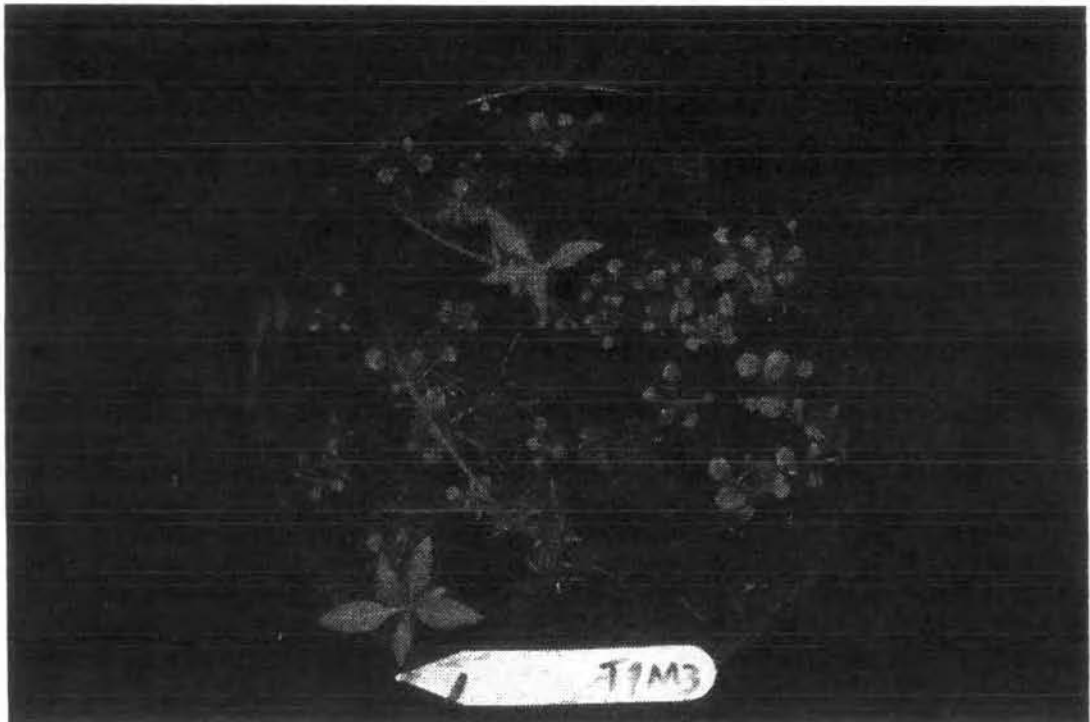


Chapter 4 The Seed Banks: Sediment Germination Trial



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

(flooded 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 community structure, resulting from removal of feral buffalo 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:

- Q₁: 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?
- Q₃: Does germination under flooded or moist conditions influence which taxa will germinate?
- Q₄: What patterns can be found in species composition and abundance of seedlings emerging from sediment samples?
- Q₅: Do seeds in the seed bank vary spatially within a grassland community?
- Q₆: Do seed banks vary among different grassland communities?
- Q₇: Have changes occurred in the seed bank since the 1984 study?

The hypotheses generated to test these questions are:

- H₁: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H₂: 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.
- H₃: 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.
- H₄: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H₅: 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.
- H₆: 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.
- H₇: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.
- H₈: 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.
- H₉: 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.
- H₁₀: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.
- H₁₁: 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.
- H₁₂: 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.

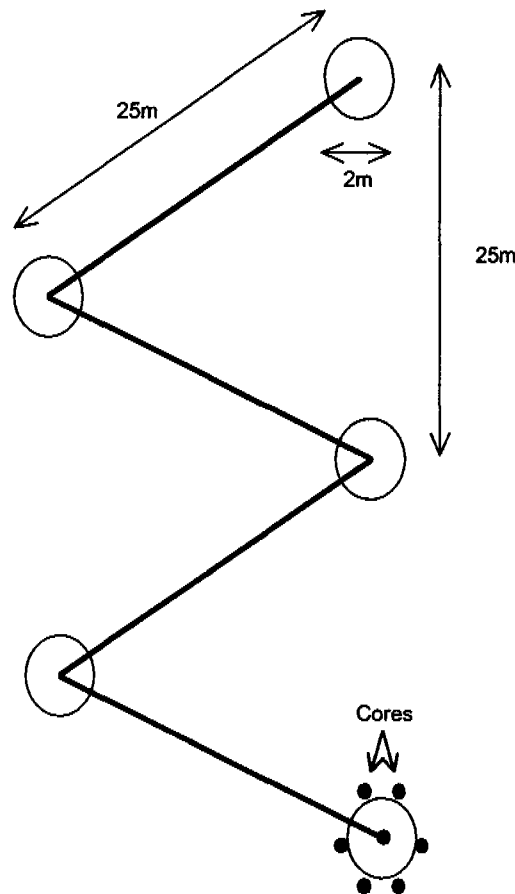


Figure 4.1 Transect dimensions showing the locations of sediment core collection sites.

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).

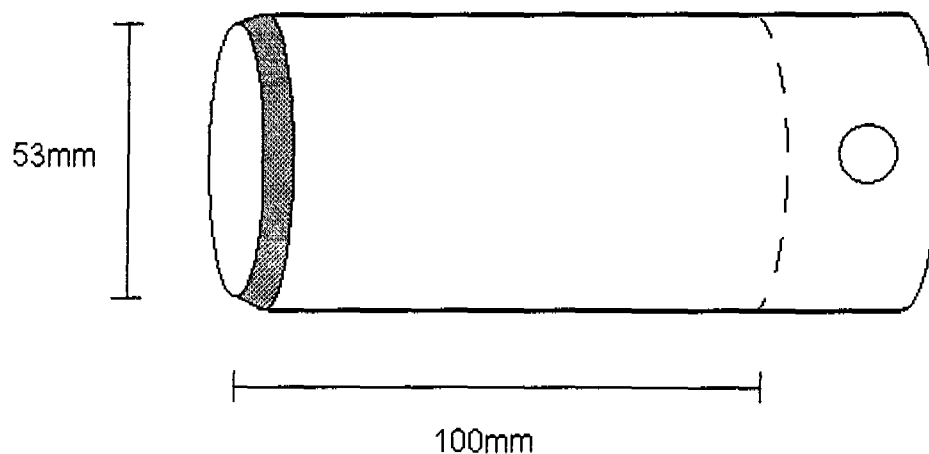


Figure 4.2 Design of pvc corer used to collect sediment samples.

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°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 cm² 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

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 $140 \text{ mg}^{-1} \text{ CaCO}_3$, conductivity $30 \mu\text{S cm}^{-1}$ at 25°C , Ca 20 mg l^{-1} , Mg 20 mg l^{-1} , (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 $\frac{1}{2}$ 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

Q₁: 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?

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)

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

Variation in Germination Conditions Among Taxa

Q₃: 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.

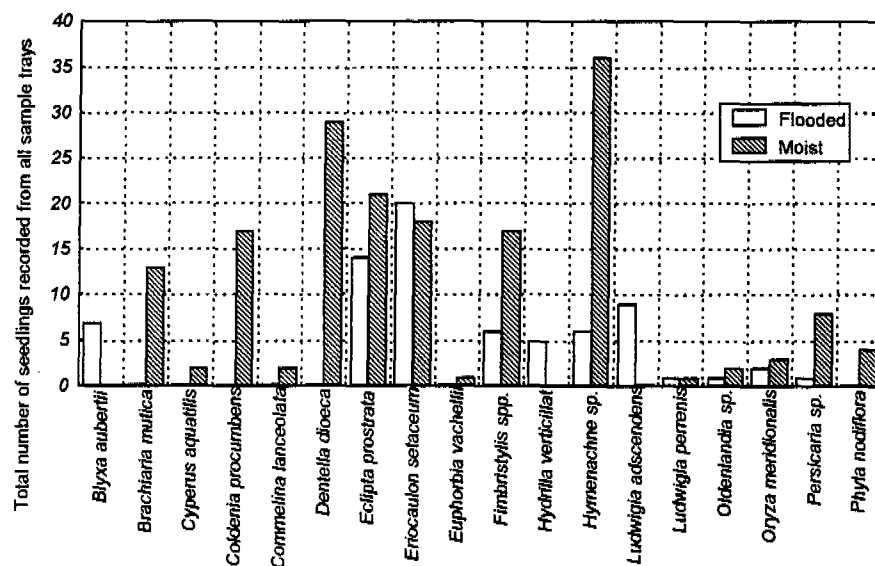


Figure 4.3 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (species with < 50 emergents)

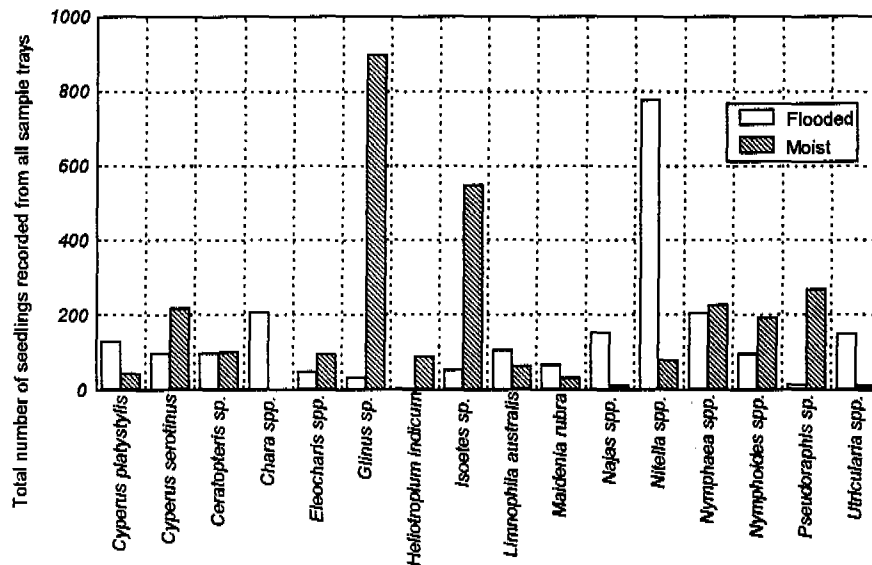


Figure 4.4 Total number of seedlings emerging from sediment samples collected in four grassland communities on the Magela floodplain and germinated under flooded and moist water regimes (taxa with > 50 emergents)

Patterns Within and Among Grassland Seed Banks

Q₄: 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.

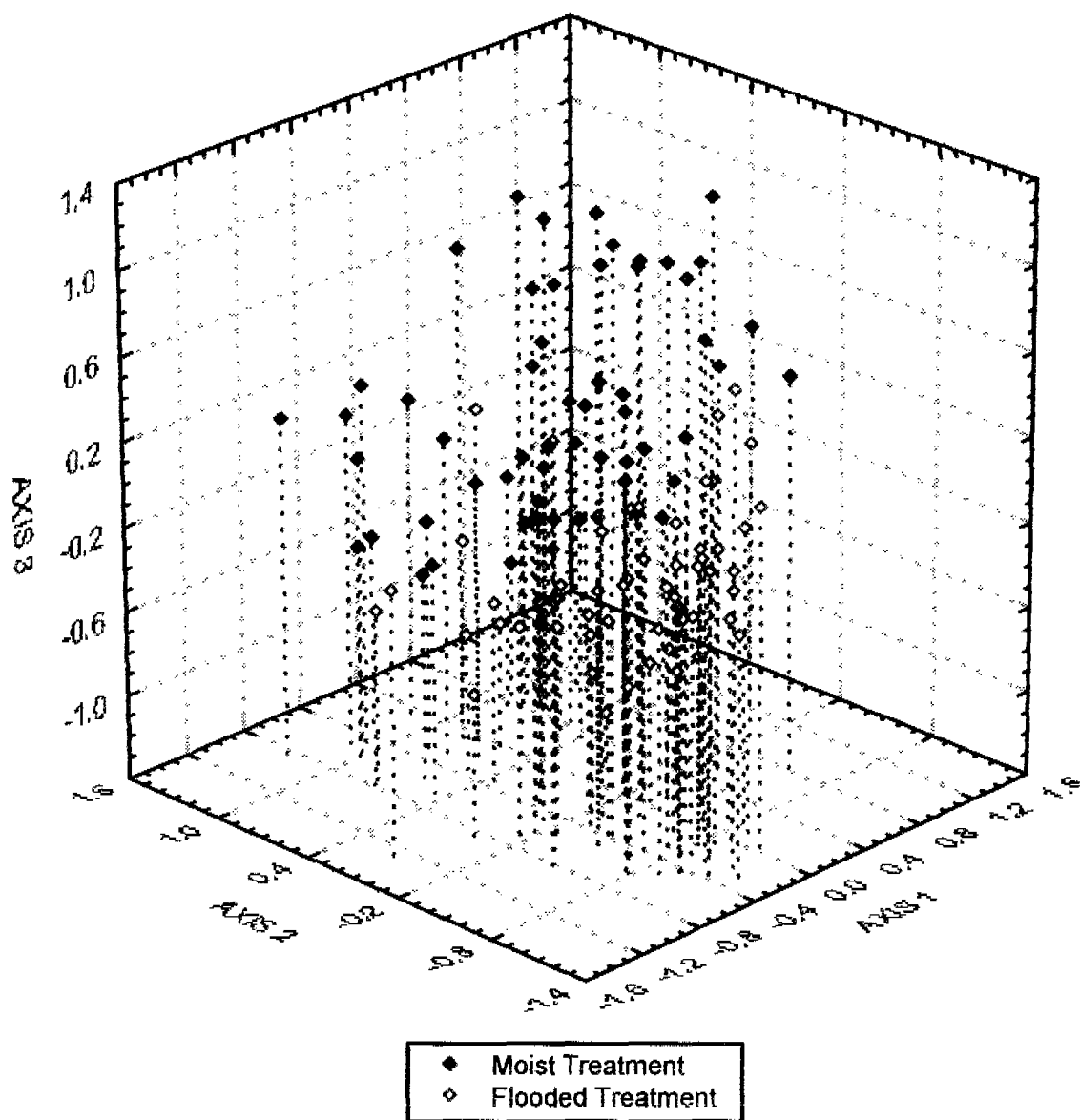


Figure 4.5 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis; multidimensional scaling stress 0.1764). Distinction between water regimes is shown.

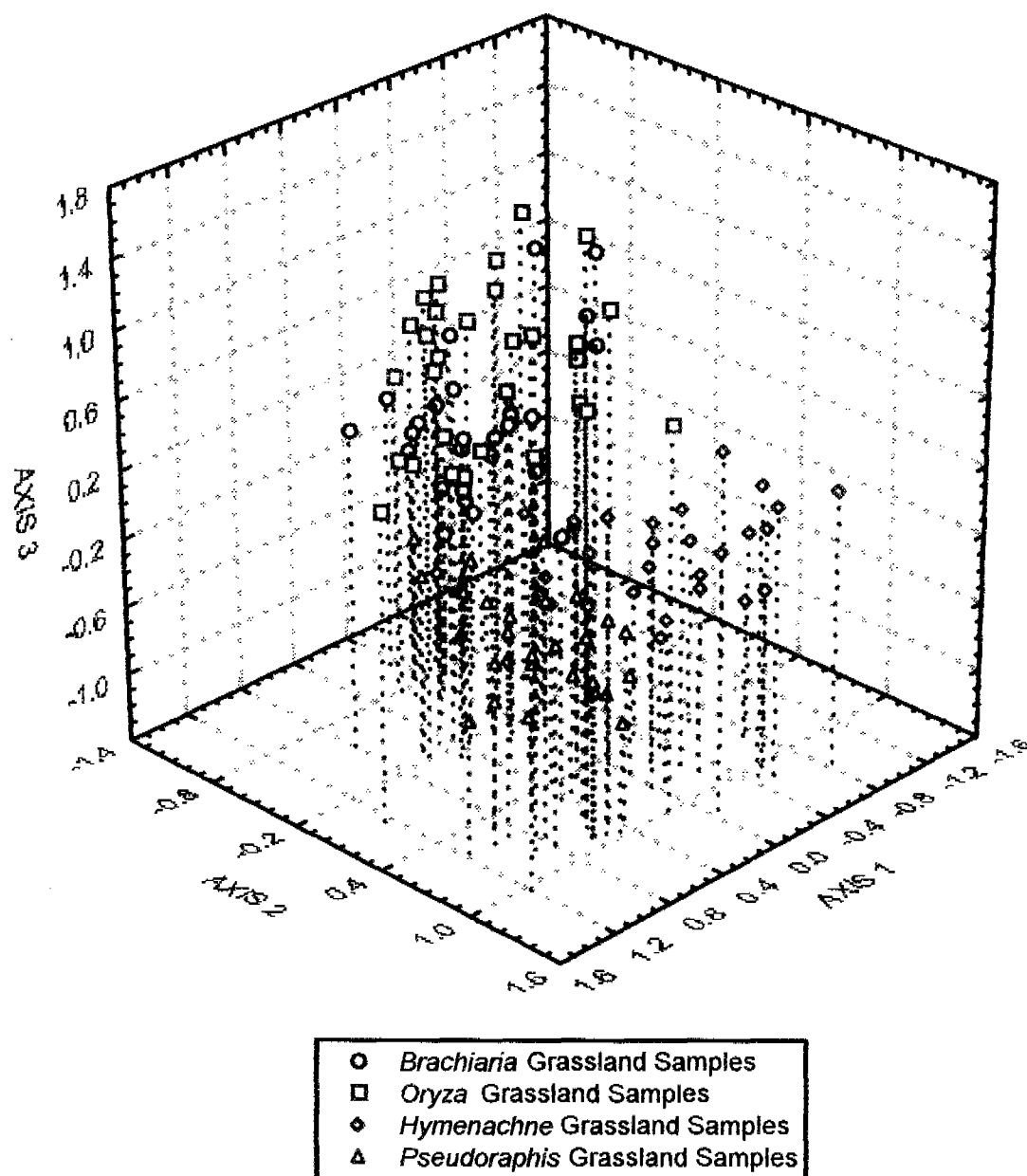


Figure 4.6 Species composition and abundance ordination plot for seedlings emerging from sediments collected in four grassland communities under flooded and moist water regimes (Bray Curtis: multidimensional scaling stress 0.1764). Distinction between plant communities is shown.

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..

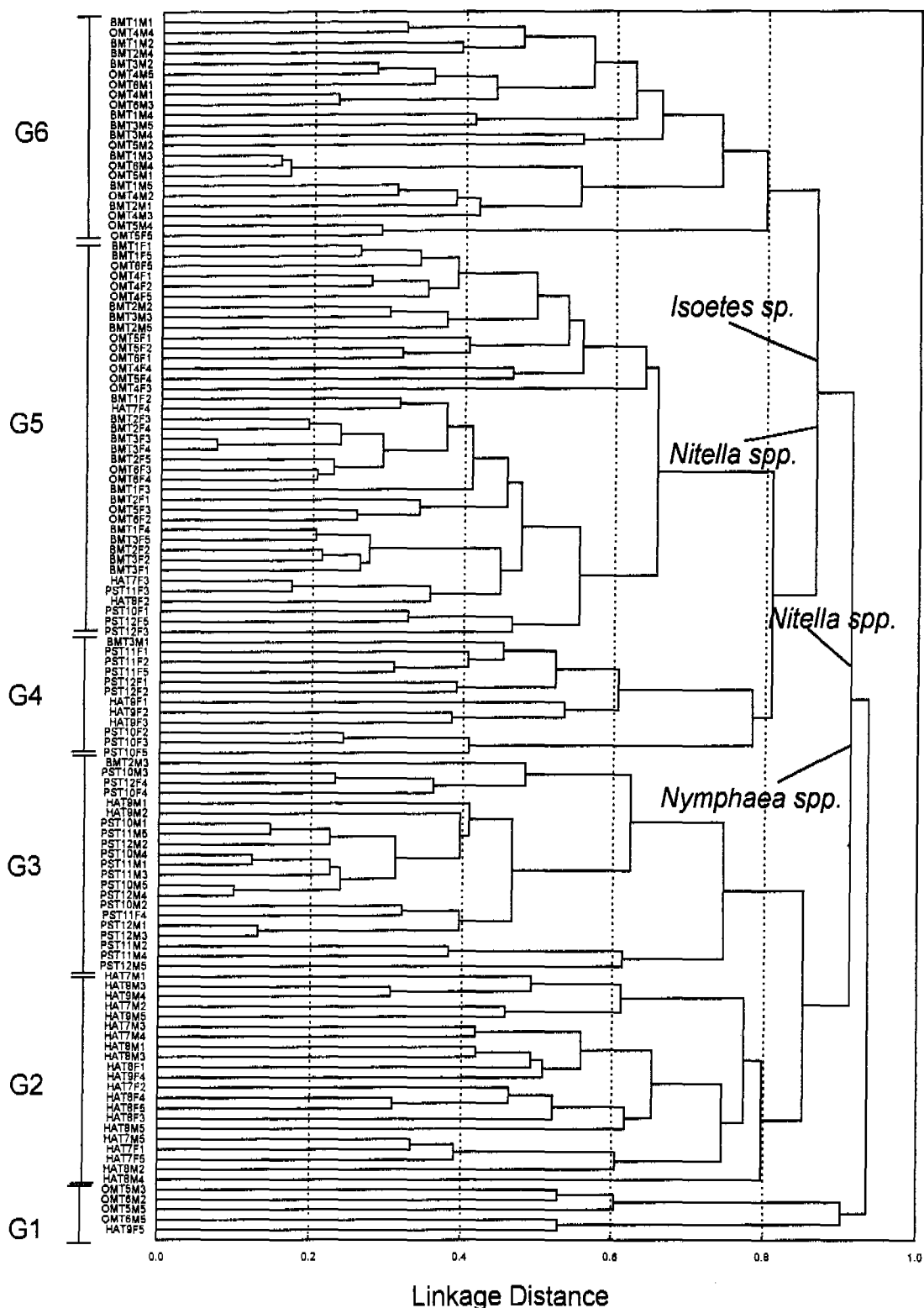


Figure 4.7 Dendrogram of Bray Curtis association matrix generated (using UPGMA) from raw seed bank data, showing seven groupings according to emergence of a few key species: G1 = Few germinants; G2 = *Glinus oppositifolius*, *Nymphaea* spp., *Pseudoraphis spinescens* (Hymenachne grassland samples); G3 = *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

Q₅: Do seeds in the seed bank vary spatially within a grassland community?

- H₁: There is no difference in the total number of seedlings emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H₂: 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.
- H₃: 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.
- H₄: There is no difference in the number of taxa emerging from sediment samples collected from within a grassland community on the Magela floodplain.
- H₅: 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.
- H₆: 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

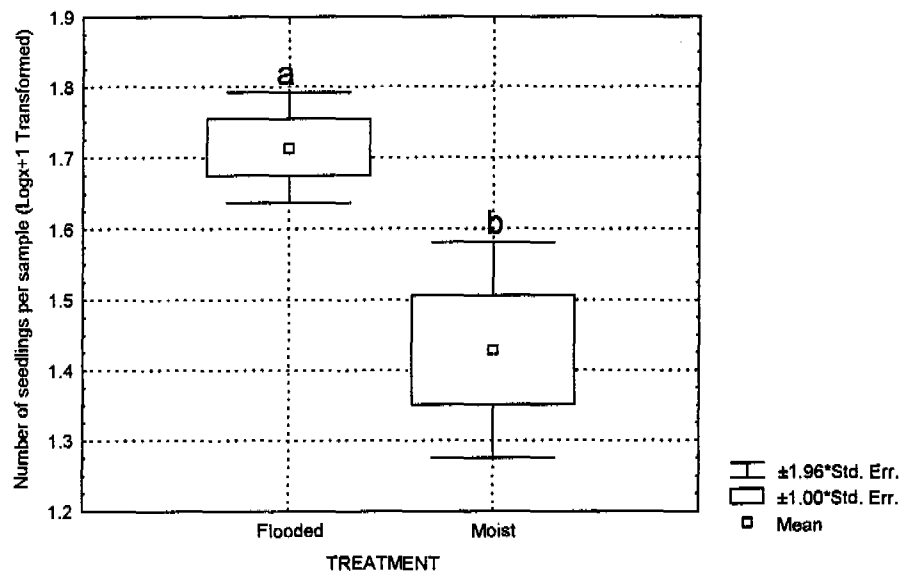


Figure 4.8 Number of seedlings (log x + 1 transformed) emerging from *Brachiaria* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

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	df 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 Effect	MS Effect	df Error	MS Error	F	p-level
Transect	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

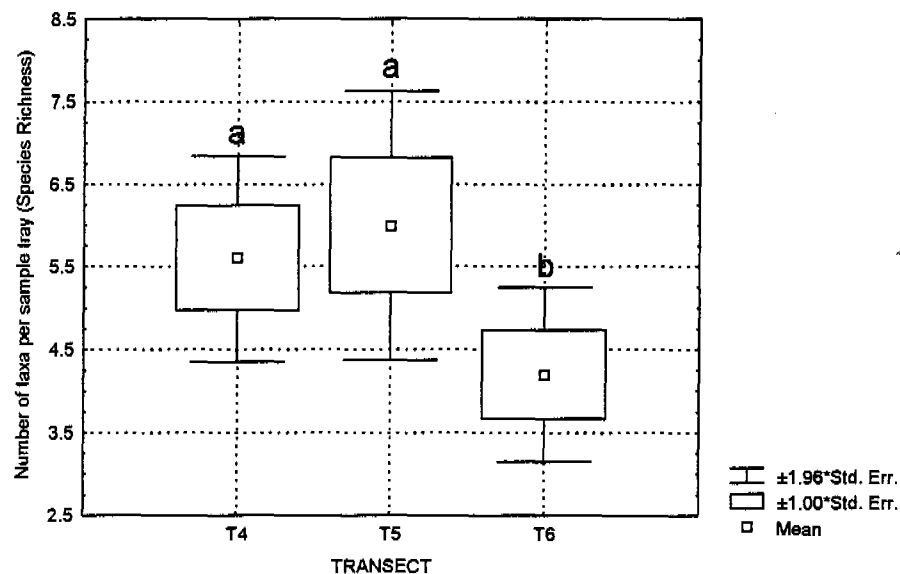


Figure 4.9 Species richness of samples collected along three different transects within the *Oryza* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test $p < 0.05$)).

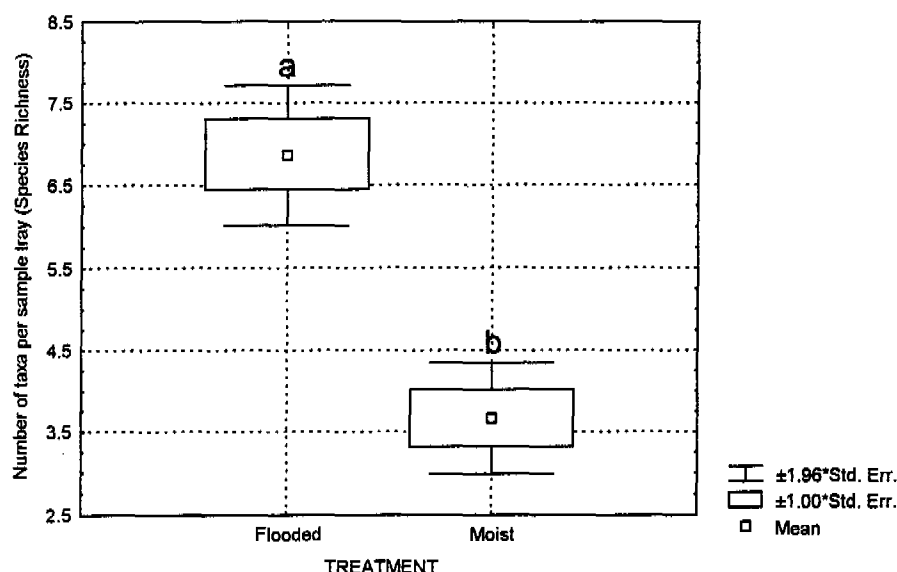


Figure 4.10 Species richness of samples collected from the *Oryza* grassland and germinated under flooded and moist water regimes significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

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 Effect	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**

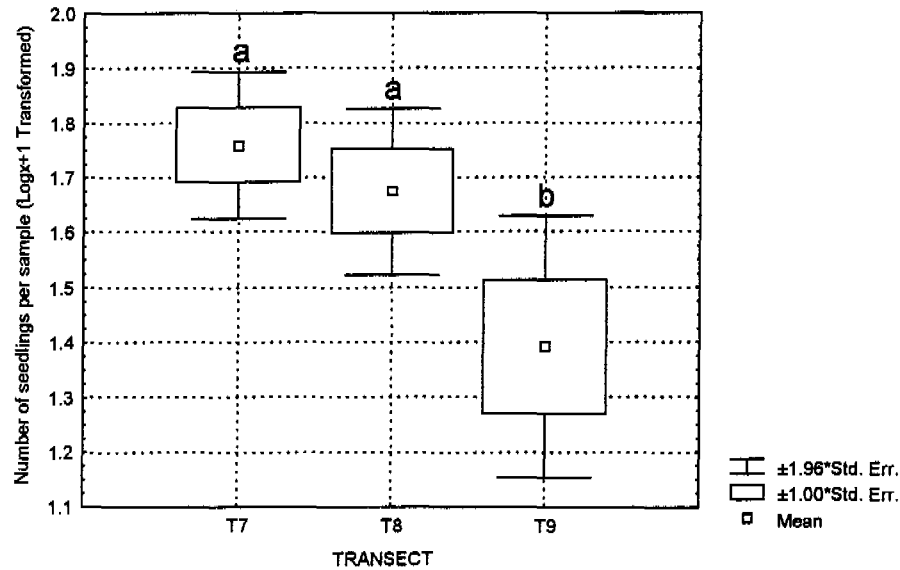


Figure 4.11 Number of seedlings ($\log x + 1$ transformed) emerging from samples collected along three transects in the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test $p < 0.05$)).

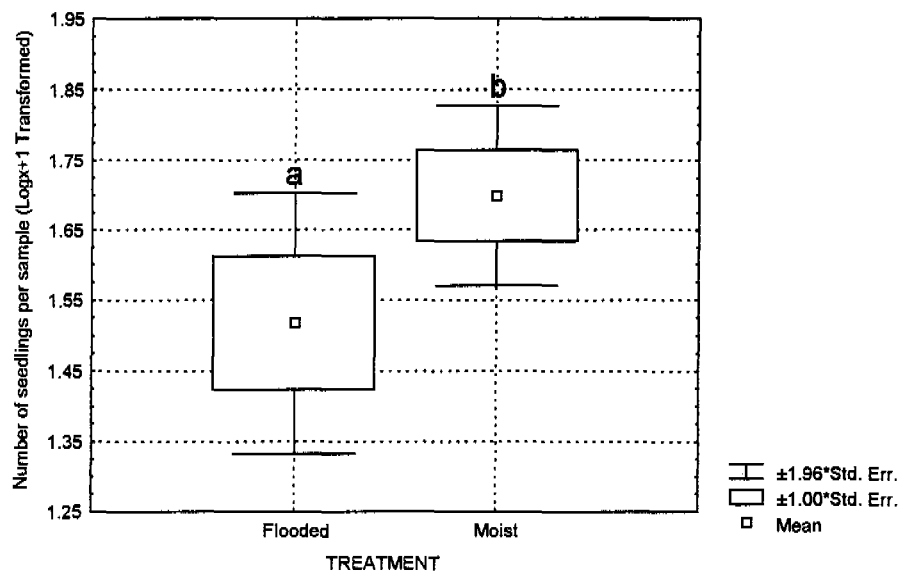


Figure 4.12 Number of seedlings ($\log x + 1$ transformed) emerging from *Hymenachne* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

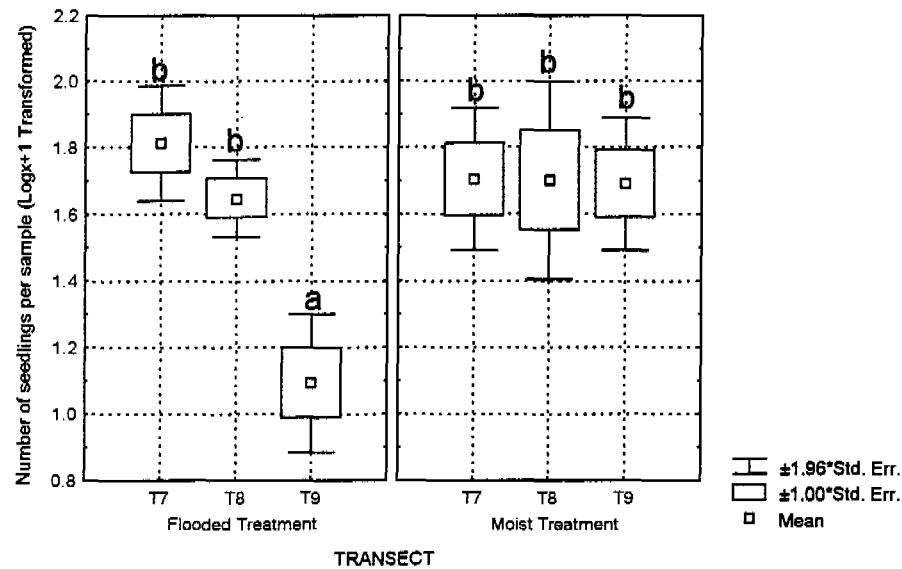


Figure 4.13 Transect and treatment interactions found within samples collected along three transects within the *Hymenachne* grassland and germinated under flooded and moist conditions (Groups marked by the same letter did not differ significantly from one another (LSD test $p < 0.05$)).

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	MS Effect	df Error	MS Error	F	p-level
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

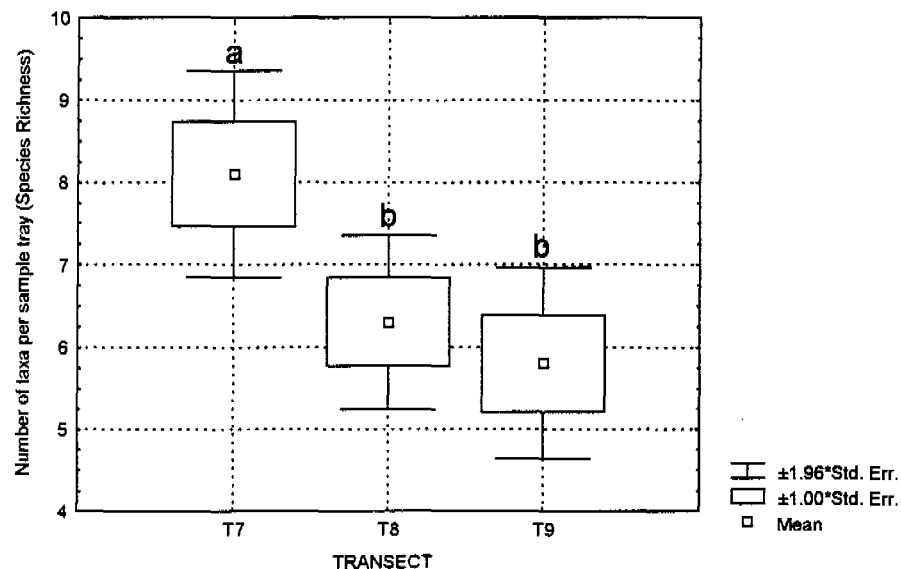


Figure 4.14 Species richness of samples collected along three different transects within the *Hymenachne* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test $p < 0.05$)).

***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 Error	MS Error	F	p-level
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

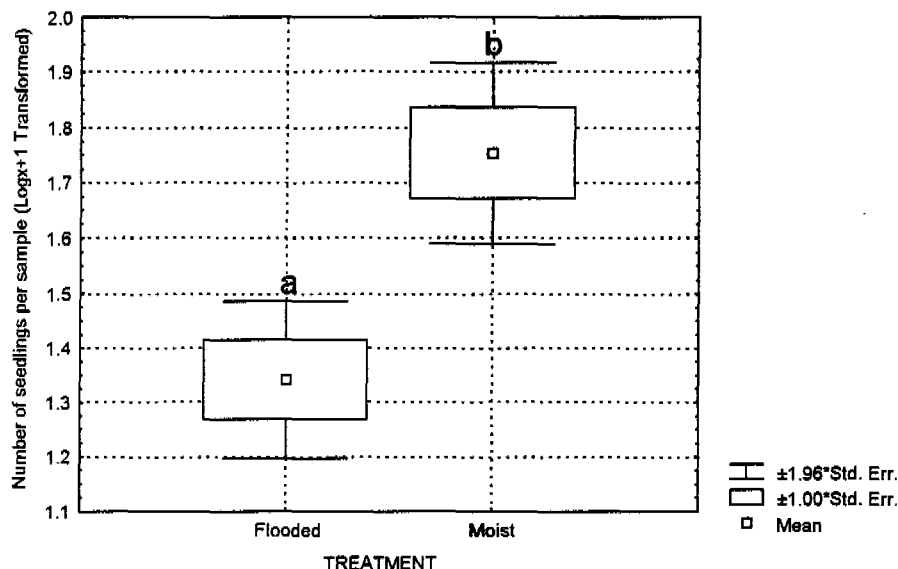


Figure 4.15 Number of seedlings (log x + 1 transformed) emerging from *Pseudoraphis* grassland samples under flooded and moist water regimes (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

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 Effect	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

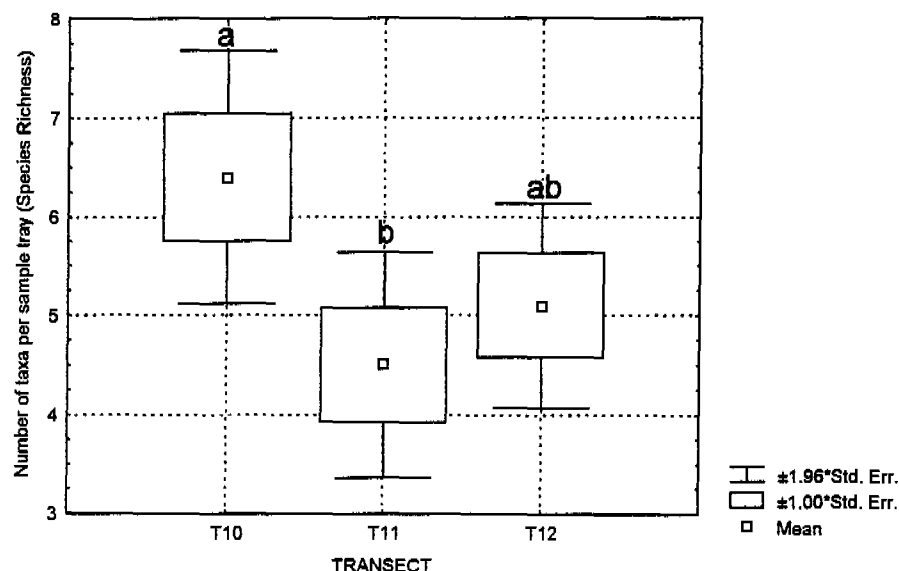


Figure 4.16 Species richness of samples collected along three different transects within the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (Groups marked by the same letter did not differ significantly from one another (LSD test $p < 0.05$)).

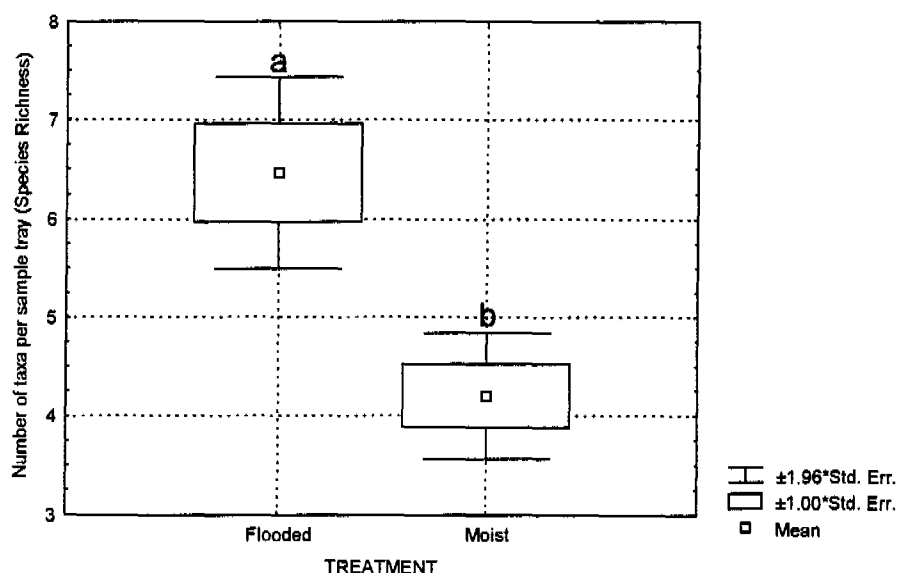


Figure 4.17 Species richness of samples collected from the *Pseudoraphis* grassland and germinated under flooded and moist water regimes (significant differences identified using the LSD test ($p < 0.05$) are indicated by different letters).

Variation Among Grassland Seed Banks

Q₆: Do seed banks vary among different grassland communities?

H₇: There is no difference in the total number of seedlings emerging from sediment samples collected from different grassland communities on the Magela floodplain.

H₈: 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.

H₉: 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.

H₁₀: There is no difference in the number of taxa emerging from sediment samples collected from four different grassland communities on the Magela floodplain.

H₁₁: 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.

H₁₂: 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) ** = $P < 0.01$, *** = $P < 0.001$.

	df Effect	MS Effect	df Error	MS 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 Treatment	3	32.222	112	4.1	7.859	< 0.001***

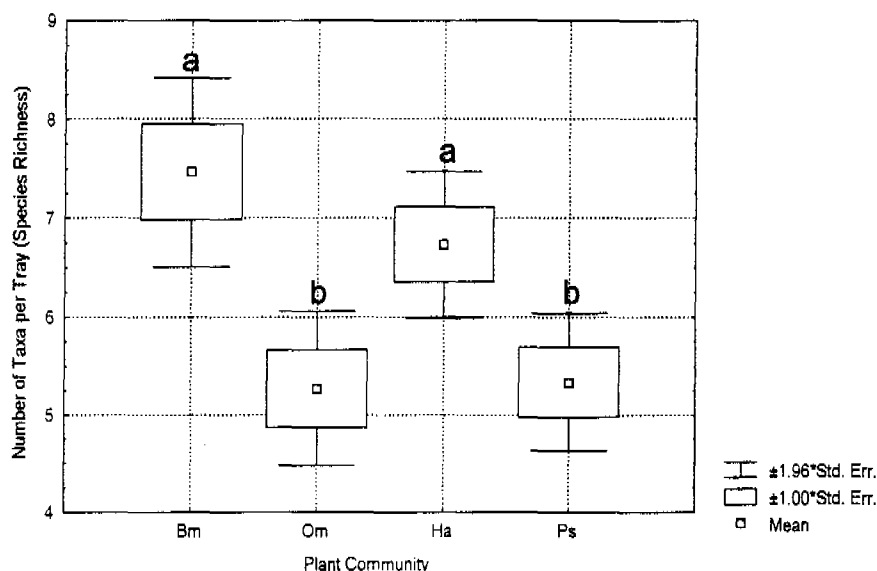


Figure 4.18 Species richness of seedlings emerging from trays, each representing $66\text{cm}^2 \times 10\text{ cm}$ deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* grassland and Ps = *Pseudoraphis*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

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

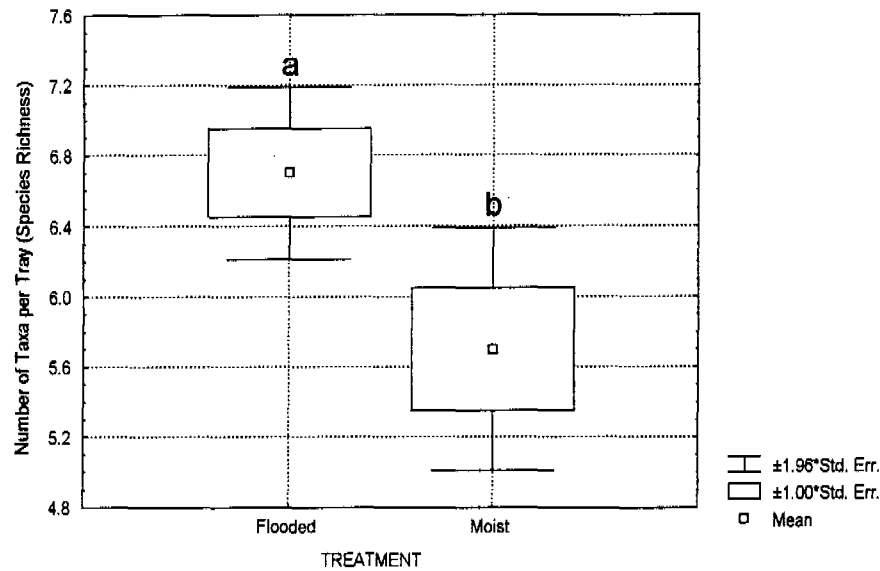


Figure 4.19 Species richness of seedlings emerging from trays, each representing $66\text{cm}^2 \times 10$ cm deep sediment samples, collected from four grassland communities on the Magela floodplain and germinated under two water regimes (flooded and moist) (significant differences identified using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

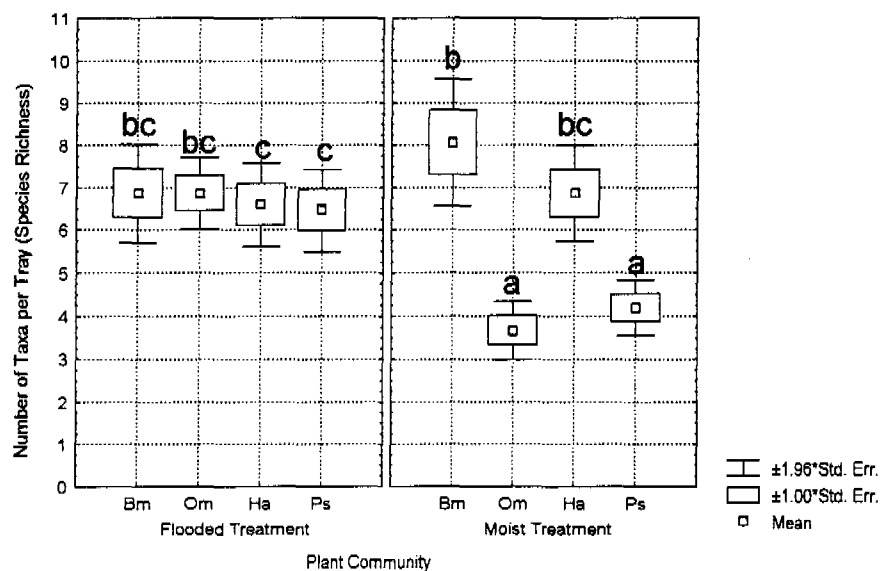


Figure 4.20 Community and treatment interactions of species richness of seedlings emerging from trays, each representing $66\text{cm}^2 \times 10$ cm deep sediment samples, collected from four grassland communities on the Magela floodplain (Bm = *Brachiaria* grassland, Om = *Oryza* grassland, Ha = *Hymenachne* 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 of seedlings	Transects	Ns	Ns	T9 < T7 / T8	Ns	Ns
	Treatments	F > M	Ns	M > F	M > F	Ns
	Interactions	Ns	Ns	T9 < all	Ns	Bm F > Bm M Ps F < Ps M
Species Richness	Transects	Ns	T6 < T4 / T5	T9 / T8 < 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)

Q₇: 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.

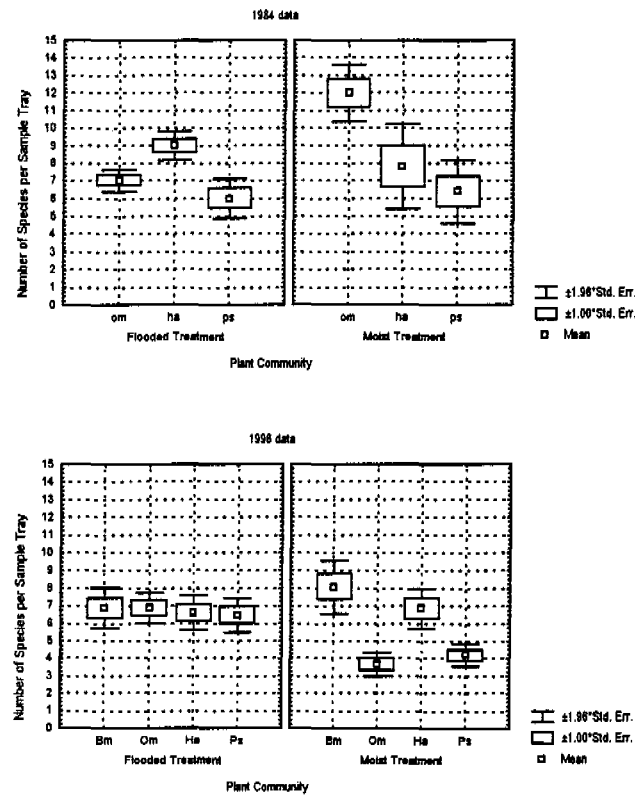


Figure 4.21 Species richness of seedlings emerging from sediment samples collected from the same sample sites on the Magela floodplain in 1984 and 1995 and germinated under two water regimes (flooded and moist)(Top 1984 Om = *Oryza* grassland, Ha = *Hymenachne* grassland, Ps = *Pseudoraphis* grassland; 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^{-2} , 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.

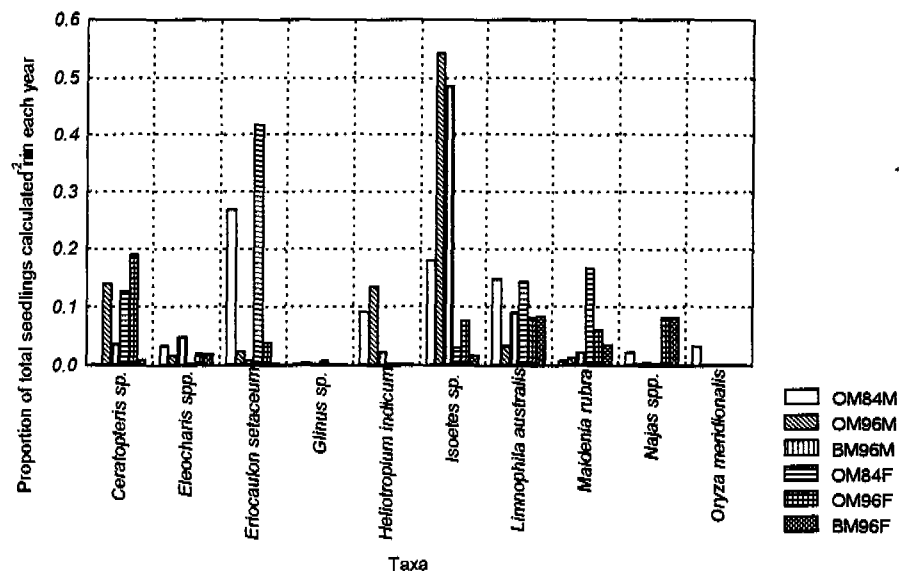


Figure 4.22 Proportions of total seedlings (calculated 1m^{-2}) that each species made up in 1984 *Oryza* grassland samples (OM84), 1996 *Oryza* grassland samples (Om96) and 1996 *Brachiaria* grassland samples (Bm96) in flooded (F) and moist (M) treatments. (only species overlapping in occurrence between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

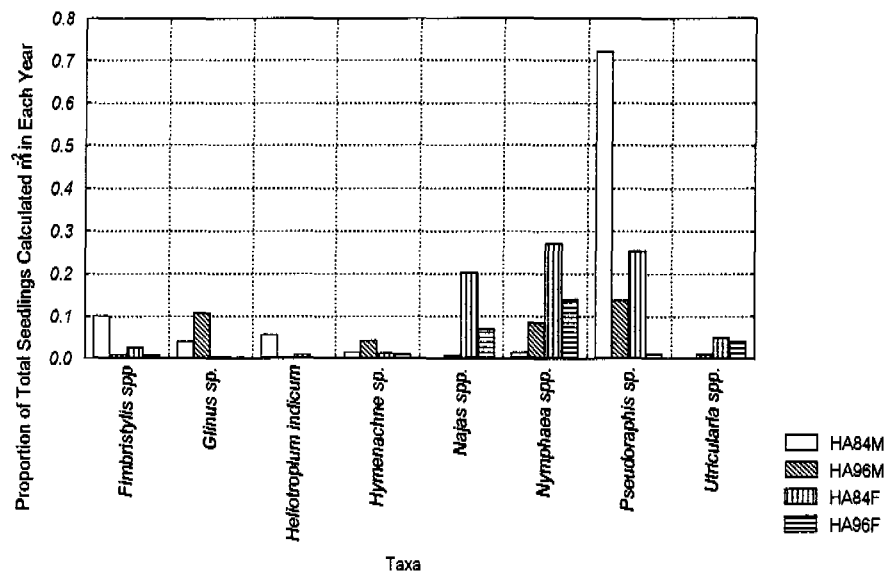


Figure 4.23 Proportions of total seedlings (calculated 1m^2) that each species made up in 1984 *Hymenachne* grassland samples (HA84), 1996 *Hymenachne* grassland samples (HA96) in flooded (F) and moist (M) treatments.(only species overlapping in occurrence between years are shown).

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.

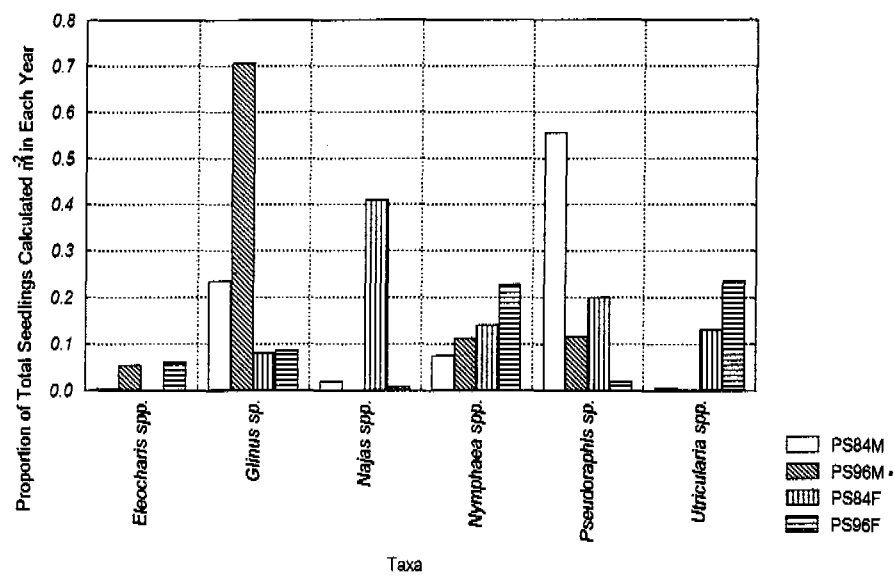


Figure 4.24 Proportions of total seedlings (calculated 1m^{-2}) that each species made up in 1984 *Pseudoraphis* grassland samples (PS84), 1996 *Pseudoraphis* grassland samples (PS96) in flooded (F) and moist (M) treatments. (only species overlapping in occurrence between years are shown).

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 *Brachiaria* 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 *Oryza* 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 non-desiccating 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.

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:

- Q₁: Is there a correlation between species composition of sediment samples (determined by germination) and the extant vegetation from which they came?
- Q₂: 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:

- H₁: 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

Q₁: 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*, *Isoetes 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).

Taxa	Brachiaria grassland				Oryza grassland				Hymenachne grassland				Pseudoraphis grassland			
	Extant Vegetation Dry	Wet	Seed bank Moist	Flooded	Extant Vegetation Dry	Wet	Seed bank Moist	Flooded	Extant Vegetation Dry	Wet	Seed bank Moist	Flooded	Extant Vegetation Dry	Wet	Seed bank Moist	Flooded
<i>Azolla pinnata</i>		✓								✓				✓		
<i>Blyxa aubertii</i>																✓
<i>Brachiaria mutica</i> *	✓	✓	✓		✓						✓					
<i>Ceratopteris thalictroides</i>			✓	✓			✓	✓			✓					
<i>Chara</i> spp.				✓				✓				✓				✓
<i>Coldenia procumbens</i>			✓				✓		✓		✓					
<i>Commelina lanceolata</i>							✓									
<i>Cyperus aquatilis</i>							✓									
<i>Cyperus platystylis</i>			✓						✓		✓	✓				✓
<i>Cyperus serotinus</i>			✓	✓			✓				✓	✓				✓
<i>Dentella dioeca</i>									✓		✓					
<i>Eclipta prostrata</i>									✓		✓	✓			✓	✓
<i>Fleocharis</i> spp.		✓	✓	✓		✓	✓	✓		✓		✓		✓	✓	✓
<i>Eriocaulon setaceum</i>			✓	✓			✓	✓								
<i>Euphorbia vachellii</i>					✓				✓		✓					
<i>Fimbristylis</i> spp.	✓		✓				✓	✓	✓		✓					✓
<i>Glinus oppositifolius</i>			✓				✓		✓		✓		✓		✓	✓
<i>Heliotropium indicum</i> *			✓				✓		✓		✓					
<i>Hydrilla verticillata</i>												✓				
<i>Hygrochloa aquatica</i>						✓										
<i>Hymenachne acutigluma</i>		✓				✓			✓	✓	✓	✓		✓		
<i>Ipomoea aquatica</i>						✓								✓		
<i>Isoetes coromandelina</i>			✓	✓			✓	✓							✓	
<i>Limnophila australis</i>			✓	✓			✓	✓								
<i>Ludwigia adscendens</i>		✓				✓			✓	✓		✓		✓		✓
<i>Ludwigia perennis</i>							✓	✓								
<i>Maidenia rubra</i>			✓	✓			✓	✓			✓	✓				
<i>Merremia gemella</i>					✓											
<i>Najas</i> spp.			✓	✓		✓		✓		✓	✓	✓			✓	✓
<i>Nitella</i> spp.			✓	✓			✓	✓			✓	✓			✓	✓
<i>Nymphaea</i> spp.		✓	✓	✓		✓	✓	✓		✓	✓	✓		✓	✓	✓
<i>Nymphoides</i> spp.			✓	✓		✓	✓	✓	✓	✓	✓	✓		✓	✓	✓
<i>Oldenlandia</i> sp.							✓				✓					✓
<i>Oryza meridionalis</i>		✓	✓	✓		✓	✓	✓		✓						
<i>Persicaria</i> spp.		✓				✓			✓	✓	✓			✓		✓
<i>Phyla nodiflora</i> *					✓		✓									
<i>Pseudoraphis spinescens</i>	✓	✓	✓		✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓
<i>Salvinia molesta</i>		✓								✓						
<i>Utricularia</i> spp.		✓	✓	✓		✓		✓		✓	✓	✓		✓	✓	✓

Q₂: Is there a correlation between species composition and abundance of sediment samples (determined by germination) and the extant vegetation from which they came?

H₁: 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 Partitions	Germination Partitions						Sum	Error
	2	4	1	5	3	6		
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	100		

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 bank to be more closely related to extant vegetation than other 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.