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PISONIA ISLANDS OF THE GREAT BARRIER REEF

PART I. THE DISTRIBUTION, ABUNDANCE AND DISPERSAL BY SEABIRDS OF PISONIA GRANDIS

BY T. A. WALKER

PISONIA ISLANDS OF THE GREAT BARRIER REEF

PART II. THE VASCULAR FLORAS OF BUSHY AND REDBILL ISLANDS

BY T. A. WALKER, M. Y. CHALOUPKA, AND B. R. KING.

PISONIA ISLANDS OF THE GREAT BARRIER REEF

PART III. CHANGES IN THE VASCULAR FLORA OF LADY MUSGRAVE ISLAND

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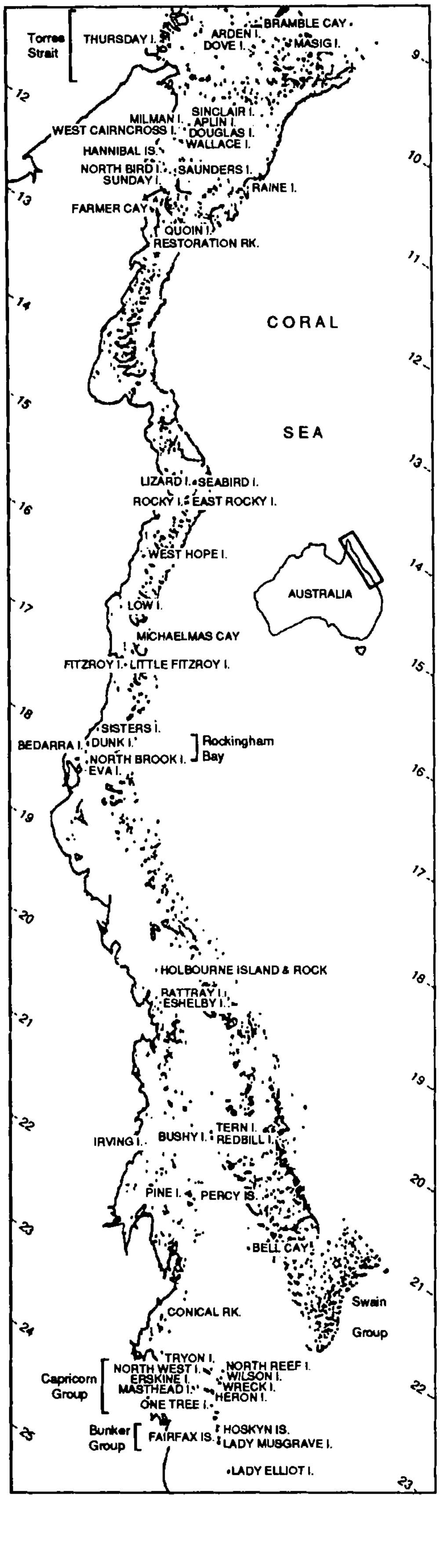


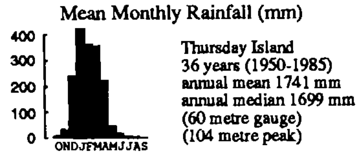
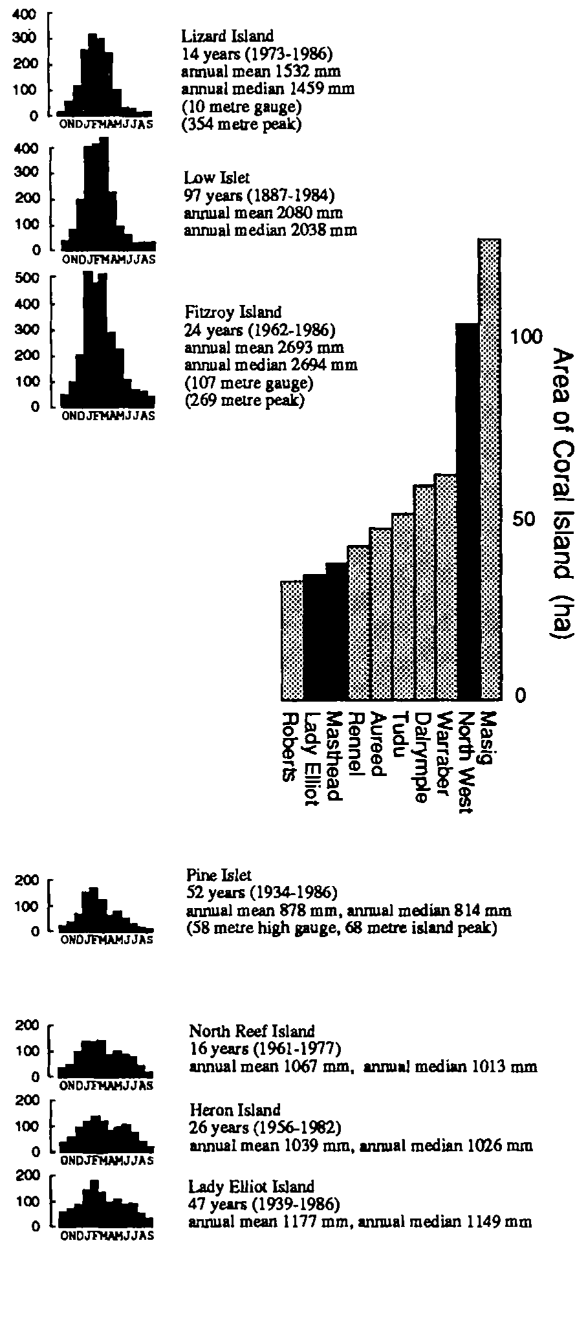


Figure 1-1. The Great Barrier Reef showing localities referred to in the text. Mean monthly rainfall data is illustrated for the four cays and the four rocky islands where records are available. Sizes of the ten largest cays on the Great Barrier Reef are shown below - three at the southern end (23 -24S) and seven at the northern end (9-11S).



PISONIA ISLANDS OF THE GREAT BARRIER REEF

PART I. THE DISTRIBUTION, ABUNDANCE AND DISPERSAL BY SEABIRDS OF PISONIA GRANDIS

BY

T. A. WALKER

ABSTRACT

Pisonia grandis was located on forty-four Great Barrier Reef islands from literature reports and during field surveys between 1983 and 1989. The abundance and maximum dimensions of *Pisonia* were measured for most islands. The highest trees are 16-18 m which is much lower than the 30 m trees reported elsewhere in the Indo-Pacific region. Less than 160 ha of *Pisonia* forest is present in total and 94% is concentrated on cays on the southern Great Barrier Reef especially on North West Island. Northern islands have greater floristic diversity and with rare exception *Pisonia* appears unable to form forests there. Possible reasons for this are discussed. Sixteen species of birds were observed with *Pisonia* fruits attached to their feathers and the primary dispersal agents are identified as the Black Noddy *Anous minutus* and the Bridled Tern *Sterna anaethetus*. The distribution of *Pisonia* is closely associated with the distribution of colonies of these two seabirds. Destruction of *Pisonia* by human activities has been significant since European settlement but relatively minor compared to that elsewhere throughout its range.

INTRODUCTION

Pisonia grandis R. Br. is a remarkable tree of Indo-Pacific islands between the latitudes of 24°N and 24°S. Its unusual features have fascinated botanists since Rumphius (1750) and island cultures have assigned it a variety of roles from culinary to that of sacred plant not to be possessed on penalty of death (Stemmerik 1964). A tall attractive species with large leaves, smooth bark, buttress-like roots and spreading canopy it often forms a shady forest characterised by near absence of undergrowth and other trees. *Pisonia grandis* occurs almost entirely on small islands supporting colonies of seabirds or imperial pigeons (Ridley 1930, St. John 1951, Airy Shaw 1952, Stemmerik 1964). This unique distribution has been attributed both to the spread of seeds by birds and to enhancement of growth by bird guano (Airy Shaw 1952, Stemmerik 1964).

Pisonia grandis forest on coraline substrate tends to produce a rich peat-like acidic humus overlaying phosphate rock (Fosberg 1957). Consequently this forest has been cleared for agriculture (particularly coconut) or phosphate mining on most islands throughout the Indo-Pacific (Fosberg 1974, 1983; Manner *et al.* 1985). The Great Barrier Reef is one region where islands with uncut *Pisonia* forests remain. It has been suggested that phosphatic cay rock requires the presence of seabird guano and *Pisonia* humus for its formation (Fosberg 1957) and *Pisonia* therefore has

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considerable historical importance in generation of commercial Indo-Pacific rock phosphate deposits. The presence of phosphatic cay rock would also indicate past abundance of *Pisonia* where it is presently absent or scarce.

The Great Barrier Reef province (GBR) extends across fifteen degrees of latitude from 9°S to 24°S (Fig.1-1) and contains approximately 950 islands. Most are rocks and islands of continental origin. Approximately 160 coral cays occur (the term "cay" is used here in its correct sense for true islands and does not include submerging sandbanks) and of these all except twenty-five are sited along the northern half of the GBR (9°S to 18°S). The most studied cays are the southernmost fifteen: the Capricorn and Bunker Groups and Lady Elliot Island. These cays are wooded and their often extensive *Pisonia grandis* forests and vegetation have been described in detail (see references in note 13 on page 8). The only other wooded cay on the southern half of the GBR, Bushy Island, is also forested with *Pisonia grandis* (Part II) . The situation on these cays has sometimes led to a belief that *Pisonia grandis* is a common or dominant species on cays of the GBR (Hopley 1982) however *Pisonia* forest has rarely been described elsewhere on the GBR (MacGillivray 1852, Domm 1977) and with one or two exceptions the few reports of this species on northern islands describe small amounts of low or stunted trees.

The present appraisal of the distribution and status of *Pisonia grandis* along the GBR is presented in response to commercial pressure to clear forest for tourism developments and airstrips on these small islands. Results of an extensive survey of GBR islands for *Pisonia grandis* are described with particular reference to its association with seabird colonies.

ISLAND SURVEYS

Four hundred and seventy GBR islands were examined for *Pisonia grandis* and avifauna from 1983 to 1990 (Fig.1-2). Investigations varied from comprehensive surveys of several days duration to observations from a vessel without landing. Further observations were made during aerial overflights of the GBR. Small amounts of *Pisonia grandis* were undoubtedly overlooked but it is considered that all significant stands south of 15°S were examined. Islands north of 15°S were visited less extensively and while information for these islands is incomplete it is considered reliable for forests of *Pisonia grandis*. Several botanists and naturalists with wide geographical

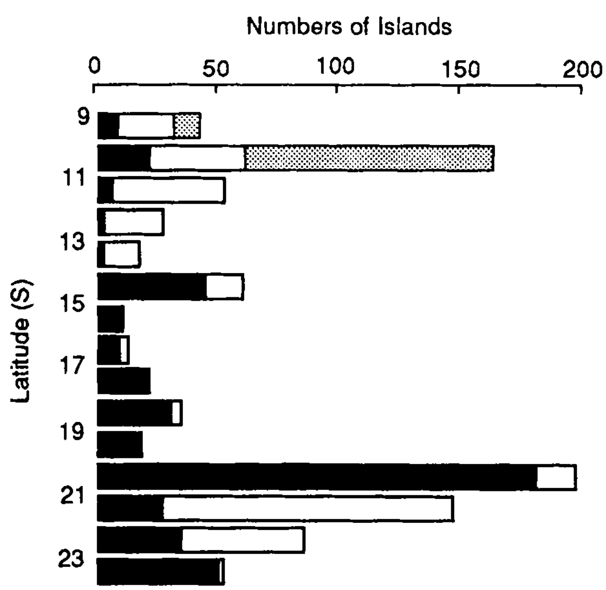

Fig.1-2. Latitudinal distribution of islands in the Great Barrier Reef province showing the numbers of islands visited from 1983 to 1990.

Western Torres Strait

Islands Surveyed 1983-90

experience along the GBR advised that no other locations for *Pisonia* were known to them (personal communications from S. Domm, B. King, C. Limpus, R. Buckley, H. Heatwole, D. Stoddart, G. Batianoff, E. Hegerl and A. Taplin).

Heights of trees were estimated using an inclinometer. Circumferences of trees were measured at the narrow region between basal root expansion and multiple trunk divergence. In large trees this region is often about a metre above the ground and was descriptively referred to as the "waist" by Cribb (1969). The areas covered by *Pisonia grandis* on each island were estimated from field measurements or determined from aerial photographs or published island maps. Areas were estimated for canopy cover of *Pisonia* forest including the canopies of interspersed trees of other species. Some measurements are approximate because of the brief time available during island visits or because of difficulties associated with distinguishing *Pisonia grandis* from other species on aerial photographs. The trees of greatest height and girth were searched for but not necessarily located on every island. For those islands not visited some published height estimates have been accepted without confirmation. The study has progressed over seven years potentially allowing significant changes in dimensions to occur since the early measurements were taken.

Vegetation species lists were compiled for several islands during the *Pisonia* surveys. Roughly half of the plant species were identified by sight and specimens of the remainder were collected for subsequent identification or confirmation of identity at the Queensland Herbarium. Some taxa were not satisfactorily resolved. *Abutilon* specimens are assigned to *A. asiaticum* var. *australasicum* as this is the only species identified from Australia by Fosberg (1988). *Boerhavia* species were identified according to the Flora of Australia (Bureau of Flora and Fauna 1984) however Fosberg (1988) considers that neither of the two GBR species identified by this key occur in Australia. Records have therefore been assigned to *Boerhavia repens* L. with the assumption that segregation is likely following further detailed examination. Records of *Lepturus repens* may include representatives of the recently described *L. stoddartii* (Fosberg 1988).

DISTRIBUTION AND ABUNDANCE OF PISONIA

Of the 950 or so islands of the GBR region the present field investigation and literature survey could locate only forty-four islands where *Pisonia grandis* occurs. Table 1 summarises the distribution and abundance of *Pisonia* and includes estimates for populations of the two main avian dispersal agents identified in following sections. The following island descriptions are numbered and refer to corresponding note numbers in the final column of Table 1-1.

1) Masig Islet is the larger of the two Yorke Islands and is referred to as Yorke Island on some maps. It is the largest coral cay on the GBR (Fig.1-1) and the Australian continental shelf and is inhabited by approximately 200 people. A five-hour search of the forest and woodland in November 1988 located only two *Pisonia grandis* trees in the centre of the cay beside the airstrip. Further isolated specimens might have been overlooked. The nature of the pre-existing vegetation cleared to make way for the airstrip and its present bordering *Casuarina* forest is unknown but the size of the existing *Pisonia* trees suggests they could pre-date the airstrip and be remnant from a larger stand.

2) MacGillivray (1852) described Arden Island as "low and sandy, covered with tall bushes and a few clumps of trees (*Pisonia grandis*)". Surveys of this uninhabited cay in 1987-88 yielded 53 species of plants (Tables 1-2,1-3) but *Pisonia grandis* was not present. The vegetation is dominated by large deciduous *Gyrocarpus americanus* trees which have a close resemblance to *Pisonia*

Table 1-1. Maximum heights (m), circumferences (m) and abundance of *Pisonia grandis* on Great Barrier Reef cays and rocky islands. Colonies of Black Noddy *Anous minutus* and Bridled Tern *Sterna anaethetus* are also shown (+ breeding colony <500 birds; ++ breeding colony 500-10,000 birds; +++ breeding colony 10,000-200,000 birds; ++ or + denotes large or small roosting population or known past breeding colony).

Island	Cay	Max. Ht.	Max. Circ.	*A. minutus*	*S. anaethetus*	Status of Pisonia
Masig I.	+	12.0	5.3	-	-	Two adjacent trees beside airstrip clearing (1)
Arden I.	+	-	-	-	-	Reported in 1848, not present in 1988 (2)
Dove I.	+	4.0	1.9	-	+	One isolated tree near beach in grassland (3)
Sinclair I.	+			-	-	<0.1 ha (R. Buckley, A. Taplin, pers. comms.)
Milman I.	+			-	-	Some amongst rainforest (A. Taplin, pers. comm.)
Aplin I.	+			-	-	Small amount on shingle bank (Buckley, pers. comm.)
Douglas I.	+	16.0	7.0	+	-	About 2.5 ha of *Pisonia* forest dominates cay (4)
West Cairncross I.	+	19.0	10.0	+	+	About 20 large trees amongst rainforest (5)
Wallace I.	+	8.0		++	+	0.02 ha thicket on grassy cay (King *et al.* 1989)
West Hannibal I.	+	9.0	2.5	-	+	2 trees amongst *Pemphis* on eastern tail of cay rock
East Hannibal I.	+	8.0	3.2	+	-	5 trees on sandy shingle bank within dense *Pemphis*
North Bird I.	+	13.0		++	-	Few in 1 ha *Erythrina* forest (King & Limpus 1985)
Farmer Cay	+	4.0		++	+	Small woodland with *Pisonia* (King and Limpus 1990)
Quoin I.	-	5.0		++	+	0.2 ha stunted thicket on rock (King & Buckley 1985)
Seabird I.	-	1.2	0.2	++	+	1 guano covered shrub on central rise on rocky soil
East Rocky I.	-	1.8	0.4	+	+	1 shrub at summit amongst other shrubs and trees
Rocky I.	-	18.0	10.5	++	++	About 1.5 ha forest on coral sand and on hillside (6)
West Hope I.	+	10.0	3.5	-	+	<0.1 ha, two stands among other trees and thickets
Low Isles	+			-	+	*Pisonia* collected in 1973, not seen in 1988 (7)
Little Fitzroy I.	-	10.0	4.2	-	+	15 trees below vine forest along north face on rock
North Brooke I.	-	8.5	2.3	-	++	2 trees on sand at north end in mixed forest (8)
Eva I.	-	10.0	6.0	-	+	Several trees and shrubs on rock in mixed forest
Holbourne I.	-	5.5	1.0	-	-	0.5 ha narrow strand forest, trees on coral sand
Holbourne Rk.	-	1.5	0.3	-	+	One stunted shrub growing on rock (Walker 1989b)
Rattray I.	-	1.5	0.7	-	-	Windshorn clump of 7 main trunks on western sand
Eshelby I.	-	7.0	2.7	-	++	About 0.5 ha of stands and scattered trees (9)
Tern I.	-	4.5	1.2	-	+	7 low trees in small *Ficus obliqua* thicket on hilltop
Bushy I.	+	13.0	6.0	++	-	2 ha of mature *Pisonia* forest dominates cay (10)
Redbill I.	-	3.0	0.6	-	+	<20 plants on rock in *Ficus obliqua* thicket (11)
Percy Isles	-			-	?	Possibly specimens on rocks off Pine Islet (12)
Conical Rk.	-	0.5	0.3	-	-	Stunted shrub in rock crevice is sole woody plant
North Reef I.	+	4.0	0.4	+	-	2 young trees among *Tournefortia*, *Scaevola* (13a)
Tryon I.	+	13.0	6.4	+	+	6.5 ha of *Pisonia* forest over most of cay (13c,d)
North West I.	+	17.0	9.0	+++	-	94 ha of *Pisonia* forest over most of cay (13b,e)
Wilson I.	+	9.0	3.3	+	+	0.7 ha *Pisonia* forest among *Pandanus* (13b,f)
Wreck I.	+	9.0	2.6	+	+	0.5 ha of *Pisonia* forest in centre of cay (13c,g)
Heron I.	+	13.0	7.0	+++	-	6.5 ha forest and through developed areas (13b,h)
Erskine I.	+	2.5	1.0	+	+	0.1 ha stunted thicket in mixed shrubs (13c,i)
Masthead I.	+	15.0	6.0	+++	+	27 ha of *Pisonia* forest over most of cay (13b,j)
One Tree I.	+	7.0	2.2	++	++	0.5 ha in 6 windshorn thickets on shingle (13b,k)
East Hoskyn I.	+	7.0	1.6	+	+	0.6 ha windshorn *Pisonia* forest on shingle (13b,l)
West Hoskyn I.	+	14.0	3.8	++	+	2 ha of *Pisonia* forest on lee side of cay (13b,l)
East Fairfax I.	+	12.0	11.0	+	+	1.5 ha of remnant *Pisonia* forest on shingle (13b,m)
West Fairfax I.	+	12.0	9.0	+	+	1.3 ha of *Pisonia* forest on shingle and sand (13b,m)
Lady Musgrave I.	+	13.0	7.5	++	+	7 ha of *Pisonia* forest over much of cay (13b,n)
Lady Elliot I.	+	10.0	3.5	+	+	Remnant stand of 11 large trees, shrubs (13c,o)

(see text for notes 1-13)

grandis when branches are bare of foliage and seeds during the dry season. It seems likely that MacGillivray misidentified *Gyrocarpus americanus* as he visited during the dry season. The irregular trunk bases are expanded with massive above-ground roots, there is coppice shooting from fallen branches and trunks, the wood is soft and brittle and the bark is light-coloured and smooth: characteristics remarkably similar to those of *Pisonia grandis*. The presence of *Pisonia* 140 years ago cannot be completely discounted because the island is occasionally or periodically burned by the nearby islanders and the tallest trees (presently *Gyrocarpus*) have been felled for years by government officers when they reached the height of the navigation light tower.

3) Dove Island is an uninhabited sand cay dominated by *Imperata cylindrica* grassland as a consequence of annual burning by the inhabitants of nearby islands. Stands of low trees occur and a solitary *Pisonia grandis* specimen is present beside the beach. This is the only wooded Torres Strait cay where Bridled Tern nesting has been confirmed to date.

4) The highly developed *Pisonia* forest on Douglas Island is discussed on page 14. There were no seabirds nesting during the survey in October 1988 but the observation of eight dead Black Noddies and the spread of white excreta indicated the presence of a nocturnal roosting population.

5) MacGillivray (1852) described Cairncross Island as "... covered in the centre with tall trees ... These large trees *Pisonia grandis* form very conspicuous objects from their great dimensions, their smooth, light bark, and leafless, dead appearance. Some are from eighty to one hundred feet in height, with a circumference at the base of twenty feet." These height estimates conflict with the more likely contemporary value of 58 feet (17.4 m) given for the island trees by Stokes (1846). In October 1848 T. H. Huxley (J. Huxley 1935) also recorded Cairncross Island as ".. well wooded, the most conspicuous objects being the white naked Pisonia trees". In 1988 there were roughly twenty large *Pisonia grandis* trees on the western (large) Cairncross Island and none on the eastern island. These trees were a minor component of a well developed forest dominated in height (20 m) by *Garuga floribunda*, *Ficus virens* and *Gyrocarpus americanus*. In October the cay was very dry and the leafless branches of these three deciduous species and *Pisonia* protruded above the leafy canopies of *Manilkara kauki* and other lower species of trees. The *Pisonia* trees are old and appear to be surviving with little or no vegetative spread or growth of seedlings. There were indications of some nocturnal Black Noddy roosting.

6) Rocky Islet has the second highly developed *Pisonia* forest on the northern GBR. Phosphate rock is widespread but the forest differs from that at Douglas Island because burrowing shearwaters prevent accumulation of a thick humus layer. The forest is protected behind the lee side of a high island ridge and forms a pure stand on the lowland calcareous sand but mixes with other species near to and upon the rocky hillside. There is extensive *Pisonia* growth on non-calcareous substrate but this does not reach the stature or girth of trees on the coraline substrate. Thousands of Black Noddies roost in the forest at night.

7) The Queensland Herbarium in Brisbane has a record of *Pisonia grandis* collected at Low Isles by S. Everist in 1973. It was not observed in other vegetation surveys of the sand cay in 1973 (D. Stoddart, pers. comm.) or in 1983 or 1988. If the 1973 record is correct the species has apparently disappeared or is present only on shingle banks in the mangrove complex (Woody Island).

8) Some confusion occurs in the Rockingham Bay area (approx. 18°S) where *Pisonia inermis* is reported by Bentham (1870). Cribb (1969) considered this to be *Pisonia grandis* and discussed the likelihood that the specimen was collected from an island in the bay rather than from the mainland.

Table 1-2. Terrestrial vascular flora of northern cays where *Pisonia grandis* is recorded, Part 1: Species also naturally occurring or naturalized on southern cays. Species presence on the 16 wooded southern cays is shown for comparison. (Partial list for Masig Island.)

	Northern Cays									Southern Cays															
	Masig	Arden	Dove	Cairncross (west)	Douglas	Wallace	Hannibal (west)	Hannibal (east)	West Hope	Bushy	North Reef	Tryon	North West	Wilson	Wreck	Heron	Erskine	Masthead	One Tree	Hoskyn (west)	Hoskyn (east)	Fairfax (west)	Fairfax (east)	Lady Musgrave	Lady Elliot
Abutilon asiaticum	+	+		+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+
Achyranthes aspera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Amaranthus viridis	+	+	+									+	+			+						+	+	+	+
Bidens pilosa	+		+	?							+	+	+			+		+		+		+	+	+	+
Boerhavia repens	+	+		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Caesalpinia bonduc	+	+	+	+			+	+	+				+							+		+		+	
Canavalia rosea	+		+	+			+		+					+		+		+	+	+	+	+		+	+
Cassytha filiformis	+	+	+	+			+		+	+	+	+	+	+	+	+	+	+							
Casuarina equisetifolia	+	+		+		+	+			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Catharanthus roseus	+																								+
Celtis paniculata				+	?				+			+	+			+		+							
Cenchrus echinatus	+											+	+	+	+	+	+	+				+		+	+
Cocos nucifera	+	+	+				+		+	+	+	+	+	+	+	+				+		+		+	+
Cordia subcordata	+	+	+	+		+	+		+	+		+	+	+		+		+							
Crinum pedunculatum	+								+	•						+		+							
Cyperus rotundus		+																						+	+
Dactyloctenium aegyptium				+		+	+								+		+								
Diplocyclos palmatus				+	+				+											+					+
Eleusine indica	+											+	+			+		+		+		+	+	+	+
Emilia sonchifolia				+					+																+
Euphorbia atoto	+	+	+	+			+					+	+	+	+	+	+	+	+	+					+
Euphorbia cyathophora	+															+									+
Euphorbia hirta	+	+											+												+
Euphorbia tannensis	+				+	+	+			+		+	+	+	+	+	+	+	+	+		+		+	+
Ficus obliqua					?		?					+	+					+							
Ficus opposita	+											+	+	+	+	+	+	+		+	+	+	+	+	+
Ipomea macrantha				+	?		+		+	+		+	+	+	+	+		+	+	+		+		+	+
Ipomea pes-caprae	+	+	+	+	+	+	+		+	+	+	+	+		+	+		+	+		+	+	+	+	+
Lantana camara	+																								+
Lepturus repens	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pandanus tectorius	+	+	+	+					+	+	+	+	+	+	+	+		+	+	+		+	+	+	+
Pipturus argenteus	+	+										+	+			+		+							
Pisonia grandis	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Portulaca oleracea						+				+	+	+			+	+			+		+	+	+	+	+
Rhynchelytrum repens	+																							+	+
Salsola kali	+	+	+		+	+	+			+		+				+		+	+	+		+			+
Scaevola sericea	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+	+	+	+		+			+
Sesuvium portulacastrum	+		+	+	+	+	+	+	+	+								+	+					+	
Sophora tomentosa		+	+	+					+	+			+			+	+	+	+	+					
Spinifex sericeus	+					+	+					+	+			+	+	+	+					+	+
Sporobolus virginicus	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+						+	+
Stachytarpheta jamaicensis	+																								+
Suriana maritima	+	+	+	+	+							+	+		+	+		+		+					
Thuarea involuta	+	+		+					+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+
Tournefortia argentea	+	+	+	+					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tribulus cistoides	+	+	+	+	+					+		+	+	+	+	+	+	+	+	+				+	
Tridax procumbens	+		+							+															+
Triumfetta repens		+		+		+				+												+			+
Vigna marina	+	+							+									+							
Wollastonia biflora	+		+	+			+		+	+		+	+	+	+	+	+	+	+	+		+			+

Table 1-3. Terrestrial vascular flora of northern cays where *Pisonia grandis* is recorded, Part 2: Species not naturally occurring or naturalized on southern cays. (Partial list for Masig Island)

Species	Masig	Arden	Dove	Cairncross (w)	Douglas	Wallace	Hannibal (w)	Hannibal (e)	West Hope
Abrus precatorius		+	+	+	+		+		+
Bauhinia binata							+		
Boerhavia sp.		+							
Bulbostylis barbata		+							
Calotropis procera			+						
Cananga odorata				+					
Cansjera leptostachya				+					
Canthium vaccinifolium				+					
Capparis arborea		+							
Capparis lucida	+	+	+	+	+		+		?
Capparis quiniflora				+					
Capparis sarmentosa					+				
Capparis separia									+
Capparis spinosa		+	+						
Capparis sp.	+			+					
Carissa laxifolia		?		+			+		
Cayratia acris		+							
Cayratia cardiophylla		?			+				+
Cayratia saponaria				+			+		
Cayratia trifolia		+			+		+		
Cayratia sp.	+							+	
Cleome viscosa	+		+	+	+	+	+	+	
Clerodendrum inerme	+	+	+	+	+		+		+
Cochlospermum gillivraei	+								
Colubrina asiatica	+	+	+	+			+		+
Commelina lanceolata		+	+						
Commelina undulata				+					+
Commelina sp.	+			+	+				
Cynanchum carnosum									+
Cyperus pedunculatus	+	+		+					
Cyperus scaber	+								
Cyperus stoloniferus		+							
Cyperus sp.	+		+						
Derris trifoliata									+
Digitaria ctenantha									+
Diospyros maritima	+	+		+	+		+		+
Dodonae viscosa	+			+					
Drynaria rigidula									+
Drypetes australasica				+			+		
Endospermum medulosum									+
Erythrina sp.				?	?		+	+	
Eupomatia?									+
Eugenia reinwardtiana				+					
Exocarpus latifolius				+			+		+
Ficus drupacea					+		+		
Ficus virens	+	+		+					
Ficus sp.	+			+	+	+	?		
Flagellaria indica	+			+	+			+	+
Ganophyllum falcatum				+					+
Garuga floribunda				+			+		
Glycosmis pentaphylla				+	+		+		+
Guettardia speciosa	+			+			+		+
Gyrocarpus americanus		+		+	+		+		
Hibiscus tiliaceous	+	+	+				+		
Imperata cylindrica	+		+						
Ipomea aquatica		+							
Ipomea nil			+						
Ipomea sp.	+				+		+	+	
Josephinia imperatricus	+	+	+	+					
Leucaena leucocephala			+						
Macaranga tanarius	+								
Malaisia scandens				+					
Manilkara kauki	+	+	+	+	+	+	+		
Micromelum minutum				+	+		+		
Mimusops elengi				+					+
Morinda citrifolia	+		+		?				+
Mukia maderaspatana		+							
Olax pendula				+			+		
Operculina riedeliana						+			
Opilia amentacea				+					
Pachygone ovata				+					+
Pandorea pandorana				+					
Panicum trichoides					+				
Passiflora foetida	+						+		
Pemphis acidula		+		+	+		+	+	+
Phyllanthus amarus				+					
Phyllanthus novaehollandiae		+							?
Phyllanthus reticulatus				+					+
Phyllanthus tenellus							+		
Phyllanthus sp.						+			
Pleomele angustifolia	+			+					
Platycerium bifurcatum									+
Pongamia pinnata									+
Portulaca australis		+	+				+		+
Premna serratifolia	+	+	+	+	+	+	+		+
Proiphys amboinensis	+		+	+					
Ptychosperma elegans				+					
Salacia chinensis			+						
Sida spinosa		+							?
Schefflera actinophylla									+
Scyphiphora hydrophyllacea			+						
Solanum seaforthianum									+
Solanum torvum									+
Solanum viridifolium		+					+	+	
Solanum sp.									+
Spermacoce sp.			+						
Suaeda australis								+	+
Tacca leontopetaloides	+	+	+	+					
Terminalia catappa	+								+
Terminalia melanocarpa				+					
Terminalia muelleri		+					+		
Terminalia sp.	+			+		+		+	
Thespesia populnea	+				+	+		?	+
Thespesia populneoides							?		
Tinospora smilacina		+							+
Turrea brownii			+				+		
Vitex negundo		?							+
Vitex trifolia		+							
Vitex ovata	+	?				+			
Xenostegia tridentata				+		+	+		+

Banfield (1908), a long-time resident of Dunk Island, described in detail the "murderous" nature of *Pisonia brunoniana* the "bird-lime tree", "Upas-tree" or "Ahm-moo" of the natives which "counts its victims by the thousand each season." He stated that "On some of the islands where the tree is plentiful numbers of pigeons meet a dreary fate every season." A subsequent long-time resident of nearby Bedarra Island noted that "Banfield's Upas tree... *Pisonia umbellifera* is not found in the islands themselves, only on the mainland" (N. Wood in Porter 1983). The Bureau of Flora and Fauna (1984) records *Pisonia umbellifera* from near Mission Beach and at Clump Point, both mainland localities in Rockingham Bay. The present survey of islands in Rockingham Bay located only two *Pisonia grandis* trees on sand at the northern end of North Brook Island (site of a major Torresian Imperial-Pigeon colony) but found *Pisonia aculeata* vines on Sisters Island further north. The source of Banfield's observations remains a mystery.

9) Eshelby Island is a 50 m high, 11.5 ha granite rock with the most extensive growth of *Pisonia grandis* on rocky soil on the GBR. *Pisonia* clumps are scattered amongst other trees and shrubs throughout the island. Eshelby Island supports the largest Bridled Tern colony in eastern Australia (Walker and Hegerl 1986).

10) The *Pisonia* forest and vegetation of Bushy Island (4.5 ha) is identical to that of the Capricorn and Bunker cays 330 km to the south (Part II) . Phosphatic cay rock and a nocturnal Black Noddy roosting population of many thousands are present (Walker 1987). There are no known roosting or nesting colonies of this species for a distance of 840 km to the north. Bridled Terns and other seabirds probably nested at the cay prior to interference from human activities.

11) Redbill Island is a steep 1 ha rock with upper slopes covered by a dense low thicket of *Ficus obliqua* containing several interspersed *Pisonia grandis* (Walker 1989a, (Part II) . No other woody plants are present. Wallace and Lovell (1977) list *Ficus opposita* as the only woody plant on the isle in 1973. Although it is possible for *Pisonia grandis* to have arrived and grown to 3 m in the subsequent fourteen years the species may have been initially overlooked. The widely scattered distribution of *Pisonia* specimens pressed upon by *Ficus* thicket suggests a long period of residence. The *Pisonia* are the same height as the *Ficus* thicket and appear to be partially dependent upon it for protection from salt-laden wind.

12) Bentham (1870) reported collection of *Pisonia grandis* from the Northumberland Islands by Robert Brown. The only islands in this group that were visited by Brown are three of the Percy Isles namely Middle Percy Island, South Percy Island and Pine Islet (Flinders 1814). The first two of these islands are large and did not have *Pisonia grandis* recorded in recent vegetation surveys (S. Domm, pers. comm.; G. Batianoff, pers. comm.). The third, Pine Islet, is a small rock which has not been surveyed since Brown's visit. *Pisonia grandis* specimens may be present but the species was unknown to the resident lighthouse keepers.

13) For the most recent descriptions of the vegetation and seabirds of the Capricorn Group, the Bunker Group and Lady Elliot Island consult the following: (a) Walker and Domm 1986, Walker and Ogilvie 1988*, Walker 1989c; (b) Hulsman 1984; (c) Heatwole 1984, Chaloupka and Domm 1985, Heatwole and Walker 1989; (d) Cribb 1979*, Hulsman *et al.* 1991a; (e) Cribb 1969a*, Hulsman and Walker 1991a; (f) Cribb 1965*, Walker and Hulsman 1991a; (g) Hulsman *et al.* 1991b; (h) Gillham 1963, Smith and Heatwole 1985, Kikkawa and Boles 1976*; (i) Walker and Hulsman 1989*; (j) Hulsman *et al.* 1984*, Dale *et al.* 1984; (k) Heatwole *et al.* 1981*; (l) Cribb 1972*, Walker and Hulsman 1991b; (m) Cribb 1986*, Walker *et al.* 1991; (n) Elsol 1986*, pages 31-38*, Hulsman and Walker 1991b; (o) Walker 1986, Walker 1989d* [* denotes inclusion of a vegetation map].

The Capricorn-Bunker cays support most of Australia's *Pisonia* forest and are the principal breeding sites for the two most abundant seabirds on the GBR, the Wedge-tailed Shearwater and the Black Noddy. North West Island in particular supports 60% of the GBR *Pisonia* and over 50% of the biomass of breeding seabirds on the GBR.

In addition to the records of Table 1 there are possible stands of *Pisonia grandis* on Restoration Rock and Sunday Island (Fig.1-1). At both islands *Pisonia grandis* was tentatively observed from a vessel, white guano appeared to be present on the leaves and Black Noddies were flying over the water nearby (King 1983 and pers. comm.).

Pisonia grandis occupies less than 160 ha on GBR islands. Further distribution sites undoubtedly remain to be found particularly in northern regions but they are unlikely to consist of more than isolated specimens or small stands. *Pisonia grandis* is not known to grow on the mainland and the only other Australian records are for two or three small islands in the Gulf of Carpentaria including the type locality, Pisonia Island. Geographically therefore Australia has a total of less than 170 ha of *Pisonia grandis*. The value is increased by inclusion of territories in the Coral Sea (north-east Herald Cay, south-west Coringa Cay, south-east Magdelaine Cay) and Indian Ocean (Christmas Island, Cocos Islands) that support stands of *Pisonia grandis* (St. John 1951, Airy Shaw 1952, Hindwood *et al.* 1963, Stemmerik 1964).

An estimated 30-40 ha of *Pisonia grandis* was cleared for phosphate rock mining on Lady Elliot Island and East Fairfax Island in the 1890s and on Holbourne Island in the 1920s (Ellis 1936, Cribb 1986, Walker 1989b,d). There has been relatively little recovery of *Pisonia* at these islands. Phosphate mining on Lady Musgrave Island and North West Island was less extensive (Ellis 1936) and partial or complete reforestation has occurred. An additional 4 ha of *Pisonia grandis* has been cleared for buildings and roads at Heron Island. There is no historical information on the abundance of *Pisonia* forest on the GBR cays to the east of Torres Strait. These northernmost cays appear to provide a suitable growth site although the vegetation has been altered for centuries by seasonal burning and cultivation.

Most *Pisonia grandis* along the GBR occurs on coral cays or on cay-like areas of coral substrate fringing continental islands(Table 1-1).Highly developed forest is restricted to coraline substrate. Growth on non-coraline substrate was recorded at Quoin Island, Seabird Island, Rocky Islet, East Rocky Islet, Little Fitzroy Island, Eva Island, Holbourne Rock, Eshelby Island, Tern Island, Redbill Island and Conical Rock. These specimens were mostly healthy but the greatest height reached was no more than 10 m.

AVIAN DISPERSAL OF PISONIA GRANDIS

The anthocarps of *Pisonia grandis* have a sticky resinous exudate that binds them to bird feathers or other surfaces (Banfield 1908, Cribb 1969). Birds may contact fruits in trees or on the ground below. Frequently the whole infructescence will attach to a bird restricting its ability to fly or feed. Panicles accumulate on the ground in thick mats following storms. On the Capricorn-Bunker islands thousands of entangled seabirds die in years when *Pisonia* fruiting is heavy. The main species affected are the Black Noddy *Anous minutus* and the Wedge-tailed Shearwater *Puffinus pacificus* (Hulsman and Walker 1991a). In one example beneath a tree on Lady Musgrave Island forty-five dead or dying Black Noddies were trapped in an area of 75 square metres (April 1984). Inhabitants of some Indo-Pacific islands are reported to use the sticky infructescence of *Pisonia grandis* to catch birds (Ridley 1930, Stemmerik 1964). The fruits can trap insects (Banfield 1908) and may be so adhesive that even tree snakes are immobilized (Ridley 1930). The fruits are not eaten by birds but the flowers are sometimes eaten by the Silvereye *Zosterops lateralis* (Heatwole *et al.* 1981) and at Little Fitzroy Island the flowers were visited by the nectar-feeding Yellow-bellied Sunbird *Nectorinia jugularis.*

In the present study sixteen species of birds were observed with attached *Pisonia grandis* fruits (Table 1-4). An Australian Reed Warbler *Acrocephalus australis* was previously reported with fruits attached (Kikkawa 1970) but such vagrant species are too rare to be of significance to dispersal. Another GBR species the Rufous Night Heron *Nycticorax caledonicus* is reported to carry *Pisonia* fruits elsewhere (Ridley 1930) and domestic poultry and feral chickens may disperse fruits about an island (Cooper 1948) although not between islands. Two species from Table 1-4, the Black Noddy and Bridled Tern, have the potential to be important dispersal agents of *Pisonia* between islands. Other species either have small populations on the islands, are sedentary, do not normally enter *Pisonia* forest or are sufficiently agile to avoid most contact with fruits. Seabirds and Torresian Imperial-Pigeons are the only species with large populations mobile between GBR islands.

The migratory Torresian Imperial-Pigeons are not considered to be important dispersal agents because they do not feed in *Pisonia grandis* trees and rarely nest in *Pisonia grandis*. These birds are reported to suffer many casualties from *Pisonia* fruits (Banfield 1908, Roughley 1936) but only one was seen with attached fruits during the present study. Torresian Imperial-Pigeons do not visit southern GBR islands but some nests are built in *Pisonia* at Douglas Island and possibly at Farmer Cay so these pigeons could play a minor role in local seed dispersal in the north.

Most waders and seabirds avoid entering forests. The main exceptions are Black Noddies which nest in trees and Wedge-tailed Shearwaters which nest in burrows. Shearwaters are able to nest in

Table 1-4. Characteristics of Great Barrier Reef birds seen with attached Pisonia fruits.

		Observed carrying Pisonia	Population size on the GBR	Mobility between islands	Entry to forest habitat
Anous minutus	Black Noddy	+++	+++	+++	+++
Puffinus pacificus	Wedge-tailed Shearwater	+++	+++	+	+++
Sterna anaethetus	Bridled Tern	++	++	+++	+++
Ducula spilorrhoa	Torresian Imperial Pigeon	+	+++	+++	+++
Sula leucogaster	Brown Booby	+	++	+++	+
Tringa brevipes	Grey-tailed Tattler	+	++	+++	+
Arenaria interpres	Ruddy Turnstone	+	++	+++	+
Pluvialis dominica	Lesser Golden Plover	+	+	+++	+
Larus novaehollandiae	Silver Gull	+	+	+++	+
Egretta sacra	Eastern Reef Egret	+	+	++	+++
Geopelia humeralis	Bar-shouldered Dove	+	+	+	+++
Zosterops lateralis	Silvereye	+	+	+	+++
Rallus philippensis	Buff-banded Rail	+	+	+	+++
Megapodius reinwardt	Orange-footed Scrubfowl	+	+	+	+++
Halcyon sancta	Sacred Kingfisher	+	+	+	+++
Coracina novaehollandiae	Black-faced Cuckoo-Shrike	+	+	++	++

large numbers under *Pisonia grandis* forest because there is little undergrowth to block their entry. Black Noddies and shearwaters frequently carry *Pisonia* fruits. Shearwaters are unlikely to be important dispersal agents as they are not known to visit GBR islands other than their breeding site each year. Brown Boobies nest under *Pisonia* forest on the Fairfax Islands and East Hoskyn Island but are not known to enter forest or woodland elsewhere along the GBR making them unlikely seed dispersal agents other than between these three islands. Fruits were commonly found attached to Brown Booby chicks that were raised beneath *Pisonia* trees.

Bridled Terns and Silver Gulls nest under vegetation on many islands. The largest Silver Gull population on the GBR occurs at the southern end on the Capricorn-Bunker Islands (Walker 1988a). Gulls have been observed with various types of seeds attached to their feathers and may be significant carriers of plant species amongst the fifteen coral cays in this area. Many gulls commute between these islands on a daily basis. There is a good correlation between the mean number of gulls at each cay and the number of plant species that are dispersed by birds (Heatwole and Walker 1989). Despite this local correlation Silver Gulls are unlikely to be important distributors of *Pisonia* along the GBR. They have small populations at islands, are relatively skilful in avoiding *Pisonia* fruits and show less propensity for long distance travel along the GBR than the seabirds which disperse seasonally.

Black Noddies and Bridled Terns are clearly the primary dispersal agents for *Pisonia grandis* on GBR islands(Tables 1-1,1-4).Before examining this relationship two other potential *Pisonia* dispersal mechanisms should be noted for completeness. First, White-bellied Sea-Eagles *Haliaeetus leucogaster* and Ospreys *Pandion haliaetus* were found on occasion to carry and place living *Pisonia* branches in nests built on the ground. Rooting or shooting was not observed from the branches on these occasions but should be possible under certain conditions. Second, *Pisonia* trees toppled into the sea by shoreline erosion had floated to the other side of two cays where they took root and produced shoots. Six such specimens were growing on the beach at Bushy Island in 1989. Neither of these dispersal processes is likely to be significant to colonisation of new islands by *Pisonia* because sea-eagles build their nests from vegetation collected on the same island as the nest and because *Pisonia* does not float well and can probably tolerate only brief immersion in seawater.

ASSOCIATION OF PISONIA WITH SEABIRD COLONIES

All except two GBR islands with Black Noddy breeding colonies are vegetated with *Pisonia grandis*. Nesting occurs primarily within *Pisonia* stands and associated trees except at North Bird Island, Farmer Cay, Baird Island and Chapman Island where mangroves are used (King and Limpus 1985, King and Limpus 1991, King 1991) and at Lady Elliot Island where *Tournefortia argentea* and *Casuarina equisetifolia* are used (only a few *Pisonia grandis* trees remain at Lady Elliot Island in the middle of a tourist resort). Black Noddies roost on several cays but uncommonly on continental islands. Roughly half of the islands with *Pisonia grandis* presently support Black Noddy populations(Table 1-1)Most of the remaining *Pisonia* islands support Bridled Tern colonies. Bridled Terns are infrequently observed with attached fruits and many islands with Bridled Tern colonies do not have *Pisonia grandis*.

Black Noddies breed on eight Coral Sea cays to the east of the GBR (Hindwood *et al.* 1963). The largest colonies nest in *Pisonia grandis* on the three cays where it grows (forest or stands to 6-8 m). The other colonies nest in *Tournefortia argentea* at cays devoid of other species of trees. There is also a report of several nests on ground herbage at Turtle Island, an unwooded Coral Sea cay (Hill 1984).

Relatively few islands with *Pisonia grandis* do not presently support populations of Black Noddies or Bridled Terns(Table 1-1)Conical Rocks are small spray-exposed seabird roosting rocks where the only woody plant is one *Pisonia grandis* shrub sheltering in a crevice. Rattray Island is the closest island to Eshelby Island which has the largest Bridled Tern colony on the east coast. Holbourne Island has no nesting seabirds but commercially mined phosphate rock deposits are evidence of previous occupation (Walker 1989b).

Pisonia grandis is absent from approximately 170 seabird breeding islands on the GBR. On many nesting cays and small rocky islands the environment is too harsh to support growth of trees. Coconuts, for example, have been persistently planted on unwooded cays (eg. Bramble Cay, Raine Island, Michaelmas Cay, Swain Group) without success. *Pisonia grandis* is intolerant of direct salty wind and even on well wooded cays does not colonise the strand environment. *Pisonia* forest is wind-pruned or stunted at the windward sides of Capricorn-Bunker Islands in the absence of a windbreak of strand trees such as *Casuarina, Pandanus* or *Tournefortia.*

Seabirds are essential to *Pisonia grandis* for seed dispersal and their guano may confer competitive advantages to the plant (see page 14). In return Black Noddies are benefited by provision of tree nesting sites and suitable leaves for nest construction. Black Noddy nesting is primarily in *Pisonia* forest but the nests are preferentially placed in *Celtis, Ficus* and certain other less abundant trees within the forest (Hulsman *et al.* 1984; Dale *et al.* 1984; Walker, pers. obs.). This may facilitate access through the more open canopies of these species or may be a behaviour to reduce the nest and clutch loss that results from the characteristic windthrow of *Pisonia* branches or trees. There is no apparent advantage to Bridled Terns from association with *Pisonia.* Detrimental effects of *Pisonia grandis* on seabirds include high mortality from entanglement in fruits and eventual displacement of species that require open ground for nesting.

Pisonia may assist Wedge-tailed Shearwaters by provision of a ground surface bare of obstructive vegetation so long as they colonise the site prior to hardening of the phosphate rock which inhibits their tunnelling. In return, burrowing shearwaters protect *Pisonia* forest from commercial mining by reworking the sand and preventing formation of a humus layer and phosphate rock. In the absence of shearwater burrowing the formation of phosphate rock on many Capricorn-Bunker Islands would have led to their certain mining and defoliation in the 1890s (Ellis 1936). It should be noted that phosphate rock is present on several unwooded seabird nesting cays on the GBR. Some, including Bramble Cay, Raine Island, Michaelmas Cay and Bell Cay, were mined or were leased for phosphate mining. There is no evidence that *Pisonia* was previously present on these cays and this seems unlikely in view of the harsh treeless environment. *Boerhavia repens* L. tends to dominate and form meadows at these major ground-nesting seabird colonies and may be involved in formation of phosphate rock. This herb is in the same family as *Pisonia,* is dispersed by seabirds and can form a brown humus under favourable conditions (Walker 1988b).

PISONIA STATUS ON SOUTHERN CAYS

On Capricorn, Bunker, Lady Elliot and Bushy Islands *Pisonia grandis* displaces other vegetation to form a climax forest. This dominance is achieved by vegetative extension rather than by spread of seeds. Frequent windthrow of branches and trunks is facilitated by the shallowness of the root system and the brittle nature of the wood. Extensive regions of parenchyma throughout the wood give it a weak, spongy structure consisting of two-thirds water (Cribb 1969). Fallen branches and trunks take root and produce rows of coppice shoots thereby advancing into surrounding habitat. The closed canopy extends to the ground and the advance of the canopy shades out other plants.

This process of lateral expansion of groves and trees is illustrated in sequential aerial photographs at Lady Musgrave Island (Elsol 1986; Part III). Herbs and shrubs, notably *Wollastonia biflora* and *Abutilon asiaticum* establish in clearings and under canopy breaks following windthrow of *Pisonia*. Comparison of sites at Masthead Island showed a negative correlation between mean *Pisonia* height and density of other species of trees (Hulsman *et al.* 1984, Dale *et al.* 1984) suggesting that *Celtis paniculata* , *Ficus opposita* and other trees also require disturbance of *Pisonia* to establish. The forest floor is dark, bare sand or humus where the canopy is unbroken. Locusts completely stripped the *Pisonia* foliage on west Fairfax Island in 1986 allowing sunlight to penetrate to the forest floor. An impenetrable metre-high thicket of *Wollastonia* and other species rapidly developed but when visited eight months later the canopy had regrown, the forest floor was again in shade and the undergrowth thicket was dead.

Pisonia grandis seedlings are infrequently seen on Capricorn-Bunker islands but sometimes germinate in clusters on the forest floor following rain. *Pisonia grandis* is itself shade intolerant (Gillham 1963, Airy Shaw 1952) and these clusters of seedlings disappear after germination. The only native species in the Capricorn-Bunker islands with any potential to displace *Pisonia* might be *Caesalpinia bonduc* which has slowly expanding thickets on west Hoskyn and Lady Musgrave Islands. These climbing thickets are very dense and have grown over and covered *Pisonia* trees. Seeds of the strangler fig *Ficus obliqua* can also germinate on *Pisonia grandis* but this appears to be an uncommon occurrence.

PISONIA STATUS ON NORTHERN CAYS

Large *Pisonia grandis* forests occur only on coral cays of the southern GBR. These cays are larger and more advanced than cays elsewhere but are equalled or surpassed by the large cays to the east of Torres Strait at the northern end of the GBR(Fig.1-1).The vegetation of the Torres Strait cays (9°S-11°S) has been modified by the indigenous people with possible destruction of *Pisonia grandis* but there are no reports (and no investigations) of phosphate rock which would indicate previous forest (Fosberg 1957). With the exception of the most remote island, Bramble Cay, large seabird colonies are also non-existent on Torres Strait cays presumably as a result of egg harvesting and hunting (Walker 1988b).

The islands from 11°S to 22°30'S have been traditionally visited by mainland aborigines seeking nesting turtles, birds and other food but unlike the Torres Strait Islanders they did not settle and cultivate food. One hunting technique was to set fire to the end of an island and spear the fleeing mammals and reptiles that emerged onto the beach at the other end. This method would be of no value on cays as they do not harbour large mammals or reptiles (at least not any more). A non-anthropogenic explanation seems necessary to explain the general absence of *Pisonia grandis* forest on the northern wooded cays many of which are colonised by seabirds.

Unlike southern cays there is no characteristic forest type on northern cays. Plant diversity is higher and floristic differences between individual islands are greater.Tables1-2 &1-3compare the terrestrial vascular flora (above high tide) of northern cays where *Pisonia grandis* occurs or was previously reported (vegetation lists are not available for all cays). The vegetation of these islands is generally representative of other northern cays.

West Cairncross Island and Douglas Island are of particular note because they are only 8 km apart but have major forest differences. West Cairncross Island supports one of the most diverse and highly developed forests of any cay on the GBR. Few coral islands have an equivalent species diversity and even fewer have an equivalent diversity of native species. Cairncross Island was well vegetated with *Pisonia grandis* in 1848 (MacGillivray 1852) but the species has apparently not been able to expand or displace the other vegetation in subsequent years. Douglas Island on the other hand is the only northern cay where mature *Pisonia* forest was found to occur. This forest is remarkably similar in appearance to *Pisonia* forests on the southern cays. Few other trees occur within the forest (notably *Ficus*) which has little undergrowth and thick peat-like humus overlaying phosphate rock. The main differences from southern forests are the presence of lianas on *Pisonia* trees and the presence of different species of trees and shrubs fringing the forest and cay. Douglas Island and the continental Rocky Islet are important because they demonstrate that there are no climatological barriers to formation of *Pisonia* forest on northern islands and its scarcity is therefore controlled primarily by biological factors.

Plant species on southern cays are incapable of competitively displacing *Pisonia grandis* but this is not necessarily so on northern cays. At least six times more species of trees are present on cays in the north (Table 1-3) with the result that *Pisonia* experiences wider competition. At Cairncross Island *Pisonia* is struggling against other species while nearby at Douglas Island it maintains an unchallenged dominance.

GROWTH OF PISONIA GRANDIS

The pattern of distribution and growth of *Pisonia grandis* suggests that there is no simple explanation for the floristic dominance on southern cays and the scarcity on northern cays. Several factors, each of small effect alone, more likely combine to lower the ability of *Pisonia* to compete with other vegetation and reduce the probability of forest dominance. Contributing factors may include low dispersal frequency, effects of guano, precipitation patterns, diversity of plant competitors, insect grazing, genetic variation and mycorrhizal associations.

Dispersal Frequency

Dispersal of *Pisonia grandis* seeds to locations other than to seabird nesting or roosting sites is probably an uncommon event. Black Noddies and Bridled Terns are never seen at the mainland unless blown in by tropical cyclones (Campbell 1918, Griffin 1972, Walker pers. obs.) and there is little evidence of nomadic roosting by these species on islands. Bridled Terns migrate overseas following breeding with apparently little visitation to other GBR islands. Black Noddies also migrate, some overseas, some to established roosting colonies elsewhere on the GBR and a number remain at the breeding sites in certain cases. If the distribution of *Pisonia grandis* was due solely to seabird dispersal the species should become established in non-seabird areas over a period of time as a result of uncharacteristic dispersal events (eg. cyclone scatter of seabirds). This does not seem to occur (Table 1) indicating that factors additional to dispersal are involved.

Guano and Growth Factors

It has been suggested that *Pisonia grandis* may require bird guano for growth and that when the supply of guano is interrupted by avian abandonment of sites the trees eventually disappear (Airy Shaw 1952). This is unlikely as there are examples of growth in the absence of guano on the GBR (Table 1-1) and elsewhere (St. John 1951, Airy Shaw 1952, Stemmerik 1964, Spicer and Newbery 1979). There is no absolute requirement for guano if the soil contains sufficient nutrients but its presence may nevertheless confer a competitive advantage. This could result from either a positive effect on *Pisonia grandis* or a negative effect on other species or both. High levels of guano are poisonous to many species and "guano burning" of shrubs and herbs is often visible beneath noddy nests. Tree seedlings might be particularly susceptible and many unable to establish in abundant guano. The shallow roots of *Pisonia grandis* have a unique mycorrhizal association (page 17) which might function in protection from, or utilisation of, high guano levels in the surface substrate.

It has been suggested that *Pisonia* seeds might require the presence of animal matter to germinate and that the species is indirectly carnivorous by trapping insects, birds and animals in its fruits to fertilise the soil (Banfield 1908). Seeds have no special growth requirements and will germinate without animal matter or guano (M. Chaloupka, pers. comm.) but the possibility of some small nutrient benefit to growth from addition of carrion at certain islands cannot be dismissed.

Precipitation

Lower rainfall on southern cays (Fig.1-1) may favour *Pisonia grandis* which has an exceptionally shallow root system adapted to utilise near-surface moisture and avoid contact with the water tables of cays. The cay water table is usually saline from seawater intrusion except when flushed by rain. Trees with deep root systems may be weakened by contact with saline water on cays with low rainfall. Forks in large *Pisonia* trees sometimes collect and retain rainwater for months following rain. *Pisonia grandis* requires moderate rainfall for growth and expansion but is adapted to withstand prolonged dry conditions and sheds its leaves in such years. It is reported to have been abundant prior to phosphate mining on Nauru where the mean annual rainfall is only 203 mm (Manner *et al.* 1985). There is also a report of *Pisonia* trees at an old village site on Vaugo Island near Port Moresby (Papua) where the annual rainfall is only 70 mm (Bell 1969). *Pisonia* may be better able to cope with wide seasonal or inter-annual variations of rainfall than many other trees. On northern cays the higher rainfall also improves growth conditions for competitors intolerant of salt or guano by washing these substances from the foliage and soil.

Diversity of Plant Competitors

Growth of *Pisonia* will be influenced by the nature of other species competing for space, light and nutrients. Keith (in Airy Shaw 1952) states that *Pisonia grandis* is intolerant of both competition and shade. The greater floristic diversity on northern GBR cays can be primarily attributed to their proximity to mainland vegetation compared with the southern cays, to their histories of anthropogenic interference and burning (unknown for southern cays prior to European arrival) and to their large populations of Torresian Imperial-Pigeons. Higher rainfall may also contribute to diversity. The most striking of these factors is the effect of Torresian Imperial-Pigeons.

Torresian Imperial-Pigeons migrate to Australia in spring and depart in late summer. They nest in island colonies of up to 200,000 birds particularly in mangrove trees and depart each day to feed on fruit on the mainland. Upon their return vast numbers of viable seeds are excreted on the islands. Torresian Imperial-Pigeons are found on virtually all wooded northern islands in summer. The main plant families consumed include Lauraceae, Moraceae, Arecaceae, Anonaceae, Burseraceae, Oleaceae, Chrysobalanaceae, Sapindaceae, Combretaceae, Rutaceae, Verbenaceae, Solanaceae and Myristicaceae (Crome 1975a,b, Frith *et* al. 1976). Other foods include *Manilkara kauki* and *Celtis* species. Torresian Imperial-Pigeons do not visit the southern cays and apart from stragglers the southernmost colony is at Irving Island (21°27'S). In addition to endozoochory the daily commuting of hundreds of thousands of Torresian Imperial-Pigeons increases the probability of dispersal of diaspores that attach externally to bird feathers. Most plants with epizoochores are encountered close to the ground rather than in the tree canopy but Torresian Imperial-Pigeons also feed in low shrubs such as *Solanum torvum* and *Vitex* species.

Another aspect of competitive interaction is the timing of forest development. If a mature, dark *Pisonia grandis* forest can develop before the arrival of seeds of strongly competitive species then the later arrivals may be unable to establish. Soil modifications associated with *Pisonia* forest might also enhance its relative competitiveness. The pH of coral sand is about 8.3 decreasing to 7.0 as normal humus is incorporated but *Pisonia* humus ranges from pH 6.0 to 4.0 (Fosberg 1957, 1974). Such an effect might operate at Douglas Island where *Pisonia grandis* has generated a thick humic layer but is less likely at most Capricorn-Bunker islands where burrowing Wedge-tailed Shearwaters rework the sand and prevent formation of a humus layer.

Insect Grazing

Pisonia grandis forest occurs on isolated islets relatively impoverished with insect or animal grazers that might otherwise prevent its formation on larger land masses. Occasional invasions by locusts or other insects blown from the mainland cause severe defoliation of *Pisonia* (see previous Fairfax Island example, also Musgrave 1925) but high insect populations do not persist on small islands (Heatwole *et al.* 1981). The proximity of northern cays to the mainland and the occurrence of north-west monsoonal winds presumably results in more frequent insect invasions than on southern cays and island flora derived from the adjacent mainland should be more resistant to insect damage than *Pisonia grandis* which has relatively less exposure to pests.

Genetic Variation

Pisonia grandis has an initial advantage over most trees dispersing to small islands because one plant can spread asexually by vegetative means in the absence of other individuals or pollinators. Growth on some GBR islands is undoubtedly clonal. Vegetative reproduction is also advantageous in relatively homogeneous predictable habitats such as occur at seabird cays (ie. calcium carbonate substrate, guano, salt air). Carlquist (1974) noted that *Pisonia grandis* ranges over wide stretches of the Pacific without even subspecific differentiation among remote islands thus testifying to the effectiveness of bird dispersal in reintroducing genes that swamp local incipient speciation. If this is correct the absence of genetic replenishment amongst *Pisonia grandis* growing at sites no longer inhabited by seabirds might also result in loss of vigour and eventual displacement over a long time period.

While it is probable that *Pisonia grandis* is genetically homogeneous throughout its range the possibility of the existence of distinct strains or varieties cannot be dismissed. The small sterile cultivated variety *Pisonia alba* (Airy Shaw 1952, Stemmerik 1964, Fosberg 1974) is well known and conflicting reports on the effects of guano as a growth factor might have arisen from observations of strains with differing requirements. The *Pisonia* forests on high Indo-Pacific islands (*Pisonia grandis* is reported at altitudes of 1200 m, Stemmerik 1964) may be genetically distinct. It is notable that *Pisonia grandis* trees on the GBR are only half of the height, 30 m, that they have been measured elsewhere although they attain the same maximum diameter of 3-4 m (Stemmerik 1964, Fosberg 1974). Tall and short varieties may be involved as no nutritional deficiency is apparent on large GBR sand cays where the central trees are protected from salt wind. Growth to 30 m would confer no advantage to Capricorn-Bunker trees but may be necessary elsewhere in the Indo-Pacific to avoid shading by tall species.

Mycorrhizal Association

Mycorrhizae, the symbioses between fungi and plant roots, are nearly universal in terrestrial vascular plants (Malloch *et al.* 1980). Two basic types of mycorrhizae occur (characteristics summarized by Malloch *et al.* 1980, Connell and Lowman 1989). Vesicular-arbuscular mycorrhizae (VAM) are formed by a small number of physiologically unspecialised and ubiquitous fungi with over 80% of land plants. VAM penetrate the root tissue forming intracellular vesicles and arbuscles. Ectomycorrhizae (EM) do not normally penetrate root cells but form a sheath around the epidermis isolating the root from the soil. EM are less widespread than VAM but the thousands of EM fungal strains are more highly plant specific. Unlike VAM the EM have an extensive mycelium in the soil that appears capable of decomposing organic matter and absorbing organic nitrogen.

A notable feature of insular floras is the high component of non-mycorrhizal families (Pirozynski 1983). Plants that form EM are particularly rare on Pacific Islands possibly as a result of infrequent co-dispersal of phycobiont and mycobiont (Malloch *et al.* 1980, Pirozynski 1983, Schmidt and Scow 1986). VAM associations are widespread at Heron Island (Peterson *et al.* 1985) and presumably elsewhere on GBR cays which are all relatively close to the mainland. VAM fungi are probably essential for the establishment of vegetation on beach dunes and may survive seawater immersion and attach to vegetative propagules of host plants (Trappe and Schenk 1982, Koske and Gemma 1990). *Pisonia grandis* forms a unique type of EM with morphological characteristics unlike that found in other plants (Ashford and Allaway 1982 and 1985, Ashford *et al.* 1988). This unique association adds a second dimension to mechanisms influencing the distribution of *Pisonia* because factors affecting the distribution, survival and genology of the fungus must also be considered. This is particularly important if, as with other EM, the fungus has few phycobionts other than *Pisonia grandis*. Failure to form the EM association or infection with a fungal strain less suited to the environment presumably weakens the competitive ability of *Pisonia*. At Cousin Island and Bird Island (Seychelle Islands, Indian Ocean) the *Pisonia* growing on coral sand were strongly infected with EM but *Pisonia* from granitic soil at 50 m altitude were poorly infected or were not infected at all (Ashford and Allaway 1985).

Forests dominated by a single species of tree are thought to develop from a highly efficient association with a species-specific EM mycobiont (Malloch *et al.* 1980, Connell and Lowman 1989). Such dominance is more likely on poor soils where the nutrient scavenging ability of EM mycelia is most advantageous. Once an EM plant species achieves dominance it may be difficult for other species to establish due to scarcity of spores of VAM fungi or suitable specific EM mycobionts (Connell and Lowman 1989, Alexander 1989). These spores should be scarce in the absence of suitable phycobionts and might also be toxically inhibited by the dominant EM in the soil. EM associations are uncommon in the tropics. Applying the hypothesis to *Pisonia grandis* the development of forest would require co-dispersal of suitable mycobiont spores with the *Pisonia* seeds. Suitable spores are unlikely to occur at islands where *Pisonia* is absent. At Heron Island *Pisonia grandis* is the only species with EM (Peterson *et al.* 1985). EM spores are often wind-dispersed although dispersal by seabirds is a further possibility in this particular case. If the fungus is relatively specific to *Pisonia grandis* then successful forest formation may require seabird transport of both the seeds and the fungal spores thus greatly reducing the probability of establishment away from seabird colonies. The only weakness with the mycorrhizal dominance hypothesis is that substrates at seabird colonies are usually considered to be rich in nutrients (although the addition of bird guano may not increase the levels of all micronutrients required for plant growth on a carbonate substrate). Impoverished substrate is not, however, important if *Pisonia* achieves dominance mainly by competition for light (vegetative expansion) rather than by competition for soil nutrients. The mycorrhizal hypothesis gives a feasible explanation of why *Pisonia* forest dominates at Douglas Island while nearby at Cairncross Island *Pisonia* is a minor component of the forest. If an EM-*Pisonia* forest establishes prior to arrival of seeds of competitors it may prevail but if *Pisonia* initially faces strong competition from tall trees the EM dominance may not become established.

An interesting example supporting the mycorrhizal hypothesis is a Brazilian white-sand forest dominated by EM trees. In this forest there were fewer saprophytic fungi and more litter accumulation than in nearby forest on fertile soils where EM were rare (Singer and Araujo 1979). This accords with other work indicating that EM reduce the rate at which saprophytic organisms decompose organic litter in low-nutrient soils (Gadgil and Gadgil 1971, Harmer and Alexander 1985). Despite the addition of seabird guano such a mechanism might contribute to the formation of the thick humus layer under *Pisonia* and hence to generation of phosphate rock.

CONCLUSION

Pisonia grandis is highly adapted to growth at seabird colonies and has developed exceptional morphological and physiological characteristics in association with seabirds and mycorrhizal fungi. It is particularly well adapted to growth on coraline substrate on the Great Barrier Reef although elsewhere in the Indo-Pacific it is dominant on volcanic and other non-calcareous substrates. The geographical distribution in association with tropical seabird colonies is unlike that of any other plant species.

Pisonia grandis is sometimes described as the most common tree on cays of the Great Barrier Reef. This misconception derives from a generalisation of the situation on the Capricorn-Bunker cays where *Pisonia* displaces other vegetation to form a climax forest. *Pisonia grandis* is uncommon elsewhere on Great Barrier Reef islands which have a more diverse flora. At least 18% of Australian *Pisonia grandis* forest has been cleared for mining or island development. The figure could be higher if some Torres Strait islands were forested with *Pisonia grandis* before burning and gardening became routine. This splendid forest type has a sad history of destruction throughout its range on Indo-Pacific islands and its conservation on the Great Barrier Reef depends on location of future tourist developments on environmentally robust continental islands rather than on coral cays.

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