

Floristics, structure and site characteristics of *Melaleuca viridiflora* (Myrtaceae) dominated open woodlands of the wet tropics lowlands

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Abstract: Tropical lowland plant communities in north-eastern Queensland remain under pressure from continuing clearing, fragmentation, exotic species invasion, inappropriate fire regimes, and altered hydrological patterns. Comparatively little scientific research has been conducted on the highly diverse and ecologically significant range of remnant vegetation types. Additionally, most plant communities remain very poorly represented in the existing conservation reserve system. *Melaleuca viridiflora* Sol. ex Gaertn. open woodlands were selected for investigation based on their relatively simple structure, compared to other lowland communities, and the large extent to which they have been affected by past clearing patterns. A detailed analysis of community structure and composition was conducted at 24 sites throughout the wet-tropics coastal region between Townsville and Cooktown. Surprisingly, a high diversity of structural and floristic types was recorded, with a total of 127 species documented across the 24 sites. Classification analyses of species composition data produced seven or eight main groups of sites (dependent on the statistical technique used), essentially related to a gradient of latitude and rainfall. These floristic groups were not well explained by either species richness, past fire frequencies or soil types. Structural classification analyses based upon DBH data identified six or seven main groups, the singularly most striking of which were sites with annual fire histories. Ordinations based on both the DBH and species composition data produced groupings that supported those detected by the classification techniques. On closer examination of sites with similar fire histories, soil moisture and soil type were both found to have significant effects on community structure and composition. Many of the woodland types recorded are not adequately included (some not at all) in the existing conservation reserve system.

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Introduction

There is a relative dearth of baseline information on community ecology for most vegetation types of the tropical lowlands of north-eastern Queensland. This is despite wide acknowledgment that they continue to be the communities most impacted by development, and are some of the most poorly represented communities in conservation reserves (Braby 1992; Lavarack 1994; Stanton & Godwin 1989; Tait 1994; Webb 1966). An analysis of the lowland vegetation of the Cardwell region (Figure 1) showed that remnant vegetation was reduced by 6,900 ha (29%) in the fifty years between 1942 and 1992 (Skull 1998). *Melaleuca* woodlands and *Melaleuca* open woodlands were reduced by 30% and 53% respectively. This study sought to provide a detailed description of woodlands dominated by *Melaleuca viridiflora* (Broad-leafed Tea-tree or Paperbark), which are an integral component of the highly diverse tropical lowland habitat mosaic. The conservation priority for these woodlands ranges from high through to low depending upon their floristics, structure and position in the overall landscape (Kemp & Morgan 1999; Kemp et al. 1999).

General description

Classified structurally as open woodland (Walker & Hopkins 1990), *Melaleuca viridiflora* dominated woodlands have a relatively simple tree layer, with a complex understorey comprising many sedges, grasses and other herbs (Figure 2)(Skull 1995; Tracey 1982). Non-graminaceous herbs are particularly abundant in the wet, hot summer months. Gillison and Walker (1981) documented that these communities are usually two-layered with a ground layer (10–50 cm) of graminoids. Tracey (1982) noted that epiphytes were often conspicuous in the canopy trees and that weed invasion was likely following disturbance. Lavarack (1994) described a wide range of terrestrial and epiphytic orchids that collectively flower almost year round in this vegetation type.

The predominantly low moisture and nutrient status of the soils associated with these woodlands often means that they will only carry very mild fires as a result of low fuel loads (Gillison & Walker 1981). *Melaleuca viridiflora* is tolerant of a wide range of soil salinities, prefers seasonally saturated soils, and readily coppices (Tweddell 1982). These features, together with fire-resistant bark and the capacity to establish profusely from seed, ensure that this species is a highly effective coloniser and competitor (Gillison & Walker 1981).

Table 1. The seven themes of *Melaleuca viridiflora* woodlands identified by Stanton and Godwin (1989).

Theme number	Constant species	Commonly associated species	Features
13	<i>Melaleuca viridiflora</i>	<i>Lophostemon suaveolens</i> , <i>Grevillea pteridifolia</i>	Small areas in eucalypt forest, occupying run-on areas or patches of heavier soil.
14	<i>Melaleuca viridiflora</i>	Nil	Open forests developed on recent marine alluvium. Ground cover variable.
15	<i>Melaleuca viridiflora</i> , <i>Dillenia alata</i> , <i>Carallia brachiata</i>	<i>Buchanania arborescens</i> , <i>Atractocarpus sessilis</i>	Medium to tall forests on silty loam soils of poor internal drainage.
16	<i>Melaleuca viridiflora</i>	Nil	Monospecific low forest and woodland developed on a shallow mantle of sand over mangrove mud.
17	<i>Melaleuca viridiflora</i> , <i>Lophostemon suaveolens</i>	<i>Melaleuca quinquenervia</i> , <i>Acacia crassicaarpa</i> , <i>Allocasuarina littoralis</i> , <i>Acacia mangium</i> , <i>Ischaemum australe</i>	Small low areas of seasonal swamp on sand plain.
18	<i>Melaleuca viridiflora</i>	<i>Melastoma malabathricum</i> , <i>Gahnia sieberiana</i> , <i>Banksia plagiocarpa</i>	Low forest, seasonal swamp.
19	<i>Melaleuca viridiflora</i> , <i>Lophostemon suaveolens</i> , <i>Grevillea pteridifolia</i>	<i>Corymbia clarksoniana</i> , <i>Xanthorrhoea johnsonii</i>	Grassy low woodlands of extensive plains.

Previous research

Other than the collection of baseline taxonomic and distribution information (Barlow 1989; Blake 1968), research within this vegetation type has focussed on a select number of plant species (particularly orchids) (Bartreau & Skull 1994; Jobson 1995; Lavarack 1994; Lawler 1993), even fewer animals (Anderson 1993; Braby 1992; Sommer 1990; van Dyck 1993), and rarely on entire communities. The only study to assess *Melaleuca viridiflora* specifically within the Wet Tropics Biogeographic Region (WTBR) (Thackway & Cresswell 1995), showed that this species reaches its highest densities on duplex soils, is capable of tolerating a wide range of salinities and is dominant where sites dried out markedly during the dry season (Tweddell 1982).

The floristics of the woodlands throughout the WTBR have been recorded as varying significantly in relation to controlling environmental factors (including soil type), constant canopy species and commonly associated species by Stanton & Godwin (1989), who recognized 119 “themes”. Although no detailed data was collected or analysed, seven “themes” of *Melaleuca viridiflora* were described for the region as a basis for assessing the woodlands’ conservation status at the time (Table 1). Others have described the structural variation that can occur in these woodlands, ranging from stunted, twisted trees (3–7 m) to more “pole” forest-like proportions in swampy areas (18–20 m) (Gillison & Walker 1981).

The physical structure of these woodlands has only been investigated in two other biogeographic regions of Australia (Top End Coastal and Cape York Peninsula). In the latter, Crowley & Garnett (1995) concluded that increases in the area

of this vegetation type (at the expense of native grasslands) corresponded to changes in fire regimes as a result of the cessation of Aboriginal burning, a finding supported by Stanton (1992). In both regions, a lack of an understanding of regenerative processes following disturbance in *Melaleuca* communities is a management concern (Dr J. Russell-Smith, pers. comm.). Finlayson *et al.* (1993) have published details of the structure of a mixed *Melaleuca cajuputi* Powell/*Melaleuca viridiflora* community on the Magela floodplain near Jabiru in the Northern Territory. The community exhibited a bell-shaped distribution curve across DBH size classes. Importantly, the site has remained unburnt for at least the past 20 years (Dr M. Finlayson, pers. comm.). General reductions in *Melaleuca* tree density across the same floodplain have also been documented and attributed to a combination of fire, water buffalo grazing and wind (Williams 1984).

Comparisons of the research results from other regions with those recorded in this study are, however, confounded by significant differences in annual fire regimes (including fire frequency, season and intensity), the scale of the habitats and the subsequent areas that are burnt on an annual basis, management practices (traditional vs. grazier vs. natural resource management) and environmental attributes such as rainfall, relative humidity and soil type.

Consequently, variation in structure and floristics of woodlands dominated by *Melaleuca viridiflora*, can reflect community differences in response to edaphic factors (soil type, climate) or successional responses to impacts of fire or grazing. This investigation therefore had the following objectives: (1) to conduct a detailed analysis of the structure

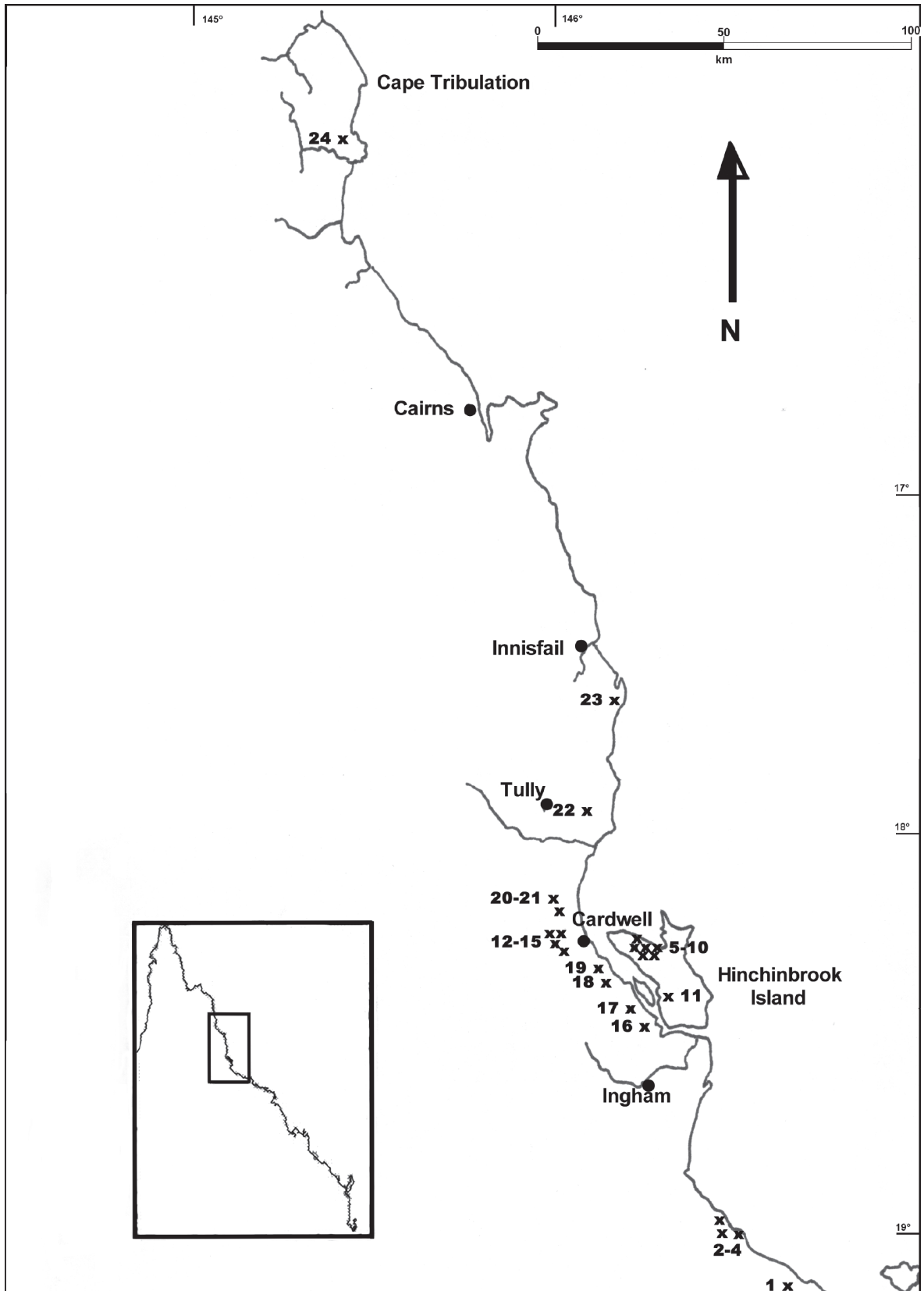


Fig. 1. Location of study sites (x) within the Wet Tropics Biogeographic Region.

of *Melaleuca viridiflora* woodlands within the WTBR, and (2) to assess the communities in terms of species composition, soil type, fire history and climate. A more detailed assessment of two of the most significant management issues facing these woodlands (fire and exotic species invasions) was also conducted (Skull 1998), and will be reported elsewhere.

Methods

Site selection

A combination of topographic maps, aerial photographs, previous vegetation surveys and consultation was used to select possible study sites. This study only investigated *Melaleuca viridiflora* communities that satisfied the following selection criteria: (1) the community was located within the coastal lowlands of the WTBR between Cooktown and

Townsville; and (2) *Melaleuca viridiflora* comprised more than 70% of the trees in the uppermost stratum.

The general location of the study sites on the north-eastern Queensland coast, between Cooktown and Townsville (from 16°13'S to 19°06'S, a distance of some 470 km), is presented in Figure 1. Sites 1–4 were chosen to represent communities at the southern extremity of the WTBR. In the central section of the WTBR, sites were primarily selected within Hinchinbrook Island National Park (Hinchinbrook Island) (Sites 5–11) and the Wet Tropics World Heritage Area (Sites 16–21), as this is where a majority of these woodlands occur (excluding privately owned freehold land). Hinchinbrook Island National Park provided unique opportunities to study *Melaleuca viridiflora* communities in detail, as it is isolated from the mainland and therefore subject to far less disturbance in terms of habitat fragmentation, high fire frequencies, exotic plant invasion and feral animal disturbance.

Table 2. Summary of site data for *Melaleuca viridiflora* communities in the lowland wet tropics of north Queensland.

Notes: ¹ = theme after Stanton & Godwin (1989), see Table 1; ² = Soil type after Cannon *et al.* (1992) where C=Cudmore, Po= Porter, R=Rungoo, L=Lugger, T=Thorpe, M=Malbon, Pr=Prior; duplex (texture contrast) soils are indicated with an asterisk, all others are gradational); ³ = Fire frequency where 1 = 1 fire every year, 2 = 1 fire every 1–2 years, 3 = 1 every 5 years, 4 = 1 every 10 years and 5 = 1 every 20 years; ⁴ = number of site visits.

Site	Latitude	Longitude	Altitude (m)	Annual rainfall (mm)	Theme ¹	Soil type ²	Fire frequency ³	Species richness	Sampling effort ⁴
1	19°06'00"	146°27'00"	10	1351	13	C	3	30	2
2	19°05'06"	146°18'00"	10	1402	13	Po*	4	18	2
3	19°05'06"	146°26'00"	30	1394	13	C	3	38	1
4	19°04'00"	146°26'00"	15	1410	13	C	3	33	1
5	18°16'06"	146°10'30"	10	2320	19	R*	4	49	13
6	18°14'48"	146°08'00"	10	2300	19	R*	4	20	6
7	18°16'00"	146°09'30"	10	2301	13	R*	4	14	3
8	18°16'30"	146°10'18"	20	2310	18	R*	4	10	6
9	18°16'30"	146°10'24"	20	2310	18	R*	4	15	6
10	18°16'30"	146°10'12"	15	2311	19	L	4	14	6
11	18°25'30"	146°13'30"	5	2205	16	T	4	16	2
12	18°15'06"	145°58'00"	10	2055	19	C	4	25	2
13	18°15'18"	145°58'12"	10	2038	19	C	4	11	2
14	18°15'12"	145°57'48"	10	2055	19	C	4	17	2
15	18°15'18"	145°57'36"	10	2038	19	C	4	18	2
16	18°30'00"	146°10'48"	5	2144	19	T	4	17	3
17	18°27'30"	146°09'00"	5	2134	19	L	1	15	2
18	18°20'12"	146°03'42"	10	2099	19	Po*	2	13	1
19	18°19'42"	146°02'36"	15	2076	19	M	3	27	8
20	18°11'30"	145°57'06"	10	2163	14	R*	3	16	1
21	18°10'42"	145°56'12"	10	2147	19	Pr	3	24	1
22	17°56'00"	146°01'30"	10	3262	19	R*	3	15	2
23	17°39'30"	146°39'30"	10	3213	17	T	5	15	1
24	16°13'00"	145°26'30"	15	3515	18	L	3	11	1
Mean ± SE	-	-	11.9 ± 1.1	2189 ± 119.3	-	-	-	20 ± 2	3 ± 1

Central WTBR sites were also located on the mainland in the State Forest and adjoining private land west of Cardwell (Sites 12–15). Northern WTBR mainland sites (Sites 22, 23 and 24) were located in the Mission Beach, Cowley Beach and Cape Tribulation areas respectively (Figure 1).

Plot data collection

The location of each site was recorded with a handheld Garmin 100 GPS unit. Altitude was determined from topographic maps. Recent fire histories were assessed using past fire records (predominantly for sites within conservation reserves), or determined following discussions with local authorities and landholders.

Most of the woodland populations sampled were small and irregularly shaped. To ensure sample units were not located too close to ecotones, a transect was established through the middle of each population. Five 10 x 10 m plots (spaced 10 m apart) were established along the transect, with the starting point for the first plot of the transect selected at random. Plots were marked to enable re-examination following fire. Steel pegs were used to mark the corners of the plots, with aluminium tags (labelled with date and plot number) nailed into a reference tree close to a pre-determined corner of every plot, and above previous fire scars. All structural data were collected over a two month period in 1993.

To provide an estimate of species richness, all species within each community were recorded and a reference herbarium compiled. Species were collected at all sites throughout the range of tropical seasons (excepting remote sites), so as to obtain a complete reference collection. Species composition data were collected between August 1993 and November 1996. Plant names follow Henderson (2002).

All mature *Melaleuca viridiflora* trees taller than 1.5 m were counted and their diameter at breast height (DBH) recorded. Individual *Melaleuca viridiflora* plants (hereafter called woody sprouts) less than 1.5 m were counted. These would include some seedlings or young saplings, as well as vegetative resprouts, which are particularly produced in response to fire. Due to their predominance in the understorey of most sites, Grass tree (*Xanthorrhoea johnsonii* A.T.Lee) densities were also recorded.

A single soil profile to a depth of 1 m was examined (as close as possible to the site centre) at each site using a 7.5 cm diameter auger. A representative sample of each horizon sub-section was collected, systematically stored in a compartmentalised tray and subsequently classified according to Cannon et al. (1992).

To enable climate comparisons to be made with other regions where this community has been studied, mean monthly rainfall and relative humidity data for Townsville, Cardwell, Cooktown (all within the WTBR), Coen (Cape York Peninsula) and Jabiru (Top End Coastal) were obtained from the Bureau of Meteorology. The climate prediction system BIOCLIM (Busby 1991) was also used to predict climate

parameters, including rainfall and temperature profiles for each of the study sites based on longitude, latitude and altitude.

Data analyses

The DBH (cm) data were sub-divided into nine DBH size classes. A cluster analysis was conducted on the *Melaleuca viridiflora* DBH data matrix to determine sites with similar structures using a Bray-Curtis (Czekanowski) association measure followed by flexible unweighted, pair group arithmetic averaging (UPGMA). This technique is a hierarchical, agglomerative clustering process available in the PATN software package (Belbin 1995b; a). All analyses closely followed the recommended procedure outlined by Belbin (1991).

This classification technique was tested against the polythetic divisive approach of TWINSpan (two-way indicator species analysis) originally developed by Hill (1979). The analysis of DBH data used six cut levels (set at 0, 5, 10, 20, 30 and 50) with the minimum group size for division and maximum number of divisions set at two and five respectively. This

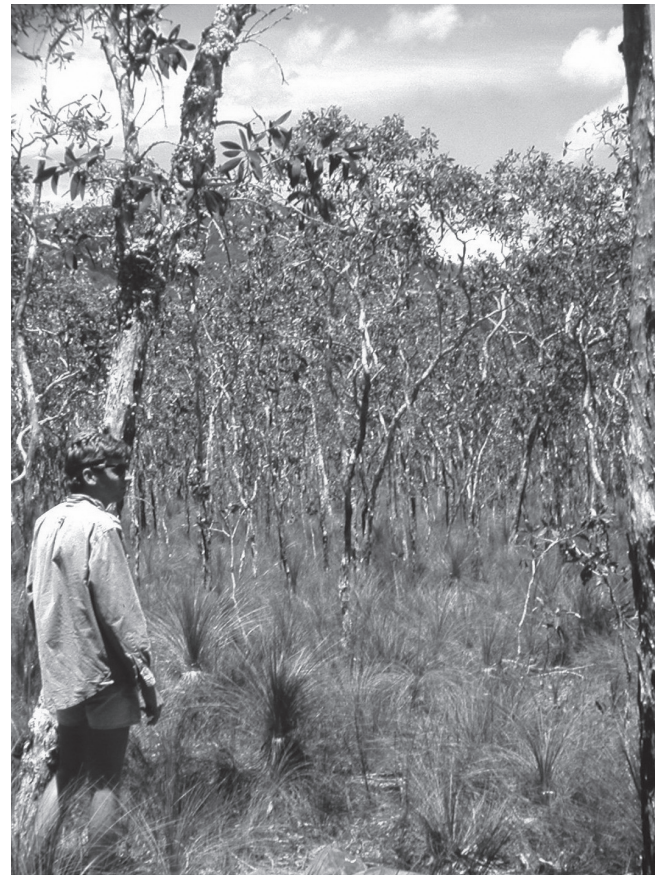


Fig. 2. A typical *Melaleuca viridiflora*-dominated open woodland community in Hinchinbrook Island National Park, with abundant grass trees (*Xanthorrhoea johnsonii*) in the understorey.

additional analysis was employed to determine which DBH groups (or species in the case of the species composition data matrix) were responsible for producing divisions/groupings of sites within the data matrix.

To test the discreteness of the groupings formulated by the cluster analysis, an ordination was performed using semi-strong hybrid multi-dimensional scaling (SSH). This ordination technique combines metric and non-metric multi-dimensional scaling (Faith 1991), and is also available within the PATN package. Three dimensions were chosen on the basis of the stress parameter (lack of fit), and for the third dimension 100 random starts were utilised to minimise the likelihood of local minima (Faith 1990). Site variables which appeared to be important with respect to site groupings (soil type, rainfall and fire history), were then superimposed on plots of the ordination vectors.

The species composition data were analysed according to the procedure outlined above for the DBH data matrix, except that two cut levels (0 & 1) and a maximum number of four divisions were used in the TWINSpan analysis, and four dimensions were required to produce sufficiently low stress in the ordination. Species with a frequency of less than 5% for all study sites were not included in the analysis. As a result, 75 species were selected from the original list of 127.

Site groupings from selected multi-variate analyses were then tested for significant differences with respect to other parameters using one-way ANOVA. For the species composition data, species richness and predicted total annual rainfall were tested for significant differences between groupings of the Bray-Curtis classification. Groupings from both classifications of the DBH size class data were tested for significance based upon the raw DBH data for each site and predicted total annual rainfall. Tukey's HSD test was employed to determine which pairs of groups (if any) were significantly different at the 5% significance level. All univariate analyses were conducted using the SPSS software package (SPSS 1993).

Results

General characteristics of the sites

A total of 24 *Melaleuca viridiflora* populations were investigated during this project. Altitude ranged from five metres above sea level to 30 m, with the majority of sites 10–15 metres above sea level (Table 2). Four sites (1–4) had predicted annual rainfalls of less than 1500 mm, with most sites between 2000 and 2300 mm. Three sites were predicted to register more than 3000 mm annually (Sites 22–24).

Of the seven themes identified by Stanton and Godwin (1989), six were recorded during this survey (Table 2). Fifty-four percent of the sites were classified as Theme 19 with Theme 13 the next most abundant (21%). No Theme 15 (*Melaleuca viridiflora* associated with *Dillenia alata* and

Carallia brachiata) was recorded. The seven soil types recorded during the survey were all derived from acid igneous rock (Cannon et al. 1992). Gradational soils were more predominant (63%) than duplex soils, although Cudmore (gradational) and Rungoo (duplex) series soils were equally abundant (30%).

Recent fire histories varied from annual fires at Site 17 to relatively low frequencies (Site 23), with most sites averaging a fire once every 5 to 10 years (Table 2). This moderate fire frequency was particularly common for sites on Hinchinbrook Island.

Community structure varied markedly for every parameter recorded (Table 3). Average DBH was lowest at Site 20, low for two other groups of sites (7–9 and 21–23) and high at Sites 17 and 18. The number of *Melaleuca viridiflora* individuals per 500 m² in the >1.5 m size class varied from 32 at Site 4 to 255 at Site 23. Understorey parameters (the number of *Melaleuca viridiflora* sprouts <1.5 m and Grass-trees) also had wide ranging densities. Canopy dominance of *Melaleuca viridiflora* was lowest at Site 11 (71%) and highest at Site 13 (100%). Species richness and sampling effort were not significantly correlated (Pearson correlation coefficient = 0.40, $P > 0.05$). The density of *Xanthorrhoea johnsonii* in the understorey also varied greatly across the sites examined. Whilst absent at some sites (Sites 3, 4, 13 14 and 24), this species reached very high densities at others (Sites 6 and 9).

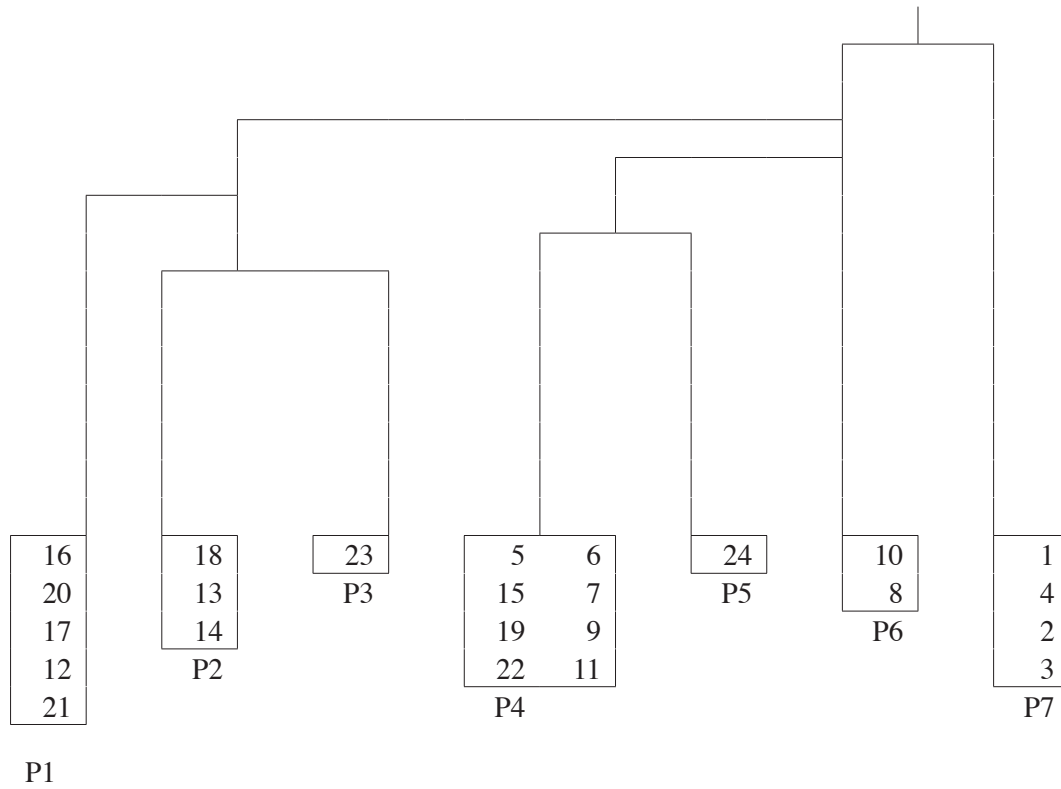
Whilst there was a large variation between sites, most individuals had a DBH of less than 20 cm (most commonly less than 5 cm). Site 20 was unusual in that it only had individuals with a DBH less than 10 cm, and Sites 17 and 18 appear distinct with the majority of individuals in the larger size classes.

Community analyses of study sites

Species composition data matrix

The Bray-Curtis clustering technique produced seven groupings (P1–P7) (Figure 3a) and TWINSpan eight (P8–P15) (Figure 3b). The two approaches generally produced similar groupings. The initial Bray-Curtis division produced two groups, the first of which (P7) separated the four sites at the southern extreme of the WTBR (Figure 3a). These sites had few understorey native herbaceous species and midstorey shrubs. Native grasses and introduced pasture species dominated the understorey, contributing to a high species richness at Sites 3 and 4. These four sites shared several species in common, including *Themeda triandra* (Kangaroo grass), *Dendrobium canaliculatum* (Tea-tree orchid), *Pandanus tectorius* and a species of wattle. Conversely, the absence of species present at many other sites, including *Casuarina equisetifolia* L. subsp. *incana*, *Dianella* spp. and several other herbaceous species, was also a noticeable feature of this first group. The TWINSpan classification also distinguished these sites from all others based on the presence of the grass *Eriachne ciliata* (Figure 3b).

a



b

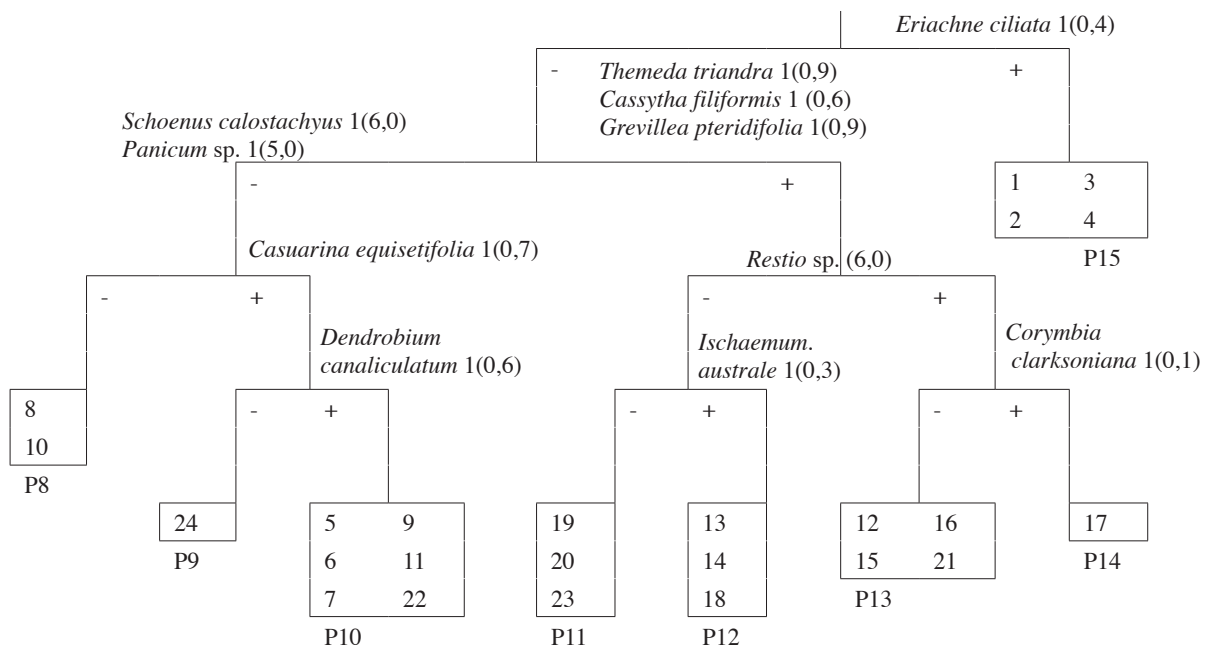


Fig. 3. Classifications of the species presence/absence data. (a) Classification of the species presence/absence data matrix utilising the Bray-Curtis association measure. End groups of sites are identified by codes (P1–P7). Groups of sites have been used to show the similarity of the SSH ordination results in Figure 4a. (b) Classification of the species presence/absence data matrix utilising TWINSpan. Cut levels of 0 and 1. Indicator taxa, their abundance level and number of sites at which they occurred are given at each division. End groups of sites are identified by codes (P8–P14).

The second split in the Bray-Curtis division separated groups P4, P5 and P6 from groups P1, P2 and P3. P6 included Sites 8 and 10 (P6). These sites are at the two extremes of the soil moisture gradient (Skull 1998). It is therefore interesting that despite significant differences in terms of soil moisture, the sites are grouped according to species composition. Similarly, the TWINSPAN classification grouped these sites (P8-after three divisions) based upon the absence of the sedge *Schoenus calostachyus*, a species of Panic grass and the tree *Casuarina equisetifolia* subsp. *incana* (Figure 3b).

The next Bray-Curtis division produced a further two groups (Figure 3a). The first of these (P5) contained only one site, the most northern site investigated during this project (Site 24). This site had an understorey almost completely dominated by the giant sedge *Gahnia sieberiana* and *Melastoma malabathricum* subsp. *malabathricum*. Apart from other canopy trees (the most unusual being *Dillenia alata* which was only recorded from one other site, on Hinchinbrook Island (Site 11)), few other species were recorded. The second group (P4) contained eight sites, including all the remaining sites located on Hinchinbrook Island (Sites 5, 6, 7 and 9). Three mainland sites were also included in this group, two from the Cardwell region and the only one investigated in the Mission Beach region. The TWINSPAN classification also placed Site 24 on its own (P9), separated from six other

sites at the fourth division based on the absence of the Tea-tree orchid *Dendrobium canaliculatum*, whose range does not extend that far north. The six sites that comprise P10 were all contained within a similar grouping produced by the Bray-Curtis approach (P4). Apart from Site 22 (located at Mission Beach), all sites were located on Hinchinbrook Island.

The final division of the Bray-Curtis classification produced three groupings (P1–P3), with P1 relatively similar to P2. The P1 group contained the majority of mainland sites in the Cardwell region, with the remainder in P2. The P3 group contained a single site (Site 23) which was the only one situated on an old sand dune system. Furthermore, this site was located near Cowley Beach, nearly 100 km to the north of Cardwell. Although this site contained no unique species, it had several (including *Melaleuca nervosa*) that were only documented at one other site. The TWINSPAN analysis produced a group identical to P2 (P12) at the fourth division based upon the presence of the grass *Ischaemum australe*. The P11 group matched none of those from the Bray-Curtis classification, whilst P13 contained three of the five members of the P1 group. Site 17 stood alone in the TWINSPAN classification based on the presence of *Corymbia clarksoniana*, which separated it from those sites in group P13 (Sites 12, 15, 16 and 21).

Table 3. Summary of structural data for *Melaleuca viridiflora* communities in the lowland wet tropics of north Queensland.

Notes: Standard errors are given in parentheses where appropriate; ¹ = number of individuals in 500 m².

Site	Mean DBH (cm)	Mean height (m)	<i>Melaleuca viridiflora</i>			<i>Xanthorrhoea johnsonii</i> ¹
			> 1.5 m ¹	< 1.5 m ¹	% of canopy	
1	8.6 (0.7)	9.2 (0.5)	54	341	74	107
2	13.1 (0.6)	13.3 (0.4)	46	89	98	14
3	10.8 (1.2)	10.0 (0.4)	85	45	97	0
4	13.7 (0.7)	12.5 (0.6)	32	330	86	0
5	19.3 (1.3)	5.9 (0.3)	128	158	99	504
6	19.2 (1.3)	4.9 (0.2)	107	84	98	705
7	5.0 (0.3)	4.0 (0.2)	88	79	72	540
8	4.3 (0.3)	3.3 (0.2)	53	154	95	175
9	5.9 (0.3)	4.2 (0.2)	142	154	96	725
10	13.2 (0.6)	9.5 (0.6)	55	94	74	30
11	7.6 (0.5)	6.2 (0.3)	114	44	71	139
12	10.4 (1.0)	7.3 (0.5)	43	75	77	242
13	11.5 (0.8)	10.3 (0.2)	62	50	100	0
14	9.8 (0.7)	6.7 (0.5)	83	123	73	0
15	9.5 (0.4)	6.4 (0.2)	74	53	89	130
16	21.2 (1.6)	5.6 (0.4)	80	275	99	466
17	34.7 (1.9)	11.2 (0.4)	48	360	96	368
18	32.4 (1.8)	10.4 (0.4)	57	65	99	307
19	9.6 (0.6)	7.6 (0.5)	51	276	78	397
20	3.1 (0.1)	2.7 (0.1)	215	900	75	333
21	5.4 (0.4)	5.8 (0.3)	182	298	75	390
22	5.1 (0.3)	4.6 (0.2)	149	3	73	97
23	5.2 (0.2)	2.7 (0.7)	255	149	84	6
24	12.7 (0.8)	9.6 (0.4)	87	0	82	0
Mean	10.4 (0.2)	6.0 (0.1)	95 (12)	175 (39)	86 (2)	237 (47)

The groupings defined by the Bray-Curtis classification were re-iterated by a plot of the first and second vectors from the ordination of the composition data (Figure 4a). Some overlap occurred between the P1 and P4 groupings of the classification, particularly Sites 16 and 19. These sites are both on the mainland and, although on different soil types, experience relatively infrequent fires. Soil types (especially gradational and duplex soils when combined) and fire history did not produce distinct patterns when overlaid on the ordination (Figure 4b and 4c respectively). Rungoo soils tended to clump together, with Cudmore soils predominantly falling to the left of the origin for Vector 1.

Sites with fire histories of 1 in 5 or 1 in 10 years formed a large group. Interestingly, although Sites 23 and 17 are very close together in the ordination space, they actually have the most different recent fire histories. Rainfall data overlaid on the species composition ordination produced some more definitive groupings (Figure 4d). High rainfall sites (Sites 22, 23 & 24) were arranged in a diagonal, linear fashion. Nearly all sites with either moderate or moderate-high rainfall fell below this diagonal and low rainfall sites above it. The exceptions to this were two sites with moderate-high rainfall (Sites 8 and 10), which formed a separate group above the linear diagonal.

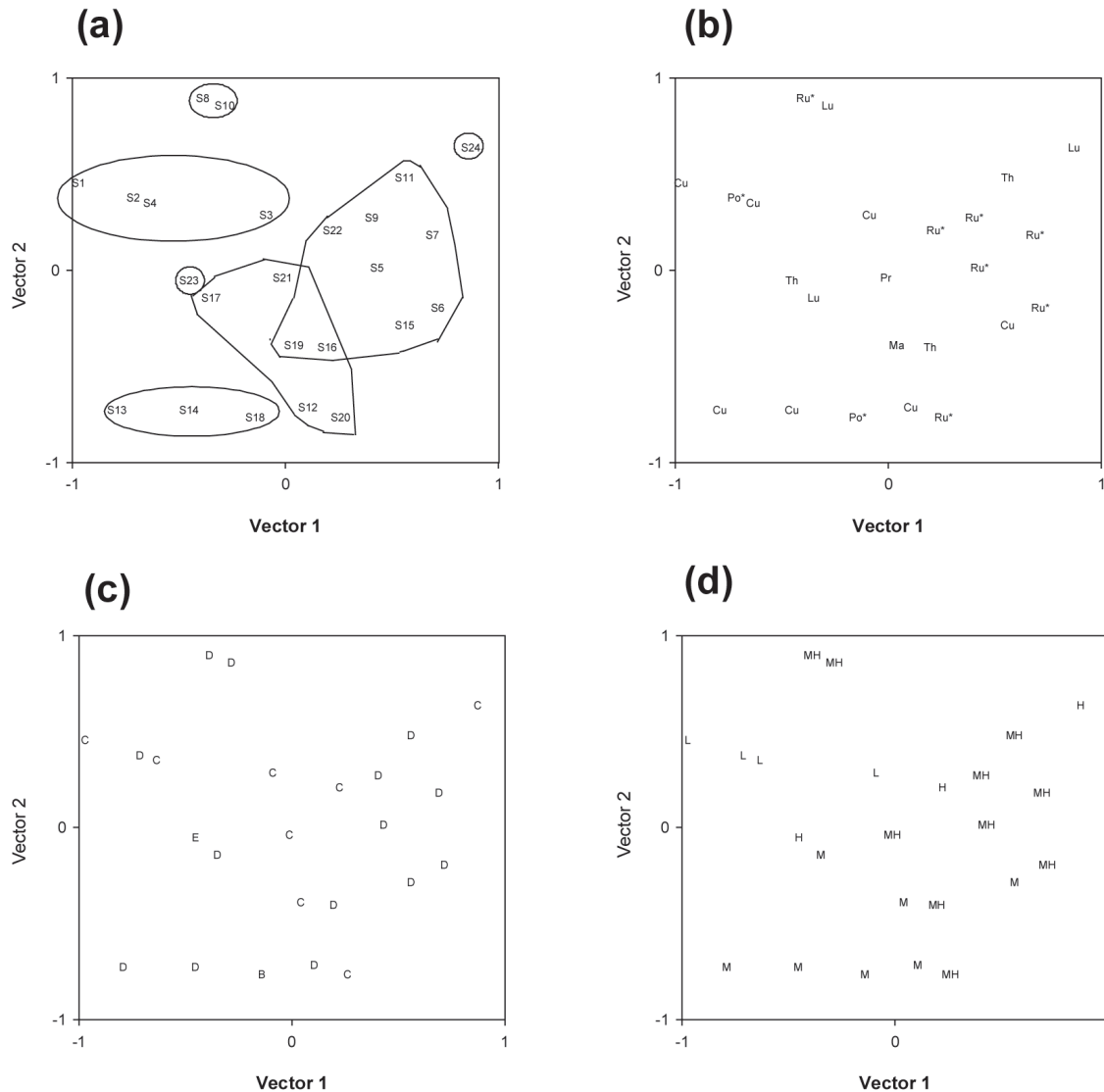


Fig. 4. Ordination of presence/absence data by SSH, Vector 2 vs. Vector 1 (S = site). (a) Sites overlain by groupings produced in the Bray Curtis classification of species presence/absence data, Figure 3a). (b) Sites with soil types superimposed (C=Cudmore, Po=Porter, R=Rungoo, L=Lugger, T=Thorpe, M=Malbon & Pr=Prior). (c) Sites with fire frequency imposed (A=1 fire every year, B=1 every 1–2 years, C=1 every 5 years, D=1 every 10 years and E=1 every 20 years). (d) Sites with rainfall superimposed (L=low: 1300–1700 mm, M=moderate: 1701–2100 mm, MH=moderate-high: 2101–2300 and H=high: > 2300).

As the two classification procedures and the subsequent SSH ordination results were generally very similar, only the Bray-Curtis results of the remaining community parameters are considered further here. Species richness did not differ significantly among the classification groups ($P=0.19$, $F=1.65$, $d.f.=6$), but predicted total annual rainfall based on latitude, longitude and altitude did ($P<0.001$, $F=15.39$, $d.f.=6$). The four southern WTBR sites (Group P7) had a significantly lower rainfall than all other groups ($P<0.05$). Group P3 (Site 23 near Cowley Beach, Innisfail) had a significantly higher rainfall than the majority of mainland sites in the Cardwell region (P2 and P1), and Site 24 (closest to Cooktown) had a statistically higher rainfall than all other sites except Site 23.

Structural data matrix

The Bray-Curtis classification of DBH data produced six species groups (Figure 5a) whilst the TWINSPLAN analysis produced seven (Figure 5b). In both cases the first group to

separate was that containing Sites 17 and 18 (D6 and D13). These sites had the highest recent fire frequencies and lacked any individuals with a DBH less than 2 cm (and taller than 1.5 m), had one each in the 2–5 cm DBH category and frequencies less than 10 for all other categories except 26–30 cm DBH and 31–35 cm DBH. There were large numbers of sprouts (<1.5 m) present (Table 3). The woodland structure is therefore simple, characterised by varying densities of sprouts and high mean DBHs.

The first division of the Bray-Curtis classification also separated eight other sites which split into two groups of five and three sites respectively (D4 and D5). Group D4 contained four of the six Hinchinbrook Island sites, which had very similar soil types, annual rainfall totals and fire histories (Table 2). Group D5 contained two sites near Edmund Kennedy National Park and the site at Cowley Beach near Innisfail (Site 23). Despite being situated on a range of soil types, all three sites had low mean DBHs (Table 3). The TWINSPLAN classification also separated seven of these sites (second division) based upon a lack of individuals

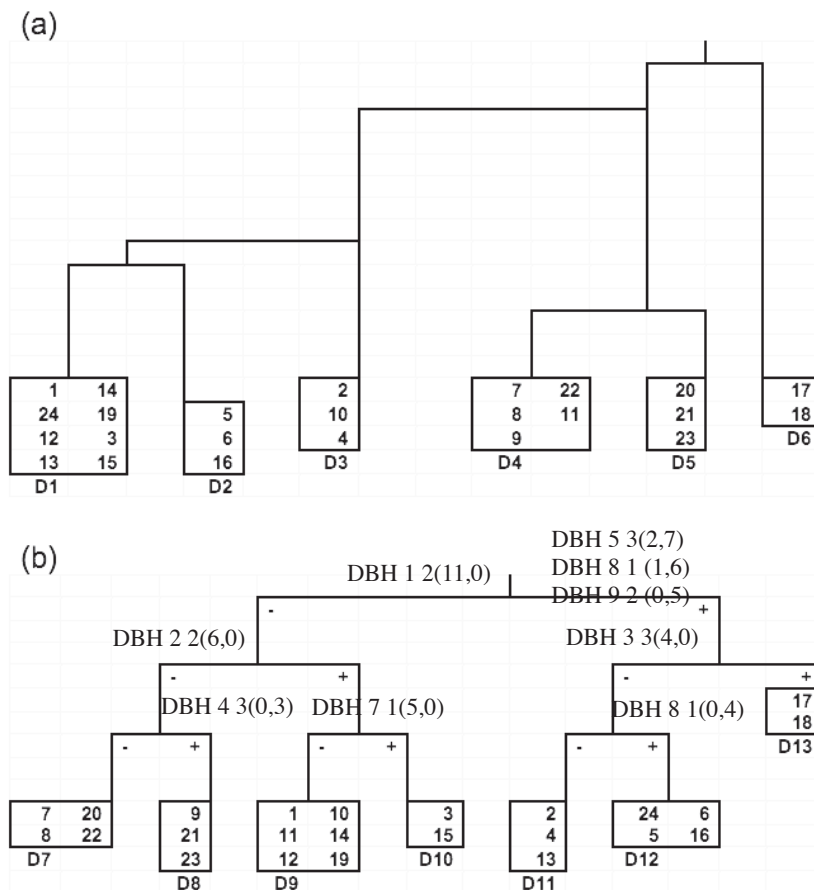


Fig. 5. Classifications of the DBH size class data matrix. (a) Classification of the *Melaleuca viridiflora* DBH size class data matrix utilising the Bray-Curtis association measure. End groups of sites are identified by codes (D1–D6). Groups of sites have been used to show the similarity of the SSH ordination results in Figure 6a. (b) Classification of the *Melaleuca viridiflora* DBH size class data matrix utilising TWINSPLAN. Cut levels of 0, 5, 10, 20, 30 and 50. Indicator groups, their frequency and the number of sites at which they occurred are given at each division. End groups of sites are identified by codes (D7–D13).

in the 2–5 cm DBH category. The group was then further divided depending on the presence or absence of individuals in the 11–15 cm DBH category. These final two groups (D7 and D8) were very similar to those of the Bray-Curtis classification (D4 and D5).

The second division of the Bray-Curtis classification separated Sites 2, 4 and 10 (D3, Figure 5a) from the remainder. Two of these sites are in the southern section of the WTBR (Sites 2 and 4), with the third (Site 10) located on Hinchinbrook Island at the end of a soil moisture gradient (high moisture) (Skull 1998). TWINSpan produced a similar grouping (but here Site 13 replaces 10) based on the absence of DBHs between 31–35 cm at the third division (D11, Figure 5b). The positive side of this division (D12) forms a grouping nearly identical

to one of those from the final division of the Bray-Curtis classification (D2). Sites 5, 6 and 16 are identical themes identified by Stanton and Godwin (1989). Furthermore, they have identical fire histories and very similar mean DBHs and soil types (Tables 2 & 3).

The remaining eight sites from the Bray-Curtis classification (D1) are a similar group to those produced at the third division of TWINSpan based upon the presence or absence of DBHs between 26–30 cm (D9 and D10). Group D1 contains a diverse group of sites from either end of the WTBR, which belong to different themes and with very different soil types and fire histories (Table 2).

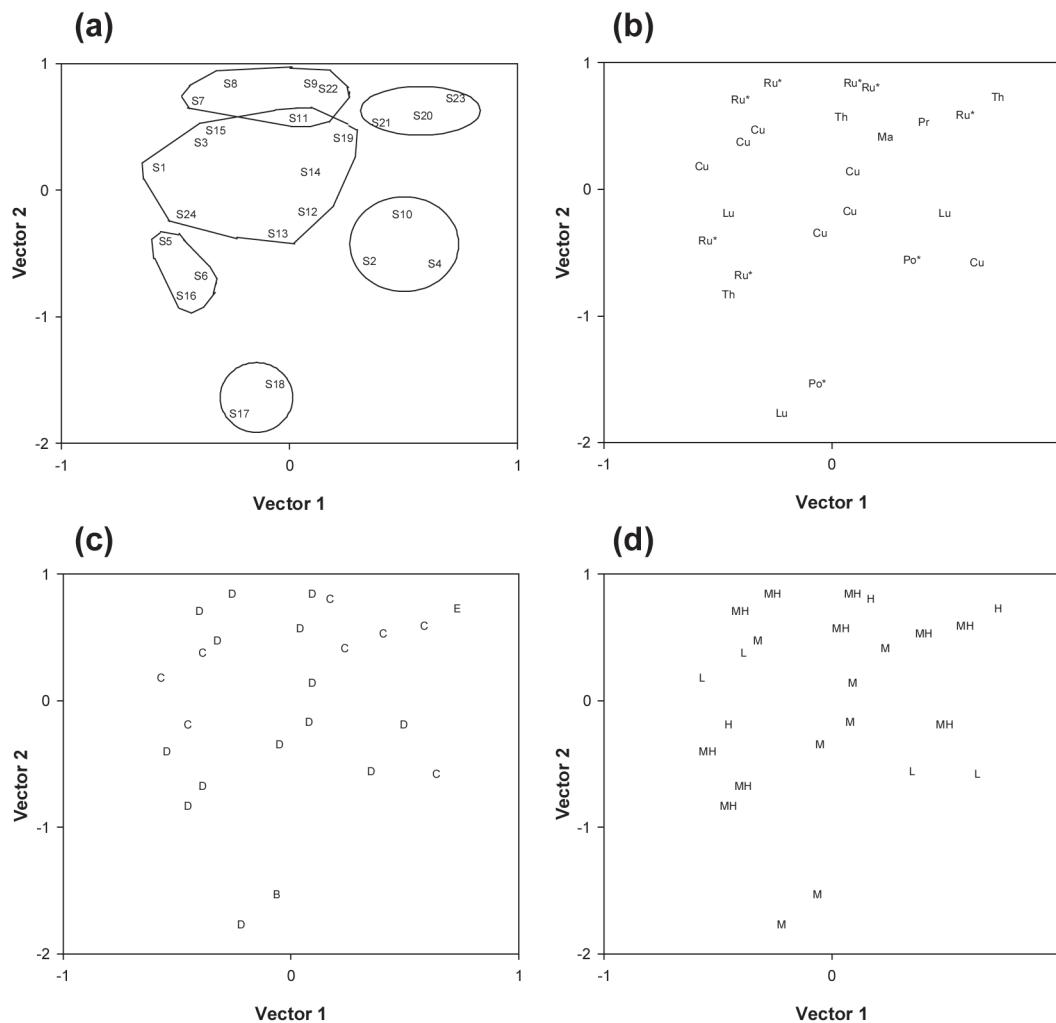


Fig. 6. Ordination of the *Melaleuca viridiflora* DBH size class data by SSH, Vector 2 vs. Vector 1 (S = site). (a) Sites overlain by groupings produced in the Bray-Curtis classification of DBH size class data, Figure 5a). (b) Sites with soil types superimposed (C=Cudmore, Po=Porter, R=Rungoo, L=Lugger, T=Thorpe, M=Malbon & Pr=Prior). (c) Sites with fire frequency imposed (A=1 fire every year, B=1 every 1–2 years, C=1 every 5 years, D=1 every 10 years and E=1 every 20 years). (d) Sites with rainfall superimposed (L=low: 1300–1700 mm, M=moderate: 1701–2100 mm, MH=moderate-high: 2101–2300 and H=high: > 2300).

The SSH ordination produced groups identical to those of the Bray-Curtis classification (Figure 6a). Cudmore and Rungoo soil types were grouped together, with less pattern evident for other soil types (Figure 6b). Fire histories were well separated when overlaid on the ordination vectors (Figure 6c). Sites experiencing recent fire frequencies of either 1 in 5 or 1 in 10 years were grouped together, with those having lower or higher frequencies positioned on either side of the ordination space. Discernible patterns were less evident when the total annual rainfall data were superimposed on the ordination space (Figure 6d). Although some grouping of moderate and moderate-high rainfall sites occurred, sites with either low or high rainfall did not group particularly well.

The results of the one-way ANOVA on the site DBH data statistically confirmed the groupings formed in the Bray-Curtis classification ($P < 0.001$, $F = 415.49$, d.f.=5). Group D6 had a significantly higher mean DBH to all other groups, as did Groups D2 and D3 compared to Group D1 ($P \leq 0.05$). No significant difference was recorded between Groups D4 and D5, which are located adjacent to each other in the classification dendrogram (Figure 5a). Rainfall did not vary significantly between the site groupings ($P = 0.40$, $F = 1.09$, d.f.=5).

Discussion

The sites examined during this investigation varied considerably across the range of parameters recorded. Sites considered relatively adjacent at the landscape scale sometimes exhibited marked differences in either species composition, species richness, community structure, soil type or fire history. Sites essentially formed a continuum between the two extremes of this vegetation type described by Gillison and Walker (1981). Their “stunted, twisted woodland (3–7 m)” was recorded at several sites (Sites 7–9 and 20–23), and their “pole” forest-like community (18–20 m) at Site 10. Despite this variation in community structure, general trends in the data emerged.

Plant species have long been known to form distribution patterns with respect to environmental gradients such as rainfall (Kershaw & Looney 1985). This was re-iterated in this study, with species composition of the woodlands providing a basis for classifying the study sites into five major groups. Two sites (23 and 24) with high rainfall in the more northern section of the WTBR stood alone (Figure 3a), with the sites having the lowest predicted annual rainfall (1 to 4) separated from the majority in the central section of the WTBR. The Hinchinbrook Island sites tended to separate from the mainland sites in both the classification and ordination analyses (although this and other recorded similarities between the classifications and ordinations may, to some degree, reflect the sampling scale, the use of presence/absence data and the concentration of DBH data into too few size classes).

Following the separation of southern WTBR sites, the next primary split in the species classification analysis was, interestingly, based upon the presence of *Grevillea pteridifolia*, (and *Cassytha filiformis* and *Themeda triandra*), and subsequently based upon *Casuarina equisetifolia* subsp. *incana*. Tracey (1982) noted that both these species were indicative of disturbance in *Melaleuca viridiflora* communities. The *Casuarina* formed small but often quite dense thickets in these woodland communities, sometimes resulting in the localised exclusion of the Tea-tree. The *Grevillea* was more dominant at mainland sites, particularly near roads and where fires were relatively recent or frequent, but probably also related to lack of salinity and lack of all-year round waterlogging in soil (RO Makinson pers. comm.).

Although some patterns emerged when other site data were superimposed on the species composition ordination (soil type and fire history), these appeared to be much less distinctive. Difficulties in classifying soil types from samples collected by auger are well documented, with this method one of the least preferred for site classification (McDonald et al. 1990). The isolation of many sites, coupled with the number investigated, precluded any more detailed methodologies (e.g. relatively large open pits) being employed. Furthermore, many of the characteristics used to distinguish the main soil types (gradational and duplex) are readily observed in auger samples. Accurately assessing the extent of these characteristics is, however, difficult. In addition, lowland soils are widely acknowledged as being highly variable over short distances (Mr M. Cannon, pers. comm.). This could result in a woodland community actually being situated on several variations of a given soil series, making classification of a site difficult at best. Future work could target this problem and ensure the soil types identified here are accurate.

Similarly, the accuracy of the fire history data is likely to be variable. Whilst some histories were obtained from records kept on conservation reserves, many were formulated solely from discussion with land-owners. The lack of accurately recorded fire histories has frustrated other researchers in tropical ecosystems (Bowman 1992), and remains a major obstacle to improved fire management of conservation reserves. An attempt at fire dating using *X. johnsonii* stem tissue scars proved unsuccessful and, furthermore, this species was not recorded at all sites. The use of *Xanthorrhoea* fire scars has been shown to be a useful method for determining past fire histories by researchers in temperate systems (Bulow-Olsen et al. 1982; Gill & Ingwersen 1976). Fire history and soil type may interact with climate, making detection of pattern with respect to single variables difficult. Furthermore, it is important that classification schemes are based not only on the species present, but also on measures of abundance, distribution, size and vigour (Kershaw & Looney 1985).

The most striking result from the multi-variate analyses of the structural data was the separation of those sites with annual

fire regimes (Sites 17 and 18). These sites had a collective total of only 10 *Melaleuca viridiflora* individuals in the four smaller DBH size classes (≤ 15 cm). Modal frequencies occur in the largest DBH size class (>36 cm), with moderate numbers of sprouts in the understorey. In comparison, sites with lower fire frequencies typically have more bell-shaped distributions across the size classes (e.g. Sites 1, 3, 6 and to a lesser extent Sites 13 and 16). The only other published data on the structure of similar *Melaleuca* communities also recorded a bell-shaped curve and, importantly, the community had remained unburnt for at least 20 years (Finlayson et al. 1993). The structure of frequently burnt communities suggests that recruitment of a midstorey, and, in the long-term, canopy is being prevented. This has drastic implications for the longevity of these communities and represents a large management challenge as the sites are both located outside the existing conservation reserve system.

These sites provide an ideal opportunity for future assessment, particularly if fire management practices can be altered. This would allow repeated monitoring to determine if a cohort of individuals can survive to the midstorey and beyond. Alternatively, if management practices are not adjusted, what is the long-term fate of these sites? Perhaps a change to grassland. This would, in effect, be the converse of research findings on Cape York where infrequent firing of grassland communities has resulted in *Melaleuca viridiflora* invasion and a more woodland-like community developing (Crowley & Garnett 1995). Alternatively, these woodlands may become dominated by other species that are known to become more prevalent following disturbances including fire (e.g. *Grevillea pteridifolia*, Tracey (1982)).

The seven themes of *Melaleuca viridiflora* woodlands identified by Stanton and Godwin (1989), although taking into account soil type and a degree of floristic information, make no allowance for a detailed assessment of community structure. This is also absent from other floristic (e.g. Specht et al. (1995)) or semi-quantitative classifications (e.g. Kemp et al. (1999)) of plant community conservation status relevant to the WTBR. Specht et al. (1995) consider that conservation of these open woodlands in Australia is adequate (the highest rating), whilst locally they are considered to have a conservation priority ranging from high (several themes) to medium (most themes) to low (one theme only) (Kemp & Morgan 1999; Kemp et al. 1999).

This research highlights the extensive variation in species composition and community structure exhibited by these communities, many of which have disappeared from localised areas of the landscape in the past 50 years (Skull 1998). Although some sites are in fact situated within the existing conservation system (especially within Hinchinbrook Island), many remain unprotected examples of either different species assemblages or structural types, some of which may represent different successional stages of the same community type or theme. Wilson (1996) has highlighted the need that some faunal groups have for

structural diversity within habitat types, a parameter he considered essential for biodiversity conservation. As recently as 1989, Themes 16 and 19 (accounting for more than half of the study sites investigated) remained poorly protected in the conservation reserve system (Stanton & Godwin 1989). This situation persists today. Until a more comprehensive range of the variation documented here becomes protected within conservation reserves and managed holistically across the landscape, the conservation status of these woodlands will remain well below ideal.

Past research efforts coupled with those of this study have recorded more than 300 plant and animal species from *Melaleuca viridiflora* open woodlands, with a further 12 orders of leaf and soil macro-invertebrates. This high biodiversity further underlines both the importance of these woodlands as an integral component of the WTBR lowland habitat mosaic, and the urgent need to improve their current conservation status.

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<i>Habenaria</i> sp.	12.5
<i>Haemodorum coccineum</i>	25.0
<i>Hibbertia melanioides</i>	8.3
<i>Ischaemum australe</i>	25.0
<i>Jacksonia thesioides</i>	8.3
<i>Lantana camara</i> *	8.3
<i>Lomandra</i> sp.	16.7
<i>Lophostemon suaveolens</i>	75.0
<i>Loranthaceae</i> sp.	16.7
<i>Melaleuca nervosa</i>	8.3
<i>Melaleuca viridiflora</i>	100
<i>Melastoma malabathricum</i>	62.5
<i>Myrmecodia beccarii</i>	33.3
<i>Orchidaceae</i> sp.	8.3
<i>Pandanus tectorius</i>	37.5
<i>Panicum</i> sp.	25.0
<i>Paspalidium</i> sp.	8.3
<i>Persoonia falcata</i>	25.0
<i>Petalostigma banksii</i>	8.3
<i>Phyllanthus virgatus</i>	8.3
<i>Pimelia</i> sp.	8.3
<i>Pinus caribaea</i> *	16.7
<i>Planchonia careya</i>	8.3
<i>Poaceae</i> sp.	8.3
<i>Restio</i> sp.	45.8
<i>Rhynchospora</i> sp.	16.7
<i>Ruellia</i> sp.	16.7
<i>Schoenus calostachyus</i>	29.2
<i>Scleria tricuspidata</i>	20.8
<i>Spermacoce brachystema</i>	12.5
<i>Striga curviflora</i>	12.5
<i>Stylidium</i> sp.	37.5
<i>Themeda triandra</i>	41.7
<i>Tricoryne anceps</i>	16.7
<i>Thysanotus banksii</i>	16.7
<i>Xanthorrhoea johnsonii</i>	75.0
<i>Xylomelum scottianum</i>	12.5
<i>Xyris</i> sp.	16.7