INVITED REVIEW

Plant Ecology of Australia's Tropical Floodplain Wetlands: A Review

C. M. FINLAYSON*

Environmental Research Institute of the Supervising Scientist, GPO Box 461, Darwin, NT 0801, Australia

● *Aims* Despite the biodiversity values of the freshwater floodplains of northern Australia being widely recognized, there has not been a concomitant investment in developing the extent of knowledge of the basic functions and ecological processes that underpin the ecological character of these habitats. This review addresses the extent of our knowledge on the plant ecology of these wetlands and covers: the relationships between the climate and the hydrological regime on the floodplain; the vegetation patterns, succession and adaptation; and primary production.
● *Scope* Information is available on the seasonal, but less regularly on the inter-annual, dynamics of the macrophytic vegetation and its evident inter-relationship with the extent, depth and duration of inundation by seasonal flooding. The available scientifically collected information on plant distribution and relationship with the water regime could be complemented by more attention to traditional knowledge. The productivity of the vegetation is high—the dominant wetland grass species have an annual dry weight production of 0.5–$2.1\,\mathrm{kg\,m^{-2}}$ and the surrounding riparian (*Melaleuca*) trees contribute litterfall of 0.7–$1.5\,\mathrm{kg}$ (dry weight) $\mathrm{m^{-2}\,year^{-1}}$, $\sim$70 % due to leaf-fall. The availability of dissolved oxygen in the water is known to vary diurnally and seasonally, at least in some habitats. The importance of seasonal differences in the availability of dissolved oxygen for the growth of micro- and macrophytic vegetation has not been investigated. The seasonal distribution and growth of plant species on a few floodplains have been investigated, and maps at scales of 1 : 10 000 to 1 : 100 000 are available for these. However, only on a few occasions have longer term analyses been conducted and long-term changes in the vegetation measured and assessed. Species lists and categorization of growth strategies and forms are available and provide a basis for further ecological investigation.
● *Conclusions* Despite the large investment in managing the many pressures that have degraded the ecological character of these highly valued wetlands, the fundamental ecological processes that underpin the biodiversity values have not received the same level of attention. Further information on plant growth and the environmental factors that drive seasonal and annual changes in vegetation distribution and productivity is required to assist managers in attending to changes due to increasing invasive species and changes in fire regimes.

Key words: Aquatic plants, plant biomass, productivity, succession.

INTRODUCTION

Australia's tropical floodplain wetlands are found across northern Australia, from Cape York in the east to Broome in the west. They cover an estimated 98 700 km^2 (Lowry and Finlayson, 2004) and support an array of plants and animals (Finlayson *et al.*, 1988; Finlayson and von Oertzen, 1993). The floodplains are found across an area that is broadly known as the 'wet–dry tropics' and which has been defined as those areas with an annual rainfall of 600–1600 mm spread over 4–7 months (see Ridpath, 1985 for an introduction to the wet–dry tropics) or taken to include the bio-geographical regions shown in Fig. 1 (Finlayson *et al.*, 1997*a*). Whilst the general distribution patterns of some of the species that occur in these habitats are known (e.g. some fish and bird species), many features of plant growth and primary production have only been investigated in a cursory fashion. Far less information is available on the adaptations that the plants have to the floodplain environment.

There have been many specific investigations and general reviews of the biodiversity (plant and animal taxa and habitats) and pressures on the freshwater wetlands, especially those in the northernmost part of the Northern Territory (Finlayson *et al.*, 1988, 1991, 1997*b*; Finlayson and von Oertzen, 1993; Finlayson, 1995; Jonauskas, 1996; Whitehead and Chatto, 1996; Storrs and Finlayson, 1997; Cowie *et al.*, 2000). These reviews have illustrated the extent of available information and the major gaps that exist, and invariably pointed out that the inventory base was incomplete (Finlayson *et al.*, 1997*b*; Storrs and Finlayson, 1997; Spiers and Finlayson, 1999). The information gaps in the Northern Territory are in part a consequence of the extent and nature of the terrain, much of it isolated and rugged, as well as policy decisions that have biased inventory and analysis to iconic areas or areas being considered for development. As a consequence, the information base is much better where analyses have been driven by interest in economic development, such as intensive cattle feeding, recreational fishing, tourism and mining, and the advent of adverse change (see reviews by Finlayson and von Oertzen, 1993; Finlayson *et al.*, 1997*b*; Storrs and Finlayson, 1997).

The analyses that have been done have often been site specific, and in many cases suffer from an absence of comparative data with other wetland landscapes, both near and further afield. The extent of knowledge about plant growth on the freshwater floodplains in the Northern Territory component of the wet–dry tropics is reviewed and covers the following: the relationships between the climate and the hydrological regime on the floodplain; the vegetation patterns, succession and adaptation; and primary production.

* For correspondence. Present address: IWMI, PO Box 2075, Colombo, Sri Lanka. E-mail m.finlayson@cgiar.org
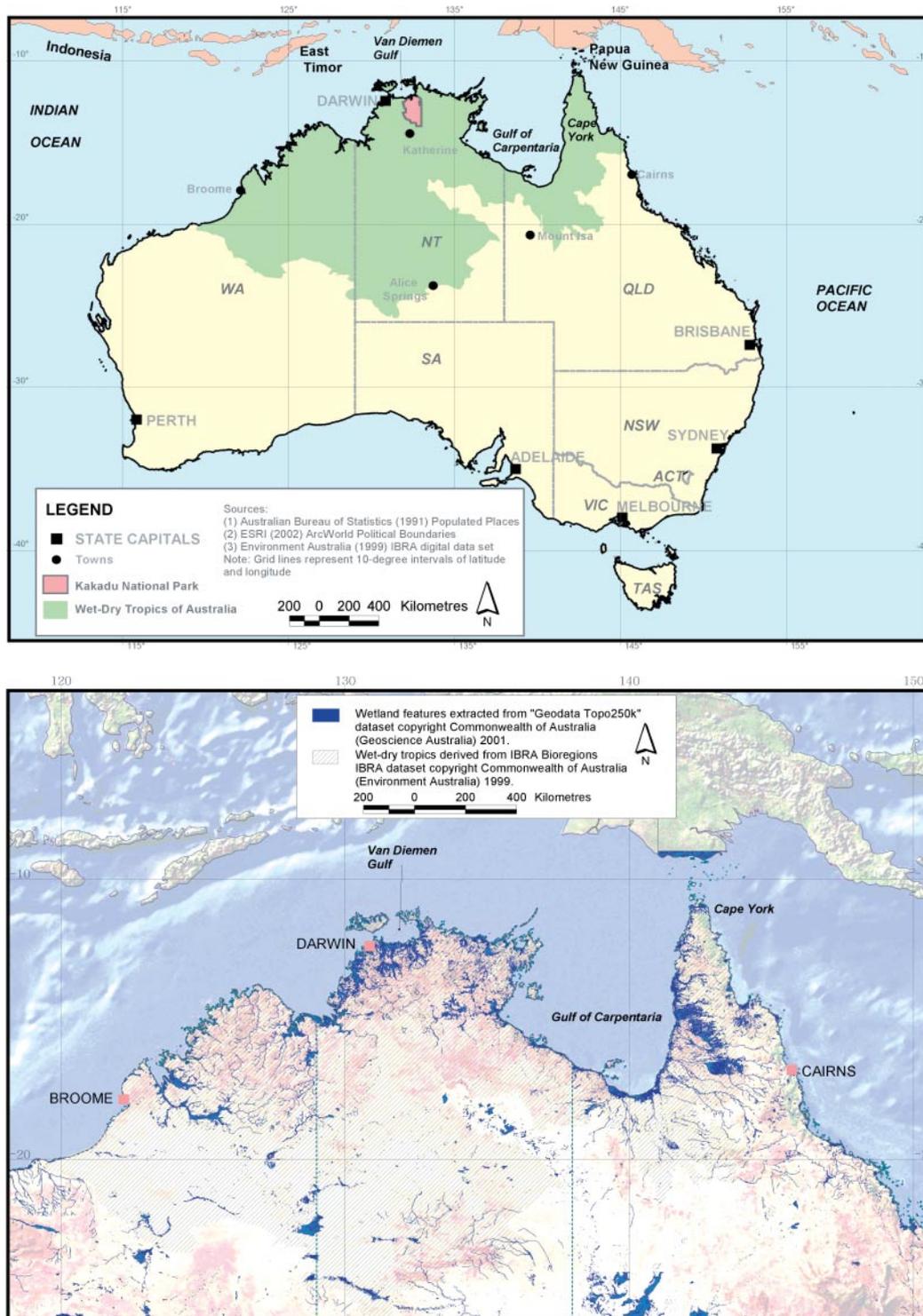
FIG. 1. The wet–dry tropics as defined on biogeographical regions (the shaded area on the upper map) with Kakadu National Park marked (Finlayson *et al.*, 1997*a*) and the distribution of wetlands (including rivers, swamps, marshes and lagoons/ponds) (from Lowry and Finlayson, 2004).

CLIMATE AND HYDROLOGY

The climate of the wet–dry tropics plays an important role in shaping the nature and dynamics of the region. It is generally taken to comprise two very broad seasons: the wet season, which commences late in the year (November–December) and lasts for 3–4 months, and the dry season (Taylor and Tulloch, 1985). This generalized description is shown schematically in Fig. 2. The most significant
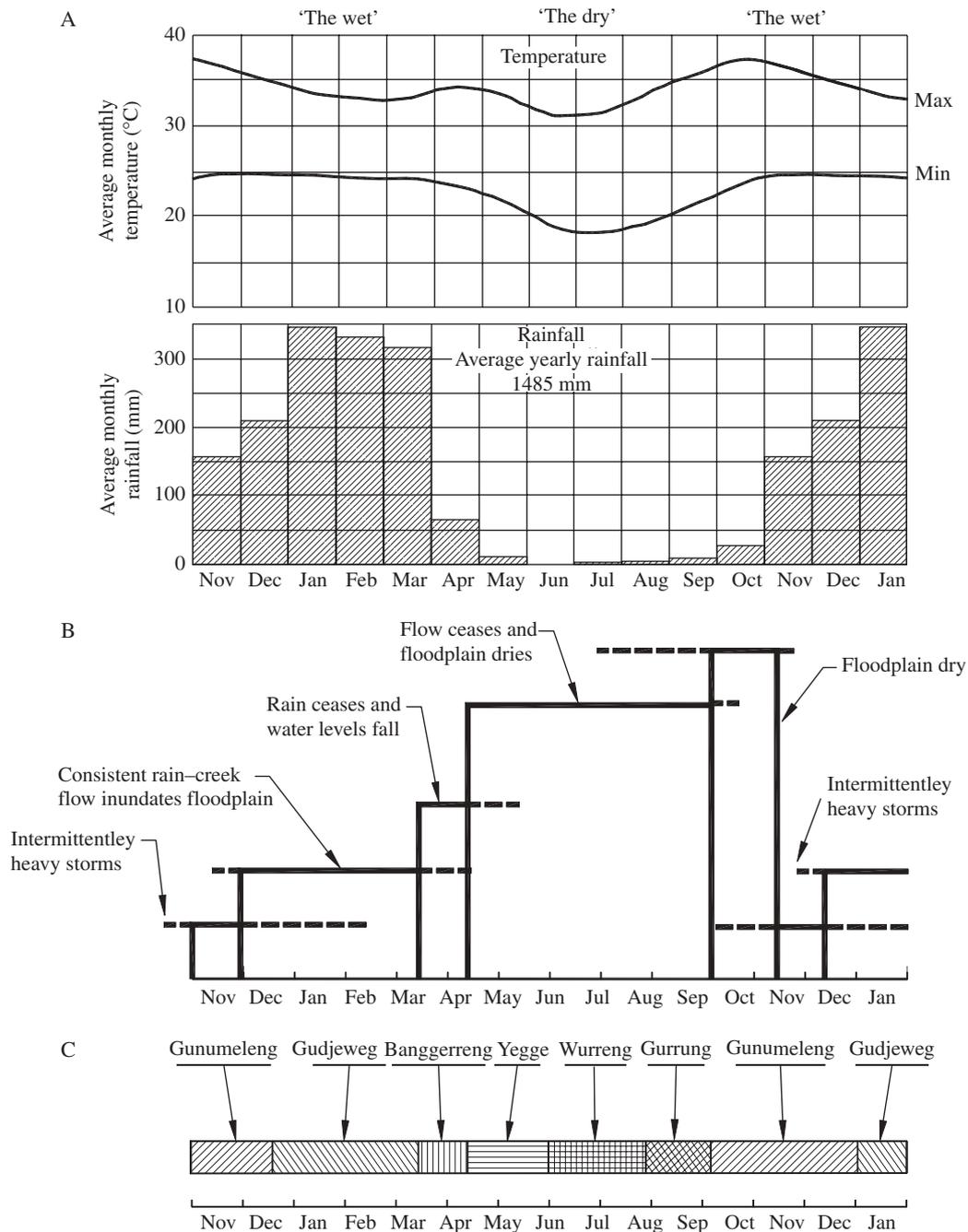
FIG. 2. Generalized representation of: (A) the climate in Darwin in the Australian wet–dry tropics; (B) hydrological changes on the Magela floodplain in Kakadu National Park (variability is represented by dashed lines); and (C) an Aboriginal calendar from Kakadu National Park. A 14 month period is shown to illustrate the extension of seasons across the calendar year. The meteorological information was derived from Hoatson *et al*. (2000), hydrological information was adapted from Sanderson *et al*. (1983) by Finlayson *et al*. (1990*a*), and the aboriginal calendar from Ovington (1986) and Morris (1996). The aboriginal seasons are described in the following manner: Gunumeleng, pre-monsoon season; Gudjewg, monsoon season; Banggerreng, harvest time; Yegge, cool weather time; Wurreng, early dry season; Gurrung, hot dry season.

features of the wet season are thunderstorms, tropical cyclones and rain depressions. As cyclones move inland, they form rain depressions and are an important source of rain. Rainfall is also associated with monsoonal troughs, with 2–3 occurring each year, which usually produce widespread cloud and rainfall, regional convection that provides localized showers and easterly disturbances that, in some years, extend the rainy season beyond its normal limits. The dry season is characterized by south-east trade winds.

Mean monthly data for temperature, rainfall, evaporation and relative humidity recorded in Darwin (on the coast) and Katherine (approx. 300 km inland to the south) are given in Table 1. In general, temperatures are warm to hot, with more humid conditions near the coast. These data represent

T ABLE 1. *Mean monthly rainfall (mm), maximum and minimum temperatures (°C), mean monthly evaporation (mm) and mean relative humidity (%) at 9 a.m. and 3 p.m. for Darwin and Katherine (300 km to the south)*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Darwin												
Rainfall	414	341	306	100	21	1	1	6	18	71	143	229
Maximum temperature	31·8	31·4	31·9	32·6	32·0	30·5	30·4	31·2	32·4	33·1	33·1	32·6
Minimum temperature	24·8	24·6	24·5	24·0	22·1	20·0	19·3	20·6	23·1	25·0	25·3	25·3
Evaporation	208	171	192	220	223	216	226	239	249	267	243	226
Humidity 9 a.m.	82	83	83	75	67	62	63	67	71	71	73	77
Humidity 3 p.m.	70	72	67	52	43	39	38	41	48	53	59	65
Katherine												
Rainfall	233	214	163	33	6	2	1	1	6	30	87	194
Maximum temperature	35·0	34·3	34·5	34·0	32·1	30·0	30·1	32·5	35·4	37·7	38·0	36·5
Minimum temperature	24·0	23·7	22·9	20·4	17·1	14·1	13·2	15·5	19·6	23·6	24·7	24·4
Evaporation	199	146	168	195	197	165	193	232	273	313	277	247
Humidity 9 a.m.	77	81	77	64	58	56	52	52	51	56	61	70
Humidity 3 p.m.	53	55	49	36	34	31	27	25	25	27	33	44

Adapted from Storrs and Finlayson (1997).
Sources: Bureau of Meteorology, Darwin. Mean monthly evaporation data for Katherine supplied by CSIRO, Tropical Ecosystems Research Centre.

the general patterns, but disguise the considerable variation in timing and duration of the monsoonal rains. While very little rain falls during the dry season, the amount that does fall is more variable than during the wet season (Taylor and Tulloch, 1985).

The more northern region has warm to hot temperatures all year round, while further south the temperatures are milder during the dry season (Table 1). In the wet season, warm temperatures in Darwin are accompanied by relative humidity of ∼80 %. Cloud cover is greatest during the wet season, decreasing over the interior and allowing overnight convective cooling.

Local Aboriginal people have a refined perception of the climate compared with many non-Aboriginal people in the region and recognize six seasons based on the relationship between changes in the weather and the availability of food items (Ovington, 1986; Morris, 1996). The calendar they recognize is usually presented in a circular manner, but in Fig. 2 it is presented in a linear manner and compared with the monthly meteorological data from Darwin. The patterns outlined by the Aboriginal calendar are readily identifiable from the meteorological data and illustrate the relationships that exist between plant growth and seasonal changes, although, as with the climate data, the representation of the Aboriginal calendar does not indicate the extent of the variability that occurs. The relationship between the knowledge base developed over millennia by Aboriginal people and the more recently obtained meteorological data is also shown by the generalized hydrological cycle that was developed separately from field observations at Magela Creek and floodplain in Kakadu National Park (developed by Sanderson *et al*., 1983, and modified by Finlayson *et al*., 1990*a*), and is also presented in Fig. 2.

The hydrological cycle has been identified as an important factor in shaping the nature of the vegetation in the freshwater wetlands (Williams, 1979; Taylor and Dunlop, 1985; Finlayson *et al*., 1989). Water flows on a seasonal basis, commencing early in the wet season and lasting until after the end of the rains. It consists of a series of flood

events superimposed on a 'base' flow. At the start of the wet season, intermittent rain storms saturate the soils and as more consistent rain occurs, water collects in the creeks and thence in the large tidal rivers. Once the creeks and rivers are full, the freshwater spills across the floodplains and can cover them to a depth of several metres. The base flow in the creeks is $<5\,\mathrm{m}^3\,\mathrm{s}^{-1}$, with peak flows late in the wet season, reaching, and exceeding on occasions, $1000\,\mathrm{m}^3\,\mathrm{s}^{-1}$. Flooding occurs once the catchment is saturated; heavy falls of rain later in the season generate more widespread flooding and discharge than equivalent flows earlier in the season. Freshwater flow in the creeks and rivers ceases within a few months of the end of the rains, and the creeks and floodplains dry out except for a few permanent swamps and billabongs (Finlayson *et al*., 1990*a*). Except for the tidally influenced channels, most creeks dry up, with a few pockets of water left in billabongs and permanent swamps. The spring tidal range in van Diemen Gulf is 5–6 m, and estuarine water can extend >100 km upstream and generally remains within the stream channel (Woodroffe *et al*., 1989). The groundwater level in the surrounding landscape is recharged by the wet season rains, but can fall 2–4 m during the dry season. Some creeks or river reaches are fed by springs or groundwater seeps.

VEGETATION PATTERNS

A broad-scale analysis of the floodplain vegetation across the Northern Territory was undertaken by Wilson *et al*. (1990), while specific published botanical studies are available for a few wetlands, such as those for the Mary River (Bach and Hoskings, 2002), the Arafura Swamp (Williams and Chudleigh, 2003) and the Magela floodplain (Finlayson *et al*., 1989; Finlayson, 1993). The vegetation patterns shown by these investigations are reviewed before considering information on plant growth and primary production from freshwater habitats on the Magela floodplain, located along a tributary of the East Alligator River and largely within Kakadu National Park (Finlayson and Woodroffe, 1996).

Lists of freshwater macrophytic species have been compiled (see Adams *et al.*, 1973; Lazarides and Craven, 1980; Cowie and Finlayson, 1986; Brennan, 1993). There are many differences in these lists as a result of the collecting effort and areas covered, as well as mis-identifications and changes in the taxonomy. Cowie *et al.* (2000) considered this information while producing a flora of the floodplains with a key to the families of macro-algae and vascular plants. Vegetation maps at a scale of 1 : 50 000 to 1 : 100 000 have been produced for some floodplains (Finlayson *et al.*, 1989; Bach and Hosking, 2002; Williams and Chudleigh, 2003), based on analyses of species distributions obtained largely from transect data and remotely sensed images [including photography and satellite images; see Phinn *et al.* (1999) for a review of the application of remote sensing to wetlands]. In many instances, these analyses have pointed out the large variability in species occurrence and dominance; Sanderson *et al.* (1983) determined that natural variability could undermine the usefulness of detailed mapping and analyses, and consequently resorted to less detailed (i.e. smaller scale) mapping in order to represent general and not specific changes in vegetation. Unless the issue of scale is considered in relation to the purpose (and hypothesis if a formal monitoring programme is undertaken; see Finlayson, 1994, 1996) of the sampling exercise, it is likely that the extent of natural variability could confound many analyses.

Briggs (1981) produced a generalized structural and floristic description of the vegetation associated with the seasonally inundated floodplains, including the fringing woodland and forests, and billabongs (seasonally or permanently inundated lagoons associated with the floodplain or river channels). This description was generalized and updated to accommodate the known variability and is presented below using updated taxonomic nomenclature (Cowie *et al.*, 2000).

(a) Paperbark swamp forest dominated by trees including *Melaleuca viridiflora*, *Melaleuca cajaputi* and *Melaleuca leucadendra*, and to a lesser extent *Barringtonia acutangula* and *Pandanus* spp. The forests are inundated by up to a metre of water during the wet season and are dry (lack surface water) at other times. Sedges and floating-leaved and submerged aquatic plants form an understorey during the wet.

(b) Eleocharis sedgelands dominated by *Eleocharis dulcis* and *Eleocharis sphacelata* in association with other sedge and grass species, most notably *Oryza meridionalis*.

(c) Wet grasslands containing many species including *Pseudoraphis spinescens*, *Leersia hexandra*, *Echinochloa* spp. and sedges, mainly *Cyperus*, *Fimbristylis* and *Fuirena* species.

(d) Floating and floating-leaved herblands on the seasonally inundated plains and in amongst the paperbark forests, including *Nelumbo nucifera*, and *Nymphaea* and *Nymphoides* species.

(e) Submerged and emergent herblands with floating and floating-leaved species, such as *Triglochin dubium*, *Caldesia oligococca*, *Limnophila australis*, *Ludwigia adscendens*, *Utricularia* spp., *Eleocharis* spp. and *Vallisneria nana*.

These generalized habitats present an overview of the wetland vegetation that is not available from more recent narrowly focused analyses. The latter have tended towards analyses of individual wetlands or floodplains and provide specific data without describing the general or characteristic patterns of seasonal and inter-annual change across the landscape. As a consequence, many recent analyses do not account sufficiently for the high natural variability between season and years or between floodplains, nor present their results within the context of the wider landscape vegetation patterns. Further, Sanderson *et al.* (1983) noted that an overemphasis on detailed and short-term sampling did not account sufficiently for the high natural variability. The wisdom provided by Sanderson *et al.* (1983) and others does not seem to have been applied in some more recent analyses that are restricted to a few years sampling and seemingly have not been based on a thorough review of previous sampling! The latter is extremely important when developing a monitoring regime that can detect change based on hypotheses that enable natural variability to be separated from anthropogenic change. Finlayson and Mitchell (1999) provide an appraisal of weaknesses in wetland monitoring, while Finlayson (1996) provides a framework that emphasizes the need to construct a valid hypothesis and undertake a pilot project to test all underlying assumptions, including dealing with natural variability.

Finlayson *et al.* (1989) built on the information provided by Sanderson *et al.* (1983) and prepared a generalized vegetation map for the Magela floodplain based on observations from 5–6 years and in particular the wet seasons when many of the aquatic plants reach their peak biomass and are easier to differentiate and map. This description is based on more comprehensive information than an earlier effort by Williams (1979) for the same floodplain, including the fringing seasonally inundated areas. It is unknown how well this description reflects the situation on other floodplains, especially given changes that have occurred on many with the removal of feral buffaloes (*Bubalus bubalis*) (Skeat *et al.*, 1996). The ten communities that were identified are shown in Fig. 3 and briefly described below.

(a) Melaleuca open forest and woodland (tree canopy cover of 10–70 %): areas dominated by one or more *Melaleuca* species—*M. viridiflora* and *M. cajaputi* around the edges and at the northern end of the floodplain, and *M. leucadendra* in back-swamps inundated for 6–8 months. The understorey varies.

(b) Melaleuca open woodland (tree canopy cover <10 %): *M. leucadendra* in areas inundated for >6 months. Understorey species are usually the same as those in adjacent areas of the floodplain.

(c) Nelumbo–Nymphoides herbland: a mixed community dominated by the water lilies *N. nucifera* and *Nymphoides indica* that occur in permanently and semi-permanently wet areas.

(d) Orzya grassland: dominated by *O. meridionalis* towards the end of the wet season. In the dry season, it consists of bare ground and dead *O. meridionalis* stems with persistent *Phyla nodiflora* and *L. adscendens* as xerophytic forms, and *P. spinescens*.
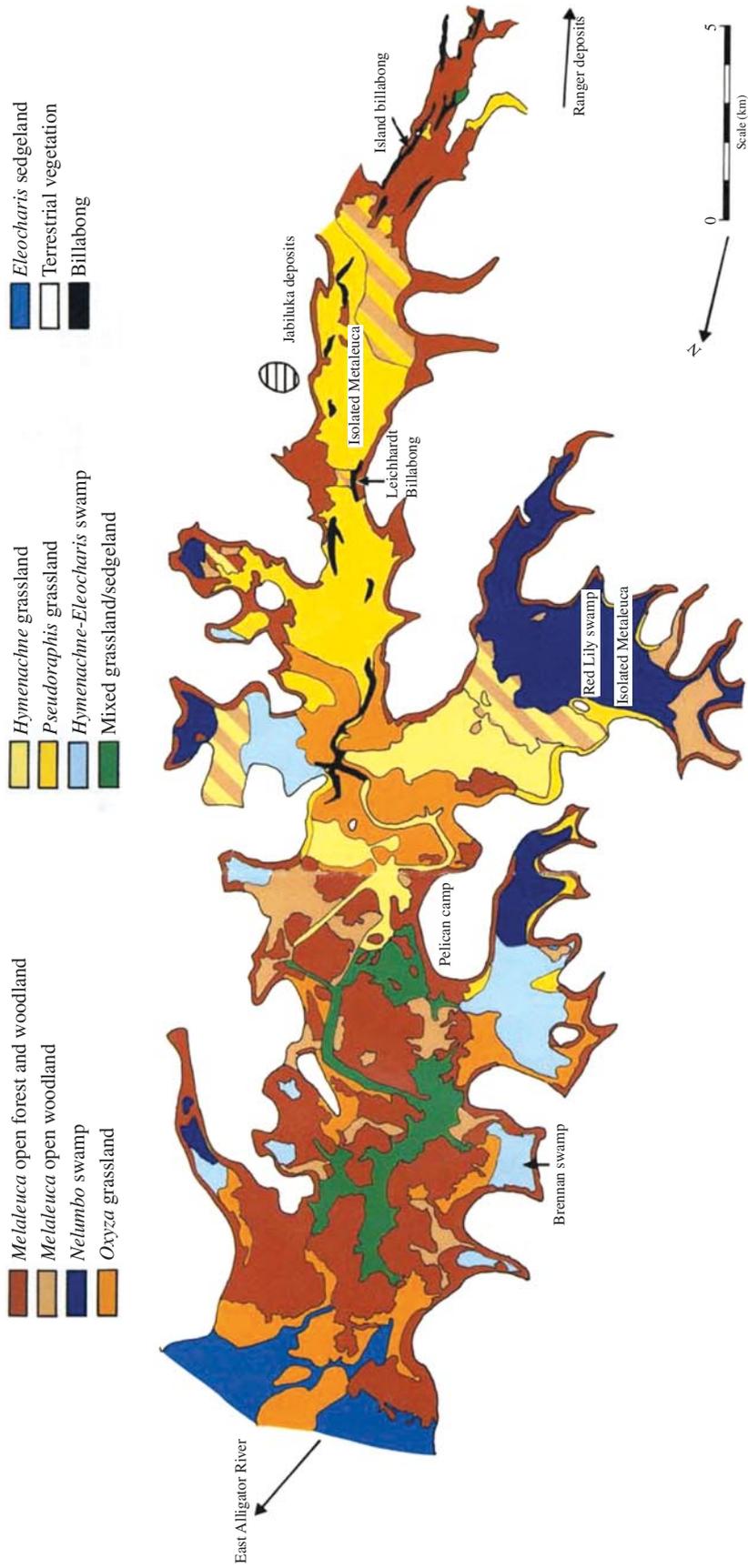
FIG. 3. Vegetation pattern on the Magela floodplain (from Finlayson *et al.*, 1989).

(e) Hymenachne grassland: dominated by *Hymenachne acutigluma* throughout the year.

(f) Pseudoraphis grassland: dominated by the perennial emergent grass *P. spinescens* which has a turf-like habit during the dry season and grows up through the water during the wet season.

(g) Hymenachne–Eleocharis grass–sedgeland: swampy areas that dry out seasonally and are dominated by *H. acutigluma* or *Eleocharis* spp., which are slower to establish.

(h) Mixed grass–sedge–herbland: a variety of species with the dominant species depending on the topographic situation. *Oryza meridionalis* occurs on the drier sites, with *P. spinescens* in slightly wetter places, while *Eleocharis* spp. and *H. acutigluma* occur in the deeper sites. On sites that remain flooded for 10–11 months *N. indica* and *Nymphaea macrosperma* may be present.

(i) Eleocharis sedgeland: *Eleocharis* spp. dominate during the wet season, but are replaced by annual herbs during the dry season;

(j) Open-water community: permanent billabongs, flow channels and shallow waterholes contain *N. macrosperma* and *Nymphaea pubescens* and a number of submerged plant species. Floating grass mats comprised of *L. hexandra*, *H. acutigluma* and *Urochloa mutica* along with the herb *L. adscendens* occur along the banks of the billabongs.

More recent analyses on the Magela have shown that these communities still predominate along with several invasive species, in particular *Salvinia molesta* and *U. mutica*, and the native species *Sesbania sesbans* which intermittently dominates some areas of the plain (J. Lowry, pers. comm. 2003). The reasons for the temporal changes in the occurrence of the latter are not known.

Waterholes or lagoons that retain water seasonally or permanently are a common feature of the floodplains and rivers and provide important habitats for many animal species at different times of the year (e.g. fish species; Bishop *et al.*, 2001). Locally, these waterholes are referred to as 'billabongs', a term that strictly refers to oxbow lakes (Bayly and Williams, 1977) that are widely taken to include all waterholes and lagoons (Finlayson *et al.*, 1989). Walker and Tyler (1985) identified three categories of billabongs for Magela Creek and floodplain: (*a*) channel billabongs or depressions in flow channels; (*b*) backflow billabongs located on small tributaries and initially filled by water from the main creek rather than from the tributary; and (*c*) floodplain billabongs that are generally remnants of deep channels on the floodplain. The floodplain and channel billabongs are, on the whole, deeper and have steeper sides than the backflow billabongs. Thus, in the former, the vegetation, with the exception of the floating aquatic plants, is restricted to a narrow belt around the edge of the billabongs, whereas the backflow billabongs are at times almost completely covered with emergent, submerged and floating-leaved plants (Finlayson *et al.*, 1993a). The vegetation of the floodplain billabongs is greatly influenced by the adjacent plant communities on the seasonally inundated floodplain (e.g. grass mats extending across the floodplain and into the billabongs), whereas the backflow billabongs often have terrestrial vegetation in close proximity and abutting the fringing *Melaleuca* woodlands.

Finlayson *et al.* (1993a) reported a semi-quantitative analyses of vegetation dominance in three backflow billabongs (Georgetown, Coonjimba and Djalkmara) along Magela Creek and two floodplain billabongs (Leichhardt and Jabiluka) on the Magela floodplain. The three backflow billabongs had a generalized vegetation zonation consisting of: (*a*) fringing *Melaleuca* spp. woodland in seasonally inundated areas; (*b*) a mix of grasses and sedges in seasonally inundated areas shaded by woodland; (*c*) a belt of *Eleocharis* sp. in water that is usually <1·5 m deep during the wet season; (*d*) a small area of open water that is usually 1·5–2·0 m deep in the wet season; and (*e*) patches of water lilies and submerged plants along the boundary between the sedges and the open water.

The dominant plant species, based on 'visual biomass' and 'ground' cover, are the *Melaleuca* spp. trees and the geophytic, perennial *Eleocharis* spp. sedges. In contrast, the two floodplain billabongs had a generalized vegetation zonation comprising: (*a*) fringing *Melaleuca* spp., *Pandanus aquaticus* and *B. acutangula* trees along a levee that comprised the western bank; (*b*) a mix of grasses and sedges and a few trees interfacing with the floodplain grass communities along the gently sloping eastern bank; (*c*) a mix of grasses, herbs and sedge overlaying a floating mat of *S. molesta* extending from the banks towards the middle of the billabong; and (*d*) a discontinuous fringe of submerged plants and water lilies along the edge of the floating mat.

Over the past decade, the vegetation in the backflow billabongs has changed considerably, with an increase in abundance of *Eleocharis* spp., attributed to the virtual elimination of feral buffaloes (*B. bubalis*) from the vicinity of the billabongs. Grazing, pugging (hoof prints left in the mud) and wallowing by buffaloes previously prevented these plants from dominating or even establishing (Skeat *et al.*, 1996).

VEGETATION HISTORY AND SUCCESSION

In recent years, there has been increased interest in determining the vegetation history of the floodplains, largely due to management interest in response to known changes and pressures resulting in adverse change (Finlayson *et al.*, 1997a; Storrs and Finlayson, 1997). There have been a series of studies which generally support the notion of widespread vegetation changes on the wetlands over the past 8000 years or so (Chappell and Grindrod, 1985; Hope *et al.*, 1985; Russell-Smith, 1985; Woodroffe *et al.*, 1985; Clark and Guppy, 1988; Grindrod, 1988). Finlayson and Woodroffe (1996) provide a summary of these investigations. In brief, the stratigraphy of the deltaic–estuarine plain of the South Alligator River, and probably the other river systems in the region, indicates that the wetlands developed in three major phases: (1) the transgressive phase (8000–6000 years ago) which was characterized by

marine incursion into the prior valley and terrestrial ecosystems were displaced by mangrove forests as the sea level rose; (2) the big swamp phase (6800–5300 years ago) when the sea stabilized around its present level and mangrove forests established over most of the present-day floodplains for around 6000 years; and (3) the sinuous/cuspate phase (approx. 5300 years ago) during which the river re-established a distinct channel meandering across the estuarine plains and the widespread mangroves were replaced with the grasses and sedges characteristic of the present-day freshwater wetlands.

In recent decades, the vegetation has undergone considerable change as a consequence of individual and multiple pressures, such as invasion by feral animals, especially buffalo, pigs (*Sus scrofa*) and, more recently, cane toads (*Bufo marinus*); as well as weeds, especially mimosa (*Mimosa pigra*), salvinia (*S. molesta*) and paragrass (*U. mutica*); changes in fire regimes; and saline intrusion (Cowie, 1996; Skeat *et al*., 1996; Bayliss *et al*., 1997; Storrs and Finlayson, 1997; Eliot *et al*., 1999; van Dam *et al*., 2002). Individual analyses and management regimes have been imposed to assess changes in vegetation as a consequence of these pressures with various monitoring programmes (e.g. for saline intrusion and weed invasion; Bach and Hosking, 2002) and management responses (e.g. Jonauskas, 1996; Finlayson *et al*., 1997*a*); however, there have been few attempts to predict changes or project future scenarios for vegetation management.

Given the importance of the water regime in determining the occurrence and distribution of plants species on the floodplains, e.g. Finlayson *et al*. (1989) determined that both the duration and depth of inundation greatly influenced the distribution of plant species, and attempted to explain this through an empirical model of plant succession in wetlands, developed by Van der Valk (1981), to assess changes in vegetation that occur as a result of changes in the annual hydrological pattern (Finlayson, 1990; Finlayson and Woodroffe, 1996). The model was tested using information from the general vegetation studies described above, and an analysis of the seedbank in grasslands on the Magela floodplain (Finlayson *et al*., 1990*b*). In undertaking this exercise, it was necessary to recognize that not only does the model have limitations (e.g. it does not take into account interactions between the plants), but the input information (i.e. ecological information on the many plant species involved) was limited. Despite these limitations, the model provided a framework around which to predict changes in the vegetation patterns, i.e. compare the predicted with the actual situation.

For the purposes of validating the model, the 1983–1984 hydrological cycle was considered (Finlayson, 1990; Finlayson and Woodroffe, 1996). Seasonal changes in species dominance in three widespread grass communities under these hydrological conditions are shown in Fig. 4. The species 'successional states' used in the model are explained in Fig. 5 (derived from van der Valk, 1981) and presented with alpha-numeric codes in parentheses in the text below.

The importance of water depth and period of inundation in determining these patterns was borne out by application of the model to the data from 1983–1984. In particular, the sparsely distributed annuals (AS-1) that occur during the dry season were replaced by wet season annuals (AS-II) dominated by *O. meridionalis* and the vegetatively reproducing *Eleocharis* spp. [VS-(II)]. In terms of successional changes that may occur on the floodplains, the introduced weeds *M. pigra* (PS-I) and *S. molesta* [VD-(II)] have the potential to alter both the seasonal vegetation changes and succession between years, albeit with the former more likely to affect the seasonally inundated parts of the floodplain and the latter the billabongs or few permanent swamps.

Mimosa pigra can survive throughout both the dry and wet season almost regardless of the growing conditions (Walden *et al*., 2004) and can rapidly spread by seed. In contrast, the vegetatively reproducing *S. molesta* is widespread during the wet season, but more restricted during the dry season as it does not have propagules in the sediment seedbank and can only survive in areas of permanent water. However, it does have the growth potential (Finlayson, 1984) to cover open water areas completely and change the vegetation structure and composition (e.g. the loss of wet season annuals). The 'successional states' of the plants can be used to determine which plants are likely to survive changes in the seasonal flooding pattern and also the likely survival of introduced species between seasons and between years from propagules stored within the wetland.

As a further example, changes in the floodplain vegetation due to the occurrence of feral animals could be predicted by using the empirical vegetation model and identifying plants that have the capability to spread under the conditions that are likely to prevail. Of particular importance has been the impact of the water buffalo which was well known to denude many seasonally inundated floodplains of much of the grass, sedge and herb cover. Whilst the presence of buffalo caused widespread changes to the floodplain vegetation, it is the changes that have occurred as a result of the removal of the buffalo that are now of interest. In particular, the popular expectation that once buffalo were removed the floodplains would re-establish a natural vegetation pattern has not been met, partly because there was no clear understanding of the nature of the natural vegetation, let alone unexpected ecological outcomes! As an example, there was an expectation that the reed *Phragmites vallatoria* would re-establish, having been reported by early European explorers as having dominated the plains. The veracity of these general claims has not been proved and nor has this species spread greatly since the buffalo were removed. This may not be an unexpected outcome given that the sediment on the floodplains may not have contained sufficient seeds or vegetative propagules of this species. In contrast, the perennial grass *H. acutigluma* has spread and now dominates large areas of the floodplain; an unexpected outcome given low correspondence between the occurrence of seeds in the substrate and the species occurrence (Finlayson *et al*., 1990*b*). In addition, the introduced grass *U. mutica* has continued to spread, presumably through vegetative propagules (Knerr, 1998).

The expected seasonal cycles in the main plant communities on the floodplains can be partly shown in the model

Pseudoraphis Community

DRY SEASON → → →

No standing water

AS - I   *Cyperus spp*
          Fimbristylis
          Glinus
          Heliotropium

VS - I   *Persecaria*
          Pseudoraphis **

PS - I   *Mimosa*

Flooding
→ → →

WET SEASON → → →

Standing water

AS - II   *Blyxa* *
          Hygrochloa *
          Najas *
          Nymphoides spp *
          Utricularia spp

VS - I   *Persecaria*
          Pseudoraphis **

VS - II   *Eleocharis spp* *
          Nymphaea *

VD - II   *Salvinia* *

PS - I   *Mimosa*

Drawdown
→ → →

Hymenachne Community

DRY SEASON

Shallow standing water
Some exposed and moist areas

VS - I   *Ludwigia*
          Pseudoraphis

VS - II   *Azolla*
          Eleocharis spp
          Hymenachne **
          Lemna
          Nelumbo
          Nymphaea
          Urochloa

VD - II   *Salvinia*

Flooding
→ → →

WET SEASON

Deeper standing water than during dry

AS - II   *Aeschynomene spp* *
          Oryza

VS - I   *Ludwigia*
          Pseudoraphis

VS - II   *Azolla*
          Eleocharis spp *
          Hymenachne *
          Lemna
          Nelumbo
          Nymphaea
          Urochloa

VD - II   *Salvinia*

Drawdown
→ → →

Oryza Community

DRY SEASON

Exposed dry areas

AS - I   *Coldenia* *
          Commelina
          Digitara
          Heliotropium
          Phyla *

VS - I   *Ludwigia*
          Pseudoraphis

PS - I   *Mimosa*

PS - II   *Isoetes*

Flooding
→ → →

WET SEASON

Standing water

AS - II   *Aeschynomene spp*
          Blyxa spp
          Hygrochloa
          Ipomoea
          Maidenia
          Nymphoides spp
          Oryza **
          Utricularia spp

VS - I   *Ludwigia*
          Pseudoraphis

VS - II   *Eleocharis spp* *
          Nymphaea

VD - II   *Salvinia*

PS - I   *Mimosa*

PS - II   *Isoetes*

Drawdown
→ → →

FIG. 4. Predicted species succession due to water level fluctuations on the Magela floodplain during the 1983–1984 wet–dry cycle. The dominant species in each community is indicated by ** and the next dominant by * (A = annual; V = vegetative; P = perennial; S = short-lived propagules; D = long-lived propagules; I = propagules established in areas devoid of standing water; II = propagules established in standing water) (from Finlayson *et al*., 1990*b*).
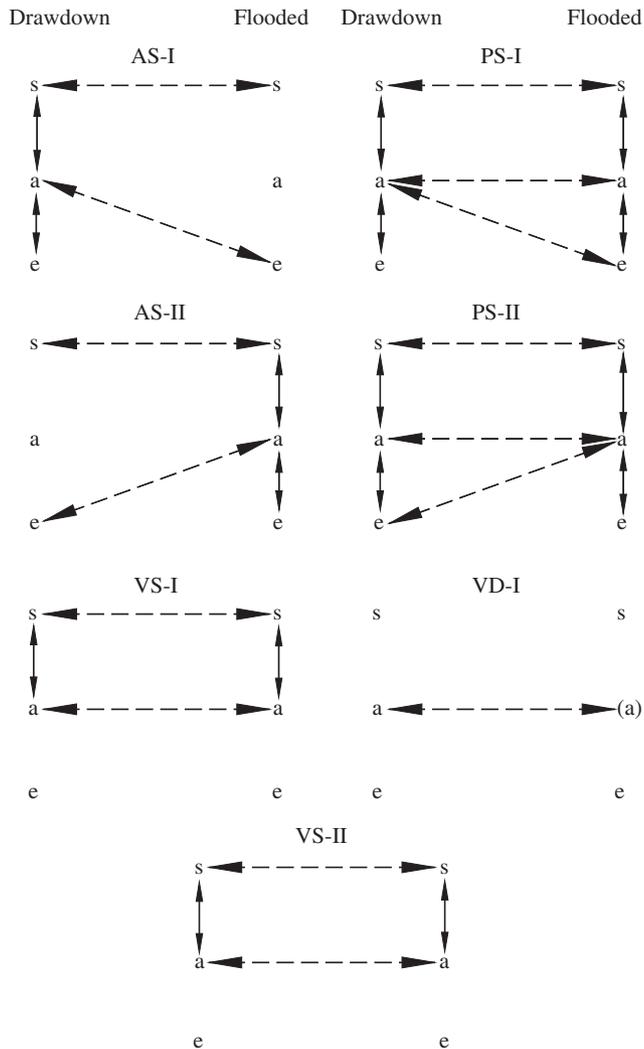
Drawdown   Flooded   Drawdown   Flooded

FIG. 5. Potential species transitions between two 'environmental situations'—increasing (i.e. flooding) and decreasing (i.e. drawdown) water periods in a wetland. Solid lines represent potential transitions within an environmental situation; dashed lines represent transitions between environmental situations. The species states are: s = present as long-lived propagules in a persistent seedbank; a = mature adults; and e = locally extinct. If establishment is dependent on dispersal from another site, adult populations are indicated in parentheses. Other abbreviations are explained in Fig. 4 (from Finlayson *et al*., 1990*b*).

diagrams (Figs 4 and 5). Any substantial changes can be noted and decisions made about the need and possibility of managing them based on the mode of distribution and reproduction. Further information on successional directions following major disturbance (e.g. the introduction of weeds or feral animals) is needed if management of this dynamically variable flora (and hence the habitat) is to be prescriptive, rather than reactive. Recent effort has focused on changes in the fire regime and the inter-relationships between native and introduced species (Knerr, 1998; Bayliss and Finlayson, 2005). Such analyses, however, have been driven more by explicit empirical concepts rather than analyses based on conceptual models and an understanding of the biology of the plant species most involved.

As an example of the complexities of plant growth on the floodplain, it is speculated that the large populations of waterbirds, especially the magpie goose (*Anseranus semipalmata*), have the capacity to alter the vegetation on which they depend. At times, some 1–2 million magpie geese can be present on some floodplain wetlands for feeding or nesting (Bayliss and Yeomans, 1990), with major effects on the vegetation that they consume (e.g. seeds of *O. meridionalis* or tubers of *E. dulcis*) or use for nesting (*E. sphacelata*). For example, does the consumption of tubers of *E. dulcis* by a large population of birds affect the growth of this species? Or, does damage done to the emergent stems of *E. sphacelata* by the geese when nesting impair transport of oxygen to submerged organs and thus impact on the growth of this important species? In some years, the extent of these sedge species has been greatly reduced—this has been attributed to prevailing hydrological conditions, but is it beyond the realm to consider that large numbers of geese in any one year may adversely affect the occurrence of these sedges in the next? These and many other biotic interactions could be investigated through empirical models and linked with knowledge from both eco-physiological analyses of plant processes and growth and hydrological analyses. Such analyses have not attracted support.

We understand that hydrological conditions greatly influence the nature of plant growth on the floodplains, but we seem blissfully unaware of how the hydrology interacts with the many other features of plant growth, e.g. nutrient and energy pathways, propagule germination and establishment. This is not a recent realization—Finlayson *et al*. (1984) postulated that the growth of plants in tropical lakes with low concentrations of nutrients in the water was dependent on a chemostat interaction where the rate of nutrient supply from the nutrient-enriched substrate to the water was determined by the rate of growth of the plant. This concept calls into question the simple use of nutrient concentrations as an indicator of the growth potential of at least some aquatic vegetation, noting that many plant species in these environments have particular adaptations that enable them to flourish under low incipient nutrient concentrations. Further, the water chemistry data and interpretations may be more complex than often reported. As an example, the water on the Magela floodplain is often considered to be acidic to neutral (Finlayson *et al*., 1990*a*) based on analyses that have on the whole been taken in the permanent billabongs and not across the open seasonally inundated plains. Analyses of the water quality within thick stands of submerged herbs and emergent grasses late in the wet season illustrate that not only does the dissolved O_2 and CO_2 vary inversely as expected (due to changes in photosynthesis and respiration rates), but also that the pH reaches alkaline values in late afternoon when the CO_2 is at its lowest (Fig. 6; B. Bailey, unpubl. res. 1995). Does this make the floodplain environment acidic or alkaline? Understanding the nature of these changes and characteristics and how they affect plant growth in these environments is often done on the basis of comparisons of tissue analyses and not through detailed eco-physiological investigations of growth factors or substrate conditions, e.g. the role of flooding and anaerobiosis
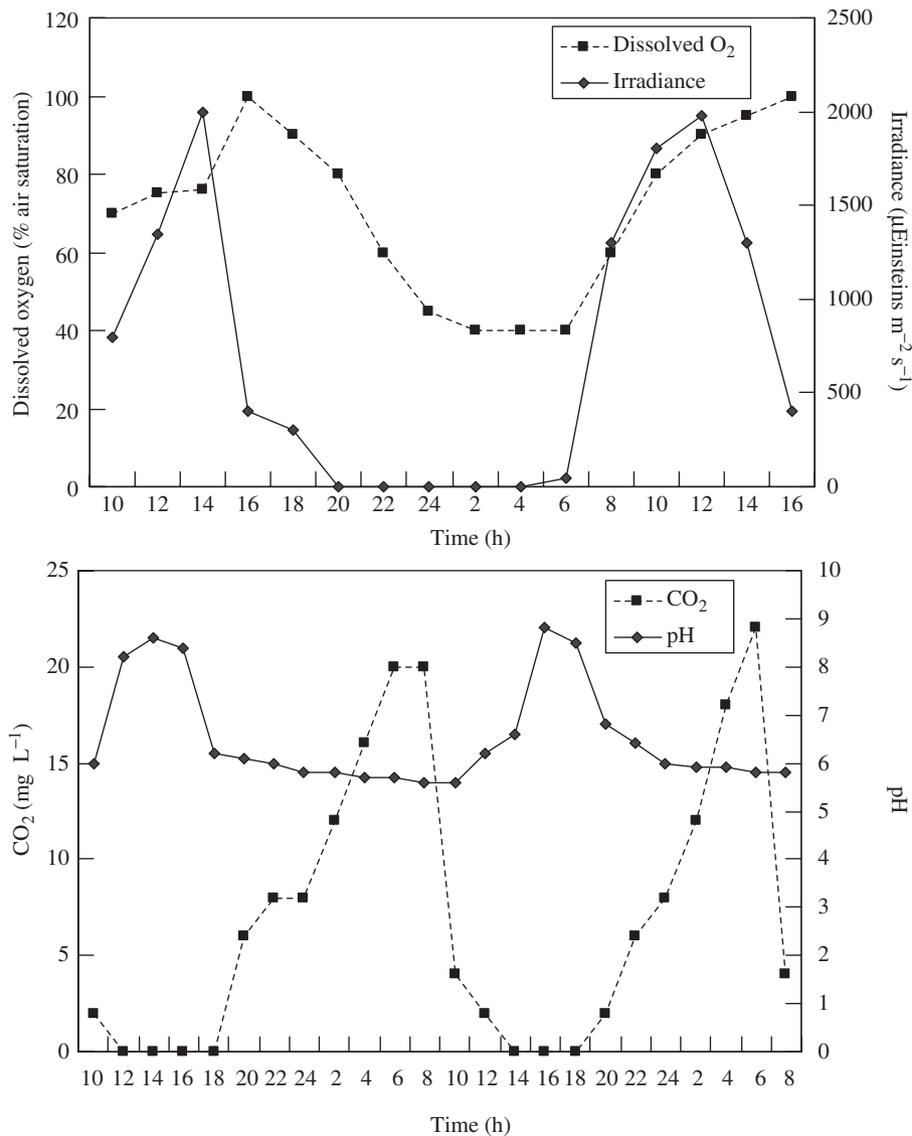
FIG. 6. Daily changes in water quality in mixed stands of emergent herbs and grasses on the Magela floodplain during the wet season (from B. Bailey, unpubl. res. 1995). (Dissolved oxygen units, percentage air saturation; irradiance, μEinsteins m^{-2} s^{-1}; carbon dioxide, mg L^{-1}).

in plant growth has not been investigated for these species and environments. More sophisticated analyses are required.

GROWTH STRATEGIES, FORMS AND ADAPTATIONS

The growth forms of the 222 plant species found on the Magela floodplain across four broad habitat categories, seasonally inundated plain, seasonally inundated fringe zone, billabong and permanent swamp, were reported by Finlayson *et al*. (1989). The fringe zone habitat covered the edges of the floodplain and included the *Melaleuca* forests/woodlands. The seasonally inundated plain habitat covered the remainder of the floodplain, except for the permanently wet areas. The seasonally inundated plain and the fringe

TABLE 2. *Plant species found in four broad habitat areas on the Magela floodplain*

Habitat	Total species	Annuals	Perennials	Geophytic perennials
Permanent billabongs	46	19	21	6
Seasonally inundated floodplain	94	57	29	8
Fringe zone	158	100	50	8
Permanent swamps	21	5	11	5

From Finlayson *et al*. (1989).

zone contained approx. 40 and 70 %, respectively, of the species, compared with 20 % in the billabongs and 10 % in the permanent swamps (Table 2). Overall, there were 139 annual species with 102 terrestrial and 37 aquatic species.

Eighty-nine of the terrestrial species occurred in the fringe zone; only 27 were found on the plain which is seasonally inundated for a longer period than the fringe zone. Finalyson *et al*. (1989) provide a listing of growth strategy and form for each species. This included three growth strategies (annual, perennial or geophytic perennial), and two primary (terrestrial or aquatic) and seven secondary growth forms (tree, shrub, grass, sedge, vine, palm or herb). Terrestrial annuals represented a diverse group of species, with 60 of them classified as herbs, 18 as sedges and 17 as grasses. Twenty-seven of the aquatic annuals are herbs and six are shrubs. There were 68 perennial species, 50 in the fringe zone (Table 2). Thirty-four of the perennials are terrestrial, 26 aquatic, with eight others difficult to classify. There are 12 terrestrial trees including *Eucalyptus* spp., *Pandanus spiralis*, *Lophostemon lactifluus* and *Syzygium suborbiculare*. The aquatic perennial species are dominated by 12 herbs, including *Hydrilla verticillata*, *L. adscendens*, *N. nucifera* and *N. indica*, and by five grasses, including the widespread *H. acutigluma* and *P. spinescens*. There were 14 geophytic species; the more widespread include the *Nymphaea* and *Eleocharis* species.

Within the broad categorization of growth strategies and forms, there are many morphological and physiological adaptations to the annual wet–dry environment with specific features that enable particular species to inhabit various niches within the cycles of dry and wet conditions. Finlayson *et al*. (1989) postulated that the duration of the period of inundation was a major determinant of the vegetation composition of the Magela floodplain along with the depth of water and the velocity of water flow. They further hypothesized that the pattern of vegetation variation was a function of both the flooding and drying phases of the hydrological cycle. The nature of the floodplain environment, especially the variability due to changes in the hydrological cycle, has resulted in many specific adaptations that enable the plants to establish and grow. Specific assessments of these adaptations have not been undertaken, although Cowie *et al*. (2000) provide a review for plant species from the freshwater floodplains in the northernmost part of the Northern Territory; some of the more obvious are presented here.

Aerenchyma, air cavities and corky tissue assist in gas exchange and buoyancy, and are common features, especially in some floating-leaved and emergent species. These features include air cavities in the leaves of *Nymphoides* species, and longitudinal air passages in the stems of *Nymphaea* and *Limnophila* species and in the thickened rhizomes of *E. sphacelata* and *Lepironia articulata*. The latter two species, in common with *E. dulcis*, have hollow, thin-walled stems with regularly spaced transverse septa. Species such as *Bambusa arhemica*, *Paspalidium udum* and *Phragmites vallatoria* have more or less hollow stems with partitions at the nodes, while others, such as *Ipomoea aquatica*, do not have partitions, although many of them develop adventitious roots on submerged nodes or other submerged parts of the stem. Many emergent species develop spongy or corky tissue in response to inundation, such as *L. adscendens* with inflated, white aerenchyma-filled floating roots, *Aeschynomene aspera* and *Sphenoclea zeylandica* with thickened corky aerenchyma and adventitious roots, and *S. sesban* with soft spongy bark on inundated stems. Many Cyperaceae have spongy aerenchymous stems often divided by longitudinal partitions. Trees on the floodplains often have modified bark structures; such as corky bark in *Sesbania formosa* and *B. acutangula*, and papery bark with internal longitudinal air passages in *Melaleuca* species.

The majority of dispersal mechanisms involve water, even though many parts of the floodplains are drier for a longer period than they are wet. Floating plants are transported in their entirety and typically produce small quantities of seeds or reproduce almost exclusively by vegetative means; this group includes the Lemnaceae, the ferns *Azolla* and *Salvinia*, *Pistia stratiotes* and the floating species of *Utricularia*. Fragmentation of submerged species is common, as in *H. verticillata*, *Najas* species and *Ceratophyllum demersum*. The grasses *H. acutigluma*, *Panicum paludosum* and *P. spinescens* are examples of emergent species with trailing stems that form roots at the nodes. The development of corky tissue or aerenchyma on the seed or fruit to provide floatation is common, for example, in *Acanthus ilicifolius*, *B. acutangula* and *P. aquaticus*. In legumes such as *Cathormion umbellatum*, *Peltophorum pterocarpum* and *Aeschynomene aspera*, the pod or articles of the pod are indehiscent and may be air filled in addition to having corky walls. Buoyancy in the seed or fruit in other species is achieved by chambers of various forms, while other species have seeds small enough to float by surface tension.

PRODUCTIVITY

Information on the productivity of the floodplain vegetation is available from the Magela (Finlayson, 1988, 1991), covering seasonal changes in dry weight of aquatic grasses and litterfall from *Melaleuca* trees. Changes in aboveground biomass (dry weight/unit area) for the dominant aquatic grasses *P. spinescens*, *H. acutigluma* and *O. meridionalis* were determined from samples collected during 1983–1984; the sampling was not extended over a longer period due to the danger presented by large individuals of *Crocodylus porosus* (Finlayson, 1991). The dry aboveground biomass of each species appears to be influenced by water depth, which in itself is a function of the rainfall and surface water flow. For two species, the increased biomass occurs at higher water levels, but not for the third, *H. acutigluma* (Fig. 7).

At the start of the wet season, *P. spinescens* undergoes a change from a turf-like habit on a nearly dry plain to elongated culms that extend up through the water as the depth increases, reaching a maximum biomass of $1 \cdot 67 \pm 0 \cdot 21$ kg m^{-2} when the water level was falling, and then senescing and reverting to a turf-like appearance. *Hymenachne acutigluma*, unlike *P. spinescens*, was growing in a perennial swamp and had a semi-erect/creeping habit with short internodes, and horizontal culms anchored to the substrate by roots at the nodes. Biomass increased after the first rains in November, but then decreased from $0 \cdot 78 \pm 0 \cdot 10$ to $0 \cdot 23 \pm 0 \cdot 03$ kg m^{-2} following a large increase in water level. A maximum dry weight of $1 \cdot 41 \pm 0 \cdot 10$ kg m^{-2} was recorded
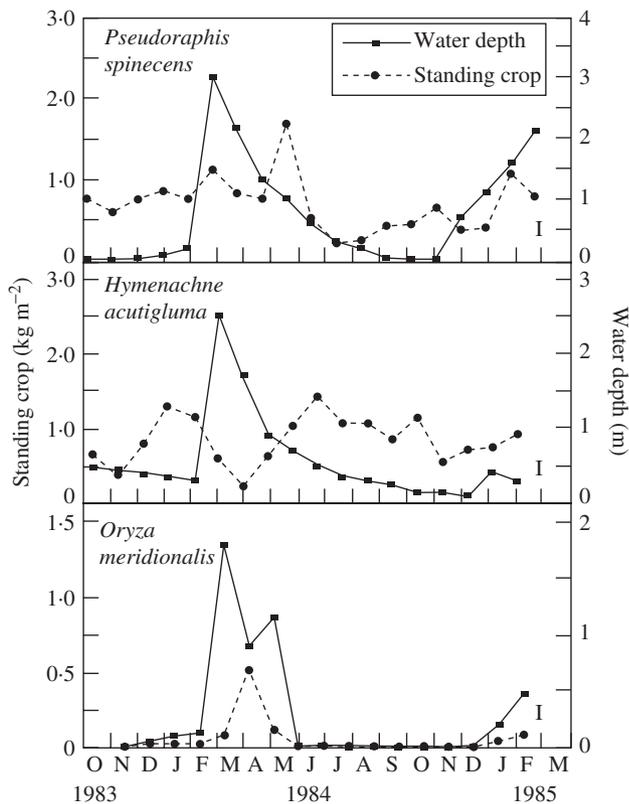
Fig. 7. Above-ground dry biomass of three aquatic grass species (from Finlayson, 1991). The data were obtained from five quadrats (1 m²) placed in each community at approx. 4 weekly intervals throughout the sample period. The least significant difference ($P = 0.05$) is shown for each species.

at the end of the wet season when the water level was falling. *Oryza meridionalis*, an annual species, germinated in November after the first rains of the wet season and continued to grow as the plain filled with water, reaching a maximum biomass of, 0.51 ± 0.10 kg m^{-2} in April before senescing; this value represented the annual productivity (based on the maximum–minimum method of estimation). *Pseudoraphis spinescens* had two growth periods with dry matter production of 1.06 ± 0.23 kg m^{-2} (December–May) and 0.85 ± 0.03 kg m^{-2} (July–November). *Hymenachne acutigluma* similarly had two growth periods with 0.96 ± 0.26 kg m^{-2} (November–January) and 1.19 ± 0.12 kg m^{-2} (March–June). As these occurred within 1 year, the annual productivity for these two species was 1.91 and 2.09 kg m^{-2}, respectively.

Productivity data for the widespread *Melaleuca* woodlands and forests on the Magela floodplain are available indirectly through an analysis of litterfall data (Finlayson, 1988; Finlayson *et al*., 1993*b*). In an intensively sampled *Melaleuca* forest on the Magela floodplain, the total litterfall was approx. 0.7 kg m^{-2} year^{-1}, whereas at another site on the floodplain, less intensively investigated, a value of approx. 1.5 kg m^{-2} year^{-1} was recorded (Finlayson, 1988). Comparative data for *Melaleuca* forests are limited to a few studies of different species in wetlands in southern Australia, with annual litterfalls of 0.39–0.43 kg m^{-2}

year^{-1} (Finlayson *et al*., 1993*b*). Based on an analysis of the relationship between total litterfall and latitude (Lonsdale, 1988), the value of 0.7–1.5 kg m^{-2} year^{-1} is within the range recorded for other forests at the same latitude with the higher 1.5 kg m^{-2} year^{-1} at the upper limit.

The aboveground biomass of *Melaleuca* species on the Magela floodplain was also investigated by Finlayson *et al*. (1993*b*) using an algorithm that related diameter at breast height (dbh) to tree height and fresh weight. The algorithm was calculated initially separately for *M. viridiflora* and *M. cajaputi*, but was combined after determining that there were no significant differences in the range of tree sizes on the experimental site or in the relationships between weight and height: log f = 3.018 (log h) − 0.941 ($r = 0.929$; d.f. = 27; $P < 0.01$) and log f = 2.266 (log dbh) − 0.502 ($r = 0.984$; d.f. = 27; $P < 0.01$), where f represents fresh weight (kg), h represents tree height and dbh was 1.3 m above the soil. This represented a weight of 260 ± 0.31 t ha^{-2} and an average tree weight of 775 ± 1.6 kg for *M. viridiflora* and 1009 ± 1.6 kg for *M. cajaputi*. The size classes (dbh) ranged from 11.8 to 62.0 cm dbh for *M. viridiflora* with a median class of 25.1–30.0 cm, and for *M. cajaputi* from 13.0 to 66.3 cm with a median class size of 30.1–35.0 cm. The average dbh for the two species was not significantly different, with 29.3 ± 1.0 cm for *M. viridiflora* and 33.5 ± 1.0 cm for *M. cajaputi*. The experimental site contained 294 trees ha^{-1}, whereas other sites on the floodplain had much higher densities of 433 and 751 trees ha^{-1}; an analysis of tree density across the floodplain was not undertaken, although Williams (1984) reported a 38 % decline in tree density on the floodplain between 1950 and 1975. A recent analysis has shown that the distribution and density of trees on at least part of the floodplain further changed to a considerable extent between 1975 and 1990 (J. Lowry pers. comm. 2003), indicating the dynamic nature of the wetland environment.

CONCLUSIONS

The vegetation of the floodplain wetlands of northern Australia has been mapped at various scales, although there are few specific and long-term analyses of the distribution and successional changes. General vegetation patterns have been identified, as have the general inter-relationships that exist between the climate cycle and plant growth. In particular, the importance of the period of inundation as well as depth of flooding has been identified. Information on morphological and physiological adaptations to the floodplain environment is largely confined to literature reviews, with few specific analyses. Given the extent of change in these environments (e.g. due to invasive species and changes in the fire regime), it is recommended that further specific investigations are undertaken to identify the importance of such adaptations especially in relation to management actions that may result in further change.

The importance of the floodplains for biodiversity is well recognized, although the interactions between the biota are also poorly investigated, especially the inter-relationships between the high primary production and the populous

fauna. The recent advent of risk assessments, such as that undertaken for mimosa (Walden *et al.*, 2004), can assist in pointing out knowledge gaps or issues critical for managing the vegetation but, on the whole, the step of linking such assessments with basic knowledge of plant growth, e.g. the many apparent adaptations to anaerobic conditions, and the condition of the substrate and inter-linked energy and nutrient pathways, has not been attempted. It is postulated that management of these valuable habitats can be vastly advanced through more attention to the features of plant growth and distribution.

ACKNOWLEDGEMENTS

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