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 generate good comparative data among species (Moore 1985). Tetrazoluim 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_1: What is the potential seed production m^{-2} of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types?

Q_2: What is the density of *Brachiaria mutica* and *Oryza meridionalis* seeds in the seed bank?

Q_3: What is the viability of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds?

The hypotheses generated to test these questions are:

H_1: There is no difference in the numbers of flowering culms m^{-2} produced by *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types.

H_2: There is no difference in the number of florets per inflorescence produced by *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens.*

H_3: 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_4: 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_5: 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^2 quadrats gave similar coefficients of variance as 4m^2 quadrats (Figure 6.1). Consequently, 1m^2 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).

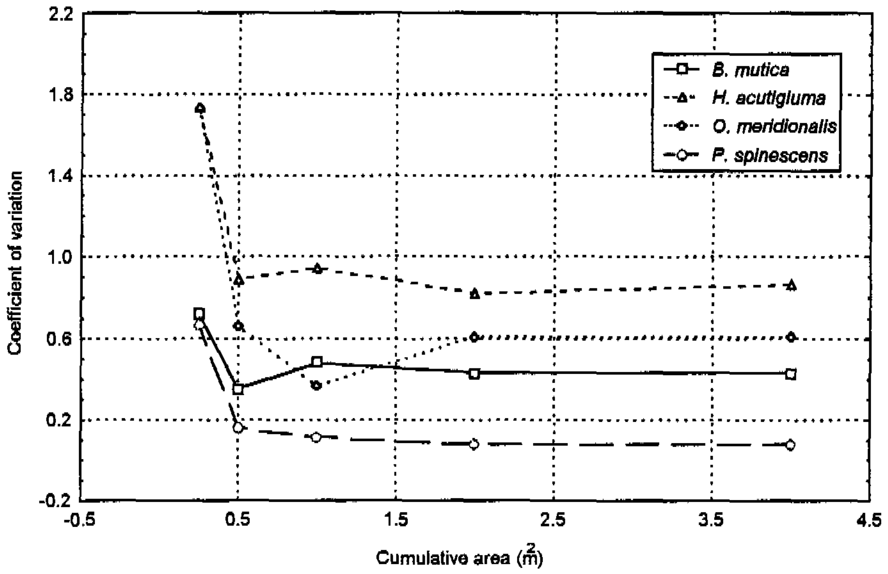


Figure 6.1 Coefficient of variation (standard deviation / mean) of the number of flowering culms recorded for each species with increasing sample area during peak biomass production in May 1996.

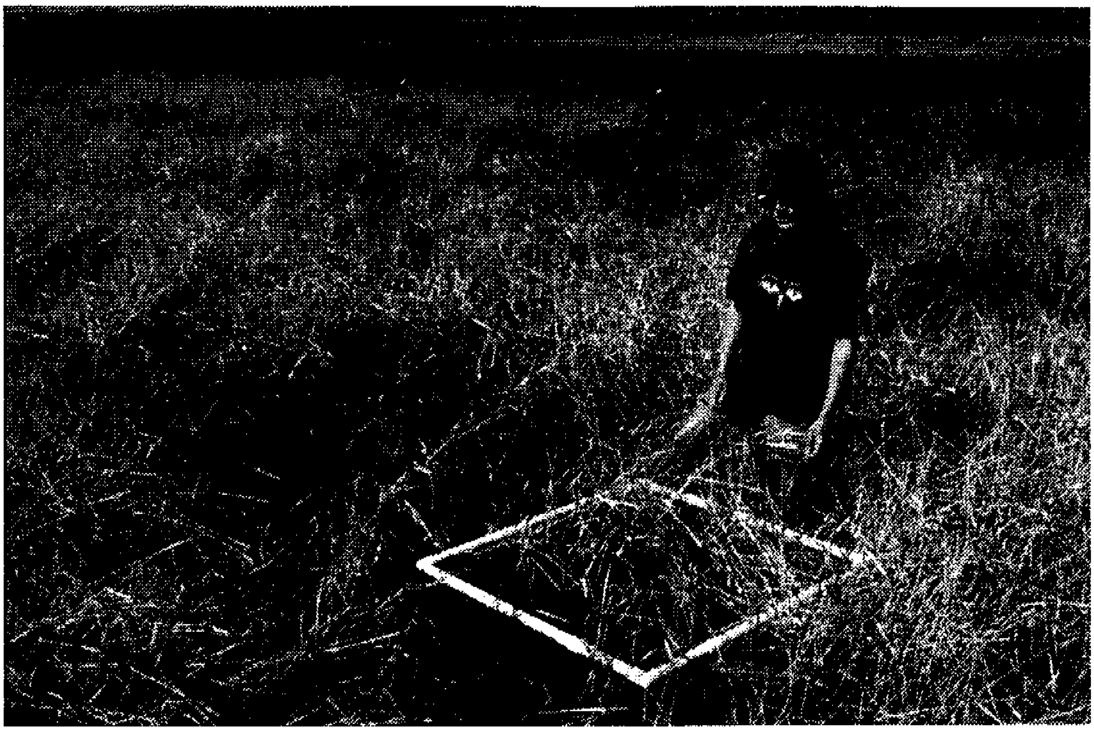


Plate 6.1 Flowering culms were counted within a $1m^2$ floating quadrat (this quadrat is located in the *Oryza* grassland).

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^{-2} 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 connecting these was stained (note: an uninterrupted connection between apices was necessary) (Moore 1985). A stereo microscope was needed to make these observations.

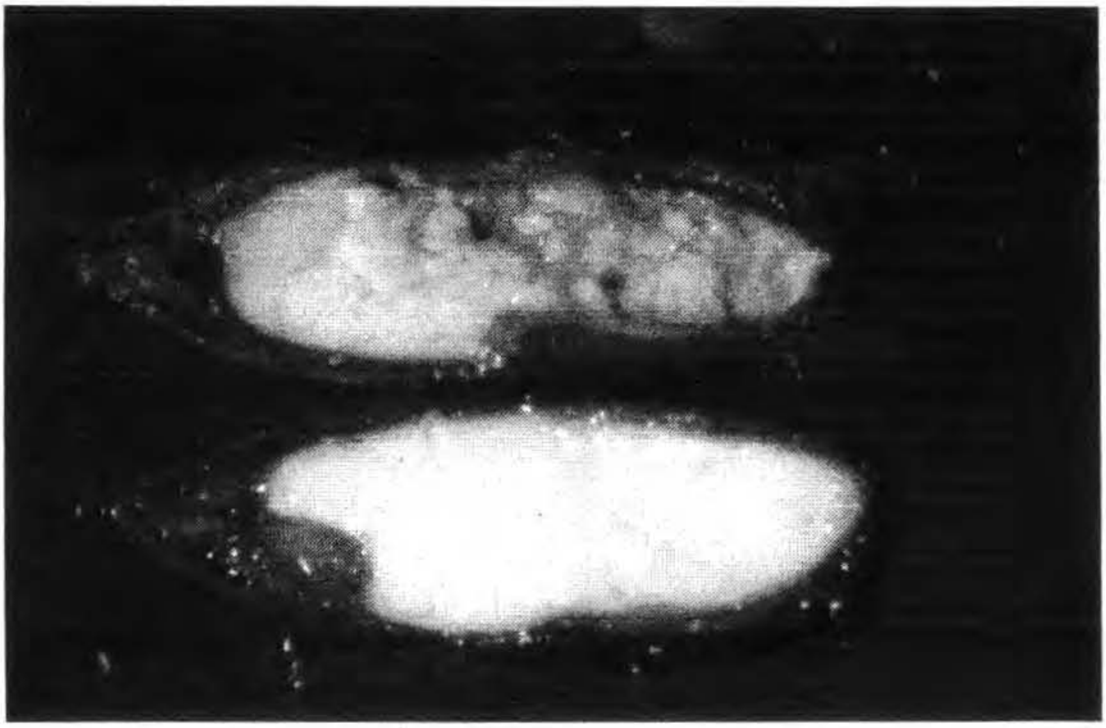


Plate 6.2 Seed viability was assessed using tetrazolium chloride, this plate shows two *Oryza meridionalis* seeds after staining; bottom seed is viable as indicated by the stained embryo, top seed is dead and embryo failed to stain.

Statistical Analysis

Differences in flowering culms m^{-2} 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_1: What is the potential seed production m^{-2} of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types?

H_1: There is no difference in the numbers of flowering culms m^{-2} produced by *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* in their respective vegetation types.

H_2: 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^{-2} of each species, in their respective vegetation types, were found (Table 6.1). *Oryza meridionalis* produced significantly more mean flowering culms m^{-2} than all other species. The mean number of flowering culms m^{-2} produced by *Brachiaria mutica* was significantly greater than those produced by both *Hymenachne acutigluma* and *Pseudoraphis spinescens.* Mean flowering culm production (m^{-2}) of *Hymenachne acutigluma* and *Pseudoraphis spinescens* did 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***

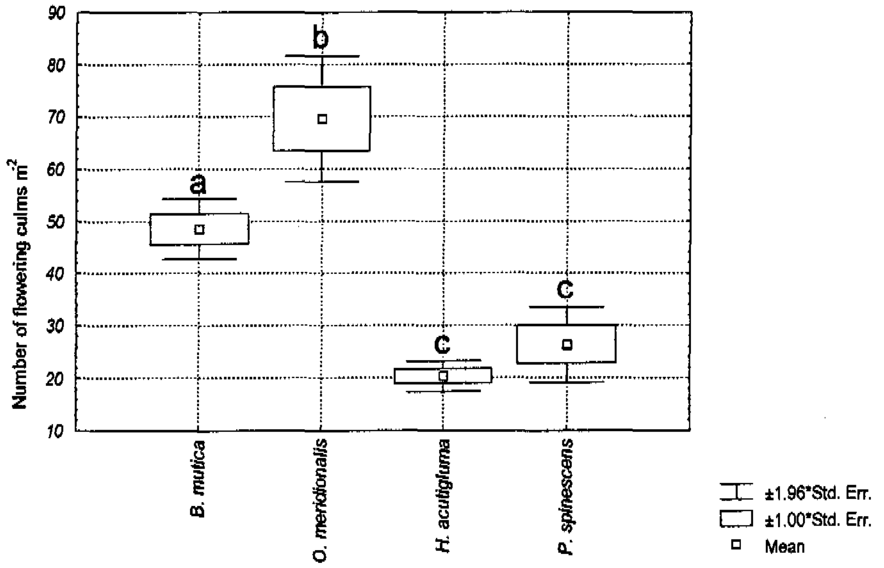


Figure 6.2 Number of flowering culms m^{-2} recorded for each dominant grass species in their respective vegetation types during peak biomass production (May 1996) (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

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).

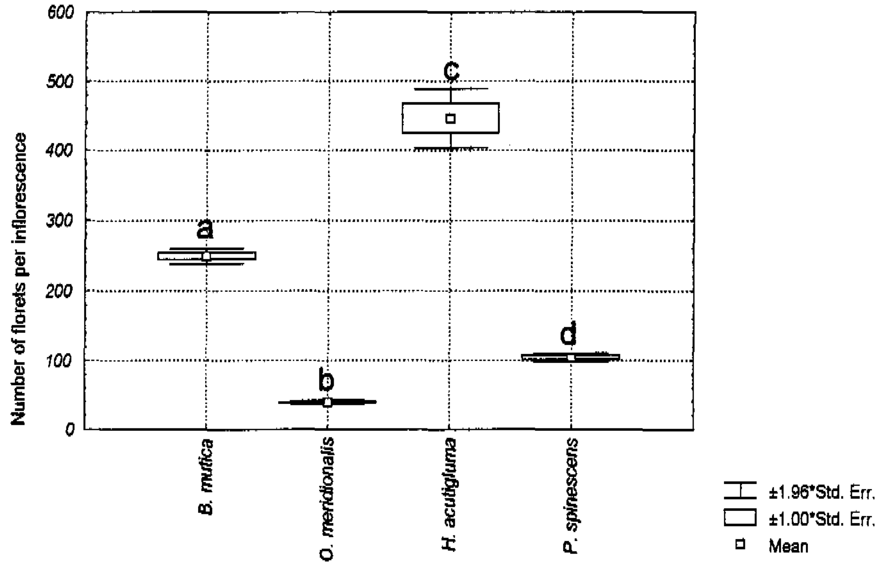


Figure 6.3 Number of florets per inflorescence recorded for *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* during peak biomass production (May 1996) (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

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

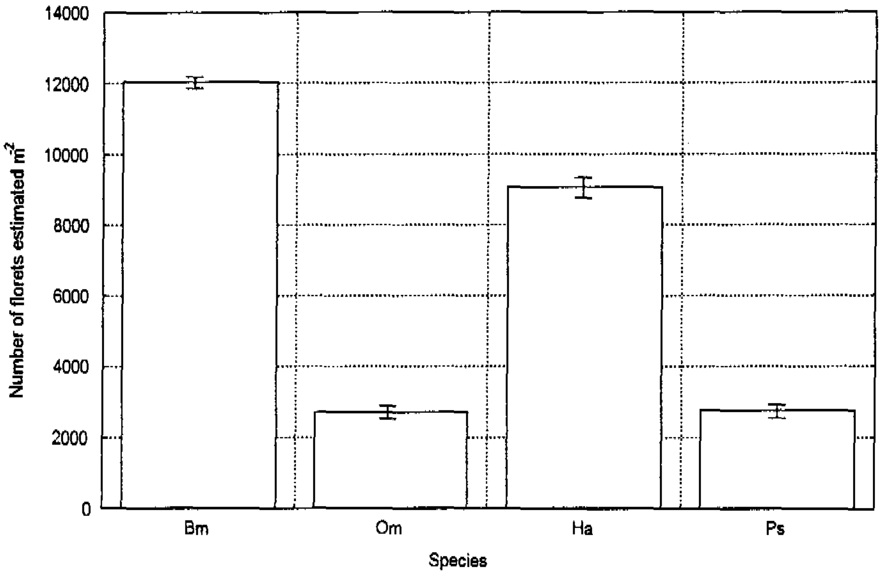


Figure 6.4 Calculated floret production m^{-2} of *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) in their respective vegetation types during peak biomass production (May 1996) (error bars show standard error). .

Soil Seed Density Estimates

Q_2: 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).

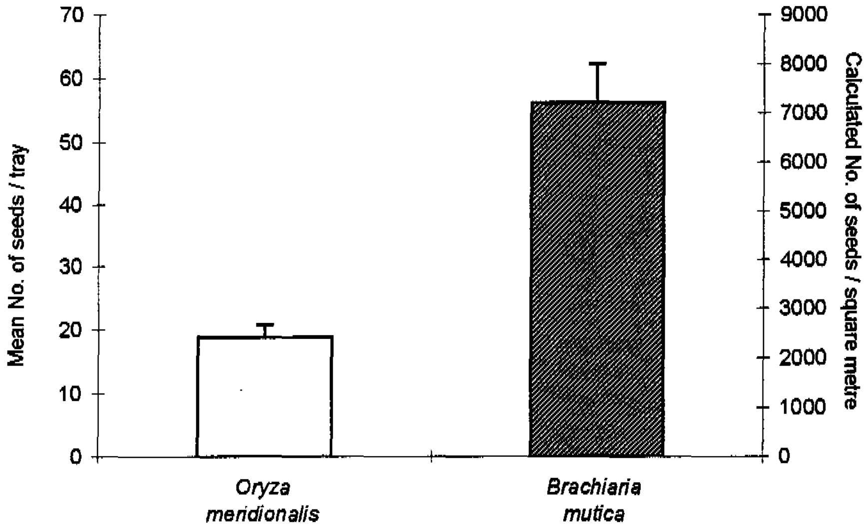


Figure 6.5 Estimates of *Oryza meridionalis* and *Brachiaria mutica* seeds within sediment seed bank germination sample trays and m^{-2} in their respective plant communities (error bars indicate standard error).

Seed Viability Estimates

Q_3: What is the viability of *Brachiaria mutica, Oryza meridionalis, Hymenachne acutigluma* and *Pseudoraphis spinescens* seeds?

H_3: 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_4: 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_5: 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

	df Effect	MS Effect	df Error	MS Error	F	p-level
% 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***

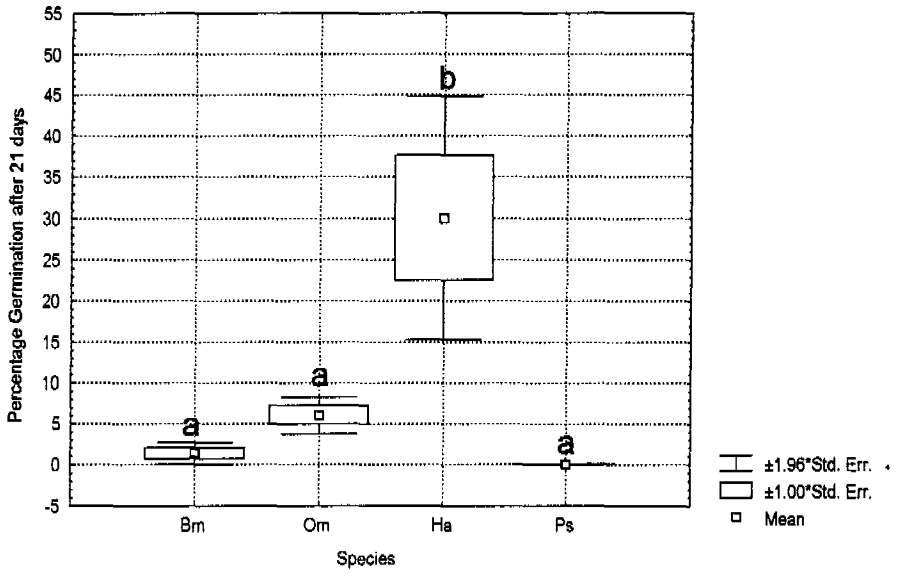


Figure 6.6 Percentage germination of *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds placed in a growth cabinet for three weeks (300 seeds of each species used) (significant differences identified using the LSD test (p < 0.05)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

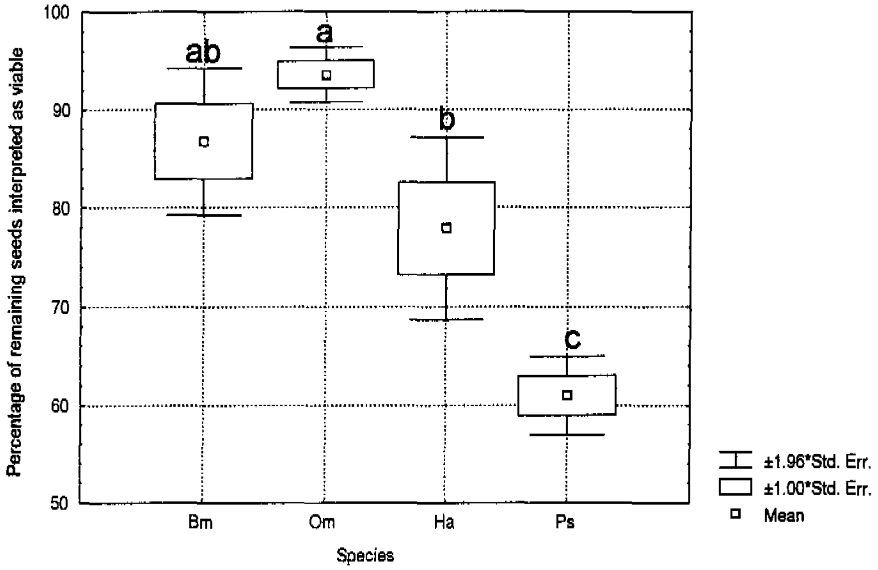


Figure 6.7 Remaining ungerminated *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds interpreted as viable (using tetrazolium chloride) after three weeks in a growth chamber (300 seeds of each species used) (significant differences 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.

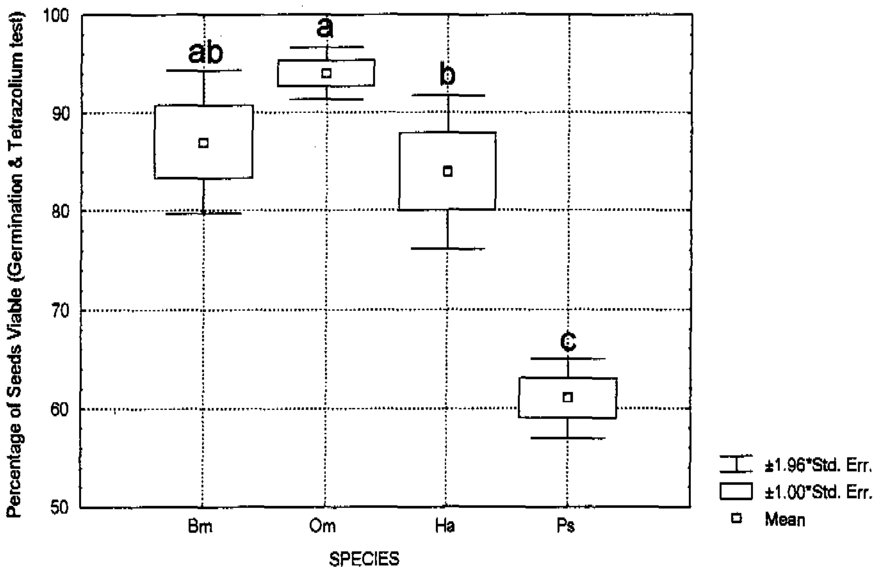


Figure 6.8 Percentage of viable (germination + tetrazolium tests) *Brachiaria mutica* (Bm), *Oryza meridionalis* (Om), *Hymenachne acutigluma* (Ha) and *Pseudoraphis spinescens* (Ps) seeds (300 seeds of each species used) (significant differences identified using the LSD test ($p < 0.05$) are indicated 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^{-2}) 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.

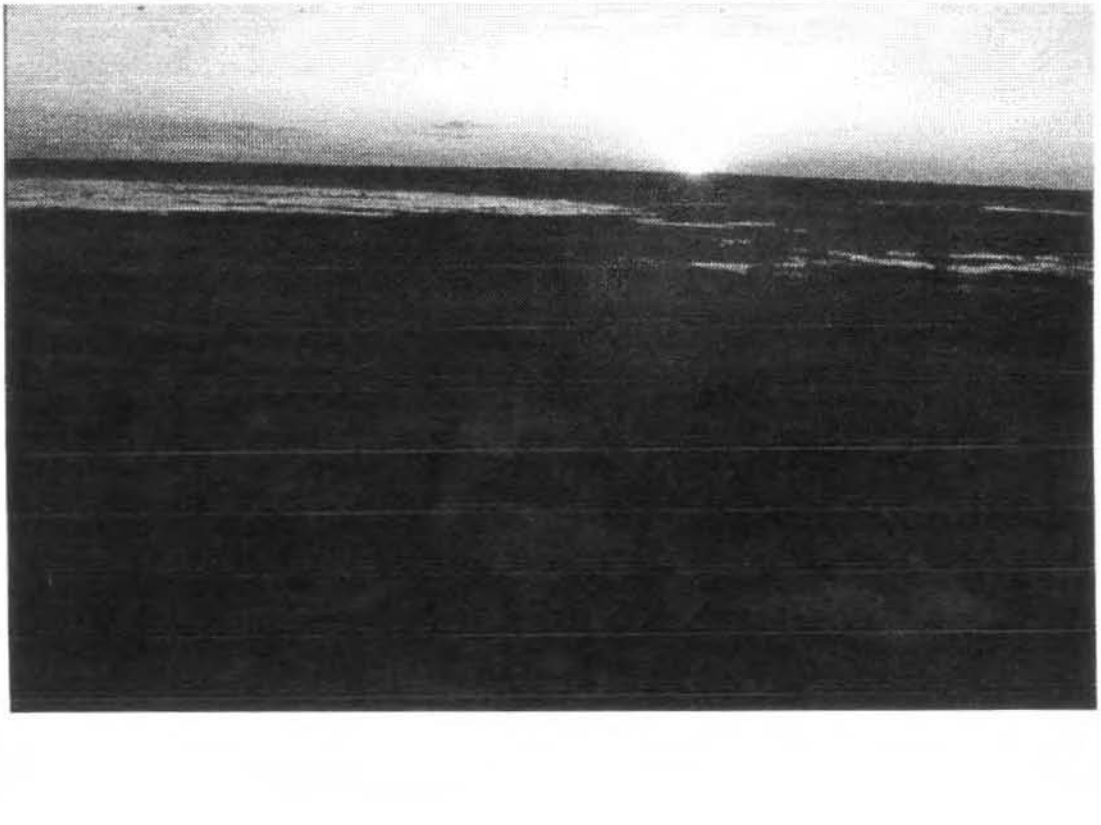
Finding large quantities of mature *Pseudoraphis spinescens* seed was difficult and the failure of seeds of this species to germinate could have been a result of poor seed stock as viability assessment using tetrazolium chloride gave low viability estimates. Tetrazolium chloride only stains living cells 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.

Chapter 7 Grassland Community Dynamics: Processes & Management



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.

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.