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Biotropica, Vol. 25, No. 1. (Mar., 1993), pp. 61-72.

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BIOTROPICA 25(1): 61–72 1993

Reproductive Biology of *Ravenala madagascariensis* Gmel. as an Alien Species[1]

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ABSTRACT

The exotic arborescent monocot species from Madagascar, *Ravenala madagascariensis*, was studied in suburban gardens in Darwin, Australia. Inflorescences are long-lived branched spikes produced at right angles to a spectacular fan-like array of foliage. They are composed of a variable number of green boat-like bracts which contain a dilute liquid. Each bract subtends a series of individual, stiff, upright, large flowers which appear every 2.3 days, the total number of flowers being variable (up to 29). The slightly musty sweet smelling, creamy white hermaphrodite flowers, sometimes protogynous, opened at night (82.6% of flowers observed). Anthesis lasted, on average, 1.3 days and stigmas were receptive within the 24 hours of flower opening. Initially, nectar production was copious (1400 μl 12 hr^{-1}) and concentration moderate (14.5% sucrose equivalents), but maximum production (1600 μl 12 hr^{-1}) with slightly reduced concentration (12.5% sucrose) occurred at 2400 hr.

Seed set occurs in Darwin plants, with the brown seed enveloped in a bright blue aril and displayed very obviously in the dehisced capsule. While autogamy treatments revealed that *Ravenala* is at least a facultative selfer, in Darwin the flowers were most frequently visited by the megachiropteran bat, *Pteropus alecto gouldii*, and only occasionally by the smaller bat, *Macroglossus lagochilus*, and honeyeater birds (Meliphagidae). Apart from reproducing vegetatively, the ability of *Ravenala* to set seed when grown outside its normal range in the absence of its co-evolved pollinator(s), either by selfing or by using a suitable indigenous pollinator, could allow the species to assume pest status in parts of the tropics where it is planted as an ornamental.

Key words: alien plant; Australia; autogamy; nectar; outcrossing; phenology; pollination; vertebrate.

ENDEMIC IN MADAGASCAR, the Traveller's Tree (*Ravenala madagascariensis* Gmel.) is found in clearings in the rain forest. Immense colonies have appeared in the cleared foothills along the east coast, where it is a dominant species of later stage forest succession (Guillaumet 1984). *Ravenala* has frequently been cultivated in the three Mascareigne islands where it has become naturalized (Marais 1983), although in Mauritius it has vigorously colonized the highly disturbed montane forests (White 1983). The species is now widely cultivated in suburban gardens throughout the tropics, and is particularly popular in Darwin, where trees with apparently single or sub-opposed pairs of inflorescences occur. In New Guinea, a variant with apical inflorescence has been described by Hallé (1978).

Little is known of pollinators of *Ravenala madagascariensis* in Madagascar although Scott-Elliot (1890) observed visits by sunbirds, *Nectarinia souimanga* (Nectariniidae). Beetles and hymenopterans also visited flowers but pollination by them appeared to be only occasional (Scott-Elliot 1890).

In alien plants far removed from their usual pollinators, reproductive success may be determined by the degree of dependence on pollinator availability and efficiency (Valentine 1978). Records of failure to set seed due to these factors are uncommon but failure occurs in some specialized alien plants (Faegri & van der Pijl 1979). Generally, a number of methods may be utilized to enable seed production in plants outside their natural range. Seed set may be adequate where anemophily or mistake pollination has occurred (Proctor & Yeo 1973, Baker 1976). In plants exhibiting apomyxis, 96 percent of ovules will generally develop into seeds without

[1] Received 4 June 1991, revision accepted 1 May 1992.

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fertilization, though varying levels of pollination may be involved (Nybom 1987).

Dependence of unspecialized alien plants on the availability of generalist pollinators is relatively common. The efficiency of generalist pollinators is usually less than that of specialists but more than one class of pollinator may be active (Howell 1977). Ultimate reproductive success is inextricably linked to breeding systems, with fertilization success generally much lower in outbreeders than inbreeders (Wiens *et al.* 1987). The objective of this study was to investigate the pollination biology of *Ravenala madagascariensis* in the Darwin region and to determine its ability to set fruit and seed and insofar as this requirement is met, its potential to become a pest in the surrounding natural areas.

MATERIALS AND METHODS

The monocot plant *Ravenala madagascariensis* is the only species in its genus in the Order Scitaminae (Zingiberales) (Tomlinson 1962). *Ravenala* is one of three genera in what was claimed to be the most primitive family of the order, the Strelitziaceae; but more recently described as the Family Strelitziaceae in the primitive suborder Strelizineae (Kress 1990). The creamy white, hermaphrodite flowers (length 20–25 cm) are numerous. The perianth consists of six free sections, the calyx forming an outer whorl of three sepals and the corolla an inner whorl of three petals. There are six stamens (length 15–20 cm), each with a bilobed anther, and a single style with six longitudinal grooves and a stigma with lips at the apex surrounding the entrance to the stylar canal (total length 20–25 cm) (Scott-Elliot 1890). Flowers, often with stigmas already slightly protruding, open rapidly, apparently unaided or responding to touch (pers. obs.), when the mature anthers are straining for release. Odor of flowers is faint, sweet, slightly musty, reminiscent of *Musa* spp., and perceptible both day and night (pers. obs.). Fruits are tripartite, dehiscent capsules, releasing dark brown, nonuniform seeds surrounded by a blue aril, the function of which is unknown (Proctor & Yeo 1973, Marais 1983).

Studies of *Ravenala* were carried out from August to November 1987 on 6 trees aged between 4 and 11 yr (inflorescence height 3–6 m) in suburban gardens in Darwin (12°S, 131°E) in the Northern Territory of Australia. Sampling of nectar, studies of floral biology, and observations of visitors to inflorescences were carried out on two of these trees. Bulk nectar analyses, pollen collection, and further observations of visitors were carried out on the remaining 4 trees.

VISITORS TO FLOWERS.—During the 10 minutes before sampling periods daytime visitors to trees 1 and 2 were recorded for 78 days from August to November. Observations of the single inflorescence of tree 3 were made regularly at intervals covering 10 hours over 6 days, producing a total of 36 hours of daytime observations for potential pollinators. Using streetlight, observations of the same inflorescence took place on 9 consecutive nights in October between 1900 and 2400 hr. Stigmas of flowers (N = 126) from trees 1 and 2 were scored, *in situ,* with the aid of a hand lens (10×) for the presence of a variety of hairs. If present, hairs were sampled, and their identity checked against reference hairs held at CSIRO Tropical Ecosystems Research Centre in Darwin.

NECTAR AND BRACT FLUID ANALYSIS.—Dawn and dusk nectar samples from fresh flowers of 1 tree were combined to give a volume of 30 ml for each of the 2 time periods. For the same time periods, 5 ml samples of the liquid from the bracts of the same tree were collected, combined, and a 30 ml aliquot set aside for analysis. All samples were stored frozen (−20°C). Samples were analyzed by the Chemistry Section, Northern Territory Department of Primary Industry and Fisheries, to determine nutrient content.

NECTAR PRODUCTION, CONCENTRATION, AND CONSUMPTION.—For determination of nectar production and concentration, flowers about to open (N = 12) were bagged with 1 mm diameter nylon mesh prior to anthesis. Nectar production and concentration were sampled by removal using 3 ml hypodermic syringes with blunted, 20 gauge needles at dawn and dusk over a period of 4 days after anthesis. Concentration was measured using a Bellingham and Stanley temperature compensated field refractometer (range: 2–100% sucrose). Nectar consumption and concentration was determined by sampling and returning quantities of nectar present in 126 unbagged flowers (N_1 = 63, N_2 = 63) at both dawn and dusk. Quantities in 76 bagged flowers (N_1 = 36, N_2 = 40) were similarly sampled to determine timing of production and if any withdrawal occurred in the flower.

FLORAL BIOLOGY.—The time intervals between opening of successive flowers (N = 126) and duration (N = 109) of anthesis were measured in the

same uncovered flowers at dawn and dusk. Anthesis was recorded when, in newly opened flowers, both stigma and 6 dehiscing anthers were exposed and considered terminated when anthers and pollen dried and stamens began to curl. Protogyny was recorded when stigmas were exposed prior to flower opening. Time of abscission ($N = 109$) was recorded when the floral apparatus had markedly browned and separated from the plant. The number of flowers produced by each bract was also scored.

Flowers ($N = 38$) subjected to peroxidase tests for stigma receptivity were bagged before opening or stigma exposure with 1 mm diameter mesh to exclude pollinators. Excised stigmas collected for various ages (0–96 hr) were tested for peroxidase activity by immersion in a freshly prepared benzidine solution (Galen & Plowright 1987). Relative peroxidase oxidation was estimated by the percentage color change from creamy white to pinky brown, on the outer surface of the stigma after 5 min. As well, flowers ($N_1 = 10$, $N_2 = 16$) for each age class (0–72 hr) were scored by touch for stigma stickiness and visually for degree of secretion and color change.

The number of fertile stamens with dehiscing anthers was recorded in 10 newly opened, unbagged flowers from each of 4 trees ($N = 40$). Status of pollen collected from 20 freshly opened flowers was determined using light microscopy and Alexander's solution (Alexander 1969). Stained pollen was scored as intact, germinating, or empty; this allowed comparison with germination estimates in hand pollination treatments.

POLLINATION TREATMENTS.—To determine the presence of autogamy, individual flowers were bagged with 1 mm diameter mesh prior to stigma exposure or anthesis and kept covered until fruit developed ($N_1 = 9$, $N_2 = 21$). Hand pollinations were performed on individual flowers bagged prior to stigma exposure or anthesis. A total of 26 stigmas of various age classes were brushed evenly with pollen from anthers of newly opened flowers. Pollination treatments included use of pollen from the same flowers, same bract, another bract, and another tree.

Stigma and style ensembles in the hand pollination treatments were collected at time intervals ranging from 15 min to 10 hr. Each style was cleaned of pollen and the ensemble then dissected longitudinally and the stigma excised from one half section. All were then stained with Alexander's solution. Pollen adhesion and germination on the outer surface of the stigmas, in the stigma canal and in the stylar canal, were scored using light microscopy to count the number of intact, germinating or empty pollen grains. Scores were adjusted to give values for the entire stigma, stigma canal, and the stylar canal. Percentage germination rates were calculated.

RESULTS

ANIMALS VISITING INFLORESCENCES.—Ants often visited the inflorescences of *Ravenala* although numbers and species visiting varied between trees, each tree having its own dominant species. Dominant, nectar-consuming species were *Iridomyrmex* sp. or *Oecophylla smaragdina,* while other nectar-consuming species included both native (*Camponotus nigroaenus* and *Opisthopsis haddoni* groups) and introduced species (*Parachtrina longicornis* and *Tapinoma* sp.). Introduced honey bees, *Apis mellifera* (Apidae), were observed collecting pollen on only two occasions and *Eutricha sequior* (Megachilidae) was seen collecting nectar three times. The beetle *Protacta fusca* (Scarabaeidae) was twice observed ingesting either liquid from the bracts or pollen; midges, occasional blowflies *Lucilia cuprina* (Calliphoridae), and cockroach nymphs were observed around older browning flowers.

Numerous diurnal birds, of various species common to the Darwin area (Thompson & Goodfellow 1987) were in the vicinity of, but bypassed *Ravenala* (16 individuals hr^{-1} within 5 m radius of tree). A few groups of two or three honeyeaters, *Entomyzon cyanotis* (Meliphagidae), visited the inflorescences of *Ravenala.* The birds were disturbed each time by passers-by before nectar consumption could be confirmed. There was one sighting of the large honeyeater, *Philemon citreogularis* (Meliphagidae), consuming nectar and another of *Philemon buceroides* close to an inflorescence.

Observations of *Ravenala* from 1900 to 2400 hr on 7 to 15 September 1987 recorded a total of 44 fruit bats, all *Pteropus alecto gouldii* (Pteropodidae), near tree 3. They were seen to forage singly (and once as a pair) for *Ravenala* nectar on 12 instances between 2100 and 2400 hr. Visits were made by up to four individuals between 1900 and 2400 hr, with one evening peak of four visits between 2100 and 2300 hr; the average duration of a visit was 11 min. Each fruit bat crept over many flowers, thereby probably carrying pollen on its coat. On two evenings, when no visits were recorded at *Ravenala, P. alecto* crowded onto nearby flowering *Melaleuca* sp.

Nineteen of 126 stigmas sampled at dawn and dusk had chiropteran hairs adhering to their surfaces. Of these, 18 stigmas had one or more *P.*

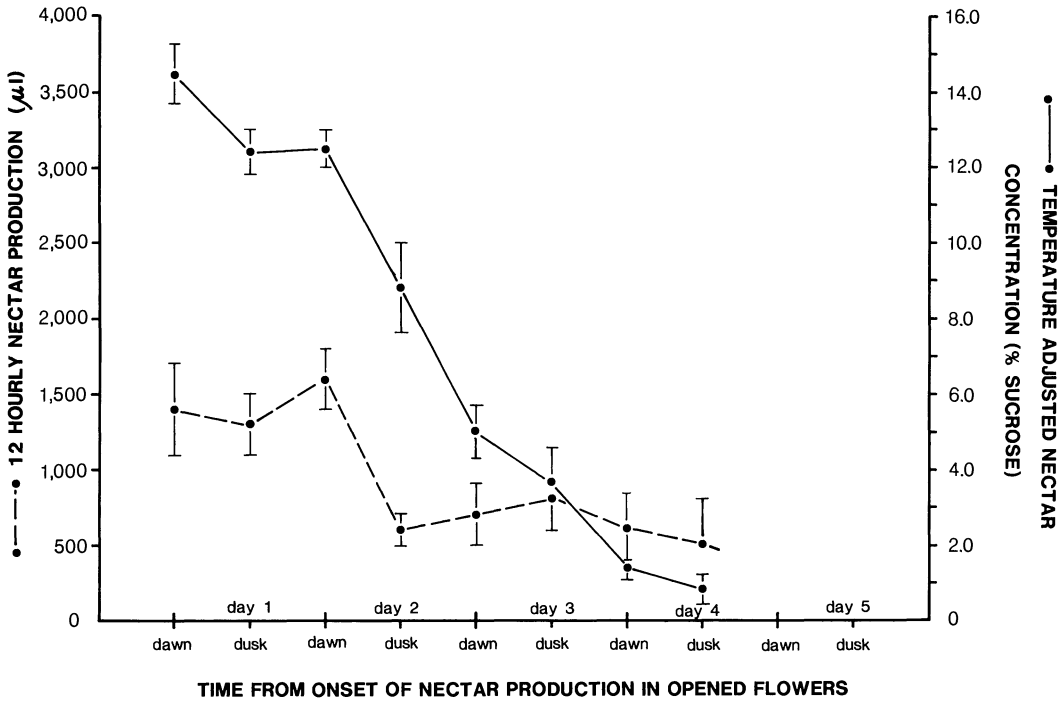


FIGURE 1. Mean (±SE) nonaccumulated nectar production and concentration in bagged flowers of *Ravenala madagascariensis* (N = 12; tree 2).

alecto (Pteropodidae) hairs (N_1 = 10, N_2 = 8) and tree 1 had hair from *Macroglossus lagochilus* (Pteropodidae). During preliminary investigations, *M. lagochilus* hairs were also sampled from tree 4. No other hairs were recorded.

NECTAR AND BRACT FLUID NUTRIENTS.—Bulked nectar analysis revealed 15.4 percent and 13.3 percent total reducing sugar (after inversion) for dawn and dusk samples respectively. Percentage nonreducing sugars were 9.7 and 8.5 respectively. Other nutrients analyzed in nectar included: N 0.026 percent, 0.025 percent; P 0.0008 percent, 0.0006 percent; Mg 31 ppm, 11 ppm; Na 25 ppm, 13 ppm; Ca 140 ppm, 93 ppm; and K 1182 ppm and 1095 ppm at dawn and dusk, respectively. Bract fluid contained 2.8 percent reducing sugar after inversion and 0.5 percent nonreducing sugars. Other nutrients in bract fluid included N 0.002 percent; P 0.0006 percent; Mg 21 ppm; Na 25 ppm; Ca 175 ppm; and K 635 ppm.

NECTAR TEMPORAL PATTERNS.—Initially, the volume of nonaccumulated nectar sampled at dawn and dusk from 12 bagged flowers (tree 2) was high (1400 µl) and of moderate concentration (14.5% sucrose equivalents, Fig. 1). After 24 hr nectar volume and concentration fell sharply to 700 µl 12 hr^{-1} and 5 percent sucrose and then more slowly until nectar production was at its lowest (500 µl 12 hr^{-1} and 0.8% sucrose) at which time 5 of the 12 flowers sampled had abscissed. Nectar was produced during both day and night but the greatest mean volume of nectar recorded (1600 µl) was produced at night on day 1.

Analysis of variance of log-transformed measures of nonaccumulated nectar volume produced significant differences for days since anthesis (F = 5.83, df = 3,70, $P < 0.01$), but not time of day (F = 3.68, df = 1,70, P = 0.06) and the interaction between the two was significant (F = 3.68, df = 2,70, $P < 0.05$). Concentration values showed significant differences for days since anthesis (F = 99.75, df = 3,78, $P < 0.001$) and time of day (F = 7.38, df = 1,78, P = 0.01) but the interaction was not significant (F = 0.77, df = 3,78, P = 0.52). In this case the nectar concentration falls continuously and time since anthesis and time of day are autocorrelated.

NECTAR REMOVAL.—The volume of accumulated floral nectar, in bagged and unbagged flowers sam-

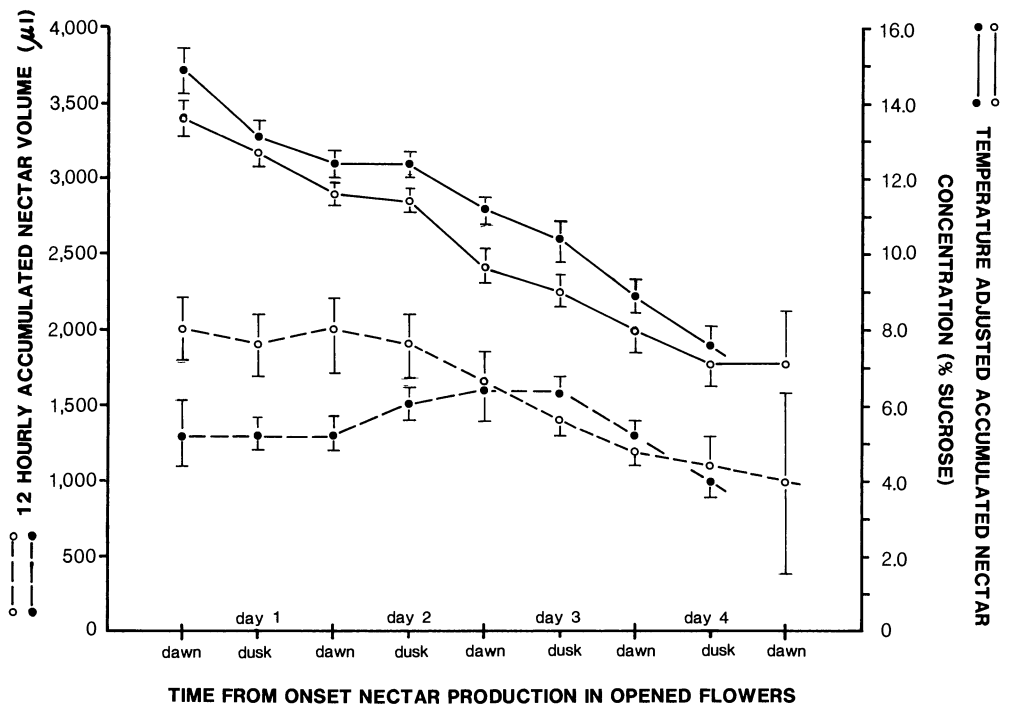


FIGURE 2. Mean (±SE) accumulated nectar production and concentration in (●) bagged and (○) unbagged flowers of *Ravenala madagascariensis* (N = 40, N = 63; tree 2).

pled to determine the consumption of nectar by animals, is shown in Figure 2. The volume of nectar decreased less rapidly in these samples than in the nonaccumulated nectar samples due to carryover of nectar from the previous period. Initially there was a significantly greater volume of nectar in the unbagged compared with the bagged flowers and this was maintained until dawn of day 3. The reason for this is unknown.

Nectar volume declined with time in the unbagged flowers consistent with removal by animals while in the bagged flowers there was a significant increase to day 3 with subsequent decrease. Analysis of variance on natural log-transformed data showed there were significant differences in volume due to bagging treatment ([F = 4.88, df = 1,79, P < 0.05], *i.e.*, an increase in bagged flowers and decrease in unbagged flowers), and the time since anthesis (F = 6.41, df = 3,79, P < 0.001).

Significant differences in the concentration of nectar produced by bagged and unbagged flowers were obtained due to days since anthesis (F = 132.35, df = 3,78, P < 0.001) and time of day (F = 6.99, df = 1,78, P < 0.05) but not due to bagging treatment (F = 0.38, df = 1,78, P = 0.55). From Figure 2 it is apparent that nectar concentration decreases fairly steadily with time since anthesis and is autocorrelated with time of day (as in the nonaccumulated case).

FLORAL BIOLOGY.—Onset of anthesis occurred at night in 82.6 percent of flowers (N = 109). The mean time interval between opening of successive flowers was 2.3 days (N = 109). There was some variation between individual trees sampled. For tree 1 (N = 49; 3 bracts) the mean time interval was 2.8 days, while for tree 2 (N = 60; 3 bracts) the mean time interval was 2.0 days. Bracts sampled on an individual tree showed little variation in the time interval between opening of successive flowers. The number of flowers per bract was variable; 17–24 flowers per bract were recorded in tree 1 and up to 29 in the bracts sampled in tree 2 ($\bar{x}$ = 21 ± 3; 6 bracts).

Mean duration of anthesis was 1.3 days (range 0.5–3.0 days; N = 109) in the 126 flowers sampled (N_1 = 62, N_2 = 64; Fig. 3). Eighty-seven percent (N = 109) exhibited anthesis; and of these, 33 percent of tree 1 flowers and 3.7 percent of tree 2 flowers were protogynous, with stigma exposed prior

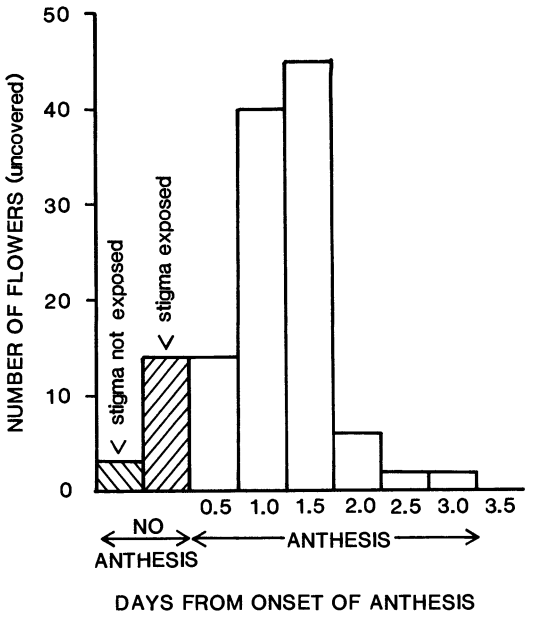


FIGURE 3. Incidence and duration of anthesis (N = 126; 109 anthesis: 17 no anthesis) (bracts 1, 2, 5, tree 3; bracts 2, 3, 4, tree 2).

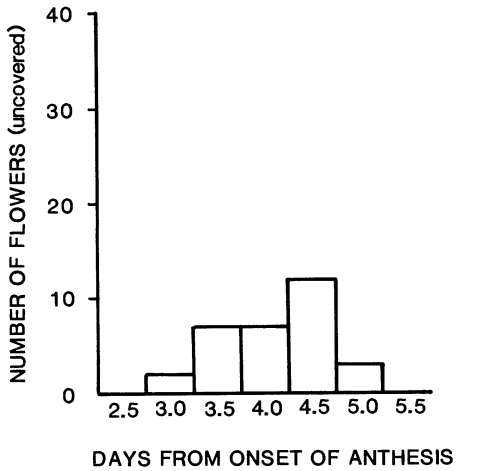


FIGURE 4. Flower longevity or time of floral abscission (anthesis = time 0) (N = 31) (bracts 2, 3, 4, tree 2).

to exposure of stamens. Anthesis was not recorded in fourteen percent (N = 17) though of these, 82.4 percent (N = 14; 11.1% of total sampled) did have stigmas only exposed while in 17.7 percent (N = 3; 2.4% of total sampled) the only possible options were cleistogamy or flower abortion as neither stigma nor stamens were exposed. After a mean time of 4.1 days from onset of anthesis the flowers abscissed (Fig. 4).

In peroxidase tests for stigma receptivity (Table 1), the mean estimated percentage color change to pale pink or pinky brown was 49 percent at onset of anthesis (age class = 0) and reached a maximum of 53 percent after 24 hr and thereafter declined rapidly. Stigma status also changed over time as all stigmas (N = 26) were creamy white, very sticky and glistening with secretion at anthesis (Table 1) but after 24 hr stigma color (N = 26) had changed to fawn and stickiness was reduced, but 73 percent still glistened with secretion. Thereafter stigmas continued to brown, glistening decreased rapidly and stickiness also decreased.

The number of fertile stamens scored in 10 flowers from each of trees 1, 2, 4, and 6 was always

TABLE 1. *Change in average stigma receptivity of* Ravenala madagascariensis *flowers with time as indicated by peroxidase tests (N = 38) and stigma status (stigma stickiness, degree of glistening with secretion and color (N = 129). (NS indicates age class not sampled).*

			Stigma status					
	Peroxidase tests			Stickiness (0–5)	Secretion (sample %)	Color (sample %)		
Age class (hours)	Number sampled	Mean % color change	Number sampled	Sample mean	Glistening	White	Fawn	Brown
0 (pre-anth)	5	12	NS	NS	NS	NS	NS	NS
0 (anth.)	9	49	26	5	100	100	—	—
12	NS	NS	26	5	85	54	46	—
24	6	53	26	5	73	—	100	—
48	9	19	26	4	6	—	96	4
72	5	6	25	2	—	—	65	35
96+	4	—	NS	NS	NS	NS	NS	NS

6. At anthesis 98 percent of pollen grains examined were intact, with grain contents clearly visible and no pollen tubes.

One-way analysis of variance of the 4 pollination treatments (self, same bract, same tree, different tree) also showed no significant differences in germination at the stigma surface ($F = 0.77$, df = 3,25, $P = 0.52$). The untransformed mean percentage germination ($N = 26$) for these four pollination treatments was 8.9 (13), 0 (2), 10.3 (3) and 5.2 (8) respectively.

The percentage germination of pollen on the stigma surface was only significantly influenced by the time since pollination ($t = 3.31$, $P < 0.01$) in a stepwise multiple regression ($F = 3.98$, df = 22,26, $P < 0.05$, $r^2 = 35\%$). Age of the stigma (0–24 hr), total number of pollen grains, or pollination treatment did not significantly contribute to the multiple regression. Similarly neither the percentage germination inside the stigma ($F = 2.01$, df = 3,24, $P = 0.14$) nor the percentage germination inside the stylar canal ($F = 0.91$, df = 3,18, $P = 0.46$) differed significantly between hand pollination treatments.

As no significant differences in pollen germination were found between the three self-pollination treatments, two-sample t-tests were performed on three combined self-pollination treatments and the different tree treatment. Results again showed no significant differences in pollen germination between pollination treatments at the stigma surface ($t = 0.65$, $P = 0.52$), in the stigma canal ($t = 0.98$, $P = 0.34$), nor in the stylar canal ($t = 0.31$, $P = 0.76$).

All 9 treated flowers of tree 1 in autogamy experiments (5 exhibited anthesis, 4 stigma only exposed), set fruit though 3 out of 9 fruits were diminished in size, 2 of them being half size. Of 21 autogamously treated flowers of tree 2, all exhibited anthesis and 20 set fruit. However, 50 percent were reduced to between a quarter and half size.

DISCUSSION

Visitors to *Ravenala*.—In Madagascar, *Ravenala* has been recorded as being visited by sunbirds (*Nectarinia souimanga,* Nectarinidae) (Scott-Elliott 1890). It is unknown whether bats are implicated in the species' native range, but suitable species are present. Of the fruit bats, *Pteropus rufus* is of a similar size to *P. alecto* while *Stenonycteris lanosus* and *Eidolon helvum* are both smaller. Kingdon (1974) noted that nectar and soft fruits may be the preferred food of *S. lanosus* and, as it occurs along the east coast of the island, this species is a likely pollinator. None of the microchiropteran bats listed for Madagascar by Kingdon (1974) or Smithers (1983) is considered to feed from plants so they are excluded as possible pollinators.

In Darwin, *Iridomyrmex* and *Oecophylla* ant species visit *Ravenala* and both were observed consuming nectar. Their activities centered around the base of flowers well away from stigmatic and pollen areas, so that they are unlikely to be effective pollinators. It is generally agreed that ants are seldom pollen vectors and few plants are pollinated by them (Beattie 1982, Buckley 1982). Other insects, also, may be considered relatively unimportant as pollinators of *Ravenala.* The large inflorescence structure and large distance between stigma and nectar suggest adaptation to vertebrate as opposed to invertebrate vectors (Turner 1982).

Daytime observations revealed that the majority of birds in the study area, including the numerous small honeyeaters, bypassed *Ravenala* inflorescences. The visitation by large honeyeaters (Meliphagidae) and in particular *Entomyzon cyanotis,* albeit in small numbers and without actual observations of *Ravenala* nectar intake (due to disturbance), may be of minor significance. Their large body size relative to the smaller honeyeaters appears better suited to the proportions of *Ravenala* inflorescences and flowers. Further observations of *Ravenala* trees situated amidst native vegetation and further removed from sources of disturbance would clarify the situation.

Pteropus alecto visitors to *Ravenala* were considered likely pollinators. Average individual visitation time was 11 min per inflorescence during which time individuals took nectar from a flower and then clambered over the flowers to reach further fresh flowers. The presence of *P. alecto* hairs on stigmas (15%) gives further support to these observations. Visitation numbers were relatively small (as was percentage hairs on stigmas), probably because *Ravenala* nectar is not the preferred diet of *P. alecto.* The primary food of *P. alecto* in Australia is blossom, though nectar and both native and cultivated fruits are also consumed (Ratcliffe 1931, Nelson 1965). Large numbers of *Pteropus alecto* were observed foraging for nectar in freshly flowering *Melaleuca* in preference to adjacent *Ravenala.* The presence of *Macroglossus lagochilus* hairs on two stigmas indicated that it, too, was a visitor to *Ravenala.* Foraging by *M. lagochilus* may occur at different times from that of *P. alecto* or the paucity of its apparent visits could be due to seasonal factors,

preferences, or low abundance. *Macroglossus* species generally feed on plants which are aseasonally flowering, produce a relatively small number of new flowers per night but have some flowers available continuously or for long periods, and frequently grow gregariously (Start & Marshall 1976). *Ravenala* does fit this description.

PLANT CHARACTERISTICS AND POLLINATION SYNDROMES.—Plant characteristics that are helpful in defining pollination syndromes include time of anthesis and nectar secretion; color, odor, morphology and positioning of flowers, and the volume and concentration of nectar (Faegri & van der Pijl 1979). The floral and plant characteristics of *Ravenala* determined by this study indicate that the species is adapted to chiropterophily and perhaps to a lesser extent, to ornithophily. It could possibly be transitional, indicating an ancestor that was bird pollinated as has been postulated for other taxa by Faegri and van der Pijl (1979). Most of the features of *Ravenala* flowers indicate vertebrates rather than invertebrates are the normal pollinators of this species. The large flowers produced on a robust inflorescence and strongly attached to the stem, as in *Ravenala,* are characteristics which aid vertebrate visitors (Turner 1982). The phenological pattern, where each bract, once flowering, produces a new flower every 2–3 days so that the overall flowering period of a single tree is of long duration (approximately 2 mo) suggests adaptation to pollination by long lived pollinators.

The faintly musty sweet odor and pale color of the flowers and the fact that over 80 percent of flowers open and begin to secrete nectar at night all point to mammalian pollination. In southern Australia there are many mammal pollinated species but these tend to have cryptic and/or geoflorous inflorescences hidden within the plant canopy (Rourke & Wiens 1977) and are associated with nonflying mammals. *Ravenala* does not fit into this syndrome with its well displayed inflorescence high on the plant and is more satisfactorily correlated with flying mammals such as bats. Both nectar concentration and productivity support the hypothesis of a bat pollination syndrome.

Mean maximum concentration of nectar of 14.5 percent sucrose in *Ravenala* is in agreement with mean nectar concentration of 17 percent (range 11–26%) for New World bat pollinated trees and lianas in Costa Rica (Baker 1978) but less than the upper range figure of a 26–27 percent recorded for the macroglossine (*Melonycteris woodfordi*) pollinated Old World *Heliconia solomonensis* (Kress 1985). The concentration for hummingbird pollinated trees and lianas and for bee pollinated flowers is much higher (Baker 1978). Bat and sunbird pollinated flowers, however, are in approximately the same category regarding nectar concentration. Mean nectar concentration for sunbird pollinated plants is 17.3 percent with mean nectar concentration being 15.2 ± 0.3 percent for *Leonotis nepaetifolia* (Cruden *et al.* 1983). For *Strelitzia nicolai* nectar quality is 10 percent sucrose equivalents, somewhat lower than in the related *Ravenala* (Frost & Frost 1981).

As well, nectar production in *Ravenala* (1400 μl 12 hr^{-1}; 116.7 μl hr^{-1}) is in the range of nectar production by other bat pollinated flowers and flowers pollinated by sunbirds. Production figures (μl) for bat pollinated flowers include 161.2 ± 16.8 (*Ipomoea muricoides*) and 64.4 ± 8.3 (*Agave palmeri*), while figures for those pollinated by sunbirds include 57.35 ± 5.92 (*Phygelius aequalis*) and 13.72 ± 1.52 (*Leonotis nepetaefolia*) (Cruden *et al.* 1983). However, for *Strelitzia nicolai* maximum mean nectar production was 140 μl hr^{-1} occurring two days after the flower opened (Frost & Frost 1981) indicating that sunbird pollinated plants may have copious nectar production.

Further aspects that may suggest specialization towards vertebrate pollination include the presence of liquid in the bract containing the flowers. Slimy to touch and not readily evaporated, this liquid acts as a fairly effective moat to isolate the flowers from nonflying invertebrates such as ants. This liquid also provides a copious and always readily available, low sugar content reward (2.8% reducing sugar, after inversion and 0.5% nonreducing sugars), less expensive than nectar, but containing essential nutrients (0.002% N, 0.0006% P, 21 ppm Mg, 25 ppm Na, 175 ppm Ca and 635 ppm K) possibly encouraging regular visitation by potential pollinators. The concentration of potassium in nectar (K-dawn 1182 ppm; K-dusk 1095 ppm) and in bract fluid (K 635 ppm) may chemically deter bees (Baker & Baker 1983). Calcium, important for bone ossification in vertebrates (Altman & Dittmer 1968) and to counterbalance the antagonistic effect of K ions on Ca ions in the body (West & Todd 1957), is found in concentrations of 144 ppm in nectar and 175 ppm in bract fluid.

Three impressive stages can be recognized in the *Ravenala* life history: the nonfan juvenile without spikes; the laterally compressed fan, with distinctive protruding green bracts and inflorescences of pale flowers providing rewards for pollinators; and the fan, with brown bracts and seeds with blue arils, providing the rewards for seed dispersers (Fig.

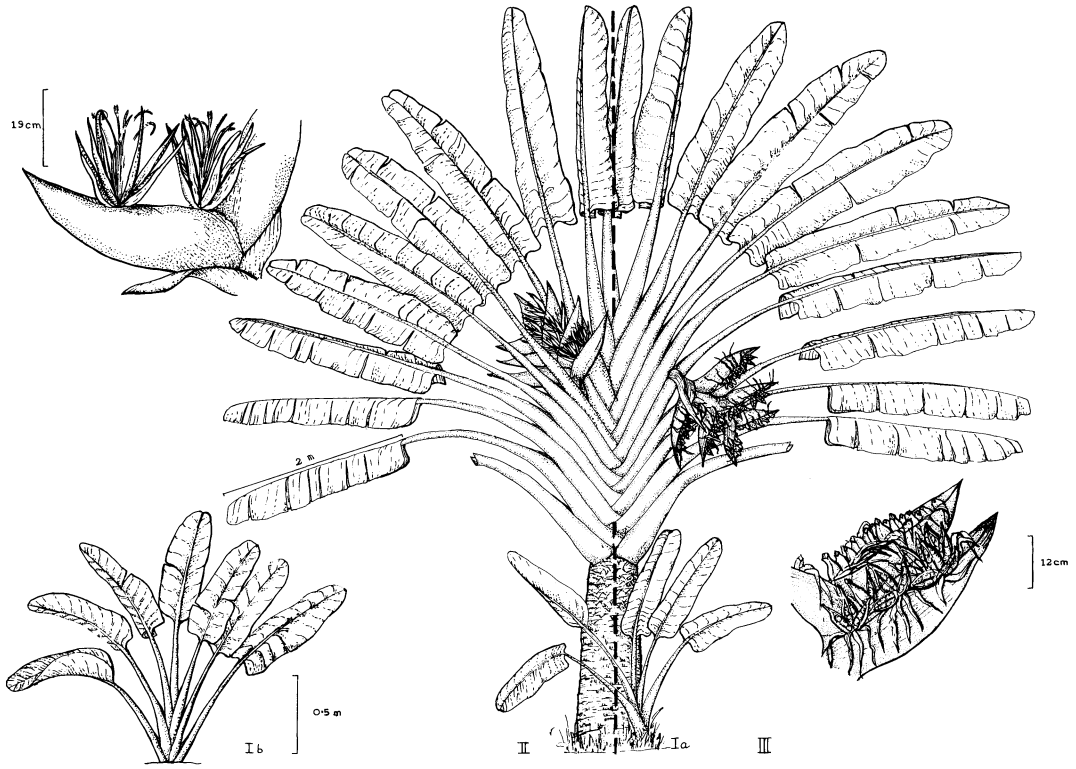


FIGURE 5. Stages in the life history of *Ravenala madagascariensis*: I, juvenile stage without trunk and with poorly developed fan; II, mature fan with protruding green bracts containing creamy white flowers with nectar; III, mature fan with brown bracts becoming pendant containing dark brown seeds with blue arils.

5). For this plant, the stiff spikes protruding with their boat-like bracts and pale inflorescences with nectar rewards, or aril-coated seeds, well out from and at right angles to the large green fan-like array, provide the display.

In the syndrome of chiropterphily bat flowers are well documented as having a peculiar position outside the foliage. Examples include *Agave schottii* Engelm. pollinated by *Leptonycteris nivalis* and *Parkia clappertoniana* Keay pollinated by *Epomophorus gambianus* (Faegri & van der Pijl 1979) and *Heliconia solomonensis* pollinated by *Melonycteris woodfordi* (Kress 1985). *Ravenala* does fit this category. In the syndrome of ornithophily, nectar in red flowers is a common attractant (Faegri & van der Pijl 1979), but the pale flowers of *Ravenala* do not fit the usual bird pollination syndrome. Perhaps the fan-shaped foliage, with bracts protruding at right angles, provides the visual display and an alternative day-time bird attraction. As birds have only a weak sense of smell (van der Pijl 1982) the faint odor of *Ravenala* flowers possibly attracts bats but not birds. Most megachiropterans do not echolocate and must locate food sources by smell or sight (but not color, as they are colorblind). Overall, the advertisement in *Ravenala* is obvious and long-lived, and as both bats and birds use their visual sense in foraging, this is the commonality of the syndrome.

BREEDING SYSTEM AND POLLINATOR ACTIVITY.—With such an impressive suite of vertebrate adaptations, the apparent propensity for self-pollination by *Ravenala* is surprising. Reports on the breeding systems of tree species of tropical and sub-tropical, wet and semi-deciduous forests indicate that the majority are obligate outcrossers, though distinctions are often not clear cut and self-incompatible plants occasionally set fruit following self-pollination (Kress 1983).

The self-pollination treatments in *Ravenala* indicate higher levels of germination at the stigma level in self-pollinations (up to 35% germination) than in cross pollinations (up to 22%). However, more pollinations need to be done before the results

can be considered conclusive. Although levels of germination were only indicative of compatibility at the stigma level, the high degree of fruit set observed in the autogamy treatments would be consistent with the presence of self-compatibility in these particular individuals. However, the dwarfed size of an appreciable number of the developed fruits from autogamous treatments may indicate that seed set or seed quality is reduced in selfed plants. In the closely related *S. nicolai* self-pollination treatments successfully set seed (Frost & Frost 1981), and in one individual of the closely related *Heliconia colgantea* levels of autogamy were almost complete (86%) indicating that individuals that are self-compatible are apparently highly autogamous as well (Kress 1983). The need for further studies on *Ravenala* is indicated.

The general activity of pollinators around the studied *Ravenala* must be considered to have been low because little nectar was consumed. The presence of other and perhaps more prolific or calorifically more suitable food sources (*e.g., Melaleuca* sp.) during the study may have diminished the attractiveness of the *Ravenala* flowers to bats. The isolated occurrence of these garden plants (either as individual plants or clumps) is in contrast to their extensive growth in secondary lowland rain forest in Madagascar. This, combined with the gregarious feeding habits of fruit bats, would make visitation of isolated plants less likely than would be the situation in their normal range. Nevertheless the fact that bat hairs were found on stigmas and visits were observed indicates that native bats could pollinate this exotic species.

Ravenala success.—The success of an exotic species in a new environment depends on its ability to increase its population by sexual or vegetative means. In many cases the limitation of the spread of an exotic species may be due to lack of suitable pollinator species in its new environment. Certainly pollinator limitation does not occur with many successful exotics such as some of the composites (*e.g.,* species of *Carduus, Arctotheca*) but would be a problem for *Yucca* with its highly specialized pollination mechanism.

The phenology of *Ravenala,* where only a few flowers on any one plant are open at one time and where up to one-third may be protogynous, favors cross fertilization, as pollinators are forced to go from one plant to another. However, the species is not locked into cross-pollination and may self-fertilize, although the quality/quantity of seed may be decreased below that achieved by outbreeding. In Darwin, where *Ravenala* is normally an isolated specimen plant, pollinator activity will often be diluted by prominent unrelated species (e.g., *Melaleuca*) which may result in reduced outcrossing possibilities.

Seed set does occur in Darwin; the hard brown 9–14 mm seeds are each enveloped in a brilliant azure blue aril. In other plants (*e.g.,* cycads; Ladd *et al.,* in press), seeds similar in size and clothed in a striking integument are removed and consumed by frugivorous birds and mammals. The seeds are rarely digested but nourishment is obtained from the protein, oil, sugar, or starch rich aril.

The removal success by a particular species is generally considered to be dependent on the ratio of edible aril to the indigestible seed (Howe & Westley 1986). In Darwin, the blue aril coated seeds of *Ravenala,* conspicuous in their dehisced capsules, are occasionally consumed by *Oriolus sagitattus* (Oriolidae) (B. F. Gunn, pers. comm.). Generally, the seeds remain in position until the browned inflorescence decays, allowing the seeds to fall to the ground.

Constraints on the success of *Ravenala* as an exotic plant and potential weed in northern Australia emanate from two factors. It has been shown that pollination either by suitable pollinators native to the Darwin area or from selfing is possible and seed is produced. However, seed quality and quantity may be reduced in selfed plants or through lack of attention from local pollinators. The second aspect involves seed dispersal, germination, and establishment and this needs to be addressed to complete the picture for the species.

ACKNOWLEDGMENTS

We thank the staff of the Department of Primary Industry and Fisheries (Northern Territory) for assistance with analyses; the Northern Territory University for provision of laboratory facilities; A. Andersen, I. Cook, and A. Hertog for identification of ants, other insects and chiropteran hairs respectively; L. A. Dorr, W. J. Kress, and T. Willing for information; B. F. Gunn for the illustrations; and the owners of *R. madagascariensis* trees in Darwin for access (in particular R. & T. Miller and L. & K. Russel). We also thank W. M. Lonsdale and R. D. Wooller for their constructive criticism of a draft of the manuscript. This is publication number 743 of the CSIRO Tropical Ecosystems Research Centre, Darwin, Australia.

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