Low fruit set in a dioecious tree: pollination ecology of *Commiphora harveyi* in South Africa

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Abstract: Dioecious plant species differ in floral morphology and rewards between females and males. Pistillate flowers on female plants often lack pollen and can be less attractive to pollinators, which can have consequences for the visitation rates of the sexes. We studied the pollination ecology of the dioecious tree *Commiphora harveyi* in a coastal scarp forest in eastern South Africa. Floral display, visiting insect species, visitation rate and natural fruit set were recorded. Additionally, we pollinated flowers by hand to determine experimental fruit set. We found that male trees had more and larger flowers per inflorescence than female trees. Both sexes produced nectar in low amounts. During 203.5 h of observation we recorded 28 insect species visiting the flowers. No difference in mean visitation rate (0.20 visits per flower h^{-1}) was recorded between the sexes. The daily and seasonal pattern was similar between the sexes. The natural fruit set was low (3.8%) and increased significantly with hand-pollination (45.5%), an indication of pollen limitation. We compared our results with the pollination ecology of *C. guillauminii* in Madagascar, a dioecious tree species on an island with a depauperate pollinator fauna. This comparison revealed a similar pattern with low visitation rates, low insect diversity and low fruit set, suggesting that this pattern may be more common in dioecious tree species than previously reported in the literature.

Key Words: Burseraceae, dioecy, Oribi Gorge NR, plant–animal interaction, pollination success, visitation rates

INTRODUCTION

Pollination by animals is an important plant–animal interaction (Boucher *et al.* 1982, Bronstein 1994), having particular significance in the tropics, where most trees are self-incompatible and up to 90% depend on animals as pollinators (Bawa 1990, Buchmann & Nabham 1996, Dick *et al.* 2003). A decline in diversity and abundance of pollinators, for example caused through habitat fragmentation, can lead to a decrease in pollination rate (Cascante *et al.* 2002, Cunningham 2000a, b; Johnson *et al.* 2004, Wilcock & Neiland 2002).

Dioecious tree species which have the sexes on different individuals are common in the tropics (Bawa 1974, 1980a; Bawa & Opler 1975). While dioecy reduces selfing almost completely, pollinator (or wind) movements between individuals of both sexes are needed for successful reproduction (Bawa 1980a, Bawa & Opler 1975, Osunkoya 1999, Renner & Ricklefs 1995). In temperate regions, dioecious trees are mostly wind-pollinated, whereas in the tropics and subtropics they often depend on insects as pollination vectors (Bawa 1980a, Bawa & Opler 1975). Male and female trees can differ in their attractiveness to pollinators; staminate flowers provide pollen and mostly nectar, whereas pistillate flowers often have only nectar. Additionally, flower size and number of flowers per tree can differ between the sexes (Ågren *et al.* 1986, Bawa 1980b, Bawa & Opler 1975, Delph *et al.* 1996, Osunkoya 1999). These differences in flower morphology and floral rewards could possibly influence visitation rates and visitor diversity between the sexes (Bawa 1980b, Bierzychudek 1987, Farwig *et al.* 2004, Thomson *et al.* 1982, Vamosi & Otto 2002).

The dependency on pollinators and the difference in rewards offered between male and female trees could have consequences for the reproductive success of dioecious species. Fruit set could be restricted through pollinator or pollen limitation (Burd 1994). Nevertheless, dioecious plants have been recorded to have a higher fruit set than monoecious and hermaphroditic plants (73.8% vs. 42.1%; Sutherland & Delph 1984). However, a

pollination study conducted on the dioecious entomophilous tropical tree *Commiphora guillauminii* in Madagascar revealed very different results: low pollinator diversity, low mean visitation rates and a fruit set of only 2.9% (Farwig *et al.* 2004). The authors explained these results by the special island situation combined with the high percentage of endemic plants and animals on Madagascar (Farwig *et al.* 2004). Even though mutualistic plant–animal interactions on Madagascar are poorly investigated, existing studies suggest that plants on Madagascar interact with surprisingly few animal pollinators (Jenkins 1987, Nilsson 1992, Ratsirarson & Silander 1996).

In the present study, we investigated the pollination ecology of *Commiphora harveyi* in South Africa, a tree species in the same genus as *C. guillauminii*, but within a subtropical, continental situation. The comparison of the pollination ecology of the two species allows us to evaluate whether the pollination ecology of *C. guillauminii* is unique to tropical Madagascar or more common in tropical and subtropical dioecious trees than previously reported. The objectives of the study were, first to quantify the attractiveness of the different sexes: flower size, number of flowers per inflorescence, total number of flowers per tree, as well as the amount of nectar provided. Second, we determined the visitation rates for male and female trees and whether both sexes have a similar daily and seasonal visitation pattern. Third, we identified the natural fruit set and conducted hand-pollination experiments. Additionally, we excluded pollinators to test for non-pseudogamous apomixis. The last objective was the comparison of the pollination systems of the two *Commiphora* species.

METHODS

Study site

The study took place during November and December 2002 in Oribi Gorge Nature Reserve (OGNR) on the South African East Coast. This 1850-ha nature reserve, located 110 km south of Durban and 22 km inland from Port Shepstone, is classified as coastal scarp forest (Cooper 1985). Average annual rainfall in the area is 1176 mm with the main rainfall season between October and March (Glen 1996). The monthly mean temperature is 19.2 °C (www.worldclimate.com). For further details on Oribi Gorge Nature Reserve and coastal forests see Glen (1996) and Acocks (1988).

Study species

Commiphora harveyi Engl. (Burseraceae) (van der Walt 1973) is a deciduous tree found on the east coast of

Southern Africa (Palgrave 1977, Pooley 1994) and grows up to 20 m in height. Its economic use is limited to the production of small goods such as spoons (van Wyk & van Wyk 1997). The species is dioecious, flowering from October to December (Pooley 1994). The flowers of female and male trees are small, whitish and are born in short axillary inflorescences (van Wyk & van Wyk 1997). Pistillate flowers are cryptically dioecious (Mayer & Charlesworth 1991) with staminodes. The fruiting season is from March–June (Bleher & Böhning-Gaese 2000, Pooley 1994). The fruits have an outer covering that splits in half when mature, exposing a single black seed, enveloped by a fleshy red aril that is dispersed by birds (Bleher & Böhning-Gaese 2000, 2001).

Floral display

To quantify floral display, we randomly chose trees of each sex (8 male and 12 female trees) in a 1-ha plot. We measured the width and the height of 2–15 flowers per tree with an electronic caliper. All flowers were taken from the lower third of the tree crown. To collect the data we either cut branches with a tree cutter or stood on an aluminium ladder. Average flower height and width were calculated for each tree. The differences in the means between male and female trees were assessed with a t-test. To determine the attractiveness of each sex to potential pollinators, we counted flowers on 8–10 inflorescences per tree and inflorescences per tree on a representative part of the tree crown and then extrapolated the numbers to the whole crown. The total number of flowers per tree was calculated by multiplying the mean number of flowers per inflorescence with the number of inflorescences per tree. We tested for differences between the sexes in number of flowers per inflorescence, number of inflorescences per tree and total number of flowers per tree, using non-parametric Mann–Whitney U-tests.

We tried to measure nectar production of flowers with standardized microcapillaries, but the amount was low and variable in both sexes, preventing rigorous statistical analysis.

Flower visitors

Pollinators and their visitation rate were recorded on 16 randomly chosen trees (eight of each sex). Because the flowering period for a number of trees was shorter than the study period, we exchanged five female trees in the second and third observation block for five other female trees (see below). The study covered the complete flowering season of *C. harveyi* in Oribi Gorge NR (5 November–10 December 2002) and was split into three observation blocks. The first two blocks lasted 12 d (5–16 November; 18–29 November). At the end of the flowering season only

9 d were left for the third block (2–10 December). The total observation time was 33 d. We divided a day into three time periods: morning (06h00–10h00), midday (10h00–14h00) and afternoon (14h00–18h00). Additionally, we made nocturnal observations on one female and one male tree (19h00–24h00), using night vision glasses (moonlight, nv 100, times 4.3).

In each of the seasonal observation blocks, we observed each tree in 30-min periods over the whole day, starting at the full hour (i.e. 06h00–06h30, 07h00–07h30, etc.). The observation units were randomized over the trees and during the course of the day. The total number of observation units was 528. For statistical analyses we excluded 54 units because the trees had no open flowers and 67 units due to heavy rain (during rain no insects visited the flowers). Therefore, the statistical analysis was based on 407 observation units (203.5 h).

In each observation unit, we observed several inflorescences simultaneously in the lower third of the crown. We recorded the number of open flowers observed and the identity and number of visiting insects – classified into visibly distinguishable morphospecies. To do this, we either stood on an aluminium ladder or sat on the ground using binoculars (Zeiss, 6×18). To determine the morphospecies, we captured specimens of the most common visiting insects, using sweep nets. To detect possible pollinators, we looked for pollen on the insect body using lenses ($10 \times$). Specimens were identified by specialists of the Plant Protection Research Institute in Pretoria and are now housed in the Ecology Department of the University of Mainz, Germany. For statistical analyses we transformed observation units into visits per flower h^{-1}. To compare visitation rates between the sexes, we calculated the mean visitation rate for each tree (4–33 observation units per tree). We used a non-parametric Mann–Whitney U-test to test for differences in visitation rates between male and female trees; first combining visitation rates of all visiting species and, then, testing each species separately.

To test for a change in visitation rate during the course of the day, we calculated the mean visitation rate for each time period and each tree (1–12 observation units per period and tree). We used a Wilcoxon Matched-Pair Signed-Rank Test to test for differences in visitation rates between the time periods. We used the same approach to test for a change in visitation rate in the course of the flowering season. The mean visitation rate for each observation block and each tree (2–12 observation units per block and tree) was calculated and tested with a Wilcoxon Matched-Pair Signed-Rank Test for differences in visitation rate. The visitation rates were also analysed with generalized linear models, using 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 comparison we present all results using non-parametric tests.

Pollination experiments and fruit set

To calculate the natural fruit set, we estimated the total numbers of flowers and fruits on 19 female trees (observation trees included). Natural fruit set was defined as number of fruits divided by number of flowers.

On the same 19 trees we conducted pollination experiments. To exclude insect visitors, we completely covered 3–5 unopened inflorescences with mosquito gauze (mesh size: 1 mm). Every second or third day, we checked the status of the stigma of the single flowers. If a pistillate flower appeared receptive (slight change of the stigma), we pollinated it, using anthers from male trees. As flowers could not be covered or marked individually, we had to cover the whole inflorescence, potentially excluding seed predators and reducing mechanical damage. As a control, we covered other unopened inflorescences on the same tree without hand-pollination and tested for apomixis. For each mosquito gauze exclosure we recorded the number of pollinated flowers. To calculate the experimental fruit set we counted the fruits under each gauze at the end of the study period and divided them by the number of pollinated flowers. For analyses, six out of the 19 trees could not be considered, because the gauze or the whole branch had broken off in windy conditions. For the statistical analysis, we determined natural and experimental fruit set for each tree. We tested for a difference between the two fruit sets, using the non-parametric Wilcoxon Matched-Pair Signed-Rank Test with the arcsine-transformed values. Moreover, we correlated fruit set with floral display (flowers per tree) using Spearman's Rho correlation.

Comparison with *Commiphora guillauminii*

The methods and results of a study on the pollination ecology of *C. guillauminii* in Madagascar have already been published (Farwig *et al.* 2004). However, to make the comparison between *C. harveyi* and *C. guillauminii* easier, we give some basic information on the study conducted. The study took place between October and December 2001 in Kirindy forest, a dry deciduous forest in western Madagascar, with an average annual temperature of 24.7 °C and an average precipitation of 779 mm (Sorg & Rohner 1996). It is an entomophilous tree species with the flowers of female and male trees being small, reddish and borne in inflorescences (de la Bathie 1946, Farwig *et al.* 2004). The pollination study was conducted as previously described for *C. harveyi* with the exception of hand-pollination that was not performed. To see whether

the pollination ecology of the two species are comparable, we tested for differences in the attractiveness of the species to potential pollinators (number of flowers per inflorescence, number of inflorescences per tree, total number of flowers), visitor diversity, visitation rates and fruit set, using non-parametric Mann–Whitney U-tests. In each test, we compared among the male trees and among the female trees.

All statistical analyses have been performed with JMP (1995).

RESULTS

The start of the flowering season for *C. harveyi* was difficult to determine, since it varied with tree size and habitat. Small trees in open habitat started to flower earlier than the larger trees in the closed forest. On our first observation date 5 November 2002 all trees in the study areas had open flowers, and after our last observation date (10 December 2002) there were only a few trees with some open flowers left. Male and female flowers opened at dawn and stayed open for 2–3 d, before they wilted and dropped off the tree.

Floral display

Male trees had significantly more flowers per inflorescence than female trees (male: median = 15, range = 9–22, n = 8; female: median = 5, range = 3–10, n = 19; Mann–Whitney U-test: Z = 3.86, P = 0.0001). Number of inflorescences differed marginally between the sexes (male: median = 1750, range = 800–5000, n = 8; female: median = 700, range = 10–3200, n = 19; Mann–Whitney U-test: Z = 1.89, P = 0.0588). The total number of flowers was significantly higher on male than on female trees (male: median = 25 500, range = 8100–100 000, n = 8; female: median = 2800, range = 30–32 000, n = 19; Mann–Whitney U-test: Z = 2.97, P = 0.0029). Staminate flowers were significant higher than pistillate flowers (male: $\bar{x} = 3.43 \pm 0.41$ mm [$\bar{x} \pm 1$ SD, unless otherwise stated], n = 8; female: $\bar{x} = 2.17 \pm 0.23$ mm, n = 12; t-test: $t_{18} = 8.82$, P < 0.0001), but did not differ in flower width (male $\bar{x} = 1.46 \pm 0.12$ mm, n = 8; female: $\bar{x} = 1.54 \pm 0.15$ mm, n = 12; t-test: $t_{18} = -1.27$, P = 0.22). Both sexes produced nectar, but data were not sufficient to test for differences in nectar amount or sugar concentration between the sexes. Pollen of staminate flowers was moist and sticky.

Flower visitors

During 203.5 h of observations, we recorded a total of 28 visiting insect species (Table 1). We found no difference in the number of insect species visiting per tree between the sexes (male: $\bar{x} = 7.12 \pm 2.78$, n = 8; female: $\bar{x} = 7.0 \pm 2.62$, n = 8; t-test: t = 0.09; df = 14; P = 0.92). The most common visitors were *Asarkina africana* (Syrphidae) and *Apis mellifera* (Apidae). The most common visitors on male trees were *Asarkina africana*, *Apis mellifera* and a species from the family Calliphoridae (Diptera) and on female trees another Diptera species, a species of Formicidae and *Asarkina africana*. We found pollen on only three species (*Apis mellifera* (Hymenoptera), *Allodape peillix* and *Eristallinus modestus* (Diptera)). No flower visitors were recorded during night observations.

Visitation rates

The mean visitation rate for both sexes combined was 0.198 visits per flower h^{-1}, for male trees 0.243 visits per flower h^{-1} and for female trees 0.170 visits per flower h^{-1}. Total visitation rates did not differ significantly between the sexes (Table 1). Considering the insect species separately, visitation rates differed significantly for *Asarkina africana*; they were 2.8 times higher on male than on female trees (0.0663 vs. 0.0235 visits per flower h^{-1}; Table 1). The visitation rate for *Ischiodon aegypticus* differed marginally between the sexes. For all other insects, no difference between the sexes could be found. When controlling for multiple tests using table-wide sequential Bonferroni adjustment (Rice 1989), all differences in visitation rate between the sexes lost their significance.

Daily pattern

Visitation rates were highest around midday with the same daily pattern for male and female trees (Figure 1; Table 2). Pooling both sexes, we found a significant difference between morning and midday and a marginal difference between midday and afternoon (Table 2). Considering the sexes separately, only the visitation rates on female trees differed significantly between morning and midday. When controlling for multiple tests using table-wide sequential Bonferroni adjustment, only the pooled values for all trees remained significant (Table 2).

Seasonal pattern

The visitation rate declined in the course of the flowering season for male as well as for female trees (Figure 1). Pooling both sexes, the visitation rate was significantly lower in the third compared to the second observation block. This decrease in visitation rate was marginally significant for both sexes (male: P = 0.063; female: P = 0.094; Table 2). There was no significant difference between

Table 1. Visitation rates per flower h^{-1} for all visitor species together and for each species separately (grouped by orders). Data were analysed for all trees, sexes pooled (♂♀, n = 21), and for male (♂♂, n = 8) and female (♀♀, n = 13) trees separately. Mean values are given, because the median was in many cases zero. Additionally, the Z- and P-values from the Mann–Whitney U-tests are presented. Significant values are in bold. No P-value remained significant, after table-wide sequential Bonferroni correction (Rice 1989).

Species	Mean ♂♀ (Visits per flower h^{-1})	Mean ♂♂ (Visits per flower h^{-1})	Mean ♀♀ (Visits per flower h^{-1})	Z	P
n	21	8	13		
All species	0.198	0.243	0.17	1.19	0.23
Diptera					
Asarkina africana Bezzi	0.0398	0.0663	0.0235	2.57	**0.01**
Calliphoridae	0.0197	0.0209	0.0190	1.37	0.17
Dipt. IV	0.0183	0.0090	0.0240	−0.335	0.74
Allobacha sp.	0.0102	0.0130	0.0086	1.08	0.28
Eristalinus modestus Wiedemann	0.0049	0.0065	0.0039	0.681	0.50
Ischiodon aegypticus Wiedemann	0.0040	0.0049	0.0035	1.89	0.06
Dipt. VI	0.0025	0.0030	0.0023	0.213	0.83
Dipt. IX	0.0025	0.0015	0.0030	−0.119	0.90
Dipt. VII	0.0018	0.0047	0	1.18	0.24
Dipt. VIII	0.0007	0.0019	0	1.18	0.24
Hymenoptera					
Apis mellifera Linnaeus	0.0382	0.0636	0.0226	1.57	0.12
Formicide I	0.0160	0.0036	0.0236	−0.733	0.46
Belonogaster sp.	0.0080	0.0059	0.0093	0.318	0.75
Casioglossum sp.	0.0066	0.0010	0.0099	0.264	0.79
Formicide II	0.0060	0	0.0097	−1.07	0.29
Allodape peillix Bingham	0.0044	0.0093	0.0014	1.50	0.13
Hym VI	0.0012	0.0032	0	1.78	0.08
Hym V	0.0005	0.0012	0	1.18	0.24
Coleoptera					
Col. IV	0.0039	0.0103	0	1.18	0.24
Col. VII	0.0021	0.0012	0.0027	−0.581	0.56
Col. I	0.0016	0.0041	0	1.18	0.24
Col. VI	0.0013	0.0026	0.0005	0.355	0.72
Col. III	0.0012	0.0031	0	1.18	0.24
Col. VIII	0.0010	0	0.0016	−1.07	0.29
Col. II	0.0005	0.0014	0	1.18	0.24
Col. V	0.0004	0	0.0007	−0.686	0.50
Lepidoptera					
Lep. II	0.0005	0.0013	0	1.18	0.24
Lep. I	< 0.0001	< 0.0001	0	1.18	0.24

Table 2. Test for changes in visitation rates in the course of the day and in the flowering season using Wilcoxon Matched-Pair Signed-Rank tests (JMP 1995). Presented are median differences between the periods, S- and P-values for all trees, sexes pooled (♀♂), for male (♂♂) and for female (♀♀) trees. Values that remained significant after table-wide, sequential Bonferroni correction (Rice 1989) are in bold.

		n	Median	S	P
Daily pattern					
Morning versus midday	♀♂	20	−0.1273	−62.5	**0.005**
	♂♂	8	−0.2692	−12.0	0.109
	♀♀	12	−0.0628	−21.5	0.027
Midday versus afternoon	♀♂	21	0.0500	51.0	0.058
	♂♂	8	0.3346	12.0	0.109
	♀♀	13	0.0260	14.0	0.301
Seasonal pattern					
First versus second period	♀♂	14	0.0185	−1.5	0.952
	♂♂	8	−0.0081	−2.0	0.844
	♀♀	6	0.0948	0.5	1.000
Second versus third period	♀♂	12	0.1192	30.0	**0.005**
	♂♂	6	0.1151	7.5	0.063
	♀♀	6	0.1255	8.5	0.094

the first and the second observation block for male trees, female trees, or for both sexes together (Table 2). After controlling for multiple tests using table-wide sequential Bonferroni adjustment the values for all trees remained significant (Table 2).

Fruit set

Median natural fruit set was 3.8% (range = 2.7–7.1%; n = 19) and the median fruit set in hand-pollinated flowers was 45.5% (range = 5.6–75%; n = 13). The experimental fruit set was significantly higher than the natural fruit set (Wilcoxon Matched-Pair Signed-Rank test: median of differences = −0.44, S = −36.0, P = 0.002, n = 13). There was a marginally significant negative correlation between floral display (flowers per tree) and natural fruit set (Spearman's Rho: R = −0.43, P = 0.065, n = 19). Inflorescences covered by mosquito-gauze did not develop fruits.
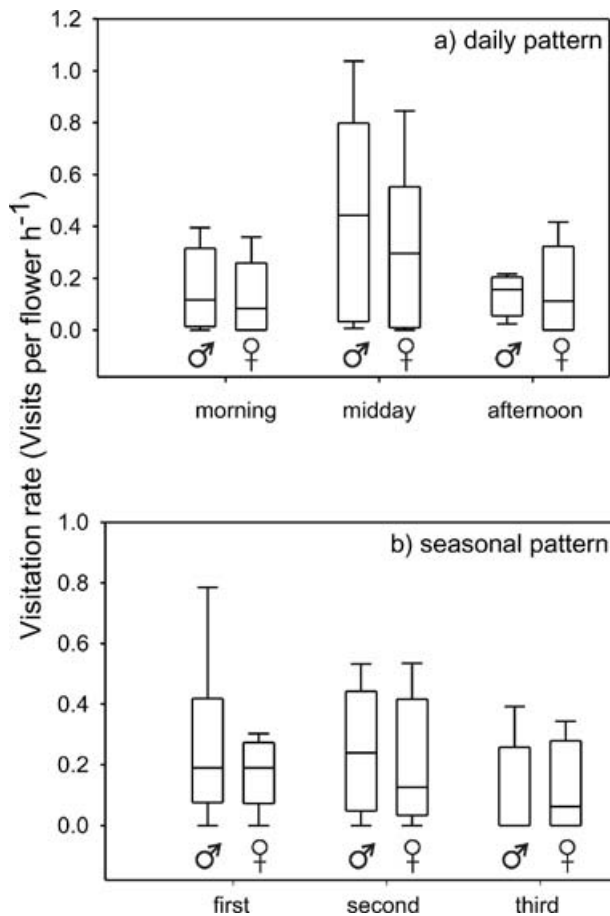
Figure 1. Daily (a) and seasonal (b) pattern of visitation rates (visits per flower h^{-1}) for male ($\male$) and female ($\female$) trees. Plotted are box-and-whisker plots with minimum value, 25%-quartile, median, 75%-quartile and maximum value. (a) morning (06h00–10h00), midday (10h00–14h00) and afternoon (14h00–18h00). N = 8 for male trees and n = 12 (morning), n = 13 (midday, afternoon) for female trees. (b) The first (5–16 November), the second (18–29 November) and the third (2–10 December) time period (n = 8 (first and second); n = 6 (third) for male trees and n = 9 (first); n = 10 (second); n = 6 (third) for female trees.

Comparison with *Commiphora guillauminii*

The attractiveness to visitors of the two tree species differed only slightly. *Commiphora guillauminii* had significantly more flowers per inflorescence than *C. harveyi* for both sexes (Mann–Whitney U-test: $Z_{male} = -3.32$; P < 0.001; n = 16, $Z_{female} = 2.36$; P < 0.05; n = 27). The number of inflorescences per tree and the number of total flowers per tree did not differ between the species for either sex. Considering the number of visiting insect species per tree, we found no difference between *C. guillauminii* and *C. harveyi* for male or for female trees (t-test: $t_{male} = 1.32$; df = 14; P = 0.21; n = 16; $t_{female} = -0.84$; df = 14; P = 0.41; n = 16). Despite a similar attractiveness and a similar visitor diversity, the

visitation rate per flower h^{-1} was significantly higher on males of *C. guillauminii* than on males of *C. harveyi* (Mann–Whitney U-test: $Z = -5.81$; P < 0.0001; n = 16), the visitation rate between the females of the two species did not differ. Fruit set did not differ significantly between the two species (Mann–Whitney U-test: $Z = -0.39$: P = 0.69; n = 27). Important results on the comparison between the species are summarized in Table 3.

DISCUSSION

The flowers of *C. harveyi* were small and whitish and, thus, correspond to the general pattern described for tropical, dioecious tree species (Bawa & Opler 1975). Male trees of *C. harveyi* had significantly more and higher flowers than female trees, a common pattern found for animal-pollinated dioecious plants (Ågren *et al.* 1986, Delph *et al.* 1996, Lloyd & Webb 1977). This could be due to possible higher energetic cost of pistillate flowers (Cipollini & Whigham 1994, Humeau & Thompson 2001) or size differences of pistil and anthers (Delph *et al.* 1996). Alternatively, the more abundant and taller staminate flowers could be the result of the intra-sexual competition as males in general need a higher visitation rate than pistillate flowers to reproduce successfully (Ågren *et al.* 1986, Osunkoya 1999). *Commiphora guillauminii* had generally more flowers per inflorescence, with female flowers being significantly larger than male ones. In both species, male trees had more flowers per inflorescence than female trees.

The flowers of *C. harveyi* were visited by 28 insect species. This is a relatively low number compared with other tropical and subtropical entomophilous tree species with similarly small 'generalized' flowers that are visited usually by up to 200 insect species (Bawa 1990, Ervik & Feil 1997, Soehartono & Newton 2001, Williams & Adam 2001). Most of the flower visitors on *C. harveyi* were small and unspecialized insects. This corresponds with other studies on dioecious tropical tree species with similar, inconspicuous flowers (Bawa 1980a, 1994; Bawa & Opler 1975, Farwig *et al.* 2004). We found pollen on the bodies of only three of the 28 insects and, thus, they appear to act as pollinators. Since we caught most insect species only once, it is possible that we underestimated the number of possible pollinators. The most important pollinator appears to be *Apis mellifera* (Table 1). This corresponds with bees being the most important pollinators for other tropical tree species of the family Burseraceae (Bawa 1990). The flowers of *C. guillauminii* were visited by an even lower total number of insect species. Since the pollen of *C. harveyi* was moist and sticky, we excluded the possibility of wind pollination in this species as observed in other primarily insect-pollinated systems (Anderson *et al.* 2000, Karrenberg *et al.* 2002).

Table 3. Comparison of *Commiphora harveyi* (South Africa) and *Commiphora guillaumini* (Madagascar) in regards to flower width, flower length, flowers per inflorescence, inflorescences per tree, flowers per tree, number of visiting species, visitation rate, natural and experimental fruit set, time of anthesis, daily and seasonal visitation peak, for male (♂♂) and for female (♀♀) trees. Data for *C. guillauminii* are taken from Farwig *et al.* (2004) and N. Farwig (unpubl. data).

	Commiphora harveyi		*Commiphora guillauminii*	
	♂♂	♀♀	♂♂	♀♀
n	8	8–19	8	8
Mean flower width (mm)	1.46	1.54	2.33	2.74
Mean flower length (mm)	3.43	2.17	1.92	2.13
Flowers per inflorescence (median)	15	5	38.6	10.9
Inflorescences per tree (median)	1750	700	2070	215.5
Flowers per tree (median)	25500	2800	82800	2775
Total number of visiting species	25	18	18	16
Number of visiting species per tree (mean)	7.12	7.0	8.75	5.75
Mean visits per flower h^{-1}	0.2434	0.1697	1.07	0.18
Natural fruit set		3.8%		2.9%
Experimental fruit set		45.5%		–
Anthesis	dawn		dusk	
daily pattern	midday peak		morning peak	
seasonal pattern	decline in course of the season		decline in course of the season	

Mean visitation rate was low with 0.2 visits per flower h^{-1} (Table 1). To our knowledge, this is the lowest visitation rate recorded in a dioecious tree species so far. In other plant species low visitation rates can be found as well (Ashman & Stanton 1991, Ghazoul 1997, Motten 1986), but they are still higher than recorded on *C. harveyi*. For example Liu *et al.* (2002) revealed a visitation rate of 2–13 visits per flower h^{-1} in the tropical monoecious genus *Musella* and McCall & Primack (1992) recorded 1.08 visits per flower h^{-1} in a South African Mediterranean plant community.

Visitation rates did not differ significantly between the sexes although male and female flowers differed in morphology and floral rewards. This result might be explained by the foraging behaviour of the visiting insect species. The insects might be nectar thieves on the nectar that is offered by both sexes. Nectar collection is known for bee-species that feed on nectar to satisfy their own energy demands and collect pollen only for their brood. For the other insect species visiting *C. harveyi*, no data on the foraging behaviour were available. Alternatively, insects may not be able to discriminate between males and females because of the staminodes in the pistillate flowers (cryptic dioecy). Anthers are important in attracting insects and are supposed to be the key to discriminating between staminate and pistillate flowers (Anderson & Symon 1989, Bawa 1980b, Charlesworth 1984, 1993; Le Corff *et al.* 1998). In contrast to *C. harveyi*, *C. guillauminii* had a generally higher visitation rate with a higher visitation rate on male than on female trees. In the Malagasy species, pistillate flowers were not cryptically dioecious and, thus, the insects were probably able to discriminate between the sexes.

Daily and seasonal patterns in visitation rates were similar for both sexes (Figure 1). The daily pattern showed a peak around midday. While anthesis of *C. harveyi* took place at dawn, only a few insects were observed in the morning. This could lead to the accumulation of pollen and nectar by midday. Furthermore, the daily pattern of visitor activity matched the daily temperature pattern. High temperature around midday could result in high insect activity and this could lead to high visitation rates (Arroyo *et al.* 1985). An interrelation between temperature and insect activity is widely observed (Arroyo *et al.* 1985, Heinrich 1974, Heinrich & Raven 1972, McCall & Primack 1992, Wilcock & Neiland 2002). *Commiphora guillauminii* had its anthesis at dusk and a visitation peak in the morning. Since no nocturnal visitors were recorded, the authors explain the visitation peak with high nectar and pollen concentration in the morning (Farwig *et al.* 2004). Alternatively, the difference in the visitation peak of the two species could be explained by the difference between the subtropical and tropical climate at the two study sites. Oribi Gorge NR in South Africa has a monthly mean temperature of 19.2 °C (www.worldclimate.com) and Kirindy forest in Madagascar of 25 °C (Sorg & Rohner 1996). Thus, insect activity could be limited by cold morning temperatures in South Africa and high temperatures in the late morning and afternoon in Madagascar (McCall & Primack 1992). In both species, visitation rates declined in the course of the flowering season and coincided with a decline in open flowers on the trees. There was no evidence that the study year had unusual climatic conditions.

Fruit set of *C. harveyi* was, at 3.8%, very low. *Commiphora guillauminii* had an even lower fruit set of 2.9%, much lower than the average fruit set of 73.8% recorded for other dioecious plant species (Sutherland & Delph 1984). Focusing on dioecious tree species, Bawa & Opler (1975) recorded an average fruit set of 26%. Low

fruit sets have been reported for the monoecious palm *Neodypsis decaryi* (9.2%) (Ratsirarson & Silander 1996) and the tropical dioecious palm *Chamaedorea alternans* (13%) (Otero-Arnaiz & Oyama 2001). Thus, to our knowledge, the fruit sets of the two *Commiphora* species are the lowest so far reported in the literature for tropical and subtropical dioecious tree species.

The low visitation rates, the low visitor diversity and the low fruit set in both *Commiphora* species and the significant increase through hand-pollination in *C. harveyi* indicate that the low fruit set in these species could be caused by pollinator or pollen limitation. Pollen limitation is one of the main reasons for a low fruit set in dioecious plant species (Liu *et al.* 2002, Otero-Arnaiz & Oyama 2001, Ratsirarson & Silander 1996). For example, Burd (1994) compiled data on pollination experiments on 258 plant species and recorded pollen limitation in 62% of them. However, the results of hand-pollination experiments have to be interpreted with caution. To compensate for resources invested, an unusually high fruit set can reduce growth, flower formation or seed production in the following year (Ackerman & Montalvo 1990, Calvo 1993, Ehrlen 1992, Ehrlen & Eriksson 1995, Fox & Stevens 1991). Additionally, it is unclear whether the fruit set could be increased on the basis of the whole tree (Johnston 1991) or whether increased fruit set would increase fruit abortion because of resource limitation (Schemske 1980, Stephenson 1981). The apparent oversupply of flowers could be a necessary adaptation to attract enough pollinators to ensure a sufficient visitation rate, resulting in an adequate number of fruits to sustain the population size. A number of studies indicate that fruit set is probably pollen limited within a season, but resource limited over a longer period of time (Cunningham 1997, Fox 1992, Wilcock & Neiland 2002).

To summarize, the two *Commiphora* species differed in the visitation rates of the two sexes. Although in both species male trees had more flowers per inflorescence, only in the Malagasy species did male trees have significantly higher visitation rates than female ones. In the South African species this could be caused by cryptic dioecy in the pistillate flowers, which might have made it difficult for the insects to distinguish the sexes. Therefore, despite the higher visitation rate in the Malagasy species, the fruit set was slightly higher in the South African one. Nevertheless, in comparison with other dioecious tree species the pollination ecology of the two entomophilous *Commiphora* species are very similar with both having low visitation rates, low species diversity and low fruit sets. This indicates that the unusual pollination ecology of the Malagasy *C. guillauminii* is not caused only by the island situation of Madagascar, combined with its endemic flora and fauna, as assumed by Farwig *et al.* (2004). The present study suggests that low fruit set in dioecious subtropical and tropical tree species may be more common than previously reported. As we compared only two species at two sites, however, further studies on more species and more sites are needed before we can make any generalizations.

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