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Dispersal and germination of seeds of *Pisonia grandis*, an Indo-Pacific tropical tree associated with insular seabird colonies

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Abstract: The distribution of the forest tree *Pisonia grandis* (Nyctaginaceae) coincides with seabird colonies on small tropical islands. Its seeds are enclosed in a calyx exuding extremely sticky resin which adheres strongly to feathers. Birds are obviously seed-dispersal vectors, but the multi-seeded infructescences frequently entangle birds, often fatally. On Cousin Island, Seychelles, I investigated the production, germination, survival, and tolerance to seawater of *Pisonia* seeds, and the occurrence of entanglement with birds. Fresh seeds had high germination success (62–87% in experimental trays), but seedling survival in Cousin's forests was low (0.1% of 6020 seeds survived as seedlings after 2–8 mo). Some seeds tolerated 30 min daily immersions in seawater (8–15% germination after 14–28 d treatment), but not continuous immersion in seawater (reduced germination after 5 d and none after 12 d). Inter-island dispersal is likely via living unencumbered seabirds carrying a few seeds, but not on floating carcasses. Seeds attached to carcasses did not have improved germination or survival. Intra-island propagation is almost entirely vegetative, with negligible local seed dispersal. *Pisonia* plants therefore do not benefit from fatal entanglements. The extreme stickiness of the seeds evidently evolved to resist removal by seabirds and so facilitate long-distance dispersal. The mortality of some potential vectors is an unfortunate consequence, but has little impact on the large populations of tree- and ground-nesting seabirds which nest in or under these trees.

Key Words: epizoochores, Nyctaginaceae, *Pisonia grandis*, seabirds, seed dispersal, Seychelles, tropical islands

INTRODUCTION

Information on the dispersal abilities and physical tolerances of propagules is essential for understanding long-distance dispersal of plants (Cain *et al.* 2000, Howe & Smallwood 1982). These phenotypic features are important even in studies where genetic markers are used to infer dispersal (Dick *et al.* 2003). Dispersal of seeds by birds among oceanic islands is a well-known phenomenon and many plant species have obvious specializations to facilitate this (Carlquist 1965, 1966; Darwin 1859, Ridley 1930, van der Pijl 1972). The adhesive seeds of the insular tropical genus *Pisonia* appear to be classic adaptations for long-distance dispersal by birds (Carlquist 1965, Ridley 1930, Sorensen 1986), but the interactions between *Pisonia* and its dispersers are complex, and often fatal for birds.

The large forest tree *Pisonia grandis* has a close relationship with seabirds. It occurs almost entirely on small islands used as seabird colonies in the tropical Indo-Pacific (approx. 24°S–24°N Walker 1991a). On such islands it is often the dominant forest tree and provides favoured nesting sites for tree-nesting white terns *Gygis alba*, lesser noddies *Anous tenuirostris*, and red-footed boobies *Sula sula*. Shearwaters (*Puffinus* spp.), tropicbirds (*Phaethon* spp.) and terns (*Sterna* spp.) nest among its roots in cavities or on the surface. Unlike most other plants, *Pisonia* flourishes in the highly acidic guano deposited by the seabirds (Airy Shaw 1952, Fosberg 1957, Walker 1991a, b). The combination of *Pisonia* forests and large populations of seabirds leads to the formation of distinctive Jemo soils, characterized by acidic humus overlaying phosphate rock or raised coral (Fosberg 1957, 1983).

The closest relationship, however, seems to be in the dispersal of *Pisonia* seeds by birds (Airy Shaw 1952, Ridley 1930, van der Pijl 1972, Walker 1991a). *Pisonia grandis* has a one-seeded anthocarp fruit (hereafter referred to as a seed) enclosed in an elongated persistent calyx (approximately 10 mm long, diameter 2–3 mm) which exudes a sticky resin that adheres strongly to feathers and similar surfaces. The seeds are borne on multi-branched infructescences, each bearing from 12 to over 200 seeds (Figure 1a). These usually fall to the ground when ripe. Birds become entangled in one or more infructescences (Figure 1b), which can severely inhibit their mobility, and in many cases prevent them from flying and thereby killing them. Large releases of *Pisonia* infructescences can cause the deaths of hundreds of birds (Walker 1991a). The frequency of such fatal encounters raises the possibility that the plant gains some benefit, perhaps by ensuring that its seeds germinate in the presence of a carcass which might provide essential nutrients.

The interactions between *Pisonia* and birds have long fascinated visitors to tropical seabird colonies (reviewed by Walker 1991a), but have not been quantitatively studied. The interactions provide an opportunity to explore pathways and constraints of bird-mediated seed dispersal on tropical islands. This paper reports on seed production, dispersal, germination, seedling survival, and recruitment of *Pisonia grandis*, and its impacts on birds. Specifically, I focused on: (1) documenting the species of birds affected by the seeds, and the impacts of the seeds on these birds; (2) testing germination and seedling survival with and without seabird carcasses; (3) recording the survival of seedlings during their first 3–8 mo after germination; and (4) experimentally testing the tolerance of seeds to immersion in seawater for varying amounts of time. I discuss the dispersal strategies of *Pisonia grandis* and the possibility that bird mortality from entanglement evolved to benefit this plant.

METHODS

Study area

Cousin Island (4°20′S; 55°40′E) is one of the smaller (27 ha) granitic islands in the Seychelles archipelago. About two-thirds of the island surface is low coastal plateau on raised coral, and one-third is granite hillside (Hill *et al.* 2002). The plateau is covered with dense forest (990 trees ha^{-1}), dominated by *Pisonia grandis* (44% of stems), and to a lesser extent other large trees, e.g. *Ficus lutea, Ochrosia oppositifolia, Morinda citrifolia* (Hill *et al.* 2002, Schumacher & Wüthrich 2000). The hillside is more sparsely vegetated with grass, ferns and woodland (390 trees ha^{-1}), including scattered *Pisonia* trees (42% of stems; Hill *et al.* 2002). Until 1968 the plateau was used as a coconut plantation and most of the native forest was patchily cleared. After the island was purchased as a nature reserve in 1968, the plateau forest regenerated rapidly, and at the time of this study was a relatively closed canopy in many areas, interspersed with gaps created by large trees falling (Hill *et al.* 2002, Schumacher & Wüthrich 2000).

Cousin Island is an important colony for seven species of seabird (Table 1; nomenclature follows Skerrett & Bullock 2001). Smaller numbers of land birds and shorebirds also occur on the island as breeders or non-breeding migrants (Prys-Jones & Diamond 1984, Skerrett & Bullock 2001). Nests of seabirds occur across much of the island (Burger & Lawrence 2003, Hill *et al.* 2002). Tree-nesting species (lesser noddies, white terns and a few brown noddies) form the bulk of the seabird population, and most nest on the forested plateau. Ground-nesting species occur on both plateau and hillside (white-tailed tropicbird, Audubon's shearwater), or are concentrated on the hillside (wedge-tailed shearwater, bridled tern and most of the brown noddies).

The seasonal climate of the Seychelles archipelago is dominated by wind direction (Walsh 1984). The south-east (SE) Trades season, May through October, has relatively low rainfall and almost constant strong SE winds. The north-west (NW) Monsoon season, December through March, has moderate and variable winds, but higher rainfall. During the transition months April and November winds are light and rainfall is moderate.

Field observations

The study was done between 15 May 1999 (after preliminary observations in the month before) and 28 February 2000. Throughout this period I recorded all incidents of birds with *Pisonia* seeds attached to their plumage, seen by myself, the island's wardens, and other biologists. These data were used to determine the bird species affected, the effects of the seeds on the birds, and where possible, the number of seeds attached to the bird. They also provided a crude chronology of the episodes of fruiting and seed drop in *Pisonia*.

Tests of germination and seedling survival

I monitored the fate of 22 seabird carcasses (adults or nearly full-grown chicks), found freshly dead, with *Pisonia* seeds attached to them. Some were birds which had evidently died as a result of their entanglement, but most had died from other causes and had seeds attached post-mortem by me. Carcasses were left on the surface of the forest floor, but tethered with 2 m of fine nylon line to prevent crabs from dragging them away. Both wings were marked with numbered tape so that dismembered carcasses could be identified. The carcasses were checked daily for 1 wk and then at intervals of 1–3 wk for up to 5 mo. At each check the condition of the carcass was

Figure 1. (a) Maturing infructescences of *Pisonia grandis*. (b) White tern *Gygis alba* rendered flightless by entanglement with a single infructescence of *Pisonia grandis*.

recorded, and the ground near the carcass was carefully searched and all emerging seedlings counted. With nine of these carcasses, I compared seedling establishment from the seeds attached to the carcass with similar numbers of seeds planted 1–2 cm below the soil surface in two control plots, within 1 m and on either side of the carcass.

I experimentally tested the tolerance of *Pisonia* seeds to varying exposure to seawater before planting. After various treatments, all seeds were rinsed with fresh water before planting in the germination trays. In all experiments seeds were spread evenly across a layer of sandy soil ∼5 mm thick in circular plastic trays (diameter 18 cm) with drainage holes, and then covered with a similar layer of soil (total soil volume approx. 2550 cm^3). The soil used in all experiments was taken from the surface layer in *Pisonia* forest on the low coastal plateau, and was thoroughly mixed and seed-free. Freshwater was untreated well water from Cousin Island, which had no chlorine or other additives. Seeds from many infructescences were evenly distributed among the experimental trays to minimize possible effects of differing viability among infructescences. Each tray contained 30–170 seeds (usually 150).

Preliminary trials showed that maximum germination (60–80% of untreated seeds) occurred in uncovered trays exposed to shaded light with the soil kept moist (150 ml water per tray at planting, 20 ml per day thereafter). Germination was significantly reduced if the trays were covered with wooden boards or if the soil was kept wet (300 ml after planting, and 60 ml per day thereafter). Consequently, all the germination experiments reported here used open shaded trays with moist soil as described above.

Germination experiment 1 tested the effects on *Pisonia* seeds of soaking for 24 h in seawater, dipping in seawater for 1 min, soaking in freshwater for 24 h, and (control) none of these treatments. Experiment 2 tested the effects of continuous soaking in seawater for 1, 3, 5, 9, 12 and 15 d. The seawater in each container was replaced daily. Experiment 3 and 4 simulated the effects of seeds attached to a seabird and periodically, but briefly, immersed in seawater each day. Seeds were immersed in seawater for 30 min each day, for varying numbers of days prior to planting (5, 8 and 10 d in experiment 3, and 7, 14, 21 and 28 d in experiment 4). These seeds were attached to feathers of terns and noddies and between the daily immersions, they were hung to dry in a shaded, well-ventilated site. In experiment 3 the seeds used were freshly dropped from the trees and had slightly higher percentage germination than those in experiment 4, which were 3–4 wk old.

Control groups in each experiment were never exposed to seawater and were planted at the start of the experiment (day zero). I also tested the effects of delayed germination by storing 150 seeds for 15 d (experiment 2) and 28 d (experiment 4) in a dry, well-ventilated container prior to planting in the usual manner.

Chi-squared tests were used to compare frequencies, and for repeated tests (experiments 2–4) I applied the Yates correction (Zar 1996: p. 464). Correlation tests were made with SPSS 11.5. Tests were considered significant if $P < 0.05$.

RESULTS

Birds affected by *Pisonia* seeds

Seven seabird species and five species of land or shore bird were recorded with seeds attached (Table 1). Most of the affected birds were adults (79% of seabirds, 89% of land birds, 80% overall) and the rest chicks. Seabirds were more likely than land or shore birds to carry large numbers of seeds (Table 1). Of the 222 birds recorded, 64% were either dead or so entangled with seeds that they were unable to fly and were likely to have died. Overall 71% of the 194 seabirds, but only 11% of the 28 land/shore birds, were dead or unable to fly when found.

Fruiting chronology of *Pisonia*

Between 1 May 1999 and 28 February 2000 there were three fruiting episodes, as shown by the reported number of birds carrying seeds (Figure 2) and my unquantified

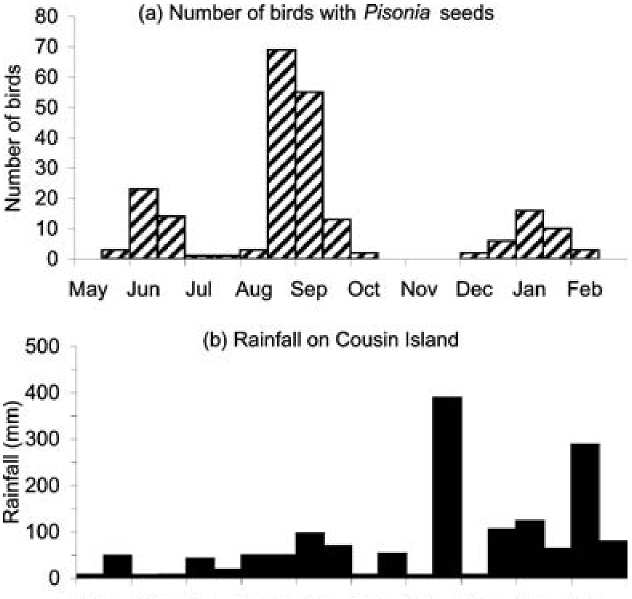


Figure 2. Number of birds recorded with *Pisonia grandis* seeds attached (a) compared with rainfall on Cousin Island (b), plotted in half-monthly intervals.

Table 1. Bird species recorded with *Pisonia grandis* seeds attached on Cousin Island, May 1999 through February 2000. The estimated total populations of these species on the island is also given. The condition of the bird when found was recorded as: able to fly, unable to fly because of seed entanglement, or dead.

Species	Estimated population on Cousin Island[a]	Number and condition of birds affected by *Pisonia* seeds				No. of seeds per bird Mean (range)
		Able to fly	Unable to fly	Dead	Total	
Seabirds (breeding pairs)						
Audubon's shearwater *Puffinus lherminieri*[b]	5000	1	5	0	6	No data
Wedge-tailed shearwater *Puffinus pacificus*	9300–16 900	5	8	0	13	80 (60–100)
White-tailed tropicbird *Phaethon lepturus*[b]	800–1500	0	14	0	14	190 (2–500)
Brown noddy *Anous stolidus*	1200	2	1	0	3	No data
Lesser noddy *Anous tenuirostris*	80 000–100 000	42	89	1	132	67 (40–100)
Bridled tern *Sterna anaethetus*	600	3	0	0	3	20
White tern *Gygis alba*[b]	1100–3600	2	20	1	23	37 (1–60)
Land or shore birds (no. of birds)						No data
Ruddy turnstone *Arenaria interpres*	10–100	1	0	0	1	50
Common moorhen *Gallinula chloropus*	20–40	5	1	0	6	13 (6–20)
Barn owl *Tyto alba*	0–2	0	1	0	1	No data
Madagascar turtle dove *Streptopelia picturata*	50–100	19	0	0	19	13 (1–30)
Seychelles Warbler *Acrocephalus sechellensis*	350	0	1	0	1	No data
Total		80	140	2	222	66 (1–500)

[a] Population estimates from Burger & Lawrence (2003) and Nature Seychelles (unpubl. data).

[b] These species breed year-round and the number of active breeders at any time of year is given.

field notes. With data pooled into half-monthly periods, there was no significant correlation between rainfall and the number of birds carrying seeds (Pearson $r = -0.094$, $n = 19$, $P = 0.701$), even when rainfall was offset by half a month ($r = -0.113$, $n = 19$, $P = 0.644$) or a month ($r = -0.145$, $n = 19$, $P = 0.552$) to account for possible delays in flowering and fruit production after rain. Nevertheless, moist conditions do seem to be partly responsible for flowering and fruiting. The peak in June 1999 occurred 2–4 wk after 2 d of heavy rain (total 37 mm) on 20–21 May which ended a dry spell (only 16 mm in the previous 27 d). The late-August–September peak in fruiting coincided with relatively high rainfall at the end of the dry SE Trades season, and the December–January peak occurred during the wet NW Monsoon season.

The number of birds affected by the seeds was obviously also a function of the number of birds present on the island. Most of the land and shore birds were found in similar numbers year-round, but the seabirds were present only for breeding. Peak seabird numbers on Cousin Island, dominated by lesser noddies, occurred in May–August during the first half of the SE Trades season (Nature Seychelles, unpubl. data), which did not coincide with the highest peak of *Pisonia* attachment.

The fate of carcasses and seeds attached to carcasses

Twenty-two bird carcasses were monitored daily for 1 wk and at 1–3-wk intervals thereafter to record the fate of the carcasses and the seeds. Scavengers usually found the carcasses within a day, and 20 (91%) were dismembered leaving scattered feathers and bones. The mean time to dismemberment was 3.3 d (SD = 1.6 d, range 1–7 d). Ghost crabs (*Ocypode* spp.) were obvious scavengers at nearly all carcasses, and fresh crab-holes were found below or near most carcasses. Two relatively intact carcasses and dismembered parts of 11 other carcasses were dragged underground by crabs. Other scavengers at the carcasses included skinks (*Mabuya wrightii*), hermit crabs (*Coenobita perlata*), fly maggots, beetles and cockroaches.

Removal of seeds was evident at six carcasses, and this was obviously a minimum count because it was difficult to check seeds on carcasses that had been dismembered

Table 2. Results of experiments testing the germination and seedling production of seeds attached to seabird carcasses. In each trial, seeds were either attached to a carcass tethered on the soil surface or buried in two control plots to the left (control 1) and right (control 2) of the carcass.

				No. of seeds		% of seeds germinating		
Trial no.	Date started	Bird species	Prevailing soil moistrue	On bird	In each control plot	Seeds on bird	Control 1	Control 2
P1	20 June 1999	Lesser noddy	Mostly dry	150	150	0	0	0
P2	29 June 1999	Lesser noddy	Mostly dry	300	300	0.3	0	0
P3	30 June 1999	White tern	Mostly dry	300	300	0	0	0
P4	04 July 1999	Lesser noddy	Mostly dry	300	150	0.7	0	0
P5	21 July 1999	Lesser noddy	Mostly dry	100	100	0	0	0
P6	21 July 1999	Lesser noddy	Mostly dry	150	150	0	0.7	0
P7	25 August 1999	White-tailed tropicbird	Moist	200	100	2.0	3.0	2.0
P8	28 August 1999	Audubon's shearwater	Moist	300	300	4.3	11.7	14.3
Mean all trials (%)						0.92	1.92	2.04
Mean with moist soil (%)						3.17	7.33	8.17

or taken underground. Most seeds were removed within 1–2 d. Madagascar turtle doves were the only species seen to eat *Pisonia* seeds, but insects and crabs might also have eaten them.

Germination and seedling establishment with and without a bird carcass

Germination of seeds on or off carcasses was tested using eight intact seabird carcasses (Table 2). Contrary to expectation, seedling establishment was slightly, but significantly higher in control plots adjacent to carcasses (mean 1.98%) than on the carcasses themselves (mean 0.92%, including seeds on carcasses dragged underground by crabs; Chi-squared test with all trials pooled, $\chi^2 = 13.3$, df $= 1$, $P < 0.001$). This was probably due to the soil disturbance caused by crab activity around the carcasses. Very few seedlings were found when the soil was mostly dry (1.0% on carcasses, 0.3% in control plots) compared with moist soil (3.2% on carcasses, 7.8% in control plots).

Establishment of seedlings in the forest was low: out of 6020 seeds attached to carcasses or planted near carcasses, only 127 (2.1%) produced seedlings that persisted long enough to be counted, and only 6 (0.1%) of these survived until checks ceased 3–8 mo after planting. The cause of disappearance of the experimental seedlings was not known. Free-living turtle doves ate *Pisonia* seedlings when provided in a germination tray, and common moorhens, giant tortoises, crabs and insects might also have eaten them in the forest.

Germination experiments and tolerance of seawater

The timing of germination in all experiments was similar: the first seedlings emerged above ground 9–11 d after planting, and few after 20 d (Figure 3). Counts of emerging seedlings were therefore restricted to the first 25–28 d after planting.

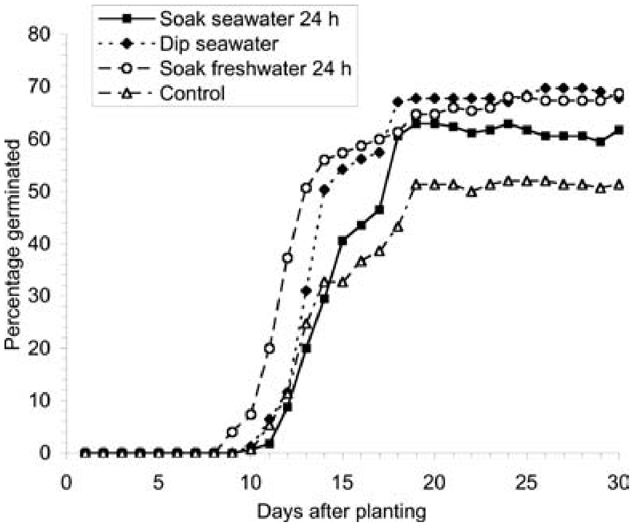
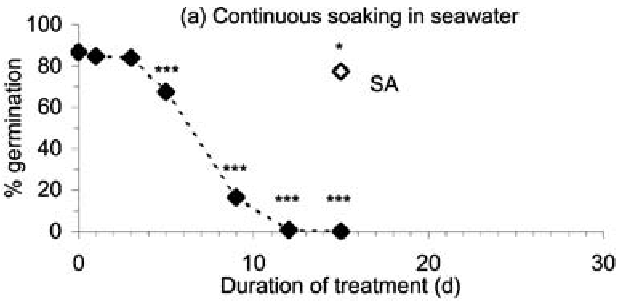
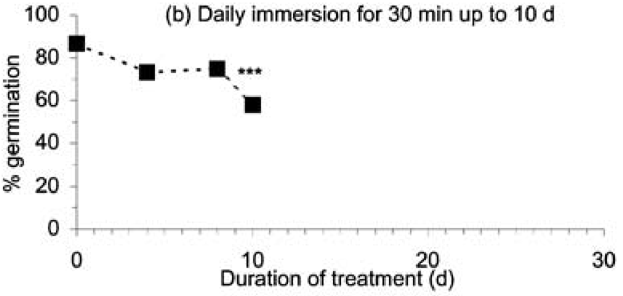


Figure 3. Germination experiment 1: the cumulative percentage of *Pisonia grandis* seeds which germinated following various treatments, plotted from the day the seeds were planted and watered.

In experiment 1, germination was similar for seeds soaked in seawater for 24 h (62.9% germinated, $n = 170$ seeds), dipped in seawater for a few seconds (69.7%, $n = 155$), or soaked in freshwater for 24 h (68.7%, $n = 150$; Figure 3; $\chi^2 = 1.96$, df $= 2$, $P > 0.05$). Germination in the control group (52.0%, $n = 150$), however, was inexplicably lower than in the three experimental treatments ($\chi^2 = 12.8$, df $= 3$, $P < 0.05$).

Experiment 2 tested the effects of continuous soaking in seawater from 1–15 d (Figure 4a). The *Pisonia* seeds usually floated for 2–3 d and then sank, indicating that they absorbed water. They also lost their stickiness after 2–3 d in seawater. No reduction in germination was observed for seeds soaked in seawater for 1 or 3 d, but progressively and significantly fewer seeds germinated after 5–9 d, and none after 12 or 15 d.





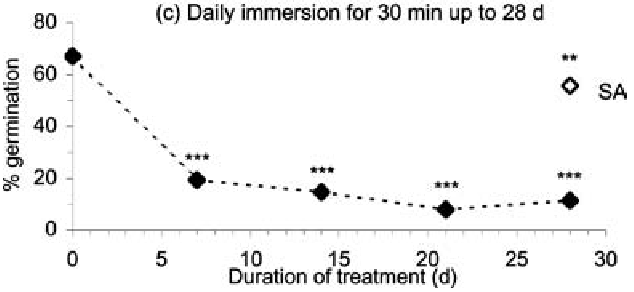


Figure 4. Germination experiments 2–4: effects of seawater on the percentage germination of *Pisonia grandis* seeds. (a) Effect of continuous soaking in seawater for 1–15 d (experiment 2; 150 seeds per treatment). (b) Effects of daily immersion for 30 min for 4– 10 d (experiment 3; 30–44 seeds per treatment). (c) Effects of daily immersion for 30 min for 7–28 d (experiment 4; 150 seeds per treatment). The groups labelled SA were stored in shaded dry air for 15 d (graph a) or 28 d (graph b) before planting to test the effects of delayed germination. Frequencies of germinated or failed seeds in each treatment group were compared with those in the control untreated group (day 0 in each graph) using Chi-squared tests with the Yates correction (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Experiments 3 and 4 tested the effects of exposure to seawater for 30 min per day (Figure 4b, c). Compared with untreated controls (day 0), no significant decrease in germination was found for treatments of 4 and 8 d in experiment 3, but treatments of 10 d in experiment 3 and 7–28 d in experiment 4 showed significantly reduced germination. Nevertheless, some seeds germinated after prolonged period exposure to seawater (15%, 8% and 11% after 14, 21 and 28 d, respectively).

Seeds stored in air for 15 d (experiment 2) and 28 d (experiment 4) prior to planting (labelled SA in Figure 4) had slightly, but significantly lower germination than the control group planted on day zero ($\chi^2 = 4.34$, df = 1, $P < 0.05$ and $\chi^2 = 7.95$, df = 1, $P < 0.01$ in experiments 2 and 4, respectively). In both cases, however, the air-stored groups had much higher germination than those treated with seawater for the same amount of time ($\chi^2 = 187$, df = 1, $P < 0.001$ and $\chi^2 = 80$, df = 1, $P < 0.001$, respectively).

DISCUSSION

Relationships between birds and *Pisonia grandis*

All seven species of seabird breeding on Cousin Island were seen to carry *Pisonia* seeds. On neighbouring Aride Island, sooty terns *Sterna fuscata* and roseate terns *Sterna dougallii*, which do not breed on Cousin Island, frequently carried *Pisonia* seeds (Skerrett & Bullock 2001, M. Betts & J. Bowler, pers. comm.). The seabird species frequently affected included those which spent considerable time on the ground (ground-nesting species or lesser noddies which collect nesting material on the ground), but also white terns which seldom landed on the ground and encountered the seeds in the trees. On the Great Barrier Reef, birds were also entangled with infructescences on the ground and in the canopy (Walker 1991a).

The consistent occurrence of *Pisonia grandis* with seabird colonies is evidence that this plant evolved in association with seabirds (Walker 1991a, b). Although many seabirds are killed by the infructescences, these form a relatively small proportion of the overall breeding populations and there has been no selection for avoidance of *Pisonia* trees. On the contrary, most tree-nesting seabirds nest in *Pisonia* trees in Seychelles (Bowler *et al.* 2002, Skerrett & Bullock 2001, AEB pers. obs.) and elsewhere (Hill *et al.* 1997, Sachet 1983, Walker 1991a).

The Madagascar turtle dove appears to be the main seed predator of *Pisonia* on Cousin Island, and is the only bird known to eat these seeds in Seychelles (Prys-Jones & Diamond 1984, this study). The doves seem to avoid fatal entanglements (although a few have been reported on nearby Aride Island, M. Betts, pers. comm.) and generally had few seeds attached to them (Table 1). Other seed- and fruit-eaters common in Seychelles (pigeons, ground doves *Geopelia striata*, and fodies *Foudia* spp.; Skerrett & Bullock 2001) appear to avoid the seeds. Insects and crabs might also eat the seeds.

Adaptations in *Pisonia grandis* for long-distance dispersal

Adhesive seeds of *Pisonia grandis* have clearly evolved for long-distance dispersal by seabirds. Adhesive fruits and seeds (epizoochores) are more effective for long-distance dispersal of plants than other dispersal modes (Sorensen 1986), and are particularly important for dispersal to oceanic islands (Carlquist 1966). On Cousin Island, the majority of birds carrying *Pisonia* seeds were seabirds, which are likely to be the most common dispersal vectors.

My experiments suggest that dispersal is most likely achieved via living seabirds carrying a few seeds rather than heavily entangled birds likely to die. Some seeds tolerated periodic daily immersion in seawater for at least 28 d (as might be experienced by seeds attached to living birds) but no seeds tolerated prolonged immersion in the sea for 12 d or more (as might be experienced by seeds attached to a dead bird floating on the sea). Hnatiuk (1979) also reported a significant decline in germination after continuous immersion of *Pisonia grandis* seeds (no details given). Seeds would survive for longer on seabirds which spent most of their time in the air (e.g. terns and noddies) than those which spent prolonged periods sitting on the water and diving beneath the water (e.g. shearwaters and tropicbirds).

Furthermore, a seed-covered carcass which washed ashore would not likely end up in soil where *Pisonia* might grow. On Cousin, the few bird carcasses which were seen on beaches were rapidly eaten and buried by ghost crabs within the salty intertidal zone where germination or seedling survival would be unlikely. Even large *Pisonia* trees have low tolerance of sea spray (Walker 1991a, AEB pers. obs.). This intolerance also makes it unlikely that the species disperses as a result of drifting trees or branches which wash ashore, as was suggested for one tropical tree species (Cain *et al.* 2000).

Is fatal entanglement beneficial to *Pisonia* or accidental?

The high incidence of bird mortality caused by entanglement of *Pisonia grandis* seeds has been documented on many tropical islands (Walker 1991a). This frequent mortality of potential dispersers raises the possibility that the extreme stickiness of the seeds and the formation of a multi-seeded infructescence which entangle birds evolved for the purpose of killing birds, and that *Pisonia* plants gain some fitness from killing birds. This concept was briefly discussed by Walker (1991a) but has never been critically examined. I examine three possible benefits to *Pisonia* that might accrue from fatal entanglements: (1) enhanced germination and seedling survival; (2) enhanced dispersal; and (3) increased nutrients benefiting the established trees.

My field experiments and unpublished evidence cited by Walker (1991a) showed that carcasses were not essential for germination and seedling survival in *Pisonia grandis*. On the contrary, seedling establishment was lower when seeds were attached to carcasses than in control plots without carcasses, probably as a result of disturbance by crabs and other scavengers at the carcass. Seeds on carcasses taken underground by crabs did not show improved success. There is therefore no evidence that *Pisonia* germination or seedling establishment is enhanced by fatal entanglement with the seeds.

As discussed above, seeds which killed birds at sea would be far less likely to produce seedlings than those which were carried on birds which did not die. Furthermore, the vast majority of birds killed by the *Pisonia* seeds die on the island where they contact the seeds. There is therefore no evidence for enhanced long-distance dispersal resulting from fatal entanglements.

Although flightless, heavily entangled birds can usually still walk, and *Pisonia* might thereby benefit from enhanced intra-island dispersal. This does not appear to be the case. Seeds contribute a trivial portion of the recruitment of *Pisonia grandis* on the islands where they are already established. My experiments revealed very low persistence of seedlings (0.1% of seeds) within the first few months after planting. Similar rapid disappearance of seedlings was found on the Great Barrier Reef (Walker 1991a). The seeds seem adapted to relatively rapid dispersal and germination, and not for prolonged dormancy (Hnatiuk 1979, this study). Seeds on the ground disappeared quickly, and few could be found 1 mo after a fruiting episode, although infructescences stripped of seeds were commonly seen. I never encountered free *Pisonia* seeds in the forest soil when collecting soil for experiments or digging for other reasons.

Although *Pisonia grandis* has been the most common and structurally dominant tree in the coastal plateau forest of Cousin Island for the past 30 y, two intensive studies reported virtually no seedlings (Derksen & van Dort 1990, Schumacher & Wüthrich 2000). Replacement, spread, and gap regeneration is almost entirely by vegetative regeneration (rooting of fallen branches and coppicing). The wood from these rapid-growing trees is weak, spongy and rots easily. Branches and trees frequently fall, but usually re-sprout rapidly. On Cousin Island *Pisonia* is largely self-replacing, can replace some other tree species during succession, and is likely to remain the dominant tree species on the coastal plateau (Derksen & van Dort 1990, Schumacher & Wüthrich 2000). Similar trends are reported elsewhere (Walker 1991a, b).

It seems doubtful that the extreme stickiness would have evolved primarily for intra-island dispersal, because this could be achieved just as readily through less-sticky seeds that are preened off the feathers of birds sitting on the island where they encountered the seeds. Selection for intra-island dispersal and recruitment generally results in reduced tenacity of epizoochore seeds (Carlquist 1965, 1966; Sorensen 1986). Some insular members of the genus, e.g. *Pisonia sandwicensis*, lack the sticky seed coats, which Carlquist (1965) attributed as a secondary loss of dispersal ability to facilitate intra-island propagation.

Although birds killed by entanglement add nutrients to the soil, the amounts would be trivial compared with the massive inputs from guano, failed eggs and dead chicks coming from the many thousands of breeding seabirds typically found on *Pisonia*-dominated islands.

In conclusion, my study and the sparse published data suggest that killing birds provides little or no benefit to *Pisonia grandis*. The entanglement and mortality of some of the potential vectors can be viewed as a negative side-effect of selection for seeds with sufficient adhesion to stick to a bird's plumage for several weeks and resist the efforts of preening birds to remove the seeds. The strong co-incidence of *Pisonia grandis* with seabird colonies throughout the plant's range (Walker 1991a, b and references therein), and ability to thrive in the acidic guano-laden soils of seabird colonies (Fosberg 1957) are evidence of a close association with seabirds. The evolution of long-distance seed dispersal via seabirds is part of this association and is in accordance with the directed dispersal hypothesis, that seeds are preferentially dispersed to sites with favourable conditions for recruitment (Howe & Smallwood 1982, Sorensen 1986), in this case to islands with seabird colonies.

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