

Pollination ecology of the dioecious tree *Commiphora guillauminii* in Madagascar

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Abstract: In dioecious plant species differences in morphology and resources between female and male flowers can have consequences for flower visitation rates. Female flowers sometimes lack pollen and can be less attractive to pollinators than male flowers. We studied the pollination ecology of the dioecious tree *Commiphora guillauminii* in a dry deciduous forest in western Madagascar. We recorded floral display, visiting insect species and visitation rates for female and male trees. The results showed that female trees produce significantly larger but fewer flowers per inflorescence than male ones. Number of flowers per tree did not differ between the sexes. During 270 observation-hours we observed 17 insect and two bird species visiting the flowers. Mean visitation rates of male flowers were 6.1 times higher than those of female flowers (1.07 vs. 0.18 visitors per flower h⁻¹). Visitation rates to female and male trees showed similar daily and seasonal patterns. Fruit set (2.9%) was low, which could have been caused by pollinator or pollen limitation. This study suggests that dioecy may pose a risk for fruit set and, potentially, reproductive success for plant species with depauperate pollinator faunas on islands such as Madagascar.

Key Words: Burseraceae, dioecy, Kirindy Forest, plant–animal interaction, pollination success, visitation rates

INTRODUCTION

Tropical trees are mostly self-incompatible and generally depend on animals to disperse their pollen (Bawa 1974, 1990; Fleming *et al.* 1987). Up to 90% of tropical tree species are pollinated by insects (Bawa *et al.* 1985, Buchmann & Nabham 1996). Dioecious tree species with separate male and female individuals are common in the tropics (11–30% vs. 4–6% for flowering plants in general) (Bawa 1980a, Renner & Ricklefs 1995, Richard 1997). Dioecious plants are incapable of producing seed without pollinators and are therefore extremely sensitive to changes in pollinator abundance (Vamosi & Otto 2002).

The main advantage of dioecy may be avoidance of inbreeding. This might result in high fruit set in comparison with monoecious and hermaphroditic plant species (Sutherland & Delph 1984). The main disadvantage of dioecy is that pollinator (or wind) movement between individuals of both sexes is needed for repro-

duction (Bawa 1980a, Bawa & Opler 1975, Howe & Westley 1997, Renner & Ricklefs 1995). Flowers of female and male trees can differ in morphology and floral rewards. Female flowers often have only nectar whereas male flowers provide both pollen and nectar and may therefore be more attractive to pollinators (Bawa 1983, Lloyd & Bawa 1984, Mayer & Charlesworth 1991). However, not all insects collect pollen. Some collect only nectar and, thus, may not discriminate between the sexes. In some dioecious species, female trees produce larger flowers than male trees. This might be necessary to produce large fruits and seeds (Primack 1987), and possibly it increases the attractiveness to pollinators (Bawa & Opler 1975).

The differences in resources and morphology of female and male trees may have consequences for visiting species and visitation rates of the two sexes. Female and male trees may attract different pollinating species, or the same species may visit female and male flowers at different rates, which may disrupt the pollination process. Existing literature suggests that female trees are visited with a lower frequency than male ones (Bawa 1980b, Bierzychudek 1987, Charlesworth 1993).

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Low visitation rates of female trees could present a problem for successful fruit set when pollinators or pollen is limiting. Low numbers of pollinating species and individuals might be particularly likely on islands where the pollinator fauna is often depauperate due to biogeographic constraints (Bernardello *et al.* 2001, Christian 2001, Cox *et al.* 1991, Hansen *et al.* 2002, Inoue 1993, Murren 2002). Madagascar is an especially interesting island due to its highly endemic flora and fauna (Ceballos & Brown 1995, Krause *et al.* 1997, Yoder *et al.* 2000). Mutualistic plant–animal interactions in Madagascar are poorly studied, but previous studies suggest that the plant species are dependent on surprisingly low numbers of animal pollinators (Jenkins 1987, Nilsson 1992, Ratsirarson & Silander 1996).

In the present study, we examined the pollination ecology of *Commiphora guillauminii*, a dioecious tree species abundant in dry deciduous forests in western Madagascar. The objectives of the study were, first, to test whether female and male trees produced different floral displays, in terms of flowers per inflorescence, inflorescences per tree, flowers per tree and size of flowers. Second, we determined whether the sexes differed in visitation rates and pollinating species due to differences in morphology and floral rewards. Third, we examined temporal patterns in visitation rates of female and male trees in the course of the day and the flowering season. Finally, we established patterns of fruit set in female trees of *Commiphora guillauminii*.

METHODS

Study site

The study took place from September to November 2001 in the Forêt de Kirindy/Centre de Formation Professionnelle Forestière (CFPF) (20°03'S, 44°39'E) (Kirindy in text), a dry deciduous forest in western Madagascar. Kirindy is a 10 000 ha forestry concession of the CFPF de Morondava, located 60 km north of Morondava. Average annual temperature of the forest is 24.7 °C, average precipitation 799 mm, with the main rainy season between December and March (Sorg & Rohner 1996). The forest has been used for selective logging, but this has had little impact on vegetation or on the abundance and distribution of animals (Ganzhorn *et al.* 1990). Further information on Kirindy is given in Ganzhorn & Sorg (1996).

Study species

Commiphora guillauminii H. Perrier (Burseraceae) (de la Bathie 1946) is the dominant canopy tree species in Kirindy, representing 42% of the trees > 40 cm diameter

at breast height (dbh) (Hunziker 1981). It is an important timber species yielding 80–90% of the wood logged in Kirindy (Schwitter 1984). This deciduous tree is endemic to Madagascar and grows up to 20 m in height. Adult trees have long branchless trunks with crowns starting at 6–12 m height. The species is dioecious, flowering from September to December (de la Bathie 1946, Rohner & Sorg 1986). The flowers of female and male trees are reddish, approximately 4 mm in length, and are borne in inflorescences (de la Bathie 1946). Female trees produce roundish fruits from January to April (de la Bathie 1946). The fruits have outer coverings that split open when mature and expose a black seed partly enveloped by a fleshy red aril. Seeds are bird-dispersed (Böhning-Gaese *et al.* 1995, 1999).

Floral display

To quantify floral display, eight randomly selected trees of each sex were chosen in a plot of 1 ha. We counted the number of flowers per inflorescence (6–10 inflorescences per tree). The differences in mean number of flowers per inflorescence between female and male trees were assessed with a t-test. Inflorescences per tree were quantified by counting the inflorescences of a representative part of the tree crown and then extrapolating to the whole crown. To determine the number of flowers per tree, flowers per inflorescence were multiplied by number of inflorescences per tree. We tested for differences between the sexes in number of inflorescences and number of flowers per tree using non-parametric Mann–Whitney U-test. To investigate the differences in flower size between the sexes, we measured length and width of flowers of 14 randomly chosen trees (six female and eight male trees, 1–16 flowers per tree) in situ with an electronic caliper. All measurements were taken from flowers in the lower third of the crown at 8–15 m height. To collect the data we climbed the trees using climbing equipment or an aluminium ladder. We tested for differences in length and width of the flowers between female and male trees with a nested ANOVA (Statsoft 2001). In this analysis, sex of trees was treated as fixed effect and the trees were nested within sex as random effect and error term. We tried to measure nectar production of flowers with standardized microcapillaries, however, the yield was extremely low and variable in both sexes and did not allow a rigorous statistical analysis.

Flower visitors

To determine the pollinators and their visitation rates we counted the visiting insect species on 16 randomly chosen trees (eight female and eight male trees).

Observations were made at distances of up to 5 m, partly using binoculars (Zeiss, 6 × 18) that had a close-up range of 0.3 m. The study period covered the entire flowering season of *C. guillauminii* in Kirindy (13 October–23 November 2001). Observations were conducted in blocks of 30 min in the lower third of the tree crown at 8–15 m height. We observed several inflorescences simultaneously and recorded the number of open flowers observed and the identity and number of visiting insects – classified into visually distinguishable morpho-species. Each tree was observed over the course of the whole day between 6h00 and 18h00 in 12 observation blocks each starting at the half-hour, i.e. between 6h30–7h00, 7h30–8h00, 8h30–9h00, etc. The observation blocks were randomly distributed over the trees and the course of the day.

For statistical analyses we divided the day into three time periods (morning: 6h00–10h00, midday: 10h00–14h00, and afternoon: 14h00–18h00) and the flowering season in three 14-d periods (first period: 13 October–25 October, second period: 26 October–09 November, third period: 10 November–23 November 2001). In the first two periods, we were able to record 12 observation blocks per period and tree, covering the whole day. For the third period we do not have data for all 12 observation blocks per tree because some trees had lost all flowers by this time. Total observation time was 270 h. Additionally, we made nocturnal observations on one female and one male tree between 18h00–6h00 (2 × 12 h). For our nocturnal observations we chose trees whose inflorescences were easily accessible. Thus, no night vision glasses were needed. To determine morphospecies, visiting insects were captured at each tree three times during the observation period using sweep nets. Specimens were identified in the laboratory by specialists. We transformed observations into visitation rates per flower and hour. We first analysed the visitation rates using generalized linear models with Poisson-distribution and log-link function. However, this was only possible for the combined visitation rate of all species and the results corresponded to those of the non-parametric Mann–Whitney U-test. Visitation rates of single species were too low for using generalized linear models. Thus, for the sake of comparability we present all results using non-parametric tests (JMP 1995).

Fruit set

Fruit set was calculated from the estimated numbers of flowers and fruits of the eight female trees used for observations. Fruit set was equated with female flowers developing ovaries. Thus, we considered only initial pollination success without taking into account potential fruit abortion. Fruit numbers were determined for small

trees by counting all fruits. For large trees, we estimated fruit set as we did for number of inflorescences. Counting flowers and fruits did not prove difficult because leafing did not begin until the end of the flowering season. Additionally, we measured the diameter at breast height (dbh) of all trees. We compared the fruit numbers of the present study with data from 1993 (30 trees) and 1994 (20 trees), controlling for DBH (Böhning-Gaese *et al.* 1999). We had to use absolute fruit numbers for the comparison since fruit set was not determined in 1993 and 1994. Additionally, we completely covered 3–5 unopened inflorescences of the eight female trees with mosquito netting (mesh size: 1 mm) to test for apomixis.

RESULTS

Floral display

Numbers of flowers per inflorescence differed significantly between the sexes, with male inflorescences having more flowers than females (female = 10.9 ± 5.0 ($\bar{x} \pm 1$ SD, unless otherwise stated), $n = 8$; male = 38.6 ± 10.4 , $n = 8$; t-test: $t = 6.8$, $df = 14$, $P < 0.001$). Even though number of inflorescences (female: median = 212.5, range 22–3000, $n = 8$; male: median = 2070, range 33–7000, $n = 8$) and number of flowers (female: median = 2775, range 88–45 000, $n = 8$; male: median = 82 800, range 990–350 000, $n = 8$) did not differ significantly between the sexes ($Z = -0.89$, $P = 0.37$; $Z = -1.73$, $P = 0.08$; respectively), there is a large difference between the sexes, with females having fewer inflorescences and fewer flowers than males. Nevertheless, because of low sample sizes and large variance these differences were not significant. We found size differences in flowers, with female trees producing larger flowers than male trees. The flowers differed significantly in width (female = 2.74 ± 0.27 mm; male = 2.33 ± 0.26 mm; nested ANOVA: $F_{1,12} = 21.3$, $P < 0.0001$) but not in length (female = 2.13 ± 0.22 mm; male = 1.92 ± 0.21 mm; $F_{1,12} = 0.6$, $P = 0.44$).

Flower visitors of female and male trees

Visitors. Flowers opened at dusk and remained open until they dropped off the tree after 3–5 d. During 270 h of observations, we recorded 17 insect and two bird species visiting the flowers (Table 1). The insect species belonged to: Hymenoptera, Lepidoptera, Diptera and Heteroptera. The bird species were common jery (*Neomixis tenella*) and Souimanga sunbird (*Nectarinia souimanga*). All individuals that we caught with sweep nets were inspected with binocular eyepieces for the occurrence of pollen. Pollen was found on a eumenine wasp species (subfamily Eumeninae), a stingless bee

Table 1. Visitation rates per flower h^{-1} for all visitor species together and each separately (grouped by orders). Data were analysed for all 16 trees together ($\sigma\sigma$), and for the eight female trees ($\sigma\sigma$) and eight male ($\sigma\sigma$) separately. Mean values are presented, because the median was in many cases zero. Z and P values from the Mann–Whitney U-test are also presented. Values that remained significant after table-wide, sequential Bonferroni correction are in bold (Rice 1989).

Species	Mean $\sigma\sigma$ (Visits per flower h^{-1})	Mean $\sigma\sigma$ (Visits per flower h^{-1})	Mean $\sigma\sigma$ (Visits per flower h^{-1})	Z	P
n	16	8	8		
All species	0.621	0.176	1.066	-3.20	0.001
Hymenoptera					
<i>Liotrigona mahafalya</i>	0.354	0.03	0.687	-2.399	0.017
<i>Apis mellifera</i>	0.067	0.025	0.109	-2.054	0.040
Eumenine wasp	0.047	0.031	0.063	0.210	0.834
Wasp 2	0.003	0.001	0.012	-0.966	0.334
Wasp 1	0.001	0.001	< 0.001	-0.385	0.700
Bee 2	0.017	0.014	0.020	-0.274	0.784
Bee 1	0.011	0.012	0.009	0.280	0.779
Bee 3	< 0.001	0.001	< 0.001	0.000	1.000
<i>Crematogaster</i> sp.	0.006	0.000	0.011	-0.875	0.382
<i>Tetraponera</i> sp.	0.001	0.002	0.000	0.875	0.382
Lepidoptera					
<i>Acraea ranaivalona</i>	0.020	0.015	0.026	-0.384	0.701
<i>Acraea turna</i>	0.002	0.001	0.003	0.000	1.000
Pieridae	0.009	0.001	0.018	-2.905	0.004
Diptera					
<i>Geron</i> sp.	0.054	0.029	0.079	-0.899	0.369
Sp. D	0.016	0.035	0.018	-0.637	0.524
Calliphoridae	0.009	0.003	0.014	-1.341	0.180
Heteroptera	0.001	0.000	0.001	-1.369	0.171
Aves					
<i>Neomixis tenella</i>	0.004	0.007	0.002	0.539	0.590
<i>Nectarinia souimanga</i>	< 0.001	0.000	0.001	-0.875	0.382

(*Liotrigona mahafalya*), a honeybee (*Apis mellifera*) and a species of fly (*Geron* sp.). No pollen was found on any of the other insect species. The two bird species feed mainly on insects but are known to feed on nectar occasionally (Langrand 1990). No flower visitors were recorded during night observations.

Visitation rates. We found that mean total visitation rates of male trees were 6.1 times higher than those of female ones (1.07 vs. 0.18 visits per flower h^{-1} ; Table 1). The most frequent visitors to female trees were two fly species (Species D and *Geron* sp.), an eumenine wasp species and the stingless bee *Liotrigona mahafalya* (Table 1). The most frequent visitors to male trees were *Liotrigona mahafalya*, *Apis mellifera*, *Geron* sp. and the eumenine wasp species (Table 1).

Statistically significant differences in visitation rates between the sexes were found for total visitation rates (all visitors pooled) and for the three species *Liotrigona mahafalya*, *Apis mellifera* and one species of the family

Pieridae with visitation rates being higher on male than on female trees (Table 1). However, when controlling for multiple tests using sequential Bonferroni adjustment over the whole table (Rice 1989) only the values for gross visitation rates remained significant (Table 1).

Daily pattern. Visitation rates were highest in the morning with the same daily pattern for female and male trees (Figure 1). We found significant differences in visitation rates for both sexes between morning and midday, but no difference between midday and afternoon (Figure 1, Table 2). When controlling for multiple tests using sequential Bonferroni adjustment over the whole table (Rice 1989) only the values for all trees remained significant (Table 2).

Seasonal pattern. The visitation rates declined in the course of the flowering season for female as well as for male trees (Figure 2). We did not find significant differences

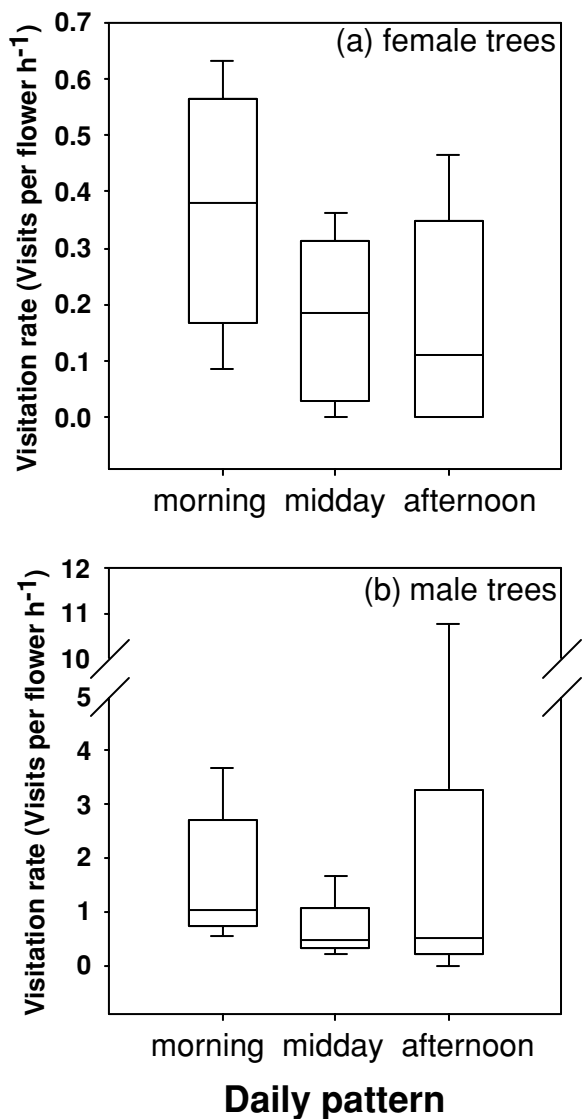


Figure 1. Daily pattern of visitation rates (visits per flower h⁻¹) for female (a) and male trees (b). Plotted are box-and-whisker plots with minimum value, 25%-quartile, median, 75%-quartile and maximum value for morning (6h00–10h00), midday (10h00–14h00) and afternoon (14h00–18h00) (n = 8 for female and male trees, please note different scaling of y-axes).

between the first two periods for either female or male trees. However visitation rates between periods two and three differed significantly for male trees and, marginally, for female trees (Table 2). When controlling for multiple tests using sequential Bonferroni adjustment over the whole table (Rice 1989) only the values for all trees remained significant (Table 2).

Fruit set. Median fruit set among the eight female trees was 2.9% (range 1.0–25.0%; n = 8 trees). To test whether fruit set was especially low in the study year, we compared absolute fruit numbers with the ones of 1993 and 1994

Table 2. Test for changes in visitation rates in the course of the day and the flowering season using the Wilcoxon matched pair signed rank test. Given are median differences between the periods, S and P values for all trees, pooled (♂♀), for male (♂♂) and for female (♀♀) trees. Values that remained significant after table-wide, sequential Bonferroni correction are in bold (Rice 1989).

		n	Median	S	P
Daily pattern					
Morning versus midday	♂♀	16	0.279	65	< 0.0001
	♂♂	8	0.371	18	0.008
	♀♀	8	0.020	16	0.023
Midday versus afternoon	♂♀	16	0.000	8.5	0.626
	♂♂	8	0.174	1	0.945
	♀♀	8	0.000	1.5	0.844
Seasonal pattern					
First versus second period	♂♀	16	-0.007	17	0.404
	♂♂	8	0.234	8	0.313
	♀♀	8	-0.030	1	0.945
Second versus third period	♂♀	16	0.219	51	0.002
	♂♂	8	0.324	16	0.023
	♀♀	8	0.065	11	0.078

(Böhning-Gaese *et al.* 1999) using dbh as a co-variable (JMP 1995) (Table 3). The results showed a significant annual effect, but the adjusted mean (controlled for dbh) of 2001 (454 ± 248 fruits) was similar to the one of 1993 (471 ± 236 fruits) whereas the value of 1994 (216 ± 248 fruits) was significantly lower. Inflorescences covered by mosquito netting did not develop fruits.

DISCUSSION

The flowers of *C. guillauminii* were visited by 17 insect species, a relatively low number compared with other tropical entomophilous species with open ‘generalized’ flowers (Ervik & Feil 1997, Soehartono & Newton 2001, Williams & Adam 2001). Furthermore, only four of the 17 insect species had pollen on their bodies and, thus, appeared to act as pollinators. Low numbers of pollinating species seem to be a common phenomenon in Madagascar. For example, due to the low number of pollinating insects, *Dalechampia* vines (Euphorbiaceae) switched from a highly specialized pollinator relationship in Africa to a generalized pollination system in

Table 3. Number of fruits produced by *C. guillauminii* as a function of study year and tree size (dbh). ANCOVA, type III SS, whole model R² = 0.52.

	Model df	Error df	F	P
Whole model	3	54	19.3	< 0.0001
Year	2	54	6.48	0.003
Dbh	1	54	53.2	< 0.0001

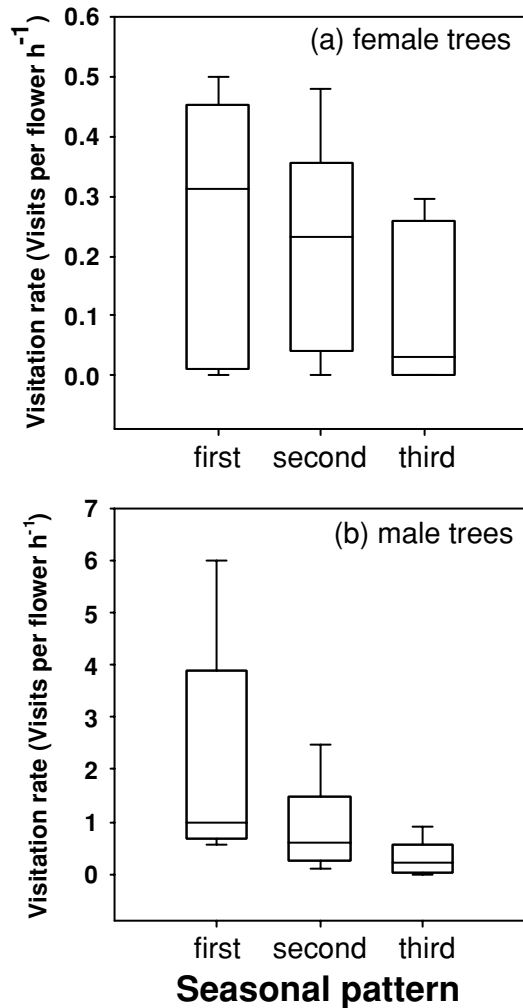


Figure 2. Seasonal pattern of visitation rates (visits per flower h^{-1}) for female (a) and male trees (b). Plotted are box-and-whisker plots with minimum value, 25%-quartile, median, 75%-quartile and maximum value for first, second and third 14-d period of the flowering season ($n = 8$ for female and male trees, please note different scaling of y-axes).

Madagascar (Armbruster & Baldwin 1998). The same pattern seems to be found in other mutualistic plant–animal interactions, for example in seed dispersal. The seeds of the same *Commiphora* species were dispersed by basically one bird species with an average dispersal distance of only 0.9 m (Bleher & Böhning-Gaese 2000, 2001; Böhning-Gaese *et al.* 1995, 1999).

Gross visitation rates of flowers were 0.62 visits per flower h^{-1} (Table 1). Comparing these values with data from the literature is difficult because in most studies data were collected only during peak pollinator activity. However, even if we consider only our data on visitation rates at peak activity, in the morning at the beginning of flowering season, our visitation rates are still much lower than most found in the literature (Ågren *et al.* 1986, Ashman & Stanton 1991, Delph & Lively 1992, Ghazoul

1997, McCall & Primack 1992, Motten 1986, Ratsirarson & Silander 1996, Spira *et al.* 1992).

Visitation rates differed between the sexes; flowers on male trees were visited 6.1 times more frequently than female ones. The ability of pollinators to differentiate between male and female flowers has often been observed (Baker 1976, Bawa 1977, Bell *et al.* 1984, Kay 1982, van der Werf 1983). One explanation could be different resources offered by female and male flowers. Male flowers provide pollen and nectar, whereas female flowers offer only nectar. Since many pollinators, especially bees and hover flies, feed on pollen in addition to nectar, they might prefer the more rewarding male flowers (Ågren *et al.* 1986, Bierzychudek 1987, Mayer & Charlesworth 1991, Thomson *et al.* 1982). Pollinators like bees or wasps sample different trees or groups of flowers while foraging and then concentrate on especially resource-rich flower patches (Real 1981, Waddington 1983). With respect to pollen-collecting species such as the stingless bee *Liotrigona mahafalya* and the honey-bee we could confirm this pattern with male trees potentially acting as resource-rich patches. The stingless bee was the most frequent visiting species on male flowers; it was 23.0 times more abundant on male than on female trees. Similarly, the honeybee, the second most frequent visitor on male flowers, was 4.4 times more abundant on male than on female trees. Many of the other insects did not discriminate so clearly between the sexes (Table 1). This suggests that they may be collecting nectar. Alternatively, non-specific (generalist) pollinators might be relatively indiscriminating in their flower preferences in comparison with specialized species such as bees (Charlesworth 1993).

Daily and seasonal patterns in visitation rates were similar for both sexes (Figures 1 and 2). The daily pattern showed a visitation peak in the morning. Anthesis of *C. guillauminii* took place at dusk, but no nocturnal visitors were observed. Thus, it can be assumed that the amount of pollen and nectar was highest in the morning, leading to high visitation rates at that time period (Figure 1). Similar patterns were found for the Malagasy palm species *Neodypsis decaryi* (Ratsirarson & Silander 1996). It has been argued that time of anthesis is an adaptation to attract specific pollinators (Baker 1961, Waser 1983). Thus, we should expect nocturnal visitors for *C. guillauminii*. However, recent theoretical and comparative studies on the timing of anthesis indicated that anthesis at dusk is a frequent phenomenon and not necessarily an adaptation to nocturnal pollinators (Miyake & Yahara 1998, 1999). The seasonal pattern in visitation rates showed a decline in the course of the flowering season (Figure 2). The flowering peak coincided with the onset of the rainy season and a possible emergence of many small insects and therefore followed a general pattern known for tropical trees (Janzen 1973).

Fruit set of *C. guillauminii* was 2.9%, lower than in other studies. Bawa & Opler (1975) recorded an average fruit set of 26% for dioecious trees. Sutherland & Delph (1984) calculated a value of 73.8% for dioecious plants, which was significantly higher than that for monoecious (53.8%) and hermaphroditic species (22.1%). The lowest value of fruit set for another tropical dioecious tree species we found was 13% for *Chamaedorea alternans* (Palmae; Otero-Arnaiz & Oyama 2001). For other tropical trees, fruit sets as low as 6% seem to occur (Fuchs *et al.* 2003, Rao & Raju 2002), with lowest fruit set being 0.9% in a Kenyan *Grevillea*-species (Kalinganire *et al.* 2001).

One factor leading to low fruit set of *C. guillauminii* could be the generally low visitation rates and the low number of visiting and pollinating species (Howell & Roth 1981, Schemske 1980, Willson & Schemske 1980). A second factor contributing to low fruit set might be the exceptionally low visitation to female trees and the absence of apomixis. All these factors suggest that the low fruit set of *C. guillauminii* is caused by pollinator or pollen limitation. Pollen limitation appears to be common in dioecious plant species (Ågren *et al.* 1986, Ayre & Whelan 1989, Bierzychudek 1981, Cunningham 1996, Fox 1992, Weis & Hermanutz 1993, Wilcock & Neiland 2002).

These results raise the question of whether the patterns found for *C. guillauminii* in Kirindy in 2001 are historical patterns or caused by recent anthropogenic influences (e.g. forest fragmentation, habitat degradation). The comparison of mean fruit numbers of the present study with data from 1993 and 1994 (Böhning-Gaese *et al.* 1999) demonstrated that fruit numbers have not declined over the last 10 y. Furthermore, Kirindy is still one of the largest forest fragments along the West Coast of Madagascar and holds populations of highly threatened vertebrate species, e.g. giant jumping rat (*Hypogeomys antimena*) (Ganzhorn *et al.* 1996, Sommer & Hommen 2000) and white-breasted mesite (*Mesitornis variegata*) (Evans *et al.* 1996, Hawkins 1994). This suggests that low fruit set of *C. guillauminii* could be a natural rather than anthropogenic phenomenon. However, to test this, further studies analysing the spatial and temporal variation in fruit set of *C. guillauminii* and other species are necessary.

To conclude, the low fruit set of *C. guillauminii* seems to be caused by several factors. First, the low general visitation rates and low numbers of visiting and pollinating species might be a pattern common in Madagascar (Armbruster & Baldwin 1998, Ratsirarson 1995, Wasserthal 1997). Second, the extremely low visitation rates to female trees seems to be caused by dioecy and the lower amount of rewards offered in female than in male flowers. Third, the higher visual attractiveness of the larger but fewer female flowers do not seem to be sufficient to improve the visitation rates of female flowers and thus,

the fruit set. Therefore, dioecy may pose a risk for fruit set and, potentially, reproductive success for plant species with depauperate pollinator faunas on islands such as Madagascar.

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