

Water Regime and the  
Aquatic Vegetation  
of Bool Lagoon,  
South Australia



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# Summary

This thesis considers the aquatic macrophyte vegetation of remnant wetlands in the South East of South Australia, and of Bool Lagoon in particular. It consists of four sections.

The first is a description of the diversity of aquatic vegetation in 11 remnant and ephemeral wetlands in the South East using a multivariate approach of classification and ordination of vegetation quadrats. The wetlands are further classified on the basis of their aquatic vegetation and the structure of their vegetation is suggested as a suitable criterion for the classification of wetlands.

Flooding frequency was implicated as an important determinant of species composition but the paucity of water level data at the majority of these wetlands has prevented a more detailed examination of the effects of flooding pattern on aquatic species. Only at Bool Lagoon, the most floristically diverse wetland of those surveyed, were there sufficient water level data available to make this possible.

The South East is characterised by a Mediterranean climate which causes fluctuations in wetland water level. Previous work derived from literature has shown convincingly the effects of standing water on aquatic macrophyte species but few studies have considered the effect of a seasonal pattern of water level fluctuation. The second section of this study characterises this seasonal pattern of fluctuation through a numerical description of *water regime*. Flooding frequency was described as a histogram of time spent in each water depth class and histograms were compared on the basis of overall similarity. In this way, seasonal and interannual patterns of inundation and exposure may be described and compared from different sites within a wetland or between sites at different wetlands.

The third section of the study is a consideration of the population demography of *Typha domingensis* and *Phragmites australis* in relation to flooding frequency at Bool Lagoon. *In situ* permanent quadrats were used over two years to follow the seasonal development of shoots of both species, and how the depth and period of inundation influenced both the expression of biomass, and the demography of the annual population. While the annual production of both species was largely unaffected by water regime, the characteristics of individual shoots indicated that *Typha* performed better than *Phragmites* under conditions of deeper and more prolonged inundation. The capacity of each species to respond to changes in water level is suggested as the reason for the superiority of *Typha* in deep water conditions.

*Baumea arthrophylla* (Nees)Boeckeler [Cyperaceae], *Triglochin procerum* R.Br. [Juncaginaceae] and *Myriophyllum salsugineum* Orch. [Haloragaceae] were shown to be important components of the vegetation of Bool Lagoon and other wetlands. The final section of this study considers the influence of flooding frequency on the distribution of these species at Bool Lagoon. Statistical models were developed using logistic regression to fit Gaussian logit curves to binary response data. Quadrat elevation was used as the indicator of environmental gradient. Species optima, tolerances and maximum probability of occurrence were found to vary considerably around the Lagoon to the extent that flooding frequency alone was insufficient to explain their distribution. Interspecific competition and disturbance effects mediated by flooding and exposure are suggested as possible mechanisms to explain the distribution of these species.

# Declaration

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

I consent to the thesis being available for copying and loan, if accepted for the award of the degree.

Marcus D. Brownlow  
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**Part I**

**Text**



# Chapter 1

## Introduction

### 1.1 Preamble

Much of our knowledge of the ecology of aquatic macrophytes has emanated from the temperate Northern Hemisphere and from lakes where fluctuations in water level are minimal. Hence description of the niche requirements of macrophyte species have relied on static water depths and determination of the physiological tolerances of different species to inundation at different depths. In the Southern Hemisphere, particularly in areas with semi-arid or Mediterranean climates such as inland Australia, water levels are rarely static. Fluctuating water levels are the norm rather than the exception and wetlands are often ephemeral or temporary, yet the influence of these fluctuations on the productivity, performance, or even the occurrence of aquatic macrophytes is largely unknown. There is growing acceptance that wetlands are an important natural resource which should be carefully managed and preserved, but this cannot reasonably occur without information on the effects of flooding and drawdown cycles on aquatic vegetation.

By using field data from Bool Lagoon and other wetlands in the South East of South Australia, this work attempts to quantify and describe the effects of flooding cycles on the occurrence, productivity and performance of five aquatic macrophyte species. In this way, we may better understand the influence of water level fluctuations on Australian wetlands, and recognise the importance of environmental fluctuation in the shaping of natural systems.

## 1.2 Study area

The South East of South Australia has a landform which has been shaped by marine incursions over the last 400,000 years. The landscape is a gently sloping coastal plain with superimposed 30 m high consolidated dune ridges of Bridgewater limestone. The high annual rainfall (600–800 mm per year), coupled with a large catchment area which extends into western Victoria causes rapid flooding in winter of the flat corridors of land between the dunal ridges. There are no large rivers which run through the area and so water moves in a mass across the surface of the land. Historically, this sheet water flow conducted some 365,000 ML of water (South Eastern Water Conservation and Drainage Board, pers. comm.) from western Victoria through the South East every year to discharge into the Coorong (adjacent to Salt Creek; Figure 1.1). The direction of water flow was north-west through the interdune corridors. Since settlement, these interdune corridors have been cleared, cropped and grazed, but flooding severely reduced the agricultural productivity of the land. During this century more than 1450 km of drains have been cut into the landscape to rid agricultural land of standing water and today 53% of previously waterlogged land has been freed for agriculture and pastoralism (D'Arcy 1984). Water is now discharged to sea *via* the drains at various coastal locations and reaches the Coorong only in exceptionally wet years.

A consequence of this drainage has been a severe depletion of the wetland resources of the region. Once extensive, wetlands have been reduced to only about 8% of their former area (South Eastern Wetlands Committee 1984), and are generally restricted to local depressions in the interdune corridors. Creek-fed wetlands are now extensions of the drainage system and often receive their water from, or discharge their water to, the artificial drains cut into the landscape. A consequence of this is that some wetlands have the potential to be actively managed by the manipulation of their inflows and outflows. This may be for the purposes of flood mitigation or, more recently, for the purpose of wildlife management. Because of their rarity, there is now general recognition that these remnant wetlands should be carefully managed and preserved.

### 1.2.1 Bool Lagoon

Bool Lagoon is the largest (2,500 ha) and most well-known wetland in the South East. The Bool Lagoon complex consists of four linked basins: Hacks Lagoon and the Main, Central and Western Basins of Bool Lagoon. The basins have different morphometries and depths which range from 1.6–2.1 m (Table 1.1). The main source of water inflow is from Mosquito Creek (Figure 1.2) and then water flows through the basins of Bool Lagoon to be discharged into Drain M at the end of the Western Basin. However, this pattern of water flow is the result of human intervention. Historically, water entering Hacks Lagoon would exit *via* its northern perimeter and flow north-west across the Naracoorte Plain. Relatively little water entered the other basins.

In order to use the enormous capacity of Bool Lagoon for flood mitigation, stop banks and levees have been constructed along the northern perimeter of Hacks Lagoon and the Main Basin (Figure 1.2). Water is now diverted into Bool Lagoon and held there over summer through the operation of a regulator gate at the entrance to Drain M. The water levels of Bool Lagoon are now manipulated, both for flood mitigation and for the provision of open water habitat over summer for migratory water fowl. It is for its role as a water fowl refuge that Bool Lagoon is listed as a wetland of international significance under the Ramsar Convention (Ramsar Convention Bureau and International Union for the Conservation of Nature 1990).

This active management of the Lagoon's water levels has had a marked effect on its aquatic macrophyte vegetation over the last 15–20 years. Increased summer water levels, atypical of a Mediterranean-type wetland which should (nearly) dry out over summer, have been implicated in the large-scale shift in species dominance where sedgeland communities have retreated and semi-emergent species have increased their range. This pattern has been well documented by Rea (1993) and Rea and Ganf (1994b) who have demonstrated the effects of static water levels on the performance of emergent species in *in situ* experiments.

The chemical characteristics of the sediment of Bool Lagoon are summarised in Table 1.2 and are shown for a variety of locations in Table A.1 in Appendix A. The clay-based sediment is slightly alkaline ( $\text{pH} \approx 8$ ) caused by the presence of underlying calcium car-

bonate at many sites (CaO=16% and Ca:Na=31). Phosphorus is likely to be a limiting nutrient at Bool Lagoon with a Total N:Total P (TN:TP) ratio of 5.6. Sediment redox potentials range from  $-50$  to  $+200$  mV and increase with increasing depth indicating a mainly oxidising sediment (Muller et al. 1994). There is a chemical gradient at Bool Lagoon running from west–east, with sediments on the western side of the Lagoon having significantly higher pH and higher levels of organic matter, silicon, potassium and nitrogen, and a higher TN:TP ratio (Table 1.2). Sediments on the eastern side of the Lagoon have higher conductivity and levels of calcium, sodium, volatile compounds (indicated by loss on ignition) and a higher Ca:Na ratio. There are also chemical differences between sites on the same side of the Lagoon, but these are considerably smaller than the west–east differences.

Despite Bool Lagoon being generally regarded as the most important wetland in the South East because of the high diversity of waterfowl species its habitats support, there has been no attempt to quantify its habitat diversity. The avifaunal literature concerning Bool Lagoon is extensive (e.g. Hood 1932, 1934, 1935 cited in Parker and Reid 1983, and Jones 1978), but in contrast there have been few botanical studies conducted at the Lagoon. This is remarkable when one considers that the habitat diversity upon which avifaunal diversity is based is largely a function of the aquatic macrophyte species which occur there and the macroinvertebrate communities which they support. It is therefore not known whether Bool Lagoon is in any way representative of other regional wetlands, or very different from them. Indeed, apart from a few studies of individual wetlands, the region's wetland resources are poorly documented.

### 1.3 Water level fluctuation

The South East has a Mediterranean-type climate and the majority of wetlands in the area are ephemeral or temporary. Water level fluctuation is a feature of all wetlands in the region and is caused by strongly seasonal precipitation, with the bulk of the 600–800 mm per year rainfall occurring from April–September (winter) each year, and high daily temperatures and irradiance which cause slow evaporation and a gradual decrease in water level during the relatively dry summer.

The effect of flooding and drawdown on wetland vegetation may be broadly classed into both indirect effects (mediated by some alteration of the physical environment), and direct effects on individuals.

### 1.3.1 Indirect effects

The physical environment may be altered in a number of ways, with the most profound changes occurring in the soil. As the essential growth medium for most aquatic plants, changes in soil characteristics are most likely to have the greatest impact. Soil can become anoxic when waterlogged for relatively short periods (Ponnamperuma 1972) due to reduced atmospheric gas exchange (Wesseling 1974) and the continuing oxygen demands of aerobic soil bacteria. This oxygen depletion is accompanied by increases in the concentration of other soil gases, especially nitrogen, methane, carbon dioxide and hydrogen, which eventually escape either directly *via* ebullition or indirectly *via* molecular diffusion. Aerobic soil bacteria are replaced by facultative anaerobes, and then by obligate anaerobes which continue the process of organic decomposition. Upon drawdown the soil is reoxygenated through increased levels of atmospheric gas exchange and concentrations of potentially toxic gases are reduced.

Underwater light climate can also be affected by flooding, with rapid light attenuation affecting photosynthesis (Spence 1982; Chambers and Kalff 1985; Vermaat and De Bruyne 1993) especially in turbid or coloured water. Denny (1971) found that light regime was the principal determinant of plant zonation in a high altitude tropical lake. Nutrient release characteristics of soil may also be affected by flooding cycle. Kadlec (1962) and Briggs and Maher (1985) noted increased nutrient levels in wetland soil upon reflooding after a period of drawdown, and a subsequent increase in macrophyte production. This effect was attributed to increased aerobic nitrification of the soil during drawdown. Neill (1990) has also suggested that by altering nitrogen limitation, fluctuating water levels may influence macrophyte primary productivity through effects on nitrogen cycling. Organic decomposition can also be accelerated under alternate flooded and exposed conditions (Reddy and Patrick 1975). In riverine systems especially, the rate of underwater photosynthesis has been shown to respond to changes in current velocity (Madsen and Søndergaard 1983).

Under exposed conditions wave action can alter substrate particle size, nutrient concentration and organic content (Wilson and Keddy 1985; Weisner 1987). Long-term exposure will increase water stress and may ultimately lead to desiccation and adult plant death.

### 1.3.2 Direct effects

As a consequence of soil waterlogging and anoxia, flooding directly and adversely affects plant roots. Prior to tissue anoxia and subsequent death of root tips (Armstrong et al. 1991), reduced gas exchange caused by static water around roots can lead to both tissue hypoxia (reduced O<sub>2</sub> concentration) and increased ethylene concentration. Ethylene has been shown to stimulate petiolar growth (cell elongation or cell division) in *Ranunculus* (Horton 1992) and is believed to be chiefly responsible for the ability of many submerged aquatic species to accommodate increasing water levels. Rapid increases in water level and velocity have been shown to lead to changes in species abundance or even complete species removal in riverine systems through mechanical damage and uprooting (Brock et al. 1987; Chambers et al. 1991). Even under exposed conditions, plants growing on lakeshores are subject to direct mechanical damage by waves (Wilson and Keddy 1985).

Thus far flooding has been described in rather negative terms—as a harbinger of toxins and plant stress. This is only the case for non-wetland or facultative wetland species whose morphological and life history characteristics better equip them for an aerobic existence. The obligate aquatic species whose transition from land to freshwater is complete (Sculthorpe 1967) flourish under flooded conditions. For them, exposure is a greater stress than inundation. Therefore, depending on the species under consideration, either flooding or exposure will represent the greatest threat to survival.

## 1.4 Plant responses to water level fluctuation

It is impossible to generalise about the effects of flooding and drawdown on wetland vegetation because of the multiplicity of factors involved. The frequency, depth, duration and timing of inundation (and drawdown) interact with the specific combination of morphological and life history traits of each macrophyte species. The species themselves

interact with each other and their interactions are modified by the conditions of flooding or drawdown (Keddy 1989a). Amidst this complexity, it is possible to identify a few salient features.

Under conditions of static water level species have been shown to form gradation sequences along the depth gradient (Yamasaki and Tange 1981) either due to physiological limits or the effects of interspecific competition (Grace and Wetzel 1981; Buttery and Lambert 1965). However, when water levels fluctuate, species must be capable of dealing with a range of physical conditions which may range from total submergence to total exposure.

Fluctuation of water level is a feature common to Southern Hemisphere inland wetlands (Mitchell and Rogers 1985). Fluctuation may be either seasonal or aseasonal and this potentially unpredictable environment has promoted a variety of life history and growth strategies in aquatic macrophytes.

A common means of surviving adverse conditions is through avoidance—retreat to the seed bank. Even principally vegetatively reproducing species may set seed and deposit it in the seedbank in order to maintain populations between years when there is no other reproduction (Bonis et al. 1995). Annual species which complete their life cycle entirely during drawdown persist from year to year *via* the seedbank (van der Valk 1981) and effectively avoid adversity (e.g. prolonged drawdown or fire; Smith and Kadlec 1985) until the return of drawdown conditions suitable for germination (Kadlec 1962). In unpredictable habitats the opportunity for germination may be irregular and Casanova and Brock (1990) have suggested that selection may favour individuals whose propagules are drought resistant and can survive extended dry periods.

Because seed production offers the possibility of long-distance dispersal, the seedbank need not represent the same suite of species which are present in their adult form (Meredith 1985; Wilson et al. 1993). Thus depending on conditions, germinating seeds may produce the same or different communities from year to year (Galinato and van der Valk 1986).

Perennial plants have no mechanism to avoid unfavourable conditions and instead display enormous phenotypic plasticity in order to tolerate stress and persist in their adult form. Principally submerged species, and others, may display heterophylly to allow

perennation under dry conditions (Bostrack and Millington 1962; Cook 1968; Johnson 1967; Brock 1991). Under flooded conditions, emergent plants may increase their stem or leaf lengths to maintain contact with the atmosphere for gas exchange (Waters and Shay 1990; Hogeland and Killingbeck 1985; Sjöberg and Danell 1983), but not all plants are capable of such accommodation and this can lead to large-scale changes in vegetation as species poorly adapted to deep water are eliminated (Rea 1993; Burgess et al. 1990).

Fluctuation and unpredictability of water level may be perceived merely as a complication to interpreting plant performance under static water levels. However, fluctuation has an important role in the structuring of wetland vegetation in addition to its effects on individual species.

Willcox and Meeker (1991) demonstrated that regulated water levels which promoted either too much or too little fluctuation lead to reduced structural diversity in wetland vegetation (cf. the natural cycle was equivalent to an intermediate fluctuation and lead to structurally diverse vegetation). Also, fluctuating water levels increased the area of Canadian lakeshore vegetation as well as species and vegetation diversity (Keddy and Reznicek 1986). Fluctuating water levels further influence the structuring of lakeshore herb communities by modifying the influence of biotic and abiotic factors in a particular year, or series of years (Keddy 1989b).

While water depth has been used successfully as an explanatory variable in a number of studies examining the performance of aquatic vegetation (Lieffers and Shay 1981; Grace and Wetzel 1982; Menges and Waller 1983; Keddy and Constabel 1986; Poiani and Johnson 1988; Squires and van der Valk 1992) in a system where levels are rarely static, the relative lengths of wet and dry periods may be as important a stress as the average (or maximum) depth of water. Indeed, the very notion of plant response to water depth is misleading when water levels fluctuate. There must instead be an acknowledgement that plants respond to a *pattern* of fluctuation in semi-arid wetland systems. However, the important components of this pattern are largely unknown. As Howard-Williams (1975), paraphrasing Hejny (1971), notes:

... it is not necessarily only the amplitude of water level fluctuations which causes changes in the vegetation, but rather the duration of various phases in

the annual hydrological cycle; e.g. the length of time for which the soil is dry is more critical to the vegetation than is the difference between maximum and minimum water levels each year.

## 1.5 Study aims

This study had several aims, all of which were related to the investigation of the influence of flooding pattern on aquatic vegetation.

The first aim was to provide a formal floristic description of the aquatic vegetation of a number of wetlands in the South East. This was not only for the purpose of documenting the aquatic community types in these wetlands (generally neglected in previous studies), but also to compare and contrast their community composition. For this purpose, multivariate classification was used to distinguish floristically similar sites within wetlands, and quantify the degree of floristic overlap between wetlands. Finally, a classification of these wetlands was proposed on the basis of their aquatic vegetation.

It is well known from single-species studies or studies where only a few species have been considered (e.g. Grace and Wetzel 1981, 1982; Yamasaki and Tange 1981) that water depth has a profound effect on the occurrence, growth and survival of aquatic species. It is reasonable to suggest that communities of such aquatic species might be similarly susceptible to changes in water depth and a further aim of this study was to examine the extent to which community composition responded to flooding frequency. Ordination was used in tandem with classification to determine whether the community composition was related to flooding frequency, using *post hoc* correlations of ordination axis scores with elevation (a coarse indicator of flooding frequency).

These floristic descriptions and the relationship between community composition and flooding frequency are presented in Chapter 2.

As has already been stated, wetlands in the South East seldom experience static water levels. Instead they experience water levels which fluctuate seasonally but only coarse and inaccurate statements of this pattern were possible for the majority of wetlands due to the absence of formal water level records. Clearly, formal description and quantification of flooding pattern is a necessary first step towards determining the influence of this

pattern on aquatic vegetation. The second aim was to describe and quantify the flooding characteristics of the most intensively-sampled wetland, Bool Lagoon, and to classify different regions of the elevation gradient on the basis of their annual flooding pattern. This is presented in Chapter 3.

The final aim was to determine the influence of flooding pattern on five aquatic macrophyte species at Bool Lagoon. This was investigated using two approaches. The first considered whether biomass production and plant demography in *Phragmites australis* (Cav.) Trin. ex Steudel [Gramineae] and *Typha domingensis* Pers. [Typhaceae] was a function of the classified flooding class proposed above, and is presented in Chapter 4. The second examined whether the presence or absence of *Baumea arthrophylla* (Nees.) Boeckeler [Cyperaceae], *Triglochin procerum* R.Br. [Juncaginaceae] and *Myriophyllum salsugineum* Orch. [Haloragaceae] was a function of elevation (itself rank correlated with ordinal elevation class). This is presented in Chapter 5.

*Phragmites* and *Typha* were considered to be important components of the marginal vegetation of Bool Lagoon—both were invasive clonal growers capable of rapid establishment and domination of disturbed areas, but their distribution appeared to be restricted to the margins of the Lagoon. From a management perspective it was desirable to know the influence of flooding frequency on their growth because both species have the potential to become problem species. From a botanical perspective, it was not known whether the production characteristics of these highly productive species were influenced by flooding frequency, given that many previous studies (e.g. Hocking 1989a; Roberts and Ganf 1986) had been conducted under static water level conditions.

The study of species or community changes over major environmental gradients often occurs over great distances (e.g. altitude gradients on mountainsides) but wetland systems offer the near-unique opportunity to study the distribution of plants over a major gradient which is considerably smaller, but which can still display community changes of equivalent magnitude. For example, Nilsson and Wilson (1991) found similar plant community structure changes over a 495 m altitude gradient on a mountainside as those found along a 67 cm elevation gradient on a lakeshore. At Bool Lagoon, a 1.6 m elevation gradient is considered in conjunction with a flooding frequency gradient which ranges from 365 days

per year flooded to a variety of depths to <2 days per year flooded. Direct gradient analysis is used to model the distribution of *Baumea*, *Triglochin* and *Myriophyllum* along this gradient.

These species were also considered to be important components of the vegetation of Bool Lagoon—*Baumea* was the historically-dominant sedge throughout the Lagoon and both *Triglochin* and *Myriophyllum* have become dominant in more recent times to the extent that *Baumea* now has a reduced distribution. Increased water levels have been implicated in this change and both *Baumea* and *Triglochin* have been shown to respond differently to increased flooding (Rea 1993) consistent with the observed vegetation changes. It was therefore desirable to more closely examine the distribution and probability of occurrence of these species and whether these parameters were related to flooding frequency to the extent that flooding frequency might be used to predict their occurrence.

This has significant management implications because Bool Lagoon and some other South East wetlands have the potential to have their water levels manipulated to achieve a variety of wildlife management objectives. Implicit in such a proposal is that there is a clear relationship between the occurrence of aquatic macrophyte species and the flooding pattern to which they have been exposed.

Finally, this work aims to achieve the broad objective of increasing our knowledge of inland Australian wetlands and how water level fluctuations affect their vegetation.

# Chapter 2

## Wetland vegetation in the Lower South East of South Australia

### 2.1 Introduction

#### 2.1.1 Wetland classification

The idea of wetland classification is both topical and problematic, as highlighted by the recent special issue of *Vegetatio* (Vol. 118, 1995) devoted to global wetland inventory and classification. This volume presents considerable discussion on the need for a global wetland classification system with common methodology and terminology. The authors of the individual articles describe various regional attempts (successful or otherwise) to classify and catalogue their wetland resources. Once the thorny problem of “What is a wetland?” is resolved (for various definitions see Finlayson and van der Valk 1995, Cowardin et al. 1979 and Taylor et al. 1995), three broad schemes are proposed for the classification of wetlands.

The first relies chiefly on the physical characteristics of the wetland (e.g. landform and degree of wetness; Semeniuk and Semeniuk 1995). The second uses either the structure or floristics of vegetation (or both e.g. Briggs 1981) as a criterion for classification. The third uses a hierarchical combination of the two, with physical parameters such as location, salinity and duration of flooding used at the higher levels of classification, and vegetation characteristics such as physiognomy and growth form used as lower level modifiers. This

last type has generally been the most popular and the schemes of Gopal and Sah (1995) in India, Cowardin et al. (1979) in the United States and Ramsar Convention Bureau and International Union for the Conservation of Nature (1990) worldwide all follow this physical-biological combination format.

However, vegetation characteristics are not the only biological criteria which can be used to classify wetlands. As Britton and Podlejski (1981) note, "Different classifications reflect in part the different uses to which they will be put, and in part to the range of variation present in the area of wetland surveyed". Thus studies concerned with the role of wetlands as waterfowl habitat (e.g. Storey et al. 1993) use bird numbers and species as criteria for classification, and studies of the "biological health" of wetlands might classify using invertebrate community structure (Davis et al. 1993).

None of these schemes is universally applicable, though not for reasons of intrinsic weakness. Problems of application are due sometimes to the myriad exceptions in natural systems which conspire against any would-be universal classification system. This is perhaps inevitable because of the multiplicity of gradients along which the world's wetlands can be described. Classification of such a gradient system may be artificial, because it will always be possible to find wetlands which are intermediate between broad classification groups.

Other application problems are due solely to a question of scale where the resolution of global systems is inadequate at the local scale (and *vice versa*). As Pressey and Adam (1995) note, the question of scale should be uppermost in the minds of those who demand global uniformity. Classifications derived at continental, national or local scales can only be applied at those scales if the resulting wetland groups are to have any substantial meaning. Thus the widespread desire for global classification of wetlands may be an unattainable goal and smaller scale classifications may be a more profitable way of quantifying the enormous diversity of habitats and organisms present within wetlands.

### 2.1.2 Wetland vegetation classification

There are several ways in which vegetation can be considered when it is used as a lower level modifier in global wetland classification schemes, or when a physically similar range of

wetlands is considered. Physiognomic characteristics of vegetation are the most popular, especially when large physical areas are involved. For example, Kalliola et al. (1991) in a study of 920,000 km<sup>2</sup> of Peruvian Amazonia identified four distinct swamp types (herbaceous-, shrub-, palm- and forest-swamps) based on the physiognomy of dominant taxa. When remote sensing methods are used to map vegetation types, a physiognomic consideration of vegetation is virtually universally adopted (Christensen et al. 1988; Jensen et al. 1986; Johnston and Barson 1993; Kalliola et al. 1991) because satellites cannot distinguish species!

Broad-scale physiognomic treatments of wetland vegetation have a coarse resolution and only a single vegetation type may be assumed to exist within a wetland. Thus whole water bodies can be classified as cattail swamps if the dominant growth form and taxon is *Typha*. This level of resolution is entirely appropriate at the global or national scale, but at a local scale it is too simplistic.

It is practical to consider vegetation in terms of its component species and their association with each other in recognisable communities when a relatively small area is considered. Kirkpatrick and Harwood (1983) identified 16 major plant communities in 530 Tasmanian wetlands and characterised them by reference to structural vegetation type (formation) and dominant species (defined as the species with the most cover in the tallest stratum as observed in the field). Thus communities were described as, for example, *Ruppia* aquatic herbland and *Juncus kraussii* tussock sedgeland. Their formation definitions are shown in Table 2.1. Kirkpatrick and Harwood (1983) note with some despair the difficulty of comparing their data with other Australian regional wetland studies such as Jones (1978) because "... although good for their purpose, [they] treat the vegetation on a wetland-type basis and contain insufficient detail to enable comparison with our data".

This raises the questions of what is the purpose of classification, and what indeed is being classified, and both of these are related to the scale of study being conducted. In the work of Kirkpatrick and Harwood the wetlands themselves were not the subject of classification, but rather their vegetation. This is a subtle but important distinction. Furthermore, only a subset of the world's wetland types was examined. In contrast, the remote sensing papers and the bulk of work in the special issue of *Vegetatio* aim to classify

wetlands into distinct categories on a much broader global or regional scale and some use vegetation to aid in this.

There is a median approach between these two extremes where a classification of vegetation can be used subsequently to classify wetlands. Britton and Podlejski (1981) classified 506 French Carmargue wetland basins without *a priori* distinction between wetland types. They conducted two analyses. Firstly they classified vegetation into structural units (e.g. free-floating vegetation vs floating-attached vegetation) and used the % cover of these types in a multivariate analysis to group wetlands on the basis of their vegetation and physical and chemical attributes. Their second analysis was conducted just on species presence-absence data. This allowed both a classification of wetlands, and a classification of vegetation independent of wetland type.

Even Britton and Podlejski's approach takes an *a priori* view of vegetation classification because it is based on structural characteristics of different stands (height, life form and taxonomy). Where subtle changes in vegetation exist across environmental gradients, this structural approach may preclude the acknowledgement of stands of mixed height or life form, *viz* Kirkpatrick and Harwood (1983) who noted that species are often not restricted to their stated structural formations—"some [taxa] may slightly transgress the classificatory boundaries".

Britton and Podlejski (1981) concluded that their classifications based on species presence/absence were more satisfactory and furthermore were achieved with greater efficiency than were classifications based on vegetational (structural) and physical attributes. In small scale studies then, classification of vegetation within wetlands, rather than the wetlands themselves, allows for a more accurate description of their habitat diversity and consequently a clearer picture of the range of local wetland types. In addition, a floristic assessment of wetlands will put their flora into context with studies in surrounding (terrestrial) habitats. Only in this way can the relative importance of wetland flora be quantified, and we can move away from the coarse systems which assign whole wetlands to a pigeonhole such as "cattail swamp" or similar.

### 2.1.3 Wetland vegetation classification in South Australia

The classification of vegetation in South Australia has largely overlooked the contribution that athalassic freshwater wetland communities make to the floristic diversity of the State. This is no criticism of the broad-scale classification schemes of Specht (1972) and Sparrow (1991) which provide an extensive treatment of regional vegetation. Instead the neglect of wetland vegetation is more likely a function of the scale of previous surveys which have aimed to classify the State vegetation on a regional basis. The restricted geographic range of wetlands and the often ephemeral or annual nature of their component species, have further diminished their representation in previous studies.

Specht's (1972) consideration of the vegetation of South Australia identified 13 structural formations from closed forest to ephemeral herbland. Vegetation types common to South East inland wetlands come from the closed-grassland formation (and include the *SPOROBOLUS VIRGINICUS-DISTICHLIS DISTICHOPHYLLA*<sup>1</sup>, *PHRAGMITES AUSTRALIS-TYPHA* spp., *JUNCUS* spp.-*SCIRPUS* spp. and *BAUMEA JUNCEA-BAUMEA RUBIGINOSA* associations) and the tussock grassland formation (containing the *GAHNIA TRIFIDA-GAHNIA FILUM* association). These associations, with the possible exception of *PHRAGMITES AUSTRALIS-TYPHA* spp., are essentially terrestrial in nature when compared to obligate aquatic vegetation. Other closed-grassland formations include those from the salt marsh land system containing *JUNCUS MARITIMUS-SPOROBOLUS VIRGINICUS*, *SELLIERA RADICANS-MIMULUS REPENS* and *DISTICHLIS DISTICHOPHYLLA* associations. These associations are derived from coastal land systems whose primary influences are the degree of tidal inundation and salt leaching from organically poor sediment. Their appropriateness for the description of the vegetation of inland freshwater wetlands will be discussed in this chapter.

Specht noted that "although . . . [his] surveys cover[ed] most areas of the State, modifications and additions to each [species association] list must be expected as more critical ecological studies are made" (Specht 1972). Excluding the few studies of individual wetlands (Dodson 1974; Eardley 1943) the only ecological study of South East wetlands, was made by Jones (1978) who described all major wetlands in the area. Jones was able to identify 11 broad categories of wetland habitat (Table 2.2), using the dominant plant

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<sup>1</sup>Associations are shown in a small capitals typestyle to distinguish them from single species.

species (or alliances) present within the wetland and surrounding area, and an estimate of the relative proportions of open water and vegetation. This approach was not so much a classification of wetlands, or vegetation, but rather habitat type. Some wetlands are shown to contain numerous habitat types e.g. Fairview Conservation Park contains Wet Heath, Semi-permanent and Permanent Swamp (Table 2.2). Jones' habitat categories encompass a wide variety of wetland types, from deep freshwater or saline lakes to permanent inland swamps, and also include terrestrial habitats such as wet heath. The wetland habitats of the South East of South Australia are clearly more diverse than the relatively compact regional area (12,500 km<sup>2</sup>) might at first suggest.

#### 2.1.4 Aims and objectives

The broad aim of this study was to describe and compare the aquatic vegetation communities of a range of wetlands in the Lower South East of South Australia. In doing so the intention was to examine whether the wetlands are simply duplicates of each other and merely members of a "typical" South East swamp type, or whether their aquatic vegetation communities make each wetland significantly individual. This study neglects the lake and terrestrial habitat locations of Jones (1978) (Table 2.2) and concentrates on the so-called Forest Swamps, Semi-permanent and Permanent Swamps.

The aim was to classify aquatic vegetation first, and then to use these vegetation communities to classify wetlands. Because a relatively small geographic region was considered, it was possible to employ a vegetation sampling strategy of relatively high resolution where the sampling unit was the quadrat, rather than the basin used by Britton and Podlejski (1981) in their vegetation-only classification of wetlands.

The communities identified from these wetlands were described using the nomenclature of Kirkpatrick and Harwood (1983), and community dominants were selected on the basis of their constancy within classification groups, rather than projected foliage cover in the highest stratum. In this regard the method is more in keeping with the Zürich-Montpellier approach to vegetation classification, which uses species composition only, and structural references are purely descriptive (see Poore 1955a, 1955b, 1955c, 1956 for a detailed explanation of the Zürich-Montpellier methodology).

## 2.2 Methods

The 11 wetlands considered in this study are: Bloomfield Swamp, Bool Lagoon Game Reserve, Dine Swamp, Fairview Conservation Park, Honans and Bonney's Woodland Swamp, The Marshes Swamp, Mullins Swamp, Nangwarry Swamp, Poocher Swamp, Shearing Tree Waterhole and Topperweins Swamp (Figure 2.1). The wetlands were chosen in consultation with wildlife managers from the S.A. National Parks and Wildlife Service and the S.A. Department of Primary Industries (Forestry). All but Shearing Tree Waterhole were included in the list of wetland resources of South East South Australia (South Eastern Wetlands Committee 1984). The wetlands are variously managed and conserved (Table 2.3) and were considered to represent a range of wetland types in the area.

Three separate vegetation surveys were conducted during 1991 and 1992. The unpublished raw data of Flower (1991) and Hay (1992) were used from 10 of the 11 sampled wetlands. Data from Bool Lagoon were collected during 1991. Each wetland was visited once only and its vegetation and topography surveyed using a variety of methods.

Because of the different methodologies employed during these surveys, the method employed at each wetland (or group of wetlands) is described in detail below. The difficulties with reconciling these different data sets is also discussed.

### 2.2.1 G3 wetlands

Nangwarry Swamp, Honans and Bonney's Woodland Swamp and The Marshes Swamp were surveyed during 1991 and for brevity will be referred to as the group of three (G3) swamps. These were surveyed by Flower (1991, unpublished raw data).

#### 2.2.1.1 Nangwarry Swamp

Nangwarry Swamp (Grid Ref. 37°33'S 140°47'E) is a 20 ha swamp surrounded by *Pinus radiata* plantation forest and situated about 2 km from the town of Nangwarry (Figure 2.1). The original single basin of the swamp has been divided into three separate basins as a result of road construction and the dumping of saw mill waste. The practice of mill waste dumping has ceased but areas of the swamp are still polluted with wrecked

car bodies, tyres and other local refuse. Data from the first basin were chosen for analysis because of the basin's relative isolation from these impacts and from traffic in general.

Five locations were selected around the perimeter of the basin. At each location three parallel 25 m transects were run perpendicular to shore. These three transects were separated by 1 m. Along each transect the numbers of individual shoots of each plant taxon were counted in each of 250 contiguous 10 cm × 1 cm quadrats (i.e. those individuals touching the tape).

### 2.2.1.2 Honan's and Bonney's Woodland Swamp

The vegetation of this wetland is poorly described. The only published account of Honan's and Bonney's Woodland Swamp (hereafter referred to as Honan's Swamp, Grid Ref. 37°43'S 140°37'E) is that of Reeves (1970), and then it is only the most cursory of treatments. The focus of this work is on the woodland surrounding the swamp (Honan's Scrub) which contains numerous *Eucalyptus* species. The swamp itself is not described and its existence is only alluded to with a description of a "low-lying uncleared area, with some sedge flats and *E. ovata*". A more recent State Government management plan for Honan's Scrub (Anon. 1995) only provides a list of 17 plant species in its section on wetlands associated with the forest reserve.

The survey method used for Nangwarry Swamp was changed for the sampling of Honan's Swamp to sample more efficiently across the elevation gradient. A line transect was run perpendicular to shore at 10 equidistant locations spanning the perimeter of the swamp. At 5 m intervals along each transect (high water mark (0 m) to 50 m inclusive) fifteen 0.5 m × 0.5 m contiguous quadrats were set perpendicular to the transect (parallel to shore). The numbers of individuals of each plant taxon were counted in each quadrat.

### 2.2.1.3 The Marshes Swamp

The Marshes complex (Grid Ref. 37°37'S 140°32'E) is composed of two major swamps, Blue Tea-tree swamp and Mt Burr Swamp, and a series of "semi-permanent swampy depressions" (South Eastern Wetlands Committee 1984). The sampling of The Marshes complex was conducted in one of the basins of Blue Tea-tree Swamp. This was chosen

in consultation with wildlife managers from the Department of Primary Industries South Australia, Forestry (B. Gepp, pers. comm.), and also because of restricted access to many other regions of the swamp margin.

The survey method employed at Honan's Swamp was as used at The Marshes, except that only nine sampling locations were set out around the perimeter of the basin.

#### 2.2.1.4 Measurement of topography

At each sampling location of Nangwarry, Honan's and The Marshes, the topography of the line transect was measured with a dumpy level. Elevation of the sediment surface was standardised within each wetland by scaling elevation scores relative to the lowest measured point in the basin (=0 m) (Figure 2.2.1).

### 2.2.2 G7 wetlands

Vegetation surveys were conducted in Bloomfield Swamp (Grid Ref. 36°52'S 140°26'E), Mullins Swamp (37°31'S 140°08'E) and Topperweins Swamp (37°36'S 140°55'E) during May 1992. Dine Swamp (36°57'S 140°55'E), Fairview Conservation Park (C.P.) (36°49'S 140°25'E), Poocher Swamp (36°18'S 140°41'E) and Shearing Tree Waterhole (36°19'S 140°39'E approx.) were sampled in July 1992. Again for brevity, these swamps will be collectively referred to as the group of seven (G7) swamps.

At each swamp, survey locations were evenly distributed around the perimeter. For Bloomfield, Mullins and Topperweins Swamps, the position of sampling locations along the elevation gradient was determined by linear distance from the estimated high water mark (Figure 2.2.2). Twenty contiguous 1 m × 1 m quadrats were placed in a strip perpendicular to the transect line at distances 0 m, 10 m, 30 m, and 100 m from the estimated high water mark baseline. The percentage cover score for all vascular plant species and macroalgae was estimated within each quadrat, and the mean % cover across the 20 quadrats was calculated for each sampling location. The elevation of each location was measured with a dumpy level.

For Dine and Poocher Swamps, Fairview C.P. and Shearing Tree Waterhole, sampling between the estimated high water mark and the water surface was based on the elevation

classes defined from the previous three swamps with (at least one) sampling location(s) positioned within each elevation class, when each class was present at the swamp (Figure 2.2.3). For elevations below the water surface, locations were positioned at 5 m, 10 m, 30 m and 60 m (horizontal distance) from the current position of the water surface. The percentage cover score for all plant species was estimated within each quadrat, and the mean % cover across the 20 quadrats was calculated for each sampling location.

## 2.2.3 Bool Lagoon

### 2.2.3.1 Biotic data

36 sites were located at 0.5–1 km intervals around the perimeter of Bool Lagoon (Figure 1.2). At each location a 100 m line transect was run perpendicular to shore towards the approximate centre of the current basin. The baseline of each transect was placed at the high water mark (denoted by the landward extent of free surface water) on the day of sampling, with the exception of some sites containing *Gahnia* species where there was a great distance from the access point of the perimeter and the high water mark. In this case elevations higher than the level of the water surface were sampled. At all sites a 10 m × 0.5 m quadrat was laid perpendicular to the transect (parallel to shore) at intervals of 0, 5, 10, 15, 20, 30, 40, 60, 80 and 100 m from the baseline. The quadrat was divided into 20 0.5 m × 0.5 m contiguous cells in which the presence or absence of vascular plant taxa and macroalgae was recorded.

### 2.2.3.2 Abiotic data

The topography of each transect was measured using a dumpy level. All elevations within a transect were measured relative to the transect baseline, the elevation of which was estimated from the water surface elevation on the day of sampling. This reference elevation was measured from the nearest basin water level marker post. The effects of “wind tides” (bulk movement of water to one side of the Lagoon caused by strong winds) were minimal because sampling was conducted on particularly still days.

At each site three replicate soil cores were taken with a 1.5 m long split cylinder soil corer. Cores were collected generally at a distance of 15 m from shore, although extra

cores were taken at some sites of potential extra interest on the day of sampling. Fewer than three cores were taken from sites only where sample collection was difficult. Core samples were taken from the 10–25 cm zone within the core to avoid the detrital sediment layer and adequately sample the underlying substrate and rooting zone of many aquatic species. The soil core subsamples were refrigerated at 4°C until chemical determinations could be made.

Three subsamples were taken from each refrigerated soil core: the first was used for the determination of pH and conductivity; the second for nitrogen determination; the third for organic composition and extensive elemental analysis.

**pH and conductivity** A volume of water equal in millilitres to five times the weight of each core subsample in grams was added to approximately 5 g fresh weight of the sample in a beaker. The sediment-water mixture was stirred for one hour and the conductivity of the resulting solution measured with a TPS LC81 digital conductivity meter (TPS Pty Ltd, Brisbane, Australia). Solution pH was measured with an Orion model 720 pH meter (Orion Research Inc., U.S.A.).

**Nitrogen analysis** The subsample (approximately 5 g fresh weight) was dried overnight at 105°C and ground to a fine powder using a mortar and pestle. A Carlo Erba NA1500 Analyser Series 2 was used to determine the nitrogen concentration in approximately 5 mg of dry sediment sample. This involved the combustion of the whole sample and was based on the Dumas method (Hauck et al. 1994).

**Organic component** The subsample (approximately 20 g fresh weight) was dried overnight at 105°C and then ground to a fine powder using a mortar and pestle. The sample dry weight was measured prior to combustion in a muffle furnace at 550°C for one hour to remove the organic and volatile component from the sample. Samples were then cooled in a desiccator and weighed to determine ash-free dry weight. The difference between pre- and post-furnace weight was used to calculate the magnitude of the organic component of the original sample as a percentage of dry weight.

**Elemental analysis** Concentrations of volatile sediment components were measured by igniting ground samples (after combustion at 550°C for % organic determination) at 960°C for two hours. The difference between pre- and post-ignition weights was used to calculate the loss on ignition (LOI) as a percentage of sample weight.

The ignited sample was mixed with flux in the ratio 1:4 using 1.0–1.1 g of sample. The two components were melted together over an oxy-propane flame at approximately 1100°C into a fused glass disc. This disc of fused flux and sample was then analysed by x-ray fluorescence (Potts 1987) using a Philips PW1480 x-ray spectrometer which measured elemental concentrations within each sample as percentage composition.

## 2.2.4 Consolidation of data sets

Before any comparative analyses could be conducted, the data from the three disparate survey sets had to be made compatible prior to combination into a single composite data set.

### 2.2.4.1 Biotic data

Bool Lagoon vegetation data had the simplest structure based on the sum of presence-absence scores in 20 contiguous quadrats. This frequency score on a 0–20 scale was used as the standard species response measurement for all locations. Nangwarry, The Marshes and Honan's swamps had counts of individuals within each quadrat. The remaining swamps had percentage cover score estimates for each quadrat. Data from the other ten swamps were recoded to ensure compatibility with the Bool Lagoon data. Thus individual count and % cover scores per quadrat were reduced to presence-absence scores and these combined across sets of quadrats at a particular elevation to yield a score on a 0–20 scale. The Marshes and Honan's Swamp presence-absence scores would maximally sum to 15 and so these scores were linearly rescaled so that they ranged from 0–20.

Nangwarry Swamp was unique amongst sampled wetlands in having quadrats placed parallel to the elevation gradient rather than perpendicular to it, and having three transects per sampling location. To ensure compatibility with other data sets, count data were transformed to presence-absence scores and a moving-average smoothing function with a

20 quadrat window used on each transect. The average for three transects was calculated and then the values were read off at 5 m intervals from 0–25 m inclusive.

#### 2.2.4.2 Abiotic data

Consolidation of the elevation estimates for each sampling location was the most problematic, because of the widely different methodologies employed to measure elevation in each survey. At the G3 swamps (Nangwarry, Honans, Marshes) elevation was measured relative to the lowest point measured in the basin. The elevations of the sampling locations in the G7 swamps (Bloomfield, Dine, Fairview, Mullins, Poocher, Shearing Tree, Topperweins) were measured in two ways depending on the swamp (see Figure 2.2). In addition, the actual estimates of elevation for each site were inaccurately measured because of poor technique<sup>2</sup> and so all sampling locations in G7 swamps were intuitively assigned to one of nine ordinal elevation classes by field workers (Figure 2.3). These elevation classes were defined relative to the water surface on the day of sampling and ranged from (lowest to highest) >1 m below the surface (class 1) to >3.95 m above the surface (class 9).

Elevation was the only variable routinely measured at each swamp, although its scale of measurement varied between data sets. Thus these elevation data were mainly used to interpret within-swamp community analyses because of the difficulties associated with reconciling these different scales of measurement and different degrees of accuracy. Recoded ordinal elevation class was used in some between-swamp analyses where appropriate.

#### 2.2.5 Numerical analysis

Numerical classification and ordination of survey data were conducted to describe both the community composition and determine the  $\beta$ -diversity of each swamp. For the latter purpose an ordination approach was favoured over the calculation of numerous diversity indices because it was both immediately descriptive of sample diversity and offered a visual confirmation of the integrity of dendrogram groups (cf. Magurran 1988).

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<sup>2</sup>The estimated accuracy of (interval) elevation measurements was  $\pm 50$  cm (A. Hay pers. comm.)

### 2.2.5.1 Classification

All classification analyses were conducted using the PATN program (Belbin 1993a). The modules used for various procedures are shown in brackets. The Bray-Curtis distance measure (Bray and Curtis 1957) was used in the calculation of the site-site distance matrix (ASO) together with flexible unweighted pair-group method with arithmetic averages (UPGMA) fusion ( $\beta = -0.1$ ) (FUUSE; Belbin et al. 1992) to produce a dendrogram (DEND). The Bray-Curtis distance measure was chosen in accordance with general recommendations for biological data of this type (e.g. Faith et al. 1987, Clarke and Warwick 1994). It has repeatedly been shown to be superior to Euclidean distance measures when data sets contain large numbers of zero values ("zero-rich" data) (Ludwig and Reynolds 1988) and Faith et al. (1987) and Beals (1984) have shown that it performs consistently well across a range of ecological data sets.

The original sites  $\times$  species matrix was transposed (DATN) for examination of species associations *via* flexible UPGMA clustering ( $\beta = -0.1$ ) after  $\chi^2$  distance matrix calculation. The  $\chi^2$  distance measure was preferred over Bray-Curtis distance because of the propensity of the latter to give high weighting to species of high abundance, ultimately leading to associations characterised only by very frequent species. Chi-squared distance provided a way of detecting low frequency species which were found regularly with high frequency species and thus may be included in the association description. A two-way cross-tabulation of species groups and site groups was prepared to summarise the results of these classifications (TWAY).

### 2.2.5.2 Ordination

Detrended Correspondence Analysis (DCA; Hill and Gauch 1980) was used as an indirect ordination technique on the wetland survey data. Analyses were conducted using the CANOCO package (ter Braak 1988) and used 26-segment detrending with the down-weighting of rare species. DCA results were displayed as scatter plots of sites and species on (usually) the first two ordination axes using the CanoDraw program (Smilauer 1992). Dendrogram groupings were overlaid on these plots.

### 2.2.5.3 Correlation with environmental variables

The correlation of elevation class at G7 swamps with DCA axis scores was evaluated with one-way analysis of variance (ANOVA). At G3 swamps, Pearson product-moment correlation coefficients ( $\rho$ ) were used to quantify the correlation of elevation with ordination axis scores. Spearman rank-correlation coefficients were used at Bool Lagoon.

## 2.3 Results

### 2.3.1 Description of vegetation communities within wetlands

Classification of sites on the basis of species frequency showed, with some exceptions, a clear distinction between sites low on the elevation gradient (covered with standing water) and sites higher on the gradient. While some species were restricted to one of these elevation zones (the reason for the site group distinction), some species were found across the entire gradient. Groups were defined on the basis of a standard Bray-Curtis dissimilarity value of 0.7–0.8, or if there were clear discontinuities with long dendrogram branches. A single Bray-Curtis dissimilarity value could not be used because of the distorting nature of flexible UPGMA fusion with  $\beta$  set at  $-0.1$  i.e. upper branch ‘stretching’ occurs and the maximum dissimilarity values cannot be directly compared between dendrograms for data sets of varying numbers of quadrats.

The use of  $\chi^2$  distance for species clustering did not always recover meaningful groups. The members of the recovered species groups tended to be either endemic to a minority of sampling locations or were found across several locations at low frequencies (<25 %).  $\chi^2$  distance was considered appropriate for the cross-tabulation of species with site groups but little account was taken of the actual species groups defined from the dendrogram. Instead the constancy and frequency of species were used to characterise the vegetation of site groups. In general, the only clear community distinction was between truly aquatic and other species. In some instances where swamps were virtually monospecific, no clear community structure could be identified.

### 2.3.1.1 Bloomfield Swamp

Three site groupings were identified from the clustering (Figure 2.4)—one group (I) with high frequencies of aquatic species *Myriophyllum verrucosum*, *Potamogeton pectinatus*, *Triglochin* sp., *Isolepis inundata*, and two groups (II and III) where these species were either absent or comparatively infrequent. These latter groups were distinguished from each other on the basis of high frequency of *Myriophyllum* sp. 2 in Group II and high frequencies of the terrestrial grass *Stipa* and (less frequently) *Juncus* in Group III.

The majority of groups recovered were characterised by infrequent species restricted to only a few locations, with species groups A (*Anagallis arvensis*–*Isolepis nodosa*), C (*Festuca* sp.–Herb 2), D (*Melaleuca brevifolia*–*Solanum nigrum*) and E (*Crassula helmsii*–*Rumex bidens*) occurring in 8, 1, 3 and 3 sites respectively. Species group B had a large and diverse membership and may be considered the dominant species assemblage in Bloomfield Swamp. The poor performance of  $\chi^2$  distance in the species clustering can be seen clearly by examining the membership of this species group. *Myriophyllum verrucosum* and *Eucalyptus baxteri* are shown in the same dendrogram group but do not co-occur in any site, while *E. baxteri* and *Isolepis nodosa* are shown in different groups but co-occur at two sites.

The sites in the two-way tabulation of the classifications (Figure 2.4) are labelled with swamp number (1), site number and elevation class. It is clear that the aquatic herbland containing the truly aquatic species *Myriophyllum verrucosum* and *Potamogeton pectinatus* was restricted to sites below the water surface (elevation classes 2–4). *Triglochin* sp. and *Isolepis inundata* (also dominant below the water surface) were also found patchily at lower frequencies higher on the elevation gradient (Site group II). These were the only species (with the exception of *Rumex bidens*) which were found in both aquatic and terrestrial habitats. These observations were confirmed by the DCA ordination of sites (Figure 2.5.1) and species (Figure 2.5.2). Dendrogram groups I and III (Figure 2.5.1) were separated on axis I by approximately four half change units indicating that they shared no species in common. Site group II was intermediate between groups I and III, sharing species in common with each group. DCA axes I and II explained 29.9% and 8.7% of the total variation in species composition. DCA axis I was strongly correlated with elevation

class, showing a significant difference between the DCA axis I scores for sites below the water surface (elevation classes 2–4) and those above the surface (elevation classes 5 and 6; Figure 2.6.1).

### 2.3.1.2 Dine Swamp

Dine Swamp is comparatively small and contained only seven sampling sites. Two groupings were identified from the site clustering (Figure 2.8). The first (Group I) was characterised by the presence of *Azolla*, *Crassula*, *Myriophyllum* and *Chara* (which were found at only two sampled locations within the swamp) and contained sites covered with water up to 25 cm deep (elevation class 4). More terrestrial species were found higher on the elevation gradient up to 2.95 m above the water surface (elevation class 7) e.g. *Trifolium repens*, *Centipeda cunninghamii*, *Festuca* sp. and Compositae sp. These were found at high frequencies (>75%) at the majority of sites. Only *Lythrum* and *Limosella* were found in both site groups and may be classed as marginal aquatic species. There was strong separation of sites along DCA axis I (Figure 2.9) which explained 49.5% of variation in species composition and this was strongly correlated with elevation (Figure 2.6.2).

### 2.3.1.3 Fairview Conservation Park

Five site groupings were identified at Fairview Conservation Park (Figure 2.10). At elevation classes 2, 3 and 4 (i.e. below the water surface to a depth of 1 m) two species dominated—*Potamogeton pectinatus* and *Myriophyllum* sp. 1. *Myriophyllum* was also found high on the gradient in elevation class 5 and was the only species found across the entire elevation gradient. Also found high on the gradient were high frequencies of herbaceous species (*Lilaeopsis*, *Mimulus* and *Selliera*) and some more terrestrial species (*Juncus*, *Solanum* and *Anagallis*). Other species were generally found at fewer than three sites and at low frequencies. *Montia* sp. (a prostrate herb) was almost certainly misidentified at site 2, elevation class 3 (1 m depth). Similarly, the chlorophyte alga *Nitella* would be unlikely to occur at elevation class 5.

Ordination of sites showed that DCA axes I and II accounted for 34.6% and 10.2% of variation in species composition. Sites were well separated along axis I (Figure 2.11.1),

with particular distinctions between the high elevation terrestrial sites (Groups IV and V) and sites below the water surface (Groups I–III). Elevation class was strongly correlated with DCA axis I (Figure 2.6.3).

#### 2.3.1.4 Honan's and Bonney's Woodland Swamp

Sites at the periphery of Honan's Swamp (0–10 m from shore) contained the greatest diversity of species within the swamp, which were mainly from the ubiquitous species group B (Figure 2.12). Species groups A and C–E were minor components of the flora, containing low frequency species at a small number of locations. Species group B contained the bulk of species, particularly at distances <10 m (site groups I and II) from shore where terrestrial species such as *Dianella revoluta* (Liliaceae) and *Leptospermum myrsinoides* (Myrtaceae) occurred in high frequencies. Some of these species continued sporadic occurrence in site groups III and IV but were minor components of the species assemblages of these sites. Honan's Swamp was clearly dominated by *Baumea arthrophylla* at all distances from shore. Site group IV was characterised by a co-dominant mix of *Baumea arthrophylla* and *Myriophyllum salsugineum*.

Unlike in other wetlands, ordination of sites did not show clear group distinctions (Figure 2.13.1). All sites appeared within about two half change units in ordination space, indicating at least some shared species. The central position of *Baumea arthrophylla* on the species ordination scatter plot (Figure 2.13.2) confirmed its ubiquitous nature across sites at Honan's Swamp. The first two axes of DCA explained 25.8% and 9.9% of variation in species composition. DCA axis I scores were weakly negatively correlated with elevation (Pearson product-moment correlation coefficient ( $\rho$ ) =  $-0.45$ ; Figure 2.7.1). This was perhaps a function of the virtually uniform distribution of *Baumea arthrophylla*, or alternatively, inaccurate estimation of elevation of sampling locations. The measured change in elevation (4.0 m) over a 50 m horizontal distance makes the latter possibility highly likely.

### 2.3.1.5 The Marshes

The vegetation of The Marshes was very similar to that of Honan's Swamp with frequent (>75%) occurrence of *Baumea arthropphylla* at nearly all sites. Sites close to shore (Figure 2.14; site groups I, V, VI, VII) contained the highest species diversity, but nearly all species occurred at submaximal frequencies, often <50% occurrence. The remaining site groups II–IV contained a core of codominant species: *Baumea arthropphylla*, *Triglochin procerum* and *Myriophyllum salsugineum* from species group A. These groups were distinguished from each other by the presence of an extra dominant species: *Baumea articulata* (group IV), *Gahnia trifida* (group III) or the absence of either (group II).

Ordination of sites showed some separation of site groups III and IV along DCA axis I (explaining 25.8% of species variation), with group II intermediate between the two (Figure 2.15.1). With the possible exception of site group V, there were no clear discontinuities between any of the site groupings, caused by their sharing of the core species. The remarkably uniform species composition of the sampling sites caused DCA axis I to show no correlation with elevation ( $\rho=0.025$ ; Figure 2.7.2).

### 2.3.1.6 Mullins Swamp

Mullins Swamp had the highest total number of species of any of the sampled swamps (excluding Bool Lagoon) and was similarly unique in having the majority of its species occur at submaximal frequencies (<75%) (Figure 2.16). For example, *Baumea arthropphylla* when present at other swamps, especially Honan's and The Marshes, occurred almost exclusively at frequencies >75% and over a large number of sites. At Mullins Swamp however it was restricted to a single location with frequency between 50% and 75% (Site group I, species group H). Species groups were distinguished by low frequencies of locally endemic species occurring at a few locations, with the exception of species group C. Site group III was characterised by mainly obligate and marginal aquatic species (*Azolla*, *Spirodela*, *Ruppia*, *Cotula*, *Lilaeopsis*). Species such as *Berula erecta*, *Typha domingensis*, *Urtica* sp. and *Leptospermum lanigerum* (Species group C) were able to grow across the elevation gradient in elevation classes 3–5 (50 cm water depth–exposed to 1 m above water surface). Other species were restricted to higher elevations away from free surface

water. Site groups were separated along DCA axis I (Figure 2.17.1) but this was only weakly related to elevation (Figure 2.6.4).

The community structure of Mullins Swamp was indistinct and, unlike other sampled wetlands, poorly explained by elevation. Only 17.0% and 11.3% of variation in species composition was explained by DCA axes I and II.

### 2.3.1.7 Nangwarry Swamp

The sites of Nangwarry Swamp formed three distinct groups characterised by high frequencies of *Baumea arthropphylla* and few other species (Group III), *B. arthropphylla* and *Villarsia reniformis* jointly dominant with many other sporadically occurrent low frequency species (Group II) and a group of near-shore sites (Group I) which contained lower frequencies (<50%) of *Baumea* and *Villarsia* with many other species at low frequency (Figure 2.18). Nangwarry Swamp may therefore be described as a *Baumea arthropphylla*-*Villarsia reniformis* mixed community, with some peripheral diversity near shore. Site groups were separated along DCA axis I (Figure 2.19.1) which was strongly negatively correlated with elevation (Figure 2.7.3). There were no major discontinuities between site groups, caused by the sharing of *Baumea arthropphylla* and *Villarsia reniformis* (a feature in common with The Marshes and Honan's Swamp). 32.7% of variation in species composition was accounted for by DCA axis I, and 7.9% by DCA axis II.

### 2.3.1.8 Poocher Swamp

There was a clear distinction between aquatic and terrestrial sites at Poocher Swamp (Figure 2.20), with sites occurring below the water surface (Group 1, elevation classes 3 and 4) containing only two species (*Myriophyllum verrucosum* and *Nitella* sp.), neither of which were shared with any other sites. Ordination of sites and species (Figure 2.21) confirmed the aquatic-terrestrial discontinuity with clear site separation along DCA axis I caused by the absence of shared species between the two site groups. Unlike other sampled swamps, variation in species composition was not explained mainly by the first ordination axis. DCA axis I accounted for 37.7% of the variation, with another 23.3% by DCA axis II. The elevation gradient was effectively curved in ordination space. The low elevation sites

containing the aquatic species *Myriophyllum verrucosum* and *Nitella* had low DCA axis I scores and slightly higher axis II scores (Figure 2.21.2). The species found at medium elevations (classes 5–8) such as *Crassula helmsii* and *Haloragis aspera* had high axis I scores and low axis II scores. The species found highest on the elevation gradient (class 9) such as *Verbena supina* and *Festuca* sp. had high scores for both axes I and II. The sites also reflect this ‘curvature’ of elevation in ordination space (Figure 2.21.1).

### 2.3.1.9 Shearing Tree Waterhole

The sites of Shearing Tree Waterhole formed two distinct groups—those containing aquatic species (Group I) and those mainly without such species (Group II) (Figure 2.22). Some species were shared between the two groups at frequencies generally less than 75% (*Azolla*, *Wolffia*, *Triglochin*) such that ordination of sites (Figure 2.23.1) did not show such a marked separation of groups as that observed at Poocher Swamp (Figure 2.21.1). The terrestrial sites (Group II, elevation classes 5–7) contained mainly grass species with some *Trifolium campestre*, *Eleocharis acuta* and other infrequent species. Aquatic sites (Group I, elevation classes 1–3) contained the obligate aquatic species *Azolla*, *Wolffia*, *Chara*, *Potamogeton* and *Otellia*. *Triglochin* occurred across the elevation gradient, as did *Azolla* and *Wolffia*, but these latter species may have been found in puddles of water at higher elevations. Species composition was well explained by the first two DCA axes (Figure 2.23.1), which explained 45.5% and 14.7% of variance. There were significant differences between the DCA axis I scores of sites below water and those at higher elevations (Figure 2.6.6).

### 2.3.1.10 Topperweins Swamp

Topperweins Swamp contained a nearly uniform cover of *Baumea arthropphylla* and *Myriophyllum* sp. 3 across all elevation classes and site groups (Figure 2.24). Site group I, below the water surface (elevation classes 3–4) also contained *Potamogeton tricarinatus*, *Lilaeopsis polyantha* and grass species Gramineae 5. The latter two species were also found at higher elevations (elevation class 5) in site group III with other species from group A such as *Villarsia reniformis*, *Ranunculus* sp., *Lepidosperma laterale* and *Leptospermum myrsi-*

*noides*. Species from groups B–H were found across the elevation gradient at frequencies <75%.

Sites were arranged along DCA axis I (Figure 2.25.1) in a way which was strongly correlated with elevation class (Figure 2.6.7), but no large discontinuities were observed between groups. This was a consequence of the uniform cover of *Baumea arthropphylla* and *Myriophyllum salsaugineum*, which also caused the relatively short distance between sites (<2 half-change units). The number of species found below the water surface was higher than any other sampled wetland, where, generally, fewer than six underwater species were found. DCA axes I and II explained a large proportion of variation in species composition, with 40.0% and 15.1% of variance explained respectively.

#### 2.3.1.11 Bool Lagoon

Clustering of sites initially produced four site groupings (Figure 2.26). Two groups were essentially monospecific stands of *Phragmites australis* (Group III) and *Baumea arthropphylla* (Group IV). These were considered to be floristically distinct and so were excluded from subsequent analyses. Note that elevation class is not shown in the two-way tabulations of sites and species classifications. The distance from the transect baseline is shown instead.

Seven site groups were identified from the clustering of sites after removal of the *Phragmites* and *Baumea arthropphylla* monoculture sites (Figure 2.27). Group I contained mainly floating species (*Azolla*, *Spirodela*, *Wolffia*, *Lemna trisulca*) with similarly high frequencies of *Triglochin procerum* and lower frequencies of *Myriophyllum salsaugineum*. Scattered throughout these sites were lower frequencies of herbaceous species such as *Ranunculus*, *Cotula* and *Rumex*. Site group II contained the semi-emergent species, *Triglochin* and *Myriophyllum propinquum*. All group III sites contained a mixture of *Triglochin procerum* and *Myriophyllum salsaugineum* and in addition some contained low frequencies of *Baumea arthropphylla* and *Potamogeton tricarinatus*. These two species were most common at sites in group IV. Only four sites occurred in group V and contained only *Potamogeton pectinatus*. Site group VI contained numerous herbaceous species such as *Crassula*, *Lilaeopsis* and *Ranunculus* which occurred at generally <75% frequency. This

group may be described as an aquatic herbland. The final group of sites (VII) contained high frequencies of the terrestrial grass *Distichlis distichophylla* and the tussock grasses *Gahnia trifida* and *Gahnia filum*.

The associations of species which characterise the groups of sites at Bool Lagoon are:

1. BAUMEA ARTHROPHYLLA;
2. PHRAGMITES AUSTRALIS;
3. TRIGLOCHIN PROCERUM-MYRIOPHYLLUM SPP.-FLOATING SPECIES;
4. MYRIOPHYLLUM-TRIGLOCHIN-BAUMEA;
5. BAUMEA ARTHROPHYLLA-POTAMOGETON TRICARINATUS;
6. GAHNIA SPP.-DISTICHLIS DISTICHOPHYLLA;
7. CRASSULA-RANUNCULUS-LILAEOPSIS MIXED (aquatic herbland).

The first four axes of DCA explained considerably less of the variation in species composition than in any other sampled wetland (Figures 2.28–2.30). There was a slow decline in % explained variance between axes (9.8%, 7.3%, 4.8% and 3.8% for DCA axes I, II, III and IV respectively) compared with the much more rapid drop in % explanation observed at other wetlands (e.g. Bloomfield Swamp DCA I–IV: 29.9%, 8.7%, 5.3%, 4.3%).

There were two environmental gradients which accounted for the majority of variation in species composition: elevation (and the closely related water regime) and distance to the source of water inflow. On a scatterplot of sites on DCA axes I and II (Figure 2.28.1) there was a clear trend of inflow distance diagonally across the ordination space from bottom left to top right. The elevation/water regime gradient was perpendicular to this and went from top left to bottom right. Site group III, dominated by *Phragmites* and *Gahnia* was found at higher elevations than other site groups (Figure 2.28.1). These other groups were separated from each other along the gradient of distance from water inflow, with site group I (characterised by species from the TRIGLOCHIN PROCERUM-MYRIOPHYLLUM SPP.-FLOATING SPECIES and CRASSULA-RANUNCULUS-LILAEOPSIS MIXED associations) occurring at the northern end of the Main Basin adjacent to Hacks Lagoon and the inflow from Mosquito Creek. Virtually monospecific stands of *Baumea arthropphylla* (site group IV)

were found the greatest distance from the source of water inflow in the Central and Western basins. Site group II was spatially widely dispersed.

Examination of the scatterplot of DCA site scores on axes I and III also showed the separation of site groups along the gradient of distance from water inflow parallel to axis I (Figure 2.29.1) but no separation of site groups along axis III. In all site ordination scatterplots, sites in groups I, III and IV formed relatively compact clusters (width often <2 half-change units) indicating very similar species compositions among sites. In contrast, site group II spanned five half-change units on axis I and 4–5 half-change units along axes II–IV, indicating that species were not shared among all sites within the group and that sites on opposite sides of the group (in ordination space) may have shared no species in common. Furthermore, the group II sites (and species therein) were distributed across a wide variety of environments (as defined by elevation and distance from water inflow).

The separation of sites on axes III and IV (Figures 2.29.1 and 2.30.1) could not be related strongly to either elevation or distance from water inflow and site groups could not be separated on either of these axes. The following speculations are proposed to account for this lack of separation. Firstly, the coexistence of a large number of species could be caused by disturbance and succession within some combinations of elevation and distance from inlet conditions. Secondly, this pattern may be the result of completely random patches of species within combinations of elevation and distance from inlet conditions (i.e. non-equilibrium communities). Indeed, a combination of these two effects may be acting. A reappraisal of sampling sites for sheep grazing intensity<sup>3</sup> might aid in exploring the disturbance hypothesis.

The influence of elevation on species occurrence is clearly related to flooding frequency, where sites at low elevations would be inundated more deeply and for longer periods than would sites at higher elevations. The gradient of distance from water inflow was less easy to interpret. This distance gradient may be a function of one, or several of the following possibilities. Mosquito Creek is not only the source of water for Bool Lagoon, but also a significant source of nutrient and sediment influx. Consequently there may have been a nutrient gradient from Hacks Lagoon through the basins of Bool Lagoon which

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<sup>3</sup>Sheep are allowed to graze the perimeter of Bool Lagoon to reduce fuel loads and the risk of fire over summer (B. Clarke, pers. comm.)

was reflected in water rather than soil chemistry, but this was not sampled. Similarly, there may have been a difference in sediment characteristics in each basin (not reflected chemically), such as the rate of sedimentation or the texture of sediment. In addition, there would almost certainly have been a flood disturbance gradient parallel with the distance from water inflow gradient, when winter floods caused a rapid filling of the Lagoon.

### 2.3.1.12 General observations

Thus far the vegetation associations of individual wetlands have been described and related (with varying success) to elevation, elevation class or distance from shore—all coarse indicators of flooding depth and frequency. Some general observations can be made.

The aquatic flora of most locations was species-poor in contrast with the more diverse terrestrial sites. With the exception of Bool Lagoon, and Mullins and Topperweins Swamps, fewer than six truly aquatic species were found below the water surface at each wetland. There was often a marked distinction between aquatic and terrestrial communities in ordination space. This was caused primarily by the abrupt species change at the edge of each G7 wetland. The detection of this change was an artifact of the sampling methods employed at each wetland. While truly aquatic habitats were (usually) sampled at Bool Lagoon and G3 wetlands, sampling at G7 wetlands encompassed both terrestrial and aquatic communities because of the two methods used to choose sampling sites. The first relied on an estimate of the position of the high water mark and a major change from the absence of open mud or low-growing or herbaceous species to fringing sclerophyll woodland was used to signal this. The second used the elevation of the water surface to determine sampling sites with only four of the nine possible elevation classes occurring below water (Figure 2.3)—the others were sampled to maintain compatibility with the first sampling scheme.

Nevertheless, it was clear that elevation (as an indicator of flooding frequency) had a major influence on the distribution of aquatic plants. This was particularly evident at Bool Lagoon where elevation and the distance from water inflow were the principal explanatory environmental variables.

### 2.3.2 Comparison of vegetation communities between wetlands

The classification and ordination methods used thus far were also used to compare the floristic composition of different wetlands. The first comparison was between the G7 wetlands (Bloomfield, Dine, Fairview, Mullins, Poocher, Shearing Tree, Topperweins) in isolation because ordinal elevation class had been recorded for all sites and so could be used as an explanatory environmental variable. The second considered all 11 regional wetlands, including G3 wetlands and Bool Lagoon.

#### 2.3.2.1 G7 wetlands only

The distribution of species across sampling locations showed a distinct skew with over 50% of species occurring in fewer than four sampling sites. In order to remove the 'noise' associated with these infrequent species, they were excluded from subsequent analyses.

Eight site groups were identified from the classification of G7 wetland sites (Figure 2.31). The wetlands were largely distinct entities, but with some degree of floristic overlap. The variance in species composition explained by the first four axes of DCA was 8.6%, 6.7%, 4.5% and 3.5% respectively—considerably lower than was achieved during analyses of individual wetlands.

Analyses of individual wetlands showed a clear distinction between aquatic and terrestrial habitats at the majority of swamps. This pattern was repeated in the ordination of all G7 wetlands (Figure 2.32), but the aquatic/terrestrial gradient was only weakly correlated with ordination axes. A scatterplot of sites on DCA axes I and II with individual wetlands indicated by polygon envelopes (Figure 2.33), showed five cigar-shaped envelopes whose long axis represents a separation of aquatic and terrestrial sites within each wetland (Mullins and Topperweins Swamps did not show this pattern). It was clear from this diagram that the aquatic communities of G7 wetlands were largely distinct from each other, but their terrestrial communities were quite similar.

The terrestrial end of each wetland pointed towards the centre of the ordination plot (Figure 2.32.1). The terrestrial sites of Bloomfield Swamp and Fairview C.P. were floristically similar sharing the herbaceous species *Lilaeopsis*, *Mimulus*, *Selliera* and the grass *Sporobolus* and formed site group IV. The terrestrial sites of Poocher and Dine swamps

and Shearing Tree Waterhole formed site group VI and shared *Centipeda*, *Lythrum* and Compositae and Gramineae species. Site group VII contained sites from Mullins Swamp with large numbers of codominant, often terrestrial species largely unshared with other wetlands.

The remaining site groups were characterised by mainly aquatic species and represented the aquatic end of the individual swamp polygon envelopes. Site group I (POTAMOGETON PECTINATUS-ISOLEPIS INUNDATA-TRIGLOCHIN SP.-MYRIOPHYLLUM VERRUCOSUM) was restricted to the aquatic sites of Bloomfield Swamp. Site group 2 (POTAMOGETON PECTINATUS-MYRIOPHYLLUM SP. 1) was restricted to Fairview C.P. Poocher Swamp was the only location containing monospecific *Myriophyllum verrucosum* (Site group III). The floating species *Azolla filiculoides* and *Wolffia* sp. formed an association with *Chara corallina* and *Potamogeton ochreatus* only at Shearing Tree Waterhole (Site group VIII). Topperweins Swamp was the only wetland in the G7 group to contain a BAUMEA ARTHROPHYLLA-MYRIOPHYLLUM SP. 3-VILLARSIA RENIFORMIS association (Site group V).

Because the aquatic communities at different wetlands radiated from a shared core in ordination space, the relationship between elevation class and either of the first two DCA axes was neither linear nor regular. The position of centroids of elevation classes in ordination space did represent a gradation of elevation and consequently flooding frequency in the G7 wetlands, but this was unrelated to ordination axis score (Figure 2.32.1). In exposed sites (groups IV, VI and VII), a vector representing increasing exposure and decreasing flooding went diagonally across the site groups from bottom right to top left (roughly linking the centroids of elevation classes 4–9). Thus there was separation of these terrestrial and species-rich sites on the basis of flooding frequency, but this was not closely correlated with either of the first two DCA axes. The sites below the water surface were separated along DCA axis II and by a correlated wetness gradient going from elevation class 3 to 1.

The proximity of elevation class centroids to each other indicated the level of habitat specificity (in terms of flooding frequency) displayed by sampled species. In general, the terrestrial (classes 5–9) and shallow aquatic sites (class 4, up to 25 cm deep) were more closely associated with each other than were the deeper aquatic sites (classes 1–3). This

indicated that the presence of water greater than 25 cm deep severely reduced the number and kind of species able to survive under those conditions. At shallower water depths, and under exposed conditions, a much larger number of species could survive, and furthermore these did not have specific flooding frequency preferences (i.e. they were not associated with a single elevation class).

### 2.3.2.2 Bool Lagoon, G3 and G7 wetlands

A scatterplot of sites on the first two axes of DCA (Figure 2.34) showed considerable floristic overlap between the 11 sampled wetlands, but the low eigenvalues indicated that they accounted for a relatively low proportion of variation in species composition (6.2% and 4.3% for DCA axes I and II respectively). This relatively low level of explanation was also seen in the previous G7 swamp ordinations. Thus the representation of sites in only two dimensions may have inflated the actual degree of floristic overlap between the different wetlands. Seemingly similar sites may have separated along a third but unplotted axis.

To examine this possibility, a different ordination method was used which did not yield the  $(n-1)$ -dimensional solution ( $n$ =sample size) characteristic of eigenanalysis techniques. Semi-strong hybrid scaling (SHS; Belbin 1991) attempts to recover the starting configuration of objects (taken from an association matrix) in a user-defined number of dimensions. The success of this recovery is indicated with an estimate of stress which ranges from 0–1 (0 = perfect recovery; 1 = no recovery). Using this ordination method it was possible to see whether a two-dimensional representation of the combined wetland survey data was valid.

Analysis of both G7 wetlands in isolation and all surveyed wetlands (Bool + G3 + G7) required at least seven dimensions to recover the starting association matrix structure with a stress value of  $\leq 0.1$  (Table 2.4). Two-dimensional ordination was then wholly inadequate in representing the relationships among sites beyond simple graphical display. Ordination appeared to be an inappropriate method for combined analyses devised to quantify floristic overlap between wetlands.

### 2.3.2.3 Variation in combined wetland analyses

It is useful here to discuss the potential sources of the extra variation which has caused individual systems explicable in two dimensions to assume greater complexity when combined, so that more than four dimensions are required to achieve the same level of explanation.

In a model wetland where communities respond to the depth gradient and intergrade across contour lines, ordination of sites will show a strong gradient along axis I, corresponding to the depth of inundation. The second and subsequent axes will tend to display more subtle patterns of response (sometimes termed 'random noise'). This is true only if quadrats are placed at sufficient frequency to detect the gradual change in species composition. Where quadrats are placed at insufficient frequency, discontinuities will arise along the first ordination axis, and will dominate it. The second axis will show a part-gradient in the largest (or most variable) data subset, and the third axis will show a part-gradient in the smaller (or less variable) data subset. Thus, due to a sampling scale problem, a one-axis ordination has been converted to a three-axis ordination with the same total explanatory power.

This situation is complicated when more than one community is found at the same depth band, either through edaphic (e.g. fertility), disturbance history or other chance effects. If this second gradient is unrelated (orthogonal) to the depth gradient, then a one-axis ordination will extend into two dimensions. A more irregular second gradient may extend the ordination into more than two dimensions. Thus a single wetland can have a complex ordination.

When many wetlands are ordinated together, these sampling problems are compounded. Discontinuities will occur when wetlands do not share species in common. When orthogonal gradients exist between wetlands due to environmental or historical differences, more ordination axes will be required to achieve reasonable explanatory power.

This situation has occurred in all South East wetland site ordinations which have considered more than one wetland. The unshared species problem is compounded in this study where the taxonomy of species is either unknown or uncertain (65 taxa fall into these categories, out of a total species number of 239; Appendix B).

### 2.3.3 Species associations in South East wetlands

Classification was the only alternative method for combined wetland analyses in not being susceptible to the dimensional distortions of ordination. The hierarchical clustering of sites using the methods applied to single wetlands (Bray-Curtis distance; flexible UPGMA fusion) recovered sensible site groupings (i.e. they were in keeping with field perceptions/observations). Clustering of species using  $\chi^2$  distance was less informative because of the tendency of species with scattered distributions to form single-species groups (e.g. Figure 2.35 groups C–K). Species associations were therefore defined by searching for frequent and/or dominant species on the two-way table. Some of these associations were restricted to single wetlands, while others were shared among numerous wetlands. A total of 13 species associations were defined from the site clustering, but some of these have been merged after taxonomic review to yield the following 11 vegetation types (see also Appendix C).

1. POTAMOGETON PECTINATUS aquatic herbland;
2. MYRIOPHYLLUM VERRUCOSUM;
3. BAUMEA ARTHROPHYLLA;
4. BAUMEA ARTICULATA;
5. PHRAGMITES AUSTRALIS;
6. BAUMEA - MYRIOPHYLLUM - TRIGLOCHIN;
7. BAUMEA ARTHROPHYLLA MIXED;
8. TRIGLOCHIN PROCERUM FREE-FLOATING;
9. TRIGLOCHIN PROCERUM AQUATIC HERBLAND;
10. AQUATIC/TERRESTRIAL HERBLAND;
11. GAHNIA TRIFIDA.

The simplest vegetation associations were virtual monocultures of *Myriophyllum verrucosum* at Poocher Swamp (Figure 2.35, Group III), *Phragmites australis* at Bool Lagoon (Group XII) and *Baumea arthropphylla* at Bool Lagoon, Nangwarry and Honan's

Swamps (Group XIII). This last species formed a close alliance with *Myriophyllum sal-sugineum* and *Triglochin procerum* in four species associations, which were distinguished from each other on the basis of co-occurring taxa. Site group XI (Marshes and Bool) contained a BAUMEA ARTHROPHYLLA-MYRIOPHYLLUM SALSUGINEUM-TRIGLOCHIN PROCERUM-BAUMEA ARTICULATA association. Site group X (Marshes, Honan's, Bool) contained the BAUMEA ARTHROPHYLLA-MYRIOPHYLLUM SALSUGINEUM-TRIGLOCHIN PROCERUM association with frequent *Gahnia trifida* (Marshes) and *Potamogeton tricarinatus* (Bool). Site group IX (Bool, Honan's, Marshes, Nangwarry, Topperweins) contained a mixed BAUMEA ARTHROPHYLLA association with a diverse assemblage of co-occurrent species such as *Villarsia reniformis*, *Ranunculus pentandrus* (Nangwarry and Honan's) and *Phragmites* (Bool). Site group VIII (Bool) was similar in composition to group IX, but in addition contained high frequencies of floating species (*Azolla*, *Lemna*, *Spirodela*, *Wolffia*) and contained virtually no *Baumea arthropphylla*. The inclusion of floating species in association descriptions may be problematic in some instances because their distribution may be severely influenced by wind action. Thus the TRIGLOCHIN-AZOLLA-LEMNA and PHRAGMITES associations of today could be transformed into PHRAGMITES-AZOLLA-LEMNA and TRIGLOCHIN associations.

Mainly submerged communities and semi-emergent communities were restricted to site group I (POTAMOGETON-TRIGLOCHIN-MYRIOPHYLLUM-ISOLEPIS at Bloomfield, Fairview and Mullins), group II (POTAMOGETON-MYRIOPHYLLUM at Fairview), group III (MYRIOPHYLLUM VERRUCOSUM at Poocher, described above) and group V (TRIGLOCHIN-PHRAGMITES-AZOLLA-LEMNA at Shearing Tree).

The remaining site groups IV, VI and VII contained a large number of species often with patchy distribution and at submaximal frequency. Site group VI (Bool) contained the aquatic herbland species such as *Lilaeopsis*, *Mimulus*, *Crassula*, *Triglochin striatum* and *Selliera*, as well as patchy occurrence of *Triglochin procerum*, *Myriophyllum sal-sugineum* and *Baumea arthropphylla*. Site group IV contained some of the aquatic herbland species, but many more terrestrial species. Site group VII contained sites with *Gahnia trifida* tussockland which were restricted to Bool Lagoon and Mullins Swamp.

It is clear that Bool Lagoon contains the greatest number of defined species associations (9 out of 11; Table 2.5). The only associations absent are MYRIOPHYLLUM VERRUCOSUM and the AQUATIC/TERRESTRIAL HERBLAND. The absence of this latter association indicates that the aquatic herbland at Bool Lagoon is comparatively pristine in having no terrestrial species (often invasive pasture grasses) in uniform abundance.

### 2.3.4 Individuality of South East wetlands

The distribution of species associations across wetlands (Table 2.5) clearly shows that the majority of wetlands were not merely replicates of each other. The wetlands broadly fell into two groups: those which contained BAUMEA associations (BAUMEA ARTHROPHYLLA, BAUMEA ARTICULATA, BAUMEA - MYRIOPHYLLUM - TRIGLOCHIN and BAUMEA ARTHROPHYLLA MIXED) and those which did not. The former group included Topperweins, Nangwarry and Honan's swamps, The Marshes and Bool Lagoon and these were distinguishable from each other on the basis of the number and type of species associations they contained. The non-BAUMEA wetlands were similarly distinguishable from each other with the exception of Bloomfield Swamp and Fairview C.P. which shared the same POTAMOGETON PECTINATUS and AQUATIC/TERRESTRIAL HERBLAND associations, and Dine Swamp and Shearing Tree Waterhole which shared the same AQUATIC/TERRESTRIAL HERBLAND association.

## 2.4 Discussion

The species and site associations presented here are based on the results of numerical analysis. While site classification based on the Bray-Curtis distance measure was largely successful, the species clustering based on  $\chi^2$  distance was abandoned in favour of visual inspection of the two-way tables. The initial choice of the  $\chi^2$  distance was based on the desire to detect low-frequency species which may have been included in the association description. An unwanted side effect of this distance measure with "zero-rich" data was the overweighting of shared absences of rare species. Thus two species that were rare but shared a few sites in common appeared more strongly associated than two species that were common and shared a few sites in common.

For species similarities, Ludwig and Reynolds (1988) recommend the use of measures that do not use mutual absences in their calculation of association, such as Jaccard's Index. However, even Jaccard's Index can produce misleading association values when "zero-rich" data are considered. Comparison of zero values with non-zero values results in an association value of 1.0 regardless of the magnitude of the non-zero value (Belbin 1993b). In this case the impression may be given that a species frequency of 1 was as different from zero as a species frequency of 20. Clearly this was inappropriate.

Clarke and Warwick (1994) recommend the use of the Bray-Curtis distance measure for the calculation of species similarities, with two important pre-processing steps: removal of rare species from the data set and the row-standardisation of species frequency scores (i.e. standardisation of scores within a species). This latter step is suggested in order to account for intrinsic differences in species abundance caused by morphological differences e.g. larger species will necessarily have smaller counts in the same quadrat than smaller species, even though their counts may be in strict ratio to each other across samples. In this case, such an approach would have allowed the detection of low-frequency species which may have been included in the association description, but would have precluded the incorporation of rare species.

For the purpose of classification of wetlands, vegetation can be used successfully as a classification criterion. In the South East wetlands, each was found to contain a unique combination of associations, with the exception of Bloomfield Swamp and Fairview C.P. which were floristically very similar. This is perhaps unsurprising given that these wetlands are geographically close to each other, experience essentially identical climatic conditions and are surrounded by similar terrestrial wet heath.

The previous descriptions of wetland vegetation, both in South Australia and elsewhere, were not entirely appropriate for the associations defined here, although some similarities could be detected. The formation definitions of Kirkpatrick and Harwood (1983) were appropriate for the description of some communities (e.g. Dine Swamp site groups A and B formed an *aquatic herbland*), but the majority of species associations contained a mixture of life forms which conflicted with the rigid criteria used to delineate formations e.g. high on the elevation gradient at Fairview C.P. the vegetation contained

a mixture of *marginal herbland* species (*Lilaeopsis*, *Mimulus*, *Selliera*) and *sedgeland* species (*Juncus pallidus*, *Isolepis nodosa*). The broad category *aquatic herbland* could be applied to both the POTAMOGETON PECTINATUS and MYRIOPHYLLUM VERRUCOSUM associations (Appendix C) defined here and less precisely to the BAUMEA ARTHROPHYLLA-MYRIOPHYLLUM SALSUGINEUM-TRIGLOCHIN PROCERUM, TRIGLOCHIN PROCERUM - FREE-FLOATING, TRIGLOCHIN PROCERUM AQUATIC HERBLAND and AQUATIC/TERRESTRIAL HERBLAND associations. Such a structural classification would have shown a greater similarity between these wetlands than was the case with floristic classification.

Ellenberg's (1988) extensive phytosociological classification of European vegetation describes alliances of striking similarity to some of the associations defined here. e.g. Potamogetonion (rooted aquatic waterplant community) accurately describes the POTAMOGETON PECTINATUS association. These similarities continue through the monospecific associations PHRAGMITES AUSTRALIS ( $\equiv$  reed swamp), and BAUMEA ARTHROPHYLLA, BAUMEA ARTHROPHYLLA MIXED and BAUMEA ARTICULATA ( $\equiv$  tall sedge swamps). However, when combinations of species occur whose life form or structural characteristics are very different (e.g. TRIGLOCHIN PROCERUM - FREE-FLOATING) there is no exact Ellenberg alliance equivalent. Such combinations occurred in five of the 11 defined associations.

The treatments of South Australian vegetation by Specht (1972) and Sparrow (1991) have largely overlooked the species associations defined here with a few exceptions. Specht's closed grassland formation (SELLIERA RADICANS-MIMULUS REPENS association) overlaps floristically with the TRIGLOCHIN PROCERUM - AQUATIC HERBLAND. There is a less precise match between Specht's closed grassland formations BAUMEA JUNCEA - BAUMEA RUBIGINOSA and PHRAGMITES AUSTRALIS - TYPHA DOMINGENSIS and the BAUMEA ARTHROPHYLLA association, and PHRAGMITES AUSTRALIS associations respectively. Sparrow's (1991) classification contains only one of the associations defined here, and is also in agreement with Specht (1972)—the GAHNIA TRIFIDA/GAHNIA FILUM association is common to all works.

These surveys were intended as a preliminary quantitative consideration of the vegetation of remnant wetlands whose community composition was previously unknown or was represented only by a simple species list (i.e. Lloyd and Balla 1986). It is clear that the wetlands are not merely replicates of each other but have unique combinations

of aquatic and semi-aquatic species associations. It is also clear that the presence of standing water significantly alters species composition and richness in these wetlands. Gosselink and Turner (1978) have suggested two alternative effects of flooding to explain this. Monospecific stands of macrophyte vegetation can be the result of sheet water flow and the concomitant uniform mixing of dissolved and suspended material and a minimisation of spatial diversity. The uniform cover of *Baumea arthropophylla* in Honans and Nangwarry swamps, The Marshes and regions of Bool Lagoon may be the result of this habitat uniformity caused by sheet water flow. The other effect of flooding on wetlands can have precisely the opposite effect, where rising and falling water levels can produce marked elevational and substrate differences which Hinde (1954) has suggested is the chief source of species diversity in wetlands. This latter effect appears the most likely cause of the patterns observed in Bloomfield, Dine and Poocher swamps, Fairview C.P., Shearing Tree Waterhole and (less markedly) Topperweins Swamp, where the clear distinction between aquatic and terrestrial species was mediated by the presence of standing water.

The degree of fluctuation of water levels in these wetlands, and consequently the degree of habitat disturbance experienced, is largely unknown. If uniformity of habitat is a function of low levels of disturbance (see the extensive literature on the Intermediate Disturbance Hypothesis from Connell (1978) onwards), then the *Baumea* swamps (Honan's, Marshes, Nangwarry, Bool Lagoon) might be expected to be the products of comparatively minor water level fluctuation. Conversely, the habitat-rich swamps which contain multiple species associations may be the results of more major fluctuations of water level. This is purely speculative—it is not possible to investigate the relationship between flooding frequency and community composition in each of these wetlands because of the absence of basic water level data.

However, water level records have been kept for Bool Lagoon, and combined with its very diverse nature in terms of the number of species associations its habitats support (9 out of the 11 defined associations are found at Bool Lagoon) patterns detected there may be used to better understand the patterns of vegetation in the other wetlands. This is more fully explored in the next chapter.

# Chapter 3

## Water regime at Bool Lagoon<sup>1</sup>

### 3.1 Introduction

Semi-arid wetland systems are characterised by marked changes in their water levels which see, over summer, the wetland turn into a dryland. Broad descriptions of these variations in water level include 'seasonal', 'ephemeral', 'temporary', 'permanent', 'deep' or 'shallow'. These categories are at best qualitative and may be derived from local knowledge in the absence of more formal measurements of water level. More significantly however, these descriptions are made at a scale which implicitly assumes that the vegetation of these systems will respond uniformly. Thus the vegetation of a permanently deep swamp might be expected to differ significantly from that in a seasonally inundated shallow swamp. At this scale of classification, gross floristic differences are virtually assured.

From a 'plant's-eye-view' however, these broad classifications of wetland flooding pattern are of little consequence. The important flooding pattern to a non-motile organism is that experienced *in situ* and this may be only tenuously related to the gross description of the annual flooding pattern of the wetland in which it grows. For example, the annual flooding pattern experienced by a wetland herb situated near the edge of a permanently deep swamp may resemble that of an emergent plant growing near the centre of an infrequently inundated basin. Although these wetlands *in toto* have markedly different flooding characteristics, they do share some flooding characteristics peculiar to distinct regions along their gradients.

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<sup>1</sup>This chapter contains material which has been previously published (Brownlow et al. 1994) but is based on more extensive data from 1985–1992.

It has been difficult to quantify flooding patterns in fluctuating systems. Many descriptions of wetland flooding characteristics simply use qualitative appraisals of water permanency such as seasonal or ephemeral, yet these categories are inadequate as a definition of the stress or niche which might account for the distributions of perennial species in wetlands.

It is well known that water depth affects the occurrence and performance of aquatic macrophytes (e.g. Grace and Wetzel 1982; Spence 1982) but in systems subject to fluctuating water levels, instantaneous water depth does not adequately describe the conditions experienced by plants over a single growing season, year or several years. Rørslett (1984) has suggested instead that impact on species in regulated Swedish lakes “should be assessed from a ‘plant’s point of view’ ”. Relatively simple indices of this pattern of fluctuation, such as degree of exposure, can be used to explain some aspects of species occurrence (e.g. species’ lower depth limits) but community level responses were less easily explained (Rørslett 1983 cited in Rørslett 1984).

Rea and Ganf (1994a) also acknowledge the importance of describing flooding pattern from the ‘plant’s-eye-view’ and have described the immediate past flooding history experienced by a plant as its Sum Water Regime (SWR). Measured in units of cm days, SWR is essentially an integration of the area under a graph of water surface elevation through time and has been used successfully to explain the biomass allocation patterns of emergent macrophyte species (Rea and Ganf 1994a). However, these descriptions of past flooding patterns lack the probabilistic component which Rørslett (1984) considers to be an important link between instantaneous water depth and the many environmental gradients associated with it. Also, it is not possible using SWR to distinguish patterns of shallow flooding for long periods from deep flooding for short periods.

In an attempt to quantify the flooding characteristics of different localities within a wetland complex, and better describe flooding pattern from the ‘plant’s-eye-view’, a numerical definition of *water regime* is described that allows the comparison of flooding and drying cycles both between locations within a wetland and between locations in different wetlands (cf. Rørslett 1984 where comparisons across locations were not possible).

## 3.2 Methods

### 3.2.1 Study area

From 1985–1992 the flooding and drawdown characteristics of Bool Lagoon followed a distinct seasonal pattern. The basins reached their maximum water level in August/September each year after winter rain, then gradually dried over summer and autumn and reached their minimum in April/May (Figure 3.1). The amplitude of this seasonal fluctuation was strictly controlled by the South Eastern Water Conservation and Drainage Board (SEWCDB) so that, if possible, water remained ponded in Bool Lagoon over summer to provide refuge habitat for migratory water fowl. The amplitude of annual water level fluctuation varied between 0.3 m and 1.1 m at the deepest point depending on the year and basin under consideration (Table 3.1).

### 3.2.2 Water Regime Classification

The following terms are used throughout this section and their definitions are presented here to avoid confusion.

**Elevation** distance above mean sea level measured in Australian Height Datum metres (mAHD).

**Gradient position** a single point along a gradient having a distinct elevation and flooding pattern.

**Water level** the elevation of the water surface (mAHD).

**Water depth** distance between the sediment surface and water surface measured in metres.

**Location** a distinct geographical position either within the same basin/wetland or in another basin/wetland.

**Level baseline** the elevation of the lowest point in a basin.

The only data required to characterise, compare and cluster the water regimes in the wetlands are the water level (elevation of water surface) and the date at which the level was recorded. In this case water level data recorded over eight years by the SEWCDB in the Bool Lagoon system were used. Readings were taken fortnightly over winter and

less frequently over summer. This sampling frequency was considered adequate for this method. However, because of the non-continuous nature of the data and the large fluctuations which occurred over some time periods, behaviour of the water level during periods between sample dates was estimated by linear interpolation between adjacent data points.

The inundation characteristics of any particular location were then determined as follows. Firstly, the water level data for the lagoon were corrected for the elevation of the location concerned by adding/subtracting location elevation to/from the lagoon level baseline. Then depth of inundation was divided into a series of 5 cm depth classes ranging from 0 cm (dry) through to 205–210 cm (deepest). Time spent at each depth class was calculated by a summation of time where the depth of water fell within individual depth class limits (including interpolated values; Figure 3.2). These data were then represented as a histogram whose area was corrected to a value of 365 days (one year) by division by the number of years of records. Gradient positions were compared by multivariate clustering on the basis of their histograms, after square-root transform of time spent in each depth class. The square-root transform downweighted the effects of long periods of either dry or deeply flooded, and also acknowledged the non-linear biological effects on vegetation of immersion or exposure i.e. plant stress at 100 days inundation would not necessarily be twice that experienced after 50 days. A Manhattan (City-Block) distance measure was used to determine the proximity of each gradient position to its neighbours; this distance is defined as simply the sum of differences in each depth class i.e.

$$\sum_{k=1}^n |\sqrt{T_{ij}} - \sqrt{T_{jk}}|$$

where  $d_{ij}$  = dissimilarity between locations  $i$  and  $j$ ,  $n$  = number of inundation depth classes ( $n=43$  in the Bool Lagoon example),  $T_{ik}$  = time (mean days per year) when location  $i$  is flooded within the range of inundation class  $k$ . The Manhattan distance metric was chosen over other distance measures (e.g. Bray-Curtis) because each attribute (depth class) is given equal weight in the calculation of inter-sample distance. Flexible UPGMA fusion ( $\beta=0$ ) (Sneath and Sokal 1973; Belbin et al. 1992) was used to group gradient positions and produce a dendrogram. Clustering was performed using the PATN program (Belbin 1993a).

The dendrogram groupings were interpreted at a level which yielded eight broad water regimes; on the ground, these groups represented bands 2–3 m wide where the gradient is steepest and so could easily be identified in the field. The median gradient position of each regime was chosen as representative of that regime, and its flooding characteristics calculated as the mean inundation time in each depth class for each location in the same dendrogram grouping. Annual flooding and drawdown characteristics of different basins (or swamps) *in toto* were numerically compared using the bottom of swamp gradient position.

### 3.3 Results

#### 3.3.1 ‘Bottom of Swamp’ Comparisons

The four basins of the Bool Lagoon system (Hacks Lagoon, and the Main, Central and Western Basin of Bool Lagoon) have different morphometries, different proximity to the source of water inflow, different physical area, and consequently different flooding and drawdown characteristics (Table 1.1). Basin morphometry was determined from a number of 100 m line transects run perpendicular to shore. A dumpy level was used to measure elevations down the gradient in all basins except Hacks Lagoon where the minimum recorded water level (47.6 mAHD) was taken as the basin bottom. Transects within each of the other basins were combined to provide a rough estimate of basin morphometry. The most rapid changes in elevation occurred close to shore, with only minimal changes in elevation noted in transects between 80 and 100 m from shore. The minimum elevation measured within each basin was taken as the bottom-of-basin elevation.

Hacks Lagoon appears to be much shallower than other basins in having a maximum depth of inundation of only 160 cm and actually drying out completely (Figure 3.3.1). This annual pattern is true of the 47.6 mAHD gradient position only. The actual basin bottom is almost certainly lower than this and so would be inundated to depths greater than 160 cm and never dry out.

The Main Basin of Bool Lagoon is deeply inundated, reaching a maximum depth of 210 cm on average less than two days per year (Figure 3.3.2). The Central Basin is

slightly shallower than the Main Basin, seldom reaching depths over 190 cm and spending some 85 days at depths less than 100 cm (Figure 3.3.3). The maximum depth attained in the Western Basin is 180 cm (Figure 3.3.4). Approximately 139 days per year are spent between 70 and 100 cm depth.

Each flooding pattern histogram shows a distinctly bimodal distribution. In general, there is a deeper range of depths to which the basin is inundated more frequently than other depth classes (e.g. Central Basin 145–165 cm; Figure 3.3.3). This corresponds to the most frequent filled depth of the basin after winter rain in August/September each year. A range of shallower depth classes (e.g. Central Basin 90–125 cm) is similarly frequent and may correspond to groundwater infiltration over summer. The interim depth classes (e.g. Central Basin 130–145 cm) are less frequent because they are only experienced briefly during rapid filling or drawdown.

Simple subtraction of time values in each depth class from those in the same depth class of a different basin provides a clear indication of the ways in which flooding patterns vary between basins. Deviation away from zero indicates either more ( $>0$ ) or less ( $<0$ ) time (in days) spent at a particular depth class. Such a pairwise comparison of basin histograms (Figure 3.4) indicates a gradation in water depth and permanency from the Main Basin (deepest) to Western Basin (shallowest). The major differences between basin filling patterns occur where the bimodal histograms do not overlap as they are translated sideways to shallower depth classes. Thus the Main Basin differs from the Central Basin in spending more time in depth classes greater than 170 cm (Figure 3.4.1). The difference is even more pronounced when comparing the Western Basin with the Main Basin (Figure 3.4.2) and Central Basin (Figure 3.4.3).

### 3.3.2 Classification of Flooding Patterns

Eight distinct groupings (regimes) were identified from the dendrogram produced from multivariate clustering of flooding frequencies of individual gradient positions (Figure 3.5). The regimes represented a gradient from permanently deep water (regime 1) to shallow and infrequent inundation (regime 8) and each defined a particular numerically-distinct flooding pattern. These definitions are based on arithmetic averages of the time spent

in each depth class for each location within a dendrogram group. Locations grouped within a single regime grouping would therefore not necessarily show identical flooding patterns, but would share depth classes in common and have similar time scores for each depth class. Figure 3.6 shows the histogram of each regime definition together with the standard deviation associated with the mean time score for each depth class, and indicates the degree of variability associated with each regime definition. The following descriptions of water regimes refer to these mean histograms.

Regime 1 is the deepest of the eight regimes, reaching a maximum depth of 210 cm, and never drying out during the year. The most frequent depth classes in this regime occur between 100 and 160 cm depth ( $20 \pm 5$  days per year). Regime 1 was only found at the bottom of the the Main and Central Basins. Regimes 2 and 3 are generally shallower with a maximum depth of only 190 and 170 cm respectively. Other depth classes are again represented with a frequency of between 20 and 30 days per year. These regimes are represented in all basins of Bool Lagoon except Hacks Lagoon. With <1, 2, 43, 180 and 340 days per year dry respectively, regimes 4, 5, 6, 7 and 8 represent zones along the gradient of increasing drying frequency and decreasing depth of inundation, with maximum inundation levels of 150 cm, 130 cm, 110 cm, 100 cm and 50 cm respectively. These regimes are found in each basin.

Each dendrogram group (regime) comprises a number of gradient positions in each basin whose flooding characteristics were numerically distinguishable from those of other basin/gradient position combinations, but closely resembled those of gradient positions within the same dendrogram group. These similar positions are found in nearly all of the Bool Lagoon basins, and so it is then possible to locate gradient positions in different basins which experience the same flooding pattern. The significance of the water regime classification lies in the ability (to use scant data) to integrate time and space across swamps, and ultimately to map the distribution of distinct flooding patterns. Such a mapping may be represented as a thematic map of bands spanning from the perimeter to centre of a swamp, or alternatively as a transverse section through the swamp. The latter method has been chosen to represent the water regimes of Bool Lagoon because of the complexity of the perimeter.

The relationship between flooding pattern and elevation is not the same in each basin—gradient positions which share the same flooding pattern may not have the same elevation (Figure 3.7). For example, in Hacks Lagoon and the Main Basin the flooding pattern at 48.88 mAHD is described by regime 5 (4 days dry, max. depth of inundation 130 cm), while the same elevation in the Central and Western Basins is described by regime 6 (44 days dry, max. depth of inundation 110 cm). These flooding patterns are markedly different and great care must be taken when locating sites for ecological sampling which rely on equality of flooding patterns.

The highest elevation of each basin shown in Figure 3.7 indicates the measured highest water level recorded during the sampling period 1985–1992. Hacks Lagoon had the highest water level of all basins but not necessarily the greatest water depth (see section 3.2.2 for terminology). The elevation of the basin bottom was estimated from water level records rather than from topographic survey. It is highly likely that regimes 1–3 do exist in Hacks Lagoon, and indeed zones “wetter” than regime 1 may exist in all basins if the basin bottoms are lower than the surveyed estimates.

### 3.4 Discussion

Any study involving recorded water levels is reliant on the frequency and accuracy of readings. At Bool Lagoon, water level readings are taken from a marker post driven into the sediment in each of the basins. Unfortunately the posts are not positioned at the bottom of each basin, but are more strategically placed to facilitate their ease of reading from shore. During periods of extreme drawdown the level of the water surface can drop below the lowest reading on the depth post. This may be recorded as “dry” even though the basin itself is not dry and this can distort the interpretation of water level patterns. This particular problem is relatively infrequent at Bool Lagoon, but data collected from other South East swamps have displayed this feature, and together with very infrequent collection, have proved unsuitable for the application of this method.

A primary influence on plant performance in wetlands is water depth (Squires and van der Valk 1992) and elevation of the sediment surface is merely correlated with this

(1:1 correlation under static water level conditions). As water levels fluctuate elevation no longer reflects the absolute water depth and instead represents a unique pattern of fluctuation. Elevation has now become a complex variable, an integrator of many factors, and its representation as an explanatory variable neglects this new complexity. If there is a perceived change in vegetation response across a gradient, it can no longer be adequately explained in terms of elevation (*sensu* water depth) and should be explained instead by the pattern of seasonal flooding, or water regime. Logical groupings of positions along the gradient allows the transformation of the interval explanatory variable *elevation* into the ordinal variable *regime*. Such groupings are numerically derived and their ability to explain both the community and individual species response to inundation will be discussed in the next chapter.

The classification approach described herein was adopted specifically to allow objective definition of zones which were useful for, say, stratified sampling regimes and which could be mapped readily for comparisons of variation between wetlands and between years (e.g. see Figures 3.7 and 3.8). Given that these zones represent nodes along the gradient of elevation (and, less precisely, along some gradient of flooding frequency), ordination could be useful as an alternate analytical pathway. In the case of the Bool Lagoon dataset, the solution lies in a one- or two-dimensional ordination (eigenvalues DCA Axis I: 0.55; DCA Axis II: 0.07), since the waterbodies in the four basins are physically linked except when the water level is very low. However, if additional wetlands with very different cycles of flooding and drying were added, the dimensionality of the ordination would increase, thus making presentation of inter-wetland and interannual variability more difficult. These problems may be compounded by ordination axis distortions such as the “horseshoe effect” on some long secondary axes (e.g. Gauch 1982; Austin and Noy-Meir 1971). Thus classification may be a more practical approach when comparing a diversity of wetland types, just as it proved to be with the vegetation data from many wetlands in Chapter 2. Further work is required to assess the relative merits of classification and ordination of water regime datasets of different spatial and temporal complexities.

The bulk of literature on the influence of water depth on the performance of aquatic macrophytes has emanated from the temperate climates of Europe and North America

where the amplitude of seasonal fluctuations is minimal, when compared to more semi-arid regions. It is hardly surprising that elevation has been used so widely as a description of plant niche—in systems of static water levels elevation can be used successfully to explain species distributions. In semi-arid regions however, the dynamic nature of the water level precludes this approach. The water regime classifications presented here not only represent the annual flooding pattern of different gradient positions in terms of days per year at each depth class, but also may be interpreted in terms of a probability distribution of a gradient position being inundated to a particular depth at some stage during the year. A comparison of spatially disparate locations based on such probabilities is the major advantage of the water regime concept over that of simple elevation, as well as the ability to relate flooding pattern to other environmental gradients (Rørslett 1984). For the reasons outlined above, comparison on the basis of elevation is not adequate, and so a relatively small sacrifice in resolution is necessary to achieve the more desirable ability to compare the flooding patterns of different locations.

An extension of the regime classification method could include the rate of change of water level i.e. in addition to the time spent in each depth class, the classification would also consider the rate and direction of change of the water level whilst in each depth class. This would distinguish between locations which experienced rapid changes in water level such as might be experienced during the onset of winter rains (high +ve rate) or the opening of a regulator gate to facilitate drainage (high -ve rate). These would contrast with the more usual effects of gradual filling during winter (low +ve rate) and evaporation over summer (low -ve rate). Similarly the timing of water level changes could be incorporated to distinguish between sites which begin to flood in September (say) from those which flood in November. This would involve the division of the year into equal intervals (monthly, weekly or daily) which would form a separate axis for the multivariate clustering.

Application of these extensions to Bool Lagoon was considered potentially too misleading—the individual depth class rates and times would have been severely influenced by the linear interpolation, particularly when relatively long periods existed between sampled data points.

### 3.4.1 Interannual variability

The eight regime definitions represent the average flooding pattern over the eight years of sampling. However, the actual flooding pattern experienced by a gradient position is unlikely to correspond exactly with the pattern predicted by its regime type.

The magnitude of this interannual variability can be quantified by using water level data from separate years to describe dendrogram groups whose members represented location, elevation and year. For Bool Lagoon the water level data for the eight years of sampling were divided into eight 12-month periods (May–May each year). Seven types of annual flooding pattern (A–G) were identified from the dendrogram and a summary of the spatial and temporal distribution of these in each of the Bool Lagoon basins is presented in Figure 3.8, with the regime boundaries overlaid for comparison.

The seven flooding pattern types fell into two distinct categories, based on the shape of their histograms. Groups A, C and E (Figure 3.9) showed bimodal distribution of time spent in each depth class and represented patterns which included rapid water level changes (the trough between the two mode peaks). Groups B, D and F showed a single-peak histogram indicating a much slower rate of filling or drawdown. In addition, the time spent in depth classes was generally higher in these slower-rate patterns, especially groups B and D where 25–50 days was spent in most depth classes. Group G could perhaps also be classed as a slow-rate pattern, but the large number of days spent dry (325) may have precluded the detection of any rapid filling to its maximum class.

The physical positions of these annual flooding patterns are shown in Figure 3.8. The rapid patterns A, C and E were restricted to the lower elevations present within each basin which were subject to rapid depth increases during winter and spring. The slow patterns B, D, F and G were found progressively higher on the elevation gradient and would not have become inundated until later in the season when the rate of water depth increase had slowed.

There is an important distinction between the way in which the annual patterns have been derived compared to the overall regime definitions. Water regimes were defined for all gradient positions from the measured bottom of each basin to the measured highest water mark. The annual patterns were defined for gradient positions from the measured

lowest water mark in each basin to the highest water mark. Hence Figure 3.8 shows regime 5 (Figures 3.8.2 and 3.8.3) and regime 6 (Figure 3.8.4) as being open-ended, that is, the lower boundary of the regime is lower in elevation than can be displayed on the y-axis of the plots. This also explains why the deepest depth class present in any of the annual patterns (160 cm, Group A) is some 50 cm lower than the deepest depth class present in regime 1 (210 cm)—they have different baselines.

The regime definition describes the probability of the time and depth of inundation in any one year, and differs somewhat from the actual patterns experienced from year to year. e.g. 48.1 mAHD in the Western Basin has an overall flooding pattern described by regime 7, but its annual patterns vary (Figure 3.8.4). The actual patterns however are only descriptive and have no probabilistic component, and thus cannot be used in any predictive sense. The interesting biological question remains as to whether species respond to the annual flooding pattern, or the mean pattern described by the water regime (see Chapter 4).

The annual patterns are defined for regions of the elevation gradient which (at least in some years) become exposed during drawdown. The degree of interannual variability in flooding pattern reflects the fact that the Lagoon was never allowed to dry out completely between 1985 and 1992. The boundaries between annual pattern types from year to year only differ (in spatial terms) by fewer than 20 cm in elevation, and while this may translate to a much broader band on the ground, the degree of variability of flooding pattern is considerably less than might be expected in a Mediterranean wetland.

The true scale of interannual variability in flooding pattern possible at Bool Lagoon is clear from an examination of 1992–1994 water level records (Figure 3.10). In 1993 a management decision was taken to allow the Lagoon to dry out over summer in an attempt to stimulate the regeneration of *Melaleuca halmaturorum* trees whose seedling recruitment had been adversely affected by virtually constant inundation (B. Clarke, pers. comm.; Denton and Ganf 1994). The characteristic annual water level peak in winter was reduced in 1993 (Figure 3.10) and absent in 1994. During the long periods of drawdown between 1993 and 1994, the elevation of the water surface fell below that of the depth gauge, and the basins were recorded as being 'dry'. This accounts for the long periods between measured water levels.

The flooding patterns during this imposed drawdown were unlike any others recorded in the previous eight years, but they were more typical of the flooding patterns which might be experienced by a semi-arid wetland. If these more 'natural' flooding cycles were allowed to occur at Bool Lagoon, the degree of interannual variability would increase enormously and diagrams of the type shown in Figure 3.8 would show much greater vertical displacement from year to year of the boundaries between distinct flooding patterns.

However, these drier years occurred outside the period of this study. The eight years of water level records from 1985–1992 set the scale on which interannual variation in water level might be expected to occur under a similar management policy, and more pragmatically, the context in which current patterns of Bool Lagoon vegetation will be interpreted in subsequent chapters.

# Chapter 4

## Production and demography of *Phragmites* and *Typha*

### 4.1 Introduction

Freshwater wetlands have been shown to be one of the most productive ecosystems (Westlake 1963) and since the 1960s and 1970s when the International Biological Programme (IBP) tried to quantify productivity in the economically important Central European fishponds (Dykyjová and Květ 1978), many estimates of the productivity of aquatic macrophytes have been made (e.g. Westlake 1963, 1975; Bradbury and Grace 1983; Spence et al. 1971). However, the majority have emanated from the Northern Hemisphere and there remain few studies on the productivity of inland aquatic macrophytes from Australia, with the work of Briggs and Maher (1985) and Brock (1982) on submerged macrophytes and Roberts and Ganf (1986) on *Typha* and Hocking (1989a, 1989b) on *Phragmites* being notable exceptions.

Water level fluctuation is an important and common feature of many Australian wetlands, but the effect on aquatic macrophyte productivity is largely unknown. One of the few accounts is provided by Froend et al. (1993) who noted that even within a population or single stand, there can be considerable variation in the productivity and reproductive phenology of aquatic macrophyte species in wetlands which experience fluctuating water levels.

This has implications for whole system productivity estimates where production rates based on small samples in macrophyte stands may be scaled up according to the area occupied by the stand. If productivity is related to flooding frequency, then the position of the initial samples would severely influence estimates of the system's productivity by either under- or over-estimating it. This, together with the enhanced productivity noted in emergent macrophyte species in Australia (Roberts and Ganf 1986; Hocking 1989a, 1989b), warrants a closer examination of the production characteristics of aquatic macrophytes in Australian wetlands, and their relationship to water regime.

The aim of this study was to quantify and describe the production and demographic characteristics of the emergent macrophytes *Typha domingensis* and *Phragmites australis* at Bool Lagoon and to determine the influence of flooding frequency on their production and demography.

## 4.2 Methods

A series of permanent 50 × 50 cm quadrats was placed in stands of monodominant *Phragmites* and *Typha* around the perimeter of Bool Lagoon. Quadrats were placed within stands of each species at specific elevations which corresponded, where possible, to the midpoint of the elevation range for each of five water regimes (4–8) defined in Chapter 3. No stand of either species grew continuously from the margin to the centre of a basin, so stands were chosen at several locations, but at different elevations, in order to sample the full elevation gradient (Figure 4.1). Suitable stands of *Phragmites* and *Typha* were not found growing in regimes 1–3, hence these were excluded from sampling.

At least four quadrats were placed within each regime sampling zone and were marked with a metal fence post (“star dropper”) and individual shoots within each quadrat were labelled with a Code 39 barcode tag. This allowed the ready identification of shoots during subsequent visits and the detection of newly recruited shoots or leaves. All field data were recorded with a Psion LZ-64 Organiser II data logger to which was attached a barcode wand. Permanent quadrats were set up in summer 1990 and were monitored at 6–8 week intervals until winter 1992.

For *Phragmites*, the height of each shoot (culm) within a quadrat was measured from ground level to the tip of the apical meristem, together with the number of leaves present on the shoot. Any lateral branches present on the shoot (produced in response to damage of the primary stem) and leaves on these branches were ignored during the measurement of shoot length and leaf number. Such shoots were noted as having been broken. For *Typha*, the total length of each leaf on each shoot was measured, as was its photosynthetic length (indicated by the presence of chlorophyll). The second youngest leaf was tagged on each shoot to allow the detection of leaf recruitment during subsequent visits.

Because of the restricted size of many stands destructive harvesting of material from sacrificial quadrats during the course of the sampling was considered to be too disturbing for the permanent quadrats. Therefore indirect estimates of standing biomass were made from predictive equations derived by linear regression relating measurements of plant parts to biomass (Kauppi et al. 1983).

For *Phragmites* in inland Australia, a relationship between shoot (culm) height ( $x$ ) and dry weight biomass ( $y$ ) has been provided by Hocking (1989a) and is of the form:

$$y = a + be^{-kx} \quad (4.1)$$

where  $a = -14.52$ ,  $b = 14.52$ ,  $e^k = 1.01$ .

However, these parameters do *not* describe the line presented by Hocking (1989a) as Figure 3. The line described by these parameter values is shown in Figure 4.2, together with a close approximation of the line originally presented by Hocking as Figure 3. The parameters have been estimated by non-linear fitting from points estimated to lie on the line of Hocking's Figure 3. In this study, biomass of *Phragmites* in permanent quadrats was indirectly estimated using Equation 4.1, using the derived parameter values  $a = -17.20$ ,  $b=16.59$ ,  $e^k=1.004$ . Maximum shoot height encountered during sampling was 305 cm, well within the range of lengths used by Hocking (1989a) to derive his equation. Shoot height and biomass data derived from a previous study at Bool Lagoon (Brownlow 1988) were overlaid for comparison (Figure 4.2) to ensure that the predicted biomass was reasonable for *Phragmites* growing at Bool Lagoon.

For *Typha*, harvests were made during the first summer in different stands chosen as having plants with a range of leaf lengths similar to the plants in permanent quadrats. A predictive equation was developed from these harvests relating biomass to leaf length (Figure 4.3).

Three estimates of production were made and were calculated in the following way:

**Maximum dry weight per shoot.** Leaves were the measured units in *Typha* and the sum of the estimated dry weight biomass of individual leaves at each sampling period was taken as the standing crop per shoot. For *Phragmites*, the shoot was the measured unit and there was no need to calculate the sum of individual plant parts per shoot. The maximum standing crop during the growing season was calculated for each shoot for each species across the water regimes.

**Above-ground standing crop.** This was estimated as the sum of indirect biomass estimates for all shoots (*Phragmites*) or leaves (*Typha*) within each quadrat. These values were scaled ( $\times 4$ ) to give a standing crop estimate in grams per square metre. AG standing crop was calculated at each sample period.

**Net annual primary productivity (NAPP).** This attempted to account for losses associated with plant growth which would not be accounted for by final AG standing crop estimates. The maximum measured height attained by a shoot or leaf during the growing season was used to estimate its maximum biomass, prior to any senescence, breakage or other loss. This was calculated for all shoots (*Phragmites*) and leaves (*Typha*) which appeared in quadrats during sampling, regardless of whether they remained at the end of the growing season. The sum of these biomass estimates was calculated per quadrat and scaled ( $\times 4$ ) to give a biomass estimate in grams per square metre per year.

Calculation of NAPP was restricted to the 1991–92 growing season. The first growing season was considered unsuitable for this calculation because sampling did not commence until well into summer and there was the possibility that shoots present only in spring may not have been accounted for.

Dickerman et al. (1986) have reviewed the efficacy of various methods for using changes in plant biomass to estimate above-ground production in *Typha*. The method used here is most similar to their standard “summed shoot maximum” method but differs by considering the shoot as merely the sum of its leaves and uses the relationship between leaf length and biomass to calculate whole shoot biomass. Because every leaf is accounted for and its maximum length known, the chances of underestimating production through unaccounted leaf loss is greatly reduced.

Comparisons of the density of shoots, the length of leaves and stems, and estimates of primary production were made between quadrats in different water regimes. Within each sampling period, one-way Analysis of Variance (ANOVA) was used to test whether differences existed between regimes with respect to the parameter under consideration. Tukey’s Honestly Significant Difference (HSD) test was used as a *post hoc* means of pair-wise comparison.

## 4.3 Results

The quadrats containing sampled plants have been grouped according to their elevation, and consequently flooding frequency described by the water regime (outlined in Chapter 3) on the basis of the flooding patterns of the previous eight years (1985–1992). These quadrat groupings form the basis for comparison among the samples.

### 4.3.1 *Phragmites australis*

#### 4.3.1.1 Shoot density

Sampling commenced in December 1990 in regimes 6, 7 and 8 and in February 1991 in regime 4. During this time, recruitment of new shoots (equal to single stems or culms) was still ongoing for *Phragmites*, with mean shoot density increasing from approximately 49–55 shoots  $\text{m}^{-2}$  in December 1990 to 62–122 shoots  $\text{m}^{-2}$  in February 1991 (Figure 4.4). For plants growing low on the elevation gradient whose flooding pattern was described by regime 4, this shoot recruitment continued until April 1991. Thereafter, shoot senescence lead to decreased live shoot densities for these deeper plants, while those growing in

regimes 6, 7 and 8 suffered either a reduced decrease or no decrease in mean shoot density until June 1991. Only in August 1991 were live shoot densities reduced to zero for all water regimes (Figure 4.4) consistent with the seasonal die-back associated with *Phragmites* stands.

The recruitment of new *Phragmites* shoots was completed by November 1991 in regimes 7 and 8, but continued until February 1992 in regimes 4 and 6 (Figure 4.4). No live shoots remained by June 1992 at the end of sampling.

There was a reversal of shoot density pattern related to water regime between 1991 and 1992. In 1991, regimes 4 and 6 had higher shoot densities than regimes 7 and 8. However, in 1992, the pattern was reversed and regimes 7 and 8 had higher shoot densities than regimes 4 and 6.

These snap-shot views of plant density neglect the *total* production of shoots during the growing season i.e. cumulative shoot number over time. For *Phragmites* the mean ranged from 94 to 136 shoots per square metre (Table 4.1) but no significant difference was found across water regimes ( $F=0.60$ ,  $df=3,14$ ,  $P=0.63$ ).

#### 4.3.1.2 Stem length

Mean stem lengths of *Phragmites* during the first growing season were already high at the beginning of sampling (96–188 cm in December 1990; Figure 4.5). These did not increase appreciably during the next six months until winter when live stem length was reduced to zero during die-back. The slight increase in mean stem length during this period was most likely due to the recruitment and subsequent growth of new shoots. Plants growing under shallower conditions in regimes 7 and 8 were significantly taller than plants growing in regimes 4 and 6 throughout the first growing season ( $F=144.8$ ,  $df=3,360$ ,  $P<0.0001$  in February 1991;  $F=133.8$ ,  $df=3,381$ ,  $P<0.0001$  in April 1991;  $F=93.2$ ,  $df=3,315$ ,  $P<0.0001$  in June 1991).

During the second season of growth, stem lengths in regimes 7 and 8 were again significantly higher than in regimes 4 and 6 (Figure 4.5;  $F=21.25$ ,  $df=3,334$ ,  $P<0.0001$  in November 1991;  $F=27.56$ ,  $df=3,340$ ,  $P<0.0001$  in January 1992;  $F=56.87$ ,  $df=3,331$ ,  $P<0.0001$  in February 1992;  $F=95.04$ ,  $df=3,293$ ,  $P<0.0001$  in April 1992). Mean stem

lengths increased slightly from November 1991 to April 1992 in all regimes except regime 4 which showed decreases in mean stem length after January 1992.

#### 4.3.1.3 Leaf number

The number of leaves per shoot followed the same seasonal pattern as both stem density and stem length (Figure 4.6). Leaf numbers were variable throughout the first season of growth, ranging from a mean of 4–10 leaves per shoot in December 1990 and 6–9 leaves per shoot in February 1991. Leaf numbers decreased until the winter die-back in June for all plants in all water regimes except regime 4, which showed definite leaf recruitment in April 1991. This was caused by new shoot recruitment and consequent leaf production during the same period (Figure 4.4).

#### 4.3.1.4 Flowering

Flowering culms were present from February 1991 onwards in the first growing season (Figure 4.7) and were most frequent ( $>20$  flowering culms  $m^{-2}$ ) in regimes 6 and 7 (shallower). No plants flowered in regime 5 during the first year and no live flowering culms remained in any water regime by August 1991.

There was rapid production of inflorescences in the second growing season with most floral emergence taking place in January 1992 (Figure 4.7). Flowering took place in all water regimes and was complete by June 1992. The density of flowering culms did not differ significantly across water regimes.

#### 4.3.1.5 Maximum dry weight per shoot

*Phragmites* shoots in regimes 7 and 8 were significantly heavier than in other regimes ( $F=71.15$ ,  $df=3,501$ ,  $P<0.0001$ ) in the second growing season (August 1991–June 1992) with mean maximum dry weight per shoot values of 17.8 g and 17.2 g for regimes 7 and 8 respectively (Table 4.1) compared with values of 9.0 g and 12.9 g for regimes 4 and 6.

#### 4.3.1.6 Above-ground live production

Figure 4.8 shows the net changes in standing above-ground (AG) live biomass of quadrats in each of the four water regimes in which *Phragmites* was sampled. In both growing seasons there was a clear seasonal pattern of high standing crop over summer and autumn (January–April) and rapid decline to zero standing AG live biomass in winter (August 1991 and June 1992). Only in December 1990 did regime 6 show a significantly lower standing AG biomass ( $F=27.92$ ,  $df=2,11$ ,  $P<0.0001$ ) than other sites during the first growing season. There were no significant differences in standing AG biomass for any other regimes during the first growing season. A peak in standing AG biomass over summer was also seen in the second growing season (Figure 4.8), but the only significant differences occurred between plants growing in regime 4 (usually with the lowest mean standing AG biomass) and regime 7 (with consistently the highest mean standing AG biomass).

These instantaneous comparisons of AG live production neglect production across the whole growing season. There was however no significant difference in net above-ground primary productivity (NAPP) over the season, despite the higher per shoot biomass estimates in regimes 7 and 8 (Table 4.1). Furthermore, these did not differ from final live AG standing crop estimates, with the exception of regime 7 where NAPP was significantly higher ( $t = -2.75$ ,  $df=10$ ,  $P=0.02$ ). In most water regimes then, significant biomass losses were not associated with the growth of *Phragmites* and water regime did not affect the amount of biomass produced during the growing season.

### 4.3.2 *Typha domingensis*

#### 4.3.2.1 Shoot density

The sampling of *Typha* commenced in February and March 1991, when plants were at their maximum standing crop. Mean shoot densities of 25–50 shoots  $m^{-2}$  during the first four months of sampling either declined (regime 5) or remained stable (Figure 4.9). No live shoots remained by August 1991.

Shoot recruitment was delayed in regime 6 during the second growing season (Figure 4.9). Between November 1991 and January 1992 large numbers of shoots were re-

cruited in regime 5 (mean density = 50 shoots  $\text{m}^{-2}$ ) but density was reduced to 28 shoots  $\text{m}^{-2}$  because of the effects of grazing by swamp hens (*Porphyrio porphyrio* [Rallidae]). There were no significant differences in shoot densities among any of the sampled water regimes from January 1992 onwards.

The cumulative shoot number per square metre in the second growing season (August 1991–June 1992) in regime 5 (70 shoots  $\text{m}^{-2}$ ; Table 4.2) was significantly higher than in either regimes 4 or 7 (with 24.8 and 32.6 shoots  $\text{m}^{-2}$  respectively;  $F=8.29$ ,  $df=3,22$ ,  $P=0.0007$ ).

#### 4.3.2.2 Total leaf length

The photosynthetic length of each *Typha* leaf was summed to produce a total photosynthetic leaf length per shoot, as an estimate of the leaf production of the plants (Figure 4.10). All plants showed a decline in the amount of photosynthetic material until total die-back in August 1991. Plants growing at regime 4 maintained significantly higher levels of photosynthetic material than plants growing under shallower conditions ( $F=51.42$ ,  $df=2,104$ ,  $P<0.0001$  in February 1991;  $F=149.35$ ,  $df=3,184$ ,  $P<0.0001$  in April 1991;  $F=126.24$ ,  $df=3,158$ ,  $P<0.0001$  in June 1991).

This trend continued into the second growing season. Plants in regime 6 did not develop leaves until November 1991 and after reaching a maximum mean total photosynthetic length of 1258 cm in June 1992 (Figure 4.10) leaves were severely reduced by swamp hen grazing to a mean total photosynthetic length of <100 cm from February 1992 onwards.

#### 4.3.2.3 Leaf number per shoot

*Typha* plants had an average (depending on regime) of between four and nine live leaves per shoot in February 1991 (Figure 4.11). This increased slightly during March 1991 in regimes 4 and 7. All regimes showed a marked and seasonal decrease in the number of leaves per shoot until the winter minimum in August when no live leaves were present. Throughout the first growing season, plants growing in regime 4 had significantly more leaves than those growing in other conditions ( $F=40.16$ ,  $df=2,99$ ,  $P<0.0001$  in February

1991;  $F=96.09$ ,  $df=3,170$ ,  $P<0.0001$  in April 1991;  $F=23.0$ ,  $df=3,67$ ,  $P<0.0001$  in June 1991), except in June 1991 when there was no significant difference in leaf number between regimes 4 and 5.

By January 1992, the standing crop of *Typha* had between eight and 11 leaves per shoot. Leaf numbers declined thereafter as leaves senesced until the end of sampling. The rapid decrease in leaf number of plants in regime 6 in February 1992 was caused by swamp hen grazing.

#### 4.3.2.4 Flowering

With the exception of a single plant growing in regime 5 in the second growing season, all *Typha* plants which flowered grew in regime 7, both in Hacks Lagoon and the Central Basin (Figure 4.12). Flowering was completed by the time of winter die-back in August 1991 and commenced again in January 1992. There was only one flowering shoot per quadrat ( $\equiv 4$  shoots  $m^{-2}$ ) from January–April 1992, hence no error bars are shown.

#### 4.3.2.5 Maximum dry weight per shoot

*Typha* shoots in regime 4 (deepest) were significantly heavier than in other regimes during the second growing season ( $44.9$  g shoot $^{-1}$ ,  $F=7.63$ ,  $df=2,204$ ,  $P=0.0006$ ; Table 4.2). The very low per shoot biomass of plants in regime 6 ( $\bar{x}=2.58$  g) was an artefact of swamp hen grazing and these plants were excluded from formal comparisons.

#### 4.3.2.6 Above-ground live production

The standing above-ground (AG) live biomass of *Typha* also showed a distinct seasonal pattern with a summer maximum and winter minimum (Figure 4.13). The standing AG biomass of plants growing in deep water was consistently and significantly higher than in other locations throughout the first growing season ( $F=25.3$ ,  $df=2,9$ ,  $P=0.0002$  in February 1991;  $F=230.11$ ,  $df=3,20$ ,  $P<0.0001$  in April 1991;  $F=92.6$ ,  $df=3,19$ ,  $P<0.0001$  in June 1991). However, this pattern was not repeated in the second season where there were no significant differences in standing AG live biomass between regimes, with the exception of regime 5 which peaked in January 1992 with a mean standing AG biomass of  $1333$  g D.Wt  $m^{-2}$ .

Table 4.2 shows that there were losses associated with plant growth which were not accounted for by an examination of the standing AG biomass prior to the winter die-back. In regimes 5 and 7, these losses made the NAPP estimates for quadrats significantly higher than the final biomass estimate ( $t=-2.46$ ,  $df=6$ ,  $P=0.05$  and  $t=-2.61$ ,  $df=24$ ,  $P=0.02$  for regimes 5 and 7 respectively). Comparison across water regimes showed that NAPP estimates ranged between 1040 and 1944  $\text{g m}^{-2} \text{ yr}^{-1}$  but were not significantly different (excluding the grazed plants in regime 6).

### 4.3.3 Net annual primary productivity across water regimes

Net annual primary productivity (NAPP) was not significantly different between water regimes for either species, but the expression of biomass was very different, especially for *Typha*. In regime 4 (deepest) the average per shoot weight of *Typha* was highest (44.9 g; Table 4.2) but shoots were produced in their lowest numbers (24.8 shoots  $\text{m}^{-2}$ ). In contrast, there were more *Typha* shoots produced in regime 5 (70 shoots  $\text{m}^{-2}$ ) but they had the lowest average per shoot biomass (23.5 g). (Shoots in regime 7 were approximately median between these two extremes with low average per shoot biomass (24.3 g) but intermediate shoot numbers (32.6 shoots  $\text{m}^{-2}$ .) The effects of water regime on *Typha* shoots was not reflected in NAPP values, but *was* expressed in the demography of the plants and the characteristics of their shoots.

Average per shoot biomass values for *Phragmites* were significantly higher in regimes 7 and 8 and cumulative shoot number was not significantly different across regimes, but this did not translate into significant differences in NAPP. It is suggested that variation associated with mean cumulative shoot number estimates may be responsible for this lack of difference. In regimes 6–8, standard deviations of mean cumulative shoot number estimates were between 21% and 37% of the mean value (Table 4.1), and in regime 4 (the deepest) this value was nearly twice as large as the other estimates at 64%.

There was also a statistical problem with the NAPP comparisons across regimes—the power of the ANOVA was too low. Power analysis revealed that for  $P=0.05$ , the minimum sample size required to be able to detect a difference in NAPP of *Phragmites* was  $N=24$  (cf. 18 sampled here) and for *Typha*,  $N=27$  (cf. 26 sampled here).

Despite the difficulties with comparing NAPP values, it was clear that individual shoot characteristics were affected by water regime. The maximum dry weight biomass per shoot was attained at opposite ends of the flooding gradient for *Phragmites* and *Typha* (Tables 4.1 and 4.2). Mean dry weight biomass per shoot for *Phragmites* in regimes 7 and 8 (17.8 and 17.2 g yr<sup>-1</sup> respectively) was significantly higher than for other regimes (F=73.52, df=3,501, P<0.0001). In contrast, the highest mean dry weight biomass per shoot for *Typha* (44.9 g yr<sup>-1</sup>) was achieved in regime 4, which was higher than values in either regimes 5 or 7 (F=7.62, df=2,204, P=0.0006).

## 4.4 Discussion

The distribution of suitable stands of *Phragmites* and *Typha* was such that no single location encompassed the eight water regimes. In order to sample across the full elevation gradient, it was necessary to place quadrats at several locations around Bool Lagoon. Such confounding (Hurlbert 1984) was not ideal, because of the possibility that other, unmeasured, gradients may exist in addition to the sampled water regime gradient. It has already been shown that a gradient in sediment chemistry exists between the western and eastern sides of the Lagoon (see Chapter 1). Permanent quadrats were not placed at sites used for the Bool Lagoon vegetation survey (from where sediment chemical characteristics have been determined) and so it was not possible to specifically examine the role of sediment chemistry in the production patterns described here. However, all permanent quadrats were located on the eastern side of the Lagoon where between-site chemical differences were considerably less than those observed between western and eastern sides. This offers some assurance that the major environmental gradient sampled was indeed a flooding gradient.

Despite the seasonal nature of their growth, both *Phragmites* and *Typha* were shown to be extremely productive species, with a net annual primary productivity (NAPP) as high as 2072 g m<sup>-2</sup> yr<sup>-1</sup> and 1944 g m<sup>-2</sup> yr<sup>-1</sup> respectively (cf. fertilised maize field 1390 g m<sup>-2</sup> yr<sup>-1</sup>, Bray et al. 1959).

For *Typha*, this was in the upper range of published values of peak AG standing

crop (the method most commonly used as a measure of production) which ranged from  $44 \text{ g m}^{-2}$  (Poland, Szczepańska and Szczepański 1976) to  $2000 \text{ g m}^{-2}$  (United States, Davis and van der Valk 1983) (Table 4.3). The only estimate higher than these was for *Typha* growing in inland Australia (Roberts and Ganf 1986) with a peak AG standing crop of  $3277 \text{ g m}^{-2}$ . For *Phragmites*, the maximum value of NAPP at Bool Lagoon was  $2072 \text{ g m}^{-2}$  which was higher than European and North American estimates of peak standing crop, which ranged from  $447\text{--}1446 \text{ g m}^{-2}$  (Table 4.3) but much lower than Hocking's (1989a) estimate of  $9890 \text{ g m}^{-2}$  in inland Australia.

There are difficulties with comparing production estimates based on peak standing crop versus estimates of NAPP because of the potential of the former for underestimation of production. There may have been losses prior to peak standing crop, or unaccounted growth after peak standing crop is reached. For *Phragmites*, such unaccounted losses range from  $<10\%$  of peak standing crop (Ondok and Květ 1978) to  $14.6\%$  (Mason and Bryant 1975), but for *Typha*, Mason and Bryant (1975) found that NAPP was  $23\%$  higher than peak standing crop. Thus greater biomass losses would be expected with the growth of *Typha* compared with *Phragmites*. The standing crop and NAPP estimates for *Typha* presented in Table 4.2 show that only in regimes 5 and 7 was the final AG standing crop a significant underestimate of NAPP. For *Phragmites*, final AG standing crop only underestimated NAPP in regime 7. Therefore the possibility remains that NAPP could be underestimated in both species if final AG standing crops are used. However, this does not greatly influence the results of production comparisons—*Phragmites* and *Typha* were both extremely productive species whose productivity was greatest in inland Australia where daily irradiance, temperature and day length are all high (Roberts and Ganf 1986).

#### 4.4.1 Net annual primary productivity and water regime

The lack of difference in NAPP estimates, in contrast to individual shoot characteristics, may represent a form of trade-off by plants as they modify their growth form or other characteristics to maintain a positive carbon balance (Menges and Waller 1983). Thus fewer, longer shoots of *Typha* were produced in deep water compared with many shorter shoots in shallow water, but the NAPP over the growing season was the same in each

case. It may then be more appropriate to consider the effects of water regime on individual shoots, rather than on entire population parameters such as NAPP.

Marshall (1991) has suggested that ramets (*sensu* Harper 1977) may be self-sufficient for their carbon, water and nutrient needs under resource-rich conditions, and even under stressed conditions that carbon capture is largely the responsibility of individual ramets. Thus, even though the shoots in quadrats are the result of clonal growth and may be physically linked together, they may function largely as individuals. Exposure and inundation, and their myriad direct and indirect effects on plants (see Chapter 1) will therefore operate on individual shoots. It is the shoot which may be unable to photosynthesise when deeply flooded or die through desiccation when exposed. Thus the effects of water regime may be best observed at the scale at which it operates—the scale of the shoot.

For *Typha* especially, where the expression of biomass was very different across the elevation gradient, it is possible to speculate on which form of growth represented the “optimum” growth mode—many, shorter shoots, or fewer, longer shoots? De Kroon and Schieving (1991) suggest that clonal growth in *Typha* (and *Phragmites*) follows a “consolidation strategy” where runner length is relatively short and rhizome buds are numerous in order to promote local persistence of the clone. If this is the case, then the shallower water conditions in regimes 5–7 with higher shoot numbers per square metre, may be the preferred position of *Typha* plants, where rapid shoot recruitment and space pre-emption can also occur.

For comparative purposes with literature values, the maximum value of NAPP per square metre was used for both species. No differences were found in NAPP across water regimes for either species and this contrasts with the patterns of productivity noted by Froend and McComb (1994) for *Typha orientalis* and *Baumea articulata* [Cyperaceae] where AG productivity declined in both species at the extremes of a water depth gradient. The absence of fringing vegetation around Bool Lagoon may have prevented the shading effects proposed by Froend and McComb (1994) as an explanation for reduced productivity high on the elevation gradient.

The enhanced per shoot biomass of *Phragmites* in regimes 7 and 8 may have been caused by access to ground water. Adcock and Ganf (1994) have shown that the rhizome

system of *Phragmites* at Bool Lagoon can penetrate the soil to a depth of >96 cm and this may be sufficient to allow these plants access to the water table during summer. The shorter stems and slower rate of production in regimes 4 and 6 may have been caused simply by the presence of standing water, or the depth of water at a crucial time in the development of the annual population.

#### 4.4.2 Water regime versus actual flooding pattern

Thus far the production and demographic characteristics of *Phragmites* and *Typha* have been compared within a single growing season and differences in production characteristics have been shown to exist between plants growing in different water regimes. Were these patterns a function of the water regime as defined by flooding frequency from 1985–1992 (the strict numerical definition), or were these patterns a function of more recent flooding histories? If populations responded to the *average* conditions, similar demographic patterns would be expected from year to year (especially at Bool Lagoon where there is a concerted effort to regulate water levels to minimise interannual variation). Alternatively, if populations responded to more recent flooding patterns, then there would be the expectation that interannual variation in flood pattern would also lead to interannual variation in plant demography.

In order to explore these two possibilities, the flooding patterns in 1990, 1991 and 1992 were compared to determine the level of interannual variation to which the plants had been exposed. 1990 water levels were included because their effects (if any) on populations may have manifest themselves over summer 1990–1991 when sampling commenced.

Where possible, demographic characters of *Phragmites* and *Typha* were compared between years, and the timing of recruitment events specifically examined in 1991 and interpreted in terms of immediate past flooding history.

##### 4.4.2.1 Flooding history 1990–1992

Figure 4.14 shows the elevation of the water surface in the Main Basin of Bool Lagoon in 1990, 1991 and 1992. Also shown is the average water level from 1985–1992. The most significant difference in the flooding patterns is the timing and magnitude of the

spring peak in high water. In 1990 the peak water level ( $\approx 48.8$  mAHD) occurred in October, but in 1991 the water surface reached a maximum elevation of  $>49.0$  mAHD two months earlier in August. In 1992 the maximum level was only 48.9 mAHD and occurred in late September. A coarse description of these three years would describe 1990 as an 'average' year with a late spring water level peak, 1991 as a very wet year with early, rapid and deep flooding, and 1992 as a drier year with reduced water levels until the spring peak in October. The eight year average flooding pattern showed a peak in August of  $<47.7$  mAHD.

It was clear that there was considerable interannual variability in flooding pattern both in terms of the depth and duration of flooding, and that an eight year average was a misleading representation of the actual flooding pattern experienced by the plants from year to year.

It is suggested that the timing and amplitude of this spring peak in water level is a major determinant of the recruitment and growth characteristics of *Phragmites* and *Typha* populations.

#### 4.4.2.2 *Phragmites*

Ostendorp (1991) states that the first half of the growth period for *Phragmites* is fuelled solely by below-ground rhizome reserves which have stored assimilation products from the previous summer. Thereafter growth is maintained through photosynthesis and thus the production of leaves and the capture of light is critical for the successful ongoing development of shoots. The presence of deep water at the time of shoot emergence from the soil can delay the production of leaves and growth of the shoot can be impaired due to a shortage of reserves. In addition, extended periods of anaerobic metabolism in isolation from atmospheric oxygen leads to the production of toxic metabolites and the rapid consumption of glucose reserves—only 2 moles of ATP produced per mole of glucose under anaerobic conditions (cf. aerobic respiration in which 38 moles of ATP are produced) (Yamasaki and Tange 1981).

At the time of shoot emergence at the start of the second growing season (August–November 1991) the range of monthly mean water depths in regimes 4 and 6 was 1.0–1.3 m

and 0.8–1.0 m respectively (Figures 4.15.1 and 4.15.2). These are considerably higher than the monthly mean water depth ranges in regimes 7 and 8 which were 0.2–0.5 m and <0.1 m respectively (Figures 4.15.3 and 4.15.4). It is suggested that these deep water conditions at the time of shoot emergence severely and negatively affected the development of *Phragmites* shoots in regimes 4 and 6. This was manifested in both reduced stem height and lower standing AG live biomass when compared with plants growing in regimes 7 and 8. Furthermore, most new shoot recruitment in the second growing season was delayed in regime 4 until January 1992 when the water was approximately 70 cm deep (Figure 4.15.1). Such a delayed recruitment also delayed leaf production until February 1992 (Figure 4.6) thereby reducing the time available for the translocation of photosynthates to below-ground rhizomes in readiness for the next season's growth. Furthermore, oxygenation of rhizomes through convective flow (Armstrong and Armstrong 1991; Grosse et al. 1991) is not possible without leaves being in contact with the air. Delayed leaf production then compounded the problems experienced by *Phragmites* in trying to maintain aerobic respiration.

*Phragmites* growing in highly reducing sediments, characterised by high levels of organic decomposition, may suffer oxygen depletion in the rhizosphere due to the enormous oxygen demand of the microflora in the sediment. Rhizosphere oxygenation is the principal mechanism for liberating bound nutrients from anaerobic sediments and without such a mechanism, nutrients remain unavailable to the plant. Reduced redox potentials of the sediment have been implicated in the decline of *Phragmites* beds in northern Europe (Phillips et al. 1978; Krumscheid et al. 1989; den Hartog et al. 1989; Sukopp and Markstein 1989), as has mechanical damage by waves or floating algal mats (Klötzli 1971), grazing, reduced water quality, eutrophication and water level regulation. Thus, highly reducing sediments combined with deep water conditions would place *Phragmites* under severe stress.

Haslam (1971) has shown the functional relationship between basal diameter and final potential shoot height in *Phragmites*, where narrow rhizome buds must necessarily produce narrow and shorter shoots. There was a progressive and significant decrease in mean shoot basal diameter in *Phragmites* from regimes 8–6 (increased flooding depth and

duration;  $F=38.43$ ,  $df=3,782$ ,  $P<0.0001$ ), but plants growing in regime 4 had a mean basal diameter between those in regimes 7 and 8—they did not adhere to a trend of decreasing basal diameter with increased flooding frequency (Table 4.4).

Enhanced shoot density in these deeper regimes may be the result of the reduced presence of standing dead biomass observed in the field. Granéli (1989) observed increased shoot densities, and therefore increased shoot AG biomass in experimental plots where standing litter had been removed. In this case, while density increased in the absence of litter, standing biomass did not for the reasons suggested above. Also, Weisner and Strand (1996) noted that the horizontal spread of *Phragmites* rhizomes was reduced under deep water conditions, and they suggest that this is an adaptation to reduce oxygen transport distances within the rhizome. Such reduced horizontal rhizome spread would increase the density of rhizome buds and consequently increase shoot density.

Another consequence of reduced stem diameter was the ready breakage of stems in response to the movement of water and floating debris. The rapid decline in stem length noted from January 1992 onwards in regime 4 was caused by the breakage of long stems and hence their exclusion from the calculation of mean stem length. This might explain why the basal diameters of shoots in regime 4 did not fit the expected pattern. i.e. all the small shoots were broken, leaving only the large diameter survivors.

A notable aspect of the growth of *Phragmites* between 1991 and 1992 was the reversal of stem density trends between the two years (Figure 4.4). Changes in stem density between years must be caused by either reduced or enhanced rhizome bud production in the previous growing season. Thus the 1991 pattern of high shoot density in regimes 7 and 8 was a function of the 'average' flooding pattern in 1990 (Figure 4.14). The reduced shoot densities in these regimes in 1992 was most likely caused by the extremely wet year 1991 which flooded deeply early in the year, which may in turn have affected nutrient translocation to below-ground reserves and the production of rhizome buds.

#### 4.4.2.3 *Typha*

The differences in production characteristics of *Typha* between water regimes were much less pronounced than were found with *Phragmites*. Leaf production in *Typha* was greater

in plants growing in regime 4 with both more leaves per stem and longer leaves produced under deep water conditions. Standing AG live biomass was also higher, despite the lower density of shoots. This is consistent with a reallocation of resources in order to maintain a positive carbon balance. *Typha* leaves are highly cuticularised and have sunken stomata—both of these anatomical features suggest that the plant would be incapable of carbon uptake and photosynthesis underwater.

Only in regime 6 was there delayed emergence and elongation of *Typha* shoots in the second growing season. It is unlikely that this delay was caused by the 0.3–0.5 m mean monthly depth of standing water at the time of emergence of other shoots (August–November) (Figure 4.16.3) because plants inundated more deeply in regime 4 (mean monthly depth 0.9–1.2 m) were not affected in terms of shoot emergence or elongation.

It is suggested that some other site-specific effect may have caused this delayed emergence, such as grazing by swamp hens. This was previously suggested as a reason for the rapid drop in photosynthetic leaf length per shoot in February 1992. Given that the location of the regime 6 quadrats was on the northern side of Hacks Lagoon where swamp hens were repeatedly observed in the field, such damage by them could have prevented the detection of small, newly-emerged shoots until later in the growing season. Froend et al. (1993) have shown that water regime alone does not account for the production characteristics of *Typha orientalis* and *Baumea articulata* in south-west Western Australia and have demonstrated that the nutrient content and texture of the sediment can change both the production characteristics and reproductive phenology of aquatic macrophyte species. It is possible that the stands sampled in Hacks Lagoon may have been exposed to a different nutrient load than other stands because of their proximity to the site of water inflow at Mosquito Creek. Confirmation of this would require the determination of both water and sediment nutrient loads.

The flowering of *Typha* was restricted to regime 7. Plants growing in deeper water did not flower at all and this may have been caused by a shortage of resources which had been consumed to produce longer leaves under deep water conditions. *Typha* plants growing in regimes 4, 5 and 6 were restricted to clonal reproduction and this has implications for the long-term viability of stands along the elevation gradient. In the absence of regeneration

from seedlings, the maintenance of the stand is solely reliant on vegetative growth (Chick et al. 1983). Seed production, and hence contribution to the seed bank, was restricted to shallow near-shore locations. In the event of adult plant mortality in stands in regimes 4–7, only regime 7 plants could become re-established after disturbance through locally-dispersed seed germination and seedling establishment. This might explain why *Typha* is prevalent only on the margins of Bool Lagoon, and is present more sporadically in deeper water. These deep water stands may be the results of opportunistic colonisation by seed dispersal at a time of low water levels when conditions were favourable for germination and establishment. With the maintenance of higher water levels, the plants cannot colonise far beyond the periphery of the Lagoon and remnant patches in deeper water are restricted to vegetative growth.

#### 4.4.3 Comparison of species performance

Given that the amplitude of water level fluctuations at lower elevations is much greater than higher on the elevation gradient, *Typha* has the ability to react to changes in water level by modification of the length of leaves through basal meristem activity. Smith (1987) further suggests that the ability of different species of *Typha* to withstand fluctuations in water level may be enhanced by their ability to hybridise readily with other species. The shoot length of *Phragmites* is fixed by basal shoot diameter and it has no mechanism to respond to changing water levels in this way. This contrasting ‘rest or react’<sup>1</sup> response to fluctuating water levels has been demonstrated by Rea (1993) and Rea and Ganf (1994b) for *Baumea arthrophylla* [Cyperaceae] and *Triglochin procerum* [Juncaginaceae] at Bool Lagoon. The leaf turnover and elongation rates of *Triglochin* far exceeded those of *Baumea* and the former was rapidly able to accommodate increasing water levels and maintain sufficient biomass on or above the water surface to allow for aerobic respiration and photosynthesis. *Baumea* on the other hand was incapable of such rapid response and although it was able to reallocate resources from below-ground to increase stem length under deep water conditions, its slow turnover and production rates lead to increasingly patchy stands which were susceptible to invasion by other species. In terms of the ‘rest

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<sup>1</sup>A term coined by G.G. Ganf and K.F. Walker.

or react' response, *Phragmites* must rest, while *Typha* can react to fluctuations in water level.

The patterns of production noted here were significantly influenced by the annual flooding pattern experienced by the stand. Water regime not only influenced the estimates of dry weight biomass of shoots of *Phragmites* and *Typha*, but also the ways in which the production was expressed. Thus accurate production estimates in temperate and semi-arid wetland systems should consider not only the demography and reproductive phenology of aquatic macrophyte species but also the seasonal pattern of water level fluctuation experienced by the plants.

# Chapter 5

## Species distribution across the elevation gradient

### 5.1 Introduction

The wetland resources of the South East of South Australia have been severely reduced during European settlement such that only 8% of former wetlands remain intact (South Eastern Wetlands Committee 1984). While these remnants are considered to be of great conservation value, many remain part of the network of drains which traverse the South East landscape and are, to different degrees, subject to manipulation of their natural water levels. While this practice is often used purely for flood mitigation, there is the potential at least for this manipulation to be used as a wildlife management tool. However, little information is available on the relationship between wetland plant community composition and flooding frequency. Any manipulations must therefore be 'hit-and-miss' affairs with only anecdotal evidence to suggest what the outcomes may be.

Of the 11 wetlands sampled in the South East, Bool Lagoon has been shown to be the most diverse wetland in terms of the number of distinct vegetation associations. In addition to its diversity, it also has the most complete set of water level records of any of the sampled wetlands. It is therefore uniquely placed to assist in the understanding of the relationship between flooding frequency and community composition in the South East.

Can a relationship between vegetation type and flooding frequency at Bool Lagoon be used in a predictive sense to aid in the management of other wetlands? For example,

it may be desirable to try to rehabilitate a degraded aquatic herbland (say) in a wetland. Apart from vague notions of “shallow water” there is however little guidance available to the wildlife manager charged with the task of manipulating water levels to achieve this desirable end. If a similar community can be found at Bool Lagoon and its annual flooding pattern quantified, the quantified pattern may be used as a guide for the imposition of a flooding regime in the other wetland.

This chapter examines the proposition that Bool Lagoon can be used in this way to aid in the active management of other wetlands.

Three species have been chosen for special consideration—*Baumea arthrophylla* (Nees) Boeckeler [Cyperaceae], *Triglochin procerum* R.Br. [Juncaginaceae] and *Myriophyllum salsugineum* Orch. [Haloragaceae]. *Baumea* and *Triglochin* have been shown to respond differently to changes in flooding frequency at Bool Lagoon (Rea and Ganf, 1994) and field observations indicate that *Myriophyllum* may also respond to such changes. All are dominant species at Bool Lagoon and are also major components of five of the species associations identified across the 11 South East wetlands considered in Chapter 2 (see p 42 and Appendix C). Morphologically the species differ considerably, and they were considered to represent a range of plant strategies, life forms and life histories. Each has the potential to form virtually monospecific stands and for this reason their individual distribution patterns, rather than their combination into communities, are considered in this chapter.

## 5.2 Single gradient modelling

While aquatic macrophyte species will respond to many environmental gradients, it is the depth and duration of flooding which will have the most immediate impact on their survival and distribution. Crawford (1996) summarises some of the changes to plant function brought about by flooding, which range from the deprivation of oxygen to plant organs and subsequent anoxic injury under flooded conditions to post-anoxic injury such as damage to cell membranes. These stresses will increase with increased depth or duration of flooding and as flood water recedes and exposes plants to the air, these will be replaced

by exposure-related stresses such as desiccation. In a wetland system whose water levels fluctuate, the magnitude of these physiological stresses is related to the elevation at which the plant grows. Thus this complex gradient of physiological stress may be neatly summarised by a single environmental variable. While elevation *per se* has no impact on the growth of aquatic macrophytes, its ability to integrate the physiological impacts experienced by plants growing in the presence of standing water enables it to be considered as a major environmental gradient in wetland systems. This is true only within a wetland (or basin) where there is a perfect monotonic relationship between elevation and flooding cycle. Elevation alone does not indicate flooding pattern because of the different filling and drying characteristics of different wetlands (or basins).<sup>1</sup> The basins of Bool Lagoon are therefore treated separately here.

The description and quantification of the distribution of species across environmental gradients is a core feature of plant ecology. Since Gause (1930) and Ramensky (1930), the symmetric bell-shaped curve (or *Gaussian* curve) has been used as a convenient and intuitively appealing model for the distribution of species across gradients. From this type of curve, the ecologically meaningful parameters of optimum and tolerance can be estimated. Such direct gradient analysis (DGA) may be used to study the distribution of species along recognised and easily measured environmental gradients (Gauch 1982; Whittaker 1967, 1978), but this, of course, requires the determination of the important environmental gradient. Gauch (1982) suggests that this is a distinct problem with DGA because of the potential difficulty of defining important environmental factors. Ter Braak and Looman (1986) suggest the possibility of confounding variables which could show a relationship with the environmental gradient under consideration and distort the pattern observed along the primary gradient. These concerns though are *caveats* to the interpretation of the results of DGA. Gauch (1982) considers DGA to be an important member of the “methodological triad” of multivariate analysis (together with classification and ordination) and that its simplicity belies its utility.

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<sup>1</sup>See also Chapter 3, especially Section 3.4.

## 5.3 Methods and Results

### 5.3.1 Model fitting and calculation of optima

The vegetation data collected during the survey of Bool Lagoon were used to model the distribution of *Baumea*, *Triglochin* and *Myriophyllum*. Species abundance data were calculated as the sum of presence/absence scores in 20 contiguous 50 × 50 cm quadrats placed along the elevation gradient at 36 locations around the perimeter of the Lagoon (Figure 1.2). Species presence could therefore be described on a 0–20 scale, or a binary scale depending on the quadrat size considered. Because of the potential difficulty of dealing with essentially right-censored data (maximum abundance = 20/20) a binary response model was chosen.

A Gaussian logit curve (Cox 1970; ter Braak and Looman 1986) was used to model these binary data in which the logit transform of probability of occurrence of a species,  $P$ , is a quadratic function of some environmental variable,  $x$ , under consideration:

$$\text{logit } P(x) = \log_e \frac{P(x)}{1 - P(x)} = b_0 + b_1x + b_2x^2 \quad (5.1)$$

which can be reformulated as:

$$\text{logit } P(x) = a - \frac{\frac{1}{2}(x - u)^2}{t^2} \quad (5.2)$$

$$\text{with } u = \frac{-b_1}{2b_2} \quad (5.3)$$

$$t = \frac{1}{\sqrt{-2b_2}} \quad (5.4)$$

$$a = e^{b_0 + b_1u + b_2u^2} \quad (5.5)$$

where  $u$  is the species' *optimum*, or indicator value,  $t$  is its tolerance and  $a$  is the species' maximum abundance.

Logistic regression was implemented in the JMP package (Anon. 1996) to estimate parameters  $b_0$ ,  $b_1$  and  $b_2$  in equation 5.1 and from these, estimates of optimum, tolerance

and maximum were made for *Baumea*, *Triglochin* and *Myriophyllum* using Equations 5.3, 5.4 and 5.5. Elevation was used as the environmental gradient  $x$ .

To examine the possibility that the real species optimum was outside the sampled range of the gradient, a chi-squared test was used to compare residual deviance of a monotonic model with that of a quadratic model (ter Braak and Looman 1986; Austin et al. 1984). The significance of the quadratic part of the model was tested by stepwise removal of the quadratic component, thereby yielding a linear monotonic model within the observed range of the environmental gradient. If the drop in residual deviance for this reduced model was larger than the critical value of a chi-square distribution with one degree of freedom (only *one* extra term added to the extended model) the quadratic model was retained as being superior to the monotonic model. This was true only if  $b_2 < 0$  and the response curve rose to a maximum. If  $b_2 > 0$  and the quadratic component is significant, this indicates a u-shaped response with optima outside the sampled range.

### 5.3.2 Comparisons of optima

Figures 5.1 and D.1–D.3 show the optimum and tolerance of *Baumea arthrophylla* along the elevation gradient at the 14 sites where a Gaussian response model was found to be superior to a monotonic one. Five sites (not shown) showed a superior fit with the monotonic model. Of these, two showed a negative slope (optimum was lower than the minimum sampled elevation), two showed a positive slope (optimum was higher than the maximum sampled elevation) and one showed a non-significant slope (no pattern). For sites which showed a Gaussian response, optimum estimates varied considerably between the sites and ranged from 48.43 mAHD to 47.68 mAHD. The probability of finding *Baumea* at these optima ( $P_{\max}$ ) varied between 1.0 (sites 34 and 35) and 0.36 (site 20). The tolerance (or ecological amplitude) of *Baumea* at these sites was similarly variable and ranged from narrow (0.05 mAHD at site 20) to broad (0.32 mAHD at site 27).

Estimates of optimum, tolerance and maximum were similarly variable for the other species where a Gaussian model was found to be superior. For *Triglochin* the optimum ranged from 48.12 mAHD to 47.10 mAHD, tolerance ranged from 0.03 mAHD at Site 8 to 0.35 mAHD at site 22, and maximum probability of occurrence ranged from 0.99

(site 22) to 0.11 (sites 8 and 28) (Figures 5.2 and D.4–D.7). At five sites *Triglochin* did not show a Gaussian response, and instead showed a monotonic decrease with increasing elevation (one site), a monotonic increase (one site) and one site which showed no pattern. For *Myriophyllum* the optimum ranged from 48.24 mAHD to 47.50 mAHD, tolerance ranged from 0.03 mAHD at Site 6 to 0.30 mAHD at site 14, and maximum probability of occurrence ranged from 0.99 (site 14) to 0.37 (site 6) (Figures 5.3 and D.8–D.10). Four sites did not show a Gaussian response: two showed no pattern and the remaining two showed a monotonic increase and monotonic decrease respectively.

The highest and lowest optimum positions occupied by each species were considered to delimit the species' range at Bool Lagoon where they were still able to occur at high frequencies. At the edge of the species' range, the lowest probability of occurrence was 0.40 for *Baumea* at site 27. The next lowest probability value of 0.81 was for *Myriophyllum* at site 24. Even at these extreme positions, the probability of finding these species was high, which indicated that their habitat preferences in terms of flooding frequency were very broad. Each species was capable of attaining a high probability of occurrence across virtually the full elevation gradient at Bool Lagoon, in the context of the sampling period and the previous water regime.

Statements about the range of elevations occupied by these species belie the enormous differences in flooding frequencies experienced by the plants over a 12 month period. Characterisation of the annual flooding pattern using the methods outlined in Chapter 3 revealed that, from its highest to lowest optimum, *Baumea* ranged from sites which were inundated up to 1.3 m and never dried (47.68 mAHD in the Central Basin) (Figure 5.4.1) to sites which were exposed for over 250 days per year and were never submerged deeper than 0.55 m (48.43 mAHD in the Central Basin) (Figure 5.4.2). For *Triglochin* its lowest optimum in the Main Basin (47.10 mAHD) was inundated to a depth of between 0.8 m and 1.9 m during the year (Figure 5.4.3). At the other end of its range (48.12 mAHD, Main Basin) the plants were exposed for 135 days and were flooded to a depth of 0.9 m (Figure 5.4.4). *Myriophyllum* was similarly variable in the range of flooding patterns to which it was exposed—with inundation from 0.4 m to 1.5 m at its lowest optimum (47.5 mAHD in the Main Basin; Figure 5.4.5) to exposure for 190 days and deepest flooding to 0.75 m

at its highest optimum (48.24 mAHD in the Central Basin; Figure 5.4.6).

Each optimum estimate had associated with it a measure of variability—the tolerance. It was therefore possible to calculate the confidence associated with each optimum and from this determine whether the optima were significantly different from each other.

It was assumed that tolerance was equivalent to the standard deviation (S.D.) of a normal distribution. Thus, the standard error of the mean was simply  $\frac{S.D.}{\sqrt{n}}$  where  $n$ =number of observations. The enumeration of  $n$  was potentially problematic and was severely influenced by the scale of observation. Larger values of  $n$  would produce smaller error bars and greater confidence in the optimum estimate, while smaller values of  $n$  would have the reverse effect and make the detection of statistically significant differences in optimum estimates more difficult.

Recall that at each site around the perimeter of Bool Lagoon, twenty 50×50 cm contiguous quadrats were laid parallel to shore at each of 0, 5, 10, 15, 20, 30, 40, 60, 80 and 100 m from shore along a transect perpendicular to it. The maximum number of sampled units was therefore 200 (i.e. 20 quadrats × 10 distances from shore). For the purposes of the calculation of confidence intervals, if  $n=200$  then all quadrats are assumed to be independent, that is, the probability of finding species  $x$  in one quadrat is completely unrelated to the probability of finding the same species in neighbouring quadrats. With a quadrat size of 50 × 50 cm, this was clearly an unreasonable assumption for a clonal plant such as *Baumea arthrophylla*.

If  $n=10$  (10 distances from shore), this assumes dependence of quadrats within a cluster of 20 and independence of quadrats between clusters. The probability of finding *Baumea* at 10 m from shore would therefore be unrelated to the probability of finding *Baumea* at 15 m from shore.

Even this is not ideal because the clusters of quadrats were not placed evenly down the elevation gradient and were separated by either 5 m, 10 m or 20 m. It is possible then that some clusters of quadrats are dependent on each other (e.g. those 5 m apart) while others are not (e.g. those 20 m apart). Also within a cluster of quadrats, some may be independent (e.g. quadrats 1 and 20 which are separated by 9 m) while others may not (e.g. any quadrat pair separated by (say) <5 m).

The determinant of dependence and independence of quadrats should be the size of an individual of the species under consideration for a clonal plant, or the dispersal range of propagules for a non-clonal plant. For many species, including *Baumea arthrophylla*, this is not known and so in this instance the most conservative approach was taken by assuming dependence within a cluster of quadrats and independence between clusters. Thus  $n=10$  for the purpose of comparing optimum estimates between sites for all species.

Analysis of variance (ANOVA) was used for the comparison of optima rather than using multiple *t*-tests which increase the probability of committing a Type I error (Zar 1984). The optimum and tolerance of each site are derived statistics and were used as summary statistics for the construction of a synthetic ANOVA using the method outlined by Larson (1992). Summary statistics are used as a starting point and from these a data set is constructed with the same statistical properties as the original data. The method creates one observation below the mean for each group and  $n - 1$  observations above the mean in such a way that the mean and standard deviation for each group are identical to those in the original summary table. In this case, the mean and S.D. were taken as the optimum and tolerance respectively and sites were used to group observations. This analysis was conducted using the JMP program (Anon. 1996) and the protocol outlined by Best (1993).

ANOVA indicated that there were significant differences among the optimum estimates at the 14 sites containing *Baumea arthrophylla* ( $F=15.62$ ,  $df=13,126$ ,  $P<0.0001$ ). The results of *post hoc* pairwise comparisons (Tukey-Kramer HSD tests) are shown in Figure 5.5 and indicate that while the optimum estimates at some sites were not significantly different (e.g. sites 24–30, 32–17, 34–25) there were always some sites whose optimum estimate for *Baumea* was significantly higher (e.g. sites 27, 20) or lower (e.g. sites 30–28). Similar differences were found among the optimum estimates at different sites containing *Triglochin* (Figure 5.6) and *Myriophyllum* (Figure 5.7). It must be remembered that these differences were detectable with the very broad confidence intervals caused by a low  $n$  ( $=10$ ). With a better understanding of the independence of quadrats the number of significantly different optima would increase. For example, if all quadrats were independent ( $n=200$ ) all 14 *Baumea* sites would have significantly different optima at  $P=0.05$ .

### 5.3.3 Diversity and species' optima

Site specific features were examined in an attempt to explain the existence of the different optima of each species. Given the relatively large number of vegetation communities which were found at Bool Lagoon, there was the potential for the presence of other communities to influence the distribution of *Baumea*, *Triglochin* and *Myriophyllum* at different sites through space pre-emption, shading or other competitive effects. To examine this possibility, two measures of diversity were calculated at each site where a Gaussian response function had been modelled. The first was simply species richness and was used as a measure of  $\alpha$ -diversity at a site. The second was a crude measure of  $\beta$ -diversity across the elevation gradient at a site. A Bray-Curtis association matrix was calculated for each cluster of 20 quadrats at a site (i.e. 10 samples per site) based on species composition as measured on a 0–20 scale. This was identical to the method used to describe community composition across the whole Lagoon (see Chapter 2) but was restricted in this case to single sites. The square root of the mean association measure in the sample  $\times$  sample matrix was used as a measure of the  $\beta$ -diversity of the site. An alternative, rejected because of its rather arbitrary nature, would have been to count the number of dendrogram groups (communities) at some chosen dissimilarity level after classification of sites. The Spearman rank correlation coefficients between optimum,  $P_{\max}$  and  $\alpha$ - and  $\beta$ -diversity are shown in Tables 5.1, 5.2 and 5.3.

The optimum for *Myriophyllum* was weakly negatively correlated with the  $\alpha$ -diversity of the site ( $\rho = -0.52$ ,  $P=0.08$ ; Table 5.3). Thus the optimum for *Myriophyllum* became lower on the elevation gradient as the number of species increased at the site.

In contrast, the optima for *Baumea* and *Triglochin* were unrelated to either the  $\alpha$ - or  $\beta$ -diversity of the site (Tables 5.1 and 5.2)—neither the number of other species nor the number of communities present influenced their optimum position.

However, it is unreasonable to suggest that all species are of equal competitive ability. Indeed, if competitive hierarchies exist among the species at Bool Lagoon (Keddy 1989a) the presence or absence of one or more strong competitors may outweigh any competitive effects caused by a diversity of less competitive species. In order to better understand the influence of diversity on the distribution of *Baumea*, *Triglochin* and *Myriophyllum*, not

only must the diversity *per se* of the site be considered but also the *identity* of the species which make up that diversity.

In order to quantify the degree of co-occurrence across Bool Lagoon, Spearman rank correlation coefficients were calculated at the site level between other species and *Baumea*, *Triglochin* and *Myriophyllum*. Figure 5.8 summarises the correlations for all species with a correlation coefficient  $|\rho| > 0.5$  with at least one of the three modelled species.

The occurrence of both *Triglochin* and *Myriophyllum* was correlated with the occurrence of floating species (*Spirodela*, *Azolla*, *Wolffia*, *Lemna*) and herbland species (*Crassula*, *Rumex*, *Cotula*, *Eleocharis* and *Lilaeopsis*). In contrast, the occurrence of *Baumea arthrophylla* was correlated with those of *B. juncea*, *Nitella*, *Leptocarpus*, *Distichlis* and *Samolus*. Furthermore, the occurrence of *Baumea* was strongly and negatively correlated with all species with which *Triglochin* and *Myriophyllum* were found, with the exception of *Triglochin striata* and *Potamogeton pectinatus*. *Baumea* was then more or less excluded from regions of Bool Lagoon containing aquatic herbland.

Another approach taken in examining the potential influence of community composition on species' optima was the characterisation of whole site vegetation by clustering based on mean frequency score (/20) across all quadrats at each site. The resulting dendrogram yielded five groups of sites whose floristic composition is shown in Figure 5.9.

There was no systematic relationship between the optimum estimates for *Baumea*, *Triglochin* or *Myriophyllum* and the floristic group to which each site belonged.

### 5.3.4 Diversity and $P_{\max}$

While no significant relationship existed between optimum and diversity for either *Baumea* or *Triglochin*, site diversity was significantly correlated with the maximum probability of occurrence ( $P_{\max}$ ) for both species. For *Baumea*, both  $\alpha$ - and  $\beta$ -diversity were negatively correlated with  $P_{\max}$  (Table 5.1). *Triglochin* showed a positive correlation between  $P_{\max}$  and  $\beta$ -diversity (Table 5.2), while *Myriophyllum* showed no significant correlation with either diversity measure (Table 5.3). Thus for *Baumea* and *Triglochin*, the diversity of the site did not influence *where* they occurred on the gradient, but *how much* of each species was present.

A simple and logical relationship between species' probability of occurrence (P) and diversity would see P decrease in direct proportion with the number of other species present at the site. The simplest case is that P should equal 1.0 when the species occurs in monoculture. The addition of each extra species to the system should decrease P in the following way:

$$P = \frac{1}{N + 1} \quad (5.6)$$

where N = no. of extra species.

Thus when one extra species occurs,  $P=0.5$ , and when two extra species occur  $P=0.33$ . If the above relationship exists then there will be a straight line relationship between the reciprocal of P and the number of extra species.

Only *Baumea* showed a significant linear relationship between diversity and  $\frac{1}{P_{\max}}$  with  $r^2=0.30$  and  $0.45$  for  $\alpha$ - and  $\beta$ -diversity respectively. The greater the number species and communities that were present at a site, the lower was the maximum probability of occurrence for *Baumea*.

For *Triglochin*, the other species which showed any correlation between  $P_{\max}$  and diversity,  $P_{\max}$  was *enhanced* by  $\beta$ -diversity. The relationship was not a linear one ( $r^2=0.14$ ,  $P=0.12$ ) and non parametric statistics were required to detect the correlation (Spearman rank correlation; Table 5.2). In contrast to the other two species, *Triglochin* was able to attain a greater probability of occurrence in a mixed community.

## 5.4 Discussion

For all species considered, none showed a uniform response to flooding frequency—their optima were different at different sites. In addition, while their ranges may have been broad at some sites, they were restricted or absent at others. There is therefore a large range of possible flooding frequencies to which *Baumea*, *Triglochin* and *Myriophyllum* can be exposed without causing local extinction. Thus flooding frequency alone was insufficient to explain the distribution of species.

The lack of a predictable response to flooding frequency means that Bool Lagoon cannot be used with any certainty as a model system to aid in the management of other wetlands purely on the grounds of water regime. The distribution of the major species considered here was not just related to flooding frequency. There were other, site-specific effects which determined the distribution of species and although these may have interacted with flooding pattern, the mechanism of interaction was more complex than could be shown with simple correlation.

Disturbance caused by water level fluctuations and their effect on interspecific competition are suggested as mechanisms by which these distribution patterns occur.

It is important to note here that the patterns detected are derived from the occurrence of adult plants at the time of sampling. For *Triglochin* at least, there is the possibility of perennation *via* underground organs under dry conditions and thus the apparent distribution of the plants may not be the real distribution. This is an unavoidable temporal limitation to the vegetation sampling.

#### 5.4.1 Water level fluctuation as a disturbance

Grime (1977) proposed two distinct sets of physical factors which influenced plants: stress and disturbance. Stress was associated with slower growth or at least reduced production, while disturbance was associated with the destruction of plant biomass. Notwithstanding this rigid definition of disturbance, the term has been used rather loosely in the literature to refer to many external influences on a system, seemingly regardless of whether biomass loss results or not. This is particularly evident in the wetland literature, where flooding is frequently described as a disturbance (van der Valk and Davis 1980; Wilson and Keddy 1985; Keddy 1983; Bonis et al. 1995; Kirkman and Sharitz 1994). Thus it might be more appropriate to use a more recent definition of disturbance as provided by Pickett et al. (1989):

Disturbance is a change in the minimal structure [of any level of any system] caused by a factor external to the level of interest. "External" refers to any action that originates outside the unit in question, including the action of the higher level unit.

However, flooding has a dual role as either a stress or disturbance (*sensu* Grime 1977) in a wetland (Menges and Waller 1983). A particular flooding regime cannot be described as a stress or a disturbance effect on a plant without reference to the species under consideration and its adaptations to flooding or exposure. Conditions which are stressful for one species may be at the ecological optimum of another and the particular combination of physiological/morphological or life history characteristics of a plant will determine which of these alternatives holds true. Indeed, these same characteristics will determine how the plant may make the transition from flooded to drawdown conditions and back again (van der Valk 1981).

Numerous studies have sought to describe these characteristics and their relationship to the environment. Such functional classifications have been developed by Noble and Slatyer (1980) for dryland forests and their response to fire, Leishman and Westoby (1992) and Bugmann (1996) for temperate and semi-arid woodlands, Friedel et al. (1988) for arid zone plants and their response to grazing, Chapin et al. (1996) for arctic vegetation and Boutin and Keddy (1993), Hills et al. (1994) and Grace (1993) for wetland plants.<sup>2</sup> The aim of each of these is to afford some level of prediction as to the type of species which may prevail under a given set of environmental conditions.

Grime's (1977) classification of plant life history strategies uses species' response to stress and disturbance (using specific definitions) to classify plants as either competitors, stress tolerators or ruderals. The association between these life history types with particular environments provides the link necessary to make the model predictive. Thus highly productive, undisturbed habitats would favour competitive species with the ability to maximise resource capture. Unproductive habitats would favour slow-growing stress-tolerant species. Highly disturbed habitats would favour ruderal species with high growth rates, short life span and copious seed production.

The shift in classification from competitor to stress-tolerator to ruderal is mediated by both productivity and disturbance gradients. Therefore the degree of disturbance experienced by a wetland will create habitats with particular characteristics and therefore will promote the occurrence of species with strategies appropriate to those habitats.

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<sup>2</sup>See also Resh et al. (1994) and other papers in the series on species traits and long-term ecological research in the Rhône River (*Freshwater Biology* 31, 1994).

Not only can the degree of disturbance in a wetland affect the kinds of species which are able to grow there, but also the number of species. Connell's (1978) Intermediate Disturbance Hypothesis suggests that richness is maximised at intermediate levels of disturbance. It assumes that there is a trade-off in each species' ability to either compete or tolerate disturbance such that a superior competitor would be most susceptible to disturbance. If disturbances were frequent, then competitive species would become locally extinct and species richness would decrease. Conversely, if disturbances were infrequent, then competitively superior species would exclude competitively inferior ones and richness would similarly decrease. Support for the Intermediate Disturbance Hypothesis has been found in wetland systems ranging from Canadian lakeshores (Keddy 1983), and Minnesota lakes (Willcox and Meeker 1991) to intermittent wetlands on the Riverine Plain in New South Wales (McIntyre et al. 1988) and river banks in Sweden (Nilsson et al. 1989). Maintenance of species rich wetland habitat is therefore dependent on an intermediate frequency and intensity of disturbance.

*Myriophyllum* was the only species whose position on the gradient could be related (albeit weakly,  $P=0.08$ ) to the species diversity of the site. It is reasonable to suggest that *Myriophyllum* may retreat to deeper water conditions when competition higher on the gradient becomes too intense.

Neither *Baumea* nor *Triglochin* shared the same, logically predictable response. Instead, it was their  $P_{\max}$  values which were affected by changes in species diversity.

Consider a monospecific stand of *Baumea* growing at the margins of an ephemeral wetland. Increased water levels may prevent the regeneration of *Baumea* either sexually or clonally—the regeneration niche of *Baumea* (*sensu* Grubb 1977) could be said to have moved up the gradient where water levels were not so deep and regeneration could (potentially) once more take place. The perennial adult plants of *Baumea* still remain at their old position despite their lack of recruitment. Through time, these adults will senesce and die, the stand will become more patchy and will be more susceptible to invasion by other species. The  $P_{\max}$  value of *Baumea* within this stand will decrease through time as the adults senesce.

Movement of the regeneration niche caused by water level increase can potentially change the optimum value for *Baumea* within this stand, but *only if recruitment of adult plants higher on the gradient is successful*. If conditions are not suitable for recruitment (e.g. no space due to presence of competitors), then no optimum change will occur and an ever-decreasing  $P_{\max}$  will be the only influence of increased flooding on the *Baumea* stand. This decline may even be accelerated if competitors start to grow amongst the thinning *Baumea*.

While this process is ongoing, any instantaneous view of the system would detect an ecotone of coexisting species along the elevation gradient. Populations of one species would blend into populations of others and the locality could aptly be described as a mosaic. However, through time, these interactions may lead to some conclusion such as the successful migration of *Baumea* up the elevation gradient in response to increased flooding. Only when competition has ceased and *Baumea* exists in local equilibrium with its neighbouring communities will its boundaries be well defined.

Thus a single snapshot in time in the field means that there may be a combination of well-defined boundaries where species are at equilibrium and ecotones where these processes are still active. The frequency of disturbance with respect to the speed at which the system recovers and reaches a new equilibrium will determine which of these will predominate.

The speed of recovery of the system is linked to the growth characteristics of the species under consideration and more particularly to their ability to respond rapidly to an environmental disturbance.

#### 5.4.2 Other disturbances

Flooding is not the only natural disturbance which could influence the vegetation of Bool Lagoon, and furthermore, interspecific competition is not the sole explanation for the patterns in vegetation.

Aquatic vegetation may be disturbed in (at least) four ways and each type of disturbance will influence the vegetation in a different way. These are:

1. Extended wet periods
2. Extended dry periods
3. Wave action
4. Fire/grazing

These disturbances are shown diagrammatically in Figure 5.10 together with the influence of each on the position of the boundary between different vegetation types. Boundary is used in a loose sense here. If the adjoining vegetation types have reached local equilibrium (complete replacement of one species by another along a subset of its potential range) then a distinct boundary will occur. However, if competitive interactions are ongoing and local equilibrium has not been reached, then an ecotone will result with no clear boundary.

Extended wet periods, with a concomitant increase in the depth and duration of flooding will favour deep water species such as *Myriophyllum* and their occupancy range along the elevation gradient will increase at the expense of reedbed species such as *Baumea*. Recall that this does not necessarily mean the ousting of *Baumea* by *Myriophyllum* but more likely a subtle effect of the prevention of adequate recruitment by *Baumea* in the deepest zones. This, of course, may ultimately lead to the complete replacement of reedbed species by deep water species. Similarly, herbland species will be replaced by reedbed species as the adult populations are removed by deeper inundation.

Extended dry periods would have the reverse effect on these communities and the boundaries between them would appear lower down on the elevation gradient.

Wave action under deep water conditions may adversely affect reedbed species both through mechanical damage and through changes in sediment texture characteristics (Wilson and Keddy 1985; Keddy and Constabel 1986). This could lead to a movement upwards in the boundary between deep water and reedbed species.

Finally, herbland species and other in the aquatic/terrestrial ecotone may be influenced by any number of disturbances such as fire or animal grazing and trampling. Fire could easily encroach into reedbed edges or further during an extended dry period and open up space suitable for colonisation by herbland species. The complete dissociation

of herbland species from *Baumea* (Figure 5.8) may have been caused by some historical effect such as fire or grazing rather than any direct competitive interactions between the species groups—*Baumea* was burnt out and the herbland took over.

### 5.4.3 Classification of species

The relationship between species distributions and species diversity goes some way towards classifying species as being either a competitor, stress-tolerator or ruderal using Grime's (1977) scheme. However, more information is required for a definitive classification.

The probability of finding *Triglochin* increased with increasing  $\beta$ -diversity, indicating that it is a ruderal species. It was the only species which showed such a correlation and its classification was the most straightforward. *Baumea* and *Myriophyllum* were more problematic.

The presence of other species reduced the probability of finding both *Baumea* and *Myriophyllum*, a situation diagrammatically represented in Figure 5.11 in which the numerous sites are at a variety of stages of equilibrium i.e. this is the 'snap shot' view of the system described above. The  $\circ$  sites experience intermediate disturbance (frequency and/or intensity) because they have the highest diversity. The  $\square$  sites have the lowest diversity and so are either at equilibrium (low disturbance) or experience high levels of disturbance. If they are low disturbance sites, the species (*Myriophyllum*, say) must be a good competitor, having been able to exclude other species. Alternatively, if they are high disturbance sites, then *Myriophyllum* must be a stress tolerator. It cannot be ruderal because the site diversity is too low (except if it is a first invader and has not yet been outcompeted). Thus the distinction between these two alternative classifications, competitor or stress tolerator, depends on the level of disturbance at the site, or at least the time since last disturbance.

In trying to classify *Baumea* and *Myriophyllum* as either competitors or stress tolerators, there is the inference of causality: what has caused the relationship between species' probability of occurrence and site diversity? There are two alternatives. Firstly, if the x-axis of Figure 5.11 (diversity) is the presumed cause, then the presence of many other species suppresses the growth of *Myriophyllum*. Secondly, if the y-axis of Figure 5.11 is

the cause then *Myriophyllum* suppresses many other species. The only way to determine which of these alternatives holds true is to examine this pattern through time and use the direction of change to infer causality. In this way, the true classification of the species may be made.

Consider a single site, initially disturbed and then left to recover (Figure 5.12). The frequency of *Myriophyllum* is determined periodically and the relationship between site diversity and the probability of occurrence of *Myriophyllum* is determined.

If this time trace moves to the upper left, then *Myriophyllum* must be a good competitor (Figure 5.12.1). If the trace moves to the lower right, then *Myriophyllum* is a poor competitor and must instead be a ruderal (Figure 5.12.2). If the time trace is stationary, then this indicates that *Myriophyllum* is a stress tolerator.

In the absence of the temporal data required to make such statements, it is possible to infer a C-S-R classification of some species based on their known biology. For example, the erect habit, cuticularised stems, slow growth and perennial life history of *Baumea* suggest that it is a stress tolerator—these are all clear adaptations to survival throughout the year in conditions which will vary from flooded to fully exposed. The growth habit of *Triglochin* suggests that it is most likely a competitive species. Its rhizome and root system ensure its nutrient capture and retention, and its semi-erect/semi-emergent habit (depending on whether it is exposed or flooded) enable it to overshadow herbaceous species which may attempt to compete for light. Alternatively, it could be classed as ruderal because of its large and successful seed set and dispersal mechanisms. It may also be classed as a stress tolerator because of its phenotypic plasticity and variable leaf form! *Myriophyllum* is similarly difficult to classify definitively. Its capacity for heterophylly suggests that it is capable of tolerating extreme stress and its rapid growth rate and methods of propagule dispersal suggest a more ruderal existence.

The difficulty with definitive classification of these plants is their flexibility in coping with an essentially fluctuating environment. Such flexibility is not restricted to phenotype: reproductive flexibility, especially phenological variation, has been demonstrated in many Australian wetland systems for emergent macrophytes (Froend and McComb 1994) and submerged macrophytes (Brock 1982, 1983, 1991; Casanova 1994). No single strategy

will equip the plant for survival in all conditions and their readiness to change strategy in response to environmental pressures may preclude a definitive classification in Grime's C-S-R scheme.

#### 5.4.4 Bool Lagoon as a model wetland

Although the water regime at Bool Lagoon cannot be used in a prescriptive way to predict species responses, the Lagoon still has the potential to act as a model system for other wetlands in the area.

It has been shown that the probability of finding *Baumea* is negatively correlated with species diversity. Thus, a management strategy designed to maximise species diversity in a wetland would likely result in the exclusion of *Baumea* from the wetland. Conversely, if the preservation of a *Baumea* swamp is the desired management outcome, then there must be an acceptance of low species diversity in that wetland. The maintenance of species diversity need not be the sole aim of wetland conservation, that is, every conserved wetland need not be species rich. Instead, a considered plan to manage the wetland resources of the South East should recognise the regional diversity of wetlands and the aquatic vegetation communities they contain. Some wetlands may contain several vegetation types and/or diverse types, whereas others may contain only one type or monocultures. A desire to create the ultimately representative wetland which contains all vegetation associations in the South East may be an unattainable goal.



## Chapter 6

### Conclusion

This study has provided formal floristic descriptions of the aquatic vegetation of remnant wetlands in the South East of South Australia. It was clear that the 11 wetlands considered here were not merely duplicates of each other. Each was significantly individual and contained generally unique combinations of the 11 defined vegetation associations. The majority of these associations were not represented in previous vegetation survey work in South Australia (Specht 1972; Sparrow 1991). Sparrow regarded wetland vegetation as a very rare vegetation type in South Australia and certainly one which was poorly documented and described, and Specht urged the conduct of more critical ecological studies designed to modify his list of state-wide species associations. This work addresses both of these concerns.

Aquatic vegetation was found to be a suitable criterion for the classification of wetlands. While most wetlands could be easily classified on the basis of two or three species associations (e.g. Bloomfield Swamp contained *POTAMOGETON PECTINATUS* and *AQUATIC/TERRESTRIAL HERBLAND* associations), Bool Lagoon contained nine of the eleven defined associations and was clearly the most diverse wetland in the region. Therefore, in addition to its listing by the Ramsar Convention as an important water fowl habitat, the diversity of its aquatic macrophyte vegetation justifies its protection and conservation.

The species list developed during the vegetation surveys contained an embarrassing number of unknown or incompletely identified taxa. While many of these occurred in surrounding terrestrial habitats and did not strictly form part of the aquatic flora, the

taxonomy of many aquatic plants was unclear e.g. *Myriophyllum* species, *Triglochin* species and others. Because classification of vegetation is reliant on sound taxonomy, it is hoped that new taxonomic research (e.g. Aston 1977, 1993) will help to clear up some of these difficulties in field identification.

The inaccuracy of topographic surveys at the G3 and G7 swamps was an initial disappointment, but did not severely influence the interpretation of floristic patterns, or their gross response to flooding which showed a clear demarkation between aquatic and terrestrial habitats. However, accurate topographic data are essential if past flooding histories are to be calculated for positions along the elevation gradient. Although water level records are kept for many of the wetlands considered here, the frustratingly low frequency of observations and incompatibility of scales of measurement meant that, apart from Bool Lagoon, it was not possible to relate current vegetation patterns to past flooding history. Accurate and frequent water level data would be a welcome addition to assist future work in this region.

There is a wealth of literature evidence which shows that static water level influences the distribution patterns of aquatic vegetation, but neither elevation nor water regime were able to explain the distribution of the majority of the seven vegetation associations at Bool Lagoon (with the exception of the GAHNIA SPP.-DISTICHLIS DISTICHOPHYLLA association which was restricted to high elevations at the terrestrial margin of the Lagoon). Examination of the distributions of *Baumea arthropphylla*, *Triglochin procerum* and *Myriophyllum salsugineum* showed that each species had a very broad ecological amplitude and was capable of growing at virtually any position along the sampled elevation gradient. These species are major components of four of the seven vegetation associations at Bool Lagoon (see p 35) and it is therefore likely that these associations are not restricted to a subset of elevations such that their occurrence would be explained in terms of elevation alone.

Clearly other factors were involved in determining the distribution of the vegetation associations. Even though soil chemical data were collected at Bool Lagoon, they were collected at a frequency largely incompatible with the frequency at which vegetation data were collected. i.e. 360 vegetation sites were visited, but soil chemical data were only

collected at 35 of these. Future work of this nature would benefit from an understanding of the role of sediment chemistry, and perhaps its interaction with flooding frequency, in determining vegetation patterns. In order to include chemical data within the analysis of vegetation (either *post hoc* correlations following Detrended Correspondence Analysis (DCA), or the inclusion of environmental data in vegetation analyses with Canonical Correspondence Analysis (CCA; ter Braak (1986))), sediment samples should have been collected from each location where vegetation data had been collected. Similarly, sediment texture and colour characteristics could also have been scored.

The maintenance of Bool Lagoon as a habitat-rich and important water fowl refuge may be dependent on the maintenance of a Mediterranean-type seasonal flooding cycle. This would impose an intermediate level of disturbance on the system and maintain high diversity of aquatic macrophyte communities. If the Lagoon were to remain dry for too long, or wet for too long, there is the potential for loss of diversity and a reduction in the Lagoon's conservation value.

The difficulty is knowing how long is "too long". We return here to the problem of how best to define water regime. The numerical definition proposed here is suitable for the comparison of annual flooding patterns between different locations and as a description of plant niche is certainly an improvement over 'deep' or 'shallow' water, or mean water depth. It is though essentially hydrological in nature, not biological, despite the numerical modification of time spent in each depth class to acknowledge the non-linear effects of flooding on vegetation.

The water regime definitions presented here did not influence the productivity of either *Phragmites* or *Typha* but *did* severely influence their shoot characteristics. Given the seasonal production of above-ground shoots in both species, it is unreasonable to suggest that the entire annual flooding pattern would have any influence on these shoots. For example, very deep water in winter, when there is no live above-ground biomass, is unlikely to affect the shoot population. Instead, the shoots are more likely to be affected by the water depth at critical times during their development e.g. the time they emerge in spring. Only a subset of the water depths experienced during the whole year will have had the potential to affect the development of the annual population of *Phragmites* or *Typha*.

The classical zonation of a wetland plant community often involves concentric rings of vegetation, the composition of which is principally determined by the degree of adaptation to exposure or inundation (e.g. Yamasaki and Tange 1981; Spence 1982). It is reasonable to suggest that the mechanisms giving rise to such “text-book” species zonation in the Northern Hemisphere also operate in the Southern Hemisphere, as indeed the literature evidence for individual species demonstrates. Rea (1993) and Rea and Ganf (1994b) have shown that *Triglochin procerum* reallocates its below ground resources to above ground as water depth increases and *vice versa*. Similarly, *Baumea arthropphylla* is able to tolerate a range of water depths from dry to ca. 80 cm by reallocating resources from rhizome to shoot. Cooling (1996) has shown that *Villarsia reniformis* responds to changes in water depths so that it can persist from dry to ca. 70 cm depth. Blanch (unpublished) has investigated the response of *Vallisneria americana* and *Bolboschoenus medianus* to both water depth and turbidity. Walker et al. (1994) have shown that the distribution of aquatic plants in the lower Murray River is correlated with the water regime above and below weirs. The conclusion from these Australian studies (some unpublished) and those overseas (e.g. Grace and Wetzel 1981; Lieffers and Shay 1981; Sjöberg and Danell 1983; Waters and Shay 1990) is that perennial aquatic macrophytes demonstrate a remarkable degree of plasticity in the allocation and reallocation of biomass in response to changing water depths.

The anomalous observation made in this thesis is that there appears to be little correlation between the distribution of species and water depth in Bool Lagoon. There is often an equal probability of finding a species low and high on the elevation gradient. The absence of a clear zonation pattern suggests that many species are able to occupy all elevations. The entire elevation gradient may then represent both the fundamental and realised niche for perennial aquatic species. It represents a fundamental niche because the amplitude of water level fluctuations is within the accommodation capacity of most species and thus the entire gradient is a potential site for establishment and growth. However, the entire gradient is not available for colonisation and growth at the same time. Instead, a “window of opportunity”, representing the instantaneous realised niche of species, moves sequentially across the gradient in response to rising and falling water

levels. The current field distributions of species are the summation of many seasons of smaller-scale recruitment. These patterns persist because of the perennial nature of the species and their morphological responses which enable them to endure both flooded and drawdown conditions. The entire suite of perennial species is thus able to occupy the entire elevation gradient not because they are unresponsive to water level change, but rather because that they are *so* responsive to it.

The observed lack of a distinct correlation between water depth and species distribution is likely to be a product of the amplitude of the water levels fluctuations, the degree of plasticity of the individual species response and the timing of the major growth periods in relation to the current water regime. As Mitsch and Gosselink (1986) have pointed out, the most important factor determining the floristic composition, distribution and productivity of wetland plants is the hydrological regime. However, it is important to recognise that it is the interaction between plant plasticity and water regime that will ultimately define the distribution and abundance of species. As has been shown at Bool Lagoon (Denton and Ganf 1994; Rea and Ganf 1994a), major changes in water regime will result in major changes in floristic composition if the changes are outside the tolerance limits of the existing flora.

# Bibliography

- Adcock, P. W. and G. G. Ganf (1994). Growth characteristics of three macrophyte species growing in a natural and constructed wetland system. *Water Science and Technology* 29, 127–132.
- Anon. (1995). Honans Native Forest Reserve Management Plan. Interim Report. 8 September 1995. Department of Primary Industries South Australia (Forestry), South East Region, Mount Gambier Forest.
- Anon. (1996). *JMP. Statistics for the Apple Macintosh from SAS Institute Inc. Version 3.1.6. [computer program]*. Cary, N.C.: SAS Institute Inc.
- Armstrong, J. and W. Armstrong (1991). A convective gas through-flow in *Phragmites australis*. *Aquatic Botany* 39, 75–88.
- Armstrong, W., S. H. F. W. Justin, P. M. Beckett, and S. Lythe (1991). Root adaptation to soil waterlogging. *Aquatic Botany* 39, 57–73.
- Aston, H. I. (1977). *Aquatic Plants of Australia*. Melbourne: Melbourne University Press.
- Aston, H. I. (1993). New Australian species of *Triglochin* L. (Juncaginaceae) formerly included in *T. procerum* R.Br. *Muelleria* 8, 85–97.
- Austin, M. P., R. B. Cunningham, and P. M. Fleming (1984). New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55, 11–27.
- Austin, M. P. and I. Noy-Meir (1971). The problem of non-linearity in ordination: experiments with two-gradient models. *Journal of Ecology* 59, 763–773.
- Beals, E. W. (1984). Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14, 1–55.
- Belbin, L. (1991). Semi-strong Hybrid Scaling, a new ordination algorithm. *Journal of Vegetation Science* 2, 491–496.
- Belbin, L. (1993a). *PATN Pattern Analysis Package v1.6 [computer program]*. Canberra: CSIRO Division of Wildlife and Ecology.
- Belbin, L. (1993b). *PATN Pattern Analysis Package v1.6. Technical Reference*. Canberra: CSIRO Division of Wildlife and Ecology.
- Belbin, L., D. P. Faith, and G. W. Milligan (1992). A comparison of two approaches to beta-flexible clustering. *Multivariate Behavioural Research* 27, 417–433.
- Best, A. (1993). JMPing to conclusions. Power check with a synthetic ANOVA. *JMPer Cable. Biannual newsletter for JMP users* 1, 2–3. [SAS Institute Inc., Cary, N.C.].
- Boar, R. R., C. E. Crook, and B. Moss (1989). Regression of *Phragmites australis* reedswamps and recent changes of water chemistry in the Norfolk Broadland, England. *Aquatic Botany* 35, 41–55.

- Bonis, A., J. Lepart, and P. Grillas (1995). Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. *Oikos* 74, 81–92.
- Bostrack, J. M. and W. F. Millington (1962). On the determination of leaf form in an aquatic heterophyllous species of *Ranunculus*. *Bulletin of the Torrey Botanical Club* 89, 1–20.
- Boutin, C. and P. A. Keddy (1993). A functional classification of wetland plants. *Journal of Vegetation Science* 4, 591–600.
- Bradbury, I. and J. Grace (1983). Primary production in wetlands. In *Mires: Swamp, Bog, Fen and Moor*, Volume 4A of *Ecosystems of the World*, pp. 285–310. Amsterdam: Elsevier.
- Bray, J. R. and J. T. Curtis (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27, 325–349.
- Bray, J. R., D. B. Lawrence, and L. C. Pearson (1959). Primary production in some Minnesota terrestrial communities. *Oikos* 10, 38–40.
- Briggs, S. V. (1981). Freshwater wetlands. In R. Groves (Ed.), *Australian Vegetation*, pp. 335–360. Cambridge: Cambridge University Press.
- Briggs, S. V. and M. T. Maher (1985). Limnological studies of waterfowl habitat in South-western New South Wales. II. Aquatic macrophyte productivity. *Australian Journal of Marine and Freshwater Research* 36, 707–715.
- Britton, R. H. and V. D. Podlejski (1981). Inventory and classification of the wetlands of the Carmargue (France). *Aquatic Botany* 10, 195–228.
- Brock, M. A. (1982). Biology of the salinity tolerant genus *Ruppia* L. in saline lakes in South Australia. II. Population ecology and reproductive biology. *Aquatic Botany* 13, 249–268.
- Brock, M. A. (1983). Reproductive allocation in annual and perennial species of the submerged aquatic halophyte *Ruppia*. *Journal of Ecology* 71, 811–818.
- Brock, M. A. (1991). Mechanisms for maintaining persistent populations of *Myriophyllum variifolium* J. Hooker in a fluctuating shallow Australian lake. *Aquatic Botany* 39, 211–219.
- Brock, T. C. M., G. van der Velde, and H. M. van de Steeg (1987). The effects of extreme water level fluctuations on the wetland vegetation of a nymphaeid-dominated oxbow lake in The Netherlands. *Ergebnisse der Limnologie* 27, 57–73.
- Brownlow, M. D. (1988). Phosphorus enrichment and the growth of three aquatic macrophytes from Bool Lagoon. B.Sc. (Hons.) thesis. Department of Botany, The University of Adelaide.
- Brownlow, M. D., A. D. Sparrow, and G. G. Ganf (1994). Classification of water regimes in systems of fluctuating water level. *Australian Journal of Marine and Freshwater Research* 45, 1375–1385.
- Bugmann, H. (1996). Functional types of trees in temperate and boreal forests: classification and testing. *Journal of Vegetation Science* 7, 359–370.
- Burgess, N. D., C. Evans, and G. J. Thomas (1990). Vegetation change on the Ouse Washes wetland, England, 1972–88 and effects on their conservation importance. *Biological Conservation* 53, 173–189.

- Buttery, B. R. and J. M. Lambert (1965). Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. I. The competitive mechanism. *Journal of Ecology* 53, 163–182.
- Casanova, M. T. (1994). Vegetative and reproductive responses of charophytes to water-level fluctuations in permanent and temporary wetlands in Australia. *Australian Journal of Marine and Freshwater Research* 45, 1409–1419.
- Casanova, M. T. and M. A. Brock (1990). Charophyte germination and establishment from the seed bank of an Australian temporary lake. *Aquatic Botany* 36, 247–254.
- Chambers, P. A. and J. Kalff (1985). Depth distribution and biomass of submerged aquatic macrophyte communities in relation to secchi depth. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 701–709.
- Chambers, P. A., E. E. Prepas, H. R. Hamilton, and M. L. Bothwell (1991). Current velocity and its effects on aquatic macrophytes in flowing waters. *Ecological Applications* 1, 249–257.
- Chapin, III, F. S., M. S. Bret-Harte, S. E. Hobbie, and H. Zhong (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* 7, 347–358.
- Chick, A. J., C. M. Finlayson, and J. T. Swarbrick (1983). Typhaceae—the cumbings or bulrushes. *Weeds of Australia* 2, 102–104.
- Christensen, E. J., J. R. Jensen, E. W. Ramsey, and H. E. Mackey, Jr. (1988). Aircraft MSS data registration and vegetation classification for wetland change detection. *International Journal of Remote Sensing* 9, 23–38.
- Clarke, K. R. and R. M. Warwick (1994). *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council, U.K.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cook, C. D. K. (1968). Phenotypic plasticity with particular reference to three amphibious species. In V. H. Heywood (Ed.), *Modern Methods in Plant Taxonomy*, pp. 97–111. London: Academic Press.
- Cooling, M. P. (1996). *Adaptations of aquatic macrophytes to seasonally fluctuating water level*. Ph. D. thesis, The University of Adelaide.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. La Roae (1979). Classification of wetlands and deepwater habitats of the United States. Technical report, U.S. Fish and Wildlife Service, Washington D.C.
- Cox, D. R. (1970). *The Analysis of Binary Data*. London: Methuen.
- Crawford, R. M. M. (1996). Whole plant adaptations to fluctuating water tables. *Folia Geobotanica et Phytotaxonomica* 31, 7–24.
- D'Arcy, R. (1984). Infrastructure. In M. L. Morris (Ed.), *South East Environmental Profile Study. Report No. SADEP64*. Adelaide: South Australian Department of Environment and Planning.
- Davis, C. B. and A. G. van der Valk (1983). Uptake and release of nutrients by living and decomposing *Typha glauca* tissues at Eagle Lake, Iowa, U.S.A. *Aquatic Botany* 16, 75–90.

- Davis, J. A., R. S. Rorisch, J. S. Bradley, J. E. Grouns, J. E. Schmidt, and F. Cheal (1993). *Wetland classification on the basis of water quality and invertebrate community data*, Volume 6 of *Wetlands of the Swan Coastal Plain*. Perth: Water Authority of Western Australia, and Environmental Protection Authority.
- de Kroon, H. and F. Schieving (1991). Resource partitioning in relation to clonal growth strategy. In J. van Groenendael and H. de Kroon (Eds.), *Clonal growth in plants: regulation and function*, pp. 113–130. The Hague: SPB Academic Publishing.
- den Hartog, C., J. Květ, and H. Sukopp (1989). Reed: a common species in decline. *Aquatic Botany* 35, 1–54.
- Denny, P. (1971). Zonation of aquatic macrophytes around Habukara Island, Lake Bunyonyi, S.W. Uganda. *Hidrobiologia* 12, 249–257.
- Denton, M. and G. G. Ganf (1994). Response of juvenile *Melaleuca halmaturorum* to flooding: management implications for a seasonal wetland, Bool Lagoon, South Australia. *Australian Journal of Marine and Freshwater Research* 45, 1395–1408.
- Dickerman, J. A., A. J. Stewart, and R. G. Wetzel (1986). Estimates of net annual aboveground production: sensitivity to sampling frequency. *Ecology* 67, 650–659.
- Dodson, J. R. (1974). Vegetation history and water level fluctuations at Lake Leake, South-eastern South Australia. I. 10,000 B.P. to present. *Australian Journal of Botany* 22, 719–741.
- Dykyjová, D. and J. Květ (Eds.) (1978). *Pond Littoral Ecosystems. Structure and Functioning. Methods and Results of Quantitative Ecosystem Research in the Czechoslovakian I.B.P. Wetland Project*, Volume 28 of *Ecological Studies. Analysis and Synthesis*. Berlin: Springer-Verlag.
- Eardley, C. M. (1943). An ecological study of Eight Mile Creek Swamp: A natural South Australian coastal fen formation. *Transactions of the Royal Society of South Australia* 67, 200–223.
- Ellenberg, H. (1988). *Vegetation Ecology of Central Europe* (4th ed.). Cambridge: Cambridge University Press.
- Faith, D. P., P. R. Minchin, and L. Belbin (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68.
- Finlayson, C. M. and A. G. van der Valk (1995). Editorial. *Vegetatio* 118, 1–2.
- Flower, G. E. (1991). Vegetation survey data from Nangwarry Swamp, Honan's and Bonney's Woodland Swamp and The Marshes. [Unpublished raw data].
- Friedel, M. H., G. N. Bastin, and G. F. Griffin (1988). Range assessment and monitoring in arid lands: The derivation of functional groups to simplify vegetation data. *Journal of Environmental Management* 27, 85–97.
- Froend, R. H., R. C. C. Farrell, C. F. Wilkins, C. C. Wilson, and A. J. McComb (1993). *The effect of altered water regimes on wetland plants*, Volume 4 of *Wetlands of the Swan Coastal Plain*. Perth: Water Authority of Western Australia, and Environmental Protection Authority.
- Froend, R. H. and A. J. McComb (1994). Distribution, productivity and reproductive phenology of emergent macrophytes in relation to water regimes at wetlands of southwestern Australia. *Australian Journal of Marine and Freshwater Research* 45, 1491–1508.

- Galinato, M. I. and A. G. van der Valk (1986). Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. *Aquatic Botany* 26, 89–102.
- Gauch, Jr., H. G. (1982). *Multivariate Analysis in Community Ecology*. Cambridge: Cambridge University Press.
- Gause, G. F. (1930). Studies on the ecology of the Orthoptera. *Ecology* 11, 307–325.
- Gopal, B. and M. Sah (1995). Inventory and classification of wetlands in India. *Vegetatio* 118, 39–48.
- Gosselink, J. G. and R. E. Turner (1978). The role of hydrology in freshwater wetland ecosystems. In R. E. Good, D. F. Whigham, and R. L. Simpson (Eds.), *Freshwater wetlands. Ecological processes and management potential*, pp. 63–78. New York: Academic Press.
- Grace, J. B. (1993). The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquatic Botany* 44, 159–180.
- Grace, J. B. and R. G. Wetzel (1981). Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. *American Naturalist* 118, 463–474.
- Grace, J. B. and R. G. Wetzel (1982). Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany* 60, 46–57.
- Granéli, W. (1989). Influence of standing litter on shoot production in reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *Aquatic Botany* 35, 99–109.
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111, 1169–1194.
- Grosse, W., H. B. Büchel, and H. Tiebel (1991). Pressurized ventilation in wetland plants. *Aquatic Botany* 39, 89–98.
- Grubb, P. J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52, 107–145.
- Harper, J. L. (1977). *Population Biology of Plants*. London: Academic Press.
- Haslam, S. (1971). Shoot height and density in *Phragmites* stands. *Hidrobiologia* 12, 113–119.
- Hauck, R. D., J. J. Meisinger, and R. L. Mulvaney (1994). Practical considerations in the use of nitrogen tracers in agricultural and environmental research. In *Part 2. Microbiological and Biochemical Properties*, Methods of Soil Analysis, pp. 907–950. Madison, Wisconsin: Soil Science Society of America.
- Hay, A. (1992). Vegetation survey data from South East wetlands. [unpublished raw data].
- Hejný, S. (1971). The dynamic characteristic of littoral vegetation with respect to changes in water level. *Hidrobiologia* 12, 71–86.
- Hill, M. O. and H. G. Gauch, Jr. (1980). Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42, 47–58.

- Hills, J. M., K. J. Murphy, I. D. Pulford, and T. H. Flowers (1994). A method for classifying European riverine wetland ecosystems using functional vegetation groups. *Functional Ecology* 8, 242–252.
- Hinde, H. P. (1954). Vertical distribution of salt marsh phanerogams in relation to tide levels. *Ecological Monographs* 24, 209–225.
- Hocking, P. J. (1989a). Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Steudel in a nutrient-enriched swamp in inland Australia. II. Individual shoots. *Australian Journal of Marine and Freshwater Research* 40, 445–464.
- Hocking, P. J. (1989b). Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Steudel in a nutrient-enriched swamp in inland Australia. I. Whole plants. *Australian Journal of Marine and Freshwater Research* 40, 421–444.
- Hogeland, A. M. and K. T. Killingbeck (1985). Biomass, productivity and life history traits of *Juncus militaris* Bigel. in two Rhode Island (U.S.A.) freshwater wetlands. *Aquatic Botany* 22, 335–346.
- Horton, R. F. (1992). Submergence-promoted growth of petioles of *Ranunculus pygmaeus* Wahl. *Aquatic Botany* 44, 23–30.
- Howard-Williams, C. (1975). Seasonal and spatial changes in the composition of aquatic and semiaquatic vegetation of Lake Chilwa, Malawi. *Vegetatio* 30, 33–39.
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187–211.
- Jensen, J. R., M. E. Hodgson, E. Christensen, H. E. Mackey, Jr., L. R. Tinney, and R. Sharitz (1986). Remote sensing inland wetlands: a multispectral approach. *Photogrammetric Engineering and Remote Sensing* 52, 87–100.
- Jessop, J. P. (1989). A list of the vascular plants of South Australia (Edition III). *Journal of the Adelaide Botanic Gardens* 12, 1–163.
- Johnson, M. P. (1967). Temperature dependent leaf morphogenesis in *Ranunculus flabellaris*. *Nature* 214, 1354–1355.
- Johnston, R. M. and M. M. Barson (1993). Remote sensing of Australian wetlands: an evaluation of Landsat TM data for inventory and classification. *Australian Journal of Marine and Freshwater Research* 44, 235–252.
- Jones, W. (1978). *The Wetlands of the South-East of South Australia*. Adelaide: Nature Conservation Society of South Australia.
- Kadlec, J. A. (1962). Effects of a drawdown on a waterfowl impoundment. *Ecology* 43, 267–281.
- Kalliola, R., M. Puhakka, J. Salo, H. Tuomisto, and K. Ruokolainen (1991). The dynamics, distribution and classification of swamp vegetation in Peruvian Amazonia. *Annales Botanici Fennici* 28, 225–239.
- Kauppi, P., J. Selkäinaho, and P. Puttonen (1983). A method for estimating above-ground biomass in *Phragmites* stands. *Annales Botanici Fennici* 20, 51–55.
- Keddy, P. A. (1983). Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64, 331–344.
- Keddy, P. A. (1989a). *Competition*. London: Chapman and Hall.

- Keddy, P. A. (1989b). Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. *Canadian Journal of Botany* 67, 708–716.
- Keddy, P. A. and P. Constabel (1986). Germination of ten shoreline plants in relation to seed size, soil particle size and water level: an experimental study. *Journal of Ecology* 74, 133–141.
- Keddy, P. A. and A. A. Reznicek (1986). Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research* 12, 25–36.
- Kirkman, L. K. and R. R. Sharitz (1994). Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. *Ecological Applications* 4, 177–188.
- Kirkpatrick, J. B. and C. E. Harwood (1983). Plant communities of Tasmanian wetlands. *Australian Journal of Botany* 31, 437–451.
- Klötzli, F. (1971). Biogenous influence on aquatic macrophytes, especially *Phragmites communis*. *Hidrobiologia* 12, 107–111.
- Krumscheid, P., H. Stark, and M. Peintinger (1989). Decline of reed at Lake Constance (Obersee) since 1967 based on interpretations of aerial photographs. *Aquatic Botany* 35, 57–62.
- Ksenofontova, T. (1988). Morphology, production and mineral contents in *Phragmites australis* in different waterbodies of the Estonian S.S.R. *Folia Geobotanica et Phytotaxonomica* 23, 17–43.
- Larson, D. A. (1992). Analysis of variance with just summary statistics as input. *The American Statistician* 46, 151–152.
- Leishman, M. R. and M. Westoby (1992). Classifying plants into groups on the basis of associations of individual traits—Evidence from Australian semi-arid woodlands. *Journal of Ecology* 80, 417–424.
- Lieffers, V. J. and J. M. Shay (1981). The effects of water level on the growth and reproduction of *Scirpus maritimus* var. *paludosus*. *Canadian Journal of Botany* 59, 118–121.
- Lloyd, L. N. and S. A. Balla (1986). Wetlands and water resources of South Australia. Technical report, S.A. Department of Environment and Planning.
- Ludwig, J. A. and J. F. Reynolds (1988). *Statistical Ecology. A primer on methods and computing*. New York: John Wiley and Sons.
- Madsen, T. V. and M. Søndergaard (1983). The effects of current velocity on the photosynthesis of *Callitriche stagnalis* Scop. *Aquatic Botany* 15, 187–193.
- Magurran, A. E. (1988). *Ecological diversity and its measurement*. London: Croom Helm.
- Marshall, C. (1991). Source-sink relations of interconnected ramets. In J. van Groenendael and H. de Kroon (Eds.), *Clonal growth in plants: regulation and function*, pp. 23–41. The Hague: SPB Academic Publishing.
- Mason, C. F. and R. J. Bryant (1975). Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *Journal of Ecology* 63, 71–95.

- McIntyre, S., P. Y. Ladiges, and G. Adams (1988). Plant species-richness and invasion by exotics in relation to disturbance of wetland communities on the Riverine Plain, N.S.W. *Australian Journal of Ecology* 13, 361–373.
- Menges, E. S. and D. M. Waller (1983). Plant strategies in relation to elevation and light in floodplain herbs. *American Naturalist* 122, 454–473.
- Meredith, T. C. (1985). Factors affecting recruitment from the seed bank of sedge (*Cladus mariscus*) dominated communities at Wicken Fen, Cambridgeshire, England. *Journal of Biogeography* 12, 463–472.
- Mitchell, D. S. and K. H. Rogers (1985). Seasonality/aseasonality of aquatic macrophytes in Southern Hemisphere inland wetlands. *Hydrobiologia* 125, 137–150.
- Mitsch, W. J. and J. G. Gosselink (1986). *Wetlands*. New York: Van Nostrand Reinhold.
- Muller, K. L., G. G. Ganf, and P. I. Boon (1994). Methane flux from beds of *Baumea arthropphylla* (Nees)Boeckeler and *Triglochin procerum* R.Br. at Bool Lagoon, South Australia. *Australian Journal of Marine and Freshwater Research* 45, 1543–1553.
- Neill, C. (1990). Effects of nutrients and water levels on emergent macrophyte biomass in a prairie marsh. *Canadian Journal of Botany* 68, 1007–1014.
- Nilsson, C., U. Sperens, G. Grelsson, and M. Johansson (1989). Patterns of plant species richness along riverbanks. *Ecology* 70, 77–84.
- Nilsson, C. and S. D. Wilson (1991). Convergence in plant community structure along disparate gradients: Are lakeshores inverted mountainsides? *The American Naturalist* 137, 774–790.
- Noble, I. R. and R. O. Slatyer (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43, 5–21.
- Ondok, J. P. and J. P. Květ (1978). Selection of sampling areas in assessment of production. In D. Dykyjová and J. Květ (Eds.), *Pond Littoral Ecosystems. Structure and Functioning. Methods and Results of Quantitative Ecosystem Research in the Czechoslovakian I.B.P. Wetland Project*, Volume 28 of *Ecological Studies. Analysis and Synthesis.*, pp. 163–174. Berlin: Springer-Verlag.
- Ostendorp, W. (1991). Damage by episodic flooding to *Phragmites* reeds in a prealpine lake: proposal of a model. *Oecologia* 86, 119–124.
- Parker, S. A. and N. C. H. Reid (1983). Birds. In M. J. Tyler, C. R. Twidale, J. K. Ling, and J. W. Holmes (Eds.), *Natural History of the South East*, pp. 135–150. Adelaide: Royal Society of South Australia Inc.
- Phillips, G. L., D. F. Eminson, and B. Moss (1978). A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany* 4, 103–126.
- Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins (1989). The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54, 129–136.
- Poiani, K. and W. Johnson (1988). Effects of hydroperiod on seed-bank composition in semipermanent prairie wetlands. *Canadian Journal of Botany* 67, 856–864.
- Ponnamperuma, F. N. (1972). The chemistry of submerged soils. *Advances in Agronomy* 24, 29–96.

- Poore, M. E. D. (1955a). The use of phytosociological methods in ecological investigations. I. The Braun-Blanquet system. *Journal of Ecology* 43, 226–244.
- Poore, M. E. D. (1955b). The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun-Blanquet system. *Journal of Ecology* 43, 245–269.
- Poore, M. E. D. (1955c). The use of phytosociological methods in ecological investigations. III. Practical application. *Journal of Ecology* 43, 606–651.
- Poore, M. E. D. (1956). The use of phytosociological methods in ecological investigations. IV. General discussion of phytosociological problems. *Journal of Ecology* 44, 28–50.
- Potts, P. J. (1987). X-ray fluorescence analysis: principles and practice of wavelength dispersive spectrometry. In P. Potts (Ed.), *A handbook of silicate rock analysis*. Glasgow: Blackie and Son.
- Pressey, R. L. and P. Adam (1995). A review of wetland inventory and classification in Australia. *Vegetatio* 118, 81–101.
- Ramensky, L. G. (1930). Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere, verschiedenartig wirkende Faktoren bestimmt werden. *Beiträge zur Biologie der Pflanzen* 18, 269–304.
- Ramsar Convention Bureau and International Union for the Conservation of Nature (1990). *Proceedings of the Fourth Conference of the Contracting Parties to the Convention on Wetlands of International Importance Especially as Waterfowl Habitat*, Volume 1, Montreaux, Switzerland. Ramsar Convention Bureau and International Union for the Conservation of Nature.
- Rea, N. (1993). *Influence of water regime on the population ecology of two emergent macrophytes*. Ph. D. thesis, The University of Adelaide.
- Rea, N. and G. G. Ganf (1994a). How emergent plant experience water regime in a mediterranean-type wetland. *Aquatic Botany* 49, 117–136.
- Rea, N. and G. G. Ganf (1994b). The influence of water regime on the performance of aquatic plants. *Water Science and Technology* 29, 127–132.
- Reddy, K. R. and W. H. Patrick (1975). Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. *Soil Biology and Biochemistry* 7, 87–94.
- Reeves, P. R. (1970). Nature conservation in the South East of South Australia. I. Native forest and virgin swamps of the Lower South East. Technical report, Nature Conservation Society of South Australia.
- Resh, V. H., A. G. Hildrew, B. Statzner, and C. R. Townsend (1994). Theoretical habitat templates, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology* 31, 539–554.
- Roberts, J. and G. G. Ganf (1986). Annual production of *Typha orientalis* Presl. in inland Australia. *Australian Journal of Marine and Freshwater Research* 37, 659–668.
- Rørslett, B. (1984). Environmental factors and aquatic macrophyte response in regulated lakes—a statistical approach. *Aquatic Botany* 19, 199–220.

- Sculthorpe, C. (1967). *The Biology of Aquatic Vascular Plants*. London: Edward Arnold.
- Semeniuk, C. A. and V. Semeniuk (1995). A geomorphic approach to global classification for inland wetlands. *Vegetatio* 118, 103–124.
- Sjöberg, K. and K. Danell (1983). Effects of permanent flooding on *Carex-Equisetum* wetlands in northern Sweden. *Aquatic Botany* 15, 275–286.
- Smilauer, P. (1992). *CanoDraw v3.0 [computer program]*. Ithaca, N.Y.: Microcomputer Power.
- Smith, L. M. and J. A. Kadlec (1985). The effects of disturbance on marsh seed banks. *Canadian Journal of Botany* 63, 2133–2137.
- Smith, S. G. (1987). *Typha*: Its taxonomy and the ecological significance of hybrids. *Ergebnisse der Limnologie* 27, 129–138.
- Sneath, P. H. A. and R. R. Sokal (1973). *Numerical Taxonomy*. San Francisco: Freeman.
- South Eastern Wetlands Committee (1984). *Wetland resources of the South East of South Australia: Investigation of wetland areas in the South East of South Australia for conservation and recreation uses: Volume I. Conduct of investigation and findings of the committee. (The Report of the South Eastern Wetlands Committee)*, Adelaide, South Australia. South Eastern Wetlands Committee.
- Sparrow, A. D. (1991). *A geobotanical study of the remnant natural vegetation of temperate South Australia*. Ph. D. thesis, The University of Adelaide.
- Specht, R. L. (1972). *The Vegetation of South Australia (Second Edition)*. Adelaide: British Science Guild Handbooks Committee.
- Spence, D. H. N. (1982). The zonation of plants in freshwater lakes. *Advances in Ecological Research* 12, 37–125.
- Spence, D. H. N., R. M. Campbell, and J. Chrystal (1971). Productivity of submerged freshwater macrophytes. *Hidrobiologia* 12, 160–176.
- Squires, L. and A. G. van der Valk (1992). Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. *Canadian Journal of Botany* 70, 1860–1867.
- Storey, A. W., R. M. Vervest, G. B. Pearson, and S. A. Halse (1993). *Waterbird usage of wetlands on the Swan Coastal Plain*, Volume 7 of *Wetlands of the Swan Coastal Plain*. Perth: Water Authority of Western Australia, and Environmental Protection Authority.
- Sukopp, H. and B. Markstein (1989). Changes of the reed beds along the Berlin Havel, 1962–1987. *Aquatic Botany* 35, 27–39.
- Szczepańska, W. and A. Szczepański (1976). Growth of *Phragmites communis* Trin., *Typha latifolia* L., and *Typha angustifolia* L. in relation to the fertility of the soils. *Polskie Archiwum Hydrobiologii* 23, 233–248.
- Taylor, A. R. D., G. W. Howard, and G. W. Begg (1995). Developing wetland inventories in Southern Africa: A review. *Vegetatio* 118, 57–79.
- ter Braak, C. J. F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.

- ter Braak, C. J. F. (1988). *CANOCO—a FORTRAN program for [cano]nical [c]ommunity [o]rdination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis*. Agricultural Mathematics Group, Ministerie van Landbouw en Visserij.
- ter Braak, C. J. F. and C. W. N. Looman (1986). Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* 65, 3–11.
- van der Valk, A. G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology* 62, 688–696.
- van der Valk, A. G. and L. C. Bliss (1971). Hydrarch succession and net primary production of oxbow lakes in central Alberta. *Canadian Journal of Botany* 49, 1177–1199.
- van der Valk, A. G. and C. B. Davis (1978). Primary production of prairie glacial marshes. In R. E. Good, D. F. Whigham, and R. L. Simpson (Eds.), *Freshwater wetlands. Ecological processes and management potential*, pp. 21–37. New York: Academic Press.
- van der Valk, A. G. and C. B. Davis (1980). The impact of a natural drawdown on the growth of four emergent species in a prairie glacial marsh. *Aquatic Botany* 9, 301–322.
- Vermaat, J. E. and R. J. De Bruyne (1993). Factors limiting the distribution of submerged waterplants in the lowland River Vecht (The Netherlands). *Freshwater Biology* 30, 147–157.
- Walker, K. F., A. J. Boulton, M. C. Thoms, and F. Sheldon (1994). Effects of water-level changes induced by weirs on the distribution of littoral plants along the River Murray, South Australia. *Australian Journal of Marine and Freshwater Research* 45, 1421–1438.
- Waters, I. and J. M. Shay (1990). A field study of the morphometric response of *Typha glauca* shoots to a water depth gradient. *Canadian Journal of Botany* 68, 2339–2343.
- Weisner, S. E. B. (1987). The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. *Freshwater Biology* 18, 537–544.
- Weisner, S. E. B. and W. Granéli (1989). Influence of substrate conditions on the growth of *Phragmites australis* after a reduction in oxygen transport to below-ground parts. *Aquatic Botany* 35, 71–80.
- Weisner, S. E. B. and J. A. Strand (1996). Rhizome architecture in *Phragmites australis* in relation to water depth: Implications for within-plant oxygen transport distances. *Folia Geobotanica et Phytotaxonomica* 31, 91–97.
- Wesseling, J. (1974). Crop growth and wet soils. In J. van Schilfgaarde (Ed.), *Drainage for Agriculture*, Volume 17 of *Agronomy*, pp. 7–37. Madison, Wisconsin: American Society of Agronomy.
- Westlake, D. F. (1963). Comparisons of plant productivity. *Biological Reviews*. 38, 385–425.
- Westlake, D. F. (1975). Primary production of freshwater macrophytes. In J. P. Copper (Ed.), *Photosynthesis and Productivity in Different Environments*. London: Cambridge University Press.
- Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews*. 49, 207–264.

- Whittaker, R. H. (Ed.) (1978). *Ordination of Plant Communities. Handbook of Vegetation Science 5* (2nd ed.). The Hague: Junk.
- Willcox, D. A. and J. E. Meeker (1991). Disturbance effects on aquatic vegetation in regulated and unregulated lakes in northern Minnesota. *Canadian Journal of Botany* 69, 1542–1551.
- Wilson, S. D. and P. A. Keddy (1985). The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: an experimental study. *Aquatic Botany* 21, 277–284.
- Wilson, S. D., D. R. J. Moore, and P. A. Keddy (1993). Relationships of marsh seed banks to vegetation patterns along environmental gradients. *Freshwater Biology* 29, 361–370.
- Yamasaki, S. and I. Tange (1981). Growth responses of *Zizania latifolia*, *Phragmites australis* and *Miscanthus sacchariflorus* to varying inundation. *Aquatic Botany* 10, 229–239.
- Zar, J. H. (1984). *Biostatistical Analysis* (Second ed.). New Jersey: Prentice-Hall.



Water Regime and the  
Aquatic Vegetation  
of Bool Lagoon,  
South Australia

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**Volume II: Figures, Tables and Appendices**

## Part II

## Figures

# Chapter 1

## Introduction

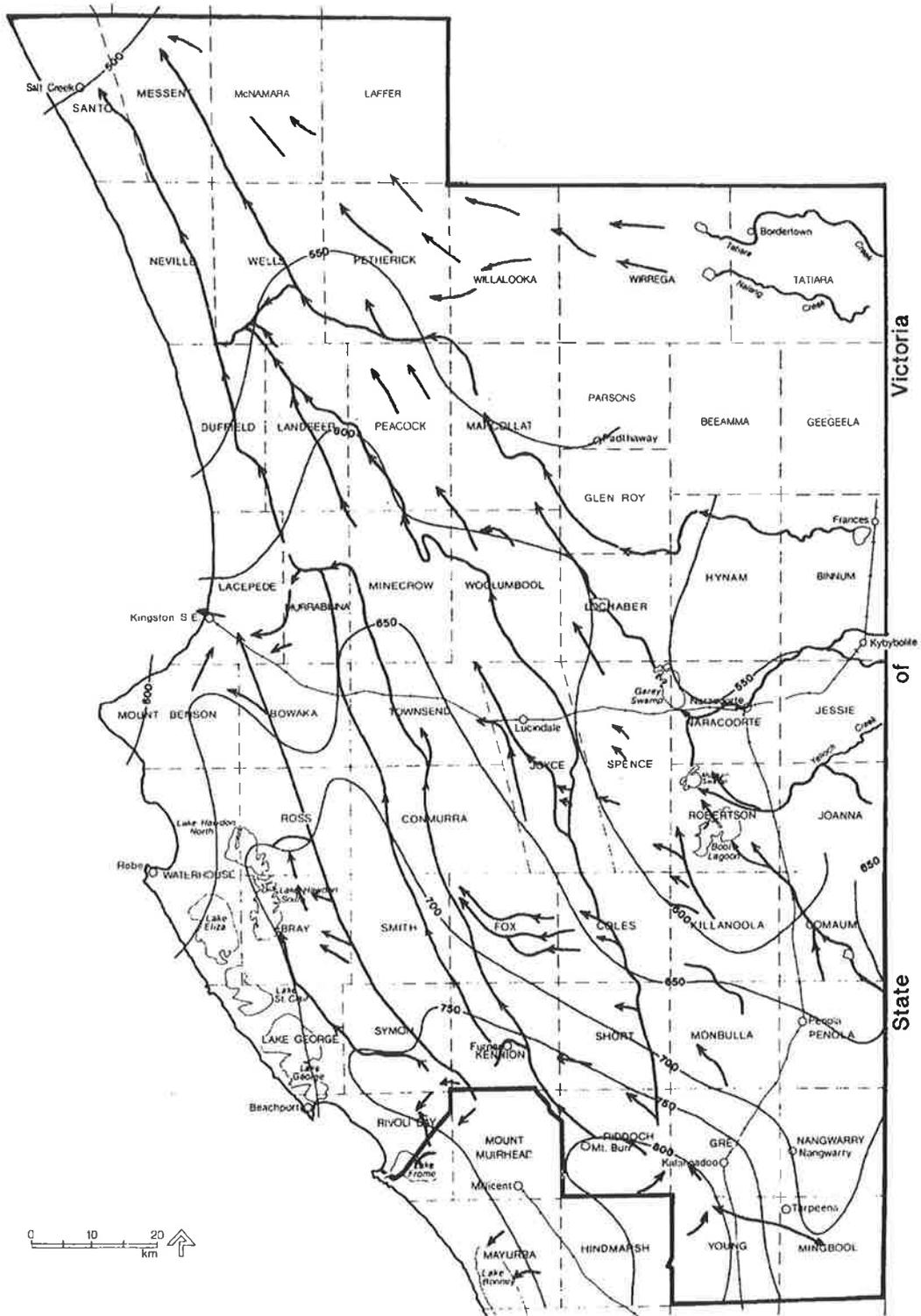
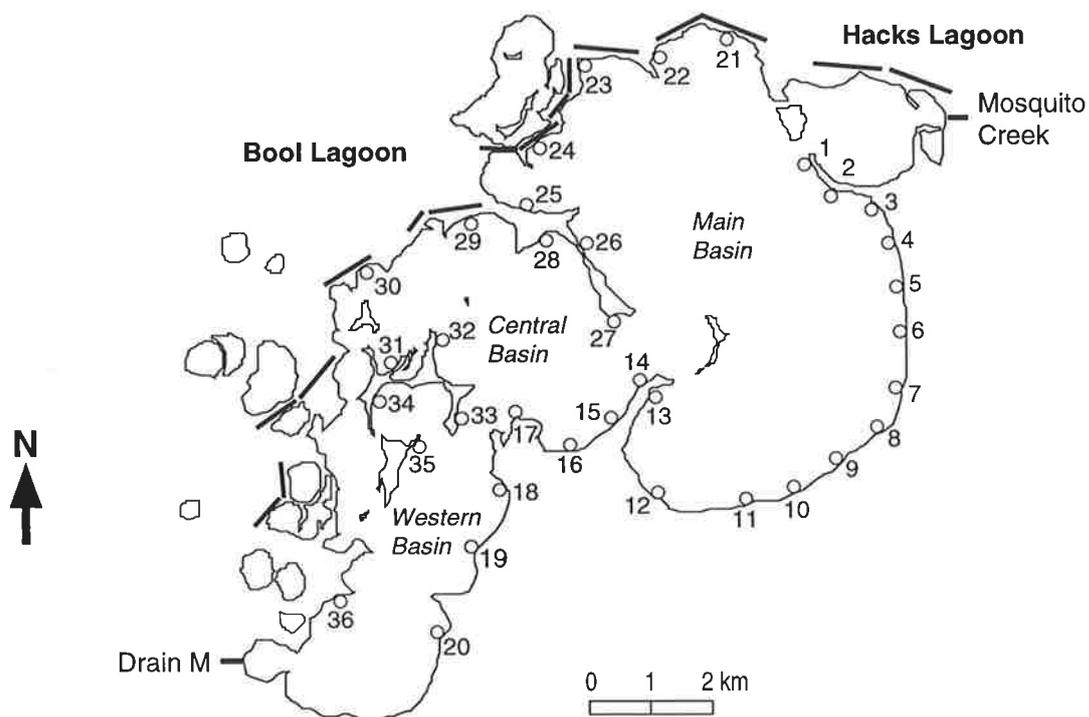


Figure 1.1: South East of South Australia showing direction of sheet water flow (after South Eastern Wetlands Committee 1984). Arrows indicate direction of water flow. Isobars indicate annual rainfall.



**Figure 1.2:** Bool Lagoon system in the South East of South Australia (Grid Ref. 37°07'S 140°40'E), showing Hacks Lagoon and the Main, Central and Western Basins of Bool Lagoon. Levee banks are shown as solid lines along the northern and western perimeters. Vegetation- and sediment-sampling sites are shown around the perimeter as hollow circles. Sites 1–20 are on the eastern side. Sites 21–36 are on the western side.

## **Chapter 2**

# **Wetland vegetation in the Lower South East of South Australia**

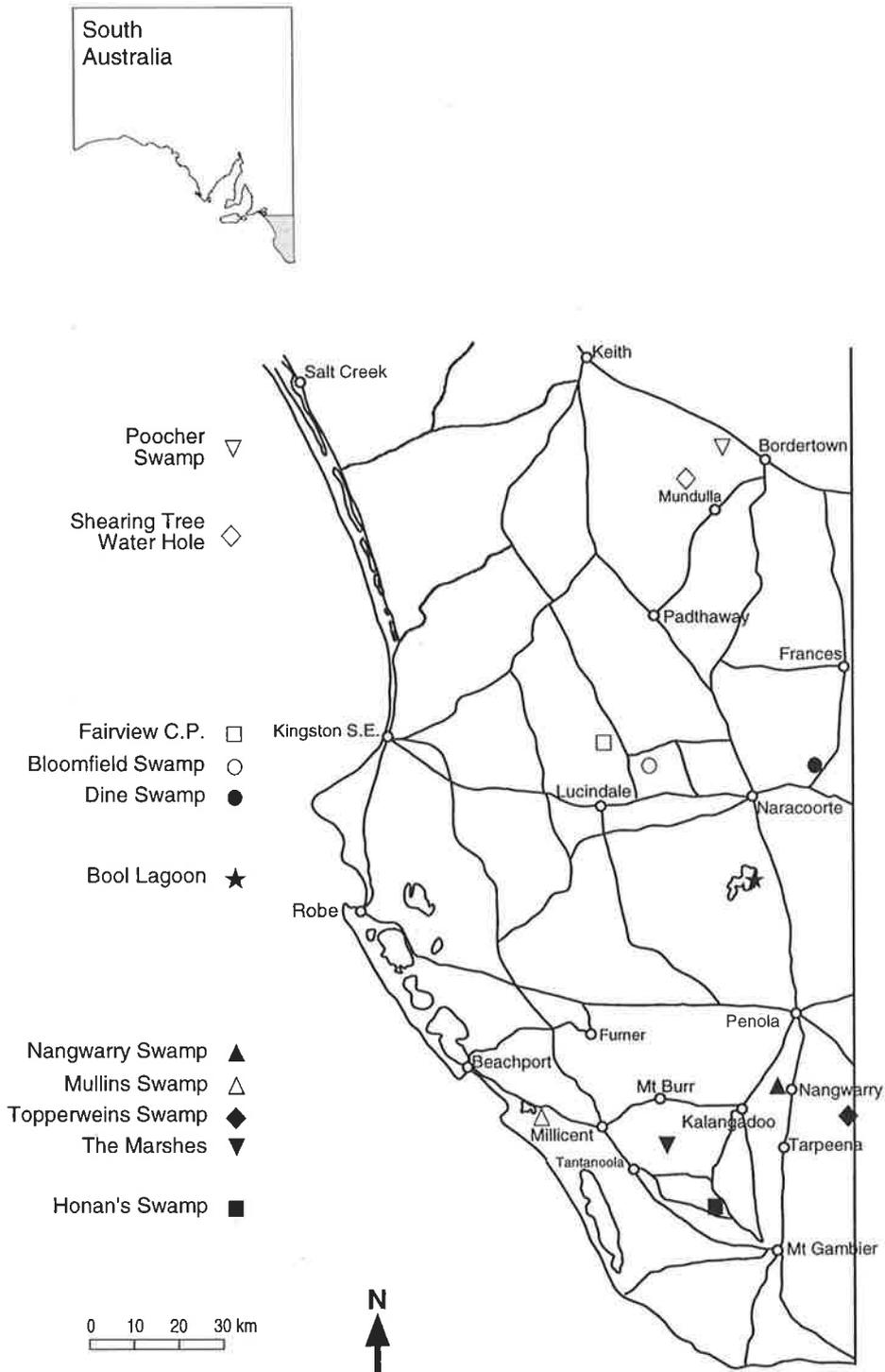
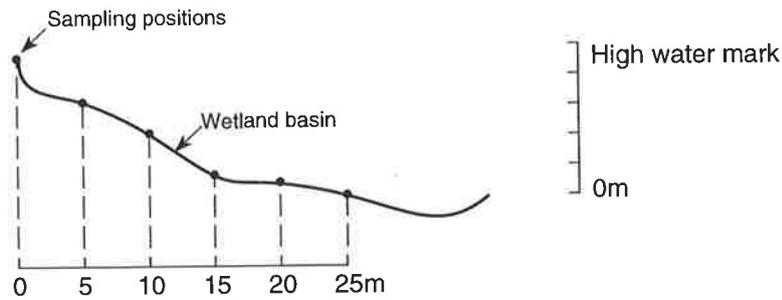
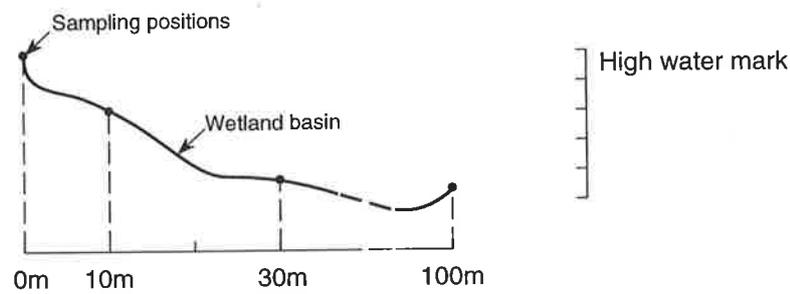


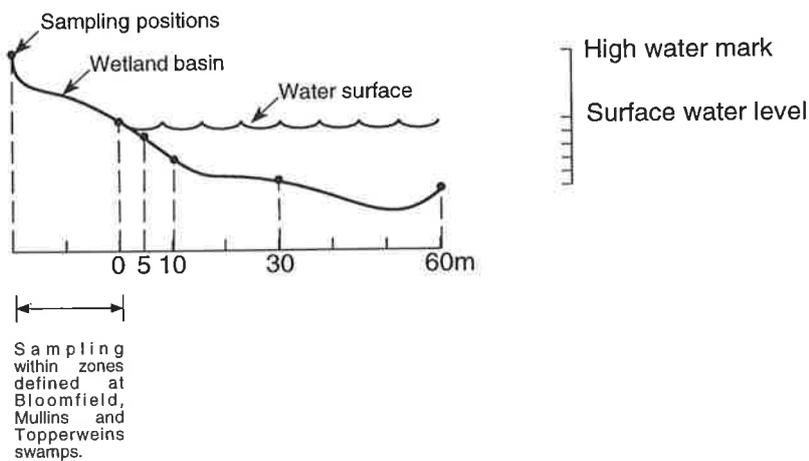
Figure 2.1: South East of South Australia showing locations of sampled wetlands.



2.2.1: Elevation measurements at G3 wetlands (Nangwarry Swamp, The Marshes and Honan's Swamp).

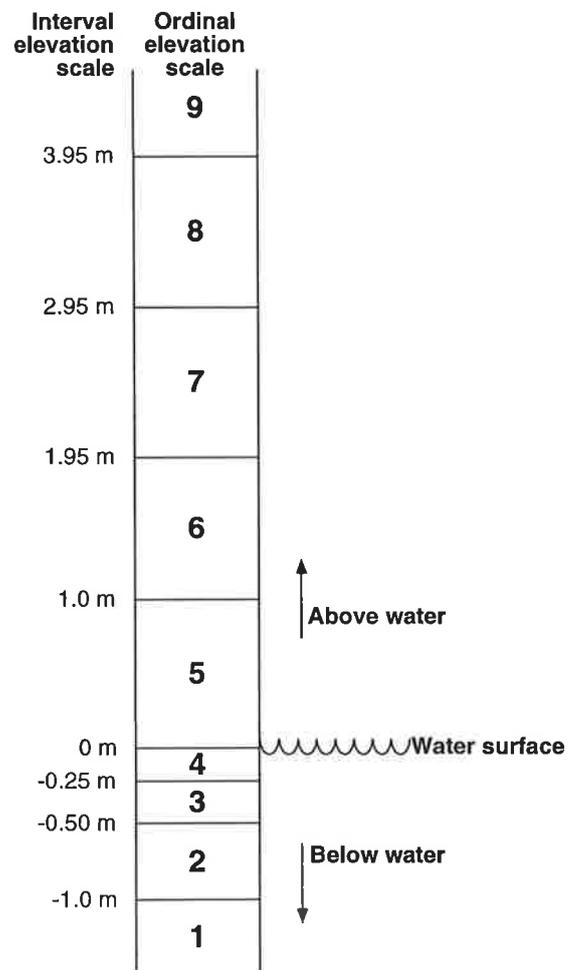


2.2.2: Elevation measurements at G7 wetlands (Bloomfield Swamp, Mullins Swamp, Topperweins Swamp).



2.2.3: Elevation measurements at G7 wetlands (Dine Swamp, Fairview C.P., Poocher Swamp, Shearing Tree Waterhole).

**Figure 2.2:** Methods used to measure elevation of sampling locations at G3 (Nangwarry, Marshes, Honan's) and G7 wetlands (Bloomfield, Dine, Fairview, Mullins, Poocher, Shearing Tree, Topperweins). Note that two methods were used at G7 wetlands.



**Figure 2.3:** Conversion scale used to convert interval dumpy level measurements of the elevation of sampling sites to ordinal elevation class. Elevation classes (1–9) were defined relative to the elevation of the water surface. Classes 1–4 occur below and classes 5–9 occur above the water surface.

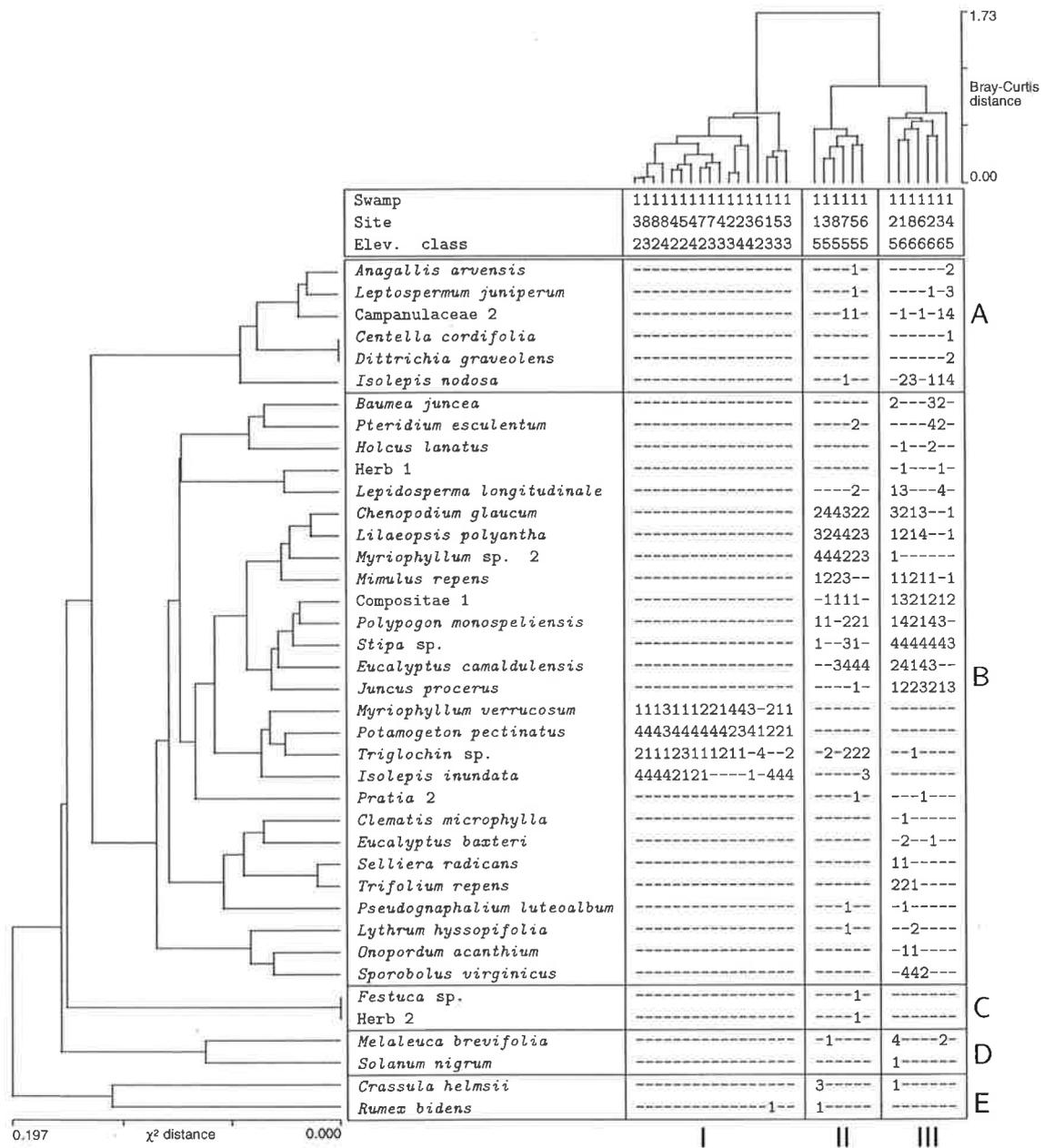
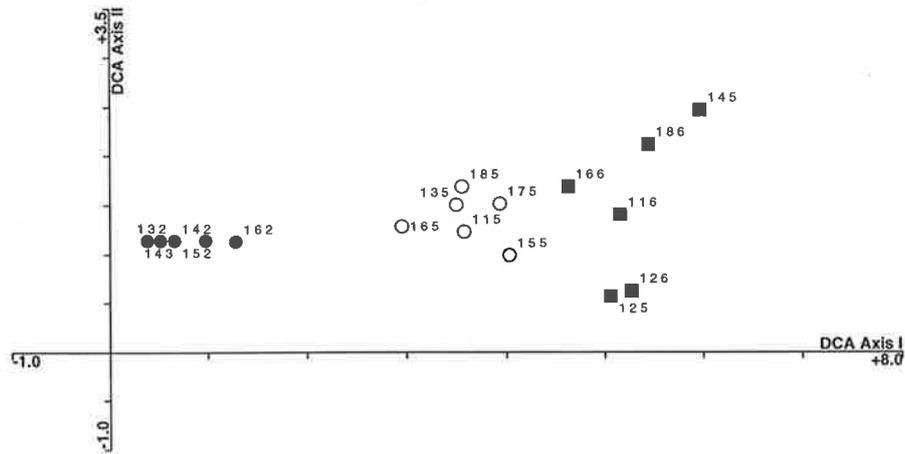
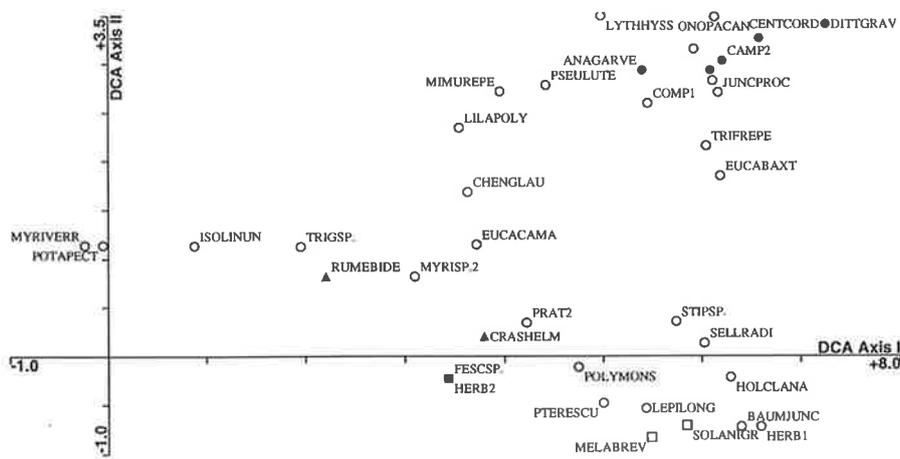


Figure 2.4: Bloomfield Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%.

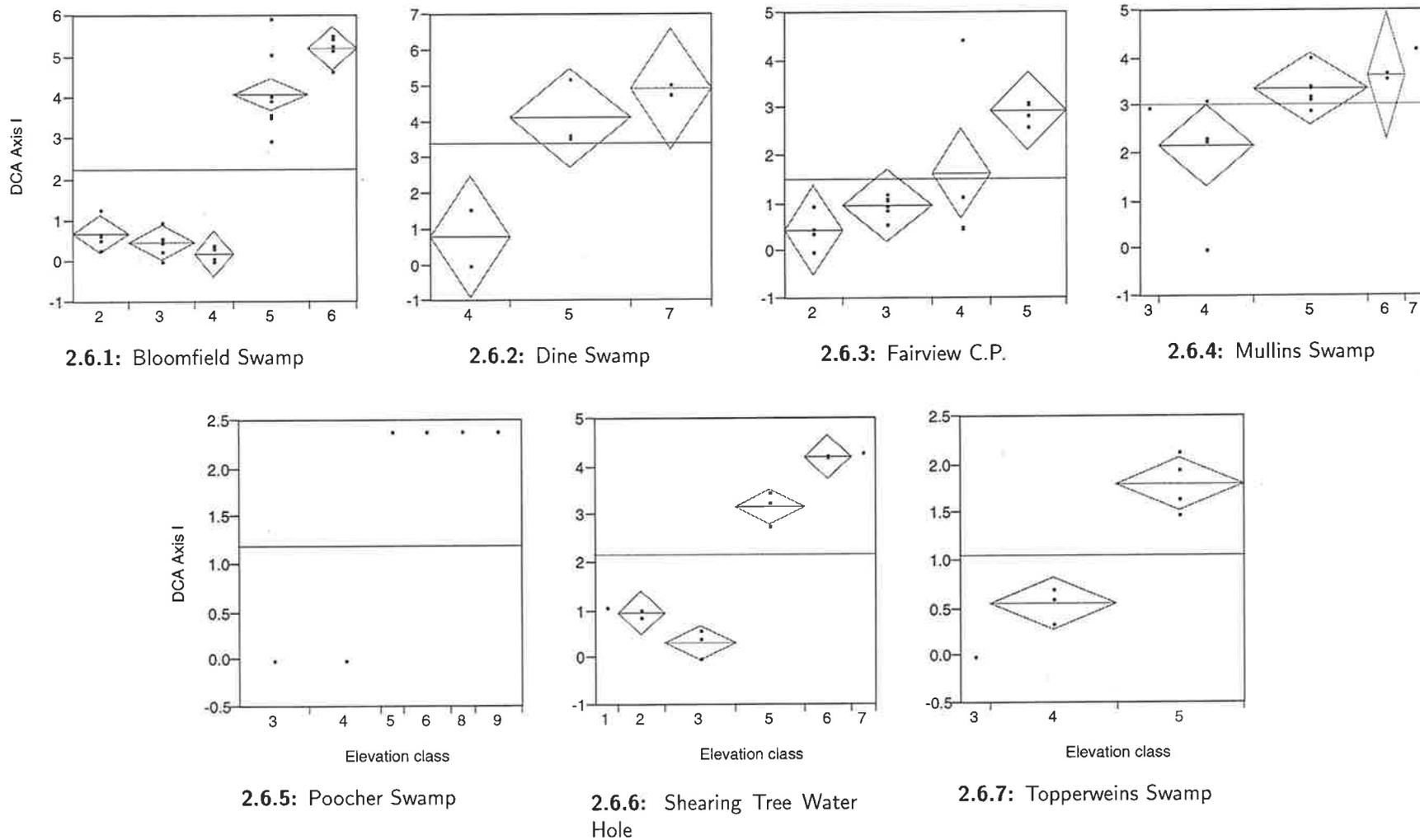


2.5.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III. Labels indicate swamp number (1), sampling location (1–8) and elevation class.

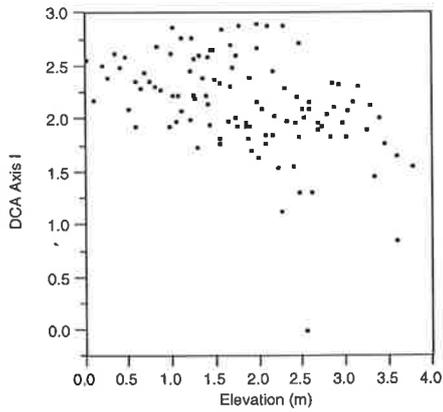


2.5.2: Species ordination on first two axes of DCA. ●=Group A; ○=Group B; ■=Group C; □=Group D; ▲=Group E. See species list for species abbreviations.

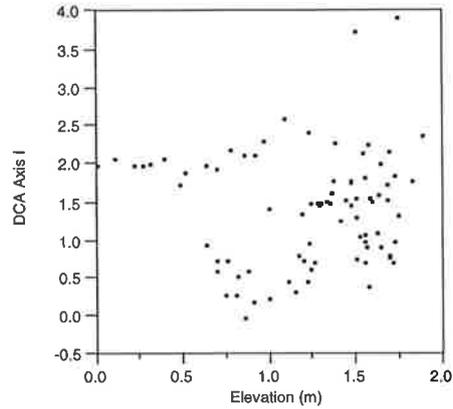
Figure 2.5: Bloomfield Swamp site and species ordinations. Classification groups are those defined in Figure 2.4. Axes explain 29.9% and 8.7% of the variation in species composition.



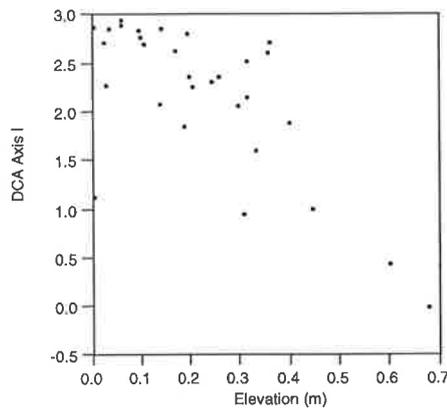
**Figure 2.6:** Relationship between DCA Axis I site ordination score and ordinal elevation class for G7 wetlands. Means diamonds: horizontal line shows the sample mean; diamond height shows the 95% confidence interval; diamond width shows the sample size for each elevation class. These correlations are shown here rather than with individual swamps to allow comparison of the importance of the elevation gradient between swamps.



**2.7.1:** Honans and Bonney's Woodland Swamp. Pearson correlation coefficient =  $-0.45$ .

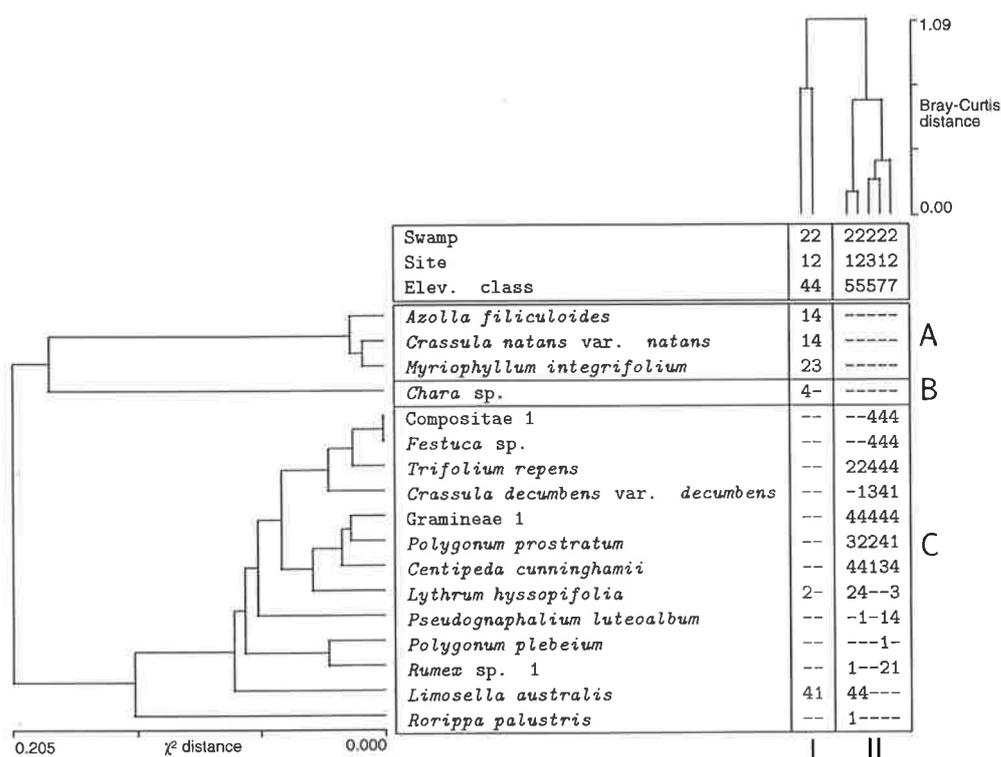


**2.7.2:** The Marshes. Pearson correlation coefficient =  $0.025$ .

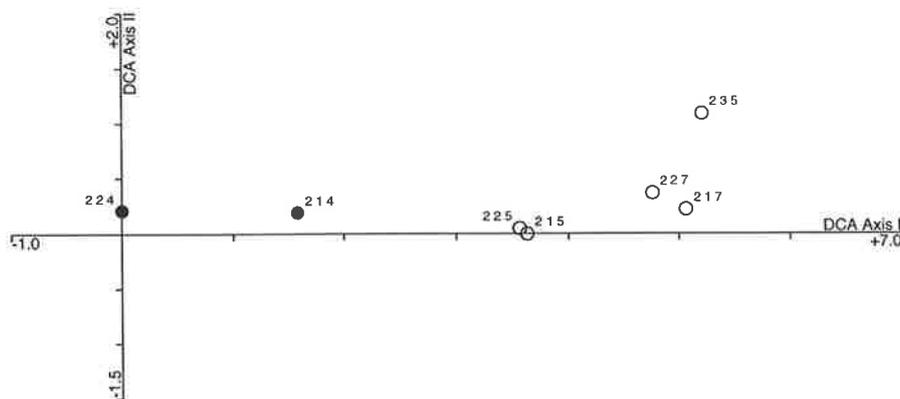


**2.7.3:** Nangwarry Swamp. Pearson correlation coefficient =  $-0.70$ .

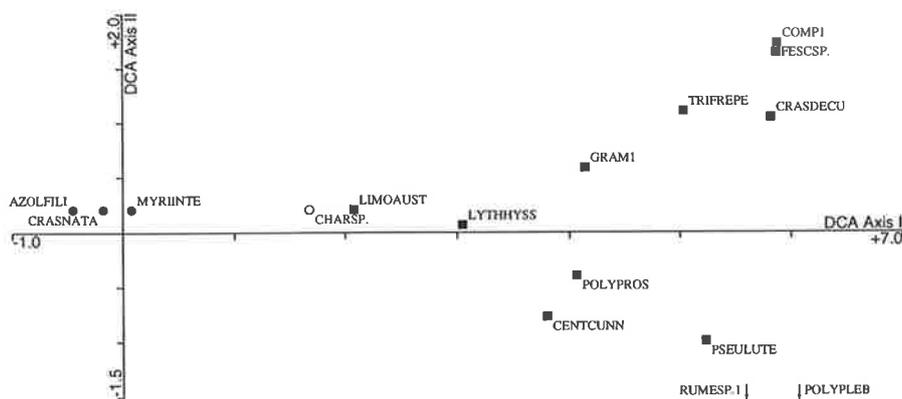
**Figure 2.7:** Relationship between DCA Axis I site ordination score and elevation (in metres, relative to minimum measured elevation in basin) for G3 wetlands.



**Figure 2.8:** Dine Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%.

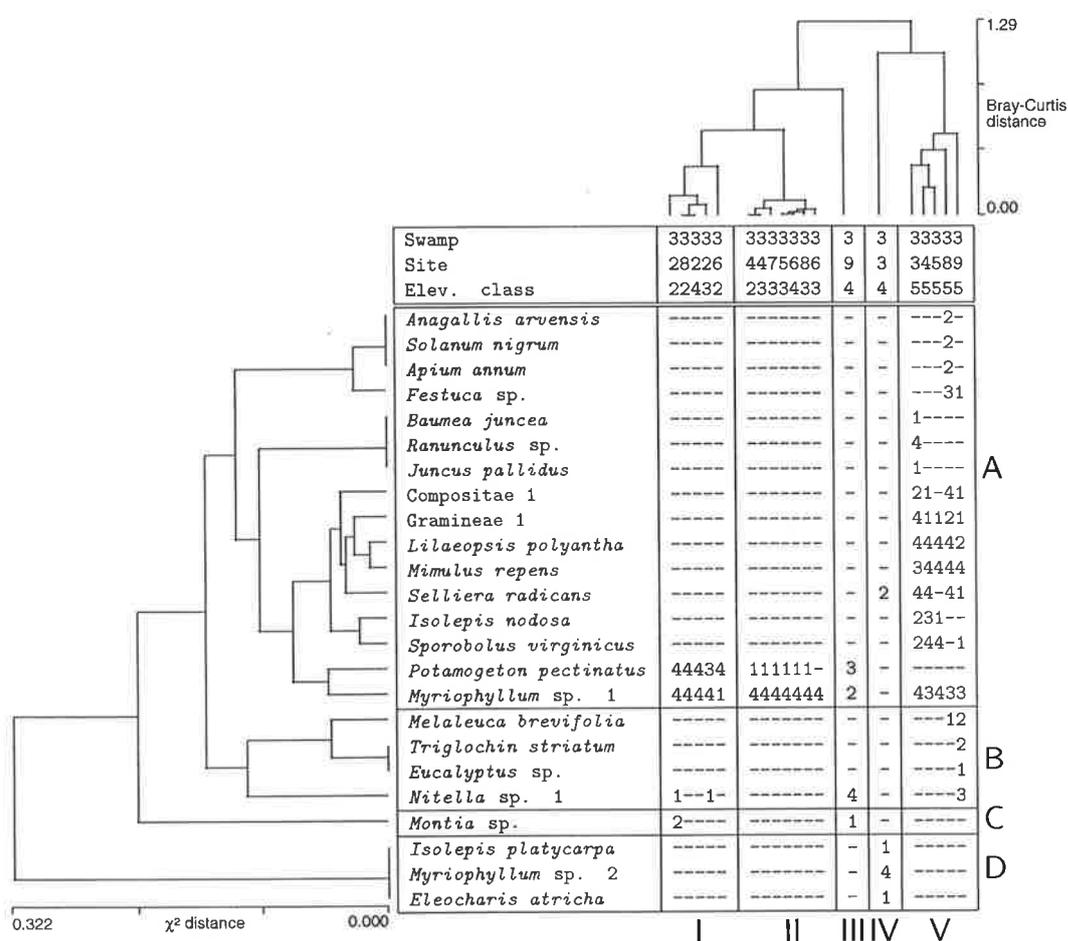


2.9.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II. Labels indicate swamp number (2), sampling location (1–3) and elevation class.

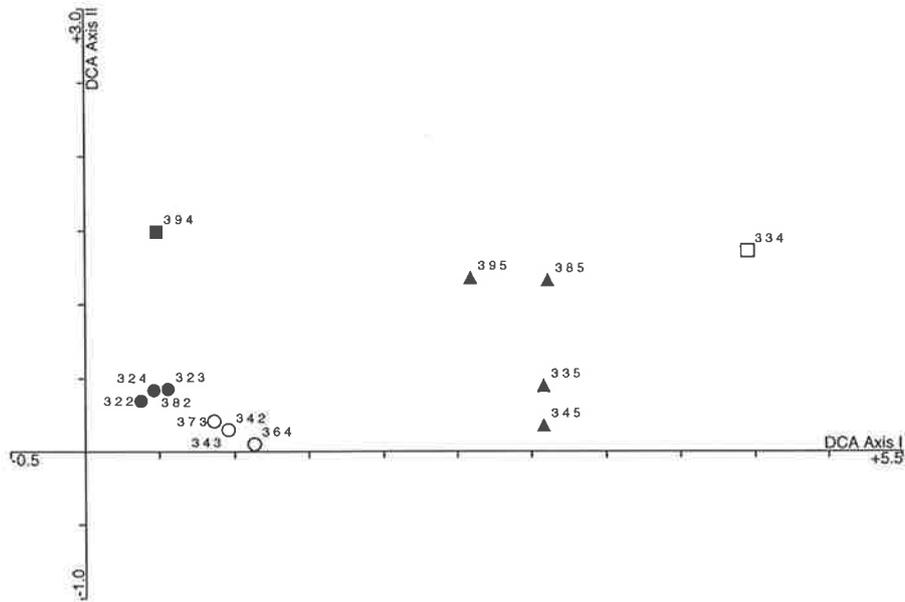


2.9.2: Species ordination on first two axes of DCA. ●=Group A; ○=Group B; ■=Group C. See species list for species abbreviations.

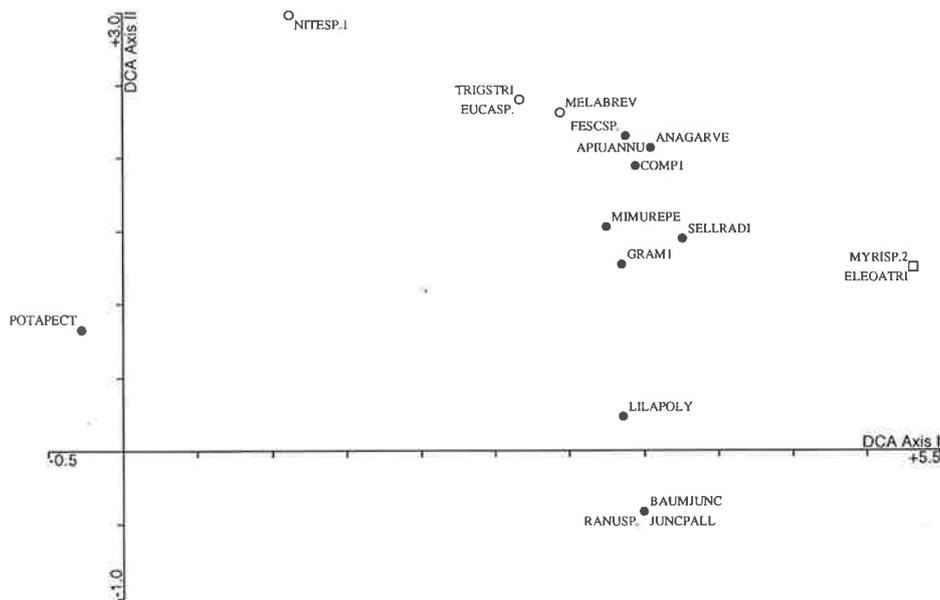
**Figure 2.9:** Dine Swamp site and species ordinations. Classification groups are those defined in Figure 2.8. Axes explain 49.5% and 3.6% of the variation in species composition.



**Figure 2.10:** Fairview Conservation Park. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.



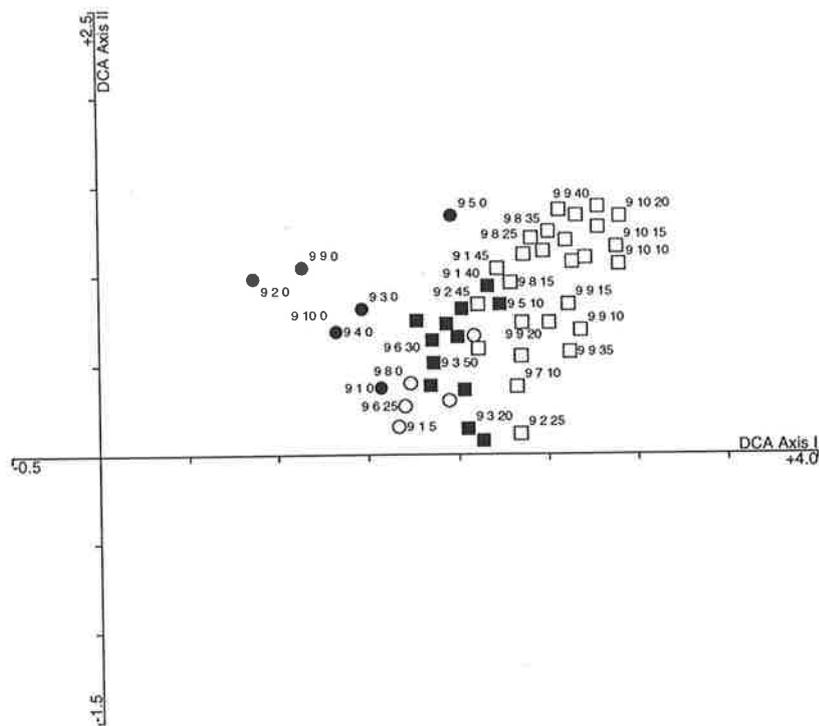
2.11.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III; □=Group IV; ▲=Group V. Labels indicate swamp number (3), sampling location (1–9) and elevation class.



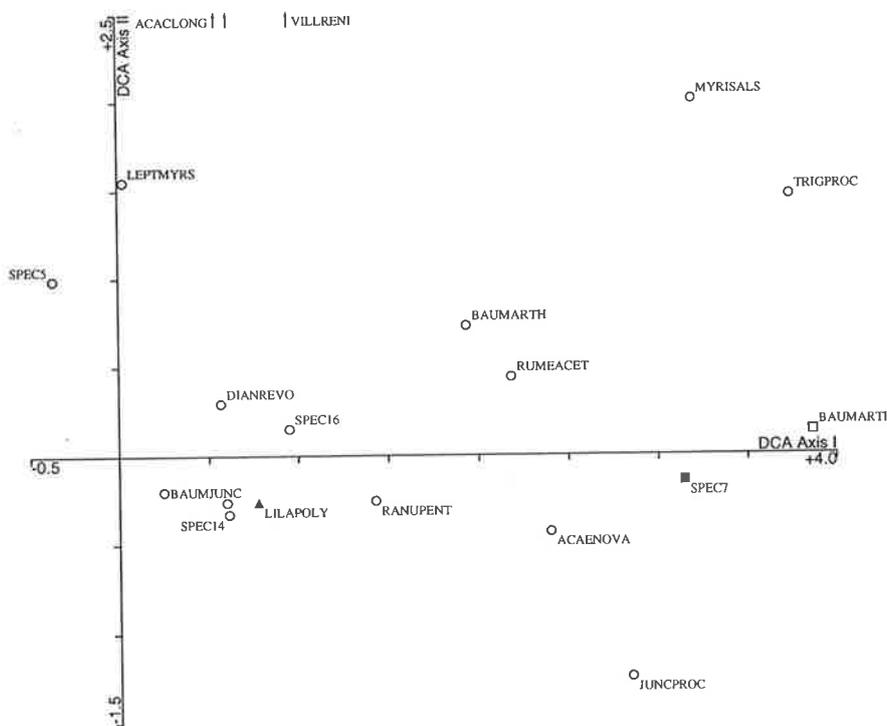
2.11.2: Species ordination on first two axes of DCA. ●=Group A; ○=Group B; ■=Group C; □=Group D. See species list for species abbreviations.

Figure 2.11: Fairview C.P. site and species ordinations. Classification groups are those defined in Figure 2.10. Axes explain 34.6% and 10.2% of the variation in species composition.





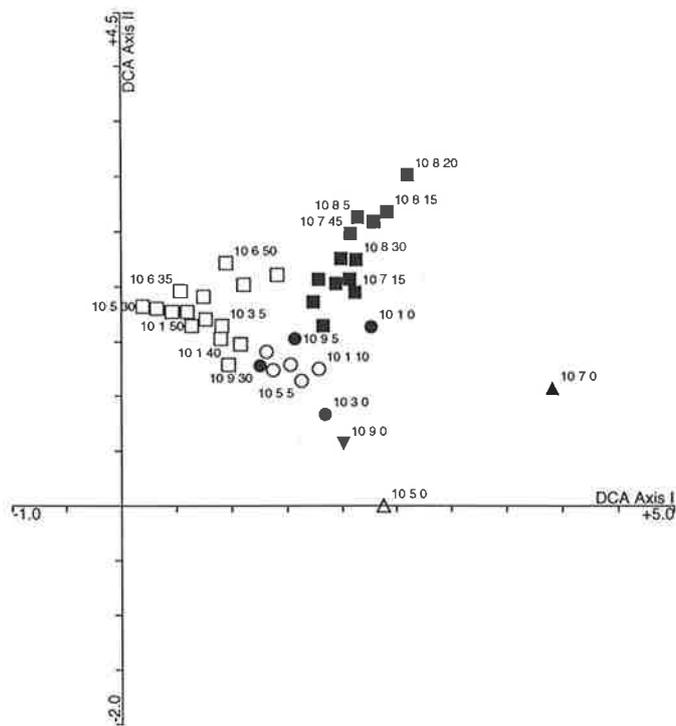
2.13.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III; □=Group IV. Labels indicate swamp number (9), sampling location (1–10) and distance from shore (m).



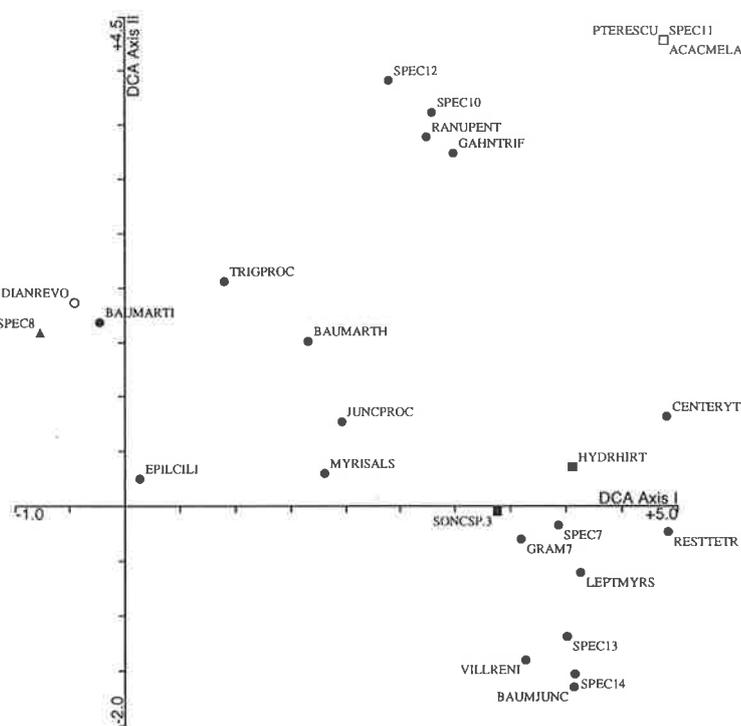
2.13.2: Species ordination on first two axes of DCA. ●=Group A (DCA Axis II score > 2.5); ○=Group B; ■=Group C; □=Group D; ▲=Group E. See species list for species abbreviations.

**Figure 2.13:** Honan’s and Bonney’s Woodland Swamp site and species ordinations. Classification groups are those defined in Figure 2.12. Axes explain 25.8% and 9.9% of the variation in species composition.





2.15.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III; □=Group IV; ▲=Group V; △=Group VI; ▼=Group VII. Labels indicate swamp number (10), sampling location (1–9) and distance from shore (m).



2.15.2: Species ordination on first two axes of DCA. ●=Group A; ○=Group B; ■=Group C; □=Group D; ▲=Group E. See species list for species abbreviations.

**Figure 2.15:** The Marshes site and species ordinations. Classification groups are those defined in Figure 2.14. Axes explain 25.8% and 12.9% of the variation in species composition.

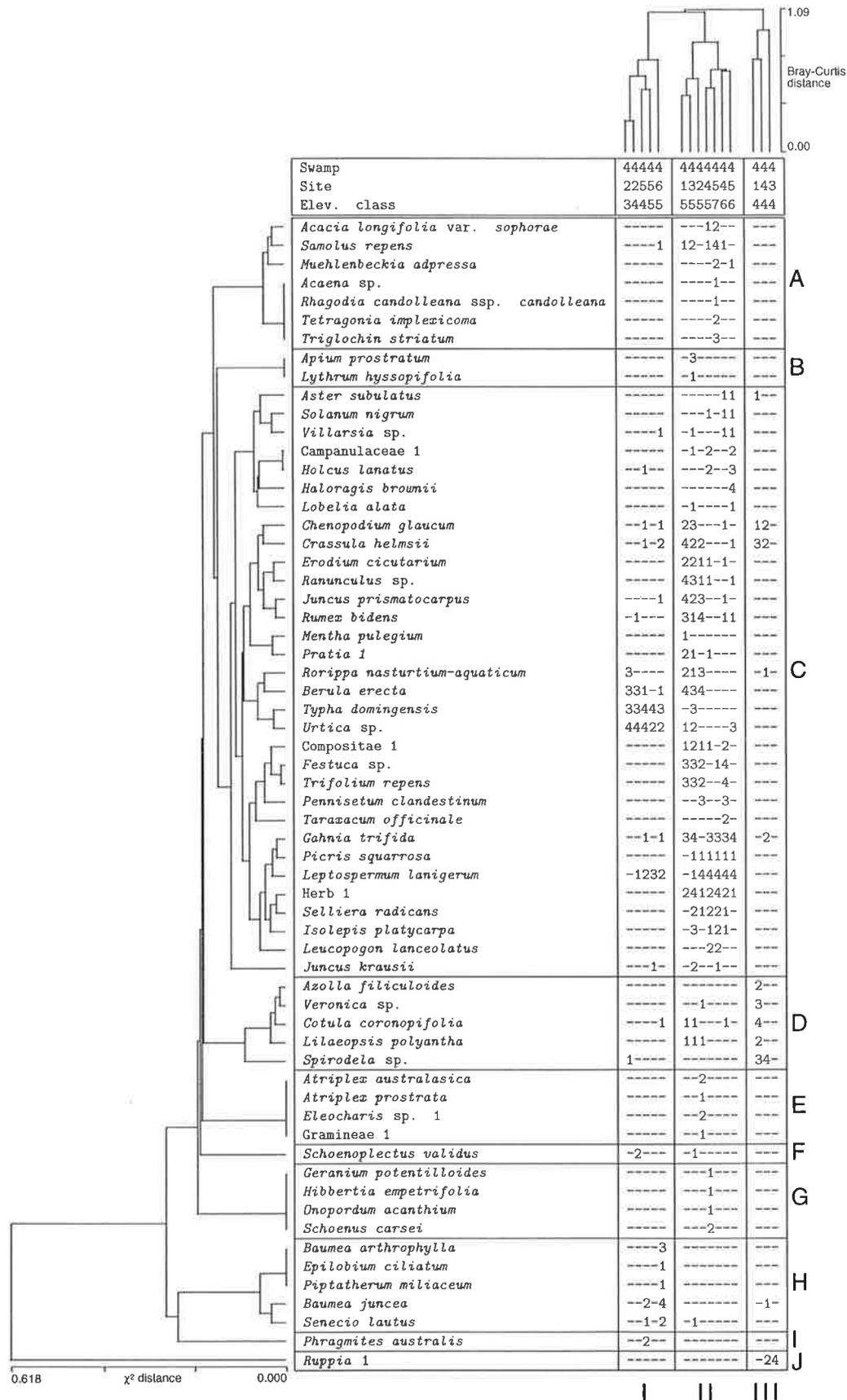
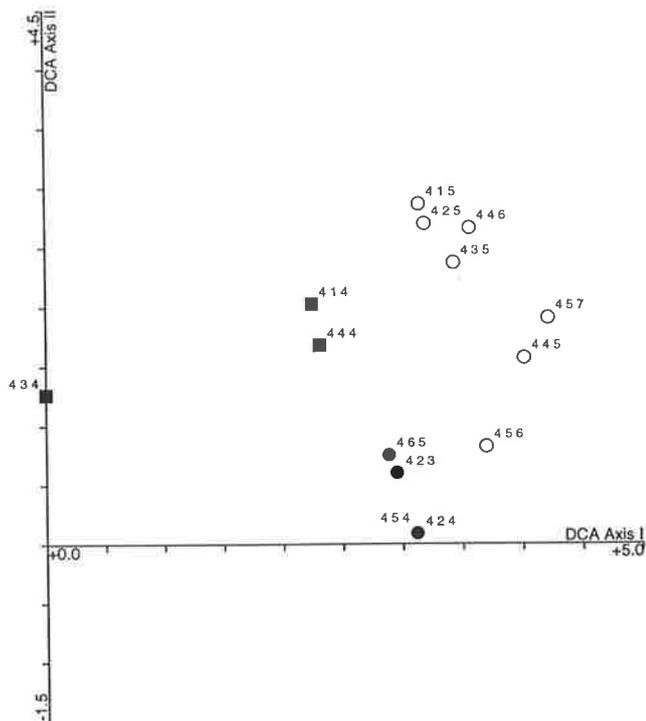
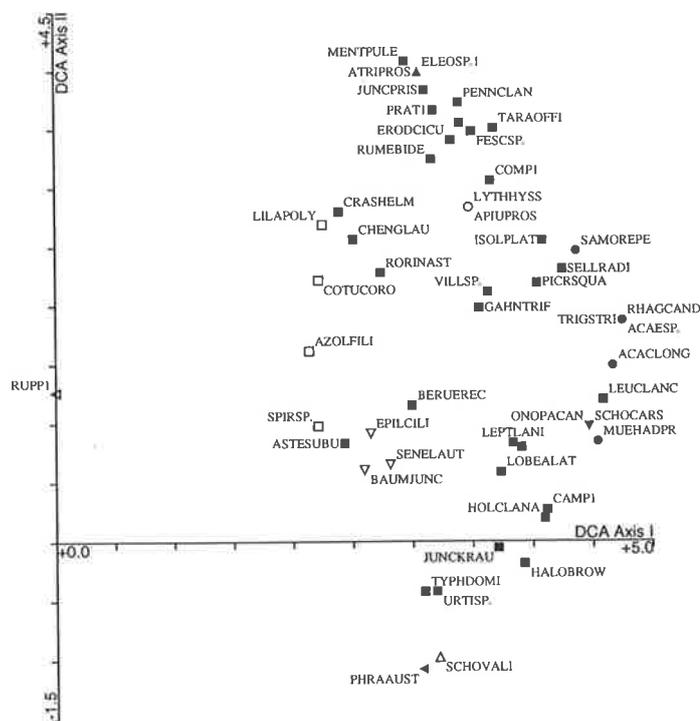


Figure 2.16: Mullins Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%.



2.17.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III. Labels indicate swamp number (4), sampling location (1–5) and elevation class.



2.17.2: Species ordination on first two axes of DCA. ● Group A; ○ Group B; ■ Group C; □ Group D; ▲ Group E; △ Group F; ▼ Group G; ▽ Group H; ◀ Group I; < Group J. See species list for species abbreviations.

Figure 2.17: Mullins Swamp site and species ordinations. Classification groups are those defined in Figure 2.16. Axes explain 17.0% and 11.3% of the variation in species composition.

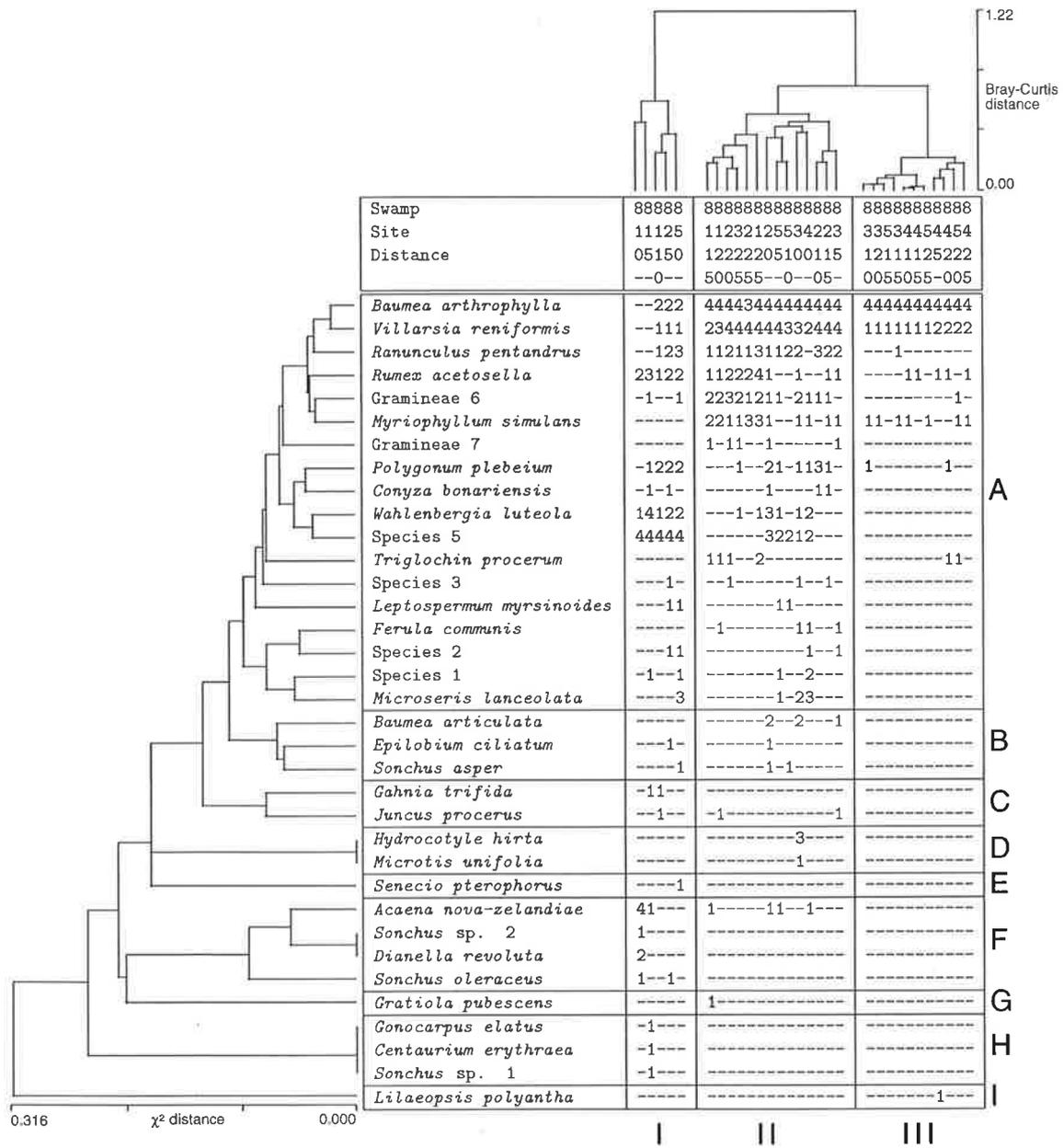
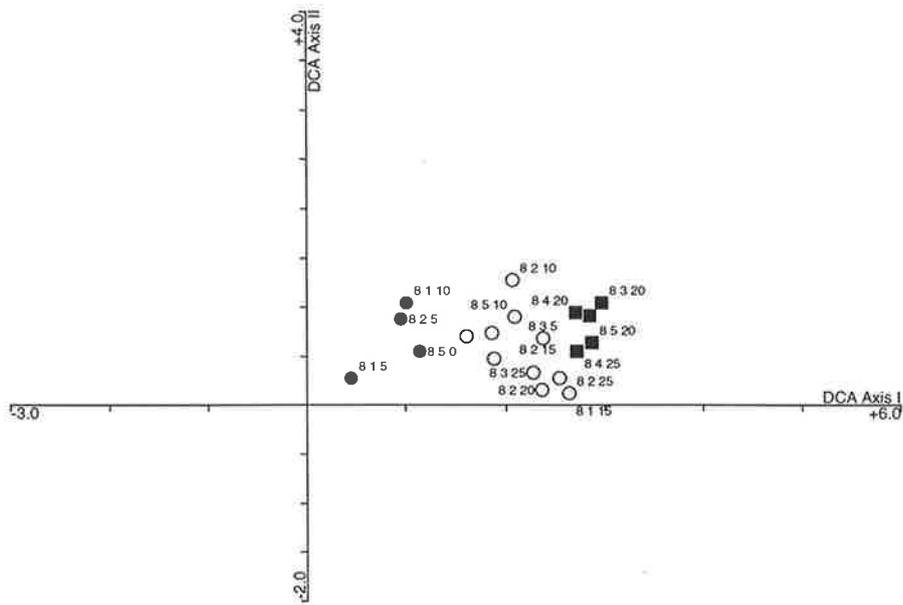
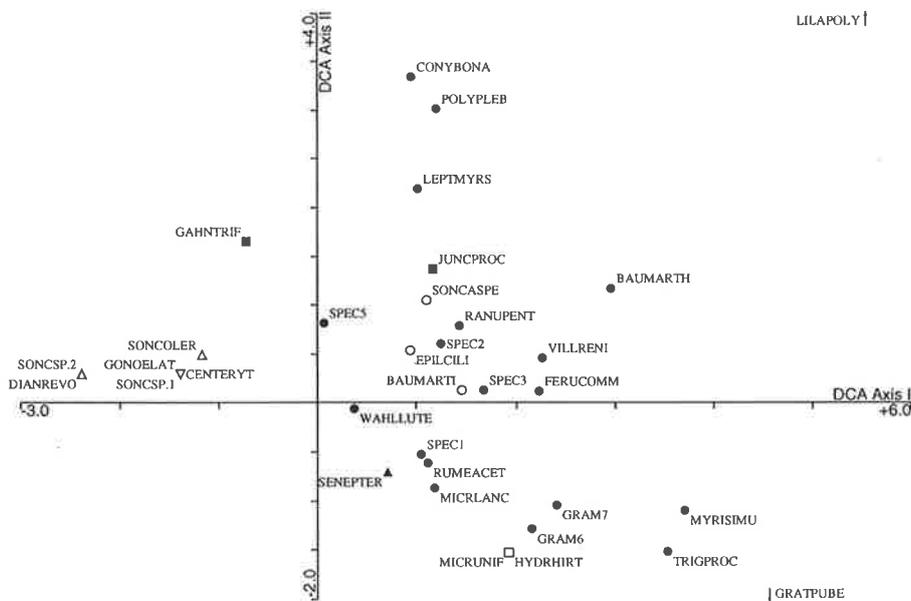


Figure 2.18: Nangwarry Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%.



2.19.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III. Labels indicate swamp number (8), sampling location (1–5) and distance from shore (m).



2.19.2: Species ordination on first two axes of DCA. ● Group A; ○ Group B; ■ Group C; □ Group D; ▲ Group E; △ Group F; ▼ Group G; ▽ Group H; ◀ Group I. See species list for species abbreviations.

Figure 2.19: Nangwarry Swamp site and species ordinations. Classification groups are those defined in Figure 2.18. Axes explain 32.7% and 7.9% of the variation in species composition.

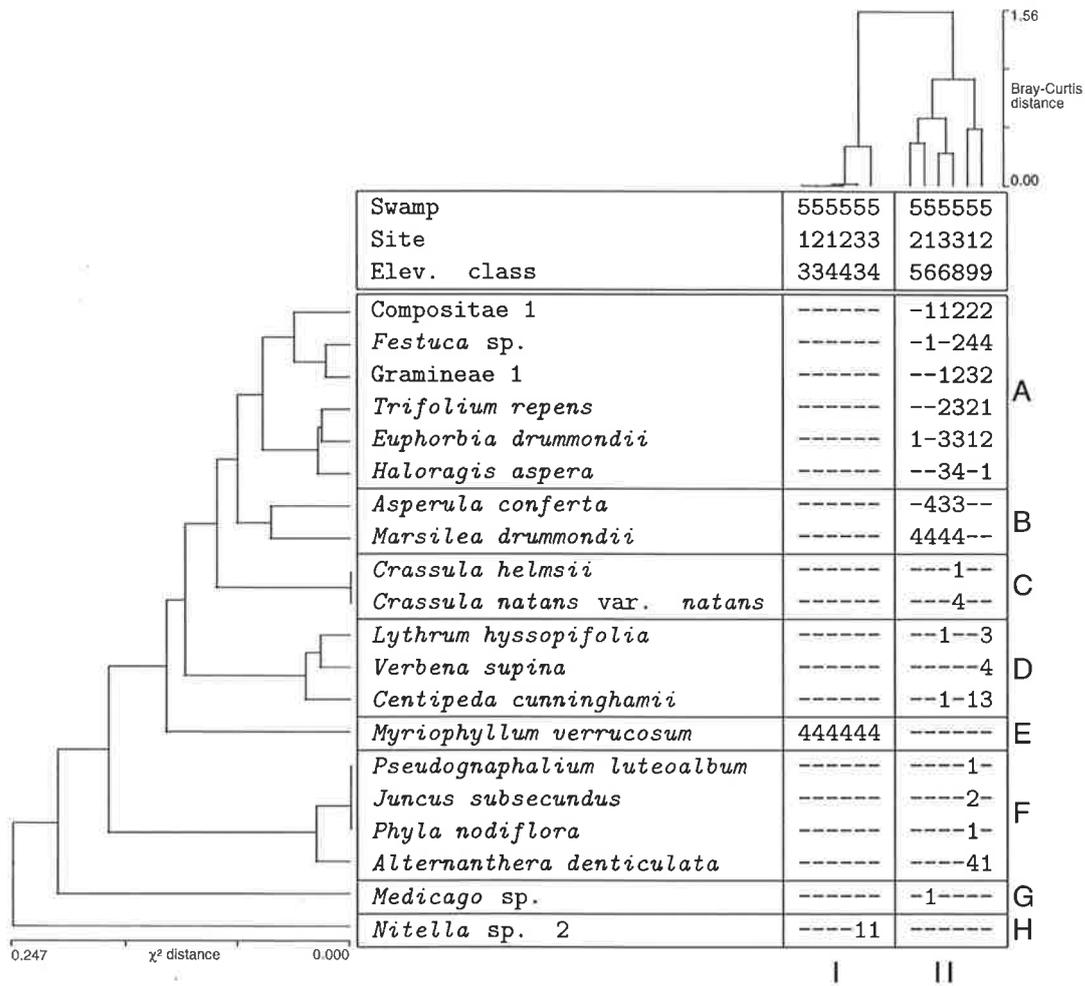
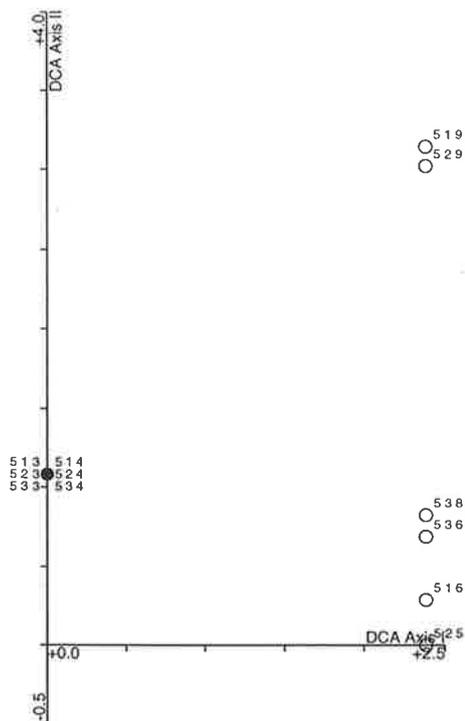
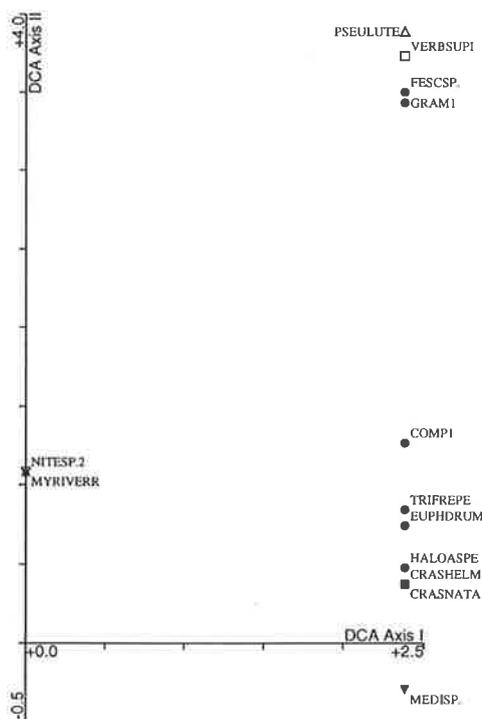


Figure 2.20: Poocher Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.



2.21.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II. Labels indicate swamp number (5), sampling location (1–3) and elevation class.



2.21.2: Species ordination on first two axes of DCA. ● Group A; ○ Group B; ■ Group C; □ Group D; ▲ Group E; △ Group F; ▼ Group G; ▽ Group H. See species list for species abbreviations.

**Figure 2.21:** Poacher Swamp site and species ordinations. Classification groups are those defined in Figure 2.20. Axes explain 37.7% and 23.3% of the variation in species composition.

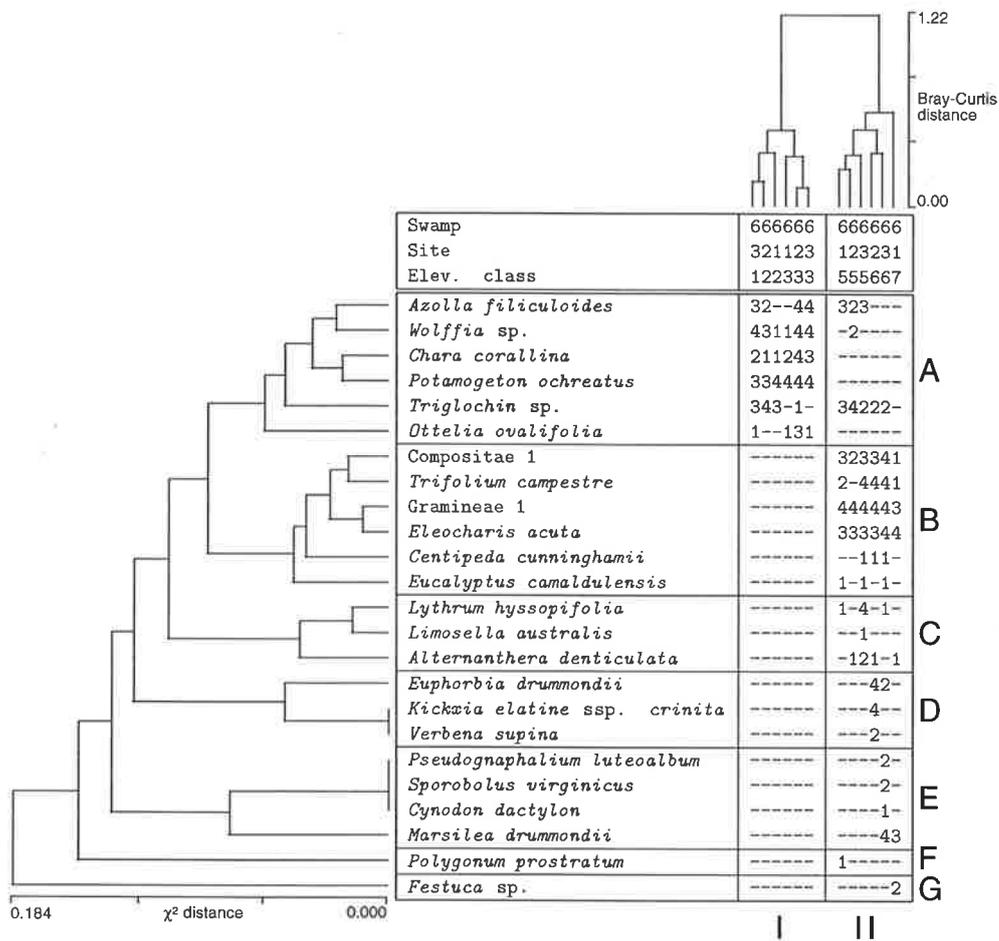
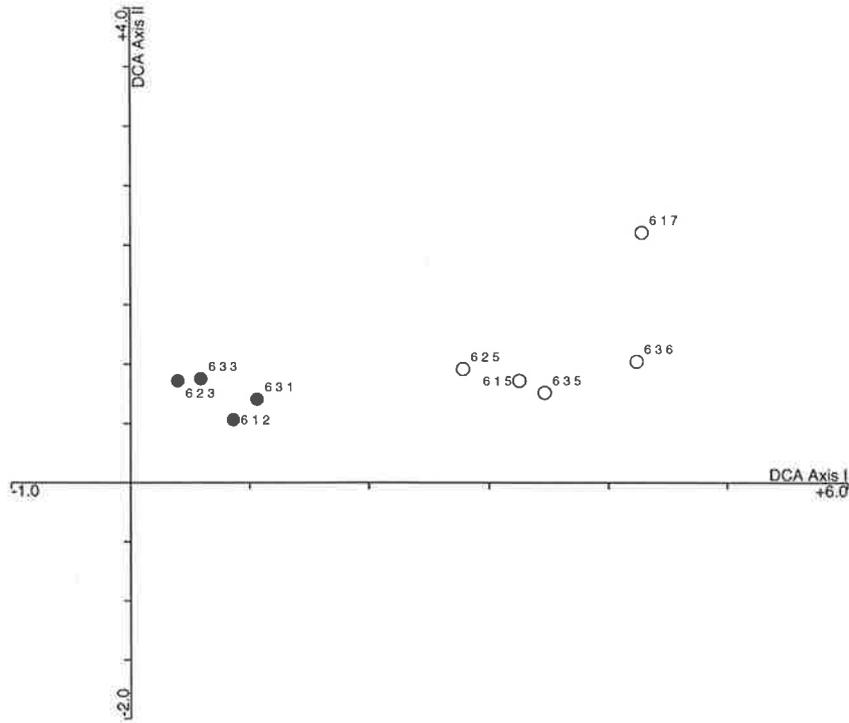
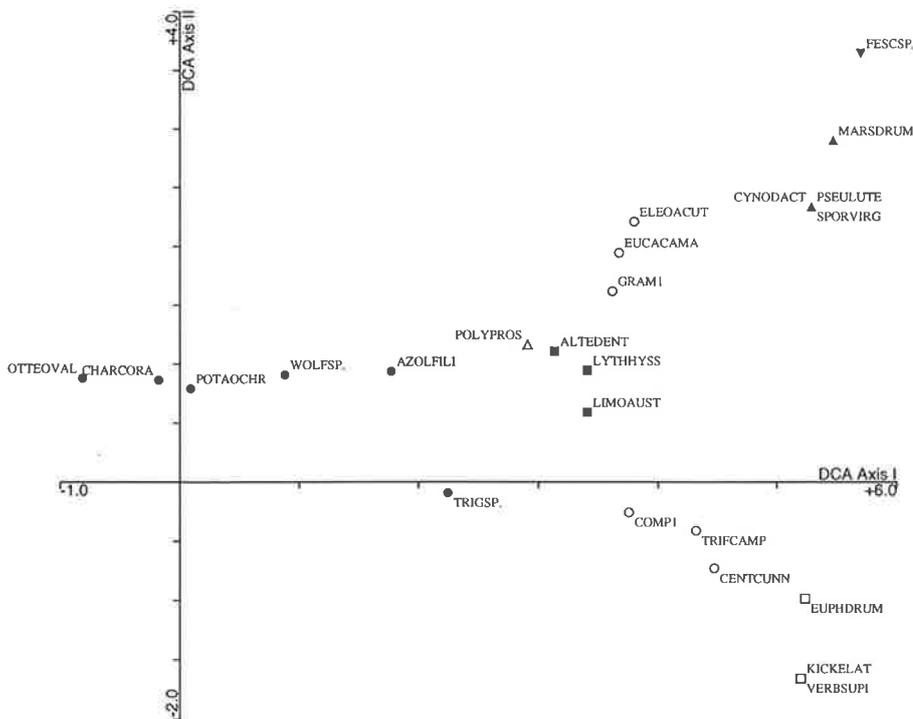


Figure 2.22: Shearing Tree Waterhole. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.



2.23.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II. Labels indicate swamp number (6), sampling location (1–3) and elevation class.



2.23.2: Species ordination on first two axes of DCA. ● Group A; ○ Group B; ■ Group C; □ Group D; ▲ Group E; △ Group F; ▼ Group G. See species list for species abbreviations.

Figure 2.23: Shearing Tree Waterhole site and species ordinations. Classification groups are those defined in Figure 2.22. Axes explain 45.5% and 14.7% of the variation in species composition.

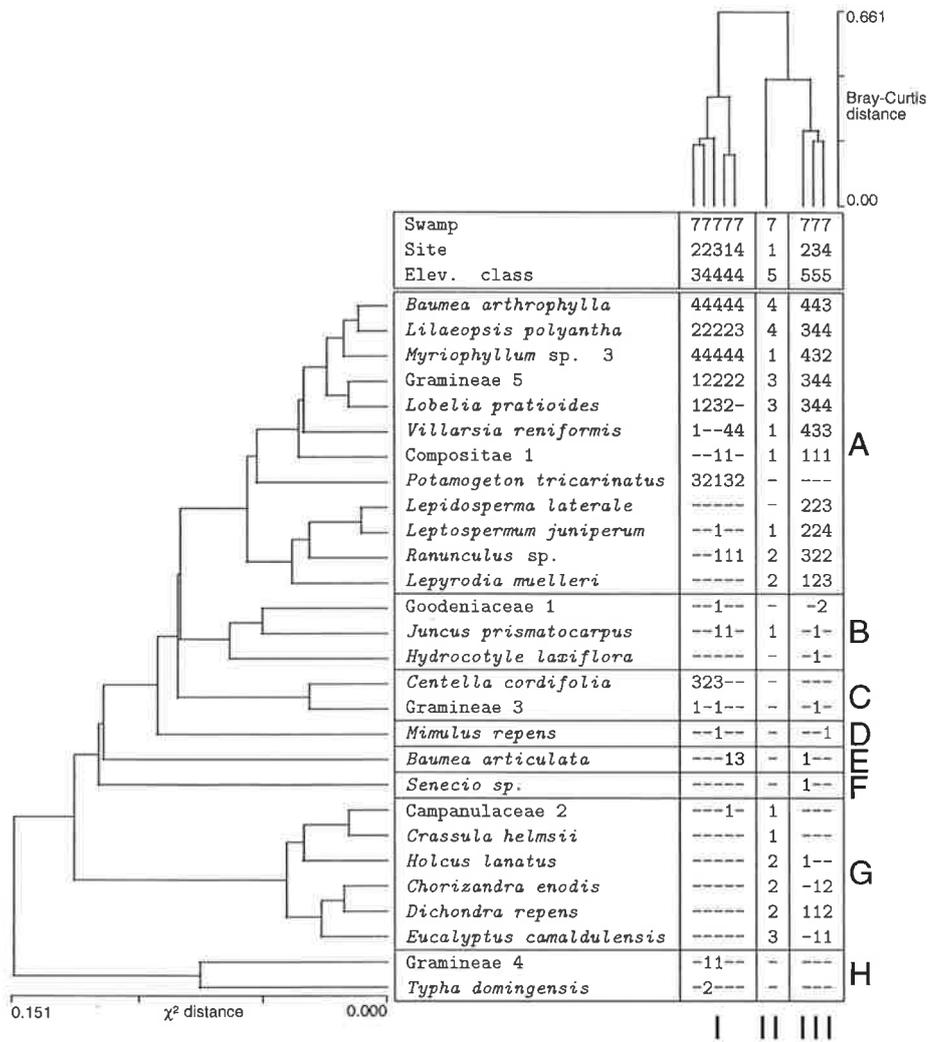
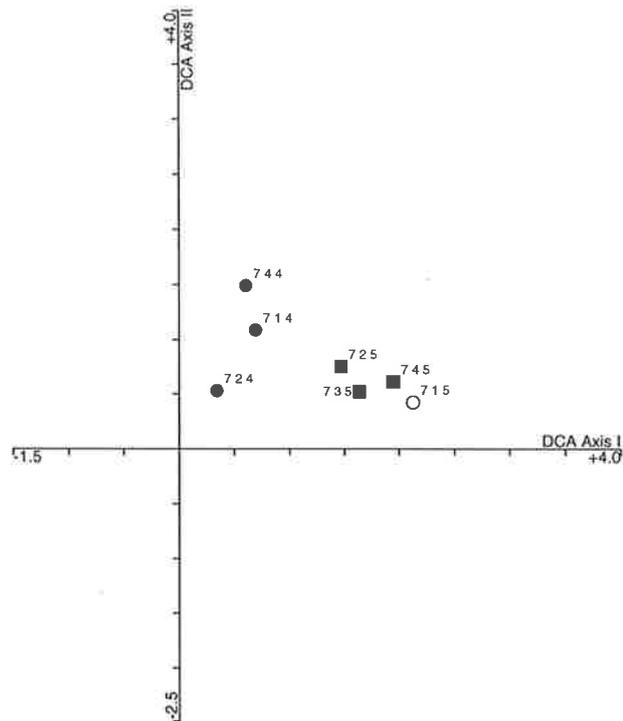
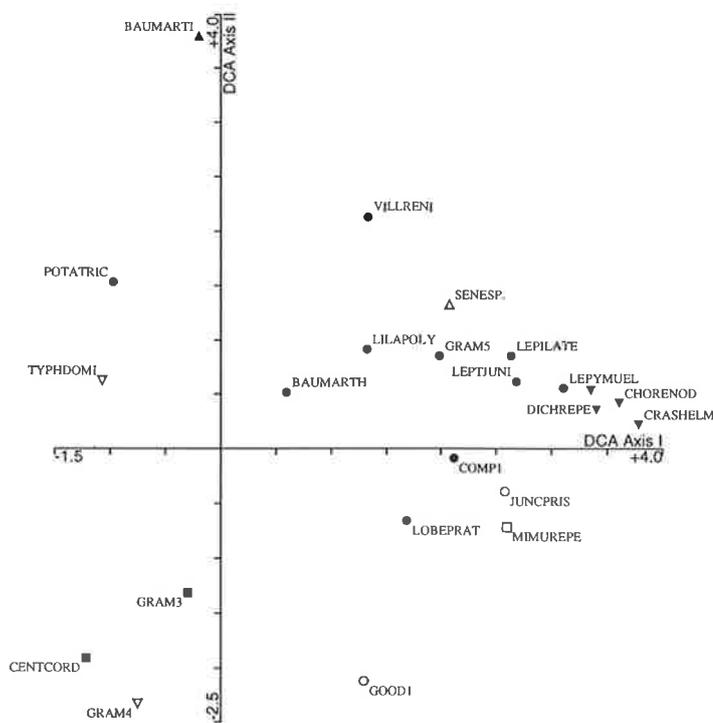


Figure 2.24: Topperweins Swamp. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.



2.25.1: Site ordination on first two axes of DCA. ●=Group I; ○=Group II; ■=Group III. Labels indicate swamp number (7), sampling location (1–4) and elevation class.



2.25.2: Species ordination on first two axes of DCA. ● Group A; ○ Group B; ■ Group C; □ Group D; ▲ Group E; △ Group F; ▼ Group G; ▽ Group H. See species list for species abbreviations.

**Figure 2.25:** Topperweins Swamp site and species ordinations. Classification groups are those defined in Figure 2.24. Axes explain 40.0% and 15.1% of the variation in species composition.

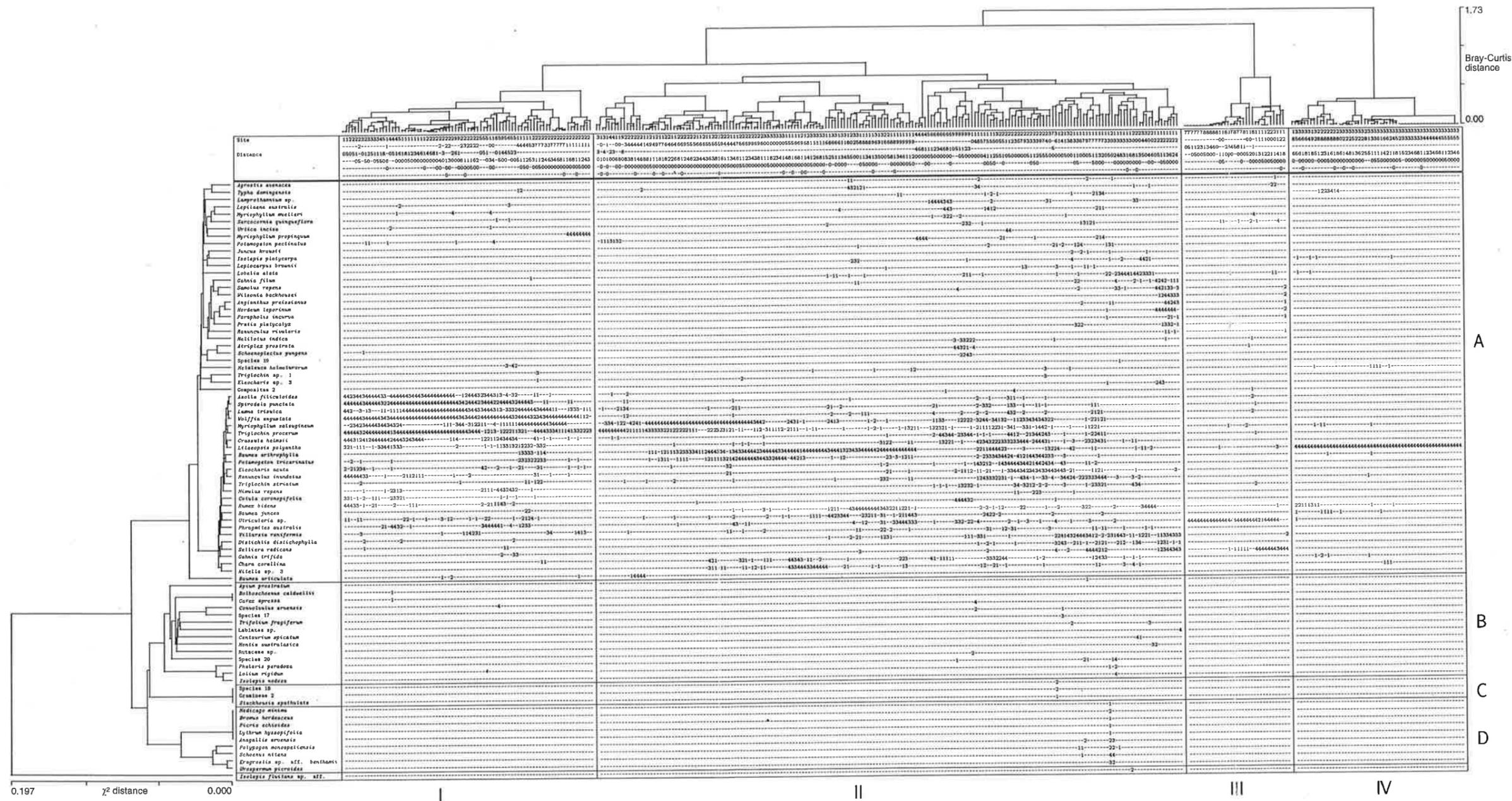


Figure 2.26: Bool Lagoon (all sites). Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.

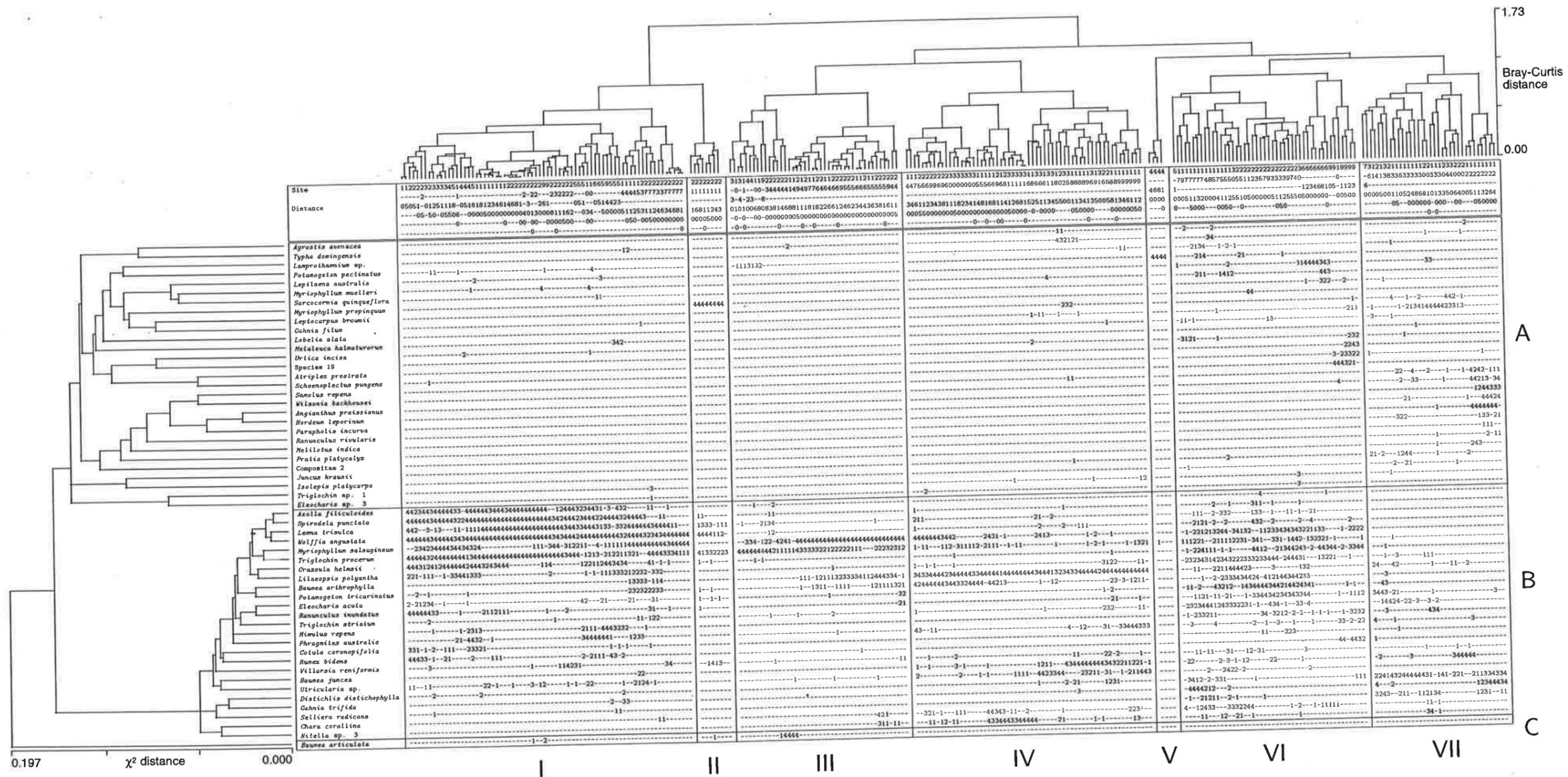
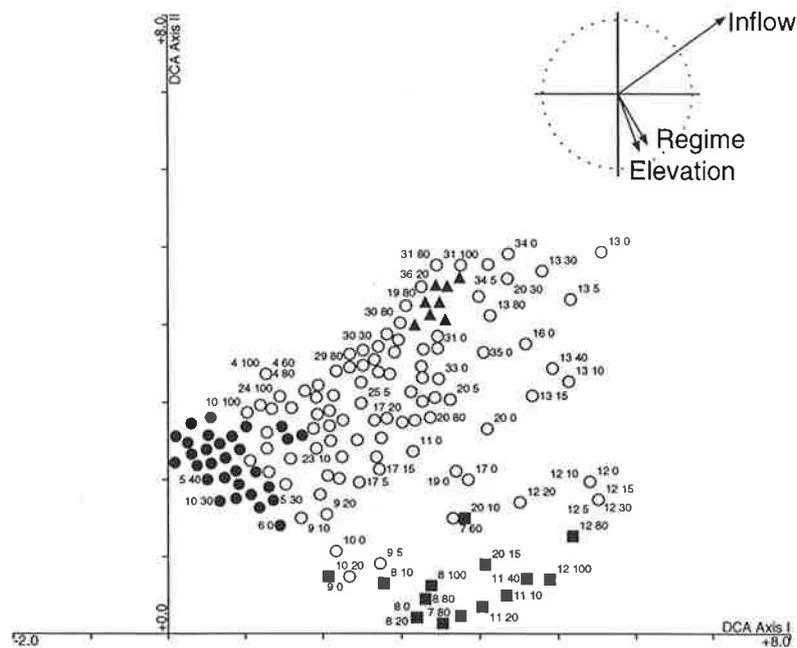
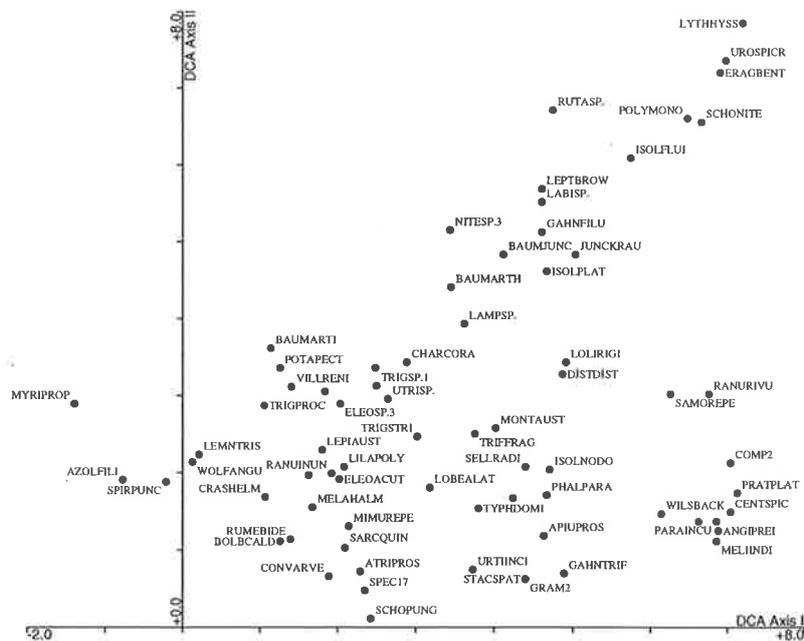


Figure 2.27: Bool Lagoon (subset of sites, excluding *Phragmites* and *Baumea arthropophylla* monocultures). Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1-25%; (2) 26-50%; (3) 51-75%; (4) 76-100%.

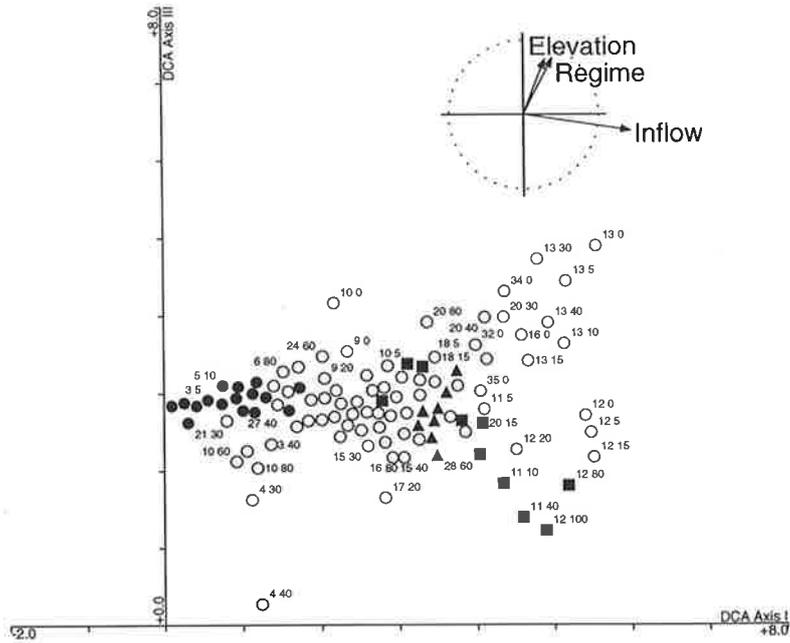


2.28.1: Site ordination on DCA axes I and II. ●=Group I; ○=Group II; ■=Group III; ▲ Group IV. Labels indicate sampling location (1–36) and distance from baseline (m). Inset shows correlation of environmental variables with DCA axes. Each correlation vector is determined by the product of the Spearman rank correlation coefficients with the DCA axes individually. The circle describes the length of vectors with a net two-dimensional correlation of 0.5. Display follows the methodology of Sparrow (1991).

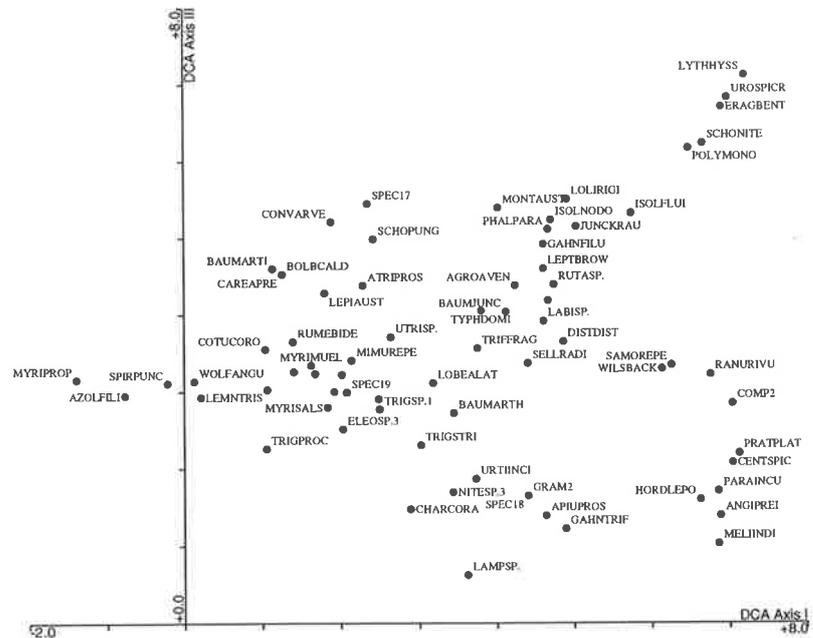


2.28.2: Species ordination on DCA axes I and II. See species list for species abbreviations.

**Figure 2.28:** Bool Lagoon site and species ordinations on DCA axes I and II. Site classification groups are those defined in Figure 2.26. Species classification groups are not shown. Axes explain 9.8% and 7.3% of the variation in species composition.

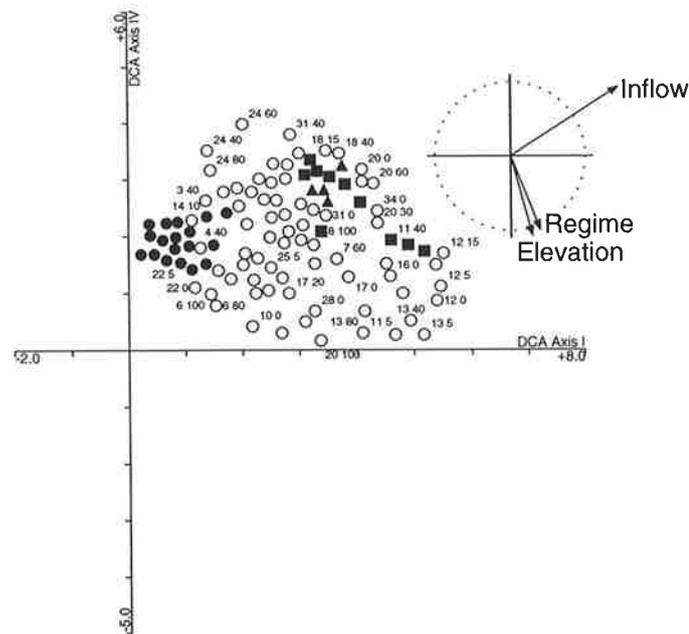


2.29.1: Site ordination on DCA axes I and III. ●=Group I; ○=Group II; ■=Group III; ▲ Group IV. Labels indicate sampling location (1–36) and distance from baseline (m). Inset shows correlation of environmental variables with DCA axes. Each correlation vector is determined by the product of the Spearman rank correlation coefficients with the DCA axes individually. The circle describes the length of vectors with a net two-dimensional correlation of 0.5. Display follows the methodology of Sparrow (1991).

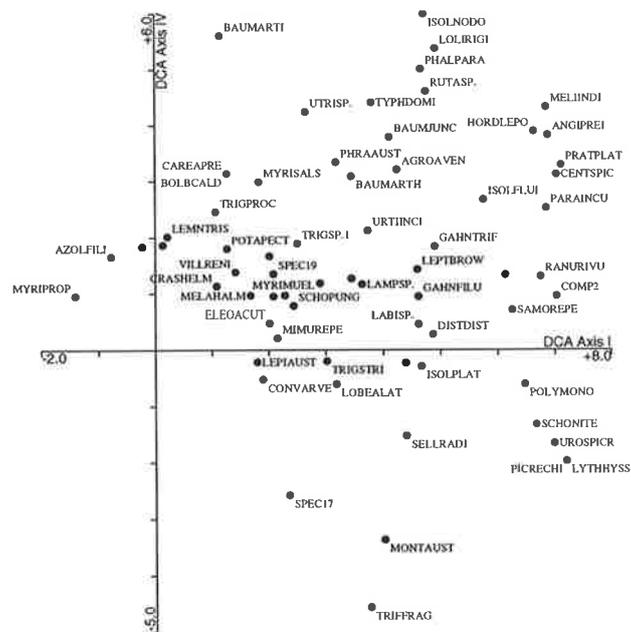


2.29.2: Species ordination on DCA axes I and III. See species list for species abbreviations.

Figure 2.29: Bool Lagoon site and species ordinations on DCA axes I and III. Site classification groups are those defined in Figure 2.26. Species classification groups are not shown. Axes explain 9.8% and 4.8% of the variation in species composition.



**2.30.1:** Site ordination on DCA axes I and IV. ●=Group I; ○=Group II; ■=Group III; ▲ Group IV. Labels indicate sampling location (1–36) and distance from baseline (m). Inset shows correlation of environmental variables with DCA axes. Each correlation vector is determined by the product of the Spearman rank correlation coefficients with the DCA axes individually. The circle describes the length of vectors with a net two-dimensional correlation of 0.5. Display follows the methodology of Sparrow (1991).



**2.30.2:** Species ordination on DCA axes I and IV. See species list for species abbreviations.

**Figure 2.30:** Bool Lagoon site and species ordinations on DCA axes I and IV. Site classification groups are those defined in Figure 2.26. Species classification groups are not shown. Axes explain 9.8% and 3.8% of the variation in species composition.

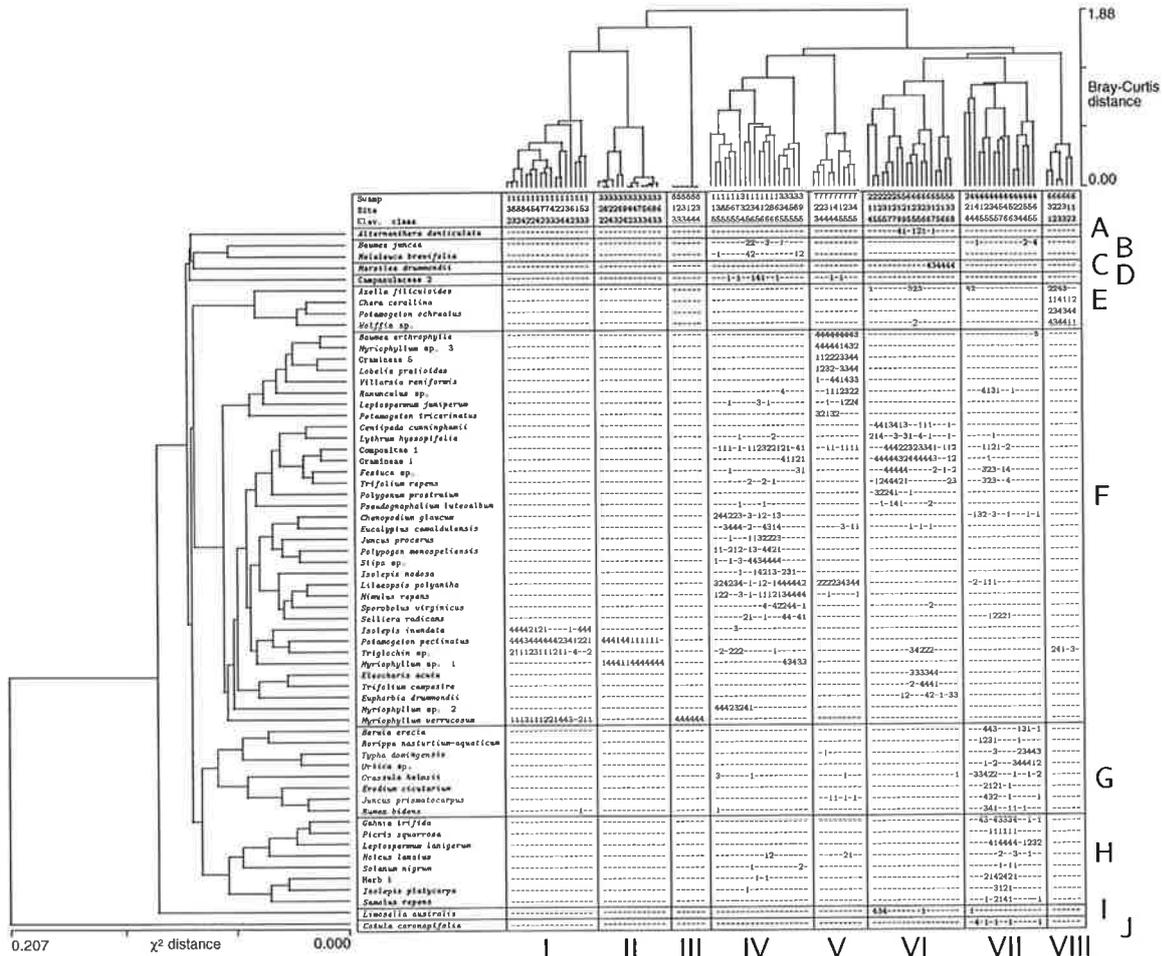
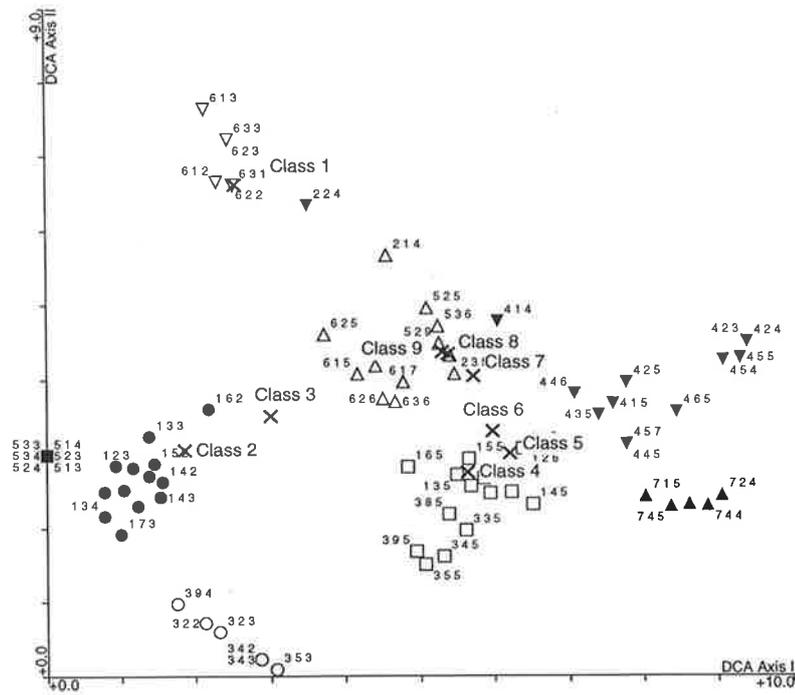
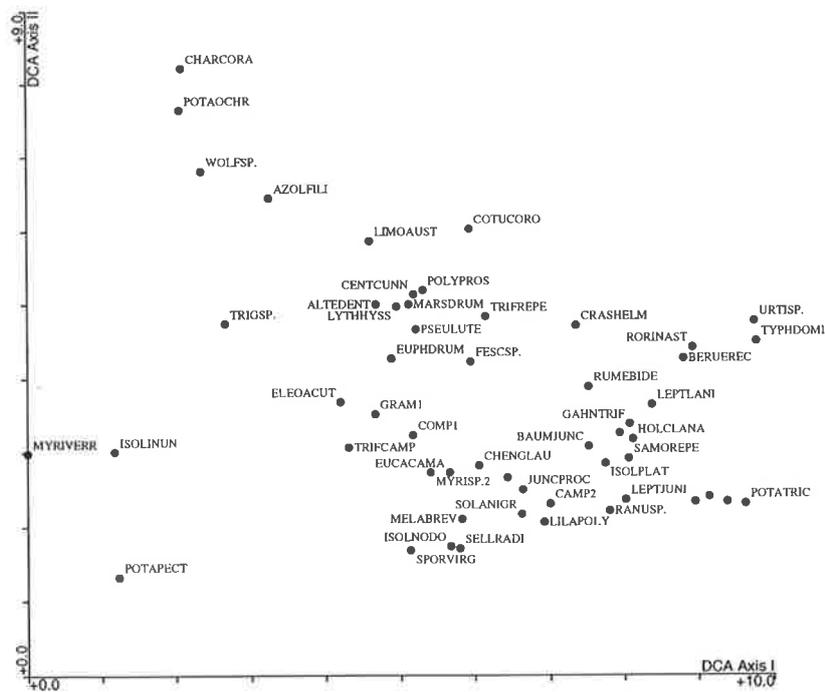


Figure 2.31: G7 wetlands. Two-way tabulation of sites and species classification. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100% Swamp numbers: 1=Bloomfield Swamp, 2=Dine Swamp, 3=Fairview C.P., 4=Mullins Swamp, 5=Poocher Swamp, 6=Shearing Tree Waterhole, 7=Topperweins Swamp.

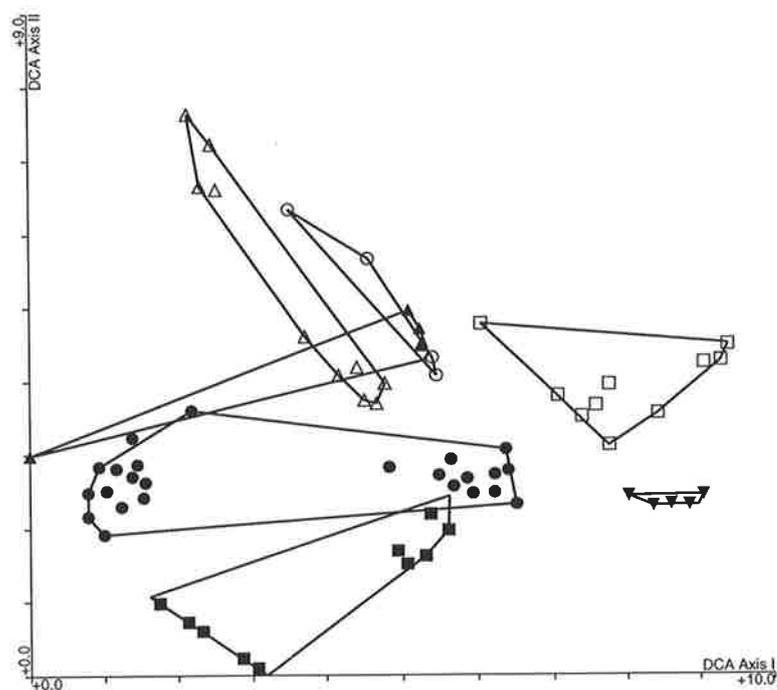


2.32.1: Site ordination on first two axes of DCA. ● Group I; ○ Group II; ■ Group III; □ Group IV; ▲ Group V; △ Group VI; ▼ Group VII; ▽ Group VIII. Labels indicate swamp number (1–7), sampling location (1–9) and elevation class. Centroids of ordinal elevation classes (Class 1–Class 9) are shown as x.

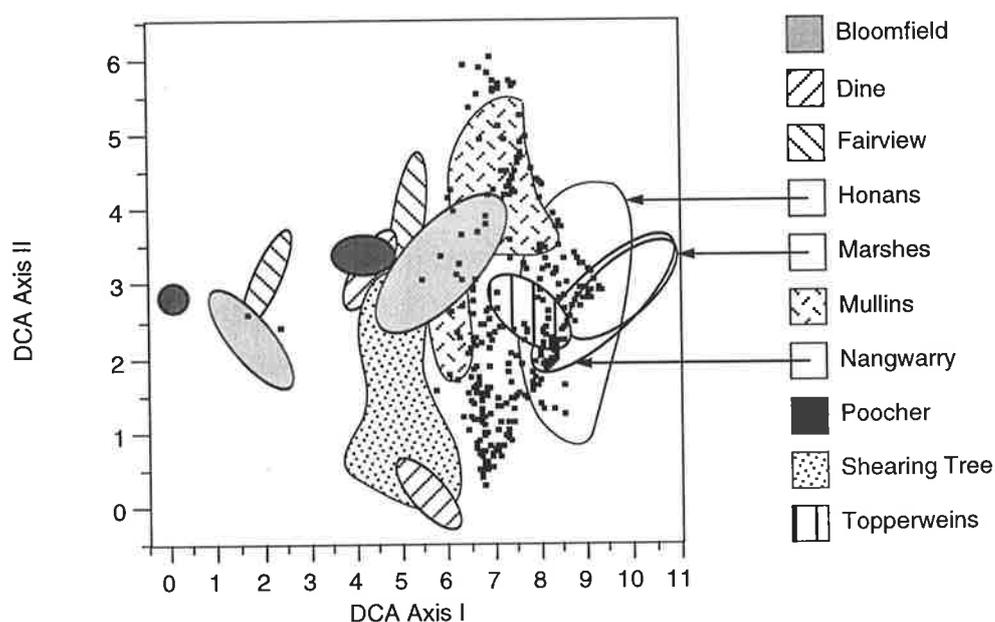


2.32.2: Species ordination on first two axes of DCA. See species list for species abbreviations.

Figure 2.32: G7 wetlands site and species ordinations. Species occurring in fewer than five sampling locations were excluded from the analysis. Classification groups are those defined in Figure 2.31. Axes explain 8.6% and 6.7% of the variation in species composition.



**Figure 2.33:** G7 wetlands site ordination on first two axes of DCA. ● Bloomfield Swamp; ○ Dine Swamp; ■ Fairview C.P.; □ Mullins Swamp; ▲ Poocher Swamp; △ Shearing Tree Waterhole; ▼ Topperweins Swamp. Polygons show sites contained within each wetland.



**Figure 2.34:** All sampled wetlands site ordination. Bool Lagoon sites are shown as ■. Shaded polygons show the boundaries of other wetlands whose sites are not shown individually. Note that Bloomfield Swamp, Dine Swamp, Fairview C.P. and Poocher Swamp show two polygons each, representing the distinction between their aquatic and terrestrial communities. Axes explain 6.2% and 4.3% of variation in species composition.





## Chapter 3

# Water regime at Bool Lagoon

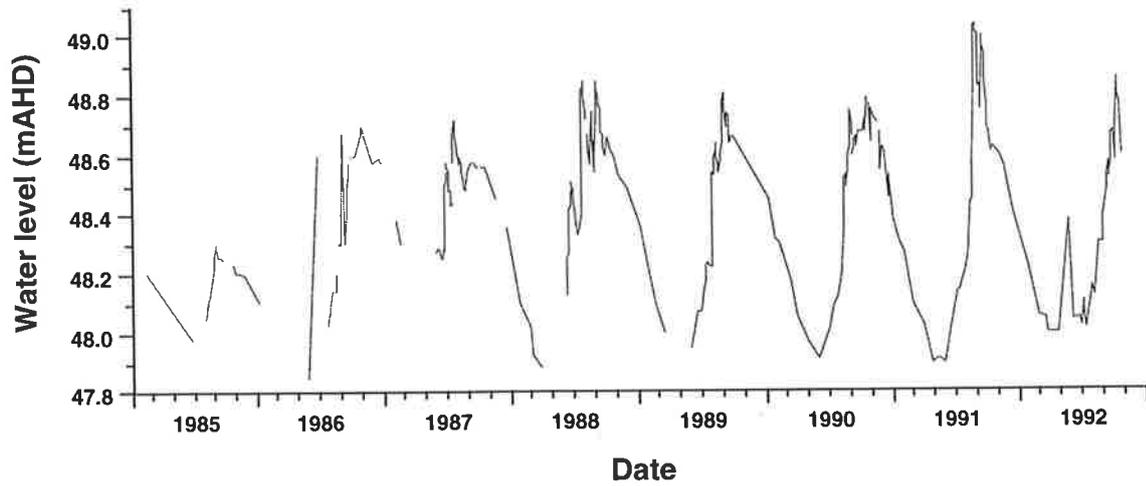


Figure 3.1: Water levels (mAHD) in Main Basin 1985–1992.

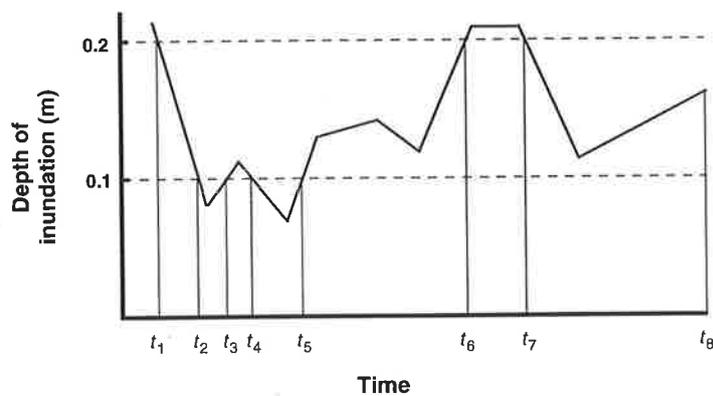
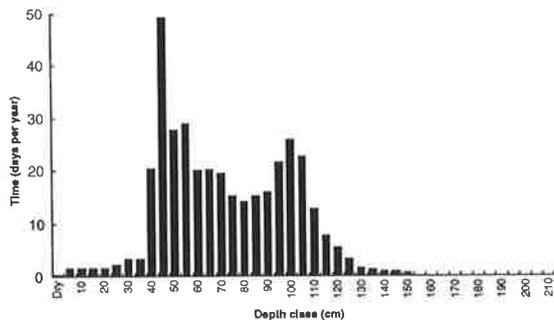
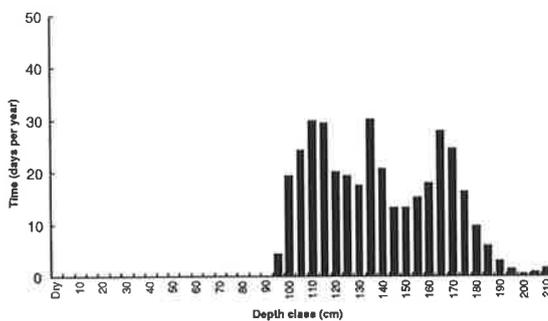


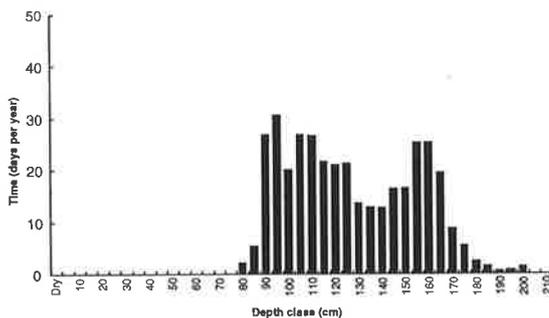
Figure 3.2: Depth-time calculation. Time spent between 0.1–0.2 m depth is the summation of time when the elevation of the water surface falls between these two points i.e.  $\text{Time}_{(0.1-0.2\text{m})} = (t_2 - t_1) + (t_4 - t_3) + (t_6 - t_5) + (t_8 - t_7)$ .



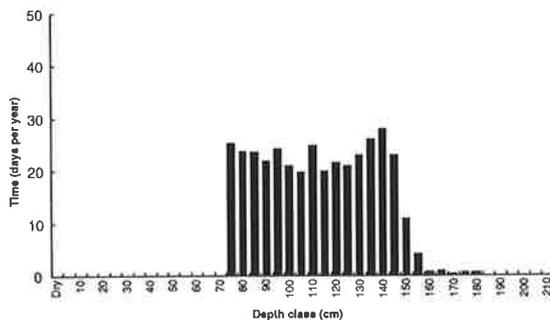
3.3.1: Hacks Lagoon.



3.3.2: Main Basin

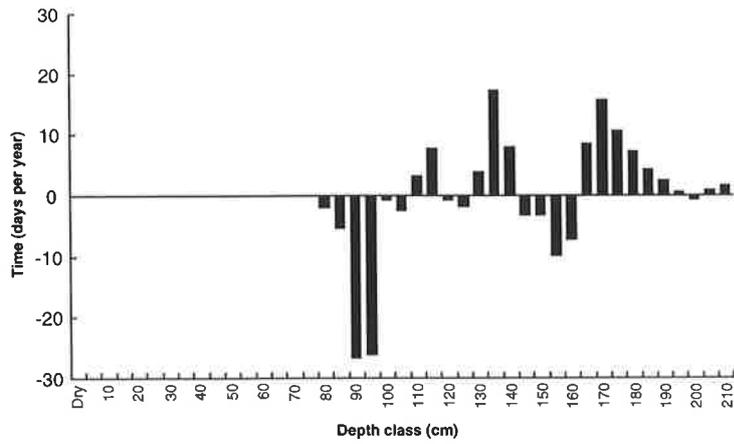


3.3.3: Central Basin

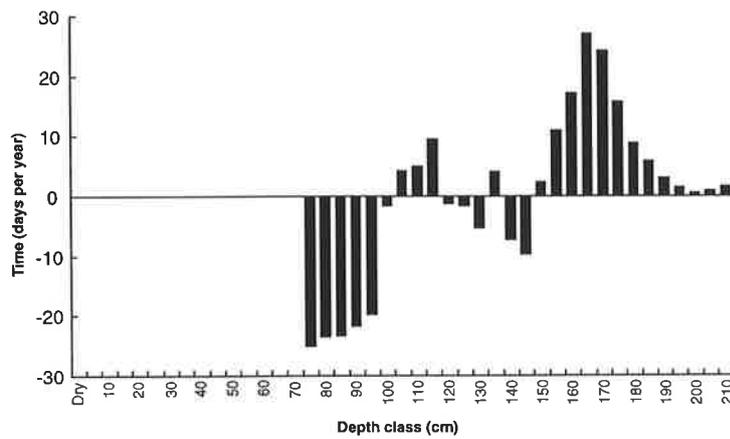


3.3.4: Western Basin

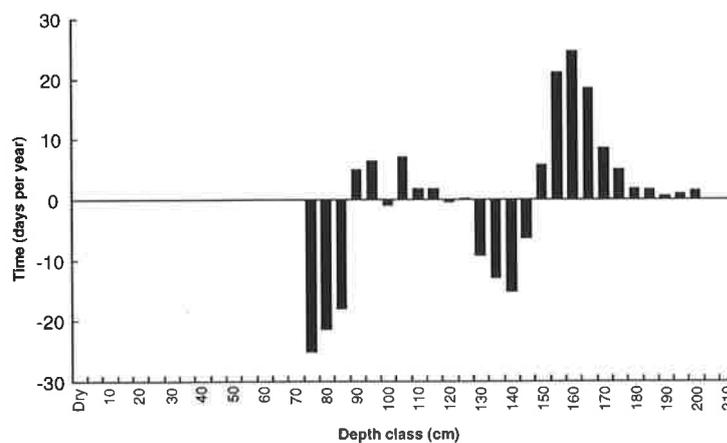
Figure 3.3: 'Bottom of basin' flooding patterns derived from 1985–1992 water level data from Bool Lagoon.



3.4.1: Main Basin cf. Central Basin

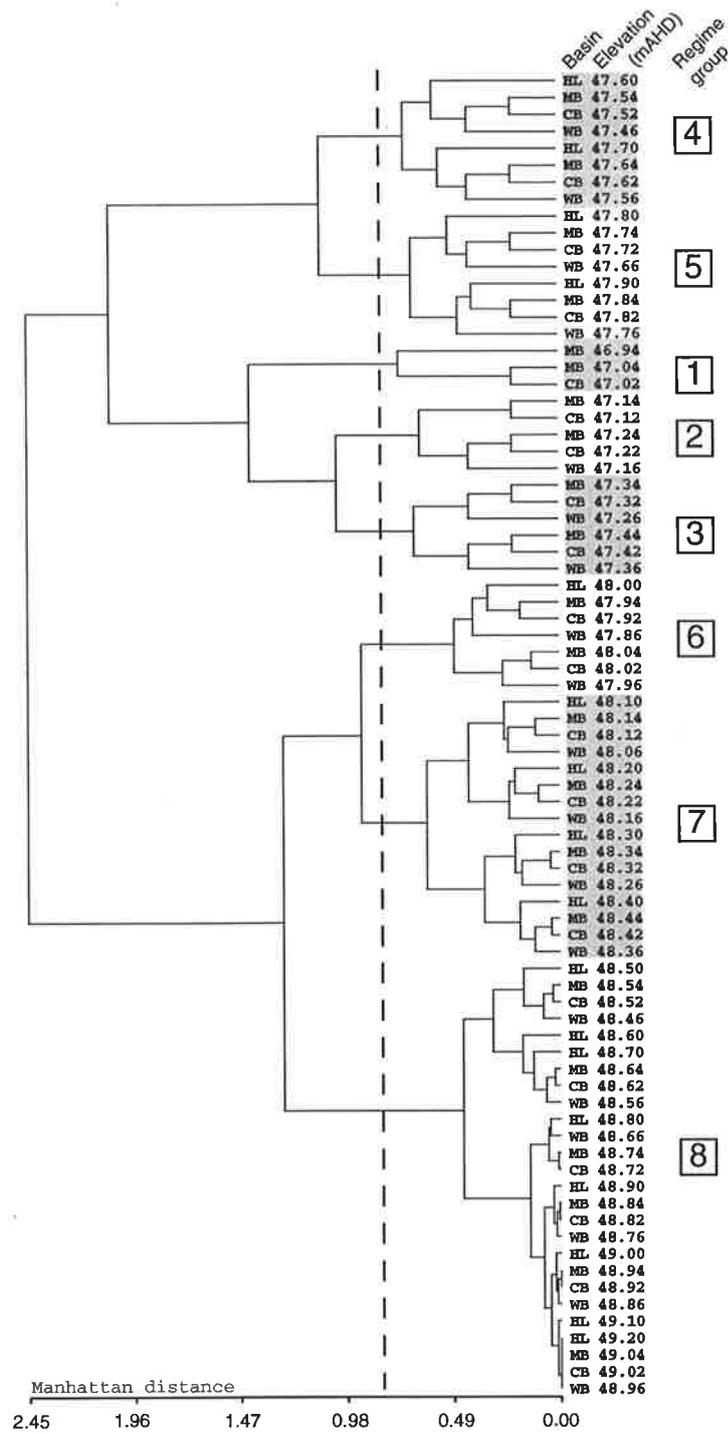


3.4.2: Main Basin cf. Western Basin

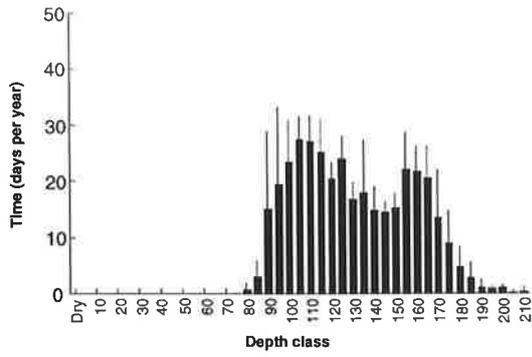


3.4.3: Central Basin cf. Western Basin

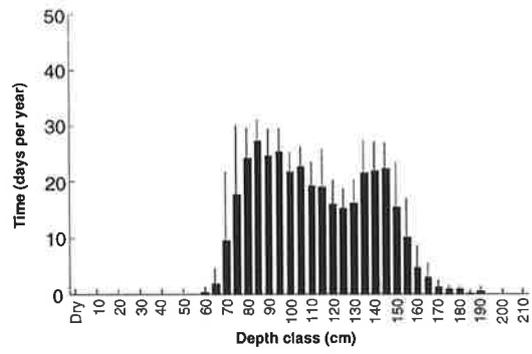
**Figure 3.4:** Comparison of basin flooding characteristics obtained by subtracting frequency histogram of one basin from another. +ve time value indicates more time spent in depth class by former basin. -ve value indicates more time spent in depth class by latter basin. 0 value indicates same time spent in depth class by each basin.



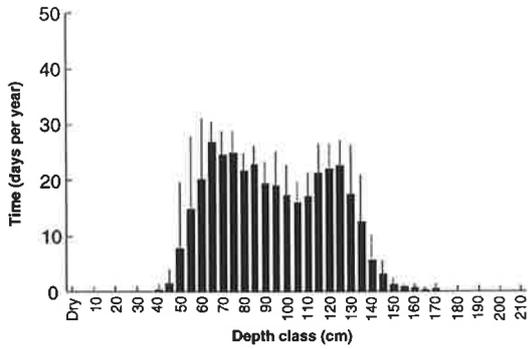
**Figure 3.5:** Dendrogram derived from Manhattan distance and flexible UPGMA fusion ( $\beta=0$ ) on flooding frequency data from Bool Lagoon, showing eight water regime definitions, and the physical locations of gradient positions within each regime.



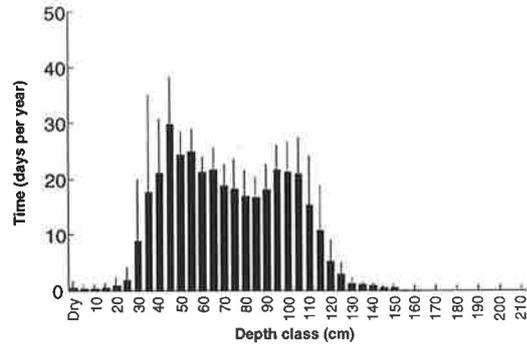
3.6.1: Regime 1



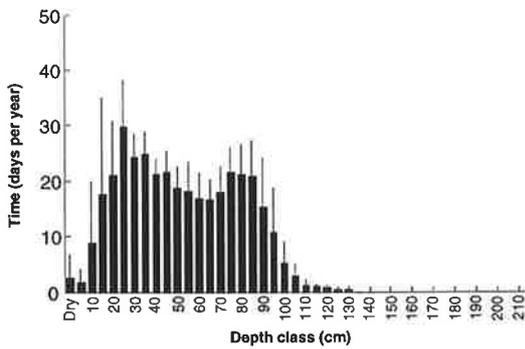
3.6.2: Regime 2



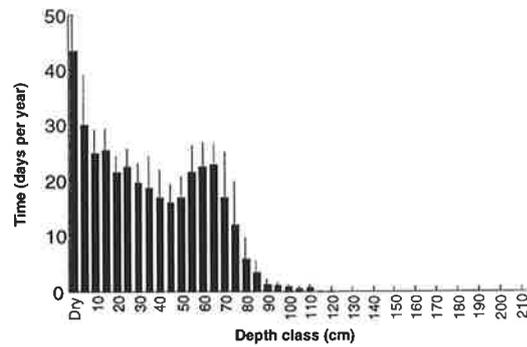
3.6.3: Regime 3



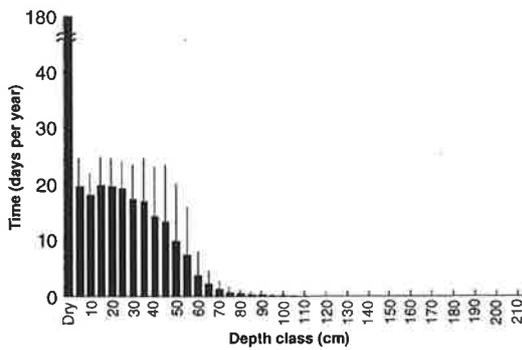
3.6.4: Regime 4



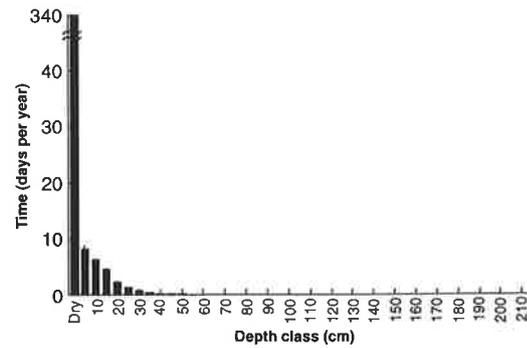
3.6.5: Regime 5



3.6.6: Regime 6



3.6.7: Regime 7



3.6.8: Regime 8

**Figure 3.6:** Definitions of eight water regimes, showing variability (S.D.) within each depth class based on the differing flooding frequencies of gradient positions within the same dendrogram group, as defined in Figure 3.5

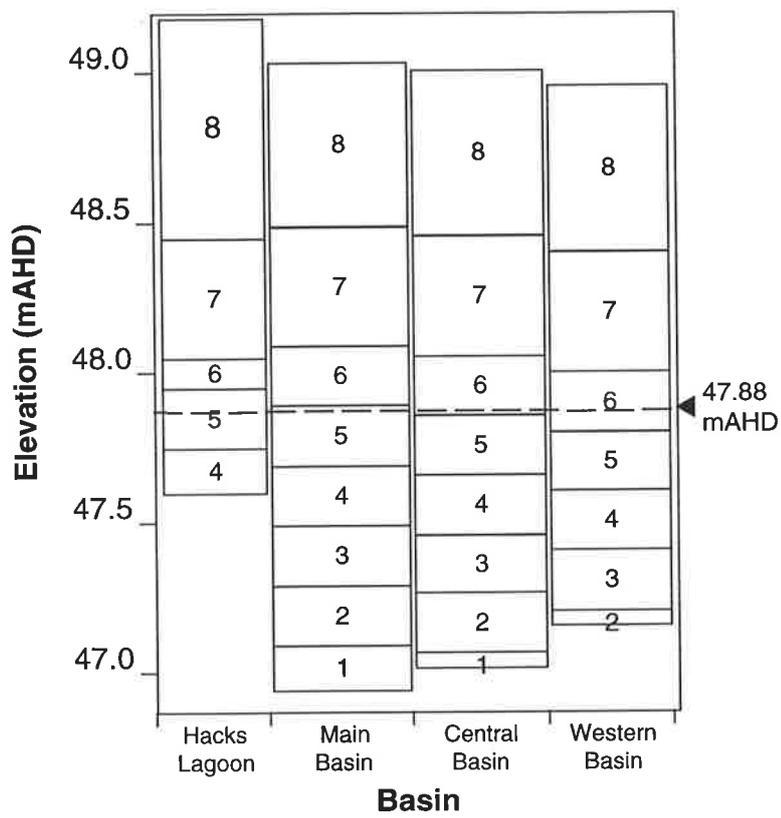
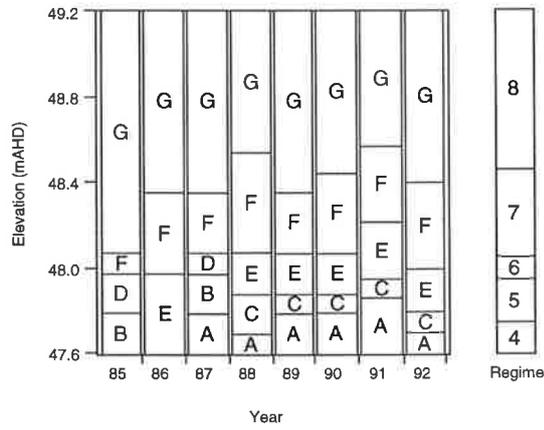
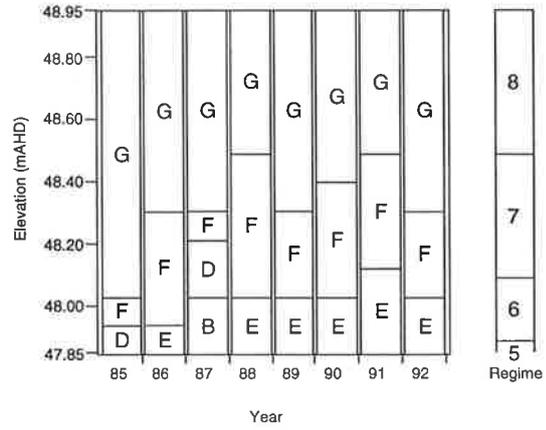


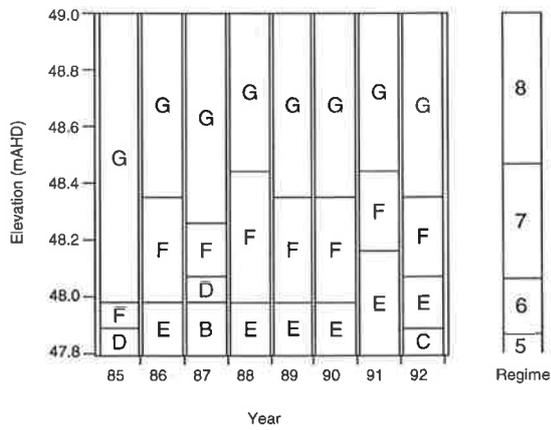
Figure 3.7: Relationship between elevation and water regime (1–8) in the basins of Bool Lagoon.



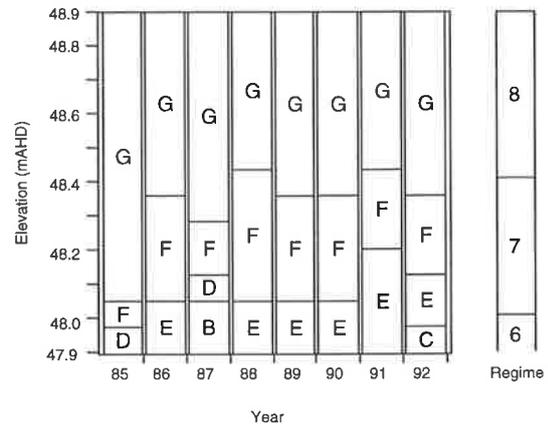
3.8.1: Hacks Lagoon



3.8.2: Main Basin

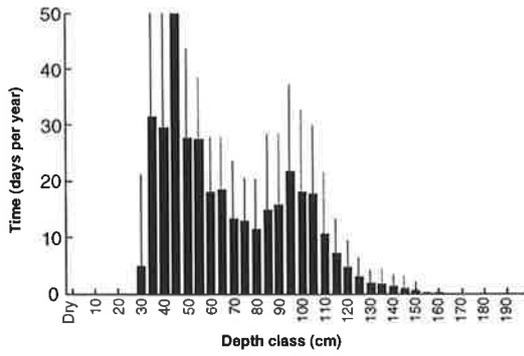


3.8.3: Central Basin

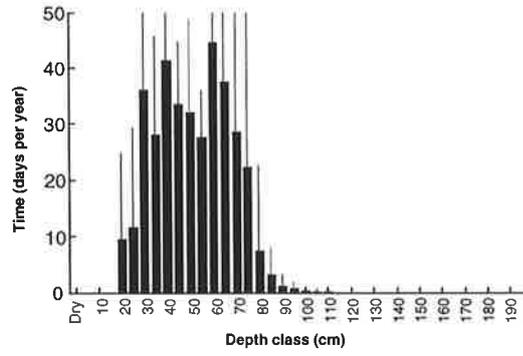


3.8.4: Western Basin

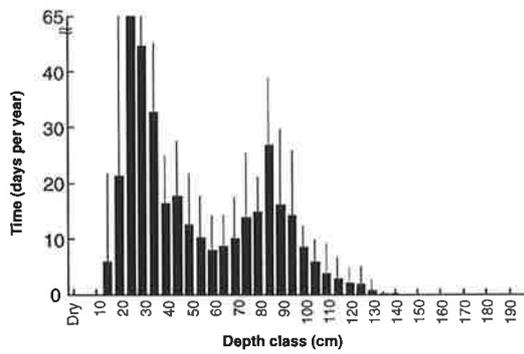
Figure 3.8: Spatial and temporal distribution of annual flooding pattern types (A–G) in basins of Bool Lagoon. Water regime definition (1–8) is overlaid for comparison.



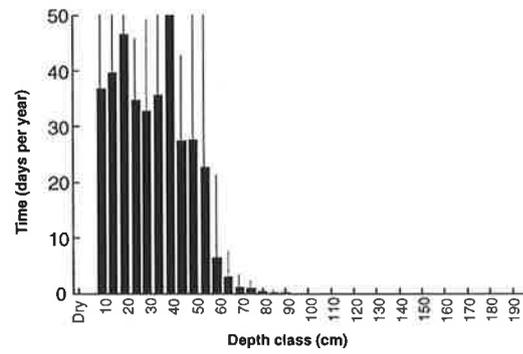
3.9.1: Group A



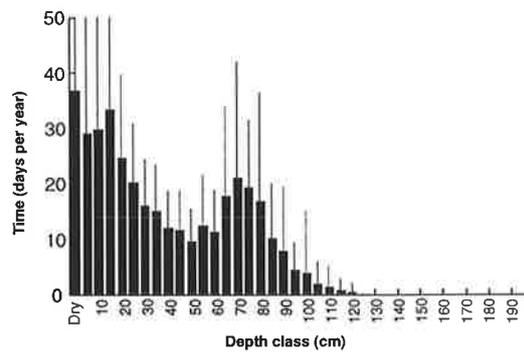
3.9.2: Group B



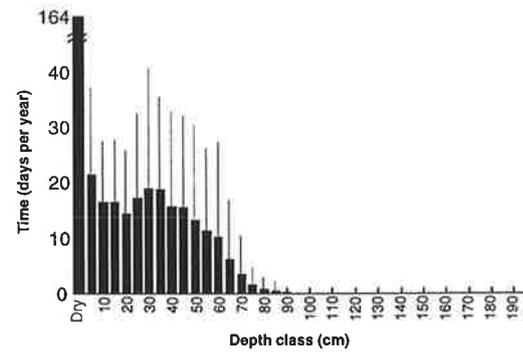
3.9.3: Group C



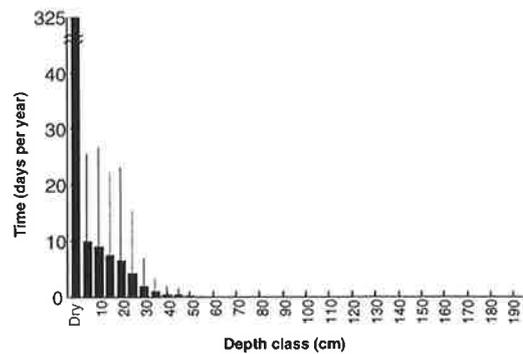
3.9.4: Group D



3.9.5: Group E



3.9.6: Group F



3.9.7: Group G

**Figure 3.9:** Definitions of seven annual flooding patterns, showing variability (S.D.) within each depth class based on the differing flooding frequencies of gradient positions and years within the same dendrogram group.



## Chapter 4

# Production and demography of *Phragmites* and *Typha*

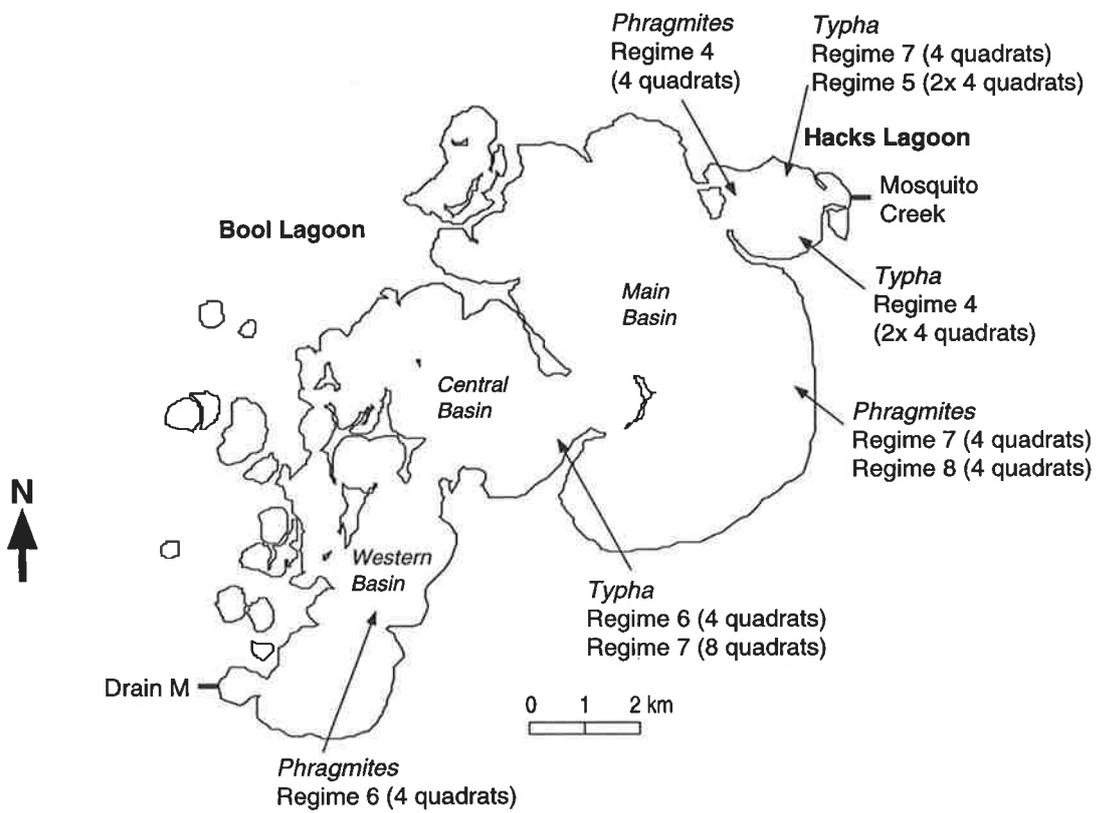
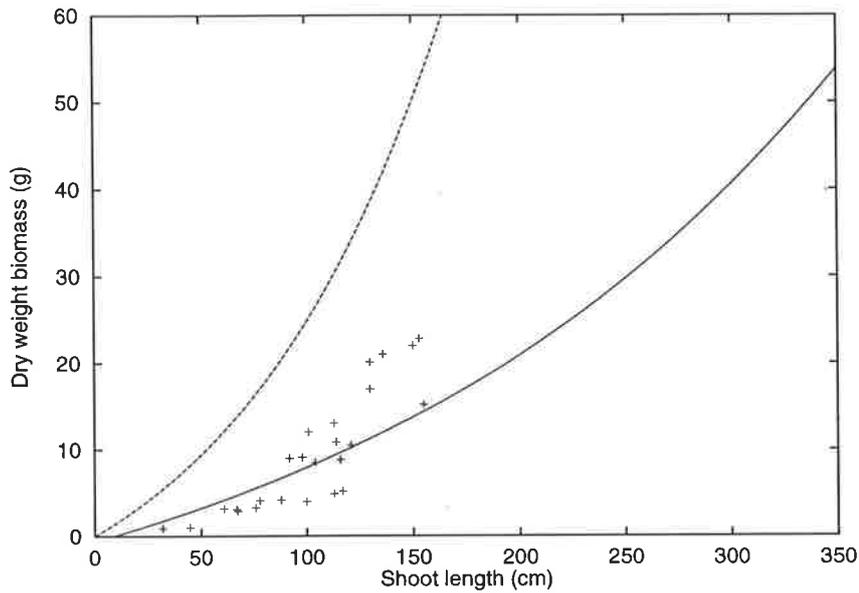
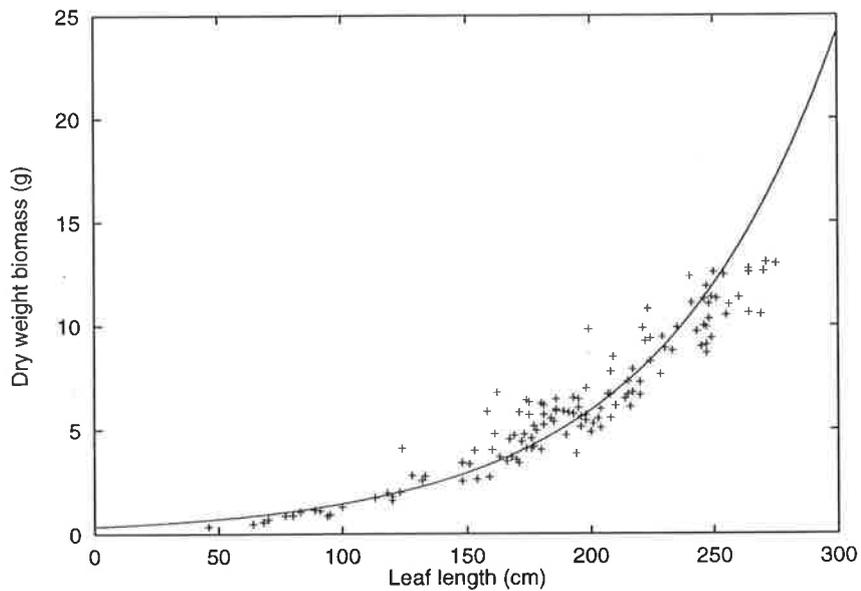


Figure 4.1: Bool Lagoon showing location of permanent quadrats.



**Figure 4.2:** Relationship of *Phragmites* shoot length to dry weight biomass. Equations have the form:  $y = a + be^{-kx}$ . Dotted line has the parameter values  $a=-14.52$ ,  $b=14.52$ ,  $e^k=1.01$  as stated by Hocking (1989a). Solid line is an approximation of the line presented by Hocking (1989a) and has the parameter values  $a = -17.20$ ,  $b = 16.59$ ,  $e^k = 1.004$ .



**Figure 4.3:** Relationship of *Typha* leaf length to dry weight biomass.  $Biomass=e^{-1.0318+0.01407 \times length}$

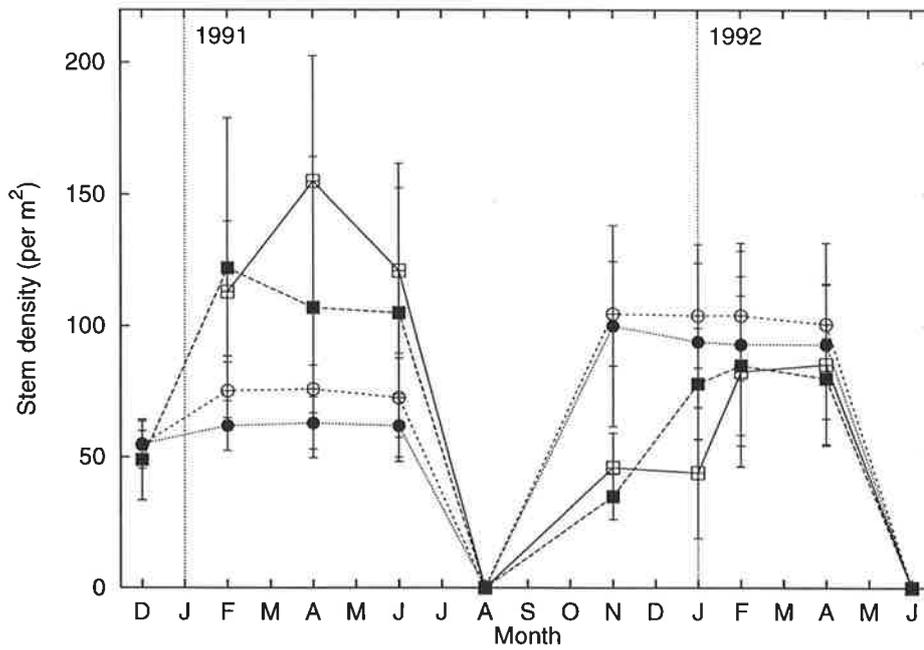


Figure 4.4: Changes in density of *Phragmites australis* stems (per m<sup>2</sup>) through time. □=Regime 4; ■=Regime 6; ○=Regime 7; ●=Regime 8.

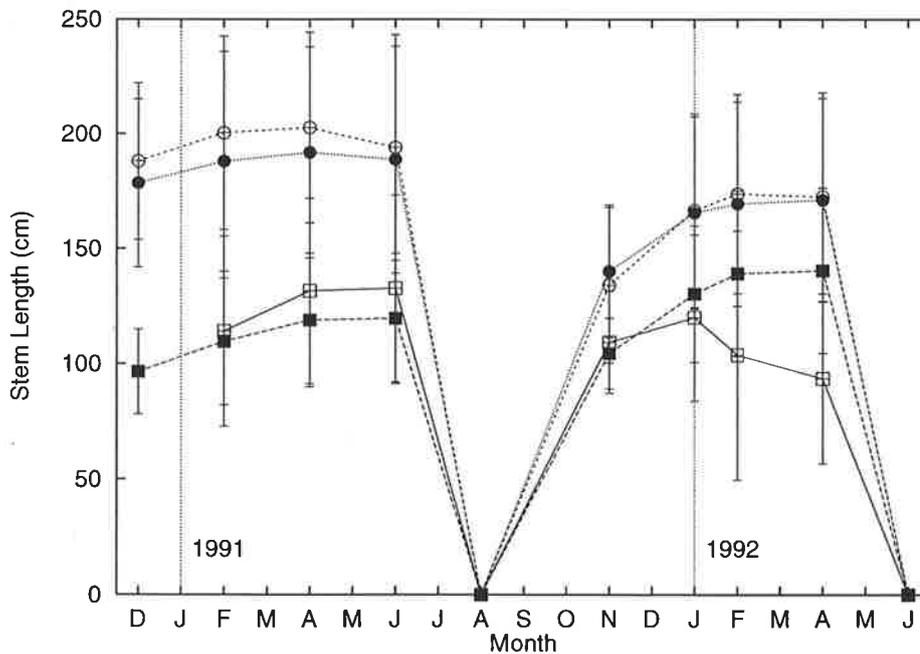
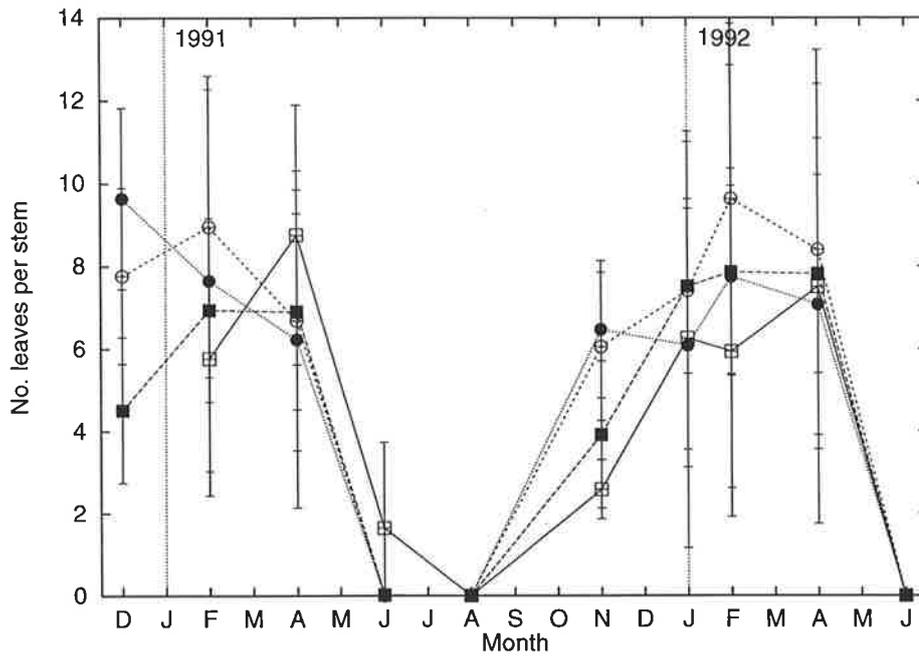
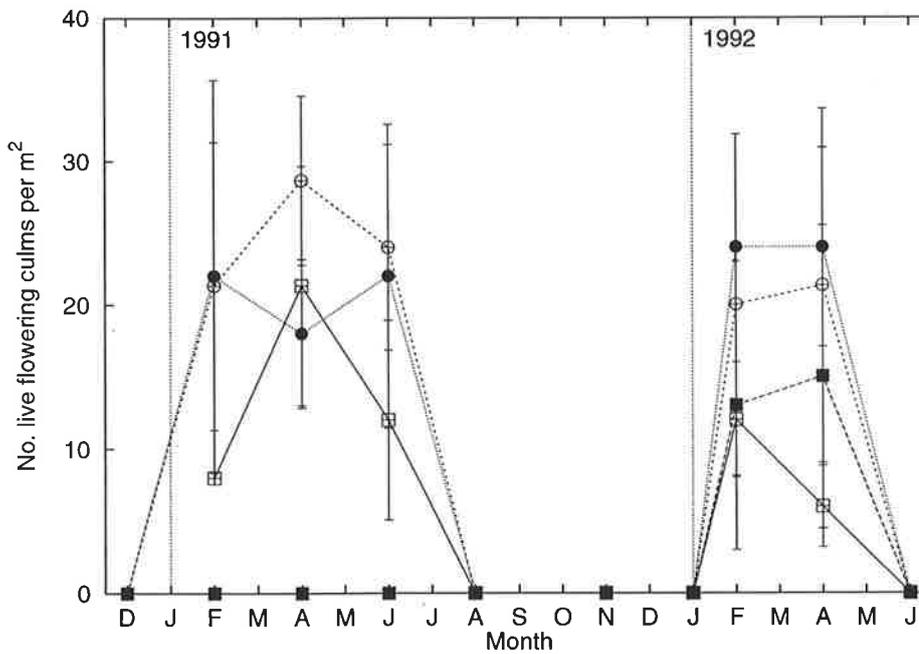


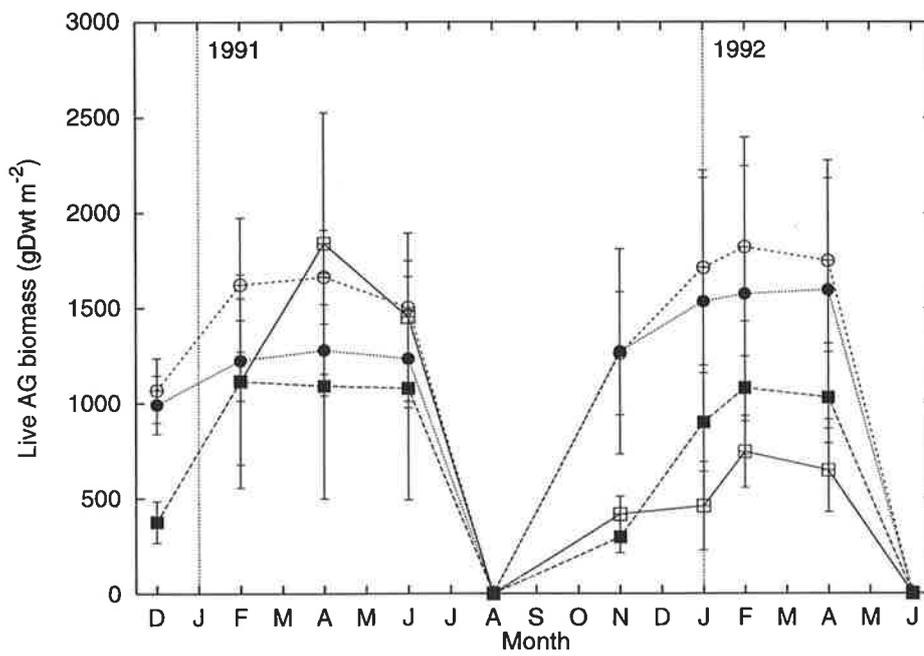
Figure 4.5: Changes in stem length of *Phragmites australis* through time. □=Regime 4; ■=Regime 6; ○=Regime 7; ●=Regime 8.



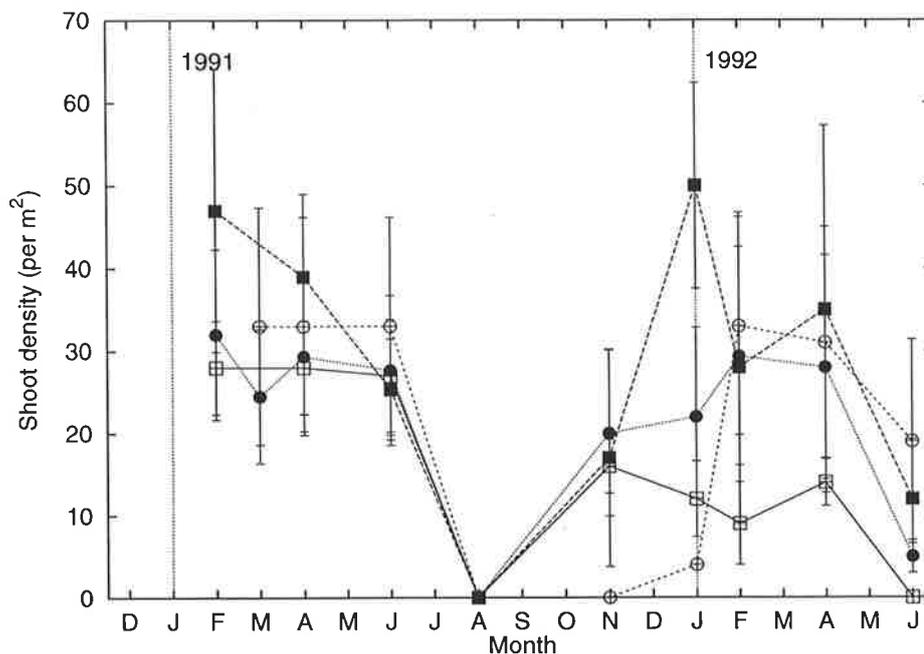
**Figure 4.6:** Changes in leaf number of *Phragmites australis* through time. □=Regime 4; ■=Regime 6; ○=Regime 7; ●=Regime 8.



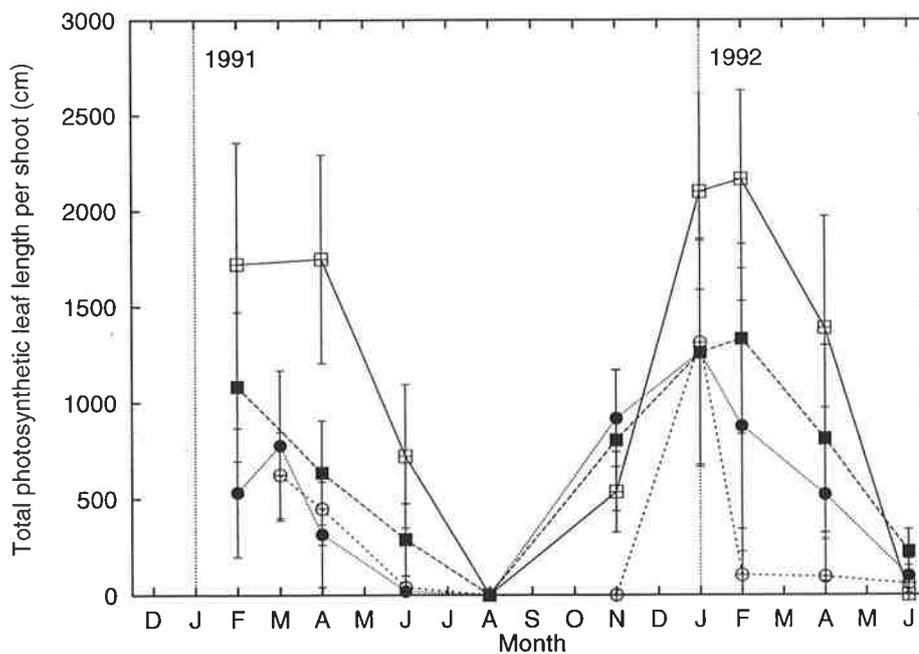
**Figure 4.7:** Changes in density of flowering culms of *Phragmites australis* through time. □=Regime 4; ■=Regime 6; ○=Regime 7; ●=Regime 8.



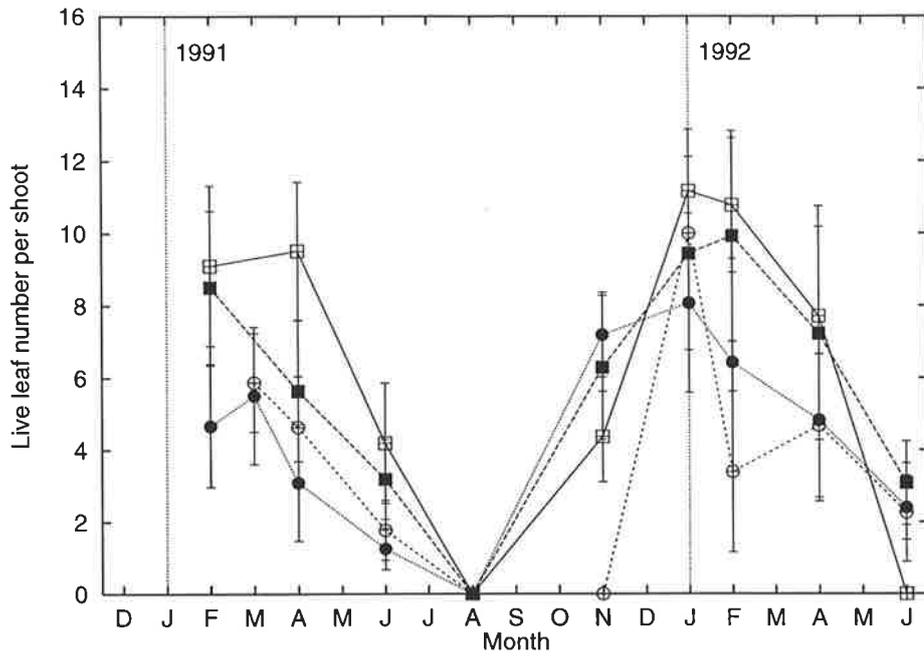
**Figure 4.8:** Changes in above ground live biomass of *Phragmites australis* through time. □=Regime 4; ■=Regime 6; ○=Regime 7; ●=Regime 8.



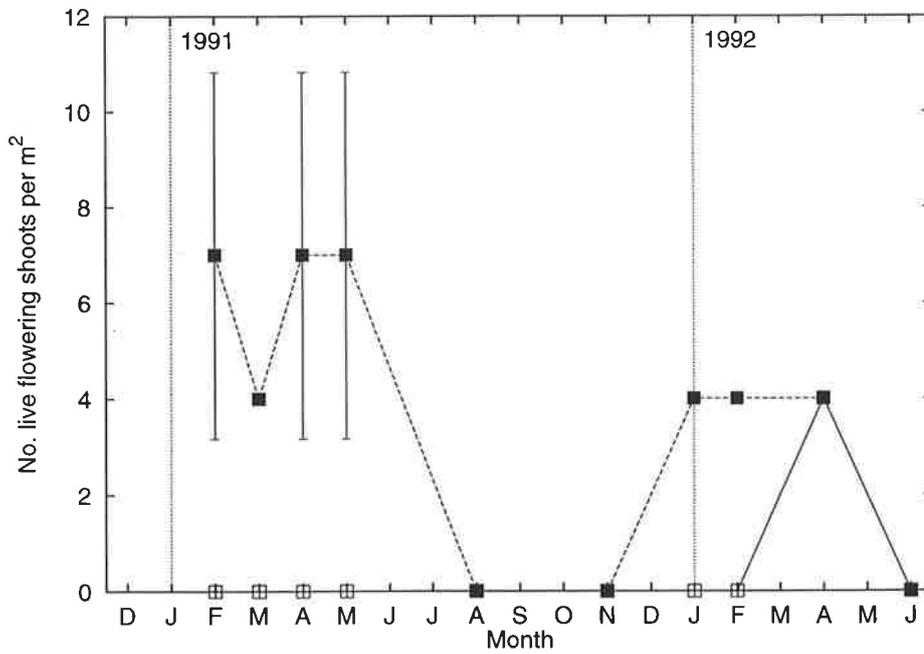
**Figure 4.9:** Changes in density of *Typha domingensis* shoots (per m<sup>2</sup>) through time. □=Regime 4; ■=Regime 5; ○=Regime 6; ●=Regime 7.



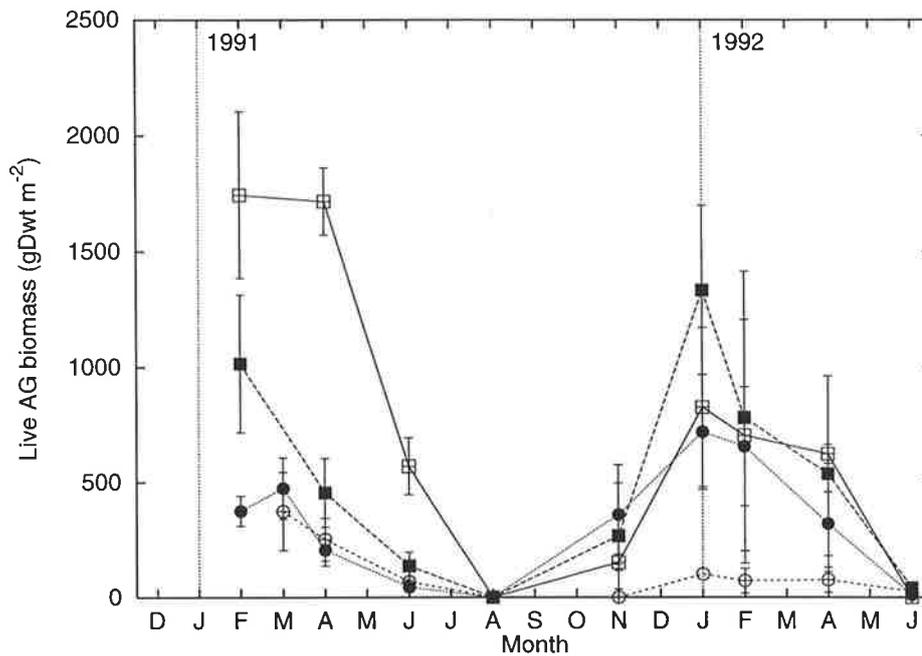
**Figure 4.10:** Changes in total photosynthetic leaf length per shoot of *Typha domingensis* through time. □=Regime 4; ■=Regime 5; ○=Regime 6; ●=Regime 7.



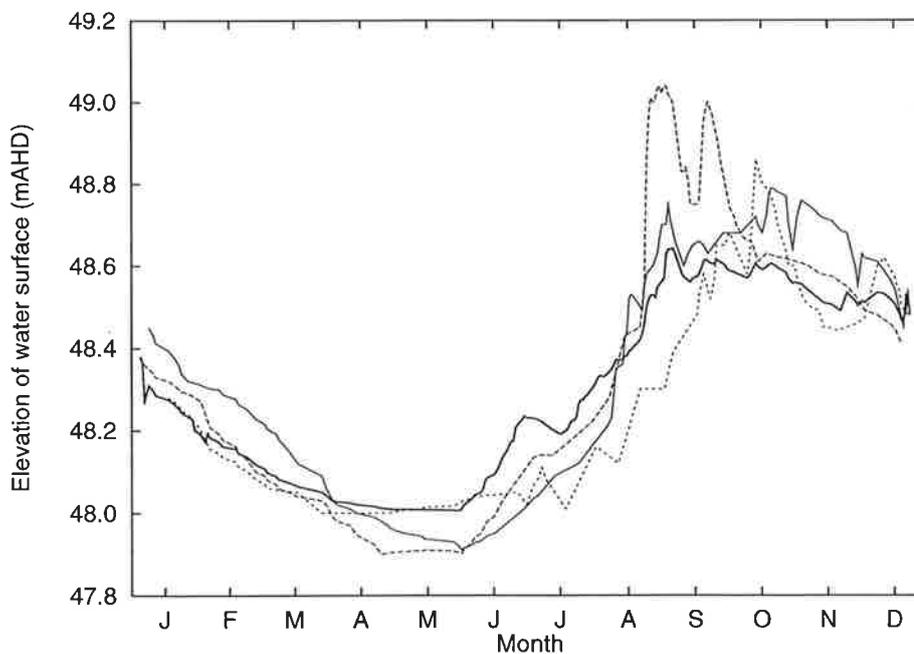
**Figure 4.11:** Changes in live leaf number per shoot of *Typha domingensis* through time. □=Regime 4; ■=Regime 5; ○=Regime 6; ●=Regime 7.



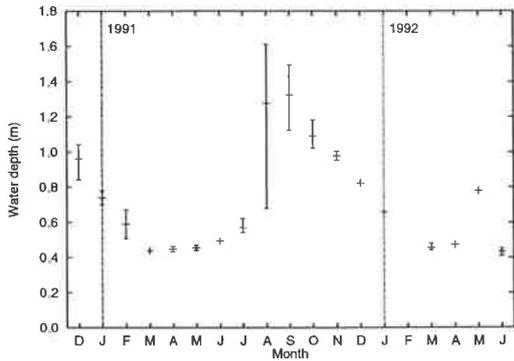
**Figure 4.12:** Changes in density of flowering shoots of *Typha domingensis* through time. □=Regime 4; ■=Regime 5; ○=Regime 6; ●=Regime 7.



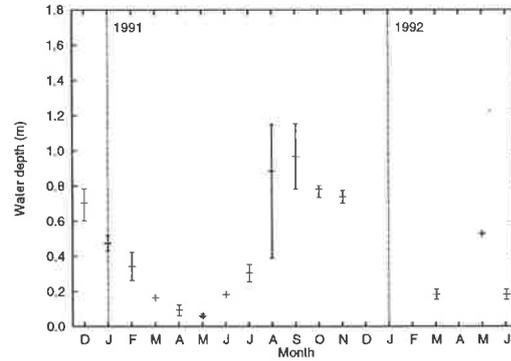
**Figure 4.13:** Changes in above ground live biomass of *Typha domingensis* through time. □=Regime 4; ■=Regime 5; ○=Regime 6; ●=Regime 7.



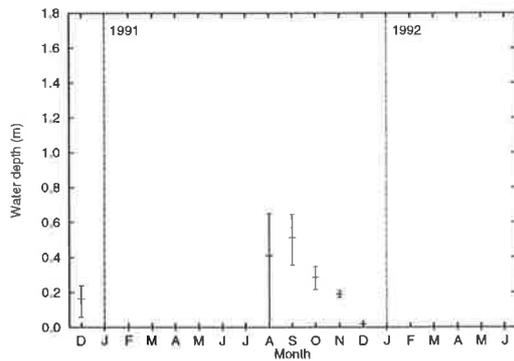
**Figure 4.14:** Comparison of water level changes in the Main Basin from 1990–1992. Solid line=1990; dashed line=1991; dotted line=1992; heavy solid line=average water level from 1985–1992.



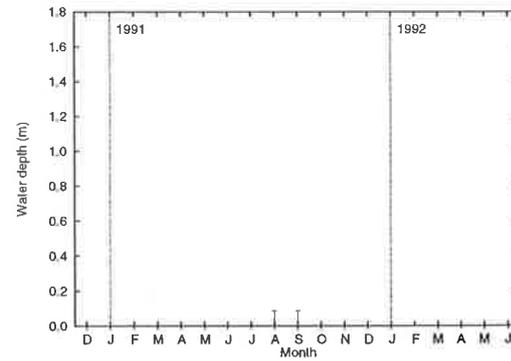
4.15.1: Regime 4, Hacks Lagoon. Elevation = 47.6 mAHD



4.15.2: Regime 6, Western Basin. Elevation = 47.85 mAHD

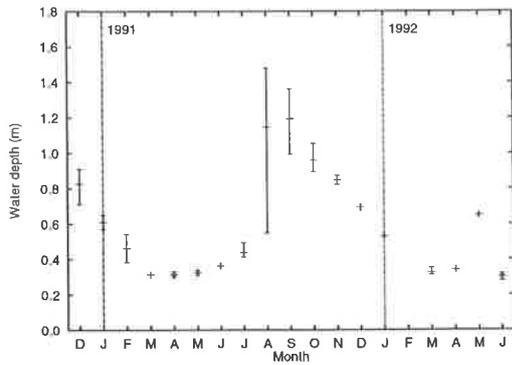


4.15.3: Regime 7, Main Basin. Elevation = 48.39 mAHD

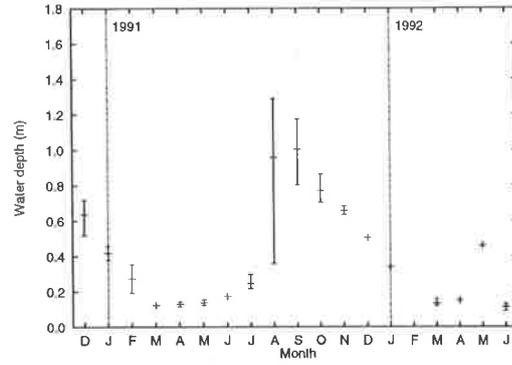


4.15.4: Regime 8, Main Basin. Elevation = 48.95 mAHD

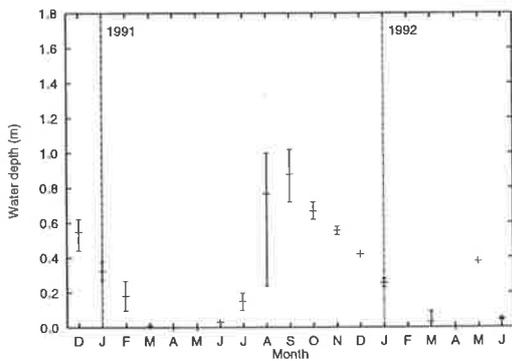
Figure 4.15: Changes in water depth in permanent quadrats of *Phragmites* throughout the sampling period. Vertical bars represent the monthly mean, minimum and maximum water depth (m). For Regimes 7 and 8, stated elevation is the median elevation of two sets of sampled quadrats within each regime.



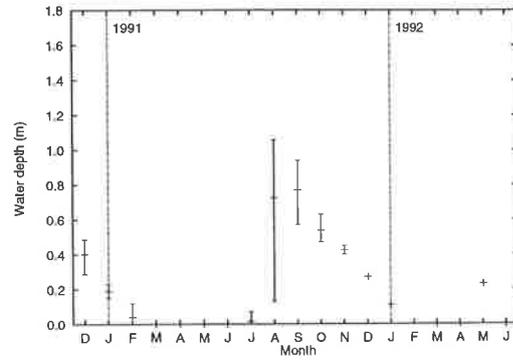
4.16.1: Regime 4, Hacks Lagoon. Elevation = 47.73 mAHD



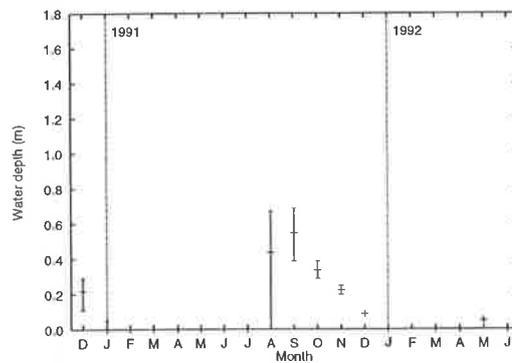
4.16.2: Regime 5, Hacks Lagoon. Elevation = 47.92 mAHD



4.16.3: Regime 6, Central Basin. Elevation = 48.00 mAHD



4.16.4: Regime 7, Hacks Lagoon. Elevation = 48.15 mAHD



4.16.5: Regime 7, Central Basin. Elevation = 48.33 mAHD

**Figure 4.16:** Changes in water depth in permanent quadrats of *Typha* throughout the sampling period. Vertical bars represent the monthly mean, minimum and maximum water depth (m). For Regime 7 in the Central Basin, stated elevation is the median elevation of two sets of sampled quadrats within the regime.

## Chapter 5

# Species distribution across the elevation gradient

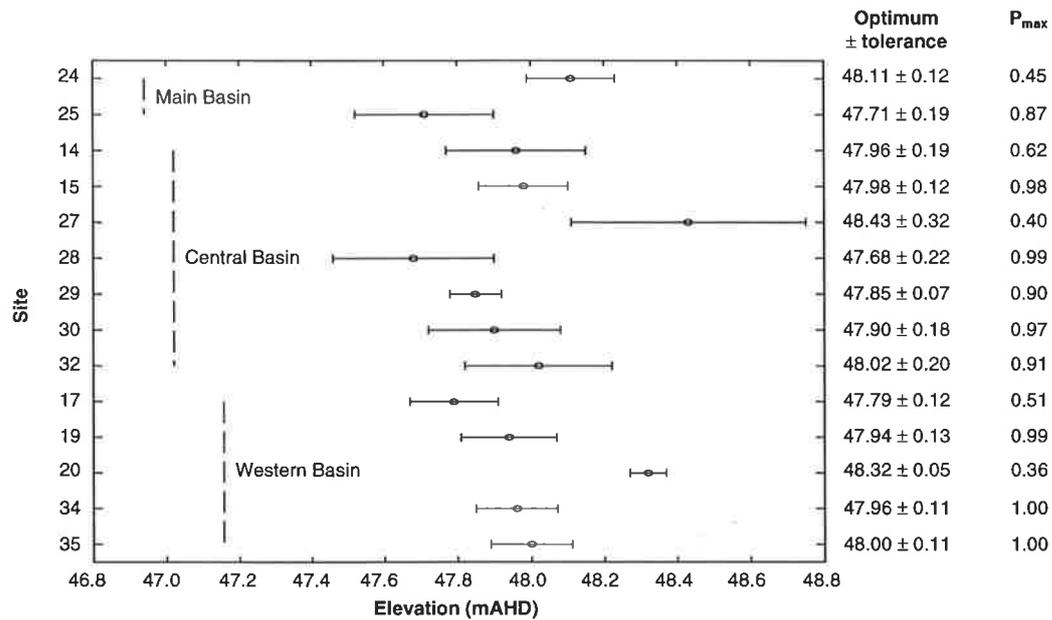


Figure 5.1: Optimum and tolerance estimates for *Baumea arthropylla* at Bool Lagoon. Vertical dashed lines indicate the elevation of the measured or estimated basin floor. P<sub>max</sub> = maximum probability of occurrence.

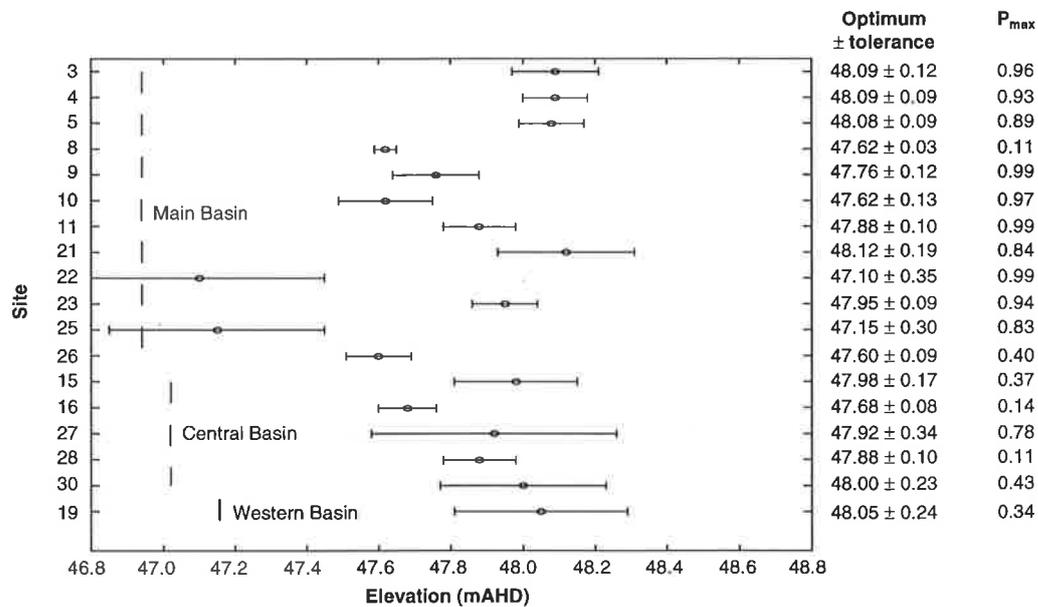
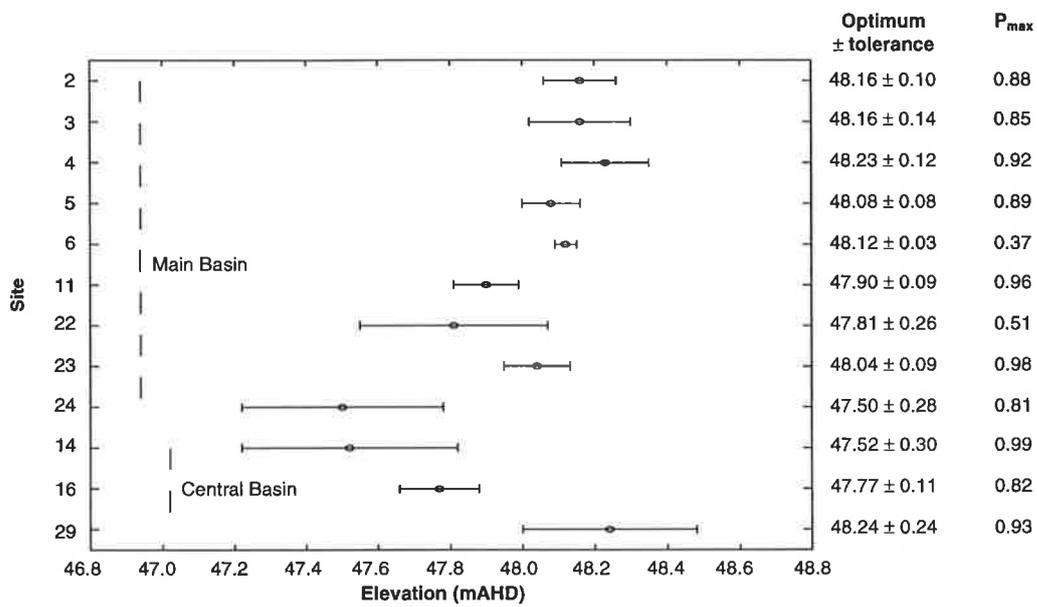
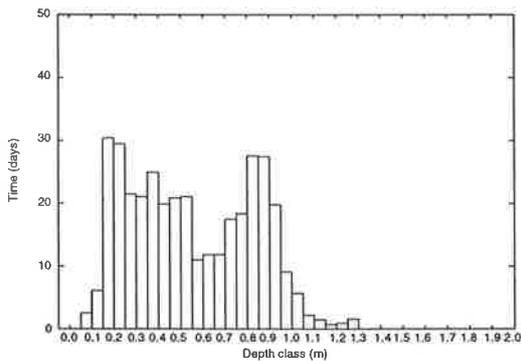


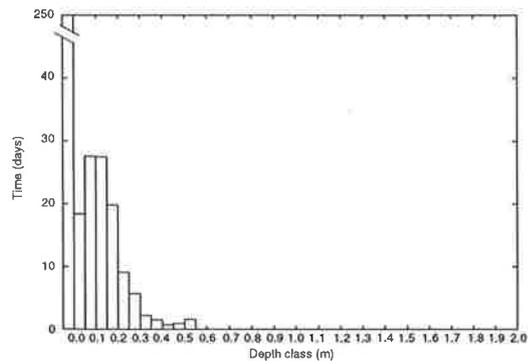
Figure 5.2: Optimum and tolerance estimates for *Triglochin procerum* at Bool Lagoon. Vertical dashed lines indicate the elevation of the measured or estimated basin floor. P<sub>max</sub> = maximum probability of occurrence.



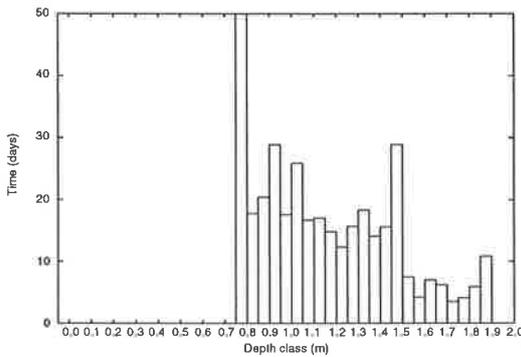
**Figure 5.3:** Optimum and tolerance estimates for *Myriophyllum salsgineum* at Bool Lagoon. Vertical dashed lines indicate the elevation of the measured or estimated basin floor. P<sub>max</sub> = maximum probability of occurrence.



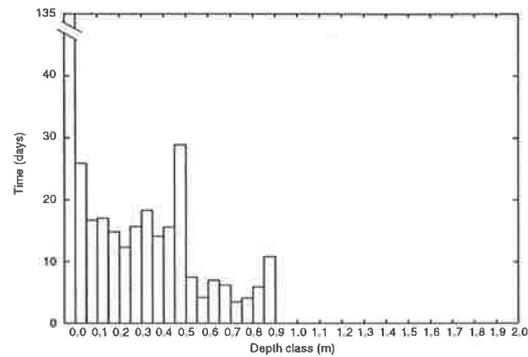
5.4.1: *Baumea arthropphylla*. Lowest optimum at 47.68 mAHD in the Central Basin.



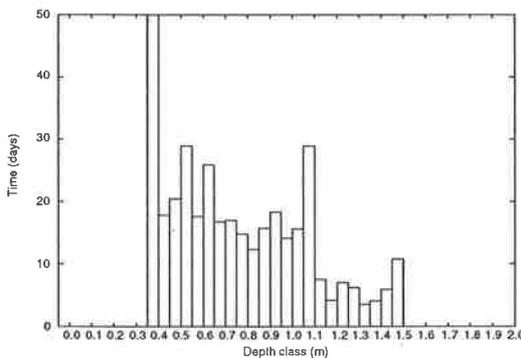
5.4.2: *Baumea arthropphylla*. Highest optimum at 48.43 mAHD in the Central Basin.



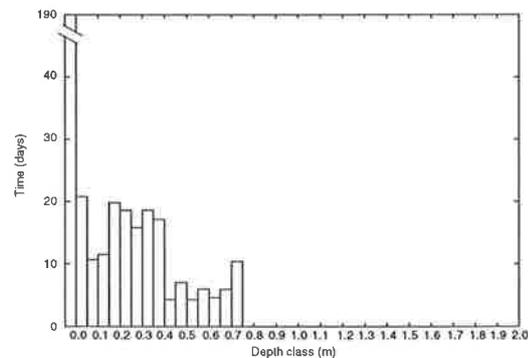
5.4.3: *Triglochin procerum*. Lowest optimum at 47.10 mAHD in the Main Basin.



5.4.4: *Triglochin procerum*. Highest optimum at 48.12 mAHD in the Main Basin.

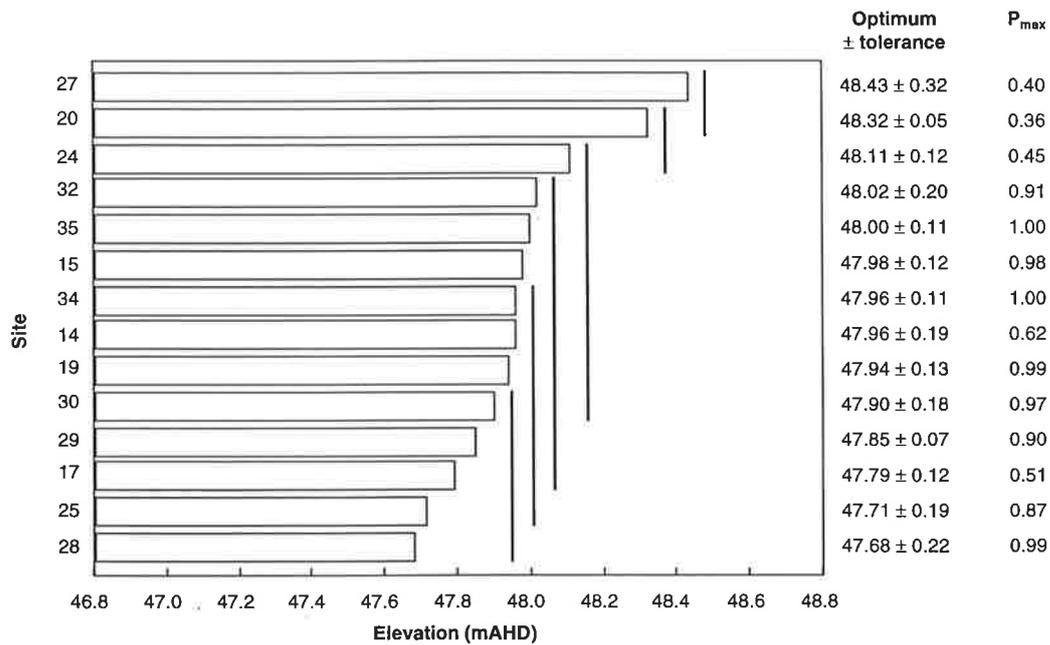


5.4.5: *Myriophyllum salsugineum*. Lowest optimum at 47.5 mAHD in the Main Basin.

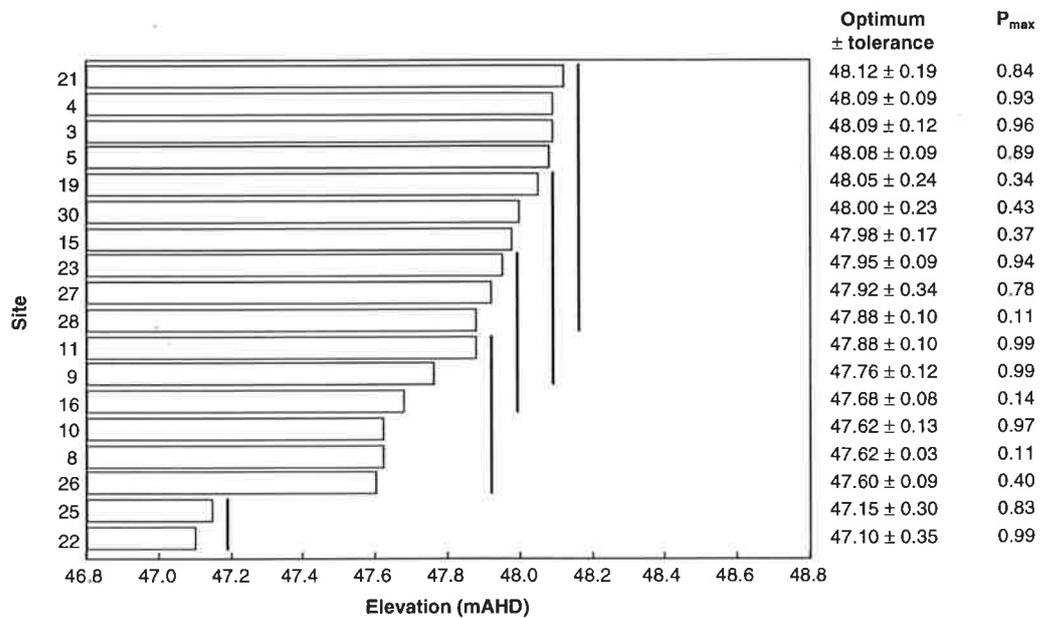


5.4.6: *Myriophyllum salsugineum*. Highest optimum at 48.24 mAHD in the Central Basin.

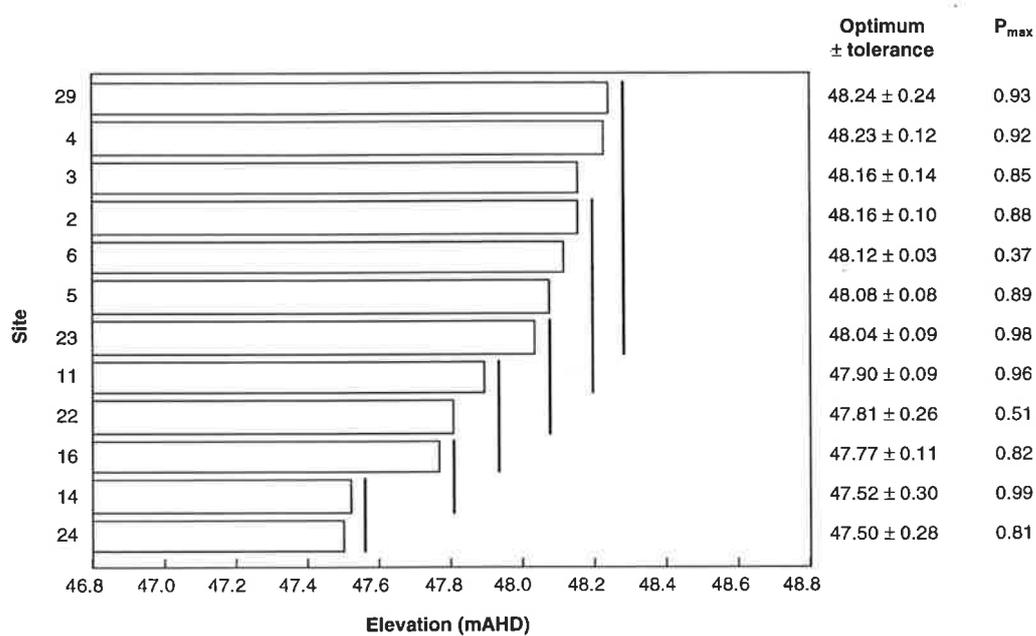
Figure 5.4: Flooding patterns over previous 12 months for minimum and maximum optima for *Baumea*, *Triglochin* and *Myriophyllum*.



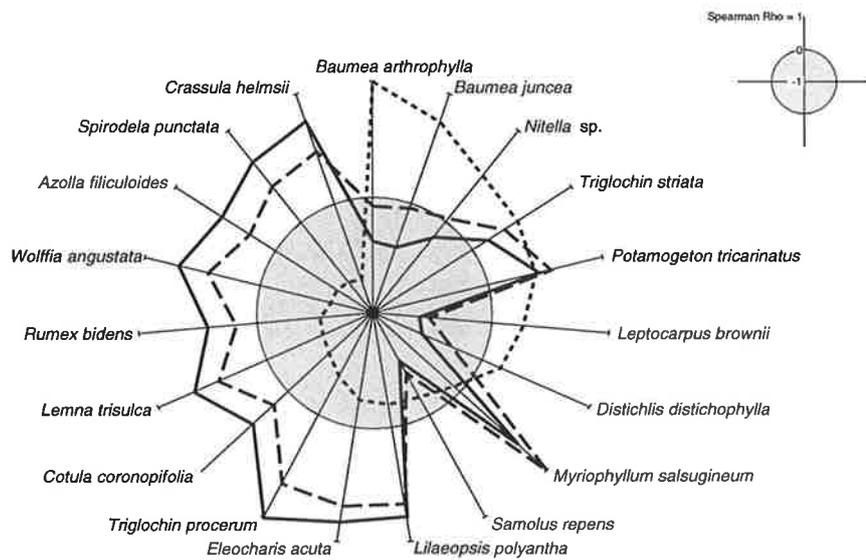
**Figure 5.5:** Comparison of optimum estimates for *Baumea arthropphylla* at Bool Lagoon. Vertical lines indicate non-significant differences between groups of sites. P<sub>max</sub> = maximum probability of occurrence.



**Figure 5.6:** Comparison of optimum estimates for *Triglochin procerum* at Bool Lagoon. Vertical lines indicate non-significant differences between groups of sites. P<sub>max</sub> = maximum probability of occurrence.



**Figure 5.7:** Comparison of optimum estimates for *Myriophyllum salsugineum* at Bool Lagoon. Vertical lines indicate non-significant differences between groups of sites.  $P_{max}$  = maximum probability of occurrence.



**Figure 5.8:** Correlation of species occurrence for *Baumea*, *Triglochin* and *Myriophyllum*. Each spoke represents the Spearman rank correlation of the abundance of major species with *Baumea* (dotted line), *Triglochin* (solid line) and *Myriophyllum* (dashed line) and is scaled from  $-1$  (at the centre) to  $+1$  (tip of spoke). Zero correlation is indicated by the perimeter of the shaded circle [see inset].

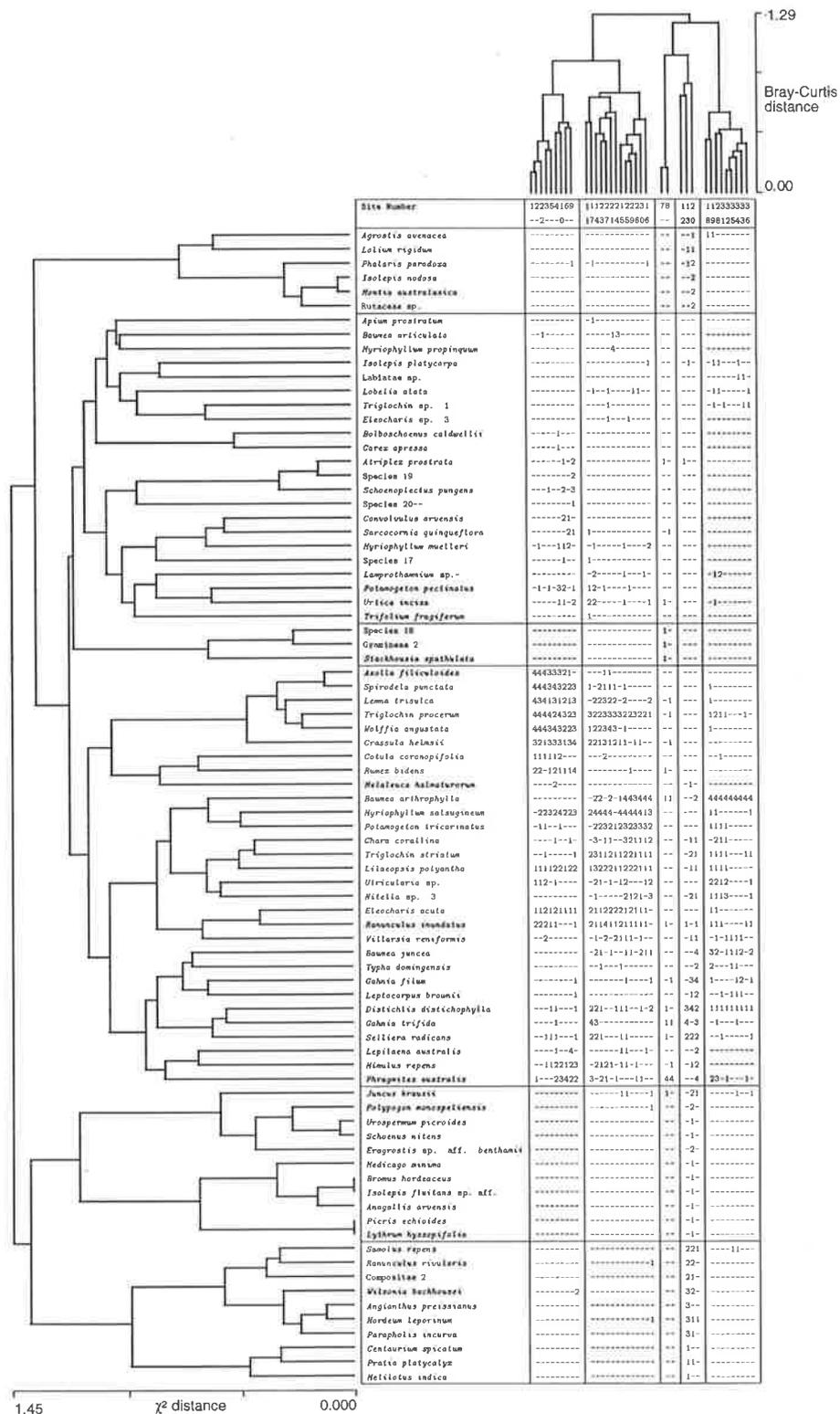
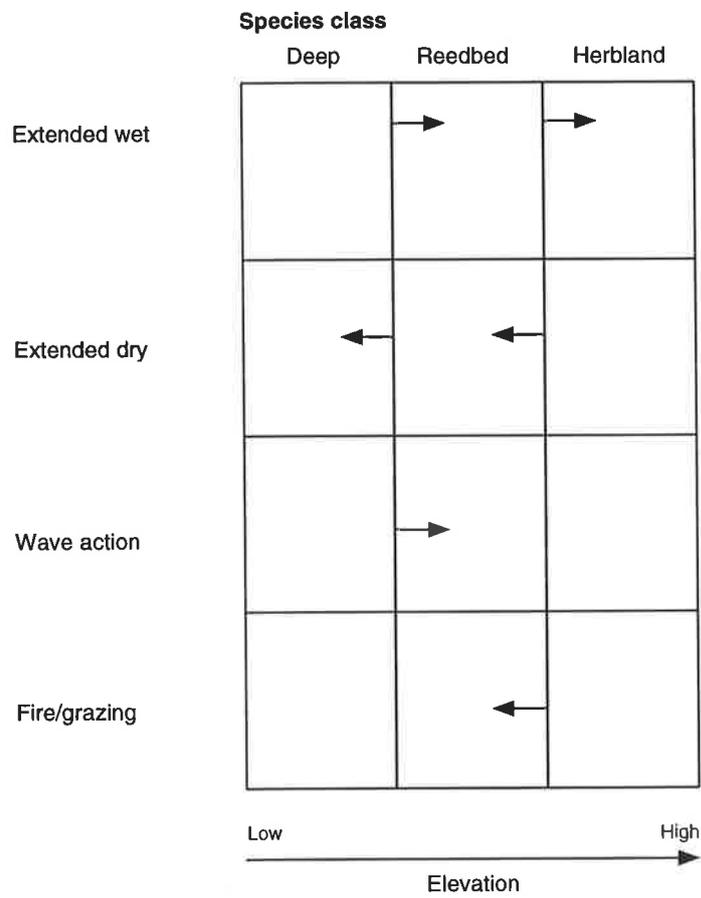
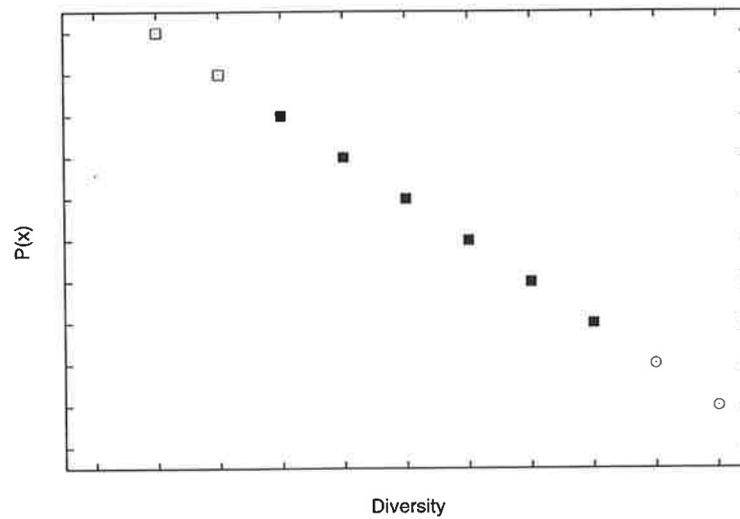


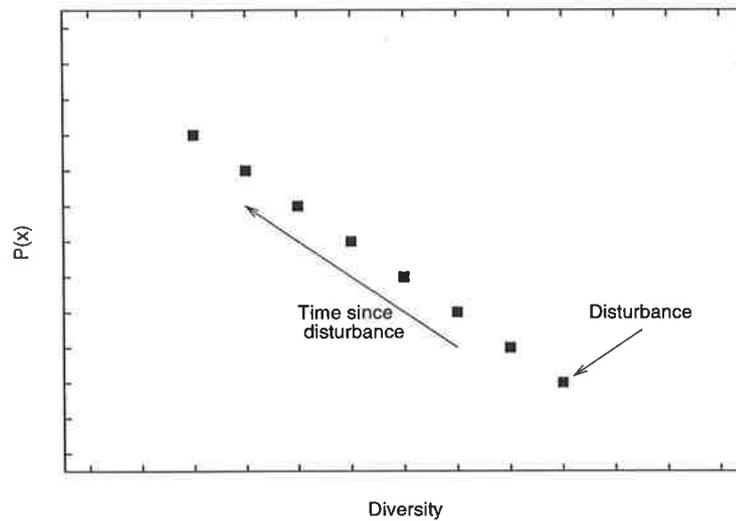
Figure 5.9: Two-way tabulation of sites and species classification at Bool Lagoon based on mean frequency score across all quadrats at each site. Frequency class scores: (-) absent; (1) 1–25%; (2) 26–50%; (3) 51–75%; (4) 76–100%.



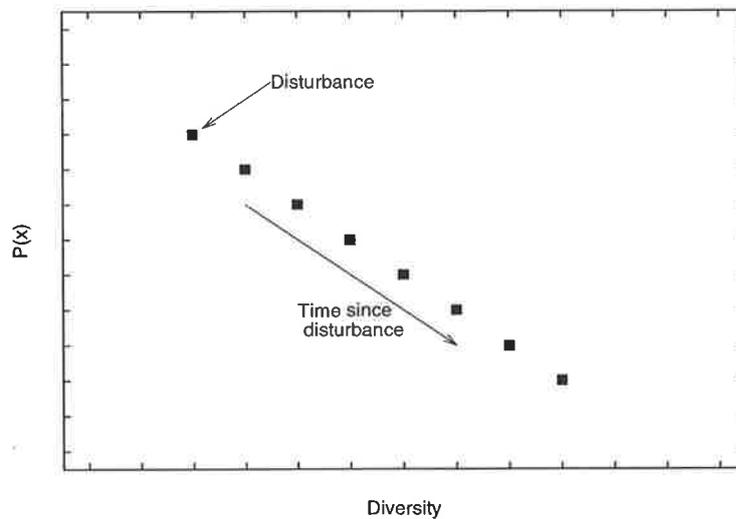
**Figure 5.10:** Movement of species boundaries in response to disturbance.



**Figure 5.11:** Hypothetical relationship between diversity and maximum probability of occurrence for *Myriophyllum* as determined by a gradient of disturbance frequency. ○ sites experience intermediate disturbance and have high diversity. □ sites experience either low or high disturbance and have low diversity.



5.12.1: *Myriophyllum* as a competitor.



5.12.2: *Myriophyllum* as a ruderal.

**Figure 5.12:** Hypothesised relationships between probability of occurrence of *Myriophyllum* and species diversity after an initial disturbance if *Myriophyllum* is either a competitor (5.12.1) or ruderal (5.12.2).

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## **Part III**

### **Tables**

# Chapter 1

## Introduction

	Hacks Lagoon	Main Basin	Central Basin	Western Basin
Perimeter (m)	5500	16000	8500	15000
Distance from water inflow <sup>a</sup> (m)	1000	3000	5000	7500
Area (ha)	193	1680	495	530
Min. recorded water level (mAHD)	47.60	47.85	47.80	47.90
Max. recorded water level (mAHD)	49.21	49.04	49.02	49.00
Measured Baseline (mAHD)	47.60 <sup>b</sup>	47.94	47.02	47.16
Max. Depth (m)	1.61 <sup>c</sup>	2.10	2.00	1.84

<sup>a</sup>to centre of basin.

<sup>b</sup>taken as minimum recorded water level.

<sup>c</sup>as a consequence of *b*.

**Table 1.1:** Morphometry and minimum and maximum water levels (1985–1992) of Bool Lagoon basins.

	Whole Lagoon		East		West	
	Mean	SD	Mean	SD	Mean	SD
pH	8.0	0.5	8.3	0.5	7.6	0.3
Conductivity ( $\mu\text{S cm}^{-1}$ )	1762.61	781.62	2040.58	771.43	1255.72	498.83
Organic (%)	7.08	2.19	6.68	1.82	7.67	2.56
SiO <sub>2</sub> (%)	53.99	15.72	45.87	15.52	65.77	4.68
Al <sub>2</sub> O <sub>3</sub> (%)	9.59	5.20	7.55	4.79	12.56	4.30
Fe <sub>2</sub> O <sub>3</sub> T (%)	3.58	1.85	3.00	1.83	4.41	1.55
MnO (%)	0.01	0.01	0.01	0.01	0.01	0.01
MgO (%)	2.47	1.17	2.71	1.45	2.13	0.31
CaO (%)	16.12	13.61	22.78	13.82	6.46	4.45
Na <sub>2</sub> O (%)	0.61	0.20	0.63	0.24	0.58	0.12
K <sub>2</sub> O (%)	1.23	0.67	0.94	0.64	1.65	0.46
TiO <sub>2</sub> (%)	0.44	0.24	0.36	0.24	0.57	0.17
P <sub>2</sub> O <sub>5</sub> (%)	0.13	0.05	0.13	0.04	0.12	0.06
SO <sub>3</sub> (%)	0.38	0.27	0.46	0.26	0.26	0.25
LOI (%)	11.23	8.44	15.50	8.49	5.04	2.34
N (%)	0.66	0.40	0.48	0.21	0.93	0.47
Ca:Na	31.28	32.31	44.67	35.67	11.82	8.97
TN:TP	5.65	3.37	3.89	1.72	8.17	3.56

**Table 1.2:** Summary of chemical characteristics of Bool Lagoon sediment. LOI=Loss on ignition and represents volatile soil components. TN=Total nitrogen. TP=Total phosphorus.

## **Chapter 2**

# **Wetland vegetation in the Lower South East of South Australia**

Formation	Description
Forest	dominated by trees taller than 8 m with more than 10% projective foliage cover.
Scrub	dominated by shrubs or trees less than 8 m tall and with greater than 10% projective foliage cover.
Marginal herbland	dominated by non-woody helophytes but not by species of graminoid form unless such species were less than 0.1 m tall at maturity.
Reed swamp	dominated by non-woody graminoid helophytes more than 1 m tall at maturity.
Sedgeland	dominated by non-tussocky graminoid helophytes 0.1–1.0 m tall at maturity.
Tussock sedgeland	dominated by graminoid helophytes of tussock form and more than 0.1 m tall at maturity.
Aquatic herbland	dominated by nymphaeids, lem-nids, elodeids, isoetids or emergent non-graminoid, herbaceous helophytes.

**Table 2.1:** Formation descriptions of Kirkpatrick and Harwood (1983).

Category	Location
Coastal peat fen swamps	Piccaninnie Ponds C.P.
Coastal saline lakes	Beachport C.P., Little Dip C.P., Lake George, Lake Eliza, Lake St. Clair, Lake Robe.
Coastal freshwater lakes	Lake Bonney.
Volcanic freshwater lakes	Mt Gambier lakes, Lake Leake, Lake Edward.
Temporary inland saline lakes	Lake Hawdon, Clay Lake com- plex.
Wet heath	Fairview C.P.*, Big Heath C.P., Mt Scott C.P.
Tussock grassland	Big Heath C.P.
Freshwater meadows	extensive (flooded grassland).
Forest swamps	Marshes*, Honan's Scrub*, Hog- arth's Scrub.
Semi-permanent swamps	
<i>Shallow</i>	Piccaninnie Ponds C.P., Hacks Lagoon, Bool Lagoon*, Lake Cadnite, Deadman's Swamp.
<i>Usually deeper</i>	Bool Lagoon*, Bucks Lake, Fairview C.P.*, Bloomfield Swamp*, Dine Swamp*.
Permanent swamps	Fairview C.P.*, Hacks Lagoon, Bloomfield Swamp*, Mullins Swamp*, Piccaninnie Ponds C.P., Penola C.P.

**Table 2.2:** 11 South East wetland categories of Jones (1978) showing examples of wetlands in each category. Asterisk indicates that the wetland is considered in this study.

Wetland	Directory listing <sup>a</sup>	Management <sup>b</sup>	Designation
Bloomfield Swamp		Private	
Bool Lagoon	+	NPWS <sup>c</sup>	Game Reserve
Dine Swamp		Private	
Fairview C.P.		NPWS	Conservation Park
Honans Swamp	+	PISA <sup>d</sup>	
The Marshes	+	PISA	
Mullins Swamp	+	Private	
Nangwarry Swamp		PISA	
Poocher Swamp	+	NPWS	Game Reserve
Shearing Tree			
Topperweins Swamp		PISA	

<sup>a</sup>Source: Anon. (In prep.) *Directory of Important Wetlands in Australia*. March 1996. Canberra: Australian Nature Conservation Agency.

<sup>b</sup>Source: South Eastern Wetlands Committee (1984)

<sup>c</sup>S.A. National Parks and Wildlife Service.

<sup>d</sup>Department of Primary Industries South Australia (Forestry).

**Table 2.3:** Management and designation of 11 South East wetlands, showing whether the wetland is listed in the *Directory of Important Wetlands in Australia*, the government agency (if any) responsible for its management, and its status as a Reserve.

Wetland comparison	No. scaling dimensions							
	1-D	2-D	3-D	4-D	5-D	6-D	7-D	8-D
G7 only	0.55	0.34	0.24	0.18	0.14	0.12	0.10	0.09
Bool + G3 + G7	0.50	0.32	0.23	0.18	0.15	0.13	0.11	0.10

**Table 2.4:** Stress values associated with SHS site ordinations.



## **Chapter 3**

### **Water regime at Bool Lagoon**

Year	Hacks Lagoon			Main Basin			Central Basin			Western Basin		
	Min.	Max.	Amplitude	Min.	Max.	Amplitude	Min.	Max.	Amplitude	Min.	Max.	Amplitude
1985	47.98	48.36	0.38	47.98	48.30	0.32	47.95	48.26	0.31	47.93	48.26	0.33
1986	47.60	48.78	1.18	47.85	48.70	0.85	47.80	48.70	0.90	47.90	48.70	0.80
1987	48.08	48.89	0.81	48.25	48.72	0.47	48.07	48.76	0.69	48.10	48.57	0.47
1988	47.97	48.95	0.98	47.88	48.85	0.97	47.89	48.83	0.94	47.94	48.72	0.78
1989	47.99	48.86	0.87	47.95	48.81	0.86	47.90	48.78	0.88	47.93	48.72	0.79
1990	48.02	48.78	0.76	47.91	48.79	0.88	47.93	48.76	0.83	47.91	48.76	0.85
1991	48.03	49.21	1.18	47.90	49.04	1.14	47.90	49.02	1.12	47.90	49.00	1.10
1992	48.01	49.00	0.99	48.00	48.86	0.86	47.95	48.85	0.90	48.00	48.66	0.66

**Table 3.1:** Minimum and maximum water levels (mAHD) and amplitude (min.–max. in m.) in each basin of Bool Lagoon for the years 1985–1992.



## Chapter 4

# Production and demography of *Phragmites* and *Typha*

Regime	Cumulative shoot no. (shoots m <sup>-2</sup> yr <sup>-1</sup> )			Max. dry weight per shoot (g Dwt)			NAPP (g m <sup>-2</sup> yr <sup>-1</sup> )			Final live AG standing crop <sup>a</sup> (g m <sup>-2</sup> )			
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	
	4 (deep)	136	87.2	4	8.99	4.64	136	1223.35	715.68	4	598.05	258.73	
5	—	—	—	—	—	—	—	—	—	—	—	—	—
6	94	23.7	4	12.86	4.33	94	1208.90	321.62	4	999.27	253.29	4	n.s.
7	115.3	24.3	6	17.78	6.27	173	2072.83	589.42	6	1296.30	359.50	6	**
8 (shallow)	102	37.9	4	17.23	6.66	102	1757.04	738.91	4	849.90	531.43	4	n.s.

<sup>a</sup>Measured at the penultimate sampling in April 1992.

**Table 4.1:** Comparison of shoot number, maximum shoot dry weight, net annual primary productivity (NAPP) and final live above ground standing crop for *Phragmites australis* during the second growing season (August 1991 – June 1992). Maximum shoot dry weight was estimated indirectly using regression equations to relate individual shoot maximum height with dry weight biomass. NAPP was calculated as the sum of individual shoot maximum biomass estimates per quadrat. Final column indicates whether a significant difference exists between NAPP and final standing crop estimates.

Regime	Cumulative shoot no.			Max. dry weight per shoot			NAPP			Final live AG standing crop <sup>a</sup>			
	(shoots m <sup>-2</sup> yr <sup>-1</sup> )			(g Dwt)			(g m <sup>-2</sup> yr <sup>-1</sup> )			(g m <sup>-2</sup> )			
	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.	N	
4 (deep)	24.8	13.1	5	44.93	41.7	31	1260.96	1022.56	5	1148.84	241.06	2	n.s.
5	70	16.2	4	23.48	19.0	70	1944.87	689.84	4	788.91	639.97	4	**
6 <sup>b</sup>	46	14.8	4	2.58	4.00	46	141.56	104.97	4	80.42	62.51	4	n.s.
7	32.6	15.3	13	26.98	24.27	106	1040.01	495.51	13	607.25	335.25	13	**
8 (shallow)	–	–	–	–	–	–	–	–	–	–	–	–	–

<sup>a</sup>Measured at the penultimate sampling in April 1992.

<sup>b</sup>Affected by swamp hen grazing.

**Table 4.2:** Comparison of shoot number, maximum shoot dry weight, net annual primary productivity (NAPP) and final live above ground standing crop for *Typha domingensis* during the second growing season (August 1991 – June 1992). Maximum shoot dry weight was estimated indirectly using regression equations to relate individual leaf maximum length with dry weight biomass. NAPP was calculated as the sum of individual shoot maximum biomass estimates per quadrat. Final column indicates whether a significant difference exists between NAPP and final standing crop estimates.

	<i>Phragmites</i>			<i>Typha</i>		
	Shoot Biomass (g m <sup>-2</sup> )	Shoot Density (m <sup>-2</sup> )	Shoot Height (cm)	Shoot Biomass (g m <sup>-2</sup> )	Shoot Density (m <sup>-2</sup> )	Shoot Height (cm)
U.K. <sup>a</sup>	1446±1211	220±98	159±30			
Sweden <sup>b</sup>	500±100					
Sweden <sup>c</sup>	447±82	61±8	215±9			
Estonia <sup>d</sup>	1310±136	124±20				
U.K. <sup>e</sup>	941±107	127±7		1118±84	100±5	
Poland <sup>f</sup>	1088	72	232	44	795	237
Australia <sup>g</sup>	9890					
Australia <sup>h</sup>				3277		
U.S.A. <sup>i</sup>				2000		
U.S.A. <sup>j</sup>				322±70		
U.S.A. <sup>k</sup>				1156		

<sup>a</sup>Boar et al. (1989) *P. australis*.

<sup>b</sup>Weisner and Granéli (1989). *P. australis*. Approximate.

<sup>c</sup>Granéli (1989) *P. australis*.

<sup>d</sup>Ksenofontova (1988) *P. australis*.

<sup>e</sup>Mason and Bryant (1975) *P. communis* and *T. angustifolia*.

<sup>f</sup>Szczepańska and Szczepański (1976) *P. communis* and *T. angustifolia*.

<sup>g</sup>Hocking (1989b) *P. australis*.

<sup>h</sup>Roberts and Ganf (1986) *T. orientalis*.

<sup>i</sup>Davis and van der Valk (1983) *T. glauca*.

<sup>j</sup>van der Valk and Bliss (1971) *T. latifolia*.

<sup>k</sup>van der Valk and Davis (1978) *T. glauca*.

**Table 4.3:** Comparison of *Phragmites* and *Typha* peak standing crop estimates. Maximum production value is shown where a range has been published.

Regime	N	Basal Diameter (mm)	
		Mean	S.D.
4	219	4.48	1.63
6	175	3.68	0.94
7	239	4.28	1.25
8	153	5.21	1.21

**Table 4.4:** Basal diameter of shoots of *Phragmites australis*

## Chapter 5

# Species distribution across the elevation gradient

	Optimum	P <sub>max</sub>	β-diversity	α-diversity
Optimum	–	–0.39 (P=0.21)	0.05 (P=0.87)	0.06 (P=0.83)
P <sub>max</sub>	–0.39 (P=0.21)	–	–0.67 (P=0.009)	–0.51 (P=0.06)
β-diversity <sup>a</sup>	0.05 (P=0.87)	–0.67 (P=0.009)	–	0.73 (P=0.003)
α-diversity <sup>b</sup>	0.06 (P=0.83)	–0.51 (P=0.06)	0.73 (P=0.003)	–

<sup>a</sup>Estimated as  $\sqrt{\text{Bray} - \text{Curtis}}$  dissimilarity.

<sup>b</sup>Estimated as species richness.

**Table 5.1:** Spearman rank correlation coefficients and associated P values of optimum, maximum probability of occurrence and α- and β-diversity for *Baumea arthrophylla*.

	Optimum	P <sub>max</sub>	β-diversity	α-diversity
Optimum	–	–0.002 (P=0.99)	0.08 (P=0.76)	0.15 (P=0.56)
P <sub>max</sub>	–0.002 (P=0.99)	–	0.48 (P=0.05)	0.18 (P=0.48)
β-diversity <sup>a</sup>	0.07 (P=0.76)	0.48 (P=0.05)	–	0.58 (P=0.01)
α-diversity <sup>b</sup>	0.15 (P=0.56)	0.18 (P=0.48)	0.58 (P=0.01)	–

<sup>a</sup>Estimated as  $\sqrt{\text{Bray} - \text{Curtis}}$  dissimilarity.

<sup>b</sup>Estimated as species richness.

**Table 5.2:** Spearman rank correlation coefficients and associated P values of optimum, maximum probability of occurrence and α- and β-diversity for *Triglochin procerum*.

	Optimum	P <sub>max</sub>	β-diversity	α-diversity
Optimum	–	0.09 (P=0.77)	–0.36 (P=0.25)	–0.52 (P=0.08)
P <sub>max</sub>	0.09 (P=0.77)	–	0.11 (P=0.74)	0.15 (P=0.65)
β-diversity <sup>a</sup>	–0.35 (P=0.25)	0.11 (P=0.74)	–	0.46 (P=0.13)
α-diversity <sup>b</sup>	–0.52 (P=0.08)	0.15 (P=0.65)	0.46 (P=0.13)	–

<sup>a</sup>Estimated as  $\sqrt{\text{Bray} - \text{Curtis}}$  dissimilarity.

<sup>b</sup>Estimated as species richness.

**Table 5.3:** Spearman rank correlation coefficients and associated P values of optimum, maximum probability of occurrence and α- and β-diversity for *Myriophyllum salsugineum*.

**Part IV**  
**Appendices**

# Appendix A

## Bool Lagoon sediment chemistry

Site	n	pH		Conductivity ( $\mu\text{Scm}^{-1}$ )		Organic (%)		SiO <sub>2</sub> (%)		Al <sub>2</sub> O <sub>3</sub> (%)		Fe <sub>2</sub> O <sub>3</sub> T (%)		MnO (%)		MgO (%)		CaO (%)		Na <sub>2</sub> O (%)		K <sub>2</sub> O (%)		TiO <sub>2</sub> (%)		P <sub>2</sub> O <sub>5</sub> (%)		SO <sub>3</sub> (%)		LOI (%)		N (%)	
		$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
1	4	8.1	0.18	1579.25	168.61	6.27	0.30	62.30	1.09	16.44	0.67	6.56	0.23	0.02	0.00	2.32	0.08	4.28	1.34	0.64	0.02	1.5	0.04	0.86	0.04	0.15	0.02	0.18	0.03	4.5	0.48	0.66	0.03
2	1	7.9	-	1960.00	-	5.96	-	63.90	-	16.01	-	6.54	-	0.02	-	2.87	-	3.12	-	0.76	-	1.78	-	0.79	-	0.13	-	0.15	-	3.40	-	0.67	-
3	2	8.4	0.30	1578.00	11.31	5.08	1.43	41.10	4.10	8.04	2.66	3.19	1.15	0.01	0.00	2.30	0.93	24.80	1.13	0.53	0.11	1.07	0.37	0.36	0.11	0.12	0.01	0.37	0.21	18.00	0.00	0.23	0.14
4	2	8.4	0.05	1267.50	283.55	6.12	1.75	41.95	13.08	9.99	0.44	4.10	0.04	0.02	0.01	2.51	0.12	22.40	9.19	0.57	0.23	1.38	0.18	0.44	0.02	0.15	0.08	0.35	0.14	16.00	4.24	0.26	0.08
5	2	8.5	0.15	2750.00	410.12	5.36	3.60	46.30	19.37	9.82	10.15	3.84	4.04	0.02	0.01	2.28	0.97	19.40	20.22	1.12	0.83	1.05	1.22	0.55	0.59	0.14	0.10	0.28	0.04	14.70	15.98	0.31	0.35
6	4	8.5	0.20	2107.50	397.52	6.70	1.29	34.33	1.64	5.72	1.70	2.30	0.67	0.01	0.00	2.06	0.13	30.53	1.01	0.63	0.04	0.68	0.26	0.25	0.07	0.12	0.01	0.48	0.23	22.67	2.52	0.29	0.10
7	3	7.7	0.2	1311.67	187.44	6.40	0.84	64.13	0.83	16.42	0.51	6.06	0.12	0.01	0.01	4.13	0.06	1.67	0.18	0.65	0.04	2.36	0.07	0.75	0.02	0.13	0.02	0.16	0.09	3.73	0.95	0.56	0.12
8	3	9.6	2.4	2295.67	449.10	7.86	0.84	65.63	0.47	14.26	0.35	5.36	0.09	0.01	0.00	4.17	0.05	2.19	0.65	1.00	0.05	2.09	0.05	0.63	0.02	0.14	0.02	0.26	0.16	4.10	0.20	0.63	0.09
9	5	8.2	0.2	2200.80	457.90	6.85	1.86	31.98	9.60	3.82	2.23	1.75	0.93	0.01	0.00	2.09	0.49	34.20	7.60	0.53	0.19	0.42	0.32	0.18	0.10	0.16	0.04	0.54	0.11	24.00	6.52	0.50	0.19
10	3	7.9	0.1	2290.00	85.44	7.56	1.13	49.73	2.24	5.67	0.48	2.41	0.21	0.01	0.00	1.84	0.23	23.33	2.95	0.60	0.03	0.87	0.09	0.27	0.02	0.22	0.01	0.86	0.51	14.33	1.53	0.75	0.04
11	3	8.1	0.2	2048.33	143.73	7.91	1.53	31.67	1.29	1.74	0.11	0.77	0.04	0.01	0.00	1.45	0.06	39.43	0.76	0.35	0.04	0.15	0.01	0.08	0.01	0.18	0.01	0.62	0.18	24.00	1.73	0.59	0.04
12	3	8.8	0.2	3986.67	604.35	10.66	3.20	25.53	2.98	4.94	0.38	1.91	0.14	0.03	0.01	7.15	1.09	42.13	3.50	0.89	0.14	0.34	0.04	0.25	0.02	0.11	0.01	0.54	0.16	16.30	8.54	0.11	0.03
13	3	9.0	0.3	2426.67	150.11	8.40	0.25	19.50	0.89	4.40	0.42	1.76	0.14	0.02	0.00	4.88	0.28	42.27	2.00	0.65	0.03	0.49	0.11	0.20	0.02	0.10	0.01	0.58	0.23	25.00	1.00	0.18	0.02
14	3	8.2	0.3	1610.33	50.52	5.97	0.25	56.70	0.53	7.29	0.40	2.77	0.15	0.01	0.00	2.21	0.05	16.13	0.81	0.65	0.05	1.09	0.06	0.31	0.02	0.14	0.02	0.53	0.21	12.00	1.00	0.61	0.02
15	3	8.0	0.2	1906.33	586.07	5.98	0.75	44.10	1.41	4.49	0.34	1.74	0.12	0.01	0.01	1.64	0.10	26.30	1.23	0.54	0.03	0.60	0.04	0.20	0.02	0.11	0.01	0.61	0.29	19.67	1.15	0.43	0.15
16	3	8.0	0.2	1455.67	193.04	4.15	1.10	58.50	3.78	8.52	1.94	3.20	0.73	0.01	0.00	2.29	0.41	13.83	3.52	0.55	0.07	1.28	0.31	0.39	0.10	0.09	0.01	0.34	0.13	11.03	3.55	0.55	0.03
17	3	8.5	0.0	3653.33	765.14	5.85	1.61	56.30	0.28	10.41	0.66	4.08	0.25	0.01	0.00	4.53	0.21	13.10	2.69	1.20	0.04	1.62	0.11	0.46	0.03	0.07	0.01	0.40	0.11	7.95	0.92	0.38	0.08
18	3	8.2	0.1	1190.67	154.05	7.59	1.17	35.13	0.96	2.93	0.03	1.17	0.03	0.01	0.00	1.45	0.02	33.70	0.26	0.33	0.02	0.31	0.01	0.14	0.01	0.13	0.01	0.77	0.40	24.00	1.00	0.72	0.01
19	3	7.7	0.2	1574.67	346.00	7.40	0.94	59.37	0.76	4.88	0.09	2.07	0.05	0.01	0.00	1.55	0.02	17.57	0.59	0.47	0.02	0.66	0.01	0.23	0.01	0.11	0.00	0.60	0.22	12.67	0.58	0.80	0.11
20	3	7.9	0.3	1496.33	120.27	5.59	0.66	67.13	0.15	8.24	0.54	3.44	0.22	0.01	0.00	2.35	0.12	9.65	1.48	0.49	0.01	1.14	0.08	0.38	0.02	0.09	0.01	0.34	0.18	6.77	1.29	0.47	0.03
21	3	7.6	0.2	902.00	229.99	4.51	0.38	68.40	1.18	16.53	0.18	5.30	0.09	0.01	0.00	1.95	0.03	1.23	0.21	0.48	0.02	2.10	0.03	0.78	0.01	0.08	0.01	0.05	0.03	2.70	0.53	0.34	0.06
22	3	7.8	0.1	1432.33	734.73	5.75	0.49	64.33	2.91	17.39	0.25	6.32	0.05	0.01	0.01	2.39	0.14	2.87	1.85	0.51	0.02	1.97	0.13	0.77	0.02	0.11	0.01	0.11	0.14	3.13	0.95	0.53	0.07
23	3	8.0	0.2	1267.33	512.53	4.63	0.26	58.80	0.20	21.54	0.09	7.83	0.05	0.02	0.01	2.62	0.04	1.36	0.06	0.61	0.06	2.61	0.03	0.89	0.02	0.06	0.01	0.05	0.02	3.37	0.40	0.30	0.05
24	3	7.8	0.2	1290.33	152.40	7.82	2.33	64.60	2.19	17.20	0.63	6.29	0.25	0.02	0.01	2.40	0.07	2.00	0.30	0.68	0.09	2.24	0.04	0.76	0.05	0.12	0.02	0.11	0.03	3.37	0.83	0.80	0.27
25	3	7.5	0.3	981.73	828.57	8.32	1.05	69.07	0.55	14.26	0.31	5.02	0.13	0.01	0.00	2.58	0.16	2.69	0.64	0.66	0.05	1.72	0.05	0.60	0.01	0.10	0.02	0.09	0.03	2.93	0.49	1.15	0.19
26	3	7.5	0.4	1944.33	339.05	9.80	3.04	64.73	2.35	10.88	2.76	4.06	0.44	0.01	0.01	2.20	0.20	9.14	0.45	0.59	0.13	1.43	0.06	0.47	0.07	0.13	0.06	0.26	0.09	5.60	1.60	1.30	0.27
27	3	7.9	0.1	1575.67	85.01	8.21	0.40	62.50	2.31	10.21	0.11	3.61	0.13	0.02	0.01	1.88	0.05	10.64	1.28	0.58	0.06	1.12	0.02	0.43	0.01	0.14	0.01	0.68	0.32	7.90	0.61	0.91	0.14
28	1	7.2	-	1265.00	-	12.37	-	66.10	-	10.24	-	3.55	-	0.01	-	1.98	-	8.85	-	0.52	-	1.18	-	0.43	-	0.17	-	0.95	-	6.90	-	1.56	-
29	2	7.3	0.0	590.15	788.92	8.34	0.98	73.85	0.07	11.09	0.04	3.94	0.15	0.01	0.00	1.91	0.01	2.57	0.13	0.52	0.01	1.86	0.01	0.56	0.02	0.13	0.01	0.12	0.02	2.60	0.42	0.90	0.44
30	3	7.0	0.4	1314.50	126.57	11.85	0.95	63.57	2.86	13.35	1.04	4.11	0.44	0.01	0.00	2.41	0.16	6.83	0.42	0.81	0.08	1.66	0.10	0.65	0.07	0.30	0.02	0.26	0.08	5.53	1.90	1.77	0.25
31	3	7.2	0.3	-	-	9.34	0.44	68.70	3.29	10.02	0.47	2.81	0.20	0.01	0.00	1.79	0.09	7.98	2.69	0.55	0.01	1.30	0.08	0.43	0.02	0.15	0.02	0.21	0.06	5.07	0.93	1.56	0.36
32	3	7.6	0.2	1455.50	566.39	6.74	3.23	59.13	3.04	7.40	1.44	2.99	0.70	0.02	0.02	1.93	0.11	16.00	1.84	0.57	0.15	0.98	0.11	0.36	0.07	0.09	0.04	0.42	0.23	9.03	2.81	1.08	0.25
33	3	7.8	0.1	1253.67	220.21	8.72	2.01	71.23	2.06	8.07	0.17	2.61	0.09	0.01	0.00	1.82	0.07	7.78	1.63	0.52	0.02	1.39	0.06	0.43	0.02	0.11	0.02	0.47	0.29	5.20	1.31	0.63	0.17
34	3	7.8	0.4	1094.00	-	6.58	2.13	68.73	7.52	10.50	2.99	4.22	0.76	0.01	0.01	2.15	0.25	6.44	2.95	0.61	0.25	1.54	0.21	0.52	0.10	0.11	0.07	0.17	0.09	4.63	2.18	0.84	0.28
35	3	7.8	0.2	836.50	47.38	5.41	0.82	65.77	1.55	7.65	0.95	2.83	0.30	0.01	0.00	1.78	0.10	10.73	1.65	0.41	0.03	1.36	0.18	0.43	0.04	0.06	0.01	0.37	0.29	8.07	0.85	0.67	0.16

Table A.1: Chemical characteristics of the sediment at 35 sites around Boal Lagoon. See Figure 1.2 for sample locations.

# Appendix B

## Species list

Full species list for all sampled South East wetlands. \* indicates naturalised taxon. Nomenclature follows Jessop (1989).

N	Full name	Code	Family	Bool Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
1	<i>Acacia longifolia</i> (Andrews)Willd. var. <i>sophorae</i> F.Muell.	ACACLONG	LEGUMINOSAE					+					+	
2	<i>Acacia melanoxylon</i> R.Br.	ACACMELA	LEGUMINOSAE											+
3	<i>Acaena nova-zelandiae</i> Kirk	ACAENOVA	ROSACEAE									+	+	+
4	<i>Acaena</i> sp.	ACAESP.	ROSACEAE					+						
5	<i>Agrostis avenacea</i> J.Gmelin var <i>avenacea</i>	AGROAVEN	GRAMINEAE	+										
6	<i>Alternanthera denticulata</i> R.Br.	ALTEDENT	AMARANTHACEAE						+	+				
7	<i>Anagallis arvensis</i> L.	ANAGARVE	PRIMULACEAE	+	+		+							
8	<i>Angianthus preissianus</i> (Steetz)Benth.	ANGIPREI	COMPOSITAE	+										
9	<i>Apium annuum</i> P.Short	APIUANNU	UMBELLIFERAE				+							
10	<i>Apium prostratum</i> Labill. ex Vent.	APIUPROS	UMBELLIFERAE	+				+						
11	<i>Asperula conferta</i> Hook.f.	ASPECONF	RUBIACEAE						+					
12	* <i>Aster subulatus</i> Michaux.	ASTESUBU	COMPOSITAE					+						
13	<i>Atriplex australasica</i> Moq.	ATRIAUST	CHENOPODIACEAE					+						
14	* <i>Atriplex prostrata</i> DC.	ATRIPROS	CHENOPODIACEAE	+				+						
15	<i>Azolla filiculoides</i> Lam.	AZOLFILI	AZOLLACEAE	+		+		+		+				
16	<i>Baumea arthrophylla</i> (Nees.)Boeckeler	BAUMARTH	CYPERACEAE	+				+			+	+	+	+
17	<i>Baumea articulata</i> (R.Br.)S.T.Blake	BAUMARTI	CYPERACEAE	+							+	+	+	+
18	<i>Baumea juncea</i> (R.Br.)Palla	BAUMJUNC	CYPERACEAE	+	+		+	+					+	+
19	<i>Berula erecta</i> (Hudson)Coville	BERUEREC	UMBELLIFERAE					+						
20	<i>Bolboschoenus caldwelii</i> (V.Cook)Sojak	BOLBCALD	CYPERACEAE	+										
21	* <i>Bromus hordeaceus</i> L. var. <i>hordeaceus</i>	BROMHORD	GRAMINEAE	+										
22	Campanulaceae 1	CAMP1	CAMPANULACEAE					+						
23	Campanulaceae 2	CAMP2	CAMPANULACEAE		+						+			
24	<i>Carex apressa</i> R.Br.	CAREAPRE	CYPERACEAE	+										
25	* <i>Centaurium erythraea</i> Rafn.	CENTERYT	GENTIANACEAE									+		+
26	* <i>Centaurium spicatum</i> (L.)Fritsch	CENTSPIC	GENTIANACEAE	+										
27	<i>Centella cordifolia</i> (Hook.f.)Nannf.	CENTCORD	UMBELLIFERAE		+						+			
28	<i>Centipeda cunninghamii</i> (DC.)A.Braun & Asch.	CENTCUNN	COMPOSITAE			+			+	+				
29	<i>Chara corallina</i> Klein ex Will. esk. R.D.Wood	CHARCORA	CHARACEAE	+						+				
30	<i>Chara</i> sp.	CHARSP.	CHARACEAE			+								

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N	Full name	Code	Family	Bool Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
31	* <i>Chenopodium glaucum</i> L.	CHENGLAU	CHENOPODIACEAE		+			+						
32	<i>Chorizandra enodis</i> Nees.	CHORENOD	CYPERACEAE								+			
33	<i>Clematis microphylla</i> DC.	CLEMMICR	RANUNCULACEAE		+									
34	Compositae 1	COMP1	COMPOSITAE		+	+	+	+	+	+	+			
35	Compositae 2	COMP2	COMPOSITAE		+									
36	<i>Convolvulus arvensis</i> L.	CONVARVE	CONVOLVULACEAE		+									
37	<i>Conyza bonariensis</i> (L.)Cronq.	CONYBONA	COMPOSITAE									+		
38	<i>Cotula coronopifolia</i> L.	COTUCORO	COMPOSITAE		+			+						
39	<i>Crassula decumbens</i> Thunb. var. <i>decumbens</i>	CRASDECU	CRASSULACEAE			+								
40	<i>Crassula helmsii</i> (Kirk)Cockayne	CRASHELM	CRASSULACEAE		+	+		+	+		+			
41	<i>Crassula natans</i> Thunb. var. <i>natans</i>	CRASNATA	CRASSULACEAE			+			+					
42	* <i>Cynodon dactylon</i> (L.)Pers.	CYNODACT	GRAMINEAE							+				
43	<i>Dianella revoluta</i> R.Br. var. <i>revoluta</i>	DIANREVO	LILIACEAE									+	+	+
44	<i>Dichondra repens</i> Forster & Forster f.	DICHREPE	CONVOLVULACEAE								+			
45	<i>Distichlis distichophylla</i> (Labill.)Fassett	DISTDIST	GRAMINEAE		+									
46	* <i>Dittrichia graveolens</i> (L.)Greuter	DITTGRAV	COMPOSITAE			+								
47	<i>Eleocharis acuta</i> R.Br.	ELEOACUT	CYPERACEAE		+					+				
48	<i>Eleocharis atricha</i> R.Br.	ELEOATRI	CYPERACEAE				+							
49	<i>Eleocharis</i> sp. 1	ELEOSP.1	CYPERACEAE					+						
50	<i>Eleocharis</i> sp. 2	ELEOSP.2	CYPERACEAE											
51	<i>Eleocharis</i> sp. 3	ELEOSP.3	CYPERACEAE		+									
52	* <i>Epilobium ciliatum</i> Raf.	EPILCILI	ONAGRACEAE					+				+		+
53	<i>Eragrostis</i> sp. aff. <i>benthamii</i> Mattei	ERAGBENT	GRAMINEAE		+									
54	<i>Erodium cicutarium</i> (L.)L'Hér. ex Aiton	ERODCICU	GERANIACEAE					+						
55	<i>Eucalyptus Baxteri</i> (Benth.)Maiden & Blakely ex J.Black	EUCABAXT	MYRTACEAE			+								
56	<i>Eucalyptus camaldulensis</i> Dehnh.	EUCACAMA	MYRTACEAE			+				+	+			
57	<i>Eucalyptus</i> sp.	EUCASP.	MYRTACEAE				+							
58	<i>Euphorbia drummondii</i> Boiss.	EUPHDRUM	EUPHORBIACEAE						+	+				
59	<i>Ferula communis</i> L.	FERUCOMM	UMBELLIFERAE									+		
60	<i>Festuca</i> sp.	FESCSP.	GRAMINEAE			+	+	+	+	+				

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N	Full name	Code	Family	BooL Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
61	<i>Gahnia filum</i> (Labill.)F.Muell.	GAHNFILU	CYPERACEAE	+										
62	<i>Gahnia trifida</i> Labill.	GAHNTRIF	CYPERACEAE	+				+				+	+	+
63	<i>Geranium potentilloides</i> L'Hér. ex DC. var <i>potentilloides</i>	GERAPOTE	GERANIACEAE					+						
64	* <i>Gnaphalium spicatum</i> Lam.	GNAPSPIC	COMPOSITAE											
65	<i>Gonocarpus elatus</i> (Cunn. ex Fenzl)Orch.	GONOELAT	HALORAGACEAE									+		
66	<i>Goodenia humilis</i> R.Br.	GOODHUMI	GOODENIACEAE											
67	Goodeniaceae 1	GOOD1	GOODENIACEAE								+			
68	Gramineae 1	GRAM1	GRAMINEAE			+	+	+	+	+				
69	Gramineae 2	GRAM2	GRAMINEAE	+										
70	Gramineae 3	GRAM3	GRAMINEAE								+			
71	Gramineae 4	GRAM4	GRAMINEAE								+			
72	Gramineae 5	GRAM5	GRAMINEAE								+			
73	Gramineae 6	GRAM6	GRAMINEAE									+		
74	Gramineae 7	GRAM7	GRAMINEAE									+		+
75	<i>Gratiola pubescens</i> R.Br.	GRATPUBE	SCROPHULARIACEAE									+		
76	<i>Haloragis aspera</i> Lindley	HALOASPE	HALORAGACEAE						+					
77	<i>Haloragis brownii</i> (Hook.f.)Schindler	HALOBROW	HALORAGACEAE					+						
78	Herb 1	HERB1	-		+			+						
79	Herb 2	HERB2	-		+									
80	Herb 3	HERB3	-										+	
81	<i>Hibbertia empetrifolia</i> (DC.)Hoogl.	HIBBEMPE	DILLENIACEAE					+						
82	* <i>Holcus lanatus</i> L.	HOLCLANA	GRAMINEAE		+			+			+			
83	* <i>Hordeum leporinum</i> Link	HORDLEPO	GRAMINEAE	+										
84	<i>Hydrocotyle hirta</i> R.Br. ex A.Rich.	HYDRHIRT	UMBELLIFERAE									+		+
85	<i>Hydrocotyle laxiflora</i> DC.	HYDRLAXI	UMBELLIFERAE								+			
86	* <i>Hypochoeris radicata</i> L.	HYPORADI	COMPOSITAE											
87	<i>Isolepis fluitans</i> (L.)R.Br. sp. aff.	ISOLFLUI	CYPERACEAE	+										
88	<i>Isolepis inundata</i> R.Br.	ISOLINUN	CYPERACEAE		+									
89	<i>Isolepis nodosa</i> (Rottb.)R.Br.	ISOLNODO	CYPERACEAE	+	+		+							
90	<i>Isolepis platycarpa</i> (S.T.Blake)Sojak	ISOLPLAT	CYPERACEAE	+			+	+						

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N	Full name	Code	Family	Bool Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
91	<i>Juncus kraussii</i> Hochst.	JUNCKRAU	JUNCACEAE	+				+						
92	<i>Juncus pallidus</i> R.Br.	JUNCPALL	JUNCACEAE				+							
93	<i>Juncus prismatocarpus</i> R.Br.	JUNCPRIS	JUNCACEAE					+		+				
94	<i>Juncus procerus</i> E.Meyer	JUNCPROC	JUNCACEAE		+							+	+	+
95	<i>Juncus subsecundus</i> Wakef.	JUNCSUBS	JUNCACEAE						+					
96	* <i>Kickxia elatine</i> (L.)Dumort. ssp. <i>crinita</i> (Mabille)W.Greutner	KICKELAT	SCROPHULARIACEAE							+				
97	Labiatae sp.	LABISP.	LABIATAE	+										
98	* <i>Lactuca serriola</i> L.	LACTSERR	COMPOSITAE											
99	<i>Lamprothamnium</i> sp.	LAMPSP.	CHARACEAE	+										
100	<i>Lemna trisulca</i> L.	LEMNTRIS	LEMNACEAE	+										
101	<i>Lepidosperma laterale</i> R.Br.	LEPILATE	CYPERACEAE								+			
102	<i>Lepidosperma longitudinale</i> Labill.	LEPILONG	CYPERACEAE		+									
103	<i>Lepilaena australis</i> J.L.Drumm. ex Harvey	LEPIAUST	ZANNICHELLIACEAE	+										
104	<i>Leptocarpus brownii</i> Hook.f.	LEPTBROW	RESTIONACEAE	+										
105	<i>Leptospermum juniperinum</i> Smith	LEPTJUNI	MYRTACEAE		+						+			
106	<i>Leptospermum lanigerum</i> (Aiton)Smith	LEPTLANI	MYRTACEAE					+						
107	<i>Leptospermum myrsinoides</i> Schldl.	LEPTMYRS	MYRTACEAE									+	+	+
108	<i>Lepyrodia muelleri</i> Benth.	LEPYMUEL	RESTIONACEAE								+			
109	<i>Leucopogon lanceolatus</i> (Smith)R.Br. var. <i>lanceolatus</i>	LEUCLANC	EPACRIDACEAE					+						
110	<i>Lilaeopsis polyantha</i> (Gand.)H.Eichler	LILAPOLY	UMBELLIFERAE	+	+		+	+			+	+	+	
111	<i>Limosella australis</i> R.Br.	LIMOAUST	SCROPHULARIACEAE				+			+				
112	<i>Lobelia alata</i> Labill.	LOBEALAT	CAMPANULACEAE	+				+						
113	<i>Lobelia pratioides</i> Benth.	LOBEPRAT	CAMPANULACEAE								+			
114	* <i>Lolium rigidum</i> Gaudin	LOLIRIGI	GRAMINEAE	+										
115	<i>Lythrum hyssopifolia</i> L.	LYTHHYSS	LYTHRACEAE	+	+	+		+	+	+				
116	<i>Marsilea drummondii</i> A.Braun	MARSDRUM	MARSILEACEAE						+	+				
117	* <i>Medicago minima</i> (L.)Bartal. var. <i>minima</i>	MEDIMINI	LEGUMINOSAE	+										
118	* <i>Medicago sativa</i> L.	MEDISATI	LEGUMINOSAE											+
119	* <i>Medicago</i> sp.	MEDISP.	LEGUMINOSAE						+					
120	<i>Melaleuca brevifolia</i> Turcz.	MELABREV	MYRTACEAE		+		+							

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N	Full name	Code	Family	Boo Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
121	<i>Melaleuca halmaturorum</i> F.Muell. ex Miq.	MELAHALM	MYRTACEAE	+										
122	* <i>Melilotus indica</i> (L.)All.	MELIINDI	LEGUMINOSAE	+										
123	* <i>Mentha pulegium</i> L.	MENTPULE	LABIATAE					+						
124	<i>Microseris lanceolata</i> (Walp.)Schultz-Bip.	MICRLANC	COMPOSITAE									+		
125	<i>Microtis unifolia</i> (Forster.f.)Reichb.f.	MICRUNIF	ORCHIDACEAE									+		
126	<i>Mimulus repens</i> R.Br.	MIMUREPE	SCROPHULARIACEAE	+	+		+				+			
127	<i>Montia australasica</i> (Hook.f.)Pax. & K.Hoffm.	MONTAUST	PORTULACACEAE	+										
128	<i>Montia</i> sp.	MONTSP.	PORTULACACEAE				+							
129	<i>Muehlenbeckia adpressa</i> (Labill.)Meissner	MUEHADPR	POLYGONACEAE					+						
130	<i>Myriophyllum integrifolium</i> (Hook.f.)Hook.f.	MYRIINTE	HALORAGACEAE			+								
131	<i>Myriophyllum muelleri</i> Sonder	MYRIMUEL	HALORAGACEAE	+										
132	<i>Myriophyllum propinquum</i> sensu J.Black (1952)	MYRIPROP	HALORAGACEAE	+										
133	<i>Myriophyllum salsugineum</i> Orch.	MYRISALS	HALORAGACEAE	+									+	+
134	<i>Myriophyllum simulans</i> Orch.	MYRISIMU	HALORAGACEAE									+	+	
135	<i>Myriophyllum</i> sp. 1	MYRISP.1	HALORAGACEAE				+							
136	<i>Myriophyllum</i> sp. 2	MYRISP.2	HALORAGACEAE		+		+							
137	<i>Myriophyllum</i> sp. 3	MYRISP.3	HALORAGACEAE							+				
138	<i>Myriophyllum verrucosum</i> Lindley	MYRIVERR	HALORAGACEAE		+				+					
139	<i>Nitella</i> sp. 1	NITESP.1	CHARACEAE				+							
140	<i>Nitella</i> sp. 2	NITESP.2	CHARACEAE						+					
141	<i>Nitella</i> sp. 3	NITESP.3	CHARACEAE	+										
142	* <i>Onopordum acanthium</i> L. ssp. <i>acanthium</i>	ONOPACAN	COMPOSITAE		+			+						
143	<i>Ottelia ovalifolia</i> (R.Br.)Rich.	OTTEOVAL	HYDROCHARITACEAE							+				
144	* <i>Parapholis incurva</i> (L.)C.E.Hubb.	PARAINCU	GRAMINEAE	+										
145	* <i>Pennisetum clandestinum</i> Hochst. ex Chiov.	PENNCLAN	GRAMINEAE					+						
146	* <i>Phalaris paradoxa</i> L.	PHALPARA	GRAMINEAE	+										
147	<i>Phragmites australis</i> (Cav.)Trin. ex Steudel	PHRAAUST	GRAMINEAE	+				+						
148	* <i>Phyla nodiflora</i> (L.)Greene	PHYLNODI	VERBENACEAE						+					
149	* <i>Picris echioides</i> L.	PICRECHI	COMPOSITAE	+										
150	<i>Picris squarrosa</i> Steetz	PICRSQUA	COMPOSITAE					+						

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N	Full name	Code	Family	Boo Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
151	* <i>Piptatherum miliaceum</i> (L.)Cosson	PIPTMILI	GRAMINEAE					+						
152	<i>Polygonum plebeium</i> R.Br.	POLYPLEB	POLYGONACEAE			+						+	+	
153	<i>Polygonum prostratum</i> R.Br.	POLYPROS	POLYGONACEAE			+				+				
154	* <i>Polypogon monospermioides</i> (L.)Desf.	POLYMONO	GRAMINEAE	+	+									
155	<i>Potamogeton ochreatus</i> Raoul	POTAOCR	POTAMOGETONACEAE							+				
156	<i>Potamogeton pectinatus</i> L.	POTAPECT	POTAMOGETONACEAE	+	+		+							
157	<i>Potamogeton tricarinatus</i> F.Muell. & A.Bennett ex A.Bennett	POTATRIC	POTAMOGETONACEAE	+							+			
158	<i>Pratia</i> sp. 1	PRAT1	CAMPANULACEAE					+						
159	<i>Pratia</i> sp. 2	PRAT2	CAMPANULACEAE		+									
160	<i>Pratia platycalyx</i> (F.Muell.)Benth.	PRATPLAT	CAMPANULACEAE	+										
161	<i>Pseudognaphalium luteoalbum</i> (L.)Hilliard & B.L.Burt	PSEULUTE	COMPOSITAE		+	+			+	+				
162	<i>Pteridium esculentum</i> (Forster f.)Cockayne	PTERESCU	DENNSTAEDTIACEAE		+									+
163	<i>Ranunculus inundatus</i> R.Br. ex DC.	RANUINUN	RANUNCULACEAE	+										
164	<i>Ranunculus pentandrus</i> J.Black	RANUPENT	RANUNCULACEAE									+	+	+
165	<i>Ranunculus rivularis</i> Banks & Sol. ex DC.	RANURIVU	RANUNCULACEAE	+										
166	<i>Ranunculus</i> sp.	RANUSP.	RANUNCULACEAE				+	+		+				
167	<i>Restio tetraphyllus</i> Labill.	RESTTETR	RESTIONACEAE											+
168	<i>Rhagodia candolleana</i> Moq. ssp. <i>candolleana</i>	RHAGCAND	CHENOPODIACEAE					+						
169	* <i>Rorippa nasturtium-aquaticum</i> (L.)Hayek	RORINAST	CRUCIFERAE					+						
170	<i>Rorippa palustris</i> (L.)Besser	RORIPALU	CRUCIFERAE			+								
171	* <i>Rumex acetosella</i> L.	RUMEACET	POLYGONACEAE									+	+	
172	<i>Rumex bidens</i> R.Br.	RUMBIDE	POLYGONACEAE	+	+			+						
173	<i>Rumex</i> sp. 1	RUMESP.1	POLYGONACEAE			+								
174	<i>Ruppia</i> sp. 1	RUPPSP.1	POTAMOGETONACEAE					+						
175	Rutaceae sp.	RUTASP.	RUTACEAE	+										
176	<i>Samolus repens</i> (Forster & Forster f.)Pers.	SAMOREPE	PRIMULACEAE	+				+						
177	<i>Sarcocornia quinqueflora</i> (Bunge ex Ung.-Sternb.)A.J.Scott	SARCQUIN	CHENOPODIACEAE	+										
178	<i>Schoenoplectus pungens</i> (M.Vahl.)Palla	SCHOPUNG	CYPERACEAE	+										
179	<i>Schoenoplectus validus</i> (M.Vahl.)A. & D.Löve	SCHOVALI	CYPERACEAE					+						
180	<i>Schoenus carsei</i> Cheeseman	SCHOCARS	CYPERACEAE					+						

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N	Full name	Code	Family	Bool Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
181	<i>Schoenus nitens</i> (R.Br.)Poiret	SCHONITE	CYPERACEAE	+										
182	<i>Selliera radicans</i> Cav.	SELLRADI	GOODENIACEAE	+	+		+	+						
183	<i>Senecio biseratus</i> Belcher	SENEBISE	COMPOSITAE											
184	<i>Senecio lautus</i> Forster f. ex Willd.	SENELAUT	COMPOSITAE					+						
185	* <i>Senecio pterophorus</i>	SENEPTER	COMPOSITAE									+		
186	<i>Senecio</i> sp.	SENE SP.	COMPOSITAE								+			
187	* <i>Solanum nigrum</i> L.	SOLANIGR	SOLANACEAE		+		+	+						
188	* <i>Sonchus asper</i> (L.)Hill ssp. <i>asper</i>	SONCASPE	COMPOSITAE									+		
189	* <i>Sonchus oleraceus</i> L.	SONCOLER	COMPOSITAE									+		+
190	<i>Sonchus</i> sp. 1	SONCSP.1	COMPOSITAE									+		
191	<i>Sonchus</i> sp. 2	SONCSP.2	COMPOSITAE									+		
192	<i>Sonchus</i> sp. 3	SONCSP.3	COMPOSITAE											+
193	Species 1	SPEC1	-									+		
194	Species 2	SPEC2	-									+		
195	Species 3	SPEC3	-									+		
196	Species 4	SPEC4	-											
197	Species 5	SPEC5	-									+	+	+
198	Species 6	SPEC6	-											
199	Species 7	SPEC7	-										+	+
200	Species 8	SPEC8	-											+
201	Species 9	SPEC9	-											
202	Species 10	SPEC10	-											+
203	Species 11	SPEC11	-											+
204	Species 12	SPEC12	-											+
205	Species 13	SPEC13	-											+
206	Species 14	SPEC14	-										+	+
207	Species 15	SPEC15	-										+	
208	Species 16	SPEC16	-										+	
209	Species 17	SPEC17	-		+									
210	Species 18	SPEC18	-		+									

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N	Full name	Code	Family	Bool Lagoon	Bloomfield	Dine	Fairview	Mullins	Poocher	Shearing Tree	Topperweins	Nangwarry	Honans	Marshes
211	Species 19	SPEC19	-	+										
212	Species 20	SPEC20	-	+										
213	<i>Spirodela punctata</i> (G.Meyer)C.Thompson	SPIRPUNC	LEMNACEAE	+										
214	<i>Spirodela</i> sp.	SPIRSP.	LEMNACEAE					+						
215	<i>Sporobolus virginicus</i> (L.)Knuth	SPORVIRG	GRAMINEAE		+		+			+				
216	<i>Stackhousia spathulata</i> Sieber ex Sprengel	STACSPAT	STACKHOUSIACEAE	+										
217	<i>Stipa</i> sp.	STIPSP.	GRAMINEAE		+									
218	* <i>Taraxacum officinale</i> G.Weber ex Wiggers	TARAOFFI	COMPOSITAE					+						
219	<i>Tetragonia implexicoma</i> (Miq.)Hook.f.	TETRI MPL	AIZOACEAE					+						
220	* <i>Trifolium campestre</i> Schreber	TRIFCAMP	LEGUMINOSAE							+				
221	* <i>Trifolium fragiferum</i> L. var. <i>fragiferum</i>	TRIFFRAG	LEGUMINOSAE	+										
222	<i>Trifolium repens</i> L.	TRIFREPE	LEGUMINOSAE		+	+		+	+					
223	<i>Triglochin procerum</i> R.Br.	TRIGPROC	JUNCAGINACEAE	+								+	+	+
224	<i>Triglochin</i> sp.	TRIGSP.	JUNCAGINACEAE		+					+				
225	<i>Triglochin</i> sp. 1	TRIGSP.1	JUNCAGINACEAE	+										
226	<i>Triglochin striatum</i> Ruíz Lopez & Pavón	TRIGSTRI	JUNCAGINACEAE	+			+	+						
227	<i>Typha domingensis</i> Pers.	TYPHDOMI	TYPHACEAE	+				+		+				
228	* <i>Urospermum picroides</i> (L.)F.W.Schmidt	UROSPICR	COMPOSITAE	+										
229	<i>Urtica incisa</i> Poirlet	URTIINCI	URTICACEAE	+										
230	<i>Urtica</i> sp.	URTISP.	URTICACEAE					+						
231	<i>Utricularia</i> sp.	UTRISP.	LENTIBULARIACEAE	+										
232	* <i>Verbena supina</i> L.	VERBSUPI	VERBENACEAE						+	+				
233	<i>Veronica</i> sp.	VEROSP.	SCROPHULARIACEAE					+						
234	<i>Villarsia reniformis</i> R.Br.	VILLRENI	MENYANTHACEAE	+							+	+	+	+
235	<i>Villarsia</i> sp.	VILLSP.	MENYANTHACEAE					+						
236	<i>Wahlenbergia luteola</i> P.J.Smith	WAHLLUTE	CAMPANULACEAE									+		
237	<i>Wilsonia backhousei</i> Hook.f.	WILSBACK	CONVOLVULACEAE	+										
238	<i>Wolffia angusta</i> Landolt	WOLFANGU	LEMNACEAE	+										
239	<i>Wolffia</i> sp.	WOLFSP.	LEMNACEAE							+				

# Appendix C

## Species associations in South East wetlands

Characterisation of the 11 species associations in South East wetlands defined from hierarchical clustering, following the Complex descriptions of Sparrow (1991). The characteristic species were determined from the two-way tabulation of sites and species classifications (Figure 2.35). Where possible, association descriptions are provided for comparison, based on those of Ellenberg (1988), Kirkpatrick and Harwood (1983), Sparrow (1991) and Specht (1972). Associations are shown in braces where there is incomplete correspondence between previous descriptions and those defined here. Ellenberg descriptions follow the phytosociological nomenclature of the Zürich-Montpellier School (*-etea*=class; *-etalia*=order; *-ion*=alliance).

## 1. POTAMOGETON PECTINATUS (34 sites)

**Association description:**

**Ellenberg:** Potamogetonetea, Potamogetonetalia, Potamogetonion—rooted aquatic waterplant community

**Kirkpatrick and Harwood:** Aquatic herbland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *P. pectinatus*, *Myriophyllum verrucosum*, *Triglochin* sp.

**Other common species:** *Isolepis inundata*.

**Distribution:** Bloomfield Swamp, Bool Lagoon, Fairview C.P., Mullins Swamp.

## 2. MYRIOPHYLLUM VERRUCOSUM (6 sites)

**Association description:**

**Ellenberg:** Potamogetonetea, Potamogetonetalia, Nymphaeion—rooted floating-leaf cover

**Kirkpatrick and Harwood:** Aquatic herbland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *M. verrucosum*.

**Other common species:** None.

**Distribution:** Poocher Swamp.

## 3. BAUMEA ARTHROPHYLLA (102 sites)

**Association description:**

**Ellenberg:** Phragmitetea, Phragmitetalia, Magnocaricion—tall sedge swamps

**Kirkpatrick and Harwood:** Sedgeland

**Sparrow:** —

**Specht:** [Closed grassland formation BAUMEA JUNCEA - B. RUBIGINOSA association].

**Characteristic species:** *B. arthropphylla*.

**Other common species:** None.

**Distribution:** Bool Lagoon, Honan's Swamp, Nangwarry Swamp.

## 4. BAUMEA ARTICULATA (49 sites)

**Association description:**

**Ellenberg:** Phragmitetea, Phragmitetalia, Magnocaricion—Tall sedge swamps

**Kirkpatrick and Harwood:** Reed swamp

**Sparrow:** —

**Specht:** —

**Characteristic species:** *B. articulata*.

**Other common species:** *Baumea arthropylla*, *Myriophyllum salsugineum*,  
*Triglochin procerum*.

**Distribution:** Bool Lagoon, The Marshes.

## 5. PHRAGMITES AUSTRALIS (22 sites)

**Association description:**

**Ellenberg:** Phragmitetea, Phragmitetalia—Reed and tall sedge swamps

**Kirkpatrick and Harwood:** Reed swamp

**Sparrow:** —

**Specht:** Closed grassland formation [P. AUSTRALIS - TYPHA DOMINGENSIS as-  
sociation].

**Characteristic species:** *P. australis*.

**Other common species:** None.

**Distribution:** Bool Lagoon.

6. BAUMEA ARTHROPHYLLA - MYRIOPHYLLUM SALSUGINEUM - TRIGLOCHIN PRO-  
CERUM (161 sites)**Association description:**

**Ellenberg:** —

**Kirkpatrick and Harwood:** Sedgeland/aquatic herbland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *B. arthropylla*, *M. salsugineum* *T. procerum*.

**Other common species:** *Ranunculus inundatus*, *Gahnia trifida*, *Nitella* sp.,  
*Chara corallina*.

**Distribution:** Bool Lagoon, Honan's Swamp, The Marshes.

## 7. BAUMEA ARTHROPHYLLA - MIXED (80 sites)

**Association description:**

**Ellenberg:** Phragmitetea, Phragmitetalia, Magnocaricion—tall sedge swamps

**Kirkpatrick and Harwood:** Sedgeland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *B. arthrophylla*.

**Other common species:** *B. juncea*, *Utricularia* sp., *Juncus procerus*, *Villarsia reniformis*, *Lilaeopsis polyantha*, *Myriophyllum* sp., *Lobelia pratoides*.

**Distribution:** Bool Lagoon, Honan's Swamp, Nangwarry Swamp, Topperweins Swamp.

## 8. TRIGLOCHIN PROCERUM - FREE-FLOATING (86 sites)

**Association description:**

**Ellenberg:** [Potamogetonetea, Potamogetonetalia, Nymphaeion—rooted floating-leaf cover], Lemnatea, Lemnatalia—free-floating still-water communities.

**Kirkpatrick and Harwood:** Marginal herbland/aquatic herbland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *T. procerum*, *Azolla filiculoides*, *Lemna trisulca*, *Spirodela punctata*, *Wolffia angustata*, *Myriophyllum salsugineum*.

**Other common species:** *Crassula helmsii*, *Lilaeopsis polyantha*, *Potamogeton tricarinatus*, *Mimulus repens*.

**Distribution:** Bool Lagoon.

## 9. TRIGLOCHIN PROCERUM - AQUATIC HERBLAND (54 sites)

**Association description:**

**Ellenberg:** [Potamogetonetea, Potamogetonetalia, Nymphaeion—rooted floating-leaf cover], Lemnatea, Lemnatalia—free-floating still-water communities.

**Kirkpatrick and Harwood:** Marginal herbland/aquatic herbland

**Sparrow:** —

**Specht:** Closed grassland formation (SELLIERA RADICANS - MIMULUS REPENS association)

**Characteristic species:** *T. procerum*, *Lilaeopsis polyantha*, *Crassula helmsii*, *Eleocharis acuta*, *Ranunculus inundatus*, *Myriophyllum salsugineum*, *Triglochin striatum*.

**Other common species:** *Baumea arthropphylla*, *Lilaeopsis polyantha*, *Potamogeton tricarinatus*, *Mimulus repens*, *Selliera radicans*.

**Distribution:** Bool Lagoon.

10. AQUATIC/TERRESTRIAL HERBLAND (40 sites)

**Association description:**

**Ellenberg:** [Chenopodieta—communities of waste ground and related arable and garden weed communities]

**Kirkpatrick and Harwood:** Marginal herbland/aquatic herbland

**Sparrow:** —

**Specht:** —

**Characteristic species:** *Lilaeopsis polyantha*, *Mimulus repens*, Gramineae 1, Compositae 1.

**Other common species:** *Chenopodium glaucum*, *Eucalyptus camaldulensis* (overstorey).

**Distribution:** Bloomfield Swamp, Dine Swamp, Fairview C.P., Poocher Swamp, Shearing Tree Water Hole.

11. GAHNIA TRIFIDA (50 sites)

**Association description:**

**Ellenberg:** —

**Kirkpatrick and Harwood:** Tussock sedgeland

**Sparrow:** GAHNIA TRIFIDA/G. FILUM Complex

**Specht:** Tussock grassland formation (*G. trifida*/*G. filum* association).

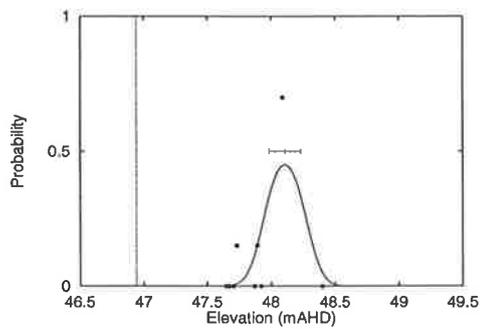
**Characteristic species:** *Gahnia trifida*, *Distichlis distichophylla*.

**Other common species:** *Gahnia filum*, *Leptospermum lanigerum*, *Phragmites australis*.

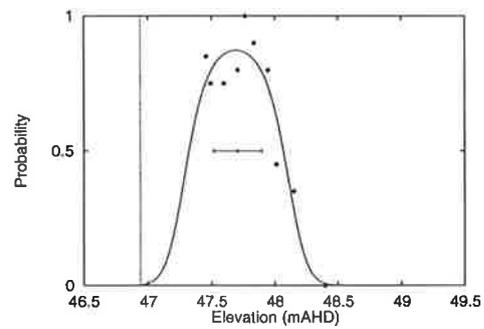
**Distribution:** Bool Lagoon, Mullins Swamp.

# Appendix D

## Response curves and parameters

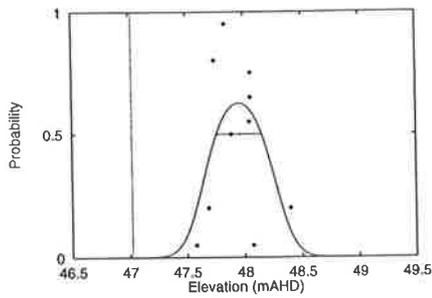


**D.1.1:** Site 24.  $u=48.11$ ,  $t=0.12$ ,  $P_{\max}=0.45$ .

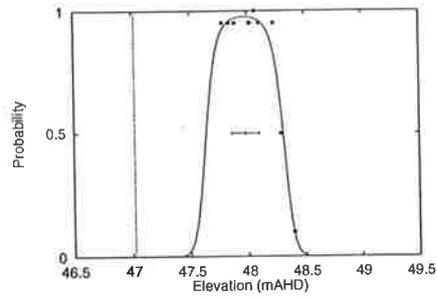


**D.1.2:** Site 25.  $u=47.71$ ,  $t=0.19$ ,  $P_{\max}=0.87$ .

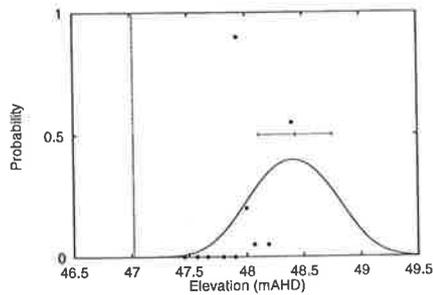
**Figure D.1:** Gaussian response functions and parameters for *Baumea arthrophylla* in the Main Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (46.94 mAHD).



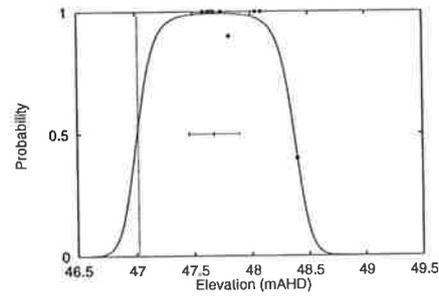
**D.2.1:** Site 14.  $u=47.96$ ,  $t=0.19$ ,  $P_{\max}=0.62$ .



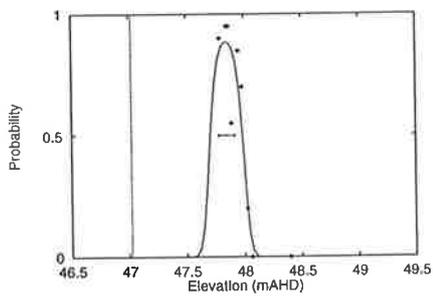
**D.2.2:** Site 15.  $u=47.98$ ,  $t=0.12$ ,  $P_{\max}=0.98$ .



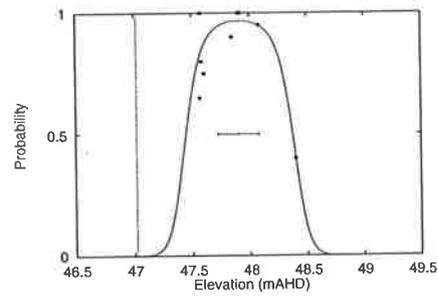
**D.2.3:** Site 27.  $u=48.43$ ,  $t=0.32$ ,  $P_{\max}=0.40$ .



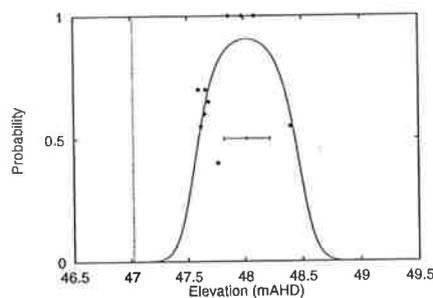
**D.2.4:** Site 28.  $u=47.68$ ,  $t=0.22$ ,  $P_{\max}=0.99$ .



**D.2.5:** Site 29.  $u=47.85$ ,  $t=0.07$ ,  $P_{\max}=0.90$ .

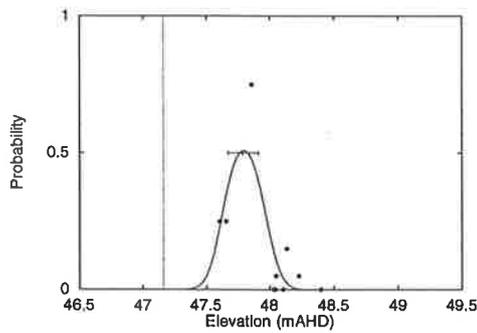


**D.2.6:** Site 30.  $u=47.90$ ,  $t=0.18$ ,  $P_{\max}=0.97$ .

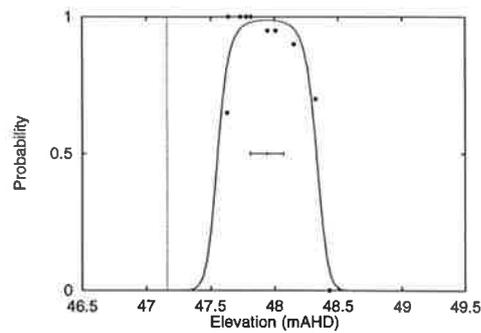


**D.2.7:** Site 32.  $u=48.02$ ,  $t=0.20$ ,  $P_{\max}=0.91$ .

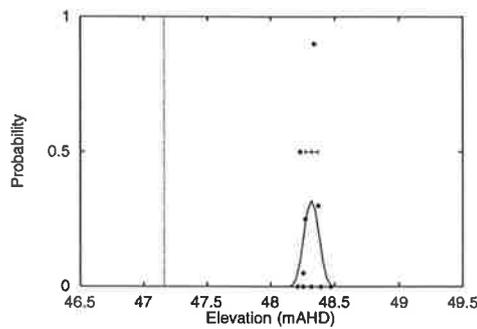
**Figure D.2:** Gaussian response functions and parameters for *Baumea arthropphylla* in the Central Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (47.02 mAHD).



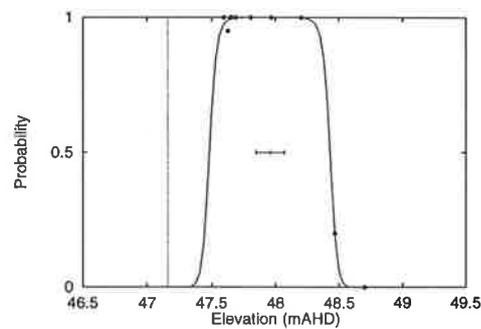
**D.3.1:** Site 17.  $u=47.79$ ,  $t=0.12$ ,  $P_{\max}=0.51$ .



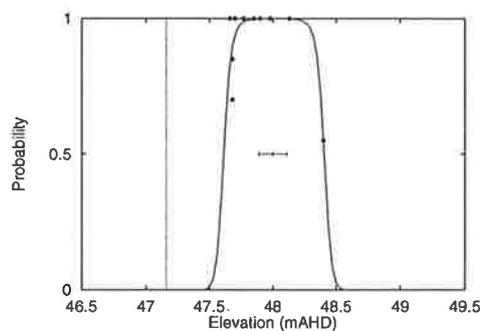
**D.3.2:** Site 19.  $u=47.94$ ,  $t=0.13$ ,  $P_{\max}=0.99$ .



**D.3.3:** Site 20.  $u=48.32$ ,  $t=0.05$ ,  $P_{\max}=0.36$ .

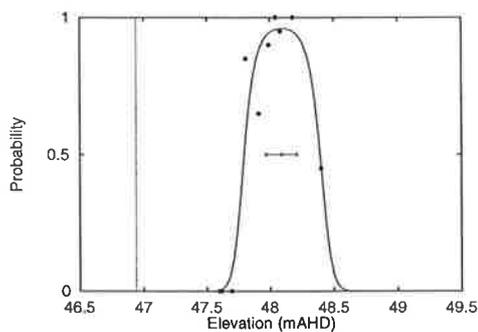


**D.3.4:** Site 34.  $u=47.96$ ,  $t=0.11$ ,  $P_{\max}=1.00$ .

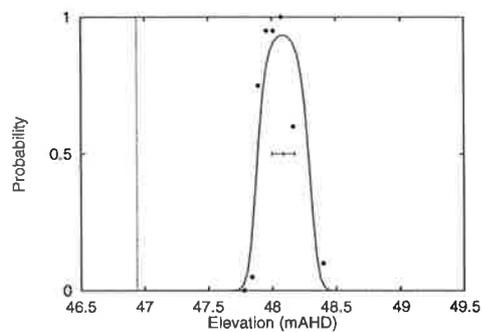


**D.3.5:** Site 35.  $u=48.00$ ,  $t=0.11$ ,  $P_{\max}=1.00$ .

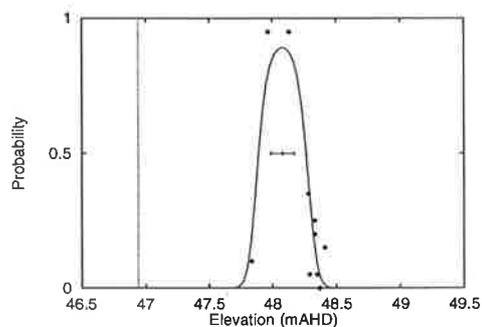
**Figure D.3:** Gaussian response functions and parameters for *Baumea arthrophylla* in the Western Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (47.16 mAHD).



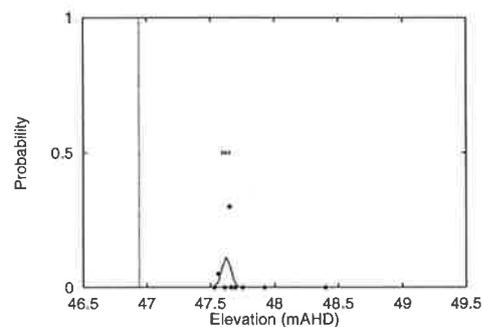
**D.4.1:** Site 3.  $u=48.09$ ,  $t=0.12$ ,  $P_{\max}=0.96$ .



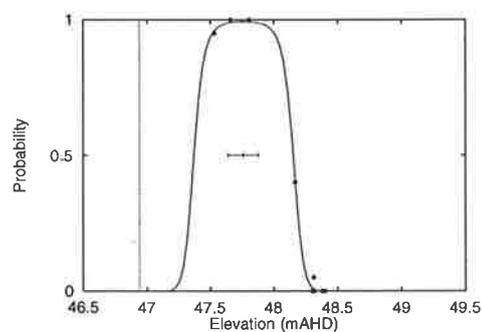
**D.4.2:** Site 4.  $u=48.09$ ,  $t=0.09$ ,  $P_{\max}=0.93$ .



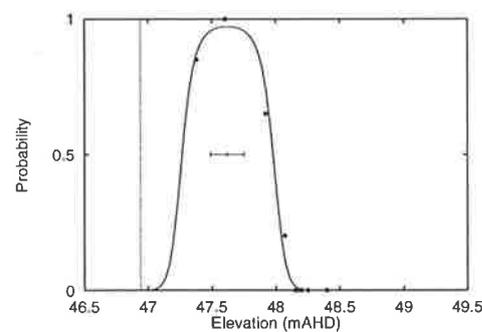
**D.4.3:** Site 5.  $u=48.08$ ,  $t=0.09$ ,  $P_{\max}=0.89$ .



**D.4.4:** Site 8.  $u=47.62$ ,  $t=0.03$ ,  $P_{\max}=0.11$ .

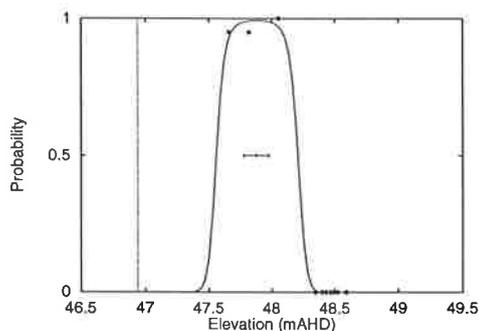


**D.4.5:** Site 9.  $u=47.76$ ,  $t=0.12$ ,  $P_{\max}=0.99$ .

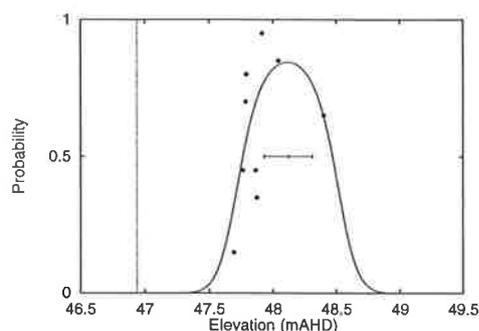


**D.4.6:** Site 10.  $u=47.62$ ,  $t=0.13$ ,  $P_{\max}=0.97$ .

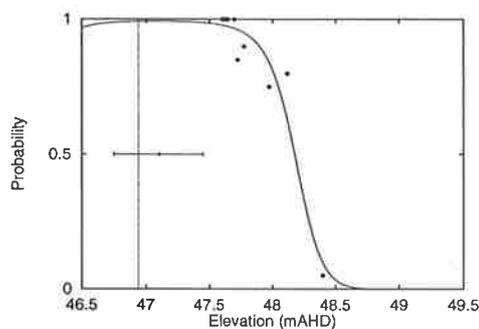
**Figure D.4:** Gaussian response functions and parameters for *Triglochin procerum* in the Main Basin of Bool Lagoon (Sites 3–10).  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (46.94 mAHD).



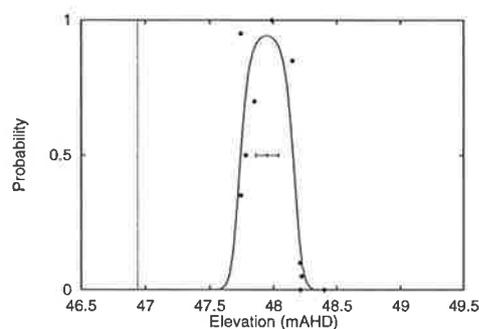
**D.5.1:** Site 11.  $u=47.88$ ,  $t=0.10$ ,  $P_{\max}=0.99$ .



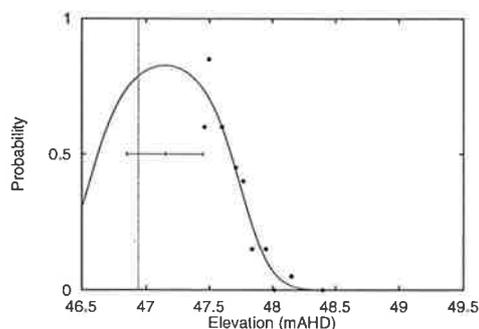
**D.5.2:** Site 21.  $u=48.12$ ,  $t=0.19$ ,  $P_{\max}=0.84$ .



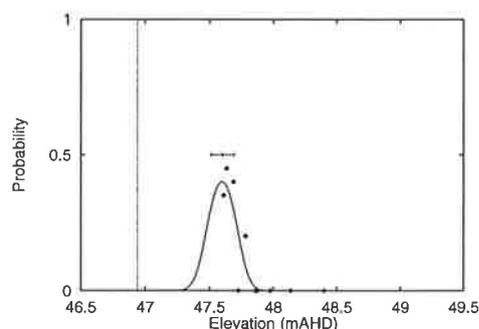
**D.5.3:** Site 22.  $u=47.10$ ,  $t=0.35$ ,  $P_{\max}=0.99$ .



**D.5.4:** Site 23.  $u=47.95$ ,  $t=0.09$ ,  $P_{\max}=0.94$ .

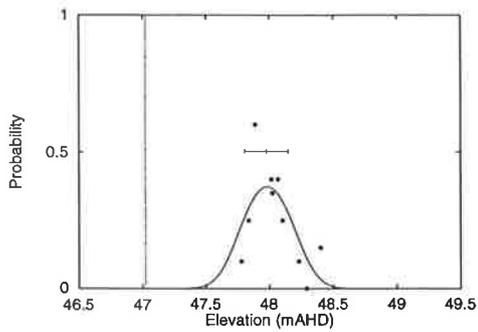


**D.5.5:** Site 25.  $u=47.15$ ,  $t=0.30$ ,  $P_{\max}=0.83$ .

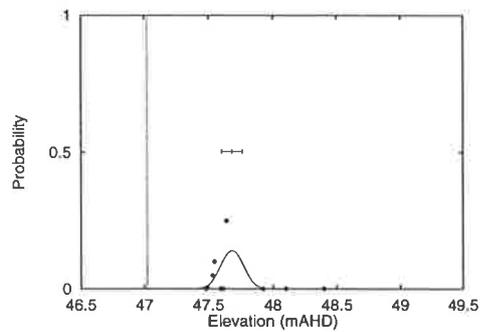


**D.5.6:** Site 26.  $u=47.60$ ,  $t=0.09$ ,  $P_{\max}=0.40$ .

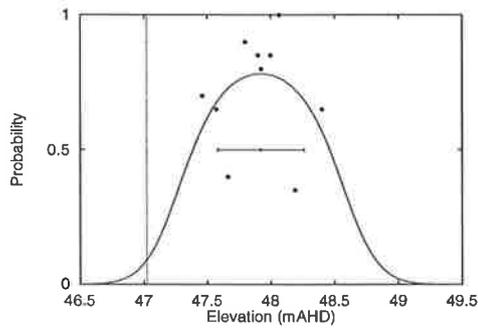
**Figure D.5:** Gaussian response functions and parameters for *Triglochin procerum* in the Main Basin of Bool Lagoon (Sites 11–26).  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (46.94 mAHD).



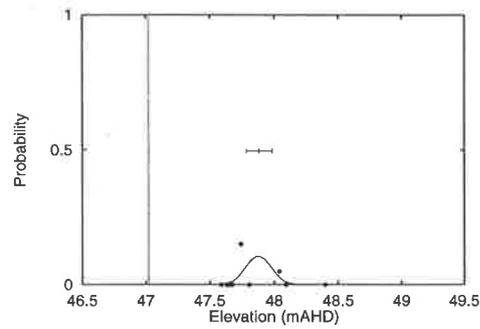
**D.6.1:** Site 15.  $u=47.98$ ,  $t=0.17$ ,  $P_{\max}=0.37$ .



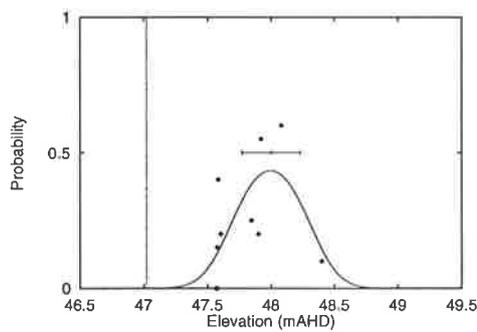
**D.6.2:** Site 16.  $u=47.68$ ,  $t=0.08$ ,  $P_{\max}=0.14$ .



**D.6.3:** Site 27.  $u=47.92$ ,  $t=0.34$ ,  $P_{\max}=0.78$ .

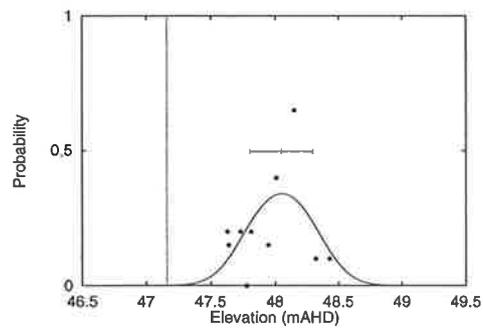


**D.6.4:** Site 28.  $u=47.88$ ,  $t=0.10$ ,  $P_{\max}=0.11$ .



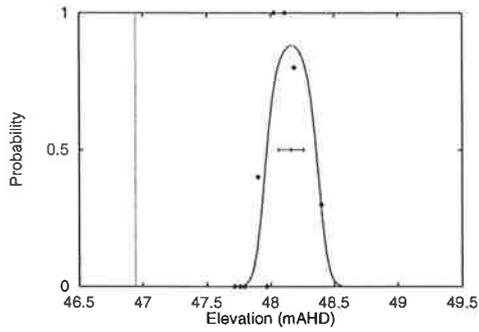
**D.6.5:** Site 30.  $u=48.00$ ,  $t=0.23$ ,  $P_{\max}=0.43$ .

**Figure D.6:** Gaussian response functions and parameters for *Triglochin procerum* in the Central Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (47.02 mAHD).

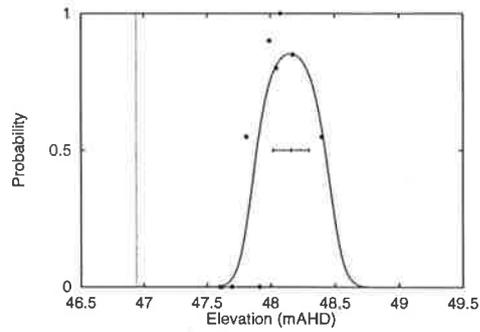


**D.7.1:** Site 19.  $u=48.05$ ,  $t=0.24$ ,  
 $P_{\max}=0.34$ .

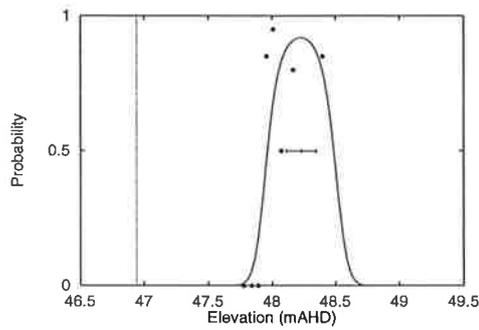
**Figure D.7:** Gaussian response functions and parameters for *Triglochin procerum* in the Western Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (47.16 mAHD).



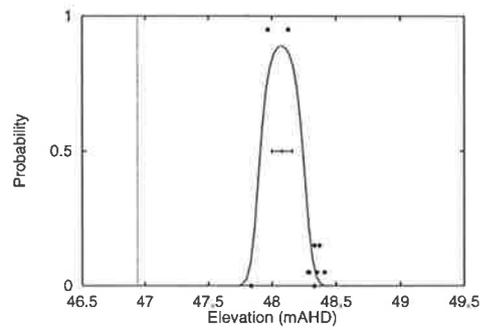
**D.8.1:** Site 2.  $u=48.16$ ,  $t=0.10$ ,  $P_{\max}=0.88$ .



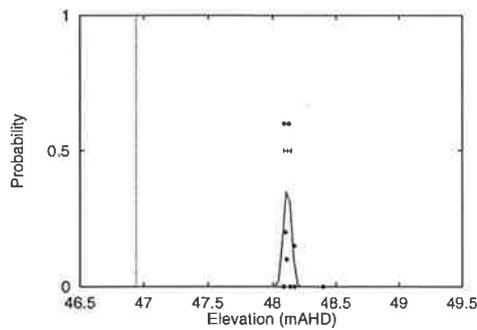
**D.8.2:** Site 3.  $u=48.16$ ,  $t=0.14$ ,  $P_{\max}=0.85$ .



**D.8.3:** Site 4.  $u=48.23$ ,  $t=0.12$ ,  $P_{\max}=0.92$ .

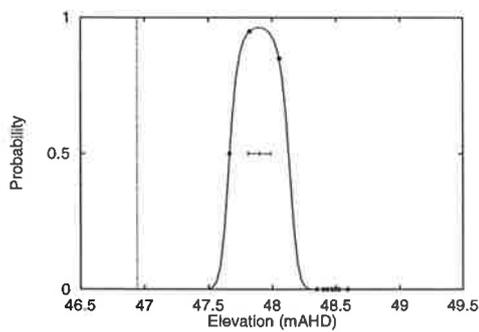


**D.8.4:** Site 5.  $u=48.08$ ,  $t=0.08$ ,  $P_{\max}=0.89$ .

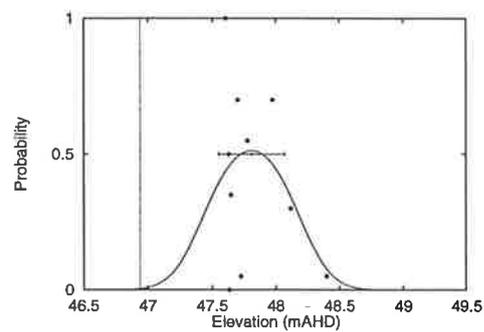


**D.8.5:** Site 6.  $u=48.12$ ,  $t=0.03$ ,  $P_{\max}=0.37$ .

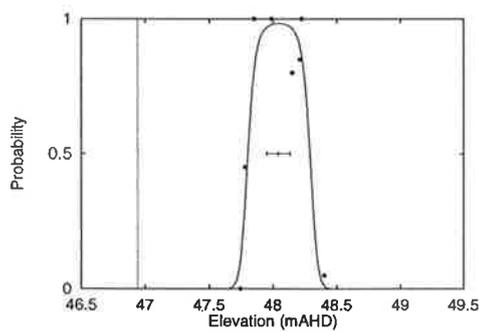
**Figure D.8:** Gaussian response functions and parameters for *Myriophyllum salsugineum* in the Main Basin of Bool Lagoon (Sites 2–6).  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (46.94 mAHD).



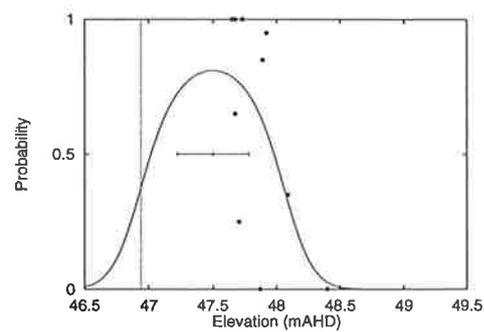
**D.9.1:** Site 11.  $u=47.90$ ,  $t=0.09$ ,  $P_{\max}=0.96$ .



**D.9.2:** Site 22.  $u=47.81$ ,  $t=0.26$ ,  $P_{\max}=0.51$ .

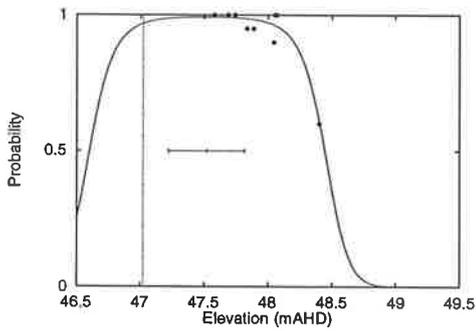


**D.9.3:** Site 23.  $u=48.04$ ,  $t=0.09$ ,  $P_{\max}=0.98$ .

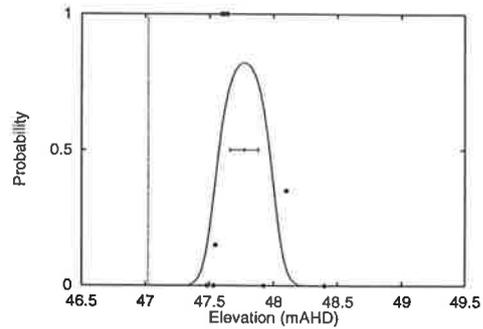


**D.9.4:** Site 24.  $u=47.50$ ,  $t=0.28$ ,  $P_{\max}=0.81$ .

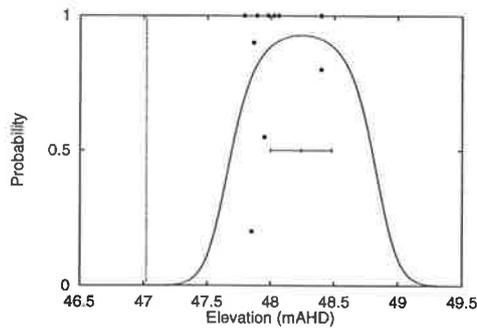
**Figure D.9:** Gaussian response functions and parameters for *Myriophyllum salsaugineum* in the Main Basin of Bool Lagoon (Sites 11–24).  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (46.94 mAHD).



**D.10.1:** Site 14.  $u=47.52$ ,  $t=0.30$ ,  $P_{\max}=0.99$ .



**D.10.2:** Site 16.  $u=47.77$ ,  $t=0.11$ ,  $P_{\max}=0.82$ .



**D.10.3:** Site 29.  $u=48.24$ ,  $t=0.24$ ,  $P_{\max}=0.93$ .

**Figure D.10:** Gaussian response functions and parameters for *Myriophyllum salsgineum* in the Central Basin of Bool Lagoon.  $u$ =optimum,  $t$ =tolerance,  $P_{\max}$ =maximum probability of occurrence. Vertical line indicates the measured or estimated elevation of the basin floor (47.02 mAHD).