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PHYTOGEOGRAPHY AND VEGETATION OF THE REEF ISLANDS OF THE NORTHERN GREAT BARRIER REEF

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Introduction

Until 1973 the vegetation and flora of the reef islands of the northern Great Barrier Reef were among the least known of those of all the world's reef islands. Apart from collections made by Joseph Banks, on Cook's first expedition in *Endeavour*, Robert Brown with Flinders in *Investigator*, Allan Cunningham with Philip Gidley King, and (on a larger scale) F. von Mueller, included in Bailey's *Flora of Queensland* (1899-1905), the only extensive floristic records were those of MacGillivray (1852), who recorded 19 species from a total of 12 islands during the voyage of H.M.S. *Rattlesnake* in 1846-1850. Steers (1938, 92) listed 10 species from Fife Island, determined by W. D. Francis, and Stephenson *et al* (1931) 25 species from Low Isles and 12 species from Three Isles, all presumably based on collections by G. Tandy. Den Hartog (1970) has summarised sea-grass records, mainly from Low Isles. Otherwise the only island in the northern province for which a full floristic record existed was Green Island, where a large proportion of the species is exotic (Smith, Specht and Clapham 1973, Gardner 1973). It is not perhaps surprising, therefore, that it was generally concluded that

> 'the terrestrial flora of the cays is a very restricted one, of only 30 to 40 species, practically all of which are of wide distribution in the Indo-West Pacific province and are characteristic of strand line environments and of environments of shifting lime sand' (Hill 1970, 76; 1974, 725).

Such an interpretation is certainly reinforced by (and indeed largely derives from) work on the Bunker and Capricorn Islands at the southern end of the Reef. These islands are well known both from earlier studies (Longman 1913, White and Macgillivray 1926, Macgillivray and Rodway 1931), more detailed recent work at Heron Island (Fosberg and Thorne 1961, Gillham 1963), at Wilson, Northwest, Hoskyn and Fairfax Islands (Cribbs 1965, 1969, 1972, 1986), and throughout the southern islands by Chaloupka and Domm (1985, 1986). Most of these southern islands have 20-40 species of vascular plants, with a substantial proportion of introductions, a total flora of ca 80 species, and a restricted series of vegetation types dominated by *Pandanus* and *Pisonia* forest and herbaceous communities. At Heron Island, with the largest number of species (51), half (26) are introductions (Chaloupka and Domm 1986, 1540).

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Studies during the Royal Society and Universities of Queensland Expedition to the northern Great Barrier Reef in 1973 revealed a markedly different picture. 1107 numbers of plants, generally each in five sets, were collected from 40 islands or island-groups, and sight records were obtained from a further 19 island-groups during detailed mapping of the islands between 16°57'S in the south (Sudbury Cay) and 11°36'S in the north (Raine Island). These collections, together with others made subsequently by R. Buckley, H. Heatwole, and T.A. Walker, comprise over 380 species of flowering plants in 86 families, together with some lichens and fungi. Not only is the flora different in important respects from that of any other reef province so far studied, reflecting its Australian affinities, but the vegetation units which can be recognised do not in some cases have counterparts in other reef areas. This paper discusses the biogeography and floristics of the northern islands, and describes the main vegetation units of the islands and their relationship to topography, substrate and other ecological controls. It should be read in conjunction with the systematic treatment of the flora by Fosberg and Stoddart (1991).

Biogeography

The known flora of the reef islands (i.e. excluding high islands) of the Great Barrier Reef is ca 410 species and subspecies; this figure does not include the large number of records of exotic pot plants made by Fosberg (1961) at Heron Island. Of these, over 330 are known only from the northern area (north of Cairns, 16°45'S), 33 are known only from the Bunker and Capricorn Islands in the south, and only 43 are common to both provinces. These figures derive from the listing of the plants of the northern islands by Fosberg and Stoddart (1991), and of the southern islands by Chaloupka and Domm (1986). While some revision of the numbers is to be expected and while there are possibilities of nomenclatural differences in the two lists, there is no question of the remarkable distinctiveness in the floras of the two sets of islands. This difference had not previously been recognized before these recent collections were made on the northern Great Barrier Reef. Table 1 lists plants only recorded from the northern islands, Table 2 those only recorded from the southern islands (25 of the 33 species there listed are judged by Chaloupka and Domm (1985) to be introductions), and Table 3 lists the species common to both provinces. A major element in this distribution pattern is the absence of mangroves, sea-grasses, and rock-platform succulents from the southern province: 15 species of mangroves, 7 of sea-grasses, and 4 succulents are recorded only north of Cairns, while two species of sea-grasses are common to both north and south. If these ecological groups are excluded from the analysis, the northern sector has some 330 species of vascular plants, of which perhaps one-third are introduced.

The first striking point about the floras of the southern and northern islands is that the former are Indo-Pacific or pantropical in character and the latter are distinctively Australian. In the south the two dominant vegetation units are *Pisonia* forest and *Pandanus tectorius* forest, both of wide distribution. Other common trees are the wide-ranging *Casuarina equisetifolia*, *Cordia subcordata*, *Celtis paniculata*, and *Pipturus argenteus*. The strand flora comprises wide-ranging Indo-Pacific species including the shrubs *Tournefortia argentea*, *Scaevola taccada*, and *Suriana maritima*, as well as common herbs.

In the north, the main tree species are strikingly different. *Casuarina* and *Cordia* are widespread, but both *Pisonia* and *Pandanus* are relatively uncommon, though there is a single specimen of both as species and in forming vegetation units, and neither *Celtis* nor *Pipturus*

have been recorded (the latter more than fifty years ago at Green Island). The common woodland trees include *Aglaia elaeagnoidea, Diospyros maritima, Eugenia carrisoides, Exocarpos latifolia, Ficus opposita, Manilkara kauki, Mimusops elengi, Pouteria obovata, Terminalia arenicola,* and *Terminalia muelleri.* Among larger shrubs *Capparis lucida* is very common. Most of these species are unknown in the vegetation of Indian and Pacific Ocean reef islands, and they impart a distinctively Australian aspect to the flora. This was recognised by Fosberg (1974), who identified a 'Coral Sea element' on some of the Great Barrier Reef cays, but the five species he then named comprising it included three mangroves and only one tree species (*Ficus opposita*) from the above list. Because this flora appears to be largely restricted to the northern Barrier Reef, and to be absent in the south, and because there are at present no records to suggest that these characteristic plants reach the more remote reef islands of the open Coral Sea, it may be more appropriate to speak of a 'North Queensland element' than a 'Coral Sea element'. As a further qualification, it should be noted that there are some conspicuous anomalies in labelling the southern flora Indo-Pacific in character and the northern one Australian. For example the common Indo-Pacific atoll trees *Guettarda speciosa* and *Thespesia populnea* are among the most widespread in the north, but are unaccountably absent in the south.

The Australian component on the northern islands extends also to the inland (but not the coastal) shrubs. In addition to *Capparis lucida* these include *Elaeodendron australe, Elaeodendron melanocarpus, Micromelum minutum,* the very common and distinctive *Myoporum acuminatum,* and *Vitex trifolia.* The inland shrub flora does also include, however, several very wide-ranging species which may have successfully established themselves after being introduced. They include *Clerodendrum inerme, Colubrina asiatica, Caesalpinia bonduc,* and *Premna corymbosa.* Distinctively Australian vines in these inland communities include species of *Cayratia* and *Hoya.*

The second striking point to note is that if the island woodland flora is of clear Australan affinity, the littoral flora has a more Indo-Pacific or cosmotropical composition: this alone suggests that the two components have very different dispersal mechanisms and histories. Widespread and common coastal shrubs include *Pemphis acidula* (strangely absent in the south), *Scaevola taccada, Suriana maritima,* and *Tournefortia argentea;* common herbs *Achyranthes aspera, Canavalia maritima, Cassytha filiformis, Cleome viscosa, Euphorbia atoto, Ipomoea macrantha, Ipomoea pes-caprae, Sesuvium portulacastrum, Tribulus cistoides, Tridax procumbens, Vigna marina,* and *Wollastonia biflora;* and common grasses *Lepturus repens, Spinifex hirsutus, Sporobolus virginicus,* and *Thuarea involuta.* The littoral trees *Casuarina equisetifolia, Cordia subcordata, Guettarda speciosa,* and *Thespesia populnea* also fall into this category. A few Australian endemics, notably *Euphorbia eremophila* and *Josephinia imperatricis,* are found in both inland and nearshore situations.

Nevertheless, in spite of this heavy Indo-Pacific strand representation, a number of expected species are rare or missing in the northern reef islands. *Hernandia sonora* was seen only as a seedling on West Hope Island; *Calophyllum inophyllum* (other than probably planted trees on Green Island and Low Isles) is also found on the reef islands only as a seedling, though common on Lizard Island (Byrnes et al. 1977); *Morinda citrifolia* is more widespread but frequently only as a seedling, as on West Hope, Low Wooded Island, and Two Isles; *Cordia subcordata* is present on Low Wooded Island only as a seedling. Drift seeds of *Barringtonia asiatica* are widespread but do not survive, and the species is unrepresented in the flora, in spite of its abundance north of Torres Straits. Many other species are represented by drift seeds along the beach crests (*Entada* and *Mucuna* are very abundant) but never germinate. The drift seeds of Low Isles and Raine Island have recently been reported by Crome (1975) and Hacker (1990).

The coconut *Cocos nucifera* presents a similar case. There are obviously planted trees on Green Island, Low Isles and Three Isles, though those on the latter (survivors of plants reported by the 1928-1929 Expedition) were felled by casual visitors in 1973. There are probably planted trees on Nymph, Turtle II, Turtle IV and Turtle V Islands. There is a single tree on Morris Island. Otherwise in the whole province we observed but sixteen recently planted juveniles on Magra, one on Saunders, one on Kay, and two germinating nuts on Sudbury Cay, an otherwise unvegetated island where the species will not survive. Walker (1990) has recorded the species on five further islands. Steers (1938, 92) also found planted coconuts at Night Island, which was not visited in 1973. The absence of natural coconuts on this coast is remarkable. Cook found two nuts covered with barnacles at the Endeavour River in 1770 (Banks 1962, II, 86, 88), Flinders (1814, II, 49) found one in Shoalwater Bay, and King (1820, I, 194) a single mature tree at Cape Cleveland in 1819. The contrast with the high islands of the Torres Straits, where Flinders (1814, II, 111) found 'abundant' coconuts at Murray Island is of obvious cultural rather than natural origin. However, during 1898-1899, Cdr Parry, H.M.S. *Dart*, surveying the inner reefs, planted a number of islands with coconuts 'for the use of navigators or for the benefit of shipwrecked mariners' (Day 1967, 290), but this seems to have had little lasting effect. It is worth noting that few of the high islands of the northern reef province possess coconuts either, though there is a small plantation on the Forbes Islands near Cape Grenville.

Two immediate questions arise from this discussion of plant biogeography on the Great Barrier Reef. First: why are the Barrier Reef islands so different from those of Indo-Pacific reefs in general? Second: why is the Australian element so obvious in the northern islands and absent in the south? Two possibilities may be suggested. First, the flora of the northern islands may be to some degree inherited from that of last low sea-level times (before 6000 years B.P.) when the entire coastal shelf was dry and presumably vegetated; such persistence from earlier and different environmental conditions has been proposed to account for the existence of distinctive elements in the flora of Laysan Atoll (Schlanger and Gillett 1976). By contrast the isolated Bunker and Capricorn reefs in the south rise from a much deeper shelf, open to the Pacific. Second, the floras may have been much modified by man. Thus in the Torres Straits region the fruits of *Manilkara kauki* were a valued food (Harris 1977, 433) and this and similar species may have been introduced, encouraged, or selectively preserved on inhabited or visited reef islands. There is certainly evidence (in the vegetation of some islands, in soil constituents, and in archaeological remains) for considerable human impact on some islands, and this will be discussed in a later section.

Two further biogeographical points may be made. The first is that ferns are almost entirely absent from the northern islands, and appear to be wholly so in the south. This is particularly remarkable given the dispersal abilities of this group. There are introduced decorative ferns at Low Isles and Green Island, but the only native ferns appear to be species of *Drynaria* on Turtle I. It is remarkable that the leather fern *Acrostichum*, which is widespread on the coast of Queensland, does not reach the reef islands, even in those with extensive mangrove communities. Second, we have found only a single species of orchid (possibly two) on the northern islands; there are none in the south. The contrast in both cases with the neighbouring islands of Melanesia is striking, and emphasises the distinctiveness of the Barrier Reef area.

Numerical relationships

The data at present available are inadequate for a rigorous numerical analysis of species distribution on the different islands, partly because of the small number of islands with

comprehensive collections, partly because of the diversity of island types which makes the direct comparison of islands on the basis of area alone a meaningless exercise (a point which has been subsequently made by Buckley).

Restricting the analysis to sand cays (i.e. excluding the more complex low wooded islands with their extensive mangroves), we have data for 18 islands ranging in size from less than 0.03 ha to 16.3 ha, approximately the same range as in Niering's (1956) analysis of the Kapingamarangi islands. There is only the weakest trend of increasing number of species with increasing area: indeed, the two largest islands are Green Island, a forested island with ca 60 native plant species in a total of 114 species, and Raine Island, a seabird island with only 13 species; this latter total is exceeded by several islands only one-tenth the size of Raine. The sand cays of low wooded islands, while differing in degree of separation from their associated shingle ridges and mangroves, range in size form 0.4 to 16 ha. These again show no obvious trend in floristic diversity with increasing size, though several are known to be seriously undercollected. They are also not strictly comparable with isolated sand cays, since the shingle and mangrove components represent an adjacent reservoir of potential colonisers, usually immediately to windward of the cay.

Finally, the ten islands of the Bunker and Capricorn Groups in the southern province provide additional data. These range ins size from 1.9 to 116.7 ha. Two of those with high species numbers have a large number of introductions. Eight of the islands, with areas varying by a factor of 52, all have between 22 and 40 species (Chaloupka and Domm 1986). There is again no simple relationship between island area and floristic diversity.

The northern and the southern Barrier Reef islands do, however, appear to show distinct differences in their physical characteristic. The southern islands are in general much larger than the northern ones (respectively: mean length 1020 and 460 m, mean width 365 and 170 m, mean area 28.0 ha and 5.8 ha, range in area 2-105 ha and 0.4-27.3 ha; numbers in sample 10 and 17). Yet the usual number of native species on the southern islands is 19-30 and on the northern, better-collected islands the total species number is at least 30 and in some cases greater than 45. The species-area relationship is thus very broadly inverse. As already indicated, this appears to result from a biogeographical control, in that many northern species are absent from the southern species pool, and a further ecologically important factor is that the rainfall in the southern islands is only one-half that in the north (mean annual rainfall at Heron Island 965 mm, and at Green Island and Low Isles 2152 and 2027 mm respectively).

Variation in species numbers in the northern islands, which is real though clearly exaggerated by the incompleteness of collections, must largely reflect ecological factors rather than simply size. These include edaphic factors, including surface phosphatisation and the relative proportion of sand and shingle; the presence or absence of ground-nesting sea-birds; and human interference. Certainly a great deal more work is required before useful conclusions can be drawn about diversity-area relationships. With present knowledge these appear to overlap the distributions previously established for reef islands in Belize, Kapingamarangi, and the Leeward Hawaiian Islands.

Vegetation types

The main characteristics of reef islands in the northern province have been described by Stoddart *et al* (1978) and by McLean and Stoddart (1978). Islands are of the following types:

(a) Unvegetated sand cays, usually oval-shaped, up to 400 m long and 120 m wide, with a mean area of 0.5 ha.

(b) Vegetated sand cays, up to 580 m long and 250 m wide, with a mean area of 5.8 ha. The upper surfaces of these cays range in height from 5 to 7.3 m, but many of the larger ones have a lower terrace at 3.5-4.5 ha.

(c) Low wooded islands, reefs with windward shingle ramparts and platforms of cemented shingle-rock, a leeward sand cay, and a reef-top mangrove swamp of variable extent. The leeward cays of low wooded islands resemble ordinary vegetated sand cays, but are often larger (mean area 12 ha), and may be partly surrounded by mangroves.

(d) Complex sand and shingle island, in which no simple distinction can be made between a sand cay and shingle ramparts.

The main types of sediment encountered by (McLean and Stoddart 1978, Scoffin and McLean 1978) are:

(a) Carbonate sands.

(b) Coral shingle and rubble ridges.

(c) Lithified coral rubble and shingle forming moderate to well cemented rock platforms at levels varying from intertidal to 2.8 m.

(d) Intertidal sediments varying from silty sands to coral rubble.

The only significant non-limestone material on the cays is pumice, either in the form of large boulders or small pebbles, which very locally may form a complete surface cover. Some islands have superficial phosphorites formed following guano deposition by seabirds.

This section provides a simple empirical classification and description of the main vegetation units of the islands, in terms both of species composition and of location with respect to the main topographic features of the islands.

1. Initial plant colonisation on sand cays

Unvegetated cays in the northern province vary from sandbores overtopped by swash at high tide, up to 0.4 ha in area (e.g. Binstead Cay, Chapman Cay, Pickersgill Cay), to larger islands such as Arlington, Sudbury and Mackay (0.5-1.4 ha) and relict islands of 0.4-2.8 ha which have undergone major cyclone damage and which may have been vegetated in the past (e.g. Ashmore, Ellis, Waterwitch). Some of these larger islands are intermittently colonised by vascular plants. Sudbury in 1929 had 'seven small seedlings, one of *Ipomoea* (?) and six of *Sesuvium portulacastrum*' (Steers 1929, 257); in 1936 there were no plants at all (Steers 1938, 67-68); and in 1973 there were three coconut seedlings and a small patch of Sesuvium. Mackay in 1929 'was well covered in its higher parts by grasses and creeping plants' (Steers, 1929, 257) by 1936, following a cyclone in 1934, the continuous vegetation cover had disappeared and had been replaced by two or three clumps of grass, a single *Ipomoea*, and a few other plants (Steers 1938, 70); in 1973 there were four coconut seedlings but no other plants. In 1936 Arlington had a vegetated area of 0.05 ha, with grasses and creepers, but was being eroded (Steers 1938, 68); in

1973 it had no plants or even drift seeds. Pickersgill, once slightly vegetated, had no plants in 1929 (Spender 1930, 265) or 1973.

The size of islands lacking any terrestrial vegetation (up to 2.8 ha in the case of Waterwitch) is surprising. On the Belize barrier reef all cays larger than 0.1 ha are vegetated, and at Kapingamarangi Atoll 50 are all islets larger than 0.01 ha. The difference presumably reflects the greater instability of Great Barrier Reef islets in an area of high tidal range and cyclonic activity.

2. Beach-crest scrub and herbaceous vegetation with trees

Beach crest vegetation on the vegetated sand cays in variable in composition and structure, partly as a function of island size. On small islands (Stapleton, Coombe, Eagle), where the cay surface lacks a woodland cover, the beach crest vegetation consists of a continous cover of herbs and grasses, extending inland, interrupted by scattered shrubs. On larger islands (Bird, Green, Farmer, East Hope) there is a more continuous zone of shrubs and low trees, with only scattered patches of herbs and grasses.

The tallest beach crest tree is *Casuarina equisetifolia*, which reaches 7-10 m on Bewick, Eagle, Ingram, Low, Low Wooded, Newton, Three, Turtle I and Two Isles. This species always occurs as scattered trees, and never forms a continuous woodland. In places, as at Green, some have been toppled by beach retreat; elsewhere height gradients suggest progressive colonisation following beach aggradation, as on the western spit of Ingram. Other occasional trees in this habitat are *Guettarda speciosa* (up to 5 m tall), *Thespesia populnea* (which reaches a height of 8 m on East Hope), and *Cordia subcordata*. Only *Cordia* forms a distinct zone of woodland, and then only on the north side of East Hope.

The most common shrubs are *Scaevola taccada*, which only occasionally exceeds 2 m in height and rarely forms a continuous zone, in contrast to many Indo-Pacific locations, and *Suriana maritima*, which is widespread but only forms a distinct vegetation unit on the south and east sides of Bird Island; except for one locality this latter species is absent from the mainland coast of Queensland. Shrubs found more rarely include *Tournefortia argentea*, *Sophora tomentosa* (up to 4 m tall on Green Island), and *Pemphis acidula*.

Common herbs include *Ipomoea pes-caprae*, especially on smaller islands such as Coombe, *Canavalia rosea*, *Euphorbia eremophila*, *Salsola kali* and *Josephinia imperatricis*. Common grasses are *Lepturus repens*, *Sporobolus virginicus*, *Thuarea involuta*, and *Spinifex hirsutus*. *Thuarea* forms a dense sward on low dunes on the east side of Ingram, but interspersed with shrubs. On Raine, however, there is an extensive zone 20-50 m wide round the entire perimeter of the island of *Lepturus* grassland on a sand substrate, and while this species is one for the most common plants of the northern islands its occurrence as a monospecific vegetation unit is here unique, though common in drier parts of the Pacific, e.g. in the Phoenix Islands.

3. Scrub and succulent sward of rock platforms

Most low wooded islands are fringed on their windward sides by lithified rubble and shingle platforms which differ in height and degree of dissection. The lower platform stands at 1.6-2.4 m, and the upper at 2.6-3.8 m above LLWS datum. Three types of vegetation are associated with these platforms:

(a) Low extensive monospecific scrub, usually 1-1.5 m tall, of *Aegialitis annulata* or *Avicennia marina*, at an elevation of 1.0-2.0 m; this scrub is almost completely submerged at HWS, and has a very even crestline and sharp boundaries.

(b) Succulent mats on the rock surface, consisting of *Suaeda australis*, *Salicornia quinqueflora*, *Arthrocnemum* (2 species), and *Sesuvium portulacastrum*. These mats are best developed on the horizontal surface of the upper platform, especially in areas frequently wetted by spray. Succulent mats are found on virtually all islands with platforms.

(c) Outposts on the inner upper platforms of the vegetation of shingle ridges, notably *Pemphis acidula* and *Sporobolus virginicus*. *Pemphis* is so extensive that it is treated separately (type 5).

4. Scrub and herbaceous cover of windward shingle ramparts

Ramparts of shingle, often in multiple ridges, are frequently lodged on the inner edges of conglomerate platforms. Much of the shingle is old and weathered, and its surface consists of bare, blackened and eroded coral fragments. In addition to *Pemphis*, the vegetation is dominated by *Suriana maritima*, *Myoporum acuminatum*, and *Capparis spinosa*, with scattered patches of *Boerhavia repens*, *Tribulus cistoides*, *Lepturus repens*, *Sesuvium portulacastrum*, *Achyranthes aspera*, and *Ipomoea pes-caprae*. The substantial stems of the vine *Cayrathia* stretch across the surface. In places there are low patches of *Abutilon*.

On inner older ridges the vegetation becomes more continuous and dense. On Green Ant Island, Low Isles, for example, *Caesalpinia* reaches 8 m in height, *Micromelum minutum* 3 m, *Vitex*, 2.5 m, *Glycosmis* 3 m, and *Clerodendrum* 2-3 m. Such vegetation either ends abruptly as the single surface passes under mangrove swamp, or its merges into inland scrub and scrub woodland (types 8 and 9).

5. *Pemphis* scrub and scrub-woodland

Pemphis acidula is one of the most common species on the northern islands, especially in exposed situations on rocky and thin shingle substrates; its absence from the southern Barrier Reef islands has already been noted. It occurs in three distinct situations:

(a) On the seaward shores of sand cays, for example on Bewick, Bird, Chapman and Sherrard. It is relatively uncommon on such sandy substrates, even where underlain by beachrock, but may form a zone up to 5 m wide, as on the north and northeast sides of Bird and the south shore of Three, and may reach heights of 4-6 m.

(b) On the inner margin of upper conglomerate platforms on the windward sides of low wooded islands, either on rock or on thin shingle ridges. It is extremely common in this habitat, where it is usually 3-5 m tall (exceptionally 6 m at East Pethebridge and 8 m at Fisher). At Low Wooded a *Pemphis* zone extends with few interruptions for about 1500 m along the south side of the island, and at Turtle V the zone is up to 50 m wide. In profile the shrubs are often wind-sheared, and in plan may show distinct windrows, giving the outer edge a crenulate margin. Such windrows have fairly constant bearing: 302° at Coquet, 300-320° at East Pethebridge, 298° at West Pethebridge, 305° at Sinclair-Morris, 320° at Turtle II. Generally *Pemphis* forms a shrub, but on some islands it occurs as a substantial tree with clear trunks up to

1 m in diameter; these were seen at Houghton, East Pethebridge, West Pethebridge and Turtle I. It might be noted that the references to *Suriana maritima* in similar habitats by Steers (1937, 1938), in accounts of King, Hay and Turtle I, probably all refer to *Pemphis*.

(c) At the junction between sand cay and mangrove swamps, on low wooded islands where the two units are in contact. Here *Pemphis* forms laterally extensive but narrow and often rather open zone, occasionally intermixed with *Osbornia octodonta*, as on Bewick, Coquet, Howick, Houghton and Turtle IV.

6. Mixed scrub and herbaceous vegetation of sand cays

An open mosaic of low shrubs, herbs, vines and grasses is widely distributed on sandy substrates in the interiors of smaller (and lower) sand cays, including the discrete sand cays of some low wooded islands. Typical of such islands are Beesley, Coombe, Eagle, Fife, Ingram, Magra, Morris, Pelican, Saunders, Sinclair, Stainer and Stapleton; all are presumably younger cays than the more densely vegetated and higher islands of other low wooded islands and the mixed sand an shingle cays.

Usually there are no single dominants. Some ten shrub species are represented, of which the most common are *Clerodendrum inerme* (1-3 m tall), *Capparis lucida* (reaching a height of 4 m at Coombe), *Colubrina asiatica* (1-3 m tall), *Premna serratifolia* (2-5 m tall), and *Scaevola taccada, Tournefortia argentea* is moderately widespread as a shrub, but on Coombe and Saunders it occurs as a tree up to 6 m tall.

The ground cover between these taller shrubs is very varied and often of low density. It includes the herbs *Boerhavia repens, Tribulus cistoides, Euphorbia eremophila, Euphorbia chamissonis, Wollastonia biflora, Sesuvium portulacastrum, Cleome viscosa, Canavalia rosea, Triumfetta procumbens, Achyranthes aspera, Portulaca australis, Stachytarpheta jamaicensis;* the vines *Ipomoea macrantha, Ipomoea pes-caprae, Cassytha filifomis, Cayratia* species, *Vigna marina, Abrus precatorius,* and *Hoya;* and the grasses *Sporobolus virginicus* and *Lepturus repens*.

Each of the smaller cays may have ten species or fewer in total; islands such as Sinclair, Pelican, Stainer and Lowrie are good examples of islands with 1-3 species of shrub and 3-7 species of other plants.

7. Herbaceous communities on seabird islands

These represent a modification of type 6 on Coombe, Michaelmas, Raine, Stapleton, and parts of Stainer, Morris and Magra. Shrubs are uncommon, and if present may be leafless and dead; usually only a few specimens of *Cordia, Colubrina* and *Capparis* are present. The tallest plants may be spindly *Abutilon asiaticum,* with a ground cover of *Achyranthes aspera, Lepturus repens,* and *Boerhavia repens*. Similar patches of *Abutilon* and *Boerhavia* on shingle ridges of otherwise more densely vegetated islands usually suggest a local concentration of ground-nesting seabirds. On the main bird islands the vegetation cover is very patchy, with large bare areas.

8. Scrub woodland of sandy cays

This type is similar to type 6, but with a number of taller trees. These include some littoral species, such as *Casuarina equisetifolia* (reaching 15 m in height at Green), *Cordia subcordata*, and *Thespesia populnea* (3 m tall at Bewick), but also *Terminalia muelleri* (up to 10 m tall) and *Terminalia arenicola* (up to 4 m tall). Common shrubs are *Capparis lucida, Colubrina asiatica, Clerodendrum inerme, Micromelum minutum, Myoporum acuminatum, Caesalpinia bonduc*, and *Pemphis acidula*. The ground cover is rather less diverse, with *Lepturus repens, Achyranthes aspera* and *Euphorbia atoto*.

9. Woodland of sand and sand-shingle islands

A number of larger islands are covered with dense, largely close-canopied woodland, which is undoubtedly less well-known than it ought to be. Of the 40 tree species recorded from the islands, up to 10-12 species are recorded in woodland from East Hope, Howick, Ingram, Low, Three, The Turtles, and Two Isles.

Common trees are *Diospyros maritima*, usually 5-6 tall but reaching 15 m at East Hope, *Aglaia eleagnoidea* (4-5 m tall), *Pouteria obovata* (5-10 m), *Terminalia arenicola* (3-12 m) *Terminalia muelleri* (3-10 m), *Mimusops elengi* (4-8 m), and *Manilkara kauki*. There is dense *Manilkara* woodland at Two Isles, where MacGillivray (1852, I, 107) described trees of this species 20 m tall and 1 m in diameter. Most trees now seem to be only 8 m tall; the tallest noted on the northern islands were on Low Wooded (10 m) and Turtle I (15 m). Other trees 3-8 m tall found in similar closed woodland include *Guettarda speciosa, Ficus opposita, Ficus obliqua, Ficus drupacea, Malaisia scandens, Exocarpos latifolia, Eugenia carissoides, Diospyros ferrea, Macaranga tanarius, Cordia subcordata*, and *Ganophyllum falcatum*. One of the of tallest trees on the islands is *Erythrina insularis*, reaching 10-15 m in height and often an emergent, but it is apparently confined to Bird and Farmer Islands, on both of which it was first recorded by MacGillivray (1852). In addition Cunningham recorded 'a strong luxuriant tree, having a stem six feet in diameter, whose base is much like the spurred bulb of a tropical fig' at Cairncross (King 1827, I,383-384), to which he gave the name *Gueltarda octandra*. This may be *Guettarda*; we did not visit Cairncross in 1973, nor see any tree as large as this on the northern islands.

The paucity of *Pisonia* woodland has already been mentioned, and has recently been examined by Walker (1991a). There is forest on Bird Island, and occasional trees on West Hope (respectively at 11°46'S and 15°45'S). Interior phosphate rock is associated with the *Pisonia* forest on Bird, and the occurrence of similar rock on Green Island suggests the former existence of *Pisonia* there too. There is *Pisonia* woodland with phosphate rock on the tiny island of Bushy Cay on Redbill Reef, at 21°S, but the most extensive *Pisonia* is in the Bunker and Capricorn Islands, south of 23°S. There it forms a tall forest on Heron and Northwest Islands, isolated groves on Hoskyn, and occurs occasionally on Wilson (Cribb 1965, 1969, 1972; Fosberg 1961); it is also recorded from Masthead, Tyron, One Tree, Fairfax, Lady Musgrave and Wreck Islands (Macgillivray and Rodway 1931). Why *Pisonia* is so rare in the north is unknown. Similarly *Pandanus tectorius* is rare in the north and nowhere forms a vegetation unit. In the south there are extensive *Pandanus* groves with deep litter on Wilson, One Tree and Hoskyn Islands (Cribb 1965, 1972).

In addition to the tree species, the islands with tall woodland have a number of characteristic shrubs, mostly 3-5 m tall. They include *Premna serratifolia, Myoporum acuminatum, Elaeodendron australe, Glycosmis pentaphylla, Phyllanthus reticulatus*, and

Micromelum minutum. These are well seen at such islands as Howick, Turtle I, Low Wooded and Ingram.

Because of the canopy density, herbs and grasses are few; where they occur they are the same as those represented in type 8.

10. Mangroves

The mangrove vegetation of the northern islands has been discussed in a separate paper (Stoddart 1979) and will only be briefly outlined here. Mapping of 21 low wooded islands with mangroves yielded a mean mangrove area of 19.7 ha, but with extremes ranging from 0.3 to 125.4 ha; 12 of the reefs have less than 12 ha of mangroves. As a percentage of the reef top the mean mangrove cover is 18.2%, the range 1.1-67.7%, and the modal class (classes of 10%) is 0-10%. Elevations in the following account refer to the datum of LLWS; the height of MHWN is 1.6 m and MHWS 2.3 m. The following main types of mangrove vegetation may be recognised:

(a) *Aegialitis annulata* scrub, 1-2 m tall, on higher reef flat and lower conglomerate platform surfaces on the windward sides of low wooded islands. It is very common from Chapman in the north to Low Isles in the south; it has not been recorded on the reef south of Low Isles. Though usually a low shrub, this species forms trees up to 5 m tall in clearings in mature mangrove woodland, e.g. at Nymph and Turtle I. The windward scrub forms mainly in the height interval 1.3-1.6 m LLWS.

(b) *Avicennia marina* scrub, 1.5 m (exceptionally 3 m) tall, occurring in similar situations to *Aegialitis* scrub on low wooded islands. On platforms it occurs up to 1.6 m above datum.

(c) *Avicennia* woodland in the lee of platforms and shingle ramparts. This reaches heights of 8 m at Chapman and Sherrard and 10 m at Fisher, but it never forms a very extensive unit.

(d) *Ceriops* thicket, consisting of dense slender trees of *Ceriops tagal* at higher levels (up to 2.5 m), often immediately in the lee of platforms or close to the mangrove shore of low-wooded-island sand cays. Exceptionally this species is found in ponded situations between 3.5 and 4.4 m above datum; at Low Wooded Island it reaches 3.0 m. The trees frequently reach a height of 5 m (e.g. at Lowrie, West Pethebridge, and Turtle I), but at East Pethebridge they reach 8 m and at Low Wooded 10 m. In other places they may only reach 2-4.5 m.

(e) *Rhizophora mucronata* var. *stylosa* woodland. This is the dominant mangrove community of the reef tops, and exceptionally forms a closed canopy forest 20 m tall, with stilt roots reaching 3 m above the surface. Tall *Rhizophora* woodland (8-15 m) is found at Chapman, Fisher, Low, Low Wooded, East Pethebridge, West Pethebridge and Sherrard. The edge of the mangrove, where it extends only part of the way across the reef top, is either a wall of tall trees, as at Three Isles, or an extensive field of seedlings up to 2 m tall, as at West Hope. There may be occasional trees of *Sonneratia alba* along the margin, e.g. at Chapman; this species has not been recorded on the Reef south of Three Isles.

(f) *Osbornia* thicket. A woodland of closely-set trees of *Osbornia octodonta* is characteristic of high-standing substrates at the junction of mangrove swamp and shingle ridge on the windward sides of low wooded islands. Because of its exposed situation, the trees are often wind-sheared, and frequently movement of the shingle ridges during storms has left tall trees of *Osbornia* standing on the reef flat outside the ridges. In dense *Osbornia* woodland many

of the trunks and branches are almost horizontal towards the edge of the unit, presumably in response to light. The woodland reaches heights of 8-9 m at Low, Low Wooded and West Pethebridge, but also forms a low scrub 2-4 m tall at Chapman, Bewick, and Sinclair-Morris.

(g) Mangroves at higher levels. Perhaps the most extensive of these is *Bruguiera* woodland, though not enough is known of its local extent to define and map a vegetation unit. It is well developed at Bewick, Watson, Newton and Howick, and is usually 5-8 m tall. More work is needed to define the occurrences of the three different species (*B. cyclindrica, B. exaristata, B. gymnorrhiza*) which are present. *Excoecaria agallocha* is common round cay and shingle ridge margins, usually as scattered trees 3-6 m tall. *Xylocarpus australasicus* and *X. granatum* also occur in similar situations, and even on dry land, again as tall individual trees; this genus has not so far been recorded south of the Howick Group.

11. Sea-grass meadows

Extensive meadows of sea-grasses on reef tops not occupied by mangroves are dominated by *Thalassia hemprichii.* They have been described at Low Isles by Den Hartog (1970), who notes that this species, though widespread on the reefs, is apparently absent from the mainland coast. Species of other genera (*Halophila, Halodule, Zostera, Enhalus*) are also present but less conspicuous; *Halodule* often forms a narrow zone of turf at the foot of beaches on fine sand in sheltered water.

12. Man-modified vegetation

It is at present impossible to estimate the degree of human modification of the vegetation of the northern islands, though there is little doubt that many were regularly visited or occupied by aborigines over a long period, some have since been occupied by Europeans, and the often abrupt contrasts between the vegetation units of adjacent and similar islands suggests some degree of disturbance. Several types of modification may be suggested:

(a) Anthropogenic grasslands. Several cays are covered with a probably man-induced grassland in place of the expected scrub or scrub woodland. This is most apparent at Three Isles, where they cay is largely covered with *Panicum maximum* 1.5 m tall. Much of Bewick Cay is covered with grasses, including *Heteropogon triticeus* up to 1.7 m tall. *Imperata cylindrica* on Morris reaches 1 m and so does *Heteropogon contortus* on Howick.

(b) *Agave* thicket. *Agave rigida* var. *sisalana* covers about half the vegetated area (i.e. about 2.3 ha) on Morris Island. It was not seen by MacGillivray (1852) in 1846, but W. Macgilivray (1910, 220) found 'a clump of sisal hemp' in October 1910. It is probably now impossible to eradicate, and will doubtless extend to cover the island. Fortunately it has not been introduced elsewhere.

(c) Modification by Europeans on cays now inhabited (Low, Green) or inhabited in the past (Pipon): the removal of natural woodland and scrub, the introduction of exotic trees and decorative plants, and the arrival of weeds.

(d) Possible modification of woodland by aborigines, especially through the selective encouragement of useful trees.

Ecological factors

It would be premature to attempt any full explanation of the vegetation patterns here reported, but it might be useful to draw attention to certain factors which may have influenced their development.

Age

As a result of the 1973 Expedition a great deal is known of the age of topographic features on the reef tops in the northern province. The sediments of older, higher parts of sand cays cluster in the range 2900-3400 years B.P., and it appears that the main outlines of the larger islands were formed before 3000 years B.P. It is these areas which support the closed-canopy woodland. The lower terrace which in places surrounds these higher central core-islands is composed of sediments averaging about 2700 years in age, but the feature itself may have formed much more recently than this. The age difference between the two levels on the bigger cays, and between the larger islands and the smaller ones, certainly supplies a major reason for the difference in vegetation between them (for details, see McLean and Stoddart 1978). As previously mentioned, it is, moreover, possible that some part of the flora of the larger forested islands is relict from last glacial times (ca 8000 years B.P.) when the northern coastal shelf was dry land and when the present reefs were limestone hills upon it.

It has also been found that the more extensive mangrove forests of the low wooded islands overlie fossil reefs, the oldest of which date from the time when sea-level reached approximately its present level after the last main transgression. The oldest microatolls in such reef-top reefs date from 6310 years B.P.; others extend to 2370 years B.P., and some are still forming as reef tops grow up to present sea-level. It is also likely that mangroves owe their initial location on reef tops to the sheltering effect of windward shingle ramparts, and the ages of the upper conglomerate platform (a cemented rampart) on the low wooded islands range from 4420 to 3050 years and cluster between 3300 and 3600 years B.P. It has been suggested that mangroves are more extensive where such reef-top reefs formed earliest, and that the formation of a field of microatolls on the reef top triggers the rapid expansion of mangrove vegetation (Stoddart 1979). Hence differences in initial reef geometry could control the great differences found in the extent of mangroves between adjacent reefs, because of the different amounts of limestone deposition needed to bring the reef to present sea-level.

Rainfall

It has already been mentioned that the mean annual rainfall at Green Island (2152 mm) and Low Isles (2027 mm) is substantially greater than that at Heron Island in the south (965 mm). There are no other island records available between Low Isles and Thursday Island (1739 mm). Nevertheless, some of the islands north of Princess Charlotte Bay had a distinctly arid aspect (admittedly during the 1973 dry season), and the rainfall at Raine Island could well be as low as 1000 mm. Rainfall variation within the northern province could thus be an important ecological control.

Cyclones

Cyclones have occurred roughly 6-12 times per decade during the present century in the northern province. They have major topographical effects, especially in altering the location and size of shingle ramparts, and thus incidentally through movement of the substrate leading to destruction of vegetation. They also have direct effects on the vegetation itself, mainly through wind action. This is most marked in mangrove woodland. Steers (1938) noted extensive devastation of mangroves on Houghton, Wilkie and Night Islands, and the same was seen in 1973 on Newton and Houghton. The effects of this periodic destruction on pattern and succession in the mangrove woodlands has yet to be investigated. Wind damage during cyclones is undoubtedly also responsible for the feeling of some taller trees, such as *Casuarina* at Three Isles.

Seabirds

A number of the reef islands are important seabird nesting sights (Serventy *et al* 1971, Lavery and Grimes 1971, Kikkawa 1976). The birds have both mechanical and chemical effects on soil and vegetation, and we have noted the characteristic vegetation of seabird islands (type 7). Three groups of seabirds are important modifiers of vegetation:

(a) Boobies. The Brown Booby *Sula leucogaster* nests at Waterwitch, Ashmore, Pandora (all unvegetated), and Raine (in unvegetated areas). The Masked Booby *Sula dactylatra* nests on Pandora (unvegetated) and on unvegetated parts of Raine. These heavy birds would undoubtedly locally suppress vegetation in any nesting area; and they may have been more widespread in the past.

(b) Terns and Noddies. The Sooty Tern *Sterna fuscata* nests in extremely large numbers on Michaelmas and Stapleton, as well as on Raine, Pandora, Low, Upolu and Saunders. The Noddy *Anous stolidus* nests mainly on Michaelmas but also on Raine, Howick and Upolu. The nesting areas have a vegetation of grasses (*Lepturus repens*) and herbs (notably *Boerhavia repens*), and other plants, especially shrubs, are probably suppressed. Walker (1991a) has discussed the role of the Black Noddy *Anous minutus*, the Bridled Tern *Sterna anaethetus*, and the Wedge-tailed Shearwater *Puffinus pacificus*, in the dispersal of *Pisonia grandis*.

(c) The Pelican *Pelecanus conspicillatus*. This breeds and is still numerous on Coombe, Pelican and Sinclair. Its effects are much more local than those of the other seabirds, but nevertheless identifiable.

Not a great deal of work has been done on the effects on vegetation of tropical seabirds on reef islands, but reference may be made to Gillham's observations (1977a, 1977b) on Aldabra and Cosmoledo Atolls.

Landbirds

The Torres Strait Pigeon *Ducula spilorrhoa* is likely to be of particular significance in the dispersal of plants with fleshy fruits, and it could be particularly important in explaining the distribution of some of the distinctively Australian trees of the larger cays. It is seasonally abundant at Cairncross, Howick, Hope, East Pethebridge, and Low (where it has recently been studied by Crome 1975), and probably at many other islands. It would be interesting to compare

its food preferences with the plant species present on the cays: Crome (1975) has provided a list of propagules at Low Isles not present as viable plants in the present flora.

Turtles

Sea turtles, notably the Green Turtle *Chelonia mydas*, are probably relatively uncommon on most northern islands at the present day. The major exception is Raine Island, which is probably the largest Green Turtle rookery in the world, with a population of 11,000 in 1974. The turtles nest in *Lepturus* grassland, which undergoes constant mechanical disturbance in consequence. It is likely that turtle rookeries were much more extensive in the past.

Man

The presumed effects of both aboriginal and European man on island vegetation has been mentioned several times. Beaton (1978) has summarised archaeological evidence of the occupation of the northern islands, especially for the reef islands Howick, Pipon, Ingram, Bewick, Nymph and the Turtles.

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