Research Report 5

Macrophyte vegetation of the Magela Creek flood plain, Alligator Rivers Region, Northern Territory

C. M. Finlayson, B. J. Bailey and I. D. Cowie

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ABSTRACT

Finlayson, C.M., Bailey, B.J. & Cowie, I.D. (1989). Macrophyte vegetation of the Magela Creek flood plain, Alligator Rivers Region, Northern Territory. Research Report 5, Supervising Scientist for the Alligator Rivers Region.

Ten major macrophyte communities have been identified on the Magela Creek flood plain, an area of 220 km^2, in northern Australia. Because of significant seasonal changes in vegetation each community is classified by its observed Wet season to early-Dry season vegetation, or otherwise given a general descriptive name. The *Melaleuca* open forest and woodland community covered 34% of the flood plain and Pseudoraphis and Oryza grasslands covered 14% and 12% respectively. Differences in the species composition of each community result from changes in the availability of water on the flood plain. The 222 plant species recorded from the flood plain were catagorised into the four habitat types: seasonally inundated plain, seasonally inundated fringe zone, permanent swamps, and permanent billabongs. One hundred and thirty nine annual species, 69 perennials and 14 geophytic perennial species were recorded on the flood plain. The seasonally inundated plain and fringe zone habitats respectively contained 41% and 71% of the plant species. The fringe zone contained 100 annual species (91 of which were terrestrial), the seasonally inundated plain 57, the permanent billabongs 19 and the permanent swamps 5. Seasonal variation of plant communities and the occurrence and extent of plant groups near billabong margins was related to the hydrological cycle on the flood plain. It is postulated that the duration of the period of inundation is a major determinant of the vegetation composition on the flood plain; the related factors of water flow velocity and water depth are also influential. Furthermore, it is hypothesised that the pattern of vegetation variation is a function of both the flooding and drying phases of the hydrological cycle on the flood plain.

1

Introduction

1.1 General

Magela Creek is located within the area defined by Fox et al. (1977) as the Alligator Rivers Region (ARR) in northern Australia, about 250 km east of Darwin (Fig. 1). The Ranger uranium mine is located in the Magela Creek catchment and has been operational since 1980. Downstream of the mine, Magela Creek is within the boundaries of Kakadu National Park (Stage II), proclaimed in February 1984. Government authorisation for the mining activities was largely dependent on conditions and guidelines recommended by the Ranger Uranium Environmental Inquiry (Fox et al. 1977), which were later developed into a series of Environmental Requirements.

The Inquiry speculated that the biota of the Magela Creek system could be at risk from the mining operation if waste water were to be released. While a policy of 'containing' water on the Ranger mine site was initially adopted it was recognised that future procedures may need to include controlled release of waste water. To assist in determining an acceptable operational policy for any such release a research program to collect and assess ecological information and to determine the fate of potential pollutants was initiated.

This paper contains a description of the macrophyte vegetation of a section of the creek watershed, generally referred to as the Magela flood plain, downstream of the Ranger uranium mine. The vegetation description was part of a project established to determine the role of the major plant species in retaining, cycling, and possibly recycling, of selected substances of concern on the flood plain. In describing the vegetation it was necessary to consider the dynamic and variable nature of the floodplain ecosystem. Transects established across the flood plain near a permanent billabong were used to document the extent of seasonal variation in the vegetation composition, whilst growth-strategy and growth-form attributes of the plant species were examined in an attempt to explain the nature of the variability.

Details of the study area and climate of the ARR are presented below. In addition, a brief description of previous botanical studies in the ARR and their relevance to the Magela flood plain is given.

1.2 The study area

The physical features of the ARR have been described by Galloway (1976) and Christian & Aldrick (1977). Bishop et al. (1986) have described the main aquatic habitats in the plateau, lowland and floodplain areas.

Magela Creek (Fig. 2) is a seasonally-flowing tributary of the East Alligator River with a catchment originating in a sandstone plateau, extending to wooded lowlands and thence into an extensive flood plain. The creek consists of five distinct sections: escarpment channels flowing through deep narrow gorges, braided sandbed channels with sandy levees, a series of billabongs and connecting channels (the Mudginberri Corridor), a seasonally inundated black-clay flood plain with permanent billabongs, and a single channel that discharges into the East Alligator River. Billabongs are defined as pools or lagoons in or near the creek channel, rather than as oxbow lakes as defined by Bayly & Williams (1977). Walker et al. (1984) have categorised the billabongs of Magela Creek into channel (depressions in flow channels), backflow (located on small tributaries and initially filled by water from the main creek) and floodplain (generally remnants of deep channels on the flood plain).

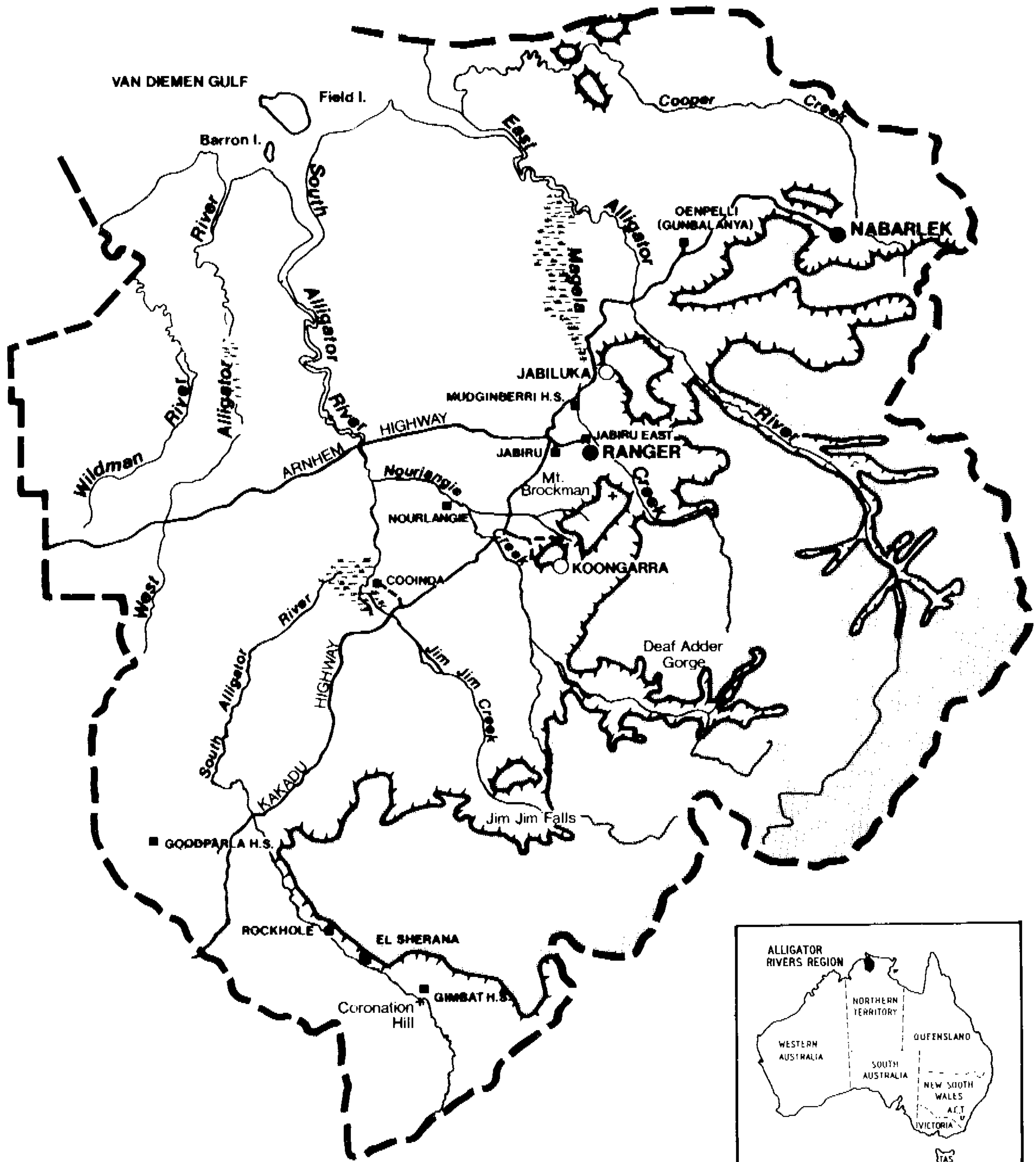

Figure 1. The Alligator Rivers Region[1]

[1]Outline of the Region is shown as it was at the time of the study, it has since been extended. [ed.]

This paper is concerned with the area encompassed by the Mudginberri Corridor and the black-clay flood plain, referred to here as the Magela flood plain. The Corridor is in effect a relatively narrow passage between opposing lowland slopes and is intermediate in character between the well-defined channels upstream and the flood plain downstream. The area referred to as the flood plain extends about 220 km^2, though up to 500 km^2 of land can be flooded by a 1 in 100 year flood event (Fox et al. 1977). The flood waters recede and evaporate during the dry months, leaving several large permanent swamps on the western side, along with a number of billabongs.

1.3 Climate

The climate of the region is monsoonal and has two dominant seasons, the Wet and the Dry. Annual rainfall at Jabiru averages 1560 mm, mostly falling during the Wet season which generally commences in November-December and lasts for 3-4 months. Both the onset and duration of the Wet season vary from year to year. Thunderstorms, tropical cyclones and barometric depressions are associated with the monsoon and are significant features of the Wet season. The wettest months are January-March with 250-350 mm, though November and December have over 150 mm on average. Cyclones occur during the Wet season and can result in destructive winds, torrential rain and flooding. Very little rain falls during the Dry season, though the amount that falls is more variable than during the Wet season (Taylor & Tulloch 1985).

Generalised descriptions of the pattern of rainfall and water flow in Magela Creek are provided by Sanderson et al. (1983) and Bishop et al. (1986). In brief, there is a period of intermittent storms that saturate the soil, followed by more consistent rains and wide-spread flooding. As rainfall increases, continuous flow is established in the braided channels and eventually in the Mudginberri Corridor before spilling out onto the black-clay flood plain. The flood plain can be covered with water up to several metres in depth. At the end of the Wet season, inflow from the catchment is reduced and after several months ceases altogether. Outflow from the flood plain to the East Alligator River can continue after all surface inflows stop. Evaporation of surface water late in the Dry season eventually dries the flood plain, except for isolated pockets of permanent water in billabongs and swamps. The large floodplain billabongs such as Nankeen, Jabiluka and Leichhardt (Fig. 2) persist throughout the Dry season. The number of waterholes that persist and the amount of water left in permanent billabongs varies from year to year.

1.4 Previous botanical studies in the Alligator Rivers Region

Lists of macrophytic plant species of the ARR have been compiled by a number of authors (e.g. Adams et al. 1973; Lazarides & Craven 1980). The most recent is a list of 1346 species, 71 of them alien, from 165 families, by Cowie & Finlayson (1986). The earliest description of the flora was that of Specht & Mountford (1958) which reported information collected by the 1948 American-Australian Expedition to Arnhem Land, and included a list of plant species collected on a 1928 expedition by Mackay (1929). Story (1976) described and mapped the major plant communities in the ARR. Widespread communities are: tall, open forests dominated by *Eucalpyptus miniata* and *Eucalyptus tetrodonta*; woodland dominated by *Erythrophleum chlorostachys* and broad-leaved bloodwoods, e.g. *Eucalyptus papuana, Eucalyptus latifolia*; and sandstone scrub containing various *Acacia* species. Communities that could be broadly described as 'wetlands' are less common and include paperbark (*Melaleuca*) forests, sedgelands, grasslands, herbaceous swamps, samphire flats and mangrove swamps. A similar group of communities was identified by Burgman & Thompson (1982) in the vicinity of Jabiluka Billabong, including part of the Magela flood plain (Fig. 2).

Specific information on aquatic vegetation of the Magela Creek catchment has been collected by Williams (1979), Morley (1981) and Sanderson et al. (1983). In seeking to

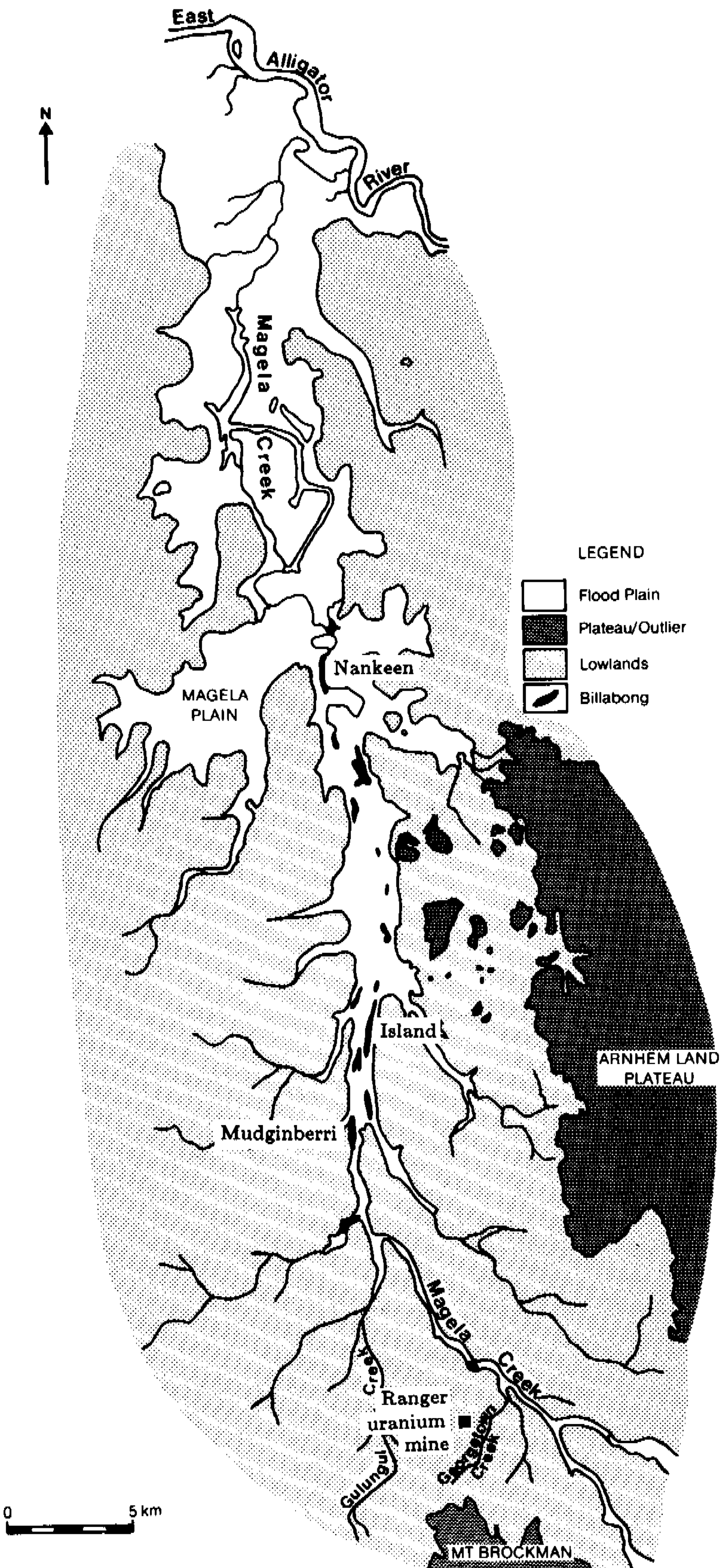

Figure 2. The Magela Creek flood plain

establish a relationship between vegetation and water flow patterns Williams (1979) identified six broad vegetation types that were regarded as direct indicators of water depth. However, the survey times and aerial photographs in Williams' study did not coincide with times of peak Wet season vegetation cover and biomass (April-May) and so the classification failed to identify communities containing different grass species, e.g. *Oryza meridionalis*, or take into account seasonal changes in the vegetation.

Morley (1981) mapped and classified peak Wet season (April) herbaceous aquatic vegetation on the flood plain south of Nankeen Billabong (Fig. 2). Distribution of the 36 communities recognised was largely attributed to the influence of flow conditions and water depth on the plants. As these particular community descriptions were not reproduced in subsequent Wet seasons a simpler and broader classification (Sanderson et al. 1983) was adopted.

2

Methods

2.1 Vegetation mapping

A broad generalised vegetation classification was prepared from Wet season vegetation maps and descriptions. During the Wet season many of the aquatic plants reach their peak biomass levels and are therefore easier to differentiate and map. The presence of terrestrial species, excluding trees, that reach their biomass peak at other times of the year was also considered in the general descriptions. Tree dominated communities were mapped by stereoscopic viewing of black and white aerial photographs. The crown separation criteria of Walker & Hopkins (1984) were used to classify the tree communities.

Grass, sedge and herb communities were mapped from a series of aerial colour photographs of the flood plain taken with a hand-held camera. Photographs were taken at the end of the Wet season (when grasses were at their peak), early in the Dry season (when *Eleocharis* communities were at their maximum) and late in the Dry season (when water level was lowest). Survey details are summarised in Table 1.

The aircraft used in the photographic surveys was flown at 150-300 m altitude and had its side door removed to aid photography. Photographs were taken during the middle of the day to minimise problems of light reflection from the water surface. A 35 mm colour transparency film (Kodachrome 25 and 64) was used with a 50 mm Pentax lens and either a Ricoh (with motor wind) or Pentax camera.

Major plant communities were delineated on the combined basis of interpretation of patterns of colour and texture in the aerial photographs and from surveys made on foot or in boats. Details of species composition, of communities, and of height of tree species were derived from field transects and field work incidental to the mapping over a period of 4 years (Table 1). Canopy cover of the grass, sedge and herb communities was not mapped because the species dominance and percentage canopy cover in these communities can vary from season to season. The boundaries between some communities are by necessity arbitrary, since the communities commonly intergrade and their margins vary with changes in water level.

Each mapping unit was named according to an observed indicator species over the Wet season to early-Dry season or else given a general descriptive name. The selected indicator species for each community may not be present throughout the complete annual cycle, but is the most abundant species present at the time of greatest plant biomass and diversity. The resultant map therefore emphasizes the temporal variations of species dominance and does not delineate the minor plant communities as identified by Sanderson et al. (1983).

2.2 Growth-strategy, growth-form and habitat classification of floodplain vegetation

All macrophyte species known to occur on the Magela flood plain were listed and assigned to growth-strategy, growth-form and habitat categories. The taxonomic nomenclature follows that used by Cowie & Finlayson (1986), although the authors are aware that several taxa (e.g. *Nymphaea*, *Eleocharis* and *Phyllanthes*) are under revision or require revision.

Species were divided into the broad categories of annuals or perennials to describe their growth strategy, with the former containing all of those species that usually complete their life-cycle in one year and depend on seeds to survive to the next growing season. The perennials were sub-divided to provide a separate list

Table 1. Details of vegetation surveys and mapping

Survey type	Date	Other details
Aerial; vertical black and white photography	Sept 1978	c. 1:50 000; non-stereoscopic
	June 1975	c. 1:25 000; stereoscopic
	Oct 1982	c. 1:33 000; stereoscopic
Aerial; oblique hand-held colour photography	12 April 1984 }	
	19 Nov 1984 }	
	7 June 1984 }	taken from 150-300 m altitude
	16 Dec 1985 }	
	4 June 1986 }	
Terrestrial; collection by hand	November, December 1983 and October 1984	8 transects
Aquatic; collection by hand	December 1984 - April 1986	fixed transects, bi-monthly
Incidental fieldwork	1983-1986	

for the geophytes i.e. those with underground perennating organs. The growth form was initially categorised as aquatic (A) or terrestrial (T), based on the definition of aquatic plants from Denny (1985) '..... pteridophytes, charophytes and spermatophytes with vegetative parts that are permanently or seasonally submerged in or emergent from, or float on the water surface'. Further division into grasses (g), trees (t), herbs (h), sedges (z), shrubs (c) or palms (p) was based on the classification of Walker & Hopkins (1984). The aquatic species were also separated into emergent (e), floating-leaved (f), submerged rooted (s), free-floating (b) and free-floating submerged (d) categories. Where appropriate a solidus (/) was used to indicate two possible growth forms for the one species.

The broad habitat classification included billabong (B), seasonally inundated plain (P), zone fringing the plain (F) and swamp (S).

2.3 Vegetation transects

Field surveys

A marker post was positioned on the western edge of the flood plain near Nankeen Billabong (Fig. 2). This post marked the origin of a transect running at a compass bearing of 90° and extending 650 m across the billabong to the flood plain on the eastern side of the billabong. Visual estimates of the relative ground cover (expressed as a percentage) of each species in 1 m^2 quadrats, spaced approximately 10 m apart along this transect, were made during the late-Wet (March), early-Dry (May), mid-Dry (July) and late-Dry (October) seasons of 1982. Water depth was recorded at each quadrat.

A collection of voucher specimens of all plant species located along the transect was placed in a herbarium maintained at the Alligator Rivers Region Research Institute (ARRRI), (Finlayson, Cowie & Brennan, unpublished).

Data analysis

Ordination (Detrended Correspondence Analysis (DCA)) and classification (TWINSPAN (two-way indicator species analysis)) techniques were used to analyse the transect data. These two techniques are complementary and are effective in summarising major trends in community data sets (Hill 1979*a,b*; Gauch 1982).

To define the plant groups (communities) which occurred on the flood plain, data from all four surveys were combined into a single matrix, classified and ordinated. Combining the data in this way allows them to be displayed in a manner which facilitates interpretation of the seasonal and spatial variation of the floodplain plant species. The distribution of the plant groups identified from the DCA and TWINSPAN analyses was mapped on transect profile diagrams.

The ordination axes produced by DCA were also tested for correlations between ordination scores, water depth and period of inundation of the sites to establish if these variables influenced the distribution of plant species. A correlation matrix was generated and Spearman correlation coefficients calculated.

Percentage species richness values were calculated for each plant community as follows:

$$\text{\% species richness} = \frac{\text{No. of species in plant community}}{\text{Total no. of species recorded for the transect}} \times 100$$

3

Results

3.1 Vegetation mapping

The 10 mapping units delineated as communities on the flood plain (Plate 1) are described below and discussed in terms of the wet-dry rainfall pattern. Changes in associated species are also discussed to provide a broad basis to the vegetation classification. An estimate of the area (ha) of each unit is given as well as the proportion (as a percentage) of the 220 km^2 of the flood plain which each unit occupied at the time of the survey.

Melaleuca open forest and woodland

Plate 2a; canopy cover 10-70%, 7390 ha, 34%: comprised areas dominated by one or more *Melaleuca* species - *Melaleuca viridiflora* and *Melaleuca cajaputi* around the edges and at the northern end of the flood plain, and *Melaleuca leucadendra* in back-swamps inundated for 6-8 months. The understorey varies, apparently in response to water depth and degree of shading. In areas with relatively dense canopies shade-tolerant species such as *Blyxa* spp. and *Najas tenuifolia* are common during the Wet season. In areas of faster flowing water at the southern end of the flood plain *Blyxa* spp. and *Caldesia oligococca* may be dominant. Other species that may be plentiful include *Nymphaea violacea, Nymphaea nouchali, Hygrochloa aquatica, Salvinia molesta* and *Nymphoides hydrocharoides*. Under the more open *Melaleuca* stands, the understorey is similar to that of the adjacent grasslands with *Pseudoraphis spinescens, Hymenachne acutigluma* and/or *Oryza meridionalis* present. During the Dry season the understorey may be absent, owing to the presence of a thick layer of leaves on the ground beneath the most dense forest, or consist of perennial grasses (*Pseudoraphis spinescens* or *Hymenachne acutigluma*), terrestrial herbs (e.g. *Glinus oppositifolius, Centipida minima, Phyllanthus* spp., *Desmodium* spp.), annual grasses (e.g. *Echinochloa colona, Paspalum scrobiculatum*), and/or sedges (e.g. *Cyperus polystachyos, Cyperus compressus*).

Melaleuca open woodland

Canopy cover less than 10%, 1290 ha, 6%: consists of *Melaleuca leucadendra* in areas inundated for over 6 months. Understorey species are usually the same as those in adjacent areas of the flood plain; these include the grasses *Pseudoraphis spinescens, Hymenachne acutigluma* and *Oryza meridionalis* and the herbs *Nelumbo nucifera* and *Nymphoides indica*. Annual herbs can replace *Oryza meridionalis* during the Dry.

Nelumbo-Nymphoides herbland

Plate 2b; 2090 ha, 9%: a mixed community seemingly dominated by the water lilies *Nelumbo nucifera* and *Nymphoides indica* that occur in permanently and semi-permanently wet areas. The perennial, emergent or floating-leaved *Nelumbo nucifera* can form very dense stands, particularly during the Dry season. In areas that dry out seasonally it occurs as an annual, flowering at the end of the Wet season. Floating mats of the perennial grasses *Hymenachne acutigluma* and *Leersia hexandra* with *Ludwigia adscendens* and the mat colonising sedge *Cyperus platystylis* are commonly present. The small floating species *Azolla pinnata* and *Spirodela polyrhiza* also occur. In permanently flooded areas the tall emergent sedge *Hymenochaeta grossa* can form dense clumps late in the Dry season. *Nymphoides indica, Nymphaea macrosperma, Nymphaea violacea*, and *Utricularia* spp. commonly occur in more open water during the Dry season. The submerged *Chara* sp., a

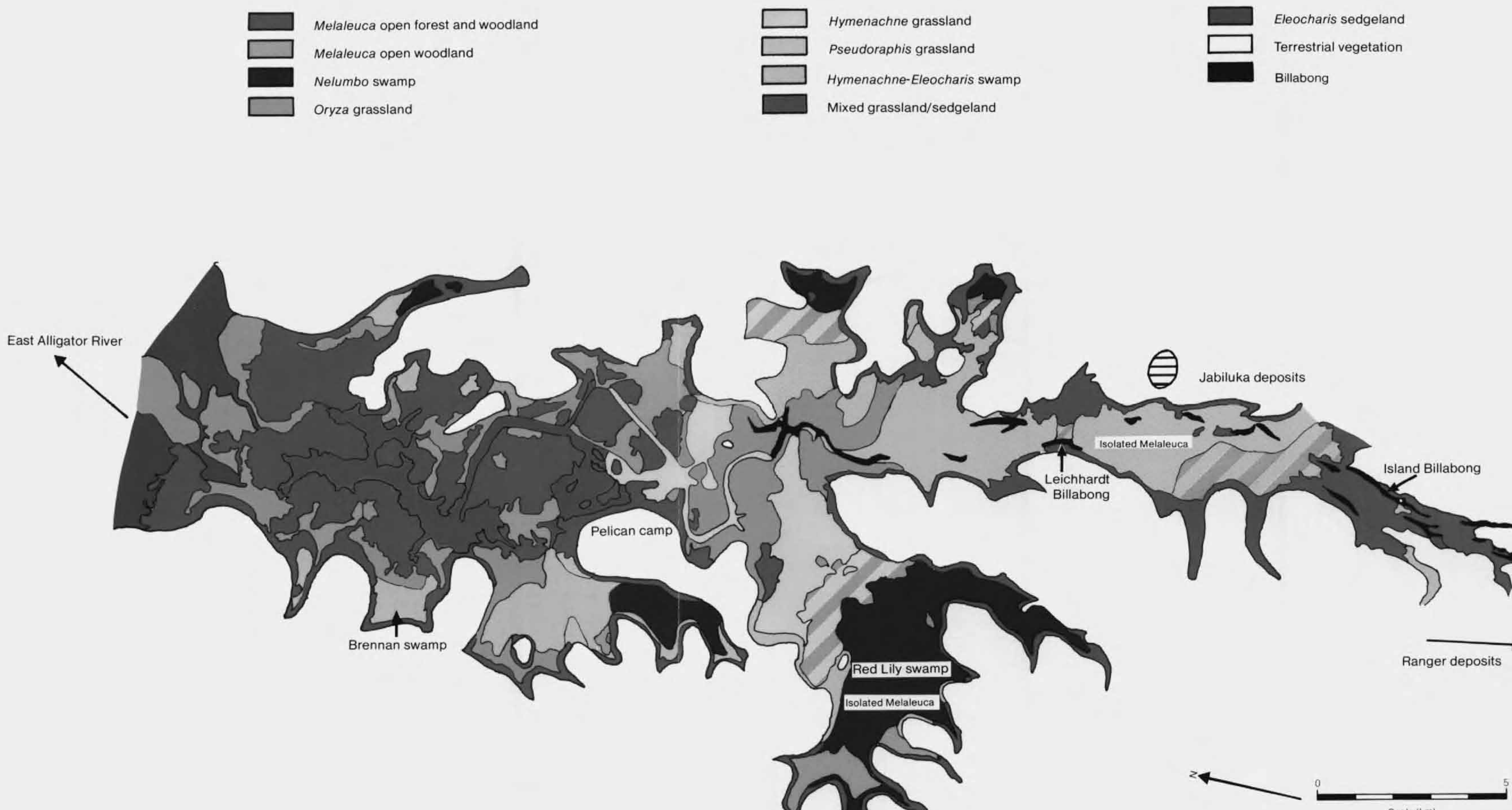

Plate 1. Vegetation communities on the Magela flood plain

macrophytic species of algae, becomes increasingly abundant at the end of the Dry season, sometimes completely dominating areas devoid of emergent or floating species. Other species present include *Melaleuca leucadendra*, *Najas tenuifolia*, *Hydrilla verticillata* and *Vallisneria gigantea*. *Eleocharis* spp. clumps can also occur.

Oryza grassland

Plate 2c; 2730 ha, 12%: dominated by *Oryza meridionalis* towards the end of the Wet season. In the Dry season it consists largely of bare ground and dead *O. meridionalis* stems with persistent *Phyla nodiflora* and *Ludwigia adscendens* as xerophytic forms, and *Pseudoraphis spinescens*. Early-Wet season storms cause germination of the annual species *O. meridionalis*, *Digitaria* sp., *Aeschynomene* spp., *Hygrochloa aquatica*, *Heliotropium indicum* and *Coldenia procumbens*. *H. aquatica* and *P. nodiflora* may be dominant at this time. The pattern of storms is influential on the subsequent success of these species. Once flooding occurs, aquatic species such as *Maidenia rubra*, *Isoetes muelleria*, *Blyxa* spp., *Nymphoides* spp., *Nymphaea hastifolia* and *Eleocharis* spp. may occur. During the drying out phase *Ludwigia adscendens*, *Ipomoea aquatica* and *Utricularia* spp. increase in abundance whilst herbs, e.g. *Commelina lanceolata*, are common on the wet mud.

Hymenachne grassland

Plate 2d; 1930 ha, 9%: dominated by *Hymenachne acutigluma* throughout the year. Minor species present include *Aeschynomene* spp., *Ludwigia adscendens*, *Spirodela polyrhiza*, *Azolla pinnata*, *Lemna aequinoctialis*, *Nymphaea violacea*, *Oryza meridionalis* and *Pseudoraphis spinescens*. The naturalised exotic grass *Urochloa mutica* (formerly *Brachiaria mutica*) appears to be invading this community. *Nelumbo nucifera* can form dense clumps in this community.

Pseudoraphis grassland

Plate 2e; 3050 ha, 14%: dominated by the perennial emergent grass *Pseudoraphis spinescens* which has a turf-like habit during the Dry season and grows up through the water during the Wet season. Times of flowering and senescence appear related to the pattern of flood events. At the end of the Wet season this grass flowers and senesces within a 2-4 week period. Other species such as *Eleocharis* spp., *Najas tenuifolia*, *Nymphaea violacea* and *Utricularia* spp. also respond to stable water levels and become more abundant. The annual grass *Hygrochloa aquatica* occurs on shallow fringes and banks in this community. On the southern part of the flood plain this community covers an undulating topography with *P. spinescens* and *Blyxa octandra* dominant on the mounds and *Najas tenuifolia* and *Nymphaea violacea* dominant in depressions during the Wet season (Sanderson et al. 1983). During the Dry season *P. spinescens*, *Fimbristylis aestivalis* and *Cyperus* sp. (*Cyperus digitatus*?) occupy the mounds and *Glinus oppositifolius* and *Heliotropium indicum* the depressions. If the areas remain wet late into the Dry season, *Eleocharis dulcis* can dominate the mounds with *Nymphaea violacea* occurring in the depressions. The floating weed *Salvinia molesta* is becoming more prevalent amongst *P. spinescens*, especially in channels and depressions on the western side of the flood plain.

Hymenachne-Eleocharis grass-sedgeland

Plate 2f; 1290 ha, 6%: consists of swampy areas that dry out seasonally and are dominated by *Hymenachne acutigluma* or *Eleocharis* spp., which are slower to establish themselves. Long periods of shallow water appear to favour the latter. These swamps generally remain inundated for about 9 months. In deeper areas *Nymphoides indica* may be abundant. This grass-sedgeland community is mainly found in back-swamps on the northern part of the flood plain.

Mixed grass-sedge-herbland

Plate 2g; 1120 ha, 5%: contain a variety of species, the dominant species depending on the topographic situation. *Oryza meridionalis* occurs on the driest sites with *Pseudoraphis spinescens* in slightly wetter


a
b
c
d
e
f
g
h

places, while *Eleocharis* spp. and *Hymenachne acutigluma* occur in the deeper sites. On sites that remain flooded for 10-11 months *Nymphoides indica, Nymphaea macrosperma* and submerged species may also be present. This community occurs along drainage channels on the northern part of the flood plain.

Eleocharis sedgeland

Plate 2h; 960 ha, 4%: *Eleocharis* spp. dominate during the Wet season, but are replaced by annual herbs such as *Glinus oppositifolius, Coldenia procumbens, Phyla nodiflora, Heliotropium indicum* and *Cardiospermum halicacabium* during the Dry season. This community only occurs in shallow flooded areas near the merging of the Magela flood plain with that of the East Alligator.

Open-water community

160 ha, 1%: permanent billabongs, flow channels and seasonal, shallow waterholes contain *Nymphaea macrosperma* and *Nymphaea pubescens* and a number of submerged species. The latter include *Najas tenuifolia* during the Wet season, changing to *Ceratophyllum demersum* and *Hydrilla verticillata* during the Dry. The western banks of the billabongs are generally fringed with the trees *Barringtonia acutangula, Pandanus aquaticus, Melaleuca* spp. and the vines *Aniseia martinicensis* and *Merremia gemella.* Associated with this fringe is a floating mat of *Leersia hexandra, Hymenachne acutigluma* and *Ludwigia adscendens* and the alien species *Brachiaria mutica* and *Salvinia molesta.*

Plate 2 *(opposite).* Macrophyte vegetation of the Magela Creek flood plain

a. Melaleuca open forest and woodland in Mudginberri Corridor (November 1985)
b. *Nelumbo nucifera* (September 1983) in an area of Nelumbo-Nymphoides herbland
c. Oryza grassland (April 1984)
d. Hymenachne grassland (April 1984)
e. Pseudoraphis grassland (December 1983)
f. Hymenachne-Eleocharis grass-sedgeland (June 1985)
g. Mixed grass-sedge-herbland (November 1984)
h. Eleocharis sedgeland (June 1985)

3.2 Growth strategy, growth form and habitat classification of floodplain vegetation

The flood plain supports a total of 222 identified plant species. The occurrence of these species in 4 broad habitats - seasonally inundated plain, seasonally inundated fringe zone, billabong and permanent swamp - is given in Appendix 1 and summarised in Table 2. The fringe zone category takes in the edge of the seasonally inundated plains and therefore includes the extensive fringing Melaleuca forest/woodland. The seasonally inundated plain category includes the remainder of the flood plain except for the permanently wet areas. The four habitat categories are purposefully broad as the demarcation between areas is not always clear and transitional zones occur.

The seasonally inundated plain and the fringe zone contain 41% and 71% respectively of the 222 species compared with 20% in the billabongs and 10% in the permanent swamps (Table 2); the first two habitats contain a greater proportion of annual species. Annuals generally complete their life cycle in one year and have a carry over of seeds to the next growing season. On the flood plain, however, some species usually regarded as annuals are able to survive for several years and should be regarded as short-lived perennials, or perhaps as facultative annuals. *Vallisneria spiralis* and *Najas tenuifolia* are two examples of species that are true annuals in the seasonally inundated habitats, but are facultative annuals in the permanently wet habitats. All facultative annuals are listed with the true annuals.

Of the 139 annual species 102 are terrestrial and 37 aquatic with one, *Rotala ocultiflora*, difficult to classify. Eighty-nine of the terrestrial species occur in the fringe zone; only 27 are found on the seasonally inundated plain. The seasonally inundated plain has a longer period of inundation than the fringe zone. The terrestrial annuals are a diverse group of species, that do not constitute a large proportion of the total standing crop on the flood plain. Sixty of them are classified as herbs, 18 as sedges and 17 as grasses. Twenty-seven of the aquatic annuals are herbs with *Ceratophyllum demersum*, *Najas tenuifolia* and *Nymphoides hydrocharoides* being amongst the more common species. The aquatic grasses, *Oryza meridionalis* and *Hygrochloa aquatica* are the most common species in the seasonally inundated areas.

There are 68 perennial species, 50 of which occur in the fringe zone (Table 2); 37 do not occur elsewhere on the flood plain (Appendix 1). Thirty-four of the perennial species are terrestrial, 26 aquatic, with 8 others difficult to classify. The latter includes five *Melaleuca* species that dominate large areas of the fringe zone and the seasonally inundated plain. There are 12 terrestrial trees including *Eucalyptus* spp., *Lophostemon lactifluus*, *Pandanus spiralis* and *Syzygium suborbiculare*. The aquatic species are dominated by 12 herbs, including *Hydrilla verticillata*, *Ludwigia adscendens*, *Nelumbo nucifera* and *Nymphoides indica*, and by five grasses, including the widespread *Hymenachne acutigluma* and *Pseudoraphis spinescens*.

The geophytic perennials comprise 14 species, six of them herbs confined to the fringe zone. The more widespread species include three *Eleocharis* and five *Nymphaea* species, all of which are aquatic.

The list in the Appendix contains 21 alien species (13 annuals and 8 perennials). Ten of the annuals are terrestrial species with the shrub *Hyptis suaveolens* prevalent in the fringe zone. The perennial alien species include the terrestrial shrubs *Sida* spp., the vine *Passiflora foetida* and the herb *Stylosanthes hamata*, and two aquatic species, *Mimosa pigra* and *Salvinia molesta*.

Table 2. Plant species found in four broad habitat areas on Magela flood plain

See Appendix for details

Habitat	Total no. of species	Annuals	Perennials	Geophytic perennials
Permanent billabongs	46	19	21	6
Seasonally inundated plain	94	57	29	8
Fringe zone	158	100	50	8
Permanent swamps	21	5	11	5

3.3 Vegetation transects

Twenty-seven species were identified along the transect. The actual number present, however, was possibly higher as some species e.g. *Nymphaea* spp. were difficult to identify. The maximum number of species (17) was recorded during the late-Wet season and the minimum (8) during the late-Dry season.

There were seven major plant groups (communities) in the study area. Transect profiles which illustrate the dominant species at each site and the spatial and temporal distribution of the seven communities are shown in Fig. 3, which also shows a dendrogram of the site classification, with indicator species at each division. Some communities were dominated by aquatic annual species (e.g. groups 2 and 3) and only occurred in the Wet season, whereas other communities were present during both the Wet and Dry seasons (e.g. groups 1 and 4). More detailed profile diagrams are given in Fig. 4. A scatter plot of the DCA ordination is given in Fig. 5. The sites which comprise each of the seven communities are listed in Table 3 while Table 4 lists the species composition of the communities. Although TWINSPAN and DCA produced comparable results, some sites were misclassified. Misclassified sites (indicated in Table 3) generally contained

Table 3. Sites comprising the seven plant groups identified by TWINSPAN and DCA

The month sampled and distance along transect (m) are given for each site; misclassified sites are indicated by an asterisk.

Plant group/dominant species						
1	2	3	4	5	6	7
Nymphaea	Hygrochloa	Oryza	Pseudoraphis 1	Ludwigia	Pseudoraphis 2	Eclipta
Mar. 400	Mar. 0	*Mar. 375	Mar. 300	May 0	*May 20	Oct. 40
Mar. 425	Mar. 10	Mar. 575	Mar. 350	May 10	*May 40	Oct. 60
Mar. 545	Mar. 20	Mar. 580	Mar. 370	May 30	July 0	Oct. 70
Mar. 550	Mar. 40	Mar. 590	*May 60	May 40	July 10	Oct. 80
Mar. 560	Mar. 50	Mar. 610	*May 70	May 50	July 20	Oct. 90
May 390	Mar. 80	Mar. 630	May 260	May 80	July 30	Oct. 100
May 400	Mar. 115	Mar. 650	May 290	May 90	July 40	Oct. 110
May 410	Mar. 150		May 300	May 100	July 50	Oct. 120
May 420	Mar. 180		May 310	May 110	July 60	Oct. 130
May 430	Mar. 220		May 320	May 120	July 70	Oct. 140
May 540	Mar. 260		May 330	May 130	July 200	Oct. 150
May 550	Mar. 280		May 340	May 140	July 210	Oct. 160
May 560			May 350	May 150	July 220	Oct. 170
July 390			May 370	May 160	July 230	Oct. 180
July 400			May 380	May 170	July 240	Oct. 190
July 410			May 570	May 180	July 250	Oct. 200
July 420			May 580	May 190	July 260	Oct. 210
July 530			May 590	May 210	July 270	Oct. 220
July 540			May 620	May 220	July 280	
July 550			July 300	May 230	July 290	
Oct. 390			July 310	May 240	July 570	
			July 320	May 250	July 580	
			July 330	May 270	July 590	
			July 340	May 280	July 600	
			July 350	July 90	July 610	
			July 360	July 110	July 620	
			July 370	July 120	July 630	
			July 380	July 130	July 640	
				July 140	July 650	
				July 150	*Oct. 50	
				July 160	Oct. 230	
				July 170	Oct. 240	
				July 180	Oct. 250	
				July 190	Oct. 260	
					Oct. 270	
					Oct. 280	
					Oct. 290	
					Oct. 300	
					Oct. 310	
					Oct. 320	
					Oct. 330	
					Oct. 340	
					Oct. 350	
					Oct. 360	
					Oct. 370	
					Oct. 380	
					Oct. 560	
					Oct. 570	
					Oct. 580	
					Oct. 590	
					Oct. 600	
					Oct. 610	
					Oct. 620	
					Oct. 630	

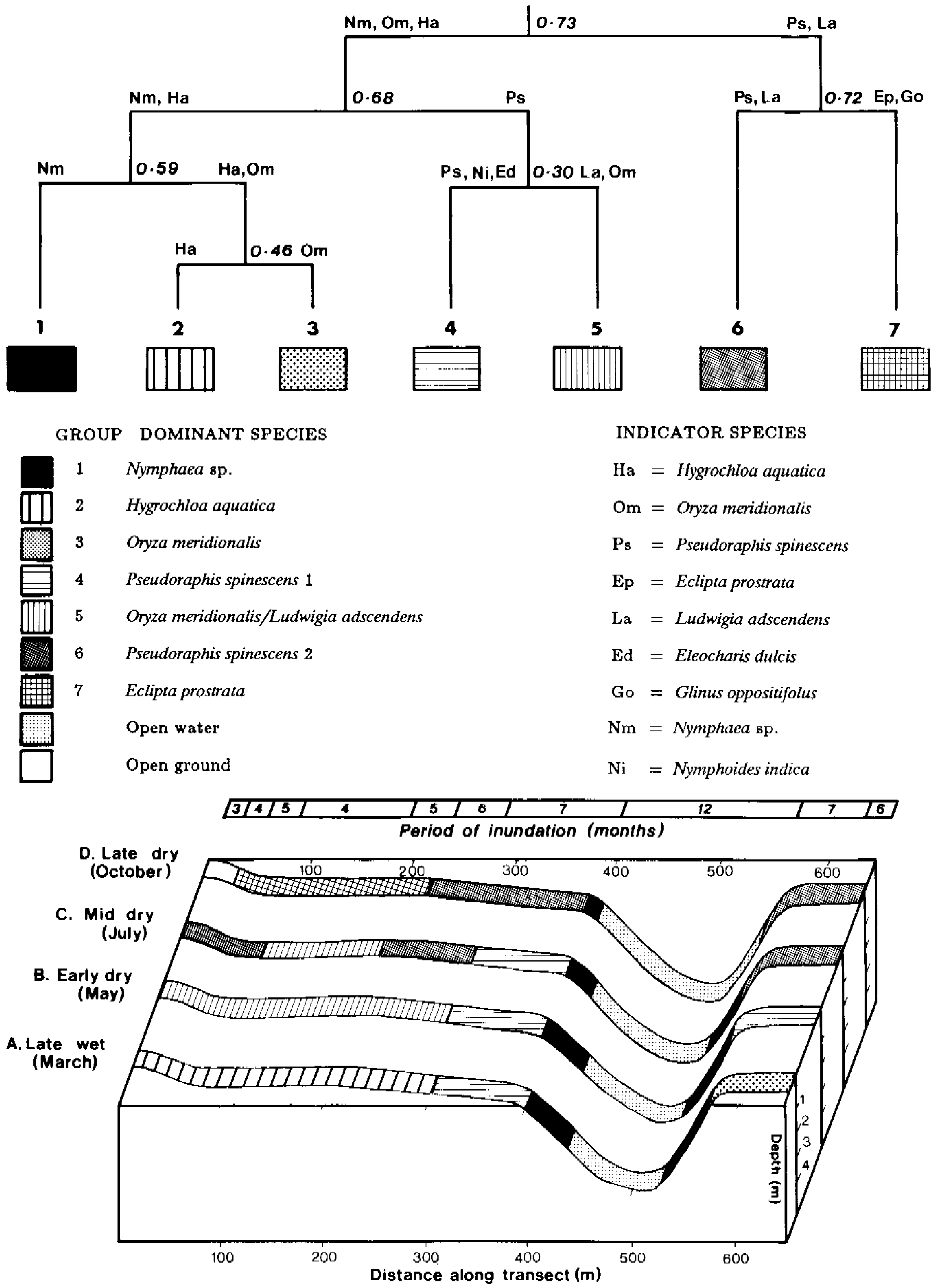

Figure 3. Dendrogram divisions produced by TWINSPAN analysis of the sites on the vegetation transects: indicator species and eigen-values at each division are given. Also shown is the spatial and temporal distribution of the seven plant groups recognised by TWINSPAN and DCA.

only one or two species (with low relative groundcover values), or were sites located in transitional zones between plant communities.

Sanderson et al. (1983) after 4 years of observation prepared a scheme which depicted five hydrological periods important to the seasonal growth of plants on the Magela flood plain. The results from the four transect surveys are described in the context of this scheme.

Late-Wet season survey (March)

Aquatic plants grew rapidly after inundation of the flood plain and by March the plant communities were well-developed. Four plant groups, containing a total of 17 species, were identified on the transect at this time. *Hygrochloa aquatica*, an aquatic annual grass dominated one community and was present at 80% of sites surveyed. The other plant communities were dominated by *Pseudoraphis spinescens* (Group 4), *Nymphaea* sp. (Group 1) and *Oryza meridionalis* (Group 3). The composition and structure of the groups (communities) are described below (refer to Fig. 3, Fig. 4a and Table 4).

Group 1: Nymphaea *sp. dominated sites*

Nymphaea sp., a large floating-leaved water lily with underground corms, dominated sites along the banks of the billabong (Fig. 4a). *Nymphaea* plants with leaves floating on the water surface have been recorded growing in 4.5 m of water, but were usually in water < 3.0 m deep. Although the *Nymphaea* group was present throughout the Wet and Dry seasons it had low species richness (species richness = 18%). *Limmophila australis* and *Najas tenuifolia* were the only other members of this group present during the late-Wet season.

Group 2: Hygrochloa aquatica *dominated sites*

Group 2 occupied the shallow section of the transect (< 1.8 m deep) and was prevalent only during the Wet season. Group 2 sites were dominated by *Hygrochloa aquatica* (a floating-leaved annual grass which formed a dense, almost continuous mat of vegetation); small clumps of *Oryza meridionalis* were present while *Ludwigia adscendens*, *Nymphoides indica*, *Utricularia exoleta*, *Najas tenuifolia* and *Eleocharis dulcis* occurred infrequently (species richness = 22%).

Group 3: Oryza meridionalis *dominated sites*

Group 3 also occurred only during the Wet season and was dominated by a sparse cover of *Hygrochloa aquatica* with dense emergent stands of *Oryza meridionalis*. This group, although similar in appearance to Group 2, had higher percentage cover values for *Oryza meridionalis* and contained more species (species richness = 51%).

Group 4: Pseudoraphis spinescens *dominated sites*

Group 4 sites were dominated by the aquatic form of *Pseudoraphis spinescens* and contained 17 of the 27 species collected during the surveys (species richness = 62%). Twelve Group 4 species were present during the late-Wet season. Dense aggregations of *Ceratophyllum demersum* and *Myriophyllum diococcum* occurred as pockets within the *Pseudoraphis spinescens* mat. *Nymphoides indica* (TWINSPAN indicator species) was also conspicuous while *Azolla pinnata* (aquatic fern) occurred infrequently.

Early-Dry season survey (May)

During the late-Wet to early-Dry season period, described as the 'draw-down' phase by Sanderson et al. (1983), rainfall ceased and the water level dropped rapidly, before eventually stabilising. This resulted in pronounced changes in the appearance of the vegetation. In the shallow section of the transect (0-300 m along the transect), *Hygrochloa aquatica* (Group 2) was replaced by Group 5 (Fig. 3) after the *H. aquatica* plants had senesced and large amounts of decaying plant material were deposited on the flood plain. Similarly,

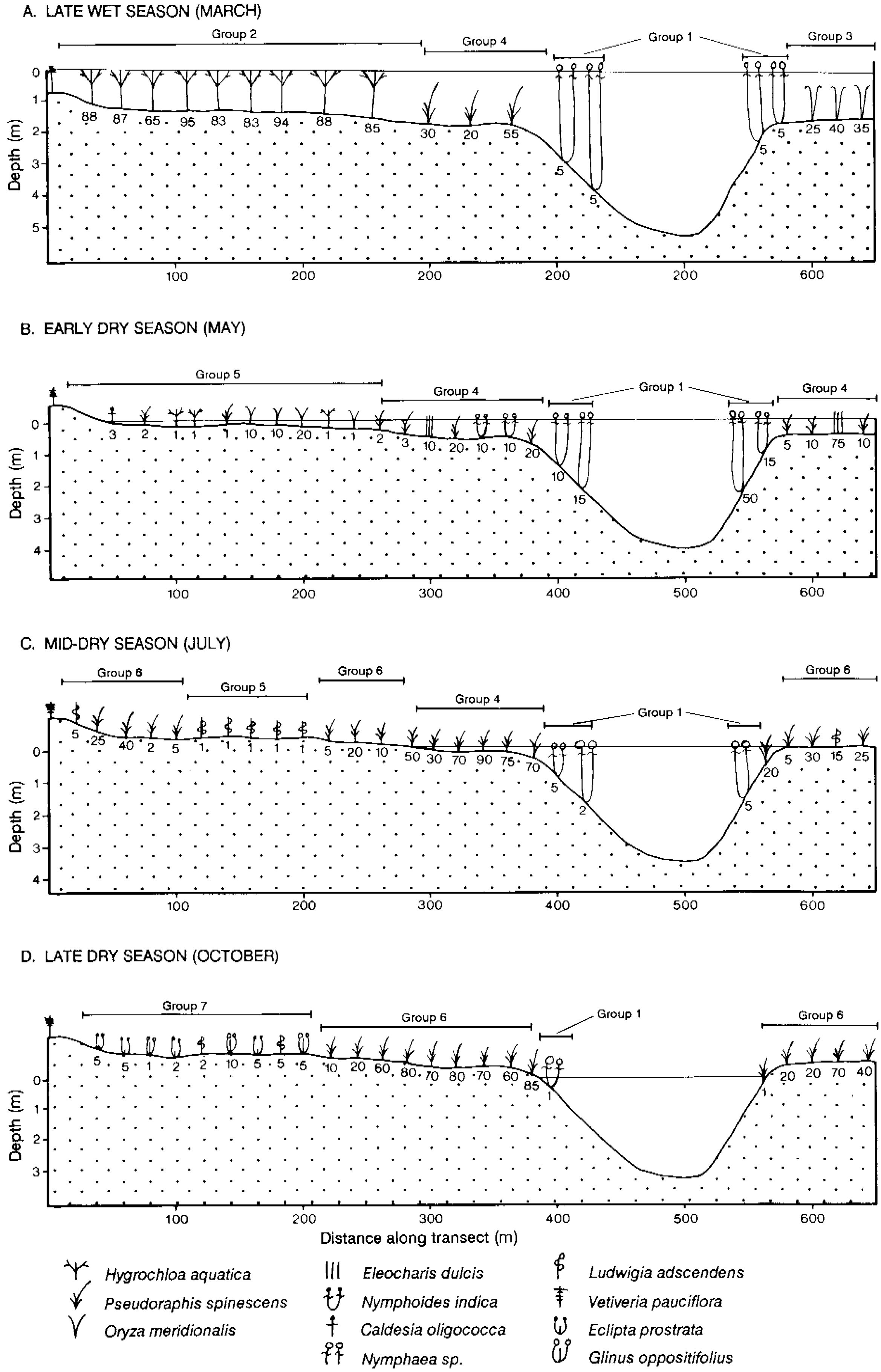
A. LATE WET SEASON (MARCH)
Group 2
Group 4
Group 1
Group 3
B. EARLY DRY SEASON (MAY)
Group 5
Group 4
Group 1
Group 4
C. MID-DRY SEASON (JULY)
Group 6
Group 5
Group 6
Group 4
Group 1
Group 6
D. LATE DRY SEASON (OCTOBER)
Group 7
Group 6
Group 1
Group 6
Depth (m)
Distance along transect (m)
Hygrochloa aquatica
Pseudoraphis spinescens
Oryza meridionalis
Eleocharis dulcis
Nymphoides indica
Caldesia oligococca
Nymphaea sp.
Ludwigia adscendens
Vetiveria pauciflora
Eclipta prostrata
Glinus oppositifolius

Table 4. Species composition of the seven plant groups identified on the Nankeen Billabong transect.

	Group						
	1	2	3	4	5	6	7
Aquatic annual species							
Najas tenuifolia	x	x		x	x		
Hygrochloa aquatica		x	x	x	x		
Utricularia aurea	x			x			
Utricularia exoleta		x		x			
Ceratophyllum demersum			x	x			
Limnophila australis	x		x	x			
Maidenia rubra			x				
Oryza meridionalis		x	x	x	x		
Caldesia oligococca			x	x			
Ipomea aquatica			x	x		x	
Myriophyllum dicoccum				x			
Marsilea mutica							
Aquatic perennial species							
Nymphoides indica		x	x	x			
Hydrilla verticillata	x						
Azolla pinnata			x	x			
Aquatic geophytes							
Nymphaea sp.	x		x	x			
Eleocharis dulcis		x	x	x			
Aquatic/terrestrial perennials							
Pseudoraphis spinescens			x	x	x	x	
Ludwigia adscendens		x	x	x		x	x
Polygonum attenuatum			x	x	x	x	
Terrestrial annual species							
Phyla nodiflora					x	x	
Glinus oppositifolius							x
Heliotropium indicum						x	x
Eclipta prostrata					x	x	x
Centipeda minima							x
Coldenia procumbens					x	x	x
Alternanthera nodiflora							x

Percentage species richness

Group 1: 18.5 Group 2: 22.0 Group 3: 51.0 Group 4: 62.0 Group 5: 29.6 Group 6: 37.0 Group 7: 26.0

Pseudoraphis spinescens (Group 4) replaced *Oryza meridionalis* (Group 3) as the dominant species in sites 575-650 m along the transect. In contrast, the floristic composition of Group 1 sites (*Nymphaea* sp.) altered little during the 'draw-down' phase.

The composition and structure of the plant groups which occurred on the transect during the early-Dry season are described below (refer to Fig. 3, Fig. 4b and Table 4).

Figure 4 *(opposite)*. Transect profile diagrams showing the species dominant at each site and the distribution of the seven groups recognised by TWINSPAN and DCA. The percentage cover estimates for each quadrat are presented beneath the species symbols on each transect

Group 1: Nymphaea *sp. dominated sites*

Nymphaea sp. was abundant at this time and formed a conspicuous 'belt' along the water's edge in Nankeen Billabong. *Utricularia aurea* was the only other species to occupy the Group 1 sites at this time.

Group 4: Pseudoraphis spinescens *dominated sites*

The number of sites dominated by *Pseudoraphis spinescens* increased during the 'draw-down' phase and included sites previously dominated by *Oryza meridionalis* (Group 3). Fourteen Group 4 species were present during the early-Dry season with *Pseudoraphis spinescens* and *Nymphoides indica* being abundant. Clumps of *Eleocharis dulcis* were also conspicuous.

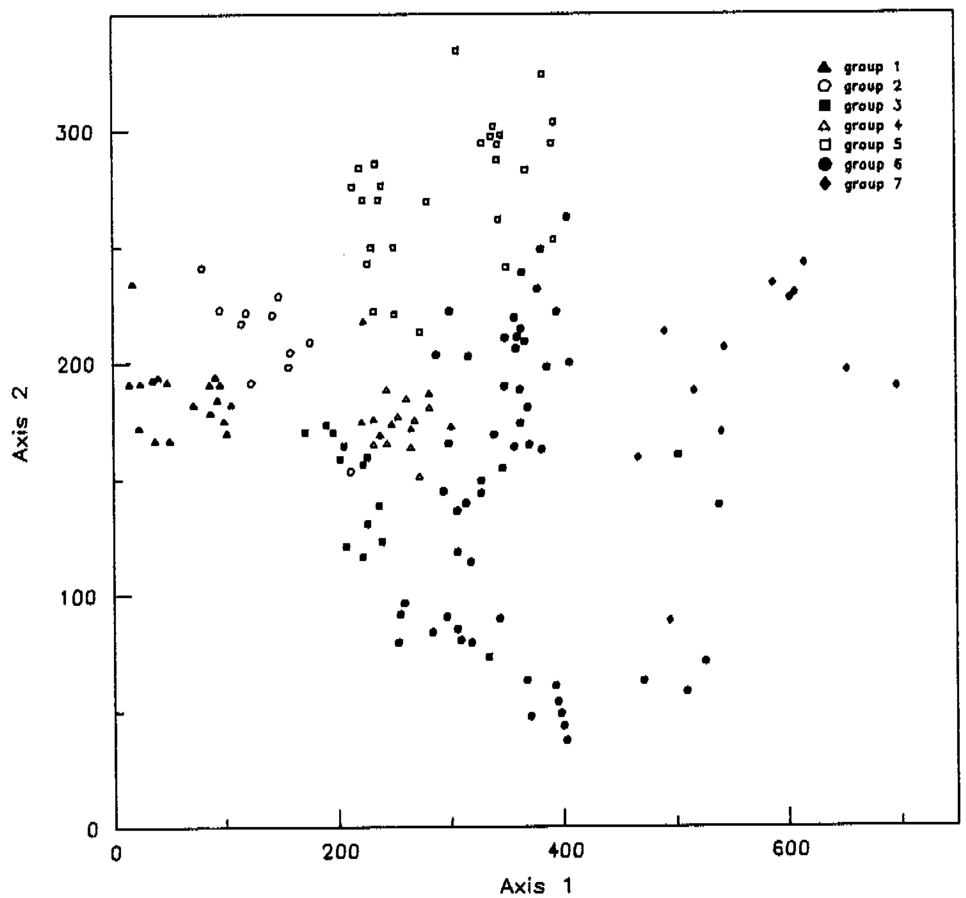

Figure 5. DCA ordination of vegetation transect sites with groups recognised by TWINSPAN superimposed

Utricularia exoleta was widespread and formed tangled masses amongst the stems of the dominant species.

Group 5: Oryza meridionalis/Ludwigia adscendens *dominated sites*

TWINSPAN and DCA separated from Group 4 those floodplain sites where *Pseudoraphis spinescens* was absent, or low in abundance - the Group 5 sites. Group 5 included the shallow floodplain sites previously dominated by *Hygrochloa aquatica* (Group 2). Some *Hygrochloa aquatica* plants remained scattered amongst a mat of decaying vegetation. Other members of this group, all with low percentage-cover values, included *Oryza meridionalis, Caldesia oligococca, Eleocharis dulcis* and *Ludwigia adscendens*, the TWINSPAN indicator species (species richness = 30%).

Mid-Dry season survey (July)

As the Dry season progressed ('drying out phase' - Sanderson et al. (1983)), and the surface waters evaporated from inundated sites, aquatic plants declined and were replaced by terrestrial species. The terrestrial form of *Pseudoraphis spinescens* (Group 6) was widespread, invading sites previously inhabited by Group 4 and Group 5 species (Fig. 3). Although some 'aquatic' species persisted on dry land as reduced xerophytic forms (e.g. *Ludwigia adscendens* and *Polygonum attenuatum*) most relied on seeds or underground perennating organs to survive the Dry season.

TWINSPAN and DCA analysis recognised 4 groups for this survey (see Fig. 3, Fig. 4c and Table 4).

Group 1: Nymphaea *sp. dominated sites*

The *Nymphaea* sp. zone in shallow water at the margins of the billabong diminished as the Dry season progressed. *Nymphaea* sp., *Hydrilla verticillata* and *Utricularia aurea*, all with low percentage-cover values, were the only species to occupy the deep water sites during the mid-Dry season.

Group 4: Pseudoraphis spinescens *(aquatic) dominated sites*

Pseudoraphis spinescens was abundant on the inundated floodplain sites (300-380 m) where it attained percentage-cover values as high as 90%. In comparison, the percentage cover of this species on dry sites (Group 6) was generally less than 40%. *Nymphoides indica, Eleocharis dulcis* (TWINSPAN indicator species) and *Ludwigia adscendens* were common, whereas submerged species such as *Utricularia aurea* and *Utricularia exoleta* occurred infrequently. In total, nine species occupied the Group 4 sites during the mid-Dry season.

Group 5: Ludwigia adscendens *dominated sites*

During the early to mid-Dry season period the terrestrial form of *Pseudoraphis spinescens* (Group 6) invaded many of the Group 5 sites. In addition to *Ludwigia adscendens*, four herbaceous terrestrial species were recorded - *Heliotropium indicum, Coldenia procumbens, Glinus oppositifolius* and *Phyla nodiflora.*

Group 6: Pseudoraphis spinescens *(terrestrial) dominated sites*

Group 6 occupied 51% of the sites surveyed during the mid-Dry season and comprised the terrestrial form of *Pseudoraphis spinescens, Ludwigia adscendens* and *Polygonum attenuatum* as well as several terrestrial herbaceous species.

Late-Dry season survey (October)

Towards the end of the Dry season, described as the 'dry-plains phase' by Sanderson et al. (1983), all of the floodplain section of the transect was dry (i.e. without surface water). Aquatic plants were restricted to the billabong or were present on the flood plain as reduced 'dry-land' forms or perennating organs. Typical of this period was the growth and maturation of terrestrial grasses and herbs. Three groups of plants occurred on the transect at this time (see Fig. 3, Fig. 4d and Table 4).

Group 7: Eclipta prostrata/Glinus oppositifolius *dominated sites*

Terrestrial herbaceous species were the only species to persist in the black, cracking clays of the driest section of the transect (0-220 m). *Eclipta prostrata, Glinus oppositifolius* and *Coldenia procumbens*, though never abundant, were present.

Group 6: Pseudoraphis spinescens *(terrestrial) dominated sites*

The remaining floodplain sites on the transect were dominated by *Pseudoraphis spinescens* (terrestrial growth form). The absence of cracks in the soil was indicative of the higher moisture content of the soil at these sites. Six species were recorded, but only *Pseudoraphis spinescens* and *Ludwigia adscendens* were present in the majority of sites.

Group 1: Nymphaea *sp. dominated sites*

Nymphaea sp. and *Hydrilla verticillata* were the only Group 1 species to persist through the late-Dry season. Only one individual of each species was observed.

Correlation analysis of sites

Correlation tests between ordination scores, water depth and period of inundation revealed a discernible relationship between the ordination axes and the measured environmental variables. The first ordination axis (floristic composition) was significantly correlated with water depth ($r = -0.912$, $P < 0.05$) and with period of inundation ($r = -0.492$, $P < 0.001$). The second axis was significantly correlated with period of inundation ($r = -0.524$, $P < 0.001$) but not correlated with water depth ($r = -0.012$, $P > 0.05$). Water depth and period of inundation of the site were found to be correlated ($r = 0.610$, $P < 0.001$).

To illustrate the relationship between period of inundation and the distribution of the seven plant groups, the period of inundation was plotted against the transect profile diagrams presented in Fig. 4. Group 4 (*Pseudoraphis spinescens* - aquatic growth form) only occupied sites inundated for more than 6 months of the year. Group 1 (*Nymphaea* sp.) only occurred on permanently flooded sites whereas Group 7 (terrestrial herbaceous species) only inhabited sites inundated for less than 5 months of the year. Similarly, Group 2 and Group 5 sites were inundated for less than 6 months of the year.

4

Discussion

4.1 Vegetation mapping

The map produced from this study contained 10 plant communities (mapping units); this was more than the number recognised by Williams (1979), but the same as recognised by Sanderson et al. (1983). The actual units, however, differ from those recognised in the earlier studies (Table 5). For example, the *Melaleuca* communities were described and mapped in more structural and spatial detail, with open woodland being separated from the open forest/woodland. The latter community actually comprised two structural types which intergrade and are thus difficult to distinguish. The grassland category recognised by Williams (1979) was separated into three parts, each dominated by either *Pseudoraphis spinescens*, *Hymenachne acutigluma* or *Oryza meridionalis*. The annual and perennial swamp communities delineated by Williams (1979) correspond to the Hymenachne-Eleocharis grass-sedgeland and the Nelumbo-Nymphoides herbland communities respectively of this study, but the detailed descriptions differ. The shallow fringing communities containing *Hygrochloa* and *Blyxa* species identified by Sanderson et al. (1983) were not identified in this study, owing to the smaller scale adopted. Similarly, the *Pseudoraphis* communities of Sanderson et al. (1983) were not separated due to changes in area and dominance of associated species e.g. *Nymphaea violacea*, *Eleocharis dulcis* and *Eleocharis brassii*.

Whilst seasonal and temporal changes in the area and species composition of some plant communities were observed, they were not considered large enough to alter the basic outlines of the communities shown in Plate 1. Examples include changes in the abundance of *Eleocharis* spp. on the flood plain south of Nankeen Billabong - uncommon during 1984 and 1985, but very common in areas designated as Pseudoraphis grassland during 1986. *Hymenachne acutigluma* also covered a larger area during 1986 than it had in 1983-85. Over the period of this study (1983-1986) *Pseudoraphis spinescens* also extended its distribution to the north and east of Nankeen Billabong into an area previously dominated by *Oryza meridionalis*. At Nankeen Billabong itself, however, the communities appear to contain more of the latter species. These changes are probably related to the influence of the hydrological regime on the germination, establishment and growth of the plants, especially those dependent on seeds for survival (i.e. the true annuals). The full extent of this influence is not well understood in relation to the germination and growth characteristics of the plant species.

In general, descriptions of the variability within the vegetation units have been incorporated into the outlines of the plant communities. It would not, however, be surprising if further changes in the relative abundance or density of species in the vegetation communities were noticed. These could occur as a result of changes in the dynamics of the ecosystem, or even as a result of more careful or persistent investigation. Examples of the latter are the recording of *Spirodela polyrhiza* in 1983 and of *Nymphaea pubescens* in 1986. Both species are now regarded as common on the flood plain.

Taylor & Tulloch (1985) analysed the rainfall pattern for Darwin and concluded that the notion of a normal or average rainfall year was of dubious value due to large year-to-year variation in the pattern of rainfall over the Wet season. To account for this variability they recommended that ecological studies, in this environment, continue for 6-8 years as consecutive years can rarely be regarded as replicates.

Consequently, both short- and long-term fluctuations in plant populations should be expected and accounted for in an ecological study such as vegetation mapping on the Magela flood plain. As the map presented in this report is only based on 4 years of observation we have deliberately adopted broad mapping units to allow for these fluctuations.

Community structure and species dominance on flood plains such as the Magela not only change from year-to-year, but also change during the seasonal flooding and drying phases. Gopal (1986) has argued that such changes are a response to oscillating water levels and are a normal feature of shallow wetlands in strongly seasonal wet-dry climates. Fluctuations in water level and flow rates are regarded by Mitchell & Rogers (1985) as seasonal events whereas the duration, periodicity and predictability of periods suitable for plant growth can vary both seasonally and aseasonally. Aquatic habitats that experience alternate periods of wetting and drying are therefore more likely to have a predominance of annual growth patterns, desiccation resistant propagules and multiple regenerative adaptations to enable the plants to cope with both seasonal and aseasonal variations (Mitchell & Rogers 1985).

4.2 Growth strategy, growth form and habitat of floodplain vegetation

The relative uniformity of the aquatic environment compared to the terrestrial environment is held by Hutchinson (1975) to encourage species with a perennial life cycle. In temperate North America 86% of aquatic and wetland plant species are categorised as perennials and 14% as annuals (Kadlec & Wentz 1974), while the most prevalent aquatic plants are vegetatively-reproducing perennials with an indefinite life-span (Van der Valk 1981). However, in areas that experience alternate periods of wetting and drying the annual growth habit is predominant (Mitchell & Rogers 1985); 62% of the plant species on the Magela are annuals. Depending on the germination/establishment requirements of the annual species and the pattern of rainfall and flooding there could be significant year-to-year floristic change. Attempts to predict vegetation successional changes in seasonally flooded environments are hindered by a lack of information on the germination/establishment requirements and the response of plants to changes in the hydrological regime. As a consequence vegetation mapping has been restricted to schemes that are only applicable to one annual cycle or are sufficiently generalised to cope with the seasonal and annual variations in species densities and distribution.

Gopal (1986) considers that vegetation changes in temporary and shallow freshwater habitats are primarily a result of changes in water levels resulting from seasonal flooding and drying. Whilst many aquatic species seed when the sediments are covered by water, germination can also occur on moist sediments during the inundation or drying phases of the annual flooding cycle. Germination is usually favoured by high light intensities, fluctuating temperatures and low oxygen concentrations (Gopal 1986). Drying of the sediment and exposure to fluctuating temperatures also enhance seed scarification and formation of tubers and turions. As some of these conditions occur early in the Wet season, the success of aquatic annual species on the Magela is likely to be greatly influenced by the pattern of storms and subsequent flooding at that time of year. It is also likely that species which germinate and grow during the Wet season are heavily dependent on both the pattern of early storms and on the rapidity with which the plain is flooded. Terrestrial species that occur on the flood plain during the Dry season, in contrast, are influenced more by the rapidity of drying of the flood plain and the occurrence of late-Wet season storms and flooding. Rapid flooding early in the Wet season could curtail, or even prevent, germination and establishment of some aquatic/wetland species. The amplitude of the change, however, may not be as important as the frequency and duration of the change (Hejny 1971).

Germination and establishment of annual species during the Dry season could also be affected by, or even dependent on, periodic flooding and the provision of water-logged substrates. The seasonally dry areas on the Magela are usually bare of vegetation in the Dry season except for scattered terrestrial annuals and reduced 'aquatic' perennial grasses and herbs. As an example, the extensive Oryza grasslands of the Wet season only establish following storms and wetting of the dry substrate. During the initial period of inundation *Oryza meridionalis* is overshadowed by the terrestrial herbs *Phylla nodiflora*, *Coldenia procumbens* and *Digitaria bicornis* and the aquatic grass *Hygrochloa aquatica*. *Oryza meridionalis* is dependent on further rainfall after it germinates to enable establishment and further growth. Under extremely wet conditions it can also survive throughout the Dry season when it would normally senesce after seeding.

Most of the above discussion has dwelt on changes in the abundance of annual species in relation to changes in the hydrological regime. Williams (1984) has reported on changes in the distribution of the large perennial trees *Melaleuca* spp. In summary, between 1950 and 1975 an estimated 38% of the area occupied by *Melaleuca* spp. suffered significant loss of trees. Evidence for this change came from aerial photographs and personal observation. The cause was attributed to the combined effects of late-Dry season fire on the flood plain, strong winds and buffalo damage. On an annual basis though, changes in the distribution and abundance of perennial species are not as marked as for annual species.

4.3 Vegetation transects

Annual flooding is an important influence on the structure and floristic composition of the vegetation on the Magela Creek flood plain. The annual occurrence of flooding is predictable, though flooding patterns are variable from year-to-year. Generally, it takes less than 8 weeks from commencement of water flow onto the flood plain for floodwaters to attain maximum coverage; drying of the flood plain can be spread over a period of 9 months. Consequently, the floodplain species are constantly responding to changing physical and biological conditions. As a result the composition of the plant communities changes more or less continuously during the wet-dry cycle. Similarly, at any one point of time, plant communities change spatially along environmental gradients such as water depth. Therefore, when describing vegetation pattern on seasonally flooded wetlands a plant community must be defined temporally as well as spatially.

During the years following this study there have been significant shifts in species dominance. In particular, *Oryza meridionalis* displaced *Hygrochloa aquatica* as dominant in the shallow floodplain sites (0-300 m along the transect), while *Eleocharis dulcis* became more prevalent in the Group 4 sites. Although the composition of the plant groups varied, the distribution of groups appeared to remain stable - the vegetation zones identified during the 1982 surveys were still apparent during the 1986-87 Wet season. Yearly variations in rainfall pattern and flow regimes undoubtedly affect the short-term and possibly even the long-term composition of plant communities on the flood plain.

In the present study, by combining data collected at various times during the wet-dry cycle into a single matrix, plant communities (or groups) were defined in time as well as space. Both temporal and spatial zonation of the vegetation were found. Zonation of wetlands is generally a feature of permanent rather than seasonally inundated wetlands, with plant communities arranged in a series of bands or zones along a water depth gradient (Briggs 1981; Sculthorpe 1967). This oversimplification is probably not applicable to annually flooded wetlands, as several factors are determinants of vegetation patterns. Thompson (1985) notes that flooding depth, duration of flooding, water table height during the Dry season, soil type, temperature and several other factors are involved.

The present study enabled identification of the period of inundation of a site and, to a lesser extent, water depth as important variables influential in determining vegetation patterns. To examine the importance of these variables, the growth strategies of the floodplain plants need to be considered.

Characteristics requiring consideration include propagule dispersal, seed germination, growth rate under various environmental conditions, seed production, susceptibility to specific pathogens, competitive ability and life span (Van der Valk 1981). Few studies have investigated the importance of these characteristics in determining vegetation pattern. Nevertheless, some general comments can be made. The species recorded during the surveys are listed according to growth strategy in Table 4. The categories used in this assessment are more specific than the general ones used in the overall assessment of growth strategies and growth forms of all floodplain plants.

The period of inundation influences the time available for an aquatic species to complete its life cycle i.e germinate, grow, flower and seed. In seasonally inundated areas 70% of the species are annual. However, the life cycles of some species are more rapid than others. Species such as *Hygrochloa aquatica* (Group 2) appear to have a short life cycle and colonise habitats that dry out quickly. Other species such as the submergent *Maidenia rubra* and *Myriophyllum dicoccum* seed later in the year and are restricted to sites with a longer period of inundation. Similarly, perennial species such as *Eleocharis dulcis*, which completes its life cycle during the mid- to late-Dry season, proliferate in sites flooded for more than 7 months.

Once the surface waters evaporate, the most important environmental variable for plant growth is soil moisture. Soil moisture is related to the period of inundation of the site - the longer a site is flooded, the higher the soil moisture during the Dry season. The influence of this variable can best be illustrated by the example of *Pseudoraphis spinescens*. The terrestrial growth form of this species (Group 6) invaded the shallow floodplain section of the transect during the mid-Dry season (Fig. 3). As the soils dried out further this species senesced and was replaced by terrestrial herbaceous species (Group 4). By the late-Dry season survey, there was a clear demarcation between terrestrial herb and *Pseudoraphis spinescens* sites, with the latter restricted to sites that had been inundated for more than 6 months. Presumably, the boundary between the two groups reflects differences in soil moisture regime. Further research, however, is required to elucidate the relationship between period of inundation, growth strategy and the plant-soil system.

Van der Valk (1981) hypothesises that the wetland environment only permits the establishment of certain plant species at any given time. Grime (1973) predicts that a pertubation (such as seasonal drought) will increase species richness, since it allows new species to become established. The results of the present study support these hypotheses. Marked seasonal changes in composition and structure were restricted to sites exposed to wet-dry cycles i.e. the seasonally inundated section of the transect. In total, six plant groups containing a total of 27 species, occupied seasonally flooded areas at various times during the wet-dry cycle. In contrast, only one group containing five species occurred in the permanently flooded sites (Group 1). Sites inundated for less than 5 months only contained seven aquatic species, while 17 aquatic species occurred in sites inundated for more than 7 months. Grime (1973) also postulates that under extreme environmental conditions species richness is low because there are fewer species which can tolerate the environment. This would explain the low species richness in sites inundated for a shorter period.

Considering the evidence, we propose that water depth and the period of inundation are major determinants of Wet season vegetation composition on the seasonally flooded plain. Certainly other factors are also involved. Vegetation patterns governed by water flow, for example, are recognisable in some areas of the flood plain. Water depth may also influence the spatial distribution of the aquatic species during the Wet season. Water depth is also important as it determines the relative length of time a site is inundated during the Dry season.

Furthermore, on the basis of the transect data we speculate that vegetation zonation is a function of both the dissipation (early-Dry to late-Dry period) and expansion (early-Wet season) phases of flooding. Other authors note that early-Wet season patterns and their influence on flow regimes have a pronounced effect on the botanical composition of the aquatic communities. Taylor & Dunlop (1985) report that the herbaceous floodplain communities have a high frequency of annual life forms (64-80%) and that these communities could undergo significant changes in botanical composition depending on the timing, duration and intensity of the Wet season. Morton & Brennan (pers. comm.) note that the timing of inundation affects the relative success of certain species. They observed that *Pseudoraphis spinescens* begins to grow as soon as rain falls. If inundation does not take place until months later, then this species may proliferate and prevent development of other species.

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APPENDIX

Growth strategy, growth form and habitat grouping of plant species on the Magela flood plain

KEY

Habitat: B = billabong, P = seasonally inundated plain, F = fringe zone, S = permanent swamp
Growth form: T = terrestrial, A = aquatic, s = shrub, c = sedge, g = grass, v = vine, h = herb, t = tree, p = palm, e = emergent, f = floating-leaved, s = submerged rooted, b = free-floating, d = free-floating submerged
Asterisk indicates alien species

Species	Habitat			
	B	P	F	S
ANNUAL				
Aeschynomene americana (Ase)*			x	
A. aspera (Ase)*		x	x	
A. indica (Ase)		x	x	
Alysicarpus rugosus (Th)			x	
A. vaginalis (Th)*		x	x	
Aneilema siliculosum (Th)			x	
Bacopa floribunda (Th)		x	x	
Basilicum polystachyon (Th)			x	
Blumea integrifolia (Th)			x	
B. tenella (Th)			x	
Blyxa aubertii (Ahs)		x		
B. octandra (Ahs)	x	x		
Boerhavia coccinea (Th)			x	
B. australiana (Th)			x	
Borreria breviflora (Th)			x	
Brachiaria holosericea (Tg)			x	
B. pubigera (Tg)			x	
Caldesia oligococca (Ahf)	x	x		
Calogyne pilosa (Th)			x	
Cardiospermum halicacabum (Th)			x	
Cartonema spicatum (Th)			x	
Cassia occidentalis (Ts)			x	
Centipeda minima (Th)		x	x	
Centrolepis exserta (Tc)			x	
Ceratophyllum demersum (Ahs)	x	x		x
Ceratopteris thalictroides (Ahs)	x	x	x	x
Cleome tetrandra (Th)			x	
C. viscosa (Th)			x	
Coldenia procumbens (Th)		x	x	
Commelina ensifolia (Th)			x	
C. lanceolata (Th)			x	
Corchorus aestuans (Ts)*			x	
Crotalaria medicaginea (Ts)			x	
Cyanotis axillaris (Th)		x		
Cynodon dactylon (Tg)*			x	
Cyperus aquatilis (Tc)		x		
C. breviculmis (Tc)		x		
C. castaneus (Tc)			x	
C. compressus (Tc)			x	
C. cuspidatus (Tc)			x	
C. digitatus (Tc)		x		
C. iria (Tc)			x	
C. polystachyos (Tc)			x	
Dentella dioeca (Th)			x	
D. repens (Th)			x	
Desmodium filiforme (Th)		x	x	
D. flagellare (Th)		x	x	
Digitaria bicornis (Tg)*			x	
Dysophylla stellata (Ahe/s)		x		
Ebermaiera glauca (Th)			x	
Echinochloa colona (Tg)*			x	
E. elliptica (Tg)		x		
Eclipta prostrata (Th)		x	x	
Ectrosia leporina (Tg)			x	
E. shultzii (Tg)			x	
Eleocharis caespitosissima (Ace)	x	x		
Epaltes australis (Th)			x	
Eragrostis tenellula (Tg)			x	
Eriocaulon setaceum (Ahs)		x	x	
E. spectabile (Th)			x	
Eulalia leschenaultiana (Tg)			x	
Euphorbia hirta (Th)*			x	
E. vachellii (Th)		x	x	
Fimbristylis aestivalis (Tc)		x		
F. clavata (Tc)			x	
F. littoralis (Tc)			x	
F. pauciflora (Tc)			x	
F. punctata (Tc)			x	
F. simplex (Tc)		x	x	
Fuirena ciliaris (Tc)		x	x	
Glinus lotoides (Th)		x		
G. oppositifolius (Th)		x	x	

Species	Habitat B	P	F	S
Hedyotis mitrasacmoides (Th)			x	
Heliotropium crispatum (Th)		x		
H. indicum (Th)*		x	x	
Hibiscus sabdariffa (Ts)*			x	
Hydrocotyle grammatocarpa (Th)		x		
Hygrochloa aquatica (Agf)		x		
Hygrophila salicifolia (Th)			x	
Hyptis suaveolens (Ts)*			x	
Ipomoea aquatica (Ave)	x	x		
I. coptica (Tv)		x		
Isoetes coromandelina (Ahs)		x		
Limnophila australis (Ahe)	x	x		
L. chinensis (Th)			x	
L. fragrans (Th)			x	
L. gratioloides (Ahe)	x	x		
Lindernia mitrasacmoides (Th)			x	
L. plantaginea (Th)			x	
Lipocarpha microcephala (Tc)			x	
Ludwigia hyssopifolia (Th)			x	
L. octovalvis (Th)		x		
L. perennis (Th)		x	x	
Maidenia rubra (Ahs)	x	x		
Malachra fasciata (Ase)*			x	
Marsilea crenata (Ahf)	x			
M. drummondii (Ahf)	x			
Marsilea mutica (Ahf)	x	x		
Melochia corchorifolia (Th)			x	
Microcarpaea minima (Th)			x	
Mimulus debilis (Th)			x	
M. uvedaliae (Th)			x	
Mitrasacme exserta (Th)			x	
Monochoria cyanea (Ahb/e)		x	x	
M. vaginalis (Ahb/e)		x		
Myriophyllum dicoccum (Ahe)	x	x		
Najas tenuifolia (Ahs)	x	x		x
Nelsonia brunellodes (Th)			x	
Nymphoides hydrocharoides (Ahf)		x		
N. minima (Ahf)		x		
N. parviflora (Ahf)		x		
N. spongiosa (Ahf)	x	x		
Oryza meridionalis (Age)		x		
Panicum mindanaense (Tg)			x	
Phyla nodiflora (Th)		x	x	
Phyllanthus minutiflorus (Th)			x	
Physalis minima (Th)*			x	
Portulaca bicolor (Th)			x	
P. filifolia (Th)			x	
Rhynchospora longisetis (Tc)			x	
Rotala occultiflora (A/Th)			x	
Sacciolepis indica (Tg)			x	
S. myosuroides (Tg)			x	
Schizachyrium fragile (Tg)			x	
Scoparia dulcis (Th)			x	
Sesbania cannabina (Ase)		x	x	
S. sesban (Ase)			x	
Setaria apiculata (Tg)			x	
Sporobolus australasicus (Tg)			x	
Stylidium floodii (Th)			x	
S. rotundifolium (Th)			x	
Trianthema portulacastrum (Th)			x	
Triglochin procera (Ahf/s)		x		
Utricularia aurea (Ahd)	x	x		
U. exoleta (Ahd)	x	x		x
U. muelleri (Ahd)	x	x		
Vallisneria gigantea (Ahs)	x	x		x
Vernonia cinerea (Th)			x	
Whiteochloa capillipes (Tg)			x	
PERENNIAL				
Acacia holosericea (Ts)			x	
Alstonia actinophylla (Tt)			x	
Alternanthera micrantha (Th)		x	x	
A. nodiflora (Th)		x		
Aniseia martinicensis (Av)			x	
Azolla pinnata (Ahb)	x	x	x	
Barringtonia acutangula (A/Tt)	x	x	x	
Canarium australianum (Tt)			x	
Cayratia trifolia (Tv)			x	
Cynodon arcuatus (Tg)*			x	
Cyperus haspan (Tc)			x	
C. javanicus (Tc)			x	
C. platystylis (Ace)	x	x		x
Eriachne obtusa (Tg)			x	
E. shultziana (Tg)			x	
E. triseta (Tg)			x	
Eucalyptus alba (Tt)			x	
E. papuana (Tt)			x	
E. polycarpa (Tt)			x	
E. setosa (Tt)			x	
Ficus scobina (Tt)			x	
Fimbristylis denudata (Ace)		x	x	
Flagellaria indica (Tv)			x	
Gymnanthera nitida (Tv)			x	
Hydrilla verticillata (Ahe)		x		
Hymenachne acutigluma (Age)	x	x		x
Hymenochaeta grossa (Ace)	x			x
Leersia hexandra (Age/b)	x			x
Lemna aequinoctialis (Ahb)	x	x		x
L. tenera (Ahb)	x	x		x
Lepironia articulata (Ace)	x			
Livistona benthami (A/Tp)		x	x	x
Lophostemon lactifluus (Tt)			x	
Ludwigia adscendens (Ahe/b)	x	x		
Melaleuca argentea (A/Tt)		x		

Species	Habitat			
	B	P	F	S
M. cajuputi (A/Tt)	x	x	x	
M. leucadendra (A/Tt)	x	x	x	
M. symphyocarpa (A/Tt)			x	
M. viridiflora (A/Tt)		x	x	
Merremia gemella (Av)		x	x	
Mimosa pigra (Ase)*		x	x	
Murdannia graminea (Th)			x	
Nelumbo nucifera (Ahe)	x	x		x
Nymphoides indica (Ahf)	x	x		
Pandanus aquaticus (At)	x	x		
P. spiralis (Tt)			x	
Panicum paludosum (Age)	x	x		
Paspalum scrobiculatum (A/Tge)			x	
Passiflora foetida (Tv)*			x	
Philydrum lanuginosum (Ahe)			x	
Phragmites karka (Age)		x		
Phyllanthus reticulatus (Ase)			x	
P. simplex (Th)			x	
Platyzoma microphyllum (Th)			x	
Polygonum attenuatum (Ahe)	x	x	x	x
Pseudoraphis spinescens (Age)	x	x	x	x
Salvinia molesta (Ahb)*	x	x	x	
Schoenoplectus articulatus (Ace)		x		
Sida acuta (Ts)*			x	
S. cordifolia (Ts)*			x	
Spirodela polyrhiza (Ahb)	x	x		x

Species	Habitat			
	B	P	F	S
Stemodia viscosa (Th)			x	
Stylosanthes hamata (Th)*			x	
Syzygium suborbiculare (Tt)			x	
Triumfetta rhomboidea (Ts)			x	
Urochloa mutica (Age/b)*	x	x		
Vetiveria pauciflora (Tg)			x	
Vitex glabrata (Tt)			x	
Xanthostemon eucalyptoides (Tt)			x	
GEOPHYTIC PERENNIAL				
Aponogeton elongatus (Ahs)		x		
Crinum asiaticum (A/Th)			x	
C. uniflorum (A/Th)			x	
Drosera burmanni (Th)			x	
D. indica (Th)			x	
Eleocharis brassii (Ace)	x	x		
E. dulcis (Ace)	x	x		x
E. sphacelata	x	x		
Nymphaea hastifolia (Ahf)		x	x	x
N. macrosperma (Ahf)	x	x		x
N. nouchali (Ahf)			x	x
N. pubescens (Ahf)	x	x		
N. violacea (Ahf)	x	x	x	x
Sowerbaea alliacea (Th)			x	

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