

## 5 Chapter 5: Plant Recruitment during Drawdown in the Field

### 5.1 Introduction

Exposed sediment with high soil moisture is required for the germination of all but one species in the Menindee Lakes seed bank; furthermore, 22 of the 33 species present were extirpated when water levels rose above the sediment surface (Chapter 4). The remaining 11 species were amphibious; however, two were intolerant of flooding to 70 cm (Chapter 4). For the majority of species the sediment must be free of standing water for recruitment, seed set and replenishment of the seed bank. On the other hand, rapid drawdown (5 cm day<sup>-1</sup> or greater) was shown to reduce or prevent recruitment of several amphibious and floodplain species and promote the recruitment of an exotic terrestrial species (Chapter 4).

The primary management consideration of the Menindee Lakes is to maximise water conservation, which has resulted in inundation for longer periods than under the natural hydraulic regime (Harris *et al.* 1996; New South Wales Department of Land and Water Conservation 1998b; New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998; Scholz *et al.* 1999). Drawdown is governed by the balance between downstream demand and evaporative losses versus inflow, consequently the rate of drawdown is often more rapid than under natural conditions (up to 10 cm day<sup>-1</sup>) (New South Wales Department of Land and Water Conservation 2003).

In July 2001, the lakes were close to maximum regulated capacity (Figure 1.5, Figure 1.6 and Figure 1.7) (New South Wales Department of Land and Water Conservation 2003). Drawdown commenced in spring and there were no significant inflows from November 2001 to February 2003 (Figure 1.5, Figure 1.6 and Figure 1.7) (New South Wales Department of Land and Water Conservation 2003). During this period, three different hydraulic regimes occurred simultaneously. The small lakes upstream of the main weir were isolated from Lake Wetherell and dried by evaporation. The lakes downstream of the main weir were used for water supply and were at first drawn down rapidly until drought operations came into effect (New South Wales Department of Land and Water Conservation 1998b), after which the rate of drawdown slowed. Lake Wetherell levels remained relatively static until Lakes Pamamaroo and Menindee dried and the lake was used to supply downstream users, when water levels decreased rapidly.

When water levels fall and the sediment becomes exposed the “window of opportunity” for germination for species in the seed bank will open. The duration the window remains open will be dependent on soil moisture, which is dependent on water level, elevation, rate of drawdown and sediment texture. If the rate of drawdown is rapid, the window may not be open for sufficient time for germination or seedlings may not establish. When the window of opportunity for germination has closed, survival of seedlings will be dependent on sub-surface moisture. The factors that influence the availability of sub-surface moisture are the same as those that influence the window of opportunity for germination. However, survival is species dependent because a species that is desiccation tolerant or has a deep root system will be able to survive in drier conditions than those that are less desiccation tolerant or have shallow root systems.

Changes that occur as water levels fluctuate are outlined in the window of opportunity (WOO) model (Figure 5.1), which is based on series of hypotheses formulated from observations of the Menindee Lakes and data from the pond experiment undertaken in Chapter 4. The system switches between five states (windows of opportunity) depending on water level, elevation, rate of drawdown or flood, composition of the seed bank and extant vegetation (Figure 5.1).

When the sediment is inundated the window of opportunity for germination, growth and reproduction is closed (Figure 5.1).

Germination, establishment and reproduction occur as the sediment becomes exposed (Figure 5.1). In this state, soil moisture in the top 7.5 cm is high enough for seeds to germinate and seedlings establish. If established plants are present, they will not be water stressed and will be able to reach maturity and reproduce.

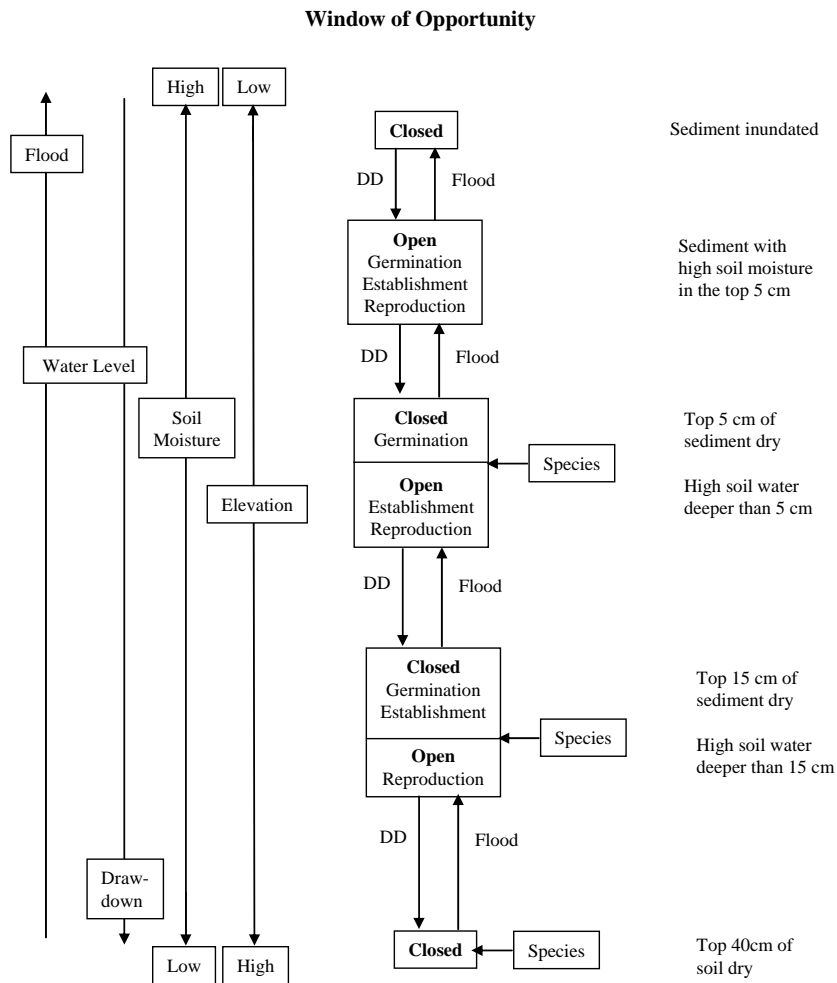
When water levels are drawn down further, the top 7.5 cm of soil will dry and the window of opportunity for germination will close (Figure 5.1) (the model assumes that the seeds buried deeper than 7.5 cm are not part of the active seed bank). Newly germinated seedlings will be able to establish providing the root system can access moisture 7.5 cm (or deeper) below the surface. Established plants will be able to grow and reach maturity because they will be able to access water. If water levels rise, and water is brought to the top 7.5 cm of soil, the window of opportunity for germination will re-open and if sediment is inundated all windows of opportunity may close (Figure 5.1).

As the sediment dries further, the window of opportunity for establishment will close and only plants that have root systems sufficiently developed to reach water deeper than 15 cm will survive. These plants will be able to reach maturity and replenish the seed bank; however, plants with less developed root systems will not survive (Figure 5.1).

The driest state occurs when the top 40 cm of soil is dry and no plants survive (all windows of opportunity are closed) (Figure 5.1).

In a lake that has static water levels, it is possible for all states to be present at different elevations (Figure 5.1). The rate at which a position on the elevation gradient changes between states is dependent on the rate of drawdown or flood (Figure 5.1). If the rate of drawdown or flood is rapid, the system may jump between states (Figure 5.1), seeds may not germinate or seedlings may die and potentially deplete the seed bank.

The soil moisture conditions that dictate when windows of opportunity for establishment and reproduction will be open and closed are dependent on species (Figure 5.1). For example, when the sediment is inundated amphibious species that have recruited will not be extirpated and species with root systems deeper than 40 cm may be present in the driest state.



**Figure 5.1: Window of opportunity model (WOO model), which describes plant recruitment from the seed bank in the Menindee Lakes.**

Vegetation change as water levels fall will therefore be dependent on the rate of drawdown and sediment exposure time. The seed bank recruitment model (Figure 4.11 and Table 4.3) predicts the species present as water levels are drawn down and the sediment dries. This is represented in the model by different states, which the system switches between depending on soil moisture content (Figure 4.11). As water levels recede and sediment exposure time increases, the system moves between states and the floristic composition will change from a mixture of species with high and low desiccation tolerances to a community dominated by species with high desiccation tolerances. If the rate of drawdown is slow ( $1 \text{ cm day}^{-1}$  or less), the system will spend more time in each state and the rate of vegetation change will be slower than if the rate of drawdown is rapid (Figure 4.11 and Table 4.3). If the rate of drawdown is rapid, the system may jump from newly exposed sediment to one of the drier states and species with low desiccation tolerances may be extirpated (Figure 4.11 and Table 4.3).

Rate of drawdown, elevation, sediment exposure time and resulting soil moisture are all components of water regime. However, factors other than water regime such as sediment texture (particle size distribution) (Black 1968), seed bank composition before the window of opportunity has opened (*sensu* Simpson *et al.* 1989) and canopy cover may influence floristic composition. Lakes or areas within lakes that have the same water regime may have a different floristic composition due to these factors.

The study had three aims:

The first aim was to validate the window of opportunity model (Figure 5.1) by comparing lakes with different rates of drawdown. The model predicts that the length of time a window of opportunity will remain open is inversely related to the rate of drawdown. Therefore, species will persist for longer in lakes where water levels are drawn down by evaporation compared with those that are used for water supply and drawn down rapidly.

The second aim was to test the seed bank recruitment model proposed in Chapter 4 (Figure 4.11 and Table 4.3). Due to low inflows, only the section of the model that predicts species composition when the sediment is exposed was tested. This section of the model consists of four sub-states that the system switches between depending on water level (Figure 4.11 and Table 4.3). The species present in each sub-state will be dependent on water regime requirements (Chapter 4).

The final aim was to determine if there was any correlation between the floristic composition of the lakebed vegetation and environmental variables. The environmental variables chosen were soil moisture (at four depths), sediment exposure time, height of the quadrat in relation to the water level, soil texture, canopy cover, and elevation.

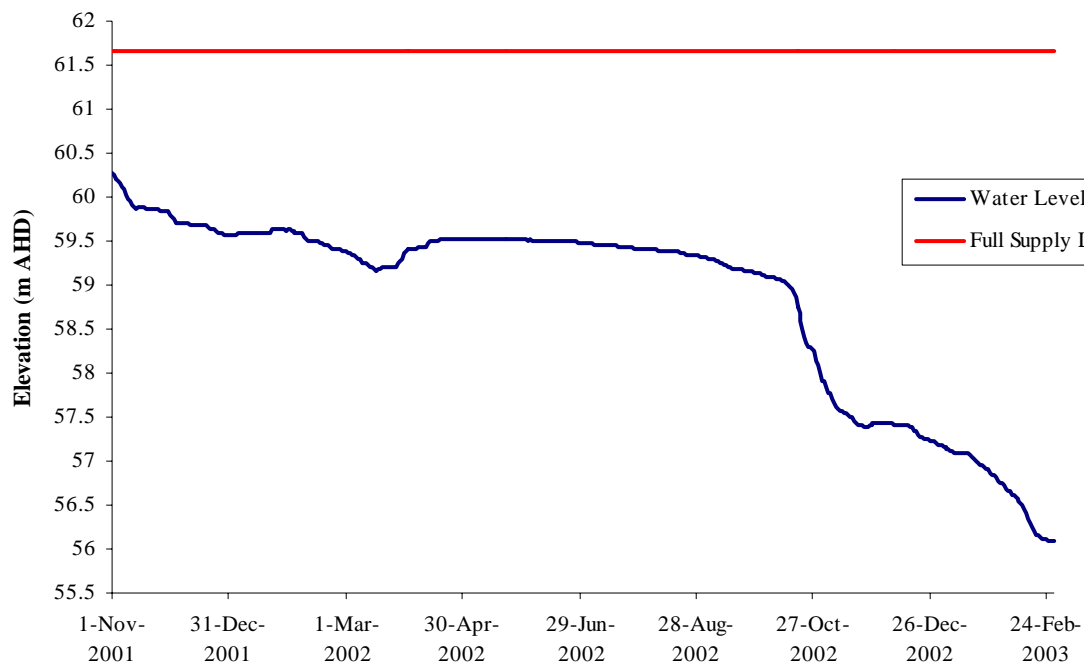
## **5.2 Methods**

### **5.2.1 Study Sites and Hydraulic Regimes**

Lakes Malta, Balaka, Wetherell, Menindee and Cawndilla exhibit three hydraulic regimes typical of the Menindee Lakes. Lakes Malta and Balaka are small shallow lakes upstream of the Menindee main weir that dry by evaporation when the water level in Lake Wetherell falls below the sill of the feeder creeks (Scholz *et al.* 1999). Lake Wetherell water levels may remain relatively static for long periods (New South Wales Department of Land and Water Conservation 2003) (Figure 1.5). When Lake Wetherell is drawn down, the rate of

fall is rapid until the floodplain is exposed after which releases are reduced or stopped and water may remain at this level for several months (New South Wales Department of Land and Water Conservation 2003) (Figure 1.5). During periods of high demand, Lakes Cawndilla and Menindee can have rates of drawdown in excess of  $5 \text{ cm day}^{-1}$  (New South Wales Department of Land and Water Conservation 2003).

In November 2001 the water level in Lake Wetherell was approximately 1.5 m below full supply level, which meant the floodplain was exposed (Figure 5.2). Between November 2001 and September 2002, the water level fell less than 1 m with a small inflow during April 2002 (Figure 5.2). Between October 2002 and February 2003, water levels were drawn down rapidly (Figure 5.2).



**Figure 5.2: Water level in Lake Wetherell from November 1<sup>st</sup> 2001 to February 28<sup>th</sup> 2003 (New South Wales Department of Land and Water Conservation 2003).**

In November 2001, Lake Malta was isolated from Lake Wetherell and drying due to evaporation (Figure 1.5). Water levels were estimated from relative dumpy level readings of the feeder creek. The water level fell at less than  $1 \text{ cm day}^{-1}$ , until dry in April 2002 (Figure 5.3).

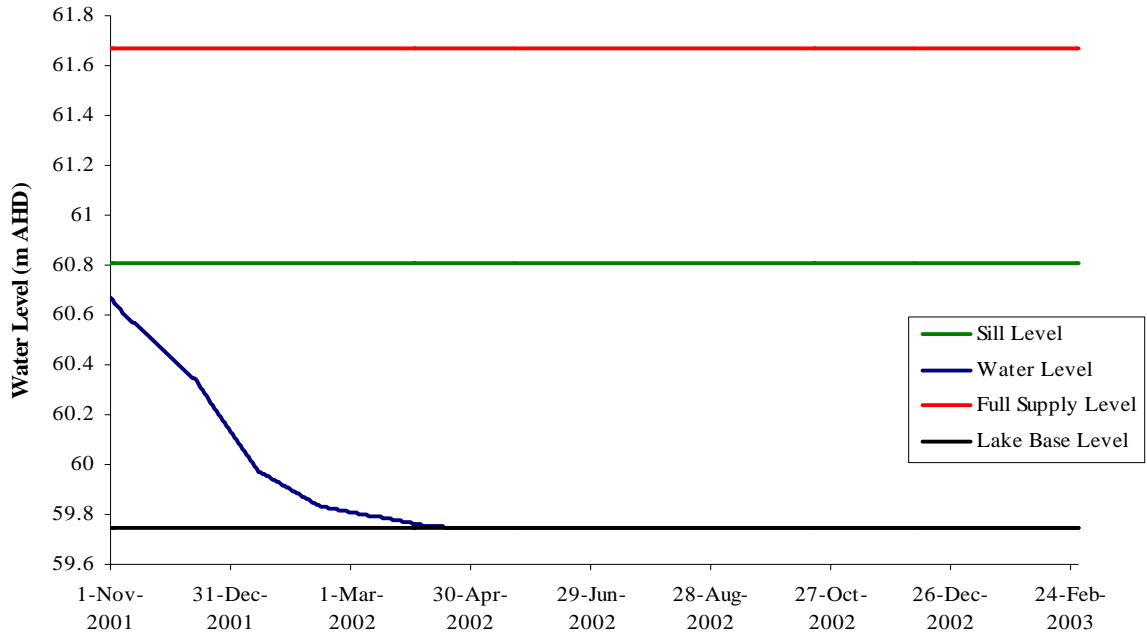


Figure 5.3: Water level in Lake Malta from November 1<sup>st</sup> 2001 to February 28<sup>th</sup> 2003.

Lake Balaka was also isolated from Lake Wetherell in November 2001 (Figure 1.5) and drying due to evaporation. Water levels were determined in the same fashion as Lake Malta. The water level fell at approximately 1 cm day<sup>-1</sup>, until dry in March 2002 (Figure 5.4).

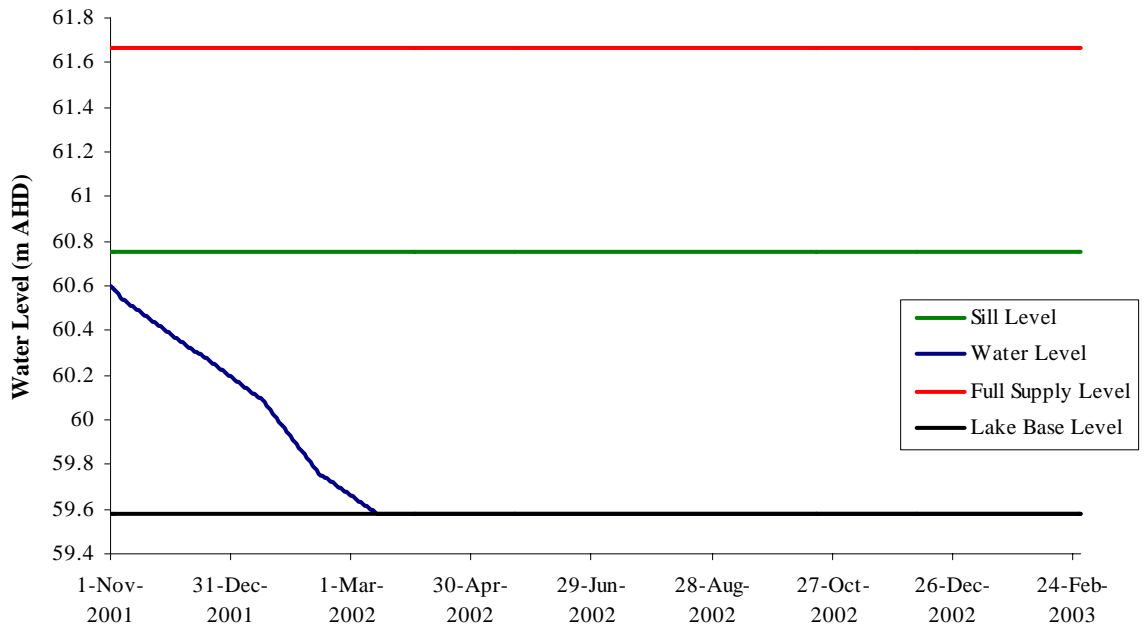
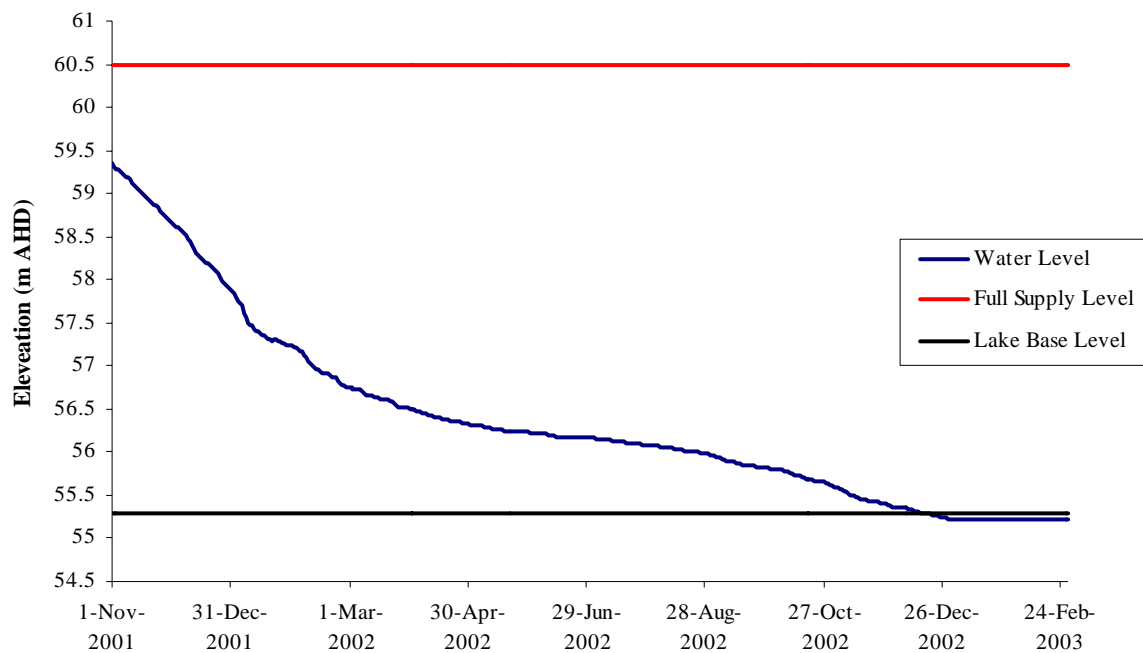


Figure 5.4: Water level in Lake Balaka from November 1<sup>st</sup> 2001 to February 28<sup>th</sup> 2003.

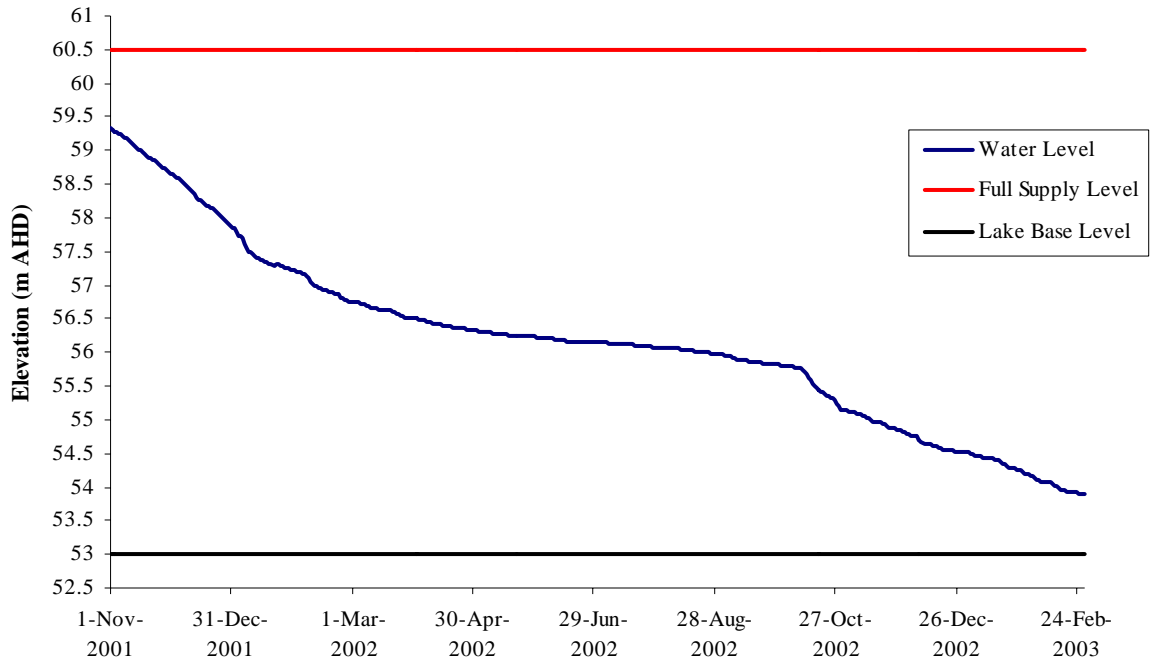
The Lake Menindee water level in November 2001 was approximately 1.2 m below full supply level and falling 1 to 6 cm day<sup>-1</sup> (New South Wales Department of Land and Water Conservation 2003) (Figure 5.5). The rate of drawdown slowed between April and August 2002 after, which it increased until the lake was dry at the end of December 2002 (Figure 5.5).



**Figure 5.5: Water level in Lake Menindee from November 1<sup>st</sup> 2001 to February 28<sup>th</sup> 2003 (New South Wales Department of Land and Water Conservation 2003).**

The water levels in Lake Cawndilla (Figure 5.6) showed a similar pattern to those in Lake Menindee (Figure 5.5) except that the lake did not dry during the study period. When surveyed in February 2003 approximately 1 m of water remained in the lake (Figure 5.6).





**Figure 5.6: Water level in Lake Cawndilla from November 1<sup>st</sup> 2001 to February 28<sup>th</sup> 2003 (New South Wales Department of Land and Water Conservation 2003).**

### 5.2.2 Plant Surveying Protocol

Species area curves showed that the optimum quadrat was a rectangle placed parallel to the shore with dimensions 1 x 20 m with 40 0.5 m cells. The presence or absence of species was recorded for each cell.

Three replicate transects ( $n = 3$ ), 50 m apart, were established perpendicular to the lakeshore on the south-western shores of Lakes Malta, Balaka, Menindee and Cawndilla (Figure 5.7). The banks of Lake Wetherell were generally steep and the only suitable location was on the southern shore of the lake. The elevation of the first and subsequent quadrats was where plant germination was active at that time. Quadrats position was recorded by GPS (Garmin E-trex). The vegetation was surveyed on ten occasions, November 2001, December 2001, January 2002, February 2002, March 2002, April 2002, May 2002, August 2002, November 2002 and February 2003. Each time the vegetation was surveyed and as water levels receded, one quadrat was added to each transect (Figure 5.7).

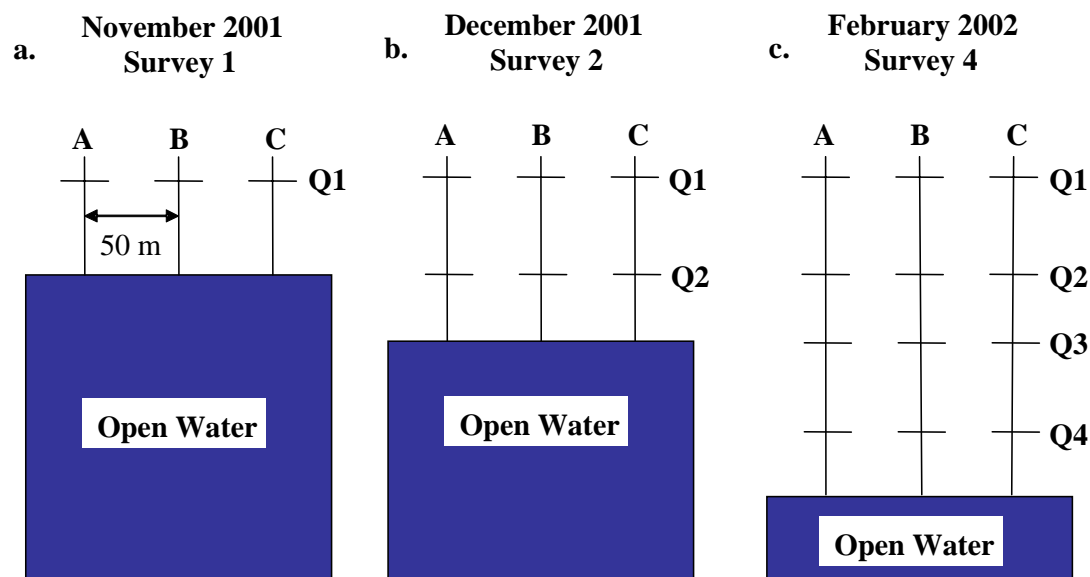


Figure 5.7: Vegetation sampling strategy as the lakes were drawn down, for a. November 2001, b. December 2001 and c. February 2002. The number of quadrats for each transect (A, B and C) increased as more lakebed was exposed until the lake dried.

The sampling strategy resulted in six quadrats on each transect for Lake Malta, five for Lake Balaka, nine for Lake Menindee and ten for Lake Cawndilla. Only two quadrats were used in Lake Wetherell due to the steep banks. A summary of the number of days the sediment was exposed for each quadrat in each lake at each survey is given in Appendix 5. The elevation of the quadrats was determined using a dumpy level to compare the elevation of the quadrat and the water level.

At each survey, soil samples were collected at depth intervals of 0-7.5 cm, 7.5-15 cm 15-25 cm and 25-40 cm and placed in airtight containers for later determination of soil moisture by the gravimetric method (Rayment and Higginson 1992). Soil texture at the same depth intervals was measured using the hydrometer method (Gee and Bauder 1986) and canopy density on a scale from zero to three (0 = no canopy and 3 = dense *Eucalyptus camaldulensis* or *Eucalyptus largiflorens* canopy) were measured once.

### 5.2.3 Plant Identification and Nomenclature

Plants were identified using Jessop and Tolken (1986), Sainty and Jacobs (1981; 1994) and Cunningham *et al.* (1981). Nomenclature follows Jessop and Tolken (1986).

### 5.2.4 Data Analysis

Comparison of floristic composition within each lake was undertaken with NMS ordination using the package PCOrd version 4.28 (McCune and Mefford 1999). Environmental variables with  $r^2$  values greater than 0.3 were overlaid on the ordination plot as vectors. Bray-Curtis distances were used to calculate the similarity matrix for all ordinations (Bray and Curtis 1957) and two-dimensional ordination solutions with stress lower than 20% were deemed acceptable (sensu Clarke 1993). Replicates were pooled for the ordinations for clarity.

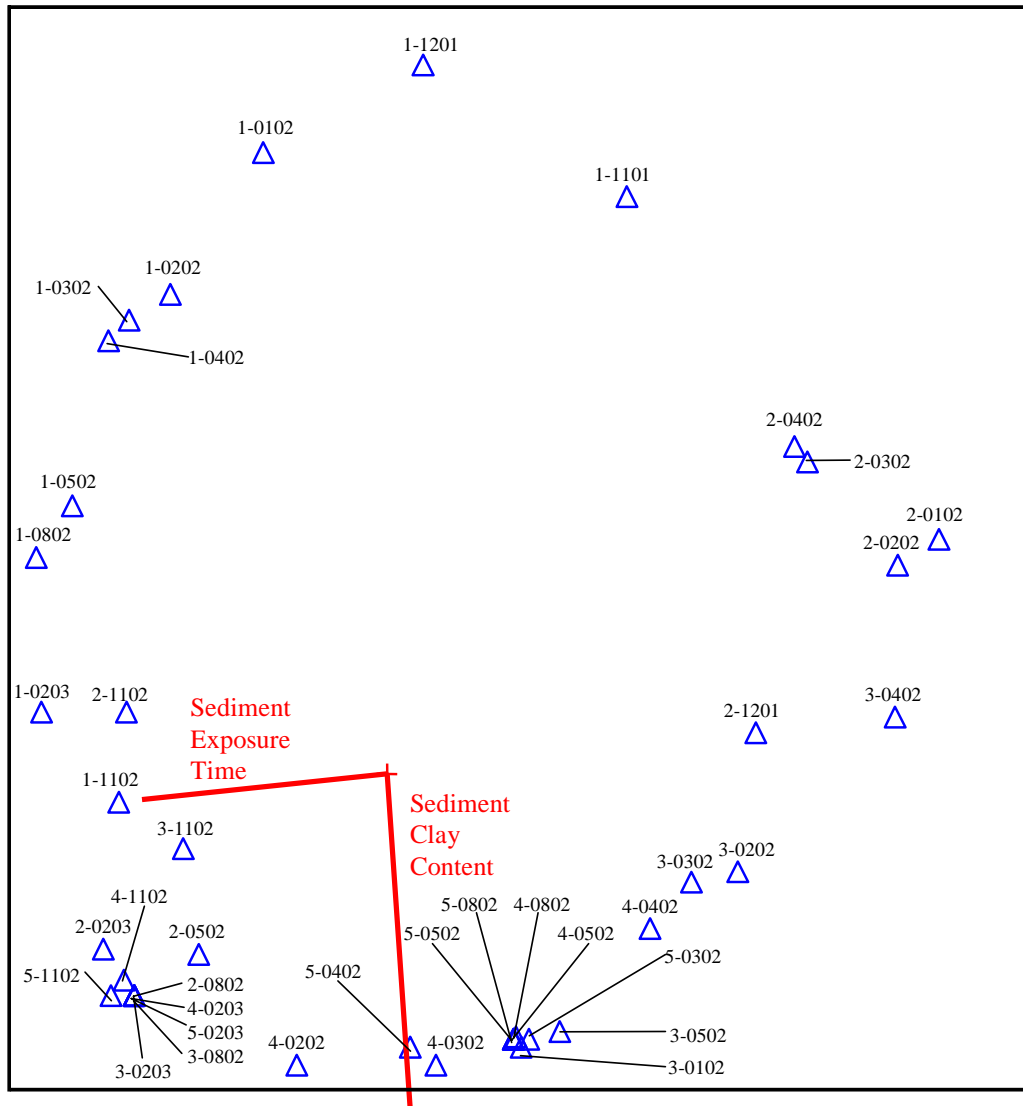
## 5.3 Results

### 5.3.1 Lake Malta

Sediment exposure time ( $r^2 = 0.46$ ) and sediment clay content (texture) ( $r^2 = 0.73$ ) were the only environmental variables with  $r^2$  values greater than 0.3 (NMS ordination: Figure 5.8). Quadrats grouped according to differences in these factors (Figure 5.8).

The change in floristic composition as sediment exposure time increased was probably due to the decrease in abundance of annuals as they set seed and died (Figure 5.9).

Floristic composition changed as sediment clay increased (Figure 5.8). There was no pattern in sediment clay content from the surface to 40 cm but a soil texture gradient from the edge to the centre of the lake was present (Appendix 1a). Quadrat one had the lowest clay content (25%) and as the elevation decreased the sediment clay content increased (65% in quadrat 6) (Appendix 1a).



**Figure 5.8:** NMS ordination of the quadrats through time from Lake Malta (stress = 15.2%), (the clay content of the sediment at different depths vectors were indistinguishable and grouped as one variable), (1- to 5- = quadrat number and 1101 to 0203 denotes sampling time e.g. 1101 = November 2001).

Soil moisture ranged from 3 to 13% (surface) and 10 to 34% (sub-surface) (Appendix 6a) but was not correlated with floristic composition. As the lake dried, the soil moisture content decreased at all sampling depths and there was very little change in soil moisture after the sediment was exposed for more than 150 days (Appendix 6a). Generally, soil moisture increased as sample depth increased (Appendix 6a and Appendix 7a).

Changes in the extant vegetation with respect to the sediment exposure time, can give an indication into the different responses of species to hydraulic regime. As lake levels fell there was no evidence of live individuals (except dormant *Cyperus gymnocaulos*

rhizomes), which suggests that no species germinated whilst the sediment was inundated (sensu Chapter 4).

All species germinated less than 25 days after the sediment was exposed (Figure 5.9). After 50 days of exposure, species richness decreased as *Heliotropium europaeum*, *Scirpus* sp. and *Wahlenbergia communis* were not found (Figure 5.9). After 100 days of exposure, no *Heliotropium amplexicaule* plants occurred (Figure 5.9). Only five species persisted in quadrats exposed for longer than 200 days and in the quadrats exposed for nearly 500 days, the only species present were *Morgania floribunda*, *Cyperus gymnocaulos*, *Haloragis aspera* and *Sporobolus mitchelli* (Figure 5.9).

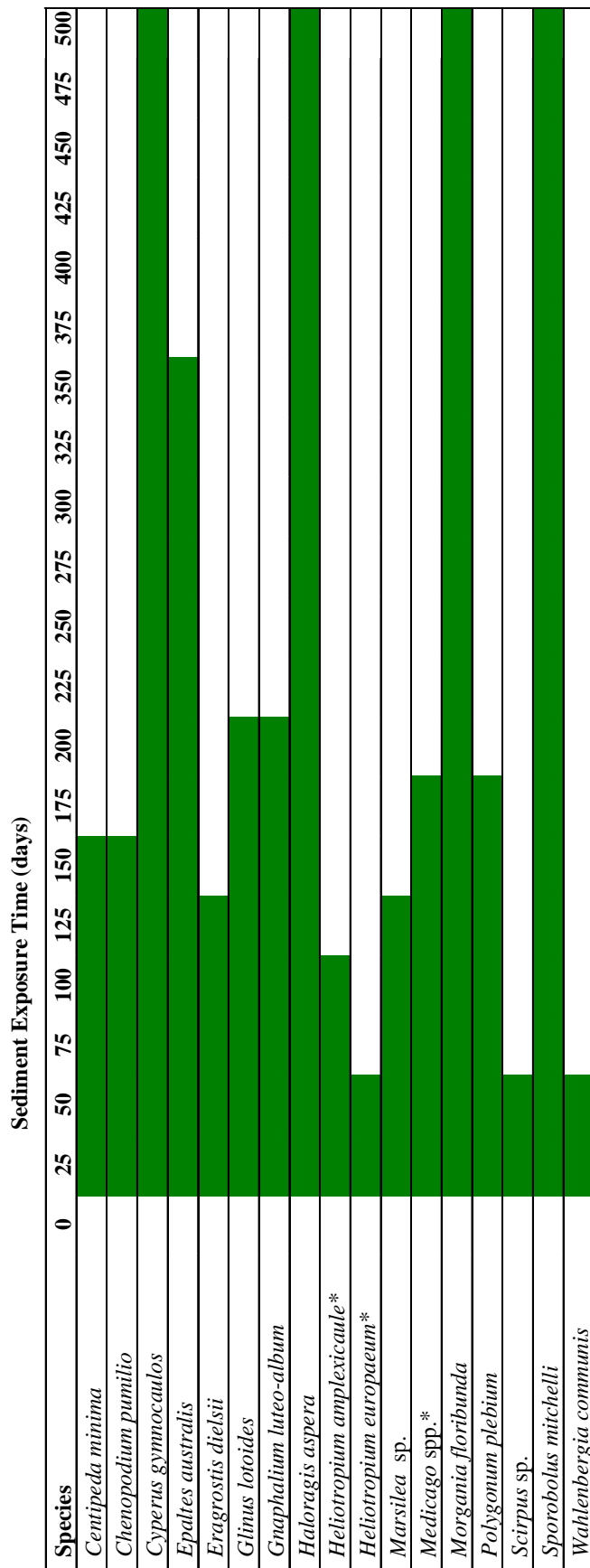


Figure 5.9: Sediment exposure time and species present in the extant vegetation of Lake Malta (\* denotes exotic species).

### 5.3.2 Lake Balaka

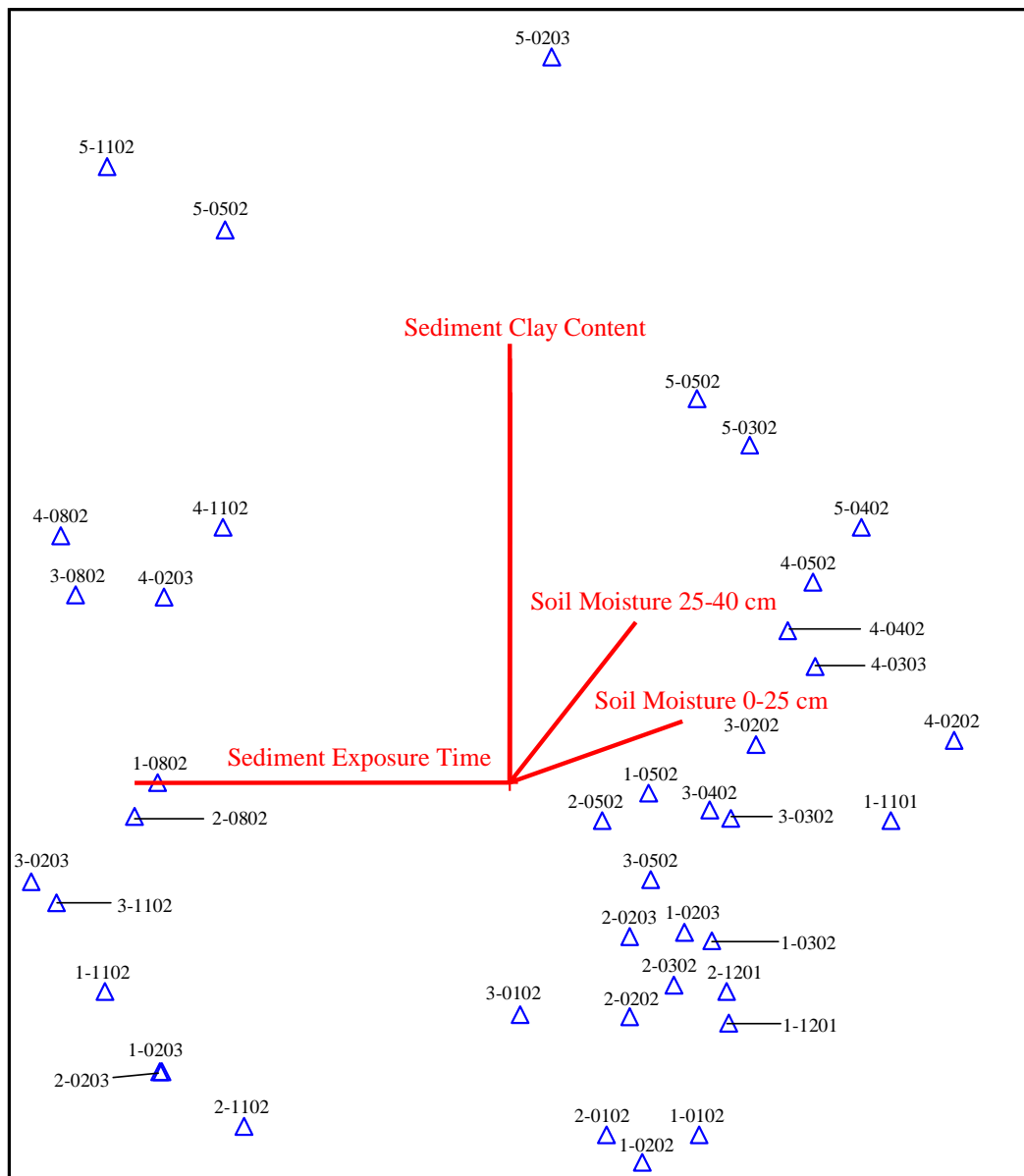
Sediment exposure time ( $r^2 = 0.65$ ), soil moisture 0-25 cm ( $r^2 = 0.36$ ), soil moisture 25-40 cm ( $r^2 = 0.38$ ) and clay content ( $r^2 = 0.81$ ) had  $r^2$  values greater than 0.3 (NMS ordination: Figure 5.10). Quadrats generally grouped according to differences in exposure time and soil texture, although quadrats with low soil moisture (quadrats one and two when surveyed later than August 2002) formed a group (Figure 5.10).

Similar to Lake Malta, the change in floristic composition as sediment exposure time increased was probably due to the quadrats with the longest exposure times being devoid of annuals (Figure 5.11).

Also similar to Lake Malta, floristic composition changed as clay content increased (Figure 5.10). A soil texture gradient from the edge to the centre of the lake is present in Lake Balaka (Appendix 1b). The sediment at high elevations (quadrats 1 and 2) contained the highest proportion of sand (60%), which decreased with a corresponding increase in the proportion of clay at lower elevations (10% sand in quadrat 5) (Appendix 1b).

Soil moisture (Figure 5.10) ranged from 3 to 18% (surface) and 10 to 44% (sub-surface), increased with sampling depth and decreased as sediment exposure time increased (Appendix 6b). The samples from low on the elevation gradient (quadrats 4 and 5) tended to have higher soil moisture contents than quadrats from higher on the elevation gradient (quadrats 1 to 3) when exposed for a similar amount of time (Figure 5.10).

Water loss from the sediment was higher when the sediment was first exposed until 200 days after exposure than from day 200 to 500 (Appendix 6b). After nearly 500 days of exposure the soil moisture content between 25 and 40 cm deep for quadrat one was 12% (Appendix 6b). The corresponding quadrat in Lake Malta had soil moisture content of 7% (Appendix 6a), which indicated that the sediment water holding capacity was higher in Lake Balaka than Lake Malta.



**Figure 5.10: NMS ordination of the quadrats through time from Lake Balaka (stress = 15.1%), (the clay content of the sediment at different depths vectors were indistinguishable and grouped as one vector as were the soil moisture 0-7.5 cm, 7.5-15 cm and 15-25 cm vectors), (see Figure 5.8 for explanation of abbreviations).**

All species germinated within 25 days of the sediment being exposed and species richness decreased after 50 days of exposure (Figure 5.11). Despite drying faster than Lake Malta (Figure 5.3 and Figure 5.4) species persisted for longer. For example *Centipeda minima* was found in quadrats that were exposed for 300 days in Lake Balaka (Figure 5.11) but only present in Lake Malta in quadrats that were exposed for less than 175 days (Figure 5.9). *Chenopodium pumilio*, *Epiltes australis*, *Eragrostis dielsii*, *Glinus lotoides*, *Heliotropium amplexicaule*, *Heliotropium europaeum*, *Marsilea* sp., *Medicago* spp.,



*Polygonum plebium* and *Scirpus* sp. all occurred in quadrats in Lake Balaka that were exposed for longer than in Lake Malta (Figure 5.9 and Figure 5.11). *Morgania floribunda* and *Sporobolus mitchelli* were the only species that persisted for the duration of the study (Figure 5.11).

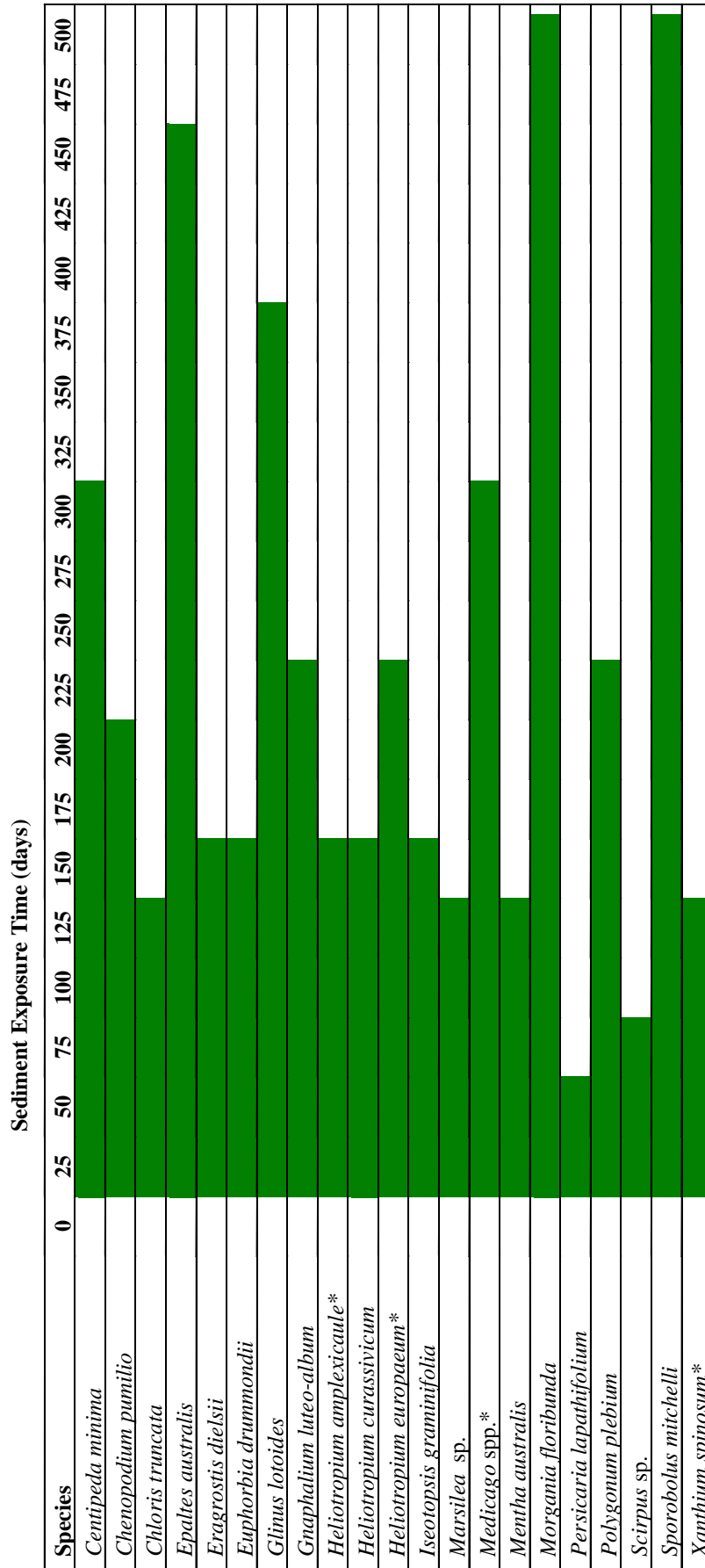
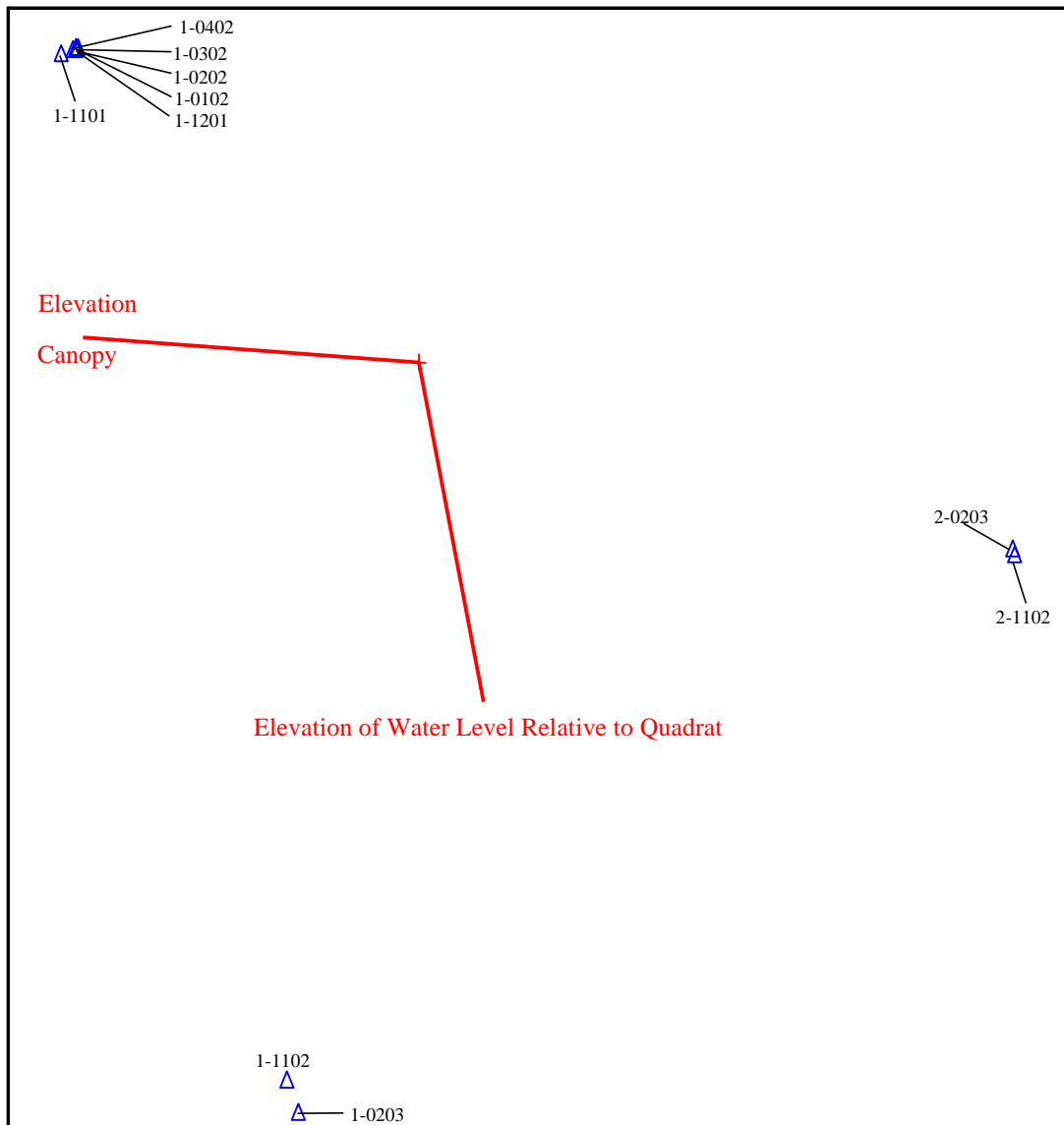


Figure 5.11: Sediment exposure time and species present in the extant vegetation of Lake Balaka (\* denotes exotic species).

### 5.3.3 Lake Wetherell

Three distinct vegetation communities developed over the study period represented by: quadrat one November 2001 to April 2002, quadrat one November 2002 to February 2003 and quadrat two (NMS ordination: Figure 5.12). The groups were related to differences in the elevation of the quadrat relative to the water ( $r^2 = 0.88$ ), elevation ( $r^2 = 0.99$ ) and canopy cover ( $r^2 = 0.99$ ) (Figure 5.12). During the surveys between November 2001 and April 2002, the water level decreased 60 cm in comparison to 300 cm between April 2002 and February 2003 (Figure 5.2) and quadrat one was at a higher elevation than quadrat two and had a dense canopy of *Eucalyptus camaldulensis*.

In contrast to Lakes Malta (Figure 5.8) and Balaka (Figure 5.10), the  $r^2$  for sediment texture was lower than 0.3 (Figure 5.12) because there was no texture gradient from high to low elevation (Appendix 1c). Soil clay content decreased with increased sampling depth for quadrat 1 (60% at 0-7.5 cm and 45% at 25-40 cm) and was uniform for quadrat 2 (60%) (Appendix 1c).



**Figure 5.12: NMS ordination of the quadrats through time from Lake Wetherell (stress = 10.7%), (see Figure 5.8 for explanation of abbreviations).**

Soil moisture ranged from 5 to 28% (surface) and 13 to 28% (sub-surface) and the longer the quadrat was exposed the lower the soil moisture content (Appendix 6c). The water holding capacity of the Lake Wetherell sediment was similar to that of Lake Balaka (Appendix 6b), with the moisture content of quadrat one 13% at 25-40 cm in February 2003 (Appendix 6c). In contrast to Lake Balaka, which was dry, there was still water in Lake Wetherell in February 2003 but there was a 4.5 m elevation difference between quadrat one and the water level.

Similar to Lakes Malta and Balaka all species germinated within 25 days of the sediment being exposed and species richness decreased after 50 days of exposure (Figure 5.13). No

annuals (Cunningham *et al.* 1981) were detected after the sediment was exposed for longer than 200 days (Figure 5.13). Six species persisted for the duration of the study in quadrat one and four species persisted for 475 days (Figure 5.13). The species that persisted for 475 days were found exclusively in quadrat two and were present from just after the quadrat was exposed until February 2003.

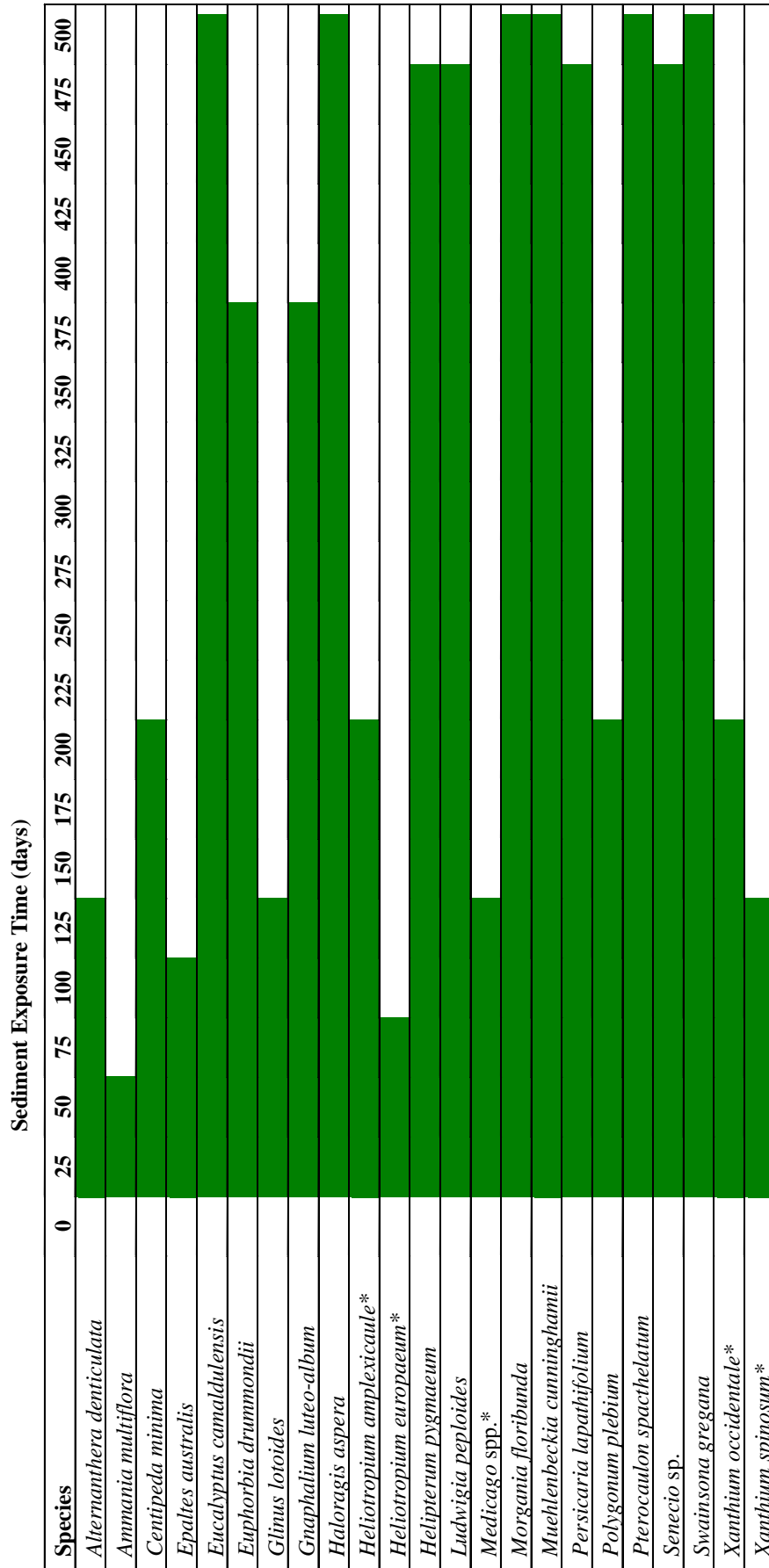


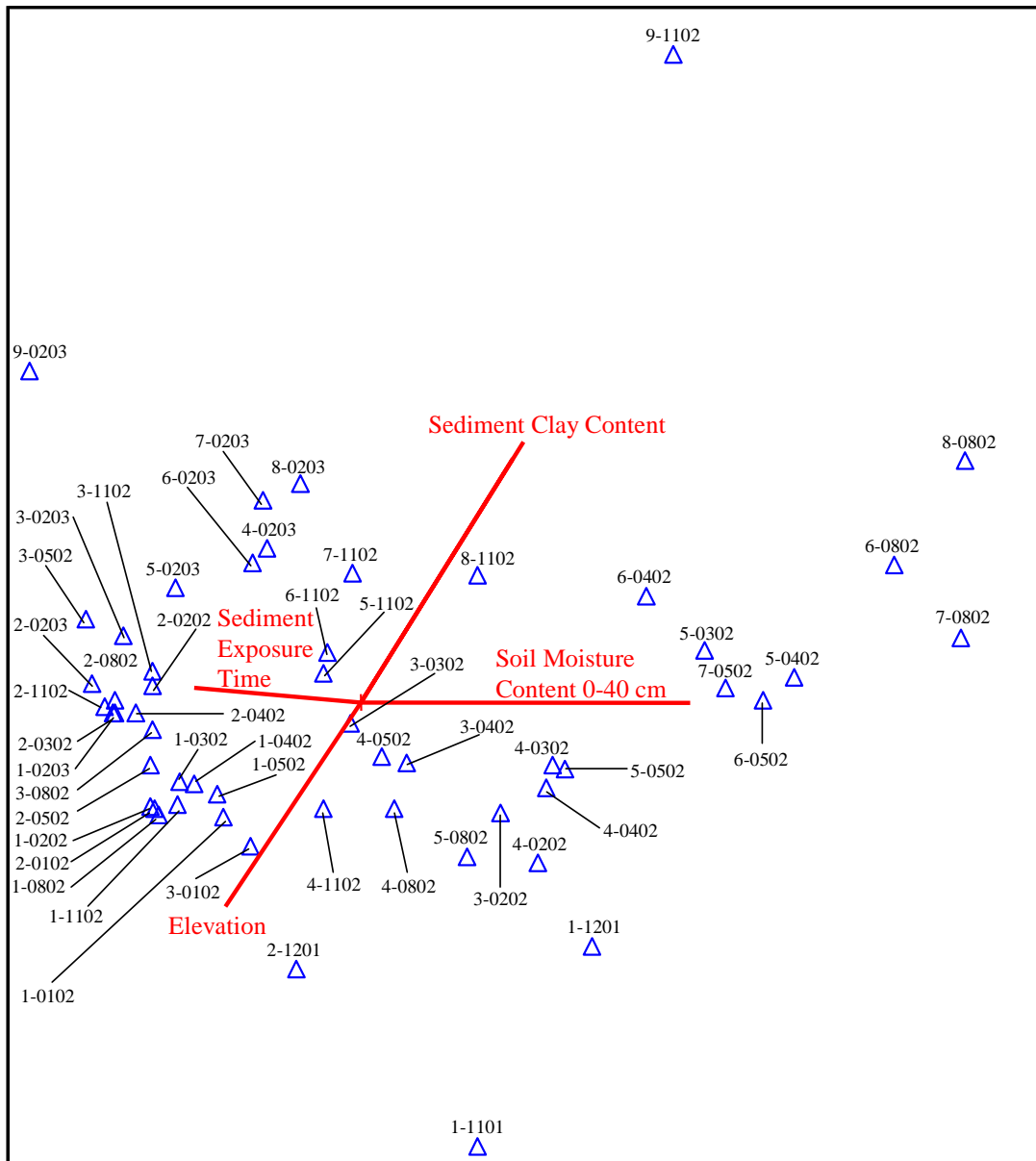
Figure 5.13: Sediment exposure time and species present in the extant vegetation of Lake Wetherell (\* denotes exotic species).

### 5.3.4 Lake Menindee

The  $r^2$  values for sediment clay content ( $r^2 = 0.56$ ), sediment exposure time ( $r^2 = 0.31$ ), soil moisture ( $r^2 = 0.60$ ) and elevation ( $r^2 = 0.45$ ) were all higher than 0.3 (NMS ordination: Figure 5.14). These variables; however, were not independent: the vectors for sediment clay content and elevation extended in opposite directions, likewise the vectors for soil moisture and sediment exposure time (Figure 5.14). Quadrats were located in the ordination space with respect to the soil texture and elevation, and soil moisture and exposure time gradients.

There was a strong soil texture gradient in Lake Menindee; the sediment around the edges consisted of mainly coarse sand (85% sand) and the sediment in the centre consisted mainly of clay (90% clay) (Appendix 1d).

Soil moisture ranged from 1 to 41% (surface) and 3 to 48% (sub-surface). As exposure time increased soil moisture decreased (Appendix 6d). Quadrats with the longest exposure times (quadrats one to three) showed little difference in soil moisture between the surface and 40 cm deep (Appendix 6d and Appendix 7d). After the sediment was exposed for longer than 250 days the decrease in soil moisture content at all sampling depths was lower than the first 250 days (Appendix 6d). The variation in soil moisture between quadrats exposed for similar durations was greater than Lakes Malta (Appendix 6a), Balaka (Appendix 6b) and Wetherell (Appendix 6c), hence the higher  $r^2$  value for soil moisture than sediment exposure time.



**Figure 5.14:** NMS ordination of the quadrats through time from Lake Menindee (stress = 11.4%), (the clay content of the sediment at different depths vectors were indistinguishable and grouped as one variable as were the soil moisture vectors), (see Figure 5.8 for explanation of abbreviations)

All species present germinated within 25 days of the sediment being exposed (except *Cirtullus lanatus*, which germinated between 50 and 75 days after exposure) (Figure 5.15). *Heliotropium europaeum* and *Limosella australis* persisted for between 75 and 100 days and *Chenopodium pumilio*, *Eragrostis dielsii*, *Myosurus minima*, *Myriophyllum verrucosum*, *Nicotiana velutino* and *Persicaria lapathifolium* persisted for between 100 and 125 days (Figure 5.15). Despite the faster rate of drawdown *Centipeda minima*, *Ammania multiflora*, *Alternanthera denticulata* and *Epaltres australis* persisted for longer in this lake than in Lake Wetherell (Figure 5.13 and Figure 5.15). Species richness



decreased after 75 days of exposure (Figure 5.15). Five species persisted for the duration of the study, one of which was *Epaltes australis* (Figure 5.15). *Epaltes australis* is an annual (Cunningham *et al.* 1981) and in the Lakes Malta, Balaka and Wetherell did not persist for longer than 350 days (Figure 5.9, Figure 5.11 and Figure 5.13).

Fifteen of the 28 species present were only found in quadrats where the sediment had high clay content and three were widespread across all quadrats (Figure 5.15). The quadrats with the highest clay contents were lower on the elevation gradient and not exposed for as long as the quadrats higher on the elevation gradient (Appendix 1d). Therefore, it appears that the species only found in the quadrats with high clay content were not as desiccation tolerant as those found higher on the elevation gradient (Figure 5.15). However, live plants were present in these quadrats when surveyed in February 2003 (pers. obs.).

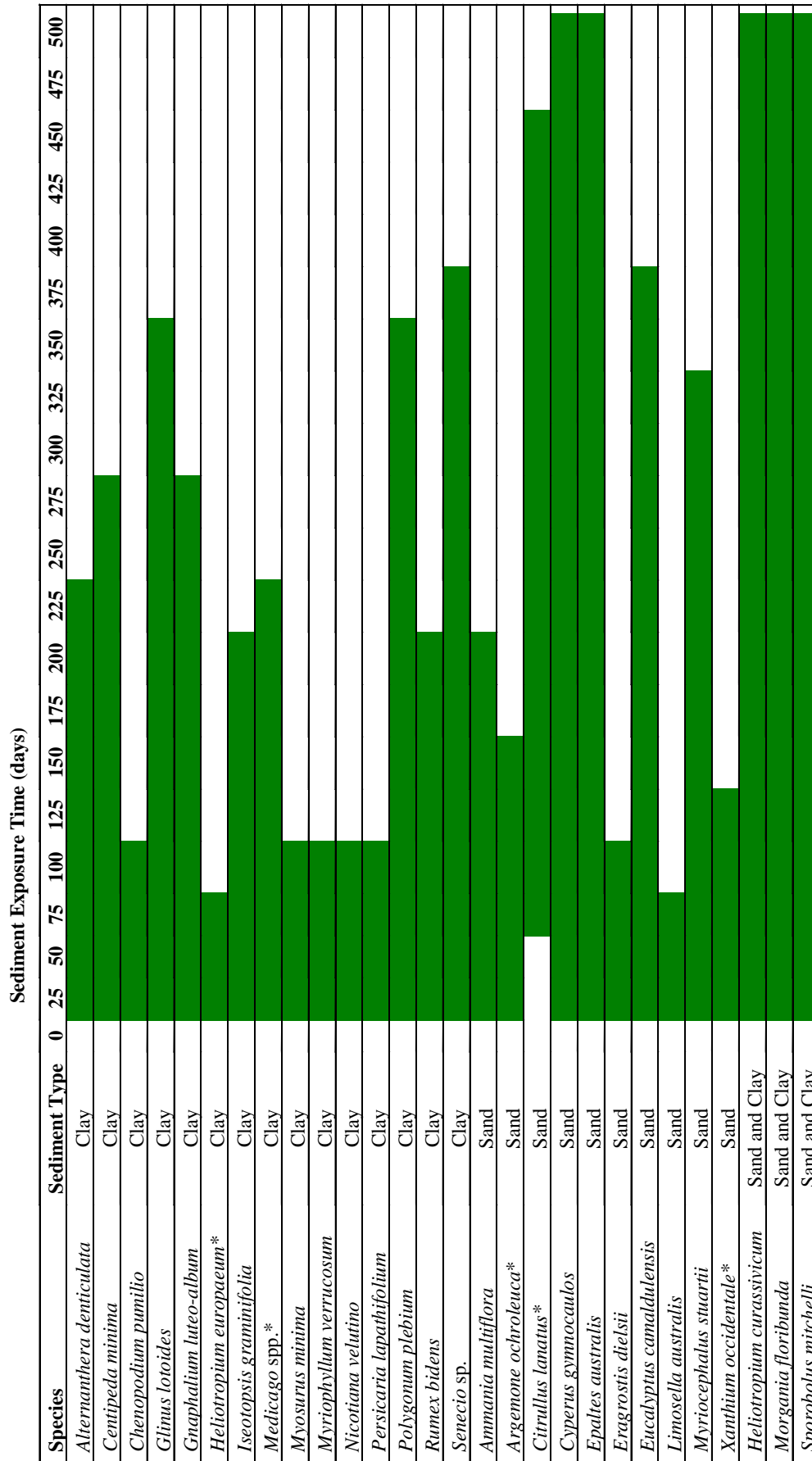
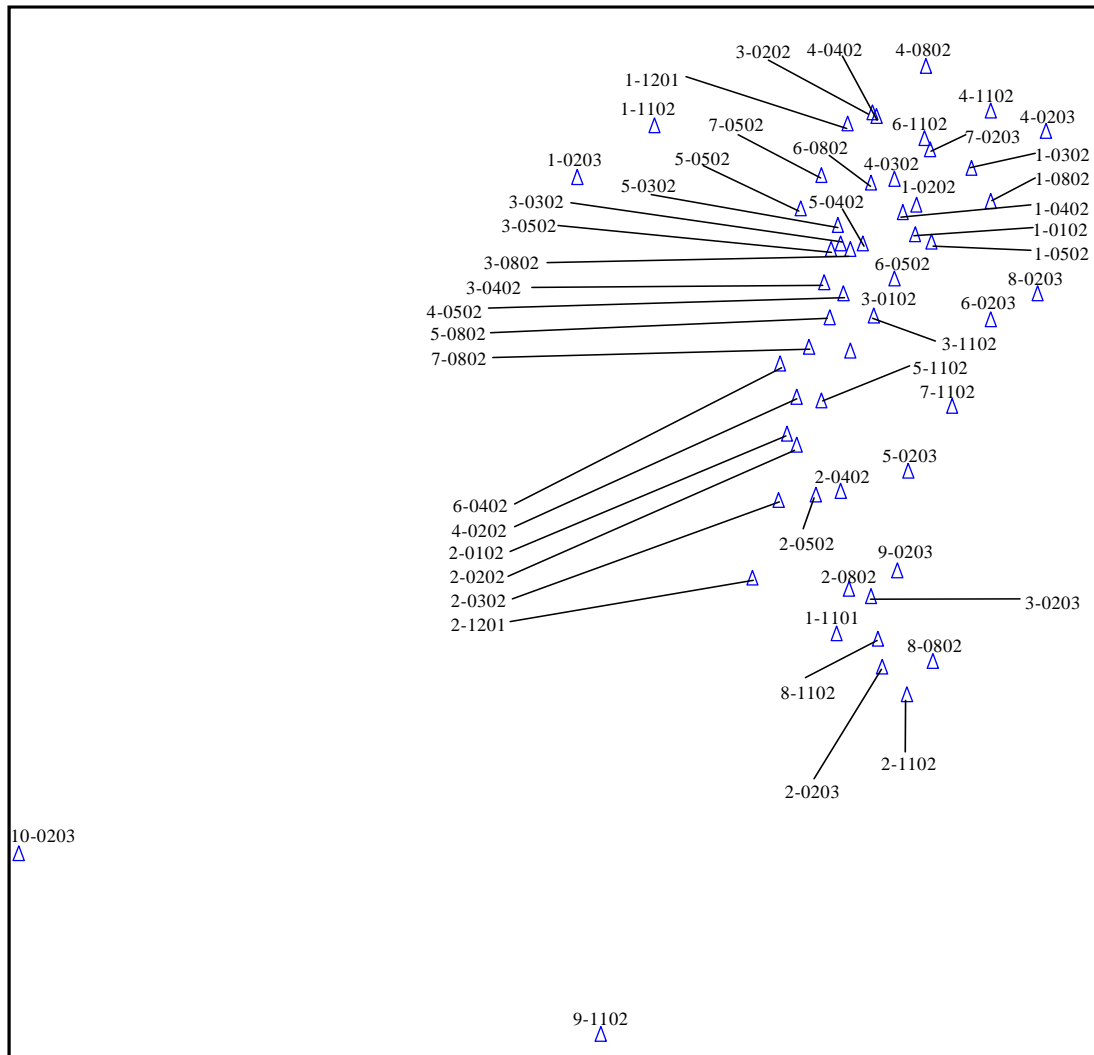


Figure 5.15: Sediment exposure time, sediment type preference and species present in the extant vegetation of Lake Menindee (\* denotes exotic species).

### 5.3.5 Lake Cawndilla

In contrast to the other lakes, none of the environmental variables had an  $r^2$  of over 0.3 (NMS ordination: Figure 5.16), in fact all variables (except sediment clay content 25-40 cm:  $r^2 = 0.21$ ) were between 0.05 and 0.15. Two outliers represented the first surveys of the two quadrats with the lowest elevations (quadrats nine and ten) (Figure 5.16). Quadrat nine when surveyed in November 2002 had only a small number plants present likewise quadrat ten when surveyed in February 2003 although the latter had *Myriocephalus stuartii* present in over half the cells in each quadrat.

The soil texture gradient from high to low elevation in Lake Cawndilla was not as defined as the other deflation lakes (Appendix 1e). The sediment at all quadrats and sampling depths generally consisted of 60 to 90% sand although the sediment clay contents in quadrats nine and ten (30%-40%) were higher than quadrats one to eight (Appendix 1e).



**Figure 5.16: NMS ordination of the quadrats through time from Lake Cawndilla (stress = 10.6%), (see Figure 5.8 for explanation of abbreviations).**

Soil moisture ranged from 2 to 24% (surface) and 3 to 28% (subsurface), decreased as sediment exposure time increased and increased with sampling depth (Appendix 6e). Similar to Lake Menindee, the quadrats with the longest exposure times (quadrats one to three) showed little difference in soil moisture between the surface and 40 cm deep (Appendix 6e and Appendix 7e). After 200 days of exposure, the decrease in soil moisture was lower than the first 200 days (Appendix 6e).

Most of the species present germinated within 25 days of the sediment being exposed (Figure 5.17). However, *Solanum karsensis* and *Asphodelus fistulosus* were not observed until between 125 to 150 and 375 to 400 days respectively (Figure 5.17). Eight species

persisted for less than 150 days and four species persisted for the duration of the study (Figure 5.17). *Solanum karsensis* and *Asphodelus fistulosus* also persisted until the end of the study (Figure 5.17). The annual species *Argemone ochroleuca* (Cunningham *et al.* 1981), germinated soon after the sediment was exposed, set seed and died between 200 and 225 days (Figure 5.17). This species germinated after rainfall; hence, it was found in quadrats one and two when surveyed in November 2002 and February 2003 (Figure 5.17). Species richness generally declined after a quadrat was exposed for longer than 75 days (Figure 5.17). The dominant species throughout the survey period were *Cyperus gymnocaulos* and *Morgania floribunda*, which were present for the duration of the study in all quadrats (Figure 5.17).

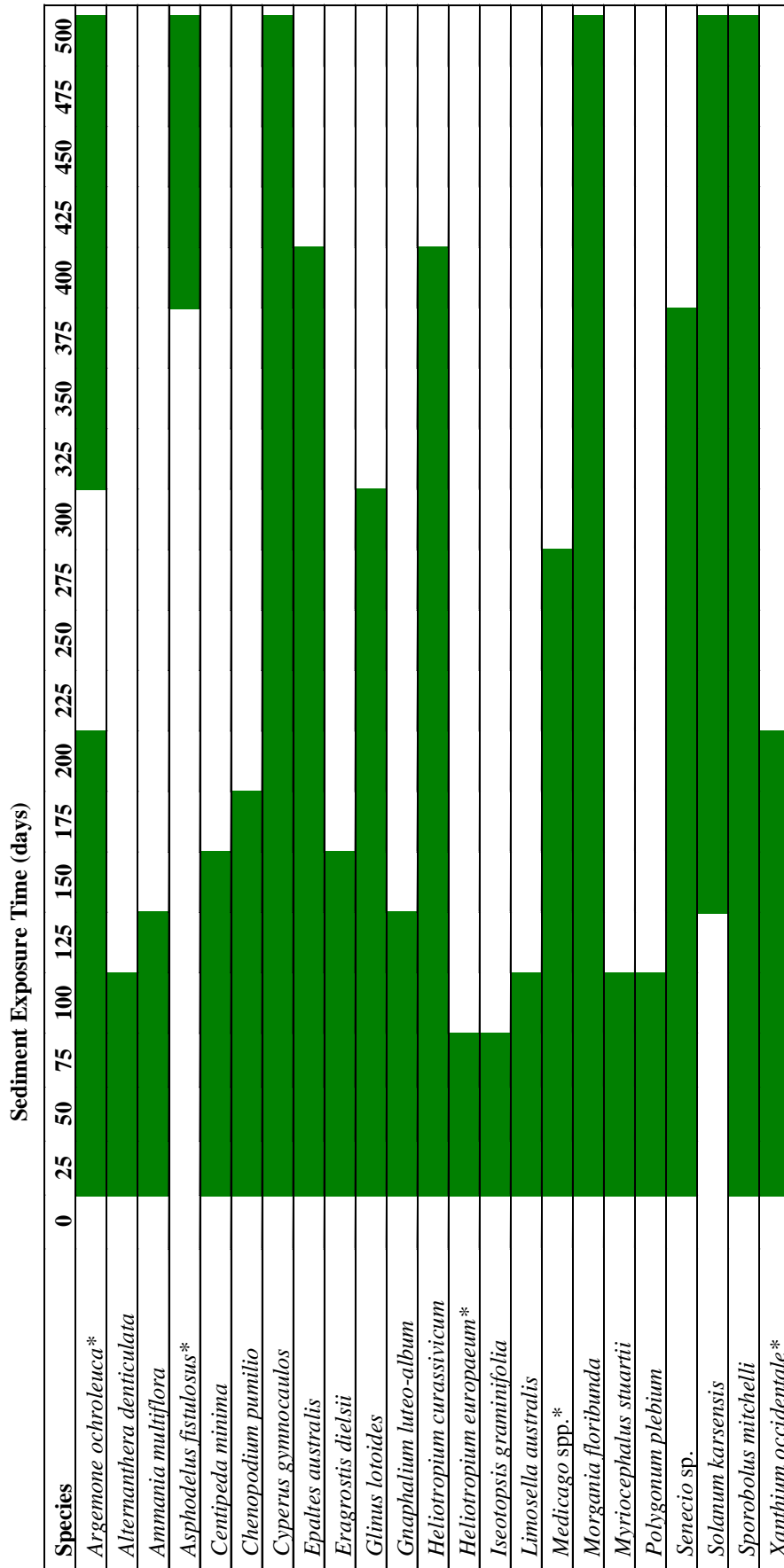


Figure 5.17: Sediment exposure time and species present in the extant vegetation of Lake Cawndilla (\* denotes exotic species).

## 5.4 Discussion

### 5.4.1 Window of Opportunity Model

Windows of opportunity opened and closed as water levels fell. The window of opportunity for germination was open when there was high soil moisture in the top 7.5 cm. After the top 7.5 cm of soil dried, rainfall during the study period did not provide sufficient soil moisture for germination of amphibious or floodplain species and the only terrestrial species that germinated were *Citrullus lanatus*, *Argemone ochroleuca*, *Solanum karsensis* and *Asphodelus fistulosus*.

The windows of opportunity for establishment and reproduction were dependent on sub-surface moisture and species. Progressive desiccation did not extirpate or prevent reproduction in *Morgania floribunda*, *Cyperus gymnocaulos*, *Asphodelus fistulosus*, *Sporobolus mitchelli*, *Haloragis aspera*, *Eucalyptus camaldulensis*, *Helipterum pygmaeum*, *Ludwigia peploides*, *Muehlenbeckia cunninghamii*, *Pterocaulon spathelatum*, *Swainsona gregana* (in all lakes) and *Heliotropium curassivicum* and *Epaltes australis* (in Lake Menindee). Except for *Epaltes australis*, these species are perennials (Cunningham *et al.* 1981) and their survival suggests they are desiccation tolerant. The reproductive potential of annuals also was not inhibited as the lakes dried, because they were able to complete their life cycle before soil moisture reached critical levels (pers. obs.).

A species may still be successful if it can complete its life cycle whilst conditions are favourable. The ratio of a species minimum life cycle to its desiccation tolerance provides an index of success. Desiccation tolerance and minimum life cycle duration for common Menindee Lakes species are shown in Table 5.1. Desiccation tolerance is an index from 1 (lowest) to 5 (highest) and the minimum life cycle is shortest observed time from germination to seed set (pers. obs.). Generally, species with the lowest desiccation tolerances have the fastest life cycles (Table 5.1). However, some desiccation tolerant annuals and perennials have short life cycles (e.g. *Glinus lotoides* and *Morgania floribunda*) (Table 5.1). Most species have flexible life histories, such as *Limosella australis*, which is a perennial (Cunningham *et al.* 1981) but behaves as annual (pers. obs.) under ephemeral conditions.

**Table 5.1: Desiccation tolerance indices, life cycle strategy (Cunningham *et al.* 1981) and minimum time observed for successful life cycle completion for common Menindee Lakes species.**

Species	Life Cycle Strategy	Desiccation Tolerance (DT)	Minimum Life Cycle (MLC) (months)	DT:MLC
<i>Scirpus</i> sp.	Annual	3	2	1.50
<i>Wahlenbergia communis</i>	Annual	3	2	1.50
<i>Alternanthera denticulata</i>	Annual	4	3	1.33
<i>Glinus lotoides</i>	Annual	5	5	1.00
<i>Heliotropium europaeum</i>	Annual	2	2	1.00
<i>Limosella australis</i>	Perennial	2	2	1.00
<i>Marsilea</i> sp.	Perennial	4	4	1.00
<i>Morgania floribunda</i>	Perennial	5	5	1.00
<i>Myriocephalus stuartii</i>	Annual	3	3	1.00
<i>Sporobolus mitchelli</i>	Perennial	5	5	1.00
<i>Swainsona gregana</i>	Perennial	5	5	1.00
<i>Argemone ochroleuca</i>	Annual	5	6	0.83
<i>Cyperus gymnocaulos</i>	Perennial	5	6	0.83
<i>Senecio</i> sp.	Perennial	5	6	0.83
<i>Xanthium occidentale</i>	Annual	5	6	0.83
<i>Ammania multiflora</i>	Annual	3	4	0.75
<i>Iseotopsis graminifolia</i>	Annual	3	4	0.75
<i>Heliotropium amplexicaule</i>	Annual	2	3	0.67
<i>Ludwigia peploides</i>	Perennial	4	6	0.67
<i>Medicago</i> spp.	Annual	4	6	0.67
<i>Polygonum plebium</i>	Annual	2	3	0.67
<i>Epaltes australis</i>	Annual	5	8	0.63
<i>Euphorbia drummondii</i>	Annual	5	8	0.63
<i>Haloragis aspera</i>	Perennial	5	8	0.63
<i>Centipeda minima</i>	Annual	3	5	0.60
<i>Chenopodium pumilio</i>	Annual	3	5	0.60
<i>Gnaphalium luteo-album</i>	Annual	3	5	0.60
<i>Persicaria lapathifolium</i>	Perennial	2	4	0.50
<i>Heliotropium curassivicum</i>	Perennial	4	9	0.44
<i>Myriophyllum verrucosum</i>	Perennial	1	Not observed flowering	NA
<i>Solanum karsensis</i>	Perennial	5	Not observed flowering	NA

Three species did not flower at all locations (pers. obs.). *Persicaria lapathifolium* set seed in Lake Wetherell but in Lakes Balaka and Menindee, it died before flowering indicating that the windows of opportunity for germination and establishment were open but the period was insufficient for reproduction. The same was observed for *Myriophyllum verrucosum* in Lake Menindee. *Solanum karsensis* also did not flower but live individuals were present when surveyed in February 2003 in very dry areas with sandy soil, which suggests that this species is desiccation tolerant.

Flooding closed the opportunity for germination for all species (except *Myriophyllum verrucosum*); however, if germination was successful establishment and reproduction may proceed despite flooded conditions (Chapter 4). The lakes did not flood during the study



period but observations of the lakes when flooded and data from pond experiments (Chapters 4 and 6) showed that *Persicaria lapathifolium*, *Ludwigia peploides*, *Alternanthera denticulata*, *Eucalyptus camaldulensis*, *Muehlenbeckia cunninghamii*, *Marsilea* sp., *Sporobolus mitchelli* and *Myriophyllum verrucosum* all either tolerate or change morphologically in response to flooding. In addition, *Xanthium occidentale* will tolerate partial but not top flooding (Victorsen 2001; Chapter 6).

The rate of drawdown influenced soil moisture and in turn the rate at which windows of opportunity open and close; however, soil texture also influenced soil water holding capacity. The rate of drawdown in Lake Malta was slower than Lake Balaka but because of the higher clay content, soil moisture in Lake Balaka was higher for quadrats exposed for a similar duration. This was probably the reason annuals persisted for longer in Lake Balaka than Lake Malta. It also highlights the life cycle flexibility of these species because all annuals flowered and set seed in both lakes.

#### 5.4.2 Seed Bank Recruitment Model

The results of this study suggest that the seed bank recruitment model (Figure 4.11 and Table 4.3) should be modified to include sediment exposure time and sub-surface soil moisture.

Sub-surface soil moisture is important for plant survival after the window for opportunity for germination has closed. After the sediment had been exposed for nearly 500 days, soil moisture at depths between 25 and 40 cm ranged from 3 to 14% but plants were alive. This implies the sub-surface soil moisture was sufficient for survival. In addition, the species present generally had roots deeper than 40 cm (pers. obs.).

Sediment exposure time is also an important factor, if the window of opportunity for germination has closed, because it will determine whether annuals are present (sensu Capon 2003).

There is also evidence that species present in the exposed intermediate soil moisture state of the model (Figure 4.11) will be present in the exposed low soil moisture state in the field. *Eplates australis*, *Gnaphalium luteo-album*, *Ammania multiflora* and *Marsilea* sp. were all recorded in areas where the soil moisture content was lower than 5% in the top 7.5 cm. It is unclear why these species were present in the field but not in the pond.

Information from Chapter 4, Chapter 5 and Chapter 6 has been summarised in a conceptual model (Chapter 9), which takes into consideration sediment exposure time, sub-surface soil moisture, soil texture, flood duration and depth.

### 5.4.3 Correlation of Vegetation with Environmental Variables

In all lakes, except Lake Cawndilla, at least two environmental variables had  $r^2$  values greater than 0.3.

In Lakes Malta, Balaka and Menindee different plant communities were present in areas with sandy or clayey soils. This was particularly evident in Lake Menindee where only three species were common to sandy and clayey soils. In Lakes Wetherell and Cawndilla soil texture was relatively uniform over the area surveyed and the  $r^2$  value was below 0.3.

In Lakes Wetherell and Menindee,  $r^2$  values for elevation were higher than 0.3. However, it is doubtful whether elevation had an effect on floristic composition because a soil texture gradient from sand to clay with decreasing elevation was evident in Lake Menindee; therefore, soil texture and elevation were not independent variables. In Lake Cawndilla where the soil texture is relatively uniform and the elevation difference between quadrats one and ten is comparable to Lake Menindee  $r^2$  for this factor was well below 0.3. In Lake Wetherell, elevation and canopy were related and low elevation quadrats were located on the steep side a channel with no canopy cover whereas high elevation quadrats were located on level ground with a dense *Eucalyptus camaldulensis* overstory. Aqueous and crude volatile oil extracts of *Eucalyptus camaldulensis* leaves have been shown to suppress to inhibit or suppress radicle growth and suppress the growth of other species by affecting several biochemical and physiological processes (Moradshahi *et al.* 2003).

Floristic composition changed as sediment exposure time increased and the degree of change was related to species composition when first surveyed. Capon (2003) reported that annuals decreased in abundance as exposure time increased on the Cooper Creek floodplain (central Australia), which also occurred in the Menindee Lakes. Quadrats with large numbers of annual species (Lake Malta quadrats one and two, Lake Balaka and Lake Menindee quadrats five to nine) changed floristically as sediment exposure time increased because annuals flowered, set seed and died regardless of soil moisture. The quadrats dominated by perennial species did not change to the same degree as those dominated by annuals because most perennial species were deep rooted and desiccation tolerant. This

was particularly evident in Lake Cawndilla where the dominant species were desiccation tolerant (*Cyperus gymnocaulos* and *Morgania floribunda*) (Table 5.1) and floristic composition was not correlated with exposure time ( $r^2 = 0.065$ ).

The  $r^2$  values for soil moisture in Lakes Balaka and Menindee were greater than 0.3, which suggests that some species in these lakes were extirpated due to low soil moisture. In Lake Balaka, soil moisture decreased rapidly and after 200 days 11 of the 21 species initially detected were not found. In all lakes, soil moisture decreased rapidly after the sediment was exposed with a corresponding loss of species. In Lake Menindee, soil moisture and sediment exposure time were related but the change in floristic composition was due to the loss of annuals. In Lakes Malta, Wetherell and Cawndilla, where  $r^2$  values for soil moisture were below 0.3, the dominant species were desiccation tolerant.

The  $r^2$  value for water level relative to quadrat elevation was above 0.3 only in Lake Wetherell. This was due to the 4 m water level difference between April 2002 and February 2003 and the corresponding loss of annuals during this time. There were two possible reasons  $r^2$  was below 0.3 for this factor in the other lakes. Elevation of the quadrat relative to the water level influences soil moisture content, which will have little impact on communities dominated by desiccation tolerant species. In addition, elevation of the quadrat relative to the water level will not change after a lake has dried. Lakes Malta, Balaka and Menindee dried during the study period, with Lakes Balaka and Malta drying after four and five months, respectively.

All measured variables, except soil texture and canopy, are the result of or components of water regime. Water regime is an important factor because it determines whether the sediment is exposed or inundated, sediment exposure time and soil moisture. Whether the soil is inundated or exposed is of paramount importance for germination and survival of most Menindee Lakes species (Chapter 4). Sediment exposure time is important if for annuals (sensu Capon 2003). Surface soil moisture is important for germination but sub-surface moisture appears to be of less importance because most species are desiccation tolerant or have flexible life histories. However, water regime is not the only factor that influences floristic composition in this system. There is evidence to suggest the soil texture is an important factor in the deflation lakes. Canopy cover may be important because of the allelopathic properties of *Eucalyptus camaldulensis* leaf extracts (Moradshahi *et al.* 2003). Other non-hydrological factors not measured in this study,

which may influence floristic composition are grazing (e.g. van Der Valk *et al.* 1993; Mesleard *et al.* 1999; Jutila 2001), nutrients (e.g. Newman *et al.* 1998; Keddy *et al.* 2000; Woo and Zedler 2002; Newman *et al.* 2004) and wave action (e.g. Keddy and Constabel 1986; Doyle 2001; Squires *et al.* 2002; Hawes *et al.* 2003; Vis *et al.* 2003).

## 6 Chapter 6: Flooding Tolerance of *Xanthium occidentale*, *Cyperus gymnocaulos* and *Ludwigia peploides*

### 6.1 Introduction

Flooding and submergence represent stressors for many plant species and rank alongside water shortage, salinity and extreme temperature as determinants of species distributions (Visser *et al.* 2003). Flooding limits the diffusion of oxygen into the rhizosphere (Ewing 1996) and may cause carbon starvation due to reduced access to atmospheric carbon dioxide and light limitation of photosynthesis (Grace 1989; Mauchamp *et al.* 2001). Plants that grow around the edges of wetlands or on floodplains are prone to both inundation and desiccation (Brock and Casanova 1997) and at least one lifecycle stage must be able to either tolerate or respond to these conditions.

Amphibious plants commonly respond to increases in water depth by increasing resource allocation to above-ground organs in order to reach the surface, utilise atmospheric carbon dioxide for photosynthesis and oxygenate submerged tissues (e.g. Blanch *et al.* 1999b 159; Mauchamp *et al.* 2001 5472; Miller and Zedler 2003 4520). If a species is not morphologically plastic and unable to respond to increases in water depth it must tolerate flooding or be extirpated. Flood tolerant species may senesce and persist as rhizomes, which resprout when water levels are drawn down (van der Valk *et al.* 1994). Intolerant species may persist in the seed bank (Nicol *et al.* 2003; Chapter 4).

The conditions for recruitment from seed for *Xanthium occidentale*, *Cyperus gymnocaulos* and *Ludwigia peploides* are similar: they do not germinate, but remain viable whilst submerged and germinate on exposed, moist sediment (Chapter 4). In nature, they germinate on the margins of creeks, rivers and lakes, or on newly exposed lake and floodplain sediments as water levels recede (pers. obs.). Despite their similar regeneration niches (*sensu* Grubb, 1977), these species have different life history strategies, desiccation tolerances and adaptations to flooding. They represent three species well adapted to ephemeral systems with contrasting adaptations to flooding, which is the focus of the present chapter.

*Xanthium occidentale* is an erect annual forb, native to southern Africa and attains a maximum height of about 2 m (Cunningham *et al.* 1981). Dense stands occur on

floodplains after late spring and early summer flooding (Cunningham *et al.* 1981). Reproduction is by seed and mature fruits readily attach to the coats of passing animals and so are dispersed (Cunningham *et al.* 1981). This species is also adapted for hydrochory because seeds and seedlings float (Cunningham *et al.* 1981). *Xanthium occidentale* grows well in water-logged to moist soil; however, stunted plants may also occur in areas with low soil moisture (pers. obs.). Plants will tolerate shallow flooding for long periods (Cunningham *et al.* 1981) but are intolerant of top-flooding (Victorsen 2001). When plants experience partial flooding the above to below ground biomass ratio increases and adventitious roots are produced (Victorsen 2001).

*Cyperus gymnocaulos* is a perennial sedge with woody, short creeping rhizomes (Cunningham *et al.* 1981). Plants reproduce by seed, rhizomes and bulbils (viviparous propagules in the flower heads) (Cunningham *et al.* 1981). It is common on river and creek banks, lakeshores and swamp margins on sandy soils (Cunningham *et al.* 1981). This species grows in a wide range of soil moisture conditions from waterlogged to soil with <5% moisture in the top 40 cm (Chapter 5). Seedlings and plants that have not developed rhizomes are intolerant of flooding (Chapter 4) but plants that have developed rhizomes appear to tolerate top-flooding for short periods and partial flooding indefinitely with no adverse effects. When top flooded for longer periods (>four weeks), stems and leaves senesce and the rhizome persists. New stems and leaves sprout from the rhizomes when water levels recede, just prior to exposure of the sediment surface (pers. obs.).

*Ludwigia peploides* is a perennial forb with prostrate stems that float on water or creep on mud (Cunningham *et al.* 1981). Reproduction is by seed and stem fragments (Cunningham *et al.* 1981), both of which disperse by hydrochory. It is commonly found in clayey soils with high moisture contents such as river and creek banks, lake and lagoon shores, low-lying areas subject to periodic flooding and in water <2 m deep (Cunningham *et al.* 1981). *Ludwigia peploides* does acclimate to low soil moisture by producing prostrate slightly woody stems and smaller leaves (pers. obs.). When growing in or adjacent to water, floating stems spread across open water and creeping stems can form dense mats on the shore resulting in thick almost monospecific stands covering considerable areas (Cunningham *et al.* 1981). Plants appear to respond to flooding by rapid elongation of the internodes and production of adventitious roots (Chapter 4).

The study provides an experimental test of three hypotheses:

1. *Xanthium occidentale* when top-flooded for more than two weeks will die. Plants partially flooded will survive, increase above to below ground biomass ratios and produce adventitious roots. Plants not flooded will survive, produce no adventitious roots and have lower above to below ground biomass ratios. The production of adventitious roots enables this species to survive in shallow water providing there is sufficient biomass above the water for photosynthesis and oxygenation of submerged organs. Due to the limited ability of this species to tolerate or respond to flooding, its distribution is restricted to areas not inundated or shallowly flooded.
2. *Cyperus gymnocaulos* when top-flooded for two weeks will show no adverse effects. When top flooded for longer than four weeks, the above ground organs will senesce and above to below ground biomass ratios will decrease. When the water recedes, stems and leaves will re-sprout from rhizomes. Plants partially flooded will show no adverse effects. The ability to persist through floods as rhizomes allows this species to colonise newly exposed areas more rapidly than species (such as *Xanthium occidentale*) that rely solely on seeds (Grace 1993). In addition, this species tolerates brief floods. The wide soil moisture and flooding tolerances of *Cyperus gymnocaulos* ensures that it is widely spread in ephemeral systems.
3. *Ludwigia peploides* when top-flooded will rapidly increase its above-ground biomass toward the water surface. Non-flooded plants will have lower above- to below-ground biomass ratios. When the stems of non-flooded plants contact water, they produce adventitious roots. The ability of this species to respond to flooding and rapidly grow across the water surface allows it to grow in flooded situations and access water and nutrients directly from the water column and the sediment. However, *Ludwigia peploides* is not as desiccation-tolerant as *Cyperus gymnocaulos* or *Xanthium occidentale* and is thereby restricted mainly to areas with high soil moisture or standing water (pers. obs.). In areas with low soil moisture, such as dry creek beds, it may be present but not dominant (pers. obs.).

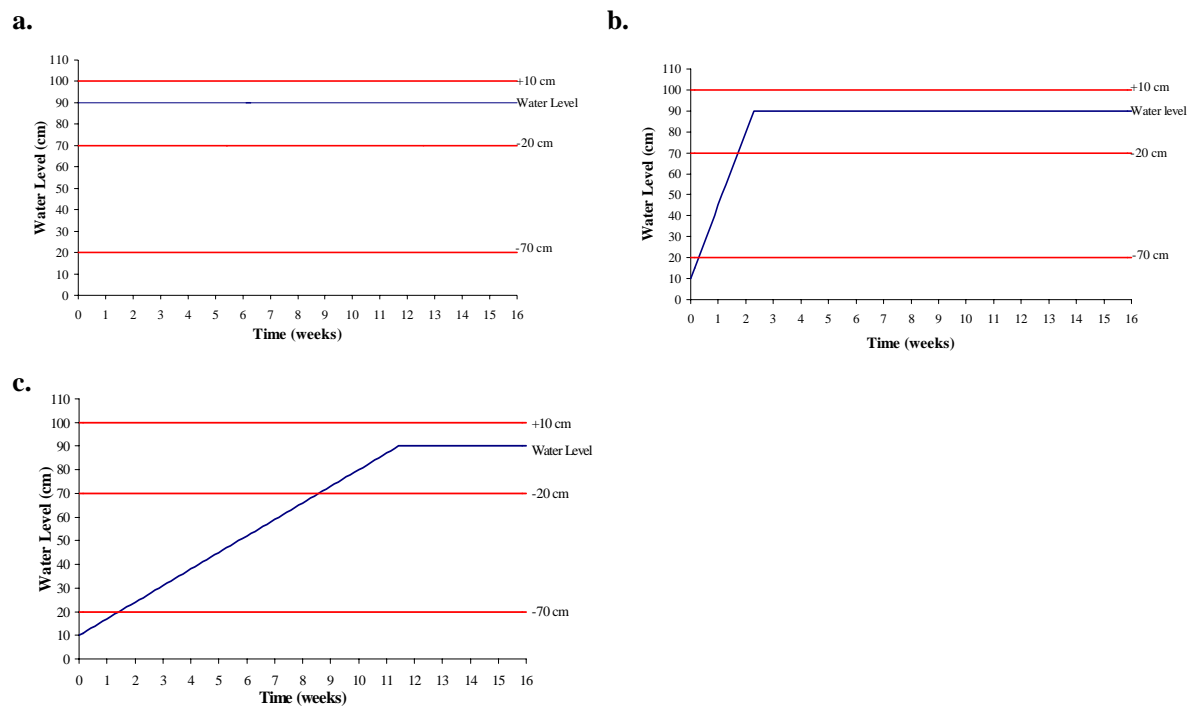
## 6.2 Methods

### 6.2.1 Plant Establishment

Approximately 500 plants of each species were established; *Xanthium occidentale* by seed, *Cyperus gymnocaulos* by rhizomes and *Ludwigia peploides* by stem fragments. Plants were watered daily for six weeks, when the plants were judged to have established, then transferred into ponds.

### 6.2.2 Hydraulic Regimes

Plants were subjected to three hydraulic regimes: static (90 cm for the duration of the experiment), fast flood (water levels rose at 5 cm day<sup>-1</sup> until the depth was 90 cm then static) and slow flood (water levels rose at 1 cm day<sup>-1</sup> until the depth was 90 cm then static) (Figure 6.1).



**Figure 6.1:** Pond water levels with respect to the different elevation treatments over the experimental period (a. static, b. fast flood and c. slow flood).

Within each hydraulic regime, there were three elevations +10, -20 and -70 cm. The soil surface was 10 cm above the water level of 90 cm in the static hydraulic regime for the +10 cm elevation and the soil surface was 20 and 70 cm below the water level of the static hydraulic regime for the -20 and -70 cm elevations respectively (Figure 6.1). To ensure the



survival of the plants at the +10 cm elevation in the slow and fast flood ponds and the -20 cm elevation in the slow flood treatments, plants were watered daily until the water level was 30 cm below the soil surface and water could reach the surface by capillary action (Nicol 1999).

### 6.2.3 Data Collection and Analysis

To calculate relative growth rate the initial biomass of each plant was required (Harper 1977). This was determined by measuring stem length and counting the number of leaves for *Xanthium occidentale* and *Ludwigia peploides* and measuring total stem length and total number of stems for *Cyperus gymnocaulos*. At least 50 plants from each species were harvested and total biomass (dry weight) determined. The relationship between these factors and biomass was determined and the coefficient of determination ( $r^2$ ) calculated. The relationships that had the greatest  $r^2$  value were used to calculate initial biomass. Stem length was the most reliable estimate for *Xanthium occidentale* (Figure 6.2) and *Ludwigia peploides* (Figure 6.3) and the total number of stems for *Cyperus gymnocaulos* (Figure 6.4) was most reliable.

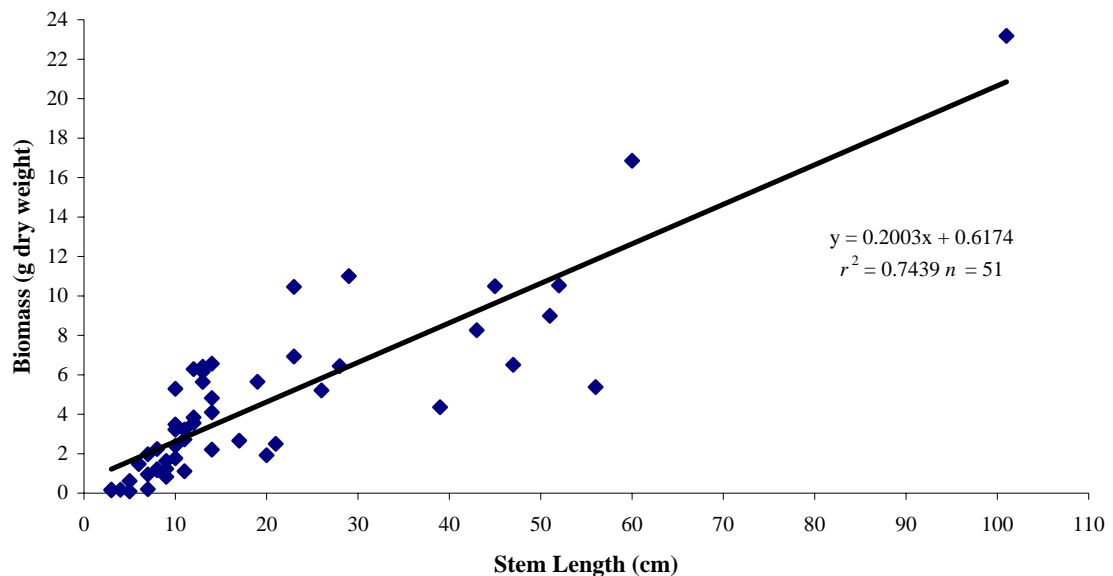


Figure 6.2: Relationship between stem length and biomass for *Xanthium occidentale*.

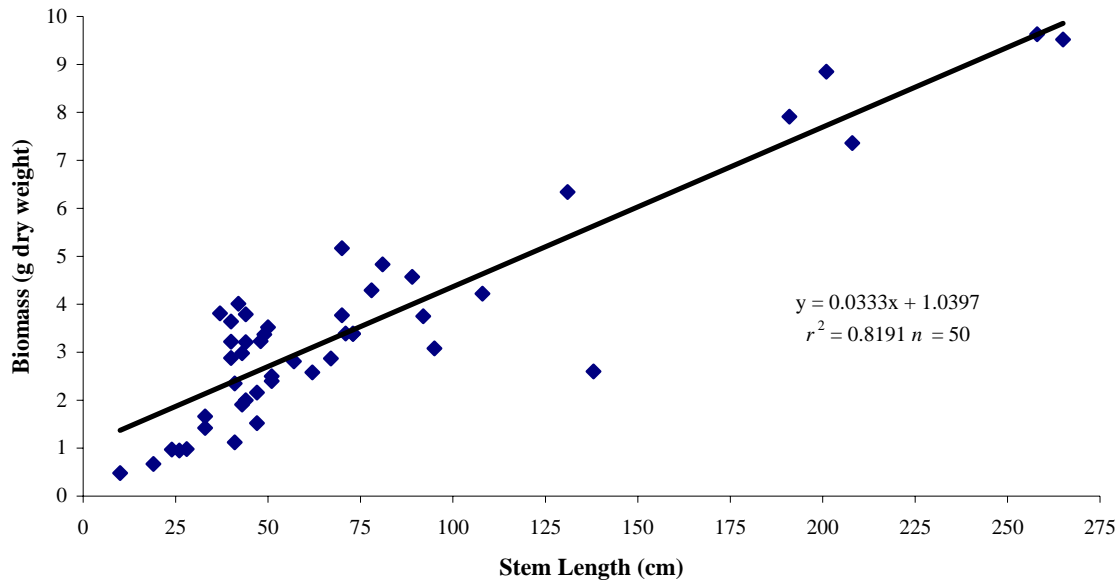


Figure 6.3: Relationship between stem length and biomass for *Ludwigia peploides*.

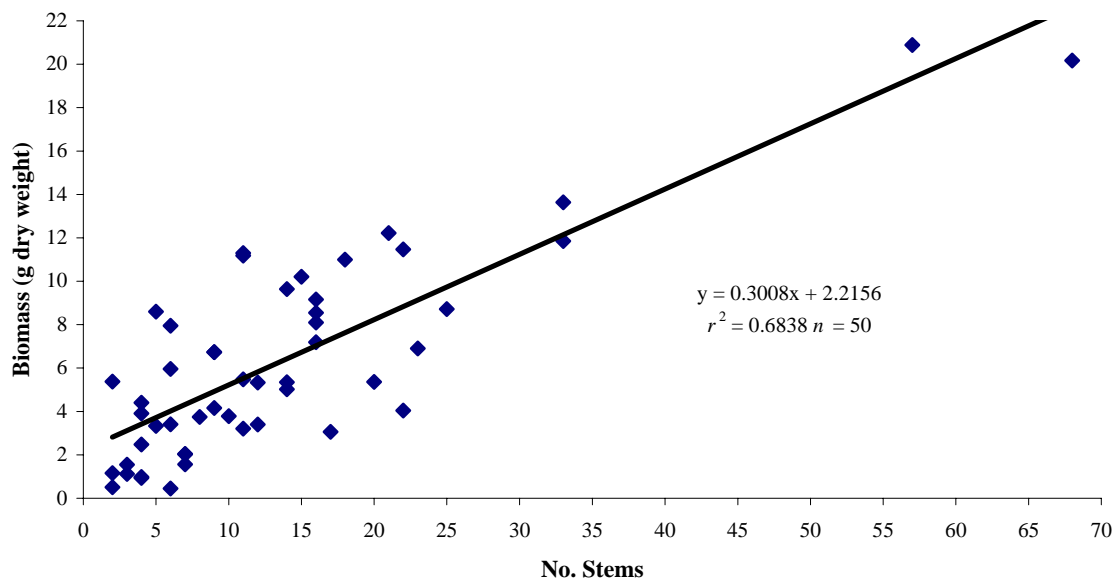


Figure 6.4: Relationship between total number of stems and biomass for *Cyperus gymnocaulos*.

Five plants from each species ( $n = 5$ ), hydraulic regime and elevation were destructively harvested at weeks 2, 4, 8, 12 and 16. In addition, at each harvest five plants from each species was removed from each hydraulic regime and elevation combination where the water level was above the soil surface. These plants were placed in a static pond with the soil surface 10 cm above the water level for four weeks to determine whether the plants had survived.

Relative growth rates (Harper 1977) and above to below ground ratios (A:B) were calculated from each harvest. Relative Growth Rate (RGR) was calculated as (Harper 1977):

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \text{ (mg g}^{-1} \text{ day}^{-1}\text{)}$$

$W_1$  = Initial biomass (g dry weight)

$W_2$  = Final biomass (g dry weight)

$t_1$  = Initial time (days)

$t_2$  = Final time (days)

Differences in Relative Growth Rate and above to below ground ratios between hydraulic regime, elevation and time of harvest for *Cyperus gymnocaulos* and *Ludwigia peploides* were analysed with a three factor analysis of variance (3 way ANOVA) using the package JMP In version 3.2.6 (SAS Institute Inc. 1996). Normality of the data was tested with the Shapiro-Wilk W test and equality of variances with the Levene test. Above to below ground ratios for *Ludwigia peploides* were log transformed. For all statistical tests  $\alpha = 0.05$ . The *Xanthium occidentale* data set contained large numbers of zeros and the differences between hydraulic regimes, elevations and sampling times for relative growth rate and above to below ground biomass ratios were obvious therefore statistical analyses were deemed unnecessary.

## 6.3 Results

### 6.3.1 *Xanthium occidentale*

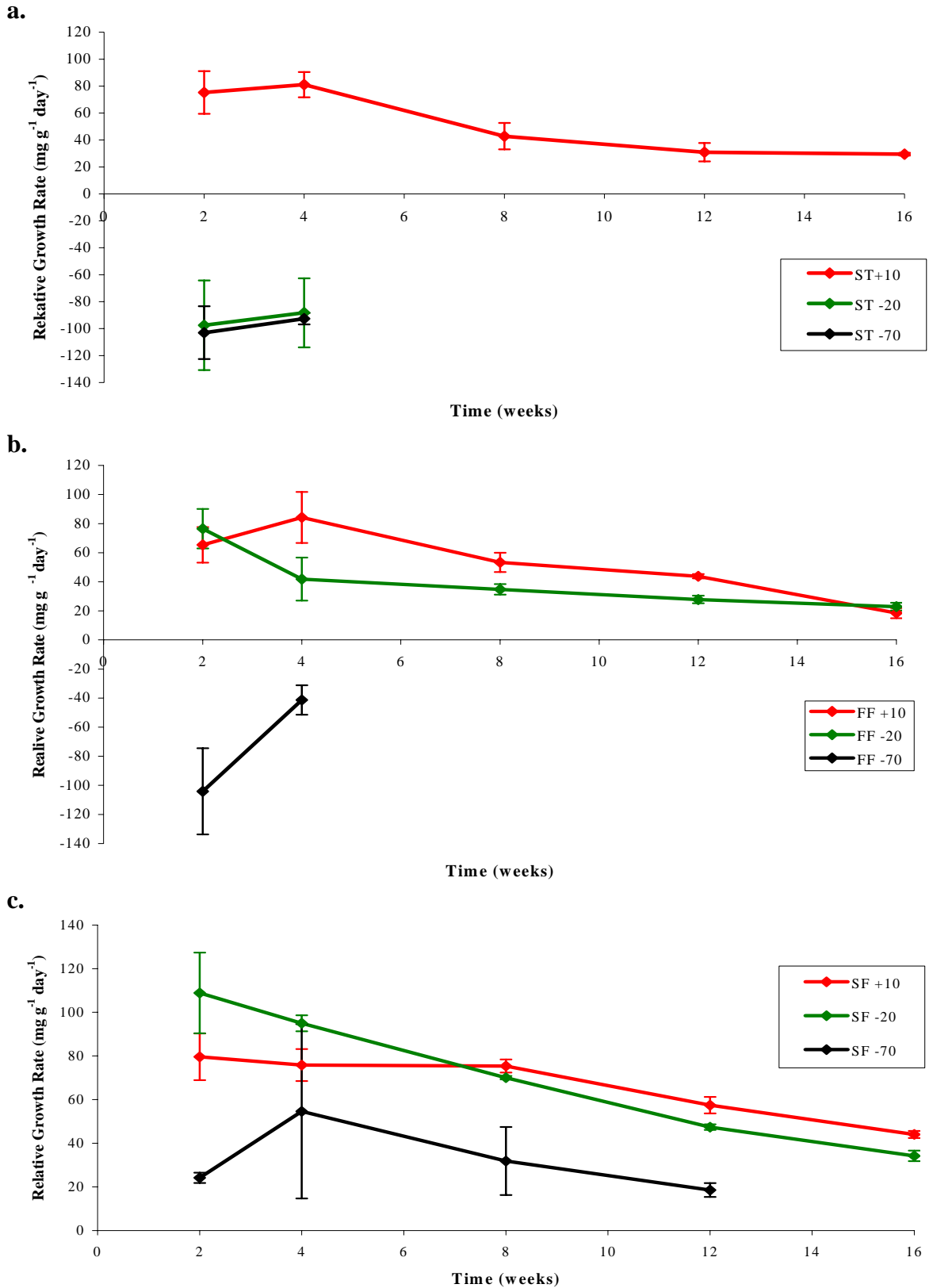
#### 6.3.1.1 Survivorship and Relative Growth Rate

*Xanthium occidentale* subjected to static water levels showed two different responses (Figure 6.5a). Plants at +10 cm survived for the duration of the experiment and showed reduced relative growth rates after week four (Figure 6.5a). Plants that were flooded but removed from the pond and placed at +10 cm at weeks two and four survived; however, after week four none of the plants re-sprouted and were assumed dead. Submerged plants had negative Relative Growth Rates (Figure 6.5).

Plants at +10 cm and flooded at 5 cm day<sup>-1</sup> showed a similar response to those in the static hydraulic regime (Figure 6.5a and Figure 6.5b). Relative Growth Rate peaked at week four (Figure 6.5b) then decreased. Plants at the lower elevations (-20 and -70 cm) showed different responses. At -20 cm, all plants survived and relative growth rate decreased rapidly from week two to four then decreased slowly for the remainder of the experiment (Figure 6.5b). Plants at -70 cm showed a similar response to the corresponding elevation in the static hydraulic regime (Figure 6.5a and Figure 6.5b). All plants died between weeks four and eight and the relative growth rate was negative (Figure 6.5b).

Plants flooded at 1 cm day<sup>-1</sup> all survived except those at -70 cm, which died between weeks 12 and 16. At +10 cm, the Relative Growth Rate remained constant until week eight after which it decreased (Figure 6.5c). Relative Growth Rates of plants at -20 cm decreased throughout the experiment (Figure 6.5c). At -70 cm Relative Growth Rates increased between weeks two and four, although the measurements at week four were variable, then decreased until week 12 after which all plants died (Figure 6.5c).

In all hydraulic regimes, partially submerged plants produced adventitious roots but those totally submerged did not.



**Figure 6.5:** Relative Growth Rate of *Xanthium occidentale* over the experimental period when subjected to a. static water levels, b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

### 6.3.1.2 Above to Below Ground Biomass

When subjected to static water levels, above to below ground ratios for *Xanthium occidentale* at +10 cm peaked at week eight then decreased (Figure 6.6a). Above to below ground ratios for plants at -20 cm increased between weeks two and four (Figure 6.6a), because of a decrease in root biomass not an increase in shoot biomass. There was a decrease in above to below ground ratios for plants at -70 cm for the corresponding period (Figure 6.6a).

Above to below ground ratios for plants flooded at 5cm day<sup>-1</sup> at +10 cm, increased slightly over the experiment (Figure 6.6b) but were generally lower than those in the static regime (Figure 6.6a). At -20 cm, above to below ground ratios increased as water levels increased until week 12 then decreased, although the week 16 results were variable (Figure 6.6b). Above to below ground ratios for plants at -70 cm remained constant until they died between weeks four and eight (Figure 6.6b).

Plants flooded at 1 cm day<sup>-1</sup> at +10 cm, above to below ground ratios remained constant over the experiment (Figure 6.6c), although they were generally lower than the corresponding elevation from the other regimes (Figure 6.6a and Figure 6.6b). At -20 cm, above to below ground ratios were similar to plants at +10 cm until between weeks 8 and 12 (Figure 6.6c), when the water level rose past the soil surface (Figure 6.1c) and ratios increased. Above to below ground ratios for plants at -70 cm increased between weeks two and four (Figure 6.6c) when the water level rose above the soil surface (Figure 6.1). Above to below ground ratios remained high until the plants died between weeks 12 and 16 (Figure 6.6c).

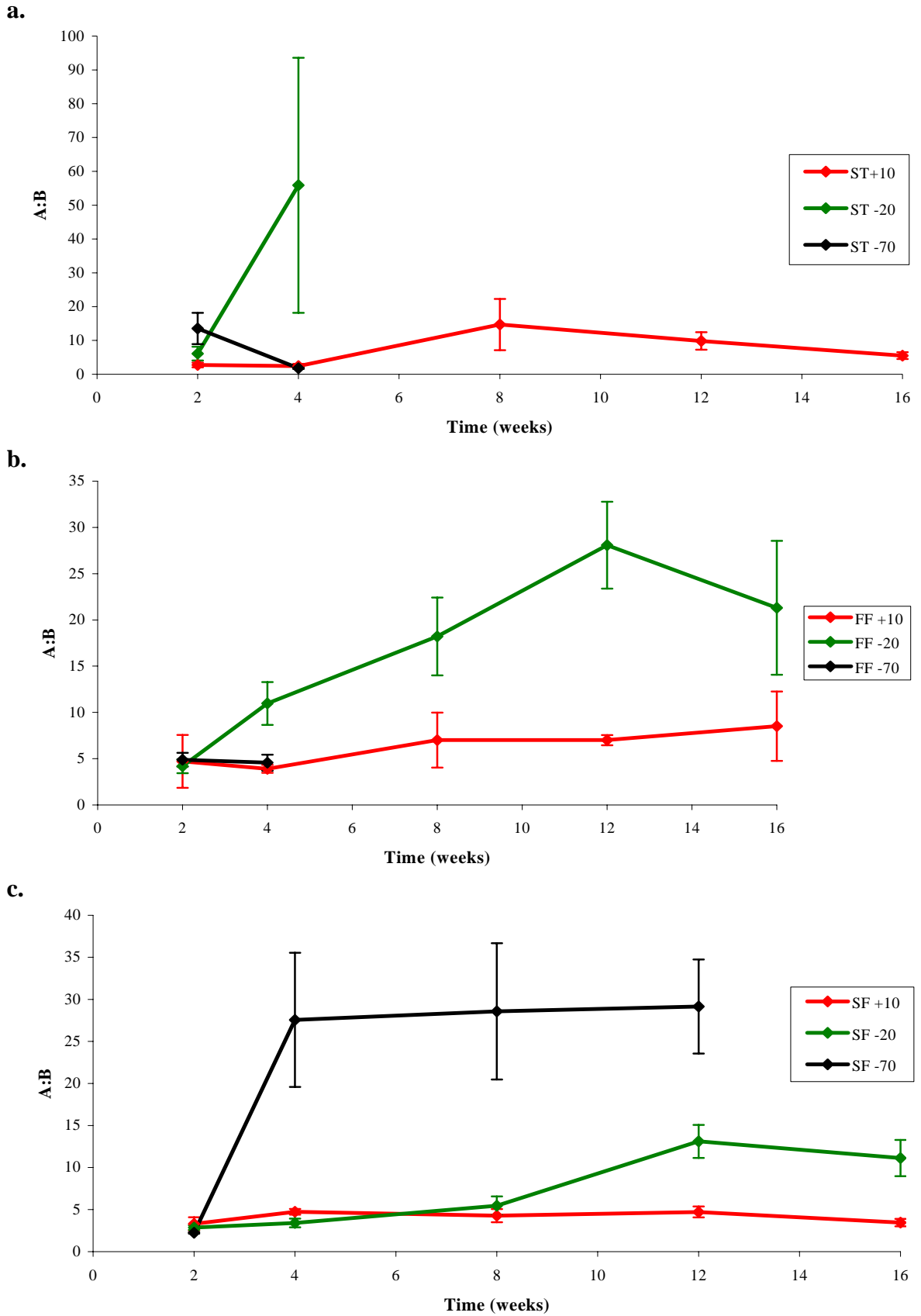


Figure 6.6: Above to below ground ratios (A:B) of *Xanthium occidentale* over the experimental period when subjected to a. static water levels b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

### 6.3.2 *Cyperus gymnocaulos*

In contrast to *Xanthium occidentale*, all *Cyperus gymnocaulos* plants survived in all hydraulic regimes and elevations because rhizomes re-sprouted after they were moved to +10 cm regardless of the flood depth or duration. A three-factor analysis of variance showed a significant interaction for all three factors for Relative Growth Rate and above to below ground ratio (Table 6.1), showing that the combination of hydraulic regime and elevation influenced the performance of this species differently through time.

**Table 6.1:** *F* statistics obtained from comparisons of Relative Growth Rate (RGR) and above to below ground ratios (A:B) of *Cyperus gymnocaulos* between hydraulic regime, elevation and sampling time.

Significance at  $P < 0.001$ , 0.01 and 0.05 represented by \*\*\*, \*\* and \* respectively, n.s. = not significant.

Factor	RGR	A:B
Hydraulic Regime	$F_{2, 180} = 10.91$ ***	$F_{2, 180} = 13.52$ ***
Elevation	$F_{2, 180} = 32.32$ ***	$F_{2, 180} = 12.66$ ***
Time	$F_{4, 180} = 2.95$ *	$F_{4, 180} = 4.52$ **
Hydraulic Regime x Elevation	$F_{4, 180} = 5.40$ ***	$F_{4, 180} = 7.56$ ***
Hydraulic Regime x Time	$F_{8, 180} = 1.46$ n.s.	$F_{8, 180} = 4.13$ ***
Elevation x Time	$F_{8, 180} = 0.71$ n.s.	$F_{8, 180} = 1.88$ n.s.
Hydraulic Regime x Elevation x Time	$F_{16, 180} = 1.71$ *	$F_{16, 180} = 2.26$ **

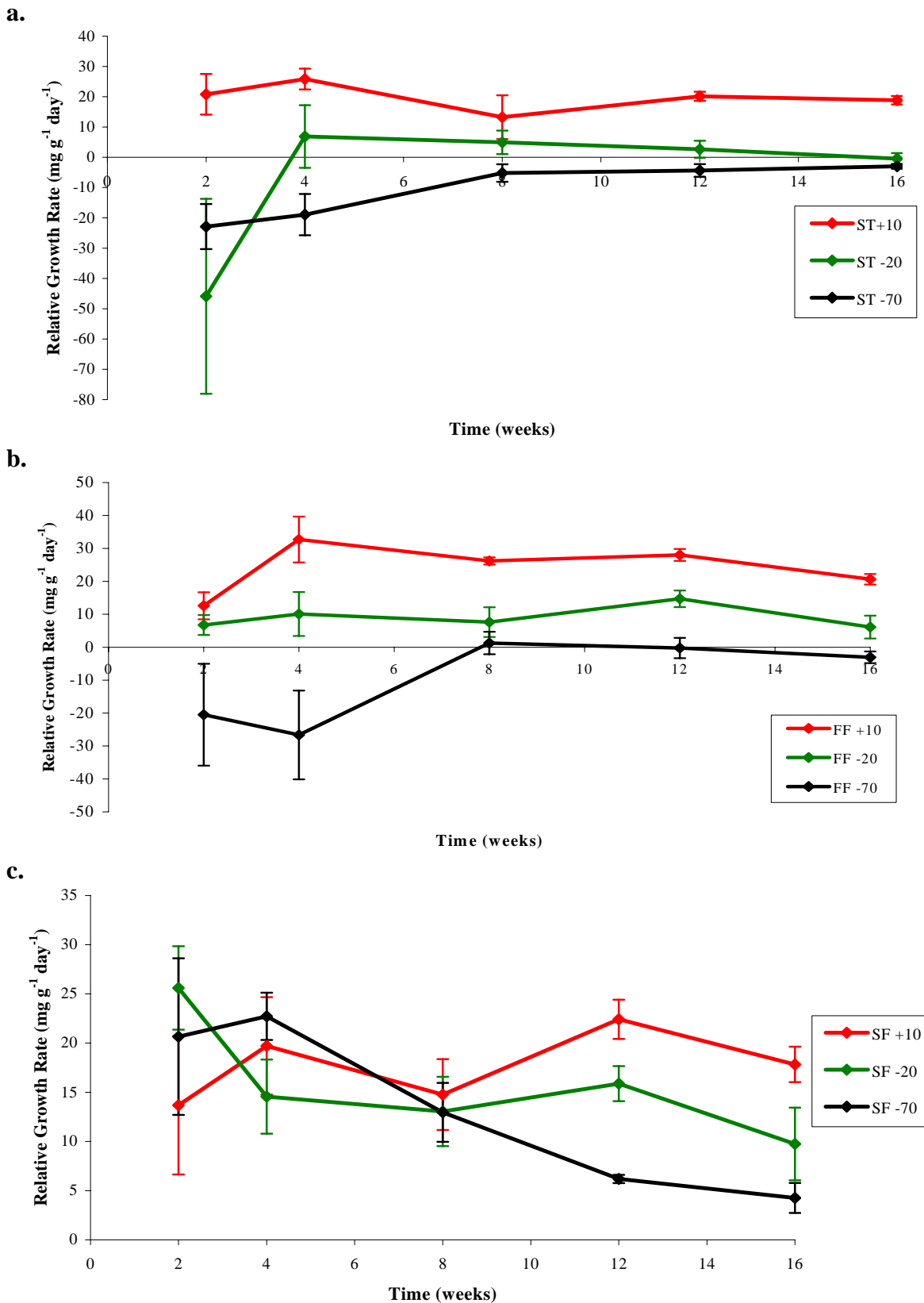
#### 6.3.2.1 Relative Growth Rate

The significant three-way interaction effect (Table 6.1) was due to different patterns of change in Relative Growth Rate for plants at -20 cm and -70 cm between hydraulic regimes (Figure 6.7).

Relative Growth Rates for plants at +10 cm in all regimes were relatively static and ranged between 10 and 35 mg g<sup>-1</sup> day<sup>-1</sup> (Figure 6.7), which was due to the continued production of stems. At the lower elevations, the change in Relative Growth Rate was dependent on the timing, duration and depth of flooding. In the static regime, plants at -20 cm after two weeks had negative Relative Growth Rates (Figure 6.7a). However, after four weeks, plants had increased in size and for the remainder of the experiment the Relative Growth Rate decreased but remained positive (Figure 6.7a). When flooded to 70 cm biomass decreased initially and never recovered; hence, the negative Relative Growth Rates (Figure 6.7a). Relative Growth Rates for plants at -20 cm, flooded at 5 cm day<sup>-1</sup>, were relatively constant but generally lower than plants at +10 cm and higher than plants at -70 cm (Figure 6.7b). At -70 cm in the same regime, Relative Growth Rates were negative until week eight, although



values remained around zero (Figure 6.7b). In contrast to the other regimes, the Relative Growth Rates of plants flooded at 1 cm day<sup>-1</sup> at all elevations were positive (Figure 6.7c). The Relative Growth Rates of plants at -20 cm were variable but generally decreased over the experiment and at weeks 12 and 16 were lower than plants at +10 cm (Figure 6.7c). The Relative Growth Rate for plants at -70 cm was relatively static between weeks two and four after which it decreased and at week 16 was lower than the other elevations (Figure 6.7c).

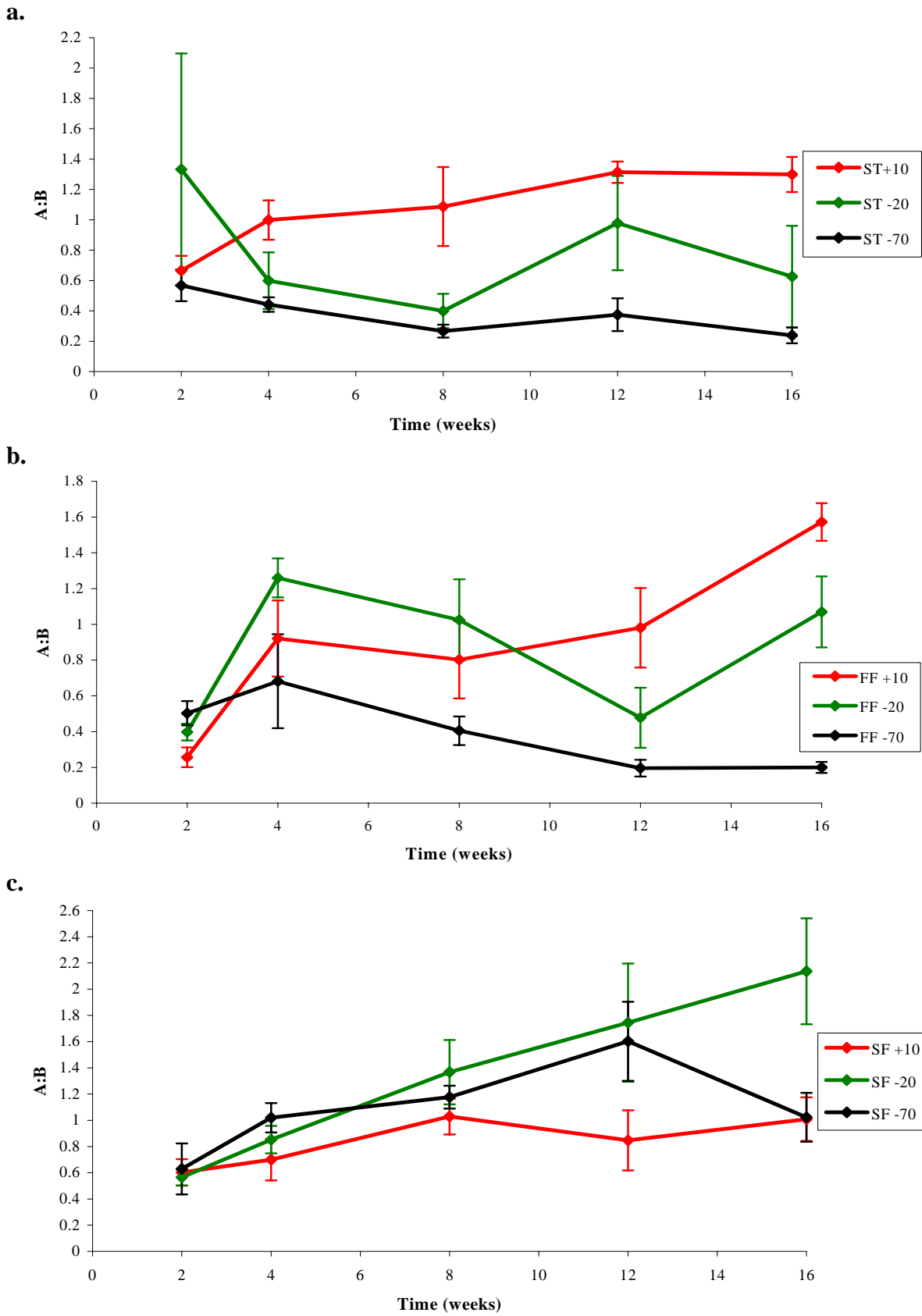


**Figure 6.7:**Relative Growth Rate of *Cyperus gymnocaulos* over the experimental period when subjected to a. static water levels b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

### 6.3.2.2 Above to Below Ground Biomass

Similar to Relative Growth Rate, the significant three-way interaction effect (Table 6.1) was due to different patterns of change in above to below ground ratios for plants at -20 cm and -70 cm between hydraulic regimes (Figure 6.8).

Above to below ground ratios for plants at +10 cm in all regimes were variable but generally increased over the experiment (Figure 6.8) due to stem production. At -20 cm and -70 cm above to below ground ratios changed in response to flood timing and depth (Figure 6.8). When initially top flooded (ST -70 cm) or rapidly top flooded (FF -70cm) above to below ground ratios were low after two weeks and remained low for the duration of the experiment (Figure 6.8a and Figure 6.8b). Plants slowly flooded at -70 cm (SF -70 cm) allocated more resources to above ground organs until week 12 when they were top flooded and stems senesced (Figure 6.8c). Plants growing at -20 cm in the static and fast flood regimes showed similar responses (Figure 6.8a and Figure 6.8b). Above to below ground ratios were variable and erratic, probably due to some of the plants being totally submerged and others being partially exposed to the atmosphere. However, at the end of the experiment, above to below ground ratios were lower than plants at +10 cm but higher than plants at -70 cm (Figure 6.8a and Figure 6.8b). Above to below ground ratios for plants at -20 cm in the slow flood regime showed an almost linear increase over the experiment (Figure 6.8c). This was probably due to stem production because the sediment surface was not inundated until day 60 (Figure 6.1) and plants were never top flooded.



**Figure 6.8:** Above to below ground biomass (A:B) of *Cyperus gymnocaulos* over the experimental period when subjected to a. static water levels b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

### 6.3.3 *Ludwigia peploides*

*Ludwigia peploides* was the only species that responded positively to flooding. A three-factor analysis of variance detected a significant interaction for all factors for Relative Growth Rate and above to below ground ratio (Table 6.2) indicating different responses to each combination of hydraulic regime and elevation over time.

**Table 6.2:** *F* statistics obtained from comparisons of Relative Growth Rate (RGR) and above to below ground ratios (A:B) of *Ludwigia peploides* between hydraulic regime, elevation and sampling time.

Significance at  $P < 0.001$ , 0.01 and 0.05 represented by \*\*\*, \*\* and \* respectively, n.s. = not significant.

Factor	RGR	A:B
Hydraulic Regime	$F_{2, 180} = 9.67$ ***	$F_{2, 180} = 58.35$ ***
Elevation	$F_{2, 180} = 1.92$ n.s.	$F_{2, 180} = 53.646$ ***
Time	$F_{4, 180} = 35.95$ ***	$F_{4, 180} = 84.66$ ***
Hydraulic Regime x Elevation	$F_{4, 180} = 12.31$ ***	$F_{4, 180} = 46.13$ ***
Hydraulic Regime x Time	$F_{8, 180} = 0.89$ n.s.	$F_{8, 180} = 39.85$ ***
Elevation x Time	$F_{8, 180} = 4.30$ ***	$F_{8, 180} = 20.33$ ***
Hydraulic Regime x Elevation x Time	$F_{16, 180} = 1.70$ *	$F_{16, 180} = 24.68$ ***

When stems came in contact with water, in all hydraulic regimes and elevations, plants produced two types of adventitious roots; thin fibrous roots with many branches that probably served the functions of nutrient and water uptake and thick spongy roots, which probably functioned as buoyancy and aeration organs. When stems were submerged, spongy tissue was also produced on the outside of the stems, which caused stems to become buoyant.

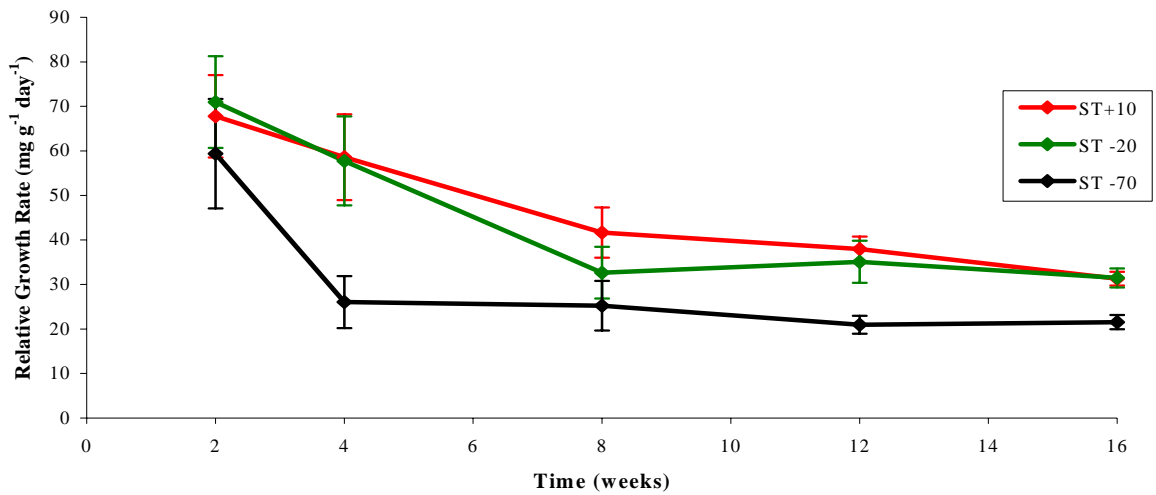
#### 6.3.3.1 Relative Growth Rate

Relative Growth Rates for all elevations in all regimes were positive and generally decreased over the experiment (Figure 6.9). The significant three-way interaction effect for Relative Growth Rate (Table 6.2) was due to the combination of lower initial growth rates in the slow flood regime at +10 cm and -20 cm and different responses to elevation over time between hydraulic regimes (Figure 6.9).

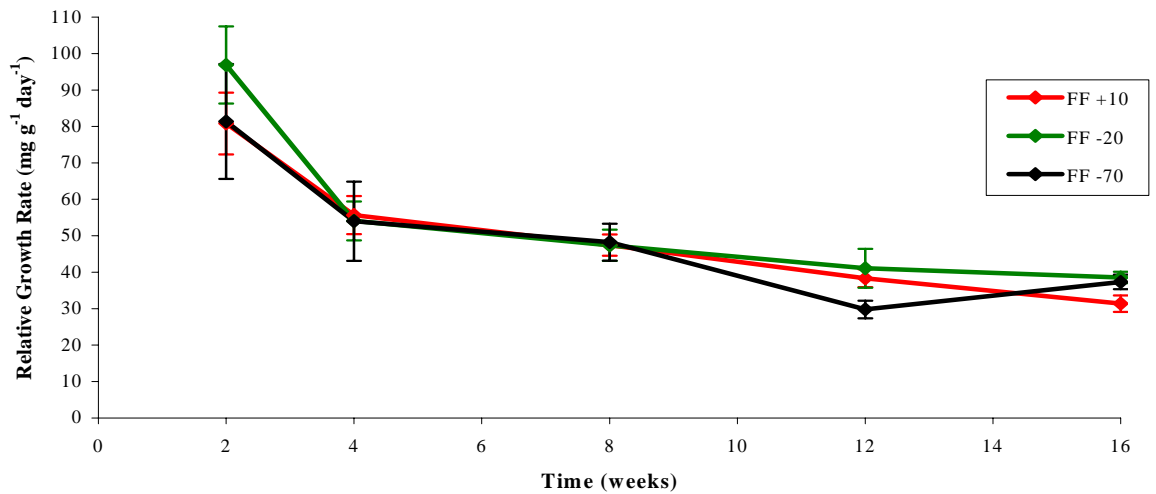
When subjected to static water levels, the Relative Growth Rate for plants at -70 cm was generally lower than plants at -20 cm and +10 cm (Figure 6.9a). When flooded at 5 cm day<sup>-1</sup> there was very little difference in Relative Growth Rate between the three elevations (Figure 6.9b). When flooded at 1 cm day<sup>-1</sup> plants at -70 cm had the highest Relative Growth

Rates (Figure 6.9c). Plants at -20 cm had higher Relative Growth Rates than plants at +10 cm except at weeks two and twelve when there was no discernable difference (Figure 6.9c).

a.



b.



c.

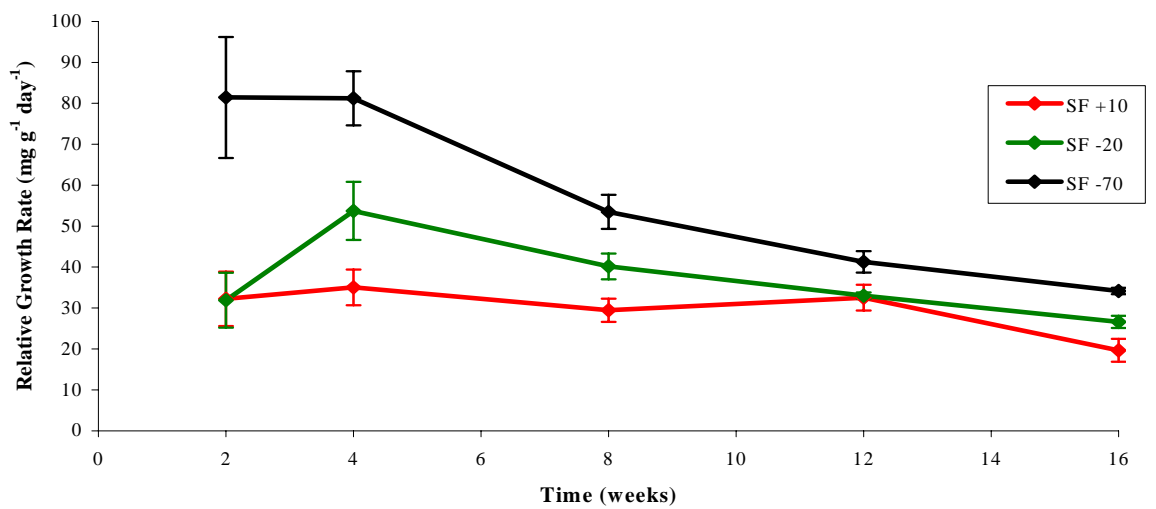


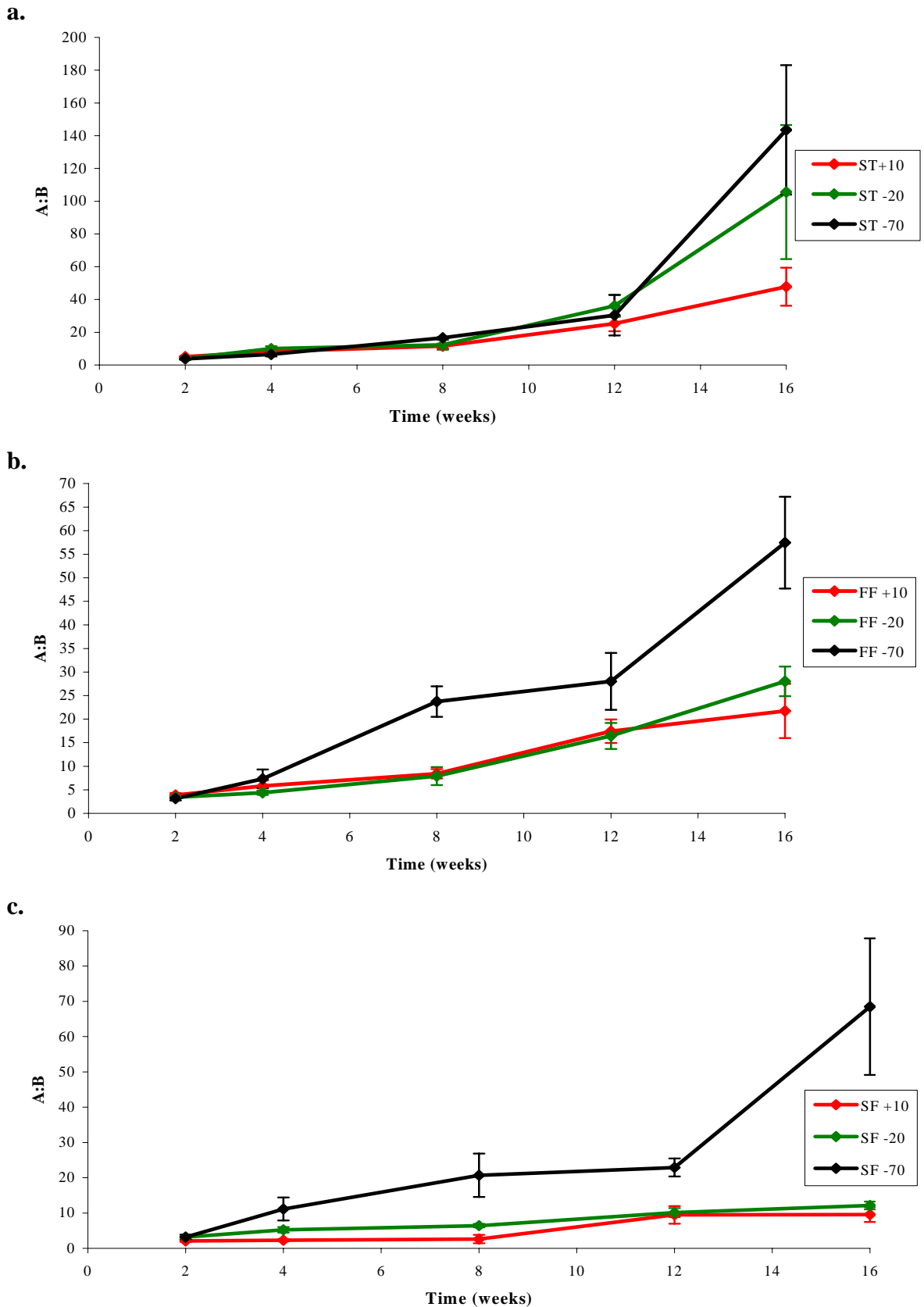
Figure 6.9: Relative Growth Rate of *Ludwigia peploides* over the experimental period when subjected to a. static water levels b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

### 6.3.3.2 Above to Below Ground Biomass

Above to below ground ratios at week two in all hydraulic regimes and elevations were approximately three and generally increased over the experiment (Figure 6.10). The significant three-way interaction effect (Table 6.2) was due to the different patterns of above ground biomass allocation between elevations and hydraulic regimes over the experiment, brought about by different flood timing, depth and duration.

There was no difference in above to below ground ratios between elevations for plants subjected to static water levels until week 16 when ratios were higher for submerged plants (-20 cm and -70 cm) (Figure 6.10a). Plants subjected to static water levels also had the highest above to below ground ratios at each elevation (Figure 6.10). Plants at -70 cm had higher above to below ground ratios when subjected to flooding at 5 cm day<sup>-1</sup> than plants at +10 and -20 cm (Figure 6.10b). When subjected to flooding at 1 cm day<sup>-1</sup>, above to below ground ratios at +10 cm and -20 cm were similar over the experiment (Figure 6.10c). The increase in above to below ground ratio for these elevations in the slow flood regime was not as great as the other regimes (Figure 6.10). After week two, plants at -70 cm had higher above to below ground ratios than plants at +10cm and -20 cm.





**Figure 6.10:** Above to below ground ratios of *Ludwigia peploides* over the experimental period when subjected to a. static water levels b. flooded at 5cm day<sup>-1</sup> and c. flooded at 1cm day<sup>-1</sup> at three different elevations (error bars = ± 1 S.E.).

## 6.4 Discussion

In wetland and floodplain systems, where water level fluctuations are common, the ability to persist when desiccated or flooded is important for persistence. These species illustrated three different strategies of persistence in response to flooding. All three species generally responded to flooding as hypothesised; *Xanthium occidentale* died when top flooded for longer than four weeks and produced adventitious roots when partially flooded. *Cyperus gymnocaulos* stems senesced and re-sprouted from rhizomes when the flooding pressure was removed. *Ludwigia peploides* increased above ground biomass in order to reach the surface and produced adventitious roots when stems came in contact with the water.

*Xanthium occidentale*, whilst intolerant to top flooding for periods longer than four weeks, was able to survive partial flooding. This has also been observed for the saplings of the wetland and floodplain tree species *Melaleuca halmaturorum* (Denton and Ganf 1994), *Alnus rubra* and *Fraxinus latifolia* (Ewing 1996). When *Xanthium occidentale* was subjected to partial flooding (and waterlogging in some cases), the above to below ground ratio increased primarily due to a decrease in root biomass caused by root necrosis. When harvested, roots from these plants were devoid of root hairs and the epidermis of the taproot and other main roots was black and appeared to be dead. This suggested that the ability of this species to aerate the sediment is limited and, when present, adventitious roots primarily undertook water and nutrient uptake. Another symptom displayed by *Xanthium occidentale* when subjected to partial flooding was loss of rigidity of the submerged portion of the stem. When removed from partial flooding and placed at static +10 cm, plants collapsed with the weak point in the stem being the portion that was submerged. Despite this, these plants survived and continued to grow because the adventitious roots were able to take root in the soil.

The seed bank is probably the primary mode of persistence during floods and extended inundation for *Xanthium occidentale*. Observations of this species in the pond experiment and the field (Chapter 4 and Chapter 5) suggested that seeds survive inundation and germinate soon after the sediment is exposed. Observations from this experiment confirmed this because more than one seed was planted in each pot. If more than one plant germinated, it was either transplanted or thinned but ungerminated seeds were not removed. Some of these seeds germinated in pots that had been flooded then placed at the static regime at +10 cm.

The optimal conditions for growth for this species were non-flooded conditions and the larger the plants were the more they were able to tolerate partial flooding. These data also suggested that 70 cm is deeper than the maximum depth of flooding this species can tolerate.

*Cyperus gymnocaulos* survived at all hydraulic regimes and elevations, which indicated that this species was more flood tolerant than *Xanthium occidentale*. Squires and van der Valk (1992) reported the same strategy of persistence whilst top flooded by the wetland sedges *Scirpus lacustris* ssp. *glaucus*, *Scirpus lacustris* ssp. *validus* and *Scirpus maritimus*. The ability to persist through unfavourable conditions, such as cold temperatures, with dormant rhizomes has also been observed for many species of aquatic plants. For example, *Scirpus maritimus* sprouts from overwintering tubers, which enables this species to colonise bare sediment more rapidly than those species that rely solely on seeds (Lieffers and Shay 1982b). *Cyperus gymnocaulos* plants also rapidly switched between dormant and actively growing states. When flooding pressure was removed, plants resprouted from rhizomes within one week (pers. obs). How long *Cyperus gymnocaulos* rhizomes can remain viable whilst submerged is not known; however, rhizomes have been observed sprouting in Lake Cawndilla at elevations where the sediment had been submerged for nearly eight years by water up to 7 m deep (New South Wales Department of Land and Water Conservation 2003).

*Cyperus gymnocaulos* also forms a persistent seed bank (Chapter 3) and plants, obviously derived from seed, were observed in the field on newly exposed sediment. Therefore, this species has two modes of persistence when subjected to long term flooding. Rhizomes have advantages over seeds because they are larger, have greater carbohydrate reserves, are able to sprout whilst submerged, are anchored to the sediment and faster growing than seeds (Grace 1993). Seeds however, are the only means of dispersal because this species does not reproduce by fragmentation. *Cyperus gymnocaulos* plants derived from seed require more time under non-flooded conditions because plants that have not developed rhizomes are intolerant of flooding (Chapter 4).

The optimal conditions for growth for *Cyperus gymnocaulos*, similar to *Xanthium occidentale*, were non-flooded conditions regardless of the rate of flooding. Unlike *Xanthium occidentale*, the Relative Growth Rate of the non-flooded plants remained relatively constant. This was probably due to the different growth forms and life history

strategies of the different species. *Xanthium occidentale* is an annual (Cunningham *et al.* 1981) and the plants that were not flooded, were starting to flower by the end of the experiment. Once flowering commenced, growth appeared to slow and was reflected in the Relative Growth Rates. In contrast *Cyperus gymnocaulos* is a rhizomatous perennial (Cunningham *et al.* 1981), which constantly recruited new stems when not fully submerged.

Plants subjected to top flooding were able to survive (as dormant rhizomes) but did not grow. Plants that were subjected to partial flooding or top flooded towards the end of the experiment generally had lower Relative Growth Rates than the plants that were never flooded; however, the values were generally positive. Blanch *et al.* (1999a) reported a similar reduction in Relative Growth Rate of the emergent sedge *Bolboschoenus medianus* when partially flooded as did Siebentritt and Ganf (2000) for *Bolboschoenus caldwellii*.

*Ludwigia peploides* survived in all hydraulic regimes and elevations by responding to partial and top flooding by allocating resources to above ground organs in order to reach the surface. Phenotypic plasticity with respect to the ability of a species to allocate biomass to above and below ground organs in response to water level changes has been reported for numerous macrophyte species. Allocation of resources to above ground organs in response to flooding has been reported for *Triglochin procerum* (Rea and Ganf 1994d), *Typha glauca* (Squires and van der Valk 1992; Waters and Shay 1992), *Bolboschoenus medianus* (Blanch *et al.* 1999a; Siebentritt and Ganf 2000), *Bolboschoenus caldwellii* (Siebentritt and Ganf 2000) *Phragmites australis* (adult plants) (Squires and van der Valk 1992; Vretare *et al.* 2001), *Phragmites australis* (seedlings) (Mauchamp *et al.* 2001), *Scirpus maritimus* (Lieffers and Shay 1982a; Squires and van der Valk 1992; Clevering and Hundscheid 1998), *Scirpus ancistrochaetus* (Lentz and Dunson 1998), *Villarsia reniformis* (Cooling *et al.* 2001) and *Oryza sativa* (Metraux and Kende 1983).

Morphological responses to flooding are usually petiole extension (Blom *et al.* 1990; Cooling *et al.* 2001; Voesenek *et al.* 2003), internode extension (Metraux and Kende 1983; Kirkman and Sharitz 1993; Mauchamp *et al.* 2001; Vriezen *et al.* 2003) and production of fewer but longer stems (Waters and Shay 1990; Blanch *et al.* 1999a; Vretare *et al.* 2001). Although no measurements were taken, it appeared that when *Ludwigia peploides* plants were flooded internode length increased. Ethylene accumulation in submerged tissues, which reacts with ethylene receptor proteins operates as a reliable sensor of flooding and causes cell elongation and a subsequent increase in internode or petiole length (Metraux and

Kende 1983; Voeselek *et al.* 2003; Vriezen *et al.* 2003). In addition to internode elongation this species produced adventitious roots. Aerenchymatous adventitious root production has also been observed in *Oryza sativa*, when subjected to flooding, to facilitate diffusion of oxygen and prevent anaerobic conditions in the submerged tissue (Vriezen *et al.* 2003). A third adaptation to flooding exhibited by plants that respond morphologically is the production of aerenchyma to facilitate oxygen diffusion (Vriezen *et al.* 2003). Stems produced by flooded *Ludwigia peploides* plants appeared to be thicker and less dense than those produced by non-flooded plants, which may be due to the production of aerenchyma. Older submerged stems developed thick external spongy tissue, which may be external aerenchyma or buoyant tissue to enable stems to float.

Optimal growing conditions of this species were much wider than those of *Cyperus gymnocaulos* and *Xanthium occidentale*. Even though *Ludwigia peploides* responded positively to rising water levels, (especially when flooded at 1 cm day<sup>-1</sup>) plants at the +10 elevations had relatively high growth rates. This was probably because when stems came into contact with water they produced adventitious roots, which enabled the uptake of water and nutrients from the water column.

The high degree of phenotypic plasticity of *Ludwigia peploides* enabled this species to acclimate rapidly to rising water levels and hence was the only species that responded positively to flooding and grew faster. *Xanthium occidentale* and *Cyperus gymnocaulos* did not exhibit as high a degree of phenotypic plasticity and the optimal conditions for growth of those species was restricted to non-flooded elevations.

## 7 Chapter 7: Effect of Nutrients and Water Regime on Recruitment from the Seed Bank

### 7.1 Introduction

Water regime is the salient factor determining wetland floristic composition (e.g. Moore and Keddy 1988; Mitsch and Gosselink 1993; Casanova and Brock 2000; Nicol *et al.* 2003) Chapter 4) but its effects may be modified. For example, Portielje and Roijackers (1995) demonstrated that addition of nutrients changed the responses of submergent plant communities subjected to the same hydraulic regime. Morris *et al.* (2003a) reported that after four months of nutrient enrichment, mesocosms initially dominated by *Vallisneria americana* were overtaken by *Azolla pinnata*.

Eutrophication is implicated in the decline of submergent macrophytes and increased blooms of Cyanobacteria in lakes in the Netherlands (Brouwer and Roelofs 2001) and Lake Emir (Turkey) (Beklioglu *et al.* 2003), the decline of *Chara* sp. and *Myriophyllum spicatum* in Lake Geneva (Switzerland) (Lehmann and Lachavanne 1999) and the disappearance of submergent macrophytes from lakes in southern Sweden (Blindow 1992a; Blindow 1992b). Conversely, Tracy *et al.* (2003) reported that in lakes in Michigan (USA) dominated by floating macrophytes were invaded by submergent macrophytes when nutrient inputs into the system decreased but reverted to floating macrophytes when nutrient concentrations increased.

Nutrient enrichment is implicated in the expansion of *Typha domingensis* into areas dominated by *Cladium jamaicense* (Newman *et al.* 1998) and *Eleocharis interstincta* (Newman *et al.* 1996) in the Everglades (USA).

Clarke and Baldwin (2002) reported that ammonia levels  $>200 \text{ mg L}^{-1}$  inhibit the growth of *Juncus effusus*, *Sagittaria latifolia* and *Typha latifolia* and levels  $>100 \text{ mg L}^{-1}$  inhibited growth of *Schoenoplectus tabernaemontani*. Increased water levels and nutrient concentrations in soil and water facilitate the replacement of native wetland vegetation by *Phalaris arundinacea* (Miller and Zedler 2003) and reduce biomass production in marshes dominated *Scolochloa festucacea* and increase production in marshes dominated by *Typha glauca* (Neill 1989). Wetlands in tropical Puerto Rico receiving eutrophic swine effluent

have lower species richness of aquatic plants than those receiving water with low nutrient concentrations (Kent *et al.* 2000).

There is also evidence to suggest that nutrients influence seed germination. Stewart *et al.* (1997) demonstrated that *Typha latifolia* seeds germinate faster when subjected 0.2 mg L<sup>-1</sup> phosphorus. Seeds of Amazonian floodplain trees subjected to high-nutrient inflows generally have smaller seed carbohydrate reserves than those that receive low nutrient floodwaters (Parolin 2001). When seeds from species adapted to high-nutrient floodwaters are subjected to low nutrients, germination and survival are lower than when subjected to high nutrients, and the reverse is true for low-nutrient adapted species subjected to high nutrients (Parolin 2001). However, Bekker *et al.* (1998) reported no differences in the germination response of 17 fen-meadow species when buried and exposed to different nutrient concentration for two years.

The nutrient status of sediment from the Menindee Lakes is not known. When dry, domestic stock grazing is the dominant land use for all lakes except Cawndilla and the southern half of Menindee. Grazing by wildlife and domestic stock has the potential to change the nutrient dynamics by converting nitrogen and phosphorus from organic compounds that are unavailable to plants to available inorganic compounds such as phosphates and ammonia. The coarse sands around the edges of the deflation lakes (Appendix 1) are probably low in soluble nutrients because of low water holding capacity and the potential for leaching. The heavier clay soils towards the centre of the deflation lakes (Appendix 1) may be more fertile and have different species present than the areas with sandy soils (Chapter 5).

The aim of this experiment was to investigate the response of the Lake Malta seed bank to different nutrient loadings by testing the hypothesis that different soil nutrient loadings will give rise to different plant communities from the same seed bank, when subjected to the same water regime. The samples with high nutrient loadings will be dominated by species found on clay soils (e.g. *Glinus lotoides*, *Centipeda minima*, *Iseotopsis graminifolia*) and the low nutrient samples by species found on sandy soils (e.g. *Cyperus gymnocaulos*, *Limosella australis*, *Epaltis australis*). The Lake Malta seed bank was chosen because it is the most species rich seed bank (Chapter 2 and Chapter 3) and contains examples of species found on sandy and clayey soils (Chapter 5).

## 7.2 Methods

### 7.2.1 Sediment Sampling Protocol

Sediment was collected from four locations around the edge of Lake Malta. The sediment was dried to constant weight at 40° C, aggregates were broken up and thoroughly mixed (after drying) to produce composite sediment samples (sensu Seabloom *et al.* 1998; Nicol *et al.* 2003; Chapter 4). A composite seed bank was used to ensure that the potential differences between water-regime and nutrient treatments were not obscured by differences in seed bank composition.

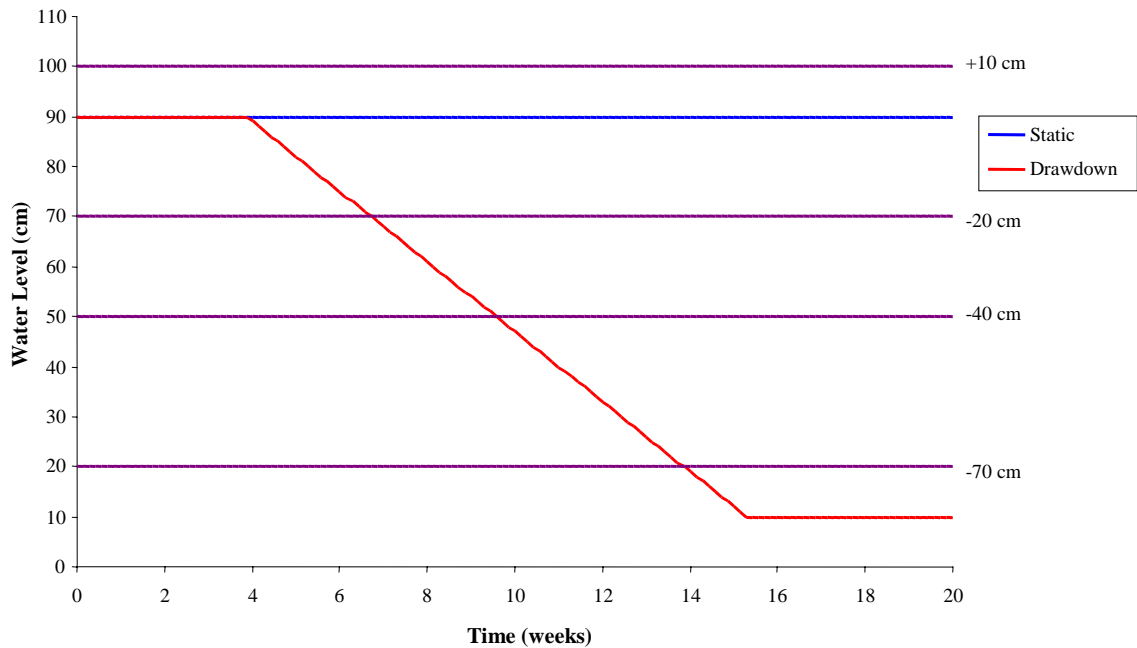
### 7.2.2 Experimental Protocol and Design

One hundred and twenty five cylinders (30 cm diameter, 100, 70, 50 or 20 cm tall) were filled with 60/40 sandy loam. Osmocote<sup>®</sup>, a slow-release fertilizer (N: P: K = 17.4: 4.4: 8.8 plus micronutrients), was added to the soil to give nitrogen loading equivalents of 0, 10, 25, 50 and 100 g N m<sup>-2</sup> year<sup>-1</sup>. This ensured that the nutrients did not leach into other treatments, but also obscured responses to single nutrient elements. The cylinders were placed in outdoor ponds (3 m x 4 m x 1.1 m) at the University of Adelaide (34°56' S, 138°36' E) and positioned to allow the soil to maintain contact with the falling water levels (sensu Nicol and Ganf 2000; Nicol *et al.* 2003; Chapter 4). Four hundred grams of the dried composite seed bank was spread over the top of the sandy loam. Five replicates for nutrient treatment and water regime were used ( $n = 5$ ), which gave a total of 125 cylinders.

### 7.2.3 Hydraulic Regimes

Initially the water level was held at 90 cm for 28 days to ensure the soil column was thoroughly saturated, then two hydraulic regimes were imposed on the seed bank: static 90 cm and drawdown at the rate of 1 cm day<sup>-1</sup> until the water level reached 10 cm where it remained static (Figure 7.1).





**Figure 7.1: Pond water levels with respect to the different elevation treatments over the experimental period.**

Within the drawdown regime there were four elevations +10, -20 -40 and -70 cm. At +10 cm the soil surface was 10 cm above the initial water level of 90 cm, at -20 cm the soil surface was 20 cm below the initial water level, at -40 cm the soil surface was 40 cm below the initial water level and at -70 cm the soil surface was 70 cm below the initial water level. There was only one elevation in the static treatment (+10 cm) because *Myriophyllum verrucosum* is the only species present in the seed bank of Lake Malta that germinates under water (Chapter 4). The hydraulic regime coupled with position on the elevation gradient will determine the water regime.

#### 7.2.4 Plant Identification and Nomenclature

Plants were identified using Jessop and Tolken (1986), Sainty and Jacobs (1981; 1994) and Cunningham *et al.* (1981). Nomenclature follows Jessop and Tolken (1986).

#### 7.2.5 Data Collection and Analysis

The experiment ran for 20 weeks and species composition was measured every four weeks. Bare soil was considered as a taxon so as not to exclude the samples devoid of plants. Differences in species composition between water regime, nutrient treatment and sampling date were compared using multivariate statistical analyses (group average clustering, multi

response permutation procedures (MRPP: (McCune and Mefford 1999) and indicator species analysis (Dufrene and Legendre 1997)). The major groups apparent in the cluster analysis determined the groups for MRPP and indicator species analysis. Non-significant species were classed as either Type A, B or C non-significant species (Chapter 2) depending on their distribution and abundance. All multivariate analyses were undertaken using PCOrd version 4.28 (McCune and Mefford 1999). Bray-Curtis distances were used for all multivariate analyses (Bray and Curtis 1957). For all statistical tests  $\alpha = 0.05$ . Data were pooled for the clustering analysis, for sake of clarity, but not for other statistical tests.

### 7.3 Results

At week four there were two divergent groups at a similarity of 0% (MRPP:  $A = 0.85$ ;  $P < 0.0001$ ) (Figure 7.2). Groups A-B represented the water regimes that were not submerged and group C represented those that were submerged (Figure 7.2). At a similarity of 80% the dendrogram can be divided into three groups (MRPP:  $A = 0.89$ ;  $P < 0.0001$ ): group C were the submerged samples, group B were the samples that were not submerged from the drawdown hydraulic regime and group A the samples that were not submerged from the static hydraulic regime (Figure 7.2). The samples from groups A and B however, had been subjected to the same hydraulic regime for the first four weeks of the experiment period. Differences in nutrient concentrations appeared to have no effect on species composition at this stage of the experiment (Figure 7.2).

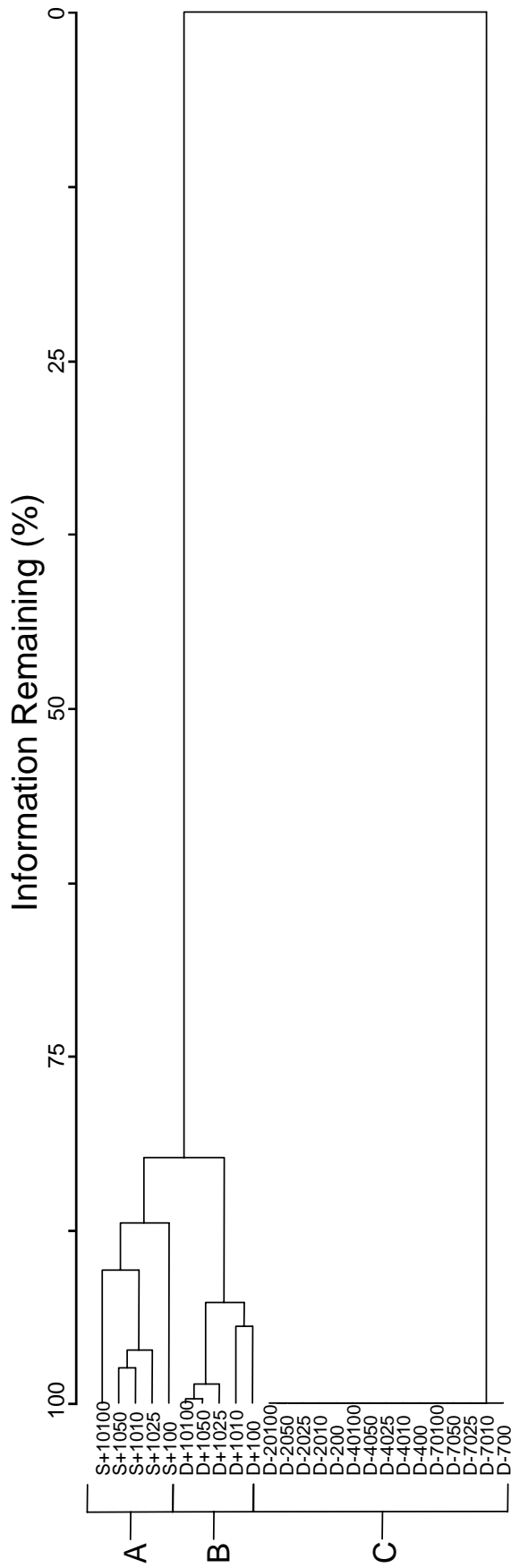


Figure 7.2: Group average clustering dendrogram of each water regime for week 4 (S = static, D = drawdown, +10, -20 -40 and -70 = Elevation and 100, 50, 25, 10 and = nitrogen loading rate in g m<sup>-2</sup> year<sup>-1</sup>).

The difference between groups A-B, and C was that the water regimes that were submerged at week four were devoid of plants and bare soil was the only significant indicator for group C (Table 7.1). All except three of the fifteen taxa detected at week four were significant indicators of either group A or B (Table 7.1). The two non-significant species, *Alternanthera denticulata* and *Cyperus gymnocaulos* were detected in low numbers (Type A non-significant species) (Table 7.1).

**Table 7.1: Indicator species analysis for week 4 (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).**

Species	Group	P
<i>Chenopodium pumilio</i>	A	0.011
<i>Cyperus gymnocaulos</i>	A	0.178 (Type A)
<i>Gnaphalium luteo-album</i>	A	0.009
<i>Medicago</i> sp.	A	0.008
<i>Alternanthera denticulata</i>	B	0.410 (Type A)
<i>Ammania multiflora</i>	B	0.002
<i>Centipeda minima</i>	B	0.004
<i>Epaltes australis</i>	B	0.007
<i>Limosella australis</i>	B	0.007
<i>Mollogo cerviana</i>	B	0.009
<i>Morgania floribunda</i>	B	0.013
<i>Polygonum plebium</i>	B	0.011
<i>Sporobolus mitchelli</i>	B	0.027
<i>Wahlenbergia communis</i>	B	0.007
Bare Soil	C	0.001

At week eight, the difference in floristic composition can be attributed to the presence of water (Figure 7.3). At a similarity of 0% there were two groups (MRPP: A = 0.59;  $P < 0.0001$ ). Group A were water regimes that were exposed, which now included the -20 cm elevation from the drawdown hydraulic regime and group B consisted of the water regimes that were submerged (Figure 7.3).

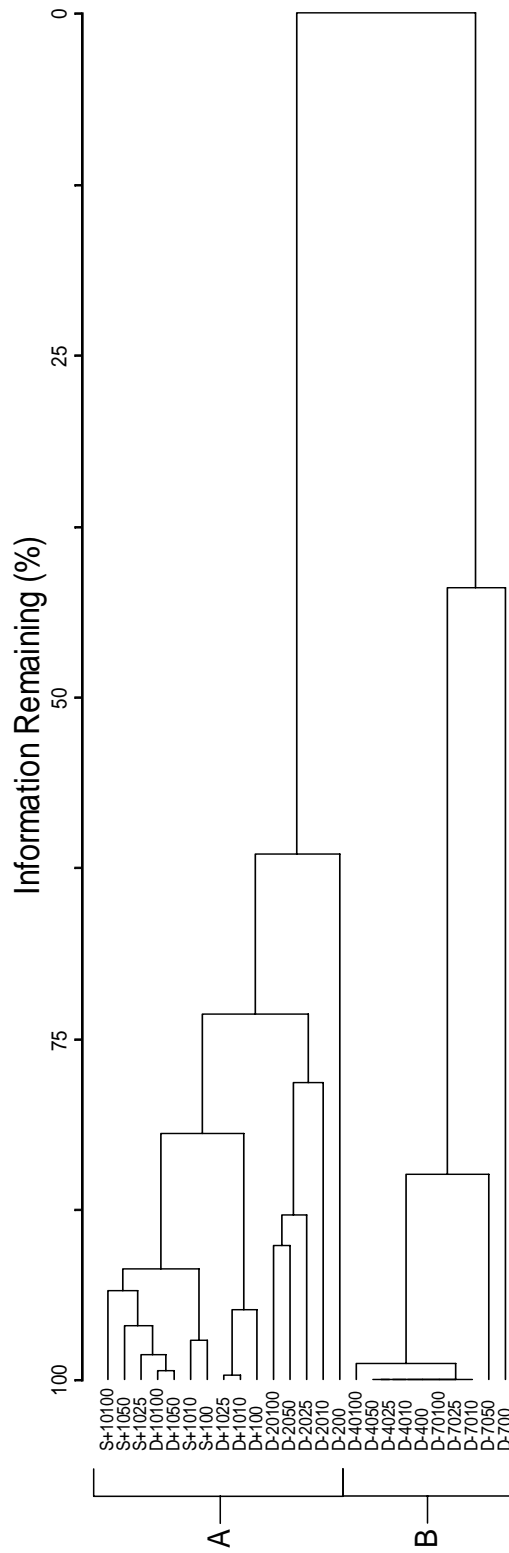


Figure 7.3: Group average clustering dendrogram of each water regime for week 8 (for explanation of abbreviations see Figure 7.2)

The main difference between groups A and B was the lack of plants on most of the samples in group B (bare soil is a significant indicator for this group) (Table 7.2). *Myriophyllum verrucosum* had germinated in some of the samples in group B but not in sufficient numbers to be a significant indicator (Table 7.2). Group A had 11 significant indicator species with *Alternanthera denticulata*, *Chenopodium pumilio* and *Cyperus gymnocaulos* also found exclusively in group A but not in sufficient numbers to be significant indicators (type A non-significant species) (Table 7.2).

**Table 7.2: Indicator species analysis for week 8 (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).**

Species	Group	P
<i>Alternanthera denticulata</i>	A	0.529 (Type A)
<i>Ammannia multiflora</i>	A	0.006
<i>Centipeda minima</i>	A	0.001
<i>Chenopodium pumilio</i>	A	0.484 (Type A)
<i>Cyperus gymnocaulos</i>	A	0.196 (Type A)
<i>Epaltes australis</i>	A	0.001
<i>Gnaphalium luteo-album</i>	A	0.001
<i>Limosella australis</i>	A	0.001
<i>Medicago</i> sp.	A	0.002
<i>Mollogo cerviana</i>	A	0.001
<i>Morgania floribunda</i>	A	0.001
<i>Polygonum plebium</i>	A	0.001
<i>Sporobolus mitchelli</i>	A	0.002
<i>Wahlenbergia communis</i>	A	0.02
Bare Soil	B	0.001
<i>Myriophyllum verrucosum</i>	B	0.675 (Type A)

As in weeks four and eight, the difference in floristic composition between the three groups (MRPP:  $A = 0.46$ ;  $P < 0.0001$ ), at similarity of 40%, can be attributed to differences in water regime (Figure 7.4). Groups A and B contained exposed water regimes and group C submerged (Figure 7.4). The samples that make up group A had all been exposed for at least four weeks, except the one drawdown -40 cm water regime treatment present (static +10 cm, drawdown +10 cm and -20 cm) and all group B samples (drawdown -40 cm) were exposed for less than four weeks (Figure 7.4).

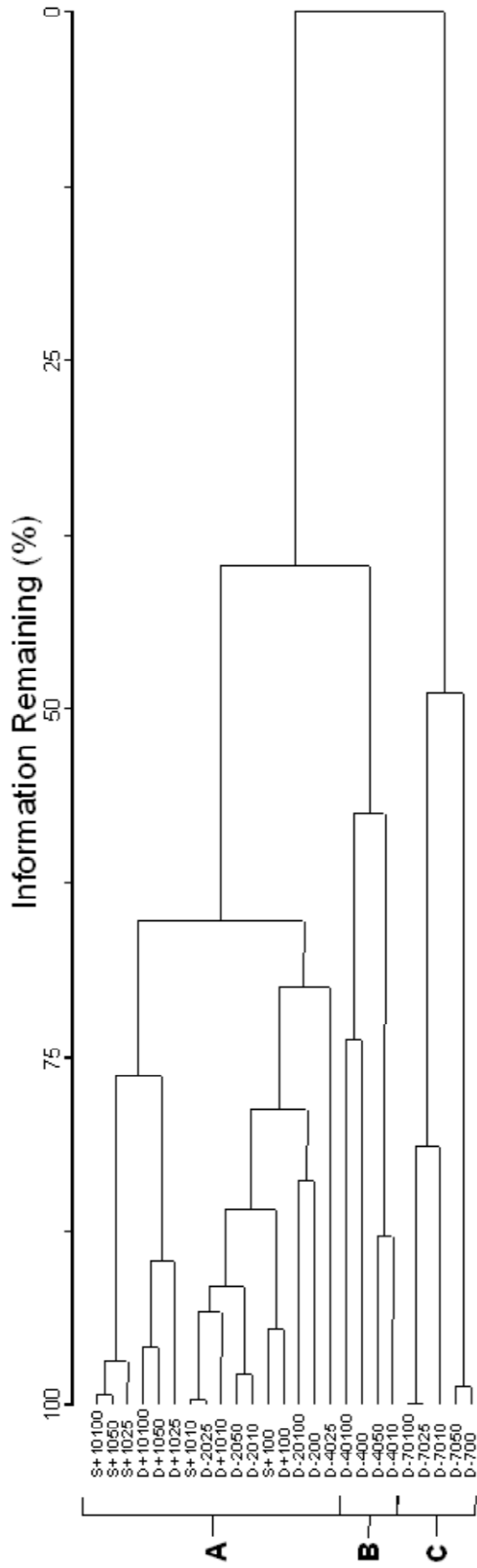


Figure 7.4: Group average clustering dendrogram of each water regime for week 12 (for explanation of abbreviations see Figure 7.2)

The samples that were submerged (group C) either were devoid of plants or dominated by *Myriophyllum verrucosum* (Table 7.3). The newly exposed water regimes (group B) were dominated by *Limosella australis*, which was the only significant indicator for that group (Table 7.3). Group A had the most significant indicator species (eight), but *Sporobolus mitchelli* and *Wahlenbergia communis* decreased in abundance and were no longer indicators (type A non-significant species) (Table 7.3).

**Table 7.3: Indicator species analysis for week 12 (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).**

Species	Group	P
<i>Alternanthera denticulata</i>	A	1.00 (Type A)
<i>Ammania multiflora</i>	A	0.042
<i>Centipeda minima</i>	A	0.001
<i>Chenopodium pumilio</i>	A	0.347 (Type A)
<i>Cyperus gymnocaulos</i>	A	0.453 (Type A)
<i>Epaltes australis</i>	A	0.001
<i>Gnaphalium luteo-album</i>	A	0.001
<i>Medicago</i> sp.	A	0.028
<i>Mollogo cerviana</i>	A	0.001
<i>Morgania floribunda</i>	A	0.001
<i>Polygonum plebium</i>	A	0.039
<i>Sporobolus mitchelli</i>	A	0.115 (Type A)
<i>Wahlenbergia communis</i>	A	0.737 (Type A)
<i>Limosella australis</i>	B	0.009
Bare Soil	C	0.001
<i>Myriophyllum verrucosum</i>	C	0.013

At week sixteen all water regimes were exposed (Figure 7.1), but there were still three distinct groups (MRPP:  $A = 0.40$ ;  $P < 0.0001$ ), at a similarity of 25%, reflecting differences in exposure time (Figure 7.5). Group A consisted of the static and drawdown +10 cm elevations, which had never been submerged (Figure 7.5). Group B contained the water regimes that were initially submerged, but exposed for at least four weeks (drawdown -20 and -40 cm) and group C contained the drawdown -70 cm samples that had been exposed for less than four weeks (Figure 7.5).



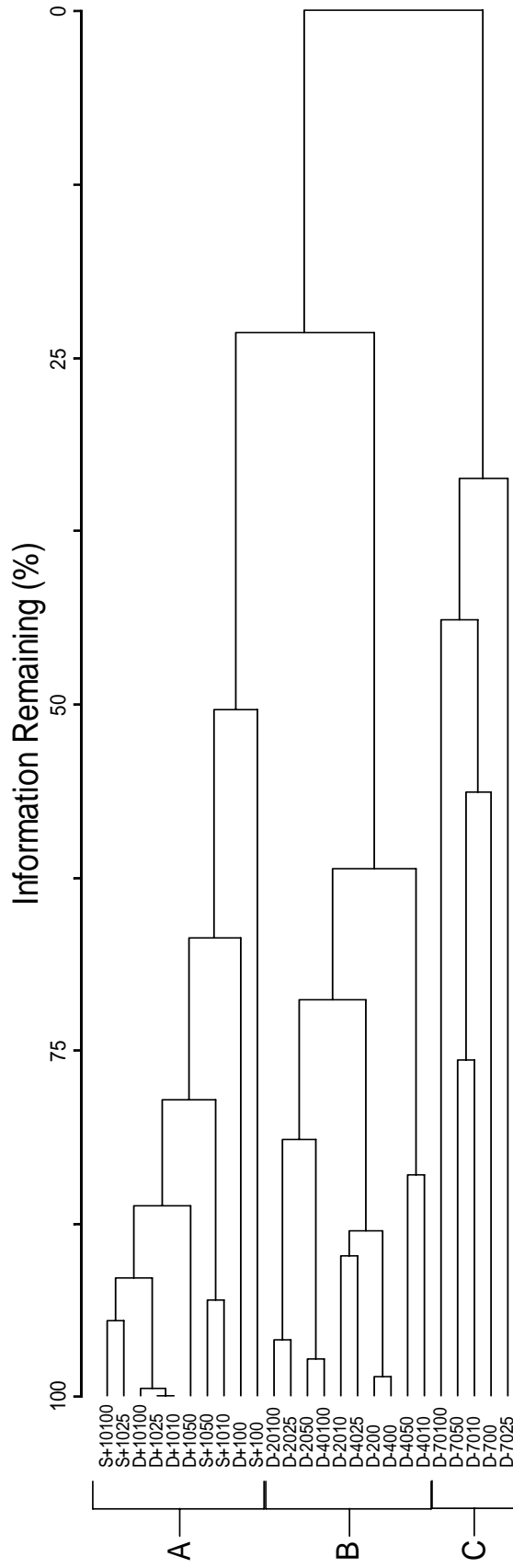


Figure 7.5: Group average clustering dendrogram of each water regime for week 16 (for explanation of abbreviations see Figure 7.2)

At week sixteen, indicator species analysis showed that three species (*Medicago* sp., *Gnaphalium luteo-album* and *Polygonum plebium*) were widespread (type B non-significant species) (Table 7.4). In addition, plants had germinated in all replicates, hence bare soil was not present (Table 7.4). Groups A and B had three significant indicator species each and *Myriophyllum verrucosum* was the only significant indicator of group C (Table 7.4). The same species that were not significant indicators at week twelve because of low numbers (Table 7.3) were still rare (type A non-significant species) (Table 7.4).

**Table 7.4: Indicator species analysis for week 16 (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).**

Species	Group	P
<i>Alternanthera denticulata</i>	A	1.00 (Type A)
<i>Centipeda minima</i>	A	0.001
<i>Cyperus gymnocaulos</i>	A	0.346 (Type A)
<i>Epaltes australis</i>	A	0.001
<i>Gnaphalium luteo-album</i>	A	0.078 (Type B)
<i>Medicago</i> sp.	A	0.096 (Type B)
<i>Morgania floribunda</i>	A	0.005
<i>Polygonum plebium</i>	A	0.083 (Type B)
<i>Sporobolus mitchelli</i>	A	0.333 (Type A)
<i>Ammania multiflora</i>	B	0.001
<i>Limosella australis</i>	B	0.001
<i>Mollogo cerviana</i>	B	0.011
<i>Wahlenbergia communis</i>	B	0.124 (Type A)
<i>Myriophyllum verrucosum</i>	C	0.001

At week twenty, all water regimes had been exposed for at least six weeks (Figure 7.1). The three significantly different groups (MRPP:  $A = 0.49$ ;  $P < 0.0001$ ) at a similarity of 20% could be generally explained by differences in water regime. Group A generally contained the water regimes that were never submerged (static and drawdown +10 cm), however the 100, 50 and 25 g N m<sup>-2</sup> year<sup>-1</sup> nutrient loading treatments from the drawdown -20 cm treatments were also present in the is group (Figure 7.6). The remainder of the water regime treatments were present in group B which were all initially submerged then exposed, except for the drawdown -70 cm 0 g N m<sup>-2</sup> year<sup>-1</sup> treatment which was an outlier (Figure 7.6).

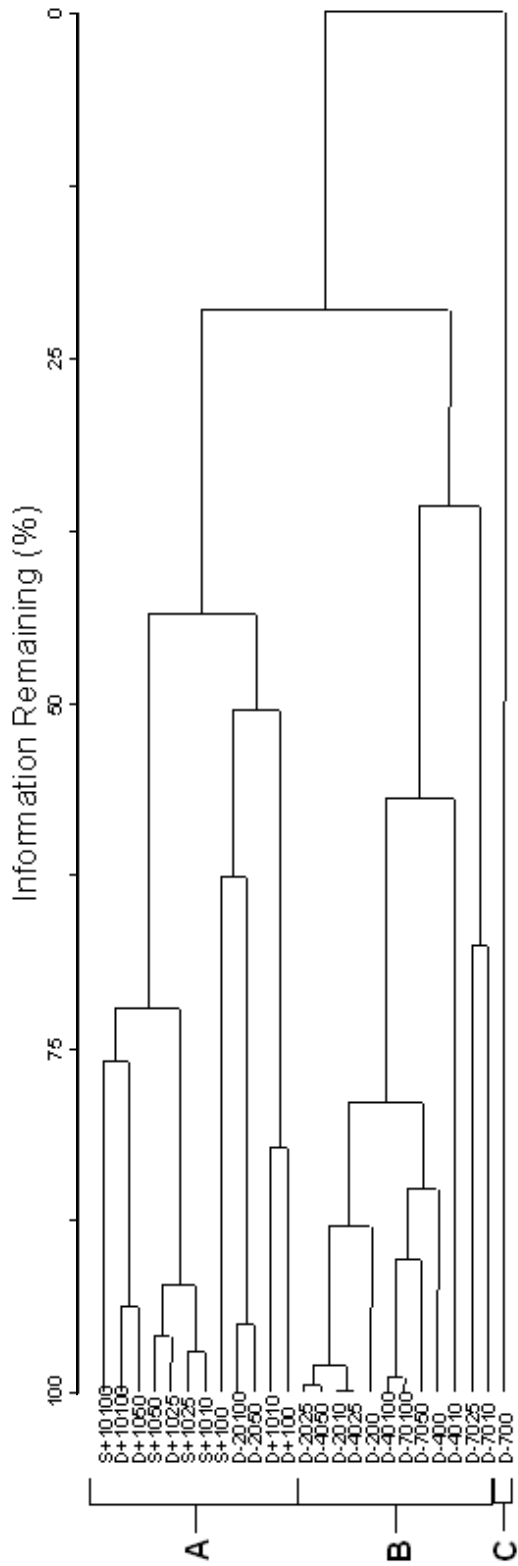


Figure 7.6: Group average clustering dendrogram of each water regime for week 20 (for explanation of abbreviations see Figure 7.2)

Group A samples were dominated by *Centipeda minima*, *Epaltes australis* and *Morgania floribunda* (Table 7.5). Group B was dominated by *Limosella australis* and group C by *Myriophyllum verrucosum* (Table 7.5). *Gnaphalium luteo-album*, *Polygonum plebium*, *Medicago* sp. and *Mollogo cerviana* were common across all treatments (type B non-significant species) and the other four rare (type A) species had not increased in abundance (Table 7.5).

**Table 7.5: Indicator species analysis for week 20 (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).**

Species	Group	P
<i>Alternanthera denticulata</i>	A	1.00 (Type A)
<i>Centipeda minima</i>	A	0.026
<i>Epaltes australis</i>	A	0.005
<i>Medicago</i> sp.	A	0.091 (Type B)
<i>Morgania floribunda</i>	A	0.002
<i>Polygonum plebium</i>	A	0.260 (Common)
<i>Ammania multiflora</i>	B	0.254 (Type A)
<i>Cyperus gymnocaulos</i>	B	0.351 (Type A)
<i>Gnaphalium luteo-album</i>	B	0.085 (Type B)
<i>Limosella australis</i>	B	0.001
<i>Mollogo cerviana</i>	B	0.124 (Type B)
<i>Sporobolus mitchelli</i>	B	0.811 (Type A)
<i>Myriophyllum verrucosum</i>	C	0.001

Nutrient loading; however, had an effect on total biomass (Figure 7.7). The 0 g N m<sup>-2</sup> year<sup>-1</sup> for all water regimes (except drawdown -70 cm) had lower total biomass than the other treatments (Figure 7.7). This was not the case for the drawdown -70 cm treatment where there was no discernable difference in total biomass (Figure 7.7). The water regimes that were never submerged with nutrients added had higher, albeit variable, total biomasses followed by drawdown -20 and -40 cm (with nutrients added) and drawdown -70 cm had the lowest total biomass (Figure 7.7).

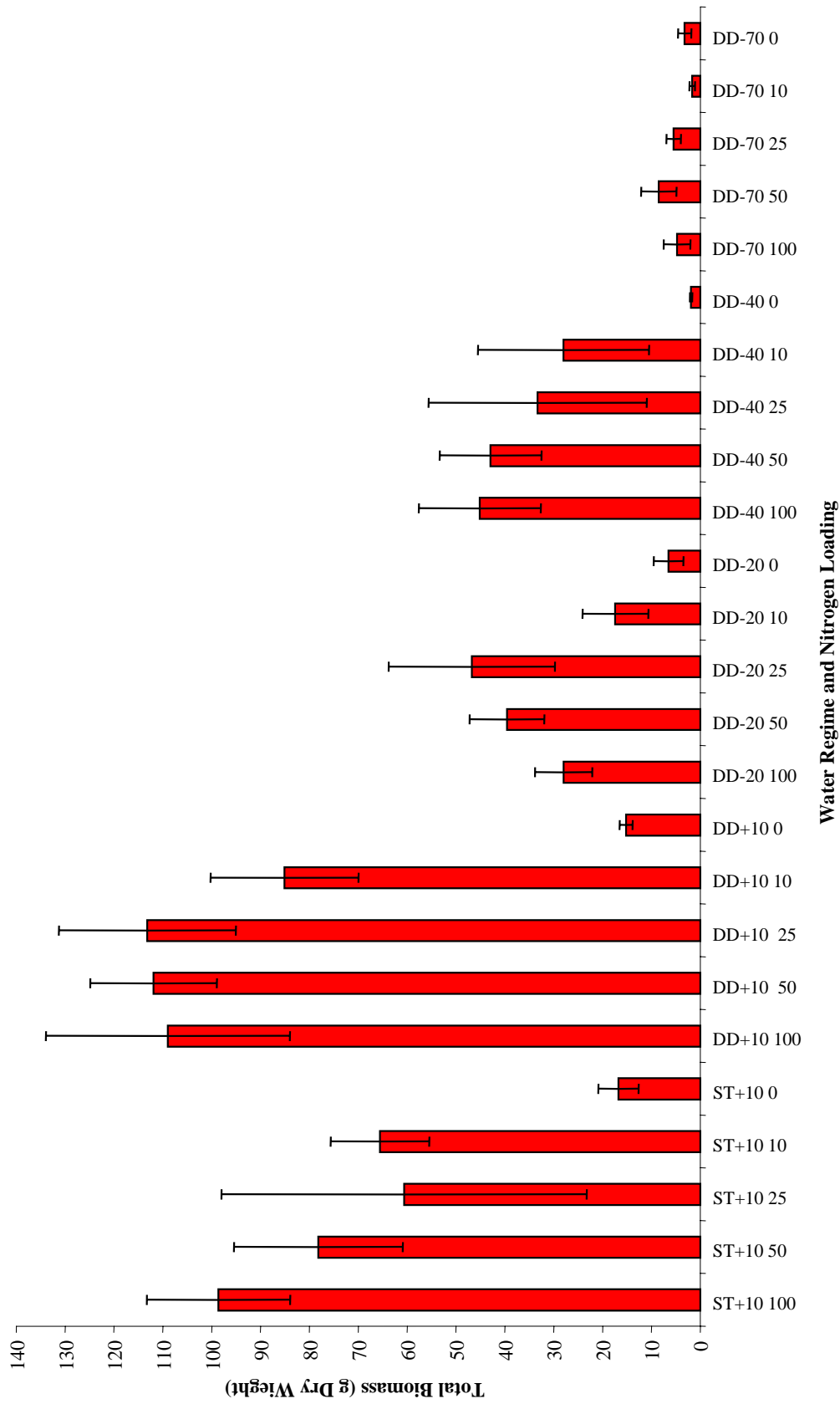


Figure 7.7: Total final biomass (week 20) for each hydraulic regime and elevation combination (ST = static, DD = drawdown, +10 -20, -40 and -70 = elevation, 100, 50, 25, 10 and 0 = nitrogen loading in  $g\ m^{-2}\ year^{-1}$ ), (error bars =  $\pm$  SE).

## 7.4 Discussion

The addition of nutrients to the soil had no apparent effect on germination and recruitment from the Lake Malta seed bank. The major differences in species composition were related to whether the sediment was inundated or exposed and the duration of exposure. Submerged samples were generally devoid of plants, newly exposed samples were dominated by *Limosella australis* and samples never submerged or exposed longer than four weeks had the greatest species richness.

The species present and the delivery of nutrients to the system are important factors in how the seed bank and extant vegetation responds. Submergent macrophytes appear to be more sensitive to in changes in nutrient concentration in the water column. For example, high concentrations of nutrients in the water column has been implicated in changes in the vegetation communities in permanent lakes from systems dominated by charophytes and submerged macrophytes to systems dominated by floating macrophytes or cyanobacteria (e.g. Blindow 1992a; Blindow 1992b; Sandilands *et al.* 2000; Brouwer and Roelofs 2001; Solinska-Gornicka and Symonides 2001; Morris *et al.* 2003a). However, emergent, floodplain and terrestrial species dominate the Lake Malta seed bank (only *Myriophyllum verrucosum* will germinate underwater (Chapter 4)) and the nutrients were delivered to the soil.

The concentration of nutrients is also important; Morris *et al.* (2003a; 2003b) reported that a single high concentration dose of nutrients caused a shift from a submerged macrophyte dominated system to a phytoplankton dominated system, whereas repeated lower concentration doses did not cause a change. Osmocote is a slow release fertiliser; therefore, a steady supply of nutrients was released over the experiment. The seed bank may have shown different responses to a single, high concentration dose of nutrients delivered by a soluble fertiliser; however, this would have required separate ponds for each nutrient treatment.

Despite different concentrations of a broad spectrum of nutrients having no apparent effect, the seed bank and extant vegetation may show different responses to the addition of a single element such as nitrogen or phosphorus. Experiments designed to investigate effect of

single elements would give a further insight into how nutrients can modify the effect of water regime in the Menindee Lakes.

## 8 Chapter 8: General Discussion

The six experimental chapters (Chapters 2-7) in this thesis have dealt with various aspects of the vegetation dynamics of the Menindee Lakes. A preliminary reconnaissance study to gain information about the seed bank was undertaken in Chapter 2, which not only aided in the design of future experiments, also led to the strandline investigation in Chapter 3. The strandline investigation compared the seed banks of the strandlines in four lakes with the adjacent sediment. Chapter 4 was an investigation into the effect of water regime on recruitment from the seed bank under controlled experimental conditions. From this information the seed bank recruitment model was formulated and tested in Chapter 5. In addition to testing the aforementioned model, Chapter 5 dealt with recruitment from the seed bank in the field and how factors other than water regime can influence floristic composition. Another model (the window of opportunity model, which predicts how the system changes when water levels fluctuate) was also tested in Chapter 5. Due to extended drought in the Darling River catchment the Menindee Lakes did not flood over the study period and a pond experiment to investigate the flooding tolerance of three common species found in the Menindee Lakes was undertaken (Chapter 6), to give an insight into how these species coped with inundation. The final experimental chapter (Chapter 7) investigated recruitment from the seed bank under different soil nutrient conditions.

### 8.1 The Menindee Lakes Seed Bank

The Menindee Lakes seed bank provides propagules for regeneration of plant communities after flood or drought disturbance. Approximately two thirds of the species had persistent seed banks (Thompson and Grime (1979) type III or IV seed banks). The remainder are not 'bet hedgers', but are not Thompson and Grime (1979) type I or II seed banks. Species with these strategies are adapted to exploit predictable seasonal damage and mortality to the extant vegetation and the seed is short-lived (Thompson and Grime 1979). The Menindee Lakes are not subject to predictable seasons and favourable conditions for germination do not occur on a regular, seasonal basis. Therefore, seeds of these species must persist for longer than one year or they will be extirpated.

The seed bank is extremely variable in terms of seed density and species richness. Seed density ranged from 117 seeds  $\text{m}^{-2}$  from the northern edge of Lake Menindee (Chapter 2) to over 200,000 seeds  $\text{m}^{-2}$  near the inlet channel of Lake Tandure (Appendix 8). The estimate



of the seed density near the inlet channel of Lake Tandure was an underestimate because the seedling emergence technique was used (Gross 1990; Brown 1992) and germination was still occurring when the trial stopped. Species richness ranged from one species from the northern edge of Lake Menindee (Chapter 2) to 31 species from the north eastern shore of Lake Malta (Chapter 3).

Around the edges of the large lakes, the strandline had greater seed density and species richness than the adjacent sediment (Chapter 3). This pattern was not observed in Lake Malta where there was a large, species-rich seed bank present outside the strandline (Chapter 3). The edges of Lake Bijiji also had a significant sediment seed bank outside of the strandline (Chapter 2) but the strandlines of this lake were not investigated and may have a greater seed density and species richness. Significant sediment seed banks were also detected near the inlet of Lake Tandure (Appendix 8).

The seed bank of the Menindee Lakes is also resilient with 2-9 species germinating during the final wetting cycle from sediments that were subjected to five wetting and drying cycles (Chapter 3). This implies that even after five false starts some viable seed remained in the sediment.

## 8.2 Recruitment from the Seed Bank

Germination for all species, except *Myriophyllum verrucosum*, occurred when the sediment was exposed to the atmosphere with high soil moisture in the top 7.5 cm of sediment (Chapter 4 and Chapter 7). For recruitment to occur conditions must remain favourable for sufficient time for seedlings to establish. Favourable conditions for recruitment were similar within functional groups (Chapter 4). Terrestrial and floodplain species required moist exposed sediment for germination, were generally desiccation tolerant and intolerant of flooding. All amphibious species, except *Myriophyllum verrucosum*, also required moist exposed sediment to germinate. Desiccation tolerance varied between species as did the response to flooding. No submergent species were present and floating species occurred in low numbers.

Recruitment from the seed bank is summarised in a conceptual model (Figure 8.1), which draws together information from pond experiments (Chapter 4, Chapter 6 and Chapter 7) and the field study (Chapter 5). The effect of flooding could only be investigated using

ponds because inflows into the Menindee Lakes after September 2001 were insufficient to flood any of the deflation lakes (Figure 1.5, Figure 1.6 and Figure 1.7).

The model includes three major states depending on whether the window of opportunity for germination is open or closed, which the system switches between depending on water level and elevation (Figure 8.1). The three states are:

Flooded: the window of opportunity for germination is closed due to inundation of the sediment surface (Figure 8.1).

Exposed: the window of opportunity for germination is open because the sediment is exposed and the soil moisture in the top 7.5 cm is sufficient for germination (Figure 8.1).

Exposed: the window of opportunity for germination is shut because the soil moisture in the top 7.5 cm is insufficient for germination (Figure 8.1).

Within each state, there are several sub-states that the system switches between depending on soil moisture content, sediment exposure time, flooding duration and flooding depth. Species potentially present in each state and sub-state are listed in Table 8.1.

When the sediment is flooded, the window of opportunity for germination is closed for all species except *Myriophyllum verrucosum* (Chapter 4 and Chapter 7). When the sediment is initially flooded, the system switches from one of the exposed states to the recently flooded sediment sub-state (Figure 8.1). When the system is in this sub-state not all of the floodplain and terrestrial species have been extirpated.

If the system remains flooded and the maximum depth does not exceed 1 m, the system switches to the sediment flooded for less than 8 weeks or flooded sediment with amphibious species present sub-state, depending on which species recruited during the previous drawdown phase (Figure 8.1).

If the sediment remains flooded for longer than 8 weeks to a depth of less than 1 m the system switches to the sediment flooded for longer than 8 weeks sub-state (Figure 8.1). If water levels remain static, the system will remain in this sub-state indefinitely (Figure 8.1).

If water levels increase and the sediment is flooded to deeper than 1 m the system switches to the sediment flooded deeper than 1 m or sediment flooded deeper than 1 m with

amphibious species, depending on the species present (Figure 8.1). However, this part of the model is untested (Figure 8.1).

If the water level falls below the sediment surface, the system switches states to exposed: window of opportunity for germination open (Figure 8.1). Immediately after the sediment is exposed the system is in the newly exposed sediment sub-state (Figure 8.1). If there is no change in the water level, the system will switch to the sediment with high soil moisture 0-40 cm sub-state and remain in that state indefinitely (Figure 8.1). Since the window of opportunity for germination is open, annuals will be able to persist because germination can continuously occur; however, competitive species may dominate the system. Other factors that could potentially influence the species composition are sediment texture and grazing (untested) (Figure 8.1).

If the water level increases and the sediment becomes inundated, the system will switch to the flooded state and the window of opportunity for germination will close (Figure 8.1). If water levels are drawn down further and the top 7.5 cm of sediment dries, the system will switch states to exposed: window of opportunity for germination closed (Figure 8.1).

Immediately after the state changes, the system will be in the sediment with low soil moisture 0-7.5 cm (short exposure time) sub-state. Most of the species present in the sediment with high soil moisture 0-40 cm sub-state will also be present in this sub-state because water is available at a shallow depth (Table 8.1). If water levels remain static, annuals will be lost from the extant vegetation after flowering and seed set (Figure 8.1). The system will then switch to the sediment with low soil moisture 0-7.5 cm (long exposure time) and if water levels remain static, stay in that sub-state indefinitely (Figure 8.1). Sediment texture and grazing (untested) will also influence species composition of the extant vegetation (Figure 8.1).

If the water level is drawn down further, the top 15 cm of sediment will dry out and the system switches to one of the sediment with low soil moisture 0-15 cm sub-states, depending on the sediment exposure time and presence or absence of annuals (Figure 8.1). Species that do not develop extensive root systems will be extirpated when the system is in this state (Table 8.1). If water levels remain static the system will remain in the sediment with low soil moisture 0-15 cm (long exposure time) sub-state indefinitely (Figure 8.1).

If water levels are drawn down further, the system switches to the driest of the sub-states, sediment with low soil moisture 0-40 cm (Figure 8.1). When the system is in this state, only the most desiccation tolerant species will be present (Table 8.1). If water levels remain static the system will remain in the sediment with low soil moisture 0-40 cm (long exposure time) sub-state indefinitely (Figure 8.1).

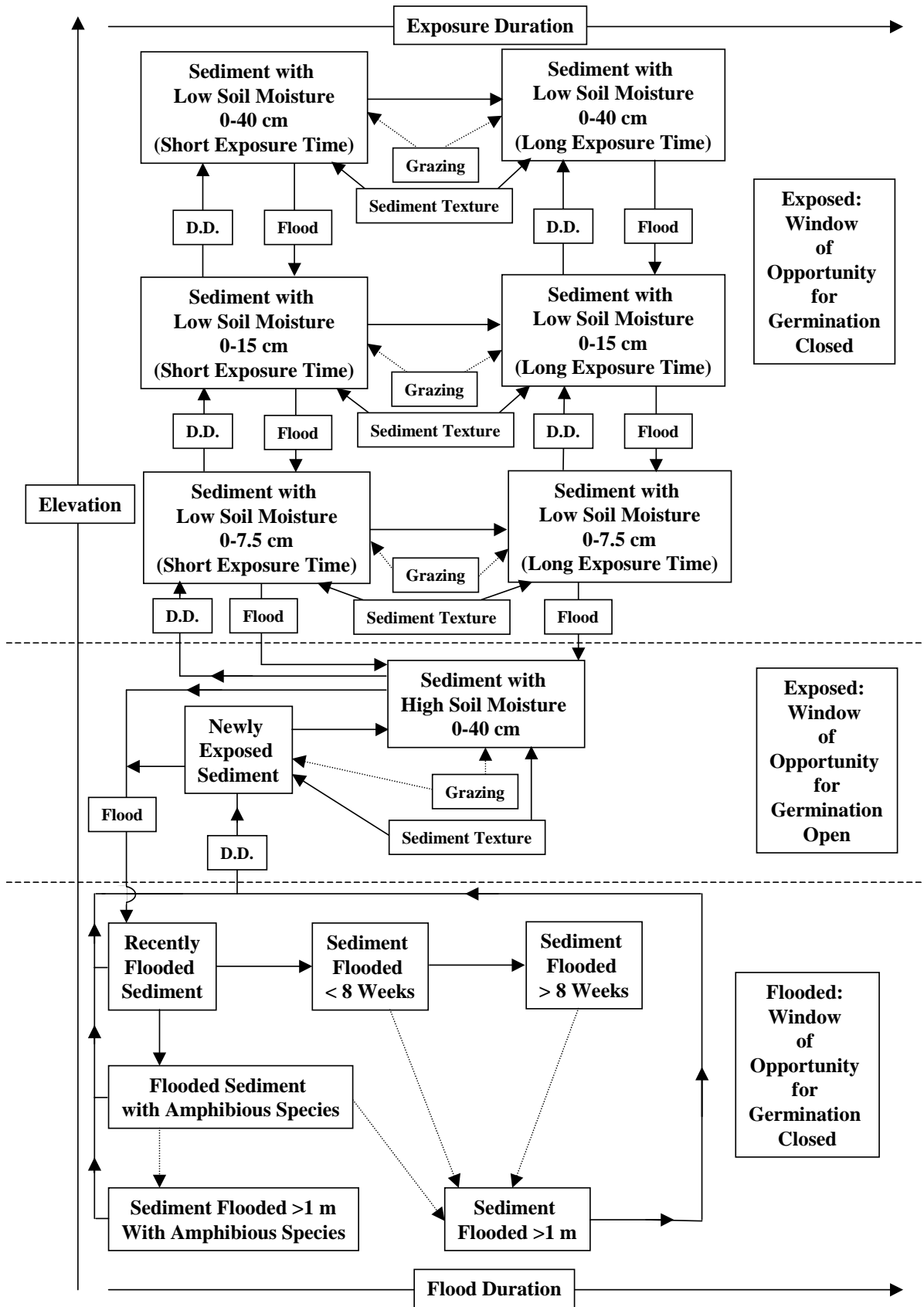


Figure 8.1: Conceptual model of plant recruitment from the seed bank for the Menindee Lakes (dashed arrows indicate process not investigated).

Table 8.1: Species list for each model state a. Flooded, b. Exposed: window of opportunity open for germination and c. Exposed: window of opportunity for germination closed (\*denotes exotic species).

a.

Recently Flooded Sediment	Sediment Flooded < 8 Weeks	Sediment Flooded > 8 Weeks	Flooded Sediment with Amphibious Species	Sediment Flooded > 1m with Amphibious Species	Sediment Flooded > 1 m
<i>Alternanthera denticulata</i>	Bare Soil	Bare Soil	<i>Cyperus gymnocaulos</i>	<i>Cyperus gymnocaulos</i>	Bare soil
<i>Centipeda minima</i>		<i>Myriophyllum verrucosum</i>	<i>Eucalyptus camaldulensis</i>	<i>Eucalyptus camaldulensis</i>	
<i>Cyperus gymnocaulos</i>			<i>Heliotropium curassivicum</i>	<i>Ludwigia peploides</i>	
<i>Eucalyptus camaldulensis</i>			<i>Juncus aridicola</i>	<i>Typha domingensis</i>	
<i>Eucalyptus largiflorens</i>			<i>Ludwigia peploides</i>		
<i>Heliotropium curassivicum</i>			<i>Marsilea</i> sp.		
<i>Juncus aridicola</i>			<i>Myriophyllum verrucosum</i>		
<i>Limosella australis</i>			<i>Persicaria lapathifolium</i>		
<i>Ludwigia peploides</i>			<i>Sporobolus mitchelli</i>		
<i>Marsilea</i> sp.			<i>Typha domingensis</i>		
<i>Medicago</i> spp.*					
<i>Persicaria lapathifolium</i>					
<i>Sporobolus mitchelli</i>					
<i>Typha domingensis</i>					
<i>Xanthium occidentale</i> *					

b.

Newly Exposed Sediment	Sediment with High Soil Moisture 0-40 cm
<i>Eucalyptus camaldulensis</i>	<i>Alternanthera denticulata</i>
<i>Eucalyptus largiflorens</i>	<i>Ammania multiflora</i>
<i>Juncus aridicola</i>	<i>Argemone ochroleuca*</i>
<i>Limosella australis</i>	<i>Centipeda minima</i>
<i>Marsilea</i> sp.	<i>Chenopodium pumilio</i>
<i>Myriophyllum verrucosum</i>	<i>Chloris truncata</i>
<i>Typha domingensis</i>	<i>Cyperus gymnocaulos</i>
	<i>Epaltes australis</i>
	<i>Eragrostis dielsii</i>
	<i>Eucalyptus camaldulensis</i>
	<i>Eucalyptus largiflorens</i>
	<i>Euphorbia drummondii</i>
	<i>Galenia secunda*</i>
	<i>Glinus lotoides</i>
	<i>Gnaphalium luteo-album</i>
	<i>Haloragis aspera</i>
	<i>Heliotropium amplexicaule*</i>
	<i>Heliotropium curassivicum</i>
	<i>Heliotropium europaeum*</i>
	<i>Helipterum pygmaeum</i>
	<i>Iseotopsis graminifolia</i>
	<i>Juncus aridicola</i>
	<i>Limosella australis</i>
	<i>Ludwigia peploides</i>
	<i>Marsilea</i> sp.
	<i>Medicago</i> spp.*
	<i>Mentha australis</i>
	<i>Muehlenbeckia cunninghamii</i>
	<i>Mollogo cerviana</i>
	<i>Morgania floribunda</i>
	<i>Myosurus minima</i>
	<i>Myriocephalus stuartii</i>
	<i>Nicotiana glauca</i>
	<i>Nicotiana velutino</i>
	<i>Persicaria lapathifolium</i>
	<i>Polygonum plebium</i>
	<i>Pterocaulon spacthelatum</i>
	<i>Rumex bidens</i>
	<i>Senecio</i> sp.
	<i>Scirpus</i> sp.
	<i>Sporobolus mitchelli</i>
	<i>Swainsona gregana</i>
	<i>Tetragonia tetragonoides</i>
	<i>Typha domingensis</i>
	<i>Wahlenbergia communis</i>
	<i>Xanthium occidentale*</i>

C.

Sediment with Low Soil Moisture 0-7.5 cm (Short Exposure Time)		Sediment with Low Soil Moisture 0-7.5 cm (Long Exposure Time)		Sediment with Low Soil Moisture 0-15 cm (Short Exposure Time)		Sediment with Low Soil Moisture 0-15 cm (Long Exposure Time)		Sediment with Low Soil Moisture 0-40 cm (Short Exposure Time)		Sediment with Low Soil Moisture 0-40 cm (Long Exposure Time)	
<i>Alternanthera denticulata</i>	<i>Asphodelus fistulosus*</i>	<i>Alternanthera denticulata</i>	<i>Asphodelus fistulosus*</i>	<i>Asphodelus fistulosus*</i>	<i>Asphodelus fistulosus*</i>	<i>Alternanthera denticulata</i>	<i>Asphodelus fistulosus*</i>	<i>Alternanthera denticulata</i>	<i>Asphodelus fistulosus*</i>	<i>Asphodelus fistulosus*</i>	<i>Asphodelus fistulosus*</i>
<i>Ammania multiflora</i>	<i>Citrullus lanatus*</i>	<i>Ammania multiflora</i>	<i>Citrullus lanatus*</i>	<i>Ammania multiflora</i>	<i>Citrullus lanatus*</i>	<i>Ammania multiflora</i>	<i>Citrullus lanatus*</i>	<i>Ammania multiflora</i>	<i>Citrullus lanatus*</i>	<i>Citrullus lanatus*</i>	<i>Citrullus lanatus*</i>
<i>Argemone ochroleuca*</i>	<i>Cyperus gymnocaulos</i>	<i>Argemone ochroleuca*</i>	<i>Cyperus gymnocaulos</i>	<i>Argemone ochroleuca*</i>	<i>Cyperus gymnocaulos</i>	<i>Argemone ochroleuca*</i>	<i>Cyperus gymnocaulos</i>	<i>Argemone ochroleuca*</i>	<i>Cyperus gymnocaulos</i>	<i>Cyperus gymnocaulos</i>	<i>Cyperus gymnocaulos</i>
<i>Centipeda minima</i>	<i>Eucalyptus camaldulensis</i>	<i>Centipeda minima</i>	<i>Eucalyptus camaldulensis</i>	<i>Centipeda minima</i>	<i>Eucalyptus camaldulensis</i>	<i>Centipeda minima</i>	<i>Eucalyptus camaldulensis</i>	<i>Centipeda minima</i>	<i>Eucalyptus camaldulensis</i>	<i>Eucalyptus camaldulensis</i>	<i>Eucalyptus camaldulensis</i>
<i>Chenopodium pumilio</i>	<i>Eucalyptus largiflorens</i>	<i>Chenopodium pumilio</i>	<i>Eucalyptus largiflorens</i>	<i>Chenopodium pumilio</i>	<i>Eucalyptus largiflorens</i>	<i>Chenopodium pumilio</i>	<i>Eucalyptus largiflorens</i>	<i>Chenopodium pumilio</i>	<i>Eucalyptus largiflorens</i>	<i>Eucalyptus largiflorens</i>	<i>Eucalyptus largiflorens</i>
<i>Chloris truncata</i>	<i>Haloragis aspera</i>	<i>Chloris truncata</i>	<i>Haloragis aspera</i>	<i>Chloris truncata</i>	<i>Haloragis aspera</i>	<i>Chloris truncata</i>	<i>Haloragis aspera</i>	<i>Chloris truncata</i>	<i>Haloragis aspera</i>	<i>Haloragis aspera</i>	<i>Haloragis aspera</i>
<i>Cyperus gymnocaulos</i>	<i>Heliotropium curassivicum</i>	<i>Cyperus gymnocaulos</i>	<i>Heliotropium curassivicum</i>	<i>Cyperus gymnocaulos</i>	<i>Heliotropium curassivicum</i>	<i>Cyperus gymnocaulos</i>	<i>Heliotropium curassivicum</i>	<i>Cyperus gymnocaulos</i>	<i>Heliotropium curassivicum</i>	<i>Heliotropium curassivicum</i>	<i>Heliotropium curassivicum</i>
<i>Epaltes australis</i>	<i>Helipterum pygmaeum</i>	<i>Epaltes australis</i>	<i>Helipterum pygmaeum</i>	<i>Epaltes australis</i>	<i>Helipterum pygmaeum</i>	<i>Epaltes australis</i>	<i>Helipterum pygmaeum</i>	<i>Epaltes australis</i>	<i>Helipterum pygmaeum</i>	<i>Helipterum pygmaeum</i>	<i>Helipterum pygmaeum</i>
<i>Eragrostis dielsii</i>	<i>Juncus aridicola</i>	<i>Eragrostis dielsii</i>	<i>Juncus aridicola</i>	<i>Eragrostis dielsii</i>	<i>Juncus aridicola</i>	<i>Eragrostis dielsii</i>	<i>Juncus aridicola</i>	<i>Eragrostis dielsii</i>	<i>Juncus aridicola</i>	<i>Ludwigia peploides</i>	<i>Ludwigia peploides</i>
<i>Eucalyptus camaldulensis</i>	<i>Ludwigia peploides</i>	<i>Eucalyptus camaldulensis</i>	<i>Ludwigia peploides</i>	<i>Eucalyptus camaldulensis</i>	<i>Ludwigia peploides</i>	<i>Eucalyptus camaldulensis</i>	<i>Ludwigia peploides</i>	<i>Eucalyptus camaldulensis</i>	<i>Ludwigia peploides</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Muehlenbeckia cunninghamii</i>
<i>Eucalyptus largiflorens</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Eucalyptus largiflorens</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Eucalyptus largiflorens</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Eucalyptus largiflorens</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Eucalyptus largiflorens</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Muehlenbeckia cunninghamii</i>
<i>Euphorbia drummondii</i>	<i>Morgania floribunda</i>	<i>Euphorbia drummondii</i>	<i>Morgania floribunda</i>	<i>Euphorbia drummondii</i>	<i>Morgania floribunda</i>	<i>Euphorbia drummondii</i>	<i>Morgania floribunda</i>	<i>Euphorbia drummondii</i>	<i>Morgania floribunda</i>	<i>Morgania floribunda</i>	<i>Morgania floribunda</i>
<i>Galenia secunda*</i>	<i>Nicotiana glauca</i>	<i>Galenia secunda*</i>	<i>Nicotiana glauca</i>	<i>Galenia secunda*</i>	<i>Nicotiana glauca</i>	<i>Galenia secunda*</i>	<i>Nicotiana glauca</i>	<i>Galenia secunda*</i>	<i>Nicotiana glauca</i>	<i>Nicotiana glauca</i>	<i>Nicotiana glauca</i>
<i>Glinus lotoides</i>	<i>Persicaria lapathifolium</i>	<i>Glinus lotoides</i>	<i>Persicaria lapathifolium</i>	<i>Glinus lotoides</i>	<i>Persicaria lapathifolium</i>	<i>Glinus lotoides</i>	<i>Persicaria lapathifolium</i>	<i>Glinus lotoides</i>	<i>Persicaria lapathifolium</i>	<i>Pterocaulon spacthelatum</i>	<i>Pterocaulon spacthelatum</i>
<i>Gnaphalium luteo-album</i>	<i>Pterocaulon spacthelatum</i>	<i>Gnaphalium luteo-album</i>	<i>Pterocaulon spacthelatum</i>	<i>Gnaphalium luteo-album</i>	<i>Pterocaulon spacthelatum</i>	<i>Gnaphalium luteo-album</i>	<i>Pterocaulon spacthelatum</i>	<i>Gnaphalium luteo-album</i>	<i>Pterocaulon spacthelatum</i>	<i>Pterocaulon spacthelatum</i>	<i>Pterocaulon spacthelatum</i>
<i>Haloragis aspera</i>	<i>Senecio sp.</i>	<i>Haloragis aspera</i>	<i>Senecio sp.</i>	<i>Haloragis aspera</i>	<i>Senecio sp.</i>	<i>Haloragis aspera</i>	<i>Senecio sp.</i>	<i>Haloragis aspera</i>	<i>Senecio sp.</i>	<i>Senecio sp.</i>	<i>Senecio sp.</i>
<i>Heliotropium amplexicaule*</i>	<i>Solanum karsensis</i>	<i>Heliotropium amplexicaule*</i>	<i>Solanum karsensis</i>	<i>Heliotropium amplexicaule*</i>	<i>Solanum karsensis</i>	<i>Heliotropium amplexicaule*</i>	<i>Solanum karsensis</i>	<i>Heliotropium amplexicaule*</i>	<i>Solanum karsensis</i>	<i>Solanum karsensis</i>	<i>Solanum karsensis</i>
<i>Heliotropium curassivicum</i>	<i>Sporobolus mitchelli</i>	<i>Heliotropium curassivicum</i>	<i>Sporobolus mitchelli</i>	<i>Heliotropium curassivicum</i>	<i>Sporobolus mitchelli</i>	<i>Heliotropium curassivicum</i>	<i>Sporobolus mitchelli</i>	<i>Heliotropium curassivicum</i>	<i>Sporobolus mitchelli</i>	<i>Sporobolus mitchelli</i>	<i>Sporobolus mitchelli</i>
<i>Heliotropium europaeum*</i>	<i>Swainsona gregana</i>	<i>Heliotropium europaeum*</i>	<i>Swainsona gregana</i>	<i>Heliotropium europaeum*</i>	<i>Swainsona gregana</i>	<i>Heliotropium europaeum*</i>	<i>Swainsona gregana</i>	<i>Heliotropium europaeum*</i>	<i>Swainsona gregana</i>	<i>Swainsona gregana</i>	<i>Swainsona gregana</i>
<i>Helipterum pygmaeum</i>	<i>Typha domingensis</i>	<i>Helipterum pygmaeum</i>	<i>Typha domingensis</i>	<i>Helipterum pygmaeum</i>	<i>Typha domingensis</i>	<i>Helipterum pygmaeum</i>	<i>Typha domingensis</i>	<i>Helipterum pygmaeum</i>	<i>Medicago spp.*</i>	<i>Medicago spp.*</i>	<i>Medicago spp.*</i>
<i>Isoetopsis graminifolia</i>		<i>Isoetopsis graminifolia</i>		<i>Isoetopsis graminifolia</i>		<i>Isoetopsis graminifolia</i>		<i>Isoetopsis graminifolia</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Muehlenbeckia cunninghamii</i>	<i>Muehlenbeckia cunninghamii</i>
<i>Juncus aridicola</i>		<i>Juncus aridicola</i>		<i>Juncus aridicola</i>		<i>Juncus aridicola</i>		<i>Juncus aridicola</i>	<i>Morgania floribunda</i>	<i>Morgania floribunda</i>	<i>Morgania floribunda</i>
<i>Limosella australis</i>		<i>Ludwigia peploides</i>		<i>Ludwigia peploides</i>		<i>Ludwigia peploides</i>		<i>Ludwigia peploides</i>	<i>Nicotiana glauca</i>	<i>Nicotiana glauca</i>	<i>Nicotiana glauca</i>
<i>Ludwigia peploides</i>		<i>Marsilea sp.</i>		<i>Marsilea sp.</i>		<i>Marsilea sp.</i>		<i>Marsilea sp.</i>	<i>Pterocaulon spacthelatum</i>	<i>Pterocaulon spacthelatum</i>	<i>Pterocaulon spacthelatum</i>
		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>	<i>Senecio sp.</i>	<i>Senecio sp.</i>	<i>Senecio sp.</i>
		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>		<i>Medicago spp.*</i>	<i>Sporobolus mitchelli</i>	<i>Sporobolus mitchelli</i>	<i>Sporobolus mitchelli</i>
		<i>Mentha australis</i>		<i>Muehlenbeckia cunninghamii</i>		<i>Muehlenbeckia cunninghamii</i>		<i>Muehlenbeckia cunninghamii</i>	<i>Swainsona gregana</i>	<i>Swainsona gregana</i>	<i>Swainsona gregana</i>
		<i>Muehlenbeckia cunninghamii</i>		<i>Myriocephalus stuartii</i>		<i>Myriocephalus stuartii</i>		<i>Myriocephalus stuartii</i>	<i>Wahlenbergia communis</i>	<i>Wahlenbergia communis</i>	<i>Wahlenbergia communis</i>



C...

Sediment with Low Soil Moisture 0 -7.5 cm (Short Exposure Time)	Sediment with Low Soil Moisture 0 -7.5 cm (Long Exposure Time)	Sediment with Low Soil Moisture 0 -15 cm (Short Exposure Time)	Sediment with Low Soil Moisture 0 -15 cm (Long Exposure Time)	Sediment with Low Soil Moisture 0 -40 cm (Short Exposure Time)	Sediment with Low Soil Moisture 0 -40 cm (Long Exposure Time)
<i>Mollogo cerviana</i>		<i>Nicotiana glauca</i>		<i>Xanthium occidentale*</i>	
<i>Morgania floribunda</i>		<i>Nicotiana velutino</i>			
<i>Myosurus minima</i>		<i>Persicaria lapathifolium</i>			
<i>Myriocephalus stuartii</i>		<i>Polygonum plebium</i>			
<i>Nicotiana glauca</i>		<i>Pterocaulon s. pachelatum</i>			
<i>Nicotiana velutino</i>		<i>Rumex bidens</i>			
<i>Persicaria lapathifolium</i>		<i>Senecio</i> sp.			
<i>Polygonum plebium</i>		<i>Scirpus</i> sp.			
<i>Pterocaulon spachelatum</i>		<i>Sporobolus mitchelli</i>			
<i>Rumex bidens</i>		<i>Swainsona gregana</i>			
<i>Senecio</i> sp.		<i>Tetragonia tetragonoides</i>			
<i>Scirpus</i> sp.		<i>Wahlenbergia communis</i>			
<i>Sporobolus mitchelli</i>		<i>Xanthium occidentale*</i>			
<i>Swainsona gregana</i>					
<i>Tetragonia tetragonoides</i>					
<i>Wahlenbergia communis</i>					
<i>Xanthium occidentale*</i>					

### 8.3 Water Regime Requirements

For all but one species, the water regime requirement for germination was exposed sediment with high soil moisture in the top 7.5 cm (Chapter 4 and Chapter 5). The water regime requirements for survival were similar for species in each of the Brock and Casanova (1997) functional groups. The majority of the species in the seed bank and extant vegetation were from the terrestrial and floodplain functional groups (intolerant of flooding). Species from the floodplain functional group are only found in areas that are subject to periodic inundation, however they are (in most cases) very desiccation tolerant.

Floodplain species generally exhibited characteristics of terrestrial species. This is in contrast to species that inhabit floodplains in well watered temperate and tropical regions, where they are generally amphibious (e.g. Bornette and Amoros 1991; Wetzel *et al.* 2001). Prior to regulation, the Menindee Lakes would have been dry or partially full more often than the current hydraulic regime (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998; Scholz *et al.* 1999; Scholz and Gawne 2004), hence the vegetation has adapted to this water regime. These species persist in the regulated system because of the ability of their seeds to remain viable whilst flooded and colonise areas of newly exposed lakebed. The extant vegetation of the areas that were most affected by regulation (Lake Wetherell and supply channels that are held full) are dominated by amphibious species such as *Persicaria lapathifolium*, *Ludwigia peploides* and *Typha domingensis*.

It is unclear why floodplain species are only found in flood prone areas and do not colonise the adjacent non-flooded areas. Possible explanations for this are differences in soil type, soil nutrient status, dispersal mechanisms, competitive interactions or high soil moisture requirements for germination. The Darling River carries large amounts of suspended solids (Scholz *et al.* 1999; Thoms and Sheldon 2000b), a proportion of which is deposited on the floodplain during floods. This results in the soils from areas subject to periodic inundation (except the edges of deflation lakes (Appendix 1)) having grey clay soils in comparison to the red sandy soils in areas not subject to inundation (Cunningham *et al.* 1981). The nutrient status of the floodplain soils in comparison to the non-flooded areas is not known. However, the difference in soil texture and colour suggest that the nutrient status is probably different. Several of the floodplain species appear to have seeds adapted for hydrochory

(Chapter 3). Seeds that are adapted for dispersal by water will not disperse into areas that are never flooded. When the floodplain is inundated, most of the extant vegetation is killed and germination and recruitment occurs when water levels recede (Chapter 4 and Chapter 5). The non-flooded areas are not subject to disturbances as frequently as the floodplains, which may facilitate recruitment of floodplain species. Floodplain species from other systems have been shown to recruit better in areas where there was an absence of competitors (Kalliola *et al.* 1991; Jones *et al.* 1994; Smith *et al.* 1998; Elias 2001; Pettit and Froend 2001b; Pettit *et al.* 2001; Dixon 2003). Floodplain species grow in response to rainfall (pers. obs.) but probably require higher soil moisture to germinate than can be provided by precipitation, because only terrestrial species germinated in response to rain (Chapter 5).

Therefore, water regime acts as an ‘environmental sieve’ (*sensu* Harper 1977; van der Valk 1981) and the presence or absence of standing water (controlled by water regime) determines which species will germinate and survive. Management and regulation have changed the water regime of the system and in turn changed the action of the environmental sieve. Increased permanency has limited the opportunity for most species to germinate at lower elevations to periods of extended drought. Using the lakes for downstream flood mitigation by pre-releasing has the potential to deplete the seed bank. Seeds will germinate on areas exposed to create headspace to capture the flood peak and potentially be killed by inundation before they set seed.

#### **8.4 Strategies of Persistence in Ephemeral Systems**

For species to persist in ephemeral environments, where unfavourable conditions can occur for extended periods, at least one life cycle stage must be able to persist until favourable conditions occur or the species will be extirpated. Unfavourable conditions in the Menindee Lakes, depending on the species, can range from submergence to desiccation. Three broad strategies are employed by species growing in and around the Menindee Lakes to persist through unfavourable conditions: avoidance, tolerance and response.

Species that avoid unfavourable conditions must have a life cycle stage that can remain viable during periods of unfavourable conditions in order to persist. For most species the formation of a seed bank, in many cases a persistent seed bank, is the primary mode of persistence through drought or flood. However, some species (e.g. *Typha domingensis* and

*Cyperus gymnocaulos*) use asexual propagules to persist through unfavourable conditions. Species that avoid both desiccation and inundation generally have short life cycles (annuals or facultative annuals) are intolerant of flooding and desiccation and generally form a persistent seed bank. Grime (1979) classified these species as *ruderals* that colonise bare patches soon after a disturbance and are poor competitors.

*Tolerators* are species that persist through unfavourable conditions and do not change their morphology as conditions change. These species are similar to Grime's (1979) stress tolerators and are generally long-lived (perennials).

*Responders* are also long-lived (perennials) but are morphologically plastic. These species change their morphology in response to different conditions. For example, *Ludwigia peploides* allocated a greater proportion of biomass to above ground organs when flooded when compared with plants that were not flooded (Chapter 6). These species probably fit into Grime's (1979) classification as *competitors*, but very little is known of their competitive ability.

Only 14 of the 68 species observed in this study can be classed as *avoiders* (avoid both inundation and desiccation) (Table 8.2). Most species employ different strategies to persist through inundation or desiccation, probably because of the very different nature of inundation and desiccation and problems posed for plants. Thirty-three species avoided inundation by forming a seed bank and tolerate desiccation (e.g. *Morgania floribunda*) (Table 8.2). Some species employ more than one strategy to persist through either inundation or desiccation (Table 8.2). For example, *Alternanthera denticulata* will tolerate shallow flooding but only persists in the seed bank when deeply flooded (Chapter 4). *Cyperus gymnocaulos* will tolerate flooding for less than four weeks but senesces to rhizomes if top flooded for longer than four weeks (Chapter 6) and forms a persistent seed bank (Chapter 3). *Xanthium occidentale* will respond to shallow flooding by production of adventitious roots but is intolerant of top flooding and persists only in the seed bank (Chapter 6). *Ludwigia peploides* allocates more biomass to below ground organs when not flooded (Chapter 6) and when subjected to extreme desiccation only persists in the seed bank. *Myriophyllum verrucosum* responds to drying a similar way to *Ludwigia peploides* except is less desiccation tolerant (pers. obs.). *Typha domingensis* avoids desiccation as rhizomes (Cunningham *et al.* 1981; Sainty and Jacobs 1981; Sainty and Jacobs 1994) or in the seed bank.

For *Myriophyllum verrucosum*, *Lemna* sp. and *Azolla* sp. inundation of the sediment for these species is favourable for germination, growth and survival (Chapter 4; pers. obs.). These species either avoid desiccation and persist in the seed bank or are morphologically plastic (Table 8.2).

**Table 8.2: Strategies for persisting through inundation and desiccation for all species detected in the extant vegetation and seed banks of the Menindee Lakes (\*denotes exotic species).**

Species	Inundation	Desiccation
<i>Alisma</i> sp.	Response	Avoidance
<i>Alternanthera denticulata</i>	Tolerance/Avoidance	Tolerance
<i>Ammania multiflora</i>	Avoidance	Tolerance
<i>Argemone ochroleuca</i> *	Avoidance	Tolerance
<i>Asphodelus fistulosus</i> *	Avoidance	Tolerance
<i>Azolla</i> sp.		Avoidance
<i>Centipeda minima</i>	Avoidance	Avoidance
<i>Chenopodium pumilio</i>	Avoidance	Avoidance
<i>Chloris truncata</i>	Avoidance	Tolerance
<i>Citrullus lanatus</i> *	Avoidance	Tolerance
<i>Convolvulus arvensis</i> *	Avoidance	Tolerance
<i>Crassula sieberana</i>	Avoidance	Avoidance
<i>Cyperus gymnocaulos</i>	Tolerance/Avoidance	Tolerance
<i>Daucus glochidiatus</i>	Avoidance	Tolerance
<i>Echium plantagineum</i> *	Avoidance	Tolerance
<i>Epaltes australis</i>	Avoidance	Tolerance
<i>Eragrostis dielsii</i>	Avoidance	Tolerance
<i>Eragrostis parvifolia</i>	Avoidance	Tolerance
<i>Eucalyptus camaldulensis</i>	Tolerance	Tolerance
<i>Eucalyptus largiflorens</i>	Tolerance	Tolerance
<i>Euphorbia drummondii</i>	Avoidance	Tolerance
<i>Galenia secunda</i> *	Avoidance	Tolerance
<i>Glinus lotoides</i>	Avoidance	Tolerance
<i>Gnaphalium luteo-album</i>	Avoidance	Avoidance
<i>Haloragis aspera</i>	Avoidance	Tolerance
<i>Heliotropium amplexicaule</i> *	Avoidance	Tolerance
<i>Heliotropium curassivicum</i>	Avoidance	Tolerance
<i>Heliotropium europaeum</i> *	Avoidance	Avoidance
<i>Helipterum pygmaeum</i>	Avoidance	Tolerance
<i>Hypochoeris radicata</i> *	Avoidance	Tolerance
<i>Iseotopsis graminifolia</i>	Avoidance	Avoidance
<i>Isolepis australiensis</i>	Avoidance	Avoidance
<i>Juncus aridicola</i>	Tolerance	Tolerance
<i>Lemna</i> sp.		Avoidance
<i>Limosella australis</i>	Avoidance	Avoidance
<i>Ludwigia peploides</i>	Response	Avoidance/Response
<i>Marsilea</i> sp.	Response	Response
<i>Medicago</i> spp.*	Avoidance	Tolerance
<i>Mentha australis</i>	Avoidance	Avoidance
<i>Muehlenbeckia cunninghamii</i>	Response	Response

Table 8.2...

Species	Inundation	Desiccation
<i>Mollogo cerviana</i>	Avoidance	Avoidance
<i>Morgania floribunda</i>	Avoidance	Tolerance
<i>Myosurus minima</i>	Avoidance	Avoidance
<i>Myriocephalus stuartii</i>	Avoidance	Tolerance
<i>Myriophyllum verrucosum</i>		Avoidance/Response
<i>Nicotiana glauca</i>	Avoidance	Tolerance
<i>Nicotiana velutino</i>	Avoidance	Tolerance
<i>Pachychnonia tenuis</i>	Avoidance	Tolerance
<i>Persicaria lapathifolium</i>	Response	Response
<i>Polygonum aviculare*</i>	Avoidance	Tolerance
<i>Polygonum plebium</i>	Avoidance	Avoidance
<i>Pterocaulon spathelatum</i>	Avoidance	Tolerance
<i>Ptilotus obovatus</i>	Avoidance	Tolerance
<i>Ricinis communis*</i>	Avoidance	Tolerance
<i>Rumex bidens</i>	Avoidance	Avoidance
<i>Rumex crispus*</i>	Avoidance	Avoidance
<i>Schlerolaena sp.</i>	Avoidance	Tolerance
<i>Scirpus sp.</i>	Avoidance	Avoidance
<i>Sinapis alba*</i>	Avoidance	Avoidance
<i>Solanum karsensis</i>	Avoidance	Tolerance
<i>Solanum oligacanthum</i>	Avoidance	Tolerance
<i>Sporobolus mitchelli</i>	Tolerance	Tolerance
<i>Swainsona gregana</i>	Avoidance	Tolerance
<i>Tetragonia tetragonoides</i>	Avoidance	Avoidance
<i>Typha domingensis</i>	Response	Response/Avoidance
<i>Wahlenbergia communis</i>	Avoidance	Avoidance
<i>Xanthium occidentale*</i>	Avoidance/Response	Tolerance

## 8.5 Non-hydrological Changes

The effect of water regime on the floristic composition derived from the seed bank has been clearly demonstrated by pond experiments (e.g. Seabloom *et al.* 1998; Casanova and Brock 2000; Nicol *et al.* 2003; Chapter 4; Chapter 7). However, field results suggest that other factors can modify the effect of water regime. In pond experiments, it is possible to control factors that can potentially change the floristic composition and only test the effect of water regime. However, in the field it is difficult (at times impossible) to control these factors.

Factors that can potentially change floristic composition and which cannot be experimentally manipulated in the field, include soil texture (Chapter 5), seed bank differences (Chapter 3 and Appendix 9), wave action (e.g. (Riis and Hawes 2003), grazing (e.g. van Der Valk *et al.* 1993; Blanch and Bock 1994; Mesleard *et al.* 1999), temporal differences between pond experiments and field studies, lateral and longitudinal movement of water and nutrients.

The soil type used for the pond experiment was 60: 40 (sand: clay) sandy loam, whereas in the field the soil texture ranged from coarse sand to fine clay (Appendix 1). Soil texture can influence the availability of water and nutrients (Black 1968) and in turn floristic composition. Floristic composition in Lakes Malta, Balaka and Menindee was strongly correlated with soil texture (Chapter 5). No correlation was observed in Lakes Wetherell and Cawndilla because the sediment texture was relatively uniform throughout the area of lakebed surveyed (Appendix 1). Observations of the extant vegetation revealed that some species have preferences for either clayey or sandy soil. For example, *Epaltes australis* and *Glinus lotoides* are species that probably occupy similar niches. Both are prostrate annual forbs that grow in areas subject to periodic inundation, are unpalatable to stock (Cunningham *et al.* 1981), relatively desiccation tolerant (Chapter 5), form persistent seed banks (Chapter 3) and seeds will only germinate when the sediment is exposed (Chapter 4 and Chapter 5). However, *Glinus lotoides* is found on clayey soils and *Epaltes australis* on sandy soils (pers. obs.).

To ensure that only the effect of water regime was tested, the pond experiments (Chapter 4 and Chapter 7) used a composite seed bank (*sensu* Seabloom *et al.* 1998; Nicol *et al.* 2003). In nature seed banks are extremely spatially variable (e.g. Roberts 1981; Bigwood and Inouye 1988; Brock *et al.* 1994; Chapter 2; Chapter 7; Appendix 9) and may confound differences due to water regime.

The impact of wave action on establishment and growth of aquatic macrophytes has been well documented (e.g. Foote and Kadlec 1988; Sager *et al.* 1998; Hudon *et al.* 2000; Doyle 2001; Hawes *et al.* 2003; Riis and Hawes 2003; Schutten *et al.* 2004). Plants growing in a 3 x 4 m pond are not subjected to wave action whereas plants growing around lake edges could potentially be subjected to sizeable waves depending on the size of the lake and location on the shoreline. There is also evidence to suggest the wave action can change the seed bank composition by the creation and destruction of strandlines (Ignaciuk and Lee 1980; Chapter 3).

The impact of grazing on floristic composition in terrestrial, wetland and riparian systems has been well documented (e.g. Bakker 1985; Cooke 1987; van Der Valk *et al.* 1993; Vormann and Kuhbauch 1999; Wahren *et al.* 1999; Robertson and Rowling 2000; Jutila 2001; Jutila 2003). Grazing by domestic stock can decrease the abundance of palatable species and increase the abundance of unpalatable species (e.g. O'Connor and Pickett 1992;

Mesleard *et al.* 1999). The selective grazing habits of domestic stock, over time, can also change seed bank composition (e.g. O'Connor and Pickett 1992; Muston *et al.* 2004; Appendix 9; Appendix 10). Trampling by the hard hooves of domestic stock can also significantly change habitat condition (Wahren *et al.* 1999; Jansen and Robertson 2001). This changes the capacity of the system to respond to disturbances such as floods and droughts (Meeson *et al.* 2002). It also affects the capacity of the system to respond to rehabilitation efforts such as environmental flows or removal or reduction in grazing pressure (Meeson *et al.* 2002). Lakes Malta, Balaka and the northern half of the lakebed in Lake Menindee are grazed by domestic stock. Native and feral animals graze the southern shore of Lake Menindee and all of Lake Cawndilla.

Pond experiments are generally of short duration (one or part of a growing season); the pond experiment in Chapter 4 ran for 252 days and Chapter 7 140 days, whereas the field surveys in Chapter 5 ran for nearly 500 days. When the top 7.5 cm of the sediment that is too dry for germination, annuals will only be present before they have set seed whereas perennials will always be present providing the soil moisture in the root zone is sufficient for survival. Annual species were present in the ponds (e.g. *Centipeda minima*, *Epiltes australis*) when sampled for the final time, whereas in the field they were generally absent in the final surveys in areas exposed for longer than 200 days (*sensu* Capon 2003), Chapter 5).

The lateral and longitudinal distances from the water are generally greater in the field than in the pond. For example, the greatest distance from the soil surface to the water in the pond is 80 cm (Chapter 4 and Chapter 7). Capillary action can bring water to the surface of the sandy loam used in the pond experiment when the water level is 50 cm below the soil surface (Nicol 1999). Therefore, when the water level was at its lowest point in the ponds plants only needed 30 cm deep roots to access water. In the field, the water level in the lakes that had not dried was up to 5 m lower than the highest quadrats and up to 2 km away. Therefore, it was very unlikely that any lake water was brought to the root zone by capillary action. At least 10 cm of water remained in the ponds hence the plants that had root systems deeper than 30 cm had a constant source of water whereas in the field Lakes Balaka, Malta and Menindee dried. Therefore, plants growing in these lakes needed to be able to access soil water or go into dormancy to survive.

High levels of nutrients (nitrogen and phosphorus) have been implicated in the decline of submergent macrophytes in permanent lakes (e.g. Brouwer and Roelofs 2001; Morris *et al.*



2003a; Morris *et al.* 2003b), the decline of *Cladium* and *Eleocharis* and expansion of *Typha* in the Everglades (e.g. Newman *et al.* 1996; Stewart *et al.* 1997; Newman *et al.* 1998; Lorenzen *et al.* 2000; Miao *et al.* 2000; Newman *et al.* 2004) and has been shown to facilitate the invasion of *Phalaris arundinacea* (Wetzel and van der Valk 1998; Green and Galatowitsch 2002; Kercher and Zedler 2004). The nutrient status of the lakebed sediments of the Menindee Lakes is not known but plants growing in the pond were not nutrient limited (100 g N m<sup>-2</sup> year<sup>-1</sup> plus trace elements). It is also possible that the nutrient status of the sediment changes with elevation, soil type and grazing intensity. However, soil nutrient loading had no effect on the species composition of the plant community derived from the Lake Malta seed bank (Chapter 7). The design of this experiment prevented the investigation of the effect of a single nutrient, such as nitrogen or phosphorus, which may effect germination and recruitment from the seed bank (Chapter 7).

## 8.6 Further Research

Time constraints and drought resulted in several questions regarding the vegetation dynamics of the Menindee Lakes being unanswered. In addition, the results gained in this study posed further questions and highlighted some knowledge gaps.

The drought prevented investigations into the effect of flooding and prolonged high water levels in the field. Future experiments could include:

- Flooding tolerance of key plant species in the field or under controlled conditions.
- The effect of wave action on recruitment of key plant species.
- The use of flooding to control pest plant species such as *Xanthium occidentale* and *Ricinis communis*.
- Origin and dynamics of strandlines.
- Seed longevity of important species under different conditions.
- Effect of prolonged flooding on seed survival.

Other investigations of the vegetation dynamics of the system could include:

- Comparison with other systems, such as the Anabranh Lakes or Teryaweynya Lakes.
- The effect of grazing on the extant vegetation and seed bank in other areas, and the recovery of plant communities after grazing.
- The effect of the addition of a single nutrient, such as nitrogen or phosphorus on recruitment from the seed bank.
- Does the breakdown of the non-seed component of the strandline provide soil nutrient enrichment and favourable microsites for plant recruitment?
- What are the germination cues for key plant species?
- Can the seed bank be used to examine the vegetation history of the Menindee Lakes?

## 8.7 Conclusions

The seed bank provides a mechanism for the plant communities of the Menindee Lakes to regenerate after both flood and drought disturbances. Approximately two thirds of the species present in the soil seed bank develop persistent seed banks with nine species having extremely resilient seed banks. The seed bank is dominated by floodplain and terrestrial species and recruitment from the seed bank primarily occurs when the sediment is moist but not inundated. Different species have evolved different strategies to persist through unfavourable conditions; however, these strategies could be classified into three broad categories: tolerance, response and avoidance. The strategy for persisting through flood was, for many species, different from the strategy for persisting through drought. Water regime plays an important role in structuring the floristic composition of the lakes; however, other factors such as soil type and grazing are also important. Under controlled experimental conditions, total biomass increased as soil nutrient loading increased but there was no impact of nutrient loading on floristic composition.