Chapter 5
Interaction between *J. articulatus* and *G. australis*

The data presented in this chapter has been published in two papers (Smith and Brock 1996; Smith and Brock in press).

5.1 Introduction

Individuals that grow together almost always interact in some way. In this study growing together for sustainable periods of time is referred to as coexistence. The interactions between coexisting species can be classified into three main types: predation, mutualism and competition. This chapter aims to investigate these three types of interactions between the dominant species that coexist at Mother of Ducks Lagoon. The most commonly encountered species at Mother of Ducks are *G. australis*, *J. articulatus* and grazing animals, be they livestock or water birds (Briggs 1976; Lloyd 1992; White 1986). The relationship between the grazers and the plants is predatory (herbivory). The interaction between *J. articulatus* and *G. australis* could be of mutual benefit or it could be competitive, however plants that are of similar size are likely to compete, given that they have similar requirements for the basic resources of light and nutrients.

The definition of competition has been controversial (Grace and Tilman 1990; Keddy 1989; Peters 1991). Here interaction and competition are defined in relation to the aims of the study. The aim of this chapter is to investigate the growth and interaction between *J. articulatus* and *G. australis*. Interaction is defined as any modification to

growth caused by the presence of the other species. If one species has a negative effect on the other then the interaction is competitive. Most important for interpreting the coexistence of *G. australis* and *J. articulatus* is any change in interaction that depends on the two major environmental gradients at Mother of Ducks Lagoon; water regime and grazing.

The importance of competition in regulating community structure and influencing species traits is evidenced by the regular reviews of the many studies into competition (Connell 1983; Goldberg and Barton 1992; Gopal and Goel 1993; Grace and Tilman 1990; Schoener 1983). Goldberg and Barton (1992) concluded that there has been insufficient work done to draw general conclusions on the role of competition in plant communities, while acknowledging that the logistics of appropriate field studies to answer questions make this situation unsurprising. For aquatic plant communities, Gopal and Goel (1993) concluded there is tentative evidence that competition is decreasingly important under more permanent and deeper water regimes. All the New England lagoons are shallow and temporary, which suggests that competition should be important.

In reviewing the role of competition in aquatic plant communities, Gopal and Goel (1993) chose to only discuss competition between similar growth forms of aquatic plants. It will probably also be more fruitful to study competition between species of similar size. Gaudet and Keddy (1988) found that biomass explained 63% of variation in competitive ability and other morphological characteristics explained most of the remainder. The interesting questions about plant community assembly are concerned with how species of increasingly similar size and growth form coexist under a range of environmental conditions and not just whether competition occurs (Goldberg and Barton 1992; Goldberg and Scheiner 1993). Understanding of the coexistence between similar species will shed light on limits to plant resource partitioning and alternate theories of community structure (Keddy 1989). The role of species traits in change in competition over gradients has been highlighted as an area for more research (Bengtsson *et al.* 1994; Goldberg 1990).

Several studies have focused on the relationship between physical factors and competition between coexisting species (Grace and Wetzel 1981; McCreary *et al.*

1983; Mesleard *et al.* 1993; Rea 1992; Zedler *et al.* 1990). If one of the species is native and one invading, this may give an indication of the limits to the range of the invading species (Mesleard *et al.* 1993; Zedler *et al.* 1990). This chapter aims to investigate the growth and interaction of *G. australis* and *J. articulatus* under different water regimes and clipping over two seasons. This will be used for interpretation of other findings on the growth and traits of *G. australis* and *J. articulatus* from other chapters.

5.2 Methods

There is considerable choice of methodology for testing questions of competition. Controlled conditions allow certainty and manipulation whereas field conditions are uncertain and manipulation may be difficult. For example, when wetlands experience drought, manipulation of density and water levels is very difficult and interference by water birds likely. The use of outdoor tubs allows accurate control of densities and water levels, while simulating some outdoor conditions.

Replacement series experiments, where plants are grown in varying ratios at only one overall density (de Wit 1960; Goldberg and Scheiner 1993), have been criticised because they do not test for density dependent responses (Connolly 1986; Inouye and Schaffer 1981). However, these criticisms appear unduly bold as there is no evidence for a qualitative change in outcome with different total densities (Cousens and O'Neill 1993). The methodology is sound for conclusions drawn with care. For example, exact measures of relative strengths of intra- and inter-specific competition can not be drawn from replacement series results because intra-specific competition is not tested. Overall density can affect the outcome of the experiment if it is too low, resulting in little or no interaction. A density should be chosen that is typical of field conditions and is therefore sufficiently high to ensure the results are relatively independent of density. Clonal species densities are unlikely to be low as the plants can quickly fill the available space.

Several factors need to be adapted for the use of replacement series with emergent macrophytes (McCreary and Carpenter 1983). When species are clonal it becomes

impossible to distinguish between individuals. Mortality can not be measured and aspects of growth other than survival must be used to measure performance. Aquatic emergent species may show plastic responses to neighbours and to changes in environmental conditions and therefore morphological responses of individuals may be better indicators of performance than biomass (McCreary and Carpenter 1983). However, over time morphological responses should translate into biomass if they confer a competitive advantage. Goldberg and Barton (1992) found only a small proportion of studies that were run for longer than one year. For clonal plants the length of the experiment is not limited by life-span and short duration studies may miss changes in interaction that may occur at later life stages or when resource levels are reduced.

The growth and sexual reproduction of *J. articulatus* and *G. australis* were measured in response to water regime, clipping and mixture. In September 1992, seedlings of the two species were transplanted from the field into Mother of Ducks Lagoon soil in 200mm diameter pots in five different mixtures (*J. articulatus: G australis* - 100%:0%, 75%:25%, 50%:50%, 25%:75%, 0%:100%) to obtain a total density of 36 seedlings per pot. This density was representative of established stands of both species at Mother of Ducks Lagoon.

Pots were suspended in twelve large outdoor tubs in a split plot design (Figure 5.1, Figure 5.2). The main plot factor (applied to tubs) was one of three water regimes; waterlogged (bottom of the pot under water), submerged (10cm water above soil surface) and fluctuating between these two relatively static levels. These water regimes were chosen to be representative of the most common range of depths for both species. The fluctuating treatment was included because stable water levels are rare in the lagoons. These levels are particularly relevant to Mother of Ducks Lagoon where past drainage of the lagoon restricted the depth and duration of flooding (Table 1.2). Water level changes in the fluctuating treatment were as follows; first submerged 24/12/92, to waterlogged 22/2/93, to submerged 13/4/93, to waterlogged 26/11/93, to submerged 15/2/94 (Table 5.1). The tubs were allocated to four blocks according to position within the experimental layout and the pots were allocated to the blocks according to the size of the seedlings, to facilitate the removal of any effects due to differences in seedling size.

In the first season, performance of both species was measured as number of tillers and maximum height of tillers measured in five places located systematically within each pot. These were measured three times: late October 1992, late December 1992, and late February, 1993 (Table 5.1). Beginning in February 1993, after the first growing season, performance was measured as above ground dry weight.

Figure 5.1 Photo of the experimental setup showing the tubs built for the experiment and pots in tubs. Water levels within each tub were maintained at one of three water levels; waterlogged (base of the pot underwater), submerged (soil surface 10 cm below water level), and fluctuating between these two relatively static levels.

In February and November 1993, half the pots (one pot of each treatment combination from each tub) were clipped 2 cm above the soil and the harvested material was sorted to species and dried for 48 hours at 80 degrees C and weighed. In late May 1994 at the conclusion of the experiment, all the pots were clipped to ground level, sorted, dried and weighed (Table 5.1).

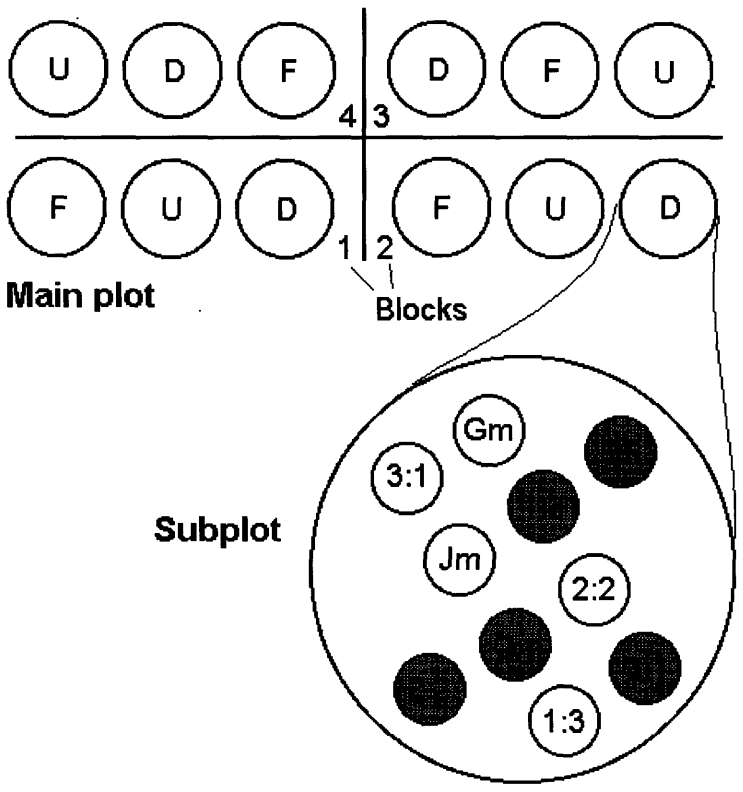


Figure 5.2 Diagram of experimental layout showing the arrangement of tubs in blocks, pots in tubs, plot levels and treatments. The water regime treatments in the tubs were either waterlogged -W, fluctuating -F or submerged -S. The mixtures treatments contained in each tub were *G. australis* monoculture - Gm, *J. articulatus* monoculture – Jm or ratios of the two species - 1:3, 2:2, 3:1 and each pot was either clipped – (shaded) or unclipped (unshaded).

Table 5.1 Experimental timetable showing dates on which tillers were counted and heights were measured (x), pots were clipped and biomass harvested (o) and the timing of water levels in the fluctuating treatment: waterlogged - solid arrows, submerged – broken arrows.

Tillers & height			X		X		X															
Clipping & harvest							O									O						O
Fluctuating treatment		◄	─	►	◄	·····	►	◄	─	►	◄	- - -	- - -	- - -	- - -	►	◄	─	►	◄	- - -	►
Date	Month	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M
	Year	92				93												94				

Five aspects of growth and interaction were examined:

1) To determine if the early growth of the two species was different, the number of tillers and the heights of the two species were compared. Interactions between time, water regime and mixture of species were analysed separately for each species.

2) The growth strategies of the two species were compared. Early growth data from the first season were related to the above ground biomass data from later scores (see below). The relationships between tiller number or height versus biomass (above ground dry weight) were analysed by regression analysis of data collected in late February 1993 (Table 5.1).

3) To assess differences in performance and allocation to sexual reproduction under the treatments, biomass production per plant at the end of year two was compared between plants clipped during the experiment (clipped treatment) against plants only clipped at the conclusion of the experiment (unclipped treatment) for each species separately.

4) To determine the nature of the interaction between the two species and how it changed over the two years, total biomass production per plant at the end of the first season (first clipping, February 1993) and second season (from the conclusion of the experiment - unclipped treatment) were compared. Interactions between water regime, year and mixture were tested by three way analysis of variance for each species separately.

5) To assess whether the interaction between the two species was mutually beneficial, competitive or neutral (no interference), the model of deWit (1960) was fitted using the maximum-likelihood estimation method of Machin and Sanderson (1977).

Differences and interactions between treatments and species were assessed using analysis of variance (Burr 1981) and the least significant difference (Steele and Torrie 1980). Normality of the data was checked using normal probability plots. Heteroscedasticity and independence of means and variances was checked using plots of cell means and variances. Biomass data were transformed ($x = \text{Ln} +1$) to satisfy

the above assumptions. *G. australis* inflorescence data were not analysed because too many pots had no inflorescences.

5.3 Results

5.3.1 The effect of water regime and mixture on tiller number and height

The number of tillers and maximum heights of *J. articulatus* and *G. australis* increased exponentially over the first 24 weeks, but differed in total height and final number of tillers (Figure 5.3 & Figure 5.4). The number of tillers of *J. articulatus* was always greater than *G. australis* (Figure 5.3c & d, Figure 5.4c & d). Water regime affected the number of tillers produced by *G. australis* but not *J. articulatus*. After 24 weeks *G. australis* had produced a significantly greater number of tillers under the waterlogged treatment (Figure 5.3d, $p<0.05$), whereas *J. articulatus* tiller number was not affected by water regime (Figure 5.3c, ANOVA: non significant water x score).

Water regime affected the mean maximum tiller heights attained by both species. After 16 weeks the height of *J. articulatus* was significantly less under the fluctuating water regime than the waterlogged or submerged regimes and after 24 weeks was significantly less under the waterlogged treatment (Figure 5.3a, $p<0.05$). After 16 weeks, *G. australis* height was significantly greater under the fluctuating regime (Figure 5.3b, $p<0.05$) and tiller number was significantly lower (Figure 5.3d, $p<0.05$). However, these differences in *G. australis'* growth were no longer evident after 24 weeks.

Mixture affected the growth of both species. For *G. australis,* the number of tillers per plant in monoculture was significantly greater than in mixtures (Figure 5.4d, ANOVA: mixture x time $p<0.001$). *J. articulatus* tiller numbers increased in all mixtures; however, the increase was significantly greater in mixtures with lower initial densities of *J. articulatus* (Figure 5.4c, ANOVA: mixture x time $p<0.001$). Therefore, the tiller number of both species was dependent on the initial density of *J. articulatus.*

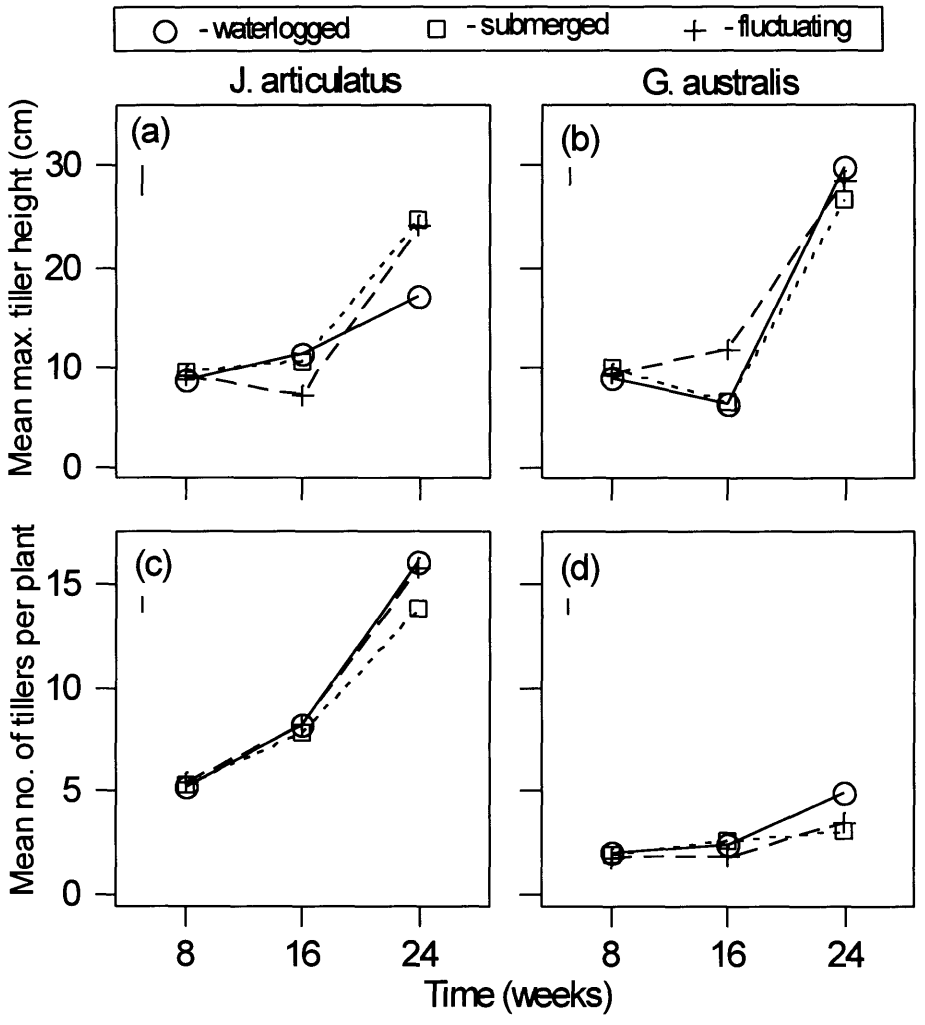


Figure 5.3 Mean maximum height (a & b) and mean number of tillers (c & d) of *J. articulatus* (a & c) and *G. australis* (b & d) after eight, sixteen and twenty four weeks of growth, under three water regimes: waterlogged, fluctuating and submerged. Bars in the top left of each figure are least significant difference for sub-plot comparisons ($p<0.05$).

Mixture affected the height of *G. australis* but not *J. articulatus*. After 24 weeks there was no significant difference in the height of *J. articulatus* plants between mixtures. After 16 weeks, *G. australis* plants growing in monoculture were significantly taller ($p<0.05$) and height decreased with initial density (Figure 5.4b, ANOVA: mixture x time $p<0.001$).

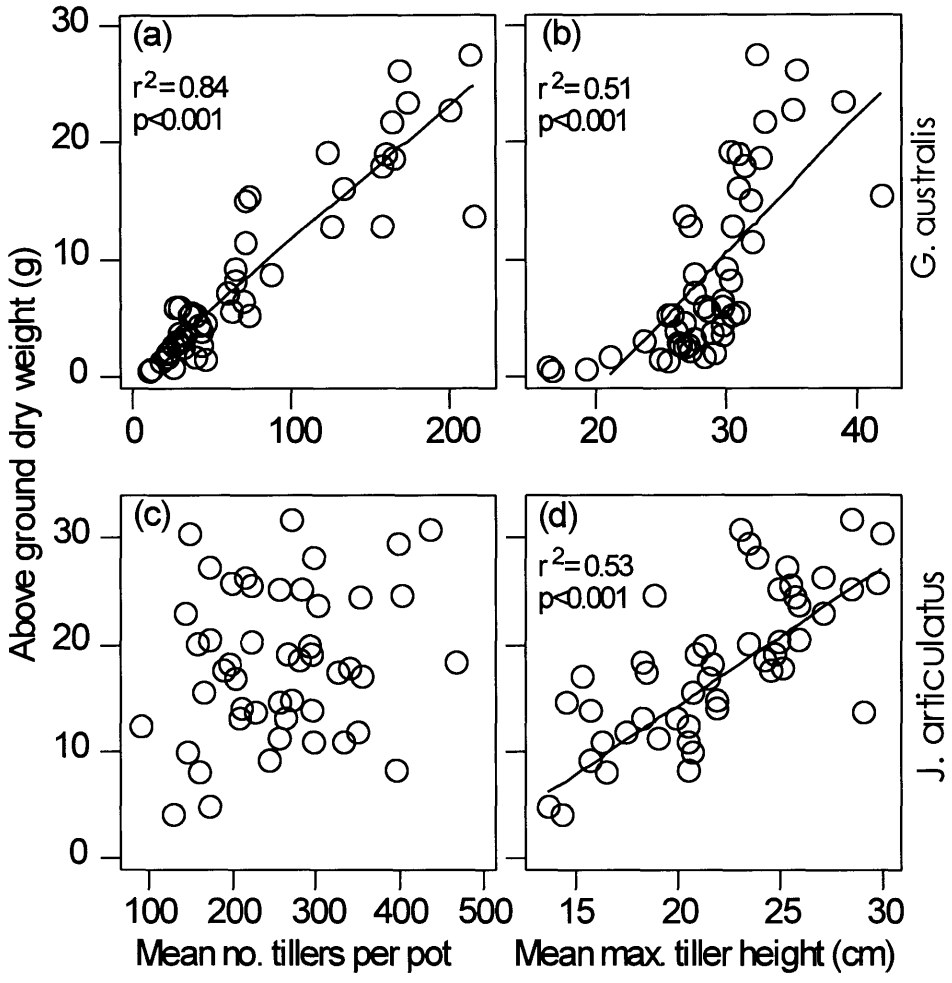


Figure 5.5 Number of tillers (a & c) and height (b & d) plotted against total dry weight per pot of *G. australis* (a & b) and *J. articulatus* (c & d). Significant regression lines are shown with probability and r squared values.

5.3.2 The effect of clipping, water regime and mixture on growth and reproduction

The above ground biomass of both species was greater when clipped (Figure 5.6). *J. articulatus* only produced significantly greater biomass when clipped at low initial densities (Figure 5.6a, ANOVA: mixture x clipping $p<0.05$). *G. australis* produced significantly greater biomass when clipped in monoculture (Figure 5.6b, ANOVA: mixture x clipping $p<0.05$).

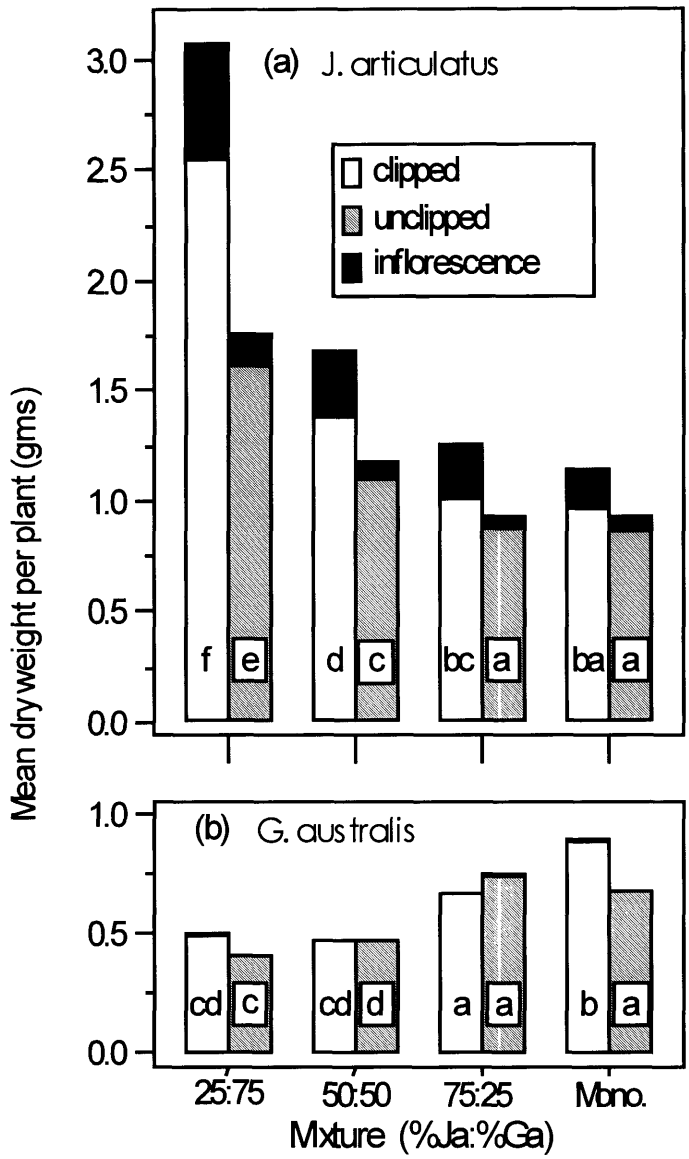


Figure 5.6 Mean dry weight per plant of (a) *J. articulatus* and (b) *G. australis* in four mixtures when clipped (clear) or unclipped (hatched). Inflorescence biomass is shown at the top of each bar (black). The same letter indicates vegetative biomass means that are not significantly different ($p<0.05$). Differences between inflorescence means are not shown as *G. australis* inflorescence data were not analysed and for *J. articulatus* the mixture x clipping interaction term was not significant.

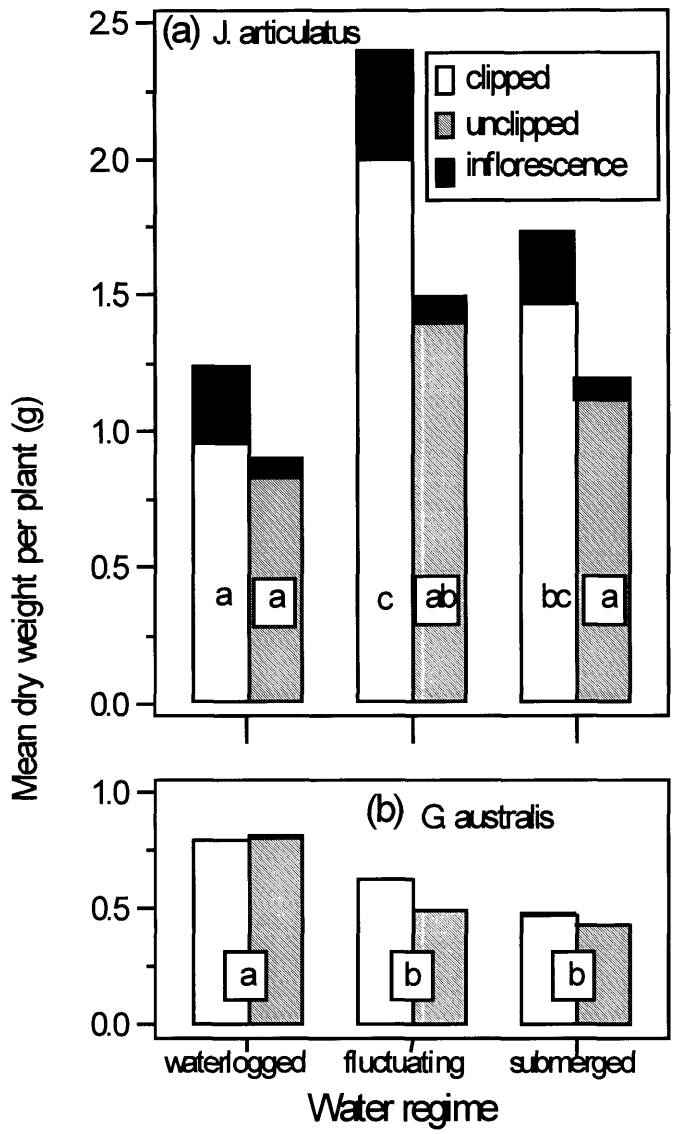


Figure 5.7 Mean dry weight per plant of a) *J. articulatus* and b) *G. australis* under three water regimes when clipped (clear) or unclipped (hatched). Inflorescence biomass is shown at the top of each bar (black). The same letter indicates vegetative biomass means that are not significantly different ($p<0.05$). Differences between individual inflorescence means are not shown as *G. australis* inflorescence data were not analysed and for *J. articulatus* the mixture x clipping interaction term was not significant.

Clipping and mixture affected the reproductive effort of *J. articulatus* plants but water regime did not. *J. articulatus* produced a significantly greater amount of inflorescence biomass when clipped (Figure 5.6a Figure 5.7a, ANOVA: clipping main effect $p<0.001$) and at lower initial densities (Figure 5.6a, ANOVA: mixture main effect $p<0.001$); however, inflorescence biomass was not significantly different between water regime treatments.

The lack of any significant difference in allocation to inflorescence biomass under all water regimes contrasts with the variation in vegetative biomass, which was significantly greater when clipped under the fluctuating and submerged water regimes (Figure 5.7a, ANOVA: water x clipping $p<0.01$). In contrast to *J. articulatus*, *G. australis* allocated a very small proportion of above ground biomass to sexual reproduction and many pots had no inflorescences. (Figure 5.6b, Figure 5.7b).

When the total biomass production of both species after one and two years was compared, the two species responded differently to water regime. *J. articulatus* production was always greatest under the fluctuating regime, least under the damp regime and intermediate under the flooded. The production of *G. australis* was always greatest under the damp regime, least under the flooded regime and intermediate under the fluctuating regime, except in monoculture in the first year. The production of *J. articulatus* in monoculture was significantly greater under the fluctuating and flooded treatments than under the damp at the end of the first year ($P<0.05$), but by the end of the second year was not significantly different between water regimes (Figure 5.8, ANOVA water x year interaction $p< 0.01$). For *G. australis,* after two years production had increased significantly over all water regimes (Figure 5.8 ANOVA ns water x year interaction).

At the end of the first year *J. articulatus* production per plant was less at higher densities of *J. articulatus*. After two years, this trend had weakened, and was not the case for the two highest densities. After one year, *G. australis* production per plant decreased with decreasing *G. australis* density, that is, decreased with increasing *J. articulatus* density under the fluctuating and flooded regimes (Figure 5.8).

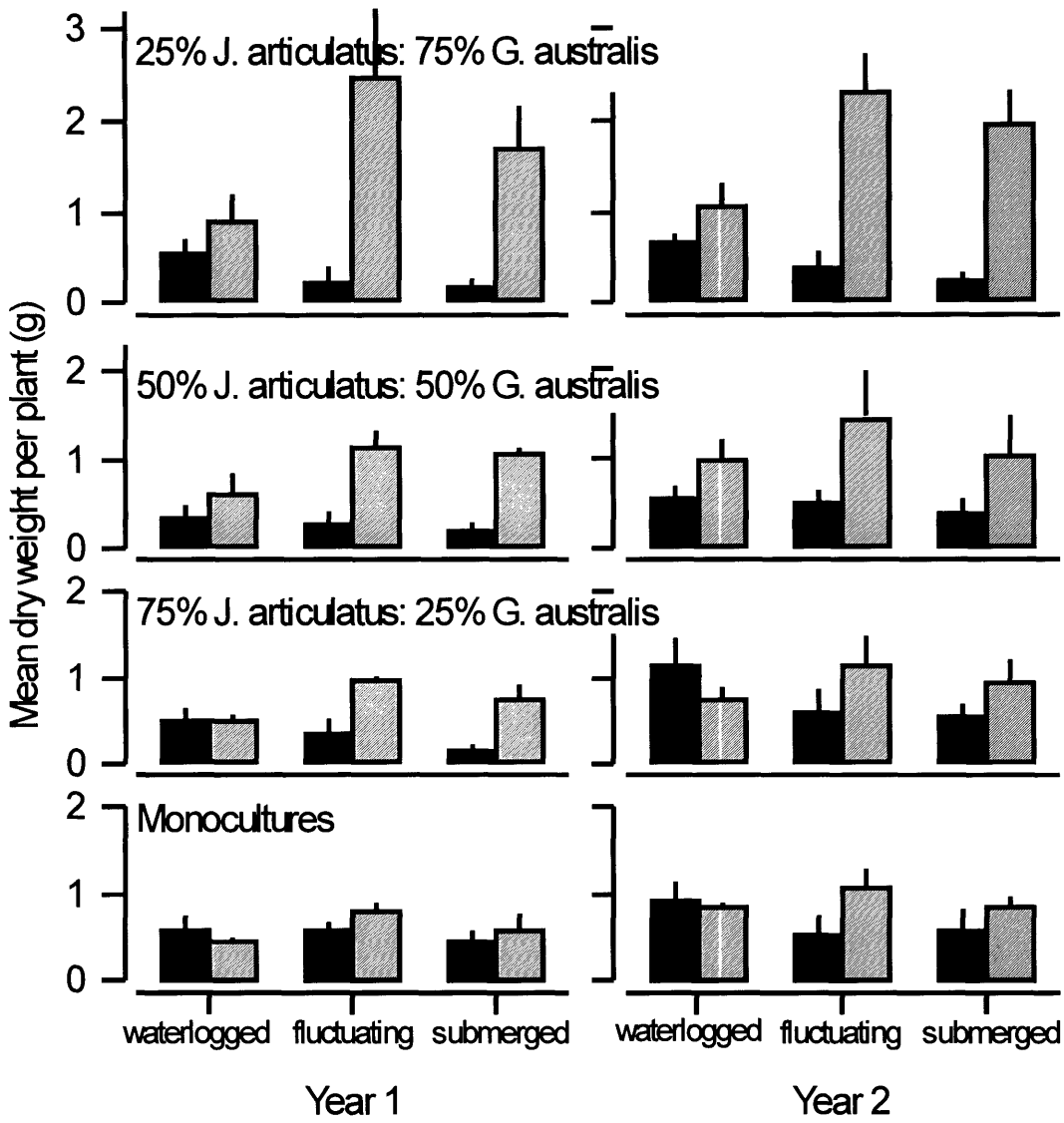


Figure 5.8 Dry weight per plant (+ se) of *J. articulatus* (unshaded) and *G. australis* (shaded) grown for two years under three water regimes in three mixtures and in monoculture.

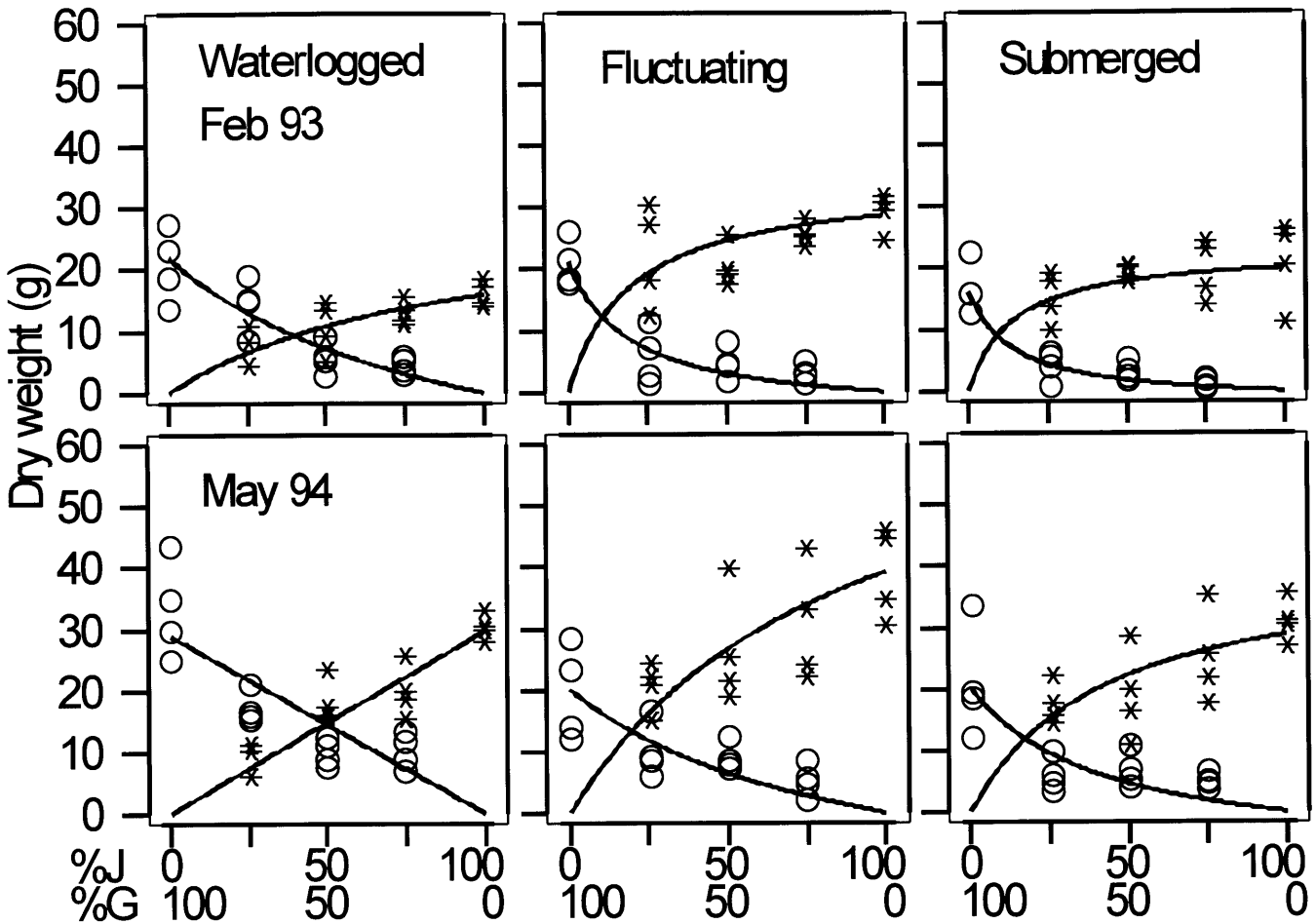


Figure 5.9 The model of deWit (1960) fitted to dry weight data for three water regimes and two years using the maximum likelihood estimation method of Machin and Sanderson, (1977). *J. articulatus* - J. & star, *G. australis* - G & circle.

During the second growing season this trend reversed. For both species, the difference in production between year 2 and year 1 was greater with decreasing *G. australis* density (ANOVA, year x mixture interactions *G. australis* - $p<0.01$, *J. articulatus* - $p<0.05$). The production of *G. australis* at the end of the second growing season was less at increasing densities of *G. australis* in mixture, but production was still less in mixture than in monoculture (Figure 5.8).

Water regime affected the competitive outcome. The greater production of *J. articulatus* at its lowest density did not occur under the damp regime. Correspondingly, the production of *G. australis* under the damp regime at the lowest density of *J. articulatus* was greater (Figure 5.8, ANOVA significant mixture x water interactions *G. australis* $p<0.01$ *J. articulatus* $p<0.05$).

The interaction of *G. australis* and *J. articulatus* in mixture and in monoculture under different water regimes is presented in Figure 5.9. The model of de Wit (1960) has been fitted to the above ground production data. The estimated parameters of the de Wit model describe interference of *G. australis* by *J. articulatus* for all treatments in the first year and for the fluctuating and flooded regimes after the second year. The reciprocal curvature of the two lines indicates interference of one species by the other. The downwards curvature indicates interference to growth. Under the damp regime after the second year the parameters describe mutual interference of equal magnitude (Figure 5.9).

5.4 Discussion

Competition between the two species varied with water regime. The decreased production of *G. australis* per plant in mixture and the corresponding increase in production of *J. articulatus* per plant, under the fluctuating and flooded regimes in both years and the damp regime in the first year, (Figure 5.8 & Figure 5.9) indicates competition (as defined by Golberg and Barton (1992), and described by Harper, (1977)). The model of de Wit (1960) shows the relative intensity of the interaction (Figure 5.9). The influence of *J. articulatus* on *G. australis* is strongest under the

flooded regime, even though the production of *J. articulatus* is greatest under the fluctuating regime. The competitive advantage of *J. articulatus* disappears during the second year. The effect of *G. australis* on individuals of the same species is greater than the effect of *J. articulatus* on *G. australis*. By the end of two years *G. australis* production in the lowest density mixture has caught up to the production in monoculture (Figure 5.8).

A change in competitive outcome could occur where one of the two species (*J. articulatus*) has greater ability to deplete resource levels and the other species (*G. australis*) is better able to tolerate the low levels (Goldberg 1990). After resource levels are depleted the tolerant species will have an advantage. In such a situation allocation of energy to high seed production would be an advantage or even essential for the species less tolerant of low resource levels. If this species was excluded (see Chapter 6) it could have the potential to regenerate from seed at the next germination event (Chapter 7). *J. articulatus* exhibits high biomass allocation to inflorescence and therefore seed production (Figure 5.6 & Figure 5.7).

J. articulatus has other traits that are consistent with a species reliant on seed production. *J. articulatus*' biomass was correlated with height (Figure 5.5) but not tiller number at all stages of growth. Such a growth pattern sacrifices height in early growth for the sake of tiller number. That is, there is a tradeoff between height and tiller number such that if *J. articulatus* didn't produce greater tiller numbers resources would be available for increased height growth of fewer tillers. While this could be competitively disadvantageous it avoids any limitation to seed production caused by insufficient tiller numbers (Watson, 1984). It would be disadvantageous when water level fluctuations are rapid during the early stages of growth as plants would be more likely to be 'drowned'. *J. articulatus* also maintains constant biomass allocation to inflorescences despite differences in biomass caused by water regime (Figure 5.7)(see Chapter 4). In contrast, *G. australis* biomass is highly correlated with numbers of tillers that are of similar height (Figure 5.5). In this respect the growth of *G. australis* is less varied, although it is more responsive to changes in water levels (Figure 5.3). *G. australis* appeared to favour sexual reproduction in the water regimes under which it was least productive (Figure 5.7), whereas there is some evidence that *J. articulatus* reproduction and growth was inhibited at the lowest initial density under the least

favourable damp water regime (Smith and Brock 1996). *J. articulatus* also responds more to clipping than *G. australis* (Figure 5.6, Figure 5.7), both in increased tiller and inflorescence biomass. This would confer a competitive advantage for *J. articulatus* under grazing pressure and implies that the advantage that *J. articulatus* had over *G. australis* maybe even greater under grazing pressure.

A change in competitive outcome after two years has important implications for community dynamics. Short term studies which are completed within one season may need reevaluation if they involve perennial species in environments that do not preclude life-spans greater than the duration of the study. Longer time frames also give rise to greater fluctuations in both environment and populations (Pimm and Redfearn 1988). Greater fluctuations can increase the possibilities for co-existence.

The information presented in this and the previous chapter has come from pot experiments in outdoor tubs. While this information provides a detailed picture of many aspects of the growth and interaction of *G. australis* and *J. articulatus*, it needs to be interpreted in the light of community data from the field.

Chapter 6
Community response to water regime in the field

6.1 Introduction

The highly variable nature of water regime in the New England lagoons results from water levels varying through time in an unpredictable way as well as across elevation gradients (Section 1.5, Chapter 2). The combination of these two major dimensions of water regime with biotic interactions within a community makes interpretation of changes in community composition difficult. Understanding the community response to the complex of factors by field observation will be greatly enhanced if the factors can be treated separately. The aim of this chapter is to assess the growth and response of a plant community dominated by *J. articulatus* and *G. australis* to changing water levels over time in the field by using a manipulative field experiment.

The successful use of field experimentation provides the strongest evidence for inference and therefore prediction in ecology (Diamond 1986; Gurevitch and Collins 1994). The catch is in using field experiments successfully. Field situations are difficult to control and results can be difficult to interpret. A serious limitation is that spatial variation can be great, correlated with scale and can confound treatment effects. Methods for handling such variation are not yet widely used (Legendre 1993). However, compared to monitoring plots, experiments at a small scale provide extra information that may be used in the interpretation of community dynamics in response to environmental variation.

This chapter reports a manipulative field experiment that was designed to separate the effects of temporal and spatial variation in water depth changes on the plant community. The experiment combined the monitoring of permanent quadrats (Austin 1981) with a manipulation of lagoon bed height to determine changes in the plant community determined by water levels. The technique separates the effect of spatial variation from temporal changes by manipulating vegetation communities that are in close proximity. Therefore as water levels fluctuate, community and species responses in quadrats of varying height were compared.

6.2 Methods

A site at Mother of Ducks Lagoon Nature Reserve was selected for its relatively even proportions of *J. articulatus* and *G. australis* as dominants in the vegetation and for its accessibility. Thirty quadrats (0.5 m x 0.5 m) were selected at random within a 60 m x 30 m area and marked with pegs 0.5 m from the quadrat corners (to minimise bird disturbance). In early spring, on 8th September 1993, the vegetation in each quadrat was recorded and, using a spade, cuts were made around 0.6 m by 0.6 m blocks of lagoon bed containing each quadrat to a depth of approximately 0.45 m. On 1st October, the blocks of lagoon bed were subjected to one of five randomly assigned treatments: raised 15 cm, raised 7.5 cm, replaced at the same level, lowered 7.5 cm or lowered 15 cm (Figure 6.1). The treatment heights were somewhat constrained by the physical possibilities of moving blocks of earth by hand, however the magnitude of height differences that was used was considered adequate as 30cm can result in very different communities across elevation gradients. Height changes were made by removing a measured volume of soil from below a quadrat block to be lowered and packing that soil under a quadrat block to be raised. Double the quantity of soil was removed and replaced for the lowered and raised 15 cm treatments as for the 7.5 cm treatments.

Vegetation in the quadrats and the water level were measured at intervals ranging from 2 to 15 weeks until January 1995. Measurements were made every 2-3 weeks until February, 1994 and then every 12 to 15 weeks until January, 1995 (Figure 6.3).

The vegetation in quadrats was described using two measures of species abundance. For each species percentage cover/ abundance was estimated visually (Table 6.1) and presence or absence was recorded in each of 25 sub-quadrats (0.1 m by 0.1 m) within each quadrat to give a frequency score from 0 to 25. The frequency score and the midpoint of the cover/ abundance class (Table 6.1) of each species in each quadrat on each date were combined into an importance value that was calculated as follows:

$$IV = Ci/(\Sigma C) + Fi/(\Sigma F) \qquad (1)$$

Ci and Fi are the cover/abundance classes and frequency scores for species i and ΣF and ΣC are the sums for all species in the quadrat.

Figure 6.1 Photograph showing two blocks of lagoon bed at Mother of Ducks Lagoon shortly after treatment, one raised 15 cm (background) and one lowered 15 cm treatment (foreground).

Importance values that combine cover/abundance and frequency were used because cover/abundance classes were found to be imprecise at the lower end of the scale (< 20 %, Table 6.1 - classes 2 & 3). In contrast, frequency scores are imprecise at the higher end of the scale. To test the method for the range of growth forms found in the lagoons, the frequency and cover/abundance values of six species were compared for two dates in spring and summer, October 1993 and February 1994 (Figure 6.3, dates 1 and 8). The species were *G. australis, J. articulatus, P. tricarinatus, M. variifolium, E. acuta* and *A. avenacea*. *G. australis* and *J. articulatus* are semi-aquatic species that reproduce by rhizomes. *P. tricarinatus* has floating leaves of variable form. *M. variifolium* has elongated stems with highly variable leaf form. *E. acuta* has rigid upright culms and elongated rhizomes and *A. avenacea* is a bunch forming grass.

Table 6.1 Cover abundance classes used for scoring species abundance. The midpoint was used for calculation of an importance value that combines frequency and cover abundance scores.

Class	Abundance / cover	Midpoint - %
0	Not present	0
1	only 1 or 2 small specimens	1
2	<5% several small specimens	3
3	5-19%	13
4	20-39%	30
5	40-59%	50
6	60-79%	70
7	80-100%	90

Patterns of change in community composition were assessed by multivariate methods using PATN (Belbin 1993). Changes in compositional similarity between quadrats due to treatments were assessed by ordination of the data using the modules ASO to calculate the Bray-Curtis dissimilarity and SSH, to perform semi-strong hybrid multidimensional scaling using default options and increasing the number of dimensions until an acceptable stress value was obtained (<0.15) (Belbin 1993). The significance of differences in community composition between dates and treatments were tested using the ANOSIM module in PRIMER (Carr 1996). The mean importance value of the six species (see above) for each treatment was plotted against date and water level fluctuation. Differences in individual species values were not

tested statistically because the confounding factors of initial abundance and multiple interacting species make interpretation difficult.

6.3 Results

6.3.1 Species frequency and cover class scores

A comparison of frequency values and cover/ abundance classes from all quadrats in spring and summer showed similar distributions of frequency values in each of the cover/ abundance classes for all species except *G. australis* in spring (Figure 6.2). The spring data showed a range of frequency values for each of the cover/ abundance classes 1, 2, 3 and 4. The summer data showed a range of frequency values for cover/ abundance classes 2 and 3. For cover/ abundance class 4 in summer all frequency values were at or near the maximum possible 25. The summer data showed similar patterns for the six species with the greatest range of frequencies being in cover class 2 and, to a lesser extent, cover class 3 (Table 6.1). The spring frequency values are spread across the full range of cover/abundance values. For example, for *J. articulatus* cover/abundance classes from 1 to 4 exhibit a range of frequency scores but in summer only cover/abundance class 3 had any spread in frequency (Figure 6.2a, b). For *M. variifolium* (Figure 6.2g, h) and *P. tricarinatus* (Figure 6.2g, h) that have floating leaves and stems, there are a range of frequency values in cover/abundance classes 2 and 3 for both species in spring and summer. For the more compact upright growing species *A. avenacea* (Figure 6.2c, d) and *E. acuta* (Figure 6.2i, j), spring frequency values are more restricted in range within cover/ abundance classes, but by summer the pattern is similar to other species. In contrast to all these species, the spring frequency values for *G. australis* showed no correlation for the cover/abundance classes 2, 3 and 4 (Figure 6.2e). However, by summer the pattern for *G. australis* was similar to all the species described above (Figure 6.2f).

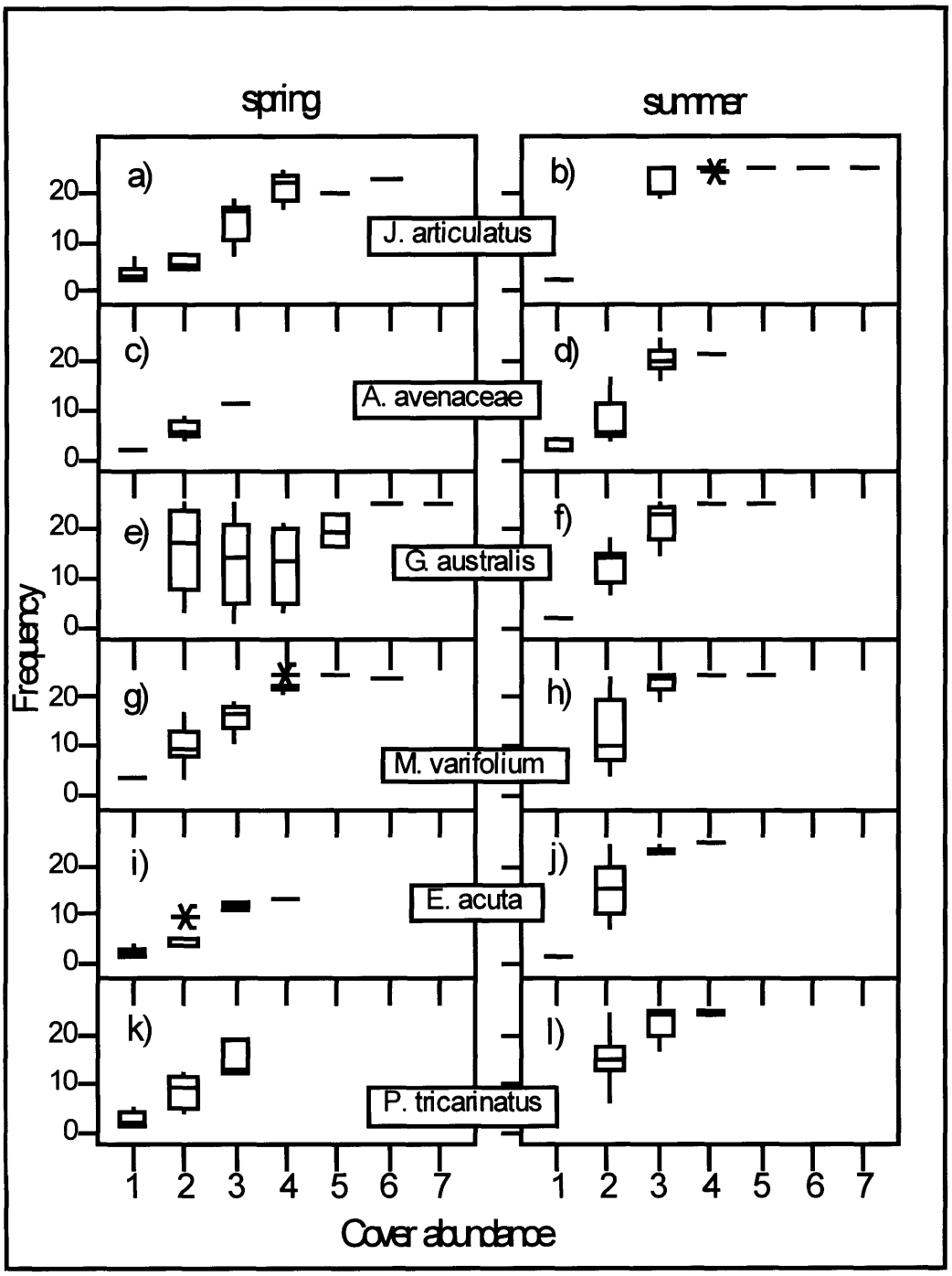


Figure 6.2 Boxplots of frequency values in the seven cover/abundance classes for six species of varying growth form measured in spring 1993 and summer 1994. Box plots represent median, interquartile ranges (* = outlier).

6.3.2 Community responses to water level treatments

The water levels in Mother of Ducks Lagoon during the course of the experiment fluctuated above soil level during the 1993/4 summer (Figure 6.3), but exceeded the highest treatment only once for a short period and then began a decline until the lowest level approximately 0.25m below the lagoon bed in winter 1994. Water levels returned to near the lagoon bed level by summer 1995. Note that the lines between the dates in Figure 6.3 are interpolated and so exact changes could be slightly more variable.

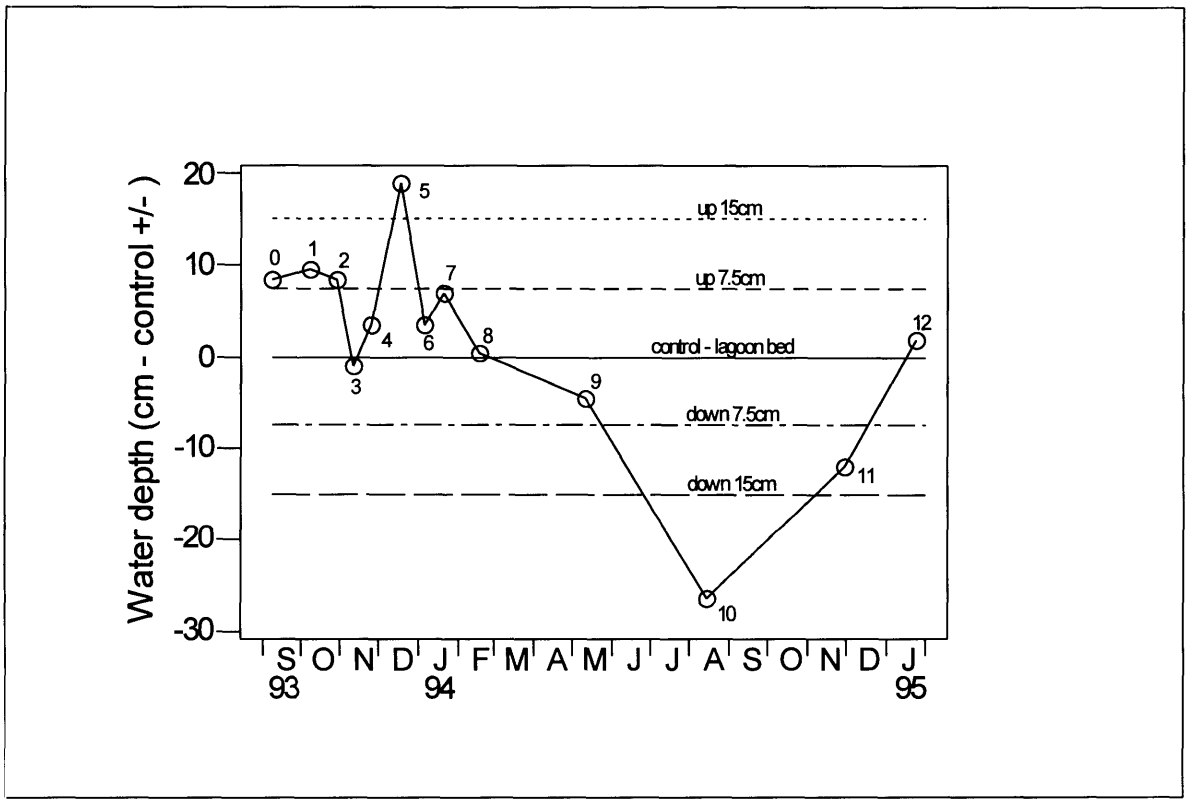


Figure 6.3 Water levels during the course of the experiment with the lagoon bed (0 cm depth) and level of the five treatments shown. The numbered points represent dates on which measurements were made.

The ordination of quadrats based on compositional similarity revealed a similarity within treatments during summer 1993/4, especially the lowest and highest treatments located at the bottom right and top centre of the plot respectively (Figure 6.4). However, quadrat composition after May 1994 (dates 10, 11 and 12) showed a stronger similarity than that based on treatments the summer before. This is represented on the ordination plot by points representing all treatments on dates 10, 11, and 12 being on the left of the plot. In the ANOSIM analysis of dates 0, 4, 8 and 12, only date 12 was significantly different, averaged over all treatments (P = 0, permutations = 5000).

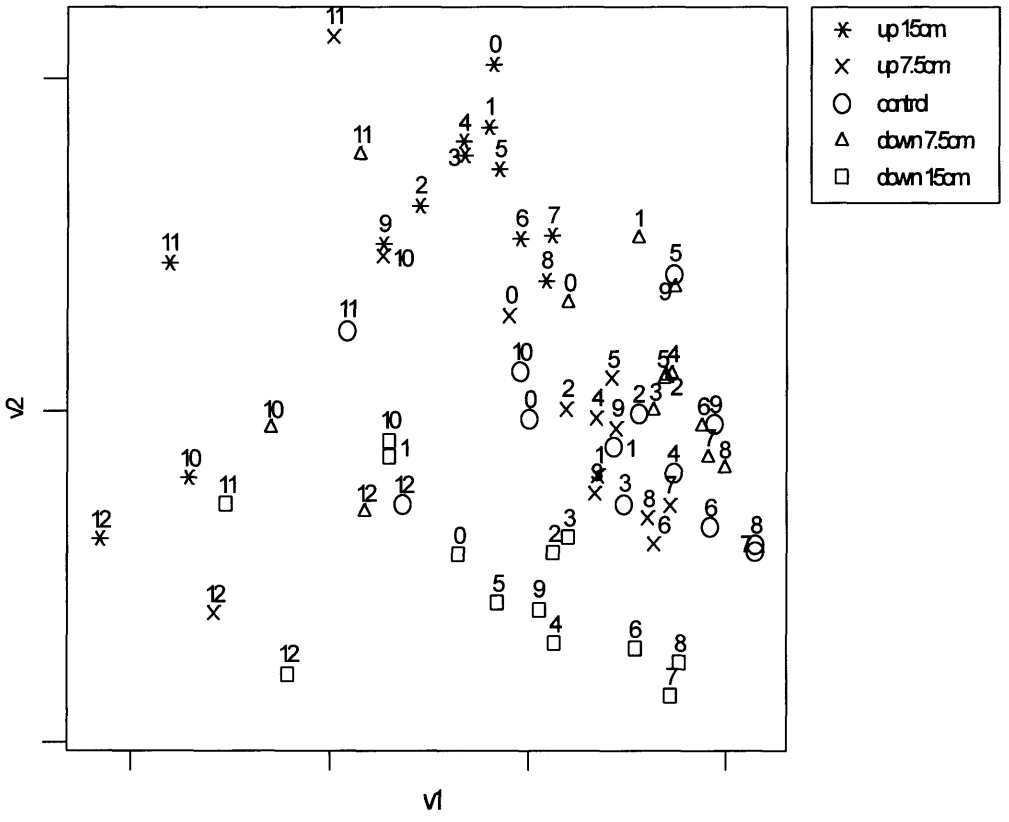


Figure 6.4 Ordination diagram on the first two SSH axes (v1 & v2). The points are means of the SSH coordinates for the six quadrats of each treatment on each date. Symbol type shows the treatment and numeric labels indicate sequential dates (see Figure 6.3). More similar points are closer together on the plot. Note the dominant pattern is a similarity within treatments during Summer 1993/4 (until approximately date 10), especially the lowest and highest treatments located at the bottom right and top centre of the plot respectively. After May, 1994, (dates 10, 11 and 12) there is major change in composition in all quadrats across all treatments (located to the left of the plot).

Pairwise comparisons between treatments on seven dates showed differences between treatments were variable. After 3 months (by December 1993), significant differences ($p<1\%$) emerged between quadrats that were at least 15 cm apart (Table 6.2). In December 1993, the lowered 15 cm treatment was significantly different from all other treatments except the lowered 7.5 cm treatment. However, by February 1994 these differences had weakened. By January 1995, the highest treatment was significantly different from the three lowest treatments and close to significantly different from the other raised treatment. Quadrats subjected to the dry conditions of the highest raised treatment (+15cm) were significantly different from other quadrats more often than other treatments. Overall, the greater the difference in height between quadrats, the more likely it was that significant differences in composition would emerge.

Table 6.2 Significance values (percentages) for pairwaise comparisons of treatments for seven dates. The values are the percentage of random allocations of quadrats into groups (/5000) that exhibit greater within group similarity than the treatment groups. Consistent differences are apparent between treatments that are at least 15cm apart by December 93. Quadrats were most affected by the dry conditions of the highest treatment which was more often significantly different to all other treatments, especially in January 1995.

Treatment pair Compared		0 Sep, 93	1 Oct 93	2 Nov 93	3 Nov 93	4 Dec 93	8 Feb 94	12 Jan 95
+15 cm	+7.5cm	47.20	31.20	36.10	44.40	12.30	30.70	6.90
"	0 cm	74.90	38.70	5.00	3.90	0.20	1.70	0.40
"	- 7.5 cm	28.60	52.60	20.60	17.30	12.60	15.40	0.20
"	- 15 cm	27.70	3.20	12.30	8.20	0.90	0.60	0.20
+ 7.5 cm	0 cm	94.60	37.00	41.10	53.20	11.30	4.50	6.70
"	- 7.5 cm	95.90	90.90	92.20	90.30	81.80	74.70	29.90
"	- 15 cm	98.90	76.00	39.80	34.40	0.40	4.80	24.70
0 cm	- 7.5 cm	68.80	81.20	34.20	49.10	67.50	31.00	75.10
"	- 15 cm	78.80	6.30	3.90	15.20	0.90	4.80	37.70
-7.5 cm	- 15 cm	56.30	42.00	35.10	49.60	11.70	66.00	39.00

6.3.3 Individual species patterns

Examination of individual species patterns shows the species responsible for the change in community composition and the response to water regime of those species. This major change was due partly to changes in abundance of species such as the disappearance of *A. avenacea* and *I. fluitans*. However, it was strongly influenced by

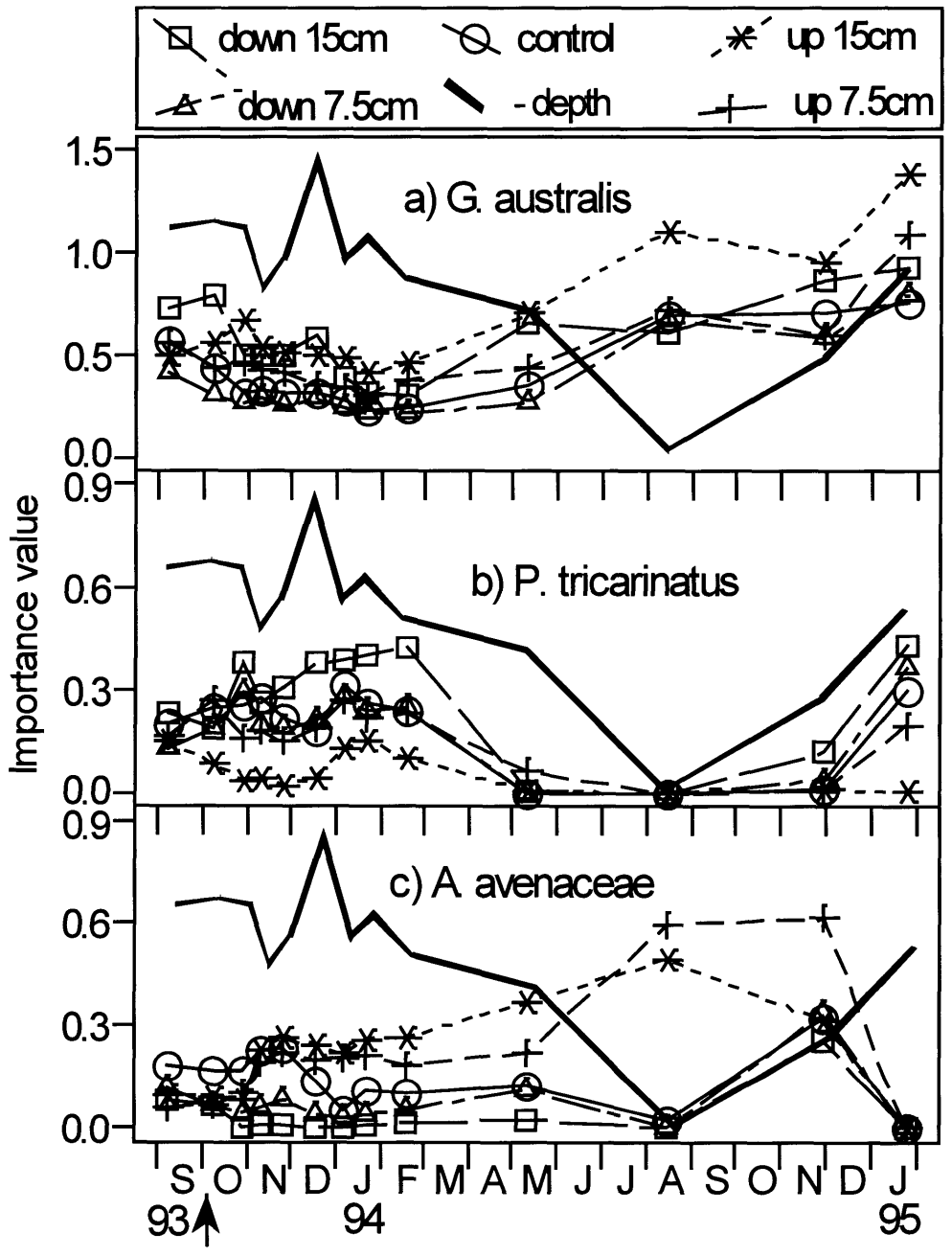


Figure 6.5 Mean importance values for a) *G. australis*, b) *P. tricarinatus* and c) *A. avenacea* for each of the five treatments. The water level fluctuations from Figure 6.3 are overlaid on each graph. The arrow indicates the date when treatments were imposed.

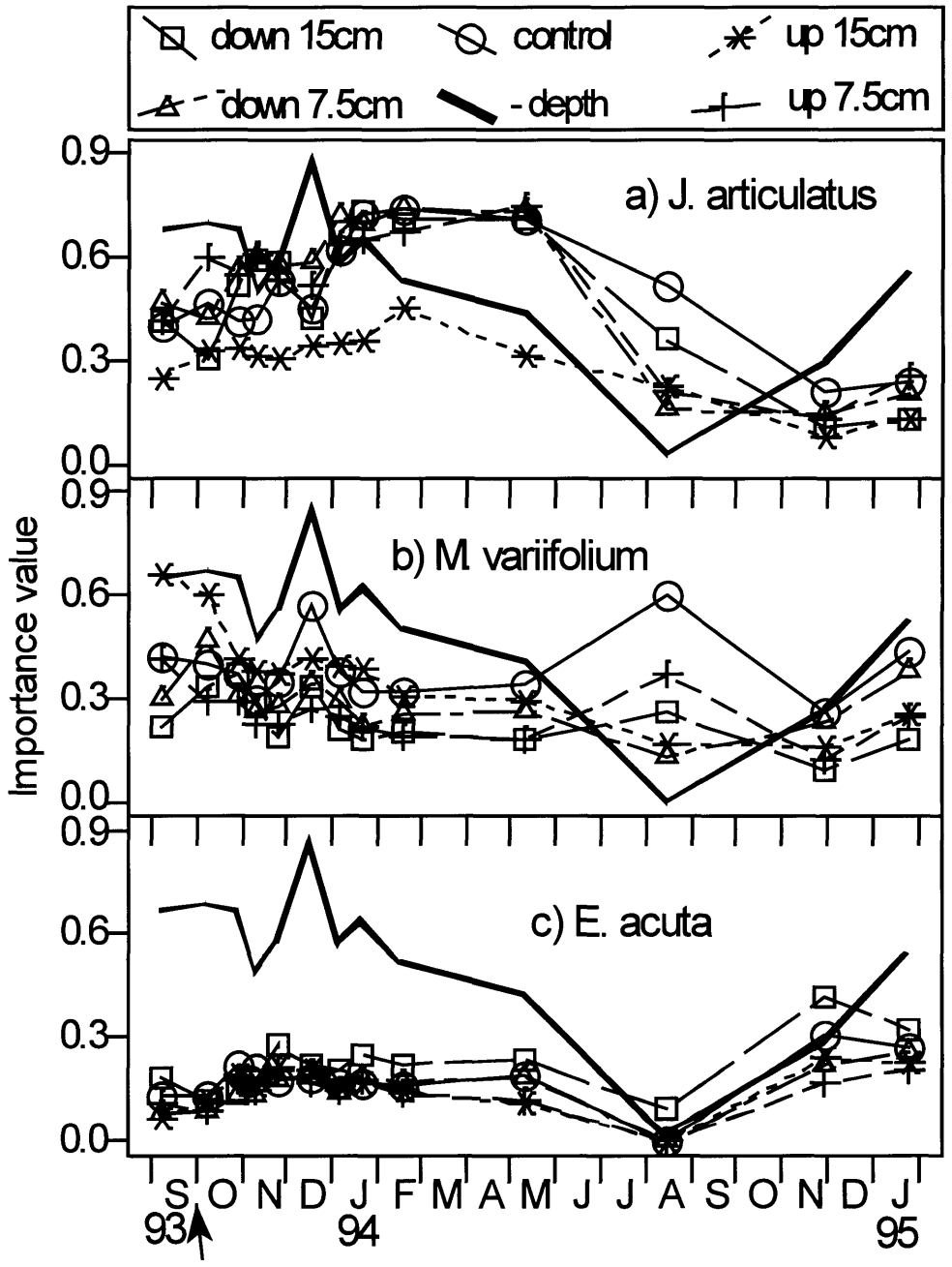


Figure 6.6 Mean importance values for a) *J. articulatus*, b) *M.variifolium* and c) *E. acuta* for each of the five treatments. The water level fluctuations from Figure 6.3 are overlaid on each graph. The arrow indicates the date when treatments were imposed.

a decline in the abundance of *J. articulatus* and the increase in the abundance of *G. australis*. There was a gradual increase in *J. articulatus* and decrease in *G. australis* during summer 1993/4, when water levels fluctuated around ground level (Figure 6.5a, Figure 6.6a). After February 1994, when water levels fell, there was a decrease in *J. articulatus* and a large increase in *G. australis*. Although *G. australis* and *J. articulatus* were similar in this clear long term trend associated with water regime, they can be contrasted in their response to the treatments. Three species, including *G. australis,* showed a clear response to the treatments (Figure 6.5) and others, including *J. articulatus*, did not (Figure 6.6).

G. australis and *A. avenacea* were favoured by the raised treatments while *P. tricarinatus* was favoured by the lowered 15 cm treatment and inhibited by the raised 15 cm (Figure 6.5). *A. avenacea* became much more abundant in the two raised treatments and remained so through the winter of 1994 (Figure 6.5c). During the first growing season *P. tricarinatus* was less abundant in the highest treatment and more abundant in the lowest. In January 1995 (date 12), *P. tricarinatus* showed a correlation between abundance and treatment, being most abundant in the lowest treatment through to absent from the highest (Figure 6.5b). After summer 1994, *G. australis* was more abundant in the raised 15 cm treatment (Figure 6.5a)

Other species showed a variety of responses to water level fluctuations but were not affected by the treatments (Figure 6.6). Although *J. articulatus* was less abundant under the highest treatment during summer 1993/4 through to May 1994, this was the case at the start of the experiment (Figure 6.6a). In contrast, *M variifolium* appears sensitive to short term fluctuations in water level (Figure 6.6b). *M variifolium* abundance rose and fell sharply in all treatments with the sharp increase in water level in December 1993, but then rose and fell again in some treatments when water levels fell and recovered over winter 1994. There was no clear relationship with treatment levels. *E acuta* abundance was very stable compared to other species and there was little difference between treatments or over longer term fluctuations (Figure 6.6c).

6.4 Discussion

The varied growth forms of the species tested had very little affect on frequency scores and cover/ abundance class, especially in the summer. For example, *E. acuta* has rigid upright culms while *P. tricarinatus* has flat floating leaves, yet these very different growth forms had similar relationships between frequency and abundance values (Figure 6.2). The increased range of values for all species in cover/ abundance classes 2 and 3 means that smaller changes in species abundance in less common species are detectable using this method. The unusual values for *G. australis* during spring (Figure 6.2e) could be due to *G. australis* ability to withstand frost and also the persistence of dead leaf material. Cover is difficult to assess for many leaves that are partially alive among dead leaves.

J. articulatus declined in abundance during the dry period at the end of the experiment (Figure 6.6a). This effect was marked over all the treatments and suggests that *J. articulatus* may be less drought tolerant than some native species. However, a relationship between drought tolerance and the water regime that was most favourable is not clear. For example, *A. avenacea* also declines after the 1994 winter yet had a preference for lower water levels. This may be expected as *A. avenacea* is an annual species. *P. tricarinatus* also shows an increase after the winter 1994 dry period. While its decline in all treatments during autumn 1994 was probably due to winter, the spring recovery was influenced by water levels because the lowered 15 cm treatment recovered first and the mean importance value for each treatment was correlated with treatment height difference (Figure 6.5b). *M. variifolium* was relatively unaffected by the winter 1994 dry period. This suggests that both *P. tricarinatus* and *M. variifolium* are more drought tolerant than *J. articulatus*, yet these two species have a preference for wetter conditions.

If treatments were not imposed it would be difficult to assess the different contributions of seasonal response and the low water levels over winter 1994 to the species changes that occurred in all treatments. However even though differential responses to treatments were detected for several species, significant differences in community composition only occurred on some dates after which they sometimes weakened or disappeared (Table 6.2). The effects of treatments are masked by

fluctuations in water level that are large compared to the differences between the treatments. The differences between the treatments may only be apparent during windows of time that are controlled by fluctuations in water level.

The effect of the treatment on community composition will also be masked by the different time scale within which the species responded. *A. avenacea* and *P. tricarinatus* showed differential responses to treatments a month after treatments were imposed. *J. articulatus* and *G. australis* responded gradually over time frames of several months that corresponded to larger fluctuations in water level. They were not strongly affected by treatments or smaller fluctuations in water level. In contrast, *E. acuta* showed consistent occurrence across all treatments although responded to the dry period.

Brock and Casanova, (1997) classified wetland species, including those above, on the basis of germination, growth and reproductive responses to water presence and absence. *A. avenacea, E. acuta, G. australis* and *J. articulatus* were classified as emergent fluctuation tolerators and *M. variifolium* and *P. tricarinatus* were classified as morphologically plastic fluctuation responders. *M. variifolium* and *P. tricarinatus* responsed to water level changes in this experiment. *P. tricarinatus* showed a correlation with treatment and *M. variifolium* showed a rapid response to short term water level fluctuations and drought tolerance. These latter two characteristics are well suited to sites subject to a large range of water levels in variable water regimes (see Section 3.3), providing the ability to withstand rapid changes in water level (Brock 1988; Brock 1991; Brock and Casanova 1997).

Even though species may occur separated over a slope, longer term changes in water level and extreme events are important in determining plant distributions. For example, after an extended dry period in 1995 and then the lagoon filling, quadrats were dominated by *G. australis* and *M. variifolium* at the water surface (1 m depth). This extreme event of a long dry period followed by flooding to maximum depth selected for the most tolerant of species and the small differences in height of the quadrats had no effect. *G. australis* and *M. variifolium* were more tolerant of the dry period in winter 1994. When water levels return to more moderate and fluctuating levels other species must reestablish from seed or vegetative fragments.

The experiment separated spatial and temporal variation in water regime in that it showed that spatial patterns are the result of differential responses of species to water regime variability at several time scales. These results suggest that appraisal of such wetland communities will benefit from awareness of the time since an extreme event and which species are appropriate indicators of community condition for different temporal scales. To assess plant communities in the lagoons over longer time scales than experiments reported in this and previous chapters, it is necessary to examine the soil seed bank, as this is how most species survive the most extreme events.

Chapter 7
Seed and seed bank germination

The soil seed bank data on *G. australis* and *J. articulatus* presented in this chapter are part of a larger data set on approximately 96 species from six wetland sites collected for the LWRRDC project "The role of seed banks in maintaining or rehabilitating vegetation in temporary and permanent wetlands." (see Acknowledgements). The data on *G. australis* and *J. articulatus* soil seed banks have been published along with data from Chapter 5 in a paper reporting the germination potential, growth patterns and reproductive effort of these two species (Smith and Brock in press).

7.1 Introduction

Wetland plant species that grow in temporary or variable environments usually have a soil seed bank. (Finlayson *et al.* 1990; Grillas *et al.* 1993; Leck 1989b; McIntyre *et al.* 1989). In such variable environments the seed bank forms an essential part of the overall life history strategy of a species and may have an important role in maintaining community diversity (Grime 1979; Grubb 1977; Kazmierczak *et al.* 1995; Leck 1989a). Studies of seed banks in the New England lagoons have shown large, diverse and persistent seed banks in a range of the wetlands. (Britton and Brock 1994; Brock 1995; Brock and Britton 1995; Casanova 1993). These studies indicate that most species in the New England lagoons have persistent seed banks.

Both *G. australis* and *J. articulatus* reproduce vegetatively and sexually in the lagoons. The relative importance of clonal and sexual reproduction for these two species in the New England lagoons will be related to frequency, depth and duration of water level fluctuations. The seed bank may be less important as a method for colonising gaps than for regeneration after periods of either high or low water or after physical disturbance which kills off extant vegetation (Thompson 1992). Chambers and McComb (1992) found a continuum of regeneration strategies in species tested for establishment in artificial wetlands. Species ranged from those reliant solely on germination to those that were difficult to germinate but sprouted readily from vegetative storage organs. *J. articulatus* was intermediate, both sprouting and germinating readily.

Other studies have investigated germination and seed bank ecology of *J. articulatus*. In a study investigating seed banks for the restoration of drained fen in Germany, *J. articulatus* seeds germinated from the seed bank five years after draining (Maas and Schopp-Guth 1995). The longevity of the native *J. articulatus* seed in the soil was an advantage. Another study investigating germination responses to different soil moisture contents found that *J. articulatus* germinated only after wet storage and preferred a soil moisture content which was wet (Etherington and Evans 1986). Many emergent aquatic species use changes in moisture content as germination cues (Moore 1985). In temporary wetlands this may be alternate flooding and drying.

In the lagoons, germination from the seed bank is important after drought periods and disturbance by water birds or cattle. Previous chapters that investigated the growth, vegetative reproduction and sexual reproductive effort of *J. articulatus* and *G. australis* (Chapter 4, Chapter 5) found traits that suggested regeneration from seed is likely to be important in the coexistence of these two species. Knowledge of the seed bank is also important for predicting the outcome of management actions.

The aim of this chapter is to assess how many seeds of *J. articulatus* and *G. australis* germinate readily from the soil of six wetland sites and how the number of seeds germinating varied in response to water regime, season and over time. The germination in response to water regime was tested because extreme events of drought and flooding are the major disturbance in the lagoons. Also, germination

response to water regime will influence a species chances of establishment under flooded or dry conditions (Leck 1989a). Germination in response to season was tested. The season of germination has been shown to be important in wetlands where water regimes are seasonal and predictable, but might be less so under the unpredictable water regimes of the New England lagoons (Britton and Brock 1994). Under such unpredictable water regimes, for a species to repeatedly germinate after disturbances when establishment and production of more seed is uncertain, it must have a persistent seed bank (Grime 1989; Thompson 1992). Two attributes of the persistence of the germinable seed bank were tested, germination after dry storage and the residual properties of the seed banks measured by repeated germination without any replenishment. To estimate the proportion of the seed bank that was germinating, the number of seeds in the soil were counted. To estimate how many years of seed production the seed bank represents, counts of possible seed production were made from the two species grown for experiments in Chapter 5. Finally, an experiment was undertaken to assess the germination response of both species to fluctuating temperatures. This response can influence the seasonal timing of germination and the preference for physical characteristics such as depth of germination and soil surface cover.

7.2 Methods

7.2.1 Germination of seed in response to fluctuating temperature

Seed of *J. articulatus* and *G. australis* was collected from mature plants at Mother of Ducks lagoon in April, 1993, stored dry at room temperature and subjected to temperature fluctuations on a thermogradient plate similar to that described by Larsen (1971) (Figure 7.1). The thermogradient plate has a 9 by 9 array of cells that are temperature controlled from underneath and experience diurnal temperature fluctuations ranging from 5° C to 45° C in 5° increments. All possible combinations of diurnal maximum and minimum temperatures are covered, including constant. Germination trays for the plate were designed and fabricated for use with semi-aquatic species as large differences in rates of drying occurred with the trays normally used for terrestrial species. The plate was designed for use with agronomic species at

lower moisture levels. The trays were small aluminium dishes that formed a close fit with a 5 cm diameter clear plastic lid. The close fitting lid allows continual recondensation of the small quantity of water in each dish thereby enabling a constant saturation of seeds across the temperature ranges.

Approximately 50 seeds were placed on germination pads and each tray subjected to one of 9 maximum x 9 minimum temperature combinations. There were 41 trays of *J. articulatus* and 40 trays of *G. australis* with the two species occupying alternate constant temperature positions along the main plate axis (Figure 7.1). A light was on continuously. The seeds were first wet on the 8th August, 1993. At two to three day intervals seeds were checked and if they had germinated were removed from the plate. All the trays were removed from the thermogradient plate on 22nd August and were placed on a laboratory bench under a window where the temperature for all trays was 15 - 24 °C. All remaining seeds were counted on 3rd September, and the total percentage of seeds germinated was calculated.

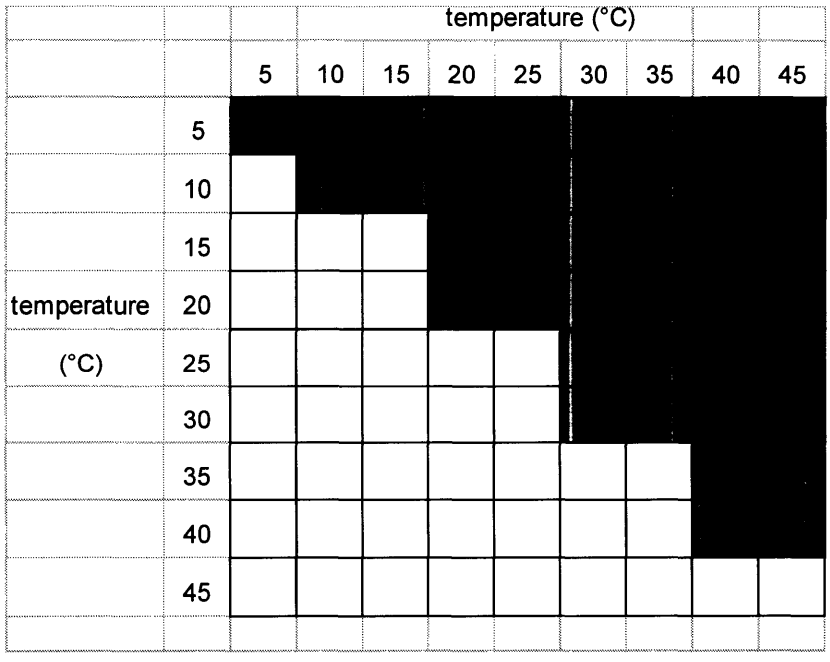


Figure 7.1 Diagram showing the diurnally fluctuating temperatures of individual cells on the thermogradient plate. The hatched area is the cells with *J. articulatus* seeds and the clear area is cells with *G. australis* seeds.

7.2.2 Germination from the seed bank.

Germination of *J. articulatus* and *G. australis* from the seed banks of six sites at five wetlands (Figure 1.4), including Mother of Ducks Lagoon, was examined under glasshouse conditions. The sites were chosen to represent the range of water regimes found in the lagoons. The most permanent of the five wetlands are Llangothlin Lagoon and Dumaresq Dam. These are near-permanent, drying only in extreme droughts. Racecourse Lagoon is typically wet two years in five. Least permanent are Barleyfields Lagoon, which fills and dries approximately seasonally and Mother of Ducks Lagoon that can wet and dry several times in a season. All the sites experience occasional droughts and years when they are flooded for the whole year. Sediments were collected from two sites at Llangothlin Lagoon, one in deeper water and one on the edge where water levels generally fluctuate several times a year (Brock *et al.*1994).

Four experiments were undertaken to compare germination from the seed banks of the six sites. The first experiment tested germination in response to water regime (water regime experiment). The second tested residual properties of the seed bank by measuring germination from the same samples over several years without replenishment of the seed bank (residual experiment). The third tested the longevity of the seed bank by measuring germination after dry storage of from one to six years duration (longevity experiment). The germination response to water regime and the residual germination were repeated with seed bank samples from three and four consecutive years respectively to test for any variation in the germination response between years.

The fourth experiment tested germination from the sediment in six seasons both in the glasshouse and outdoors (seasonality experiment) (Britton and Brock 1994). Preliminary estimates were made of total seed numbers in the seed bank and of potential seed production for comparison with the seed bank germination data.

For the water regime and residual experiments, at randomly selected positions within each site, one plastic tray containing eight sediment cores was collected for each treatment. The cores were collected in tact using a 5 cm diameter PVC tube with a

plunger (Brock *et al.* 1994). For the longevity and seasonality experiments, at a randomly selected position, sediments were dug out with a shovel to a depth of 5 cm and mixed. Each replicate tray contained 125 ml sediment (Britton and Brock 1994). The methodology used for all sample collections is described in detail by Brock *et al.* (1994).

Germination in response to water regime

For the water regime experiment, trays of sediment cores were collected in autumn of each year from 1991 to 1993. In the year of collection, after drying for three months until September, trays from each site were subjected to three water regime treatments (n=9); waterlogged, submerged (depth 10 cm) and fluctuating between these two at intervals of approximately eight weeks (Table 7.1). The trays were arranged in a randomised block design in a glasshouse. Seedlings were identified, counted and removed, ensuring no addition of seeds to the sediments.

Table 7.1 Design of three of the seed bank germination experiments undertaken with samples from six sites. Columns show timing of collection and germination of samples, and the water regime treatments applied. The experiments investigated (a) the germination response to *Water regime*, (b) the *Residual* germination each successive year and (c) the *Longevity* of seeds when stored dry. The number of replicates and the collection year of samples are indicated.

Year	Collected (C)	Germinated	Water regime treatments
(a) Water Regime			
1991	C91 n = 9,	C91 n = 9	waterlogged, fluctuating, submerged
1992	C92 n = 9,	C92 n = 9	waterlogged, fluctuating, submerged
1993	C93 n = 9,	C93 n = 9	waterlogged, fluctuating, submerged
(b) Residual			
1990	C90 n = 6,	C90 n = 6.	waterlogged only
1991	C91 n = 6,	C90 n = 6, C91 n = 6	"
1992	C92 n = 6,	C90 n = 6, C91 n = 6, C92 n = 6	"
1993	C93 n = 6,	C90 n = 6, C91 n = 6, C92 n = 6, C93 n = 6	"
1994		C90 n = 6, C91 n = 6, C92 n = 6, C93 n = 6	"
1995		C90 n = 6, C91 n = 6, C92 n = 6, C93 n = 6	"
1995		C90 n = 6, C91 n = 6, C92 n = 6, C93 n = 6	"
1996		C90 n = 6, C91 n = 6, C92 n = 6, C93 n = 6.	"
c) Longevity			
1990	C90 n = 30,	C90 n = 5,	waterlogged only
1991		C90 n = 5,	"
1992		C90 n = 5,	"
1993		C90 n = 5,	"
1994		C90 n = 5,	"
1995		C90 n = 5,	"
1996		C90 n = 5,	"

Residual seed bank - repeated germination without replenishment

For the residual experiment, trays of sediment cores were collected in autumn of each year from 1990 to 1993. Each year until summer 1996/7, the same trays were subjected to the waterlogged treatment (n=6) to assess the germinability of the remaining seed bank (Table 7.1). Trays were dried for four months (May-August) between annual wetting events. Seedlings were identified, counted and removed, ensuring no addition of seeds to the sediment.

Longevity of seed bank - germination after dry storage

For the longevity experiment, germination from the seed bank was assessed from mixed sediment collected in 1991 that was stored dry. Each year until 1996, five 125 ml samples from each site were placed in a glasshouse under waterlogged conditions and then discarded after seedlings were counted and removed (Table 7.1).

Germination in response to season

The effect of season on germination was tested in four trials beginning in September 1992 (spring) and ending in August 1993 (winter) (Britton and Brock 1994). A second spring trial was conducted in spring 1993 to assess the effect of dry storage on germination response. For each trial 125 ml of sediment was placed in each of 10 clear plastic trays and maintained in a waterlogged condition for eight weeks, after which all *G. australis* and *J. articulatus* seedlings were counted and the sediment discarded. Five replicate trays were placed outdoors and five in a glasshouse. The methods are described in detail by Britton and Brock (1994).

Total seed numbers in the seed bank

To make a preliminary estimate of the proportion of the seed bank that germinated, all the seeds in nine small cores (1 cm diameter 2.5 cm depth), taken from 1990 sediment trays of Mother of Ducks Lagoon sediment, were sieved, identified and counted. On a separate occasion another twenty cores from each of the six sites including Mother of Ducks were counted. The number of seeds was expressed per square metre for both the residual seed bank trays and for the seed count cores. The proportion of the seed

bank germinating was expressed as a percentage of the total seed bank. It was not intended to estimate total seed numbers or potential seed production with the same accuracy as the germination from the seed bank.

Potential seed production

Maximum potential seed production of *J. articulatus* and *G. australis* was estimated from counts of number of inflorescences per pot, capsules or spikelets per inflorescence, and maximum possible number of seeds per spikelet or capsule from plant material grown in the experiment reported in Chapter 5. Potential seed production was expressed per square metre for comparison with the seed bank data.

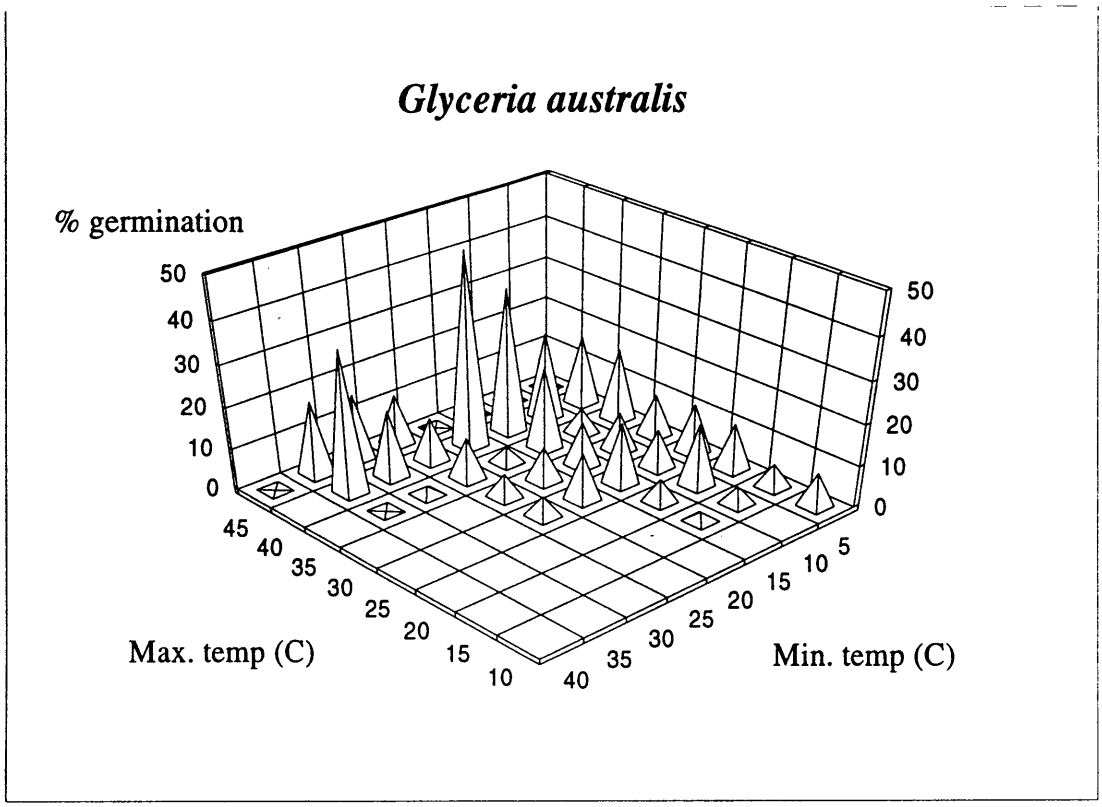
Data analysis

Differences and interactions between treatments and species were assessed using analysis of variance (Burr 1981) and the least significant difference (Day and Quinn 1989). Normality of the data was checked using normal probability plots. Heteroscedasticity and independence of means and variances was checked using plots of cell means and variances. Some data were transformed (x = Ln +1) to satisfy the above assumptions. Water regime experiment data were only analysed for Mother of Ducks Lagoon, the only site where *J. articulatus* and *G. australis* were dominant. Differences between year and water regime were tested by two way analysis of variance for each species separately. Residual, longevity and seasonality experiment data are presented for Mother of Ducks Lagoon as germination from other sites was too low. Total seed numbers in the seed bank and potential seed production was expressed per square metre for comparison with the seed bank data.

7.3 Results

7.3.1 Germination of seed in response to fluctuating temperature

The patterns of germination exhibited by *J. articulatus* and *G. australis* were different (Figure 7.2). The temperature ranges where germination of *J. articulatus* seeds were highest were a minimum diurnal temperature of 5° C with a fluctuation of at least



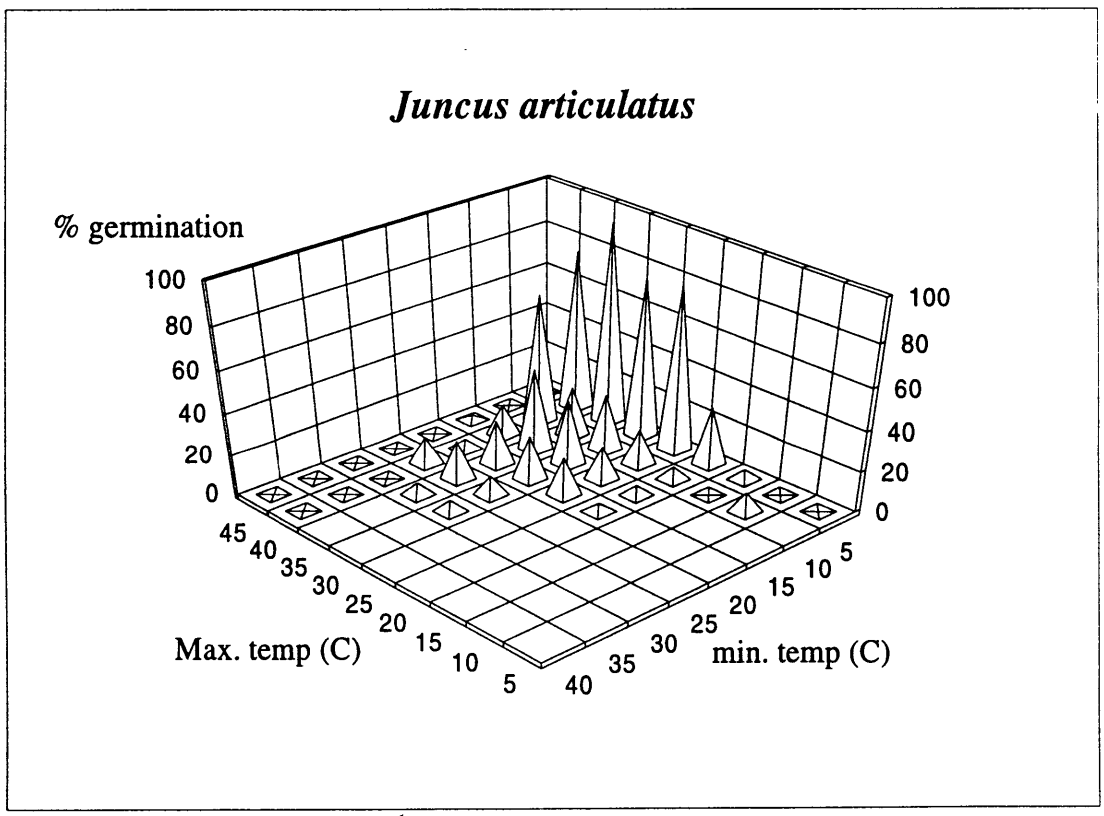


Figure 7.2 Percentage germination of *J. articulatus* and *G. australis* after twenty six days in response to diurnal fluctuating temperatures on the thermogradient plate. The two base axes are minimum and maximum diurnal temperatures. Note different maxima on the vertical axes.

20°C and up to 35° C. Germination in this range was over 70% (maximum 95%). Maximum temperatures of 45° C almost completely inhibited germination, as did maximum temperatures of 40° C or minimum temperature of 5°C without sufficient diurnal fluctuation. The pattern of germination of *G. australis* was much less restricted to particular temperatures (Figure 7.2).

The greatest germination of *G. australis* seeds (>20%) occurred when the maximum temperature was 40 °C across a range of minimum temperatures. The maximum percentage of *G. australis* seeds that germinated was less than 50% however there was germination of between 5 and 15 percent over a wide range of temperatures. Germination was only inhibited by maximum diurnal temperatures of 45°C when the minimum was less than 25°C. There was some germination at maximum temperatures of 45°C when minimum temperatures were also above 25°C.

7.3.2 Germination from the seed bank

Germination in response to water regime

Both *J. articulatus* and *G. australis* germinated from the seed banks of all six sites. *J. articulatus* germinated from the seed bank of Mother of Ducks Lagoon in very high numbers (5,000-125,000 m^{-2}) (Figure 7.3a) compared to *G. australis* (10–4,000 m^{-2}) (Figure 7.4a). Both species germinated from all the other lagoons but only in low numbers and in some years (Figure 7.3b-e, Figure 7.4b-e). *J. articulatus* occurred in all lagoons in greater numbers and more consistently over years and water regimes than *G. australis*, with the exception of Barleyfields lagoon where *G. australis* germinated in all three years (Figure 7.4b).

For Mother of Ducks sediment, the two species differed in their germination response to the water regime treatments in the three years of the water regime experiment. *J. articulatus* germination was significantly less in 1992 and 1993 than in 1991 when averaged over all water regimes (Figure 7.3a, ANOVA year main effect - $p<0.05$) and was significantly less in the submerged treatment when averaged over all years (ANOVA water regime main effect, $p<0.001$). *G. australis* germination under the

fluctuating and waterlogged water regimes was significantly greater in 1992 than 1991 and in 1993 than 1992, whereas germination from the submerged treatment was not different between years (Figure 7.4a. ANOVA year x water regime - $p < 0.001$).

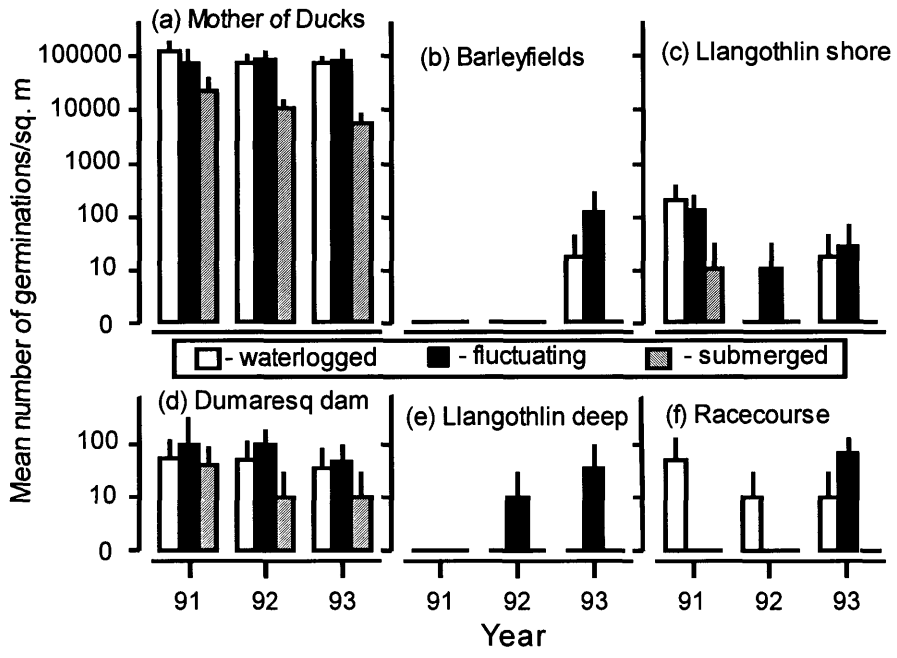


Figure 7.3 Mean number of *J. articulatus* seeds which germinated under three water regimes (waterlogged - clear, fluctuating - black, submerged - hatched) from sediment cores collected at six sites in five lagoons over three years (n=9). Error bars are standard deviations.

Residual germination - repeated germination without replenishment

Residual germination of both species was negligible from sites other than Mother of Ducks. Seeds of both species germinated from Mother of Ducks sediment in decreasing numbers when seed banks were wet in successive years. *J. articulatus* seeds germinated from all Mother of Ducks trays in 1996 after three to six years of repeated wetting (Figure 7.5a). In contrast, no *G. australis* seeds germinated from cores collected in 1990 and 1991 three or more years after collection. However in

1996, *G. australis* seeds were still germinating from cores collected in 1992 and 1993, four and three years after collection respectively (Figure 7.5b). High numbers of *G. australis* seeds germinated from sediments collected in 1993 compared to the other three years.

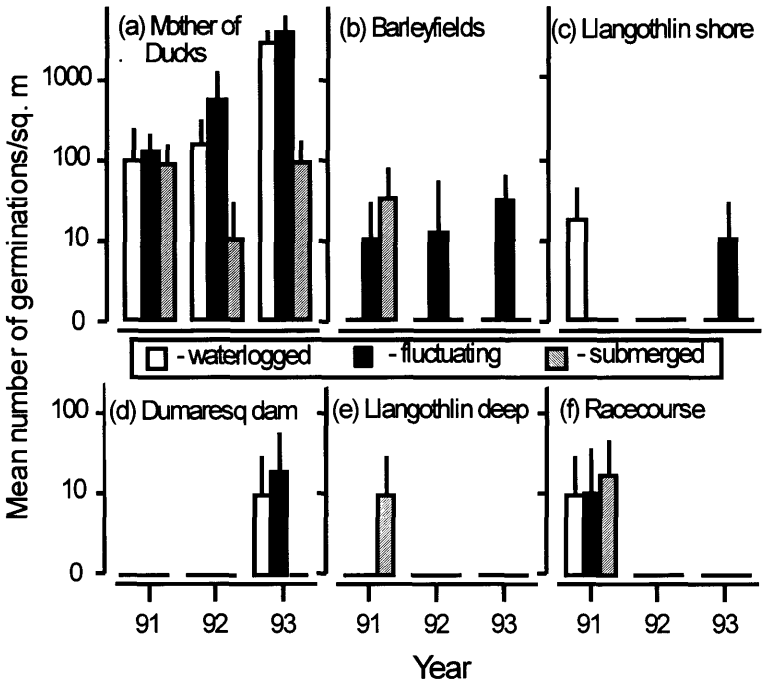


Figure 7.4 Mean number of *G. australis* seeds which germinated under three water regimes (waterlogged - clear, fluctuating - black, submerged - hatched) from sediment cores collected at six sites in five lagoons over three years (n=9). Error bars are standard deviations.

Longevity of seed bank - germination after dry storage

In the longevity experiment, both species germinated from sediment stored dry for six years (Figure 7.5a,b). Although there is a decline in numbers of seeds germinating over the six years, the pattern appears to differ from the residual experiment. For *J. articulatus*, and to a lesser extent for *G. australis*, germination from the dry stored sediments declines less rapidly than the trays that are germinated each year.

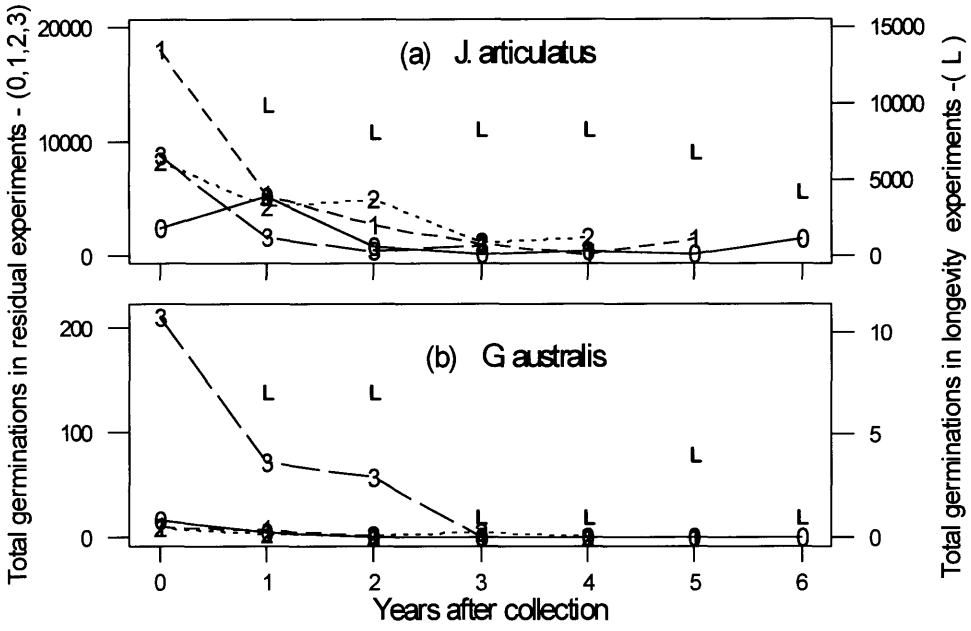


Figure 7.5 Total number of seeds of (a) *J. articulatus* and (b) *G. australis* germinating from (i) residual experiment sediment cores collected in each year from 1990 to 1993 at Mother of Ducks (symbols represent the year of collection 0 = 1990, 1 = 1991, etc. Cores were waterlogged from the year of collection until 1996), and (ii) longevity experiment mixed sediment (symbol - L) collected in 1990 at Mother of Ducks (sediment was stored dry and a new sample used each year until 1996). Note the different scales on the vertical axes for *J. articulatus* and *G. australis* and for the residual experiment (left axis) and longevity experiment (right axis).

Germination in response to season

G. australis and *J. articulatus* seeds germinated in the four consecutive seasons from spring 1992 to spring 1993 all four seasons. For *J. articulatus,* more seeds germinated in the glasshouse than outdoors. For *J. articulatus* outdoors, more seeds germinated in the spring and autumn and in winter, 1993, whereas in the glasshouse, more seeds germinated in the winter. However, very few seeds germinated in summer in the galsshouse or outdoors. For *G. australis,* very few seeds germinated in any season, however more seeds germinated in autumn and spring outdoors and in autumn in the glasshouse. The germination of *J. articulatus* seeds in spring 1993 was less than in spring 1992, especially in the glasshouse. The germination of *G. australis* seeds is greater in spring 1993 than spring 1992.

Table 7.2 Mean number of seeds (± standard deviation) of *J. articulatus* and *G. australis* that germinated from Mother of Ducks sediment in the glasshouse and outdoors in five seasons from spring 1992 to spring 1993.

Season	Glasshouse /outdoor	*J. articulatus* Mean	± stdev	*G. australis* Mean	± stdev
Spring 1992	Glasshouse	972	235	0	0
Summer 1992		706	225	4.6	3
Autumn 1993		722	397	3.8	1.1
Winter 1993		1119	143	4.6	3.6
Spring 1993		685	84	9.4	3.8
Spring 1992	Outdoors	822	555	0.4	0.9
Summer 1992		114	38	2.4	2.5
Autumn 1993		1269	172	9	2.5
Winter 1993		941	145	3.8	3.3
Spring 1993		791	164	8	3.5

Seed counts from sediment

Seed counts from sediment cores suggest the proportion of *J. articulatus* seeds that germinated from sediment cores collected at Mother of Ducks in 1990 over the first three years comprised 6.3% of the seed bank. The proportion of the *G. australis* seed bank that germinated over the same period was 3.5%. Although coefficients of variation for both the seed count and the germination data were high (>1), a substantial proportion of the seed bank remains in the sediments. Counts performed on a separate occasion (20 cores from the 1992 collection) revealed a similar percentage of seeds germinating in the first year for *J. articulatus*, however failed to find any *G. australis* seeds.

Potential seed production

Potential seed production for *J. articulatus* was from 7,000,000 to 19,000,000 seeds/m^2. This is comparable to the total number of seeds in the top 25mm of soil estimated from the soil core seed counts (10,000,000/m^2). Similarly with *G. australis*, potential seed production was from 35,000 to 94,000 seeds/m^2, which is also comparable to the figure of 50,000 seeds/m^2 from the soil core count data

7.4 Discussion

G. australis and *J. articulatus* seeds had contrasted germination responses to temperature (Figure 7.2). Most *J. articulatus* seeds germinated when the minimum temperature was 5° C and there was a diurnal fluctuation of at least 20 to 35° C. This is consistent with greater germination in autumn or spring when minimum temperatures are low but diurnal fluctuations are large. The requirement for a minimum temperature of 5° C explains the very low number of seeds that germinated in summer (Table 7.2). Low percentages of *G. australis* seeds germinated over a broad range of temperature regimes. A similar response by other wetland species was interpreted as an adaptation to life in wetlands with unpredictable water regimes that allowed opportunistic germination regardless of season (Baskin *et al.* 1989 cited in Britton, 1994 #306). Britton and Brock (1994) concluded that for species inhabiting the lagoons generally, temperature regimes act to inhibit germination during unfavourable summer conditions. The thermogradient plate results suggest that different mechanisms may be responsible for *J. articulatus* and *G. australis* responses to temperature regime. *J. articulatus* germination is inhibited by high minimum temperatures whereas *G. australis* germination may be controlled by a requirement for a limited maximum temperature range (Figure 7.2). The responses of more native species need to be investigated to see if there are general patterns of germination among native species inhabiting the lagoons.

Both *J. articulatus* and *G. australis* have a long lived seed bank from which only a small proportion of seeds germinate in any one event. *J. articulatus* seeds continued to germinate after six years (Figure 7.5a) and *G. australis* seeds for four years (Figure 7.5b) without replenishment of the seed bank. Both species continued to germinate from sediment stored dry for up to six years. *J. articulatus* germinated from dry Mother of Ducks sediment twelve years after collection (Brock and Britton 1995). This would be an advantage in temporary and unpredictable habitats where a germination event may not result in successful establishment and reproduction and where extended droughts occur. This is the case in the lagoons on the Northern Tablelands.

Without replenishment of the seed bank, the number of seeds of both species that germinated in successive seasons decreased (Figure 7.5). *G. australis* did not germinate more than four years after collection and after three years germination from dried sediments was low (Figure 7.5). In contrast, *J. articulatus* is known to germinate after more extended periods: fifteen years after the draining of fens in Germany (Pfadenhauer and Maas, 1987) and after twelve years from Mother of Ducks sediment (Brock and Britton 1995). This suggests that *G. australis* seeds are less long lived in the seed bank than *J. articulatus*.

The patterns of germination of both species depended on the year of collection (Figure 7.3, Figure 7.4). The differences may be due to falling water levels in the lagoons through those years, culminating in a drought in 1995. The lower number of *J. articulatus* seeds that germinated from sediment collected in 1992 and 1993 compared to 1991 may reflect less favourable field conditions for growth and seed production or conditions inducing dormancy preceding collection. The germination response of *J. articulatus* to water regime was the same in each year. In contrast, germination of *G. australis* changed between years, suggesting the conditions preceding seed production and collection induced different dormancy responses. There is also variation in the patterns of germination of the two species from the other sites (Figure 7.3b-f, Figure 7.4b-f). For example, *J. articulatus* germinated under all water regimes in all years from Dumaresq Dam sediments but germination from Racecourse Lagoon sediments was greater under the waterlogged water regime (Figure 7.3d & f). Froend *et al.* (1993) achieved 100 percent germination under all treatments of *J. articulatus* seed from seasonal wetlands in Western Australia. These patterns suggest that germination cues may be site specific. Further studies to elucidate relationships between site and dormancy would assist in predicting the potential for *J. articulatus* to be invasive.

Suitable conditions for germination occur infrequently in the field compared to the glasshouse. Suitable conditions for establishment are also likely to be much more restricted in area than germination events (Leck and Simpson 1995; Rea and Ganf 1994b). Establishment success will depend on other traits of both species such as seed size and growth rate. Although much less frequent, *G. australis* seeds are much larger than those of *J. articulatus* and so may establish more readily. In common with characteristics researched in previous chapters, some seed bank traits of *J. articulatus*

and *G. australis* are shared and some are contrasted. To gain a complete picture, all the traits must be considered together.