"Two Bob Each Way": The Pollination and Breeding System of the Australian Rain Forest Tree *Syzygium cormiflorum* (Myrtaceae)[1]

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ABSTRACT

The breeding system of a cauliflorous rainforest tree *Syzygium cormiflorum* was examined to assess the degree of self-compatibility, the type and effectiveness of its pollinators, and the postfertilization seed loss and net seed production. The species is xenogamous, but shows a degree of self-compatibility, with successful pollination via autogamy ranging from 10 to 32 percent, via geitonogamy 16–60 percent, via intrapopulation xenogamy 58–82 percent, and via interpopulation xenogamy 80–92 percent. The difference in fertilization rates between autogamy and geitonogamy is discussed. Bats, birds, and insects were successful pollinators, with bats (and possibly large moths) being the most effective despite visiting the flowers less frequently than birds. Bats, and possibly large moths, accounted for 55.4 percent of successful pollinations, compared to 19.6 percent for birds and 25 percent for small insects. Postfertilization seed loss due to the predatory activity of a weevil was very high, up to 70 percent.

The pattern of average nectar flow favors birds, but individual flowers produce nectar at varying times suitable for nocturnal or diurnal visitors or both. There is some evidence that breeding is restricted to crosses between individuals in a local population. The pollination system may be adaptive in maximizing fertilization in situations lacking the major pollinators, but the difficulty of distinguishing this from a system evolving from night to day pollination or *vice versa* is recognized.

THE RAINFOREST TREE FLORA OF AUSTRALIA totals over 1200 species, yet there has been no quantitative study made of the pollination biology and breeding system of any of them. This is in marked contrast to the Neotropics and southeast Asia where a few studies of controlled pollination and pollinator biology have been done, resulting in a rapid reassessment of the general view of breeding systems in tropical forest trees. The earlier view (Corner 1954, Baker 1959, Fedorov 1966) was that rainforest trees were mostly self-compatible and self-pollinated, allowing maximum seed set in an environment where pollinator movements were supposedly limited. It is now held that outcrossing is the more important phenomenon encountered (*e.g.,* Ashton 1969, Bawa 1974, Frankie & Baker 1974, Frankie *et al.* 1976).

The Myrtaceae is an important and conspicuous element in the Australian flora and is well represented in our rainforests. The largest genus in these forests is the widely distributed *Syzygium,* which has over 500 species world wide with 52 in Australia of which 41 are endemic (Hyland 1983). Studies of two species of *Syzygium* have already been reported. Lack and Kevan (1984) examined the breeding system of *Syzygium lineatum* on Sulawesi, and Hopper (1980) recorded floral visitors to *Syzygium tierneyanum* in north Queensland.

The subject of the present study, the first quantitative assessment of breeding of an Australian rainforest tree, was *S. cormiflorum* (F. Muell.) B. Hyland, a small subcanopy tree which commonly occurs in a variety of rainforest types between Townsville and Cooktown in north Queensland and again further north in the forests of the McIlwraith and Iron ranges. It exists as two forms, a small (up to 60 cm DBH) cauliflorous tree or a larger (up to 100 cm DBH) ramiflorous tree; the former occurring from sea level to 1200 m altitude but commoner at higher elevations, and the latter from sea level to 900 m and commoner at lower elevations. On a small scale it appears to be patchily distributed. All further references are to the cauliflorous form.

The flowers are not numerous and are borne in small cymes on cauline excrescences that increase in size with age. They are large (calyx tube 7–20 mm long × 9–16 mm diameter, filaments 15–30 mm long) and creamy white with four small white petals and numerous stamens (a "shaving brush" type) and have a faint unpleasant smell. The majority project downward, but in big clusters they are forced to point in all directions. There are 30–50 ovules in the ovary of the cauliflorous form and 90–100 in the ramiflorous form. The fruits are large (30–60 mm diameter), red or white, and fleshy.

The only recorded floral visitor is the nocturnal pygmy possum (*Cercatetus caudatus*) (Winter 1979), but the

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floral attributes of this tree are those that characterize plants with a bat-pollination syndrome (Faegri & van der Pijl 1971).

The aims of this study were to determine by controlled pollination the degree of self-compatibility in *S. cormiflorum,* to assess the effectiveness of its floral visitors as pollinators and to relate this to floral biology, and to measure postfertilization fruit loss and net seed production.

STUDY AREA

The study took place on the Atherton Tableland, north Queensland, between July and December 1983. Four populations of *S. cormiflorum* were located at Halloran's Hill (H), Curtain Fig (F), Wongabel (W), and Longland's Gap (L) (Fig. 1).

The four populations occur in remnant patches of complex notophyll vine forest (Type 5a and 5b of Tracey 1982) which survived widespread clearing during the 1930s and 1950s. Although the tableland is a complex mosaic of rainforest and eucalypt forest, it is apparent that the four areas were once a continuous belt of rainforest and that the *S. cormiflorum* populations of our study were extant in the original intact rainforest belt. The Longland's Gap population is in a cooler area with higher rainfall than the other three, very similar, sites.

The population at Halloran's Hill (10 trees) was used for all crosses and observations. The other three populations were used for interpopulation crosses only.

METHODS

FLORAL BIOLOGY.—Fifteen individual flowers on 4 trees were examined frequently for floral development, and the times of various floral events were noted.

Insufficient flowers existed to measure the timing and development of stigma receptivity accurately. Instead we tested to see if any flowers could be fertilized after one pollination at anthesis. To do this 10 flowers on one tree at Halloran's Hill, 37 on one tree at Curtain Fig, and 22 on one tree at Wongabel were emasculated at anthesis and pollinated immediately by hand using self-pollen at Halloran's Hill and xenogamous pollen at the other sites. The flowers were then individually bagged.

Nectar flow from 13 screened flowers in 3 inflorescences on one tree was measured every 3 hours over a 24-hour period. Nectar concentration was measured with a refractometer and is expressed as percent sucrose equivalents (wt/vol). No allowance was made for nonsugar refracting substances (Hiebert & Calder 1983).

CONTROLLED POLLINATIONS.—Three trees at Halloran's Hill were chosen (Nos. 3, 5, and 8) and the following experiments performed, starting between 27 July and 5 August 1984.

On each experimental tree and on trees 1 and 4, 130 to 380 flowers in several inflorescences were designated as controls, and left completely untreated.

For the autogamy experiment, 50 large buds on each experimental tree were individually bagged and sealed. The expanding stamens of the flowers were naturally forced into contact with the stigma by the sides of the bag, and examination of selected flowers showed that large amounts of pollen had been transferred to the stigma. A bag was not removed from a flower until a fruit had developed and filled the bag.

For the geitonogamy experiment, 50 buds on a single inflorescence on each experimental tree were individually numbered. The inflorescences were then covered in a voluminous paper bag with plastic windows and attached to the trunk of the tree by velcro® tape. Every day the trunk and buds were sprayed with a mild pyrethrum-based house plant insecticide to act as a final deterrent to insects. (Separate trials showed that the insecticide had no effect on the development of either the flowers or the ovules.) The buds were examined twice daily prior to opening. Near opening, each bud was emasculated, the stigma carefully checked for accidental pollen transfer (and not used if contaminated), and then pollinated using anthers from other flowers. The pollinations were done in the morning and evening every day with fresh pollen to ensure adequate pollen transfer and to counteract any vagaries in the timing of stigma ripening. When the stigma on the last flower had turned brown, the cover was permanently removed. This period varied from 30 to 44 days.

The xenogamy experiment consisted of intrapopulation crosses and interpopulation crosses. Intrapopulation crosses were made among the 3 trees as follows: 5 × 3 (#3 = pollen donor); 5 × 8 (#8 = pollen donor) and 3 × 8 (#8 = pollen donor). Insufficient buds existed for reciprocal crosses. The procedure was identical to geitonogamy except for the pollen source.

One tree was chosen in each population (tree 8 at Halloran's Hill) and interpopulation crosses performed as follows:

Halloran's Hill × Longland's Gap (pollen donor)
Halloran's Hill × Curtain Fig (pollen donor)
Halloran's Hill × Wongabel (pollen donor)
Curtain Fig × Wongabel (pollen donor)
Curtain Fig × Longland's Gap (pollen donor)
Wongabel × Longland's Gap (pollen donor)

Fifty flowers in 10 inflorescences were emasculated, crossed, and individually bagged for each treatment.

For the apomixis experiment, 20 flowers in 2 inflorescences on tree 3 and a further 25 in one inflorescence

on tree 7 were emasculated as medium-sized buds before anthesis, and the top half of the style was cut off. The swollen buds were examined for developing ovules.

POLLINATOR VISITS AND EFFECTIVENESS.—To determine pollinator array we visited the Halloran's Hill trees twice daily from 28 July to 15 November, for a total of 220 visits, each lasting up to 3 hours. During these visits we noted invertebrate activity at flowers and collected material for identification. Bird species present were recorded, but a subsequent watch from a hide showed that our presence affected them.

To determine visitation rates two trees were constantly watched during one 24-hr period from a hide. Time of arrival and time spent probing flowers by all birds, mammals, and large insects was recorded. Night observatons were made with a "nightkeeper" night vision scope. Every hour each tree was examined for 5 minutes for small insects.

Night vs day pollination by vertebrates and lepidoptera commenced 5 August 1984. Four sets of 144 to 170 flowers each were chosen on each of trees 1, 4, and 8. Cages of 2-cm chicken mesh were constructed for 3 of these sets on each tree. One set of flowers on each tree was caged from just after dusk to just before dawn, thus excluding nocturnal mammals and large moths (night cages); whereas another set was caged from just before dawn to dusk, thus excluding all birds and large lepidoptera (day cages). The third set was constantly exposed without treatment as an open-pollination control. On tree 8 this was the same control as used for the manipulated pollinations described above. A fourth set was caged constantly to exclude all vertebrates and large (>2 cm) insects (insect-only cages). These experiments were attended every dusk and dawn for 60 consecutive days.

The percentage of flowers successfully fertilized in each set (see below) was used to calculate the effectiveness of different classes of pollinators as follows:

If D = % fertilized in day cages
N = % fertilized in night cages
C = % fertilized in control cages
I = % fertilized in insect-only cages,

for each tree, the percent flowers fertilized by bats and large moths = C − N, and the percent flowers fertilized by birds and large lepidoptera = C − D. Fertilization by small insects and wind was measured directly from the insect-only cages and calculated indirectly as D + N − C.

EXAMINATION PROCEDURES AND RECORDING OF FERTILIZATION.—In all the above experiments each flower was examined daily for signs of fruit development and insect attack. Every aborted flower and fruit was collected and all surviving fruit harvested just prior to abscission. Each flower or fruit was dissected and examined for insect predation, ovule damage, and signs of disease. If one or more ovules in an ovary had expanded to at least 8 times the diameter of a normal unfertilized ovule, the flower was recorded as having been fertilized. We considered this a better criterion than seed production because predation rates and abortion rates were high (see below). It does not exclude the possibility of ovule development without fertilization by, for example, pollen tube stimulation. Neither do we know if a predated ovule would have formed a seed or not.

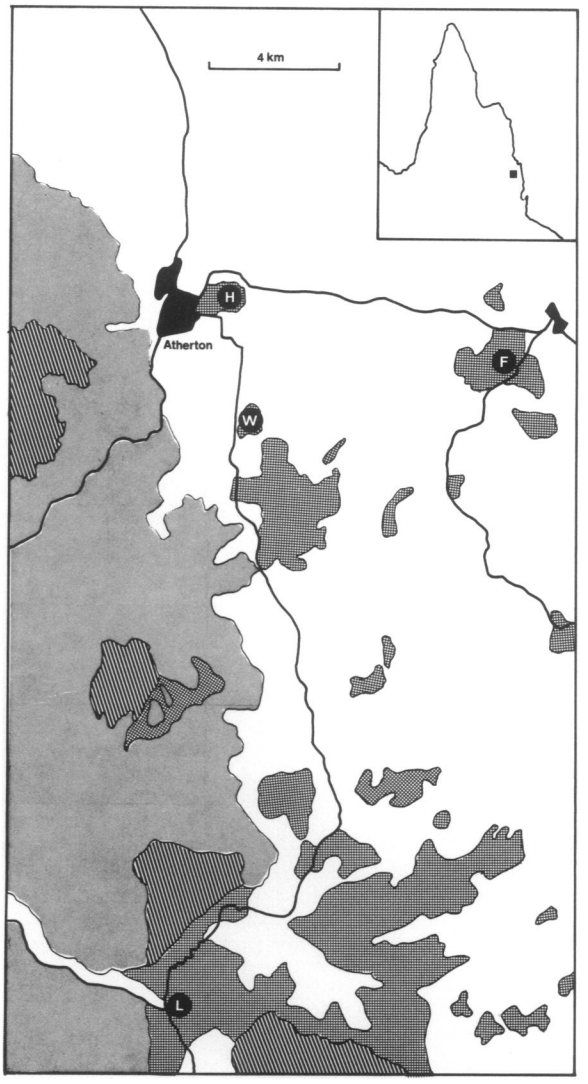


FIGURE 1. Map of the study area. Shading-eucalypt forest formations; hatching = simple microphyll vine fern forest; cross hatching = complex notophyll vine forest. Study areas are indicated by white letter on black: H = Halloran's Hill; F = Curtain Fig; W = Wongabel; L = Longland's Gap.

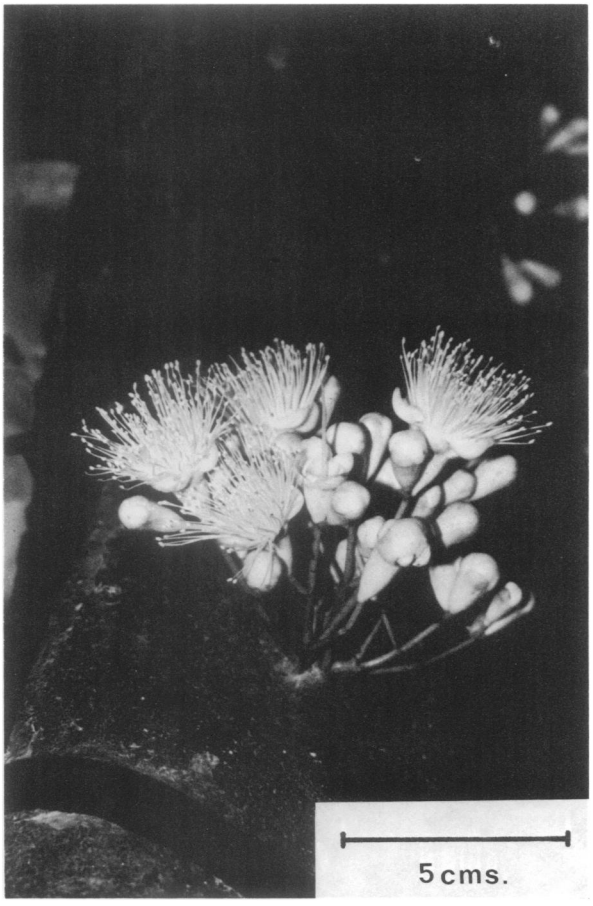


FIGURE 2. An inflorescence of *S. cormiflorum* at Halloran's Hill.

TABLE 1. *Floral development in* S. cormiflorum *at Halloran's Hill.*

Event	Time after opening (in days)		
	Mean	SE	Range
First nectar production	1.0	0.14	0–1.5
Maximum nectar flow (estimate)	2.55	0.11	2.5–3.0
Length of nectar flow	5.25	0.25	3.75–6.5
Anther dehiscence	0.06	0.04	0.0–0.5
Stamen shedding	2.5	0.1	2.0–3.5
Style browning	7.5	0.72	4.0–11.0
Calyx tube swelling	10.5	1.6	10.0–14.0
Style shed	27.2	0.66	24.0–31.0

RESULTS

Floral biology

Floral development.—An inflorescence is shown in Figure 2 and the sequence of floral development in Table 1. Flowers open at any time of the day or night. As the petals unfold they reveal the filaments packed around the style with their anthers deeply inserted toward the style base. The style itself is bent and often twisted, lying alongside the filaments. The anthers quickly expand and are open fully within a few hours. Pollen is available from the anthers while they are still in this expansionary phase and can be transferred to the stigma. The style straightens out at or within a few hours of opening, when it quickly reaches the same length as the stamens. It tends to remain a similar length to the stamens while they persist, but expands to maximum length 4–5 days after opening and after the stamens are shed. Dense papillae develop on the tip in an area about 1 mm long in the first 24 hours. The flower is remarkably long lived. The styles do not brown until, on average, a week after anthesis, and they are not shed until about three weeks later.

Stigma receptivity.—Three of the 10 flowers at Halloran's Hill, 30 of the 37 at Curtain Fig, and 14 of the 22 at Wongabel were successfully fertilized and produced fruit half to fully mature after one pollination at anthesis. The immature fruits that did not develop were lost to a seed predator (see below). We cannot say whether *S. cormiflorum* is or is not protandrous like, for example, *Eucalyptus grandis* (Griffin and Hand 1979). The stigma may be ripe on the first day, or the pollen could retain viability until the stigma ripens later. In the latter case any self-pollen deposited on the stigma at anthesis may gradually lose viability and be competitively inferior to xenogamic pollen arriving later; this could minimize self-pollinating. Irrespective of the mechanism, our data shows that a flower can be successfully pollinated at anthesis. The care we took in emasculating flowers and eliminating contaminated ones precluded this affecting the results of our pollination experiments.

Nectar production.—Nectar flow was copious, with a mean of 347 μl/day, but variable (147–497 μl/day, SD = 108.9 = 31% of mean), and all the flowers produced nectar throughout the 24-hr sampling period. The mean nectar flow was highest between 1330 and 1630 h when 30.9 percent of the total mean flow was produced (Fig. 3), but another small but noticeable peak occurred in the morning. This average, however, masks a great variability in nectar flows of individual flowers as Figure 3 shows. Six flowers had an afternoon peak and an almost equally large peak either side of dawn or in the morning; 2 others had smaller dawn/morning peaks; 2 flowers had large peaks after midnight as well as an afternoon peak; one flower had no afternoon peak but instead had an extended flow from midnight to morning; and finally 2 flowers had extended peaks from the afternoon until past nightfall.

Nectar concentration was low, and varied in the

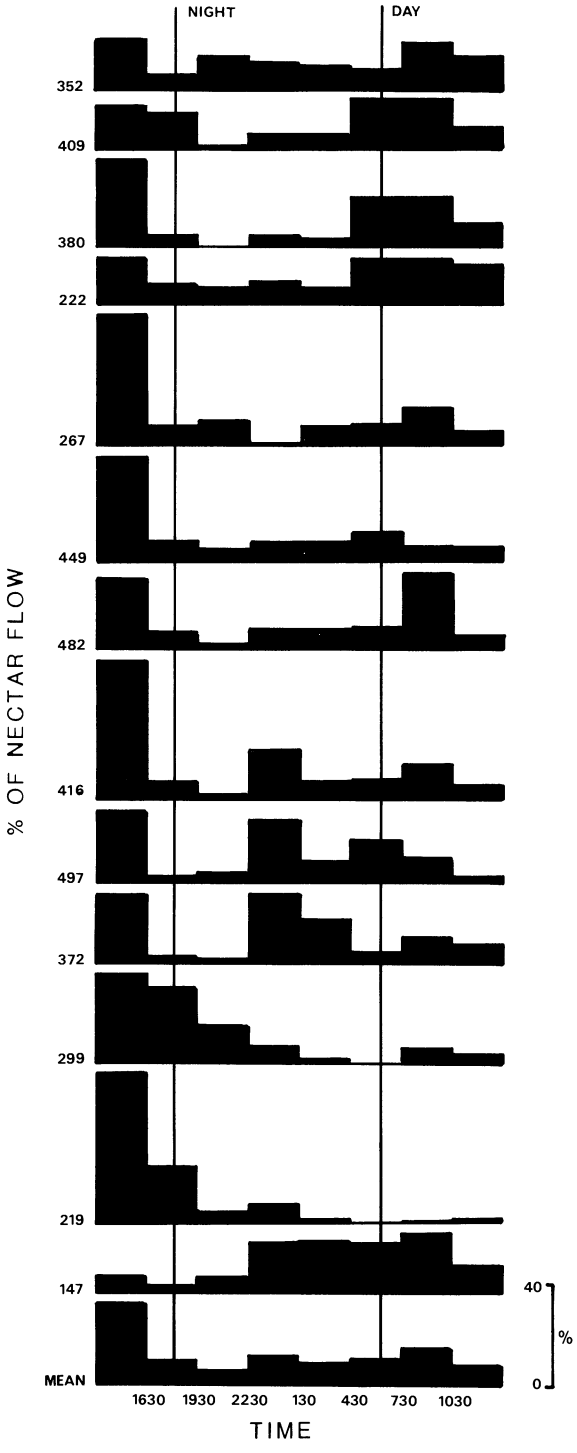


FIGURE 3. Patterns of nectar production in *S. cormiflorum* at Halloran's Hill. The figure on each graph is the total nectar flow in μl for that flower over the 24-hr period.

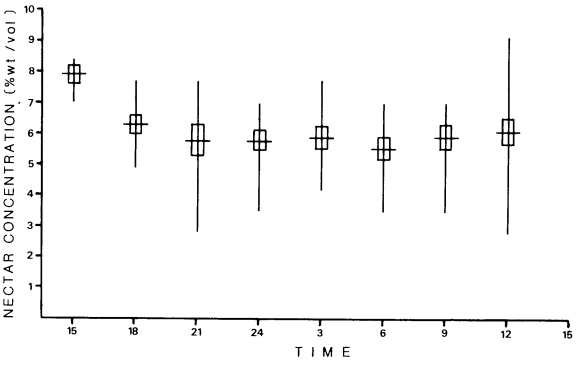


FIGURE 4. 24-hour change in nectar concentration in *S. cormiflorum* at Halloran's Hill. Data are mean ± 95% confidence intervals and range (N = 13).

3-hour samples from 2.8 to 9.8 percent (wt/vol) sucrose equivalents, and in the mean 24-hr concentrations from 3.37 to 8.09 percent (mean = 6.15, s = 0.74 = 12% of mean). The concentration peaked in the afternoon when mean nectar flow was at its highest (Fig. 4). For each flower the relationship between nectar flow and concentration was tested using Kendall's Rank Correlation Coefficient. Only three flowers showed a significant relationship ($P > 5\%$); this and the range of variation suggest that nectar concentration is less variable than flow rate. The peak in nectar concentration may be produced by evaporation and concentration in the warm afternoon.

BREEDING SYSTEM.—The results of the pollination experiments are presented in Table 2. We detected no apomixis, although on the basis of our sample sizes, we cannot rule it out as a rare phenomenon or perhaps producible in response to pollen tube growth. *S. cormiflorum* can be easily self-pollinated but at a lower rate than for outcrossing. If each tree were genetically homogeneous, the rates for autogamy and geitonogamy should have been the same; they were not. The difference may have been due to the different techniques used. The geitonogamic crosses had pollen applied twice daily, whereas the autogamic crosses relied on unmanipulated mechanical transfer of pollen within the bags to effect fertilization. Thus pollen loads in the autogamic crosses could have been lower than in the geitonogamic ones. A deleterious effect of reduced pollen load on fertilization has been recorded for *Costus* (Zingiberaceae) (Schemske & Fenster 1983). However, we noted that the stigmatic heads are quite small and were well covered with pollen in all experiments, and we doubt, therefore, that pollen supply was limiting.

Another explanation is that *S. cormiflorum* is protandrous to a certain degree, and pollen viability within the individual bags for autogamy had declined before the stigmata became fully receptive.

TABLE 2. *Fertilization rates of* S. cormiflorum.[a]

Treatment	Percent fertilization in Three Experiments			Mean
Apomixis	0 (T3)	0 (T7)		0
Autogamy	10.0 (T3)	32.0 (T5)	12.0 (T8)	18.0
Geitonogamy	34.0 (T3)	60.0 (T5)	16.0 (T8)	36.6
Out-crossing				
Intrapopulation	58.0 (T3 × T8)	78.0 (T5 × T8)	82.0 (T5 × T3)	72.7
Interpopulation	92.0 (T8 × L)	88.0 (T8 × F)	80.0 (T8 × W)	86.7
	82.0 (F × L)	90.0 (F × W)	80.0 (W × L)	
Open controls	52.5 (T3)	81.8 (T5)	71.7 (T8)	72.6
	80.0 (T4)	81.7 (T1)	67.7 (T10)[b]	

[a] Each entry is the result of one experiment (the tree or cross used is in parentheses) and gives the percent of successful fertilizations according to the criteria given in the text. T1 to T10 = Halloran's Hill trees, W = Wongabel, F = Curtain Fig, L = Longland's Gap.
[b] 867 buds, the entire crop, were monitored as part of a separate experiment.

A third possibility is that mechanical or genetic barriers may prohibit crossings within flowers but not between flowers on the same tree.

Fertilization rates for outcrossing were much higher than for autogamy and geitonogamy, and may have been higher in interpopulation than intrapopulation crosses. The difference between inter- and intrapopulation crosses was not significant (Behren's modification of *t*-test [Bliss 1967] on transformed data). Fertilization rates of the open controls were not significantly different from those of intrapopulation crosses but were ($P < 5\%$) from those of interpopulation crosses (Behren's test). We wish to be cautious, however, since similar results could have been produced by intertree differences in reproductive ability (Willson 1984, G. Moran, pers. comm.). Certainly, the data in Table 2 indicate that differences, not unexpected, exist between individual trees. Nonetheless a strong suggestion that the differences between inter- and intrapopulation crosses may be a populational rather than an individual phenomenon comes from examination of seeds resulting from the crosses.

The seeds were counted in 222 ripe fruits collected from all crosses, representing 90–95 percent of the fruits that survived predation. Of the 105 fruits from all experiments except interpopulation crosses, 99 (94.3%) had only one seed and the remaining 6 had 2 seeds each. This appears to be normal for *S. cormiflorum* (Hyland 1983). Of the 116 fruits from the interpopulation crosses, 22 (19%) had more than one seed. The average number of seeds in these polyseeded fruits was 4 (range, 2–7), and within a fruit the seeds or developing ovules had fused to form a single composite sphere rather like a volleyball. Of the polyseeds sown as a whole unit and regarded as a single seed, 92 percent germinated. The average number of germinations per polyseed was 2.5. In the field, these seedlings would perhaps grow as multistemmed plants. Insufficient single seeds were available for sowing from the progeny to compare growth rates adequately, but after 9 months, the tallest dominant seedling among the polyseeds was taller than the tallest single-seed seedling, and several were of similar size. We have never seen this phenomenon before, even though one of us (A.K.I.) has had considerable experience with this and many other species of *Syzygium*. Apparently it is a result of the increased success of fertilization in interpopulation crosses.

FLORAL VISITORS AND POLLINATOR EFFECTIVENESS.—Four species of birds, all Meliphagidae—the Macleay Honeyeater (*Lichenostomus macleayi*), the Bridled Honeyeater (*L. frenatus*), the Lewin Honeyeater (*Meliphaga lewini*), and the Eastern Spinebill (*Acanthorhynchus tenuirostris*)—visited the flowers. The only nocturnal vertebrate visitors were small blossom bats (Pteropodidae); two species of these occur locally, *Macroglossus lagochilus* and *Syconycteris australis*. They are virtually indistinguishable in the field. They were not captured for positive identification because we did not want to disturb them in their pollinating activities. During the 24-hr watch, the following species were recorded at flowers: a cockroach (Blattellidae), three flies, *Tambourella endiandrae* Wheeler (Drosophilidae), an unidentified Drosophilid and *Dichaetomyia morrisi* Port (Muscidae), a staphylinid beetle *Paraphloestiba* sp., a weevil (Baridinae), and a mite. At other times during the study period 2 other species of beetle (*Monolepta* sp. [Chrysomelidae] and *Rachioides insignis* Lea [Curculionidae]), an ant, and 2 species of noctuid moths (*Parallelia solomonensis* Hampon and *Erebus crepuscularis* [Linn.]) were captured. A sphingid was sighted once. The staphylinid, 3 flies, cockroach, weevil, and mite were observed to be present every day, but the noctuid moths less frequently. These moths were observed on 11 of the 60 evenings of observing the cages.

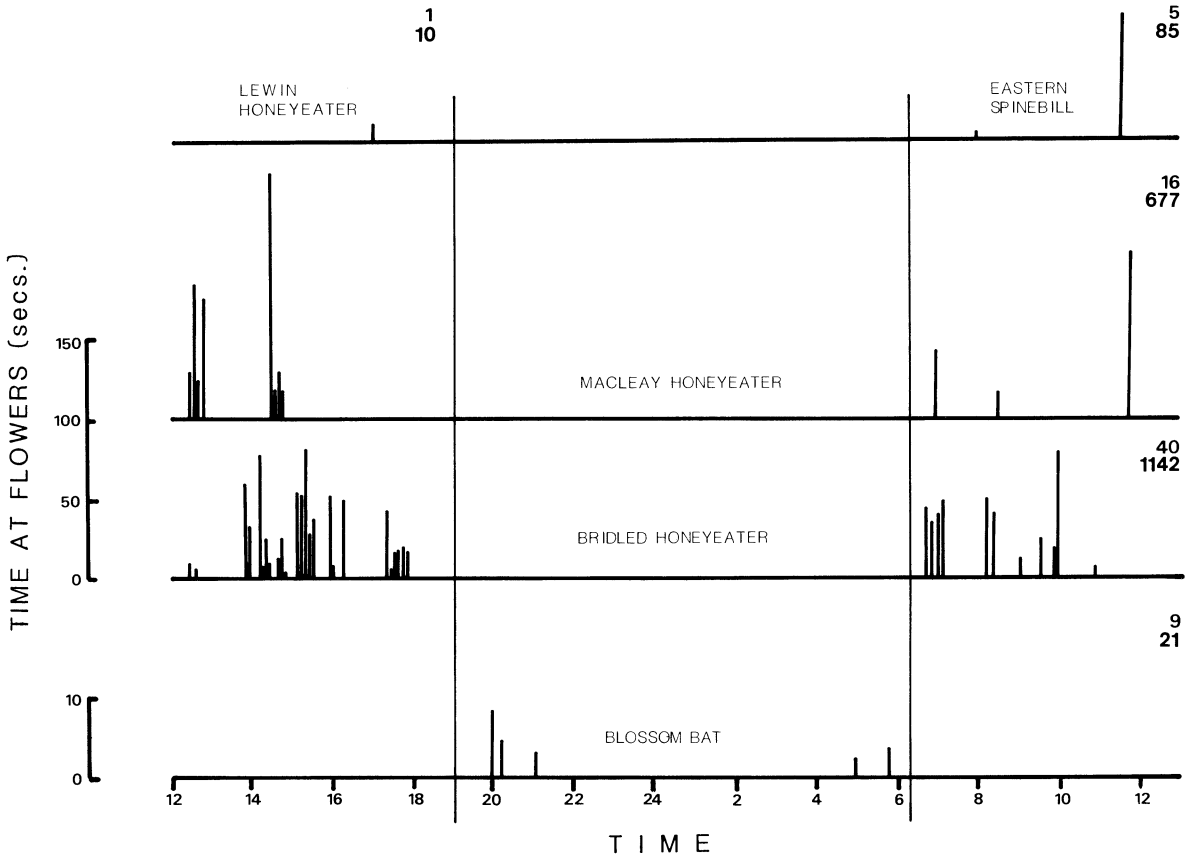


FIGURE 5. Visitation rates of vertebrates on the flowers of 2 trees of *S. cormiflorum* at Halloran's Hill. Entries are combined data for the two trees, and each line represents the total time spent at flowers at each visit. The lower figures on each graph are the total amounts of time in seconds spent at flowers, and the upper figures are the number of intertree flights during the 24-hour period.

Of these invertebrates only the moths, the ant, the cockroach, the mite, and the staphylinid had pollen on their mouth parts or bodies.

The various species of honeyeaters all foraged in a manner superficially similar to each other. They never hovered but always landed on an inflorescence, and probed flowers in either a perched or pendant position while tending to keep the body arched away from the stamens. They occasionally damaged styles while obtaining nectar, and sometimes probed fallen flowers. Bats could hover while feeding but usually landed on an inflorescence, sprawling over it and contacting many stamens with their chests, abdomens, and wings. The 2 moth species visiting the flowers similarly spread themselves over many stamens. The other insect visitors readily moved between flowers and inflorescences on the same tree, and we recorded the flies and cockroaches moving between trees.

Visitation rates of vertebrates are presented in Figure 5. Honeyeaters were the most numerous and frequent vertebrate visitors and were active throughout the day but mostly in the morning and afternoon. All four species were recorded on every day of the experimental period. The most frequent visitors were Bridled Honeyeaters, and they, the Lewin Honeyeaters, and the Macleay Honeyeaters appeared to be moving systematically between the trees. Bridled Honeyeaters did not tolerate other species at the same tree.

Bats foraged for an hour or two just after dusk and briefly again before dawn. There were at least 2 individuals foraging, and bats were recorded on all occasions when we stayed at the trees after dusk to manipulate the cages for the experiment on pollinator effectiveness. Like other nectarivorous bats that have been studied (*e.g.*, Gould 1978, Lack 1978), they usually visited inflorescences very briefly. Their average stay was 2.3 sec, significantly less than that of birds (mean = 32.5 sec for Bridled and Macleay Honeyeaters; $P < 1\%$ Behren's modification to t-test). However, we recorded their stay-

TABLE 3. *Pollinator effectiveness in* S. cormiflorum *in night and day caging experiments. Entries are percent of total buds in experiment pollinated by that source.*

Tree	Fertilized by bats and large moths	Fertilized by birds	Fertilized by insects (Calc)	Fertilized by insects (Direct)	Total fertilized
1	48.1	16.6	17.0	18.0	81.7
4	34.2	22.0	23.0	—	79.2
8	46.0	7.7	18.0	18.2	71.7

ing for up to 30 sec during casual observations while we attended the pollination cages.

During the 24-hr watch the cockroach was active on the flower throughout the night, whereas the other species were recorded at every search throughout the day. The 3 species of flies and the cockroach readily moved between inflorescences on different trees.

The results of the night and day caging experiments are given in Table 3. The fertilization rate of the constantly caged inflorescences (insect-only cages) on tree 4 could not be calculated because a significant number of fallen buds were lost. The direct measures of rates of insect pollination from the other trees, however, were virtually identical to the rates calculated indirectly from the night and day cages and lend strong support to the results from these experiments.

Table 3 shows that animals excluded by the night cages, *i.e.,* bats, large lepidoptera, and perhaps other insects, were the most effective pollinators. This group fertilized an average of 42.7 percent of the flowers in the experiments on the 3 trees, which represents 55.4 percent of all successful pollinations. The absence of moths during the 24-hr watch and their rarity on our early evening visits to the cages suggests that bats are the most important pollinators. Our knowledge of moth activity is admittedly limited, however, and toward the end of the experimental period, as air temperatures increased, moth activity may have increased. Birds, perhaps large diurnal insects, and small insects fertilized an average of 15.4 and 19.3 percent, respectively, of the flowers, which represented 19.6 and 25 percent, respectively, of total successful pollinations. We are sure that birds are the only significant large diurnal pollinators. Thus, despite being far more active at flowers than bats, birds were far less effective pollinators.

FRUIT PRODUCTION.—We found two major causes of flower/fruit mortality. The most important was the baridinine weevil, which attacked unfertilized and fertilized flowers. These weevil-infested fruits in turn occasionally attracted birds that tore the fruit open and extracted the larvae, often pulling the fruit off in the process. The other was an unidentified condition that caused enlarged ovules to collapse and rot. Where a flower had been attacked by a weevil that had entered an ovule, it was of course impossible to say whether the ovule would have suffered the second form of mortality. Thus, ovule collapse is perhaps underestimated.

Production and mortality rates from the day and night cage experiments are comparable with open-pollinated controls in that they did not restrict insect attack. Table 4 presents data on fruit production and mortality from all the open-pollinated and day and night experiments.

Fruit production was low and the attack rate by weevils very high. Moreover, the attack rate is conservative since it only includes weevilled flowers where the weevil was in or close to a loculus and the fertilized flower had aborted. Of the fruit produced, two-thirds had weevils in the flesh and occasionally in the seed, but the fruits and seeds grew fast enough and were so big that the weevils did not impair germination. There was a wide range of attack rates on both fertilized and unfertilized flowers, and attacks on fertilized flowers were not significantly higher (t-test) than on unfertilized ones.

Over a quarter of the fertilized flowers were spontaneously aborted without any obvious physical cause. This and ovule rotting may represent postzygotic selection, the tree aborting self-pollinated embryos (G. Moran, pers. comm.), or adjusting fruit and seed production to nutrient supplies (Bawa 1976, Bookman 1983).

If postzygotic selection does exist, one would expect the loss rates in outcrosses to be lower than in self-crosses. Moreover, if the fruits from outcrosses grow faster than those from self-crosses, the loss to weevils should be lower because the proportion of fruit and seed biomass to weevil biomass increases. Unfortunately we cannot use the results of our pollination experiments to test this because they were covered and treated with insecticide, thus eliminating insect attack in the early stages. Moreover, covers were left on until styles browned, thus giving varying periods of protection (31–44 days); and in the autogamy experiments the individual protective bags on flowers were left on for longer periods than in the experiments with bagged inflorescences. Thus, we cannot compare losses of fertilized flowers and immature fruit among experiments where we have not controlled for predator loss. All we can say is that two-thirds to fully matured fruits with germinable seed were collected from all experiments, including 27 of the 150 individually bagged flowers that underwent autogamy.

DISCUSSION

Our data suggest that *S. cormiflorum* is basically a xenogamous species, as are most rainforest trees studied to date. This is supported by the higher rates of outcrossing in

TABLE 4. *Fruit production and seed mortality of* S. cormiflorum *from open-pollinated experiments.*[a]

	Unweighted mean	SE	Range
% flowers forming fruit with viable seed[b]	13.22	2.27	5.4–19.2
% fertilized flowers forming fruit	15.0	2.71	2.4–26.8
% fertilized flowers with rotten ovules	11.14	3.43	0.0–33.3
% fertilized flowers lost to unknown causes	27.76	2.99	7.7–48.5
% fertilized flowers attacked by weevil	46.10	4.30	27.3–70.3
% unfertilized flowers with weevil attack	27.3	7.81	0.0–73.3
% weevil attack on all flowers	36.6	5.09	16.4–60.0

[a] Data are from the 11 night cage, day cage, and control experiments.
[b] Data are from the control experiments only, and include fruits that had viable, as indicated by germination in the glasshouse, but not necessarily fully grown seeds.

the manipulated pollinations and by the similarity in fertilization rates between open-pollinated controls and intrapopulation crosses. Outcrossing, however, is not genetically obligatory, as evidenced by the moderate fertilization rates and production of viable seed from auto- and geitonogamic experiments. The self-crossing rates we measured accord well with but tend to be higher (10–60%) than those measured in other Myrtaceae, *e.g.,* 10–30 percent in open-pollinated populations of several Eucalyptus species (Eldridge & Griffin 1983). Within a population such as at Halloran's Hill, the trees are so close together and pollinator movements so frequent that xenogamous pollen from within the population is probably available to all flowers and could favor greater production of xenogamous seed, but an isoenzyme analysis of the seeds is needed to definitely confirm the degree of xenogamy in the progeny.

The crosses between populations gave higher fertilization rates than those within populations and produced the peculiar polyseeded fruits mentioned previously. This and the similarity of fertilization rates between intrapopulation and open-pollinated crosses suggest that outcrossing is restricted to breeding between the individuals in the local population and that there is some degree of genetic discontinuity between the populations we studied. If indeed this is the case, then the ability to self-pollinate may be of considerable significance to *S. cormiflorum.* If a single tree is isolated as a result of germination from a distantly dispersed seed or is left in a field after forest clearing, self-pollinated seeds may be produced and be a significant portion of the total seed crop. They may suffer inbreeding depression in growth and competitive ability such as has been quantified for *Eucalyptus regnans* (Eldridge & Griffin 1983), but this may not matter in the short term in the face of heavy predation rates as reported here and of climatic uncertainty. Schemske (1983), for instance, was able to demonstrate long-term inbreeding depression of growth in glasshouse-grown species of *Costus,* but in the field, experiments demonstrated no breeding system effects on germination and survival. He interpreted this as evidence that variance in habitat quality is much greater than variance in plant fitness at the seed and seedling stage. Wells (1979) discusses the "paradox" of self-pollinating's being considered deleterious by biologists but common in the field, and Carpenter (1976) was able to demonstrate that some inbreeding produces dependable seed production in *Metrosideros collina* (Myrtaceae).

The floral biology of *S. cormiflorum* is that of a chiropterophilous plant, and its copious weak nectar matches that reported from vertebrate-pollinated plants (Gould 1978, Scogin 1980, Pyke & Waser 1981). Consistent with this is our conclusion that bats are the single most important pollinators, in spite of the far greater activity of birds and insects. The latter are, nonetheless, important pollinators, and this species could be easily considered to have an opportunistic pollination system as much as a chiropterophilous one. It is this and the ability of the plant to produce self-pollinated seeds that prompted us to title this paper "Two Bob Each Way." This is a common colloquialism in Australia and refers to covering all bets or contingencies. It seems very appropriate for this species that probably can reproduce under most circumstances with or without its major pollinators. In this respect *S. cormiflorum* is typical of the Myrtaceae which, in general, do not have specialized pollination systems and attract a wide range of vertebrate and invertebrate floral visitors (Eldridge 1970, Carpenter 1976, Hopper 1980, Hopper & Moran 1981). *S. lineatum* in Sulawesi attracts 16–20 species of insect visitors (Lack & Kevan 1984), and Hopper (1980) recorded 8 species of vertebrates and 37 of insects visiting *S. tierneyanum* at Kuranda, north Queensland. However, as we and others (*e.g.,* Bertin & Willson 1980) have demonstrated, pollinator effectiveness need not be related to pollinator activity. Thus conclusions about pollination systems based on pollinator activity alone, such as Hopper's (1980) that *S. tierneyanum* is basically pollinated by birds and hawk moths, cannot be made.

What makes *S. cormiflorum* somewhat unusual is its

pattern of nectar flow, which appears to suit both nocturnal and diurnal pollinators. The two peaks in the average flow rate coincide with bird rather than bat activity, but individual flowers showed timing that corresponded to either birds or bats. Certainly, total nectar flow has been shown to vary greatly (Cruden 1976, Feinsinger 1983), but the 9- to 12-hr asynchrony between individual flowers on the same tree of *S. cormiflorum* is somewhat unusual. We need to assess from larger samples the full variability in nectar flow patterns to determine if a tree produces separate day and night flowers, if the flowers change their patterns of nectar flow with age, or if nectar flow patterns vary along a continuum.

Other plants with both night and day pollinators have been reported: *Freycinetia reineckii* (Cox 1984), *Passiflora mucronata* Lam. (Passifloraceae) (Sazima & Sazima 1978), *Asclepias syriaca* (Willson & Bertin 1979, Willson *et al.* 1979, Bertin & Willson 1980), and *Luehea seemanii* (Tiliaceae) (Haber & Frankie 1982). The floral behavior of the latter is adapted to nocturnal pollination, yet it is mostly pollinated by diurnal visitors. This led Haber and Frankie to conclude that the population was evolving or switching from night to day pollination and that, in general, when a stable plant/pollinator relationship breaks down, opportunistic visitors may assume the primary pollinator function. An example of this is *Freycinetia arborea* Gaud. (Pandanaceae) in Hawaii, which is now pollinated by *Zosterops japonica* instead of the recently extinct honeycreepers (Cox 1983). One could apply such logic to *S. cormiflorum* and conclude that it is evolving from a night to a day pollination system. Besides this hypothesis, however, two others can be put forward: our species could be evolving from day to night pollination, or our species could be a generalist and adapted to a range of nocturnal and diurnal pollinators in a continent whose tropical bat, bird, and (presumably) insect communities are less diverse than elsewhere in the tropics. Willson *et al.* (1979) and Bertin and Willson (1980) concluded that, although the nocturnal pollinators of *A. syriaca* were the most effective, the attraction of both night and day pollinators was adaptive in allowing high fertilization and thus permitting selective abortion of young pods when the ability of the plant to mature them all was limited. This and the ability to promote pollination in situations where the major pollinators are absent could be of significance to *S. cormiflorum.*

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