

THRIPS POLLINATION OF ANDRODIOECIOUS *CASTILLA ELASTICA* (MORACEAE) IN A SEASONAL TROPICAL FOREST¹

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Androdioecy is a rare sexual system in nature, as predicted theoretically. Among the androecious species reported so far, *Castilla elastica* (Moraceae) is unique in that flowers are unisexual and staminate and pistillate flowers on cosexual plants are produced on different inflorescences. In addition, inflorescence structure of staminate inflorescences on males and staminate and pistillate inflorescences on cosexes is markedly different. Staminate inflorescences on males are bivalvate, while staminate inflorescences on cosexes are “fig-like” and urceolate. Pistillate inflorescences are discoidal. The difference may reflect different roles and requirements of the three inflorescences in pollination and protection from herbivores. This study reports thrips pollination of *C. elastica*, demonstrated by a pollinator introduction experiment. Thrips pollination of the species may be an example of mutualism originating from plant–herbivore interactions. In the Moraceae, shifts from simple herbivores on flowers to pollinators might have occurred many times, evolving into diverse pollination systems including the fig–fig wasp mutualism. The family, of which little is known about pollination systems, provides interesting and unique opportunities to study evolution of pollination systems and roles of nonpollinating associates of inflorescences.

Key words: androdioecy; inflorescence structure; Moraceae; Panama; pollination; thrips.

The inflorescences of the Moraceae are extremely diverse, ranging from simple racemes, capitula, and spikes to urceolate (urn-shaped) inflorescences and *Ficus syconia* (Berg, 1989; Rohwer, 1993). The most important trend of evolution of inflorescences may be progressive condensation by fusion and reduction of floral parts (Rohwer, 1993), which can be associated with reduction of flowers and change from bisexual to unisexual condition (Berg, 1989). This tendency appears to be most tightly linked with protection of flowers from destructive organisms that consume or cause infection of floral tissues. The interactions that minimize loss to such floral parasites may in some cases lead to mutualism (Berg, 1989). In the case of *Ficus*, seed predators have evolved into pollinators of the plant (Bronstein and McKey, 1989; Herre et al., 1996; Anstett, Hos-saert-McKey, and Kjellberg, 1997). In *Artocarpus integer*, male inflorescences infected by fungi provide mycelia as a reward for gall-midge pollinators (Sakai, Kato, and Nagamasu, 2000). It is remarkable, however, that little is known about pollination systems in the Moraceae other than *Ficus* and some apparently wind-pollinated species (Berg, 1989; Endress, 1994; Rohwer, 1993). Several available studies suggested that various pollination systems are involved (Bawa et al., 1985; Momose et al., 1998; Sakai, Kato, and Nagamasu, 2000) and that wind-pollination might have evolved more than once (Zapata and Arroyo, 1978; Bawa and Crisp, 1980; Williams and Adam, 1993; Bullock, 1994).

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Here, I report on the pollination system of *Castilla elastica* Sessé (Moraceae). Although the species was formally important for rubber production and was cultivated in the late 1800s and early 1900s (Pittier, 1910; Hammel, 1986), its reproductive biology is poorly studied. Three forms of inflorescences, the most peculiar characteristic of the species, were described by Cook (1903a, b) for the first time. Cook (1903a, b) and Pittier (1910) examined living and preserved materials as well as dry specimens and mentioned that the species was “partly dioecious” with two types of trees within a population. There were trees that bore only male inflorescences, while others produced pistillate inflorescences flanked by a few staminate inflorescences, which were smaller than primary ones. The stamens on both types of trees were fertile (Pittier, 1910). In other words, the species was androdioecious.

As theoretical studies have predicted (Charlesworth and Charlesworth, 1978) androdioecy (cosexes and males in a single population) is an extremely rare sexual system in plants (Charlesworth, 1984). In most androdioecious species reported so far, a cosexual individual produces hermaphrodite flowers (*Datisca* spp. [Datisceae] [Liston, Rieseberg, and Elias, 1989; Swensen, Luthi, and Rieseberg, 1998], *Fraxinus* spp. and *Phillyrea angustifolia* [Oleaceae] [Lepart and Dommée, 1992; Yamazaki, 1993; Hiura and Ishida, 1994; Ishida and Hiura, 1998; Dommée et al., 1999], *Neobuxbaumia mezcalaensis* [Cactaceae] [Valiente-Banuet et al., 1997], *Oxalis suksdorfi* [Oxalidaceae] [Ornduff, 1964, 1972], *Saxifraga cernua* [Saxifragaceae] [Molau and Prentice, 1992], and *Schizopepon bryoniaefolius* [Cucurbitaceae] [Akimoto, Fukuhara, and Kikuzawa, 1999]). A few plant species show “monoecious” cosexes with pistillate and staminate flowers on the same inflorescences (*Ricinocarpos pinifolius* and *Mercurialis annua* [Euphorbiaceae] [Thomson et al., 1989; Pannell, 1997], and *Sagittaria lancifolia* [Alismataceae] [Muenchow, 1998]).

Androdioecy of *C. elastica* is unique in that staminate and pistillate flowers occur on different inflorescences of a cosexual plant. In addition, staminate inflorescences on male and



Figs. 1–4. *Castilla elastica*. 1. Branches of a flowering male tree. 2. Primary staminate inflorescence, from which many thrips flew out when it was shaken by breeze ($\times 2$). 3. A pistillate inflorescence visited by thrips (*Frankliniella diversa*) ($\times 2.7$). 4. Complementary staminate inflorescence ($\times 2.7$).

cosexual plants and pistillate inflorescences are strikingly different from one another in structure. Pistillate inflorescences are discoidal with a shallow central depression, in which pistils are aggregated (Fig. 3). Staminate inflorescences on cosexes are urceolate, “fig-like” (Cook, 1903b) with an apical hole covered by imbricate bracts (Fig. 4), while staminate inflorescences on males are bivalvate (Fig. 2). Because of this variation and the peculiarity of inflorescence structure and the sexual system, the pollination system of *Castilla* was considered of particular interest.

MATERIALS AND METHODS

Terminology—In this paper, I term staminate inflorescences on male trees “primary staminate inflorescences” and those on cosexes “complementary staminate inflorescences” following Cook (1903a, b), Pittier (1910), and Berg (1972).

Study site and plant—The study was conducted in a seasonally dry forest in the Parque Natural Metropolitano near Panama City, Panama. Annual rainfall at the site is 1740 mm on average, most of which occurs during the rainy season from May through December. The forest is ~80-yr-old second growth of 40 m in height. I used a 42 m tall tower crane with a 51-m jib at a permanent installation in the park (Parker, Smith, and Hogan, 1992) to reach tree canopies.

Castilla elastica Sessé (Moraceae) is an abundant tree species in secondary forests and open areas such as clearings and forest edges of the region (Pittier,

1910; Berg, 1972). This deciduous tree can be 30 m in height. The natural distribution of the species ranges from Mexico through Panama and the coastal region of western Colombia and western Ecuador, although the species was widely spread through the tropics as a result of introduction and cultivation for its latex during the late 1800s and early 1900s (Pittier, 1910; Berg, 1972; Hammel, 1986). Among the three subspecies recognized by Berg (1972), only *C. elastica* subsp. *costaricana* (Liebmann) C. C. Berg is known from Panama. I observed 13 reproductively mature trees within reach of the tower crane (~1 ha) in April–July 2000 (Table 1).

TABLE 1. Sex and diameter at breast height (dbh) of the trees observed in this study.

Plant ID	Sex	dbh (cm)
C1	Cosex	28.8
C2	Cosex	15.9
C3	Cosex	20.9
C4	Male	15.8
C5	Male	49.0
C6	Cosex	33.1
C7	Cosex	15.9
C8	Male	15.9
C9	Cosex	24.0
C10	Male	14.6
C11	Male	21.6
C12	Cosex	18.2
C13	Cosex	18.0

Observation and collection of flower visitors—Flowers and flower visitors on staminate and pistillate inflorescences of *Castilla* were observed from 10 April to 15 May for 20 h in total, including 4 h at night. Flower visitors on staminate flowers were collected by sampling the whole inflorescence. Insects on pistillate flowers were collected with an aspirator. The insects were preserved in 50% alcohol or AGA solution (60% alcohol, glacial acetic acid, and glycerin in the proportions 10:1:1) or in dried state and stored at the Smithsonian Tropical Research Institute. Some were identified to insect family and to species in the case of adult thrips or used to examine pollen load under a binocular microscope. To estimate density of the thrips, the numbers of thrips on pistillate inflorescences were counted on the four trees, C1, C3, C6, and C7, and numbers of thrips on staminate inflorescences on two trees, C5 and C7.

Sticky traps—I used sticky traps (TAT Fly Paper; Walco-Linck, Valley Cottage, New York, USA) to compare population densities and activities of thrips among different sites. The traps catch insects on the sticky surfaces of a yellowish-brown paper (70 cm × 4.7 cm). The trap has no odor and does not contain insecticide. To compare thrips density among sites, I placed traps for 24 h in tree canopies at the height of 10–25 m and in the understory 1.5 m above the ground. The canopy traps included two traps on each of four *Castilla* trees (two cosexual trees, C1 and C6, and two male trees, C4 and C5) and four traps at least 10 m away from any plants flowering intensively as a control. Understory traps were placed just below each of the canopy traps. Therefore, one trapping procedure involved 24 sticky traps, and trapping was conducted twice on 27 and 28 April.

Pollination experiment—I conducted two pollination experiments on cosexual trees. In Experiment 1, I compared fruit set of inflorescences enclosed in a bag of 0.2-mm mesh, which allowed the entry and exit of tiny insects such as thrips, with that of open-pollinated control on C3. Flowers on the inflorescences were receptive around 22 April.

Experiment 2 conducted on C1 involved four treatments: (1) bagged with fine cloth; (2) hand-pollinated; (3) thrips-introduced; and (4) open-pollinated control. In the former three treatments, inflorescences were bagged with cloth fine enough to exclude thrips before the inflorescences became receptive. In addition, inflorescences were hand-pollinated with pollen of male tree C5 using a Chinese writing brush in treatment 2, and thrips collected from C5 were introduced into two bags enclosing five inflorescences each in treatment 3. Thrips for the treatment were collected from five staminate inflorescences, then released in a bag enclosing pistillate inflorescences under the treatment. This procedure was estimated to introduce 247 ± 82 thrips (98.9% of all arthropods introduced) and 2.8 ± 2.2 other arthropods (1.1%) ($N = 10$). Hand-pollination and thrips introduction were conducted twice on the same inflorescences on 9 and 11 May.

Fruit set was examined on 10 June by dissecting infructescences to count finished flowers and developing seeds in both experiments. At that time, infructescences (fruiting head) were still green but of almost mature size (4.3 ± 0.4 cm in diameter, $N = 15$). Differences in numbers of retained infructescences and in fruit set of the inflorescences between different treatments were statistically examined using Fisher's exact test and a t test, respectively, using SAS (SAS, 1988).

Pollen staining—To examine existence of cytoplasm in pollen grains, pollen grains from frozen flower samples were dyed with methylene blue/phloxine-B solution. Phloxine-B stains cytoplasm of pollen red, and methylene blue stains the exine blue (A. Dafni, University of Haifa, Israel, personal communication).

RESULTS

Floral biology—Two types of sex expression occurred within a population of *Castilla elastica*: cosexual trees producing both pistillate and staminate inflorescences and male trees with staminate inflorescences. Diameter at breast height (dbh) of the trees did not differ significantly between the two sexes (t

test, $P > 0.05$, Table 1). On a single node of male tree branches, about four primary staminate inflorescences are borne together (Fig. 1). They are flabellate opening in a slit, or bivalvate, ~2.3 cm wide and 1.3 cm thick with a 0.5-cm peduncle (Fig. 2). A primary staminate inflorescence is fully packed with ~400 flowers, each bearing a single stamen, on the internal surface. Anthers are ~1.2 mm in length and smaller than those in complementary inflorescences (~1.6 mm in length). On a branch of a cosexual tree, one or rarely two pistillate inflorescences are borne on each node. The inflorescences are almost sessile, shallow cup-shaped or discoidal with a shallow central depression, 1.0 cm thick and 1.5 cm in diameter (Fig. 3). Approximately 16 pistillate flowers on an inflorescence are fused with each other and with the receptacle at the base. At the center of the inflorescence, styles of the flowers are aggregated. The ovary is 1-locular with a single ovule. Pistillate inflorescences are usually accompanied by two or more complementary staminate inflorescences. Complementary staminate inflorescences are urceolate with a small apical opening, 1.2 cm long, and 1.0 cm in diameter with a peduncle of ~1.3 cm (Fig. 4). The opening is usually blocked by imbricate bracts, but sometimes bracts are loosened during flowering, and a small hole becomes visible. A staminate inflorescence encloses ~50 staminate flowers, each with a single stamen. Pollen grains are ~13 μm in a diameter with three or rarely four pores. Pollen grains of male and cosexual trees each stained red by methylene blue/phloxine-B solution, indicating existence of cytoplasm in both, and there was no difference between them under a compound microscope. I could not find other rewards for pollinators besides pollen on staminate inflorescences.

The 13 *C. elastica* trees under observation flowered continuously or intermittently from April to May 2000. Most of their leaves had been shed before the flowering period (Fig. 1), which was followed by an explosive leaf flush. Primary inflorescences turned from green to yellow when they opened and anther dehiscence began. Within 2 d all the anthers on an inflorescence dehisced, and inflorescences then abscised. In cosexes, pistillate and staminate inflorescences were in flower simultaneously, and temporal segregation was not observed. Pistillate inflorescences changed color from green to creamy yellow as their stigma extended and probably became receptive (Fig. 3). Stigmas sometimes remained wet and fresh for >10 d. The receptive period of an inflorescence may depend on fertilization, since all the stigmas withered and turned brown <2 d after hand-pollination. Most pistillate inflorescences developed into infructescences, which reached maturity and turned salmon pink in July. The flowering period of complementary staminate inflorescences seemed to be several days, while it was difficult to examine since anther dehiscence could not be observed without damaging the inflorescence. The inflorescences had usually abscised ~1 d after their color changed from green to yellow.

Flower visitors—The most abundant flower visitors were two species of thrips, *Frankliniella diversa* and *F. insularis*, both on staminate and on pistillate inflorescences (Table 2). They were observed actively feeding on pollen grains on staminate inflorescences. Many thrips emerged from primary staminate inflorescences when the branch was shaken by a breeze (Fig. 2). On pistillate inflorescences, thrips just stayed, sometimes moving around (Fig. 3). Thrips accounted for 99.0% of flower visitors ($N = 1320$) collected on male trees and for

TABLE 2. Insects collected on inflorescences of *Castilla elastica*.

Order Family Species	Cosexual tree										Male tree				Total
	Pistillate inflorescence					Staminate inflorescence					Staminate inflorescence				
	C1	C2	C6	C7	C1	C7	C9	C12	C13	C5	C8	C10	C11		
Thysanoptera															
Thripidae															
<i>Frankliniella diversa</i> Hood	2		8	10	39	12	47	81	56	384	19	271	170	1099	
<i>F. insularis</i> Franklin	1	2	8		25	7	6	20	36	63	8	65	29	270	
Sp. 1										2				2	
Immature individuals					8	23	68	20	1	139	15	117	22	413	
Subtotal of Thripidae	3	2	16	10	72	42	121	121	93	588	42	453	221	1784	
Hymenoptera															
Apidae															
Formicidae							1				1			1	
Eulophidae	1										3	2	3	9	
Vespidae										1				1	
Coleoptera															
Curculionidae															
Staphylinidae										2			1	3	
Total	4	2	16	10	72	42	122	121	93	595	42	455	228	1802	

99.8% ($N = 450$) and 96.9% ($N = 32$) on staminate and pistillate inflorescence of cosexuals, respectively. Their sex ratio was biased in favor of female (80%, $N = 1079$ in *F. diversa*; 91%, $N = 35$ in *F. insularis*), some of which had a well-developed ovary. All thrips collected on male trees ($N = 55$) were observed to carry pollen grains. Seventy-one percent ($N = 51$) and 66% ($N = 44$) of thrips collected on staminate and pistillate inflorescences of cosexual trees, respectively, had pollen loads. The numbers of pollen grains on thrips collected from primary staminate inflorescences were much higher (25.8 ± 46.2 grains, $N = 25$) than on those from complementary inflorescences (7.6 ± 13.7 , $N = 51$). Thrips densities on pistillate inflorescences, complementary, and primary staminate in-

florescences were estimated to be 0.9 ± 1.3 ($N = 59$), 6 ± 4.5 ($N = 7$), and 202.8 ± 16.0 ($N = 6$), respectively.

Other than thrips, wasps (*Ceraninus americensis* Girault, Eulophidae, Hymenoptera), which are parasitoids of thrips (Triapitsyn and Headrick, 1995), and ants (Formicidae) were observed to visit both pistillate and staminate inflorescences, but only infrequently. Ants remained on the outside of primary staminate inflorescences and on the pistillate inflorescences, catching the thrips as they entered or left the inflorescence. Beetles (Curculionidae and Staphylinidae, Coleoptera) and bees (Apidae and Halictidae, Hymenoptera) were occasionally observed visiting flowers for pollen, only on primary staminate inflorescences.

High thrips activities around *C. elastica* were confirmed by sticky traps (Fig. 5). In the canopy traps, the numbers of thrips trapped in male trees were 33 times as high as the control. Thrips trapped in cosexual-tree canopies were also more abundant than the control, while much less than those in male trees (Fig. 5). Thrips on understory traps did not show much difference among sites. The numbers of arthropods other than thrips were almost constant at all sites both in the forest canopy and in the understory.

Pollination experiments—In experiment 1, all the inflorescences of both treatments, open-pollinated and bagged with mesh, were retained after flowering (Table 3). However, fruit set of the bagged inflorescences was significantly lower than and about half of that in the open-pollinated control ($P =$

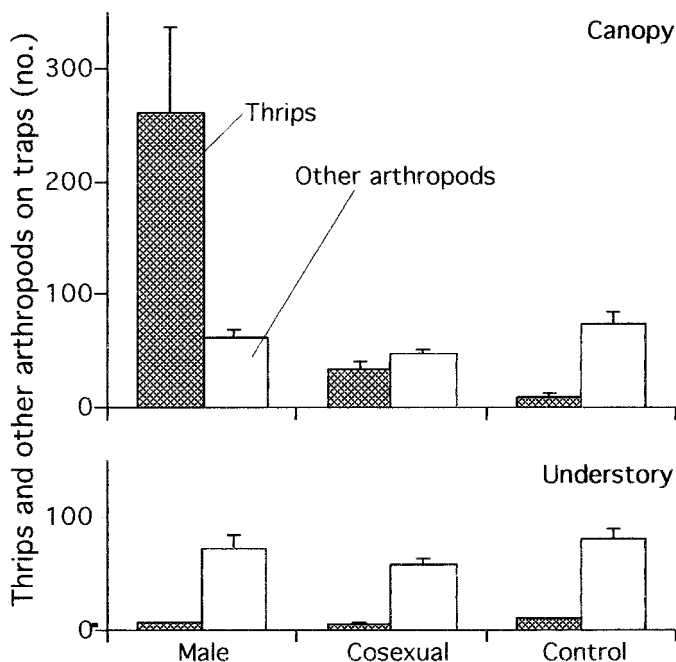


Fig. 5. Mean \pm 1 SE of the numbers of thrips and other arthropods on sticky traps in (canopy) and below (understory) the canopy of male and cosexual trees, and controls in the forest canopy and understory.

TABLE 3. Results of two pollination experiments on *Castilla elastica*.

Treatment	Inflorescence		Flowers	
	N	Retained (%)	N	Fruit set (%)
Experiment 1				
Control	8	100.0	120	90.8
Bagged with mesh	6	100.0	103	47.6
Experiment 2				
Control	21	100.0	356	90.2
Bagged with fine cloth	19	0.0	—	—
Hand-pollinated	10	100.0	148	87.2
Thrips-introduced	10	100.0	177	80.2

0.005, *t* test, one-tailed). In experiment 2, inflorescences bagged with fine cloth without additional manipulation produced no fruits, while all the inflorescences of the other three treatments were retained (Table 3, $P < 0.0001$ for all three comparisons, Fisher's exact test, one-tailed). Fruit set of inflorescences that were hand-pollinated and had thrips introduced were not significantly different from those of the open-pollinated control ($P > 0.05$, *t* test, two-tailed).

DISCUSSION

Pollination system—Although some species of Moraceae are reported to be wind-pollinated, wind-pollination is unlikely in *C. elastica*. Staminate flowers were enclosed in bivalvate or urceolate inflorescences, and stamens were not exposed to wind. Pistils were aggregated in the central depression of the pistillate inflorescence, thus they may not catch airborne pollen effectively.

Beetles and bees visited staminate inflorescences on male trees for pollen, but they were not observed on pistillate or complementary staminate inflorescences. Pistillate inflorescences or complementary staminate inflorescences closed by imbricate bracts may not be attractive for them due to absence or inaccessibility of pollen. In addition to thrips, ants and parasitoids of thrips visited both pistillate and staminate inflorescences. Although these insects might pollinate *C. elastica* accidentally in rare cases, they are unlikely to visit *C. elastica* flowers that lack their prey, thrips, and they could not be the principal pollinators, considering their low visit frequencies.

I conclude that *Castilla elastica* is pollinated by thrips for the following reasons. First, thrips were observed and collected on all the three types of inflorescences, primary and complementary staminate inflorescences and pistillate inflorescences, and accounted for 96.9–99.8% of the flower visitors. Presence of thrips both in staminate and in pistillate inflorescences was also observed by Pittier (1910). Second, a high proportion of the thrips carried pollen on the body. All the thrips collected on male trees, and two-thirds of thrips on pistillate inflorescences had pollen loads. Third, the results of the pollination experiment 1 suggest that pollen vectors included very small insects, because some flowers bagged with mesh developed into fruits. Finally, in experiment 2, thrips-introduced inflorescences enclosed in a bag of fine cloth showed fruit set as high as hand-pollinated ones and the open-pollinated control. High fruit set (80.2%) cannot be explained if thrips did not pollinate, although small numbers (1.1%) of insects other than thrips were accidentally introduced together.

Apparently, thrips visited staminate flowers for pollen. They were observed actively feeding on pollen. They probably copulated and reproduced on staminate inflorescences, because many thrips larvae as well as male and female adults were found on staminate inflorescences, and some females had developed ovaries. On the other hand, it is unclear why thrips visited pistillate flowers, which had no substantial reward. Pistillate inflorescences did not have soft tissue other than pistils, and there was no clear evidence that thrips fed upon and damaged any part of the inflorescences. Thrips might be attracted by odor and color of the pistillate inflorescences that mimic those of staminate ones. Scent is thought to be a primary attractant for thrips (Kirk, 1985). Although I could not detect odor of pistillate flowers, volatile released by flowering inflorescences remains to be examined. Color may also be an important cue for the pollinators in *C. elastica*, because pistillate

inflorescences changed color into yellow while flowering, although it was green before and after flowering.

Thrips, agricultural and horticultural pests causing damage by feeding on plant tissues, are often found in flowers of many wild plants (Kevan and Baker, 1983; Kirk, 1984). In a tropical forest of Panama, 85% of 285 species were inhabited by floral thrips (F. Gattesco, the University of Milan, Italy and D. W. Roubik, Smithsonian Institution, personal communication). Thrips feed on floral tissue, nectar and exposed liquids, and pollen grains in flowers (Kirk, 1984). Although they are thought to rarely contribute to pollination, recent studies have reported thrips as primary pollinators in many plant species of several families including Annonaceae (Webber and Gottsberger, 1995; Momose, Nagamitsu, and Inoue, 1998), Araceae (Rust, 1980), Lauraceae (Norton, 1984), Winteraceae (Thien, 1980; Pellmyr et al., 1990), and Zamiaceae (Mound and Terry, 2001). Pollen grain size in plants pollinated by thrips is $< 34 \mu\text{m}$, which corresponds well to grain size of *C. elastica* (F. Gattesco and D. W. Roubik, personal communication).

Host specificity of thrips varies greatly among species, and true host relationships of thrips species have rarely been established (Mound and Marullo, 1996). *Frankliniella* is a large thrips genus of ~180 species, 90% of which occur in the Neotropics. Its species diversity is especially high in Central America. For most species, the number of individuals collected so far is quite small. For example, among 44 species of *Frankliniella* recorded from Costa Rica, 18 are known only from a single sample or individual, and only ten are known from six or more samples (Mound and Marullo, 1996). *Frankliniella diversa*, the most abundant thrips on *C. elastica*, was described based on a single female specimen from Panama; a second female was collected in Costa Rica. These two females are the only known specimens of this species prior to the present study, despite extensive collections in Central America (Mound and Palmer, 1992; F. Gattesco and D. W. Roubik, unpublished data). The rarity might reflect host specificity of the species. A large population of *F. diversa* was also found on inflorescences of *Poulsenia* (Moraceae) (S. Sakai, unpublished data), thus they might be Moraceae specialists. On the other hand, *F. insularis* has been frequently collected in Panama and Costa Rica, especially from flowers of Bignoniaceae. A few individuals of this species were also collected from flowers of Bignoniaceae and Apocynaceae at the study site, when *Castilla* was flowering (S. Sakai, unpublished data).

Extremely high fruit set in open-pollinated flowers (Table 3), which is no lower than hand-pollinated ones, suggests the focal population of *C. elastica* with rather high density of flowering trees (13 trees in 1 ha) received enough pollination service. However, it is unknown how tree density affects pollination success and fruit set. Distance of thrips movement in forests has not been estimated yet. Momose, Nagamitsu, and Inoue (1998) reported thrips pollination of an understory tree, *Popowia pisocarpa* (Annonaceae), and suggested that limited movement of thrips caused lower fruit set of isolated trees. On the other hand, Appanah and Chan (1981) argued that thrips visiting flowers of emergent trees moved for long distances between trees, carried by a wind, and effectively pollinated six species of emergent trees (*Shorea*, Dipterocarpaceae). Observations in isolated islands and on a boat far from the land suggest that some thrips could travel $> 30 \text{ km}$ (Lewis, 1973). In *C. elastica*, low thrips densities on the forest floor underneath the tree canopies suggested that thrips rarely dropped

with abscised staminate inflorescences. They might be dispersed by wind from canopy branches.

Sexual system—*Castilla elastica* is androdioecious with cosexes and male plants within a population. Pollen grains were not different between male and cosexual plants, and existence of cytoplasm was confirmed in pollen grains from both primary and complemental staminate inflorescences. However, constancy of gender expression over more than one flowering season is still unclear. Pittier (1910) suggested that younger trees blooming for the first time might bear invariably male inflorescences, but simple size-dependent gender switching does not seem to occur, considering that no clear size difference between male and cosexual trees was found.

Theoretical studies predict that for males to invade a cosexual population, pollen success of males must be at least twice as high as cosexes; furthermore, high outcrossing rates and strong inbreeding depression are needed (Lloyd, 1975; Charlesworth and Charlesworth, 1978). High outcrossing rates, inbreeding depression, and pollen production by male plants observed in another androdioecious species, *Datisca glomerata* (Fritsch and Rieseberg, 1992; Rieseberg et al., 1993; Philbrick and Rieseberg, 1994) agree with the prediction. In addition, Akimoto, Fukuhara, and Kikuzawa (1999) showed dominance of selfing in hermaphrodite populations and significant correlation between frequency of males and inbreeding coefficients in androdioecious populations of *Schizopepon bryoniaefolius*. In *C. elastica*, male trees may have higher pollen success than cosexes, as indicated by higher thrips density on primary inflorescences than complemental ones and much higher thrips activities in male canopies than those of cosexes, as shown by data from sticky traps. Quantifying outcrossing ratio and inbreeding depression, together with sex ratio and sexual allocation, of *C. elastica* would be interesting problems for further studies.

A distinctive characteristic of androdioecy in *C. elastica* is that male and female flowers are produced on different inflorescences. Thus male and female functions do not share any structure. Additionally, the shape of staminate inflorescences on male and cosexual plants is quite different. Androdioecy in *C. elastica* might have evolved from dioecy. Among three *Castilla* species, closely related *C. elastica* and *C. ulei* are androdioecious, but *C. tunu* is strictly dioecious without complemental inflorescences (Berg, 1972).

What is the advantage for cosexual plants of having staminate inflorescences? Although functionally pistillate flowers of some species are known to produce inviable pollen to attract pollinators (reviewed by Mayer and Charlesworth, 1991), pollen concealed in urceolate complemental staminate inflorescences of *C. elastica* is unlikely to serve as an attractant. In *C. elastica*, production of staminate inflorescences causes disadvantages for cosexes in three different ways. In the first place, they should reduce production of pistillate flowers and fruits as some resources are allocated to staminate inflorescences. Second, there is the possibility that outcross pollen on pollinator bodies is lost in a complemental staminate inflorescence if thrips from other trees enter a staminate inflorescence before a pistillate one. Furthermore, complemental staminate inflorescences may increase inbreeding.

I suggest that the most likely explanation for retention of male function in cosexual *C. elastica* is reproductive continuity in colonists. Pollen of complemental staminate inflorescences must rarely contribute to outcrossing, because thrips in

complemental staminate inflorescences were present in much lower numbers than in primary inflorescences. Pollen grains were also less abundant on thrips from complemental inflorescences, probably due to imbricate bracts blocking the entrance of the inflorescences. Outstanding colonizing ability of *C. elastica* is evidenced by trees growing in the wild out of its original distribution dispersed by cultivated mother trees (Berg, 1972). Producing seeds through self-pollination must be essential when they invade a new habitat without conspecific trees. In addition, for *C. elastica* it may be important to assure a high level of pollination, because selective abscission of unfertilized ovaries (i.e., sterile fruits) is impossible due to fusion of all pistillate flowers on a discoid inflorescence. All flowers on a developing infructescence were observed to grow into fruits, some of which were without a seed. It may be advantageous to maintain high fruit set through self-pollination rather than to produce many seedless fruits as a part of an infructescence.

Inflorescence structure—Urceolate inflorescences occur in at least three genera of three different tribes of the Moraceae: *Castilla* in Castilleae, *Sparattosyce* in Artocarpeae, and *Ficus* in Ficeae. They are considered to have evolved independently for protection of reproductive organs from insects destroying reproductive organs (Corner, 1962; Berg, 1989). Although inflorescences, or syconia, of *Ficus* are clearly different from those of *Castilla* in that monoecious *Ficus* have both staminate and pistillate flowers on a single inflorescence, the pollination system of *C. elastica* shares some common characters with *Ficus*. Firstly, they are pollinated by small insects, which enter urceolate inflorescences through small holes. Host specificity of the pollinators may also be high. Next, the pollinators breed in the inflorescences. Finally, both pollination systems are possibly derived from herbivory at the inflorescence level.

Interestingly, only complemental inflorescences, rather than pistillate ones, have urceolate structure and, hence, the most closed structure in *C. elastica*. In contrast, the primary staminate inflorescences are opened by slits. This difference may be due to different requirements for pollinator activities. For male trees, it is essential to attract and release as many thrips as possible, while smaller complemental staminate inflorescences may function primarily to ensure self-pollination if outcross pollen is unavailable. The closed structure of a complemental inflorescence may protect pollinators as well as pollen. When there is no male tree nearby, density of pollinator thrips may be low. Therefore, a cosexual tree should increase and maintain a thrips population on its own staminate inflorescences throughout the flowering period to successfully produce seeds through self-pollination mediated by thrips. Predators of thrips such as ants and spiders were frequently observed outside of staminate inflorescences, although parasitoids were also found inside. In addition, the closed structure of staminate inflorescences promotes thrips visits to pistillate inflorescences prior to staminate ones. On the other hand, discoid pistillate inflorescences are protected by the thick receptacle, rather than closed structure. This open structure may facilitate thrips visits.

It is clear that both pollination and herbivory play important roles in the evolution of inflorescence structure of the Moraceae, although systematic relationships within the family and their pollination systems are poorly understood (Berg, 1989; Humphries and Blackmore, 1989). In the course of evolution, shifts from simple "floral predators" to pollinators might oc-

cur several times. These pollinators are represented by thrips in this study, the fig-wasps, that are both pollinators and seed predators of *Ficus* (Janzen, 1979; Wiebes, 1979), and gall midges pollinating *Artocarpus integer*, in which pollinator larvae feed on fungi infecting a staminate inflorescence (Sakai, Kato, and Nagamasu, 2000). Some studies on different plant groups suggest that preadaptations played essential roles in drastic changes of pollination systems, and the original function of these traits were often related to protection from destructive flower visitors (Pellmyr and Thompson, 1992; Pellmyr et al., 1996; Armbruster, 1997). The Moraceae may provide interesting and unique opportunities to study the roles of nonpollinators in shaping the evolution of pollination systems.

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