1 Chapter 1: Introduction

Little is known about the vegetation dynamics of ephemeral wetlands and floodplains and the role of the seed bank in these systems (with the exception of Brock and Rogers (1998) and Capon (2003; 2005)). The majority of our knowledge of wetland and floodplain ecosystems is focussed on well-watered temperate northern hemisphere systems and tropical systems (e.g. van der Valk 1981; Leck and Simpson 1987; Junk *et al.* 1989). In Australia, the majority of the research into wetlands and floodplains has been undertaken on seasonal wetlands (e.g. Britton and Brock 1994; Casanova and Brock 1999b; Nicol *et al.* 2003), rivers with seasonal flow regimes (e.g. Pettit and Froend 2001a; 2001b; Pettit *et al.* 2001) and the impact of altered flow regimes in the River Murray system (e.g. Walker *et al.* 1994; Nielsen and Chick 1997). This study provides an insight into the vegetation dynamics of a regulated ephemeral system (the Menindee Lakes) and the role of the seed bank plays in that system.

1.1 The Seed Bank

The seed bank is defined as the reserves of viable seed present in and on the soil surface (Roberts 1981) and associated litter (Simpson *et al.* 1989), capable of replacing adult plants (Baker 1989). The size of the seed bank, the contribution made to it by the different species and patterns of seed distribution reflect the seed production mainly by the resident plant community; although, inputs of seed from distant sources may also contribute (Simpson *et al.* 1989). In addition, the seed bank contains not only seeds from the preceding year but may contain seeds from many previous years (Roberts 1981); especially species that form long-term persistent seed banks (Thompson and Grime 1979). The seed bank, in effect, is a temporal dispersal syndrome in which dispersal over time (with seeds) is a strategy for exploiting favourable habitats that are patchily distributed in time and space (De Stasio 1989).

The concept of the seed bank was first identified by Darwin (1859) when he observed the emergence of 537 seedlings from three tablespoons of pond mud. The seed banks of arable weeds and their role in the rapid exploitation of disturbed ground were among the first group of plants to receive intensive study (Brenchley 1918; Grime 1989). Since then, the presence of a pool of viable seeds in the soil has been detected in a wide range of other habitats (Grime 1989).

1.1.1 Seed Bank Classification

The most widely accepted classification system for seed banks was proposed by Thompson and Grime (1979). They identified four functional types based on seed persistence and timing of germination (Thompson and Grime 1979).

Seed bank type I: species with transient seed banks present only during summer. Species from this group release all their seeds during late spring and early summer and germinate all at one time in the cooler and wetter conditions in autumn. Species with a type I seed bank appear to be adapted to environments with predicable low summer rainfall (Thompson and Grime 1979).

Seed bank type II: species with transient seed banks present only during winter. Species in this group have seeds that remain dormant throughout the winter and germinate in spring. Species that have evolved this strategy are usually from regions where plant growth in late autumn and winter is restricted by the cold (Thompson and Grime 1979).

After germination, no viable seed is present in the soil from species with transient seed banks (Thompson and Grime 1979). Species that have evolved these strategies are adapted to take advantage of predictable damage or mortality to the extant vegetation (Thompson and Grime 1979).

Species with type III or IV seed banks have persistent seed banks and not all viable seed germinates at one time (Thompson and Grime 1979). They found that many species were capable of forming persistent seed banks and this group of plants is heterogeneous with respect to the form and function of the seed bank (Thompson and Grime 1979). However, species that inhabit environments subject to severe and unpredictable disturbances by cultivation, fire or large water level fluctuations generally form a large persistent seed bank (Thompson 1992).

Species with a type III seed bank have many seeds that germinate soon after release from the parent plant. This component of the seed output effectively functions as a type I or II seed bank, however a proportion of the seeds do not germinate and become incorporated into the persistent seed bank (Thompson and Grime 1979).

Species that have evolved a type IV seed bank have very few seeds germinate that in the period immediately following release from the parent plant and the species maintains a seed bank, which does not vary greatly in size from season to season. The seed banks of these species are also large in comparison to the annual production of seeds (Thompson and Grime 1979).

This classification does not take into account species that have an aerial or canopy seed bank (e.g. *Melaleuca halmaturorum* (Holliday 1989; Denton and Ganf 1994)) or species that do not have a persistent seed bank (all the viable seed germinates during favourable conditions) but remain viable in the soil for longer than one year.

1.1.2 Role of the Seed Bank in Vegetation Dynamics

Major and Pyott (1966) stated that the seed bank is part of the flora of a system, as it helps to determine the community, even though it is not readily evident. The primary role of the seed bank is to ensure the continuation of species after disturbance or natural mortality has killed the extant vegetation (Simpson *et al.* 1989). However, population maintenance (Simpson *et al.* 1989) and a reserve of genetic diversity (Templeton and Levin 1979; Simpson *et al.* 1989) are also functions of the seed bank.

The role of the seed bank in vegetation dynamics varies from system to system. For example, temperate woodland trees generally only form a transient or short-term persistent seed bank. Presumably, because natural selection does not favour the accumulation of a persistent seed bank in long-lived perennials of relatively stable undisturbed ecosystems (Thompson 1992). The few woody species that do form a persistent seed bank are usually early successional short-lived species (Thompson 1992). Species from systems where disturbances are common generally form persistent seed banks, however if the disturbance is predictable (seasonal) species with transient seed banks may dominate (Thompson and Grime 1979; Thompson 1992; Thompson *et al.* 1998; Leck and Brock 2000).

An understanding of the dispersal mechanisms, germination requirements and seed longevity is also important in understanding the role of seed bank in the vegetation dynamics of a system.

Species that have seeds that are dispersed by wind or water can disperse great distances from the parent plant. For wind-dispersed species the chances of landing in a suitable environment are low, hence these species tend to produce large numbers of small seeds (e.g. *Typha* spp. (Cunningham *et al.* 1981; Sainty and Jacobs 1981; Sainty and Jacobs 1994)). Seed from species adapted for dispersal by water (hydrochory) are more likely to be deposited in a suitable environment therefore they generally produce a smaller number of larger seeds (e.g. *Triglochin procerum* (Cunningham *et al.* 1981; Sainty and Jacobs 1981; Sainty and Jacobs 1994)). The distance an animal dispersed seed can travel and the suitability of the location of deposition are dependent on the habits of the animal.

Many species have specific requirements for germination and unless those requirements are met, the seed will remain dormant. Factors such as temperature, light, salinity, oxygen, depth of burial and redox potential can influence seed germination (Haag 1983; Galinato and van der Valk 1986; Baskin *et al.* 1989; Baskin *et al.* 1993; Baskin and Baskin 1998). In addition, seeds may have multiple chilling requirements (Baskin *et al.* 1989; Baskin and Baskin 1998), need to pass through the gut of vertebrates (Haag 1979; Baskin and Baskin 1998), require diurnally fluctuating temperatures (Thompson and Grime 1983; Baskin and Baskin 1998), have their fruits broken down by bacterial action, require scarifying of the seed coat (Haag 1983; Baskin and Baskin 1998) or require multiple wet and dry cycles (Brock and Rogers 1998) to break dormancy.

The duration a seed can remain viable is also important. Seeds of some species remain viable in dry storage for several years (e.g. *Melaleuca halmaturorum*) but lose viability when submerged in a matter of weeks (Nicol and Ganf 2000); other species lose viability when desiccated (Farnsworth 2000). Loss of viability when wet can be overcome by having an aerial seed bank (Holliday 1989; Denton and Ganf 1994). Species with seeds that lose viability after being desiccated are generally from wet areas such as rain forest or permanent wetlands or are viviparous (Farnsworth 2000). Recovery after disturbance may be dependent on dispersal into the disturbed area for species that have short-lived seeds or transient seed banks. In contrast, species that have long-lived seeds or persistent seed banks do not need to rely on dispersal into the disturbed area.

1.1.3 Wetland and Floodplain Seed Banks

Australian wetland and floodplain habitats are highly variable and subject to both flood and drought disturbances. The seed bank provides one mechanism for persistence through unfavourable conditions and regeneration of plant communities after these disturbances (e.g. van der Valk and Davis 1976; Casanova and Brock 1990; Grillas *et al.* 1993; Brock and Britton 1995; Brock and Rogers 1998; Casanova and Brock 1999a). Plants growing in areas subject to permanent inundation, in many cases, rarely produce seeds (especially submergent species) and rely on asexual propagules for propagation, population maintenance and in some cases dispersal (Sculthorpe 1967). In contrast, systems that are subject to extreme desiccation may rely solely on seed for regeneration because asexual propagules may not survive (Thompson 1992).

The seed bank strategies employed by the species present may reflect adaptations to a hydraulic regime (Leck and Brock 2000). Leck and Brock (2000) compared the seed bank strategies from temporary wetlands in Australia and tidal freshwater wetlands in the U.S.A. The temporary wetlands in Australia are subject to water-level fluctuations on a seasonal or aseasonal basis resulting in substantial areas of the wetland with low soil moisture at times (Casanova and Brock 1990; Britton and Brock 1994; Casanova 1994; Brock and Britton 1995; Casanova and Brock 1996; Brock 1998; Casanova and Brock 1999b; Leck and Brock 2000; Warwick and Brock 2003). Tidal freshwater wetlands are also subject to large water level fluctuations, but levels diurnally fluctuate resulting in saturated or inundated soil in the amphibious zone (Leck and Graveline 1979; Simpson *et al.* 1983; Leck and Simpson 1987; Leck and Simpson 1994; Leck and Simpson 1995; Leck and Brock 2000; Leck 2003). Leck and Brock (2000) found that all species present in the seed banks of the Australian wetlands formed persistent seed banks, whereas 37% of the species present in the tidal freshwater wetland had transient seed banks. They also reported that a further 42% of species present in the tidal freshwater wetlands had short-term persistent seed banks (less than 5 years), in comparison to 11% from Australian temporary wetlands (Leck and Brock 2000). The results from this study suggest that species from Australian temporary wetlands are adapted to persisting through “false starts”, where a favourable period for germination may be followed immediately by unfavourable conditions for growth and survival and the plants are unable to replenish the seed bank (Leck and Brock 2000).

The seed bank strategies of floodplain species also reflect adaptation to hydraulic regime. For example, Pettit and Froend (2001a) showed that seed of four riparian tree species was short lived in the soil from tropical and temperate river systems in Australia that flooded on a seasonal basis. They also reported that the trees held seed in the canopy, which was released to coincide with receding water levels (Pettit and Froend 2001a). Brock and Rogers (1998) reported that 10 of 16 species from an ephemeral floodplain in South Africa had persistent seed banks (adapted to false starts) and two species required a second wetting cycle to break dormancy.

1.1.4 Methods of Seed Bank Assessment

The most direct method of estimating seed bank composition is to observe the emergence of seedlings *in situ* (Roberts 1981). If seed input is prevented, all new seedlings observed must have arisen from the soil seed bank (Roberts 1981). It is unlikely that the gemination requirements of many of the species present will be met during the observation period so whilst this method can provide an estimation of the seeds available at the time, it does not provide a full statement of the seed bank (Roberts 1981).

The technique employed by most researchers is to take representative soil samples and to determine seed numbers by either placing the soil under conditions that are suitable for germination or by physically separating the seed from the soil particles (Roberts 1981).

1.1.4.1 Sampling

The sampling strategy employed in a seed bank investigation will be dependent on the objectives of the study. Roberts (1981) stated that the most usual requirement is an assessment of the number of viable seeds of each species present in the soil of a defined area. The results are normally expressed as the mean number of seeds m^{-2} and related to a soil layer to a particular depth (Roberts 1981). The most commonly encountered problem with sampling soil seeds banks is insufficient sample numbers (Roberts 1981; Simpson *et al.* 1989). Due to the high spatial heterogeneity of soil seed banks it is better to take a large number of small samples than a small number of large samples, to gain an accurate estimate of the seed bank composition (Bigwood and Inouye 1988; Benoit *et al.* 1989). If there is no prior knowledge of the site, a preliminary investigation is critical to determine the most efficient method of obtaining and assessing samples (Roberts 1981; Simpson *et al.* 1989; Brock *et al.* 1994).

The pattern of sampling will be dependent on the study objective, if the aim is to determine seed bank changes along a gradient (e.g. topography, elevation, distance from a seed-bearing plant) a transect will be appropriate (Roberts 1981). If a general assessment of the size and species composition of the seed bank from an area is desired, a random or stratified (if prior knowledge of seed distribution has been obtained) sampling regime is appropriate (Benoit *et al.* 1989). If the aim of the study is to test the response of the seed bank to different conditions, such as water regime or temperature, a composite seed bank of a location is desirable to ensure that differences arising from treatments are not obscured by differences in the seed bank (sensu Seabloom *et al.* 1998; Nicol *et al.* 2003).

To determine the surface soil seed bank, seeds can be retrieved by suction from a delineated sample area (Roberts 1981). If an estimate of the seed that has been incorporated in the soil is required, samples of soil to a specified depth can be obtained by the removal of blocks of soil of known dimensions or by the use of a sampling tool that extracts a soil core (Roberts 1981). If the design of the corer minimises soil compaction, the cores can be sectioned to obtain samples from different depths (Roberts 1981). Sampling depth will also depend on the objectives of the study. The majority of studies are only interested in the fraction of the seed bank where the majority of the seeds are concentrated and that will contribute to the vegetation (the top 5 cm) (Bonis and Lepart 1994). However, van der Valk and Davis (1979) used seed banks from different depths to reconstruct the recent vegetation history of a prairie marsh and Tsuyuzaki and Goto (2001) sampled 115 to 185 cm below the soil surface to determine the seed bank of the topsoil that had been buried for 20 years under volcanic ash. Regardless of the study objectives, the total volume of soil collected needs to be large in relation to the size of the seeds in the soil (Simpson *et al.* 1989).

1.1.4.2 The Seedling Emergence Technique

The seedling emergence technique is the most commonly used method to estimate seed density and floristic composition (Roberts 1981). Soil samples are placed into a shallow container or spread in a thin layer over a suitable medium and kept moist. The seedlings that emerge are counted, identified and recorded. The aim is to ensure that as many of the viable seeds as possible germinate and produce seedlings (Roberts 1981). If a single species is being investigated, samples can be kept under conditions known to promote maximum germination in that species (Roberts 1981).

Samples can be either pre-treated or subjected to different conditions to promote maximum germination of the majority of species. Fluctuating temperatures are known to promote germination in many species, especially species from temperate regions that are adapted to germinate in spring (e.g. Thompson and Grime 1983; Brandel 2004). Some species require a period of cold before dormancy is broken, these species are also generally from temperate regions and adapted to germinating in spring (e.g. Baskin and Baskin 1998; Brandel 2004). Subjecting the seed bank to multiple wetting and drying cycles (sensu Brock and Rogers 1998; Leck and Brock 2000) can give a more accurate estimate of seed bank composition; it can also determine which species have persistent seed banks (Thompson and Grime (1979) Type III and IV seed banks). ter Heerdt *et al.* (1996) suggested that the seedling emergence technique can be improved by washing soil samples through a fine sieve, to remove the clay fraction of the soil, and spreading the concentrated samples in a 3 to 5 mm layer over sterilised potting mix.

The seedling emergence technique has several advantages over seed separation techniques because it only detects viable seed (tetrazolium staining is required to conclusively determine viability when using seed separation techniques), is less labour intensive, plants are easier to identify and does not discriminate against small seeded species (Roberts 1981; Gross 1990; Brown 1992). The major disadvantage of this method is that it generally underestimates seed density and species richness because not all of the conditions for germination for all species present will be met (Roberts 1981; Gross 1990; Brown 1992).

1.1.4.3 Seed Separation Techniques

Seed separation utilises differences in size or density to separate seed from soil particles; however, this is generally not entirely successful and some manual sorting is usually required (Roberts 1981). Sieving and floatation are the two main techniques utilised to separate the seed from the soil (Roberts 1981).

1.1.4.3.1 Sieving

Sieving entails the washing of soil samples through sieves with appropriate mesh or pore sizes to reduce the volume of soil from which the seeds must be removed (Roberts 1981). In studies where the seed bank of a single species is being investigated sieving may be all that is required, especially if the species has large conspicuous seeds (Roberts 1981). For species with small seeds, the particle size range can be reduced by sieving and the target fraction can be sorted by hand or the seeds separated by floatation or centrifuging (Roberts 1981). Sieving is not as effective when the aim of the study is to investigate the seed banks of a range of species with different seed sizes.

1.1.4.3.2 Floatation

Floatation exploits the difference in density between seeds and soil particles. Most viable seeds sink in water so a solution with a greater specific gravity than the seeds but less than the soil particles is needed to enable the seeds to be skimmed off and manually sorted (Roberts 1981). Gross (1990) used a hydropneumatic root elutriator designed by Smucker *et al.* (1982) for the separation of fine roots from soil to separate seeds from soil. This system uses compressed air to agitate the soil water mixture, which then flows into a series of sieves where the seed and other coarse organic debris is collected and hand sorted (Smucker *et al.* 1982).

The major disadvantages of seed separation techniques is that they are labour intensive, small seeds can be easily missed when hand sorting, species are difficult to identify and non-viable seeds may be counted (Roberts 1981; Gross 1990; Brown 1992). The major advantage is that it provides a more accurate estimate of the total size and species richness of the seed bank (Roberts 1981; Gross 1990; Brown 1992).

1.1.5 Asexual Reproduction

Vegetation is ultimately perpetuated in two ways, through the production of seeds and the formation of a seed bank and asexual reproduction (Simpson *et al.* 1989). Clonal reproduction has many advantages (Table 1.1) and can predominate over sexual reproduction in many species of aquatic plants (Hutchinson 1975; Philbrick and Les 1996).

Table 1.1: Differences between asexually and sexually produced offspring (from Williams 1975).

Asexual Offspring	Sexual Offspring
Large initial size	Small initial size
Produced continuously	Seasonally limited
Develop close to parent	Widely dispersed
Develop immediately	Dormant
Develop directly to adult stage	Develop through a series of diverse embryos
Environment and optimum genotype predictable from those of parent	Environment and optimum genotype unpredictable
Low mortality rate	High mortality rate
Natural selection mild	Natural selection intense

Asexual reproduction can consolidate local populations because of the lower risk of mortality due to the larger size of the propagule and attachment to the parent plant (Grime 1979). Asexual propagules can also be long lived. Wienhold and van der Valk (1989) reported the presence of viable *Scirpus fluviatilis* and *Scirpus validus* rhizomes from wetlands that had been drained to provide land for cultivation twenty years earlier, indicating they can contribute to the vegetation community after prolonged disturbances. In contrast, sexual reproduction favours long distance dispersal and increased genetic diversity (Williams 1975).

Sculthorpe (1967) suggested that the inhibition of sexual reproduction by the aquatic environment gives a selective advantage to asexual reproduction. Grace (1993) elaborated on that statement by suggesting that the methods of sexual reproduction in aquatic angiosperms are essentially terrestrial and require the emergence of flowering structures above the water surface for fertilisation. In addition to numerical increase and dispersal, Grace (1993) stated that asexual propagules could provide resource acquisition, carbohydrate storage, protection and anchorage.

Sexual reproduction becomes more difficult with increasing water depth and for many species, production of sexual propagules is an occasional event (Grace 1993). An alternative perspective that may also contribute to the predominance of asexual reproduction in some species is that asexual reproduction may be so effective in aquatic ecosystems that the selective value of sexual reproduction will be reduced. Some methods of asexual reproduction (such as fragmentation) are highly effective, economical and can disperse long distances in aquatic systems (Grace 1993). This may be the case for permanent water bodies; however, for temporary wetlands or wetlands with large and aseasonal water level fluctuations asexual modes of reproduction such as fragmentation may not be so favourable (Philbrick and Les 1996). In these systems propagules that can undergo dormancy, form a propagule bank, maintain genetic diversity, are able to tolerate desiccation (Philbrick and Les 1996) and exploit more than one window of opportunity should predominate. However, asexual propagules that can be used for anchorage, resource acquisition and rapid recolonisation would also be advantageous in systems, such as arid wetlands, where disturbances are common.

1.2 Water Regime

The water regime of a wetland creates the unique physiochemical conditions that make wetland systems different from both well-drained terrestrial systems and deepwater aquatic systems (Mitsch and Gosselink 1993). Bunn *et al.* (1997) described water regime as the depth, duration, frequency, rate of filling and drying, timing and predictability of flood and dry phases. The aforementioned factors influence the biochemistry of soils and are major factors in the selection of wetland biota from microbes to macrophytes to waterfowl (Mitsch and Gosselink 1993).

A component of water regime, hydroperiod, is the basis for the majority of wetland classification frameworks (Mitsch and Gosselink 1993). The hydroperiod of a wetland is the seasonal pattern of the water level and is the hydraulic signature of each wetland type (Mitsch and Gosselink 1993). Water levels in the majority of wetlands are not stable but fluctuate seasonally (e.g. tropical floodplain wetlands (Junk *et al.* 1989) or vernal pools (Bliss and Zedler 1998)), daily or semi daily (e.g. tidal freshwater wetlands (Leck and Brock 2000)) or unpredictably (e.g. dryland river floodplain wetlands (Walker *et al.* 1997)). Non-tidal wetlands are classified into permanently flooded, intermittently exposed, semi-permanently flooded, seasonally flooded, saturated, temporarily flooded and intermittently flooded (ephemeral) (Mitsch and Gosselink 1993).

1.2.1 Ephemeral Wetlands

The hydrology of ephemeral wetlands is characterised by large and aseasonal water level fluctuations (Walker *et al.* 1997; Puckridge *et al.* 1998; Puckridge *et al.* 2000), generally due to highly variable inflows from allogenic rivers (Timms 2001). Most ephemeral wetlands are shallow and located in arid or semi-arid climates (Timms 2001). In contrast, the permanent or semi-permanent wetlands (in arid climates) are usually deeper isolated reaches of intermittent rivers (Timms 2001). In many cases, ephemeral wetlands are more often dry than inundated (Timms 2001) and due to their shallow morphology are subject to large water level fluctuations in relation to their depth (Gopal 1986).

1.2.2 Effect of Water Regime on Germination and Recruitment from the Seed Bank

Mitsch and Gosselink (1993) stated that hydrology was the most important factor in determining the plant communities in wetland ecosystems. Hydrology in combination with elevation will influence the water regime experienced by a plant community. Water regime effects water availability (if the substrate is exposed), water depth if submerged, duration of flooding or exposure, rate of inundation and drawdown, oxygen availability, sediment redox potential, availability of inorganic carbon, light availability and quality, temperature, timing (season) of flooding or drawdown (Rea and Ganf 1994a), nutrient availability and salinity (Smith and Kadlec 1983). van der Valk (1981) suggested that water regime acts as an environmental sieve (sensu Harper 1977) that allows only certain species to germinate and recruit depending on water level.

The aforementioned factors all influence germination, performance, survival and in turn floristic composition. For example: Bonnewell *et al.* (1983) determined that *Typha latifolia* seeds required high temperatures low oxygen concentration and high light to induce high percentages of seed germination. *Melaleuca halmaturorum* seeds failed to germinate when submerged and lost viability when submerged for longer than 30 days (Nicol and Ganf 2000). In addition, persistent top flooding of one and two year old *Melaleuca halmaturorum* saplings resulted in high rates of mortality (Denton and Ganf 1994). Moore and Keddy (1988) concluded that the zonation of lakeshore plants was the result of differential germination responses to water depth not differences in the seed bank. Nicol *et al.* (2003) reported that when water levels fall below the sediment surface, submergent species are replaced by amphibious and terrestrial species. *Triglochin procerum* and *Baumea arthrophylla* allocated more biomass to above ground organs when submerged and below ground organs when exposed (Rea and Ganf 1994d). Casanova (1994) reported that *Chara australis* allocated more resources to asexual reproduction when water levels increased and more resources to sexual reproduction when water levels decreased. During periods of low water levels, Lake Saint Pierre (Canada) became a highly productive marsh whereas under high water levels it is an open water lake (Hudon 1997). Extensive papyrus swamps developed around the edges of Lake Naivasha (Kenya) in the 1970s when water levels were drawn down (Gaudet 1977). Nielsen and Chick (1997) reported that permanently inundated and summer flooded wetlands were floristically less diverse than those flooded in spring or initially flooded and allowed to vary with rainfall and evaporation (control). They also reported that terrestrial plants germinated on the exposed areas in the spring flood and control treatments (Nielsen and Chick 1997). Welling *et al.* (1988b) stated that recruitment in many wetland systems occurs primarily during drawdown, when the sediment surface is not inundated.

Casanova and Brock (2000) concluded that flood duration was the most important factor and depth was the least important factor in determining the establishment of wetland plant communities from the seed bank of a semi-permanent wetland. Petit and Froend (2001a) showed evidence that the timing of the flood pulse was important for the dispersal and establishment of the riparian trees *Eucalyptus camaldulensis, Eucalyptus rudis, Melaleuca leucodendra* and *Melaleuca rhaphiophylla.* These species do not develop soil seed banks and seed fall is timed to coincide with falling water levels to take advantage of high soil moisture, bare substrate and absence of scouring by high flows (Pettit and Froend 2001a). van der Valk and Davis (1978) and Welling *et al.* (1988a) stated that the presence of standing water, even as little as 2 cm, can have a dramatic effect on which species germinate from the seed bank.

1.2.2.1 Consequences of Altered Water Regimes

Walker and Thoms (1993) stated that altered water regimes change the habitat template and the biological character of rivers and wetlands must change accordingly. Adaptations to the natural water regime of a system involve life history strategies, behaviour and physiological and morphological adaptations (Bunn and Arthington 2002; Lytle and Poff 2004). In addition, for each mode of adaptation, different components of the water regime appear to be relevant: timing is important for many life history adaptations, predictability for behavioural adaptations and depth and duration for physiological and morphological adaptations (Lytle and Poff 2004). Due to different modes of adaptation, different species can show markedly different responses to the same water regime modifications (Lytle and Poff 2004).

River regulation for water supply (domestic, agricultural and industrial), hydropower, flood mitigation and navigation have significantly changed the water regime of many river systems worldwide (e.g. Walker 1985; Nilsson *et al.* 1991a; Petts 1996; Jansson *et al.* 2000; Merritt and Cooper 2000; Johansson and Nilsson 2002; Nilsson and Johansson 2002). For example: river regulation for water supply and abstraction in the lower Murray River (Australia) has resulted in reduced annual discharge, reduction in the number and duration of over bank flows, stable water levels, permanent inundation of low lying wetlands and droughting of high elevation wetlands (Maheshwari *et al.* 1995). The installation of storage reservoirs and run-of-the-river impoundments for hydroelectricity generation has changed the Ume River (Sweden) from system with high flows in the spring and early summer and low flows in autumn and winter to a system, which has three different regulated regimes (Nilsson *et al.* 1991a). In the storage reservoirs the water level is lowest in spring and highest in mid to late summer, in the run-of-the-river storages the water level shows daily fluctuations between the highest and lowest regulated levels (usually 1 m apart) throughout the year and sections of the original river immediately downstream of the reservoirs show a natural rhythm with the amplitude of the fluctuations greatly reduced (Nilsson *et al.* 1991a). Modification of the channel and installation of water regulating structures in the Missouri River (USA) for navigation and flood mitigation has significantly changed the hydraulic regime (Pegg *et al.* 2003). Many reaches that experienced spring floods and periods of low flow in autumn and winter now have uniform flow throughout the year and the construction of levees for flood control has prevented inundation of the floodplain in many reaches in all but the largest floods (Pegg *et al.* 2003).

The consequences of these changes for wetland, riverine and riparian biota can sometimes be catastrophic or give certain species a competitive advantage that may lead to extirpation of species not well adapted to the new water regime (Lytle and Poff 2004). For example: riparian tree species adapted to regular flood pulses by timing seed fall to coincide with the flood pulse will not recruit or disperse if the flood pulse is eliminated or the timing is altered (Grace 1993; Pettit and Froend 2001b; Pettit and Froend 2001a; Pettit *et al.* 2001). Stable water levels and increased permanency have been implicated in the expansion of *Triglochin procerum* and decline of *Baumea arthrophylla* in Bool Lagoon (Australia) (Rea and Ganf 1994b; Rea and Ganf 1994c) and the expansion of *Typha domingensis* and *Phragmites australis* along the banks of the lower River Murray (Australia) (Blanch *et al.* 2000). Stable water levels may also restrict the germination and recruitment of many amphibious and floodplain species to a narrow fringe just above the water level (e.g. Gaudet 1977; Welling *et al.* 1988b; Blanch *et al.* 2000). Shorter flood durations can extirpate submergent species and promote amphibious and terrestrial species (Blanch *et al.* 1999b; Nicol *et al.* 2003).

1.3 Site Description

1.3.1 The Murray-Darling System

The Murray Darling Basin covers an area of 1 061 469 km^2 (Crabb 1997), which is approximately 14% of mainland Australia’s land surface and contains areas of Queensland, New South Wales, Victoria, South Australia and all of the Australian Capital Territory (Figure 1.1).

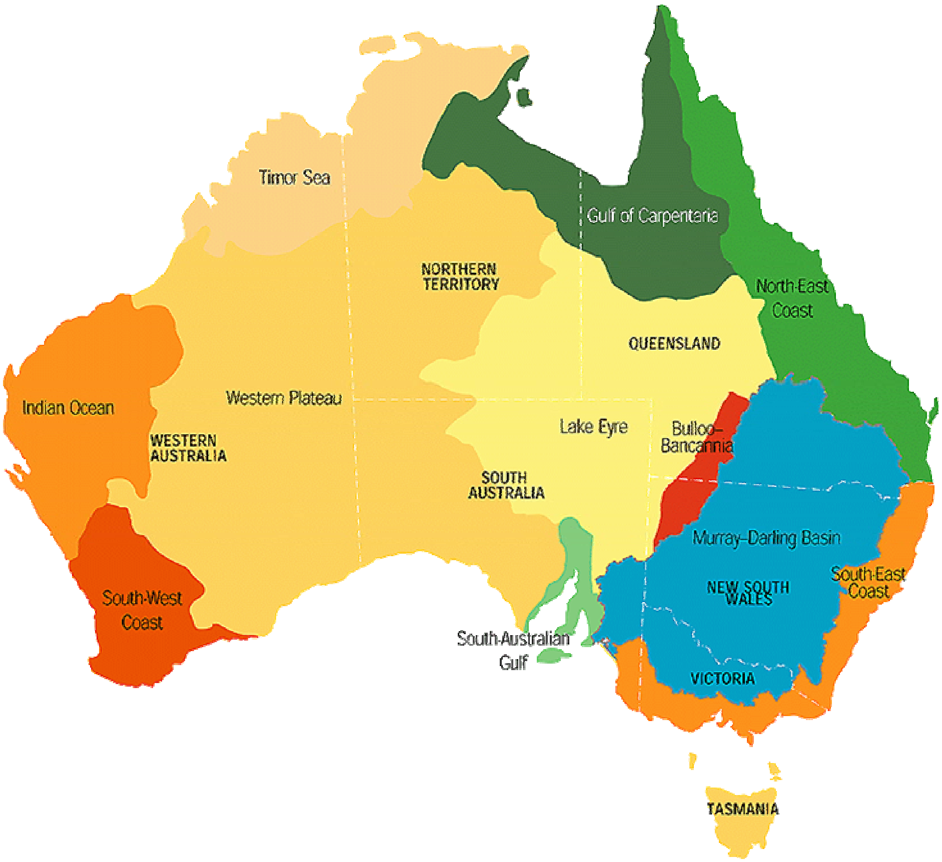

Figure 1.1: Major surface water drainage divisions in Australia (Murray Darling Basin Commission 2004)

Despite being one of the longest river systems in the world and draining a significant area of mainland Australia, the total discharge of the Murray Darling system is insignificant in world terms with a mean and median annual discharge of 10,090 GL and 8489 GL respectively (Walker and Thoms 1993; Maheshwari *et al.* 1995). In contrast, the Ganges River system in southern Asia has a catchment of similar size to the Murray Darling system and a mean annual discharge of 1,200,000 GL (Crabb 1997).

The Murray Darling system originates in wetter upland areas but for most of its length flows through semi-arid and arid lowland regions that contribute little to the total discharge (Figure 1.2) (Walker and Thoms 1993; Crabb 1997). The Murray Darling system experiences large water losses in the lowland regions through evapotranspiration and groundwater recharge (Thoms and Sheldon 2000a).

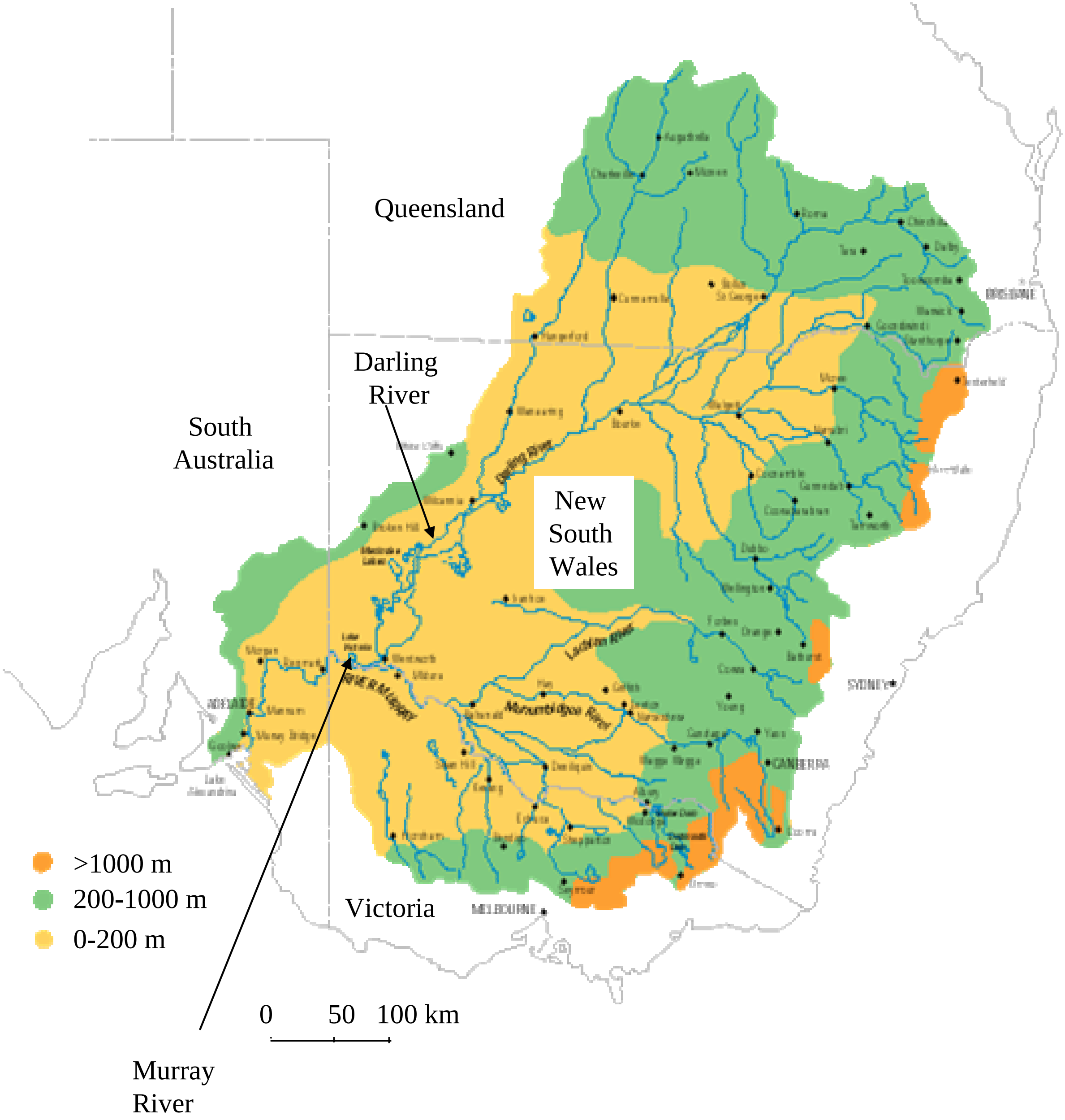

Figure 1.2: The Murray Darling Basin (Murray Darling Basin Commission 2004)

As its name suggests, the Murray Darling system consists of two major rivers the Murray and the Darling. The Murray River drains areas of Victoria and southern New South Wales inland of the Great Diving Range (Figure 1.2). The upland regions of the Murray catchment provide over 70% of the mean annual runoff for the entire basin from rainfall and snowmelt (Crabb 1997).

The pre-regulation hydrology of the Murray River, exhibited large inter-annual variability (Puckridge *et al.* 1998; Puckridge *et al.* 2000) with high flows usually occurring in spring and early summer and lows flows during late summer and autumn (Walker 1986; Walker and Thoms 1993; Walker *et al.* 1995; Walker *et al.* 1997). Between 1922 and 1940 construction of series of weirs, barrages, small storages and the Hume Dam (a large headwater storage, near Albury in New South Wales) (Figure 1.2) changed the flow regime of the lower Murray from a lotic ecosystem to a series of stable permanent pools (Walker 1985; Walker 1986; Walker and Thoms 1993). In addition, large headwater storages were constructed on several tributaries of the Murray; these include Dartmouth Dam on the Mitta Mitta River and Eildon Dam on the Goulburn River.

1.3.2 The Darling River

The Darling River drains the northern and western portion of the Murray Darling Basin (Figure 1.2). The majority of flows in the lower Darling River originate in the wetter eastern areas of the catchment (Thoms and Sheldon 2000b). The rivers that drain this part of the catchment, the Condamine-Balonne, Macintyre, Gwydir, Namoi, Castlereagh and Macquarie Rivers have their headwaters on western slopes the Great Dividing Range in southern Queensland and northern New South Wales (Thoms and Sheldon 2000b). The Paroo and Warrego Rivers in contrast have their headwaters in the more arid west and only contribute significant runoff during periods of high rainfall (Thoms and Sheldon 2000b). Annual median rainfall in the catchment decreases westward from >1200 mm in the upland headwaters to <200 mm at Broken Hill (Thoms and Sheldon 2000b).

Flows in the lower Darling, whilst extremely variable between years, do show some seasonality with the highest flows usually occurring between December and April (Thoms and Sheldon 2000b). Annual discharge of the Darling River is inversely correlated to sea surface temperature (SST) anomalies in the eastern tropical Pacific Ocean. These SST variations are components of El Nino-Southern Oscillation Index (ENSO). Historically high flows in the Darling River due to sub-tropical summer monsoon precipitation in the headwaters are strongly correlated with ENSO (Simpson *et al.* 1993).

Areas with low and variable rainfall (such as the lower Darling catchment) depend on dryland rivers for water. In order to secure a reliable water supply, the Darling River has undergone some degree of regulation (Thoms and Sheldon 2000b). There are nine headwater dams with a combined storage of 4966 GL (Table 1.2), 15 main channel weirs to assist in the supply of water for urban, stock and domestic purposes, more than 1000 small weirs on tributaries and anabranch channels and the Menindee Lakes Storage (Thoms and Sheldon 2000b). The seasonal variability of flows has decreased considerably since the construction of headwater storages and the Menindee Lakes (Thoms and Sheldon 2000b). Flows in the system are also modified by water abstraction for irrigated agriculture. In 1994, the number of licensed water abstractors between Mungindi and Menindee was 267 compared with 20 in 1960 (Thoms and Sheldon 2000b). This has resulted in about one third of the mean annual flow being diverted from the river and its tributaries and decreased natural flow into the Menindee Lakes (Taylor-Wood *et al.* 2001).

Table 1.2: Major headwater storage capacities of the Darling River (from Crabb 1997)

Storage	River	Capacity (GL)
Burrendong Dam	Macquarie	1678
Copeton Dam	Gwydir	1364
Keepit Dam	Namoi	423
Split Rock Dam	Manilla (Namoi)	397
Windamere Dam	Cudgenong	368
Pindari Dam	Severn	312
Glenlyon Dam	Pike Creek	261
Beardmore Dam	Balonne	101
Chaffey Dam	Peel	62
Total		4966

1.3.3 The Menindee Lakes

The Menindee Lakes are a series of shallow floodplain depressions on the Lower Darling River. The system comprises seven deflation basins: Lakes Malta, Balaka, Bijiji, Tandure, Pamamaroo, Menindee, Cawndilla, and Lake Wetherell. Lake Wetherell was created by the construction of the Menindee Main Weir and subsequent flooding of the main channel of the Darling River and surrounding floodplain (Figure 1.3). Each lake, with the exception of Lake Cawndilla, is individually connected to the Darling River. Lake Cawndilla is connected to Lake Menindee by Morton Boolka Channel (Figure 1.3).

The lakes were formed by the erosive action of the wind, a process known as deflation (Earth Tech Engineering 2002). The lakes are generally elliptical or kidney shaped, with the long axis running north south (Figure 1.3). Small cliffs are often found on the western edges of the lakes where the lake truncates the surrounding dune system (the Woorinen formation); however, this dune does not encroach onto the lakebed due to the removal of material by wind and water (Earth Tech Engineering 2002). On the eastern (lee) shorelines of the lakes are distinctive shoreline dunes called lunettes. The lunettes were formed by the deposition of lakebed material, and the size of the lunette generally reflects the size of the lake (Bowler 1973). The Menindee Lakes are unique in the Murray Darling Basin because of their association with a major stream. All other dune lake systems in the Murray Darling Basin (e.g. Teryaweynya Lakes), are fed by anabranches that only flow during high flows (Earth Tech Engineering 2002).

The Menindee Lakes have been listed in the Directory of Important Wetlands in Australia (Australian Nature Conservation Agency 1996). The reasons for inclusion include (from Scholz *et al.* 1999):

- They are a good example of a wetland type in a biogeographical region.
- They provide important habitat for animals at critical stages in their life cycles.
- They provide important refugia in drought or adverse conditions.
- They support 1% or more of national populations of native plant or animal taxa.
- They support plant or animal species that are endangered or vulnerable at a national level.
- They are significant habitat for water birds.

1.3.3.1 Climate

The climate of the Menindee area is arid with a mean annual rainfall of 243.7 mm (Table 1.3), which equates to 110 GL input directly to the lakes (Scholz *et al.* 1999). The mean monthly rainfall shows no pattern, however summer storms (on occasion) result in over 100 mm of precipitation recorded in 24 hours (Table 1.3). Due to the flat topography, local runoff is negligible and the impact of total precipitation on the water budget of the lakes is negligible in comparison to evaporation. Due to the shallow broad morphology of the lakes and high summer temperatures (Table 1.3), potential evaporative losses from the system can be as high as 753.8 GL year^{-1} (2.5 m year $^{-1}$), assuming the lakes are at maximum capacity (Scholz *et al.* 1999). Potential monthly rates of evaporation range from 18.8 GL in July to 100.7 GL in January (Harris *et al.* 1996). From 1990 to 1996, approximately 45% of stored capacity within the Menindee Lakes was lost due to evaporation and from August 1997 to August 1998 evaporation accounted 43% of total losses from Lakes Menindee and Cawndilla (Scholz *et al.* 1999). The proportion of water loss due to evaporation as a ratio of storage volume increases as the lakes dry (Scholz *et al.* 1999).

Table 1.3: Climate averages for Menindee (117 years of records) (Australian Bureau of Meteorology 2003).

Element	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual
Mean daily maximum temperature (° C)	34.1	33.4	30.5	25.3	20.7	17	16.9	19.2	22.8	26.4	29.9	32.8	25.6
Mean no. days Max Temp ≥ 40.0° C	3.8	1.5	0.4	0.1	0	0	0	0	0	0	0.8	1.7	8.4
Mean no. days Max Temp ≥ 35.0° C	12	10.7	4.5	0.3	0	0	0	0	0.2	1.4	4.5	7.8	41.4
Mean no. days Max Temp ≥ 30.0° C	20.8	19.3	13.9	4.3	0.2	0	0	0.3	2	5.9	10.8	15.1	92.5
Highest daily Max Temp (° C)	49.7	47.2	42.8	41.4	33.3	28.9	28.9	32.3	37.2	42.8	45	48.9	49.7
Mean daily minimum temperature (° C)	18.2	17.9	15	10.4	7.4	4.8	4	5.2	7.9	11.2	14.3	16.7	10.9
Lowest daily Min Temp (° C)	7	6.4	3.9	2	0.7	-2.2	-3.5	-2	0.2	1	1.7	6	-3.5
Mean 9 am air temp (° C)	24.4	23.5	20.5	15.6	11.6	8.3	7.7	10	14.1	17.9	20.9	23.6	16.3
Mean 9 am relative humidity (%)	45	50	55	61	72	79	79	71	60	52	48	44	60
Mean monthly rainfall (mm)	23.1	21.2	18.1	16.5	23.3	21.3	18.1	18	18.8	23.3	20.2	21.9	243.7
Mean no. of rain days	2.5	2.6	2.3	2.8	4.2	4.7	4.9	4.9	3.9	4	3.2	2.8	42.6
Highest monthly rainfall (mm)	231.7	157.1	165.6	152	107.2	111.7	113.5	67.6	79.3	113.2	163.5	197.5	
Lowest monthly rainfall (mm)	0	0	0	0	0	0.3	0	0	0	0	0	0	
Highest recorded daily rainfall (mm)	129.6	100.8	96.6	66	45	63.5	60.7	38.9	47	69.3	150.6	80	

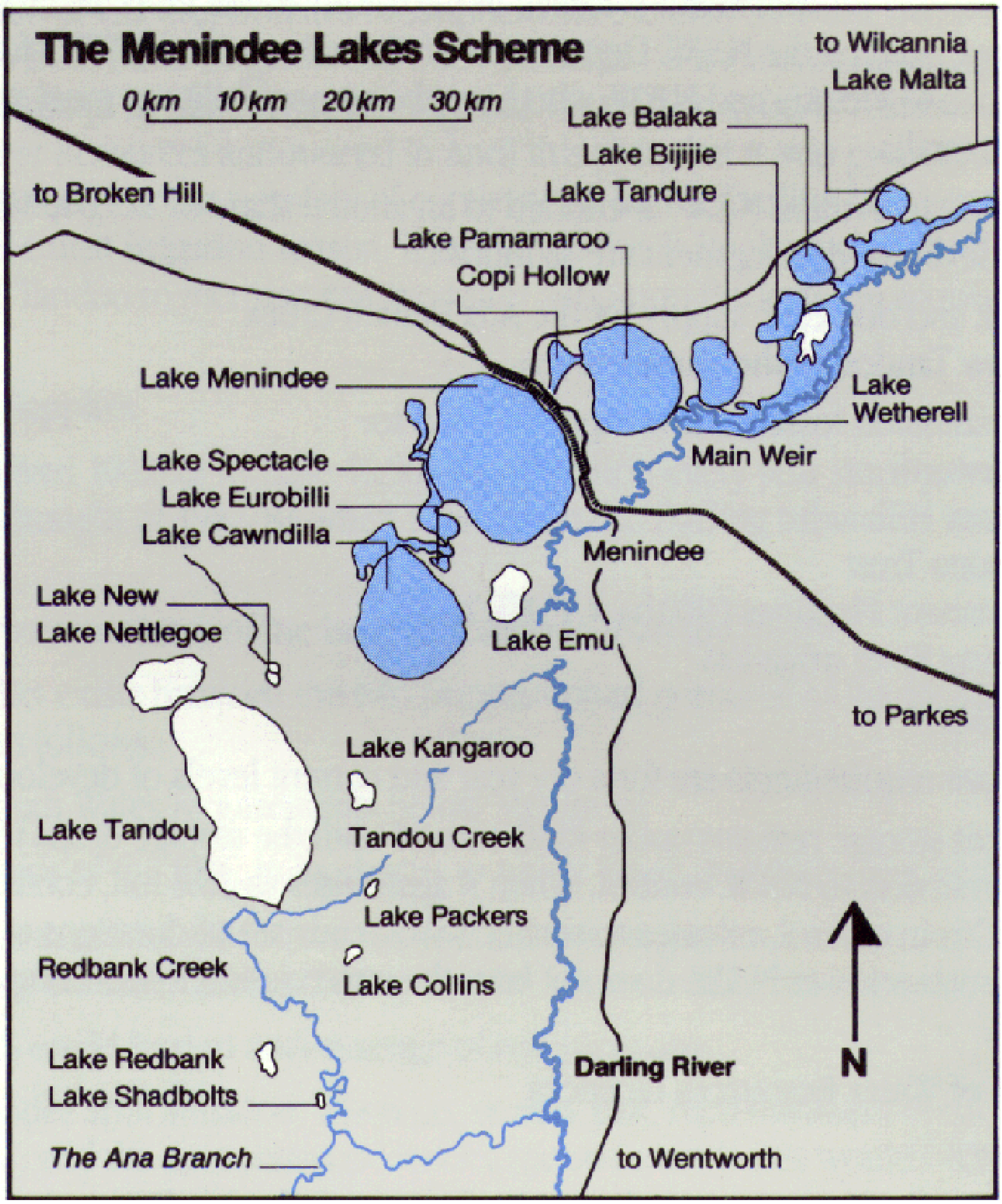

Figure 1.3: The Menindee Lakes Scheme (Tandou Pty Ltd 2003)

1.3.3.2 Pre-regulation Water Regime

Prior to completion of the storage scheme, the Menindee Lakes were a series of ephemeral lakes, which were inundated when river levels were higher than the sill level of the feeder creeks. When river levels receded, the lakes drained back to the Darling River leaving a residual pool, which would evaporate. The time the water remained in the residual pool was dependent on the depth of the lake (New South Wales Department of Land and Water Conservation 1998b).

Water level records prior to regulation are incomplete; however, it is believed that the small lakes (Malta, Balaka and Bijiji) would fill on average once every 2-3 years with the longest droughts being up to 11 years (Jenkins and Briggs 1997). The large lakes Tandure, Pamamaroo, Menindee and Cawndilla filled on average once every 1-2 years with the longest droughts being five years (Scholz *et al.* 1999).

1.3.3.3 Post-regulation Water Regime

The need for a reliable water supply for Broken Hill, Menindee and other communities in western New South Wales and to aid the supply of water to South Australia resulted in the Menindee Lakes Water Conservation Act in 1949. Construction of the scheme began later that year and was completed in 1968 (New South Wales Department of Land and Water Conservation 1998b). The Menindee Lakes are the only major water storage on the Lower Darling River and are the fourth biggest water storage in the Murray Darling Basin (Thoms and Sheldon 2000b).

The scheme is a series of small dams, regulators, weirs, channels and levees designed to conserve Darling River floodwaters (Figure 1.4). The main structure is the Menindee Main Weir. The Menindee Main Weir is located upstream of Menindee township across the Darling River (Figure 1.3) and raises the level of the river 12 m above the bed level (Table 1.4), creating Lake Wetherell and filling Lakes Tandure, Bijiji, Balaka and Malta (Figure 1.4) (New South Wales Department of Land and Water Conservation 1998b). This hydraulic head is used to gravity feed Lakes Pamamaroo, Menindee and Cawndilla (New South Wales Department of Land and Water Conservation 1998b).

The lakes now are now inundated for longer periods and small to medium sized floods downstream of the scheme and in the Darling Anabranch have been eliminated (New South Wales Department of Land and Water Conservation 1998b; Scholz *et al.* 1999). Despite the increased duration of inundation, large water level fluctuations are still common and drying cycles have not been lost entirely (Scholz *et al.* 1999) (Figure 1.5, Figure 1.6 and Figure 1.7). Lake Malta dried in the early 1980s, 1986, 1994-5 and 2002-3, Lake Balaka in 1986, 1994-95 and 2002-3, Lake Bijiji in the mid 1980s and 2002-3, Lake Tandure in 2002-3, Lake Pamamaroo in 2002-3 (Figure 1.6), Lake Menindee in 1966-7, 1967-8, the early

1980s, 1994-5 and 2002-3 (Figure 1.7) and Lake Cawndilla 1966-7, 1994-5, 1995-6 and 2003 (Figure 1.7) (Scholz *et al.* 1999). Lake Malta is least impacted by regulation (Scholz *et al.* 1999).

Table 1.4: Sill, lakebed, full supply levels and surcharge levels of the Menindee Lakes, from Scholz *et al.* (1999) and New South Wales Department of Land and Water Conservation (1998b).

Location	Elevation (m AHD)
Malta Sill	60.82
Balaka Sill	60.75
Bijiji Sill	59.97
Tandure Sill	59.30
Wetherell Bed	49.50
Pamamaroo Bed	55.30
Menindee Bed	55.30
Cawndilla Bed	53.00
Wetherell Full Supply	61.67
Pamamaroo Full Supply	60.45
Menindee Full Supply	59.84
Cawndilla Full Supply	59.84
Wetherell Surcharge	62.28
Pamamaroo Surcharge	61.50
Menindee Surcharge	60.45
Cawndilla Surcharge	60.45

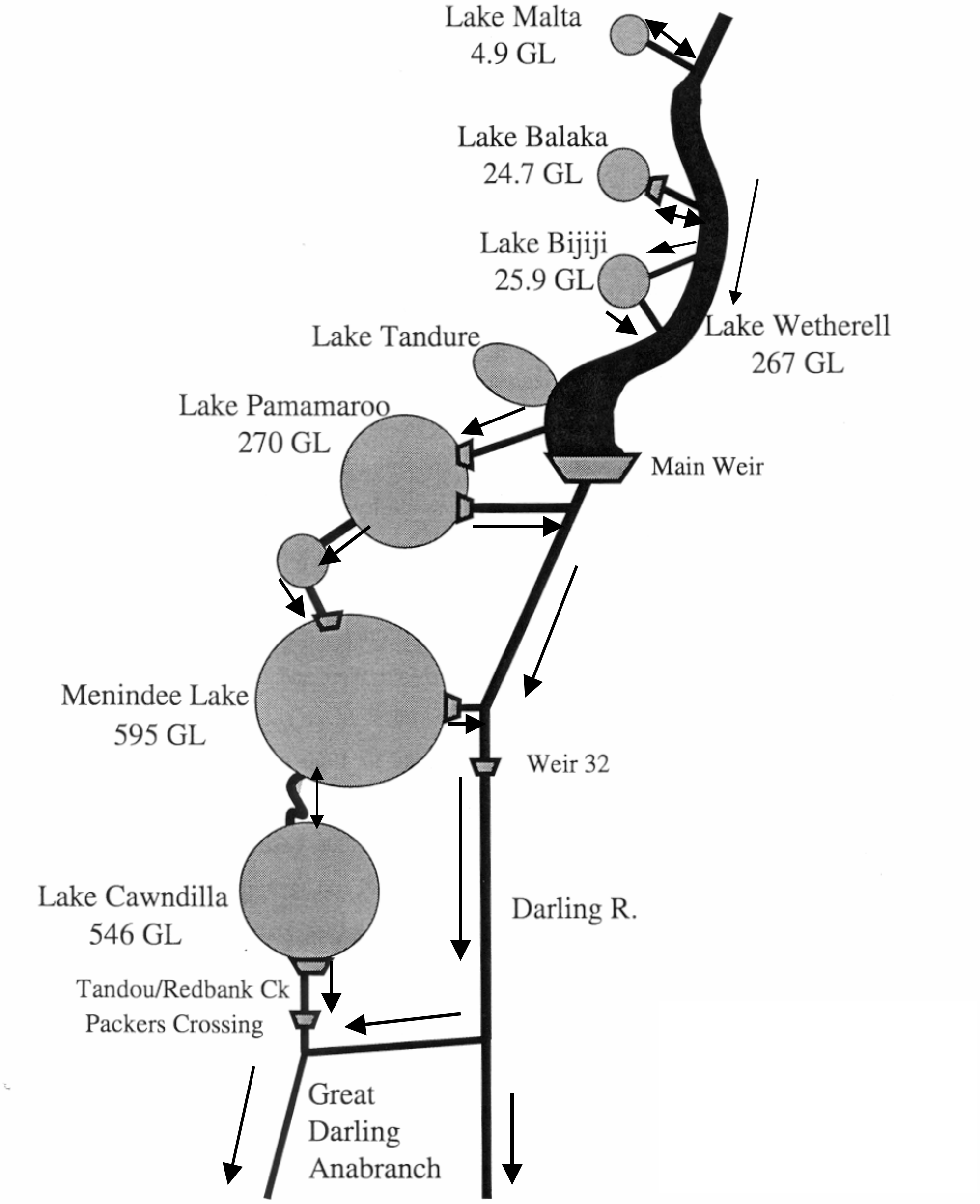

Figure 1.4: Schematic diagram of the Menindee Lakes Scheme (direction of flow denoted by arrows), from Scholz *et al.* (1999).

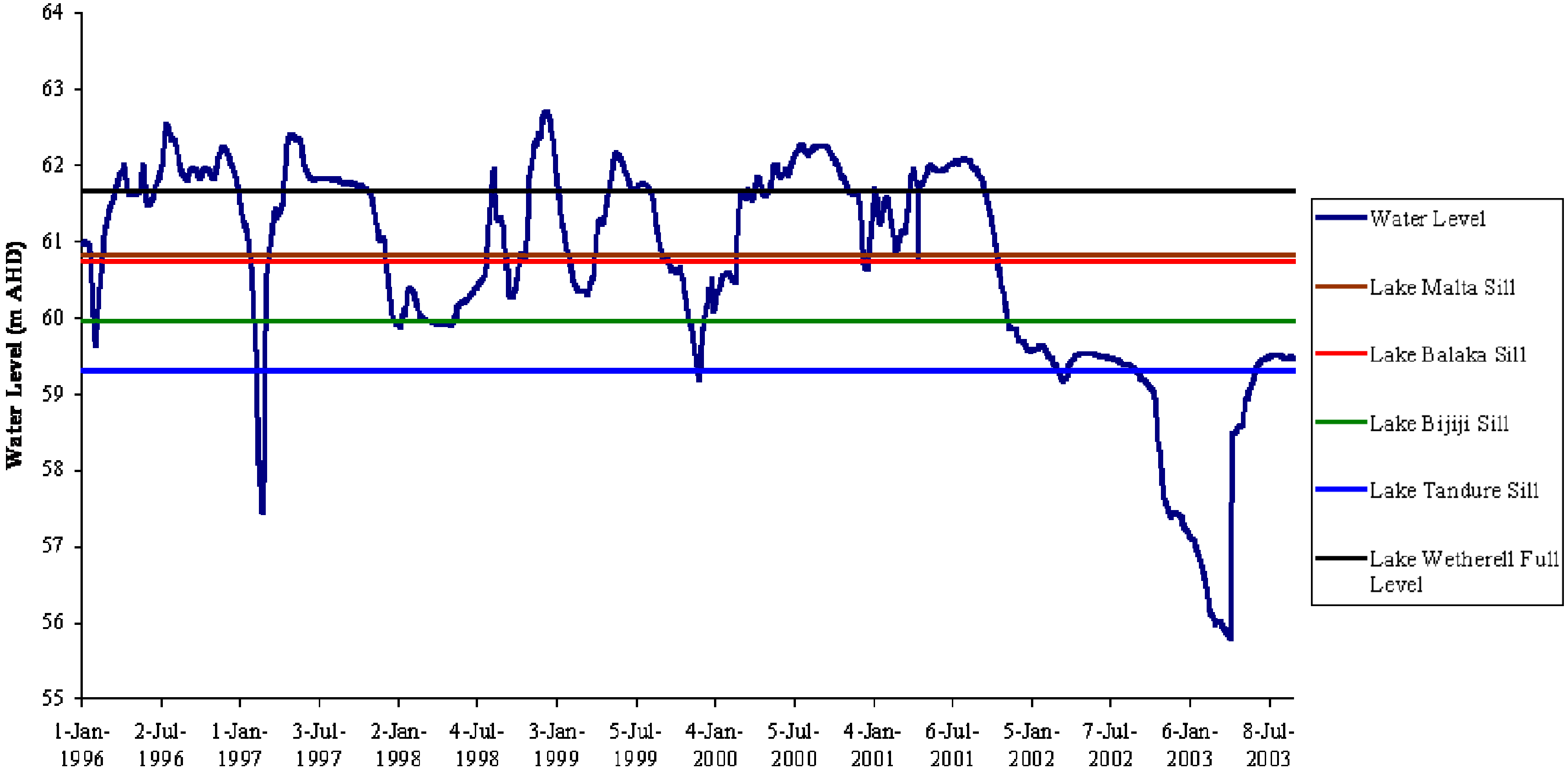

Figure 1.5: Lake Wetherell water levels from January 1st 1996 to August 31st 2003 (New South Wales Department of Land and Water Conservation 2003).

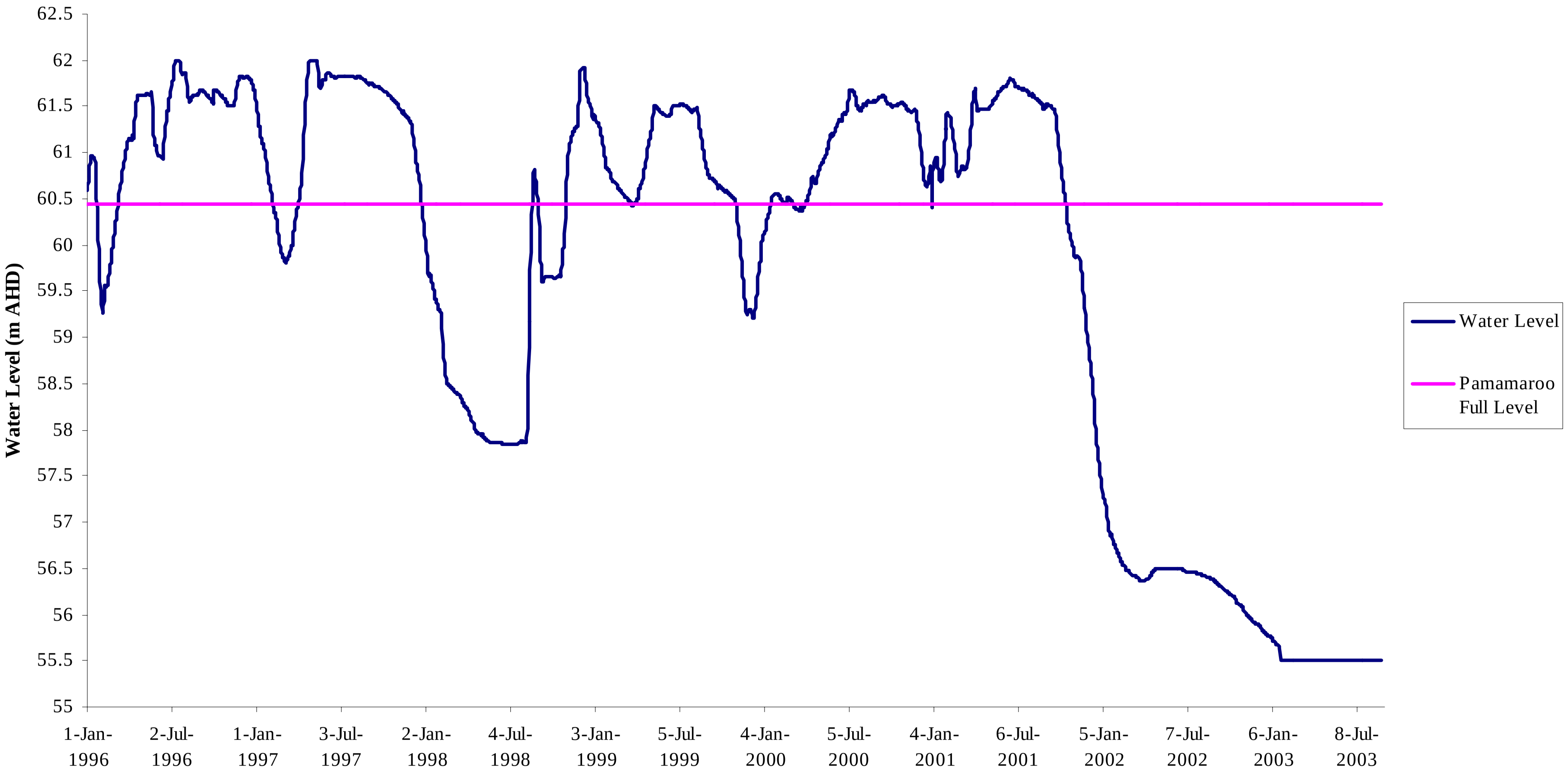

Figure 1.6: Lake Pamamaroo water levels from January 1st 1996 to August 31st 2003 (New South Wales Department of Land and Water Conservation 2003).

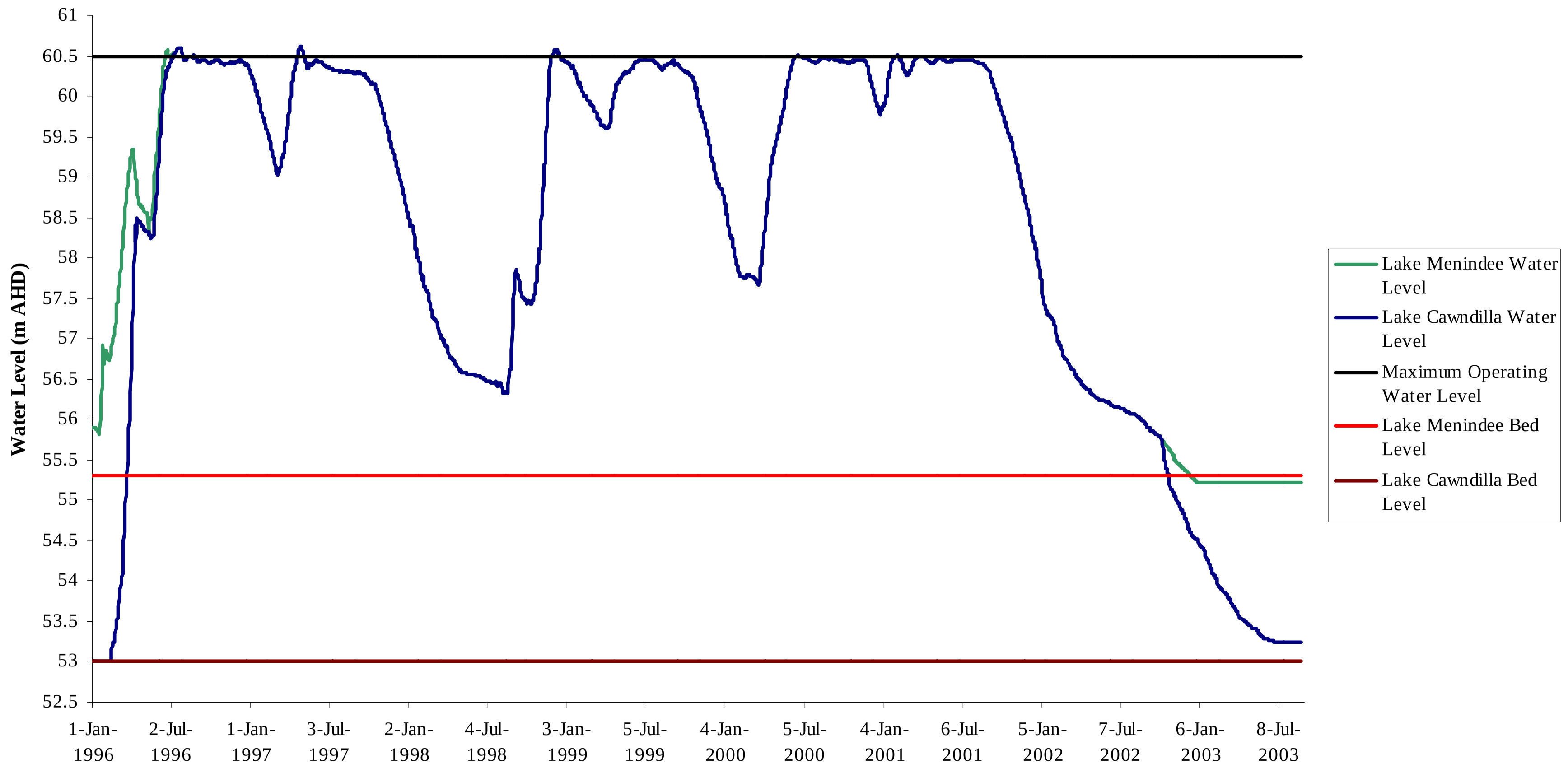

Figure 1.7: Water levels of Lakes Menindee and Cawndilla from January 1st 1996 to August 31st 2003 (New South Wales Department of Land and Water Conservation 2003).

1.3.3.4 Menindee Lakes Operations

Since the completion of the scheme, the hydraulic regime is dictated by the operating procedures developed and implemented by the New South Wales Department of Infrastructure, Planning and Natural Resources. The priority of operations is to maximize the potential supply of water for all users, to ensure operations provide long-term ecological sustainability and to maximize water quality within the lakes and Lower Darling River for human uses (New South Wales Department of Land and Water Conservation 1998b).

To achieve these objectives the general operation of the Menindee Lakes has been (New South Wales Department of Land and Water Conservation 1998b):

- Minimize evaporation.
- Maximize storage volumes.
- Maximize water quality (low salinity).
- Maximize supply to users.
- Mitigate floods where possible.

In recent years especially since 1991 when extensive cyanobacteria blooms affected much of the Lower Darling River and Menindee Lakes (Bowling and Baker 1996), operating strategies have been modified to address further objectives including (New South Wales Department of Land and Water Conservation 1998b):

- Maximizing ecological benefits, including fish and wildlife habitat.
- Maximizing water quality (in terms of mitigating algal blooms).
- Managing flood mitigation for the Lower Darling River to provide environmental benefits.
- Control of foreshore erosion.

1.3.3.4.1 Water Regulating Structures

The main water regulating structure is the Menindee Main Weir, which raises the water level and inundates the upstream lakes (New South Wales Department of Land and Water Conservation 1998b) (Figure 1.4) (Table 1.4). An inlet regulator allows water to move from Lake Wetherell into Lake Pamamaroo where it can be stored to a depth of 4.8 m (Table 1.2). Water can then be moved from Lake Pamamaroo to Lake Menindee through an interconnecting channel and artificially created lake called Copi Hollow then through the Menindee Inlet regulator (Figure 1.4), where it can be stored to a depth of 5.4 m (New South Wales Department of Land and Water Conservation 1998b) (Table 1.2). Lake Cawndilla is connected to Lake Menindee by Morton Boolka Channel, which incorporates Lakes Eurobilli and Spectacle (Figure 1.3). Morton Boolka Channel has no regulating structure (New South Wales Department of Land and Water Conservation 1998b).

Water can be released to the Darling River through outlet regulators from Lakes Wetherell (not shown on Figure 1.4), Pamamaroo and Menindee as well as from the Main Weir (Figure 1.4). Lake Cawndilla can drain to Lake Menindee via Morton Boolka Channel, not directly to the Darling River (Figure 1.4). Water from Lake Cawndilla can only be diverted from the Lake Cawndilla outlet regulator (Figure 1.4). Water then passes via the Cawndilla Channel to Tandou Creek where it is contained by a block bank and regulator at Packers Crossing (Figure 1.4) (New South Wales Department of Land and Water Conservation 1998b). Water here can be diverted by Tandou Pty Ltd for irrigation or diversion into the company’s storage Lakes or passed downstream to Redbank Creek and into the Great Darling Anabranch (Figure 1.4) (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.4.2 Filling and Surcharge Procedures

When filling the lakes the major objective is to minimize evaporative losses where possible by minimizing the surface area of the lakes. This is undertaken by preferentially filling, and in some cases surcharging, Lakes Wetherell and Pamamaroo (New South Wales Department of Land and Water Conservation 1998b). Water is not released from Lake Pamamaroo to Lakes Menindee and Cawndilla unless predicted inflows will exceed the surcharge capacity of Lakes Wetherell and Pamamaroo (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.4.3 Emptying Procedures

The procedures for releasing water from the Menindee Lakes are based on the same considerations as the filling procedures. The preferred strategy for emptying the lakes is to meet all consumptive demands from Lakes Menindee and Cawndilla before using water from Lakes Pamamaroo and Wetherell (New South Wales Department of Land and Water Conservation 1998b). However, Lake Wetherell is often drawn down to just below the level of the floodplain to reduce evaporation and allow regeneration of riparian vegetation (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.4.4 Drought Operations

Management for drought underpins all operations of the Menindee Lakes (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998). The Murray Darling Basin Commission leases the Menindee Lakes from the New South Wales Department of Infrastructure, Planning and Natural Resources and when the total storage volume falls below 480 GL, the water in the lakes comes under the control of the New South Wales Government. When the lakes are under New South Wales control, they are not obliged to use the water to meet minimum flow requirements to South Australia (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998). When the lakes refill control does not revert to the Murray Darling Basin Commission until the total storage volume reaches 640 GL. This strategy was adopted to prevent unnecessary switching of control between the two organizations (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998).

1.3.3.4.5 Flood Operations

Floods in the Darling River are generally the result of rainfall in the upper catchment therefore inflows into the Menindee Lakes can occur up to three months later than the rainfall events. This can make accurately predicting the volume, duration and peak of a flood difficult, particularly when tributaries closer to Menindee (the Warrego and Paroo Rivers) also contribute flow (New South Wales Department of Land and Water Conservation 1998b).

The severity of floods in the Menindee Lakes and Lower Darling River are dependent on (New South Wales Department of Land and Water Conservation 1998b):

- The volume, duration and peak of floods upstream.
- The prior storage of the lakes.
- The level of surcharge adopted during a flood event.

The main objective of flood operations is to ensure the safety of infrastructure and to minimize property damage downstream. The lakes were not constructed for flood mitigation, however some mitigation may be achieved by increasing outflows before the peak reaches the lakes. Airspace in the lakes up to the determined surcharge volume may be used to store inflows and reduce the flood peak downstream (New South Wales Department of Land and Water Conservation 1998b). This practice (pre-releasing) changes the nature of floods downstream of the scheme. The height of the flood peak is reduced, but the length of time of higher flows is increased (New South Wales Department of Land and Water Conservation 1998b).

Pre-releasing may reduce the social and economic impacts of flooding downstream of Menindee Lakes, but the altered flood hydrograph downstream of the Main Weir can have severe impacts for the riverine and floodplain biota (Walker 1985; Walker 1986; Junk *et al.* 1989; Walker *et al.* 1992; Walker and Thoms 1993; Walker *et al.* 1994; Maheshwari *et al.* 1995; Nilsson *et al.* 1997; Walker *et al.* 1997; Puckridge *et al.* 1998; Puckridge *et al.* 2000; Thoms and Sheldon 2000b; Nilsson and Johansson 2002).

The degree of downstream mitigation achieved by pre-releasing is dependent on the size of the flood. Pre-releasing will have little effect on large floods (greater than 100 GL day^{-1}), however small to medium sized floods may be completely mitigated (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.4.6 River Operations

The primary objective of river operations is to provide at least minimum flow requirements to meet the demands of users, conserving water to increase the security of supply and to meet environmental requirements. Typically, flow regimes to maintain water quality have been limited to maintenance of river flow (New South Wales Department of Land and Water Conservation 1998b).

When storage volumes are high and the Menindee Lakes are not under the sole control of the New South Wales government, water may be released to the Lower Darling River as requested by the Murray Darling Basin Commission (MDBC) (New South Wales Department of Land and Water Conservation 1998b). The MDBC requests releases from the Menindee Lakes to supplement River Murray Flows when required and to minimize evaporative losses and maximize water available to supplement River Murray flows by transferring water to Lake Victoria (New South Wales Department of Land and Water Conservation 1998b). The MDBC will request releases from the Menindee Lakes when flows in the River Murray and storage in Lake Victoria are insufficient to meet flow requirements for South Australia or to maintain storage in Lake Victoria at or above a specified target (New South Wales Department of Land and Water Conservation 1998b).

Replenishment flows to the Great Darling Anabranch are diverted from Lake Cawndilla via Tandou Creek, Packers Crossing and Redbank Creek. The replenishment flow is generally provided between June and October, although supplementary flows may be available in autumn following flood events if water is available (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.4.7 Flow Forecasting and Implementation

The final component of Menindee Lakes operations involves flow forecasting and implementation. Much of the water reaching the Menindee Lakes falls up to three months before reaching the storage. This provides an opportunity to plan the operation of the storage well in advance to meet the objectives at the time, whether it be flood mitigation by pre-release of approaching floodwaters, or a release best suited to environmental requirements downstream (New South Wales Department of Land and Water Conservation 1998b).

After each rainfall event in the upper catchment a forecast is produced to assess the impact of flows on the Management of the Menindee Lakes (New South Wales Department of Land and Water Conservation 1998b).

In the case of a large flood with sufficient volume to fill and spill the storage with a potentially damaging flow rate downstream management actions to ensure the safety of structures and minimize damage downstream of the storage, whilst producing a flow pattern as “natural” as possible (taking into consideration water conservation objectives) will be undertaken (New South Wales Department of Land and Water Conservation 1998b). This may involve pre-releasing to minimize the peak flow rate, however in some cases this itself may cause damage (New South Wales Department of Land and Water Conservation 1998b).

If the flood is not large enough to cause damage to infrastructure, the situation is examined to determine if the operation of the storage can improve environmental conditions within the lakes or downstream. These include improvement of water quality by flushing or circulating water within the lakes or mimicking as far as possible natural flows downstream of the storage to inundate wetlands or flush the Anabranch (New South Wales Department of Land and Water Conservation 1998b).

The prime consideration has always been that ensuring the storage is as full as possible at all times. Environmental considerations may make it more appropriate to use some of the inflows to achieve environmental objectives before ensuring the storage is filled (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.5 Water Quality

1.3.3.5.1 Temperature and Thermal Stratification

The Menindee Lakes are subject to large variations in surface water temperature. Winter temperatures are approximately 10 ºC, with summer temperatures around 30 ºC (New South Wales Department of Land and Water Conservation 1998b), although temperatures higher than 40 ºC have been recorded in Lakes Malta and Balaka just prior to drying (Scholz *et al.* 1999). The high turbidity of the lakes (50 to >999 NTU (Scholz *et al.* 1999)) may also aid in heat absorption over the summer (New South Wales Department of Land and Water Conservation 1998b).

Diel fluctuations in water temperature in the small lakes (Malta, Balaka and Bijiji) were greater than those of the larger, lakes (Menindee, Cawndilla, Tandure and Pamamaroo) (Scholz *et al.* 1999). Lower water levels reduce the thermal mass of a lake and increase the surface area: volume ratio, thus reducing its capacity to buffer against changes in ambient temperature (Scholz *et al.* 1999). Therefore, the larger lakes will behave in a similar manner to the small lakes when volumes are low.

In Lakes Pamamaroo, Tandure, Menindee and Cawndilla temperature is relatively constant throughout the water profile (New South Wales Department of Land and Water Conservation 1998b). Scholz *et al.* (1999) observed temperature differences of only 2º C between the surface (10 cm below the water's surface) and bottom (10 cm above the sediment surface) in Lakes Cawndilla, Menindee and Tandure. The temperature gradient observed usually broke down during the night because the potential for thermal stratification in the large lakes is greatly reduced by their broad, shallow morphology and mixing by wind (New South Wales Department of Land and Water Conservation 1998b). However, some diurnal stratification has been observed in hot and still conditions (Scholz *et al.* 1999). On the other hand Lake Wetherell, due to its deep, narrow, sinuous morphology and shelter from trees lining the banks, exhibited thermal gradients of up to 8 ºC between the surface and bottom (New South Wales Department of Land and Water Conservation 1998b; Scholz *et al.* 1999).

1.3.3.5.2 Dissolved Oxygen

Dissolved oxygen concentrations in the large lakes when water levels are high are generally high to super saturated (6.5 to 15.9 mg L^{-1}) (Scholz *et al.* 1999) with only minimal decreases at times of diurnal stratification (New South Wales Department of Land and Water Conservation 1998b). When water levels are low and temperatures are high dissolved oxygen concentrations can decrease dramatically. For example, Scholz *et al.* (1999) measured dissolved oxygen concentrations as low as 1.5 mg L^{-1} in the waters of Lake Malta when the water temperature was 30.8 ºC and 20 cm deep. This is probably the case at times for the large lakes when volumes are low.

Lake Wetherell is subject to thermal stratification and the dissolved oxygen concentrations throughout the water profile indicate that stratification may persist for a period of several months, in calm hot conditions with low inflows. In the event of thermal stratification for extended periods, dissolved oxygen concentrations at the bottom of the lake may fall to zero (New South Wales Department of Land and Water Conservation 1998b).

1.3.3.5.3 Turbidity

All lakes in the Menindee Lakes Storage are turbid (generally > 50 NTU) (Scholz *et al.* 1999), which is due to the naturally highly turbid inflows from the Darling River and wind and wave action resuspending sediment in the large lakes (New South Wales Department of Land and Water Conservation 1998b).

Of the deflation lakes, Lakes Malta and Balaka were the most turbid lakes with turbidities of >999 NTU prior to drying in 1998 and Lake Cawndilla was the least turbid (50-150 NTU) (Scholz *et al.* 1999). The lower turbidity in Lake Cawndilla was probably due to the coarser sediment and less turbid inflows from Lake Menindee (compared with the Darling River) (Scholz *et al.* 1999).

The turbidity in Lake Wetherell is variable, during periods of high inflows the turbidity can exceed 200 NTU, however during periods of low on no inflows the turbidity can fall to below 20 NTU (Scholz *et al.* 1999).

The lakes exhibit a steep light gradient because of the high turbidity, which could restrict submergent macrophytes to the shallow fringes (Spence 1982; Chambers and Kalff 1987b; Chambers and Kalff 1987a; Middleboe and Markager 1997). However, the lakes are subject to water level fluctuations that result in frequent and aseasonal exposure of the sediment that will prevent the establishment of submergent species (Brock and Casanova 1997).

1.3.3.5.4 Electrical Conductivity

Due to the broad shallow morphology of the lakes and the hot dry climate, the Menindee Lakes are subject to high rates of evaporation. As a consequence of high evaporation, water stored in the lakes is subject to concentration of salts and thus increasing electrical conductivity, which can only be diluted during periods of high flows. Generally electrical conductivity increases downstream through the lakes (Table 1.5) (New South Wales Department of Land and Water Conservation 1998b).

Table 1.5: Results of salinity monitoring 1995-96 (*n*=12) (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998).

Site	Maximum EC μS cm^{-1}	Median EC μS cm^{-1}	Minimum EC μS cm^{-1}
Lake Wetherell inflow	331	268	151
Lake Wetherell outlet	948	356	160
Lake Pamamaroo	653	390	160
Lake Menindee	647	460	223
Lake Cawndilla outlet	1998	827	376

The largest changes in electrical conductivity occur in the small upstream lakes (Malta, Balaka and Bijiji) when the water level in Lake Wetherell falls below the sill level of the respective inlet creek (see Table 1.4 for elevations). Once the lake is isolated from Lake Wetherell, conductivity increases due to evaporative concentration. For example, the electrical conductivity in Lake Malta in August 1997 was 400 µScm^{-1}; in May 1998 just prior to its complete drying was over 9000 µScm^{-1} and after reflooding in August 1998 was 200 µScm^{-1} (Scholz *et al.* 1999).

Extreme changes in electrical conductivity of the surface waters of the Menindee Lakes would have been common prior to regulation. Maintaining the conductivity within a defined range could have a detrimental effect on species that are adapted to fluctuations in salinity and promote increases in numbers of taxa less tolerant to change (Scholz *et al.* 1999).

1.3.3.5.5 pH

The pH of all lakes is generally slightly alkaline (7.3 to 9.7) because of the dominance of bicarbonate ions (Scholz *et al.* 1999). The pH generally increases downstream within the lakes with Lake Cawndilla having the highest pH (New South Wales Department of Land and Water Conservation 1998b; Scholz *et al.* 1999). In water where the pH is greater than 8.8 over 80% of the inorganic carbon is present as bicarbonate not carbon dioxide, therefore plants must be able to utilise this form of inorganic carbon in order to photosynthesise whilst submerged (Kirk 1983). This can cause problems for submerged plants because not all plant species are able to utilise this form of inorganic carbon (Kirk 1983).

1.3.3.5.6 Nutrients

Total nitrogen concentrations in the Menindee Lakes exceeded the range of 0.10 to 0.50 mg N L^{-1} set out by ANZECC (Australian and New Zealand Environmental and Conservation Council 1992), however were generally below 2 mg N L^{-1} (Scholz *et al.* 1999). There is a tendency for total nitrogen concentrations to increase as the lakes dry, which was most pronounced in Lakes Malta, Balaka and Bijiji. The exception was Lake Cawndilla, where total nitrogen concentration declined during a drying event from 1997 to 1998 (probably due to net sedimentation of organic loads) (Scholz *et al.* 1999). Total nitrogen concentrations were reduced by reflooding (Scholz *et al.* 1999).

Available nitrogen (NO_2^-, NO_3^- and NH_3) concentrations were generally low in all of the lakes and accounted for less than 6% of the total nitrogen pool (Scholz *et al.* 1999). Significant increases in NO_2^- and NO_3^- were observed when sediments in Lake Malta were reflooded, which provides some evidence for a post flooding pulse of bio-available nitrogen (McComb and Qiu 1998) although no corresponding pulse of ammonia was observed (Scholz *et al.* 1999).

Total phosphorus concentrations also exceeded the ANZECC guidelines of 0.1 mg P L^{-1} in all of the lakes and in some cases exceeded 2.0 mg P L^{-1} (Scholz *et al.* 1999). The total phosphorus concentration increased as the lakes dried out in 1997-98 and subsequently decreased with inflows. Lake Tandure had the lowest and least variable total phosphorus concentrations of all the lakes (Scholz *et al.* 1999).

Bio-available or filterable reactive phosphorus (FRP) ranged from 1.3 to 96.6% of the total phosphorus pool. As drying progressed the ratio of FRP to total phosphorus decreased and reflooding reversed that trend (Scholz *et al.* 1999).

The atomic ratio of bio-available nitrogen to phosphorus in the surface water of the Menindee Lakes is generally below 2 which is far below the Redfield ratio of 16:1 indicating that the lakes are nitrogen limited (Scholz *et al.* 1999). Reflooding of sediments increased the concentration of nitrate and nitrite in Lake Malta, but even then the atomic ratio of nitrogen to phosphorus was below 5 (Scholz *et al.* 1999).

1.3.3.6 Sediments

Lakebed sediments vary between and within lakes (Scholz *et al.* 1999), although a texture gradient ranging from coarse sands at the high water mark (80-90% sand) to fine easily dispersible clays (75-95% clay) in the centre is evident in all of the deflation lakes (Appendix 1). Lake Wetherell has sediments that typically consist of 50% clay 20% silt and 30% sand, which are probably of riverine origin (Appendix 1). The primary sources of sediment input to the Menindee Lakes are the Woorinen formation that provides aeolian sand and the suspended load from the Darling River (Earth Tech Engineering 2002). Wave action resuspends the clays from the Darling River resulting in a sandy shoreline with the Darling River clay deposited in the centres of the lakes when they dry (Scholz *et al.* 1999; Earth Tech Engineering 2002).

Soil samples taken from the edges of the lakes have revealed much higher organic contents in sediments from Lakes Malta and Balaka (approximately 5% organic carbon) than from the other deflation lakes (Scholz *et al.* 1999). Growth of terrestrial vegetation on the dry lakebeds, the absence of flushing combined with evaporative water losses has resulted in the deposition of allochthonous and autochthonous organic matter in Lakes Malta and Balaka. Greater flushing frequencies combined with wind generated sediment suspension probably accounts for the lower organic carbon contents of the other deflation lakes (Scholz *et al.* 1999). The organic carbon content of Lake Wetherell sediments is not known.

1.3.3.7 Vegetation

Taylor-Wood *et al*. (2001) identified five broad categories for vegetation types within the areas subject to inundation of Menindee Lakes. These were further divided into 17 primary vegetation / habitat types:

Floodplain woodland: floodplain woodland (*Eucalyptus largiflorens*), floodplain woodland (*Eucalyptus camaldulensis*), rarely flooded woodland, woodland with lignum (*Muehlenbeckia cunninghamii*) and introduced species.

Shrubland: chenopod shrubland

Herb field / Sedges / Grasslands: sandy lake fringe, dry lakebed herb field / sedge land / grassland.

Freshwater Wetlands: shallow freshwater marsh, shallow freshwater marsh (dead trees), lignum swamp, dead trees with *Persicaria* and / or lignum.

Areas with little or no vegetation: open water lake, open water lake (dead trees), recently exposed lakebed, open water channel and inflow-outflow channel.

The vegetation present in the Menindee Lakes system at any one time is dependent on the water level of the system (Taylor-Wood *et al.* 2001). For the most part the larger lakes (Cawndilla, Menindee, Pamamaroo and Tandure) have areas of open water fringed by floodplain woodland consisting of either *Eucalyptus camaldulensis* or *Eucalyptus largiflorens* over storey (Taylor-Wood *et al.* 2001). These open water areas can become herbfields, grasslands or sedgelands when water levels are drawn down and vice versa when water levels increase.

Vegetation types in the smaller lakes and channels (including Lake Wetherell) tend to be more complex, supporting a greater number of vegetation types and not dominated by large areas of open water (Taylor-Wood *et al.* 2001). Similar to the large lakes the vegetation type will change with changing water levels.

A habitat mapping survey of the Menindee Lakes, undertaken by Taylor Wood *et al*. (2001) in January 2000, provided a snapshot of the vegetation types present and the area occupied by the different vegetation at the time of the survey. The aforementioned study recognised that the vegetation of the Menindee Lakes is dynamic and changes in response to season and water level changes (Taylor-Wood *et al.* 2001).

In January 2000 open water lake accounted for 51% of the vegetation / habitat mapped and surveyed (Taylor-Wood *et al.* 2001). Other major vegetation / habitat types present at the time were rarely flooded woodland (11%), open water lake (dead trees) (11%), floodplain woodland (*Eucalyptus camaldulensis*) (9%), floodplain woodland (*Eucalyptus largiflorens*) (4%) and shallow freshwater marsh (3%) (Taylor-Wood *et al.* 2001). During this study the lakes were at approximately 50% capacity with water levels rising (Figure 1.5, Figure 1.6 and Figure 1.7).

The dominant vegetation / habitat type in Lake Malta when surveyed was open water lake with smaller areas of shallow freshwater marsh, dry lakebed herbfield / sedge land / grassland, floodplain woodland (*Eucalyptus largiflorens*) and recently exposed lakebed around the edge (Taylor-Wood *et al.* 2001).

In Lake Balaka the dominant vegetation / habitat type was shallow freshwater marsh with smaller areas of recently exposed lakebed, lakebed herbfield / sedge land / grassland, floodplain woodland (*Eucalyptus largiflorens*) and floodplain woodland (*Eucalyptus camaldulensis*) present around the edges (Taylor-Wood *et al.* 2001). Around the edges there are also extensive stands of dead eucalypts that extend from the high water mark up to 500 m towards the centre of the lake in places.

Open water lake was the dominant vegetation / habitat type in Lake Bijiji with smaller areas of dry lake-bed herbfield / sedge land / grassland, sandy lake fringe, lignum, shallow freshwater marsh, recently exposed lake bed, floodplain woodland (*Eucalyptus camaldulensis*), floodplain woodland (*Eucalyptus largiflorens*) and open water (dead trees) present (Taylor-Wood *et al.* 2001).

Similarly the dominant vegetation / habitat type in Lake Tandure in January 2000 was open water lake. Smaller areas of open water lake (dead trees), sandy lake fringe and floodplain woodland (*Eucalyptus camaldulensis*) were also present (Taylor-Wood *et al.* 2001).

Lake Wetherell north of Lake Balaka was dominated by rarely flooded woodland with smaller areas of floodplain woodland (*Eucalyptus camaldulensis*), chenopod shrubland, woodland with lignum, open water channel, lignum, floodplain woodland (*Eucalyptus *largiflorens*), open water lake (dead trees), shallow freshwater marsh, dead trees with lignum and *Persicaria*, dry lake-bed herbfield / sedge land / grassland and inflow outflow channel (Taylor-Wood *et al.* 2001).

Lake Wetherell south of Lake Balaka was dominated by floodplain woodland (*Eucalyptus camaldulensis*) and shallow freshwater marsh (dead trees). Smaller areas of lignum, dead trees with lignum and *Persicaria*, rarely flooded woodland, open water channel, shallow freshwater marsh, dry lakebed herbfield / sedge land / grassland, floodplain woodland (*Eucalyptus largiflorens*), open water lake (dead trees) and woodland with lignum are also present (Taylor-Wood *et al.* 2001).

The dominant vegetation / habitat type in Lake Pamamaroo in January 2000 was open water lake with smaller areas of open water lake (dead trees), floodplain woodland (*Eucalyptus camaldulensis*), floodplain woodland (*Eucalyptus largiflorens*) and shallow freshwater marsh (Taylor-Wood *et al.* 2001). Sandy lake fringe and dry lakebed herbfield / sedge land / grassland are also present in Lake Pamamaroo when water the level is approximately 59.5 m AHD as it was in January 2000 (Figure 1.6).

The Pamamaroo-Menindee interconnecting channel and Copi Hollow Lake were dominated by open water lake and introduced species. Also present were smaller areas of dry lakebed herbfield / sedge land / grassland, floodplain woodland (*Eucalyptus camaldulensis*), open water channel, shallow freshwater marsh, lignum and recently exposed lakebed (Taylor-Wood *et al.* 2001).

Open water lake dominated the vegetation / habitat type in Lake Menindee. Also present in January 2000 were extensive areas of open water lake (dead trees) and smaller areas of dry lakebed herbfield / sedge land / grassland, sandy lake fringe, floodplain woodland (*Eucalyptus camaldulensis*), floodplain woodland (*Eucalyptus largiflorens*), shallow freshwater marsh and lignum (Taylor-Wood *et al.* 2001).

Speculation Lake, Morton Boolka Channel and Spectacle Lake were dominated by floodplain woodland (*Eucalyptus largiflorens*), open water lake (dead trees) and floodplain woodland (*Eucalyptus camaldulensis*). There were also extensive areas of open water lake and dry lakebed herbfield / sedge land / grassland, with smaller areas of recently exposed lakebed, sandy lake fringe, shallow freshwater marsh, lignum, open water channel and recently exposed lakebed (Taylor-Wood *et al.* 2001).

In January 2000, Lake Cawndilla was dominated by the vegetation / habitat type open water lake with extensive areas of dead eucalypts around the edges. Shallow freshwater marsh, sandy lake fringe, floodplain woodland (*Eucalyptus largiflorens*), lignum, floodplain woodland (*Eucalyptus camaldulensis*) and dry lakebed herbfield / sedge land / grassland were also present (Taylor-Wood *et al.* 2001).

The 17 different vegetation types identified by Taylor-Wood *et al.* (2001) are useful for descriptive and broad scale habitat mapping purposes, but not generally appropriate for ecological studies. These types of classifications concentrate on the dominant species and ignore factors such as life history traits and water regime preferences, which are important in studies of this nature. Classifying species into ecologically functional groups is more useful (sensu Brock and Casanova 1997) for this type of study because it gives an indication how species persist and how changes in water levels can change the plant communities.

With the exception of Taylor-Wood *et al.* (2001) there have been no investigations of the vegetation of the Menindee Lakes system. There is no information regarding the seed bank (density, species richness and composition), water regime requirements of the species present, recruitment from the seed bank, effect of water regime on vegetation dynamics, flooding tolerances of species present and impact of grazing. Knowledge of the vegetation dynamics is important for management of the system, which has been under review (New South Wales Department of Land and Water Conservation 1998b; New South Wales Department of Land and Water Conservation 1998a; New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998).

1.4 Thesis Outline and Objectives

This thesis investigates the vegetation dynamics of the Menindee Lakes with reference to the seed bank, recruitment from the seed bank, response of the seed bank and extant vegetation to different water regimes, water regime requirements of the species present and the effect of flooding on three common floodplain species. From this information, a conceptual model is proposed to predict the floristic composition expressed by the seed bank under different water regimes. The Menindee Lakes are an appropriate study because of their varied morphologies and hydraulic regimes from small lakes that dry frequently and are minimally impacted by regulation (e.g. Malta) to large semi-permanent and highly regulated lakes (e.g. Cawndilla).

Background information and specific objectives and hypotheses are described in the chapter introductions. Here a synopsis of the major objectives and hypotheses is given.

The objectives were addressed by two glasshouse trials, three pond experiments and one field study.

The first trial (Chapter 2) was a reconnaissance to determine the most efficient method of obtaining and assessing samples. This study investigated the density, species richness and floristic composition of the seed bank and zonation of these components with respect to elevation and location on the shoreline in Lakes Malta, Bijiji and Menindee.

The second trial (Chapter 3) developed the Reconnaissance, which showed that the zone of organic matter deposition (the strandline) was a site of seed concentration. The hypothesis that the strandline will have a denser, more species rich seed bank and inturn a different floristic composition was tested by comparing the strandline and adjacent sediment seed banks in Lakes Malta, Tandure, Menindee and Cawndilla. In addition, the seed bank strategy of the species present was determined by subjecting the samples to multiple wet and dry cycles.

The first pond experiment (Chapter 4) investigated the response of the seed banks of Lakes Malta, Balaka, Wetherell, Menindee, Cawndilla and Redbank Creek to static water levels (90 cm for 252 days), 1 cm day^{-1} drawdown and 5 cm day^{-1} drawdown in combination with three elevations +10 cm, -20 cm and -70 cm. The change in abundances of individual species over time was used to determine their water regime requirements for germination, and survival. This information was used to formulate a conceptual model (the seed bank recruitment model) that predicts the species present under different water regimes.

The field study (Chapter 5) investigated recruitment and vegetation change in Lakes Malta, Balaka, Wetherell, Menindee and Cawndilla as they were drawn down, with a series of surveys over 500 days. The study had three aims. The first aim was to test a model, which predicted that windows of opportunity for germination, growth and reproduction will open and close as water levels fall. The amount of time a window remains open will be dependent on the rate of drawdown. The second aim was to test the seed bank recruitment model formulated in Chapter 4. Due to low inflows, only the section of the model that deals with drawdown could be tested. The final aim was to investigate the relationship between floristic composition and soil moisture (at four depths), soil clay content, canopy cover, sediment exposure time, elevation and height of the quadrat relative to the water level

The second pond experiment (Chapter 6) was undertaken in response to extended drought in the Darling River catchment, which meant the effect of flooding on floristic composition could not be tested in the field. The aim of this experiment was to examine the response to flooding (relative growth rate, above to below-ground biomass and survivorship) of three common species from the Menindee Lakes (*Cyperus gymnocaulos, Ludwigia peploides* and *Xanthium occidentale*) with contrasting adaptations to flooding. Three hypotheses were tested: *Xanthium occidentale* will die when top-flooded for longer than two weeks. *Cyperus gymnocaulos* when top-flooded for two weeks will show no adverse effects but when top flooded for longer than four weeks above ground organs will senesce and resprout when water levels fall. *Ludwigia peploides* will increase above-ground biomass, when top-flooded to reach the water surface.

The final pond experiment (Chapter 7) was undertaken because results from Chapter 5 showed that factors other than water regime influenced plant recruitment. The experiment investigated the response of the Lake Malta seed bank to different water regimes and soil nutrient loadings by testing the hypothesis that different plant communities will develop from the same seed bank when subjected to different nutrient concentrations and the same water regime.

Chapter 8 presents a general discussion. Seed bank strategies, seed density and seed distribution patterns are summarised. The predictive model is presented, strategies of persistence employed by species present (avoidance, tolerance and response to flood or desiccation) were suggested and non-hydrological factors that may influence floristic composition discussed. The final section proposes a research agenda to further understanding of the vegetation dynamics of the Menindee Lakes and ephemeral systems in general.

2 Chapter 2: Reconnaissance Study

2.1 Introduction

Simpson *et al.* (1989) and Brock *et al.* (1994) emphasised the need for preliminary studies before embarking on a detailed study of seed banks. This is essential to determine the most efficient method of obtaining and assessing samples that are adequate in number and size to address the objectives of the study (Brock *et al.* 1994). Information regarding spatial patterns and concentrations of seed density, species richness, species composition, indicator species and the duration of wetting cycles are an essential platform for future work. None of this information was available for the Menindee Lakes; hence, a reconnaissance study was undertaken to aid in the design of subsequent investigations.

Seed banks are one strategy of ensuring the survival of plants through periods of unfavourable conditions for germination, growth and survival (e.g. van der Valk and Davis 1976; Thompson and Grime 1979; Keddy and Reznicek 1982; Leck 1989; Brock and Britton 1995; Leck and Brock 2000). In systems such as the Menindee Lakes, where large and often aseasonal water level fluctuations occur (Figure 1.5, Figure 1.6 and Figure 1.7), unfavourable conditions for germination, growth and survival can range from desiccation to deep flooding beneath several metres of highly turbid water. The seeds of resident plants must be able to remain viable whilst submerged or desiccated to enable species to exploit favourable conditions for germination and growth when they occur. Depending on the species, optimal germination conditions may persist for less than two weeks if the rate of drawdown is rapid (>5 cm day^{-1}) and temperatures are high.

As the Menindee Lakes are drawn down, the newly exposed sediment is bare with no evidence of submerged species (pers. obs.). The seeds of many floodplain, amphibious and terrestrial species germinate shortly after the sediment is exposed to the atmosphere. As the water level falls, the sediment surface dries and germination ceases. However, individuals that have established are able to access sub-surface water, and depending on the species, continue to grow and inturn replenish the seed bank. Germination on newly exposed sediment is ecologically advantageous because the sediment is moist and devoid of competitors. Therefore, the species present in the seed bank may be adapted to respond rapidly to favourable but ephemeral germination conditions.

Thompson (1992) stated that a common feature of communities that accumulate large seed banks is a regime of severe, unpredictable disturbances by fire, cultivation or large water level fluctuations. Therefore, it would be expected that the seed density of the lakes would exceed that of wetland systems that are not subject to such large and aseasonal water level fluctuations.

These observations and predictions formed the first aim, which was to investigate the following aspects of the seed banks of selected lakes in response to a single wetting:

1. Germination strategy (germination pattern through time)
2. Seed bank density (between lakes)
3. Species richness (between lakes)
4. Species composition (between lakes)

Indicator species analysis (Dufrene and Legendre 1997) was used in the comparison of the seed bank species composition between lakes to give an indication of which species characterise a particular lake. It was used extensively in this and succeeding chapters.

Multi response permutation procedures (MRPP) or non-parametric multivariate analysis of variance (NPMANOVA) can determine whether the species composition between two treatments or locations is statistically significantly different but it cannot give an indication of what has caused the difference (McCune and Grace 2002). Indicator species analysis can give an indication of which species characterise a particular treatment or location and therefore provide information to explain why there is or is not a statistically significant difference (McCune and Grace 2002). It combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (McCune and Grace 2002). A “perfect” indicator species of a particular group should be faithful to that group (always present) and exclusive to that group (never occurring in other groups) (McCune and Grace 2002). This test produces indicator values for each species in each group based on the standards of the prefect indicator. Statistical significance of each indicator value is tested by using a Monte Carlo (randomisation) technique, where the real data is compared against, in this study, 1,000 runs of randomised data (Dufrene and Legendre 1997).

Groups can be assigned based on experimental treatments, different sites or locations, levels of disturbance, categorical environmental variables, presence or absence of a target species, habitat types or groups defined by cluster analysis (Dufrene and Legendre 1997; McCune and Grace 2002).

A species that is deemed a non-significant indicator of a particular group is either:

Type A: Rare. The species is only found in one group but in low numbers. This species is faithful and exclusive to one group but present in such low numbers that it cannot be deemed a significant indicator with any confidence.

Type B: Widespread and abundant. The species is found in more than one group in high numbers. This species is not faithful or exclusive to any group and it cannot be deemed a significant indicator of any group.

Type C: Widespread and rare. The species is found in more than one group in low numbers. This species is not faithful or exclusive to any group and it cannot be deemed a significant indicator of any group.

Which category a non-significant species fits into can be determined by examination of the raw data. A non-significant indicator species therefore, may not be ecologically unimportant. Widespread species could be generalists (either rare or abundant) that can survive in a wide range of conditions and rare species could potentially require conservation.

Indicator species analysis was used, in this study, to illustrate the differences between the lakes with respect to species distribution. For example, whether a particular lake has several indicator species that makes its seed bank different from the others and whether there are species that are widespread across some or all of the lakes.

The zonation of lakeshore plants with respect to exposure and submergence is well documented in permanent lakes (e.g. Spence 1982). Moore and Keddy (1988) suggested that zonation was caused by differential germination at different depths and not differences in the composition of the seed bank. Welling *et al.* (1988a) reported that the zonation of marsh vegetation that developed during drawdown in Delta Marsh (Manitoba, Canada) was not the result of differences in the species composition of the seed bank. However, vegetation zonation patterns are not always the result of differential germination. Keddy and Ellis (1985) investigated the germination and recruitment response of 11 species, which in nature are found at different elevations, along a water level gradient. They found that six species showed a distinct response to water depth that explained their distribution in nature whereas the other species showed no response to water depth (Keddy and Ellis 1985). They concluded that biological interactions accounted for the distribution in nature of the species that showed shared responses (Keddy and Ellis 1985). Grace (1987) also reported that the zonation of *Typha domingensis* and *Typha latifolia* was not due to differences in germination with respect to water depth and that an extreme temporal advantage by either species can lead to extinction of the other species.

In some cases however, the differences in vegetation patterns observed in nature can be attributed to differences in the seed bank. For example, Leck and Gravline (1979) and Leck and Simpson (1994) found that the vegetation zonation patterns in a freshwater tidal marsh reflected the species composition of the seed bank. They suggested the reason for the seed bank zonation was secondary dispersal of seeds by the tidal movement of water (Leck and Simpson 1994).

In contrast to tidal freshwater wetlands, the water level fluctuations of the Menindee Lakes are large and aseasonal (Figure 1.5, Figure 1.6 and Figure 1.7) and probably do not influence the distribution of seeds to the same degree. Therefore, no zonation of seed density or species composition with respect to elevation for any of the lakes in this study is expected.

Spatial heterogeneity of seed banks is well documented (e.g. Roberts 1981; Bigwood and Inouye 1988; Benoit *et al.* 1989; Brock *et al.* 1994; Reinhardt *et al.* 2000; Grandin 2001) and may result in differences due to geographical location of the transect on the shoreline. Differences in seed bank composition, at different locations on the lakeshore, may also arise due to the accumulation and deposition of floating seeds on the lee shores (the northern and western shores). Nilsson *et al.* (1991b) reported that water borne seeds accumulated in areas where there are eddies and pockets of low flow, caused by snags or meanders. The shoreline complexity of the Menindee Lakes is generally low and devoid of snags, especially for the deflation lakes; therefore areas where water borne seeds may accumulate in greater numbers causing differences in the seed bank composition are few. Alternatively, zonation of seed density or species composition with respect to elevation or location may be present within the lakes but (due to spatial heterogeneity) may not be detectable unless a very large (impractical) number of samples are taken.

These observations and predictions formed the basis for the second aim, which was to determine whether there were distinct differences in the density, species richness and species composition of the seed bank in relation to elevation and geographical location within the lakes.

2.2 Methods

2.2.1 Study Sites

Sediment samples were taken from Lakes Malta, Bijiji and Menindee (Figure 2.1) in December 2000. These lakes were chosen because they exhibit different hydrology and morphology, were accessible by vehicle and located outside of Kinchega National Park. Lake Malta is the smallest and least impacted by regulation (Scholz *et al.* 1999). The lake is inundated for longer periods than before the scheme was initiated, however it is frequently the driest of all the lakes (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). Lake Bijiji, which is down stream of Lake Malta, is larger and inundated for longer periods than Lake Malta because of its proximity to the main weir (Scholz *et al.* 1999) (Figure 1.3). The maximum water level in the lake is also higher due to the influence of the main weir (New South Wales Department of Land and Water Conservation 1998b; New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998). When the water level in Lake Wetherell falls below the sill level of the inlet creeks of Lakes Malta and Bijiji, the lakes dry slowly due to evaporation (Scholz *et al.* 1999). Lake Menindee is the largest of the lakes and is impacted by regulation with increased water permanency and water levels (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). In comparison to Lakes Malta and Bijiji, Lake Menindee is more permanent (New South Wales Department of Land and Water Conservation Menindee Lakes Advisory Committee 1998; Scholz *et al.* 1999), the shoreline is subject to higher wave energy (Earth Tech Engineering 2002) and when water is released the water levels can fall up to 10 cm day^{-1} (when downstream demand for water is high) (New South Wales Department of Land and Water Conservation 2003).

2.2.2 Sediment Sampling Protocol and Seedling Emergence

Three replicate transects (*n* = 3), 50 m apart, were established on the north, west and south shores of Lake Bijiji (the eastern shore was inaccessible due to due to high river levels), perpendicular to the shoreline. National park regulations precluded sampling on all but the north shore of Lake Menindee. In Lake Malta transects were established on the north, south, east and west shorelines (Figure 2.1). Four elevations at 30 cm increments on each transect were sampled, two above the water level and two elevations below the water level (Figure 2.1 and Table 2.1). At each transect and elevation five 5 cm diameter cores, randomly located up to 5 m from the centre of the transect on either side, were taken to a depth of 5 cm and pooled.

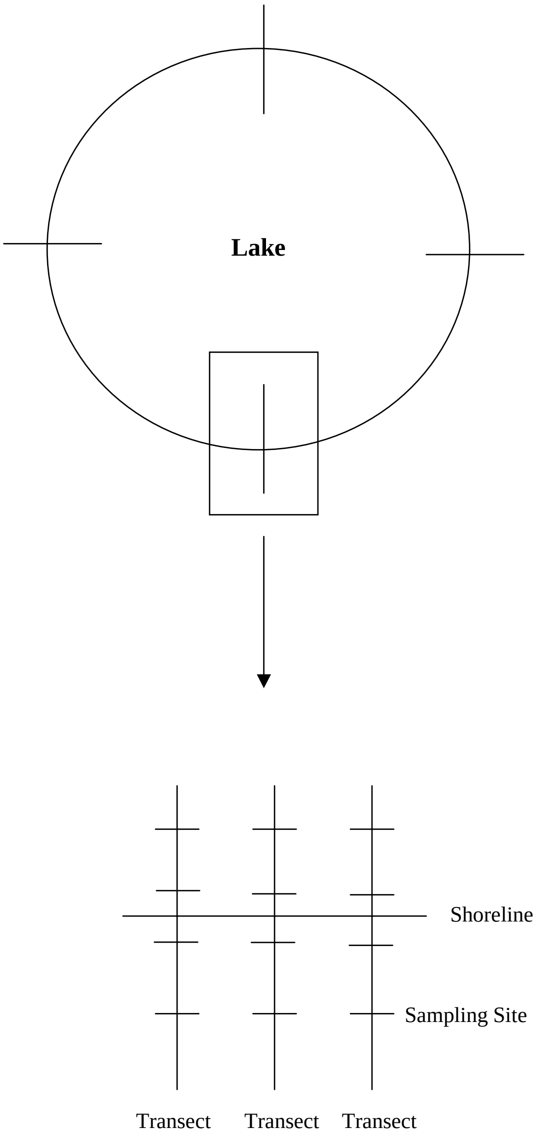

Figure 2.1: Sediment sampling transect locations.

Table 2.1: Sediment sampling elevations.

Malta	Bijiji	Menindee
61.32	61.32	60.32
61.02	61.02	60.02
60.72	60.72	59.72
60.42	60.42	59.42

The samples were transported to Adelaide and dried at 40 ºC to constant weight. Replicate sediment samples of 200 g were spread evenly over a base of 4 cm of 60-40 sandy loam contained in 170 x 115 mm plastic containers. Holes were drilled in the side of each container 10 mm from the bottom, which allowed water to drain. The samples were placed randomly in a glasshouse and watered daily. Temperature in the glasshouse ranged from 15 to 40° C and the day length ranged from 14 h 30 min to 11 h 50 min. In addition to the seed bank samples, 15 blanks consisting of only sandy loam were randomly placed amongst the samples to determine if there was any contamination in the sandy loam or from the glasshouse. Every two weeks seedlings were counted, identified and removed and the position of the samples in the glasshouse re-randomised. Seedlings that could not be identified were transplanted and grown to a stage at which they could be identified. The germination trial ran until germination had ceased in most samples and no new species were detected, which was 12 weeks after the initial watering.

2.2.3 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).

2.2.4 Data Analysis

The number of germinants was converted to seeds m^{-2} by calculating the bulk density of the sediment, then calculating the total mass of sediment for 1 m^{2} to a depth of 5 cm. The sediment from all lakes and elevations had a bulk density of 1.4 g cm^{-3}. This equated 70 kg of sediment m^{-2} for all lakes. Therefore, the formula for converting the number of germinants to seeds m^{-2} is:

$$\text{No. Seeds m}^{-2} = \text{No. Germinants x } \frac{\text{Mass of Sediment m}^{-2}}{\text{Sample Mass}}$$

Differences in seed densities within Lakes, Malta and Bijiji were analysed with two-factor analysis of variance (transect, elevation and transect x elevation) and in Lake Menindee with a single factor analysis of variance (elevation). Data from Lakes Malta and Bijiji were log transformed. Normality was tested using the Shapiro-Wilk W test and equality of variances with the Levene test. Power and least significant number (LSN) were calculated for each ANOVA. Least significant number denotes the minimum number of extra samples required to detect a statistically significant difference, if that significant difference does exist. All univariate statistical tests were performed using the package JMP In version 3.2.6 (SAS Institute Inc. 1996).

Differences in seed bank composition between the lakes were analysed using NMS ordination, multi response permutation procedures (MRPP) and indicator species analysis

(Dufrene and Legendre 1997). The aforementioned tests were undertaken using the package PCOrd version 4.28 (McCune and Mefford 1999). MRPP was used in preference to NPMANOVA due to unbalanced sample sizes. Differences in seed bank composition between elevation and transect within Lakes Malta and Bijiji were analysed using NMS ordination and two-way non-parametric multivariate analysis of variance (NPMANOVA) (transect, elevation and transect x elevation). The differences in seed bank composition between elevations for Lake Menindee were analysed with NMS ordination and one-way NPMANOVA (elevation). NPMANOVA was undertaken using the procedure described by Anderson (2001). Bray-Curtis distances were used to calculate the similarity matrix for all multivariate statistical analyses (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 NMS ordinations so the ordinations were less cluttered, however MRPP, indicator species analysis and NPMANOVA were performed on unpooled data. For all statistical tests $\alpha = 0.05$.

2.3 Results

2.3.1 Germination Strategy

In all lakes the majority of the germination occurred during the first two weeks after the initial watering (Table 2.2). Over 90% of the total numbers of germinants were detected by week six, after which germination slowed dramatically or stopped (Table 2.2).

Table 2.2: Mean number of germinants from the seed bank of each lake (seeds m^{-2} ± 1 S.E.) for weeks zero to two, two to six and six to twelve after the initial watering.

	Week 0-2		**Week 2-6**		**Week 6-12**	
Lake	**X**	**S.E.**	**X**	**S.E.**	**X**	**S.E.**
Malta	7219	1113	6511	1760	743	236
Bijiji	8828	1738	2985	729	258	78
Menindee	88	29	58	34	0	0

2.3.2 Seed Bank Density

Seed density in Lake Malta was independent of elevation and location of the transect on the lakeshore (Table 2.3 and Figure 2.2). The northern shore of Lake Bijiji had a significantly lower seed density than the other two locations but there was no significant difference between the numbers of seeds in the seed bank at each elevation (Table 2.4 and Figure 2.3). Lake Menindee showed no significant differences between elevations (ANOVA: $F_{3,\,8}$ =

0.25, *P* = 0.859, Power = 0.08, LSN = 129) (Figure 2.4). For each lake there was a large degree of within sample variability (Figure 2.2, Figure 2.3 and Figure 2.4) and where no significant differences were detected the power of the ANOVA was very low (Table 2.3 and Table 2.4).

Table 2.3: *F* statistics, power and least significant number (LSN) values obtained from comparisons of seed bank density for each transect and elevation from Lake Malta.

Factor	*df*	*F*	*P*	*Power*	*LSN*
Transect	3, 32	2.43	0.084	0.55	57
Elevation	3, 32	2.08	0.123	0.48	65
Transect x Elevation	9, 32	1.77	0.113	0.68	58

Table 2.4: *F* statistics, power and least significant number (LSN) values obtained from comparisons of seed bank density for each transect and elevation from Lake Bijiji.

Factor	*df*	*F*	*P*	*Power*	*LSN*
Transect	2, 24	4.10	0.03	-	-
Elevation	3, 24	1.55	0.228	0.35	65
Transect x Elevation	6, 24	1.94	0.114	0.59	45

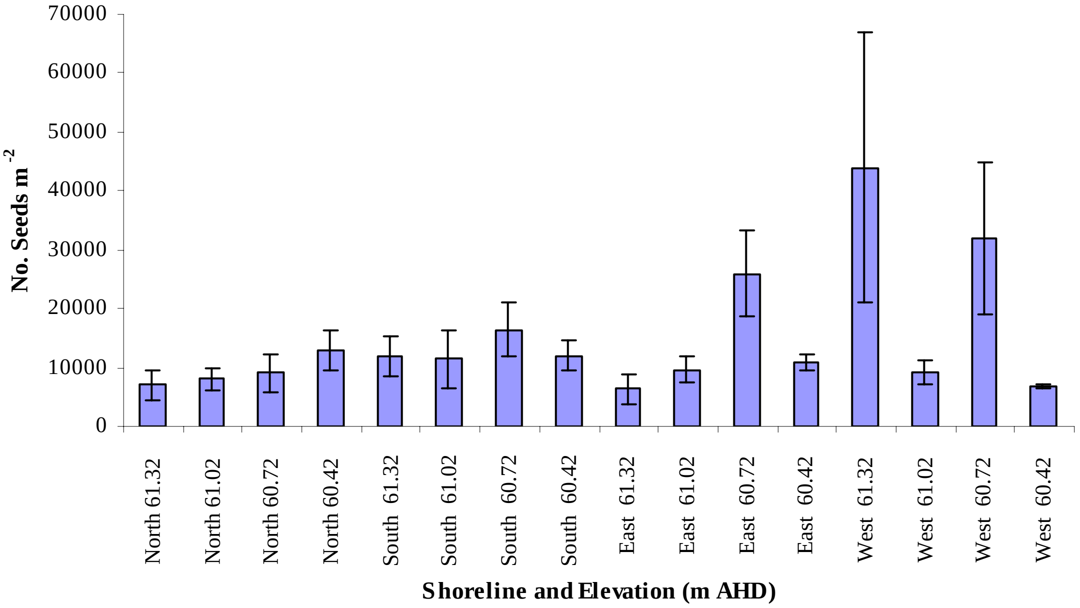

Figure 2.2: Total number of seeds m^{-2} in the Lake Malta seed bank (error bars = ± 1 S.E.)

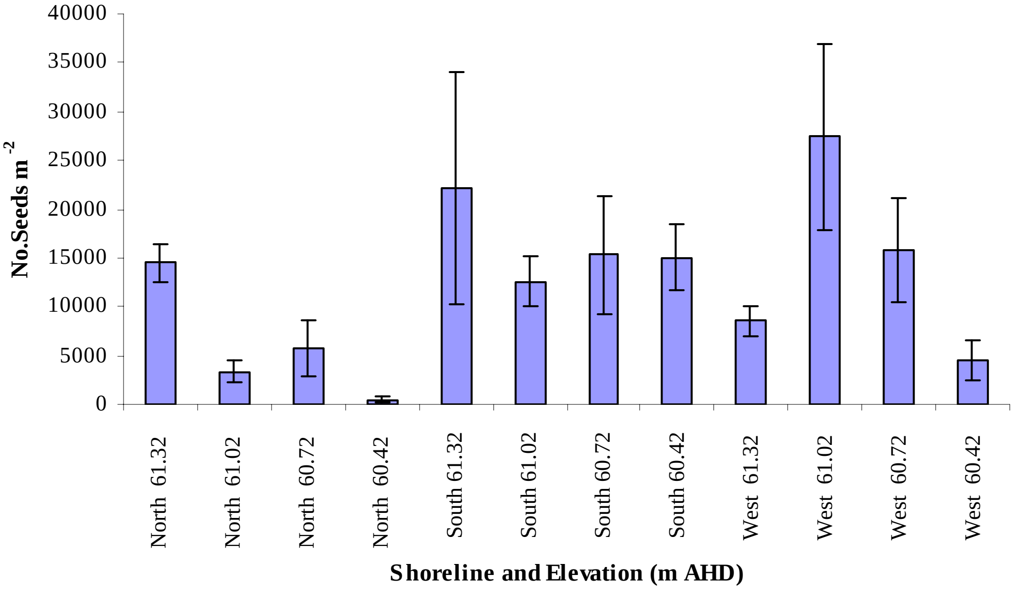

Figure 2.3: Total number of seeds m^{-2} in the Lake Bijiji seed bank (error bars = ± 1 S.E.)

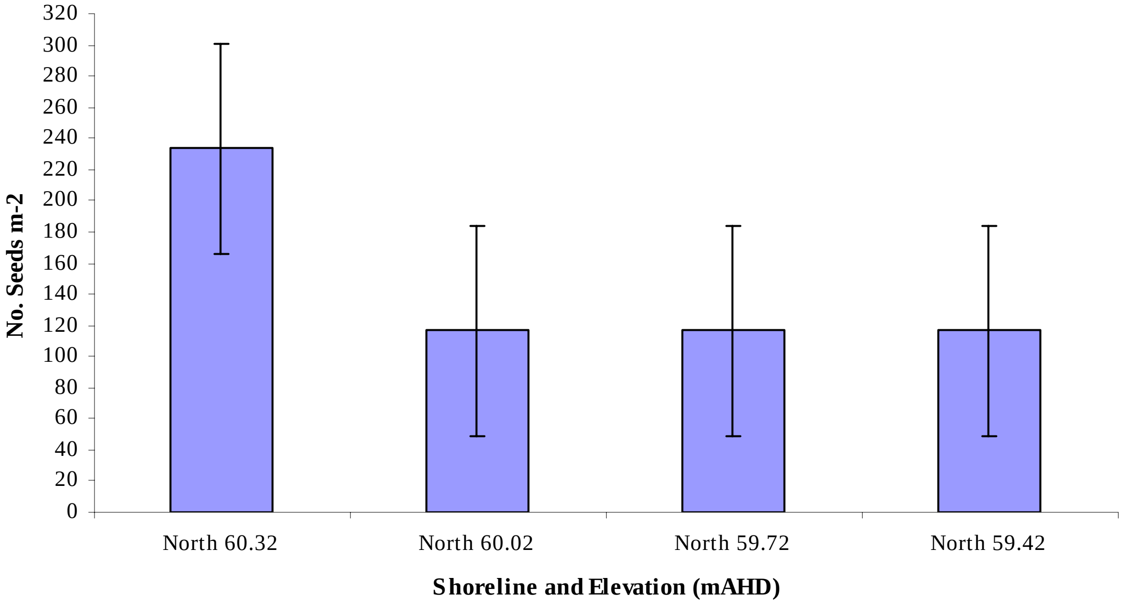

Figure 2.4: Total number of seeds m^{-2} in the Lake Menindee seed bank (error bars = ± 1 SE)

2.3.3 Species Richness

Species richness within lakes appeared independent of elevation or location (Figure 2.5 and Figure 2.6). The greatest number of species detected at one sampling site was 14, which occurred in two sites in Lake Malta, and one site in Lake Bijiji (Figure 2.5 and Figure 2.6).

The lowest number of species was two, recorded on the northern shore of Lake Bijiji at an elevation of 60.42 m (AHD) (Figure 2.6).

Twenty-four species were detected in the seed banks from all of the lakes sampled. The Lake Malta seed bank had the greatest species richness with 23 species, Lake Bijiji had 21 species present and Lake Menindee had the lowest species richness with only *Epaltes australis* detected at each elevation.

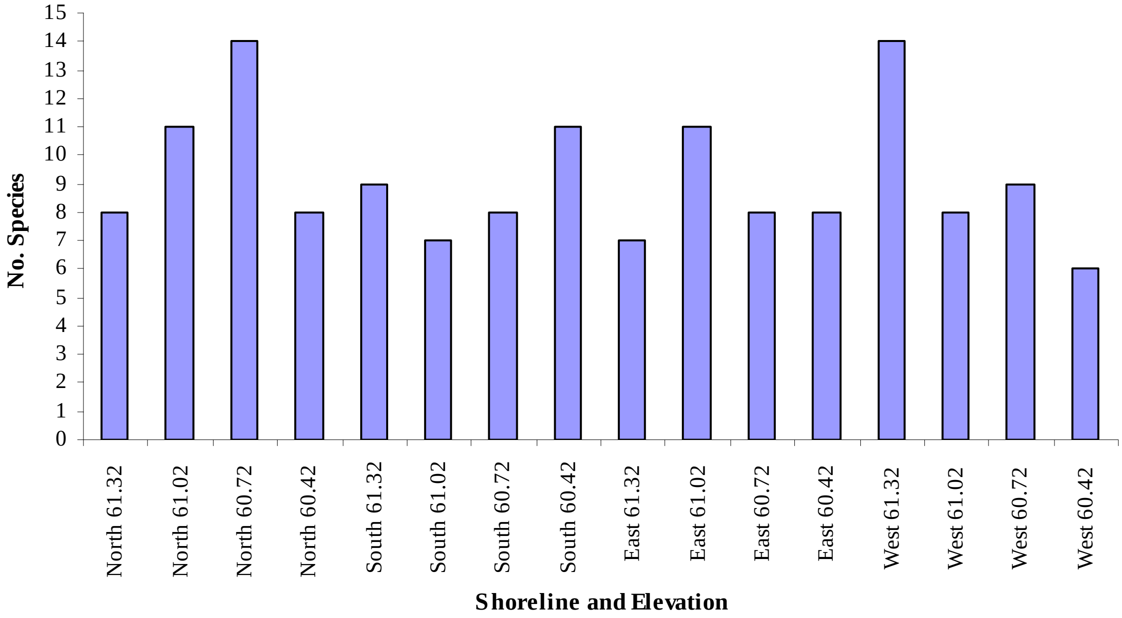

Figure 2.5: Lake Malta seed bank species richness.

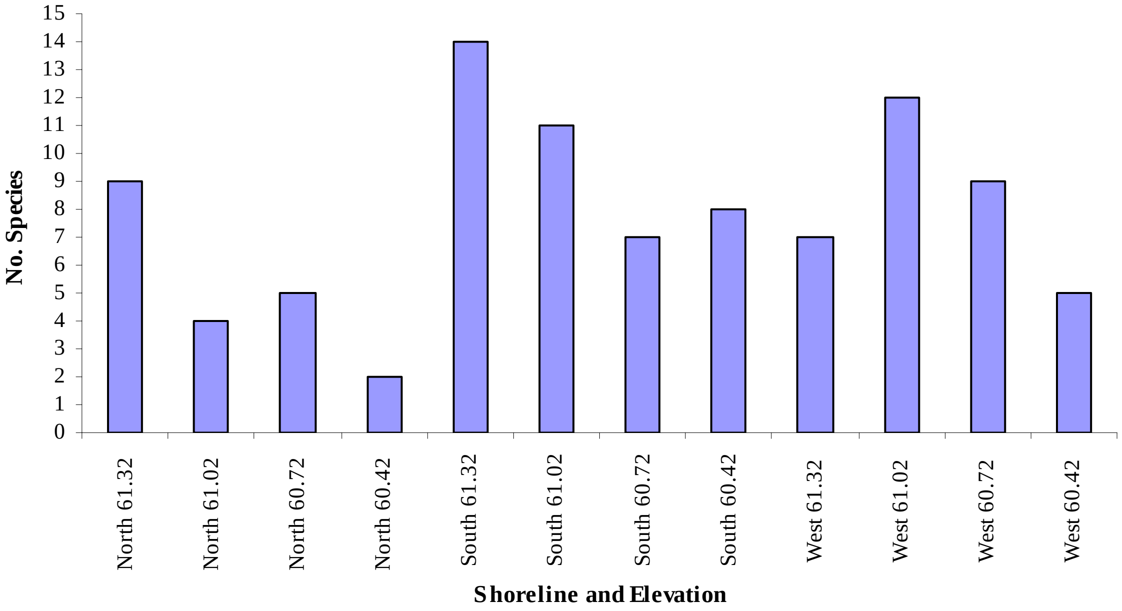

Figure 2.6: Lake Bijiji seed bank species richness.

2.3.4 Species Composition

The species composition of the Lake Menindee seed bank was significantly different from Lakes Malta and Bijiji (MRPP: $A = 0.25$, $P < 0.0001$). The NMS ordination of the samples from all the lakes showed that Lake Menindee formed a distinct group on the left hand side of the ordination plot (with one outlier from Lake Bijiji) (Figure 2.7). Seed density (Figure 2.4) and species richness of the Lake Menindee seed bank was extremely depauperate in comparison to Lakes Malta and Bijiji. Lakes Malta and Bijiji appeared to form a relatively tight single grouping (with a single outlier) (Figure 2.7), however when analysed without the Lake Menindee data the seed bank composition of these two lakes was significantly different (MRPP: $A = 0.03$ $P = 0.021$).

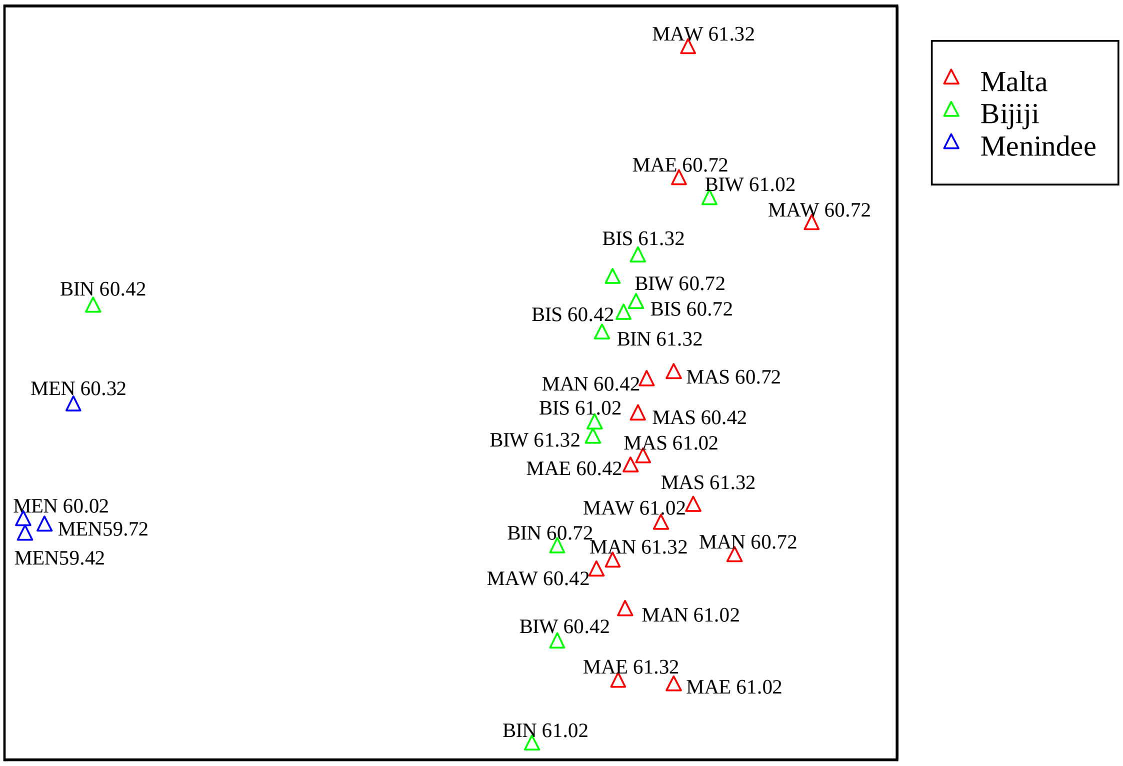

Figure 2.7: NMS ordination of all sampling locations in Lakes Malta, Bijiji and Menindee (stress = 18.9%) (MA = Lake Malta, BI = Lake Bijiji, ME = Lake Menindee, N = North, S = South, E = East, W = West and 59.42 - 61.32 = Elevation m AHD).

Chenopodium pumilio, Morgania floribunda and *Sporobolus mitchelli* were significant indicators of the Lake Malta seed bank (Table 2.5). Four species that were not significant were rare (Type A) with the majority of the species widespread over Lakes Malta and Bijiji (Types B and C) (Table 2.5). The only species that was common to all lakes was *Epaltes australis*, which was the only species detected in the Lake Menindee seed bank.

Table 2.5: Indicator species analysis results comparing the seed bank species composition of Lakes Bijiji, Malta and Menindee (Type A, B or C denotes why the species was not a significant indicator).

Species	Lake	*P*
Alternanthera denticulata	Bijiji	0.067 (Type C)
Centipeda minima	Bijiji	0.224 (Type B)
Eragrostis australiensis	Bijiji	0.574 (Type C)
Euphorbia drummondii	Bijiji	1.00 (Type A)
Gnaphalium luteo-album	Bijiji	0.447 (Type B)
Haloragis aspera	Bijiji	0.096 (Type C)
Iseotopsis graminifolia	Bijiji	0.367 (Type B)
Isolepis australiensis	Bijiji	0.568 (Type C)
Limosella australis	Bijiji	0.744 (Type B)
Medicago spp.	Bijiji	1.00 (Type A)
Alternanthera nana	Malta	1.00 (Type A)
Ammania multiflora	Malta	0.191 (Type C)
Chenopodium pumilio	Malta	0.012
Cyperus gymnocaulos	Malta	0.135 (Type C)
Epaltes australis	Malta	0.369 (Type B)
Eragrostis dielsii	Malta	0.211 (Type C)
Galenia secunda	Malta	0.222 (Type C)
Glinus lotoides	Malta	0.607 (Type C)
Heliotropium curassivicum	Malta	0.424 (Type C)
Juncus aridicola	Malta	1.00 (Type A)
Mollogo cerviana	Malta	0.514 (Type B)
Morgania floribunda	Malta	0.01
Polygonum plebium	Malta	0.719 (Type B)
Sporobolus mitchelli	Malta	0.004

No significant pattern in seed bank composition between elevation and transect location on the shoreline for Lake Malta was detected (NMS ordination: Figure 2.8, NPMANOVA: Table 2.6). Three samples were separated from the main group (Figure 2.8) because they had larger numbers of germinants than the other samples (Figure 2.2).

Table 2.6: NPMANOVA *F* statistics obtained from comparisons of seed bank species composition for each transect and elevation from Lake Malta.

Factor	*df*	*F*	*P*
Transect	3, 32	1.31	0.159
Elevation	3, 32	1.35	0.148
Transect x Elevation	9, 32	1.85	0.128

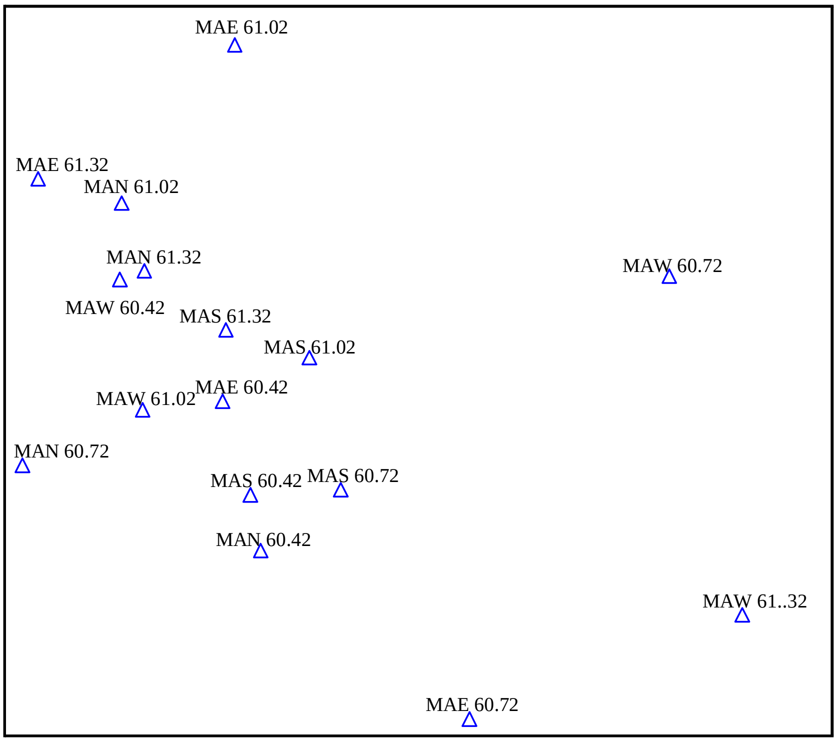

Figure 2.8: NMS ordination of all sampling locations in Lake Malta (Stress = 6.8%) (for explanation of labels see Figure 3.11).

No pattern in seed bank species composition with respect to elevation or shoreline was detected in Lake Bijiji (NMS ordination: Figure 2.9). The outlier at the bottom of the ordination plot (North 60.42) had only two species; *Epaltes australis* and *Glinus lotoides* (Figure 2.6) in extremely low numbers (Figure 2.3). The two factor NPMANOVA however, detected a statistically significant difference between the different transect locations with no significant differences between elevations (Table 2.7).

Table 2.7: NPMANOVA *F* statistics obtained from comparisons of seed bank species composition for each transect and elevation from Lake Bijiji.

Factor	***df***	***F***	***P***
Transect	2, 24	3.14	0.003
Elevation	3, 24	1.99	0.254
Transect x Elevation	6, 24	2.32	0.111

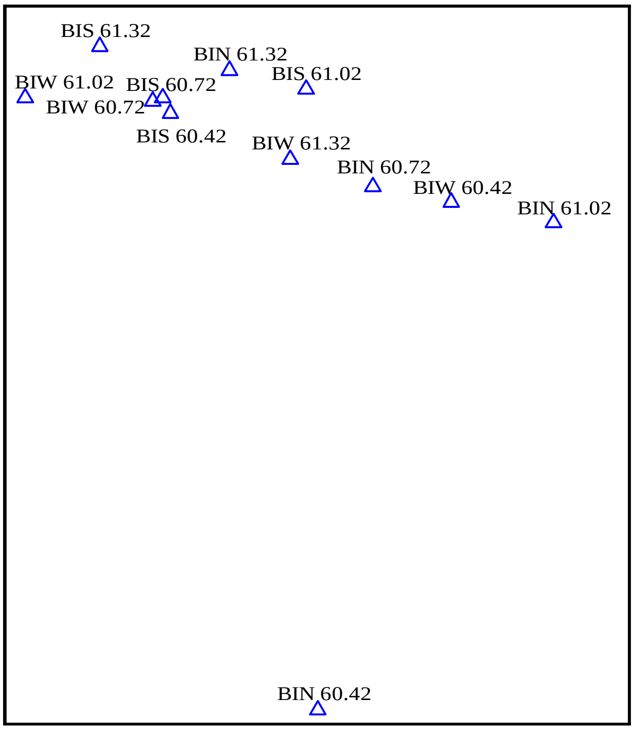

Figure 2.9: NMS ordination of all sampling locations in Lake Bijiji (Stress = 7.3%) (for explanation of labels see Figure 2.7).

No difference in seed bank composition between the different elevations was detected in Lake Menindee.

2.4 Discussion

2.4.1 Germination Strategy

Most seeds germinated within the first two weeks (Table 2.2), which is probably an adaptation to ephemeral environments. A corresponding decrease in germination from the seed bank was not reported for a cold temperate permanent lake in North America, where the germination rate had not slowed appreciably after 60 days (Haag 1983). Similarly, germination occurred at the rate of 1,564 to 1,853 germinants m^{-2} $week^{-1}$ after 16 weeks from the seed banks of southern Australian seasonal wetland (Nicol *et al.* 2003).

Jones and Sharitz (1989) suggested that early germination for trees in deciduous floodplain forests was advantageous because light intensity was greater before the canopy closed over. Therefore, the ability to germinate and establish quickly when conditions are favourable could be advantageous, especially if the sediment surface dries but there is still subsurface water. If rapid drawdown results in low subsurface moisture or the sediment is inundated, seedlings will die before maturity and not replenish the seed bank. Therefore, species that bet hedge will have an advantage over those that do not. Leck and Brock (2000) demonstrated that all species present in the seed bank of a temporary wetland in the New South Wales northern table lands (Australia) bet hedged.

2.4.2 Seed Bank Density

Generally, the seed banks of the lakes sampled were of comparable density to the seed banks of other Australian wetland systems, with the exception of Lake Menindee. For example, in a South Australian seasonal wetland 20,000 to 90,000 seeds m^{-2} were detected (Nicol *et al.* 2003), seed banks of a floodplain in the Northern Territory had 3,800 to 15,400 seeds m^{-2} (Finlayson *et al.* 1990). However, McIntyre (1985) showed the seed banks of rice fields on the Murrumbidgee floodplain were extremely large containing 100,000 to 300,000 seeds m^{-2}.

The seed banks of Lakes Malta and Bijiji generally had a higher seed density than overseas wetland systems. For example, Brock and Rogers (1998) found 1,300 seeds m^{-2} in the seed bank of the Nyl River floodplain in South Africa, the sediment seed bank of a North American cold temperate lake ranged from 0 to 2335 seeds m^{-2} (Haag 1983). Leck and Simpson (1995) reported seed densities of 707 to 4,607 seeds m^{-2} in a freshwater tidal marsh in north-eastern USA, Le Page and Keddy (1998) estimated that the seed density of beaver ponds was 2,300 seeds m^{-2} and van der Valk and Davis (1978) reported seed densities ranging from 21,445 to 42,615 seeds m^{-2} in prairie glacial marshes in the USA.

Similarly, the seed banks of terrestrial systems are extremely variable (Roberts 1981). In cultivated systems the numbers of viable seeds in the soil was generally higher than those detected for Lakes Malta and Bijiji (typically 70,000 to 80,000 seeds m^{-2}, with values as high as 500,000 seeds m^{-2} reported) (Roberts 1981). In low disturbance systems, dominated by long-lived species, such as forests and woodlands the numbers of seeds were generally lower (< 5,000 seeds m^{-2}) (Roberts 1981; Brown 1992).

A possible explanation of the low seed density from the Lake Menindee in comparison to the other lakes is that the northern shoreline of Lake Menindee is exposed to the prevailing south-westerly winds and at times is subject to waves over 50 cm high. These waves can re-suspend seeds in the water column and deposit them in other locations or uproot newly germinated seedlings, prevent establishment and in turn deplete the seed bank. The negative impact of increased wave action on the establishment and growth of lakeshore plants has been documented in studies from North America (Wilson and Keddy 1985b; Foote and Kadlec 1988; Coops and Van der Velde 1996; Doyle 2001) and New Zealand (Riis and Hawes 2003).

Large numbers of seeds were detected in three samples from lake Malta (East 60.72, West 61.32 and West 60.72) (Figure 2.2); visually these samples appeared to contain large amounts of coarse organic debris. The organic debris had probably been either deposited or concentrated by the action of waves or seiches, or stranded when water levels receded after floods. These “strandlines” could be extremely important with regard to the vegetation dynamics of the Menindee Lakes, especially if the surrounding sediment seed bank is depauperate. Seed rich strandlines have been recorded in the Vindel River (Sweden) where 189,181 seeds m^{-2} were detected in the strandlines following a spring flood (Nilsson and Grelsson 1990), and in the Schiermonnikoog Salt Marsh (The Netherlands) where a more than twofold increase in the number of seeds was detected in the strandline than in the surrounding sediment (Wolters and Bakker 2002). Strandlines were observed in all lakes, however the sampling strategy only resulted in them being sampled in Lake Malta.

The seedling emergence technique, used in this study, generally underestimates seed bank density when compared to methods where the seed is separated from the soil or sediment (Roberts 1981; Gross 1990; Brown 1992). The seedling emergence technique does have advantages over seed separation techniques because it only detects viable seed (tetrazolium staining is required to conclusively determine viability when using seed separation techniques), is less labour intensive, plants are easier to identify and does not discriminate against small seeded species (Roberts 1981; Gross 1990; Brown 1992). The seedling emergence technique was chosen for this study because many of the species present in the extant vegetation have small (less than 1 mm in diameter) seeds (e.g. *Epaltes australis, Gnaphalium luteo-album, Sporobolus mitchelli, Centipeda minima, Glinus lotoides, Chenopodium pumilio* and *Morgania floribunda*), which could be easily missed by seed separation techniques.

No zonation of the seed bank density with respect to elevation was observed in any of the lakes. Power analysis suggested that the number of samples required to detect a significant difference are much greater than the three taken. The number of samples required to detect a difference in seed bank density at the different elevations was impractical, however it does highlight that the seed bank is spatially variable.

There were no differences detected for Lake Malta with respect to the geographic location of the transect on the shoreline. Power analysis also showed that if there were significant differences in seed bank density between the different transect locations the number of samples taken was not sufficient for detection. The northern shore of Lake Bijiji had a significantly lower seed bank density than the other transects (Figure 2.3). The north-south axis of Lake Bijiji is approximately 7 km long, which during southerly or south-westerly winds, is probably sufficient fetch for the generation of destructive waves. Therefore, the same explanation for the low seed bank density for Lake Menindee may apply here.

2.4.3 Species Richness

The species richness of Lakes Malta and Bijiji were lower than other studies from Australia. For example, Nicol *et al.* (2003) detected a total of 28 species from a seasonal wetland in South Australia, Finlayson *et al.* (1990) reported 33 species from a Northern Territory creek floodplain, Britton and Brock (1994) identified 68 species and Brock *et al*. (2003) 73 species from the seed banks of temporary wetlands in the New South Wales northern tablelands.

Studies from overseas generally yielded lower numbers of species compared to those of Lakes Malta and Bijiji. For example Brock and Rogers (1998) found a total of 18 species from the Nyl River floodplain, LaDeau and Ellison (1999) detected 14 species in a north-eastern US tussock swamp, ter Heerdt and Drost (1994) reported 22 species from an emergent macrophyte dominated marsh in the Netherlands, Leck and Graveline (1979) found 22 species in a tidal freshwater marsh in north-eastern USA, Le Page and Keddy (1998) reported 37 species from Canadian beaver ponds and van der Valk and Davis (1976) found 23 species from prairie glacial marshes in the USA.

There were no patterns in species richness with respect to elevation or transect location in all the lakes sampled. This may be due to the low power of the study or small area of the lake sampled.

Species richness may also have been underestimated in this study because the seedling emergence technique was used with only one wetting cycle. Brock and Rogers (1998) found two species, not detected in the first wetting cycle, when they subjected the seed bank of the Nyl River floodplain (South Africa) to a second wetting cycle. Therefore, species may have gone undetected in this study. In future studies to determine the species richness of the seed bank more than one wetting cycle may be required (sensu Brock and Rogers 1998; Leck and Brock 2000).

2.4.4 Species Composition

The species composition of the seed banks differed significantly between lakes. The low species richness and seed density was the reason Lake Menindee differed from Lakes Malta and Bijiji. The differences between Lakes Malta and Bijiji were not as clear, most of the species deemed non-significant by indicator species analysis were common to the seed banks of both lakes (Type B and C species); however, the Lake Malta seed bank had three significant indicator species whereas Lake Bijiji had none (Table 2.5).

Epaltes australis, Centipeda minima, Gnaphalium luteo-album and *Morgania floribunda* accounted for over 80% of the total number of germinants from the seed banks of Lakes Malta and Bijiji. A similar situation to the references mentioned above where less than five species accounted for over 80% of germinants.

Only one exotic taxon (*Medicago* spp.) occurred in the seed banks. Lakes Bijiji and Malta are both grazed by domestic stock when dry and annual medics have been sown by the landholders in both lakes to provide high nutrition pasture (D. Barnes pers. com.). Few studies from freshwater and terrestrial systems indicate the number of exotic species. However, Nicol *et al.* (2003) reported seven exotic species (28 species total) in the seed bank of a seasonal southern Australian wetland, Brock and Casanova (1997) identified eleven exotics (60 species total) and Casanova and Brock (2000) twelve exotics (72 total) from the seed banks of northern New South Wales temporary wetlands. The only exotic species in the seed banks of Lakes Malta and Bijiji, was found in low numbers (0-700 seeds m^{-2}). In contrast, exotic species accounted for 20 to 42% of total number of seeds found by Nicol *et al.* (2003) and for the other two aforementioned studies seed densities for all species were not reported. In terrestrial systems where disturbances are common, such as arable land, pest plants can numerically dominate the soil seed bank (Roberts 1981; Thompson 1992).

2.4.5 Implications for Future Studies

The extremely low power of this study indicated that three replicates were inadequate and more need to be taken in subsequent studies. However, the number of replicates suggested by power analysis is impractical and would require an enormous amount of labour and glasshouse space. In the succeeding chapters, a compromise between the number of samples needed for adequate statistical power and logistical considerations (such as glasshouse space) was reached (usually $n = 15$).

The timing of the sampling in this study probably had little impact on seed density and the floristic composition of the seed bank with respect to the Strandline Study (Chapter 3). The lakes were at close to regulated capacity for both studies (Figure 1.5 and Figure 1.7) and the species present at and around the sampling areas were perennials, most of which had flowered (pers. obs.).

Despite the tendency to underestimate seed density and species richness, the seedling emergence technique is the most effective method. The seeds of the most common species are very small (which could be easily missed by seed separation), it is less labour intensive (especially since a much larger number of samples is required for future studies), only detects viable seed and species are easier to identify (Roberts 1981; Benoit *et al.* 1989; Gross 1990). The 12-week duration of wetting appeared to be adequate as germination had slowed or ceased in all cases. A single wetting cycle is probably not adequate because it is unlikely that all the conditions required to break dormancy for all species have been met. This can be overcome by subjecting the seed bank to at least two wetting cycles (sensu Brock and Rogers 1998; Leck and Brock 2000). By subjecting the seed bank to at least two wetting cycles also gives an indication of which species bet hedge.

Whilst the seed bank was spatially variable, the results provided some evidence that seeds may be concentrated around the edges of the lakes in strandlines.

3 Chapter 3: Strandlines

3.1 Introduction

Strandlines are mounds of organic debris deposited on the shorelines of water bodies. They are formed by the sorting and deposition action of waves or seiches (especially in large lakes) as water levels fall. In the Menindee Lakes strandlines form multiple, discontinuous rings around the lake edges (Figure 3.1). Evidence suggests that strandlines are areas where seeds are concentrated (Chapter 2) and provide optimal conditions for germination and recruitment (Figure 3.1).

Large numbers of seeds in strandlines have been reported from the Vindel River (Sweden) (Nilsson and Grelsson 1990) 189,181 seeds m^{-2}) and from the Schiermonnikoog Salt Marsh (The Netherlands) (Wolters and Bakker 2002). Ignaciuk and Lee (1980) suggested the strandline is a highly unstable and mobile habitat where wave action can cause dramatic changes by obliterating some communities, but replenishing others by carrying seed from other sources. Jacobs *et al*. (1994) reported that the seeds of the invasive shrub *Ludwigia peruviana* were more prevalent in areas where there was an accumulation of organic matter than in areas of bare sand in eastern Australian coastal wetlands.

Green (1999) investigated the species composition of stranded propagules on tropical beaches on Christmas Island and reported that two thirds of the species were not locally derived and Smith (1990) found that most of the propagules present in the driftlines on beaches from Viti Levu (Fiji) were capable of floating for long periods. Nilsson *et al*. (2002) demonstrated that species with long, floating propagules had higher abundances along lakeshores and tranquil reaches than species with short, floating propagules and suggested that the differences in distribution were due to differences in buoyancy properties. Wolters and Mineke (2002) suggested that floating propagules became stranded by ebb tides and these and organic debris formed strandlines in salt marshes. Cellot *et al*. (1998) reported that strandlines deposited by spring floods in the Rhone River were composed of a combination of redistributed propagules from the existing propagule bank and new vegetative dispersal units.

Ignaciuk and Lee (1980) suggested that the recruitment of four annual strandline species was the result of the presence of larger numbers of seeds and the strandline providing a more suitable habitat for germination and establishment than the surrounding sediment. However, it is possible that the non-seed component of the strandline could inhibit germination of many species (van der Valk 1986; Facelli and Pickett 1991). Seeds buried under the strandline (especially small seeded species) may not have the carbohydrate reserves to emerge or receive cues to break physiological dormancy, such as light (Simpson *et al.* 1989). In systems where there are large, unpredictable and rapid changes in water levels and the sediment has limited water-holding capacity, the non-seed component of the strandline could act as mulch. Observations of the strandlines in the field from the large lakes (Cawndilla, Menindee, Pamamaroo and Tandure) tend to support this because plant recruitment appeared to be higher in the strandline than the surrounding sediment (Figure 3.1), although this may be due to larger numbers of seeds in the strandline when compared with the surrounding sediment.

Leck and Brock (2000) demonstrated that all species in the seed banks of temporary and semi-permanent wetlands on the New South Wales northern tablelands bet hedged (Thompson and Grime (1979) type III or IV seed banks). Thompson (1992) stated that communities that accumulate large persistent seed banks are associated with habitats that experience severe regimes of unpredictable disturbances by fire, cultivation or large water level fluctuations. In aseasonal systems with large water level fluctuations, such as the Menindee Lakes, species that have persistent seed banks would have an advantage over species that do not bet hedge because of their ability to persist through “false starts”. If conditions suitable for germination are followed by unfavourable conditions for growth and survival that do not allow the plant to reach sexual maturity and the seed bank is not replenished, species that do not bet hedge will be extirpated from the system.

This study had three aims; the first was to test the hypothesis that strandline will have a larger and more species rich seed bank than the adjacent sediment.

The second was to test the hypothesis that the strandlines form favourable microhabitats for plant recruitment.

The third aim was to test the hypothesis that the seed bank will only contain species that bet hedge (Thompson and Grime (1979) type III or IV seed banks).

Figure 3.1: A well developed strandline on the northern shore of Lake Cawndilla

3.2 Methods

3.2.1 Study Sites

During May 2001, the water levels in the Menindee Lakes were close to the maximum regulated levels hence; sampling was undertaken close to the maximum flood level (New South Wales Department of Land and Water Conservation 2003) (Figure 1.5). Lakes Malta, Tandure, Menindee and Cawndilla were chosen because all had well-developed strandlines on the north-eastern (exposed) shores. The adjacent sediment in all sampled lakes consisted mainly of coarse sand.

3.2.2 Sediment Sampling Protocol

Strandlines and adjacent sediment were sampled in June 2001. The strandline was located and three replicate transects 50 m apart, perpendicular to the shoreline, were established (Figure 3.2). Ten metre long quadrats were established perpendicular to the transect on the strandline, the sediment adjacent the strandline higher on the elevation gradient, lower on the elevation gradient and from directly underneath the strandline (the strandline was scraped away until bare sediment was revealed) (Figure 3.2). Five composite samples from each quadrat (*n* = 15), which consisted of five randomly located 5cm diameter by 5cm deep cores were taken.

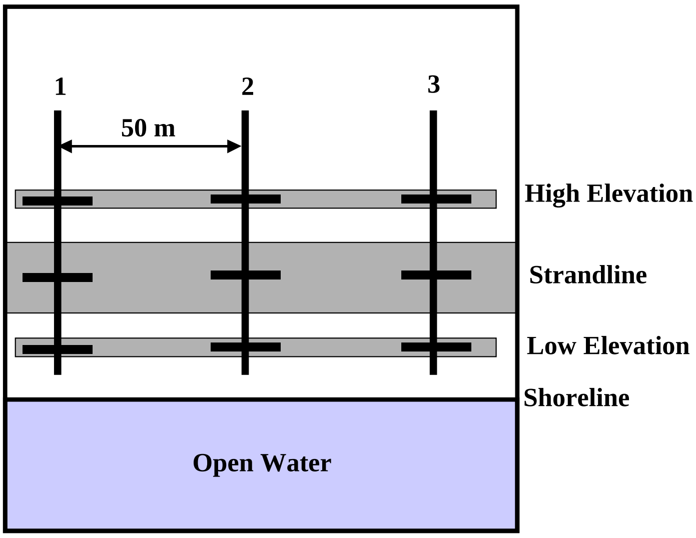

Figure 3.2: Strandline sampling strategy.

3.2.3 Soil Moisture

A sub-sample from each replicate was taken and stored in an airtight container. Soil moisture contents were measured gravimetrically using the procedure described by Rayment and Higginson (1992).

3.2.4 Seedling Emergence and Wetting and Drying Cycles

Sediment samples were transported to Adelaide where they were dried at 40 ºC to constant weight. Two hundred grams of each replicate sediment sample was spread evenly over 4 cm of 60-40 sandy loam contained in 170 x 115 mm plastic containers. Holes were drilled in the side of each container 10 mm from the bottom, which to allowed water to drain. The samples were placed in random positions in a glasshouse and watered daily. In addition to the seed bank samples, fifteen blanks consisting of only sandy loam were randomly placed amongst the samples to determine if there was any contamination in the sandy loam or from the glasshouse. Every two weeks seedlings were counted, identified and removed and the position of the samples in the glasshouse re-randomised. Seedlings that could not be identified were transplanted and grown to a stage at which identification was possible.

Plants were watered daily for 12 weeks then allowed to dry and not watered for six weeks. Twelve weeks was considered long enough for one wetting cycle because germination had slowed dramatically and in most cases ceased after six weeks. This wetting and drying cycle was repeated four more times for a total of five wetting and drying cycles.

3.2.5 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).

3.2.6 Data Analysis

The number of germinants was converted to seeds m^{-2} by calculating the bulk density of the sediment, then calculating the total mass of sediment for 1 m^{2} to a depth of 5 cm. The high elevation, low elevation and below strandline samples from all lakes had bulk density of 1.4 g cm^{-3}, the strandline samples had a bulk density of 0.9 g cm^{-3}. This equated 70 kg of sediment m^{-2} for the high elevation, low elevation and below strandline samples and 45 kg of sediment m^{-2} for the strandline samples. Therefore, the formula for converting the number of germinants to seeds m^{-2} was:

$$\text{No. Seeds m}^{-2} = \text{No. Germinants x } \frac{\text{Mass of Sediment m}^{-2}}{\text{Sample Mass}}$$

The differences in seed density and soil moisture contents between lakes and the strandline and adjacent sediment were analysed with a two factor ANOVA (lake, location and lake x location). Seed density values were log transformed and the soil moisture data were converted to proportions and arcsine square root transformed. Normality was tested using the Shapiro-Wilk W test and equality of variances using the Levene test. All univariate statistical tests were performed using the package JMP In version 3.2.6 (SAS Institute Inc. 1996). The differences in species composition of the seed banks between and within lakes and locations were analysed with NMS ordination and indicator species analysis (Dufrene and Legendre 1997) using the package PCOrd version 4.28 (McCune and Mefford 1999). Non-significant species were classed as Type A, B or C non-significant species (Chapter 2) depending on their distribution and abundance. Two-factor non-parametric multivariate analysis of variance (NPMANOVA) (lake, location and lake x location) (Anderson 2001) was used to compare the seed bank composition between lakes and locations. Single-factor NPMANOVA (Anderson 2001) was used to compare the seed banks of the strandline from the different lakes and the locations within each lake. Multiple comparisons were performed using a Tukey test for ranked data (Zar 1984). Bray-Curtis distances were used to calculate the similarity matrix for all multivariate analyses (Bray and Curtis 1957) and two-dimensional ordination solutions with stress lower than 20% were deemed acceptable (sensu Clarke 1993). Replicates for each transect were pooled for the ordinations for clarity, however NPMANOVA and indicator species analysis were performed on unpooled data. For all statistical tests $\alpha = 0.05$.

3.3 Results

3.3.1 Seed Density

For Lakes Cawndilla, Menindee and Tandure the strandline had the highest seed density followed by the sediment underneath the strandline. The adjacent sediment above and below the strandline had low seed densities (Figure 3.3). In Lake Malta, however there appeared to be no significant differences in the seed density between the strandline, the high elevation and underneath the strandline. The sediment at the elevation lower than the strandline also had a large (albeit smaller than the other locations) seed bank (Figure 3.3). The two factor ANOVA (lake, location and lake x location) supported this with a very significant interaction between lake and location (Table 3.1).

Table 3.1: *F* statistics obtained from comparisons of seed numbers for each lake and location within each lake.

Factor	*df*	*F*	*P*
Lake	3, 224	160.05	<0.0001
Location	3, 224	60.91	<0.0001
Lake x Location	9, 224	6.76	<0.0001

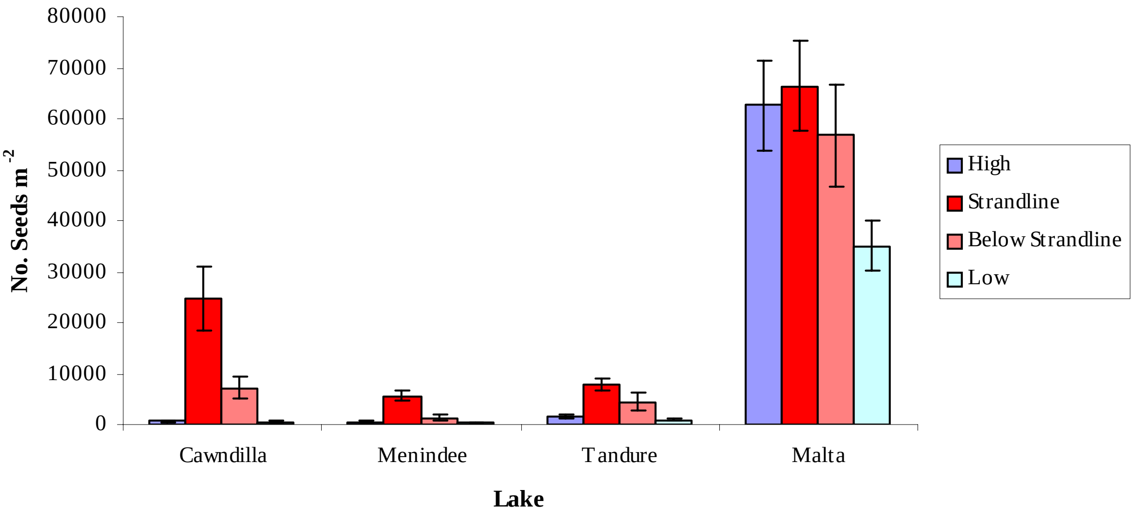

Figure 3.3: Total number of germinations m^{-2} (after five wetting events) for Lakes Cawndilla, Menindee, Tandure and Malta strandlines and adjacent sediment (error bars = ± 1 SE, *n* = 15).

In Lakes Cawndilla and Menindee, the number of germinants decreased with each wetting cycle (Figure 3.4). In Lake Malta, there was a significant reduction in the number of germinants after the fourth wetting although there was an increase after the fifth wetting. For the Lake Tandure seed bank the number of germinants fell after the second wetting cycle, rose after the third but decreased after that (Figure 3.4). The larger number of germinants was the result of large numbers of *Chenopodium pumilio* observed during the respective wetting cycles, when this species was removed the number of germinants fell with each consecutive wetting cycle for Lakes Malta and Tandure.

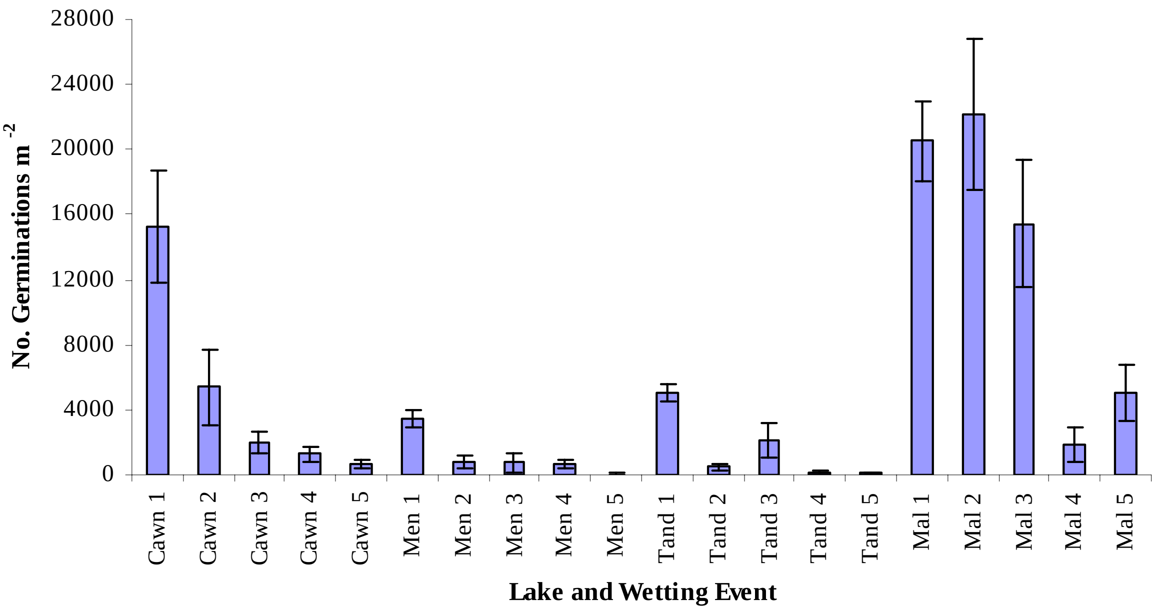

Figure 3.4: Number of germinations m^{-2} for the strandlines of Lakes Cawndilla, Menindee, Tandure and Malta for each wetting event (error bars = ± 1 SE) (only strandlines were plotted because the number of germinants from other samples in Lakes Cawndilla, Menindee and Tandure were extremely low) (Cawn = Cawndilla, Men = Menindee, Tand = Tandure and Mal = Malta) (1-5 = wetting event).

3.3.2 Species Richness

The strandlines of the large lakes (Cawndilla, Menindee and Tandure) had the richest seed bank and the sediment beneath the strandline the second richest for Lakes Menindee and Cawndilla (Figure 3.5). In all lakes, the lowest species richness occurred in the samples taken from the lowest point on the elevation gradient (Figure 3.13). Lake Malta was different from the larger lakes because the highest species richness occurred at the highest point on the elevation gradient (Figure 3.5).

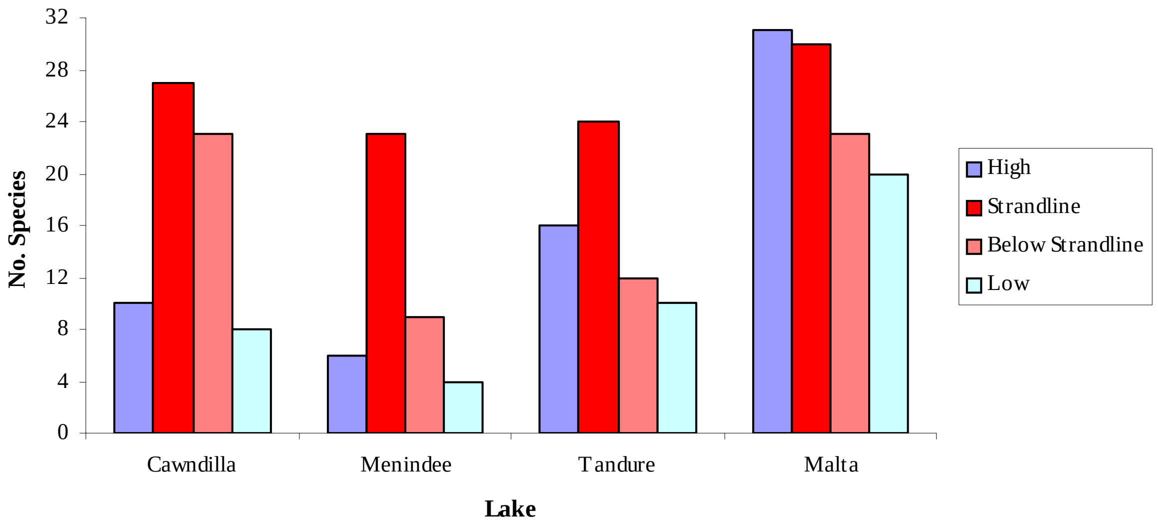

Figure 3.5: Total number of species detected for the strandlines and adjacent sediment in Lakes Cawndilla, Menindee, Tandure and Malta after five wetting events.

3.3.3 Species Composition

The species composition of the Lake Malta seed bank differed from Lakes Cawndilla, Tandure and Menindee. The NMS ordination of all locations from all lakes showed two main groups (Figure 3.6). The Lake Malta samples formed a tight group in the bottom right hand corner of the ordination plot, separate from the larger lakes (Figure 3.6). There was some separation between the strandline samples and below strandline samples and the high and low elevation samples of the large lakes (Figure 3.6). The significant interaction, (NPMANOVA: Table 3.2) supported the observation that the Lake Malta seed bank was very different from the other lakes and the strandline seed banks of the large lakes were different from the seed bank of the adjacent sediment. The below strandline samples from the large lakes appeared to be an intermediate group between the strandline and high and low elevations (Figure 3.6).

Table 3.2: *F* statistics obtained from comparisons of seed bank species composition for each lake and location within each lake.

Factor	***df***	***F***	***P***
Lake	3, 224	12.41	0.0002
Location	3, 224	6.82	0.0002
Lake x Location	9, 224	3.29	0.0002

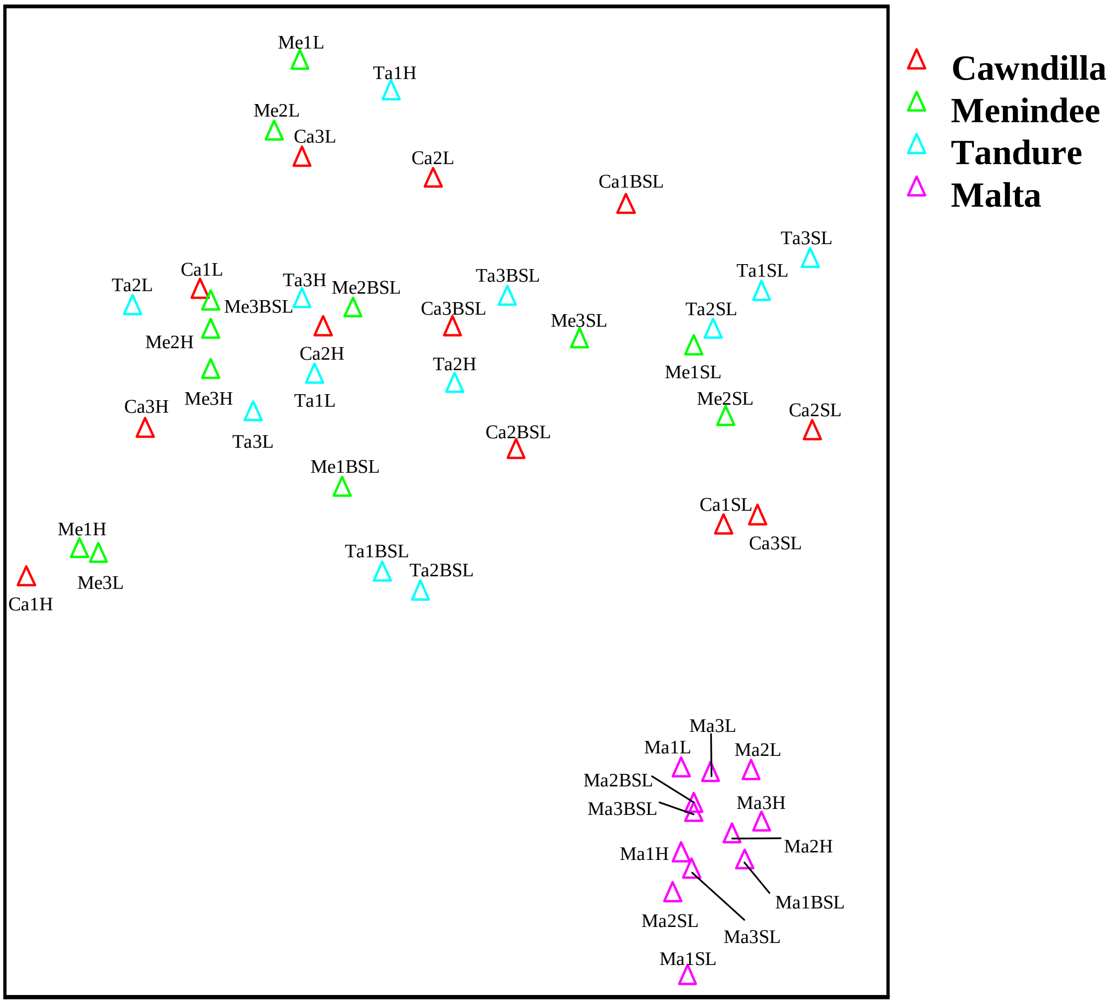

Figure 3.6: NMS ordination of the species composition of the strandlines and surrounding sediment seed bank of Lakes Malta, Tandure, Menindee and Cawndilla (stress = 17.8%) (Ma = Malta, Ta = Tandure, Me = Menindee, Ca = Cawndilla, 1, 2 or 3 = transect, H = high elevation, SL = strandline, BSL = below strandline, L = low elevation) (data were pooled for clarity).

Fifty-eight species were present in the seed banks of all of the lakes, 18 of which were significant indicators of Lake Malta (Table 3.3). Thirty species were not significant because too few individuals were detected (Type A non-significant species (Chapter 2)) and only two species (*Polygonum plebium* and *Chenopodium pumilio*) were common to all of the lakes (Type B non-significant species (Chapter 2)) (Table 3.3). *Heliotropium curassivicum, Nicotiana velutino, Rumex bidens, Senecio* sp. and *Xanthium occidentale* were significant indicators of Lake Cawndilla (Table 3.3). *Alternanthera denticulata, Eucalyptus largiflorens* and *Persicaria lapathifolium* were significant indicators of Lake Tandure (Table 3.3). There were no significant indicator species for Lake Menindee (Table 3.3).

Table 3.3: Indicator species analysis comparing Lakes, Malta, Tandure, Menindee and Cawndilla (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).

Species	Lake	*P*
Alisma sp.	Cawndilla	0.282 (Type A)
Argemone ochroleuca	Cawndilla	0.609 (Type A)
Heliotropium curassivicum	Cawndilla	0.001
Lemna sp.	Cawndilla	1.00 (Type A)
Myriocephalus stuartii	Cawndilla	0.181 (Type A)
Nicotiana velutino	Cawndilla	0.013
Pachychornia tennuis	Cawndilla	1.00 (Type A)
Rumex bidens	Cawndilla	0.034
Senecio sp.	Cawndilla	0.031
Solanum karsensis	Cawndilla	0.23 (Type A)
Xanthium occidentale	Cawndilla	0.029
Ammania multiflora	Malta	0.001
Centipeda minima	Malta	0.001
Chenopodium pumilio	Malta	0.073 (Type B)
Convolvulus arvensis	Malta	0.049
Crassula sieberana	Malta	0.012
Cyperus gymnocaulos	Malta	0.001
Daucus glochidiatus	Malta	1.00 (Type A)
Epaltes australis	Malta	0.001
Eragrostis dielsii	Malta	0.518 (Type A)
Eragrostis parvifolia	Malta	0.111 (Type A)
Euphorbia drummondii	Malta	0.001
Glinus lotoides	Malta	0.002
Gnaphalium luteo-album	Malta	0.001
Haloragis aspera	Malta	0.008
Heliotropium amplexicaule	Malta	0.008
Heliotropium europaeum	Malta	0.014
Iseotopsis graminifolia	Malta	0.001
Isolepis australis	Malta	0.222 (Type A)
Limosella australis	Malta	0.001
Medicago sp.	Malta	0.001
Mollogo cerviana	Malta	0.008
Morgania floribunda	Malta	0.001
Myosurus minima	Malta	0.002
Myriophyllum verrucosum	Malta	1.00 (Type A)
Polygonum aviculare	Malta	1.00 (Type A)
Polygonum plebium	Malta	0.098 (Type B)
Rumex crispus	Malta	0.543 (Type A)
Scleroblitum atriplicinum	Malta	0.055 (Type A)
Sporobolus mitchelli	Malta	0.012
Unknown dicot 1	Malta	0.589 (Type A)
Wahlenbergia communis	Malta	0.001
Galenia secunda	Menindee	1.00 (Type A)
Hypochoeris radicata	Menindee	1.00 (Type A)
Ricinis communis	Menindee	0.223 (Type A)
Solanum oligacanthum	Menindee	0.67 (Type A)
Alternanthera denticulata	Tandure	0.021

Table 3.3…

Species	**Lake**	***P***
Azolla sp.	Tandure	1.00 (Type A)
Chloris truncata	Tandure	1.00 (Type A)
Eucalyptus largiflorens	Tandure	0.039
Juncus aridicola	Tandure	1.00 (Type A)
Ludwigia peploides	Tandure	0.382 (Type A)
Nicotiana glauca	Tandure	1.00 (Rare)
Persicaria lapathifolium	Tandure	0.001
Ptilotus obovatus	Tandure	1.00 (Type A)
Sclerolaena sp.	Tandure	1.00 (Type A)
Tetragonia tetragonoides	Tandure	0.752 (Type A)

The strandline seed banks from Lakes Malta, Tandure, Menindee and Cawndilla each had a distinctive species composition. (NMS ordination: Figure 3.7; NPMANOVA: $F_{3,\ 56}$ = 14.61, $P = 0.0004$; differences confirmed by Tukey HSD: Cawndilla ≠ Menindee ≠ Tandure ≠ Malta).

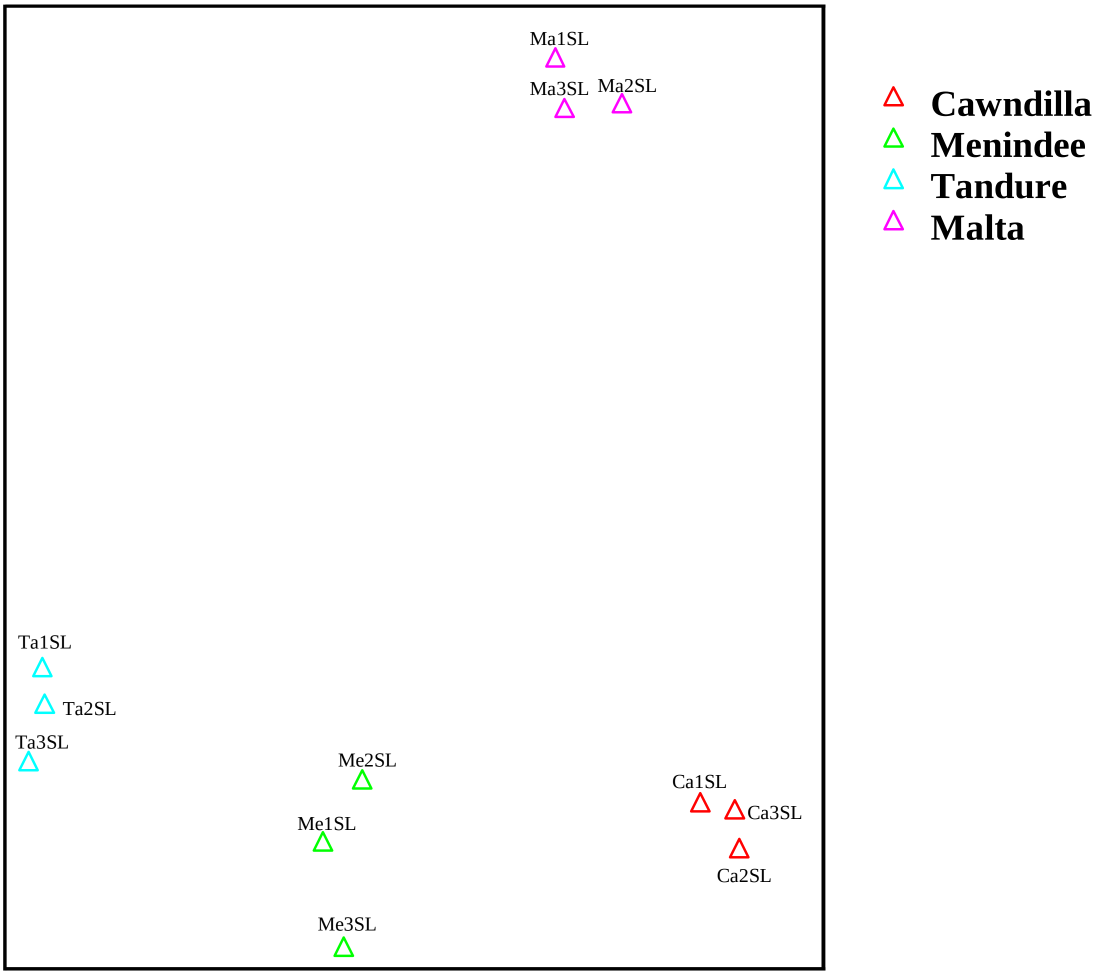

Figure 3.7: NMS ordination of the seed bank composition of the strandlines from Lakes, Cawndilla, Menindee, Tandure and Malta (stress = 4.2%) (for explanation of abbreviations see Figure 3.6) (data were pooled for clarity).

Twelve of the 51 species recorded in strandlines in this study were significant indicators of Lake Malta (Table 3.4). Thirty-two species were not significantly associated with any lake because they were rare (Type A non-significant species (Chapter 2)) and *Chenopodium pumilio* and *Polygonum plebium* were widespread (Type B non-significant species (Chapter 2)) (Table 3.4). *Alternanthera denticulata*, *Ludwigia peploides* and *Persicaria lapathifolium* were significant indicators of Lake Tandure (Table 3.4). Lake Menindee had no significant indicator species (Table 3.4). *Heliotropium curassivicum* and *Rumex bidens* were significant indicators of Lake Cawndilla (Table 3.4).

Table 3.4: Indicator species analysis of the seed banks of the strandlines of Lakes Cawndilla, Menindee, Tandure and Malta (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).

Species	Lake	*P*
Alisma sp.	Cawndilla	0.341 (Type A)
Eucalyptus largiflorens	Cawndilla	0.208 (Type A)
Heliotropium curassivicum	Cawndilla	0.025
Lemna sp.	Cawndilla	1.00 (Type A)
Myriocephalus stuartii	Cawndilla	0.277 (Type A)
Nicotiana velutino	Cawndilla	1.00 (Type A)
Pachychornia tennuis	Cawndilla	1.00 (Type A)
Polygonum plebium	Cawndilla	0.09 (Type B)
Rumex bidens	Cawndilla	0.047
Senecio sp.	Cawndilla	0.06 (Type A)
Solanum karsensis	Cawndilla	1.00 (Type A)
Tetragonia tetragonoides	Cawndilla	0.478 (Type A)
Unknown dicot 1	Cawndilla	0.539 (Type A)
Xanthium occidentale	Cawndilla	0.323 (Type A)
Ammania multiflora	Malta	0.016
Centipeda minima	Malta	0.016
Chenopodium pumilio	Malta	0.358 (Type B)
Convolvulus arvensis	Malta	1.00 (Type A)
Crassula sieberana	Malta	1.00 (Type A)
Cyperus gymnocaulos	Malta	0.016
Daucus glochidiatus	Malta	1.00 (Type A)
Epaltes australis	Malta	0.01
Euphorbia drummondii	Malta	1.00 (Type A)
Glinus lotoides	Malta	0.346 (Type A)
Gnaphalium luteo-album	Malta	0.016
Haloragis aspera	Malta	0.178 (Type A)
Heliotropium amplexicaule	Malta	0.178 (Type A)
Iseotopsis graminifolia	Malta	0.016
Limosella australis	Malta	0.016
Medicago sp.	Malta	0.016
Mollogo cerviana	Malta	1.00 (Type A)
Morgania floribunda	Malta	0.014
Myosurus minima	Malta	0.016
Polygonum aviculare	Malta	1.00 (Type A)
Rumex crispus	Malta	0.483 (Type A)
Scleroblitum atriplicinum	Malta	0.016
Sporobolus mitchelli	Malta	0.786 (Type A)
Wahlenbergia communis	Malta	0.016
Argemone ochroleuca	Menindee	0.495 (Type A)
Eragrostis dielsii	Menindee	1.00 (Type A)
Galenia secunda	Menindee	1.00 (Type A)
Ricinis communis	Menindee	0.179 (Type A)
Solanum oligacanthum	Menindee	0.484 (Type A)
Alternanthera denticulata	Tandure	0.05
Chloris truncata	Tandure	1.00 (Type A)
Eragrostis parvifolia	Tandure	1.00 (Type A)

Table 3.4…

Species	**Lake**	***P***
Juncus aridicola	Tandure	1.00 (Type A)
Ludwigia peploides	Tandure	0.05
Persicaria lapathifolium	Tandure	0.025
Ptilotus obovatus	Tandure	1.00 (Type A)
Sclerolaena sp.	Tandure	1.00 (Type A)

Individually the seed banks of the edges of all lakes showed similar patterns. The strandline samples formed a distinct group with a different species composition from the adjacent sediment, although the pattern was not as pronounced in Lake Malta (Figure 3.8, Figure 3.9, Figure 3.10, and Figure 3.11).

The different locations in Lake Cawndilla each had a different seed bank composition (NMS ordination: Figure 3.8; NPMANOVA: $F_{3, 56} = 4.98$, $P = 0.0004$; Tukey HSD: high elevation ≠ strandline ≠ below strandline ≠ low elevation). The strandline samples formed the most well defined group (Figure 3.8). The below strandline samples also formed a relatively tight group between the strandline and high and low elevation samples (Figure 3.8).

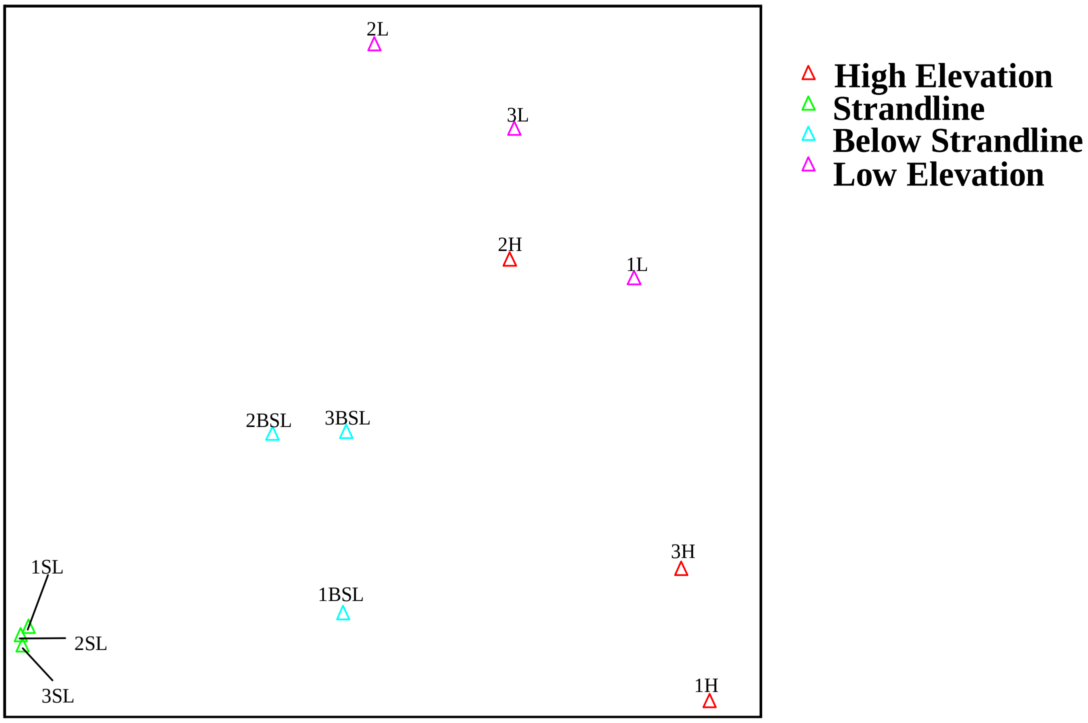

Figure 3.8: NMS ordination of the species composition of the seed banks of Lake Cawndilla (stress = 10.9%) (for explanation of abbreviations see Figure 3.6) (data were pooled for clarity).

Thirty-four species were present in the Lake Cawndilla seed bank (Table 3.5). *Alternanthera denticulata, Chenopodium pumilio, Cyperus gymnocaulos Heliotropium curassivicum, Ludwigia peploides, Myriocephalus stuartii, Rumex bidens* and *Senecio* sp. were significant indicators of the strandline (Appendix 2). The other locations had no significant indicator species. All of the non-significant species were rare (Type A (Chapter 2)), most of which were only detected in the strandline, except for *Morgania floribunda* and *Polygonum plebium* that were widespread (Type B (Chapter 2)) (Table 3.5, Appendix 2).

Table 3.5: Summary of indicator species analysis for all lakes.

Lake	No. Species	No. Significant Indicators in Strandline Seed Bank	No. Rare Species	No. Widespread Species
Cawndilla	34	8	24	2
Menindee	25	6	17	2
Tandure	32	3	25	4
Malta	39	9	14	15

The Lake Menindee species composition showed similar patterns to Lake Cawndilla, although the strandline samples formed a looser group and the high and low elevation samples did not form clear groups (NMS ordination: Figure 3.9). The below strandline samples again, were located between the strandline and high and low elevation on the ordination plot (Figure 3.9). The strandline and below strandline samples forming distinct groups was supported by NPMANOVA ($F_{3, 56} = 3.52$, $P = 0.0028$). Tukey HSD showed no difference in the seed bank composition between the high and low elevation samples with the strandline and below strandline seed banks significantly different from each other and the adjacent sediment (strandline ≠ below strandline ≠ high elevation = low elevation).

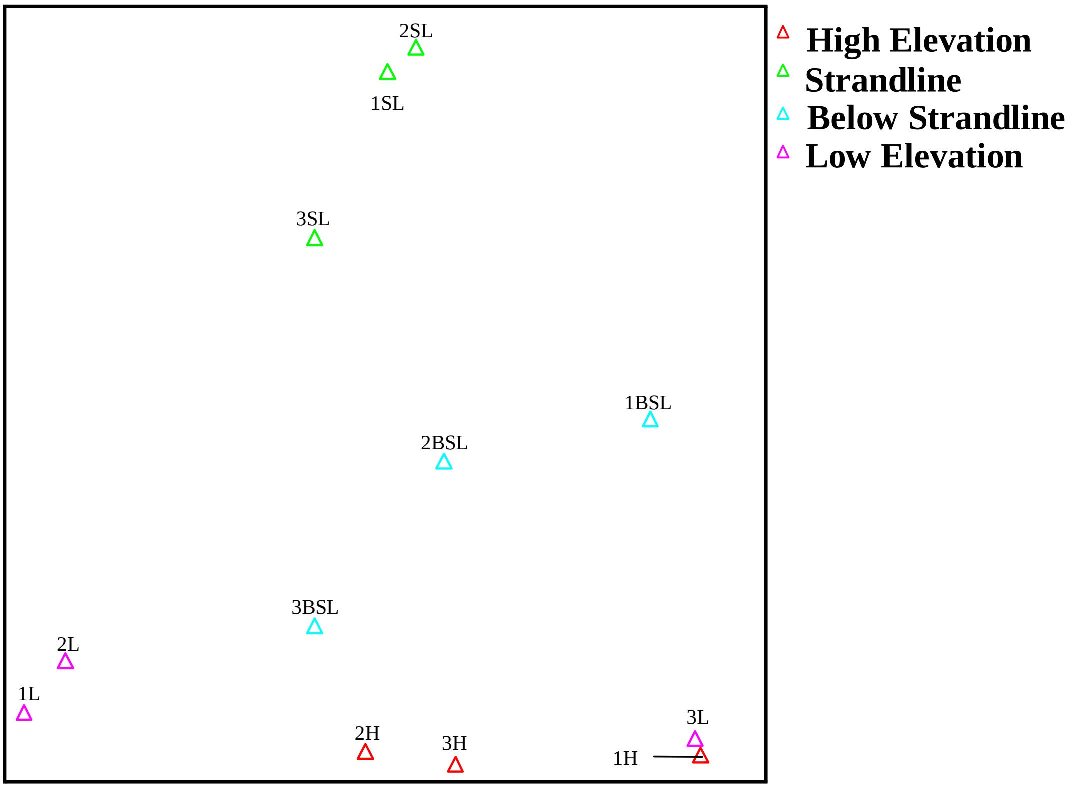

Figure 3.9: NMS ordination of the species composition of the seed banks of Lake Menindee (stress = 10.3%) (for explanation of abbreviations see Figure 4.6) (data were pooled for clarity).

Twenty-five species were found in the Lake Menindee seed bank (Table 3.5). *Alternanthera denticulata, Cyperus gymnocaulos, Heliotropium curassivicum, Ludwigia peploides* and *Morgania floribunda* were significant indicators of the strandline (Appendix 2). In addition to the significant indicator species, all of the rare (Type A (Chapter 2)) species (except *Hypochoeris radicata, Polygonum aviculare* and *Wahlenbergia communis*) were only detected in the strandline (Appendix 2). *Chenopodium pumilio* and *Epaltes australis* were the only widespread (Type B (Chapter 2)) species (Appendix 2, Table 3.5).

The Lake Tandure species composition also showed a similar pattern to Lake Cawndilla. The different locations generally formed different groups and the strandline formed a tight group separate from the adjacent sediment (NMS ordination: Figure 3.10). These patterns were supported by NPMANOVA ($F_{3, 56} = 3.84$ $P = 0.0004$), with Tukey HSD showing that the seed bank of each location was significantly different (high elevation ≠ strandline ≠ below strandline ≠ low elevation). Similar to Lake Cawndilla, the below strandline samples were located between the strandline and high and low elevation samples on the ordination plot (Figure 3.10).

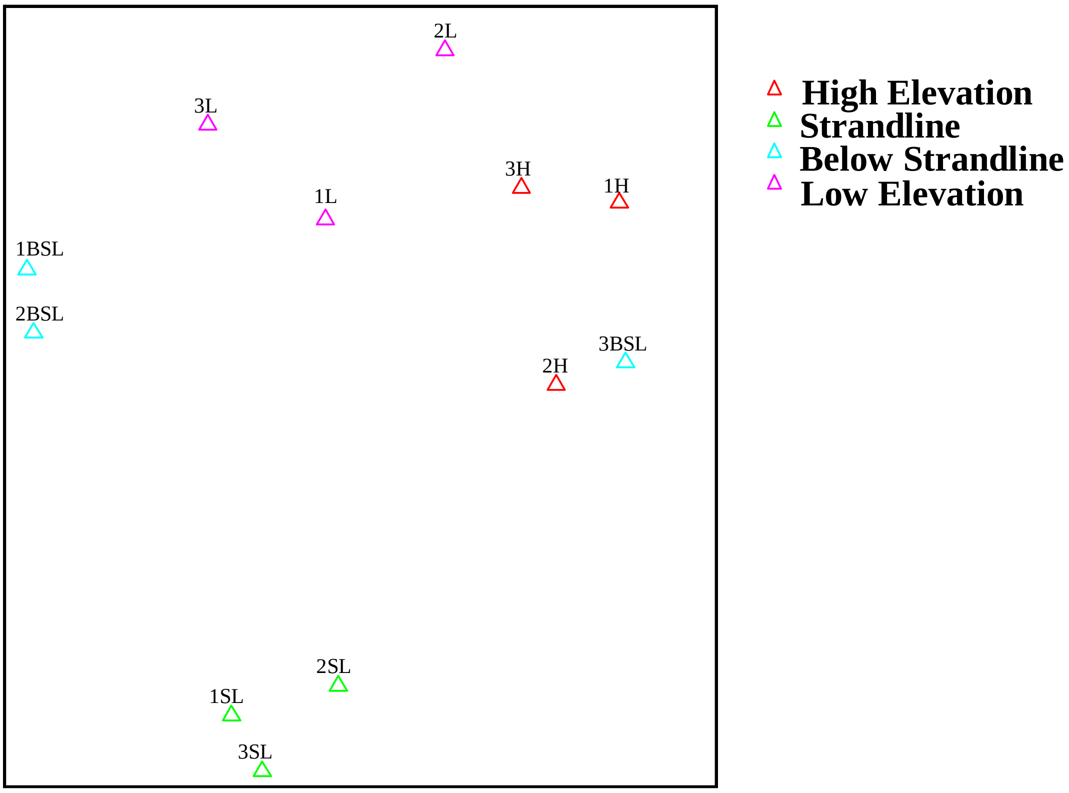

Figure 3.10: NMS ordination of the species composition of the seed banks of Lake Tandure (stress = 9.6%) (for explanation of abbreviations see Figure 4.6) (data were pooled for clarity).

The Lake Tandure seed bank had 32 species, three of which were significant indicators of the strandline (Table 3.5) (*Alternanthera denticulata*, *Ludwigia peploides* and *Persicaria lapathifolium*) (Appendix 2). Four species were not significant because they were wide spread (Type B and C non-significant species (Chapter 2)) and the remaining 25 species were rare (Table 3.5) (Type A non-significant species (Chapter 2)), 17 of which were only found in the strandline (Appendix 2).

The Lake Malta seed bank showed different patterns to the large lakes, the low elevation samples formed the tightest group and the strandline samples had the most in common with the high elevation samples not the below strandline samples (Figure 3.11). However, each of the locations within this lake had a significantly different seed bank composition. This was supported by NPMANOVA ($F_{3, 56} = 5.18$ $P = 0.0006$) with Tukey HSD indicating that each location was significantly different (high elevation ≠ strandline ≠ below strandline ≠ low elevation).

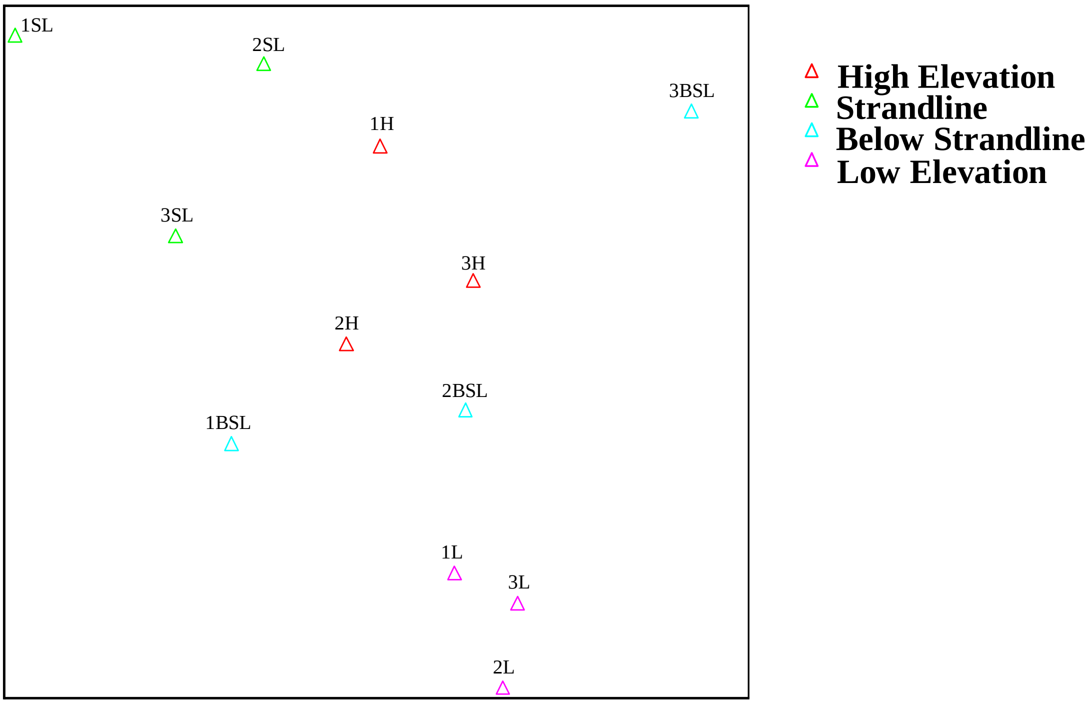

Figure 3.11: NMS ordination of the species composition of the seed banks of Lake Malta (stress = 6.4%) (for explanation of abbreviations see Figure 4.6) (data were pooled for clarity).

The most striking difference between Lake Malta and the large lakes was illustrated by the indicator species analysis results (Table 3.5). The strandline had nine significant indicator species (Table 3.5) (*Alternanthera denticulata*, *Ammania multiflora*, *Centipeda minima*, *Gnaphalium luteo-album*, *Medicago* spp., *Myosurus minima* and *Schleroblitum atriplicinum*) and the high elevation seed bank had one (*Crassula sieberana*) (Appendix 2). In addition to the high elevation seed bank having a significant indicator, 15 of the 39 species (37.5%) detected were widespread (Type B and C non-significant species (Chapter 2)) (Table 3.5). The proportion of widespread species was much greater in Lake Malta than the larger lakes: Lake Cawndilla had 6%, Lake Menindee 7.5% and Lake Tandure 15% (Table 3.5).

3.3.4 Favourable Microsites for Plant Establishment

The soil moisture results suggested that the strandline does provide a favourable microsite for plant establishment, compared with the adjacent sediment higher on the elevation gradient because more moisture was present (Figure 3.12). However, results were not consistent across all lakes and soil moisture was dependent on both location and lake (Figure 3.12, ANOVA: Table 3.6). In all lakes, except Lake Malta, the location with the lowest soil moisture was the high elevation (Figure 3.12). In Lake Cawndilla the location with the highest soil moisture was the strandline followed by the below strandline samples then the low elevation samples (Figure 3.12). In Lake Menindee, the pattern was different with the low elevation sample having higher soil moisture content than the strandline and below strandline samples, which appeared to be equal (Figure 3.12). Lake Tandure had a similar pattern to Lake Cawndilla except the below strandline and low elevations samples were not significantly different (Figure 3.12). Lake Malta also had a similar pattern to Lake Cawndilla although the variability within the strandline samples was much larger and the high elevation samples had higher soil moisture than the low elevation sample (Figure 3.12).

Table 3.6: *F* statistics obtained from comparisons of soil moisture content for each lake and location within each lake.

Factor	***df***	***F***	***P***
Lake	3, 224	3.75	0.0117
Location	3, 224	46.77	< 0.0001
Lake x Location	9, 224	5.59	< 0.0001

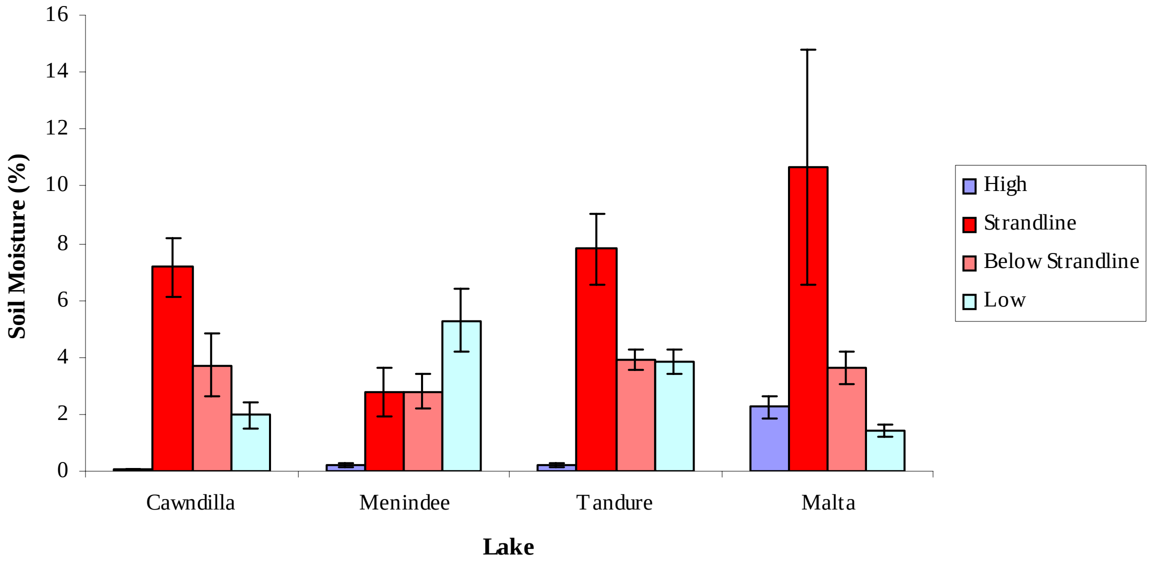

Figure 3.12: Soil moisture contents for the strandline and adjacent sediment for Lakes Cawndilla, Menindee, Tandure and Malta (error bars = ± 1 S.E.).

3.3.5 Persistent and Transient Seed Banks

For all lakes, the number of species decreased after the first wet cycle, which indicated that some of the species do not bet hedge (Figure 3.13). Fifty-eight species were recorded from the seed banks of Lakes Malta, Tandure, Menindee and Cawndilla (Table 3.7). Of these, 21 only germinated during the first wet (Table 3.7) with no new species recorded in subsequent wet cycles. The number of species recorded was the same for the second and third wettings in all lakes, except Lake Tandure where one less species was detected in the third wetting (Figure 3.13). Generally, the number of species recorded decreased sharply after the third wetting cycle, which indicated that the species that have persistent seed banks have the potential to recruit after at least two false starts before their seed reserves become exhausted (Figure 3.13). During the fifth wetting cycle four species were recorded from Lake Cawndilla, three from Lake Menindee, five from Lake Tandure and eleven from Lake Malta (Figure 3.13).

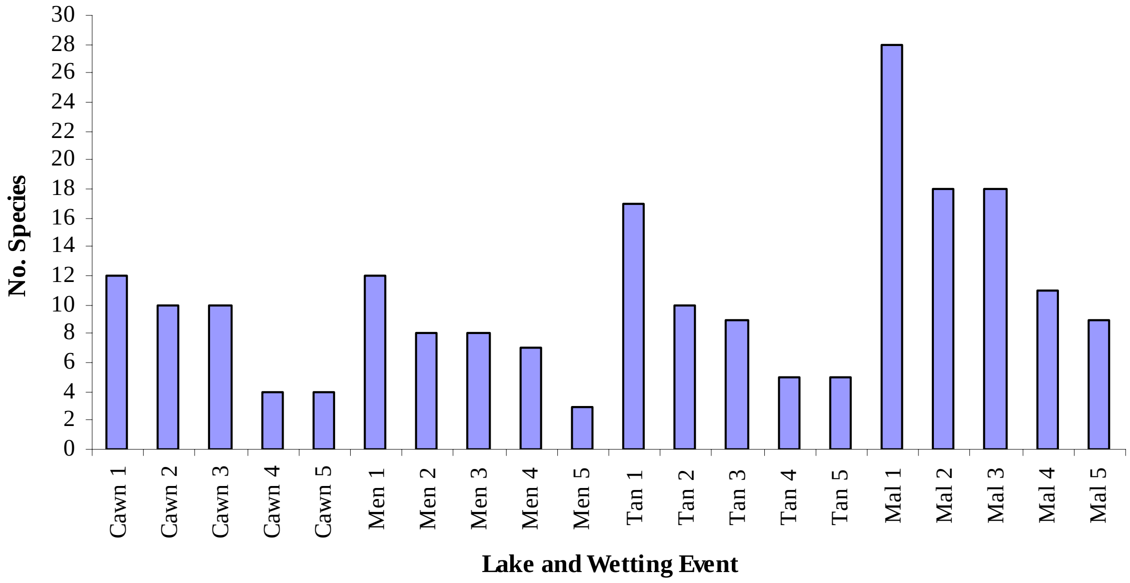

Figure 3.13: Number of species detected in the seed banks (strandline and adjacent sediment) of Lakes Cawndilla, Menindee, Tandure and Malta for each wetting event (see Figure 3.4 for the explanation of the X-axis abbreviations).

Table 3.7: Seed bank strategy of species detected from the seed banks of Lakes, Cawndilla, Menindee, Tandure and Malta (* denotes exotic species).

Species	Seed Bank Strategy
Alisma sp.	Persistent
Alternanthera denticulata	Persistent
Ammania multiflora	Persistent
*Argemone ochroleuca**	Persistent
Azolla sp.	Persistent
Centipeda minima	Persistent
Chenopodium pumilio	Persistent
Chloris truncata	Persistent
*Convolvulus arvensis**	Persistent
Crassula sieberana	Persistent
Cyperus gymnocaulos	Persistent
Epaltes australis	Persistent
Eragrostis dielsii	Persistent
Eragrostis parvifolia	Persistent
*Galenia secunda**	Persistent
Glinus lotoides	Persistent
Gnaphalium luteo-album	Persistent
Haloragis aspera	Persistent
Heliotropium curassivicum	Persistent
Hypochoeris radicata	Persistent
Limosella australis	Persistent
Medicago sp.*	Persistent
Mollogo cerviana	Persistent
Morgania floribunda	Persistent
Myriocephalus stuartii	Persistent
Myriophyllum verrucosum	Persistent
Nicotiana glauca	Persistent
Pachychornia tennuis	Persistent
Persicaria lapathifolium	Persistent
Polygonum plebium	Persistent
Rumex bidens	Persistent
Schlerolaena sp.	Persistent
Scleroblitum atriplicinum	Persistent
Solanum oligacanthum	Persistent
Sporobolus mitchelli	Persistent
Tetragonia tetragonoides	Persistent
Wahlenbergia communis	Persistent
Daucus glochidiatus	Transient
Eucalyptus largiflorens	Transient
Euphorbia drummondii	Transient
*Heliotropium amplexicaule**	Transient
*Heliotropium europaeum**	Transient
Iseotopsis graminifolia	Transient
Isolepis australiensis	Transient
Juncus aridicola	Transient
Lemna sp.	Transient
Ludwigia peploides	Transient

Table 3.7…

Species	Seed Bank Strategy
Myosurus minima	Transient
Nicotiana velutino	Transient
*Polygonum aviculare**	Transient
Ptilotus obovatus	Transient
*Ricinis communis**	Transient
*Rumex crispus**	Transient
Senecio sp.	Transient
*Sinapis alba**	Transient
Solanum karsensis	Transient
Unknown dicot 1	Transient
*Xanthium occidentale**	Transient

3.4 Discussion

3.4.1 Seed Density

The strandline and the sediment beneath the strandline accounted for over 90% of germinants in Lakes Cawndilla, Menindee and Tandure, which suggested that this narrow zone of organic matter deposition is important in the vegetation dynamics of the edges these lakes (Figure 3.3). The greater seed density in the sediment directly underneath the strandline than in the adjacent sediment, in the larger lakes, indicated that some of the seed in the strandline has been incorporated into the sediment underneath. However, similar to the formation and age of strandlines, it was beyond the scope of this study to determine the origin of the seed in the sediment directly under the strandline. If flood, drought or grazing destroyed the extant vegetation around the edges of the larger lakes, the strandline and sediment underneath provide most of the seed reserves for regeneration in the absence of allochthonous seed inputs. Lake Malta on the other hand showed a different pattern with the presence of a significant sediment seed bank outside the strandline (Figure 3.3).

The use of the seedling emergence technique with multiple wet and dry cycles meant that this estimate of seed density was more accurate than the reconnaissance study (Chapter 2). However, it was not clear whether five wetting cycles was sufficient to exhaust the seed bank. How many wetting and drying cycles are needed to exhaust the seed bank is not known, although, Leck and Brock (2000) subjected temporary wetland seed banks from the New South Wales northern tablelands (Australia) to eight annual wetting and drying cycles and found that the seed bank had become depleted but not exhausted. Therefore, total seed density was probably underestimated (sensu Gross 1990).

3.4.2 Species Richness and Composition

Species richness patterns were similar to seed density, with the strandline having the largest number of species in the larger lakes and Lake Malta having a species rich seed bank outside of the strandline (Figure 3.5). The species composition of the adjacent sediment seed bank in Lake Malta was more similar to the strandline than the larger lakes due to the larger number of widespread species (Table 3.5). The different patterns in species richness and composition were probably due to differences in wave exposure between Lake Malta and the larger lakes. Wave exposure can influence plants directly through biomass removal (Wilson and Keddy 1985a; Coops and Van der Velde 1996; Doyle 2001) and uprooting seedlings (Foote and Kadlec 1988; Riis and Hawes 2003; Schutten *et al.* 2004) or indirectly by producing a gradient of substrate particle size, organic content and nutrient concentration (Wilson and Keddy 1985a). The larger lakes are subject to higher wave exposure than Lake Malta that may result in newly germinated seedlings being uprooted or damaged and unable to reach sexual maturity, which over time could deplete the seed bank. In contrast, seedlings around the edge of Lake Malta would be subject to lower wave exposure suffer less damage or mortality and therefore, have a higher chance of reaching sexual maturity and replenishing the seed bank.

Ignaciuk and Lee (1980) reported that four species were found exclusively in the strandlines of coastal salt marshes in northern England. Several species were found only in the strandlines of the large lakes; however, many of those species were found in the adjacent sediment in Lake Malta or were rare species that in some cases were only detected once.

The samples from underneath the strandline in the large lakes had a species composition that was intermediate between the strandline and adjacent sediment (high and low elevation samples) (Figure 3.8, Figure 3.9 and Figure 3.10). This and the species richness results suggest that only some species are incorporated into the sediment (Figure 3.5), hence these samples contained elements of the strandline seed bank and those of the adjacent sediment.

3.4.3 Favourable Microsites for Plant Establishment

The soil moisture data provided evidence that the strandline may provide favourable microsites for plant recruitment, since the strandline may act as a barrier to evaporation. However, the major species observed growing in strandlines in the field were *Ricinis communis* and *Xanthium occidentale* (pers. obs.), large seeded species with sufficient carbohydrate reserves to emerge through the strandline. This pattern may also be due to the higher soil moisture content of the strandline or higher abundances of these species in the strandline seed bank. Small seeded species were not observed germinating in the strandline in the field but were present in the strandline seed bank of all lakes. No plants were observed growing in the Lake Malta strandline (pers obs) but no *Xanthium occidentale* or *Ricinis communis* seeds were present at this lake. The seed bank of this lake consisted of only small seeded species, which may not be able to emerge through the strandline (sensu van der Valk 1986).

3.4.4 Persistent and Transient Seed Banks

Leck and Brock (2000) concluded that systems with unpredictable wetting and drying cycles had seed banks with a larger number of species that bet hedge (Thompson and Grime (1979) type III or IV seed banks). However, more than one third of the species present were only detected in the first wetting event, which is in contrast to the results of Leck and Brock (2000). Bet hedging is seen as an important adaptation to ensure survival of the species in systems where the opportunities for successful germination, establishment and replenishment of the seed bank are unpredictable and can be of short duration or prone to false starts (Thompson 1992).

The species that were only detected in the first wetting cycle probably do not bet hedge, however many probably cannot be classified as having type I or type II seed banks (Thompson and Grime 1979). Species with type I and II seed banks are adapted to exploit the gaps created by seasonally predictable damage and mortality to vegetation and the seed is short lived (less than 1 year) (Thompson and Grime 1979). In comparison to the systems in the United Kingdom, where Thompson and Grime (1979) suggested this classification system, the climate of the Menindee Lakes cannot be described as having predictable seasons. No information on the longevity of the species present in the Menindee Lakes seed bank is available. Leck and Brock (2000) investigated the seed longevity of species from temporary wetlands from the New South Wales northern tablelands, by drying the seed bank and each year in spring sub samples were placed in a green house and germinated under damp conditions. The number of species recorded for the first five years showed a marginal annual decrease but from years five to nine the number of species recorded annually decreased more rapidly (Leck and Brock 2000). The results from the aforementioned study show that the seeds of over 20 plant species from the seed banks from these temporary wetlands can survive for at least nine years in dry storage (Leck and Brock 2000). It is possible that seeds of some species from the Menindee Lakes that do not bet hedge remain viable for longer than one year in dry sediments.

A larger proportion of the species that do not bet hedge, compared with those that do, are exotics (Table 3.7). The native environment of the exotic species that do not bet hedge may be seasonal or they are able to persist for extended periods in dry sediment. Included in the exotic species that do not bet hedge was *Xanthium occidentale* (Table 3.7), this species however, has been reported to bet hedge (Cunningham *et al.* 1981). Cunningham *et al.* (1981) stated that in each fruit, which contains two seeds, there is a larger seed that is ready to germinate as soon as conditions become favourable and a smaller seed that can remain dormant for several years. *Eucalyptus largiflorens* was only detected in the first wetting cycle, however this species is a long-lived tree that will have many opportunities to set seed and disperse (sensu (Roberts 1981). *Lemna* sp., *Juncus aridicola* and *Ludwigia peploides* all have asexual modes of reproduction: *Lemna* sp. produces new plants by budding, *Juncus aridicola* by rhizomes and *Ludwigia peploides* produces roots at nodes that can produce new plants by fragmentation (Cunningham *et al.* 1981). Species that form rhizomes or other belowground perennating structures are able to survive periods of desiccation by allocating more resources to the belowground organs (Rea and Ganf 1994d). Plants that produce asexual reproductive structures such as rhizomes have an advantage over those species that are reliant on seeds for reproduction because asexual offspring are generally more developed, larger and able to utilize resources more efficiently than sexual offspring (Grace 1993). Free-floating species such as *Lemna* are not reliant on seeds for dispersal and plants that reproduce by fragmentation can also disperse effectively by hydrochory (Johansson and Nilsson 1993). Asexual reproduction is not limited to species that do not bet hedge: *Azolla* sp., *Cyperus gymnocaulos, Heliotropium curassivicum, Limosella australis, Myriophyllum verrucosum* and *Sporobolus mitchelli* all have asexual modes of reproduction (Cunningham *et al.* 1981) and bet hedge (Table 3.7). *Iseotopsis graminifolia* has been observed in the field to flower and set seed in less than four weeks (pers. obs.) and if the seed can survive in dry sediment for extended periods, there is no need to bet hedge. Finally, fourteen of the species that were only detected in the first wetting cycle were extremely rare, it is possible that these species bet hedge but there was insufficient seed present for this to be detected.

In contrast to Brock and Rogers (1998), no new species were recorded after the first wetting event. This suggested that subjecting the seed bank from this system a single wet cycle for 12 weeks, is sufficient to determine the species richness of the seed bank.

4 Chapter 4: Water Regime Requirements for Germination and Recruitment of Common Menindee Lakes Species

4.1 Introduction

It is widely accepted that when the seed bank is subjected to different water regimes different plant communities will arise, because some species will be favoured over others (e.g. van der Valk 1981; Casanova and Brock 2000; Baldwin *et al.* 2001; Nicol *et al.* 2003). Therefore, the response of the plant community will be dependent on the water regime requirements for germination, recruitment and survival of species present in the extant vegetation and the seed bank. The functional classification of wetland plants proposed by Brock and Casanova (1997) classified species into different functional groups based on their response to different water regimes; hence, the water regime requirements for species in the same group should be similar.

The Reconnaissance (Chapter 2) and Strandline (Chapter 3) studies showed that the Menindee Lakes have a species rich seed bank, but very little is known about the water regime requirements for the majority of the species present. In many freshwater systems recruitment occurs primarily during drawdown, when the sediment is free of standing water (e.g. Keddy and Rezincek 1986; Welling *et al.* 1988b; Welling *et al.* 1988a). For example, Gaudet (1977) identified drawdown as the primary factor in the development of papyrus swamps in an African tropical lake and Baldwin *et al.* (2001) found that twice as many species occurred when the seed bank from a tidal freshwater marsh was subjected to damp as opposed to submerged conditions. In experimental whole lake studies, *Phragmites australis* stands developed during drawdown whereas in the control lake submergent aquatics and open water dominated (ter Heerdt and Drost 1994). Other studies have shown that emergent macrophytes replaced submergent macrophytes when water levels were artificially drawn down in Delta Marsh (Manitoba, Canada) (Welling *et al.* 1988a). Conversely, van der Valk *et al.* (1994) found that an increase in water level reduced the species richness of vegetation communities that were established after a draw down.

Field observations suggest that most Menindee Lakes species do not germinate whilst submerged and, as juveniles and adults, are intolerant of flooding (pers. obs.). Therefore, drawdown is required for germination, recruitment and replenishment of the seed bank.

This suggests that the majority of the species present are from the terrestrial functional group (Brock and Casanova 1997). Species classified in this group are intolerant of flooding (Brock and Casanova 1997); however, the Brock and Casanova (1997) classification system does not take into consideration where the species occurs in nature. Ephemeral lakes and floodplains may be dry for extended periods (Puckridge *et al.* 1998; Scholz *et al.* 1999) and the species present may be desiccation tolerant and killed when flooded, but are found only in areas subject to periodic inundation. These species do not colonise areas that are never inundated perhaps due to requirements for high soil moisture to germinate, specific soil type requirements, nutrients or biological interactions (Cunningham *et al.* 1981).

In arid ephemeral lakes, the rate of drawdown in addition to the presence or absence of water influences germination, recruitment and survival. The largest rainfall events may provide sufficient water for seeds to germinate; however, only four species (all uncommon) have been observed germinating in response to rainfall (Chapter 5). Therefore, the major water source for germination is Darling River floodwater, which saturates the soil profile. Germination occurs when water levels in the lakes fall and the sediment surface is exposed but not dry (Chapter 5). If the rate of drawdown is rapid, the sediment surface may dry before seeds germinate or the resultant soil moisture may be too low for seedlings to survive. This may result in amphibious species being extirpated and the system being dominated by only the most desiccation tolerant (terrestrial) species.

Water depth also plays an important role in determining which species will germinate from the seed bank and recruit. The maximum depth of submergent plant species in lakes is related to light attenuation (e.g. Spence 1982; Chambers and Kalff 1987b; Chambers and Kalff 1987a). However, Chambers and Prepas (1988) and Hudon *et al.* (2000) found that light quality was also important. For example, Chambers and Kalff (1985) reported that the depth distribution of species was primarily controlled by water transparency and Squires *et al.* (2002) reported the highest biomass of submerged macrophytes in the lakes with the clearest water.

The Menindee Lakes are highly turbid water bodies (20 to >1,000 NTU) (Scholz *et al.* 1999); therefore, a steep light gradient caused by rapid attenuation is present that will influence which species germinate from the seed bank and recruit. Several amphibious species (e.g. *Persicaria lapathifolium, Ludwigia peploides, and Cyperus gymnocaulos*) were found in the seed bank (Chapter 2 and Chapter 3). The highly turbid water may prevent these species from persisting whilst flooded or restrict them to shallow water.

The seed banks from six locations within the Menindee Lakes and Great Darling Anabranch systems were subjected to three different hydraulic regimes and three elevations within each hydraulic regime (nine different water regimes). The aims of this experiment were:

1. To examine the species composition derived from the seed bank when subjected to different water regimes.
2. To determine the water regime requirements of the common species found in the seed bank and whether the functional classification system of Brock and Casanova (1997) can be applied to species from this system.
3. To test the hypothesis that exposed sediment is required for germination for all species in the seed bank.
4. To test the hypothesis that rapid drawdown (5 cm day^{-1}) will prevent the establishment of amphibious species and lead to the dominance of terrestrial species.
5. To formulate a conceptual model to predict which species will be present under different water regimes and how the system will respond to different water management options.

4.2 Methods

4.2.1 Sediment Sampling Sites

The sites chosen for sediment collection were representative of three common geomorphic and hydraulic regime types present in the Menindee Lakes system. Lakes Balaka and Malta are small lakes, which dry more frequently than the large lakes and when not connected to Lake Wetherell dry slowly by evaporation (Scholz *et al.* 1999). Lakes Cawndilla and Menindee are large lakes that do not dry as frequently as the small lakes (Scholz *et al.* 1999) and when drawn down the water level can fall up to 10 cm day^{-1} (New South Wales Department of Land and Water Conservation 2003), depending on downstream demand for water. Lake Wetherell and Redbank Creek are typical of flowing habitats with modified hydraulic regimes. Lake Wetherell is part of the main channel of the Darling River and was created by the construction of the main weir (Scholz *et al.* 1999). Whilst subject to large water level fluctuations, it has never dried completely since the completion of the scheme (Scholz *et al.* 1999) and at times is subject to static water levels for several months (New South Wales Department of Land and Water Conservation 2003). Redbank Creek is part of the Great Darling Anabranch system and is used as an irrigation supply channel. The water level in Redbank Creek is generally kept at close to bank full capacity and is subject to static water levels most of the time (pers. obs.). Collecting sediment samples across the different geomorphic and hydraulic regime types present in the system maximized the number of species present in the samples.

4.2.2 Sediment Sampling Protocol

Sediment was collected from four locations around the edges of Lakes Malta, Balaka, Menindee, Cawndilla, Wetherell and Red Bank Creek; high river levels prevented the collection of sediment from the centres of the lakes. Only sampling the edges of the lakes meant that some species might have been missed; however, the water was in excess of 5 m deep and the soil sandy in places that made it impossible to take representative samples from these areas. The sediment was dried to constant weight at 40º C, large aggregates were broken up and all samples from each lake were thoroughly mixed (after drying) to produce composite seed bank samples from each lake (sensu Seabloom *et al.* (1998) and Nicol *et al.* (2003)). A composite seed bank of each lake was used to ensure that the potential differences between water regime treatments were not obscured by differences in seed bank composition.

4.2.3 Experimental Protocol and Design

Three hundred and fifteen cylinders (30 cm diameter, 100, 70 or 20 cm tall) were filled with 60/40 sandy loam. Osmocote®, a slow release fertilizer (N: P: K = 17.4: 4.4: 8.8 plus micronutrients), was added to the top 10 cm of the soil to give an equivalent nitrogen loading of 100 g N m^{-2} $year^{-1}$. The cylinders were placed in outdoor ponds (3 m x 4 m x 1.1 m) at The University of Adelaide (34º56’ S, 138º36’ E) and allowed the soil to maintain contact with the falling water levels (sensu Nicol and Ganf 2000; Nicol *et al.* 2003). Four hundred grams of the dried composite seed bank was spread over the top of the sandy loam.

Five replicates from each lake (and Redbank Creek), elevation and hydraulic regime were used (*n* = 5), which gave 315 cylinders.

4.2.4 Hydraulic Regimes

The hydraulic regimes were chosen to mimic three common hydraulic regimes that can simultaneously occur in the Menindee Lakes. Initially the water level was held at 90 cm above the base of the pond for 28 days to ensure the columns were saturated. Three hydraulic regimes were then employed static (90 cm for the duration of the experiment), slow drawdown (1 cm day^{-1}) and rapid drawdown (5 cm day^{-1}) (Figure 4.1). The water level fell in the drawdown treatments to a minimum of 10 cm where it remained static until week 32 when the water level rose at 5 cm day^{-1} until it reached 90 cm (Figure 4.1). The experiment ran for a total of 36 weeks. The static hydraulic regime reflected the regimes Lake Wetherell and Red Bank Creek are subjected to most of the time (Figure 1.5). The slow drawdown regime reflected the hydraulic regime of Lakes Malta, Balaka and Bijiji when the water level in Lake Wetherell is lower than the feeder creek and the lake is drying due to evaporation. The rapid drawdown hydraulic regime simulated the rate of drawdown in Lakes Pamamaroo, Menindee and Cawndilla when they are used to supply downstream users with water (Figure 1.6 and Figure 1.7). The rate of reflooding (5 cm day^{-1}) was also chosen to simulate rates commonly experienced by plants growing in the Menindee Lakes (Figure 1.5, Figure 1.6 and Figure 1.7).

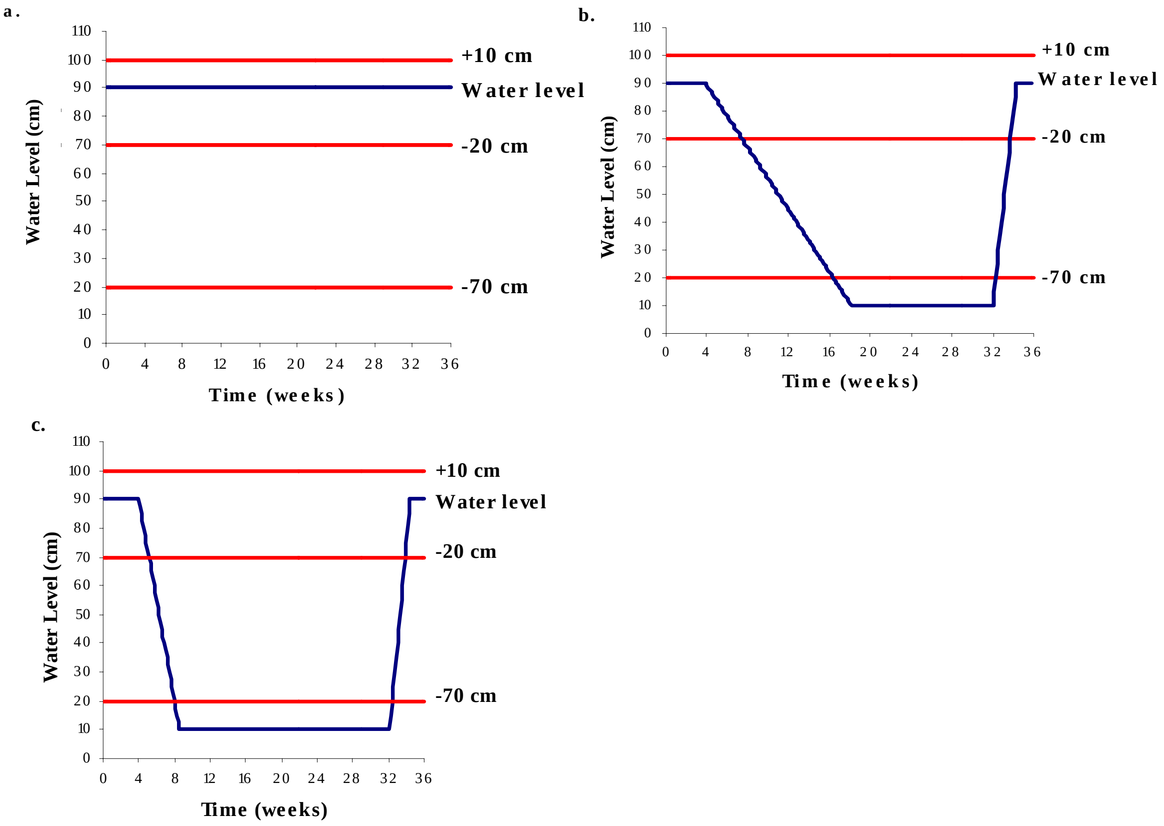

Figure 4.1: Pond water levels (a. Static, b. Slow Drawdown and c. Rapid Drawdown) with respect to the different elevation treatments (+10 cm, -20 cm and -70 cm) over the experimental period.

Within each hydraulic regime, there were three elevations +10, -20 and -70 cm: +10 cm the soil surface was 10 cm above the initial water level of 90 cm, -20 cm the soil surface was 20 cm below the initial water level and -70 cm the soil surface was 70 cm below the initial water level (Figure 4.1).

To simulate the underwater light climate of the Lower Darling River and Menindee Lakes, bentonite was added to the ponds to give a mean turbidity of 100 NTU. To keep the bentonite in suspension pumps were placed in each pond to circulate the water and every two days each pond was manually mixed. Directing the flow under benches, behind pots and around the pond walls, prevented damage to the plants (sensu Cenzato and Ganf 2001). The turbidity was measured every two days, before and after the manual mixing, with a Hach model 2100A turbidity meter. The turbidity throughout the experiment ranged from 70 to 120 NTU. The same type of bentonite was used for this experiment as used by Cenzato and Ganf (2001); therefore, the downwelling extinction coefficient (K_d) was calculated from the turbidity measurements using the same relationship:

$$K_\mathrm{d} = 0.93 + 0.057\ \mathrm{Turbidity}$$

The resultant downwelling extinction coefficient at 100 NTU was 6.63 m^{-1} and ranged from 4.92 m^{-1} (70 NTU) to 7.77 m^{-1} (120 NTU).

4.2.5 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).

4.2.6 Functional Classification

Brock and Casanova (1997) classified species into four groups based on their strategies of persistence when subjected to fluctuating water levels: terrestrial (intolerant of flooding), amphibious (able to persist in a wide rage of conditions from flooded to damp soil), submerged (intolerant of drying) and floating (not anchored to the sediment). The terrestrial group can be split into terrestrial dry (able to tolerate dry conditions) and terrestrial damp (unable to persist in dry conditions). The amphibious group can be split into amphibious tolerators (tolerates water level changes with no changes in morphology) and amphibious responders (changes morphology in response to water level changes).

4.2.7 Data Collection and Analysis

The numbers of plants from each species present in each water regime treatment were counted every four weeks. Differences in species composition between hydraulic regime, elevation and sampling date for Redbank Creek were compared using group average (UPGMA) clustering, multi-response permutation procedures (MRPP) and indicator species analysis (Dufrene and Legendre 1997) undertaken with the package PCOrd version 4.28 (McCune and Mefford 1999). Bray-Curtis distances were used to calculate the similarity matrix for all multivariate analyses (Bray and Curtis 1957). Bare soil was used as a taxon, so as not to exclude the replicates devoid of plants from the multivariate analyses. Any replicate that was totally devoid of plants was said to have bare soil at an abundance of one. Replicates were pooled for the cluster analysis for clarity but not for indicator species analysis or MRPP. For all statistical tests $\alpha = 0.05$. Groups with different species compositions were assigned according to divisions from the clustering analysis. Species deemed non-significant by indicator species analysis were classed as Type A, B or C non-significant species (Chapter 2).

4.3 Results

4.3.1 Water Regime and Species Composition

Three distinct plant communities developed from the Red Bank Creek seed bank at a distance of 20% (Figure 4.2, MRPP: $A = 0.45$, $P < 0.0001$)). Group A was not submerged when sampled, group B was submerged and *Myriophyllum verrucosum* was present and group C were also submerged but devoid of plants. Group A samples was from the +10 experimental elevation in all hydraulic regimes (never submerged) or from the -20 and -70 cm elevations in the drawdown ponds that were initially submerged, had become exposed and developed a floristic composition similar to the samples that were never submerged (Figure 4.2). The group B samples were submerged for longer than eight weeks, which was sufficient time for *Myriophyllum verrucosum* to germinate (Figure 4.2). The group C samples consisted of samples that were submerged early in the experiment (weeks 4 to 8) or were elevations from the drawdown hydraulic regimes that were reflooded and all of the plants were killed (Figure 4.2).

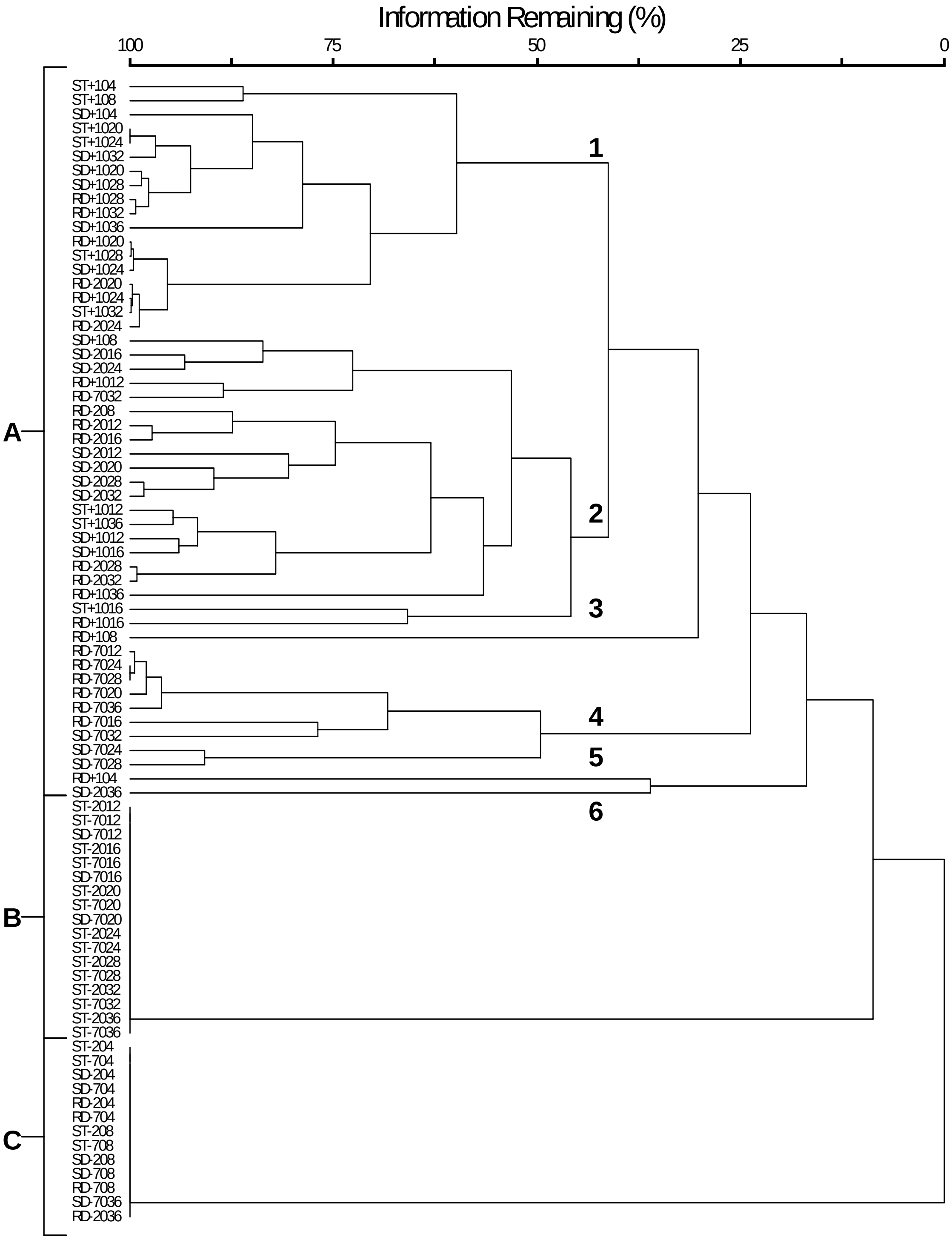

Figure 4.2: Group average clustering dendrogram of each hydrology, elevation and sampling time for the Red Bank Creek seed bank (ST = static, SD = slow drawdown, RD = rapid drawdown, +10, -20 or -70 = elevation and 4, 8, 12, 16, 20, 24, 28, 32 or 36 = sampling time in weeks).

Bare soil was the only significant indicator of group C and *Myriophyllum verrucosum* was the only significant indicator of group B (Table 4.1). Group A had the largest number of significant indicator species: *Alternanthera denticulata, Ammania multiflora, Centipeda* *minima, Epaltes australis, Heliotropium curassivicum, Limosella australis, Medicago* spp., *Morgania floribunda* and *Xanthium occidentale* (Table 4.1). No species was widespread over the three groups, however 15 species were only found in group A that were not significant indicator species because they were rare (Type A non-significant species (Chapter 2)) (Table 4.1).

Table 4.1: Indicator species analysis of the Red Bank Creek seed bank (Type A, B or C denotes why the species was not a significant indicator (Chapter 2)).

Species	Group	*P*
Alternanthera denticulata	A	0.001
Ammania multiflora	A	0.006
Centipeda minima	A	0.001
Epaltes australis	A	0.003
Heliotropium curassivicum	A	0.016
Limosella australis	A	0.002
Medicago spp.	A	0.001
Morgania floribunda	A	0.036
Xanthium occidentale	A	0.01
Alisma sp.	A	0.135 (Type A)
Crassula sieberana	A	1.00 (Type A)
Cyperus gymnocaulos	A	0.057 (Type A)
Eragrostis australasica	A	0.851 (Type A)
Eragrostis dielsii	A	0.119 (Type A)
Eragrostis parvifolia	A	0.365 (Type A)
Euphorbia drummondii	A	1.00 (Type A)
Gnaphalium luteo-album	A	0.123 (Type A)
Juncus aridicola	A	1.00 (Type A)
Mollogo cerviana	A	0.765 (Type A)
Polygonum plebium	A	0.246 (Type A)
Rumex bidens	A	0.434 (Type A)
Sporobolus mitchelli	A	1.00 (Type A)
Typha domingensis	A	0.079 (Type A)
Bare Soil	B	0.001
Myriophyllum verrucosum	C	0.001

Group A can be split into six groups at a distance of 55% (1-6) (MRPP: $A = 0.14$, $P < 0.0001$) (Figure 4.2). These groups generally corresponded to different elevations: group 1 was dominated by samples from the +10 cm elevation, group 2 with samples from the +10 and -20 cm elevations, group 4 with samples from the -70 cm elevation (Figure 4.2). Groups 3, 5 and 6 were outliers (Figure 4.2). Despite MRPP indicating that the groups had significantly different species composition, indicator species analysis showed very few significant indicators. The majority of the species were widespread across all of the groups (Type B and C non-significant species) although *Medicago* spp. was a significant indicator of group 1, *Limosella australis* was a significant indicator of group 3 and *Eragrostis australasica* was a significant indicator of group 5. All other groups had no significant indicator species.

The patterns of germination from the seed bank and recruitment for the five remaining lakes showed similar patterns to Red Bank Creek, except that *Myriophyllum verrucosum* was not present in the seed bank (Appendix 3 and Appendix 4). Therefore, the samples that were submerged were generally devoid of plants, except if they were reflooded and amphibious species were present. The main factor that determined the community composition was whether the sediment surface was exposed or submerged when sampled. The samples that were exposed could also be split into groups that generally corresponded to elevation. These groups had significantly different species compositions (MRPP $P < 0.05$) however, each group contained less than two significant indicator species (several times there were none) with the majority of species present widespread across all sub-groups.

4.3.2 Water Regime Requirements

The response of individual species to the different water regimes indicates the water regime requirements for that species. Response to the different water regimes for a particular species did not vary between lakes; therefore, the seed bank that contained the highest abundance of the target species was examined.

Myriophyllum verrucosum was the only species that germinated whilst the sediment was submerged (Figure 4.3). When the sediment was exposed, the plants did not immediately die and in the rapid drawdown -70 cm water regime plants that germinated between weeks four and eight persisted for the remainder of the experiment (Figure 4.3). *Myriophyllum verrucosum* did not germinate in treatments that were exposed at the beginning of the experiment (Figure 4.3); therefore, it probably requires inundation to germinate. Germination and recruitment was significantly lower at the -20 cm elevations in both drawdown regimes (Figure 4.3). No plants survived to the end of the experiment in the slow and rapid drawdown -20 cm water regimes and the plants in the rapid drawdown -20 cm water regime died earlier (Figure 4.3)

This species was not classified as a submergent because it persisted in exposed treatments. All species from this genus are morphologically plastic (Cunningham *et al.* 1981; Brock and

Casanova 1991); therefore, it was classified as an amphibious responder (Brock and Casanova 1997).

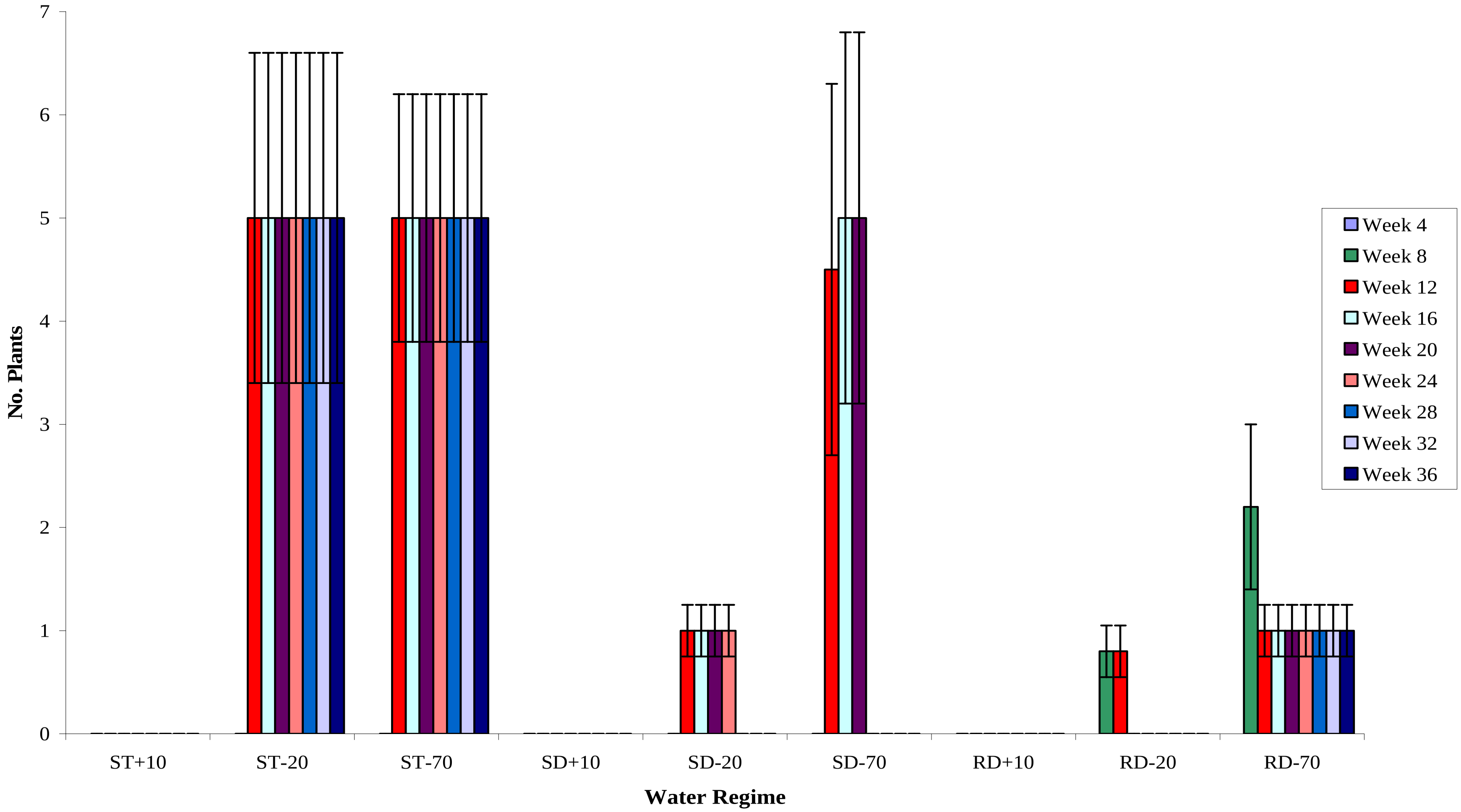

Figure 4.3: Abundance of *Myriophyllum verrucosum* through time for each water regime from the Red Bank Creek seed bank (error bars = ±1 SE) (ST = static, SD = slow drawdown, RD = rapid drawdown; +10, -20 and -70 = elevation).

Typha domingensis was only present in three water regimes (slow drawdown -20 and -70 cm and rapid drawdown -70 cm) (Figure 4.4). No plants were observed until the water level was drawn down below the sediment surface and all plants survived flooding at the end of the experiment (Figure 4.4). In the slow drawdown -20 cm and rapid drawdown -70 cm water regimes the number of plants increased by asexual reproduction (Figure 4.4). The plants in the slow drawdown -70 cm water regime did not reproduce asexually.

Typha domingensis was one of the few species that did not respond negatively to flooding and survived exposure, therefore it was classed as an amphibious responder (Brock and Casanova 1997).

Alisma sp., *Ludwigia peploides*, *Marsilea* sp. and *Persicaria lapathifolium* seeds (and spores) also germinated when the sediment surface was not inundated and survived flooding by allocating more resources to above ground organs. *Ludwigia peploides* and *Persicaria lapathifolium* responded by increasing internode length, *Alisma* sp. increased petiole length and *Marsilea* sp. increased frond length (pers. obs.). Therefore, they were also classified as amphibious responders (Brock and Casanova 1997).

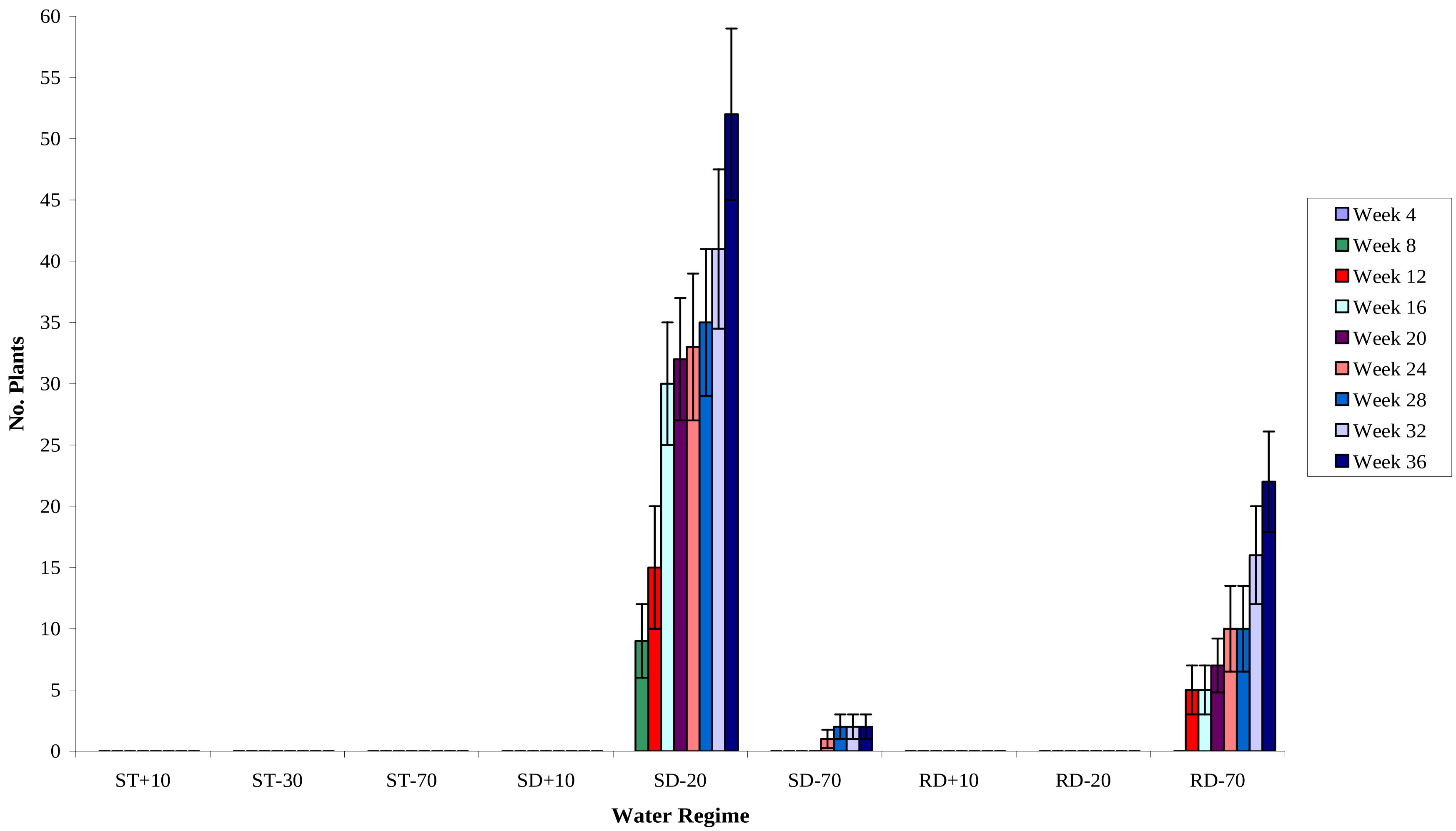

Figure 4.4: Abundance of *Typha domingensis* through time for each water regime from the Lake Wetherell seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Germination and recruitment for *Heliotropium curassivicum* was highest in the water regimes that were not initially submerged (+10 cm) (Figure 4.5). After the initial germination event, the number of plants generally decreased in the +10 cm elevations until week 36 when the number of plants increased (Figure 4.5). Seed remained viable whilst submerged and the timing of germination in the water regimes that were initially submerged then exposed corresponded to when the sediment was exposed (Figure 4.5). At the -70 cm elevations in the drawdown hydraulic regimes, the number of plants was generally lower than the other water regimes (Figure 4.5). Plants did not persist for longer than four weeks in the slow drawdown -70 cm water regime (Figure 4.5). When water levels increased in the drawdown regimes after week 32 all plants at the -70 cm elevations died, however plants survived at the -20 cm elevation (Figure 4.5).

Heliotropium curassivicum, due to its ability to survive shallow inundation, was classified as an amphibious species (Brock and Casanova 1997). The morphology of the submerged and non-submerged plants was similar therefore; it is an amphibious tolerator (Brock and Casanova 1997).

Alternanthera denticulata showed similar patterns of germination and recruitment to *Heliotropium curassivicum* (Figure 4.5). Plants survived flooding to a depth of 20 cm for four weeks, hence; this species was also classified as amphibious (Brock and Casanova 1997). Plants growing at the -20 cm elevations were morphologically similar to those growing at the +10 cm elevations therefore this species is also an amphibious tolerator (Brock and Casanova 1997).

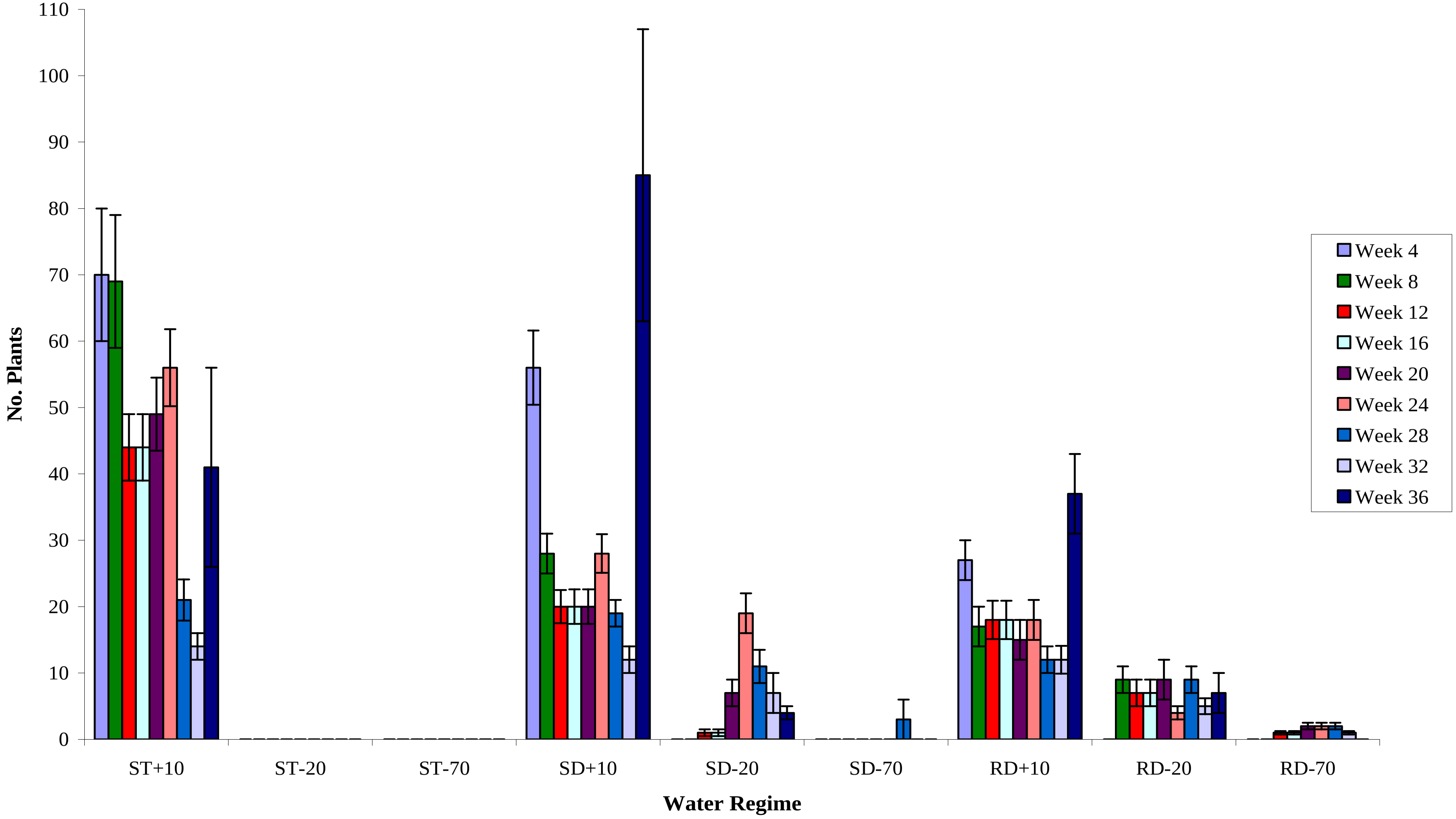

Figure 4.5: Abundance of *Heliotropium curassivicum* through time for each water regime from the Lake Cawndilla seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Sporobolus mitchelli seeds only germinated when the sediment surface was exposed (Figure 4.6). However, the seeds remained viable whilst submerged and in the water regimes that were initially submerged then exposed germination occurred soon after the sediment was exposed (Figure 4.6). After germination, the number of plants present remained relatively constant, even when flooded (Figure 4.6).

This species was classified as an amphibious tolerator (Brock and Casanova 1997) because it survived inundation and the plants that were inundated were morphologically similar to those that were not inundated.

Juncus aridicola was also classified as an amphibious tolerator (Brock and Casanova 1997). Seeds only germinated in water regimes that were initially flooded, after the sediment surface was exposed and when flooded most plants survived but showed no morphological changes.

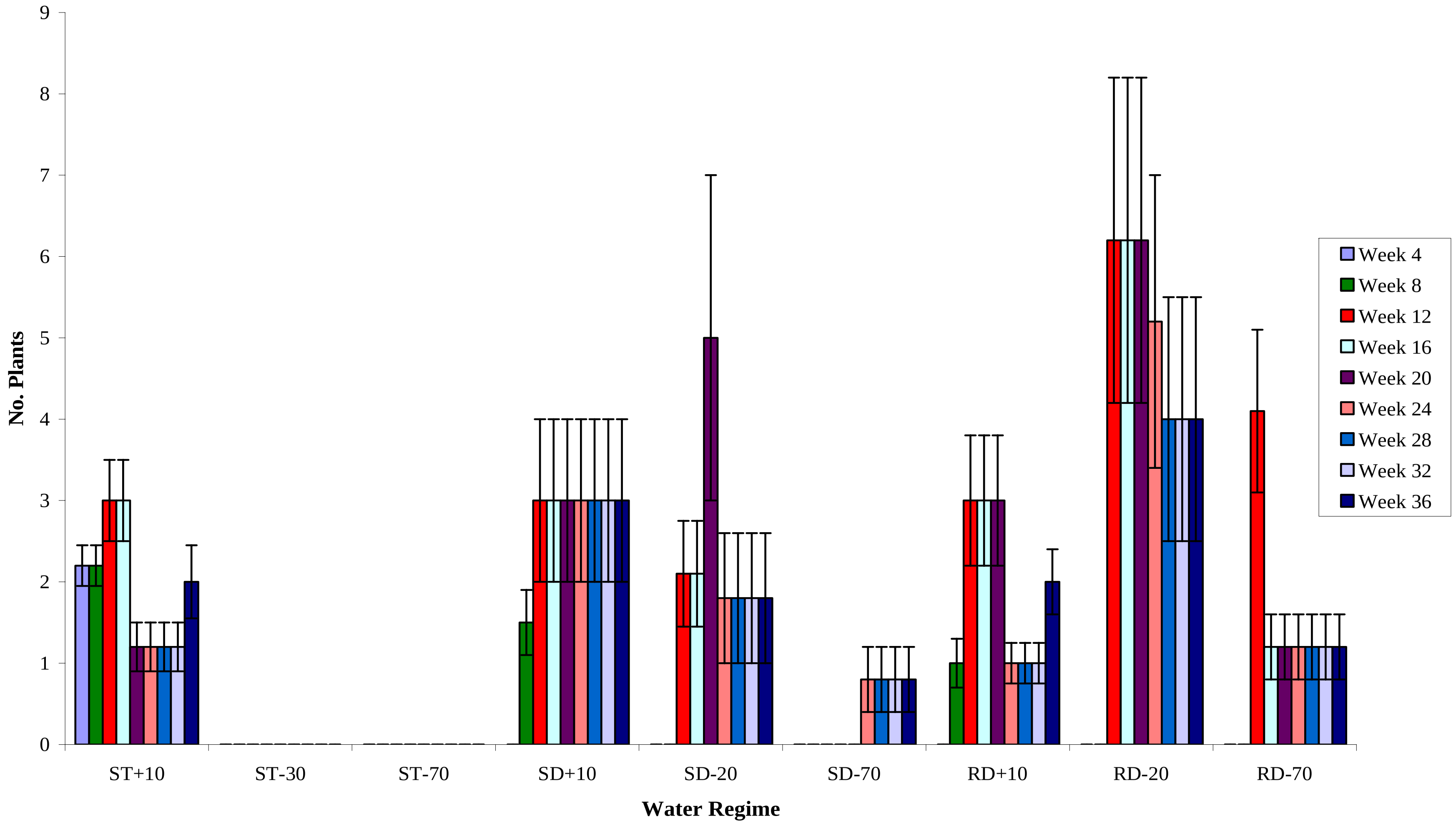

Figure 4.6: Abundance of *Sporobolus mitchelli* through time for each water regime from the Lake Malta seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Cyperus gymnocaulos also did not germinate whilst submerged, however the seeds remained viable and germinated when the sediment surface was exposed (Figure 4.7). Survivorship of the seedlings was low with only individuals in the static and rapid drawdown +10 cm water regimes persisting for the duration of the experiment (Figure 4.7). No seeds germinated in the rapid drawdown -20 cm water regime and all plants died when flooded at the end of the experiment (Figure 4.7).

These results suggest that *Cyperus gymnocaulos* is a terrestrial species, however observations in the field show that this species will survive inundation as rhizomes therefore, it was classified as an amphibious tolerator (Brock and Casanova 1997).

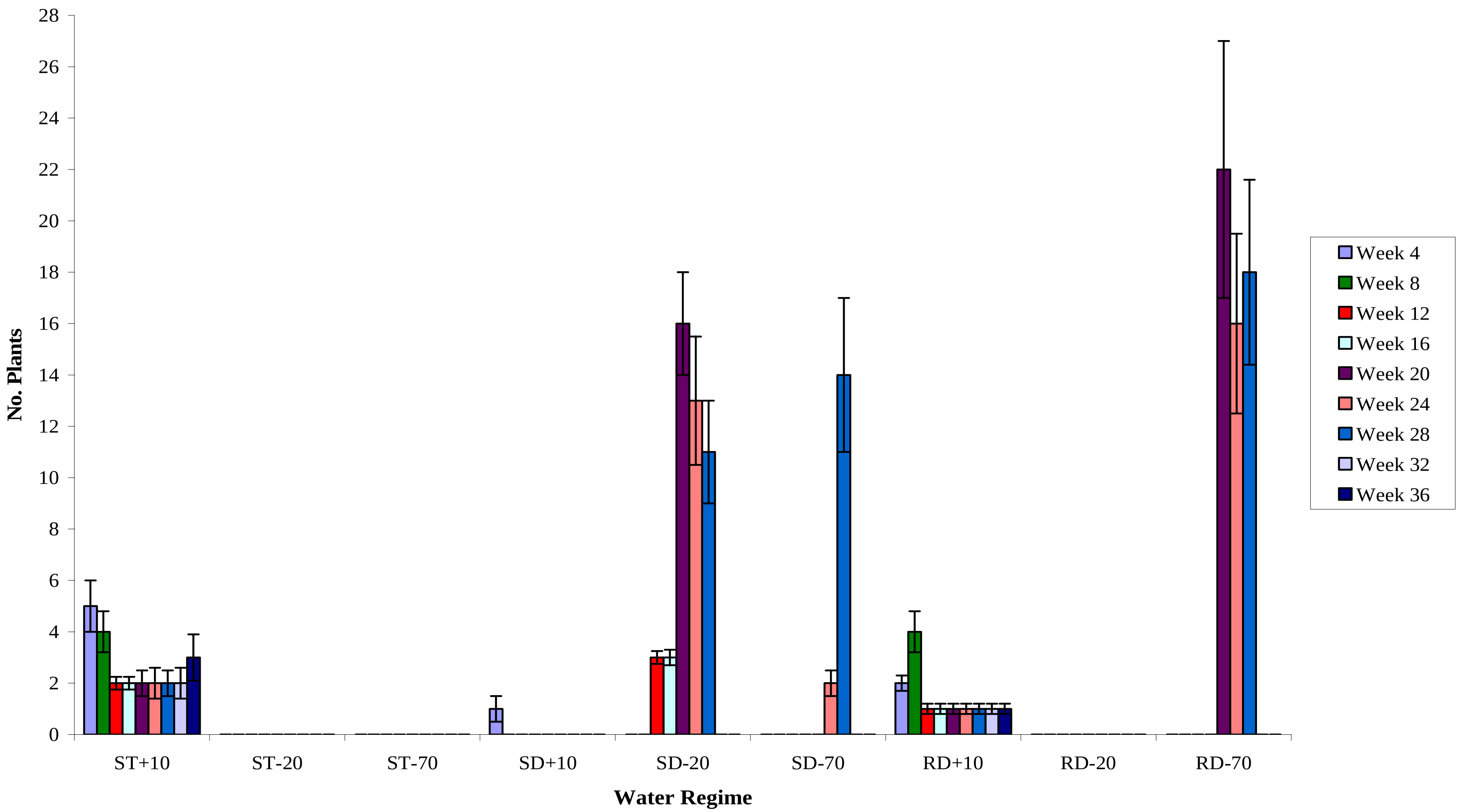

Figure 4.7: Abundance of *Cyperus gymnocaulos* through time for each water regime from the Lake Cawndilla seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Epaltes australis seeds also did not germinate whilst submerged, however the seeds remained viable and germinated once the sediment was exposed (Figure 4.8). A smaller number of plants were observed in the rapid drawdown +10 cm water regime than the other +10 cm elevations (Figure 4.8). The number of plants generally decreased over the experiment at the +10 cm elevations in all hydraulic regimes, except for between weeks 32 and 36 in the drawdown regimes when water levels rose (Figure 4.1) and the number of plants increased (Figure 4.8). The numbers of plants in the slow drawdown -70 cm and rapid drawdown -20 cm water regimes were lower than other water regimes that included periods of exposure (Figure 4.8). All plants were killed when flooded at the end of the experiment (Figure 4.8).

According to the classification system of Brock and Casanova (1997) *Epaltes australis*, should be a classified as a terrestrial species because it was intolerant of flooding. This species however is found exclusively in areas that are periodically inundated (Cunningham *et al.* 1981); therefore, it was classified as a floodplain species.

Morgania floribunda, Gnaphalium luteo-album, Centipeda minima, Ammania multiflora, Chenopodium pumilio, Haloragis aspera, Iseotopsis graminifolia, Mollogo cerviana, Polygonum plebium, Rumex bidens, Wahlenbergia communis and *Xanthium occidentale* also did not germinate whilst submerged and were intolerant of flooding. These species were not classified as terrestrial because they are only found in areas that are periodically inundated (Cunningham *et al.* 1981) therefore they were also classified as floodplain species.

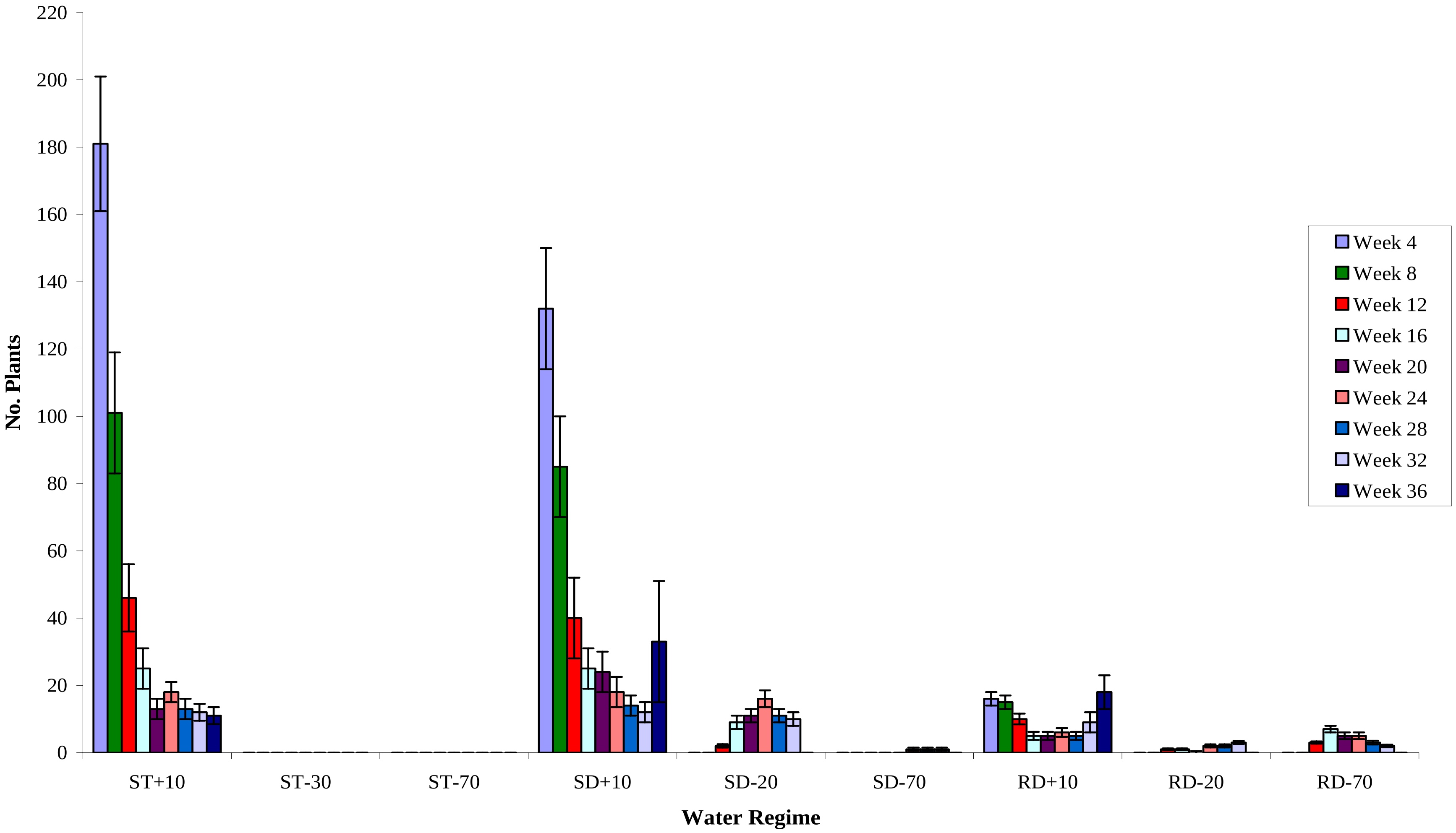

Figure 4.8: Abundance of *Epaltes australis* through time for each water regime from the Lake Menindee seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Limosella australis was not found in the +10 cm elevations in any hydraulic regime, however seeds did not germinate whilst the sediment was inundated (Figure 4.9). Seeds germinated soon after the sediment was exposed and in the slow drawdown -20 and -70 cm and rapid drawdown -20 and -70 cm water regimes. The number of plants increased by asexual reproduction in all of the aforementioned water regimes except for rapid drawdown -20 cm (Figure 4.9). In the rapid drawdown -20 cm water regime, no plants survived past week 20 (Figure 4.9). All plants died when flooded at the end of the experiment (Figure 4.9).

This species was intolerant of flooding but is only found in areas that are subject to periodic inundation (Cunningham *et al.* 1981); hence, it was classified as a floodplain species.

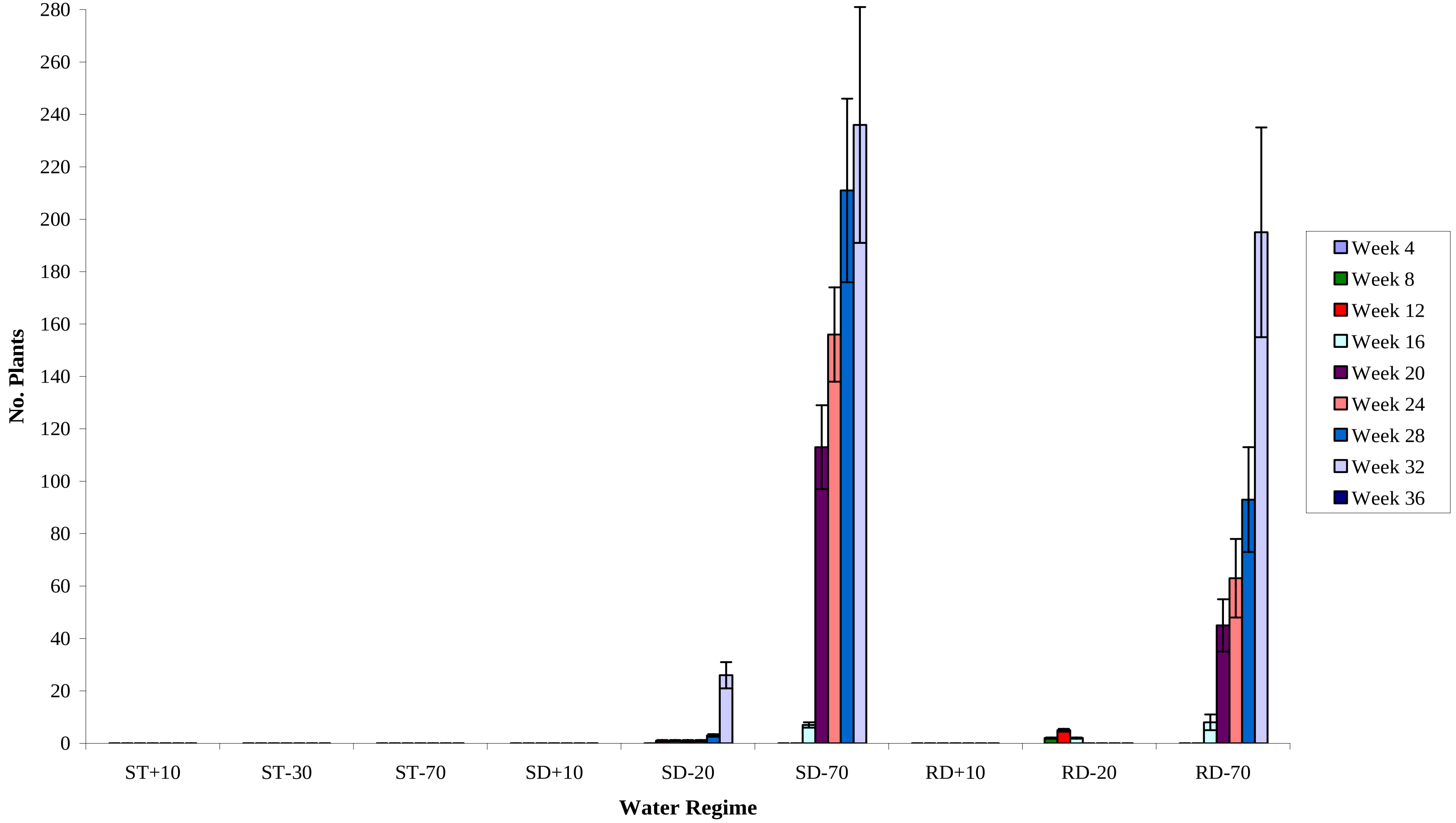

Figure 4.9: Abundance of *Limosella australis* through time for each water regime from the Lake Menindee seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

Medicago spp. did not germinate whilst submerged however, the seeds remained viable whilst submerged and germinated soon after the sediment became exposed (Figure 4.10). Larger numbers of seeds germinated in the rapid drawdown water regimes than other water regimes (Figure 4.10). All plants died when the sediment was flooded (weeks 32 to 36) (Figure 4.10) and this species is found in areas that are never inundated (Cunningham *et al.* 1981); therefore, it belongs in the terrestrial functional group (Brock and Casanova 1997).

The germination observed between weeks 16 and 24 in the slow drawdown +10 cm and rapid drawdown +10 and –20 cm water regimes (Figure 4.10) corresponded with rainfall events.

Argemone ochroleuca, Eragrostis dielsii, Euphorbia drummondii, Galenia secunda, Nicotiana glauca, Senecio sp. and *Tetragonia tetragonoides* also did not germinate whilst submerged and did not survive flooding. Therefore, they were also classified at terrestrial species (Brock and Casanova 1997). *Tetragonia tetragonoides* is generally found in damp situations after soaking rains (Cunningham *et al.* 1981) therefore it was classified as a terrestrial damp species. All of the other terrestrial species are more desiccation tolerant (Cunningham *et al.* 1981) therefore; they were classified as terrestrial dry species.

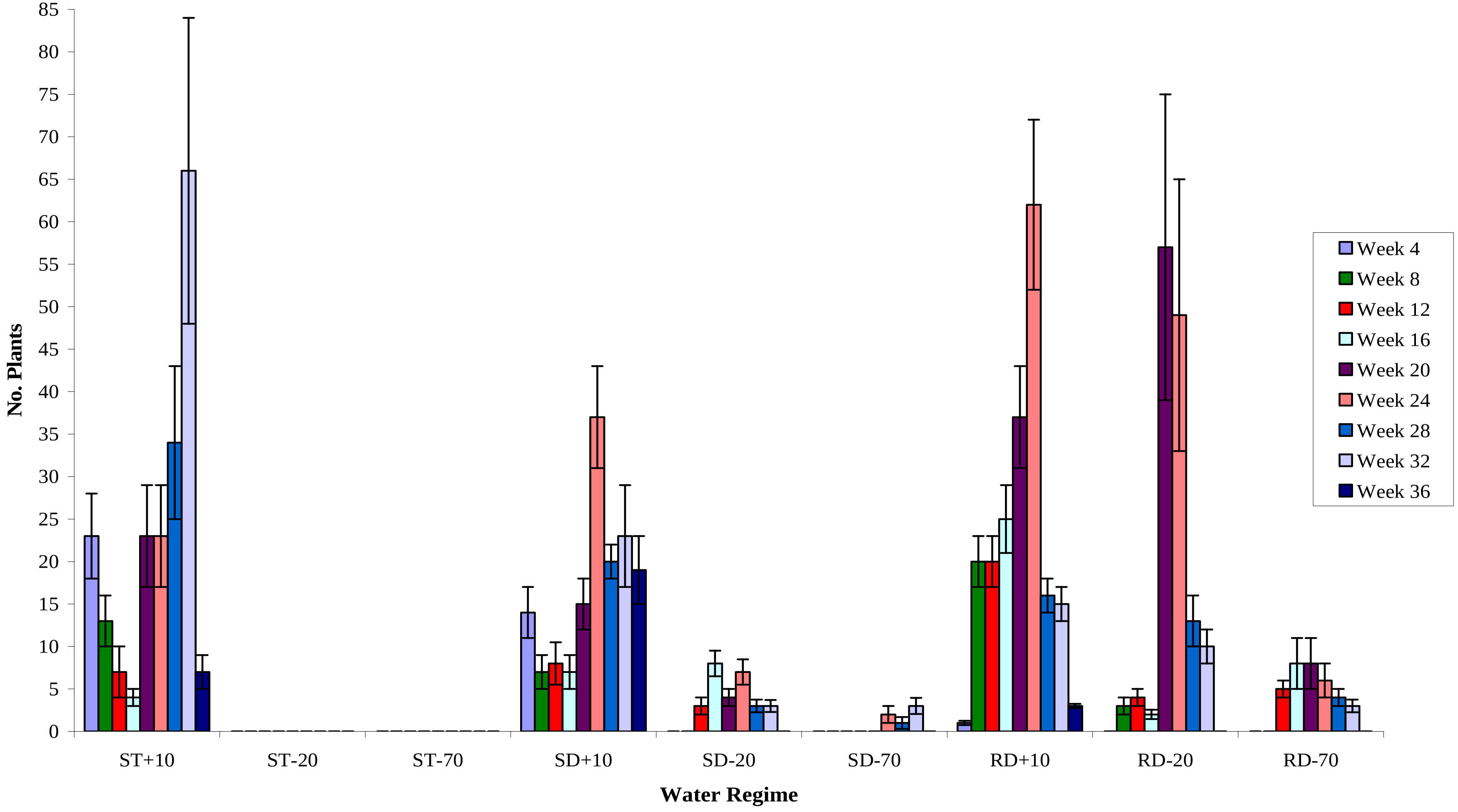

Figure 4.10: Abundance of *Medicago* spp. through time for each water regime from the Red Bank Creek seed bank (error bars = ±1 SE) (for explanation of abbreviations see Figure 4.3).

The floodplain species were the dominant functional with 14 of the 31 species (Table 4.2). Five species were classified as amphibious tolerators, one as terrestrial damp, seven as terrestrial dry and six as amphibious responders (Table 4.2).

Table 4.2: Functional classification of the species from all seed banks modified from the system suggested by Brock and Casanova (1997) (* denotes exotic species).

Species	Functional Classification
Alisma sp.	Amphibious responder
Ludwigia peploides	Amphibious responder
Marsilea sp.	Amphibious responder
Myriophyllum verrucosum	Amphibious responder
Persicaria lapathifolium	Amphibious responder
Typha domingensis	Amphibious responder
Alternanthera denticulata	Amphibious tolerator
Cyperus gymnocaulos	Amphibious tolerator
Heliotropium curassivicum	Amphibious tolerator
Juncus aridicola	Amphibious tolerator
Sporobolus mitchelli	Amphibious tolerator
Ammania multiflora	Floodplain
Centipeda minima	Floodplain
Chenopodium pumilio	Floodplain
Epaltes australis	Floodplain
Gnaphalium luteo-album	Floodplain
Haloragis aspera	Floodplain
Iseotopsis graminifolia	Floodplain
Limosella australis	Floodplain
Morgania floribunda	Floodplain
Mollogo cerviana	Floodplain
Polygonum plebium	Floodplain
Rumex bidens	Floodplain
Wahlenbergia communis	Floodplain
Xanthium occidentale *	Floodplain
Tetragonia tetragonoides	Terrestrial damp
Argemone ochroleuca *	Terrestrial dry
Eragrostis dielsii	Terrestrial dry
Euphorbia drummondii	Terrestrial dry
Galenia secunda *	Terrestrial dry
Medicago spp. *	Terrestrial dry
Nicotiana glauca	Terrestrial dry
Senecio sp.	Terrestrial dry

4.4 Discussion

4.4.1 Water Regime and Species Composition

The plant communities derived from the seed bank were dependent on water regime, which determined whether the sediment was exposed or flooded and the duration of flood or exposure. Therefore, water regime acted as an environmental sieve (sensu Harper 1977; van der Valk 1981), which allowed only certain species to germinate and survive. Inundation of the sediment surface prevented the germination of all but one species, which supports the observations of Welling *et al.* (1988b) and Keddy and Reznicek (1986) that recruitment from the seed bank primarily occurs when the sediment surface is exposed and drawdown is critical for the recruitment of many species. In lakes with static water levels, the zone of germination and recruitment (for most species) will be restricted to the area around the edge where water is brought to the surface by capillary action.

Inundation or exposure of the sediment is only one component of water regime that can influence germination and recruitment from the seed bank. Depth, duration, frequency and rate of flood and drawdown can also potentially influence germination and recruitment (Casanova and Brock 2000).

Casanova and Brock (2000) concluded that duration of flood and drawdown was the most important component of water regime in determining plant community composition. The duration of flooding was the major determining factor in the recruitment of *Myriophyllum verrucosum*, however there was no difference in recruitment from samples flooded to 20 cm or 70 cm with turbid water. The duration of exposure did influence species composition but not to the extent observed in the field (Chapter 5). The maximum duration of exposure for any sample in this experiment was 252 days (36 weeks); in contrast, some quadrats were exposed for 488 days in the field (Chapter 5). In the field the quadrats that had the longest exposure times were devoid of annuals such as *Epaltes australis, Alternanthera denticulata, Xanthium occidentale* and *Centipeda minima* (Chapter 5), which were all present in the ponds when sampled for the final time.

Water depth was not important for germination and recruitment in samples that were flooded, even though they were subjected to a steep underwater light gradient. This is in contrast to many studies where the species composition was dependent on water depth and inturn underwater light intensity (e.g. Spence 1982; Keddy and Ellis 1985; Chambers and Kalff 1987b; Chambers and Kalff 1987a; Chambers and Prepas 1988; Moore and Keddy 1988; Grillas 1990; Seabloom and van der Valk 2003). Water depth was however, important in the survival of species that had recruited and were flooded. All floodplain, terrestrial and some amphibious species died when top flooded; however, *Heliotropium curassivicum* and *Alternanthera denticulata* survived when flooded to 20 cm. Similar results were reported for *Melaleuca halmaturorum* saplings (Denton and Ganf 1994) and *Xanthium occidentale* seedlings and adults (Victorsen 2001; Chapter 6).

The seeds of floodplain, amphibious and terrestrial species remained viable when submerged for at least 80 days. Not all species have seeds that remain viable whilst submerged for extended periods. For example, *Melaleuca halmaturorum* seeds lost viability when submerged for longer than 30 days (Nicol and Ganf 2000). Maintenance of seed viability whilst submerged is important if plants are to colonise the lakebed, because it is a more advantageous than relying on dispersal into areas of newly exposed sediment. In ephemeral systems, if a species has to rely on dispersal, there is a high chance that seeds may not reach the area whilst conditions for germination are favourable.

Despite the presence of only one species that germinated whilst submerged, these results supported the conclusions by van der Valk and Davis (1976) that wetland systems, due to their seed banks, jump from one successional stage to another when subjected to fluctuating water levels. For each site the samples from the elevations in the drawdown hydraulic regimes that were initially flooded developed a similar species composition to the elevations that were never flooded and when reflooded most or all of the plants died resulting in a species composition similar to the samples that were never exposed.

4.4.2 Water Regime Requirements

The water regime requirements for germination and survival generally reflected the Brock and Casanova (1997) functional classifications. The functional classes of submerged, floating, amphibious and terrestrial defined by Brock and Casanova (1997), strictly speaking, does apply to the species present in the seed bank of this system. However, this classification system does not take into account the distribution of the species in nature. A fifth functional group has been proposed called floodplain species. Under the system proposed by Brock and Casanova (1997) these species would be classed as terrestrial species because they were intolerant of flooding, did not germinate whilst submerged and were able to tolerate desiccation. However, floodplain species only occur in areas that are subject to periodic inundation whereas terrestrial species can occur in areas that are never flooded (Cunningham *et al.* 1981). The distinction between floodplain and terrestrial species cannot be determined from the data presented in this experiment and were separated according to their distribution described in Cunningham *et al.* (1981).

The most obvious water regime requirement for germination for all species present in the seed bank, except *Myriophyllum verrucosum*, was exposed sediment with high surface soil moisture. However, *Typha domingensis* has been shown to germinate whilst submerged to a depth of 80 cm in clear water (Nicol and Ganf 2000). Bonnewell *et al.* (1983) reported that *Typha latifolia* seeds required long light exposure for germination and Froend and McComb (1994) reported similar conditions for *Typha orientalis* germination. Therefore, low light intensity due to the high turbidity may have been responsible for the lack of germination whilst submerged. Insufficient light may have prevented other amphibious species from germinating whilst submerged therefore drawdown is critical for these species to complete their life cycle in turbid water bodies. For germination and potential recruitment to occur over an entire lakebed, water levels must be drawn down. The duration and rate of drawdown to ensure recruitment and survival to maturity will be dependent on the functional group and species.

Terrestrial and floodplain species both had similar water regime requirements for recruitment and reproduction. Species from these functional groups required exposed sediment with sufficient soil moisture in the root zone. The required soil moisture content was dependent on species, although most species were desiccation tolerant.

The amphibious functional group had the widest water regime tolerance for recruitment and reproduction. Species from this functional group were able to recruit and grow when the sediment surface was inundated or exposed.

The degree of inundation or exposure tolerance was species and life stage dependent. For example, *Cyperus gymnocaulos* was intolerant of flooding (Figure 4.7) probably because the plants were all derived from seed and had not produced rhizomes. This species has been observed in the field resprouting from rhizomes on sediment that had been submerged for nearly eight years to a maximum water depth of 7 m (pers. obs.). *Ludwigia peploides* and

Persicaria lapathifolium responded positively to flooding because the rate at which they increased internode length was able to keep up with the rate of flooding (pers. obs.). *Ludwigia peploides* was also a dominant species in the static +10 cm water regime with three plants accounting for over 80% of the total biomass from that water regime. This species will grow in water up to 2 m deep and will extend across open water with floating stems regardless of the depth (Sainty and Jacobs 1981; Sainty and Jacobs 1994). *Persicaria lapathifolium* has been observed growing in water up to 1 m deep (Sainty and Jacobs 1981; Sainty and Jacobs 1994). *Typha domingensis* will persist almost indefinitely in water up to 1.5 m deep providing stems and leaves are able to reach the surface. (Cunningham *et al.* 1981; Sainty and Jacobs 1981; Sainty and Jacobs 1994). *Juncus aridicola* and *Alisma* sp. can also survive almost indefinitely when flooded to depths of up to 1 m (Sainty and Jacobs 1981; Sainty and Jacobs 1994). *Marsilea* sp. will survive in shallow water for extended periods but sporocarps are rarely produced until water levels are drawn down (Aston 1973). *Heliotropium curassivicum* and *Alternanthera denticulata* tolerated flooding to a depth of 20 cm but were killed when flooded to 70 cm with turbid water. However, adult plants of the aforementioned species have not been observed in the field on newly exposed sediment (pers. obs.) and how long they can survive shallow inundation is unknown. *Sporobolus mitchelli* tolerated flooding to a depth of 70 cm with turbid water for at least four weeks however top flooding stalls plant growth, which recovers when water levels are drawn down (Taylor 2003). How long *Sporobolus mitchelli* can survive when flooded is also unknown but adult or juvenile plants have not been observed in the field on newly exposed areas of lakebed (pers. obs.)

The rate of drawdown appeared to have little effect on species composition, however when individual species were examined it was clear this did influence germination and recruitment of some species. When water levels were drawn down at 5 cm day^{-1} several amphibious and floodplain species showed reduced germination and recruitment (e.g. *Morgania floribunda*, *Limosella australis*), whilst others showed no response (e.g. *Sporobolus mitchelli*, *Heliotropium curassivicum*) and the terrestrial taxon *Medicago* spp. showed increased recruitment. Therefore, rapid drawdown (5 cm day^{-1} or greater) could facilitate the invasion of exotic terrestrial species. However, the responses of the aforementioned species may also be due to longer sediment exposure times brought about by the faster drawdown rate. For germination and recruitment of native floodplain and amphibious species over large areas of lakebed, the optimum rate of drawdown appears to be 1 cm day^{-1}.

Limosella australis, *Typha domingensis* and *Juncus aridicola* appeared to require inundation then exposure to germinate. However, *Limosella australis* was detected in the Reconnaissance Study (Chapter 2) and Strandline Investigation (Chapter 3). The samples taken for these investigations were not submerged but seedlings were removed at regular intervals. Nicol and Ganf (2000) and Nicol *et al.* (2003) reported that *Typha domingensis* germinated in water logged soil that was never inundated.

4.4.3 Conceptual Model

The response of the seed bank and recruited vegetation to different water regimes is described in the seed bank recruitment model (Figure 4.11). The model predicts the species that will establish (reach sexual maturity) in ephemeral lakes under different water regimes, providing they are present in the seed bank (Table 4.3). The seed bank recruitment model consists of two major states: flooded and exposed. When the sediment is flooded, the state depends on the duration of flooding and the species that have established (Figure 4.11). When the sediment is exposed the state depends on the amount of time the sediment has been exposed, whether the sediment has been flooded and soil moisture content (Figure 4.11). Whether a species will establish in a particular sub-state is dependent on the water regime requirements of the species.

The different sub-states when flooded are flooded for less than eight weeks, flooded for longer than eight weeks, newly reflooded sediment and reflooded sediment with amphibious vegetation.

When the seed bank is initially flooded, no plants will be present. After the sediment has been inundated for longer than eight weeks, *Myriophyllum verrucosum* will germinate and establish (if in the seed bank). The newly reflooded sediment sub-state is when the sediment has just been reflooded, but not for a sufficient period as to extirpate the floodplain and terrestrial species. If flooded for longer, depending on the species present, the state changes to flooded for less than eight weeks (if there are no amphibious species present) or flooded with amphibious species present (Figure 4.11).

When the sediment is exposed the four sub-states are newly exposed sediment, exposed sediment with high soil moisture content, exposed sediment with intermediate soil moisture content and exposed sediment with low soil moisture content.

The newly exposed sediment sub-state is when water levels are drawn down and flooded sediment becomes exposed to the atmosphere allowing amphibious, floodplain and terrestrial species to germinate. As water levels are drawn down and the sediment dries the system progresses from newly exposed sediment to exposed sediment with high soil moisture (waterlogged to field capacity), exposed sediment with intermediate soil moisture (field capacity to 10% soil moisture) and exposed sediment with low soil moisture (<10% soil moisture) (Figure 4.11).

Depending on the water level, rate and duration of drawdown or flooding the system can jump from one state to another (sensu van der Valk and Davis 1976) and the floristic composition changes accordingly; however, it does not take into consideration the impact of multiple wetting and drying cycles on floristic composition. In a lake with static water levels, it is possible to have the high, intermediate and low soil moisture sub-states and flooded for less than eight weeks, flooded for longer than eight weeks or flooded with amphibious species sub-states simultaneously present at different elevations.

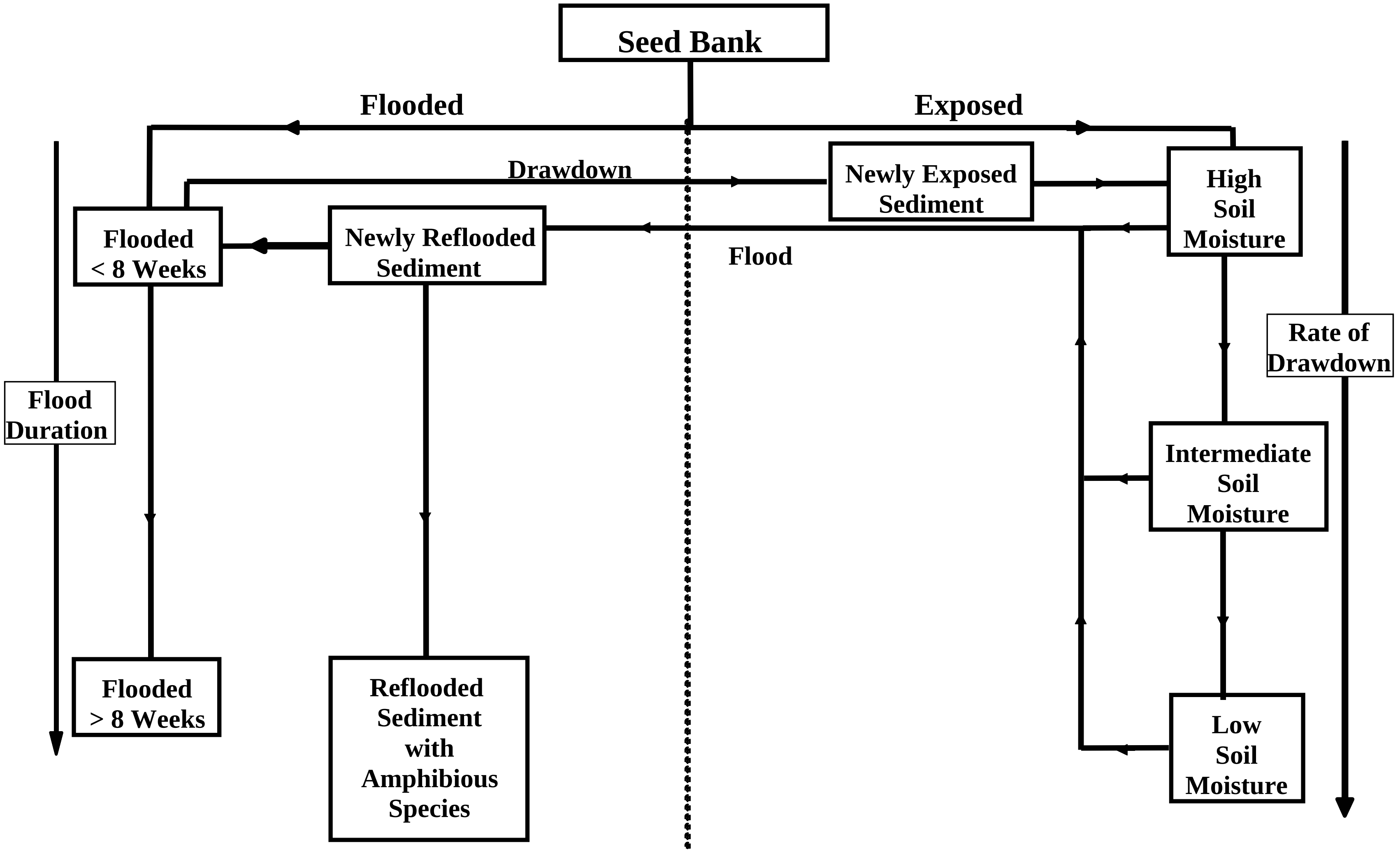

Figure 4.11: Conceptual model of recruitment from the seed bank and response of the recruited vegetation when the seed bank is subject to the different hydraulic regimes and elevations (seed bank recruitment model).

Table 4.3: Species that will germinate and potentially establish (depending on the amount of time the systems remains in a particular sub-state) in each of the different model sub-states for a: flooded sediment and b: exposed sediment.

a:

Flooded < 8 Weeks	Flooded > 8 Weeks	Newly Reflooded Sediment	Reflooded Sediment with Amphibious Species
Bare Soil	Bare Soil	*Alisma* sp.	*Alisma* sp.
	Myriophyllum verrucosum	*Alternanthera denticulata*	*Cyperus gymnocaulos*
		Centipeda minima	*Juncus aridicola*
		Cyperus gymnocaulos	*Ludwigia peploides*
		Juncus aridicola	*Marsilea* sp.
		Limosella australis	*Myriophyllum verrucosum*
		Ludwigia peploides	*Persicaria lapathifolium*
		Marsilea sp	*Sporobolus mitchelli*
		Persicaria lapathifolium	*Typha domingensis*
		Sporobolus mitchelli	
		Typha domingensis	

b:

Newly Exposed Sediment	Exposed High Soil Moisture	Exposed Intermediate Soil Moisture	Exposed Low Soil Moisture
Juncus aridicola	*Alisma* sp.	*Alternanthera denticulata*	*Alternanthera denticulata*
Limosella australis	*Alternanthera denticulata*	*Ammania multiflora*	*Argemone ochroleuca*
Marsilea sp.	*Ammania multiflora*	*Argemone ochroleuca*	*Cyperus gymnocaulos*
Myriophyllum verrucosum	*Argemone ochroleuca*	*Centipeda minima*	*Eragrostis dielsii*
Typha domingensis	*Centipeda minima*	*Cyperus gymnocaulos*	*Euphorbia drummondii*
	Cyperus gymnocaulos	*Epaltes australis*	*Galenia secunda*
	Epaltes australis	*Eragrostis dielsii*	*Haloragis aspera*
	Eragrostis dielsii	*Euphorbia drummondii*	*Heliotropium curassivicum*
	Euphorbia drummondii	*Galenia secunda*	*Medicago* spp.
	Galenia secunda	*Gnaphalium luteo-album*	*Morgania floribunda*
	Gnaphalium luteo-album	*Haloragis aspera*	*Sporobolus mitchelli*
	Haloragis aspera	*Heliotropium curassivicum*	*Xanthium occidentale*
	Heliotropium curassivicum	*Juncus aridicola*	
	Iseotopsis graminifolia	*Limosella australis*	
	Juncus aridicola	*Ludwigia peploides*	
	Limosella australis	*Marsilea* sp.	
	Ludwigia peploides	*Medicago* spp.	
	Marsilea sp.	*Morgania floribunda*	
	Medicago spp.	*Persicaria lapathifolium*	
	Mollogo cerviana	*Polygonum plebium*	
	Morgania floribunda	*Sporobolus mitchelli*	
	Persicaria lapathifolium	*Tetragonia tetragonoides*	
	Polygonum plebium	*Xanthium occidentale*	
	Sporobolus mitchelli		
	Tetragonia tetragonoides		
	Typha domingensis		
	Wahlenbergia communis		
	Xanthium occidentale		