

Floristic patterns in coastal rainforest of Shoalwater Bay, Central Queensland

Peter McCarthy¹, Peter Clarke² and Jeremy Bruhl³

¹13 Knox St., Clovelly NSW 2031; ²Botany, School of Environmental Sciences and Natural Resources Management, University of New England, Armidale, NSW 2351, AUSTRALIA; ³Botanic Gardens and Domain Trust, Mrs Macquaries Rd, Sydney NSW 2000, AUSTRALIA.

Abstract: A study was undertaken of the floristic patterns in coastal rainforest (low closed forest) of Shoalwater Bay, central Queensland. The site encompasses 60 km of coastline, extending from latitude 22° 08' 30" to 22° 30' 0" and longitude 150° 02' 00" to 150° 24' 30". The rainforest grows on coastal Holocene sand dunes, swales and sand flats, distributed as a series of 27 discrete patches greater than one hectare along 60 kilometres of coastline. Mean patch size was 10.7 hectares (maximum 150 hectares). The flora was predominantly woody, and lacked the complex growth forms of Webb (1968). Floristic links with central and north Queensland were strong, with some species distributions extending into Malesia and the Pacific. Three physical strata, emergent (composed of trees), canopy (composed of trees, vines and epiphytes) and sub-canopy (trees, vines and herbs) were recognised. The herb layer was very poorly developed. Eighty-one species were recorded, representing 42 families and 72 genera.

Sixty three quadrats were sampled across the rainforest patches to measure abundance of all vascular taxa using frequency score. Five floristic groups were defined from agglomerative classification analysis, one representing mixed forest, two representing low microphyll vine forest (LMVF) and two representing microphyll vine thicket (MVT). The vegetation at the study site was predominantly MVT. Five species groups were defined, one correlated with the mixed forest, one with the LMVF and one with the MVT. The remaining species groups represented ubiquitous and widespread species. Floristic patterns were found to be strongly influenced by three environmental variables using canonical correspondence analysis. The strongest variable was drainage, which separated the mixed forest from the vine forest/thicket. The LMVF/MVT vegetation forms a continuum along an environmental gradient, influenced by exposure to onshore-winds and landform height. The mesic/protected extreme was represented by the tallest LMVF situated in swales, whilst at the exposure/elevation extreme was represented by wind-sheared MVT located on foredunes.

Cunninghamia (2004) 8(3): 362–370

Introduction

Rainforest established on coastal sands are located along the tropical and sub-tropical coast of Australia, extending as a discontinuous belt from north-western Western Australia to southern New South Wales (Adam 1992). In common with rainforest established on other substrates, the physical and floristic characters of coastal rainforest on sand may vary considerably from 'core' rainforest areas, due to climatic variations of the Australian littoral zone. Rainforest ecology studies have found that these communities experience extreme environmental variables (Baur 1962; Floyd 1990a; Tracey 1982).

Along the Queensland coast, these rainforest communities are often described as beach scrubs (Batianoff and McDonald 1980; Young and McDonald 1987). They are often floristically depauperate, and much reduced in stature. Their ecology is poorly known when compared with the more aesthetically pleasing rainforests in high rainfall areas (Gillison 1987).

The presence of coastal rainforest on sands of Holocene origin has been widely noted (Russell-Smith & Dunlop 1987, Byrnes et al. 1977, Batianoff & McDonald 1980, Floyd 1990a, Hopkins et al. 1979). The flora is composed of species that are widely distributed and highly vagile, having successfully colonised these Holocene landforms (Russell-Smith & Dunlop

1987). The topographical protection from fire is an important aspect of coastal rainforest persistence, as coastal rainforest communities are generally destroyed by fire. The expansion of rainforest communities in the absence of fire has been noted by several authors (Dunlop et al. 1975, Dunlop 1976, Tracey 1982, Bowman 1990).

The effects of wind shear from exposure to on-shore winds and periodic storms of a highly destructive nature contribute to the low, wind-sheared forms of coastal rainforest, exacerbated by frontal dune topology. Open forest structures are attributed to meteorological disturbances (Tracey 1982, Floyd 1990a). Soil water status and the access to aquifers and water tables appears to favour the development of coastal rainforest in many locations. Where seasonal access to sub-surface moisture occurs, the deciduous component predominates (Russell-Smith & Dunlop 1987, QDEH 1994, Specht et al. 1977). Bowman (2000) however, questions the requirement of aquifers to support many types of dry rainforest. In coastal situations, impeded drainage favours the establishment of palm forests intermixed with rainforest. Where surface water persists for longer periods, replacement by *Melaleuca* communities is reported (Tracey 1982).

The *de novo* establishment of rainforest and the re-establishment of degraded coastal rainforest under current climatic conditions appears to be limited. More favourable

climatic conditions are thought to have occurred during the Holocene, which has been attributed to the original establishment of coastal sands rainforest (Floyd 1990a). Where displacement has occurred, eucalypt woodlands and grasslands become established (Dunlop 1976, Tracey 1982).

The purpose of this study was to investigate the local scale floristic patterns of coastal rainforest along the poorly known Shoalwater Bay section of the Queensland coastline. The coastal rainforests of Shoalwater Bay are relatively undisturbed, unlike many coastal areas of Queensland where urban development has destroyed or modified significant areas. The study seeks to answer two basic questions: (1) are there local-scale patterns of species distribution and abundance? (2) Do these patterns relate to environmental variables?

Study area

The study area was located on the western shore of Shoalwater Bay, 180 km north of Rockhampton (Fig. 1). It encompasses 60 km of coastline from Parker Creek in the north ($22^{\circ} 08' 30''$) to Raspberry Creek in the south ($22^{\circ} 30' 0''$). The Holocene sand deposits of the coastline are broadly classified as calcareous sands (BPA 1979), often with a capping of siliceous sands from aeolian deposition (Hopkins et al. 1979). Sand landforms along Shoalwater Bay are frontal dunes and parallel beach ridges. Parallel beach ridges have degraded into flat sand deposits, with one or two dunes or swales evident.

The Shoalwater Bay coastline was classified by Dick (1975) as warm and moist with a summer rainfall maximum. The key features of the study area's rainfall are the distinct seasonality and the high variability on a year-to-year basis. The average rainfall is 894 mm, with 63% recorded in the months December to March, calculated from a

discontinuous series of recordings at Couti Outi (1964–1975), Stanage Bay (1915–1919), Langham (1986–1998) and Hollins Bay (1972–1974). The mean annual maximum temperature for the nearest recording station of St. Lawrence is 28.3°C , and the mean annual minimum is 17.2°C .

The central Queensland coast is frost free and the temperature range is conducive to growth 12 months of the year. However, summer heat waves and high evaporation, particularly in the winter and spring period can limit plant growth (BPA 1979). Wind strength is consistently moderate to fresh with velocities exceeding 20 kph for about 30% of the time, with almost no calm days (BPA 1979). Cyclones pass within 150 km of the St. Lawrence recording station on average every 2.6 years. Associated with these disturbances are wind speeds up to 160 kph, and storm tides of up to 1.2 m (ABARE et al. 1993, BPA 1979, BPA 1982).

Materials and methods

The study area rainforest was mapped at a 1:10 000 scale by aerial photograph interpretation. The aerial photographs were a colour series taken by the Department of Defence on September 1975 at a scale of 1:30 000, and a 1987 black and white series at a scale of 1:26 000 from Sunmap. Ground traverses were carried out along the entire length of the coastline to confirm the aerial interpretations.

A floristic survey was carried out using a frequency score method (Outhred 1984, Morrison et al. 1995). This method employed seven sub-quadrats of size 5, 10, 20, 40, 80, 160 and 320 m^2 . Species presence/absence was recorded for each sub-quadrat, producing an abundance score from 0 to 7. Seven combinations of morphology, drainage and vegetation type were sampled, replicated three times, giving 21 patches. Triplicate quadrats were randomly located in the selected patch. A total of 63 quadrats were sampled. All species occurring in less than three quadrats were discarded from multivariate analysis. Plant identifications were verified where necessary by checking specimens at the Queensland Herbarium, and nomenclature follows Forster et al. (1991), updated with reference to Harden (1990–93) where possible.

All data were stored using Microsoft Excel (Microsoft 1994) on a personal computer. Numerical classification was carried out using PATN (Belbin 1993). An association matrix for classification of quadrats was generated using the symmetric form of the Kulczynski co-efficient (PATN module ASO). Agglomerative hierarchical fusion was carried out using flexible UPGMA, with $\beta = -0.1$ (PATN module FUSE). Dendrograms were produced from the fusion results (PATN module DEND). For ordination analysis, CANOCO was employed (ter Braak 1988). The canonical correspondence analysis option in CANOCO was chosen, with the underlying assumption that species distribution are unimodal. Environmental factors were recorded for each quadrat. Variables were distance from high water mark (h.w.m); continuous, elevation above h.w.m; continuous, latitude; continuous, vegetation type; binary, landform; 3 states, exposure; 4 states and drainage; binary.

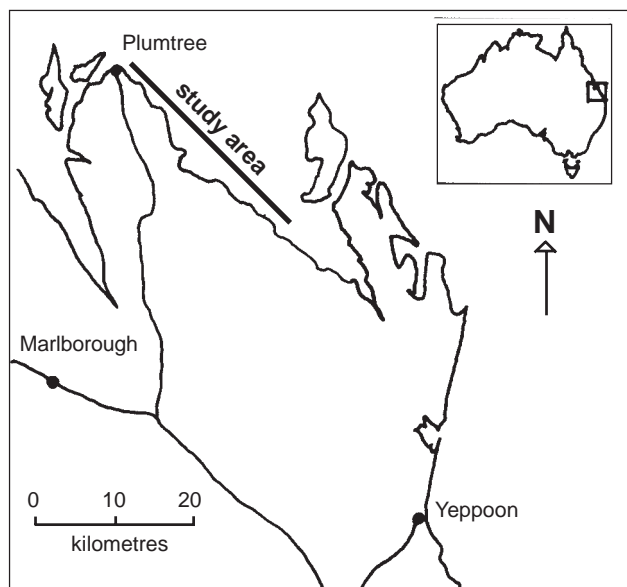


Fig. 1. Location of study site on the western shore of Shoalwater

Results

The coastal rainforest of Shoalwater Bay was distributed as a series of 27 discrete patches greater than one hectare extent, along the 60 km of coastline surveyed. The patch mean patch size was 10.7 ha, with the largest patch encompassing 150 ha.

Three geomorphological formations supporting rainforest were distinguished: 1. foredunes, with a windward and leeward aspect, encompassed 9.2% and 10.7% respectively of the rainforest area, 2. flat sand masses, with free draining and poorly draining forms, accounted for 70.4% and 7.0% respectively of the area, and 3. swales, which accounted for 2.8% of the area.

Three rainforest vegetation types were distinguished in the aerial photographs and ground traverses. Rainforest was present as; 1. patchy rainforest without sclerophyll emergents interspersed with areas of bare sand, 2. dense rainforest without sclerophyll emergents or 3. rainforest with sclerophyll emergents. The occurrence of each rainforest vegetation type across the geomorphological formations is shown in Table 1, along with the quadrat codes employed in the classification analysis.

In total, 81 native vascular rainforest plant taxa were recorded at the study site, from 72 genera and 42 families (Appendix 1). The most common species were the canopy vine *Jasminum simplicifolium*, and the canopy trees *Exocarpos latifolius*, *Pouteria sericea*, *Drypetes deplanchei* and *Diospyros geminata*. The most common families were Rubiaceae, Rutaceae, Sapindaceae, Asclepiadaceae, Oleaceae and Apocynaceae.

The vegetation was predominantly woody, with three physical strata delineated. The emergent layer was composed of trees, the canopy layer was composed of trees, vines and epiphytes, and the sub-canopy layer was composed of trees and vines. The herb layer was poorly developed, with occasional occurrences of *Ancistrachne uncinulata* and *Cyperus eglobosus*.

The classification of quadrat data showed a strong spatial pattern of floristic composition within the study site (Fig. 2). At the two group level, the 9 quadrats placed in the rainforest vegetation with sclerophyll emergents are clearly separated from the remaining 54 quadrats (quadrat group 1). At the three group level, 15 quadrats located in swales and leeward aspect of frontal dunes, supporting dense rainforest vegetation without sclerophyll emergents, are separated from the 39 remaining quadrats. These 14 quadrats are further divided at the 5 group level into a group with all 9 swale quadrats of the study (quadrat group 2) and the 6 leeward frontal dunes sites (quadrat group 3).

The remaining 39 quadrats are separated at the five group level, forming 21 quadrats in quadrat group 4, consisting of leeward and windward foredune and flat geomorphologies, and supporting a mix of dense and patchy rainforest without sclerophyll emergents. Quadrat group 5 containing the remaining 18 quadrats supported patchy rainforest without

Table 1. Areal extent of the three rainforest vegetation types classified by geomorphology and drainage. Quadrat code follows the percentage area for each combination: p-patchy or type 1, d-dense or type 2, s-sclerophyll emergents or type 3 vegetation; f-windward foredune, h-leeward foredune, s-swale, t-flat geomorphology; f-free draining, i-impeded drainage.

Geomorph.	Drainage	Community (%)			Total (%)
		(1)	(2)	(3)	
Windward foredune	free	9.2% (pff)	absent	absent	9.2%
Leeward foredune	free	4.4% (phf)	6.3% (dhf)	absent	10.7%
Swale	free	absent	2.8% (dsf)	absent	2.8%
Flat	free	9.0% (ptf)	61.4% (dtf)	absent	70.4%
Flat	impeded	absent	absent	7.0% (sti)	7.0%
Total		22.6%	70.4%	7.0%	100%

sclerophyll emergents, located on leeward and windward foredune and flat geomorphologies.

The two-way table analysis (Fig. 3) highlights three species group/quadrat group relationships. Species group 1, with 6 species, is associated with the quadrats of group 1. This species group contains the sclerophyll emergents *Corymbia tessellaris* and *Melaleuca leucadendra*, and the palm *Livistona decipiens*. Along with the herb *Cyperus eglobosus*, these four species were restricted to quadrat group one. They impart a distinctive physical structure to this quadrat group, with *Cyperus eglobosus* forming a prominent herb layer in several quadrats. Species group 2 contains 14 species, and is associated with quadrat group 2. *Terminalia porphyrocarpa* and *Turraea pubescens* are confined to this quadrat group, and along with *Bridelia leichhardtii* and *Olea paniculata* form a distinctive floristic component. Species group 3, with 12 species, is correlated with quadrat groups 4 and 5. *Notelea microcarpa*, *Pleurostyliya opposita*, *Hoya australis*, *Cassytha pubescens*, *Amyema congener* and *Parsonsia plaesiophylla* are restricted to these quadrat groups. Vines are far more prominent in both the floristic and physical constitution of the vegetation of these quadrat groups. Species group 4 contains 17 species found in almost every quadrat, and can be considered the ubiquitous coastal sand rainforest species. The species with the highest frequency scores of the study, namely *Diospyros geminata*, *Drypetes deplanchei*, *Pouteria sericea*, *Exocarpos latifolius* and *Jasminum simplicifolium*, are members of this species group. Species group 5 comprises 16 species that are widespread but occur less frequently than group 4 members. Representatives are *Rapanea* spp., *Mimusops elengi* and *Pleiogynium timorense*.

Ordination results are shown in Figure 4 for species and Figure 5 for quadrats. The quadrat ordination diagram shows quadrat group 1 as a distinct cluster along positive values of the x-axis, with the remaining quadrats forming a series along the y-axis. Quadrat group 1 is correlated with the impeded drainage vector, and orthogonally with the flat morphology and dense vegetation vectors. The separation between quadrat group 1 and the remaining quadrat groups corroborates the clear demarcation of these communities shown in the classification results. The remaining series of quadrats are

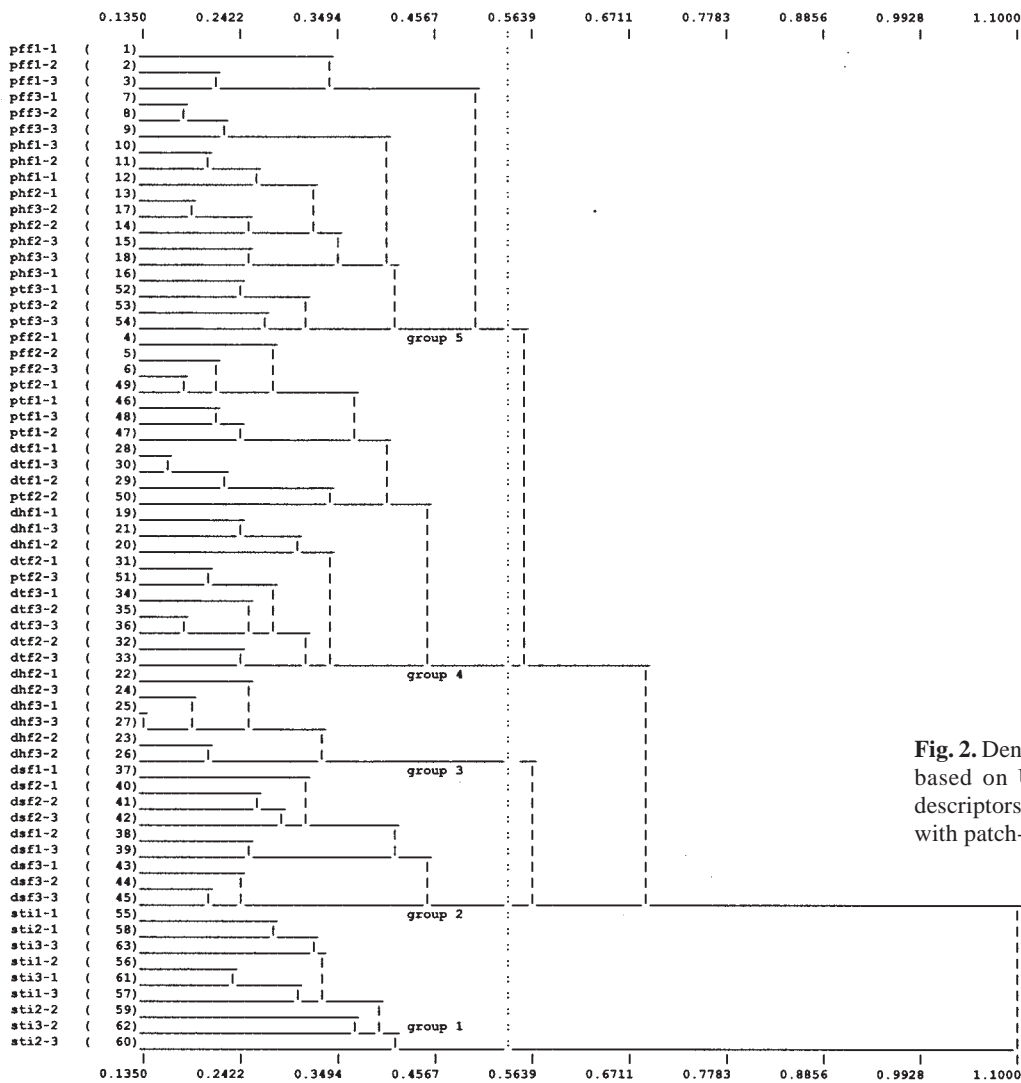


Fig. 2. Dendrogram of 63 quadrat samples, based on UPGMA fusion. The quadrat descriptors are shown in Table 1, suffixed with patch-quadrat number.

arranged along the Y-axis. Quadrat groups 2 and 3 are located at positive Y-axis values, correlated with swales and dense vegetation vectors. Quadrat groups 4 and 5, located at negative Y-axis values, correlate with foredune geomorphology, high exposure, scattered vegetation and elevated relative height vectors. The vectors latitude and distance to h.w.m. were poorly correlated with the quadrat and species groups.

Species groups show a similar pattern to the quadrats, located along the y-axis and at positive values of the x-axis. However, the species pattern is more diffuse than the quadrat pattern, due to the presence of a cloud of species located around the origin. These ubiquitous species are members of species groups 4 and 5, which exhibit little correlation with the environmental vectors. Species group 1 occupies the same space as quadrat group 1. Species group 2 occupies a broad sweep of space at positive x-axis values, spreading towards quadrat group 1, in which they were recorded sporadically. Species group 3 occupies similar space to quadrat group 5.

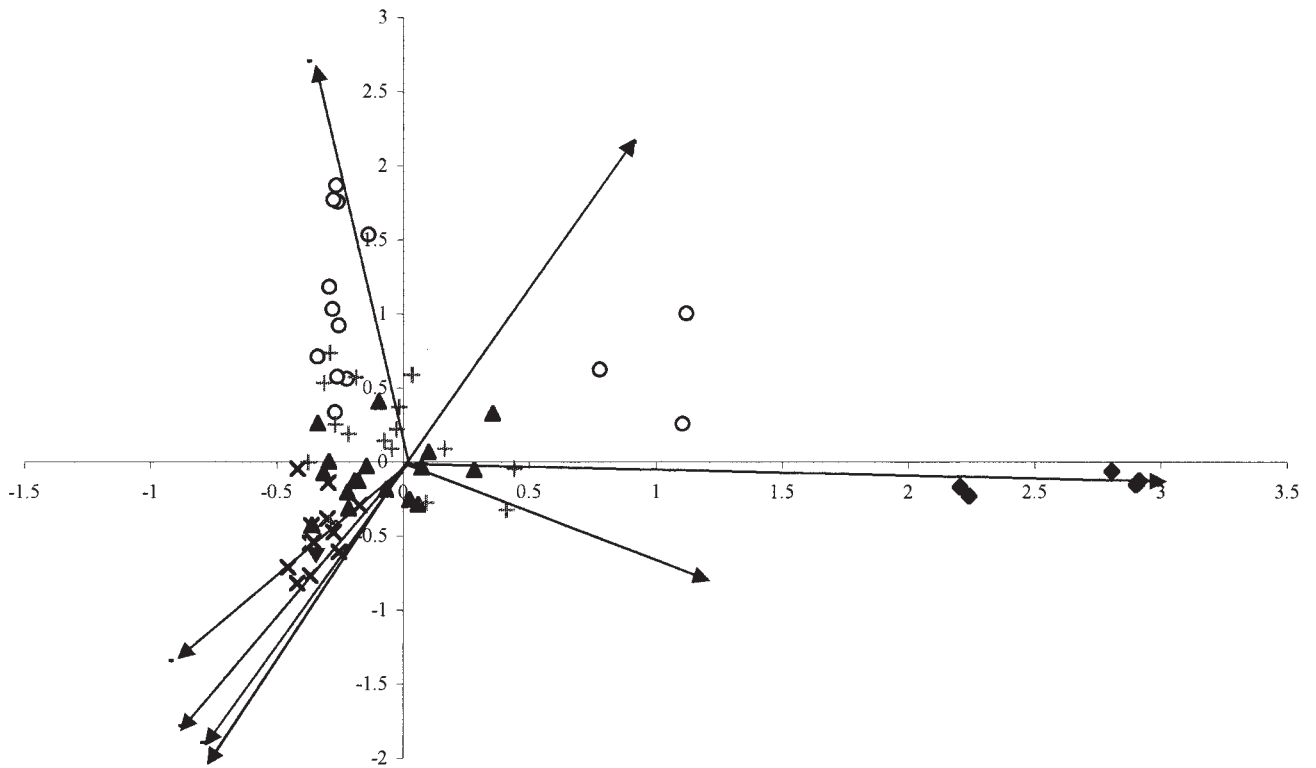
Discussion

This study detected strong local-scale patterns of species distribution and abundance in the coastal rainforest of Shoalwater Bay. The patterns show correlation with a number of environmental variables.

The strongest environmental variable was impeded drainage, correlated with species group 1 and quadrat group 1. The occurrence of the emergent sclerophyll species *Corymbia tessellaris* and *Melaleuca leucadendra*, the palm *Livistona decipiens* and a ground layer of *Cyperus* impart a distinctive structure to this community, which was clearly visible in the aerial photograph analysis. The impeded drainage is due to the proximity of underlying mudflats to the soil surface (Grinrod & Rhodes 1984, Cook & Polach 1973). Large amounts of litter accumulate from sclerophyll leaf and branch fall, creating a combustible ground layer in these patches. The presence of charred trunks of *Livistona*, *Corymbia* and *Melaleuca* indicate a dynamic community, with the fire tolerant emergents surviving the fire sensitive understorey rainforest species, and a re-invasion from surrounding rainforest of the fire sensitive species during fire free periods.

	Group 2	Group 5	Group 4	Group 3	Group 1
	EBOAACSCSPFTTC	PGMBFCAPADGRCCPA	PEDDJAPCCETMJMXIR	PSSACCACGHPN	LCMCAP
	urllilitltaieui	leirieianeaeuasc	oxiraloaalraaiyxa	aaemaylalolo	ioeyci
	rieyyseerncrs	eimecldvncipnyr	looyseurpaoysclop	rrcyscppyet	vrlpat
	odaxsrrydmrs	gjuyutieidtaatco	ycspmtipeptmrrora	scaeshpcaue	iyact
	flpsroqtppoppo	tseorpraudcvaodl	nlgdscsomsddmoqc	pvepceltaom	dtledf
	aeapupuosapoub	ialbuaauniyandaa	iaeeioeveeciivur	lilouoxurupi	eeegie
	linisaaminprbl	mlelbnscsmraope	ttmpmnrplasdnaea	amlnbpcispc	csulsr
	ccicccdeloepo	oinoiieticoicrhv	iiilpnitianpyutes	eiigereiftor	iscopr
	+				
pff1-1		* * * * *	***** * * * *	***** **	*
pff1-2	*	*** ** * **	***** * **	*** * *	
pff1-3		*** ** * * **	***** ** ***	**** *	*
pff3-1		* * * * *	*****	**	
pff3-2		* * * * *	*****	**	
G pff3-3		* * * * *	*****	**	
R phf1-3	*	** *** *	*****	***** *	*
O phf1-2		*** **** * *	***** *	**** *	
U phf1-1		** * * * *	*****	* ** *	
P phf2-1		** * * * * *	*****	****	
5 phf3-2		** * * * *	*****	**** *	
phf2-2		* * * * *	***** *	**** **	
phf2-3		** * * * *	***** *	**** *	
phf3-3		* *** ** *	** *	* ** *	
phf3-1		*** * * *	***** **	****	
ptf3-1	*	**** * * * * *	***** *	**	
ptf3-2		**** ** * * *	*****	**** **	
ptf3-3	**	**** * * * * *	***** * * * *	*****	
	+				
pff2-1	*	* * * * *	***** * * * * *	*** * *	*
pff2-2	* *	** * * * *	***** * * * * *	*** * *	*
pff2-3	*	** * * * *	***** * * * * *	*** *	
ptf2-1	**	*** *	*****	*** *	*
ptf1-1		* * * * *	*****	* ** **	**
G ptf1-3		** * * *	*****	*** *	*
R ptf1-2	*	***** * **	*****	** *	*
O dtf1-1	**	**** ** * **	*****	* * **	*
U dtf1-3	*	* ** * * * *	*****	*****	*
P dtf1-2	*	**** * * * *	*****	*** **	
ptf2-2	**	* * * * *	*****	*** ** **	
4 dhf1-1	* *	* * * * * *	*****	* * **	
dhf1-3	* * *	* * * * * *	*****	*** **	
dhf1-2	** * *	** * * * * *	*****	*	
dtf2-1	***	** *** * * * *	*****	* ** **	
ptf2-3	***	** * * * *	*****	*** * **	
dtf3-1	** * *	*** * * * *	*****	* ** **	
dtf3-2	**	*****	*****	* * **	**
dtf3-3	*	***** ** * * *	*****	* ** **	
dtf2-2	***** **	***** ** * * *	*****	* **	**
dtf2-3	* * * * *	*** ** * * *	*****	* ** **	**
	+				
G dhf2-1	* *	*** ** * *	***** **	*	
O dhf2-3	* * * * *	*** ** * *	***** * * *	** *	
U dhf3-1	* * *	*** ** * *	***** *		
P dhf3-3	* * *	*** ** * *	***** *	*	
dhf2-2	*	** *** * * * *	*** ** * * *	**	
3 dhf3-2	*	**** * * * *	***** * *		
	+				
dsf1-1	*** * *	*****	***** * * * *	** **	
G dsf2-1	***** * ***	* * * * *	***** * * * *	**	
R dsf2-2	** *	* * * * *	***** **		
O dsf2-3	***** * ***	*****	***** * * * *	*	
U dsf1-2	*** *	*****	*****		
P dsf1-3	*** *	***** * * * *	***** * * * *	*	
dsf3-1	***** * *	***** * * * *	*****		
2 dsf3-2	***** * * *	***** * * * *	*****		
dsf3-3	***** ** **	***** * * * *	*****		*
	+				
sti1-1	**	*** * * *	***** * * * * *	*	*****
G sti2-1		* ** * * *	***** * * * *		*** **
R sti3-3		* * * * *	* * * * *		*****
O sti1-2	* * *	* ** * * *	***** * * * * *		*****
U sti3-1	*	* ** * * * *	** * * * * *		*****
P sti1-3	*	** * * * *	** * * * *		*****
sti2-2	* **	** * * *	*** ** * * *	*	*** **
1 sti3-2	*	** * * *	*** * * * *		*****
sti2-3	*	** * * *	** * * *	*	*** **

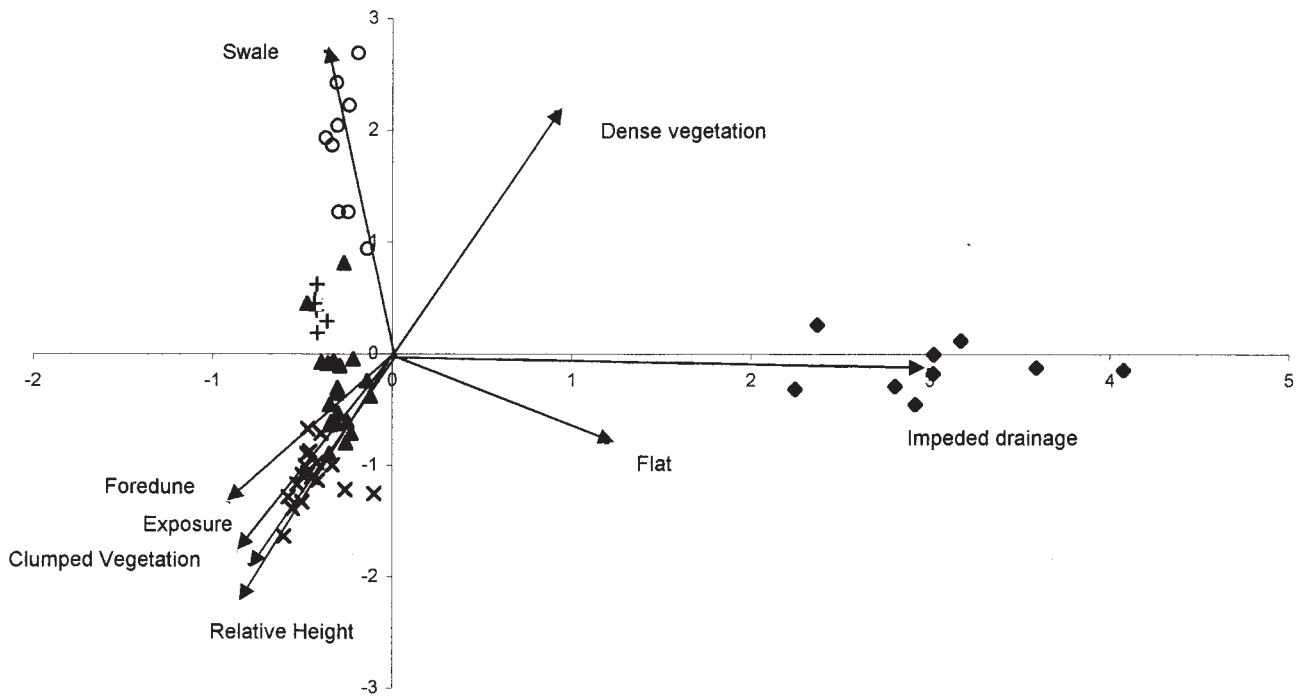
Fig. 3. Two-way table of classification results for 63 quadrats and 65 species. Quadrat labels as for Figure 2. Species labels are listed in Appendix 1.



Ordination results for species showing species membership of five species classification groups. Vectors x 3.

◆ Species Group 1 ○ Species Group 2 ✕ Species Group 3 ▲ Species Group 4 + Species Group 5

Fig. 4.



Ordination results for quadrats showing quadrat membership of five quadrat classification groups. Vectors x 3.

◆ Quadrat Group 1 ○ Quadrat Group 2 + Quadrat Group 3 ▲ Quadrat Group 4 ✕ Quadrat Group 5

Fig. 5.

All species appear to be able to tolerate periods of shallow submersion. This forest was classified as a mixed forest (Adam 1992), and exhibits a clear floristic and physical difference to the remaining vegetation. The sclerophyll emergent layer and rainforest understory are akin to wet sclerophyll forests of more temperate regions (Specht 1981, Adam 1992). Analogous communities in Queensland coastal rainforest have been documented by Tracey (1992) where beach ridge and swale systems support mixed vegetation, where *Melaleuca*, *Corymbia* and *Acacia* form a prominent sclerophyll component of the rainforest community. The impeded drainage of this community, which favours *Livistona decipiens* and *Cyperus eglobosus*, bears close resemblance to the communities described in Webb's (1968) subtropical swamp series, where notophyll palm forest gives way to sclerophyll sedge forest as drainage becomes increasingly impeded. Batianoff and McDonald (1980) documented a similar forest on the Capricorn Coast, where the *Livistona-Melaleuca-Eucalyptus (Corymbia)* assemblage occupied large areas of the extensive parallel beach ridge systems. Melzer et al. (1993) identified a similar community in the Shoalwater Bay area, where poorly drained coastal and inland dunes systems support communities dominated by *Livistona decipiens* and *Euroschinus falcata*.

The remaining free-draining quadrats appear in ordination as a continuum, ranging from dense, low rainforest in swales to scattered wind-sheared thickets on foredunes. This series of quadrats lacked sclerophyll species, and the decrease in stature from low forest to thickets was correlated with relative landform height and exposure. They show a gradual turnover of species and change in physical structure along the environmental gradients.

Group 2 and 3 quadrats, representing the tallest and least exposed rainforest facies, were classified as low microphyll vine forest (LMVF) according to the criteria of Webb (1968). This vegetation resembled the protected rainforest located behind foredunes as described by Queensland coastal rainforest studies (Lavarack & Godwin 1987, Tracey 1982). This vegetation is closely allied with the low closed forests identified by Batianoff and McDonald (1980). In common with that study, the low closed forests were located between a *Livistona-Melaleuca-Corymbia* association and foredune heaths and scrubs.

Group 4 and 5 quadrats were classified as microphyll vine thicket (MVT). The MVT vegetation is similar to that recorded in many locations along the Queensland coastline. Lavarack and Godwin (1987) described frontal dunes covered by dense vine thicket, and noted the reduction in canopy height due to exposure to onshore winds. Similarly, Hopkins et al. (1979) describe wind sheared beach scrub at Cowley Beach. Batianoff and McDonald (1980) have documented foredune closed and open heath/scrub on the Capricorn Coast. Along the northern areas of the NSW coastline, similar communities are described by Floyd (1990b), where the *Cupaniopsis anacardioides* alliance forms low, wind-moulded scrubs on the coastal margins of rainforest.

Group 4 quadrats represent the largest aerial extent of rainforest that is of intermediate stature along the LMVF/MVT continuum. Fifty-seven of the 65 species recorded in the study are found in group 4 quadrats. Environmental variables show a moderate level of exposure, and an intermediate relative height. As the exposure and relative height of the landform increase, increasing patchiness, a larger vine component and a decrease in canopy height are apparent. This vegetation represents the extreme littoral expression of rainforest in central Queensland, and was recorded in group 5 quadrats.

The species turnover along the LMVF/MVT gradient occurs against a background of stochastic species occurrence, represented by species groups 4 and 5. The range of environmental factors at the study site had little effect on these species groups, and they form a consistent part of the recorded flora. Floristically, this vegetation could be summarised as a *Diospyros-Drypetes-Pouteria-Exocarpos* association for both the LMVF and the MVT. Against this variable background of ubiquitous species, two correlations were distinguished, one comprising a group of species restricted to the LMVF, and the other restricted to the MVT.

Species group 2 was concentrated in the LMVF, and absent from the MVT. The low relative heights of the landforms supporting the LMVF infer proximity to subsoil moisture, and thus more mesic species persist here. Lower salt loads in the protected hinddune and swale locations would also allow salt sensitive species to persist.

Species group 3 is closely related to the exposed situations on elevated landforms of the MVT. Many of the species are vines, favoured by a low and easily accessible canopy, and high sub-canopy light levels where the vegetation is clumped. Vines may also form the extreme leading edge of the foredune vegetation, where a tangle of leafless or succulent vine species such as *Cassytha pubescens* and *Sarcostemma viminale* create the lowest part of the canopy. Species of the MVT are generally evergreen, maintaining a consistent canopy cover in all seasons, which is essential for canopy integrity under the constant stress of onshore salt-laden winds. Although the Shoalwater Bay coastline is within the environmental range for deciduous rainforest, deciduous species are restricted to the taller and more protected forests.

Two structural types of the MVT are evident, based on the continuity of vegetation cover. The patchy type, consisting of discrete clumps of rainforest separated by bare sand areas, were floristically indistinguishable from the continuous MVT type where moderate exposure and elevation were recorded, as in quadrat group 4. At higher levels of exposure and elevation, only the patchy type was recorded, and quadrat group 5 contains only this form of MVT. There are two hypotheses regarding the formation of the patchy type:

(i) the original establishment of the rainforest in areas that show strong correlation with high exposure and elevated landforms occurred in such a way that either establishment never proceeds to colonise all the area, or is in the process of

continuing to colonise the area. The study results do not preclude the former, however the latter is unlikely. No rainforest seedling germination was observed in the very exposed sand areas which lack organic material. However, the regeneration of rainforest under the clumps of the patchy vegetation is proceeding in a similar manner to the closed forest, where a deep peat layer moderates soil temperature and moisture in the shady understorey. If establishment is patchy in nature, it has remained so at least in the recent past.

(ii) that original establishment was complete, and that a decay process is occurring under the stresses that prevail in areas where clumped vegetation occurs. There is no evidence however of dead rainforest species in the inter-patch areas, and the boundary of each clump appears to be stable, neither relinquishing species from the edges, nor increasing the area by colonisation. Environmental conditions at the study site may have varied since a complete establishment event, resulting in the loss of rainforest area. It may have reached an equilibrium, or be proceeding at very slow rates. Floyd (1990a) considered the regeneration of littoral rainforest of N.S.W. coastal stands to be inhibited by the change in climate since the original establishment events of the Holocene. It appears likely that a similar climatic deterioration has resulted in conditions less favourable for the establishment of coastal rainforest in the study area, and possibly severe enough to degrade the most vulnerable areas. Damage from intense meteorological events may be one of the destructive forces responsible for the partial loss of rainforest areas in clumped vegetation. The establishment of a more benign climate may allow regeneration of the bare areas.

Acknowledgements

Thanks to Queensland Department of Environment and Heritage for permission to carry out the field work in Shoalwater Bay Conservation park, and the private landholders of the western shoreline of Shoalwater Bay for access to coastal dunes located on their properties.

References

- Adam, P. (1992) *Australian rainforests* (Clarendon Press: Oxford).
- ABARE, AGSO & BRS (1993) *Shoalwater Bay Military Training Area Resource Assessment* (AGPS: Canberra).
- Batianoff, G. & McDonald, T. (1980) *Capricorn Coast sand and headland vegetation* (Botany Branch, Department of Primary Industries: Brisbane).
- Baur, G. N. (1962) Forest Vegetation in north-eastern New South Wales. *Research Note 8* (Forestry Commission of NSW: Sydney).
- Belbin, L. (1993) *PATN Technical Reference Manual* (CSIRO Division of Wildlife and Ecology: Canberra).
- Bowman, D.M.J.S. (1992) Monsoon forests in north-western Australia. II. Forest-savanna transitions. *Australian Journal of Botany* 40: 89–102.
- Bowman, D.M.J.S. (2000) *Australian rainforests: Islands of green in a land of fire* (Cambridge University Press: Cambridge).
- BPA (1979) *Capricorn Coast beaches* (Beach Protection Authority: Brisbane).
- BPA (1982) *Cyclones and their effects on beaches* (Beach Protection Authority: Brisbane).
- Byrnes, N.B., Everist S.L., Reynolds, S.T., Specht, A. & Specht, R.L. (1977) The vegetation of Lizard Island, North Queensland. *Proceedings of the Royal Society of Queensland* 88: 1–15.
- Cook, P.J. & Polach, H.A. (1973) A chenier sequence at Broad Sound, Queensland, and evidence against a Holocene high sea level. *Marine Geology* 14: 253–268.
- Dick, R.S. (1975) The climate of Australia: According to Koepkens principles of definition. *Queensland geographical Journal* 3rd Series, Vol. 3.
- Dunlop, C.R. (1976) Botany of Maria Island, Gulf of Carpentaria. *Northern Territory Botanical Bulletin* 2: 1–14.
- Dunlop, C.R., Latz, P.K., & Maconochie, J.R. (1976) A botanical survey of Elcho Island. *Northern Territory Botanical Bulletin* 1: 1–56.
- Floyd, A.G. (1990a) *Australian rainforests in New South Wales I* (Surrey Beatty & Sons: Chipping Norton).
- Floyd, A.G. (1990b) *Australian rainforests in New South Wales II* (Surrey Beatty & Sons: Chipping Norton).
- Forster, P.I., Bostock, P.D., Bird, L.H. & Bean A.R. (1991) *Vineforest plant atlas for South-East Queensland* (Queensland Herbarium: Indooroopilly).
- Gillison, A.N. (1987) The 'dry' rainforests of Terra Australis. Pp. 350–355 In G. Werren & A.P. Kershaw (eds), *The rainforest legacy. Australian national rainforests study I* (Australian Government Publishing Service: Canberra).
- Harden, G.J. (Ed.) (1990-1993) *Flora of New South Wales* Vols 1–4 (New South Wales University Press: Kensington).
- Hopkins, M.S., Graham, A.W. & Murtha, G. (1979) *The vegetation of Cowley Beach area, joint tropical trials research establishment, North Queensland*. Technical Memorandum 79/13, CSIRO Institute of Earth Resources, Division of Land Use Research, Canberra.
- Lavarack, P.S. & Godwin, M. (1987) Rainforests of northern Cape York Peninsula. Pp. 201–226 in G. Werren and A.P. Kershaw (eds), *The rainforest legacy. Australian national rainforests study I* (Australian Government Publishing Service: Canberra).
- Melzer, R., Barry, S. & Kershaw, N. (1993) *Research report 8: Flora survey: Shoalwater Bay Military Training Area* (Commonwealth Commission of Inquiry, Shoalwater Bay, Capricornia Coast: Brisbane).
- Morrison, D.A., Le Brocque, A.F. & Clarke, P.J. (1995) An assessment of some improved techniques for estimating the abundance (frequency) of sedentary organisms. *Vegetatio* 120: 131–145.
- Outhred, R.K. (1984) Semi-quantitative sampling in vegetation survey. Pp. 87–100 in K. Myers, C.R. Margules & I. Musto (eds), *Survey methods for nature conservation* (CSIRO: Canberra)
- QDEH. (1994) *Introducing dry rainforests* (Queensland Department of Environment and Heritage: Brisbane).
- Russell-Smith, J. & Dunlop, C. (1987) The status of monsoon vine forests in the Northern Territory: a perspective. Pp. 227–288 in G. Werren and A.P. Kershaw (eds), *The rainforest legacy. Australian national rainforests study I* (Australian Government Publishing Service: Canberra).
- Specht, R. L. (1981) Foliage projective cover and standing biomass. Pp. 10–21 in A.N. Gillison and D.J. Anderson (eds), *Vegetation classification in Australia* (CSIRO/ANU Press: Canberra).
- Specht, R.L., Salt, R.B., & Reynolds, S.T. (1977) Vegetation in the vicinity of Weipa, North Queensland. *Proceedings of the Royal Society of Queensland* 88: 17–38.
- Ter Braak, C.J.F. (1988) *Canoco — a FORTRAN program for Canonical Community Ordination* (Microcomputer Power: New York).
- Tracey, J.G. (1982) *The vegetation of the humid tropical region of north Queensland* (CSIRO: Melbourne).

Webb L.J. (1968) Environmental relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296–311.

Young, P.A.R. and McDonald, W.J.F. (1987) The distribution, composition and status of the rainforests of southern Queensland. Pp. 119–141 in G. Werren and A.P. Kershaw (eds), *The rainforest legacy. Australian national rainforests study 1* (Australian Government Publishing Service: Canberra).

Manuscript accepted 5 May 2004

Appendix 1:

Vascular species recorded in coastal rainforest of Shoalwater Bay. Species group and two-way table codes are shown for species recorded in quadrat results.

Dicotyledons	Group	Code
Anacardiaceae		
<i>Euroschinus falcatus</i>	2	Eurofalc
<i>Pleiogynium timorense</i>	5	Pleitimo
Annonaceae		
<i>Polyalthia nitidissima</i>	4	Polyniti
Apocynaceae		
<i>Alyxia ruscifolia</i>	2	Alyxrusc
<i>Alyxia spicata</i>	2	Alyxspic
<i>Carissa ovata</i>	4	Carisovat
<i>Parsonsia plaesiophylla</i>	3	Parsplae
Asclepiadaceae		
<i>Sarcostemma viminale</i> subsp. <i>brunonianum</i>	3	Sarcvimi
<i>Gymnanthera oblonga</i>		
<i>Hoya australis</i> subsp. <i>Australis</i>	3	Hoyaaust
<i>Secamone elliptica</i>	3	Secaelli
Bignoniaceae		
<i>Pandorea pandorana</i>	2	Pandpand
Capparaceae		
<i>Capparis arborea</i>		
<i>Capparis lucida</i>	3	Cappluci
<i>Capparis sepiaria</i>	4	Cappsepi
Celastraceae		
<i>Elaeodendron melanocarpum</i>	4	Elaemela
<i>Maytenus disperma</i>	4	Maytdisp
<i>Pleurostyliya opposita</i>	3	Pleuooppo
Combretaceae		
<i>Terminalia porphyrocarpa</i>	2	Termporp
Ebenaceae		
<i>Diospyros geminata</i>	4	Diosgemi
Euphorbiaceae		
<i>Breynia oblongifolia</i>	5	Breyoblo
<i>Bridelia leichhardtii</i>	2	Bridleic
<i>Drypetes deplanchei</i>	4	Drypdepl
Fabaceae		
<i>Abrus precatorius</i>		
Flacourtiaceae		
<i>Xylosma ovatum</i>	4	Xyloovat
Lauraceae		
<i>Cassytha pubescens</i>	3	Casspube
Lecythidaceae		
<i>Planchonia careya</i>		
Loganiaceae		
<i>Strychnos psilosperma</i>	2	Strypsil
Loranthaceae		
<i>Amyema congener</i> subsp. <i>congener</i>	3	Amyecong
<i>Dendrothoe glabrescens</i>		
Meliaceae		
<i>Turraea pubescens</i> Benth.	2	Turrpube
Menispermaceae		
<i>Tinospora smilacina</i>		
<i>Stephania japonica</i> var. <i>discolor</i>		
Mimosaceae		
<i>Acacia disparrima</i>	1	Acacdisp

Moraceae		
<i>Ficus rubiginosa</i>	5	Ficurubi
<i>Ficus opposita</i> var. <i>opposita</i>	2	Ficuooppo
<i>Trophis scandens</i>	4	Tropscan
Myoporaceae		
<i>Myoporum acuminatum</i>		
Myrsinaceae		
<i>Rapanea variabilis</i>	5	Rapavari
<i>Rapanea crassifolia</i>	5	Rapacras
Myrtaceae		
<i>Corymbia tesellaris</i>	1	Corytess
<i>Gossia bidwillii</i>		
<i>Melaleuca leucadendra</i>	1	Melaleuca
Oleaceae		
<i>Olea paniculata</i>	2	Oleapani
<i>Jasminum simplicifolium</i> subsp. <i>australiense</i>	4	Jasmsimp
<i>Jasminum didymum</i> subsp. <i>didymum</i>	4	Jasmdidy
<i>Notelea microcarpa</i> var. <i>microcarpa</i>	3	Notemicro
Passifloraceae		
<i>Passiflora aurantia</i> var. <i>aurantia</i>		
Pittosporaceae		
<i>Pittosporum ferrugineum</i>	1	Pittferr
Rhamnaceae		
<i>Alphitonia excelsa</i>	3	Alphexce
Rubiaceae		
<i>Aidia racemosa</i>	5	Aidirace
<i>Cyclophyllum coprosmoides</i>	3	Cyclcopr
<i>Cyclophyllum odoratum</i>	5	Cantodor
<i>Psychotria daphnoides</i>	5	Psycdaph
<i>Ixora queenslandica</i>	4	Ixorquee
<i>Pavetta australiensis</i>	5	Paveaust
Rutaceae		
<i>Geijera salicifolia</i>	5	Geijsali
<i>Acronychia laevis</i>	5	Acrolaev
<i>Micromelum minutum</i>	5	Micrminu
<i>Glycosmis trifoliata</i>	3	Glyctrif
Santalaceae		
<i>Exocarpos latifolius</i>	4	Exoclati
Sapindaceae		
<i>Alectryon connatus</i>	4	Aleconn
<i>Cupaniopsis anacardioides</i>	5	Cupaanac
<i>Elatostachys xylocarpa</i>		
Sapotaceae		
<i>Pouteria sericea</i>	4	Poutseri
<i>Mimusops elengi</i>	5	Mimuelen
Sterculiaceae		
<i>Brachychiton australis</i>		
<i>Sterculia quadrifida</i>	2	Sterquad
Ulmaceae		
<i>Celtis paniculata</i>	5	Celtpani
<i>Trema tomentosa</i> var. <i>tomentosa</i>		
Verbenaceae		
<i>Clerodendron floribundum</i>	2	Clerflor
Viscaceae		
<i>Viscum articulatum</i>		
Vitaceae		
<i>Cissus oblonga</i>	2	Cissoblo
<i>Cissus opaca</i>	2	Cissopac
Monocotyledons		
Arecaceae		
<i>Livistona decipiens</i>	1	Livideci
Cyperaceae		
<i>Cyperus eglobosus</i>	1	Cypeeglob
Luzuriagaceae		
<i>Geitonoplesium cymosum</i>	5	Geitcymo
Orchidaceae		
<i>Cymbidium canaliculatum</i>		
<i>Dendrobium bowmanii</i>		
<i>Dendrobium discolor</i>	5	Denddisc
Poaceae		
<i>Ancistrachne uncinata</i>	5	Anciunci