Pollination ecology of Aloe divaricata, Berger (Liliaceae): an endemic plant species of south-west Madagascar

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The reproductive biology and pollination ecology of an endemic plant species (Aloe divaricata) of Madagascar was studied in order to understand the relative significance of various flower visitors to fruit set success. The flowers were hermaphrodite and protandrous, and were primarily visited by souimanga sunbirds (Nectarinia souimanga) and stingless bees (Trigona sp.). Flower development and phenology were examined. Fruit set success of flowers from which sunbirds were excluded was significantly lower than that of flowers visited by both bees and sunbirds. Sunbirds (Nectarinia souimanga) appeared to be the most effective pollinators of Aloe divaricata, although numerous stingless bees (Trigona sp.) also visited the flowers. The latter visitors did not seem to play any role in Aloe divaricata pollination.

Die voortplantingsbiologie en bestuiwingsekologie van Aloe divaricata, wat endemies is aan Madagaskar, is bestudeer om die rol te bepaal wat verskillende besoekers aan die plant in vrugset speel. Die blomme is hermafrodities en protandries en is hoofsaaklik besoek deur suikerbekkies (Nectarinia souimanga) en angellose bye (Trigona spp). Blomme wat deur sowte souimanga besoek is, het meer vrugte geformeer as blomme wat deur hulde suikerbekkies en bye besoek is. Alhoewel baie van die angellose bye die blomme besoek het, wil dit dus voorkom asof Nectarinia souimanga die mees effektiewe bestuiwer is en dat die bye geen rol in die bestuiwing van Aloe divaricata speel nie.

Keywords: Aloe, bees, Madagascar, pollination, sunbirds.

Information on interactions between flowers and the vectors promoting their pollination is essential to an understanding of plant reproductive success (Willson 1983; Dafni 1992; Kearns & Inouye 1993). Flower attractiveness and the effectiveness of visitors play key roles in these interactions. Flower responses to visitors differ from flower to flower and depend on floral developmental phenology (Dafni 1992; Kearns & Inouye 1993; Guitián et al. 1994).

Madagascar, with its high degree of plant diversity and endemism (Guillaumet 1984; Jenkins 1987), is of particular interest for such studies, not only because of the little-studied, unique flora, but also because of the widespread destruction of the natural communities (Mittermeier 1988; Green & Sussman 1990). Many species have already been classified as rare, threatened, or endangered (see Jenkins 1987), including Aloe divaricata Berger (Liliaceae), which is one of the 46 Aloe species of Madagascar (Reynolds 1966). An understanding of flower biology and the role of flower visitors in pollination may be necessary in order to design conservation and management strategies for these species (Bawa & Krugman 1991). The purposes of this study were (1) to describe flower development and phenology, and (2) determine the relative significance of pollinators to fruit set success in A. divaricata.

A. divaricata is widely distributed in south-western and southern Madagascar (Reynolds 1966), and has important ornamental and medicinal values (see Jenkins 1987). It is found mostly in arid sandy shrublands, it propagates vegetatively by rhizomes, usually forms clumps and can reach 3 m in height (Figure 1).

Study site
The study was undertaken between January and April 1994 in a pastured forest, adjacent to the protected Reserve of Bezété Mafaly (Figure 2, ca. 23°30’S and 44°40’E), 35 km north-east of Betioxy-Sud in south-western Madagascar (see Richard et al. 1987; Andriamampiasina 1992). The area encompasses a gradient of vegetation: a gallery forest dominated by Tamarindus indica along the Sakamena River gives way to xerophytic, spiny vegetation with increasing distance from the water course (Sussman & Rakotozafy 1994). A. divaricata is densely populated in the study area. Mean annual rainfall is 550 mm, almost all of it...
falling between December and February, and the average temperature is about 25°C (Griffith & Ranaivoson 1972).

**Methods**

Stigma receptivity was estimated by hand crossing 120 flowers at three different stigma developmental stages (40 flowers in each stage) and determining fruit set success (see Thomson & Baret 1981; Bertin 1982). Fruit set was defined when the fruit attained about 1.5 cm in length. The anthers in each targeted flower were removed prior to their anthesis to prevent autogamy. The inflorescences were covered with mosquito netting after drawing a small brush loaded with pollen from another plant across the stigmas of the experimental flowers (see Ratsirarson & Silander 1995). Developmental stages of the stigma were divided into three categories depending on the dryness and the colour of the stigma: (1) wet and greenish-yellow, (2) wet and whitish-yellow, and (3) dry and brownish-yellow.

Flower development was examined in 80 flowers from eight different inflorescences (10 flowers in each) in March 1994. Flower buds about to open were marked and then visited every 2 hours. On each visit, the size of the corolla, and length of the filament and style were measured with a caliper. The characteristics and the duration of events during flower development (e.g. anther dehiscence, stigma receptivity, nectar availability etc.) were recorded. Nectar volume was quantified with micropipettes and the sugar concentration with a hand-held refractometer (see Dafni 1992; Ratsirarson & Silander 1995). The anther was considered to have dehisced when pollen grains were seen around it; the stigma was receptive when its tip had a whitish-yellow colour and was wet (see below), and wilted when it shortened and became brownish.

Stingless bees (Trigona sp.; Apidae) and the souima nga sunbirds (Nectarinia souimanga; Nectariniidae) were the main flower visitors. An exclusion experiment was used to determine the relative significance of these visitors to pollination. Ten inflorescences were bagged for each of the following experimental conditions: (1) complete exclusion, in which no visitor was allowed access to the flower, permitting an assessment of self-compatibility; (2) bird exclusion, by covering the whole plant with 1-cm-gauge chicken wire, thereby excluding birds, while allowing access to the flowers by various insects (see Ford 1979; Wright 1994); and (3) control flowers, allowing both sunbirds and bees access to the flower. Analyses of variance were used to compare the percentage of fruit set success among treatments.

**Results and Discussion**

The peak flower production in *A. divaricata* is between February and April (see Figure 4). An individual plant produces one inflorescence in general (rarely two) at the apex of the plant, which bears about 850 tubular red flowers per inflorescence (mean = 852, s.d. = 375, n = 18). Fruits with winged seeds mature, begin-
ing in March (see Figure 4) and fruits and flowers can be seen simultaneously in one inflorescence (Figure 3). An individual inflorescence produces mature flowers over a 2- to 3-week period (mean = 20 days, s.d. = 7.14, n = 18). The flowers are about 2.5 cm long (mean = 2.63 ± 1.55, n = 80), and mature one after the other from the bottom of the inflorescence upwards, each one lasting for less than 16 hours (see Figure 5).

*A. divaricata* has a perfect hermaphroditic, protandrous flower. The whitish-yellow filaments are elongated (Figure 6), and the anthers produce pollen 2 hours after the flower opens (Figure 5b). When the flower is open, nectar is already present (Figure 5e). Covered flowers had 15 ± 7.5 μl (n = 30) of nectar 1 hour after opening, prior to anthesis. Pollen shedding lasted about 5 hours (Figure 5b), followed by a colour change in the anthers and a shortening of the filament (Figure 6).

The style, located in the center of the flower, continued to elongate (Figure 6) after the anthers had become brown and the filaments had shortened. In *Aloe divaricata* the stigma was receptive for less than 10 hours after flower opening (Figure 5c). In contrast, stigma receptivity has been reported to be between 8 and 24 hours in *Aloe ferox* (Hoffman 1988) and up to 30 hours in Gasteria (Martinie et al. 1993). Fruit set success in *A. divaricata* was higher when the stigma was wet and had a whitish tip than that of the other developmental stages of the stigma (ANOVA, f = 181.86; df = 2, df = 2, P < 0.01). This whitish colour stage is most likely the optimal state of stigma receptivity. The green and brown colour of the stigma appeared to be an earlier and later, suboptimal stage of receptivity, respectively.

Individual flowers last about 16 hours, whereafter wilting of the petals and sepals occurs. Pollen shedding and stigma receptivity are not well separated within a flower or within the inflorescence. Fruit production of completely covered inflorescences indicated that self pollination does occur and flowers are self-compatible although fruit set occurs at low rates (see Table 1). This finding contrasts with *Aloe ferox* which has been reported to be self-incompatible (Hoffman 1988).

Flowers are visited mainly by sunbirds and bees, with nectar and pollen as rewards. The bird exclusion experiment showed significantly lower fruit set success than the flowers visited by both sunbirds and bees (ANOVA, f = 14.80; df = 1, df = 18; P < 0.01; Table 1). Sunbirds (*Nectarinia souimanga*; Nectariniidae) therefore appear to be the primary pollinators. The birds inverted the stiff tubular flowers of *Aloe divaricata* with their beaks and collected the nectar produced without damaging the flowers. Pollen was deposited at the base of the sunbird's beak and transferred to the next flowers visited. Although it was not examined in this study, it has been suggested that sunbirds prefer *Aloe* flowers located in direct sunlight regardless of nectar quantity and quality (Goldstein et al. 1987). Sunbirds in general are reported to have a hibid tongue and feed on insects and flower nectar (Schlumowitz et al. 1976; Langrand 1990). One other bird species, *Neomixis tenella* (Sylviidae) was occasionally seen visiting *A. divaricata* flowers and may play a minor role in its pollination.

Stingless bees (*Trigona* sp.) were attracted by the large amount of pollen produced by the flowers, but, fruit set success of flowers from which birds were excluded was not significantly differ-

![Figure 4](image-url) **Figure 4** Flower phenology in *Aloe divaricata* (n = 18 individuals). The percentage of individuals producing flowers (○) and fruits (●) were estimated between December 1993 and April 1994.

![Figure 5](image-url) **Figure 5** Flower development in *Aloe divaricata* flower. (a) Corolla first open; (b) anthers dehiscing; (c) stigma receptive; (d) stigma wilting; (e) nectar available; (f) sunbird visits; (g) bee visits; (h) fruit development.

![Figure 6](image-url) **Figure 6** Flower parts elongation in *Aloe divaricata* flowers. The length of filament (○) and style (●) of the flower was measured every 2 hours after flower opening. The average petal length is 26.30 ± 1.55 mm, n = 80, error bars are ± s.e.

| Level of exclusion   | Mean   | Standard deviation | Number of inflorescences |
|----------------------|--------|--------------------|--------------------------|
| Complete exclusion   | 2.60   | 2.10               | 10                       |
| Bird exclusion       | 2.50   | 3.14               | 10                       |
| No exclusion         | 15.15  | 9.91               | 10                       |

**Table 1** Percentage of fruit set success in *Aloe divaricata* with different levels of exclusion
ent to that of completely covered flowers (ANOVA, $F = 0.007; df_1 = 1, df_2 = 18; \ P > 0.05$; Table 1). These bees did not seem to play any role in pollination of A. divaricata and were mostly seen collecting pollen on male flowers in anthesis as soon as the anthers were exerted beyond the floral tube, but fewer bees visited receptive female flowers.

Other insects, such as ants (Formicidae), were also seen collecting nectar inside the tubular flowers but they did not seem to be effective pollinators, because they constantly cleaned and groomed, removing pollen from their bodies. Ants in general secrete substances on their body surfaces that may inhibit pollen germination (Buckley 1982; Peukall et al. 1991). Primates did not seem to play any role in the pollination of A. divaricata. *Lemur catta* (Lemuridae) was observed eating whole inflorescences, but no other lemur species were seen feeding on flowers.

I conclude that sunbirds (*Nectarinia souimanga*) play a significant role in the pollination of A. divaricata. Trigona bee visits do not have any role in its pollination. The morphology of the flower, including the tubular form, red colour and the amount of nectar secreted during the daytime resembles that of general hummingbird (*Trochilidae*) or sunbird (*Nectariniidae*) pollination syndromes (Gill & Wolf 1975; Bertin 1982; Cruden et al. 1983; Dafni 1992; Kearns & Inouye 1993). The dependence of *N. souimanga* on Aloe divaricata resources is unknown, although the pollination of this plant species appears to be largely dependent on this sunbird. The management and conservation of the *N. souimanga* population is as important as the management of A. divaricata. The fitness of the plant is indirectly coupled with the presence of surrounding forests for *N. souimanga* habitat. Destruction of natural habitat in the south-west of Madagascar will reduce the densities of potential pollinators, such as *N. souimanga*, and inevitably affect A. divaricata abundance. Protection of much of the habitat surrounding the protected Reserve area is the first priority. The procedure for extension of the Beza Mahafaly Special Reserve is under way and will include most of the forested area adjacent to the Reserve.

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