Chapter 1
Introduction

1.1 Introduction

The introduced perennial *Juncus articulatus* L. (jointed rush) and the native perennial *Glyceria australis* C. E. Hubb (Australian sweet grass) (Harden 1993) are the dominant species in Mother of Ducks Lagoon, one of the largest of 57 temporary freshwater lakes (locally termed 'lagoons') on the Northern Tablelands of New South Wales, Australia. The shallow lagoons fill and dry at irregular intervals (Brock 1991) and the majority are used primarily for grazing. The native *G. australis* is common in many lagoons where it is valued as a forage species. *J. articulatus* is co-dominant over large areas of Mother of Ducks Lagoon, but is rare in other lagoons.

This study originated as part of a research project entitled "The Role of Seed Banks in Maintaining or Rehabilitating Vegetation in Temporary and Permanent Wetlands" (Brock 1995). The invasive potential of *J. articulatus* was suggested by its dominance in field germination cohorts and longevity in the seed bank at Mother of Ducks Lagoon (Brock and Britton 1995). The ecology of both *G. australis* and *J. articulatus* were studied for the advantages that a comparative study offered over an autecological investigation of *J. articulatus*. Given the similarity in size and growth form of *G. australis* and *J. articulatus*, an understanding of their co-existence will contribute to knowledge of plant community processes more generally. As part of the larger project, this study provides a detailed example of how two species inhabiting

the lagoons behave in all life stages. This will enhance the interpretation of seed bank information for species management. Cousens and Mortimer (1995) recently confirmed this idea. They suggested that given the dearth of information on many aspects of weed ecology, comparative studies of contrasting species would be the most cost-effective strategy for future weed research.

At a national scale, *J. articulatus* is potentially a serious aquatic weed of natural wetlands (Humphries *et al.* 1991) and can be a minor weed of irrigation drains (Sainty and Jacobs 1981). Given the increasing number of irrigation developments and of water control works more generally, research into the ecology of *J. articulatus* was needed for management of this species at Mother of Ducks Lagoon and in other sites. However, a knowledge of the ecology of both introduced and native species is essential for the successful management of an introduced species in native plant communities. This is especially true when exotics invade conservation and amenity areas in variable environments (Groves 1991; McIntyre and Barrett 1985; Van Vierssen 1990).

At a regional scale, *J. articulatus* is not common throughout the New England lagoons but *G. australis* is widespread. Comparative information on the ecology of both *G. australis* and *J. articulatus* may therefore aid in the interpretation of the invasive potential of *J. articulatus* in other lagoons. The growth and interaction of *G. australis* and *J. articulatus* (and all the plant communities) within the lagoons is primarily influenced by the presence of water. Differences in hydrology determine patterns of wetting and drying in the lagoons. These patterns are termed water regime. In Australian wetlands, there is a decreasing amount of water reaching wetlands in a variety of landscapes, often accompanied by a change in the patterns of flooding. For example, in southern temperate areas irrigation development has often resulted in the presence of water at constant high levels in summer rather than winter (Nielson and Chick 1997). The New England lagoons have been either drained or dammed with few lagoons remaining that have unaltered hydrology. This is because alteration of water regime was, and still is, an easily achieved and commonly utilised management option (Brock *et al.* in press.). The result has been a variety of water regimes and equally varied plant communities (Brock *et al.* 1994). Manipulation of

water regime is therefore likely to be a management tool that can be used for the manipulation of species composition within the lagoons.

Mother of Ducks Lagoon has many problems typical of wetlands in Australia. In a recent scoping review to define issues in wetland ecology requiring research, Bunn *et al.* (1997) identified the role of water regime as the top priority issue, habitat modification as second priority, pollution as the third and weeds and feral animals as the fourth. This study addresses the first, second and fourth of these issues. Although there is some knowledge in these priority areas it is often patchy. For example, the role of water regime in determining water chemistry has received limited attention (Briggs and Maher 1985; Song and McComb 1996). Research has focussed on plant populations (Froend and McComb 1994; Rea 1992) more than communities (Brock 1995; Finlayson *et al.* 1990). Areas highlighted as national research priorities included the relative importance of components of water regime, the water requirements of wetland populations and communities and the development of ways of applying water regime knowledge to wetland restoration issues and weed control (Bunn *et al.* 1997). This thesis aims to contribute to all of these.

1.2 Aims

The initial aim of this study was to determine the ecological parameters that controlled the abundance of *J. articulatus* and *G. australis* at Mother of Ducks Lagoon. It soon became apparent that the ecological parameters were socioeconomic and physical as well as biological. The research strategy adopted had two main parts. The first part researched the hydrology of the New England lagoons and the distribution of *J. articulatus* and *G. australis* within the lagoons. This was to determine the potential range of *J. articulatus* within the lagoons and the ecological niche of *G. australis*. The second part of the research comprised a series of experiments to study responses of the life history stages of *J. articulatus* and *G. australis* to water regime.

The approach adopted in this investigation of an invasive and a native species fits well with a modified version of Humphries *et al.*(1991) outline of the information needed

to determine the ecological role of an invading species (Figure 1.1). In addition to information about the biology of the species, information was needed on how human land-use and management influence the species.

This thesis reports the results of the following research aims:

- Describe the New England lagoons including their characteristics, history, conservation statuses and major land-uses (Chapter 1).

- Quantify the major physical characteristics of lagoons and assess their importance in determining water regime. (Chapter 2).

- Describe the distribution and abundance of *J. articulatus* and *G. australis* in plant communities in the New England lagoons (Chapter 3).

- Design and utilise innovative techniques that allow investigation of different components of water regime (Chapter 2, Chapter 4, Chapter 5 and Chapter 6).

- Determine key life history attributes of *J. articulatus* and *G. australis* and the stability of those characters in relation to water regime (Chapter 4 and Chapter 7).

- Investigate the interaction of *J. articulatus* and *G. australis* under different water regimes (Chapter 5 and Chapter 6).

- Investigate the response of the vegetation community at Mother of Ducks to the spatial and temporal variation in water regime (Chapter 6).

- In light of the information gained on the biology of *J. articulatus* and *G. australis* and on land-uses and management practices, discuss the management implications of the findings and assess the invasive potential of *J. articulatus* in the New England lagoons (Chapter 8).

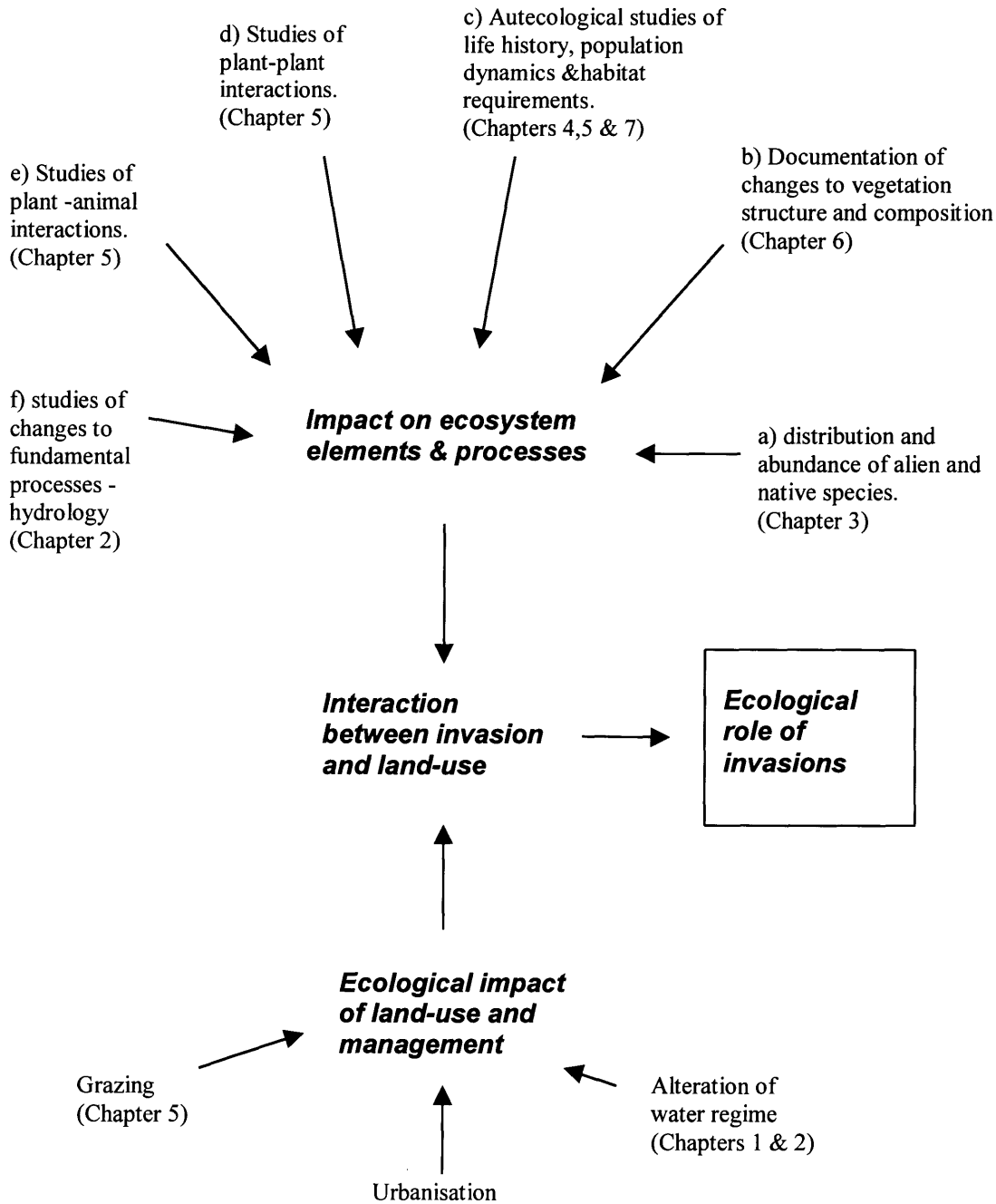


Figure 1.1 A model of the links between information on the distribution and abundance of *G. australis* and *J. articulatus* collected for this thesis. Adapted from Humphries *et. al.* (1991).

The techniques used range across scales from micro to macro and from the individual seed and plant to the whole ecosystem. The work includes glasshouse experiments, outdoor experiments under controlled conditions, manipulative field experiments, descriptive survey work and a simulation study. The variety of techniques used combines studies that are broad in their scope but necessarily simpler in detail with

those that investigate narrow aspects of the ecology of *G. australis* and *J. articulatus* and water regime in detail.

This study addresses many of the current issues affecting wetlands in Australia and elsewhere in the world. The New England lagoons provide a good example of the difficulties faced in trying to manage diverse wetland systems for a range of outcomes. Mother of Ducks Lagoon provides an unusual example of wetland rehabilitation where extensive capital works have been undertaken in an attempt to reverse a long history of degradation and conflict in utilisation.

1.3 Juncus articulatus and *Glyceria australis*

G. australis and *J. articulatus* have similar emergent growth forms (Figure 1.2, Figure 1.3). Both species have a maximum height of approximately 35cm although under flooded conditions both species have been observed to produce elongated stolons reaching the surface of water 1 metre deep (but at low densities). Both species reproduce from seed and stolons and are rhizomatous. In *J. articulatus* the rhizomes are short and stout. The seeds of *J. articulatus* are approximately 0.5 mm long whereas those of *G. australis* are approximately 3 mm in length.

Little is known of the ecology of *G. australis.* It was previously mistaken for *G. fluitans. G. australis* is restricted in distribution to the temperate areas of south east Australia. As well as providing forage for stock, at Mother of Ducks Lagoon *G. australis* provides habitat for waterfowl. Mother of Ducks Nature Reserve is recognised under the Japan-Australia Migratory Bird Agreement as a site of significance for the migratory *Gallinago hardwickii* (Gray). (Japanese snipe) (Brock *et al.* in press.).

J. articulatus is one of few exotic aquatic species in the lagoons (Brock and Casanova 1997). It occurs widely within Mother of Ducks Lagoon but is concentrated in lower, wetter areas which are more disturbed by birds and cattle. This suggests that the species may be separated over elevation (and therefore water regime) and/or disturbance gradients.

Figure 1.2 ***J. articulatus*** **(top) and growing at Mother of Ducks lagoon (bottom)**

Figure 1.3 ***G. australis*** **(bottom) and growing at Mother of Ducks lagoon (top)**

J. articulatus is a circumboreal species (Cusick 1986; Schmider and Ottow 1984; Spence and Allen 1978). Studies in Europe indicate *J. articulatus* is a colonising species and has a long-lived seed bank. In Germany, *J. articulatus* germinated from the seed bank of fens fifteen years after draining (Pfadenhauer and Maas 1987) and is a characteristic species in the primary successional stage of wet heath (Neuhaus 1990). In Great Britain, *J. articulatus* is morphologically variable and is typically found in base-rich mire where disturbance and some soil infertility limit the growth of potential dominants. It has a wide ecological amplitude in wetland habitats, occurring on stream banks and in drainage ditches where it can behave as a semi-aquatic, forming floating mats usually attached to the bank (Grime *et al.* 1988).

J .articulatus is also widespread in Australia. As in Europe, it was found to have a long lived seed bank, germinating from Mother of Ducks Lagoon sediment stored for twelve years (Brock and Britton 1995). *G. australis* did not germinate from these same sediments. In Western Australia, *J. articulatus* reproduced readily from seed and rhizomes compared to other species that were reproductively more specialised, relying on either sexual or vegetative reproduction (Chambers and McComb 1992). It is common in drains and creeks on the Northern Tablelands but is not common in lagoons other than Mother of Ducks. Of some concern may be a small population at Little Llangothlin Lagoon, a recently declared Ramsar site (Brock *et al.* in press.).

1.4 The New England lagoons

The lagoons on the northern tablelands of New South Wales (Figure 1.4) range in size from approximately 0.01 to 4 km^2, and are at altitudes ranging from 1020 to 1360 m above sea level. The geomorphological origins are unclear, although the majority occur on tertiary basalts with laterite or silcrete outlet sills, and some have aeolian lunettes (Haworth 1994). The persistence of the lagoons in the landscape relies on their situation adjacent to regional or local divides, thus having restricted catchments. The major characteristics of the lagoons and others used in later chapters are summarised in Table 1.1.

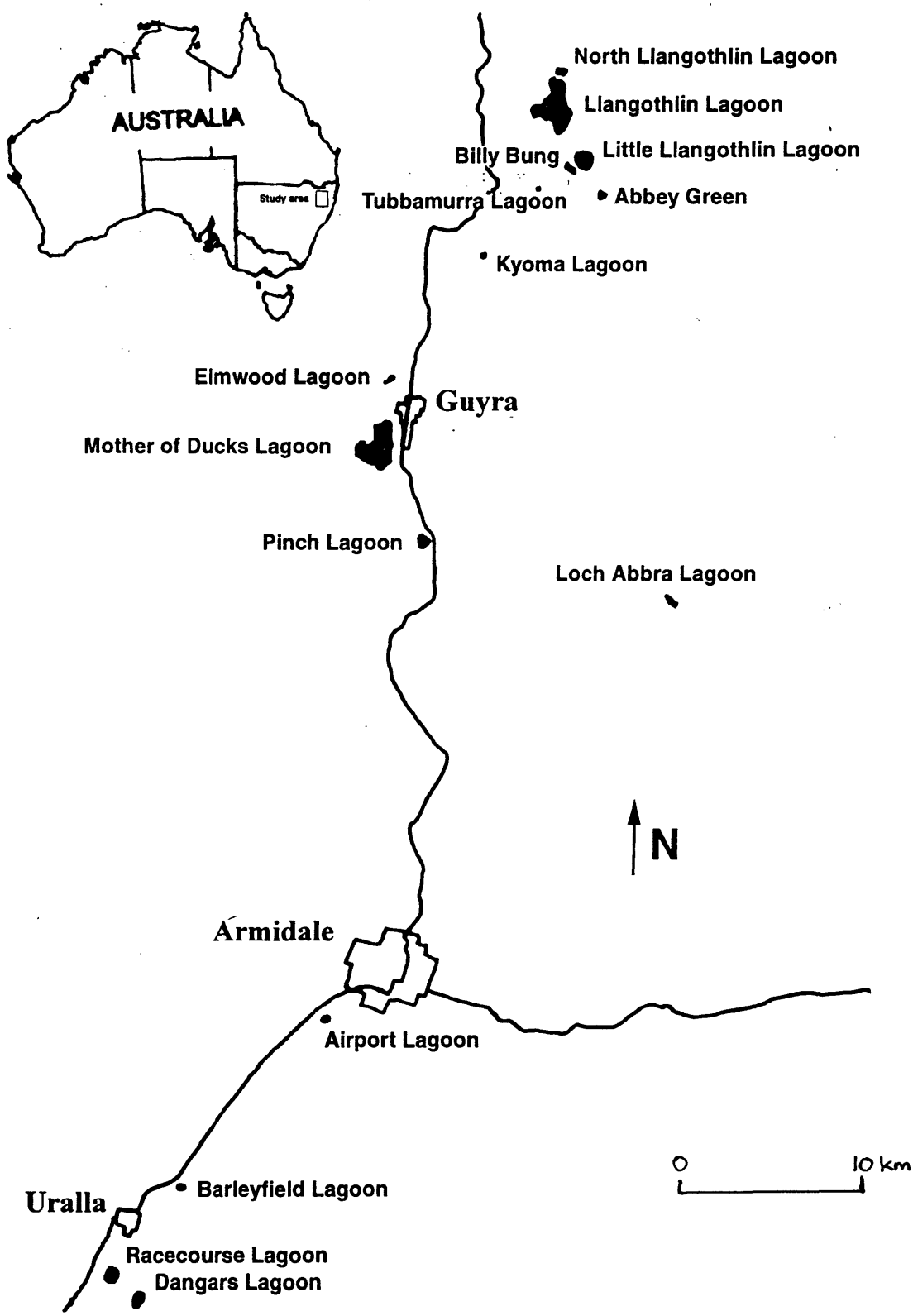


Figure 1.4 Location of the New England Lagoons on the Northern Tablelands of New South Wales, Australia. Lagoon characteristics are described in Table 1.1.

Table 1.1 Characteristics of the New England Lagoons studied. Map sheets and grid references are included in Appendix C

Lagoon Group	Lagoon -	Elevation - (m)	Geology	Disturbance	Surface area - (ha)	Catchment -(ha)	Catchment/ area - (ratio)	Maximum Depth (cm)
Guyra-Main Divide	Elmwood	1320	Basalt	Drained	11	61	5.55	15
	Mother of Ducks Nature Reserve	1315	Basalt	Dammed	94.15	829.52	3.07	100
	Mother of Ducks (west paddock)			Drained	270.48	829.52	3.07	15
	Pinch (Ditton's, Little)	1340	Basalt	Partly drained	24.21	130.82	5.40	25
Brockley-Clarence-Macleay Divide	Kyoma	1348	Granite/ silcrete		3.39	3.86	1.14	40
	Loch Abbra	1295	Basalt	Dammed	3.99	13.83	3.47	250
Llangothlin	North Llangothlin	1356	Basalt/ granite	Dammed	9.48	67.25	7.09	275
	Llangothlin	1350	Basalt/granite	Dammed	410.42	1586.06	3.86	180
	Little Llangothlin	1354	Basalt/ granite	Drained then dammed	105.47	364.65	3.46	150
	Billy Bung (The Billabong)	1358	Basalt		16.24	59.49	3.66	60
	Tubbamurra	1355	Basalt		3.55	59.63	16.80	20
	Abbey Green	1348	Basalt/ granite	Partly drained	11.28	106.11	9.41	35
Armidale / Uralla	Barleyfield	1055	Edge of basalt		5.86	53.57	9.14	60
	Airport (Wyanbah)	1055	Basalt		3.68	29.75	8.08	70
	Dangars	1022	Granite	Dammed	55.29	956.94	17.31	90
	Racecourse	1030	Granite		20.97	65.38	3.12	275

The lagoons vary in size, depth and catchment area which results in a range of water regimes from large, near permanent water bodies to small, shallow, ephemeral wetlands. The rainfall in the region is distributed throughout the year with a slight summer maximum. As evaporation is also higher in the summer and rainfall is highly variable between years, fluctuations of water levels in the lagoons, in contrast to many other parts of Australia, are not seasonal and may be described as aperiodic or fluctuating irregularly. In terms of permanence, as defined by Paijmans *et al.*(1985), there are examples of permanent, episodic and intermittent lakes.

The soil types largely reflect the geology of the parent materials. The lagoons are located on basalt, basalt granite boundaries or granite. Soils are typically deep with light to medium clay textures on basalt and sandy clays to sandy clay loams on the basalt/granite boundary and on granite. Soil pH ranges from 5.5 to 6.5 on basalt and

5.5 to 7 on granite. Mother of Ducks and Pinch lagoons have higher soil pH of about 8. Mother of Ducks has a layer of peat overlying the clay.

The New England Lagoons provide an example of the many pressures faced by wetlands in much of the world. Many of the lagoons have been subjected to competing interests of production, conservation and development for nearly one hundred years. The majority of lagoons have been drained and most of those remaining have had their hydrological regimes altered (Brock *et al.* in press.). The most common change is the drainage of the lagoons. Creek (1982) reconstructed water levels in Mother of Ducks Lagoon using aerial photography and rainfall and historical records. He noted that the successive drainage events of the lagoon occurred after a dryer period was followed by a return to normal wetter years. Several lagoons have been drained and then dammed again later, probably in response to very wet or dry periods. In the case of the two reserves, recent damming is due to changes in ownership back into public hands and an increase in awareness of the ecological value of wetlands. The approximately 57 easily recognisable lagoons on the tablelands probably represents only a fraction of the original number and most of these have been partially drained (Haworth 1994). The catchments of most of the lagoons are cleared and grazed at varying intensities.

Mother of Ducks Lagoon (Latitude 30°23'5" Longtitude 151°39'30") was the largest of the New England wetlands before drainage, and its eastern shore contains elements of a lunette at the foot of a ridge which forms part of the Great Divide (locally the watershed between east-flowing and west-flowing drainage basins). The lagoon is unusual for its peat soil overlying a clay base (Jessup 1965). The township of Guyra has developed along the New England Highway on this ridge, and the lagoon has been integral to the town's development.

The lagoon's history of water regime change (Table 1.2) is partly reflected in its present management for three major uses. Part of the 400ha lagoon bed is managed as a Nature Reserve (97ha), and the rest as grazing leases and a golf course. Because the lagoon outlet is about 2m lower than its original level (Briggs 1976), most of the Nature Reserve has been enclosed by a levee bank, which allows extended periods when the water level remains up to 1m above the adjacent golf course and grazing

Figure 1.5 Mother of Ducks Lagoon looking south. The levee enclosed nature reserve can be seen at the bottom of the photo and the township of Guyra and the golf course on the eastern shore of the lagoon (Photo courtesy NPWS)

land. The levee was built by the NSW NPWS as an Australian Bicentennial project in 1988, in response to and in collaboration with a community effort to beautify the township of Guyra (Figure 1.5). The present patterns of multiple use arise from the different and changing perceptions of the value of this wetland in its various states. Until recently, most changes involved lowering the water outlet level to facilitate more reliable use of the lagoon bed for grazing, cropping and for the golf course (Table 1.2). Although those people promoting the beautification of Guyra wanted the reserve flooded for as much of the time as possible to attract waterbirds (and tourists), water levels in the levee-enclosed part of the reserve fluctuate.

Table 1.2 Water regime and policy changes at Mother of Ducks (compiled from Briggs (1976), Creek (1982) and White (1986)). Italics denote the type of change that took place, either natural, intentional or unintentional (after Brock *et al.* in press).

DATE	WATER REGIME CHANGE	LANDUSES AND EFFECTS
pre 1800	*natural*	- wide fluctuations in water levels
1830	*natural* - drought	- sheep grazing on lagoon bed
1850		- cattle grazing
	unintentional reduced depth	- sedimentation event
1860s		- declared a water supply reserve
1870		- clearing of trees from catchment
1890		- water for steam trains
		- gazetted as a travelling stock reserve
		- water supply status revoked
1894		- declared a public reserve
1900	*natural* - lagoon full	- part declared as a fauna protection area
1900	*natural* - lagoon full	- shallow-draught paddle steamer
		- declared as Guyra Common
1901-2	*natural* - drought	- peat fires
1910		- site for Guyra show ground
1917-18	*natural* - drought	- peat fires
1923	*intentional* - outlet level lowered 60cm	- for extra land for soldier settlers
		- racecourse
1923	*natural* - regular filling	- lagoon regularly filled to new lowered level
1937	*intentional*	- golf course started
1950	*natural* -flood	
1951	*intentional* - outlet level lowered 170cm	- by Guyra Shire Council to increase rich grazing land and to reduce innundation of the golf club
1962	*intentional* - outlet level lowered 63 cm	- weir constructed - golf course extended
1964-5	*natural* -drought	- lagoon dried up
1973	*intentional*	- remaining 97 ha of Guyra Common declared as a Nature Reserve
1965-77	shallow ephemeral	- peat fires
1978	*natural* -flood	- conflict between golf/grazier and reserve in wet years
1988	*intentional* - levee constructed-1m depth	- restoration of water regime in Nature Reserve.
		- JAMBA agreement for protection of migratory water birds

Earlier work on the New England lagoons focussed on their value and management as bird habitat (Briggs 1976; Johnston 1977 ; McAlister 1976; White 1986). More recent work has investigated the ecology of several common plant species in the lagoons (Blanch 1991; Brock 1991; Casanova 1993), the ecology of seed banks in the lagoons (Britton and Brock 1994; Brock and Britton 1995) and plant phenology (Bell 1991). The construction of the levee at Mother of Ducks was undertaken after the development of a plan by Creek (1982), some parts of which are examined in more detail in Chapter 2. Since the construction of the levee bank in the Mother of Ducks Lagoon Nature Reserve studies have investigated the physical and chemical influences on vegetation at Mother of Ducks Nature Reserve (Lloyd 1992) and the spatial distribution of the seed bank within the nature reserve (Blinman 1993).

The recent damming of Little Llangothlin and the construction of the levee at Mother of Ducks Lagoon Nature Reserve show the awareness of the importance of water regime in the ecology of the lagoons. While these actions are relatively simple the results are not understood in detail. This is partly because the study of wetland water regimes lacks well developed terminology and methodology.

1.5 Water regime

Water regime has been defined as the patterns of water inundation in a wetland (Bunn *et al.* 1997). Although the presence of water is the defining characteristic for a wetland, water regime is generally not well enough understood to interpret species patterns in temporary wetlands. For example, Carter (1986) described the complexity of wetland transitional zone vegetation as a result of seasonal, yearly or several year cycles of fluctuations in water levels and noted the paucity of studies in wetland transition zones. Similarly, La Baugh (1986) argued that despite the recognised importance of water regime in the pattern and processes within wetlands, it is often the component of ecosystem research which is not thoroughly investigated. The situation is similar in Australia (Bunn *et al.* 1997).

Bunn *et al.* (1997) list the important components of water regime as: timing and frequency (e.g. seasonal, annual and longer); duration; maximum and minimum

depths; spatial extent; and variability (predictability). In areas of Australia that experience a more seasonal climate than the New England region, within year patterns are important. For intermittent or episodic wetlands in more arid areas between year patterns may be more important. The duration of inundation is important and is related to depth and spatial extent within one wetland, especially in well defined basins such as the New England lagoons. Finally, the variability of all these is important. For example, how often will a pattern of water regime be interrupted by a drought. Variability (and therefore predictability) is probably the characteristic most commonly changed in wetlands (Bunn *et al.* 1997, Brock *et al.* in press).

Obviously, it is desirable to summarise water regime using as few parameters as possible. Over an elevation gradient within one wetland, the relative level (or difference in height) may act as an index of water regime. This is because there will be increasing depth and overall duration of inundation at lower elevations. Therefore, elevation could be used to summarise water regime within the same water body. However, the relationship between elevations in different water bodies will be more complex. Other simple properties may be also be useful indicators of physical characteristics within one system. For example, the variation in water depth experienced by plants was related to the position relative to weirs on the River Murray. The vegetation composition changed with the variation in water levels and so position could be used as an indicator of water regime (Walker *et al.* 1994).

The simplest direct measure of water regime is water depth averaged over time. This has been used to describe seasonal water regimes (Froend and McComb 1994; Rea and Ganf 1994a; Rorslett 1984). Rea and Ganf (1994a) defined a descriptor of water levels that they termed the "Sum Water Regime". It was calculated as the area underneath the plot of water depth over time (time series). However, this is mathematically identical to the mean of water depth over the time for which the calculation was made. Rorslett (1984) derived that the best time averaged measure was median depth but noted that valuable information was contained in the depth probability distribution function. These functions give the probability of depths being within defined depth classes.

Brownlow *et al.* (1994) used multivariate classification of above ground water levels in four interconnected lagoon basins in South Australia to show the relationship between elevation and water regime. This method showed that elevation was not a good indicator when comparing between basins. However, the shapes of the distributions were generally unimodal and there appeared to be a strong pattern of the number of days when water levels were below ground (all measured as zero depth in the analysis). Simpler measures such as average depth or days dry that were used by Rea and Ganf (1994a) in the same wetland system were not discussed. Brownlow *et al.* (1994) pointed out that their method takes no account of other characteristics of water regime, such as temporal variation, but that these could be included in the classification. Frequency is probably not as important as the lagoon systems are strongly seasonal and regulated. Using a similar technique, Rorslett (1984) compared water regimes in lakes by standardising depths and comparing the cumulative distribution curves, showing differences such as the prevalence of low water levels in regulated lakes and the effects of characteristics such as catchment size.

A more complex approach was adopted by Gowing and Spoor (pers. comm.). They defined limits for water table levels optimal for growth of wet grassland species and calculated a value based on the amount of time water levels were outside these limits (termed a sum exceedence value). This gave the best correlation with species and community distributions out of a range of measures tested. Unfortunately, this has limited application where detailed water table levels and management history are not available. However, the identification of thresholds for species, in both time and depth, is a promising approach, especially where uncertainty of environmental conditions is great and where extreme events may be important for species survival and reproduction (Denton and Ganf 1994).

A characteristic not considered by any of these descriptors is the frequency of fluctuations. All the examples above consider seasonal systems. While seasonal fluctuations are important there may be several cycles operating at different time scales and it becomes necessary to define the period of interest (Carter 1986; Deuver 1988). This may be difficult as the response of plants to different periodicities of water presence is not well understood (Rea and Ganf 1994a). Colwell (1974) presented a method for describing any periodic phenomena using three parameters.

Any periodic phenomena is perfectly predictable (predictability =1) if it is invariant (constancy =1) or changes in a regular sequence (contingency = 1). In less than perfectly predictable phenomena, predictability of is the sum of constancy and contingency, which are reciprocal. This method may be used to investigate the predictability of time series at many periods. In a study of riparian and aquatic vegetation along the Murrumbidgee River, Roberts (1992) examined the correlation between characteristics of the vegetation and five indices of variability in water regime including within and between year deviations, seasonality, event types and return times. She found that all the indices were significant predictors for at least one characteristic of the vegetation although the correlations were weak.

Where predictability is low, Burges (1990) points to the analytical tools of hydrology to manage water resources under conditions of uncertainty. The Hurst coefficient describes the tendency for periods of below or above average levels to be connected. Another approach is to look for probabilities of specific events. In stream hydrology techniques exist for low flow and high flow analysis. Similar techniques could be used for any defined series of water levels within or outside specified limits. This will be appropriate where predictability is low and when specific characteristics of different species are known or thought to be important, for example: length of wetting or drying to germination; leaf or stem longevity; rhizome longevity; or maximum duration above a certain depth before death (Mitchell 1978).

Several of the measures and methods described above are used throughout this thesis. The critical role of water regime in temporary wetlands has resulted in water regime being a recurrent theme in this study. The relationship between physical characteristics and the hydrology of the New England lagoons is investigated in Chapter 2. In Chapter 4, water regime is broken down into components that allow variation in the timing and amplitude of depth fluctuations independently of the average depth. In Chapter 6, the relationship between the spatial and temporal variation in water regime is examined.

Chapter 2
Hydrology of the New England Lagoons

2.1 Introduction

The hydrology of the New England lagoons, like other shallow basin wetlands, was thought to be largely dependent on local rainfall, runoff and evapotranspiration (Creek 1982; Lloyd 1992). There are observational and anecdotal data on water regimes in the lagoons (Brock 1991) but very little quantitative data, or hydrological studies of shallow wetlands in Australia. The different geological types, locations, sizes and catchment areas of the lagoons result in a variety of water regimes. Longer term fluctuations, such as the effects of the El Nino Southern Oscillation (Nicholls 1991), are also significant. Therefore a hydrological model of a lagoon was constructed that tested these major physical characteristics.

Holling (1978) and Starfield and Bleloch (1986) describe the application of modeling in areas of resource management that are poor in both data and understanding. In such situations modeling is not used for the animated description of data or for prediction. Rather it can be a tool for exploring the consequences of what we think may be true given limited understanding, and then compared with what real world data we have (Starfield and Bleloch 1986). Furthermore, a model can provide a framework for increased understanding in which available data can be integrated (Carter 1986).

The aims of this chapter are to a) quantify physical characteristics of lagoons that determine variations in water regime between lagoons, b) use these characteristics together with hydrological data to construct a computer model of a lagoon water balance and c) use the model to assess the sensitivity of a lagoon water regime to changes in the physical characteristics of the lagoons and hydrological components by comparison with a short period of water level data available for several lagoons.

Although understanding of major hydrological processes is well developed, there are practical difficulties of estimation of some parameters (Carter 1986). Water balances describe the movement of water through an ecosystem. Often this methodology provides the most accurate or the most convenient method for estimation of difficult to measure components, which most commonly are groundwater movement and evaporation (Lee 1983). Many water balances give results such as average depths for long periods or use conservative estimates of probabilities of water bodies filling. These are appropriate for estimating probabilities of reproductive success in seasonal environments (Woo *et al.* 1993) or more commonly, for estimating yield for use in storage design (Bligh 1994; Creek 1982). A water balance was constructed for the New England lagoons using data from a variety of sources. The output was then compared to anecdotal evidence and water level data of the way the lagoons behave.

2.2 Methods

2.2.1 Collection of lagoon water level data

Water level and rainfall were measured in Llangothlin, Barleyfields, Mother of Ducks Nature Reserve and Racecourse lagoons between 1992 and June 1998 by members of the aquatic botany group. Depth gauges were installed for above ground water depth and tube wells to a depth of approximately two metres to measure water depth through dry periods. Raingauges were installed at the lagoons and were replaced periodically as they went missing at two of the lagoons. For the first three years measurements were opportunistic and therefore mostly infrequent. After January 1995 measurements were performed approximately weekly until June 1997, after which they were collected fortnightly.

2.2.2 Model formulation and structure

The general form of a water balance equation is (Lee 1983):

Inflow - outflow - storage change = 0 (1)

In the model inflow and outflow were broken down into the following components thought to be important for the lagoons, resulting in the following formulation:

$$S = P + Q - E - O + G \quad (2)$$

Storage (**S**), the model output, was expressed as lagoon water depth. Inflows were precipitation (**P**) and surface inflow (**Q**) and outflow was made up of evaporation (**E**), overflow (**O**) and net groundwater flow (**G**). As with many water balances, errors of measurement of the components within the balance are confounded with the term calculated as a residual, in this case depth (Storage). In many water balances, groundwater is calculated as the residual because it is the most difficult to measure. However, even if all components of the balance are measured and an error term is included in the equation, the size of the error term is not indicative because the errors in many terms may be compensatory (Carter 1986; LaBaugh 1986).

The model structure and the daily calculations involved are represented schematically in Figure 2.1. The components from Equation 2 used to calculate lagoon water depth are represented as square boxes. Rainfall, runoff, evaporation, groundwater flow and lagoon morphological data were gained from several different sources (see Section 2.2.3 below). Rainfall and groundwater flow are straight input and outputs from the model respectively. Evapotranspiration and runoff are dependent on the lagoon water depth, represented as feedback mechanisms in the model. To calculate the evapotranspiration from evaporation a multiplier that depends on water depth was used. To calculate the amount of runoff, the model first calculates the size of the catchment as the total catchment area including the lagoon less the surface area of the lagoon. Therefore as the lagoon water surface becomes smaller the ratio of catchment to surface area greatly increases. This relationship also depends on the morphology of the lagoon basin.

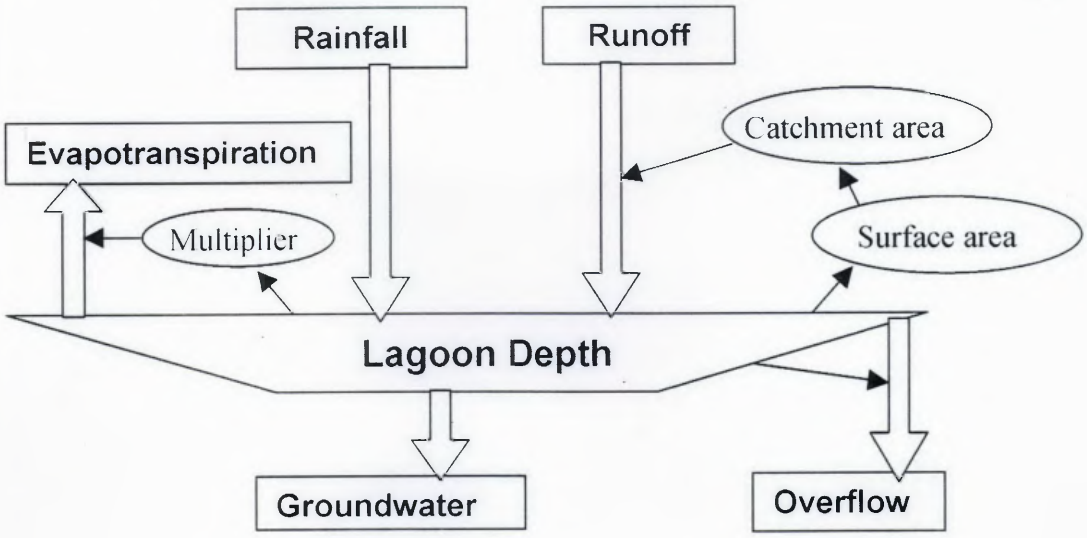


Figure 2.1 Schematic representation of the water balance. Lagoon depth is the model output. Square boxes represent direct inputs and outputs, elliptical boxes are components dependent on water depth that modify the value of inputs and outputs. Block arrows represent water movement, thin arrows represent factors affecting water movement. The lagoon depth at the beginning of each day determines i) the catchment area which determines the volume of runoff and ii) the multiplier which determines evapotranspiration and overflow.

Figure 2.2 Pinch lagoon showing its well defined catchment typical of most lagoons.

As lagoon bed slope decreases the increase in depth due to a given amount of runoff will decrease because of the increasing volume needed for a unit depth increase. When lagoon depth was increased it was assumed that the slope of the lagoon sides continued at the same angle. Details of input data sources and treatments are outlined below. The water balance model program code is included in Appendix A.

Sensitivity analysis was used to compare the effects of four characteristics on the hydrology of the lagoons: the two geological bases on which the lagoons occur; groundwater flow; the evaporation multiplier; and changing outlet height (maximum depth). The model was tested using the morphology data for Pinch lagoon (Figure 2.2). Mother of Ducks lagoon was not used because its hydrology is complex (and atypical) due to the levee construction. For changed outlet height, data for North Llangothlin were also run for comparison. Simulated water regimes were compared when outlet height (maximum depth at which overflow occurs) was raised (Pinch) and lowered (North Llangothlin). This is the easiest and most common change that has taken place in many lagoons and was one of the main environmental factors that appeared to be related to patterns in community composition (see Chapter 3).

2.2.3 Model input data

The water balance model of two lagoons was run over the only period for which all input data were available (September 1976 to August 1986). This included periods of above and below average rainfall. Any days for which the rainfall, runoff or evaporation data were missing were deleted. The data sources and how the data were applied for each term are outlined below. For events such as the germination and establishment of plants the sequential nature of water level fluctuations on a time scale of days is important, therefore daily data were used (although event based analyses were not carried out in this study).

Rainfall and runoff

Daily rainfall and runoff data for Boorolong Creek and Pipeclay Creek from the New South Wales Department of Water Resources were used. These stations recorded rainfall and the volume of water flowing in creeks that drain small catchments (several times the size of the largest lagoon catchment) near Armidale. The two

catchments have basalt and granite geological bases respectively. These two geological types are those on which all the lagoons are found, although none of the lagoons occur within the Boorolong or Pipeclay creek catchments.

The runoff characteristics of the two catchments are very different. Even though Boorolong Creek delivered a greater overall amount of runoff than Pipeclay Creek, it was delivered at a more even rate. This resulted in greatly reduced probabilities of zero runoff in the basaltic catchment compared to the granitic. The lower overall runoff from Pipeclay Creek catchment probably indicates greater deep percolation.

An attempt was made to create an antecedent precipitation index (Linsley *et al.* 1988) that gives a relationship between antecedent precipitation in a catchment and the proportion of rainfall that ends up as runoff. If such a relationship existed for these catchments, it would have been possible to use the antecedent precipitation index to estimate runoff using Bureau of Meteorology rainfall data for stations nearest individual lagoons. This proved very unreliable for both creeks and so the rainfall and runoff data for Boorolong and Pipeclay Creek catchments were used. The runoff data used were adjusted to a unit area and then multiplied by the catchment area of the lagoon being simulated. Creek (1982) applies a multiplier for the small catchment sizes of lagoons and for the slopes within the catchment. Refinements such as an antecedent precipitation index may be possible when more rainfall and water level data are recorded from individual lagoons. Rainfall data measured within the small catchments of individual lagoons are likely to be more reliable.

Evapotranspiration

Daily evaporation data (class A pan) were available for stations at Glen Innes and CSIRO Chiswick. CSIRO is located approximately 5 kilometres north of Uralla and the most southern of the lagoons while Glen Innes is approximately 40 km north of Llangothlin and the northern most study sites (Figure 1.4). CSIRO data for the same period as the rainfall and runoff data were used in the model as it was available for the same period and the station was more central to a majority of lagoons. Overall, data from the two stations was not greatly different.

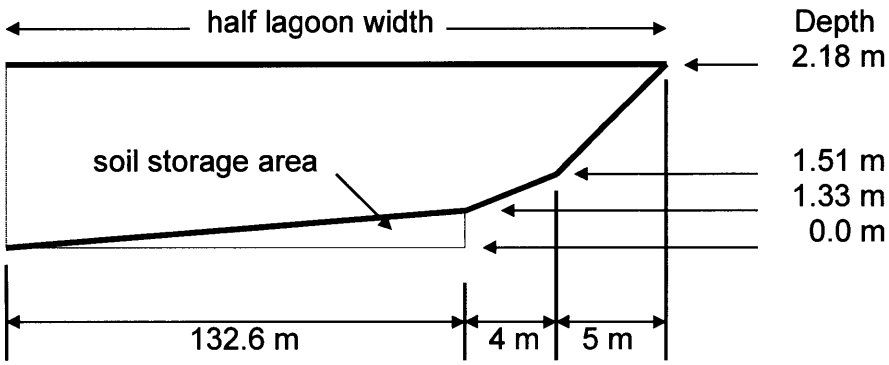
Evapotranspiration varies with water level and with plant cover. Wade (1990) argues that there is an increased effect due to plant transpiration but that the magnitude of the effect will depend on a variety of site and species specific factors. Boyd (1987) gives Et/Eo ratios (the ratio of evapotranspiration, Et, to open water evaporation, Eo) for a variety of species that agree with those used by Creek (1982) which were based on values given in Nichols and Brown (1980) and extended for a range of depths. Multiplier values used were taken from Creek (Table 2.1).

Table 2.1 Multiplier values (Et/Eo ratios) used to calculate evapotranspiration from evaporation depending on water depth. After Creek (1982)

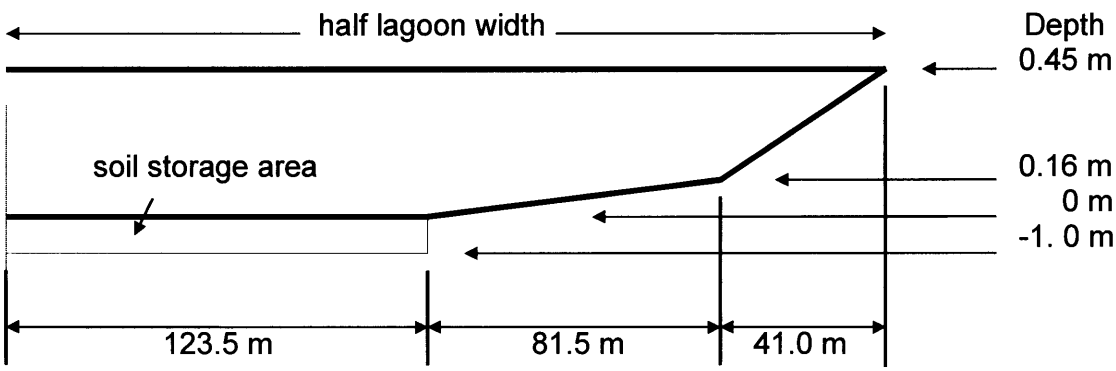
Water depth (m)	Evaporation multiplier
> 0.50	1.00
0.00 to 0.50	1.25
-0.15 to 0.00	1.50
-0.25 to -0.15	1.25
-0.35 to -0.25	1.00
-0.50 to -0.35	0.75
< -0.5	0.50

Groundwater flow

When the water levels in four of the lagoons (Barleyfields, Racecourse, Llangothlin and Mother of Ducks) were below ground, the water levels were measured using a single testwell located on the main lagoon bed. The testwells were constructed from 50mm diameter PVC pipe installed vertically in a 0.1m diameter hole to a depth of approximately two metres. The pipe was slotted and wrapped in geotextile filter fabric below the soils surface and the hole was back-filled with sand. The testwells were installed in December and January, 1992/3 and read at intervals of approximately one month until January 1995. After January 1995 the testwells were read weekly. In mid-winter, 1995 the net flow of groundwater was estimated from weeks with no rain during a period of very low rainfall when water levels were well



North Llangothlin Lagoon
Area when full - 9.48 ha
Assumed shape - rectangle: 283.2 * 334.7m



Pinch Lagoon
Area when full - 24.2 ha
Assumed shape - square: 492 m

Figure 2.3 Morphological profiles used for North Llangothlin and Pinch Lagoons based on areas measured from aerial photos and slopes measured at sites. Volumes were calculated as 5mm deep solids of the surface area at each depth.

below the lagoon bed (>0.5 m). It was assumed that evaporation was negligible during these periods and that the drop in level was largely due to deep percolation. Measured values ranged from 5 to 15 mm per day. The model was tested for sensitivity to values ranging from 0 to 20 mm per day, covering a greater range than was observed. Groundwater flow was assumed to be constant and negative in the model that follow. Groundwater inflow was not included because the model results showed high sensitivity to groundwater outflow and therefore inflow would have no effect compared to the zero net groundwater flow value that was tested. Apart from the groundwater sensitivity analysis, an intermediate value of 10 mm per day was used in the model.

Lagoon morphology

The two lagoons that were used in the model were North Llangothlin and Pinch Lagoons (Figure 2.3). North Llangothlin was only used for testing the effect of lowered outlet height. These were selected because they were intermediate in physical attributes and because Pinch has been partially drained and North Llangothlin has been dammed. The volumes and shapes of the two lagoons were estimated using the area data from topographic maps and aerial photographs (Table 1.1, Appendix C) and from gradients of the lagoon bases measured during the lagoon survey. To calculate the volume of the lagoons at any given depth it was necessary to assume the lagoons were a regular shape. Circular, rectangular or right triangular shapes were used to minimise errors when lagoon shapes became less regular. A soil storage component was incorporated to a depth of 1m using 0.5 as the soil void proportion, based on soil field texture tests and typical values given in Brady (1984). Creek (1982) calculated a value of 0.7 for the peat and the clay subsoil at Mother of Ducks Lagoon, however he assumed the clay was impervious. The value of 0.5 was used for all soils as soil field texture tests indicated a consistently high clay content in the lagoon soils sampled (Figure 2.3).

2.3 Results

2.3.1 Field data

The water levels measured at four lagoons show a fluctuating pattern (Figure 2.4). The water levels in all lagoons decreased over 1993-4, were at low levels in early 1995, increased during late 1995 and through 1996 and begin falling again during 1997-8. However, the magnitude and speed of water level changes is quite different between lagoons. Llangothlin is the most permanent as the deepest part of the lagoon didn't dry to the same extreme as the other lagoons, although the range of depths is similar to Mother of Ducks and Barleyfields apart from the driest period in 1995. Racecourse lagoon appears to be more rapidly effected coming into the drought during 1994. When the depths are expressed as histograms all lagoons show bimodal distributions of depth with the possible exception of Mother of Ducks (Figure 2.5).

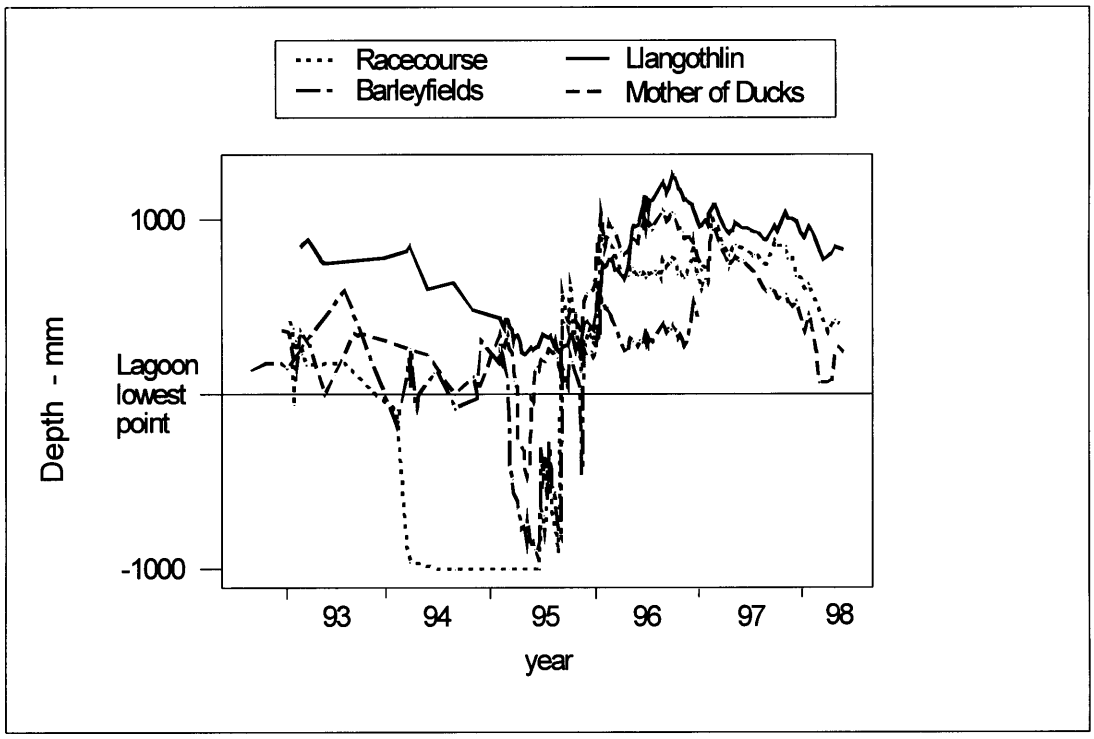


Figure 2.4 Water depths at four lagoons measured from 1993 to 1998. All lagoons show a similar long term pattern over the period of measurement.

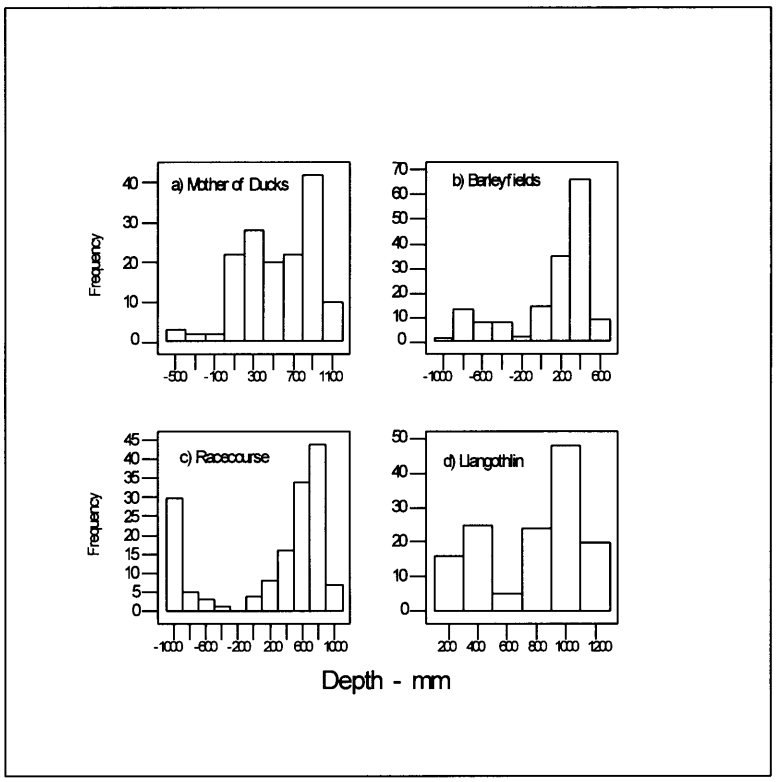


Figure 2.5 Water depth distributions measured from 1993 to 1998 at a) Mother of Ducks, b) Barleyfields, c) Racecourse and d) Llangothlin lagoons. All lagoons show a bimodal distribution due to the long term fluctuation of depths in all lagoons.

2.3.2 Model sensitivity results.

The effect of catchment geology

The effect of the different rainfall and runoff data for Boorolong Creek and Pipeclay Creek was tested on Pinch lagoon with a maximum depth of 45 cm and with evaporation multipliers. The Pipeclay Creek catchment delivered runoff to the lagoon much more quickly but only half as much of the rainfall ends up as runoff despite very similar total rainfall for the period over which the model was run.

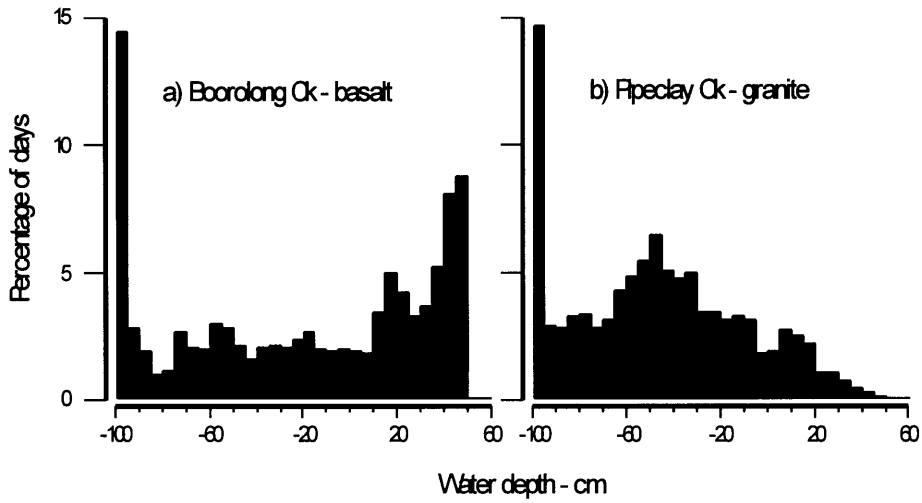


Figure 2.6 Simulated depth distribution histograms for Pinch Lagoon using rainfall and runoff input data from a) Boorolong Creek (basaltic) and b) Pipeclay Creek (granitic) catchments.

This exaggerated the effect of any dry spell (Figure 2.6). However, despite the decreased volume of runoff, the probability of the very lowest water levels did not increase. The strongly bimodal water levels recorded in Racecourse lagoon (Figure 2.4, Figure 2.5) suggest that a constant groundwater flow may be an oversimplification (see below). However, the results suggest geology will have a strong influence on water regime (Table 1.1).

The effect of ground water flow

Water levels in the lagoons show a high degree of sensitivity to groundwater seepage (Figure 2.7). The reduction or increase of the constant amount of seepage by 50% results in a dramatic change in water level distributions. Although variation in recorded seepage was large and based on only a few measurements, the high sensitivity of the model to the level of groundwater suggested groundwater movement must be a significant component of the water balance in the lagoons. Setting groundwater seepage to zero resulted in water levels being almost constantly overflowing (Figure 2.7a).

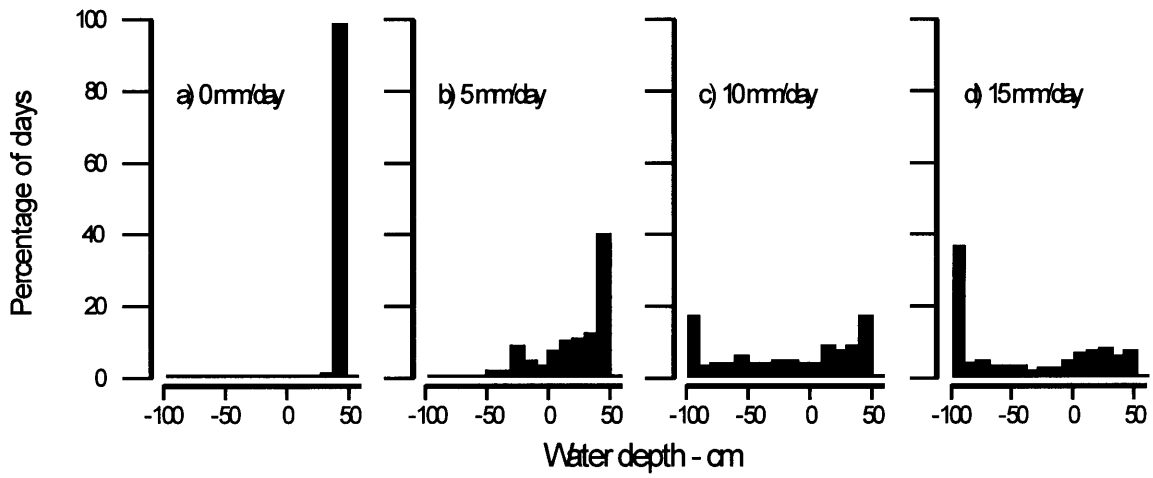


Figure 2.7 Simulated depth distribution histograms for Pinch Lagoon using constant values of a) 0 mm, b) 5 mm, c) 10 mm and d) 15 mm per day groundwater seepage from the lagoon.

This conclusion is stronger considering that the likely errors in the runoff and evaporation data used. Runoff is likely to be greater than the data used in the model because a multiplier is sometimes applied to account for greater runoff in a smaller catchment (Creek 1982). The evaporation data used in the model was probably less than occurs in the lagoons because open water evaporation is generally less than pan evaporation data (Linsley *et al.* 1988). Therefore, given the likely errors the effect of seepage would be even greater than is suggested by the model. From visual inspection of histograms, the water level data collected at all four lagoons are most similar to the results obtained with groundwater seepage of 5 or 10 mm per day, depending on the lagoon. However, it is likely that groundwater movement will be more complex than a constant loss (see Discussion)

The effect of damming or draining.

Changes in outlet height had several effects on the distribution of water depths (Figure 2.8). At lower outlet heights the lagoon was often full. The proportion of time that the lagoon is overflowing (at maximum depth) decreases as outlet height is raised. The maximum depth for the ten year period of input data was 0.75 m at Pinch and 1.94m at North Llangothlin.

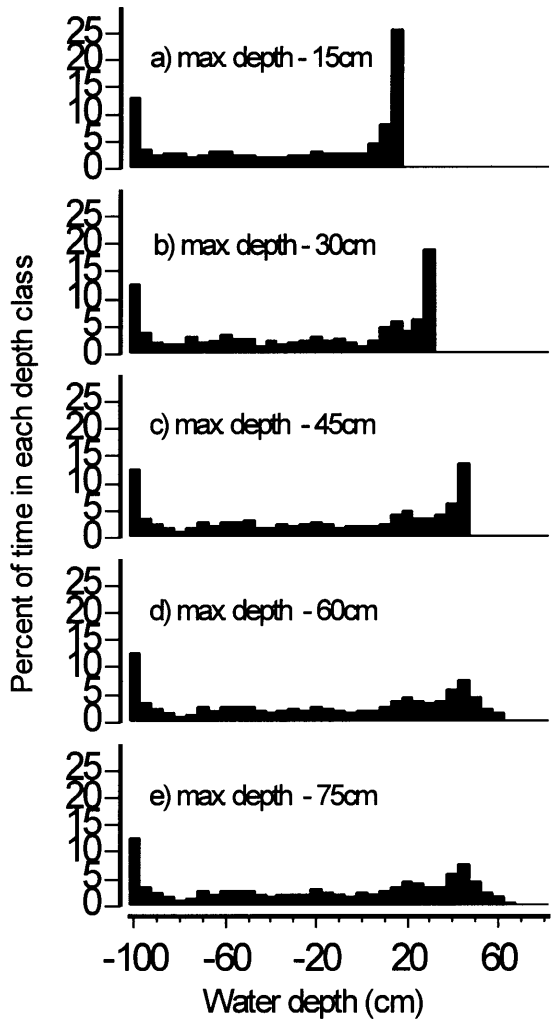


Figure 2.8 Simulated depth distribution histograms for Pinch Lagoon at different outlet heights. Maximum depth was set above and below the value of 45 cm measured in the field: a) 15cm, b) 30cm, c) 45 cm, d) 60cm, e) 75 cm.

Both North Llangothlin and Pinch lagoons only achieved the maximum depths on a very small number of days. This is in agreement with an observation by the owner of Loch Abbra Lagoon that the lagoon has only been full once in the past 15 years since he constructed a dam across approximately half the lagoon. It is likely that wetter periods would occur (Pimm and Redfearn 1988) and the lagoon would fill deeper but the incidence would be so infrequent as to be of little interest. This effect is consistent with the recorded water depths in lagoons, none of the lagoons had a high frequency of values at the maximum depth (Figure 2.5).

For Pinch lagoon, maximum depths greater than 30 cm resulted in bimodal distributions of water depths above the soil surface. This is probably due, at least in part, to the effect of the evaporation multipliers. At intermediate water levels the

increased evaporation reduces water levels back to just above ground level before the next inflow event. A bimodal distribution of above ground depths was only apparent in the two largest lagoons, Mother of Ducks and Llangothlin (Figure 2.5). The effect of the evaporation multiplier was tested independently of other factors for Pinch lagoon.

The effect of the evaporation multiplier

The effect of the evaporation multiplier was tested by running the model without any multiplier (an evaporation multiplier of 1 was assigned at all depths) (Figure 2.9).

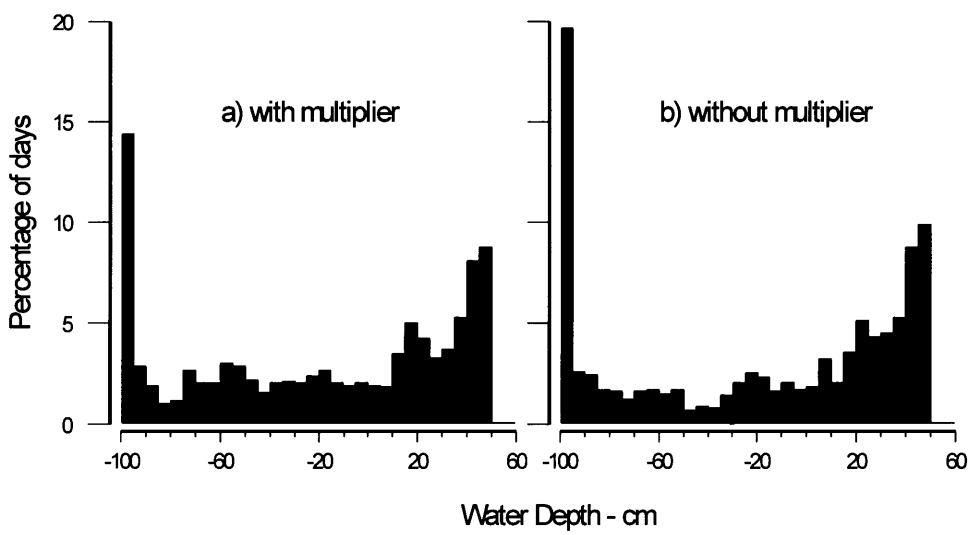


Figure 2.9 Simulated depth distribution histograms for Pinch Lagoon with a) and without b) an evaporation multiplier. The maximum depth in both simulations was 45cm

The result was an increase in extreme depths, especially the lowest water levels due to the increased evaporation when water levels were lower than 0.25m below ground level. There was a smoothing effect on the distribution of depths above the soil surface.

2.4 Discussion

The analyses indicate that all the components within the water balance (equation 2) substantially effect the water levels in the lagoons. Therefore any action which may effect the hydrology of the lagoons should be carefully considered. Draining or damming have been the most common management actions undertaken in the past due to the ease with which they can be achieved (Brock *et al.* in press.). If draining does not destroy a wetland, it will create a situation where water levels vary less, most notably the lagoon overflowing for a significant proportion of the time. On the other hand, damming a lagoon has the effect of reducing the amount of time water levels are within a particular range of depths. That is, because water levels increase to higher levels they take longer to return to pre-rainfall event levels. As was seen for the two lagoons studied and from anecdotal evidence from the owner of Loch Abbra Lagoon, the limited catchments mean that increases in depth for a substantial proportion of the time are uncommon after damming. Another effect of damming lagoons is increasing the slope of the lagoon edges. This has occurred at Mother of Ducks Nature Reserve and North Llangothlin Lagoon. The effect of increased slope is discussed further in Chapter 8.

The effect of evaporation on lagoon water levels does not seem as great as described by Creek (1982). His water balance had no groundwater flow and therefore outflow was comprised only of evaporation and overflow. Also, he varied a runoff coefficient to examine the behaviour of water levels in the lagoon. The behaviour of runoff used in this study was found to be far from a simple relationship with rainfall such as an antecedent precipitation index. There is strong evidence that groundwater is important in the hydrology of the lagoons (Figure 2.7). If groundwater flow is affected by underlying geology as seems likely, this may account for the very different hydrological behaviours of Llangothlin and Little Llangothlin lagoons. Llangothlin Lagoon dries out periodically whereas Little Llangothlin water levels are much more stable (Haworth 1994). Llangothlin is situated partly on granite, whereas the position of the basalt granite boundary near Little Llangothlin probably skirts the lagoon catchment boundary.

All the lagoons sampled exhibited a bimodal distribution of water depths (Figure 2.5). The weakest pattern was Mother of Ducks lagoon which may be important for the dominance of *J. articulatus*. The bimodal depth distributions observed in the lagoons and in the model shows that water levels in the lagoons tend to be either high or low, probably due to several hydrologic processes that act as positive feedback mechanisms (Wilson and Agnew 1992), tending to push water levels toward more extreme values. The greater evaporation at lower water levels when plants are present prevents levels from increasing unless rainfall is high (Creek 1982), such as occurred in the winter of 1990 (Bell 1991) (and the spring and summer of 1995/6). Unlike the assumption of constant flow used in the model, groundwater flow in the lagoons probably fluctuates in response to rainfall patterns (Kreeb *et al.* 1995). The small size of the catchments means they would be sensitive to local rainfall. Periods of consistent or above average rainfall would result in net groundwater inflow whereas after drier periods groundwater flow would become negative as was recorded in winter 1995. Another characteristic of above average rainfall periods is lower evaporation. The final characteristic leading to positive feedback is the relationship between the probability of drying and the position within the lagoon. The more central areas of the lagoon are less likely to dry because the ratio of catchment size to water surface area increases exponentially as the area of the lagoon reduces. All these factors would contribute to a bimodal pattern of longer term water level fluctuations with shorter term fluctuations due to individual rainfall events. Bimodal distributions present problems if averages are used as descriptive statistics. The data does not have a central tendency and the average is misleading.

This chapter only touches the surface of the hydrology of the New England lagoons. It is limited by the disparate sources of input data and lack of comprehensive data sets with which to validate the model. The model water balance of the New England lagoons constructed in this chapter has highlighted geology as an important factor that will influence runoff and groundwater seepage at lagoons but also provides a framework for further work such as the examination of temporal patterns in water level fluctuations or measurements of hydrological components made at individual lagoons. Future research may profit from a slightly different strategy given that physical characteristics, changes in water levels and rainfall are the easiest factors to measure to a high level of accuracy at individual lagoons.

Chapter 3
Distribution of *J. articulatus* and *G. australis* in the New England lagoons

3.1 Introduction

Invasive plants typically become established in a few places in low numbers for a variable and sometimes considerable period, before becoming widespread in high numbers (Humphries *et al.* 1991). In this establishment phase of invasion the broad habitat requirements of the species are important in determining its range. The quantification of that range is important for management planning, but can also be useful in gaining insight into the species ecology and interaction with native species.

This chapter reports the results of a survey that aimed to assess the distribution of *J. articulatus* and *G. australis* in the New England lagoons. The extent, diversity and consistency of communities in which *J. articulatus* and *G. australis* occur and the correlation of several environmental characteristics with those communities are reported. Thesurvey aimed to provide a regional focus to this study and a baseline for any future work if *J. articulatus* becomes a problem at other lagoons or in other regions. It also provides the basis for interpretation of more detailed aspects of the ecology of *G. australis* and *J. articulatus*.

Comparisons of lagoons surveyed at only one time must be interpreted carefully. Lagoons may have a similar cycle of vegetation change but may be in different stages

of that cycle. However there are strategies that can assist in overcoming these difficulties. Short-term fluctuations of environmental parameters result in changes in the dominance of species within the community. The use of species presence/absence rather than abundance will remove some of the effects of the short-term fluctuations. Investigating the seed and propagule banks of the lagoons will remove effects of severe short term or long term fluctuations that result in changes in species presence (Brock 1995)(Chapter 7). In temporary wetlands seed banks will give a picture of the vegetation over past wetting and drying cycles spanning several years. There are several limitations to seed bank counts. Seed banks may contain large numbers of seeds of species that rarely occur within the extant vegetation of the community due to environmental factors that restrict germination or establishment. In wetlands this could include well dispersed terrestrial species. Of the species that do occur in the community, seed banks will be dominated by species that invest a large amount in sexual reproduction and germinate readily. For example, *Eleocharis sphacelata* rarely germinated from the seed banks of several lagoons (Britton and Brock 1994) despite being common in the extant vegetation. Such a pattern may be due to an absence of seeds or because the germination requirements of the species are outside those used in the experiment.

3.2 Methods

Sixteen sites in fifteen lagoons were selected (Figure 1.4) on the basis of size, geology, location and water regime (Table 1.1). The lagoons occur in groups located in discrete areas on the tablelands, therefore the location is related to lagoon group, altitude and latitude. Major changes to water regime that had taken place were assessed in terms of alteration to the lagoons and from anecdotal evidence gathered during a preliminary reconnoitering of lagoons during the summer of 1992-3.

At each of the sixteen sites an area from above maximum water level to the lowest part of the lagoon bed was selected to sample plant communities across the main elevation gradient. Sites were rejected if there was evidence of excessive disturbance caused by stock or by digging for worms, such that the topsoil had been thoroughly

mixed and there was very little extant vegetation. The Llangothlin group of lagoons were sampled more intensively than the Brockley Group to enable detailed examination within one group of lagoons. The Llangothlin lagoons include the greatest variation in size, geology and water regime. At Mother of Ducks Lagoon one site was selected inside and one outside the nature reserve to assess the effect of the levee since its construction.

At each site three transects were selected at random distances from an arbitrary starting point along the lake shore (Figure 3.1). These distances were constrained so that three transects would fit along the lagoon edge. The transects ran along the elevation gradient starting above the level of the overflow (high water line) and finishing on the lagoon bed where the vegetation became uniform and the lagoon bed slope became minimal or flat. Between 4 and 10 quadrats (0.5 metre by 0.5 metre) were selected along each transect in a stratified random design. A 0.5m by 0.5m transect had been found to be optimum size to adequately sample the diversity of the lagoon vegetation in preliminary test of several sizes. The stratification along each transect was on the basis of identifiable vegetation zones. The distance (D) between each quadrat was selected randomly from a range of values.

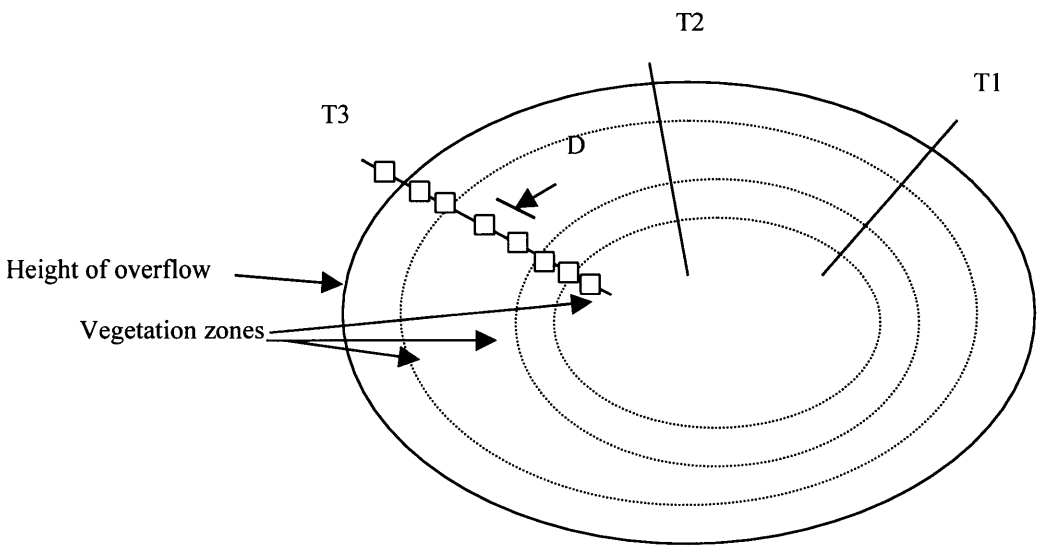


Figure 3.1. Diagram of sampling used in a typical lagoon morphology. The distance between quadrats on the transect (D) was varied depending on the width of recognisable vegetation zones.

The range of values was determined so that each zone was sampled at least twice to reduce the chance of missing species that were more restricted than the dominant

species defining the zone. This facilitated sampling at random within readily identifiable zones of vegetation, while overcoming the problem of over- or under-sampling in sites due to differences in size between lagoons and in width of zones of vegetation within lagoons. Distance between transects and quadrats and the height difference between quadrats were recorded. Where possible, water level was used as a reference for measuring height differences. Where a lagoon was dry the gradient of the bed was measured using a spirit level, straight edge and tape measure. All species within each quadrat were identified (to species when possible) and given a modified Braun-Blanquet scale reference score from 1 to 7 for estimations of projected foliage cover/abundance (Table 3.1) (Mueller-Dombois and Ellenberg 1974). Presence/absence data were used in the multivariate analysis and cover /abundance were plotted against environmental variables.

Table 3.1 Cover abundance classes used for scoring species abundance. Adapted from (Mueller-Dombois and Ellenberg 1974).

Score	Abundance / cover
0	Not present
1	only 1 or 2 small specimens
2	<5% several small specimens
3	5-19%
4	20-39%
5	40-59%
6	60-79%
7	80-100%

The maximum size of each lagoon (when overflowing) and its catchment area were determined from 1:25000 topographic maps and from 1989, 1:25000 colour aerial photography. The 1989 photography was chosen because it was recent and it was a wet year, allowing accurate estimation of lagoon area. The areas were measured using a planimeter program and checks were made for accuracy using known areas and distances, e.g. the area inside the levee banks at Mother of Ducks Nature Reserve. This information was used to calculate lagoon area to catchment area ratios for each lagoon and for each quadrat. This was done by calculating the lagoon water surface area if the water depth was such that the water extended to the quadrat. Thus the surface area would increase as quadrats were closer to the maximum water level at the

edge of the lagoon. Landholders were questioned concerning any changes to the lagoons and this information was used in interpreting results.

The survey data were analysed using the PATN software package (Belbin 1993). Presence/absence data were classified and ordinated using the ASO module to calculate of association measures (Bray and Curtis), the FUSE module to assign groups based on the fexible UPGMA clustering strategies with a beta value of 0, the DEND module to produce a dendogram and the SSH module to perform semistrong hybrid multidimensional scaling using the default options. Environmental variables were plotted on ordination axes. Individual species cover/abundance scores were plotted against environmental variables.

3.3 Results

3.3.1 Distribution of *J. articulatus* and *G. australis*

Overall 111 species were recorded in 295 quadrats. Of these, 19 occurred in more than 10% of quadrats. A list of species is included in Appendix B. When quadrats were clustered according to similarity in species composition three main classification groups were evident. The most well defined group was the Mother of Ducks lagoon quadrats (Figure 3.2 group c). All the quadrats from Mother of Ducks were very dissimilar to quadrats from other lagoons due to the presence of *J. articulatus* and *G. australis* and few other species. *G. australis* was the most frequently encountered and abundant species recorded in the survey (Table 3.2) and was present at 14 of the 16 lagoons surveyed (not found at Racecourse or Dangars lagoons). In contrast, *J. articulatus* was only recorded at Llangothlin and Mother of Ducks lagoons. *J. articulatus* has been recorded at Little Llangothlin in an area on the north east shore (D. Bell pers. comm.; Briggs 1976). It was observed in a drain that runs into Little Llangothlin Lagoon in this survey.

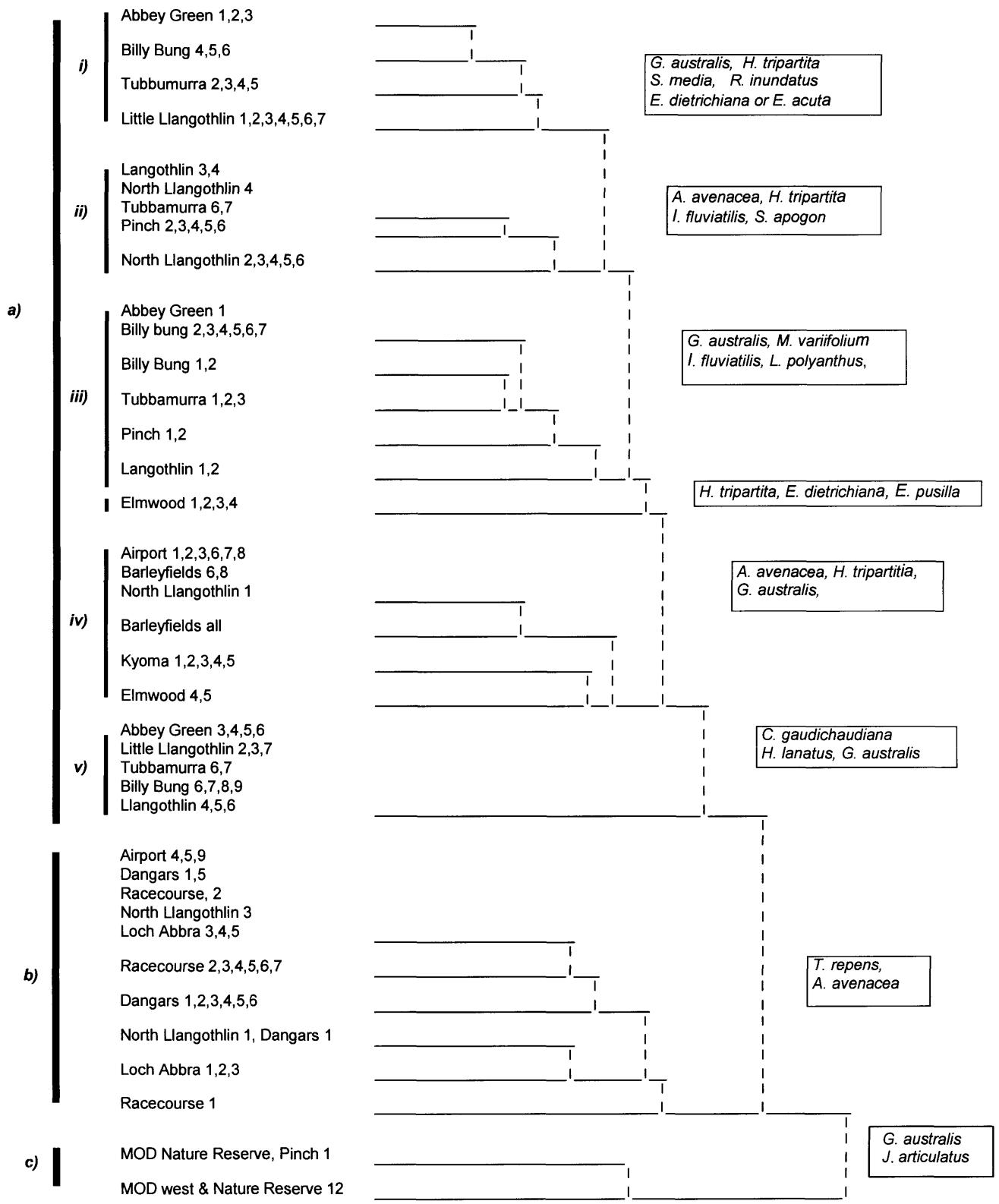


Figure 3.2 Dendogram of quadrats clustered according to compositional dissimilarity of species presence/absence. Major and minor groupings are indicated on the left. Branch labels indicate the lagoon and the position on transect (1 - lowest end to 6-9 highest end of transect). Most abundant species in each group are indicated in boxes on the right. Full species names are included in Appendix B

Within Mother of Ducks lagoon, west paddock quadrats and those within the reserve are segregated (Figure 3.2 group c). This is due to the presence of different species less common than *J. articulatus* and *G. australis*. Within the nature reserve, *Potomageton tricarinatus* and *Myriophyllum variifolium* are present, whereas in the west paddock species such as *Agrostis avenacea*, *Stellaria angustifolia*, *Hydrocotyle tripartita* and *Trifolium repens* are present in small numbers. These are typical of dryer conditions and some appeared in the nature reserve in later seasons (see Chapter 6). *Eleocharis acuta* occurs within the nature reserve and in the west paddock at similar abundances.

The second major group (Figure 3.2 group b) consisted of quadrats from Racecourse and Dangars lagoons and several from each of North Llangothlin, Loch Abbra, and Airport lagoons. Quadrats in this group were typically dominated by *T. repens* and *A. avenacea*. However, these species were in low abundance in some quadrats. In these cases similarity between quadrats was attributable to other opportunistic species such as *Persicaria lapathifolium* or to the presence of terrestrial species such as in edge quadrats of Racecourse Lagoon (terrestrial species are those that have no tolerance of flooding and so would not survive below the high water mark of the lagoon except during dry periods).

In two other groups *A. avenacea* was a dominant with other species. The first was a group of quadrats from North Llangothlin and Pinch lagoons that frequently contained *A. avenacea* and the semi-aquatic species *H. tripartita*, *Isotoma fluviatilis* and *Schoenus apogon* (Figure 3.2 group a-ii). This group had the highest species richness per quadrat of any group. The Pinch lagoon quadrats in this group contained several codominant aquatic species whereas the North Llangothlin quadrats contained *T. repens* as a co-dominant. The second group consisted mainly of quadrats from Airport, Barleyfields and Kyoma lagoons (Figure 3.2, group a-iv). These quadrats were characterised by *A. avenacea, H. tripartita* and *G. australis* (Table 3.2). These quadrats were generally less species rich than group a-ii. They contained grass species such as *Amphibromus sinuatus* and *Panicum obseptum*.

Table 3.2 Percentage frequency of quadrats in groupings identified by cluster analysis (Figure 3.2) and the number of lagoons in which species were found.

	Group							Number of
	a-I	a-ii	a-iii	a-iv	a-v	b	c	lagoons
Glyceria australis	86	26	56	56	48	10	98	14
Agrostis avenacea	46	78	20	84	16	85	13	15
Hydrocotyle tripartita	76	85	51	69	35	10	6	14
Trifolium repens	14	74	0	27	52	65	4	14
Eleocharis dietrichiana	62	11	49	69	29	7	0	9
Myriophyllum variifolium	32	30	61	2	6	8	29	8
Juncus articulatus	0	4	2	0	0	0	77	3
Eleocharis acuta	65	44	34	2	0	5	31	10
Stellaria angustifolia	97	33	5	18	55	0	8	11
Ranunculus inundatus	76	52	41	31	3	5	2	10
Holcus lanatus	35	33	0	7	71	0	0	9
Isotoma fluviatilis	27	70	59	9	6	5	0	9
Eleocharis pusilla	59	37	34	7	0	17	0	11
Carex gaudichaudiana	3	15	2	0	94	0	0	6
Brachycome radicans	51	56	29	0	0	0	2	9
Lilaeopsis polyantha	27	0	68	2	3	0	10	9
Persicaria lapathifolia	0	7	0	0	0	42	0	3
Potamogeton tricarinatus	0	4	22	0	0	0	48	3
Amphibromus sinuatus	5	4	10	49	3	13	0	9
Gnaphalium involucratum	5	30	20	4	0	17	0	10
Schoenus apogon	0	70	0	0	16	0	0	6
Panicum obseptum	0	0	0	40	0	0	0	2
Festuca sp.	0	0	0	0	13	5	31	3

The remaining quadrats were mainly from lagoons in the Llangothlin group and had a diverse range of species. These quadrats occur right across the transects and are in three groups; deeper water sites are dominated by *M. variifolium* and *G. australis* (Figure 3.2, group a-iii), quadrats intermediate on the transects were highly diverse, having between 6 and 9 co-dominant aquatic species (Figure 3.2, group a-i.) and, quadrats located on the edge of these lagoons were dominated by *Carex gaudichaudiana* and *Holcus lanatus* (Figure 3.2, group a-v). *T. repens* often occurred when *H. lanatus* was dominant whereas *G. australis* commonly occurred with *C. gaudichaudiana*. *G. australis* occurred commonly in many quadrats in all these groups (Table 3.2).

3.3.2 Correlation with environmental gradients.

The relationship between species abundance and maximum possible depth showed a distinct separation of *G. australis*, *J. articulatus*, *M. variifolium* and *E. acuta* at Mother of Ducks Nature Reserve quadrats (Figure 3.3a,b,d & e). *T. repens* and *A.*

avenacea occurred at quadrats that could experience great maximum depths at Racecourse Lagoon (Figure 3.3g & h). If the exceptional quadrats from dammed lagoons are excluded, *M. variifolium* appears to prefer deeper sites, as it shows a weak positive correlation between cover/abundance and maximum depth compared to other species where there was little relationship (Figure 3.3d).

Mother of Ducks quadrats were omitted from the ordination because they were so dissimilar to all other lagoons. The lack of similarity makes comparisons with environmental variables impossible. Only species that occurred in more than 10 quadrats were retained (44 species). Presence in greater than ten quadrats generally indicated occurrence throughout a zone (six quadrats) in more than one lagoon. When the data were ordinated six dimensions were necessary to achieve a good representation of differences between quadrats (stress < .15) (Belbin 1993). The lack of clarity and separation of the groupings from the classification indicates that many of the species that were recorded do not grow in distinct communities. A plot of the 3rd and 5th ordination vectors gave the best separation of the groupings from the classification (Figure 3.4a).

Overall, there was a general pattern of similarity between lagoons that were in close proximity. Dangars and Racecourse grouped closely, Barleyfields and Airport also grouped together, and so did all the Llangothlin lagoons. This also resulted in weak correlation with altitude and lagoon group and to a lesser extent geology. Lagoons occur at increasingly higher altitudes from the southern limit of the study sites near Uralla to the northern most near Llangothlin. Racecourse and Dangars lagoons are the only two lagoons that occur completely on granite (Table 1.1).

Two measures of water regime, maximum possible depth at a quadrat and the ratio of catchment area to the area of the lagoon at the quadrat (C/A ratio), gave the best general agreement with the pattern of classification groupings (Figure 3.4b). Other parameters that were measured are not reported as there was no discernable relationship with species distributions.

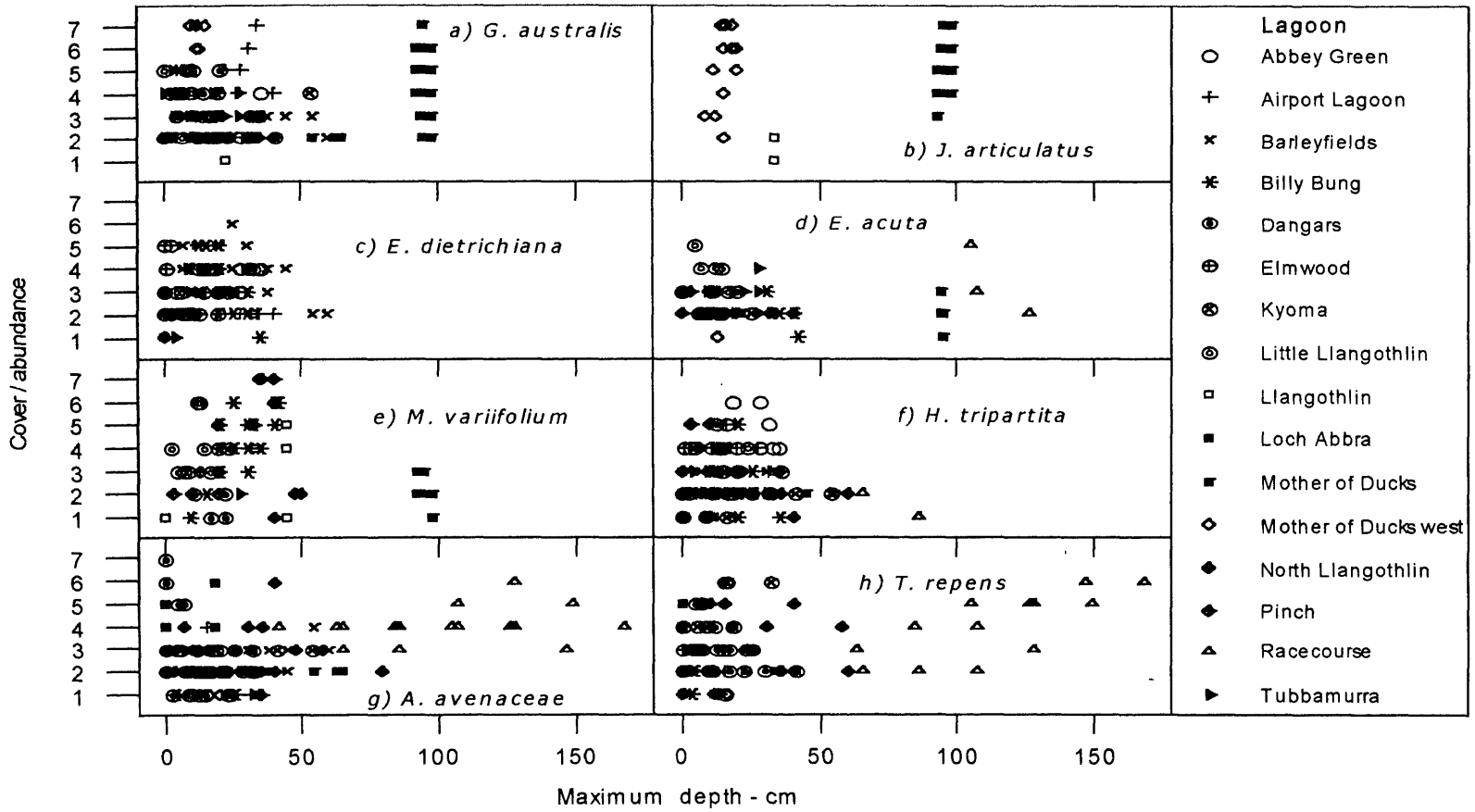


Figure 3.3 Abundance of common species at different maximum depths at the sixteen sites surveyed. *G. australis, J. articulatus, M. variifolium* and *E. acuta* occurrences in Mother of Ducks quadrats are clearly separated, as are *T. repens* and *A. avenacea* at Racecourse lagoon

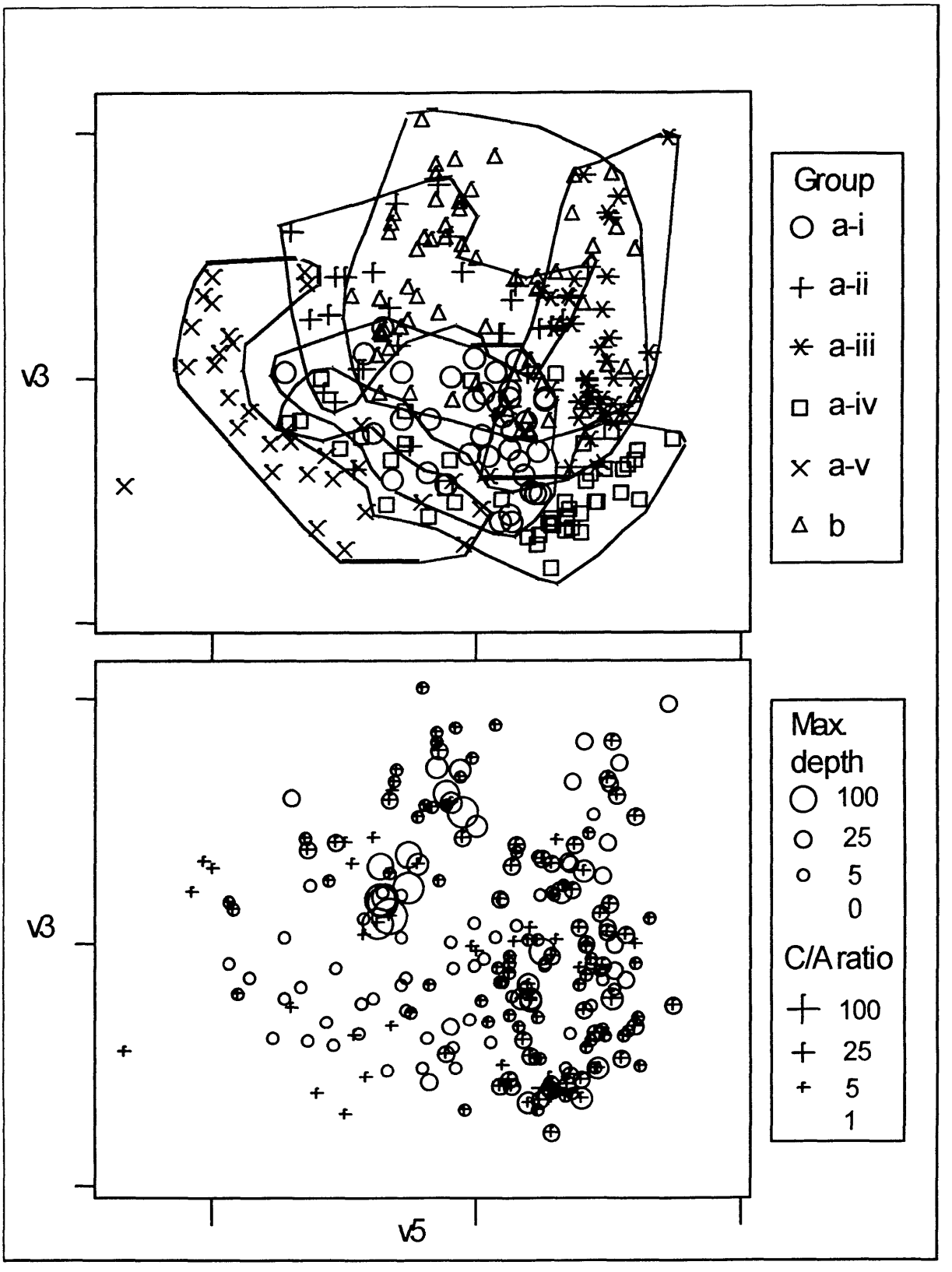


Figure 3.4 Ordination diagrams of quadrats showing a) groups defined by cluster analysis (see Figure 3.2 and text for details) and b) maximum possible depth at each quadrat and the ratio of catchment to surface area (C/A ratio) at each quadrat. (see methods for explanation of how these were calculated).

Many of the quadrats in group b (from the cluster analysis) showed high values of maximum possible depth (Figure 3.4b, top centre and centre right on the plot). Group b quadrats were not well separated from other groups on the ordination plot, overlapping groups a-i, a-ii, and a-iii (Figure 3.4a). The quadrats with large maximum depth were from Racecourse, North Llangothlin and to a lesser extent Dangars lagoons. The catchment to area ratio of these quadrats was variable. Quadrats in groups a-iii and a-iv had intermediate maximum depths and also medium to high values of C/A ratios (Figure 3.4b, down the right axis of plot). Quadrats in groups a-i and a-v (Figure 3.4b, left and centre of the plot) generally had lower values of both maximum possible depth and C/A ratio.

3.4 Discussion

The presence of *J. articulatus* at only three lagoons and only at Mother of Ducks at high densities contrasts with the extensive distribution of *G. australis*. The presence of *J. articulatus* at Mother of Ducks and Little Llangothlin lagoons (Briggs 1976) and in creeks (Casanova 1993) and drains suggests that it has a preference for water levels that fluctuate less than occurs in most of the lagoons. For example, apart from the area within the levee bank, the drainage of Mother of Ducks restricted fluctuations to short periods of inundation. Similarly, creeks and drains have relatively stable water levels during base flow conditions except for short flood periods after which levels decline rapidly. At Little Llangothlin water levels are consistently high but they also fluctuate very little (Haworth 1994).

Another possible reason for the abundance of *J. articulatus* at Mother of Ducks is eutrophication. Briggs (1976) found that water samples from Mother of Ducks and one set of samples from the north end of Little Llangothlin Lagoon (where there was a population of *J. articulatus*) were high in nutrients. However, Grime *et al.*(1988) described *J. articulatus* as commonly found in base rich mire where disturbance and some soil infertility limit the growth of potential dominants, so nutrient availability seems unlikely to be critical, however lagoons situated on basalt are base rich. Disturbance appears to be a factor that is necessary for *J. articulatus* to be successful.

However, there is disturbance from waterbirds, cattle, drought and people in all the lagoons, yet *J. articulatus* has not yet spread widely.

In contrast, the co-occurence of *G. australis* with a range of other species indicates that it has a broad tolerance of water regimes. The species ranged from edge species such as *C. gaudichaudiana* and *H. lanatus* through to species showing a preference for deeper water such as *M. variifolium* (Table 3.2). Bell (1991) found *G. australis* grew across an elevation gradient at Barleyfields Lagoon. *G. australis* was much less common in lagoons that had been dammed (or in the case of Racecourse Lagoon, had a high outlet level) and that would therefore experience wide fluctuations in water level (Figure 3.4b, Chapter 2). It was absent from Dangars and Racecourse and uncommon in North Llangothlin and Loch Abbra lagoons. This is also true for many species with which *G. australis* co-occurs (Table 3.2). This suggests that dammed lagoons have fluctuations too large for even species with tolerance of a wide range of depths to persist and that states of flooded and dry may occur with resulting communities of shorter lived plants.

Racecourse and Dangars are the only lagoons where *G. australis* was absent and are consistently different to the other lagoons. These lagoons (and the Uralla area) received less rainfall preceeding the survey. They are also the most southern lagoons, are at the lowest altitude, are the only lagoons located completely on granite and are in close proximity to each other. However most of the Racecourse and Dangars quadrats grouped with quadrats from Airport, Loch Abbra and North Llangothlin lagoons. Airport is near Armidale, North Llangothlin is the northern most of the lagoons surveyed and Loch Abbra is near Guyra. All three of these lagoons occur on basalt and are not in close proximity. The only characteristic that is shared with Racecourse and Dangars lagoons is that Loch Abbra and North Llangothlin have been dammed. This suggests that damming may be responsible for some of the difference between this group and the remaining lagoons.

Damming a lagoon allows water levels to fluctuate over a greater range of depths (Figure 2.8). However, the exact effect of damming will depend on characteristics such as the catchment size of the lagoon (Chapter 2). If the catchment of a lagoon is large enough then the dammed lagoon may fill regularly. However, results from

Chapter 2 (Figure 2.8) and anecdotal evidence suggest that for most lagoons damming results in a broader range of water depths and the dammed lagoon will overflow less often (this appears to be the case for Pinch, North Llangothlin, Mother of Ducks and Racecourse lagoons). Such a change in water regime would result in only ruderal species or those with the broadest tolerance of water depth fluctuations surviving. Species with a narrow tolerance for water depths would be first affected because water levels will be less likely to be within particular ranges of depth. The clearest example of this is *C. gaudichaudiana*. This species is commonly dominant at the high water line around lagoons in the Llangothlin area. At North Llangothlin, there is a depression near the edge of the lagoon that drains a large part of the catchment where the vegetation is dominated by *H. lanatus*, *C. gaudichaudiana* and *G. australis*. However these species are uncommon in the lagoon basin. Therefore, although species rich, the transects at North Llangothlin lack vegetation zones dominated by species typical of other lagoons in the Llangothlin group. Similarly, in the deepest part of Loch Abbra Lagoon, there are species typical of deeper water such as *Eleocharis sphacelata*, but higher up the elevation gradient other vegetation zones with species assemblages typical of shallower lagoons are absent and are replaced by opportunistic species such as *Persicaria lapathifolium*, *A. avenacea* and *T. repens*.

The lack of clear separation of groups and considerable overlap that exists when the groups are plotted (Figure 3.4) suggests that the quadrats are a continuum of species assemblages rather than distinct communities. The large number of species that are uncommon (only 19 of 111 species occur in >10% of quadrats) also suggests that there is an element of chance in the species composition of a quadrat. The role of chance as a mechanism in community composition has been proposed for Fynbos in South Africa (Laurie and Cowling 1994) and for kettle-holes in Poland (Kazmierczak *et al.* 1995). Chance may be even more important in perennial communities compared to those dominated by annuals as recruitment may be a less predictable event than for environments where annuals are favoured. This may result in various species that become dominant due to a chance event and then become more established during a prolonged vegetative phase.

Several of the results suggest that the continued dominance of *G. australis* and *J. articulatus* in Mother of Ducks Lagoon Nature Reserve is unlikely. The maximum

depth within the levee is greater than other quadrats where *G. australis* and *J. articulatus* were recorded (Figure 3.3). However, the morphology of the nature reserve is unusual having steep sides and a relatively flat base. In other lagoons deeper areas are dominated by *Eleocharis sphacelata* and *M. variifolium*. The latter species is dominant at Racecourse Lagoon during wet periods when the lagoon fills. Species such as *P. tricarinatus* and *M. variifolium* were more prevalent in the nature reserve than in the west paddock and there is a large patch of *E. sphacelata* on the western side of the nature reserve. Lloyd (1992) noted this patch and a more complex mosaic of vegetation within the nature reserve two years after the levee was constructed. If the composition of the vegetation within the levee is changing, the rate has been slow since 1992. There were seven years between the levee construction and the survey, although for much of that time there was below average rainfall. The amount of time before substantial changes occur in the plant community may be considerable if change is concentrated into infrequent wet years (Mitsch and Wilson 1996).

Variation in water regime has been put forward as a hypothesis explaining the different distributions of *G. australis* and *J. articulatus*. Testing the growth of *J. articulatus* and *G. australis* in response to aspects of that variability may provide insight into whether this is the case. Also, it will be difficult to assess changes from surveys that are spaced at approximately 10 year intervals and are influenced by long term cyclic events (Lloyd 1992). Investigation of response to water regime provides an alternative approach and will aid in interpretation of such data.

Chapter 4
Individual plants - response to water regime

4.1 Introduction

The response of plants to water regime is critical to vegetation dynamics and to the success of an invasive species such as *J. articulatus*. The important components and measures of water regime used by others were reviewed in Section 1.5, however none of these used a general framework that could accommodate the variety of water regimes experienced in the New England lagoons. The next four chapters present results from experimental investigations into the growth of, and interaction between, *G. australis* and *J. articulatus* under different water regimes. This chapter, as one of several different approaches used to investigate water regime, aimed to develop an experimental method that breaks water regime down into fundamental components and tests the effect of those components on plant growth.

The aspect of water regime most commonly used to described wetlands is "permanence". However, such a simple term fails to account for other aspects of variability in water level fluctuations. Permanence is a measure of the proportion of time flooded. Other important characteristics are the upper and lower limits of water depth fluctuations, which can be described together as the amplitude of depth changes. Similarly, the number of times water levels fluctuate may be summarised as the frequency of water level fluctuations. These latter two measures include implicit assumptions. The use of frequency assumes a fixed time period during which species can grow and reproduce (in this case corresponding to the duration of the experiment).

Similarly, amplitude describes a range of depths but does not specify around what depth the fluctuations occur. In this experiment, depth fluctuates symmetrically above and below soil level as this is the range of depths where *G. australis* and *J. articulatus* commonly grow.

In the same way that water regime can be broken down to its component parts, so a similar strategy was adopted to measure plant growth. The allocation of resources to plant parts is often used for interpretation of both the evolutionary implications of different life strategies and of community dynamics and species distributions. Allocation of resources to either growth or reproduction is arguably the character of life history strategy which is of the greatest importance in determining a species ecological role (Thompson and Stewart 1981). Clonal herbaceous aquatic plants that also reproduce sexually are ideal for study as they exhibit a range of reproductive strategies (Chambers and McComb 1992; Grace 1993; Sculthorpe 1967).

The usefulness of resource allocation as a measure of variation in plant growth is evidenced by the use of resource allocation to different plant structures and functions as the basis for the development of theories of community ecology. These theories are based on trade-offs such that the allocation of resources to one functional plant part is at the expense of another functional part. For example, Smith and Hutson (1989) developed a theory of community dynamics based on a trade-off between low light tolerance and drought tolerance. Tilman (1988) developed his general theory of community structure based on the trade-off in the individual plant between structural complexity and maximum possible growth rate. In these applications, the allocation trade-offs at the individual plant level are used to predict consequences at the community and landscape scales. Similar trade-offs occur at smaller scales in aquatic communities. For example, there is evidence of a trade-off between extent of tolerance to environmental gradients and competitive ability in aquatic plant communities (Keddy 1989).

In this study differential allocation of biomass is used in a comparative study of species. Of importance in understanding community dynamics is the variation in allocation strategies in response to environmental stress (Thompson and Stewart 1981). For example, Andel and Vera (1977) showed that changes in allocation over a

stress gradient are the most striking difference between an annual and a perennial species. Of prime concern for management is the variation in allocation in response to manipulable environmental factors. Differences between coexisting perennial species, in this case *J. articulatus* and *G. australis*, over water regime gradients may contribute to understanding community assemblages of semi-aquatic plants.

The growth of plants is most commonly measured as allocation of biomass to different parts. Biomass is a good indicator of energy but not necessarily of nutrient allocation (Abrahamson and Caswell 1982; Bazzaz and Ackerly 1992; Bazzaz and Reekie 1985). The use of carbon as the currency for measuring allocation may be inappropriate for evolution and life history strategy if some other nutrient is limiting growth (Thompson and Stewart 1981; Watson 1984). Even the use of carbon or other nutrients may be an inappropriate measure as allocation to reproduction can be interpreted as being constrained by plant development (Watson 1984). However, even if this were the case there would still be a resultant difference in biomass. Therefore even though the trigger for flowering may not be understood it is possible to investigate species relationships with environmental variation. Abrahamson and Caswell (1982) point to the sacrifice of growth by many plants for the sake of reproduction as reason to accept biomass as a reasonable measure of growth until more evidence is at hand.

There have been a number of simulation studies investigating optimal allocation strategies. Under the strict assumptions about environmental variation used in these studies, the most effective strategy for perennial plants is one of repeated reproduction utilising all available resources after a certain size is attained (Cohen 1966; Cohen 1967; Cohen 1968; Pugliese and Kozlowski 1990). However, it seems likely there will be a range of strategies exhibited by species which coexist under variable water regimes. It may also be the case that variation in several environmental variables may have a synergistic effect on strategies, particularly where a complex of environmental factors such as water regime is the variable of interest. The limited amount of work that has been done on water regime and plant growth focuses on static or seasonal water level changes (Froend *et al.* 1993, Rea and Ganf, 1994c; Madsen 1991). The knowledge of which components of water regime trigger changes in allocation may

provide insight into their relative importance for plant growth and community dynamics.

For *J. articulatus* and *G. australis,* the allocation of biomass to growth or reproduction will be critical for survival under conditions of uncertainty, such as the duration of flooded or drought periods. This chapter aims to compare how individual plants of *J. articulatus* and *G. australis* allocate biomass to growth and reproduction under variable water regimes. Water regime was divided into three fundamental components that were manipulated independently of each other: the proportion of time flooded; frequency of depth fluctuations; and the amplitude of depth fluctuations. These components will probably rarely be independent in the field, but separation provides an opportunity to study effect of components individually and in combination. The components are closely related to other measures that are known to be important in other systems. For example, duration of flooding varies with the proportion of time flooded, but was not studied in this chapter as it wasn't thought to be as important as in more seasonal wetland systems. Finally, if allocation is measured under field conditions it is not possible to distinguish between genetic and environmentally induced allocation patterns. This can only be determined under controlled conditions (Thompson and Stewart 1981).

4.2 Methods

The responses of *G. australis* and *J. articulatus* to variation of three characteristics of water level fluctuations were tested: the proportion of time flooded; the frequency of flooding (the number of flood/dry events during the sixteen weeks duration of the experiment); and the amplitude of depth fluctuations (the difference between maximum and minimum water levels). Water levels in all the treatments fluctuated between two stable extremes that were an equal distance above and below the soil surface. Water level changes (by moving pots) occurred twice weekly, moving up rapidly and down more slowly to simulate the nature of water level fluctuations in the field. These characteristics were tested in three experiments (Figure 4.1, Figure 4.2):

a) The first experiment (proportion of time flooded experiment) measured the response of the plants to 7 treatments (Figure 4.1a) ranging from pots that were never flooded (soil surface 8cm above water) to pots that were constantly flooded (soil surface 8cm under water), in increments of one sixth of the proportion of time: 0 (never flooded); 1/6 total time flooded; 1/3 total time flooded; 1/2 total time flooded; 2/3 total time flooded; 5/6 total time flooded; and 1 (constantly flooded). Except for pots that were never or constantly flooded, the treatments all had a frequency of two cycles during the 16 weeks of the experiment and an amplitude of 16 cm fluctuation in depth.

b) The second experiment (frequency experiment) measured the response of the plants to combinations of frequency and proportion of time flooded treatments. The pots were flooded for 1/6, 1/2 and 5/6 of the time at frequencies of one, two and four cycles during the 16 weeks of the experiment (Figure 4.1b). All treatments had an amplitude of 16 cm.

c) The third experiment (amplitude experiment) measured the response of plants to combinations of amplitude of depth fluctuations and proportion of time flooded. Water levels fluctuated over amplitudes of 8, 16 and 32 cm and were flooded for 1/6, 1/2 and 5/6 of the time (Figure 4.1c). All treatments had a frequency of 2 cycles over the 16 week of the experiment.

All experiments were carried out concurrently. The pots were grown in 6 large outdoor tubs. Each tub was an experimental block, containing one replicate of each treatment combination (from each experiment). Each pot was suspended from a frame which allowed raising and lowering of pots individually in and out of the water (Figure 4.2). This allowed the simultaneous simulation of all water regimes treatments. *G. australis* and *J. articulatus* were collected from Mother of Ducks Nature Reserve as seedlings of approximately 10 cm height in November 1994 and were transplanted into pots of soil collected from Mother of Ducks lagoon. Each pot (1.5 litre, 200 mm diameter) was divided into two equal halves with a sheet of plastic attached to the pot base and walls. Three seedlings of *J. articulatus* were transplanted into one half and three seedlings of *G. australis* were transplanted into the other. These were thinned to one plant after the first two weeks.

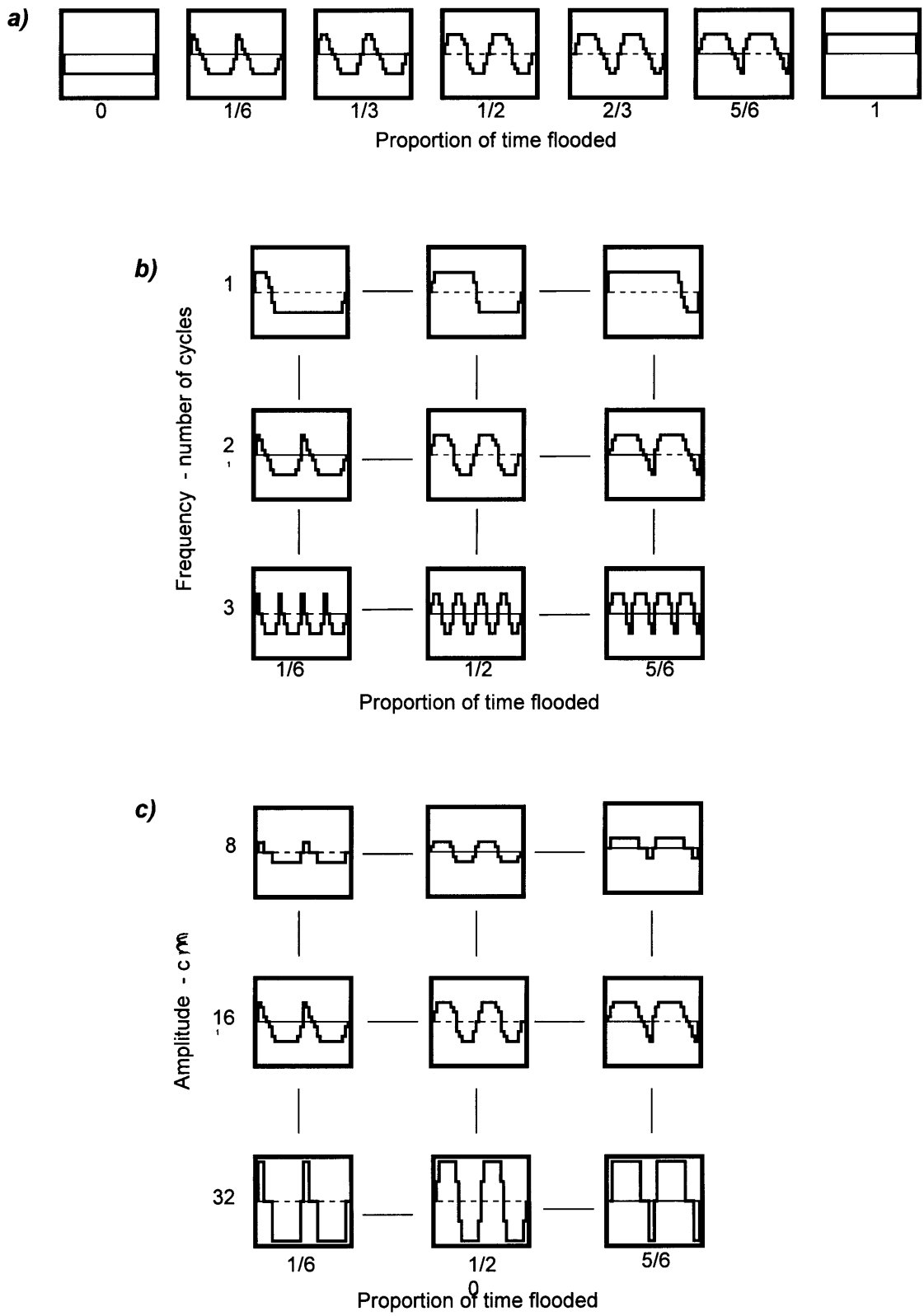


Figure 4.1. Water regimes in the three experiments testing response to variation in a) Proportion of time flooded, b) frequency of fluctuations and proportion of time flooded and c) amplitude of depth fluctuations and proportion of time flooded.

At the completion of the 16-week experiment all the pots were harvested and sorted into tillers, inflorescences, stolons or roots. All samples were dried at 80 degrees C for 48 hours and weighed. Differences in total biomass and the proportion of biomass allocated to plant parts were tested. Total biomass measures overall growth whereas allocation of biomass to parts can be used to interpret changes in growth strategy in response to aspects of water regime.

Figure 4.2 Experimental setup showing the tubs and the mechanism for suspending pots that was designed and constructed so that individual pots can be raised and lowered independently.

Differences in total biomass and proportion of biomass of each of the four plant parts were assessed in separate analyses, for each of the three experiments. Analysis was by two and three way analysis of variance and the least significant difference using NEVA (Burr 1981). Data were checked for normality and heteroscedasticity using plots of data (Green 1979). Homogeneity of variances was checked for a maximum ratio of smallest to largest according to Green (1979). Where needed data were transformed using $x = \sqrt{x}$ or $x = \ln(x+1)$ to satisfy the assumptions of analysis of variance. Where data did not satisfy the assumptions due to outliers or hetergeneity of variances, outlier values were changed and the subsequent effect on Anova and posthoc test results were assessed. In all cases the change made no difference to conclusions and so Anovas and least significant difference tests on the original data were carried out. Inflorescence data for *G. australis* were not analysed because too many pots had no inflorescences.

4.3 Results

4.3.1 Overall response

G. australis and *J. articulatus* produced significantly different biomass of (Table 4.1a - significant species main effects in all analyses), and allocated significantly different proportions of biomass to, all plant parts in response to all experimental water regime treatments (Table 4.1b - significant species main effects in all analyses). *J. articulatus* biomass production was always greater than that of *G. australis* but *G. australis* consistently had a higher root/shoot ratio than *J. articulatus*. Whole plant biomass production was not affected by frequency of flooding or proportion of time flooded treatments, but was affected by the amplitude of water level fluctuations and proportion of time flooded in combination.

Table 4.1 Analysis of variance of differences in (i) biomass and (ii) proportion of biomass in three experiments. Each experiment tested differences in allocation to roots, stolons, tillers and inflorescences between the two species (S), *J. articulatus* and *G. australis*. The first experiment (a) tested response to seven levels of proportion of time flooded (P). The second experiment (b) tested response to three levels of frequency (F) and proportion of time flooded. The third experiment (c) tested response to three levels of amplitude (A) and three levels of proportion of time flooded. Inflorescence data were analysed for *J. articulatus* only. F values are shown and significance at P < 0.05, 0.01 and 0.001 are represented as *, ** and * respectively.**

i) Biomass

Source	df	Roots	Stolons	Tillers	*J. articulatus* only df	Inflorescence
a) Proportion of time flooded experiment						
P	$F_{6,65}$	0.282 n.s.	1.063 n.s.	4.931 ***	$F_{2,30}$	1.687 n.s.
S	$F_{1,65}$	95.636 ***	127.01 ***	49.982 ***		- -
PS	$F_{6,65}$	0.514 n.s.	0.649 n.s.	2.177 n.s.		- -
b) Frequency experiment						
P	$F_{2,85}$	0.845 n.s.	5.222 n.s.	1.580 n.s.	$F_{2,40}$	0.188 n.s.
F	$F_{2,85}$	1.249 n.s.	5.260 **	1.558 n.s.	$F_{2,40}$	5.529 **
S	$F_{1,85}$	82.756 ***	102.42 ***	25.606 ***		- -
FP	$F_{4,85}$	0.497 n.s.	1.135 n.s.	0.482 n.s.	$F_{4,40}$	2.814 *
PS	$F_{2,85}$	0.107 n.s.	0.010 n.s.	2.105 n.s.		- -
SF	$F_{2,85}$	1.171 n.s.	2.665 n.s.	0.925 n.s.		- -
SFP	$F_{4,85}$	0.697 n.s.	0.834 n.s.	0.837 n.s.		- -
c) Amplitude experiment						
P	$F_{2,85}$	5.387 **	12.641 ***	11.101 ***	$F_{2,40}$	0.702 n.s.
A	$F_{2,85}$	64.862 ***	19.163 ***	7.391 **	$F_{2,40}$	12.56 ***
S	$F_{1,85}$	68.180 ***	160.63 ***	17.787 ***		- -
AP	$F_{4,85}$	4.315 **	4.223 **	5.433 ***	$F_{4,40}$	6.126 ***
PS	$F_{2,85}$	0.761 n.s.	0.059 n.s.	0.225 n.s.		- -
AS	$F_{2,85}$	10.929 ***	17.893 ***	0.424 n.s.		- -
ASP	$F_{4,85}$	1.675 n.s.	1.873 n.s.	1.800 n.s.		- -

ii) Proportion of biomass

Source	df	Roots	Stolons	Tillers	*J. articulatus* only df	Inflorescence
a) Proportion of time flooded experiment						
P	$F_{6,65}$	3.948 ***	0.564 n.s.	2.858 *	$F_{2,30}$	1.688 n.s.
S	$F_{1,65}$	20.477 ***	37.331 ***	48.521 ***		- -
PS	$F_{6,65}$	1.028 n.s.	0.807 n.s.	1.442 n.s.		- -
b) Frequency experiement						
P	$F_{2,85}$	4.067 *	0.982 n.s.	1.756 n.s.	$F_{2,40}$	0.891 n.s.
F	$F_{2,85}$	0.013 n.s.	4.672 *	7.965 ***	$F_{2,40}$	6.086 *
S	$F_{1,85}$	10.518 ***	28.247 ***	35.638 ***		- -
FP	$F_{4,85}$	0.437 n.s.	1.017 n.s.	1.124 n.s.	$F_{4,40}$	2.319 n.s.
PS	$F_{2,85}$	0.450 n.s.	0.080 n.s.	1.300 n.s.		- -
SF	$F_{2,85}$	0.491 n.s.	1.697 n.s.	4.256 *		- -
SFP	$F_{4,85}$	0.546 n.s.	0.549 n.s.	0.696 n.s.		- -
c) Amplitude experiment						
P	$F_{2,85}$	8.109 ***	7.647 ***	0.661 n.s.	$F_{2,40}$	0.252 n.s.
A	$F_{2,85}$	11.487 ***	5.085 **	49.144 ***	$F_{2,40}$	3.474 *
S	$F_{1,85}$	18.618 ***	47.933 ***	30.189 ***		- -
AP	$F_{4,85}$	3.240 *	1.746 n.s.	1.832 n.s.	$F_{4,40}$	3.580 *
PS	$F_{2,85}$	1.120 n.s.	0.284 n.s.	0.752 n.s.		- -
AS	$F_{2,85}$	0.451 n.s.	4.012 *	8.835 ***		- -
ASP	$F_{4,85}$	0.441 n.s.	1.409 n.s.	1.743 n.s.		- -

4.3.2 The effect of proportion of time flooded

The effect of proportion of time flooded (referred to hereafter as time flooded) was analysed separately and in interaction with amplitude and frequency. Overall, and in contrast to other treatments, there was no significant difference between the species responses to any of the proportion of time flooded treatments (Table 4.1, non-significant species x proportion of time flooded interaction terms in all experiments and all analyses). Time flooded did not affect the biomass of roots produced by either species, however, the proportion of biomass allocated to roots, averaged over both species, was significantly greater when the pots were never flooded (Figure 4.3c, d; Table 4.1ii(b) - significant time flooded main effect - roots).

A significantly greater biomass and proportion of biomass was allocated to tillers as the time flooded increased for *J. articulatus* but not for *G. australis*. There was no significant difference between stolon or inflorescence biomass produced under the seven time flooded treatments. However, time flooded did affect these plant parts in combination with the amplitude and frequency of water level fluctuation treatments.

4.3.3 The effect of amplitude of water level fluctuations

The amplitude of water level fluctuations (hereafter referred to as amplitude) significantly affected the biomass and the proportion of biomass allocated to all plant parts (Figure 4.4). However, the effect of amplitude on the biomass of all plant parts produced and on the proportion of biomass allocated to roots and inflorescences, was also dependent on the proportion of time flooded (Figure 4.4; Table 4.1i(c), ii(c), significant amplitude x proportion of time flooded (AP) interactions).

The strong interactive effect of amplitude and time flooded was a reduction in total biomass in the largest amplitude treatment when flooded for smaller proportions of time (i.e. longer periods of drought). This restriction of growth affected production of root and stolon biomass significantly more for *J. articulatus* than *G. australis* (Figure 4.4a, b; Table 4.1i(c) significant amplitude x species interactions). The reduction in root biomass production at the largest amplitude was significantly less for *G. australis*

than for *J. articulatus*. *G. australis* stolon production was not significantly affected by amplitude whereas *J. articulatus* stolon and inflorescence biomass was significantly less at the largest amplitude. These differences between the two species in biomass production were not the same when expressed as a proportion of biomass.

The interactive effect of time flooded and amplitude did not have as strong an effect on the proportion of biomass allocated to plant parts as on biomass production. For both species, the proportion of biomass allocated to roots was significantly less at the largest amplitude and when the proportion of time flooded was one half or greater (Figure 4.4c, d; Table 4.1ii(c) - significant time flooded x amplitude interaction).

At greater amplitudes, both species allocated significantly higher proportions of biomass to tillers. For *J. articulatus*, the proportion of biomass allocated to tillers was significantly different for all amplitude treatments whereas for *G. australis* the allocation was only significantly less at the smallest amplitude treatment (Figure 4.4c, d; Table 4.1ii(c) - significant amplitude x species interaction - tillers).

For *J. articulatus*, differences in the proportion of biomass allocated to tillers were compensated for by differences in the proportion of biomass allocated to stolons. The proportion of *J. articulatus* biomass allocated to stolon production was significantly less at the largest amplitude. In contrast, the proportion of *G. australis* biomass allocated to stolons was not significantly different between amplitude treatments (Figure 4.4, Table4.1ii(c) - significant amplitude x species interaction - stolons). Averaged over all amplitude treatments and both species, the proportion of biomass allocated to stolons was significantly less when pots were flooded for only one sixth of the time, (Figure 4.4, Table 4.1ii(c) - significant time flooded main effect).

The effect of amplitude on inflorescence production is difficult to assess for *G. australis* as many pots had no inflorescences at all and therefore data were not analysed statistically. However, there were patterns worth noting. No pots had inflorescences under the largest amplitude and greatest proportion of time flooded treatments.

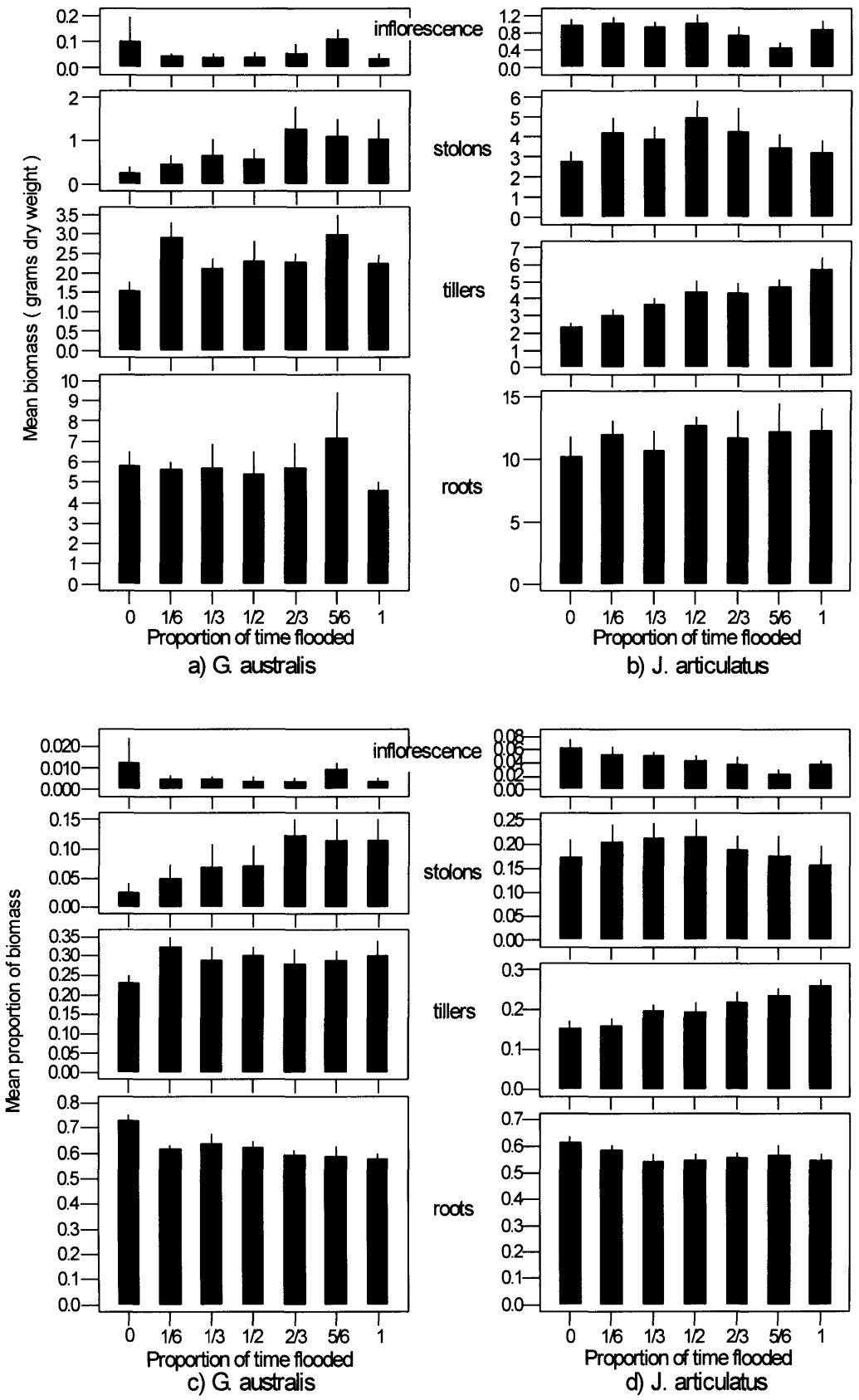


Figure 4.3 Mean biomass (a & b) and mean proportion of biomass (c & d) allocated to roots, tillers, stolons and inflorescences by *G. australis* (a & c) and *J. articulatus* (b & d) in response to seven proportion of time flooded treatments. Error bars are standard error of the mean.

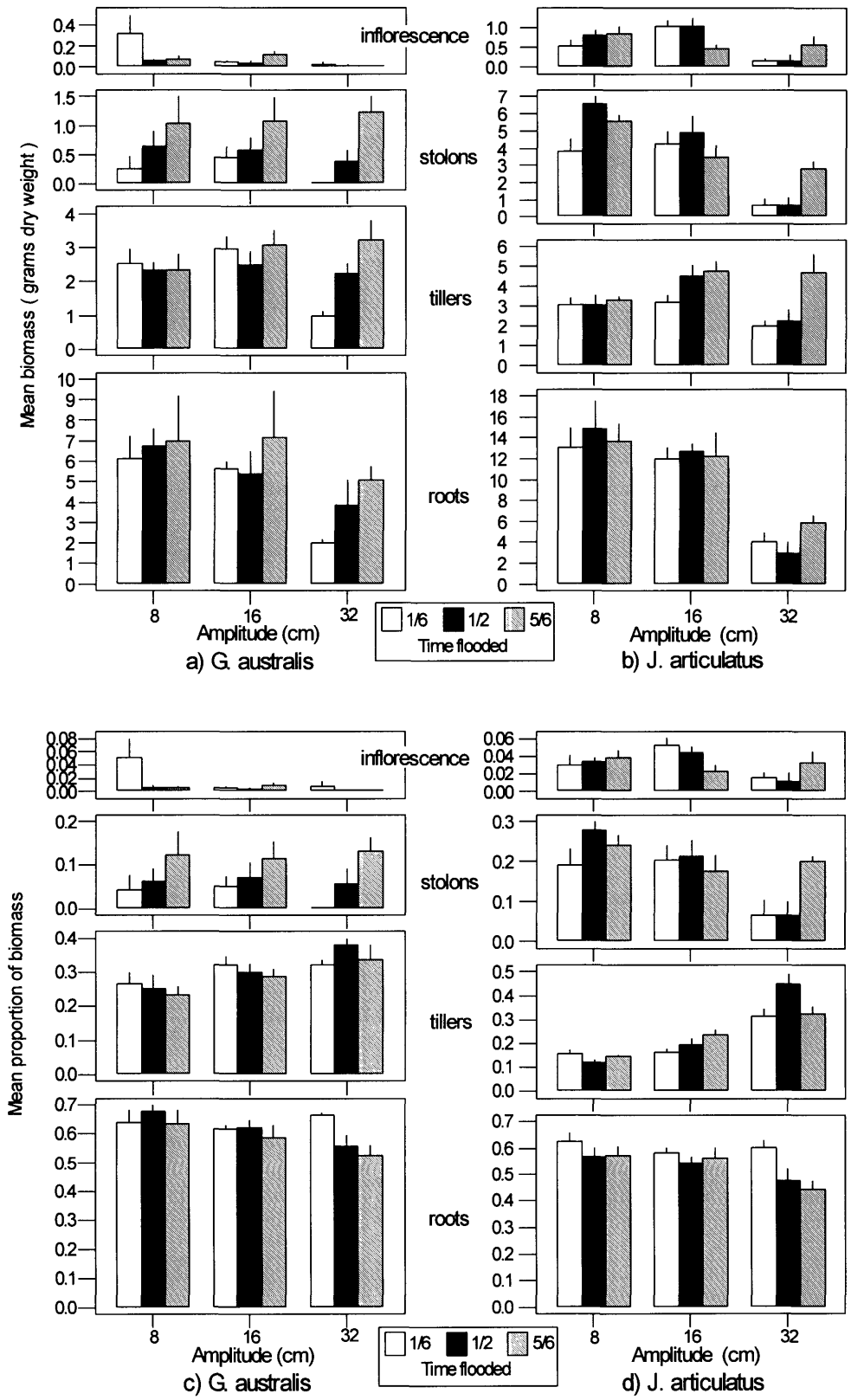


Figure 4.4 Mean biomass (a & b) and mean proportion of biomass (c & d) allocated to roots, tillers, stolons and inflorescences by *G. australis* (a & c) and *J. articulatus* (b & d) in response to three amplitude of water level fluctuation treatments and three proportion of time flooded treatments. Error bars are standard error of the mean.

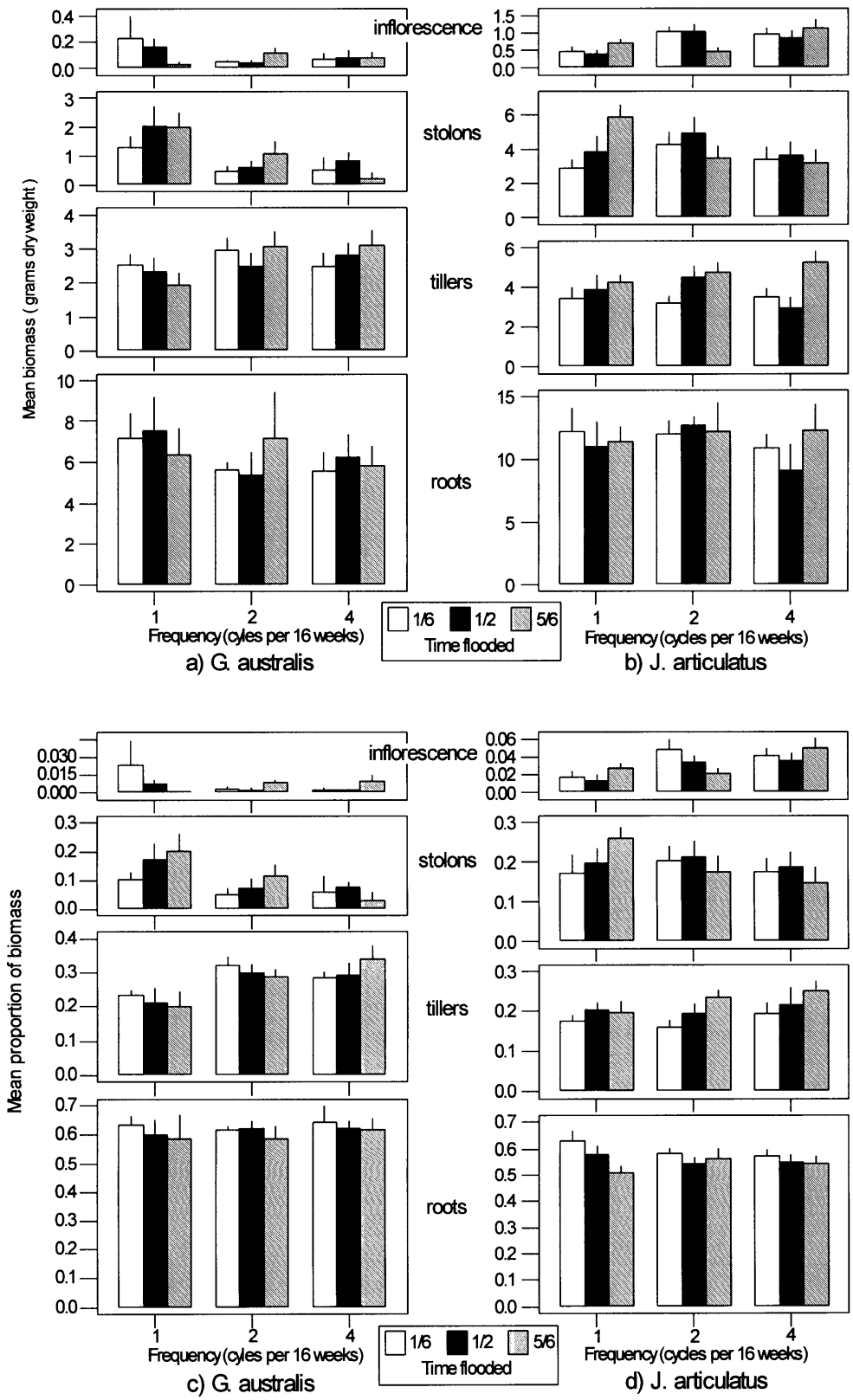


Figure 4.5 Mean biomass (a & b) and mean proportion of biomass (c & d) allocated to roots, tillers, stolons and inflorescences by *G. australis* (a & c) and *J. articulatus* (b & d) in response to three frequency of flooding treatments and three proportion of time flooded treatments. Error bars represent the standard error of the mean.

In contrast, high proportions of biomass were allocated to inflorescences in several pots in the smallest amplitude and smallest proportion of time flooded treatment combination (Figure 4.4a). The proportion of *J. articulatus* biomass allocated to inflorescences was similar to the pattern of allocation to stolons. The proportion of biomass allocated was significantly reduced by a combination of the largest amplitude and half the time flooded or less (Figure 4.4, Table 4.1ii(c) - significant amplitude x time flooded interaction).

4.3.4 The effect of frequency of flooding

Frequency of flooding had no effect on the production of root and tiller biomass or the proportion of biomass allocated to roots for either species (Table 4.1i(b), ii(b); Figure 4.5). For *J. articulatus*, the proportion of biomass allocated to tillers under all frequency of fluctuation treatments was not significantly different. However, a significantly smaller proportion of *G. australis* biomass was allocated to tillers under the lowest frequency treatment (Figure 4.5c; Table 4.1ii(b), significant frequency x species interaction).

Stolon biomass production and the proportion of biomass allocated to stolons was significantly greater under the lowest frequency treatment than under the highest, averaged over both species (Figure 4.5, Table 4.1i(b), ii(b), - significant frequency main effects). In contrast to the similar patterns of stolon production exhibited by the two species, the patterns of allocation to inflorescences of the two species appear different. Although *G. australis* inflorescence data could not be analysed, *G. australis* inflorescence production was stimulated by the long dry periods resulting from the combination of only one fluctuation of water level in 16 weeks and the low proportion of time flooded treatments (Figure 4.5a, c). In contrast, the inflorescence biomass produced was significantly less for *J. articulatus* under the combination of a frequency of one cycle and half the time flooded or less (Figure 4.5b, Table 4.1i(b) - significant frequency x time flooded interaction). Similarly, the proportion of biomass allocated to inflorescences was significantly less under a frequency of one cycle than a frequency of four cycles of flooding (Figure 4.5d, Table 4.1ii(b) - significant frequency main effect).

4.4 Discussion

The patterns of biomass allocation exhibited by both species are similar for roots and tillers but contrasted for the reproductive organs; stolons and inflorescences. The consistently higher biomass of all *J. articulatus* plant parts is consistent with a higher growth rate than *G. australis* (see Chapter 5). Both species increase tiller biomass production and the proportion of biomass allocated to tillers with increasing proportion of time flooded (average depth). Both species also allocated a greater proportion of biomass to roots when never flooded (Figure 4.3c,d) and less biomass to roots when flooded to 16cm depth for half the duration of the experiment or more (Figure 4.4). The proportion of time flooded was also important in combination with both the amplitude and frequency of fluctuations. The similarity of the responses of both species to all the proportion of time flooded treatments was evidenced by the non-significance of all proportion of time flooded x species interactions (Table 4.1). This suggests the importance of response to flooding for survival and that the effects of changes in the proportion of time flooded wont be predictable without knowledge of changes in frequency and amplitude. In many seasonal wetland systems the frequency will probably will be one, a single flood event and the amplitude may also be predictable. In the lagoons this is not often the case.

Greater allocation to above ground biomass is necessary for emergent species to keep tillers above the water surface when water levels increase (Crawford 1992). For example, Rea and Ganf (1994c) found the response to water depth increases of *Baumea arthrophylla* and *Triglochin procerum* was to increase shoot (tiller) biomass at the expense of rhizomes and tubers first, and finally roots once depth became critical. Grace (1989) found that different species achieved tillers above water level by different mechanisms, suggesting a complex of factors may be at work.

Both *G. australis* and *J. articulatus* also exhibited a reduction in growth when the pots were dry (out of water) for an extended period (Figure 4.4). However, the dry periods affected *J. articulatus* more severely than *G. australis*, suggesting that *G. australis* is more drought tolerant (see Chapter 6). The higher root/shoot ratios of *G. australis* in

comparison to *J. articulatus* also suggest that *G. australis* is adapted to dryer and/or shallower conditions. Differences between the two species in the proportion of biomass allocated to different plant parts in response to amplitude and time flooded are more strongly contrasted than differences in total biomass. In *J. articulatus*, compensation for large increases in allocation to tillers is made by reduced allocation to stolons and inflorescences, whereas for *G. australis*, allocation to tillers changes less and there is no corresponding change in stolons, but some change in allocation to inflorescence (Figure 4.4). This suggests that the strategies of the species are different, not just the degree to which they are affected.

Differences between the two species are also evident in the growth responses to the frequency of flooding. The production of root and tiller biomass was not affected by the frequency of flooding (Figure 4.5). A frequency of one cycle of water level fluctuations stimulated stolon production. For *G. australis,* the infrequent water level fluctuations stimulated both stolon and inflorescence production (Figure 4.5), whereas for *J. articulatus*, allocation to reproductive tissues was less affected. For *G. australis,* inflorescence biomass production was stimulated by a combination of infrequently fluctuating water levels and flooding for a low proportion of the time. For *J. articulatus*, inflorescence biomass production was more consistent when water levels fluctuated frequently (Figure 4.5).

For species that are commonly found growing together, it may be useful to differentiate growth responses that are common and those which are different. The growth responses that are common could provide a basis for the delineation of community types whereas those that are different enable co-existence within communities. Responses or strategies that are common to species within a community type may be essential for survival within the environment occupied by that community. Therefore we could hypothesise that all species in the lagoons which grow in similar depth ranges to *G. australis* and *J. articulatus* will exhibit similar qualitative growth responses to different proportions of time flooded. Similarly, the root/shoot ratio may be a good indicator of drought tolerance or of the range of depths optimal for a species. *G. australis* and *J. articulatus* have differential stolon and inflorescence production and allocation that may provide insights into mechanisms of co-existence.

It may be possible to manipulate species composition using knowledge of the mechanisms of coexistence. The results suggest that any manipulation of water regime aimed at manipulating species composition will need to take into account amplitude and frequency of water level fluctuations in combination with the proportion of time flooded (average depth). This is because different proportions of time flooded affects both species similarly when considered alone. In combination with amplitude and frequency of fluctuations it has a more pronounced and varied effect on growth. Such factors must also be considered in combination with other life history characteristics such as germination cues. Another important consideration is that the growth of the two species may also be affected by competition and by grazing. The next two chapters consider these aspects by examining growth under the influence of other species and other environmental stresses.