internal report





Grassland community dynamics of a freshwater tropical floodplain: Invasion of *Brachiaria mutica* (Para grass) on the Magela floodplain, Kakadu National Park

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GRASSLAND COMMUNITY DYNAMICS OF A FRESHWATER TROPICAL FLOODPLAIN: Invasion of Brachiaria mutica (Para Grass) on the Magela Floodplain, Kakadu National Park.

By

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# Declaration

I certify that the work described in this thesis has not been submitted for any other award or degree. I certify that any help in the preparation of this thesis and all sources used have been acknowledged.

Nunzio John Alexander Knerr

# Acknowledgments

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# Abstract

The Magela floodplain in Kakadu National Park is occupied by several different grassland communities each of which is flooded annually in the tropical wet season. Data collected in this study adds to the understanding of vegetation dynamics on the floodplain and provides essential information for the management of the introduced plant species, Brachiaria mutica, in this ecosystem. The species composition and abundance of the extant vegetation in four grassland communities (Brachiaria, Oryza, Hymenachne and Pseudoraphis grasslands) were examined in the dry and wet seasons of 1995-96 in order to examine spatial and temporal changes. The area covered by each grassland community in the southern section of the Magela floodplain was mapped. The change in distribution of *Brachiaria mutica* was estimated by detailed mapping of the most heavily infested area in 1996 and by interpreting aerial photographs of the same area taken in 1991. In addition, the spatial variation of seeds in sediments was studied through a sediment germination trial. Data generated from this experiment was compared to a previous sediment germination trial conducted in 1984. The experimental design allowed both within and between study site variations to be detected in germination from the seed banks. The potential seed production of the grass species that dominate the floodplain were estimated (Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma and Pseudoraphis spinescens). Seed germinability and viability of these species was also assessed by a direct germination trial and tetrazolium chloride tests. The density of Brachiaria *mutica* and Oryza meridionalis seeds in the sediments was estimated by direct seed counts from soil cores.

Distinct changes in species composition and abundance of the grasslands were found between wet and dry seasons. Species richness and diversity in the extant vegetation was highest in the *Hymenachne* grassland. The *Pseudoraphis* and *Oryza* grasslands had low species richness and diversity in the dry season and this increased significantly in the wet season. *Brachiaria* grassland had the lowest species richness and diversity of all grasslands. *Pseudoraphis* grassland covered the greatest area of the floodplain followed by

*Oryza, Brachiaria* and *Hymenachne* grasslands. The *Brachiaria* grassland was found to increase in area by 290ha in the most heavily infested area over 5 years and a corresponding decrease in the *Oryza* grassland was found.

Sediment samples were found to have heterogeneously distributed seeds. Many aquatic taxa emerged from the sediments and low numbers of grass seeds germinated. Distinct differences in the seed banks of each community were found. *Brachiaria* and *Hymenachne* grasslands contained more species rich seed banks than the *Pseudoraphis* and *Oryza* grasslands. This was attributed to the growth form of the species that dominate the former communities. Species composition of the *Brachiaria* grassland seed bank was more similar to that of the *Oryza* grassland than other grasslands, indicating that the latter community is being invaded. Comparisons of seed banks of these grasslands are dynamic. Differences in the proportions of individual species found to emerge in each year were attributed to differences in methodology between the studies and variation in rainfall in the years leading up to sample collection for each study, as this factor effects seed production.

Brachiaria mutica was found to have the greatest potential seed production followed by Hymenachne acutigluma, Pseudoraphis spinescens and Oryza meridionalis. These differences may be due to the growth forms and habit of these species. Seeds of Hymenachne acutigluma had the highest germinability compared to other species. No Pseudoraphis spinescens seeds germinated and this species had the lowest seed viability (tetrazolium test) of all species. Oryza meridionalis and Brachiaria mutica were both found to have low germinability but high viability indicating that these species have some seed dormancy mechanism. Seed counts from soil cores indicated that Brachiaria mutica contains a considerable seed bank in the sediments below the community in which it occurs. Hence, the eradication of Brachiaria mutica from the Magela floodplain may be impossible, therefore, it is suggested that management efforts should be directed toward restricting Brachiaria mutica to areas already invaded.

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#### Introduction

Over fifty different definitions of wetlands are currently in use world wide (Dugan 1990). The broadest of these has been provided by the Ramsar convention (1971), defining wetlands as:

"Areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres"

The above definition classes a vast area as wetlands. This study deals with a small sub-set of wetlands in Australia, termed freshwater tropical floodplains. Floodplains are low lying areas subject to periodic inundation. These commonly occur between river channels and raised land on the edge of valleys. In many areas they occur in coastal lowlands ending in estuarine deltas. Floodplains are also found far inland making up parts of large river systems. Freshwater tropical floodplains, therefore, are floodplains occurring in tropical climates that, when inundated, are flooded from a fresh water source.

Tropical floodplains serve many functions and are highly productive ecosystems (Finlayson 1988). They recharge and discharge groundwater, act as buffers controlling floods and retain nutrients, sediments and toxicants (Dugan 1990). Floodplains also provide valuable resources such as wildlife, fisheries, forests and agricultural products, and have both biological diversity and cultural heritage values (Dugan 1990).

The climate of tropical regions make these floodplains highly variable ecosystems. Tropical northern Australia is characterised by two distinct seasons, the wet and the dry (Lee and Neal 1984). The wet season occurs in summer, when a large volume of rain (≈ 1500mm) falls over a 3-4 month period (December - March) causing floodplains to be inundated by several metres of water. This cyclic fluctuation is very predictable, with flooding occurring every year and plays a major role in determining the vegetation of such systems. However, the timing of onset and duration of flooding varies from year to year

and it has been suggested that this variation among years largely determines the relative abundance of many plant species on tropical floodplains in Australia (Finlayson *et al.* 1989).

In recent years increasing recognition of the importance of tropical floodplains has instigated the development of conservation and management strategies for these systems (Finlayson 1995a). Before such strategies can be devised substantial baseline data is required in order to assess changes and identify threats to these systems. The Montreux Record guidelines outline mechanisms by which such information should be collected (Finlayson 1996). Degradation of ecosystems can be caused by many factors ranging from changes in the physical and chemical environment, both within and surrounding a system, to overutilisation of its products and resources or invasion from introduced fauna and flora.

Few floodplains in the world are free of invasions from introduced species. The impact that an introduced species has is largely determined by its ability to survive and reproduce in its new environment and the range of environmental conditions under which it can persist (Amor and Piggin 1977). Several introduced species have had major impacts on freshwater tropical floodplains in Australia. Examples include *Mimosa pigra* (Giant Sensitive Plant) which has invaded vast areas of northern Australia converting diverse communities into impenetrable vine thickets thereby excluding native flora and containing little habitat for wildlife (Lonsdale and Segura 1987). Similarly, *Salvinia molesta* a floating weed that reproduces rapidly has been found to completely cover areas of open water blocking out light and reducing dissolved oxygen, subsequently killing fish and submerged macrophytes in natural ecosystems (Storrs and Julien 1996).

Feral buffalo (*Bubalus bubalis*) introduced into northern Australia last century, have also been recorded to dramatically change floodplains by stirring up sediments and creating wallows and swim channels thus causing considerable destruction to vegetation cover (Letts *et al.* 1979; Fogarty 1982; Friend and Taylor 1984; Corbett *et al.* 1996).

The introduction of more than four hundred pasture species to northern Australia since the 1940's poses a significant threat to Australian tropical floodplains. Lonsdale (1994) noted that 13% of introductions have become weeds. *Brachiaria mutica* is one such species. Native to Africa and South America, it was introduced into Australia late last century (Wesley-Smith 1973) and since the 1960's has been extensively planted in Queensland and the Northern Territory (Clarkson 1995). It is now a widespread weed in coastal Queensland (Clarkson 1995). The rapid expansion of this species in natural ecosystems is only now being recognised and conflicting interests between conservationists and pastoralists makes management of this species difficult (Lonsdale 1994).

Mimosa pigra, Salvinia molesta, Bubalus bubalis and Brachiaria mutica have all been recorded on the Magela floodplain. The floodplain has been the subject of ongoing research since the discovery of two large uranium deposits within its catchment (Christian and Aldrick 1977; Fox et al. 1977). Physio chemical characteristics of the water in the Magela Creek (which feeds the floodplain) and billabongs of the floodplain have been well documented (Walker and Tyler 1982; Walker et al. 1984; Brown et al. 1985; Noller and Hunt 1985). Research has been conducted into the formation of the floodplain sediments (Wasson 1992), as well as heavy metal and radionuclide distribution within sediments (Finlayson et al. 1985; Finlayson 1994). Studies on the fishes, frogs, birds, crocodiles and macroinvertebrates of the floodplain have also been conducted (Grigg and Taylor 1980; Bishop et al. 1981; Marchant 1982; Tyler and Cappo 1983; Tyler et al. 1983; Morton et al. 1984; Humphrey 1985; Jenkins and Forbes 1985; Julli 1985). In addition, algae found on the floodplain are well documented (Brady 1979; McBride 1983; Thomas 1983; Broady 1984; Ling and Tyler 1986).

Several inventory studies of vegetation on the floodplain have been conducted (Williams 1979; Sanderson *et al.* 1983; Finlayson *et al.* 1989) including specific research on vegetation of billabongs on the floodplain (Walker and Tyler 1983; Finlayson *et al.* 1993b). Vegetation surveys of the floodplain including wider areas have also been undertaken to assess alien

plant species (Cowie *et al.* 1986; Cowie and Werner 1993) and more specific research has been conducted on the biomass and litter dynamics of *Melaleuca* forest (Finlayson *et al.* 1993a) as well as primary production and nutrient composition of dominant grasses in three communities on the floodplain (Finlayson 1991). A sediment germination trial assessing the species composition of the soil seed banks of these grassland communities has also been conducted (Finlayson *et al.* 1990). Sediment samples were germinated with the objective of comparing the size and species composition of plant populations arising from seed banks of these communities (*Oryza, Hymenachne* and *Pseudoraphis* grasslands) with the dominant vegetation of these communities than was available previously (Finlayson *et al.* 1990). The importance of seed banks in aquatic plant communities has long been

The importance of seed banks in aquatic plant communities has long been recognised (Darwin 1859) and recently emphasis has been placed on understanding the role of seed banks in vegetation regeneration within wetland habitats (Van der Valk and Davis 1978; Smith and Kadlec 1983; Brock *et al.* 1994).

The wetting / drying cycles in tropical floodplain ecosystems make seed banks a particularly important feature of these systems. Many species have adapted to survival in tropical floodplains and seeds or oospores commonly serve as a resting stage while conditions are not suitable for growth and reproduction (Gopal 1986) For example, aquatic species that require standing water for growth (eg, Nymphoides spp., Nymphaea spp. and Charophytes) may use seeds to ensure survival over the dry season. Conversely, mudflat or terrestrial species which cannot grow when inundated for long periods (eg. Glinus oppositifolius) rely on seeds to allow re-establishment or regeneration after drawdown (Leck 1989). Seeds also act as effective dispersal agents allowing species to gain access to potentially inhabitable sites. Due to their function seed banks can supply information about changes that may occur in vegetation over time including what vegetation may have been present in an area in the Such information is particularly useful if detailed past (Roberts 1981). knowledge of the life histories of species occurring in the community are available (Pederson and Van der Valk 1984). In any case seed bank data add to current knowledge about life histories of the species that they contain.

Most seed bank studies in tropical systems have focussed on forests or farmlands (Garwood 1989). Hence, little quantitative data on tropical wetland seed banks exists (Gopal 1986), with the study by Finlayson *et al.* (1990) being the only seed bank experiment conducted on a freshwater tropical floodplain ecosystem in northern Australia. A recent workshop identified key issues and priority research areas for this region (Finlayson 1995b) and highlighted the need for focussed research on freshwater tropical floodplains in Australia. This created an opportunity for this study to be conducted. Therefore the information gathered by this study fits into a national context as part of a holistic research program on tropical wetlands currently run by the Research Institute of the Supervising Scientist (*eriss*).

The invasion by *Brachiaria mutica* on the Magela floodplain has been recognised (Finlayson *et al.* 1989) but not quantified. In addition, limited information on the seed production capacity of grass species that dominate large areas of the floodplain exists.

#### **Objectives**

This study examined both extant vegetation and seed bank vegetation, of the Magela floodplain to help understand aspects of the dynamics of this floodplain. The objectives of the study were:

- To compare the extant vegetation of four grassland communities in wet and dry seasons.
- To determine change in the distribution of *Brachiaria mutica* (Para Grass) between 1991 and 1996 in extant vegetation over the study area.
- To assess germination from the seed banks of four grassland communities on the Magela floodplain in Kakadu National Park during 1995/96.
- To compare germination from the seed bank in 1995/96 with that in 1984.
- To examine the relationships between extant vegetation and seed banks of these communities.
- To determine if *Brachiaria mutica* seeds are present within grassland seed banks of the Magela floodplain.
- To estimate the potential seed production and seed viability of the dominant grass species in each community.

A vegetation survey identified extant vegetation communities on the floodplain which were subsequently mapped. Four communities were selected for investigation of seed banks (*Brachiaria, Oryza, Hymenachne* and *Pseudoraphis* grasslands). A study on seed production and viability of the dominant grass species in each community (*Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* was undertaken. This assists by placing survey and seed bank results into perspective through providing information on seed input into the soil. Additional information on the seed banks of *Brachiaria mutica* and *Oryza meridionalis* was attained by conducting soil seed counts, thus allowing the size of the seed bank of these two species to be estimated.



# Chapter 2 The Study Site: Magela Floodplain

# Site Selection & Description

The Alligator Rivers Region (ARR) lies approximately 200km east of Darwin and comprises the catchments of the East Alligator, West Alligator and South Alligator rivers (Map 2.1). A large proportion (80%) of this area is Kakadu National Park, Australia's largest National Park. Kakadu is one of seventeen places in the world listed as a world heritage area having both significant conservation and cultural value (UNESCO 1992) and the Magela floodplain which feeds into the East Alligator river is currently listed as a Ramsar site of international importance (Ramsar 1990).



Map 2.1 Alligator Rivers Region (ARR) the majority of which is now Kakadu National Park. (Map courtesy of eriss)

The climate of the area is monsoonal having distinct wet and dry seasons. Annual rainfall varies from 1500 to 3500mm with most rainfall occurring during the wet season in summer (Dec-March). High temperatures (≈35C°) during the wet season are accompanied by relative humidities of about 80%. Both temperature and relative humidity drop to around 25C° and 50% respectively during the dry season (May-October). Most of the water inundating the Magela floodplain during the wet season is runoff from the surrounding sandstone plateaus.

Four different grassland communities were selected for detailed study (Map 2.2). Each is characterised by a different dominant grass species (*Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens*). Vegetation on the study sites were previously described by Finlayson *et al.* (1989; 1990), as *Oryza, Hymenachne* and *Pseudoraphis* grassland communities. The *Brachiaria* grassland examined in this study occupies a large area that was *Oryza* grassland prior to 1989.

The same locations as those used by Finlayson *et al.* (1990) were sampled. Each sample area was determined by visual inspection of extant vegetation to select areas where dominant species were most uniform (specific sample sites were randomly located within these areas). Characteristics of the dominant species in each community and species that occur with them are:

# Brachiaria grassland

*Brachiaria mutica* grows in dense clumps and dominates this community throughout the year. It reproduces vegetatively from stolons and no other species were found on initial inspection of this community.

### Oryza grassland

This community is dominated by *Oryza meridionalis,* an annual grass, during the wet season. In the dry season it consists of bare ground and dead *Oryza meridionalis* stems with *Pseudoraphis spinescens, Phyla nodiflora* and *Ludwigia adscendens* commonly occurring. During inundation aquatic species such as *Maidenia rubra, Isoetes* spp., *Nymphaea* spp., *Nymphoides* spp. and *Eleocharis* spp. can be found (Finlayson *et al.* 1989).

#### Hymenachne grassland

*Hymenachne acutigluma* dominates this community throughout the year with species such as *Ludwigia adscendens*, *Nymphaea* spp., *Oryza meridionalis* and *Pseudoraphis spinescens* also present. *Nelumbo nucifera* forms dense patches in this vegetation type (Finlayson *et al.* 1989).

# Pseudoraphis grassland

*Pseudoraphis spinescens* grows in two forms depending on season and it dominates this community. During the dry season it grows as a turf and when inundated its stems elongate to reach the water surface. During the wet season *Nymphaea* spp. and *Nymphoides* spp. are extremely common and other aquatics such as *Utricularia* spp. and *Najas* spp. can also be found (Finlayson *et al.* 1989).



Map 2.2 showing the study area and locations of the four grassland communities sampled (the two uranium deposits, Jabiluka and Ranger are marked, Ranger is currently being mined; map courtesy of *eriss*)



Chapter 3 The Grasslands: Vegetation Survey and Mapping

## Introduction

Vegetation survey data can be used to generate vegetation maps which assist in identifying environmental factors that may be controlling vegetation, such as topography or soil type. Vegetation maps can also be used to document temporal changes in vegetation, which is particularly relevant when monitoring the spread of introduced species in an area. The vegetation of the Magela floodplain has been mapped at a number of scales (Williams 1979; Morley 1981; Sanderson *et al.* 1983; Finlayson *et al.* 1989).

Williams (1979) attempted to establish a relationship between vegetation and water flow patterns on the floodplain using six vegetation types as indicators of water depth. However, the study was not conducted during peak biomass production on the floodplain (April-May), hence the study did not account for seasonal changes in vegetation (Finlayson *et al.* 1989). Morely (1981) conducted a detailed vegetation survey on the southern section of the floodplain during peak biomass production, but the 36 communities recognised were not found in subsequent years and as a consequence Sanderson *et al.* (1983) adopted a simpler and broad classification (Finlayson *et al.* 1989).

Finlayson *et al.* (1989) has published the most recent vegetation map of the floodplain to date, using modified classifications from previous studies. Aerial photos taken over a number of years and in different seasons were used in conjunction with field surveys to produce a more detailed map than Sanderson *et al.* (1983), but which was broad enough to be repeatable in subsequent years.

The aims of this chapter were to identify the areas covered by each of the surveyed plant communities in the southern section of the floodplain, to distinguish differences in species richness and diversity of these communities and to estimate the change in distribution of *Brachiaria mutica* in the most heavily infested area between 1991 and 1996.

The questions addressed in this chapter are:

- Q1: What taxa are present in each of the vegetation types in each season?
- Q<sub>2</sub>: Does species composition differ among extant vegetation of the four grassland communities?
- Q<sub>3</sub>: What area of the southern section of the floodplain do each of the four grassland communities occupy?
- Q<sub>4</sub>: What change in the distribution of *Brachiaria mutica* has occurred in the most heavily infested area of the floodplain between 1991 and 1996?

The hypotheses generated to examine these questions are:

- H<sub>1</sub>: There is no difference in species richness of extant vegetation among grassland communities.
- H<sub>2</sub>: There is no difference in species richness of extant vegetation between wet and dry seasons.
- H<sub>3</sub>: There is no difference in species richness of extant vegetation among grassland communities and between wet and dry seasons.
- H<sub>4</sub>: There is no difference in species diversity of extant vegetation among grassland communities.
- H<sub>5</sub>: There is no difference in species diversity of extant vegetation between wet and dry seasons.
- H<sub>6</sub>: There is no difference in species diversity of extant vegetation among grassland communities and between wet and dry seasons.

# Materials and Methods

# Vegetation Survey and Mapping

This study used similar techniques to that of Finlayson *et al.* (1989) to produce a current map containing the invading species *Brachiaria mutica* (Para Grass). The four grassland communities (see Chapter 2) were surveyed using a nested quadrat technique. This technique has the advantage of allowing quantitative data to be collected as quickly as qualitative data (Morrison *et al.* 1995). Surveys were conducted in both the dry (November) and wet (April-May) seasons of 1995-96. A total of 30 nested quadrats were recorded in each community, 15 during the dry season and the remaining 15 during the flooding

period. Each nested quadrat consisted of five concentric quadrats, 0.25m<sup>2</sup>, 0.5m<sup>2</sup>, 1m<sup>2</sup>, 2m<sup>2</sup>, and 4m<sup>2</sup> respectively (Figure 3.1).





The dry season quadrats were marked out using four lengths of rope joined by a central peg and layed out in the shape of a cross (Plate 3.1). These quadrats were located at the apices of twelve W shaped transects used for soil core collection (see Chapter 4).

Quadrats recorded in the wet season were randomly positioned within the four study sites because dry sites were difficult to locate and survey. An airboat was used as a platform and the four smallest quadrats in the nest were marked out using a portable sampling device (Plate 3.2). The portable sampling device was constructed of four pieces of pvc tubing each joined at one end, with quadrats being marked by four lengths of orange rope each attached to the tubes at appropriate distances from the central junction. The 4m<sup>2</sup> sub-quadrat was visually estimated. Species presence in each quadrat was recorded and quadrat locations were noted using a global positioning system (Garmin 45 GPS).



Plate 3.1 Nested quadrats for sampling vegetation in the dry season were marked out with four pieces of rope (this quadrat was located in the *Pseudoraphis* grassland).



Plate 3.2 Sampling device used to survey vegetation in the wet season (this quadrat was located in the *Pseudoraphis* grassland).

Data for mapping was obtained from visual assessment of the dominant species (1048 GPS locations) recorded between April and May 1996 across vegetation types on the Magela floodplain. These data were plotted at 1:25000 (using Garmin PCX5 interface software and ARC/INFO GIS) and used for aerial photographic interpretation.

Colour aerial photos 1:25000 (60% forward overlap, 20% side overlap for stereo viewing) of the Magela floodplain were taken in June 1996 to allow a vegetation map to be generated and comparisons with 1991 photos to be made. Eight markers were placed in different positions on the floodplain prior to undertaking aerial photography. Vegetation surrounding each marker was described and marker locations were recorded by GPS and plotted at 1:25000. These positions enabled referencing of aerial photographs and the descriptions were used in interpretation. Interpretation of photos from 1991 allowed the change in distribution of *Brachiaria mutica* on the floodplain between 1991 and 1996 to be established.

The plant communities used as mapping units follow Finlayson *et al.* (1989) with the addition of the *Brachiaria* grassland community defined by the vegetation survey in this study (Table 3.1). More detailed descriptions are outlined in Chapter 2 and Appendix A.

Vegetation types and markers were mapped by tracing onto drafting film using a stereo viewer. The *Brachiaria mutica* infested area was mapped in greater detail by adding eyepieces with 8x objective lenses to the stereo viewer. The same area was also mapped from 1991 aerial photos using this method. Maps were digitised into Generic Cadd 6.1 using a digitising tablet (Summasketch II).

Images were converted into an appropriate format (DXF) for import into ARC/INFO 6.0, a Geographic Information System (GIS). Once in the GIS, images were transformed into real world coordinates (latitude & longitude) using the reference markers and 10 other readily identifiable GPS locations. Each image was processed using Arcedit and the areas of each plant community were calculated in hectares. Finally, maps were generated using Arcplot.

Table 3.1 Dominant species in the plant communities used as mapping units when generating vegetation maps of the Magela floodplain from aerial photographs (plant communities except *Brachiaria* grassland follow Finlayson *et al.* (1989)).

Plant Community	Dominant Plant Species			
Melaleuca Open Woodland	Overstorey: Melaleuca leucadendra			
	Understorey usually dominated by same			
	species in adjacent areas.			
Melaleuca Open Forest/Woodland	Overstorey: Melaleuca viridiflora, Melaleuca			
	cajaputi and/or Melaleuca leucadendra			
	Understorey usually dominated by same			
	species in adjacent areas.			
Brachiaria Grassland	Brachiaria mutica (has invaded either Oryza			
	Grassland or Hymenachne Grassland)			
Oryza Grassland	Oryza meridionalis in the wet & Pseudoraphis			
	spinescens in the dry			
Hymenachne Grassland	Hymenachne acutigluma with Ludwigia			
	adscendens, Nymphaea spp., Oryza			
	meridionalis & Pseudoraphis spinescens			
	also common			
Pseudoraphis Grassland	Pseudoraphis spinescens in wet and dry with			
	Nymphaea spp., Najas spp., Utricularia spp.			
	common in the wet			
Nelumbo Swamp	Nelumbo nucifera in wet and dry with			
	Nymphoides spp. in wet			
Hymenachne/Eleocharis Swamp	Hymenachne acutigluma or Eleocharis spp.			
	with Nymphoides spp. in wet			
Mixed Grassland/Sedgeland	Depending on topography (ie. middle or edge			
	of floodplain) Oryza meridionalis,			
	Pseudoraphis spinescens & Hymenachne			
	acutigluma with Eleocharis spp. & Cyperus			
	spp.			
Terrestrial Vegetation	Eucalypt overstorey with terrestrial shrubs			
	and herbs in the understorey			

#### Data analysis

Frequency scores for each species at a sampling location were calculated from species presence scores of nested quadrats. These data were analysed using PATN (Belbin 1993b). An association matrix was generated using the Bray Curtis coefficient (Appendix B).

Cluster analysis was conducted using flexible unweighted pair grouping using arithmetic averaging (UPGMA) ( $\beta$  = -0.1) (Belbin 1993a). Semi-strong hybrid multidimensional scaling (SSH), was used to ordinate data in three dimensions, with a maximum of 50 iterations and 100 random starts (Belbin 1993a). Principle component correlations (PCC) were then conducted to identify vectors for each species in the ordination (Belbin 1993a).

Individual species could not be compared using parametric techniques as statistical assumptions were violated. Consequently, species richness and diversity were used as a measure of species composition. Species richness (total number of species) and the Shannon Diversity Index were calculated for each nested quadrat and ANOVA was used to compare both of these variables among sampling sites and seasons. The Least Significant Differences (LSD) test was used to determine significant differences (P<0.05). The Shannon Diversity Index was calculated according to the following formula:

Shannon Diversity  $H = -\sum_{i=1}^{s} P_i(\ln P_i)$ 

. Where P = Proportion (relative abundance determined from frequency score) of the given species *i*.

### Results

### Taxa Within the Extant Vegetation

Q1: What taxa are present in each of the vegetation types in each season?

A total of twenty five taxa were recorded through the vegetation survey (Appendix G; Table 3.2). Twelve taxa were found in the *Brachiaria* grassland, sixteen in the *Oryza* grassland, twenty in the *Hymenachne* grassland and eleven in the *Pseudoraphis* grassland. Higher numbers of taxa were recorded in the *Brachiaria*, *Oryza* and *Pseudoraphis* grasslands during the wet than during the dry season. The total number of taxa found in the *Hymenachne* grassland in both seasons did not differ greatly, however, the species composition differed between wet and dry seasons in this community.

Five species were unique to the *Hymenachne* grassland during the dry season namely, *Coldenia procumbens*, *Cyperus platystylis*, *Dentella dioeca, Eclipta prostrata* and *Heliotropium indicum*. Three species were found to occur only in quadrats recorded from the *Oryza* grassland, *Hygrochloa aquatica* during the wet season, *Merremia gemella* and *Phyla nodiflora* during the dry season.

Table 3.2 Cumulative frequency scores for each species from vegetation surveys of four grassland communities on the Magela floodplain in wet and dry seasons (Nov 95 & April-May 96). Fifteen nested quadrats were taken in each community (values range from 0-15) (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland, D = dry season, W = wet season)

Таха	Bm D	Bm W	Om D	Om W	Ha D	Ha W	Ps D	Ps W
Azolla pinnata		0.6				1		1.2
Brachiaria mutica	15	15	0.2					
Coldenia procumbens					2.6			
Cyperus platystylis					2.8			
Dentella dioeca					3			
Eclipta prostrata					8			
Eleocharis spp.		1		4.4		1.8		0.8
Euphorbia vachellii			6.8		0.8			
Fimbristylis spp.	0.6				2			
Glinus oppositifolius					2,6		0.4	
Heliotropium indicum					2.4			
Hygrochloa aquatica				0.4				
Hymenachne acutigluma		0.2		1	12.6	15		0.4
Ipomoea aquatica				2.6				0.6
Ludwigia adscendens		1.2		2.4	9.4	7		4.4
Merremia gemella			3.4					
Najas spp.				1.4		0.4		
Nymphaea spp.		0.6		3.6		1.8		7.6
Nymphoides spp.				1	3.4	1		1
Oryza meridionalis		0.2		14.2		1		
Persicaria spp.		0.4		1.6	5	1.6		0.2
Phyla nodiflora			0.4					
Pseudoraphis spinescens	1	0.8	15	7.6	10.8	3.2	15	15
Salvinia molesta		0.6				3		
Utricularia spp.		3.2		5		1.8		12.8
### Patterns in the Extant Vegetation

Q<sub>2</sub>: Does species composition differ among extant vegetation of the four grassland communities?

Four main groups according to plant community and season were defined by cluster analysis (Figure 3.2).

Quadrats sampled in the *Brachiaria* grassland were separated first as these samples had similar species composition and abundance in both wet and dry seasons. *Hymenachne* grassland quadrats also had similar species composition and abundance in wet and dry seasons and as such were separated from the remaining quadrats. Following this *Oryza* grassland quadrats recorded in the wet season were separated from *Pseudoraphis* grassland quadrats in both wet and dry seasons and *Oryza* grassland quadrats recorded in the dry. The remaining group was separated into three partitions: two anomalous samples; *Pseudoraphis* grassland quadrats recorded in the wet season; and *Pseudoraphis/Oryza* grassland quadrats recorded in the dry season; and *Pseudoraphis/Oryza* grassland quadrats recorded in the dry season.



Figure 3.2 Dendrogram of cluster analysis on nested quadrat data collected from four grassland communities on the Magela floodplain in the dry and wet season of 1995-96; G1 = *Brachiaria* grassland quadrats (wet and dry seasons), G2 = *Oryza* grassland (dry season) and *Pseudoraphis* grassland quadrats (wet & dry seasons), G3 = *Oryza* grassland quadrats (wet season), G4 = *Hymenachne* grassland quadrats (wet & dry seasons) (The 3 additional partitions of quadrats are indicated on the figure; small text: *Brachiaria* grassland (Bm), *Hymenachne* grassland (Om) and *Pseudoraphis* grassland (Ps) in the dry (T) and wet (Q) Bray Curtis coefficient, UPGMA,  $\beta$ = -0.1).

Similar patterns among grassland communities were observed from ordination of frequency data (Figure 3.3). Three dimensional ordination gave an acceptable stress value of 0.113 (Belbin 1993a) and the two dimensional plot of ordinal axes 1 and 3 gave the clearest view of this analysis. To highlight patterns, groups defined by the cluster analysis have been superimposed on the plot (thickness and number of breaks in the lines indicates the hierarchy of groupings). High correlations (r > 0.7) were found for *Brachiaria mutica*, Oryza meridionalis. Hymenachne acutigluma, Pseudoraphis spinescens and Ludwigia adscendens using principle co-ordinate correlation analysis (Figure 3.4). Presence and frequency of *Brachiaria mutica* was the main factor influencing the position of samples taken from the Brachiaria grassland site and analyses were unable to detect change in species composition and abundance of this community between seasons. Oryza grassland samples differed markedly between seasons and the analyses indicate that this difference is due to the occurrence of the species *Pseudoraphis spinescens* during the dry season. Differences in species composition and abundance of the Pseudoraphis grassland were found between seasons and these samples were similar to the Oryza grassland during the same season. Changes in species composition and abundance within the Hymenachne grassland, between wet and dry seasons, were not as evident as those found in the *Pseudoraphis* and *Oryza* grasslands.



Figure 3.3 Ordination plot of nested quadrat data collected from four different grassland communities on the Magela floodplain in both wet and dry seasons (1995-96); superimposed lines show groupings according to cluster analysis, thickness and number of breaks in line indicate hierarchy of grouping (Bray Curtis coefficient: multidimensional scaling: 3 dimensions: stress = 0.113).



Figure 3.4 Vectors of principle component co-ordinate analysis on ordination results of nested quadrat data collected from four different grassland communities on the Magela floodplain in both wet and dry seasons (1995-96). Only species with r values greater than 0.7 are shown (*Brachiaria mutica* r = 0.963, *Pseudoraphis spinescens* r = 0.941, *Hymenachne acutigluma* r = 0.928, *Oryza meridionalis* r = 0.719 and *Ludwigia adscendens* r = 0.716) (Bray Curtis coefficient).

## Species Richness in the Extant Vegetation

- Q<sub>2</sub>: Does species composition differ among extant vegetation of the four grassland communities?
- H<sub>1</sub>: There is no difference in species richness of extant vegetation among grassland communities.
- H<sub>2</sub>: There is no difference in species richness of extant vegetation between wet and dry seasons.
- H<sub>3</sub>: There is no difference in species richness of extant vegetation among grassland communities and between wet and dry seasons.

Species richness was found to differ significantly among the four grassland communities, between seasons and for community and season interactions (Table 3.3: refer Appendix C for LSD tables). When data between seasons were pooled, the *Hymenachne* grassland quadrats had significantly higher species richness than all other communities (Table C.1; Figure 3.5). *Oryza* grassland quadrats had the second highest species richness and this was significantly different from all other communities. Species richness in *Brachiaria* and *Pseudoraphis* grasslands were low and did not differ significantly. When data for each community were pooled, species richness was significantly higher in the wet season than the dry season (Figure 3.6).

Table 3.3 Summary of ANOVA on species richness of nested quadrat data collected from four grassland communities on the Magela floodplain during wet and dry seasons of 1995-96 (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands) (\* = p < 0.05, \*\*\* = p < 0.001).

	df Effect	MS Effect	df Error	MS Error	F	p-level
Community	3	70.335	112	2.282	30.823	< 0.001***
Season	1	10.233	112	2.282	4.485	0.036*
Community x Season	3	42.003	112	2.282	18.407	< 0.001***



Figure 3.5 Species richness in *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain in 1995-96 (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 3.6 Combined species richness of four grassland communities on the Magela floodplain in dry and wet seasons 1995-96. (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands) (Significant differences identified using LSD test (p<0.05) are indicted by different letters).

Species richness in the *Brachiaria* grassland did not change significantly between seasons, whereas *Oryza* and *Pseudoraphis* grasslands had significantly higher species richness in the wet season, compared to the dry season, and species richness in the *Hymenachne* grassland dropped significantly during the wet season (Table C.2; Figure 3.7).

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During the dry season the *Pseudoraphis* grassland contained the lowest overall species richness of all vegetation types, in all seasons. This grassland community had significantly lower species richness than all other communities, except *Brachiaria* grassland in the dry season. *Brachiaria* grassland in the dry contained the second lowest number of species, with *Oryza* and *Pseudoraphis* grasslands in the wet season, and the *Hymenachne* grassland, in both wet and dry seasons containing significantly more species. During the wet season species richness in the *Brachiaria* dominant community increased, but was still significantly lower than species richness in the *Hymenachne* grassland in either season and the *Oryza* grassland during the wet season. During the dry season the *Oryza* grassland in both wet and dry seasons. *Hymenachne* grassland in other the *Hymenachne* grassland in either season and the *Oryza* grassland in both wet and dry seasons. Hymenachne grassland in other the thymenachne grassland in other the season and the *Oryza* grassland is significantly lower numbers of species than the *Hymenachne* grassland in both wet and dry seasons. Hymenachne grassland in the dry season contained significantly more species than all other communities in any season.



Figure 3.7 Species richness in *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain in both dry and wet seasons, 1995-96 (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

# Species Diversity in the Extant Vegetation

- H<sub>4</sub>: There is no difference in species diversity of extant vegetation among grassland communities.
- H<sub>5</sub>: There is no difference in species diversity of extant vegetation between wet and dry seasons.
- H<sub>6</sub>: There is no difference in species diversity of extant vegetation among grassland communities and between wet and dry seasons.

The Shannon Diversity Index of nested quadrats was found to differ significantly among communities, between seasons and for community and season interactions (Table 3.4: Refer Appendix C for LSD tables). All communities differed significantly from each other in species diversity (Table C.3; Figure 3.8). The *Hymenachne* grassland had the highest diversity followed by the *Oryza* grassland, *Pseudoraphis* grassland and *Brachiaria* grassland. Species diversity was significantly higher in the wet season than the dry season (Figure 3.9).

Table 3.4 Summary of ANOVA on species diversity (Shannon Index) of nested quadrat data collected from four grassland communities on the Magela floodplain during wet and dry seasons of 1995-96 (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands) (\*\*\* = p < 0.001).

	df Effect	MS Effect	df Error	MS Error	F	p-level
Community	3	6.499	112	0.143	45.294	< 0.001***
Season	1	3.969	112	0.143	27.664	< 0.001***
Community x Season	3	3.498	112	0.143	24.379	< 0.001***



Figure 3.8 Species diversity (Shannon Index) in *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain (1995-96) (Significant differences identified using LSD test (p<0.05) are indicted by different letters).



Figure 3.9 Combined species diversity (Shannon index) of four grassland communities on the Magela floodplain in dry and wet seasons 1995-96. (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands) (Significant differences identified using LSD test (p<0.05) are indicted by different letters).

Species diversity was significantly higher in the wet season than the dry season in the *Brachiaria, Oryza* and *Pseudoraphis* grasslands, whereas a significant decrease in diversity was found for the *Hymenachne* grassland in the same season (Table C.4; Figure 3.10). During the dry season *Brachiaria* and *Pseudoraphis* grasslands had significantly lower species diversity than all

other communities in either the wet or dry. Although diversity in the *Brachiaria* grassland increased in the wet season, it remained significantly lower than all other samples, except those collected from the *Oryza* and *Pseudoraphis* grasslands, during the dry season. In the dry season the *Oryza* grassland had significantly lower species diversity than the *Hymenachne* grassland in both seasons and the *Pseudoraphis* grassland in the wet season. Despite increased diversity in the *Oryza* grassland during the wet season, species diversity remained significantly lower than that of the *Hymenachne* grassland during the dry season. *Hymenachne* grassland, during the dry season, contained significantly higher species diversity than all other samples.



Figure 3.10 Species diversity (Shannon index) in *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain in both dry and wet seasons, 1995-96 (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

# Mapping of the Extant Vegetation

- Q<sub>3</sub>: What area of the southern section of the floodplain do each of the four plant communities occupy?
- Q<sub>4</sub>: What change in distribution of *Brachiaria mutica* has occurred in the most heavily infested area of the floodplain between 1991 and 1996?

Descriptions of the mapping units used are supplied in Chapter two and Appendix A. Area calculations for all maps are presented in Table 3.5. The total area mapped was 9120 ha (map 3.1). Maps 3.2 and 3.3 are more detailed and only cover the area of major *Brachiaria mutica* infestation in 1996 (1672 ha). The *Brachiaria* grassland was found to cover 920 ha (10%) of the total area mapped. This was less than the 1020 ha (11%) and 1926 ha (21%) covered by the *Oryza* and *Pseudoraphis* grasslands respectively, but more than the area calculated for the *Hymenachne* grassland (620 ha, 7%).

Within the area covered by maps 3.2 and 3.3 the *Brachiaria* grassland expanded from 132 ha in 1991 to 422 ha in 1996. A corresponding decrease in the area covered by the *Oryza* grassland was also found (590 ha  $\rightarrow$  278 ha). The *HymenachnelEleocharis* swamp increased in area from 242 ha to 295 ha and the *Pseudoraphis* grassland which covered 13 ha in 1991 was not identified in 1996.

Table 3.5 Calculated areas of each mapping unit defined in three vegetation maps produced from aerial photos of the Magela floodplain: Map 3.1 (1996 photos) covered the southern section of the floodplain while Map 3.2 (1991 photos) and Map 3.3 (1996 photos) cover only the area of major *Brachiaria mutica* infestation in 1996.

Plant Community	(Map 1) Area ha	Map 2 (1991) Area ha	Map 3 (1996) Area ha
Open water	117	26	30
Melaleuca Open Woodland	1511	34	32
Melaleuca Open Forest/Woodland	819	0	0
Brachiaria grassland	920	132	422
Oryza grassland	1020	590	278
Hymenachne grassland	620	9	12
Pseudoraphis grassland	1926	13	0
Nelumbo swamp	1466	0	0
Hymenachne/Eleocharis swamp	572	242	295
Mixed Grassland/Sedgeland	89	0	0
Terrestrial Vegetation	60	204	206
Undefined		422	397
Total area	9120	1672	1672

Chapter 3



Map 3.1 Vegetation map of the southern section of the Magela floodplain in Kakadu National Park; generated from aerial photographs taken in June 1996 and vegetation survey data; Mapping units except *Brachiaria* grassland follow Finlayson *et al.* (1989).

Chapter 3



1991







Map 3.2 (top) and Map 3.3 (below) Change in distribution of *Brachiaria* grassland between 1991 and 1996 in the most heavily infested area on the Magela floodplain.

# Discussion

## Patterns in the Extant Vegetation

The Brachiaria and Hymenachne grassland communities were clearly separate from one another and the Oryza and Pseudoraphis grasslands (Figures 3.2 & 3.3). However, distinctions between seasons in *Brachiaria* and Hymenachne grasslands were not demonstrated using multivariate techniques. The Oryza grassland was found to differ distinctly between seasons and a change in species composition and abundance of the *Pseudoraphis* grassland was also found although this separation was not as clear in the cluster analysis. The inability of multivariate analyses to distinguish clear differences in species composition and abundance between seasons in the Hymenachne and Brachiaria grasslands were a result of Brachiaria mutica, Hymenachne acutigluma and Ludwigia adscendens occurring in high numbers. Brachiaria mutica was the most abundant species in the Brachiaria grassland and few other species were found with it in high numbers in either wet or dry seasons (Table 3.2). Similarly Hymenachne acutigluma and Ludwigia adscendens were abundant in both seasons within the Hymenachne grassland sample sites. However, this community appears to undergo distinct changes in species composition between wet and dry seasons. It contains many herbs in the dry season that are not found in the wet season (Table 3.2). It is possible that the high abundance of Hymenachne acutigluma and Ludwigia adscendens in both seasons impeded multivariate techniques from distinguishing compositional changes in this community between seasons. In contrast, Pseudoraphis and Oryza grasslands contained few taxa during the dry and both composition and abundance of taxa increased dramatically in the wet season. The Pseudoraphis grassland was characterised by Pseudoraphis spinescens and during the wet season Nymphaea spp. were abundant in this community. *Pseudoraphis spinescens* also dominated the Oryza grassland during the dry season and featured prominently in this community during the wet season. Oryza meridionalis, being annual, dominated the Oryza grassland community during the wet season.

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## Species Richness & Diversity in the Extant Vegetation

Both species richness and species diversity followed similar trends in the four grasslands. Species richness and diversity was higher in the wet than the dry (Figures 3.3 & 3.6). The Brachiaria grassland had the lowest species richness and diversity of the communities when seasonal data were pooled (Figures 3.2 & 3.5). When community and season interactions were tested, however, the Pseudoraphis grassland had lower species richness and diversity than the Brachiaria grassland in the dry, although this difference was not significant (Figures 3.4 & 3.7). This could be due to a combination of the turf like habit of Pseudoraphis spinescens in the dry season inhibiting germination of other species and the extreme change in conditions that this site undergoes over one season. The *Pseudoraphis* grassland is located in the main flow channel of the floodplain (Map 3.1) where water level fluctuations are more rapid compared to other communities. These conditions may inhibit many species from establishing in this area. Examination of seasonal vegetation changes within communities provides relevant information on long term vegetation changes that may be occurring as this factor plays an important role in the vegetation dynamics of the Magela floodplain.

Species richness did not change in the Brachiaria grassland between seasons whereas all other communities showed significant changes, and although diversity increased in the Brachiaria grassland in the wet season, this was still much lower than diversity in other communities. Oryza and Pseudoraphis grasslands experienced increased diversity and richness, whereas, the Hymenachne grassland decreased in species richness and diversity between dry and wet seasons. These fluctuations can probably be attributed to the duration of inundation of these areas and the growth habits of Oryza meridionalis and Pseudoraphis spinescens. Oryza meridionalis and Pseudoraphis spinescens do not grow in dense clumps during the wet season and as a result many other species can co-occur with them in the wet. The Oryza grassland is situated on the edge of the floodplain and consequently draws down early in the dry season. This could be one reason contributing to low species richness and diversity in this community during the dry season.

Grime (1973) postulated that species richness would be low under extreme environmental conditions as fewer species can tolerate harsh environments. The results of this study support this idea as both *Oryza* and *Pseudoraphis* grasslands are situated in sites that have more extreme water fluctuations than the *Hymenachne* grassland. Due to its location, the *Hymenachne* grassland is flooded by backflow (Map 3.1), therefore draw down takes longer in this community and this is probably why more taxa can be found in this area of the floodplain.

The small change in species richness and diversity within the *Brachiaria* grassland illustrates the potential of *Brachiaria mutica* to change the environment in which it grows. Its form and habit does not readily allow coexistence with other species and this is one reason pastoralists have chosen to use it in ponded pastures (Anning and Hyde 1987).

*Brachiaria mutica* appears to be able to tolerate the early draw down that occurs towards the edge of the floodplain and as it is perennial could therefore be excluding *Oryza meridionalis* by inhibiting germination of this species early in the wet season. It would appear that *Brachiaria mutica* could potentially invade the *Hymenachne* grassland, but this process may take longer as *Hymenachne acutigluma* is also perennial. *Brachiaria mutica* will not grow in water much deeper than 60cm (Clarkson 1995) and as a result is unlikely to invade the *Pseudoraphis* grassland as this community occurs on the deepest areas of the floodplain (inundated >1m). This factor may also limit the degree of invasion into the *Hymenachne* grassland as this community can also be found in areas inundated up to and above 1m (Finlayson 1991).

Gopal (1986) suggested that changes in temporary and shallow freshwater habitats are primarily a result of water level changes. Finlayson *et al.* (1989) highlighted the importance of timing and duration of flooding in such changes. This study did not have the scope to investigate this further, however, Finlayson *et al.* (1990) did point out that plant communities could be delineated according to mean inundation times.

The five species found to correlate strongly with the patterns found in the ordination made vegetation mapping from aerial photographic interpretation possible as these species could be identified growing in large clumps on aerial

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photos. Pseudoraphis grassland covered the greatest area out of the four arassland communities followed by the Orvza arassland. Brachiaria arassland and Hymenachne grassland (Map 3.1). Maps 3.2 and 3.3 illustrate both the variability in plant communities over a five year period and the change in distribution of Brachiaria mutica in that time. Pseudoraphis grassland covered 13ha in 1991 and was absent in the 1996 photos, the Hymenachne grassland 3ha over the five year period and the increased in size by Hymenachne/Eleocharis swamp expanded by 53ha. The greatest contrast was found in the considerable increase in area covered by Brachiaria grassland (290 ha) and corresponding decrease in the Oryza grassland (312 ha). This indicates that a considerable loss in the area occupied by Oryza meridionalis The change in Hymenachne/Eleocharis swamp has already occurred. illustrates the dramatic changes in distribution of vegetation that this system can undergo. Hence more detailed data are needed on distribution changes of Brachiaria mutica on the Magela floodplain as this community my also undergo fluctuations in distribution. Nevertheless, the considerable difference in area covered by the Brachiaria grassland between years indicates that the change is too great to be attributed to seasonal fluctuation alone. However, the timing of dry season fires may have influenced the results of aerial photographic interpretation and this factor should be considered when producing future maps. Additionally, changes in distribution of vegetation may be affected by rainfall in previous years and such a factor can only be assessed by mapping vegetation in conjunction with monitoring long term rainfall patterns.



Chapter 4 The Seed Banks: Sediment Germination Trial

# Introduction

Seed banks are difficult to study and this may account for the limited research existing in this area. The difficulty in studying seed banks arises as seeds are rarely evenly distributed in soils and different species have varying seed size and different germination requirements. Thus, many factors must be considered in the design of seed bank experiments, including sample collection, sampling intensity, sample distribution, timing of sampling, estimation of seed numbers and the suitability of data for analysis with various statistical techniques (Benoit *et al.* 1989; Warr *et al.* 1993; Britton and Brock 1994).

Most wetland seed bank studies have been aimed at gaining an understanding of the role seed banks play in structuring wetland plant communities. Various approaches have been used including comparison of seed banks from different vegetation types (Thompson and Grime 1979); examination of the relationship between the seed bank and extant vegetation (Grillas *et al.* 1993; Wilson *et al.* 1993); investigation of the role of seed banks in re-establishment of vegetation after a disturbance (ter Heerdt and Drost 1994); and determination of germination from seed banks under various hydrological regimes (Smith and Kadlec 1983; Schneider and Sharitz 1986; Schneider 1994) and in different seasons (Thompson and Grime 1979; Britton and Brock 1994).

The most common technique applied in studying seed banks involves collecting soil cores, placing them in a glasshouse, and counting seedlings of each species as they emerge. This technique assesses the ability of seeds to germinate but does not accurately assess numbers of seeds of different species contained within the soil (Thompson and Grime 1979). To maximise precision of seed estimates most studies of this type germinate samples under different water regimes (Smith and Kadlec 1983; Wilson *et al.* 1993; Britton and Brock 1994; Brock *et al.* 1994; Schneider 1994) and/or run experiments over many months (Leck and Simpson 1987; Leck and Simpson 1995).

A seed bank experiment was conducted over a period of 10 months on sediment samples from the Magela floodplain in 1984 using two water regimes

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(flocded and moist) (Finlayson *et al.* 1990). This study demonstrated significant site-treatment differences, reflecting to some extent, the previous vegetation history of each site and the habit of the dominant grass species. It also indicated that specific species composition could vary under different environmental conditions, however, there was insufficient information to suggest that major changes to broad vegetation patterns would occur (Finlayson *et al.* 1990). One of the main reasons for conducting the study was to provide baseline data so that changes in plant species composition and introduced plant species invasions, could be assessed (Finlayson *et al.* 1990).

Chapter three discussed changes in extant vegetation and revealed that *Brachiaria mutica* has invaded a considerable area of the *Oryza* grassland. Hence, samples collected, from sites also used by Finlayson *et al.* (1990), for the following seed bank experiment included *Brachiaria* grassland in addition to *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland. The *Brachiaria* grassland and *Oryza* grassland samples of the present study come from *Brachiaria mutica* invaded and uninvaded areas of the *Oryza* grassland site as sampled in the 1984 study. This division was made to assess differences in seed banks between invaded (previously *Oryza* grassland).and uninvaded communities.

The questions that this experiment was designed to address are:

- Q<sub>1</sub>: What taxa germinate from the seed banks of four grassland communities (*Brachiaria* grassland, *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland) in 1996?
- Q2: Does Brachiaria mutica (Para Grass) exist in the seed bank?
- Q<sub>3</sub>: Does germination under flooded or moist conditions influence which taxa will germinate?
- Q<sub>4</sub>: What patterns can be found in species composition and abundance of seedlings emerging from sediment samples?
- Q<sub>5</sub>: Do seeds in the seed bank vary spatially within a grassland community?
- Q<sub>6</sub>: Do seed banks vary among different grassland communities?
- Q<sub>7</sub>: Have changes occurred in the seed bank since the 1984 study?

The hypotheses generated to test these questions are:

- H<sub>1</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>2</sub>: There is no difference between flooded and moist water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>3</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>4</sub>: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>5</sub>: There is no difference between flooded and moist water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>6</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>7</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.
- H<sub>8</sub>: There is no difference between flooded and moist treatments in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>9</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>10</sub>: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>11</sub>: There is no difference in the number of taxa emerging from flooded and moist treatments from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>12</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.

# **Materials and Methods**

## Sampling Design for Field Collection of Seed Bank Samples

Sediment samples were collected to allow spatial variation to be detected both within and among plant communities. The methods used were modified from a previous study conducted at the same sites as the present study (Finlayson *et al.* 1990). Six sediment cores (53mm diameter and 10cm deep), including a spare core, located around the circumference of a 1m radius circle, were collected from each of five replicate sites. The replicate sites were 25m apart and located at the ends and apices of W shaped transects (Figure 4.1). Three transects were randomly placed in each of four different grassland communities (*Brachiaria, Oryza, Pseudoraphis* and *Hymenachne*) as defined in Chapter two. To ensure randomisation of samples, each transect was positioned along a different randomly allocated compass bearing. The cores were collected in the dry season between 20-29 November 1995.



Figure 4.1 Transect dimensions showing the locations of sediment core collection sites.

The corer consisted of a 150mm long piece of pvc pipe (inside diameter 53mm) that was tapered at one end to minimise soil compaction. A mark 100mm from the tapered end was made around the circumference of the pipe to ensure correct sampling depth. The corer was driven in to the appropriate depth using a lump mallet. Two opposing holes were positioned above the depth mark to allow corer extraction using a metal bar as a lever (Figure 4.2).



Figure 4.2 Design of pvc corer used to collect sediment samples.

As seeds were possibly present within soil surface organic matter, this material was included in the samples. Each sample was pushed out of the corer directly into a labelled calico bag. Calico bags were spread out on benches in the glasshouse and left for 24 hours to air dry. Samples were then stored at  $22^{\circ}$ C until March 16 1996 when the 30 samples collected from each transect were combined into ten groups of three cores (the six cores from each sample circle made up two groups). Each group represented a floodplain area of 66 cm<sup>2</sup> x 10 cm depth. Groups were then placed into different labelled circular trays (25cm diameter x 4cm deep) each lined with absorbent paper. The trays were watered, samples were spread to a depth of 2cm and the samples were randomly placed on benches in a glasshouse (Plate 4.1). Half of the trays from each transect were flooded to a depth of 2 cm over the sample (to the top of the tray) and the remaining trays were kept permanently moist. Thus, the experiment consisted of 120 trays, 30 trays from each grassland community (15 flooded and 15 moist). Twelve additional trays of sterilised

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were added as controls to assess contamination from weeds and seed dispersal between trays. Treatments were maintained by daily additions of tap water (total alkalinity 140 mg<sup>-1</sup> CaCO<sub>3</sub>, conductivity 30  $\mu$ S cm<sup>-1</sup> at 25°C, Ca 20 mg l<sup>-1</sup>, Mg 20 mg l<sup>-1</sup>, (Finlayson *et al.* 1990)) using an automated watering system. All trays were monitored daily to ensure even watering.

The experiment was run over a period of 3 <sup>1</sup>/<sub>2</sub> months. After six weeks seedlings emerging from trays were identified, counted and removed. Unidentified seedlings were either potted up and left to further mature or marked using map pins for later identification. Trays were scored a second time in June 1996.

As plants were removed representative specimens of each species were pressed and lodged as vouchers in the Environmental Research Institute of the Supervising Scientist (*eriss*) Herbarium. Additional vouchers were lodged at the New England Herbarium (NE).



Plate 4.1 Sample trays randomly placed on benches in the glasshouse just prior to commencement of the sediment germination trial (March 1996).

#### Data analysis

### Patterns in Grassland Seed Banks

Absolute value data for each taxa in all samples were analysed using PATN (Belbin 1993b). An association matrix was generated using the Bray Curtis coefficient and this was used to produce an ordination plot and cluster dendrogram.

Semi-strong hybrid multidimensional scaling (SSH), a non-metric ordination algorithm, was used to ordinate data in three dimensions with a maximum of 50 iterations and 100 random starts.

Cluster analysis was conducted using flexible unweighted pair grouping using arithmetic averaging (UPGMA), ( $\beta = -0.1$ ) (Belbin and McDonald 1993).

### Variation Within and Among Grassland Seed Banks

Taxa found to emerge from each plant community in both flooded and moist treatments were examined. Sample distributions of data for individual taxa were not normal and transformations of these data failed to homogenise sample distributions. Log (x + 1) transformations of the total number of seedlings found in transects within grassland communities and among grassland communities were effective in normalising sample distributions. Species richness (total number of species) data within and among grassland communities was found to contain normal sample distributions. ANOVA was used to compare differences for both total number of seedlings (Log (x + 1) transformed) and species richness between transects, treatments and for transect and treatment interactions, within each vegetation type. These data were pooled and differences among grassland communities were also tested. The Least Significant Difference (LSD) test was used to identify the exact effects of all ANOVA analyses that were significant.

### Comparisons of Grassland Seed Banks Between Years (1984 & 1996)

Species richness of samples were compared between years for varying plant communities and flooded / moist treatments. Taxa emerging from the same communities (or equivalent) in different years were also compared. The latter comparisons were based on the proportion of the total number of seedlings

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emerging from samples collected within their respective communities in each year.

## Results

- Q<sub>1</sub>: What taxa germinate from the seed banks of four grassland communities (*Brachiaria* grassland, *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland) in 1996?
- Q<sub>2</sub>: Does Brachiaria mutica (Para Grass) exist in the seed bank?

In total thirty four taxa emerged from the sediment samples (Appendix G; Table 4.1). Twenty nine percent of taxa were found in all grassland communities and twenty six percent of taxa occurred in only one vegetation type. Three introduced species were recorded, *Brachiaria mutica, Heliotropium indicum* and *Phyla nodiflora. Brachiaria mutica* emerged from the *Brachiaria* grassland and *Hymenachne* grassland samples, *Heliotropium indicum* occurred in *Brachiaria, Hymenachne* and *Oryza* grassland samples and *Phyla nodiflora* occurred in *Oryza* grassland samples.

The Hymenachne grassland samples contained 25 taxa, the Oryza grassland samples, 24 taxa, Brachiaria grassland samples, 21 taxa and Pseudoraphis grassland samples, 13 taxa. Four species were unique to Oryza grassland samples namely, Cyperus aquatilis, Commelina lanceolata, Ludwigia perennis and Phyla nodiflora. Hymenachne grassland samples contained the highest number of unique taxa, Dentella dioeca, Euphorbia vachellii, Hydrilla verticillata , Hymenachne acutigluma, Ludwigia adscendens and Persicaria sp... Only one species emerged exclusively from the Pseudoraphis grassland samples being, Blyxa aubertii and no taxa were unique to the Brachiaria grassland samples.

Table 4.1 Total number of seedlings of each taxa emerging (between March and June 96) from sediments of four grassland communities on the Magela floodplain germinated under flooded and moist water regimes (Bm = Brachiaria grassland, Om = Oryza grassland, Ha = Hymenachne grassland, Ps = Pseudoraphis grassland, F = flooded treatment, M = moist treatment, \* = introduced species)

Таха	Bm	Bm	Om	Om	На	На	Ps	Ps
Pluvo oubortii	- <u>  -</u>	<u></u>		<u></u>	┝──┍	<u>  M</u>		<u> </u>
Biyxa aubertii		10	<u> </u>		<u> </u>			
Brachiaria mutica		12				<u> </u>		<u>-</u>
Cyperus aquatilis		<u> </u>	ļ	2	100		<u> </u>	<u> </u>
C. platystylis				<u>↓</u>	129	41		
C. serotinus		1			96	216	1	ļ
Ceratopteris thalictroides	7	18	92	80		2	<u> </u>	<u></u>
Chara spp.	121		45		35	<u> </u>	7	<u> </u>
Coldenia procumbens		2		6		9		
Commelina lanceolata				2				
Dentella dioeca						29		
Eclipta prostrata					8	20	6	1
Eleocharis spp.	15	24	10	10	1		23	60
Eriocaulon setaceum	1	4	19	14		[		
Euphorbia vachellii		<u> </u>				1		
Fimbristylis spp.		3	1	6		8	5	
Glinus oppositifolius		2		3		91	33	801
Heliotropium indicum*		11		77		1		
Hydrilla verticillata					5			
Hymenachne acutigluma					6	36		
Isoetes coromandelina .	13	238	37	311				1
Ludwigia adscendens					6		3	
L. perennis			1	1				
Limnophila australis	61	44	40	19				
Maidenia rubra	29	11	30	8	8	14		
Najas spp.	62	3	40		44	6	3	2
Nitella spp.	414	60	138	3	102	14	114	2
Nymphaea spp.	19	26	6	2	76	72	102	127
Nymphoides spp.	15	28	11	5	55	155	15	6
Oldenlandia sp.				1		1	1	
Oryza meridionalis	1	1	1	2				
Persicaria sp.				·		8	1	
Phyla nodiflora*				4				
Pseudoraphis spinescens		2		17	4	117	10	132
Utricularia spp.	22	1	12		26	9	90	2

# Variation in Germination Conditions Among Taxa

Q<sub>3</sub>: Does germination under flooded or moist conditions influence which taxa will germinate?

Figure 4.3 shows taxa for which less than fifty seedlings emerged and Figure 4.4 shows taxa with more than fifty emergents. Four taxa, *Blyxa aubertii*, *Ludwigia adscendens, Hydrilla verticillata* and *Chara* spp. only emerged under flooded conditions. Other taxa, *Cyperus platystylis, Najas* spp., *Nitella* spp. and *Utricularia* spp., all emerged in far greater numbers in the flooded treatments compared to the moist treatments.

The following seven species emerged from moist treatments only: *Brachiaria mutica*; *Cyperus aquatilis*; *Coldenia procumbens; Commelina lanceolata; Dentella dioeca; Euphorbia vachellii; Phyla nodiflora;* and *Heliotropium indicum* (Figures 4.3 and 4.4). *Persicaria* sp., *Hymenachne acutigluma, Fimbristylis* spp., *Eclipta prostrata, Cyperus serotinus, Glinus oppositifolius, Isoetes coromandelina, Nymphoides* spp., and *Pseudoraphis spinescens* all emerged in greater numbers in moist rather than flooded treatments.



Figure 4.3 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (species with < 50 emergents)



Figure 4.4 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (taxa with > 50 emergents)

### Patterns Within and Among Grassland Seed Banks

Q<sub>4</sub>: What patterns can be found in species composition and abundance of seedlings emerging from sediment samples?

Differences (shown above) in the species composition and abundance of germination from flooded and moist treatments are confirmed by ordination of data (Figure 4.5). In addition grassland communities were clearly separated (Figure 4.6). The *Pseudoraphis* grassland samples were distinctively grouped as were *Hymenachne* grassland samples. *Oryza* grassland and *Brachiaria* grassland sample trays, on the other hand, overlapped considerably in species composition and abundance.

Principal component correlations did not produce high r-values for any individual taxa (r < 0.2), although cluster analysis grouped samples according to combinations of taxa.



Figure 4.5 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis: multidimensional scaling stress 0.1764). Distinction between water regimes is shown.



Figure 4.6 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis: multidimensional scaling stress 0.1764). Distinction between plant communities is shown.

Cluster analysis separated samples according to groupings of a few taxa (Figure 4.7). The first branch split four Oryza grassland samples under the moist water regime and one *Hymenachne* grassland sample under the flooded water regime, from the remaining samples. These samples all had very few germinants of any species. The remaining samples were then split into two main groups, one containing all of the remaining Oryza grassland samples and all but two of the Brachiaria grassland samples, and the other containing most of the Hymenachne grassland and Pseudoraphis grassland samples. This branch was derived from samples containing Nymphaea spp. in the absence of Nitella spp. The branch containing the Hymenachne and Pseudoraphis grassland samples were split into two groups, one comprised predominantly of Pseudoraphis grassland samples containing Glinus oppositifolius, Nymphaea spp., and *Pseudoraphis spinescens* seedlings and the other made up primarily of Hymenachne grassland samples with Nymphaea spp., Nymphoides spp. and Cyperus serotinus seedlings.

The branch made up mainly of *Oryza* grassland and *Brachiaria* grassland samples was divided into two groups according to the presence of *Nitella* spp.. One group made up of *Oryza* and *Brachiaria* grassland samples, under a moist water regime, contained *Isoetes* spp. in all samples, but few *Nitella* spp.. With the other group containing flooded samples, almost all of which contained *Nitella* spp. seedlings. This group was then split into two groups, one of which was further divided. One of these consisted mainly of *Oryza* grassland and *Brachiaria* grassland samples and the other was made up essentially of *Pseudoraphis* grassland samples that contained *Nitella* spp., *Nymphaea* spp. and *Nymphoides* spp..



Figure 4.7 Dendrogram of Bray Curtis association matrix generated (using UPGMA) from raw seed bank data, showing seven groupings according to emergence of a few key species: G1 = Few germinants; G2 = Glinus oppositifolius, Nymphaea spp., Pseudoraphis spinescens (Hymenachne grassland samples); G3 = Nymphaea spp. Nymphoides spp. Cyperus serotinus (Moist Pseudoraphis grassland samples); G4 = Nitella spp, Nymphaea spp, Nymphoides spp. (Flooded Pseudoraphis grassland samples); G5 = Limnophila australis, Nitella spp., Chara spp., Najas spp. (Flooded Brachiaria & Oryza grassland samples); G6 = Isoetes coromandelina (Moist Brachiaria & Oryza grassland samples).

# Variation Within Grassland Seed Banks

Q<sub>5</sub>: Do seeds in the seed bank vary spatially within a grassland community?

- H<sub>1</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>2</sub>: There is no difference between flooded and moist water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>3</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>4</sub>: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>5</sub>: There is no difference between flooded and moist water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>6</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.

### Brachiaria grassland

Differences in the total number of seedlings emerging from sediment samples collected in the *Brachiaria* grassland were found to be significant between flooded and moist treatments, but not between transects or for transect and treatment interactions (Table 4.2). Moist treatments were found to have significantly lower seedling numbers than flooded treatments (Figure 4.8). Species richness on the other hand was not found to differ significantly in samples collected from this community (Table 4.3).

Table 4.2 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Brachiaria* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions (log(x+1) transformed data) \*\*\* = p < 0.001.

	df Effect	MS Effect	df Error	MS Error	F	p-level
Transect	2	0.067	24	0.0487	1.37	0.272
Treatment	1	0.613	24	0.0487	12.57	< 0.001***
Transect x Treatment	2	0.154	24	0.0487	3.16	0.060



Figure 4.8 Number of seedlings (log x + 1 transformed) emerging from *Brachiaria* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

Table 4.3 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in the *Brachiaria* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions

	df Effect	MS Effect	df Error	MS Error	F	pelevel
Transect	2	2.634	24	6.566	0.401	0.674
Treatment	1	10.801	24	6.566	1.644	0.211
Transect x Treatment	2	16.902	24	6.566	2.573	0.097

### Oryza grassland

No significant difference was found (transects, water treatment, transect and treatment) in the total number of seedlings emerging from sediment samples collected from the *Oryza* grassland (Table 4.4). Species richness was found to differ significantly between transects and treatments but no transect and treatment interaction was found (Table 4.5). Samples collected from transect six were found to contain significantly lower species richness than those from transects four and five (Table D.1; Figure 4.9). Samples in the flooded treatment were found to be significantly less species rich than those in the moist treatment (Figure 4.10).

Table 4.4 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Oryza* grassland on the Magela floodplain and germinated under two treatments; flooded and moist conditions (log(x+1) transformed data)

	df Effect	MS Effect	di Error	MS Error	F	p-level
Transect	2	0.013	24	0.127	0.105	0.901
Treatment	1	0.029	24	0.127	0.228	0.636
Transect x Treatment	2	0.101	24	0.127	0.791	0.465

Table 4.5 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Oryza* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions \*\* = p < 0.01, \*\*\* = p < 0.001

	df Effeci	MS Effect	di Enor	MS Error	F	p-level
Transeci	2	8.933	24	1.533	5.826	0.008**
Treatment	1	76.800	24	1.533	50.087	< 0.001***
Transect x Treatment	2	5.200	24	1,533	3.391	0.052



Figure 4.9 Species richness of samples collected along three different transects within the *Oryza* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).


Figure 4.10 Species richness of samples collected from the *Oryza* grassland and germinated under flooded and moist water regimes significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

#### Hymenachne grassland

The total number of seedlings emerging from samples collected in the *Hymenachne* grassland differed significantly between transects and between treatments (Table 4.6). Further, a transect and treatment interaction was found (Table 4.6). Transect nine contained significantly lower numbers of seedlings than transects seven and eight (Table D.2; Figure 4.11). Samples under the moist water regime contained significantly more seedlings than those under the flooded treatment (Figure 4.12). The transect and treatment interaction effects were probably caused by the low numbers of seedlings emerging from the flooded treatment of transect nine (Table D.3; Figure 4.13). Species richness differed significantly between transects (Table 4.7), with transect seven found to contain significantly more species than transects eight and nine (Figure 4.14).

Table 4.6 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions (log(x+1) transformed data) \* = p < 0.05, \*\* = p < 0.01.

	df Effeci	MS Effect	df Error	MS Error	F	p-level
Transect	2	0.370	24	0.056	6.551	0.005**
Treatment	1	0.246	24	0.056	4.351	0.048*
Transect x Treatment	2	0.341	24	0.056	6.042	0.007**



Figure 4.11 Number of seedlings (log x + 1 transformed) emerging from samples collected along three transects in the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 4.12 Number of seedlings (log x + 1 transformed) emerging from *Hymenachne* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.13 Transect and treatment interactions found within samples collected along three transects within the *Hymenachne* grassland and germinated under flooded and moist conditions (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

Table 4.7 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions \* = p < 0.05.

	df Effect	MSEffect	df Error	MS Error	F	p-levei
Transect	2	14.633	24	3.666	3.990	0.032*
Treatment	1	0.533	24	3.666	0.145	0.706
Transect x Treatment	2	3.033	24	3.666	0.827	· 0.449



Figure 4.14 Species richness of samples collected along three different transects within the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

#### Pseudoraphis grassland

A significant difference between moist and flooded treatments was found for the total number of seedlings emerging from the *Pseudoraphis* grassland samples (Table 4.8). Moist treatment samples contained significantly more seedlings than flooded treatment samples (Figure 4.15). Differences in species richness were found to be significant for transects and treatments, but treatment and transect interactions were not significant (Table 4.9). Samples from transect ten contained more species than transects eleven and twelve (Table D.5; Figure 4.16) and moist transect samples were less species rich than flooded samples (Figure 4.17).

Table 4.8 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Pseudoraphis* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions (log(x+1) transformed data) \*\*\* = p < 0.001.

	df Effect	MS Effect	df Eiror	MS Error	F	prievel
Transect	2	0.016	24	0.087	0.189	0.828
Treatment	1	1.272	24	0.087	14.563	< 0.001***
Transect x Treatment	2	0.238	24	0.087	2.727	0.085



Figure 4.15 Number of seedlings (log x + 1 transformed) emerging from *Pseudoraphis* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

Table 4.9 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Pseudoraphis* grassland on the Magela floodplain (Nov 95) and germinated under two water regimes; flooded and moist \* = p < 0.05, \*\*\* = p < 0.001.

	df Elfect	MS Effect	df Error	MS Error	F	p-level
Transect	2	9.433	24	2.266	4.162	0.028*
Treatment	1	38.533	24	2.266	17.00	<0.001***
Transect x Treatment	2	0.433	24	2.266	0.191	0.827



Figure 4.16 Species richness of samples collected along three different transects within the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 4.17 Species richness of samples collected from the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

# Variation Among Grassland Seed Banks

Q<sub>6</sub>: Do seed banks vary among different grassland communities?

- H<sub>7</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.
- H<sub>8</sub>: There is no difference between flooded and moist treatments in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>9</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>10</sub>: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>11</sub>: There is no difference in the number of taxa emerging from flooded and moist treatments from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>12</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.

When samples from each community were pooled, to test for differences among communities and water treatments, a significant community and treatment interaction was found for the total number of seedlings emerging from samples, despite community and treatments not being significant as separate factors (Table 4.10). This significant interaction was caused by the within community effects of watering regimes in both *Brachiaria* grassland and *Pseudoraphis* grassland samples (Figures 4.8 and 4.15) and, hence, is not relevant to among grassland community variation.

Table 4.10 Summary of ANOVA on total number of seedlings emerging from samples collected in four grassland communities on the Magela floodplain (Nov 95) germinated under two water regimes; flooded and moist (log(x+1) transformed data) (*Brachiaria* grassland, *Oryza* grassland and, *Hymenachne* grassland, *Pseudoraphis* grassland)

	df Effect	MS Effect	df Error	MS Error	F	p-level
Veg Type	3	0.172	112	0.092	1.87	0.138
Treatment	] 1	0.112	112	0.092	1.22	0.271
Veg type x Transect	3	0.682	112	0.092	7.45	< 0.001***

Species richness was found to differ significantly among communities between treatments and for community and treatment interactions (Table 4.11). Seed banks of *Brachiaria* and *Hymenachne* grasslands did not differ significantly in species richness and samples from both communities had significantly more species than *Oryza* and *Pseudoraphis* grasslands. Emergent communities from both the *Oryza* and *Pseudoraphis* grassland samples were similar in species richness (Figure 4.18).

More taxa were found to emerge in samples under flooded rather than moist regimes (Figure 4.19). The interaction between communities and water regimes was due to the moist *Brachiaria* grassland samples having significantly more species than flooded *Hymenachne* and *Pseudoraphis* grassland samples, while moist *Oryza* and *Pseudoraphis* grassland samples had less species than all other samples (Table D.5; Figure 4.20).

Table 4.11 Summary of ANOVA on species richness of seedlings emerging from samples collected in four grassland communities on the Magela floodplain (Nov 95) and germinated under two water regimes; flooded and moist. (*Brachiaria* grassland, *Oryza* grassland and, *Hymenachne* grassland, *Pseudoraphis* grassland) \*\* = P < 0.01, \*\*\* = P < 0.001.

	di Effeci	MS Effect	dtError	Mis Error	F	p-level
Veg Type	3	35.111	112	4.1	8,563	< 0.001***
Treatment	1	30.000	112	4.1	7.313	0.008**
Veg type x Transect	3	32.222	112	4.1	7.859	< 0.001***



Figure 4.18 Species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = Brachiaria grassland, Om = Oryza grassland, Ha = Hymenachne grassland and Ps = Pseudoraphis grassland) and germinated under flooded and moist water regimes

(significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.19 Species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain and germinated under two water regimes (flooded and moist) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.20 Community and treatment interactions of species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland and Ps = *Pseudoraphis* grassland) and germinated under two water regimes (flooded and moist) (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

#### Summary

Table 4.12 summarises the significant results for total number of seedlings and species richness within and among grassland communities.

Table 4.12 Summary of all results of analyses on total number of seedlings and species richness within and among sediment samples collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland) and germinated under two water regimes (F = flooded, M = moist).

Significant Effect		Bm	Om	Ha	Ps	Veg Types
Total number	Transects	Ns	Ns	T9 < T7 / T8	Ns	Ns
of seedlings	Treatments	F > M	Ns	M > F	M > F	Ns
	Interactions	Ns	Ns	T9 < ail	Ns	Bm F > Bm M Ps F < Ps M
Species Richness	Transects	Ns	T6 < T4 / T5	T9/T8 <t7< td=""><td>T11 &lt; T10</td><td>Bm/Ha &gt; Om/Ps</td></t7<>	T11 < T10	Bm/Ha > Om/Ps
	Treatments	Ns	F > M	Ns	F > M	F > M
	Interactions	Ns	Ns	Ns	Ns	BmM > HaF/OmM/PsF/PsM Om M < all bar Ps M Ps M < all bar Om M

Comparisons of Grassland Seed Banks Between Years (1984 & 1996) Q<sub>7</sub>: Have changes occurred in the seed bank since the 1984 study?

Due to differences between the present study and that conducted in 1984 (Finlayson *et al.* 1990) (duration, sample numbers, timing of sampling and experimental starting time), the following comparisons are tentative.

A total of 33 taxa were recorded in 1984 compared with 34 taxa found in this study. Two species were found in 1984 that were not present in 1996, namely, *Cyperus digitatus* and *Hygrochloa aquatica*. In contrast *Brachiaria mutica* was recorded in 1996 but not in 1984.

Similar numbers of species were found to emerge from flooded treatments in both years (Figure 4.21), although the *Hymenachne* grassland samples in 1984 contained slightly more species than those in 1996. A vast difference in species richness of the moist treatments could be seen. *Oryza* grassland samples in 1984 contained more species than the equivalent (*Brachiaria* grassland and *Oryza* grassland) samples in 1996. The number of species in moist treatments of both *Hymenachne* and *Pseudoraphis* grassland samples in 1996 were also reduced but the difference was not as great.



Figure 4.21 Species richness of seedlings emerging from sediment samples collected from the same sample sites on the Magela floodplain in 1984 and 1995 and germinated under two water regimes (flooded and moist)(Top 1984 Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland; Bottom 1996 Bm = *Brachiaria* grassland, Om = *Oryza* grassland (Bm + Om = Om 1984), Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland).

Data on all taxa were not published for the 1984 study, consequently comparisons of taxa can only be made with those that were documented. Data published from the 1984 study were presented in the form of calculated seedlings m<sup>-2</sup>, and these calculations were also conducted for the present study in order to facilitate comparisons (Appendix E). Examination of the proportions of each taxa that emerged from the grassland communities in 1984 and 1996 for both flooded and moist treatments, showed several overlaps.

#### Taxa Emerging from Oryza Grassland Samples in 1984 & 1996

Ceratopteris thalictroides, Eleocharis spp., Eriocaulon setaceum, Glinus oppositifolius, Heliotropium indicum, Isoetes coromandelina, Limnophila australis, Maidenia rubra, Najas spp. and Oryza meridionalis overlapped among the Oryza grassland samples in 1984 and Brachiaria and Oryza grassland samples in 1996 (Figure 4.22). Differences in proportions of seedlings of these species were found between years and treatments. Ceratopteris thalictroides, Heliotropium indicum, Isoetes coromandelina and Najas spp. were found to emerge in higher numbers in 1996 than in 1984. Conversely, Maidenia rubra, Limnophila australis, Eriocaulon setaceum and Oryza meridionalis were proportionally more abundant in 1984 samples (compared to 1996 samples). Eleocharis spp. and Glinus oppositifolius were found in similar proportions in samples from both years



Figure 4.22 Proportions of total seedlings (calculated 1m<sup>-2</sup>) that each species made up in 1984 *Oryza* grassland samples (OM84), 1996 *Oryza* grassland samples (Om96) and 1996 *Brachiaria* grassland samples (Bm96) in flooded (F) and moist (M) treatments (only species overlapping in occurrence between years are shown).

#### Taxa Emerging from in Hymenachne Grassland Samples in 1984 & 1996

Taxa found to emerge from samples in both 1984 and 1996 included *Fimbristylis* spp., *Glinus oppositifolius*, *Heliotropium indicum*, *Hymenachne acutigluma*, *Najas* spp., *Nymphaea* spp., *Pseudoraphis spinescens*, and *Utricularia* spp. (Figure 4.23).

*Fimbristylis* spp., *Heliotropium indicum, Najas* spp., and *Pseudoraphis spinescens* made up greater proportions of seedlings in 1984 compared to 1996. *Hymenachne acutigluma* and *Glinus oppositifolius* were found to emerge in greater proportions in 1996. While *Nymphaea* spp. differed in proportion between years in flooded and moist treatments and *Utricularia* spp. was found in similar proportions in both years.



Figure 4.23 Proportions of total seedlings (calculated  $1m^{-2}$ ) that each species made up in 1984 *Hymenachne* grassland samples (HA84), 1996 *Hymenachne* grassland samples (HA96) in flooded (F) and moist (M) treatments.(only species overlapping in occurrence between years are shown).

#### Taxa Emerging from Pseudoraphis Grassland Samples in 1984 & 1996

*Eleocharis* spp., *Glinus* oppositifolius, Najas spp., Nymphaea spp., *Pseudoraphis spinescens*, and *Utricularia* spp. were all found to emerge from samples collected from the *Pseudoraphis* grassland site in both years (Figure 4.24).

*Najas* spp. and *Pseudoraphis spinescens* were found in higher proportions in 1984 compared to 1996, while *Glinus oppositifolius*, *Nymphaea* spp., *Utricularia* spp. and *Eleocharis* spp. emerged in higher proportions in 1996.



Figure 4.24 Proportions of total seedlings (calculated  $1m^{-2}$ ) that each species made up in 1984 *Pseudoraphis* grassland samples (PS84), 1996 *Pseudoraphis* grassland samples (PS96) in flooded (F) and moist (M) treatments.(only species overlapping in occurrence between years are shown).

# Discussion

# **Grassland Seed Banks in 1996**

Wetland taxa found to emerge from the seed bank can be divided into three groups according to their germination: taxa that germinate under flooded conditions; taxa that germinate under moist conditions; and taxa that germinate under both flooded and moist conditions. *Blyxa aubertii, Ludwigia adscendens, Hydrilla verticillata, Chara* spp., *Cyperus platystylis, Najas* spp., *Nitella* spp. and *Utricularia* spp. all germinate in higher numbers under flooded conditions (compared to moist). In contrast, *Cyperus aquatilis, Coldenia procumbens, Commelina lanceolata, Dentella dioeca, Euphorbia vachellii, Phyla nodiflora* and *Heliotropium indicum* germinate better under moist conditions. All other recorded taxa emerged in similar numbers regardless of whether they experienced flooded or moist water regimes (Figures 4.3 & 4.4).

Groupings of the aquatic taxa, *Nitella* spp., *Nymphaea* spp., *Isoetes coromandelina, Najas* spp., *Nymphoides* spp., *Cyperus serotinus* and *Limnophila australis* were the main influences in patterns found among samples (Figures 4.6 & 4.7). *Glinus oppositifolius*, a mudflat species, also influenced the patterns that were found. Distinct differences in species composition and abundance between treatments were caused by the emergence of more aquatic taxa in the flooded treatments compared to moist treatments (Figure 4.5). Charophytes played a major role as large numbers of oospores were present in flooded samples from all communities (Table 4.1).

*Hymenachne* and *Pseudoraphis* grassland seed banks differed from *Brachiaria* and *Oryza* grassland seed banks as few *Nymphaea* spp. seedlings emerged from seed banks of the latter two communities. Differences between *Pseudoraphis* and *Hymenachne* grassland seed banks were attributed to the combination of *Nymphoides* spp. and *Cyperus* spp. emerging in *Hymenachne* grassland samples.

Species composition and abundance of *Oryza* and *Brachiana* grassland samples were similar although partitions between treatments were found. This was caused by the presence of *Nitella* spp. seedlings in flooded samples and

*Isoetes coromandelina* seedlings in moist samples. High numbers of the latter species in moist samples may indicate germination conditions required by this species. The similarities in species composition between seed banks of *Oryza* and *Brachiaria* grasslands are not surprising as the *Brachiaria* grassland exists on a site which, prior to 1989, was *Oryza* grassland.

Brachiaria mutica seeds emerged from both Brachiaria and Hymenachne grassland samples, indicating that these seeds are widely dispersed on the floodplain. However, these seeds were not found in the adjacent Oryza grassland or Pseudoraphis grassland samples. Seeds of this species could be present in these communities in lower numbers (than in Hymenachne and Brachiaria grasslands) because reduced vegetation cover in Oryza and Pseudoraphis grasslands, during the dry season, allows seed predation by providing easier access to seeds. If this was the case, sample size and intensity may not have been large enough to detect these seeds.

Species richness and total number of seedlings in *Hymenachne* grassland samples and species richness among both *Oryza* and *Pseudoraphis* grasslands differed between transects, these results indicate a heterogeneous distribution of seeds within sediments of the Magela floodplain. As this difference was noted for both seedling numbers and species richness in the *Hymenachne* grassland, seeds may be more variably distributed within sediments of this community (Table 4.12). This is consistent with species in the extant vegetation as the *Hymenachne* grassland was found to have the most species rich and diverse extant vegetation of the four communities (Figures 3.2 & 3.5).

Moist samples yielded the highest numbers of seedlings for *Hymenachne* and *Pseudoraphis* grasslands, whereas, flooded *Brachiaria* grassland samples yielded more seedlings for this particular community. These contrasting trends led to significant community and water regime interactions for the total number of seedlings emerging among communities (Table 4.10). These differences can be attributed to high numbers of just a few species. The flooded *Brachiaria* grassland samples had higher total seedling numbers because of the many *Nitella* spp. and *Chara* spp. seedlings emerging in these samples (Table 4.1). Similarly, the greater total number of seedlings emerging from moist

Hymenachne grassland samples were a result of the high number of Cyperus serotinus, Nymphoides spp., Nymphaea spp., Pseudoraphis spinescens and Glinus oppositifolius seedlings in these samples. The latter three taxa are responsible for the same trend in *Pseudoraphis* grassland samples.

Species richness in the seed bank was more indicative of observations in the extant vegetation than seedling numbers emerging from sediment samples, with both Orvza and Pseudoraphis grassland samples having greater species richness when flooded than under a moist water regime. The significantly higher species richness in Brachiaria and Hymenachne grassland samples. compared to Oryza and Pseudoraphis grassland samples, may reflect the morphological form and perennial habit of the two grass species that dominate these communities. Thompson (1992) noted that floating seeds are trapped by emergent vegetation. Both Brachiaria mutica and Hymenachne acutigluma are emergents that tend to grow in thick clumps. Therefore, these species could easily trap seeds dispersed during the wet as they float down the floodplain. Similarly, airborne seeds dispersed during the dry season could also be trapped. The perennial habit of these two species may also provide a nondesiccating environment during the dry as the thick vegetation cover over the whole year reduces fluctuations in soil temperature, thus providing better conditions for seed survival (Murdoch and Ellis 1992). Similarly, the clumping growth form of both Brachiaria mutica and Hymenachne acutigluma reduces light reaching the soil surface (and seeds). Light has been shown to play a major role in breaking the seed dormancy of many species (Pons 1992), thus the reduced light in these communities could inhibit germination of seeds.

Furthermore, the topographic position of these communities may also play a role. Both *Brachiaria mutica* and *Hymenachne acutigluma* occur in sites of intermediate inundation compared to the remnant *Oryza* and *Pseudoraphis* grassland sites, which occur on the edge and in deeper sections of the floodplain respectively. This supports Grime's (1973) suggestion that harsh environmental conditions generate low species diversity.

The interaction between plant community and water regime was a result of higher species richness in moist *Brachiaria* grassland samples, compared to all

other samples, and low species richness in both *Oryza* and *Pseudoraphis* grasslands, under moist water regimes (Figure 4.20). Extremely high species richness in *Brachiaria* grassland samples may be a result of the recent changes in extant vegetation in this community. This sample site still contains the suite of seeds from the *Oryza* community that previously occupied the site (Maps 3.2 & 3.3). Further, thick vegetation cover of *Brachiaria mutica* all year round traps seeds (Thompson 1992), while reducing recruitment from the seed bank. These factors contribute to a larger soil seed bank in this community.

### Comparisons of Grassland Seed Banks Between Years (1984 & 1996)

The marked difference in species richness of *Oryza* grassland samples in 1984 and 1996 is not easily explained (Figure 4.21). It is possible that the small number of samples taken in 1984 could have been collected from a particularly species rich location within the *Oryza* grassland. In addition, differences between timing and duration of experiments in 1984 and 1996 could effect these results. The remnant *Oryza* grassland site sampled for the current study was located on the edge of the floodplain, as *Brachiaria mutica* has invaded the deeper parts of this community. This could reflect the habitat requirements of *Brachiaria mutica*. It is possible that the water regime toward the edge of the floodplain inhibits *Brachiaria mutica* from establishing. The habitat requirements of *Brachiaria mutica* have not been fully established and the water regimes that facilitate establishment and survival of this species may also differ, that is, once established *Brachiaria mutica* may be able to survive in environments with less water.

Comparison of the proportions of individual species occurring in each community between years gave varying results. Higher proportions of *Oryza meridionalis*, *Eriocaulon setaceum*, *Limnophila australis*, *Fimbristylis* spp., *Maidenia rubra*, and *Pseudoraphis spinescens* were found in samples from 1984 compared to those in 1996. While *Isoetes coromandelina*, *Glinus oppositifolius*, *Nymphaea* spp., *Utricularia* spp. and *Eleocharis* spp. made up a greater proportion of seedlings emerging from 1996 samples compared to those from 1984.

#### Chapter 4

The duration of experiments could have considerably influenced the proportions of species emerging from sediments. This factor has been suggested to effect seed bank estimates by several authors (Benoit et al. 1989; Warr et al. 1993; Britton and Brock 1994). In addition dormancy of seeds could have been induced in this study by drying samples at the time of onset of flooding in November 1995. This study was conducted over 3 1/2 months. whereas the previous study monitored germination from samples over 10 months. The presence of seed dormancy may have resulted in seeds requiring longer than 3 1/2 months to germinate. This is particularly relevant to *Pseudoraphis spinescens* as seeds of this species were previously found to continue germinating after 10 months (Finlayson et al. 1990), and they made up a considerable proportion of the seedlings emerging in the previous study (Figures 4.23 & 4.24). In any case, these results illustrate the variability in covert vegetation on the floodplain, and may indicate that the contribution of seed banks to the extant vegetation varies in different years. As seed banks reflect seed production of previous years, the proportions of seedlings found in each year could be an artefact of seed production due to variation in rainfall in the years leading up to each study. The wet season prior to sample collection for this study was unusually long and rainfall for the year was above average (3700mm), this could explain why all but one of the taxa found to make up higher proportions of seedlings in 1996 compared to 1984 were aquatic taxa.



Chapter 5 The Relationships: Extant Vegetation & Seed Banks

# Introduction

The seed banks of most plant communities are expected to contain more species than extant vegetation, as seed banks commonly reflect vegetation from previous times (Roberts 1981). Several studies have examined the relationships between freshwater tidal wetland seed banks and extant vegetation and, contrary to expectations, these seed banks have been found to mirror extant vegetation in species composition and abundance (Parker and Leck 1985; Leck and Simpson 1987; Leck and Simpson 1995). This is considered to be a result of the large proportion of annual species, and the reduced numbers of grass and sedge species, in such communities (Leck and Simpson 1995).

Grillas *et al.* (1993) studied a marsh in southwestern Spain and found significant correlations between seed bank and extant vegetation in species composition and abundance. However, this relationship failed to apply to Charophyta, for although oospores were abundant in samples, charophytes were not present in the extant vegetation of all areas sampled (Grillas *et al.* 1993).

Hydrological patterns establish the role seed banks play in vegetation dynamics (Leck 1989). Prairie marshes in North America have been shown to rely on seed banks for regeneration of mudflat and emergent species during drought, and recruitment of submersed aquatics during periods of normal rainfall (van der Valk and Davis 1979). In habitats where the drawdown cycle is annual (eg. vernal pools & monsoonal floodplains), more complex relationships between seed banks and extant vegetation have been found (Gopal 1986; Zedler 1987). Zedler (1987) hypothesised that variation in pool water level contributes to seed bank and vegetation diversity in vernal pools. Gopal (1986) suggested that two seasonally delimited communities develop in monsoonal climates, one adapted to inundation and the other to drawdown, both contributing and recruiting from the seed bank.

Finlayson *et al.* (1990) applied flooded and damp water regimes to sediment samples from *Hymenachne*, *Oryza* and *Pseudoraphis* grasslands of the Magela floodplain with the objective of finding relationships between seed banks and

extant vegetation of each community. Pseudoraphis grassland seed banks were found to closely resemble the vegetation of this community. *Hymenachne* grassland seed banks, on the other hand, did not closely resemble extant vegetation. Hymenachne acutigluma made up <2% of seedlings emerging from sediments collected in the *Hymenachne* grassland compared with Pseudoraphis spinescens which comprised 72% of emergent seedlings. However, *Pseudoraphis spinescens* was not prominent in the extant vegetation of the Hymenachne grassland, therefore, it was suggested that Pseudoraphis spinescens seed had been transported downstream from the Pseudoraphis grassland to the Hymenachne grassland. Seed transport may therefore be an important factor influencing vegetation patterns (Finlayson et al. 1990). It was also noted that just prior to the study in 1984 (Finlayson et al. 1990) that the Hymenachne grassland was inhabited by a population (unknown size) of feral buffaloes and this could have been, in part, responsible for the lack of Hymenachne acutigluma seed within sediment samples, as grazing buffalo may have prevented this species from flowering. Oryza grassland seed bank samples were found to contain more seedlings than seed bank samples from other communities, although not all species found in the extant vegetation of this community were represented in the sediment samples. It was suggested that the observed unevenness of species composition in these sediment samples was a result of the dominance of annual species in extant vegetation of the Oryza grassland (Finlayson et al. 1990). Predictions of vegetation succession on the Magela floodplain from this study alone were not possible due to the lack of correspondence between seed bank results and vegetation survey data.

The current study was conducted on the same sample sites as those of Finlayson *et al.* (1990) and aimed to collect more detailed data on sediment seed banks and extant vegetation of these sites thus clarifying relationships and allowing comparisons between the studies.

The questions addressed in this chapter are:

- Q<sub>1</sub>: Is there a correlation between species composition of sediment samples (determined by germination) and the extant vegetation from which they came?
- Q<sub>2</sub>: Is there a correlation between species composition and abundance of sediment samples (determined by germination) and the extant vegetation from which they came?

The hypothesis generated to test this is:

H<sub>1</sub>: There is no difference in the species composition and abundance of extant vegetation and seed banks.

## Methods and Analyses

Simple comparisons of species presence between extant vegetation (Chapter 3) and seed bank data (Chapter 4) were made for each of the four plant communities studied. More complex comparisons were made using the Mantel test and modified Rand test to compare results from multivariate analyses of these data. The Mantel test compared association matrices of vegetation data and seed bank data (Appendix B: refer to disk provided) using Pearsons product moment correlation coefficient (Belbin 1993a). An original correlation was made, then one association matrix (vegetation survey) was randomised 10,000 times. Each randomisation was correlated to the sediment germination matrix (held constant). These values were compared to the original r value to determine if this correlation occurred purely by chance.

Groupings identified from cluster analyses of the vegetation survey (Figure 3.2) and sediment germination (Figure 4.7) data were compared using the RIND sub-routine in PATN. This method is based on the modifications of the Rand statistic made by Hubert and Arabie (1985). It returns a Hubert/Arabie/Rand statistic ranging from a value of zero, implying chance levels of associations to one, indicating a perfect correlation (Belbin 1993a).

#### Results

Q<sub>1</sub>: Is there a correlation between species composition of sediment samples (determined by germination) and the extant vegetation from which they came?

More taxa germinated from sediment samples than were found in the extant vegetation of each plant community (Table 5.1) and many of the taxa germinating from sediment samples were not found at all in the vegetation survey. These included *Blyxa aubertii, Ceratopteris thalictroides, Chara* spp., *Commelina lanceolata, Cyperus aquatilis, Cyperus serotinus, Eriocaulon setaceum, Hydrilla verticillata, Limnophila australis, Ludwigia perennis, Maidenia rubra, Nitella spp. and Oldenlandia* sp. Of these taxa, *Nitella* spp., *Chara* spp. and *Cyperus serotinus* were found to emerge from sediment samples of all communities. *Blyxa aubertii, Hydrilla verticillata* and *Ludwigia perennis* were each found in only one community. *Eriocaulon setaceum, lsoetes coromandelina* and *Limnophila australis* emerged only from samples collected at *Brachiaria* and *Oryza* grassland sites and *Maidenia rubra* was found in all samples but those from the *Pseudoraphis* grassland.

Five species occurred in the vegetation survey that were not found to germinate from the sediments namely, *Azolla pinnata, Salvinia molesta, Hygrochloa aquatica, Merremia gemella* and *Ipomoea aquatica.* 

Table 5.1 Species occurring in extant vegetation (wet and dry season) and emerging from sediment seed bank (moist and flooded water regimes) of four grassland communities on the Magela floodplain (communities are defined in Chapter 2).

Таха	Brachiaria grassland Taxa Extant Vegetation Seed bank		nd d bank	Extant V	Oryza egetation	grassland See	d bank	Extant V	Hymenach /enetation	ne grasst See	and d bank	Extant V	Pseudorap egetation	his grassli Seer	and I bank	
	Drv	Wet	Moist	Flooded	Dry	Wet	Moist	Flooded	Drv	Wet	Moist	Flooded	Dry	Wet	Moist	Flooded
Azolla pinnata		1								1				<b>v</b>		
Blyxa aubertii																~
Brachiaria mutica*	~	~	1		✓						1					
Ceratopteris thalictroides				1					· · · ·		√					
Chara spp.				1				<ul> <li>Image: A second s</li></ul>								
Coldenia procumbens			√				✓		<b>v</b>		1					
Commelina lanceolata																
Cyperus aquatilis																
Cyperus platystylis			1						1		✓	1	1			
Cyperus serotinus			✓	1								1				1
Dentella dioeca					-				✓		✓					
Eclipta prostrata									1		~	✓			1	1
Eleocharis spp.			<ul><li>✓</li></ul>	✓		- ✓	1	1		1		1		~	1	✓
Eriocaulon setaceum			<b>v</b>	✓			1	1								
Euphorbia vachellii					1				<ul> <li>✓</li> </ul>		1		1			
Fimbristylis spp.	1		1				<ul> <li>✓</li> </ul>	√	<ul> <li>✓</li> </ul>		<ul> <li>✓</li> </ul>					- V
Glinus oppositifolius			✓			_	<ul> <li>✓</li> </ul>				✓		<ul> <li>Image: A set of the set of the</li></ul>		1	~
Heliotropium indicum*	ſ		<ul><li>✓</li></ul>				1		✓		<ul> <li>✓</li> </ul>					-
Hydrilla verticillata							<u> </u>					✓				
Hygrochloa aquatica					<u> </u>	<u> </u>										
Hymenachne acutigluma		<u> </u>				<u></u> √			1	1	1	1		<b>√</b>		
Ipomoea aquatica		· ·····				<u></u>	<u> </u>						L	<u>√</u>		
Isoetes coromandelina			✓	<u> </u>			<u> </u>	1								
Limnophila australis				······			<u> </u>	<u> </u>								
Ludwigia adscendens		<u> </u>				<u> </u>			_ <b>✓</b>	<u> </u>				<u> </u>	ļ	<u> </u>
Ludwigia perennis								√							<u> </u>	
Maidenia rubra			<u> </u>				<u> </u>	√				<u> </u>			ļ	
Merremia gemella					<u> </u>				L							
Naias spp.			<ul> <li>✓</li> </ul>	<u> </u>	ļ							<u> </u>				
Nitella spp.				<u> </u>				<u> </u>			<u> </u>	<u> </u>			<u> </u>	·
Nymphaea spp.		<u> </u>	✓	······			✓	<u> </u>		<u> </u>	<u> </u>	<u> </u>		<b>√</b>		
Nymphoides spp.			✓			<u> </u>		<u> </u>		<b>√</b>	<u> </u>	<u> </u>				<u> </u>
Oldenlandia sp.							<u> </u>					<u></u>				<b>/</b>
Oryza meridionalis		<u> </u>	1	<u> </u>	1		<u> </u>	√		<u> </u>	<u>.                                    </u>				<u> </u>	
Persicaria spp.							L			<u> </u>	<u>↓                                    </u>			<b>/</b>	<u>i</u>	·
Phyla nodiflora*	L				<b>↓</b> ✓		<hr/>		L							·
Pseudoraphis spinescens	<b>↓</b> ✓		<ul> <li>✓</li> </ul>		×	<u> </u>	<u> </u>			√			1	√	<u> </u>	
Salvinia molesta		<u> </u>								√						
Utricularia spp.		<u> </u>	✓	<u> </u>		<b>/</b>		✓		1	✓			1		<ul> <li>✓</li> </ul>

- Q<sub>2</sub>: Is there a correlation between species composition and abundance of sediment samples (determined by germination) and the extant vegetation from which they came?
- H<sub>1</sub>: There is no difference in the species composition and abundance of extant vegetation and seed banks.

The original correlation between association matrices of extant vegetation and seed bank germination data generated an r value of 0.245 indicating a poor correlation between association matrices. One hundred percent of the randomised values were less than or equal to this original value indicating that this correlation was significant and did not occur purely by chance.

To compare the groupings of cluster analyses of extant vegetation and seed bank data the RIND sub-routine in PATN generated a contingency table (Table 5.2). Vegetation survey partitions are presented in rows and sediment seed bank germination partitions are presented in columns. The values appearing off the shaded diagonal line indicate the level of miss-match between the two cluster analyses. The diagonal total shows that there was 44% overlap in the contingency table. The Hubert/Arabie/Rand statistic found was 0.1986, a lower result to the r value of the Mantel test (0.245). Indicating that there is little correlation between the two classifications.

Table 5.2 Contingency table produced by RIND sub-routine in PATN for comparison of vegetation survey and sediment germination classifications of four grassland vegetation types on the Magela floodplain; Hubert/Arabie RAND statistic = 0.1986; Diagonal/total = 53/120 = 0.4417

Vegetation Survey	1	Ge	ך					
Partitions	2	4	1	5	3	6	Sum	Ептог
1	17	1	10	0	1	0	29	41
2	5	17	11	2	8	4	47	64
3	14	0	1	1	0	0	16	94
4	3	3	0	18	3	1	28	36
Sum	39	21	22	21	12	5		
Error	56	19	95	14	100	<u>1</u> 00		

# Discussion

This study has shown that the seed banks of the Magela floodplain grasslands, like other systems, contain greater species richness than extant vegetation (Roberts 1981). One would expect seed banks of the Magela floodplain to contain species which have occurred as extant vegetation in previous years as well as those species which appear at different times throughout the same year. This was best illustrated by the observed differences in the *Brachiaria* grassland which contains extant vegetation with few species, but a seed bank containing more species than other grassland communities. Reasons for such high species richness in the seed bank of this community were discussed in Chapter 4.

Five species were found in extant vegetation of grassland communities that were absent from seed banks: *Azolla pinnata; Salvinia molesta; Hygrochloa aquatica; Merremia gemella;* and *Ipomoea aquatica. Azolla pinnata* and *Salvinia molesta* were not expected to emerge from sediments as they have not been reported to produce fertile spores in Australia (Sainty and Jacobs 1981) and vegetative propagules would have been killed by drying samples. Only a few specimens of *Hygrochloa aquatica* were recorded in extant vegetation. The rarity of this species in study sites is reflected in its absence from sediment germination samples. The absence of *Merremia gemella* and *Ipomoea aquatica* in germination trays may be explained by poor seed set or seed dormancy as these species were more common in extant vegetation than *Hygrochloa aquatica*.

Several taxa found in extant vegetation of particular communities, were absent from their representative seed banks. This may reflect the low frequency with which these taxa occur in a given community. Examples include *Hymenachne acutigluma* and *Ludwigia adscendens* found in the *Brachiaria* grassland, and *Oryza meridionalis* found in the *Hymenachne* grassland. These species occurred in low numbers in extant vegetation and were absent from sediment samples. *Euphorbia vachellii,* on the other hand was quite common in extant vegetation of the *Oryza* grassland during the dry season, yet it too was

absent in sediment samples of this community. This result may be due to seed dormancy or unfavourable conditions for germination in the glasshouse.

Many aquatic taxa found in the seed bank were not observed in extant vegetation. However, greater numbers of these taxa may occur in extant vegetation during the wet season than otherwise indicated by the vegetation survey (Chapter 3) as the presence of crocodiles on the floodplain limited sampling of submerged vegetation during this season. The common occurrence (in sediments) of *Nitella* spp., *Chara* spp., *Cyperus* serotinus and *Maidenia* rubra is more than likely a reflection of the high seed and oospore production of these taxa. It is likely that *Blyxa* aubertii, *Hydrilla* verticillata and *Ludwigia* perennis occur infrequently in the study sites as they were each only found emerging from one community and were absent from extant vegetation.

Finlayson *et al.* (1990) found species composition and abundance of the *Pseudoraphis* grassland seed bank to closely resemble extant vegetation in this community, but found poor relationships between extant vegetation and seed banks of the *Hymenachne* and *Oryza* grasslands. In contrast, this study found species composition of the *Hymenachne* grassland seed banks were to their respective extant vegetation (Table 5.1), although this relationship did not hold for species abundance. This result may reflect the ability of the *Hymenachne* grassland to sustain a variety of taxa in the extant vegetation late into the dry season, as this community undergoes less dramatic seasonal water fluctuations than other communities (ie. drawdown takes longer).

Finlayson *et al.* (1989) suggested that duration of inundation played an important role in structuring vegetation. They reported that areas of the floodplain inundated for approximately five months each year had greater fluctuations of species composition in extant vegetation than those inundated for three months (Finlayson *et al.* 1989). This may be due to the greater length of time available for individual species to germinate, grow and reproduce. The availability of water for this extended period may enable more species to complete their life-cycles and as a result, more species rich communities are found in the sediments of these areas.

Correlations of species composition and abundance between extant vegetation and sediment seed bank data of this study were poor. Although the above analyses show that this relationship did not occur purely by chance. The lack of correlation between extant vegetation and seed banks is probably due to the occurrence of high numbers of submerged aquatic taxa emerging from sediment samples (Chapter 4).

The timing of vegetation survey could also be one reason stronger correlations were not found. Finlayson *et al.* (1989) noted that many species are recruited from the seed bank at the start and end of the wet season, just before flooding and drying of the floodplain. It is possible that the *Brachiaria, Oryza* and *Pseudoraphis* grasslands contain many of the taxa found to emerge from sediment samples as extant vegetation during this period of time only. If this is the case, the vegetation surveys in this study would not have found these taxa, as surveys were conducted late in the dry season, before rain had commenced, and during the wet season after flooding had occurred. To further investigate this, emergence of seedlings would need to be monitored in the field during different times of year while study sites were inundated to different water levels.

Alternatively, it is possible that seeds of the taxa found to emerge in germination trials from samples taken in the *Brachiaria, Oryza* and *Pseudoraphis* grassland sites, but not observed in the extant vegetation, were transported to these grassland communities from elsewhere. These taxa may not be able to grow and reproduce in these communities as conditions are not suitable. Regardless of these possibilities, the poor correlations found in this study indicate that other factors may be contributing to the vegetation dynamics on the floodplain. For example, it is recognised that vegetative reproduction plays a role in the vegetation dynamics of the Magela floodplain (Finlayson *et al.* 1989; 1990).

The sediment seed bank germination trial did not account for vegetative reproduction and the lack of correlation between extant vegetation and seed banks indicate that it may be a significant feature of the vegetation dynamics in this ecosystem. The lower numbers of grass seeds found to emerge in this study, compared to the 1984 study, would suggest that the importance of

vegetative reproduction varies from year to year. This may be related to the effect of rainfall patterns upon seed production of dominant species of the grassland communities on the Magela floodplain.



Chapter 4 The Seed Banks: Sediment Germination Trial

## Introduction

Seed banks are difficult to study and this may account for the limited research existing in this area. The difficulty in studying seed banks arises as seeds are rarely evenly distributed in soils and different species have varying seed size and different germination requirements. Thus, many factors must be considered in the design of seed bank experiments, including sample collection, sampling intensity, sample distribution, timing of sampling, estimation of seed numbers and the suitability of data for analysis with various statistical techniques (Benoit *et al.* 1989; Warr *et al.* 1993; Britton and Brock 1994).

Most wetland seed bank studies have been aimed at gaining an understanding of the role seed banks play in structuring wetland plant communities. Various approaches have been used including comparison of seed banks from different vegetation types (Thompson and Grime 1979); examination of the relationship between the seed bank and extant vegetation (Grillas *et al.* 1993; Wilson *et al.* 1993); investigation of the role of seed banks in re-establishment of vegetation after a disturbance (ter Heerdt and Drost 1994); and determination of germination from seed banks under various hydrological regimes (Smith and Kadlec 1983; Schneider and Sharitz 1986; Schneider 1994) and in different seasons (Thompson and Grime 1979; Britton and Brock 1994).

The most common technique applied in studying seed banks involves collecting soil cores, placing them in a glasshouse, and counting seedlings of each species as they emerge. This technique assesses the ability of seeds to germinate but does not accurately assess numbers of seeds of different species contained within the soil (Thompson and Grime 1979). To maximise precision of seed estimates most studies of this type germinate samples under different water regimes (Smith and Kadlec 1983; Wilson *et al.* 1993; Britton and Brock 1994; Brock *et al.* 1994; Schneider 1994) and/or run experiments over many months (Leck and Simpson 1987; Leck and Simpson 1995).

A seed bank experiment was conducted over a period of 10 months on sediment samples from the Magela floodplain in 1984 using two water regimes

(flocded and moist) (Finlayson *et al.* 1990). This study demonstrated significant site-treatment differences, reflecting to some extent, the previous vegetation history of each site and the habit of the dominant grass species. It also indicated that specific species composition could vary under different environmental conditions, however, there was insufficient information to suggest that major changes to broad vegetation patterns would occur (Finlayson *et al.* 1990). One of the main reasons for conducting the study was to provide baseline data so that changes in plant species composition and introduced plant species invasions, could be assessed (Finlayson *et al.* 1990).

Chapter three discussed changes in extant vegetation and revealed that *Brachiaria mutica* has invaded a considerable area of the *Oryza* grassland. Hence, samples collected, from sites also used by Finlayson *et al.* (1990), for the following seed bank experiment included *Brachiaria* grassland in addition to *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland. The *Brachiaria* grassland and *Oryza* grassland samples of the present study come from *Brachiaria mutica* invaded and uninvaded areas of the *Oryza* grassland site as sampled in the 1984 study. This division was made to assess differences in seed banks between invaded (previously *Oryza* grassland).and uninvaded communities.

The questions that this experiment was designed to address are:

- Q<sub>1</sub>: What taxa germinate from the seed banks of four grassland communities (*Brachiaria* grassland, *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland) in 1996?
- Q2: Does Brachiaria mutica (Para Grass) exist in the seed bank?
- Q<sub>3</sub>: Does germination under flooded or moist conditions influence which taxa will germinate?
- Q<sub>4</sub>: What patterns can be found in species composition and abundance of seedlings emerging from sediment samples?
- Q<sub>5</sub>: Do seeds in the seed bank vary spatially within a grassland community?
- Q<sub>6</sub>: Do seed banks vary among different grassland communities?
- Q<sub>7</sub>: Have changes occurred in the seed bank since the 1984 study?

The hypotheses generated to test these questions are:

- H<sub>1</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>2</sub>: There is no difference between flooded and moist water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>3</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>4</sub>: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>5</sub>: There is no difference between flooded and moist water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>6</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>7</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.
- H<sub>8</sub>: There is no difference between flooded and moist treatments in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>9</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>10</sub>: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>11</sub>: There is no difference in the number of taxa emerging from flooded and moist treatments from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>12</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.

## **Materials and Methods**

### Sampling Design for Field Collection of Seed Bank Samples

Sediment samples were collected to allow spatial variation to be detected both within and among plant communities. The methods used were modified from a previous study conducted at the same sites as the present study (Finlayson *et al.* 1990). Six sediment cores (53mm diameter and 10cm deep), including a spare core, located around the circumference of a 1m radius circle, were collected from each of five replicate sites. The replicate sites were 25m apart and located at the ends and apices of W shaped transects (Figure 4.1). Three transects were randomly placed in each of four different grassland communities (*Brachiaria, Oryza, Pseudoraphis* and *Hymenachne*) as defined in Chapter two. To ensure randomisation of samples, each transect was positioned along a different randomly allocated compass bearing. The cores were collected in the dry season between 20-29 November 1995.



Figure 4.1 Transect dimensions showing the locations of sediment core collection sites.

The corer consisted of a 150mm long piece of pvc pipe (inside diameter 53mm) that was tapered at one end to minimise soil compaction. A mark 100mm from the tapered end was made around the circumference of the pipe to ensure correct sampling depth. The corer was driven in to the appropriate depth using a lump mallet. Two opposing holes were positioned above the depth mark to allow corer extraction using a metal bar as a lever (Figure 4.2).



Figure 4.2 Design of pvc corer used to collect sediment samples.

As seeds were possibly present within soil surface organic matter, this material was included in the samples. Each sample was pushed out of the corer directly into a labelled calico bag. Calico bags were spread out on benches in the glasshouse and left for 24 hours to air dry. Samples were then stored at  $22^{\circ}$ C until March 16 1996 when the 30 samples collected from each transect were combined into ten groups of three cores (the six cores from each sample circle made up two groups). Each group represented a floodplain area of 66 cm<sup>2</sup> x 10 cm depth. Groups were then placed into different labelled circular trays (25cm diameter x 4cm deep) each lined with absorbent paper. The trays were watered, samples were spread to a depth of 2cm and the samples were randomly placed on benches in a glasshouse (Plate 4.1). Half of the trays from each transect were flooded to a depth of 2 cm over the sample (to the top of the tray) and the remaining trays were kept permanently moist. Thus, the experiment consisted of 120 trays, 30 trays from each grassland community (15 flooded and 15 moist). Twelve additional trays of sterilised
#### Chapter 4

were added as controls to assess contamination from weeds and seed dispersal between trays. Treatments were maintained by daily additions of tap water (total alkalinity 140 mg<sup>-1</sup> CaCO<sub>3</sub>, conductivity 30  $\mu$ S cm<sup>-1</sup> at 25°C, Ca 20 mg l<sup>-1</sup>, Mg 20 mg l<sup>-1</sup>, (Finlayson *et al.* 1990)) using an automated watering system. All trays were monitored daily to ensure even watering.

The experiment was run over a period of 3 <sup>1</sup>/<sub>2</sub> months. After six weeks seedlings emerging from trays were identified, counted and removed. Unidentified seedlings were either potted up and left to further mature or marked using map pins for later identification. Trays were scored a second time in June 1996.

As plants were removed representative specimens of each species were pressed and lodged as vouchers in the Environmental Research Institute of the Supervising Scientist (*eriss*) Herbarium. Additional vouchers were lodged at the New England Herbarium (NE).



Plate 4.1 Sample trays randomly placed on benches in the glasshouse just prior to commencement of the sediment germination trial (March 1996).

#### Data analysis

### Patterns in Grassland Seed Banks

Absolute value data for each taxa in all samples were analysed using PATN (Belbin 1993b). An association matrix was generated using the Bray Curtis coefficient and this was used to produce an ordination plot and cluster dendrogram.

Semi-strong hybrid multidimensional scaling (SSH), a non-metric ordination algorithm, was used to ordinate data in three dimensions with a maximum of 50 iterations and 100 random starts.

Cluster analysis was conducted using flexible unweighted pair grouping using arithmetic averaging (UPGMA), ( $\beta = -0.1$ ) (Belbin and McDonald 1993).

### Variation Within and Among Grassland Seed Banks

Taxa found to emerge from each plant community in both flooded and moist treatments were examined. Sample distributions of data for individual taxa were not normal and transformations of these data failed to homogenise sample distributions. Log (x + 1) transformations of the total number of seedlings found in transects within grassland communities and among grassland communities were effective in normalising sample distributions. Species richness (total number of species) data within and among grassland communities was found to contain normal sample distributions. ANOVA was used to compare differences for both total number of seedlings (Log (x + 1) transformed) and species richness between transects, treatments and for transect and treatment interactions, within each vegetation type. These data were pooled and differences among grassland communities were also tested. The Least Significant Difference (LSD) test was used to identify the exact effects of all ANOVA analyses that were significant.

### Comparisons of Grassland Seed Banks Between Years (1984 & 1996)

Species richness of samples were compared between years for varying plant communities and flooded / moist treatments. Taxa emerging from the same communities (or equivalent) in different years were also compared. The latter comparisons were based on the proportion of the total number of seedlings

emerging from samples collected within their respective communities in each year.

## Results

- Q<sub>1</sub>: What taxa germinate from the seed banks of four grassland communities (*Brachiaria* grassland, *Oryza* grassland, *Hymenachne* grassland and *Pseudoraphis* grassland) in 1996?
- Q<sub>2</sub>: Does Brachiaria mutica (Para Grass) exist in the seed bank?

In total thirty four taxa emerged from the sediment samples (Appendix G; Table 4.1). Twenty nine percent of taxa were found in all grassland communities and twenty six percent of taxa occurred in only one vegetation type. Three introduced species were recorded, *Brachiaria mutica, Heliotropium indicum* and *Phyla nodiflora. Brachiaria mutica* emerged from the *Brachiaria* grassland and *Hymenachne* grassland samples, *Heliotropium indicum* occurred in *Brachiaria, Hymenachne* and *Oryza* grassland samples and *Phyla nodiflora* occurred in *Oryza* grassland samples.

The Hymenachne grassland samples contained 25 taxa, the Oryza grassland samples, 24 taxa, Brachiaria grassland samples, 21 taxa and Pseudoraphis grassland samples, 13 taxa. Four species were unique to Oryza grassland samples namely, Cyperus aquatilis, Commelina lanceolata, Ludwigia perennis and Phyla nodiflora. Hymenachne grassland samples contained the highest number of unique taxa, Dentella dioeca, Euphorbia vachellii, Hydrilla verticillata , Hymenachne acutigluma, Ludwigia adscendens and Persicaria sp... Only one species emerged exclusively from the Pseudoraphis grassland samples being, Blyxa aubertii and no taxa were unique to the Brachiaria grassland samples.

Table 4.1 Total number of seedlings of each taxa emerging (between March and June 96) from sediments of four grassland communities on the Magela floodplain germinated under flooded and moist water regimes (Bm = Brachiaria grassland, Om = Oryza grassland, Ha = Hymenachne grassland, Ps = Pseudoraphis grassland, F = flooded treatment, M = moist treatment, \* = introduced species)

Таха	Bm	Bm	Om	Om	На	На	Ps	Ps
Pluvo oubortii	_ <u>  ⊦</u>	<u></u>		<u></u>	┝──┍	<u>  M</u>		<u> </u>
Biyxa aubertii		10	<u> </u>		<u> </u>			
Brachiaria mutica		12				<u> </u>		<u>-</u>
Cyperus aquatilis		<u> </u>		<u></u>	100		<u> </u>	<u> </u>
C. platystylis				<u> </u>	129	41		
C. serotinus			<u> </u>		96	216	1	ļ
Ceratopteris thalictroides	7	18	92	80		2	<u> </u>	<u> </u>
Chara spp.	121		45	1	35	<u> </u>	7	
Coldenia procumbens		2	ļ	6		9		
Commelina lanceolata			ļ	2	<u>.</u>			
Dentella dioeca						29		
Eclipta prostrata					8	20	6	1
Eleocharis spp.	15	24	10	10	1		23	60
Eriocaulon setaceum	1	4	19	14		[		
Euphorbia vachellii		<u> </u>				1		
Fimbristylis spp.		3	1	6		8	5	
Glinus oppositifolius		2		3		91	33	801
Heliotropium indicum*		11		77		1		
Hydrilla verticillata					5			
Hymenachne acutigluma					6	36		
Isoetes coromandelina .	13	238	37	311				1
Ludwigia adscendens					6		3	
L. perennis			1	1				
Limnophila australis	61	44	40	19				
Maidenia rubra	29	11	30	8	8	14		
Najas spp.	62	3	40		44	6	3	2
Nitella spp.	414	60	138	3	102	14	114	2
Nymphaea spp.	19	26	6	2	76	72	102	127
Nymphoides spp.	15	28	11	5	55	155	15	6
Oldenlandia sp.				1		1	1	
Oryza meridionalis	1	1	1	2				
Persicaria sp.						8	1	
Phyla nodiflora*		<u> </u>		4				
Pseudoraphis spinescens	11	2		17	4	117	10	132
Utricularia spp.	22	1	12		26	9	90	2

# Variation in Germination Conditions Among Taxa

Q<sub>3</sub>: Does germination under flooded or moist conditions influence which taxa will germinate?

Figure 4.3 shows taxa for which less than fifty seedlings emerged and Figure 4.4 shows taxa with more than fifty emergents. Four taxa, *Blyxa aubertii*, *Ludwigia adscendens, Hydrilla verticillata* and *Chara* spp. only emerged under flooded conditions. Other taxa, *Cyperus platystylis, Najas* spp., *Nitella* spp. and *Utricularia* spp., all emerged in far greater numbers in the flooded treatments compared to the moist treatments.

The following seven species emerged from moist treatments only: *Brachiaria mutica*; *Cyperus aquatilis*; *Coldenia procumbens; Commelina lanceolata; Dentella dioeca; Euphorbia vachellii; Phyla nodiflora;* and *Heliotropium indicum* (Figures 4.3 and 4.4). *Persicaria* sp., *Hymenachne acutigluma, Fimbristylis* spp., *Eclipta prostrata, Cyperus serotinus, Glinus oppositifolius, Isoetes coromandelina, Nymphoides* spp., and *Pseudoraphis spinescens* all emerged in greater numbers in moist rather than flooded treatments.



Figure 4.3 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (species with < 50 emergents)



Figure 4.4 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (taxa with > 50 emergents)

### Patterns Within and Among Grassland Seed Banks

Q<sub>4</sub>: What patterns can be found in species composition and abundance of seedlings emerging from sediment samples?

Differences (shown above) in the species composition and abundance of germination from flooded and moist treatments are confirmed by ordination of data (Figure 4.5). In addition grassland communities were clearly separated (Figure 4.6). The *Pseudoraphis* grassland samples were distinctively grouped as were *Hymenachne* grassland samples. *Oryza* grassland and *Brachiaria* grassland sample trays, on the other hand, overlapped considerably in species composition and abundance.

Principal component correlations did not produce high r-values for any individual taxa (r < 0.2), although cluster analysis grouped samples according to combinations of taxa.



Figure 4.5 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis: multidimensional scaling stress 0.1764). Distinction between water regimes is shown.



Figure 4.6 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis: multidimensional scaling stress 0.1764). Distinction between plant communities is shown.

Cluster analysis separated samples according to groupings of a few taxa (Figure 4.7). The first branch split four Oryza grassland samples under the moist water regime and one *Hymenachne* grassland sample under the flooded water regime, from the remaining samples. These samples all had very few germinants of any species. The remaining samples were then split into two main groups, one containing all of the remaining Oryza grassland samples and all but two of the Brachiaria grassland samples, and the other containing most of the Hymenachne grassland and Pseudoraphis grassland samples. This branch was derived from samples containing Nymphaea spp. in the absence of Nitella spp. The branch containing the Hymenachne and Pseudoraphis grassland samples were split into two groups, one comprised predominantly of Pseudoraphis grassland samples containing Glinus oppositifolius, Nymphaea spp., and *Pseudoraphis spinescens* seedlings and the other made up primarily of Hymenachne grassland samples with Nymphaea spp., Nymphoides spp. and Cyperus serotinus seedlings.

The branch made up mainly of *Oryza* grassland and *Brachiaria* grassland samples was divided into two groups according to the presence of *Nitella* spp.. One group made up of *Oryza* and *Brachiaria* grassland samples, under a moist water regime, contained *Isoetes* spp. in all samples, but few *Nitella* spp.. With the other group containing flooded samples, almost all of which contained *Nitella* spp. seedlings. This group was then split into two groups, one of which was further divided. One of these consisted mainly of *Oryza* grassland and *Brachiaria* grassland samples and the other was made up essentially of *Pseudoraphis* grassland samples that contained *Nitella* spp., *Nymphaea* spp. and *Nymphoides* spp..



Figure 4.7 Dendrogram of Bray Curtis association matrix generated (using UPGMA) from raw seed bank data, showing seven groupings according to emergence of a few key species: G1 = Few germinants; G2 = Glinus oppositifolius, Nymphaea spp., Pseudoraphis spinescens (Hymenachne grassland samples); G3 = Nymphaea spp. Nymphoides spp. Cyperus serotinus (Moist Pseudoraphis grassland samples); G4 = Nitella spp, Nymphaea spp, Nymphoides spp. (Flooded Pseudoraphis grassland samples); G5 = Limnophila australis, Nitella spp., Chara spp., Najas spp. (Flooded Brachiaria & Oryza grassland samples); G6 = Isoetes coromandelina (Moist Brachiaria & Oryza grassland samples).

## Variation Within Grassland Seed Banks

Q<sub>5</sub>: Do seeds in the seed bank vary spatially within a grassland community?

- H<sub>1</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>2</sub>: There is no difference between flooded and moist water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>3</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>4</sub>: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>5</sub>: There is no difference between flooded and moist water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H<sub>6</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.

### Brachiaria grassland

Differences in the total number of seedlings emerging from sediment samples collected in the *Brachiaria* grassland were found to be significant between flooded and moist treatments, but not between transects or for transect and treatment interactions (Table 4.2). Moist treatments were found to have significantly lower seedling numbers than flooded treatments (Figure 4.8). Species richness on the other hand was not found to differ significantly in samples collected from this community (Table 4.3).

Table 4.2 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Brachiaria* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions (log(x+1) transformed data) \*\*\* = p < 0.001.

	df Effect	MS Effect	df Error	MS Error	F	p-level
Transect	2	0.067	24	0.0487	1.37	0.272
Treatment	1	0.613	24	0.0487	12.57	< 0.001***
Transect x Treatment	2	0.154	24	0.0487	3.16	0.060



Figure 4.8 Number of seedlings (log x + 1 transformed) emerging from *Brachiaria* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

Table 4.3 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in the *Brachiaria* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions

	df Effect	MS Effect	df Error	MS Error	F	p-level
Transect	2	2.634	24	6.566	0.401	0.674
Treatment	1	10.801	24	6.566	1.644	0.211
Transect x Treatment	2	16.902	24	6.566	2.573	0.097

### Oryza grassland

No significant difference was found (transects, water treatment, transect and treatment) in the total number of seedlings emerging from sediment samples collected from the *Oryza* grassland (Table 4.4). Species richness was found to differ significantly between transects and treatments but no transect and treatment interaction was found (Table 4.5). Samples collected from transect six were found to contain significantly lower species richness than those from transects four and five (Table D.1; Figure 4.9). Samples in the flooded treatment were found to be significantly less species rich than those in the moist treatment (Figure 4.10).

Table 4.4 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Oryza* grassland on the Magela floodplain and germinated under two treatments; flooded and moist conditions (log(x+1) transformed data)

	df Effect	MS Effect	dt Error	MS Error	F	p-level
Transect	2	0.013	24	0.127	0.105	0.901
Treatment	1	0.029	24	0.127	0.228	0.636
Transect x Treatment	2	0.101	24	0.127	0.791	0.465

Table 4.5 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Oryza* grassland on the Magela floodplain (Nov 95) and germinated under two treatments; flooded and moist conditions \*\* = p < 0.01, \*\*\* = p < 0.001

	df Effeci	MS Effect	di Error	MS Error	F	p-level
Transeci	2	8.933	24	1.533	5.826	0.008**
Treatment	1	76.800	24	1.533	50.087	< 0.001***
Transect x Treatment	2	5.200	24	1,533	3.391	0.052



Figure 4.9 Species richness of samples collected along three different transects within the *Oryza* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 4.10 Species richness of samples collected from the *Oryza* grassland and germinated under flooded and moist water regimes significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

#### Hymenachne grassland

The total number of seedlings emerging from samples collected in the *Hymenachne* grassland differed significantly between transects and between treatments (Table 4.6). Further, a transect and treatment interaction was found (Table 4.6). Transect nine contained significantly lower numbers of seedlings than transects seven and eight (Table D.2; Figure 4.11). Samples under the moist water regime contained significantly more seedlings than those under the flooded treatment (Figure 4.12). The transect and treatment interaction effects were probably caused by the low numbers of seedlings emerging from the flooded treatment of transect nine (Table D.3; Figure 4.13). Species richness differed significantly between transects (Table 4.7), with transect seven found to contain significantly more species than transects eight and nine (Figure 4.14).

Table 4.6 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions (log(x+1) transformed data) \* = p < 0.05, \*\* = p < 0.01.

	df Effeci	MS Effect	df Error	MS Error	F	p-level
Transect	2	0.370	24	0.056	6.551	0.005**
Treatment	1	0.246	24	0.056	4.351	0.048*
Transect x Treatment	2	0.341	24	0.056	6.042	0.007**



Figure 4.11 Number of seedlings (log x + 1 transformed) emerging from samples collected along three transects in the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 4.12 Number of seedlings (log x + 1 transformed) emerging from *Hymenachne* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.13 Transect and treatment interactions found within samples collected along three transects within the *Hymenachne* grassland and germinated under flooded and moist conditions (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

Table 4.7 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions \* = p < 0.05.

	df Effect	MSEffect	df Error	MS Error	F	p-levei
Transect	2	14.633	24	3.666	3.990	0.032*
Treatment	1	0.533	24	3.666	0.145	0.706
Transect x Treatment	2	3.033	24	3.666	0.827	· 0.449



Figure 4.14 Species richness of samples collected along three different transects within the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

#### Pseudoraphis grassland

A significant difference between moist and flooded treatments was found for the total number of seedlings emerging from the *Pseudoraphis* grassland samples (Table 4.8). Moist treatment samples contained significantly more seedlings than flooded treatment samples (Figure 4.15). Differences in species richness were found to be significant for transects and treatments, but treatment and transect interactions were not significant (Table 4.9). Samples from transect ten contained more species than transects eleven and twelve (Table D.5; Figure 4.16) and moist transect samples were less species rich than flooded samples (Figure 4.17).

Table 4.8 Summary of ANOVA on total number of seedlings emerging from samples collected along three transects in a *Pseudoraphis* grassland on the Magela floodplain (Nov 95) and germinated under two Treatments; flooded and moist conditions (log(x+1) transformed data) \*\*\* = p < 0.001.

	df Effect	MS Effect	df Eiror	MS Error	F	prievel
Transect	2	0.016	24	0.087	0.189	0.828
Treatment	1	1.272	24	0.087	14.563	< 0.001***
Transect x Treatment	2	0.238	24	0.087	2.727	0.085



Figure 4.15 Number of seedlings (log x + 1 transformed) emerging from *Pseudoraphis* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

Table 4.9 Summary of ANOVA on species richness of seedlings emerging from samples collected along three transects in a *Pseudoraphis* grassland on the Magela floodplain (Nov 95) and germinated under two water regimes; flooded and moist \* = p < 0.05, \*\*\* = p < 0.001.

	df Elfect	MS Effect	dt Error	MS Error	F	p-level
Transect	2	9.433	24	2.266	4.162	0.028*
Treatment	1	38.533	24	2.266	17.00	<0.001***
Transect x Treatment	2	0.433	24	2.266	0.191	0.827



Figure 4.16 Species richness of samples collected along three different transects within the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).



Figure 4.17 Species richness of samples collected from the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

## Variation Among Grassland Seed Banks

Q<sub>6</sub>: Do seed banks vary among different grassland communities?

- H<sub>7</sub>: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.
- H<sub>8</sub>: There is no difference between flooded and moist treatments in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>9</sub>: There is no difference in interactions of transects and water regimes in the total number of seedlings emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>10</sub>: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>11</sub>: There is no difference in the number of taxa emerging from flooded and moist treatments from sediment samples collected from four different grassland communities on the Magela floodplain.
- H<sub>12</sub>: There is no difference in interactions of transects and water regimes in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.

When samples from each community were pooled, to test for differences among communities and water treatments, a significant community and treatment interaction was found for the total number of seedlings emerging from samples, despite community and treatments not being significant as separate factors (Table 4.10). This significant interaction was caused by the within community effects of watering regimes in both *Brachiaria* grassland and *Pseudoraphis* grassland samples (Figures 4.8 and 4.15) and, hence, is not relevant to among grassland community variation.

Table 4.10 Summary of ANOVA on total number of seedlings emerging from samples collected in four grassland communities on the Magela floodplain (Nov 95) germinated under two water regimes; flooded and moist (log(x+1) transformed data) (*Brachiaria* grassland, *Oryza* grassland and, *Hymenachne* grassland, *Pseudoraphis* grassland)

	df Effect	MS Effect	df Error	MS Error	F	p-level
Veg Type	3	0.172	112	0.092	1.87	0.138
Treatment	] 1	0.112	112	0.092	1.22	0.271
Veg type x Transect	3	0.682	112	0.092	7.45	< 0.001***

Species richness was found to differ significantly among communities between treatments and for community and treatment interactions (Table 4.11). Seed banks of *Brachiaria* and *Hymenachne* grasslands did not differ significantly in species richness and samples from both communities had significantly more species than *Oryza* and *Pseudoraphis* grasslands. Emergent communities from both the *Oryza* and *Pseudoraphis* grassland samples were similar in species richness (Figure 4.18).

More taxa were found to emerge in samples under flooded rather than moist regimes (Figure 4.19). The interaction between communities and water regimes was due to the moist *Brachiaria* grassland samples having significantly more species than flooded *Hymenachne* and *Pseudoraphis* grassland samples, while moist *Oryza* and *Pseudoraphis* grassland samples had less species than all other samples (Table D.5; Figure 4.20).

Table 4.11 Summary of ANOVA on species richness of seedlings emerging from samples collected in four grassland communities on the Magela floodplain (Nov 95) and germinated under two water regimes; flooded and moist. (*Brachiaria* grassland, *Oryza* grassland and, *Hymenachne* grassland, *Pseudoraphis* grassland) \*\* = P < 0.01, \*\*\* = P < 0.001.

	di Effeci	MS Effect	dtError	Mis Error	F	p-level
Veg Type	3	35.111	112	4.1	8,563	< 0.001***
Treatment	1	30.000	112	4.1	7.313	0.008**
Veg type x Transect	3	32.222	112	4.1	7.859	< 0.001***



Figure 4.18 Species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = Brachiaria grassland, Om = Oryza grassland, Ha = Hymenachne grassland and Ps = Pseudoraphis grassland) and germinated under flooded and moist water regimes

(significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.19 Species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain and germinated under two water regimes (flooded and moist) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).



Figure 4.20 Community and treatment interactions of species richness of seedlings emerging from trays, each representing  $66 \text{cm}^2 \times 10$  cm deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland and Ps = *Pseudoraphis* grassland) and germinated under two water regimes (flooded and moist) (Groups marked by the same letter did not differ significantly from one another (LSD test p < 0.05)).

### Summary

Table 4.12 summarises the significant results for total number of seedlings and species richness within and among grassland communities.

Table 4.12 Summary of all results of analyses on total number of seedlings and species richness within and among sediment samples collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland) and germinated under two water regimes (F = flooded, M = moist).

Significant Effect		Bm	Om	Ha	Ps	Veg Types
Total number	Transects	Ns	Ns	T9 < T7 / T8	Ns	Ns
of seedlings	Treatments	F > M	Ns	M > F	M > F	Ns
	Interactions	Ns	Ns	T9 < ail	Ns	Bm F > Bm M Ps F < Ps M
Species Richness	Transects	Ns	T6 < T4 / T5	T9/T8 <t7< td=""><td>T11 &lt; T10</td><td>Bm/Ha &gt; Om/Ps</td></t7<>	T11 < T10	Bm/Ha > Om/Ps
	Treatments	Ns	F > M	Ns	F > M	F > M
	Interactions	Ns	Ns	Ns	Ns	BmM > HaF/OmM/PsF/PsM Om M < all bar Ps M Ps M < all bar Om M

Comparisons of Grassland Seed Banks Between Years (1984 & 1996) Q<sub>7</sub>: Have changes occurred in the seed bank since the 1984 study?

Due to differences between the present study and that conducted in 1984 (Finlayson *et al.* 1990) (duration, sample numbers, timing of sampling and experimental starting time), the following comparisons are tentative.

A total of 33 taxa were recorded in 1984 compared with 34 taxa found in this study. Two species were found in 1984 that were not present in 1996, namely, *Cyperus digitatus* and *Hygrochloa aquatica*. In contrast *Brachiaria mutica* was recorded in 1996 but not in 1984.

Similar numbers of species were found to emerge from flooded treatments in both years (Figure 4.21), although the *Hymenachne* grassland samples in 1984 contained slightly more species than those in 1996. A vast difference in species richness of the moist treatments could be seen. *Oryza* grassland samples in 1984 contained more species than the equivalent (*Brachiaria* grassland and *Oryza* grassland) samples in 1996. The number of species in moist treatments of both *Hymenachne* and *Pseudoraphis* grassland samples in 1996 were also reduced but the difference was not as great.



Figure 4.21 Species richness of seedlings emerging from sediment samples collected from the same sample sites on the Magela floodplain in 1984 and 1995 and germinated under two water regimes (flooded and moist)(Top 1984 Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland; Bottom 1996 Bm = *Brachiaria* grassland, Om = *Oryza* grassland (Bm + Om = Om 1984), Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland).

Data on all taxa were not published for the 1984 study, consequently comparisons of taxa can only be made with those that were documented. Data published from the 1984 study were presented in the form of calculated seedlings m<sup>-2</sup>, and these calculations were also conducted for the present study in order to facilitate comparisons (Appendix E). Examination of the proportions of each taxa that emerged from the grassland communities in 1984 and 1996 for both flooded and moist treatments, showed several overlaps.

### Taxa Emerging from Oryza Grassland Samples in 1984 & 1996

Ceratopteris thalictroides, Eleocharis spp., Eriocaulon setaceum, Glinus oppositifolius, Heliotropium indicum, Isoetes coromandelina, Limnophila australis, Maidenia rubra, Najas spp. and Oryza meridionalis overlapped among the Oryza grassland samples in 1984 and Brachiaria and Oryza grassland samples in 1996 (Figure 4.22). Differences in proportions of seedlings of these species were found between years and treatments. Ceratopteris thalictroides, Heliotropium indicum, Isoetes coromandelina and Najas spp. were found to emerge in higher numbers in 1996 than in 1984. Conversely, Maidenia rubra, Limnophila australis, Eriocaulon setaceum and Oryza meridionalis were proportionally more abundant in 1984 samples (compared to 1996 samples). Eleocharis spp. and Glinus oppositifolius were found in similar proportions in samples from both years



Figure 4.22 Proportions of total seedlings (calculated 1m<sup>-2</sup>) that each species made up in 1984 *Oryza* grassland samples (OM84), 1996 *Oryza* grassland samples (Om96) and 1996 *Brachiaria* grassland samples (Bm96) in flooded (F) and moist (M) treatments (only species overlapping in occurrence between years are shown).

### Taxa Emerging from in Hymenachne Grassland Samples in 1984 & 1996

Taxa found to emerge from samples in both 1984 and 1996 included *Fimbristylis* spp., *Glinus oppositifolius*, *Heliotropium indicum*, *Hymenachne acutigluma*, *Najas* spp., *Nymphaea* spp., *Pseudoraphis spinescens*, and *Utricularia* spp. (Figure 4.23).

*Fimbristylis* spp., *Heliotropium indicum, Najas* spp., and *Pseudoraphis spinescens* made up greater proportions of seedlings in 1984 compared to 1996. *Hymenachne acutigluma* and *Glinus oppositifolius* were found to emerge in greater proportions in 1996. While *Nymphaea* spp. differed in proportion between years in flooded and moist treatments and *Utricularia* spp. was found in similar proportions in both years.



Figure 4.23 Proportions of total seedlings (calculated  $1m^{-2}$ ) that each species made up in 1984 *Hymenachne* grassland samples (HA84), 1996 *Hymenachne* grassland samples (HA96) in flooded (F) and moist (M) treatments.(only species overlapping in occurrence between years are shown).

### Taxa Emerging from Pseudoraphis Grassland Samples in 1984 & 1996

*Eleocharis* spp., *Glinus* oppositifolius, Najas spp., Nymphaea spp., *Pseudoraphis spinescens*, and *Utricularia* spp. were all found to emerge from samples collected from the *Pseudoraphis* grassland site in both years (Figure 4.24).

*Najas* spp. and *Pseudoraphis spinescens* were found in higher proportions in 1984 compared to 1996, while *Glinus oppositifolius*, *Nymphaea* spp., *Utricularia* spp. and *Eleocharis* spp. emerged in higher proportions in 1996.



Figure 4.24 Proportions of total seedlings (calculated  $1m^{-2}$ ) that each species made up in 1984 *Pseudoraphis* grassland samples (PS84), 1996 *Pseudoraphis* grassland samples (PS96) in flooded (F) and moist (M) treatments.(only species overlapping in occurrence between years are shown).

## Discussion

# **Grassland Seed Banks in 1996**

Wetland taxa found to emerge from the seed bank can be divided into three groups according to their germination: taxa that germinate under flooded conditions; taxa that germinate under moist conditions; and taxa that germinate under both flooded and moist conditions. *Blyxa aubertii, Ludwigia adscendens, Hydrilla verticillata, Chara* spp., *Cyperus platystylis, Najas* spp., *Nitella* spp. and *Utricularia* spp. all germinate in higher numbers under flooded conditions (compared to moist). In contrast, *Cyperus aquatilis, Coldenia procumbens, Commelina lanceolata, Dentella dioeca, Euphorbia vachellii, Phyla nodiflora* and *Heliotropium indicum* germinate better under moist conditions. All other recorded taxa emerged in similar numbers regardless of whether they experienced flooded or moist water regimes (Figures 4.3 & 4.4).

Groupings of the aquatic taxa, *Nitella* spp., *Nymphaea* spp., *Isoetes coromandelina, Najas* spp., *Nymphoides* spp., *Cyperus serotinus* and *Limnophila australis* were the main influences in patterns found among samples (Figures 4.6 & 4.7). *Glinus oppositifolius*, a mudflat species, also influenced the patterns that were found. Distinct differences in species composition and abundance between treatments were caused by the emergence of more aquatic taxa in the flooded treatments compared to moist treatments (Figure 4.5). Charophytes played a major role as large numbers of oospores were present in flooded samples from all communities (Table 4.1).

*Hymenachne* and *Pseudoraphis* grassland seed banks differed from *Brachiaria* and *Oryza* grassland seed banks as few *Nymphaea* spp. seedlings emerged from seed banks of the latter two communities. Differences between *Pseudoraphis* and *Hymenachne* grassland seed banks were attributed to the combination of *Nymphoides* spp. and *Cyperus* spp. emerging in *Hymenachne* grassland samples.

Species composition and abundance of *Oryza* and *Brachiana* grassland samples were similar although partitions between treatments were found. This was caused by the presence of *Nitella* spp. seedlings in flooded samples and

*Isoetes coromandelina* seedlings in moist samples. High numbers of the latter species in moist samples may indicate germination conditions required by this species. The similarities in species composition between seed banks of *Oryza* and *Brachiaria* grasslands are not surprising as the *Brachiaria* grassland exists on a site which, prior to 1989, was *Oryza* grassland.

Brachiaria mutica seeds emerged from both Brachiaria and Hymenachne grassland samples, indicating that these seeds are widely dispersed on the floodplain. However, these seeds were not found in the adjacent Oryza grassland or Pseudoraphis grassland samples. Seeds of this species could be present in these communities in lower numbers (than in Hymenachne and Brachiaria grasslands) because reduced vegetation cover in Oryza and Pseudoraphis grasslands, during the dry season, allows seed predation by providing easier access to seeds. If this was the case, sample size and intensity may not have been large enough to detect these seeds.

Species richness and total number of seedlings in *Hymenachne* grassland samples and species richness among both *Oryza* and *Pseudoraphis* grasslands differed between transects, these results indicate a heterogeneous distribution of seeds within sediments of the Magela floodplain. As this difference was noted for both seedling numbers and species richness in the *Hymenachne* grassland, seeds may be more variably distributed within sediments of this community (Table 4.12). This is consistent with species in the extant vegetation as the *Hymenachne* grassland was found to have the most species rich and diverse extant vegetation of the four communities (Figures 3.2 & 3.5).

Moist samples yielded the highest numbers of seedlings for *Hymenachne* and *Pseudoraphis* grasslands, whereas, flooded *Brachiaria* grassland samples yielded more seedlings for this particular community. These contrasting trends led to significant community and water regime interactions for the total number of seedlings emerging among communities (Table 4.10). These differences can be attributed to high numbers of just a few species. The flooded *Brachiaria* grassland samples had higher total seedling numbers because of the many *Nitella* spp. and *Chara* spp. seedlings emerging in these samples (Table 4.1). Similarly, the greater total number of seedlings emerging from moist

Hymenachne grassland samples were a result of the high number of Cyperus serotinus, Nymphoides spp., Nymphaea spp., Pseudoraphis spinescens and Glinus oppositifolius seedlings in these samples. The latter three taxa are responsible for the same trend in *Pseudoraphis* grassland samples.

Species richness in the seed bank was more indicative of observations in the extant vegetation than seedling numbers emerging from sediment samples, with both Orvza and Pseudoraphis grassland samples having greater species richness when flooded than under a moist water regime. The significantly higher species richness in Brachiaria and Hymenachne grassland samples. compared to Oryza and Pseudoraphis grassland samples, may reflect the morphological form and perennial habit of the two grass species that dominate these communities. Thompson (1992) noted that floating seeds are trapped by emergent vegetation. Both Brachiaria mutica and Hymenachne acutigluma are emergents that tend to grow in thick clumps. Therefore, these species could easily trap seeds dispersed during the wet as they float down the floodplain. Similarly, airborne seeds dispersed during the dry season could also be trapped. The perennial habit of these two species may also provide a nondesiccating environment during the dry as the thick vegetation cover over the whole year reduces fluctuations in soil temperature, thus providing better conditions for seed survival (Murdoch and Ellis 1992). Similarly, the clumping growth form of both Brachiaria mutica and Hymenachne acutigluma reduces light reaching the soil surface (and seeds). Light has been shown to play a major role in breaking the seed dormancy of many species (Pons 1992), thus the reduced light in these communities could inhibit germination of seeds.

Furthermore, the topographic position of these communities may also play a role. Both *Brachiaria mutica* and *Hymenachne acutigluma* occur in sites of intermediate inundation compared to the remnant *Oryza* and *Pseudoraphis* grassland sites, which occur on the edge and in deeper sections of the floodplain respectively. This supports Grime's (1973) suggestion that harsh environmental conditions generate low species diversity.

The interaction between plant community and water regime was a result of higher species richness in moist *Brachiaria* grassland samples, compared to all

other samples, and low species richness in both *Oryza* and *Pseudoraphis* grasslands, under moist water regimes (Figure 4.20). Extremely high species richness in *Brachiaria* grassland samples may be a result of the recent changes in extant vegetation in this community. This sample site still contains the suite of seeds from the *Oryza* community that previously occupied the site (Maps 3.2 & 3.3). Further, thick vegetation cover of *Brachiaria mutica* all year round traps seeds (Thompson 1992), while reducing recruitment from the seed bank. These factors contribute to a larger soil seed bank in this community.

## Comparisons of Grassland Seed Banks Between Years (1984 & 1996)

The marked difference in species richness of *Oryza* grassland samples in 1984 and 1996 is not easily explained (Figure 4.21). It is possible that the small number of samples taken in 1984 could have been collected from a particularly species rich location within the *Oryza* grassland. In addition, differences between timing and duration of experiments in 1984 and 1996 could effect these results. The remnant *Oryza* grassland site sampled for the current study was located on the edge of the floodplain, as *Brachiaria mutica* has invaded the deeper parts of this community. This could reflect the habitat requirements of *Brachiaria mutica*. It is possible that the water regime toward the edge of the floodplain inhibits *Brachiaria mutica* from establishing. The habitat requirements of *Brachiaria mutica* have not been fully established and the water regimes that facilitate establishment and survival of this species may also differ, that is, once established *Brachiaria mutica* may be able to survive in environments with less water.

Comparison of the proportions of individual species occurring in each community between years gave varying results. Higher proportions of *Oryza meridionalis*, *Eriocaulon setaceum*, *Limnophila australis*, *Fimbristylis* spp., *Maidenia rubra*, and *Pseudoraphis spinescens* were found in samples from 1984 compared to those in 1996. While *Isoetes coromandelina*, *Glinus oppositifolius*, *Nymphaea* spp., *Utricularia* spp. and *Eleocharis* spp. made up a greater proportion of seedlings emerging from 1996 samples compared to those from 1984.

#### Chapter 4

The duration of experiments could have considerably influenced the proportions of species emerging from sediments. This factor has been suggested to effect seed bank estimates by several authors (Benoit et al. 1989; Warr et al. 1993; Britton and Brock 1994). In addition dormancy of seeds could have been induced in this study by drying samples at the time of onset of flooding in November 1995. This study was conducted over 3 1/2 months. whereas the previous study monitored germination from samples over 10 months. The presence of seed dormancy may have resulted in seeds requiring longer than 3 1/2 months to germinate. This is particularly relevant to *Pseudoraphis spinescens* as seeds of this species were previously found to continue germinating after 10 months (Finlayson et al. 1990), and they made up a considerable proportion of the seedlings emerging in the previous study (Figures 4.23 & 4.24). In any case, these results illustrate the variability in covert vegetation on the floodplain, and may indicate that the contribution of seed banks to the extant vegetation varies in different years. As seed banks reflect seed production of previous years, the proportions of seedlings found in each year could be an artefact of seed production due to variation in rainfall in the years leading up to each study. The wet season prior to sample collection for this study was unusually long and rainfall for the year was above average (3700mm), this could explain why all but one of the taxa found to make up higher proportions of seedlings in 1996 compared to 1984 were aquatic taxa.



Chapter 5 The Relationships: Extant Vegetation & Seed Banks

## Introduction

The seed banks of most plant communities are expected to contain more species than extant vegetation, as seed banks commonly reflect vegetation from previous times (Roberts 1981). Several studies have examined the relationships between freshwater tidal wetland seed banks and extant vegetation and, contrary to expectations, these seed banks have been found to mirror extant vegetation in species composition and abundance (Parker and Leck 1985; Leck and Simpson 1987; Leck and Simpson 1995). This is considered to be a result of the large proportion of annual species, and the reduced numbers of grass and sedge species, in such communities (Leck and Simpson 1995).

Grillas *et al.* (1993) studied a marsh in southwestern Spain and found significant correlations between seed bank and extant vegetation in species composition and abundance. However, this relationship failed to apply to Charophyta, for although oospores were abundant in samples, charophytes were not present in the extant vegetation of all areas sampled (Grillas *et al.* 1993).

Hydrological patterns establish the role seed banks play in vegetation dynamics (Leck 1989). Prairie marshes in North America have been shown to rely on seed banks for regeneration of mudflat and emergent species during drought, and recruitment of submersed aquatics during periods of normal rainfall (van der Valk and Davis 1979). In habitats where the drawdown cycle is annual (eg. vernal pools & monsoonal floodplains), more complex relationships between seed banks and extant vegetation have been found (Gopal 1986; Zedler 1987). Zedler (1987) hypothesised that variation in pool water level contributes to seed bank and vegetation diversity in vernal pools. Gopal (1986) suggested that two seasonally delimited communities develop in monsoonal climates, one adapted to inundation and the other to drawdown, both contributing and recruiting from the seed bank.

Finlayson *et al.* (1990) applied flooded and damp water regimes to sediment samples from *Hymenachne*, *Oryza* and *Pseudoraphis* grasslands of the Magela floodplain with the objective of finding relationships between seed banks and

extant vegetation of each community. Pseudoraphis grassland seed banks were found to closely resemble the vegetation of this community. Hymenachne grassland seed banks, on the other hand, did not closely resemble extant vegetation. Hymenachne acutigluma made up <2% of seedlings emerging from sediments collected in the *Hymenachne* grassland compared with Pseudoraphis spinescens which comprised 72% of emergent seedlings. However, *Pseudoraphis spinescens* was not prominent in the extant vegetation of the Hymenachne grassland, therefore, it was suggested that Pseudoraphis spinescens seed had been transported downstream from the Pseudoraphis grassland to the Hymenachne grassland. Seed transport may therefore be an important factor influencing vegetation patterns (Finlayson et al. 1990). It was also noted that just prior to the study in 1984 (Finlayson et al. 1990) that the Hymenachne grassland was inhabited by a population (unknown size) of feral buffaloes and this could have been, in part, responsible for the lack of Hymenachne acutigluma seed within sediment samples, as grazing buffalo may have prevented this species from flowering. Oryza grassland seed bank samples were found to contain more seedlings than seed bank samples from other communities, although not all species found in the extant vegetation of this community were represented in the sediment samples. It was suggested that the observed unevenness of species composition in these sediment samples was a result of the dominance of annual species in extant vegetation of the Oryza grassland (Finlayson et al. 1990). Predictions of vegetation succession on the Magela floodplain from this study alone were not possible due to the lack of correspondence between seed bank results and vegetation survey data.

The current study was conducted on the same sample sites as those of Finlayson *et al.* (1990) and aimed to collect more detailed data on sediment seed banks and extant vegetation of these sites thus clarifying relationships and allowing comparisons between the studies.

The questions addressed in this chapter are:

- Q<sub>1</sub>: Is there a correlation between species composition of sediment samples (determined by germination) and the extant vegetation from which they came?
- Q<sub>2</sub>: Is there a correlation between species composition and abundance of sediment samples (determined by germination) and the extant vegetation from which they came?

The hypothesis generated to test this is:

H<sub>1</sub>: There is no difference in the species composition and abundance of extant vegetation and seed banks.

## Methods and Analyses

Simple comparisons of species presence between extant vegetation (Chapter 3) and seed bank data (Chapter 4) were made for each of the four plant communities studied. More complex comparisons were made using the Mantel test and modified Rand test to compare results from multivariate analyses of these data. The Mantel test compared association matrices of vegetation data and seed bank data (Appendix B: refer to disk provided) using Pearsons product moment correlation coefficient (Belbin 1993a). An original correlation was made, then one association matrix (vegetation survey) was randomised 10,000 times. Each randomisation was correlated to the sediment germination matrix (held constant). These values were compared to the original r value to determine if this correlation occurred purely by chance.

Groupings identified from cluster analyses of the vegetation survey (Figure 3.2) and sediment germination (Figure 4.7) data were compared using the RIND sub-routine in PATN. This method is based on the modifications of the Rand statistic made by Hubert and Arabie (1985). It returns a Hubert/Arabie/Rand statistic ranging from a value of zero, implying chance levels of associations to one, indicating a perfect correlation (Belbin 1993a).
### Results

Q<sub>1</sub>: Is there a correlation between species composition of sediment samples (determined by germination) and the extant vegetation from which they came?

More taxa germinated from sediment samples than were found in the extant vegetation of each plant community (Table 5.1) and many of the taxa germinating from sediment samples were not found at all in the vegetation survey. These included *Blyxa aubertii, Ceratopteris thalictroides, Chara* spp., *Commelina lanceolata, Cyperus aquatilis, Cyperus serotinus, Eriocaulon setaceum, Hydrilla verticillata, Limnophila australis, Ludwigia perennis, Maidenia rubra, Nitella spp. and Oldenlandia* sp. Of these taxa, *Nitella* spp., *Chara* spp. and *Cyperus serotinus* were found to emerge from sediment samples of all communities. *Blyxa aubertii, Hydrilla verticillata* and *Ludwigia perennis* were each found in only one community. *Eriocaulon setaceum, lsoetes coromandelina* and *Limnophila australis* emerged only from samples collected at *Brachiaria* and *Oryza* grassland sites and *Maidenia rubra* was found in all samples but those from the *Pseudoraphis* grassland.

Five species occurred in the vegetation survey that were not found to germinate from the sediments namely, *Azolla pinnata, Salvinia molesta, Hygrochloa aquatica, Merremia gemella* and *Ipomoea aquatica.* 

Table 5.1 Species occurring in extant vegetation (wet and dry season) and emerging from sediment seed bank (moist and flooded water regimes) of four grassland communities on the Magela floodplain (communities are defined in Chapter 2).

Таха	Brachiaria grassland Extant Vegetation Seed bank			Oryza grassland Extant Vegetation Seed hank			Hymenachne grassland Extant Vegetation Seed bank				Pseudoraphis grassland Extant Vegetation Seed bank					
	Drv	Wet	Moist	Flooded	Dry	Wet	Moist	Flooded	Drv	Wet	Moist	Flooded	Dry	Wet	Moist	Flooded
Azolla pinnata		1								1						
Blyxa aubertii																~
Brachiaria mutica*	~	~	1		✓						1					
Ceratopteris thalictroides				1					· · · ·		√					
Chara spp.				1				<ul> <li>Image: A second s</li></ul>								
Coldenia procumbens			1				✓		1							
Commelina lanceolata																
Cyperus aquatilis																
Cyperus platystylis			1						1		✓	1	1			
Cyperus serotinus			✓	1								1				1
Dentella dioeca					-				✓		✓					
Eclipta prostrata									1		~	✓			1	1
Eleocharis spp.			<ul><li>✓</li></ul>	✓		- ✓	1	1		1		1		~	1	✓
Eriocaulon setaceum			<b>v</b>	✓			1	1								
Euphorbia vachellii					1				<ul> <li>✓</li> </ul>		1		1			
Fimbristylis spp.	1		1				<ul> <li>✓</li> </ul>	√	<ul> <li>✓</li> </ul>		<ul> <li>✓</li> </ul>					- V
Glinus oppositifolius			✓			_	<ul> <li>✓</li> </ul>				✓		<ul> <li>Image: A set of the set of the</li></ul>		1	~
Heliotropium indicum*	ſ		<ul><li>✓</li></ul>				1		✓		<ul> <li>✓</li> </ul>					
Hydrilla verticillata							<u> </u>					✓				
Hygrochloa aquatica					<u> </u>	<u> </u>										
Hymenachne acutigluma		<u> </u>				<u></u> √			1	1	1	1		<b>√</b>		
Ipomoea aquatica		· ·····				<u></u>	<u> </u>						<u> </u>	<u>√</u>		
Isoetes coromandelina			✓	<u> </u>			<u> </u>	1								
Limnophila australis				······			<u> </u>	<u> </u>			L					
Ludwigia adscendens		<u> </u>				<u> </u>			_ <b>✓</b>	<u> </u>				<u> </u>	ļ	<u> </u>
Ludwigia perennis							<u> </u>	√							<u> </u>	
Maidenia rubra			<u> </u>				<u> </u>	√				<u> </u>			ļ	
Merremia gemella					<u> </u>				L							
Naias spp.			<ul> <li>✓</li> </ul>	<u> </u>	ļ							<u> </u>				
Nitella spp.				<u> </u>				<u> </u>			<u> </u>	<u> </u>			<u> </u>	
Nymphaea spp.		<u> </u>	✓	······			✓	<u> </u>		<u> </u>	<u> </u>	<u> </u>		<b>√</b>		
Nymphoides spp.			✓			<u> </u>		<u> </u>		<b>√</b>	<u> </u>	<u> </u>				<u> </u>
Oldenlandia sp.							<u> </u>					<u></u>				<b>/</b>
Oryza meridionalis		<u> </u>	1	<u> </u>	1		<u> </u>	√		<u> </u>	<u>.                                    </u>				<u> </u>	
Persicaria spp.							L			<u> </u>	<u> </u>			<b>/</b>	<u>i</u>	·
Phyla nodiflora*	L				<b>↓</b> ✓		<hr/>		L							·
Pseudoraphis spinescens	<b>↓</b> ✓		<ul> <li>✓</li> </ul>		×	<u> </u>	<u> </u>			√			1	√	<u> </u>	
Salvinia molesta		<u> </u>								√						
Utricularia spp.		<u> </u>	✓	<u> </u>		<b>/</b>		✓		1	✓			1		<ul> <li>✓</li> </ul>

- Q<sub>2</sub>: Is there a correlation between species composition and abundance of sediment samples (determined by germination) and the extant vegetation from which they came?
- H<sub>1</sub>: There is no difference in the species composition and abundance of extant vegetation and seed banks.

The original correlation between association matrices of extant vegetation and seed bank germination data generated an r value of 0.245 indicating a poor correlation between association matrices. One hundred percent of the randomised values were less than or equal to this original value indicating that this correlation was significant and did not occur purely by chance.

To compare the groupings of cluster analyses of extant vegetation and seed bank data the RIND sub-routine in PATN generated a contingency table (Table 5.2). Vegetation survey partitions are presented in rows and sediment seed bank germination partitions are presented in columns. The values appearing off the shaded diagonal line indicate the level of miss-match between the two cluster analyses. The diagonal total shows that there was 44% overlap in the contingency table. The Hubert/Arabie/Rand statistic found was 0.1986, a lower result to the r value of the Mantel test (0.245). Indicating that there is little correlation between the two classifications.

Table 5.2 Contingency table produced by RIND sub-routine in PATN for comparison of vegetation survey and sediment germination classifications of four grassland vegetation types on the Magela floodplain; Hubert/Arabie RAND statistic = 0.1986; Diagonal/total = 53/120 = 0.4417

Vegetation Survey	1	Ge	ך					
Partitions	2	4	1	5	3	6	Sum	Ептог
1	17	1	10	0	1	0	29	41
2	5	17	11	2	8	4	47	64
3	14	0	1	1	0	0	16	94
4	3	3	0	18	3	1	28	36
Sum	39	21	22	21	12	5		
Error	56	19	95	14	100	<u>1</u> 00		

## Discussion

This study has shown that the seed banks of the Magela floodplain grasslands, like other systems, contain greater species richness than extant vegetation (Roberts 1981). One would expect seed banks of the Magela floodplain to contain species which have occurred as extant vegetation in previous years as well as those species which appear at different times throughout the same year. This was best illustrated by the observed differences in the *Brachiaria* grassland which contains extant vegetation with few species, but a seed bank containing more species than other grassland communities. Reasons for such high species richness in the seed bank of this community were discussed in Chapter 4.

Five species were found in extant vegetation of grassland communities that were absent from seed banks: *Azolla pinnata; Salvinia molesta; Hygrochloa aquatica; Merremia gemella;* and *Ipomoea aquatica. Azolla pinnata* and *Salvinia molesta* were not expected to emerge from sediments as they have not been reported to produce fertile spores in Australia (Sainty and Jacobs 1981) and vegetative propagules would have been killed by drying samples. Only a few specimens of *Hygrochloa aquatica* were recorded in extant vegetation. The rarity of this species in study sites is reflected in its absence from sediment germination samples. The absence of *Merremia gemella* and *Ipomoea aquatica* in germination trays may be explained by poor seed set or seed dormancy as these species were more common in extant vegetation than *Hygrochloa aquatica*.

Several taxa found in extant vegetation of particular communities, were absent from their representative seed banks. This may reflect the low frequency with which these taxa occur in a given community. Examples include *Hymenachne acutigluma* and *Ludwigia adscendens* found in the *Brachiaria* grassland, and *Oryza meridionalis* found in the *Hymenachne* grassland. These species occurred in low numbers in extant vegetation and were absent from sediment samples. *Euphorbia vachellii,* on the other hand was quite common in extant vegetation of the *Oryza* grassland during the dry season, yet it too was

absent in sediment samples of this community. This result may be due to seed dormancy or unfavourable conditions for germination in the glasshouse.

Many aquatic taxa found in the seed bank were not observed in extant vegetation. However, greater numbers of these taxa may occur in extant vegetation during the wet season than otherwise indicated by the vegetation survey (Chapter 3) as the presence of crocodiles on the floodplain limited sampling of submerged vegetation during this season. The common occurrence (in sediments) of *Nitella* spp., *Chara* spp., *Cyperus* serotinus and *Maidenia* rubra is more than likely a reflection of the high seed and oospore production of these taxa. It is likely that *Blyxa* aubertii, *Hydrilla* verticillata and *Ludwigia* perennis occur infrequently in the study sites as they were each only found emerging from one community and were absent from extant vegetation.

Finlayson *et al.* (1990) found species composition and abundance of the *Pseudoraphis* grassland seed bank to closely resemble extant vegetation in this community, but found poor relationships between extant vegetation and seed banks of the *Hymenachne* and *Oryza* grasslands. In contrast, this study found species composition of the *Hymenachne* grassland seed banks were to their respective extant vegetation (Table 5.1), although this relationship did not hold for species abundance. This result may reflect the ability of the *Hymenachne* grassland to sustain a variety of taxa in the extant vegetation late into the dry season, as this community undergoes less dramatic seasonal water fluctuations than other communities (ie. drawdown takes longer).

Finlayson *et al.* (1989) suggested that duration of inundation played an important role in structuring vegetation. They reported that areas of the floodplain inundated for approximately five months each year had greater fluctuations of species composition in extant vegetation than those inundated for three months (Finlayson *et al.* 1989). This may be due to the greater length of time available for individual species to germinate, grow and reproduce. The availability of water for this extended period may enable more species to complete their life-cycles and as a result, more species rich communities are found in the sediments of these areas.

Correlations of species composition and abundance between extant vegetation and sediment seed bank data of this study were poor. Although the above analyses show that this relationship did not occur purely by chance. The lack of correlation between extant vegetation and seed banks is probably due to the occurrence of high numbers of submerged aquatic taxa emerging from sediment samples (Chapter 4).

The timing of vegetation survey could also be one reason stronger correlations were not found. Finlayson *et al.* (1989) noted that many species are recruited from the seed bank at the start and end of the wet season, just before flooding and drying of the floodplain. It is possible that the *Brachiaria, Oryza* and *Pseudoraphis* grasslands contain many of the taxa found to emerge from sediment samples as extant vegetation during this period of time only. If this is the case, the vegetation surveys in this study would not have found these taxa, as surveys were conducted late in the dry season, before rain had commenced, and during the wet season after flooding had occurred. To further investigate this, emergence of seedlings would need to be monitored in the field during different times of year while study sites were inundated to different water levels.

Alternatively, it is possible that seeds of the taxa found to emerge in germination trials from samples taken in the *Brachiaria, Oryza* and *Pseudoraphis* grassland sites, but not observed in the extant vegetation, were transported to these grassland communities from elsewhere. These taxa may not be able to grow and reproduce in these communities as conditions are not suitable. Regardless of these possibilities, the poor correlations found in this study indicate that other factors may be contributing to the vegetation dynamics on the floodplain. For example, it is recognised that vegetative reproduction plays a role in the vegetation dynamics of the Magela floodplain (Finlayson *et al.* 1989; 1990).

The sediment seed bank germination trial did not account for vegetative reproduction and the lack of correlation between extant vegetation and seed banks indicate that it may be a significant feature of the vegetation dynamics in this ecosystem. The lower numbers of grass seeds found to emerge in this study, compared to the 1984 study, would suggest that the importance of

vegetative reproduction varies from year to year. This may be related to the effect of rainfall patterns upon seed production of dominant species of the grassland communities on the Magela floodplain.



Chapter 6 The Grasses: Seed Production and Viability

#### Introduction

To date no quantitative data on seed production of the dominant grass species investigated in this study has been published. However, research into *Oryza meridionalis* is currently being conducted (Wurm 1996) and seed production of *Brachiaria mutica* has been assessed qualitatively (Cameron 1991). Data on the production of flowering culms and florets per inflorescence, for each species investigated through this study, adds to previously published information on biomass and nutrient composition of these species (Cameron 1991; Finlayson 1991). These data help place vegetation survey and sediment germination data (presented in previous chapters) into perspective by supplying relative estimates of potential seed input into the seed bank. Information of this kind is vital to understanding the vegetation dynamics of the Magela floodplain.

In addition to sediment germination experiments (Chapter 4), seed banks can be quantified by conducting direct seed counts from soil cores. Direct seed counts are not commonly conducted in seed bank experiments (Warr et al. 1993). This is probably due to the labour requirements of such experiments. Nevertheless, this technique has the advantage over emergence techniques (Chapter 4) of allowing seed numbers to be estimated in a shorter time period (Roberts 1981). Several problems are encountered, however, including difficulties in seed extraction and the assessment of seed viability. Seed extraction is usually conducted by means of washing samples through a series of sieves with successively smaller pore sizes. Many wetland species have very small seeds (<1mm) and the difficulty in extracting seed is probably the main reason seed counts (from soil cores) have not been extensively used in studies on wetlands. Once extracted, there is no assurance that all seeds are viable. Viability can be assessed using tetrazolium chloride (outline below), but this requires large numbers (>100 preferably 400) of undamaged seeds and in many cases only the most abundant species can be assessed in this way.

Viability data on the grass species that dominate the Magela floodplain was sought to provide information on germinability and dormancy of seeds collected from each species. Tests of germinability and viability on seed of tropical pasture species are common (de Andrade *et al.* 1983), but such information on tropical grass species (not used in pastures) is unavailable (Simpson 1990). Several methods exist to test seed viability, the most direct method is testing by germination of seeds.

There are several problems associated with direct germination tests. Firstly, seeds from a sample may have different germination requirements due to variations in genetic make up or stages of maturity (Mackay 1972). Similarly, different species may require different germination conditions, or have dormancy mechanisms (Fenner 1985). To overcome these problems this study used a tetrazolium chloride test to assess viability of seeds that did not germinate as a result of a direct germination trial.

The abovementioned test involves treating seeds with a solution of colourless tetrazolium chloride. Once imbibed by the seed, dehydrogenase enzymes of living tissues reduce the tetrazolium to red formazin. Formazin is immobile in plants and remains within the cells in which it is formed. Thus, seeds with living embryos stain red. Some difficulties can arise when interpreting the results of tetrazolium tests as in many cases only part of an embryo stains. This is further complicated as seeds of different plant families have been shown to stain differently (Moore 1985). Families containing species of agronomic importance have been extensively tested using tetrazolium chloride stain and providing the same techniques are used to interpret seeds from the same family, tetrazolium tests on seeds of the species investigated in this study have not previously been conducted.

Direct germination of *Brachiaria mutica* seed was investigated by MacLean and Grof (1968). They found higher numbers of scarified (acid washed) seeds to germinate compared to untreated seeds (MacLean and Grof 1968). Therefore concluding that seed dormancy in *Brachiaria mutica* was due to an impermeable seed coat (MacLean and Grof 1968). Similar results have been found for *Oryza meridionalis* (Wurm 1996). Germination of untreated *Brachiaria mutica* seeds were found to exceed the minimum Australian primary industries standard of 15% by both Wesley-Smith (1973) and Cameron (1991) and high proportions of florets were found to set seed (qualitative data) (Cameron 1991).

The questions addressed in this chapter are:

- Q<sub>1</sub>: What is the potential seed production m<sup>-2</sup> of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types?
- Q<sub>2</sub>: What is the density of *Brachiaria mutica* and *Oryza meridionalis* seeds in the seed bank?
- Q<sub>3</sub>: What is the viability of *Brachiaria mutica*, Oryza meridionalis, Hymenachne acutigluma and Pseudoraphis spinescens seeds?

The hypotheses generated to test these questions are:

- H<sub>1</sub>: There is no difference in the numbers of flowering culms m<sup>-2</sup> produced by *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types.
- H<sub>2</sub>: There is no difference in the number of florets per inflorescence produced by *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens*.
- H<sub>3</sub>: There is no difference in the germinability of seeds of *Brachiaria mutica*, Oryza meridionalis, Hymenachne acutigluma and Pseudoraphis spinescens when placed in a growth cabinet for three weeks.
- H<sub>4</sub>: There is no difference in the viability of seeds of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* as interpreted using tetrazolium stain after attempted germination for three weeks in a growth cabinet.
- H<sub>5</sub>: There is no difference in the overall viability (germination & tetrazolium tests) of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds.

### Materials and Methods

## Seed Production Estimates

Counts of flowering culms of the dominant species in each grassland community were conducted concurrently with direct species counts (Chapter 3) during peak biomass production in May 1996. Collection of these data during peak biomass production was expected to produce the best estimate of seed production potential from a given snapshot in time (Finlayson 1991).

Optimal quadrat size for culm counts was determined by calculating the coefficient of variation of the total number of flowering culms within all nests of nested quadrats for each species (five replicate nested quadrats were used for each species) (Chapter 3). Coefficient of variation was plotted against cumulative area which indicated that 1m<sup>2</sup> quadrats gave similar coefficients of variance as 4m<sup>2</sup> quadrats (Figure 6.1). Consequently, 1m<sup>2</sup> quadrats were employed in all subsequent culm counts. Quadrats (usually 3) were randomly placed within 10m of the airboat platform, at each nested quadrat location, and the number of flowering culms in each were recorded (Plate 6.1).



Figure 6.1 Coefficient of variation (standard deviation / mean) of the number of flowering culms recorded for each species with increasing sample area during peak biomass production in May 1996.



Plate 6.1 Flowering culms were counted within a 1m<sup>2</sup> floating quadrat (this quadrat is located in the *Oryza* grassland).

Floret number per inflorescence was assessed for one hundred flowering culms from each dominant grass species of the four vegetation types sampled (Brachiaria, Oryza, Pseudoraphis and Hymenachne grasslands). Direct counts of Brachiaria mutica, Oryza meridionalis and Pseudoraphis spinescens florets were conducted. It was impractical to conduct direct counts on Hymenachne acutigluma due to the large number of small florets possessed by this species. Instead, ten groups of ten inflorescences were placed into paper bags and oven dried at 60°C for 5 days. Florets from each group were then removed from their culms and the total weight of florets from each group was recorded. Five 0.02g sub-samples were then taken from each group, weighed and the number of florets in each of these sub-samples were counted and averaged. From this value the mean number of florets per inflorescence for each group was calculated. Finally a mean of the calculated number of florets per inflorescence of each group was taken and this value was used as the estimated average number of florets per inflorescence for Hymenachne acutigluma.

Both the number of culms m<sup>-2</sup> and the number florets per inflorescence were used to calculate potential seed production of each of the dominant grass species in their respective vegetation types.

## **Soil Seed Density Estimates**

The five extra cores collected from each transect were used for seed counts (Chapter 4). Cores were wet up and three 1cm diameter x 2cm deep sub-cores were taken from each. The sub-cores were oven dried at 60°C for two weeks and washed through a 250µm sieve to extract seeds. Calgon, a commercial water softener containing sodium hexametaphosphate was used to assist in clay dispersal and after extraction the seeds were identified and counted using a stereo microscope.

## Seed Viability Estimates

Seeds of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* were collected both by hand in the field and using a flyscreen catcher placed in front of the airboat. Seeds were sorted under a stereo microscope using transmitted light to determine if embryos were present. Three hundred mature seeds of each species were counted out and dipped in Thyram fungicide solution (0.1 molar) for 30 seconds to inhibit fungal growth. Six replicate plastic petri dishes, lined with 10 sheets of Whatman No.5 filter paper, were made for each species. Each petri dish contained fifty seeds. The replicates were saturated with distilled water and placed in a growth chamber set at 16h dark / 8h light photoperiod with temperature settings of 25°C and 30°C respectively. Replicates were kept saturated and germinating seeds were counted every two days (germination = both roots and shoots visible). After three weeks the trial was terminated and remaining ungerminated seeds were stained with tetrazolium chloride to assess viability.

Staining involved making either a longitudinal or lateral incision to the endosperm of each imbibed seed before placing them in stain solution (0.02 molar) for 24 hours after which time each seed was washed and cut in half longitudinally (Moore 1985) (Plate 6.2). Seeds were then interpreted as viable if both root and shoot apices stained red and more than 50% of the tissue

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connecting these was stained (note: an uninterrupted connection between apices was necessary) (Moore 1985). A stereo microscope was needed to make these observations.



Plate 6.2 Seed viability was assessed using tetrazolium chloride, this plate shows two Oryza meridionalis seeds after staining; bottom seed is viable as indicated by the stained embryo, top seed is dead and embryo failed to stain.

## Statistical Analysis

Differences in flowering culms m<sup>-2</sup> and florets per inflorescence among species were tested by ANOVA. The mean number of *Brachiaria mutica* and *Oryza meridionalis* seeds in each core was estimated, from the seed number to sediment core volume ratio. These values were then used to estimate grass seed numbers per sample tray from each of the grassland communities (Chapter 4).

Differences in the numbers of germinating seeds and viable dormant seeds determined by tetrazolium tests were also analysed using ANOVA. The Least Significant Difference (LSD) test was used to determine which results were significant at the 5% level (Appendix F).

## Results

# **Potential Seed Production**

- Q<sub>1</sub>: What is the potential seed production m<sup>-2</sup> of *Brachiaria mutica*, Oryza *meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types?
- H<sub>1</sub>: There is no difference in the numbers of flowering culms m<sup>-2</sup> produced by *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types.
- H<sub>2</sub>: There is no difference in the number of florets per inflorescence produced by *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens*.

Significant differences in the mean number of flowering culms m<sup>-2</sup> of each species, in their respective vegetation types, were found (Table 6.1). *Oryza meridionalis* produced significantly more mean flowering culms m<sup>-2</sup> than all other species. The mean number of flowering culms m<sup>-2</sup> produced by *Brachiaria mutica* was significantly greater than those produced by both *Hymenachne acutigluma* and *Pseudoraphis spinescens*. Mean flowering culm production (m<sup>-2</sup>) of *Hymenachne acutigluma* and *Pseudoraphis spinescens*. Mean flowering culm not differ significantly (Table F.1; Figure 6.2)

Table 6.1 Results of ANOVA on the number of flowering culms  $m^{-2}$  and number of florets per inflorescence recorded for *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* recorded in their respective vegetation types during peak biomass production (May 1996) (\*\* = p < 0.01, \*\*\* = P < 0.001).

	df Effect	MS Effect	df Error	MS Error	F	p-level
Florets	3	1093712.	309	1474.44	741.8	< 0.01**
Culms	3	0.0291	222	0.001	25.728	< 0.001***



Figure 6.2 Number of flowering culms  $m^{-2}$  recorded for each dominant grass species in their respective vegetation types during peak biomass production (May 1996) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

The mean number of florets per inflorescence were found to differ significantly among species (Table 6.1). *Hymenachne acutigluma* had the greatest mean number of florets per inflorescence followed by *Brachiaria mutica*, *Pseudoraphis spinescens* and *Oryza meridionalis* (Table F.2; Figure 6.3).



Figure 6.3 Number of florets per inflorescence recorded for *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutiglum*a and *Pseudoraphis spinescens* during peak biomass production (May 1996) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

Calculated floret production m<sup>-2</sup> differed dramatically among species. Brachiaria mutica was calculated to produce the greatest number of florets m<sup>-2</sup> followed by *Hymenachne acutigluma*, *Pseudoraphis spinescens* and *Oryza meridionalis* (Figure 6.4).



Figure 6.4 Calculated floret production m<sup>-2</sup> of *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) in their respective vegetation types during peak biomass production (May 1996) (error bars show standard error).

## Soil Seed Density Estimates

Q<sub>2</sub>: What is the density of *Brachiaria mutica* and *Oryza meridionalis* seeds in the seed bank?

*Brachiaria mutica* and *Oryza meridionalis* seeds were only found in cores of samples taken in their respective vegetation types. Extrapolations from these counts gave estimates of 20 *Oryza meridionalis* seeds per tray and 57 *Brachiaria mutica* seeds per tray within samples collected from their respective grassland communities (Figure 6.5).



Figure 6.5 Estimates of Oryza meridionalis and Brachiaria mutica seeds within sediment seed bank germination sample trays and m<sup>-2</sup> in their respective plant communities (error bars indicate standard error).

## Seed Viability Estimates

- Q<sub>3</sub>: What is the viability of *Brachiaria mutica*, Oryza meridionalis, Hymenachne acutigluma and Pseudoraphis spinescens seeds?
- H<sub>3</sub>: There is no difference in the germinability of seeds of *Brachiaria mutica*, Oryza meridionalis, Hymenachne acutigluma and Pseudoraphis spinescens when placed in a growth cabinet for three weeks.
- H₄: There is no difference in the viability of seeds of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* as interpreted using tetrazolium stain after attempted germination for three weeks in a growth cabinet.
- H<sub>5</sub>: There is no difference in the overall viability (germination & tetrazolium tests) of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds.

Significant differences were found in the percentages of seeds of each species that germinated after three weeks in a growth cabinet, ungerminated seeds tested for viability using tetrazolium chloride and overall seed viability (germination + Tetrazolium tests) among species (Table 6.2).

Significantly more *Hymenachne acutigluma* seeds germinated than all other species, whereas percentage germination among *Brachiaria mutica*, *Oryza meridionalis* and *Pseudoraphis spinescens* did not differ significantly (Table F.3; Figure 6.6).

Table 6.2 Results of ANOVA on assessment of germination (three weeks in a growth chamber), viability (tetrazolium chloride tests of remaining ungerminated seeds) and total viability (germination + tetrazolium test) of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds. \*\*\* = p<0.001

	distes	MS Effect	df Error	MS Error	F	prievel
% germination	3	1179.163	20	87.441	13.485	< 0.001***
% viable (tetrazolium)	3	1194.068	20	64.767	18.436	< 0.001***
Total viability	3	1226.717	20	54.031	22.704	< 0.001***



Figure 6.6 Percentage germination of *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds placed in a growth cabinet for three weeks (300 seeds of each species used) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

On average, 61 % of the remaining *Pseudoraphis spinescens* seeds were interpreted as viable. This was significantly lower than all other species (Table F.4; Figure 6.7). Almost all remaining *Oryza meridionalis* seeds were viable and this was significant compared to *Hymenachne acutigluma* seeds, but not *Brachiaria mutica* seeds. Viability of *Hymenachne acutigluma* and *Brachiaria mutica* seeds did not differ significantly (Figure 6.7).



Figure 6.7 Remaining ungerminated *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds interpreted as viable (using tetrazolium chloride) after three weeks in a growth chamber (300 seeds of each species used) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

*Pseudoraphis spinescens* seeds were found to have the lowest overall viability and this was significant compared to *Hymenachne acutigluma*, *Brachiaria mutica* and *Oryza meridionalis* (Figure 6.8). *Oryza meridionalis* seeds had the greatest viability and this was significant compared to *Hymenachne acutigluma* but not significantly different from *Brachiaria mutica*. *Brachiaria mutica* and *Oryza meridionalis* seeds did not differ significantly in overall viability.



Figure 6.8 Percentage of viable (germination + tetrazolium tests) *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds (300 seeds of each species used) (significant differences identified using the LSD test (p < 0.05) are indicated by different letters).

## Discussion

### **Potential Seed Production**

The species Brachiaria mutica, Hymenachne acutigluma, Oryza meridionalis and *Pseudoraphis spinescens* have different potential seed production as indicated by the differences in both the numbers of flowering culms (m<sup>-2</sup>) and florets per inflorescence. Oryza meridionalis and Pseudoraphis spinescens both had similar potential seed production which were much lower than those estimated for Brachiaria mutica and Hymenachne acutigluma (Figure 6.4). This may reflect the environmental conditions under which these species grow as both Oryza and Pseudoraphis grasslands were found in environments which undergo more extreme fluctuations in water level. Oryza meridionalis is an annual and *Pseudoraphis spinescens* changes form between wet and dry seasons. These factors could reduce resources available for seed production as a larger proportion must be allocated to vegetative growth in these species compared to Brachiaria mutica and Hymenachne acutigluma which maintain the same form in both seasons. Above ground biomass data supports this idea as Oryza meridionalis and Pseudoraphis spinescens were found to be positively correlated to water depth levels, where little correlation with this variable was

found for *Hymenachne acutigluma* (Finlayson 1991). The period of inundation and floodwater dispersion patterns have been shown to play a major role in the life-cycles of plants on the Magela floodplain (Finlayson *et al.* 1989). This factor could also help to explain the low seed production in *Oryza meridionalis* and *Pseudoraphis spinescens* (compared to *Brachiaria mutica* and *Hymenachne acutigluma*) as *Oryza* and *Pseudoraphis* grasslands are inundated for less time than *Brachiaria* and *Hymenachne* grasslands. Thus, *Oryza meridionalis* and *Pseudoraphis spinescens* must grow, flower and set seed faster than *Brachiaria mutica* and *Hymenachne acutigluma*.

This study made no attempt to quantify seed set of each species, therefore results over-estimate seed production. The indeterminate inflorescence growth of *Hymenachne acutigluma* however, could have led to under-estimates for this species. Qualitative assessment of seed set in this species showed very poor caryopsis formation (Calder 1982), therefore, it is unlikely that this study has under-estimated seed production in this species. Seed production estimates of this study are only relevant to 1996. Estimates of yearly seed production would require similar data to be collected in subsequent years. Such studies are necessary before the vegetation dynamics of this ecosystem can be fully understood.

### Soil Seed Density Estimates

Direct counts of *Brachiaria mutica* and *Oryza meridionalis* seeds from soil cores gave an alternate estimate to the sediment germination trial (Appendix E) of the number of seeds of these species within the seed bank. These estimates are tentative however, as the sample size was very small. Many more *Brachiaria mutica* than *Oryza meridionalis* seeds were estimated to be present in the seed banks of their respective vegetation types (Figure 6.5). This finding was lower that the estimated seed production of each species (Figure 6.4) as would be expected. For not all florets develop into seeds and not all seeds make it into the seed bank. Nevertheless, these results indicate that *Brachiaria mutica* seeds are present within the soil in high numbers.

#### Seed Viability Estimates

Germinability was low for all species except *Hymenachne acutigluma* for which 30% of seeds germinated (Figure 6.6). Tetrazolium tests showed that most seeds of *Hymenachne acutigluma*, *Brachiaria mutica* and *Oryza meridionalis* were viable (Figure 6.7). These results indicate that these species have dormancy mechanisms. This study could not identify what type of dormancy mechanisms were present in each species, but dormancy in both *Brachiaria mutica* and *Oryza meridionalis* have been suggested to be a result of impermeable seed coats (MacLean and Grof 1968; Wurm 1996). Information on viability of *Hymenachne acutigluma* and *Pseudoraphis spinescens* has not been published but examination of seeds of these species indicates that dormancy factors other than an impermeable seed coat could be acting on these species as these seeds tend to be soft.

Finding large quantities of mature *Pseudoraphis spinescens* seed was difficult and the failure of seeds of this species to germinate could have been a result of poor seed stock as viability assessment using tetrazolium chloride gave low viability estimates. Tetrazolium chloride only stains living cells and the low viability (as assessed by tetrazolium) indicates that seeds were either, dead before the germination trial commenced, or that they died during the experiment. This species was found to be more abundant than other grass species in the sediment seed bank trial and was also seen germinating in high numbers on top of floating *Salvinia molesta* in the field (personal observation). These observations probably reflect the area of the floodplain that this species dominates (Map 3.1). It is possible that the poor viability of *Pseudoraphis spinescens* seeds are offset by the vast area occupied by this species for potential seed production. In any case, further research into the phenology and seed production of this species is necessary, particularly as it covers the greatest area of the floodplain.

Baskin (1989) noted that seeds with physical dormancy are found in annuals and perennials of predictable habitats and it would appear that dormancy in *Oryza meridionalis* and *Brachiaria mutica* seeds (related to impermeable seed coats (MacLean and Grof 1968; Wurm 1996) conform with this. As *Oryza* 

*meridionalis* is an annual, recruitment from the seed bank is vital to the survival of this species. *Oryza* seeds contain a long stiff awn and it is likely that disturbance caused by annual flooding breaks the awn off seeds, allowing them to imbibe water and germinate.

*Brachiaria mutica* has been found to reproduce very successfully by vegetative means (Anning and Hyde 1987; Cameron 1991) and it is likely that dormancy in seeds of this species are an adaptation to ensure persistence in the event of a disturbance.

The indeterminate growth of *Hymenachne acutigluma* culms give rise to seeds that are dispersed at different times and this could be why *Hymenachne acutigluma* seeds do not have similar dormancy characteristics to *Brachiaria mutica* and *Oryza meridionalis*. This species ensures persistence by producing readily germinable seeds over a range of environmental conditions.





## **General Discussion and Conclusions**

This study has contributed to understanding the dynamics of the vegetation of Kakadu's wetlands by providing information on the grasslands of the Magela floodplain and establishing the impacts of *Brachiaria mutica*, an introduced grass, on this system. *Brachiaria mutica* now covers a considerable area of the Magela floodplain, and although sediments under these areas still contain a species rich seed bank, the areas it has invaded have a reduced species richness in the extant vegetation. In addition, *Brachiaria mutica* has the potential to produce more seeds per unit area than the native grasses and these seeds show some dormancy. It is estimated that a considerable number of *Brachiaria mutica* seeds are present within the seed bank beneath areas that this species now occupies.

Four distinct groups were identified according to species composition and abundance: *Brachiaria* grassland in both wet and dry seasons; *Oryza* grassland in the dry / *Pseudoraphis* grassland in both wet and dry; *Oryza* grassland in the wet season; and *Hymenachne* grassland in both wet and dry seasons.

In general species richness was greatest in the wet season compared to the dry season. *Hymenachne* grassland had the highest species richness followed by *Oryza*, *Pseudoraphis* and *Brachiaria* grasslands. *Hymenachne* grassland decreased in species richness in the wet season whereas both *Oryza* and *Pseudoraphis* grasslands increased in species richness in this season. *Brachiaria* grassland did not differ in species richness between seasons.

Species diversity followed similar trends but the *Pseudoraphis* grassland had higher species diversity than the *Brachiaria* grassland which differed in species diversity between seasons, having higher diversity in the wet season.

Of the grasslands studied, *Pseudoraphis* grassland covered the greatest area of the floodplain followed by *Oryza*, *Brachiaria* and *Hymenachne* grasslands.

The distinct differences observed in extant vegetation of the four grassland communities studied highlights the dynamic nature of vegetation on the Magela floodplain. This was best illustrated by the dramatic change in both species richness and diversity recorded in the *Oryza* grassland between seasons. Similar differences recorded for the *Pseudoraphis* grassland indicate that these

two communities occupy similar niches. This is demonstrated by the dominance of *Pseudoraphis spinescens* in *Oryza* grassland sites during the dry season. However, it would appear that *Pseudoraphis spinescens* is better adapted to survival in deep water as this perennial dominates the deepest areas of the floodplain (Finlayson *et al.* 1990). *Oryza meridionalis* must have a faster growth rate than *Pseudoraphis spinescens* as it is able to dominate the *Oryza* grassland sites during the wet season through recruitment from the seed bank.

The higher species richness and diversity found during the wet season in all communities but the *Hymenachne* grassland suggests that many floodplain species are adapted to flooded rather than dry conditions. The drop in species richness and diversity of the *Hymenachne* grassland during the wet season (from the highest species richness and diversity of any community in both seasons), suggests that extended periods of extremely dry conditions limit the distribution of many taxa on the floodplain. If such extreme drying of the *Oryza* and *Pseudoraphis* grasslands did not occur (as is the case in the *Hymenachne* grassland) more species rich and diverse communities may be expected in these communities during the dry rather than wet season (as was the case in the *Hymenachne* grassland).

Extant vegetation data collected in this study concur with the intermediate disturbance hypothesis illustrated by Sousa (1979) which suggests that frequency and severity of disturbance affects species richness. Further, it is postulated that areas of intermediate disturbance contain the highest number of species. This study found extant vegetation of the *Hymenachne* grassland community to be more species rich compared to other communities. The area occupied by this community undergoes intermediate fluctuations in disturbance (ie. draws down over a longer period) compared to *Oryza* and *Pseudoraphis* grasslands which experience rapid draw down (Finlayson 1991).

Thirty four taxa were found to germinate from sediment samples. Species composition and abundance was found to differ between water regimes by ordination analysis, although cluster analysis was unable to show distinct differences between water regimes for all communities. Samples were grouped according to emergence of a few key species, namely, *Glinus oppositifolius, Nymphaea* spp., *Pseudoraphis spinescens, Cyperus serotinus, Nitella* spp.,

Nymphoides spp., Limnophila australis, Chara spp., Najas spp. and Isoetes coromandelina. Hymenachne grassland samples were grouped from other samples but not between water regimes. *Pseudoraphis* grassland samples were distinguished separately from other samples and also between water regimes. *Oryza* and *Brachiaria* grassland samples were similar and separated only by flooded and moist water regimes.

Seed distribution varied within sediment samples, with the total number of seedlings emerging from *Hymenachne* grassland samples differing between transects. Transect differences were also found in species richness for *Hymenachne*, *Pseudoraphis* and *Oryza* grassland samples. The number of seedlings emerging differed between flooded and moist water regimes. These differences were attributed to large numbers of a few species in flooded samples and the presence of *Glinus oppositifolius*, *Nymphaea* spp., *Pseudoraphis spinescens* and *Isoetes coromandelina* in moist samples.

Species richness was higher in *Oryza* and *Pseudoraphis* grassland samples that were flooded compared to those under a moist water regime. This treatment difference was also found when grasslands were compared (ie. flooded treatments were more species rich than moist treatments overall). *Brachiaria* and *Hymenachne* grassland sediments contained more species rich seed banks than *Pseudoraphis* and *Oryza* grassland sediments. Samples from the latter two communities under a moist water regime had the lowest species richness (compared to other samples) while *Brachiaria* grassland samples under the same water regime had the highest species richness of all samples.

Germination from sediment seed banks of the grassland communities illustrated the diversity of species on the floodplain. Sediments were found to contain many seeds of aquatic taxa, reflecting their abundance on the floodplain during the wet season and/or high seed production of these taxa. Most aquatic species require seeds to ensure persistence during dry periods particularly in tropical environments where the flooding/drying cycle is seasonal (Gopal 1986). Data generated by this study support this hypothesis and although few tropical wetland seed bank studies have been conducted, studies of other wetland types (that undergo similar cyclic fluctuations in water depth) have found similar results (Zedler 1987; Grillas *et al.* 1993). Several studies

that have used flooded and moist water regimes to assess germination from seed banks, including the previous study on the Magela floodplain, found species richness to be greater in moist treatments compared to flooded treatments (Smith and Kadlec 1983; Finlayson *et al.* 1990; Schneider 1994). In contrast this study found flooded samples to be more species rich. This could reflect the unusually high rainfall in the wet season prior to collection of samples for this study. Many aquatic taxa may have been present in large numbers during the flooded period and subsequently samples contained propagules of many aquatic taxa in high numbers. More detailed comparisons of the grassland seed banks on the Magela floodplain between 1984 and 1996 further illustrate the variability in seed bank vegetation of these communities.

Comparisons of seed bank data from 1984 to 1996 showed species richness of 1984 *Oryza* grassland samples under a moist water regime to be higher than equivalent samples in 1996 (moist *Brachiaria* and *Oryza* grassland samples). Comparisons between the proportions of individual species emerging from sediment samples in each year gave varying results.

Given the high numbers of seedlings of aquatic taxa emerging from samples in 1996, it was expected that a greater proportion of these taxa would have been found to emerge compared to 1984 data. This was the case for many aquatic taxa. However, differences in duration between studies may explain the varying results for other taxa, as the previous study was conducted over ten months compared to the 3 1/2 month duration of germination for this study.

Seed banks may reflect seed production on the floodplain which is, in turn, affected by rainfall and water flow patterns. The seasonal variation in extant vegetation on the floodplain makes long term predictions of vegetation change from seed bank data difficult. Nevertheless, seed bank data can provide valuable information on changes that have occurred on the Magela floodplain, as illustrated by the similarities found between *Brachiaria* and *Oryza* grassland seed banks.

Species composition and abundance of extant vegetation was found to be poorly correlated with seed banks. This was due to the low frequency of aquatic species recorded in extant vegetation compared to high numbers of other taxa emerging from sediment samples (mentioned above). This result

was expected as it was thought that sediment samples would contain taxa from all seasonal cycles of extant vegetation on the floodplain, in addition to seeds of extant vegetation from previous years.

This illustrates the important role that seed banks play in grasslands on the Magela floodplain particularly for aquatic taxa. Additionally the small number of seeds of the dominant species in the seed banks of these communities suggests that vegetative reproduction plays a major role in these grassland communities. The role of vegetative reproduction of grass species in vegetation dynamics on the Magela floodplain was not quantified in this study, however, it is suggested that the contribution of this factor, in structuring grassland communities, varies from year to year.

Potential seed production of the dominant grass species were estimated to differ greatly. *Brachiaria mutica* had the highest potential seed production followed by *Hymenachne acutigluma*. *Oryza meridionalis* and *Pseudoraphis spinescens* were both estimated to have similar seed production and this was much lower than the former species. *Pseudoraphis spinescens* was found to have the lowest seed viability, although this was greater than 50%. *Hymenachne acutigluma, Brachiaria mutica* and *Oryza meridionalis* all had high seed viability. All species exhibited some seed dormancy which was most pronounced in seeds of *Pseudoraphis spinescens*, *Oryza meridionalis* and *Brachiaria mutica*. Dormancy in seeds of the latter two species appear to be related to impermeable seed coats.

The low numbers of grass seeds found to germinate from sediment samples could reflect the small sediment sample size used, as estimated seed production was high, and both *Brachiaria mutica* and *Oryza meridionalis* were estimated to contain considerable seed banks from soil core seed counts. However, seed bank estimates were tentative due to the small core size. Factors such as poor seed set or failure of species to flower in years leading up to this study could contribute to the low seed numbers found in the soil seed bank. Alternatively predation could be particularly high on seeds of grass species. Seed dormancy exhibited by the four grass species indicates that these species all utilise the seed bank as a source of recruitment. *Oryza meridionalis* being annual relies entirely on the seed bank to persist over the

dry season. The other three species probably use seeds to ensure persistence and allow dispersal to potentially inhabitable sites.

### Brachiaria mutica on the Magela floodplain

It was evident that communities with higher species richness tended to occur in the wet rather than the dry season. The lower species richness and diversity found in the extant vegetation of the *Brachiaria* grassland illustrates the reduced species richness experienced by this ecosystem following the establishment of *Brachiaria mutica*. The increase in area covered by the *Brachiaria* grassland and corresponding decrease in area of the *Oryza* grassland from 1991 to 1996 indicates that *Brachiaria mutica* is primarily invading the latter community. This change appears to be too great to be attributed to seasonal variation alone.

No detailed data on the habitat and establishment requirements of Brachiaria mutica have been published, although it is reported to be limited by water depth (to 50-60cm) (Calder 1982; Anning and Hyde 1987). However, Brachiaria mutica was observed in areas that are inundated by water to depths greater than 60cm in this study. Further, Brachiaria mutica was observed on the floodplain fringes around trees and shrubs, where it is assumed that cover from vegetation provides suitable conditions for establishment. This could indicate that invasion of the remnant Oryza grassland will occur in the short term. Brachiaria mutica was not observed to have invaded the Hymenachne grassland, nevertheless it is suggested that this process may be occurring over a more protracted time scale (compared to invasion of the Oryza grassland over 7 years) given that Hymenachne acutigluma, the species that dominates this community, is perennial. Data published by Calder (1982) suggests that Brachiaria mutica may not be able to competitively exclude Hymenachne acutigluma in areas inundated by more than one metre of water as Brachiaria mutica was found to have lower survival from cuttings than Hymenachne acutigluma under these conditions.

Finlayson *et al.* (1989) noted that considerable shifts in species composition of the *Oryza* grassland occur, with *Hygrochloa aquatica*, another annual species, being displaced by *Oryza meridionalis*. This was attributed to yearly variation in rainfall patterns and flow regimes (Finlayson *et al.* 1989). It is

probable that these two species occupy the same niche in different years, and as such the species that dominates the area in any particular year is determined by rainfall of previous years. *Brachiaria mutica* may have disrupted this cycle (as it is perennial) and the absence of *Hygrochloa aquatica* seeds in the grassland seed banks suggests that this species is being excluded from the study site area, particularly as seeds of this species were found in sediments in 1984.

Changes in species composition and abundance in extant vegetation, between seasons, does not display a clear relationship with the seed bank. The species rich seed bank of the *Brachiaria* grassland indicates that a diverse plant community still exists in this area. Therefore, the restoration of areas invaded by *Brachiaria mutica* may still be possible.

### Further Research

This study has identified several areas that require more detailed research both to help in understanding the vegetation dynamics of freshwater tropical floodplains and to aid in the management of *Brachiaria mutica* on the Magela floodplain.

More detailed mapping of the *Brachiaria* grassland communities on the Magela floodplain are required. For example, satellite infestations could be marked out and their growth observed during different seasons and among years. In addition, recruitment from the seed bank should be recorded. Such a study could provide detailed information on the growth and phenology of this species and an accurate assessment of the methods by which it invades would then be possible (ie. vegetative growth or recruitment from the seed bank or both). This information in turn could help to indicate which communities this species has the potential to invade.

Several varying seed bank experiments could be conducted to provide a more detailed assessment of the vegetation of these grasslands. They include germinating the same samples over successive years in order to give a more accurate account of seed numbers within the soil and identify the time period required for depletion of the seed bank. Different samples could also be collected in successive years to gain a better understanding of the role seed banks play in structuring extant vegetation on the Magela floodplain.

Observations of seedling emergence from field plots would also aid in determining the role seed banks play.

Seed exclusion and seed rain experiments could be conducted in the field to investigate the variability of seed production of different species on the floodplain and allow estimates of seed input into the soil of these grasslands to be made.

One area that requires clarification is the discrepancy between the low numbers of grass seeds found to emerge from sediment seed banks and high potential seed production estimated from culm and floret counts of grass species. Predation could be one reason for such discrepancies and seed bait experiments could be conducted to establish the role of predation in grassland dynamics. Such an experiment would quantify seed loss due to predation and may identify the predators responsible for this loss.

A seed burial experiment of *Brachiaria mutica* seeds would provide essential information to managers, as such experiments would allow the longevity of *Brachiaria mutica* seeds to be assessed. It is suggested that *Brachiaria mutica* seed would be buried and then replicates exhumed after different time periods for viability assessment by germination and tetrazolium chloride. This experiment would have to be conducted over a number of years and large numbers of seeds would be necessary, particularly if seed predation is found to occur.

This study has highlighted the urgent need for an assessment of the role that vegetative reproduction plays in grassland communities on the Magela floodplain. Such a study would provide valuable information by quantifying vegetative reproduction and adding to the understanding of vegetation dynamics on the floodplain. This would allow the contributions made by both the seed bank and extant vegetation (vegetative reproduction) to the distribution of plant species on the floodplain to be compared. A study of this type would contribute substantially to the effective management of *Brachiaria mutica*, given that it reproduces vegetatively.

Additional studies on competition between native grasses and *Brachiaria mutica*, particularly *Hymenachne acutigluma*, would provide valuable information on the potential of *Brachiaria mutica* to invade and competitively

exclude native grasses other than *Oryza meridionalis*. These studies should assess competition between both seedlings, cuttings and adult plants. In addition, it is recommended that they be conducted using a number of water depth treatments, particularly between 60cm and 1.5m, as this factor has been shown to influence establishment of *Brachiaria mutica* from cuttings (Calder 1982). It is also recommended that duration of flooding be assessed. Such experiments would establish competitiveness of the grasses examined and enable predictions of the potential spread of *Brachiaria mutica* to be made according to water depths and inundation period, thereby assisting managers by allowing areas of possible infestation (areas with appropriate water depths) to be identified and surveyed.

As the Magela floodplain extends into a saline estuary, the establishment of salinity tolerance limits of *Brachiaria mutica* would also be valuable. Such an experiment would involve germinating seeds and growing cuttings under a range of different salinity conditions. These data would allow for predictions of the potential spread of *Brachiaria mutica* into saline habitats to be made.

*Brachiaria mutica* was noted to re-shoot vigorously after being burnt (personal observation). Determination of the response of this species to fire would enable improved assessments of the changes that occur under different fire regimes. Such data is relevant as fire is currently used as a management tool on the floodplain.

#### Management of the Magela floodplain

It is likely that the observed vegetation both in the seed bank and extant vegetation is an outcome of previous management in the area. That is, removal of feral buffalo (*Bubalus bubalis*) from the floodplain may have lead to the rapid invasion of *Brachiaria mutica*, which was previously limited by selective grazing pressure. This would explain the absence of *Brachiaria* grassland from vast areas until recent times. Similarly, a more frequent fire regime on the floodplain, as has been adopted in recent years, appears to favour *Brachiaria mutica* which is noted to re-shoot vigorously after being burnt.

Seed bank data are essential to the management of vegetation on the Magela floodplain. The large seed bank of *Brachiaria mutica* estimated under areas already invaded by this species must be considered and managed accordingly.

NI C

The demonstrated dormancy of *Brachiaria mutica* seeds indicates that management strategies need to be long term.

It is necessary to devise and implement appropriate management strategies now if further degradation of vegetation on the Magela floodplain is to be prevented. Due consideration should be given to information on the seed banks, as well as seed production and viability, of the floodplain grasslands when developing management strategies. Vegetative reproduction must also be considered. Effective control of *Brachiaria mutica* can only be achieved by utilising knowledge of the life history of this species. It has been suggested that an effective management strategy for Brachiaria mutica would involve utilising the wet season flood to 'drown it out' (Schultz 1996). This may be achieved by using fire or herbicides on Brachiaria mutica just prior to flooding. If inundation occurs rapidly, plants may not be able to re-shoot fast enough to stay above the water level. This strategy may be effective in controlling extant vegetation, but does not account for the seed bank. Provided that plants are recruited from the seed bank during the wet season, and are removed before flowering and set seed, the application of this strategy in successive years would result in depletion of *Brachiaria mutica* seeds from the seed bank:

A further consideration is that the occurrence of *Brachiaria mutica* under trees and shrubs around the floodplain edge may act as a seed source. Therefore total eradication of this invasive species from the Magela floodplain would be almost impossible and impractical. Rather, management should adopt an approach of minimising the spread of *Brachiaria mutica* to areas not presently invaded, by targeting isolated patches in new areas. Further, management should attempt to reduce the spread of *Brachiaria mutica* in presently infested areas via the application of a management strategy such as that outlined above.
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# Appendix A

Description of mapping units used for mapping the Magela floodplain in June 1996 (descriptions of the four grassland mapping units are given in Chapter 2).

## Melaleuca open woodland

These areas consisted of scattered *Melaleuca leucadendra* (cover <10%) with a mixture of understorey species. These were usually the same as those in adjacent areas of the floodplain and included the grasses *Hymenachne acutigluma*, *Oryza meridionalis* and *Pseudoraphis spinescens* with *Nelumbo nucifera, Nymphoides* spp., *Nymphaea* spp. also present (Finlayson *et al.* 1989). This mapping unit covered 1511 ha, 17% of the total area mapped in 1996.

## Melaleuca Open Forest/Woodland

This mapping unit occurred predominantly around the margins of the floodplain and in the southernmost section of the area mapped. It covered 819 ha, 9% of the total area mapped in 1996, and was comprised of areas dominated by one or more Melaleuca species (cover 10-70%). These included Melaleuca viridiflora, Melaleuca symphyocarpa and Melaleuca leucadendra. The understorey contained a wide variety of species including Brachiaria mutica, Hymenachne acutigluma, Oryza meridionalis, Pseudoraphis spinescens, Coldenia procumbens, Dentella Ecliptica prostrata. dioeca. Glinus oppositifolius, Heliotropium indicum, Phyla nodiflora, Euphorbia vachellii, Fimbristylis spp., Nymphaea spp. and Nymphoides spp. (Finlayson et al. 1989).

### Nelumbo swamp

The Nelumbo swamp covered 1466 ha (16%) of the area mapped in 1996. It occurred mainly in the western plain section of the floodplain and was dominated by large patches of *Nelumbo nucifera*. In areas that were not so densely populated, *Nymphoides* spp., and floating mats of *Hymenachne acutigluma* with *Ludwigia adscendens* and *Cyperus platystylis* were common (Finlayson *et al.* 1989).

### *Hymenachne/Eleocharis* swamp

This vegetation type covered 572 ha (6%) scattered in the northern section of the area mapped in 1996 and it consisted of a variety of sedges including *Eleocharis dulcis* and *Eleocharis sphacelata* co-occurring with *Hymenachne acutigluma* and in some cases with *Oryza meridionalis*. *Nymphaea* spp. and *Nymphoides* spp. were also common in this community (Finlayson *et al.* 1989).

### Mixed Grassland/Sedgeland

This mapping unit was found to cover a small area (89 ha, 1%) in the south in 1996. It contained a mixture of species including the grasses *Hymenachne acutigluma*, *Oryza meridionalis*, and *Pseudoraphis spinescens*. The sedges *Eleocharis dulcis, Eleocharis sphacelata, Cyperus platystylis* and the herbs *Ludwigia adscendens, Ipomoea aquatica* and *Nymphoides* spp. were also found (Finlayson *et al.* 1989).

## **Terrestrial Vegetation**

This mapping unit was not extensively examined, but the species occurring within it include the trees *Eucalyptus papuana*, *E. miniata*, *E. alba*, *Alstonia actinophylla*, *Syzigium suborbiculare* (Finlayson *et al.* 1989).

# Appendix B

The Disk supplied contains two text files; germ.aso and vg120.aso. These files are the association matricies generated by PATN (Belbin 1993b).

## Appendix C

Significant differences found in species richness and diversity of quadrat data collected from a vegetation survey in four grassland communities on the Magela floodplain in dry and wet seasons (1995-1996)

Table C.1 LSD test on species richness of nested quadrat data collected from four grassland communities on the Magela floodplain during wet and dry seasons of 1995-96 (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands). (\*\* = p < 0.01, \*\*\* = p < 0.001).

	<i>Oryza</i> grassland	Hymenachne grassland	Pseudoraphis grassland
Brachiaria grassland	< 0.001***	< 0.001***	0.441
Oryza grassland	\$	< 0.001***	.002**
Hymenachne grassland		\$	< 0.001***

Table C.2 Results from two factor ANOVA (LSD test) showing differences in mean species richness between *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain for dry and wet seasons, 1995-96 (\* = p < 0.05, \*\*\* = p < 0.001).

	Bm (Wet)	Om (Dry)	Om (Wet)	Ha (Dry)	Ha (Wet)	Ps (Dry)	Ps (Wet)
Bm (Dry)	0.068	0.056	< 0.001***	< 0.001***	<0.001***	0.547	< 0.001***
Bm (Wet)	\$	0.953	< 0.001***	< 0.001***	0.012*	0.016*	0.093
Om (Dry)		\$	< 0.001***	< 0.001***	0.013*	0.013*	0.099
Om (Wet)			<b>\$</b>	< 0.001***	0.399	< 0.001***	0.079
Ha (Dry)				Ŷ	<0.001***	< 0.001****	< 0.001***
Ha (Wet)					\$	< 0.001***	0.363
Ps (Dry)						\$\$	< 0.001***

Table C.3 LSD test on species diversity (Shannon Index) of nested quadrat data collected from four grassland communities on the Magela floodplain during wet and dry seasons of 1995-96 (*Brachiaria*, *Oryza*, *Hymenachne* and *Pseudoraphis* grasslands). (\* = p < 0.05, \*\*\* = p < 0.001).

	<i>Oryza</i> grassland	<i>Hymenachne</i> grassland	Pseudoraphis grassland
Brachiaria grassland	< 0.001***	< 0.001***	0.039*
Oryza grassland	\$	< 0.001***	< 0.001***
Hymenachne grassland		\$	< 0.001***

Table C.4 Results from two factor ANOVA (LSD test) showing differences in species diversity (Shannon Index) between *Brachiaria* grassland (Bm), *Oryza* grassland (Om), *Hymenachne* grassland (Ha) and *Pseudoraphis* grassland (Ps) on the Magela floodplain for dry and wet seasons, 1995-96 (\* = p < 0.05, \*\* = p < 0.01, \*\*\* = p < 0.001).

	Bm (Wet)	Om (Dry)	Om (Wet)	Ha (Dry)	Ha (Wet)	Ps (Dry)	Ps (Wet)
Bm (Dry)	0.005**	< 0.001***	< 0.001***	< 0.001***	<0.001***	0.327	< 0.001***
Bm (Wet)	45	0.153	< 0.001***	< 0.001***	<0.001***	< 0.001***	< 0.001***
Om (Dry)		₿	< 0.001***	< 0.001***	0.010*	< 0.001***	0.014*
Om (Wet)			\$	0.008**	0.199	< 0.001***	0.148
Ha (Dry)				÷	<0.001***	< 0.001***	< 0.001***
Ha (Wet)					Ð	< 0.001***	0.884
Ps (Dry)						\$	< 0.001***

## Appendix D

Significant differences found within and among grassland sediment samples collected from four grasslands on the Magela floodplain (1995) and germinated under flooded and moist water regimes.

Table D.1: LSD test on species richness of seedlings emerging from samples collected along three transects in a *Oryza* grassland on the Magela floodplain (Nov 95) and germinated under two treatments (T = transect, \* = p < .05, \*\* = p < .01)

	T5	T6
T4	0.477	0.018*
T5	<i>¢</i>	0.003**

Table D.2: LSD test on total number of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two treatments (log(x+1) transformed data)(T = transect, \* = p < 0.05, \*\* = p < 0.01)

	Т8	Т9
Τ7	0.433	0.002**
T8	¢	0.014*

Table D.3: LSD test on interactions of total number of seedlings (log(x+1) transformed) emerging from samples collected in a *Hymenachne* grassland on the Magela floodplain (Nov 95) with germination under two water regimes (T = transect, M = moist, F = flooded; \*\*\* = p < 0.001)

[	T7 M	T8 F	T8 M	T9 F	Т9 М
T7 F	0.479	0.281	0.463	< 0.001***	0.422
T7 M	¢	0.704	0.979	< 0.001***	0.923
T8 F		<u>به</u>	0.723	< 0.001***	0.777 <sup>•</sup>
T8 M		·	₩.	< 0.001***	0.943
T9 F				&	< 0.001***

Table D.4: LSD test on species richness of seedlings emerging from samples collected along three transects in a *Hymenachne* grassland on the Magela floodplain (Nov 95) and germinated under two treatments (T = transect, \* = p < 0.05)

	T8	Т9
T7	0.046*	0.013*
Т8	Ŕ	0.565

Table D.5: LSD test on species richness of seedlings emerging from samples collected along three transects in a *Pseudoraphis* grassland on the Magela floodplain (Nov 95) and germinated under two treatments (\*\* = p < 0.01)

	T11	T12
T10	0.009**	0.065
T11	\$	0.382

Table D.6: LSD test on species richness of seedlings emerging from samples collected in four grassland vegetation types on the Magela floodplain (Nov 95) and germinated under two treatments (Bm = Brachiaria grassland, Ha = Hymenachne grassland, Om = Oryza grassland, Ps = Pseudoraphis grassland; \*\* = p < 0.01, \*\*\* = p < 0.001)

	Om	Ha	Ps
Bm	<0.001***	0.163	< 0.001***
Om	\$	0.006**	0.899
На		\$	0.008**

Table D.7: LSD test on interactions of species richness of seedlings emerging from samples collected in four grassland vegetation types on the Magela floodplain (Nov 95) with germination under two water regimes (Bm = *Brachiaria* grassland, Ha = *Hymenachne* grassland, Om = *Oryza* grassland, Ps = *Pseudoraphis* grassland, M = moist, F = flooded; \* = p < 0.05, \*\* = p < 0.01, \*\*\* = p < 0.001)

	Bm M	Ha F	Ha M	Om F	Om M	Ps F	Ps M
Bm F	0.107	0.719	1.000	1.000	< 0.001***	0.589	< 0.001***
Bm M	₩	0.049*	0.107	0.107	< 0.001***	0.032*	< 0.001***
Ha F		Ŷ	0.719	0.719	< 0.001***	0.857	0.002**
Ha M			Ę\$	1.000	< 0.001***	0.589	< 0.001***
Om F				\$	< 0.001***	0.589	< 0.001***
Om M					₩\$	< 0.001***	0.472
Ps F						<b>₽</b>	0.002**

# Appendix E

Table E.1 Seedlings estimated to emerge from  $1m^2$  of grassland communities on the Magela floodplain in 1984 and 1996 (1984 data from Finlayson *et al.* (1990).

Таха	Treatment		Nu	mber of se	eedlings calculated per square metre			
		Oryza 1984	Brachiaria 96	Oryza 96	Pseudorephis 84	Pseudorephis 96	Hymenachne 64	Hymenachne 96
Blyxa aubertii	F	NA NA	0	0	NA NA	0 71±41	NA NA	0
Brachiaria mutica	M F	NA NA	121 ± 40 0	0 0	NA NA	0	NA NA	10 ± 10 0
Cyperus aquatilis	M F	NA NA	0 Q	20 ± 14 0	NA NA	0 0	NA NA	U O
Cyperus piatystylis	M F	NA NA	10 ± 10 0	0	NA NA	0 0	NA NA	414 ± 282 1313 ± 708
Cyperus serotinus	M	NA NA	10 ± 10 10 ± 10	10 ± 10 0	NA NA	0 0	NA NA	2182 ± 858 960 ± 480
Cyperus digitatus	M F	0 0	0	0 0	121 ± 56 30 ± 30	0	393 ± 242 967 ± 363	0
Ceratopteris thallctroides	M F	0 483 ± 166	182 ± 102 71 ± 44	808 ± 527 929 ± 634	30 ± 30 0	0 0	0 0	20 ± 14 0
Chara spp.	M F	NA NA	0 1222 ± 321	0 455 ± 147	NA NA	0 71±49	NA NA	0 354 ± 134
Coldenia procumbens	M F	NA NA	20 ± 14 0	61 ± 36 0	NA NA	0 0	NA NA	91 ± 57 0
Commelina lanceolata	M F	NA NA	0 0	20 ± 14 0	NA NA	0 0	NA NA	o o
Dentella diceca	M F	NA NA	0	Ç O	NA NA	0 0	NA NA	293 ± 179 0
Ecliptica prostrata	M F	NA NA	0	0	NA NA	10 ± 10 0	NA NA	202 ± 73 141 ± 52
Eleocharis spp.	M F	272 ± 212 0	242 ± 86 182 ± 73	101 ± 38 101 ± 44	30 ± 30 0	606 ± 574 232 ± 149	0 0	0 10 ± 10
Eriocaulon setaceum	M F	2145 ± 848 1602 ± 151	40 ± 23 10 ± 10	141 ± 65 192 ± 56	0 0	a o	0 60 ±36	0
Euphorbia vachelili	M F	NA NA	0	0 0	NA NA	0 0	NA NA	10 ± 10 0
Fimbristylis spp.	M F	0	30 ± 30 0	61 ± 44 10 ± 10	786 ± 348 0	0 0	1571 ±589 181 ±110	81±57 51±51
Glinus oppositifolius	M F	30 ± 30 30 ± 30	20 ± 20 0	30 ± 16 0	2659 ± 680 242 ± 106	8091 ± 2958 333 ± 161	604 ±136 30 ±30	919±561 0
Hellotroplum indicum	M F	725 ± 212 0	111 ± 45 0	778 ± 245 0	60 ± 36	0	876 ±348 60 ±36	10 ± 10 0
Hydrilla verticillata	M F	NA NA	0 0	0 0	NA NA	0 0	NA NA	0 51 ± 35
Hygrochio <b>a a</b> quatica	M F	725 ± 91 181 ± 147	0 0	0 0	0	0 0	0	0 0
Hymenachne acutigiuma	M F	0 0	0 0	0	0	0 0	242 ±21 91 ±30	384 ± 135 61 ± 32
lsoetes spp.	M F	1450 ± 438 121 ± 91	2404 ± 977 141 ± 48	3141 ± 1258 374 ± 125	0 0	10 ± 10 0	0	0 0
Ludwigia adscendens	M F	NA NA	0	0 0	NA NA	0 0	NA NA	0 91 ± 39
Ludwigla perennis	M F	NA NA	0	10±10 10±10	NA NA	0	NA NA	o o
Limnophila spp.	M F	1179 ± 1027 544 ± 212	444 ± 110 877 ± 177	192 ± 75 404 ± 114	0 0	0 0	ů O	0
Maldenia rubra	M F	60 ± 36 635 ± 105	111 ± 48 293 ± 83	81 ± 36 303 ± 44	0 30 ± 30	0 0	0 0	141 ± 79 81 ± 25
Najas spp.	M F	181 ± 75 0	30 ± 22 657 ± 168	0 404 ± 69	222 ± 151 1238 ± 393	20 ± 20 30 ± 22	30 ±30 1450 ±196	61 ± 61 444 ± 181
Nitella sp.	M F	NA NA	608 ± 251 4273 ± 492	30 ± 30 1394 ± 227	NA NA	20 ± 20 1141 ± 386	NA NA	141 ± 111 1040 ± 368
Nymphaea spp.	M F	0 0	263 ± 67 192 ± 56	20 ± 14 61 ± 25	846 ± 332 423 ± 91	1283 ± 279 889 ± 149	212 ±181 1934 ±438	727 ± 222 909 ± 186
Nympholdes spp.	M F	NA NA	283 ± 74 152 ± 59	51 ± 32 111 ± 72	NA NA	61 ± 41 131 ± 71	NA NA	1556 ± 487 576 ± 168
Oldenlandia sp.	M F	NA NA	0	10 ± 10 0	NA NA	0 10 ± 10	NA NA	10 ± 10 0
Oryza meridionalis	M F	272 ± 56 0	10 ± 10 10 ± 10	20 ± 14 10 ± 10	0	C Q	60 ±30 0	0
Persicaria spp.	M F	NA NA	0	0	NA NA	0 0	NA NA	81 ± 33 10 ± 10
Phyla nodiflora	M F	NA NA	0	40 ± 40 0	NA NA	0	NA NA	0
Pseudoraphis spinescens	M F	0 0	20 ± 14 0	172 ± 57 0	6316 ± 3536 604 ± 212	1333 ± 310 71 ± 33	11060 ±2040 1813 ±544	1182 ± 421 71 ± 36
Utricularia spp.	M F	0 0	10 ± 10 222 ± 99	0 121 ± 68	60 ± 60 393 ± 212	20 ± 20 909 ± 415	30 ±30 363 ±106	91 ± 46 263 ± 79

## Appendix F

Significant differences found in production of flowering culms (m<sup>-2</sup>), florets per inflorescence, germination of seeds, viability of ungerminated seeds and overall viability of seeds of four grass species that dominate different grassland communities on the Magela floodplain.

Table F.1: Results of LSD test (p values) on the number of flowering culms  $m^2$  recorded for *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* recorded in their respective vegetation types during peak biomass production (May 1996) (\*\*\* = p < 0.001).

	Oryza	Hymenachne	Pseudoraphis
	meridionalis	acutigluma	spinescens
Brachiaria mutica	< 0.001***	< 0.001***	< 0.001***
Oryza meridionalis	₩	< 0.001***	< 0.001***
Hymenachne acutigluma		\$	0.431

Table F.2: Results of LSD test (p values) on the number of florets per inflorescence recorded for *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* during peak biomass production (May 1996) (\*\*\* = p < 0.001).

	Oryza meridionalis	Hymenachne acutigluma	Pseudoraphis spinescens
Brachiaria mutica	< 0.001***	< 0.001***	< 0.001***
Oryza meridionalis	\$	< 0.001***	< 0.001***
Hymenachne acutigluma		÷\$	< 0.001***

Table F.3: Results of LSD test (p values) on percentage germination of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds placed in a growth cabinet for three weeks (\*\*\* = p < 0.001).

	Oryza meridionalis	Hymenachne acutigluma	Pseudoraphis spinescens
Brachiaria mutica	0.396	< 0.001***	0.805
Oryza meridionalis	5	< 0.001***	0.276
Hymenachne acutigluma		\$	< 0.001***

Table F.4: Results of LSD test (p values) on viability assessment (using tetrazolium chloride) of remaining ungerminated *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds after three weeks in a growth chamber (\*\*\* = p < 0.001).

	Oryza meridionalis	Hymenachne acutigluma	Pseudoraphis spinescens
Brachiaria mutica	0.155	0.071	< 0.001***
Oryza meridionalis	Ŷ	< 0.01***	< 0.001***
Hymenachne acutigluma		\$	< 0.01***

## Appendix F

Table F.5: Results of LSD test (p values) on overall viability (germination + tetrazolium chloride tests) of *Brachiaria mutica*, *Oryza meridionalis*, *Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds. (\* = p < 0.05,\*\*\* = p < 0.001).

	Oryza meridionalis	Hymenachne acutigluma	Pseudoraphis spinescens
Brachiaria mutica	0.116	0.476	< 0.001***
Oryza meridionalis	\$	0.028*	< 0.001***
Hymenachne acutigluma		÷\$	< 0.001***

## Appendix G

List of taxa found in this study either emerging from sediment samples or

present in the extant vegetation.

Azolla pinnata R. Br. Blyxa aubertii Rich. Brachiaria mutica (Forsskal) Stapf Cyperus aquatilis R. Br. C. platystylis R. Br. C. serotinus Rottb. Ceratopteris thalictroides (L.) Brongn. Chara spp. Coldenia procumbens L. Commelina lanceolata R. Br. Dentella dioeca Airy Shaw Eclipta prostrata (L.) L. Eleocharis spp. Eriocaulon setaceum L. Euphorbia vachellii Hook. & Arn. Fimbristylis spp. Glinus oppositifolius (L.) R.DC. Heliotropium indicum L. Hydrilla verticillata (L.f.) Royle Hygrochloa aquatica Lazarides Hymenachne acutigluma (Steudel) Gilliland Ipomoea aquatica Forsskal Isoetes coromandelina L. f. Ludwigia adscendens (L.) H. Hara L. perennis L. Limnophila australis Wannan & J. T. Waterh. Maidenia rubra Rendle Merremia gemella (N. Burman) H Hallier Najas spp. Nelumbo nucifera Gaertner Nitella spp. Nymphaea spp. Nymphoides spp. Oldenlandia sp. Oryza meridionalis N. Ng Persicaria sp. Phyla nodiflora (L.) E. Greene Pseudoraphis spinescens (R. Br.) Vick. Salvinia molesta D. Mitch. Utricularia spp.