CHAPTER 1

General introduction

1.1 Introduction

1.1.1 Worldwide trend of increasing coastal wetland degradation and loss

Wetlands are highly complex ecological systems which perform a range of valuable functions. These include fixation of solar energy and biomass production, storage and recycling of water, organic matter and nutrients, and provision of important migration, feeding and nursery habitats for waterbirds, fish, molluscs, crustaceans and other wildlife (Goodrick 1970; Williams and Watford 1997; Keddy 2000). Wetlands are declining in number and extent at a rapid rate in many parts of the world due to the widespread landscape modification that accompanies human population growth (Streever 1997). High rates of wetland degradation and loss in the worlds coastal regions are of particular concern, since these are among the most productive areas on earth, and also those most densely populated by humans (de Jong and de Jong 2002).

A major factor contributing to the decline of coastal wetlands in Australia and other countries has been the widespread historical installation of barriers, such as dikes or levees, barrages and floodgates, to exclude tidal water (Williams and Watford 1997; Crooks *et al.* 2002; Mauchamp *et al.* 2002; Nienhuis *et al.* 2002; Warren *et al.* 2002). Other contributing factors include the use of dredging to clear areas for shipping, infill of coastal marsh land, and the extensive use of drainage, to remove surface water, reduce flood or mosquito risk, and to allow new areas to be opened up for agricultural, urban or industrial development (Neckles and Dionne 1999; de Jong and de Jong 2002; Eertman *et al.* 2002; Nienhuis *et al.* 2002; Tanner *et al.* 2002; Warren *et al.* 2002; Wolters *et al.* 2005).

1.1.2 Impacts of drainage and tidal restriction

Drainage and exclusion of tidal flows can have detrimental effects on the ecological functioning of coastal wetlands and their associated estuaries. With the addition of drains and tidal barriers, changes occur in regularly-inundated tidal marsh areas. These wetlands become dependent on rainfall for inundation, less saline, more rapidly draining and more frequently dry (Williams and Watford 1997; Mauchamp *et al.* 2002; Nienhuis *et al.* 2002; Warren *et al.* 2002). Disruption of salinity gradients and changes to water depth and flooding regimes lead to changes in wetland vegetation communities, with less salt-tolerant and inundation-tolerant species able to establish and spread (Bart and Hartman 2000; Boumans *et al.* 2002; Chambers *et al.* 2003). Without tidal flushing, biota that depend on regular inundation with salty water, such as mangroves, some saltmarsh macrophytes and many invertebrates that live in the intertidal zone, often disappear (Dick and Osunkoya 2000; Bouzillé *et al.* 2001; Boumans *et al.* 2002; Warren *et al.* 2002; Laegdsgaard 2006). Barriers between wetlands and estuaries also disrupt the movement of fish, crustaceans and other biota (Middleton *et al.* 1985; Roman *et al.* 2002; Challacombe and Wilkinson 2003), and can impact commercial and recreational fisheries by excluding wetland areas that provide food resources and important nursery habitats. Waterbird populations are often negatively affected as these respond to wetland size, depth and permanence, food availability and availability of suitable vegetation for foraging and nesting (Dostine and Morton 2000; Reid and Brooks 2000; Neckles *et al.* 2002; Warren *et al.* 2002). Water quality can also be negatively affected by wetland degradation (Neckles and Dionne 1999). Potential acid sulfate soils also commonly occur under estuarine wetlands and where present their drainage leads to production and mobilization of acid leachate, which can cause vegetation dieback, soil surface scalding, pollution of downstream environments, and in some cases has contributed to substantial fish kills (Sammut *et al.* 1995; White *et al.* 1997; Russell and Helmke 2002; Warren *et al.* 2002).

1.1.3 Interest in tidal restoration for coastal wetland rehabilitation

As the ecological importance of coastal wetlands has become more widely recognised, especially over the past 40 years, interest in conserving and restoring these areas has increased (Pressey and Adam 1995; Warren *et al.* 2002). Tidal restoration for coastal wetland rehabilitation has attracted considerable interest in other countries, including North America, the United Kingdom, and Europe (de Jong and de Jong 2002; Warren *et al.* 2002; Wolters *et al.* 2005) and is now emerging as a focal point for wetland rehabilitation research in Australia (Sammut *et al.* 1995; White *et al.* 1997; Williams and Watford 1997; Dick and Osunkoya 2000; Johnston *et al.* 2003; Greenwood and MacFarlane 2006; Laegdsgaard 2006).

The typical assumption underlying tidal restoration projects is that once a natural tidal regime is reinstated, ecological communities characteristic of tidal marsh habitat will eventually return, and the ecological functions of these habitats will be restored (Warren *et al.* 2002). This assumption is not always met. In some cases additional measures are required before the restoration site can support the types of flora and fauna that are found at less disturbed sites. Examples include the addition of sediment to compensate for soil surface subsidence due to drainage and peat degradation, and the introduction of organisms to compensate for the effects of local population depletion (Zedler 2000; Williams and Orr 2002). Once these types of amendments have been made, tidal restoration is usually expected to place wetland communities on a general trajectory toward recovery (Whisenant 1999; Warren *et al.* 2002). However, whether recovery is considered to have been achieved, or to be achievable depends on the criteria used to judge success. Such criteria vary according to the project aims.

1.1.4 Typical approaches used to predict the effects of tidal restoration on macrophyte communities and set vegetation targets

Setting targets against which recovery can be monitored and reported is an important initial step in ecological rehabilitation projects (Whisenant 1999; Neckles *et al.* 2002; Wolters *et al.* 2005). In tidal restoration projects the reestablishment of a macrophyte community, similar in structure and composition to that occurring in a natural tidal marsh, is often seen as a key indicator of rehabilitation success (Brinson and Reinhardt 1996; Neckles *et al.* 2002). Once restored, this macrophyte community is expected to help support the reestablishment of tidal marsh macroinvertebrate, fish and waterbird populations, by providing habitat and food resources (Callaway *et al.*

1997; Neckles and Dionne 1999; Mauchamp *et al.* 2002; Roman *et al.* 2002; Warren *et al.* 2002).

Often, in areas where wetlands have been degraded by drainage and tidal restriction, there are other wetlands remaining that have more natural hydrological regimes. The vegetation at these sites can be used as a reference to predict which macrophyte species are likely to occur at rehabilitation sites after tidal-restoration, and the elevation ranges those species are likely to occupy (Neckles and Dionne 1999; Zedler *et al.* 1999; Neckles *et al.* 2002). Extrapolation from reference sites is the most widely used method for predicting the effects of tidal-restoration on macrophyte community composition and structure (Brinson and Reinhardt 1996; de Jong and de Jong 2002; Neckles *et al.* 2002; Warren *et al.* 2002; Wolters *et al.* 2005). However, predicting vegetation changes becomes more difficult when there is a lack of natural reference wetlands for comparison. One extreme example is the Netherlands, where diking and dredging have removed the vast majority of natural saltmarsh areas (de Jong and de Jong 2002).

Where historical data on community composition collected prior to drainage and tidal-restriction are available, these may be used to set vegetation restoration targets (de Jong and de Jong 2002). However, such historical data are frequently not available, and their use in setting restoration targets can often be inappropriate, particularly where the effects of landscape degradation on wetland structure or function are irreversible (de Jong and de Jong 2002; Mauchamp *et al.* 2002; Wolters *et al.* 2005). For example, restoration of historical conditions may be unachievable if surrounding areas have been extensively modified, altering landscape properties such as rainfall runoff rates, sedimentation rates or nutrient cycling processes at a larger scale (Poff 1997; de Jong and de Jong 2002; Mauchamp *et al.* 2002; Wolters *et al.* 2005), or where acid sulfate soils have become oxidised, permanently altering soil chemistry (Walker 1972; White *et al.* 1997; Stone *et al.* 1998; Rosicky *et al.* 2004). In these situations restoration of tidal exchange alone cannot be expected to result in vegetation communities returning to an historical, pre tidal-restriction, state.

1.1.5 Alternative approaches

Salinity and hydrological regime are widely recognised as the primary factors controlling the distribution and abundance of macrophyte species in coastal wetlands (Odum 1988; Keddy 2000; Laegdsgaard 2006). Where it is impossible or inappropriate to predict the effects of tidal restoration on community composition by extrapolating from reference sites or historical data, it may be helpful to assess the potential habitat ranges of individual species instead, with respect to salinity and inundation regimes, and to use this information to predict site suitability for species occurrence or survival under different tidal flow management strategies.

Macrophyte communities vary in composition and diversity between tidal wetlands along the estuarine gradient according to differences in water salinity (Odum 1988). These sites can range from euhaline wetlands inundated by marine waters (salinity >30 000 ppm), through polyhaline (~18 000-30 000 ppm) mesohaline (~5000-18 000 ppm) and oligohaline (~500-5000 ppm) wetlands, to freshwater (<500 ppm) tidal wetlands (Odum 1988). Salt marshes, occurring at the coastal extremity, are typically species-poor, dominated by a small number of specialist halophytes (Laegdsgaard 2006) while freshwater wetlands can support much more diverse communities, particularly since many salt-tolerant macrophytes show an inclusive niche structure, and will grow well at a range of salinities lower than the maximums tolerated (Odum 1988; Keddy 2000). Within wetlands, macrophyte distributions are determined to a large extent by inundation regime, with species often occurring within more or less distinct elevation zones (Keddy 2000; Crooks *et al.* 2002; Pennings *et al.* 2005; Laegdsgaard 2006). The lower limit of a species elevation range is usually most strongly affected by tolerance to inundation or waterlogging, while the upper limit is often determined by a combination of tolerance to exposure, or drying, and interspecific competition (Keddy 2000; Siebentritt and Ganf 2000).

Some studies have quantified relationships between wetland species distribution and abiotic factors, such as salinity, watertable depth, anoxia and hydroperiod, using survey methods alone (Bouzillé *et al.* 2001; Álvarez-Rogel *et al.* 2006). Where this has been done, species presence is associated with particular environmental conditions, and a predictive model can be created based on the assumption that the measured factors directly affect species distribution (Álvarez-Rogel *et al.* 2006). However, correlations between species distributions and environmental factors do not prove causal relationships, and in wetlands, substrate elevation, salinity, hydroperiod and other environmental factors are often closely correlated with each other (Keddy 2000), making it difficult to determine their individual effects. This problem is bypassed when field surveys are used to generate hypotheses about the effects of environmental factors on species distributions, and these hypotheses are then tested in controlled experiments (Clarke and Hannon 1970; Grillas *et al.* 1993; Bart and Hartman 2002). This approach is likely to result in more robust models for predicting species distributions relative to specific environmental factors.

1.1.6 Applicability of experimental data in predicting species field distributions

Pot experiments can be used to obtain data on how individual environmental factors affect plant growth and survival, and to test for differences in species environmental tolerance ranges. These data can then be used to predict differences in species distributions in the field. There are some limitations to this approach. For example, the tolerance of a species toward an individual environmental variable can vary between experiments, since tolerance ranges can be affected by plant growth stage, as well as the effects of other abiotic and biotic variables (Maas 1977; Gorham 1996; Miyamoto 1996; Siebentritt and Ganf 2000). Therefore, species tolerance limits should be considered in the context of the particular set of growing conditions under which they were determined rather than as absolute values (Maas 1977; Miyamoto 1996). Also, these types of experiments are usually limited to testing the response of species toward one, or a small number of, environmental variables only and may not take into account possible interactions between the effects of these and other variables (Siebentritt and Ganf 2000; Jolly *et al.* 2008). Despite these limitations, experimental data can be used to rank species according to their tolerance to variables of interest, provided species tolerance ranges have been determined under comparable conditions and using standardised methods (Maas 1977; Jolly *et al.* 2008). These relative tolerance rankings can be used to make some basic predictions about species distributions relative to environmental gradients.

Experimental data on wetland macrophyte salinity and inundation tolerance ranges have been used successfully to explain species distribution patterns in the field (Clarke and Hannon 1970; Grillas *et al.* 1993; Howard and Mendelssohn 1999; Espinar *et al.* 2005; van der Valk 2005). For example, Clarke and Hannon (1970) conducted experiments on a variety of Australian mangrove swamp and saltmarsh species to determine the effects of salinity and waterlogging on species germination and establishment success. It was found that patterns in distribution and abundance of species relative to site salinity and waterlogging gradients in the field were closely related to their performance in culture relative to these factors (Clarke and Hannon 1970). Similarly, Espinar *et al* (2005) found that the relative salt tolerance rankings of salt marsh species derived from laboratory germination experiments concurred with rankings of the average salinity levels recorded in field habitats occupied by those species throughout the growing season. Similar results were found by Grillas *et. al* (1993) and Howard and Mendelssohn (1999) who investigated the salt tolerance ranges of oligohaline marsh plants. Van der Valk (2005) compared a number of pot experiments assessing the relative depth tolerances of wetland macrophyte species, with field studies reporting on species relative elevation ranges. He concluded that pot trial results usually confirm that interspecific differences in depth tolerance are the primary cause of variance in species distributions relative to elevation (van der Valk 2005).

1.2 Project outline

Along the east coast of Australia many tidal wetlands have become degraded due to drainage and the installation of tidal barriers (Williams and Watford 1997). The Clarence River floodplain in Northern NSW is one area heavily affected by drainage and floodgates, and will be the focus of this project. Small drains and tidal barriers were initially installed by landowners in the early 1900s, to reduce flooding and improve agricultural productivity (Middleton *et al.* 1985; Bowling pers. com.). However, following severe floods in the 1950s the NSW Government initiated a systematic flood mitigation program, which lasted into the 1970s and resulted in extensive areas being drained and floodgates put in place on a number of tidal creeks (Pressey and Clancy 1979; Pressey and Middleton 1982). The development of floodgate management plans is currently being considered for a number of wetlands on the Clarence River floodplain, with the intention of restoring a limited degree of tidal flow (Walsh and Copeland 2004).

The main objectives of the Clarence River wetlands rehabilitation project are to reduce land degradation and improve water quality by minimising the oxidisation of acid sulfate soils, and to increase fish habitat by removing barriers to fish passage (Walsh and Copeland 2004). However, these goals must be balanced with other management objectives including appropriate site vegetation management. Incursions of salt water may lead to the loss of some freshwater macrophyte species that currently provide habitat for a variety of waterbirds, and this is an issue of concern to some land managers. Maintenance of valuable wetland pasture species is also a high-priority management objective at many sites.

Individual wetlands are likely to have different optimal strategies for floodgate management, depending on the goals of the relevant site managers. However, although effective vegetation management is a priority at all potential rehabilitation sites, there is little information available for predicting how floodgate management will affect the structure and composition of existing macrophyte communities. Due to the extent of drainage and tidal restriction in the study area, there is a lack of reference sites that could be used to predict the effects of tidal restoration on community composition. Historical records on site vegetation are sparse, and make little reference to species composition. Information on the salinity and inundation tolerance ranges of common macrophyte species found at these sites would therefore be extremely useful in the development of future floodgate management plans.

1.2.1 Aims

The broad aim of this thesis is to determine how the changes to floodgate management currently proposed for wetlands on the Clarence River floodplain are likely to affect the growth and survival of macrophyte species at potential rehabilitation sites. More specifically this thesis will:

1) Examine the composition of macrophyte communities in wetlands along the Clarence River floodplain, describing any patterns in species composition relative to salinity, water depth and other relevant site factors.

2) Identify the most abundant and widespread species in floodgate-affected wetlands, particularly in those sites that have become shallower and less brackish, and compare species salinity and depth ranges.

3) Determine experimentally the salinity tolerance ranges of focal species, i.e. those identified as widespread and abundant in floodgate-affected wetlands on the Clarence River floodplain.

4) Test experimentally the tolerances of focal species to a combination of salinity and water depth treatments.

5) Develop a model framework for predicting the effects of tidal restoration on coastal wetland macrophyte communities. This framework should not require vegetation composition data from reference wetlands or historical sources.

6) Predict the effects of changes in floodgate management on macrophytes in Clarence River wetlands by applying this general tidal restoration model framework to relevant site and species data, including the survey and experimental data obtained in this project and in other studies.

1.3 Thesis structure

Chapter 2 reports on a survey in which aims one and two are addressed. Macrophyte species composition and cover were assessed in wetlands across the Clarence River floodplain, to determine which species occur at these sites and to compare their distributions with respect to environmental and management variables, including soil and water salinity. Based on this survey work five focal species, identified as widespread or abundant in secondarily fresh or oligohaline floodgate-impounded wetlands, were selected for a more in-depth investigation of their respective salinity and depth tolerance ranges. The third aim is addressed in Chapter 3, in which a controlled tub experiment in a glasshouse was used to evaluate the salinity tolerance ranges of each of the focal species. In Chapter 4 the fourth aim is addressed, in a second outdoor tub experiment where the responses of the focal species to increases in both water depth and salinity are investigated.

The final two aims are addressed in Chapter 5. Here a broadly applicable model framework is identified that can be used for predicting the effects of tidal restoration on macrophyte community composition, without reliance on historical or reference site data. This model framework is then applied to Clarence River wetland site and species data sets, and predictions are made about the effects of floodgate manipulation on the persistence of focal species at potential rehabilitation sites.

Chapter 6 presents a synthesis of the research. This chapter describes the strengths and weaknesses of the approach that was used here to predict effects of tidal restoration on wetland macrophyte species, and also ways that the Clarence River wetland rehabilitation model can be tested and refined once floodgate management plans are put into action.

CHAPTER 2

Assessment of patterns in macrophyte distribution with respect to environmental gradients on the Clarence River floodplain

2.1 Introduction

On the east coast of Australia, many wetlands have been altered by the effects of the widespread land clearing and drainage that has occurred since European settlement. The majority of wetlands on the NSW North Coast (including those on the Richmond, Clarence and Macleay River floodplains) were drained during the 1950s to late 1970s for flood mitigation, to improve agricultural productivity, and to make land more suitable for development (Pressey and Middleton 1982). Goodrick (1970) estimated that by 1970 47% of wetlands in this region had been lost or altered through drainage. This figure is likely to have increased since that time, since Pressey (1987) reported that between 1970 and 1986 a substantial amount of government funding had been dedicated to flood mitigation works, and also that private parties had separately cleared and drained a number of wetlands.

Floodgates are a feature of many coastal flood mitigation drains on the NSW North Coast, functioning as one-way barriers that facilitate the rapid removal of floodwaters while preventing backflooding or tidal exchange (Walsh and Copeland 2004). A 1996 inventory of barriers preventing tidal exchange and fish passage in coastal areas reported the presence of 1037 floodgates in NSW (Williams and Watford 1997), with 630 (i.e. more than half) of these located on the North Coast (Walsh and Copeland 2004). Over-drainage and tidal restriction of wetlands on the North Coast have had a number of detrimental side-effects (Pressey and Middleton 1982). The most direct include the complete elimination of some floodplain wetlands and reductions in the size and permanence of others, causing loss of wetland flora and reduced habitat for fauna, including waterbirds and fish (Pressey and Middleton 1982).

Other secondary impacts of overdrainage and flow restriction by floodgates have now become apparent and are of considerable concern. These include the widespread oxidation of potential acid sulfate soils (PASS) due to lowered water tables, resulting in acidification of land and dieback of surface vegetation (Walsh and Copeland 2004). The release of acidic and iron- and aluminium-rich runoff from acid sulfate soil (ASS) areas after rainfall has had negative impacts on aquatic biota downstream, contributing to red-spot disease in fish and fish kill events (Sammut *et al.* 1995; White *et al.* 1997; Naylor *et al.* 1998; Stone *et al.* 1998; Tulau 1999; Russell and Helmke 2002). Wetland vegetation has also been replaced in many drained areas by pasture grasses and other inundation intolerant vegetation types. These plants cause problems by rapidly dying and decomposing during flood events, resulting in extremely low dissolved oxygen content in run-off water. This ‘black water’ is another factor that has contributed to fish kills along the NSW North Coast after periods of high rainfall and flooding (Pressey and Middleton 1982; Middleton *et al.* 1985; Walsh and Copeland 2004).

While some of the environmental risks of overdrainage, including high acidification potential, were recognized for the NSW North Coast as early as the 1960s (Walker 1972), rehabilitation of overdrained and floodgate-affected wetlands has only recently become a high priority for land managers in the region (Walsh and Copeland 2004). Options for the rehabilitation of drained wetlands in this area include the modification and management of floodgates and other structures to raise water tables and to allow a controlled amount of tidal flushing to take place (Walsh and Copeland 2004). The goals of these rehabilitation strategies include reduced oxidation of PASS, increased water quality both within wetlands and downstream, increased wetland vegetation cover, and increased available habitat for waterbirds, fish and other aquatic biota (Walsh and Copeland 2004).

Vegetation assessment and management are very important components of the wetland rehabilitation process. Wetland plants provide productive and highly important sources of food and shelter for a range of floodplain fauna, including invertebrates, amphibians, birds and fish, as well as performing a number of other important roles, such as nutrient cycling, and maintenance of water quality by filtering sediments and nutrients from overland flows (Pressey and Middleton 1982). Over time, the maintenance of adequate wetland vegetation cover often leads to the accumulation of a peat layer, which can help keep the underlying soil moist and therefore help to prevent the conversion of PASS into ASS (Slavich 2000). Because dissolved oxygen levels in water can decline dramatically in the presence of rotting plant material, maintaining wetland plant communities in low-lying areas may also improve the dissolved oxygen content of run-off water after flood events, since wetland plants are more tolerant of inundation than terrestrial species.

Allowing tidal water into floodgate-affected wetlands is likely to result in increases in water salinity as well as water depth and permanence at rehabilitation sites. These changes are expected to increase the extent and permanence of affected wetlands, and therefore increase the area of habitat available for wetland plant communities on the NSW North Coast. However, some sites that were tidal oligohaline to mesohaline wetlands before the installation of flood-mitigation drains and floodgates are now secondarily fresh or oligohaline sites respectively, with higher drainage rates and lower flooding frequencies than before (Clarence River County Council 1978; Beveridge 1998; Wilkinson 2003). Some of the plant species currently occupying these sites may not withstand the changed conditions that will be imposed by opening floodgates, and this is of concern to wetland rehabilitators. In addition, not every floodgate-affected site would have been subject to regular tidal inundation before drainage occurred as some have been artificially connected to nearby tidal waterways through the construction of deep drains. Opening floodgates on these drains to allow wetland inundation in these situations may result in sites becoming more brackish than they were prior to drainage, which could also have a negative effect on some plant species.

Some plant species found in North Coast floodplain wetlands currently provide a useful and productive pasture resource for cattle, including *Paspalum distichum* L. (Rose *et al.* 2006). Others provide habitat for particular species of waterbirds, including the floating-leaved *Nymphaea caerulea* Savigny (synonym *N. capensis* Thunb.), which is used by the Comb-crested Jacana as a foraging platform, and *Eleocharis equisetina* C. Presl which is grazed by swans. Because of the value placed on existing plant communities at these sites, information is needed on how letting tidal water into these wetlands (for ASS remediation purposes) will affect the species that occur there, particularly those perceived to be of high ecological importance or of economic value. While the ecological value of these sites is of prime importance from a conservation perspective, maintaining the economic value of these sites is an important practical consideration, since this will affect the willingness of landholders to trial the proposed wetland rehabilitation methods on their land. For the Clarence River catchment in particular, around 98 % of coastal floodplain wetlands occur on private properties and are managed for cattle grazing (Pressey 1987). Floodgate management plans need to take into account the vegetation management goals of all stakeholders.

In this project the main focus is on the vegetation found in floodgate-restricted wetlands on the Clarence River floodplain, and how well we can predict the effects of adding or reintroducing tidal flows on plant communities at these sites. To predict how extant plant communities will be affected by changed floodgate management, it is necessary to first assess which species are currently found at potential rehabilitation sites. To make predictions about whether the cover of particular species will increase or decrease once site salinity and inundation regimes are changed, it is also necessary to look at the current habitat ranges of these species, and to assess what their salinity and inundation tolerance ranges are. A literature review was conducted as the initial step in this process, assessing site vegetation and environmental data from past field surveys.

2.1.1 Previous vegetation surveys

Survey data on wetland plant species distributions prior to drainage and tidal exclusion can serve as a useful reference for predicting the effects of tidal influx on wetland macrophyte species composition. Unfortunately those pre flood-mitigation vegetation records that are available for Clarence estuary wetlands contain information that is both patchy and also very general, referring to broad vegetation categories such as 'open swamp' rather than identifying particular plant species (Cibilic 2002), which limits their reference potential. However, there are post flood-mitigation vegetation survey reports available for wetlands on the Clarence River floodplain, and these do report on which species were found to be common as well as indicating some general trends in species composition with respect to environmental gradients (Goodrick 1970; Pressey and Clancy 1979; Pressey 1987, 1989a; Keith and Scott 2005). Species reported to have been particularly common and widespread in wetlands on the Clarence River floodplain include: *Eleocharis equisetina, Eleocharis minuta* Boeck., *Paspalum distichum, Eleocharis sphacelata* R. Br., *Juncus usitatus* L. A. S. Johnson, *Juncus polyanthemus* Buchenau, *Phragmites australis* (Cav.) Trin. ex Steud., *Persicaria* species, *Ludwigia peploides* (Kunth) Raven, *Melaleuca quinquenervia* (Cav.) S. T. Blake and *Casuarina glauca* Sieber ex Sprengel, amongst others (Pressey and Clancy 1979; Pressey 1989a, b).

While these survey reports provide a useful guide to species found in the area, the environmental data reported are sparse, and, therefore, the environmental tolerance ranges of particular species can only be loosely defined. Fresh and oligohaline wetland plant communities have been grouped together in existing vegetation classifications (for example Pressey 1989a) with no quantitative data included that could be used to investigate individual species salinity ranges. While reference is made by Keith and Scott (2005) to the occurrence of particular species, such as *Sporobolus virginicus* (L.) Kunth, in coastal saltmarsh, or other species, such as *Casuarina glauca, Juncus kraussii* Hochst. subsp. *australiensis* (Buchenau) Snogerup and *Phragmites australis*, in areas that are influenced by saline groundwater, no specific soil or water salinity measurements are mentioned. Similarly, no information was found on species distributions with respect to acidity; this is another variable likely to affect establishment and growth of species in Clarence River coastal floodplain wetlands since ASS are a common feature of these sites.

However, Pressey and Clancy, in their 1979 survey, did assess macrophyte habitat ranges with respect to some aspects of water regime, commenting on the distributions of dominant species relative to site differences in depth, duration and frequency of flooding in freshwater wetlands (Pressey and Clancy 1979). These wetlands were often dominated by dense, often monospecific, stands of vegetation with species composition varying along a water depth gradient. In order of relative elevation and/or inundation tolerance, *C. glauca* was found to occur at the upper boundaries of freshwater wetlands, sometimes followed by *J. polyanthemus* at slightly lower elevations*,* with *Philydrum lanuginosum* Banks & Sol. Ex Gaertn., *Paspalum distichum* (referred to as *P. paspaloides*) and *L. peploides* found in lower, wetter areas, then *Maundia triglochinoides* F.Muell. or *Triglochin procerum* R. Br. and *E. sphacelata* or *E. equisetina* in even more frequently inundated areas*. Nymphaea caerulea* Savigny (synonym *N. capensis* Thunb.) occurred in the areas with highest water permanence (Pressey and Clancy 1979). It was also reported that species occupied narrower and more distinct elevation zones at wetlands that were more permanently inundated and had more stable water levels (Pressey and Clancy 1979).

2.1.2 Current vegetation survey

The following survey was designed and conducted in 2005, to address the need for more detailed information on species distributions with respect to environmental traits. As my key interest was in predicting the effects of floodgate management on existing vegetation, the primary focus areas were site salinity and flooding regimes, and how these were related to wetland plant community composition and species distributions. Flooding regime, being temporally variable, is something that cannot be measured and described in a single survey. In this case, there were no temporal data on water levels available to allow a direct comparison of previous flooding regimes between these sites. In addition, elevation above sea level (mAHD) could not be considered a reliable indicator of flooding regime here, due to the variety of tidal barriers, drains and water retention structures found at the different sites. However, information on species distributions relative to the aspects of flooding regime that could be measured, such as species ranges relative to high and low water marks, and water depth or soil moisture content at time of sampling, can give some indication of the relative inundation tolerances of different species and were considered here. Low pH due to the presence of ASS, and grazing by cattle are other factors that may affect vegetation composition and species distributions at these sites (Blanch and Brock 1994; Gough and Grace 1998; Rosicky *et al.* 2006; Geho *et al.* 2007), and so these were also considered in the survey.

2.1.3 Aims

The aims of this survey were to:

1. Assess macrophyte species composition in wetlands along the Clarence River floodplain, looking for patterns in the distribution and relative cover of species with respect to environmental and management variables, particularly soil and water salinity and pH, relative elevation, water depth, soil moisture and grazing intensity;

2. Identify the most widespread and abundant species of floodgate-affected wetlands, and investigate the habitat ranges of these species, along with those *E. equisetina, N. caerulea* and *P. distichum;* species of importance to managers of wetlands in the study area, and;

3. Formulate hypotheses about the potential effects of floodgate manipulation on the distributions of these species.

2.2 Materials and methods

2.2.1 Study area

The Clarence River floodplain is located on the New South Wales (NSW) North Coast (refer to Figure 2.1). This river has the largest catchment area of any coastal river in south-eastern Australia, covering an area of approx. 22 700 km^2 (Healthy Rivers Commission 1999). The climate of the area is humid and sub-tropical and average annual rainfall is 992 mm, with most rainfall occurring from late spring through summer (Bureau Of Meteorology 2006: NSW Agriculture Research Station, 46 years of data, between 1917 and 2006). The survey area extends from the river mouth at Yamba (-29°26’S; 153°22’E) inland to Grafton (-29°40’S; 152°56’E). Grafton lies approximately 55 km upstream of Yamba, and is located downstream of the tidal limit of the Clarence River, which ranges up to 108 km upstream from the river mouth (Healthy Rivers Commission 1999). Wetlands in this area of the floodplain vary from fresh to saline, depending on distance upstream and degree of tidal connectivity. Some backswamps receive river water only during flood events when the river is fresh and overtops its levees due to high volumes of rainfall runoff, while other wetlands abut the river directly and are inundated regularly by tides.

Nine wetlands were selected for the survey (Figure 2.1). These wetlands were chosen to represent the range of water salinities found in wetlands on the floodplain and were loosely categorized as fresh (<500 ppm), fresh-brackish (500–20 000 ppm) or saline (>35 000 ppm) (Table 2.1). After initial investigation, the nine wetlands were subdivided into a total of 17 different study sites (Figure 2.1) based on differences in salinity, water management, and grazing management (Table 2.1).

Seven and eight sites were included in the fresh and fresh-brackish categories respectively (Table 2.1). Chaffins Swamp (site 3) was considered likely to be the freshest of these, due to lack of tidal connectivity and inputs of fresh water from the Coldstream River (Figure 2.1). Only two sites were included in the saline category (sites 16 and 17). These sites were located at the edge of Lake Wooloweyah, closest to the Clarence River mouth (Figure 2.1). Saline sites were of lesser interest because they contain halophytic saltmarsh communities, rather than some of the other less salt-tolerant vegetation types that rehabilitation managers are concerned may be negatively affected by inundation with brackish water. However, these saltmarsh sites were included to represent the upper limit of the floodplain salinity gradient.

Some of the selected study sites had relatively natural inundation regimes, such as site 10 located adjacent to the Broadwater (Figure 2.1), while others had been drained extensively with levees and floodgates preventing tidal exchange, including sites in Edwards Creek wetland and Everlasting Swamp (Figure 2.1). Sites 11 and 12 at the Little Broadwater wetland and site 9 at the Broadwater wetland had recently had their floodgates modified to allow some tidal exchange (Table 2.1).

Grazing was considered likely to influence vegetation cover and composition, so information on past and present grazing use was obtained from landholders. As quantitative data on past grazing intensity were not available, sites were ranked according to current grazing strategy into one of three grazing intensity categories: set stocking (highest grazing intensity), cell grazing (intermediate grazing intensity), or not grazed (Table 2.1).

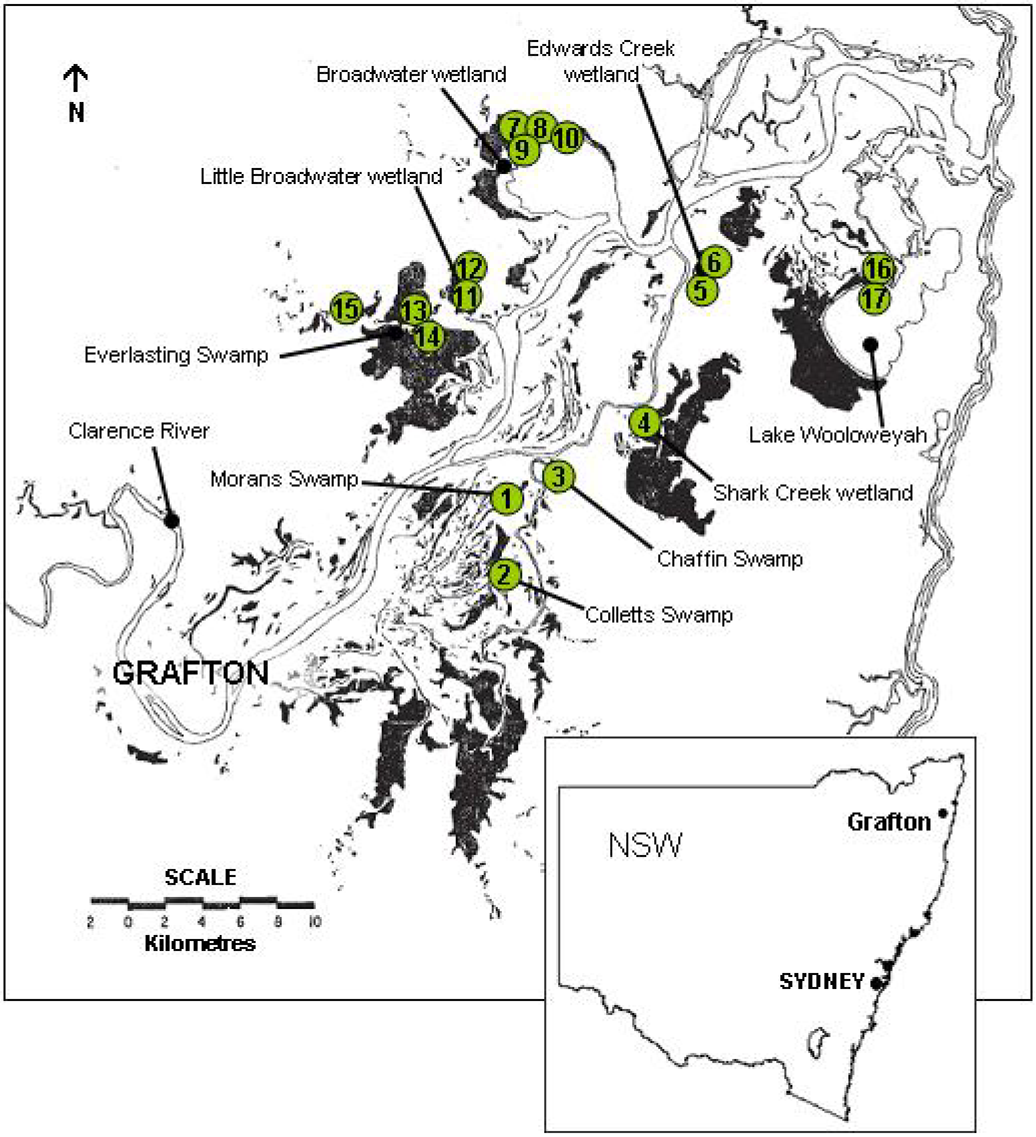


Figure 2.1. Clarence River floodplain wetlands and location of survey sites (based on map from Pressey (1987)).

Table 2.1. Clarence floodplain wetland sites surveyed in 2005.

Site No.	**Site name**	**Easting: Northing** [UTM zone 56, GDA 94]	**Salinity category**	**Grazing category**	**Water management**
1	Morans Swamp	0508117:6717649	Fresh	Set stocking	Floodgate, but river water allowed in when fresh.
2	Colletts Swamp	0509244:6715222	Fresh	Set stocking	Floodgate, but river water allowed in when fresh.
3	Chaffins Swamp	0511900:6718970	Fresh	Set stocking	No floodgate. No drain in area sampled. Fresh water from Coldstream River. Receives water from Clarence River only when in flood.
4	Shark Creek Wetland	0518598:6729555	Fresh	Not grazed	No floodgate. Receives water from Clarence River only when in flood.
5	Edwards Creek	0520342:6739330	Fresh	Set stocking	Floodgate, always kept closed to exclude brackish water.
6	Edwards Creek	0520496:6739313	Fresh	Not grazed	As above.
7	Broadwater, freshwater channel	0509373:6744995	Fresh	Cell grazed	Freshwater channel, above extent of tidal influence.
8	Broadwater	0509373:6744995	Fresh-Brackish	Cell grazed	Bounded by tidal exclusion levee, occasionally overtopped by brackish river water but usually contains ponded rain water
9	Broadwater	0509373:6744995	Fresh-Brackish	Not grazed (grazing exclosure)	Bounded by tidal exclusion levee, but tidal flows recently reintroduced (2004/2005). (Trial tidal gate in place).
10	Broadwater	0510943:6746408	Fresh-Brackish	Cell grazed	Natural, tidal water never excluded
11	Little Broadwater	0507571:6737430	Fresh-Brackish	Not grazed (grazing exlosure)	Bounded by tidal exclusion levee and floodgate. Tidal water reintroduced since 2002 floodgate opening trial.
12	Little Broadwater	0507424:6738988	Fresh-Brackish	Set stocking	As above.
13	Everlasting Swamp	0505141:6734789	Fresh-Brackish	Set stocking	Drained with floodgate. Tidal water excluded.
14	Everlasting Swamp, deep drainage channels	0505141:6734789	Fresh-Brackish	Set stocking	As above.
15	Everlasting Swamp, Teal lagoon	0505141:6734789	Fresh-Brackish	Set stocking	As above.
16	Wooloweyah, natural	0530395:6738542	Saline	Set stocking	Natural, water never excluded.
17	Wooloweyah, gated	0530764:6739431	Saline	Set stocking	Drained with floodgate, but tidal flows recently reintroduced.

2.2.2 Sampling vegetation

Data on vegetation and environmental variables were collected from within 5 m × 5 m quadrats, with a total of 77 sampling quadrats set up across the 17 sampling sites. Prior to sampling, sites were stratified into elevation zones based on relative wetness and depth of standing water, if present (Figures 2.2 and 2.3). These were: the 'above edge' zone, just above the visible high water line; the 'edge' zone, including dry areas, often with a visible salt crust, found immediately below the high water line; the 'damp' zone characterised by wet mud without standing water; the 'shallow' zone, containing shallow water up to 15 cm deep; and the 'deeper water' zone, including all areas with standing water over 15 cm depth present. Since standing water was not present at all sites during the survey, and sites varied in depth and drainage characteristics, the range of depth zones differed between sites. At each site a transect was positioned across all elevation zones, from above the high water mark to the deepest point accessible, with a quadrat placed centrally within each elevation zone.

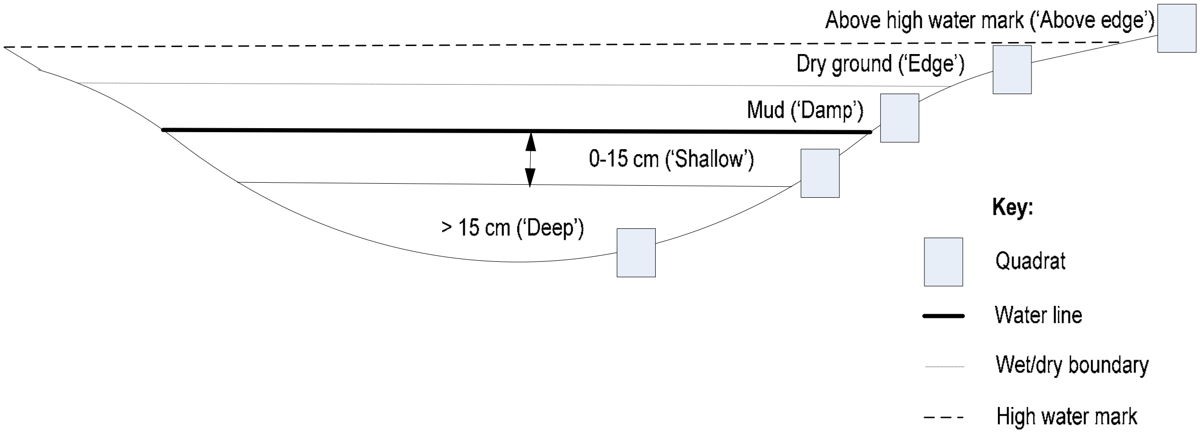


Figure 2.2. Stratification of sampling within wetlands according to elevation and water depth.

Figure 2.3. Sample quadrats; **a)** ‘above edge’ sample, Morans Swamp, and **b)** ‘edge’ sample, Lake Wooloweyah.

Figure 2.3. continued. Sample quadrats; **c)** ‘damp’ zone, Shark Creek wetland, and **d)** ‘shallow’ sample, Everlasting Swamp.

Figure 2.3. continued. Sample quadrats; **e)** 'deeper water' sample, Little Broadwater wetland.

The identity, percent foliage cover and approximate mean canopy height of each macrophyte species was noted in every quadrat. As vegetation within these wetlands was typically uniform within elevation zones with very low species richness (Figure 2.3), this sampling regime was considered adequate for assessing species distribution and composition within zones. However, if areas of different vegetation occurred within an elevation zone these were sampled separately. Identification followed Harden (1992; 1993, 2000, 2002). Where field identification of species was not possible, voucher specimens were collected, pressed and then identified if possible at a later date. Voucher specimens were lodged in the N.C.W. Beadle Herbarium at the University of New England, Armidale.

2.2.3 Sampling environmental variables

Environmental data were obtained from all quadrats and included soil salinity, pH and moisture content, and the salinity, pH and depth of standing water where present. Where standing water was present, depth in each quadrat was measured to the nearest five cm using a ruler and/or weighted stringline suspended from a rod. The salinity and pH of standing water were measured *in situ* using an YSI-30 temperature compensated salinity meter and a TPS MC81 temperature compensated pH meter respectively. Soil pH was also measured *in situ,* because, at sites where potential acid sulfate soils (PASS) occur, oxidation processes after core collection may alter soil pH if measurement is delayed (Stone *et al.* 1998). Soil pH samples were extracted from a depth of 20cm near the centre of each quadrat using a soil corer. A teaspoon-sized amount of this soil was mixed with water to form a 1:5 solution. The pH of the soil slurry was then measured using the TPS MC81 pH meter.

Soil samples were also collected for laboratory assessment of moisture content and surface salinity. Soil moisture content was measured volumetrically using 3 cm wide × 20 cm deep cores obtained from the centre of each quadrat. These cores were sealed into plastic bags in the field to prevent moisture loss. In the laboratory bagged samples were weighed to the nearest mg. These were then transferred into metal tins, oven dried at 105^{o}C for 96 hours, then reweighed without tins. Bags were individually weighed, and bag weights subtracted from initial wet core weights, then percentage weight loss due to drying was calculated.

To measure soil surface salinity I collected one 5 cm diameter × 5 cm deep core from the centre of each quadrat. Surface soil was sampled because salt accumulates close to and on the soil surface, particularly around the wetland perimeters where a visible surface crust often occurs, and concentration of salt in the shallow rooting zone may affect the establishment and survival of vegetation in these areas. Cores were allowed to air dry in the laboratory, then homogenised by grinding. A 1:5 soil/water suspension was prepared for each sample by weighing 20g of soil into a specimen jar then adding 100ml of deionised water. Jars were placed on a mechanical shaker for 1 hour, then allowed to settle for half an hour before the electrical conductivity (dSm^{-1}) and salinity (ppm TDS) of the soil suspension were measured using the YSI-30 salinity meter.

While the above method measured the quantity of salts present per unit weight of air dried soil, the concentration of salts in the soil water (i.e. saturation extract or pore-water salinity) is typically used when interpreting the effects of salinity on plant growth and survival (Slavich and Petterson 1993; Shaw 1999; Hazelton and Murphy 2007). Saturation extract salinities were calculated here by multiplying 1:5 soil/water suspension salinity values of each sample by a standard conversion factor, based on soil texture (Hazelton and Murphy 2007). This method makes the assumption that texture (Northcote 1979) is indicative of the water-holding capacity of the soil (Slavich and Petterson 1993; Hazelton and Murphy 2007). I analysed the texture of each soil sample, using the methods of Northcote (1979), to determine the appropriate conversion factor for multiplying my soil 1:5 extract salinities up to saturation extract equivalent. The conversion factor for peat soils is lower than for other soil types (Hazelton and Murphy 2007). Since soil texture is not a reliable indicator of soil organic matter content, the loss-on-ignition method was used to compare the organic matter content (% weight) of a random subset of 24 of the 77 soil samples (Nelson and Sommers 1996).

2.2.4 Analyses

Ordination methods were used to explore patterns in species distribution with respect to environmental variables. Initially an unconstrained ordination, Detrended Correspondence Analysis (DCA), was carried out on the species cover data to identify the main axes of variation in vegetation composition across samples, and to determine whether linear or unimodal ordination methods would be most appropriate for the data (Lepš and Šmilauer 2003). All species, regardless of rarity, were included and no data transformation was applied. While unconstrained ordinations such as DCA provide a summary of the overall pattern of variation in species composition across quadrats, some of the variability related to measured environmental variables can be missed (Lepš and Šmilauer 2003). Conversely, while constrained methods are better for explicitly examining relationships between vegetation composition and explanatory variables including environmental data (Ter Braak 1986), the main part of the variability that is not related to the measured explanatory variables can be masked (Lepš and Šmilauer 2003). Both approaches were used here to circumvent these issues. Canonical Correspondence Analysis (CCA) was selected for the constrained ordination after examination of DCA results showed that unimodal methods would be most appropriate for this dataset (Lepš and Šmilauer 2003).

Six environmental variables were included in the unconstrained analysis: depth zone (represented by five binary categories – above edge, edge, damp, shallow water and deep water), water depth (cm), soil moisture (volumetric % weight), soil salinity (ppm TDS, 1:5 extract), grazing strategy (three binary categories – ungrazed, cell grazed and set stocking), and soil pH. In the final constrained analysis the number of environmental variables was reduced to four, in order to remove an arch effect caused by the high degree of correlation between the variables water depth (cm), soil moisture, and depth zone. Rerunning the analysis with these three variables condensed into a single variable termed 'depth class' removed the arch effect and improved interpretability of the CCA triplot. The new variable was a semi-quantitative estimate of sample site wetness on a scale from one to five, corresponding with the five binary depth categories previously used: 1= above edge, 2 = edge, 3 = damp mud, 4 = shallow water and 5 = deep water. Forward selection of environmental variables was carried out to determine how much of the variability in community composition could be attributed to each. Statistical significance of the forward-selected variables was tested using Monte Carlo simulations (499 permutations). All ordinations were performed using the CANOCO statistical software package (Ter Braak and Šmilauer 2002).

2.3 Results

2.3.1 Species richness and common species

Seventy one species were recorded from a total of 77 quadrats across the 17 sites. The full list of species names with relevant authorities is given in Appendix 1, along with a list of sites where each was found. Species richness was typically low within sample quadrats, with most containing fewer than five species (Table 2.2). Both species richness (Table 2.2) and total vegetation cover (Figure 2.4) decreased with depth. Higher species richness per quadrat was also found at freshwater sites compared to brackish and saline sites, and at sites subject to cell grazing, compared to those that were set stocked or not grazed (Table 2.2).

Table 2.2. Species richness of quadrats according to site category.

Variable	Category	Sites	Quadrats	Species	Species per quadrat (mean ± std. dev.)
Depth zone	Above edge	11	13	27	4.46 ± 2.85
	Edge	11	13	20	3.15 ± 1.72
	Damp/waterlogged	12	23	32	3.96 ± 2.58
	Shallow (<15 cm)	9	18	18	2.33 ± 1.57
	Deeper water (>15 cm)	9	10	14	2.22 ± 1.20
Salinity	Fresh	7	21	46	4.24 ± 3.16
	Fresh-brackish	8	48	42	3.08 ± 2.30
	Saline	2	8	13	3.25 ± 1.64
Grazing	Ungrazed (low intensity)	3	17	20	2.59 ± 1.70
	Cell grazed (intermediate)	4	14	31	4.29 ± 2.46
	Set stocking (highest)	10	46	55	3.46 ± 2.71

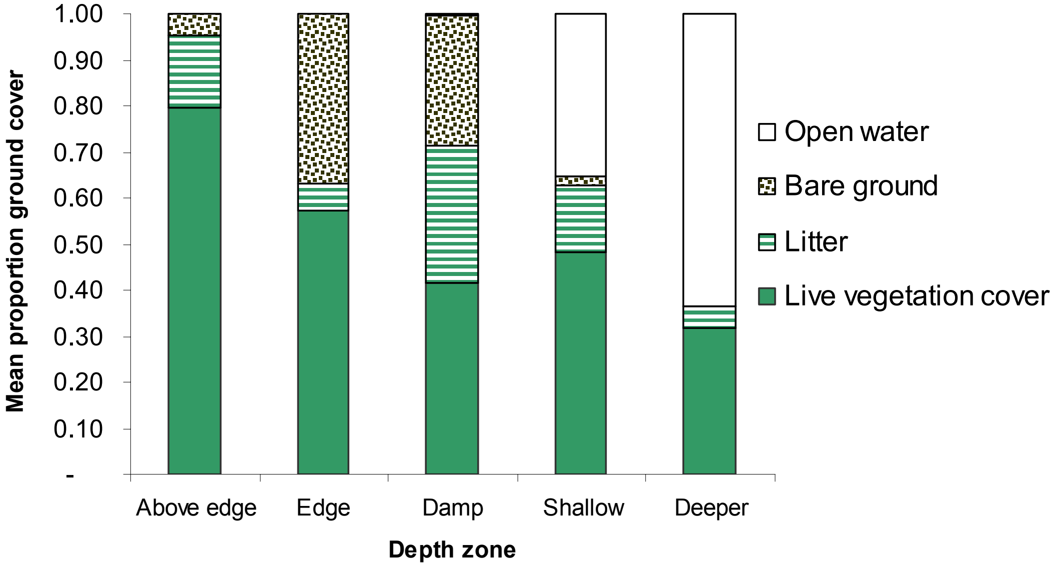


Figure 2.4. Differences in mean vegetation cover according to depth zone.

Of the species recorded, *Eleocharis equisetina, Paspalum distichum* and *Cynodon dactylon* were most widely distributed, sampled at 82%, 71% and 71% of sites respectively (Table 2.3). These species were also recorded in more quadrats in total than any other species, with *E. equisetina* in 42% of quadrats, *C. dactylon* in 35% of quadrats and *P. distichum* in 27% of quadrats. The majority of species recorded were not widely distributed, with 54% of species found at one site only. Sampling frequencies and sites of occurrence are listed for all species in Appendix 1.

Table 2.3. The ten most widely distributed wetland† species, based on number of sites recorded. (Photos in Figure 2.4).

Species	Family	Common name	Number of sites / quadrats
Eleocharis equisetina	Cyperaceae	Spike Rush	14 / 32
Cynodon dactylon	Poaceae	Couch	12 / 27
Paspalum distichum	Poaceae	Water Couch	12 / 21
Casuarina glauca	Casuarinaceae	Swamp Oak	8 / 9
**Cotula coronipifolia* L.	Asteraceae	Waterbuttons	7 / 13
Bacopa monnieri	Scrophulariaceae	Brahmi	6 / 12
Phragmites australis	Poaceae	Common Reed	5 / 10
Bolboschoenus caldwellii	Cyperaceae	Marsh Clubrush	5 / 9
**Eleocharis minuta*	Cyperaceae	Dwarf Spikerush	5 / 5
Juncus usitatus	Juncaceae	Common Rush	5 / 5

†Species sampled only above the high water mark (i.e. 'above edge' quadrats) excluded from this table. *Introduced species.

Figure 2.5. The ten most widely distributed species recorded in Clarence River floodplain wetlands, November 2005; **a)** *Eleocharis equisetina* (foreground) and *Casuarina glauca* (background), **b)** *Eleocharis minuta,* **c)** *Cynodon dactylon* (foreground) and *Juncus usitatus* (background), **d)** *Paspalum distichum* (foreground), **e)** *Phragmites australis,* **f)** *Bolboschoenus caldwellii,* **g)** close up of *Cotula coronipifolia* (yellow flowers) interspersed with *Bacopa monnieri* (rounded, fleshy leaves), and **h)** mats of *B. monnieri* and *C. coronipifolia* (foreground) with *P. australis* (midground) and *C. glauca* (background).

Some of the species sampled formed very dense dominant stands in particular elevation zones, contributing up to 100% canopy cover in some quadrats (Table 2.4). These species tended to also be among those that were most widespread, and of the ten species with the highest recorded canopy cover (Table 2.4), seven are also listed among the ten most widely distributed species (Table 2.3).

Table 2.4. The ten species with the highest maximum percentage cover measurements in quadrats.

Species	Family	Common name	Max. % cover	Mean % cover	Median % cover
Paspalum distichum	Poaceae	Water Couch	100	27	15
Cynodon dactylon	Poaceae	Couch	100	48	35
Sporobolus virginicus	Poaceae	Salt Couch	90	52	50
Bolboschoenus caldwellii	Cyperaceae	Marsh Clubrush	90	23	10
Eleocharis equisetina	Cyperaceae	Spikerush	80	20	12.5
Paspalum vaginatum	Poaceae	Saltwater Couch	80	40	40
**Eleocharis minuta*	Cyperaceae	Dwarf Spikerush	80	27	5
Bacopa monnieri	Scrophulariaceae	Brahmi	70	13	5
**Nymphaea caerulea*	Nymphaeaceae	Cape Waterlily	66	31	27.5
Phragmites australis	Poaceae	Common Reed	65	19	12.5

*Introduced species

2.3.2 Patterns in species composition with respect to environmental variables

2.3.2.1 DCA results

The DCA (unconstrained ordination) biplot (Figure 2.6) summarises the main patterns observed in species composition and percent cover across the sampled quadrats, with 21.4% of the total variability in species composition and cover summarised by the first four axes, and axes one and two accounting for 7.4% and 6.2% of the total variability respectively. The sum of all canonical eigenvalues was 3.80, while the sum of all eigenvalues was 13.11, indicating that of the 21.4% of total variability explained, 29.0% could be attributed to the measured environmental variables in an equivalent constrained analysis.

Axis one had the highest degree of correlation with the environmental data (multivariate regression coefficient of 0.80), followed by the less strongly correlated third (0.66), second (0.58) and fourth (0.44) axes. Samples formed two distinct groups along axis one, with those from the most strongly saline sites noticeably separated from the others (Figure 2.5). This high degree of dissimilarity was due to the presence and dominance of obligate halophytes, including *Avicennia marina* var. *australasica*, *Sporobolus virginicus* and *Sarcocornia quinqueflora* subsp. *quinqueflora*, which occurred only at the most saline sites. Samples were also ranked approximately in order of increasing water depth along axis one and to a lesser extent also along axis two, at least in the fresh to brackish quadrat group (Figure 2.6).

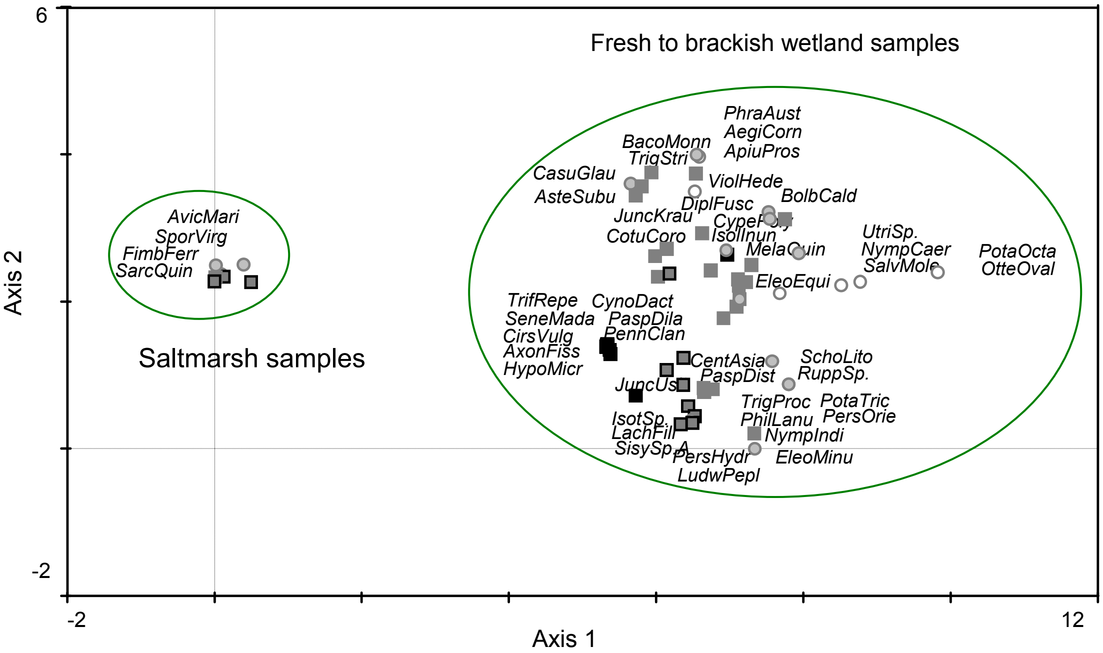


Figure 2.6. DCA biplot of quadrats and species from the Clarence wetlands survey, 2005.

(Symbols indicate quadrat position; ■ above edge, ▣ edge, □ damp, ● shallow, ○ deep. Eight letter abbrieviations consist of the first four letters of genus and species names respectively: *AegiCorn* = *Aegiceras corniculatum*, *ApiuPros* = *Apium prostratum* subsp. *prostratum, AsteSubu* = *Aster subulatus*, *AvicMari* = *Avicennia marina* var. *australasica*, *AxonFiss* = *Axonopus fissifolius*, *BacoMonn* = *Bacopa monnieri*, *BolbCald* = *Bolboschoenus caldwellii*, *CasuGlau* = *Casuarina glauca*, *CentAsia* = *Centella asiatica*, *CirsVulg* = *Cirsium vulgare*, *CotuCoro* = *Cotula coronopifolia*, *CynoDact* = *Cynodon dactylon*, *CypePoly* = *Cyperus polystachyos*, *DiplFusc* = *Diplachne fusca*, *EleoEqui* = *Eleocharis equisetina*, *EleoMinu* = *Eleocharis minuta*, *FimbFerr* = *Fimbristylis ferruginea*, *HypoMicr* = *Hypochaeris microcephala*, *IsolInun* = *Isolepis inundata*, *IsotSp.* = *Isotoma* sp., *JuncKrau* = *Juncus kraussii* subsp. *australiensis*, *JuncUsit* = *Juncus usitatus*, *LachFilli* = *Agrostis avenacea* var. *avenacea* (synonym *Lachnagrostis filiformis*), *LudwPepl* = *Ludwigia peploides* subsp. *montevidensis*, *MelaQuin* = *Melaleuca quinquenervia*, *NympCaer* = *Nymphaea caerulea* (synonym *N. capensis*), *NympIndi* = *Nymphoides indica*, *OtteOval* = *Ottelia ovalifolia*, *PaspDila* = *Paspalum dilatatum*, *PaspDist* = *Paspalum distichum*, *PennClan* = *Pennisetum clandestinum*, *PeriOrie* = *Persicaria orientalis*, *PersHydr* = *Persicaria hydropiper*, *PersOrie* = *Persicaria orientalis*, *PhilLanu* = *Philydrum lanuginosum*, *PhraAus* = *Phragmites australis*, *PotaOcta* = *Potamogeton octandrus* (syn. *Potamogeton javanicus*), *PotaTric* = *Potamogeton tricarinatus*, *RuppSp.* = *Ruppia* sp., *SalvMole* = *Salvinia molesta*, *SarcQuin* = *Sarcocornia quinqueflora* subsp. *quinqueflora, ScholLitto* = *Schoenoplectus litoralis*, *SeneMada* = *Senecio madagascariensis*, *SisySp.* = *Sisyrinchium* sp. A, *SporVirg* = *Sporobolus virginicus*, *TrifRepe* = *Trifolium repens*, *TrigProc* = *Triglochin procerum*, *TrigStri* = *Triglochin striatum*, *UtriSp.* = *Utricularia* sp., *ViolHede* = *Viola hederacea.*)

2.3.2.2 CCA results

Since the number of explanatory variables was reduced from six to four in the final CCA to remove an arch effect, the total proportion of variance explained decreased from 29.0% to 14.3% of that explained in the unconstrained analysis (DCA). However, the percentage of the species-environmental data relationship that was explained by the fitted axes increased from 73.0% to 94.9%, which improved the interpretability of the resulting species/samples/environment triplot (Figure 2.7).

Axis one of the CCA plot explained 6% of the total variation in species data, whereas axis two explained 3.7%, and axes three and four explained 1.5% and 1.4% respectively. The first two axes explained a higher proportion of the relationship between species composition and the measured environmental variables with 41.9% explained by axis one, 33% by axis two, 10% by axis three and 10% by axis four. Axes one and two were much more strongly correlated with the environmental data (multivariate regression coefficients of 0.92 and 0.82 respectively) than the third and fourth axes (coefficients of 0.53 and 0.58) with axis one most closely associated with water depth and axis two most strongly correlated with soil salinity (Table 2.5).

Forward selection identified soil salinity, water depth class, and set stocking as significant ($p < 0.05$), while soil pH, cell grazing and non-grazing were not ($p > 0.10$). Soil salinity and water depth class were much more strongly correlated with changes in quadrat species composition than grazing management, as indicated by longer arrow lengths (Figure 2.7). The arrows for soil salinity and water depth class were orthoganal (Figure 2.7), indicating that changes in species composition along these two gradients were distinct and uncorrelated.

Table 2.5. Weighted correlation matrix (weight = sample total).

Environmental variable	Species axis 1	Species axis 2
Depth class	-0.8889	-0.1449
Ungrazed	-0.0590	-0.1712
Cell grazed	-0.0750	-0.0677
Set stocking	0.1104	0.1959
Soil pH	-0.1850	0.0458
Soil salinity	-0.3674	0.6572

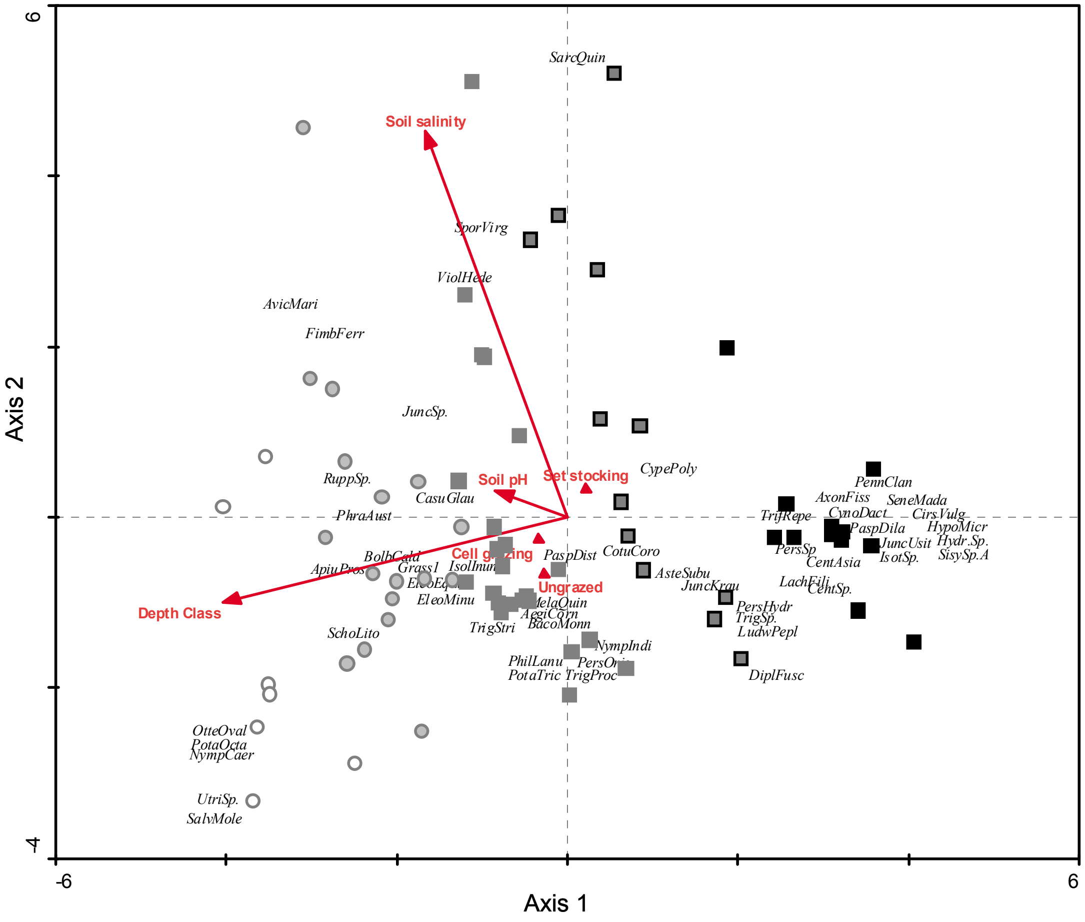


Figure 2.7. CCA triplot of quadrats, species and environmental variables from the Clarence wetlands survey, 2005.

(Symbols indicate quadrat position; ■ above edge, ▣ edge, ▢ damp, ● shallow, ○ deep. Eight letter abbrieviations consist of the first four letters of genus and species names respectively: *AegiCorn* = *Aegiceras corniculatum*, *ApiuPros* = *Apium prostratum* subsp. *prostratum, AsteSubu* = *Aster subulatus*, *AvicMari* = *Avicennia marina* var. *australasica*, *AxonFiss* = *Axonopus fissifolius*, *BacoMonn* = *Bacopa monnieri*, *BolbCald* = *Bolboschoenus caldwellii*, *CasuGlau* = *Casuarina glauca*, *CentAsia* = *Centella asiatica*, *CirsVulg* = *Cirsium vulgare*, *CotuCoro* = *Cotula coronopifolia*, *CynoDact* = *Cynodon dactylon*, *CypePoly* = *Cyperus polystachyos*, *DiplFusc* = *Diplachne fusca*, *EleoEqui* = *Eleocharis equisetina*, *EleoMinu* = *Eleocharis minuta*, *FimbFerr* = *Fimbristylis ferruginea*, *HypoMicr* = *Hypochaeris microcephala*, *IsolInun* = *Isolepis inundata*, *IsotSp.* = *Isotoma* sp., *JuncKrau* = *Juncus kraussii* subsp. *australiensis*, *JuncUsit* = *Juncus usitatus*, *LachFilli* = *Agrostis avenacea* var. *avenacea* (synonym *Lachnagrostis filiformis*), *LudwPepl* = *Ludwigia peploides* subsp. *montevidensis*, *MelaQuin* = *Melaleuca quinquenervia*, *NympCaer* = *Nymphaea caerulea* (synonym *N. capensis*), *NympIndi* = *Nymphoides indica*, *OtteOval* = *Ottelia ovalifolia*, *PaspDila* = *Paspalum dilatatum*, *PaspDist* = *Paspalum distichum*, *PennClan* = *Pennisetum clandestinum*, *PeriOrie* = *Persicaria orientalis*, *PersHydr* = *Persicaria hydropiper*, *PersOrie* = *Persicaria orientalis*, *PhilLanu* = *Philydrum lanuginosum*, *PhraAus* = *Phragmites australis*, *PotaOcta* = *Potamogeton octandrus* (syn. *Potamogeton javanicus*), *PotaTric* = *Potamogeton tricarinatus*, *RuppSp.* = *Ruppia* sp., *SalvMole* = *Salvinia molesta*, *SarcQuin* = *Sarcocornia quinqueflora* subsp. *quinqueflora, ScholLitto* = *Schoenoplectus litoralis*, *SeneMada* = *Senecio madagascariensis*, *SisySp.* = *Sisyrinchium* sp. A, *SporVirg* = *Sporobolus virginicus*, *TrifRepe* = *Trifolium repens*, *TrigProc* = *Triglochin procerum*, *TrigStri* = *Triglochin striatum*, *UtriSp.* = *Utricularia* sp., *ViolHede* = *Viola hederacea.*)

Along axis one of the CCA, plot quadrats were arrayed from left to right in order of decreasing water depth (Figure 2.7). Deeper water plots were characterised by floating-leaved species, including *Nymphaea caerulea*, *Salvinia molesta*, *Utricularia* species, *Ottelia ovalifolia* and *Potamogeton octandrus* (Figure 2.7). In shallow water characteristic species included *Eleocharis equisetina, Phragmites australis*, *Bolboschoenus caldwellii* and *Schoenoplectus litoralis* (Figure 2.7). Species associated with damp mud included *Paspalum distichum*, *Casuarina glauca*, *Melaleuca quinquenervia* and *Bacopa monnieri* (Figure 2.7). Edge samples were characterised by the presence of a range of grasses, sedges and herbaceous species, including *Diplachne fusca*, *Lachnagrostis filiformis*, *Sporobolus virginicus*, *Juncus kraussii*, *Cyperus polystachyos*, and *Cotula coronipifolia* (Figure 2.7). Above edge samples were characterised by the dominance of pasture and weed species, including *Cynodon dactylon*, *Trifolium repens*, *Paspalum dilatatum*, *Pennisetum clandestinum*, *Axonopus fissifolius* and *Cirsium vulgare* (Figure 2.7).

Along axis two, which was most strongly correlated with soil salinity, the most saline site quadrats were once again grouped together due to the occurrence of saltmarsh species, including *Avicennia marina*, *Sporobolus virginicus* and *Sarcocornia quinqueflora* (Figure 2.7). At the opposite end of axis two, samples from the freshest sites were also clustered together. These quadrats included some species that were found only at site 3 (Table 2.1), located upstream of the limit of saline influence, including *Nymphaea indica*, *Philydrum lanuginosum* and *Ottelia ovalifolia* (Figure 2.7).

There were no obvious patterns in species composition with respect to soil pH or grazing intensity (Figure 2.7). The depth and salinity ranges recorded for individual species are listed in Appendices 2 and 3 respectively. The distributions of each species with respect to sampled soil pH and grazing intensity are summarised in Appendices 4 and 5.

2.3.3 Conversion of soil salinities (1:5 extracts) to approximate porewater salinities

Soil texture classes ranged from loam for samples collected above the wetland edge, though to clay loams, silty clay loams and light-medium clays for samples in lower-lying and inundated areas. The suggested multipliers for converting 1:5 soil/water salinity values to an estimate of pore-water salinity are 9.5 for loam, and 8.6 for the other soil types (Hazelton and Murphy 2007). However, use of these conversion factors to estimate pore-water salinity led to very high to extremely high salinity values for many of the sites (Table 2.6).

Table 2.6. Estimations of pore-water salinity for sites based on 1:5 extract salinity and soil texture class.

	Average estimated pore-water salinity (ppm) for different elevation zones		
Site number	Above-edge samples	Edge zone samples	Below-edge samples
1	5700	37 000	45 000
2	9300	20 900	11 800
3	4000	2000	1700
4	5600	25 300	18 200
5	-	79 600	41 600
6	33 100	-	16 500
7	-	-	1 900
8	22 500	-	33 200
9	-	20400	54 700
10	25 100	114 100	31 700
11	15 100	27 000	44 300
12	26 700	47 000	25 500
13	16 000	35 700	28 300
14	-	-	10 500
15	-	-	41 600
16	22 400	92 600	139 900
17	11 000	66 400	62 900

Site numbers correspond to those used in Table 2.1. Salinity values rounded to the nearest 100 ppm.

A smaller multiplication factor of 4.9 is suggested for converting 1:5 dilution salinities to pore-water salinity estimates in peat soils (Hazelton and Murphy 2007) and this would result in lower values if applied. The results of the loss-on-ignition test here did indicate generally high soil organic matter content as well as high variability in organic matter content between samples (range 4.6 – 56.2 %, mean 22.9 %, standard deviation 12.3%, n

= 24), indicating that a smaller conversion factor would be appropriate for some but not all samples. Adjustment of these conversion factors would require further data on soil bulk density from each quadrat location (Slavich and Petterson 1993; Shaw 1999; Hazelton and Murphy 2007). Hence, unless indicated otherwise, the salinity values reported in this and later chapters are direct measurements of salinity obtained from 1:5 soil/water dilutions, and not extrapolations of pore-water salinity based on multiplication of these values by a conversion factor.

2.3.4 Common species habitat ranges with respect to depth, salinity, acidity and grazing

Of the ten most widespread wetland species (Table 2.3), *E. equisetina* was recorded over the greatest range of water depths, occupying sites from the wetland edge zone up to 75 cm depth (Table 2.7). *Cynodon dactylon* and *J. usitatus* were found over the narrowest depth ranges, and did not occur in any areas with standing water. The other widespread species inhabited the intermediate area at depths up to 25 cm at the time of sampling (Table 2.7).

While some of the less widespread species were recorded only at sites with particularly high or low soil salinity (Figure 2.7), the ten most widespread species, excepting *J. usitatus,* inhabited sites spanning a broader range of salinities than observed for the majority of species (Appendix 3). *Eleocharis equisetina, P. distichum* and *C. dactylon,* the three most common species, had the broadest habitat salinity ranges (Table 2.7). In contrast with these three most common and widespread species, *N. caerulea* and *J. usitatus* had narrower soil salinity ranges and were also only found at sites with low soil salinity (maxima of 1000 and 500 ppm for *N. caerulea* and *J. usitatus* respectively). *Bacopa monnieri, Bolboschoenus caldwellii* and *P. australis* were only found at sites with soil salinity ≥ 1100 ppm.

Most of the ten most widespread species were also found growing in soils spanning a reasonably broad range of pH levels (Table 2.7). Many occurred at sites where soil pH was ≤ 4, indicating the likely presence of acid sulfate soils which are a common feature of wetlands on the Clarence floodplain (Walker 1972; Stone *et al.* 1998). Most of these species occupied sites across the full range of grazing intensity levels, and all were found at sites under set stocking, where grazing pressure was most continuous.

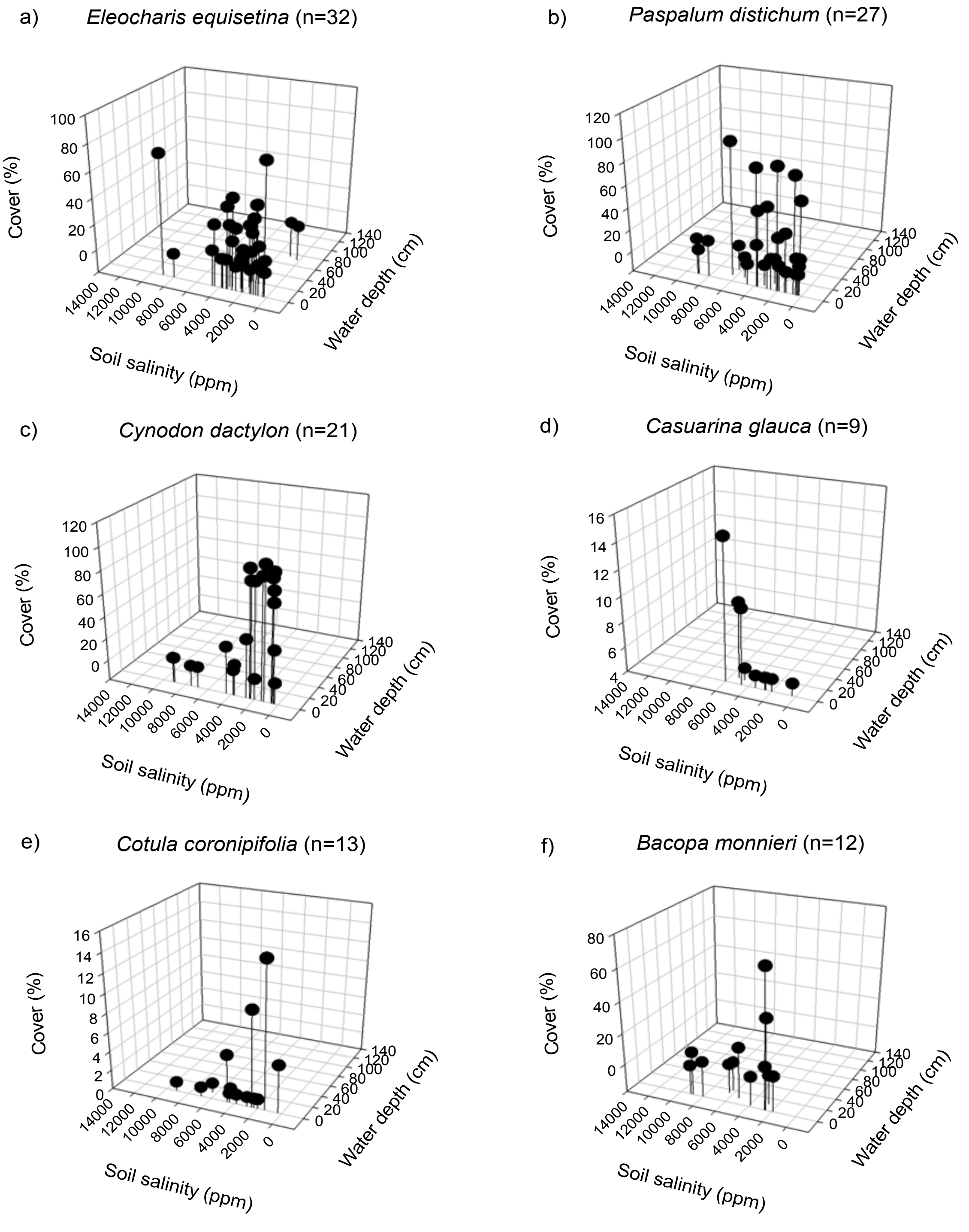
Table 2.7. Depth and salinity ranges of the ten most †widespread wetland species.

Species	No. of sites / quadrats	Water depth min – max (cm)	Soil salinity min – max (ppm)	Soil pH min – max	Grazing regime (1, 2, 3)
E. equisetina	14 / 32	0–75	200–9000	4.1–7.2	1, 2, 3
P. distichum	12 / 27	0–20	200–9000	3.9–8.0	1, 2, 3
C. dactylon	12 / 21	0	300–9100	3.9–7.2	1, 2, 3
C. glauca	8 / 9	0–10	300–6000	4.6–6.6	1, 2, 3
C. coronipifolia	7 / 13	0–10	300–9100	3.9–7.2	1, 2, 3
B. monnieri	6 / 12	0–20	1900–9100	4.6–8.0	1, 2, 3
P. australis	5 / 10	0–25	1900–8900	6.2–7.1	1, 2, 3
B. caldwellii	5 / 9	0–25	1100–8900	4.4–7.1	1, 2, 3
**E. minuta*	5 / 5	0–20	200–5300	4.4–6.7	1, 3
J. usitatus	5 / 5	0	300–500	3.9–6.6	3

†Based on total number of sites where species recorded. Species found only above the high water mark have been excluded. For grazing regime, 1 = ungrazed, 2 = cell grazed, 3 = set stocking.

Within their recorded water depth and soil salinity ranges, percentage canopy cover of the most widespread and common species varied, typically increasing over a particular depth or salinity range then declining (Figure 2.8). For some species, cover appeared to be more strongly associated with water depth than soil salinity across the ranges where these species were found. For example, cover of *E. equisetina* was highest when standing water was less than 10 cm deep, decreasing when this species was sampled at greater depths (Figure 2.8a). However, similar cover measurements were recorded for *E. equisetina* at both ends of the salinity range in which it was sampled (Figure 2.8a). A comparable pattern was found for *P. distichum* (Figure 2.8b). Other widespread species displayed a change in cover as soil salinity increased, either declining, as with *B. caldwellii* (Figure 2.8h), *C. dactylon* (Figure 2.8c) and *C. coronipifolia* (Figure 2.8e), or increasing, such as with *C. glauca* where the highest percentage cover was recorded at the most saline site it was sampled (Figure 2.8d).

Nymphaea caerulea (Figure 2.8k) was observed at only four of the survey sites, and was sampled at each of these. The depth range of *N. caerulea* ranged from 50 cm to 120 cm, with soil salinities ranging from 100 ppm to 1000 ppm. Soil pH was close to neutral in the quadrats where *N. caerulea* occurred, ranging from 6.4 to 7.0.


a) *Eleocharis equisetina* (n=32)

b) *Paspalum distichum* (n=27)

c) *Cynodon dactylon* (n=21)

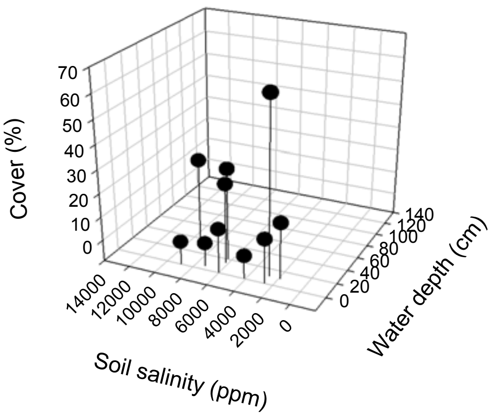
d) *Casuarina glauca* (n=9)

e) *Cotula coronipifolia* (n=13)

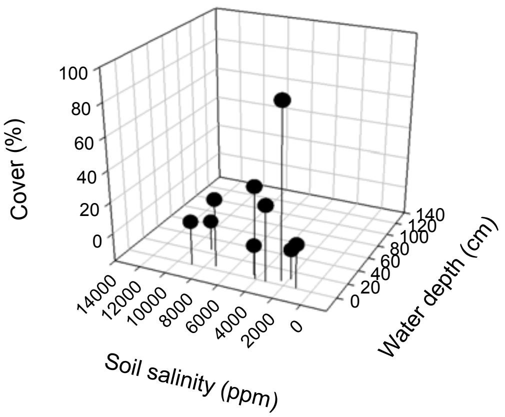
f) *Bacopa monnieri* (n=12)

Figure 2.8. Changes in percent canopy cover according to depth and salinity for the ten most widespread species, plus *N. caerulea.* (N = quadrats.)

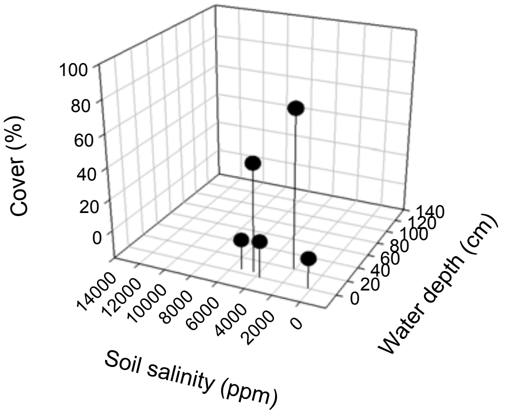
g) *Phragmites australis* (n=10)



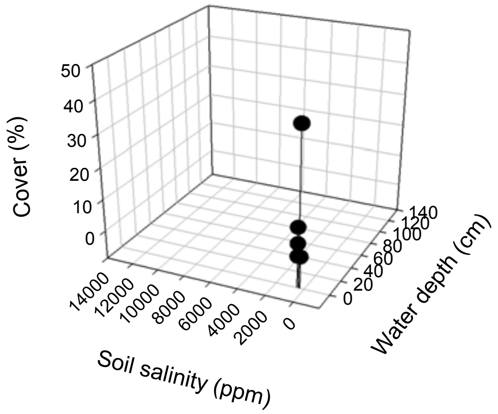
h) *Bolboschoenus caldwellii* (n=9)



i) *Eleocharis minuta* (n=5)



j) *Juncus usitatus* (n=5)



k) *Nymphaea caerulea* (n=4)

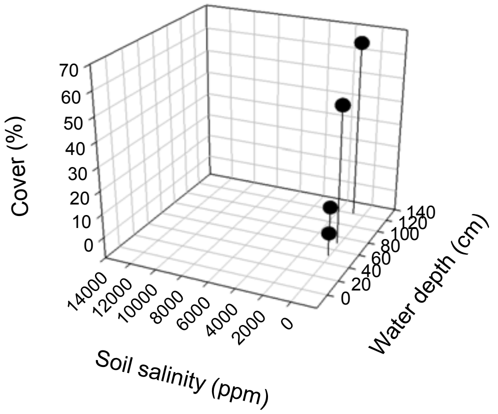


Figure 2.8. continued.

2.4 Discussion

This survey identified a number of widespread and abundant macrophyte species in Clarence River floodplain wetlands as well as some of the major patterns in their distribution with respect to habitat gradients. These survey results have expanded on the results of previous surveys by relating species distributions to measurements of salinity, pH and grazing management, in addition to relative water depth (Pressey and Clancy 1979; Pressey 1989a). There are some limitations to the ways in which species distribution data from this survey data can be interpreted. While data were collected from saline sites and fresh to slightly brackish sites, sites in the intermediate to moderately brackish range were not available for sampling, largely because they have disappeared due to past drainage and tidal flow exclusion. Therefore, the complete range of soil salinities that could be tolerated by each species may not have been represented. Similarly, because water depth is temporally variable, and the survey was carried out during the drier time of the year, the ranges of water depths tolerated by these species could be underestimated if estimates are made based solely on data from this survey. Despite these limitations, differences in species distributions relative to environmental gradients can be used to generate hypotheses about their relative environmental tolerance ranges (Clarke and Hannon 1970; Pressey and Clancy 1979; Hart *et al.* 1991). These hypotheses can then be tested in controlled experiments (Clarke and Hannon 1970; Hart *et al.* 1991).

While grazing and soil pH affect on wetland macrophyte composition and cover (Blanch and Brock 1994; Gough and Grace 1998; Rosicky *et al.* 2006; Geho *et al.* 2007) changes in species composition and cover were found here to be more strongly associated with differences in soil salinity and position on the water depth gradient than differences in soil pH or grazing management. Strong relationships between wetland vegetation composition, soil salinity and relative elevation are typical in coastal wetlands, particularly those influenced by tides (Odum 1988; Neckles *et al.* 2002; Warren *et al.* 2002; Laegdsgaard 2006). The relationships between species composition and cover, and soil salinity and relative water depth are likely to be of particular relevance in the context of floodgate management, since both salinity and flooding regime could be directly affected by the management changes being proposed. Any changes to salinity or water depths could have flow-on effects on species composition and distribution at affected sites if these factors are responsible for the observed patterns in vegetation composition (Odum 1988; Laegdsgaard 2006).

The most widespread species recorded in this survey were *Eleocharis equisetina* and *Paspalum distichum*, followed by *Cynodon dactylon, Casuarina glauca, Cotula coronipifolia, Bacopa monnieri, Phragmites australis, Bolboschoenus caldwellii, Eleocharis minuta* and *Juncus usitatus*. Of these, *P. distichum* and *C. dactylon* had the highest percentage cover in particular sample quadrats, followed by *Sporobolis virginicus, B. caldwellii, E. equisetina, Paspalum vaginatum*, *E. minuta, B. monnieri, Nymphaea caerulea* and *P. australis.* These species were also listed among the most common and widespread species in an earlier survey of vegetation in wetlands on the lower Clarence floodplain conducted by Pressey (1989a).

All of the ten most widespread species, and eight out of ten of those with the highest recorded percentage canopy cover, were predominantly found in the fresh to brackish wetland category. Exceptions were *N. caerulea,* which was found mainly at freshwater sites, and *S. virginicus*, which was found only at saline sites. The most widespread species were generally found occurring across a broader range of salinity and pH conditions than many of the less frequently sampled species. *Eleocharis equisetina,* the most frequently sampled species, also occurred over a broader range of water depths than all other species, except for *N. caerulea.* Based on these results it is hypothesized that the most widespread species may be more widespread due to a higher tolerance to extremes of soil salinity and pH, or fluctuations in water depth, than the other species. However, few environmental data were collected for the less widespread species, and it is possible that some of these may also have broader habitat tolerances than observed here. Of the three species *N. caerulea, E. equisetina* and *P. distichum*, highlighted earlier because of their interest to rehabilitation managers, *N. caerulea* was found to be least widespread.

Nymphaea caerulea was found only at fresh to very mildly brackish sites with soil salinity (1:5 extract) less than or equal to 1000 ppm, and occurred in water from 50–120 cm deep.

Based on soil salinity ranges and percentage canopy cover *P. australis, E. equisetina* and *P. distichum* appear likely to be the most salt tolerant out of the ten most common and widespread species recorded in this survey. *Cynodon dactylon, Cotula coronipifolia, B. monnieri* and *B. caldwellii* may be less salt tolerant, because while these species had similar soil salinity upper limits, percentage cover appeared to decline more for these species as salinity increased, than for *P. australis, E. equisetina* or *P. distichum. Casuarina glauca, J. usitatus* and *E. minuta* were found at less saline sites than the other species, which may indicate lower salt tolerance.

If the observed habitat ranges of these species are indicative of their actual salinity tolerance, then stands of *N. caerulea* are hypothesized to be more likely to die out than stands of *E. equisetina* or *P. distichum* if brackish water is allowed to flood these sites. This hypothesis is supported by field observation since while dense stands of *N. caerulea* occur and have persisted for the duration of this project at Everlasting Swamp (site 14), currently isolated from tidal flows by a weir and floodgate, this species is usually not seen at the Little Broadwater wetland (site 11) which is located immediately downstream of the weir. However, *N. caerulea* does appear at the Little Broadwater in some years after periods of high spring/summer rainfall, when it germinates from the soil seedbank and then dies off later, usually after flowering (pers. obs.). In contrast *E. equisetina* and *P. distichum* generally persist at both sites, although cover may decline (pers. obs.). In contrast, *N. caerulea* is expected to be the most tolerant of these three species to increases in water depth, since it was recorded in deeper water than the other species.

The soil pore-water salinities that were estimated here using a standard table of conversion factors, based on soil texture class (Hazelton and Murphy 2007), were extremely high and are also much higher than reported for other drained coastal backswamps in New South Wales (Rosicky *et al.* 2006). This method, though used successfully elsewhere (Slavich and Petterson 1993; Shaw 1999; Hazelton and Murphy 2007), may have been inappropriate in the current situation. These conversion factors are based on differences in soil water-holding capacity according to sand, silt and clay content (Hazelton and Murphy 2007). However, high organic matter content can increase soil water-holding capacity and this could not be accounted for using the texture class method (Hazelton and Murphy 2007). As high levels of soil organic matter were recorded at these wetlands, collection of additional soil cores and direct measurement of saturation water content are considered likely to result in lower, and more accurate, estimates of pore-water salinity (Slavich and Petterson 1993).

Correlations between species distributions and environmental variables can be used to point out possible causal relationships, but do not provide conclusive evidence of cause and effect. The absolute tolerance ranges of species with respect to environmental variables can also not be determined from survey data alone (Clarke and Hannon 1970; Hart *et al.* 1991; Howard and Mendelssohn 1999a, b). Experimental testing of species salinity and inundation tolerance limits would be a useful step toward predicting the suitability of wetland sites for individual species in conditions that fall outside those existing under current water management conditions (James and Hart 1993; Howard and Mendelssohn 1999a, b). The species of highest relevance for such experiments are those which have been identified as widespread and dominant, and which are currently found in secondarily fresh to mildly brackish wetlands with tidal barriers in place, because those species are most likely to be present at prospective rehabilitation sites and to account for a substantial proportion of vegetation cover. Species limited to narrow elevation ranges are also of relevance, because these are likely to be affected most by changes in inundation depth and duration (Gough and Grace 1998; Blanch *et al.* 2000).

Based on the results of the current survey, *E. equisetina, P. distichum, C. dactylon, B. caldwellii* and *Bacopa monnieri* have been selected and will be used in controlled experiments to directly determine the effects of increased salinity and water depth on plant growth and survival. The resulting information on the relative salinity and inundation tolerance thresholds of these species can then be used to help predict how they will respond to the changes in water management proposed for wetlands on the Clarence River floodplain.

Photo: Vegetation at the Little Broadwater Wetland on the Clarence River floodplain, November 2006.

CHAPTER 3

Responses of macrophytes from floodgate-restricted wetlands to increased salinity

3.1 Introduction

Tidal wetlands along the Clarence River estuary on the NSW North Coast have been heavily impacted by extensive flood mitigation works carried out in the 1950s to 1970s (Pressey and Clancy 1979; Middleton *et al.* 1985). The network of drains and floodgates now in place allows flood waters to rapidly escape low lying areas. However, floodgates also prevent tidal exchange and, as a result, most previously tidal wetlands connected to the Clarence estuary have been converted into fresher, rainfall-dependent systems (Pressey and Clancy 1979). Restoration of tidal flows, either partial or complete, has been proposed as a rehabilitation measure for these wetlands and this is expected to cause increases in salinity and inundation depth and frequency. These changes are likely to affect macrophyte community composition at wetland rehabilitation sites, since site salinity and inundation regime are primary determinants of macrophyte species distribution in estuarine systems (Odum 1988).

Extant plant communities within these tidally isolated wetlands provide habitat for a variety of biota, including threatened and migratory water birds, some of which are protected under international conservation agreements. Most floodgate-affected wetlands also occur on private grazing properties, where freshwater plant communities provide a valuable fodder resource for cattle (Pressey 1989). Predicting the effects of reinstating tidal flows on current macrophyte communities is important to rehabilitators who wish to know the likely impacts of this reintroduction before they proceed (Walsh and Copeland 2004). This chapter examines the effects of increased salinity on growth and survival of some of the more common and widespread macrophyte species currently found in floodgate-affected wetlands on the Clarence River floodplain, in order to help predict how they will respond to tidal restoration.

Prior to flood mitigation works, wetlands associated with the tidal portion of the Clarence River would have ranged in salinity from fresh (< 500 ppm) up to polyhaline (~30 000 – 35 000 ppm), depending on distance from the estuary mouth. Due to the presence of drains with floodgates, a number of previously tidal wetlands now fall in the range from fresh and mildly brackish (i.e. oligohaline sites ~0–15 000 ppm), and are typically quite shallow, filling during the higher rainfall spring/summer seasons and drying at other times. The plant communities of most interest in this project are those that occur in these fresh to mildly brackish floodgate-affected wetlands.

The species composition of floodgate-affected wetlands on the Clarence River floodplain was discussed in depth in Chapter 2 of this thesis. Vegetation cover at these sites is often high, with little or no open water present (Pressey 1989), and is most commonly dominated by dense swards of *Eleocharis equisetina* (Figure 2.5a) in shallow water areas (< 20 cm) with *Paspalum distichum* (Figure 2.5d) occurring around edge areas, on damp ground and in shallow water up to around 5 cm (Chapter 2). However, *P. distichum* has also been observed at one site growing as a floating mat in water approximately 60 cm deep, where *E. equisetina* was absent and cattle had been fenced out for several years (pers. obs.). It is therefore possible that the depth distribution of this species is limited by competition with *E. equisetina* or by grazing. *Bolboschoenus caldwellii* (Figure 2.5f) is another common species found in waterlogged and shallow areas (Chapter 2). Taller species, particularly *Phragmites australis* (Figure 2.5e) and *Schoenoplectus litoralis*, often occur at the deeper and more brackish sites (Chapter 2). In the less frequently inundated area found between the high and low water marks a surface salt crust is sometimes seen (Figure 2.3b) and the vegetation is typically sparser (Figure 2.3a and b), especially at drier sites (Chapter 2). Characteristic species of this edge zone include *Bacopa monnieri* and *Cotula coronipifolia* (Figure 2.5g and h). *Cynodon dactylon* typically dominates the groundcover above the water line (Figure 2.5c). Two tree species, *Casuarina glauca* (Figure 2.5a and h) and *Melaleuca quinquenervia*, commonly occur as dominants in the fringing vegetation.

A ranking of the relative salt tolerances of these common and widespread floodplain wetland species would assist rehabilitators in making decisions about floodgate management based on the species they want to maintain. However, information on salt tolerance is lacking for the majority of these and other Australian coastal wetland macrophyte species, particularly for species that occur in oligohaline to mesohaline (~ 15 000 ppm) environments. Most work exploring the salt tolerance of Australian wetland macrophytes has focused on predicting the responses of freshwater species in inland waterways to secondary salinisation (Hart *et al.* 1990, 1991; Metzeling *et al.* 1995; Hart *et al.* 2003), or the effects of salinity on community composition in arid-zone salt lakes (Sim *et al.* 2006; Porter *et al.* 2007). While salt-tolerance has been assessed for some Australian estuarine macrophytes, these studies have largely been restricted to halophytic species from saltmarsh and mangal communities, found at the most saline end of the estuarine gradient (Laegdsgaard 2006). *Phragmites australis* is a notable exception.

Phragmites australis is cosmopolitan and regarded as an invasive weed in some areas of the world, including North America, where it characteristically invades fresh-brackish tidal wetlands, including man-made marshes and tidal restoration sites (Chambers *et al.* 2003). Consequently, the effects of salinity on *P. australis* field distribution, establishment, growth and survival have each been extensively researched. Experiments on North American accessions have demonstrated that mildly brackish conditions are most favourable for *P. australis* establishment, with seed germination stimulated at salinities of 5000 to 10 000 ppm but inhibited completely at ~25 000 ppm (Meyerson *et al.* 2000). In tidal marshes the most vigorous mature stands of *P. australis* have been found at sites where salinity remains ≤18 000 ppm (Chambers *et al.* 2003). However, the roots of *P. australis* can extend > 60 cm into the soil and, where sufficiently fresh water is available in the rhizosphere, clonal stands can extend into areas of higher surface water salinity (Chambers *et al.* 2003). This species has been observed at some sites in North

America with surface water up to 45 000 ppm (Chambers *et al.* 2003). In Australia *P. australis* distribution shows a similar relationship with site salinity to that reported overseas, as demonstrated by the retreat of established stands in the Gippsland Lakes to areas with soil salinity < 12 000 ppm after tidal restoration (Bird 1978; Clucas and Ladiges 1980).

Of the other common Clarence floodplain wetland species mentioned above, the two grasses *C. dactylon* and *P. distichum* and the tree species *C. glauca* appear to be the only species that have had their salt-tolerance ranges experimentally tested. *Cynodon dactylon* is able to survive over quite a broad range of soil salinities, as demonstrated in a recent salt scald revegetation trial where plants survived and maintained growth at two sites with soil salinities of approximately 14 000 ppm and 21 000 ppm (Semple *et al.* 2004). *Paspalum distichum* was also planted at these sites, but exhibited a lower salt tolerance, demonstrated by higher mortality rate and greater growth reduction than *C. dactylon* (Semple *et al.* 2004). *Casuarina glauca* seedlings also proved tolerant of mildly brackish conditions. In one experiment *C. glauca* seedlings grew best in conditions up to 7000 ppm, however germination was prevented completely at this concentration (Clarke and Hannon 1970). In a subsequent experiment a 21% reduction in shoot dry weight was reported at approximately 4500 ppm, and a 33% reduction at approximately 9000 ppm (Clemens *et al.* 1983).

A number of other less prominent species occur in Clarence River oligohaline to mesohaline wetlands (Chapter 2. Refer to Appendix 1) and four of these less frequently recorded species have been included in salt-tolerance experiments, including *Diplachne fusca*, *Potamogeton tricarinatus, Triglochin procerum* and *Juncus kraussii* (Warwick and Halloran 1991; Warwick and Bailey 1997, 1998; Greenwood and MacFarlane 2006). The results of these experiments are summarised in Appendix 6. Limited salt-tolerance information, based on survey data alone, was also found in the literature for some of these other species (Appendix 6). However, in many cases habitat ranges were not quantitatively defined, with soil and water salinity measurements not reported. In other cases it is still not clear whether the sampled distribution represents the full salinity tolerance range of the species. For example, while some survey-based data on species distributions relative to salinity are presented in Chapter 2, these data may not represent the full range of salinity levels tolerated by these species. In particular, the upper limits of species salinity tolerance ranges may not have been captured because no wetlands were surveyed in the mesohaline to polyhaline salinity range.

Habitat salinity ranges are difficult to define for plant species when considering survey data alone, particularly for those found in estuarine systems where soil and water salinity can be highly variable, both spatially and temporally (Odum 1988). Salinity varies within and between estuarine wetlands according to tidal patterns, distance upstream from the coastal inlet, degree of tidal connectivity, amount of rainfall runoff recently received, topography and substrate drainage characteristics (Odum 1988). These variations make comparison of soil and water salinities between sites difficult, even when temporal data on salinity levels are available. Other factors can also affect species distributions in the field such as propagule availability, competition, herbivory, sediment type, nutrients and inundation regime making it difficult to differentiate the effects of salinity from those of other confounding factors (Hart *et al.* 1991; Gough and Grace 1998; Keddy 1999; Bart and Hartman 2000).

Experiments can be useful for determining and ranking the relative tolerances of species to salinity while controlling for the effects of other variables (Hart *et al.* 1991; Bart and Hartman 2000). Field-based experiments have some advantages over those conducted under glasshouse or laboratory conditions. For example, there are a number of potentially interacting variables that can affect macrophyte growth and survival in the field, and these can not be duplicated effectively in a glasshouse or laboratory situation (Hart *et al.* 1991; Jolly *et al.* 2008). Field experiments may therefore yield more representative data than glasshouse experiments on the effects of tidal restoration on species growth and survival under field conditions (Hart *et al.* 1991; Jolly *et al.* 2008).

Field experiments using a before and after, control and impact (BACI) design have been used in a number of studies to determine the effects of tidal restoration on wetland macrophyte communities (Neckles *et al.* 2002). This approach was not considered practical here. Opportunities for a BACI design field experiment in the study area are currently restricted due to landholder concerns about salt water intrusion. There is also a lack of wetlands with natural tidal regimes that could be used as control or reference sites in a tidal restoration experiment. However, one floodgate opening trial was recently carried out in a Clarence River wetland, the Little Broadwater, without control sites (Graham *et al.* 2004). This was followed by one year of post-tidal-reinstatement monitoring of changes in the percentage canopy cover of dominant plant species (Graham *et al.* 2004). The results of the post-tidal-reinstatement monitoring at the Little Broadwater indicated a decline and disappearance of *B. caldwellii* and an increase in *P. australis* at survey points where increases in salinity and water depth occurred (Graham *et al.* 2004). *Cynodon dactylon* also died back around the wetland boundary (Graham *et al.* 2004), while *B. monnieri* appeared to be thriving one year after the trial began (pers. obs.). These observations suggest *B. caldwellii* and *C. dactylon* may be more sensitive to salinity or prolonged inundation than *P. australis* or *B. monnieri*. However, based on field data, it was unclear whether the observed vegetation changes were caused mostly by changes in salinity, flooding regime or other potentially correlated factors at that field site. For example, the Little Broadwater is also affected by ASS, and the vegetation changes at this site could also have been caused by a potential reduction in acidity due to the buffering effects of increased salinity, coupled with increased dilution and flushing of acid sulfate soil leachates. It is not possible to draw conclusions about the relative salt sensitivity of species based on these monitoring data alone.

One of the disadvantages of BACI design tidal restoration experiments is that they do not allow the effects of changes in salinity on macrophyte growth and survival to be distinguished from the effects of changes in inundation regime, or any other potentially correlated environmental variables (Hart *et al.* 1991). Because water management is likely to vary between rehabilitation sites on the Clarence floodplain, and could involve ponding brackish water at some times rather than restoring a natural tidal regime, it would be useful to determine the effects of increased salinity on macrophyte growth and survival alone, controlling for the effects of differences inundation regime (which may vary between sites as well as temporally). Both field and pot experiments have been used effectively elsewhere to determine the effects of salinity on macrophyte growth and survival and to rank species according to their relative salt tolerance thresholds (Maas 1977; Hart *et al.* 1991; Miyamoto 1996; Sim *et al.* 2006). A glasshouse experiment was used here rather than a field trial for logistical reasons. While glasshouse experiments can not replicate the complexity of field conditions (Hart *et al.* 1991; Jolly *et al.* 2008), they can be used to rank species according to their relative salt tolerance thresholds (Maas 1977; Hart *et al.* 1991; Miyamoto 1996; Sim *et al.* 2006).

Threshold salinity values can vary between experimental studies for an individual species according to the plant response measured (Maas 1977; Miyamoto 1996; Jolly *et al.* 2008). The the effects of salinity on plant growth and survival can also be affected by other factors such as water availability, temperature and plant life stage (Maas 1977; Miyamoto 1996; Jolly *et al.* 2008). However, while salinity tolerance thresholds may vary between experimental studies for individual species (Miyamoto 1996), these values can still be used to group and rank species according to their relative salt tolerance, provided they have been determined under comparable conditions and using a standard methodology (Maas 1977; Miyamoto 1996). Predictions can then be made about the impact of an increase in salinity on these species based on their relative salt tolerance rankings.

Five species, *C. dactylon, P. distichum, B. caldwellii*, *E. equisetina* and *B. monnieri*, were selected here for use in a salinity-tolerance experiment*.* Of these species *C. dactylon, P. distichum* and *E. equisetina* were selected because they are particularly common, abundant and widespread in Clarence River floodplain wetlands. These same species are also widely used as a pasture resource. *Bolboschoenus caldwellii* and *Bacopa monnieri* were selected because they are also widely distributed, and because they displayed contrasting growth responses during the Little Broadwater floodgate trial. A broad range of salinities were chosen for investigation, ranging from fresh to sea water, to reflect the range of salinities across which these species are distributed in the field, and to include higher and lower concentrations to ensure that the full salt-tolerance range of each species was tested.

3.1.1 Aims

The aims of this experiment were:

1. To determine how increased salinity affects the growth and survival of five macrophyte species that currently occur in tidally-restricted, secondarily fresh to oligohaline wetlands associated with the Clarence River, and;

2. To rank these species based on salt-sensitivity.

3.2 Materials and methods

3.2.1 Collection of plants from field sites, and growing conditions

I collected specimens of all five species from two separate sites on the Clarence River floodplain north east of Grafton, NSW. These were a fresh-water ponded area adjacent to the Broadwater wetland (29º25'S; 153º08'E), site 1, and the Little Broadwater wetland (29º28'S; 153º05'E), site 2. Both sites supported similar plant communities, although higher salinities at site 2 have been recorded than at site 1 due to recent floodgate opening trials which led to inundation with slightly brackish water (typically ≤ 5000 ppm).

The selected experimental species differ in size and growth form: *E. equisetina* is a rhizomatous sedge with photosynthetic stems (culms) to around one metre high; *B. caldwellii* grows to one metre in clumps and has rhizomes that terminate in subglobose woody tubers; *C. dactylon* and *P. distichum* are both low-growing stoloniferous and rhizomatous grasses, and; *B. monnieri* is a prostrate, stoloniferous, mat-forming herb with fleshy leaves and stems.

To standardise plants I trimmed them to a set size before growing them on to a suitable size for the glasshouse experiment. For *C. dactylon*, *P. distichum* and *B. monnieri*, 5–7 cm stem sections were planted, each bearing three nodes. For *B. caldwellii* single tubers of approximately 2.5 cm diameter were planted. For *E. equisetina* rooted ramets were used, each trimmed to 10 cm in height. The taller species, *B. caldwellii* and *E. equisetina*, were grown in 500 ml plastic pots, while the others were grown in 210 ml seedling tubes. The growing medium consisted of a 1:1:1 mixture of peat, loam and sand, with a six-month slow release granular fertilizer (Osmocote®) added at the manufacturer's recommended rate.

Plants were maintained for approximately six months in an unheated glasshouse under natural lighting. During this time pots were kept standing in three-cm deep trays of fresh tap water in order to keep the growing medium waterlogged. The experiment was conducted during November 2005 to February 2006 in an air-conditioned glasshouse with an approximate 28°C/20°C day/night temperature regime. In mid-November 2005, prior to the experimental treatments being applied, water depth was gradually increased to 10 cm, approximately 2 cm above the top edge of the pots. At the start of the experiment all plants were trimmed to a standard height: *E. equisetina* 20 cm, *B. caldwellii* 50 cm, *B. monnieri* seven cm, *P. distichum* 10 cm and *C. dactylon* 10 cm.

3.2.2 Experimental treatments

The salinity treatments were applied in plastic tubs (360 mm wide × 550 mm long × 550 mm deep), with two pots of each species from each site in each tub. Tubs were positioned in three blocks of eight, with one tub in each block representing each of the eight different salinity treatments. Tubs were randomly positioned within blocks.

Salinity treatments were prepared using a commercially available aquarium sea salt (AQUASONIC Ocean Nature®) dissolved in tap water to reach concentrations of 1500, 3000, 5000, 10 000, 15 000, 20 000 and 35 000 ppm, respectively. The control tubs contained only tap water, which was approximately 200 ppm. The salt concentrations in each tub were incrementally increased by one third of the target level per day until the respective final concentrations were reached.

Water levels in the tubs were topped up every 1–2 days to compensate for evaporation and evapotranspiration. The salt concentrations in the tubs were monitored and maintained throughout the length of the experiment to within approximately 100 ppm of target concentrations.

3.2.3 Measurements

Survivorship was recorded every 1–2 days. Plants were considered dead when no green leaves or stems remained (grasses particularly), or when all leaves and stems had wilted beyond recovery. Dead plants were removed.

Growth parameters were measured on all plants at the start of the experiment and again at 16-day intervals for the duration of the 64-day experiment. These measurements included: height (all species), numbers of stems or shoots (all species), numbers of live and dead stems (*E. equisetina),* numbers of live and dead leaves (*B. caldwellii* and *B. monnieri*) and total combined shoot lengths (*B. caldwellii* and *B. monnieri).* Trimming retarded the height growth of some stems in *B. caldwellii* and *E. equisetina* and after the dominant stems were trimmed plants responded by producing new shoots from the base of the plant. Therefore, height was rejected for growth comparisons in these species. Since the other growth measurements were closely correlated, the following sets of measurements were selected for the final analysis: for *B. monnieri* and *B. caldwellii* the numbers of live leaves per plant, and for *E. equisetina* numbers of live culms per plant at each measurement time.

For the grasses neither plant height measurements nor shoot counts alone were adequate indicators of plant growth. Some plants produced many short shoots, whereas others produced fewer longer shoots. For these species a simple growth index was calculated combining the two sets of measurements (growth = number of shoots × plant height). The reliability of the growth index was tested for each of the grasses by plotting the growth indices of all plants at day 64 (the final measurement time) against the dry weights of the shoot material harvested at that time, and was considered adequate (*C. dactylon* $y = 1334.5\,x + 565.37$, $R^2 = 0.75$; *P. distichum* $y = 1480.3\,x + 401.02$, $R^2 = 0.64$).

Total above-ground biomass accumulation over the experimental period was also recorded for all five species. To achieve this all plants were trimmed back to their standardised starting heights at the end of the experiment. The material removed was sorted into live and dead matter fractions for each plant and these samples were bagged, dried (65^{o}C for 48 hours) and weighed.

3.2.4 Analyses

Survivorship was compared between salinities for each species using Cox's proportional hazards regression. This method allowed the joint effects on plant survival of block, salinity, site, and the salinity × site interaction to be examined. JMP Version 5.0.1a (JMP 2002) software was used to perform the analysis.

Growth and biomass data were analysed separately for each species. Growth data were analysed using repeated measures ANOVA, after Crawley (2002) and Snedecor and Cochran (1989), with salinity and time as fixed factors and block, site and plant (nested in salinity and site) as random factors. Interactions between blocks and the main factors were not included in the statistical analyses (refer to Newman *et al.* 1995). Biomass gain data were analysed using random block ANOVA, with salinity as a fixed factor and block and site as random factors. Selection of appropriate denominators for calculating *F*-ratios followed Quinn and Keough (2002). Where sample sizes were unequal, appropriate quasi *F*-ratios and degrees of freedom were calculated using Satterthwaite's approximation (Minitab 2007).

The data were transformed using Taylor's power law prior to analysis to meet assumptions of normality and homogeneity of variances (square root transformation for *E. equisetina* growth data and *E. equisetina, B. monnieri*, *B. caldwellii* and *P. distichum* biomass data, and $\log_{10}$ transformation for all other growth and biomass data sets). All

ANOVAs were performed using the Minitab statistical package, Version 15 (Minitab 2007).

Some salinity treatments were excluded from analyses because high mortality led to inadequate replication. For *B. monnieri* and *E. equisetina* the highest salinity treatment was excluded, for *B. caldwellii* the two highest salinity treatments were excluded, and for *C. dactylon* the three highest salinity treatments were excluded. All salinity treatments were included for *P. distichum*. The mean growth and biomass values for surviving plants in all treatments are represented in the figures for these variables. Plant growth measurements were standardised before plotting to simplify comparison of treatments. This was done by subtracting the value of the measurement taken on day one of the experiment from all subsequent growth measurements for each plant.

3.3 Results

3.3.1 Survivorship

The results of the Cox's proportional hazards survival analyses demonstrate a significant effect of salinity on the survival of all species (Table 3.1). For all species, neither block nor site differed significantly, and all log-ratio Chi-squared values for site were less than one. No salinity × site interactions were significant (Table 3.1). The salinity required for a decrease in survivorship varied according to species (Figure 3.1).

Paspalum distichum had the highest rates of survivorship. All *P. distichum* individuals retained live shoots until the end of the experiment (Figure 3.1e), except in the 35 000 ppm treatment where the first plants died after 16 days, with dieback of others proceeding slowly afterward. However, more than 60% of these plants in the highest salinity treatment remained alive after 64 days.

Table 3.1. Results of Cox's proportional hazards survival analysis. Log-ratio Chi-squared values are given for each species.

Source	d.f.	*Bacopa .monnieri*	*Bolboschoenus caldwellii*	*Cynodon dactylon*	*Eleocharis equiesetina*	*Paspalum distichum*
Block	2	1.88	3.85	3.79	< 1.00	< 1.00
Salinity	7	50.87***	100.40***	88.95***	77.98***	12.08**
Site	1	< 1.00	< 1.00	< 1.00	< 1.00	< 1.00
Sal.×site	7	1.48	3.62	4.41	1.37	< 1.00

** $P \leq 0.010$; *** $P \leq 0.001$

Bacopa monnieri had the second highest survival rates under increased salinity with 100% survivorship in every treatment for at least the first 24 days (Figure 3.1a). From 24 to 48 days, mortality increased to 100% in the 35 000 ppm treatment. A small number of plants also died in the second highest salinity treatment, 20 000 ppm, after 48 days, but more than 90% remained alive in this treatment at the end of the experiment. As the stems of *B. monnieri* died off in the high salinity treatments they rotted and fragmented. On many of these floating stem fragments the leaves remained green and unwilted.

Eleocharis equisetina had the next highest survivorship under increased salinity. *Eleocharis equisetina* plants died rapidly at 35 000 ppm with more than more than 90% of plants dead over the first 16 days (Figure 3.1d). At 20 000 ppm plants began to die at a steady rate from day 16. However, all *E. equisetina* individuals survived the full 64-day experimental period in salinity treatments of 15 000 ppm or less.

For *B. caldwellii* 100% survivorship occurred only at salinities of 5000 ppm or less (Figure 3.1b). At 10 000 ppm and 15 000 ppm some mortality occurred, but the majority of plants survived 64 days. At 20 000 ppm leaf death was rapid, and in the highest salinity treatment all leaves and stems were dead after eight days *Cynodon dactylon* had the highest mortality rates per salinity treatment of the five species (Figure 3.1c). One hundred percent survival occurred only in the control and 1500 ppm treatments. At higher salinities mortality increased over time in proportion to salt concentration.

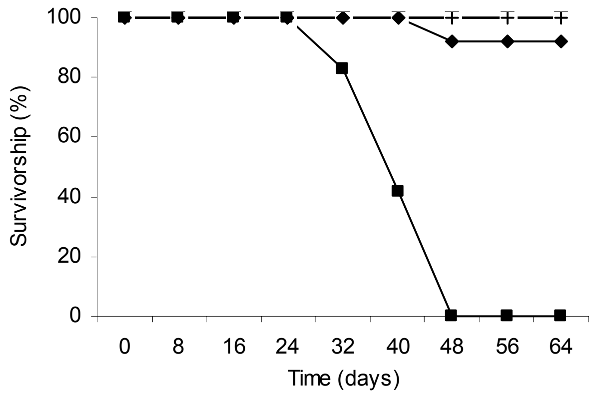
3.3.2 Growth rates

Visible differences in plant size and leaf and stem production were apparent between salinity treatments for every species after the first measurement period (Figure 3.2). The ANOVA results (Table 3.2) showed a significant negative effect of salinity on the growth of every species, although this effect was marginal for the two grasses ($P \leq 0.10$). For *C. dactylon* this result indicates marginally significant differences in growth rate of plants between salinity treatments of ≤ 10 000 ppm (Figure 3.3) only, since mortality was too high to compare measurements from plants in the other treatments (Figure 3.1). For *P. distichum* survivorship was higher (Figure 3.1) and the marginally significant differences in growth rate apply across all salinities (Figure 3.3). For *B. monnieri* and *E. equisetina* only the highest salinity treatment was excluded from growth and biomass comparisons, and for *B. caldwellii* the two highest salinity treatments were excluded.

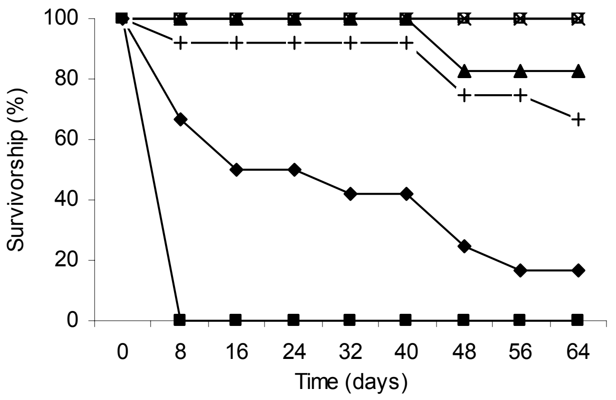
Collection site had a significant effect on growth for every species except *P. distichum,* with higher growth of plants from site one for *C. dactylon* and *B. caldwellii* and higher growth of plants from site two for *B. monnieri* and *E. equisetina* (Figure 3.4). A significant time × site interaction also occurred for *C. dactylon* due to higher growth recorded for plants from site one at lower salinities, but decreasing differences between the sites as salinity increased and growth became negligible for plants from both sites.

There were highly significant differences in growth between individuals for every species, and also between measurement times for all species except *B. caldwellii*. Significant time × salinity interactions occurred for *B. caldwellii* and *E. equisetina* due to growth rates in some treatments decreasing over time (Figure 3.3). There were also significant differences in growth between blocks for all species except *B. monnieri*.

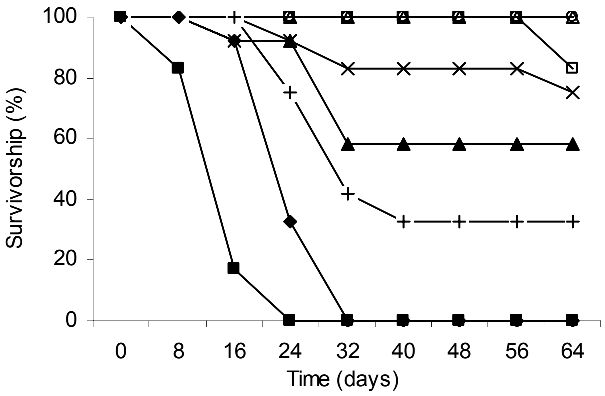
a) *Bacopa monnieri*



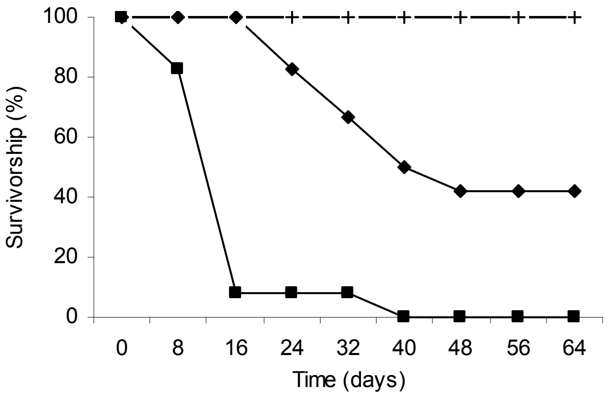
b) *Bolboschoenus caldwellii*



c) *Cynodon dactylon*



d) *Eleocharis equisetina*



e) *Paspalum distichum*

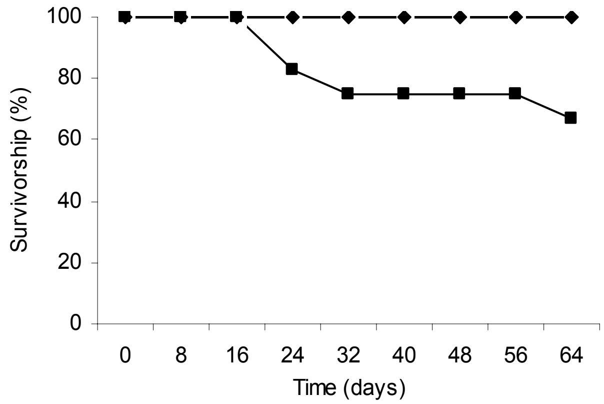


Figure 3.1. Effect of increasing salinity on survivorship over 64 days (n = 12 plants per salinity treatment). Key: △ Control, ⊖ 1500ppm, ✳ 3000ppm, ⊟ 5000ppm, ▲ 10 000ppm, + 15 000ppm, ◆ 20 000ppm, ■ 35 000ppm.

Of the three species on which sequential counts of live and dead leaves or culms were made, *B. monnieri* growth appeared to be least affected by salinity. *Bacopa monnieri* (Figure 3.3a) maintained a positive rate of leaf production over the 64-day experimental period in all but the highest salinity treatment. At the highest salinity very few or no new leaves were produced per plant. However, the number of live leaves present on *B. monnieri* plants remained relatively constant for the first 32 days, after which the plants began to die. In contrast to *B. monnieri, B. caldwellii* exhibited dieback of existing leaves from the first measurement period (day eight) onward in salinities ≥ 10 000 ppm (Figure 3.3b). *Eleocharis equisetina* growth was reduced at salinities ≥ 5000 ppm with declining numbers of live culms recorded from day eight onward (Figure 3.3d). However, *E. equisetina* plants also began to yellow and die back in every salinity treatment during the latter half of the experiment. Yellowing was also observed in other *E. equisetina* plants in the glasshouse as well as in the field at that time (late Summer).

The numbers of stems recorded for the grasses were totals and did not differentiate between live and dead stems, therefore rates of dieback cannot be examined. However, the calculated growth indices give an indication of overall differences in growth between salinities over time. *Cynodon dactylon* growth ceased during the first eight to 16 days at ≥ 20 000 ppm (Figure 3.3c), whereas *P. distichum* maintained a low but positive growth rate in these conditions (Figure 3.3e).

3.3.3 Above-ground biomass accumulation

Above-ground biomass accumulation for all species was significantly reduced with increasing salinity (Table 3.3, Figure 3.4). However, one exception was found in *P. distichum* with plants accumulating more above-ground biomass in the 10 000 ppm treatment than in the 5000 ppm or 15 000 ppm treatments. Initial plant collection site also had a significant effect on shoot biomass production for all species except *P. distichum* (Table 3.3), with plants from site one accumulating more biomass for *C. dactylon* and *B. caldwellii* and plants from site two accumulating more biomass for *B. monnieri* and *E. equisetina* (Figure 3.4). There were no significant salinity × site interactions (*P* > 0.14), and there was a significant effect of block for *C. dactylon* only (Table 3.3).

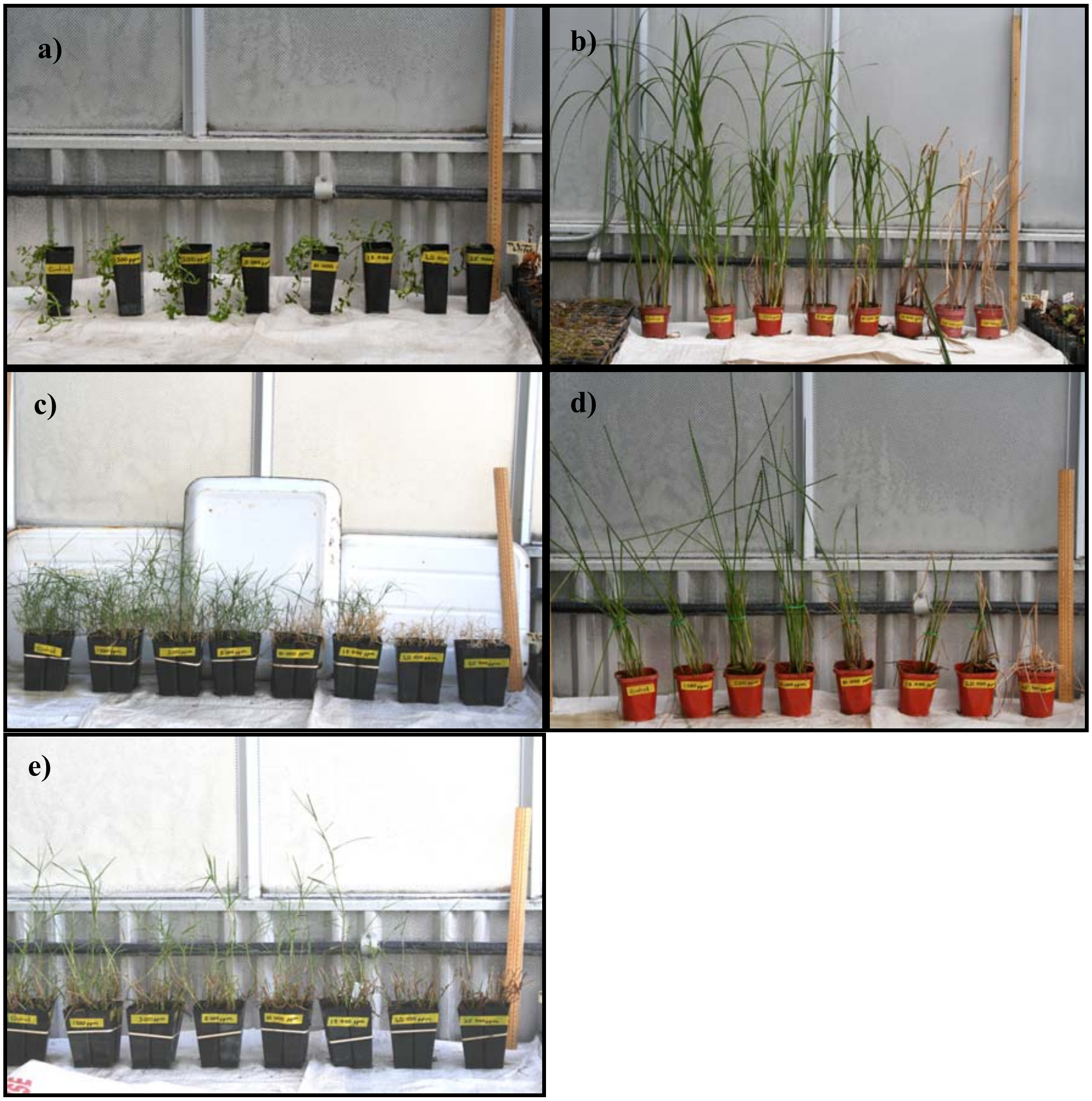


Figure 3.2. Visible differences in plant size and leaf and stem survival between the salinity treatments, for **a)** *Bacopa monnieri,* **b)** *Bolboschoenus caldwellii,* **c)** *Cynodon dactylon,* **d)** *Eleocharis equisetina,* and **e)** *Paspalum distichum.* (Photographs taken three weeks after treatments applied. One metre rule displayed in **3.2b**, and 50cm rule in others).

Table 3.2. Results of ANOVAs on sequential growth measurements, recorded on days 0, 16, 32, 48 and 64 of the experiment.

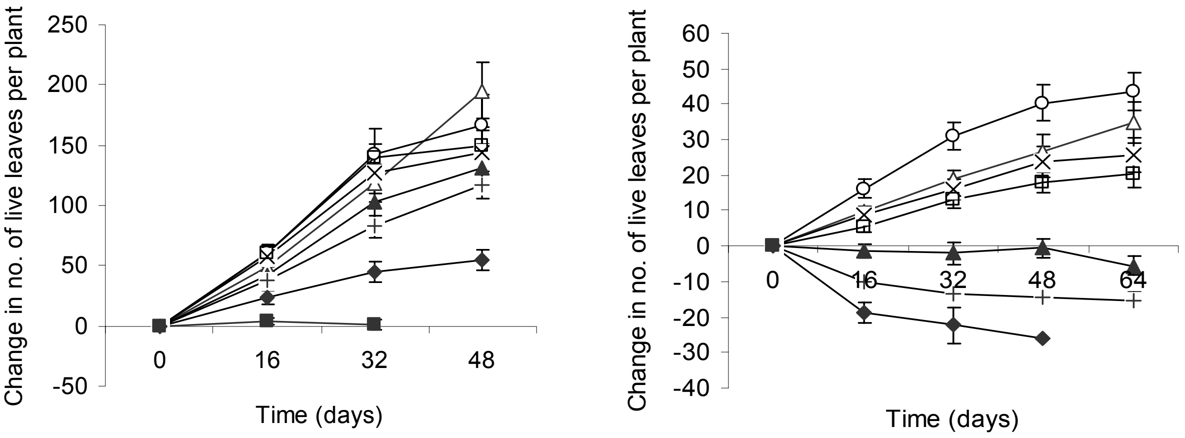
Source	*Bacopa monnieri*		*Bolboschoenus caldwellii*		*Cynodon dactylon*		*Eleocharis equisetina*		*Paspalum distichum*	
	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Block	2, 280	2.17	2, 289	5.83^{**}	2, 229	23.43^{***}	2, 340	5.24^{**}	2, 400	5.65^{**}
Salinity	6, 6	11.08^{**}	5, 5	32.16^{***}	4, 4	$3.94^{\dagger}$	6, 6.1	12.64^{**}	7, 7	$3.18^{\dagger}$
Site	1, 2.2	32.24^{*}	1, 6.3	56.27^{***}	1, 5.3	27.64^{**}	1, 4.6	7.38^{*}	1, 4.8	0.00
Salinity × site	6, 14	0.33	5, 12	1.14	4, 10.1	0.81	6, 14	0.54	7, 16	1.19
Plant (sal, site)	14, 280	2.71^{***}	12, 289	4.49^{***}	10, 229	3.09^{***}	14, 340	6.43^{***}	16, 400	3.69^{***}
Time	3, 3	157.83^{***}	4, 4	2.25	4, 4.1	46.71^{***}	4, 4.5	39.84^{***}	4, 4.2	481.88^{***}
Time × salinity	18, 280	1.58	20, 289	13.85^{***}	16, 229	1.09	24, 340	3.66^{***}	28, 400	0.78
Time × site	3, 280	1.53	4, 289	2.35	4, 229	2.65^{*}	4, 340	0.64	4, 400	0.27
Error	280		289		229		340		400	

† $P \leq 0.10$, $^{*}P \leq 0.050$; ** $P \leq 0.010$; *** $P \leq 0.001$. Degrees of freedom are numerator, denominator and were calculated using Satterthwaite's approximation. The time × salinity × site and the time × plant (salinity, site) interactions were not significant ($P > 0.25$) for any species and were pooled with the error term in the final analyses.

Table 3.3. Results of ANOVAs on dry weights (g) of shoot material gained during the experimental period.

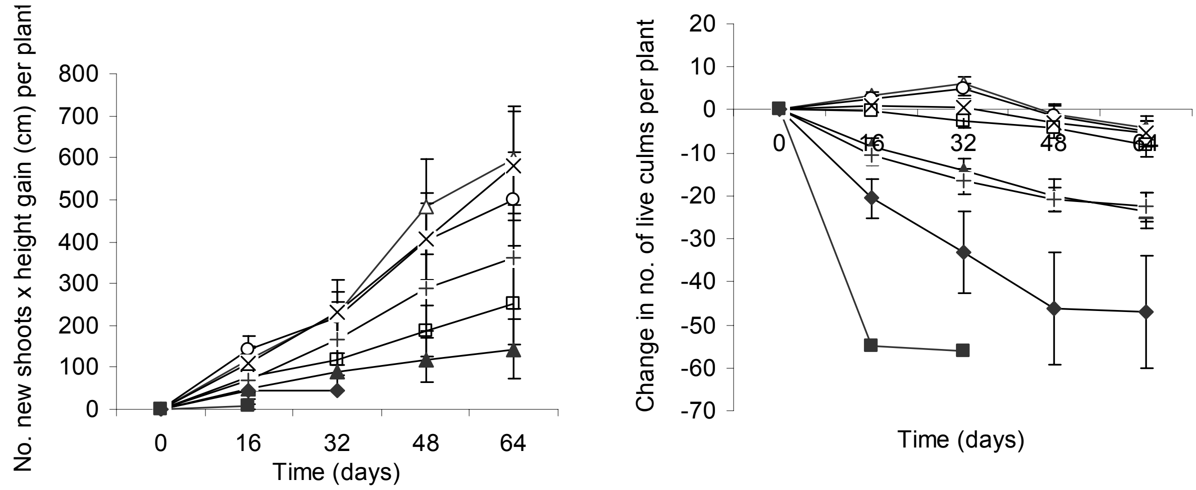
Source	*Bacopa monnieri*		*Bolboschoenus caldwellii*		*Cynodon dactylon*		*Eleocharis equisetina*		*Paspalum distichum*	
	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*	d.f.	*F*
Block	2, 66	0.09	2, 47	3.16	2, 40	15.54^{***}	2, 61	1.17	2, 74	0.18
Salinity	6, 6	11.04^{**}	5, 5.1	41.72^{***}	5, 4.4	66.16^{***}	6, 6	16.72^{**}	7, 7	12.43^{**}
Site	1, 6	25.69^{**}	1, 5.7	9.27^{*}	1, 24.1	88.06^{***}	1, 7.9	10.75^{*}	1, 7.6	0.13
Salinity × site	6, 66	0.38	5, 47	1.73	5, 40	0.15	6, 61	1.57	7, 74	0.54
Error	66		47		40		61		74	

$^{*}P \leq 0.050$; ** $P \leq 0.010$; *** $P \leq 0.001$. Degrees of freedom are numerator, denominator and were calculated using Satterthwaite's approximation.



a) *Bacopa monnieri*

b) *Bolboschoenus caldwellii*



c) *Cynodon dactylon*

d) *Eleocharis equisetina*

e) *Paspalum distichum*

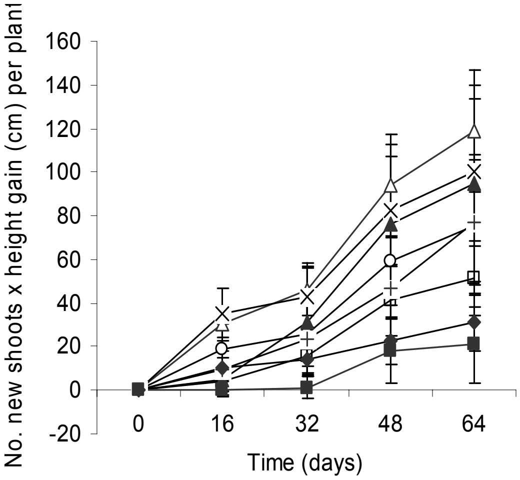
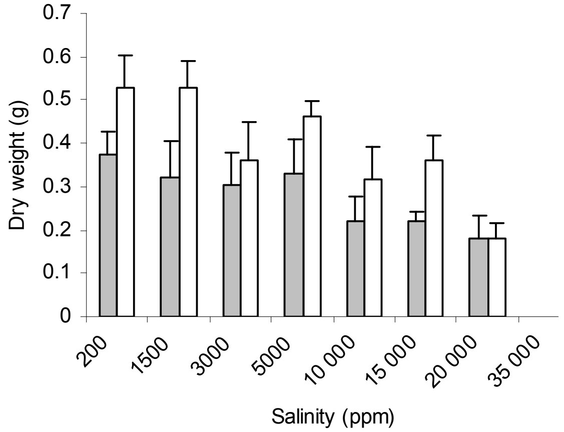
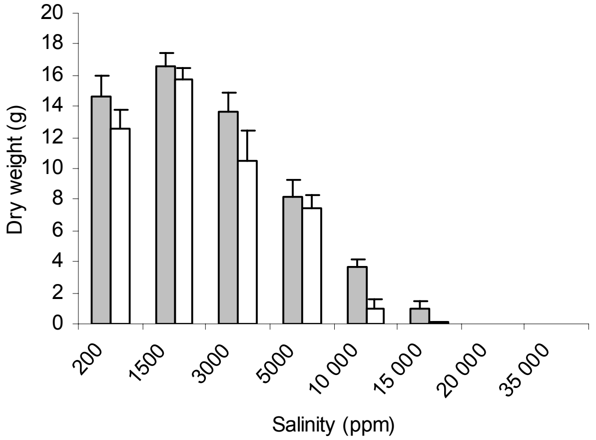


Figure 3.3. Effect of increasing salinity on plant growth (△ control, ○ 1500ppm, × 3000ppm, □ 5000ppm, ▲ 10 000ppm, + 15 000ppm, ◆ 20 000ppm, ■ 35 000ppm). Bars show s.e.m. of up to 12 plants (number of deaths indicated in mortality results).

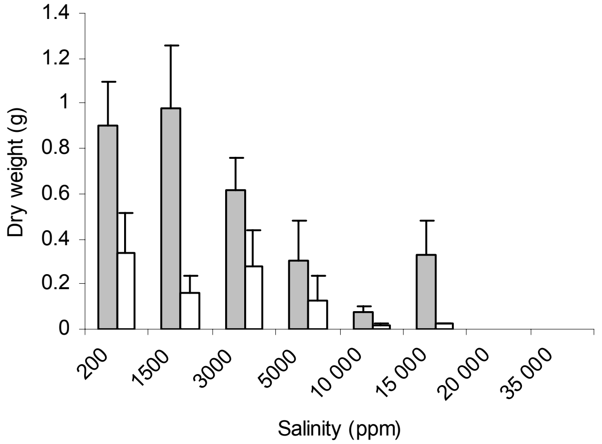
a) *Bacopa monnieri*



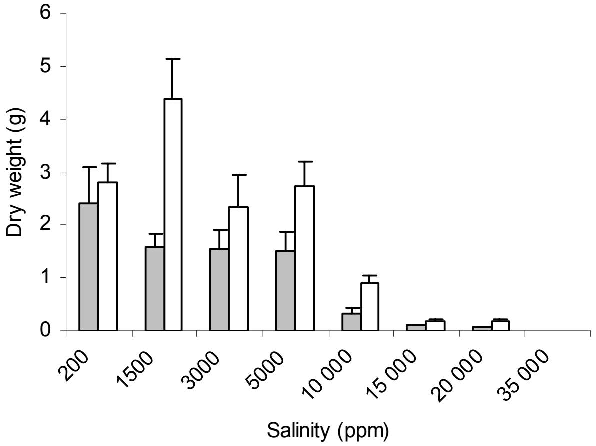
b) *Bolboschoenus caldwellii*



c) *Cynodon dactylon*



d) *Eleocharis equisetina*



e) *Paspalum distichum*

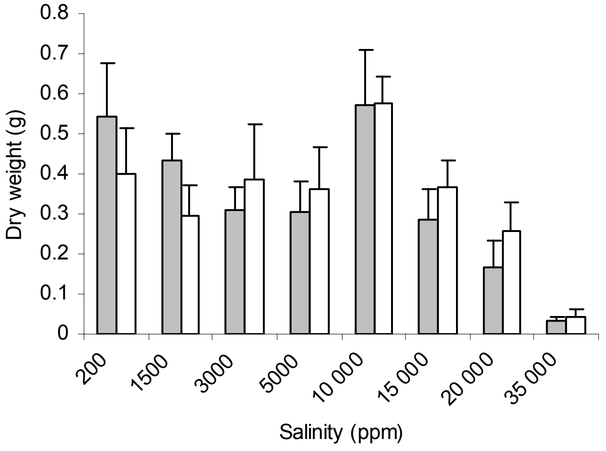


Figure 3.4. Effect of increased salinity on above-ground biomass gain (▨ site one, ☐ site two.) Bars show s.e.m. of up to 12 plants (number of deaths indicated in mortality results).

3.4 Discussion

This experiment demonstrated the effects of different salinities on the growth and survival of five common and widespread coastal floodplain macrophyte species, *B. caldwellii, B. monnieri, C. dactylon, E. equisetina* and *P. distichum,* under waterlogged conditions. By using a glasshouse experiment I was able to isolate the effects of salinity from those of other environmental factors that would have confounded the interpretation of species salt-tolerance ranges in a survey or field experiment.

While glasshouse experiments such as this one can be used to measure and rank species salinity tolerance ranges, there are limitations to this approach. In particular, absolute salt concentrations affecting growth and survival can vary according to other factors, such as water availability, plant growth stage, temperature and herbivory (Hart *et al.* 1991; Jolly *et al.* 2008). The salinities tolerated in this glasshouse experiment could be higher than those that these species would typically inhabit in the field due to the absence of other factors that could limit plant growth and survival at field sites. However, while absolute salinity tolerance thresholds may vary, the data obtained here data are still expected to be representative of the relative salinity tolerance of these species (Maas 1977; Hart *et al.* 1991; Miyamoto 1996; Sim *et al.* 2006).

Overall it was found here that growth rates, above-ground biomass accumulation and survival rates declined significantly for every species as salinity increased. While these species commonly co-occur in the field, the salt concentrations that led to increased mortality and decreased growth were found to differ considerably between species. In comparison with previous work assessing salt tolerance of *P. australis* (Bart and Hartman 2000; Bart and Hartman 2002)*,* only *B. monnieri* showed a comparable degree of tolerance to increased salinity. In order of survivorship, *P. distichum* was followed by *B. monnieri*, *E. equisetina*, *B. caldwellii*, and finally by *C. dactylon*. Growth responses under the different salinities could not be compared in the same way as mortality results between all species because the measurements needed to demonstrate growth over time varied according to differences in plant growth form (Maas 1977; Hart *et al.* 1991; Jolly *et al.* 2008). However, rates of live leaf gain or loss could be compared between *B. monnieri, B. caldwellii* and *P. distichum,* and plant growth indices could be compared between treatments for the two grasses, *C. dactylon* and *P. distichum.*

In the species with the highest survivorship under elevated salinity, *P. distichum,* plant deaths occurred in the highest salinity treatment only. However, even in the 35 000 ppm treatment only one third of the plants died over the 64-day period, indicating a strong ability to withstand short-term salinity increases. Growth of *P. distichum* appeared to be unaffected by low to intermediate level salinity increases, with little apparent difference seen in mean above-ground biomass production at salinities ≤ 15 000 ppm. An exception was the 10 000 ppm treatment in which slightly higher above-ground biomass was recorded. Higher growth in the 10 000 ppm treatment may indicate that *P. distichum* grows better at this intermediate salinity level. However, plants in this treatment did grow slightly taller than plants in some of the lower salinity treatments between the initial trimming and the first measurement, i.e. before treatments were applied, so it is also possible that the difference observed was due to a slightly higher initial growth potential for some plants in this treatment.

Bacopa monnieri plants had the second highest set of survival rates under elevated salinity. *Bacopa monnieri* plants survived for 64 days in waterlogged conditions and at salinities ranging from fresh up to 15 000 ppm, whilst maintaining relatively rapid growth rates. At higher salinities growth rate was reduced, and the plants began to fragment as stems died. However, these stem fragments were node-bearing and buoyant, indicating that they may be capable of dispersing to and colonising new areas where salinity conditions are more favourable. Detached floating pieces of *B. monnieri* have been previously observed in the field (site 2) away from established clumps, and node-bearing stem sections readily produced roots in the glasshouse during this experiment (pers. obs.), supporting this hypothesis. Increased salinity appeared to affect growth rates of *B. monnieri* less than those of *B. caldwellii* or *E. equisetina.* While *B. monnieri* maintained and increased live leaf numbers throughout the experiment in all treatments except the

35 000 ppm treatment, *B. caldwellii* and *E. equisetina* experienced rates of leaf and culm decline faster than their rates of new leaf or culm production in all treatments ≥ 10 000 ppm.

Based on survivorship, *E. equisetina* displayed the third greatest tolerance toward increased salinity. At the end of the experiment all plants in the 35 000 ppm treatment, and 60 % of plants in the 20 000 ppm treatment had died, however, at salinities ≤ 15 000 ppm all *E. equisetina* plants survived the 64-day experimental period. New culms were also produced throughout the experiment in all treatments ≤ 20 000 ppm. However, once salinity reached ≥ 10 000 ppm *E. equisetina* plants demonstrated a more rapid rate of culm loss than culm production and also a substantial reduction in average above-ground biomass. This result suggests that *E. equisetina* plants are likely to die if exposed to salinities ≥ 10 000 ppm over a longer time period. Around 32 days into the experiment some culms began to senesce on *E. equisetina*, as evidenced by a colour change from green to shades of orange, red and yellow. This change occurred at a similar time in plants kept in another non-air-conditioned glasshouse and also occurred under natural conditions at coastal field sites more than 200 km away (A. Smith pers. com., March 2006). Thus, this senescence was most likely a consequence of seasonal changes, such as decreasing day length and lower temperatures. The decline in growth in the low salinity treatments during the second half of this experiment should be interpreted with this ‘natural’ senescence in mind.

Based on survival, *B. caldwellii* and *C. dactylon* appear least able to withstand increases in site salinity under waterlogged conditions. While the other species experienced mortality only in the two highest salinity treatments, some *B. caldwellii* and *C. dactylon* plants also died in some of the lower salinity treatments.

Bolboschoenus caldwellii had very low survivorship in the two higher salinity treatments, with more rapid mortality in the 35 000 ppm treatment than any other species, and some mortality also occurring in the 15 000 and 10 000 ppm treatments. At salinities ≤ 15 000 ppm most *B. caldwellii* plants survived for the full 64 days. However, if the experiment had been extended, *B. caldwellii* plants growing in salinities ≥ 10 000 ppm are unlikely to have survived over much longer periods of time since at 10 000 ppm leaf loss was occurring at a faster rate than leaf production. *Bolboschoenus caldwellii* grew best at salinities ≤ 5000 ppm. These results support earlier suggestions that a decline in *B. caldwellii* observed at the Little Broadwater wetland after floodgate opening was most likely due, at least in part, to low salt tolerance compared to other dominant species (Graham *et al.* 2004).

Cynodon dactylon had the lowest survivorship under increased salinity of the five species tested, with plant deaths occurring in all treatments ≥ 5000 ppm. More than half of the *C. dactylon* plants had died after only four weeks in salinities ≥ 15 000 ppm. This low salt tolerance of *C. dactylon* compared to *P. distichum,* measured here in waterlogged conditions, contrasts with the findings of Semple *et al.* (2004) who found *C. dactylon* to be more salt tolerant than *P. distichum* when planted on dryland salt scalds. In Clarence estuary wetlands *P. distichum* typically inhabits waterlogged and shallowly inundated areas, whereas *C. dactylon* dominates above the waterline (Pressey and Clancy 1979; Pressey 1987). This difference in distributions appears likely to have been caused by a low tolerance of *C. dactylon* toward waterlogging since in this experiment, where all plants were subjected to waterlogging, *C. dactylon* produced minimal biomass in any treatment including the fresh water controls.

There were some differences in growth rate between plants taken from the two field sites, with *C. dactylon* and *B. caldwellii* plants from site one growing significantly faster than those from site two, and the opposite trend for *B. monnieri* and *E. equisetina.* Past differences in the salinities of these sites prior to plant collection may have affected their growth potential, through delayed effects of recent exposure (Espinar *et al.* 2005; Salter *et al.* 2008), or through long-term selection which may have caused variation in the salt tolerance of these species between sites. While some site differences did occur, no significant site × salinity interactions were found, indicating that collection site affected the magnitude, but not the direction of the salinity effect on growth or survival. Significant differences in growth were also found between plants within each species, but these were not great enough to mask the overall differences in growth between salinity treatments.

Trimming affected the height growth of stems in *B. caldwellii*, but new stems were produced and total combined stem length provided a good measure of growth over time, as did total leaf number. Culms of *E. equisetina* also showed very little height growth after trimming. In future experiments a different method should be used to standardise these species. Also, as numbers of leaves and total combined stem lengths were closely correlated for *B. caldwellii* and also for *B. monnieri*, measurement of one of these variables should be sufficient in future growth experiments. Standardising initial plant size by weight would provide a better basis for direct between-species comparisons of growth and survivorship in further experiments.

In wetlands occupied by these particular species, tidal restoration is expected to lead to decreases in *C. dactylon* cover due to increased waterlogging. Salinity increases are expected to have the largest and most rapid effect on *B. caldwellii* stands, with *B. caldwellii* displaying declining growth and survivorship here at the lowest salinities. *Eleocharis equisetina* stands are then expected to be the next most affected by salt-induced dieback, followed by those of *B. monnieri* and then *P. distichum.*

In predicting the overall effects of tidal restoration on these plant communities there are also several additional avenues which would be useful to explore to supplement these results. Differences between species in reproductive ability and propagule dispersal ability under increased salinities may affect the way tidal restoration affects the distribution of these species. The floating stem fragments and adventitious roots observed in *B. monnieri* may allow this species to disperse and reestablish vegetatively in more favourable areas if site salinity levels become too extreme. However, the other species investigated did not break up into vegetative dispersal units under extreme salinities. The relative importance of seed and vegetative propagules in establishment of these species at new sites is not known, nor has the effect of salinity on seed production, germination or seedling establishment rates ever been tested.

Seed and seedlings may also be less tolerant toward increased salinity than established plants (Bart and Hartman 2002). Further investigation into the effects of salinity and/or water regime on different plant life stages could also be of value in predicting which species are most likely to establish under altered salinity and flooding regimes (James *et al.* 2003). More information on the recovery ability of species after salt-induced dieback could also help in predicting how salinity fluctuations would affect plant communities (Howard and Mendelssohn 1999; James *et al.* 2003).

Furthermore, floodgate manipulation is expected to increase not only the salinity, but also the depth, duration and frequency of inundation of rehabilitation sites. Investigation into the effects of combined increases in salinity and these various components of water regime on germination, establishment, growth and survival of coastal floodplain wetland species would provide further useful information to help predict the outcomes of tidal restoration in these systems.

CHAPTER 4

Combined effects of increased salinity and water depth on the growth and survival of four macrophyte species

4.1 Introduction

Tidal restoration has been proposed for the rehabilitation of drained, impounded wetlands on the Clarence River estuary, located on the far north coast of NSW in eastern Australia. This restoration is expected increase salinity as well as the depth, duration and frequency of inundation at rehabilitation sites. Species composition in wetland macrophyte communities typically varies along the estuarine gradient according to differences in site salinity (Odum 1988); within wetlands it also varies along an elevation gradient, with species elevation ranges primarily determined by their tolerance toward depth, duration, frequency and timing of inundation, and other correlated factors, such as soil moisture content and redox potential (Odum 1988; Sorrell *et al.* 2002). Since salinity and inundation regimes are the primary abiotic factors determining the distribution of coastal wetland macrophyte species (Odum 1988; Laegdsgaard 2006), tidal restoration is expected to cause changes to macrophyte community composition.

This chapter focuses on predicting how tidal restoration may affect some of the most common and widespread macrophyte species currently found in drained, secondarily fresh and oligohaline impounded wetlands on the Clarence River estuary. To predict how the habitat ranges of these species may be affected by tidal restoration, it is necessary to know how both salinity and inundation affect their establishment, growth and survival. While other factors, such as interspecific competition, herbivory, and disturbance, can also modify the habitat ranges occupied by wetland macrophytes (Keddy 2000; Geho *et* *al.* 2007), the direct effects of increased salinity and water depth on plant growth and survival are focused on here.

4.1.1 Effects of increased water depth on emergent macrophyte growth and survival

Inundation and salinity stress affect the growth and survival of wetland macrophytes in different ways. Inundation reduces the availability of light, atmospheric gases and nutrients to plants, with species differing in their ability to overcome these resource restrictions (Keddy 2000). Within wetlands, macrophyte species are, therefore, commonly restricted to particular elevation ranges, or zones, largely determined by their inundation tolerance limits (Keddy 2000). For example, Brock and Casanova (1997) grouped macrophytes into terrestrial, amphibious and submerged categories according to relative inundation tolerance, with terrestrial species intolerant of waterlogging and occurring above the high water mark, submerged species growing in inundated areas, and amphibious species occurring in the wet/dry ecotone.

Of these groups, terrestrial and low-growing and/or emergent amphibious macrophytes are likely to be more vulnerable to rapid increases in water depth than floating species. While these species are attached to the substrate and may become submerged, many are unable to maintain adequate rates of photosynthesis or gas exchange to grow and survive for long periods underwater (Siebentritt and Ganf 2000). Some emergent macrophytes survive depth increases by shifting a higher proportion of their biomass into above-ground parts and/or growing taller to maintain photosynthetic leaf or stem tissue above the water surface (Rea and Ganf 1994; Siebentritt and Ganf 2000). For example, survival of the emergent sedge *Bolboschoenus caldwellii* under flooded conditions was found to be dependent on stem height and the presence of photosynthetic material above the waterline, with no completely submerged plants surviving to the end of a four-week experiment (Siebentritt and Ganf 2000).

4.1.2 Current zonation of species in fresh and oligohaline Clarence floodplain wetlands

In impounded, fresh-oligohaline wetlands on the NSW north coast, stands of *Cynodon dactylon, Paspalum distichum* and *Eleocharis equisetina* often occur in relatively close proximity but more or less clearly separated along a depth gradient, with *C. dactylon* above the high water mark, *E. equisetina* in shallow water (up to approximately 20 cm deep), and *P. distichum* occupying the damp ground in between. *Bolboschoenus caldwellii* is also commonly found on damp ground or in shallow water, while *Bacopa monnieri* is often found at the edges of wetlands. Based on the distributions of these species in Clarence River wetlands (Chapter 2), *C. dactylon* appears terrestrial, while the other species can be classed as amphibious (Brock and Casanova 1997). At the survey sites, *C. dactylon* appeared only above the waterline. *Cynodon dactylon* also performed poorly in the salt-tolerance experiment conducted under waterlogged conditions, even in fresh water controls (Chapter 3).

The results of the survey also suggest that amongst these amphibious species *E. equisetina* and *Bolboschoenus caldwellii* may be more tolerant of inundation than *P. distichum* and *Bacopa monnieri.* While the inundation tolerance of *E. equisetina* has not been tested, this species occurred across a greater range of depths than *Bacopa monnieri, Bolboschoenus caldwellii* or *Cynodon dactylon,* occurring at sites with depths to 75 cm. Experimental depth tolerance testing has been carried out for *B. caldwellii*, and the results suggest the optimum depth range of *B. caldwellii* in fresh water is from 20 cm above the waterline to 20 cm below (Siebentritt and Ganf 2000). In the field survey the distribution of *B. caldwellii* fell within five cm of this optimum depth range (maximum depth 25 cm). The inundation tolerances of *B. monnieri* and *P. distichum* have not been experimentally tested. However, both species are known to tolerate some flooding; *Bacopa monnieri* has floating stems and is commonly grown as an aquarium plant (Sainty and Jacobs 1994), and *Paspalum distichum* is reported to prefer regularly wet or flooded areas, growing best in fresh water up to 15 cm deep (Rose *et al.* 2006).

In the field survey *P. distichum* was typically found on damp mud only, around the wetland edge. *Paspalum distichum* was also observed during preliminary surveys growing at a depth of approximately 60 cm at one site where *E. equisetina* was absent. However, *P. distichum* was found only around the damp edge zone at the majority of sites, where shallow areas were dominated by *E. Equisetina* (pers. obs.). Other evidence suggests that *P. distichum* may be more tolerant of inundation than its typical habitat range in the Clarence floodplain wetlands suggests. For example, in a project quantifying biomass production of *P. distichum* in flooded situations in India, this species was recorded as persisting for periods of a year or more at depths over 60 cm (van der Valk *et al.* 1993). The authors also stated that if *P. distichum* has produced sufficiently long runners, these can float to the water surface during flooding, forming thick floating mats that later drop to the soil surface as the water level recedes.

4.1.3 Effects of increased salinity on emergent macrophyte growth and survival

Salinity increases can affect the growing environment of wetland macrophytes in a number of ways. Changes to water salinity also involve changes in electroconductivity, hydrogen-ion concentration, water density, the relative proportions of ions other than sodium and chloride and osmolarity (Sculthorpe 1985). These factors affect plant growth by disturbing the electrolyte balance, which can modify water uptake, cause deficiencies of some essential nutrient elements and cause excesses of some unwanted salts in plant tissues (Alam 1994).

Symptoms of salinity-induced stress include reduced rates of photosynthesis and biomass production, chlorosis, and tissue death (Alam 1994). Salinity stress can also lead to changes in biomass allocation, causing reductions in above-ground biomass production and increased proportional allocation to roots (Morris and Ganf 2001). This biomass allocation shift away from aerial parts is opposite to the height growth response required for some emergent macrophytes to tolerate flooding stress (Morris and Ganf 2001). Increased salinity may therefore reduce the ability of emergent macrophytes to tolerate water depth increases by limiting above-ground biomass production, which may prevent plants from maintaining sufficient photosynthetic material above the waterline to survive (Morris and Ganf 2001).

I found reduced rates of growth and above-ground biomass production with increased salinity in the salt-tolerance experiment on *Bacopa monnieri, Bolboschoenus caldwellii, C. dactylon, E. equisetina* and *P. distichum* (Chapter 3). If these species depend on leaf or stem height increases to survive flooding, I hypothesise that they will have a reduced ability to withstand water depth increases when salinity is concurrently increased. If this prediction is true, then in saltier water the elevation ranges occupied by these species may be reduced and they will be restricted to areas higher up the elevation gradient with shallower maximum water depths, or in areas subject to fewer rapid depth increases than they could tolerate in fresh water.

This chapter examines the relative tolerances of four of the above species, *B. caldwellii, C. dactylon, E. equisetina* and *P. distichum*, to increases in water depth in freshwater conditions, and determines whether increased salinity affects the abilities of each of these species to survive depth increases. The fifth species, *B. monnieri,* included in the Chapter 3 salt-tolerance experiment, was excluded here because it has floating stems and is commonly grown as an aquarium plant (Sainty and Jacobs 1994), making it less likely than the other species to be affected negatively by water depth increases.

4.1.4 Aims

This experiment aimed to:

1. Test whether there are differences in the inundation tolerances of *B. caldwellii, C. dactylon, E. equisetina* and *P. distichum,* as suggested by the differences in their relative depth distributions observed in the field (Chapter 2), and;

2. Determine if exposure to increased salinities will reduce the ability of these species to tolerate increased water depth, which could lead to a contraction of their potential depth ranges after tidal flow restoration.

4.2 Materials and methods

4.2.1 Plant material

The four experimental species differ in size, growth form and habitat. *Eleocharis equisetina* is a stoloniferous sedge with basal meristems and culms (photosynthetic stems) to around one metre in height, typically forming dense stands in shallow water. *Bolboschoenus caldwellii* is a sedge with upright stems bearing true leaves that also grow to approximately one metre in height. *Bolboschoenus caldwellii* stems have apical meristems, and arise from bulbous tubers produced on underground rhizomes in the previous growing season. *Bolboschoenus caldwellii* occurs in clumps on damp ground and in shallow water. *Paspalum distichum* and *C. dactylon* are both low-growing stoloniferous grasses. However, while *C. dactylon* is typically found above the high water mark, *P. distichum* occurs in damp to shallow water habitats.

Approximately 250 plants of each species were obtained from two wetlands on the Clarence River floodplain during August 2006. These were a freshwater area (-29° 25' 09'': 147° 6' 07'') adjacent to the Broadwater wetland, and a ponded freshwater section of Everlasting Swamp (-29° 31' 23'': 147° 3' 32''). Historically these wetlands were oligohaline to mesohaline and subject to tidal inundation. However, infrastructure built around the 1950s has isolated these wetlands from adjacent tidal waterways, converting them into fresher, rainfall-dependent wetlands. It was necessary to use more than one collection site to obtain sufficient plant material of all four species due to the effects of grazing. These particular sites were selected because they had similar salinity levels and hydrological regimes as well as vegetation communities typical of secondarily fresh wetlands on the floodplain. Individual plants were collected from points spaced c. 5–10 m apart to maximise the variety of genetic material obtained.

The plants were washed, trimmed to an approximate standard size, and weighed before being placed in pots. The root-bearing runners used for *C. dactylon* and *P. distichum* weighed 5.8 ± 0.7 and 4.6 ± 0.5 g respectively at planting. Rooted tufts of *E. equisetina* had culms c. 30 cm tall and weighed 6.5 ± 1.8 g at planting. For *B. caldwellii* tubers, c. two to three cm in diameter and weighing 7.6 ± 1.4 g, were used.

Plants were potted into 2.8 L capacity pots with a potting mix consisting of equal proportions of sand, peat and loam. Pots were then placed into trays of water c. 10 cm deep in an unheated polyhouse (Figure 4.1) with temperatures at approximately 35 ^{o}C/12 ^{o}C day/night and natural light. Pot positions were regularly rotated to minimise possible position effects on growth. After two months 144 plants of each species were selected and randomly allocated to experimental treatments.

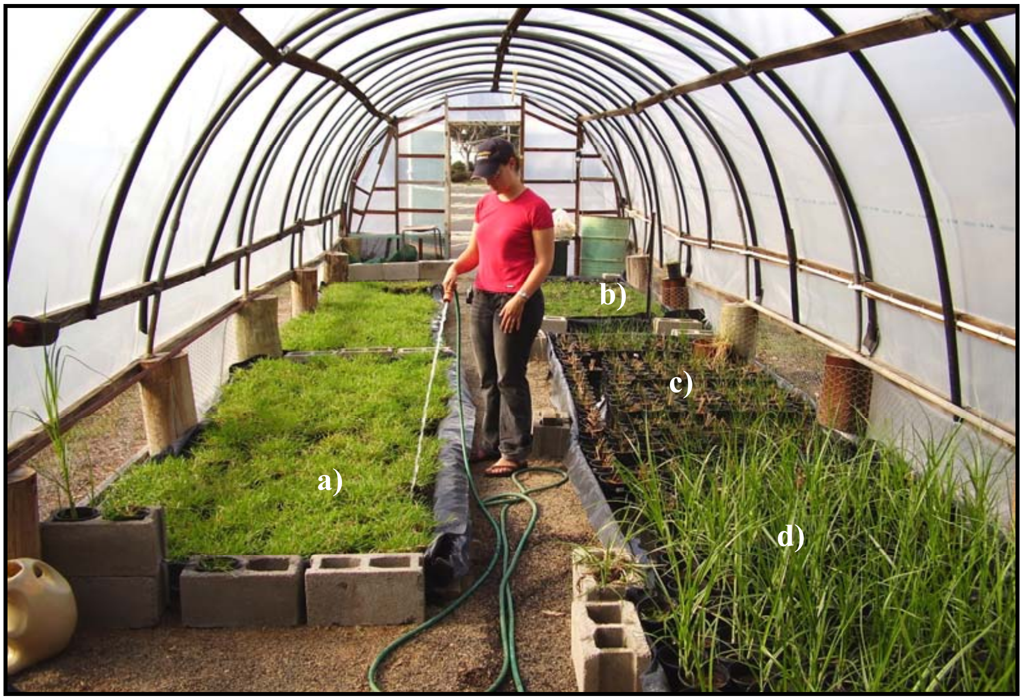


Figure 4.1. Plants in the polyhouse approximately six weeks after potting up, including **a)** *Paspalum distichum,* **b)** *Cynodon dactylon,* **c)** *Eleocharis equisetina,* and **d)** *Bolboschoenus caldwellii.*

4.2.2 Experimental design

The experiment was conducted outdoors during October–December 2006 in large fibreglass tubs, 110 cm wide and 75 cm deep (Figure 4.2). A split-plot design was used with plants grown at three water depths (5, 20 and 60 cm, measured from pot rims to the water surface) and four water salinity levels (fresh, 2500, 5000 and 10 000 ppm). This design employed 16 tubs arranged into four replicate blocks. In every block one tub was randomly allocated to each of the four salinity treatments. Plastic platforms were placed within each tub to position plants at each of the three different water depths. Three plants of each species were placed in each tub at each depth, resulting in a total of 12 plants per species growing in each of the 12 salinity × depth combinations.

Figure 4.2. Plants growing in their depth × salinity treatment tubs, December 2006.

A narrower range of salinities were examined here than in the salt-tolerance experiment which tested salinity tolerance thresholds with respect to growth and survival for these species (Chapter 3). The salinity range for this experiment, from fresh to 10 000 ppm, was chosen because it includes salinity levels found to be limiting to growth of these four species, and also to the survival of *B. caldwellii* (Chapter 3). The water depth range of five to 60 cm was selected to encompass and/or exceed the range of depths at which *B. caldwellii* and *C. dactylon* have been observed in the field. The other two species, while typically seen at depths around 20 cm in the field (Chapter 2), were also observed infrequently at greater depths, with *E. equisetina* recorded at 75 cm and *P. distichum* recorded at 60 cm depth (Chapter 2). Tub height restricted depth treatments to a maximum of 60 cm.

The salinity treatments of 2500 ppm, 5000 ppm and 10 000 ppm were achieved using a commercially available aquarium sea salt (AQUASONIC Ocean Nature®) dissolved in tap water (approx. 200 ppm). Control tubs contained tap water only. Tubs were filled with water to the top on the day the pots were placed in position. Beginning on the following day, salt concentrations in the tubs were incrementally increased by one third of the target concentration per day until the desired salinity was reached. Salt concentrations were monitored throughout the experiment with an YSI-30 hand-held temperature compensated salinity meter. Salinity was kept to within 200 ppm of the desired concentration by topping up tubs with water every one to two days to compensate for evaporation and evapotranspiration.

4.2.3 Measurement

A number of growth parameters were measured on all plants, both immediately before being placed in their treatment tubs, and again at weekly intervals for eight weeks. Plant survival rates per treatment were also recorded weekly.

Height was recorded for all species, since height affects the ability of the plants to reach the water surface and was considered likely to affect plant survival at depth. For the grasses height was considered to be the length of the longest runner since grass runners can grow through water to the surface. For *E. equisetina* height was measured from the base of the culms to the tip of the tallest culm, and for *B. caldwellii* from the tallest stem base to the tip of the terminal leaf. At the start of treatments lengths of the longest runner for *P. distichum* plants ranged from 47 to 130 cm (median length 80 cm), and for *C. dactylon* from 19 cm to 78 cm (median 43 cm). *Eleocharis equisetina* starting heights ranged from 16 cm to 45 cm (median 28 cm). *Bolboschoenus caldwellii* starting heights ranged from 93 cm to 147 cm (median 119 cm).

Numbers of live and dead culms were recorded for each *E. equisetina* plant. Numbers of live and dead *B. caldwellii* leaves were recorded along with all individual stem lengths and the total combined stem lengths for each plant were calculated. These measurements were used to plot growth differences between treatments and to calculate relative growth rates over time. Relative growth rates (RGR) are usually calculated:

$$\mathrm{RGR} = \frac{\underline{lnW_2 - lnW_1}}{\Delta t}$$

where W_2 is final plant weight, W_1 is initial plant weight, and Δt is the duration of the experiment (Harper 1977). In this case plant weights at day one of the experiment were not known. Instead, numbers of live leaves and culms at the start and end of the experiment were substituted for weights, and relative rates of live leaf or culm gain or loss during the experiment calculated.

After eight weeks all plants were harvested. For each plant all above-ground biomass was bagged, oven-dried at 65^{o} C for 48 hours, and then weighed. For *B. caldwellii* and *E. equisetina* below-ground biomass (including roots, rhizomes and tubers) was also washed, bagged, oven-dried, and weighed so that shoot to root ratios could be calculated. Below-ground biomass was not harvested for the grasses due to practical and logistical constraints. Grass root weights and shoot to root ratios were considered to be of lesser interest because these two grasses spread via above-ground runners and appear to be less dependent on below-ground storage organs for asexual reproduction than *E. equisetina* and *B. caldwellii*.

4.2.4 Analyses

To determine whether the four species differed in inundation tolerance I examined growth differences between plants in the three different depth treatments in fresh water. Datasets for each species were analysed separately using random block ANOVAs, with block and depth treated as random and fixed factors respectively. When ANOVA revealed a significant depth effect, Tukey's method was used for post-hoc pairwise comparison of means, with the family error rate set at $P = 0.05$.

To determine whether increased salinity leads to a reduction in the ability of these species to tolerate water depth increases, the combined effects of increased depth and salinity on plant growth were assessed, with depth tolerances in fresh water used as the control. Again, datasets for each species were analysed separately, this time using split-plot ANOVAs (Snedecor and Cochran 1989; Crawley 2002; Quinn and Keough 2002). This design recognizes that the three water depth treatments occurred within each salinity treatment tub. Block was treated as a random factor, while salinity and depth were treated as fixed. The block × salinity interaction was included in the analyses to provide the appropriate error term for testing the salinity and block effects.

For analyses the data were transformed where necessary to meet assumptions of normality and homogeneity of variances, using Taylor's power law to determine the best transformation. Shoot weights of *B. caldwellii, C. dactylon* and *P. distichum* and root weights of *B. caldwellii* and *E. equisetina* were square root transformed. Whole plant weights and shoot:root weight ratios were also square root transformed for *E. equisetina*. A $\log_{10}$ transformation was applied to *E. equisetina* shoot weights. Mortality data were not analysed because all plants survived the full length of the experiment, regardless of depth or salinity treatment.

4.3 Results

4.3.1 Effects of increased depth on plant growth in fresh water

4.3.1.1 Relative growth rates (RGR)

Increased water depth led to significant reductions in RGR for both *B. caldwellii* and *E. equisetina* in fresh water (Table 4.1). For *B. caldwellii,* RGRs were significantly lower in the 60 cm treatment than in the 5 cm treatment (Table 4.1). For *E. equisetina,* rates of culm gain decreased significantly with each water depth increase (Table 4. 1). At 20 cm depth culm production was approximately half that of plants at 5 cm, and at 60 cm RGR became negative, indicating loss of existing culms rather than new culm production (Table 4.1).

At the start of the experiment *B. caldwellii* and *P. distichum* plants were tall enough to reach the waterline, whereas *E. equisetina* and *C. dactylon* were completely submerged in the deepest treatment. By the end of the experiment *E. equisetina* had grown substantially taller, exceeding the waterline in the 60 cm treatment, whereas *C. dactylon* remained submerged with little noticeable height gain.

4.3.1.2 Biomass

Biomass production in fresh water also declined significantly for every species as depth increased (Table 4.1). For *C. dactylon,* above-ground biomass was significantly reduced in the 60 cm treatment, with samples weighing around one half to one third of those from the two shallower treatments (Table 4.1). For *P. distichum,* above-ground biomass was also significantly lower in the 60 cm treatment than in the 5 cm treatment with sample weights reduced by approximately one quarter (Table 4.1). However, for *P. distichum,* above-ground biomass did not vary significantly between plants in the 20 cm treatment and those in the other depth treatments (Table 4.1).

Bolboschoenus caldwellii and *E. equisetina* plants had significantly lower whole plant biomass in the 60 cm treatment than in the two shallower treatments (Table 4.1). In contrast to the grasses, above-ground biomass for *B. caldwellii* and *E. equisetina* was not significantly affected by depth (Figure 4.3, Table 4.1). However, *B. caldwellii* and *E. equisetina* below-ground biomass declined with increasing depth, causing significant reductions in total plant biomass, and significant increases in shoot:root weight ratios (Table 4.1).

Figure 4.3. *Eleocharis equisetina* **(a)** and *Bolboschoenus caldwellii* **(b)** plants grew taller in the 60cm depth treatment (left). However, above-ground biomass did not vary significantly between depths (Table 4.1).

Table 4.1. Results of random block ANOVAs assessing effects of water depth on growth of plants in fresh water.

Species	Growth parameter	F ratio		Depth		
		Block d.f. = 3,30	Depth d.f. = 2, 30	5 cm Mean ± s.e.	20 cm Mean ± s.e.	60 cm Mean ± s.e.
Bolboschoenus caldwellii	Total biomass (g)	0.13	4.85*	62.98±4.55^{a}	64.56±4.38^{a}	47.70±3.09^{b}
	Above-ground biomass (g)	0.78	1.5	25.66±1.86	29.70±2.69	31.01±2.14
	Below-ground biomass (g)	0.23	24.93***	37.33±2.94^{a}	34.86±2.06^{a}	16.68±1.15^{b}
	Above- to below-ground biomass ratio	1.55	103.08***	0.70±0.04^{a}	0.85±0.05^{a}	1.89±0.09^{b}
	RGR (leaf gain)	0.73	8.95***	0.10±0.01^{a}	0.09±0.01^{ab}	0.06±0.01^{b}
Cynodon dactylon	Above-ground biomass (g)	1.48	14.41***	26.66±3.18^{a}	18.64±2.49^{a}	9.70±0.91^{b}
Eleocharis equisetina	Total biomass (g)	1.58	4.05*	17.18±1.21^{a}	14.36±2.14^{a}	10.88±2.35^{b}
	Above-ground biomass (g)	0.85	0.93	6.82±0.45	7.17±0.98	6.30±1.28
	Below-ground biomass (g)	2.94*	7.97**	10.36±0.88^{a}	7.19±1.26^{ab}	4.58±1.16^{b}
	Above- to below-ground biomass ratio	5.15**	24.38***	0.68±0.05^{a}	1.10±0.1^{b}	1.63±0.17^{c}
	RGR (culm gain)	2.58	44.17***	0.10±0.01^{a}	0.05±0.01^{b}	-0.04±0.01^{c}
Paspalum. distichum	Above-ground biomass (g)	0.27	3.46*	69.97±4.67^{a}	65.90±6.83^{ab}	50.87±4.25^{b}

*$P \leq 0.050$; ** $P \leq 0.010$; *** $P \leq 0.001$. Different letters indicate significant differences between means, as determined by Tukey's test. RGRs are relative growth rates, based on live leaf or culm counts.

4.3.2 Combined effects of increased salinity and water depth on plant growth and survival

Increases in water depth across all salinity treatments had significant affects on each of the various plant growth measurements (Table 4.2). However, some were positively affected and others were negatively affected. Increases in salinity had a significantly negative effect on most plant growth measurements, except for the above-ground to below-ground biomass ratios and above-ground biomass in *C. dactylon* which were not affected by salinity (Table 4.2).

4.3.2.1 Relative growth rates (RGR)

For *B. caldwellii,* a significant interaction was found between the effects of water depth and salinity on RGR (Table 4.2). This is explained by a more marked decline in RGR when water depth increased in the highest salinity treatment, compared to the other salinity treatments (Figure 4.5). Overall, *B. caldwellii* displayed positive rates of live leaf gain in all salinities and at all water depths, with these rates decreasing as both salinity and water depth increased (Figure 4.4, Figure 4.6). However, while plants in the 10 000 ppm × 60 cm treatment had the lowest final overall RGR, leaf production was initially higher in this treatment than in the other treatments, and remained so until six weeks into the experiment (Figure 4.6).

There was no significant interaction between the effects of depth and salinity on RGR for *E. equisetina* (Table 4.2). Relative growth rates for *E. equisetina* declined with increasing depth and with increasing salinity (Figure 4.4, Figure 4. 5). Positive rates of live culm gain were recorded for *E. equisetina* in the shallowest treatment across all salinities (Figure 4.5). However, the total number of live culms per plant decreased over time for *E. equisetina* in the 60 cm depth treatment regardless of salinity (Figure 4.5). Negative RGRs were also recorded for *E. equisetina* at 20 cm depth in the highest salinity treatment (Figure 4.5). These negative RGRs became apparent from week six onward (Figure 4.6).

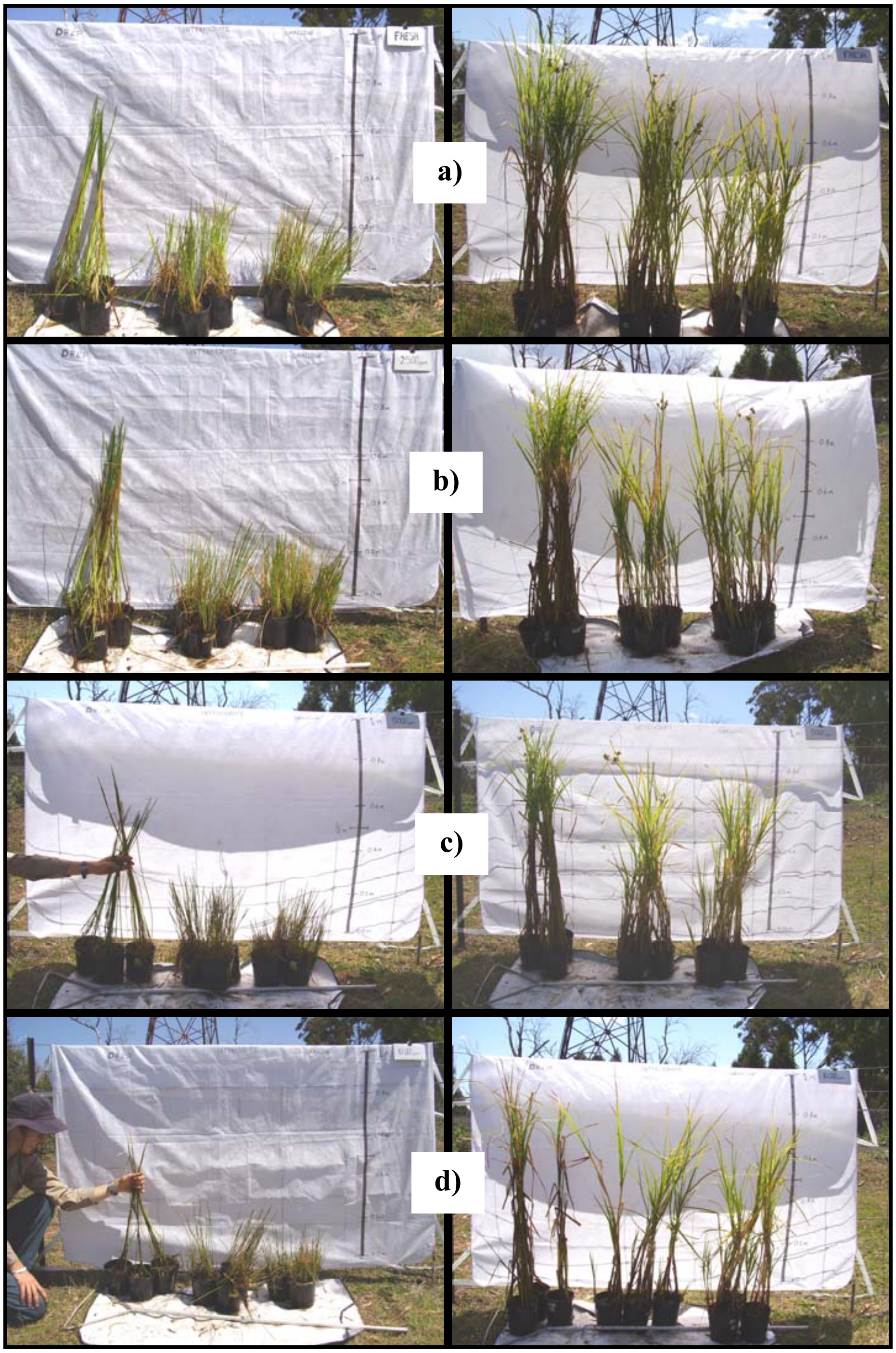
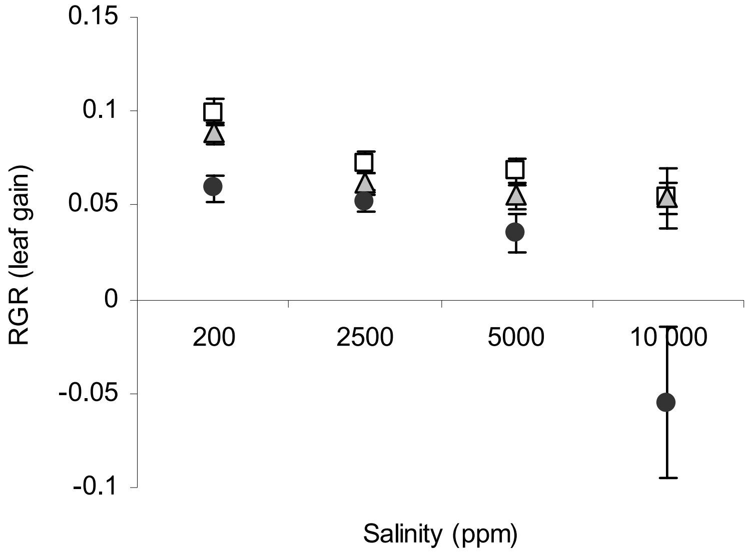


Figure 4.4. Growth reductions with increasing salinity for *Eleocharis equisetina* (left) and *Bolboschoenus caldwellii* (right). Salinity treatments; **a)** fresh, **b)** 2500 ppm, **c)** 5000 ppm, and **d)** 10 000 ppm. Plants are arranged in order of depth treatment (left 60 cm, centre 20 cm and right 5 cm).

a) *Bolboschoenus caldwellii*



b) *Eleocharis equisetina*

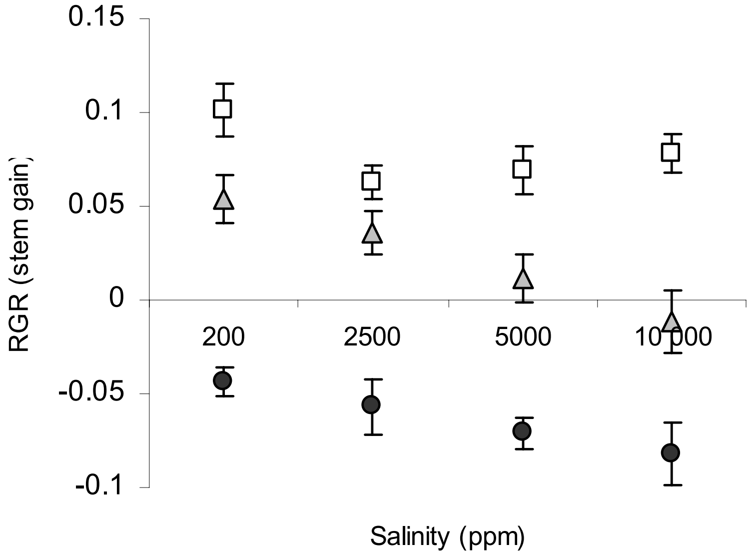
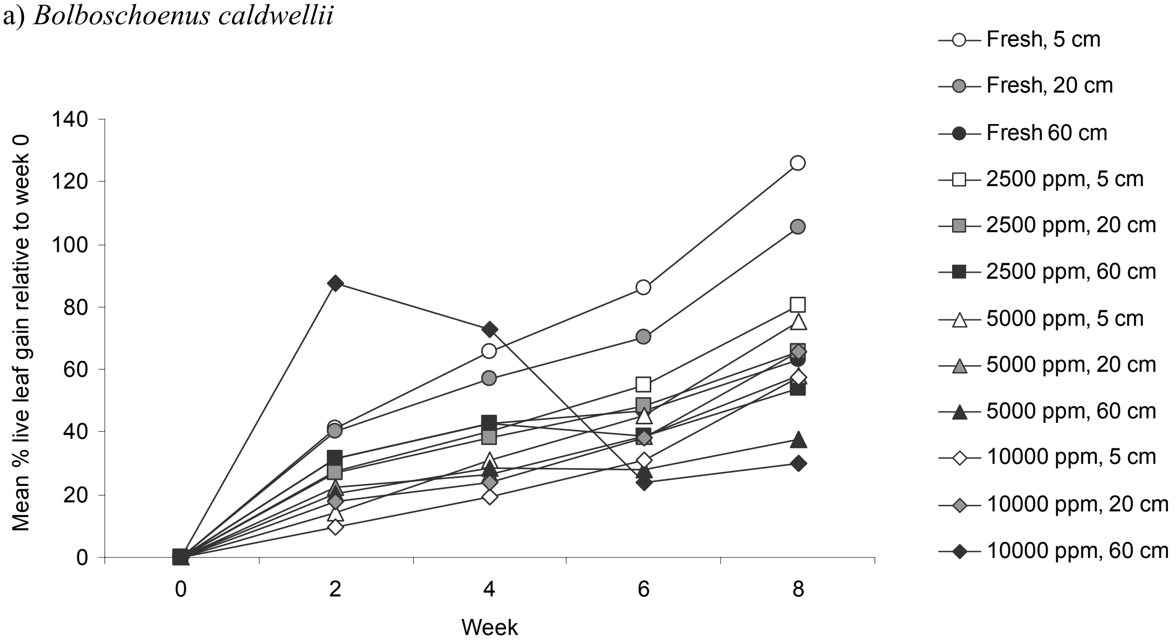


Figure 4.5. Effects of salinity (ppm) and water depth (☐ 5 cm, △ 20 cm and ● 60 cm) on relative growth rate (RGR), based on numbers of live leaves and culms. Means presented with standard error bars (*N* = 12).

a) *Bolboschoenus caldwellii*



b) *Eleocharis equisetina*

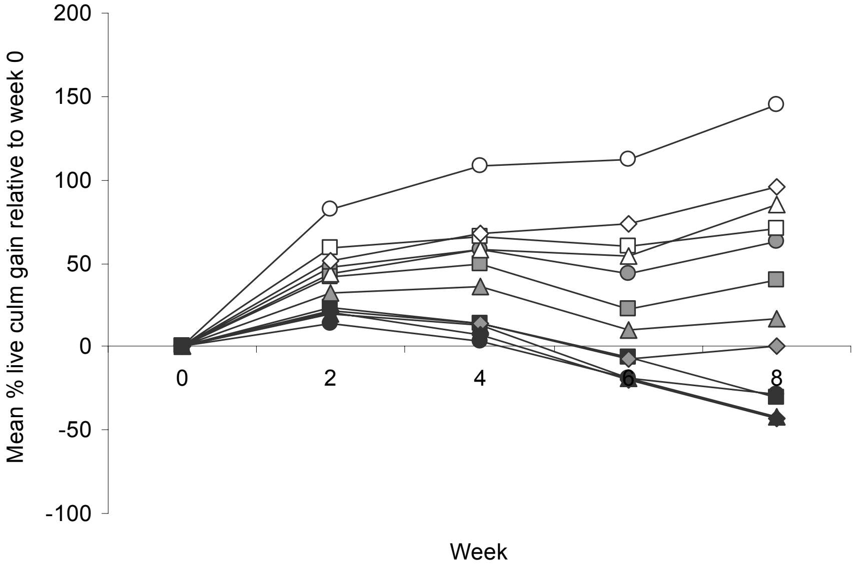


Figure 4.6. Effects of increased salinity and water depth on mean rates of live leaf and culm gain over time ($N = 12$).

4.3.2.2 Biomass

Significant salinity × depth interactions occurred for *C. dactylon* above-ground biomass measurements and *E. equisetina* above- to below-ground biomass ratios (Table 4.2). Across all treatments water depth had significant effects on the above-ground biomass of *B. caldwellii, E. equisetina* and *P. distichum*, as well as on below-ground and total biomass in the species where these variables were measured (Table 4.2). Salinity also had a significant effect on most biomass measurements, except for the above- to below-ground biomass ratios of *B. caldwellii* and *E. equisetina* (Table 4.2). There were also some significant block effects, affecting *B. caldwellii* above-ground biomass, and above- to below-ground biomass ratios of *B. caldwellii* and *E. equisetina.*

For *B. caldwellii* total plant biomass declined significantly as both depth and salinity increased (Figure 4.7). While the above-ground biomass of *B. caldwellii* increased with depth (Figure 4.8), these increases were not large enough to offset significant reductions in below-ground biomass (Figure 4.9). Due largely to these reductions in below-ground biomass, above- to below-ground biomass ratios also increased significantly for *B. caldwellii* as depth increased (Table 4.6), with plants in the 60 cm depth treatment having approximately twice as much above-ground biomass per unit of below-ground biomass as plants placed at five or 20 cm depth (Figure 4.9).

For *C. dactylon* a significant interaction occurred between the effects of salinity and water depth on above-ground biomass (Table 4.2). This is explained by a small increase in above-ground biomass with increasing salinity at 60 cm depth, contrasting with decreasing above-ground biomass as salinity increased at the two shallower water depths (Figure 4.8). Apart from the increase mentioned, above-ground biomass decreased as water depth increased in *C. dactylon* (Figure 4.8). While some green leaves and stems were retained on submerged *C. dactylon* plants in the 60 cm treatment, advanced tissue chlorosis was seen in the majority of leaves at this depth. The decrease in above-ground biomass with depth was most noticeable in the fresh water control (Figure 4.8) where the highest shoot growth occurred in the 5 cm and 20 cm treatments. At 10 000 ppm negligible above-ground biomass production occurred, resulting in similar final above-ground biomass measurements across the three depths.

Eleocharis equisetina total plant biomass decreased significantly across all treatments (Table 4.2) with increased depth and with increased salinity (Figure 4.7). This was due to significant reductions in both above-ground biomass (Figure 4.8) and below-ground biomass with increasing depth and salinity, with no interaction found between the effects of these factors (Table 4.2). There was a significant interaction between the effects of salinity and water depth on above- to below-ground biomass ratios for *E. equisetina* (Table 4.2), which increased with salinity in the 5 cm depth treatment, changed little between salinities in the 20 cm depth treatment, and decreased as salinity increased in the 60 cm depth treatment (Figure 4.8). In the fresh water and 2500 ppm treatments marked increases in the above- to below-ground biomass ratios of *E. equisetina* with increasing water depth were largely caused by reductions in below-ground biomass (Figure 4.9). In the 5000 ppm and 10 000 ppm treatments there was less variation in above- to below-ground biomass ratios across depths. However, while above- to below-ground ratio varied little between depths, total plant biomass was reduced in the 60 cm depth treatment to approximately two thirds to one half of that found at shallower depths (Figure 4.9).

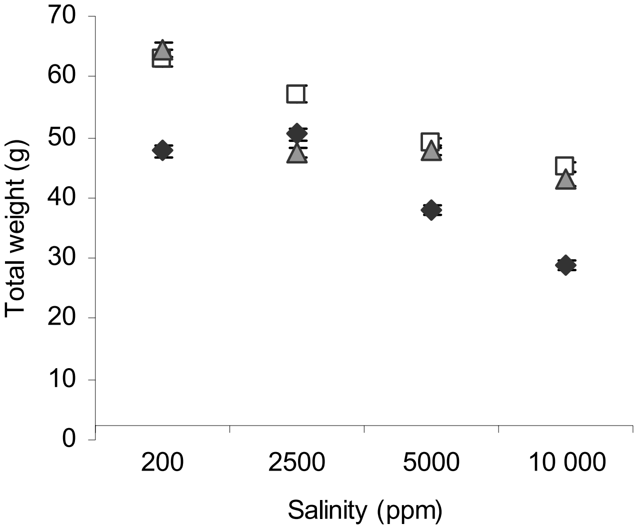
While above-ground biomass measurements were similar across all depths for *E. equisetina* in the fresh water control, longer culms were produced as depth increased. It was observed that, when *E. equisetina* plants were removed from their tubs for measurement, the elongated culms produced in the 60 cm depth treatment were more prone to falling over and becoming kinked than the shorter culms that were produced at shallower depths. *Eleocharis equisetina* culms produced in the higher salinity treatments were more fragile and less self-supporting than those produced in the fresh water control. *Paspalum distichum* above-ground biomass decreased significantly with both increased salinity and depth (Figure 4.8). At 10 000 ppm salinity above-ground biomass was low, with little difference between depths (Figure 4.8).

Table 4.2 Results of split-plot ANOVAs assessing the combined effects of increased water depth and salinity on plant growth. *F*-ratios shown with significance levels as indicated.

Species	Growth parameter	Source			
		Block d.f. = 3, 9	Salinity d.f. = 3, 9	Depth d.f. = 2, 120	Salinity × depth d.f. = 6, 120
Bolboschoenus caldwellii	Total biomass (g)	0.09	25.06^{***}	12.89^{***}	1.54
	Above-ground biomass (g)	5.34^{*}	32.19^{***}	5.05^{**}	1.78
	Below-ground biomass (g)	1.84	10.55^{**}	81.53^{***}	1.57
	Above- to below-ground biomass ratio	8.79^{**}	3.24	261.67^{***}	1.71
	RGR (leaf gain)	3.60	25.16^{***}	14.24^{***}	2.97^{**}
Cynodon dactylon	Above-ground biomass (g)	1.11	1.90	21.62^{***}	3.20^{**}
Eleocharis equisetina	Total biomass (g)	0.59	5.13^{*}	24.57^{***}	0.65
	Above-ground biomass (g)	2.33	5.04^{*}	15.42^{***}	0.94
	Below-ground biomass (g)	1.04	4.81^{*}	36.39^{***}	0.76
	Above- to below-ground biomass ratio	23.47^{***}	2.57	32.66^{***}	2.67^{*}
	RGR (culm gain)	1.82	6.31^{*}	130.40^{***}	1.17
Paspalum distichum	Above-ground biomass (g)	1.18	23.72^{***}	10.82^{***}	1.36

*$P \le 0.050$; ** $P \le 0.010$; *** $P \le 0.001$. RGRs are relative growth rates, based on live leaf or culm counts. For salinity and block, the block × salinity interaction was used as the error term. For depth and the salinity × depth interaction, the error term incorporates the block × depth and block × depth × salinity interactions and the unexplained error (Snedecor and Cochran 1989; Crawley 2002).

a) *Bolboschoenus caldwellii*



b) *Eleocharis equisetina*

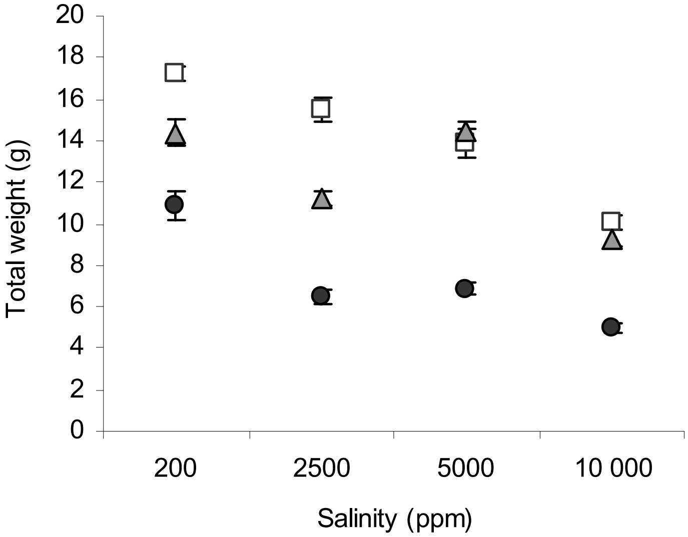
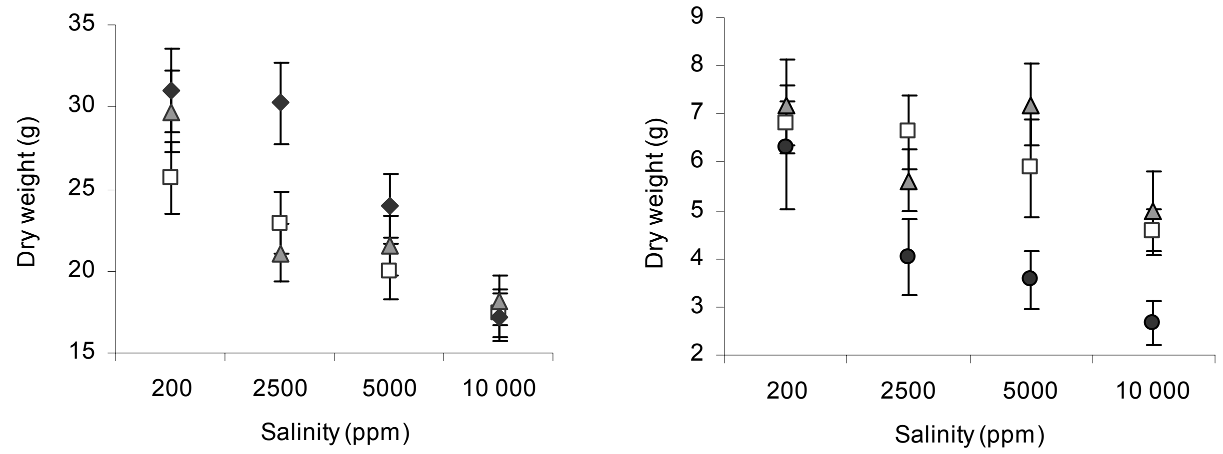
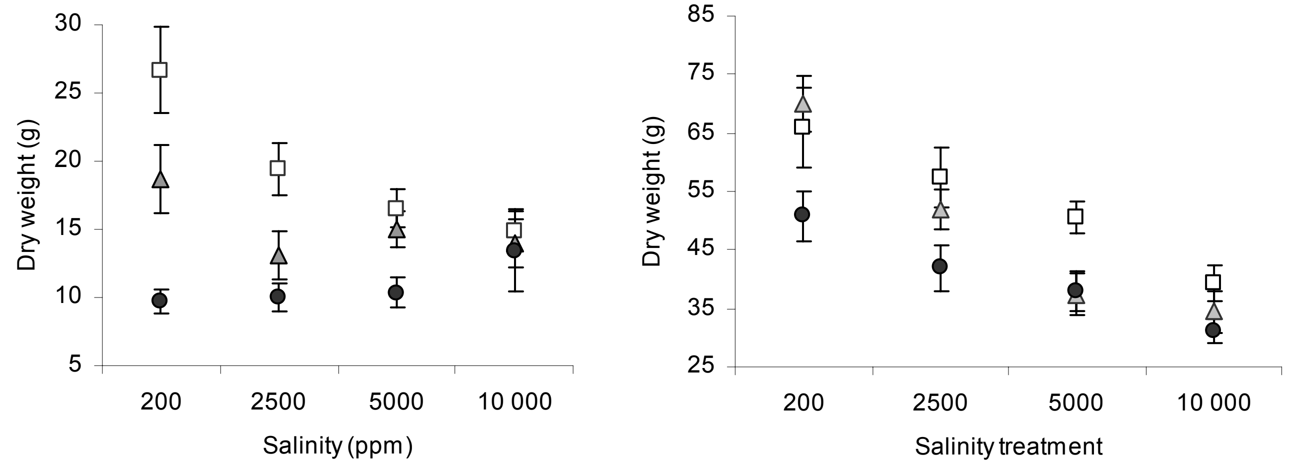


Figure 4.7. Effects of salinity (ppm) and water depth (☐ 5 cm, △ 20 cm and ● 60 cm) on final dry weight of whole plants. Means presented with standard error bars (*N* = 12).


a) *Bolboschoenus caldwellii*

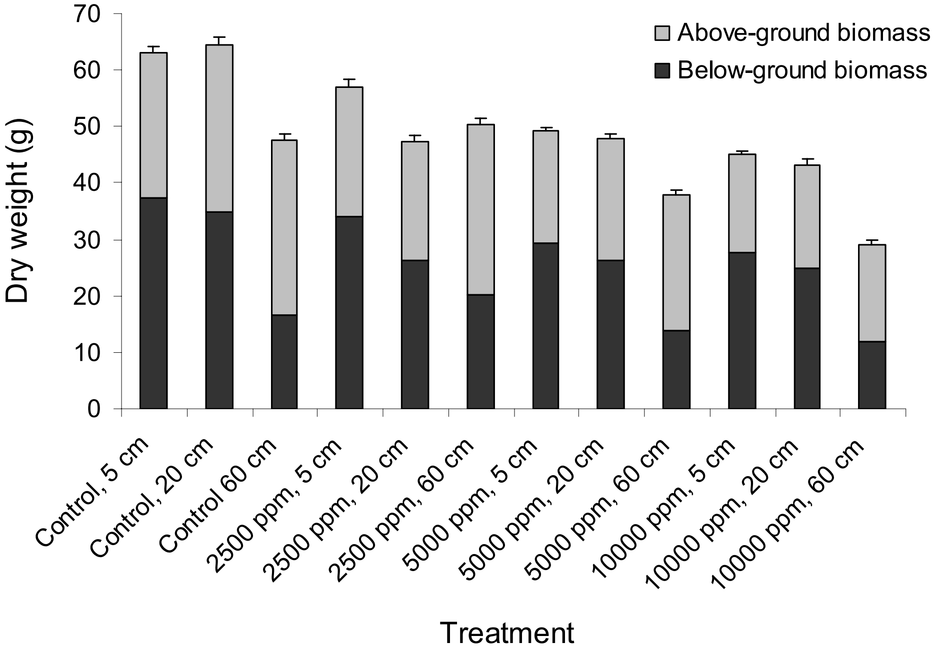
c) *Eleocharis equisetina*


b) *Cynodon dactylon*

d) *Paspalum distichum*

Figure 4.8. Effects of salinity (ppm) and water depth (☐ 5 cm, △ 20 cm and ● 60 cm) on above-ground biomass harvested at week eight. Means presented with standard error bars (*N* = 12).

a) *Bolboschoenus caldwellii*



b) *Eleocharis equisetina*

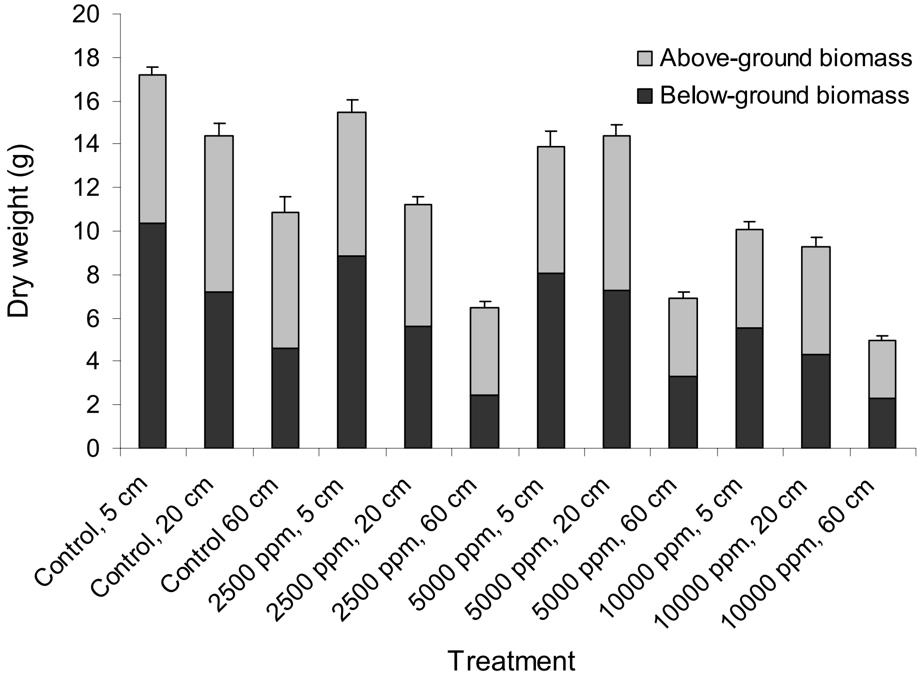


Figure 4.9. Effects of salinity and water depth on mean above- and below-ground biomass allocation. Error bars show standard errors for mean whole plant dry weights (*N* = 12).

4.4 Discussion

Tidal restoration, whether partial or full, has the potential to modify the distributions of estuarine wetland macrophyte species both through increased salinity and increased depth, duration, and frequency of inundation. While considerable previous research has focused on the effects of salinity and water depth on saltmarsh plants (Bart and Hartman 2002; Chambers *et al.* 2003), including some Australian species (Laegdsgaard 2006), to my knowledge this experiment is the first to have examined the combined effects of increased depth and salinity on growth and survival of macrophyte species found in oligohaline wetlands.

4.4.1 Relationship between field zonation patterns, and experiment depth tolerances

Fresh water depths at which each species grew best in this experiment corresponded reasonably well with the water depths at which these species were observed in the field. For example, in the field survey *C. dactylon* was usually confined to areas above the high water mark, suggesting a low tolerance toward waterlogging. In this experiment *C. dactylon* was least tolerant of inundation, showing the largest proportional reduction in above-ground biomass of any species as depth increased. While *C. dactylon* survived complete submergence in the deepest treatment for the duration of the experiment, little growth was apparent. Stems did not grow sufficiently to reach the water surface and extensive tissue chlorosis was observed in submerged leaves.

In the survey *P. distichum* was largely confined to areas of damp ground when in association with *E. equisetina* (Chapter 2). However, it was observed in water up to 60 cm at one site, which lacked *E. equisetina* and which had also been fenced off from cattle for several years. At that site *P. distichum* grew in clumps surrounded by open water (pers. obs.). In this experiment *P. distichum* produced significantly more above-ground biomass in the 5 cm depth treatment than in the 60 cm treatment, with no significant differences found between 5 cm and 20 cm, or the 20 cm and 60 cm depth treatments. This lack of difference in above-ground biomass between the 5 cm and 20 cm depth treatments suggests that this species should be able to grow successfully at a greater range of depths than it was typically found occupying in the field survey. This suggestion is supported by the observations of others who have reported stands of *P. distichum* growing in inundated areas, at depths from 15 cm to 60 cm (Middleton *et al.* 1991; van der Valk *et al.* 1993; Rose *et al.* 2006). Clipping underwater can dramatically reduce the survivorship of *P. distichum* (Middleton 1990). Therefore, grazing by cattle may be preventing *P. distichum* from occupying the deeper end of its potential depth range in some Clarence floodplain wetlands. Competition with *E. equisetina* is another factor that could be affecting the distribution of *P. distichum.* Dense stands of these two species are often found close together, with *P. distichum* dominating above the waterline and *E. equisetina* dominating below (Chapter 2).

In the field survey, *B. caldwellii* was observed growing on damp ground and in shallow water up to 25 cm deep (Chapter 2). In this experiment the optimum depth range for growth of *B. caldwellii* was similar to the observed field distribution. Both *B. caldwellii* RGR and total plant biomass were significantly higher in the 5 cm and 20 cm depth treatments than at 60 cm. These results concur with those of Siebentritt and Ganf (2000) who found optimum biomass production in *B. caldwellii* plants grown from 20 cm above to 20 cm below the waterline, with reductions in RGR at greater depths. In this experiment *B. caldwellii* displayed a substantial drop in below-ground biomass at 60 cm depth compared to the shallower treatments. A similar pattern of biomass allocation was found by Siebentritt and Ganf (2000) who reported no reallocation of biomass to tubers once depths exceeded 40 cm. Rhizomes and tubers in *B. caldwellii* are important for asexual reproduction and recovery after stem dieback, therefore, these reductions in below-ground biomass are likely to affect its long-term persistence and spread at depths over 40 cm (Siebentritt and Ganf 2000). Growth and survival of *B. caldwellii* plants under submerged conditions was not tested in this experiment. However, Siebentritt and Ganf (2000) have demonstrated that growth and survival of *B. caldwellii* depends on the presence of emergent photosynthetic tissue, with completely submerged plants all dead before the end of six weeks.

Eleocharis equisetina was typically found at greater maximum water depths than the other study species in the survey of Clarence floodplain wetlands, where these species coocurred, and was found from damp ground to a maximum depth of 75 cm (Chapter 2). Experimentally, total plant biomass was significantly higher in the two shallower treatments than at 60 cm, indicating optimum growth in the 5 cm to 20 cm depth range for *E. equisetina*. However, RGR for *E. equisetina* dropped significantly with each increase in depth. At 20 cm RGR for *E. equisetina* was approximately only half that recorded at 5 cm, and at 60 cm RGR was a negative value, indicating that death of culms occurred at a faster rate than new culm production. At the start of the experiment every *E. equisetina* plant in the 60 cm treatment was completely submerged. Culms on submerged plants grew rapidly up to the water surface and all *E. equisetina* plants survived for the eight-week duration of the experiment. However, although culms grew taller, above-ground biomass did not vary between depths. Instead, biomass allocated to below-ground rhizomes and tubers decreased, resulting in significant reductions in above- to below-ground biomass ratio with each depth increase. This response suggests that *E. equisetina* plants may use energy reserves from their underground rhizomes and tubers to maintain growth during periods of inundation stress. Overall, while *E. equisetina* may tolerate short-term inundation, this species is not suited to long-term survival at 60 cm depth. Therefore, *E. equisetina* appears to be currently occupying its full potential depth range in the Clarence floodplain wetlands.

4.4.2 Combined effects of increased salinity and water depth on plant growth and survival

It was expected that under conditions of increased water depth and salinity, plant growth would be reduced compared to that of plants faced with increased salinity alone (Morris and Ganf 2001). This expectation was supported for all four species, since both increased depth and salinity had significant negative effects on most growth and biomass measurements. Exceptions were above-ground biomass for *B. caldwellii* which increased with depth, and above-ground biomass for *C. dactylon* which was not significantly affected by salinity. However, while above-ground biomass increased with depth for *B. caldwellii*, reductions in root biomass as depth increased were large enough for whole plant biomass to be significantly reduced. In most cases the effects of salinity and depth were additive, with few significant interactions occurring. Depth thresholds affecting plant growth and survival therefore decreased as salinity levels increased.

Some interactions were found between salinity and depth effects, affecting RGR for *B. caldwellii,* above- to below-ground biomass ratio for *E. equisetina,* and above-ground biomass for *C. dactylon.* For *B. caldwellii* RGR was reduced more as depth increased in the highest salinity treatment than at the lower salinities. Therefore, this interaction represents a change in the magnitude rather than the direction of the effects of salinity and depth on *B. caldwellii* growth.

For *E. equisetina,* increased depth resulted in higher above-ground to below-ground biomass ratios at low salinities. However, depth caused less of a decrease in above-ground to below-ground biomass ratios for *E. equisetina* at higher salinities. There were several contributing factors. While all *E. equisetina* plants were initially completely submerged and grew taller to reach the waterline at 60 cm depth, this coincided with a reduction in below-ground biomass for these plants. It was only in the fresh water control that above-ground biomass remained similar across water depths, suggesting that if *E. equisetina* compensates for water depth increases by reallocating reserves from below-ground tissues into culm height growth, it is only able to maintain equivalent culm weight across water depths under fresh water conditions. As salinity increased, both above-ground biomass and below-ground biomass were reduced, particularly at 60 cm depth, resulting in substantially lower total biomass for plants in this treatment. Overall, above-ground, below-ground and total plant biomass declined significantly with both depth and salinity for *E. equisetina,* as expected.

In *C. dactylon,* the significant interaction between the effects of water depth and salinity on above-ground biomass is explained by above-ground biomass decreasing as salinity increased in the 5 cm and 20 cm depth treatments, but increasing slightly for plants in the 10 000 ppm treatment at 60 cm depth. The slight increase in above-ground biomass in this treatment may have originated in the two-month growing-on-stage prior to the imposition of experimental treatments, since submerged *C. dactylon* plants showed little evidence of shoot growth in any of the tubs throughout the experiment. Plants at 60 cm depth in particular showed evidence of extensive leaf dieback.

Above-ground to below-ground biomass ratios increased with depth for both *B. caldwellii* and *E. equisetina.* This result corresponds with findings elsewhere that as water depths increase, and light and atmospheric gases become limiting, many emergent plants must allocate more biomass to stems and leaves to obtain those resources and to survive (Chapin *et al.* 1987; Rea and Ganf 1994; Blanch *et al.* 1999; Siebentritt and Ganf 2000). However, despite this shift in biomass allocation, plants were unable to compensate fully for increases in depth. For example, below-ground biomass and total biomass of *B. caldwellii* and *E. equisetina* plants were reduced at 60 cm depth compared to plants at 5 cm or 20 cm in fresh water, indicating a reduction in fitness at 60 cm. Both below-ground and total plant biomass declined even further as salinity increased, indicating even greater reductions in fitness. For *B. caldwellii* and *E. equisetina* above-ground parts typically die off during adverse growing conditions, for example winter frosts, with plants later recovering by resprouting from underground rhizomes and tubers when growing conditions become favourable (pers. obs.). These species also rely on below-ground parts for vegetative reproduction, typically spreading to form large clonal stands in the field. Below-ground biomass was reduced in these species by around 30 to 50 % at 60 cm depth compared to the shallower treatments. The large reductions in below-ground biomass found here, therefore, suggest that the abilities of *B. caldwellii* and *E. equisetina* to recover from stem dieback and to spread vegetatively will be reduced substantially if plants are subjected to eight weeks of inundation at 60 cm depth or more, with resilience at shallower depths also decreasing as salinity is increased.

It was expected that at increased water depths, the study species would have lower survival rates than when faced with increased salinity alone (Morris and Ganf 2001). However, the expected difference in survival between depth treatments was not observed since all plants in this experiment survived, regardless of depth or salinity. This is most likely a result of larger initial plant sizes used here than in the salt-tolerance experiment

(Chapter 3). While plant mortality was not observed for any of the species in any treatment, RGRs were negative for *E. equisetina* at 60 cm depth in every salinity treatment, and also at 20 cm depth in the 10 000 ppm treatment, indicating higher rates of culm loss than culm production. If the experiment had been extended for a longer period I predict that mortality would have occurred in *E. equisetina* plants in these treatments. *Cynodon dactylon* plants in the 60 cm treatment would also be likely to die under a lengthier period of submergence, since these plants displayed extensive tissue chlorosis by week eight. The experiment was not extended here to gather mortality data because after eight weeks plants in the tubs were beginning to shade each other and future growth and biomass measurements would have been confounded.

Cynodon dactylon, B. caldwellii and *E. equisetina* demonstrated higher salt-tolerance thresholds in this experiment than in the previous experiment where water depth was kept constant (Chapter 3). In that experiment *C. dactylon* plants began to die after two weeks at salinities of 3000 ppm and above, *E. equisetina* showed a higher rate of culm loss than culm production from week two in salinities of 5000 ppm and greater, and *B. caldwellii* lost leaves faster than it produced new ones from week one onward at salinities of 10 000 ppm and above. In this experiment shoot dieback was observed for submerged *C. dactylon* in all treatments, however no plants died. While *E. equisetina* RGRs were lower at 5000 ppm than in the fresh water control in the 5 cm and 20 cm depth treatments, positive rates of culm production were maintained. *Bolboschoenus caldwellii* leaf production rates did decrease with salinity, however these remained positive even at 10 000 ppm. The salt-tolerance thresholds of *P. distichum* could not be compared because salinities were not high enough to affect survival in this experiment, and *P. distichum* growth rates were not determined here.

4.4.3 Predicted effects of floodgate manipulation on individual species distributions

All four species survived for eight weeks in this experiment when salinity was increased up to 10 000 ppm, and water depth was increased up to 60 cm. Based on these high survival rates I would predict that these species could survive inundation for at least eight weeks provided water depth and salinity ranges remained within these limits and no other adverse site conditions caused reductions in plant growth and survival.

Total and below-ground biomass for *B. caldwellii* declined significantly, however, with increasing water depth, particularly when depth was increased to 60 cm, and also with increased salinity. Based on these results it is predicted that *B. caldwellii* plant biomass will be higher at sites where water remains ≤ 20 cm depth, decreasing as salinity increases. Persistence and rates of vegetative spread are also expected to decline in *B. caldwellii* stands at depths > 20 cm, and as salinity increases.

In the salt-tolerance experiment (Chapter 3) mortality of *C. dactylon* occurred at salinities of 3000 ppm and above and in this experiment increases in water depth were found to be even more detrimental to growth of *C. dactylon* than increases in salinity. Therefore, the relative cover of *C. dactylon* is expected to decline at waterlogged sites with salinities ≥3000 ppm, and also at flooded sites regardless of salinity, particularly where plants are submerged. *Cynodon dactylon* plants may survive being submerged for eight weeks or more, however, the recovery ability of these plants is expected to be low, due to extensive dieback of leaves and shoots under these conditions.

For *E. equisetina* above-ground biomass remained constant at depths up to 60 cm in fresh water. However, below-ground biomass decreased by approximately one third with each depth increase. Relative growth rates were negative for all salinity treatments at 60 cm depth, while at 5000 ppm RGR was close to zero at 20 cm depth; at 10 000 ppm RGR at 20 cm was negative. Based on these results, *E. equisetina* would be expected to gradually die out at sites where water depth remains at 60 cm for prolonged periods of time, with substantial reductions in below-ground biomass and negative rates of stem production occurring within eight weeks. This result is also expected to occur if sites are flooded to 20 cm depth with water ≥ 5000 ppm salinity. *Eleocharis equisetina* stem sturdiness also decreased as salinity increased. This trait is likely to make *E. equisetina* less tolerant of water level fluctuations in brackish water than in fresh, since stems will be more prone to collapsing and breaking as water levels recede.

In fresh water, *P. distichum* shoot biomass did not differ between the two shallower depth treatments, but dropped significantly between the 5 cm and 60 cm depth treatments. Shoot biomass also declined significantly as salinity increased. Based on these results I predict that the relative cover of *P. distichum* will decline when sites are inundated to depths greater than 20 cm, but that cover should remain relatively consistent at lower water depths, at least for periods of flooding up to eight weeks. Above-ground biomass production is expected to be highest at sites inundated with fresh water, declining at a relatively constant rate as salinity increases, and with negligible growth occurring once salinity reaches 10 000 ppm.

While salinity and inundation regime are primary determinants of species potential elevation ranges, other site-specific factors may modify species distributions, further restricting potential elevation range in the field. These include biotic factors, such as herbivory and competition (Gough and Grace 1998), and abiotic factors such as differences in acidity, or turbidity (Porter *et al.* 2007) or temperature extremes (Maas 1977). Low temperatures in winter cause reduced growth and leaf and stem senescence in all four study species (pers. obs.), which may reduce their ability to respond to flooding. Alternatively, high temperatures may lead to increased uptake of salts as a result of higher evapotranspiration rates (Maas 1977, 1986). The effects of these and other site-specific factors on macrophyte salinity and depth tolerances are currently unknown but may be resolved through further experiments and future monitoring at tidal restoration sites. The responses of the study species to differences in the frequency and timing of depth and salinity changes, and their relative resilience to repeated depth and salinity fluctuations are other areas of interest for future research.

CHAPTER 5

Development and application of a general model for predicting wetland macrophyte responses to tidal flow management

5.1 Introduction

Coastal wetlands are highly productive, complex and biologically diverse systems that perform a range of ecologically valuable functions, including maintenance of water quality, nutrient cycling, and provision of habitat for a range of flora and fauna (Keddy 2000b). Worldwide these systems are in a state of decline due to the rapid pace of agricultural, urban and industrial development. Drainage and installation of tidal barriers have contributed to the reduction of tidal wetland habitats in many parts of the world, including Europe, the United Kingdom, North America, Australia and elsewhere (Williams and Watford 1997; Warren *et al.* 2002; Wolters *et al.* 2005). Recent interest has focused on the rehabilitation of tidal wetlands by restoring more natural water regimes, particularly in North America, the United Kingdom, and Europe (reviewed in Warren *et al.* 2002; Wolters *et al.* 2005).

Tidal restoration is also becoming a focus for wetland rehabilitation research in Australia (Sammut *et al.* 1995; White *et al.* 1997; Williams and Watford 1997; Dick and Osunkoya 2000; Johnston *et al.* 2003; Laegdsgaard 2006). However, research into the environmental tolerance ranges of our wetland biota, and the likely impacts of tidal restoration on them, has to date focused mainly on species occupying saltmarsh habitats (reviewed in Laegdsgaard 2006). Less research has been conducted in Australia, or overseas, in habitats higher up the estuarine salinity gradient, including oligohaline and mesohaline wetlands with lower and more temporally variable salinity levels (Odum 1988) (but see Baldwin *et al.* 2001; Capers 2003; Capers and Les 2005). These habitats have also been affected by high levels of artificial drainage and by tidal exclusion (Pressey and Middleton 1982; Williams and Watford 1997), and are beginning to attract more interest as potential candidates for tidal restoration (Walsh and Copeland 2004).

The lack of data on the environmental tolerance ranges of Australian oligohaline and mesohaline wetland macrophytes is reflected in an absence of conceptual models for predicting the effects of tidal flow manipulation on plant communities in these systems. There also appears to be no broadly applicable model framework available, in Australia or elsewhere, for predicting how tidal flow manipulation may affect macrophyte community structure and composition at these sites, despite effective vegetation management being of high importance to wetland rehabilitators. What is required is a broadly applicable conceptual model, based on ecological principles, which will allow predictions to be made about plant species responses in these habitats to a variety of tidal flow management scenarios. This model should be general enough to allow basic predictions to be made for any geographic region or wetland plant community, while also allowing more specific predictions to be made for individual sites and species of interest.

5.1.1 Essential characteristics of a model of wetland macrophyte responses to altered tidal flow management

Wetlands are distinguished from other environments by the presence of standing water, for at least some of the time (Finlayson *et al.* 1999). The presence of standing water and associated anaerobic soil conditions necessitates specialised adaptations in plants for survival, growth and reproduction, hence hydrological regime is a key determinant of both plant community composition in wetlands and the distribution of species along the elevation gradient (Brock and Casanova 1997; Keddy 1999, 2000a). In tidal wetlands salinity also exerts a strong control on community composition (Odum 1988; Keddy 2000a). Since salinity and hydrology are both directly affected by degree of tidal exchange, with changes in these factors are expected to drive vegetation changes, salinity and hydrology are the most important abiotic factors to include in a conceptual model for predicting macrophyte responses to tidal flow manipulation.

Water depth and salinity are spatially and temporally variable within and among tidal wetlands (Odum 1988). Hydrological regimes typically vary between wetlands in terms of depth, duration, frequency and timing of inundation, and these factors can also vary temporally within wetlands, independent of tidal influence (Deuver 1988). Tidal patterns introduce additional variability to water depth, with cyclical variations in amplitude (Odum 1988). In addition, the upper limit of tidal influence moves longitudinally closer to or further from the estuary mouth, according to tidal patterns and the amount of stream flow (Odum 1988). Salinity also varies temporally, most noticeably in the mid to upper reaches of tidal waterways, where it decreases after periods of high rainfall and increases during periods of lower stream flow (Odum 1988). Any model framework developed to summarise vegetation changes in wetlands due to tidal flow manipulation needs to take into account the high degree of variability in water depth and salinity occurring both within and between estuarine wetlands.

In addition to water depth and salinity ranges, complex interactions between abiotic and biotic factors can affect which plant species flourish in tidal wetlands, and some of these interactions are only now being identified. For example, recent work has shown that it is not only average salinity that determines the distribution and composition of seagrass beds, but also the frequency and extent of salinity fluctuations (de Jong and de Jong 2002). It has also been demonstrated that the addition of nutrients to saltmarsh communities can substantially alter interspecific competition, affecting final community composition (Emery *et al.* 2001). Conceptual models for summarising vegetation dynamics in estuarine and linking habitats therefore need to be flexible, and able to evolve as our understanding of these complex interactions increases.

5.1.2 Existing wetland vegetation models

Numerous wetland restoration studies have assessed the effects of particular environmental factors on plant communities (Zedler 2000). However, most wetland restoration papers report on a single site and a small group of species, with little reference to ecological theory (Keddy 2000c). This makes it difficult to extract broadly applicable principles or to develop a more general conceptual model for predicting wetland plant community responses to rehabilitation measures.

Interpretation of the underlying theories used in existing models can also be difficult due to the inconsistent terminologies used (Keddy 2000c).

In the broader field of restoration ecology, Clementsian succession, state and transition and assembly rule theories have each been used as a conceptual basis for understanding plant community dynamics, with state and transition and assembly rule-based models becoming more prominent in recent years (Young *et al.* 2005). Of these, Clementsian succession models have been traditionally preferred for modeling vegetation changes associated with wetland restoration (Neckles and Dionne 1999; Neckles *et al.* 2002). However, these models are based on assumptions that are not met in all tidal wetland plant communities (Table 5.1) and are often both site and community-specific (Table 5.1), which prevents their effective use in predicting the effects of tidal flow manipulation across different sites, communities and spatial scales. Some of the limitations of Clementsian succession models may be bypassed by switching to the use of Gleasonian succession-based state and transition or assembly rule models (Table 5.1). These three model frameworks are outlined below, and their various advantages and disadvantages for modeling the effects of tidal flow reinstatement on wetland community composition are summarised in Table 5.1.

5.1.3 Clementsian succession models

Successional theories have long been incorporated into restoration models (Young *et al.* 2005). Some of the simpler succession models follow the suggestion of Clements (1916) that plant species are arranged in discrete stable communities, and that after disturbance these communities recover along a predictable trajectory, progressing through various successional stages until they return to the stable climax state (Figure 5.1.). In development of such models the climax plant community is usually determined from community composition at nearby undisturbed reference sites, or pre-disturbance vegetation survey data from the restoration site (Brinson and Reinhardt 1996). This climax community is then used as the target state by which restoration success can be measured at the restoration site (Brinson and Reinhardt 1996).

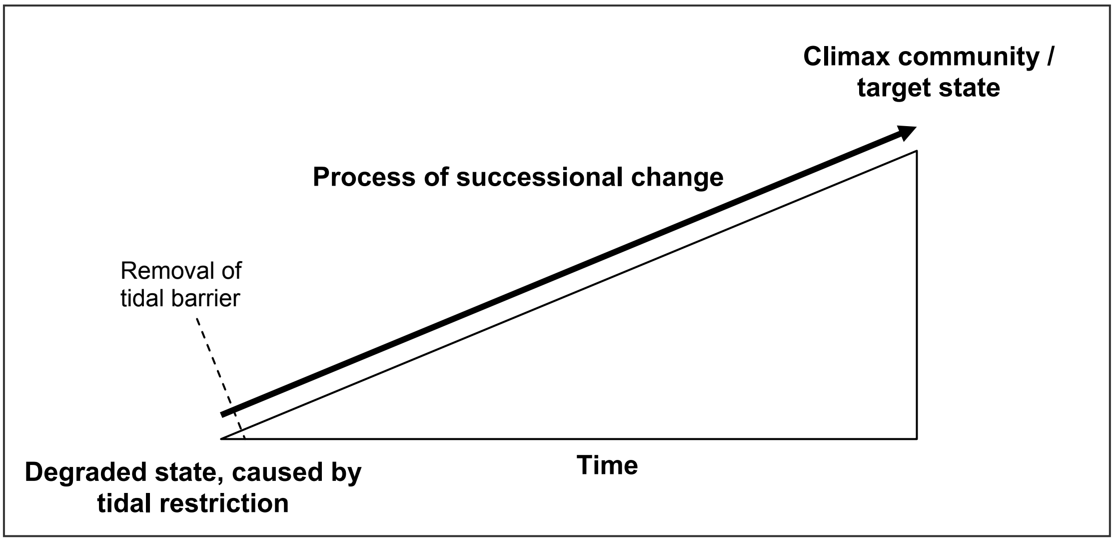
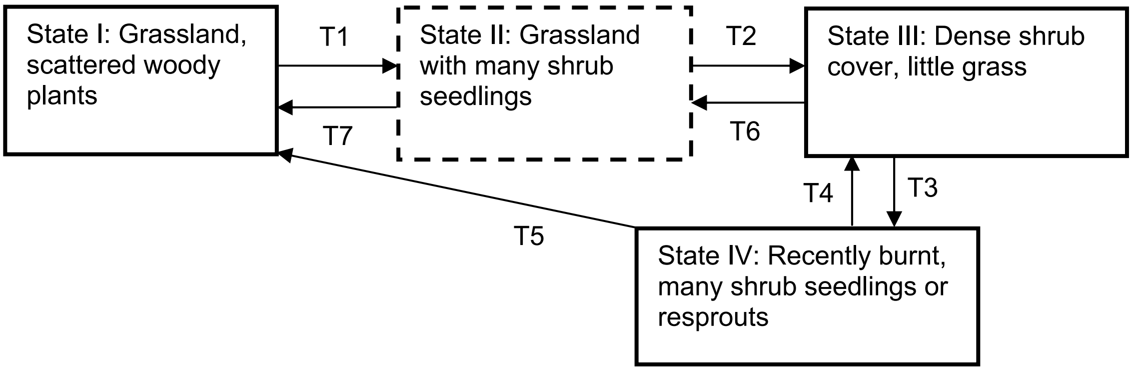


Figure 5.1. Clementsian succession model of plant community recovery, post tidal-restoration

This type of succession model framework has often been used in saltmarsh restoration projects, to predict the effects of tidal barrier removal on plant community composition and species distributions and to set vegetation restoration targets (Brinson and Reinhardt 1996; Boumans *et al.* 2002; Crooks *et al.* 2002; Thom *et al.* 2002). Nearby marshes without tidal barriers are used to determine the target community, and the elevation ranges inhabited by species at reference sites are used to predict their eventual distributions at tidal restoration sites.

5.1.4 State and transition models

State and transition models were initially proposed by Westoby *et al.* (1989), in the context of rangeland management, for summarizing existing knowledge on vegetation changes under different management scenarios. State and transition models continue to be used most often in rangeland management (Westoby *et al.* 1989; Briske *et al.* 2005; McIntyre and Lavorel 2007) but can easily be applied to other ecosystem management scenarios, including wetland restoration and rehabilitation (Young *et al.* 2005). Like simple succession models, state and transition models assume the existence of stable vegetation states, as per Clements (Westoby *et al.* 1989). A state and transition model is comprised of: a list of discrete recognisable vegetation ‘states’ possible at a site, defined in terms of community composition and structure; a list of the ‘transitions’, or management actions, that would cause vegetation to change from one state to another; and a list of the ‘opportunities and hazards’, including natural climatic circumstances such as rainfall or drought, that could also cause transition between states (Westoby *et al.* 1989) (Figure 5.2). This model framework can be particularly useful in an ecosystem management context because particular states of interest may be defined and focused on (such as higher or lower density of a particular species), with the environmental and management circumstances leading to those states investigated and summarised.



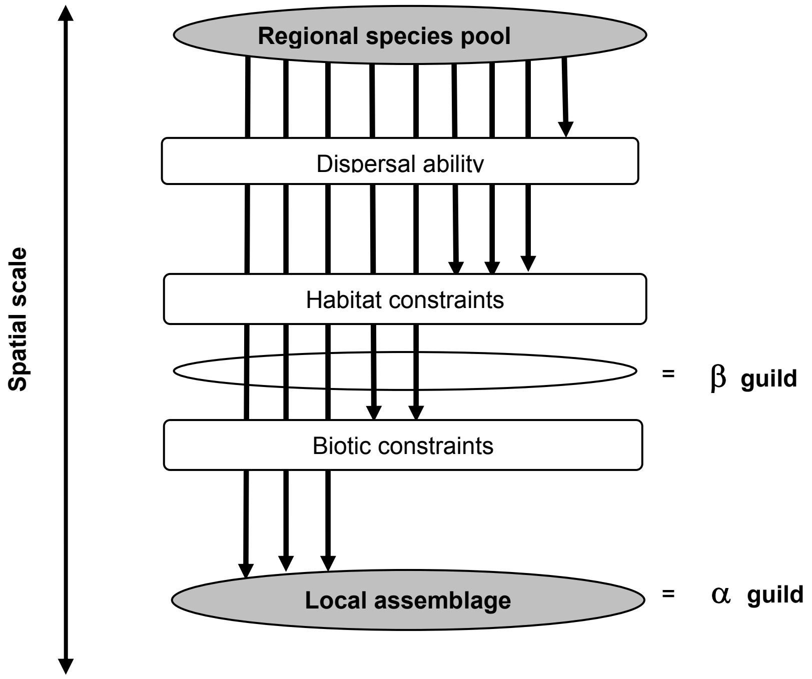
Key: T1-7 represent transitions between vegetation states. The characteristics marking each transition and their specific causes (such as higher or lower grazing pressure, rainfall and/or fire frequency) are explained in depth in the source article. The dashed outline of State II indicates that this is a transient or relatively short-lived state, whereas States I, III and IV, with the solid outlines are considered more stable.)

Figure 5.2. State and transition model for predicting community composition under different climatic and management condition scenarios (adapted from Westoby *et al.* 1989)

5.1.5 Assembly rule models

Other authors have suggested the use of assembly rule models for predicting the composition of ecological communities under different scenarios (Weiher and Keddy 1995; Poff 1997; Diaz *et al.* 1998; Keddy 2000c; Wolters *et al.* 2005; Holdaway and Sparrow 2006). Keddy (1999) strongly advocates the use of assembly rule theory as a framework to guide wetland rehabilitation in particular. Assembly rules models follow from the observation that certain ecological communities appear more often in nature than would be expected if the processes that govern species assemblage were random (Diamond 1975). The underlying premise is that plant communities assemble non-randomly, according to a set of definable rules, and that these rules are underpinned by a hierarchy of constraints, or filtering factors, that determine which species can establish and persist at any given site (Diamond 1975; Keddy 1999;

Keddy 2000c). Within the filtering factor hierarchy, the available species pool (Zobel 1997; Zobel *et al.* 1998) in the study region is considered to be the primary constraint affecting community composition, with the relative dispersal abilities of species further limiting which are able to arrive at a particular site (Figure 5.3). Next in the filter hierarchy are environmental factors that differentially affect the establishment and growth success of those species (Figure 5.3). Finally, where multiple species establish that are capable of tolerating and exploiting the particular abiotic conditions prevailing at a site, biotic interactions such as interspecific competition act as a final filtering factor (Figure 5.3), further modifying community structure (Lake *et al.* 2007). There has been some debate about the appropriateness of including biotic interactions in assembly rule models. In response, some suggest splitting the vegetation communities predicted by assembly rule models into two groups or guilds, beta guilds and alpha guilds (Figure 5.3), depending on whether habitat or biotic factors are considered most influential in their formation (Holdaway and Sparrow 2006) (Wilson 1999; Wilson and Gitay 1999).



Key: Arrows represent species. Bars represent filters that act as barriers to the establishment of some species.

Figure 5.3. Structure of an assembly rules model for predicting plant community composition based on combinations of abiotic and biotic filtering factors (Modified from Lake *et al.*, 2007)

Table 5.1. A comparison of the suitability of three theoretical frameworks for predicting the effects of tidal flow manipulation on wetland plant communities.

Model framework	**Advantages**	**Disadvantages**	**Literature**
Clementsian succession	Simplicity and ease of application: Only two vegetation states are necessary to define in the model, the degraded state and the target or reference site community.	Dependence on natural, undegraded reference sites, or pre-disturbance condition reports: In highly degraded systems these are often unavailable.	(Brinson and Reinhardt 1996; de Jong and de Jong 2002; Warren *et al.* 2002; Wolters *et al.* 2005)
	Ability to set well-defined restoration targets: Targets are set based on reference site community composition, against which the success of tidal restoration projects can be measured. Such targets are often required by funding bodies.	Assumption that reference marsh community represents a stable climax vegetation state: Often violated because tidal wetland communities are temporally dynamic. When target community composition fluctuates, the definition of restoration success must then be defined more loosely, with more approximate measures of similarity between sites accepted to allow for this variability. While coastal saltmarsh communities are often species-poor, and therefore relatively predictable, species richness generally increases as salinity decreases moving up the estuarine gradient. The more species present, the higher the degree of possible year to year fluctuation in species composition and cover, resulting in lower reliability of model predictions.	(Odum 1988; Brinson and Reinhardt 1996; Neckles and Dionne 1999; Boumans *et al.* 2002; Neckles *et al.* 2002; Thom *et al.* 2002)
		Assumption of a predictable unidirectional trajectory of change in community composition post tidal-restoration, toward the target state: A problematic assumption because in the temporally variable abiotic environment of tidal marshes the direction of vegetation change can also be unpredictable. Stochastic events can strongly affect community composition.	(Odum 1988; Boumans *et al.* 2002)
		Effects of salinity and hydrology on community composition are not separated out: At the saline end of the estuarine gradient salinity and inundation regimes are closely interlinked. However, further up the estuarine gradient fluctuations in salinity and inundation regimes become less closely correlated. To predict the impacts of tidal flow reinstatement on vegetation community composition in these wetlands it is important to consider the effects of changes in salinity and hydrology separately. Traditional tidal restoration models do not differentiate between the effects of these variables.	(Odum 1988)
		Narrow applicability: Such models are generally highly site and community-specific and therefore cannot be applied across different sites or spatial scales.	(Brinson and Reinhardt 1996)

Model framework	Advantages	Disadvantages	Literature
State and transition	Flexibility: Despite being based on the principle of successional changes between vegetation states, these models allow for a range of alternative vegetation states that fall outside the earlier idea of a simple linear progression over time, from early-successional to climax vegetation. Other commonly observed phenomena, such as discontinuous and irreversible transitions, non-equilibrium communities, and stochastic effects, are also accommodated. This flexibility in structure and content means that state and transition models could be built to summarise whatever information is available on practically any factor that affects plant community dynamics.	Reliance on predefined vegetation states based on prior monitoring data: Like simple succession models, these also require a list of predefined vegetation states. State and transition models were initially developed to summarise vegetation composition and cover changes under different grazing management strategies, based on long-term monitoring data. It is difficult to make a predictive model for vegetation shifts under different management scenarios when monitoring of past changes under these scenarios has not occurred, particularly if the current degraded state is the only one that can be accurately described. Predictions made for state shifts in such systems may need to be based on extrapolation from experimental data.	(Westoby *et al.* 1989; Whisenant 1999; Briske *et al.* 2005)
	A shift in the underlying succession theories used: More state and transition models are now being based on a Gleasonian rather than Clementsian succession paradigm. Gleason's definition of succession involves no assumptions about the long-term direction of community change. Instead the effects of changes in the growing environment are considered individually, with community composition at any point being the product of the sequence of previous changes. Models based on this "dynamic regime concept" are very suitable for summarising plant community responses to spatially and temporally variable growing conditions, such as those found in tidal wetlands.		(Gleason 1917, 1927; van der Valk 1981; Mayer and Rietkerk 2004)
	Compatibility with assembly rule models: State and transition models based on the dynamic regime concept share a common theoretical basis and assumptions with assembly rule models. These approaches could therefore be used complementarily.		
	Broad applicability: State and transition models can be made applicable across different sites by defining vegetation states in terms of plant functional groups.	Definition of plant functional groups: Since the application of state and transition models based on plant functional groups is novel in the context of tidal flow management, guidelines for definition of these groups will need to be developed. Appropriate plant functional groups for a tidal flow management model should be differentiated according to responses to altered salinity and/or hydrological regimes. While plant inundation responses may be determined to some extent from easily measured morphological or life-history traits, definition of salt tolerance ranges may require a more intensive bioassay approach.	(van der Valk 1981; Mountford and Chapman 1993; Brock and Casanova 1997; Gondard *et al.* 2003; Holdaway and Sparrow 2006; McIntyre and Lavorel 2007)

Model framework	**Advantages**	**Disadvantages**	**Literature**
Assembly rules	Broader applicability: One of the clearest advantages of the assembly rule model framework is that it is particularly well suited to making predictions about community composition across a range of different landscape scales. These models can be site and community-specific, or adjusted to apply to multiple sites with differing communities by considering plants as functional types rather focusing on particular species. Plant functional types should be defined according to differences in ability to 'pass through' relevant ecological filters.	Definition of plant functional groups: Appropriate plant functional groups for a tidal flow management model should be differentiated according to their responses to altered salinity and/or hydrological regimes. While plant inundation responses may be determined to some extent from easily measured morphological or life-history traits, definition of salt tolerance ranges may require a more intensive experimental screening approach.	(van der Valk 1981; Boutin and Keddy 1993; Mountford and Chapman 1993; Weiher and Keddy 1995; Poff 1997; Keddy 2000a; Keddy 2000c)
	Clear hierarchical structure: This model requires orderly, stepwise consideration of the range of factors likely to affect community composition at any particular site or scale. This process is potentially useful for highlighting any knowledge gaps that hinder prediction.		(Poff 1997; Keddy 1999; Keddy 2000c)
	Avoidance of the stable, climax vegetation community assumption: Based on the Gleasonian view of succession, these models overcome the problems inherent in simple Clementsian succession models that require a definition of the climax vegetation state.		(Gleason 1927; Keddy 1999; Keddy 2000c)
	No dependence on historical monitoring data: Unlike simple Clementsian succession and state and transition model frameworks, in an assembly rule model there is no need for vegetation states to be predefined. These models can be built without data on past changes to community composition under different management scenarios.		(Keddy 1999; Keddy 2000c)

5.1.6 Determination of the most suitable conceptual framework for a broadly-applicable model summarising wetland vegetation responses to tidal flow manipulation

Of the ecological models assessed here (Table 5.1), the assembly rule model framework appears suitable for making summarising information and making predictions about plant community composition across the broadest range of conditions. The assembly rule model framework can be applied across different types of wetlands and plant communities, is not dependent on data from reference sites, can be readily adapted to make predictions at different spatial scales, and requires explicit, stepwise consideration of all factors that are expected to have an effect on final community composition at rehabilitation sites (Table 5.1). This stepwise process in particular could be a useful tool for identifying knowledge gaps.

State and transition models also have some useful traits and in particular are highly suitable for summarising the effects of variability in abiotic factors, such as temporal fluctuations in water depth (van der Valk 1981), on community composition (Table 5.1). These models are more flexible in structure and content than assembly rule models, and can be created to focus on the effects of individual habitat variables. Since Gleasonian succession-based assembly rule models and state and transition models share a common theoretical basis and set of underlying assumptions, these models could be used together in a complementary way. Both types of model can be designed to be species or community-specific, by focusing on species identities, or made more generally applicable across different plant communities, by focusing on plant functional traits, and responses of different functional types of plants to tidal flow manipulation.

Here it is proposed that an overarching assembly rule model framework be used as the basis for a general model designed for making predictions about changes to tidal connectivity on wetland plant community composition, with complementary state and transition sub-models added, where appropriate, to summarise the effects of variability in individual habitat filters within the overall model. Salinity and water depth are naturally variable, both within and between tidal wetlands, particularly when the wetlands under consideration occur at different points along the estuarine gradient (Odum 1988). State and transition sub-models would be useful for summarising the effects of salinity and water depth changes on wetland plant community composition, including those caused by tidal flow manipulation.

In this chapter a general model will be developed for predicting the effects of tidal flow management on wetland plant community composition. This model will be based on the conceptual framework proposed above, focusing on plant functional groups, and with salinity and hydrology as the key environmental filters. This conceptual model is intended to be broadly applicable to any site or plant community, and suitable for predicting the distribution of relevant plant functional groups across a range of spatial scales. Once defined, the general model framework will be used to summarise Clarence River wetland data in a case study. Here macrophyte species will be classified into functional groups, based on their expected responses to altered salinity and water depth. The model will then be used to make predictions about the effects of floodgate management on the distribution of these groups, at both the entire floodplain and individual wetland scales.

5.2 General model for predicting macrophyte responses to tidal flow management

The general conceptual model for predicting macrophyte functional group responses to tidal flow management was developed and applied using the following stepwise process:

1. Definition of the general model structure with the various components identified and outlined, including abiotic and biotic habitat filters;

2. Identification of the spatial scales at which individual abiotic and biotic habitat filters affect wetland community composition;

3. Determination of plant traits that affect response to key habitat filters, particularly salinity and hydrology, and classification of species into functional response groups;

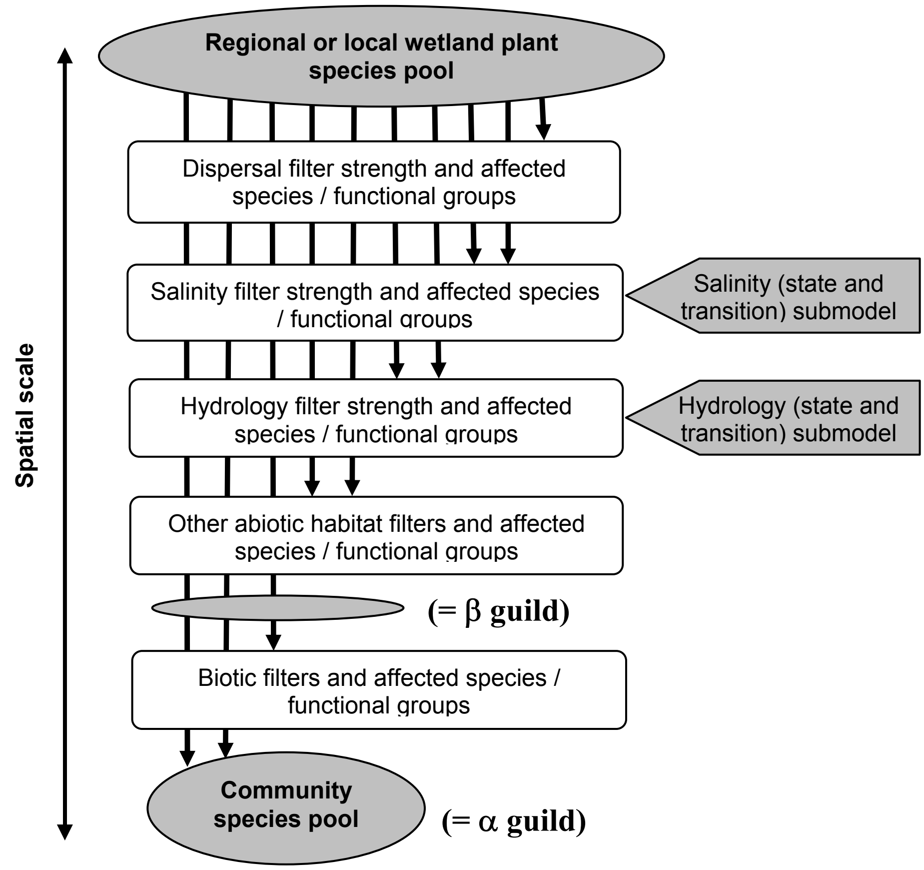
4. Development of state-and-transition submodels for summarising the effects of temporally variable filtering factors on community composition; and

5. Case study, applying steps 1–4 to survey and experimental data and predicting effects of floodgate manipulation on macrophyte community composition in Clarence River floodplain wetlands.

Steps in model development

5.2.1 Step 1: Definition of model structure and components

A hierarchical structure was selected for the generalised model of macrophyte responses to changes in tidal connectivity (Figure 5.4). This structure is based on that of a generalised plant community assembly rule model (Lake *et al.* 2007), with modifications made to suit the context of macrophyte response to tidal flow manipulation. Salinity and hydrological regime have been added to highlight their importance as key abiotic filters. Since salinity and water depth vary temporally in tidal wetlands as well as along the estuarine gradient (Odum 1988), allowance is made for the inclusion of state and transition submodels (Westoby *et al.* 1989), to summarise this variability along with relevant plant functional group responses. This framework has been designed to be a general model for predicting the effects of altered tidal flow management on the composition of any wetland plant community, irrespective of species composition, location or spatial scale. Each component of the general model framework in Figure 5.4 is described in Table 5.2, along with a summary of data requirements and suggested data sources.



(Vertical arrows represent species. Bars represent filters that act as barriers to the establishment of some species.)

Figure 5.4. A general model for predicting the effects of tidal flow management on wetland plant community composition (Modified from Lake *et al.* (2007)).

Table 5.2. Components of the generalised tidal flow management vegetation response model defined, including data requirements and relevant data sources.

Model component	Definition	Data required and suggested sources
Regional or local species pool	Regional species pool: The set of species occurring across a geoclimatic region, which are considered potentially capable of growing at the target site/s based on occurrence in similar habitat types (Pärtel *et al.* 1996; Zobel *et al.* 1998). Local species pool: The set of species found within the same landscape unit (e.g. coastal floodplain, wetland complex) as the target site/s, that are potentially capable of growing in the target habitat type (i.e. in wetlands) and which are considered likely to disperse relatively rapidly to the target site/s (Pärtel *et al.* 1996; Zobel *et al.* 1998).	Regional or local species list determined from vegetation surveys or literature (see Wolters *et al.* 2005).
Dispersal filter strength	The combined effectiveness of all factors limiting the arrival of propagules from species in the appropriate scale species pool at the target site/s (for example, propagule availability, availability of dispersal vectors, physical barriers including tidal barriers that restrict propagule movement). If interested only in potential effect of dispersal limitation on site species richness, filter strength may be defined as the percentage of species from the regional or local species pool reaching the target site. If interested in effects on site community composition, may be defined in terms of plant functional types and/or actual species arriving.	No reliable plant trait-based method has been found for predicting and ranking different species dispersal rates and distances (Zobel *et al.* 1998). However, information on how many species, and which species, are reaching the rehabilitation site/s can be obtained using propagule traps or standard seedbank methods (Brock *et al.* 1994; Leck 2004; Neff and Baldwin 2005).
Salinity filter strength	The effectiveness of target site soil and water salt concentrations at preventing the establishment of species from propagules that arrive at the target site. If interested in effects on species richness, salinity filter strength may be defined as the percentage of species reaching the target site that are also able to establish within the soil and water salinity ranges experienced (Wolters *et al.* 2005). If interested in effects on target community composition, may be defined in terms of both plant functional types and actual species establishing.	Target site salinity regime defined using data from site monitoring, both within wetland and outside tidal barrier, collected prior to tidal flow restoration. Species salinity tolerance ranges determined in controlled experiments where possible (Clarke and Hannon 1970; Bart and Hartman 2000; Bart and Hartman 2002; Greenwood and MacFarlane 2006). Otherwise survey data or literature may be used (Hart *et al.* 1990, 1991; Bailey *et al.* 2002; James *et al.* 2003; Nielsen *et al.* 2003).
Salinity submodel	Where considerable temporal variation in site salinity occurs due to management factors (e.g. tidal barriers open or closed) or natural cycles (e.g. low salinity in high rainfall season, high salinity in low rainfall season), changes in salinity filter strength and resulting effects on potential community composition may be summarised in a state and transition model.	As above.
Hydrology filter strength	The effectiveness of target site inundation regime (depth, duration, frequency and timing of inundation events) at preventing the establishment of species from propagules that arrive at the	Inundation regimes defined based on site monitoring data collected both within wetland

Model component	Definition	Data required and suggested sources
	target site. If interested in effects on species richness, filter strength may be defined as the percentage of species reaching the target site that are able to establish within the range of hydrological conditions experienced. If interested in effects on target site community composition, may be defined in terms of both plant functional types and actual species establishing.	and outside tidal barrier prior to tidal flow restoration (Neckles and Dionne 1999; Boumans *et al.* 2002; Neckles *et al.* 2002). Species flooding responses determined by compiling life history data from literature, supported by additional survey and experimental data if required (van der Valk 1981; Brock and Casanova 1997).
Hydrology submodel	Where site inundation patterns vary considerably over time due to management factors (e.g. tidal barriers open or closed) or natural cycles (e.g. standing water present in high rainfall season, followed by drawdown in low rainfall season), these changes in hydrology, and resulting effects on potential community composition, may be summarised in a state and transition model.	As above. Monitoring should be carried out over a period long enough to capture the range of variation in inundation patterns. For saltmarsh this period may be as short as one month (Neckles and Dionne 1999). In other classes of tidal wetland several years may be required to determine the extent of seasonal and interannual variability in water depth.
Other abiotic habitat filters	While salinity and inundation regime are the abiotic filters most directly affected by tidal flow manipulation, other abiotic factors may also reduce species (or functional group) establishment success at particular target sites (e.g. propagule burial due to sedimentation (Geho *et al.* 2007), light reduction due to high turbidity (Porter *et al.* 2007), or in the case of acid sulfate soils, reduced bioavailability of nutrients and exposure to elevated iron and aluminium concentrations (Rosicky *et al.* 2004)). Additional filters may be incorporated in the model as appropriate.	Importance of other habitat constraints assessed by field survey, followed by controlled experiments to test for causality if species distributions are correlated with any particular habitat factor.
β guild	A group of species (or plant functional types) capable of tolerating the same set of abiotic habitat conditions. These species occur together more frequently than expected by chance, because of their shared habitat preferences (Wilson 1999).	Field surveys, before and after tidal flow reestablishment.
Biotic filters	Any interspecific interactions capable of removing species (or functional groups) from the target site community that would otherwise be capable of establishing and surviving under the proposed combination of abiotic habitat traits.	Importance of particular biotic constraints (herbivory, competition etc.) may be determined experimentally if required (e.g. Gough and Grace 1998).
α guild	Alpha guilds occur nested within beta guilds and are groups of species with very similar resource requirements. These species occur together less frequently than expected by chance, because interspecific interactions strongly affect community composition, and competitive exclusion of species is common.	Field surveys, before and after tidal flow reestablishment.
Community species pool	The actual group of species (or plant functional types) present at the target site/s at any point in time (Zobel 1992).	Field surveys, before and after tidal flow reestablishment.

5.2.2 Step 2: Spatial scales for the consideration of model components

The model framework presented above could be applied to make predictions about the composition of wetland macrophyte communities at any spatial scale, including for example a whole bioclimatic region, a particular estuarine wetland system, an individual wetland of interest, or a specific microhabitat within a wetland. However, the different filtering factors governing plant community assembly may differ in importance according to the spatial scale under consideration. The scale at which predictions about community composition will be made, and the level of detail required in predictions, together determine the type of data required for the model (Table 5.3).

Table 5.3. Appropriate spatial scales for defining each model component

Model component	Appropriate scale of assessment	Scale of predictions
Species pool	Regional species pool (Zobel 1997; Zobel *et al.* 1998)	Broad scale predictions encompassing large biogeographic regions (see Wolters *et al.* 2005).
	Local species pool (Zobel 1997; Zobel *et al.* 1998)	*Coastal floodplain, *estuarine wetland complex, individual wetland, or microhabitat scales.
	Community species pool (Zobel 1997; Zobel *et al.* 1998)	*Individual wetland, or *microhabitat scale predictions (e.g. predictions about how tidal regime changes will affect the existing plant community at a target site.)
Dispersal ability	Individual target sites	For predictions at any scale.
Salinity and hydrology	Individual target sites	For predictions at any scale.
Other abiotic filters	Appropriate spatial scales for assessment vary and must be determined on an individual basis. For example, climate can be expected to affect plant community composition over large biogeographic regions, while factors such as siltation rates or eutrophication may vary between catchment areas, and others vary at finer scales still. (Poff 1997)	For predictions at any scale.
Biotic filters	Biotic filters, such as interspecific competition, facilitation and herbivory, are best considered at the individual wetland or microhabitat scale, since they are usually strongly affected by extant community composition and/or other site factors, such as grazing management. (Gough and Grace 1998; Chang *et al.* 2005; Geho *et al.* 2007)	For predictions at any scale.

*If species pool is defined at the same scale as the scale of prediction, then predictions about potential new coloniser species can not be made.

5.2.3 Step 3: Classification of species into functional response groups for filtering factors

Species pool, dispersal-mediated propagule availability, salinity, hydrology and the effects of salinity and hydrology on germination, establishment and persistence of particular species are the key primary factors that determine tidal wetland plant community composition (Odum 1988; Keddy 2000a). Identification of plant functional traits relating to an ability to pass through each of these primary filters is important for moving away from species-specific response models toward a broader predictive model based on plant functional groups.

5.2.3.1 Classifying plants into salt tolerance categories

Despite various attempts there is still no clear trait-based definition for the term halophyte, and the boundary separating halophytes from glycophytes (or non salt-tolerant plants) is equally difficult to define (Cheeseman 1988; Poljakoff-Mayber and Lerner 1995). This is because salinity alters the growing environment of plants in a number of different ways; other environmental factors such as temperature, nutrient availability and soil type can interact with salt concentrations and influence the effect of salinity on plants; a variety of different mechanisms are used by salt tolerant plants to avoid or tolerate salinity effects, and; strategies for salt tolerance as well as degree of salt tolerance can vary over the life of a plant (Cheeseman 1988; Poljakoff-Mayber and Lerner 1995). The complexity of salinity as an environmental stressor, and the variability in plant response mechanisms, as well as in the timing and degree of their expression, make it difficult to rank plants according to salt tolerance based on morphological or physico-chemical traits (Cheeseman 1988; Poljakoff-Mayber and Lerner 1995).

Because the salt tolerance ranges of different plant species are not readily apparent, an experimental screening process, as per Boutin and Keddy (1993), may be required to classify species in the target flora into appropriate functional response groups. Survey data can be used to obtain some information on species distributions with respect to salinity gradients. However, survey data may not necessarily indicate the full range of salinities that species are able to survive in as other factors are also likely to limit the distribution of species in the field. An experimental approach is useful because the full salinity tolerance range of each species can be tested, and species ranked accordingly.

Salt tolerance often varies across the life-cycle of a species with maximum salinities tolerated at the germination and establishment stages typically lower than those tolerated by mature plants (Gorham 1996). Some wetland species with salt-sensitive early life stages only germinate after exposure to fresh water (Baskin and Baskin 1998). Information about the salt tolerance of propagules and establishing plants is important for predicting germination and establishment success under altered salinity conditions. It is suggested that salinity thresholds and tolerance categories be determined for each life stage separately if predictions are to be made about species establishment as well the persistence of mature plants under altered tidal flow management. Petri dish experiments can be used to rank the salt tolerance of seeds (Baskin and Baskin 1998), whereas pot experiments are appropriate for screening more advanced growth stages (James and Hart 1993; Warwick and Bailey 1997; Morris and Ganf 2001; Bart and Hartman 2002).

Salt tolerance can be defined in terms of a simple threshold value, for example, the salt concentration that results in a specified reduction (commonly 50%) in germination, biomass production or survivorship (Marcum 2004). The salinity threshold can also be defined as a concentration above which yield (or germination, or survivorship) begins to decline, with the rate of decline above that threshold indicated (Maas 1986). Since the effects of salinity on plant growth and survival are affected by numerous factors, including water availability, temperature, types of salts involved, substrate fertility and plant life stage, salt tolerance is best expressed as an indication of performance in a given set of conditions rather than as an absolute value (Maas 1977; Miyamoto 1996). However, while threshold salinities may vary between experimental studies for individual species (Miyamoto 1996), these values can still be used to group and rank species of interest into salinity response categories for the purpose of modeling, provided they have been determined under comparable conditions and using a standard methodology (Maas 1977). Predictions can then be made about the relative impact of increased salinities on plants from each category.

5.2.3.2 Classifying plants into inundation response categories

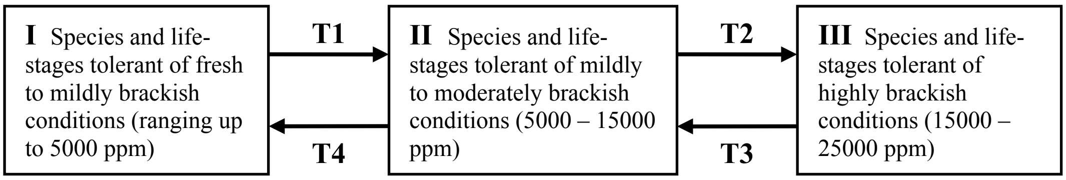
Plant responses to altered inundation regimes can also be complex. There are multiple variables incorporated into the term inundation regime, including rate, extent, timing and frequency of water depth variation, and each of these may differentially affect species establishment, growth or survival (van der Valk 1981; Capon and Brock 2006). However, some useful simplifications can be made. For example, Brock and Casanova (1997) divided wetland plants into three basic functional groups, terrestrial, amphibious and aquatic, based their on tolerances to wetting and drying. Terrestrial species are intolerant of flooding and aquatic species require standing water to survive, while amphibious species occur in the intermediate wet/dry ecotone, tolerating temporal fluctuations in water availability (Brock and Casanova 1997). Plants can be classified into these simple inundation tolerance categories based on information in the literature, or from survey or experimental data.

Another useful simplification was made by van der Valk (1981) who used the longevity of mature plants and propagules, and presence or absence of ability to establish underwater, to predict species tolerances to different wetting and drying sequences. Lifespan affects a species ability to withstand water level fluctuations because short-lived species may die out during unfavourable conditions, possibly reestablishing when conditions are more favourable, while long-lived species may depend more on an ability to tolerate unfavourable conditions in their mature form (van der Valk 1981). Under van der Valk's classification scheme wetland plants can be grouped into three lifespan categories; annuals (A), perennials with a limited lifespan (P) and vegetatively reproducing perennials of indefinite lifespan (V) (van der Valk 1981). These functional groups can be further subdivided, with species classified by propagule type into short-lived, dispersal-dependent species (D) or long-lived seedbank species (S) (van der Valk 1981). Species with D propagules depend on availability of a nearby viable propagule source and dispersal into sites suitable for establishment to persist, whereas S species propagules persist and can accumulate over numerous years, allowing these species to become established whenever suitable conditions occur, even without the presence of propagule-producing adults (van der Valk 1981). Finally, species can be further subdivided into draw-down species (Type I) or standing-water species (Type II), according to whether they are able to establish underwater (van der Valk 1981). Most of the life history information required for this classification process is easy to determine. However, if it is not known whether species form persistent seed banks, or whether propagules establish when submerged or during drawdown periods this information can be gathered by conducting a basic seed bank germination study (van der Valk 1981).

5.2.4 Step 4: Development of state-and-transition submodels to summarise the effects of temporally variable filters on community composition

5.2.4.1 Salinity regime, plant salt-tolerance categories, and the salinity response submodel

Soil and water salinity in tidal wetlands can be temporally variable, particularly in the upper reaches of estuaries where the fresh-saline interface occurs (Odum 1988). Changes to tidal flow management could increase or decrease the variability and extent of salinity fluctuations. Where salinity is likely to vary enough to cause changes to plant community composition, differences in the salinity thresholds of species (or groups of species) can be used as the basis for a state-and-transition submodel that summarises the changes in community composition expected under different salinity scenarios (for example Figure 5.5.).



Key: **I**, **II** and **III** indicate alternative vegetation states. **T1**, **T2**, **T3** and **T4** arrows indicate potential transitions between states

Transitions:
Transitions 1 and 2. Tidal barrier remains closed, and wetland salinity increases during drawdown due to evapoconcentration of existing salt. Alternatively, tidal barrier is opened and wetland is flushed with higher salinity water.
Transitions 3 and 4. Tidal barrier is closed. However, salinity decreases due to high rainfall and overland flows, coupled with a rapid drainage rate. Alternatively, tidal barrier is opened, and wetland is flushed with fresher water during a period of high streamflow.

Figure 5.5. Example of a basic state and transition model for summarising effects of temporal fluctuations in salinity on community composition

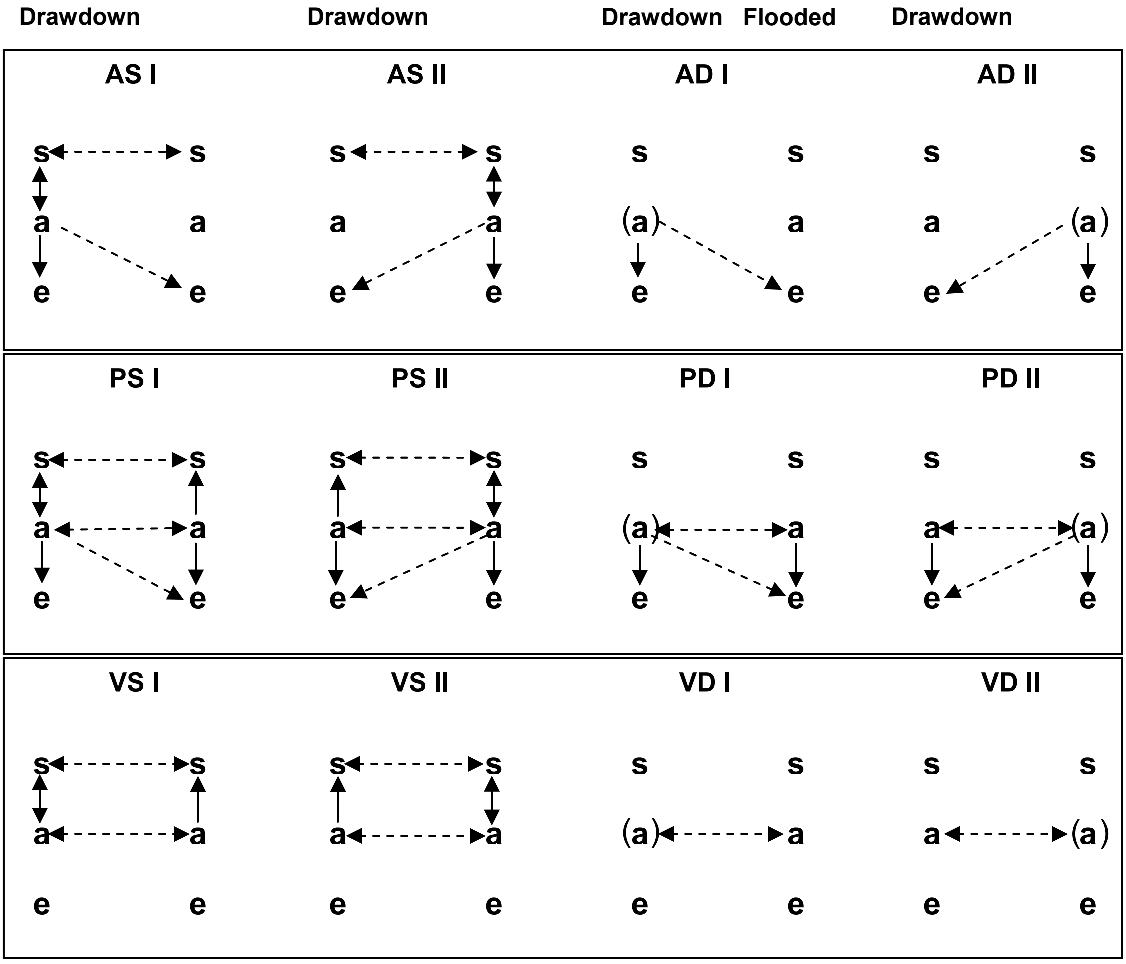
Timing and rate of salinity increase during increased salinity events and length of exposure to high salinity conditions can all affect the growth, survival, and recovery potential of wetland plants (Howard and Mendelssohn 1999a, b; de Jong and de Jong 2002). Where this type of information is available it can be incorporated into the salinity submodel to improve its predictive power.

5.2.4.2 Inundation regime, plant functional response groups and the hydrology submodel

The hydrology submodel proposed here for inclusion in the tidal flow management model combines Brock and Casanova's (1997) and van der Valk's (1981) models of plant functional types and responses to water level fluctuations, again using a state and transition model framework. These two models were selected because they use readily measured plant morphological and life history traits as their basis for predictions and are non species-specific, allowing generation of a hydrology submodel that is broadly applicable across a range of wetland plant communities. This submodel is useful for making predictions about community composition changes at sites with high temporal variability in water depth, such as those with floodgates where water influx is artificially managed and tidal flows may only be introduced at particular times of year.

To build the hydrology submodel, plants should be first categorised into one of the three broad inundation tolerance categories suggested by Brock and Casanova (1997) (terrestrial, amphibious or aquatic) based on general life history information available from regional flora and similar sources. Following tidal flow reinstatement, terrestrial category species would be expected to decrease and amphibious and aquatic species would be expected to increase, due to increased extent, duration and frequency of inundation (Brock and Casanova 1997). If site elevation surveys are carried out, information on tidal amplitude may be used to predict the position and extent of aquatic, amphibious and terrestrial vegetation zones, based on the position of permanently wet, permanently dry, and periodically inundated areas. If water depth variability is likely to decrease as a result of tidal flow reinstatement, the total elevation range and spatial extent of the amphibious plant zone can also be expected to decrease, whereas if depth variability increases the width of the amphibious plant zone can also be expected to increase (Keddy 2000a).

To build a more detailed hydrology submodel, life history and seedbank study data can also be used to categorise each of the species in the aquatic and amphibious groups into one of the twelve functional groups proposed by van der Valk (1981), each with a different strategy for responding to water level fluctuations. Predictions for each of the twelve species groups under different sequences of wetting and drying are summarised diagrammatically in Figure 5.6. As an example, AS I species, that is annual species with persistent seed banks and seeds that only germinate during drawdown, are predicted to either withstand inundation periods in seed form, or to die out completely in the inundated area, reestablishing only if additional seed is dispersed to the site. In contrast PD II species which are perennial, dispersal limited, and able to germinate under water can survive as adults during both flooded and drawdown periods although they may die out if conditions become too unfavourable. Establishment of PD II species occurs during flooded periods and is dependent on the presence of a nearby propagule source within dispersal range.



Key:
Plants are classified according to their traits as follows:
Lifespan; A = Annual, **P** = Perrenial, **V** = Vegetative reproduction (indefinite life-span).
Propagule longevity; S = persists in seed bank, **D** = short-lived propagules disperse and establish immediately.
Propagule establishment requirements; Type I = can only establish during drawdown (no standing water), **Type II** = can establish when there is standing water.

Plants exist in three states in the model; **s** = propagule in a persistent seed bank, **a** = adult plant, **e** = locally extinct. Parentheses indicate where establishment is dependent on the arrival of propagules from another site. Dashed arrows indicate potential transitions between states. Solid lines represent potential transitions within states.

Figure 5.6. Van der Valk's Gleasonian succession model for freshwater wetland vegetation composition.

5.3 Case study: Applying the general tidal flow management model to Clarence River wetland macrophyte data

5.3.1 Background

This case study focuses on the Clarence River coastal floodplain located in Northern NSW on the east coast of Australia. Many of the previously tidal wetlands on the Clarence River floodplain are now in a degraded state due to drainage and the historical installation of floodgates that exclude tidal water (Williams and Watford 1997). This situation is typical of many areas along the heavily settled east coast of Australia. Active floodgate management to allow tidal flushing has been proposed for a number of fresh, brackish and saline wetlands on the Clarence floodplain. The primary goals of tidal flushing are to improve water quality by reducing the production and mobilization of acid leachate from over-drained acid sulfate soils (ASS), and to increase fish habitat by removing barriers to fish passage (Walsh and Copeland 2004); however these goals must be balanced with site vegetation management goals. Increased incursions of higher salinity water could lead to the loss of some currently valued wetland vegetation types, including wet pasture and waterbird habitat.

This particular project differs from typical tidal marsh restoration projects in several key areas. Firstly, tidal flow reintroduction will be limited due to the desire to balance the project goals mentioned above (grazing utility, habitat maintenance, and ASS remediation) (Walsh and Copeland 2004). Therefore, this is a tidal flow management project rather than a full tidal restoration project. Secondly, because an adaptive management approach is being taken toward floodgate management, the actual flooding regimes that will be put in place are not clearly defined and will continue to evolve in the future. Finally, the wetlands being considered as potential rehabilitation sites are distributed along a longitudinal gradient ranging from approximately five to 24 kilometres from the tidal inlet, and therefore vary considerably in salinity and potential degree of tidal influence post flow-reintroduction. In some cases the presence of deep drains could lead to sites being flushed with more brackish water, once floodgates are opened, than they would have been exposed to prior to drain installation. While hydrological and salinity regimes will differ spatially and temporally within and among potential rehabilitation sites, there are two common underlying factors. One is the intention to increase flooding depth, duration and frequency, either by increasing tidal flushing and/or by increasing fresh water retention. Another is that increased tidal flushing will probably raise soil and water salinities at most sites. These changes to salinity and inundation regimes are likely to affect the growth, survival and distribution of plant species occupying rehabilitation sites.

5.3.2 Aims

The aims of this case study are:

1. To build a model for predicting the effects of floodgate manipulation on Clarence River wetland macrophyte communities, by applying the general tidal flow management model framework and methods, developed above, to Clarence River site and species data.

2. To make predictions about the effects of tidal flow reinstatement on the distribution of common and abundant macrophyte species found in fresh to moderately brackish Clarence River wetlands. This will be done at two spatial scales; the floodplain scale and individual wetland scale.

5.3.3 Methods

5.3.3.1 Step 1: Definition of model structure and components

At the individual wetland scale, the model framework is as presented in Figure 5.4., with the model used here for making predictions about β guild species composition. At the floodplain scale wetland sites were categorised into different types, based on their salinity and water management regimes. The models for each site type were then combined into one overarching model to represent site diversity at the whole of floodplain scale.

5.3.3.2 Step 2: Spatial scales for consideration of model components

Scale and determination of relevant species pools

The local species pool was used for predictions at the floodplain scale. This consisted of all species recorded in the survey of Clarence River floodplain wetlands presented in Chapter 2, where 17 sites were surveyed representing a range of salinity and water management conditions. The community species pool was used as the basis for prediction at the individual site scale, and was determined for each site using Chapter 2 survey data. Appendix 1 contains a list of species and their sites of occurrence.

Scale and dispersal ability

As the starting point for this project is the prediction of the loss of species from existing communities at potential rehabilitation sites, the model does not require data on the dispersal ability or propagule availability of potential colonisers.

Scales for assessment of salinity and hydrology filter strength

Differences in salinity and hydrology were assessed at the individual wetland scale using data from the site survey in 2005 (Chapter 2). Soil pore-water salinity was intended to be a criterion here for classifying sites into salinity filter strength groupings, because the salinity of the water in the root zone is often closely correlated with plant growth responses (Slavich and Petterson 1993; Shaw 1999; Hazelton and Murphy 2007). However, soil pore-water salinities could not be reliably extrapolated from 1:5 soil/water extract salinities using the standard soil texture-based conversion method (see Chapter 2). Instead, water management information from landholders, standing water salinity, and soil 1:5 soil/water extract salinity data were used to classify the survey sites into six salinity and inundation regime categories (Table 5.4). Since the survey was conducted in spring 2005, before the onset of the summer high rainfall period, soil and water salinities (Table 5.4) are expected to have been close to annual maximums at the time of sampling.

Table 5.4. Classification of sites into categories according to differences in abiotic filter strength (salinity and inundation regimes)

Wetland salinity/tidal influence category	**Survey sites**	**Survey site water (W) and soil (S) salinity ranges (ppm)**
Category 1: Freshwater wetlands. Above extent of tidal influence.	3 Chaffins Swamp, 7 Broadwater fresh channel	100–600 W 100–200 S
Category 2: Fresh to mildly brackish wetlands. Floodgate only opened during "freshes", or kept closed but levee occasionally overtopped when river floods and is relatively fresh (<5000 ppm).	1 Morans Swamp, 2 Colletts Swamp, 4 Shark Creek Wetland, 13 Everlasting Swamp ponded paddocks, 14 Everlasting Swamp drainage channels, 15 Everlasting Swamp Teal Lagoon	2300–6300 W 500–6200 S
Category 3: Mildly to moderately brackish wetlands. Floodgate opened when water <5000 ppm, or remains closed but levee occasionally overtopped by brackish water during floods (potentially >5000 ppm).	5 and 6 Edwards Creek Wetland, 8 Broadwater ponded freshwater area, 11 and 12 Little Broadwater Wetland	4500–12400 W 300–9000 S
Category 4: Moderately to strongly brackish wetlands. Sites subject to tidal inundation, with water <25 000 ppm.	9 Broadwater floodgated area, 10 Broadwater outside floodgate	12 000–25 900 W 800–9100 S
Category 5: Strongly brackish to saline wetlands. If tidal, receiving water 25 000–35 000 ppm.	N.A.	
Category 6: Saline to hypersaline wetlands. Tidal, receiving water ≥35 000 ppm.	16 Lake Wooloweyah tidal edge zone, 17 Lake Wooloweyah floodgated area	37 200–44 900 W 4700–11 700 S

Site numbers as listed in Table 2.1. Soil salinity ranges are based on 1:5 soil/water extract data from each site (see Chapter 2), with samples collected above the wetland edge excluded.

5.3.3.3 Step 3: Classification of species into functional response groups

Species salt tolerance categories

A literature search was conducted to establish the salinity tolerances of all species in the local species pool, except for those terrestrial species recorded only above the high water mark. For some species, such as *Phragmites australis*, salt tolerance ranges have been experimentally tested and reported (Chambers *et al.* 2003; Greenwood and MacFarlane 2006), while for others either survey distribution salinity range data, or no data, were found. For information from the literature on salt tolerance of individual species, and data sources, refer to Appendix 6. The growth and survival rates of *Bacopa monnieri, Bolboschoenus caldwellii, Cynodon dactylon, Eleocharis equisetina* and *Paspalum distichum* were also tested over a range of salinities in two experiments during this project. These experimental results are summarised in Appendix 7. Species salinity distribution data were also obtained during the 2005 survey of Clarence River wetlands, as summarised in Appendix 3.

Based on the above data sources, each species found at or below the high water mark was allocated to one or more of six tolerance categories (Appendix 8), with the water or soil pore-water salinity ranges used to define these categories corresponding with water salinity ranges used to separate sites into the categories in Table 5.4. For the purpose of classification, species salt tolerance thresholds determined from experimental data were defined as the salt concentration shown to have caused at least 50% mortality in the test group over a period of three months or less, or a negative rate of biomass production (e.g., shoot loss exceeds shoot production) sufficient to cause plant death over the same time period. Where experimental data were unavailable, species were allocated to salt tolerance categories based on the standing water or pore-water salinities measured at survey sites, from the 2005 survey of Clarence River wetlands or from other survey results reported in the literature (Appendix 6). Data relating to mature plants only were used in the salt tolerance classification, due to low data availability for other life stages.

Species inundation response categories

Information on inundation tolerance and flooding responses of species were gathered at the same time as the above salt tolerance data and this is also summarised in Appendix 6, along with the relevant data sources. Using this information, and data from the 2005 survey of Clarence River wetlands (Appendix 2), species were first classified into general inundation tolerance groups as per the methods of Brock and Casanova (1997). This was followed by a further classification of species into the water depth fluctuation response groups described by van der Valk (1981) (refer to Figure 5.6.). The inundation tolerance and depth fluctuation response categories determined for each species are listed in Appendix 8.

5.3.3.4 Step 4: State and transition submodels for temporally variable filters

Van der Valk's (1981) Gleasonian succession model was used to summarise the effects of water depth variation in the model (Figure 5.6). A simple state and transition model was also incorporated in the floodplain-scale model, to indicate hypothesised shifts in rehabilitation site salinity and inundation regime categories (Table 5.4) under different tidal flow management scenarios.

5.4 Results

5.4.1 The model: Floodplain and wetland scales

With sites categorised according to salinity and flooding regimes, and species categorised according to salinity and inundation tolerances, the relationships between site characteristics and species composition were summarised into the floodplain scale conceptual model presented in Figure 5.7. Nested within the floodplain scale model, an assembly rule model is depicted at the wetland scale for sites in each category from one to six. For each of these wetland scale models the local (i.e. currently occurring) species pool is indicated, to the left, as the primary determinant of plant community composition, with the salinity and inundation regimes defining each wetland category then acting as filters on this species pool. Arrows connecting the different types of wetland categories indicate predictions about the ways that floodgate manipulation might result in a transition of a wetland from one category to another due to changes in salinity or inundation regime filter strength (Figure 5.7). These hypothetical transitions are summarised in Table 5.5. Within wetlands of each category, species are distributed according to their flooding tolerance categories (Brock and Casanova 1997), with terrestrial species above the high water line, aquatic species below the low water line, and amphibious species in the intermediate area. Within each of these flooding tolerance categories, the model predicts that species will have different responses to water depth fluctuations according to their particular depth fluctuation response category, as summarised in Figure 5.6.

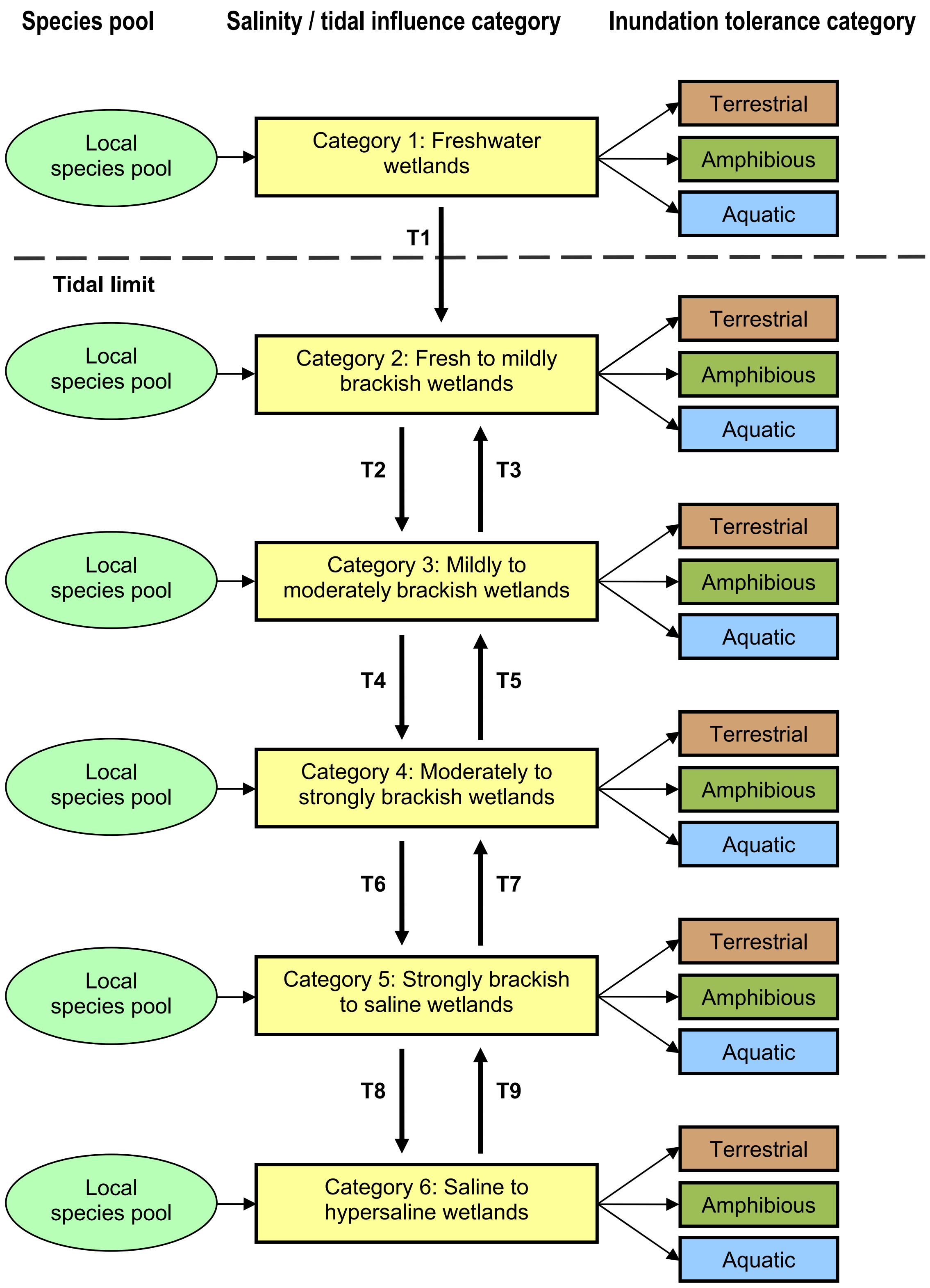


Figure 5.7. Model for predicting changes to macrophyte community composition under different tidal flow management scenarios in wetlands on the Clarence River floodplain.

NB: The amphibious and aquatic species groups have each been subdivided into the relevant water fluctuation response categories of Figure 5.6. These were excluded from the model diagram for simplicity. Fluctuation response categories for Clarence River wetland macrophytes are listed in Appendix 8.

Table 5.5. Transitions between wetland salinity / tidal influence categories.

Transition	Potential contributing factors
T1	Removal of tidal barrier on a drain results in mildly brackish tidal flows reaching a site that under natural conditions (pre-drain construction) would not have received tidal water. Wetland salinity range is increased by increased water salinity and evapoconcentration of salt.
T2	Floodgate opening allows slightly brackish water (approx. ≤5000 ppm) back onto a site that was historically tidal (with incoming water approx. ≤20 000 ppm (Peter Wilson *pers. com.* July 2005)).
T3	Floodgate kept closed. Gradual reduction in soil and water salinity if rainfall sufficiently high to flush accumulated salts from site and site does not pose an potential acid sulfate soil oxidation risk. Transition less likely if ASS are present because associated surface scalding and vegetation loss can drive increases in soil surface salinity that are difficult to reverse (Rosicky *et al.* 2006).
T4	Floodgate or other tidal barrier removed. Incoming water salinity is temporally variable, ranging up to maximum of 25 000 ppm.
T5	Floodgate in place, and opened only when incoming water salinity is <5000 ppm.
T6	Brackish water ≤25 000 ppm is retained on site and salinity increases due to evapoconcentration.
T7	Rainfall runoff reduces soil and standing water salinity to ≤25 000 ppm.
T8	Site is tidal, receiving strongly brackish to saline water, and after tidal barrier put in place site salinity increases due to evapoconcentration. Alternatively, site has had floodgate closed to exclude saline water ≥35 000 ppm for some time, and site salinity has decreased, however salinity increases again once floodgate is opened.
T9	Floodgate kept closed, and well-drained soils assist rainfall in flushing accumulated salts from site.

5.4.2 Effects of floodgate management on species distributions at the floodplain scale

In the 2005 survey of Clarence River wetlands some species were identified as being particularly common and/or abundant in fresh to moderately brackish wetland sites, including *Eleocharis equisetina, E. minuta, Phragmites australis, Schoenoplectus litoralis, Cynodon dactylon, Paspalum distichum, Cotula coronipifolia, Bacopa monnieri, Bolboschoenus caldwellii, Casuarina glauca, Melaleuca quinquenervia, Juncus usitatus* and *Nymphaea caerulea* (Chapter 2). The predicted habitat ranges of these species according to their salt tolerance ranges (Appendix 8) are presented in Table 5.6.

Table 5.6. Predicted distribution of focus species at the floodplain scale.

Wetland salinity / tidal influence category Species	Category 1: Freshwater wetlands	Category 2: Fresh to mildly brackish wetlands	Category 3: Mildly to moderately brackish wetlands	Category 4: Moderately to strongly brackish wetlands	Category 5: Strongly brackish to saline wetlands	Category 6: Saline to hypersaline wetlands
†*Bacopa monnieri*	✓	✓	✓	✓	✓	✗
†*Bolboschoenus caldwellii*	✓	✓	✓	✗	✗	✗
†*Casuarina glauca*	✓	✓	✓	✗	✗	✗
†*Cynodon dactylon*	✓	✓	✓	✓	✗	✗
Cotula coronipifolia		✓	✓	✓	✓	✓
†*Eleocharis equisetina*	✓	✓	✓	✗	✗	✗
Eleocharis minuta	✓	✓	✓	✓		
Juncus usitatus			✓			
Melaleuca quinquenervia		✓	✓	✓		
Nymphaea caerulea	✓	✓				
†*Paspalum distichum*	✓	✓	✓	✓	✗	✗
†*Phragmites australis*	✓	✓	✓	✓	✗	✗
Schoenoplectus litoralis			✓	✓		

Habitat ranges predicted based on experimental data† and/or survey records (✓ indicates habitat predicted suitable for species survival, ✗ indicates areas with salinity exceeding experimental salt tolerance threshold). Site salinity / tidal influence categories only include areas located below the high water mark.

If altered floodgate management causes an increase or decrease in site salinity that is sufficient to cause a change in the salinity / tidal influence category of a site, this may result in that site becoming unsuitable for some species. The floodgate management-related transitions (Table 5.5), outlined in the macrophyte response model for Clarence floodplain wetlands (Figure 5.7), are expected to affect focal species as summarised in Table 5.7.

Table 5.7. Effects of floodgate management on distribution of focal species

Transition	Predicted consequences for species
T1	No loss of focus species. Sites suitable for *Bolboschoenus caldwellii, Cynodon dactylon, Eleocharis equisetina, Phragmites australis, Paspalum distichum* and **Nymphaea caerulea* to occur as persistent stands. However, Category 1 wetlands contained a number of species that were found only at freshwater sites (Appendix 1), some of which may affected negatively by increased salinity.
T2	**Nymphaea caerulea* may disappear. Alternatively, **N. caerulea* may occur as an annual if the wetland is fresh for a sufficient period of time to grow and reproduce over Spring-Summer, later dieing as salinity levels increase. Conditions remain largely favourable for *Bolboschoenus caldwellii, Eleocharis equisetina* and *Paspalum distichum,* however salt tolerance thresholds may be exceeded at some times causing stunting and/or dieback. Conditions remain favourable for *Phragmites australis.*
T3	Sites may become more favorable for **N. caerulea* persistence.
T4	*Phragmites australis* likely to persist. *B. caldwellii, Casuarina glauca, E. equisetina* and *P. distichum* growth and survival likely to decline as salt tolerance thresholds are exceeded over extended periods. *Bolboschoenus caldwellii* and *E. equisetina* likely to retreat to shallower water depths (data available for these two species only). **Juncus usitatus* may also decline.
T5	Sites may become more favourable for *B. caldwellii, C. glauca, E. equisetina, *J. usitatus* and *P. distichum* growth and persistence.
T6	Salt tolerance thresholds for *Cynodon dactylon, *Eleocharis minuta, *Melaleuca quinquenervia, Paspalum distichum, Phragmites australis* and **Schoenoplectus litoralis* exceeded. *Bacopa monnieri* and **Cotula coronipifolia* the only focus species likely to remain.
T7	Sites may become more favourable for *C. dactylon, *E. minuta, *M. quinquenervia, Paspalum distichum, Phragmites australis* and *S. litoralis* persistence.
T8	**Cotula coronipifolia* is the only focus species remaining. Sites occupied by saltmarsh species.
T9	Sites may become more favourable for *Bacopa monnieri* persistence. **Cotula coronipifolia* the only other focus species likely to remain.

*Predictions based on survey data only for these species. Data from salt tolerance experiments available for the other species.

5.4.3 Effects of floodgate manipulation on species distributions at the wetland scale

While wetland salinity is expected to affect the distribution of species at the floodplain scale, species are distributed along a relative elevation gradient within individual wetlands according to differences in their inundation tolerance (Table 5.8). While species inundation tolerance categories are unlikely to change, their elevation ranges are likely to shift with any long-term change in wetland depth. Increases in water depth and permanence are expected to lead to increased habitat for aquatic species, and an upward shift in the lower elevation limit of amphibious and terrestrial vegetation zones (Keddy 2000a). Increases in water depth variability are expected to result in an increase in the range of elevations suitable for occupation by amphibious species, while reductions in water depth variability are expected to lead to a contraction of the elevation range suitable for these species (Keddy 2000a). The tolerance of some key species to increases in water depth may also change according to changes in site salinity, as demonstrated in the factorial salinity × water depth tolerance experiment in Chapter 4. The depth tolerance thresholds of *E. equisetina* and *B. caldwellii* are expected to decline with increasing salinity, limiting these species to shallower and less-frequently inundated areas at salt-affected sites (Table 5.8).

The persistence of species at the wetland scale is also affected by their ability to tolerate fluctuations in water depth, and to reestablish at a site if mature plants die due to excessive flooding or drying. If changes to floodgate management lead to increases in water permanence, type II species, capable of establishing underwater, are likely to have a competitive advantage, whereas type I species, establishing only during drawdown, may be disadvantaged (van der Valk 1981). For example, stands of *B. caldwellii* and *E. equisetina* occur as long-lived stands of vegetatively reproducing individuals in fresh to mildly brackish conditions (Table 5.8), but may die out at some times. *Bolboschoenus caldwellii* appears to reestablish primarily from tubers during drawdown while *E. caldwellii* is capable of reestablishing from seed while the substrate remains submerged (pers. obs.). *Eleocharis equisetina* stands may therefore be more capable of reestablishing under conditions of increased inundation frequency and/or permanence than stands of *B. caldwellii*. Species that form persistent seed banks (S species) may also be less vulnerable to local extinction due to adverse conditions than those that rely on local dispersal of short-lived propagules from nearby sites (D species) (van der Valk 1981).

Table 5.8. Inundation tolerance and depth fluctuation response categories for focus species.

Species	**Inundation tolerance category (Optimum depth range)**	**Depth fluctuation response category**
Bacopa monnieri	Amphibious	P/V D/S I
†*Bolboschoenus caldwellii*	Amphibious (Optimum depth ≤20 cm in fresh water. Depth tolerance decreases with increasing salinity.)	V S I (category 1and 2 sites) V/A S/D I (category 3 sites)
Casuarina glauca	Terrestrial	P/V S I
†*Cynodon dactylon*	Terrestrial (Poor growth in waterlogged conditions.)	V/P S I
Cotula coronipifolia	Amphibious	A/P S I
†*Eleocharis equisetina*	Amphibious (Optimum depth ≤20 cm in fresh water. Depth tolerance decreases with increasing salinity.)	V S II (category 1 and 2 sites) V/A S II (category 3 sites)
Eleocharis minuta	Amphibious	V/P S II
Juncus usitatus	Amphibious	P S I
Melaleuca quinquenervia	Terrestrial	P S I
Nymphaea caerulea	Aquatic	P S II (category 1 and 2 sites) A/P S II (category 3 sites)
†*Paspalum distichum*	Amphibious (Optimum depth ≤20 cm in fresh water. Depth tolerance decreases with increasing salinity.)	P D/S I
Phragmites australis	Amphibious	V D/S I/II
Schoenoplectus litoralis	Amphibious	P S I

†Optimum depth range as determined in depth × salinity experiment (Chapter 4). Depth fluctuation response categories are as defined in Figure 5.6.

Changes to site salinity can change the response of species to fluctuations in water depth (Table 5.8). For example, the results of the salinity × water depth tolerance experiment in Chapter 4 suggest that *B. caldwellii* and *E. equisetina* will withstand increases in water depth ≥20 cm for longer time periods at category one and two sites, than at category 3 sites where higher salinities occur. In these situations *B. caldwellii* and *E. equisetina* would be reliant on the availability of propagules for reestablishment. This type of salinity effect appears likely to be occurring for *Nymphaea caerulea,* which was observed persisting throughout 2005-2008 at category one and two sites but grew as a short-lived annual at the Little Broadwater wetland, the only category three site where it was found. At the Little Broadwater site, *N. caerulea* was observed reestablishing from seed when the wetland was fresh after high spring-summer rainfall events, and survived long enough to flower and set seed before salinity increased and the plants died off (pers. obs.).

5.4.4 Effectiveness of experimentally-derived salt tolerance thresholds as predictors of species field distributions

To test how well experimentally derived salt tolerance thresholds worked as predictors of field distribution, site salinity classification data from Table 5.4 were matched against the species salinity tolerance categories in Table 5.6 to generate a table of sites that these species should be capable of occupying on the Clarence River floodplain (Table 5.9). Survey data from each site were then used to test how closely this table of expected species distribution limits, based on experimental data, matched with species distributions recorded in the field.

Predicted habitat suitability was not always a good indicator of species occurrence. Most of the focal species were found at less than half of the sites predicted to be within their salt tolerance ranges. Exceptions were *E. equisetina* and *P. distichum* which were found at 100 % and 80 % of sites predicted to be suitable, respectively. The species distributions recorded in the 2005 field survey also sometimes exceeded those predicted based on experimental salt tolerance data. *Paspalum distichum* and *Phragmites australis* were found exclusively at sites classified as suitable according to their experimentally-determined salt tolerance ranges. However, *Bacopa monnieri* and *C. dactylon* were expected to occur only at category one to five sites, but were found at Lake Wooloweyah, a category 6 site. *Bolboschoenus caldwellii* was expected to occur only at category one to three sites, but was also found at two category four sites fringing the Broadwater wetland. *Casuarina glauca* was expected to occur only at category three sites, but was also recorded at two category four sites, adjacent to the Broadwater, and at Lake Wooloweyah. *Eleocharis equisetina* was expected to occur only at category one to three sites, but was also found at a category four site, adjacent to the Broadwater.

Table 5.9. Comparing species expected salinity ranges, extrapolated from experimental data (as summarised in Table 5.6), to their recorded field distributions

Site	***Bacopa monnieri***	***Bolboschoenus caldwellii***	***Casuarina glauca***	***Cynodon dactylon***	***Eleocharis equisetina***	***Paspalum distichum***	***Phragmites australis***
1. Morans Swamp	P	P	P	P, R	P, R	P, R	P
2. Colletts Swamp	P	P	P	P	P, R	P, R	P
3. Chaffins Swamp	P	P	P	P	P, R	P, R	P
4. Shark Creek wetland	P	P	P, R	P, R	P, R	P, R	P
5. Edwards Creek wetland	P, R	P	P	P	P, R	P, R	P
6. Edwards Creek wetland (not grazed)	P	P	P	P, R	P, R	P, R	P
7. Broadwater freshwater channel	P	P	P	P	P, R	P	P
8. Broadwater ponded fresh area	P, R	P, R	P, R	P	P, R	P, R	P, R
9. Broadwater floodgated area (not grazed)	P, R	R		P		P, R	P
10. Broadwater, tidal area	P, R	R	R	P, R	R	P, R	P, R
11. Little Broadwater (grazing exclosure)	P, R	P, R	P, R	P, R	P, R	P, R	P, R
12. Little Broadwater wetland	P	P	P, R	P, R	P, R	P, R	P
13. Everlasting Swamp ponded paddocks	P	P, R	P, R	P, R	P, R	P, R	P, R
14. Everlasting Swamp drainage channels	P	P	P	P	P, R	P	P
15. Everlasting Swamp, Teal Lagoon	P	P	P, R	P	P, R	P	P, R
16. Lake Wooloweyah tidal							
17. Lake Wooloweyah floodgated	R		R	R			
Total % sites = Predicted and recorded	29.4	17.6	35.3	41.2	76.5	70.6	29.4
Total % sites = Not predicted, not recorded	5.9	11.8	11.8	5.9	17.6	11.8	11.8
Total % sites = Predicted, but not recorded	58.8	58.8	41.2	47.1	0	17.6	58.8
Total % sites = Not predicted, but recorded	5.9	11.8	11.8	5.9	5.9	0	0

Key: P = site predicted suitable for species occurrence, R = species recorded in this wetland, below the high water mark, during 2005 survey. For further information on survey sites refer to Table 2.1.

5.5 Discussion

This chapter successfully achieved its primary aim of developing a general model framework, based on assembly rule model principles (Keddy 2000c), that can be used to predict effects of tidal flow changes on wetland macrophyte community composition. Unlike previous tidal restoration models, the framework presented here is not restricted to saltmarsh sites, but can also be applied to other tidal wetland types that differ in salinity and inundation regime traits, including oligohaline and mesohaline sites. This is because the effects of salinity and inundation regime on macrophyte persistence are considered individually. The model developed here can also be used to make predictions about the changes to community composition likely to occur under a variety of alternative tidal flow management scenarios, rather than being restricted to a full tidal restoration scenario. This increased flexibility has been aided by both the use of an assembly rule model structure overall, and the incorporation of state-and-transition submodels to summarise the effects of changes in salinity and water depth on the persistence of different plant functional types. The methods for model construction outlined here are not site or community-specific and so could potentially be applied to any tidal flow management project. The model can also be constructed and applied at the individual site scale, or adapted to include multiple sites at a larger geographical scale as was demonstrated here in the case study using Clarence River wetland site and species data.

The second aim, of applying the model framework and methods developed here to Clarence River wetland site and species data, was also successfully achieved, with a model developed to predict the effects of floodgate manipulation at both the floodplain and individual site scales. Through this process a range of data on current site conditions, species salinity and inundation responses, and the predicted effects of different floodgate management strategies on the survival of focal species at each site were summarised into a potentially useful management tool.

As well as allowing predictions to be made, the hierarchical structure of the assembly rule model framework used here, and the stepwise process of model development were both useful for highlighting any knowledge gaps that could hinder prediction. This was due to the consideration of range of factors likely to affect community composition at a particular site, in this case including species pool, dispersal ability and abiotic factors. For example, one such unknown factor in the case study presented here is the composition of the propagule pool available at each site.
In the absence of propagule availability data, the model outputs were limited to predictions about the likelihood of extant species persisting at particular sites under different tidal flow management scenarios. However, with the addition of propagule availability data, and data on the effects of salinity on seed germination, the model could be extended to predict which additional species are likely to colonise sites under different floodgate management strategies.

Other areas were also highlighted during model development where additional data could be used to increase predictive power. The classification of species into functional response groups was one such area. Where experimental data on the salt tolerance or depth tolerance of particular species were available, species could be readily classified into functional response categories based on their relative tolerance ranges. However, for many species only survey distribution data were available, and while these species could still be classified into functional response categories based on their observed field distributions the upper and lower limits of their tolerance ranges could not be as confidently determined. For these species most areas of suitable habitat should be confidently predicted in the model. However, areas of unsuitable habitat were less confidently predicted.

The classification of Clarence River wetland sites according to differences in abiotic filter strength also highlighted areas where the model could be further developed. For example, site salinity ranges were broadly defined here using site water salinity data collected during 2005, during the driest time of year, information on incoming water salinity ranges provided by landholders, and data provided by Clarence Valley

Council Floodplain Services on the salinity of the Clarence River and its tributaries. A more refined study on the nature and extent of salinity and water depth fluctuations over time at individual sites has not yet been conducted. A prediction of abiotic habitat suitability for a group of species by the model, based on site salinity and species salt tolerance range data, did not guarantee the presence of those species at that site. None of the focus species were found at every field site within the salinity range determined to be suitable, and most species were absent from more than half of the sites that were determined to be within their habitable salinity range, as determined from 2005 species distribution data. This result may have been caused by dispersal limitation, other biotic or abiotic factors reducing habitat suitability, or insufficient sampling to detect species presence. Habitat unsuitability (excessive salinity) was usually a reasonably reliable predictor of species absence. However, species distributions recorded in the 2005 field survey did sometimes exceed those predicted based on experimental salt tolerance data, indicating a need for further refinement. Where species were found outside of their predicted ranges, this could either be the result of an overestimation of site salinity, or an underestimation of plant salinity tolerance.

The predictions made here about species persistence at different sites across the Clarence River floodplain were largely based on experimentally-derived species salt tolerance data and data on site salinity, since specific data on how floodgate management will affect inundation regimes at these sites were not available. However, while it is expected that changes to water regime will alter macrophyte distributions, these distribution changes are likely to be primarily changes to the particular elevation ranges able to be occupied by species within sites (Pressey and Clancy 1979; Keddy 2000a). The distribution of species in coastal floodplain wetlands is strongly affected by site salinity (Odum 1988; Keddy 2000c), and it is expected that changes in site salinity are more likely to affect species persistence at individual sites.

Finally, to predict effects of floodgate opening on macrophyte species, based on their salinity and inundation response categories, it is necessary to not only summarise current site conditions, but also to predict the extent to which site salinity and inundation regimes will change. In the Clarence River wetlands model these predictions about salinity and inundation regime changes are loosely defined. More targeted data for predicting these changes should be acquired by monitoring temporal changes in soil and water salinity and water depth both inside and outside the floodgates at intended rehabilitation sites, for one or more years prior to floodgate opening (Neckles *et al.* 2002). However, while these data will provide a useful indication of depth and salinity changes likely under a program of full tidal flow reinstatement, this method may have some limitations with respect to predicting the effects of partial tidal flow reinstatement on site depth and salinity. In particular, it does not take into account some salinity increases that are likely to occur due to evapoconcentration while floodgates are kept closed. An investigation into the relationships between initial water salinity, ponding time, evaporation rates, standing water salinity, and how these factors affect pore-water salinity in the plant root zone, depending on soil type, would provide useful data for increasing the predictive power of the model under partial tidal flow reinstatement scenarios. These data could also be obtained through targeted monitoring at rehabilitation sites after floodgate opening.

CHAPTER 6

Synthesis and conclusions

6.1 Introduction

The primary aim of this research was to determine how opening floodgates, that have excluded tidal water from wetlands on the Clarence River for periods up to 70 years, would affect macrophyte community composition, particularly at sites that have become secondarily fresh or oligohaline. Few overseas studies have focused on the effects of tidal restoration on oligohaline wetland macrophytes (Odum 1988; Meyerson *et al.* 2000) and the current project appears to be the first in Australia to focus on this area. Here a field survey, two manipulative tub experiments and a literature review were used to obtain data and build a model for predicting how floodgate manipulation would affect the persistence of macrophyte species in Clarence River wetlands.

6.2 Assessment of patterns in macrophyte species distribution with respect to environmental gradients on the Clarence River floodplain

The aims of the field survey reported in Chapter 2 were to determine the composition of macrophyte communities in wetlands along the Clarence River floodplain, look for any patterns in species composition relative to site environmental and management factors, identify the most abundant and widespread species occurring in fresh and oligohaline floodgate-affected wetlands, and compare the salinity and depth ranges of abundant and widespread species found at these sites.

Seventy one macrophyte species were recorded in 17 wetland sites distributed along the length of the Clarence River floodplain. Species richness at individual sites ranged from four to 25 species, and was typically low below the high water mark where species such as *Eleocharis equisetina* and *Phragmites australis* formed dense, often monospecific, stands. As expected, differences in species composition were strongly and significantly correlated with both differences in soil salinity and position on a relative water depth gradient. While it was hypothesised that species composition may also vary with acidity and grazing management these variables were not, or only weakly, correlated with differences in species composition.

The most widespread species occurred over a broader range of soil salinity, water depth and soil pH conditions than less widespread species, suggesting that these widespread species are likely to be more tolerant of variations in those habitat traits. The species from secondarily fresh and oligohaline wetlands were ranked according to their soil salinity and water depth ranges, and based on these rankings hypotheses were made about their relative salinity and inundation tolerances. However, while these correlative data highlighted some trends and provided a basis for hypothesis generation, they did not provide direct evidence of the effect of environmental variables on species distributions.

6.3 Differing responses of estuarine wetland macrophytes to increased salinity

The aim of Chapter 3 was to experimentally determine the salinity tolerance ranges of focal species identified as widespread and/or abundant in floodgate-affected, secondarily fresh or oligohaline wetlands on the Clarence River floodplain. The direct effects of increased salinity on the growth and survival of five focal species were tested here using a glasshouse tub experiment. These species were *Bacopa monnieri, Bolboschoenus caldwellii, Cynodon dactylon, Eleocharis equisetina* and *Paspalum distichum,* which were identified as being common or abundant in fresh and oligohaline wetlands in Chapter 2. They were selected because they are likely to form a substantial component of the vegetation found at potential rehabilitation sites, and because their salt-tolerance under waterlogged conditions had not been tested previously.

Based on plant survival times, *P. distichum* was found to have the highest salt tolerance under waterlogged conditions, followed by *B. monnieri, E. equisetina, B. caldwellii* and then *C. dactylon.* Growth rates and overall biomass production showed a similar trend, with productivity maintained at higher salinities for *P. distichum* and *B. monnieri* than for *E. equisetina,* followed by *B. caldwellii* and *C. dactylon.* In

Chapter 3 the relative salinity tolerance ranking of the five species differed from what was predicted based on the survey data in Chapter 2, or on field observations after floodgate opening at the Little Broadwater wetland (Graham *et al.* 2004). It was also found that while a particular salinity threshold caused survival rate decline for each species, above-ground biomass production was often reduced at a lower salt concentration.

An advantage of the experiment reported in Chapter 3 was that the salinity tolerances of these species could be assessed across a broader range of salt concentrations than they were observed at in the field. The effects of salinity on plant growth and survival could also be determined without the confounding effects of spatial and temporal variability in other environmental factors, such as water depth. A limitation of the experimental determination of plant salinity tolerance is that salinity tolerance thresholds can be reduced by the presence of other environmental stressors (Maas 1977) such as drought or flooding stress, or nutrient deficiencies. The salt concentrations at which species growth and survival rates began to decline in the experiment in Chapter 3 are therefore likely to be higher than those that will affect plants placed under more stressful conditions in the field. However, these salt tolerance data give a good indication of the maximum salt concentrations tolerated by these species under favourable growing conditions, and indicate the relative salt sensitivities of these species. These data can be used to predict their relative performance in the field (Maas 1977).

6.4 Combined effects of increased salinity and water depth on the growth and survival of four macrophyte species

Tidal restoration will affect not only salinity, but also inundation regime at affected sites. The aim of Chapter 4 was to experimentally determine the tolerances of focal species to simultaneous increases in water depth and salinity, testing whether these factors had any interactive effects on plant growth. An outdoor tub experiment was used here to measure the growth and survival rates of four species, *B. caldwellii, C. dactylon, E. equisetina* and *P. distichum,* under 12 different salinity and water depth treatment combinations (four salinities × three depths).

For all four species biomass production declined both with increasing salinity and with increasing water depth. In most cases the effects of salinity and depth were additive, with few significant interactions occurring. Based on the relative growth rate data recorded for *B. caldwellii* and *E. equisetina* in Chapter 4, it was also demonstrated that sub-lethal salt concentrations, in particular those high enough to affect plant growth rates, can cause a reduction in the ability of these emergent macrophytes to withstand increases in water depth. These results suggest the water depth ranges tolerated by these species will decrease at wetland rehabilitation sites if salinity becomes high enough to limit growth. Therefore, as site salinity increases, the lower limits of these species elevation ranges are expected to move upward on the topographic gradient.

6.5 Development and application of a general model for predicting macrophyte responses to tidal flow management

Chapter 5 had two main aims. The first aim was to find a model framework for predicting the effects of tidal restoration on coastal wetland macrophyte communities that would not require vegetation composition data from reference wetlands or historical sources. This was achieved via a literature review.

The review compared the relative suitability of Clementsian succession models, state and transition models, and assembly rule models for predicting the effects of tidal restoration on the composition of estuarine wetland macrophyte communities. It was concluded that the Clementsian-succession models typically used to predict the outcomes of tidal restoration on saltmarsh community composition could not be used for the sites and tidal flow management scenarios being considered for the Clarence River floodplain. These models tend to be site and/or community-specific, can not be used to make predictions across different landscape scales, are restricted to predictions about the effects of complete tidal restoration, and are dependent on the existence of vegetation data from reference sites without tidal barriers. They also do not separate the effects of salinity and inundation regime on community composition. These factors are closely correlated in coastal saltmarsh environments. However, salinity and water depth are less closely correlated and more spatially and temporally variable in oligohaline and mesohaline wetlands.

An assembly rule-based model framework, considering salinity and water depth as separate abiotic filters, was suggested here as a way of overcoming the limitations identified above and creating a more broadly-applicable model. State and transition sub-models were also proposed as a complementary addition, to summarise the effects of variability in salinity and water depth on community composition. This conceptual model framework would not require vegetation composition data from reference wetlands or historical sources; is not site- or community-specific; is applicable to the full range of tidal wetland types found along the estuarine salinity gradient; and can be applied to make predictions at a variety of spatial scales. A stepwise process for applying this model to particular wetland sites and their communities was also suggested and outlined in Chapter 5.

6.6 Floodgate management model for the Clarence River floodplain

The second aim in Chapter 5 was to predict the effects of changes in floodgate management on macrophytes in Clarence River wetlands. This was achieved by applying the general tidal restoration model framework developed in the first part of Chapter 5 to relevant site and species data, including the survey and experimental data obtained in this project and data obtained from a literature review.

The process of applying the model to Clarence River wetland sites and macrophyte species was found to be relatively straightforward and a number of predictions about the effects of different floodgate management actions on species persistence were generated. The framework used for the model enabled predictions to be made about the effects of floodgate management on species persistence at two different spatial scales, within individual wetlands and across the whole floodplain. These outcomes could not have been achieved using a traditional tidal restoration model based on Clementsian succession principles.

Both advantages and limitations of the new model framework were highlighted during the Clarence River wetlands model development and application processes. One advantage was that the different wetland sites, varying in position along the estuarine gradient, extent of drainage, current water management and degree of tidal connectivity, were all readily incorporated into one floodplain-scale model. Another advantage was that the hierarchical structure of the assembly rule model framework and the stepwise process of model development were useful for highlighting any areas where the predictive power of the model could be improved, and the types of data required. For example, the Clarence River wetlands model currently focuses on the persistence or loss of extant species under different floodgate management strategies, but with additional data on the species composition of the available propagule pool, and the habitat tolerances of those species, predictions could also be made about recruitment of new species (Keddy 2000).

Some areas of model development were more challenging than others. For example, using the framework and methods proposed to develop a model for specific sites it was suggested that assessment of site salinity and hydrological regime traits be carried out separately, and this information used to place sites into separate filter strength categories for these two factors. Classification of Clarence River wetlands into salinity filter strength categories was achieved using the relatively limited soil and water salinity data available, and a state and transition sub-model was created to summarise the expected effects of different floodgate management strategies on species persistence due to changes in site salinity ranges. However, less information was available on site hydrology, or on how different floodgate management strategies would alter site hydrology, therefore only a very simple type of hydrology sub-model could be created, with sites (or habitats within sites) split into aquatic, amphibious and terrestrial habitat categories.

Classification of species into salinity tolerance categories was a simple process when experimental data on salt-tolerance were available. However, salt-tolerance experiments require a substantial investment in time and labour and only five species could be tested in the experiments summarised in Chapters 3 and 4. This approach is best reserved for those species with the highest management priority. When the predicted habitat ranges of the focal species used here were compared with their surveyed distributions, some discrepancies were found, with species found outside their predicted habitat ranges. This indicates that either site salinities were overestimated in some cases, or that species salinity tolerance ranges were underestimated, and highlights the need for more detailed data on site salinities. Classification of species into the depth tolerance and fluctuation response classes of Brock and Casanova (Brock and Casanova 1997) and van der Valk (van der Valk 1981) required a less intensive data collection and was achieved here using a information from a literature review and field observations. However, there were some cases where fluctuation response class could not be decided, and a germination experiment would be necessary to classify these species further.

A limitation of the hydrology sub-model included in the Clarence River wetlands model is that it does not attempt to explicitly predict species distributions with respect to elevation at particular sites. The zonation of wetland macrophytes can be influenced by a number of hydrological factors, including the range, duration, frequency and timing of water depth changes (van der Valk 1981; Zedler 2000). More specific information would be required to refine the hydrology sub-model to a point where it could be used to predict the potentially habitable elevation ranges of individual species at particular sites, including; site elevation profiles, the current range, frequency and timing of water depth changes, the potential effects of different floodgate management strategies on these factors, and information on species responses to these various aspects of inundation regime.

6.7 Implications with respect to Clarence River wetland floodgate management plans

The Clarence wetland rehabilitation project will be using an adaptive approach to tidal flow management. Within this adaptive management framework it is intended that the model developed here will be used to help guide floodgate management decisions, based on the macrophyte species managers wish to retain, and their associated salinity and inundation response categories. The Clarence River wetlands floodgate management model presented in Chapter 5 is not intended to be seen as representing the final step in model development. Instead, it is intended that, as new floodgate management strategies are put into action, the site salinity classifications and the plant salinity, water depth and water depth fluctuation response categories defined in the model will be tested to see how accurate they are as predictors of species survival in the field. It is also intended that the model be refined, updated and extended as more data become available. As part of the adaptive management process monitoring should be carried out at prospective rehabilitation sites, to obtain baseline data on site salinity, hydrology, vegetation composition and species elevation ranges before floodgates are opened and to assess the effects of floodgate management actions on these variables after these actions are put into effect. This process will provide data for testing the accuracy of model predictions, and refining and updating the model.

6.8 General applicability of methods to future wetland tidal restoration projects

The traditional approach used to predict the effects of tidal restoration on wetland macrophyte community composition is to find another wetland nearby that is not affected by tidal barriers and use vegetation composition at that site as a guide (Brinson and Reinhardt 1996; Neckles *et al.* 2002). However, predicting the effects of tidal restoration on wetland macrophyte community composition can be difficult in degraded landscapes where reference wetlands without tidal barriers do not occur (de Jong and de Jong 2002; Wolters *et al.* 2005). Determining the likely effects of partial, rather than full, tidal restoration on wetland macrophyte community composition can make this task even more complex, because the effects of partial tidal restoration on site salinity and hydrology are more difficult to predict. This is particularly so for oligohaline and mesohaline wetlands which can display greater temporal variability in salinity than their more seaward counterparts (Odum 1988).

The novel approach used in this project circumvented some of these difficulties and allowed predictions to be made about how floodgate management will affect the persistence of common and abundant macrophyte species, in a variety of fresh to saline wetlands, without requiring vegetation composition data from reference sites or historical sources. The assembly rule model framework and the data collection methods employed here are not site or species-specific, and could potentially be refined and applied to other projects seeking to predict the impacts of tidal flow reconnection on wetland macrophytes. In particular, this approach could be suitable for other heavily modified coastal areas where natural reference sites are not available and historical data on macrophyte community composition is either unavailable or would be inappropriate to use as the rehabilitation target.

However, there are also some limitations to this approach. For example, experimental screening of species environmental tolerance ranges can be both time-consuming and labour-intensive. Species environmental tolerance thresholds can also vary depending on the effects of other abiotic and biotic variables on plant growth and survival (Gorham 1996; Siebentritt and Ganf 2000; Jolly *et al.* 2008). Therefore, predictions about the potential habitat ranges of species based on data from pot experiments may be broader than those that these species would tolerate in the field because the effects of all limiting factors can not be taken into account (Jolly *et al.* 2008). Data from pot experiments such as those conducted here can be used in the absence of field data to make some basic predictions about the effects of tidal flow reconnection on macrophyte distributions. However, field validation will be required to determine the accuracy of these predictions and to refine them.

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Appendices

APPENDIX 1. Clarence floodplain wetland plant species distribution across sites

(• Indicates those species recorded only above the high water mark, n = total number of quadrats each species recorded in, * indicates sites of species occurrence. Site numbers correspond to those used in the methods section of Chapter 2.)

Species	**Family**	**n**	**Sites**																
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Aegiceras corniculatum (L.) Blanco (River Mangrove)	MYRSINACEAE	1								*									
Apium prostratum Labill. Ex Vent. subsp. *prostratum* (Sea Celery)	APIACEAE	2								*		*							
Aster subulatus Michx. (Wild Aster)	ASTERACEAE	2										*	*						
Avicennia marina (Forsskal) Vierh. var. *australasica* (Walp.) Mold. (Grey Mangrove)	ACANTHACEAE	2																*	*
• *Axonopus fissifolius* (Raddi) Kuhlm. (Narrow-Leaved Carpet Grass)	POACEAE	2				*												*	
Bacopa monnieri (L.) Pennell (Brahmi)	SCROPHULARIACEAE	12					*			*	*	*	*						*
Bolboschoenus caldwellii (V. J. Cook) Soják (Marsh Clubrush)	CYPERACEAE	9								*	*	*	*		*				
Casuarina glauca Sieber ex Sprengel (Swamp Oak)	CASUARINACEAE	9				*		*		*		*	*		*		*		*
Centella asiatica (L.) Urb. (Pennywort)	APIACEAE	5	*	*	*	*													
Centipeda sp. (Sneezeweed)	ASTERACEAE	2			*														
•*Cirsium vulgare* (Scotch Thistle)	ASTERACEAE	3	*	*								*							
Cotula coronopifolia L. *(*Waterbuttons)	ASTERACEAE	13						*				*	*	*	*			*	*
Cynodon dactylon (L.) Pers (Couch)	POACEAE	21	*	*	*	*		*		*		*	*	*	*			*	*
Cyperus polystachyos Rottb.	CYPERACEAE	5				*		*		*							*		

Species	**Family**	**n**	**Sites**																
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
(Cyperus)																			
Diplachne fusca (L.) P. Beauv. (Brown Beetle Grass)	POACEAE	1									*								
Eleocharis equisetina C. Presl (Spikerush)	CYPERACEAE	32	*	*	*	*	*	*	*	*		*	*	*	*	*	*		
Eleocharis minuta Boeck. (Dwarf Spikerush)	CYPERACEAE	5	*		*						*						*		
Epaltes australis Less. (Spreading Nut-Heads)	ASTERACEAE	1						*											
Fimbristylis ferruginea (L.) Vahl (Fimbristylis)	CYPERACEAE	3										*							*
•*Hydrocotyle* sp. (Pennywort)	APIACEAE	1			*														
• *Hypochaeris microcephala* (Sch.Bip.) Cabrera (White Cats Ear)	ASTERACEAE	1										*							
Isolepis inundata R. Br. (Isolepis)	CYPERACEAE	1				*													
•*Isotoma* sp. (Isotoma)	LOBELIACEAE	1			*														
Juncus kraussii Hochst. subsp. *australiensis* (Buchenau) Snogerup (Sea Rush)	JUNCACEAE	3						*		*		*							*
Juncus sp. (Juncus)	JUNCACEAE	2									*	*							
Juncus usitatus L. A. S. Johnson (Common Rush)	JUNCACEAE	5		*	*	*		*											
Lachnagrostis filiformis (G. Forst.) Trin.) (Blown Grass)	POACEAE	8			*			*				*		*					*
Ludwigia peploides subsp. *montevidensis* (Spreng.) Raven (Water Primrose)	ONAGRACEAE	1			*														
Melaleuca quinquenervia (Cav.) S. T. Blake (Paperbark)	MYRTACEAE	6				*		*				*					*		
Nymphaea caerulea Savigny (synonym *N. capensis* Thunb.) (Cape Waterlily)	NYMPHAEACEAE	4			*				*							*			

Species	**Family**	**n**	**Sites**																
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Nymphoides indica (L.) Kuntze (Water Snowflake)	NYMPHAEACEAE	1			*														
Ottelia ovalifolia (R. Br.) Rich. (Swamp Lily)	HYDROCHARITACEAE	1			*														
• *Paspalum dilatatum* Poir. (Common Paspalum)	POACEAE	3	*	*								*							
Paspalum distichum L. (Water Couch)	POACEAE	27	*	*	*	*	*	*		*	*	*	*	*	*				
Paspalum vaginatum Swartz (Saltwater Couch)	POACEAE	3								*	*	*							
• *Pennisetum clandestinum* Hochst. ex Chiov. (Kikuyu)	POACEAE	3												*				*	*
Persicaria hydropiper (L.) Spach (Water Pepper)	POLYGONACEAE	1			*														
Persicaria orientalis (L.) Spach (Princess Feathers)	POLYGONACEAE	1			*														
•*Persicaria* sp. (Persicaria)	POLYGONACEAE	1				*													
Philydrum lanuginosum Banks & Sol. Ex Gaertn. (Frogsmouth)	PHILYDRACEAE	1			*														
Phragmites australis (Cav.) Trin. ex Steud. (Common Reed)	POACEAE	10								*		*	*		*		*		
Potamogeton octandrus Poir. (syn. *Potamogeton javanicus* Hassk.) (Pondweed)	POTAMOGETONACEAE	1			*														
Potamogeton tricarinatus F. Muell & A. Benn. ex A. Benn. (Floating Pondweed)	POTAMOGETONACEAE	1			*														
Ruppia sp. (Ruppia)	POTAMOGETONACEAE	1					*												
Salvinia molesta D. Mitch. (Salvinia)	SALVINIACEAE	1							*										
Sarcocornia quinqueflora (Bunge ex Ung.-Sternb.) A. J. Scott subsp. *quinqueflora* (Samphire)	CHENOPODIACEAE	2																*	
Schoenoplectus litoralis (Schrad.)	CYPERACEAE	5					*				*	*	*						

Species	**Family**	**n**	**Sites**																
			1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
Palla (River Clubrush)																			
• *Senecio madagascariensis* Poir. (Fireweed)	ASTERACEAE	5	*	*				*				*						*	
Sisyrinchium sp. A sensu James & Brown (1993) (Sisyrinchium)	IRIDACEAE	1			*														
Sporobolus virginicus (L.) Kunth (Salt Couch)	POACEAE	7										*						*	*
•*Trifolium repens* L. (White Clover)	FABACEAE	1				*													
Triglochin procerum R. Br. (Water Ribbons)	JUNCAGINACEAE	2			*			*											
Triglochin sp. (Triglochin)	JUNCAGINACEAE	1			*														
Triglochin striatum Ruíz & Pav. (Streaked Arrowgrass)	JUNCAGINACEAE	1										*							
Utricularia sp. (Bladderwort)	LENTIBULARIACEAE	1							*										
Viola hederacea Labill.	VIOLACEAE	1										*							
•Unknown 1	APIACEAE	1	*																
Unknown 2		1						*											
Unknown 3	ASTERACEAE	1						*											
•Unknown 4	CHENOPODIACEAE	1												*					
Unknown 5	AMERANTHACEAE	1											*						
Unknown 6		2											*	*					
Unknown 7		1												*					
•Unknown 8	APIACEAE	1										*							
Unknown 9		1															*		
Unknown 10		1			*														
Unknown 11		1			*														
Unknown grass	POACEAE	3	*				*	*											
Unknown grass 1	POACEAE	3		*				*											
Unknown grass 2	POACEAE	1																	*
•Unknown grass 3	POACEAE	1			*														
Total species per site			10	9	25	12	6	17	4	12	8	25	12	9	7	2	7	8	11

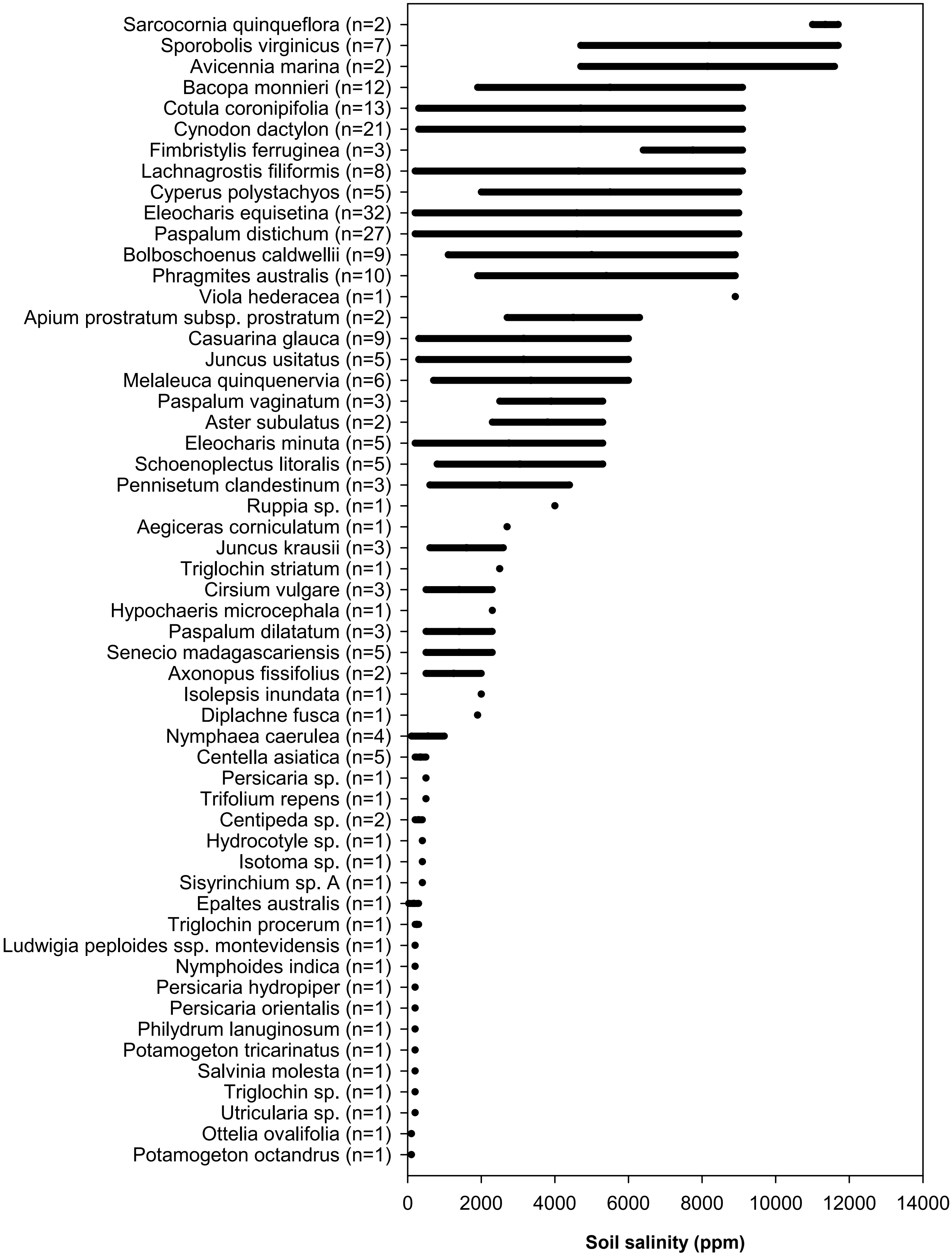
APPENDIX 2. Species distributions according to relative elevation and water depth zones

Species (n = total quadrats)	Depth (cm) min – max	Depth zones				
		Above edge	Edge	Damp	Shallow	Deeper
Aegiceras corniculatum (n=1)	10			*		
Apium prostratum subsp. *prostratum* (n=2)	10 — 20			*		*
Aster subulatus (n=2)	0 – 10	*			*	
Avicennia marina (n=2)	10 – 15				*	
Axonopus fissifolius (n=2)	0	*				
Bacopa monnieri (n=12)	0 – 20		*	*	*	*
Bolboschoenus caldwellii (n=9)	0 – 25			*	*	*
Casuarina glauca (n=9)	0 – 10			*	*	
Centella asiatica (n=5)	0	*	*			
Centipeda sp. (n=2)	0	*	*			
Cirsium vulgare (n=3)	0	*				
Cotula coronipifolia (n=13)	0 – 10	*	*	*	*	
Cynodon dactylon (n=21)	0	*	*	*		
Cyperus polystachyos (n=5)	0	*		*		
Diplachne fusca (n=1)	0		*			
Eleocharis equisetina (n=32)	0 – 75		*	*	*	*
Eleocharis minuta (n=5)	5 – 20		*		*	*
Epaltes australis (n=1)	0			*		
Fimbristylis ferruginea (n=3)	0 – 15		*		*	
Hydrocotyle sp. (n=1)	0	*				
Hypochaeris microcephala (n=1)	0	*				
Isolepis inundata (n=1)	0			*		
Isotoma sp. (n=1)	0	*				
Juncus krausii (n=3)	0	*		*		
Juncus sp. (n=2)	0 – 5		*		*	
Juncus usitatus (n=5)	0	*		*		
Lachnagrostis filiformis (n=8)	0	*	*	*		
Ludwigia peploides ssp. *montevidensis* (n=1)	0		*			
Melaleuca quinquenervia (n=6)	0	*		*		
Nymphaea caerulea (n=4)	25 – 120					*
Nymphoides indica (n=1)	0			*		
Ottelia ovalifolia (n=1)	50					*
Paspalum dilatatum (n=3)	0	*				
Paspalum distichum (n=27)	0 – 20	*	*	*	*	*

Species (n = total quadrats)	**Depth (cm) min – max**	**Depth zones** **Above edge**	**Edge**	**Damp**	**Shallow**	**Deeper**
Paspalum vaginatum (n=3)	0 – 5			*	*	
Pennisetum clandestinum (n=3)	0	*				
Persicaria hydropiper (n=1)	0		*			
Persicaria orientalis (n=1)	0			*		
Persicaria sp. (n=1)	0	*				
Philydrum lanuginosum (n=1)	0			*		
Phragmites australis (n=10)	0 – 25			*	*	*
Potamogeton octandrus (n=1)	50					*
Potamogeton tricarinatus (n=1)	0			*		
Ruppia sp. (n=1)	75					*
Salvinia molesta (n=1)	70					*
Sarcocornia quinqueflora (n=2)	0		*	*		
Schoenoplectus litoralis (n=5)	5 – 75				*	*
Senecio madagascariensis (n=5)	0	*				
Sisyrinchium sp. A (n=1)	0	*				
Sporobolus virginicus (n=7)	0 – 15		*	*	*	*
Trifolium repens (n=1)	0	*				
Triglochin procerum (n=1)	0		*			
Triglochin sp. (n=1)	0		*			
Triglochin striatum (n=1)	0		*			
Utricularia sp. (n=1)	70					*
Viola hederacea (n=1)	0			*		
Unknown 1 (n=1)	0	*				
Unknown 2 (n=1)	0			*		
Unknown 3 (n=1)	0			*		
Unknown 4 (n=1)	0	*				
Unknown 5 (n=1)	10				*	
Unknown 6 (n=2)	0 – 10			*	*	
Unknown 7 (n=1)	10				*	
Unknown 8 (n=1)	0	*				
Unknown 9 (n=1)	0			*		
Unknown 10 (n=1)	0			*		
Unknown 11 (n=1)	0		*			
Unknown grass 1 (n=3)	0	*		*		
Unknown grass 2 (n=1)	0			*		
Unknown grass 3 (n=1)	0	*				

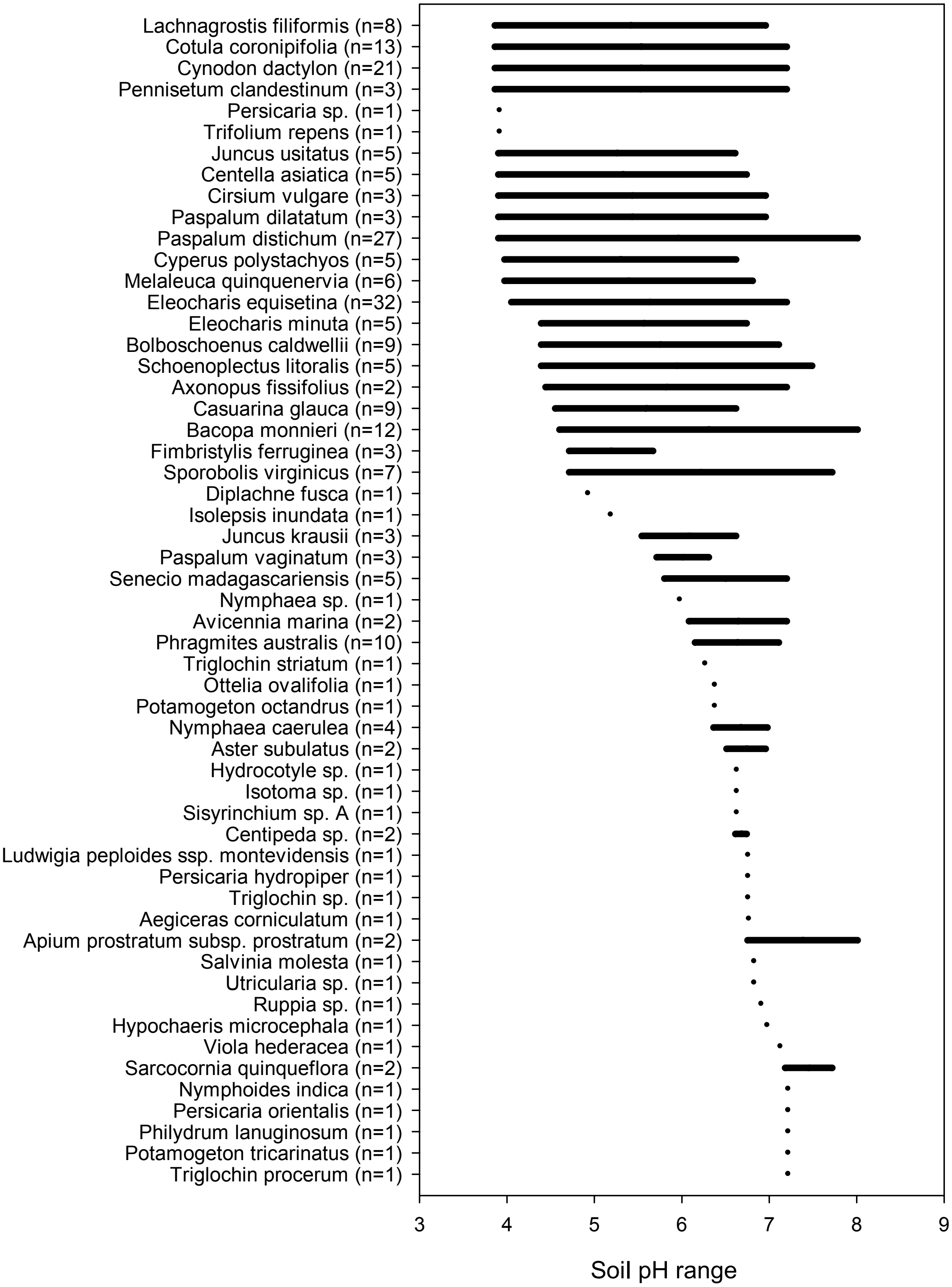
APPENDIX 3. Species distributions and soil salinity

(n = number of quadrats species sampled in. Salinity derived from a 1:5 soil/water suspension.)



APPENDIX 4. Species distributions and soil pH

(n = number of quadrats each species recorded in. Soil pH derived from a 1:5 soil/water suspension.)



APPENDIX 5. Species distributions according to grazing intensity

	Grazing strategy		
Species	Not grazed (n = 17 quadrats)	Cell grazed (n = 14 quadrats)	Set stocking (n = 46 quadrats)
Aegiceras corniculatum	0	1	0
Apium prostratum subsp. *prostratum*	0	2	0
Aster subulatus	1	1	0
Avicennia marina	0	0	2
Axonopus fissifolius	0	0	2
Bacopa monnieri	3	7	2
Bolboschoenus caldwellii	3	3	3
Casuarina glauca	2	2	5
Centella asiatica	0	0	5
Centipeda sp.	0	0	2
Cirsium vulgare	0	1	2
Cotula coronipifolia	3	3	7
Cynodon dactylon	3	3	15
Cyperus polystachyos	2	1	2
Diplachne fusca	1	0	0
Eleocharis equisetina	4	4	24
Eleocharis minuta	2	0	3
Epaltes australis	0	0	1
Fimbristylis ferruginea	0	1	2
Hydrocotyle sp.	0	0	1
Hypochaeris microcephala	0	1	0
Isolepis inundata	0	0	1
Isotoma sp.	0	0	1
Juncus krausii	0	2	1
Juncus sp.	1	1	0
Juncus usitatus	0	0	5
Lachnagrostis filiformis	0	3	5
Ludwigia peploides ssp. *montevidensis*	0	0	1
Melaleuca quinquenervia	1	2	3
Nymphaea caerulea	0	1	3
Nymphoides indica	0	0	1
Ottelia ovalifolia	0	0	1
Paspalum dilatatum	0	1	2
Paspalum distichum	7	5	15
Paspalum vaginatum	1	2	0
Pennisetum clandestinum	0	0	3
Persicaria hydropiper	0	0	1
Persicaria orientalis	0	0	1
Persicaria sp.	0	0	1
Philydrum lanuginosum	0	0	1
Phragmites australis	3	4	3
Potamogeton octandrus (syn. *P. javanicus*)	0	0	1
Potamogeton tricarinatus	0	0	1

Species	**Grazing strategy** Not grazed (n = 17 quadrats)	Cell grazed (n = 14 quadrats)	Set stocking (n = 46 quadrats)
Ruppia sp.	0	0	1
Salvinia molesta (Salvinia)	0	1	0
Sarcocornia quinqueflora	0	0	2
Schoenoplectus litoralis	3	1	1
Senecio madagascariensis	0	1	4
Sisyrinchium sp. A	0	0	1
Sporobolus virginicus	0	1	6
Trifolium repens	0	0	1
Triglochin procerum	0	0	2
Triglochin sp.	0	0	1
Triglochin striatum	0	1	0
Utricularia sp.	0	1	0
Viola hederacea	0	1	0
Unknown 1	0	0	1
Unknown 2	0	0	1
Unknown 3	0	0	1
Unknown 4	0	0	1
Unknown 5	1	0	0
Unknown 6	1	1	0
Unknown 7	1	0	0
Unknown 8	0	1	0
Unknown 9	0	0	1
Unknown 10	0	0	1
Unknown 11	0	0	1
Unknown grass 1	1	0	2
Unknown grass 2	0	0	1
Unknown grass 3	0	0	1

APPENDIX 6. Sources of salinity and inundation tolerance information for species recorded in the 2005 Clarence River wetlands survey

Species	**Salinity and inundation tolerance range information**	**Data type**	**Source**
Aegiceras corniculatum	Often occurs with *Avicennia marina* but usually extends further upstream and inland than *A. marina.*	Field survey	(Harden 2000)
Apium prostratum subsp. *prostratum*	Occurs at edges of saltmarsh, on coastal cliffs and near rivers or brackish water.	Field survey	(Harden 1992)
Aster subulatus	Weed of seasonally wet or poory drained land, including swamp edges and roadside drains.	Field survey	(Harden 1992)
Avicennia marina	20-60% seawater optimum for seedling growth (0-4 leaf stage). Grew well when waterlogged but high seedling mortality when constantly immersed.	Pot experiment. Seawater dilution rate.	(Clarke and Hannon 1970)
A. marina	Adults form a belt at the sea edge rooted in continuously waterlogged soil flooded by tides at least once daily, often diurnally.	Field survey	(Clarke and Hannon 1970)
A. marina	Grows in saltwater swamps and estuaries.	Field survey	(Harden 1992)
Bacopa monnieri	Occurs at the edge of fresh or brackish pools or streams, sometimes submerged.	Field survey	(Harden 1992)
Bolboschoenus caldwellii	On the banks of the Murray River, found at infrequently flooded elevations including areas flooded 80-215 days per year, to < 60 cm depth.	Field survey	(Blanch *et al.* 1999)
B. caldwellii	Occasional in swamps or inland along artesian bore drains.	Field survey	(Harden 1993)
B. caldwellii	Sensitive to rapid flood recession. Recession rates should be slow e.g. 2 cm per day. Should not be flooded above 50-75% of stem height.	Literature review	(Roberts and Marston 2000)
B. caldwellii	Found in waterlogged areas.	Field survey	(Sainty and Jacobs 2003)
B. caldwellii	Relative growth rate of 15cm high ramets was depressed at depth of 40cm and death occurred at 60cm, over a two month experiment. Survival at depth depended on initial shoot height. None of the completely submerged plants survived the one month experiment period. Most of the plants with some emergent stems survived. Tolerates depths up to 60 cm but grows best from 20 cm above the waterline to 20 cm water depth.	Pot experiment	(Siebentritt and Ganf 2000)
Casuarina glauca	Fails to germinate under saline conditions (ie 20% seawater equiv. to about 7000ppm. Lower salinities not tested). Germination not prevented by submergence (4mm). Seedlings grew best in 0-20% seawater. Waterlogging greatly reduced seedling growth, but did not affect survival.	Pot experiment. Seawater dilution rate.	(Clarke and Hannon 1970)
C. glauca	Adults occur at landward edge of salt marsh communities, in areas free of tidal flooding and where soil salinities are lowest.	Field survey	(Clarke and Hannon 1970)
C. glauca	Occurs in brackish situations along coastal streams, on coastal headlands, and inland along major river valleys.	Field survey	(Harden 2000)
C. glauca	4384 ppm =21% reduction in shoot dry wt; 8767 ppm 33% reduction in shoot dry wt	Pot experiment. Water salinity	Clemens *et al.* (1983) cited in

Species	Salinity and inundation tolerance range information	Data type	Source
	(seedlings).	measurements.	Bailey *et al.* (2002)
C. glauca	Restoration project with wet sites vs dry and seed vs tubestock. Tubestock survived better at the higher elevation. Regenerated from seed mostly at sites inundated approx. 10% to 50% of the time.	Pot experiment	(de Jong 2000)
C. glauca	Commonly found on the landward side of salt marsh in eastern States of Australia.	Field survey	(Sainty and Jacobs 1994)
Centella asiatica	Grows in moist places in coastal districts.	Field survey	(Harden 1992)
Centipeda sp.	Four species, all occurring on damp ground near waterways.	Field survey	(Harden 1992)
Cotula coronipifolia	Grows in damp and often saline disturbed areas.	Field survey	(Harden 1992)
C. coronipifolia	Occurs on mud or in still or slow moving saline, brackish or fresh water to ~50 cm deep.	Field survey	(Sainty and Jacobs 2003)
C. coronipifolia	Observed at 5000 ppm.	Field survey. Water salinity measurement.	Brock and Shiel (1983) cited in Bailey *et al.* (2002)
C. coronipifolia	Occurred in the peripheral wetlands of Everlasting Swamp where there are also areas of unvegetated salt scalds, prior to the current levee and drainage system.	Field survey	(Clarence River County Council 1978)
Cynodon dactylon	On the banks of the Murray River *C. dactylon* occurred at rarely flooded sites, ie inundated >0 cm a median of 240 days in 2 years (0-20 cm 31 days, 20-60 cm 61 days).	Field survey	(Blanch *et al.* 1999)
C. dactylon	Flood and drought tolerant. Occurs at the tops of riverbanks.	Literature review	(Roberts and Marston 2000)
C. dactylon	Performed well when planted at saline scald sites (mean soil salinity c. 14 000–21 000 ppm).	Field experiment. Soil pore-water salinity estimated from texture and 1:5 soil/water extract data, as per Slavich and Petterson (1993).	(Semple *et al.* 2004)
C. dactylon	When inundated to up to 18 cm for 9 days, leaves disintegrated and fell from stems, but once the water evaporated down to 5 cm shoots were produced.	Field experiment	(Wilkinson 2000)
Cyperus polystachyos	Occurs in open, often disturbed situations.	Field survey	(Harden 1993)
Diplachne fusca	Usually grows in or near water or in depressions and is moderately salt-tolerant.	Field survey	(Harden 1993)
D. fusca	Found in permanent or ephemeral water up to c. 80cm deep. Often in saline areas.	Field survey	(Sainty and Jacobs 2003)
D. fusca	Salt tolerance varied according to provenance of source material, but overall this species is salt tolerant, surviving at 23 000 ppm in this experiment (higher salinities not tested). However, highest growth of all accessions occurred in fresh conditions, decreasing as salinity increased.	Pot experiment. Water salinity measurements.	(Warwick and Halloran 1991)
Eleocharis equisetina	In Moran's Swamp, once dominated by *Paspalum distichum, E. equisetina* moved in and established in the lowest areas after	Field observations	(Bowling 2000 pers. com.)

Species	**Salinity and inundation tolerance range information**	**Data type**	**Source**
	construction of Wants Drain. Once penstocks were built, density of *E. equisetina* declined and *Paspalum distichum* has started to reestablish. The penstocks hold water to c. 30 cm over most of the swamp, and 50 cm in the deepest parts.		
E. equisetina	Grows in swampy areas.	Field survey	(Harden 1993)
E. equisetina	Dominant in the parts of the Coldstream wetland system where the most drains occur, likely favoured by the shorter inundation periods there.	Field survey	(Pressey and Clancy 1979)
E. equisetina	The dominant species in the lower areas that make up the bulk of Everlasting Swamp (prior to the current drainage and levee system)	Field survey	(Clarence River County Council 1978)
Eleocharis minuta	Grows in swamps and sandy shores of coastal lakes.	Field survey	(Harden 1993)
E. minuta	Found in the upper Coldstream wetlands from c. 40 cm above the water line to c. 20 cm below.	Field survey	(Pressey and Clancy 1979)
Epaltes australis	Grows in temporarily flooded areas.	Field survey	(Harden 1992)
Fimbristylis ferruginea	Grows in brackish or fresh water swamps.	Field survey	(Harden 1993)
Hydrocotyl sp.	Some aquatic, some terrestrial.	Field survey	(Harden 1992)
Isolepis inundata	Widespread on moist ground.	Field survey	(Harden 1993)
Isotoma sp.	Occurs on moist sand or mud.	Field survey	(Harden 1992)
Juncus kraussii	Found in coastal districts and often dominant at saline or brackish sites.	Field survey	(Harden 1993)
J. kraussii	Commonly found at edges of coastal lagoons or lakes.	Field survey	(Sainty and Jacobs 2003)
J. kraussii	High germination rate maintained until salinity > 15 000 ppm.	Pot experiment. Water salinity.	(Greenwood and MacFarlane 2006)
Juncus usitatus	Common on stream banks and in other moist areas.	Field survey	(Harden 1993)
J. usitatus	Damp and periodically wet areas, usually only in shallow water.	Field survey	(Sainty and Jacobs 2003)
Lachnagrostis filiformis	Often occurs in moist areas.	Field survey	(Harden 1993)
L. filiformis	Occurs in wetter areas (e.g. swamp edges, drainage lines) that have low ground cover. Low drought tolerance and competetiveness.	Field survey	(Rose *et al.* 2006)
Ludwigia peploides subsp. *montevidensis*	Occurs at margins of lakes and streams.	Field survey	(Harden 2002)
L. peploides ssp. *montevidensis*	Has floating stems that can encroach some distance into waterways.	Field survey	(Sainty and Jacobs 2003)
Melaleuca quinquenervia	Widespread in coastal swamps and around lake margins.	Field survey	(Harden 2002)
M. quinquenervia	Damp soil to shallow stationary to slow-moving fresh or brackish water.	Field survey	(Sainty and Jacobs 2003)
Nymphaea caerulea	Naturalised and spreading in a range of perennial coastal waterbodies.	Field survey	(Harden 2000)
N. caerulea	Typically in water up to 1m deep, but tolerates subsequent increases up to c. 2m. Seeds of germinate spring to autumn on mud or in clear water.	Field survey	(Sainty and Jacobs 2003)
Nymphaea sp.	Waterlilies occurred in many of the blind channels and depressions in the east of	Field survey	(Clarence River County Council

Species	Salinity and inundation tolerance range information	Data type	Source
	Everlasting Swamp, prior to the current levee and drainage system.		1978)
Nymphoides indica	Floating leaves and stolons up to 2m.	Field survey	(Sainty and Jacobs 2003)
Ottelia ovalifolia	Floating-leaved species with roots attached. Petioles to c. 1m length. Grows in stationary to slow moving waterbodies and creeks.	Field survey	(Sainty and Jacobs 2003)
Paspalum distichum	On the banks of the Murray River was most abundant at sites flooded 0-20 cm for median of 163 days in 2 years, but also occurred in sites shallowly flooded for 11-45 days in 2 years.	Field survey	(Blanch *et al.* 1999)
P. distichum	Amphibious, fluctuation-tolerator, emergent.	Pot experiment	(Brock and Casanova 1997)
P. distichum	Grows in and near fresh water.	Field survey	(Harden 1993)
P. distichum	Occurs in temporarily flooded areas, including the edges of marshes kept flooded over summer. Biomass decreased as salinity increased. Salintiy treatments were 0, 2000, 4000 and 6000 ppm. The very strong negative effect of salinity over 4000 ppm, combined with field observations, suggest that this species is unlikely to persist at salinities greater than 6000 ppm.	Field survey and pot experiment. Water salinities.	(Mesléard *et al.* 1993)
P. distichum	Dominant in the parts of the Upper Coldstream wetlands with the most drains, likely favoured by the shorter inundation periods there. Observed from c. 55 cm above water line to c. 20 cm below.	Field survey	(Pressey and Clancy 1979)
P. distichum	Requires moist to wet soil for most of the year (c. 75%), particularly during the spring-summer growing season. Found in areas with shallow continuous flooding at 5-15 cm for 4-6 months of the year or pulsed flooding events 2-3 times per year. Can also recover from dry periods of 1-3 years.	Field survey	(Roberts and Marston 2000)
P. distichum	Productivity of water couch best when ponded water levels were 0-15 cm, and declined at 20 cm. As the pond emptied, productivity was higher in the previously deep areas than in areas with no water. Ponding also reduced frost damage.	Field experiment	(Rose and Rose Unpub.)
P. distichum	Common in areas that are frequently wet or flooded by fresh water. Grows best up to 15cm depth but withstands short term flooding to greater depths.	Field survey	(Rose *et al.* 2006)
P. distichum	Found in damp areas and along edges of water bodies.	Field survey	(Sainty and Jacobs 2003)
P. distichum	When flooded to 18 cm for 9 days plants had a rapid growth spurt, growing from 10 cm below the surface to 10 cm above in just 2 days.	Field experiment	(Wilkinson 2000)
P. distichum	Peripheral wetlands of the Everlasting Swamp complex were vegetated with water couch before the levee and drainage system was built.	Field survey	(Clarence River County Council 1978)
Persicaria hydropiper	Common in damp places.	Field survey	(Harden 2000)
Persicaria orientalis	Widespread near water.	Field survey	(Harden 2000)

Species	**Salinity and inundation tolerance range information**	**Data type**	**Source**
Philydrum lanuginosum	Widespread in swamps and along margins of streams and dams	Field survey	(Harden 1993)
P. lanuginosum	Found in permanent or periodically shallowly inundated areas.	Field survey	(Sainty and Jacobs 2003)
Phragmites australis	Roots and rhizomes extended down to 60cm in invaded sites. Found that better-drained/flushed sites were more favourable to *P. australis* range expansion	Pot experiment	(Bart and Hartman 2000)
P. australis	In the Murray River this species occurs on areas of the bank flooded around 80-225 days per year, mostly at depths <60cm.	Field survey	(Blanch *et al.* 1999)
P. australis	In weir pools with highly variable water levels and lots of fluctuation, was found from 0m to 6m above pool surface.	Field survey	(Blanch *et al.* 2000)
P. australis	Salinity tolerance increases with growth. Initial vigorous invasion sites (seed or rhizome) have salinity <10 000 ppm and flooding frequency <10%. Water salinity of 35 000 ppm kills young plants. Seed germination completely inhibited at soil salinity 20 000 ppm Established healthy vigourous populations usually found in tidal freshwater to mesohaline salinity up to 18 000 ppm. Higher salinity surface water is tolerated if roots have access to lower salinity conditions. Mature clones have been reported in marshes with salinity up to 45 000 ppm and flooding up to 100%. Flood tolerance is low when small. Submersion tolerance increases with age. Soil waterloggging / high watertables inhibit establishment and growth.	Literature review. Water measurements for pot experiments. Direct measurements of surface water and soil pore-water (piezometer) salinity from field studies.	(Chambers *et al.* 2003)
P. australis	Grows at the edge of ponds and streams and in tidal waters.	Field survey	(Harden 1993)
P. australis	Has been studied in the Gippsland Lakes – an area where salinity has increased due to construction of a permanent entrance. At this site the range of *P. australis* contracted and it is restricted to areas where substrate salinity is from 3600–12 000 ppm. Dieback occurs at salinities >12 000 ppm.	Literature review. Field survey data. Water salinity measurements (Clucas and Ladiges 1980).	Bird (1978) and Clucas and Ladiges (1980), cited in Bailey *et al.* (2002) and (Hart *et al.* 1991).
P. australis	Temperature affected germination response to increased salinity, with 2% germination at 30 000 ppm high temp. treatment (15-30°C) and 43% in low temp. (10-25°C) treatment. At high temp. germination rates began to drop at >10 000 ppm, but at lower temp. did not decrease until >15 000 ppm.	Pot experiment. Water salinity measurements.	(Greenwood and MacFarlane 2006)
P. australis	Tendency to form large clonal stands. Seed germination inhibited at 25 000 ppm, but is stimulated by salinities of 5000–10 000 ppm. This sp. can significantly change wetland vegetation structure, particularly in terms of above-ground biomass, because dead culms can remain standing for 2 or more years, leading to year-round vegetation cover and litter accumulation even when it dies back. Therefore, in freshwater tidal marshes, areas that were bare mudflats during winter/spring because of dieback and	Literature review. Pot experiment water salinity measurements.	(Meyerson *et al.* 2000)

Species	Salinity and inundation tolerance range information	Data type	Source
	decomposition may retain year-round cover after *P. australis* invasion. In North America *P. australis* is considered to be of poor quality as wildlife habitat.		
P. australis	Tolerates fluctuating water levels, and grows to a maximum depth around 1.5-2 m where banks are steep. Does not require surface water e.g. will grow in waterlogged areas. Can survive long dry periods as rhizomes reach to 1-2 m below ground. Grows most vigorously in water only a few cm deep.	Field survey	(Roberts and Marston 2000)
P. australis	A *P. australis* dominated wetland was reopened to tidal flow, raising mean pore water salinity from 18 000 ppm to 26 000 ppm. Height of *P. australis* decreased. Bare areas sig. increased as *P. australis* died off and was replaced by salt marsh spp.	Field survey. Soil pore-water salinity measurements.	(Roman *et al.* 2002)
P. australis	Tolerant of slightly brackish water to 10 000 ppm. Occurs in stationary or slow-moving water bodies, margins of creeks, streams, channels and drains, swamps, areas with high water tables and areas that are seasonally inundated.	Field survey. Water salinity measurements.	(Sainty and Jacobs 1994)
P. australis	In freshwater marshes restored to brackish / salty disappeared abruptly when soil salinity >26 000 ppm. Cover and frequency were negatively correlated with salinity. Distribution moved up the elevation gradient after tidal influxes increased (ie died out on lower saltier spots). Stem density also higher at sites with lower water tables. Where water tables close to surface, *P. australis* died back faster. Persists on sites flooded on just 15-20% of high tides but less vigorus than on more frequently-flooded sites.	Field survey. Soil pore-water salinity measurements.	(Warren *et al.* 2002)
P. australis	Observed at 280-2200 ppm.	Field survey. Water salinity measurements.	Goonan *et al.*(1992) cited in Bailey *et al.* (2002)
P. australis	Died in the field at 15 000 ppm. In a controlled experiment biomass was reduced at 10 000 ppm. At 22 500 ppm 88% mortality of seedlings (10 weeks) occurred, compared with 25% mortality for rhizome - grown plants	Field survey, soil pore-water salinities. Pot experiment, water salinity measurements.	Lissner and Schierup (1997)
*Potamogeton octandrus (*syn.. *Potamogeton javanicus)*	Aquatic with some floating leaves, but mostly submerged. Grows in shallow water of creeks and lakes, often in sand.	Field survey	(Harden 1993; Sainty and Jacobs 2003)
Potamogeton tricarinatus	Aquatic with submerged and floating leaves. Grows in slow-flowing rivers and creeks to c. 3m depth.	Field survey	(Harden 1993)
P. tricarinatus	Observed at 180-5800 ppm.	Field survey. Water salinity measurements.	Bailey (1998) cited in Bailey *et al.* (2002)
P. tricarinatus	In controlled experiment 1000 ppm and above reduced growth and 7000 ppm caused 44% mortality.	Pot experiment. Water salinity measurements.	James and Hart (1993)
P. tricarinatus	When exposed to 6000 ppm salinity, plants displayed a severe reduction in biomass,	Pot experiment. Water salinity	Warwick and Bailey (1997)

Species	**Salinity and inundation tolerance range information**	**Data type**	**Source**
	increased leaf loss and reduced leaf production, compared to those grown at 2000 ppm.	measurements.	
P. tricarinatus	Experimentally delaying NaCl exposure until 34 days post emergence from tubers caused catastrophic leaf loss. Biomass reduced by water salinity 6000 ppm.	Pot experiment. Water salinity measurements.	Warwick and Bailey (1998)
P. tricarinatus	Amphibious, fluctuation-responder, morphologically plastic.	Pot experiment	(Brock and Casanova 1997)
Ruppia sp.	Submerged aquatic species. The three species of this genus range in habitat from fresh to brackish and hypersaline waterbodies including coastal lakes, lagoons and estuaries. More specific information in the review by (Bailey *et al.* 2002).	Field survey	(Harden 1993)
Salvinia molesta	Typcially occurs floating in dams or ponds.	Field survey	(Harden 2000)
S. molesta	Free-floating.	Field survey	(Sainty and Jacobs 2003)
Sarcocornia quinqueflora	Occurs mostly in coastal areas and frequently in areas periodically inundated with salt water.	Field survey	(Harden 2000)
S. quinqueflora	Found in low-lying areas adjacent to saline water.	Field survey	(Sainty and Jacobs 2003)
Schoenoplectus litoralis	Grows in fresh and brackish water, in coastal lakes and open swamps.	Field survey	(Harden 1993)
Schoenoplectus litoralis (river clubrush)	Tolerates brackish water and occurs in upper reaches of estuaries.	Field survey	(Sainty and Jacobs 2003)
Sporobolus virginicus	Seedlings grew best in 0-40% seawater (ie salt not required). No growth occurred in 100% seawater. Seedlings grew best when continuously waterlogged.	Pot experiment. Seawater dilution rate.	(Clarke and Hannon 1970)
S. virginicus	Occurs in higher areas of salt marsh where flooding is less frequent. Not flooded diurnally.	Field survey	(Clarke and Hannon 1970)
S. virginicus	Occurs in salt marshes.	Field survey	(Harden 1993)
S. virginicus	Found in low-lying areas adjacent to saline water.	Field survey	(Sainty and Jacobs 2003)
S. virginicus	Accessions from Yamba performed well when planted at saline scald sites with mean soil salinity c. 14 000–21 000 ppm.	Field experiment. Soil pore-water salinity estimated from texture and 1:5 soil/water extract data, as per Slavich and Petterson (1993).	(Semple *et al.* 2004)
Triglochin procerum	Emergent aquatic, with leaves semi erect or floating to 2m long. Grows in stationary or flowing fresh water.	Field survey	(Harden 1993)
T. procerum	Observed at 180–5800 ppm.	Field survey. Water salinity measurements.	Bailey (1998) cited in Bailey *et al.* (2002)
T. procerum	Observed at 500–2000 ppm.	Field survey. Water salinity measurements.	Brock and Lane (1983) cited in Bailey *et al.* (2002)
T. procerum	Observed at 5000–10 000 ppm.	Field survey. Water salinity measurements.	Brock and Shiel (1983) cited in Bailey *et al.*

Species	**Salinity and inundation tolerance range information**	**Data type**	**Source**
			(2002)
T. procerum	In controlled experiment growth reduced at 1000 ppm and above; 7000 no mortality occurred.	Pot experiment. Water salinities.	James and Hart (1993)
T. procerum	In controlled experiment biomass was reduced at 6000 ppm.	Pot experiment. Water salinity.	Warwick and Bailey (1997)
T. procerum	In controlled experiment timing of exposure to NaCl (0 or 40 days) had no effect, but growth was reduced at 6000 ppm.	Pot experiment. Water salinity.	Warwick and Bailey (1998)
Triglochin striatum	Found in periodically inundated salt marsh or in shallow saline aquatic habitats.	Field survey	(Harden 1993)
T. striatum	In water to 15 cm deep and persists on dried mud after water recedes. Tolerates brackish water to c. 6000 ppm. Common in salt marshes.	Field survey. Water salinity measurement.	(Sainty and Jacobs 2003)
Utricularia sp.	Various spp. vary in habit and habitat. Some terrestrial, others semi-aquatic to aquatic and either fixed or suspended.	Field survey	(Harden 1992)
Viola hederacea	Occurs in moist sheltered situations.	Field survey	(Harden 2000)

APPENDIX 7. Species salinity and inundation tolerance range data summarised from Chapter 3 and 4 experiments

Key: The results for the 2cm depth treatment are summarised from the salt tolerance experiment in Chapter 3, while results for 5, 20 and 60 cm water depths are from the factorial (salinity × depth) experiment in Chapter 4. Time until death was extrapolated from the average weekly plant mortality rate (all species), calculated from the time at which survivorship began to decline, or from weekly rates of leaf or culm loss (*Bacopa monnieri, Bolboschoenus caldwellii* and *E. equisetina),* averaged from the time relative growth rates (i.e. leaf/culm production) became negative. Leaf or culm loss data were used preferentially when available as these are likely to give a more accurate indication of survival time (often slightly less than when extrapolated from mortality rate data, since mortality rate data ranks all plants with live photosynthetic tissue as equivalent, regardless of the extent of tissue dieback). Survival times could not be extrapolated for the two grasses at 5 cm, 20 cm and 60 cm depth because numbers of live leaves and shoots were not recorded in the factorial experiment, and all individuals survived.

Species	**Water depth (cm)**	**Positive RGR (salinity, ppm)**	**Static or negative RGR (salinity, ppm)**	**LC50 4 weeks (salinity, ppm)**	**LC50 8 weeks (salinity, ppm)**	**Estimated weeks until mortality reaches 100%**
Cynodon dactylon	2 cm	≤15 000	20 000	20 000	15 000	<4 weeks at 35 000 ppm, <6 weeks at 20 000 ppm, ≤13 weeks at 15 000 ppm, ≤19 weeks at 10 000 ppm, ≤15 weeks at 5000 ppm, ≤33 weeks at 3000 ppm. (Insufficient mortality at lower salinities to extrapolate survival times.)
Bacopa monnieri	2 cm	≤20 000	35 000	>35 000	35 000	<9 weeks at 35 000 ppm, <49 weeks at 20 000 ppm. (Survival times could not be extrapolated for lower salinity treatments since all plants survived and rates of stem growth and leaf production remained positive when salinity was ≤15 000 ppm.)
Bolboschoenus caldwellii	2 cm	≤5000	10 000	20 000	20 000	≤1 week at 35 000 ppm, ≤7 weeks at 20 000 ppm, ≤11weeks at 15 000 ppm, ≤30 weeks at 10 000 ppm. (Survival times could not be extrapolated in lower salinity treatments because all plants survived, and rates of leaf production were positive when salinity was ≤5000 ppm.)
	5 cm	10 000	>10 000	NA	NA	(Positive rates of leaf production at all salinities tested i.e. ≤10 000 ppm.)
	20 cm	10 000	>10 000	NA	NA	(Positive rates of leaf production at all salinities tested i.e. ≤10 000 ppm.)
	60 cm	5000	10 000	NA	NA	(Positive rates of leaf production at all salinities tested i.e. ≤10 000 ppm.)

Species	**Water depth (cm)**	**Positive RGR (salinity, ppm)**	**Static or negative RGR (salinity, ppm)**	**LC50 4 weeks (salinity, ppm)**	**LC50 8 weeks (salinity, ppm)**	**Estimated weeks until mortality reaches 100%**
Eleocharis equisetina	2 cm	≤5000	10 000	35 000	20 000	<7 weeks at 35 000 ppm, <10 weeks at 20 000 ppm, ≤15 weeks at 15 000 ppm, ≤13 weeks at 10 000 ppm, ≤21 weeks at 5000 ppm, ≤24 weeks at 3000 ppm, ≤22 weeks at 1500 ppm, ≤22 weeks at ≤200 ppm.
	5 cm	10 000	>10 000	NA	NA	(Positive rates of culm production all salinities tested i.e. ≤10 000 ppm.)
	20 cm	≤5000	10 000	NA	NA	≤36 weeks at 10 000 ppm, ≤32 weeks at 5000 ppm, ≤64 weeks at 2500 ppm. (Positive rate of culm production when salinity ≤200 ppm.)
	60 cm	≤200	≤200	NA	NA	≤14 weeks at 10 000 and 5000 ppm, ≤16 weeks at 2500 ppm, ≤18 weeks at ≤200 ppm .
Paspalum distichum	2 cm	≤20 000	35 000	>35 000	>35 000	<23 weeks at 35 000 ppm. (100% survival when salinity ≤20 000 ppm.)

APPENDIX 8. Classification of Clarence wetland macrophyte species into functional groups, based on salinity and inundation tolerance data

Key: Bold print indicates salinity categories were calculated from growth and/or survival data measured in controlled experiments while others are based on survey data and may therefore not be indicative of the full range of conditions in which species may grow and survive. Wetland salinity and inundation categories are as defined in Table 5.4. In the functional group (water level fluctuation response) column, / is used to indicate species that may belong to either of two different categories. Where species have been classified into salinity categories using experimental data these categories reflect soil pore-water salinity tolerance thresholds of those species. Where survey data were used, species were only placed into a salinity category when found below the high water mark at a site placed in that salinity category (some species were also found at sites with higher salinities, but occurred in areas above the high water mark that were less salt-affected).

Species	Wetland salinity category	Functional group (water requirements) (Brock and Casanova 1997)	Functional group (water level fluctuation response) (van der Valk 1981)
Aegiceras corniculatum (river mangrove)	3-4	Amphibious	P D I
Apium prostratum subsp. prostratum (sea celery)	3-4	Terrestrial	P S I
Aster subulatus (wild aster)	3	Terrestrial	A S I
Avicennia marina (grey mangrove)	6	Amphibious	P D I
Bacopa monnieri (brahmi)	**1-5**	Amphibious	P/V D/S I
Bolboschoenus caldwellii (marsh clubrush)	**1-3**	Amphibious	VS I
Casuarina glauca (swamp oak)	**1-3**	Terrestrial	P/V S I
Centella asiatica (Indian pennywort)	1-2	Terrestrial	P D/S I
Centipeda sp. (sneezeweed)	1	Terrestrial	P S I
Cotula coronopifolia (waterbuttons)	2-6	Amphibious	A/P S I
Cynodon dactylon (couch)	**1-4**	Terrestrial	V/P S I
Cyperus polystachyos (Cyperus)	2-3	Terrestrial	A/P S I
Diplachne fusca (brown beetle grass)	4	Amphibious	P S II
Eleocharis equisetina (soft rush)	**1-3**	Amphibious	V/P S II
Eleocharis minuta	1-4	Amphibious	V/P S II
Epaltes australis (spreading nut-heads)	3	Amphibious	A S I
Fimbristylis ferruginea	4-6	Amphibious	P S I
Isolepis inundata (Swamp clubrush)	2	Amphibious	P/V S I
Juncus kraussii (sea rush)	3-4	Amphibious	P S I
Juncus usitatus (common rush)	3	Amphibious	P S I
Lachnagrostis filiformis (blown grass)	1-4	Terrestrial	A/P S I

Species	**Wetland salinity category**	**Functional group (water requirements) (Brock and Casanova 1997)**	**Functional group (water level fluctuation response) (van der Valk 1981)**
Ludwigia peploides ssp. *montevidensis* (water primrose)	1	Amphibious	P D/S I
Melaleuca quinquenervia (paperbark)	2-4	Terrestrial	P S I
Nymphaea caerulea (Cape waterlily)	1-2	Aquatic	A/P S II
Nymphoides indica (water snowflake)	1	Aquatic	P D/S II
Ottelia ovalifolia (swamp lily)	1	Aquatic	A/P S II
Paspalum distichum (water couch)	**1-4**	Amphibious	P D/S I
Persicaria hydropiper (water pepper)	1	Amphibious	P S I
Persicaria orientalis (princess feathers)	1	Amphibious	A S I
Philydrum lanuginosum (frogsmouth)	1	Amphibious	P S I/II
Phragmites australis (common reed)	**1-4**	Amphibious	V D/S I/II
Potamogeton octandrus (syn. Potamogeton javanicus) (pondweed)	1	Aquatic	P D/S II
Potamogeton tricarinatus (floating pondweed)	**1-3**	Aquatic	P D/S II
Ruppia sp.	3	Aquatic	A/P/V S II
Salvinia molesta (salvinia)	1	Aquatic	V D II
Sarcocornia quinqueflora (samphire)	6	Amphibious	P S/D I
Schoenoplectus litoralis (river clubrush)	3-4	Amphibious	P S I
Sporobolus virginicus (salt couch)	6	Amphibious	P D/S I
Triglochin procerum (water ribbons)	1-3	Amphibious	P S I/II
Triglochin striatum (streaked arrowgrass)	4	Amphibious	P/V D/S II
Utricularia sp. (bladderwort)	1	Various spp. vary in habit and habitat. Some terrestrial, others semi-aquatic to aquatic, either fixed or floating.	P/V D/S I/II
Viola hederacea	1	Terrestrial	P/V S I