

**Seed banks, Community Dynamics and Species Persistence
in 5 Tasmanian Temporary Wetlands.**

by

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Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution and to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except when due reference is made in the text.



5/7/02

Janet Anne Smith

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Abstract

Water regime has been found to be the most important factor in determining vegetation patterns in wetlands. The present study investigates the short and long-term persistence of plant communities within 5 temporary Tasmanian lentic wetlands and resistance and resilience of wetland communities to dry periods. Within each wetland an aquatic herbaceous and sedge-dominated zone were sampled seasonally between February, 1997 and November, 1998, to test difference between and within wetlands, and their relations to water depth.

Four glasshouse experiments using sediments taken from 9 permanent quadrats per vegetation type per wetland (zone) were used to determine temporal and spatial differences in seed banks in relation to season, vegetation type, depth, germination treatment and water regime. The relationship between the seed bank and extant vegetation was investigated.

A functional group classification generated similar groups to Brock and Casanova (1997). These were: a) submerged; b) amphibious fluctuation responder; c) amphibious fluctuation tolerator-emergent; d) amphibious fluctuation tolerator-saturated/mudflat; and e) terrestrial.

The vegetation communities within the 5 temporary wetlands proved not resistant to changes in water level. Large differences in percentage cover were associated with hydrological changes over the 2 year period. However, the communities were able to resurrect relatively quickly after both short and long term dry periods.

The seed bank experiments indicated that Tasmanian temporary wetlands have species-rich persistent seed banks, and, therefore, the potential for future regeneration. In general, species in the seed bank could be related to species found in the extant vegetation. However, at any given time, species can be found in the seed bank and not present in the extant vegetation, or vice versa. Both seed banks and vegetative regeneration were important mechanisms for species persistence in the vegetation communities of the 5 wetlands.

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ON THE NATURE OF THINGS

Nothing remains for ever what is was.
Everything is on the move. Everything
Is transformed by nature and forced into
new paths. One thing withered by time,
decays and dwindles, another emerges
from ignominy, and waxes strong. So
the nature of the world as a whole is
altered by age.

Roman Poet, Lucretius

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Chapter 1

Introduction

Importance of plant communities in wetlands

Wetland plant communities, especially those of marshes and swamps, are some of the most productive communities in the world (McComb and Lake, 1990; Maltby, 1991 Mitsch, 1998). In shallow wetlands, macrophytes are important for both their structure and function and are often the most important primary producers (Sculthorpe, 1967). Their abundance can influence both the biomass and productivity of all other primary producers as well as most processes occurring within these systems, for example, production of oxygen, nutrient cycling to and from sediments (Carpenter and Lodge, 1986; Fox 1996). Macrophyte communities promote sedimentation of mineral and organic particles and stabilise the sediment against erosion (Sand-Jensen *et al.*, 1989). They provide both an important habitat and food source for the wide range of animals that inhabit these areas, e.g. invertebrates, fish, waterfowl and frogs. They also provide a substrate for epiphytic algae and bacteria (Nielsen and Sand-Jensen, 1991). As a result, any change in environmental conditions within a wetland, such as fluctuations in water levels, that can alter aquatic macrophyte communities would inevitably have a flow on effect throughout the whole ecosystem.

Descriptions of aquatic plants

The term 'macrophyte' is generally used to describe macroscopic aquatic plants. The term includes flowering plants, ferns, mosses, liverworts, bryophytes and larger algae, such as charophytes (Sculthorpe, 1967; Hutchinson, 1975; Brock, 1994; Fox, 1996). The present study focuses on angiosperm and charophyte species. Although they were observed during the present study, ferns, mosses, liverworts, bryophytes and other larger algae were not included. However, it is noted that these are also important components of aquatic vegetation.

Generally, aquatic macrophytes are described by their life or growth form with regard to water, for example, floating (i.e. on the air-water interface), submerged and emergent

(i.e. photosynthetic parts above the water surface; Sculthorpe, 1967). This classification was further subdivided by Sainty and Jacobs (1981; Figure 1.1; Brock, 1994).

Definition of wetlands

The term 'wetland' groups together a wide range of habitats that share a number of common features, the most important of which are continuous, seasonal or periodic standing water or saturated soils (Finlayson and Rea, 1999a). Despite a number of national and regional wetlands surveys (see Kirkpatrick and Harwood, 1983a; McComb and Lake, 1988; Finlayson and Von Oertzen, 1993; Jacobs and Brock, 1993) there is no standard definition of wetlands used throughout Australia (Finlayson and Rea, 1999a). Finlayson and Rea (1999a) recommended the use of the definition used by the Ramsar Wetland Convention. The *Directory of Important Wetlands in Australia* (ANCA, 1996) uses this as an overall wetland description:

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

This definition has been adopted by most government authorities dealing with wetlands within Tasmania (Blackhall, pers. comm.¹).

¹ Stewart Blackhall, Wildlife biologist, Nature Conservation Branch, Department of Primary Industries, Water and Environment, Hobart.

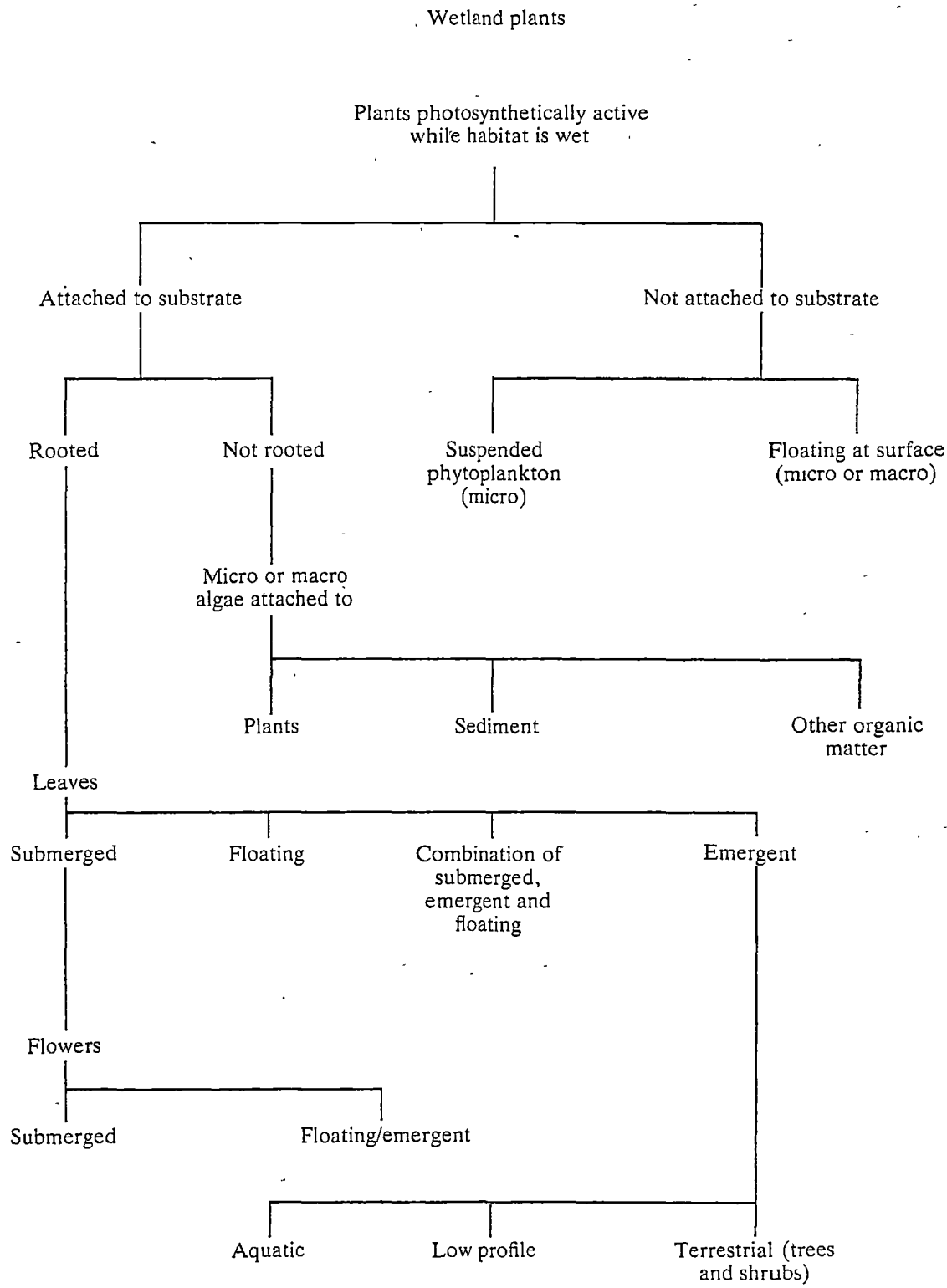


Figure 1.1 Growth form of wetland plants found in aquatic phase of habitats in Australian wetlands (Source: Brock, 1994).

Stability in wetland communities

Disturbance and its immediate effects on plant communities has been the topic of much research. At the same time there is a general feeling that disturbance and stability are closely interrelated and in some cases it is not so much the disturbance that matters, but rather the responses of the community to the disturbance that is of greater interest (van der Maarel, 1993).

Ecologists have shown an interest in community stability for several reasons. One of the most pressing is that, with the ever increasing human alteration of the natural disturbances within the environment, it is essential to know how communities respond to natural perturbations and therefore how they are likely to respond in the future if alterations occur (Begon *et al.*, 1990). Therefore, the stability of a community can be used as a measure of its sensitivity to disturbance. Several different measures can be used to determine the stability of a community.

Ecological stability (Leps *et al.*, 1982; Lawler, 1994; Johnson *et al.*, 1996) of vegetation communities can be measured through their 'resistance', i.e. ability to resist change after environmental disturbance, (Harrison, 1979; Leps *et al.*, 1982; Hughes, 1990); 'resilience', i.e. the ability to 'bounce back' or recover rapidly after disturbance (Connell, 1978; Leps *et al.*, 1982; Hughes, 1990; Brock, 1998); and 'persistence', i.e. the constancy of community structure over time (Harrison, 1979; Grossman, 1982; Hughes, 1990). Equilibrium communities are regarded as either resistant to disturbance or highly resilient following disturbance, both of which result in high persistence of relative abundances of species within the community over time (Chesson, 1986), whereas the converse applies to non-equilibrium communities (Grossman, 1982; see Hughes, 1990).

Studies in the stability of aquatic vegetation communities generally address the impact of water regimes, in particular, the response of communities to wetting and drying events (Gopal, 1986; Hughes, 1990; Brock, 1998). For temporary wetlands, resilience can be taken to mean the ability of the ecosystem to return to its normal wet phase functions after a drying event (Brock, 1998). Many wetlands are resilient to the climatically determined (natural) fluctuations in water regime, as they have experienced them for millennia (Brock, 1998; 1999). Brock (1998) concluded that temporary wetlands in both Australian and South Africa were resilient to normal cycles of wetting

and drying. However, she suggested that it may be beyond the capacity of these wetlands (through their seed bank) to respond to changes in water regime that may occur through human intervention, for example, more permanently wet or dry conditions. Hughes (1990) found low resilience at a community scale but high resilience at the species scale, to changes in discharge within aquatic river communities. The high resilience at species scale, in this case, was related to vegetative recovery.

Water regime is a term generally used to describe the temporal pattern of the presence and absence of water in a wetland and takes into account the timing, frequency, duration, depth and variation of flooding and drying events (Bunn *et al.*, 1997; Brock *et al.*, 2000). It is thought to be the most important natural disturbance that effects vegetation communities within wetland environments (e.g. van der Valk, 1981; Keddy and Reznicek, 1982, 1986; Gopal, 1986; Spence, 1982; Lieffers, 1984; Briggs and Mather, 1985; Mitchell and Rogers, 1985; Day *et al.*, 1988a; Casanova and Brock, 2000).

It has been suggested that making a wetland more permanently wet or dry is likely to reduce species richness (Keddy and Reznicek, 1982, 1986; Thompson, 1992) and thus change the vegetation community and hence seed bank composition.

Definition and classification of temporary wetlands

The use of the term 'temporary' in this thesis is consistent with the definition used by Boulton and Brock (1999) taken from Williams (1998). It is used in a broad sense to collectively refer to any wetland that dries out, no matter how briefly, or recedes to small pools. Temporary wetlands can be further classified according to their predictability (reliability of filling) and duration of filling (permanence) and from this are generally arranged from the least predictable and least permanent ephemeral or episodic wetlands - to irregularly filling intermittent wetlands - to the most predictable seasonal and permanent or semi permanent wetlands (see Table 9.1; Boulton and Brock, 1999). Permanent wetlands that dry out during extreme droughts are generally termed as semi (or near) permanent wetlands (Boulton and Brock, 1999).

Wetlands with fluctuating water levels

Temporary wetlands are generally characterised by fluctuating water levels. Naturally occurring water level fluctuations include regular and predictable ones such as those

related to tidal regimes (Parker and Leck, 1985; Leck and Simpson, 1987a), seasonal variation in precipitation and stream flow, as in areas with Mediterranean climates (Zedler, 1987; 1990) and tropical monsoonal areas (Gopal, 1986; Finlayson, *et al.*, 1990). Wetlands with unpredictable water levels fluctuations, that is, with smaller or greater than seasonal frequency of occurrence (Mitchell and Rogers, 1985; Pajmians *et al.*, 1985; Boulton and Brock, 1999), are generally associated with areas that are prone to drought (for example, temperate Australia and South Africa; Brock and Rogers, 1998; Brock, 1998) and/or have intermittent, unpredictable rainfall, such as in arid areas (Boulton and Brock, 1999).

Water level changes in wetlands and lakes produce changes in light quality and quantity, temperature fluctuations, oxygen availability, soil chemical conditions, nutrient concentrations and availability (Hultgren, 1988; see Casanova, 1993). In lakes with shallow-sloping shorelines, fluctuating water levels increase the area of shoreline vegetation and also the diversity of vegetation types and species (Keddy and Reznicek, 1986). The effects of water level change also vary with water depth, i.e. a 10 cm change in water level will have a greater effect on plants growing at 5 to 10 cm depth than on plants growing in 1 m of water (Casanova, 1993).

Diverse aquatic communities are maintained in the various aquatic habitats when the lagoon is wet, yet when dry the lake beds may be colonised by a variety of native and introduced terrestrial species leaving the aquatics to persist as seed or resistant vegetative propagules in the dry sediments. (Brock, 1994).

Studies of wetland plant communities have shown that the temporal dynamics of many wetland species can mirror water level fluctuations with characteristic increases and decreases in both number of species and plant cover depending on the adaptations or 'strategies' that plants use for coping with their changing environment.

Mechanisms for persistence in wetland plants

Plants are relatively sessile in comparison to animals and after establishment generally remain in the same place throughout their life cycle. This lack of migratory ability has made it necessary for plants to evolve mechanisms to persist in the environment, especially during unfavourable periods (Silvertown, 1982).

To persist over time, plants inhabiting temporary wetlands must be able to survive a wide range of water level fluctuations, including both predictable and unpredictable wetting and drying events (Mitchell, and Rogers, 1985; Brock, 1986, 1988; Brock and Casanova, 1991a; Brock and Casanova, 1997). As a consequence, a wide variety of survival and reproductive strategies to survive both flooded and dry conditions have evolved in wetland plants (Sculthorpe, 1967; Kadlec and Wentz, 1974; Hutchinson, 1975; Cook, 1987; Bartley and Spence, 1987; Crawford, 1987; Titus and Hoover, 1991).

Similar to terrestrial plants, three main strategies have been adapted by aquatic plants to persist in temporary wetland environments: a) dispersal of propagules, i.e. both vegetative fragments and propagules as well as seeds; b) buried vegetative propagules (for perennation and/or asexual or vegetative reproduction); and buried seed reserves (sexual reproduction). The first is associated with the movement of reproductive diaspores such as seeds and vegetative propagules, whereas, the latter two are associated with regeneration of plants *in situ*. Plants that have adaptations for persistence *in situ* generally do not need to re-disperse. However, dispersal may be an important mechanism for re-introduction of species that have either become exhausted within the propagule bank or that failed to deposit propagules prior to adverse conditions.

The methods used by wetland plants to persist in the environment are not always mutually exclusive and in many cases plants possess more than one method of regeneration (Brock, 1991; Smith and Brock, 1998). Similarly, methods of persisting may not always be common to all species within the same genus (Brock, 1983; Casanova 1994).

Dispersal mechanisms

The wide distribution of many species of aquatic plants would suggest that such plants have efficient means of dispersal (Hutchinson, 1975). Three mechanisms are generally associated with dispersal of plants both within and between wetlands: a) wind (anemochory); b) water (hydrochory); and c) animals (zoochory) (Sculthorpe, 1967; van der Pijl, 1983; Cook, 1987; van der Valk, 1992; Wainwright, 1998). The dispersal of both vegetative and seed propagules can be aided by all three mechanisms.

Seeds dispersed by wind aided by a flight appendage such as a pappus generally do not move long distances from the parent plant (Silvertown, 1982). This type of dispersal is rare in amphibious species and non-existent in true aquatic plants (although some species of *Potamogeton* have wind dispersed pollen; Cook, 1987). Dispersal by wind would be a disadvantage to a true aquatic species due to the high potential for their diaspores to be blown to terrestrial areas, where the chance of survival would be non-existent, rather than to aquatic sites. Examples of wind dispersed amphibious species are *Phragmites australis* and *Typha* spp. (Cook, 1987).

The seeds and vegetative material of many wetland plants float (pers. observation; Sculthorpe, 1967; Hutchinson, 1975) an adaptation that facilitates their dispersal by water (hydrochory). However, secondary mechanisms are required for actual water dispersal of propagules throughout the environment. In lotic environments water flow aids movement of propagules (Murray, 1986; Nilsson, *et al.*, 1991). However, in lentic wetlands wind induced movement is the most important secondary factor in dispersing propagules (Sculthorpe, 1967; Cook, 1987). Significant dispersal of propagules within wetlands has been reported in many wetland studies (Schneider and Sharitz, 1986; Grelsson and Nielsson, 1991). Grelsson and Nielsson (1991) found differences between the floating capacity seeds of species that were found in the seed bank to those found in the extant vegetation. Species present in the extant vegetation were dominated by short-floating seeds whereas the seed bank species were characterised by seeds that remained buoyant for longer. However, although this mechanism can be effective within wetlands, it is unlikely to be the cause of major dispersal between lentic wetlands.

Animals, particularly water birds, are thought to be the prime agents in the short to middle range dispersal of many wetland plants (Sculthorpe, 1967; Hutchinson, 1975; de Vlaming and Proctor, 1968; Cook, 1987; Wainwright, 1997). Adaptations for animal dispersal, such as burrs, hooked fruits and small glutinous seeds, are characteristic of many aquatic plants (Cook, 1987). Mechanisms by which animals can facilitate the dispersal of aquatic plants are either: a) seed digestion and defecation (endozoochory); and/or b) seeds and vegetative propagules adhered to feathers, fur, or mud attached to their feet (ectozoochory). Although both mechanisms are associated with short distance dispersal, only ectozoochory is thought to be a plausible mechanism for long-distance dispersal. However, it is unlikely that ectozoochory is effective in long-range dispersal

between continents (Sculthorpe, 1967). Sculthorpe (1967) suggested that human-dispersal has been the most effective means by which aquatic plants have become widespread through out the world.

Very limited direct evidence of actual water bird transportation has been published (Sculthorpe, 1967; de Vlaming and Proctor, 1968). Germination of seeds found in faecal droppings has determined that seeds can remain viable throughout the digestive process of water birds (Middleton, *et al.*, 1991). Therefore, the potential for short-distance dispersal is possible by this means (Sculthorpe, 1967). Evidence for ectozoochory was investigated within Australian wetlands by Wainwright (1997). He identified the propagules of 30 aquatic, amphibious and terrestrial plant species that had either adhered to feathers or were trapped in soil attached to the feet of 89 waterfowl. Seventy-eight per cent of species were found attached to feathers, whereas 48% were found carried on the birds feet. These results confirm that seeds can be retained on the feathers and feet of waterfowl and indicates the potential, depending on the retention time, for long-distance dispersal of aquatic plants by this mechanism.

Asexual revegetation and perennation

Aquatic environments are dominated by plants that possess mechanisms for clonal propagation (Sculthorpe, 1967; Hutchinson, 1975; Grace, 1993). This dominance of the clonal habit, along with the wide variety of clonal reproductive structures characteristic of aquatic plants, has led to the belief that vegetative mechanisms are the major means by which wetland plants persist in aquatic environments (Hutchinson, 1975; Silvertown, 1982; Rea and Ganf, 1994a). Vegetative growth has many advantages compared to establishment from seedlings, for example, rapid increase in plant size and distribution; movement from resource-poor microhabitats (due to crowding of parent plant) to resource-rich microhabitats; low risk of mortality of the offspring; and stronger competitive ability (Grime, 1979; Silvertown, 1982; Crosslé, 1998). However, for clonal plants to survive and persist in the fluctuating conditions of temporary wetlands their vegetative propagules must also be able to survive in the soil during both dry and inundated conditions (Sculthorpe, 1967).

Colonisation by means of rhizomes, stolons and runners is widespread amongst many wetland plant life forms (Sculthorpe, 1967). However, due to their food storing ability, it is rhizomes and rootstocks that are generally associated with the survival of aquatic

plants over time (Sculthorpe, 1967). Although stolons and runners rarely function as perennating organs themselves, they occasionally produce terminal swollen structures, such as, stem and root tubers, which remain dormant during adverse conditions and later grow into new plants. Many aquatic plants also produce specialised vegetation structures that are capable of remaining dormant during adverse conditions, such as drought. A variety of names have been applied to these structures, including turions, winderbuds, hibernacula and bulbils. (Sculthorpe, 1967; Kadlec and Wentz, 1974; Hutchinson, 1975; Abrahamson, 1980; Spencer *et al.*, 1990; Brock, 1991; Grace, 1993; Casanova, 1994). Vegetative fragmentation is another mechanism by which aquatic plants reproduce themselves in wetland environments. However, this may only be successful for survival of plants if the drawdown is relatively short and may not be sufficient for survival during long-term dry periods (Brock, 1991).

Sexual reproduction and seed banks

During drying events many obligate aquatic plants cannot survive vegetatively (Keddy and Reznicek, 1986). These species generally persist in the vegetation community during unfavourable conditions by non-vegetative means such as desiccated resistant seeds (angiosperms) and oospores (charophytes) found within the soil (collectively termed seed bank). Two contrasting 'types' of seed banks distinguished by their seed longevity are recognised. Transient seed banks generally do not remain in the soil more than one year. Persistent seed banks contain seeds that last at least one year (Thompson, 1992). Both have been found within wetland environments. Studies from both overseas and within Australia have shown that many temporary wetlands with unpredictable water regimes are characterised by large persistent seed banks (see Leck, 1989 for review of overseas studies; Finlayson *et al.*, 1990, Britton and Brock, 1994; see also Chapter 4).

The regeneration of species from seeds both during and after a drying event is influenced by several factors: the viability of seeds over time (Leck, 1989); dormancy of seeds (Grime, 1979b; Silvertown, 1982; Baskin and Baskin, 1985); the conditions for seed germination (van der Valk, 1981; Leck, 1989; Britton and Brock, 1994); dispersal of seeds into the wetland (Hutchinson, 1975; Sculthorpe, 1967; Eriksson, 1992; Wainwright, 1997); seed size (Keddy and Constabel, 1986; Bekker *et al.*, 1998); herbivory (Wurm, 1998; Middleton, 1999).

How seed banks can be a measure of the resilience of communities

A knowledge of the seed bank dynamics may aid in predicting the consequences of changes to the patterns of wetting and drying in wetlands. Brock (1998) proposed that if we can assess the resilience of wetland communities by evaluating the potential of seed banks for revegetation we will be in a better position to manage wetlands within their natural range of resilience. The characteristics of the seed banks which enhance wetland revegetation could be used as indicators of resilience. These include: species richness, germinable seed bank; spatial and temporal species richness; greater numbers and species in the seed bank than in growing vegetation; a variety of dormancy-breaking patterns, a variety of morphological (functional) groups; a seed bank in which all seeds do not germinate on first wetting; seed longevity;

Relationships between the seed bank and extant vegetation

In wetlands, the floristic composition of the seed bank has often been shown to determine the composition and structure of the vegetation that has developed over time (van der Valk and Davis, 1978; Smith and Kadlec, 1983, Leck, 1989). Due to this several studies have attempted to predict changes in the standing vegetation of wetlands from the species found within the seed bank (van der Valk, 1981; Welling *et al.*, 1988a; Haukos and Smith, 1993). Seed-bank data can yield information on three aspects of future wetland vegetation: (1) species composition, (2) relative abundance of species, and (3) distribution of species. They reflect the history of the vegetation as well as species that may have dispersed from other areas (van der Valk and Davis, 1976; Ungar and Riehl, 1980; Fenner, 1985; Leck and Simpson, 1987a; Welling *et al.*, 1988a; Haukos and Smith, 1993). If the seed bank and standing vegetation are correlated the standing vegetation can generally be used to predict the seed bank of the wetland, and conversely the seed banks can be used to predict the vegetation of that growing season and at that site (Brock and Rogers, 1998).

Investigating the persistence of plant communities

Several methods have been used to investigate how aquatic plants persist over time in aquatic environments (see Berry, 1993; van der Valk, 1992; Casanova and Brock, 1997). However, the methods used have generally addressed four main areas: a)

individual species (autecology); b) changes in community structure and composition (synecology); c) life history strategies; and d) functional groups.

Autecological studies investigating how individual aquatic species survive and persist in fluctuating wetland environments are many (e.g. Sculthorpe, 1967; Leck, 1979; Spencer *et al.*, 1990; Brock, 1991; Brock and Casanova, 1991b; Casanova 1994; Jacobs *et al.*, 1994; Rea and Ganf, 1994a; Denton and Ganf, 1994; Froend and McComb, 1994; Smith, 1998). These studies aid in our understanding of how species coexist. They also contribute to knowledge of plant community processes and dynamics (Smith, 1998).

The rapid and substantial changes that can occur in aquatic vegetation communities associated with water level fluctuations facilitates the study of community dynamics in these environments (see review Chapter 5; van der Valk, 1987). Both short-term and long-term community dynamic studies of wetland vegetation have been used to describe how these communities persist over time. These studies have been related persistence of species by both seed bank (van der Valk and Davis, 1978, 1979) and vegetative propagules (van der Valk, 1981; Rea and Ganf, 1994a, 1994b).

The mechanism (strategy) by which species persist in the vegetation communities of fluctuating wetlands, that is, dispersal, vegetative propagules or seed banks, are generally not mutually exclusive and combination of mechanisms may be used to persist over time. The importance of each strategy can vary both spatially, temporarily and can also be dependent on the life history stage of the plant (Grime, 1979b). This combination of mechanisms for persistence over time, in both terrestrial and wetlands systems, has been described in several ways, for example 'regeneration or life strategies (Grime, 1974; 1979b), r - K selected (MacArthur and Wilson, 1967; Leck and Brock, 2000) or life history strategies (van der Valk, 1981; Brock, 1991; Leck and Simpson, 1994; Brock and Rogers, 1998; Leck and Brock, 2000).

More recently functional classifications have been used to determine how species respond, and therefore, persist in environments subjected to unpredictable water level fluctuations. Brock and Casanova (1997) proposed a set of functional groups based on plant responses to the conditions under which species germinate, grow and reproduce in relation to water presence and absence (see review Chapter 3).

Studies within Australia

Detailed data on wetland seed banks are sparse for Australian wetlands (Brock, 1999). Seed bank germination studies have been conducted on sediments from the New England Tablelands (Brock and Britton, 1995), the Macquarie Marshes and the Gingham water course (Hutson, 1994; McCosker, 1994) and Magela Creek floodplain, Kakadu National Park, northern Australia (Finlayson *et al.*, 1990, Knerr, 1996; see Brock, 1999). All these sites had species-rich seed banks consisting of a range of aquatic and semi-aquatic species. For many species found in these environments, seeds were long-lived and only a portion germinate in each wetting event, which allows future germination and establishment.

Few comparisons have been made between the roles of different propagule types (i.e. seeds and vegetative propagules) in the persistence and re-establishment of vegetation after a drying period (Crosslé, 1998). Rea and Ganf (1994a) found that in most studies of clonal plants, the contribution of sexual reproduction to establishment of new populations and spread of existing ones was often overlooked. They suggested that although establishment of clonal plant populations by sexual reproduction is unpredictable in time and space, it is important in terms of maintaining a diverse wetland vegetation. Crosslé (1998) suggested that it is likely that the effects of water regime on established vegetation communities will differ to that on the seed bank in terms of germination, establishment and survival of species. The roles of these two modes of reproduction vary in time and space, and an understanding of how this subsequently effects community dynamics could lead to more effective management of wetland plant communities (Crosslé, 1998).

Crosslé (1998) examined the effects of water regime on germination and establishment within vegetation communities and from the seed bank of wetland plants. They found that the method of persistence (i.e. vegetative or seed bank) of a species determined whether or not it could survive a given set of conditions. More species survived flooding vegetatively than germinated from the seed bank when submerged. Fluctuating water levels enabled a greater range of species recruited into the vegetation from the soil seed bank through the provision of a variety of conditions and, thus, germination cues.

The functional group classification of Brock and Casanova (1997) has been used in several studies to describe the composition of both seed bank and extant vegetation of Australian

wetlands. Brock and Casanova (1997) proposed that longer drying or flooding events would decrease the number of amphibious species and increase the number of terrestrial or submerged species respectively. Most of the studies describing the functional groups of seed banks and extant vegetation have been from experimental studies (e.g. Casanova and Brock, 2000; Crosslé, 1998). No studies have used these functional groups to describe communities dynamics that occur in natural wetlands over time.

Aims and structure of thesis

The present study investigates both the short and long-term 'persistence' of plant communities within 5 temporary wetlands with both natural water regimes and those that have been subject to recent changes to their normal cycles of wetting and drying. The 'resistance' and 'resilience' of wetland communities to dry periods are also investigated. Emphasis is placed on the regeneration by seed banks. However, dispersal mechanisms, vegetative reproduction and life history strategies of plants are also addressed. The thesis also aims to assess if plant functional groups determined by traits associated with their response to the presence or absences of water (Brock and Casanova, 1997) are useful in describing wetland community dynamics and how wetland plants persist in their environment.

The rest of the thesis is structured as follows:

Chapter 2 - describes the study sites;

Chapter 3 - investigates if the species found in the 5 wetlands fall into functional groups similar to those derived by Brock and Casanova (1997). The functional groups recognised in Chapter 3 are used for analyses in Chapters 4, 5, 6;

Chapter 4 - investigates the potential for regeneration from the soil seed bank from 11 vegetation zones within the 5 wetlands;

Chapter 5 - investigates the relationships between the seed bank and extant vegetation found in the 11 zones;

Chapter 6 - investigates the community dynamics within the 11 zones over the 2 year period of the study. Changes in vegetation are related to changes in hydrology and

differences in vegetation communities associated with different water regimes are described in terms of functional groups.

Chapter 7 - discusses the resistance, resilience and persistence of the wetland communities. It also discusses the mechanisms by which species persist in the fluctuating environments of Tasmanian temporary lentic wetlands. Management issues are discussed and suggestions for future research made.

Chapter 2

Study Sites

Tasmanian temporary wetlands

The variable climatic patterns found within Australia (Figure 2.1) maintain a variety of permanent, semi-permanent, intermittent, seasonal and episodic temporary wetlands (Boulton and Brock, 1999). Tasmania, although richly endowed with some of the largest permanent water bodies in Australia (Kirkpatrick and Tyler, 1988), also has many temporary wetlands. These wetland types are generally found in the lower rainfall areas of the Midlands and the east coast of Tasmania (Figure 2.2), and range from shallow depressions that can sometimes dry out for many years (ephemeral or episodic wetlands) to those that can remain wet, but will dry out during extreme climatic conditions (semi-permanent). Seasonally predictable wetlands, although not common, are also found in several areas throughout Tasmania (Kirkpatrick and Harwood, 1981; Cameron, 1996). However, seasonally inundated edge zones surrounding a deeper submerged zone may be more common (Walsh, 1997).

Five temporary wetlands with varied water regimes were chosen from three regions within the low rainfall area of Tasmania (Figure 2.3). Cherry Tree Lagoon and Big Punchbowl are located on the central east coast, Tin Dish and Sandy Gate in the lower Midlands and Middle Lagoon in the northern Midlands. The wetlands vary in size from between 2 to 16 hectares and are at altitudes ranging from 5 metres to 200 metres above sea level. The major defining characteristics of the wetlands are listed in Table 2.1.

The lagoons studied have all experienced some kind of disturbance throughout their history (Table 2.1). Disturbance ranged from episodic burns to removal of vegetation and varying degrees of grazing. Three of the wetlands are presently grazed (Tin Dish, Sandy Gate and Middle Lagoon). The other two were grazed in the past but are now mainly used for recreational shooting. Two of the wetlands have had drainage channels dug through them. However, these wetlands only fill to the level of the drainage channels during high rainfall years and, therefore, the channels may not have a large effect on the permanence of water in the lagoons.

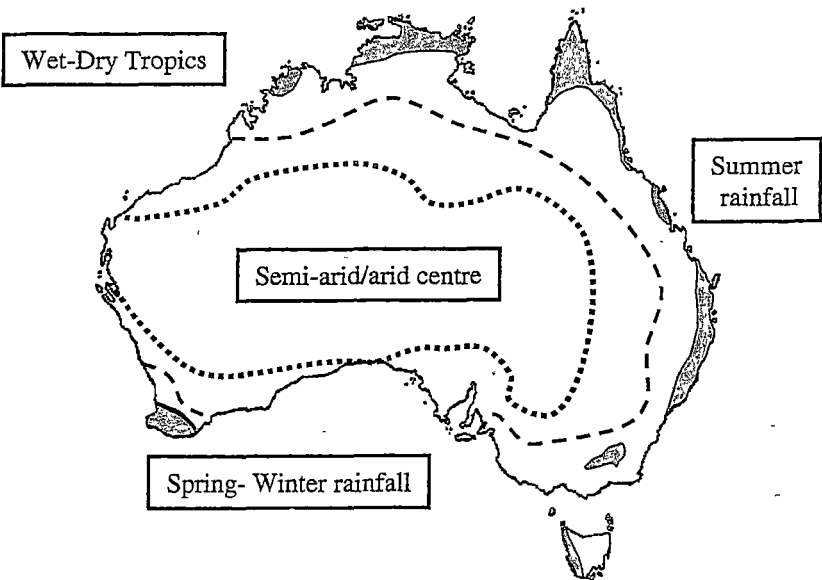


Figure 2.1 Contours of annual rainfall (dotted lines = 250 mm, broken line = 500 mm, shaded = > 1 000 mm) largely determine where the temporary wetlands occur in Australia. Saline and episodic wetlands dominate the semi-arid and arid centre whereas other temporary wetlands are more common near the coast except where rainfall exceeds 1 000 mm annually (source: Boulton and Brock, 1999).

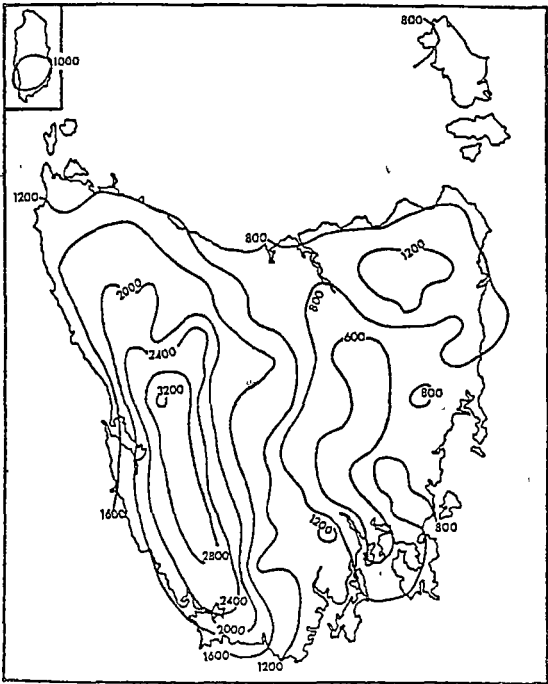


Figure 2.2 Mean annual rainfall of Tasmania (mm; source: Tasmanian Year Book, 1985).

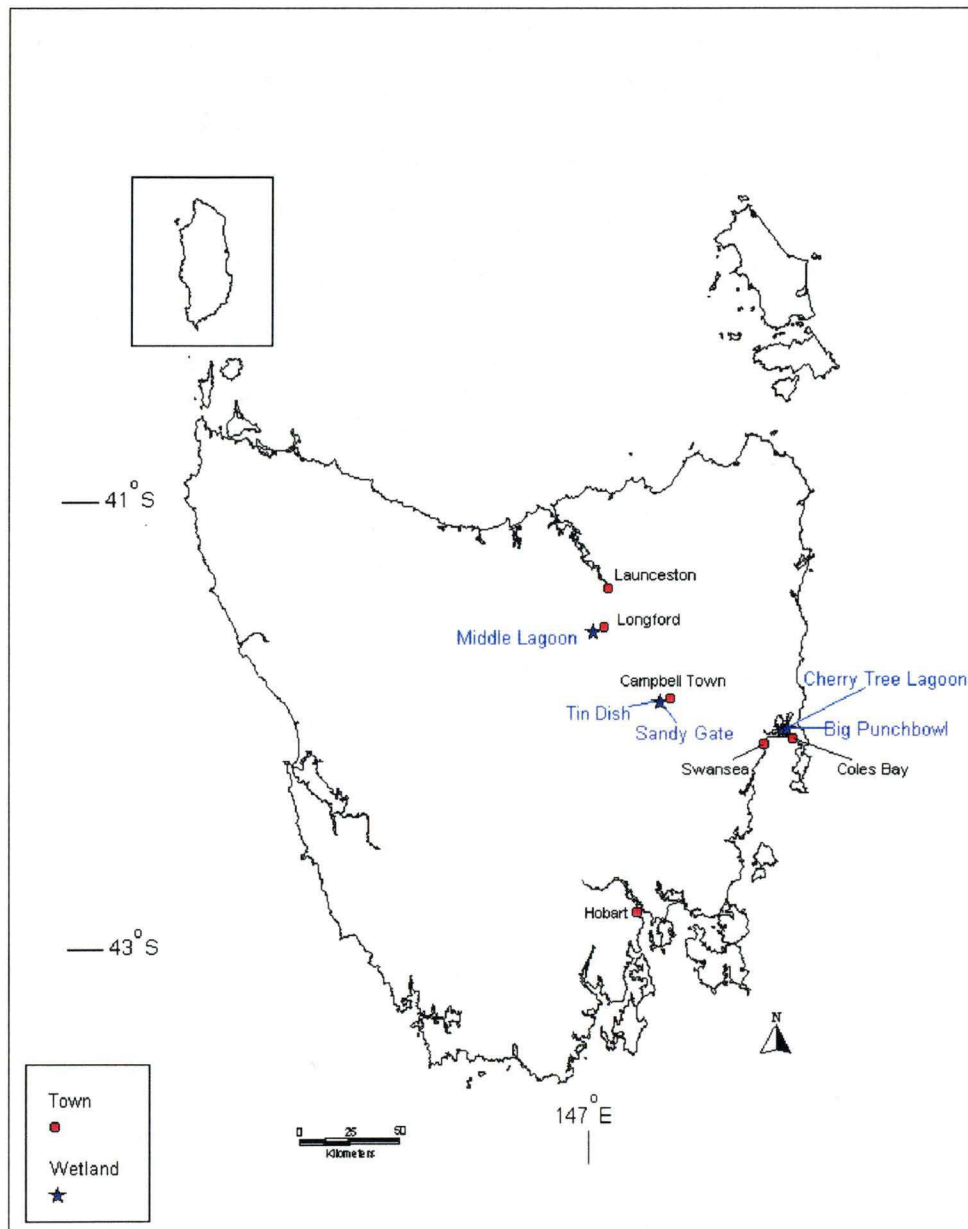


Figure 2.3 Location of the 5 wetlands within Tasmania.

Table 2.1 Summary of wetland characteristics

WETLAND	LOCATION	ELEVATION	GEOLOGY	GEOMORPHOLOGY	SOILS	Surface Area (Ha)	Max. depth (m)	SURROUNDING VEGETATION	DISTURBANCE	FAUNA
Big Punchbowl	East Coast	20	QUATERNARY/ HOLOCENE: Alluvium, sand, gravel and talus TERTIARY: Non-marine quartz grit	Deflation	Sand: medium peat content	16	1-1.5	• native forest • native grassland	• burnt • wombat digging • vehicle access	• wombat • wallaby • green & gold frog
Cherry Tree Lagoon	East Coast	5	QUATERNARY/ HOLOCENE: Alluvium, sand, gravel and talus	Unknown	Sand: high peat content	9	1-1.5	• native forest • native grassland • brackish lagoon	• burnt • wombat digging • vehicle access • recreational shooting • drainage channel • past grazing	• waterfowl nesting • wombat • wallaby • green & gold frog
Sandy Gate	Central Midlands	200	JURASSIC: Dolerite	Old River Channel	Sand: medium peat content	2	1	• woodland • native grassland	• present grazing of both cattle and sheep • natural spring • drainage channel	• sugar glider • white faced heron • wallaby • frogs
Tin Dish	Central Midlands	170	JURASSIC: Dolerite	Old River Channel	Sand: medium peat content	6	1	• woodland • native grassland	• present grazing of both cattle and sheep • vehicle access • past recreational shooting	• wallaby • <i>Triops</i> spp. • echidna • waterfowl
Middle Lagoon	Northern Midlands	155	QUATERNARY: Sand and clay deposits	Deflation	Silt: Clay: Sand	16	60	• improved pasture • freshwater lagoons	• low intensity grazing • vehicle access • 3 dams within wetland perimeter • water pumped from lagoon	• waterfowl nesting • burrowing crayfish • green & gold frog

Site Descriptions

Location and geomorphology

Big Punchbowl (42.03'S, 148.11'E) and Cherry Tree Lagoon (42.04'S, 148.12'E) are located near the eastern shore of Moulting Lagoon, midway along Tasmania's east coast (Figure 2.3). Big Punchbowl has the typical circular shape of a deflation lagoon, with a lunette at its eastern edge and has a small catchment area. Cherry Tree Lagoon on the other hand has a larger catchment with a small stream which, during wetter years, occasionally drains into the wetland. It retains water longer and refills more quickly than Big Punchbowl. The majority of Big Punchbowl is underlain by Tertiary non-marine quartz grit derived from erosion of nearby mountains and deposited by rivers prior to the Holocene sea level rise. A small area at the eastern edge of the lagoon is underlain by more recent Holocene alluvium, sand gravel and talus. It is this Holocene alluvium that underlies Cherry Tree Lagoon (Parks and Wildlife Service, 1999). The top texture of soil in both lagoons is grey sand. However, much of the area of the lagoons has a thick layer of organic peat (Kirkpatrick and Harwood, 1981).

Tin Dish and Sandy Gate (41 56'S, 147 19'E) are situated on the Maclains Plains, 3-4 km west of Campbell Town in the southern part of the Midlands (Figure 2.3). These two wetlands appear to be part of a chain of lagoons that may have once comprised an old drainage channel (Goede, pers. comm.¹). The underlying geology in the area is Jurassic dolerite. The lagoons have sandy soils with a medium peat content (Kirkpatrick & Harwood, 1981).

Middle Lagoon (41 36' S, 147 03' E) is situated in the northern Midlands, close to Longford and approximately 25 km west of Launceston (Figure 2.3). This lagoon is part of a group of deflation lakes and associated lunettes, formed in the Quaternary (Nicholls, 1958). The lagoon is oval in shape and has a distinct lunette on its south and south east border.

¹ Albert Goede, Geomorphologist, Honorary research fellow, School of Geography and Environmental studies, University of Tasmania, Hobart.

Climate

The central east coast of Tasmania experiences a subhumid climate (Gentili, 1972). The nearest long-term meteorological stations to Big Punchbowl and Cherry Tree Lagoon are at Swansea (1884-1999), and Coles Bay (1961-1999). Swansea has a mean annual rainfall of 599 mm with no apparent seasonal maximum (Table 2.2; Figure 2.4). Coles Bay, about 25 km to the south of the lagoon has a somewhat higher mean annual rainfall (688.8 mm) with marginally more rainfall in summer. Coles Bay has a mean daily maximum temperature of 22.2°C in January (the warmest month) and a mean daily minimum temperature of 3.5°C in July the coldest month (Figure 2.5). Evaporation averages 1116 mm per year (Table 2.2). Wind directions vary throughout the year. The prevailing winds during April to September are the dry north westerly winds associated with high evaporation rates. During October to March the dominant wind direction changes to the north east (Blackhall, 1986, unpublished data, Bureau of Meteorology).

The area surrounding Tin Dish and Sandy Gate, due to its situation within the rain shadow of the Western Tiers, experiences some of the lowest rainfall in Tasmania. The average annual rainfall at Campbell Town is 541 mm. Rainfall is lowest in summer and autumn and has a slight spring maximum (Figure 2.4). Wind directions for most of the year are mainly from the north and north west with an increase in southerlies during the month of June. All months experience north and north westerly winds of greater than 30 km/h. Evaporation rates are highest in summer and have a mean annual rate of 1031.8 mm (Table 2.1). Campbell Town has a mean daily maximum of 24.4°C in February (the warmest month) and a mean daily minimum of 0.3°C in June the coldest month (Figure 2.5).

Table 2.2 Climatic data summary for stations close to study wetlands (Min = minimum; Max. = maximum; n/a = not available; Source: Bureau of Meteorology).

Wetland	Station and Elevation	Period of Record	Mean annual rainfall (mm)	Mean daily temperature (Min and Max; °C)			Mean annual evaporation (mm)
				Annual	January	July	
Big Punchbowl Cherry Tree Lagoon	Swansea (7 m)	1884-1999	598.8	17.8 7.6	22.2 11.6	13.2 3.5	1,116
	Coles Bay (20 m)	1961-1998	688.8	n/a	n/a	n/a	n/a
	Dolphin Sands (10 m)	1998-1999	612.5	n/a	n/a	n/a	n/a
Middle Lagoon	Longford (140 m)	1886-1999	633.3	n/a	n/a	n/a	n/a
	Launceston Airport (170 m)	n/a	n/a	16.9 6.2	23.2 10.1	10.8 2.2	1,500
Sandy Gate Tin Dish	Campbell Town (200 m)	1915-1999	541.7	17.5	23.5	11.2	1,318
		1972-1993		5.0	9.0	0.5	

The nearest long-term meteorological stations to Middle Lagoon are Longford and Launceston. The average annual rainfall at Longford is 633 mm. There is a distinct winter rainfall maximum (Figure 2.4). The predominant wind direction throughout most of the year is from the north or north west. However, during May and June there is an increase in southerlies. While all months experience winds of greater than 30km/h, May to July have the most days with calm conditions. At Launceston the mean daily maximum temperature is 23.2°C in January, the warmest month, and the mean daily minimum temperature is 2.2°C in July, the coldest month, with maxima sometimes exceeding 38°C during February (Pinkard, 1980, unpublished data, Bureau of Meteorology). Middle Lagoon lies in a high evaporation area. At Launceston (which has the nearest available record), evaporation rates are highest in summer with a mean annual rate of 1500 mm. (Figure 2.5; Table 2.2).

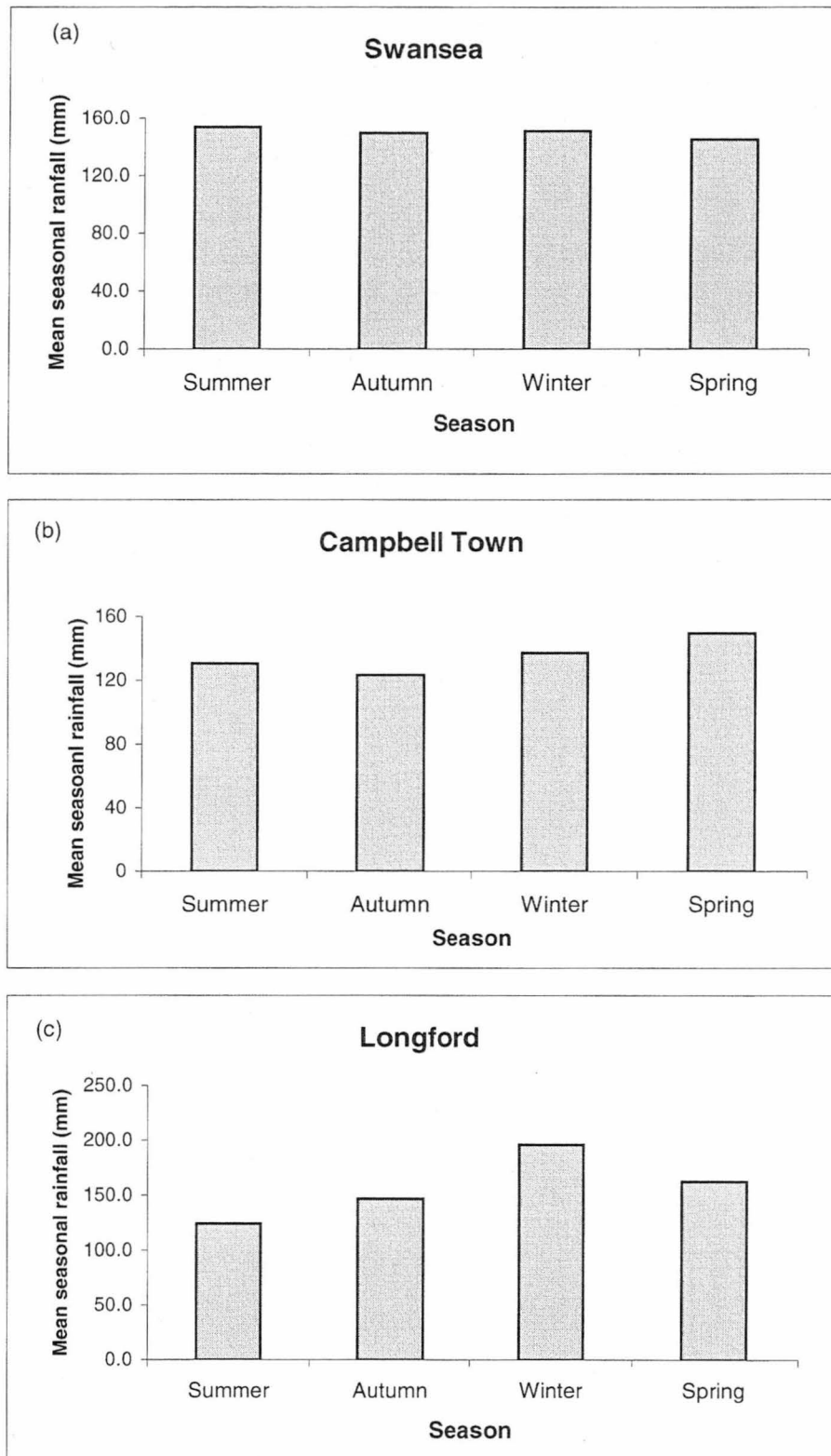


Figure 2.4 Mean seasonal rainfall: (a) Swansea, 1885 - 1998; (b) Campbell Town, 1916 - 1998; and (c) Longford, 1901 - 1998 (Source: Bureau of Meteorology).

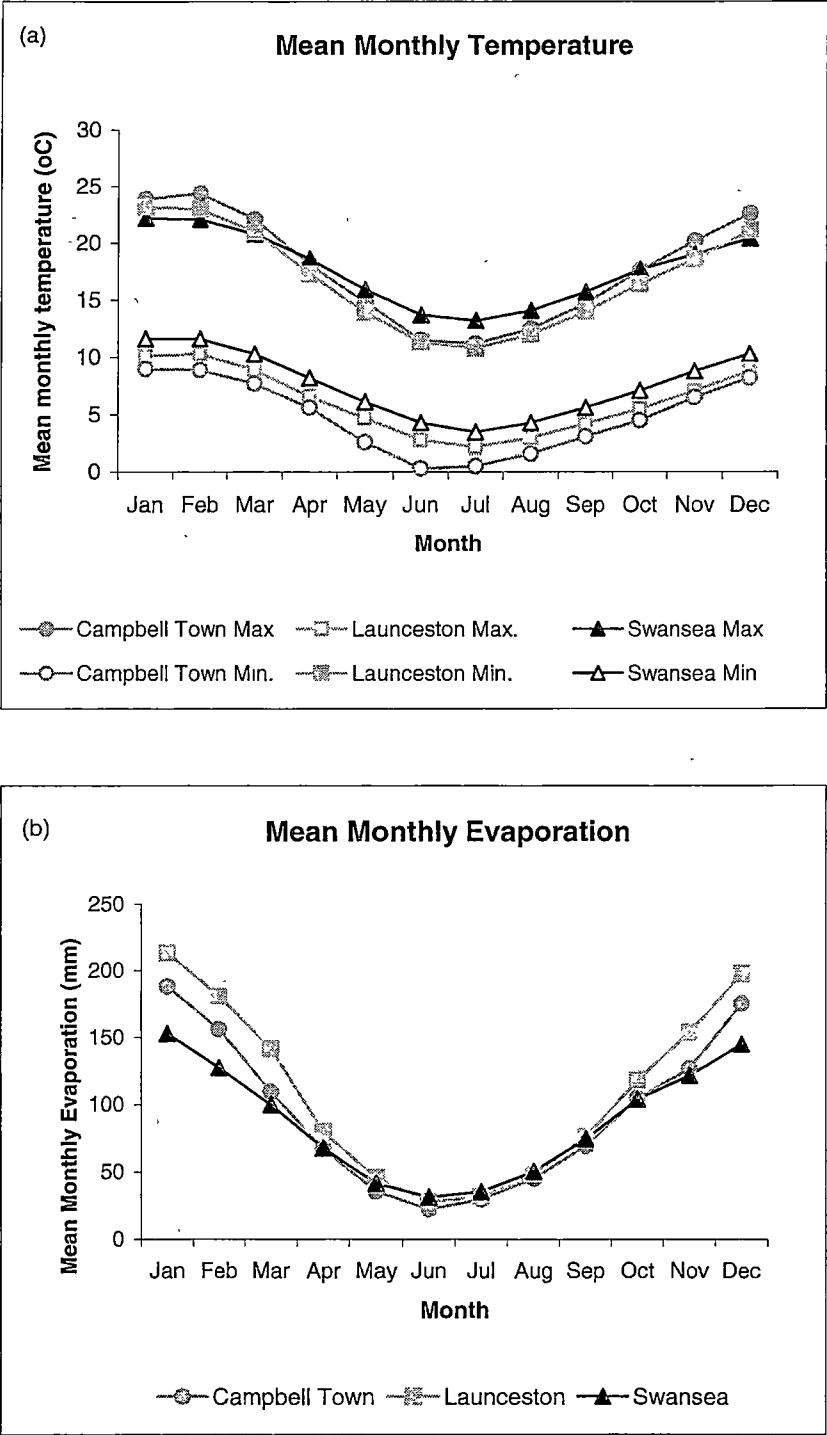


Figure 2.5 (a) Mean monthly daily maximum and minimum temperature and (b) mean monthly daily evaporation for Campbell Town, Launceston and Swansea (Source: Bureau of Meteorology).

Land Use

Cherry Tree Lagoon and Big Punchbowl are surrounded by native forest and grasslands. Much of area surrounding the two lagoons was previously grazed by sheep. However, this practice ceased approximately 20 years ago (Gavin Flack, pers. comm²).

Recreational shooting presently occurs at both Cherry Tree Lagoon and Big Punchbowl lagoons, although this has ceased in recent years in Big Punchbowl due to low water levels.

Tin Dish and Sandy Gate are surrounded by native grasslands and grassy woodlands dominated by *Acacia mearnsii* and *Eucalyptus pauciflora* (Gilfedder, pers. comm.³). Grazing of both cattle and sheep has been the major land use surrounding the wetlands since the 1820s (Henry Foster, pers. comm.⁴). Both wetlands are generally grazed at some time of the year. Sandy Gate was severely grazed by cattle during the present study. However, Tin Dish was largely grazed by sheep, which at times numbered several hundred over a period of one day. During the two year period of the study the surrounding area became very dry and during the winter period of 1998 the sheep were oat fed by the landowner. Prior to drought conditions in 1967, recreational shooting regularly occurred at Tin Dish (Henry Foster, pers. comm.). However, the practise stopped due to low water levels in the lagoon after this time. Two disused duck hides remain in the aquatic zone as a reminder of past water levels of the lagoon.

Middle Lagoon is surrounded by improved pasture and native grasslands with the major land use being grazing of both cattle and sheep. Some cropping also occurs in the area. The area within the lagoon has been grazed for many years. However, in the last eight years the grazing has been gradually reduced. Just after the completion of this study the lagoon was fenced off from the surrounding grazing pasture and all stock will eventually be removed from the lagoon area (Doug Kelly pers. comm.⁵). Recreational shooting has previously occurred in the lagoon. However, this has ceased during the present owner's occupation.

² Gavin Flack, Landowner, Cherry Tree Lagoon and Big Punchbowl.

³ Louise Gilfedder, Botanist, Nature Conservation Branch, Department of Primary Industries, Water and Environment, Hobart.

⁴ Henry Foster, Landowner, Sandy Gate and Tin Dish.

⁵ Doug Kelly, 'Woodstock', landowner, Longford.

Fire History

Tin Dish, Sandy Gate and Middle Lagoon have not been burnt in their known history. However, periodic burning of Big Punchbowl and Cherry Tree Lagoon occurred over the past 20 years. Cherry Tree lagoon is periodically burnt to maintain the vegetation habitat for waterfowl. It was last burnt in May 1997 during the period of this study. A known cool burn occurred on the eastern edge of Big Punchbowl in March 1992 (Blackhall, pers. comm.⁶) and several central areas within the lagoon appeared to have been burnt during the time of this study.

Fauna

All of the wetlands are important habitat for a wide range of fauna. Three Lagoons, Big Punchbowl, Cherry Tree Lagoon and Middle Lagoon, are important habitat for the endangered green and gold frog (*Litoria raniformis*). It was heard growling in both Cherry Tree Lagoon (October 1997) and Middle Lagoon (November, 1998) during the present study. Several other species of frog were heard in all lagoons.

Water birds were observed utilising all wetlands, except, Big Punchbowl. Water bird species observed in Cherry Tree Lagoon included Pacific black duck (*Anas superciliosa*), Australasian bittern (*Botaurus poiciloptilus*) and purple swamphen (*Porphyrio porphyrio*). A pair of black swan (*Cygnus atratus*) nested in the central *Baumea arthrophylla* zone during both breeding season sampled. Of the wetlands the lowest number of water fowl were observed in both Tin Dish and Sandy Gate. White-faced heron (*Ardea novaehollandiae*) were seen at both wetlands and nested in Sandy Gate during spring 1997. A solitary black swan was observed at Tin Dish in summer 1997 and Australasian shelduck (*Anas rhynchos*) were observed grazing on several occasions. More water fowl were observed in Middle Lagoon, than all other wetlands. Black swan (in large numbers) and purple swamp hen both nested in the lagoon. Australasian bittern, Tasmanian native hen (*Gallinula mortierii*), swamp harrier (*Circus approximans*), Australasian shelduck, white faced heron, and masked lapwing were also recorded over the period of the study.

Evidence of the presence native marsupial species was observed in all wetlands, except Middle Lagoon. A large amount of wombat (*Vombatus ursinus*) diggings and scats

⁶ Stewart Blackhall, Wildlife biologist, Nature Conservation Branch, Department of Primary Industries, Water and Environment, Hobart.

were observed in both Cherry Tree Lagoon and Big Punchbowl. These were especially noticeable in Big Punchbowl where the water levels were low for most of the period of the study. The wombats appeared to use most of the area of the lagoons during low water levels as scats were observed well into the central area. Wallaby (*Macropus rufogriseus*) scats were recorded at Big Punchbowl, Cherry Tree Lagoon, Tin Dish and Sandy Gate. Both wallabies and echidnas (*Tachyglossus aculeatus*) were observed foraging in Tin Dish. The introduced mammal species rabbits and hares were abundant throughout the area surrounding Tin Dish and Sandy Gate.

The lagoons were abundant with invertebrate life both aquatic and terrestrial. A high number of shield shrimps (*Lepidurus apus viridis*) hatched in the shallow water of Tin Dish during autumn 1997 (Williams, 1980). Shield shrimps are common in temporary wetlands (Williams, 1980). These species, along with other aquatic invertebrates, also hatched from soils in the glasshouse during the seed bank trials. Burrowing freshwater crayfish holes were observed in the herbaceous outer edge of Middle Lagoon.

Aquatic plant communities

Tasmanian wetland plant communities

Approximately 200 higher plant species have been recorded from Tasmanian lentic wetlands of which fewer than 10 (5%) are endemic (Kirkpatrick and Harwood, 1983a; Kirkpatrick and Harris, 1999). Charophyte species are a large part of Tasmania's aquatic flora, often growing in abundance in all kinds of aquatic habitats. Twenty-four species and approximately 9 varieties of charophytes have been reported from Tasmania (van Raam, 1995). Five (18%) of the charophyte species reported from Tasmania are endemic to the State.

The major vegetation communities found in Tasmanian lentic wetlands by Kirkpatrick and Harwood (1981;1983b) between 1978-1980, were allocated into community 'types' or 'formations' defined by the structure of their dominant and co-dominant species. Seven vegetation formations were recognised (Kirkpatrick and Harwood, 1983b; Kirkpatrick and Harris, 1999): forest (9% area); scrub (5% area); marginal herbfield (5% area); reed swamp (3% area); sedgeland (39% area); tussock sedgeland (4% area) and aquatic herbland (34% area).

Table 2.3 Aquatic plant communities found in the 5 wetlands in the present study. Zones range from the most central (Zone 1) to the outer edge (Zone 6). Data presented are the dominant and co-dominant species recorded in each zone either during the present study or during the surveys in 1978 - 79 by Kirkpatrick and Harwood (1981; underline = dominant; bold = zone sampled during the present study see Chapter SB).

Wetland	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
Big Punchbowl	<u>Baumea rubiginosa</u>	<u>Triglochin procerum</u> <i>Isolepis fluitans</i>	<u>Schoenus maschalimus</u> <u>Lepidosperma longitudinale</u> <i>Hydrocotyle muscosa</i> <i>Isolepis inundata</i> <i>Isolepis fluitans</i>			
Cherry Tree Lagoon	<u>Myriophyllum salsugineum</u> <u>Myriophyllum</u> <u>simulans/variifolium</u> <i>Potamogeton tricarinatus</i> <i>Villarsia reniformis</i> <i>Isolepis fluitans</i> <i>Eleocharis acuta</i> <u>Chara spp.</u> <i>Nitella spp.</i>	<u>Baumea arthropphylla</u> <i>Potamogeton tricarinatus</i> <i>Triglochin procerum</i> <i>Villarsia reniformis</i>	<u>Phragmites australis</u> <i>Baumea arthropphylla</i>	<u>Eleocharis sphacelata</u>	<u>Selliera radicans</u> <i>Wilsonia backhousei</i> <i>Distichlis distichophylla</i>	<u>Lepidosperma longitudinale</u> <i>Juncus kraussii</i> <i>Baumea juncea</i> <i>Leptocarpus brownii</i>
Middle Lagoon	<u>Eleocharis sphacelata</u> <i>Triglochin procerum</i> <i>Potamogeton tricarinatus</i> <i>Isolepis fluitans</i> <i>Myriophyllum simulans</i> <i>Chara spp.</i> <i>Nitella spp.</i>	<u>Triglochin procerum</u> <i>Isolepis fluitans</i> <i>Chara spp.</i>	<u>Myriophyllum sp.</u> <i>Potamogeton tricarinatus</i>	<u>Villarsia reniformis</u> <u>Myriophyllum sp.</u> <i>Potamogeton tricarinatus</i> <i>Isolepis fluitans</i> <i>Chara spp.</i>	<u>Baumea arthropphylla</u>	<u>Selliera radicans</u> <u>Goodenia humilis</u> <i>Villarsia reniformis</i> <i>Neopaxia australasica</i> <i>Juncus sp.</i>
Sandy Gate	<u>Potamogeton tricarinatus</u> <u>Eleocharis acuta</u> <i>Triglochin procerum</i> <i>Myriophyllum spp.</i>	<u>Baumea arthropphylla</u>	<u>Eleocharis acuta</u> <i>Eryngium vesiculosum</i> <i>Neopaxia australasica</i>	<u>Lepidosperma longitudinale</u>		
Tin Dish	<u>Potamogeton tricarinatus</u> <u>Chara spp.</u> <i>Myriophyllum spp.</i>	<u>Eleocharis acuta</u> <u>Selliera radicans</u>	<u>Selliera radicans</u> <i>Eryngium vesiculosum</i> <i>Schoenus nitens</i>			

Plant communities in the 5 wetlands

Using the classification for Tasmanian wetlands summarised by Kirkpatrick and Tyler (1988), the wetlands can be described as: 1) shallow freshwater herb marsh, Tin Dish; and 2) shallow freshwater sedge marsh, Sandy Gate, Big Punchbowl, Cherry Tree Lagoon and Middle Lagoon.

The vegetation communities within the 5 wetlands (Table 2.3) were representative of 4 of the 7 formations recognised by Kirkpatrick and Harwood (1983b), that is, marginal herbfield - *Selliera radicans*, *Schoenus nitens*, reed swamp, *Eleocharis sphacelata*; sedgeland - *Baumea arthropphylla*, *B. rubiginosa* and *Eleocharis acuta*; aquatic herbland, *Potamogeton tricarinatus*, *Chara* spp. *Triglochin procerum*, *Myriophyllum* spp., and *Villarsia reniformis*. The aquatic communities were chosen to represent the most common dominant communities (i.e. are present in more than 10 hectares within Tasmania) found in the lentic wetlands within Tasmania (Kirkpatrick and Harwood, 1983a, 1983b; Kirkpatrick and Harris, 1999).

The number of total vegetation zones recorded within each wetland ranged from 6 in Cherry Tree Lagoon and Middle Lagoon to 3 in Big Punchbowl and Tin Dish. Eleven zones, 2 from each wetland, except for 3 in Middle Lagoon) were sampled within the present study (Table 2.3; see Chapter 4).

Water regime of the wetlands

Big Punchbowl and Cherry Tree Lagoon

Big Punchbowl was inundated in 1979 during the period of the Kirkpatrick and Harwood (1981) study (Figure 2.6). Stewart Blackhall recorded water levels at Big Punchbowl between 1990 and 1993. At the beginning of his study the water level in the wetland was 740 mm. From that time the level of lagoon decreased and it eventually dried up during autumn 1992. The wetland was still dry with occasional patches of water when first visited by the author in August 1995. Between this time and the commencement of study the wetland has held water only in October 1996 (Plate 2.1). This corresponded with high rainfall in September 1996. During the period of the present study Big Punchbowl remained mostly dry until winter 1998 when the water level rose to 250 mm. While this rise in water level corresponded with only slightly above average winter rainfall recorded at Swansea, Coles Bay recorded well above average

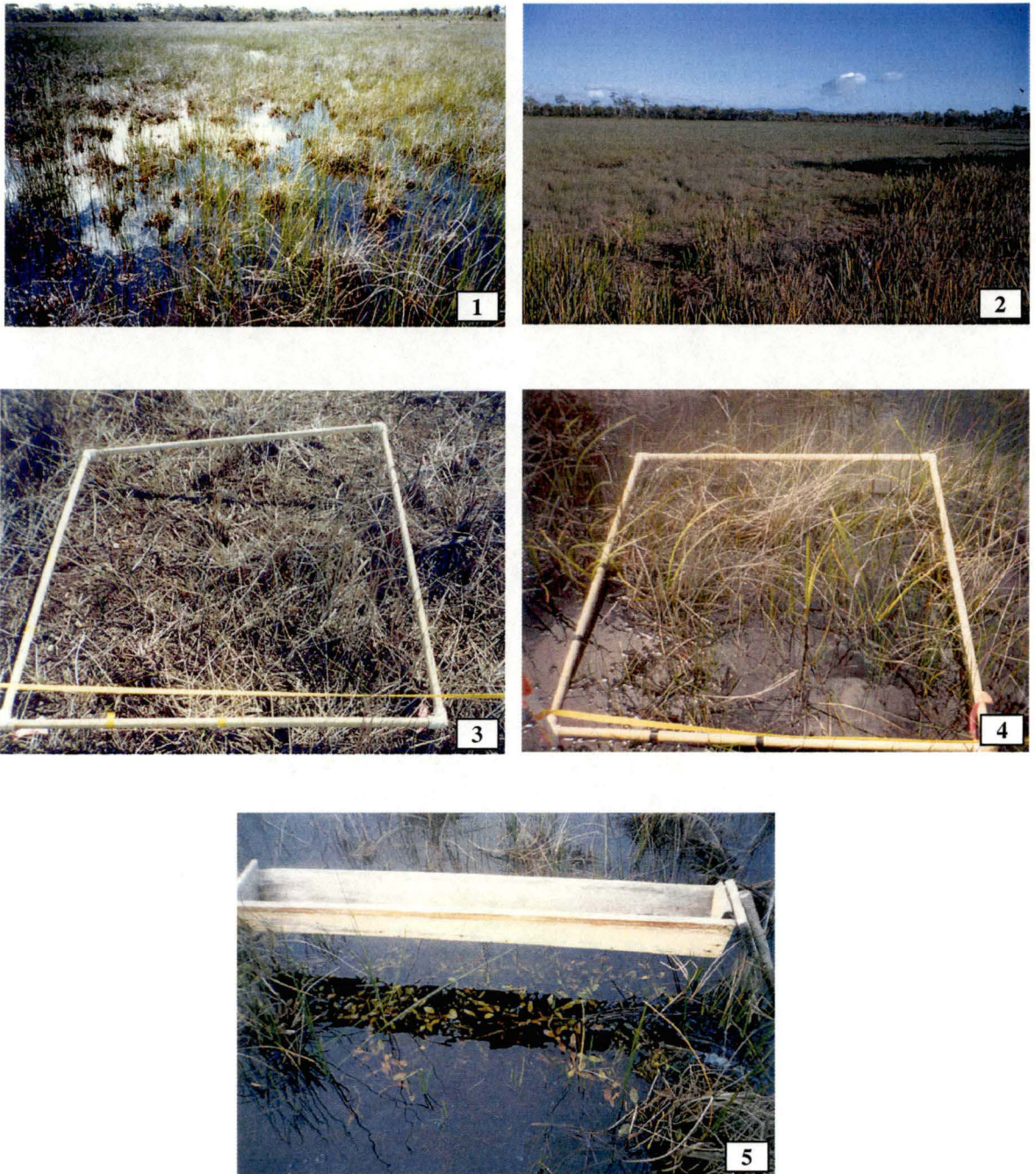


Plate 2.1

Big Punchbowl: 1) *Baumea arthropphylla* zone during first visit to the wetland in 1996; 2) *Baumea arthropphylla* zone summer 1997 at the commencement of the present study - the wetland had dried out completely by this time; 3) *Baumea arthropphylla* aquatic zone - Transect 1, summer 1998; 4) *Baumea arthropphylla* aquatic zone - Transect 1, spring 1998, shows increased *Baumea arthropphylla* cover and the presence of *Triglochin procerum* after the wetting up period of winter 1998; 5) *Baumea arthropphylla* aquatic zone -end of Transect 3 - *Potamogeton tricarinatus* that regenerated during the wetting up period of winter and spring 1998.

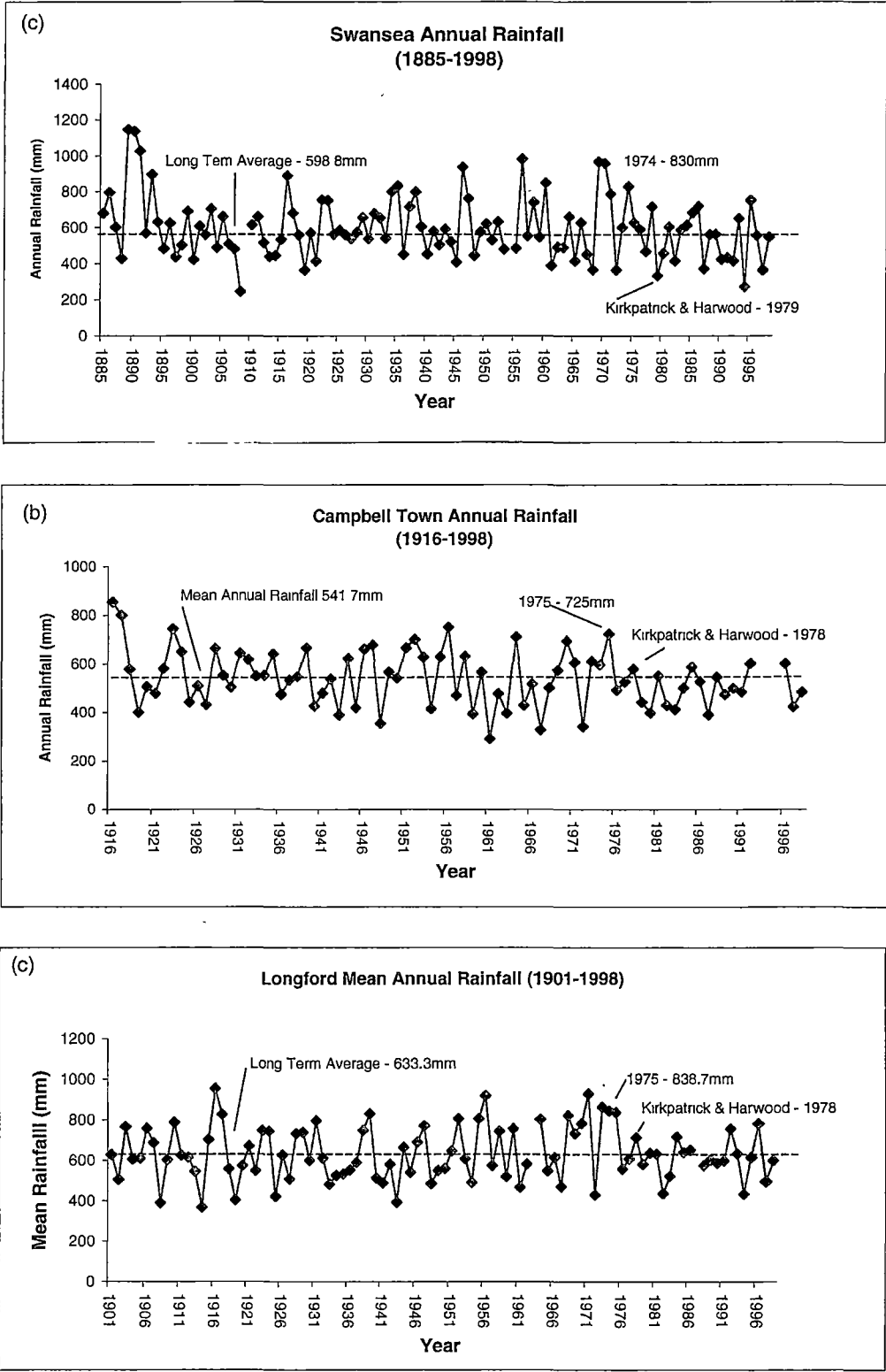


Figure 2.6 Long-term annual rainfall for (a) Swansea; (b) Campbell Town; and (c) Longford (Source: unpublished data Bureau of Meteorology),.

rainfall. The wetland remained inundated over the spring 1998 period but dried out during the following summer (1998-1999). Big Punchbowl has a small catchment area and relies on rainfall to fill. In the past Big Punchbowl has contained large amounts of water and was not generally characterised as a long-term dry wetland. The water regime in the wetland has obviously changed in the last ten years. Within this time lower annual rainfall has been recorded in the east coast area (Figure 2.6).

Cherry Tree Lagoon (Plate 2.2) had a reduced water level over the period of the present study. However, it remained inundated for most of the time studied. The highest level recorded was on the first visit in October 1995 (700 mm). This level dropped to 450 mm in summer 1997 and continued to go down until it dried completely in autumn 1998. Local shooters observed that Cherry Tree Lagoon had dried out “approximately 12 years” prior to this. This may have been in the low winter rainfall of 1987. The water level rose from zero to 670 mm in winter 1998 and remained high for the rest of the study. This was the period that Big Punchbowl retained water, although Big Punchbowl began to dry in spring 1998, whereas Cherry Tree Lagoon levels increased. Cherry Tree Lagoon has a larger catchment than Big Punchbowl. This may increase the likelihood of longer term water retention. The difference in underlying geology may also have an effect.

Sandy Gate and Tin Dish

In the 1950-60s, due to constantly being inundated, Sandy Gate and Tin Dish, along with the surrounding wetlands, were considered permanent. To reduce water levels some drainage work was done in the late 1950s, however, the wetlands were still inundated during the mid 1960s prior to a drought in 1967. The wetlands re-flooded after this time and were inundated at the time of the surveys by Kirkpatrick and Harwood (1981).

However after 1975, there seems to have been a noticeable decrease in the peaks of above average rainfall years (Figure 2.6). These higher peak rainfall events may have filled the lagoons in this area. During the period prior to the present study, Campbell Town recorded an above average seasonal rainfall in the summer of 1996. Following this, all seasons until spring 1998 recorded lower than average rainfall, decreasing to only 50 mm in autumn 1998 (Figure 2.6). Sandy Gate is predominantly a sedge-dominated wetland that tends to hold water longer than its surrounding wetlands.

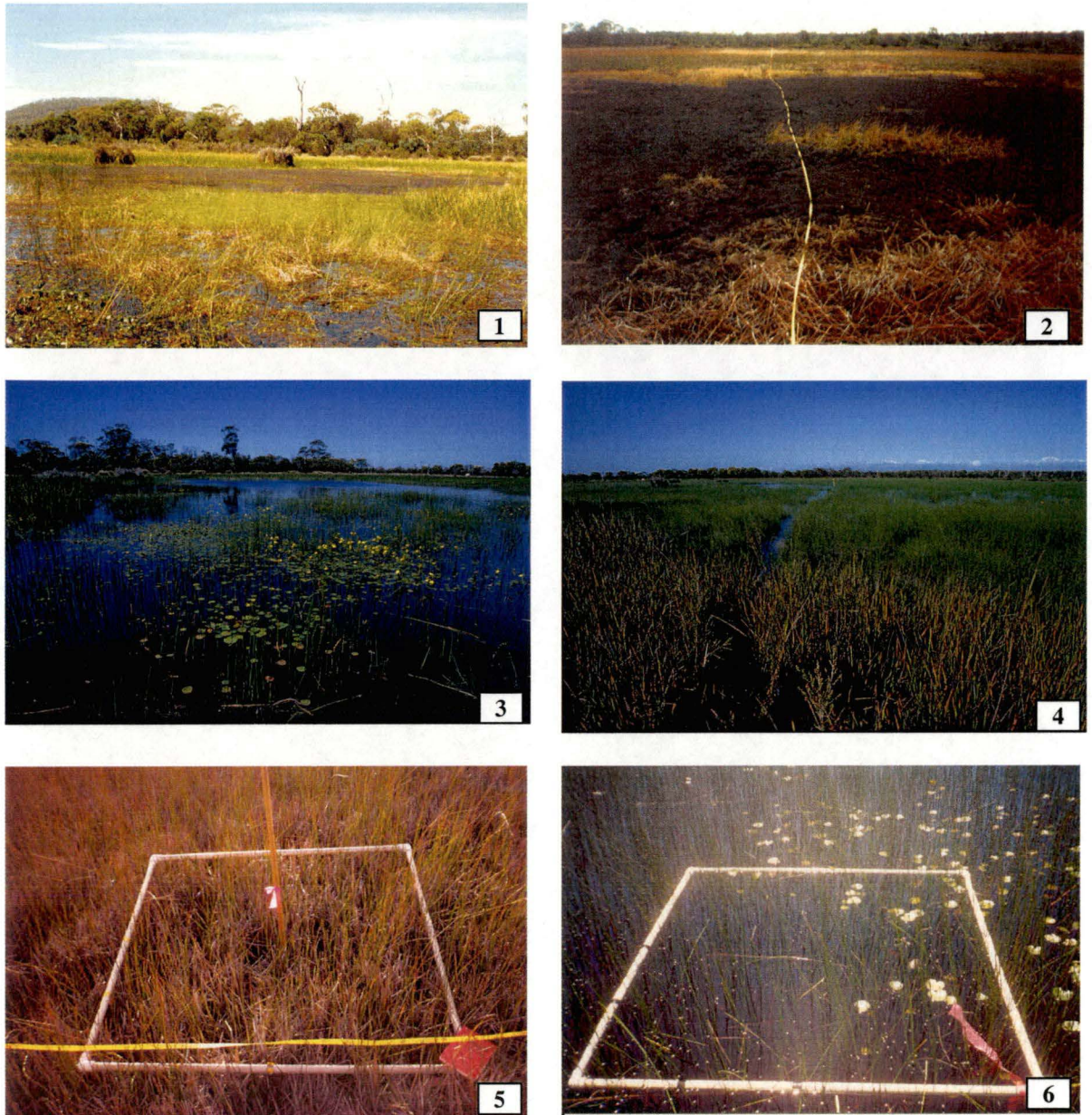


Plate 2.2 Cherry Tree Lagoon: 1) summer 1997 - looking towards water hole and aquatic herbaceous zone with *Baumea arthrophylla* in the foreground; 2) water hole when dry in autumn 1998; 3) water hole and aquatic herbaceous zones spring 1997 after wetting up again in winter 1998; 4) Transect 2 - *Baumea arthrophylla* zone - spring 1998; 5) *Baumea arthrophylla* zone Transect 1 - during the dry period of autumn 1998; 6) *Baumea arthrophylla* zone Transect 1 - spring 1998.

It is a small wetland located in a hollow surrounded by woodlands and is therefore more protected from the drying winds than the large wetlands close by. However, a natural spring that runs along the side of the wetland is probably the main reason for the wetland remaining inundated during periods of drought and not drying out more regularly. The wetland was inundated in 1978 at the time of Kirkpatrick and Harwood (1981) study (Figure 2.6; Plate 2.3). This was just at the beginning of the lower rainfall period after 1975. In October 1995 the wetland depth was 250 mm and, with the high 1996 rainfall, had increased to 400 mm by September 1996. Water levels varied in the wetland over the study period. It did not dry up until the summer 1998 and remained dry throughout the low rainfall autumn (Plate 2.3). However, it rapidly wetted up again with the increased rainfall of the following winter and spring (Figure 2.5).

Tin Dish was inundated in 1978 during the survey by Kirkpatrick and Harwood (1981; Plate 2.4). However, it had dried out by the early 1980s (Henry Foster, pers. comm.) and remained dry until the wet summer of 1995/96. The first visit to this wetland was in October 1995, prior to the summer 1996 rainfall. The wetland at this time had been dry for over ten years and supported mainly pasture weeds within its centre (Plate 2.4). It was visited a year later in September 1996 when the wetland had filled to a depth of approximately 300 mm. However, aquatic vegetation had not yet become dominant. In February 1997 the aquatic plant communities had regenerated over the spring and summer and were dominant within the wetland centre (Plate 2.4). However, the wetland was drying rapidly and by spring 1997 had dried out completely and remained so for the rest of the study (Plate 2.4). Tin Dish has a small catchment area. It is an open unprotected area and is subject to strong drying north westerly winds. Unlike Sandy Gate it failed to wet up again in 1998 and up to summer 1999 it had not retained water since the beginning of 1997 (Henry Foster, pers. comm.).



Plate 2.3

Sandy Gate: 1) 1978 survey by Kirkpatrick and Harwood (1981) during a wet period. Photo shows natural spring running through the edge of the wetland; 2) similar area to photo 1 -spring 1998 at the end of the present study; 3) summer 1998 at the commencement of the present study; 4) autumn 1998 - wetland was dry during this period; 5) aquatic herbaceous zone spring 1997 - *Potamogeton tricarlinatus* and *Triglochin procerum*; 6) *Baumea arthropphylla* zone summer 1998 (*Baumea arthropphylla* flowering).

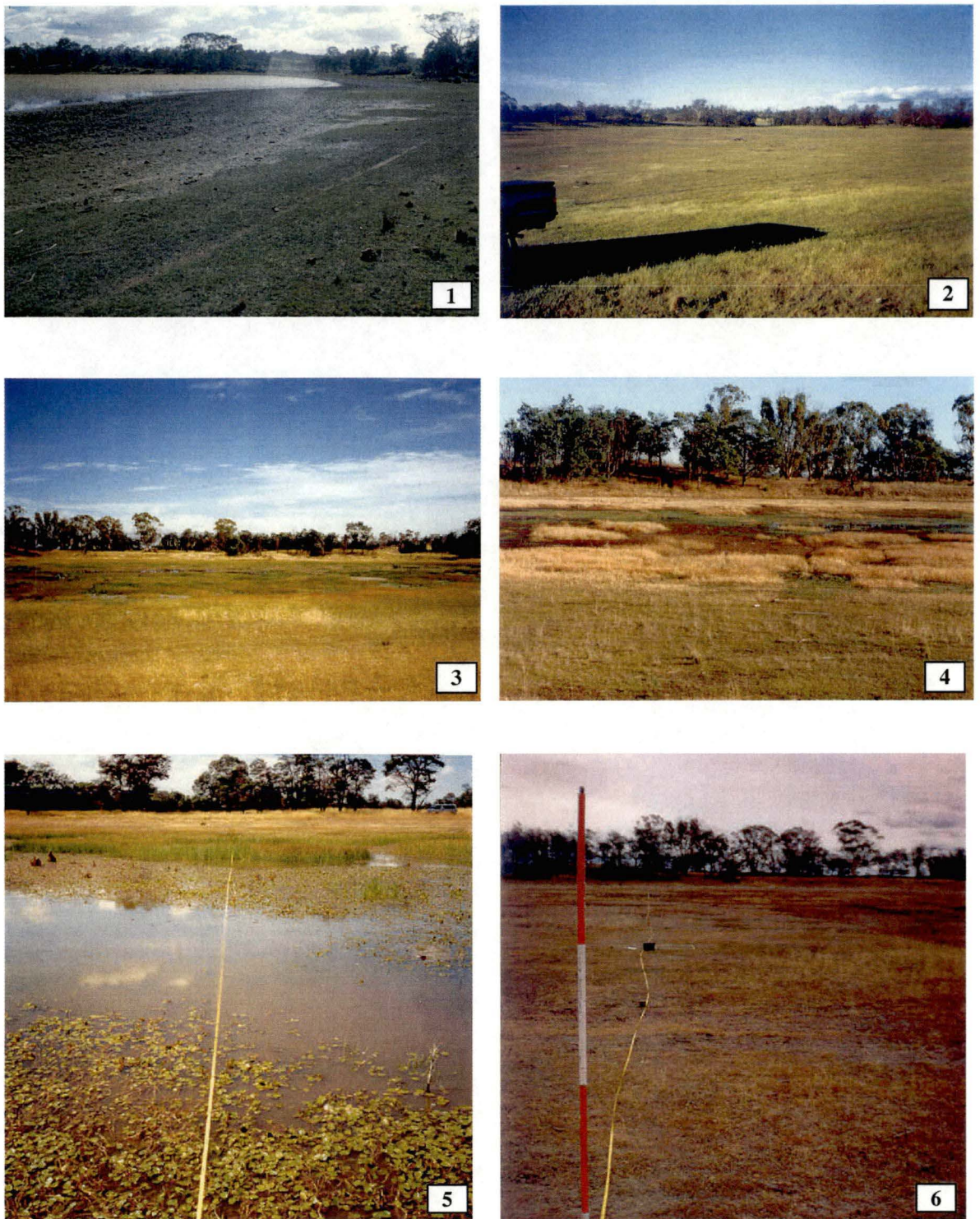


Plate 2.4

Tin Dish: 1) 1978 during survey by Kirkpatrick and Harwood (1981); 2) first visit in 1996- wetland was completely dry; 3) summer 1997 at the commencement of the present study; 4) drying up in winter 1997; 5) Transect 1 - summer 1997; 6) Transect 1 - spring 1998.

Middle Lagoon

Stewart Blackhall, has been recording water levels in Woodstock Lagoon since early 1990. Both Woodstock and Middle Lagoon appear to have had a reduction in water level over the last 20-30 years. Depths of 1-2 m in Woodstock during summer periods in the past were remembered by the landowner (Bill Cox, pers. comm⁷). These levels have not been recorded during the period of this study. Since 1975 there has been a reduction of high annual rainfall events in the area with 17 out of the 29 years recorded as below mean annual rainfall (Figure 2.6).

Middle Lagoon has a small catchment and most of the supply of water would come from rainfall. Two dams have been built within the wetland area which tend to remain wet for longer than the lagoon. However, both dried up during autumn of 1998. Middle Lagoon has experienced a wide range of water level fluctuations during the two year period of the present study.

Middle Lagoon was first visited in October 1995. At this time the water depth was approximately 300-400 mm (Plate 2.5). The wetland appeared to be in a wetting up phase which may have commenced in the summer of 1995 and continued through to 1996 due the above average rainfall in both summer and winter of that year. Hence at the commencement of this study in February 1997 the water depth in the lagoon was in the order of 600 mm increasing to 700 mm over the winter period (Plate 2.5). This was followed by a large decrease in water level during the spring period of the order of 550 mm. This may have been partly due to the landowner pumping water from the lagoon for stock in other areas. The water level increased in 1998 (Plate 2.5) and may have risen further with the high rainfall in summer 1999. However, by the end of spring 1999, the water level in the lagoon was 300 mm.

Water regime descriptions

Using the water regime classification proposed for temporary wetlands within Australian by Boulton and Brock (1999), the water regime of the 5 wetlands, prior to the early 1980s, could be described as semi-permanent. However, due to climatic changes and increased drought periods, within the last 10 - 20 years (Figure 2.5), dry periods in three of the wetlands (i.e. Big Punchbowl, Tin Dish and Middle Lagoon)

⁷ Bill Cox, landowner Woodstock Lagoon, Springbanks, Longford.

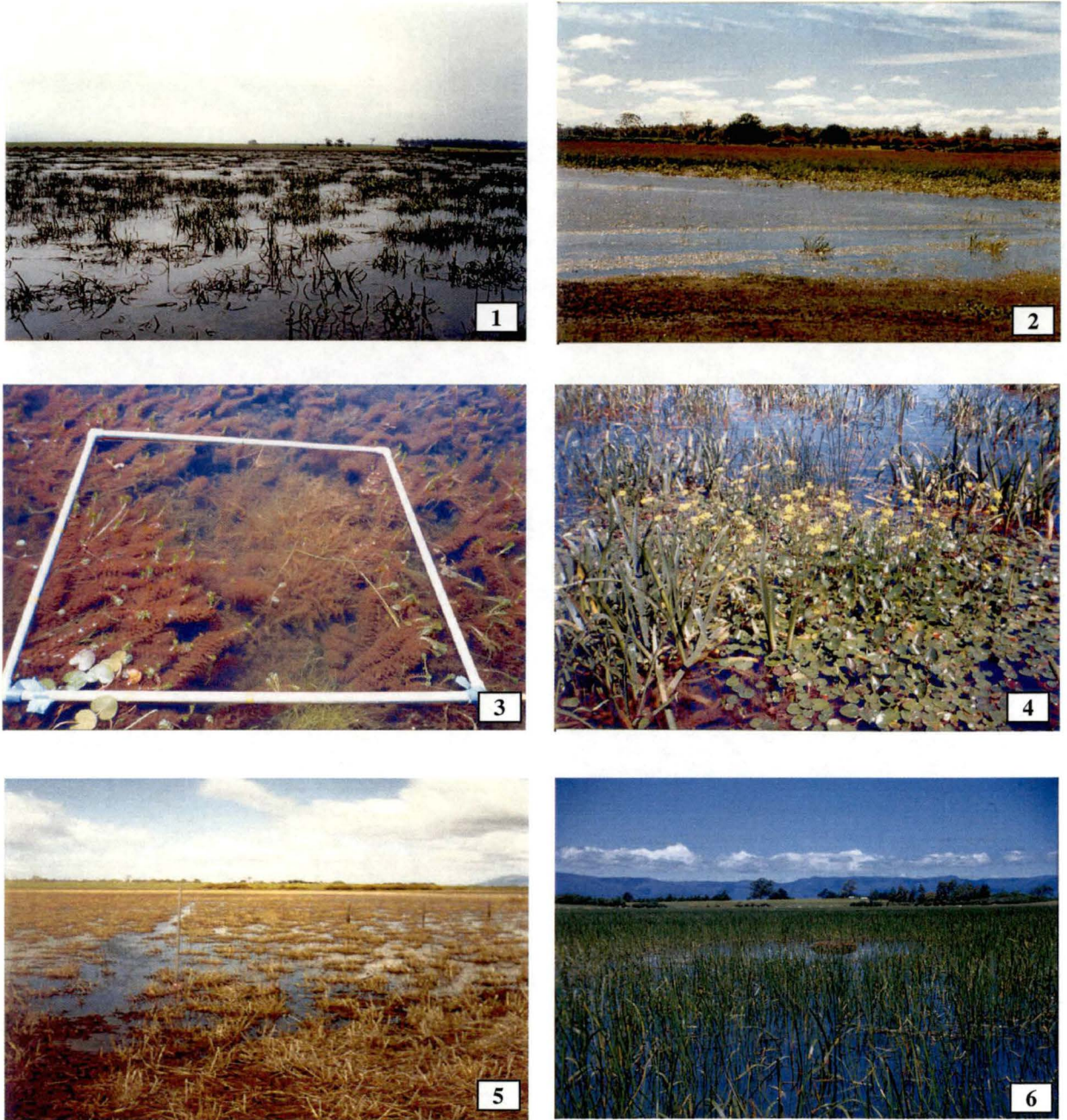


Plate 2.5

Middle Lagoon: 1) *Eleocharis sphacelata* zone during first visit in 1995 - Middle Lagoon had just wetted up after being dry for 5 years; 2) *Eleocharis sphacelata*, aquatic and dry herbaceous zones (foreground) in summer 1997 at the commencement of the present study; 3) and 4) *Myriophyllum* sp. and *Villarsia reniformis* in the aquatic herbaceous zone during spring 1997; 5) *Eleocharis sphacelata* zone winter 1998; 6) *Eleocharis sphacelata* zone spring 1998.

have become more frequent and longer in duration. As a consequence, the most recent water regimes of Big Punchbowl and Tin Dish can be described as episodic, and Middle Lagoon as intermittent. Over the same period the water regime of Cherry Tree Lagoon and Sandy Gate remained semi-permanent in nature. For the purpose of the present study, the episodic wetlands have been named "long-term dry" and the intermittent "fluctuating". All of the wetlands were dry during some period of this study.

Two means of describing the water regimes of the wetland over the period of the present study were used: a) water depth; and b) percentage of seasons a zone was inundated over the period of the study (Table 2.4).

Table 2.4 Summary of the mean seasonal water depth and percentage of inundation recorded in each vegetation zone over the period of the study (Shaded area = season inundated; numbers within shaded area = mean seasonal water depth recorded from 9 quadrats within each zone; * = maximum mean water depth recorded over the period of the present study, ** = missing value; BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B.a = *Baumea arthropophylla*; B.r = *Baumea rubiginosa*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; Aq = Aquatic; Out = Outer; DH = Dry herbaceous zone).

	SU97	A97	W97	SP97	SU98	A98	W98	SP98	Percentage inundation	Mean Max. depth*
BP B.r Aq.			1.7			17.2	5.7		37.5	17.2
BP B.r Out.						1.4			12.5	1.4
TD Aq.	8.0	1.4	4.1						37.5	8
TD E.a	1.4								12.5	1.4
MID E.s	50.9	**	56.2	60.6	5	3.4	25.4	41.1	100	60.6
MID Aq.	10.3	**	18.2	19.6				1.0	57.1	19.6
MID DH		**	2.1	2.6					28.6	2.6
CTL Aq.	24.9	19.5	14.4	17.4	4.1		44.7	50.1	87.5	50.1
CTL B.a	10.7	3.0	1.5	1.8			28.1	35.4	75	35.4
SG Aq.	7.9	11.3	26.8	17.5			6.3	11.8	75	26.8
SG B.a	3.4	6.1	18.0	10.6			2.5	6.4	75	18

Chapter 3

Classification into Functional Groups

Introduction

The classification of plants and animals into groups according to their structure and function is not a new concept. One of the first records for both terrestrial and aquatic vegetation dates back to Roman times with the natural historian Theophrastus (370-285 BC) (Du Rietz, 1931; Brock, 1994; Westoby and Leishman, 1997). This urge to classify components of large complex systems into smaller units has continued to the present day.

The early systems were generally based on plant physiognomy (i.e. external appearances or characteristics). Although they were used to relate structure to climate and other environmental factors, they were typically used for descriptive purposes (Du Rietz, 1931; Barkman, 1988; Kleyer, 1999). The next challenge in plant ecology was to develop functional classifications that incorporated the physiognomic adaptation concepts emphasised in the early systems with population and community ecology (Shugarth, 1997). From this combination grew the concept of using functional types or groups of species for the analysis and comparison of community responses to varying environmental conditions (McIntyre *et al.*, 1995; Lavorel *et al.*, 1997).

During the 1960s the functional group approach became increasingly based on community responses to environmental conditions such as disturbance regime or resource availability (Shugarth, 1997; McIntyre *et al.*, 1999a). Well known early approaches include the r-K and adversity responses (MacArthur and Wilson, 1967; Southwood, 1977); late successional species (Whittaker, 1975; Bazzaz, 1979, Finegan, 1984); exploitative and conservative species (Borman and Likens, 1979); ruderal, stress-tolerant and competitive strategies (R-S-C) (Grime, 1974, 1977, 1979b); gap and non-gap (Brokaw, 1985a, 1985b); the 'bet-hedging' model (Stearns, 1976); life-form classifications (Raunkiaer, 1934; Webb, 1959; Webb *et al.*, 1970) and vital attributes (Noble and Slatyer, 1980; Walker *et al.*, 1981).

Interest in this more dynamic functional approach has continued (Box, 1996; Brock and Casanova, 1997; Gillison and Carpenter, 1997; Lavorel *et al.*, 1997; see also reviews in Smith *et al.*, 1997; Westoby, 1998; Lavorel and Cramer, 1999). Classifications based on plant responses are particularly useful for interpretation and prediction within dynamic ecosystems, such as wetlands (Noble and Gitay, 1996; Brock and Casanova, 1997).

Several authors have attempted to categorise the main approaches used to identify functional groups or types, for example as, subjective, deductive and data driven (see reviews in Noble and Gitay, 1996; Gitay and Noble, 1997; Lavorel *et al.*, 1997; McIntyre, 1999b; Weiher *et al.*, 1999). However, the basis for most plant functional classifications, irrespective of the approach, is the identification of key traits that are believed to be important to, and predictive of, the disturbance regime being studied (Lavorel *et al.*, 1997). This concept ensures that the resulting functional groups are related to the disturbance regime rather than the ecosystem (McIntyre, 1999b), facilitating comparative studies between ecosystems.

The functional group approach has been used in relation to a variety of disturbances within a variety of ecosystems, using widely varying trait sets (McIntyre, 1999b).

Examples have been given of predictive dynamics after: fire (Noble and Slatyer, 1980); grazing (Diaz *et al.*, 1999, Hadar *et al.*, 1999, Landsberg *et al.*, 1999); land use changes (Noble and Gitay, 1996; Weiher *et al.*, 1999; Diaz, *et al.*, 1999; McIntyre *et al.*, 1999b, Kleyer, 1999); ploughing (Lavorel *et al.*, 1999); resource use (Woodward and Kelly, 1997); hydrological disturbance (van der Valk, 1981; Day *et al.*, 1988b; Hills *et al.*, 1994; Hills and Murphy, 1996; Brock and Casanova, 1997); global change (Grime, 1993; Chapin *et al.*, 1996; Smith *et al.*, 1993; Woodward and Cramer, 1996; Steffen, 1996); climate change (Skarpe, 1996); water stress (Diaz Barradas *et al.*, 1999); natural disturbances (Denslow, 1980), and within systems such as rainforests (Gitay *et al.*, 1999); arctic tundra (Chapin *et al.*, 1996); grasslands (Campbell *et al.*, 1999; Hadar *et al.*, 1999; Lavorel *et al.*, 1999); shrublands (Diaz Barradas *et al.*, 1999); arid rangelands (Westoby, 1980; Landsberg *et al.*, 1999); south African savanna (Skarpe, 1996); coastal islands (Shao *et al.*, 1996); temperate and boreal forests (Bugmann, 1996); semi-arid woodlands (Leishman and Westoby, 1992) and wetlands (van der Valk, 1981; Day *et al.*, 1988b; Hills *et al.*, 1994; Weiher and Keddy, 1995; Hills and Murphy, 1996; Brock and Casanova, 1997).

Measurable traits can fall into several broad categories of which some may overlap, namely: 1) reproductive or regenerative; 2) morphological; 3) dispersal; 4) establishment; 5) persistence or survival; 6) life history (van der Valk, 1981; Shipley *et al.*, 1989; Murphy *et al.*, 1990; Keddy, 1992a; Hills *et al.*, 1994; Brock and Casanova, 1997; Smith *et al.*, 1997; Lavorel and Cramer, 1999; Weiher *et al.*, 1999). Boutin and Keddy (1993) outlined five steps in the process of searching for functional groups: 1) defining function; 2) selecting traits which reflect function; 3) screening for these traits; 4) constructing trait matrices; and 5) grouping species according to these traits. Additionally, a choice of easily-measured traits allows useful comparison with other studies (Weiher *et al.*, 1999).

Classifications of wetland plants

Shallow wetlands, as well as many wetland edge communities, are dynamic systems due to their water level fluctuations (Brock and Casanova, 1997). Studies of wetland plant communities have shown that the temporal dynamics of many wetland species can mirror water level fluctuations with characteristic increases and decreases in both number of species and plant cover depending on the adaptations or 'strategies' that plants use for coping with their changing environment (van der Valk and Davis, 1978; Connor, *et al.*, 1981; van der Valk, 1981; Pederson and Davis, 1984; Pederson and van der Valk, 1984; Gopal, 1986; Poiani and Johnson, 1989; Leck and Simpson, 1994; Weiher and Keddy, 1995; Nielson and Chick, 1997; Brock and Rogers, 1998). Grime's (1974) plant strategy concept, namely, ruderal or disturbance tolerant (R-strategist), competitive (C-strategist) or stress tolerant (S-strategy) can be used to give a general classification of these characteristic 'strategies' or 'life cycles' in wetland plants (Crosslé, 1998). Grime (1974) related these strategies to plant reproductive, establishment and life history traits, for example, germination and life span.

Keddy (1992b) applied the concepts of assembly and response rules to wetland plants. Assembly rules are associated with individual species traits that determine which species will germinate under a given set of conditions (e.g. mud flat or drowned). Therefore, assembly rules determine the subset of species that will be recruited into the wetland vegetation (assembly). Response rules determine the species that will establish and survive to reproduce. Conditions may change from those which are in place at the time of germination, meaning that species may have to respond to changing conditions

in order to survive, or risk temporary or permanent exclusion from the community (Crosslé, 1998).

In a wetland, water regime is one of the strongest selective forces which determine species that germinate (assembly rules) and then survive (response rules) (Keddy, 1992b from Crosslé, 1998).

Functional classification of wetland plants

Several functional classifications of wetland plants have been made using a range of traits. Wetland plants have been grouped using functional life history traits (van der Valk, 1981; Boutin and Keddy, 1993), their competitive ability (Keddy *et al.*, 1994) and survival strategies (Hills *et al.*, 1994; Hills and Murphy, 1996). Studies that examine the presence of plants in fluctuating water regimes include Keddy (1992a) and van der Valk (1981). Brock and Casanova (1997) have been the only Australian authors to have investigated functional groups in relation to water regime. They used a data-driven multivariate technique (Gitay and Noble, 1997) to seek clusters of species based on plant responses to the conditions under which species germinate, grow and reproduce in relation to water presence or absence (Table 3.1).

They recognised three major groups of species: *terrestrial*, *amphibious* and *submerged* (Figure 3.1; Figure 3.2). The terrestrial and submerged groups were characterised by species dependent on either wet or dry conditions, that generally do not survive when the opposite condition occurs. The terrestrial species were those that require dry conditions to survive or those that could tolerate damp conditions. The larger amphibious group was characterised by species adapted to survive changes in water level. These amphibious species were further divided into two groups depending on their ability to either 'respond' or 'tolerate' the presence or absence of water, namely: *amphibious: fluctuating-tolerators* or *amphibious: fluctuating-responders* (Brock and Casanova, 1997).

The *fluctuating-tolerators* are species that cope with fluctuations of water by enduring a range of water conditions without major change in morphology or growth whereas, *fluctuating-responders* change their growth pattern or morphology in response to the presence or absence of water (Brock and Casanova, 1997).

Table 3.1 Criteria used by Brock and Casanova (1997) for the classification of wetland plants based on plant responses to the conditions under which species germinated, grow and reproduce in relation to water presence or absence.

Criteria	Response
Criterion 1	<p>Germination from a wetland seed bank in response to:</p> <ul style="list-style-type: none"> • fluctuating; or • damp • underwater conditions
Criterion 2	<p>Growth response as measured by:</p> <p><i>growth form of photosynthetic parts in relation to the soil/water surface:</i></p> <ul style="list-style-type: none"> • low-growing • upright • floating; and <p><i>growth place:</i></p> <ul style="list-style-type: none"> • submerged • emergent • on saturated soil
Criterion 3	<p>Reproduction in response to water presence as measured by:</p> <p><i>where seeds mature:</i></p> <ul style="list-style-type: none"> • underwater • out of water above flooded soil • out of water above dry soil; and <p><i>water depth when plants reproduce:</i></p> <ul style="list-style-type: none"> • dry • saturated soil • shallow water, < 10 cm • deep water, > 10 cm

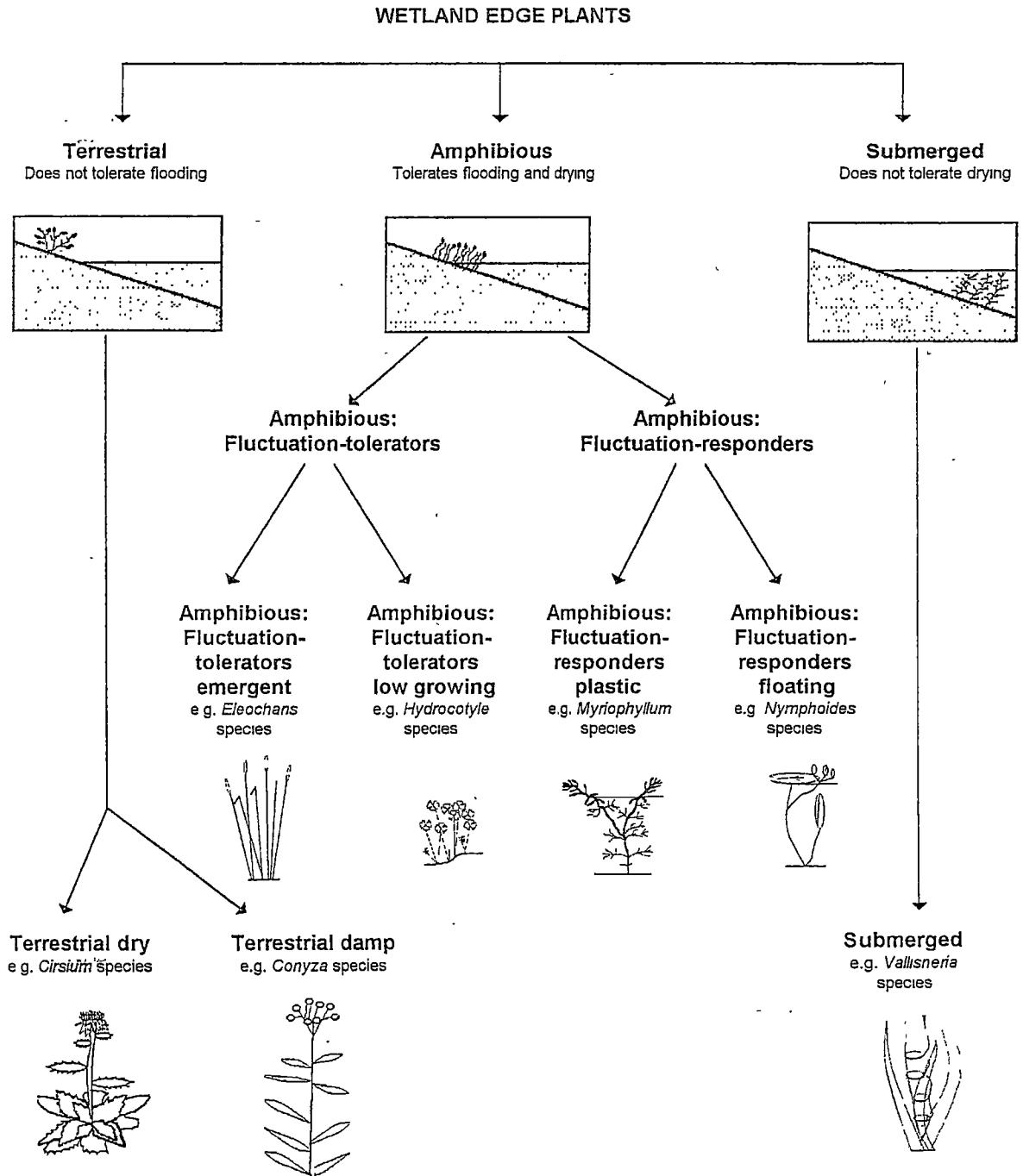


Figure 3.1 Summary and pictorial representation of functional groups identified by Brock and Casanova (1997).

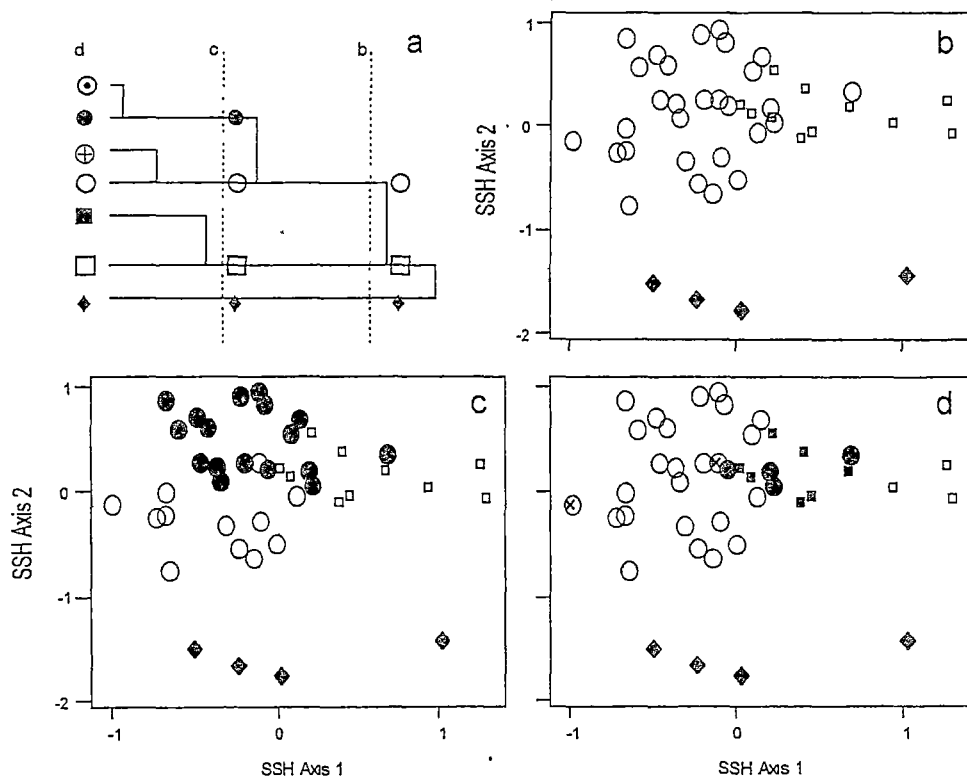


Figure 3.2

Identification of functional groups of species on the basis of germination, growth and reproduction responses to water presence and absence.

Simplified dendrogram derived from pattern analysis (symbols represent:

(b) ○ Amphibious, □ Terrestrial, ◆ Submerged; (c) ○ Amphibious:

Fluctuation-responder, ● Amphibious: Fluctuation-tolerator, □ Terrestrial, ◆

Submerged; (a) and (d) ○ Amphibious: Fluctuation-responder, plastic, Symbol,

Amphibious: ⊕ Fluctuation-responder, floating, ● Amphibious: Fluctuation-

tolerator, low growing; ⊙ Amphibious: Fluctuation-tolerator, emergent, □

Terrestrial, damp; □ Terrestrial, dry, ◆ Submerged (Source: Brock and

Casanova, 1997).

These two amphibious groups were further broken down into subgroups depending on their morphological adaptations. The *amphibious :fluctuating-tolerators* (AT) were further divided into the morphological groups 1) *emergent* (ATe) consisting mostly of monocotyledons and 2) *low growing* (ATl) consisting mostly of dicotyledons. Whereas, the *amphibious: fluctuating-responders* (AR) morphological groups depended on whether they were characterised by: 1) floating (ARf), species which have floating leaves in their aquatic phases and also grow stranded on damp ground, or 2) plastic (ARp) species that are morphologically variable in response to environmental conditions (Brock and Casanova, 1997).

Testing of functional approaches

McIntyre *et al.* (1999a) argued that meaningful interpretations of functional traits will only result from the synthesis of many studies. Few specific tests of the utility of existing functional classifications have been undertaken (Gitay and Noble, 1997). General sets of common traits for comparison studies have been proposed by various authors such as Westoby (1998); Weiher *et al.* (1999). However, these studies were mainly directed towards traits useful for predicting vegetative responses to disturbances such as fire and grazing. To enable a functional analysis to predict plant responses to water level fluctuations, species would need to be allocated to functional groups based on traits similar to those used by Brock and Casanova (1997).

Ideally, a functional classification should be applicable to similar types of species wherever they occur and under a wide range of environmental conditions and perturbations (Gitay and Noble, 1997). A classification is said to be repeatable if independent analyses carried out at different sites yield similar functional groups in terms of trait sets (Gitay and Noble, 1997; Lavorel *et al.*, 1999). Gitay and Noble (1997) tested several studies and found that there is some evidence of repeatability of functional groups. They also concluded that it is feasible to group species based on character syndromes (indicating the existence of a condition) and that these groupings are repeatable to some extent when based on the same character set measured in different locations or different times.

Table 3.2 lists the species from the Northern Tableland wetlands by the functional groups of Brock and Casanova (1997). Twenty-five of their taxa are common to the present study with a further 28 taxa being found elsewhere within Tasmania (Table 3.2). Of the 60 taxa in Brock and Casanova (1997) only 7 do not occur in Tasmania. This indicates that similar wetland systems to those found in the Northern Tablelands of New South Wales are found in Tasmania. From this, it may be asked whether the species that occur both in the Northern Tablelands and 5 Tasmanian wetlands behave the same way in both places, particularly in relation to their responses to water level fluctuations? Do they fall into similar functional groups as described by Brock and Casanova (1997)? Following on from this what are the implications for the classification of the substantial number of wetland species found only in the 5 Tasmanian wetlands? Thus the aim of this chapter is to test if the species found in the 5 Tasmanian wetlands fall into similar functional groups using the criteria and methodology outlined by Brock and Casanova (1997) in their study of wetland plants of the Northern Tablelands of New South Wales.

Methods

Except where authorities are given, nomenclature of plant taxa follows Curtis (1963, 1993), Aston (1973), Sainty and Jacobs (1981), Orchard (1985), Harden (1993), and Curtis and Morris (1993;1994). Charophyte species nomenclature follows van Raam (1995).

Criteria allocation

Seed bank germination was determined as per the methods detailed in Chapter 4. All species that either germinated in the seed bank studies, or were recorded in field surveys (Chapter 5), were scored either present/absent according to the criteria of Brock and Casanova (1997) detailed in Table 3.1. The morphological and reproductive traits for each were validated by either observations in the field or from the literature. Due to the differences in the germination experimental design between this study and Brock and Casanova (1997) the germination criteria, in the present analyses, were reduced to only two conditions: 1) damp and, 2) underwater (i.e. omitting the fluctuating condition of Brock and Casanova (1997, Table 3.1; Table 3.3).

Table 3.2 Functional groups of species found in the Northern Tableland wetlands as allocated by Brock and Casanova (1997) compared with the species in common from the present study.

25 species (41%) are common to both studies (red).

28 species (48%) are found in Tasmania but not in the wetlands of this study (blue).

7 species (11%) do not occur in Tasmania. (black)

88 percent of the species found in the two wetlands of Brock and Casanova (1997) are found in Tasmania.

	SUBMERGED	AMPHIBIOUS				TERRESTRIAL	
	S	FLUCTUATION- RESPONDER morphologically plastic ARp	FLUCTUATION- RESPONDER floating/stranded ARf	FLUCTUATION- TOLERATOR emergent ATe	FLUCTUATION- TOLERATOR low growing ATI	damp places	dry places
Dicot	<i>Najas tenuifolia</i>	<i>Crassula helmsii</i> <i>Elatine gratioloides</i> <i>Limosella australis</i> <i>Myriophyllum variifolium</i> <i>Utricularia australis</i> <i>Myriophyllum verrucosum</i>	<i>Nymphoides montana</i>	<i>Lilaeopsis polyantha</i> <i>Lythrum salicaria</i> <i>Persicaria hydropiper</i> <i>Persicaria lapathifolia</i> * <i>Ranunculus inundatus</i> ?	<i>Centipeda minima</i> <i>Utricularia dichotoma</i> <i>Hydrocotyle tripartita</i> <i>Isotoma fluviatilis</i>	<i>Hypericum japonicum</i> <i>Gratiola peruviana</i> <i>Trifolium</i> spp * <i>Centaurium spicatum</i> * <i>Conyza bonariensis</i> * <i>Rumex crispus</i> * <i>Geranium</i> spp * <i>Rorippa palustris</i> * <i>Stellaria angustifolia</i> <i>Alternanthera trachycarpa</i>	<i>Cirsium vulgare</i> * <i>Gnaphalium</i> spp. */n <i>Modiola caroliniana</i> * <i>Portulaca oleracea</i> <i>Polygonum arenastrum</i> *
Monocot	<i>Potamogeton ochreateus</i> <i>Vallisneria gigantea</i>	<i>Potamogeton tricarlinatus</i> <i>Isolepis fluitans</i> <i>Eleocharis sphacelata</i>		<i>Agrostis avenacea</i> <i>Amhibromus sinuatus</i> <i>Eleocharis acuta</i> <i>Schoenus apogon</i> <i>Juncus articulatus</i> * <i>Juncus holoschoenus</i> <i>Paspalum distichum</i> * <i>Glyceria australis</i> <i>Typha orientalis</i> <i>Carex gaudichaudiana</i> <i>Cyperus sanguinolentus</i> <i>Eleocharis pusilla</i> <i>Eleocharis dietrichiana</i> <i>Lipocarpa microcephala</i>		<i>Juncus bufonius</i> * <i>Juncus australis</i> <i>Panicum gilum</i> * <i>Eragrostis trachycarpa</i>	
Charophyte	<i>Chara</i> spp. <i>Nitella</i> spp.						
Fern	<i>Isoetes drummondii</i>	<i>Marsilea</i> species	<i>Azolla filicaulis</i>				

? *Ranunculus inundatus* is identified as *Ranunculus amphitrichus* in Tasmania.

* = introduced species

Table 3.3 Summary of the similarities and differences between this study and Brock and Casanova (1997).

This Study	Brock and Casanova (1997)
Wetland Characteristics	
5 wetlands	2 wetlands
2 semi permanent	1 semi permanent
2 long-term dry	1 intermittent
1 intermittent	
Vegetation Zones Sampled	
Aquatic herb dominated zone (4)	Aquatic herb zone (2)
Sedge dominated zone (5)	(edge and fluctuating water levels)
Outer dry edge zone (1)	
(edge and fluctuating water levels)	
Germination	
no fluctuating germination water regime	fluctuating germination water regime
Species	
Total = 92 taxa	Total = 60 taxa
taxa in common = 25	
Analyses	
PATN used for analysis	PATN used for analysis
cluster analysis Bray -Curtis	cluster analysis Bray -Curtis
flexible UPGMA	flexible UPGMA
SSH – semi-strong hybrid multi-dimensional scaling	SSH – semi-strong hybrid multi-dimensional scaling
SSH Stress = 0.086	SSH Stress = 0.133

Data Analysis

To enable a reliable comparison with the functional groups of Brock and Casanova (1997) closely comparable methods of analysis were used to classify the plants in this study. Multivariate analyses were used to group species using the ecological pattern analysis package PATN (Belbin, 1991) with all criteria weighted equally.

Classification

A hierarchical agglomerative analysis using the Bray-Curtis measure of association (Bray and Curtis, 1957) and fusion using flexible UPGMA (Unweighted Paired Group arithMetic Averaging, Sneath and Sokal, 1973), using the default settings in PATN, were used to produce a dendrogram of species. From this result functional groups of species were recognised. Where appropriate the terminology of Brock and Casanova (1997) was retained.

Ordination

Semi-strong Hybrid Multi-Dimensional Scaling (HMDS – SSH option in PATN) using the Bray-Curtis association metric (Belbin, 1991) was applied. Ten random starts were used in an iterative process which converges on the best solution.

The relationship between the ordination and the separate functional group criteria were further explored using the principal axis correlation method (PCC option in PATN). The PCC is essentially a multiple-linear regression program designed to see how well a set of attributes can be fitted to an ordination space (Belbin, 1991). The attributes in this case are the criteria. The PCC finds the location of the best fitted vector for each attribute in the ordination space. The correlation coefficient may be used as an indication of the significance of each attribute. Because of lack of replication, one hundred randomisations (MCAO option in PATN) were applied using a Monte Carlo approach to test which criteria were significantly correlated to the ordination. The resulting significant vectors were plotted in the same ordination space.

Results and Discussion

Classification by UPGMA into Functional Groups

Several ecological groups of species can be readily recognised (Table 3.4) despite some evidence of chaining in the dendrogram (Figure 3.3). Most of the groups in this analysis are analogous with the groups recognised by Brock and Casanova (1997). The functional groups recognised as having similar characteristics to Brock and Casanova groups have been labelled as such both in Table 3.4 and in the descriptions below.

At level a in the dendrogram species were allocated into two groups (Figure 3.3); those of wet (wetland) or dry (terrestrial) habitats. At level b (Figure 3.3) terrestrial, amphibious and submerged groups of taxa were discriminated. At level c (Figure 3.3) within the amphibious group the fluctuation tolerator-saturated species are separated out from both the fluctuation tolerator-emergent and responder groups (which at this level remain in one group); the terrestrial species are broadly separated into species that either prefer dry habitats or can tolerate damp conditions; and the submerged plant group remains. At level d (Figure 3.3), the one adopted herein, there are 9 functional groups – 5 amphibious, 3 terrestrial and 1 submerged (Figure 3.3; Table 3.4). The structure of the adopted functional group classification is outlined in Table 3.5.

Terrestrial groups were separated from the amphibious and submerged groups mainly due to absence of species which can germinate in drowned conditions (Table 3.6). Submerged species were separated from amphibious species by a lack of species which mature their seeds above flooded/saturated soils and of species that reproduce in saturated conditions. The amphibious responder group had almost complete representation across the criteria, with only attributes related to dry conditions missing. The amphibious responder species were separated from the other amphibious tolerator groups mainly due to the presence of species that can survive underwater. The amphibious tolerator-saturated/mudflat species were divided from the tolerator-emergent by the absence of species capable of reproducing in shallow water (i.e. less than 10 cm depth) and the absence of emergent or floating species.

Table 3.4 Recognised functional groups from UPGMA analysis of Tasmanian study area wetland spp. using criteria from Brock and Casanova (1997).

Black = species common to both studies and allocated into a different group.

* = introduced species

*/n = unknown

SUBMERGED	AMPHIBIOUS Fluctuation- responders	AMPHIBIOUS Fluctuation- tolerators emergent deep water	AMPHIBIOUS Fluctuation- tolerators emergent shallow water	AMPHIBIOUS Fluctuation- tolerators Saturated low-growing	AMPHIBIOUS Fluctuation- tolerators Saturated upright	TERRESTRIAL Damp places upright	TERRESTRIAL Damp places low-growing	TERRESTRIAL Dry places
Group I	Group II	Group III	Group IV	Group V	Group VI	Group VII	Group VIII	Group IX
<i>Chara</i> spp.	<i>Callitriche stagnalis</i> *	<i>Cotula coronopifolia</i> */n	<i>Centipeda minima</i>	<i>Apium prostratum</i>	<i>Hypericum japonicum</i>	<i>Chenopodium glaucum</i> *	<i>Dichondra repens</i>	<i>Anagallis arvensis</i> *
<i>Nitella</i> spp.	<i>Crassula helmsii</i>	<i>Agrostis avenacea</i>	<i>Lilaeopsis polyantha</i>	<i>Leptinella longipes</i>	<i>Cyperus tenellus</i>	<i>Einadia nutans</i>	<i>Erodium cicutarium</i> *	<i>Centaureum erythraea</i> *
<i>Ruppia</i> spp.	<i>Myriophyllum simulans</i>	<i>Amphibromus sinuata</i>	<i>Mimulus repens</i>	<i>Centella cordifolia</i>	<i>Hemarthria uncinata</i>	<i>Epilobium</i> spp. */n	<i>Hypochoeris radicata</i> *	<i>Euchiton collinus</i>
<i>Lepilaena cylindrocarpa</i>	<i>Myriophyllum variifolium</i>	<i>Amphibromus recurvatus</i>	<i>Chorizandra australis</i>	<i>Scaevola hookeri</i>	<i>Isolepis cernua</i>	<i>Lythrum hyssopifolia</i>	<i>Leontodon taraxacoides</i> *	<i>Parentucella latifolia</i> *
	<i>Myriophyllum salsugineum</i>	<i>Juncus articulatus</i> *	<i>Schoenus apogon</i>	<i>Hydrocotyle sibthopliodes</i>	<i>Isolepis montivaga</i>	<i>Carex inversa</i>	<i>Scleranthus biflorus</i>	<i>Stellaria media</i> *
	<i>Neopaxia australasica</i>	<i>Juncus holoschoenus</i>	<i>Isolepis inundata</i>	<i>Selliera radicans</i>	<i>Juncus bufonius</i>	<i>Poa labillardierei</i>	<i>Trifolium</i> spp.*	<i>Acetosella vulgaris</i> *
	<i>Villarsia reniformis</i>	<i>Typha</i> sp.*/n	<i>Triglochin striatum</i>	<i>Eryngium vesiculosum</i>	<i>Schoenus nitens</i>	<i>Polypogon monspeliensis</i> *		<i>Agrostis capillaris</i> *
	<i>Hydrocotyle muscosa</i>	<i>Carex tetreticaulis</i>	<i>Juncus bulbosus</i> *	<i>Gonocarpus micranthus</i>	<i>Hainardia cylindrica</i> *			<i>Aira</i> spp.*
	<i>Ranunculus amphitrichus</i>	<i>Baumea arthropophylla</i>	<i>Juncus planifolius</i>	<i>Goodenia humilis</i>				<i>Briza minor</i> *
	<i>Elatine gratioloides</i>	<i>Baumea rubiginosa</i>		<i>Plantago coronopus</i> *				<i>Cirsium vulgare</i> *
	<i>Limosella australis</i>	<i>Eleocharis acuta</i>		<i>Schoenus maschalinus</i>				<i>Cynosurus echinatus</i> *
	<i>Utricularia</i> spp.	<i>Eleocharis sphacelata</i>						<i>Deyeuxia quadriseta</i>
	<i>Batrachium trichophyllum</i>							<i>Gaudiana fragilis</i> *
	<i>Triglochin procerum</i>							<i>Holcus lanatus</i> *
	<i>Potamogeton tricarlinatus</i>							<i>Poa annua</i> *
	<i>Isolepis fluitans</i>							<i>Vulpia myuros</i> *
	<i>Isolepis producta</i>							
	<i>Schoenus fluitans</i>							
	<i>Trithuria submersa</i>							

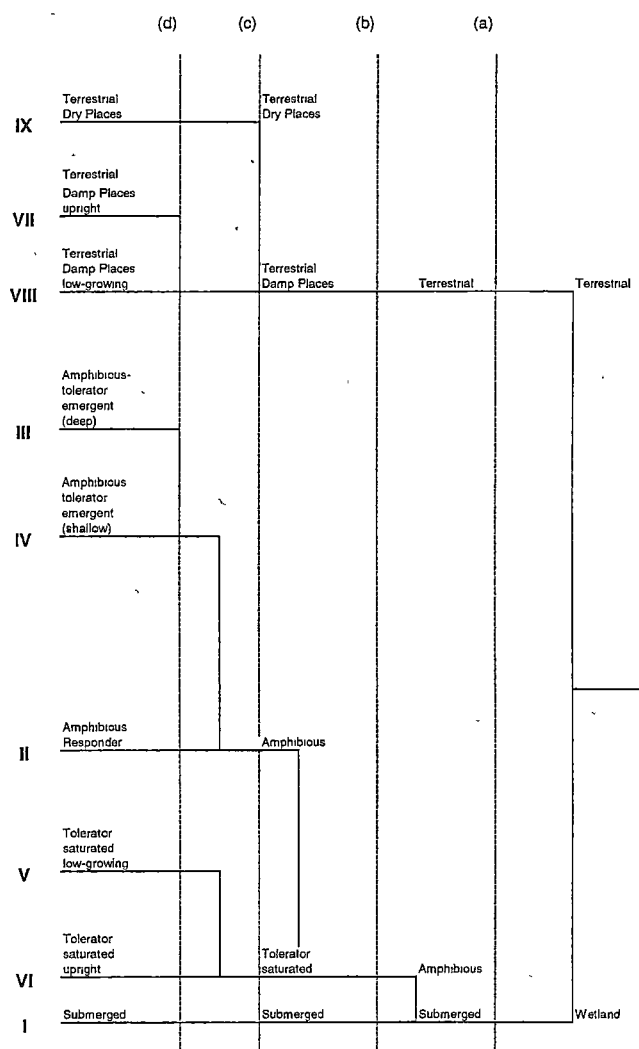


Figure 3.3 Simplified dendrogram from UPGMA analysis used to help identify functional groups of species. Four levels of classification identified, 2, 3, 5 and 9 groups of species. Group numbers refer to Table 3.4

Table 3.5 Percentage of species in the adopted functional groups

Functional Groups	Percentage of species
Submerged	4
Amphibious	64
Amphibious responder	21
Amphibious tolerator	
- tolerator-emergent	23
<i>a) species that can tolerate 'deeper' habitats</i>	13
<i>b) species that prefer 'shallower' habitats</i>	11
- tolerator-saturated/mudflat	20
<i>a) low growing</i>	12
<i>b) upright</i>	8
Terrestrial	32
- damp places	16
<i>a) upright</i>	8
<i>b) low growing</i>	8
- dry places	16

Table 3.6 Percentage of species characterised by particular criteria in 9 functional groups recognised by the UPGMA classification in Figure 3.3.

		Group								
		Submerged	Amphibious					Terrestrial		
Criteria		I Submerged	II Responder	III Tolerator Emergent Deep	IV Tolerator Emergent Shallow	V Tolerator Saturated Low	VI Tolerator Saturated Upright	VII Damp Places Upright	VIII Damp Places Low	IX Dry Places
Germination	Damp	50	100	100	100	100	100	100	100	100
	Drowned	100	89	83	22	27	0	0	0	0
Growth Form	Low	0	63	0	33	100	0	0	100	12
	Upright	100	95	100	100	27	100	100	17	100
Growth Place	Floating	0	53	0	11	0	0	0	0	0
	Saturated	0	95	92	100	100	100	100	100	100
	Emergent	0	68	100	100	0	0	0	0	0
	Submerged	100	89	0	0	0	0	0	0	0
Reproduction	Dry	0	0	0	0	18	13	100	100	100
	Saturated	0	84	67	100	100	88	100	67	6
	Water depth < 10	75	89	100	89	0	0	0	0	0
	Water depth > 10	100	80	100	0	0	0	0	0	0
Seeds Mature	Under water	21	0	0	0	0	0	0	0	0
	Above flood/sat	0	100	100	100	100	100	6	0	0
	Above dry	0	0	0	0	36	0	100	100	100

Allocation of the species in common between Tasmania and Northern Tableland Wetlands

Table 3.7 and Table 3.8 summarise the proportion of species allocated to each functional group during both studies. More than three-quarters of the species in common were classified identically between the two locations.

Table 3.7 Proportion of species allocated to each functional group in both studies.

Group	Northern Tableland s	Tasmania	Species in common
Submerged	10	4	7
Amphibious	58	64	
Fluctuation responder	20	21	33
Fluctuation- tolerator	38	43	
- emergent	31.5	23	33
- 'low-growing'/saturated	6.5	20	7
Terrestrial	32	32	
- damp	22.5	16	7
- dry	7.5	16	7

Table 3.8 Summary of the functional group allocations of the common species from both studies.

RED = common species that were allocated into similar groupings - 21 species (84%)

Species allocated into different groups: GREEN = group allocation from present study; BLACK = group allocation from Brock and Casanova (1997).

SUBMERGED	AMPHIBIOUS: Fluctuation- responders Morphologically plastic ARp	AMPHIBIOUS: Fluctuation- responders Floating/stranded ARf	AMPHIBIOUS: Fluctuation- tolerators Emergent ATe	AMPHIBIOUS: Fluctuation- tolerators Low-growing ATI	AMPHIBIOUS: Fluctuation- tolerators Saturated Upright	AMPHIBIOUS: Saturated Low-growing	TERRESTRIAL: Damp Places Tda	TERRESTRIAL: Dry Places Tdr
Chara spp. Nitella spp.	Crassula helmsii Myriophyllum variifolium Elatine gratioloides Isoetes fluitans Limosella australis Potamogeton tricarlinatus Utricularia spp.		Agrostis avenacea Eleocharis acuta Typha orientalis Schoenus apogon Amphibromus sinuatus Juncus articulatus * Juncus holoschoenus Lilaeopsis polyantha				Centaurium spicatum * Trifolium spp.*	Gnaphalium spp. */n Cirsium vulgare *
	Eleocharis sphacelata Utricularia dichotoma		Centipeda minima Eleocharis sphacelata	Centipeda minima Utricularia dichotoma	Hypericum japonicum Juncus bufonius *		Hypericum japonicum Juncus bufonius *	

Ordination of Species

The ordination of the species based on the criteria from Brock and Casanova (1997; Figure 3.4; Figure 3.5; Figure 3.6) associated the species in a manner which broadly agrees with the clustering produced by UPGMA (Table 3.3.). Both extreme groups, submerged (◆) and terrestrial (■), separated clearly along axis 1 and 2 of the ordination. The submerged species had high positive values whereas the terrestrial species had negative values on these axes (Figure 3.5; Figure 3.6). Within the amphibious species, the responder-saturated group separates relatively well from the tolerator-emergent and responder groups on axis 3. The tolerator-emergent and responder groups separate satisfactorily on axis 1 (Figure 3.6).

All the criteria were found to be significantly correlated with the ordination of the species (Table 3.9). The influence of each criterion can be understood from its correlation with the ordination of the species (Table 3.9) and from the direction of its vector when plotted in the same ordination space (Figure 3.5; Figure 3.6).

Table 3.9 **Table FG8 Correlation of the criteria with the ordination of a species as in Fig FG5 as determined by the Monte Carlo simulation MCAO, ** =P < 0.01.**

Criteria	PCC correlation coefficient	Significance
Germination		
Damp	0.576	**
Drowned	0.828	**
Growth Form		
Low growing	0.869	**
Upright	0.824	**
Floating	0.371	**
Growth Place		
Saturated	0.709	**
Emergent	0.718	**
Submerged	0.819	**
Reproduction		
Dry	0.939	**
Saturated	0.766	**
<10 water	0.833	**
>10 water	0.838	**
Seed Mature		
Underwater	0.667	**
Above flooded/sat	0.924	**
Above dry soil	0.929	**

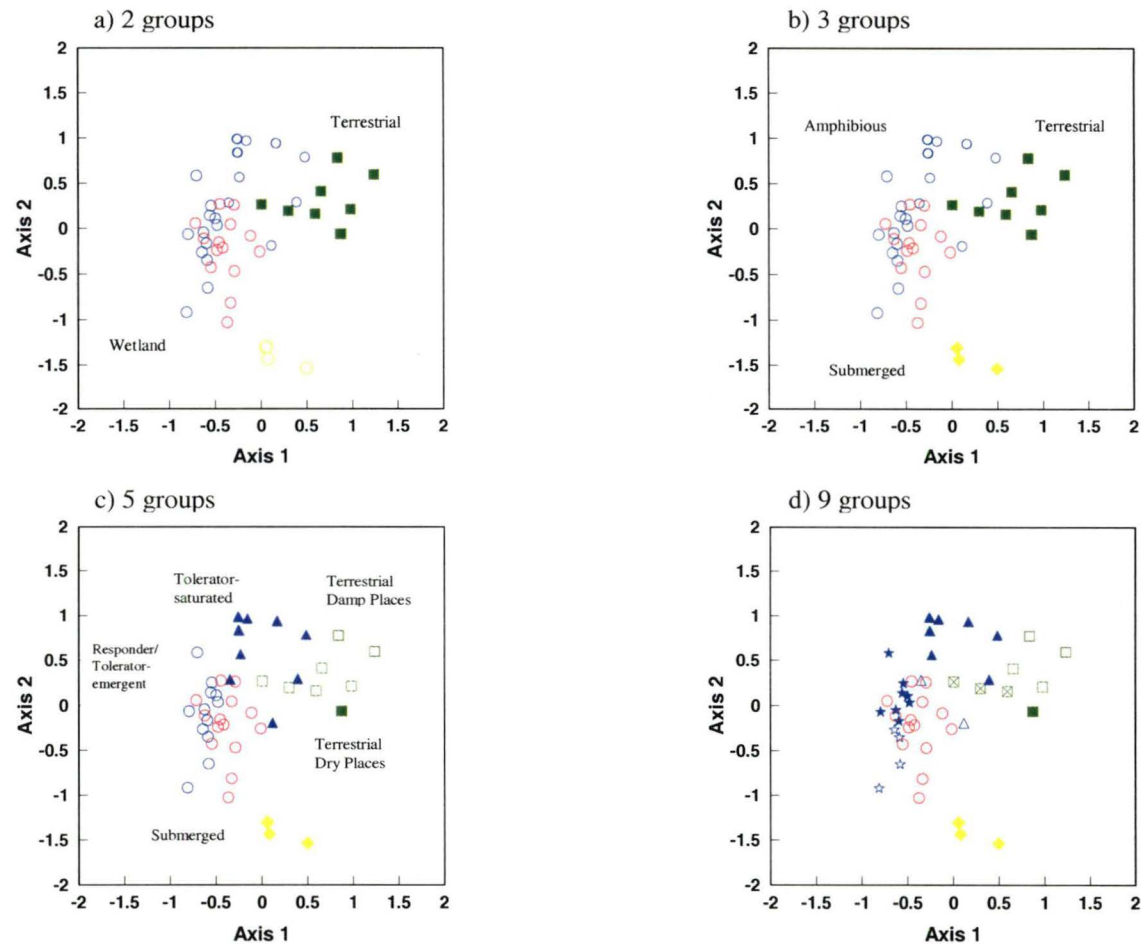


Figure 3.4

Ordination (SSHMDs) of species coded by functional groups annotated with the functional groups at each level of the UPGMA classification. (Symbols represent: a) circle = wetland species; square = terrestrial; b) circle = amphibious species; square = terrestrial; diamond = submerged; c) circle = amphibious responder/tolerator-emergent; triangle tolerator-saturated; terrestrial: open square = damp places; closed square = dry places; diamond = submerged, d) Diamond \blacklozenge = submerged; Square: terrestrial - closed \blacksquare = dry places, open \square = damp places low-growing, crossed \boxtimes = damp places upright; Circle \circ = responder; Triangle: tolerator - closed \blacktriangle = saturated low-growing, open \triangle = saturated upright, Star: tolerator - closed \blackstar = emergent shallow, open \star = emergent deep).

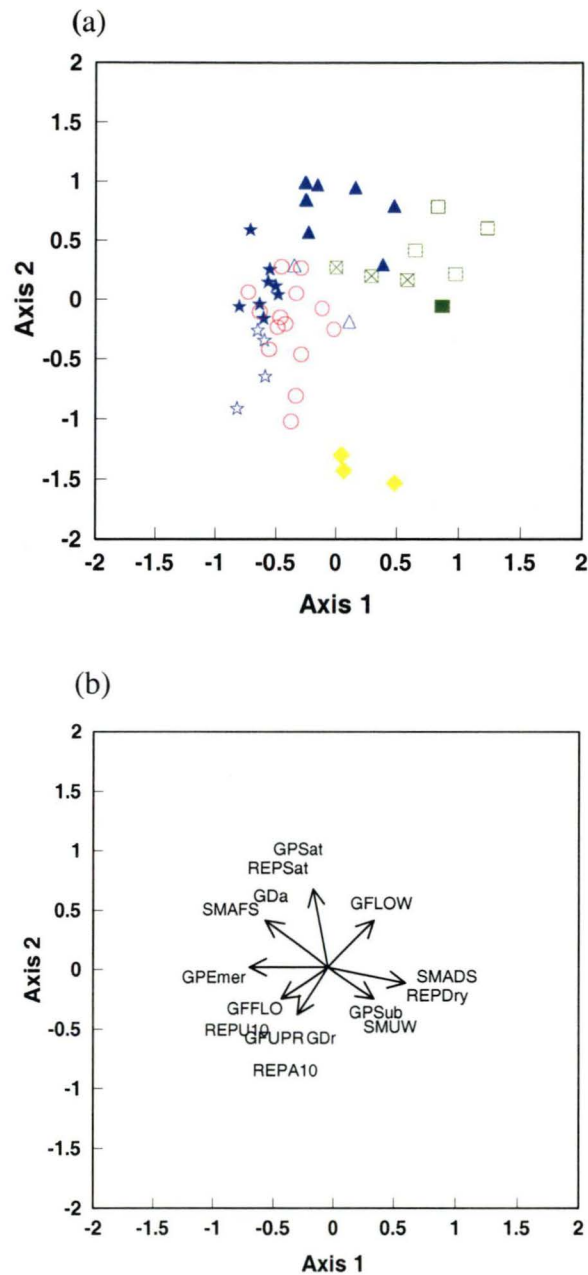


Figure 3.5

Axes 1 and 2: (a) Ordination (HMDS) of Functional Groups (3-dimensions, stress = 0.086).

Symbols correspond with the functional groups recognized from the UPGMA cluster analysis: diamond ◆ = submerged; square: terrestrial - closed ■ = dry places, open □ = damp places, low-growing, crossed ☒ = damp places upright; circle ○ = responder; tolerator: triangle - ▲ = saturated - low growing, △ = saturated upright, star - ★ = emergent shallow, ☆ = emergent deep. (b) Vectors of the significantly associated criteria plotted in the same ordination space.

Abbreviations for criteria are as follows:

Germination: Gda = damp, GDr - drowned; growth response: a) growth form - GFLOW = low-growing, GFUPR = upright, GFFLO = floating, and b) growth place - GPSub = submerged, GPEmer = emergent, GPSat = saturated; Reproduction: a) where seeds mature - SMUW = underwater, SMAFS = above flooded soil, SMADS = above dry soil, and b) water depth where plants reproduce - REPDry = dry, REPSat = saturated, REPU10 = shallow water <10 cm, REPA10 = deep water > 10 cm.

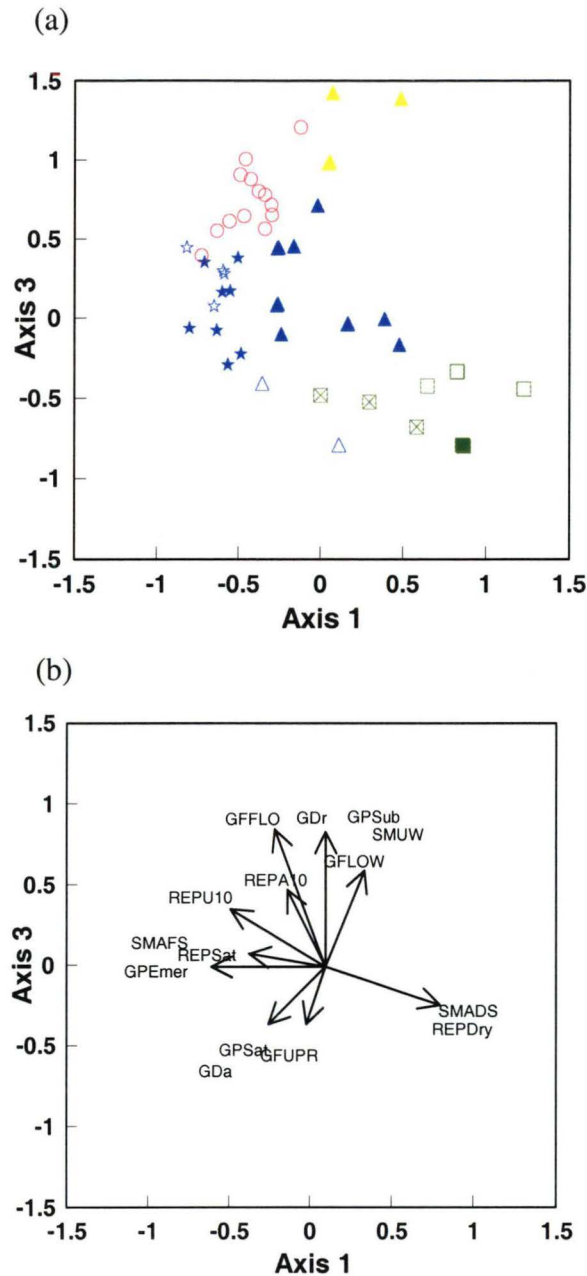


Figure 3.6

Axes 1 and 3: (a) Ordination (HMDS) of Functional Groups (3-dimensions, stress = 0.086).

Symbols correspond with the functional groups recognized from the UPGMA cluster analysis: diamond ◆ = submerged; square: terrestrial - closed ■ = dry places, open □ = damp places, low-growing, crossed ☒ = damp places upright; Circle ○ = Responder; tolerator: triangle - ▲ = saturated - low growing, △ = saturated upright, Star - ★ = emergent shallow, ☆ = emergent deep **(b) Vectors of the significantly associated criteria plotted in the same ordination space.** Abbreviations for criteria are as follows: Germination: GDa = damp, GDr - drowned; growth response: a) growth form - GFLOW= low-growing, GFUPR = upright, GFFLO = floating, and b) growth place - GPSub = submerged, GPEmer = emergent, GPSat = saturated; Reproduction: a) where seeds mature - SMUW= underwater, SMAFS = above flooded soil, SMADS = above dry soil, and b) water depth where plants reproduce - REPDry = dry, REPSat = saturated, REPU10 = shallow water <10 cm, REPA10 = deep water > 10 cm.

Description of groups

Group I : Submerged

This group consists of submerged species that reproduce either underwater (*Chara* spp. and *Nitella* spp.) or above water (*Ruppia* spp. and *Lepilaena* spp.). All species are usually found within the more aquatic end of the wetland zonation and will not survive for long in dry or saturated mudflat conditions. *Chara* and *Nitella* spp. were common to both studies and were both similarly allocated. A larger percentage of the species are allocated into this group from the wetlands in the Northern Tablelands (10%) than from the wetlands in the present study (4%; Table 3.7).

Group II - Amphibious – fluctuation: responder

The characteristics of the species classified into this group correspond closely to the *amphibious: fluctuation responder* group of Brock and Casanova (1997). Most of the species characteristically change their growth pattern or morphology in response to the presence or absence of water. All species in common, except *Eleocharis sphacelata*, were allocated into this group in both studies. Similar proportions of species were also allocated into this group from both studies (21% Tasmania: 20% Northern Tablelands).

The difference in the responder groups between the two studies is in the final level of classification. In Brock and Casanova (1997) the responder species from the Northern Tableland wetlands are separated by their different mechanisms for responding to water level fluctuations, that is, morphologically plastic or floating/stranded. While this separation did not occur in the present study, some differences in the species mechanisms for ‘responding’ to water presence and absence can be identified. The highest proportion of species classified into this group ‘respond’ to inundation by a change of morphology (e.g. the *Myriophyllum* species, the *Isolepis* species, *Elatine gratioloides*, *Potamogeton tricarinatus*). This growth characteristic identifies them with the ‘morphologically plastic’ group identified above in Brock and Casanova (1997). Those species that are exceptions to this are characterised by either: 1) responding by the elongation of the leaf petiole (e.g. *Hydrocotyle muscosa*), 2) no change to growth pattern at all (*Trithuria submersa*), or 3) is characterised as a submerged species (*Batrachium trichophyllum*).

Hydrocotyle muscosa responds to inundation by elongation of the leaf petiole. The leaf then floats on the surface of, or stands above, the water. It will also survive and flourish during saturated conditions. It is in this habitat that it is more typically seen. With variation between the two water level conditions it does not tend to change its leaf morphology, but rather its growth pattern. Other species that have floating leaves and 'respond' to water level fluctuations in a similar manner are *Villarsia reniformis* and *Ranunculus amphitrichus*. These species can survive on saturated soils, underwater and as an emergent with floating leaves. Due to these characteristics these species relate more to the 'floating' category in Brock and Casanova (1977) than the 'morphologically plastic'. However, unlike the species in their floating category they are not "stranded" on saturated soils. No species in the present study fit into the floating/stranded (ARf) functional group of Brock and Casanova (1997). However, a species allocated by them to this category – *Azolla filiculoides* - is widespread throughout Tasmania.

Trithuria submersa does not change its leaf morphology or growth pattern and generally does not "respond" to inundation. This species will flower both underwater and on saturated soils and generally has a low structure in both environmental contexts (Curtis and Morris, 1994). It is an unexpected species to be allocated into this category and is a difficult species to allocate into a group. However, it is best allocated to a 'tolerator' group due to the fact that it can live on both submerged and saturated soil without changing.

Batrachium trichophyllum is another species unexpectedly allocated into this group. It is generally described as a submerged aquatic plant (Aston, 1973; Sainty and Jacobs, 1981; Curtis and Morris, 1993) with underwater leaves and aerial flowering. Although it germinates quite readily on saturated soils it will not survive in saturated or dry conditions for very long and, as with the other submerged species, is generally found in the more inundated areas of a wetland. With these characteristics *Batrachium trichophyllum* has more in common with the submerged group rather than the responders. It will be placed in this category for the purpose of this study.

Group III and Group IV: Amphibious – fluctuation: tolerator- emergent (deep and shallow habitats)

These two groups contain both monocotyledon and dicotyledon emergent species that relate to the amphibious fluctuation tolerator- emergent group of Brock and Casanova (1997). In the present study the species have been split into two groups, separated by whether they will reproduce in deeper water (greater than 10 cm) or shallow water (less than 10 cm and saturated soils).

As with the previous groups, most of the common species allocated to this group in Brock and Casanova (1997) were also allocated to this group in this analysis. The exception is *Eleocharis sphacelata* which was allocated into the morphologically plastic responder group (Table 3.8) by Brock and Casanova (1997). Therefore, is *Eleocharis sphacelata* responding differently to water level fluctuations in Tasmania than in the Northern Tablelands?

This functional group is characterised by species that “generally do not change their morphology or growth with changes in water level “ (Brock and Casanova (1997). *Eleocharis sphacelata* tends to “respond” to the water level fluctuations by dying back during dry periods (sometimes totally) and re-sprouting and elongating through the water column after inundation. There is generally no change in its morphology during these processes and therefore probably should not be considered a “morphologically plastic” species. However, it does “respond” fairly rapidly to water level fluctuations and when fully grown can, in some cases, depend on water for stability, and will collapse during a drying period.

When analysing the characteristics of the other species in this group, for example, *Eleocharis acuta*, *Baumea rubiginosa* and *B. arthropphylla*, it can be noted that many of them have been observed to ‘respond’ to inundation in a similar manner to *Eleocharis sphacelata*. However, the other species will survive and reproduce in saturated conditions and tend not to die back as quickly after drawdown as *Eleocharis sphacelata*. In terms of presence and absence of water, it could be said that these species are ‘tolerant’ to drawdown because their growth generally remains the same for a time after drying and ‘responsive’ to water inundation due to their increased growth during inundation periods. This is different to *E. sphacelata* which is responsive to both drawdown and inundation. *Eleocharis sphacelata* has characteristics in common with

both groups and is therefore a borderline species in terms of the criterion. The different allocation may be due to the extra species in this analysis making the 'tolerator' criteria more important in the analysis of Tasmanian species and therefore *E. sphacelata* was placed in this group. There is no evidence at present to suggest that *E. sphacelata* is responding differently to water level fluctuation in these Tasmania wetlands than in the Northern Tableland wetlands as it still generally 'responds' to water level fluctuation as described by Brock and Casanova (1997). The characteristics of *E. sphacelata* indicate it is a responder to water presence and absence and, as such, will be placed in the responder group for the remainder of this study; however, not as a morphologically plastic species.

Groups V and VI: Amphibious: fluctuation tolerator – saturated

These groups consist of low growing herbaceous species that inhabit the most infrequently inundated outer edges of wetlands. They will tolerate inundation for a short period of time but prefer saturated conditions for both survival and reproduction. These characteristics correspond to the fluctuation tolerator – low growing group of Brock and Casanova (1997). However, due to the greater number of smaller monocot species in the present study the group has been further separated into both upright and low growing. The upright group, with the exception of *Hypericum japonicum*, consists of small upright monocot species – e.g. *Isolepis cernua*, *I. montivaga* and *Cyperus tenellus*. The low-growing species are predominantly dicot species- e.g. *Goodenia humilis* and *Selliera radicans*. This group shows the greatest difference in the proportion of species allocated into it between the two studies (7 % Northern Tablelands to 20 % Tasmania, Table 3.7). The greater number of species allocated into this group from Tasmania is mainly due to the inclusion of the dry outer herb zone.

Group VII, VIII and IX: Terrestrial: damp and dry place

These groups consist of introduced and native species that are associated with terrestrial habitats and generally found in the drier habitats within wetlands. This corresponds with the terrestrial groups of Brock and Casanova (1997). An extra split occurs in Tasmania with the damp species separated by the morphological characteristics of upright and low growing. Most of the species are exotic and typically occur as weeds in waste or agricultural landscapes. The two groups, damp and dry, are separated by 1) damp- species that prefer dry conditions to live and reproduce but will tolerate damp

conditions and 2) dry- species that will generally only live and reproduce in dry conditions (it is this group that contains most of the introduced species). While several of the species allocated into the damp habitat group may be unexpected (*Hypochoeris radicata*, *Leontodon taraxacoides* and *Trifolium* species), they were observed in damp conditions within the wetland during this study.

The revised groups to be used within this study are shown below (Table 3.10).

Conclusions

These results indicate that even in a modified form the functional classification used by Brock and Casanova (1997) is in fact repeatable in the terms of Gitay and Noble (1997) in that independent analyses from a different location yielded similar functional groups.

Most of the Tasmanian species grouped together into similar functional groups using the criteria and methodology in Brock and Casanova (1997). There were only a few species, which tended to overlap in certain characteristics that were placed in unexpected groups. It would be unusual for all species to match groups perfectly. Therefore, although the method and criteria are generally repeatable, the analyses above should be regarded as a useful tool for classifications of functional groups with caution needed to be taken with the final allocations.

The high number of common species for Tasmania and the Northern Tableland also indicates that these classifications are likely to be useful in the broader context of Tasmanian wetlands rather than just those wetlands within this study.

Table 3.10 Final allocation of species into functional group for the purpose of this thesis.

Black = species mentioned in discussion

* = introduced species

*/n = unknown status

SUBMERGED	AMPHIBIOUS Fluctuation- responders	AMPHIBIOUS Fluctuation- tolerators emergent deep water	AMPHIBIOUS Fluctuation- tolerators emergent shallow water	AMPHIBIOUS Fluctuation- tolerators Saturated low-growing	AMPHIBIOUS Fluctuation- tolerators Saturated upright	TERRESTRIAL Damp places upright	TERRESTRIAL Damp places low-growing	TERRESTRIAL Dry places
Group I	Group II	Group III	Group IV	Group V	Group VI	Group VII	Group VIII	Group IX
<i>Chara</i> spp.	<i>Callitriche stagnalis</i> *	<i>Cotula coronopifolia</i> */n	<i>Centipeda minima</i>	<i>Apium prostratum</i>	<i>Hypericum japonicum</i>	<i>Chenopodium glaucum</i> *	<i>Dichondra repens</i>	<i>Anagallis arvensis</i> *
<i>Nitella</i> spp.	<i>Crassula helmsii</i>	<i>Agrostis avenacea</i>	<i>Lilaeopsis polyantha</i>	<i>Leptinella longipes</i>	<i>Cyperus tenellus</i>	<i>Einadia nutans</i>	<i>Erodium cicutarium</i> *	<i>Centaureum erythraea</i> *
<i>Ruppia</i> spp.	<i>Myriophyllum simulans</i>	<i>Amphibromus sinuata</i>	<i>Mimulus repens</i>	<i>Centella cordifolia</i>	<i>Hemarthria uncinata</i>	<i>Epilobium</i> spp */n	<i>Hypochoeris radicata</i> *	<i>Euchiton collinus</i>
<i>Lepilaena cylindrocarpa</i>	<i>Myriophyllum variifolium</i>	<i>Amphibromus recurvatus</i>	<i>Chrizandra australis</i>	<i>Scaevola hookeri</i>	<i>Isolepis cernua</i>	<i>Lythrum hyssopifolia</i>	<i>Leontodon taraxacoides</i> *	<i>Parentucellia latifolia</i> *
<i>Batrachium trichophyllum</i>	<i>Myriophyllum salsuginium</i>	<i>Juncus articulatus</i> *	<i>Schoenus apogon</i>	<i>Hydrocotyle sibthopides</i>	<i>Isolepis montivaga</i>	<i>Carex inversa</i>	<i>Scleranthus biflorus</i>	<i>Stellaria media</i> *
	<i>Neopaxia australasica</i>	<i>Juncus holoschoenus</i>	<i>Isolepis inundata</i>	<i>Selliera radicans</i>	<i>Juncus bufonius</i>	<i>Poa labillardierei</i>	<i>Trifolium</i> spp.*	<i>Acetosella vulgare</i> *
	<i>Villarsia reniformis</i>	<i>Typha</i> sp. */n	<i>Triglochin striatum</i>	<i>Eryngium vesiculosum</i>	<i>Schoenus nitens</i>	<i>Polypogon monspeliensis</i> *		<i>Agrostis capillaris</i> *
	<i>Hydrocotyle muscosa</i>	<i>Carex tetraticaulis</i>	<i>Juncus bulbosus</i> *	<i>Gonocarpus micranthe</i>	<i>Hainardia cylindrica</i> *			<i>Aira</i> spp.*
	<i>Ranunculus amphitrichus</i>	<i>Baumea arthropophylla</i>	<i>Juncus planifolius</i>	<i>Goodenia humilis</i>	<i>Trithuria submersa</i>			<i>Briza minor</i> *
	<i>Elatine gratioloides</i>	<i>Baumea rubiginosa</i>	<i>Utricularia</i> spp.	<i>Plantago coronopus</i> *				<i>Cirsium vulgare</i> *
	<i>Limosella australis</i>	<i>Eleocharis acuta</i>		<i>Schoenus maschalinus</i>				<i>Cynosurus echinatus</i> *
	<i>Triglochin procerum</i>							<i>Deyeuxia quadriseta</i>
	<i>Potamogeton tricarlinatus</i>							<i>Gaudiana fragilis</i> *
	<i>Isolepis fluitans</i>							<i>Holchus lanatus</i> *
	<i>Isolepis producta</i>							<i>Poa annua</i> *
	<i>Schoenus fluitans</i>							<i>Vulpia myuros</i> *
	<i>Trithuria submersa</i>							
	<i>Eleocharis sphacelata</i>							

Chapter 4

Potential for regeneration from the Soil Seed Bank

Introduction

A knowledge of the potential seed bank of a wetland is important in the understanding of the means by which wetland plants re-establish after both drying and flooded periods. Temporary wetlands are characterised by fluctuating water levels. To survive periods of unfavourable conditions wetland plants have evolved a suite of survival and reproductive strategies (Bartley and Spence, 1987; Crawford, 1987; Brock, 1986, 1991; Brock and Rogers, 1998). During prolonged dry periods many obligate aquatic plants cannot survive vegetatively (Keddy and Reznicek, 1986; Leck, 1989). However, many of the wetland plants of temporary or variable environments have been found to have persistent soil seed banks (van der Valk and Davis, 1978, 1979; van der Valk, 1981; Leck, 1989; Finlayson *et al.*, 1990; Grillas *et al.*, 1993; McIntyre *et al.*, 1989; Brock and Britton, 1994; Smith, 1998; Brock and Rogers, 1998; van den Berg, 1999). A persistent seed bank (i.e. seeds that remain in the soil for longer than a year, Thompson and Grime, 1979) allows for community regeneration during low water levels with the germinating seeds or spores initiating the continued development of the vegetation (Smith and Kadlec, 1983; Leck, 1989; Thompson, 1992). A persistent seed bank can also buffer populations against the negative impact of 'bad' seed years (Levin, 1990).

Seed bank studies in fluctuating environments

Several studies have concentrated on the soil seed banks of fluctuating habitats. Much of this work has been done elsewhere than Australia from soils taken from wetlands with predictable water regimes, such as freshwater tidal wetlands (Simpson *et al.*, 1983; Leck and Simpson, 1994), prairie wetlands (van der Valk, 1981; Galatowitsch and van der Valk, 1995; Poiani and Johnson, 1988; Pederson and van der Valk, 1984; Wetzels, *et al.*, 2001), and seasonally flooded marshes (Middleton *et al.*, 1991; ter Heerdt and Drost, 1994; Grillas *et al.*, 1993). These studies have been within both natural (e.g. Leck and Simpson, 1987a; 1987b; Keddy and Reznicek, 1986) and managed drawdown (lowering of water level) situations (van der Valk and Davis, 1979; Welling *et al.*, 1988b). Due to the regular water regimes of these systems it is generally possible to

predict the succession of wetland vegetation through several stages or seasons (van der Valk, 1981; van der Valk and Davis, 1979).

However, within Australia, many of the wetlands fill and dry at irregular “aseasonal” intervals due to unpredictable weather conditions (Mitchell and Rogers, 1985; Paijmans, *et al.*, 1985; Brock, 1986; Brownlow *et al.*, 1994; Bunn *et al.*, 1997). Studies within these Australian wetland systems have demonstrated that a persistent seed bank plays an important role in their revegetation after drying (Brock and Casanova, 1991a; Casanova, 1993; Britton and Brock, 1994; Brock and Britton, 1995; Brock, 1998; Finlayson *et al.*, 1990). Other temporary systems that rely on seed banks for revegetation are found in South Africa (Breen, *et al.*, 1993; Denny, 1993; Brock and Rogers, 1998). Selection of species from seed banks in temporary habitats may occur at different times within the year or between years, depending on favourable weather conditions which control the magnitude of water regime fluctuations (Brock and Rogers, 1998).

Effect of water regime on wetland seed banks

Changes in water levels in a wetland can be regarded as a major disturbance which affects its vegetation community and seed bank. Thompson (1978) hypothesised that buried seed density is positively correlated with disturbance and therefore a wetland that experiences a greater number of wet/dry cycles would have a large seed bank (Haukos and Smith, 1993). This was found to be evident in many seasonal and frequently fluctuating freshwater wetlands (Haukos and Smith, 1993; Leck and Graveline (1979). The seed banks of these wetlands are generally dominated by annual species adapted to seasonal fluctuations in water levels (Keddy and Reznicek, 1986; Finlayson *et al.*, 1990). In contrast, the seed banks of wetlands with less predictable water regimes are dominated by perennials (Leck, 1989).

Brock and Rogers (1998) studied soil from three sites (zones) with different wetting and drying histories (permanent, seasonal, and occasionally inundated) from a South African floodplain. It was found that the water regime history of each site did not influence the number of species or individuals present. These results were compared with three New England wetlands with similar range of water regimes by Brock (1998) and similar results were found. The temporary wetlands studied by Brock and Rogers (1998) were characterised by a naturally fluctuating water regime. Seed banks were important in revegetating these naturally variable wetlands. However, many temporary

wetlands are subject to human-induced changes to their water regime, such as damming, draining and alterations of the frequency, duration and level of inundation (Brock, 1998; Brock *et al.*, 1999). Although able to assist re-vegetation throughout normal variations in water level, it may be beyond the capacity of seed banks to respond to more permanent wet or dry conditions imposed by changed hydrology (Brock, 1998). Making a wetland more permanently wet or dry is likely to reduce species richness (Keddy and Reznicek, 1982; 1986; Thompson, 1992) and change the vegetation and hence the seed bank composition (van der Valk and Davis, 1978; Poiani and Johnson, 1989; Schneider, 1994; Brock and Casanova, 1997).

Seed bank characteristics

Seed bank size and composition

Seed bank size and composition have been investigated for most terrestrial (see reviews in both Roberts, 1981 and Leck *et al.*, 1989a) and wetland systems (lakes, Skoglund and Hytteborn, 1990; Haag, 1983; marshes, van der Valk and Davis, 1979. Parker and Leck, 1985; salt marsh, Jerling, 1983; Hopkins and Parker, 1984, Bakker, 1985; bogs, Milton, 1939; McGraw, 1987a, 1987b; floodplains, Finlayson, *et al.*, 1990; Brock and Rogers, 1998; raised-bog, Poschlod, 1995; fens, Maas and Schopp-Guth, 1995; tidal freshwater wetlands, Simpson *et al.*, 1983; Leck and Simpson. 1994; permanent wetlands, Haag, 1983; semi-permanent wetlands, Poiani and Johnson, 1988, and temporary wetlands, Simpson *et al.*, 1983; Keddy and Reznicek, 1986; Brock *et al.*, 1994; Casanova and Brock, 1990; Leck and Simpson. 1994; Brock and Britton, 1995; Brock, 1998). It is generally thought that seed banks of wetlands are low in seed numbers compared to terrestrial communities (Rogers and Breen, 1980). However, van der Valk (1978) concluded that prairie marsh seed banks are considerably larger than the seed banks of terrestrial systems found in the United States.

The size of seed banks have been found to vary considerably both between and within wetlands (see Leck, 1989, Table 1; Harper, 1977; Schneider and Sharitz, 1986; McGraw, 1987b; Leck *et al.*, 1988; Finlayson *et al.*, 1990; Brock and Rogers, 1998), with both low (Moore and Wein, 1977; Gunther, *et al.*, 1984) and very high (McGraw, 1987b) numbers of seeds found in freshwater wetlands.

The composition of seed banks has also been found to vary. Often only a few species make up an overwhelming proportion of the seed bank (Britton and Brock, 1994; Leck and Simpson, 1994). Although differences in number of dominant species can depend on wetland type and vegetation zone (Britton and Brock, 1994; Smith and Kadlec, 1983; Schneider and Sharitz, 1986), generally it has been found that wetland seed banks are dominated by perennial monocotyledonous species (Leck, 1989). However, annual species, often mudflat colonisers (Salisbury, 1970, 1979; van der Valk and Davis, 1978, 1979; van der Valk, 1981), are more dominant in freshwater tidal wetlands (Leck and Graveline, 1979; Parker and Leck, 1985; Leck and Simpson, 1987b, 1994), in some saline marshes (Ugar and Riehl, 1980; Kadlec and Smith, 1984), and along lake shores (Keddy and Reznicek, 1982) with variations in species and numbers depending on the frequency of drawdown events (Poiani and Johnson, 1989).

In disturbed wetlands the non-wetland component of the seed bank may become more important. Non-wetland species have been found to be more abundant when the wetland is adjacent to cultivated agricultural lands or native meadows (Ugar and Riehl, 1980) and in areas with some disturbance, such as drainage channels (Hopkins and Parker, 1984). Due to their highly competitive nature introduced weed species may affect the species composition of these wetlands (Gaudet, 1977) and, as a consequence, their seed banks. The presence of non-wetland introduced species can increase the species richness of wetland seed banks. However, the potential for their recruitment may depend on the water regime of the wetland. Brock (1999) found that trials under damp conditions (rather than flooded) were more likely to be dominated by introduced species.

Until recent times (Casanova, 1993, Casanova and Brock, 1990; Casanova and Brock, 1996; Brock and Rogers, 1998; van den Berg, 1999), few studies have taken into account the Characeae (charophyte or stonewort) component of the aquatic propagule bank. Many authors have considered them too difficult to count or identify and generally group them at generic level or do not take them into account at all in their studies (Haag, 1983; Grillas *et al.*, 1993). Wood (1965) found that Australian wetlands, especially roadside ditches (a habitat which experiences frequent, unpredictable drought), were rich in charophyte species (Casanova and Brock, 1990). High numbers of charophyte oospores have germinated in seed bank observations (Casanova, 1993;

Grillas *et al.*, 1993; Brock and Rogers, 1998) with charophyte oospores often being the most abundant propagules in some wetlands (Bonis and Lepart, 1994).

Species germination patterns

Establishment of propagules from a seed bank is influenced by both the delay of germination until conditions are favourable (dormancy) and the resultant temporal pattern of germination (Silvertown, 1988). Dormancy ensures that germination occurs in an appropriate season, whereas the pattern of germination may be an adaptation to the predictability of variation within a habitat. Where a habitat has a high degree of predictability, seeds that germinated soon after a stimulus would have a competitive advantage over those that germinate later. In a less predictable habitat the risk of germinating early could negate any competitive advantage (Silvertown, 1988 see Casanova, 1993).

Functional groups

Brock and Casanova (1997) concluded from a study of Northern Tableland wetlands, that longer drying or flooding events would decrease the number of amphibious species and increase the number of terrestrial or submerged species respectively. The results of Crosslé (1998) confirmed their conclusions. Crosslé (1998) used the functional group classification proposed by Brock and Casanova (1997) to examine community development from seed bank (as well as vegetative material). They found rapid germination and establishment of species from a variety of functional groups over a wide range of experimental trials. However, differences between trials suggested that fluctuations in water levels are required to maintain a diversity of functional groups in wetlands (Crosslé, 1998). This was similar to the results of Brock and Casanova (1997) as well as other studies (van der Valk and Davis, 1978; Keddy and Reznicek, 1986).

Longevity of seed banks

Seed bank size, composition, and depth distribution are determined, in part, by the seed longevity (Leck, 1989). Information on the viability and longevity of seed banks can be obtained through examining seeds that germinate from a soil depth profile (Keddy *et al.*, 1989). Several depth studies have concentrated on aquatic systems (van der Valk and Davis, 1979; Leck and Graveline, 1979; Nicholson and Keddy, 1983; Gunther *et al.*, 1984; Leck and Simpson, 1987a; McGraw, 1987a). Though many of these studies

indicated that sizeable numbers of seeds have been observed below 25 cm, there is considerable variation within and between wetlands (Leck, 1989) and among species (Leck and Simpson, 1987a; McGraw, 1987a; Brock and Britton, 1995). For example, van der Valk and Davis (1979) found that a very deep seed bank was a characteristic of a prairie glacial marsh, and that the number of seeds declined gradually with depth. However, the pattern of decline differed between vegetation types (van der Valk and Davis, 1979). Similar deep profiles have been found in swamps (Gunther *et al.*, 1984) and bogs (McGraw, 1987a, 1987b). In contrast, Nicholson and Keddy (1983) found that the seed bank from the shoreline of a freshwater lake was exceptionally shallow with 81 percent of the germinants occurring in the top 2 cm. Shallow seed banks have also been found in temporary pools (Leck, 1989) as well as freshwater tidal wetlands (Leck and Graveline, 1979; Parker and Leck, 1989). These results are more consistent with terrestrial seed banks which generally have an abrupt decrease in seed abundance with depth (Kellman, 1970; Roberts and Feast, 1972; Strikler and Edgerton, 1976; Moore and Wein, 1977; Harper, 1977; Hill and Stevens, 1981; Roberts, 1981).

The regular wetting of sub-samples of sediments after a dry storage period (Brock and Britton, 1995) and the re-wetting of the same soil at different time periods (Bonis *et al.*, 1995) have been used to determine the interactions of environmental variability with seed longevity. Brock and Britton (1995) found that only 2 species (*Juncus articulatus* L. and *Myriophyllum variifolium* J. Hook) out of 21 species germinated after 11 years of dry storage, suggesting that species differ in their potential to survive in the seed bank. Bonis *et al.* (1995) showed that though the seed banks of two temporary marshes were not depleted after being submerged for 5 successive periods, the majority of seedlings emerged within the first period of flooding and that temporary drought had stimulated the germination of two species.

Seed longevity is considered an adaptive feature (Harper, 1977), and is of greater importance in environments where optimal conditions for growth occur infrequently than in more constant environments. Exposed sediments during times of 'drawdown' can be considered an optimal situation for growth in this context (Skoglund and Hytteborn, 1990), as well as the 'wetting up' periods after drought. These regeneration opportunities in wetlands depend on their water regime and may occur at different frequencies. Therefore, the function of seed longevity in wetland plants, not only to

withstand wet periods but also to withstand dry periods, gives them the resilience necessary to survive and establish in their highly variable environment.

Temporal variation in wetland seed banks.

Plant community establishment from the wetland seed bank is influenced by changes in hydrological regime (van der Valk and Davis, 1978; Keddy and Reznicek, 1986; Poiani and Johnson, 1989; Casanova and Brock, 1990; Brock, 1991; Thompson, 1992; Britton and Brock, 1994; Schneider, 1994; Brock and Casanova, 1997; Brock and Rogers, 1998). In non-seasonal temporary wetlands the regime of wetting and drying may be different every year. Wetting, flooding and drying are all germination cues (Keddy and Reznicek, 1986). Therefore the dominant plant community may change depending on the season and timing of flooding and drying events due to differences in plant germination requirements.

Temporal variation in wetland seed banks has been studied by several authors (Thompson and Grime, 1979; Leck and Graveline, 1979; Ungar and Riehl, 1980; Hopkins and Parker, 1984; Schneider and Sharitz, 1986; Leck and Simpson, 1987a; Welling *et al.*, 1988a; Britton and Brock, 1994). Several studies observed seasonal differences in seed numbers (Leck and Graveline, 1979; Hopkins and Parker, 1984; Britton and Brock, 1994). A common pattern observed in predictable seasonal environments is an increase in seed numbers after the autumn fall and a corresponding decrease after the spring water level rise (Schneider and Sharitz, 1986). This indicates that germination requirements were met during the spring period. Research on plant species in unpredictable habitats has indicated that germination may take place at most times during the growing season and over a wide range of temperatures (Baskin *et al.*, 1989). This was interpreted as being an adaptation to the unpredictable water level fluctuations of their habitats. However, Britton and Brock (1994) showed that individuals germinating from the unpredictable New England lagoons were significantly affected by season, with the greatest number of individuals germinating in autumn and the least in the summer months.

Spatial variation of wetland seed banks

Between wetlands

Several studies have compared seed banks between wetlands (see Leck, 1989; van der Valk and Davis, 1976a, 1978; Brock, 1998; Le Page and Keddy, 1998; Skoglung and Hytteborn, 1990). Van der Valk and Davis (1978), found a great deal of similarity when comparing the seed profiles of their wetlands with other wetlands in the United States. For example, dominant species in the seed banks were common to all wetlands. Brock (1999) compared several wetlands systems throughout Australia and found that all sites had species-rich seed banks with a range of aquatic and semi-aquatic species. However, when comparing an Australian shallow upland wetland with a South African floodplain wetland, several differences were noted (Brock, 1998). In the Australian upland wetlands many species were site specific, in comparison with the high proportion of widespread species in the South African floodplain. Brock and Britton (1995) found that species richness was highest in a relatively undisturbed wetland and the lowest in one with a history of hydrological modification and other disturbances.

Between vegetation zones

Zonation patterns of seed banks have also been observed in several studies. In some cases the differences between zones are quite large (Thompson and Grime, 1979). In wetlands these zonation patterns have been related to both inundation (Pederson, 1981; Schneider and Sharitz, 1986) and vegetation communities (van der Valk and Davis, 1978; Smith and Kadlec, 1983; Finlayson *et al.*, 1990; Middleton *et al.*, 1991; Bonis *et al.*, 1995). Fewer seeds have been found in continually inundated sites (e.g. Pederson, 1981; Haag, 1983; Schneider and Sharitz, 1986; Britton and Brock, 1994). However, Brock and Rogers (1998) studied soil from three sites with different wetting and drying histories (permanent, seasonal, and occasionally inundated) on an African floodplain and found that the water regime history of the site did not influence the number of species or individuals that germinated. The main within-site differences were between the species-poor, dry edge habitat and the species-rich deeper water. They concluded that species composition and behaviour rather than differences in number of species or individuals determined differences between sites.

Studies that have compared seed banks between vegetation zones have found both similarities (Van der Valk and Davis, 1978; Middleton *et al.*, 1991) and differences (Smith and Kadlec, 1983; Finlayson *et al.*, 1990; ter Heerdt and Drost, 1994) between numbers of species and total individuals germinated from seed banks of different vegetation types. The similarities and differences found in these studies include: the average number of seedlings per single species did not vary over vegetation zones (van der Valk and Davis, 1978); zones differed in the number of individuals germinated (Smith and Kadlec, 1983; ter Heerdt and Drost, 1994; Leck and Simpson, 1994) but not in the number of species (ter Heerdt and Drost, 1994; Leck and Simpson, 1994); seed banks from open water sites produced fewer species and lower densities than seed banks from areas dominated by emergent vegetation (Pederson, 1979; Smith and Kadlec, 1983).

Variations due to germination treatment

An understanding of seed germination ecology is enhanced by knowledge of the germination responses of seeds (Baskin and Baskin, 1998). Differences in both species richness and individual numbers have been shown to occur depending on the germination treatment of the soils (van der Valk and Davis, 1978; van der Valk, 1981; Casanova and Brock, 1990; Finlayson *et al.*, 1990; Skoglund and Hytteborn, 1990; Brock *et al.*, 1994; Brock and Britton, 1995). In most studies soils that have been kept in saturated mudflat conditions have yielded both more species and individuals than soils that have been drowned to various depths (van der Valk and Davis, 1978; Finlayson *et al.*, 1990; Brock *et al.*, 1994; Brock and Britton, 1995). However, this can vary depending on the type of species. Monocotyledonous and dicotyledonous species tend to germinate more readily in mudflat conditions, whereas charophyte species favour flooded conditions (Brock and Britton, 1995). As well as differences in species numbers and individuals the composition of the species germination between the two treatments has also found to be different (van der Valk and Davis, 1978).

Tasmanian wetland seed bank studies

There has been no published studies on the seed banks of Tasmanian lentic wetlands. However, Askey-Doran *et al.* (1999) examined the seed banks of riparian vegetation in the south east of Tasmania. Five treatments were used on the soil samples. Though no treatment (fire, smoke, heat plus smoke, aeration, scarification) was directly related to

water regime during both the scarification and aeration treatments the soil samples were inundated for a period of time prior to germination. Most wetland species that germinated were monocotyledons that were characteristic of edge habitats. *Crassula helmsii* was the only aquatic species that germinated.

Aims

This chapter uses four seed bank experiments to determine the potential for regeneration from seed banks in 5 temporary wetlands within Tasmania. Both temporal and spatial differences in species richness and total germinants are investigated in relation to season, vegetation type, depth, germination treatment and water regime. Differences in species composition is investigated in terms of life cycle, exotic vs native and functional groups. The following questions were addressed:

- 1) do the wetlands have a potential to regenerate from seed banks - ie. do they have a viable seed bank - if so what size, what type of species ?
- 2) does the season of wetting and drying affect the type of species that will germinate ?
- 3) are there significant differences between a) wetlands; b) between zones within wetlands; c) between vegetation zones with similar vegetation dominance, that is, sedge and aquatic ?
- 4) does the water regime of a zone affect the total species richness/germinants and the functional type of a wetlands seed bank ?
- 5) do the conditions of germination affect the type of species that will germinate ?
- 6) does a wetland with a low surface seed bank have significantly more seed numbers down the soil profile ?

It could be expected that:

- seed bank species richness and germinant numbers would be reduced in more permanently wet or dry wetlands (Keddy and Reznicek, 1982;1986; Thompson, 1992).
- differences in species composition rather than differences in species richness or germinants would determine differences between zones with varied water regimes;

- that there would be greater differences between wetlands than within wetlands due to the dispersal mechanisms of aquatic plants and the persistence of species within the seed bank;
- longer drying periods would increase the number of terrestrial species within a seed bank;
- vegetation type would affect its seed bank with less species and individuals germinating from a sedge dominated zone than an aquatic herbaceous dominated zone;
- that a gradient in both species richness and germinants would be evident in the wetlands, that is, species richness and germinants would increase towards the edges of wetlands;
- a greater number of angiosperm species would germinate in mudflat conditions, whereas, charophyte species would be the most abundant in drowned conditions.

Methods

Seed bank germination was investigated in several experiments. All experiments were conducted in glasshouse conditions.

Wetland sites

Five temporary wetlands were chosen within three different regions throughout Tasmania. Wetlands with different water regime histories were chosen for comparison (see Chapter 2). Big Punchbowl (BP) and Tin Dish (TD) remain dry for long periods (long-term dry), Cherry Tree Lagoon (CTL) and Sandy Gate (SG) remain wet for most of the time and only dry out at times of severe drought (semi-permanent). The fifth wetland, Middle Lagoon (MID), has water levels that fluctuate more frequently than the other four wetlands. It can dry for periods of up to five years, re-wet, then, in normal years, fluctuate, with low water periods in summer and wet periods in winter.

Vegetation zones

A total of 11 vegetation zones were sampled (Table 4.1). The intention was to sample a sedge-dominated and an aquatic herb-dominated zone in each wetland. However, in Big Punchbowl due to the dryness of the wetland, it was difficult to determine the areas of aquatic herbfield. To maintain the ability for comparison between an outer and aquatic zone in this wetland, the sedge zone in Big Punchbowl was sampled in the outer drier area and in a more moist area.

To assess further the differences between zones within wetland vegetation, an extra dry herbaceous zone was sampled from Middle Lagoon. The inner *Eleocharis sphacelata* zone remained inundated for longer periods of time, the central aquatic zone, in normal years, fluctuated seasonally and the outer dry herb zone was inundated only occasionally.

Table 4.1 Vegetation zones sampled within the five wetlands. Dominant species are given from the first sampling time February, 1997.

	Big Punchbowl BP	Tin Dish TD	Middle Lagoon MID	Cherry Tree Lagoon CTL	Sandy Gate SG
SEDGE	<i>Baumea rubiginosa</i>	<i>Eleocharis acuta</i>	<i>Eleocharis sphacelata</i>	<i>Baumea arthropphylla</i>	<i>Baumea arthropphylla</i>
	BP B.r outer	TD E.a	MID E.s	CTL B.a	SG B.a
AQUATIC	<i>Baumea rubiginosa</i>	<i>Chara</i> spp. and <i>Potamogeton</i> <i>tricarinatus</i>	<i>Chara</i> spp. and <i>Villarsia reniformis</i>	<i>Myriophyllum</i> spp. and <i>Chara</i> sp.	<i>Potamogeton</i> <i>tricarinatus</i> and <i>Eleocharis acuta</i> .
	BP B.r aquatic	TD aquatic	MID aquatic	CTL aquatic	SG aquatic
DRY HERBLAND			<i>Villarsia reniformis</i> and <i>Selliera radicans</i>		
			MID dry herb		

Transect and quadrat location

Three transects were randomly located within each wetland using a turn of a circular protractor. The degrees given by the protractor were translated to a compass bearing with 0° being north and the centre of the wetland as the central point. Transects were set out along the chosen direction from the edge of the wetland encompassing the vegetation zones to be sampled. Due to the heterogeneity of the vegetation zones within each wetland studied transects were very rarely equal distances. To determine the position of quadrats within each zone: a) the zone distance along a transect was measured; and b) random numbers were then picked from a bag containing an equal number of metres as was measured for that zone. Thus all distances within each zones had equal opportunity to be chosen. The quadrats were initially located during summer 1997 and were used for all soil seed bank studies and for the vegetation surveys over the two year period of the study described in Chapters 5 and 6.

Core samples

The field sampling methods and experimental design are summarised in Figure 4.1. Within each wetland, nine permanent quadrats, from each of 2 vegetation zones (3 in Middle Lagoon), were located along three transects. This gave a total of 9 quadrats from 11 zones within 5 wetlands. Eighteen quadrats were located within each of 4 wetlands (Big Punchbowl, Cherry Tree Lagoon, Tin Dish and Sandy Gate) and 27 within 1 wetland (Middle Lagoon).

Soil samples were taken within 1 m from each of the permanent quadrats. They were within this distance to allow comparison of the seed bank with the vegetation found within the quadrats. At each quadrat 8 randomly located soil cores were extracted and placed in a plastic container. Soil cores were located by a grid method and throwing of two dice, the dice numbers were used for the grid location of the sample (e.g. 1, 6).

Each core (5 cm diameter and 2.5 cm deep) was extracted using a modified version of the sediment sampler designed by Brock *et al.*, (1994). The use of many small samples is superior to using fewer larger samples (Roberts, 1981) due to the spatial variability of seed density in the soil (van der Valk and Davis, 1978; Thompson, 1986; Benoit *et al.*, 1989). Therefore, 8 small cores constituted 1 replicate (Figure 4.1) rather than taking one large sample of similar area.

As generally only the seeds nearest the surface will germinate in field conditions (Nicholson and Keddy, 1983; Galinato and van der Valk, 1986; ter Heerdt and Drost, 1994; Jurik *et al.*, 1994; Thompson, Bakker and Bekker, 1997) a shallow depth of 2.5 cm was chosen. The top 2-3 cm has also been shown to contain the largest number of seeds within a soil profile (Nicholson and Keddy, 1983). This depth was recommended by Brock *et al.* (1994) in an attempt to standardise seed bank methods within Australia and the use of it in the present study will facilitate comparisons between studies.

The number of replicates (9 per zone, 18 per wetland) was chosen to allow sufficient replication for analyses and a large enough total surface area to represent the species richness present. The surface area of each replicate (8 cores) was 0.0157 m^2 which give a total soil surface area for each zone of 0.14 m^2 and for each wetland of 0.28 m^2 (Middle Lagoon = 0.42 m^2). These surface areas are larger than the combined area recommended by Forcella (1984) and Brock *et al.* (1994) for adequate sampling of seed banks. On this basis it is assumed that the number of samples taken in the present study and the area of substrate sampled is sufficient to represent the species richness and seed abundance of the wetland sites. However, rare species may not be adequately represented (Brock *et al.*, 1994).

Germination methods

The eight soil cores per replicate were not mixed. They were placed upright into a plastic container and left in this position for the germination experiments. This preserved the vertical distribution of the seeds in each core and hence allowed a more realistic estimation of the potential for germination (Brock *et al.* 1994). The soils were air dried for two weeks to kill all existing plants and were then placed into a plastic lined tank within the glasshouse using a randomised block design. Due to shade at one side of the tank the trays were moved around within their blocks every week. The soils were subjected to two water regimes. They were kept in a saturated (mudflat) condition - that is, water was kept at the level of the soil with no free water and then drowned to a depth of 15 cm above soil level. These treatments were designed to mirror the conditions experienced by a wetland in the field at a time of wetting up, where saturated conditions would occur for a period of time before inundation. The length of time for each treatment varied and is discussed for each experiment below. Generally the soils were exposed to each treatment for at least 10 weeks (at total germination time of at least 20 weeks).

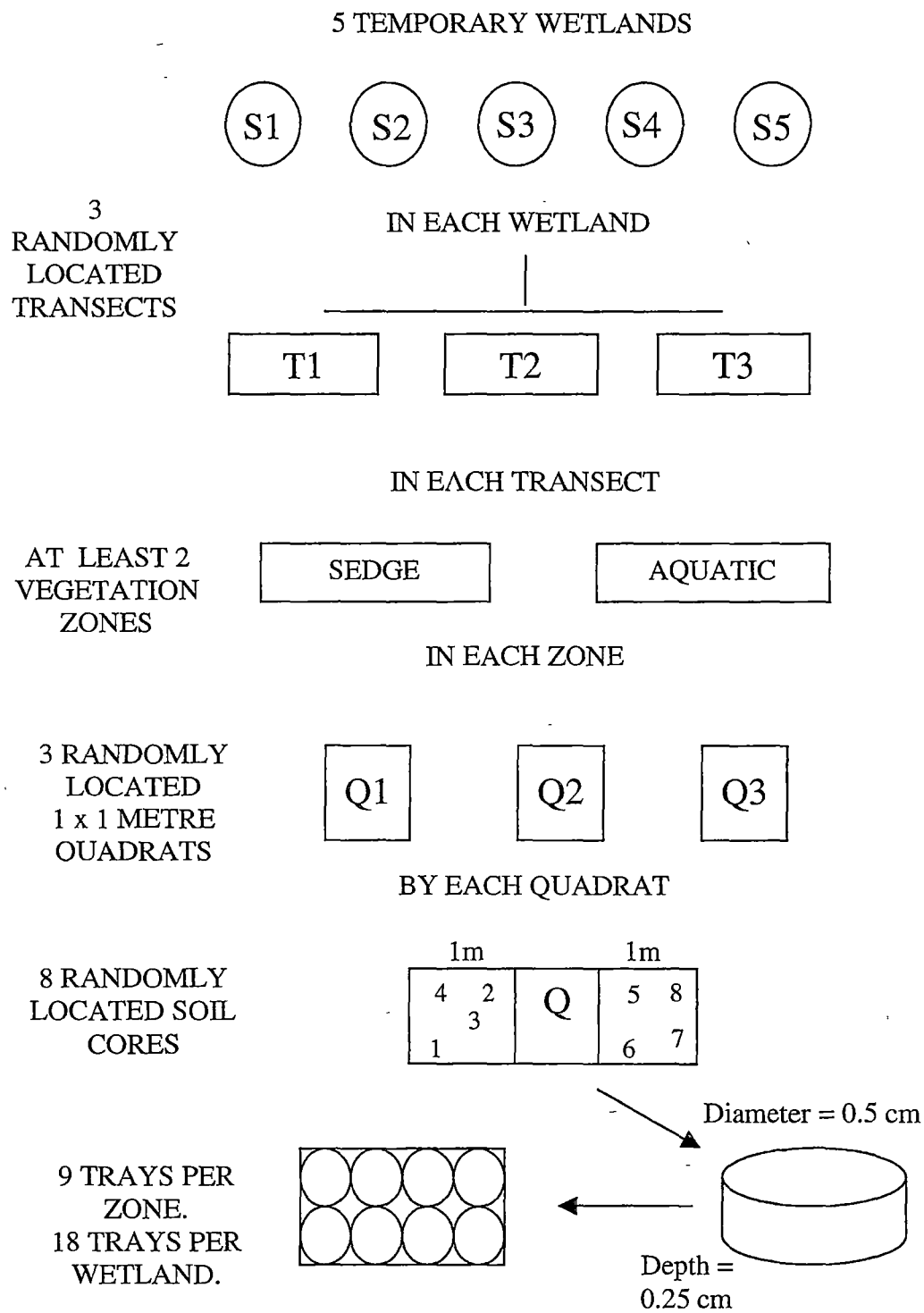


Figure 4.1 Soil sediment sampling design for seed bank experiments.

Bonis *et al.* (1995) found that the majority of germination took place within the first 2 months on soils taken from a temporary and variable wetland habitat, with a significant drop in germination after this time. Other studies (Thompson and Grime, 1979; Nicholson and Keddy, 1983) have also recorded the greatest number of seedlings emerging within the first few weeks to 2 months.

The number of seeds stored in the soil was estimated using the seedling emergence method (Roberts, 1981; Brock *et al.*, 1994; Gross, 1990), whereby substrate samples are collected and placed in a glasshouse or growth chamber for germination. Composition of the seed banks is based on the species and number of seedlings which emerge. This method has been found to be relatively accurate for estimating wetland seed bank composition (Poiani and Johnson, 1988). The estimate of the number of seeds is based on the number of viable seeds, whereas other methods (e.g. soil sieving) may provide the total number of seeds regardless of their viability. A seed bank is defined as the amount of viable seed present in the substrate at any given time (van der Valk and Davis, 1976a) and it is the measuring of the viable seed that is important in terms of the vegetation dynamics at the time the seed bank is sampled (Smith and Kadlec, 1983). The main assumptions with this method are that all viable seeds germinated under the conditions provided and within the time constraint. While this method may underestimate the number of seeds, Thompson and Grime (1979) noted that it is useful for comparison among vegetation types and for detection of persistent seed banks. Seed bank studies of wetland plants have shown that certain species require either mudflat, drowned or both conditions to germinate (van der Valk and Davis, 1978; van der Valk, 1981; Leck, 1989; Casanova and Brock, 1990; Casanova, 1993; Brock *et al.*, 1994; Brock and Britton, 1995; Brock and Casanova, 1997; Baskin and Baskin, 1998; Brock, 1999). In wetland seed banks, there are two basic types of species present; those whose seeds germinate under water and those whose seeds will not (see van der Valk and Davis, 1978). As a result, seed bank samples have to be exposed to both drawdown and flooded conditions to get a complete inventory of the species present.

It has been found that alternating temperatures are more favourable for germination than constant temperature (Baskin and Baskin, 1998, pg. 12). Hence natural conditions were maintained in the glasshouse with no modifications to light and temperature regimes. Minimum and maximum air temperatures were recorded each day.

Several trays containing washed river sand were randomly placed amongst the experimental trays to act as controls. Any germination on these trays would have indicated either that there were seeds entering the glasshouse or that seeds were being dispersed within the water of the tank.

Angiosperm and charophyte individuals were identified and carefully removed from the soil. Plants that could not be identified were potted for further identification.

Identification of angiosperm species was verified by botanists at the Tasmanian Herbarium. Charophyte species identifications were verified by Joop van Raam¹.

Several seedlings died prior to identification. However, all seedlings were identified to type (i.e. monocotyledon, dicotyledon and charophyte) and were kept in the total germinant analyses. If rhizome propagation occurred it was counted but not incorporated into the analyses. For each tray the total number of taxa and individuals for each taxa were scored. Total data as well as the number of angiosperm (monocotyledons and dicotyledons) and charophyte species and individuals were used in the analyses described below.

Germination experiments

Four germination experiments were used to determine the characteristics of the seed banks of the five wetlands.

Summer and winter 1997

Soil samples were collected during two different seasons in 1997. The first were taken at the end of the summer season, February 1997 (summer 1997). This was designed to correspond with the end of the flowering season, but not all seed maturation or fall. The next samples were taken at the end of the winter season, August 1997 (winter 1997). This was to include any 1997 seed fall that may have occurred between the two sample times. The summer 1997 soils were germinated from autumn through winter, 1997, and the winter soils were germinated from mid spring through summer 1997 - 1998 (Table 4.2).

¹ Joop van Raam, Research fellow, The Rijksherbarium, Department of Algology, Leiden, The Netherlands

Soils were subjected to 10 weeks saturated mudflat followed by 18 weeks drowned to 15 cm depth. Number of species and individuals of each species were scored during the mudflat treatment at 3, 6 and 10 weeks for both experiments. However, scoring of the drowned treatment varied between each experiment. The summer 1997 soils were scored once during the drowned treatment after 18 weeks, whereas, the winter 1997 soils were scored at 3, 6, 10 and 18 weeks. The total germination time for both experiments was 28 weeks.

Table 4.2 Summary of the germination times for each experiment (S = soil taken, MF = mudflat conditions, D = drowned conditions; SU = summer; W = winter; Exp. = Experiment).

Year	Season	Month	SU97	W97	Depth experiment	Treatment experiment
			Exp. 1	Exp. 2	Exp. 3	Exp. 4
1997	Summer	Feb.	S			
		Mar.				
	Autumn	Apr.	MF			
		May	MF			
		Jun.	MF/D			
		Jul.	D			
	Winter	Aug.	D	S	S	
		Sept.	D	MF	MF	
		Oct.	D	MF	MF	
		Nov.		MF/D	MF/D	
	Spring	Dec.		D	D	
1998	Summer	Jan.		D	D	
		Feb.		D	D	
		Mar.		D	D	
		Apr.				
	Autumn	May				
		Jun.				
		Jul.				
		Aug.				S
	Winter	Sept.				
		Oct.				MF
		Nov.				MF
		Dec.				MF/D
1999	Summer	Jan.				D
		Feb.				D
		Mar.				D

Winter 1997 - depth experiment

The results of the summer 1997 seed bank experiment indicated that Big Punchbowl (BP) had significantly less species and germinants than the other four wetlands. Big Punchbowl had been dry for several years prior to this study and very little reproduction of aquatic plants would have occurred. The wetland was at one time between 1-2 m deep in parts and once had a productive aquatic flora (indicated by surveys by Jamie Kirkpatrick and Chris Harwood in 1978 (unpublished data); Stewart Blackhall, pers. comm.²).

To determine if Big Punchbowl had a buried seed bank left from when it was continually inundated 10 cm deep cores were taken from each of the vegetation quadrats of the *Baumea rubiginosa* central aquatic zone during winter 1997. Due to limited space and time only one core was taken from each area. The cores were separated into segments of 2.5 cm width giving four depth samples for each core and a total of three from each transect. Depth categories were: 0 - 2.5 cm; 2.5 - 5 cm; 5 - 7.5 cm; and 7.5 - 10 cm. For a comparison with a semi-permanent wetland, similar cores were taken from the *Baumea arthropphylla* zone at Cherry Tree Lagoon (CTL), the other east coast wetland. The cores were then placed in the glasshouse at the same time as the second germination experiment (winter 1997). They were kept in mudflat condition for 10 weeks followed by 10 weeks drowned and scored at 3, 6, and 10 weeks in both treatments.

Winter 1998 - treatment experiment

In the previous experiments mudflat conditions were followed by inundation. In this experiment the two treatments were kept independent. Soils were taken in winter 1998. Two replicate soil samples were taken from three quadrats within representative zones throughout the wetlands studied. The zones were chosen to take into account as many species as possible found in the other two seed bank experiments (Table 4.3). It was assumed that the species would behave in a similar manner which ever wetland they came from. Soils were dried and one replicate was kept in mudflat conditions for 20 weeks and the other was drowned for 20 weeks. Trays were scored in a similar manner to the other two experiments at 3, 6, 10, 13, 16 and 20 weeks.

Table 4.3 Summary of zones used for winter 1998 - treatment analyses

Aquatic	Sedge	Dry Herb
Cherry Tree Lagoon	Middle Lagoon: <i>Eleocharis sphacelata</i>	Middle Lagoon
Sandy Gate	Sandy Gate:	
Tin Dish	<i>Baumea arthropphylla</i>	

Analytical methods

All analyses were repeated for total, angiosperm and charophyte species richness and individual germinants. A Shapiro-Wilk test (Shapiro and Wilk, 1965; Zar, 1974) was used to test for normality in the data. To satisfy the assumptions of independence of means and variances when using parametric tests the species richness data were square root transformed and the individual germinant data were Log (x+1) transformed. In ANOVA where a significant differences were found ($P < 0.05$), a Fisher's LSD *post hoc* test was performed to determine where the significant variation occurred.

From an initial analysis of variance a transect effect was found in Cherry Tree Lagoon. Therefore it was necessary to use the transect mean to determine differences between and within wetlands. These data were used unless otherwise stated.

For Spearman's rank correlation analyses (Sokal and Rohlf, 1981, Legendre and Legendre, 1983) rho values corrected for ties were reported (Abacus Concepts, 1992).

For the purpose of the analyses the nine functional groups described in Chapter 3 were amalgamated into broader groups as follows: the amphibious fluctuation tolerator emergent, deep and shallow, were amalgamated as 'emergent' species (Atle), amphibious fluctuation saturated/mudflat species, low growing and upright were amalgamated to saturated/ mudflat species (Atls) and terrestrial, wet and dry places, were amalgamated to terrestrial species (T). This gave a total of five functional groups for comparison: 1) submerged (S); 2) amphibious responder (Ar); 3) amphibious tolerator emergent (Atle); 4) amphibious tolerator saturated/mudflat; and 5) Terrestrial (T).

² Stewart Blackhall, Wildlife Biologist, Nature Conservation Branch, Department of Primary Industry, Water and Environment

Temporal analyses

Data

The summer and winter 1997 experiments were used to assess temporal changes in the seed banks of the wetlands studied. During the first experiment (summer 1997) the germination tank broke. This resulted in a loss of several samples prior to the drowned treatment. To enable comparison between germination in summer and winter 1997 the comparable data from the lost trays were taken out from the winter 1997 data. A direct comparison of number of species and individuals could then be made. Several plant groups were amalgamated due to a large number of unidentified plants in the summer 1997. The amalgamated groups were as follows:

<i>Juncus</i> unitubular species:	<i>Juncus holoschoenus</i> and <i>Juncus articulatus</i> , both species have unitubular leaves and are difficult to identify unless flowering;
<i>Isolepis/Schoenus</i> species:	<i>Isolepis fluitans</i> , <i>I. cernua</i> , <i>I. montivaga</i> , <i>I. producta</i> and <i>Schoenus fluitans</i> , these species all have similar vegetative growth;
<i>Myriophyllum simulans</i> / <i>variifolium</i> :	<i>Myriophyllum simulans</i> and <i>M. variifolium</i> , these two species were difficult to distinguish in their cotyledon stages therefore were amalgamated in both experiments
<i>Trifolium</i> species:	<i>Trifolium dubium</i> , <i>T. campestre</i> and <i>T. subterraneum</i> ;
<i>Utricularia</i> species:	<i>Utricularia dichotoma</i> , <i>Utricularia</i> sp. unidentified 1 and <i>Utricularia</i> sp. unidentified 2, these species all had similar first leaves, however, after flowering it was determined that there were three species of <i>Utricularia</i> .
Charophyte spp.:	Within the charophytes the <i>Nitella</i> species were grouped into the morphological characteristics, thick or thin branches. Thin branched <i>Nitella</i> types were feather like, whereas the thick branched types were more robust. The terms of description for charophytes below are from Casanova (1993) and van Raam (1995).

Eight separate species and types were identified:

Chara fibrosa: distinct stipulodes, spine cells, monoecious;

Chara preissii: distinct stipulodes, spine cells, dioecious;

Nitella thick spp.: *Nitella* species with thick branches;

Nitella thin spp.: *Nitella* species with thin branches;

Chara blobby arm: Charophyte with bulbous first branchlets;

Nitella congesta: *Nitella* sp. with dense accessory branchlets;

Chara globularis: *Chara* sp. with chordate branches;

Chara muelleri: *Chara* sp. with smooth branches.

The data from all wetlands were amalgamated and differences between the two seasons studied were determined as follows:

- chi square analyses were used to determine if there was an association between season and: a) the number of angiosperm and charophyte species and germinants; b) the number of exotic vs native species; and c) the life cycle of plant species (annual or perennial):
- Spearman's rank correlation coefficients were used to test if the number of germinants of exotic species were correlated between summer and winter 1997;
- a parametric correlation analysis was used to test if the number of germinants of each taxon were correlated between summer and winter 1997. In this case the data were Log (x+1) transformed to satisfy the assumptions for a correlation analysis;
- a Sørensen's index of similarity (Mueller-Dombois and Ellenberg, 1974) was used to determine the similarity between the species composition of the species that germinated in summer and winter 1997.

Spatial variation in seed banks

Data

The winter 1997 samples, subjected to 10 weeks mudflat and 10 weeks drowned treatments (total of 20 weeks), were used to determine differences between and within wetlands. The winter 1997 samples were used as a) they gave an equal number of trays for each zone more suitable for analysis of variance; b) they give a comparable time for each treatment (10 weeks); c) a greater number of charophyte species were identified during the winter 1997 experiment and could be used in the analyses; and d) the results for the winter and summer were highly correlated. The extra charophyte species were as follows: the *Nitella* thin/thick species were identified into 5 species (one species having two variations) as follows:

Nitella gelatinifera var. *gelatinifera*: large *Nitella* species with thick branches;

Nitella gelatinifera var. *microcephala*: large *Nitella* species with thin threadlike branches;

Nitella subtilissima: small *Nitella* species with thin globular accessory branchlets;

Nitella gloestachys;

Nitella c.f. *penicillata*;

Nitella cristata.

For the purpose of these analyses: a) the two variations of *Nitella gelatinifera* were separated into two species; and b) the following were amalgamated: a) *Myriophyllum simulans* and *variifolium* = *Myriophyllum sim/var.*; b) *Utricularia dichotoma*. *Utricularia* sp. 1 and *Utricularia* sp. 2 = *Utricularia* spp.; and c) *Trifolium dubium*, *T. campestre* and *T. subterraneum* = *Trifolium* spp

Differences in seed bank variables, number of germinants and species richness (dependant variables) were examined with respect to the independent variables as follows:

- a two-factor ANOVA with WETLAND and VEGETATION TYPE as the independent factors was used to test for differences between and within wetlands. To give an even number of zones for comparison between wetlands the dry herbaceous zone was not used in these analyses.
- a one-factor ANOVA with VEGETATION TYPE as the independent factor was used to test differences between the three zones of Middle Lagoon.
- data were separated into AQUATIC and SEDGE zones and a one-factor ANOVA with WETLAND as the independent factor was used to test for differences between each vegetation type.
- Spearman's rank correlation analyses were used to test if there was a correlation between seed bank variables and the location within a wetland the soils were taken. For these analyses the deepest WATER DEPTH recorded over the two year study period was used as a relative indication of the location of a sample within a wetland, that is, the deeper the water level the more central the sample.

Species composition

Jaccard's and Sørensen's indices of similarity (Mueller-Dombois and Ellenberg, 1974) were used to assess the similarity of the seed bank taxonomic composition between zones within wetlands. Sørensen's is a better similarity index than Jaccard's for ecological data because it weighs joint presences higher than joint absences. Both were calculated in some analyses to allow comparison with other papers, some of which only used Jaccard's. Species specificity was investigated by listing species that germinated from more than one zone in each wetland.

Differences related to water regime

The percentage of seasons each zone was inundated was used as a measure of the water regime experienced by each zone. To take into account all species recorded in each zone, species richness, in this case, was the combined number of species recorded in a

zone during the summer and winter 1997 experiments. The total germinants was the mean of the combined trays recorded in a zone during summer and winter 1997. The mean was used for total germinants to taken into account the different number of tray per zone due to the tank breaking during the summer 1997 experiment. Spearman's rank correlation analyses were used to test if there was a relationship between number of species and individual germinants and the percentage of seasons a zone was inundated. The analyses were repeated for all functional groups.

Winter 1997 - soil depth analysis

The data recorded for Big Punchbowl and Cherry Tree Lagoon were kept separated for these analyses. No species were amalgamated. A one-factor ANOVA using DEPTH category as the independent factor was used to test for differences in the species richness and germinants germination with depth in both Big Punchbowl and Cherry Tree Lagoon. Depth categories were: 0 - 2.5cm; 2.5 - 5 cm; 5 - 7.5 cm; and 7.5 - 10 cm.

Winter 1998 - treatment analysis

As the purpose of this experiment was to determine differences between species richness and number of germinants between treatments trays germinated were not separated into wetlands or zones but were used as 18 replicates for each treatment. Several species were amalgamated for these analyses as follows: a) *Myriophyllum simulans* and *M. variifolium* = *Myriophyllum sim/var.*; b) all *Nitella* spp.; and c) *I. fluitans* and *I. cernua* = *Isolepis* spp.. A t-test was used to test for differences between treatments in the a) the winter 1998 trays; and b) comparable trays from each wetland from the winter 1997 experiment. Sørensen's indices of similarity were used to test the similarity between the species composition that germinated in the mudflat and drowned treatment for: a) combination of the large summer and winter experiments; and b) both sub-sets from the winter 1997 and 1998 soils.

Results

Overall seed bank description

Eighty three angiosperm species from 30 families (Appendix I; Appendix II) germinated in the seed bank experiments. Slightly more dicotyledon species (43) than monocotyledon species (40) germinated. Eight initial charophyte groups were identified, which included twelve species of charophytes.

Of the eighty-three angiosperm and twelve charophyte taxa that germinated only twelve taxa contributed more than 1% to the combined total germination recorded for winter and summer 1997. Eleven angiosperm species contributed more than 1% to the combined angiosperm germination (Table 4.4).

Charophyte taxa dominated the germination with 50% of the recognised types being in the top 12 groups. *Chara fibrosa* had the highest number of germinants (29.89%) followed by *Nitella* spp. thick (14.77%) and *Nitella* spp. thin (12.18%) types. *Chara globularis* (5.79%) and *C. preissii* (2.97%) were also included in the most abundant individual species.

Within the angiosperm species seven groups contributed more than 1% to the combined total germination. The dicotyledon taxon, *Myriophyllum simulans/variifolium* had the highest amount of germinants in both total and angiosperm germination (6.98 and 20.87%) with *Batrachium trichophyllum* and *Elatine gratioloides* (1.43 and 1.29%) being the only two other dicotyledon taxa that contributed more than 1% of the total germination. Within the monocotyledon taxa, *Agrostis avenacea* (5.89 and 17.60%) and the *Juncus* unitubular group (3.91 and 11.69%) were the highest ranking taxa.

Seventy-five percent of the most abundant taxa in both cases were perennials and only one introduced species, *Leontodon taraxacoides*, contributed more than 1% to the angiosperm germination. No introduced species contributed more than 1% to the total germination.

Table 4.4 Taxa that contributed greater than 1% of total or angiosperm germination.

Species groups	Life cycle	Total germinants	Per cent total germinants	Per cent total angiosperm germinants
<i>Chara fibrosa</i>	P	8918	29.89	
<i>Nitella</i> thick sp.	A	4408	14.77	
<i>Nitella</i> thin sp.	A	3633	12.18	
<i>Myriophyllum simulans/variifolium</i>	P	2082	6.98	20.87
<i>Agrostis avenacea</i>	A	1756	5.89	17.60
<i>Chara globularis</i>	P	1729	5.79	
<i>Juncus unitubular</i> spp.	P	1166	3.91	11.69
<i>Chara preissii</i>	A	887	2.97	
<i>Isolepis/Schoenus</i> spp.	P	775	2.60	7.77
<i>Batrachium trichophyllum</i>	P/A	702	2.35	7.04
<i>Elatine gratioloides</i>	A	513	1.72	5.14
<i>Eleocharis acuta</i>	P	456	1.53	4.57
<i>Myriophyllum salsugineum</i>	P	202	0.68	2.02
<i>Leontodon taraxacoides</i> *	P	186	0.62	1.86
<i>Eleocharis sphacelata</i>	P	157	0.53	1.57
<i>Villarsia reniformis</i>	P	120	0.40	1.20

Variation between wetlands

Between wetlands, total species richness ranged from 14 in Big Punchbowl (BP) to 50 in Sandy Gate (SG, Table 4.5). Angiosperm species dominated the species richness of the seed banks in all wetlands, however, the ratio of monocotyledon and dicotyledon species varied between wetlands. Sixty percent of wetlands (Big Punchbowl, Middle Lagoon and Sandy Gate) had a greater monocotyledonous component, whereas, 40% had a greater dicotyledonous component. Native species dominated the seed banks of the wetlands with only 27 (31%) exotic angiosperm species recorded.

Due to the variation in tray numbers recorded as a result of the tank breaking during the summer 1997 experiment, as well as the extra zone sampled in Middle Lagoon, only germinants per tray provides a meaningful comparison between wetlands. This figure was naturally lower for Big Punchbowl than all other wetlands. Within wetlands, charophyte germinants dominated the individual germination of Big Punchbowl, Tin Dish, and Middle Lagoon (Table 4.5). Monocotyledon germinants dominated the individual germination of Sandy Gate, whereas, dicotyledons dominated the germinants from Cherry Tree Lagoon (Table 4.5).

Table 4.5 Overall seed bank summary: total species richness and mean number of germinants per tray. Data reported are the total number of species germinated from each wetland over the period of the present study and the mean number of germinants for winter 1997 germinated for 20 weeks. (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate).

	Total	BP	TD	MID	CTL	SG
Zone number	11	2	2	3	2	2
Species richness	95	14	34	41	34	50
	Percentage total species					
Dicotyledon spp.	45.3	21.4	44.1	36.6	50.0	40.0
Monocotyledon spp.	42.1	50.0	38.2	53.7	38.2	46.0
Charophyte spp.	12.6	28.6	17.6	9.8	11.8	14.0
Exotic species	27	1	13	7	2	13
Mean germinants per tray	128.2	47.7	121.9	209.5	202.3	120.1
	Percentage of total germinants					
Dicotyledon germinants	17.1	0.5	5.1	6.1	47.1	6.6
Monocotyledon germinants	17.7	3.4	8.1	8.3	17.7	54.2
Charophyte germinants	65.1	96.2	86.9	85.4	35.1	39.2

Exotic species contributed only a low proportion of both species and individuals in all wetlands, except Tin Dish where 44% of the species that germinated were exotic (Table 4.6). The wetlands on agricultural land (Tin Dish, Middle Lagoon and Cherry Tree Lagoon) have the highest percentages of exotic species in their seed banks, though this is not the case with total individual numbers. All wetlands germinated comparatively small percentages of exotic individuals from their seed banks. These ranged from between 0.3% (Big Punchbowl) to 5.4% (Tin Dish).

Charophyte Species

Differences in the dominance of charophyte species between the water regime types were observed (Table 4.7). *Chara* species dominated the seed banks of the long-term dry wetlands (Big Punchbowl and Tin Dish) as well as the fluctuating wetland (Middle Lagoon), whereas *Nitella* species dominated the germination of the semi-permanent wetlands (Cherry Tree Lagoon and Sandy Gate).

Table 4.6 Wetland exotic vs native seed bank summary

Wetland	Native species	Exotic species	% exotic species	Native individuals	Exotic individuals	Per cent exotic individuals
Big Punchbowl	7	1	12.5	856	2	0.3
Tin Dish	9	7	44.0	2077	118	5.4
Middle Lagoon (2)	25	3	12.0	3832	9	0.2
Middle Lagoon (3)	16	5	24.0	5603	70	1.2
Cherry Tree Lagoon	25	2	7.4	3580	60	1.6
Sandy Gate	28	8	22.0	2077	82	3.8

() = number of zones used; (2) = *Eleocharis sphacelata* and aquatic, (3) = dry herb added.

Table 4.7 Percentage contribution of the charophytes species to the total charophyte germination.

	BP	TD	MID*	CTL	SG	Total
Chara species						
<i>Chara fibrosa</i>		38.6	86.4		30.2	53.4
<i>Chara globularis</i> var. <i>globularis</i>		54.9			5.1	11.2
<i>Chara muelleri</i>		0.1				0.01
<i>Chara preissii</i>	57.0			7.9		5.9
Nitella species						
<i>Nitella</i> c.f. <i>penicillata</i>			0.5			0.2
<i>Nitella congesta</i>		0.5				0.1
<i>Nitella cristata</i>					0.6	0.1
<i>Nitella gelatinifera</i> var. <i>gelatinifera</i>	5.2		5.8	85.2	48.2	18.8
<i>Nitella gelatinifera</i> var. <i>microcephala</i>	28.1		7.3	6.5	0.9	7.0
<i>Nitella gloestachys</i>					13.8	1.2
<i>Nitella subtilissima</i>	9.7			0.4	1.2	1.0
<i>Nitella</i> UNID 63		0.1				0.01
Unidentified species						
<i>Chara</i> blobby arm		5.7				1.1

* all three zones used for Middle Lagoon

Variation between zones

The mean number of total germinants per m² ranged from 1,614 in Big Punchbowl aquatic zone to 20,970 in Cherry Tree Lagoon aquatic zone (Table 4.8). As with total wetland patterns, the germination from all zones within Big Punchbowl, Tin Dish and Middle Lagoon, were dominated by charophyte germinants, whereas, the germination from zones within Cherry Tree Lagoon and Sandy Gate were dominated by angiosperm germinants. The total number of species that germinated from each zone ranged from 7 in Big Punchbowl aquatic zone to 46 in Sandy Gate *Baumea arthropphylla* (Table 4.9). The representation of species within each functional group varied between zones. Equal number of zones (4) had their highest species representation in the amphibious responder and amphibious tolerator-emergent groups (zones in Middle Lagoon, Cherry Tree Lagoon, and Sandy Gate and Big Punchbowl outer zone). Between the two long-term dry wetlands, the seed bank species richness within Big Punchbowl had its highest representation in the submerged group, whereas, the species richness within Tin Dish had the highest representation in the terrestrial group. The dry herbaceous zone of Middle Lagoon had its highest representation of species in the amphibious tolerator-saturated/mudflat group.

Unlike species richness, 82% of zones had the greatest representation of germinants in the submerged species group (Table 4.9). The two zones that differed were the aquatic zones of the semi-permanent wetlands. The aquatic zone of Cherry Tree Lagoon had the greatest percentage of germinants in the amphibious responder group, whereas, Sandy Gate aquatic zone had the greatest percentage of germinants in the amphibious tolerator emergent group

Table 4.8 Mean seed bank size per m² (* = Middle Lagoon mean for the combined *Eleocharis sphacelata* and aquatic herb zones).

Water Regime	Zone	Total	Angiosperm	Charophyte
LT-DRY	BP Aquatic	1,614	57	1,557
	BP Outer	4,459	177	4,282
	BP Total	3,036	117	2,919
	TD Aquatic	4,437	255	4,187
	TD <i>E. acuta</i>	11,090	1,776	9,314
	TD Total	7,764	1,016	6,748
FLUC.	MID <i>E. sphacelata</i>	11,026	1,486	9,540
	MID Aquatic	16,150	1,536	14,614
	*MID Total	13,588	1,511	12,077
	MID Dry herb	12,994	2,838	10,156
	MID Total	13,390	1,953	11,437
S-PERM	CTL Aquatic	20,970	14,168	6,801
	CTL <i>B. arthropphylla</i>	4,791	2,541	2,251
	CTL Total	12,880	8,355	4,526
	SG Aquatic	8,252	4,968	3,284
	SG <i>B. arthropphylla</i>	7,035	4,338	2,696
	SG Total	7,643	4,653	2,990

LT-DRY = long-term dry; FLUC. = fluctuating; S-PERM = semi-permanent.

Table 4.9 Summary of the total and functional group species richness and mean germinants per tray of seed banks within each zone.
 (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B.r = *Baumea rubiginosa*; B.a = *Baumea arthropphylla*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; Aq. = aquatic; Out. = outer zone; Functional groups: S = submerged; Ar = amphibious responder; Atle = amphibious tolerator-emergent; Atls = amphibious tolerator-saturated/mudflat; T = terrestrial).

	BP B.r Aq	BP B.r Out.	TD Aq.	TD E.a	MID E.s	MID Aq.	MID Dry	CTL Aq.	CTL B.a	SG Aq.	SG B.a
Total species	7	13	26	27	20	24	34	30	26	37	46
Functional groups	Percentage of total species										
S	57.1	30.8	23.1	22.2	15.0	16.7	8.8	13.3	19.2	18.9	17.4
Ar	14.3	30.8	3.8	3.7	30.0	20.8	23.5	36.7	34.6	16.2	13.0
Atle	28.6	15.4	23.1	18.5	30.0	33.3	23.5	33.3	30.8	24.3	26.1
Atls	0.0	15.4	23.1	18.5	15.0	20.8	32.4	10.0	15.4	13.5	21.7
T	0.0	7.7	26.9	37.0	10.0	8.3	11.8	6.7	0.0	27.0	21.7
Mean germinants	25.3	70.0	69.4	173.9	171.8	252.4	202.6	326.1	73.8	128.6	105.8
Functional groups	Percentage of total germinants										
S	96.4	96.0	95.0	84.1	87.2	90.9	78.7	39.0	49.3	41.0	40.5
Ar	3.6	2.3	0.6	0.1	11.2	5.7	6.5	49.0	25.9	11.0	9.3
Atle	1.2	1.3	2.6	9.9	1.3	1.3	10.9	11.7	23.6	45.1	40.1
Atls	0.0	0.0	0.0	3.0	0.1	1.9	2.3	0.0	0.5	1.1	5.3
T	0.0	0.3	2.4	3.0	0.2	0.3	1.7	0.3	0.4	1.7	4.8

Temporal variation in wetland seed banks

Species Richness

Taxon richness for both angiosperm and charophyte groups was similar in both experiments. A total of 77 taxa germinated from the winter 1997 and 78 from the summer 1997. This pattern of similarity extended to relative numbers of angiosperm and charophyte taxa (Table 4.10). There was no association between season and the number of species that germinated from each plant type ($\chi^2 = 0.062$; $P = 0.9690$; 1 degree of freedom).

Table 4.10 Summer and winter 1997 germination experiments species richness summary (Monocot = monocotyledon; Dicot - dicotyledon)

	Species richness	Dicot species	Monocot species	Total angiosperm species	Charophyte species/types	Introduced species
Summer 1997	77	36	33	69	8	24
Winter 1997	78	38	32	70	8	18

Total germinants

Greater differences between the two seasons occurred in the total germinant data (Table 4.11). More individuals germinated from winter (18,019) than from summer (11,819) soils. This was mainly due to a higher amount of charophyte germination, with 13,230 charophyte individuals germinating from winter soils compared to 6,630 from summer soils (Table 4.11). This large difference is not seen in the angiosperm individuals where slightly more angiosperm individuals germinated from winter (5,189) than summer (4,789) soils.

The results of the chi-square analysis for germinants (Table 4.11) indicated that there was an association between season and the number of individuals of each plant type that germinated ($\chi^2 = 1003.47$; $P < 0.0001$). Greater than expected angiosperm individuals germinated from the summer soils, whereas, greater than expected charophyte individuals germinated from the winter soils. There was a highly significant positive

correlation between the number of germinants per taxon in the two experiments (Figure 4.2).

Table 4.11 Summer and winter 1997 germination experiments total germinant summary (Monocot = monocotyledon; Dicot - dicotyledon)

	Total germinants	Dicot. germinants	Monocot. germinants	Total angiosperm germinants	Charophyte germinants
Summer 1997	11763	2218	2925	5143	6620
Winter 1997	17871	2387	2272	4664	13207

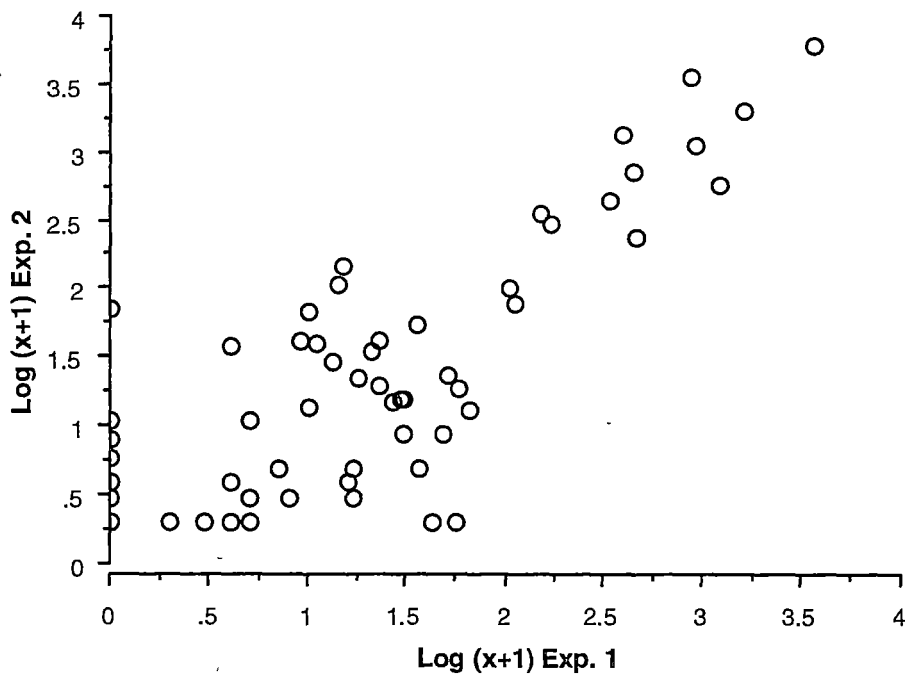


Figure 4.2 Comparing the log of the number of individuals of each taxa germinated in summer 1997 (Exp. 1) and winter 1997 (Exp. 2) (Correlation coefficient = 0.911, $P < 0.0001$).

Exotic vs native species

A total of 27 exotic species germinated in the two experiments. However, native species dominated in both species richness and number of individuals. Comparison of the two seasons showed that a higher number of exotic species germinated from summer soils (25) than from winter soils (18). The proportion of exotic total germinants was small in both experiments (summer - 4.4% and winter – 1.7%). Several of the exotic species were known wetland plants - *Juncus articulatus*, *J. bufonius*, *Cyperus tenellus*, *Typha* sp., *Cotula coronopifolia* and *Callitriche stagnalis*. However, there is a debate as to whether *Cotula coronopifolia* is an introduced species (Romanowski, 1999).

There is no association between the number of exotic and native species and season ($\chi^2 = 1.892$; $P = 0.1689$), whereas, there is an association between season and the number of exotic and native germinants ($\chi^2 = 46.174$; $P = 0.0001$). Greater than expected exotic individuals germinated from the summer 1997 soils, whereas, lower than expected germinated from the winter soils.

Eighty per cent of exotic species had more individuals germinating from soils taken in summer 1997 than those from winter 1997 (Table 4.12). The number of individuals that germinated per exotic species were significantly correlated between the two seasons ($\rho = 0.655$; $P = 0.0011$).

Life cycle classes

Perennial species dominated the angiosperm seed banks of both summer and winter 1997 soils (Table 4.13). Similar numbers of annual species germinated in both experiments ($\chi^2 = 1.918$; $P < 0.1661$). However, significantly more annual individuals ($\chi^2 = 165.994$; $P < 0.0001$), germinated from winter 1997 soils than for summer 1997 soils (Table 4.13).

Table 4.12 Comparison between summer and winter 1997 in the number of germinants of each exotic species (* = exotic species, */n = uncertain status).

Exotic Species	Summer 1997	Winter 1997	Total
<i>Leontodon taraxacoides</i> *	109	77	
<i>Vulpia myuros</i> *	55	1	
<i>Juncus articulatus</i> *	52	102	
<i>Callitriche stagnulis</i> *	51	23	
<i>Cotula coronopifolia</i> */n	47	8	
<i>Aira caryophyllaea</i> *	42	1	
<i>Plantago coronopus</i> *	36	4	
<i>Holcus lanatus</i> *	28	15	
<i>Cirsium vulgare</i> *	26	14	
<i>Centaureum erythraea</i> *	20	34	
<i>Polypogon monspeliensis</i> *	16	4	
<i>Trifolium dubium</i> *	6	4	
<i>Poa annua</i> *	5	0	
<i>Vellereophyton dealbatum</i> *	3	1	
<i>Gaudiana fragilis</i> *	3	0	
<i>Agrostis capillaris</i> *	3	3	
<i>Trifolium subterraneum</i> *	2	3	
<i>Stellaria media</i> *	2	0	
<i>Juncus bulbosus</i> *	2	0	
<i>Hypochoeris radicata</i> *	1	0	
<i>Cynosurus echinatus</i> *	1	0	
<i>Typha</i> sp.*/n	1	0	
<i>Cyperus tenellus</i> *	1	0	
<i>Epilobium</i> sp.*/n	11	3	
<i>Hainardia cylindrica</i> *	1	0	
<i>Trifolium repens</i> *	0	5	
<i>Acetosella vulgaris</i> *	0	1	
Total species	25	18	27
Total individuals	524	303	827

Table 4.13 **Angiosperms: comparison between the number of individuals and species with different life cycles (annual or perennial) that germinated from soils taken during summer 1997 and winter 1997 (Germ = germinants).**

Life cycle classes	Summer 1997 Autumn/Winter Germ.		Winter 1997 Spring/Summer Germ.	
	Individuals	Species	Individuals	Species
Annual	1575	16	925	10
Perennial	3038	51	3728	59
Biennial	46	2	48	2
Unknown	499	3	91	1

Spatial differences in seed banks

Species richness

Differences between wetlands and zones

All species richness variables showed a significant difference between wetlands (Table 4.14). There was, however, no significant differences between sedge and aquatic dominated zones in any of the species richness variables as well as no significant interaction effects. This indicated that the type of vegetation the soils were taken from did not significantly influence the number of species that germinated per tray (Figure 4.3) and that this pattern was found in all wetlands studied.

The Fisher's *post hoc* tests (Table 4.15) indicated that, in general, the semi-permanent wetlands (Cherry Tree Lagoon and Sandy Gate) had significantly more total and angiosperm species that germinated per tray than the long-term dry wetlands (Big Punchbowl and Tin Dish). However, the long-term dry Tin Dish had more in common in its total and angiosperm species richness with Middle Lagoon than with Big Punchbowl. Big Punchbowl had significantly less total and angiosperm species that germinated than all other wetlands. Greater similarity was observed in the number of charophyte species that germinated.

Table 4.14 Results from 2-factor ANOVA with wetland and vegetation type (sedge vs aquatic) as the independent factors with species richness as the dependent variable (d.f. = degree of freedom; M.S = mean squares; Sig. - significance).

Source of Variation	d.f	M.S	F- Value	P-Value	Sig.
Total species richness					
Wetland	4	2.56	24.899	<0.0001	***
Vegetation type	1	0.00	0.01	0.9104	ns
Wetland x vegetation type	4	0.11	1.10	0.3835	ns
Residual	20	0.10			
Angiosperm species richness					
Wetland	4	5.05	27.57	<0.0001	***
Vegetation type	1	0.00	0.03	0.8662	ns
Wetland x vegetation type	4	0.18	0.97	0.4471	ns
Residual	20	0.18			
Charophyte species richness					
Wetland	4	0.11	9.82	0.0001	***
Vegetation type	1	0.21	1.94	0.1790	ns
Wetland x vegetation type	4	0.00	0.58	0.6835	ns
Residual	20	0.01			

Table 4.15 Species richness means showing significant differences between wetlands from Fisher's LSD *post hoc* test for 2-factor ANOVA with wetland and vegetation type (sedge vs aquatic) as factors (Letters run across rows and indicate which wetlands are significantly different. Wetlands with same letters are not significantly different).

	LT-DRY		FLUC	S-PERM	
Variable	BP	TD	MID	CTL	SG
Species Richness					
Total	3.5 d	6.5 c	6.9 c	10.25 b	12.8 a
Angiosperm	0.8 c	3.6 b	4.1 b	8.2 a	9.6 a
Charophyte	2.7 b	3.0 ab	2.9 b	2.1 c	3.3 a

Differences within zones dominated by either aquatic herbaceous species or sedge species

Both aquatic herb dominated and sedge dominated zones were significantly different in all species richness variables (Table 4.16). The Fisher's *post hoc* test indicated that the aquatic herb zone of Tin Dish was significantly lower in its total and angiosperm species richness than the aquatic zone in most other wetlands (Table 4.17). Within the other three wetlands, angiosperm species richness of the aquatic zones in Cherry Tree Lagoon and Sandy Gate were significantly higher than the aquatic zone in Middle Lagoon.

The *Baumea arthropphylla* zones of the semi-permanent wetlands (Cherry Tree Lagoon and Sandy Gate) were significantly higher in angiosperm species richness than the *Baumea rubiginosa* zones sampled in Big Punchbowl (Table 4.17). The two *Eleocharis* spp. zones are similar to each other in all species richness variables.

Table 4.16 Seed Bank: results of a one-factor ANOVA for differences between: a) aquatic; and b) sedge dominated zones (d.f = degree of freedom; M.S = mean square; Sig. = significance).

Type III Sums of Squares					
Source of Variation	d.f.	M.S.	F-Value	P-Value	Sig.
Aquatic zones					
Total	3	0.0807	5.867	0.0203	*
Angiosperm	3	1.343	6.499	0.0154	*
Charophyte	3	0.079	6.738	0.0140	*
Sedge zones					
Total	3	1.381	17.387	<0.0001	***
Angiosperm	3	0.047	4.474	0.0156	*
Charophyte	3	2.770	16.564	<0.0001	***

Table 4.17 Results of the Fisher's *post hoc* test from one-factor ANOVA for differences in species richness between: a) aquatic zones; and b) sedge zones (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate. B.r = *Baumea rubiginosa*; B.a = *Baumea arthropphylla*, E.a = *Eleocharis acuta*; *Eleocharis sphacelata*; out = outer; aq. = aquatic. Letters run across rows and indicate which zones are significantly different. Zones with different letters are significantly different).

a) Aquatic zones

Variable	TD	MID	CTL	SG
Aquatic zones				
Total	6.0 c	7.4 bc	11.5 ab	12.6 a
Angiosperm	3.0 c	4.9 b	9.6 a	9.3 a
Charophyte	3.0 a	2.6 ab	2.0 b	3.2 a

(b) Sedge Zones

Variable	BP	BP	TD	MID	CTL	SG
	B.r aq.	B.r out.	E.a	E.s	B.a	B.a
Species Richness						
Total	3.1 d	3.9 cd	7.1 b	6.2 bc	9.0 b	13.1a
Angiosperm	0.6 d	1.0 d	4.2 bc	3.2 c	6.9 ab	9.8 a
Charophyte	2.6 bc	2.7 ab	2.9 ab	3.0 ab	2.1 c	3.3 a

Number of germinants

Differences between wetlands and zones

Similar to the species richness results, all germinant variables showed a significant difference between wetlands and no significant differences between sedge and aquatic dominated vegetation zones (Table 4.18). However, in this case all analyses had a significant interaction effect. This indicated that the differences in total individuals that germinated between the vegetation zones within wetlands depended on the wetland.

The semi-permanent wetlands (Cherry Tree Lagoon and Sandy Gate) had significantly more angiosperm germinants per tray than the long-term dry wetlands (Big Punchbowl and Tin Dish; Table 4.19). For total individual germinants Middle Lagoon had the highest number of germinants per tray and, in this case, was not significantly different to the semi-permanent wetlands. Tin Dish had significantly more germinants than the

other long-term dry wetland Big Punchbowl and was not significantly different to both semi-permanent wetlands. Big Punchbowl had significantly less total and angiosperm germinants than all other wetlands.

Table 4.18 Results from 2-factor ANOVA with wetland and vegetation type (sedge vs aquatic) as the independent factors with total germinants as the dependent variable (d.f. = degree of freedom; M.S = mean squares; Sig. - significance).

(a) Source of Variation	d.f	M.S	F- Value	P-Value	Sig.
Total germinants					
Wetland	4	0.35	11.26	<0.0001	***
Vegetation type	1	0.00	0.04	0.8387	ns
Wetland x vegetation type	4	0.25	7.9	0.0005	***
Residual	20	0.03			
Angiosperm germinants					
Wetland	4	1.18	40.30	<0.0001	***
Vegetation type	1	0.05	0.85	0.3684	ns
Wetland x vegetation type	4	0.32	5.66	0.0033	***
Residual	20	0.6			
Charophyte germinants					
Wetland	4	0.41	12.02	<0.0001	***
Vegetation type	1	0.00	0.16	0.6963	ns
Wetland x vegetation type	4	0.18	5.40	0.0041	**
Residual	20	0.03			

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant

Table 4.19 Total germinant means showing significant differences between wetlands from Fisher's LSD *post hoc* test from 2-factor ANOVA with wetland and vegetation type (sedge vs aquatic) as factors (Letters run across rows and indicate which wetlands are significantly different. Wetlands with same letters are not significantly different).

	LT-DRY		FLUC	S-PERM	
Variable	BP	TD	MID	CTL	SG
Germinants					
Total	47.7 c	121.9 b	213.3 a	202.3 ab	120.1 ab
Angiosperm	1.8 d	16.0 c	22.7 b	131.1 a	73.1 a
Charophyte	45.8 c	106.0 b	189.2 a	71.0 bc	47.0 c

Much of the pattern of the total individual differences between wetlands was related to the number of charophytes that germinated (Figure 4.3; Table 4.19). Middle Lagoon had significantly higher charophyte germination than all other wetlands. TD had significantly higher number of charophyte germination than both the semi-permanent wetlands as well as Big Punchbowl the other long-term dry wetland. The two semi-permanent wetlands had low charophyte germination and were not significantly different to Big Punchbowl in their number of charophyte germinants.

Zones within two wetlands (Middle lagoon and Sandy Gate) were not significantly different in the number of germinants per tray (Figure 4.3; Table 4.20), whereas, the zones in both the long-term dry wetlands, Big Punchbowl and Tin Dish, and Cherry Tree Lagoon were significantly different in their total germinants (Table 4.20). Within Tin Dish the difference between zones was due to a significantly greater number of angiosperm germinants in the sedge zone, whereas, for Big Punchbowl the difference was related to a greater number of charophyte germinants in the outer sedge zone. In Cherry Tree Lagoon the aquatic zone had a significantly greater number of both angiosperm and charophyte germinants than its sedge zone.

Table 4.20 Results of the Fisher's *post hoc* test for differences in the mean germinants per tray between vegetation zones within each wetland. (Letters run down columns and indicate which zones are significantly different within each wetland. Zones with different letters are significantly different).

	L-T DRY		FLUC	S-PERM	
	BP	TD	MID	CTL	SG
	Mean total germinants per tray				
AQUATIC	25.3 a	69.67 a	253.56 a	329.2 a	129.6 a
SEDGE	70.0 b	174.1 b	173.11 a	75.2 b	110.4 a
	Mean angiosperm germinants per tray				
AQUATIC	0.9 a	4.0 a	24.1 a	222.4 a	78.0 a
SEDGE	2.8 a	27.9 b	23.3 a	39.89 b	68.1 a
	Charophyte germinants per tray				
AQUATIC	24.4 a	65.7 a	229.4 a	106.8 a	51.56 a
SEDGE	67.2 b	146.2 a	149.8 a	35.3 b	42.3 a

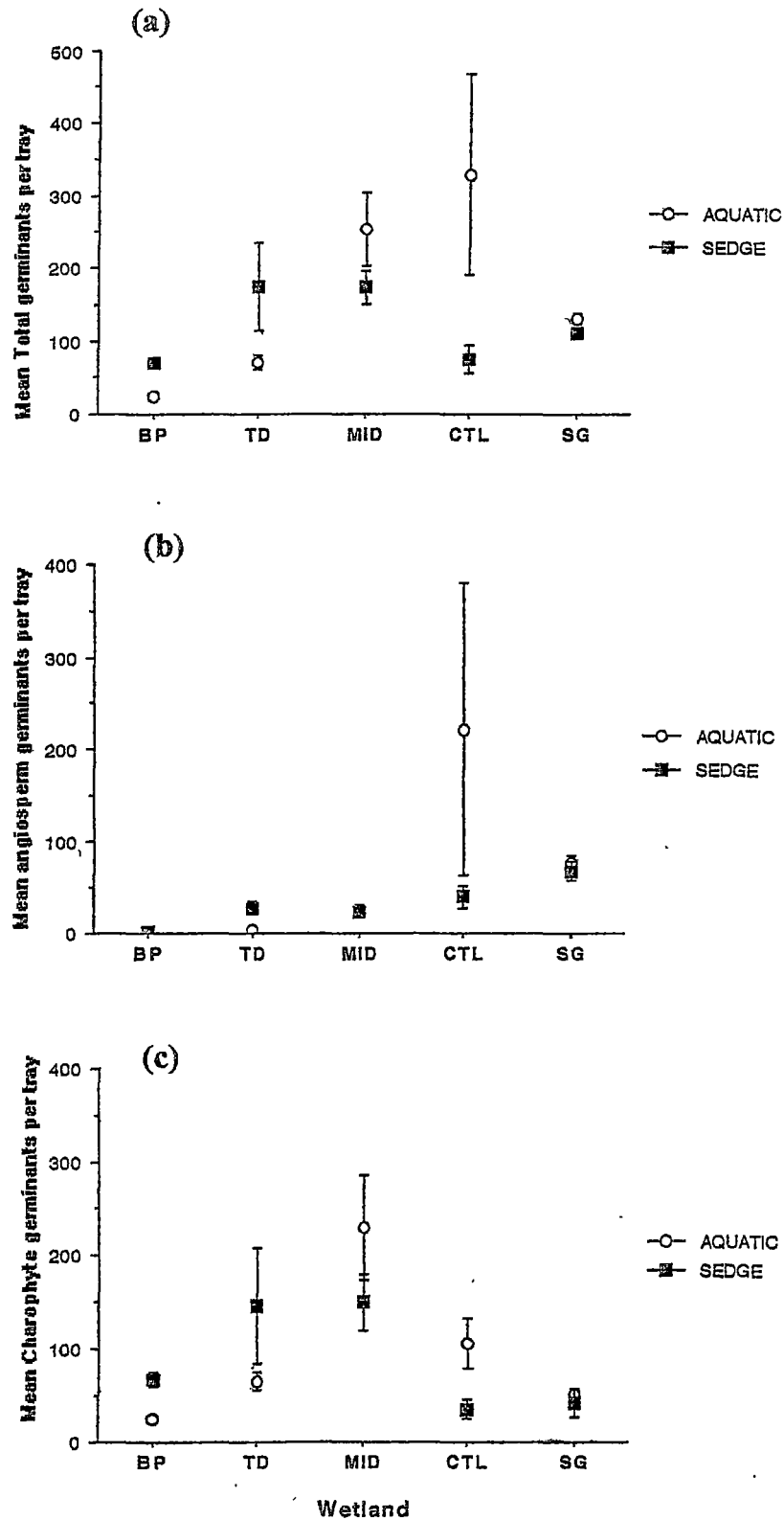


Figure 4.3

Mean number of germinants per tray for each zone within each wetland. (a) total germinants; (b) angiosperm (M/D) individuals; and (c) charophyte germinants (bar = ± 1 standard error).

Differences within zones dominated by either aquatic herbaceous species or sedge species

The aquatic herb dominated zones were significantly different in all their germinant variables (Table 4.21). The Fishers *post hoc* test indicated that the aquatic herb zone of Tin Dish was significantly lower in its total and angiosperm germinants than most other wetlands (Table 4.22). Within the other three wetlands, angiosperm germinants of the aquatic zones in Cherry Tree Lagoon and Sandy Gate were significantly higher than the aquatic zone in Middle Lagoon. However, Middle Lagoon had significantly higher charophyte germinants than both the aquatic zones of these wetlands as well as the Tin Dish aquatic zone. The aquatic zone of Sandy Gate had the lowest number of charophyte germinants and was not significantly different to the aquatic zone of Tin Dish.

Between *Baumea* zones, the *Baumea arthrophylla* zones of the semi-permanent wetlands (Cherry Tree Lagoon and Sandy Gate) were significantly higher in angiosperm individual germinants than the *Baumea rubiginosa* zones sampled in Big Punchbowl (Figure 4.3; Table 4.22), but not significantly different in most of their charophyte individual germination (Figure 4.3 c; Table 4.22). The two *Eleocharis* spp. zones were similar to each other in all germinant variables. They had the highest number of individuals that germinated in sedge dominated vegetation types. This can be related to their charophyte germination which was significantly higher than in the *Baumea* zones.

Table 4.21 Seed Bank: results of one-factor ANOVA for differences in germinants between: a) aquatic; and b) sedge dominated zones (d.f = degree of freedom; M.S = mean square; Sig. = significance;

Type III Sums of Squares					
Source of Variation	d.f.	M.S.	F-Value	P-Value	Sig.
Aquatic zones					
Total	3	.232	4.255	0.0114	*
Angiosperm	3	1.167	14.152	0.0015	**
Charophyte	3	0.227	11.375	0.0029	**
Sedge zones					
Total	3	0.269	10.493	0.0005	***
Angiosperm	3	1.202	30.470	<0.0001	***
Charophyte	3	0.279	6.444	0.0039	**

P > 0.05; ** = P > 0.01; *** = P > 0.001; ns = not significant.).

Table 4.22 Results of the Fisher's *post hoc* test from one-factor ANOVA for differences in germinants between: a) aquatic; and b) sedge dominated zones (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; Sedge zones: B.r = *Baumea rubiginosa*; B.a = *Baumea arthropphylla*, E.a = *Eleocharis acuta*; *Eleocharis sphacelata*; out = outer; aq. = aquatic. Letters run across rows and indicate which zones are significantly different. Zones with different letters are significantly different).

(a) Aquatic Zone

Variable	TD	MID	CTL	SG
Germinants				
Total	69.67 b	253.6 a	329.2 a	129.6 ab
Angiosperm	4.0 c	24.1 b	222.4 a	78.0 ab
Charophyte	65.7 bc	229.4 a	106.8 b	51.56 c

(b) Sedge Zones

Variable	BP	BP	TD	MID	CTL	SG
	B.r aq.	B.r out.	E.a	E.s	B.a	B.a
Germinants						
Total	25.3 c	70.0 b	174.1 a	173.1 a	75.2 b	110.4 ab
Angiosperm	0.9 c	2.8 c	27.9 b	23.3 b	39.9 ab	68.1 a
Charophyte	24.4 c	67.2 ab	146.2 a	149.8 a	35.3 bc	42.3 b

Species composition

Differences in species composition between zones within wetlands

There is a high level of similarity in the species composition between zones in all wetlands studied (Table 4.23). The overlap of species, as indicated by the Sørensen's index of similarity (Table 4.23), were all above 50%. The highest overlap (83.3%) occurred in Tin Dish (TD) and the least (51%) between the aquatic herb and *Eleocharis sphacelata* zone of Middle Lagoon (MID). On average the long-term dry and semi-permanent wetlands are both similar in their species overlap between zones. Comparing the wetlands with long-term dry and semi-permanent water regimes, the wetlands in the lower Midlands (Tin Dish and Sandy Gate) have a greater similarity between their zone species composition than was found in the east coast wetlands (Big Punchbowl and Cherry Tree Lagoon).

Table 4.23 Results of Sørensen's and Jaccard's indices of similarity for the seed bank species composition between the vegetation zones of each wetland (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL Cherry Tree Lagoon; SG = Sandy Gate).

Wetland Type	Wetland/Zones	Sørensen's (%similarity)	Jaccard's (% similarity)
LTDRY	BP – aquatic and outer <i>Baumea rubiginosa</i>	58.8	45.5
	TD – aquatic and <i>Eleocharis acuta</i>	83.3	71.4
FLUC.	MID – dry herb and aquatic	64.0	47.0
	MID – dry herb and <i>Eleocharis sphacelata</i>	56.0	43.8
	MID – aquatic and <i>Eleocharis sphacelata</i>	51.0	34.5
S-PERM	CTL – aquatic and <i>Baumea arthropphylla</i>	68.1	51.6
	SG – aquatic and <i>Baumea arthropphylla</i>	75.4	60.5

LT-DRY = long-term dry, FLUC. = fluctuating, S-PERM = semi-permanent.

Individual species specificity

Between wetlands

There was a high level of species specificity in wetlands (Table 4.24). This is indicated by a high percentage of species germinating from only one wetland (59%). However, a total of 30% of species germinated from three or more wetlands, indicating that many species were also widespread throughout the seed banks of the wetlands studied (Table 4.24).

Table 4.24 Taxa that germinated from three or more wetlands.

Germinated from		
5 Wetlands	4 Wetlands	3 Wetlands
<i>Potamogeton tricarinatus</i> <i>Juncus</i> unidentified sp.	<i>Lilaeopsis polyantha</i> <i>Utricularia</i> spp.	<i>Selliera radicans</i> <i>Myriophyllum</i> <i>simulans/variifolium</i> <i>Limosella australis</i>
<i>Chara</i> spp. <i>Nitella</i> spp.	<i>Eleocharis acuta</i> <i>Isolepis fluitans</i> <i>Juncus planifolius</i> <i>Agrostis avenacea</i>	<i>Isolepis cernua</i> <i>Isolepis inundata</i> <i>Juncus bufonius</i> <i>Juncus holoschoenus</i> <i>Schoenus fluitans</i> <i>Leontodon taraxacoides</i>

Within Wetlands

Several individual species occurred broadly across vegetation zones. Of the 82 species that germinated during the winter 1997 experiment, 45 species (55%) germinated from more than one zone within a wetland (Table 4.25). Many of the most abundant species (Table 4.4) in the seed bank were also ubiquitous within individual wetlands. These included both the variations of *Nitella gelatinifera*, *Chara preissii*, *C. fibrosa*, *Myriophyllum simulans/variifolium*, *Agrostis avenacea* and *Isolepis fluitans*. Ninety-eight per cent of these species were associated with wetland environments (Table 4.26).

Table 4.25 Species that germinated from the seed bank of more than one zone within a wetland. X = present in the seed bank of that wetland not in both zones.

A.a = *Agrostis avenacea*; A.s = *Amphibromus sinuatus*; B.a = *Baumea arthropphylla*; B.t = *Batrachium trichophyllum*; C.b = *Chara* blobby arm; C.e = *Centaureum erythraea*; C.f = *Chara fibrosa*; C.g = *Chara globularis*; C.i = *Carex inversa*; C.m = *Chara muelleri*; C.p = *Chara preissii*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; E.v = *Eryngium vesiculosum*; Eg = *Elatine gratioloides*; Ep. spp. = *Epilobium* spp.; I.c = *Isolepis cernua*; I.f = *Isolepis fluitans*; J. buf = *Juncus bufonius*; J. sp = unidentified *Juncus* sp.; J.a = *Juncus articulatus*; J.h = *Juncus holoschoenus*; L.a = *Limosella australis*; L.t = *Leontodon taraxacoides*; Lp = *Lilaeopsis polyantha*; M.sal = *Myriophyllum salsugineum*; Ms/v = *Myriophyllum simulans/variifolium*; N. c = *Nitella congesta*; N. gel = *Nitella gelatinifera* var. *gelatinifera* and *microcephala*; N. s = *Nitella subtilissima*; N.a = *Neopaxia australasica*; P. m = *Polypogon monspeliensis*; P.c = *Plantago coronopus*; P.t = *Potamogeton tricarlinatus*; R.a = *Ranunculus amphitrichus*; S.r = *Selliera radicans*; Trif.sp = *Trifolium* spp.; U. spp. = *Utricularia* spp.; V.r = *Villarsia reniformis*.

BP	CTL	SG	TD	MID all 3 zones	MID E.s/A	MID A/DH	MID E.s/A
C. p N. gel N. s	C.p N. gel X	C.f N. gel N.s N.g	C.f	C.f N. gel	C.f N. gel	C.f N. gel	C.f N. gel
P.t	X A.a B.t B.a E.g E.a I.f J.h M.s/v R.a	P.t A.a B.t B.a E.a I.f J.h M.s/v	C.b C.m C.g N.c X A.a E.a	P.t A.a X I.f M.s/v	P.t A.a I.f M.s/v	P.t A.a I.f J.h M.s/v	P.t A.a E.a I.f M.s/v
X	U. spp. V.r	A.s C.i J.a E.v I.c L.t L.p L.a M.sal N.a Trif. sp.	L.t L.p	X X		U spp.	
X	J.SP	J.SP X X	Trif.sp C.e Epilob. sp J..buf J.SP P.c P.m X	X X S.r I.i	S.r I.i E.s	I.c L.t L.p S.r I.i C.cord G.h	L.p

Table 4.26 **Summary of the functional groups of the species that germinated in more than one zone in each wetland.**

Functional Group		Total	Percentage *
Submerged		10	71
Amphibious	Responder –	10	56
	Tolerator - emergent	12	71
	Tolerator - saturated/mudflat	7	50
Terrestrial	damp places	5	63
	dry places	1	10

* percentage of total species found within that functional group (Chapter 3).

Differences in seed banks related to water regime

Percentage of inundation

Differences in both species richness and individuals germinants were observed between zones (Table 4.9; Figure 4.4; Figure 4.5). However, only the amphibious responder (Ar) and amphibious tolerator-emergent (Atle) species richness and the amphibious responder individual germinants were correlated with the percentage of seasons that zones were inundated (Figure 4.1; Figure 4.5). All variables were positively correlated. This indicated that zones that were inundated for longer periods had greater number of amphibious responder (Ar) and amphibious tolerator-emergent (Atle) species as well as a greater number of amphibious responder germinants than those that were inundated for less time. Generally, similar number of total, submerged (S), amphibious tolerator-saturates/mudflat (Atls) and terrestrial (T) species as well as germinants were found in zones with varied inundation periods (Figure 4.4; Figure 4.5).

Influence of maximum water depth

The Spearman's rank correlation analyses showed that in many cases there was a relationship between seed bank variables and maximum water depth. All of the significant analyses were negative (Table 4.27).

For the long-term dry wetlands water depth was significant only for the total germinant data. In Big Punchbowl this was driven by differences in charophyte germinants, whereas in Tin Dish it was driven by differences in angiosperm germinants. Within the other wetland types (semi-permanent and fluctuating) the angiosperm species richness related to water depth). Within the semi-permanent wetlands there were variable results. However, they all relate to the species richness data and especially that of the angiosperm species. Cherry Tree Lagoon does not show any relation between water depth and the number of germinants when total data is used. However, when analysing only the aquatic zone (Table 4.27) there is a negative relation between water depth and the number of angiosperm germinants. This result is similar that for the other semi-permanent wetland, Sandy Gate.

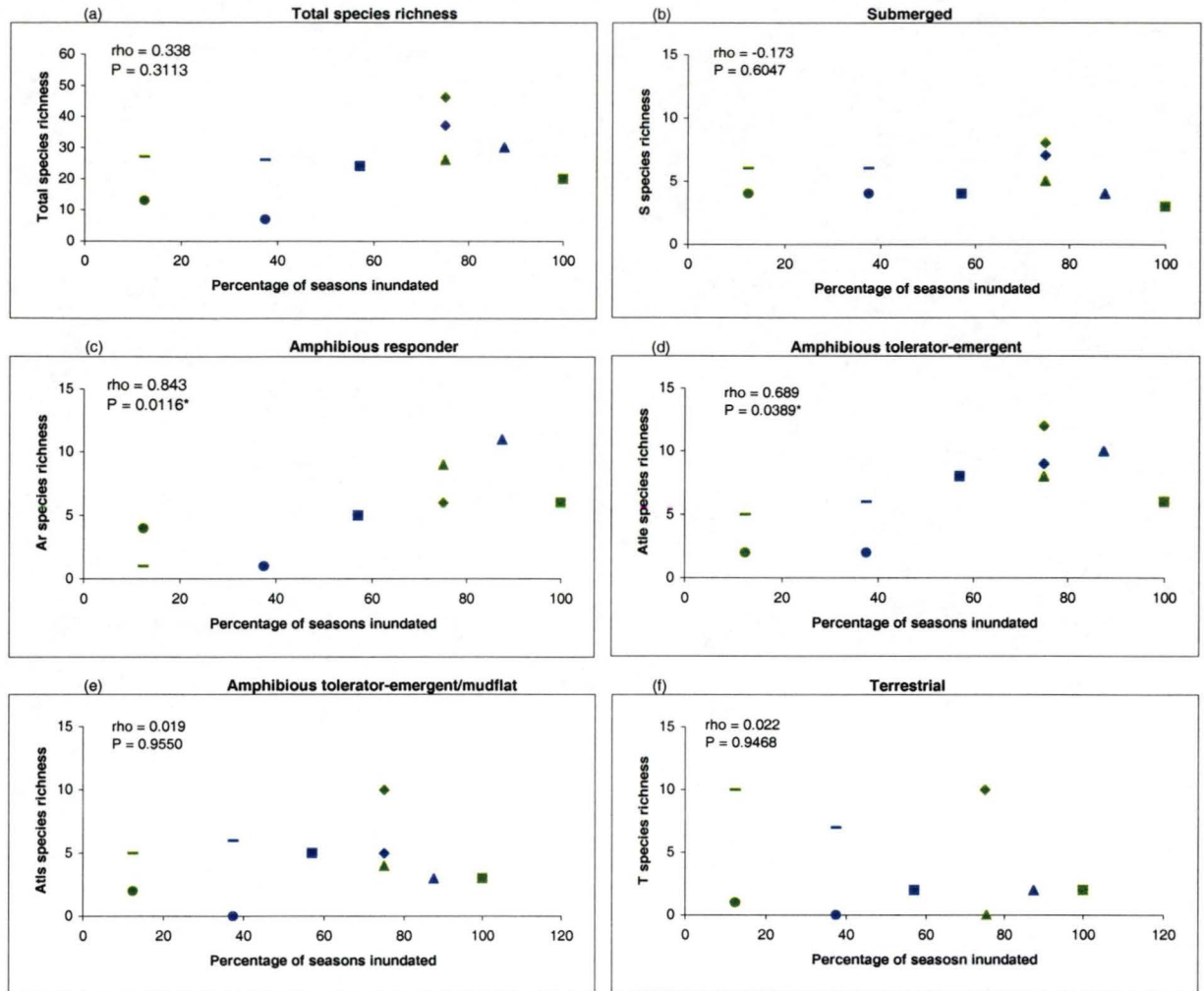


Figure 4.4 Relationship between the total combined species richness from both summer and winter 1997 experiment and the water regimes of zones represented by the percentage of seasons inundated over the period of the present study: (a) total species richness; (b) submerged, S; (c) amphibious responder, Ar; (d) amphibious tolerator emergent, Atle; (e) amphibious tolerator-saturated mudflat, Atls; and (f) terrestrial, T. (Symbols: Big Punchbowl *Baumea rubiginosa*: outer = ●; Aquatic = ●; Tin Dish: Aquatic = —; *Eleocharis acuta* = —; Middle Lagoon: *Eleocharis sphacelata* = ■; Aquatic = ■; Cherry Tree Lagoon: Aquatic = ▲; *Baumea arthropphylla* = ▲; Sandy Gate: Aquatic = ◆; *Baumea arthropphylla* = ◆).

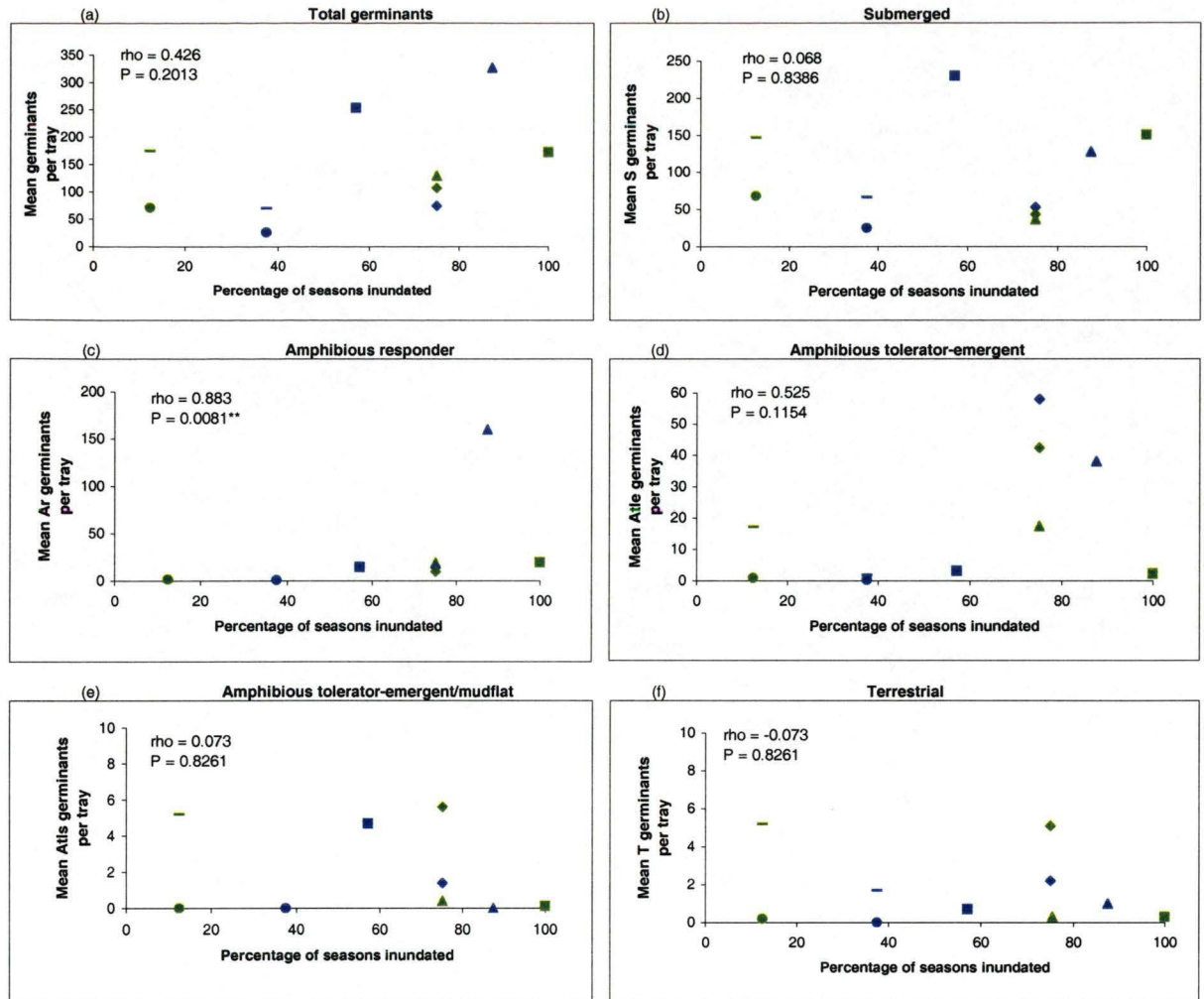


Figure 4.5 Relationship between the mean germinants per tray from both summer and winter 1997 experiment and the water regimes of zones represented by the percentage of seasons inundated over the period of the present study: (a) total species richness; (b) submerged, S; (c) amphibious responder, Ar; (d) amphibious tolerator emergent, Atle; (e) amphibious tolerator-saturated mudflat, Atls; and (f) terrestrial, T. (Symbols: Big Punchbowl *Baumea rubiginosa*: outer = ●; Aquatic = ●; Tin Dish: Aquatic = —; *Eleocharis acuta* = —; Middle Lagoon: *Eleocharis sphacelata* = ■; Aquatic = ■; Cherry Tree Lagoon: Aquatic = ▲; *Baumea arthropphylla* = ▲; Sandy Gate: Aquatic = ◆; *Baumea arthropphylla* = ◆).

Table 4.27 Summary of Spearman's rank correlation analyses of seed bank variables and water depth. The top figure is the correlation coefficient, the lower one the probability level: ns = not significant (>0.05).

Dependent variables	L-T DRY		FLUC	S-PERM		
	BP	TD	MID	CTL	CTL (aquatic zone only)	SG
Species richness						
Total	ns	ns	-.787 < 0.0001	ns	-.826 0.0195	-.633 0.0090
Angiosperm	ns	ns	-.818 < 0.0001	ns	-.758 0.0321	-.586 0.0157
Charophyte	ns	ns	ns	ns	ns	ns
Individual germinants						
Total	-.603 0.0129	-.645 0.0078	ns	ns	ns	ns
Angiosperm	ns	-.739 0.0023	ns	ns	ns	ns
Charophyte	-.620 0.0106	ns	ns	ns	ns	ns

LT-DRY = long-term dry, FLUC. = fluctuating, S-PERM = semi-permanent.

BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate.

Soil depth

Big Punchbowl

Big Punchbowl has a large buried charophyte seed bank. However, this was not the case for angiosperm species. A total of 7 species germinated from the depth samples, 3 monocot and 4 charophyte species (Table 4.28). These species constituted 67% of the total species that germinated from this zone in the larger seed bank experiments, summer and winter 1997. Within the four depth categories the largest number of individuals germinated from the 5 - 7.5 cm depth. However, of these 99.2% were charophytes. The smallest number of individuals germinated from the top 2.5 cm. However, the largest number of monocotyledons germinated from this depth. As with the larger experiments the charophytes again dominated the number of germinants. Of the charophytes only *Chara preissii* germinated in all four depths. *Nitella gelatinifera* var. *microcephala* was the most abundant charophyte. Within the monocots only *Baumea rubiginosa* (2) and the unidentified monocot species germinated at any depth with *B. rubiginosa* germinating from the 7.5-10 cm category. During both of the larger germination experiments, summer and winter 1997, only 7 individuals of *Baumea rubiginosa* germinated and these were all from the summer 1997 experiment. So the low number of germinants in this study is comparable with the two larger studies. However, as it germinated at the lower depth it indicates that *Baumea rubiginosa*, although present in small numbers, may have a long lived seed bank. The low percentage of monocotyledons that germinated in this experiment (2%) is similar to winter 1997 where only 4.5% of the germination from this zone was monocotyledon individuals.

A one-factor ANOVA was performed with DEPTH as the factor to determine if there was any significant differences between the number of species and total individuals that germinated at each depth. The results showed that there was no significant difference in the number of species that germinated between each depth ($F = 2.926_{3,20}$, $P = 0.998$). However, there was a significant difference in the number of individuals that germinated ($F = 5.376_{3,20}$, $P = 0.0255$). A Fisher's *post hoc* test showed the top 2.5 cm had significantly lower germinants than both the 2.5 - 5 cm (Fisher's LSD, $P = 0.0190$) and 5 - 7.5 cm (Fisher's LSD, $P = 0.0061$) depths. These differences were due to the charophyte germinants rather than the monocotyledons.

Table 4.28 Species and total individuals germinating in depth experiment from Big Punchbowl.

Species	Depth (cm)				Total
	0-2.5	2.5-5.0	5.0-7.5	7.5-10.0	
<i>Baumea rubiginosa</i>	0	0	1	0	1
Monocot unidentified	2	1	0	0	3
<i>Potamogeton tricarinatus</i>	2	0	0	0	2
<i>Chara preissii</i>	4	3	1	4	12
<i>Nitella gelatinifera</i> var. <i>gelatinifera</i>	12	55	38	0	105
<i>Nitella gelatinifera</i> var. <i>microcephala</i>	0	40	86	47	173
<i>Nitella subtilissima</i>	0	0	3	0	3
Total number of individuals	20	99	129	51	299
Total number of species	4	4	5	2	7
Number of new species	4	1	2	0	
Cumulative percentage	57	71	100	100	
Percentage Angiosperm individuals	20	1	1.6	0	2
Percentage Charophyte individuals	80	99	98.4	100	98

Cherry Tree Lagoon

In contrast to Big Punchbowl, Cherry Tree Lagoon has a large buried seed bank which was dominated by both angiosperm and charophyte individuals. A total of 18 identified species germinated with 5 dicotyledon, 9 monocotyledon and 3 charophyte species (Table 4.29). These species constitute 62% of the total species that germinated from this zone in the larger winter 1997 experiment. The two middle depth categories (2.5 - 7.5 cm) had the highest number of germinants.

Several species germinated through the soil profile, with 7 species germinating from all the depth categories and 4 species from 3. Several of these species correspond with the most abundant taxa that germinated from the *Baumea arthropphylla* zone during winter 1997 – that is, *Myriophyllum simulans/variifolium*, *Villarsia reniformis*, *Elatine gratioloides*, *Juncus holoschoenus*, *Nitella gelatinifera* and *Isolepis fluitans*. However, some non-abundant species, such as *Utricularia dichotoma* and *Isolepis cernua*, also germinated through the profile

The ratio of angiosperm and charophyte germinants changed down the profile. Angiosperm germinants dominated the 2.5 - 5.0 cm category, whereas, charophytes dominated both of the two lower categories, with the largest dominance in the deepest category (67 to 33%). In the top 2.5 cm the two types were more even (49, angiosperm to 51% charophyte). This was comparable with the larger winter 1997 experiment where the percentages of each were 51 for angiosperm and 49 for charophytes.

One species germinated in this experiment that was not seen in either summer or winter 1997 experiments. *Trithuria submersa* germinated between the soil categories 2.5-7.5 cm. This was the first record during the present study of *Trithuria submersa* at Cherry Tree Lagoon. It was, however, recorded in 1978 by Kirkpatrick and Harwood (1981).

A one-factor ANOVA was performed with DEPTH as the factor on the species richness and total individual data per transect. The results showed that there were no significant differences between the soil depth categories and both the number of species ($F = 1.344_{3,20}$, $P = 0.3271$) and total germinants ($F = 1.386_{3,20}$, $P = 0.3155$).

Table 4.29 Species and total individuals germinating in depth experiment from Cherry Tree Lagoon (* = introduced species).

Species	Depth (cm)				Total
	0-2.5	2.5-5.0	5.0-7.5	7.5-10.0	
<i>Chenopodium glaucum</i> *	1	0	0	0	1
<i>Elatine gratioloides</i>	6	13	8	4	31
<i>Myriophyllum simulans/variifolium</i>	38	140	63	19	560
<i>Utricularia dichotoma</i>	5	6	1	1	13
<i>Villarsia reniformis</i>	2	4	3	0	9
<i>Agrostis avenacea</i>	2	0	0	0	2
<i>Baumea arthropphylla</i>	1	3	0	1	5
<i>Isolepis cernua</i>	1	4	3	0	8
<i>Isolepis fluitans</i>	18	14	3	0	35
<i>Juncus holoschoenus</i>	50	45	63	4	162
<i>Juncus pallidus</i>	1	0	0	0	1
<i>Potamogeton tricarinatus</i>	0	1	0	0	1
<i>Trithuria submersa</i>	0	4	2	0	6
<i>Chara preissii</i>	10	9	28	10	57
<i>Nitella gelatinifera</i> var. <i>gelatinifera</i>	102	24	27	7	160
<i>Nitella gelatinifera</i> var. <i>microcephala</i>	19	128	177	60	384
Monocot unidentified	0	0	16	8	24
Poaceae sp. unidentified	0	1	0	0	1
Dicot unidentified	0	1	0	1	2
Total number of individuals	256	397	394	115	1162
Total number of species	14	14	11	9	18
Number of new species	15	3	0	0	
Cumulative percentage	77.8	100	100	100	
Percentage angiosperm	48.8	59.4	41.1	33	48.3
Percentage charophytes	51.2	40.6	58.9	67	51.7

Differences due to germination treatment

The numbers of species and germinants varied with germination treatment in all seed bank experiments (Figure 4.6). Some species germinated in both the mudflat and drowned conditions and others in only one regime (Appendix III). A Sørensen's index of similarity for the combined summer and winter 1997 experiments indicated a 60% similarity in species composition between the mudflat and drowned germination treatments.

Significantly more angiosperm species and individuals germinated in mudflat conditions, whereas, charophyte germination was significantly higher in the drowned conditions (Table 4.30). This pattern was common to trays that either had: a) both treatments had run consecutively and were not independent (winter 1997), or b) both treatments were independent (Winter 1998; Table 4.30). Similarity between the species composition of the mudflat and drowned treatments of the sub-set of trays compared from winter 1997 and 1998 were 43 and 41% respectively.

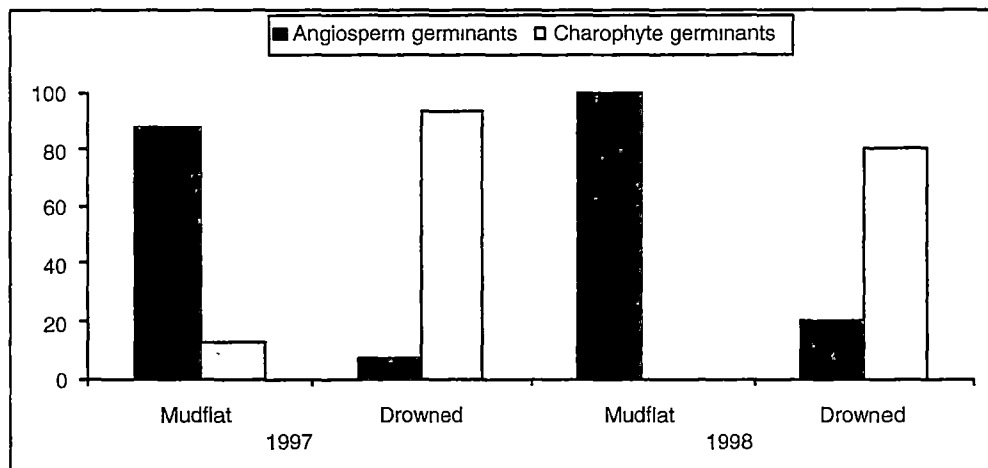


Figure 4.6 Comparison of the percentage of angiosperm and charophyte germinants in the mudflat and drowned treatments for a) combination of summer and winter 1997 soils; and b) winter 1998 soils.

Table 4.30 Results of t-tests comparing the difference in between trays with varied germination treatments from winter 1997 and winter 1998.

Source of variation	Winter 1998 (10 weeks)			Winter 1998 (20 weeks)		
	P-value	Mudflat	Drowned	P-value	Mudflat	Drowned
Species richness						
Total	0.1408	7.8	5.7	<0.0001	11.1 *	5.3
Angiosperm	0.0007	7.3 *	2.8	<0.0001	11.1 *	2.9
Charophyte	<0.0001	0.5	1.9 *	<0.0001	0	2.4 *
Individuals germinants						
Total	0.7075	154.8	113.0	0.7971	196.4	126.7
Angiosperm	0.0007	116.8 *	12.1	<0.0001	196.4 *	24.9
Charophyte	<0.0001	4.9	97.5 *	<0.0001	0	101.8 *

* = treatment that is significantly higher; data reported are the treatment mean of the 18 trays sampled.

Discussion

All wetlands studied had a viable seed bank and therefore have a potential for future regeneration of species. The soil seed densities were within the middle to the lower end of the range of densities reported for freshwater wetland systems (see Leck, 1989, Table 1; Finlayson *et al.*, 1990; Brock and Rogers, 1998; Bonis *et al.*, 1995; Keddy and Reznicek, 1986; Le Page and Keddy, 1998). However, they were generally greater than those reported for salt marsh, swamp, bog and lake environments (Moore and Wein, 1977; Kadlec and Smith, 1984; Gunther *et al.*, 1984; Haag, 1983) and much lower than those found in cultivated rice fields (McIntyre, 1985). Charophyte germination was generally lower than was reported for the Australian New England Tablelands (Brock and Casanova, 1990; Casanova, 1993).

Many of the freshwater wetland environments that had greater seed bank densities than those of the present study were dominated by annual angiosperm species and characterised by either seasonal or frequently fluctuating water regimes (e.g. prairie marshes, van der Valk and Davis, 1978, 1979; freshwater tidal wetlands, Leck and Graveline, 1979; Leck and Simpson, 1987b, 1994; and seasonal wetlands, Keddy and Reznicek, 1986; Bonis *et al.*, 1995). Perennial angiosperm species were more abundant than annuals, in both species richness and number of germinants in the seed banks of the present study (Table 4.13; Appendix IV). This pattern has been considered to characterise seed banks of wetlands with non-predictable water regimes (Leck, 1989).

The summer and winter 1997 seed bank experiments gave very similar results. As very little reproductive input was observed in the extant vegetation between the two seasons, these results indicate that a high proportion of species can remain in the seed bank for at least a few months. The depth profile experiment supported this result and also indicated that many of the species within the wetlands could remain viable over time and thus persist in the soil over much longer periods.

In contrast to the results of other studies (Britton and Brock, 1994; Maas and Schopp-Guth, 1995; Thompson and Grime, 1979), the seasons of wetting and drying did not greatly affect the germination of most of the aquatic perennial angiosperm species found in the seed bank of the five wetlands. This may indicate that water presence or absence

may be an important germination cue for the aquatic perennial species within the 5 wetlands which overrides any seasonal cues generally associated with terrestrial systems.

A decrease in numbers of annual and exotic germinants between summer and winter 1997, could be due to either a) a germination event (output); and/or b) seed dormancy (Bonis *et al.*, 1995; Silvertown, 1982; 1988); or c) variation between the conditions in the glasshouse between each experiment. Seventy-five percent of the annual species that showed a decrease in germination between the summer 1997 and winter 1997 soils were exotic terrestrial species adapted to drier environments.

As most terrestrial species will not germinate underwater it can be said that flooding of a wetland enforces dormancy (i.e. 'dormancy thrust upon them', Harper, 1959; Harper, 1977; Silvertown, 1982) on terrestrial seeds which then remain in the seed bank until a natural drawdown event occurs and conditions for germination become more suitable. The mudflat treatments in the summer and winter 1997 seed bank experiments mirrored a drawdown event in two different seasons: a) 'autumn/early winter' for summer 1997 soils; and b) 'spring/early summer' for winter 1997 soils.

Suitable field conditions for germination of annual and exotic terrestrial species, between the two sampling periods, occurred in only Tin Dish and Big Punchbowl. Big Punchbowl had very few terrestrial species, in both the seed bank and extant vegetation, and no evidence of increased germination of terrestrial species (output) was evident between the two seasons. However, an increase in terrestrial exotic species occurred between the two sampling periods in the extant vegetation of Tin Dish, where conditions changed from inundated to saturated/dry throughout most areas of the wetland (see Chapter 5). This indicated that a germination event (output) of terrestrial exotic species may have occurred in Tin Dish. As no reproductive input of similar species was evident over the same period (pers. observation) this would explain the decrease in germination of terrestrial annual and exotic species in this wetland and indicate the 'transient' nature of these species within the seed bank (i.e. do not remain in the soil for longer than 1 year, *sensu* Thompson and Grime, 1979). Transient seed banks are characteristic of annual dominated wetland systems (Leck and Simpson, 1987a) and many annual terrestrial species (Symonides, 1988). They are generally associated with predictable habitats where annual probability of successful reproduction is high (Symonides, 1988).

However, the pattern of increased autumn germination (from summer soils) of both annual and exotic species also occurred in wetlands where a germination event was not obvious, for example, the native annual *Agrostis avenacea* and exotic species *Callitriche stagnalis* and *Cotula coronopifolia*. This indicated that seed dormancy may also contribute to seasonal differences in the germination of annual and exotic species. A preference for autumn germination has been observed for many exotic and annual species (Silvertown, 1982). Early germination gives a competitive advantage especially if subsequent conditions remain favourable for growth and establishment (Grubb, 1977).

For charophytes, an increase in germination between summer and winter 1997 could be due to either a) a reproductive event (input); and/or b) seed dormancy (Bonis *et al.*, 1995; Forsberg, 1965; Shen, 1966); or c) variation between the conditions in the glasshouse between each experiment. Analysis of charophyte input between the sampling seasons indicated that three out of the five wetlands (Cherry Tree Lagoon, Middle Lagoon and Tin Dish) had potential oospore replenishment. Both Big Punchbowl and Sandy Gate would not have been replenished between seasons. However, all wetlands had an increase of charophyte germination in the winter 1997 experiment. This indicated that more than just oospore replenishment may have influenced the increased charophyte germination in the winter 1997 experiment.

Similar seasonal effects on germination of Charophyte species have been observed (Casanova, 1993; Britton and Brock, 1994; Casanova and Brock, 1996). Casanova and Brock (1998) found that although a range of germination patterns and timing was evident between charophyte species, all species had more oospores germinating in warm/long day treatments than cold/short day treatments. Similarly, in the present study, greater charophyte germination occurred from the soils germinated in the drowned conditions between summer and early autumn (warm/long day) than those germinated in similar conditions between winter and early spring (cold/short days). This indicated that the increased germination numbers of charophyte species may have been due to different germination conditions.

Casanova (1993) found that only a small percentage of oospores germinated from the total viable charophyte seed bank during a germination event with early germination being selected when the stimulus for germination coincides with a high probability of successful establishment. This corresponds with the present study in that a small

proportion of total oospores germinated during winter and early spring prior to summer when there is a probability that the wetland may dry out and establishment was not possible. Conversely, greater charophyte numbers germinated in summer and early autumn prior to winter when generally the wetland remains inundated and successful establishment could occur. The extended germination shown by charophyte species, as well as other aquatic species in the seed banks, is generally selected for habitats that experience unpredictability of germination stimulus, such as the range of wetting and drying experienced by these temporary wetlands.

Greater differences were found between wetlands than between zones within wetlands. Differences in seed bank variables at a wetland scale would be expected due to the variable nature of the wetlands in both water regime and vegetation types. The main difference between wetlands was that the long-term dry wetlands, Big Punchbowl and Tin Dish, were generally lower in both number of species and individuals that germinated per tray than the semi-permanent wetlands, Cherry Tree Lagoon and Sandy Gate. However, this was related more to differences in angiosperm species than charophyte species (Table 4.15; Table 4.19). Therefore, the results for angiosperm species on a wetland scale, supported the hypothesis that seed bank species richness and germinant numbers would be reduced in wetlands with a more permanently dry environments (Keddy and Reznicek, 1982, 1986; Thompson, 1992) and that hydrological disturbance (i.e. wetting and drying events) is important in maintaining species richness in temporary wetlands (Brock and Rogers, 1998). The difference in species richness of the semi-permanent and long-term dry wetlands were similar to those found by Brock and Britton (1995) for Australian upland wetlands, where species richness was significantly higher in a relatively undisturbed wetland (near-permanent) than one with a history of hydrological modification.

The type of vegetation did not significantly influence species richness within wetlands, a phenomenon noted in other wetland studies (van der Valk and Davis, 1976, 1978; Ungar and Riehl, 1980; Finlayson, *et al.*, 1990; ter Heerdt and Drost, 1994). This similarity could be related to either or both of high disseminule mobility within wetlands (Sculthorpe, 1967; Hutchinson, 1975; van der Valk, and Davis, 1976a; Schneider and Sharitz, 1986; Cook, 1987; Grelsson and Nilsson, 1991) or accumulation of seeds in the soil when hydrological conditions differed from those during sampling.

The water regime of a zone did not affect total species richness or number of germinants. These results are consistent with those of Brock and Rogers (1998). They suggested that species could maintain themselves, due to persistence in the seed bank, over a range of water regimes. This was evident in the functional group analyses, where water regime of the zones did not affect the number of species or individuals that germinated from the submerged, amphibious tolerator-emergent (species only), amphibious tolerator-saturated/mudflat and terrestrial groups. This indicated that the presence of these 'type' of species in the seed bank did not depend on water regime.

High number of terrestrial species were found in zones with long-term dry, as well as semi-permanent water regimes. Similar to the wetlands studied by Ungar and Riehl (1980) the number of terrestrial species in the seed bank appeared to be more related to whether a wetland was adjacent to pastoral land (Table 4.6) rather than its water regime. High numbers of submerged species were also found in all water regimes. This would be expected due to the inability of this group to survive in the extant vegetation during dry periods (Brock and Casanova, 1997). An abundant persistent seed bank is their mechanism for survival of adverse conditions.

Water regime appeared to affect the number of both species and germinants of the amphibious responder group, with higher numbers being associated with wetter habitats. This pattern was also evident for germination of the amphibious tolerator-emergent group. These results correspond to the predictions proposed by Brock and Casanova (1997) in wetlands with altered water regimes who suggested that wetlands with a permanently dry water regime would have a reduction in amphibious species.

Less germination in long-term dry environments may be taken to indicate that these groups do not persist within the seed bank. However, the depth experiment of the present study and other seed banks studies (Brock, 1991; Brock and Britton, 1995; Smith, 1998) have shown that both amphibious responder and tolerator-emergent species, such as *Myriophyllum* spp. and *Juncus* spp. can have persistent seed banks. Therefore, other factors may have reduced this 'type' of species within the seed bank of zones within the long-term dry wetlands.

In highly variable environments, such as those in the present study, the seed bank may receive a number of germination stimuli before seed bank replenishment. Although, a single germination event may not totally deplete the seed bank, repeated germination

events without replenishment may exhaust or diminish certain species (Brock and Rogers, 1998). In both Tin Dish and Big Punchbowl, germination events were observed over the period of the present study, especially for amphibious responder species, such as *Potamogeton tricarinatus* and *Myriophyllum* spp. These short-term events may also have occurred within the dry period prior to the commencement of this study and therefore, depleted the seed bank of these groups. This would explain the lower germinant numbers of these species. However, it may not explain the lower species richness of these groups in these wetlands. It may be that both Tin Dish and Big Punchbowl are naturally low in species from this group.

As expected, significantly more angiosperm species and individuals germinated during the mudflat conditions, whereas, charophyte species and germinants were significantly higher in the drowned conditions (Figure 4.6). Similarly, as expected, many aquatic species were found to germinate in both mudflat and drowned treatments (68% species composition similarity), with most terrestrial species only germinating in the mudflat conditions. The differences in germination between the mudflat and drowned treatments of this study were similar to those reported in other studies that have used similar techniques for germinating wetland seed banks (van der Valk and Davis, 1978; van der Valk, 1981; Casanova and Brock, 1990; Finlayson *et al.*, 1990; Skoglund and Hytteborn, 1990; Brock *et al.*, 1994; Britton and Brock, 1994).

Similarity in the patterns of germination in trays that had either: a) treatments were not independent, i.e. running consecutively (winter 1997); or b) treatments were independent of each other (winter 1998; Table 4.30) indicated that the experimental design used for the larger experiments was adequate to determine the characteristics of the seed banks of the wetlands.

One interesting observation between the two experiments is that, although, the winter 1997 soils were germinated for a longer period than those of the winter 1998 experiment (i.e. 20 weeks rather than 10 weeks), both experiments had a similar mean number of charophyte germinants. This indicated that a period of saturation prior to inundation may promote charophyte germination after flooding occurs. This is consistent with results of Brock and Britton (1995) who suggested that a fluctuating water regime may stimulate a greater number of germinants. However, simultaneous experiments, with soils taken during the same season, would be needed to confirm if this is in fact so for Tasmanian wetland seed banks.

Big Punchbowl, with a low surface seed bank, did not have significantly more seed numbers germinating down the soil profile. Both wetlands sampled, Big Punchbowl and Cherry Tree Lagoon, had seed bank depth profiles similar to those found in the larger seed bank experiments, using only the top 2.5 cm of soil.

In all depth categories, the seed bank of Big Punchbowl was dominated by charophyte germinants and had a low angiosperm component. This indicated that the seed bank of Big Punchbowl, may have always been naturally low in angiosperm germinants, despite what would have been expected considering the productive aquatic flora observed in the past.

In contrast, Cherry Tree Lagoon, as in the larger experiments, had a species rich, abundant seed bank, primarily dominated by angiosperm species, but also with a large charophyte component, within most of its soil depth categories. However, in the last 7.5 - 10 cm charophyte species dominated the germination. Therefore, unlike Big Punchbowl, Cherry Tree Lagoon has a substantial buried seed bank.

As depth distribution within a seed bank can in some part be a measure of the longevity of the seed bank (Leck, 1989; Keddy *et al.*, 1989), the results of the depth study indicate that many species within the seed banks of both Cherry Tree Lagoon and Big Punchbowl have long-lived persistent seeds. This was relevant to both angiosperm and charophyte species. The presence of a persistent seed bank in the wetlands of the present study is consistent with other seed bank studies of wetlands with unpredictable water regimes (Sculthorpe, 1967; van der Valk and Davis, 1976a; Keddy and Reznicek, 1982; Skoglund and Hytteborn, 1990; Haukos and Smith, 1993; Brock and Britton, 1995; Maas and Schopp-Guth, 1995; Brock and Rogers, 1998; Brock, 1999).

Chapter 5

Community Dynamics

Introduction

Plant communities in wetlands

Plant communities in wetlands are typically described as distinct zones or bands of vegetation that follow shoreline contours using either dominant plant species or life form descriptors (Spence, 1982; Sculthorpe, 1967; Hutchinson, 1975; Pederson and van der Valk, 1984; Kirkpatrick and Harwood, 1983a; Kirkpatrick and Harris, 1999; Boulton and Brock, 1999; Brock *et al.*, 2000).

Generally, these vegetation zones consist of plant species distributed independently along environmental gradients, such as water depth or salinity, with each species surviving under a specific set of environmental conditions (Swindale and Curtis, 1957; Mendossian and McIntosh, 1960; Beschel and Weber, 1962; Kadlec and Wentz, 1974; van der Valk and Davis, 1976b; Spence, 1982; van der Valk, 1982; Pederson and van der Valk, 1984; Wilson and Keddy, 1985; Keddy and Reznicek, 1986; Josselyn *et al.*, 1990; Brinson, 1993; Brownlow *et al.*, 1994; Brock and Casanova, 1997; Coops *et al.*, 1996; Casanova and Brock, 2000).

As environmental conditions change, plant species are redistributed as populations not adapted to the new conditions are eliminated and other more adapted species become established (Pederson and van der Valk, 1984). Recruitment occurs from buried seed reserves (van der Valk and Davis, 1978; Leck, 1989; Hutchinson and Russell, 1989; Brock and Britton, 1995; Brock and Casanova, 2000), buried vegetative propagules (perennation; Sculthorpe, 1967; Brock and Casanova, 1991; Grace, 1993; Spencer and Ksander, 1997; Crosslé, 1998), and dispersal of propagules (Cook, 1987; Eriksson, 1992; Wainwright, 1997).

Vegetation communities can change both qualitatively, that is, floristically, and quantitatively, that is, in abundance of species and species richness (Pederson and van der Valk, 1984). Van der Valk (1984) separated vegetation changes into three separate

phenomena: a) succession (i.e. the establishment of new species with the extirpation of existing species); b) maturation (i.e. the growth of individuals in established populations); and c) fluctuation (the year-to-year changes in density or size of individuals within established populations due to short-term changes in environmental conditions). All attributes of vegetation change (i.e. succession, maturation, fluctuation) are the result of changes within individual populations of species which make up the vegetation community (Pederson and van der Valk, 1984).

Factors affecting community dynamics in wetlands

Vegetation dynamics of communities reflect the life history strategies of individual species, interaction between species, and responses of species to environmental conditions (Leck and Simpson, 1994). Many environmental factors, both biotic and abiotic, have been studied in relation to community dynamics in wetlands, for example, sediment properties (Barko *et al.*, 1991; McComb and Qui, 1998), salinity (Lieffers, 1984; Galinato and van der Valk, 1986; Allison, 1992), fire (Bowles *et al.*, 1996), and grazing (Fossati and Pautou, 1989; Middleton, 1990; Llewellyn and Shaffer, 1993; Bridle, 1999). Water regime has been the most widely studied environmental influence due to its known profound effects on the reproduction; growth and distribution of aquatic plants (van der Valk, 1987; Blom *et al.*, 1994; Britton and Brock, 1994; Rea and Ganf, 1994a, 1994b; Casanova and Brock, 2000; Boon *et al.*, 1996) it has become the most recognised major determinant for plant community dynamics and patterns of zonation in wetlands (Spence, 1982; Sculthorpe, 1967; Hutchinson, 1975; Howard-Williams, 1975; Gosselink and Turner, 1978; Conner *et al.*, 1981; Day *et al.*, 1988; Grillas, *et al.*, 1990; Casanova and Brock, 2000; Robertson, *et al.*, 2001).

Water regime is a term generally used to describe the temporal pattern of the presence and absence of water in a wetland and takes into account the timing, frequency, duration, depth and variation of flooding and drying events (Bunn *et al.*, 1997; Brock *et al.*, 2000). It is thought to be an important natural disturbance within wetland environments (e.g. van der Valk, 1981; Keddy and Reznicek, 1982, 1986; Gopal, 1986; Spence, 1982; Lieffers, 1984; Briggs and Mather, 1985; Mitchell and Rogers, 1985; Day *et al.*, 1988a; Casanova and Brock, 2000). Changes in water levels, coupled with corresponding changes in the vegetation communities, can be both rapid and substantial within wetland systems (Howard-Williams, 1975). This contrasts with terrestrial systems, in which recovery after disturbance can take years. Therefore, lentic

communities are ideal for the study of vegetation dynamics, especially where short term studies are required (Howard-Williams, 1975).

Studies relating community dynamics to water regime

Community dynamics within wetlands have been studied with relation to water regime, both overseas and within Australia. Difference in vegetation communities between areas with varied water regimes (in terms of water depth and fluctuations) have been demonstrated in both natural (Lieffers, 1984; Conner *et al.*, 1981; Rea and Ganf, 1994a; Fojt, 1994; Brock and Rogers, 1998; Busch, *et al.*, 1998) and regulated or constructed wetland systems (Wilcox and Meeker, 1991, 1992; Reinartz and Warne, 1993), as well as through experimentation (Weiher and Keddy, 1995; Nielson and Chick, 1997; Casanova and Brock, 2000; Robertson *et al.*, 2001).

a) water depth

Water depth is commonly recognised as a primary physical factor that varies along elevation gradients in many wetland habitats (Spence, 1982). Studies have demonstrated that increased water depth depletes soil oxygen (Ponnamperuma, 1972; 1984), which in turn affects plant metabolism and growth through such mechanisms as reduced photosynthesis, altered nutrient uptake, and hormonal imbalances (Mendelssohn and Burdick, 1988; Howard and Mendelssohn, 1995). In terrestrial systems inundation is generally inhibitory to plant growth. However, in aquatic systems many plants are stimulated by such conditions (Jackson and Drew, 1984; Howard and Mendelssohn, 1995).

The direction of growth response of aquatic species to changes in water depth has been shown to vary between species. For example, an increase in water depth has shown to either increase (Wooten, 1986; Grace, 1989; Lieffers and Shay, 1981; Rea and Ganf, 1994a, 1994b) or decrease (Selinskar, 1988; McKee and Mendelssohn, 1989) biomass of aquatic species.

Dry conditions

A number of studies have reported effects of drawdowns and dry periods on wetland plant communities (Howard-Williams, 1975; van der Valk and Davis, 1976b, 1978; van der Valk, *et al.*, 1989; Brock *et al.*, 2000; Casanova and Brock, 2000). In many

wetlands a drawdown event is considered important for the re-establishment of emergent species and the maintenance of a diverse wetland community (Harris and Marshall, 1963; Weller and Fredrickson, 1974; van der Valk and Davis, 1978; Pederson and van der Valk, 1984; Keddy and Reznicek, 1986; van der Valk, *et al.*, 1989; Casanova and Brock, 1997; Crosslé, 1998). However, it has been predicted that increasingly long dry periods will decrease aquatic species richness within wetland communities (Keddy and Reznicek, 1982, 1986; Thompson, 1992; Brock *et al.*, 1999; Brock and Casanova 1997).

Inundated conditions

Rising water levels change soils from oxic to anoxic (Ponnamperuma, 1972). Organic matter and fine particles (e.g. silt and clay) may be removed by water circulation (Keddy and Reznicek, 1986). Simultaneously, mudflat species will disappear (e.g. Salisbury, 1970; van der Valk, 1981) and many aquatic species will germinate or propagate vegetatively under shallow water. However, these species may gradually die in deeper water (Harris and Marshall, 1963, van der Valk and Davis, 1978; Casanova and Brock, 1997; see Keddy and Reznicek, 1986). The vegetation changes following permanent flooding have been related to the type of vegetation originally present and the absolute increase in water depth (Sjöberg and Danell, 1983). Several studies have considered water depth to be the more important of those two factors in separating communities (Munro, 1967; Wilcox and Simonin, 1987). However, Casanova and Brock (2000) found that water depth was the least important factor in differentiating communities that established from the seed bank in experimental pots. They concluded that once a site is flooded, plants adapted to inundated conditions would be present regardless of water depth and that the duration of flooding was more important than the depth of flooding in the segregation of plant communities.

b) duration of inundation

Water level fluctuations are a natural form of disturbance in many wetlands. The role of natural disturbance in promoting vegetation change has been discussed by Grubb (1977) and Grime (1979; see Keddy and Reznicek, 1986). Water levels in wetlands can fluctuate on many time scales. Seasonal fluctuations are likely to have effects on the vegetation community that are very different from fluctuations with a period of a decade or longer. In the latter case, population responses can occur, with some species

surviving only as buried seeds, and others temporarily exploiting the existing conditions (Keddy and Reznicek, 1986).

Josselyn *et al.* (1990) found that the controlling factor in determining the location of plant communities along the moisture gradient appears to be the duration of saturation and anaerobic soil -conditions. In a wetland where saturated (inundated) soils were present all year round, obligate wetland plants dominated exclusively. Obligate wetland species also remained dominant throughout the year at a seasonal freshwater marsh, despite a six-month dry spell. The 4-5 months of anaerobic conditions were sufficient to exclude many of the facultative wetland and all of the non-wetland plants from this site (Josselyn *et al.*, 1990). However, as the period of inundation decreased, more facultative and upland species were present. Many of these species were annuals and germinated rapidly upon the first rainfall in the winter but died after the onset of the dry season. Perennial wetland species, persisted throughout the dry season even though the soils were dry and aerobic.

d) timing

Several studies have investigated the role of timing of flooding and drying events determining the distribution of communities (Hughes, 1990; Brock *et al.*, 2000; Robertson, *et al.*, 2001). Brock *et al.* (2000) demonstrated, in experimental wetlands, the differences in vegetation communities that establish after being submitted to three different flooding and drying sequences (i.e. summer-wet, winter-wet and no seasonal pattern). They found that winter-wet ponds were invaded by terrestrial species, while the summer-wet and no seasonal pattern ponds developed beds of submerged and amphibious plants.

Robertson *et al.* (2001) studied the response of aquatic vegetation within riparian wetlands of the Murray River to different seasonal flooding regimes. They concluded that spring flooding was critical for the growth of wetland macrophytes and the maintenance of macrophyte species richness.

Vegetation Cycles within wetlands

Much research into functioning of wetlands in North America has focused on cyclical disturbance (van der Valk and Davis, 1976b; 1978; 1979; van der Valk, 1981; Keddy and Reznicek, 1982; Pederson and van der Valk, 1984). Cyclic vegetation change has

been observed in prairie wetlands in the United States where seed banks are central to their long-term survival (van der Valk and Davis, 1976b, 1978, 1979). During droughts water levels drop (i.e. a drawdown event occurs), and mudflat and emergent species are recruited from the seed bank. With normal rainfall, standing water eliminates mud flat species, stops germination of emergent species, and triggers germination of submerged and free-floating species. If periods of high water continue, emergent species intolerant to these higher water levels decline (Leck, 1989; van der Valk and Davis, 1979). Similar cyclical events have been recorded in many other wetland environments throughout the world (Howard-Williams, 1975; Gopal, 1986).

Response of individual species to changes in water level

Several studies have concentrated on the response of individual species to changes in water levels (Kirkman and Sharitz, 1993; Rea and Ganf, 1994a; 1994b; Howard, and Mendelssohn, 1995; Coops *et al.*, 1996). Generally, plant responses to different water levels reflect their position along a water-depth gradient.

Within Australia, Rea and Ganf (1994b), investigated the response time after water level changes in populations of two emergent sedge species, *Eleocharis sphacelata* and *Baumea arthropphylla*. They found that *Eleocharis sphacelata* had a rapid response time with population changes matching changes in depth. However, *Baumea arthropphylla* had a slower response time with its characteristics correlated to the past water regime integrated over 6-12 months.

Use of functional groups to describe changes in vegetation structure

The 'functional group' approach has been widely used to understand community responses in relation to disturbance (Noble and Slatyer, 1977; 1980). This approach is generally based on the unique life history characteristics of individual plant species, or 'vital attributes' to determine patterns of succession at a particular site. While, initially used to deal with terrestrial communities, a functional group approach to describing community dynamics has in more recent times been applied to aquatic communities (see Chapter 3).

The functional groups, as described in Chapter 3 and used within the present chapter, were classified from criteria used by Brock and Casanova (1997) based on plant life

history responses to the variable water regimes that occur at the edge of wetlands. The resulting groups were in turn related to their ability to tolerate or respond to water presence or absence (Brock and Casanova, 1997; Casanova and Brock, 2000). The submerged group cannot tolerate drying and the terrestrial group cannot tolerate flooding, whereas the amphibious groups can either tolerate or respond to a range of wetting and drying patterns (Casanova and Brock, 1997). As the classification was based on responses to water regime, the recognised functional groups are likely to be useful in interpreting and predicting changes in community dynamics (Noble and Gitay, 1996; Casanova and Brock, 1997; Casanova and Brock, 2000).

Brock and Casanova (1997) found the distribution of species among functional groups differed between two wetlands in the Northern Tablelands, New South Wales, with varied water regimes. The more temporary wetland had a greater representation of species that preferred drier environments, whereas, the near-permanent wetland had greater representation of species within the amphibious functional groups. Brock and Casanova (1997) related these differences to the varied water regime of the two wetlands.

Casanova and Brock (2000) assessed the contribution of each species functional group to experimental plant communities that established after seed bank material from two wetlands were exposed to varying water-level treatments. They found that water regime affected the contribution of functional groups that germinated, established and became dominant in the experimental pots. Differences in community structure, with different water regimes, were related to the ability of groups to tolerate or respond to the presence or absence of water. Pots that remained dry were dominated by terrestrial species with amphibious fluctuation-tolerator species present, whereas, pots that were continually flooded were dominated by submerged species with amphibious-responder species present. Trays that were exposed to fluctuating water levels varied in their functional group representation depending on the duration of the water level fluctuation, that is, slow or rapid. Slow fluctuations (submersion > 2 weeks) were dominated by amphibious fluctuation-responder species, whereas, rapid fluctuations were dominated by both responder species if the flooding was deep and tolerator-emergent species if flooding was shallow.

Information on how aquatic plants respond to fluctuations in water levels can assist in the formulation of management strategies and predictions of the consequences of water-level regulation.

Tasmanian studies in wetland community dynamics.

Most studies of wetland macrophyte communities in Tasmania have been descriptive in nature and have focused on one point in time (Jackson, 1973; Macphail and Shepherd, 1973; Smith, 1975; Kirkpatrick, 1975; Kirkpatrick and Glasby, 1981; Kirkpatrick and Harwood, 1983a; Cameron, 1984; 1996; McDonald, 1995). Macrophyte communities are dynamic entities that change and develop over time periods ranging from seasons to many tens of hundreds of years, and most one-off community studies, due to their very nature, are not able to appreciate this. However, the opportunity for long-term studies of changes in macrophyte communities are facilitated by past records, as with those listed above.

Kirkpatrick and Harwood (1983a) described the major plant communities that occurred in 530 Tasmanian wetlands during 1978 and 1979. Visoiu (2000) investigated long-term changes that had occurred in the macrophyte vegetation communities of a sub-set of east coast wetlands surveyed by Kirkpatrick and Harwood (1983a). He related the long-term changes in macrophyte communities to 1) the impact of human modification; and 2) a lower than average rainfall over the 20 year period between studies. Between 1978-79 and 1999-2000, Visoiu (2000) recorded an increase in the proportion (presence/absence) of exotic and dry land halophytic species, and annual species adapted to drier marginal areas of wetlands. He also recorded an overall decrease in the proportion of aquatic species adapted to wetter environments.

Between wetland water regime 'types' Visoiu (2000) found that wetlands that had maintained a regular presence of water had undergone lower levels of species change (presence/absence) than less regularly inundated 'types' and that wetlands dominated by herbfield communities in 1978-79 were found to have undergone the most change.

Although, there has been no short-term dynamic studies of lentic wetland communities within Tasmania, Hughes (1990) studied the short-term dynamics caused by varying hydrological fluctuations within lotic (river) aquatic plant communities. Changes in community structure were related to high, low, and steady discharges and a simple model of aquatic community structure with varying discharge and seasons was

proposed. Higher species richness and percentage covers were recorded in summer than in winter. Higher species richness and percentage covers were also recorded during periods of low discharge than during times of high discharge.

Aims

This chapter reports the results of observations on 9 permanent plots in 11 vegetation zones over a 2 year period in Tasmanian lentic wetlands. Changes in vegetation were related to changes in hydrology with the implicit hypothesis being that vegetation change was a response to hydrological change. The analyses were undertaken for flora as a whole and for functional groups.

It would be expected that:

- greater changes in vegetation communities would occur if there was a transition between water presence (wet) and absence (dry) rather than if conditions remained either 'wet' and 'dry';
- community establishment in response to varied water level fluctuations would be directed by the functional characteristics of their component species, that is, the species ability to tolerate or respond to the presence or absence of water;
- the overall direction of change in plant communities, over the period of the study, would reflect fluctuations in water levels.

Methods

Permanent plot selection

Nine randomly selected 1 x 1 metre permanent quadrats (Austin, 1981) were established in each of the 11 vegetation zones studied at the time of seed bank collection in summer 1997 (see Chapter 4).

Data collection

Quadrats were sampled during the last month of each season from summer 1997 to spring 1998, that is, 8 sampling times over a 2 year period. Autumn 1997 was not recorded for Middle Lagoon, hence only 7 sampling times were reported for the three zones within this wetland. The following data were collected: a) floristic - the percentage cover scores for all species, using the following Braun-Blanquet cover codes: 1 = trace, 2 = < 1%, 3 = 1-5%, 4 = 5-25%, 5 = 25-50%, 6 = 50-75%, 7 = 75-100% (Whittaker, 1974; Mueller-Dombois and Ellenberg, 1974); b) the depth (cm) at the centre of the quadrat from the soil to the water surface; c) soil wetness class (saturated - if there was evidence of surface water in the top 2.5 cm and dry - if a quadrat had no evidence of surface water within the top 2.5 cm. In analyses using water depth saturated was given the value of 0.2 cm and dry 0.1 cm.

Data manipulation

It was decided to concentrate on zones as the major focus of this part of the study as it is a useful scale at which to determine differences in, and between, vegetation communities. To enable comparison between zones several types of data manipulation were used in various analyses:

a) the Braun-Blanquet cover scores recorded for the 9 quadrats within each zone were averaged for each season to give a single season score for each of the 11 zones sampled (zone x season). This gave a total of 85 zones x season combinations (8 zones x 8 seasons and 3 zones x 7 seasons). Mean scores for each season were used rather than real cover values, as this proved an effective transformation, reducing the noise created by very high values;

- c) where seasonal changes in vegetation communities were related to water levels the seasonal mean water depth, calculated from the nine quadrats within each zone, was used;
- d) for analyses comparing percentage cover the mid-point of the cover range within each quadrat was used to work out mean cover within each zone as follows: 0.1 = trace; 0.5 = <1%; 3 = 1-5%; 15 = 5-25%; 37.5 = 25-50%; 62.5 = 50-75%; and 87 = 75-100%;
- e) for both Kruskal-Wallis and ANOVA tests the transect mean data as described in Chapter 4 were used.

Species amalgamation

All species recorded were used in the analyses outlined below. However, in some cases, due to a difficulty in identifying certain taxa to species level during all seasons surveyed, species were amalgamated. They were *Chara* spp., *Nitella* spp., *Isolepis* spp., *Myriophyllum* spp., *Utricularia* spp., *Trifolium* spp., *Vulpia* spp., *Deyeuxia* spp. and *Danthonia* spp. For the classification and ordination analyses the following were also amalgamated: a) *Baumea arthropphylla* and *B. rubiginosa*; and b) all introduced Poaceae species.

Water regime 'type' category

The water regime experienced, by each vegetation zone, during both years sampled (1997 and 1998) were allocated into water regime categories based on the presence (wet) or absence (dry) of standing water during the summer and spring of that year, for example, a zone was allocated into a 'wet to wet' (W-W) category if both the summer and spring survey periods were inundated (wet), whereas, a zone was allocated into the 'wet to dry' (W-D) category if the summer survey was inundated (wet) and the spring survey was dry. The use of only spring and summer for the categorisation was possible because the classification to categories would have not been substantially changed with the inclusion of autumn and winter. Overall, four water regime categories were recognised within the zones studied: 'wet to dry' (W-D); 'dry to wet' (D-W); 'wet to wet' (W-W); and 'dry to dry' (D-D). The 'wet to wet' and 'dry to dry' water regimes were considered as hydrologically stable regimes as they remained in a similar water level condition over the one year period, whereas, the 'wet to dry' and 'dry to wet' were

considered as hydrologically disturbed regimes as changes from one water level condition to another occurred.

Data analysis

Classification

A hierarchical agglomerative analysis using a Bray-Curtis measure of association (Bray and Curtis, 1957; Faith *et al.*, 1991) and fusion using flexible UPGMA (Sneath and Sokal, 1973), with the default settings in PATN (Belbin, 1991), were used to produce a dendrogram of the 85 zone x season combinations. The resulting dendrogram gives a visual representation of clusters made up of similar zone x season combinations based on their species percentage cover. The Bray-Curtis coefficient of similarity was chosen as it has been reported to be the most robust coefficient used in ecological analyses (Faith *et al.*, 1991).

Ordination

Semi-strong Hybrid Multi-Dimensional Scaling (HMDS – SSH option in PATN) using the Bray-Curtis metric (Bray-Curtis, 1957; Belbin, 1991) was used to ordinate the zone x season averaged data. Ten random starts were used in an iterative process which converges on the best solution as determined by a satisfactorily low value of stress, typically less than 0.15. Three dimensions gave a satisfactory reduction in stress, which is a measure of information not recovered. The first two dimensions have been used to plot the results reported here. Correlation between ordination axes and species in the analyses were sought using the principal axes correlation method (PCC option in PATN). One hundred randomisations (MCAO option in PATN) were applied using a Monte Carlo approach to test which species were significantly correlated to the ordination. All species associated with the ordination of each wetland were colour coded into their functional group and plotted in the same ordination space.

Ordinations were performed using: a) the total 85 zone x season cover data combinations; and b) data from the individual zone x seasons combinations within each wetland.

Direction of change between seasons

Directionality of change between seasons over time was described using the angles between consecutive points on ordination trajectories (Hughes, 1990). The greatest possible change in direction was produced by an angle of 180° with the smallest change produced by an angle of 0° (Hughes, 1990). All angles were measured between consecutive seasonal points using the trajectories drawn for each of the 11 zones sampled (i.e. 7 or 6 angles per zone) and were divided into three categories $0-60^\circ$, $61-120^\circ$, $121-180^\circ$. A Kolmogorov-Smirnov analysis was used to test whether the angle of direction of trajectories differed from a random distribution. In this case the random distribution was taken as the probability of 2.3/7 angles (2/6 angles for Middle Lagoon) falling into each category. Thus the expected distribution of 2.3 (2) was tested against the observed distribution for each category.

The nature of change in the community over the period of the study

To determine the overall direction of change in community structure over the period of the present study the Bray-Curtis dissimilarity scores between the vegetation community found at the beginning of the study, summer 1997, and each one of the other seasons sampled within each zone were graphed. To visualise if changes in vegetation communities were associated with water levels at the time of recording, seasonal mean water depths were plotted with the Bray-Curtis scores above. From these graphs evidence of both: 1) direction of changes with water depth, for example, directional or cyclical; and 2) communities ability to "bounce" back after a dry phase, that is, its "resilience" could be assessed. Spearman's rank correlation coefficient was used to determine if the Bray-Curtis scores were related to mean water depth.

Functional group response to the direction of change of water level

To investigate the response of species within each functional group to changes in water level state (i.e. from dry to wet or wet to dry), the seasonal mean percentage cover of each species and total seasonal species richness within each functional group were plotted together with mean seasonal water depth. An increase or decrease in percentage cover with a change of water state, that is, wet-dry and dry-wet, was calculated for each species. Individual species results from each functional group were totalled to give one set of scores within each category for each functional group. Categories in this case

were: 1) an increase in percentage cover with a change in state from wet to dry; 2) an increase in percentage cover with a change in state from dry to wet; 3) a decrease in percentage cover with a change in state from wet to dry; and 4) a decrease in percentage cover with a change in state from dry to wet.

Chi-square analyses were used to determine any association between functional group and a) the number of times that taxa responded to a change in water level; and b) the direction of change associated with changes in water level using the categories outlined above.

Differences of percentage cover (dependent variable) over time were examined for both individual species and functional groups using season as the independent variable.

Community composition

Differences in plant community variables, total percentage cover and species richness (dependent variables) were examined with respect to the independent variables:

- 1) water regime category - using the data recorded during the spring seasons at the end of each water regime type;
- 2) season - using 1997 data from zones that had experienced a stable water regime, that is, 'wet to wet' or 'dry to dry'.

Difference in community composition, in terms of functional group representation, was examined using the functional group percentage cover and species richness (dependent variables) recorded within each zone during the spring seasons at the end of each water regime category (independent variable).

Differences in the magnitude of change in community structure were examined with respect to water regime type (independent variable) using the Bray-Curtis scores (as described in the ordination and classification section above) between the vegetation communities recorded in the beginning (summer) and end (spring) seasons of each year (dependent variable).

Where data could be transformed to a normal distribution a one-factor ANOVA was reported and where a significant result was found ($P < 0.05$) a Fisher's LSD *post hoc* was used to determine where the differences occurred.

Results

The extant flora

Ninety-four species of angiosperm and two charophyte taxa (*Nitella* and *Chara* spp.) were recorded in the permanent quadrats between summer 1997 and spring 1998 (Table 5.1; Appendix V). The highest numbers of species were found in the families Poaceae (21 species) and Cyperaceae (15 species; Appendix VI). The species recorded in the present study represented 33 % of the aquatic species that have been recorded in Tasmania and 79 % of families (Aston, 1967). The 94 species of angiosperm comprised of 46 dicotyledons and 48 monocotyledons, belonging in all to 35 families (Appendix V and VI). Within each zone, species richness ranged from 9 in Big Punchbowl aquatic zone to 41 in the dry herbaceous zone of Middle Lagoon (Table 5.1). Eighty-four percent of the total species were perennial, whereas, 16 % were annual (Table 5.1). Similarly, all zones sampled had a higher number of perennial than annual species.

Generally, more species were recorded in aquatic zones than in sedge zones (Table 5.1). However, this pattern was reversed in the sedge dominated Big Punchbowl, where more species were recorded in the outer edge zone than in the central aquatic zone. In Tin Dish an equal number of species was recorded for each zone. Mean seasonal species richness was higher during all seasons in aquatic zones than in sedge zones (Table 5.2).

Overall, within functional groups the highest number of species were recorded from the terrestrial group (39) with the lowest species number (6) being recorded from the submerged group (Table 5.1). The amphibious groups were approximately equal in species number (Table 5.1).

Table 5.1 Summary of species richness found in the extant vegetation in the zones of each wetland (Wetlands: BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate, Zones: Aq. = aquatic; Out. = outer; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; DH = dry herbaceous; B.a = *Baumea arthropphylla*; B.r = *Baumea rubiginosa*).

(a) SPECIES RICHNESS	Total	BP		TD		MID			CTL		SG	
		B.r Aq.	B.r Out	Aq.	E.a	E.s	Aq.	DH	Aq.	B.a	Aq.	B.a
Functional Groups												
Submerged (S)	6	2	1	1	0	2	4	2	5	3	4	1
Amphibious responder (Ar)	15	5	3	1	2	5	6	7	12	7	5	4
Amphibious tolerator-emergent (Atle)	18	2	4	4	3	2	7	9	8	5	8	8
Amphibious tolerator-saturated/mudflat (Atls)	19	0	3	2	3	1	7	11	6	2	5	6
Terrestrial (T)	39	0	7	14	14	2	5	12	2	3	10	12
Total species	97	9	18	22	22	12	29	41	33	20	32	31
Perennial species	81	8	15	12	13	11	25	39	31	19	28	27
Annual species	16	1	3	10	9	1	4	4	2	1	4	4

(b) PERCENTAGE	Total	BP		TD		MID			CTL		SG	
		B.r Aq.	B.r Out	Aq.	E.a	E.s	Aq.	DH	Aq.	B.a	Aq.	B.a
Functional Groups												
Submerged (S)	6.2	22.2	5.6	4.5	0.0	16.7	13.8	4.9	15.2	15.0	12.5	3.2
Amphibious responder (Ar)	15.5	55.6	16.7	4.5	9.1	41.7	20.7	17.1	36.4	35.0	15.6	12.9
Amphibious tolerator-emergent (Atle)	18.6	22.2	22.2	18.2	13.6	16.7	24.1	22.0	24.2	25.0	25.0	25.8
Amphibious tolerator-saturated/mudflat (Atls)	19.6	0.0	16.7	9.1	13.6	8.3	24.1	26.8	18.2	10.0	15.6	19.4
Terrestrial (T)	40.2	0.0	38.9	63.6	63.6	16.7	17.2	29.3	6.1	15.0	31.3	38.7

Table 5.2 Species richness season summary (* average of the *Baumea* spp. dominated zones using the amalgamated species richness of Big Punchbowl; BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate. Seasons: SU = summer; A = Autumn; W = winter; SP = spring).

Zone	SU97	A97	W97	SP97	SU98	A98	W98	SP98	Seasonal Average
BP <i>B. rubiginosa</i> aquatic	1	1	2	2	2	2	6	8	3.0
BP <i>B. rubiginosa</i> outer	8	7	9	5	10	9	10	14	9.0
BP Total	8	7	9	6	11	10	14	20	10.6
TD aquatic	5	13	11	16	12	14	13	13	12.1
TD <i>E. acuta</i>	5	10	15	19	13	15	16	21	14.3
MID <i>E. sphacelata</i>	9	n/a	n/a	9	7	10	6	9	8.3
MID aquatic	21	n/a	n/a	19	20	17	20	21	19.1
MID dry herbaceous	25	n/a	n/a	30	27	29	30	36	28.4
CTL aquatic	12	15	14	16	22	20	15	19	16.6
CTL <i>B. arthropphylla</i>	9	12	13	15	14	11	89	12	11.8
SG aquatic	19	17	20	24	16	21	20	25	20.3
SG <i>B. arthropphylla</i>	12	16	14	15	10	17	18	25	15.9
Vegetation averages									
<i>Baumea</i> spp. zone *	9.7	12	12	12	11.7	13	13	19	12.8
Aquatic zone *	14.3	15.0	15.3	18.8	17.5	18.0	17.0	19.5	16.9

Classification and Ordination

Classification

At the two group level, *Baumea* spp. dominated zones (32 individuals) were separated from the *Eleocharis* spp., aquatic and dry herbaceous zones (53 individuals; Figure 5.1).

At the three group level (Figure 5.1 b) the non-*Baumea* spp. group was split into: Tin Dish (14 individuals); Tin Dish (2 individuals, Summer 1997, aquatic and *Eleocharis acuta* zone), Middle Lagoon (21 individuals); and Cherry Tree Lagoon (8 individuals).

At the 7 group level the groups were further separated as follows: a) the *Baumea* spp. dominated zones were divided into two groups: Group I) Big Punchbowl (16 individuals) with Cherry Tree Lagoon (8 individuals); and Group II) Sandy Gate (8 individuals); and b) the Tin Dish, Middle Lagoon and Sandy Gate zones (40 individuals) were divided into 5 groups: Group III) Tin Dish aquatic (1 season, summer 1997) with Cherry Tree Lagoon aquatic (8 individuals) zones; Group IV) Middle Lagoon dry and aquatic herbaceous zones (14 individuals); Group V) Tin Dish *Eleocharis acuta* (1 season, summer 1997) with Sandy Gate aquatic (8 individuals) zones; Group VI) Middle Lagoon *Eleocharis sphacelata* zone; and Group VII) Tin Dish (14 individuals) group (Figure 5.1).

The 14 group level of classification was as follows:

Group I: a) Big Punchbowl *Baumea rubiginosa* aquatic (7 of 8 seasons - summer 1997 to winter 1998), b) Big Punchbowl *Baumea rubiginosa* outer zone (8 of 8 seasons - summer 1997 to winter 1998), c) Big Punchbowl *Baumea rubiginosa* aquatic zone (1 of 8 seasons - spring 1998) and d) Cherry Tree Lagoon *Baumea arthropphylla* (8 of 8 seasons - summer 1997 to spring 1998);

Group II: Sandy Gate *Baumea arthropphylla* zone (8 of 8 seasons - summer 1997 to spring 1998);

Group III: a) Tin Dish aquatic zone (1 of 8 seasons - summer 1997) and b) Cherry Tree Lagoon aquatic zone (8 of 8 seasons - summer 1997 to spring 1998);

Group IV: a) Middle Lagoon dry zone (7 of 7 seasons - summer 1997:winter 1997 to spring 1998) and b) Middle Lagoon aquatic zone (7 of 7 seasons - summer 1997:winter 1997 to spring 1998);

Group V: a) Tin Dish *Eleocharis acuta* zone (1 of 8 season - summer 1997) and b) Sandy Gate aquatic zone (8 of 8 seasons - summer 1997 to spring 1998);

Group VI: Middle Lagoon *Eleocharis sphacelata* zone (7 of 7 seasons - summer 1997:winter 1997 to spring 1998);

Group VII: a) Tin Dish aquatic zone (7 of 8 seasons - autumn 1997 to spring 1998 and b) Tin Dish *Eleocharis acuta* (7 of 8 seasons - autumn 1997 to spring 1998).

Zones were the most important clustering feature. Evidence for this was that the vegetation communities found between seasons within each zone were generally more similar to each other than those found in other zones (Figure 5.1). However, the seasonal vegetation community recorded in three zones were found to be similar to communities within other zones. Within the *Baumea* spp. zones, the spring 1998 vegetation community of Big Punchbowl, *B. rubiginosa* aquatic zone, was grouped with the communities of the *B. arthropphylla* zone of Cherry Tree Lagoon. Whereas, within the aquatic and *Eleocharis* spp. zones, the summer 1997 vegetation community of Tin Dish aquatic zone was grouped with the communities of the aquatic zone of Cherry Tree Lagoon. Similarly, the summer 1997 vegetation community of Tin Dish *Eleocharis acuta* zone was grouped with the communities of the aquatic zone of Sandy Gate.

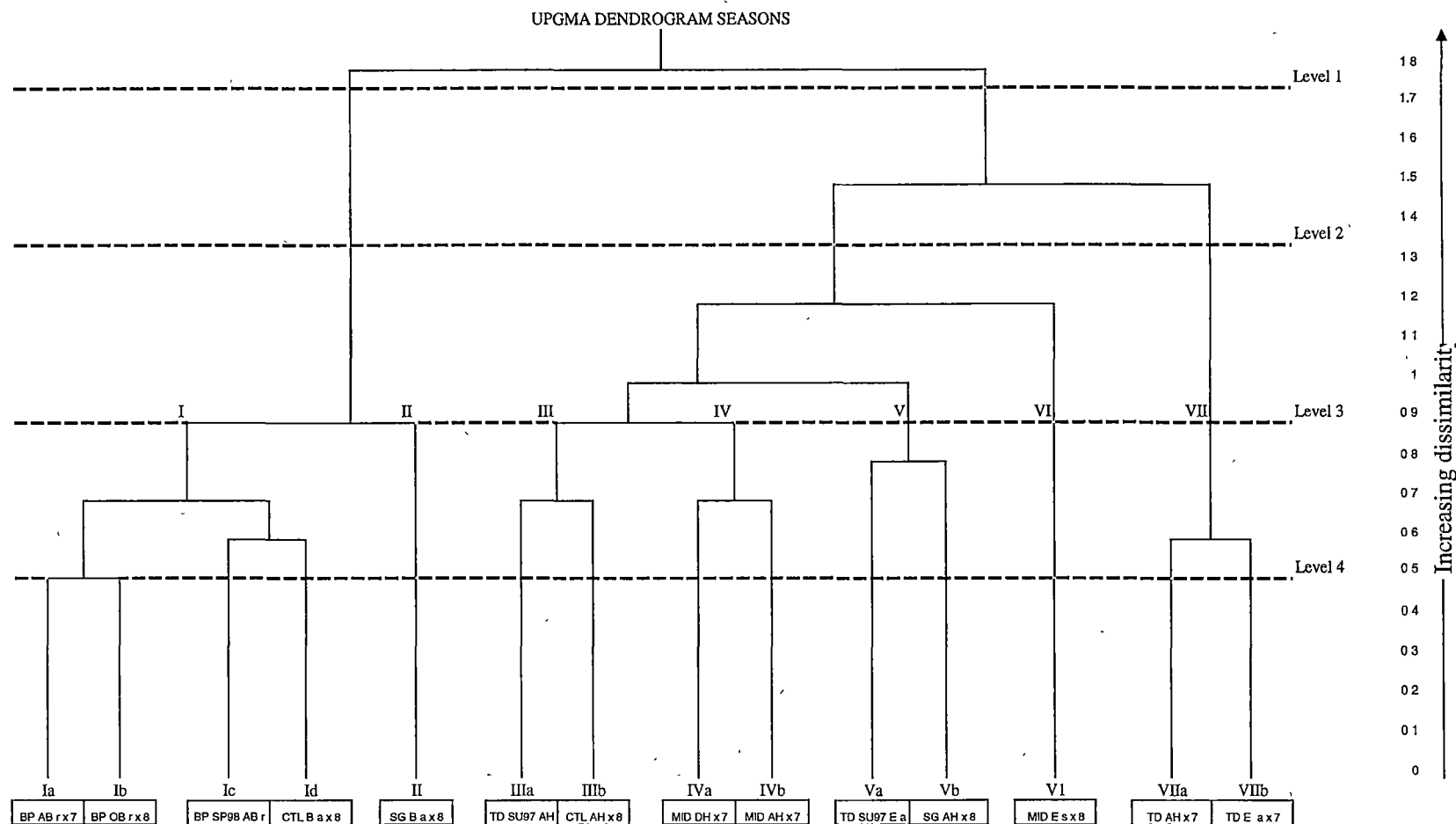


Figure 5.1 Simplified dendrogram from UPGMA analysis used to classify zones using seasonal averaged community data (AH = aquatic herb, DH = dry herb, O = outer zone; B_r = *Baumea rubiginosa*; B_a = *Baumea arthropphylla*; E_s = *Eleocharis sphacelata*; E_a = *Eleocharis acuta*; SP = spring; SU = summer; BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate. Numbers indicate the number of individual seasons within that zone grouped

Ordination analyses

The zone x season combinations in the ordination space were arranged broadly along a water depth gradient parallel to axis 2, that is, the scores on axis 2 were inversely correlated with water depth (Spearman rank correlation, $n = 85$, $\rho = -0.721$, $P < 0.0001$).

Vegetation communities from each "vegetation type", that is, aquatic, *Baumea* spp. *Eleocharis acuta* and *E. sphacelata* generally occupied distinct regions of ordination space (Figure 5.2). Satisfactory separation between *Baumea* spp. zones and aquatic herb zones occurred on axis 1 and less so on axis 2. The *Eleocharis sphacelata* zone was tightly defined by both axes but only separated from other zones by axis 2 (Figure 5.2).

Individual wetland dynamics within zones

Patterns of the direction of seasonal change in community composition varied between zones for most wetlands (Figure 5.3 a-e). Only in Tin Dish was there a similar trend in seasonal community change between both vegetation zones (Figure 5.3 b). Both Tin Dish zones had a similar large directional change in community composition between summer and autumn, 1997. Submerged species were generally associated with aquatic zones, whereas, the other four functional groups were distributed across all vegetation types (Figure 5.3 a-e).

The observed distribution of angles from each zone trajectory did not differ significantly from a random distribution for all zones (Figure 5.3; Table 5.3), possibly due to limited number of seasons sampled. However, 64% of zones showed a strong tendency to become less similar to the starting point through time, whereas the remaining zones (36%) showed a pattern of increased dissimilarity followed by increasing similarity (Figure 5.4).

Figure 5.2

(a) Ordination (SSHMDS) 85 zone x season combinations coded by zones (2-dimensions, stress = 0.11). Symbols represent: a) vegetation "types" as follows: shaded = sedge; open = aquatic, crossed = dry herbaceous, b) Wetland/zone as follows: Big Punchbowl - O = aquatic *Baumea* zone, ● = outer *Baumea* zone; Tin Dish - ☆ = aquatic, ★ = *Eleocharis acuta*; Middle Lagoon - ■ = *Eleocharis sphacelata*, □ = aquatic, ☒ = dry herbaceous; Cherry Tree Lagoon - Δ = aquatic, ▲ = *Baumea arthropphylla*; Sandy Gate - = aquatic, ◆ = *Baumea arthropphylla*.

(b) Significantly associated species plotted in the same ordination space.

Abbreviations for species are as follows: A.a = *Agrostis avenacea*; Bau. Spp. = *Baumea* spp.; C.c = *Centella cordifolia*; C.i = *Carex inversa*; C. ter = *Carex tereticaulis*; Cho.sp. = *Chorizandra* sp.; D.r = *Dichondra repens*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; E.v = *Eryngium vesiculosum*; G.h = *Goodenia humilis*; H.m = *Hydrocotyle muscosa*; H.s = *Hydrocotyle sibthorpiodes*; I.i = *Isolepis inundata*; Iso. spp. = *Isolepis* spp.; M. spp. = *Myriophyllum* spp.; J.h = *Juncus holoschoenus*; L.p = *Lilaeopsis polyantha*; L.s = *Leptospermum scoparium*; N. a = *Neopaxia australasica*; Nit.spp. = *Nitella* spp.; P.lab = *Poa labillardierei*; P.t = *Potamogeton tricarinatus*; S.h = *Scaevola hookeri*; S.b = *Scleranthus biflorus*; S.m = *Schoenus maschalinus*; S.n = *Schoenus nitens*; S.r = *Selliera radicans*; T.p = *Triglochin procerum*; T. striat = *Triglochin striatum*; U.spp = *Utricularia* spp.; V.r = *Villarsia reniformis*. **Introduced** - A.ar = *Anagallis arvensis*; P.c = *Plantago coronopus*; C.e = *Centaurium erythraea*; C.v = *Cirsium vulgare*; E. c = *Erodium cicutarium*; IP. spp = Introduced Poaceae spp.; J.a = *Juncus articulatus*; J.bul = *Juncus bulbosus*; Son. spp. = *Sonchus* spp.; Tri. spp. = *Trifolium* spp..

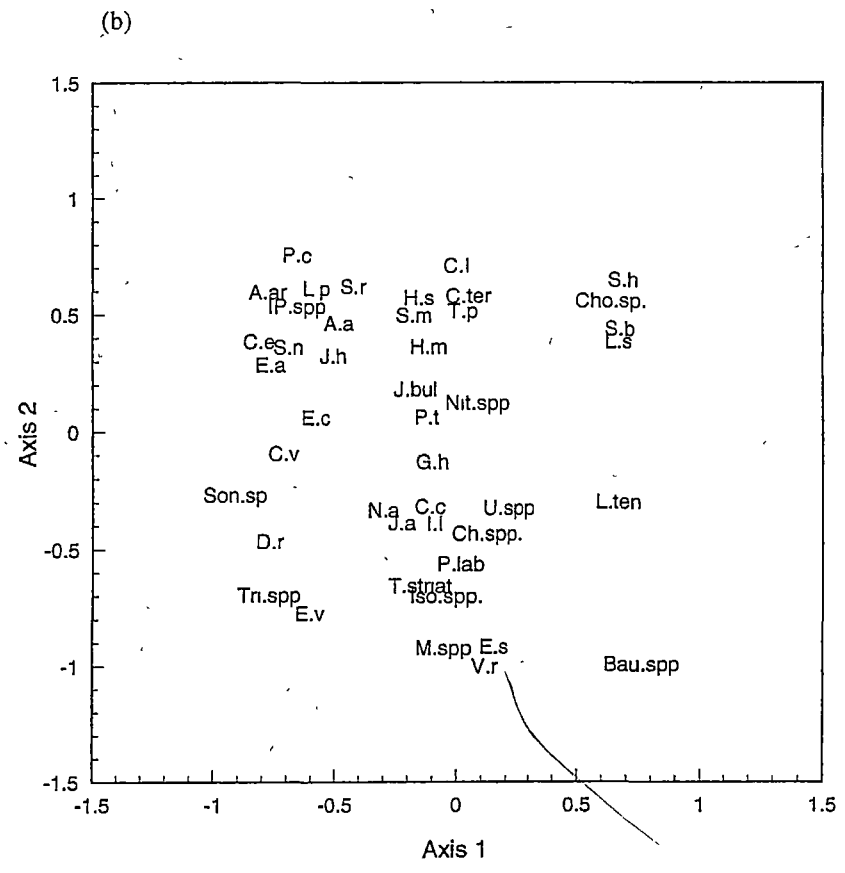
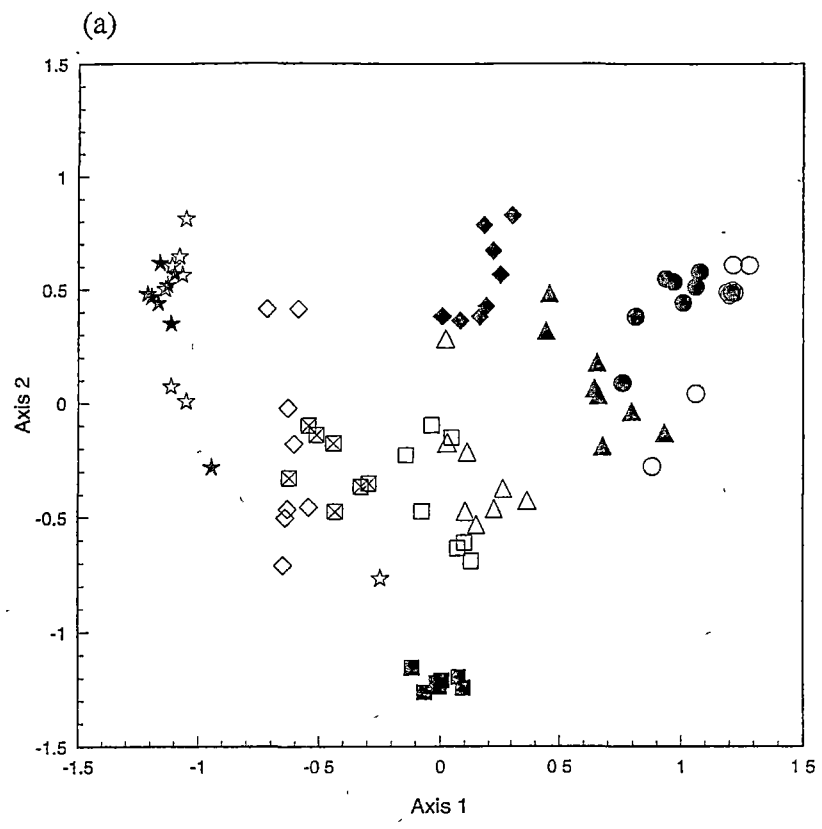


Figure 5.3 - a

(a) **Ordination (SSHMDS) of Big Punchbowl 16 zone x season combinations coded by zones** (2-dimensions, stress = 0.022). Colour codes for zones represent: **blue** = aquatic *Baumea rubiginosa* (AB) zone, **green** = outer *Baumea rubiginosa* (OB) zone; Symbols represent: SU = summer, A = autumn, W = winter, SP = spring.

(b) **Species associated with the (SSHMD) ordination plotted in the same ordination space, colour coded into functional groups.** *Italics* = species that were not significant to the ordination. Colour codes for functional groups represent: **blue** = submerged; **red** = amphibious responder; **green** = amphibious tolerator-emergent; **light green** = amphibious tolerator saturate/mudflat; black = terrestrial. Abbreviations for species are as follows: **Native** - A.a = *Agrostis avenacea*; B.r. = *Baumea rubiginosa*; Cho.sp. = *Chorizandra* sp.; E.s = *Eleocharis sphacelata*; I.f = *Isolepis fluitans*; L.s = *Leptospermum scoparium*; N.s = *Nitella subtilissima*; N.g = *Nitella gelatinifera*; P.t = *Potamogeton tricarinatus*; S.h = *Scaevola hookeri*; S.b = *Scleranthus biflorus*; S.n = *Schoenus nitens*; T.p = *Triglochin procerum*; U.spp = *Utricularia* spp.; V.r = *Villarsia reniformis*. **Introduced** - A.v = *Acetosella vulgaris*; B.m = *Banksia marginata*; D sp. = *Deyeuxia* sp.; Eu. Sp. = *Eucalyptus* sp..

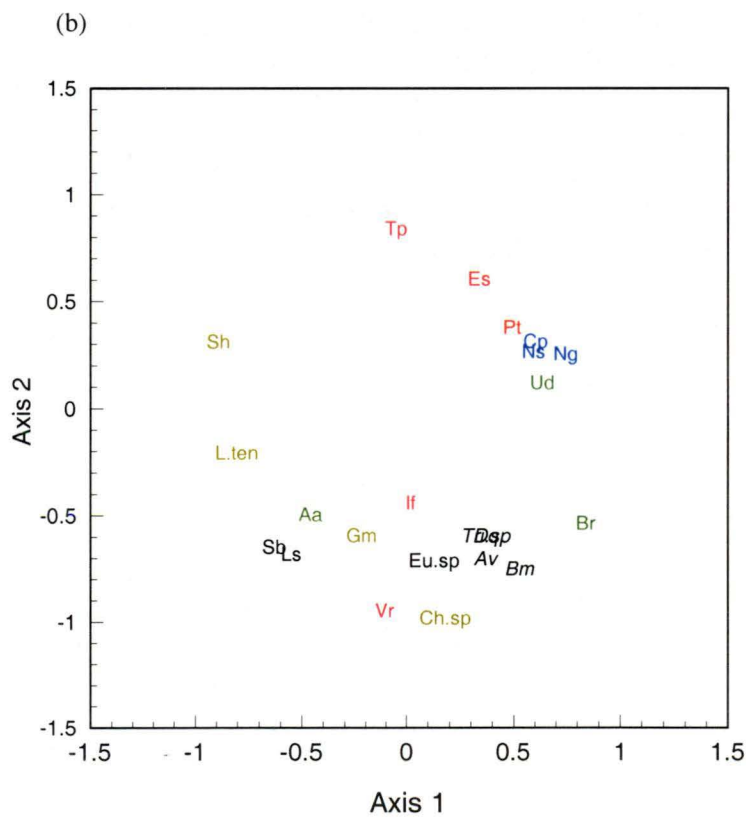
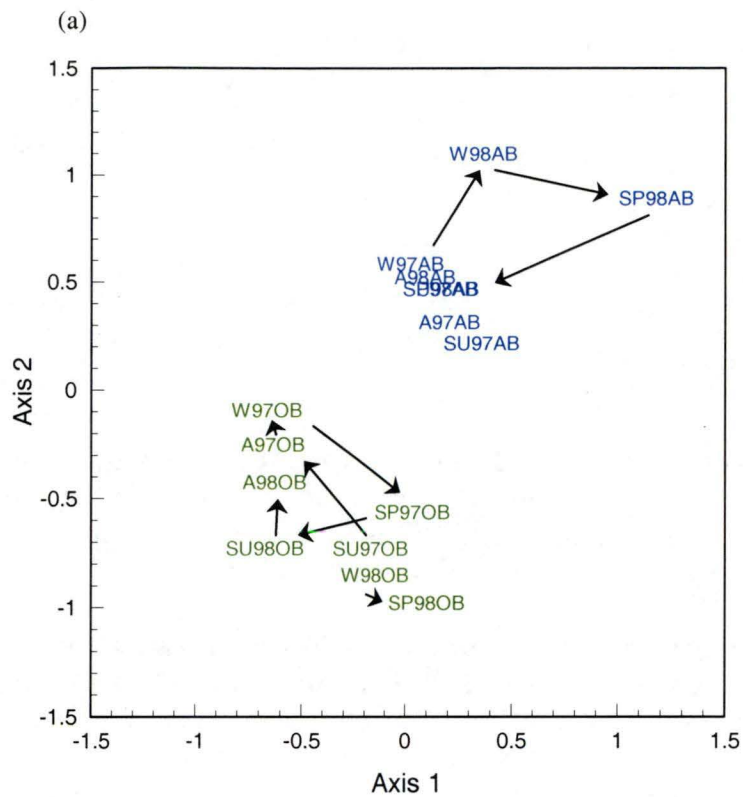


Figure 5.3 - b

(a) **Ordination (SSHMDS) of Tin Dish 16 zone x season combinations coded by zones** (2-dimensions, stress = 0.058). Colour codes for zones represent: **blue** = aquatic (AH) zone, **green** = *Eleocharis acuta* (E.a) zone; Symbols represent: SU = summer, A = autumn, W = winter, SP = spring.

(b) **Species associated with the (SSHMD) ordination plotted in the same ordination space, colour coded into functional groups.** *Italics* = species that were not significant to the ordination. Colour codes for functional groups represent: **blue** = submerged; **red** = amphibious responder; **green** = amphibious tolerator-emergent; **light green** = amphibious tolerator-saturated/mudflat; black = terrestrial. Abbreviations for species are as follows: **Native** - A.a = *Agrostis avenacea*; A.s = *Amphibromus sinuatus*; C. spp. = *Chara* spp. D.r = *Dichondra repens*; E.a = *Eleocharis acuta*; L.p = *Lilaeopsis polyantha*; P.t = *Potamogeton tricarinatus*; S.n = *Schoenus nitens*; S.r = *Selliera radicans*. **Introduced** - A.v = *Acetosella vulgaris*; C.e = *Centaureum erythraea*; C.v = *Cirsium vulgare*; E.c = *Erodium cicutarium*; Ipoac. spp = Introduced Poaceae spp.; J.a = *Juncus articulatus*; L.t = *Leontodon taraxacoides*; P.c = *Plantago coronopus*; P. lan = *Plantago lanceolata*; Son. spp. = *Sonchus* spp.; Tri. spp. = *Trifolium* spp..

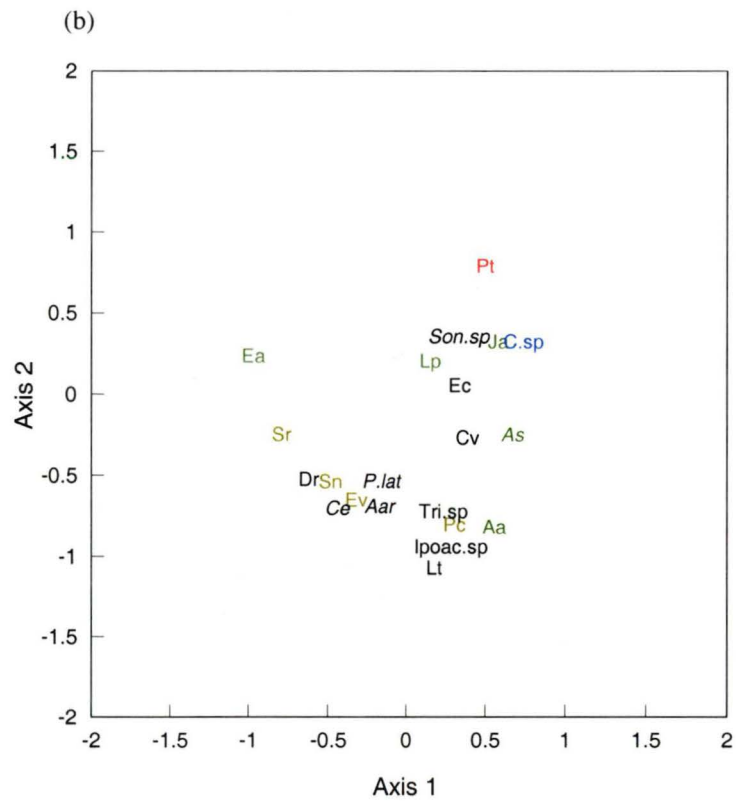
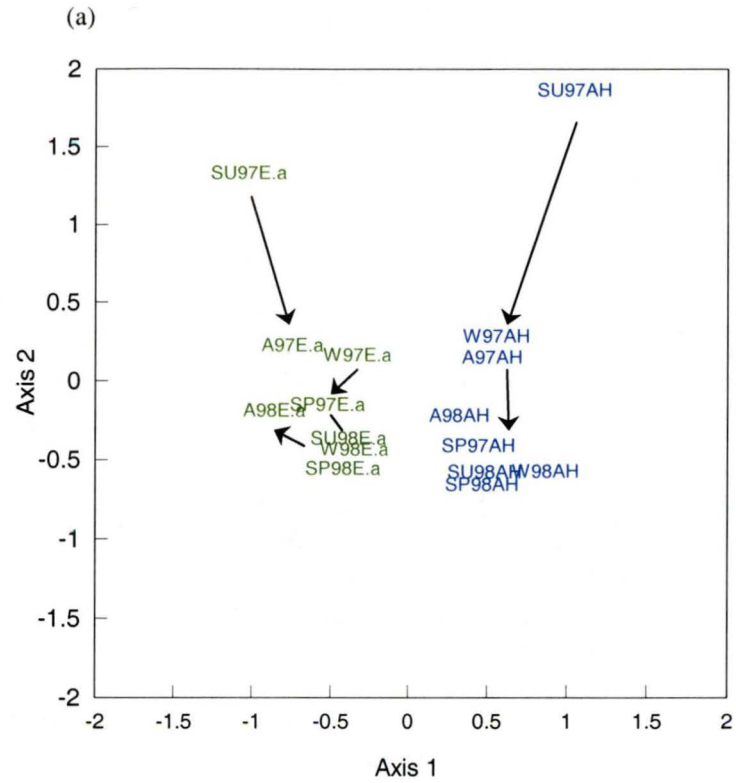


Figure 5.3 - c

(a) Ordination (SSHMDS) of Middle Lagoon 21 zone x season combinations coded by zones (2-dimensions, stress = 0.055). Colour codes for zones represent: **blue** = aquatic (AH) zone, **green** = *Eleocharis sphacelata* (E.s) zone, **red** = dry herbaceous (DH) zone; Symbols represent: SU = summer, A = autumn, W = winter, SP = spring.

(b) Species associated with the (SSHMD) ordination plotted in the same ordination space, colour coded into functional groups. *Italics* = species that were not significant to the ordination. Colour codes for functional groups represent: **blue** = submerged; **red** = amphibious responder; **green** = amphibious tolerator-emergent; **light green** = amphibious tolerator-saturated/mudflat; black = terrestrial. Abbreviations for species are as follows: **Native** - A.a = *Agrostis avenacea*; B.a = *Baumea arthropophylla*; C.c = *Centella cordifolia*; C.f = *Chara fibrosa*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; E.v = *Eryngium vesiculosum*; E.n = *Einadia nutans*; G.h = *Goodenia humilis*; H.m = *Hydrocotyle muscosa*; I.i = *Isolepis inundata*; Iso. spp. = *Isolepis* spp.; J.buf = *Juncus bufonius*; M. spp. = *Myriophyllum* spp.; J.h = *Juncus holoschoenus*; L.c = *Lepilaena cylindrocarpa*; L.p = *Lilaeopsis polyantha*; N. a = *Neopaxia australasica*; Nit.spp. = *Nitella* spp.; P.t = *Potamogeton tricarinatus*; R. spp. = *Ruppia* spp.; S.f = *Schoenus fluitans*; S.m = *Schoenus maschalinus*; S.n = *Schoenus nitens*; S.r = *Selliera radicans*; T.p = *Triglochin procerum*; T. s = *Triglochin striatum*; T. sub = *Trithuria submersa*; U.spp = *Utricularia* spp.; V.r = *Villarsia reniformis*. **Introduced** - C.e = *Centaureum erythraea*; C.v = *Cirsium vulgare*; C. ten = *Cyperus tenellus*; Ipoac spp. = Introduced Poaceae species; P.c = *Plantago coronopus* J.a = *Juncus articulatus*; J. bul. = *Juncus bulbosus*; Tri. spp. = *Trifolium* spp..

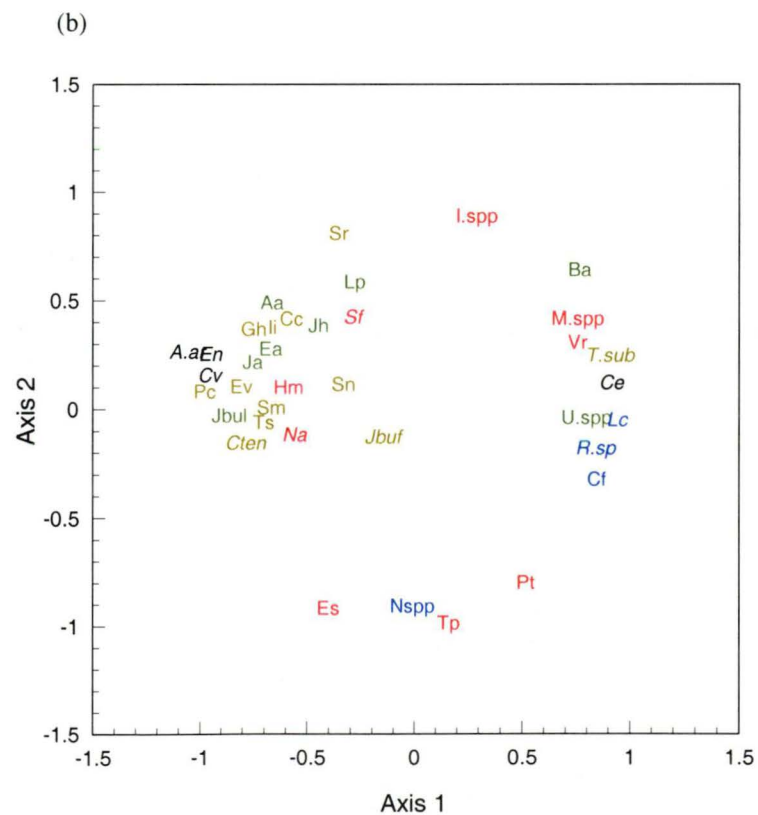
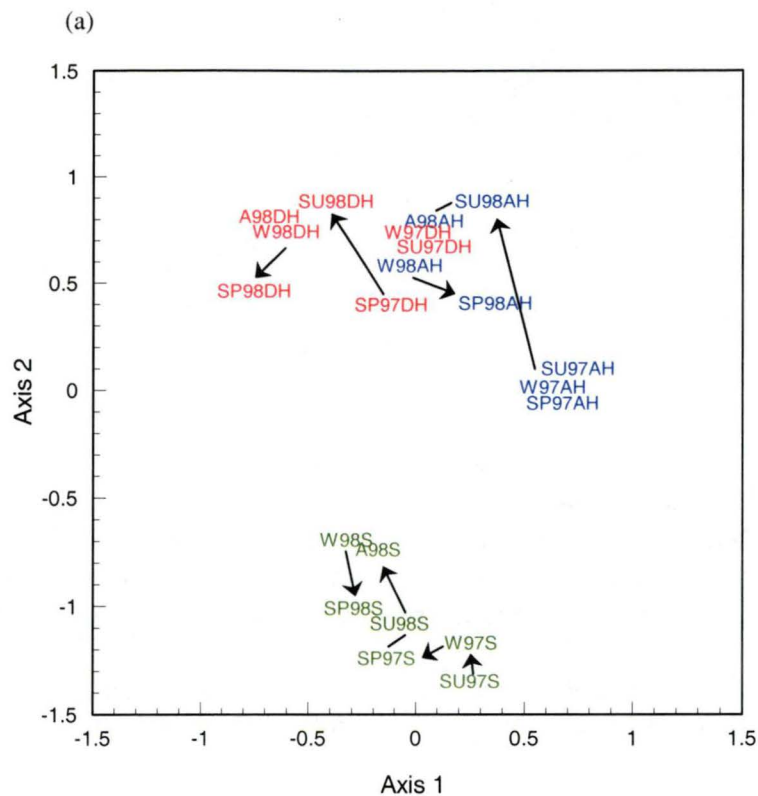


Figure 5.3 - d

(a) Ordination (SSHMDS) of Cherry Tree Lagoon 16 zone x season combinations coded by zones (2-dimensions, stress = 0.065). Colour codes for zones represent: **blue** = aquatic (AH) zone, **green** = *Baumea arthropophylla* (B.a) zone. Symbols represent: SU = summer, A = autumn, W = winter, SP = spring.

(b) Species associated with the (SSHMD) ordination plotted in the same ordination space, colour coded into functional groups. *Italics* = species that were not significant to the ordination. Colour codes for functional groups represent: **blue** = submerged; **red** = amphibious responder; **green** = amphibious tolerator-emergent; **light green** = amphibious tolerator-saturated/mudflat; black = terrestrial. Abbreviations for species are as follows: **Native** - A.a = *Agrostis avenacea*; A.s = *Amphibromus sinuatus*; B.a = *Baumea arthropophylla*; B.t = *Batrachium trichophyllum*; C.c = *Centella cordifolia*; C.cor = *Cotula coronopifolia*; C.p = *Chara preissii*; C.s = *Callitriche stagnalis*; D.q = *Deyeuxia quadriseta*; E.a = *Eleocharis acuta*; E.v = *Eryngium vesiculosum*; E.g. = *Elatine gratioloides*; H.m = *Hydrocotyle muscosa*; I.f = *Isolepis fluitans*; L. long = *Leptinella longipes*; My. spp. = *Myriophyllum* spp.; M.r = *Mimulus repens*; J.h = *Juncus holoschoenus*; L.p = *Lilaeopsis polyantha*; N.g = *Nitella gelatinifera*; N.s = *Nitella subtilissima*; P.t = *Potamogeton tricarinatus*; R.a = *Ranunculus amphitrichus*; R. spp. = *Ruppia* spp.; S.f = *Schoenus fluitans*; S.r = *Selliera radicans*; T.p = *Triglochin procerum*; U.d = *Utricularia dichotoma*; V.r = *Villarsia reniformis*. **Introduced** - C.gl = *Chenopodium glaucum*; C.v = *Cirsium vulgare*; P.c = *Plantago coronopus*.

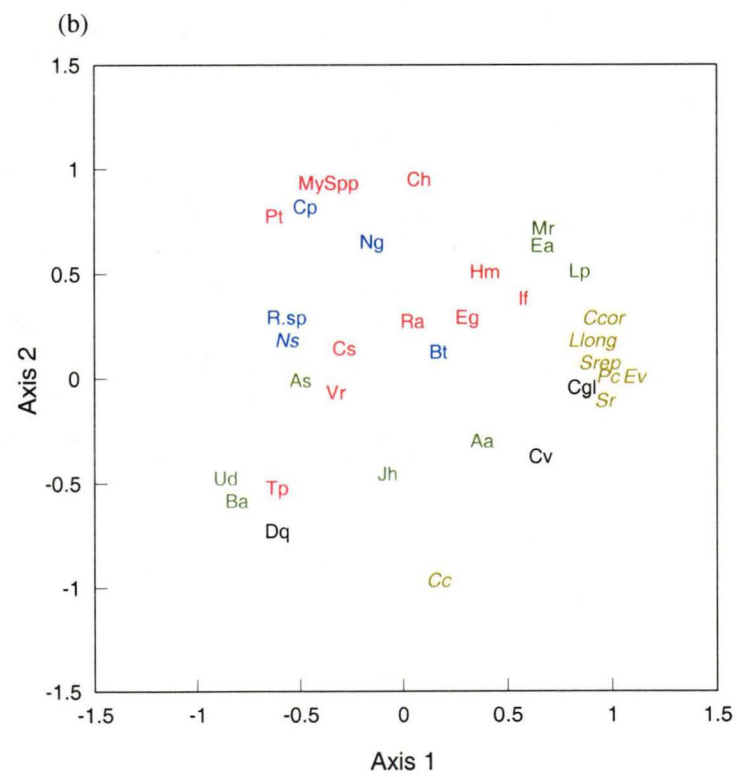
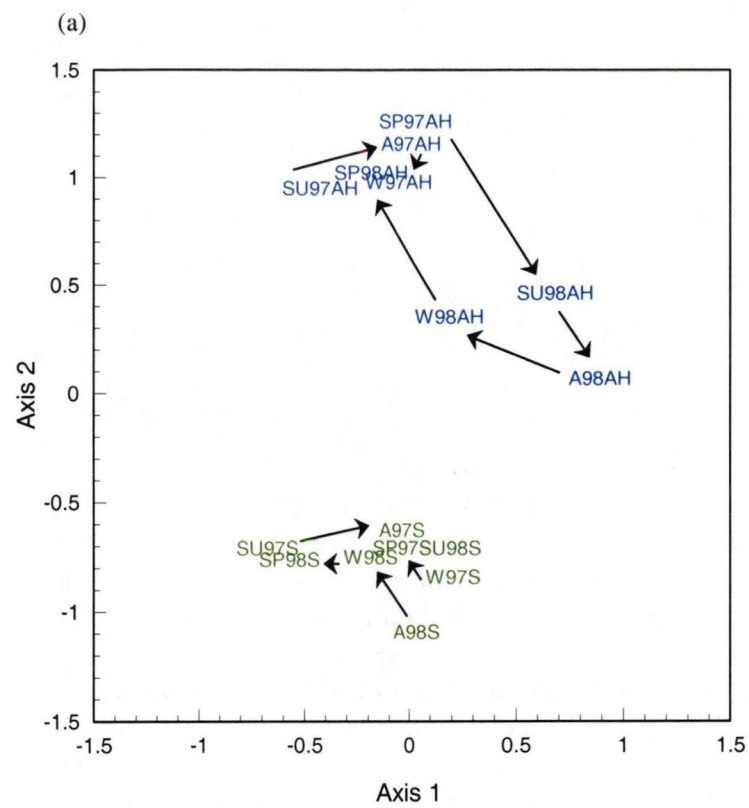


Figure 5.3 - e

(a) Ordination (SSHMDS) of Sandy Gate16 zone x season combinations coded by zones (2-dimensions, stress = 0.057). Colour codes for zones represent: **blue** = aquatic (AH) zone, **green** = *Baumea arthropophylla* (B.a) zone. Symbols represent: SU = summer, A = autumn, W = winter, SP = spring.

(b) Species associated with the (SSHMD) ordination plotted in the same ordination space, colour coded into functional groups. *Italics* = species that were not significant to the ordination. Colour codes for functional groups represent: **blue** = submerged; **red** = amphibious responder; **green** = amphibious tolerator-emergent; **light green** = amphibious tolerator-saturated/mudflat; black = terrestrial. Abbreviations for species are as follows: **Native** - A.a = *Agrostis avenacea*; A.s = *Amphibromus sinuatus*; B.a = *Baumea arthropophylla*; B.t = *Batrachium trichophyllum*; C.c = *Centella cordifolia*; C. spp. = *Chara* species; C.i = *Carex inversa*; C. ter = *Carex tereticaulis* D. spp. = *Danthonia* spp.; E.a = *Eleocharis acuta*; Ep. Sp. = *Epilobium* sp.; E.v = *Eryngium vesiculosum*; I. spp. = *Isolepis* spp.; M. spp. = *Myriophyllum* spp.; J.h = *Juncus holoschoenus*; L.p = *Lilaeopsis polyantha*; N. spp. = *Nitella* spp.; P. lab = *Poa labillardierei*; P.t = *Potamogeton tricarlinatus*; R. spp. = *Ruppia* spp.; S.a = *Schoenus apogon*; S.m = *Schoenus maschalinus*; S.n = *Schoenus nitens*; S.rep = *Samolus repens*; T.p = *Triglochin procerum*; U.d = *Utricularia dichotoma*; V.r = *Villarsia reniformis*. **Introduced** - C.v = *Cirsium vulgare*; H.r = *Hypochoeris radicata*; Ipoac = Introduced Poaceae spp.; J.a = *Juncus articulatus*; L.t = *Leontodon taraxacoides*; P.c = *Plantago coronopus*; Tri. Spp. = *Trifolium* spp.

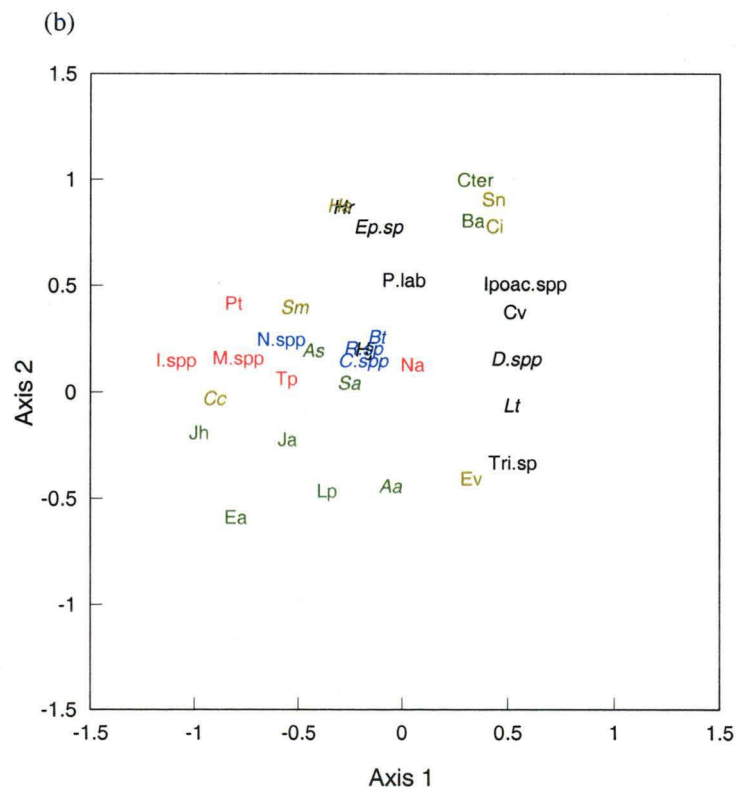
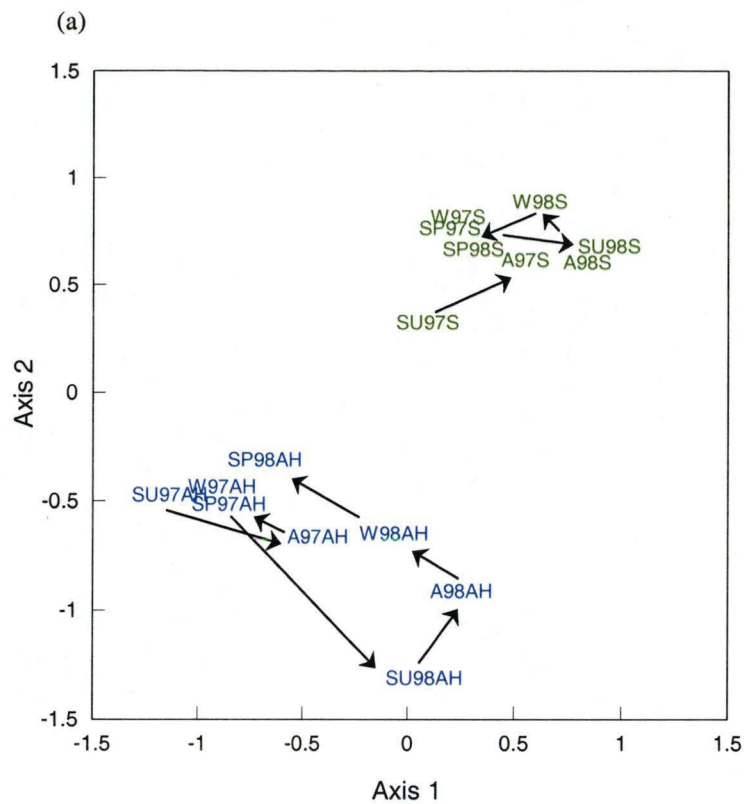


Table 5.3 Results of Kolmogorov-Smirnov analyses to test for directionality in the changes in community composition between seasons.

Zone	Kolmogorov-Smirnov Z Score	P-value	Sig.
BP <i>B. rubiginosa</i> aquatic	1.155	0.139	ns
BP <i>B. rubiginosa</i> outer	0.722	0.893	ns
TD aquatic	0.577	0.893	ns
TD <i>E. acuta</i>	0.577	0.893	ns
MID <i>E. sphacelata</i>	0.577	0.893	ns
MID aquatic	0.577	0.893	ns
MID dry herbaceous	0.577	0.893	ns
CTL aquatic	1.155	0.139	ns
CTL <i>B. arthropphylla</i>	0.577	0.893	ns
SG aquatic	1.155	0.139	ns
SG <i>B. arthropphylla</i>	1.155	0.139	ns

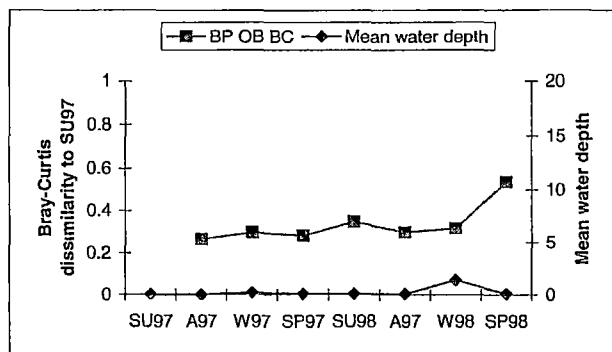
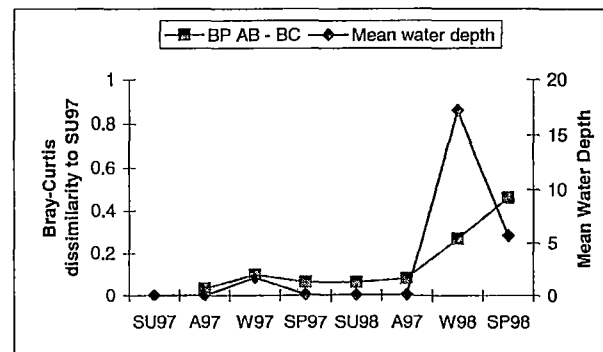
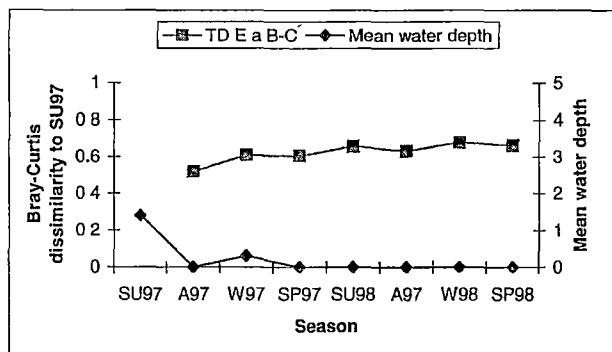
Generally, zones that changed from one water level state to another over the study period exhibited a uni-directional change in their vegetation (e.g. Big Punchbowl, Tin Dish and Middle Lagoon dry herbaceous zone, Figure 5.4). For Big Punchbowl the directional change was due to an increase in water level at the end of the study period (i.e. dry to wet), whereas, for Tin Dish and Middle Lagoon dry herbaceous zones the directional change was due to a decrease in water levels (i.e. wet to dry).

The remaining zones, in Cherry Tree Lagoon, Sandy Gate and Middle Lagoon, all experienced a two phase change in water level state over the study period. Within these zones, those dominated by aquatic herbaceous species and Middle Lagoon's *Eleocharis sphacelata* zone cycled back to a vegetation community similar to that existing prior to the drying period. The zones dominated by *Baumea arthropphylla* remained similar in community composition throughout the study period despite changes in water levels.

If a zone was wet during summer 1997, the dissimilarity score between 'wet' seasons were lower than those between 'dry' seasons. Conversely, if a zone was dry during summer 1997, the dissimilarity score between 'dry' seasons were lower than those between 'wet' seasons.

The relationships between the Bray-Curtis dissimilarity scores and mean water depth were significantly correlated for 3 of the 11 zones studied (Figure 5.4 a-c; Table 5.4). The scores of Sandy Gate and Middle Lagoon aquatic zones were negatively correlated to mean water depth ($\rho = -0.964$, $P = 0.0182$; $\rho = -0.943$, $P = 0.0350$), whereas the dissimilarity scores for Big Punchbowl aquatic zone were positively correlated to mean water depth.

Long-term dry wetlands

Big Punchbowl *Baumea rubiginosa* outer zoneBig Punchbowl *Baumea rubiginosa* aquatic zoneTin Dish *Eleocharis acuta* zone

Tin Dish aquatic zone

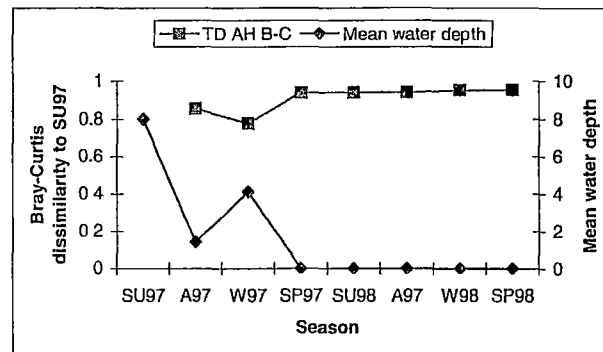
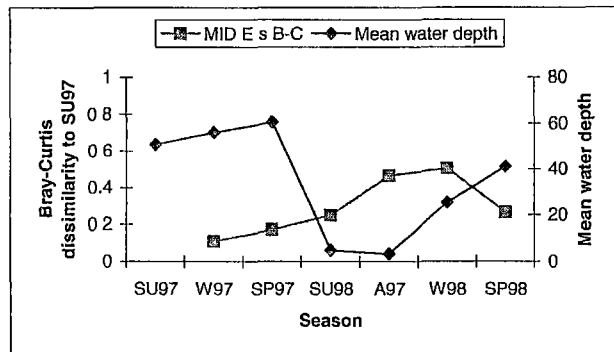
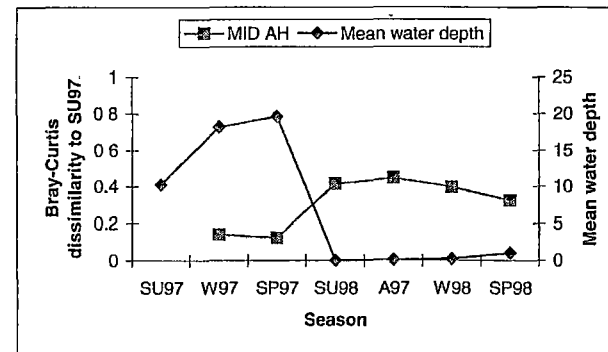


Figure 5.4 (a) Seasonal community Bray-Curtis dissimilarity scores measured against the community found during summer 1997 (SU97) compared with mean water depth for zones within Big Punchbowl and Tin Dish (B.C = Bray-Curtis; B.r = *Baumea rubiginosa*; E.a = *Eleocharis acuta*; AH = aquatic herbaceous; a Bray-Curtis score of 0 = no difference between the two communities; scores used are from the individual wetland ordination analyses, see previous section).

Middle Lagoon *Eleocharis sphacelata*



Middle Lagoon aquatic zone



Middle Lagoon dry herbaceous zone

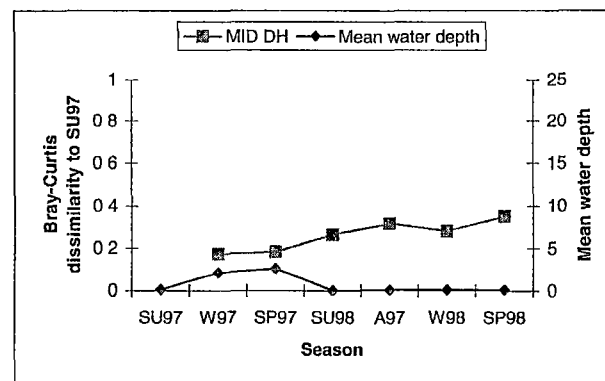
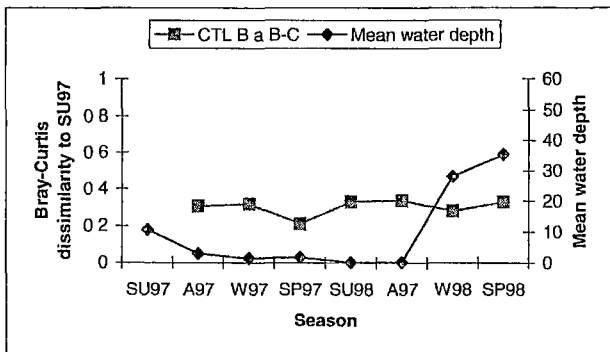
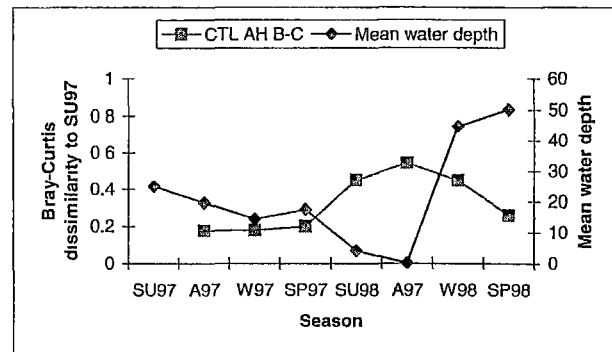
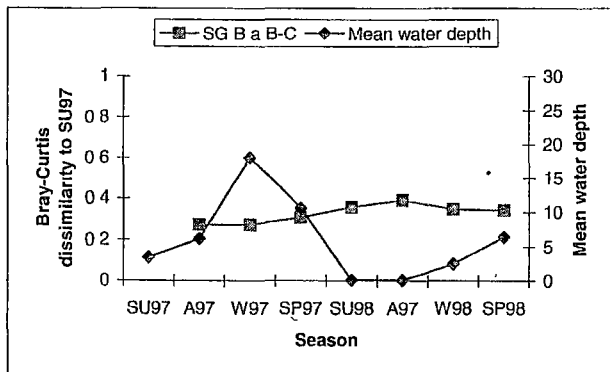


Figure 5.4 (b) Seasonal community Bray-Curtis dissimilarity scores measured against the community found during summer 1997 (SU97) compared with mean water depth for zones within Middle Lagoon (B.C = Bray-Curtis; E.s = *Eleocharis sphacelata*; AH = aquatic herbaceous; DH = dry herbaceous; a Bray-Curtis score of 0 = no difference between the two communities; scores used are from the individual wetland ordination analyses, see previous section).

Semi-permanent wetlands

Cherry Tree Lagoon *Baumea arthropphylla* zone

Cherry Tree Lagoon aquatic zone

Sandy Gate *Baumea arthropphylla* zone

Sandy Gate aquatic zone

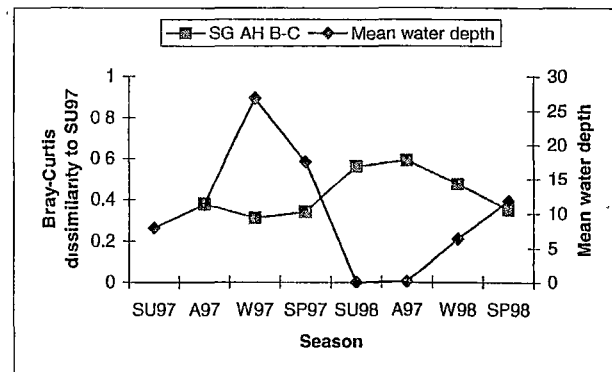


Figure 5.4 (c) Seasonal community Bray-Curtis dissimilarity scores measured against the community found during summer 1997 (SU97) compared with mean water depth for zones within Middle Lagoon (B.C = Bray-Curtis; B.a = *Baumea arthropphylla*; AH = aquatic herbaceous; a Bray-Curtis score of 0 = no difference between the two communities; scores used are from the individual wetland ordination analyses, see previous section).

Table 5.4 Results of Spearman rank analyses correlating Bray-Curtis dissimilarity scores (between vegetation communities found in summer 1997 and each of the other seasons sampled) and mean water recorded at the time sampled (Sig = significance; * = significant to 0.05).

Zone	Spearman's rho-value	P-value	Sig.
BP <i>B. rubiginosa</i> aquatic	0.935	0.0220	*
BP <i>B. rubiginosa</i> outer	0.335	0.4120	ns
TD aquatic	-0.802	0.0495	ns
TD <i>E. acuta</i>	-0.204	0.6171	ns
MID <i>E. sphacelata</i>	-0.657	0.1417	ns
MID aquatic	-0.943	0.0350	*
MID dry herbaceous	-0.516	0.2482	ns
CTL aquatic	-0.429	0.2938	ns
CTL <i>B. arthropphylla</i>	-0.500	0.2207	ns
SG aquatic	-0.964	0.0182	*
SG <i>B. arthropphylla</i>	-0.775	0.0577	ns

Functional group response to changes in water presence or absence.

Functional groups significantly differed in their proportions of species that responded by cover change to changes in water level, with submerged (S) having more than expected and terrestrial (T) having less than expected (Figure 5.5 a-e; $\chi^2 = 12.505$, $P = 0.0140$; Table 5.5).

Submerged, amphibious responder and amphibious tolerator taxa had an increase in cover more times than expected with a transition between 'dry to wet', and a decrease in cover more time than expected with a transition between 'wet to dry' ($\chi^2 = 16.081$, $P = < 0.0001$; $\chi^2 = 56.823$, $P = < 0.0001$; $\chi^2 = 4.121$, $P = 0.0424$ respectively), whereas, amphibious responder saturated mudflat taxa did the reverse ($\chi^2 = 13.074$, $P = 0.0003$; Table 5.6). Terrestrial taxa has a similar pattern of response to that of amphibious responder saturated/mudflat species, however, in this case the chi-square analysis was not significant ($\chi^2 = 2.822$, $P = 0.02451$).

Figure 5.5 a-e

Seasonal differences in mean water depth and mean percentage cover for individual species within each functional group and total mean percentage cover.

Key to species: * = introduced species; /n = uncertain status; A.a = *Agrostis avenacea*; B.a = *Baumea arthropphylla*; B.r = *Baumea rubiginosa*; B.m = *Banksia marginata*; B.t = *Batrachium trichophyllum*; A. r = *Amphibromus recurvatus*; A.s = *Amphibromus sinuatus*; C.c = *Centella cordifolia*; C.i = *Carex inversa*; C.e = *Centaureum erythraea*; C. sp. = *Chara* sp.; C.f = *Chara fibrosa*; C.gl = *Chenopodium glaucum*; C.p = *Chara preissii*; C. ten*/n = *Cyperus tenellus*; C. t = *Carex tereticaulis*; C.s = *Callitriche stagnalis*; Ch.sp. = *Chorizandra* sp.; C.v* = *Cirsium vulgare*; D. sp. = *Danthonia* sp.; D.r = *Dichondra repens*; D.q = *Deyeuxia quadriseta*; E.a = *Eleocharis acuta*; E. c* = *Erodium cicutarium*; E.g = *Elatine gratioloides*; E.n = *Einadia nutans*; E.s = *Eleocharis sphacelata*; Eu.sp. = *Eucalyptus* sp.; E.v = *Eryngium vesiculosum*; G.h = *Goodenia humilis*; G.m = *Gonocarpus micranthus*; H.m = *Hydrocotyle muscosa*; H.s = *Hydrocotyle sibthorpiodes*; I.i = *Isolepis inundata*; InP* = Introduced Poaceae spp.; I.f = *Isolepis fluitans*; M. spp. = *Myriophyllum* spp.; M.r = *Mimulus repens*; J.a* = *Juncus articulatus* J. buf = *Juncus bufonius*; J.bul* = *Juncus bulbosus*; J.h = *Juncus holoschoenus*; J.p = *Juncus procerus*; L.c = *Lepilaena cylindrocarpa*; L.t* = *Leontodon taraxacoides*; L.p = *Lilaeopsis polyantha*; L.lon = *Leptinella longipes*; L.s = *Leptospermum scoparium*; L.t = *Leptocarpus tenax*; N. a = *Neopaxia australasica*; N.g = *Nitella gelatinifera*; N.s = *Nitella subtilissima*; P.c* = *Plantago coronopus*; P.lat* = *Plantago lanceolata*; P.lab = *Poa labillardierei*; P.t = *Potamogeton tricarinatus*; R.a = *Ranunculus amphitrichus*; R.sp. = *Ruppia* sp.; S.h = *Scaevola hookeri*; S.b = *Scleranthus biflorus*; S.f = *Schoenus fluitans*; S.m = *Schoenus maschalinus*; S.n = *Schoenus nitens*; S.r = *Selliera radicans*; Son. Spp* = *Sonchus* sp.; Tri.spp* = *Trifolium* spp.; T.p = *Triglochin procerum*; T. striat = *Triglochin striatum*; T.sub = *Trithuria submersa*; U.d = *Utricularia dichotoma*; U.spp = *Utricularia* spp.; V.r = *Villarsia reniformis*.

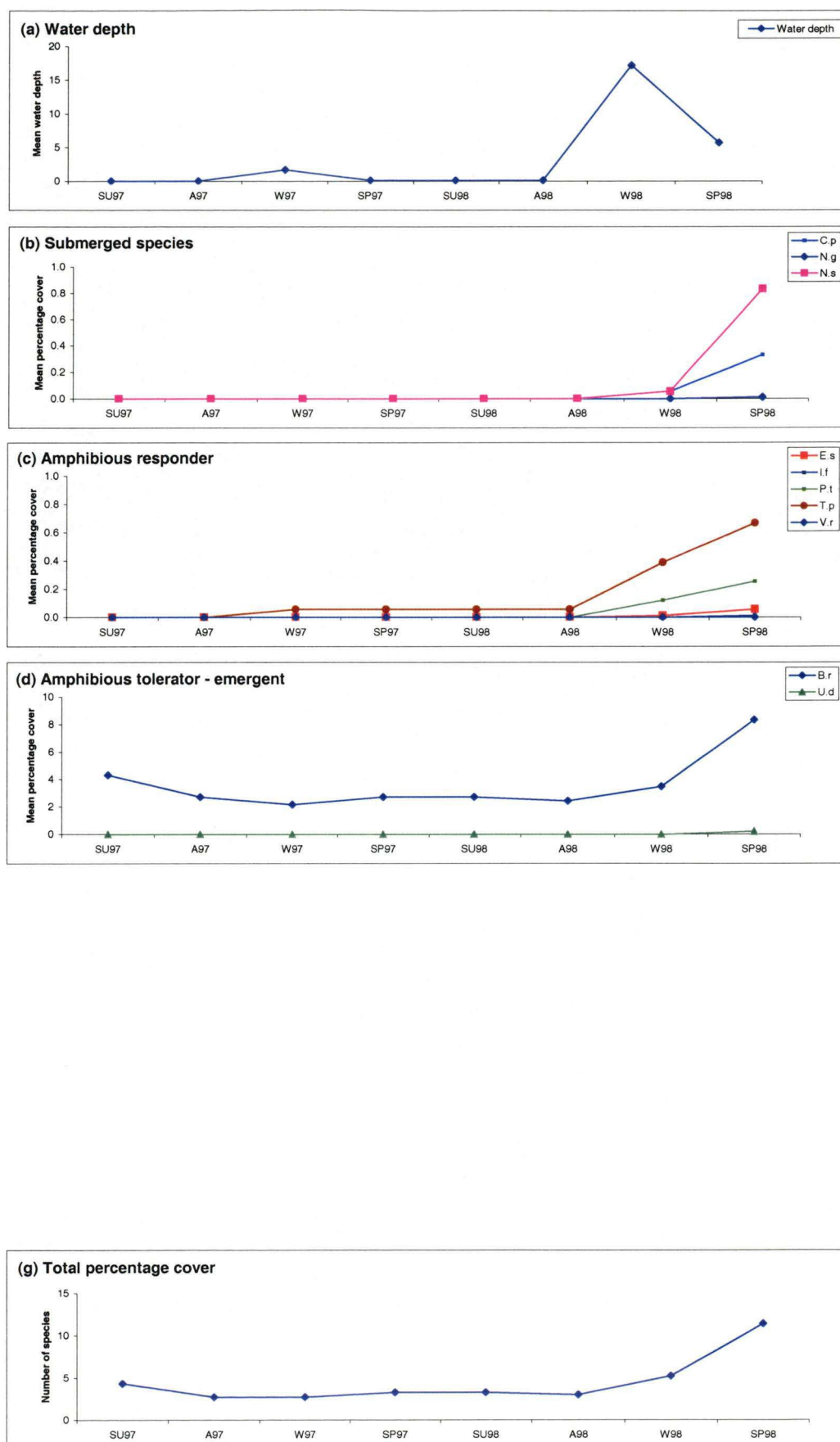


Figure 5.5 (a-1): Big Punchbowl aquatic *Baumea rubiginosa* zone- (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

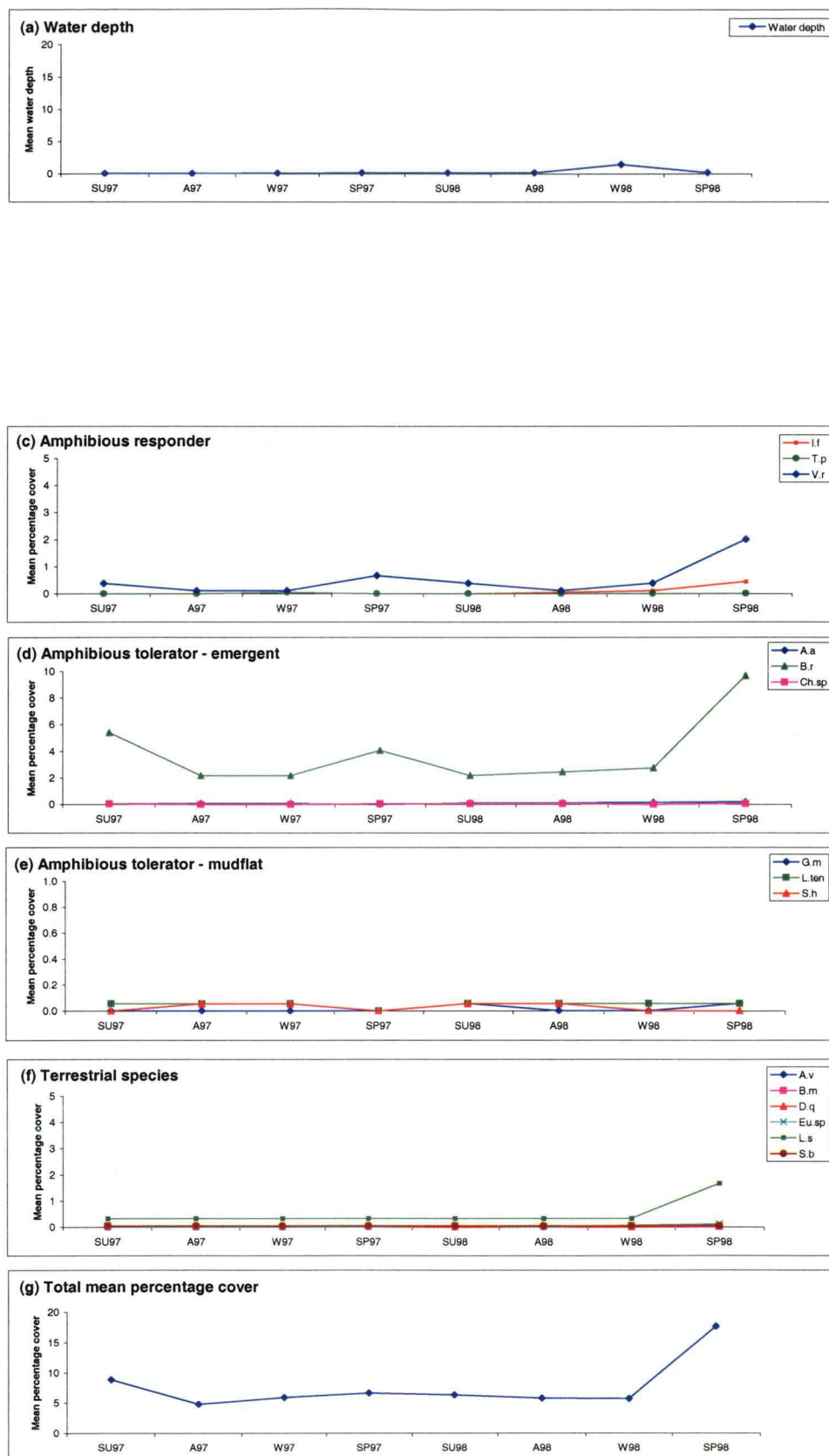


Figure 5.5 (a-2): Big Punchbowl outer *Baumea rubiginosa* zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

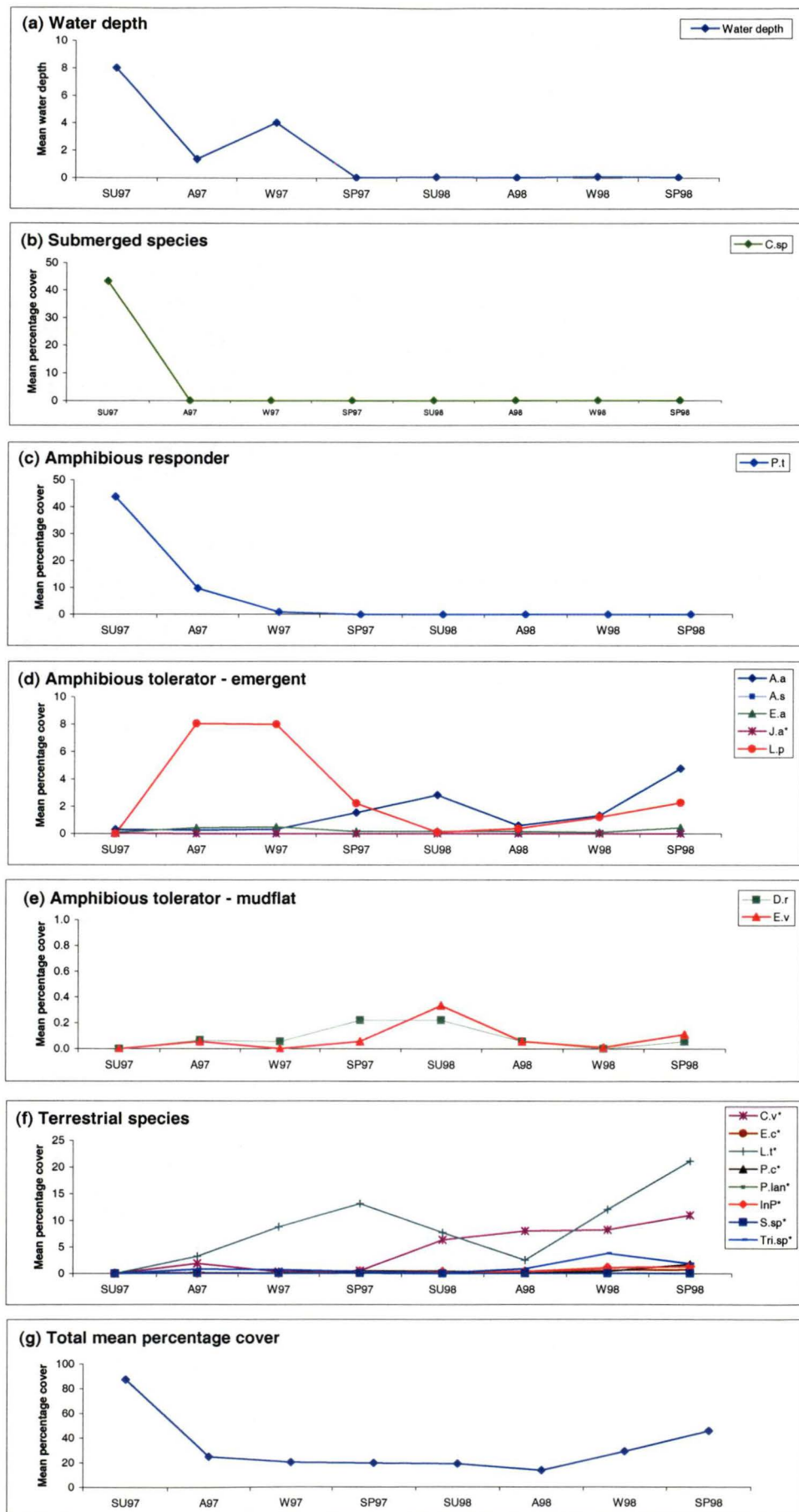


Figure 5.5 (b-1): Tin Dish aquatic zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean

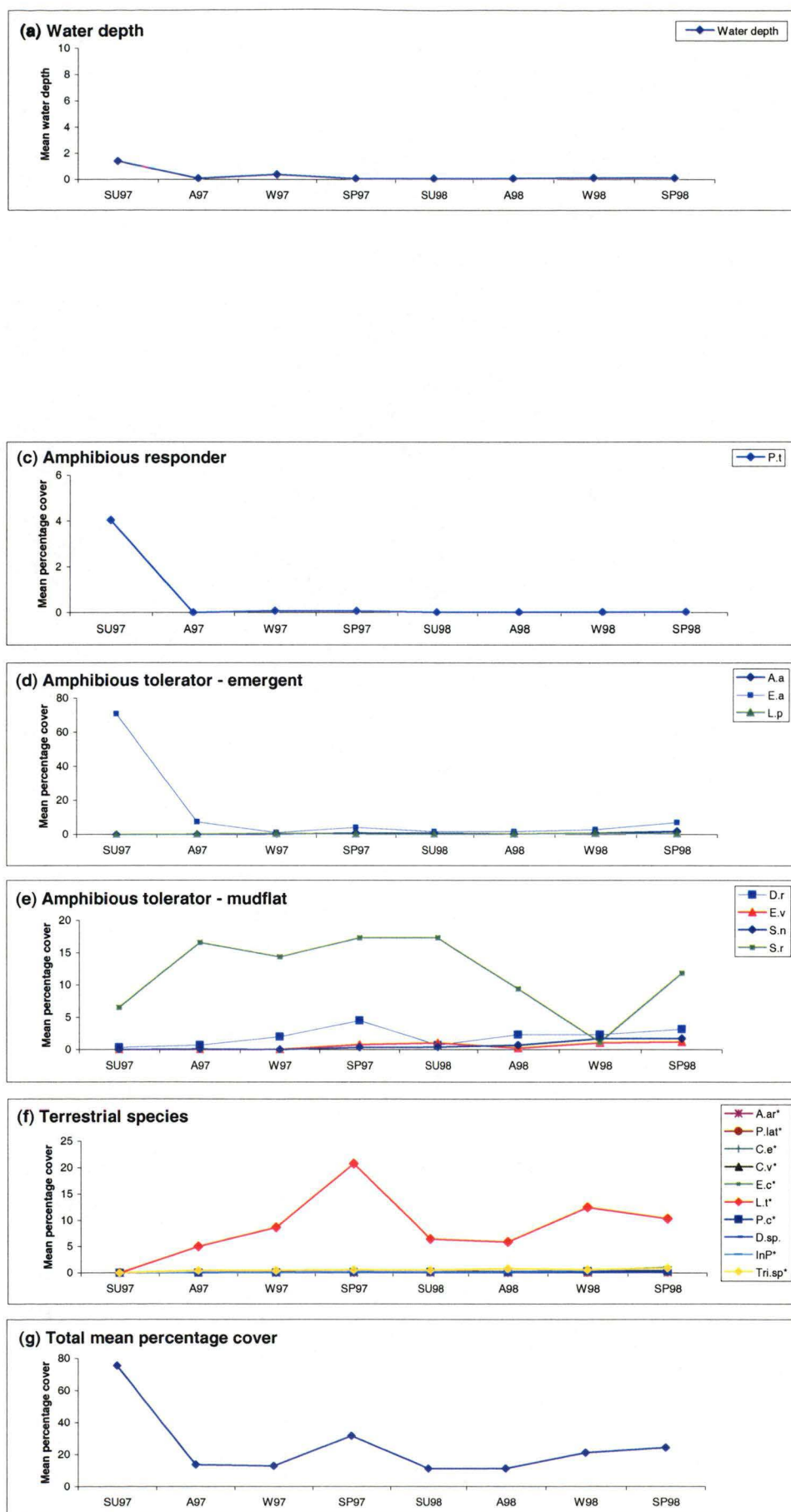


Figure 5.5 (b-2): Tin Dish *Eleocharis acuta* zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences

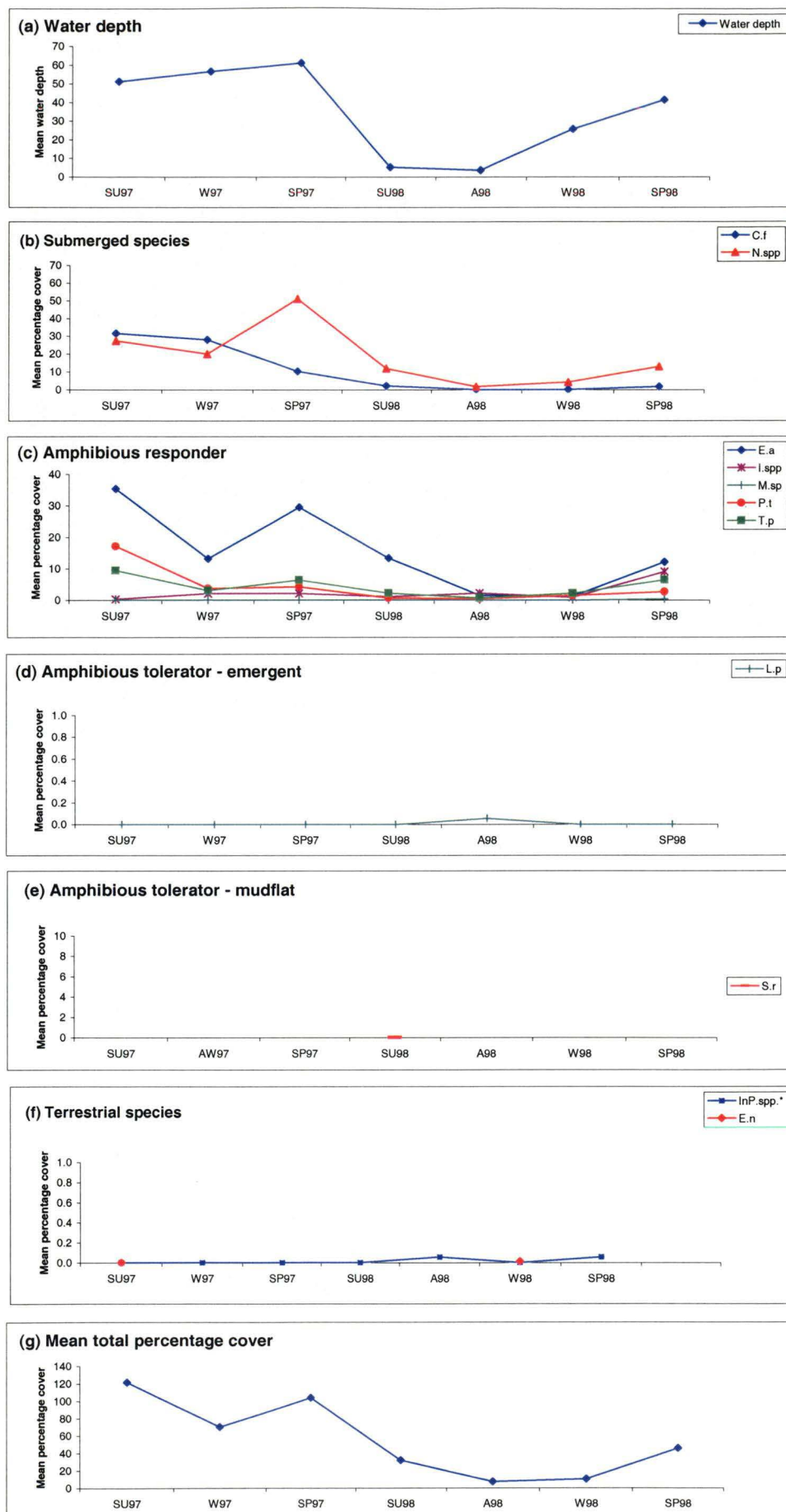


Figure 5.5 (c-2): Middle Lagoon *Eleocharis sp* - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences total mean percentage cover.

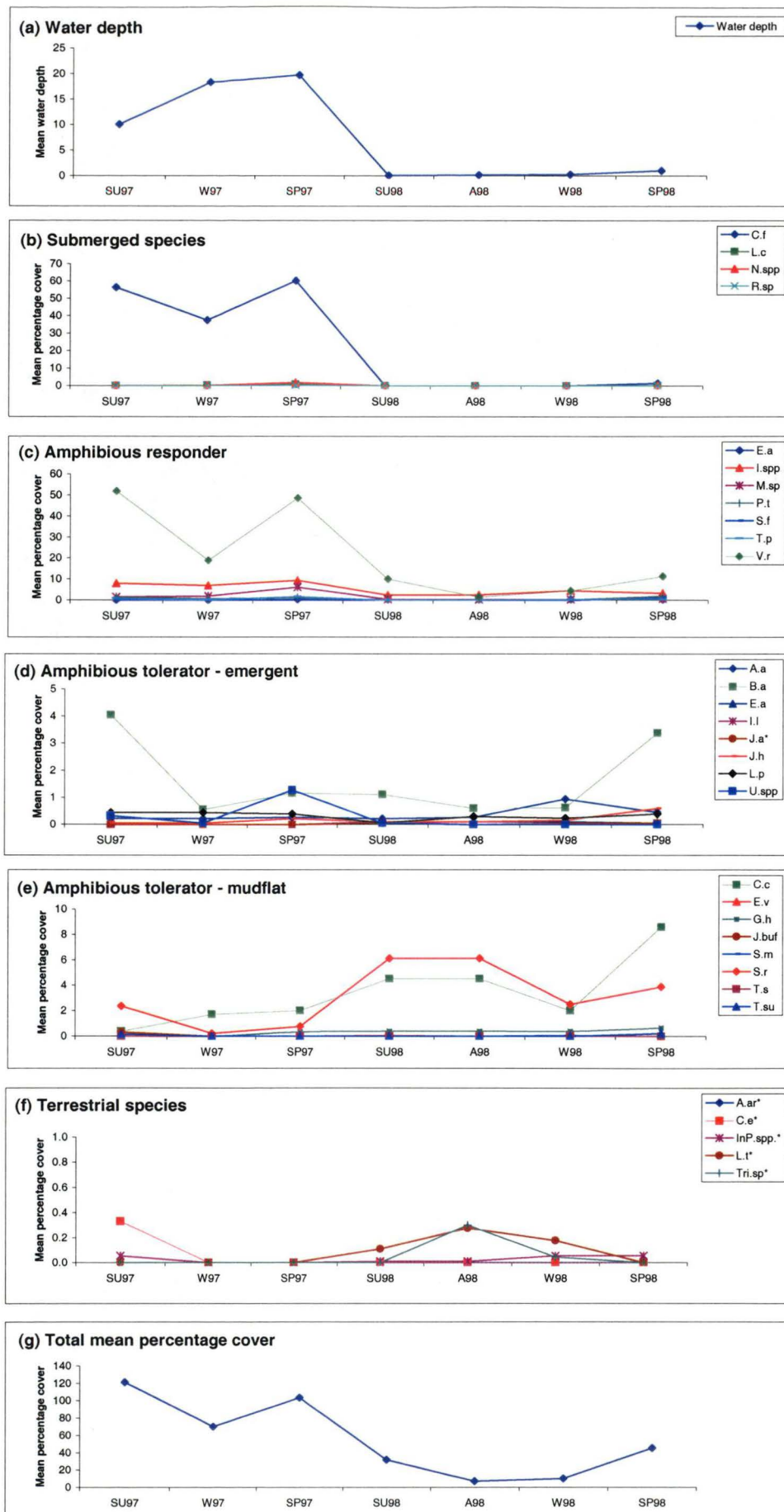


Figure 5.5 (c-1): Middle Lagoon aquatic herb zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individuals species within each functional group; (g) seasonal differences in total mean percentage cover.

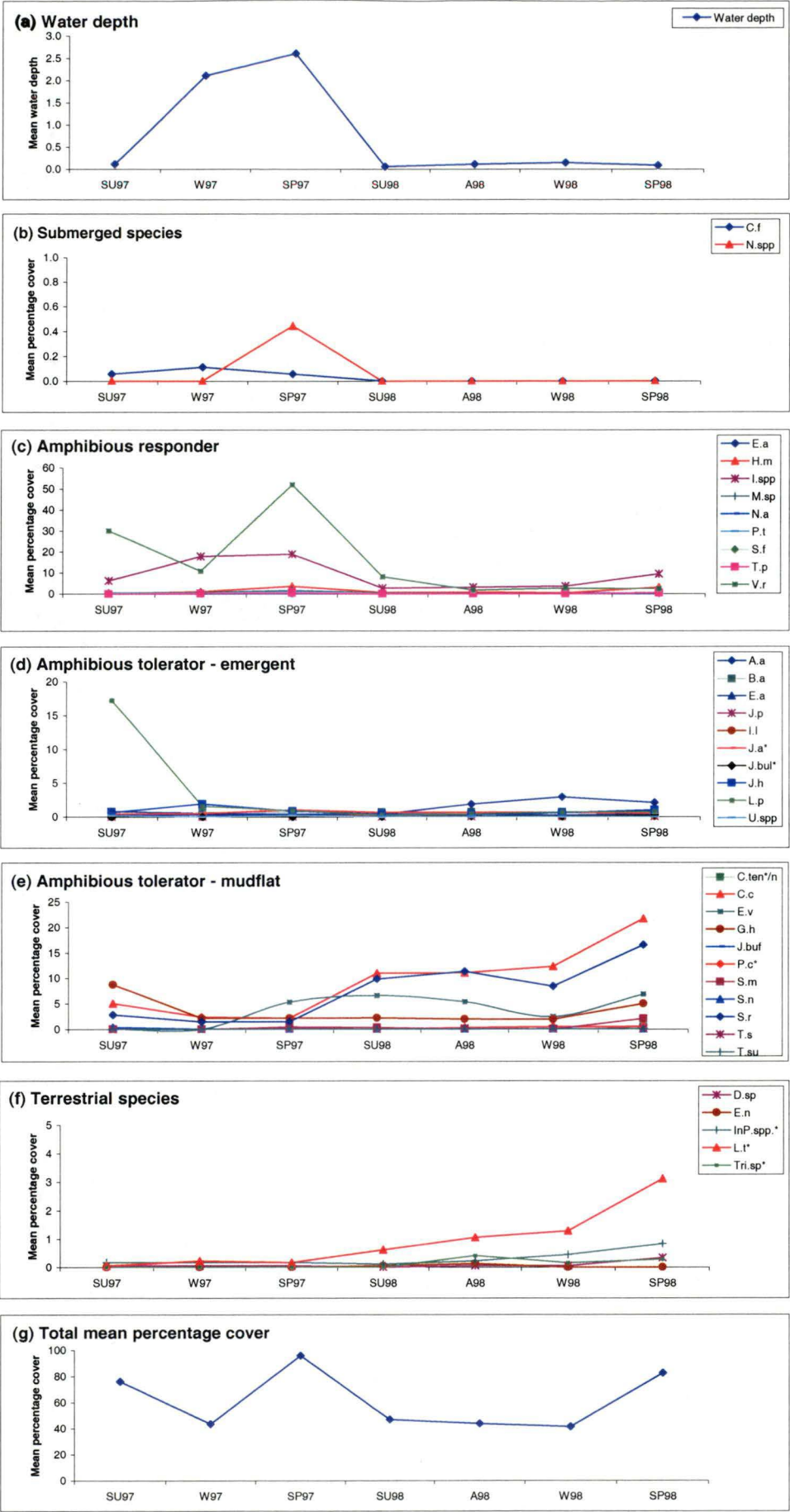


Figure 5.5 (c-3): Middle Lagoon Dry herbaceous zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

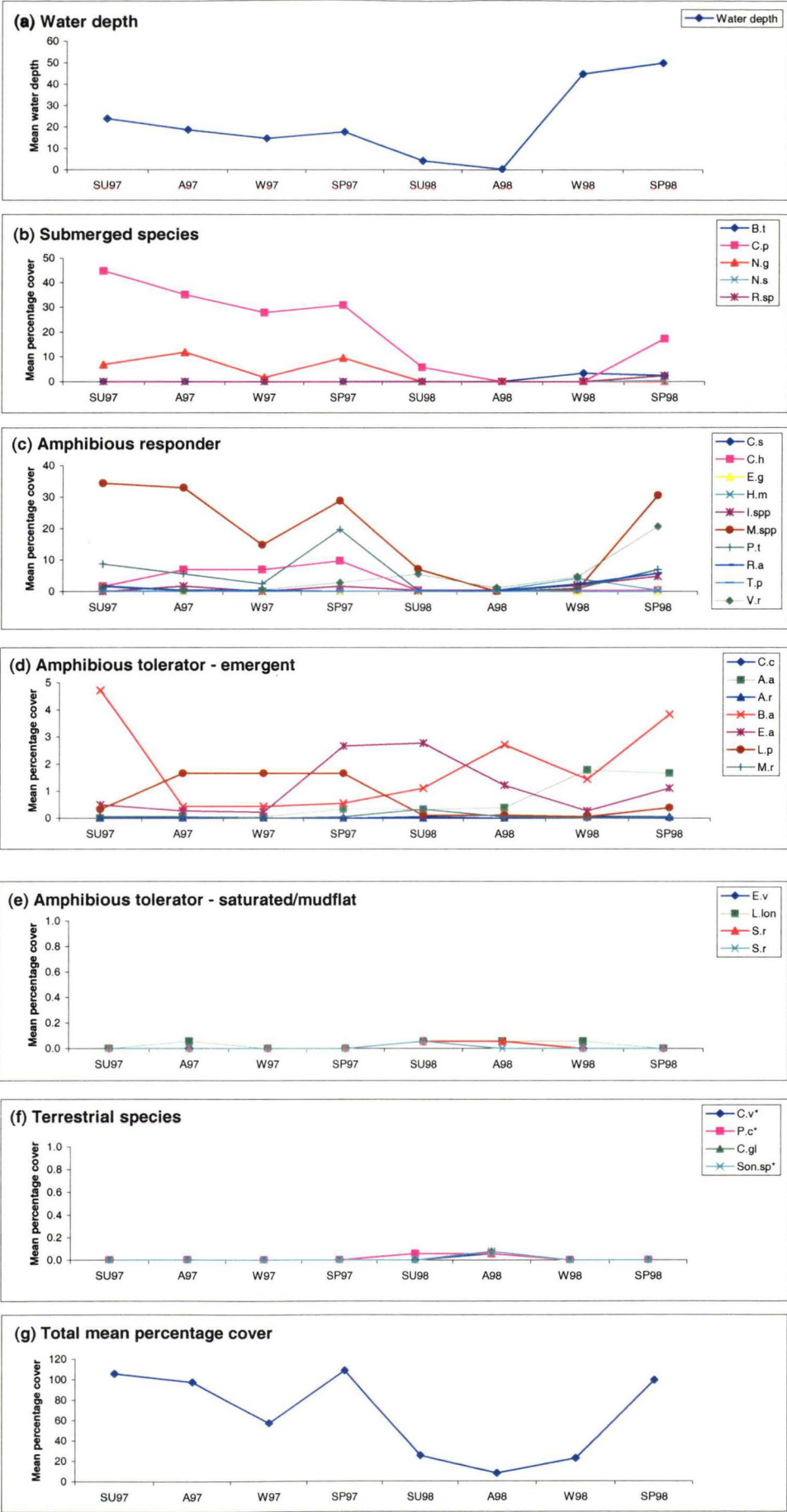


Figure 5.5 (d-1): Cherry Tree Lagoon aquatic herb zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

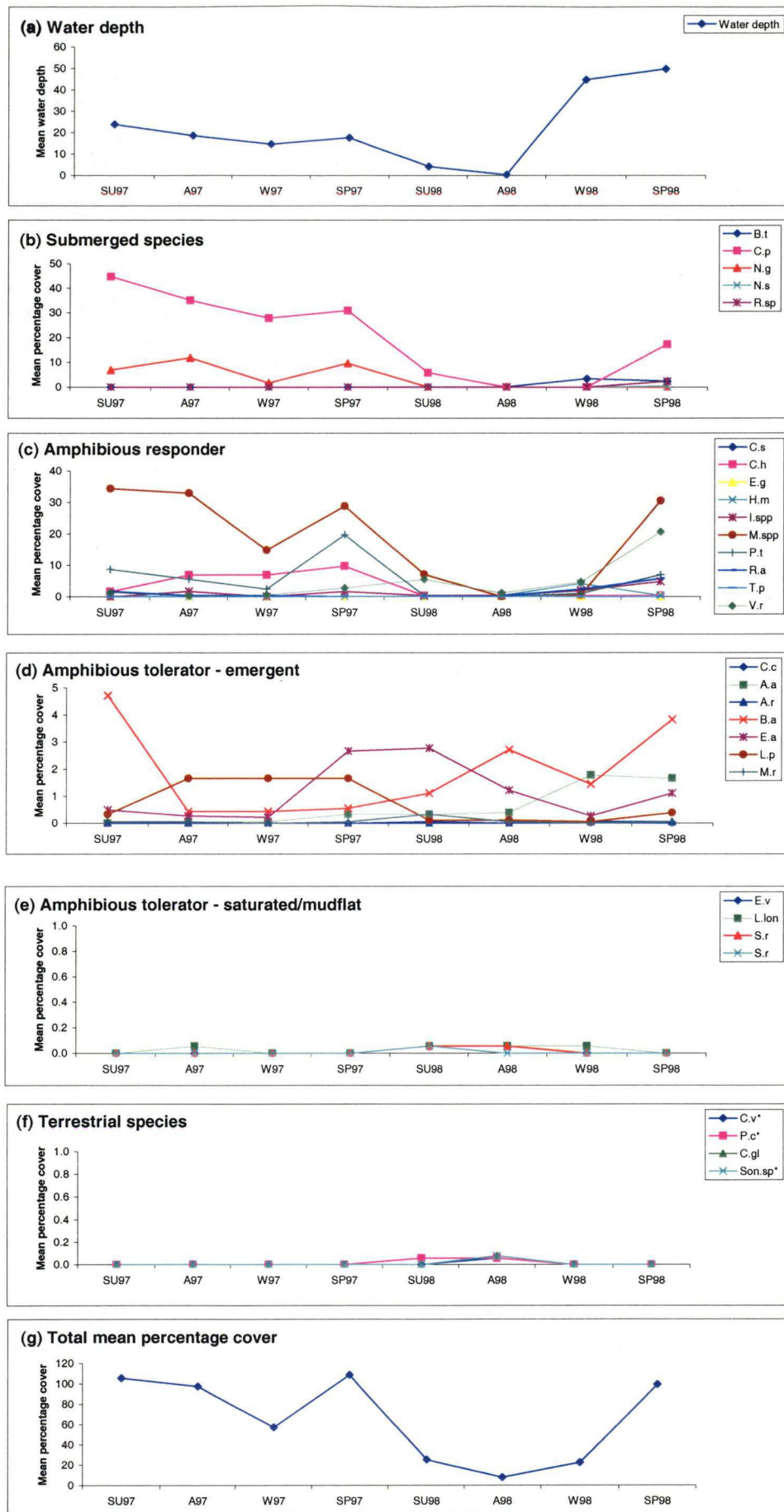


Figure 5.5 (d-1): Cherry Tree Lagoon aquatic herb zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

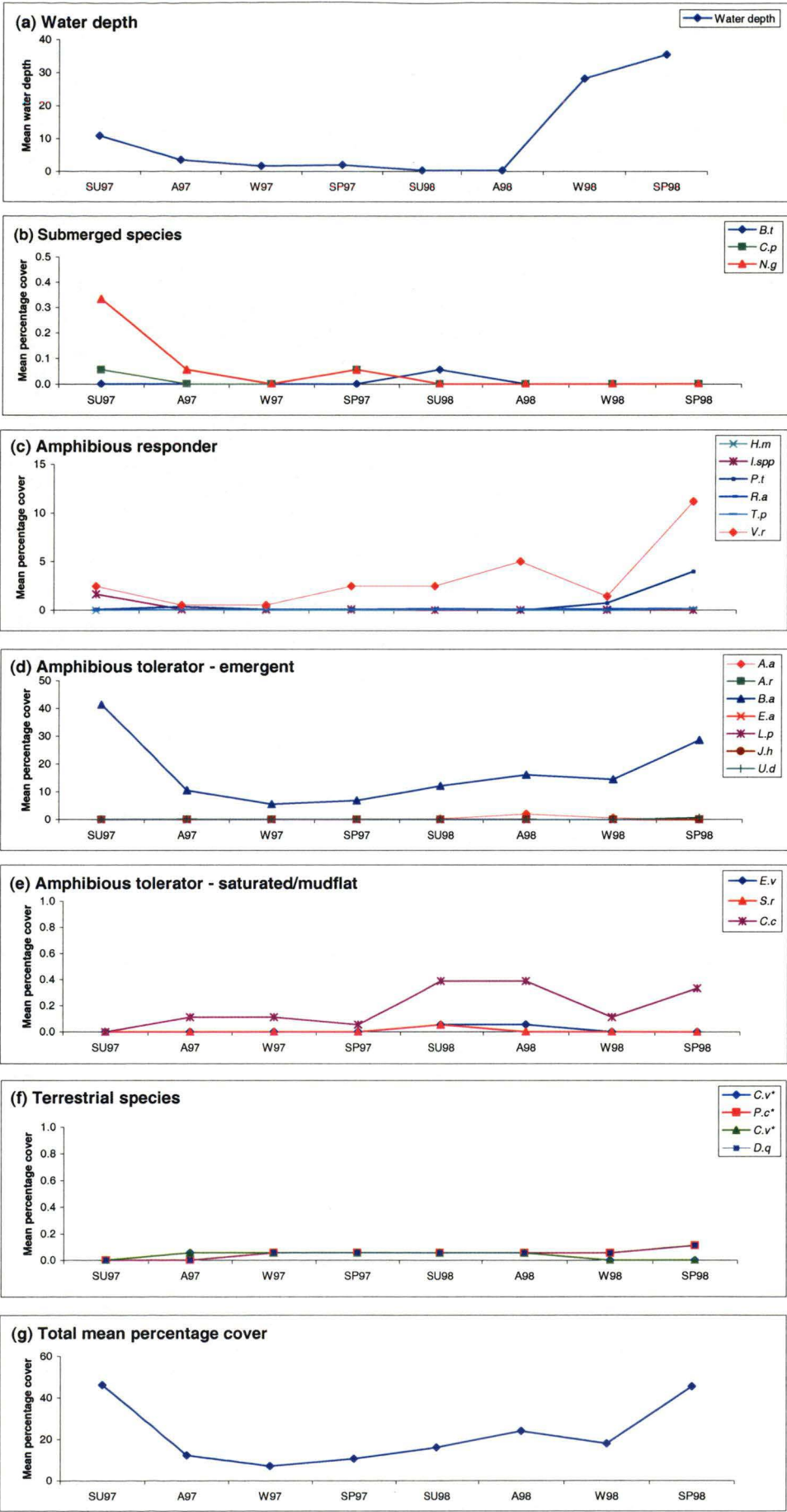


Figure 5.5 (d-2): Cherry Tree Lagoon *Baumea arthropphylla* zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

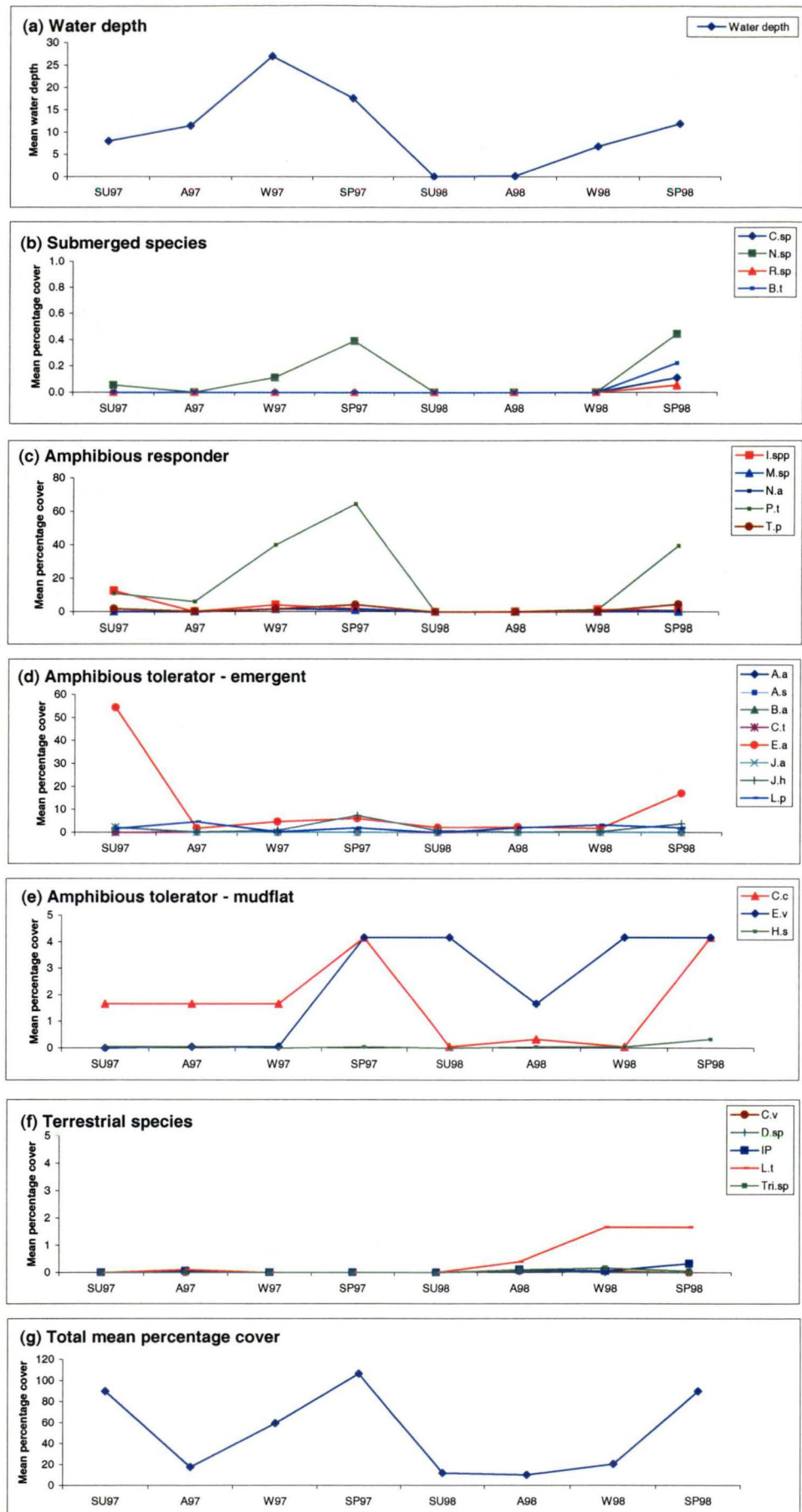


Figure 5.5 (c-1): Sandy Gate aquatic herb zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover.

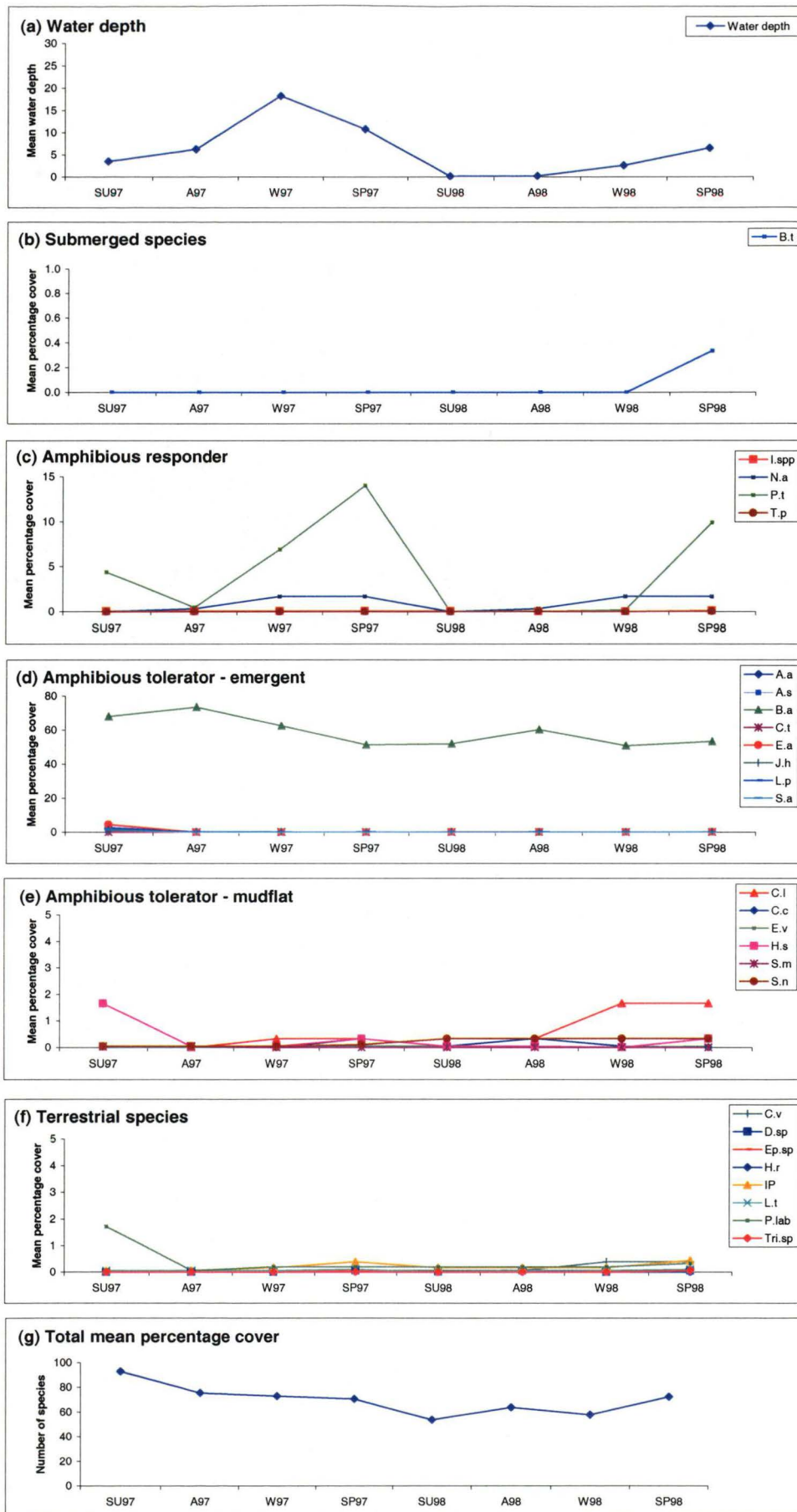


Figure 5.5 (e-2): Sandy Gate *Baumea arthropphylla* zone - (a-f) seasonal differences in mean water depth and mean percentage cover for individual species within each functional group; (g) seasonal differences in total mean percentage cover..

Table 5.5 Chi-square analysis to determine an association between functional group and the number of times that a taxa responded to a change in water level (Functional groups: S = submerged; Ar = amphibious responder; Atle = amphibious tolerator-emergent; Atls = amphibious tolerator-saturated mudflat; T = terrestrial).

df = 4	Response to a change in water presence or absence				Total
	Change in cover		No change in cover		
S	30	29.5	0	5.0	30
Ar	79	77.3	13	14.7	92
Atle	50	52.1	12	9.9	62
Atls	38	37.8	7	7.2	45
T	18	22.7	9	4.3	27
Total	215		41		256

Seasonal difference in percentage cover

Significant differences in seasonal percentage cover were recorded for nineteen taxa, that is, 20 % of the total taxa (Table 5.7). Within zones it was generally the dominant species in the community that showed significant changes in their percentage cover between seasons sampled.

All functional groups, except amphibious tolerator-saturated/mudflat, showed a significant difference in seasonal percentage cover (Table 5.8).

Table 5.6 2 x 2 contingency tables for Chi-square analyses (χ^2) to determine if the response in percentage cover of functional groups was independent of a change in water level state (W-D - wet to dry; D-W = dry to wet; \uparrow = increase in cover; \downarrow = decrease in cover; critical value at 0.05 = 3.841; *italics* = expected values; * = significant to 0.05; *** = significant to 0.0001; ns = not significant).

(a) Submerged species

Chi-square = 16.081; P = <.0001 ***

df = 1	Change in cover		Total
	\uparrow	\downarrow	
W-D	2 7.5	14 8.8	16
D-W	12 6.5	2 7.4	14
Total	14	16	30

(b) Amphibious responder species

Chi-square = 56.823; P = <.0001 ***

df = 1	Change in cover		Total
	\uparrow	\downarrow	
W-D	4 20.6	33 16.4	37
D-W	40 23.4	2 18.6	42
Total	44	35	79

(c) Amphibious tolerator-emergent species

Chi-square = 4.121; P = 0.0424 *

df = 1	Change in cover		Total
	\uparrow	\downarrow	
W-D	11 14.6	17 13.4	28
D-W	15 11.4	7 10.6	22
Total	26	24	50

(d) Amphibious tolerator-saturated/mudflat species

Chi-square = 13.074; P = .0003 ***

df = 1	Change in cover		Total
	\uparrow	\downarrow	
W-D	18 12.6	6 11.4	24
D-W	2 7.4	12 6.6	14
Total	20	18	38

d) Amphibious terrestrial species

Chi-square = 2.822; P = .2451 ns

df = 1	Change in cover		Total
	\uparrow	\downarrow	
W-D	10 8.6	1 2.4	11
D-W	4 5.4	3 1.6	7
Total	14	4	18

Table 5.7 Species that significantly changed in terms of percentage cover over the period of the present study (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate: E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; B.a = *Baumea arthropophylla*, B.r = *Baumea rubiginosa*: * = introduced species: */n = uncertain status; FG = Functional group; S = submerged; Ar = amphibious responder; Atle = amphibious tolerator- emergent; Atls = amphibious responder-saturated/mudflat; T = terrestrial; H-value = Krushal Wallis H value; Sig. = Significance; * = P = <0.05; ** =p <0.01; * = P <0.0001; bold = species that**

Species	FG		BP		TD		Zone			CTL		SG	
			B r	Aquatic B r Outer	Aquatic	E a	E s	MID	Dry	Aquatic	B a	Aquatic	B a
<i>Chara</i> spp	S	H-value P-value Sig			18.411 0.0102 *		27.637 0.0001 ***	47.052 0.0001 ***		16.243 0.023 *			
<i>Nitella</i> spp	S	H-value P-value Sig					34.708 0.0001 ***			18.344 0.0105 *			
<i>Potamogeton</i> <i>incarnatus</i>	Ar	H-value P-value Sig	14.886 0.0375 *		30.96 0.0001 ***		32.192 0.0001 ***	31.182 0.0001 ***	22.843 0.0009 ***	38.91 0.0001 ***		46.42 0.0001 ***	25.585 0.0006 ***
<i>Mynophyllum</i> spp	Ar	H-value P-value Sig						19.496 0.0034 **	19.406 0.0035 **	33.296 0.0001 ***			
<i>Villarsia</i> <i>reniformis</i>	Ar	H-value P-value Sig						38.813 0.0001 ***	41.913 0.0001 ***				
<i>Isolepis</i> spp	Ar	H-value P-value Sig					13.52 0.0355 *	26.005 0.0002 ***				19.041 0.0081 **	
<i>Eleocharis</i> <i>sphacelata</i>	Ar	H-value P-value Sig					29.699 0.0001 ***						
<i>Baumea</i> <i>arthrophylla</i>	Atle	H-value P-value Sig								23.382 0.0015 **			
<i>Eleocharis</i> <i>acuta</i>	Atle	H-value P-value Sig			33.736 0.0001 ***							19.061 0.008 **	
<i>Juncus</i> <i>holoschoenus</i>	Atle	H-value P-value Sig										17.201 0.0161 *	
<i>Utricularia</i> spp	Atle	H-value P-value Sig						38.813 0.0001 ***					
<i>Agrostis</i> <i>avenaceae</i>	Atle	H-value P-value Sig							17.052 0.009 **				
<i>Cyperus tenellus</i> */n	Atls								18.000 0.0062 **				
<i>Eryngium</i> <i>vesiculosum</i>	Atls	H-value P-value Sig							16.595 0.0109 *				
Introduced <i>Poaceae</i>	T	H-value P-value Sig			34.821 0.0001 ***	16.879 0.0182 ***							
<i>Cirsium</i> <i>vulgare</i> *	T	H-value P-value Sig			19.428 0.0069 **								
<i>Leontodon</i> <i>taraxacoides</i> *	T	H-value P-value Sig			38.108 0.0001 ***	30.608 0.0001 ***			22.763 0.0009 ***				
<i>Lilaeopsis</i> <i>polyantha</i>	T	H-value P-value Sig			24.211 0.001 **				10.692 0.0984 *				
<i>Trifolium</i> spp *	T	H-value P-value Sig			40.03 0.0001 ***	24.216 0.001 **		16.347 0.012 *	28.219 0.0001 ***				

Table 5.8 Functional groups within each zone that significantly changed over terms of their percentage cover over the period of the present study (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; S = Sandy Gate; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; B.a = *Baumea arthropphylla*; B.r = *Baumea rubiginosa*; FG = functional group; H-value = Kruskal-Wallis H Value; Sig. = significance; * = $P < 0.05$; * = $P < 0.0001$; ns = not significant; n/a = data not available).**

		Zone										
FG		BP		TD		MID			CTL		SG	
		B.r Aquatic	B.r Outer	Aquatic	<i>E. acuta</i>	<i>E. sphacelata</i>	Aquatic	Dry	Aquatic	<i>B. arthro.</i>	Aquatic	<i>B. arthro.</i>
Submerged	H-value	46.410	n/a	61.873	n/a	42.734	54.654	11.553	17.283	6.661	25.986	29.492
	P-value	<.0001		<.0001		<.0001	<.0001	0.0727	0.0157	.4650	0.0005	0.0001
	Sig	***		***		***	***	ns	*	ns	***	***
Amphibious responder	H-value	29.971	3.316	49.905	26.001	50.304	37.548	39.744	37.232	6.152	56.630	75.970
	P-value	<.0001	0.8543	<.0001	0.0005	<.0001	<.0001	<.0001	<.0001	0.5221	<.0001	<.0001
	Sig	***	ns	***	***	***	***	***	***	ns	***	***
Amphibious tolerator-emergent	H-value	19.283	23.802	20.798	38.975	0.012	11.923	12.704	10.376	21.787	34.631	22.833
	P-value	0.0073	0.0012	0.0041	<.0001	>0.9999	0.0637	0.0480	0.1682	0.0028	<.0001	0.0018
	Sig	**	**	**	***	ns	ns	*	ns	**	***	**
Amphibious tolerator Saturated/mudflat	H-value	n/a	1.111	6.914	2.421	6.000	6.582	20.001	4.180	3.100	0.035	0.434
	P-value		0.9928	0.4379	0.929	0.4232	0.3612	0.0628	0.7589	0.8756	>.9999	0.9996
	Sig		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Terrestrial	H-value	n/a	3.484	45.337	36.791	8.876	31.156	28.446	29.208	2.923	15.585	7.681
	P-value		0.8370	<.0001	<.0001	0.1807	<.0001	<.0001	0.0001	0.8920	0.0292	0.3616
	Sig		ns	***	***	ns	***	***	***	ns	*	ns

Community composition

Water regime categories

A transition between wet and dry conditions occurred in most zones over the period of the study (Table 5.9). The *Eleocharis sphacelata* zone of Middle Lagoon remained inundated for the total period of the study, whereas, the outer *Baumea rubiginosa* zone of Big Punchbowl was dry during the spring and summer of both 1997 and 1998.

Table 5.9 Allocation of zones into duration of inundation categories based on the presence (W) or absence (D) of lying water during the beginning (summer) and end (spring) seasons over a year period.

Zone	1997	1998
BP <i>Baumea rubiginosa</i> aquatic	D-D	D-W
BP <i>Baumea rubiginosa</i> outer	D-D	D-D
TD aquatic	W-D	D-D
TD <i>Eleocharis acuta</i>	W-D	D-D
MID <i>Eleocharis sphacelata</i>	W-W	W-W
MID aquatic	W-W	D-W
MID dry herbaceous	D-W	D-D
CTL aquatic	W-W	D-W
CTL <i>Baumea arthropphylla</i>	W-W	D-W
SG aquatic	W-W	D-W
SG <i>Baumea arthropphylla</i>	W-W	D-W

Seasonal differences in community composition

Evidence of seasonal differences in percentage cover was observed within both stable water regime categories (Table 5.10; Figure 5.6). In the 'wet to wet' category both spring and summer had a significantly higher vegetation cover than was found in both autumn and winter (Figure 5.6; Table 5.11). In the 'dry to dry' category the summer vegetation cover was significantly higher than in all other seasons.

There was no seasonal difference in species richness in both water regime categories (Table 5.11; Figure 5.7).

Table 5.10 Community dynamics: result of one factor ANOVA for differences in percentage cover and species richness between seasons.

Type III sums of squares

Source of variation	d.f	M.S	F-Value	P-Value	Sig.
Percentage cover					
Wet to Wet	3	8473.030	6.387	0.0008	***
Dry to Dry	3	9.856	4.926	0.0101	*
Species richness					
Wet to Wet	3	0.068	0.345	0.7928	ns
Dry to Dry	3	0.014	0.208	0.8900	ns

* = significant to 0.05; *** = significant to 0.05

Table 5.11 Community dynamics: seasonal means for percentage cover and results from Fisher's *post hoc* test from one factor ANOVA for differences in cover between seasons (Letters run across rows and indicate which seasons are significantly different. Seasons with same letters are not significantly different).

Water regime	SU97	A97	W97	SP97
Wet to Wet	97a	50 b	56 b	88 a
Dry to Dry	5 a	3 b	3 b	4 b

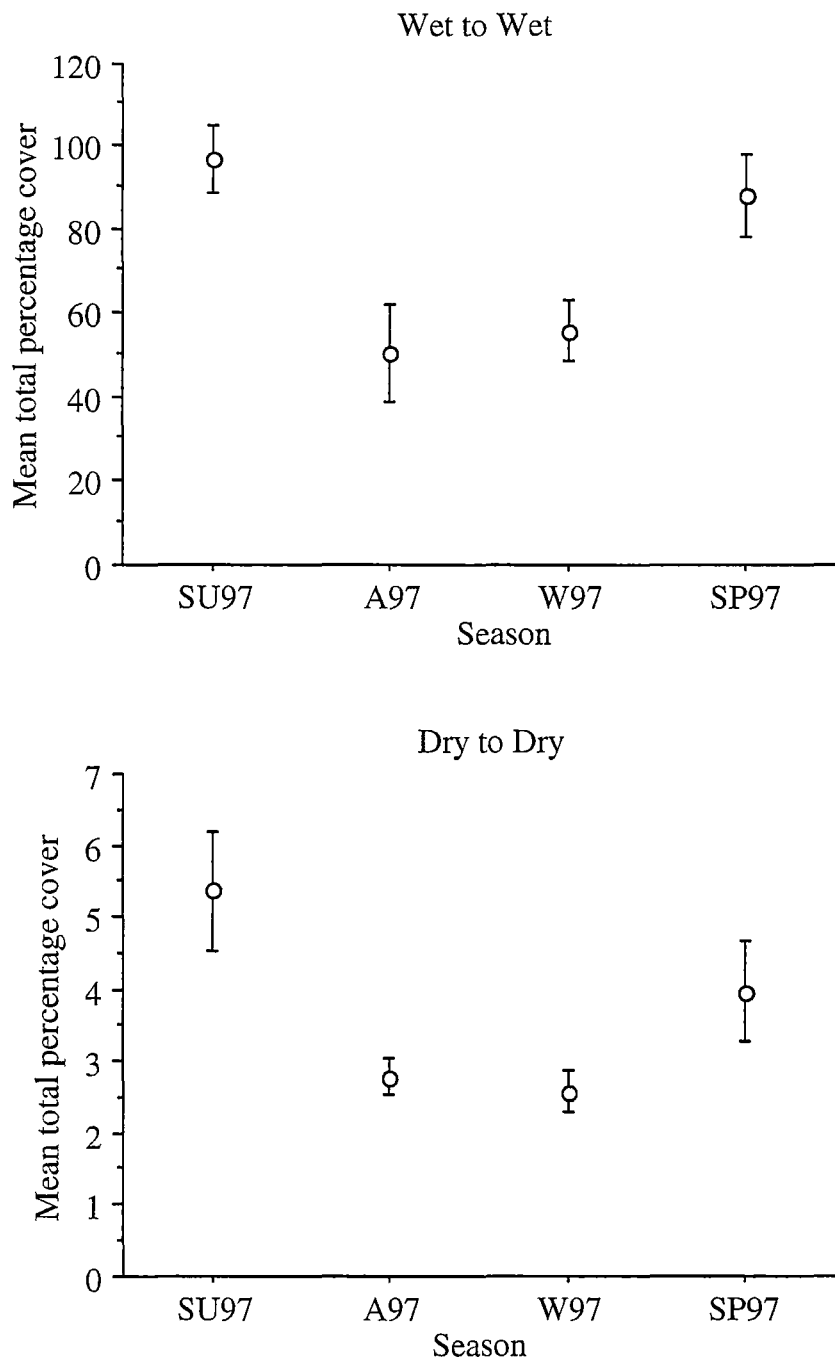


Figure 5.6 Mean seasonal percentage cover for zones with stable 'Wet to Wet' and 'Dry to Dry' water regime (error bars = ± 1 standard error).

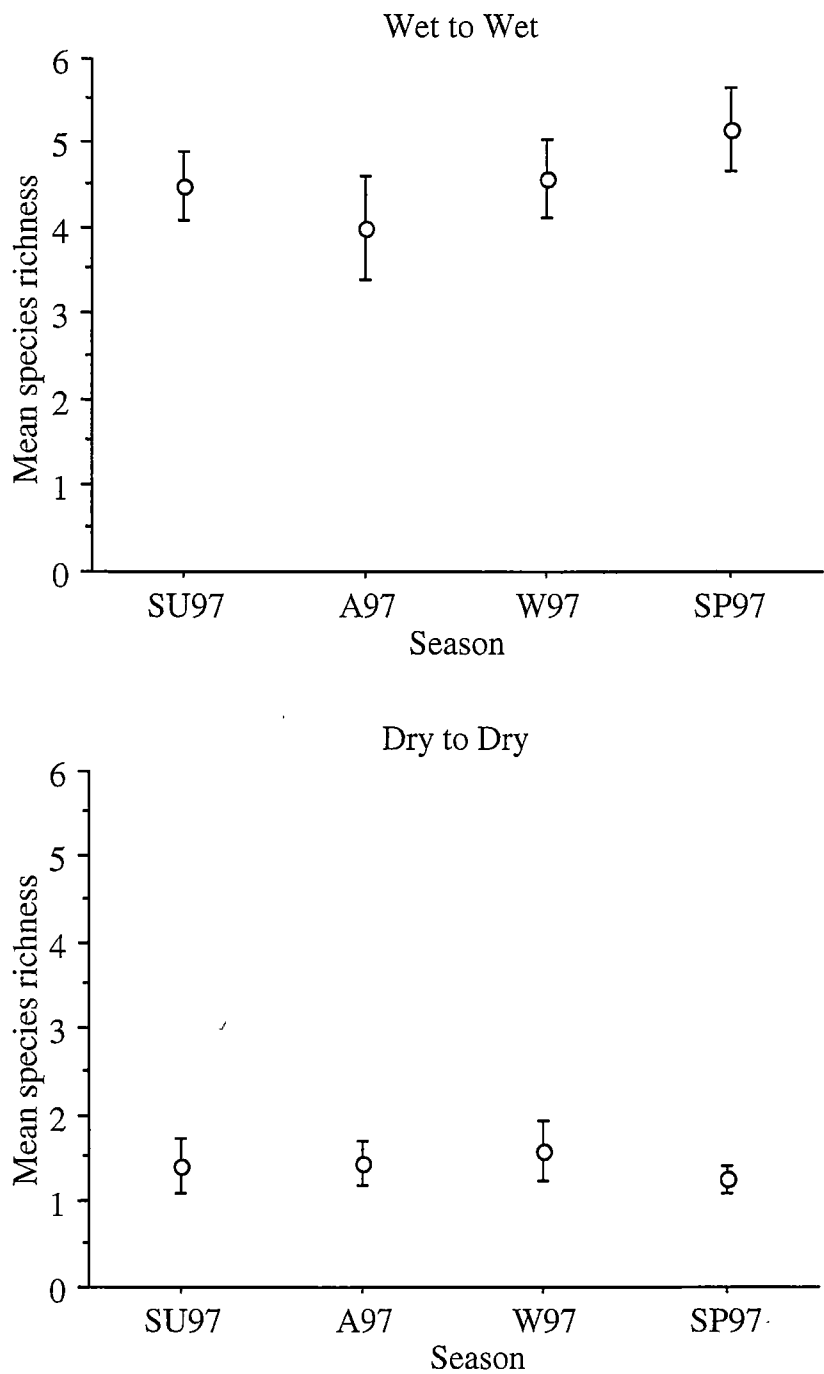


Figure 5.7 Mean seasonal species richness for zones with stable 'Wet to Wet' and 'Dry to Dry' water regime (error bars = ± 1 standard error).

Difference in community composition with water regime 'type'

Magnitude of community change

Community change was significantly greater within a year if a zone went from wet to dry (W-D) than if it went from dry to wet (D-W; Figure 5.8). It was also significantly greater if it went from dry to wet than if it either remained dry or remained wet.

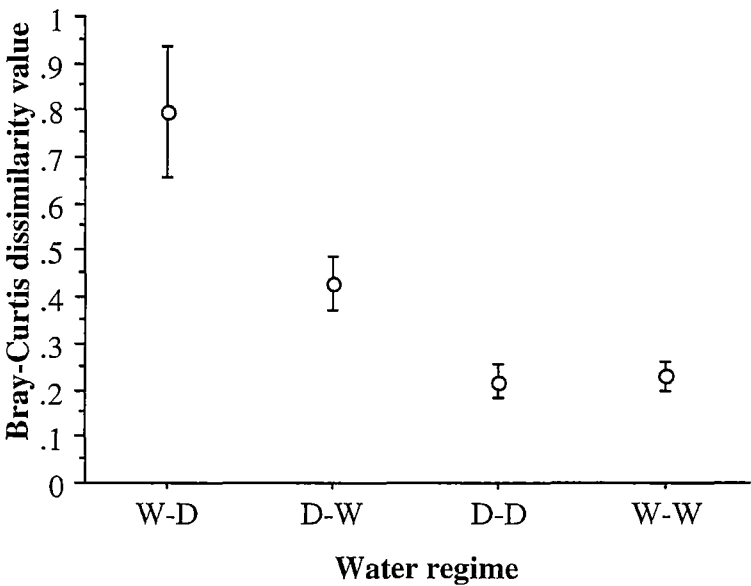


Figure 5.8 Comparison between the changes in vegetation over time with varying water regimes (W-D = wet to dry; D-W = Dry to Wet; D-D = dry to dry; W-W = wet to wet).

Percentage cover

Significant differences in both total and functional group percentage cover were found between zones within the different water regime categories (Table 5.12; Figure 5.9). The highest total percentage cover was found in zones that had remained wet over the year period, with the lowest occurring in zones that had remained dry (Figure 5.9 a). The percentage cover for the "wet to wet" (W-W) water regime was significantly higher than all other water regimes. However, the percentage cover for "dry to dry" (D-D), although significantly different to the "dry to wet" (D-W) regime, was not significantly different to that of the "wet to dry" (W-D) regime (Table 5.12). Therefore, the percentage cover of zones that ended in dry conditions were closer to each other than those that ended in wet conditions. This was also true for most functional groups.

Significant differences only occurred between dry ending water regimes, in the terrestrial group (T), where the "wet-dry" regime had significantly higher terrestrial cover than the "dry to dry" different (Figure 5.9f; Table 5.12). For wet ending regimes the "wet to wet" regime had significantly higher percentage cover of submerged (S) and amphibious responder (Ar) species and significantly lower amphibious tolerator-emergent (Atle) species than the "dry to wet" regime. It was only in the more dry habitat groups, amphibious saturated/mudflat (Atls) and terrestrial (T), that the regimes ending in wet conditions were not significantly different (Figure 5.9 e-f; Table 5.12). Both groups had low percentage cover in wet ending water regimes.

Species richness

Less variation in species richness was observed between each water regime category than was observed for percentage cover as described above (Table 5.12; Figure 5.10). There was no significant difference between the total species richness found at the end of each water regime ($Z_{3\ 60} = 2.145$, $P = 0.5419$; Table 5.12; Figure 5.10).

Within functional groups non-significant results were found between the species richness of each water regime for both amphibious tolerator-emergent (Atle) and saturated/mudflat (Atls) groups ($Z_{3\ 60} = 3.583$, $P = 0.3102$; $Z_{3\ 60} = 5.843$, $P = 0.1195$).

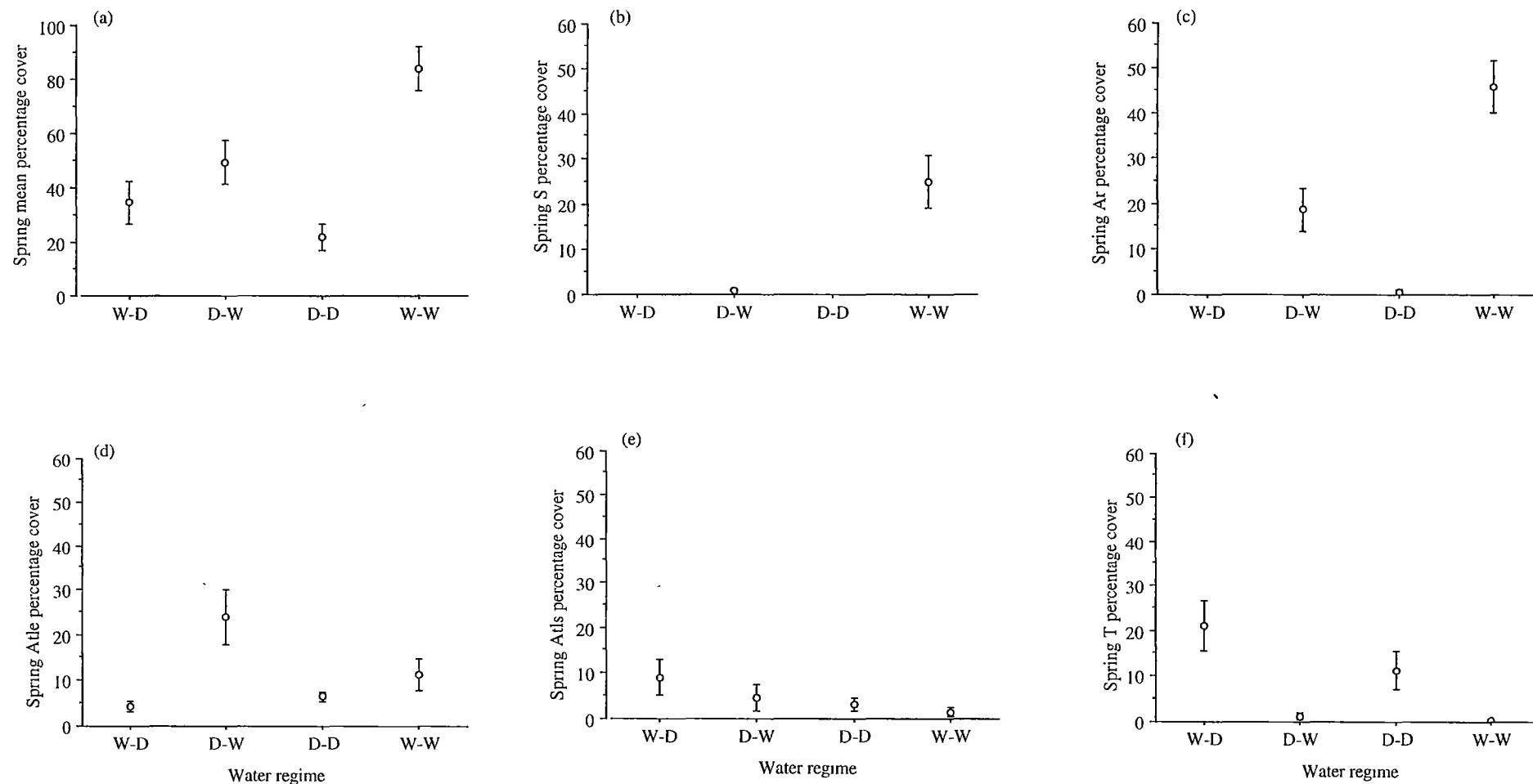


Figure 5.9 Spring total and functional group percentage cover for water regime categories. (a) Total; (b) submerges (S) group; (c) amphibious responder (Ar) group; (d) amphibious tolerator-emergent (Atle) group; (e) amphibious tolerator-saturate/mudflat (Atls) group; (f) terrestrial (T) group. Data presented are from the spring seasons at the end of each year period (water regime categories: W-D = 'wet to dry'; D-D = 'dry to dry'; W-W = 'wet to wet'; error bars = \pm standard error).

Table 5.12 (a) Spring mean and median species richness and percentage cover for water regime categories. Top number = mean; Lower number = median; Letters run across rows and indicate significant differences between categories indicated from Mann-Whitney U *post hoc* tests. Medians with the same letter are not significantly different; (b) results from Kruskal-Wallis test using water regime as the independent factor.

Variable	(a) Water regime category				(b) Kruskal-Wallis (df = 3)	
	W-D	D-W	D-D	W-W	Z-score	P-value
Percentage cover						
Total	34.7 33.5 ab	57.1 54.3 b	31.8 24.5 a	84.1 95.1 c	19.492	0.0002
Submerged (S)	0.0 0.0 a	0.7 0.6 b	0.0 0.0 a	25.0 1.3 c	28.565	<.0001
Responder (Ar)	0.03 0.0 a	28.7 21.6 b	3.5 0.0 a	45.9 45.8 b	38.265	<.0001
Tolerator-emergent (Atle)	4.4 3.3 a	20.9 9.3 b	6.5 6.2 a	11.3 4.5 a	8.927	0.0303
Tolerator-sat/mudflat (Atls)	9.1 7.8 a	5.8 0.4 ab	11.5 6.1 ab	1.5 0.0 b	8.076	0.0445
Terrestrial (T)	21.1 18.5 a	1.1 0.0 b	10.3 3.2 c	0.2 0.0 b	30.356	<.0001
Species richness						
Total	6.9 7	7.8 6.5	7.0 6.5	6.1 5.7	2.145	0.5419
Submerged (S)	0.0 3.0 a	0.7 0.7 b	0.0 0.0 a	0.9 1.0 b	24.345	<.0001
Responder (Ar)	0.1 0.0 a	3.2 3.0 b	1.0 0.0 a	3.1 3.7 b	24.867	<.0001
Tolerator-emergent (Atle)	1.8 1.9	2.5 2.0	2.3 1.7	1.5 1.3	3.583	0.3102
Tolerator-sat/mudflat (Atls)	1.0 1.0	0.9 0.0	1.3 0.4	0.2 0.0	5.843	0.1195
Terrestrial (T)	4.1 4.3 a	0.4 0.0 b	2.4 1.5 c	0.3 0.0 b	26.231	<.0001

Significant differences between species richness of each water regime were found for the submerged, amphibious responder and terrestrial groups ($Z_{3,60} = 24.345$, $P = <0.0001$; $Z_{3,60} = 24.867$, $P = <0.0001$; $Z_{3,60} = 26.231$, $P = <0.0001$). Significantly less species were found in dry ending regimes (i.e. 'wet to dry' and 'dry to dry') than wet ending regimes ('dry-wet' and 'wet to wet') for both submerged (S) and amphibious responder (Ar) groups (Figure 5.10 b-c; Table 5.12). In contrast, within terrestrial species significantly more species were found in dry ending regimes (i.e. 'wet to dry' and 'dry to dry') than wet ending regimes ('dry-wet' and 'wet to wet') (Figure 5.10 f; Table 5.12). Generally, there was no significant difference in species richness between

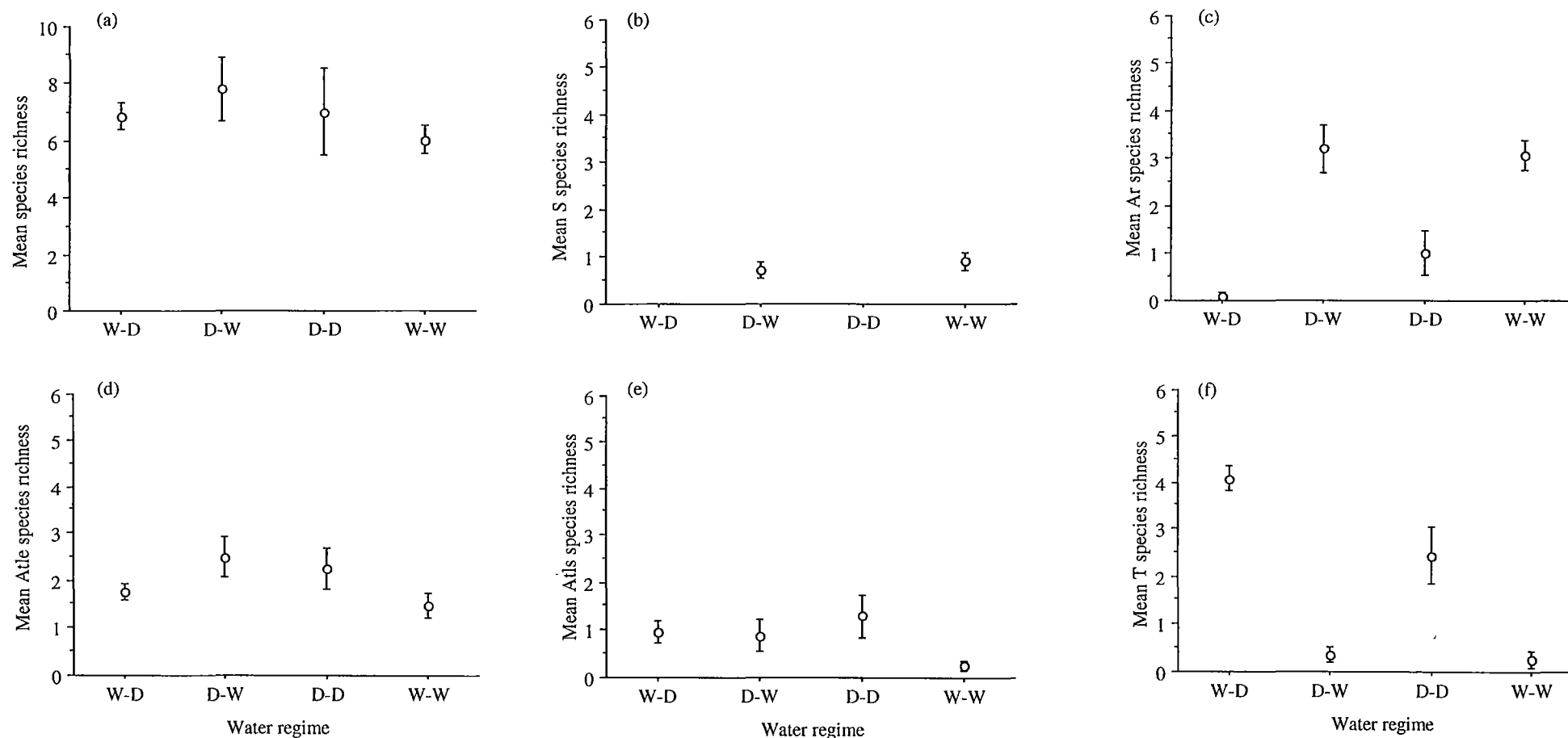


Figure 5.10 Spring total and functional group species richness for water regime categories. (a) Total; (b) submerges (s) group; (c) amphibious responder (Ar) group; (d) amphibious tolerator-emergent (Atle) group; (e) amphibious tolerator-saturate/mudflat (Atls) group; (f) terrestrial (T) group. Data presented are from the spring seasons at the end of each year period (water regime categories: W-D = 'wet to dry'; D-D = 'dry to dry'; W-W = 'wet to wet'; error bars = \pm standard error).

water regimes ending in the same water level state, that is, between 'wet to wet' and 'dry to wet' or 'wet to dry' and 'dry to dry'. However, within the terrestrial group there were significantly more species recorded in the 'wet-dry' regime than in the 'dry-dry' regime.

Differences in the representation of functional groups with water regime

Significant differences in the representation of functional groups, in terms of both percentage cover and species richness, were observed both between and within water regime categories (Table 5.13; Figure 5.11). Zones that experienced "wet to dry" and "dry to dry" conditions were similar in their functional group representation in that both were dominated by terrestrial and amphibious saturated/mudflat species cover. However, terrestrial species cover was greater in the 'wet to dry' than 'dry to dry' category.

The dominant functional groups in zones that experienced 'dry-wet' and 'wet to wet' were more varied between each other than were the 'wet to dry' and 'dry to dry' categories (Table 5.13; Figure 5.11). Zones that had remained inundated, that is, wet to wet' were dominated by amphibious responder and submerged species. Zones that experienced 'dry to wet' conditions were also dominated by amphibious responder species. However, in this case the secondary dominant group was amphibious tolerator-emergent.

Generally, similar patterns to percentage cover reported above were observed for functional group species richness both within and between water regime categories (Figure 5.11). The 'wet to dry' and 'dry to dry' were dominated by terrestrial species with the second highest mean species richness in the amphibious tolerator-emergent group. No submerged species were recorded in these categories. Similar to percentage cover, the difference between the species richness of the terrestrial group and the other groups was much greater in the 'wet to dry' category than in the 'dry to dry' category (Figure 5.11). In the 'wet to dry' category the terrestrial species richness was significantly different to all other functional groups, whereas, in the 'dry-dry' category it was not significantly different to both the amphibious tolerator-emergent and tolerator-saturated groups (Table 5.13).

The zones that experienced a 'dry to wet' and 'wet to wet' water regimes had a similar pattern of species richness between functional groups (Figure 5.11). Both categories had the highest mean species richness in the amphibious responder group with the second highest being in amphibious tolerator-emergent. The lowest mean species richness was found in the drier habitat groups, that is, amphibious tolerator-saturated/mudflat and terrestrial groups.

Table 5.13 (a) Spring mean functional group species richness and percentage cover for water regime categories. Top number = mean; Lower number = variance. Letters run across rows and indicate significant differences between functional groups indicated from Mann-Whitney U *post hoc* tests. Variances with a different letter are significantly different; (b) results from Kruskal-Wallis test using functional group as the independent factor (Functional groups: S = submerged; Ar = amphibious responder; Atle = amphibious tolerator-emergent; Atls = amphibious tolerator-saturated/mudflat; T = terrestrial).

Variable	(a) Functional group					(b) Kruskal-Wallis (df = 4)	
	S	Ar	Atle	Atls	T	Z-score	P-value
Percentage cover							
Wet - Dry (W-D)	0 0 0.0a	0 03 0.0 a	4.4 3.3 b	9.1 7.8 bc	21.1 18.5 c	21.952	0.0002
Dry - Wet (D-W)	0.7 0.6 a	28.7 21.6 b	20.9 9 3 b	5.8 0 4 a	1 1 0.0 a	47 933	<.0001
Dry - Dry (D-D)	0.0 0.0 a	3 5 0.0 b	6 5 6.2 c	11.5 6 1 c	10 3 3.2 c	32 619	< 0001
Wet - Wet (W-W)	25 0 1.3a	45.9 45.8 b	11.3 4.5 c	1.5 0.0 d	0.2 0 0 d	65 637	<.0001
Species richness							
Wet - Dry (W-D)	0.0 3.0 a	0.1 0.0 a	1 8 1.9 b	1.0 1.0 c	4.1 4.3 d	25.929	<.0001
Dry - Wet (D-W)	0.7 0.7 a	3.2 3 0 b	2 5 2.0 b	0.9 0.0 a	0.4 0.0 a	38 489	< 0001
Dry - Dry (D-D)	0.0 0.0 a	1.0 0.0 b	2.3 1.7 c	1 3 0.4 b	2 4 1.5 c	5.028	<.0001
Wet - Wet (W-W)	0.9 1.0 a	3.1 3.7 c	1 5 1.3 a	0.2 0.0 b	0.3 0.0 b	53.849	<.0001

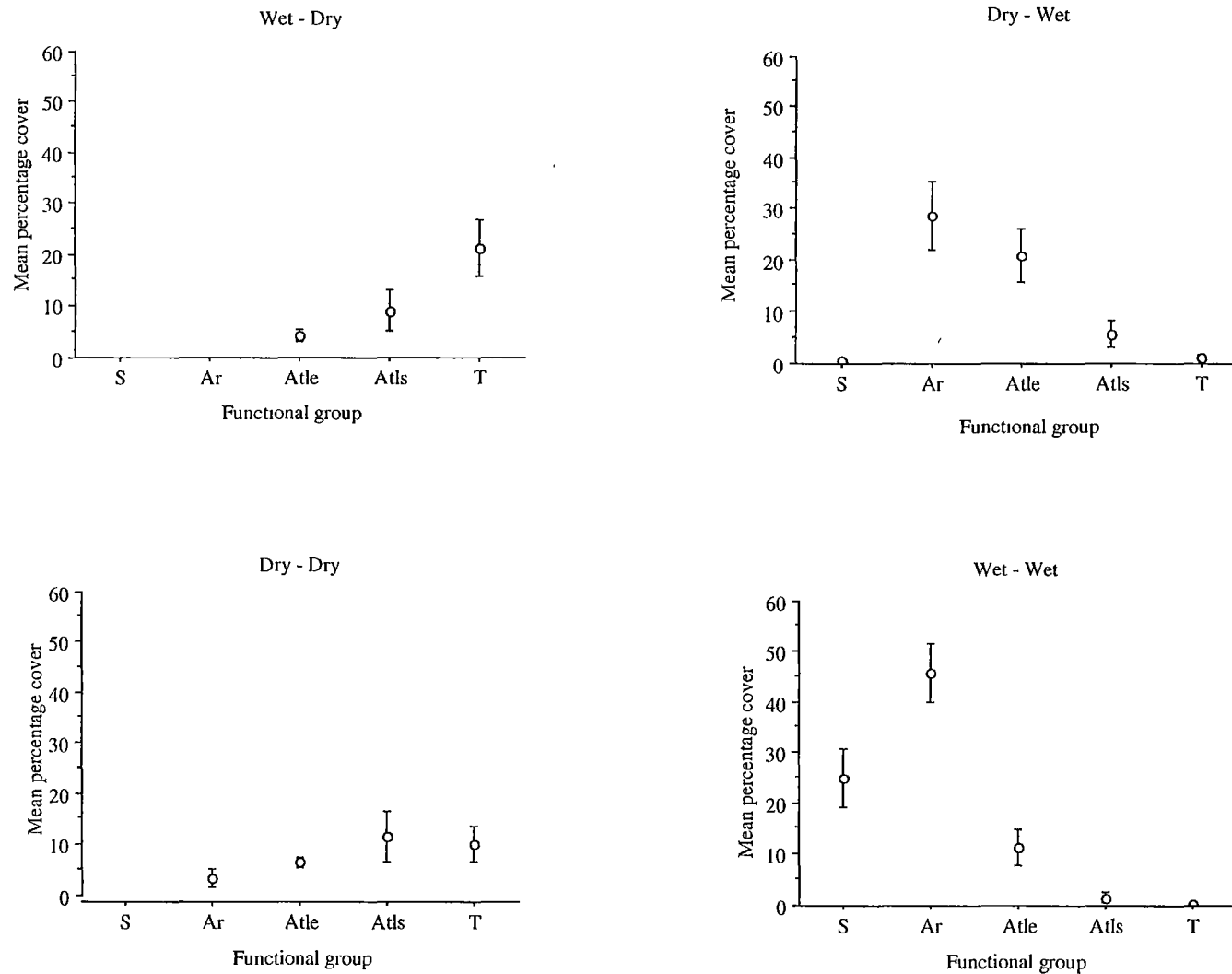


Figure 5.11 Functional group mean percentage cover recorded for each water regime category (S = submerged; Ar = amphibious responder (Ar); Atle = amphibious tolerator-emergent; Atls = amphibious tolerator-saturate/mudflat; T = terrestrial). Data presented are from the spring seasons at the end of each year period.

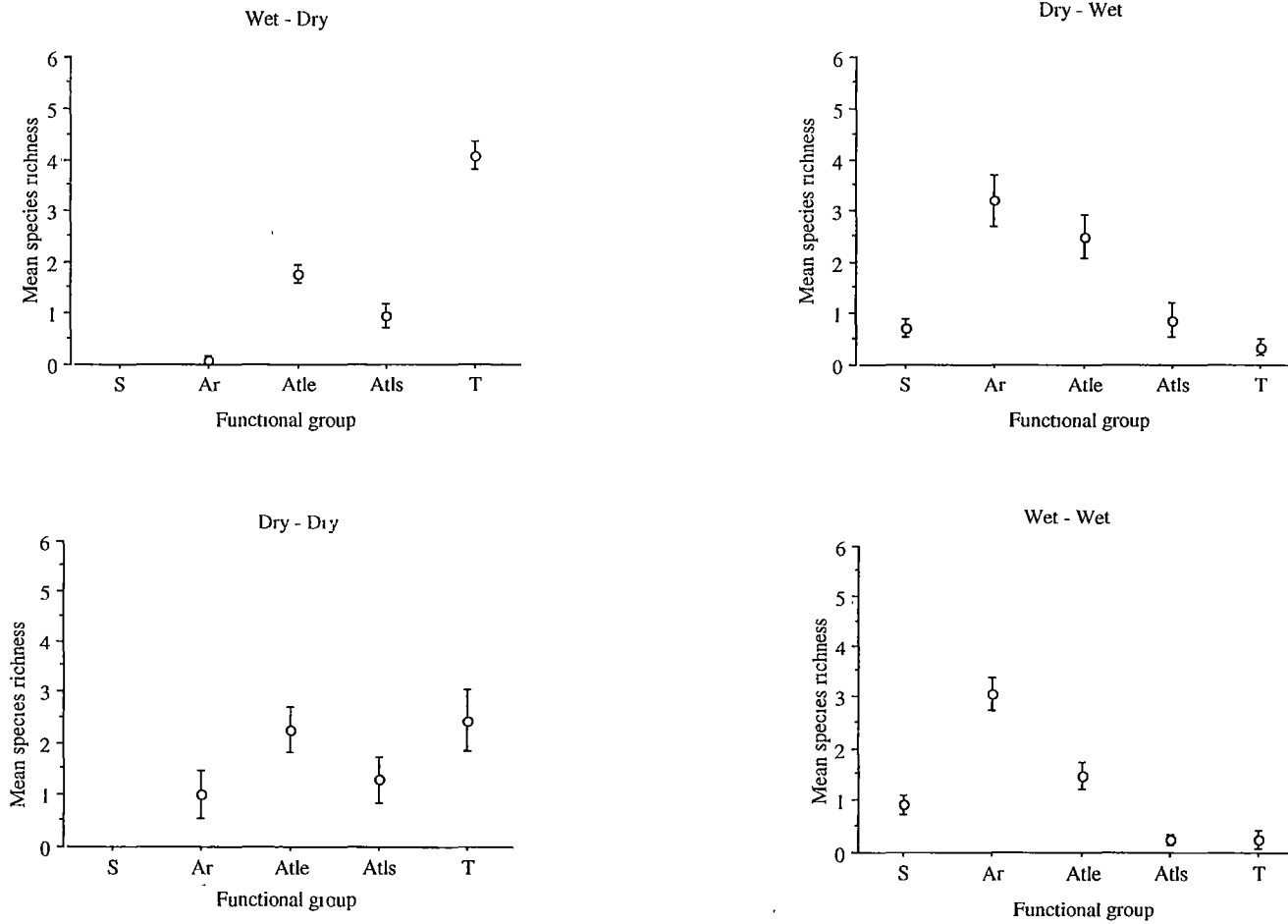


Figure 5.12 Functional group mean species richness recorded for each water regime category (S = submerged; Ar = amphibious responder (Ar); Atle = amphibious tolerator-emergent; Atls = amphibious tolerator-saturate/mudflat; T = terrestrial). Data presented are from the spring seasons at the end of each year period.

Discussion

The data from 5 wetlands showed that water level fluctuations were largely mirrored by changes in percentage cover, species composition and species richness. This applied for both amalgamated data and functional groups. However, differences due to water level fluctuations were more prominent for percentage cover than for species richness (Figure 5.8; Figure 5.9). These results correspond with most other studies concerning vegetation dynamics within wetlands (van der Valk, 1981; van der Valk and Davis, 1979; Gopal, 1986), where large responses in cover within wetland communities were observed after both drying and flooding events. However, very few studies have reported differences in species richness between flooding and drying events so it is difficult to compare the species richness results of the present study with other wetland systems. The present results indicate that a large response in total species richness does not occur with changes in water level. Zones that remained stable, whether 'wet' or 'dry', had a similar species richness to those that experienced a flooding or a drying event. Figure 5.9 shows that, even though similar species richness was found in each water regime 'type', the functional composition of species differed, indicating that the 'wet' and 'dry' species pools were approximately equivalent in number.

Most species, within all functional groups, showed a response in percentage cover due to changes between the presence and absence of water (Figure 5.5a-e; Table 5.5). Differences in the direction of response from 'wet to dry' and 'dry to wet' between functional groups was related to the ability of species in these groups to cope with inundation. Submerged (S), amphibious responder (Ar) and tolerator-emergent (Atle) species tolerate inundated conditions and all showed significant increases in percentage cover with a transition between 'dry to wet'. Amphibious tolerator-saturated/mudflat (Atls) and terrestrial (T) species will generally not tolerate long-term inundated conditions and showed significant decreases in percentage cover with a transition from 'dry to wet' (Figure 6.11; Figure 6.12). These results correspond with the characteristics of each functional group as described in Chapter 3 and Brock and Casanova (1997).

As expected, the overall direction of change in plant communities reflected fluctuations in water levels experienced over the period of the study. Zones that experienced a

transition from either 'wet to dry' or 'dry to wet' showed a uni-directional response in community composition. However, zones that experienced a two phase change in water level state varied in their direction of change depending on their dominant species. These zones demonstrated either a) a large response to a drying event and subsequent cycling back to a similar community prior to drawdown after re-flooding (aquatic herb zones); or b) a weak directional response (sedge dominated zones). Difference between the aquatic and sedge dominated zones in their response to water level fluctuations can be explained by the functional characteristics of their dominant species. The aquatic zones were dominated by submerged (S) and amphibious responder species (Ar). Within the present study these species 'types' demonstrated a rapid response to drying and re-flooding (Table 5.7; Figure 5.5a-e; Figure 5.9) and it was these characteristics that dominated the overall direction of change within these communities. A rapid response to water level fluctuations was also observed by Smith (1998) in the amphibious responder species, *Potamogeton tricarlinatus* and *Myriophyllum variifolium*. This characteristic is well suited to environments subjected to large ranges in water levels and provides the ability for these species to withstand rapid changes in water level and persist within the community (Brock, 1988; Brock, 1991; Brock and Casanova, 1997; see Smith, 1998). The sedge zones that showed very little directional change with water level fluctuations were dominated by *Baumea arthropphylla*. This species has been shown to respond to water level fluctuation in a slower manner than the amphibious responder sedge species, *Eleocharis sphacelata* (Rea and Ganf, 1994b). This also corresponded to the results of the present study. *Baumea arthropphylla* generally showed an increase in percentage cover with a transition from 'dry to wet', however, the change in cover was not significant between seasons and, therefore, was not as rapid as those recorded for amphibious responder species. The weak directional change in these zones was due to an increase in amphibious responder species over the period of the study.

As expected a greater magnitude of change, occurred in zones that experienced a transition between water presence (wet) and absence (dry) than when conditions remained stable, either wet or dry (Figure 5.8). However, the magnitude of change with a transition between 'wet to dry' was greater than with a transition between 'dry to wet'. This indicated that larger changes in community composition occurred after a drying event than a flooding event. This result could be explained as follows: In inundated conditions several aquatic plants use water as a medium for growth and after initial

regeneration (either by germination or vegetative means) will grow within the water profile to maximise the use of space (Hutchinson, 1975; Brock and Casanova, 1997). Therefore, in many cases, the water itself is the means by which the taxon remains upright. After a drying event these species lose their method of support and are reduced in the community. Submerged species, such as charophytes are totally lost from the community due to their inability to survive in dry conditions. Terrestrial species become present within the newly dry conditions. Therefore, changes that occur in community composition from wet to dry were 1) loss of species; 2) a significant loss of cover for aquatic species; and 3) an addition of new terrestrial species. After a flooding event changes in community composition are less rapid. Submerged species will germinate and become present in the community; amphibious species able to cope with dry conditions will disappear from the community. However, this may not be as rapid as a disappearance as that of charophytes after drying. This was confirmed by the functional group analyses comparing water regime categories, where terrestrial species were still present in the 'dry' to 'wet' community and submerged species were not recorded in the 'wet to dry' community. Therefore, changes that occurred in the community composition from wet to dry were 1) a small increase in percentage cover; 2) an addition of new species.

The response of communities in the present study correspond with the cyclical changes reported for other wetland systems (van der Valk, 1981; van der Valk and Davis, 1979). In stable wet conditions, seasonal variation in composition will occur (Figure 5.6; Figure 5.7). However, the community composition remains similar over time. After a drying event submerged species are lost from the community, amphibious responder (significantly reduced in cover) and tolerator-emergent species remain within the community; and amphibious tolerator saturated/mudflat and terrestrial species will become present. If the zone remains dry over time, responders will be lost and tolerators will be reduced in cover, tolerator saturated/mudflat and terrestrial species will remain dominant. If a community re-floods, a rapid response in percentage cover will occur for amphibious responders, a slow response will occur for tolerators, submerged species will germinate and slowly increase in cover and saturated/mudflat and terrestrial species will eventually, if the zone remains inundated, be lost from the community.

Chapter 6

Comparison between the soil seed bank and the extant vegetation

Introduction

Major and Pyott (1966) maintained that a complete description of a plant community must include both the buried viable seeds as well as the above ground components (standing or extant vegetation). However, we not only need to know what is there but we need to also understand the relationships between the seed bank and standing vegetation. The ability to predict changes in vegetation under varying environmental conditions using our knowledge of seed banks and existing vegetation is a useful tool in wetland management especially where regulation of a wetland's water levels is concerned.

At any one time the existing plant species of a wetland can be found in one of three states, they can be: 1) present in the form of long or short-lived propagules in the seed bank; 2) present in the form of vegetative/and or sexually reproducing adults (extant vegetation); 3) present in both seed bank and extant vegetation (van der Valk, 1981; Brock, 1998). The potential or future flora of a wetland includes all species growing in a wetland at a given time (the actual flora), plus the additional species represented only by propagules in the seed bank (Major and Pyott, 1966). The actual flora that will develop will depend on several factors including the water regime of the wetland and the life history characteristics of the species that make up the pool of potential species.

A wetland, with its dynamic fluctuating environments, can behave as a sieve, permitting the establishment of only certain species at any given time (van der Valk, 1981). Changes in the wetland environment, particularly in response to differences in water levels, will allow different types of species adapted to each new environment to germinate and establish in the wetland (van der Valk, 1981). Therefore, knowledge of the species in both the seed bank and extant vegetation of a wetland during several seasons can give significant insights into their responses to the different environmental changes found within wetlands.

Seed banks and standing vegetation used for predictions

In wetlands, the floristic composition of the seed bank has often been shown to determine the composition and structure of the vegetation that has developed over time (van der Valk and Davis, 1978; Smith and Kadlec, 1983; Leck, 1989). Due to this several studies have attempted to predict changes in the standing vegetation of wetlands from the species found within the seed bank (van der Valk, 1981; Welling *et al.*, 1988a; Haukos and Smith, 1993). Seed-bank data can yield information on three aspects of future wetland vegetation: (1) species composition, (2) relative abundance of species, and (3) distribution of species within and among wetlands. They may also reflect the history of the wetland's vegetation as well as species that may have dispersed from other areas (van der Valk and Davis, 1976a; Ungar and Riehl, 1980; Fenner, 1985; Leck and Simpson, 1987a; Welling *et al.*, 1988; Haukos and Smith, 1993). If the seed bank and standing vegetation are correlated the standing vegetation can generally be used to predict the seed bank of the wetland, and conversely the seed banks can be used to predict the vegetation of that growing season and at that site (Brock and Rogers, 1998)

Correlation studies

Studies comparing the species composition and abundance of seed banks and vegetation have analysed relationships between both past vegetation (van der Valk and Davis, 1978, 1979; Keddy and Reznicek, 1982; 1986; Schneider and Sharitz, 1986) and extant vegetation (see Leck, 1989; Brock, 1998; Brock and Rogers, 1998). Differences in relationships were related to different vegetation communities (Finlayson *et al.*, 1990), hydrological conditions and environmental conditions (van der Valk, 1981; van der Valk and Davis, 1976a, 1978) and disturbance (see Fenner, 1985; Falinska, 1999).

Studies comparing wetland seed banks with past vegetation have shown a strong similarity between the species composition of seed bank and previous vegetation in both freshwater tidal wetlands (Keddy and Reznicek, 1982) and prairie wetlands (van der Valk and Davis, 1978, 1979).

Studies comparing wetland seed banks to extant vegetation have found that similarities between these two variables can vary between wetlands and often between sites within wetlands (see Leck, 1989). High correlations between the species composition of seed bank and standing vegetation have been found in freshwater tidal wetlands (Leck and Graveline, 1979; Parker and Leck, 1985; Leck and Simpson, 1987a; 1994), flooded peat

(Thompson and Grime, 1979); marshes (Smith and Kadlec, 1983) and salt marsh (Hopkins and Parker, 1984; Ungar and Riehl, 1980). Poor correlation between the seed bank and standing vegetation has been found to be common within terrestrial communities (Harper, 1977; Thompson and Grime, 1979; Fenner, 1985; Archibold, 1989; Pickett and McDonnell, 1989; Rice, 1989). However, it has also been noted in some wetland studies (Thompson and Grime, 1979; van der Valk and Davis, 1978, 1979; Pederson, 1981; van der Valk, 1981; Finlayson *et al.*, 1990; Brock and Rogers, 1998).

Studies investigating the correlation between species abundance in the seed bank and the extant vegetation have also shown varying results (Kemp, 1989; Grillas *et al.*, 1993; Brock and Rogers, 1998). Brock and Rogers (1998) found that the abundance of each species in the field did not always reflect their numbers in the seed bank. Grillas *et al.* (1993) found that, although seed abundance tended to increase significantly with an increase in biomass of several dominant submerged angiosperm species, this was not the case for charophyte species.

Comparisons related to hydrological and environmental differences

Differences in correlation between the seed bank and the standing vegetation within wetlands has been related to water regime (van der Valk, 1981; van der Valk and Davis, 1978, 1979; Gopal, 1986; Zedler, 1987; Brock 1998) and vegetation communities (Finlayson *et al.*, 1990).

Wetlands differ fundamentally from terrestrial ecosystems in that they may be found in one of two different environmental states, (a) with standing water (flooded) and (b) without standing water (drawdown) (van der Valk, 1981). The amount of time a wetland spends in each state is what is termed the water or hydrological regime of the wetland (Brownlow *et al.*, 1997; Bunn *et al.*, 1997). The establishment, growth, and reproduction of all wetland species are influenced by the presence or absence of standing water, therefore, the impact of these two environmental states on a species is an important feature of the relationship between the seed bank and the standing vegetation (van der Valk, 1981). Vegetation development is strongly influenced by patterns of species recruitment (Grubb, 1977; Welling *et al.*, 1988). In many freshwater wetlands, most of the recruitment occurs primarily during drawdown and generally in this environment from the soil seed bank during this time (van der Valk and Davis,

1978; Smith and Kadlec, 1983; Leck *et al.*, 1989a; Brock and Britton, 1995; Casanova and Brock, 2000). Van der Valk and Davis (1978, 1979) found that within a prairie wetland, where water levels can be highly variable, the seed bank was more correlated with the drawdown vegetation community than the vegetation found at times of deep flooding.

Several general relationships between wetland seed banks and extant vegetation have been identified and related to their hydrological regime (Leck, 1989). Differences in relationships have been shown between wetlands with daily, seasonal (annual), or cyclic (multi-year) water level fluctuations. Wetlands with daily tidal fluctuations, such as freshwater tidal wetlands, have been shown to contain seed banks that resemble the surface vegetation (Parker and Leck, 1985; Leck and Simpson, 1987a). In wetlands with seasonal fluctuations, seed banks can contain seeds of two stages, for example, inundated versus drawdown, (Zedler, 1987) or dry versus wet season (Gopal, 1986) communities, with the importance of each type depending on vegetation tolerances to the inundation regime. Where cyclic changes occur, the seed bank contains components of various stages and, depending on water level, different communities can develop (van der Valk and Davis, 1976a, 1978, 1979; see Leck, 1989).

Different correspondence between the seed bank and standing vegetation has been found within wetlands and related to vegetation communities. Finlayson *et al.* (1990) found that, within an Australian floodplain wetland, the differences between the seed bank and the extant vegetation varied between an annual dominated vegetation community and one dominated by a perennial grass. The seed banks of two sites dominated by annual species were not highly correlated with the standing vegetation whereas the seed bank and vegetation of a site dominated by a perennial grass were correlated. Differences in correlations were related to the types of vegetation, annual and perennial life cycles and dispersal of seeds throughout the floodplain.

Temporal changes in relationship between the seed bank and extant vegetation

Cyclic vegetation succession had been observed in prairie wetlands in the United States by van der Valk and Davis (1976a, 1978, 1979) where seed-banks are central to the long-term survival of the vegetation communities. These wetlands experience unpredictable inundated and drought periods. During drought periods when water

levels drop a large proportion of the vegetation biomass is destroyed and over time mudflat and emergent species are recruited from the seed bank. With normal rainfall, standing water eliminates mudflat species, stops germination of emergent species, and triggers germination of submerged and free-floating species. If periods of high water continue, intolerant emergent species decline. The degenerating marsh and lake marsh have abundant submersed and free-floating plants. At each stage the seed bank contributes to the vegetation and, in turn, the vegetation contributes to renewal of the seed bank (Leck, 1989).

In contrast to prairie marshes, the seed bank of the freshwater tidal wetland does not contain seeds of different (cyclic) successional stages. The seed bank closely resembles the surface vegetation. The high yearly turnover of many species in the surface layer and generally low densities in the sub-surface layers indicate that, except for very few species, long-term accumulation does not occur (Leck and Simpson, 1987a). This wetland type is not affected by drought; although changes in water level would direct vegetation change, such changes would not be cyclic (Leck, 1989).

Where the drawdown cycle is annual, as in temporary seasonal ponds, vernal pools, and monsoon climates, complex relationships between the seed bank and the vegetation are also observed. In the temporary ponds, vegetation changes between periods of high and low water are not long enough to eliminate the most abundant species, although some species occur only under specific conditions (e.g., flooding - Leck 1989).

Correlations related to disturbance

Natural disturbances to plant communities are simultaneously a source of mortality for some individuals and a source of establishment sites for others (Denslow, 1980). Correlations between seed banks and standing vegetation in terrestrial systems have been related to disturbance (see Falinska, 1999). It has been theorised that in more frequently disturbed habitats the species composition of the seed bank and the vegetation are usually similar, then, as the vegetation matures and long-lived species that tend to recruit from quiescent juveniles increase (Silvertown, 1982), the composition and relative abundances of species in the seed bank versus the aboveground vegetation become increasingly different (Mayor and Pyott, 1966; Thompson and Grime, 1979; Fenner, 1985; van der Valk and Davis, 1976a; Thompson, 1992; Falinska, 1999). However, others have theorised that the floristic composition of

the extant vegetation and the seed bank is more similar in more stable environments than those subjected to disturbance (Williams, 1984; Falinska, 1999).

In wetland communities hydrological fluctuation is generally thought of as a natural disturbance. It has been suggested that undisturbed wetlands tend not to accumulate seeds and therefore correlation between the seed bank and extant vegetation is low, whereas, disturbed wetlands accumulate large seed banks and hence have greater correlation between their seed bank and vegetation (Thompson, 1992).

Vegetation disturbance can vary both spatially and temporarily. A plant community can consist of a mosaic of disturbed patches (or gaps) of different environmental conditions. The composition of the mosaic can be described by the size-frequency distribution of the gaps and can be dependent on the rates and scales of disturbance (Denslow, 1980). The life-history strategy of plant species dependent on some form of disturbance for establishment of propagules should reflect this size-frequency distribution of disturbance patches. An extension of island biogeography theory to encompass habitat area predicts that a community should be most rich in species adapted to growth and establishment in the spatially most common patch types (Denslow, 1980).

In wetland environments the disturbed patches (or gaps) can be thought of as temporal in nature, that is, times with or without water and therefore the wetland community, that is, the potential flora should be most rich in the species adapted to growth and establishment in the temporally most common patch type, either dry or inundated.

Aims

This chapter compares the germinable species recorded from seed bank samples taken from 9 permanent plots in 11 vegetation zones during two sampling periods, summer and winter 1997 with the extant vegetation: a) at the time the soils were taken; b) during each season surveyed over a 2-year period; and c) total species found within the two year period. The potential flora of the wetlands (that is, all taxa found in the seed bank and extant vegetation) are investigated and related to both past and present water regimes. Differences between the species richness, representation, composition and abundance of the seed bank and extant vegetation are investigated and related to hydrological conditions found during the present study. The analyses were undertaken for flora as a whole and for functional groups. The following questions were addressed:

- 1) What is the composition of the potential flora of the wetlands?
- 2) Does the functional composition of the potential flora relate to water regime ?
- 3) Are species richness, composition and abundance correlated between the seed bank and extant vegetation?
- 4) Are the relationships between the seed bank and extant vegetation related to: a) the conditions at the time the soil were taken; and/or b) the percentage of time the zones were inundated?
- 5) Was the recruitment of species from the seed bank influenced by the presence or absence of standing water?
- 6) Does the relationship between the species abundance in seed bank and extant vegetation relate to its: a) functional group; b) life cycle; and/or c) whether it is rhizomatous or not?
- 7) Can the future flora of the wetland be determined by either the seed bank or the extant vegetation found over the period of the present study?

It could be expected that:

- the potential flora of zones inundated for long periods of time would have a greater proportion of species that can survive long periods of inundation, whereas, zones that have remained dry for long periods would have a greater proportion of species that are adapted to drier conditions in their potential flora;
- that water regime does not affect the relationship between seed bank species richness and extant vegetation species richness;
- at any given time the type of species found exclusively in the seed bank would reflect the conditions of the wetland at that time, for example, a greater number of aquatic species would be present only in the seed bank if the zone is dry, whereas, more terrestrial species would be found only in the seed bank of inundated zones;
- zones that were either inundated or dry for a long periods would have the greatest number of species remaining only in the seed bank at the end of the study than zones that had fluctuated over the same period;
- the conditions in the wetland at the time the soils were taken would affect the floristic similarity between the seed bank and extant vegetation;
- that the direction of change in floristic similarity between the seed bank and extant vegetation would not be associated with the direction of change in water level, that is, both an increase and decrease in water level could cause an increase and decrease in floristic similarity depending on the species composition of the potential flora;
- rapid changes in water level would cause large differences in the relationship between the floristic similarity of the seed bank and extant vegetation of zones;
- differences in the relationship between species abundance in the seed bank and extant vegetation would be due to whether a species is rhizomatous or non-rhizomatous rather than due to its functional group or life cycle.

Methods

Seed bank and extant vegetation data collection

The nine randomly selected 1 x 1 metre quadrats used in the analyses of the both the seed bank and community dynamics were used to determine the relationship between the seed banks and extant vegetation of the wetlands. Seed bank sampling and germination experiments are described in Chapter 4 and the extant vegetation was recorded as described in Chapter 5.

Data manipulation

It was decided to concentrate on zones as the major focus of this part of the study as due to the spatial variation of species within wetland communities it is a useful scale to analyse differences between of the seed bank and extant vegetation. To determine differences between the seed bank and extant vegetation several types of data manipulation were used in various analyses:

- the potential flora for each zone were determined by listing all species recorded in the extant vegetation over the period of the present study and/or that germinated during the seed bank experiments of summer and winter 1997;
- dominant species within the potential flora were determined from species that either:
a) contributed $\geq 1\%$ of the total germination during at least one of the seed bank experiments; and/or b) had a mean cover of $\geq 1\text{-}5\%$ during at least one season over the period of the present study;
- where seasonal differences in the relationship between the seed bank and extant vegetation were related to water levels the seasonal mean water depth, calculated from the 9 quadrats within each zone, was used;
- where seasonal Sørensen's indices of similarity (SI - Mueller-Dombois and Ellenberg, 1974; Legendre and Legendre, 1983) were calculated the combined composition of species that germinated from the nine soil replicates were compared with the combined composition of species that were recorded within the nine 1 x 1 metre quadrats;

- for species abundance analyses the mean number of germinants per tray was correlated against the mean percentage cover per quadrat from each of the 9 quadrats within each zone;
- dominant species in the abundant analyses were those that were either dominant in the potential flora or present within more than 50% of zones sampled in both summer and winter 1997;
- for the purpose of the functional group analyses species were allocated, as described in Chapter seed bank, into their 5 broader groups, that is, submerged (S), amphibious responder (Ar), amphibious tolerator-emergent (Atle), amphibious tolerator-saturated/mudflat (Atls) and terrestrial (T) species;
- for analysis determining differences between species that were either adapted or not adapted to long-term inundation, the 5 functional groups were amalgamated as follows:

INUNDATION ADAPTED SPECIES (IA): groups comprising species adapted to

survive long periods of inundation (i.e. submerged (S), amphibious responder (Ar) and amphibious tolerator-emergent (Atle) species) and;

NON-INUNDATION ADAPTED SPECIES (INA): groups comprising species that cannot survive long periods of inundation (i.e. amphibious tolerator-saturated/mudflat and terrestrial species);

Ratios and percentages calculated

Seed bank percentage =	the number of species recorded only in the seed bank/ the total number of species in the seed bank x 100;
Species richness ratio =	the total number of species that germinated from the seed bank/ the total number of species that were recorded in the extant vegetation;
Functional group ratio =	the number of inundation adapted species/the number of non-inundation adapted species (IA/INA).

Species amalgamation

No taxa were amalgamated for the potential flora analyses. However, as some taxa were not able to be identified to species level in the extant vegetation during all seasons surveyed (due to a lack of flowering over all seasons and the similarity in their vegetative parts) several taxa were amalgamated to enable comparison analyses between the seed bank and extant vegetation. Taxa amalgamated were *Chara* spp., *Nitella* spp., *Isolepis* spp., *Myriophyllum* spp., *Utricularia* spp., *Trifolium* spp., *Vulpia* spp., *Danthonia* spp., *Epilobium* spp., *Sonchus* spp. and *Aira* spp. Species amalgamated were *Hainardia cylindrica* and *Hermarthria uncinata* (H.c/H.u). For abundance analyses, introduced Poaceae species and *Baumea* spp. were also amalgamated.

Past water regime category

Zones were allocated into past water regime categories from their known history according to the length of time they were inundated or dry during the last 10 - 15 years, that is, long-term dry zones had remained mainly dry, semi-permanent zones were mainly inundated and the fluctuating zones varied between inundation and dry with irregular periods in each. (Table 6.1). The allocation of wetlands into the past water regime categories were derived from personal knowledge, historical knowledge from landowners and past studies carried out on the wetlands by either the Tasmanian Parks and Wildlife Service, or Kirkpatrick and Harwood (1981).

Table 6.1: Zones allocated into categories using knowledge of the wetlands past water regime.

L-T DRY	FLUC	S-PERM
MID Dry	MID	CTL aquatic
BP B.r aquatic	MID E.s	CTL B.a
BP B.r outer		SG aquatic
TD aquatic		SG B.a
TD Sedge		

Present water regime category

Zones were classified on the basis of the number of seasons they were inundated; 0 - 3 seasons (drier longer); 4 - 5 seasons (fluctuating); 6 - 8 seasons (wetter longer, Table 6.2).

Table 6.2 Zones allocated into water regime type using the number of seasons the zone had standing water over the period of the present study.

Dryer longer	Fluctuating	Wetter longer
MID Dry	MID Aquatic	MID E.s
BP B.r outer		CTL Aquatic
BP B.r Aquatic		CTL B.a
TD E.a		SG B.a
TD Aquatic		SG Aquatic

Species representation categories

Using the species recorded in the seed bank and extant vegetation of each zone the percentage of species in each of three species representation categories were calculated as follows: a) found in 'seed bank only'; b) found in 'extant vegetation only' or; c) found in 'both seed bank and extant vegetation'. Categories were calculated for: 1) both sampling periods, summer and winter 1997; and 2) the total species recorded over the period of the present study.

Species abundance relationship categories

Using the mean number of germinants per tray and the mean percentage cover recorded in each zone during each season sampled (i.e. 2 x 11 zones), the occurrences of the each taxa were allocated into species abundance relationship categories as shown in Table 6.3.

Table 6.3 Species abundance categories

		Seed bank number of germinants		
		Low Between 1-5	Medium 5-15	High 15 and above
Extant vegetation Percentage cover	Low = < 1 %	Category 1	Category 3	Category 5
	High = > 1%	Category 2	Category 4	Category 6

Analytical methods

Several analyses were repeated using: a) total as well as dominant species; and b) data from the seasons sampled, summer and winter, 1997 as well as total number of species recorded in the seed bank and extant vegetation over the period of the present study.

The relationship between the abundance of species in the seed bank and cover in the extant vegetation were examined for: a) all species recorded within vegetation zones; b) for individual species, c) all species within functional groups, d) species within each life cycle, annual or perennial; and e) rhizomatous or non-rhizomatous species, using Spearman's rank correlation analysis. Spearman's rank correlation analysis was also used for all other comparisons of pairs of continuous variables (Table 6.4). Rho values corrected for ties are reported (Abacus Concepts, 1992).

ANOVA was used to test for relationships between categorical and continuous data. A Shipiro-Wilk test (Shipiro and Wilk, 1965; Zar, 1974) was used to test for normality in the data. To satisfy the assumptions of independence of means and variances for ANOVA the species richness data were square root transformed. In ANOVA where significant differences were found ($P < 0.05$), a Fisher's LSD *post hoc* test was performed to determine where the significant variation occurred. The transect mean as described in Chapter 4 was used in the ANOVA tests.

Chi-square analyses were used to test for relationships between categorical and continuous variables (Table 6.4). Where the expected values calculated were lower than 5 (thus reducing the power of the test) a Yates's correction was applied (Chase, 1967).

Sørensen's index of similarity was used compare the species composition of the seed bank and that of the extant vegetation.

Analyses

Variables tested are outlined in Table 6.4

Table 6.4 Variables tested to compare the seed bank with extant vegetation

Categorical data	Continuous data
Potential flora	Species richness
Past water regime category	Mean water depth
Present water regime category	Deepest water depth
Inundation adapted and non-inundation adapted category	Percentage of seasons zones inundated
Zone	Percentage of inundation adapted and non-inundation adapted
Seed bank	Species richness ratio
Extant vegetation	Seed bank percentage
Species representation categories	Functional group ratio
Direction of change in Sørensen's index of similarity (SI)	Species composition Sørensen's index of similarity (SI)
Direction of change in water depth	Number of germinants per tray
	Percentage cover in the extant vegetation
	Differences between seasonal water depth
	Differences between seasonal SI

Comparison with field germination and the extant vegetation of past surveys

To determine if the species found only in the seed bank and extant vegetation of the present study had been observed either germinating in the field or in the extant vegetation of the wetlands the following data were listed:

- 1) germination observations (i.e. cotyledons and seedlings) during the extant field surveys of the present study; and
- 2) species from the present study that were recorded in the past vegetation surveys of each wetland (Kirkpatrick and Harwood, 1981; Visoiu, 2000) and from the author's personal observations between 1995 and 1998;

From these observations a list was compiled of the species that were found in either the seed bank only and extant vegetation only of the individual wetlands over the past 20 years. After comparing wetlands, a final list was compiled of species within the present study that were found in either the seed bank only or extant vegetation only

within all wetlands. Functional group representation of the final species were listed and classified into inundation adapted and non-inundation adapted species.

To determine long-term differences in the vegetation communities, the species present in the potential flora of the present study not recorded in the zones by Kirkpatrick and Harwood (1981) were listed and the percentage of each functional group was calculated.

Results

Potential Flora

One hundred and twenty species were recorded in the potential flora of the wetlands (Table 6.5; Appendix VII). The largest total functional group representation was in the terrestrial species group (36 %), with submerged species having the lowest total representation (13 %). Species not adapted to long-term inundation had a higher species representation in the potential flora than inundation adapted species (Table 6.5).

Forty-seven species (39 %) of the potential flora were either abundant in the seed bank (i.e. greater than 1 % of total germination, see Chapter 4) and/or dominant in the extant vegetation of the zones studied (Table 6.5). Unlike total potential flora the dominant species had a higher representation in the inundation adapted species (64 %) than species not adapted to long-term inundation (36 %).

The inundation adapted groups, that is, submerged, amphibious responder and amphibious tolerator-emergent, had a higher percentage of dominant species than the non-inundation adapted groups, that is, amphibious tolerator saturated/mudflat and terrestrial.

Table 6.5 Summary of the total potential flora of the wetlands studied.

	S	Ar	Atle	Atls	T	Total
	Total species					
Total species	16	17	21	23	43	120
Percentage of total species	13	14	18	19	36	
	Inundation adapted			Inundation non-adapted		
Total species	54			66		
Percentage	45			55		
	Dominant species					
Total dominant species	9	11	10	6	11	47
Percentage of dominant species	19	23	21	13	23	
Percentage of total species	56	65	48	26	26	
	Inundation adapted			Inundation non-adapted		
Total dominant species	30			17		
Percentage	64			36		

Zones

All zones, except Big Punchbowl *Baumea rubiginosa* aquatic, had species representing all functional groups within their potential flora (Figure 6.1). The aquatic zone of Big Punchbowl had no species within both functional groups not adapted to long-term inundation, that is, from the amphibious responder saturated/mudflat (Atls) and terrestrial (T) groups.

Although the potential flora of most zones was represented by all functional groups the percentage representation of each group varied between zones (Figure 6.1). Within groups, the amphibious responder and terrestrial groups had a greater range of percentage variation between zones than did the submerged, amphibious tolerator-emergent (Atle) and saturated/mudflat groups (Figure 6.1).

Zones were generally dominated by species from one or two functional groups (Figure 6.1). Fifty-five percent of zones had the highest species representation in the terrestrial functional group, that is, Big Punchbowl *B. rubiginosa* outer; Tin Dish, aquatic and *Eleocharis acuta*; Middle Lagoon dry herbaceous; Sandy Gate, aquatic and *Baumea arthropphylla* zones, whereas, thirty-six % had their highest representation of species within the amphibious responder (Ar) group, that is, Cherry Tree Lagoon, aquatic and *B. arthropphylla*; Middle Lagoon, *Eleocharis sphacelata*; and Big Punchbowl, *B. rubiginosa* aquatic zones. The Middle Lagoon, dry herbaceous zone had its higher representation of species within the amphibious tolerator saturated/mudflat group. Submerged species (S) were only important within the potential flora of Big Punchbowl *B. rubiginosa* aquatic zone, whereas, amphibious tolerator-emergent species had a high representation in the Big Punchbowl *B. rubiginosa* aquatic, Middle Lagoon *Eleocharis sphacelata* and Cherry Tree Lagoon aquatic zones (Figure 6.1).

Greater variation in functional group representation of the dominant species occurred between vegetation zones than was shown for the total potential flora (Figure 6.1; Figure 6.2). Less zones had a full representation of functional groups within their dominant potential species. Full representation was only found in Sandy Gate *B. arthropphylla*; Middle Lagoon dry herbaceous; and Tin Dish aquatic zones. In three zones, Tin Dish aquatic, Tin Dish *Eleocharis acuta* and Sandy Gate *B. arthropphylla*, terrestrial species were still the highest represented species in the dominant flora. In Big Punchbowl, aquatic and outer, submerged species were the most represented, whereas in other zones, both the amphibious responder and tolerator species were the highest represented.

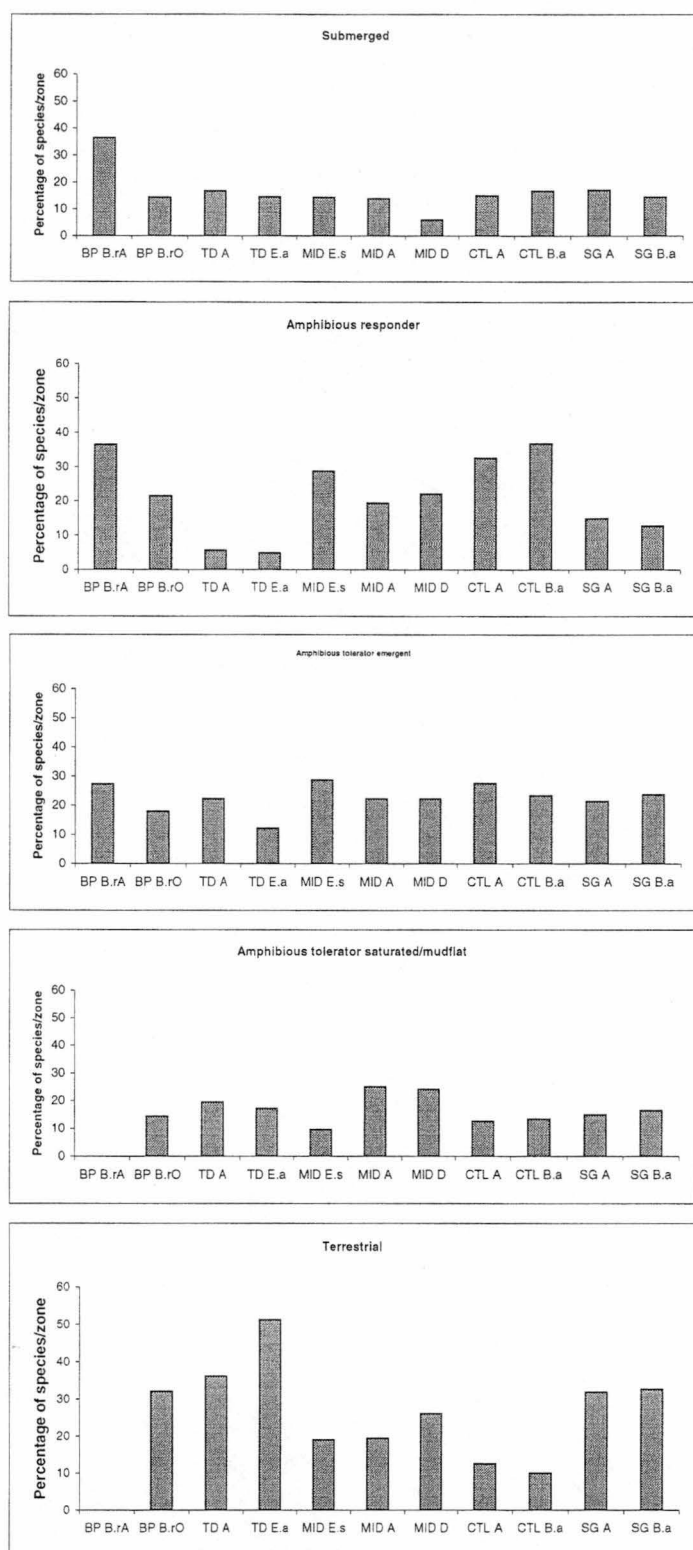


Figure 6.1 Functional group representation of plant species (percentage of species) that contributed to the potential flora of each zone (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B.r = *Baumea rubiginosa*; B.a = *Baumea arthropylla*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; O = outer; A = aquatic).

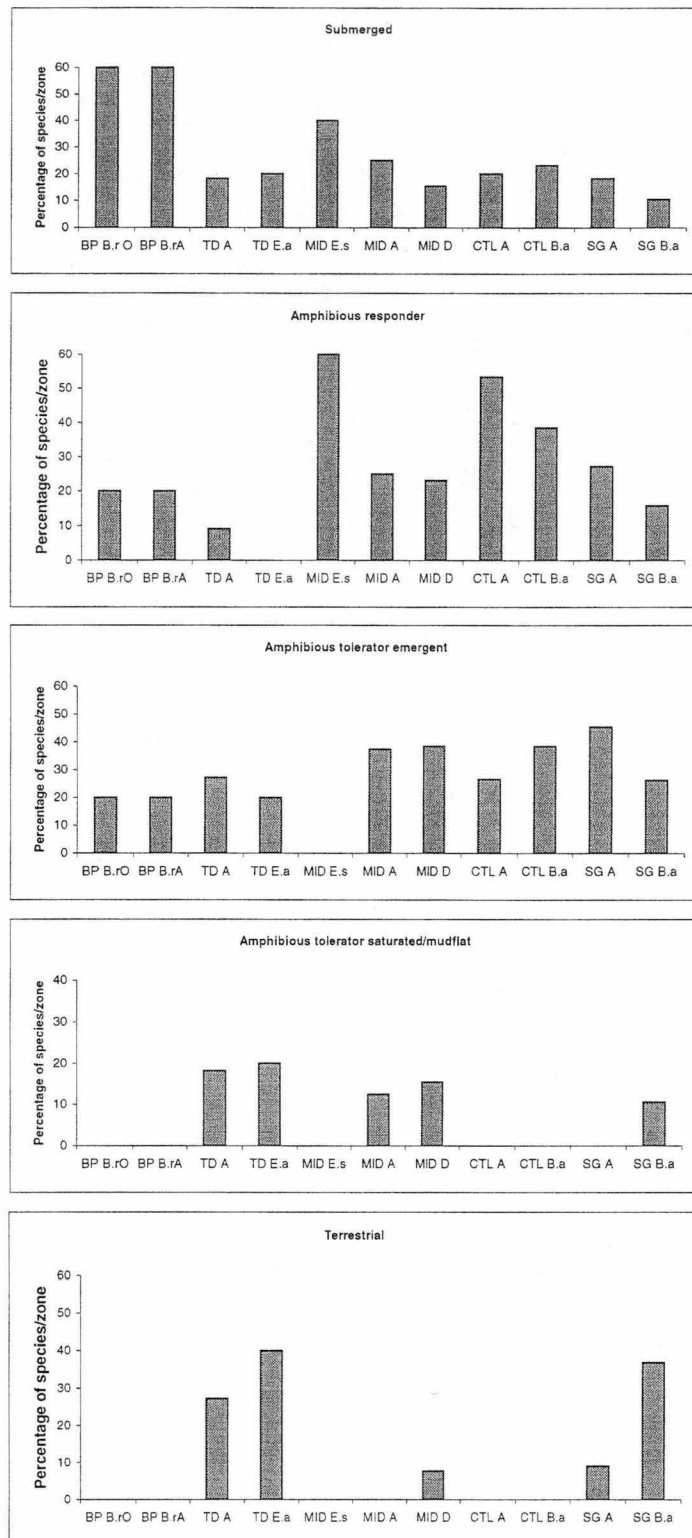


Figure 6.2 Functional group representation of dominant plant species (percentage of species) that contributed to the potential flora of each zone (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B.r = *Baumea rubiginosa*; B.a = *Baumea arthrophylla*; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; O = outer; A = aquatic).

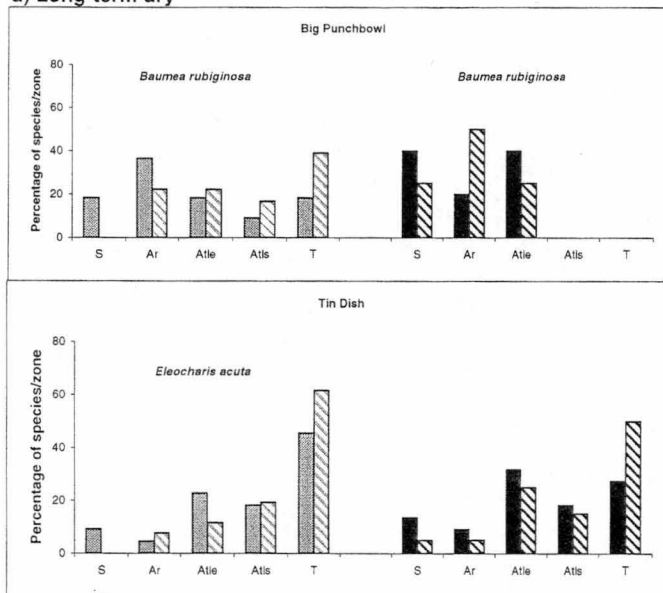
Inundation adapted groups dominated the total potential flora of all zones, except Tin Dish aquatic and *Eleocharis acuta* zones (Table 6.6). Within the dominant species, the inundation adapted groups were also dominant in Tin Dish aquatic zone. However, the more terrestrial groups remained dominant within Tin Dish *Eleocharis acuta* zone.

In most zones where they occurred, all functional groups were represented in both the seed bank and extant vegetation (Figure 6.3). However, in Big Punchbowl, *Baumea rubiginosa* outer and Tin Dish, *Eleocharis acuta* zones the submerged group was only represented in the seed bank, whereas in Cherry Tree Lagoon aquatic zone the amphibious tolerator-saturated/mudflat group were only represented in the extant vegetation.

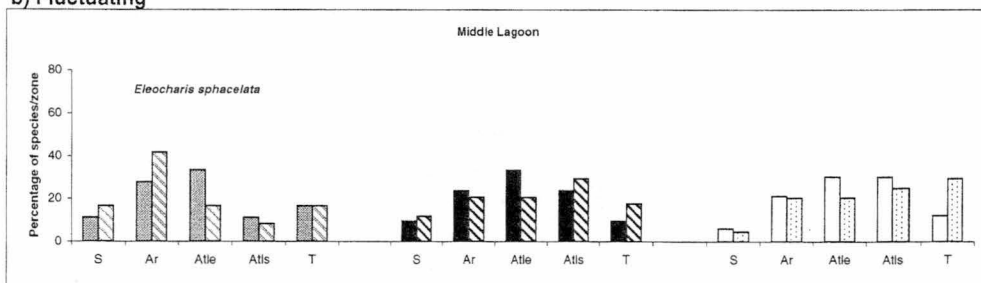
Table 6.6 Proportion of species in each zone allocated to species adapted or not adapted to long-term inundation (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B = *Baumea*; E = *Eleocharis*).

	Inundation adapted species	Inundation non-adapted species	Inundation adapted species	Inundation non-adapted species
	Species number		Percentage	
Species total				
BP <i>B. rubiginosa</i> aquatic	11	0	100	0
BP <i>B. rubiginosa</i> outer	15	13	54	46
TD aquatic	16	20	44	56
TD <i>E. acuta</i>	13	28	32	68
MID <i>E. sphacelata</i>	15	6	71	29
MID aquatic	20	15	57	43
MID dry herb	25	25	50	50
CTL aquatic	30	10	75	25
CTL <i>B. arthropphylla</i>	23	6	79	21
SG aquatic	25	22	53	47
SG <i>B. arthropphylla</i>	28	27	51	49
Dominant species				
BP <i>B. rubiginosa</i> aquatic	6	0	100	0
BP <i>B. rubiginosa</i> outer	6	0	100	0
TD aquatic	7	5	58	42
TD <i>E. acuta</i>	5	6	45	55
MID <i>E. sphacelata</i>	6	0	100	0
MID aquatic	9	1	90	10
MID dry herb	11	3	79	21
CTL aquatic	14	0	100	0
CTL <i>B. arthropphylla</i>	14	0	100	0
SG aquatic	12	1	92	8
SG <i>B. arthropphylla</i>	12	9	57	43

a) Long-term dry



b) Fluctuating



c) Semi-permanent

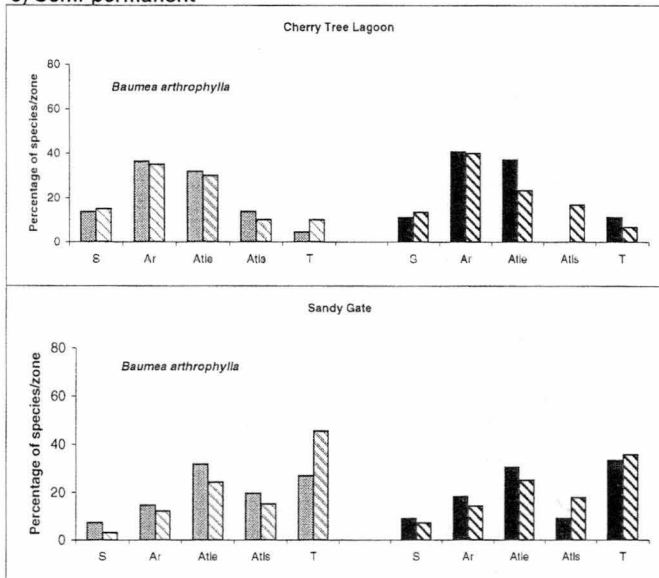
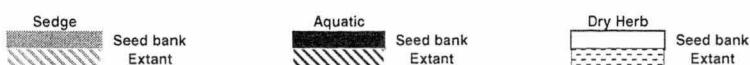


Figure 6.3

Functional group representation (percentage of species) of the potential flora in the seed bank and extant vegetation. Functional groups: S = submerged, Ar = responder, Atle = tolerator emergent, Atls = tolerator saturated, T = terrestrial.



Water regime analyses

Past water regime did not affect the functional representation of the potential flora ($\chi^2 = 0.836$; $P = 0.6585$; 2 degrees of freedom). Equal proportions of species adapted or not adapted to long term inundation were found in zones with long-term dry, fluctuating or semi-permanent water regimes in the past 10-15 years.

As with past water regime, the percentage of seasons inundated over the period of the present study did not affect the proportion of inundation to non-inundation adapted species ($\chi^2 = 1.599$; $P\text{-value} = 0.2061$; 1 degree of freedom).

Zone analysis

The proportion of the inundation adapted and inundation non-adapted species varied significantly with zone ($\chi^2 = 32.276$; $P\text{-value} = < 0.0001$; 10 degrees of freedom; Table 6.7). The more constantly inundated zones, Middle Lagoon *Eleocharis sphacelata*; and Cherry Tree Lagoon aquatic and *Baumea arthropphylla* zones, had greater than expected inundation adapted species (Table 6.7). This pattern was also found in the aquatic zone of the long-term dry wetland Big Punchbowl (Table 6.7).

In contrast, the long-term dry zones, Tin Dish aquatic and *Eleocharis acuta* and Middle Lagoon dry herbaceous zones, had a lower than expected number of species adapted to long-term inundated conditions. This pattern was also found in the *Baumea arthropphylla* zone of the semi-permanent wetland Sandy Gate (Table 6.7).

Maximum water depth recorded over the period of the study was not correlated to both the percentage of inundation adapted species or the percentage of non-inundation adapted species found in the potential flora in each zone ($\rho = -0.615$, $P = 0.518$; Figure 6.4).

Table 6.7 Chi square analysis for association between the proportion of inundation and non-inundation species and zone (LT-DRY = long-term dry); S-PERM = semi permanent; FLUC = fluctuating).

df = 10	Water regime in the last 10-15 years	Inundation adapted species		Inundation non-adapted species		Totals
		Observed	Expected	Observed	Expected	
BP <i>B. rubiginosa</i> aquatic	LT-DRY	11	6.19	0	4.81	11
BP <i>B. rubiginosa</i> outer	LT-DRY	15	15.75	13	12.25	28
TD aquatic	LT-DRY	16	20.24	20	15.76	36
TD <i>E. acuta</i>	LT-DRY	13	23.06	28	17.94	41
MID <i>E. sphacelata</i>	S-PERM	15	11.81	6	9.19	21
MID aquatic	FLUC	20	19.68	15	15.32	35
MID dry herb	LT-DRY	25	28.12	25	21.88	50
CTL aquatic	S-PERM	30	22.49	10	17.51	40
CTL <i>B. arthropphylla</i>	S-PERM	23	16.31	6	12.69	29
SG aquatic	S-PERM	25	26.43	22	20.57	47
SG <i>B. arthropphylla</i>	S-PERM	28	30.93	27	24.07	55
Totals		221		172		393

Critical value for 10 degrees of freedom at 0.05 level of significance = 18.307; $\chi^2 = 32.276$; P-value = < 0.0001

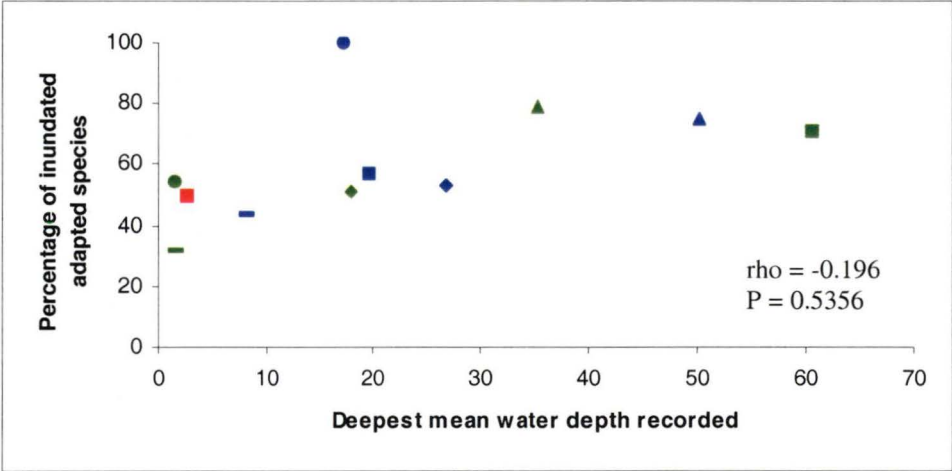


Figure 6.4 Effect of the deepest water depth recorded during the present study on the percentage of species adapted to long-term inundation recorded in the potential flora. (● = Big Punchbowl; — = Tin Dish; ■ = Middle Lagoon; ▲ = Cherry Tree Lagoon; ◆ = Sandy Gate: green = sedge; blue = aquatic, red = dry herbaceous: rho = Spearman's rank correlation coefficient, * = P < 0.05).

Comparison between the total potential flora and the dominant flora.

Big Punchbowl aquatic zone was left out of this analysis as it did not meet the assumptions of chi-square analysis due to the absence of non-inundation adapted species. The proportion of inundation and non-inundation adapted species were significantly different between the total and dominant species in the potential flora for Big Punchbowl *Baumea rubiginosa* outer, Cherry Tree Lagoon aquatic and *Baumea arthropphylla*, and Sandy Gate aquatic zones (Table 6.8). In these zones a higher than expected number of inundation adapted species was associated with a lower than expected number of non-inundation adapted species in their dominant potential flora. The other zones had a similar proportion of these species between the total and dominant potential flora (Table 6.8).

Table 6.8 Summary of the results of chi-square analyses comparing the proportion of the inundation adapted and non-adapted species between the total potential and dominant flora.

	Chi-square	P-value
BP <i>B. rubiginosa</i> aquatic	No analysis	
BP <i>B. rubiginosa</i> outer	5.570	0.0233
TD aquatic	0.696	0.4042
TD <i>E. acuta</i>	0.724	0.3948
MID <i>E. sphacelata</i>	3.020	0.1376
MID aquatic	3.490	0.1090
MID dry herb	3.628	0.0568
CTL aquatic	4.970	0.0382
CTL <i>B. arthropphylla</i>	4.510	0.0487
SG aquatic	6.580	0.0124
SG <i>B. arthropphylla</i>	0.237	0.6265

Comparison between the species richness of the seed bank and extant vegetation

Typically more species germinated from the seed bank than were recorded in the extant vegetation during each season (Figure 6.5). However, at the end of the two year period of the study there was a greater percentage of zones (55 %) that had more species recorded in the extant vegetation than had germinated from the seed bank in summer and winter 1997 (Figure 6.5).

There was a significant difference in the species richness per tray between zones and between the seed bank and extant vegetation during both seasons sampled (Table 6.9). However, there was also a significant interaction effect, indicating that the significant differences between the species richness of the seed bank and extant vegetation varied between the zone in question (Table 6.9; Table 6.10, Figure 6.6).

The Fisher's *post hoc* test indicated that 6 zones, Big Punchbowl outer and aquatic Cherry Tree Lagoon aquatic and *Baumea arthropphylla* and Sandy gate aquatic and *Baumea arthropphylla* had significantly more species that germinated from the seed bank than were recorded in the extant vegetation at the time the soils were taken. In the latter five zones this result occurred during both seasons sampled; Tin Dish aquatic and Middle Lagoon *Eleocharis sphacelata*, aquatic and dry herbaceous zones all had significantly more species recorded in the extant vegetation than germinated from the seed bank during at least one season sampled; and in Tin Dish *Eleocharis acuta*; the species richness in the seed bank was not significantly different to that of the extant vegetation during both seasons sampled (Table 6.10; Figure 6.6).

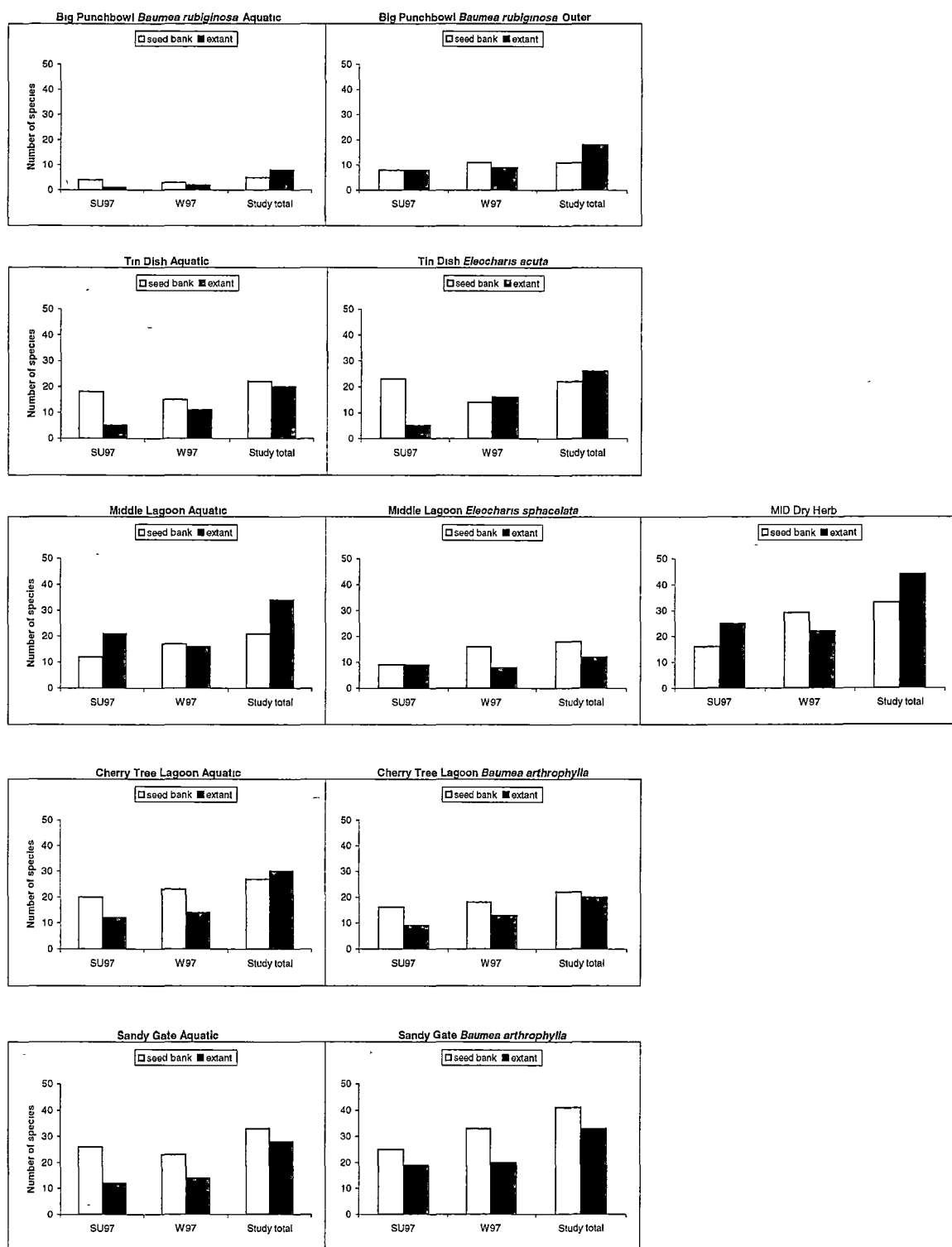


Figure 6.5 Number of species that germinated from the seed bank and were recorded in the extant vegetation for a) summer 1997, SU97; b) winter 1997, W97; and c) study total, during the period of the present study.

Table 6.9 Results for two-factor ANOVA to determine differences in species richness between zones and between the seed bank and extant vegetation (ESB) at the time the soils were taken.

Type III Sums of Squares

Source of Variation	d.f	M.S	F-Value	P-Value	Sig.
Summer 1997					
Zone	10	2.334	31.892	<0.0001	***
ESB	1	0.904	12.348	0.0010	**
Zone x ESB	10	0.686	9.214	<0.0001	***
Residual	44	0.073			
Winter 1997					
Zone	10	1.988	21.444	<0.0001	***
ESB	1	2.844	30.668	<0.0001	***
Zone x ESB	10	0.585	6.314	<0.0001	***
Residual	44	0.093			

Table 6.10 (a) mean number of species (\pm standard error) that germinated per tray during germination experiments, summer 1997 and winter 1997; (b) mean number of species recorded per quadrat in the extant vegetation for each vegetation zone at the time of seed bank collection (letters run across rows, within each season, and indicate which zones are significantly different between their seed bank and extant vegetation. Means with the same letter are not significantly different).

Zone	Summer 1997		Winter 1997	
	(a) Seed bank	(b) Vegetation	(a) Seed Bank	(b) Vegetation
BP <i>B. rubiginosa</i> aquatic	2.3 \pm 0.2 a	2.8 \pm 0.4 a	2.8 \pm 0.7 a	1.1 \pm 0.1 b
BP <i>B. rubiginosa</i> outer	3.4 \pm 0.2 a	3.8 \pm 0.4 a	3.8 \pm 1.2 a	2.0 \pm 0.4 b
TD Aquatic	1.5 \pm 0.2 b	4.2 \pm 0.6 b	4.2 \pm 1.7 b	6.2 \pm 0.5 a
TD <i>E. acuta</i>	2.7 \pm 0.1 a	5.4 \pm 0.6 a	5.4 \pm 1.7 a	6.0 \pm 0.2 a
MID <i>E. sphacelata</i>	3.9 \pm 0.4 b	5.6 \pm 0.4 a	5.6 \pm 1.4 a	5.2 \pm 0.2 a
MID Aquatic	4.8 \pm 0.5 b	6.7 \pm 0.7 a	6.7 \pm 2.2 a	9.6 \pm 0.6 a
MID Dry Herb	8.1 \pm 0.3 b	11.6 \pm 0.9 a	11.6 \pm 3.0 a	11.4 \pm 0.8 a
CTL Aquatic	9.6 \pm 1.2 a	11.2 \pm 1.4 a	11.2 \pm 4.1 a	6.0 \pm 0.7 a
CTL <i>B. arthropphylla</i>	7.2 \pm 0.7 a	8.4 \pm 0.6 a	8.4 \pm 1.7 a	3.2 \pm 0.7 b
SG Aquatic	9.4 \pm 0.4 a	11.1 \pm 0.5 a	11.1 \pm 1.6 a	5.0 \pm 0.4 b
SG <i>B. arthropphylla</i>	9.0 \pm 0.5 a	11.7 \pm 1.6 a	11.7 \pm 4.8 a	5.2 \pm 0.4 b

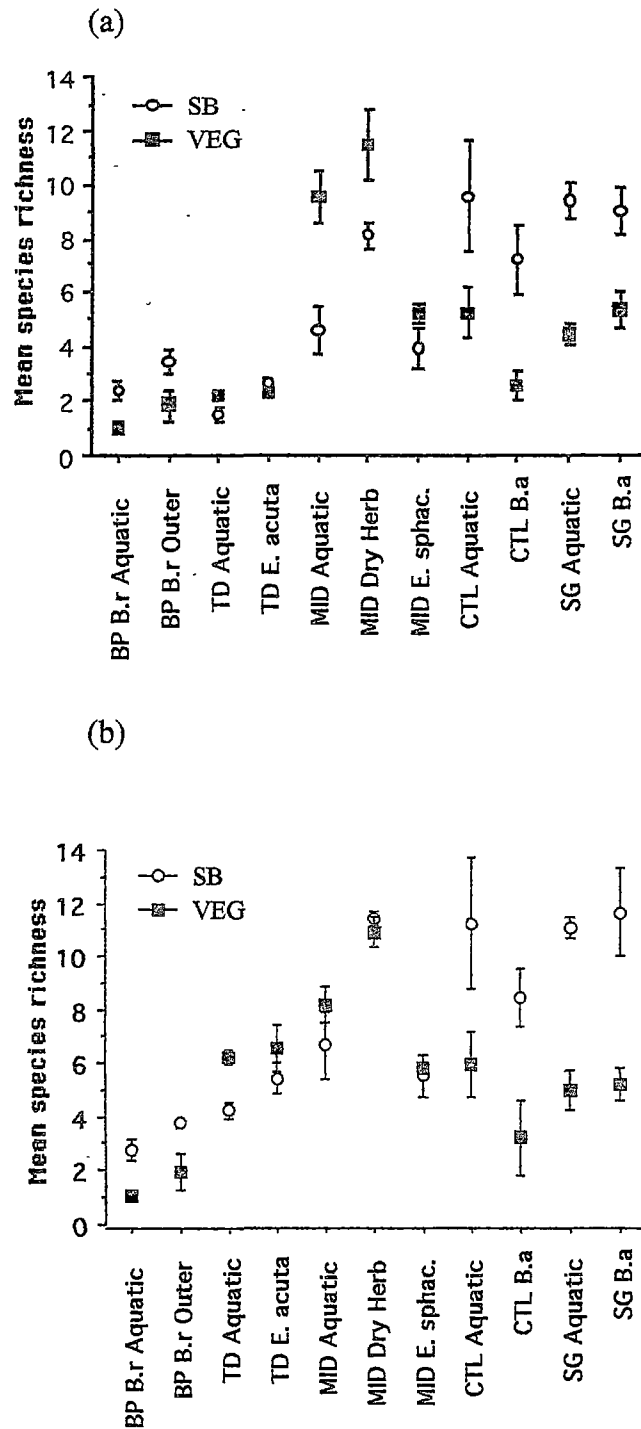


Figure 6.6 Differences in mean species richness between the seed bank (SB) per tray and extant vegetation (VEG) per quadrat at the time soils were sampled (a) summer 1997 and (b) winter 1997 (bar = 1 standard error on either side of mean).

Water depth at the time the soils were taken was not significantly correlated with the ratio calculated between the species richness of the seed bank and the extant vegetation at that time ($\rho = 0.105$, $P = 0.6266$). Greater number of species were recorded in the seed bank than extant vegetation in most zones regardless of the mean water depth at that time (Figure 6.6).

However, the percentage of seasons a zone was inundated was significantly correlated with the ratio calculated between the total species richness in the seed bank and extant vegetation recorded over the period of the present study ($\rho = 0.718$; $P = 0.0232$; Figure 6.7). In general, zones that were inundated for longer periods had more species in the seed bank than in the extant vegetation and zones with less time inundated had more species found in the extant vegetation than in the seed bank.

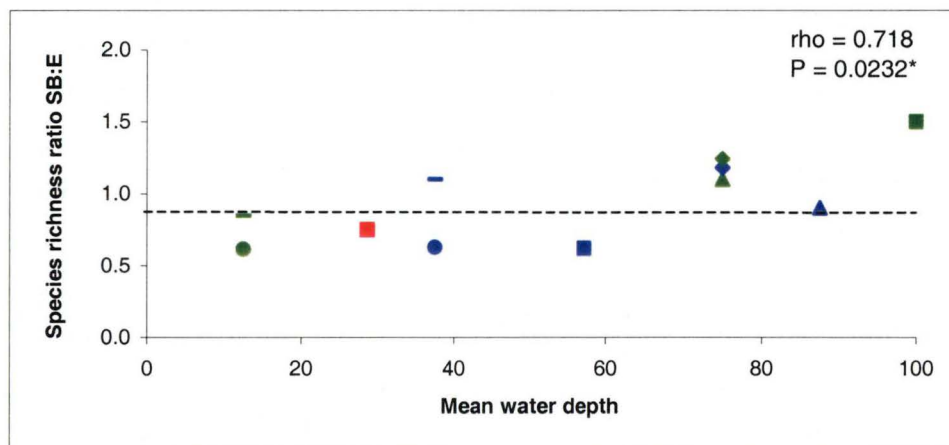


Figure 6.7 Effects of water regime (percentage of seasons inundated) on the ratio between the total species richness in the seed bank and extant vegetation recorded during the present study (● = Big Punchbowl; — = Tin Dish; ■ = Middle Lagoon; ▲ = Cherry Tree Lagoon; ◆ = Sandy Gate: green = sedge; blue = aquatic, red = dry herbaceous: ρ = Spearman's rank correlation coefficient, * = $P < 0.05$; a ratio greater than one indicates a greater number of species in the seed bank than extant vegetation).

Species representation in the seed bank and extant vegetation

The percentage representation of species within the 'seed bank only', 'extant vegetation only' and 'both seed bank and extant vegetation' varied between both seasons and zones (Figure 6.8). Overall 58% of taxa occurred in both the seed bank and extant vegetation during the period of the present study with 14.5% recorded only in the germinable seed bank and 27.5% recorded only in the extant vegetation. Individual zones (Figure 6.8; Figure 6.9), at the time the soils were taken ranged from 19-80% (0-80% dominant) of taxa recorded only in the germinable seed bank. Nought - 54% (0-33% dominant) occurred only in the extant vegetation and 0 - 65% (0-100% dominant) were recorded in both seed bank and extant vegetation. The ranges at the end of the study varied from the sampling times in that 0 - 36% (0-60% dominant) of taxa were recorded only in the seed bank, 5-56% (0-20% dominant) occurred only in the extant vegetation and 12 - 58% (0-100%) were recorded in both seed bank and extant vegetation.

Although variations in percentages occurred most zones were represented by species found within all categories (i.e. in the seed bank only, the extant vegetation only and in both seed bank and extant vegetation; Figure 6.8) during both sampling times and at the end of the study. However, the dominant category (i.e. highest percentage representation) was significantly different between the time the soils were taken and at the end of the study period ($\chi^2 = 8.1904$; $P = 0.005$; 1 degree of freedom). Very few zones had the greatest representation of species at any given time in the extant vegetation only.

Dominant species were generally found in both the seed bank and extant vegetation and there was no significant difference in this pattern between the time the soils were taken and at the end of the study period ($\chi^2 = 2.460$; $P = 0.1729$; 1 degree of freedom).

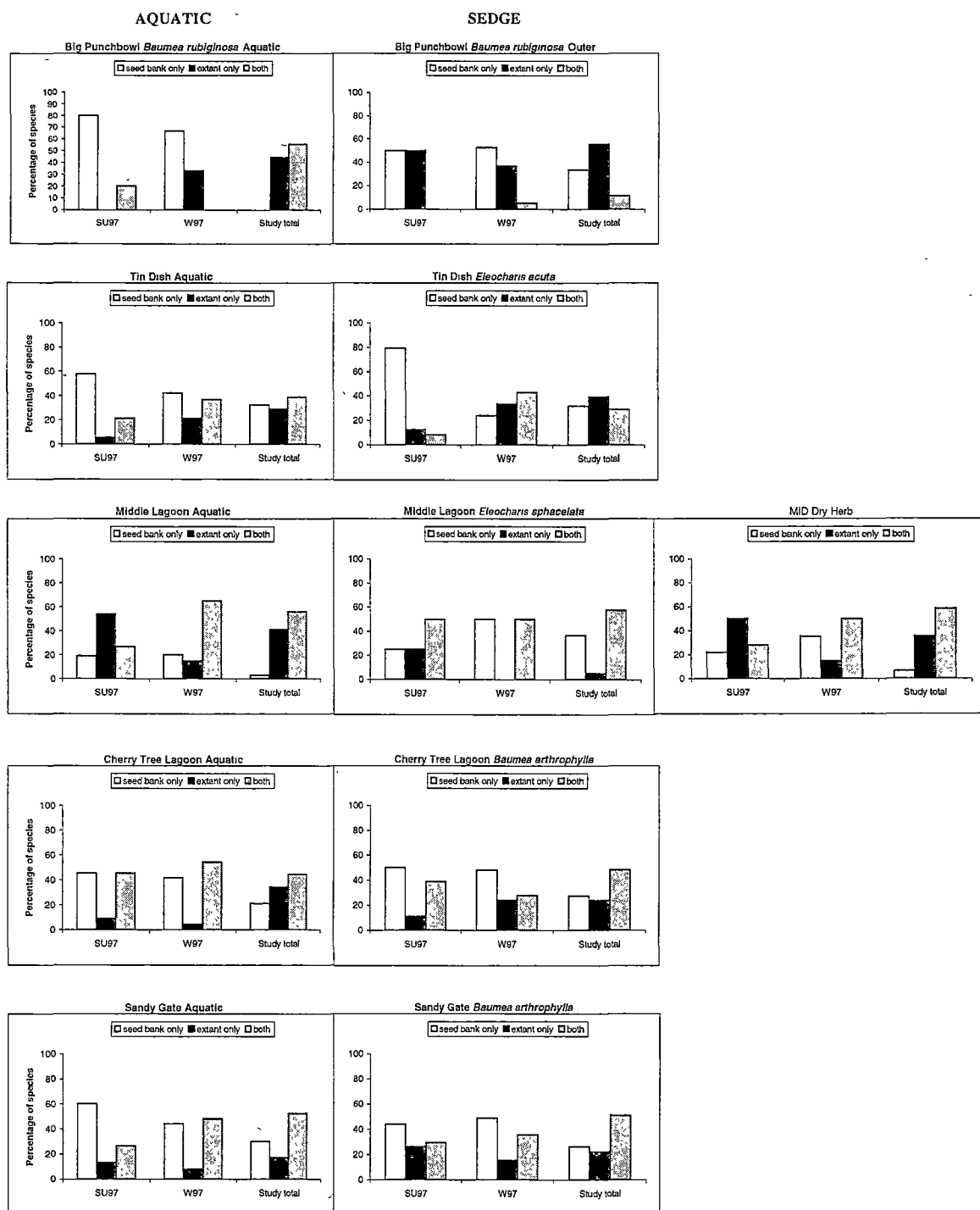


Figure 6.8 Percentage of species in the seed bank only, in the extant only and in both the extant vegetation and the seed bank in each vegetation zone sampled. Data presented are from soils taken and species recorded at each site during summer 1997 (SU97), winter 1997 (W97) and the total of the species in the seed bank from both experiment winter and summer 1997 and the total number of species recorded in the extant vegetation during the

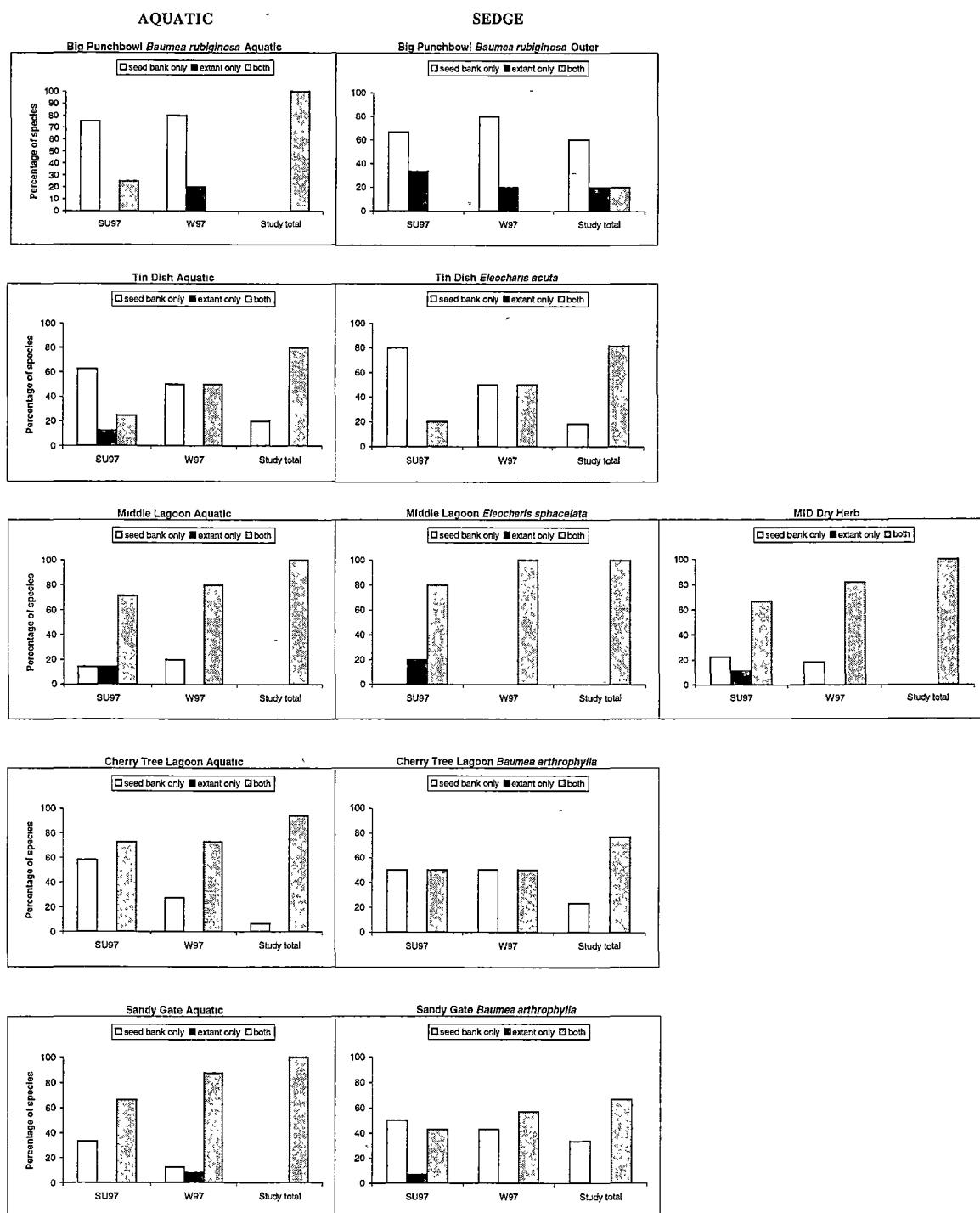


Figure 6.9 Percentage of dominant species in the seed bank only, in the extant only and in both the extant vegetation and the seed bank in each vegetation zone sampled. Data presented are from soils taken and species recorded at each site during summer 1997 (SU97), winter 1997 (W97) and the total of the species in the seed bank from both experiment winter and summer 1997 and the total number of species recorded in the extant vegetation during the period of the present study (1997-1998).

Effect of hydrological conditions on the species found only in the seed bank.

The percentage of total seed bank species present only in the seed bank at the time the soils were taken was negatively correlated with mean water depth ($\rho = -2.607$; $P = 0.0088$; Figure 6.10). Zones that were dry or had a low water depth have a greater number of species present only in the seed bank than zones with deeper water levels.

The percentage of the total seed bank species that remained in the seed bank during the present study was not significantly correlated with the percentage of time a zone was inundated ($\rho = -1.189$; $P = 0.2344$; Figure 6.10). Zones that were inundated for the shortest and longest periods of time had a greater percentage of species that remained in the seed bank than those that had an equal length of time in each hydrological state.

Water depth was not correlated with the ratio of inundation adapted (IA) to non-adaption species found in the seed bank only at the time soils were taken (Figure 6.11). Similarly, the percentage of time a zone was inundated was also not correlated with the ratio of IA to INA species that remained in the seed bank during period of the present study (Figure 6.11 b). Most zones had a higher number of non-inundation adapted species than inundation adapted species that remained in the seed bank over the study period. However, three zones, Sandy Gate *Baumea arthrophylla* and Cherry Tree Lagoon aquatic and Big Punchbowl outer had a greater number of species adapted to inundated conditions than non-adapted species that remained in the seed bank. This difference in the predominance of the two types of species was independent of zone inundation time.

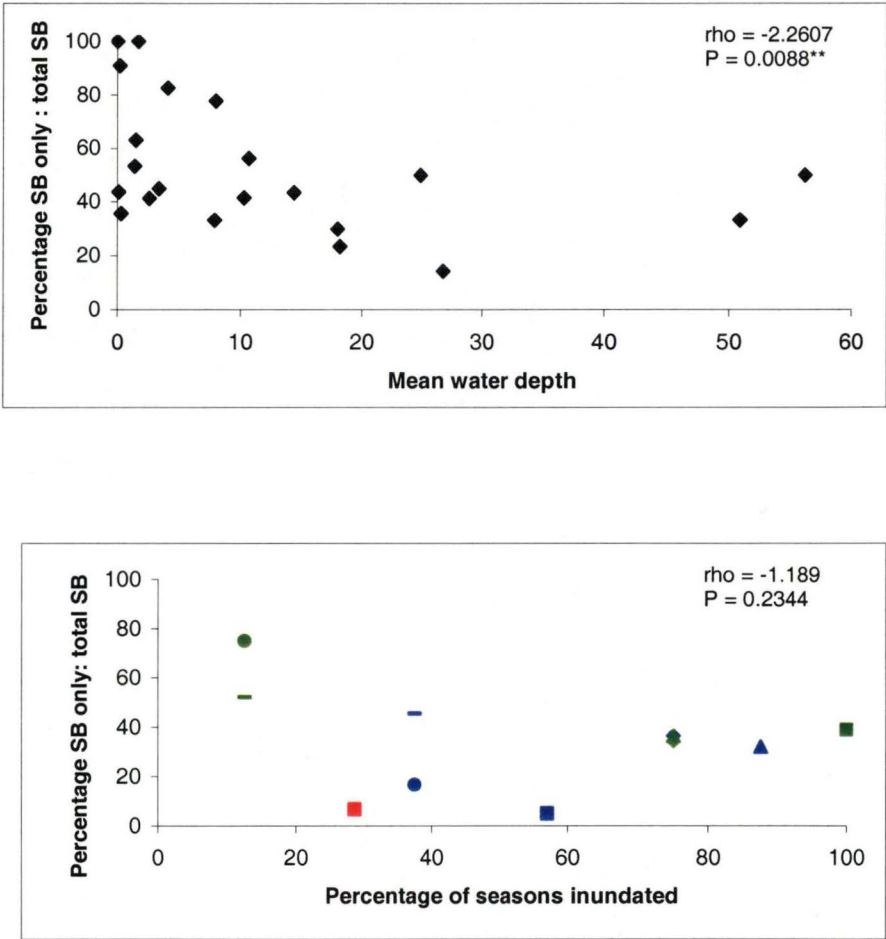


Figure 6.10 (a) percentage of species that remained in the seed bank only at the time the seed bank was collected; (b) percentage of species that remained in the seed bank only over the period of the present study (● = Big Punchbowl; — = Tin Dish; ■ = Middle Lagoon; ▲ = Cherry Tree Lagoon; ◆ = Sandy Gate: green = sedge; blue = aquatic, red = dry herbaceous: ρ = Spearman's rank correlation coefficient, ** significant to 0.0001 level of significance).

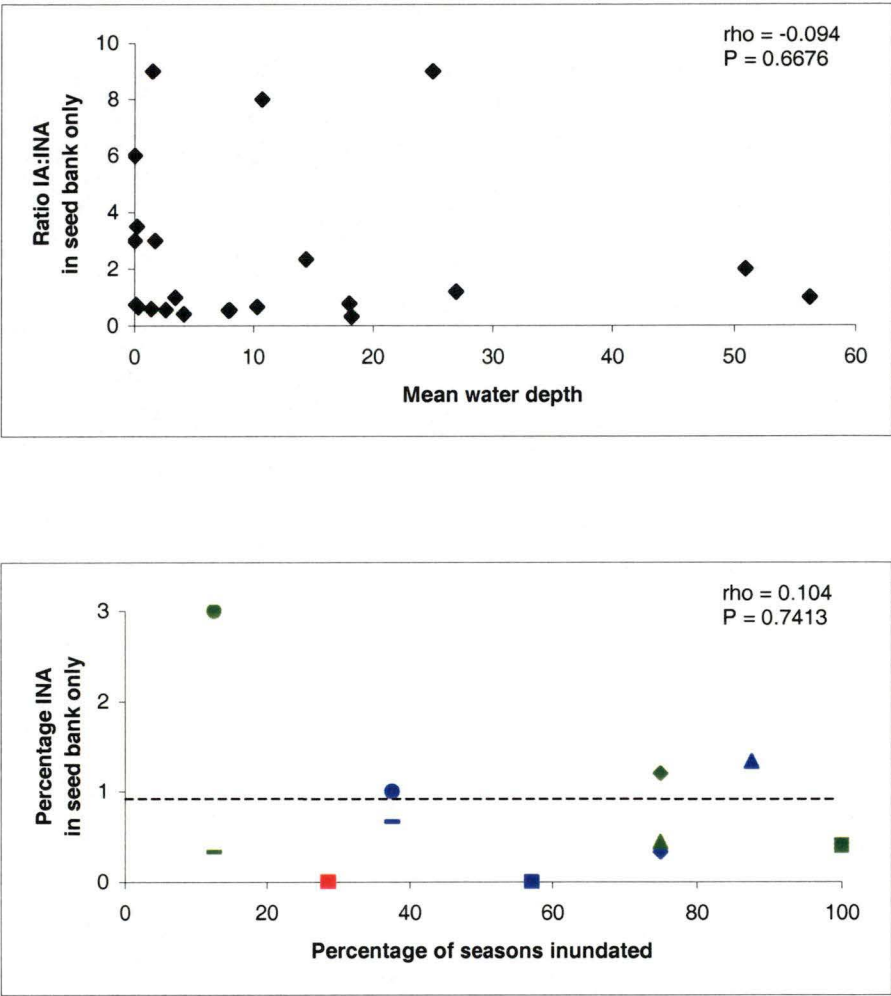


Figure 6.11 Ratio of inundation adapted (IA) and non-inundation adapted (INA) that were recorded in the seed bank only during (a) seasons sampled; and (b) at the end of the present study. A ratio lower than one indicates a greater number of non-inundation adapted species were found in the seed bank only at that time (● = Big Punchbowl; — = Tin Dish; ■ = Middle Lagoon; ▲ = Cherry Tree Lagoon; ◆ = Sandy Gate: green = sedge; blue = aquatic, red = dry herbaceous: ρ = Spearman's rank correlation coefficient).

Comparison of the total species pool

Comparisons with past studies and field germination observations during the period of the present study (Appendix VIII a-e) revealed that: a) very few species found only in the germinable seed bank of the present study had not been observed in the extant vegetation within each wetland; and 2) very few species remained only in the extant vegetation of each wetland (Table 6.11).

After taking out species listed in Table 6.11 that had either germinated from, or were recorded, in the extant vegetation of the other wetlands only 2 species (2% of total) remained in the seed bank only and 13 species (12% of total) remained in the extant vegetation only (Table 6.12). Eighty-seven percent of species found within the present study were found in both the seed bank and extant vegetation at some time within the wetlands over the past 20 years. Within the remaining species found only in the seed bank or extant vegetation, only two species, *Limosella australis* (seed bank only) and *Schoenus nitens* (extant vegetation only) were recorded in more than one wetland of the present study (Appendix VII). The functional group representation of species found in only the seed bank or extant vegetation did not substantially vary (Table 6.13).

The largest increases in numbers of species since 1979 occurred in Tin Dish, Sandy Gate and Middle Lagoon (Table 6.14). All wetlands, except Cherry Tree Lagoon, had the highest representation of increased species in the terrestrial angiosperm group, than all other functional groups, over the last 20 years (Table 6.14).

Table 6.11 List of species that were found in either the seed bank only or the extant vegetation only (* = introduced species; */n = uncertain status; underline = species that were only present within the extant vegetation during one season of the present study; bold = species that were found in only 1 quadrat or tray during the present study).

	Big Punchbowl	Tin Dish	Middle Lagoon	Cherry Tree Lagoon	Sandy Gate
Seed bank only		<i>Schoenus apogon</i> <i>Epilobium</i> sp. */n <i>Juncus procerus</i> <i>Lythrum hyssopifolia</i> <i>Ruppia megacarpa</i>	<i>Limosella australis</i> <i>Gratiola peruviana</i> <i>Juncus procerus</i>	<i>Limosella australis</i> <i>Centipeda minima</i>	<i>Limosella australis</i>
Extant vegetation only	<i>Scleranthus biflorus</i> <i>Villarsia reniformis</i> <u><i>Deyeuxia quadriseta</i></u> <i>Leptospermum scoparium</i> <i>Leptocarpus tenax</i> <i>Triglochin procerum</i> <i>Chorizandra enodis</i> <i>Scaevola hookeri</i> <i>Eleocharis sphacelata</i> <i>Scaevola hookeri</i> <i>Gonocarpus micranthus</i> <u><i>Banksia marginata</i></u>	<i>Schoenus nitens</i> <u><i>Danthonia</i> sp.</u> <i>Erodium cicutarium</i> * <i>Eryngium vesiculosum</i> <u><i>Amphibromus sinuatus</i></u>	<i>Schoenus nitens</i> <i>Danthonia</i> sp <i>Baumea arthropphylla</i> <i>Eryngium vesiculosum</i> <u><i>Ruppia</i> sp.</u> <i>Holcus lanatus</i> * <i>Lepilaena cylindrocarpa</i> <i>Neopaxia australasica</i> <i>Centaurium erythraea</i> *	<i>Centella cordifolia</i> <i>Cirsium vulgare</i> * <i>Deyeuxia quadriseta</i> <i>Eryngium vesiculosum</i> <u><i>Ruppia</i> sp.</u> <i>Triglochin</i> sp. <i>Leptinella longipes</i> <i>Mimulus repens</i> <u><i>Samolus repens</i></u> <i>Plantago coronopus</i> *	<i>Schoenus nitens</i> <i>Danthonia</i> sp. <i>Poa labillardierei</i> <i>Hainardia uncinata</i> * <u><i>Ruppia</i> sp.</u> <i>Triglochin procerum</i> <u><i>Alopecurus geniculatus</i></u> * <u><i>Veronica</i> sp.</u>

Table 6.12 Species found in either only seed bank or extant vegetation after comparison with field germination and past vegetation survey of wetland studied (+ = found in more than one zone within the present study).

	S	Ar	Atle	Atls	T
Seed bank only	<i>Limosella australis</i> +		<i>Gratiola peruviana</i>		
Extant vegetation only	<i>Lepilaena cylindrocarpa</i>		<i>Chorizandra</i> sp. <i>Mimulus repens</i>	<i>Leptocarpus tenax</i> <i>Scaevola hookeri</i> <i>Gonocarpus micranthus</i> <i>Schoenus nitens</i> + <i>Samolus repens</i>	<i>Deyeuxia quadriseta</i> <i>Leptocarpus scoparium</i> <i>Banksia marginata</i> <i>Poa labillardierei</i> <i>Veronica</i> spp.

Table 6.13 Summary of the functional group representation of species found in the seed bank only, extant only and both the seed bank and extant vegetation.

	S	Ar	Atle	Atls	T	Total
	Species number					
Seed bank only	0	1	0	1	0	2
Extant only	1	0	2	5	5	13
Both	15	16	19	17	38	105
	Percentages					
Seed bank only	0	6	0	4	0	
Extant only	6	0	10	22	12	
Both	94	94	90	74	88	
	Species number					
	Inundation adapted			Inundation non-adapted		
Seed bank only	1			1		
Extant only	3			10		
Both	50			55		
	Chi-square = 2.836; P = 0.2422; not-significant					
	Percentage					
	Inundation adapted			Inundation non-adapted		
Seed bank only	2			2		
Extant only	6			15		
Both	92			83		

Table 6.14 Percentage number of angiosperm species found in the present study not found in the vegetation surveys by Kirkpatrick and Harwood (1981) and the percentage representation of each functional group.

	Percentage of species not found in K & H (1981)	Functional groups (%)				
Wetland	%	S	Ar	Atle	Atls	T
BP	48	0.0	27.3	18.2	0.0	54.5
TD	62	3.8	0.0	15.4	7.7	73.1
MID	72	8.6	5.7	14.3	31.4	40.0
CTL	31	16.7	25.0	25.0	8.3	25.0
SG	60	6.7	10.0	23.3	16.7	43.3

Species Composition

The similarity of the species composition in the seed bank and extant vegetation varied between both seasons and zones (Table 6.15; Table 6.16). At the time soils were taken, the Sørensen's index of similarity (SI) for total species within zones ranged between 18 - 73.2% in summer 1997; 20 - 72.2% in winter 1997; and 22.2 - 75% for the study total (Table 6.15), with 68% of zones having $\leq 60\%$ floristic similarity. However, in most zones over the period of the floristic similarity between the seed bank and the extant vegetation increased with only 28% of zones having $\leq 60\%$ floristic similarity by the end of the study (Table 6.15). Floristic similarity between dominant species of the seed bank and extant vegetation was greater than for total species for most times recorded (Table 6.16). Dominant species SIs ranged from 0 - 100% in both seasons and 33-100% at the end of the study period, with 32% of zones having $\leq 60\%$ similarity at the time soil were taken. This was reduced to 18% of zones at the end of the study period. Big Punchbowl *Baumea rubiginosa* outer was the only zone that showed a consistently low similarity, both at the time the soils were taken and at the end of the study period, for both total and dominant species.

Table 6.15 Sørensen's index of similarity comparing species composition of the potential seed bank to: (a) species that were recorded in the extant vegetation at the time soils were taken; and (b) total species found in the extant vegetation during the present study (SI = Sorensen's index of similarity; SU97 = summer 1997; W97 = winter 1997; MWD = mean water depth; ↓ = decrease from summer to winter 1997; ↑ = increase from summer to winter 1997; = sign means no change).

Zone	All species			Mean water depth		Direction of change	
	(a) SI SU97	SI W97	(b) Study Total	SU97	W97	SI	MWD
BP <i>B. rubiginosa</i> aquatic	28.6	25	71.4	0	1.7	↑	↑
BP <i>B. rubiginosa</i> outer	18.0	20	22.2	0.0	0.2	↑	↑
TD Aquatic	37.0	48.5	55.8	8.0	4.1	↑	↓
TD <i>E. acuta</i>	28.6	57.9	44.9	1.4	0.0	↑	↓
MID <i>E. sphacelata</i>	61.5	61.5	75.9	50.9	56.2	=	↑
MID Aquatic	73.2	72.2	71.7	10.3	18.2	↓	↑
MID Dry herb	64.3	64.2	74.7	0.1	2.6	=	↑
CTL Aquatic	54.1	66.7	65.1	24.9	14.4	↑	↓
CTL <i>B. arthropphylla</i>	51.6	45.7	61.8	10.7	1.5	↓	↓
SG Aquatic	40	51.1	64.6	7.9	26.8	↑	↑
SG <i>B. arthropphylla</i>	52.6	51.7	67.6	3.4	18	↓	↑

Table 6.16 Sørensen's index of similarity comparing species composition of the dominant species in the seed bank to: (a) dominant species recorded in the extant vegetation at the time soils were taken; and (b) dominant species found in the extant vegetation during the present study (SI = Sorensen's index of similarity; SU97 = summer 1997; W97 = winter 1997; MWD = mean water depth; ↓ = decrease from summer to winter 1997 ; ↑ = increase from summer to winter 1997; = sign indicates no difference).

Zone	Dominant species			Mean water depth		Direction of change	
	(a) SI SU97	SI W97	(b) Study Total	SU97	W97	SI	MWD
BP <i>B. rubiginosa</i> Aquatic	40.0	0.0	100	0.0	1.7	↓	↑
BP <i>B. rubiginosa</i> Outer	0.0	0.0	33.3	0.0	0.2	=	↑
TD Aquatic	40.0	75.0	90.0	8.0	4.1	↑	↓
TD <i>E. acuta</i>	33.3	88.9	88.9	1.4	0.3	↑	↓
MID <i>E. sphacelata</i>	100.0	100.0	100.0	50.9	56.2	=	↑
MID Aquatic	83.3	90.9	100.0	10.3	18.2	↑	↑
MID Dry Herb	80.0	90.9	100.0	0.1	2.6	↑	↑
CTL Aquatic	58.8	84.2	96.8	24.9	14.4	↑	↓
CTL <i>B. arthropphylla</i>	66.7	66.7	87.0	10.7	1.5	↑	↓
SG Aquatic	80.0	93.3	100.0	7.9	26.8	↑	↑
SG <i>B. arthropphylla</i>	60.0	72.7	75.9	3.4	18.0	↑	↑

Affect of water regime on the relationship between species composition of the seed bank and extant vegetation

The direction of change in Sørensen's index of similarity between the seasons sampled, that is, summer and winter, 1997, was not associated with the direction of change in mean water depth ($\chi^2 = 0.2250$; $P = 0.6353$). However, mean water depth correlated with the floristic similarity between the seed bank and extant vegetation (SI) at the time the soils were taken for both total and dominant species ($\rho = 0.702$; $P = 0.0013$; Figure ESB SI a and $\rho = 0.611$; $P = 0.0051$). Greater similarity between the species composition of the seed bank and extant vegetation was associated with zones that had a deeper water depth at the time of seed bank sampling (Figure 6.12 a). The ratio of species inundation adapted to non-adapted species (IA:INA) present in the seed bank and extant vegetation at the time the soils were taken was not correlated with the SI values (Figure 6.12 b). However, within zones dominated by inundation adapted species, those that were inundated generally had higher SIs than those that were dry, whereas within zones dominated by non-adapted species zones that were dry generally had the highest SI.

The percentage of seasons a zone was inundated over the period of the present study did not affect the species similarity (SI) between the total species found seed bank and extant vegetation over the period of the study ($\rho = 0.477$; $P = 0.1312$; Figure 6.12 b). Most zones inundated for more than 35% of the seasons surveyed had a greater than 50% similarity between the species in the seed bank and extant vegetation over the period of the present study. Two zones, Big Punchbowl *Baumea rubiginosa* and Tin Dish *Eleocharis acuta* had a total SI lower than 50% (22.2 and 44.9% respectively). These zones also had the lowest inundation period of the zones sampled (Figure 6.12 b).

Whether a zone was dominated by species adapted to, or non-adapted to long-term inundation did not affect the relationship between the species composition of the seed bank and extant vegetation for both total and dominant species over the period of the study ($\rho = 0.325$; $P = 0.3041$; $\rho = 0.101$; $P = 0.7491$; Figure 6.12 c). Although, low SIs were recorded for the two zones dominated by non-adapted species, Tin Dish aquatic and *Eleocharis acuta* zones, the lowest SI was from Big Punchbowl, *Baumea rubiginosa* outer zone which was dominated by species adapted to long-term inundation. Within the other zones, similar SI were calculated regardless of their species functional types within their potential flora (Figure 6.12 c).

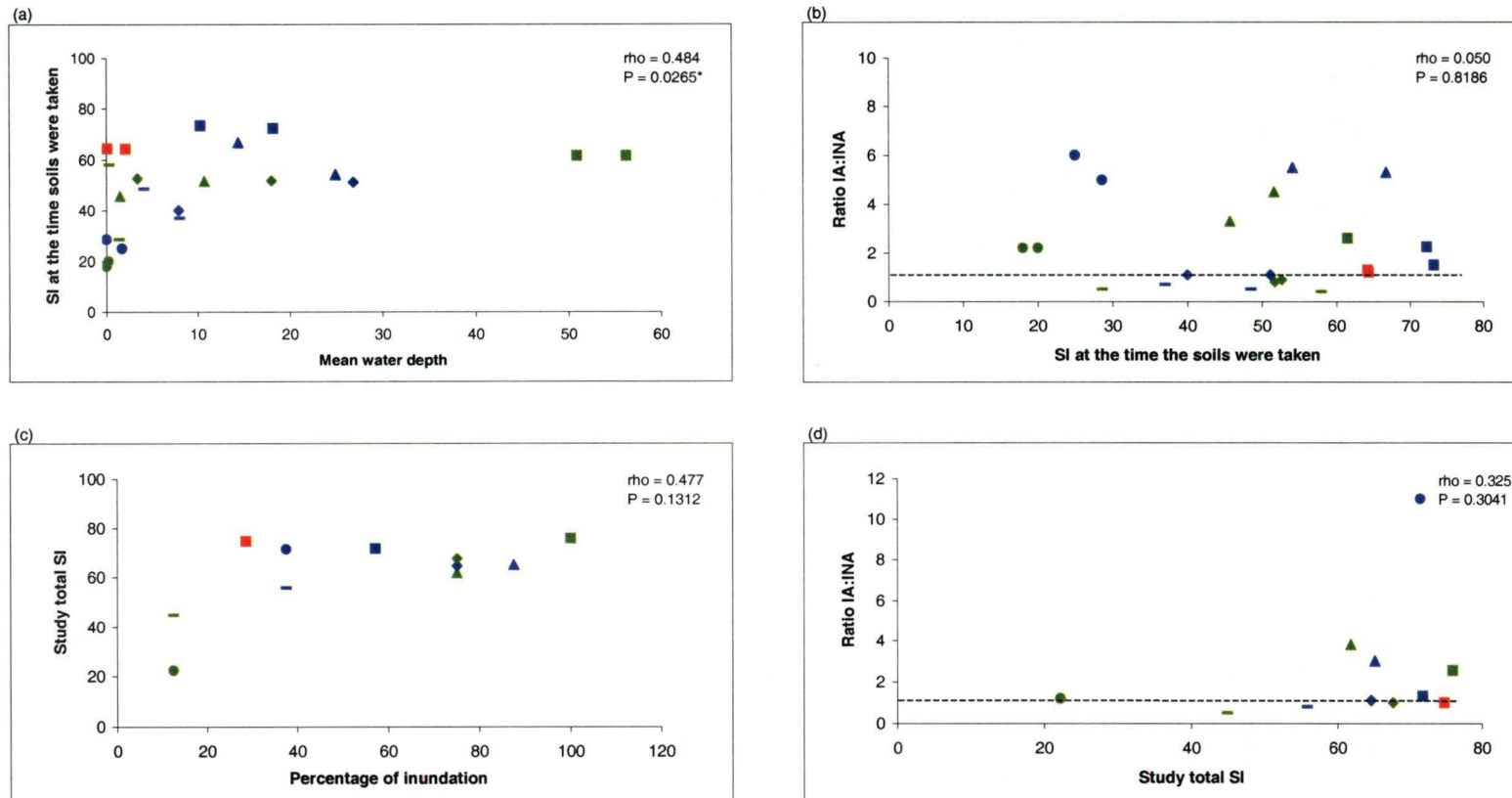


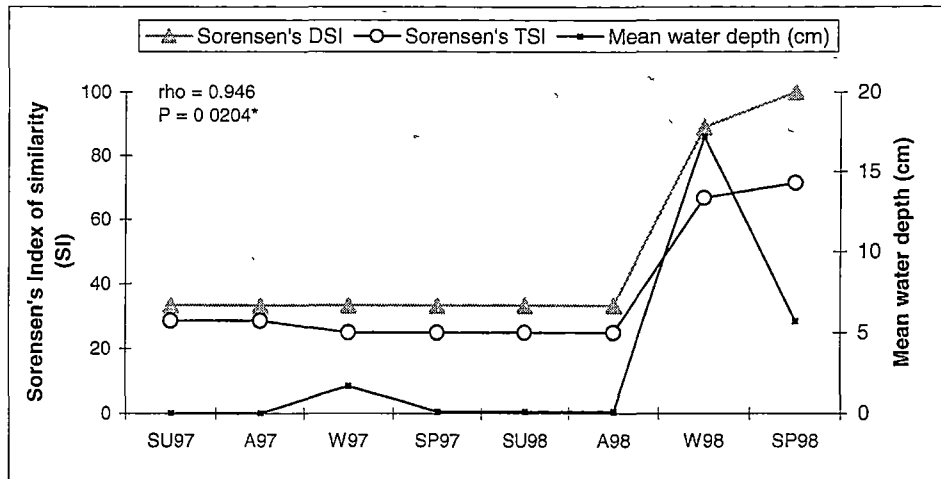
Figure 6.12 Effects of water depth on the relationship between the species composition of the seed bank and extant vegetation: (a) water depth at the time soils were taken; (b) ratio IA:INA of potential flora vs. SI; (c) percentage of inundation over the period of the present study; (d) species type, ratio between species that are adapted (IA) or not adapted (INA) to long term inundation (Big Punchbowl: ● = Aquatic, ● = Outer; Tin Dish: — = aquatic; — = *Eleocharis acuta*; Middle Lagoon: ■ = *Eleocharis sphacelata*; ■ = aquatic; ■ = Dry herbaceous; Cherry Tree Lagoon: ▲ = aquatic; ▲ = *Baumea arthropophylla*; Sandy Gate: ◆ = aquatic; ◆ = *Baumea arthropophylla*).

However, there was a higher than expected proportion of zones that had a study total SI greater than 50% that were dominated by inundation adapted species ($\chi^2 = 5.99$; $P = 0.0107$).

Changes in water level over time

Rapid changes in water level correlated with large changes in similarity between the total species composition of the seed bank and extant vegetation for only the two zones of Big Punchbowl (Figure 6.13 a-e). However, for dominant species this occurred in only one zone of Big Punchbowl ($\rho = 0.832$; $P = 0.0413$).

(a) *Baumea rubiginosa* aquatic zone



(b) *Baumea rubiginosa* outer zone

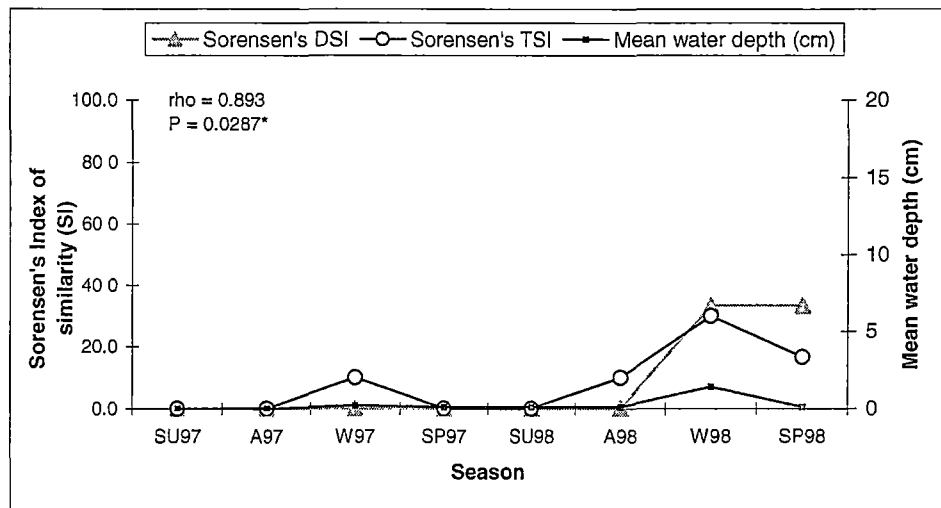
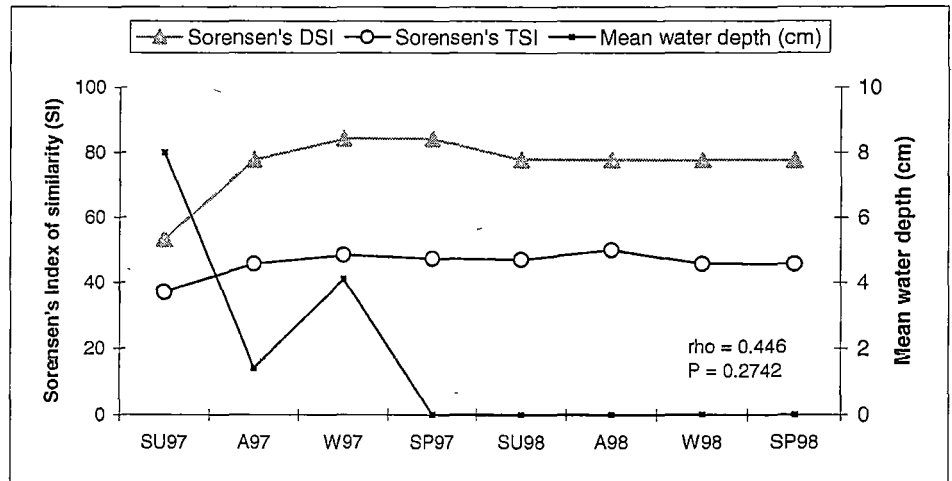


Figure 6.13-a Big Punchbowl: comparison of the Sørensen's index of similarity (SI) comparing the species composition of the extant vegetation found during each season with the combined species that germinated from the seed bank during summer and winter 1997 and mean water depth during each season (DSI = dominant species; TSI = total species, rho = Spearman's rank correlation coefficient comparing changes in SI with changes in water depth between seasons; P = significance of Spearman's rank analysis; * = $P < 0.05$).

(a) Aquatic herb zone



(b) *Eleocharis acuta* zone

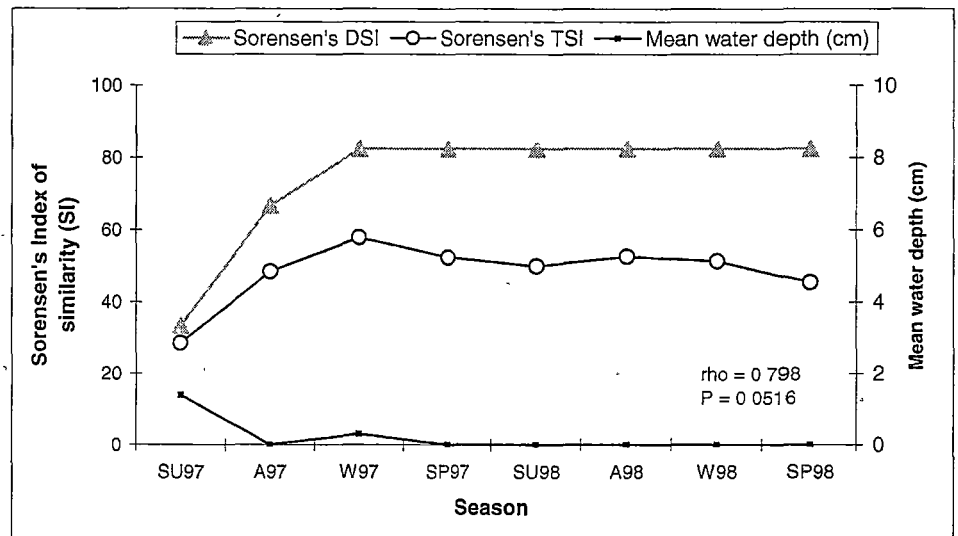
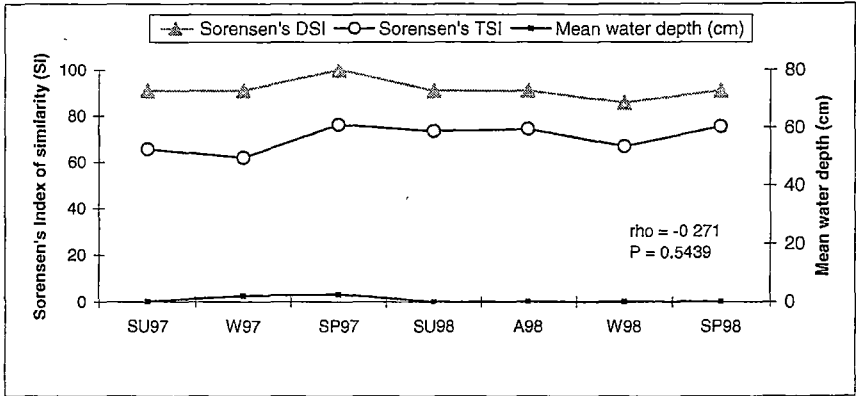
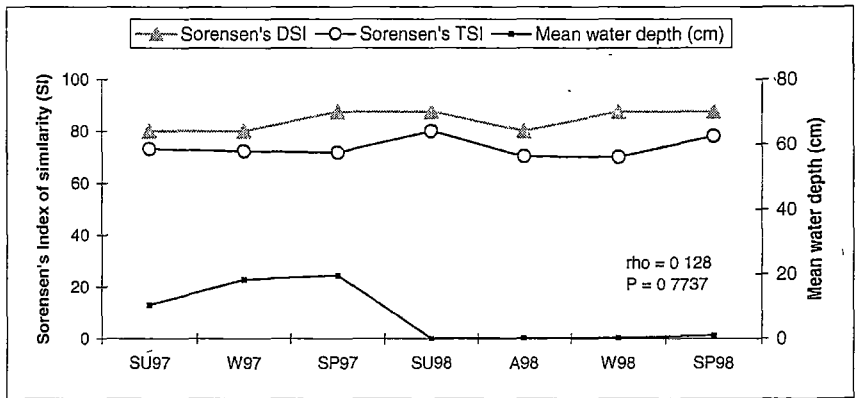


Figure 6.13-b Tin Dish: comparison of the Sørensen's index of similarity (SI) comparing the species composition of the extant vegetation found during each season with the combined species that germinated from the seed bank during summer and winter 1997 and mean water depth during each season (DSI = dominant species; TSI = total species, ρ = Spearman's rank correlation coefficient comparing changes in SI with changes in water depth between seasons; P = significance of Spearman's rank analysis; * = $P < 0.05$).

(a) Dry herb zone



(b) Aquatic herb zone



(c) *Eleocharis sphacelata* zone

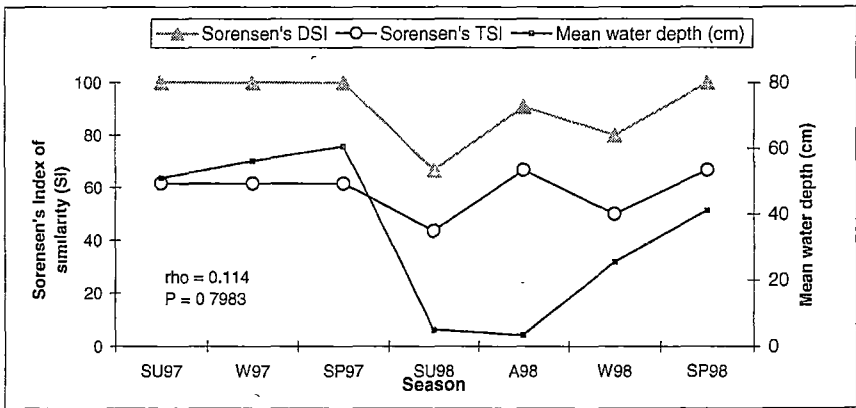
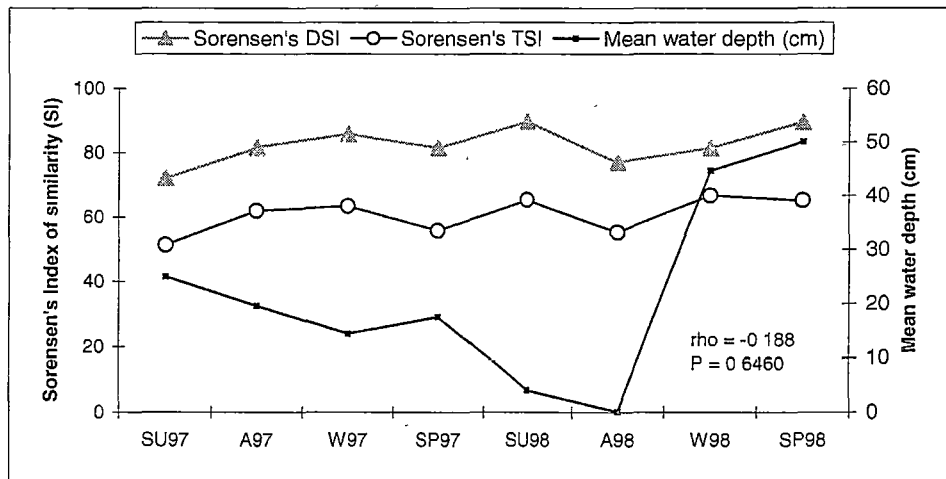


Figure 6.13-c Middle Lagoon: comparison of the Sørensen's index of similarity (SI) comparing the species composition of the extant vegetation found during each season with the combined species that germinated from the seed bank during summer and winter 1997 and mean water depth during each season (DSI = dominant species, TSI = total species, ρ = Spearman's rank correlation coefficient comparing changes in SI with changes in water depth between seasons; P = significance of Spearman's rank analysis; * = $P < 0.05$).

(a) Aquatic herb zone



(b) *Baumea arthropophylla* zone

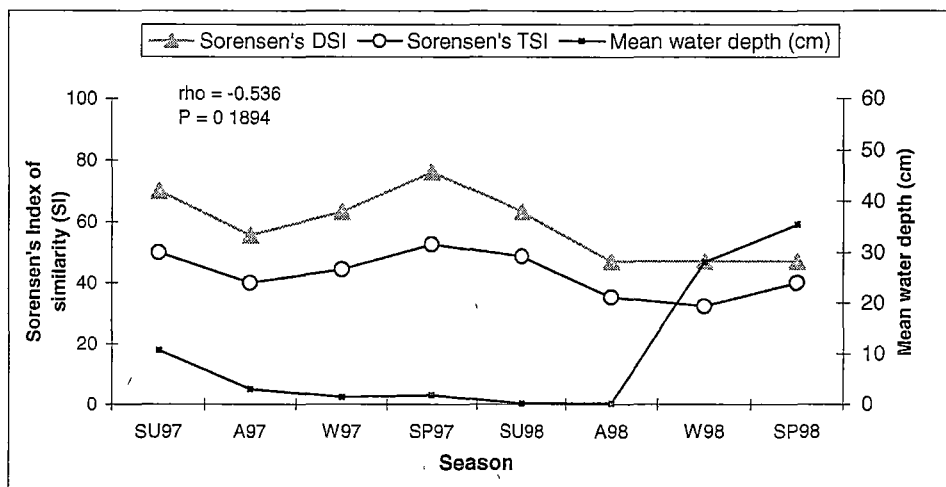
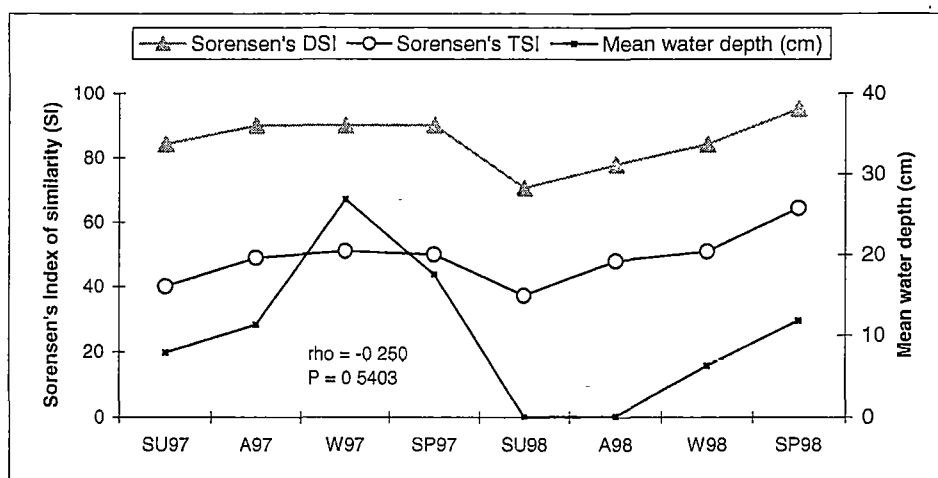


Figure 6.13-d Cherry Tree Lagoon: comparison of the Sørensen's index of similarity (SI) comparing the species composition of the extant vegetation found during each season with the combined species that germinated from the seed bank during summer and winter 1997 and mean water depth during each season (DSI = dominant species; TSI = total species, ρ = Spearman's rank correlation coefficient comparing changes in SI with changes in water depth between seasons; P = significance of Spearman's rank analysis; * = $P < 0.05$).

(a) Aquatic herb zone



(b) *Baumea arthropylla* zone

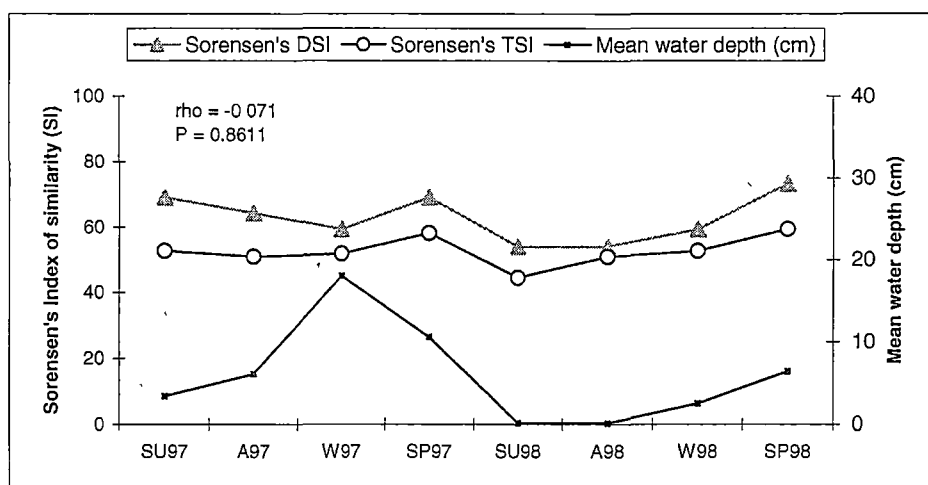


Figure 6.13-e Sandy Gate: comparison of the Sørensen's index of similarity (SI) comparing the species composition of the extant vegetation found during each season with the combined species that germinated from the seed bank during summer and winter 1997 and mean water depth during each season (DSI = dominant species; TSI = total species, ρ = Spearman's rank correlation coefficient comparing changes in SI with changes in water depth between seasons; P = significance of Spearman's rank analysis; * = $P < 0.05$).

Correlation between the species abundance in the seed bank and extant vegetation

Zone analyses

Species abundances in the seed bank and extant vegetation were significantly correlated in only Big Punchbowl *Baumea rubiginosa* outer, and Middle Lagoon *Eleocharis sphacelata* zones (Table 6.17). In the Big Punchbowl outer *Baumea rubiginosa* zone species abundances were negatively correlated during both seasons ($\rho = -0.865$; $P = 0.0018$ and $\rho = -0.785$; $P = 0.0012$), whereas, in Middle Lagoon *Eleocharis sphacelata* zone species abundances were positively correlated during winter 1997 ($\rho = 0.651$; $P = 0.0116$).

Individual species

Twenty-one taxa had sufficient occurrences during the seasons sampled (i.e. 10 or greater) to include in the Spearman's rank correlation analyses. Several patterns of abundance relationships between the seed bank and extant vegetation were observed in the 21 taxa analysed (Figure 6.14). However, the abundance relationship was significantly correlated for only the amphibious responder *Myriophyllum* spp. ($\rho = 0.551$; $P = 0.0049$; Figure 6.14). Although not significantly correlated, submerged taxa, such as *Chara* spp. showed both a high and low seed bank number with both low and high extant percentage cover, whereas, the amphibious responder, *Potamogeton tricarinatus* generally had a low abundance in the seed bank associated with both high and low abundances in the extant vegetation.

Distribution of species into seed bank/extant vegetation categories indicated that the largest percentage of taxa fell into the low seed bank/low extant vegetation category (Appendix IX). However, 16 taxa showed some variation in their abundance in the seed bank and extant vegetation (Table 6.18). The submerged charophyte taxa (*Chara* and *Nitella* spp.) fell into the high seed bank category the largest percentage of time with varying percentage covers in the extant vegetation. Conversely, several taxa, *Potamogeton tricarinatus*, *Lilaeopsis polyantha*, *Baumea* spp., and *Eleocharis acuta*, were only found in the low seed bank category with varying percentage covers in the extant vegetation.

Table 6.17 Results of Spearman's rank correlation for zones between the mean number of individuals germinated of each species in the seed bank and the mean percentage cover found within the extant data at the time the germinated soil was taken, summer 1997 and winter 1997 (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate; B = *Baumea*; E = *Eleocharis*).

Zone	Summer 1997			Winter 1997		
	Rho	P-value	Sig.	Rho	P-value	Sig.
BP <i>B. rubiginosa</i> aquatic †	-0.258	0.6547	ns	-0.823	0.657	ns
BP <i>B. rubiginosa</i> outer	-0.865	0.0018	**	-0.785	0.0012	**
TD Aquatic	-0.032	0.8908	ns	0.036	0.8798	ns
TD <i>E. acuta</i>	-0.078	0.7076	ns	0.013	0.9552	ns
MID <i>E. sphacelata</i>	0.355	0.2392	ns	0.651	0.0116	*
MID Aquatic	-0.145	0.4678	ns	-0.153	0.5060	ns
MID Dry herb	-0.168	0.3508	ns	0.327	0.0601	ns
CTL <i>B. arthropphylla</i>	0.126	0.5930	ns	-.178	0.4033	ns
CTL Aquatic	-0.030	0.8864	ns	0.265	0.1942	ns
SG <i>B. arthropphylla</i>	0.028	0.6159	ns	-0.071	0.6635	ns
SG Aquatic	0.116	0.5244	ns	0.051	0.8031	ns

† total variables were <10; Sig. = Significance; * = $P < 0.05$; ** = $P < 0.001$.

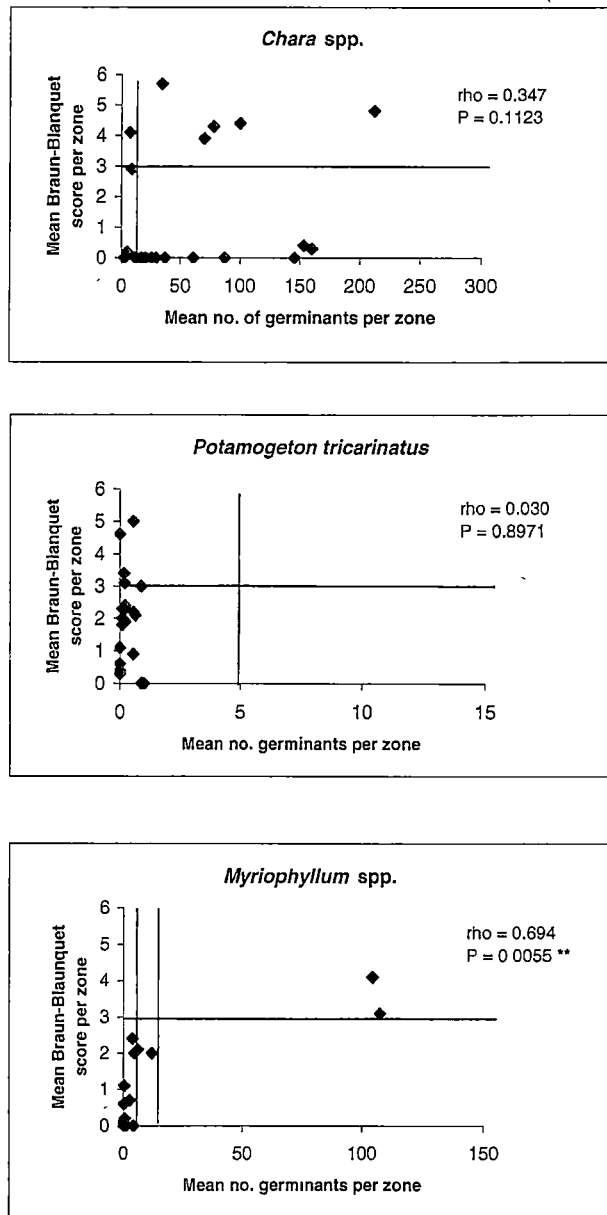


Figure 6.14 Example of species showing the differences in relationships between the seed bank and extant vegetation. (a) *Chara* spp - low and high seed bank with both low and high percentage cover; (b) *Potamogeton tricarlinatus* - low seed bank with both high and low percentage cover and; (c) *Myriophyllum* spp. - significant positive correlation between seed bank and extant vegetation. Lines indicate categories used for Table 6.18 (ρ = Spearman's rank correlation coefficient; P = significance of ρ ; $** = P > 0.001$).

Table 6.18 Taxa representation into seed bank and extant vegetation "relationship categories" (seed bank: low = less than 5 germinants per tray; medium = between 5-15 germinants per tray; High = greater than 15 germinants per tray. Extant vegetation: High = mean percentage cover of Braun-Blanquet score 3 or above i.e. 1-5%; Low = mean percentage cover of less than Braun-Blanquet score 3 i.e. <1%, Zones present = zones present out of 22 (11 = summer 1997, 11 = winter 1997; ** = $P < 0.001$; species above dotted line occur in greater than 50% of sample times).

Seed Bank number of germinants			Abundance relationship categories					
			Low		Medium		High	
			High	Low	High	Low	High	Low
Extant vegetation percentage cover								
	Zones present	P	1	2	3	4	5	6
<i>Chara</i> spp.	22	ns	1	5	2	0	5	8
<i>Nitella</i> spp.	21	ns	0	3	0	2	2	13
<i>Potamogeton tricarlinatus</i>	20	ns	5	15	0	0	0	0
<i>Agrostis avenacea</i>	20	ns	0	16	0	0	0	4
<i>Isolepis</i> spp.	17	ns	3	5	2	6	0	0
<i>Myriophyllum</i> spp.	17	**	0	13	0	2	1	1
<i>Eleocharis acuta</i>	17	ns	0	12	2	2	0	1
<i>Lilaeopsis polyantha</i>	17	ns	1	16	0	0	0	0
<i>Baumea</i> spp.	16	ns	5	11	0	0	0	0
<i>Juncus holoschoenus</i>	13	ns	0	6	0	5	0	2
<i>Leontodon taraxacoides</i> *	12	ns	3	9	0	0	0	0
<i>Villarsia reniformis</i>	11	ns	4	6	0	1	0	0
<i>Selliera radicans</i>	9	ns	0	8	0	1	0	0
<i>Juncus articulatus</i> *	9	ns	0	0	0	0	0	0
<i>Batrachium trichophyllum</i>	7	ns	0	0	0	0	0	0
<i>Eleocharis sphacelata</i>	6	ns	1	5	0	0	0	0

Amalgamated analyses

The abundance in the seed bank and extant vegetation were significantly positively correlated for the dominant species within the submerged functional group (Figure 6.15). All other functional groups were not correlated in their dominant species seed bank and extant vegetation abundances. These groups generally had a low number of germinants per tray irrespective of their cover in the extant vegetation. Species with both annual and perennial life cycles were not correlated in their seed bank and extant vegetation abundance and had a similar pattern in their species abundance relationships. Species within both life cycle groups had a range of high and low seed bank with both high and low percentage cover (Figure 6.16).

However, strong differences in the species abundance relationships, between the seed bank and extant vegetation, were shown between non-rhizomatous and rhizomatous species (Figure AFG). The non-rhizomatous species had a wide range of low and high seed bank numbers with a range of low and high levels of cover which were significantly positively correlated. These relationships were also significantly positively correlated when analysing only the dominant angiosperm species ($\rho = 0.192$; $P = 0.0194$). Rhizomatous species were not correlated in their seed bank and extant abundances and were generally characterised by low seed bank numbers which were associated with a wide range of percentage covers.

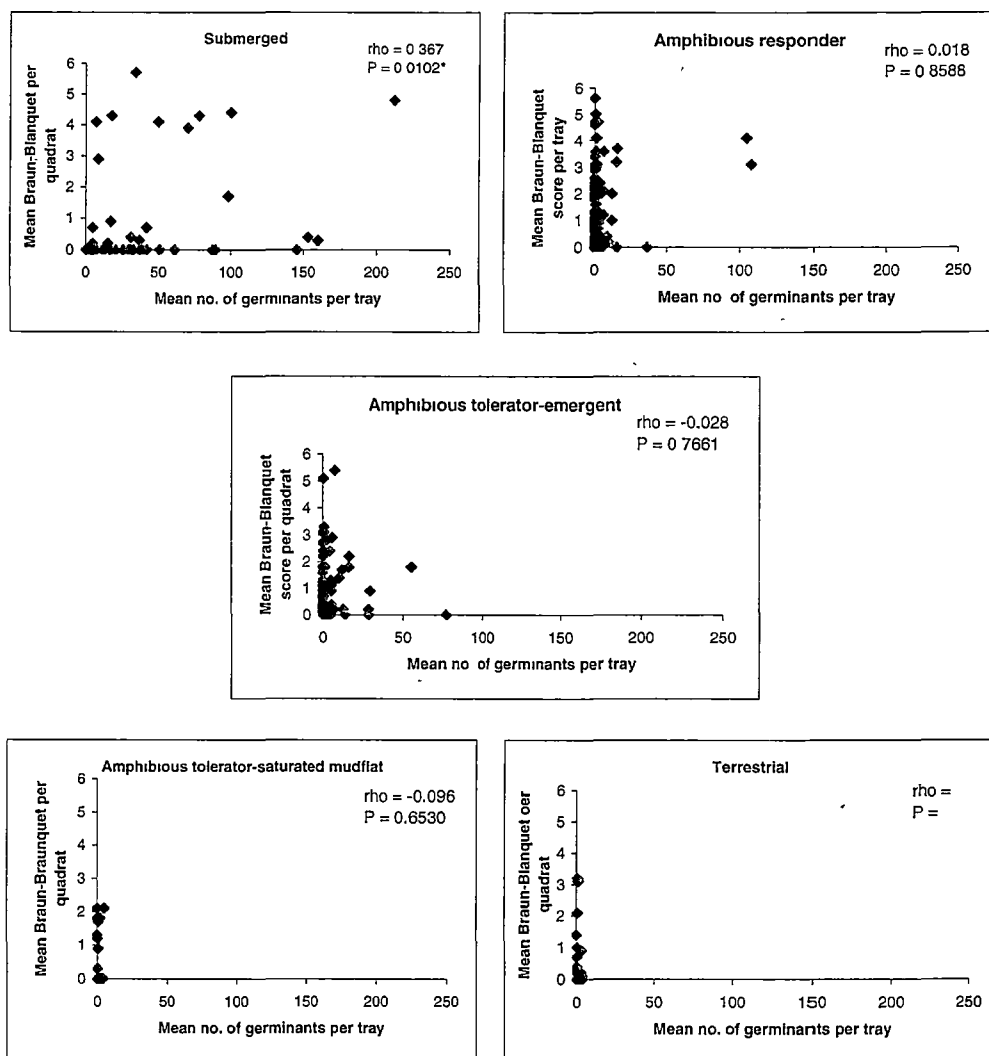


Figure 6.15 Correlation between the abundance in the seed bank and extant vegetation of the dominant or more frequent species within each functional group (ρ = Spearman's rank correlation coefficient; P = significance of ρ ; * = $P < 0.05$).

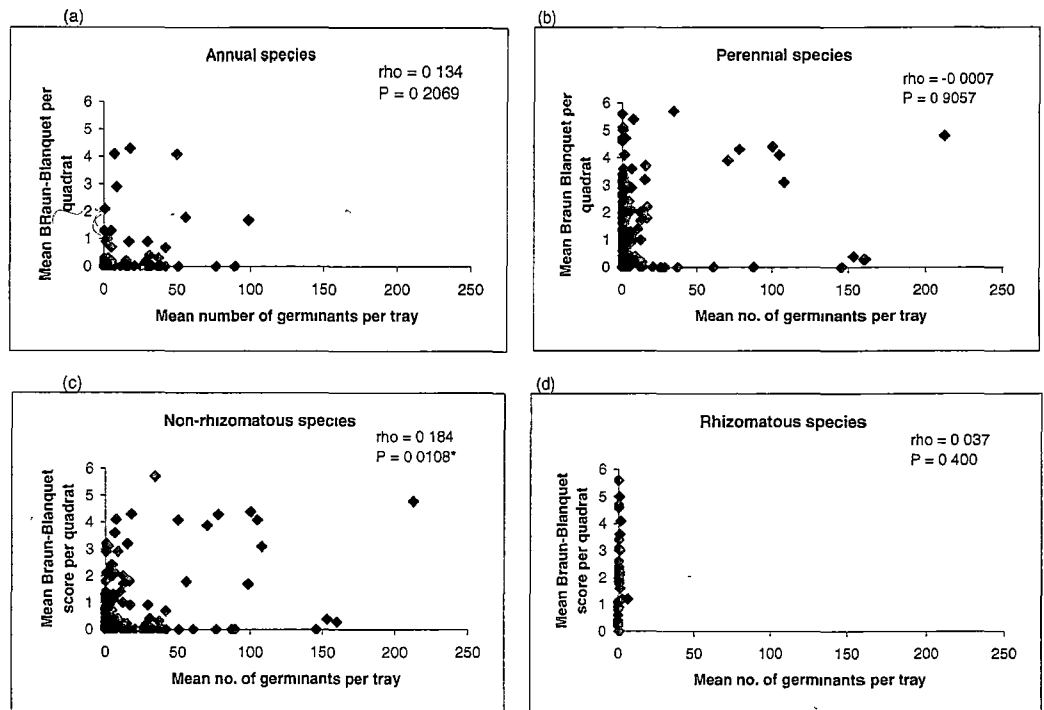


Figure 6.16 Correlation between the abundance in the seed bank and extant vegetation of the dominant or more frequent species with varied: 1) life cycles: (a) annual and (b) perennial; and 2) root systems: (c) non-rhizomatous; or (d) rhizomatous species (ρ = Spearman's rank correlation coefficient; P = significance of ρ ; * = $P < 0.05$).

Discussion

The potential flora of wetlands recorded in both the seed bank and extant vegetation of the wetlands contained species adapted to a wide range of hydrological conditions representative of both past and present vegetation communities (Figure 6.1; Figure 6.3; Appendix VII; Appendix VIII a-e). This is characteristic of many temporary wetlands (van der Valk, 1981; Leck, 1989; van der Valk and Davis, 1978,1979; Keddy and Reznicek, 1982; Schneider and Sharitz, 1986; Brock, 1998). All functional groups were represented in the potential flora of most zones. This has also been found to be characteristic of vegetation communities in other Australian temporary wetlands (Brock, 1998). However, it varies from the functional group representation found in freshwater tidal wetland in the United States, where the vegetation communities are dominated by only two groups, amphibious tolerator and terrestrial (Leck and Brock, 2000).

Variation in the past and recent hydrological conditions did not appear to significantly affect the proportion of inundation adapted to non-inundation adapted species found in the potential flora of the wetlands. The potential flora of zones inundated for longer periods did not have a significantly greater proportion of species that can survive long periods of inundation to those that were dry for long periods. This indicated that although dry these species types can remain in the propagule bank and thus remain in the potential flora over time.

Similar numbers of terrestrial species in both inundated and dry wetlands indicated that terrestrial species can invade wetlands regardless of their water regime. This was supported by the results comparing surveys of 1979 to the present study (Table 6.14) where all wetlands showed an increase in terrestrial species over the last 20 years. However, as the greatest number of terrestrial species were found in wetlands which were surrounded by native vegetation used for stock grazing (i.e. Tin Dish, Sandy Gate and Middle Lagoon) wetland in these habitats (or in disturbed areas) may be more vulnerable to invasion by terrestrial species. This may be facilitated if the wetland dries for any length of time. However, dispersal into inundated wetlands is also possible in these areas.

Species richness

Overall more species germinated from the seed bank that were recorded in the extant vegetation at time the soils were taken (Figure 6.5; Figure 6.6). This is consistent with the results of other studies on temporary wetlands (Smith and Kadlec, 1983; Brock, 1998; Brock and Rogers, 1998; Brock, 1999) and suggests that it may be common in these wetland types. As expected (Brock and Rogers, 1998; Brock, 1999) differences in the species richness between the seed bank and the extant vegetation at the time the soils were taken could not be explained by their water regime.

Species representation

Overall, 58% of species were found in both the seed bank and extant vegetation, 27% exclusively in the extant vegetation and 15% exclusively in the seed bank in the two year observation period. However from the species recorded in the wetlands over the last thirty years only 2% remained in the seed bank only and 12% remained in the extant vegetation only. Eighty-seven percent of the species found within the wetlands over the past thirty years were found in both the seed bank and extant vegetation. The results of the present study compared with Brock (1998) for both a South African floodplain and Australian upland wetlands, where 56% of species were found in both the seed bank and extant vegetation (14% seed bank and 30%, extant). However, the results for the individual zones were greater than those found in individual Australian wetlands (Brock and Britton, 1995) and other wetlands dominated by perennial species (Grelsson and Nilsson, 1991). Differences between wetlands may reflect the different conditions in the wetlands at the time the soils were taken as well as the duration of observations. However, in the case of Grelsson and Nilsson (1991), who found that 76 % of species within the wetland community were found exclusively in the extant vegetation, the differences may be due to a predominance of rhizomatous species within the lakeshore community they studied. In several zones of the present study, these type of species dominated the extant vegetation community, but were found in very low numbers in the seed bank (Figure 6.16).

At any given time, the seed banks of the wetlands held a potential store of species (which germinated in the seed bank experiments), not present in the extant vegetation (Figure 6.8) that could establish and under certain conditions, may become dominant within the wetland communities. These results are common to many wetland seed

banks in both predictable and unpredictable habitats (Smith and Kadlec, 1983; Leck *et al.*, 1988; Leck, 1989; Finlayson *et al.* 1991; Brock, 1998; Brock and Rogers, 1998). Absence of species from the vegetation may reflect: a) the conditions in the wetland at the time the soils were taken; b) seed dormancy; c) failure in establishment after germination was successful; and/or d) competition between species (Brock, 1998). In the present study, zones with dry to shallow water levels, at the time the soils were taken, had a higher percentage of seed bank species not represented in the extant vegetation than zones with deeper water levels. This could be expected as many of the aquatic species found in the seed banks of these wetlands, for example charophytes, would not be present in dry habitats and if the zone had remained dry for a long period some amphibious species would also not be present (see Chapter 5). However, contrary to what was expected fifty-five % of zones with drier conditions also had a high proportion of terrestrial species adapted to these habitats found in the seed bank only (Figure 6.11). This suggests that dormancy may also influence the absence of some species within the extant vegetation. Similarly, species adapted to inundated conditions were found in the seed bank and not present in the extant vegetation during sampling in zones inundated at that time (e.g. *Batrachium trichophyllum*, *Elatine gratioloides* and *Callitriche stagnalis* in Cherry Tree Lagoon). In this case these species may have been competitively excluded from the community and/or have an annual life cycle and require drawdown conditions for germination. Both may have been the case for *Batrachium trichophyllum* and *Callitriche stagnalis* as they both can act as an annual or a perennial, whereas, *Elatine gratioloides* is exclusively annual.

Species composition

The range of percentage similarity between the seed bank and extant vegetation found in the present study are comparable to those found in several other wetland studies (van der Valk 1981; Smith and Kadlec, 1983; Hopkins and Parker, 1984; Brock, 1998; van der Valk and Davis, 1978; Pederson, 1981; Thompson and Grime, 1979). The low correlation between the species composition in the seed bank and extant vegetation has been explained by species that have accumulation in the seed bank during different hydrological conditions not being present in the extant vegetation (van der Valk and Davis, 1978; van der Valk, 1981).

The high number of dominant species common to the seed bank and extant vegetation indicated that, similar to the results of many other wetland studies (van der Valk and

Davis, 1978; Leck and Graveline, 1979; Thompson and Grime, 1979; van der Valk, 1981; Hopkins and Parker, 1984; Parker and Leck, 1985; Thompson, 1992; Grillas *et al.* 1993), most zones possess seed banks that were reflective of the dominant surface vegetation. This contrasts to most dry land habitats where there is a general lack of correspondence between the seed bank and the established vegetation (e.g. Major and Pyott, 1966; Thompson and Grime, 1979).

As expected the conditions in the wetland at the time the soils were taken affected the floristic similarity between the seed bank and extant vegetation (Figure 6.12).

However, this was not associated with whether the potential flora at time was dominated by either inundation adapted (IA) or non-adapted species (INA). The latter would be expected due to varied nature of the potential flora in the wetlands. However, patterns within each category, that is, IA or INA dominated, showed that differences between SIs depended on whether a zone was inundated or dry at the time the soils were taken (Figure 6.12 b). As expected zones dominated by IA species and were inundated had a greater SI than those that were dry, whereas, the reverse occurred for zones dominated by INA. This indicated that the vegetation community at any particular time is not an indication of the total flora of a wetland and confirms the suggestion by Major and Pyott (1966) that knowledge of the seed bank of a wetland is essential for a complete plant community description, especially where prediction of future change may be required.

Differences over time

The results of several analyses indicated that the hydrological conditions over the period of the present study affected the relationships between the seed bank and extant vegetation.

As expected zones that were either inundated or dry for long periods had the greatest number of species that remained exclusively in the seed bank over the period of the study than zones that had fluctuated over the same period. This indicated germination requirements for a greater proportion of the species within the seed bank of these zones were present over the period of the study. This would be expected as dry conditions do not support submerged and many amphibious species, whereas, inundated conditions, as low as 1-2 cm will prevent the germination and establishment of terrestrial species (Figure 6.11). Fluctuating environments with an equal period in each water level

condition enables species adapted to each water level condition, to germinate and become established in the environment.

It was expected that a rapid change in water level would cause a large change in SI between the seed bank and extant vegetation (Figure 6.13 a-e). However, the only zones in which this occurred were from Big Punchbowl. This indicated that factors other than just the presence or absence of standing water influenced the relationship between the species composition of the seed bank and extant vegetation over the period of the study. As the differences in the SI over time was due to species within the seed bank (recorded at the beginning of the study) becoming present in the extant vegetation, the functional type of the seed bank species and their germination requirements may be also important.

Big Punchbowl, has a seed bank dominated by submerged and amphibious aquatic species. During the dry conditions most of these species were not present in the extant vegetation. These species becoming present in the extant vegetation after a rapid increase in water levels between autumn and winter 1998, thus causing the simultaneous large increase in SI. This result indicates how rapid both submerged and amphibious species can become present in the extant vegetation after a long-term dry period. The lack of correlated response, as would be expected, with a decrease in water levels in Tin Dish was probably due to the fact that the decrease in water levels were more gradual than in Big Punchbowl. However, the pattern of change in SI as the wetland dried out indicated that the floristic similarity between the seed bank and extant vegetation was greater in the dry conditions. The seed bank of Tin Dish, although it contains seeds of two stages, that is, inundated and drawdown conditions, is dominated by terrestrial and amphibious-saturated species. This indicated that the differences in SI over time demonstrated a gradual change from an aquatic dominated vegetation community to one dominated by more terrestrial species.

Most of the other zones did not show large changes in SI with rapid changes in water levels (Figure 6.13 c-e). These zones are dominated by amphibious species that survive in both inundated and drawdown conditions, however, submerged and terrestrial species were also present. All of these species, except, submerged will germinate under drawdown conditions (see Chapter 4). Submerged species do not survive drawdown whereas terrestrial species do not survive inundation (Brock and Casanova, 1997). The evenness of SI in these zones was due to most amphibious species remaining in the

community over time regardless of water depth. Slight differences, between seasons, observed, with presence or absence of water, were due to changes in the presence and absence of both submerged and terrestrial species and the germination of amphibious species in the drawdown conditions.

The results indicated that recruitment of species from the seed bank was influenced by the presence or absence of standing water. This was especially evident for submerged and terrestrial species. However, recruitment from the seed bank of amphibious species was also evident in that: a) species not present in the extant vegetation of inundated zones required a drawdown event for germination and establishment, for example, *Batrachium trichophyllum*, *Callitriche stagnalis*; *Elatine gratioloides*; and *Amphibromus* spp.; b) many species present in the extant vegetation prior to the drawdown germinated in the saturated conditions, for example, *Myriophyllum* spp.; c) many amphibious species that have been lost from the vegetation community in zones that have remained dry required saturated or inundated conditions for recruitment, for example, *Utricularia* spp. and *Myriophyllum* spp..

These results indicate that the drawdown events in the wetlands, with a naturally semi-permanent water regime, created an opportunity for species that had been lost in the extant community and relied on the seed bank for regeneration, to become present in the vegetation. This in turn indicates that the high species richness of these wetlands may be a result of their fluctuating water levels and that a drawdown is a natural regeneration event for these communities.

Species abundance

Species abundances in the seed bank and extant vegetation within the vegetation communities of each zone were generally not correlated, that is, the most dominant species in the extant vegetation were generally not the most abundant in the seed bank (Table 6.17). This is consistent with many studies of terrestrial ecosystems (Major and Pyott, 1966; Rabinowitz, 1981; Ryser and Gigon, 1985; Bakker, 1989, Leck *et al.*, 1989a; Thompson, 1992) as well as several wetland studies (Smith and Kadlec, 1983; Thompson and Grime, 1979; Finlayson, *et al.*, 1990; Brock and Rogers, 1998), but varies from results from a marsh dominated by submerged species (Grillas *et al.*, 1993).

Analysis of the individual species showed that the abundance in the seed bank and extant vegetation was correlated for only one angiosperm taxon, *Myriophyllum* spp. Both charophyte taxa were not significantly correlated. These taxa generally had a high seed bank regardless of their abundance in the extant vegetation. These results for charophytes corresponded to those found by Grillas *et al.* (1993). However, unlike in the present study, a high percentage of angiosperm species were significantly correlated in their seed bank and extant vegetation abundances in the work of Grillas *et al.*, 1993. All of the submerged species studied by Grillas *et al.* (1993) were not able to survive vegetatively over period of extended drawdown and therefore, the high investment in sexual reproduction was necessary to maintain these species in an environment characterised by fluctuating water levels.

The amalgamated analyses indicated that as expected the type of relationship between a species abundance in the seed bank and extant vegetation was largely due to whether a species was rhizomatous or non-rhizomatous rather than due to its functional group or life cycle (Figure 6.15; Figure 6.16). However, this was more relevant to amphibious and terrestrial species rather than for submerged species. Submerged species were correlated in their number of germinants per tray and percentage cover in the extant vegetation (Figure 6.15) with some submerged species also having high seed banks with low extant covers. This is similar to results of Grillas *et al.* (1993). These taxa, for example, charophyte spp, *Ruppia* spp. and *Lepilaena* spp. are not able to survive vegetatively over periods of extended drawdown. The results, therefore indicated that the submerged species within the wetlands of the present study maintain themselves within the communities through a persistent seed bank. This agrees with most studies of charophyte taxa (Casanova and Brock, 1990; Casanova, 1993; Grillas, *et al.*, 1993; Brock and Casanova, 1997; van den Berg, 1999). However, Brock (1982) found differences between the propagation of *Ruppia* spp. depending on whether they were a perennial rhizomatous or an annual seed or turion producing species. The *Ruppia* taxa were not identified to species due to the lack of flowers and were found in only low proportions in both the seed bank and extant vegetation. Further studies in areas dominated by these species would give further insight to their regeneration mechanisms in Tasmanian wetlands.

Lack of correlation in the abundance relationships between species within the amphibious and terrestrial functional groups would be expected as the allocation of

species into functional groups was from their response to the presence and absence of water rather than their reproductive strategies (see Chapter 3). Therefore, the results of the present study suggest that whether a species responds to or tolerates water presence or absence does not relate to its mechanisms for persistence.

As expected the greatest differentiation between the species abundance relationships in the seed bank and the extant vegetation was if the species was rhizomatous or non-rhizomatous. The results indicate that species without rhizomes generally rely on the seed bank to persist in the vegetation communities of temporary wetlands, whereas, rhizomatous species are generally maintained over time by vegetative means. This was consistent with the conclusions of several studies of vegetative propagation in aquatic habitats (Sculthorpe, 1967; Hughes, 1987; Rea and Ganf, 1994a; 1994c) and supports the suggestion by Rea and Ganf (1994b) that vegetative expansion appears to be responsible for the extensive stands of *Baumea arthropphylla* found in the area of both Cherry Tree Lagoon and Big Punchbowl. The results also support studies within several wetland communities (e.g. van der Valk and Davis, 1976a; van der Valk, 1981; Leck and Simpson, 1987a; Brock, 1998), where species have been found to rely primarily on their seed bank for regeneration after prolonged drawdown periods primarily from their seed bank.

However, most rhizomatous species were present in the seed bank, although in low numbers. In terrestrial systems, Falinska (1999) found that sedges were less abundant in the seed bank than in the vegetation in the later phase of succession than in the beginning phases. This suggests that if species are colonising a new habitat sexual reproduction is more prevalent than when they are more established. The seed bank of the rhizomatous species may be remnant of earlier phases of the wetlands. However, most of the dominant sedge species have been well established for at least 20 years as indicated by their dominance in the vegetation during the surveys of Kirkpatrick and Harwood (1981). As found in several other studies (Grace and Wetzel, 1982; Silander, 1985; Rea and Ganf, 1994b), and in contrast to reports that sexual reproduction by clonal plant is rare (e.g. Callaghan *et al.*, 1992; see Rea and Ganf, 1994c), many of the dominant rhizomatous species, for example, *Baumea arthropphylla*, *Eleocharis acuta*, *E. sphacelata* and *Potamogeton tricarlinatus*, were all observed flowering in the wetlands during the period of the present study. If seeds were produced at these times they would be deposited in the seed bank, where they would remain and, if viability was

maintained, would germinate when conditions were suitable. However, due to the large vegetative mass of these species and the low number of seeds in the soil, seed germination may not be the most important mechanism in the persistence of these species over time.

Comparison with past studies

After comparison with past wetland surveys, very few species remained either only in the seed bank or extant vegetation, that is, most species were represented in both the seed bank and extant vegetation during some time over the past 30 years (86.2%; Table 6.12). This correspond to the results found by Keddy and Resnicke (1982) and van der Valk and Davis (1978; 1979), who found a large correspondence between the taxa in the seed bank and taxa recorded in past vegetation studies. Of the two species found exclusively in the seed bank, only *Limosella australis* germinated from more than 1 zone. Conditions may not have been suitable for its germination and establishment within the zones sampled or seeds may have been dispersed from other areas not sampled or surrounding the wetland (Hopkins and Parker, 1985). It would be expected that during further vegetation surveys this species would be recorded in the extant vegetation of the wetlands. This species is also very rarely found in the extant vegetation in the New England Tableland wetlands within Australia (Crosslé, 1998).

Most of the species that were found only in the extant vegetation were either recorded in only 1-2 quadrats within 1 vegetation zone, or if recorded in more than 1 zone were not a dominant species, for example, *Schoenus nitens* (Table 6.12). *Schoenus nitens* was observed flowering profusely at times during the period of the present study, therefore, it would be expected to be in the seed bank. Seed bank studies of zones where these species are more abundant in the extant vegetation may reveal that they are actually present within the seed bank. However, species such as *Schoenus nitens* may fail to develop a persistent seed bank or they may have a dormant seed bank and conditions for germination did not occur during the present study.

Predictions

The results of the comparisons between the seed bank and extant vegetation indicate that the species composition of the seed bank could generally be used to predict the composition of the vegetation that would develop over time in different hydrological conditions. However, the abundance of each species would be more difficult to predict with only seed bank information. These results compare to several studies in both predictable and unpredictable wetland habitats which have also found that future species composition is more easy to predict than abundances from results recorded from seed bank studies (van der Valk and Davis, 1978; Smith and Kadlec, 1983; Welling *et al.*, 1988; Haukos and Smith, 1993; Brock and Rogers, 1998; Finlayson, *et al.*, 1991). The vegetative mechanisms for both dispersal and perennation would also be needed for a more accurate predictions of the dominant vegetation communities that would establish after a period of extended drawdown.

However, from the results of the present study it could be assumed that species found in large quantities in the seed bank, such as, charophytes would become dominant in the extant vegetation during times of prolonged inundation. This would also occur for many non-rhizomatous aquatic species. However, information on the potential for their competition exclusion, their life cycle and seed dormancy may be needed to determine if they would persist in the vegetation community. Low number of seeds of perennial rhizomatous species in the seed bank may indicate that if the species is not still present in the extant vegetation that buried rhizomes may be found or the species has been newly dispersed into the wetland.

Chapter 7

Discussion

Are the wetland communities resistant to change?

In general the vegetation communities of the 5 wetlands were not able to resist change after a hydrological disturbance. Large rapid reductions in total percentage cover of many species were observed after a drying event in all wetlands. Rapid increases in cover occurred after re-flooding. These results demonstrate the dynamic nature of aquatic communities within Tasmanian wetlands and are consistent with many other wetland vegetation dynamic studies (van der Valk, 1981; van der Valk and Davis, 1978, 1979; Hughes, 1987; Leck, 1989; Casanova and Brock, 2000).

The only evidence of resistance to change in water levels were observed in the individual species *Baumea rubiginosa*, *B. arthropphylla* and, to a lesser extent, *Eleocharis acuta*. Although eventual changes in cover were observed, these species generally showed no immediate change in morphological structure after a dry or flooding event. This indicated their tolerance of water presence or absence which is consistent with their functional group allocation, amphibious tolerator-emergent. Differences in the response between species to water level changes have been explained by both their morphological structure and leaf turnover (Rea and Ganf, 1994a). *Baumea arthropphylla* has long-lived upright cylindrical cuticularised stems that during a lifespan of 15-18 months will recruit 3 to 6 stems (Rea, 1992; from Rea and Ganf, 1994a). Species such as the amphibious responder *Triglochin procerum* have fleshy flattened leaves which in the case of *T. procerum*, can be produced every 24 days (Rea and Ganf, 1994a). Many of the aquatic species found in the present study are similar to *T. procerum* in that they have fleshy leaves supported by the water during inundation. Lack of resistance to change of these aquatic herbaceous communities, therefore, could be put down to the morphological structure of the plants and their reliance on water for support. It is the resilience of these communities to dry periods and the persistence of the species over time that may indicate how resistant these communities are to hydrological changes over the long term.

Are the wetland communities resilient to dry periods?

The results of the present study indicate that the aquatic vegetation communities of the 5 wetlands were generally resilient to hydrological disturbance, i.e. they have the ability to 'bounce back' or recover rapidly after a drying event. In both long-term dry wetlands, Big Punchbowl and Tin Dish, aquatic communities rapidly regenerated after re-wetting. In the semi-permanent wetlands, Cherry Tree Lagoon and Sandy Gate, very little change was observed in the plant communities after a short-term dry period. In these wetlands several aquatic species not present prior to the drawdown became present in the extant vegetation after re-flooding. In Middle Lagoon, rapid changes in vegetation community 'types' between those dominated by either aquatic and dry herbaceous species were observed in the fluctuating aquatic zone depending on the water levels at the time.

The resilience observed in the vegetation communities indicated that the climatically determined (natural) fluctuations in water regimes recently experienced by the 5 wetlands are within the normal cycle of wetting and drying events tolerated by many of their aquatic species. These results correspond to those found by Brock (1998), who concluded that temporary wetlands in both the Northern Tablelands of Australia and within South Africa were resilient to their normal cycles of wetting and drying.

Do the species found in the 5 wetlands persist over time?

Presence and absence of many species within the extant vegetation over the period of the present study were influenced by water levels during each season sampled. For example, submerged species and some amphibious responder species were present only during inundated conditions; some species became present during drawdown and remained in the extant vegetation after inundation; other species such as amphibious tolerator-emergents, remained in the extant vegetation during both dry and inundated conditions; whereas, species adapted to dry conditions, i.e. terrestrial and amphibious tolerator/saturated, were present in drawdown conditions and absent in areas that became inundated.

However, regardless of whether they were present or absent in the extant vegetation most species remained present in the vegetation community of the 5 wetlands over the 2 year period by means of either buried seeds or vegetative propagules. It appears then that the species found in the 5 wetland can persist in the vegetation in the short-term

becoming present when water levels are suitable for regeneration. However, can they persist in the long term?

Comparison with past extant vegetation surveys (Appendix VIII a-e) revealed that a large percentage of angiosperm species found in the 5 wetlands during 1978-1980 by Kirkpatrick and Harwood (1981) were still present, either in the extant vegetation or in the seed bank, 20 years later during the present study. In general, of the species recorded between 1978-1980, only 1-3 species in the zones surveyed were not recorded between 1997-1998. Most of the angiosperm species recorded in the vegetation of the 5 wetlands by Kirkpatrick and Harwood (1981) and in other past studies (Blackhall pers. comm.¹) were species adapted to inundated conditions (i.e. submerged, amphibious responder and tolerator emergent functional groups). Therefore, the results indicate a high level of long-term persistence of both aquatic and amphibious species in the 5 wetlands studied. This shows that species found in the 5 wetlands can persist in the vegetation community over the long-term (i.e. in this case nearly 20 years).

However, a large number of species recorded in the present study were not recorded during 1978-1980 (Appendix VIII a-e; Table 6.14). It difficult to determine if these species were actually present during 1978-80, or have been dispersed into the community over the past 20 years, as they may been: a) overlooked; or b) present in seed bank but due to conditions at the time not present in the extant vegetation. Both of these reasons may apply to the amphibious species. However, due the dry conditions since the surveys by Kirkpatrick and Harwood (1981), it is likely that much of the increase in terrestrial species is due to their dispersal into the wetlands from the surrounding areas.

How do species persist in the vegetation communities?

Dispersal

Many of the plants species found in the present study have fruits and seeds that facilitate dispersal including: large edible fruit (e.g. *Potamogeton tricarinatus* and *Triglochin procerum*); floatability of fruits and seeds (e.g. most aquatic and amphibious species); and seed attachments (e.g. *Eleocharis sphacelata* and *E. acuta*).

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Over the period of the present study, wind dispersal of seed heads of Poaceae spp. such as *Agrostis avenacea*, were observed, in addition to wind induced water transport of both seeds and vegetative material of several aquatic species in the 5 wetlands. Although no direct evidence of animal dispersal of plant species either within and between wetlands was observed, the potential for this to occur was indicated by: the presence of water fowl; the close proximity to other wetlands; and the copious amount of both native and introduced animal faeces (including waterfowl) found within the wetlands.

It is likely that wind induced water transport is the most important form of dispersal of species within the 5 wetlands. However, it is obviously not an important mechanism by which species persist over time. If a species were lost from a wetland it would have to be reintroduced from other wetlands by wind or animal dispersal.

Vegetative mechanisms

A wide range of vegetative mechanisms for both vegetative expansion and perennation are found in the plants within the present study (Appendix X). Perennating organs ranged from rhizomes, tap roots and perennating stems (also use for vegetative expansion) to turions (specific perennation organs). Bulbils may have been present in some species of charophytes. These perennating organs have been found in some charophytes species (Brock and Casanova, 1991a) and are thought to aid both short and long-term persistence of these species. However, it was difficult to investigate their presence within the scope of the present study. Rhizomatous species were found in all functional groups, but were most common in amphibious tolerator emergent group (Appendix X, page3). Several species have tubers associated with their rhizomes (e.g. *Villarsia reniformis* and *Triglochin* spp.). Tubers, although not perennating organs, aid in the persistence of species by storing resources for vegetative regeneration.

Potamogeton tricarinatus was the only species observed to have turions buried in the soil. Tap roots became more common in species that were not adapted to long-term inundation. However, these are generally associated with short-term rather than long-term persistence of species.

Seed banks

The seed banks of the 5 wetlands have a range of characteristics which contribute to the ability of their vegetation communities to 'bounce' back after a dry period and for species to persist in the vegetation community over time. These include: species-rich germinable seed banks that respond to both spatial and temporal changes in water presence and absence (wet/dry cycles) rather than to season; greater number of species (and in some cases individuals) in the seed bank than were growing in the vegetation (at any particular time); a high level of correlation between the total species found in the wetlands over time to those found in the seed bank; a range of species with different morphological form (functional groups); species that will germinate in a wide range of conditions, i.e. saturated and inundated; and seed banks characterised by persistent long-lived seeds. Many of these characteristics of the seed banks of Tasmanian lentic wetlands are similar to those found in both Australian and overseas wetlands (van der Valk, 1978; 1979; Leck, 1989; Brock and Britton, 1994; Brock and Casanova, 1997; Brock, 1998; Leck and Brock, 2000) that rely on the seed bank for the persistence of species over time.

Life history or regeneration strategies

Several general types of 'life history' or 'regeneration strategies' for maintenance of species in the vegetation communities of wetlands with unpredictable water fluctuation can be recognised in the Tasmania wetland flora (Appendix X). Due to the low values of certain aquatic species in both the seed bank and extant vegetation the discussion below is generally directed at the dominant species found in present study (both extant vegetation and seed bank). Although different strategies can be recognised, the fact that many dominant amphibious species have both vegetative propagules and a persistent seed bank indicates that many species within these communities may 'hedge their bets' (Reed *et al.*, 1996), a characteristic also common in species found in the New England Tableland wetlands within Australia (Leck and Brock, 2000). Having both strategies increases the ability of species to persist in the vegetative communities. Failure of one mechanism does not necessarily mean the loss of species within the community. The 'life history' or 'regeneration strategies' recognised within the dominant species were as follows:

a) Large persistent seed bank - no vegetative propagules: this strategy was generally found in charophytes and aquatic species such as the perennial *Myriophyllum variifolium/simulans* and *Isolepis* spp, and the annual species *Batrachium trichophyllum*, *Limosella australis*, *Elatine gratioloides*, *Callitriche stagnalis* and *Agrostis avenacea*. These species generally persist over time through their seed bank. Two amphibious saturated species, *Selliera radicans* and *Goodenia humilis*, were characterised by large seed banks and no perennating organs. However, *S. radicans* can persist in the short term via stolons, whereas, *G. humilis* has a tap root. Long term persistence would be due to their seed bank.

b) Large seed bank - with rhizomes: this strategy was found in perennial species such as *Eleocharis sphacelata*, *E. acuta*, *Myriophyllum salsugineum*, *Juncus holoschoenus* and *J. articulatus*.

c) Low seed bank - with rhizomes: this was found in perennial species such as *Potamogeton tricarinatus*, *Villarsia reniformis*, *Ranunculus amphitrichus*, *Lilaeopsis polyantha*, *Baumea arthropphylla* and *B. rubiginosa*. Most of these species maintained themselves over the period of the present study through their rhizomes. However, means of regeneration of *Potamogeton tricarinatus* varied between wetlands, i.e. in Tin Dish *P. tricarinatus* regenerated mainly from vegetative propagules, whereas, in Big Punchbowl it solely regenerated from seed. This difference between wetlands indicates that local conditions may also affect regeneration strategies of species.

d) Transient seed bank - without vegetative propagules: this was generally characteristic of introduced terrestrial annual species. These species rely on the seed bank to maintain themselves in vegetation communities. However, to persist in the vegetation after a seasonal germination event would depend on: a) adult reproductive input; or b) dispersal of seeds from the surrounding area.

The regeneration strategies of several species found in the flora of the 5 wetlands can be allocated into the C-S-R strategies proposed by Grime (1974, 1979). The stress tolerant strategy was represented by species such as *Myriophyllum* spp., *Villarsia reniformis*, *Eleocharis sphacelata*, *Isolepis* spp. and other species that displayed morphological plasticity enabling them to survive in the range of water depths recorded in the wetlands, and in species such as *Baumea arthropphylla* and *B. rubiginosa* that 'tolerated' water level fluctuations without morphological change. Ruderal species that reproduce

quickly and have a short life span were represented by aquatic species such as *Limosella australis*, *Elatine gratioloides* and *Batrachium trichophyllum* as well as a large range of introduced terrestrial species. By definition both *Baumea arthropphylla* and *B. rubiginosa* represent the competitive strategy (C-strategy) outlined by Grime (1974, 1979). Within the r and K selection strategies outlined by MacArthur and Wilson (1967) the species in the 5 wetlands have characteristics of both r and K species. An example of an r-strategist would be *Myriophyllum variifolium* and a K-strategist, *Baumea arthropphylla*. R-strategists have been found to dominate temporary wetlands within Australia, whereas, K strategists dominate North American tidal wetlands (Brock and Leck, 2000). More information would be required of the life-history patterns of Tasmanian wetlands species before both the C-S-R and r-K strategies could become useful overall classifications within Tasmanian wetlands systems.

Leck and Simpson (1994) identified four general strategies for plant species to persist in tidal wetlands. These were 1) annual seed production (i.e. transient seed bank) and to a lesser extent dispersal to perpetuate the population; 2) persistent seed bank and dispersal for population maintenance; 3) vegetative reproduction and/or gap exploitation later in growing season by seedlings; and 4) continual water dispersal into the site together with a very long lived seed bank. The first three are strategies recognised in the species found in the 5 wetlands of the present study. The latter strategy is generally not observed in lentic wetlands due to lack of continual flow into these systems and is more characteristic of species within lotic communities.

Several life history strategies of the species within the present study also relate to the model proposed by van der Valk (1981) from species found within North American prairie wetlands. He suggested that both vegetatively reproducing species and perennials with a persistent seed bank could survive transitions between inundated and drawdown conditions without becoming extinct in the community. Within Australia, the life history strategies found in Tasmanian wetlands are similar to those recorded in New England Tableland wetlands (Crosslé, 1998; Leck and Brock, 2000). Crosslé (1998) found that the first three strategies outlined by Leck and Simpson (1994) were also characteristic of species found in the lentic New England Tableland wetlands. The similarity of the life history strategies used by species to persist in the fluctuating environments of temporary wetlands could be expected as the stresses caused by water level fluctuations on wetlands plants are similar regardless of their latitude. The life

history strategies recognised in aquatic plants have probably evolved over millions of years and, as this and many other studies have shown, are successful in maintaining species within aquatic communities (Sculthorpe, 1967; Hutchinson, 1975; van der Valk, 1981; Leck and Simpson, 1994; Leck and Brock, 2000). If they were not, vegetation would not exist in temporary wetlands.

Functional Groups

All functional groups, i.e. submerged, amphibious fluctuation responder, tolerator-emergent, tolerator saturated/mudflat and terrestrial, were represented in both seed banks and extant vegetation of all 5 wetlands (see Chapter 4, 5 and 6). The methods for persisting through unfavourable conditions varied between functional groups.

Submerged species generally persisted in the wetland environment during dry periods as persistent seeds in the soil seed bank. The submerged species *Lepilaena cylindrocarpa* and *Ruppia* spp. can also persist through rhizomes. However, most submerged species do not remain vegetatively in the community during dry periods, i.e. they avoid having to cope with unfavourable conditions. Both amphibious responder and tolerator-emergent species can persist vegetatively during dry periods. While amphibious responders persist in dry conditions by changing their morphology, tolerator-emergents generally remained morphologically similar in both inundated and dry conditions. If dry conditions continue firstly amphibious responder species and over a longer period, amphibious-tolerator species will be lost vegetatively from the community. If lost from the extant vegetation, species within both amphibious responder and tolerator emergent-groups are characterised by a wide range of life history strategies (outlined above) to be able to persist in the soil during dry periods. It is their morphological mechanisms by which they respond to or tolerate water presence or absence that differentiates this group, rather than their methods of persisting during long-term dry periods if lost from the vegetation community. Amphibious tolerator-saturated/mudflat and terrestrial species will generally not persist vegetatively during inundated conditions, that is, similar to submerged species they avoid having to cope with unfavourable conditions. Similar to the amphibious responder and tolerator-emergent groups, species within the amphibious tolerator-saturated/mudflat and terrestrial groups have a wide range of life history strategies to persist during unfavourable conditions. However, it is mainly the terrestrial group that is characterised by species with transient seed banks and therefore depend on reproductive input or dispersal to persist in the community.

Are the mechanisms for resilience and persistence of vegetation communities sufficient to maintain them if changes to their natural water regime fluctuations occur?

Brock (1998) suggested that wetland seed banks may not be able to respond to changes in water regime that may occur through human intervention, e.g. more permanently wet or dry conditions. The drying events in the wetlands in the present study were relatively short. The longest totally dry period experienced by an individual wetland was approximately 10 years in Tin Dish. However, prior to this Tin Dish has had reduced water levels since the mid 1960s (Henry Foster, pers. comm.²). The results of the present study for *Myriophyllum* spp. in this long-term dry wetland may indicate that further extended anthropogenic dry periods may have an effect on the potential for long-term persistence of species within Tasmanian wetlands.

Tin Dish was inundated in 1978 during the survey of Kirkpatrick and Harwood (1981). At this time the aquatic central zone was dominated by *Myriophyllum salsugineum* (75-100% cover; unpublished data). This species is characterised by both shallow rhizomes and a large persistent seed bank. During the present study the dominant angiosperm species within the aquatic zone was *Potamogeton tricarinatus* (50 - 75% cover), generally characterised by a low seed bank and buried turions, stems and rhizomes. Very few *Myriophyllum* individuals germinated in the seed bank experiments from soils taken from Tin Dish. Similarly, *Myriophyllum* was only represented in the extant vegetation during saturated conditions in winter 1997 and at this time only as cotyledons. No adult plants were recorded in Tin Dish over the period of the study. The results of the seed bank experiments in the present study, as well as those in other Australian wetlands (Brock, 1991.), have indicated that *Myriophyllum* spp., especially when dominant in extant vegetation, can generate a large persistent seed bank. From these results it could be expected that due to the high percentage cover of *M. salsugineum* in 1978 a large number of seeds would also be present in Tin Dish sediments. The lack of germinants during the seed bank experiments was not due to conditions in the glasshouse as many individuals of both *Myriophyllum simulans/variifolium* and *M. salsugineum* germinated from other wetland soils. Therefore, other reasons may have caused the lack of germinants during the germination trials of the present study.

² Henry Foster, landowner 'Fosterville' property where Tin Dish and Sandy Gate are located

Although persistent seed banks are characterised by: a) seeds that do not all germinate on first wetting (Brock and Britton, 1995; Bonis *et al.*, 1995; Brock, 1998); and b) seeds that can last in the soil for at least one year (Thompson, 1992) they are not infinite in number and can be reduced over time if not replenished. Germination events (output) without replenishment (input) of *Myriophyllum* spp., as was observed in Tin Dish during winter 1997, may have regularly occurred in Tin Dish over the long-term dry periods since the 1960s or at least since the survey in 1978 by Kirkpatrick and Harwood (1981). This would have diminished the seed bank of this species. These events may have been more pertinent for *Myriophyllum salsugineum* (a rhizomatous seed bank species), as although it has a high seed number relative to other species, it has a considerably lower seed numbers than the other more seed bank reliant *Myriophyllum* species found in the present study, i.e. *Myriophyllum variifolium* and *M. simulans* (Appendix X). Germination events are more likely to reduce a small seed bank than a large one.

The result for *Myriophyllum salsugineum* in Tin Dish also asks the question of why this species did not regenerate from its buried rhizomes? Buried vegetative propagules of several amphibious species were recorded by the author in the sediments of the central aquatic zone of Tin Dish (e.g. *Potamogeton tricarinatus*, *Lilaeopsis polyantha*). The depth of these propagules ranged between 0-15 cm deep and were especially in the case of *P. tricarinatus*, relatively stout. It may be that the thin, shallow depth rhizomes of *M. salsugineum* cannot survive during long-term dry periods within the dry top sediments of Tin Dish. This may be especially the case for lagoons such as Tin Dish that have no surface litter to buffer the effects of surface conditions.

However, although low in numbers, viable seeds of *Myriophyllum* spp. (both *M. salsugineum* and *M. simulans*) are still found within the seed bank of Tin Dish. Therefore, given the right conditions, there is still the potential for germination, establishment and subsequent replenishment of these species within the vegetation community. However, *Myriophyllum* spp. were not recorded in the extant vegetation after the flooding event in 1996 when conditions were optimal for establishment. This indicates that environmental conditions in Tin Dish may have changed from those in 1978 during the survey by Kirkpatrick and Harwood (1981). Several of the species recorded in the extant vegetation of Tin Dish in both 1978 and in the present study indicated possibly brackish conditions, e.g. *Selliera radicans* (Appendix VIII b). The

reduced water levels since 1978 may have had a secondary effect on the environment and increased the salinity of the wetlands soils. This has been observed to occur in shallow fluctuating coastal lagoons in the north east of Tasmania (Walsh, 1997). Any increase in the salinity of the wetland may have prevented *Myriophyllum* spp. from establishing in the community. While this was not tested within this study, it may indicate that in some systems this secondary effect may also cause species reduction within vegetation communities after prolonged dry periods.

The semi-permanent and fluctuating wetlands of the present study were the most species rich in both seed bank and extant vegetation (Chapter 6). The semi-permanent wetlands remain this way over time due to the ability of species within the vegetation community to persist both during inundated periods and during short-term dry periods. The short-term dry periods also enable species from the seed bank not present in the extant vegetation to regenerate, establish and reproduce thus maintaining themselves in the community (Chapter 6). These results indicate that it is the dry periods that help maintain the high species richness in these wetlands. Loss of these natural fluctuations would cause a reduction in species richness in the central aquatic area due to the inability of species to either become present, or maintain themselves, in the extant vegetation, via their seed bank.

Brock and Casanova (1997) predicted that submerged species would become more dominant in wetlands after a change to a permanent water regime. At the beginning of the present study Cherry Tree Lagoon had been inundated for at least 12 years. At this time many areas of the deeper aquatic zones were dominated by charophytes. After drawdown these areas became more species rich with amphibious species that had regenerated during the saturated conditions. However, charophytes, although in low percentage cover (Chapter 5), were present immediately after inundation. It could be expected that over time charophytes would again become dominant in the vegetation community of these areas. Without natural water level fluctuations charophyte species may remain dominant in the deeper areas of Cherry Tree Lagoon.

Future flora

The vegetation zonation in the wetlands observed at present are a recent 'snap shot' and the result of the most recent and present hydrological conditions found in these wetlands. The dynamic nature of the vegetation communities within each zone observed over the 2 year period was largely influenced by changes in water levels that acted primarily as an environmental sieve (van der Valk, 1981) allowing subsets of wetland species from the total species 'pool' to become present in the extant vegetation.

The total potential or future flora of the wetlands could be regarded as all species recorded in the extant vegetation within the wetlands (over the past 20 years) plus additional species represented only by propagules in the seed bank during the present study (Appendix VII; Appendix VIII a-e). The actual flora that will develop in the future will depend on several factors including the water regime and the life history characteristics of the species that make up the 'pool' of potential or future species. All functional groups are represented in the potential flora of each of the 5 wetlands (Appendix VII). Therefore, a range of communities, depending on hydrological conditions, could become present at any given time in all 5 wetlands. Results of the present study show that aquatic communities, dominated by submerged, amphibious responder and tolerator-emergent species will regenerate much quicker after inundation than the regeneration of terrestrial species during dry periods.

Conclusions

Tasmanian wetland plant communities are dynamic systems. This is highlighted by their inability to resist changes in their structure associated with water level fluctuations and their ability to 'bounce' back rapidly after both short and long term dry periods.

Temporary wetlands within Tasmania have species rich persistent seed banks that can be related to the extant vegetation recorded in the wetlands over time. However, at any given time, species can be found in the seed bank not present in the extant vegetation. This study highlights the importance of seeds banks in Tasmanian lentic wetlands. It also demonstrates that an assessment of the seed bank together with extant vegetation surveys can give a more holistic view of a wetland's vegetation. Seed banks can also give information on past vegetation and hydrological conditions of wetlands. They can also be used to aid predictions of how wetland vegetation communities will change in the future if hydrological conditions vary. This information is especially useful if only one visit to a wetland is possible. The ability to predict changes in vegetation is an important tool and is especially useful where management decisions regarding changes in water regimes are concerned.

At any given time the presence of species is determined by hydrological conditions with changes in community composition and cover primarily due to the response of species to water level fluctuations. The 'type' of species present in different hydrological conditions can be related to their functional ability to either respond to or tolerate the presence and absence of water. Submerged species such as charophytes were found only in inundated conditions, whereas, terrestrial species were generally found in dry conditions. Amphibious species, i.e. responders and tolerator-emergent, were present in both inundated and dry conditions, whereas, amphibious saturated/mudflat species were generally present during saturated conditions. The functional group characteristics of species could also be related to their position in the vegetation zonation of wetlands as follows: submerged > amphibious responder > tolerator-emergent > amphibious saturated/mudflat > terrestrial.

The strategies for species persistence in the vegetation communities of Tasmanian temporary wetlands are similar to those found in many other wetland systems.

However, unlike other Australian temporary wetland systems (Brock, 1998) there is a greater presence of dominant species persisting over time through vegetative means, for

example, rhizomes. However, most rhizomatous species also have in some cases quite large persistent seed banks. Crosslé (1998) found during glasshouse experiments that more species survived vegetatively than germinated from the seed bank during submerged conditions. Seed bank regeneration for these species may become more important if wetlands remain dry for longer or if their vegetative propagules are damaged or become unviable. Seed production is also a mechanism by which species can be dispersed both within and between wetlands and many of the dominant rhizomatous species found in the 5 wetlands are wide spread in the lentic wetlands throughout Tasmania.

Although water regime is the primary influence on the vegetation dynamics of these wetland communities the dominant species or 'type' of vegetation also influenced which species may be present. For example, although seed bank composition was similar between *Baumea* spp. and aquatic herbaceous dominated zones the species present in the extant vegetation varied. This indicated that competition for resources, e.g. light and space, may also occur within the communities and have a secondary effect on the community composition and structure. Reduction in the cover of *Baumea* spp. due to either changes in water regime or disturbance, e.g. fire or grazing, creates gaps. This enables the regeneration of species, either from seed bank or vegetative propagules, that are prevented from being present due to the unfavourable microenvironment created by the dominant sedge species. Increased species richness was observed after inundation in the *Baumea* zones of both Cherry Tree Lagoon and Sandy Gate. However, regeneration of species may have been facilitated by the reduced *Baumea* cover from disturbance experienced in these zones over that time, a low intensity burn in Cherry Tree Lagoon and cattle grazing in Sandy Gate. This supports the findings of Blanch and Brock (1994) found that species diversity can be increased in wetlands by low intensity disturbance.

The use of functional groups to describe community dynamics

To describe the community dynamics of the 5 wetlands using life history strategies, as described above, would be a daunting task and would require extensive research into the life history strategies of species not dominant within the communities of the 5 wetlands. The results of the present study indicate that functional group analysis to reduce community complexity to groups based on traits related to plant response to the conditions under which species germinate, grow and reproduce in relation to water presence or absence (Brock and Casanova. 1997) is a useful tool for describing community response to hydrological disturbance (Chapter 5).

The functional groups derived in the present study are also useful in predicting which 'type' of species from the total species 'pool' that could potentially be present in the extant vegetation during different hydrological conditions. This relates to the assembly and response rules described by Keddy (1992b; see review Chapter 3). Assembly rules determine the subset of species that could be recruited into the wetland vegetation (assembly). Response rules determine the species that will establish and survive to reproduce.

Standardising wetland plants to their functional attributes, based on their response to the presence or absence, facilitates comparison between other wetlands systems both within Australia and those of other continents (Leck and Brock, 2000). Leck and Brock (2000) found that functional groups present within Australian temporary wetlands were more diverse than in North American tidal wetlands. The wet/dry ecotone found in Australian temporary wetlands was characterised by a species-rich amphibious group dominated by both fluctuation responders and tolerators. Plants that responded to changes in water level by altering growth form were conspicuous and a dominant element in the Australian environments. This contrasted to the tidal freshwater marsh where, as tidal fluctuations do not allow time for morphological responses to water fluctuation amphibious fluctuation tolerator species were more dominant (Leck and Brock, 2000). This indicated that an analysis of functional groups within wetlands communities may also be a good indication of the 'type' of water regime experienced by that particular system.

The classification into functional groups used in the present study, compared to some functional trait analyses (see review Chapter 5), is relatively easy to perform. The major effort would be for the seed bank experiments to determine species germination characteristics, i.e. if they germinated in either saturated and/or inundated conditions. Most other information can be gained by personal knowledge (in preference) or from the literature. The results of this study and those of Leck and Brock (2000) indicate that the classification proposed by Brock and Casanova (1997) is repeatable and a useful tool for describing wetland vegetation in both similar Australian wetland systems as well as other wetland types.

Management issues

The increased knowledge of the seed bank of temporary wetlands within Tasmania gives a further insight into the ecology of these important ecosystems within the State. The high correlation between seed bank and extant vegetation in these communities separates them from terrestrial systems both in Tasmania and elsewhere.

The results of this study indicate that the vegetation communities of Tasmanian temporary wetlands are resilient to their climatically determined (natural) fluctuations in water regimes. However, the results also suggest changes in natural water regimes, to either more permanently dry or wet, could lead to a decrease in both number of species and functional groups and as a consequence the diversity of the plant communities. The draining and damming of wetlands removes the aseasonal fluctuations typical of these temporary wetlands, potentially reducing their diversity. Changes to water regimes (see Appendix XI) would not only affect the plant communities but also the animal communities and ecological processes within these temporary systems. Impacts on wetlands systems arising from changes in land use that can alter natural water regimes, e.g. increases in irrigation systems throughout the catchment and increased off-river dams, should be addressed in management plans. The results of this study, as well as many other studies of wetland systems (van der Valk, and Davis, 1978; Keddy and Reznicek, 1986; Brock and Casanova, 1997; Crosslé, 1998; Casanova and Brock, 2000) suggest that fluctuations in water levels are required if the goal of management is to be the maintenance of a diverse wetland plant community and productive ecosystem.

The results of the study also indicate that in most dry times in many areas within Tasmania 'there is a wetland plant community waiting to happen' and therefore, care

must be taken of dry wetlands as well as the wet habitats generally associated with these ecosystems. Disturbance of wetlands during dry periods may disrupt their natural ability to regenerate. This is important both in populated areas where vehicle access to dry wetlands has caused extensive damage to wetland areas and in remote areas where dry wetlands have been stripped for top soil (Plate 7.1) and ploughed over.

The importance of seed banks in wetland environments highlights their potential use in the rehabilitation of wetland environments. In many rehabilitation projects plants are re-introduced to produce the required vegetation communities. If a degraded wetland is being rehabilitated there may be a source of species already within the soil. Therefore, it is important to assess if species are present within the soil prior to the commencement of rehabilitation and take them into account in project management. A fluctuating water regime, after rehabilitation and establishment of wetland communities, may also be an important management tool for a diverse productive wetland. Revegetation from seed banks has been recently addressed in several booklets for rehabilitation and management of wetlands (Brock, 1997; Thorpe, 1999; Brock *et al.*, 2000; Brock and Casanova, 2000).

This study also highlights the potential for water regimes to be used as a management tool for controlling introduced species within wetlands. Introduced terrestrial species will invade wetlands during dry periods. However, they do not survive inundation and therefore, can be eradicated by flooding. Introduced aquatic species were not dominant in the 5 wetlands. Where present they were generally out competed by more aggressive native species, e.g. *Callitriche stagnalis* (introduced annual) vs *Myriophyllum variifolium* (native perennial). *Callitriche stagnalis* when lost from the vegetation community requires drawdown conditions for germination and re-establishment. Maintaining inundated conditions would prevent this species from persisting over time. However, care must be taken when increasing inundation periods not to decrease diversity.



Plate 7.1

Little Punchbowl: 1) spring 1995 - dominated by dry herbaceous species; 2) February 1996 - Little Punchbowl wetted up during the wet spring/summer of 1995/1996. The vegetation community at this time was dominated by *Eleocharis acuta* and other aquatic amphibious species; 3) autumn 1997 - the wetland was stripped of top soil in winter 1996. Up to 1999 very few plant species had regenerated and vegetation cover was minimal.

Future research

Changes in the water regime of wetlands have many secondary effects, for example, salinity. The loss of dominance of *Myriophyllum salsugineum* in Tin Dish may be due to an increase in salinity in the wetland after a long-dry period. However, this is difficult to determine from the results of the present study. Increased salinity has been shown to affect the composition of freshwater plant communities (Adam, 1993), with many salt intolerant species becoming lost from the community. Expansion of irrigation systems and dams has been shown to cause rising groundwater leading to water logging and salinisation (Finlayson and Rea, 1999b). Further research into the affects of increased salinity on the wetland vegetation may aid management decisions to protect wetland values in areas subject to changing land use.

The results of the present study indicate that not only do seed banks vary in their longevity, i.e. transient and persistent, vegetative perennating organs may also vary in their ability to persist in the environment (e.g. *Myriophyllum salsugineum* and *Potamogeton tricarinatus*). Many of the plants within the wetlands of Tasmania rely on underground vegetative propagules to survive periods of unfavourable conditions and to persist in both the short and long-term within the vegetation communities. Relatively little attention has been given to factors that influence the longevity of vegetative propagules (Spencer and Ksander, 1997). Bartley and Spence (1987) surveyed the literature and concluded that propagules of aquatic plants apparently do not display true dormancy and that there was wide variation in which environmental factors were responsible for release from apparent dormancy. Changes in the below ground environment arising from changes in the surrounding land use may affect the moisture available (groundwater) for these propagules and therefore prevent their long-term persistence in the soil. Further research into the longevity and the means by which vegetative propagules persist in wetland environments within Tasmania would enable predictions of how wetland vegetation communities may be affected if groundwater availability was restricted within these systems.

Further research into the role of sexual and vegetative reproduction in persistence of species and how their importance varies over time and space would increase understanding of how different regeneration strategies affect both short and long-term community dynamics.

Charophyte ecology and taxonomy have largely been ignored in Tasmania. In the 5 wetlands studied, 12 charophyte taxa were recorded (i.e. 30% of total taxa, together with 2 taxa though not to occur, in Tasmania; van Raam, 1995). Charophytes have also been recorded in both lotic systems (Chappell, 2000) and deep water lakes within Tasmania. The key to charophyte species (van Raam, 1995) was mainly described using a relatively small number of samples from Australian herbariums. The present study, not only highlights the importance of these large algae within Tasmanian shallow lentic communities, due to the high number found in only 5 wetlands, it also indicates the potential for a much wider range of charophytes species to be present within the State.

Charophytes have at least two different ecological niche firstly, as the deepest inhabitants of clear water lakes, and secondly as pioneer successional vegetation in recently inundated ponds and wetlands (Casanova, 1993). However, they can also form stable communities that can persist in shallow water for many years (Wood, 1950). Changes in water regimes will both reduce (dry conditions) and increase (more permanently wet conditions) the presence of charophytes in aquatic communities. They have also been found to be affected by other environmental impacts such as eutrophication and turbidity. Charophyte life history patterns have been shown to vary between species (Casanova, 1993). Further research into the distribution and the life histories of the Tasmanian species as well as the effects of other environmental impacts on their ecology, would help with management decisions related to many wetlands systems within Tasmania.

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Appendix I Total species and germinants that germinated from each wetland during summer and winter 1997 seed bank experiments of the present study. Data presented is the total number of germinants for each species that germinated from the summer and winter 1997 soils.

Quadrat Number	Wetland				
	36	36	27	18	18
Species	BP	CTL	MID	SG	TD
NATIVE DICOTYLEDONS					
APIACEAE					
<i>Apium prostratum</i>		1			3
<i>Centella cordifolia</i>			3	4	
<i>Eryngium vesiculosum</i>				14	
<i>Hydrocotyle muscosa</i>			10		
<i>Hydrocotyle sibthorpiodes</i>				9	
<i>Lilaeopsis polyantha</i>		5	11	16	41
ASTERACEAE					
<i>Centipeda minima</i>		1		4	
<i>Euchiton collinus</i>		1			4
CRASSULACEAE					
<i>Crassula helmsii</i>		3			
CHENOPODIACEAE					
<i>Eriachne nutans</i>			18		
CLUSIACEAE					
<i>Hypericum japonicum</i>				7	
ELATINEACEAE					
<i>Elatine gratioloides</i>		1026			
GOODENIACEAE					
<i>Goodenia humilis</i>			40		
<i>Selliera radicans</i>		1	24		45
HALORAGACEAE					
<i>Myriophyllum salsugineum</i>		179		21	
<i>Myriophyllum simulans/</i> <i>variifolium</i>		1800	266	11	
LENTIBULACEAE					
<i>Utricularia</i> spp.	7	21	8	3	
MENYANTHACEAE					
<i>Villarsia reniformis</i>		98	22		
ONAGRACEAE					
<i>Epilobium sarmentaceum</i>				23	
PORTULACEAE					
<i>Neopaxia australasica</i>				18	
RANUNCULACEAE					
<i>Batrachium trichophyllum</i>		684		17	
<i>Ranunculus amphitrichus</i>		44			

Appendix I Seed bank species list (cont.) page 2/

	Wetland				
Quadrat Number	36	36	27	18	18
Species	BP	CTL	MID	SG	TD
SCROPHULARIACEAE					
<i>Gratiola peruviana</i>			1		
<i>Limosella australis</i>		15	17	17	
INTRODUCED DICOTYLEDONS					
ASTERACEAE					
<i>Cirsium vulgare</i>				40	
<i>Cotula coronopifolia</i>		55			
<i>Hypochoeris radicata</i>				1	
<i>Leontodon taraxacoides</i>			69	66	46
<i>Vellereophyton dealbatum</i>	6				2
CALLITRICHACEAE					
<i>Callitriche stagnalis</i>		74			
CARYOPHYLLACEAE					
<i>Stellaria media</i>				2	
FABACEAE					
<i>Trifolium dubium</i>					20
<i>Trifolium repens</i>					3
<i>Trifolium subterraneum</i>			2	4	4
GENTIANACEAE					
<i>Centaurium erythraea</i>					53
ONAGRACEAE					
<i>Epilobium</i> sp.					3
PLANTAGONACEAE					
<i>Plantago coronopus</i>			4	7	28
POLYGONACEAE					
<i>Acetosella vulgaris</i>				1	

Appendix I Seed bank species list (cont.) page 3/

Quadrat Number	Wetland				
	36	36	27	18	18
Species	BP	CTL	MID	SG	TD
NATIVE MONOCOTYLEDONS					
CYPERACEAE					
<i>Baumea arthropphylla</i>		45		4	
<i>Baumea rubiginosa</i>	7				
<i>Carex inversa</i>				5	
<i>Carex tereticaulis</i>				5	
<i>Eleocharis acuta</i>		74	17	140	202
<i>Eleocharis sphacelata</i>			132		
<i>Isolepis cernua</i>		9	19	152	
<i>Isolepis fluitans</i>	3	198	28	217	
<i>Isolepis inundata</i>	14	8	34	3	
<i>Isolepis montivaga</i>				4	
<i>Isolepis producta</i>			2		
<i>Schoenus apogon</i>				3	1
<i>Schoenus fluitans</i>	4	19	2		
<i>Schoenus maschalinus</i>			1	10	
HYDATELLACEAE					
<i>Trithuria submersa</i>			6		
JUNCACEAE					
<i>Juncus bufonius</i>	2		54	54	36
<i>Juncus holoschoenus</i>		531	222	254	
<i>Juncus pauciflorus</i>		1	1		
<i>Juncus planifolius</i>		1	1	35	
<i>Juncus pallidus</i>	1	11	1	23	3
JUNCAGINACEAE					
<i>Triglochin procerum</i>			1		
<i>Triglochin striatum</i>			1		
POACEAE					
<i>Agrostis avenacea</i>		60	93	1550	40
<i>Amphibromus sinuatus</i>				19	
<i>Amphibromus recurvatus</i>		4			
POTAMOGETONACEAE					
<i>Potamogeton tricarinatus</i>	22	5	10	22	1
RUPPIACEAE					
<i>Ruppia megacarpa</i>					2

Appendix I Seed Bank species list (cont.) page 4/

(Data for *Nitella* spp. are reported for the amalgamated *Nitella* thick spp. and *Nitella* thin spp. X = *Nitella* spp. Indentified from the seed bank of that wetland).

Quadrat Number	Wetland				
	36	36	27	18	18
Species	BP	CTL	MID	SG	TD
INTRODUCED MONOCOTYLEDONS					
JUNCACEAE					
<i>Juncus articulatus</i>			52	90	4
<i>Juncus bulbosus</i>			2		
POACEAE					
<i>Agrostis capillaris</i>			6		
<i>Aira</i> spp.				86	
<i>Cynosurus echinatus</i>					2
<i>Gaudiana fragilis</i>				6	
<i>Hainardia fragilis</i>				6	
<i>Holcus lanatus</i>				43	
<i>Poa annua</i>				10	
<i>Polypogon monspeliensis</i>					34
<i>Vulpia myuros</i>				108	
TYPHACEA					
<i>Typha</i> sp.					1
CHAROPHYTE					
<i>Chara fibrosa</i>			6488	915	1502
<i>Chara globularis</i> var. <i>globularis</i>				261	1468
<i>Chara muelleri</i>					6
<i>Chara preissii</i>	645	242			
<i>Chara</i> blobby arm			2	2	156
<i>Nitella</i> thick spp.	90	1897	924	1453	44
<i>Nitella</i> thin spp.	895	502	2051	185	
<i>Nitella</i> c.f. <i>penicillata</i>			X		
<i>Nitella congesta</i>					41
<i>Nitella cristata</i>				X	
<i>Nitella gelatinifera</i> var. <i>gelatinifera</i>	X	X	X	X	
<i>Nitella gelatinifera</i> var. <i>microcephala</i>	X	X	X	X	
<i>Nitella gloestachys</i>				X	
<i>Nitella subtilissima</i>	80	5		10	
<i>Nitella</i> UNID Tin Dish					2

Appendix I Seed bank species list (cont.) page 5/

	Wetland				
Quadrat Number	36	36	27	18	18
Species	BP	CTL	MID	SG	TD
UNIDENTIFIED GERMINANTS					
Dicot UNID DIED		41	10	8	2
Isolepis sp. UNID DIED		1	13	2	
Isolepis UNID		2	4		
Monocot UNID DIED		130	39	312	12
Sedge UNID DIED			1	3	1
RHIZOME PROPAGATION					
<i>Eleocharis acuta</i> rhizome				1	1
<i>Selliera radicans</i> rhizome		1	23		52

Appendix II Comparison between summer and winter 1997 seed bank experiments: 0-28 weeks (* = introduced species, */n = uncertain status).

Species	Experiment		Total	Percent % Total	Percent	
	Summer 1997	Winter 1997			Summer 1997	Winter 1997
<i>Chara fibrosa</i>	3408	5522	8930	29.79	28.83	30.41
<i>Nitella thick</i> spp.	868	3565	4433	14.79	7.34	19.63
<i>Nitella thin</i> spp	1583	2050	3633	12.12	13.39	11.29
<i>Myriophyllum</i>						
<i>simulans/variifolium</i>	939	1148	2087	6.96	7.94	6.32
<i>Agrostis avenacea</i>	1221	590	1811	6.04	10.33	3.25
<i>Chara globularis</i>	394	1335	1729	5.77	3.33	7.35
<i>Juncus unitubular</i> spp.	450	739	1189	3.97	3.81	4.07
<i>Chara pressii</i>	239	648	887	2.96	2.02	3.57
<i>Isolepis/Schoenus</i> spp.	340	439	779	2.60	2.88	2.42
<i>Batrachium trichophyllum</i>	469	234	703	2.35	3.97	1.29
<i>Elatine gratioioides</i>	152	361	513	1.71	1.29	1.99
<i>Eleocharis acuta</i>	169	296	465	1.55	1.43	1.63
<i>Mynophyllum salsuginum</i>	103	100	203	0.68	0.87	0.55
<i>Leontodon taraxacoides*</i>	109	77	186	0.62	0.92	0.42
<i>Chara blobby arm</i>	34	126	160	0.53	0.29	0.69
<i>Eleocharis sphacelata</i>	14	144	158	0.53	0.12	0.79
<i>Villarsia reniformis</i>	13	107	120	0.40	0.11	0.59
<i>Selliera radicans</i>	9	69	78	0.26	0.08	0.38
<i>Juncus bufonius</i>	64	12	76	0.25	0.54	0.07
<i>Lilaeopsis polyantha</i>	57	18	75	0.25	0.48	0.10
<i>Callitriche stagnalis*</i>	51	23	74	0.25	0.43	0.13
<i>Potamogeton incannatus</i>	22	41	63	0.21	0.19	0.23
<i>Vulpia myuros*</i>	55	1	56	0.19	0.47	0.01
<i>Cotula coronopifolia*</i>	47	8	55	0.18	0.40	0.04
<i>Centaurea erythraea*</i>	20	34	54	0.18	0.17	0.19
<i>Baumea arthropophylla</i>	8	41	49	0.16	0.07	0.23
<i>Limosella australis</i>	10	39	49	0.16	0.08	0.21
<i>Flanunculus amphitrichus</i>	29	15	44	0.15	0.25	0.08
<i>Aira caryophyllaea*</i>	42	1	43	0.14	0.36	0.01
<i>Holcus lanatus*</i>	28	15	43	0.14	0.24	0.08
<i>Goodenia humilis</i>	3	38	41	0.14	0.03	0.21
<i>Nitella congesta</i>	22	19	41	0.14	0.19	0.10
<i>Cirsium vulgare*</i>	26	14	40	0.13	0.22	0.08
<i>Juncus sheath point</i>	3	37	40	0.13	0.03	0.20
<i>Plantago coronopus*</i>	36	4	40	0.13	0.30	0.02
<i>Utricularia</i> spp.	12	28	40	0.13	0.10	0.15
<i>Juncus planifolius</i>	17	22	39	0.13	0.14	0.12
<i>Epilobium</i> spp.	29	8	37	0.12	0.25	0.04
<i>Amphibromus sinuatus</i>	9	13	22	0.07	0.08	0.07
<i>Polypogon monspeliensis*</i>	16	4	20	0.07	0.14	0.02
<i>Tritolium</i> spp *	8	12	20	0.07	0.07	0.07
<i>Erinadia nutans</i>	16	2	18	0.06	0.14	0.01
<i>Neopaxia australasica</i>	15	3	18	0.06	0.13	0.02
<i>Eryngium vesiculosum</i>	4	10	14	0.05	0.03	0.06
<i>Hydrocotyle muscosa</i>		10	10	0.03	0.00	0.06
<i>Hydrocotyle sibiricorpiodes</i>	7	2	9	0.03	0.06	0.01
<i>Baumea rubiginosa</i>	7		7	0.02	0.06	0.00
<i>Centella cordifolia</i>		7	7	0.02	0.00	0.04
<i>Hypericum japonicum</i>		7	7	0.02	0.00	0.04
Split Base Poaceae 52	7		7	0.02	0.06	0.00
<i>Agrostis capillans*</i>	3	3	6	0.02	0.03	0.02
<i>Chara muelleri</i>	4	2	6	0.02	0.03	0.01
<i>Carex inversa</i>		5	5	0.02	0.00	0.03
<i>Carex tereticaulis</i>		5	5	0.02	0.00	0.03
<i>Centipeda minima</i>	4	1	5	0.02	0.03	0.01
<i>Euchiton collinus</i>	4	1	5	0.02	0.03	0.01
<i>Poa annua*</i>	5		5	0.02	0.04	0.00
<i>Amphibromus recurvatus</i>	3	1	4	0.01	0.03	0.01
<i>Apium prostratum</i>	4		4	0.01	0.03	0.00
<i>Vellereophyton dealbatum*</i>	3	1	4	0.01	0.03	0.01
<i>Crassula helmsii</i>	2	1	3	0.01	0.02	0.01
<i>Dichondra repens</i>	3		3	0.01	0.03	0.00
<i>Gaudiana fragilis*</i>	3	0	3	0.01	0.03	0.00
<i>Trithuna submersa</i>	0	3	3	0.01	0.00	0.02
<i>Juncus bulbosus*</i>	2	0	2	0.01	0.02	0.00
<i>Juncus pauciflorus</i>	1	1	2	0.01	0.01	0.01
<i>Ruppia megacarpa</i>	0	2	2	0.01	0.00	0.01
<i>Stellaria media*</i>	2		2	0.01	0.02	0.00
<i>Acetosella vulgans*</i>	0	1	1	0.00	0.00	0.01
<i>Cynosurus echinatus*</i>	1	0	1	0.00	0.01	0.00
<i>Cyperus tennellus</i>	1	0	1	0.00	0.01	0.00
<i>Gratiola peruviana</i>	0	1	1	0.00	0.00	0.01
<i>Haimardia cylindrica *</i>	1	0	1	0.00	0.01	0.00
<i>Hypochoeris radicata*</i>	1	0	1	0.00	0.01	0.00
<i>Lythrum hyssopifolia</i>	1	0	1	0.00	0.01	0.00
<i>Mynophyllum</i> sp. UNID BP	1	0	1	0.00	0.01	0.00
Thick Stem Monocot 52	1	0	1	0.00	0.01	0.00
<i>Triglochin procerum</i>	0	1	1	0.00	0.00	0.01
<i>Triglochin striatum</i>	0	1	1	0.00	0.00	0.01
<i>Typha</i> sp.*/n	1	0	1	0.00	0.01	0.00
Charophyte UNID	78	0	78	0.26	0.66	0.00
xDicot UNID DIED	39	23	62	0.21	0.33	0.13
xMonocot UNID DIED	433	65	498	1.66	3.66	0.36
xPoaceae UNID Died	15	0	15	0.05	0.13	0.00
xSedge UNID DIED	19	1	20	0.07	0.16	0.01
Grand Total	11819	18157	29976	100.00	100.00	100.09

Bold species that contribute more than 1 % of the total germination in either experiment
 Underline species that contribute between 0.5 and 1% of the total germination in either experiment

Appendix III

Summary of the number of individuals that germinated of each species in each treatment, mudflat or drowned (* = introduced species; */n uncertain status).

Species	Mudflat	Drowned	Species	Mudflat	Drowned
<i>Myriophyllum simulans/vanifolium</i>	1723	310	<i>Juncus pallidus/procerus</i>	39	0
<i>Agrostis avenaceae</i>	1683	17	<i>Juncus planifolius</i>	37	0
<i>Juncus holoschoenus</i>	982	25	<i>Epilobium sarmeniaceum</i>	23	0
<i>Batrachium trichophyllum</i>	644	57	<i>Einadia nutans</i>	18	0
<i>Chara fibrosa</i>	561	8344	<i>Neopaxia australasica</i>	18	0
<i>Nitella thick spp.</i>	538	3852	<i>Polypogon monspeliensis*</i>	17	0
<i>Elatine gratioloides</i>	410	103	<i>Epilobium sp. */n</i>	12	0
<i>Isolepis fluitans</i>	386	60	<i>Trifolium dubium*</i>	10	0
<i>Eleocharis acuta</i>	355	78	<i>Baumea rubiginosa</i>	7	0
<i>Leontodon taraxacoides*</i>	179	2	<i>Centella cordifolia</i>	7	0
<i>Isolepis cernua</i>	170	10	<i>Hypericum japonicum</i>	7	0
<i>Myriophyllum salsuginum</i>	150	50	<i>Agrostis capillaris*</i>	6	0
<i>Juncus articulatus*</i>	143	9	<i>Carex inversa</i>	5	0
<i>Eleocharis sphacelata</i>	124	8	<i>Carex tereticaulis</i>	5	0
<i>Villarsia reniformis</i>	88	32	<i>Centipeda minima</i>	5	0
<i>Selliera radicans</i>	74	2	<i>Euchiton collinus</i>	5	0
<i>Lilaeopsis polyantha</i>	65	8	<i>Poa annua*</i>	5	0
<i>Callitriche stagnalis*</i>	64	10	<i>Amphibromus recurvatus</i>	4	0
<i>Isolepis inundata</i>	56	3	<i>Apium prostratum</i>	4	0
<i>Cotula coronopifolia*</i>	54	1	<i>Isolepis montivago</i>	4	0
<i>Centaureum erythraea*</i>	52	1	<i>Schoenus apogon</i>	4	0
<i>Nitella thin spp.</i>	52	3581	<i>Vellereophyton dealbatum*</i>	4	0
<i>Plantago coronopus*</i>	38	1	<i>Dichondra repens</i>	3	0
<i>Ranunculus amphitrichus</i>	38	6	<i>Gaudiana fragilis*</i>	3	0
<i>Limosella australis</i>	37	12	<i>Trifolium repens*</i>	3	0
<i>Baumea arthropophylla</i>	31	18	<i>Isolepis producta</i>	2	0
<i>Myriophyllum vanifolium</i>	29	18	<i>Juncus bulbosus*</i>	2	0
<i>Chara pressii</i>	25	862	<i>Juncus pauciflorus</i>	2	0
<i>Schoenus fluitans</i>	24	1	<i>Stellaria media*</i>	2	0
<i>Amphibromus sinuatus</i>	16	3	<i>Acetosella vulgaris*</i>	1	0
<i>Utricularia spp.</i>	15	24	<i>Cynosurus echinatus*</i>	1	0
<i>Chara globularis</i>	12	1717	<i>Cyperus tennellus</i>	1	0
<i>Schoenus maschalinus</i>	10	1	<i>Gratiola peruviana</i>	1	0
<i>Eryngium vesiculosum</i>	9	5	<i>Hairardia cylindrica *</i>	1	0
<i>Potamogeton tricarinatus</i>	9	51	<i>Hypochoeris radicata*</i>	1	0
<i>Hydrocotyle muscosa</i>	6	4	<i>Lythrum hyssopifolia</i>	1	0
<i>Trifolium subterranean*</i>	4	1	<i>Triglochin procerum</i>	1	0
<i>Crassula helmsii</i>	2	1	<i>Triglochin striatum</i>	1	0
<i>Hydrocotyle sibthorpiodes</i>	9	0	<i>Typha sp. */n</i>	1	0
<i>Juncus bufonius</i>	73	0	Split Base Poaceae 52	7	0
<i>Vulpia myuros*</i>	54	0	<i>Chara blobby arm</i>	0	160
<i>Aira caryophyllea*</i>	43	0	<i>Nitella congesta</i>	0	41
<i>Holcus lanatus*</i>	43	0	<i>Chara muelleri</i>	0	6
<i>Cirsium vulgare*</i>	40	0	<i>Tnthuria submersa</i>	0	3
<i>Goodenia humilis</i>	40	0	<i>Ruppia megacarpa</i>	0	2
Grand Total				10063	19571

Appendix IV Percentage of annual and perennial individuals and species that germinated during the present study (BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon; SG = Sandy Gate).

	Germinant		Species richness	
	Annual	Perennial	Annual	Perennial
Wetland				
Big Punchbowl	6.1	93.9	25	75
Tin Dish	6	94	18.2	81.8
Middle Lagoon	5.5	94.5	11.4	88.6
Cherry Tree Lagoon	16	84	7.7	92.3
Sandy Gate	41	59	11.1	88.9
Zone				
BP aquatic	0	100	0	100
BP outer	8	92	25	75
TD aquatic	28.6	71.4	30.8	69.2
TD <i>Eleocharis acuta</i>	2.8	97.2	40	60
MID <i>Eleocharis sphacelata</i>	0.5	99.5	6.7	93.3
MID aquatic	7.7	92.3	11.8	88.2
MID dry herbaceous	6.9	93.1	10.3	89.7
CTL aquatic	17.2	82.8	9.1	90.9
CTL <i>Baumea arthropophylla</i>	9.5	90.5	12.5	87.5
SG aquatic	37.7	62.3	13.6	86.4
SG <i>Baumea arthropophylla</i>	44.8	55.2	8.8	91.2

Appendix V Species recorded in the extant vegetation of each zone over the period of the present study (X = species present; * = introduced species; */n = unsure status; FG = Functional group: S = submerged; Ar = Amphibious responder; Atle = Amphibious tolerator-emergent; Atls = Amphibious tolerator saturated mudflat; T = terrestrial; Aq. = aquatic; Out. = outer zone; E.s = *Eleocharis sphacelata*; DH = dry herbaceous; B.a = *Baumea arthropophylla*; E.a = *Eleocharis acuta*).

Species	FG	Big	Tin dish		Middle Lagoon			Cherry Tree		Sandy Gate					
		Punchbowl	Aq.	Out	Aq.	E.a	E.s	Aq.	DH	Lagoon	Aq.	B.a	Aq.	B.a	
DICOTYLEDONS															
APIACEAE															
Centella cordifolia	Atls							X	X		X		X	X	
Eryngium vesiculosum	Atls			X	X					X			X	X	
Hydrocotyle muscosa	Ar								X		X	X			
Hydrocotyle sibthorpiodes	Atls												X	X	
Lilaeopsis polyantha	Atle			X	X	X	X	X		X	X		X	X	
ASTERACEAE															
Cirsium vulgare*	T			X	X				X		X	X	X	X	
Cotula coronopifolia */n	Atle									X					
Hypochoeris radicata*	T													X	
Leontodon taraxacoides*	T			X	X			X	X				X	X	
Leptinella longipes	Atls									X					
Sonchus sp.*	T			X	X										
CALLITRICHACEAE															
Callitriche stagnalis*	Ar									X					
CHARYOPHYLLACEAE															
Scleranthus biflorus	T			X											
CHENOPODIACEAE															
Chenopodium glaucum*	T												X		
Einadia nutans	T					X			X						
CLUSIACEAE															
Hypericum japonicum	Atls												X		
CONVOLVULACEAE															
Dichondra repens	T			X	X										
CRASSULACEAE															
Crassula helmsii	Ar									X					
ELATINEACEAE															
Elatine gratioloides	Ar									X					
FABACEAE															
Trifolium spp.*	T			X	X	X	X						X	X	
GENTIANACEAE															
Centaurium erythraea *	T			X	X		X	X							
GERANIACEAE															
Erodium cicutarium*	T			X	X										
GOODENIACEAE															
Goodenia humilis	Atls						X	X							
Scaevola hookeri	Atls			X											
Selliera radicans	Atls				X	X	X	X		X	X				

Appendix V Species list extant vegetation (cont.) /page 2

Species	FG	Big Punchbowl		Tin dish		Middle Lagoon			Cherry Tree Lagoon		Sandy Gate		
		Aq.	Out	Aq.	E.a	E.s	Aq.	DH	Aq.	B.a	Aq.	B.a	
HALORAGACEAE													
<i>Myriophyllum simulans</i>	Ar				X	X	X	X	X	X	X	X	
<i>Myriophyllum variifolium</i>	Ar					X			X				
<i>Myriophyllum salsugineum</i>	Ar								X		X		
LENTIBULARIACEAE													
<i>Utricularia</i> spp.	Atle	X	X				X	X		X			
MENYANTHACEAE													
<i>Gonocarpus micranthus</i>	Atls		X										
<i>Villarsia reniformis</i>	Ar		X				X	X	X	X			
MYRTACEAE													
<i>Eucalypt</i> spp.	T		X										
<i>Leptospermum scoparium</i> .	T		X										
ONAGRACEAE													
<i>Epilobium</i> sp.*\n	T										X	X	
PLANTAGONACEAE													
<i>Plantago coronopus</i> *	Atls			X	X		X	X	X				
<i>Plantago lanceolata</i> *	T			X									
POLYGONACEAE													
<i>Acetosella vulgare</i> *	T		X										
PORTULACEAE													
<i>Neopaxia australasica</i>	Ar	X											
PRIMULACEAE													
<i>Anagallis arvensis</i> *	T												
<i>Samolus repens</i>	Atls								X				
PROTACEAE													
<i>Banksia marginata</i>	T		X										
RANUNCULACEAE													
<i>Batrachium trichophyllum</i>	S								X	X	X	X	
<i>Ranunculus amphitrichus</i>	Ar								X	X			
SCROPHULARIACEAE													
<i>Veronica</i> sp.	T											X	
<i>Parentucellia latifolia</i> *	T												
<i>Mimulus repens</i>	Atle								X				

Appendix V Species list extant vegetation (cont.)

/page 3

Species	FG	Big Punchbowl		Tin dish		Middle Lagoon			Cherry Tree Lagoon		Sandy Gate		
		Aq.	Out	Aq.	E.a	E.s	Aq.	DH	Aq.	B.a	Aq.	B.a	
MONOCOTYLEDONS													
CYPERACEAE													
<i>Baumea arthrophylla</i>	Atle						X	X	X	X	X	X	
<i>Baumea rubiginosa</i>	Atle	X	X										
<i>Carex inversa</i>	T											X	
<i>Carex tereticaulis</i>	Atle										X	X	
<i>Chorizandra australis</i>	Atle		X										
<i>Cyperus tenellus*/n</i>	Atls							X					
<i>Eleocharis acuta</i>	Atle			X	X		X	X	X		X	X	
<i>Eleocharis sphacelata</i>	Ar	X											
<i>Isolepis fluitans</i>	Ar	X	X			X	X	X	X	X	X	X	
<i>Isolepis cernua</i>	Atls						X	X		X	X	X	
<i>Isolepis inundata</i>	Atle							X					
<i>Schoenus apogon</i>	Atle											X	
<i>Schoenus fluitans</i>	Ar						X	X					
<i>Schoenus maschalinus</i>	Atls						X	X				X	
<i>Schoenus nitens</i>	Atls							X				X	
HYDATELLACEAE													
<i>Trithuria submersa</i>	Atls						X	X					
JUNCACEAE													
<i>Juncus articulatus*</i>	Atle						X	X			X		
<i>Juncus planifolius</i>	Atle												
<i>Juncus bufonius</i>	Atls							X					
<i>Juncus holoschoenus</i>	Atle						X	X	X		X	X	
<i>Juncus bulbosus*</i>	Atle							X					
JUNCAGINACEAE													
<i>Triglochin procerum</i>	Ar	X				X	X	X	X	X	X	X	
<i>Triglochin striatum</i>	Atls							X					
POACEAE													
<i>Agrostis avenacea</i>	Atle		X	X	X	X	X	X	X	X	X	X	
<i>Amphibromus recurvatus</i>	Atle								X	X			
<i>Amphibromus sinuatus</i>	Atle			X							X	X	
<i>Danthonia semiannularis</i>	T							X					
<i>Danthonia sp.</i>	T				X						X	X	
<i>Deyeuxia sp.</i>	T		X							X			
<i>Poa labillardierei</i>	T											X	
<i>Poa annua*</i>	T			X				X					
<i>Poaceae sp. UNID SG</i>	T										X		
<i>Poaceae sp. UNID CTL</i>	?								X	X			
<i>Poaceae sp UNID TD *</i>	T			X									
<i>Polypogon monspeliensis*</i>	T			X	X								
<i>Vulpia megalura*</i>	T				X			X			X		
<i>Aira spp.*</i>	T			X	X			X			X	X	
<i>Alopecurus geniculatus*</i>	T											X	
<i>Briza minor*</i>	T			X	X		X	X					
<i>Agrostis capillaris*</i>	T					X	X	X					
<i>Hainardia cylindrica /</i>	T			X	X						X	X	
<i>Hermarthria uncinata</i>													
<i>Lolium perenne*</i>	T				X								
<i>Holcus lanatus*</i>	T							X					

Appendix V Species list extant vegetation (cont.)

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Species	FG	Big Punchbowl		Tin dish		Middle Lagoon			Cherry Tree Lagoon		Sandy Gate		
		Aq.	Out	Aq.	E.a	E.s	Aq.	DH	Aq.	B.a	Aq.	B.a	
POTAMOGETONACEAE													
<i>Potamogeton tricarinatus</i>	Ar	X	X	X	X	X	X	X	X	X	X	X	
RESTIONACEAE													
<i>Leptocarpus tenax</i>	Atls		X										
RUPPIACEAE													
<i>Ruppia</i> spp.	S						X		X		X		
ZANNICHELLIACEAE													
<i>Lepilaena cylindrocarpa</i>	S						X						
CHARACEAE													
<i>Chara</i> spp.	S	X		X		X	X	X	X	X	X		
<i>Nitella</i> spp. (thick branches)	S		X			X	X	X	X	X	X		
<i>Nitella subtilissima</i>	S	X							X				
Total Species Richness		9	18	22	22	12	29	41	33	20	32	31	

Appendix V1

Summary of the family representation of angiosperm species
recorded in the extant vegetation.

Dicotyledon 25 families		Monocotyledon 10 families	
APIACEAE	5	CYPERACEAE	15
ASTERACEAE	6	HYDATELLACEAE	1
CALLITRICHACEAE	1	JUNCACEAE	5
CARYOPHYLLACEAE	1	JUNCAGINACEAE	2
CHENOPODIACEA	2	POACEAE	21
CLUSIACEAE	1	POTAMOGETONACEAE	1
CONVOLVULACEAE	1	RESTIONACEAE	1
CRASSULACEAE	1	RUPPIACEAE	1
ELATINACEAE	1	ZANNICHELLIACEAE	1
FABACEAE	1		
CENTIANACEAE	1		
GERANIACEAE	1		
GOODENIACEAE	3		
HALORAGACEAE	3		
LENTIBULARIACEAE	1		
MENYANTHACEAE	2		
MYRTACEAE	2		
ONAGRACEAE	1		
PLANTAGONACEAE	2		
POLYGONACEAE	1		
PORTULACEAE	1		
PRIMULACEAE	2		
PROTEACEAE	1		
RANUNCULACEAE	1		
SCROPHULARIACEAE	3		

Appendix VII Summary of the species in the total potential flora of the wetlands (S = submerged; Ar = Amphibious responder; Atle = amphibious tolerator-emergent, Atls = amphibious tolerator-saturated mudflat; T = terrestrial; BP = Big Punchbowl; TD = Tin Dish; MID = Middle Lagoon; CTL = Cherry Tree Lagoon, SG = Sandy Gate; E.a = *Eleocharis acuta*; E.s = *Eleocharis sphacelata*; B.r = *Baumea rubiginosa*; B.a = *Baumea arthropphylla*; * = introduced; X = present in zone either in the seed bank or extant vegetation or both; bold X = potential flora from the present study).

Submerged Species	BP	TD	MID	CTL	SG
<i>Batrachium trichophyllum</i>				X	X
<i>Chara blobby arm</i>		X			
<i>Chara fibrosa</i>		X	X		X
<i>Chara globularis var globularis</i>		X			X
<i>Chara muelleri</i>		X			
<i>Chara preissii</i>	X			X	
<i>Lepilaena cylindrocarpa</i>			X		
<i>Nitella penicillata</i>			X		
<i>Nitella congesta</i>		X			
<i>Nitella cristata</i>					X
<i>Nitella gelatinifera var. galatinifera</i>	X		X	X	X
<i>Nitella gelatinifera var. microcephala</i>	X		X	X	X
<i>Nitella gloestachys</i>					X
<i>Nitella spp.</i>		X			
<i>Nitella subtilissima</i>	X			X	X
<i>Ruppia spp.</i>		X	X	X	X
Total = 16	4	7	6	6	9

Amphibious responder species	BP	TD	MID	CTL	SG
<i>Callitriche stagnalis</i> *				X	
<i>Crassula helmsii</i>				X	
<i>Elatine gratioloides</i>	X			X	
<i>Eleocharis sphacelata</i>	X		X		
<i>Hydrocotyle muscosa</i>	X		X	X	
<i>Isolepis fluitans</i>	X		X	X	X
<i>Isolepis producta</i>	X		X	X	
<i>Limosella australis</i>			X	X	X
<i>Myriophyllum variifolium</i>				X	
<i>Myriophyllum salsugineum</i>				X	X
<i>Myriophyllum simulans</i>	X	X	X	X	X
<i>Neopaxia australasica</i>			X		X
<i>Potamogeton tricarlinatus</i>	X	X	X	X	X
<i>Potamogeton ochreatus</i>	X				
<i>Ranunculus amphitrichus</i>				X	
<i>Schoenus fluitans</i>	X		X	X	
<i>Triglochin procerum</i>	X		X	X	X
<i>Villarsia reniformis</i>	X		X	X	
Total = 18	11	2	11	15	7

Appendix VII Total potential flora (cont.)/ page 2

Amphibious tolerator-emergent species	BP	TD	MID	CTL	SG
<i>Agrostis avenacea</i>	X	X	X	X	X
<i>Amphibromus recurvatus</i>				X	
<i>Amphibromus sinuatus</i>		X			X
<i>Baumea arthropphylla</i>			X	X	X
<i>Baumea rubiginosa</i>	X				
<i>Carex tereticaulis</i>					X
<i>Centipeda minima</i>	X			X	X
<i>Chorizandra</i> sp.	X			X	
<i>Cotula coronopifolia</i> */n				X	
<i>Eleocharis acuta</i>		X	X	X	X
<i>Eleocharis pusilla</i>				X	
<i>Isolepis inundata</i>	X		X		X
<i>Juncus articulatus</i> *	X	X	X	X	X
<i>Juncus bulbosus</i> *					
<i>Juncus holoschoenus</i>			X	X	X
<i>Juncus planifolius</i>	X	X	X	X	X
<i>Lilaeopsis polyantha</i>	X	X	X	X	X
<i>Mimulus repens</i>				X	
<i>Phragmites australis</i>				X	
<i>Schoenus apogon</i>		X			X
<i>Triglochin striatum</i>		X	X	X	X
<i>Typha</i> sp. */n		X		X	
<i>Utricularia</i> spp.	X		X	X	X
Total = 23	9	9	10	17	14

Appendix VII Total potential flora (cont.)/ page 3

Amphibious tolerator-saturated/ mudflat species	BP	TD	MID	CTL	SG
<i>Apium prostratum</i>		X		X	
<i>Baumea juncea</i>				X	
<i>Centella cordifolia</i>	X		X	X	X
<i>Centrolepis fascicularis</i>	X				
<i>Centrolepis</i> sp.				X	
<i>Cyperus tenellus</i> */n			X		
<i>Distichlis distichophylla</i>				X	
<i>Eryngium vesiculosum</i>		X	X	X	X
<i>Gahnia trifida</i>				X	
<i>Gonocarpus micranthus</i>	X				
<i>Goodenia humilis</i>			X		
<i>Gratiola peruviana</i>			X		
<i>Gratiola nana</i>	X				
<i>Hainardia cylindrica</i> *		X			X
<i>Hemarthria uncinata</i>		X		X	
<i>Hydrocotyle sibthorpiodes</i>					X
<i>Hypericum japonicum</i>	X				X
<i>Isolepis cernua</i>	X		X	X	X
<i>Isolepis montivaga</i>					X
<i>Juncus bufonius</i>	X	X	X		X
<i>Leptinella longipes</i>				X	
<i>Leptinella reptans</i>				X	
<i>Leptocarpus tenax</i>	X			X	
<i>Leptocarpus brownii</i>				X	
<i>Lepidosperma longitudinale</i>	X		X	X	X
<i>Lepyrodia muelleri</i>	X				
<i>Plantago coronopus</i> *	X	X	X	X	X
<i>Pratia pedunculata</i>			X		
<i>Sebaea albidiflora</i>				X	
<i>Samolus repens</i>				X	
<i>Sarcocornia quinqueflora</i>				X	
<i>Scaevola hookeri</i>	X				
<i>Schoenus maschalinus</i>	X		X	X	X
<i>Schoenus nitens</i>		X	X	X	X
<i>Schoenus tesquorum</i>				X	
<i>Selliera radicans</i>	X	X	X	X	X
<i>Trithuria submersa</i>			X	X	
<i>Wilsonia backhousei</i>				X	
<i>Wilsonia rotundifolia</i>		X		X	
Total = 39	14	9	14	24	12

Appendix VII Total Potential flora (cont.)/ page 4

Terrestrial species	BP	TD	MID	CTL	SG
<i>Acetosella vulgaris</i> *	X				X
<i>Agrostis capillaris</i> *			X		
<i>Aira</i> spp.*		X	X		X
<i>Alopecurus geniculatus</i> *					X
<i>Anagallis arvensis</i> *		X	X		
<i>Banksia marginata</i>	X				
<i>Parentucellia latifolia</i> *		X			
<i>Briza minor</i> *		X	X		X
<i>Bromus</i> sp.*		X			
<i>Carex inversa</i>					X
<i>Centaureum erythraea</i> *		X	X		
<i>Chenopodium glaucum</i> *				X	
<i>Cirsium vulgare</i> *		X	X	X	X
<i>Danthonia</i> spp.		X	X	X	X
<i>Deyeuxia quadriseta</i>	X			X	
<i>Dichondra repens</i>		X			
<i>Einadia nutans</i>			X		
<i>Epilobium sarmentaceum</i>	X	X		X	X
<i>Erodium cicutarium</i> *		X			
<i>Eucalypt</i> spp.	X				
<i>Euchiton collinus</i>		X		X	
<i>Euchiton involucratus</i>	X				
<i>Gaudiana fragilis</i> *					X
<i>Holcus lanatus</i> *	X		X	X	X
<i>Hypochoeris radicata</i> *					X
<i>Juncus pallidus</i>	X			X	
<i>Juncus pauciflorus</i>			X	X	
<i>Juncus procerus</i>					X
<i>Juncus</i> sp. unidentified		X	X		
<i>Leontodon taraxacoides</i> *		X	X		X
<i>Leptospermum scoparium</i>	X			X	
<i>Lolium perenne</i> *		X			
<i>Lythrum hyssopifolia</i>		X			
<i>Plantago lanceolata</i> *		X			
<i>Poa annua</i> *		X	X		X
<i>Poa labillardierei</i>					X
<i>Polypogon monspeliensis</i> *		X		X	
<i>Scleranthus biflorus</i>	X				
<i>Sellaginella uliginosa</i>	X			X	
<i>Sonchus</i> sp.*		X			
<i>Stellaria media</i> *					X
<i>Trifolium</i> spp.*	X	X	X		X
<i>Vellereophyton dealbatum</i> *	X	X		X	
<i>Veronica</i> sp.					X
<i>Vulpia</i> spp.*		X	X		X
Total = 45	12	23	15	12	19

Appendix VIII-a Big Punchbowl: presence/absence summary of species found in the present study compared with previous vegetation studies.

- * = introduced species; P= perennial; A = annual; B = biennial; lines indicate categories of the present study
 ✓ = germinated between field surveys; underline = dominant within either seed bank or extant vegetation
 study of the present study or in the extant vegetation at time of the past surveys; ✓ = greater than 5% cover;
 ✓ = between 1-5% cover; (a) species found in the seed bank of summer 1997 and winter 1997;
 (b) number of seasons the species was present during field surveys between 1997 and 1998;
 (c) Jamie Kirkpatrick and Chris Harwood 1978 survey (Kirkpatrick and Harwood, 1981); (d) vegetation survey by
 the author in August 1995; (e) vegetation survey in summer 1999 by Micha Visoiu (Visoiu, 2000);
 (f) JS 1997-1998 - species observed by the author in the wetland between 1997 and 1998;
 (g) field germination observed during the present study 1997-1998.

			(a)	(b)	(c)	(d)	(e)	(f)	(g)
	FG	Life cycle	Seed Bank	present extant	K+H 1978	JS 1995	Visoiu 1999	JS 1997-98	Field germination
<i>Baumea rubiginosa</i>	Atle	P	✓	8	✓	✓	✓	✓	
<i>Isolepis fluitans</i>	Ar	P	✓	4	✓	✓		✓	✓
<i>Chara preissii</i>	S	A	✓	2				✓	✓
<i>Nitella subtilissima</i>	S	P	✓	2				✓	✓
<i>Potamogeton tricarinatus</i>	Ar	P	✓	2	✓			✓	✓
<i>Utricularia dichotoma</i>	Atle	P	✓	2				✓	✓
<i>Nitella spp.</i>	S	P	✓	1				✓	✓
<i>Juncus bufonius</i>	Atls	A	✓		✓	✓			
<i>Juncus pallidus</i>	T	P	✓		✓	✓		✓	
<i>Vellereophyton dealbatum</i> *	T	A	✓		✓				
<i>Isolepis inundata</i>	Atle	P	✓		✓				
<i>Schoenus fluitans</i>	Ar	P	✓		✓				
<i>Mynophyllum simulans/varifolium</i>	Ar	P	✓					✓	
<i>Agrostis avenacea</i>	Atle	A		7		✓		✓	✓
<i>Eucalyptus</i> sp.	T	P		3		✓		✓	✓
<i>Acetosella vulgaris</i> *	T	P		1				✓	✓
<i>Tnfolium</i> sp.*	T	A		1				✓	✓
<i>Scleranthus biflorus</i>	T	P		8				✓	
<i>Scaevola hookeri</i>	Atls	P		4	✓	✓	✓	✓	
<i>Villarsia reniformis</i>	Ar	P		8	✓	✓	✓	✓	
<i>Leptospermum scoparium</i>	T	P		8	✓	✓	✓	✓	
<i>Leptocarpus tenax</i>	Atls	P		7	✓	✓	✓	✓	
<i>Triglochin procerum</i>	Ar	P		6			✓	✓	
<i>Chonozandra enodis</i>	Atle	P		5	✓	✓		✓	
<i>Eleocharis sphacelata</i>	Ar	P		2				✓	
<i>Gonocarpus micranthus</i>	Atls	P		2	✓	✓		✓	
<i>Deyeuxia quadrifida</i>	T	P		1			✓	✓	
<i>Banksia marginata</i>	T	P		1		✓		✓	
<i>Isolepis producta</i>	Ar	P			✓				
<i>Potamogeton ochreatus</i>	Ar	P			✓				
Species total			13	22	14	13	7	24	10

Species recorded in dry herbaceous zone of Big Punchbowl not sampled in the present study

<i>Lobelia alata</i>	?		✓						
<i>Hydrocotyle muscosa</i>	Ar		✓						
<i>Elatine gratioloides</i>	Ar		✓						
<i>Lilaeopsis polyantha</i>	Atle		✓						
<i>Juncus planifolius</i>	Atle		✓						
<i>Centipeda minima</i>	Atle		✓						
<i>Juncus articulatus</i> *	Atle		✓						
<i>Lepidosperma longitudinale</i>	Atls		✓		✓	✓			
<i>Schoenus maschalinus</i>	Atls		✓						
<i>Plantago coronopus</i> *	Atls		✓						
<i>Gratiola nana</i>	Atls		✓						
<i>Lepyrodia muelleri</i>	Atls		✓				✓		
<i>Centrolepis fascicularis</i>	Atls		✓						
<i>Centella cordifolia</i>	Atls		✓				✓		
<i>Selliera radicans</i>	Atls		✓		✓				
<i>Hypencum japonicum</i>	Atls		✓						
<i>Isolepis cernua</i>	Atls		✓						
<i>Scaevola hookeri</i>	Atls				✓		✓		
<i>Leptocarpus tenax</i>	Atls				✓		✓		
<i>Schoenus nitens</i>	Atls				✓		✓		
<i>Epilobium</i> sp	T		✓						
<i>Selaginella uliginosa</i>	T		✓		✓		✓		
<i>Euchiton involucreatus</i>	T		✓						
<i>Holcus lanatus</i> *	T		✓						
<i>Leptospermum scoparium</i>	T				✓		✓		
<i>Holcus lanatus</i> *	T				✓				

Appendix VIII-b Tin Dish: presence/absence summary of species found in the present study compared with previous vegetation studies.

* = introduced species; */n unknown status; P= perennial; A = annual; B = biennial; SLP = short live perennial; lines indicate categories of the present study; √ = germinated between field surveys; underline = dominant within either seed bank or extant vegetation within the present study or in the extant vegetation at time of the past surveys; √ = greater than 5% cover; √* = between 1-5% cover. (a) species found in the seed bank of summer 1997 and winter 1997; (b) number of seasons the species was present during field surveys between 1997 and 1998; (c) Jamie Kirkpatrick and Chris Harwood autumn 1978 survey; (d) vegetation survey by the author in 1995; (e) JS 1997-1998 - species observed by the author in the wetland between 1997 and 1998; (f) field germination observed during the present study 1997-1998.

Species	FG	Life cycle	(a) Seed Bank	(b) Seasons present extant	(c) K+H 1978	(d) JS 1995	(e) JS 1997-1998	(f) Field germination
<i>Agrostis avenacea</i>	Atle	A	√	8	√	√*	√	√
<i>Polypogon monspeliensis</i> *	T	A	√	7	√	√	√	√
<i>Trifolium</i> spp.*	T	A	√	7	√	√	√	√
<i>Centaurea erythraea</i> *	T	A/B	√	7	√	√*	√	√
<i>Leontodon taraxacoides</i> *	T	P/B	√	7	√	√*	√	√
<i>Dichondra repens</i>	T	P	√	8	√	√*	√	√
<i>Lilaeopsis polyantha</i>	Atle	P	√	7	√	√	√	√
<i>Plantago coronopus</i> *	Atis	A/P	√	7	√	√*	√	
<i>Hainardia</i> */ <i>Hemarthria</i> spp.	Atis	A/P	√	5	√	√*	√	
<i>Eleocharis acuta</i>	Atle	P	√	8	√	√	√	
<i>Selliera radicans</i>	Atis	P	√	8	√	√	√	
<i>Potamogeton tricarinatus</i>	Ar	P	√	4	√		√	
<i>Chara</i> spp.	S	P	√	1			√	
<i>Myriophyllum</i> sp.	Ar	P	√	1	√		√	√
<i>Juncus articulatus</i> *	Atle	P	√	1	√		√	
<i>Vellerophyton dealbatum</i> *	T	A	√				√	
<i>Euchiton collinus</i>	T	P	√			√	√	
<i>Juncus bufonius</i>	Atis	A	√			√*	√	
<i>Typha</i> sp.	Atle	P	√				√	
<i>Juncus planifolius</i>	Atle	P	√				√	
<i>Lythrum hyssopifolia</i>	T	A	√				√	
<i>Nitella</i> spp.	S	A	√					
<i>Apium prostratum</i>	Atis	P	√		√			
<i>Schoenus apogon</i>	Atle	P	√					
<i>Epilobium</i> sp.*/n	T	P	√					
<i>Juncus procerus</i>	T	P	√					
<i>Ruppia megacarpa</i>	S	P	√					
<i>Cirsium vulgare</i> *	T	B		8	√	√*	√	√
<i>Briza minor</i> *	T	A		4			√	√
<i>Anagallis arvensis</i> *	T	A		3	√		√	√
<i>Sonchus</i> sp *	T	A		3		√	√	√
<i>Aira elegantissima</i> *	T	A		2			√	√
<i>Parentucella latifolia</i> *	T	A		1		√*	√	√
<i>Poa annua</i> *	T	A		1			√	√
<i>Poaceae</i> sp *	T	A		2		√	√	√
<i>Bromus</i> sp *	T	A		1			√	√
<i>Vulpia megalura</i> *	T	A		1			√	√
<i>Plantago lanceolata</i> *	T	A/B		1			√	√
<i>Lolium perenne</i> *	T	A/SLP		1			√	√
<i>Eryngium vesiculosum</i>	Atis	P		7	√		√	
<i>Erodium cicutarium</i> *	T	P		6		√*	√	
<i>Schoenus nitens</i>	Atis	P		6	√	√	√	
<i>Amphibromus sinuatus</i>	Atle	P		1			√	
<i>Danthonia</i> sp.	T	P		1			√	
<i>Wilsonia rotundifolia</i>	Atis	P			√	√	√	
<i>Triglochin striatum</i>	Atle	P			√			
Species total			27	32	16	20	38	20

Appendix VIII-c Middle Lagoon: presence/absence summary of species found in the present study compared with previous vegetation studies.

* = introduced species; ?/n = unknown status; P = perennial; A = annual; B = biennial; lines indicate categories of the present study; ✓ = germinated between field surveys; underline = dominant within either seed bank or extant vegetation of the present study or in the extant vegetation at time of the past surveys;

✓ = greater than 5% cover; ✓ = between 1-5% cover. (a) species found in the seed bank of summer 1997 and winter 1997; (b) number of seasons the species was present during field surveys between 1997 and 1998;

(c) Jamie Kirkpatrick and Chris Harwood 1978 survey; (d) vegetation survey by the author in

1996; (e) JS 1997-1998 - species observed by the author in the wetland between 1997 and 1998.

(g) field germination observed during the present study 1997-1998.

Species	FG	Life cycle	(a) Seed Bank	(b) Seasons present extant	(c) K+H 1978	(d) JS 1995	(e) JS 1997-1998	(f) Field germination
<i>Agrostis avonacca</i>	Atle	A	✓	7		✓	✓	✓
<i>Trithuria submersa</i>	Atls	A	✓	3		✓	✓	✓
<i>Trifolium</i> spp. *	T	A	✓	3		✓	✓	✓
<i>Cyperus tenellus</i> */n	Atls	A	✓	1		✓	✓	✓
<i>Leontodon taraxacoides</i> *	T	A/P	✓	6		✓	✓	✓
<i>Juncus holoschoenus</i>	Atle	P	✓	7	✓	✓	✓	✓
<i>Myriophyllum</i> spp	Ar	P	✓	7	✓	✓	✓	✓
<i>Juncus articulatus</i> *	Atle	P	✓	7	✓	✓	✓	✓
<i>Goodenia humilis</i>	Atls	P	✓	7		✓	✓	✓
<i>Isolepis</i> spp.	Ar/Atls	P	✓	7		✓	✓	✓
<i>Selliera radicans</i>	Atls	P	✓	7	✓	✓	✓	✓
<i>Villarsia reniformis</i>	Ar	P	✓	7	✓	✓	✓	✓
<i>Centella cordifolia</i>	Atls	P	✓	7		✓	✓	✓
<i>Schoenus fluitans</i>	Ar	P	✓	3		✓	✓	✓
<i>Enadia nutans</i>	T	P	✓	2		✓	✓	✓
<i>Juncus bufonius</i>	Atls	A	✓	3		✓	✓	✓
<i>Nitella</i> spp.	S	A	✓	7			✓	
<i>Plantago coronopus</i> *	Atls	A/P	✓	4		✓	✓	
<i>Eleocharis sphacelata</i>	Ar	P	✓	7	✓	✓	✓	
<i>Eleocharis acuta</i>	Atle	P	✓	7		✓	✓	
<i>Hydrocotyle muscosa</i>	Ar	P	✓	7	✓	✓	✓	
<i>Lilaeopsis polyantha</i>	Atle	P	✓	7	✓	✓	✓	
<i>Agrostis capillaris</i> *	T	P	✓	7		✓	✓	
<i>Triglochin procerum</i>	Ar	P	✓	7	✓	✓	✓	
<i>Chara fibrosa</i>	S	P	✓	6		✓	✓	
<i>Schoenus maschalinus</i>	Atls	P	✓	5		✓	✓	
<i>Utricularia</i> spp	Atlw	P	✓	4		✓	✓	
<i>Juncus bulbosus</i>	Atls	P	✓	4		✓	✓	
<i>Potamogeton tricannatus</i>	Ar	P	✓	7	✓	✓	✓	
<i>Isolepis inundata</i>	Atls	P	✓	5	✓	✓	✓	
<i>Juncus planifolius</i>	Atle	P	✓				✓	
<i>Limosella australis</i>	Ar	A/P	✓					
<i>Gratiola peruviana</i>	Atls	P	✓					
<i>Juncus procerus</i>	T	P	✓					
<i>Aira</i> sp. *	T	A		2			✓	✓
<i>Anagallis arvensis</i> *	T	A		1			✓	✓
<i>Briza minor</i> *	T	A		1			✓	✓
<i>Vulpia</i> spp. *	T	A		1			✓	✓
<i>Poa annua</i> *	T	A		1		✓	✓	✓
<i>Centaurium erythraea</i> *	T	A/B		1			✓	✓
<i>Cirsium vulgare</i> *	T	B		2		✓	✓	✓
<i>Eryngium vesiculosum</i>	Atls	P		6	✓	✓	✓	
<i>Neopaxia australasica</i>	Ar	P		2	✓		✓	
<i>Danthonia semiannularis</i>	T	P		6		✓	✓	
<i>Holcus lanatus</i> *	T	P		3		✓	✓	
<i>Baumea arthropophylla</i>	Atle	P		7			✓	
<i>Schoenus nitens</i>	Atls	P		6			✓	
<i>Triglochin striatum</i>	Atle	P		5			✓	
<i>Lepilaena cylindrocarpa</i>	S	P		2			✓	
<i>Ruppia</i> sp.	S	P		1			✓	
<i>Pratia peduncularis</i>	Atls				✓			
Total species			34	46	13	23	47	23
Species recorded in outer herbaceous zone of Middle Lagoon not sampled in the present study								
<i>Lepidosperma longitudinale</i>	Atls				✓		✓	

Appendix VIII-b Cherry Tree Lagoon: presence/absence summary of species found in the present study compared with previous vegetation studies.

* = introduced species; */n = unknown status; (a) species found in the seed bank of summer 1997 and winter 1997; √ = germinated between field surveys; underline = dominant within either seed bank or extant vegetation of the present study or in the extant vegetation at time of the past surveys; √ = greater than 5% cover; √* = between 1-5% cover; (b) number of seasons the species was present during field surveys between 1997 and 1998; (c) Jamie Kirkpatrick and Chris Harwood 1978 survey; (d) vegetation survey by the author in spring 1995; (e) vegetation survey in summer 1999 by Micha Visoiu (Visoiu, 2000); (f) JS 1997-1998 - species observed by the author in the wetland between 1997 and 1998; (g) field germination observed during the present study 1997-1998.

			(a)	(b)	(c)	(d)	(e)	(f)	(g)
	FG	Life cycle	Seed bank	Seasons present extant	K+H 1978	JS 1995	Visoiu 1999	JS 1997-1998	Field germination
<i>Vilarsia reniformis</i>	Ar	P	√	8	√	√	√	√	√
<i>Ranunculus amphitrichus</i>	Ar	P	√	8	√	√	√	√	√
<i>Potamogeton tncarinatus</i>	Ar	P	√	8	√	√	√	√	√
<i>Myriophyllum salicoides</i>	Ar	P	√	8	√	√	√	√	√
<i>Myriophyllum simulans</i> / <i>vanifolium</i>	Ar	P	√	8	√	√*	√	√	√
<i>Lilaeopsis polyantha</i>	Atle	P	√	8	√	√	√	√	√
<i>Isolepis fluitans</i>	Ar	P	√	8	√	√	√	√	√
<i>Agrostis avenacea</i>	Atle	A	√	7	√	√	√	√	√
<i>Utricularia dichotoma</i>	Atle	P	√	5	√		√	√	√
<i>Batrachium trichophyllum</i>	S	A/P	√	4				√	√
<i>Elatine gratioloides</i>	Ar	A	√	2	√	√		√	√
<i>Cotula coronopifolia</i> */n	Atle	P	√	2	√		√	√	√
<i>Eleocharis acuta</i>	Atle	P	√	8	√	√*	√	√	√
<i>Crassula helmsii</i>	Ar	P	√	8		√*		√	√
<i>Baumea arthrophylla</i>	Atle	P	√	8	√	√	√	√	√
<i>Chara preissii</i>	S	A	√	6				√	√
<i>Nitella gelatinifera</i>	S	A	√	4				√	√
<i>Selliera radicans</i>	Atls	P	√	2	√	√	√	√	√
<i>Callitriche stagnalis</i> *	Ar	A/P	√	2		√		√	√
<i>Amphibromus recurvatus</i>	Atle	P	√	2				√	√
<i>Nitella subulissima</i>	S	A	√	1				√	√
<i>Juncus planifolius</i>	Atle	P	√		√		√		√
<i>Isolepis cernua</i>	Atls	P	√		√		√		√
<i>Juncus pallidus</i>	T	P	√		√	√	√	√	√
<i>Schoenus fluitans</i>	Ar	P	√		√	√	√	√	√
<i>Juncus holoschoenus</i>	Atle	P	√		√	√	√	√	√
<i>Apium prostratum</i>	Atls	P	√		√	√	√	√	√
<i>Euchiton collinus</i>	T	P	√		√			√	√
<i>Centipeda minima</i>	Atle	P	√						√
<i>Limosella australis</i>	Ar	A/P	√						√
<i>Hydrocotyle muscosa</i>	Ar	P		8	√	√	√	√	√
<i>Chenopodium glaucum</i> *	T	A		1				√	√
<i>Centella cordifolia</i>	Atls	P		7	√	√		√	√
<i>Cirsium vulgare</i> *	T	B		5		√		√	√
<i>Deyeuxia quadriseta</i>	T	P		6	√	√	√	√	√
<i>Eryngium vesiculosum</i>	Atls	P		2	√	√	√	√	√
<i>Leptinella longipes</i>	T	P		4	√			√	√
<i>Mimulus repens</i>	Atle	A/P		6				√	√
<i>Plantago coronopus</i>	Atls	A/P		2	√	√	√	√	√
<i>Ruppia</i> sp.	S	P		1				√	√
<i>Samolus repens</i>	Atls	P		1	√	√	√	√	√
<i>Triglochin</i> spp.	Ar	P		6	√	√	√	√	√
<i>Phragmites australis</i>	Atle	P			√	√	√	√	√
<i>Typha latifolia</i> *	Atle	P			√				√
<i>Juncus articulatus</i> *	Atle	P			√				√
Species total			30	33	27	26	21	38	14

Appendix ESB OS (d) (cont)/page 2 Cherry Tree Lagoon

		(a)	(b)	(c)	(d)	(e)	(f)	(g)
	Life	Seed	Seasons	K+H	JS	Visou	JS	Field
FG	cycle	bank	present	1978	1995	1999	1997-1998	germination
Species recorded in dry herbaceous zone of Ch�erry Tree Lagoon not sampled in the present study								
<i>Angianthus enocephalus</i>	?			√				
<i>Lobelia alata</i>	?			√		√		
<i>Gahnia filum</i>	Atle				√	√		
<i>Chonczandra australis</i>	Atle			√				
<i>Eleocharis pusilla</i>	Atle			√		√		
<i>Cotula reptans</i>	Atls			√	√	√		
<i>Lepidosperma longitudinale</i>	Atls			√	√	√		
<i>Baumea juncea</i>	Atls			√	√	√		
<i>Brachyscome graminea</i>	Atls			√	√			
<i>Gahnia trifida</i>	Atls			√	√	√		
<i>Hemarthra uncinata</i>	Atls			√		√		
<i>Hypoxis hygrometrica</i>	Atls			√	√			
<i>Juncus kraussii</i>	Atls			√	√	√		
<i>Leptocarpus brownii</i>	Atls			√	√	√		
<i>Lepyrodia muelleri</i>	Atls			√				
<i>Pratia platycalyx</i>	Atls			√	√			
<i>Schoenus maschalinus</i>	Atls			√	√			
<i>Schoenus nitens</i>	Atls			√	√	√		
<i>Schoenus tesquorum</i>	Atls			√				
<i>Sebaea albidiflora</i>	Atls			√	√	√		
<i>Selaginella uliginosa</i>	Atls			√	√	√		
<i>Tingiochin striatum</i>	Atls			√		√		
<i>Tritihuna submersa</i>	Atls			√				
<i>Polypogon monspeliensis</i>	Atls			√		√		
<i>Centrolepis</i> sp.	Atls			√	√			
<i>Schoenus nitans</i>	Atls			√	√	√		
<i>Wilsonia backhousei</i>	Atls			√	√	√		
<i>Wilsonia rotundifolia</i>	Atls			√	√	√		
<i>Distichlis distichophylla</i>	Atls			√	√	√		
<i>Spergularia media</i>	Atls			√		√		
<i>Sarcocornia quinqueflora</i>	Atls			√	√	√		
<i>Lawrenzia spicata</i>	Atls				√	√		
<i>Danthonia semiannularis</i>	T			√		√		
<i>Epilobium</i> sp.	T			√				
<i>Helichrysum dealbatum</i>	T			√				
<i>Leptospermum scoparium</i>	T			√	√	√		
<i>Melaleuca gibbosa</i>	T			√	√	√		
<i>Melaleuca squarrosa</i>	T			√	√	√		
<i>Vellereophyton dealbatum</i>	T			√	√	√		
<i>Holcus lanatus</i>	T					√		
<i>Trifolium</i> sp	T					√		
<i>Acaena novae-zelandiae</i>	T				√	√		
<i>Bnza minor</i> *	T					√		

Appendix VIII-e Sandy Gate: presence/absence summary of species found in the present study compared with previous vegetation studies.

* = introduced species; P= perennial; A = annual; B = biennial; lines indicate categories of the present study
 ✓ = germinated between field surveys; underline = dominant within either seed bank or extant vegetation within the present study or in the extant vegetation at time of the past surveys; ✓ = greater than 5% cover; ✓ = between 1-5% cover); (a) species found in the seed bank of summer 1997 and winter 1997;
 (b) number of seasons the species was present during field surveys between 1997 and 1998;
 (c) Jamie Kirkpatrick and Chris Harwood 1978 survey; (d) vegetation survey by the author in 1996; (e) JS 1997-1998 - species observed by the author in the wetland between 1997 and 1998.
 (g) field germination observed during the present study 1997-1998.

Study Totals	FG	Life cycle	(a) Seed Bank	(b) Seasons present extant	(c) K+H 1978	(d) JS 1995	(e) JS 1997-1998	(f) Field germination
<i>Acrostis avenacea</i>	Atle	A	✓	8	✓	✓	✓	✓
<i>Trifolium</i> spp.*	T	A	✓	3	✓	✓	✓	✓
<i>Cirsium vulgare</i> *	T	B	✓	6	✓	✓	✓	✓
<i>Isolepis</i> spp.	Ar/Atls	P	✓	8	✓	✓	✓	✓
<i>Myriophyllum simulans</i>	Ar	P	✓	7	✓	✓	✓	✓
<i>Myriophyllum salsugineum</i>	Ar	P	✓	1	✓	✓	✓	✓
<i>Leontodon taraxacoides</i> *	T	P/B	✓	7	✓	✓	✓	✓
<i>Batrachium trichophyllum</i>	S	P	✓	1	✓	✓	✓	✓
<i>Aira carvophyllea</i> *	T	A	✓	2	✓	✓	✓	✓
<i>Acetosella vulgaris</i> *	T	A	✓		✓	✓	✓	✓
<i>Juncus holoschoenus</i>	Atle	P	✓	8	✓	✓	✓	✓
<i>Eleocharis acuta</i>	Atle	P	✓	8	✓	✓	✓	✓
<i>Holcus lanatus</i> *	T	P	✓	8	✓	✓	✓	✓
<i>Hydrocotyle sibthorpiodes</i>	Atls	P	✓	8	✓	✓	✓	✓
<i>Lilaeopsis polyantha</i>	Atle	P	✓	8	✓	✓	✓	✓
<i>Centella cordifolia</i>	Atls	P	✓	8	✓	✓	✓	✓
<i>Baumea arthrophylla</i>	Atle	P	✓	8	✓	✓	✓	✓
<i>Eryngium vesiculosum</i>	Atls	P	✓	7	✓	✓	✓	✓
<i>Carex inversa</i>	T	P	✓	7	✓	✓	✓	✓
<i>Neopaxia australasica</i>	Ar	P	✓	6	✓	✓	✓	✓
<i>Potamogeton incarinatus</i>	Ar	P	✓	6	✓	✓	✓	✓
<i>Carex tereticaulis</i>	Atle	P	✓	6	✓	✓	✓	✓
<i>Juncus articulatus</i> *	Atle	P	✓	5	✓	✓	✓	✓
<i>Gaudiana fragilis</i> *	T	A	✓	5	✓	✓	✓	✓
<i>Nitella</i> spp.	S	A	✓	4	✓	✓	✓	✓
<i>Epilobium samentaceum</i>	T	P	✓	4	✓	✓	✓	✓
<i>Amphibromus sinuatus</i>	Atle	P	✓	3	✓	✓	✓	✓
<i>Hypochoeris radicata</i> *	T	P	✓	3	✓	✓	✓	✓
<i>Schoenus maschalinus</i>	Atls	P	✓	2	✓	✓	✓	✓
<i>Chara</i> spp.	S	P	✓	1	✓	✓	✓	✓
<i>Vulpia myuros</i> *	T	A	✓	1	✓	✓	✓	✓
<i>Hypencum japonicum</i>	T	P	✓	1	✓	✓	✓	✓
<i>Schoenus apogon</i>	Atle	P	✓	1	✓	✓	✓	✓
<i>Poa annua</i> *	T	A	✓		✓	✓	✓	✓
<i>Juncus bufonius</i>	Atls	A	✓		✓	✓	✓	✓
<i>Stellaria media</i> *	T	A	✓		✓	✓	✓	✓
<i>Plantago coronopus</i> *	Atls	A/P	✓		✓	✓	✓	✓
<i>Juncus procerus</i>	T	P	✓		✓	✓	✓	✓
<i>Centipeda minima</i>	Atle	P	✓		✓	✓	✓	✓
<i>Utricularia</i> sp 2	Atle	P	✓		✓	✓	✓	✓
<i>Juncus planifolius</i>	Atle	P	✓		✓	✓	✓	✓
<i>Limosella australis</i>	Ar	P	✓		✓	✓	✓	✓
<i>Briza minor</i> *	T	A		2	✓	✓	✓	✓
<i>Hainardia uncinata</i>	Atls	A		5	✓	✓	✓	✓
<i>Poa labillardierei</i>	T	P		8	✓	✓	✓	✓
<i>Schoenus nitens</i>	Atls	P		8	✓	✓	✓	✓
<i>Triglochin procerum</i>	Ar	P		8	✓	✓	✓	✓
<i>Danthonia</i> sp	T	P		3	✓	✓	✓	✓
<i>Alopecurus geniculatus</i> *	T	P		1	✓	✓	✓	✓
<i>Ruppia</i> sp	S	P		1	✓	✓	✓	✓
<i>Veronica gracilis</i>	T	P		1	✓	✓	✓	✓
<i>Triglochin striatum</i>	Atle	P			✓	✓	✓	✓
<i>Selliera radicans</i>	Atls	P			✓	✓	✓	✓
Species total			42	41	19	27	49	12

Appendix IX Species that were found only in low values in the seed bank and low percentage cover in the extant vegetation at the time the soils were taken, summer and winter 1997 (numbers indicate the number of times the species were recorded in the extant vegetation during the summer and winter, 1997 soil sampling [out of a possible 22 times -i.e. 11 zones x 2 sampling periods]; * = introduced species; */n = unknown status).

<i>Triglochin procerum</i> , 11	<i>Cyperus tenellus</i> */n, 1
<i>Utricularia</i> spp., 10	<i>Mimulus repens</i> , 1
<i>Centella cordifolia</i> , 10	<i>Lythrum hyssopifolia</i> , 1
<i>Juncus</i> spp., 10	<i>Gratiola peruviana</i> , 1
<i>Juncus bufonius</i> , 10	<i>Stellaria media</i> *, 1
<i>Plantago coronopus</i> *, 7	<i>Hypericum japonica</i> , 1
<i>Trifolium</i> spp.*, 7	<i>Triglochin striatum</i> , 1
<i>Eryngium vesiculosum</i> , 6	<i>Ruppia megacarpa</i> , 1
<i>Cirsium vulgare</i> *, 6	<i>Leptocarpus tenax</i> , 1
<i>Epilobium</i> spp.*/n, 6	<i>Chorizandra</i> sp., 1
<i>Hydrocotyle muscosa</i> , 5	<i>Carex tereticaulis</i> , 1
<i>Limosella australis</i> , 5	<i>Typha</i> sp.*/n, 1
<i>Juncus planifolius</i> , 5	<i>Poa annua</i> *, 1
<i>Agrostis capillaris</i> *, 5	<i>Hainardia cylindrica</i> *, 1
<i>Centaureum erythraea</i> *, 5	<i>Cynosurus echinatus</i> *, 1
<i>Ranunculus amphitrichus</i> , 4	<i>Deyeuxia quadriseta</i> , 1
<i>Neopaxia australasica</i> , 4	<i>Acetosella vulgaris</i> *, 1
<i>Goodenia humilis</i> , 4]	<i>Poa labillardierei</i> , 1
<i>Schoenus maschalinus</i> , 4	
<i>Amphibromus</i> spp., 4	
<i>Schoenus nitens</i> , 3	
<i>Callitriche stagnalis</i> *, 3	
<i>Trithuria submersa</i> , 3	
<i>Carex inversa</i> , 3	
<i>Schoenus apogon</i> , 3	
<i>Einadia nutans</i> , 3	
<i>Hydrocotyle sibthorpioides</i> , 3	
<i>Centipeda minima</i> , 3	
<i>Dichondra repens</i> , 3	
<i>Apium prostratum</i> , 3	
<i>Vellereophyton dealbatum</i> *, 3	
<i>Vulpia</i> sp.*, 3	
<i>Aira</i> spp.*, 3	
<i>Holcus lanatus</i> *, 3	
<i>Polypogon monspeliensis</i> *, 3	
<i>Crassula helmsii</i> , 2	
<i>Euchiton collinus</i> , 2	
<i>Sonchus</i> spp.*, 2	
<i>Scleranthus biflorus</i> , 2	
<i>Scaevola hookeri</i> , 2	
<i>Hypochoeris radicata</i> *, 2	
<i>Danthonia</i> spp., 2	
<i>Gaudiana fragilis</i> *, 2	
<i>Briza minor</i> *, 1	

Appendix X Summary of the vegetative reproductive and seed bank characteristics of the species found in the present study

(FG = functional group; S = submerged, Ar = amphibious responder; Atle = amphibious tolerator-emergent; Atls = amphibious tolerator saturated/mudflat; T = terrestrial; Life cycle: A = annual; P = perennial; Root depth: S = shallow (0-5 cm); M = medium (5-15 cm) D = Deep (> 15 cm); * = introduced species; Extant vegetation: mean percentage cover ** = highest mean cover recorded in a zone; Seed bank: germinants: Maximum = maximum mean germinants per m2 recorded per zone; Minimum = minimum mean germinants per m2 recorded per zone; mudflat = germinated in saturated conditions; inundated = germinated in inundated conditions; underline = dominant species discussed in text).

Species	FG	Life cycle	Vegetative reproduction											Extant vegetation	Seed bank									
			Vegetative spread										Perennating organs				Germinants							
			Root depth	NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers		Stolons	Rhizomes	Perennating stems	Fleshy roots	Perennial rootstock	Turions	Tap root	Bulbils	Max. mean percentage cover **	Max. per m2
<i>Lepilaena cylindrocarpa</i>	S	P	M?										X							0.9	0			
<i>Ruppia polycarpa</i>	S	A	M?										?					X		0.1	0			
<i>Ruppia magacarpa</i>	S	P	M?										?							0	14			X
<i>Batrachium trichophyllum</i>	S	A/P	S					X												0.3	1309	21	X	X
<i>Chara blobby arm</i>	S	A	S		X														?	0	424	347		X
<i>Chara fibrosa</i>	S	P	S		X														?	60	13526	6370	X	X
<i>Chara globularis</i> var. <i>globularis</i>	S		S		X														?	43.2	5889	1522	X	X
<i>Chara muelleri</i>	S	A	S		X														?	0	7			X
<i>Chara preissii</i>	S	A	S		X														?	44.7	2194	170	X	X
<i>Nitella cristata</i>	S	A	S		X														?	0	35			X
<i>Nitella congesta</i>	S	A	S		X														?	0	43	28		X
<i>Nitella subtilissima</i>	S	A	S		X														?	0.8	460	35	X	X
<i>Nitella gelatinifera</i> var. <i>gelatinifera</i>	S	A	S		X														?	50.9	6023	127	X	X
<i>Nitella gelatinifera</i> var. <i>microcephala</i>	S	A	S		X														?	0	1564	14	X	X
<i>Nitella gloestachys</i>	S	A	S		X														?	0.4	630	198		X
<i>Nitella</i> c.f. <i>penicillata</i>	S	A	S		X														?	0	170			X

Appendix X (cont.)/ page 2

Species	FG	Life cycle	Vegetative reproduction														Extant vegetation	Seed bank								
			Root depth	Vegetative spread								Perennating organs						Mean mean percentage cover **	Germinants							
				NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers	Stolons	Rhizomes	Perennating stems			Fleshy roots	Perennial rootstock	Turions	Tap root	Bulbils	Max.	Min	Mudflat
<u>Eleocharis sphacelata</u>	Ar	P	D										X									35.4	991	28	X	X
<u>Myriophyllum salsugineum</u>	Ar	P	M?						X		X		X									34.4	538	57	X	X
<u>Neopaxia australasica</u>	Ar	P	M?		X							X	X									1.7	14	7	X	
<u>Potamogeton tricarinatus</u>	Ar	P	M?					X			X		?	X	X			X				43.8	35	7	X	X
<u>Ranunculus amphitrichus</u>	Ar	P	M?										X	X								5.7	43	35	X	X
<u>Triglochin procerum</u>	Ar	P	D										X	X								1.7	7		X	
<u>Isolepis producta</u>	Ar	P	S										X									9.1	35		X	
<u>Villarsia reniformis</u>	Ar	P	D						X		X		X	X	?		X	X				51.9	92	28	X	X
<u>Limosella lineata</u>	Ar	A	S										X									0	60	28	X	X
<u>Myriophyllum varifolium/simulans</u>	Ar	P	M?					X	X		X											34.4	6321	14	X	X
<u>Isolepis fluitans</u>	Ar	P	S		?						X											9.5	729	319	X	X
<u>Schoenus fluitans</u>	Ar	P	S		X		X	X														1.2	7		X	X
<u>Crassula helmsii</u>	Ar	P	S				X	X														9.7	19		X	X
<u>Hydrocotyle muscosa</u>	Ar	P	S					X														4.2	35		X	X
<u>Callitriche stagnalis *</u>	Ar	A/P	S				X	X														0.3	484		X	X
<u>Centipeda minima</u>	Ar	A	S				?	X														0	19		X	
<u>Elatine gratioloides</u>	Ar	A	S				X															0.1	2343	191	X	X

Species	FG	Life cycle	Vegetative reproduction													Extant vegetation	Seed bank										
			Vegetative spread										Perennating organs				Mean mean percentage cover **	Germinants									
			Root depth	NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers	Stolons	Rhizomes			Perennating stems	Fleshy roots	Perennial rootstock	Tunons	Tap root	Bulbils	Max.	Min	Mudflat	Inundated
<i>Baumea arthropophylla</i>	Atle	P	D												X							68.1	156		X	X	
<i>Baumea rubiginosa</i>	Atle	P	D												X							8.3	50		X	X	
<i>Chorizandra</i> sp.	Atle	P	M?												X							0.1	0				
<i>Eleocharis acuta</i>	Atle	P	M?												X							70.8	1048	7	X	X	
<i>Isolepis inundata</i>	Atle	P	S			X				X	X				X							0.1	78	7	X	X	
<i>Juncus articulatus</i> *	Atle	P	S			X			X						X							0.1	333	14	X	X	
<i>Juncus holoschoenus</i>	Atle	P	S			X									X							0.6	1040	71	X	X	
<i>Juncus planifolius</i>	Atle	A/P	S			X									X							0.1	127	7	X		
<i>Lilaeopsis polyantha</i>	Atle	P	M?												X							17.2	28	7	X	X	
<i>Typha latifolia</i> */n	Atle	P	D												X							0	7		X		
<i>Carex tereticaulis</i>	Atle	P	M?												X							0.1	35		X		
<i>Amphibromus</i> spp.	Atle	P	S									X										0.1	71	7	X	X	
<i>Utriculara</i> spp.	Atle	P	S									X				?						1.3	78	7	X	X	
<i>Juncus bulbosus</i> *	Atle	P	S			X			X		X											0.3	0		X		
<i>Gratiola peruviana</i>	Atle	P	S	?																		0	4		X		
<i>Schoenus apogon</i>	Atle	P	S			X																0	21		X		
<i>Mimulus repens</i>	Atle	A/P	S					X	X													0.1	0				
<i>Agrostis avenacea</i>	Atle	A	S			?																0.9	18898	7	X	X	
<i>Cotula coronopifolia</i> */n	Atle	A	S	X																		0.1	146		X	X	

Species	FG	Life cycle	Vegetative reproduction													Extant vegetation	Seed bank								
			Vegetative spread										Perennating organs				Mean mean percentage cover **	Germinants							
			Root depth	NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers	Stolons	Rhizomes	Perennating stems		Fleshy roots	Perennial rootstock	Turions	Tap root	Bulbils	Max.	Min	Mudflat
<i>Isolepis cernua</i>	Atls	P	S			X								X							?	21	7	X	X
<i>Isolepis montivaga</i>	Atls	P	S			X								X							0	28		X	
<i>Leptocarpus tenax</i>	Atls	P	M?											X							0.1	0		X	
<i>Schoenus nitens</i>	Atls	P	M?											X							0.4	0			
<i>Triglochin striatum</i>	Atls	P	D			X						X		X							0.1	4		X	
<i>Hemarthria uncinata</i>	Atls	P	S					X						X							1.1	0		X	
<i>Plantago coronopus*</i>	Atls	P/A	S															X			1.8	14		X	X
<i>Goodenia humilis</i>	Atls	P	S															X			8.8	241	14	X	
<i>Eryngium vesiculosum</i>	Atls	P	S					?	X			?						?			6.9	50	21	X	X
<i>Leptinella longipes</i>	Atls	P	S									X									0.1	0		X	
<i>Samolus repens</i>	Atls	P	S									X									0.1	0		X	
<i>Scaevola hookeri</i>	Atls	P	S					X	X			X									0.1	0		X	
<i>Apium prostratum</i>	Atls	P/B	S	?																	0.1	7		X	
<i>Centella cordifolia</i>	Atls	P	S																		21.7	28		X	
<i>Schoenus maschalinus</i>	Atls	P	S			X			X												2.1	71		X	X
<i>Selliera radicans</i>	Atls	P	S					?	X			?									16.6	319	7	X	X
<i>Gonocarpus micranthus</i>	Atls	P	S	?																	0.1	0		X	
<i>Hypericum japonicum</i>	Atls	P	S	X																	0.1	50		X	
<i>Hydrocotyle sibthorpiodes</i>	Atls	P	S					X													0.1	14		X	
<i>Hainardia cylindrica</i>	Atls	A	S			X															1.1	0		X	
<i>Cyperus tenellus</i> *In	Atls	A	S			X															0.4	0		X	
<i>Juncus bufonius</i>	Atls	A	S			X															0.1	21	14	X	
<i>Trithuria submersa</i>	Atls	A	S				X														0.1	21			X

Species	FG	Life cycle	Vegetative reproduction													Extant vegetation	Seed bank								
			Vegetative spread										Perennating organs				Mean mean percentage cover **	Germinants							
			Root depth	NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers	Stolons	Rhizomes	Perennating stems		Fleshy roots	Perennial rootstock	Turions	Tap root	Bulbils	Max.	Min	Mudflat
<i>Carex inversa</i>	T	P	S										X								1.7	21	14	X	
<i>Agrostis capillaris</i> *	T	P	S									X	X								0.1	7		X	
<i>Juncus pallidus</i>	T	P	M?										X								0	85	71	X	
<i>Juncus pauciflorus</i>	T	P	M?										X								0	7		X	
<i>Veronica gracilis</i>	T	P	S										X								0.1	0		X	
<i>Hypochoeris radicata</i> *	T	P	S															X			0.1	7		X	
<i>Leontodon taraxacoides</i> *	T	P	S															X			20.7	177	35	X	X
<i>Taraxacum officinale</i> *	T	P	S															X			0.1	0		X	
<i>Plantago lanceolata</i> *	T	A/B	S															X			0.1	7		X	
<i>Sonchus</i> spp.*	T	A/B	S				X											X			0.1	0		X	
<i>Cirsium vulgare</i> *	T	B	M?															?	?		11	99		X	
<i>Epilobium sarmentaceum</i>	T	P	S									X									0.1	14	7	X	
<i>Acetosella vulgaris</i> *	T	P	S	X																	0.1	7		X	
<i>Centaureum glaucum</i> *	T	P	S																		0.1	0?		X	
<i>Danthonia</i> spp.	T	P	S			X															0.3	7		X	
<i>Deyeuxia quadriseta</i>	T	P	S			X															0.1	0		X	
<i>Dichondra repens</i>	T	P	S					X	X												0.3	0?		X	
<i>Enadla nutans</i>	T	P	S													X					0.1	7		X	
<i>Eucalyptus</i> sp.	T	P	D	X																	0.1	0		X	
<i>Leptospermum scoparium</i>	T	P	D	X																	0.3	0			
<i>Euchiton collinum</i>	T	P	S	X																	0.1	7		X	
<i>Holcus lanatus</i> *	T	P	S			X															0.2	106		X	

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Species	FG	Life cycle	Vegetative reproduction											Extant vegetation	Seed bank										
			Vegetative spread									Perennating organs			Mean mean percentage cover **	Germinants									
			Root depth	NONE	Rhizoid	Tufted - fibrous roots	Adventitious roots	Creeping stems	Root at node	Basal rosette	Fragments	Proliferous	Tubers			Stolons	Rhizomes	Perennating stems	Fleshy roots	Perennial rootstock	Turions	Tap root	Bulbils	Max.	Min
<i>Poa labillardierei</i>	T	P	M?			X															0.1	0		X	
<i>Scleranthus biflorus</i>	T	P	?																		0.1	0		X	
<i>Trifolium</i> spp.*	T	A/P	S	X																	4.1	21	7	X	X
<i>Aira</i> spp.	T	A	S			X															0.1	7		X	
<i>Anagallis arvensis</i> *	T	A	S	X																	0.1	0		X	
<i>Briza minor</i> *	T	A	S			X															0.1	?		X	
<i>Bromus</i> spp.*	T	A	S			X															0.1	0		X	
<i>Centaureum erythraea</i> *	T	A	S						X												0.3	219	14	X	X
<i>Cynosurus echinatus</i> *	T	A	S	X																	0.1	7		X	
<i>Erodium cicutarium</i> *	T	A	S	X																	0.3	0			
<i>Gaudiana fragilis</i> *	T	A	S	X																	0.1	7		X	
<i>Hordium</i> spp.*	T	A	S			X															0.1	0		X	
<i>Lolium perenne</i> *	T	A	S			X															0.1	0		X	
<i>Lythrum hyssopifolia</i>	T	A	S	?																	0	7		X	
<i>Parentucellia latifolia</i> *	T	A	S	X																	0.1	0		X	
<i>Poa annua</i> *	T	A	S			X															0.1	0		X	
<i>Polypogon monspeliensis</i> *	T	A	S			X															0.4	14		X	
<i>Spergularia marina</i> *	T	A	S	X																	0.1	0		X	
<i>Stellaria media</i> *	T	A	S	X																	0.1	0		X	
<i>Vellereophyton dealbatum</i> *	T	A	S	X																	0.1	7		X	
<i>Vulpia myuros</i> *	T	A	S			X															0.2	7		X	

References

Brock and Casanova, 1991
 Curtis, 1963, 1993
 Curtis and Morris, 1993
 Sainty and Jacobs, 1981
 Aston, 1973

Appendix XI: Alteration of water regimes in Tasmanian wetlands

Evidence of Aboriginal use of Tasmanian wetlands has been recorded before European settlement (Fensham, 1985). However, although they probably harvested plants and animals for food (McComb and Lake, 1990), there is no evidence of their severely altering water regimes of wetlands within Tasmania. Since European settlement, draining and inundation have been the two largest destroyers of Tasmanian wetlands (Harwood, 1981). Although it is difficult to determine the exact area, Kirkpatrick and Harwood (1983a) estimated that draining to produce cropland and pasture has destroyed approximately 7000 hectares of Tasmanian wetlands, i.e. approximately 35% of the pre-European area of wetlands. The impoundment of natural lakes and water bodies for hydro-electrical power has had a significant effect on many of Tasmania's unique permanent wetlands, e.g. Lake Pedder and Lagoon of Islands (Tyler, 1976; Kiernan, 1985; Kirkpatrick and Tyler, 1988). Land fill, especially near cities and large towns, has altered the flow regimes of many estuarine wetlands throughout the State.

Drainage of wetlands has continued over the last 20 years. Visoiu (2000) found that 17% of the area of a sub-set of east coast wetlands surveyed by Kirkpatrick and Harwood (1981) had been at least partially drained between 1978 and 2000. It is possible that this has occurred over other parts of Tasmania.

More recently a change in land use from pasture to cropping in some areas of Tasmanian has the potential to cause severe indirect changes to the natural water regimes of many wetlands. Strategies outlined in the recently published 'Water Development Plan for Tasmania' (Department of Primary Industries, Water and Environment, 2001) emphasise the importance of increasing the number of dams to support larger irrigation systems in agricultural areas within the State. Indirect non-ecological effects from dams and irrigation systems to wetland water regimes have been recorded in many wetlands systems throughout Australia (see Finlayson and Rea, 1999b). Water control systems within rivers have lead to a decrease in frequency, duration and volume of wetland flooding. Similarly, off-river storage systems can severely alter both ground and surface water flow. Due to this they are becoming increasingly recognised as a significant threat to the hydrology of their surrounding wetlands. The ecological consequences of these changes include: reduction in hydrological variability; salinity; altered creek courses; loss of native flora and fauna; and increased sedimentation; and binding of nutrients (Kingston, 1999, see Finlayson and Rea, 1999b).