THE INFLUENCE OF WATER REGIME ON THE POPULATION ECOLOGY OF TWO EMERGENT MACROPHYTES IN SOUTH AUSTRALIA

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SUMMARY

In Hacks and Bool Lagoon, South Australia (Latitude 37° 08' S, Longitude 140° 40' E), the replacement of the rigid stemmed *Baumea arthrophylla* Nees. Boeckeler, by the fleshy leaved *Triglochin procerum* R.Br., coincided with an increase in depth, a decrease in the frequency and duration of drawdown and more stable water levels (range: (0) 20-120 cm (140)), over a 25 year period. Plant responses to the abiotic and biotic environment, at the tissue, ramet and population level, identified the subtle changes in plant growth and life-history that occurred before major changes in distribution patterns. Where water levels fluctuate, any site across a depth gradient, experiences continuously changing water depth. It was shown that the degree of exposure and depth and duration of inundation, increased exponentially as elevation decreased. The water regime varied temporally, spatially, and in magnitude. Hacks Lagoon is deeper, more permanent and subject to greater fluctuations than the Western Basins.

In relation to depth and water regimes integrated over short time intervals (30 days), *Triglochin*'s aboveground mass showed a positive correlation, whereas shoot densities showed a modal response. In relation to water regimes integrated over long time intervals (6+ months), *Baumea*'s aboveground mass and shoot densities, showed a modal response and negative correlation, respectively. While *Triglochin* reacted quickly to changes in depth, *Baumea* integrated water regime over a relatively long time-scale, resting through periods of inundation. *Baumea*'s stand variability was least at high elevations, whereas *Triglochin*'s was least in deep water; responses which concur with the water regimes in the areas they dominate.

Across a 100 cm depth gradient, ramet biomasses, shoot and leaf numbers, were similar for *Triglochin*, but decreased for *Baumea*, which did not survive at one metre. Species had similar total biomasses in shallow water, but whereas *Triglochin* allocated most mass to its roots, *Baumea* placed most mass into its rhizomes. As water levels changed, mass was moved between *Baumeas*' stems and rhizomes. As the latter are storage and reproductive organs, this restricted its performance. *Triglochin*'s performance was unaffected, because mass was moved between its leaves and tubers, and tubers are not resource acquiring organs. Depth also affected the relative production of *Baumea*'s two shoot types. In shallow water, the large rhizome mass and bud-bank, was due to the predominance of long shoots, which enabled ramets to respond positively to inundation. In deeper water, continuous short shoot production, meant most mass was held aboveground and when ramets were submerged, the mass of all tissues fell. Although the relative abundance of these shoots, control *Baumea*'s capture of space, and thus its reproduction and population

structure, there is no literature on the importance of shoot type with respect to vegetation changes and resilience to invasions.

The species used contrasting life-histories, to survive the variable lagoon habitat. *Triglochin* shoots responded to fluctuating water levels with morphological plasticity; changing size (height, diameter, mass) according to depth. At any time, its shoots, at the one elevation, were indistinguishable in size. This may be attributed to its clonal habit, large belowground mass, and rapid turnover of shoot tissue, characteristics which support the equivalent growth of shoots (both before and after flowering). It was hypothesized that shoots lived 24 months (emerging/dieing during autumn drawdown), and that populations consist of two symmetrically overlapping cohorts, equal in size. In contrast, *Baumea* withstood changes in water level without major changes in height. Life-span, reproduction and size, depended on the timing of emergence. Shoots were recruited in autumn and winter and were either long- (17-19 mths) or short-lived (1-6 mths). The lack of shoot recruitment in spring, contrasted with literature examples (Bernard 1975, 1976, Soukupova 1988), where autumn shoots overwinter and join spring recruits for a summer growing season. The need for leaves and stems to keep above rising water levels, meant *Triglochin* and *Baumea* grew fastest in winter and least in summer, and that temperature was not the factor to first limit growth in this region. In spring, *Triglochin*'s growth rate fell more rapidly than water levels, which may be a post-flowering response to resource depletion. Where species have different turnover rates, morphologies and allocation patterns, RGR's calculated from shoot tissue alone, can not be validly compared.

Triglochin shoots were able to flower in either of two years, in both, or not at all; an uncommon versatility. The proportion of shoots in flower, increased with inundation. Both species flowered in winter/spring, but whereas *Triglochin*'s large, bouyant seeds, were dispersed when shed during high water levels, *Baumea*'s small hard seeds, shed during drawdown, remained beneath the canopy. As a sedge, the lack of *Baumea* seedlings, was not unusual (Bernard 1975, Auclair *et al.* 1976). Despite *Triglochin*'s seed production (300-25092 m^{-2}) and viability (100%), the low seedling establishment in 1986 (0-15 m^{-2}), was due to exposure as water levels fell too fast (drying phase) and rose to slowly (flooding phase). In 1987 and 1988, the water regime also restricted germination to a narrow zone, but then prevented establishment.

The outcome of a Replacement Series experiment, was an asymmetric interaction, which was competitive in shallow water, but not deep. At both depths, *Baumea* was unaffected by the presence of *Triglochin*, which in shallow water, experienced a fall in its total, root, shoot and tuber mass and recruitment of shoots and leaves. Its performance improved in deep water, due to less intraspecific competition and *Baumea*'s placement of mass aboveground.

In shallow monocultures, *Triglochin* allocated most N, P and mass to roots, but in mixture, mass was reallocated to tubers, and N and P to rhizomes, a strategy to conserve P, due to the competition that roots were experiencing. The reallocation of mass to tubers, (& not N or P), reveals their role as a carbohydrate, not nutrient store. *Baumea*'s response to depth (increases in nutrient levels), represented accumulation in smaller masses. Low N:P ratios in both plants, implied N was more likely to limit growth. *Triglochin* had higher nutrient levels, an indication of higher growth rates (Field and Mooney 1986). Although there was little evidence for this, differences in PB_{max} ratios and leaf life-spans, implied otherwise. The long-lived stems of *Baumea*, signal a susceptibility to C limitation. This contrasts with *Triglochin* which has short-lived leaves. Their well developed lacunae and thin cuticle, indicate *Triglochin* also has the advantage of utilizing dissolved C.

Evidence for aboveground interaction in shallow water, was sought because of *Baumea*'s numerous stems which occupy all strata and *Triglochin*'s continuous recruitment of leaves and rosette habit. However, as *Triglochin* shoots were not even emerging, the inhibition must have occurred belowground. *Baumea*'s allocation patterns adversely affected resource supply to *Triglochin*, changes in which showed that space **and** P were limiting. In conclusion, species interactions are dependent on the water regime, which affects the relative allocation to below (sediment resource acquisition) and aboveground (C acquisition) parts. At shallow and regularly exposed sites, *Baumea* is the superior competitor, and keeps *Triglochin* at bay. The change in distribution patterns occurs in deep and permanently flooded conditions, where *Baumea* dies back, paving the way for *Triglochin* to passively take its place.

DECLARATION

To the best of my knowledge and belief, this thesis contains no material previously submitted for a degree or any other award, in any university by any person, or any material previously published or written by another person, except where due reference is made in the text. I consent to the thesis being made available for copying and loan if accepted for the award of the degree.

Naomi Rea

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CHAPTER 1: INTRODUCTION

1.1 HYDROLOGY AND WETLANDS

The hydrology of wetlands is known to be a major determinant of the distribution and abundance of aquatic plants. This study examines the responses of two emergent macrophytes, grown individually and in mixture and under natural and controlled water regimes and examines how such responses translate into altered distribution patterns. The salient difference between this and other work, is a matter of scale. Water levels in South Australia fluctuate and are naturally variable. Small changes in shallow and semi-permanent habitats can significantly change the abiotic environment and subtle changes in the growth and life-history of individuals and the interaction between different species, will occur well before major changes in distribution patterns.

Wetland water regime is defined here as the depth, duration, timing and rate of inundation and drying. Definitions given by Harris and Marshall (1963), Gosselink and Turner (1978), LaBaugh (1986), Carter (1986) and Breen *et al.* (1988) include some but not all of these aspects. Because fluctuating water levels can influence nutrient, light, oxygen, and carbon dioxide supply, it is difficult and perhaps impractical to isolate the role of one factor when it is their synergistic effect that plants experience. Measuring water regime is measuring the sum effect of part of the physical and chemical environment, but the fact that it summarizes a variety of factors, does not detract from its utility. Indeed because water levels can sometimes be controlled it has widespread practical applications.

In the past, the influence of water regime was considered in terms of the extremes of constant water level which produced shoreline zonation (Hutchinson 1975, Spence 1982) or large and rapid changes in water level typical of artificial impoundments (Brock *et al.* 1987, Nilsson and Keddy 1988, Roerslett 1989). Only a few studies have examined the effects of smaller and natural fluctuations (Hultgren 1988, Wilcox and Meeker 1991), but these were, with the exception of one site, in regulated man made lakes. Because of the shallow nature of wetlands and their gentle elevation gradients, small changes in water level expose or inundate large areas, altering the oxygen status of the sediment, the availability of nutrients and the ionic concentration of the water and sediment. The flooding and exposure of shoot tissue, differentially affects the supply of photosynthetic and respiratory gases to plants with different morphologies. How aquatic plants experience the wet-dry cycle that results from fluctuating water levels, is examined in this study. The situation for tidal wetlands, also applies to emergent plants in freshwater wetlands with fluctuating water levels; "the ecological literature ... fails to address the potential role of exposure as a control on patterns of production, partitioning or growth form" (Karagatzides and Hutchinson 1991). Emergents are here defined as plants with shoots that emerge above the water and which are rooted in a waterlogged anaerobic substrate.

1.2 VEGETATION CHANGES IN WETLANDS

It is clear that changing a wetlands hydrological regime has the capacity to vastly alter the habitat for aquatic plants. The concept of hydrarch succession (Sculthorpe 1967) predicts the directional change in vegetation zones following long-term changes in water depth due to sedimentation. However, Wilcox and Simonen (1987) pointed out that the stable climax community was an illusion in wetlands and that the ideas of Clements (1916) have tricked ecologists into 'interpreting zonation as indicators of future successional trends'. This is because there is evidence that wetlands are kept successionally young over thousands of years by natural disturbances (Walker 1970, Jackson *et al.* 1988). Over these time-scales, there are numerous fluctuations or changes in the vegetation (e.g. Walker 1970, Dodson 1974, Dodson and Wilson 1975).

Instead of permanent successional changes, reversible and temporary fluctuations (Miles 1979) may predominate. For example, cyclical changes in species composition over seasons and years, are well documented (Saxton 1924, Misra 1938, Hejny and Husak 1978, van der Valk and Davis 1978a, Gopal 1986, Rabotnov 1966, Beeftink 1987, Raspopv *et al.* 1987). Although repeated fluctuations that are asymmetrical, can produce successional changes in alpine forests (Austin *et al.* 1990), there is no literature for such changes in aquatic plant communities. If natural succession occurs at all in wetlands, the time-frame must be stated, as reported changes in species composition may result from man's activities, especially when the change is to a less complex vegetation (regression).

Succession induced by nutrient enrichment (Phillips *et al.* 1978, Moss 1983, Osborn and Polunin 1986, Brown 1987, Vermeer and Verhoeven 1987, Ulrich and Burton 1988, Boar *et al.* 1989, Toivonen and Baeck 1989) and alterations to the hydrological regime (Millar 1973, Ranwell 1974, Roerslett 1989, Burgess *et al.* 1990, Grillas 1990) suggest these are important factors that precipitate change. With excess nutrients, the change is in the sequence; emergent, floating-leaved, rooted submergent, unrooted submergent and phytoplankton. This reflects decreasing dependance on the sediment for nutrients and a high supply rate in the water. Increasing or decreasing stable water levels (pondage or drainage) will result in more or less aquatically adapted species, respectively. The change from stable to fluctuating water levels such as sudden, large and irregular changes typical of impoundments, results in a more stress-tolerant flora (Murphy *et al.* 1990, Kautsky 1988). The change from fluctuating to stable water levels led to grasses, sedges and herbaceous species dying out (Kadlec 1962, Harris and Marshall 1963, Rumberg and Sawyer 1965, Weller and Fredrickson 1974, Smith and Kadlec 1983) and three studies have reported the invasion of *Typha* and decline of sedges due to increased and stabilized water levels (Beule 1979, Farney and Bookhout 1982, Wilcox *et al.* 1984).

As the above examples suggest, changing distribution patterns in wetlands are usually documented as a community level response, on the scale of years to decades. The species by species replacements that constitute successional changes, are virtually unknown. An exception is the the retreat and expansion of macrophytes in Bohemian fishponds, modelled by Hejny (1985). The retreat of a dominant plant occurred in two stages: over 10-20 years it became clustered, over 30 years scattered and then it eventually died. This time-scale compares favourably with documented changes in emergent communities (e.g. Klotzli 1971, Markstein and Sukopp 1980, Roelefs 1983, Cramer and Hytteborn 1987, Boar *et al.* 1989, Ksenofontova 1989). The expansion process proceeded in three stages: initially the invader became better adapted to the altered environment, then it invaded the retreating association, establishing dominance, and finally its enhanced performance enabled it to 'push back' the retreating association. Both abiotic and biotic interactions were a part of the model. The passive retreat and invasion were due to a negative and positive response, respectively, to the change in environment. If the positive response conferred competitive superiority, then the final stages of the invasion would be aggressive. Although the emphasis has been placed on alterations in the environment facilitating successional changes, an understanding of the influence of environmental factors on the species involved throughout this process is lacking. The emphasis should now be placed on the individual responses from species, before they translate into major population changes.

1.3 PLANT ABIOTIC AND BIOTIC RESPONSES

To predict a plants' response to a change in the environment or to the presence of a new neighbour, an understanding of its biology is necessary (Harper 1977, Grubb 1985). A useful concept, is to summarize plant traits as strategies. This was originally undertaken to examine ecological specialization over successional time (Ramenskii 1938, MacArthur and Wilson 1967, Grime 1977, Whittaker and Goodman 1979, Southwood 1988, Taylor *et al.* 1990). Disagreement over the competitive advantage of some traits (Weldon and Slauson 1986, Huston and Smith 1987, Tilman 1987, Grime 1988b, Loehle 1988, Thompson and Grime 1988, Tilman 1989) has contributed to the ongoing search for evidence. For example, clonal growth may be an advantage in variable environments (Callaghan and Emanuelsson 1985, Vermaat *et al.* 1987), where species and time-specific stresses, never persist. The main characteristic of plants in the South-east wetlands, is the perennial clonal habit. Closely associated shoots increase a plants resistance to invasion and their physiological integration (Ginzo and Lovell 1973, Hartnett and Bazzazz 1983, Pitelka and Ashmun 1985, Alpert and Mooney 1986, Tissue and Noble 1988) suggests cooperation between ramets rather than competition. Plasticity may also be a vital attribute for dealing with the physical environment, allowing plants to match changes in the environment, thereby overcoming short-term adverse affects. Life-history traits have been used to predict succession in wetlands (Hall *et al.* 1946, Gaudet 1977, Leck and Graveline 1979, Noble and Slatyer 1980, Pederson 1981, Walker *et al.* 1986) and van der Valk (1981), proposed that only life-span, seed/propagule longevity and seed germination/propagule establishment were necessary to predict changes following flooding or drawdown.

Interactions between plants, and predation and parasitism may also play a role. The relative contribution of abiotic and biotic factors to changes in distribution patterns, has been most recently examined by Chambers and Prepas (1990), Bertness (1991a) and Nomme and Harrison (1991). Chambers and Prepas (1990) concluded that "whether interspecific competition or environmental heterogeneity is the prime factor controlling the distribution and succession of aquatic plants has not been resolved." Where succession involves a change in life-form, it might be expected that they are driven by the abiotic environment, because there are fewer resources that such species compete for (Werner 1979). In habitats with stable water levels, plant interactions have been found to be responsible for controlling distribution patterns of emergent macrophytes (Buttery and Lambert 1965, Grace and Wetzel 1981a, 1982, Silander and Antonovics 1982, Grace 1988), but van der Valk and Davis (1978a) found that fluctuating water levels prevented species interactions and predation from having a significant effect. The little attention predation has received usually concerns the adverse effects of introduced herbivores (Boorman and Fuller 1981, Tester and Jansen 1985, but see Giroux and Bedard 1987). Where people believe that it has limited influence on the distribution of emergents (Roberts 1987), there may be an overriding factor such as fluctuating water levels.

The most important indicator of competitive ability in 29 emergent species, was found to be biomass (total, above and belowground, Gaudet and Keddy 1988). Belowground competition may be more important than above, as the root:shoot ratios of dominant species was found to increase over successional time (Monk 1966). This supports the theory that early successional species are competitively superior in 'high light-low nutrient' habitats and late successional species better in 'low light-high nutrient' habitats (Tilman 1990a). Over successional time, there is also a shift from fast growing species with rapid uptake rates to slow growing species tolerant of low resource levels (Bazzaz 1979, Goldberg 1990).

To understand the processes by which vegetation changes occur, species responses to abiotic and biotic factors were measured at the levels of the population (m^{-2}), the ramet and individual tissues (roots, rhizomes, tubers, stems and leaves). If the concept of emergent properties is applicable in this study, then this information will show how similar results are achieved in different ways (e.g. a standing crop of 1000 g m^{-2} may be made up of 100 shoots weighing 10 g, or 1000 shoots weighing 1 g). This approach distinguishes the factors that evoke a response at one level, but not another, and elucidates how water regime modifies competition.

1.4 STUDY RATIONALE

In Bool and Hacks Lagoon, (South Australia), the rigid stemmed emergent *Baumea arthrophylla* (Nees) Boeckeler, is being progressively replaced by the fleshy leaved emergent *Triglochin procerum* R.Br. This has occured over the past 25 years and coincides with an increase in the depth of the Lagoons and a decrease in the frequency of drawdown. These hydrological changes, are a compromise of the interests of the South Eastern Drainage Board, the Field and Game Society, the National Parks and Wildlife, local farmers and naturalists, and began when the area was dedicated a Game Reserve in 1967. Although the changes are relatively small, they have clearly had a significant effect on the vegetation. This effect was predicted by eminent scientists in a Parliamentary investigation into the management of the Lagoons (SED&D 1964). Now the vegetation changes are well underway, there is renewed concern and the need for ecological data, so that informed decisions can be made. This study aims to determine the relationship between the hydrological environment and species morphology, productivity, resource allocation, demography, and interaction. Individual and mixed responses to different depths and water regimes at the ramet and population level, were measured *in situ* and experimentally.

The research contributes to a growing understanding of aquatic plant ecology in Australia. Australian wetland environments have escaped detailed ecological study, not because of their misconceived scarcity, but because they were considered inaccessible, hazardous (insect born disease, crocodiles, snakes) and percieved as wasteland. This perception is changing as governments are bound to protect wetlands under international treaties and to ameliorate severe water quality problems. The degradation and dramatic decline in South Australian wetlands is well known (Smith 1975, Jones 1978, Environmental Protection Council 1988). In a report to the South Australian government, it was concluded that "the continuing loss of wetland in the south-east is alarming and all remaining habitat should be retained" (South-east Wetland Committee 1983). Their recommendations were that: wetlands should contain a mixture of habitat types; preference be given to areas subject to short periods of inundation and intermittently flooded sedges; and that assessments should measure 'water quantity' (depth, permanence, source), 'optimal water level', and the effect of maintaining high water levels. However, there was no data on which these decisions were founded, the affects they would have or the meaning of hydrological parameters. This very general understanding of the issue, has meant that the situation for individual sites and species has not been addressed. The species of *Triglochin* and *Baumea* in this study are endemic to Australia (*Baumea* also in New Zealand) and although they are relatively common wetland plants here, their distribution (particularly *Baumea*'s) has been restricted by destruction of their habitat and limited dispersal characteristics. With the exception of *Typha* (Roberts 1987) and *Phragmites* (Hocking 1989a & 1989b), there are few detailed studies on Australian emergents, and unlike *Baumea* and *Triglochin*, those species are cosmopolitan and common in disturbed sites. Given that plant adaptations have evolved over many years, the growth and demography of *Triglochin* and *Baumea* may differ from other plants in the literature, which mainly come from the Northern hemisphere and from wetlands with more stable water levels.

CHAPTER 2: THE HYDROLOGICAL ENVIRONMENT AND VEGETATION OF THE STUDY SITE AND REGION

2.1 INTRODUCTION

Quantitative information about the hydrodynamics of wetlands is not readily available (Gosselink and Turner 1978), although it is a major determinant of these systems. In this chapter, the hydrological environment of Hacks and Bool Lagoon is introduced and placed into the perspective of plant adaptation and response. These lagoons in the South-east of South Australia are the habitat for extensive stands of *Baumea arthrophylla* and *Triglochin procerum*, which have undergone major changes in their distribution. A brief introduction to these species will precede an hypothesis concerning the role of water regime re vegetation changes.

The influence of water regime is often investigated as the presence or absence of species or communities. Under a wet/dry cycle, the presence then absence of water will exclude many terrestrial and aquatic species, respectively. Water will also be a limiting factor for many of the semi-aquatic and aquatic species when periods of inundation or drought persist. The adaptations and biology of the specific suite of species that do survive was examined by Raup (1975) and Menges and Waller (1983). In undisturbed habitats the flora is finely-tuned to the environment, with adaptations that have evolved over many years. Grime *et al.* (1987) and Southwood (1977) identified a relationship between the strategies which plants evolve and the harshness of their environment. Recognition of the original conditions and forces which selected certain species and specific traits, is central to understanding the processes by which habitats and their wildlife exist and are lost.

The aims were: to describe the hydrological environment of the South-east region in the context of other wetland areas, and of Hacks and Bool Lagoon, the site of major vegetation changes; to focus attention on the hydrological factors that may be facilitating changes and the traits of the species in question that may indicate a predisposition to their retreat or expansion; to quantify the water regime that plants experience.

2.2 METHODS

The water regimes in Hacks Lagoon where *Triglochin* is dominant and in the Western basins where *Baumea* dominates, were compared in several ways. The units of elevation, Australian Height Datum metres above median sea level (AHDm), are omitted in the text (eg. 48.20). The number of days the habitats at the four elevations (48.25, 48.05, 47.85, 47.70 AHDm) were exposed and flooded by depths between 1-20, 21-40, 41-60, 61-80, 81-100 and 101-120 cm over 360 days (Apr-88 to Apr-89), was determined from the water level in each area. The lag time between water level and a response from these species was unknown, but this period seemed appropriate, considering the life-span of shoots and leaves of similar plants in the literature (*Carex* Hultgren 1988, *Zizania* Stevenson and Lee 1987). Two indices of the water regime over this period were calculated. The first, which quantified the wet/dry cycle as a measure of exposure, was the ratio of the number of days exposed to inundated. The second, which quantified the depth and duration of inundation, and was called Sum Water Regime, integrated the area beneath each water level plot (units: cm days x 10^2) at each sampled elevation. These values were collated for 360 day intervals, which preceded harvests discussed in Chapter 3. The indices were plotted against elevation, and the relationship assessed from the significance of linear and exponential equations.

2.3 THE SOUTH-EAST

Topography

Forty million years ago, the Southern ocean extended inland to the Riverland. When it retreated two million years ago, the limestone sediment was exposed and weathered, forming many caves and sink holes. During the quaternary era the sea again advanced, this time to just east of Bool Lagoon, which separates the high ground to the west from the coastal plain, known today as the South-east. The slow retreat of this sea left a series of stranded shorelines, running parallel to the coast. Between Robe and Naracoorte, there are 21 remnant dunes that make up 13 ranges. To the north and south they coalesce, and are less distinct. The sandy dune ridges average 15 to 30 m high and separate wide interdunal flats. The gradient of the flats varies from 1 in 1,500 to 1 in 5,000. Each flat is slightly higher moving inland, and by Penola the land is 60 metres above sea level. The dominant soil types are alkaline, dark grey to black clays which overlie the calcareous sediment (Blackburn 1983). In areas subject to flooding and groundwater influence, fine silts and acid to neutral humic gleys occur (Shepherd 1964a). Soils in general are deficient in P, N and K and the trace elements Mb, Co, Cu, Zn, Ma (Stephens and Donald 1958).

Climate

The South-east has a Mediterranean climate, defined by warm to hot dry summers and cool wet winters, with a mean annual rainfall ranging from 550 to 750 mm. The extremes of the distinct wet and dry season are accentuated not only by water availability, but temperature, evaporation and humidity ~~as well~~ (Figure 2.1). Other regions that share this climate (Figure 2.2) occur between latitude 30 and 40 degrees north (parts of the west coast of the U.S.A., Spain, Portugal, Morocco, Italy, Greece, Turkey, Lebanon, Iraq and Iran) and between latitude 30 and 40 degrees south (parts of Chile, South Africa and south western and eastern Australia). Aquatic habitats in these environments (Figure 2.2) share a surplus of water in winter and dry summers, as well as similar rainfall (range: 253-893 mm) and summer (range: 20-30 C°) and winter (range: 5-10 C°) temperatures.

Pre and Post Drainage Hydrological Environment

Prior to any changes, 54 percent of the South-east was subject to winter flooding to a minimum of 30 cm (Figure 2.3). Due to the gentle gradient of the land, surface water courses were sometimes random and led to numerous swamps and lakes. In 1863, a government expedition noted "*The character of the country is very peculiar, no large river exists, and there are no high mountains to form a watershed and force the drainage by a strong fall into any particular channel. The consequence of this is a number of lakes, lagoons, and swamps which in winter are of considerable depth and in summer, by evaporation and soakage are nearly dry.*" (Hanson 1863 in South Eastern Drainage Board 1980). In 1866 the Surveyor General Mr Goyder, reported that wetlands; sometimes never dried, could extend for 9.7 km and were deepest on the western side, generally between 30 to 180 cm deep but sometimes reaching 210 to 240 cm. These comments illustrate the extensive nature and variety of wetlands that once existed. Originally, winter rainfall collected in the lowland areas. The individual waterbodies then connected to form wide shallow sheets of water that flowed slowly to the north-west along the interdunal corridors. Due to the impermeable fine grained sediments (Shepherd 1964b), and the high level of the unconfined groundwater, which varies from less than 2 m on the interdunes and up to 35 m beneath the dune ranges and in winter may rise above the surface, water was not absorbed easily and was left to evaporate.

Drainage was first undertaken privately and on a small scale between 1840 and 1860. Submissions for government assistance followed wet winters, but records of dry periods also exist, implying that periodic drought and seasonal variation was typical a hundred years ago. A comprehensive drainage scheme began in the 1860's (Williams 1975) and has enabled European settlement and agriculture to proceed, resulting in a massive change to the environment. Of the 398406 ha of land originally inundated in the South-east, 381108 ha has been drained and put to pasture. Of the remaining 26831 ha (3.5 %), 12223 ha (1.4 %), including Hacks and Bool Lagoon are used as equalizing or buffer storage basins. Water is drained via an extensive network of channels covering 1450 km that criss-cross the area, some in the direction of historical watercourses and others that cut through the ranges at right angles taking the shortest route to the coast. Originally the aim of the South Eastern Drainage Board (SEDB) was to drain surface water to the ocean, but recently there has been the deliberate attempt to conserve water by moving it around the channel system, reclaiming wetlands where possible.

Pre and Post Drainage Vegetation Environment

There is little information about the vegetation throughout the region prior to drainage. A vegetation map based on early surveyors notes and recent government reports described the lowland area or flats as predominantly *Gahnia trifida* and *G. filum* grasslands (SEDB 1980). Other associations were dominated by *Eucalyptus camaldulensis* (river red gum), *E. ovata* (swamp gum) and *Xanthorrhoea australis*, *Hakea rostrata* and *E. diversifolia* (soap mallee).

The component plants of these groups were listed, but with the exception of some species that survive in damp places, aquatic plants were not included.

It has been reported that the natural vegetation of the area has almost disappeared as a result of drainage operations (SEDB 1980). The wetland habitat and aquatic vegetation that does remain may reflect a small part of the original hydrological and floristic diversity. In addition to hydrological changes, these habitats are subject to salinity, grazing and nutrient enrichment (Lewis *et al.* 1981). In a recent survey of remnant native vegetation in the South-east, aquatic plant communities were rated as rare (Sparrow 1991). In general there is scant information about the floristic ecology and composition of South Australian wetlands (but see Brock 1981 & Lange 1983). Many surveys that included wetland areas have failed to cover aquatic vegetation and often neglected semi-aquatic or shoreline plants as well.

2.4 HACKS AND BOOL LAGOON

Morphometry

Hacks and Bool Lagoon (Latitude 37° 08' S, Longitude 140° 40' E) are situated on the farthest inland plain (Figure 2.3) and constitute the largest wetland in the South-east (2883 ha: Figure 2.4). The main body of the system is made up of five major basins (Hacks Lagoon, Main, Central, Central-Western, Western). In addition, there are a variety of unnamed smaller basins along the convoluted western shoreline. These, together with the Central-Western and Western basins are known as the Western basin system. Morphometrically the basins are round and plate-shaped. The formation by wave action of lunettes on the eastern shorelines has resulted in the basin floors sloping from the shallow eastern sides to ✶ the deeper western sides. A transect from the West basin to Hacks Lagoon, surveyed in 1960, showed a gradual decrease in the mean elevation of the lagoon floor from the West basin to the Main basin (Figure 2.5). At a given elevation, the depth in the Western basins would therefore be approximately 20 to 30 cm shallower.

★ Transect surveyed by the SA Department of Engineering and Water Supply

Pre and Post Drainage Hydrological Environment

In 1858 a property bordering the lagoon (Killanoola) was described as two-thirds underwater in a wet winter, whilst one-third was rarely dry (Murdoch and Parker 1974). In those days, Bool Lagoon was known as 'Lake Bool' suggesting a much wetter environment than today. This cannot be verified because accurate water level records exist only from 1980. In contrast to the well-defined shoreline that exists today, the boundary between the lagoon and surrounding farms would have been hard to discern. The Lagoons were fed by Mosquito Creek floodwaters, most of which overflowed to the north, successively filling swamps along the interdunal Marcollat watercourse. Water entering the lagoon was described as 'tea-stained'.

The first record of alteration to the natural water regime was noted in 1863 when Mr Seymour of Killanoola '*had drained a large tract of country into the lake*' (Hanson 1863 in SEDB 1980). Nearly a hundred years later the construction of stop banks or levees around the northern perimeter of the main basin prevented Mosquito Creek flooding land to the north. Mosquito Creek was then excavated and broadened to carry and funnel additional floodwaters into the Lagoon. Water entering the lagoon was thereafter described as 'muddy' (SANPWS Ranger 1967-1972). Subsequent stop banks around the whole shoreline sealed the basins from the surrounding lowland (Figure 2.4). The first outlet channel was completed in 1910; however, it was not connected to the drainage channel until 1966. The installation of a weir and regulator gates meant water was first ponded in the winter of 1968. Further upgrading of the Mosquito Creek channel in the 1970's enabled comprehensive drainage of land upstream. In addition, a 40 m wide, open water flowpath through the middle of the lagoons helped to facilitate the movement of water (Figure 2.4). The first two kilometres were excavated to several metres in order to increase flow and prevent plant colonization, which the SEDB felt was impeding flow elsewhere. Herbicide spray extended the flowpath into the middle of the Main Basin in 1983, when the lagoon was dry. Since then, this part of the flowpath has gradually lost its integrity with the gradual re-establishment of vegetation.

An estimate of lagoon water levels prior to 1980 (Department of Environment 1985), using measurements of Mosquito Creek flow rates and volumes recorded infrequently by the SEDB at Struan (8 km from the inlet), showed that the mean maximum water level in the 1980's was significantly greater (P:0.03) than in the three decades between 1930 and 1960 (Figure 2.6, Table 2.1). In terms of depth, this equated with a mean increase of 46 to 57 cm, which took maximum levels to 109 ± 33 cm in Hacks Lagoon and to 94 ± 33 cm in the Western basins. The mean range of maximum depths, changed from 0-110 to 76-142 cm in Hacks Lagoon, and from 0-95 to 61-127 cm in the Western basins. Consequently, the frequency and duration of drawdowns decreased (Table 2.1). In 1938, 1940, 1945, 1949 and 1958, the lagoon did not flood at all, which produced long periods (18 to 30 months) with no standing water (Figure 2.6). In the 1980's, there were two drawdown events and these lasted no more than a few months. Between 1960 and 1989 there were slight increases in the mean floor elevation of the Main basin and Hacks Lagoon (Table 2.2), which may be due to increased silt deposition nearest the inlet following diversions in the 1960's. With the exception of the flowpath area which did not exist in 1960, there were no changes in the three basins west of Big Hill.

Pre and Post Drainage Vegetation Environment

With the exception of a small amount of open water, the lagoon is densely vegetated throughout. The area between high and mean water level represents the rim of the plate, and these marginal areas have the greatest diversity, housing numerous semi-aquatic plants adapted to the regime of seasonal inundation. The major body of the lagoon is less diverse. The shallow nature of the lagoons is reflected in the dominance of emergent species, which are divided into sedges (*Baumea arthrophylla, B. articulata, B. juncea*), reeds (*Phragmites australis, Typha domingensis*) and fleshy leaved species (*Triglochin procerum, Villarsia reniformis*). The most common submerged plants include two species of *Myriophyllum* and *Potamogeton* (*M. salsugineum, M. muelleri, P. tricarinatus, P. pectinatus*) and several charophytes. The bulk of the lagoon's aboveground plant biomass is observably made up of *Triglochin procerum* and *Baumea arthrophylla.*

Classification of the vegetation failed to place all species into separate groups (Rea 1985). This reflected the lack of defined boundaries between plant associations within the lagoon, despite the emergents showing a propensity to form monospecific stands. Nevertheless analyses consistently extracted associations dominated by *B. arthrophylla* and *T. procerum* *B. arthrophylla* can occur with the submergent *Utricularia australis* and charophytes. Established stands of *T. procerum* occur with wet-herbland plants (*Crassula helmsii, Ranunculus rivularis, Rumex bidens*) which emerge during drawdown, but where it is colonizing new areas it can occur with submerged species (*M. salsugineum, P. tricarinatus*).

No information about the vegetation is available prior to drainage operations. In 1920, it was noted that *B. arthrophylla* averaged 60-75 cm tall (Murdoch and Parker 1974), occupied the Western basins and extended into the Main basin, about 60% of Bool Lagoon. This pattern was also noted by the Ranger in the 1960's, who reported it growing around the margin of Hacks Lagoon as well (Sorrell 1970). These sedgelands were burnt and grazed up to the 1960's, but since dedication of the park in 1967 there has been comparatively little human interference. Changing distribution patterns were first noted in 1970, when the Ranger recognized *B. arthrophylla* was being adversely affected at the eastern limit of its range. Today, it is no longer present in Hacks Lagoon or the majority of the Main Basin. Comparable examples of *B. arthrophylla* with those described in the 1920's can only be found around the lagoons' perimeter. Elsewhere it grows to between 1-2 m tall. Today, observations and landsat photos, suggest that *B. arthrophylla* occupies about 35% of Bool lagoon, a reduction of 50% over approximately twenty years. *T. procerum* occupies at least 40%, having taken over the territory lost by *B. arthrophylla*. This pattern is also evident in the colonization of *T. procerum* in the flowpath since it was last sprayed (1983). Most of the vegetation was originally *B. arthrophylla*, but very little of this species has returned.

2.5 WATER LEVEL MANAGEMENT

The only control over water levels is the opening and closing of the regulator gate, at the end of the outlet channel (Figure 2.4). As the lagoon fills, the SEDB aim to keep water flowing out as fast as it flows in. Because water drains fastest when the lagoon is full, this is not simply achieved by leaving the gates continuously open, and they can be repeatedly opened and closed throughout winter. The removal of excess floodwater prevents water exceeding the stop-banks and flooding farms, and also allows the system to function more efficiently as a buffer storage basin the following winter. If the drain is full, the gates are kept shut to stop additional water breaching the drains downstream. The lagoons' situation in the far east of the region, means they can be used as a storage basin while country downstream is drained. This careful management of water levels prevents flooding in either place. Also taken into account are the wishes of the South Australian National Parks and Wildlife Service who prefer high winter/spring levels, which provide a summer water bird refuge and which meet specific breeding requirements and recreational interests. Since 1985, water has been allowed to drain freely from the lagoon during winter, as long as the regulator gates are closed to meet an agreed spring ponded elevation of 48.60 AHD.

2.6 PRESENT WATER REGIME

Input via run-off and rainfall are insignificant due to the flatness of the land and the patchy nature of rainstorms. Water principally enters the Lagoon in winter via Mosquito Creek, which drains a 1215 km^2 catchment. The daily Creek volumes at Struan (Figure 2.8) in 1986 show that water enters the lagoon in flooding events. The mean annual rainfall (1980-89) is 579 mm, but in the catchment it is slightly higher (628 mm). The water level in Hacks Lagoon during the 1980's (Figure 2.7) showed a regular pattern of winter flooding and drying over summer, with maximum levels in spring (September-November) and minimum levels in autumn (March-May). The timing and magnitude of the drying phase depended on the timing and magnitude of flooding in the previous winter. For instance, below average rains in 1982 and 1985 resulted in drawdown during 1983 and 1986, whereas late and substantial rains in 1986 kept levels relatively high throughout 1987. Summer temperature and humidity may also play a role. The magnitude of flooding varied from 52 cm (1982) to 178 cm (1981), but maxima were not maintained as water was drained to meet the requirements of the water level policy. In 1981, water levels exceeded the lagoons' capacity and caused widespread flooding. This was considered a 1 in 50 year event

(Department of Environment and Planning 1985). Plants growing at the deepest site in Hacks lagoon (47.60 AHDm) are generally always submerged, but can experience a maximum depth of 140 cm and a maximum annual change in depth of 120 cm.

Spatial differences in water regime were also evident. Data from 1987 showed the maximum monthly flow rate slowed markedly between Mosquito Creek at Struan and the outlet channel (Table 2.3). Hacks Lagoon received the full brunt of floodwaters and was filled more rapidly and to greater depths than the Central basin, which in turn was filled more rapidly and to greater depths than the Western basin (Figure 2.9). Water level fluctuations progressively moderated, moving downstream, due to the high velocity of channelled inflowing water slowing down as it dissipated across the wide, shallow and densely vegetated basins. Spatial differences were greatest during flooding, whereas pre and post winter levels coincided.

In the Central-Western basin, between Apr-88 and Apr-89, the elevation 47.70, was always inundated (Figure 2.10a). Water depth was most often between 21-40 and 81-100 cm. Maximum depths (101-120 cm) were experienced for 7 days. At the same elevation in Hacks Lagoon, the depth did not fall below 21 cm, and was between 101-140 cm for 40 days (Figure 2.10b). At an elevation of 48.25, plants would have experienced drawdown (exposure) for 152 days in the Central-Western basin, and 128 days in Hacks Lagoon.

A plot of elevation against the ratio of days inundated to exposed, illustrated the annual variability in inundation, (Figure 2.11a). For example, at 47.95 in the Central Basin, the ratio was 1.57 in Mar-87 and 4.29 in Apr-89. With a linear decrease in elevation, there was an exponential increase (range r^2: 0.96-0.99) in the degree of inundation/exposure. For plants growing in the Central basin, the difference between growing at 48.40 and 48.15 was smaller than the difference between 47.95 and 47.85. This situation held for the Sum Water Regime or depth and duration of inundation (range r^2: 0.98-0.99) (Figure 2.11b). Although this indice does not distinguish between inundations of long durations at shallow depths (e.g. 100 days at 10 cm) and short durations at deep depths (e.g. 10 days at 100 cm), it more completely summarizes water regime than the ratio of inundation to exposure, which only takes into account time (days), and not depth (cm).

2.7 *Triglochin procerum* and *Baumea arthrophylla*

The genus *Baumea* has a cosmopolitan distribution, but is particularly well represented in Australia and New Zealand. The genus and family (Cyperaceae) are under taxonomic revision in Australia. The most recent accounts are in Wetland Plants in New Zealand (7 spp, Johnson and Brooke 1988) and the Flora of South Australia (10 spp, Jessop and Toelken 1986), where descriptions differ little from the original edition. A few *Baumea* species are true aquatic plants, but most are associated with waterlogged soils. The three species in Bool Lagoon (*B. juncea, B. arthrophylla, B. articulata*) can be separated by their size and habitat. *B. juncea* has solid stems to 1 m and is restricted to marginal areas. *B. arthrophylla* has pithy stems to 2 m and is found throughout the lagoon, while *B. articulata* has hollow stems to 3 m and occurs in the deepest, most permanent areas. The most common species in the Lagoon is *B. arthrophylla* (referred to as *Baumea* hereafter). It forms extensive monospecific stands characteristic of undisturbed shallow wetlands. Due to the uniformity of these 'sedgelands' and the past derisive attitude toward wetlands, they must have been seen as monotonous and unproductive, as their distribution has been greatly reduced. The importance of these often infertile habitats has been emphasized (Moore *et al.* 1989) and they provide a habitat for a diverse number of birds, many of which are now rare.

Baumea shoots are made up of 1-5 attenuate rigid stems. Leaves are reduced to papery bracts at the shoot base. New shoots arise from adventitous buds (maximum ten) at the base of the parent shoot. Rhizomes (diameter <1.5 cm), exist as 'pieces' which may represent shoot clumps as observed aboveground. They lie close to the surface and do not branch. A small root mass is restricted to the shoot base and is also not deeply buried. Populations appear to be composed of vegetative shoots only. Many dead stems form a thatched layer, which together with a high shoot density, contribute to the impenetrable nature of stands. The documented periods of flowering (Sep-Mar; Jessop and Toelken 1986) compare with observations; although seedlings have not been observed.

Triglochin is also a cosmopolitan genus in the small monocot family Juncaginaceae. In Australia three species were described as aquatic (Aston 1973) although eleven other small, uncommon species are generally associated with damp places. Two of the three species found in the Lagoons can be separated on the basis of size and position on a water depth and permanence gradient. The slender, short *T. striatum* is found high on the gradient whereas the tall, robust *T. procerum* (referred to as *Triglochin* hereafter) is found in more permanent and deeper water. A third uncommon species is as yet unnamed (Aston unpublished). The robust form appears to be the most prevalent in Australia and exhibits a range of morphological types. McDonell (1969) proposed four growth forms, based on leaf form and habit and the degree of twisting in the fruit. A similar diversity of foliage and fruiting characteristics was noted by Aston (1973) and three ploidy levels matched to them by Robb and Ladiges (1981). This variation has not been supported by taxonomic changes to date. In the Lagoons, *Triglochin* has erect leaves and is classified as an emergent. The fruit are tightly packed around the scape producing a spike-like raceme. The fruit have six twisted carpels, each with one seed (<10 mm).

Triglochin shoots consist of up to seven basal leaves which are plano-convex in cross-section and spongy and flattened or leathery and terete, depending on the depth. Althought not rigid, they are erect when mature, later arching over so that leaf tips touch the water surface, a shoot habit which means that individuals take up considerable space beyond the shoot base. Seedlings are distinguishable by narrow, thin leaves which float. Rhizomes (diameter <3.5 cm) are deeply buried and covered by a dense mat of short brown fibrous roots on the upper side, and a bulky mass of fleshy white roots on the lower side. Some of these terminate in tubers, storage organs incapable of reproduction, which are up to 50 cm below the surface. The random and laterally arranged shoot buds produce branching rhizomes. The connection between the shoot and rhizome is fragile and difficult to examine due to the abundance of roots. Both vegetative shoots and seedlings make up the population. The documented periods of flowering (Sep-Apr; Sainty and Jacobs 1981) and fruiting (Aug-Apr; Jessop and Toelken 1986) extends from spring to autumn, but these events occur earlier in the Lagoons.

2.8 DISCUSSION

The South-east

The Mediterranean climate, and geological landscape of impermeable flat land overlying calcareous sediments, have together shaped this ancient wetland environment. From saline coastal lakes to inland freshwater lagoons, a gradient in water salinity and permanence represents stages of wetland development and ecological specialization of the flora. The fluctuations in water level have more in common with tropical wetlands than the stable water levels of northern Europe. However, in the South-east, the wet and dry seasons fall in winter and summer respectively, whereas in the tropics the wet season coincides with favourable summer temperatures and produces a growing season with fast growth rates and high productivities (Finlayson 1991). Because water becomes limiting over summer in the South-east, the highest periods of growth may not necessarily be in summer. In comparison with more Northern and Southern latitudes, however, the growing season is long, and growth may continue throughout the relatively mild winters (Roberts and Ganf 1986, Hocking 1989a), when water is in good supply. In the tropics, fluctuations in water level not only differ temporally, but in degree, with monsoonal rains producing large and sudden changes. Despite this difference, temperate regions are less hydrologically constant than the tropics (Janzen 1967), which are characterised by highly variable precipitation (White 1979). The scale of water level fluctuations in Mediterranean wetlands are not as unpredictable as the episodic changes in arid environments, nor like the irregular drawdowns which persist for several years in the prairie marshes of Northern America (van der Valk 1985).

Despite characteristics that separate the South-east wetlands from other regions, there exist influences that unite them all. Notably, these are enrichment from surrounding land use, many types of industrial and agricultural pollution, drainage for land reclamation and storage for irrigation, stock and domestic use. The South-east, now a successful farming district, is to various degrees subject to all of these influences, and there are few wetlands that remain sealed off from adverse catchment practises and which have escaped

★ Because nutrient dynamics (input, output, retention) are a function of water regime (Howard-Williams 1985, Verhoeven *et al.* 1988), differences in ephemeral versus permanent conditions can be expected. Although not the subject of this study, it was considered appropriate to raise the issue in the discussion of this chapter, especially given the recent evidence for the significant interaction between water regime and N utilization by emergent macrophytes (Neill 1990, 1992).

hydrological changes.

Hacks and Bool Lagoon

The effect of drainage operations since 1967 has been an increase in depth, reduced frequency and duration of ~~of~~ drawdown and more stable water levels. Because water is now retained, the Lagoons have changed from an open to a closed system. This has implications for the status of the ecosystem, which as an undrained sink is gradually accumulating both allocthonous and autocthonous material. As an open waterbody the lagoons would dry out and the winter floodwaters that carried little suspended material flushed the system out, a cycle which would contribute to the removal and break down of dead organic matter. High sediment organic content was shown to adversely affect the growth of submerged (Barko and Smart 1983) and salt-marsh species (Bertness 1988). Prolonged anoxia in the sediment produced by the increase in depth and duration of inundation, may be suppressing the decomposition and resupply of nutrients from an increasingly rich sediment.★ Nonetheless, concentrations of the major nutrients, do not suggest nutrient limitation (Ganf and Rea unpublished). The observed large quantities of total biomass, much of it dead, indicates the vegetation may be suffering from highly anaerobic conditions (Armstrong 1975).

The possible change in nutrient dynamics which may be impacting on the vegetation, focusses attention on the lack of substrate exposure. However, nutrient availability is not the only factor affected by a change from a wet/dry cycle to more permanent conditions. Falling water levels expose more plant tissue, enabling access to a greater supply of photosynthetic and respiratory gases. It is thus the fluctuations in water level that are hypothesized as important, and not necessarily the depth correlated factors such as light, temperature and pressure. The importance of the latter two factors with respect to the growth and survival of aquatic plants, has been dismissed (Pip 1989), and although light influences the distribution of submerged plants (Spence 1982, Chambers 1987), it has less significance for emergents. The major plant resources tied in with the hydrological environment are thus sediment nutrients, carbon and oxygen. Because plants usually compete for only one or two resources (Tilman 1990b), any plant interactions probably involves at least one of these.

As well as fluctuations in water level, variation in timing may also influence species composition and distribution. Years of late and early flooding, may favour emergent and submerged species, respectively. A switch in conditions that favours one type of plant, and then another, may hold the vegetation in dynamic equilibrium. Species coexistence may be prevented by removing this natural variation by for instance stabilizing water levels or making predictable the timing of flooding. Such changes which have occurred in the Lagoons may have reduced the diversity and extent of habitats by shrinking the marginal herbland to a narrow fringe, and increasing the major body of the basin, which appears to provide the fundamental niche for a small number of conspicuous species.

The spatial differences, due to the position relative to the inlet, also means that at similar elevations there may be quite different water regimes. The habitat of Hacks Lagoon is deeper, more permanent and subject to greater fluctuations in water level than the Western Basins. Sites across an elevation gradient had markedly different water regimes. The degree of inundation increased exponentially, confirming the difference between depth and elevation gradients. Data taken from one point in space and time, or without reference to depth or the past water regime, is thus meaningful in a restricted context only. There was considerable temporal variation at each site due to variation in the timing and magnitude of winter floods. This means that over time, plants experience a variety of water regimes and must be able to tolerate conditions that switch from one extreme to another. Variability also "spreads out the effects of extreme conditions across a wider area over time" (Wilcox and Meeker 1991). This thesis replaces the misleading term water depth gradient with elevation gradient, which is defined as a simultaneous gradient in increasing depth and duration of inundation and decreasing frequency of exposure. 'Depth' is used to describe instantaneous depth, whereas 'water regime' (defined in the Introduction) integrates continuously changing depth over time.

Baumea arthrophylla and *Triglochin procerum*

Although *Baumea* and *Triglochin* are both perennial rhizomatous freshwater emergents which form populations of vegetative shoots, there exist distinct differences in their morphologies and population structure. The photosynthetic organs of *Baumea* are cylindrical cuticularized stems, which contrast with the fleshy flattened leaves of *Triglochin*. Despite their clear emergent status, *Triglochin* may thus be able to also utilize dissolved CO_2 and O_2. It appears that *Baumea* holds more aboveground tissue than *Triglochin*, whereas *Triglochin* holds more root tissue than *Baumea*. Unlike *Triglochin*, the high density of *Baumea* shoots leads to dense stands, with little space available to other species. These characteristics, together with their separation across a depth gradient (Ganf and Rea unpublished), point to the increase in depth and duration of inundation, favouring *Triglochin* over *Baumea*.

Given the pre-drainage environment and widespread distribution of *Baumea*, this species was evidently adapted to shallow conditions with regular and sometimes prolonged periods of drawdown, whereas the lack of references to *Triglochin* suggests this habitat was not conducive to this species. There are three possible scenarios as to why the documented changes have occurred. (1) *Baumea* may not have tolerated the increase in water level and therefore passively retreated. *Triglochin* could then have taken *Baumea*'s place passively, if it was just tolerating the new conditions or (2) more actively if it was able to match the changes. (3) *Baumea* may have tolerated the new regime but been unable to survive in the presence of *Triglochin* which, having matched the changes, had gained a competitive edge.

CHAPTER 3: INDIVIDUAL RESPONSE TO DEPTH AND WATER REGIME

3.1 INTRODUCTION

Aquatic plant science originated from cool temperate regions, where concepts such as zonation and the hydrosere were formulated (Pearsall 1920, Misra 1938, Spence 1967). These theories may be inappropriate for describing distribution patterns in the South-east of South Australia, where seasonal extremes of rainfall and incident solar radiation are pronounced, and strongly affect wetland water levels. Plant response to depth and depth correlated factors, may be complicated or overridden by the effects of fluctuating water levels. Where water levels fluctuate, any point along a depth gradient will experience continuously changing water depth. In such conditions, the term depth gradient is misleading, and elevation gradient is more appropriate. The difference between depth and elevation was recognized by Roerslett (1984), who proposed a method to quantify the hydrological environment of regulated Swedish Lakes. His scale of water level fluctuations (2-7 m) and plant responses (submerged plant community distribution) were too large to be translated meaningfully to this study, where the question concerned the performance of emergent plants within their distribution limits, and under annual fluctuations (range: 70-120 cm). In this Chapter, data is presented from a series of plant harvests, that were used to investigate the relative influence of depth and water regime, exemplified by sites across an elevation gradient.

One of the consistent responses to depth is an increase in shoot height (Lieffers and Shay 1981, Stevenson and Lee 1987, Hultgren 1989, Grace 1989, Waters and Shay 1990). This can be interpreted as a response to maintain a favourable carbon balance (Mooney 1972), which can be also achieved by increasing the number of leaves and/or their diameter. Such increases can result in increases or decreases in ramet biomass (Yamasaki and Tange 1981, Stevenson and Lee 1987, Grace 1989). Plants with a high tolerance to deep water, can maintain or increase ramet biomass by reallocation, but for species with a low tolerance, increases in height are at the expense of overall biomass. An alternative response to matching environmental changes is to tolerate them by existing in a state of dormancy, where there is no net growth.

The influence of depth on flowering is also variable, being a stimulus for some plants (*Scolochloa festucacea* Smith 1973, *Scirpus maritimus* var *paludosus* Lieffers and Shay 1981) but not others (*Zizania aquatica* Stevenson and Lee 1987, *Typha* spp. Grace 1989). Lieffers and Shay (1981), and Brock (1991) suggested that plants vary vegetative and sexual reproduction in habitats where water levels fluctuate, to match changes in their relative success. For example, the seeds of *Scirpus maritimus* var *paludosus* which flowers in deep water, float, and have a long dormancy. These attributes favour their chances of survival and development, because emergent seedlings only survive under damp or shallow conditions (Keddy and Ellis 1985, Keddy and Constabel 1986).

Even though many studies have measured the influence of depth, studies where water levels fluctuate have failed to recognize that depth represents a water regime. There was no spatial variation in the sampling procedures of van der Valk and Davis (1978b), Shay and Shay (1986) or Sjoberg and Danell (1983) and Hogeland and Killingbeck (1985), who respectively measured the influence of 'mean depth during the growing season' and 'mean depth and range before and after flooding'. Although the importance of water level fluctuation has been raised many times (Harris and Marshall 1963, Hejny 1971, Van der Valk and Bliss 1971, Kvet and Ondok 1973, Gaudet 1977, Lieffers and Shay 1981, Van der Valk 1981, Briggs and Maher 1985), there remain many questions about its influence on individual plant morphology, biomass and population structure.

The ecology of aquatic plants, in regions where the driving forces are fluctuations in water chemistry and permanence, has been discussed by Mitchell and Rogers (1985), Shay and Shay (1986), Brock (1986) and Williams (1988). In Bool Lagoon, sediment and/or water chemistry did not explain the distribution of *Baumea* and *Triglochin*. Moreover, populations of *Baumea* gave way to *Triglochin* across an elevation gradient (Ganf and Rea unpublished). The null hypothesis, was that instantaneous depth was more important in determining population biomass and structure, than water regime. Harvests were undertaken at the extremes of autumn drawdown and spring flooding, to cover the range of depths that plants experienced, and at sites across an elevation gradient, to cover the range of water regimes. Above and belowground morphological, demographic and biomass characteristics were measured. In addition, an objective of the data was to provide information about the most favourable conditions for growth and reproduction.

3.2 METHODS

Field

The dates, depths, water levels, quadrat size and number of replicates are summarized in Appendix 3.1. Harvests were made in spring and autumn, following the longest period of inundation and exposure, respectively. They spanned a 75 cm elevation gradient and were taken at either end of the lagoon where each species dominates (Rea 1985). These were monospecific stands in Hacks Lagoon (48.45-47.70 AHDm) for *Triglochin* and at the Fences (48.30-47.55 AHDm) for *Baumea* (Figure 2.4 for location). This included the upper limit of their distribution but not the lower, as both species occur throughout the basins, indicating that the lagoon habitat is never too deep to restrict them. Quadrat size (*Triglochin*: 1.0x0.2 m, *Baumea*: 0.2x0.2 m) was obtained through the pattern analysis technique of Kershaw (1960) (Rea 1985). This size and the number of replicates (4-6) fell into the categories of highest precision for estimating the standing biomass of aquatic plants (Downing and Anderson 1985). Quadrats were sampled randomly to a depth which included all live material, along depth contours that were located with a metre rule or level and staff. In May-87, a belowground sample (25x25x25 cm) of *Baumea* was dug from four sites across an elevation gradient, and the diameter and length of all rhizomes in each sample recorded. In May-86, *Triglochin* seedlings were observed on the exposed mudflats in Hacks Lagoon. Their density, and those of adult shoots, were recorded along a 30 m belt transect (48.00-47.60 AHDm) in two contiguous 1.0x0.5 m quadrats. The survey was repeated three months later (Aug-86) when the depth range across the gradient was 0-50 cm.

Plant measurements

The above and belowground plants were harvested intact. Shoots were clipped at sediment level and leaf and stem heights measured. 'Mean' heights represent the entire sample and 'maximum' values represent the 10 tallest leaves or stems from each sample. Diameter was measured with calipers at the broadest part of the leaves of *Triglochin* and the stems of *Baumea*. This was about a fifth of the total height of leaves and at the base of stems. Emergent height was total height minus depth. Fresh weight was recorded in the field and dry weight on returning to Adelaide. Material was kept cool in "eskies" and a cold room for up to 72 hours before being separated into live and dead shoot, root, rhizome, tuber, inflorescence and fruits. Fruits were counted from all inflorescences and the number of seeds estimated by multiplying fruit number by six, which is the maximum and most common number. Tissues were dried in a fan-forced oven at 60-70 C° for 48-72 hours and dry weight recorded (g dwt).

Despite small amounts of senescing tissue, dead tissue (above and belowground) was noticeably absent in *Triglochin* and no measurements were taken. Belowground, *Baumea* consists of roots and rhizomes in various stages of health and decay. Rhizomes which gave rise to a live shoot were classified as live although they were often connected to older rhizomes, which in turn were sometimes connected to dead and decomposing rhizomes. The length of rhizomes on these pieces was measured. Roots attached to live rhizome were considered live. Due to the deeply buried nature of *Triglochin* and the sediment in Hacks Lagoon (sticky clay and dense gley), only one belowground quadrat was harvested (Mar-87).

The dead shoots (or expended buds) of *Baumea* were evident as rhizome crowns (named for their shape). Rhizomes of sedges (ie. *Baumea*) arise from either diageotropic buds that grow horizontally in the soil or from apogeotropic buds which grow vertically and emerge above the soil, soon after their dormancy has broken (Alexeev 1967 in Soukupova 1988). The expended shoot population was scored as long (diageotropic), short (apogeotropic), live (reflecting present conditions) or dead (reflecting past conditions). This was undertaken in Mar-87 for all rhizomes in the belowground samples. From the May-87 harvest, the diameter of all rhizome crowns (short, long and unknown) were recorded as well as the length of all rhizomes, including those yet to emerge. No measurements were taken for *Triglochin* due to the small sample size and lack of replication. Population data is expressed per metre squared, or as ratios (eg. root:shoot). Shoot biomass is specified as aboveground live or dead dry weight (g dwt). Individual data is either expressed on a per ramet basis or as mean biomass per shoot.

Water Regime and Analysis

Water levels from Hacks Lagoon are compared to *Triglochin* data, while those from the Central-Western basin are compared to *Baumea* data. Due to the annual variability in water regime at the one elevation and the variability between basins (Chapter 2), it was invalid to compare plant data to elevation. To overcome this problem, the Sum Water Regime (SWR, Chapter 2) was used as an index of the hydrological past. Values were calculated over intervals of 30, 90, 180 and 360 days prior to harvests. The hypothesis was that depth, represented by the most recent water regime (30 days prior to harvest), had a greater influence than the most distant water regime (360 days prior to harvest). This provided a water regime axis, that was the closest feasible representation of the hydrological conditions that plants experienced. Except where modal responses were evident, linear regressions (Statistix 1987) were undertaken on autumn and spring data, separately and combined. The independent variables were depth and SWR, and the dependent variables were live aboveground mass, shoot density, mean shoot mass and maximum stem or leaf height.

Two sets of data (*Triglochin* aboveground mass g m^{-2}, *Baumea* shoot density m^{-2}) that showed clear linear correlations, were chosen to identify responses on a more detailed scale. The SWR was calculated for every record of water level over the 360 days prior to sampling. Linear regressions were performed between each of these values and the chosen data sets, and r^2 values plotted against time.

As an estimate of stand variability, the coefficient of variation (V^*) was calculated for leaf densities. The number of *Baumea* stems per shoot in autumn and spring, and across an elevation gradient, were compared by 2-way AOV. The number of *Triglochin* leaves per shoot were compared by 1-way AOV's within and between seasons. Belowground features of *Baumea* and aboveground features of a flowering *Triglochin* population were compared by 1-way AOV.

3.3 RESULTS

3.3.1 Aboveground Responses to Depth and Water Regime

When the aboveground characteristics were plotted against depth, the autumn and spring data sets were clearly separated, because they represent the shallowest and deepest extremes in the Lagoons. In autumn, three of the seven *Baumea* sites and three of the five *Triglochin* sites, were exposed, but because the sediment remained waterlogged, the depth was called '0 cm'. *Baumea* data showed similar trends in each season. Its aboveground mass had a modal response, whereas its shoot density was negatively correlated in both seasons (Figures 3.1a & 3.1b, Table 3.1). Mean shoot mass was positively correlated to depth in spring only (Table 3.1, Figures 3.1c), whereas this relationship held for the maximum height of stems in spring and for combined seasonal data (Table 3.1, Figures 3.1d). *Triglochin*'s aboveground mass, mean mass per shoot and maximum stem height were positively correlated to depth in both seasons, whether analysed separately or together (Figures 3.1e, 3.1g & 3.1h, Table 3.1). Its shoot density showed a modal response with maximum values at 50 cm depth (Figure 3.1f). *Baumea* achieved much greater aboveground masses (maximum: 1516 v 429 g m^{-2}) and shoot densities (maximum: 1945 v 67 shoots m^{-2}), whereas the mass of individual shoots was smaller than *Triglochin*'s (maximum: 2.34 v 8.29 g). The photosynthetic organs of *Baumea* and *Triglochin* reached similar heights (maximum: 169 v 158 cm).

A SWR of zero, means the plant was exposed over the measured interval. *Baumea*'s aboveground mass was unrelated to the Sum Water Regime over 30 and 90 days, but at 180 and 360 days, a clear pattern emerged, with maximum values at intermediate levels of inundation (Figures 3.2a-d). *Triglochin* held positive correlations between its aboveground mass and all water regimes, in both autumn (0.79-0.56) and spring (0.62-0.52), although values decreased as more of the hydrological history was incorporated (Figures 3.2e-h, Table 3.1). This trend was amplified when seasonal data were analysed together (0.85-0.06), a result which highlights *Triglochin*'s sensitivity to depth. Irrespective of the sampling date, the most recent water levels control *Triglochin*'s aboveground mass. Because new information is additive (ie. water regimes are not independant), the correlation only changes when two contrasting seasons such as these, are analysed together.

These results held for the maximum height of *Triglochin* leaves (Figures 3.3e-h, Table 3.1), the mean height of *Baumea* stems (Figures 3.2a-d, Table 3.1), as well as the mean mass of shoots (Figure 3.4, Table 3.1) and their density (Figure 3.5, Table 3.1). Figure 3.2 shows data for *Baumea*'s mean stem height (versus maximum stem height in Figure 3.1d). Unlike the tallest stems, which were positively correlated to depth, mean stem height showed a modal response to aboveground mass. The large standard deviations at the lowest elevation illustrate considerable variability, with only some stems achieving the necessary height.

Figure 3.6 illustrates these different responses on a more detailed scale. Water regime explained the most variation in *Triglochin*'s aboveground mass, immediately (days) prior to sampling, in autumn and spring (Figures 3.6a & 3.6b). Thereafter, the correlation decreased, albeit only a small amount. The increase at 300 days (Figure 3.6a) was due to increasing water levels in the previous autumn, and as such was an artifact of the data. For *Baumea* shoot densities, the best correlation with water regime in both seasons, was between 180 and 270 days before harvest. Thereafter water regime added no information. The initially constant relationships, over the first 47 days (Figures 3.6a & 3.6c), 48 days (Figure 3.6b) and 90 days (Figure 3.6d), were because the elevations at which the plants were sampled over that period, were always submerged. Consequently, when water levels changed, they experienced the same relative change in depth. Only when one of the sampled elevations was exposed, did the r^2 value change.

During spring, the emergent height of the tallest stems or leaves of both species increased with depth/elevation (Figures 3.7a & 3.7b). However, the emergent height as a percent of the total height, simultaneously decreased. A comparison between the emergent height of *Baumea* stems, showed that at all sites the population was emergent during low water levels in autumn, but in spring the population was submerged below 47.70 (Figure 3.7c). Above this elevation, the emergent height as a percent, was between 80-100 % in autumn but reduced to 20-40 % in spring (Figure 3.7d).

Stem and leaf densities (Table 3.2) corresponded to shoot densities (Figures 3.1b & 3.1f). The associated variability was, for *Triglochin*, greatest at the highest elevation and when the population was exposed (depth=0 cm), and for *Baumea*, at the lowest elevation and when depth was greatest. Because shoot, and stem and leaf data corresponded, the number of leaves or stems per shoot were similar across the gradient (Table 3.3). This was verified by AOV for *Triglochin*, but not *Baumea*. A comparison between autumn and spring showed significantly smaller values in autumn for *Triglochin* and in spring for *Baumea*. Because of the small range of values for *Baumea*, the mixed grouping of sites by comparison of means may not be meaningful.

The influence of depth on the morphology of individual photosynthetic organs, showed that as depth increased, both the leaves of *Triglochin* and the stems of *Baumea* increased in mass, height and diameter (Table 3.4). These changes were accompanied by a decrease in height per unit weight. The height to diameter ratios showed the changes were in proportion for *Triglochin*, but not *Baumea*. The fresh to dry weight increased for *Triglochin* leaves, but not *Baumea* stems. At comparable sites, *Triglochin* leaves had a greater mass, height, diameter and fresh to dry weight ratio than the stems of *Baumea*.

3.3.2 Belowground Responses to Water Regime

Baumea's live total mass increased as elevation decreased, which was due to increases aboveground, but not below (Table 3.5). When dead biomass was included, *Baumea* values reached a maximum of 5180 g m^{-2}. Root mass increased but rhizome mass was unaffected. The decrease in rhizome length and length per unit weight, reflected fewer and broader rhizomes at lower elevations. At 48.20 and 47.95 there was around five times as much below as aboveground biomass, whereas at the deep site there was a similar amount. Root:shoot ratios, were similar under the three regimes. Individual ramets were supported by a greater mass of root and rhizome at the deepest site. For *Triglochin*, it appeared that total biomass and the mass of all tissues was greater at 47.70 and greater than *Baumea* at the same elevation. The greater rhizome mass at 47.70 was reflected in the increase in rhizome length and diameter. The below:aboveground ratios were greater than *Baumea*'s, but also decreased. There was little evidence for a change in the root:shoot ratio; although individual ramets were all supported by a greater mass of root, rhizome and tuber at the deeper site.

3.3.3 Aspects of *Baumea*'s Vegetative Reproduction

Belowground samples (autumn-87) of *Baumea*, separated naturally into distinct pieces of rhizomes (including dead and live), the number of which decreased with elevation (Table 3.6). So too did the total number of expended shoot buds, the same pattern as aboveground shoot densities (Figure 3.1b). This was due to decreases in both the number of long and short shoots, but the fall in the number of long shoots was greater. At 48.20 they were in equal abundance, whereas at lower elevations short shoots were more common. There were significant increases in the rhizome crown diameters of both shoot types as well as that of shoots at the origin of each rhizome piece, the type of which was unknown. These shoots were generally broader than the subsequent shoots on each rhizome piece. The length of rhizomes, both mature and developing also increased across the gradient.

3.3.4 Aspects of *Triglochin*'s Sexual Reproduction

Although vegetative shoots outnumbered flowering shoots, the proportion flowering increased (0.02-0.67) with depth/elevation (Table 3.7). This relationship held for the number of fruits per inflorescence, the density of seeds (m^{-2}), individual shoot mass and total inflorescence mass (m^{-2}). The proportional allocation of biomass to the inflorescence (versus the leaves) increased from 0.02 to 0.31.

By observation, seedlings fell into three density (m^{-2}) and elevation categories: 0-8 (48.00-47.88), 26-66 (47.86-47.77) and 109-422 (47.68-47.60) (Table 3.8). The highest rate of survival (11.9%) occurred at 47.63 and 47.66, although at the same elevations several metres away, the rate was only 0.4%. The proportion of established seedlings in the August population varied from 0.04 to 0.30. From these data, Ganf *et al.* (1991) calculated the probability of recruitment and survival, and found they were both inversely related to the number of days the seedling was exposed.

3.4 DISCUSSION

Aboveground Responses to Water Regime

At levels within the plant (maximum stem height, mass per shoot), *Baumea* was related to depth, only when water levels were high. However, measurements of the plants overall performance (aboveground mass, shoot density and mean stem height), were best correlated to water regimes between 180 and 360 days (6-12 months). The modal responses, showed that *Baumea*'s performance was best at intermediate levels of the Lagoons' water regime. Although water regime is temporally variable, this data shows that *Baumea*'s long-term performance (in terms of aboveground mass and shoot density), is average at high elevations and poor at low elevations (ie. close to its depth limit). *Triglochin*'s leaf height and mean mass per shoot, were also positively correlated to depth, but so too was its aboveground mass and shoot density. Analyses showed that the immediate depths were more important than the past water regime. The Lagoons' water regime was well within *Triglochin*'s limits. For both species, the highest shoot densities occurred before peak biomass, indicating a trade-off between recruitment and resource allocation.

Triglochin thus has a more rapid response time. Its sensitivity to depth was confirmed by its stand variability which was highest at the shallow end of the gradient and in the shallowest water. In contrast, variability for *Baumea* was least at those extremes and highest at the lowest elevations and in the deepest water. These responses identified the least favourable sites for each species, which compared well with the different water regimes in the areas they dominated (Figure 2.9).

Because only the tallest of *Baumea*'s stems were related to depth, this species has the ability for only a small part of its population to respond quickly to increases in depth. During flooding events, these few stems may be important for supporting the oxygen demands of the entire population. Both species responded to high spring water levels by increasing the height of their tallest stems or leaves. This is a well documented response (see Introduction); however, changes in emergent height have not been noted before. The simultaneous increase in emergent height, signalled that an optimal above water to below water ratio was being sought, but the corresponding decrease in the percent emergent height (Figures 3.6a & 3.6b: *Triglochin* 59.0-42.8 %; *Baumea* 49.2-36.1 %) meant this was increasingly difficult to achieve. As with *Baumea*, the failure to keep enough aerial photosynthetic tissue led to a decline in the shoot density of *Juncus militaris* (Hogeland and Killingbeck 1985). Calculations from their data showed a decrease in percent emergent height from 82.3-54.4 %. A small shoot height above water and a long transport distance (ie. depth) may restrict oxygen transport from the emergent shoot to belowground organs (Weisner 1988). In this study, the changes in emergent height with increasing depth, coupled with the maintenance (*Triglochin*) and decline (*Baumea*) in live aboveground biomass suggested that *Triglochin* unlike *Baumea*, had met the minimum requirements for an adequate supply of oxygen. This conclusion is supported by *Triglochin*'s extensive lacunae (Suren 1989), an indication of a well developed gas transport system.

For both species, the positive response to depth from existing stems or leaves did not extend to the recruitment of shoots. This agreed with decreases in the shoot densities of *Carex rostrata* (787-112 m^{-2}) and *C. aquatilis* (254-107 m^{-2}) following increases in depth (0-5 to 30-61 cm; Sjoberg and Danell 1983). At the same elevations, *Baumea* shoot densities were relatively constant throughout the year, which was different from species in regions with shorter growing seasons and harsh winters (e.g. *C. rostrata* in Swedish mires, Hultgren

1988). The changes in *Triglochin* shoot density compared with the decrease in shoot density of *Sparganium eurycarpum* and *Typha glauca* during a natural drawdown (Van der Valk and Davis 1980). However, that drawdown was for 1-2 years, whereas in autumn-89, the Lagoons dried for only a couple of months.

Under the conditions examined, *Baumea* and *Triglochin* (as with *C. rostrata*, Hultgren 1988 and *Cyperus papyrus*, Thompson *et al.* 1979), not only varied the number of plant parts, but their size as well. This was inconsistent with the proposition that in response to environmental variability, plants either do one but not both (Harper and White 1974, Harper 1977). This may be an important trait for survival in variable environments such as wetlands with fluctuating water levels. For *Baumea*, the increase in shoot size (height, width, mass) was at the expense of new stems and shoots; however, the initial increase in the size of *Triglochin* shoots was accompanied by an increase in their density (and that of leaves). At the deepest site there appeared to be a trade-off between shoot size and number. These responses indicate that the cost of adjusting size and density across the gradient in question came much earlier for *Baumea*.

Belowground Responses to Water Regime

Across the 45/50 cm elevation gradient (48.20-47.75/70), the increases aboveground were for *Baumea* matched by an increase in root but not rhizome mass, whereas *Triglochin* appeared to increase the mass of all its belowground tissues. Although *Baumea* increased its total live biomass (P: 0.03), the total live and dead biomass was similar between sites (P: 0.20) as was live belowground and rhizome mass. Coupled with the decrease in shoot density, both alive and expended, this showed it was approaching its depth limit. The decrease in long shoots and increase in short shoots at the deepest site also reflected a decrease in rhizome production. This reduction was compensated by an increase in rhizome length, due to the availability of space in stands with low shoot densities. Rhizome diameter also increased and supported larger shoots, a finding also made for *Phragmites* (Haslam 1970). The prevalence of short shoots in deep water may be because they can act as quick energy gatherers and are less expensive to recruit, being partially dependant on the parent shoot (e.g. *Carex*, Bernard and Gorham 1978).

Because long shoots were broader than short shoots, the shoots at the origin of rhizome pieces were probably long shoots. Shoot diameter may thus be important to the population, as it is the long shoots that produce new clumps, colonize new ground and serve as storage and reproductive organs. Although a relationship between shoot type and aboveground spatial pattern and timing of emergence was found by Soukupova (1988), there is no literature on the relative importance of shoot type with respect to long-term population survival (decline, maintenance or expansion) or resilience to species invasions. The need to address these questions and further investigations of the stimulus and demography of shoot buds, could be well served by using *Baumea* in experimental studies.

Flowering and Seedling Establishment

The main reproductive responses from *Triglochin* were the emphasis of flowering in deep water and almost exclusive vegetative growth in shallow water. For *Scolochloa festucacea*, similar increases in the proportion of flowering shoots and their weight were attributed to the affects of flooding, rather than to the addition of nitrogen (Neill 1992). Lieffers and Shay (1981) suggested a switch in reproductive strategy ensured survival in alternating wet/dry environments, a conclusion supported in this study. Grace (1989) pointed out that this characteristic was uncommon, but one of many in emergents (with the exception of height), that showed a wide range of responses to depth. He interpreted this range as evidence for other factors. Fluctuating water levels would seem relevant, as flowering is an annual event and inflorescences live longer than individual leaves. It is thus likely that the stimulus for shoots to flower would relate to the past water regime and not depth alone.

The fate of seeds also related to water regime. Seedling establishment (range: 0-422 m^{-2}) was low, considering seed production (range: 300-25092 m^{-2}) and 100% glasshouse germination. This was due to the degree of exposure, as was the natural variability in establishment. For example, the seedlings first recorded were in the cooler, moist 'safe-sites' of the cracking clay. The timing of the winter rains determined where on the elevation gradient seedlings survived, and the rate of inundation would have further influenced distribution patterns. The variability in the timing of drying and flooding moves the small survival windows of seedlings. The patchy nature of the lagoons' vegetation may reflect irregular and widely distributed establishment events.

Conclusion

Triglochin's ability to change its height and biomass according to depth and its large, deeply buried belowground mass and reproductive versatility, identifies it as a species which 'reacts', capitalising on favourable conditions and opting for underground dormancy during drought. Although some of the stems in a *Baumea* population adjust to increases in depth, the population as a whole tolerates the changes, responding to the integrated water regime over a longer time-scale. *Baumea*'s slower, more inflexible growth, dependance on vegetative reproduction and lack of a storage organ comparable to tubers, identifies it as as species which withstands flooding or drought.

CHAPTER 4: THE ACCUMULATION AND ALLOCATION OF BIOMASS

4.1 INTRODUCTION

Key differences in the responses from *Triglochin* and *Baumea* to depth and water regime were established in the previous chapter. However, because data came from one-off harvests, it was not known how the perennial and clonal nature of these species influenced their responses to past and recent water regimes. The presence of a large dead fraction in *Baumea* and the incomplete belowground data for *Triglochin* also thwarted an understanding of their relative productivity. To overcome these problems, species were studied experimentally at the level of the ramet under controlled hydrological conditions.

The net biomass accumulation per ramet over 12 months (g ramet year) is used to assess species response to depth. There are several advantages in using ramets. The problems associated with including tissue produced in previous seasons (Bernard 1974) is avoided. Considerable underestimation of emergent belowground production results from inaccurate separation of live from dead tissue (Bernard and Fiala 1986) and when the plant is clonal, it is not a snap-shot of the existing or previous season but reflects long-term stand history. Just as dead standing tissue aboveground serves a purpose (Armstrong and Armstrong 1988, Brix 1989, Dacey 1992), recent studies have shown how 'dead' rhizomes and buds 11 generations behind the nearest living shoot still function (Jonsdottir and Callaghan 1989, 1990). Production in one year may thus be utilized in years to come, and the physiological integration of a rhizome and dormant bud network negates measuring production by, for example, changes in live and dead biomass (e.g. Linthurst and Reimold 1978, Keefe 1972). Using ramets also has the advantage of not disturbing an established stand.

The allocation of biomass in a single ramet reflects the importance of each tissue type in different resource environments. Hunt and Nicholls (1986) proposed that the ratio of below to aboveground mass is determined by the external ratio of below to aboveground stress. Plants adjust to resource imbalances by allocating new or existing biomass to organs which require or can harvest a limiting resource (Chapin *et al.* 1987). In doing so, trade-offs are made between, for example, the aquisition of carbon and nitrogen (Chapin 1980) or light and nitrogen (Tilman 1986a). In aquatic systems light can determine the distribution of submerged species (Spence 1982), but emergents are controlled by their need to have aerial tissue, because carbon becomes limiting underwater more quickly than light. Although biomass allocation has been measured in submergents (Brock 1983, Kautsky 1987), and in emergents across water depth gradients (Lieffers and Shay 1981, Stevensen and Lee 1987, Pip and Stepaniuk 1988, Grace 1989, Waters and Shay 1990), its reallocation (or lack of it) in manipulative experiments has not been addressed, despite the fact that it provides insight into species adaptation to variable environments.

The known history of ramets grown under controlled conditions also allows rhizome and shoot bud development to be measured. This gives insight into the long-term resilience of the plant, which may differ from expectations from the observable vigour and the accumulation of biomass. The contribution of long and short shoots influences the spatial arrangement of shoots, and, together with the positioning of belowground mass, reflects resource supply and the way resources are captured. Hypotheses about the way the species might interact can be set up from this information.

Data from three experiments are presented. The first, undertaken in a constructed pond, was a short experiment which compared the effect of short and long periods of inundation on growth and biomass allocation in *Baumea* ramets. The second, another short experiment, measured the influence of belowground space on the growth of *Triglochin* ramets at one depth. In the third, individual ramets of both species, were grown *in situ* across a depth gradient. There were two parts to this experiment. The first examined the effect of constant depths and the second was a manipulative experiment that examined the influence of changing water levels. Plants were submerged or emerged, and the movement of biomass from one structure to another determined by comparison with control plants that were kept at one depth. The aim was to establish the effect of depth on recruitment and biomass accumulation and the effect of changes in depth on biomass allocation and reallocation.

4.2 METHODS

4.2.1 Experiment 1: *Baumea* and Inundation

Baumea was collected from healthy stands in the West basin and divided into ramets which consisted of one live mature shoot with associated live root and 6-8 cm of rhizome. Ramets were potted individually into plastic nursery bags (pots: 12x12x12 cm) with sandy loam and slow release fertiliser and left to establish at 10 cm depth for 8 months in a Botany Department pond. Treatment 1 represented 16 pots submerged to 80 cm over 2 weeks, then emerged to 10 cm over 2 weeks, where they remained for 8 weeks. Four pots were harvested at weeks 2, 6, 8 and 12. Treatment 2 consisted of 32 pots submerged to 80 cm over 2 weeks and which remained there for 10 weeks. 8 pots were harvested at weeks 4, 6, 8 and 12. At the start of the experiment, four pots were harvested as an initial. At the start and finish, shoot and stem number and total green height were recorded from each pot. On harvesting, live aboveground shoot mass was clipped at sediment level and fresh-weight recorded. The belowground plant was rinsed and separated into live root and rhizome. Dead tissue was negligible. Tissues were oven dried at 60 C° for 72 hours and dry weight (g dwt) measured. Initial and final biomass data were compared by 1-way AOV (Statistix 1987). Unplanned comparisons compared difference between initial data and treatments, and between treatments (SS-STP, Sokal and Rohlf 1981). The relative change in shoot and stem number, total stem height and shoot fresh:dry weight ratios ((final-initial)/initial) were plotted and treatments compared by 1-way AOV.

4.2.2 Experiment 2: *Triglochin* and Space

Four month old Triglochin seedlings (n=3; established in the Botany Department pond), were grown in pots of different volumes (small 10, medium 15 & large 22 cm^3) at 0 cm depth (flooded sediment, but no standing water). Initial biomass measurements were obtained by converting the total wet-weight of each plant to dry-weight, using a wet to dry weight ratio obtained from sacrificed material. Characteristics were measured as, per shoot or per pot (leaf mass, number and yield: (final-initial)/initial)). Individual biomasses were recorded and all data were compared by 1-way AOV and planned comparisons of means (large v medium & small, medium v small). Because of the small sample size, probability levels less than 0.01, were taken to indicate weak significance.

4.2.3 Experiment 3: Depth and Changes in Depth

Field

Ramets of both species were collected from the Lagoons in mid January-87. The criteria for a ramet was as described above, but *Triglochin* rhizomes, which are larger, were cut 2-4 cm from the shoot. The fresh weights of ramets of both species, were approximately 2 g. *Triglochin* seedlings were established in Adelaide from seed collected the previous spring. Seedlings were grown in plastic tubes with potting mix, kept wet, and were 3 months old when the experiment began. Seedlings and ramets were planted individually into plastic pots (12x12x12 cm) which contained a 50:50 combination of complete commercial potting mix and lagoon sediment. These were left in a sheltered part of the lagoon, at a depth of 10-20 cm for 6 weeks. By way of a final standardization, those showing signs of new shoot recruitment were selected.

Experimental Design

Four replicate pots were randomly assigned to one crate. Species were kept separate because of the potential for interaction between aboveground tissues. Crates were placed on ledges dug into the side of the outlet channel. A segregated block design was chosen to prevent interaction between crates of different species and due to limited space. Depth above the pot sediment was 0, 50 and 100 cm. During the course of the year it was necessary to shift crates to retain these depths. Bricks and boards were used on those occassions. The experimental design is shown in Appendix 4.1. Crates were put in place on 3-Mar-87, moved on the 8-Dec-87 and harvested on the 3-Mar-88. One crate, two where possible, were moved for each treatment, which was either up or down 50 or 100 cm. Extra potted *Baumea* were added as two crates at 50 cm on 6-Jun-87. These were used in the relative response to changes in water depth but not for comparisons of final yield.

A total of nine records were taken, measuring the photosynthetic height and recruitment of all individually tagged stems and leaves. On the last record, pots were rinsed in the channel and transported to Adelaide in "eskies". Photographs were taken before each ramet was separated into shoot, root, rhizome and tubers. Tissues were oven dried at 60 C° for 72 hours and dry weight (g dwt) measured. The rhizome associated with each ramet was kept intact for examination. The number, type (long or short) and timing of emergence of recruited shoots per ramet was recorded. Also counted was the number and type of shoots that had started to develop belowground, but were yet to emerge, and the number of shoots that had developed (either emerged or yet to) from shoots recruited throughout the year.

Analysis

The aboveground characteristics of plants kept at constant depths were compared after 9 months, which gave the maximum number of replicates (12-16). The final biomasses and aboveground characteristics of plants which experienced a change in depth, were compared after 12 months, when the maximum number of replicates was 4 to 8. Differences between treatments were tested by 1-way AOV. The measurements compared on a per ramet basis, were photosynthetic height, shoot number and leaf or stem number (aboveground characteristics) and root, rhizome, tuber, shoot, total live belowground and total live biomass (final biomass characteristics). The ratios of root to shoot, below to aboveground dry weight biomass and the number of tubers and their individual mass also were compared. The percent turnover of photosynthetic height and leaf and stem number, was calculated as the cumulative decrease divided by the cumulative increase, multiplied by 100 (see Neill 1992). Data were transformed (arcsin) and compared by 1-way AOV.

Analyses for plants grown at constant depths, and plants moved had the same premise. The null hypothesis was that depth or changes in depth had no effect on the aboveground characteristics or final dry weight of plant parts. Planned comparisons were undertaken for all analyses. For plants grown at constant depths, the first comparison compared ramets grown in exposed (0 cm) versus inundated (50, 100 cm) conditions and the second compared plants inundated to 50 cm to those inundated to 100 cm. For plants that were moved, the first comparison was between ramets that on the final date were exposed versus those that were inundated, and secondly between those inundated to 50 cm versus those inundated to 100 cm. The treatments, sample sizes and source of variation for each set of analyses is summarized in Appendix 4.2. Equality of variances were tested by the F-Max test. When variances were heterogeneous, data were transformed into natural logarithims. The relative allocation of biomass was illustrated by area charts.

4.3 RESULTS

Experiment 1

There were no significant changes in above, below or total biomass either between initial ramets and treatments or between treatments (Appendix 4.3). There were also no differences in root characteristics between treatments (Table 4.1), despite significantly less root mass in treatment compared to initial ramets, which affected the root:shoot ratio and % allocation of root. The consecutive data indicated how long *Baumea* took to respond to inundation/emergence (Figures 4.1a-d). The relative changes in shoot and stem number, and total height over time, showed treatments differed only after 12 weeks. Following emergence, *Baumea* thus took 4 to 6 weeks before it could recruit new tissue. Changes in the shoot fresh:dry weight ratio occurred within the first 4 weeks and continued to increase with the duration of inundation (Figure 4.1d).

Experiment 2

The amount of belowground space (1000-10648 cm^3) had no affect on the individual characteristics of *Triglochin*'s leaves (height, diameter, mass) or shoots (no. leaves, yield) (Table 4.2). In terms of the whole pot, however, the final number of leaves and shoots, increased with available space, while the number of tubers and the total yield, was greater in the large pots and similar in the small and medium sized pots. This pattern was the same for the total biomass (Figure 4.2) and that of individual tissues. Although *Triglochin* plants were aged 4 to 8 months, they each gave rise to two shoots in the large pots, 0.67 shoots (mean of: 0, 1, 1) in the medium sized pots and no shoots in the small pots. Shoot recruitment was accompanied by belowground growth in large pots only.

Experiment 3

4.3.1 Constant depth

All vegetative ramets of *Triglochin* survived submergence (Table 4.3), but, *Baumea* ramets and *Triglochin* seedlings showed decreasing survivorship with increasing depth. With the exception of *Baumea* ramets at 100 cm, all plants alive after 9 months survived the full year.

After nine months at constant depths, *Baumea* ramets showed a clear response, with decreasing stem height and number from 0 to 100 cm (Table 4.4). There were also fewer shoots at the deeper sites (50 & 100 cm depths) than at the shallow (0 cm depth). After 12 months, the total, above and belowground ramet biomass, and the mass of individual tissues was significantly greater at 0 cm than 50 cm. These changes were in proportion, as the ratios of below to aboveground and root to shoot mass were not significantly different. Photographs illustrated the affect of depth on root and rhizome production, as well as their profile. At 0 cm, *Baumea* ramets had developed more and longer rhizomes compared with 50 cm plants (Figures 4.3 & 4.4). These explored the pot on a vertical plane and as with roots, which were restricted to the base of shoots, were not deeply buried.

In contrast to *Baumea*, the leaves of *Triglochin* ramets after nine months at constant depths increased in height between 0 and 100 cm. However, this was not matched by changes in the number of leaves or shoots (Table 4.5). After 12 months, there were also no significant differences in the total or belowground biomass or the individual mass of roots, rhizomes or tubers, or tuber number or mass, but the aboveground shoot mass was greater at the deeper sites. The differences in below to aboveground and root to shoot ratios were attributed to the large changes in shoot tissue between 0 cm and the other depths. *Triglochin* seedlings showed an almost parallel response to that of vegetative ramets (Table 4.5). The differences were in leaf height, which fell between 50 and 100 cm and leaf number, which was greater at 0 cm. After 12 months, total and belowground biomass was similar between the three depths, but corresponding with the greater shoot mass at the deeper sites, was a significant fall in tuber mass. This was reflected in a decrease in the mean number of tubers from 6.5 (50 cm) to 0.5 (100 cm) and in their individual dry weight.

The effect of depth on the belowground production and form of *Triglochin* was less clear, with decreasing tuber biomass the most obvious response. The numerous fleshy white roots had explored all available space in the pot, with tubers placed at the very bottom. Unlike the prolific production of roots, rhizome production was minimal, both for ramets (Figure 4.5) and seedlings (Figure 4.6). The small number of shoots that were recruited over the year arose from lateral buds (Figure 4.7).

At 0 cm, the percent turnover in the height of *Triglochin* ramets was higher (90 %) than at the deeper sites (80 & 79 %), which had similar values (Figure 4.8a). For seedlings, turnover was higher at the deeper sites. Turnover in the height of *Baumea* stems was much less (26-33 %) and no different between 50 and 100 cm. The turnover of leaves/stems of ramets of both species was unaffected by depth (Figure 4.8b). *Triglochin* seedlings had lower values at 100 cm, which was probably due to the variability of the survivors at that depth. Differences between species were illustrated by the gains and losses in height for each time interval (Figures 4.9a-f). Depth increased the onset of senescence of *Baumea* stems (Figure 4.9a-c). For example, decreases in height at 0 cm, began in September (with a minor exception in June), where as at 50 cm, they began in August and at 100 cm, in June. At 0 cm, there was a noticeable increase in height from September to December, a pattern repeated at 50 cm, but delayed until December to March. At 100 cm, there was no growth after September and all ramets were dead by the final date. Unlike *Baumea, Triglochin* leaves were senescing by the second record (Figures 4.9e-f). The turnover in height continued throughout the year, with no obvious seasonality.

4.3.2 Changes in Depth

Submerging ramets grown at 0 cm for 9 months to 50 cm for 3 months had no effect on the height and number of *Baumea* stems and shoots (Table 4.6). Submergence to 100 cm adversely affected the height and number of stems, but not shoots. Ramets brought from 50 cm to 0 cm maintained the same height, despite the recruitment of new stems and shoots. Submerging ramets from 50 to 100 cm resulted in the loss of both stem height and number (but not shoot number), relative to ramets kept at 50 cm.

Ramets submerged from 0 to 50 cm or 0 to 100 cm, had substantially less biomass, both above and belowground compared with ramets that remained at 0 cm. Belowground, the differences were not in the root masses but in the rhizomes, the mass of which was significantly smaller at the deeper sites. Emerging plants from 50 to 0 cm had a positive affect on the mass of all tissues, which resulted in a higher root to shoot ratio. For ramets submerged from 50 to 100 cm however, the mass of all tissues was no different from that of ramets which stayed at 50 cm.

The height responses from *Triglochin* were distinct, with increases and decreases following submergence and emergence, respectively (Table 4.7). With the exception of a greater number of leaves on ramets and seedlings moved from 100 to 0 cm, leaf and shoot recruitment were unaffected by changes in depth. So too was total ramet and seedling biomass, despite a greater shoot mass of plants that either remained at or were moved to 0 cm. Belowground data showed the trend of decreasing biomass with increasing depth; however, differences were only significant on one occasion in six (seven including seedlings). This was due to very little change in the root and rhizome mass, a response which cancelled out significant changes in the tuber mass of ramets moved from 0 to 50 cm (loss) and 50 to 0 cm (gain) and seedlings moved from 100 to 0 cm (gain). Although depth also appeared to adversely affect the number and individual mass of tubers, the only significant changes were in smaller dry weights of ramets moved from 0 to 50 cm. Seedlings moved from 100 to 0 cm also experienced greater tuber dry weights as well as an increase in their number.

After 12 months growth at constant depths of 0 and 50 cm, *Triglochin* and *Baumea* had similar total biomasses (Figure 4.10a). This was despite a greater belowground mass of *Triglochin* at 50 cm (Figure 4.10b) and a greater aboveground mass of *Baumea* at 0 cm (Figure 4.10c). *Triglochin* had a greater root mass than *Baumea* at all sites (Figure 4.10d). *Baumea* had a greater rhizome mass only at 0 cm (Figure 4.10e). Overall the patterns show the mass of *Baumea*'s tissues declining more rapidly than *Triglochin*. The biomass characteristics of *Triglochin* seedlings paralleled those of ramets. The one exception was tuber tissue, very little of which had accumulated at 50 or 100 cm depth (Figure 4.10f).

4.3.3 Biomass Allocation

Figures 4.11a-c illustrate the influence of constant depth on the allocation of biomass to different tissues. Neither species experienced changes in the proportional allocation of root and rhizome mass. However, the allocation of shoot tissue in both species increased; from 0 to 50 cm for *Baumea* and between 0 and 50 or 100 cm for *Triglochin* (but not between 50 & 100 cm). The reverse pattern held for *Triglochin*'s tuber mass, which simultaneously decreased.

The influence of changes in depth on reallocation were less clear (Figures 4.12a-e). Ramets of *Baumea* submerged to 50 or 100 cm after 3 months, had the same proportion of shoot and root tissue as ramets kept at 0 cm (Figure 4.12a). In contrast, those at 100 cm, had less mass allocated to shoots and more to roots and rhizomes, than those at 50 cm. *Baumea* ramets moved from 50 to 0 cm, only changed the percent allocation of root, whereas those moved from 50 to 100 had significant changes in all tissues (Figure 4.12b). These responses, and those of plants moved from 0 to 100 cm, were due to the disproportionate decline in all tissues at 100 cm.

Triglochin ramets submerged from 0 cm, increased the allocation of mass to shoots and decreased it to tubers (Figure 4.12c). Unlike shoot mass, the allocation of tuber at 100 cm was significantly smaller than at 50 cm ($P<0.05$). Conversely, ramets moved from 50 to 0 cm, decreased allocation to shoots and increased allocation to tubers and rhizomes (Figure 4.12d). Relative to plants that remained at 50 cm, submergence from 50 to 100 cm did not alter the allocation of biomass. Neither did emergence from 100 to 50 cm, relative to plants that remained at 100 cm (Figure 4.12e). However, there were significant differences in the allocation of all tissues, between ramets moved from 100 to 50 cm compared with ramets moved from 100 to 0 cm.

4.3.4 Belowground Demography

Due to the minimal shoot recruitment and rhizome growth of *Triglochin* ramets, only belowground data for *Baumea* is presented. The long shoots produced by each *Baumea* ramet, emerged throughout the year at 0 cm, although the number was greatest on the first and last date, autumn and late summer respectively (Table 4.8). At 50 cm, long shoots only emerged on those dates. Consequently, the total mean number was greater in shallow water (8.9 v 1.5 per ramet). The emergence of short shoots was not restricted to any time of the year. Long shoots were twice as common in shallow water, but in equal abundance at 50 cm depth. The higher shoot densities at 0 cm are reiterated in Table 4.9, which summarizes the total number of shoots (long and short), divided into those which had emerged above the sediment and those yet to. Table 4.10 shows the mean number of shoots which shoots recruited throughout the year gave rise to. The continuous recruitment resulted from all shoots contributing new shoots to the population. At 0 cm, this varied from a mean of 1.0 to 4.1 and at 50 cm from 0.3 to 1.7 shoots per shoot. The total rhizome length, both developed and yet to emerge was significantly greater in shallow water (Table 4.11).

4.4 DISCUSSION

4.4.1 *Baumea* and inundation

When submerged for a short (2-4 weeks) or a long (12 weeks) period, *Baumea* overall did not gain or lose biomass and therefore did not grow. Although plants submerged for the short period had by the 12th week produced new stems and shoots, this was attributed to reallocation of existing biomass and not to growth, because there was no difference between the total biomass of this treatment and the initial. Because *Baumea* did not respond to the prolonged inundation by increasing the height and mass of stems, but experienced a loss of roots and small root:shoot ratios, the rate and depth of submergence was too great for *Baumea* to adapt to. Because *Baumea* withstood (rested through) inundation for 12 weeks, it is a plant which tolerates adverse conditions. Evidence for physiological responses within the tissues came from the increase in shoot fresh to dry weight. This may be due to a decrease in structural tissue, which may be the cost stems pay for growing taller and broader. To determine the water regime which *Baumea* cannot survive under, would require either a faster rate of inundation, longer durations or greater depths, factors that were investigated in the third experiment.

4.4.2 *Triglochin* and space

The strong influence that belowground space had on *Triglochin* growth, was not simply a function of restricted production (ie. being pot-bound). The growth of individual shoots was equivalent in each treatment, but the different outcomes on a per pot basis, was due to the effect of new shoots. Space restricted the recruitment of shoots (and therefore leaves), as well as tubers, which led to smaller final biomasses.

4.4.3 Biomass Accumulation

Although the 100 cm depth gradient was well within *Triglochin*'s limits, it exceeded *Baumea*'s. There were no survivors at 100 cm and substantially less biomass at 50 cm compared with 0 cm, due to a decrease in the mass of all tissues. This was coupled with a decrease in the recruitment of shoots and stems, a response also reported by Yamasaki and Tange (1981), Grace (1987) and Stevenson and Lee (1987). At 0 cm, the total accumulation of biomass in both species was similar. In deeper water, the biomass of all *Baumea* tissues decreased. *Triglochin*'s total biomass in contrast, was unaffected by depth, but this was due to increases in leaf mass being coupled by decreases in tuber mass. Seedling performance was similar to ramets at 0 and 50 cm, but at 100 cm, the survivors were comparatively diminutive. In spite of clear negative trends, there were no changes in root and rhizome mass. For seedlings, the number of tubers and their individual dry weight declined with depth, a trend apparent for ramets as well. *Triglochin*'s shoot mass at 0 cm was always less than when inundated, but whether the plant was at 50 or 100 cm made no difference. There was some evidence that shoot number increased when plants were emerged, but the minimal recruitment of shoots in this species indicated limited rhizome growth. The few that did emerge were from small lateral buds.

The similar amounts of biomass accumulated at 0 cm was achieved by a high and continuous turnover in the height and number of *Triglochin* leaves, and a low and delayed turnover in the height and number of *Baumea* stems. *Triglochin* leaves thus have a shorter life-span than *Baumea* stems. Although *Triglochin* ramets at 0 cm had smaller shoot biomasses and heights, the higher turnover in height showed that conditions were less favourable than at deeper sites. Conversely, *Triglochin* seedlings were more stressed at the deeper sites, presumably because they had less reserves belowground.

4.4.4 Biomass Allocation and Reallocation

Although both species produced similar total biomasses at 0 and 50 cm, the allocation of biomass was different. At 0 cm, *Baumea* had accumulated a greater shoot and rhizome mass, whereas *Triglochin* had a greater root mass. At 50 cm *Triglochin* had a greater belowground and root mass. At both depths, the majority of biomass was held in the roots of *Triglochin* and for *Baumea*, in the rhizomes at 0 cm and in the shoots at 50 cm. Although reduced total biomass with increasing depth was found for other emergents (Lieffers and Shay 1981, Grace 1987), there is less information about reallocation with changes in depth.

The reallocation of biomass showed that as water levels rose and fell, biomass was moved between the leaves and tubers of *Triglochin*, and between the stems and rhizomes of *Baumea*. These changes identified the limiting factors at different depths. At 0 cm, where roots were flooded and shoots exposed, there was an ample carbon supply. Here, the placement of most biomass belowground increased nutrient uptake, in order to complement the abundant C supply. In deep water, the placement of biomass aboveground indicated that C was now the limiting resource. The adjustments to maintain a positive carbon balance were for *Baumea* at the expense of rhizome production (also *Typha domingensis* Grace 1989 and *Scolochloa festucacea* Neill 1992), which, as storage and reproduction organs, restricts whole plant performance. For *Triglochin* it was the tubers that dealt with the changes in resource supply. Because they were not resource acquiring organs, *Triglochin*'s resource aquiring ability and thus its overall performance was unaffected. Tubers thus gave *Triglochin* added tolerance, as it is they that deal with the ramifications of water level fluctuations, and not the roots or rhizomes, changes in which would negatively affect whole plant performance. Increasing depth thus affects the survival and competitive ability of *Baumea*, but not *Triglochin*.

Baumea's sensitivity to depth was confirmed by decreases in above and belowground biomass, when moved to deeper water, and increases in the mass of all parts when moved to shallower water. The build up of belowground mass in *Baumea* at 0 cm enabled it to respond positively to submergence to half, but not one, metre. Plants moved from 50 to 0 cm increased in stem number but not height, due to the shorter stems required in shallower conditions. Shoot tissue had less root and total belowground mass to sustain it at 50 cm. In terms of biomass accumulation and allocation, *Triglochin* was less sensitive to changes in depth. The major differences were between 0 cm and the deeper sites, which reveals that exposure is more detrimental than an increase in inundation from 50 to 100 cm, for this species.

4.4.5 Belowground Demography

The predominance of long shoots at 0 cm was reflected in *Baumea*'s substantial rhizome mass, which together with a large bud-bank, gave these ramets greater resilience. When submerged to 50 or 100 cm, they were able to, at least initially, adapt. At 50 cm, however, ramets were conserving and adding to shoot tissue, at the expense of long shoot, rhizome and root production. The prevalence and continuous short shoot production at 50 cm, indicated resources were being recycled between old and young shoots, which is common in clonal plants (Ginzo and Lovell 1973, Newell 1982, Hartnett and Bazzazz 1983, Pitelka and Ashmun 1985, Alpert and Mooney 1986). As the majority of energy was held aboveground, the plant was vulnerable, as it had a low reserve of storage products and dormant buds to keep the population going in adverse times. This was evident by the poor response from plants submerged from 50 to 100 cm, which pointed to their impending mortality.

The long *Baumea* rhizomes at 0 cm, had curled their way around the pot and exploited space in a vertical plane, indicating that given more space they would travel some distance. This equates with the exploratory guerilla growth form (Lovett-Doust 1981), but may also reflect growth as a spreading clone. Short shoot production had the effect of grouping shoots into clumps within the pot. At 50 cm, only one or two small clumps formed, and these were not matched by complete occupancy belowground. The establishment of *Baumea* populations may proceed by exploratory growth which secures belowground resources, followed by clumped growth which produces the dense stands typical of this plant. Dense growth denies space and resources to other species, thereby minimizing interspecific interactions and increasing the capacity to resist invasion. This habit implies that *Baumea* may not contend with other species very well. In contrast, the abundant growth of *Triglochin* roots was not matched by rhizome growth, and the well spaced shoots infers that rhizomes grow some distance, albeit slowly, before producing a new shoot. This implies *Triglochin*'s habit is to spread to new gaps rather than monopolise a small area, a strategy which produces more interspecific contacts than intraspecific.

Their contrasting belowground profiles, *Baumea*'s concentrated in the upper half of the pot, and *Triglochin*'s root mass placed around and below the buried rhizome in the bottom of the pot, suggests the species could physically coexist. The challenge for *Triglochin* is to establish in the stands of *Baumea*. This would be difficult in shallow water where space is securely held above and belowground, but easier at deeper depths where the limited recruitment of shoots creates gaps.

Conclusion

This study has identified different degrees of adaptation across a 100 cm depth gradient and to rapid and large (± 50 or 100 cm) changes in depth. For *Baumea*, continuous inundation at depths of at least half a metre or more results in populations which look vigorous in the short-term but have an uncertain future. In shallow water, *Baumea* becomes well established, exploiting space below and aboveground and is able to cope with inundation. The changes in *Triglochin* from 0 to 100 cm are mostly morphological, with less alteration in total biomass. The priority of both ramets and seedlings was to establish a large root mass, which was both greater than *Baumea*'s at all depths and greater than its own rhizome mass. Both build up their shoot tissue in deep water, a response which results in *Baumea* losing its tenure belowground. How their life-history influences biomass accumulation and changes in biomass over time, is the subject of a demographic study, described in Chapter 5. Despite these differing responses, their occupation of belowground space suggests they may be able to coexist. In mixture *Baumea* would be expected to do better at depths less than 50 cm and *Triglochin* at depths greater than 50 cm. Whether the interaction that follows is related to the decline of *Baumea* and spread of *Triglochin*, is investigated in Chapter 6.

Addendum to Chapter 5

The original experimental design had 5 replicate sets (n=4) of 'fully' measured shoots at each elevation. Although the shoots were within 5 contiguous quadrats, they were randomly selected from within that space. As a result of high water levels, shoots were not always relocated and sample sizes became too small. To buffer that effect, all shoots in all quadrats were 'fully' measured. This modified the design and led to one big quadrat with many shoots. Even if it was valid to analyse the separate quadrat data, this was not possible, as the quadrat boundaries were lost owing to the difficulty of relocating shoots. This effectively meant the experiment was now mensurative, with three replicates sites (separated in space) that 'happened' to be at three different depths. Pooling the data led to favourable sample sizes but was at the expense of independent replicates, which meant within-site variation could not be measured. Consequently, the differences identifed by AOV, although real, should not be attributed to depth as a treatment and the interpretations should be read as hypotheses. Together with results presented in Chapter 3, the data provides strong evidence that water regime controls *Triglochin*'s leaf morphology and sexual reproduction. Because of the uniformity amongst *Triglochin* shoots, it would have been better, in hindsight, to randomly sample different shoots (from different quadrats) on each record. This would have provided independent samples, suited to 2-way AOV.

CHAPTER 5: *IN SITU* PLANT DEMOGRAPHY

5.1 INTRODUCTION

The influence of depth and water regime on species biomass and population structure, determined by one-off (Chapter 3), and final harvests (Chapter 4), were a summary of demographic processes. How life-history events influenced species performance, was investigated in a 2 year *in situ* study of the shoot dynamics of *Baumea* and *Triglochin*, conducted across a natural elevation gradient with fluctuating water levels.

It has been suggested that the dominance and persistence of clonal plants, in environments with temporally varying degrees of flooding and drawdown, is due to their ability to vary the timing of life-cycle events (Brown *et al.* 1985). Life-history data from a range of water regimes or from within a variable environment such as one with fluctuating water levels, was lacking until Neill (1992) looked at a perennial grass at two elevations, over one growing season. This paucity of information, is surprising, since it has been realized for some time that adaptation not only involves morphological, physiological and biochemical changes, but demographic changes as well (Solbrig 1980). Opportunistic growth strategies have been shown in *Carex* (Bernard 1974, 1975, Callaghan 1976, Fetcher and Shaver 1983, Schmid 1984), *Typha* (Grace and Wetzel 1981a, Dickerman and Wetzel 1985) and submerged species (Brock 1988, 1991), yet only a few studies have looked at variation in species life-histories across a range of environments and these were primarily on the basis of nutrient status (Verhoeven *et al.* 1988, Konings *et al.* 1989, but see Neill 1992). This is despite the fact that clonal plants are often found in variable and extreme environments and are known to tolerate a wide range of conditions (Abrahamson 1980, Callaghan and Emanuelsson 1985, Pitelka and Ashmun 1985, Hutchings and Bradbury 1986, Day *et al.* 1988, Jonsdottir and Callaghan 1988). *Triglochin* and *Baumea* growing across an elevation gradient in a habitat with fluctuating water levels is an obvious example. Experiment 2 in Chapter 4, indicated that the timing of growth in *Baumea*, may be delayed at deeper depths.

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Variation in the timing of life-history events can promote species coexistence (Grubb 1985, Ratliff and Westfall 1988, Soukupova 1988), and the ability of species to adapt to varying conditions is now seen by community ecologists as more important in determining distribution patterns than competition for resources (Austin 1990). Although *Triglochin* and *Baumea* do not form a distinct community together (Rea 1985), an understanding of their life-histories may explain their long term occupation of the lagoons and their present temporary coexistence which precedes a permanent shift in their distributions.

In addition to investigating the role of life-histories for survival in a heterogeneous environment, morphological plasticity may play a role. Defined as the proportion of phenotypic expression controlled by the environment (Silander 1985), plasticity in relation to depth and the emergent vegetative shoot is well documented (Van der Valk and Davis 1980, Stevenson and Lee 1987, Djebrouni and Huon 1988, Grace 1989, Waters and Shay 1990). Both *Triglochin* and *Baumea* exhibit some plasticity, as the maximum height of their photosynthetic organs was related to depth (Chapter 3). Because *Triglochin*'s plasticity also held for its abovegound biomass (Chapter 3) and depth is never stable in this system, its plasticity is much higher.

Another aim of the demographic study is to explain why *Triglochin* shoot and leaf densities differed between drawdown and flooding (Chapter 3), a finding that does not compare with clonal plants in general, which have constant densities despite large shoot fluxes. There are several theories about the regulation of shoot densities, but none to explain major seasonal changes. Shoot birth and death can be either synchronous, more or less continuous or in pulse events. The regulation of population size is thought to reflect competition for external and limiting resources, but the recognition of the connected nature of clonal shoots lends support to competition for internal resources, with the birth of new shoots preceding the death of old shoots (e.g. *Carex arenaria* Noble *et al.* 1979). More recently, the demonstration of reciprocal translocation and strong apical dominance (Jonsdottir and Callaghan 1989, 1990) suggests shoot flux may simply represent population growth, the programmed transfer of assimilates from source to new sinks, and from senescing tissues. Under this scenario, shoot death only occurs after the flowering of monocarpic shoots. Populations may also be indirectly regulated by the timing of shoot emergence (Bedford *et al.* 1988) because this can control shoot size (*Typha*, Djebrouni and Huon 1988, *Phragmites*, Haslam 1970, *Carex*, Ratliff and Westfall 1988), which in turn can affect shoot growth, life-span and reproduction.

Data from Chapter 3 also identified an increase in the proportion of *Triglochin* shoots that flowered across an elevation gradient and the varying success of seedling establishment. Because these results were from isolated harvests, they needed to be verified in the framework of the plant's life-history. Loehle (1987) suggested plants vary the two modes of reproduction to match changes in the success of each type. This could only be verified by monitoring the establishment and survival of vegetative shoots and seedlings. However, it was not known if plants allocate energy for reproduction in terms of biomass, nutrients or some other currency (Abrahamson and Caswell 1982, Watson 1984). Rhizomes, for example, function as storage, absorption, anchorage and reproductive organs. Although Cook (1985) and Loehle (1987) recommend taking the ratio of sexual to asexual offspring, this cannot be a true measure of reproductive effort, as investment that is lost is not taken into account.

A final aim was to document the life-histories of *Baumea* and *Triglochin* in the light of species with similar morphology and from wetlands with different water regimes. To highlight their features, reference is made to two well researched genera. *Carex* in the northern hemisphere has shoots and populations similar in structure to *Baumea* and *Typha* has leaves that grow in a similar manner to *Triglochin*. There are few plants with a morphology like *Triglochin*. Although *Vallisneria americanus* and *Glyceria maxima* are similar, the differences are too great for information to be extrapolated and there is limited information on their population ecology.

In summary, the objective of the study was to document species life-history under naturally fluctuating water levels (temporal component) and under different water regimes (spatial component). This would address the aforementioned questions: what is the role of species life-history and morphological plasticity with respect to survival in a variable environment ?; can their temporary coexistence and/or long-term replacement be explained by their life-

life-histories ?; is reproductive effort partitioned on the basis of the survival and establishment of vegetative versus sexual offspring ? From data presented in Chapter 3, it was hypothesized that the change in the size and structure of *Triglochin* stands was due to a high degree of morphological and demographic plasticity, whereas the little change in *Baumea* stands was due to a lack of plasticity. From biomass data (Chapter 5), it was hypothesized that the growth rates of *Triglochin* and *Baumea* would be the same in shallow conditions. Also that *Triglochin*'s growth rate would be the same across a depth/elevation gradient, whereas *Baumea*'s would decrease as the degree of inundation increased.

5.2 METHODS

Populations of *Triglochin* and *Baumea* were followed in their natural habitat from 3-Mar-87 to 7-Feb-89. Measurements of individual shoot, leaf and stem, birth, height and death, were taken at approximately 35 day intervals.

Triglochin procerum

Robust stands of *Triglochin* in Hacks Lagoon which grew from 47.75 to 48.45 AHDm were chosen for monitoring. Shoots at three elevations (48.25 shallow; 48.05 medium; 47.85 deep) were compared (Figures 5.1 to 5.3). Populations were monospecific when submerged and during drawdown were accompanied by prostrate aquatic plants (*Cotula coronopifolia, Crassula helmsii, Lilaeopsis polyantha, Mimulus repens, Ranunculus rivularis, Rumex bidens*), which emerged to form a herbland carpet. These species were either stoloniferous perennials or shallow rooted annuals, which died back during flooding. Because the study did not seek to answer questions about what limited the distribution of *Triglochin*, these sites were within the observed depth range. At each site, five quadrats (100x20 cm) were sampled within one randomly placed square metre quadrat. Within each smaller quadrat, all shoots were numbered by placing a dymo tape collar on the second youngest leaf. The photosynthetic height of all leaves and the diameter of the second youngest leaf were measured on four randomly selected shoots. The remaining shoots had only the position of the tag recorded to give leaf number and recruitment per shoot. These two groups of shoots were termed 'fully' or 'partly' measured. As new shoots emerged, they were partly measured. This would produce five replicate sets of randomly measured shoots from three elevations. This design was modified during the first winter when under 60-100 cm of water, shoots were not always relocated. Some of the partly measured shoots were switched to fully measured, to ensure an adequate sample size. From 3-Mar-88 onwards, all shoots in all quadrats were fully measured, but during flooding in the second winter it was inevitable again that some shoots were not located.

Baumea arthrophylla

The difficulty of accurately tagging and relocating shoots of this plant was apparent from the outset. The same design for monitoring *Triglochin* populations was started, but abandoned due to damage to the stand from trampling, as well as the difficulty of tagging in deep water. The perimeter of a small isolated stand that had established the previous year in a herbland, adjacent to, but separate from, old populations at the Fences, was chosen for sampling. The advantages of this stand, called the 'Patch', were that it was in shallow conditions and because of its developing status, shoots were accessible without interference to their growth. This was the closest feasible example of *Baumea* in its natural habitat. The Patch, at an elevation of 48.08 AHDm, began as a 100x30 cm quadrat with 22 shoots. These were tagged and the photosynthetic height of all stems recorded. New shoots were added as they emerged, which gave a final number of 99 shoots. Records were interupted in winter 1988, due to high water levels.

Analysis

Data were presented on an individual shoot basis, as the mean and standard deviation. *Triglochin* was identified as having three groups of shoots, which may or may not have performed differently. The shoot heights, leaf recruitment rates and relative growth rates (Appendix 5.1) of group 1 versus group 2 in 1987, and group 2 versus group 3 in 1988, were compared by two sample t-tests. Otherwise, shoots were pooled to measure the influence of elevation. For *Baumea*, groups of shoots that emerged at distinct times were examined separately.

Survivorship and depletion curves were drawn for groups of shoots of both species. The number and proportion of *Triglochin* shoots which flowered was recorded for each group in each year, as well as the maximum height of the flowering stalk, including the inflorescence and the inflorescence alone. To determine if shoot size was related to flowering, the difference between the mean heights of shoots which flowered and those which remained vegetative, were compared by two sample t-tests in the months leading up to flowering. For *Triglochin*, differences between elevations were tested by 1-way AOV's at the height of each season. Analyses at each of the 19 records was avoided because of the lack of independence that resulted from consecutive measurements of the same shoots. Each set of data consisted of large but unequal sample sizes. Planned comparisons (Sokal and Rohlf 1981) tested for the source of variation within sites.

The following data were presented: total shoot height, the maximum leaf height per shoot, the diameter of the maximum leaf height per shoot and the percent emergent height per shoot. This latter value was calculated by subtracting depth from the height of each leaf on a shoot, and expressing this height as a percent of the total shoot height. The variability of *Triglochin* stands, in terms of the height of all shoots at one elevation, was measured by the coefficient of variation (V^*). Equations for recruitment rates (leaf recruitment rate, leaves day^{-1} $shoot^{-1}$ and its inverse, the plastochrone interval, days $leaf^{-1}$ $shoot^{-1}$) and growth rates (absolute and relative growth rates) are shown in Appendix 5.1. The components of the Absolute Growth Rate (sensu Hunt 1990: cm d^{-1} $shoot^{-1}$), the gross increase and decrease in height, were shown to illustrate the rate of tissue turnover. Relative growth rates ($g\ g^{-1}\ d^{-1}$), were calculated for comparisons of shoot growth within a species, between sites for *Triglochin* and between cohorts for *Baumea*. The dimensions of *Baumea* stems and *Triglochin* leaves were converted to dry weight biomass from regression equations. For *Triglochin*, data came from a harvest of leaves across a 70 cm depth gradient. Leaf heights (cm) and diameters (mm) were converted to biomass from the equation $g\ dwt = 3.135*10^{-6}*height^3) + (9.031*10^{-5}*diameter^3) + 0.068127$, $r^2=0.94$, SAS 1985). For *Baumea*, data came from a final harvest of stems in an experiment described in Chapter 6. Stem heights (cm) were converted to biomass from the equation g dwt = (0.0164*height - 0.1643, r^2=0.76, Statistix 1987).

Production to maximum biomass ratios (PB_{max}) were calculated by a) dividing the estimate of mean annual cumulative aboveground biomass per shoot by the mean maximum aboveground biomass per shoot recorded in that year and b) dividing the mean annual number of leaves produced by a shoot by the mean maximum number of leaves per shoot in that year.

5.3 RESULTS

5.3.1 *Triglochin*

Life-history

In addition to the shoots tagged at the beginning of the study, new shoots were recruited in the following autumn at all elevations (Figure 5.4) and one new shoot was recorded at the shallow site on the last record in late summer. The depletion curves showed that part of the population died off at each elevation, also in autumn (Figures 5.5a-c). In shallow water, half the shoots died, whereas at the medium and deep sites, approximately a quarter and a third of shoots died respectively. This was the only time shoot mortality was recorded, and this coincided with the only time shoot natality was recorded. In shallow water, this restored population numbers to their original density, but at the medium and deep sites, the new shoots increased and decreased the overall population size, respectively. These pronounced recruitment events represented new cohorts, and it is likely that the pronounced die-offs also represented cohorts. The remaining shoots, however, could not be quantitatively separated, because their births and deaths were not recorded. Before summarizing shoot performance, these groups were examined for differences.

A summary of flowering shoots for which complete data sets were available, showed no observable pattern in the proportion of each group that flowered (Table 5.1). For shoots which survived the whole study period, there were some which flowered in the first year but not the second, in the second year but not the first, in both years and in neither. Flowering increased with depth and appeared to be greater in 1988, although this data could not be statistically verified (Figure 5.6). Flowering stalk and inflorescence height increased with depth (Table 5.2). Shoots that flowered at the shallow site were smaller than vegetative shoots (Table 5.3), but at the deeper sites, the opposite trend was apparent, although there was only one significant difference.

Shoots which flowered, produced a peduncle in early winter. These were first recorded with immature inflorescences present in early August of both years. By September, these stalks had grown above the water, flowered and been pollinated. Seeds were mature by October and shed soon after when stalks laden with fruit had bowed over. By December, the only evidence that flowering had taken place were floating seeds amongst the emergent leaves.

Size

The shoot heights of the three groups were compared in the middle of each season (Table 5.4). Only two significant differences were found, and these were at the time of shoot birth/death. Shoots from the second group, which lived throughout the study period, were larger than shoots in the first group in the season just before they died (P:0.05) and larger than shoots in the third group, just after they had emerged (P:0.02). At all other times shoot heights were similar, which supported the observation that soon after shoots emerged, it was impossible to distinguish their age (which group they belonged to).

Mean shoot height (Figure 5.7) closely matched the depth at time of sampling (Figure 5.8). This confirmed the correlation between instantaneous depth and *Triglochin* leaf height (Figure 3.1h). 1-way AOV's on mid-season shoot heights showed significant differences on all occasions. Planned comparisons identified that plants in deep water were larger than plants at the other sites, whereas with one exception, plants at shallow and medium sites were of similar size. These data were used to assess stand variability, which was least when water levels were at a maximum and highest when levels were at a minimum (Figure 5.9). In support of this inverse relationship between depth and stand variability, V^* was consistently higher at the shallow site (mean 45.6) and least at the deep site (mean 28.9).

In addition to the shoot module, the individual leaves also matched water levels. Figure 5.10 illustrates this sensitivity to depth for the mean maximum leaf height per shoot. Compared with total shoot height, there were more significant differences in the height of leaves between shallow and medium elevations. This suggests a difference in the number of leaves per shoot. However, there were no consistent trends throughout the study, with values ranging betweeen @ 2.5 and 5 leaves per shoot (Figure 5.11). Leaf diameter also responded positively to depth, but showed less flexibility than height (Figure 5.12), which indicated it contributed less to changes in biomass. The emergent leaf height calculated as a percent of total leaf height, illustrated how much of the leafy shoot was submerged and for how long (Figure 5.13). At the shallow site, shoots were exposed for 5 months in 1988 and only at peak water levels were they submerged by more than half. At the middle site, shoots were exposed for 3 months, while those at the deep site were permanently in water, with more than half their tissue always submerged.

Growth

A comparison between the three groups showed that the only difference in the number of leaves recruited per shoot within each season (Table 5.5) was a smaller number from shoots in the season prior to their death, compared with shoots that survived. Otherwise values were similar.

With the exception of faster rates in autumn, leaf recruitment was continuous throughout the study (Figure 5.14). This equated to the addition of a new leaf approximately every 22-32 days during the constant period of recruitment, and every 9.6-19.7 days during autumn (Table 5.6). This pattern was illustrated by leaf growth within a single shoot (Figure 5.15) and verified by significant differences in autumn recruitment rates (leaves day^{-1} $shoot^{-1}$, Figure 5.14) and the plastochrone interval (days $leaf^{-1}$ $shoot^{-1}$, Table 5.6). In Feb-88, shoots at the shallow site were producing leaves at a faster rate than at the other sites, but in May-88 the reverse was happening, because shoots at the shallow site returned to the constant rate earlier (autumn), than shoots from the medium and deep sites (winter).

The mean RGR of the three groups at each elevation (Figures 5.16a-c) showed the same annual cycle, with maximum and minimum rates in winter and summer respectively. Because previous differences were detected at the time of shoot emergence and death, RGR's were compared for those records. The only difference was in shallow water, between the shoots that died and those that survived (P: 0.02). Elevation had little influence on the RGR's of the pooled shoot data (Figure 5.17). The exceptions were in shallow water, where rates increased earlier.

The components of the absolute growth rate (cm d^{-1} $shoot^{-1}$), the gross increase and decrease in height, illustrated how leaf senescence closely followed leaf growth, a sign of rapid tissue turnover (Figure 5.18).

5.3.2 *Baumea*

Life-history

New shoots were recorded on five occasions (Figure 5.19). The first group consisted of 17 shoots which emerged between 3-Mar-87 and 5-May-87 (autumn). One new shoot, which eventually flowered, was recorded in June, and in July another 25 had emerged (winter), four of which flowered (these was considered as one group). No new shoots emerged until 3-Mar-88 (autumn), when 18 were recorded. Following high winter water levels when records were missed, 16 new shoots were recorded on 23-Oct-88. There were distinct differences in the survivorship data of the originally tagged shoots and these four groups (Figure 5.20a). The original shoots (group 1) lived through autumn/winter-87, before progressively dying off over summer/autumn-88. Shoots in groups 2 and 4, which emerged in autumn-87 and autumn-88, respectively, died within 6 months (although two from group 4 survived until summer). Group 3 lost more than half its shoots over the first

12 months; however, the remainder survived through to summer-89. When this group was divided into shoots which flowered and shoots which were either long or short-lived, it was clear that the survivorship curve of the long-lived shoots was similar to that of original shoots (Figure 5.20b). It was evident that *Baumea* recruited new shoots in autumn and winter. The original group and group 5 may thus represent the survivors of shoots recruited in winter-86 and winter-88, respectively. Table 5.7a summarizes the survivorship and life-span characteristics of the 5 groups and Table 5.7b, details of group 3.

The shoots that flowered, emerged above the water in August, when the spike unfolded. Pollination took place in September and seed ripening in October-December. Shoots senesced over summer, but once dead (no green tissue) they remained standing, with seeds intact. Seeds were shed in autumn.

Size

Demographic characteristics of these five groups, showed differences in the timing of emergence and survivorship, which were matched by differences in height, biomass and stem number (Table 5.7). Shoots emerging in autumn had mean maximum shoot heights of 30 cm in 1987 and 36 cm in 1988, which was too short to be emergent when the lagoon flooded (Figure 5.21). Maximum shoot biomass was 0.55 g in both years and shoots consisted of just one stem. The mean maximum height of these stems was greatest soon after emergence, but thereafter decreased (Figure 5.22).

Shoots emerging in winter-87 had a better chance of surviving through a growing season. The original shoots and those from group 3 and 5, had similar mean maximum heights (range: 176 - 257 cm), biomasses (range 3.12 - 3.17 g), life-span (17 - 18 months) and stem number (range: 2.4 - 3.0). The mean height of the tallest stems increased to a maximum in early summer (Figure 5.22).

Size characteristics also separated shoots within group 3 (Table 5.7b). The flowering shoots had a mean height of 93 ± 25 cm and a mean biomass of 1.50 ± 0.43 g. They lived 8 to 9 months and consisted of one stem. Of the vegetative shoots in group 3, about half lived for 3 to 6 months. They had similar characteristics to autumn shoots, being too short (mean maximum height 31 cm) to be emergent or to recruit new stems. The long-lived group (life-span range: 15 to 19 months) had a similar height, biomass and stem number, to shoots in group 1 and 5 (Table 5.7b, Figure 5.22).

Growth

The maximum growth rates of autumn shoots (1987 & 1988) were similar (mean: 6.7 v 7.2 mg g^{-1} d^{-1}) and achieved directly after emergence (Table 5.7b, Figure 5.23a). Of the shoots recruited in winter, rates from the original group were smaller, because they had passed their peak. The maximum values for the winter-87 group were achieved in mid-winter, and minimum rates in summer (Figure 5.23a). Within this group, the growth rates of the long-lived shoots and those which flowered, was greater than the short-lived shoots. Following initially similar rates, the autumn and short-lived winter shoots began to senesce whilst the long-lived winter shoots continued to grow (Figure 5.23a). The fastest growth rates were in winter-87 (36.0 ± 5.5 and 33.0 ± 6.6 mg g-1 d-1) attained by flowering and long-lived shoots respectively. The mean RGR's of all shoots were calculated for comparison with *Triglochin* (Figure 5.23b). At the one time there were cohorts growing positively and negatively. Values were mainly positive in autumn, winter and spring, and negative in summer, but the variability associated with pooling the groups, cancelled out any clear pattern(s). Data were shown up to autumn-88, because the initial growth of winter-88 shoots was missed.

The recruitment of the original group and group 5 in winter-86 and winter-88, respectively, was verified by back-calculating their heights, using the RGR's of shoots from group 3 (Figure 5.24). These winter cohorts displayed rapid growth in winter/spring, achieving their maximum height at the beginning of summer. By autumn, shoot height started to decrease and continued until shoot death 12 months later.

Stem growth and senescence were not simultaneous (Figure 5.25a & 5.25b). The life of a shoot consisted of a stage of increasing height followed by a separate stage of senescence. The survivors of winter cohorts thus have a winter/spring growing season and a long slow senesence over the following winter and spring (Figure 5.24b).

Stand Structure

As a developing population, the Patch had not reached its maximum density, and conclusive statements cannot be made about the structure of *Baumea* stands. The predominance and survival of winter recruits suggests these make up the majority of shoots in a stand. Shoots recruited in autumn appear to contribute little to stand density and aboveground biomass. The stand structure changed from a summer population of mature shoots to a winter population of young and maturing shoots (generative and vegetative) and senescing shoots from the previous winter. This verified harvest data (Figure 3.1b, Table 3.2), where spring populations had slightly higher densities and a greater proportion of young shoots with single stems than autumn stands.

5.4 DISCUSSION

There were major differences in the life-history, growth and stand structure between species. *Triglochin* responded to fluctuating water levels primarily with morphological plasticity, whereas *Baumea* displayed little plasticity. Both species, however, showed some flexibility in their demographic program.

5.4.1 Life-history

It is hypothesized that at the shallow site, *Triglochin* shoots live 24 months, emerging and dying during drawdown in late summer/early autumn (Figure 5.26). This is because on the last record, the emergence of a new shoot forewarned that the autumn-88 event would be repeated in autumn-89 and because in the middle of the study when half the population died, the same number had emerged, effectively replacing the dead shoots and restoring populations numbers to their previous values. Populations would thus consist of two symmetrically overlapping generations, equal in size. In this situation, the groups described in the Results, correspond to cohorts 1, 2 and 3 in Figure 5.26. There was some indication that this pattern did not change with elevation. However, because complete data sets for all shoots were not available for populations at the medium and deep sites, conclusions about shoot life-spans, were not definitive.

The five groups of *Baumea* shoots, separated according to their timing of emergence, also differed in size, life-span and reproductive status. This enabled them to be placed into cohorts. Groups 2 and 4 and groups 3 and 5, represented autumn and winter cohorts from 1987 and 1988, respectively. Although the emergence of cohorts 1 and 5 was not recorded, calculations showed they were the long-lived shoots from winter recruitment in 1986 and 1988, respectively. The short lived shoots would have died by the time these cohorts were sampled.

5.4.2 Morphological versus Demographic Plasticity

Triglochin used extensive morphological plasticity to adjust to the fluctuating water levels. Shoots changed dramatically in size according to the water levels. *Triglochin*'s leaf height, like *Typha*'s (Djebrouni and Huon 1988, Grace 1989, Waters and Shay 1990), was controlled by depth, which confirmed the correlation between instantaneous depth and leaf height (Chapter 3). Other morphological changes (increase in standing crop, shoot height and biomass), were found across the elevation gradient. The linear change in elevation (48.25, 48.05, 47.85) was not, moreover, matched by a linear change in size. The difference between the shallow and middle sites was small, compared with the difference between the middle and deep sites. Such a finding was also made by Ibarro-Obando and Huerta-Tamayo (1987) for seagrass growth in a tidal environment at three elevations that differed by 15 cm, and for two salt marsh species (*Scirpus*) at high and low elevations (Karagatzides and Hutchinson 1991). *Triglochin*'s non-linear growth response (and presumably the seagrasses) matched the water regime at those elevations, because depth and duration of inundation was shown to increase exponentially with linear increases in elevation (Figure 2.15).

Shoots within a population, however, were at any time or elevation, indistinguishable in terms of height, diameter and leaf number. The variability (V*) that did exist ranged from a mean of 28.9 at deep sites to 45.6 at shallow sites. Although a mean stand variability of 35.5 for live aboveground *Typha* biomass was considered high (Roberts 1987), values here are relatively low, because the same scale (per area) does not apply to individual shoots. Uniformity among shoots is uncommon in clonal populations where marked variation and skewed distributions of shoot size is often explained by intraspecific resource competiton (Weiner and Thomas 1986). Although individual variability is the subject of debate, few studies have identified or investigated the opposite situation as found in *Triglochin*. One explanation for such uniformity, is that *Triglochin* has the resources (internal supply in large belowground mass) and the resource supply (ability to capture resources through large root mass and rapid turnover of shoot tissue) to support the equivalent growth of all shoots. The redirection of resources within integrated shoot systems, is also a buffer against environmental heterogeneity (Callaghan *et al.* 1992).

Although shoot size was related to the probability of flowering in *Typha* (Roberts 1987, Dickerman and Wetzel 1985), this was not the case for *Triglochin*, because of the uniformity among shoots. Size was shown to be important for physiologically independent shoots of *Typha* (Grace and Wetzel 1981b), but for cloanl plants, it may not make any difference if a plant distributes its energy between a group of shoots of similar or different sizes. This may explain the lack of consistent correlation between shoot size and flowering. If intraspecific competition is less relevant for connected shoot systems, then the relationship between size and competitive ability (Gaudet and Keddy 1988) may only apply to interspecific interactions (eg. *Salvinia* v *Lemna*, Clatworthy and Harper 1962).

Demographically, the lack of *Triglochin* shoot natality and mortality at times other than autumn, meant shoot densities were constant over time. This contrasted with the changes identified between autumn and spring harvests (Table 3.3). In the light of *Triglochin*'s life-history, that result was due to the autumn harvest taking place just after the death of one cohort and before the emergence of the next. Simultaneous natality and mortality is usually interpreted as density-dependent regulation or competition between ramets for limiting resources (Noble *et al.* 1979). The growth of daughter ramets followed by the senescence of parent ramets does not necessarily relate to competition (Sarukhan and Harper 1973, Bedford *et al.* 1988), but can represent a transfer of photoassimilates, water and minerals within a unified shoot system (Lovett-Doust 1981). The regulation of shoot numbers is thus a developmental not a demographic process (Cook 1985).

Apart from an increase in the number of flowering shoots at deeper sites, the only indications that *Triglochin*'s growth cycle was influenced by water regime, were increases in leaf recruitment and RGR at the shallow site in late autumn, which preceded shoots from deeper sites. The influence of the timing of drawdown and exposure on *Triglochin*'s life-history could be elucidated by intensive (weekly) sampling during this period, and matching to it detailed water regime data.

For *Baumea*, the regulation of population numbers was a demographic process, because shoot birth and death were separate events, and life-span, reproductive status and size, depended on the timing of emergence. Timing of emergence also influenced stem heights in *Carex* spp. (Bedford *et al.* 1988, Soukupova 1988). Shoots which did not grow tall enough to be emergent, died, but why this included all the autumn shoots, but only half the winter shoots, is not known. It may be that winter recruits were long shoots, and autumn recruits short shoots, which respectively, did and did not give them the resources to respond to increasing depth. The distinct characteristics of *Baumea* cohorts, unlike *Triglochin*, gave variability to its population structure.

Baumea did not have the same breadth of plasticity, withstanding changes in water level without major changes in stem height, even though water levels were slightly higher in 1988. Biomass was gained over a comparatively long period, maintained and then slowly lost. Mortality was highest in winter and spring, but occurred throughout the year. Such variability in longevity is a characteristic also found in *Carex* (12 - 539 days, Bedford *et al.* 1988). The maximum life-span of the short cycle was 18 months, which compared with *Carex* species, which survive 15-18 months or 24 months for overwintering shoots (a shoot type not found in these species due to the mild winters). A high shoot mortality may not necessarily translate into a loss, because the production of many shoots, if met by favourable conditions, strengthens a plant's position by its presence in large numbers. If favourable conditions do not arise, energy can be reallocated back to the parent (Callaghan 1976, Harper 1977).

5.4.3 Sexual versus Vegetative Reproduction

The two shoot types in *Baumea*, vegetative and generative (programmed to die after flowering) was typical for sedges. *Triglochin* shoots (as with *Typha*) were of one type only, but interestingly, they were able to flower twice, passing from one reproductive phase to another, which is uncommon for aquatic clonal plants. Flowering in biennial species is usually limited to the second year (Werner 1975); however *Triglochin* shoots either flowered one year but not the other, in both years or not at all.

Both species produced flowering shoots in early winter and set seed in spring, but whereas *Triglochin* fruits were shed soon after, *Baumea* fruits remained on the standing dead culm well into the following autumn. *Triglochin* seeds being shed when water levels were high and being able to float, must undergo dispersal, while *Baumea*'s which are shed during drawdown and beneath the canopy, are not dispersed. The lack of seedlings is not unusual for sedges (Bernard 1975, Auclair *et al.* 1976) but surprising for *Triglochin* as they were noted in previous years. Application of the model of Ganf *et al.* (1991) showed that under the autumn-88 water regime, germination was restricted to between 48.04 and 48.09 AHDm. This included the middle site; but because flooding did not commence until 1-Jun, no seedlings survived. Even though vegetative reproduction was the main-stay of their populations, when a small proportion of seedlings do establish, as *Triglochin*'s did in 1986 (Table 3.8), they may make a significant contribution to genetic diversity (e.g. *Ranunculus repens*, Soane and Watkinson 1979).

There was insufficient evidence to refute the theory that energy allocated to sexual reproduction increased when the benefit:cost ratio increased (Loehle 1987). However, it appears that this is the case for both species. The increase in the proportion of *Triglochin* shoots in flower (fertility), with increasing inundation (also *Scolochloa festucacea*, Neill 1990, *Scirpus paludosus* ver *maritimus*, Lieffers and Shay 1981) did not conform with the idea that reproductive allocation was controlled by competition (under low competitive stress plants allocate more energy to seed production, Gadgil and Solbrig 1972), nor with the theory that allocation depended on plant age (Schaffer 1974, 1979). It was surmised, nevertheless, that *Triglochin* seeds produced and shed in deep water had a greater chance of survival, because they were able to float and be dispersed. Seeds produced and shed in shallow water would have been exposed for longer, and, due to their innate dormancy (unpublished), this would have decreased their viability by the time autumn arrived. The low fertility of the sampled *Baumea* population, supports the observation that flowering is not ubiquitous in the lagoon, especially in deeper water. Because the Patch was surrounded by other patches with flowering shoots, this suggests that flowering is limited to higher elevations or to young developing stands, a characteristic of clonal plants (Abrahamson 1980). Seeds shed in deep water would have a lower chance of survival, because they do not float or like other sedges (*Cladius mariscus*, Meredith 1985), germinate under water.

5.4.4 *Triglochin* v *Baumea*: Growth, Other Species and Other Regions

Triglochin's RGR's were similar at the three sites, which compares with the similar amounts of accumulated biomass at 0, 50 and 100 cm depth (Chapter 4). Long-lived *Baumea* shoots from the winter cohort had similar maximum rates to *Triglochin* shoots at comparable elevations (shallow site v Patch). Mean values from all shoots in the stand, however, showed that *Triglochin* grew rapidly in winter, but had large negative rates throughout summer. The rapid decline in growth rate over spring may be due to post-flowering exhaustion. Despite a summer lull, *Baumea* grows at an overall slow, more or less continuous rate throughout the year. RGR is ususally calculated from sequential harvests of the whole plant, mostly seedlings and less commonly ramets (Konings *et al.* 1989, Yen and Myerscough 1989). It must be kept in mind that RGR calculated for shoot tissue alone, has short-comings for clonal plants, especially where morphologies and turnover rates differ.

Triglochin PB_{max} ratios for shoot biomass and leaf numbers, were greater than *Baumea's* (Table 5.8). High values have been correlated to high productivity (Madsen 1991). PB_{max} values are an indication of tissue loss in proportion to production, which for species without a substantial belowground mass, and which do not translocate energy is a straight-forward index (e.g. *Nasturtium officinale* Howard-Williams 1982, *Potamogeton pectinatus* van Wijk 1988, and references within Madsen 1991). For emergents and perennial species with a substantial belowground mass, energy is usually incorporated into different tissues and rarely lost. Consequently, PB_{max} values may be artificially high. Nevertheless, mean values for the genus *Carex* (1.5 - 1.7, Bernard and Gorham 1978) were greater than *Baumea* (1.0 - 1.1) and less than *Triglochin*'s (1.92 - 3.07) which emphasises the differences in their rate of tissue turnover. In climates with a continuous growing season, higher values were reported, (e.g. *Cyperus papyrus* 2.5, Westlake 1975), but this did not appear to be the case for *Baumea.*

New shoots were recruited when water levels were at a minimum (*Triglochin* in autumn and *Baumea* in autumn/early winter). However, shoot recruitment in emergents is common in autumn **and** spring (Bernard 1975 & 1976, Ratliff and Westfall 1988, Soukupova 1988, Verhoeven *et al.* 1988). The former generally overwinter and join spring recruits for rapid growth into a summer growing season. Neither *Triglochin* or *Baumea* produced new shoots in spring, which combined with the finding that growth was fastest following recruitment in winter, identified a different growing season from most plants in the literature. The correlation between peak aboveground standing crop and maximum mean monthly temperature (Gorham 1975) and the assumption that shoot growth is fastest over the summer growing season when temperatures are highest (Ratliff and Westfall 1988, Soukupova 1988, Verhoeven *et al.* 1988) may apply in regions where shoots overwinter conditions of ice and snow. With maximum growth rates in winter, temperature is not a factor that shapes the annual growth cycle of *Triglochin* and *Baumea.* For other aquatic plants in southern Australia, growth was also not correlated to temperature alone. Although seagrass growth was highest in summer and lowest in winter, this was related to irradiance and day-length (Kerr and Strother 1989) and with phytoplankton, maximum growth rates can result from a favourable light environment and nutrient levels well before maximum temperatures are reached (Ganf and Oliver 1982, Oliver and Ganf 1988). The summer growing season of *Typha* and *Phragmites* in this region (Roberts 1987, Hocking 1989a & 1989b) may reflect the habitats where they were measured; habitats without winter flooding and without water being limited over summer. It appears that growth is controlled by the degree of flooding. As water levels rise in winter, plants must keep their leaves or stems abreast of the rising water levels, in order to overcome a C deficit. Growth was slowest in summer, when temperatures were highest and water levels falling, indicating that this season is a time for plants to reallocate energy gained in winter to belowground stores.

5.5.5 Conclusion

Triglochin relies on morphological plasticity to survive the variable environment of the Lagoons . It has a less flexible life-history than *Baumea,* which displays limited morphological plasticity. The most favourable site for *Triglochin* was the deepest, because stand variability was least and accumulated shoot mass, PB_{max} ratios and total biomass (Chapter 3) were greatest. Those shoots had more than half their tissue permanently submerged, whereas at the shallow site, where accumulated shoot mass was least, shoots were exposed for 5 months a year and were rarely submerged by more than half. The conclusion to be drawn here is that even though *Triglochin* responds quickly to changes in water level, it performs best not only in deeper water but when continuously inundated.

CHAPTER 6: SPECIES INTERACTION: DEMOGRAPHY AND RESOURCE ALLOCATION

6.1 INTRODUCTION

To identify the role which species interaction plays in the vegetation changes in the Lagoons, it was necessary to search for evidence of a competitive component and the influence of water regime upon it. Competition was considered possible because of a temporary coexistence in the broad area, where the front of *Triglochin* is invading the once dense *Baumea* stands. Mutualism was dismissed because their populations were naturally segregated, and predation was not investigated because the scale of changes was considered too large for herbivores or parasites to have produced. Information about the individual morphology, biomass accumulation and allocation, and demography of the species under natural and manipulated water regimes, has been presented so far. This chapter presents the results of a competition experiment to conclude the investigation of the replacement of *Baumea* by *Triglochin* in Bool Lagoon.

A Reciprocal Replacement Series was set up to determine the influence of depth on the interaction between *Triglochin* and *Baumea*. Plant distribution patterns result from the physico-chemical environment interacting with competitive processes (Titus and Adams 1979, Grace and Wetzel 1981a, Silander and Antonovics 1982, Keddy 1984, Agami and Waisel 1985, Bertness and Ellison 1987). In investigations of the relative contribution of abiotic and biotic factors, Chambers and Prepas (1990) found that submerged plant community structure was determined more by competitive interactions than abiotic factors, whereas the zonation of salt marsh emergents (Bertness 1991a) and the composition of seagrass communities (Nomme and Harrison 1991) was due more to the physical environment. Water level fluctuations in Bool Lagoon were considered to be more similar to the tidal environment than to the hydrologically uniform habitat of submerged plants. It was thus hypothesized that water regime had a greater influence on distribution patterns than interspecific competition.

✶ This idea was drawn from the resource supply model of Keddy (1989) and on the basis that sediments are the primary source of essential nutrients for rhizomatous emergent macrophytes (Graneli 1989). At any one elevation, the supply of atmospheric C and O_2 will, over time, change in accordance with changes in water level. Spatially, resource supply will depend on the degree of wetting and drying. Continuous inundation, with all other factors constant, will cause a more uniform and restricted supply of resources compared to areas subject to exposure, because the wet/dry cycle stimulates the transformation of nutrients into available forms (Briggs and Maher 1985).

The definition of competition given by Begon *et al.* (1986); "an interaction between individuals brought about by a shared requirement for a resource in limited supply, and leading to the reduction in the survivorship, growth, and/or reproduction of the individuals concerned", refers to both the mechanism and the outcome of species interactions. The mechanism is the utilization of the same unit of resource (nutrient, light, water, space). As the intermediary in competitive interactions, resources are central to competition studies (Price 1984). Of particular relevance is resource supply and how plants and the environment modify it. When a species exploits a resource to the extent that it reduces its availability to other species, this is called direct competition. The performance of the dominant plant is often enhanced because it uses the extra resources it garners to exploit more resources, further drawing down levels available to the suppressed species. This mechanism was proposed by Hejny (1985) to explain the retreat of macrophyte communities. The influence of the abiotic environment on resource supply also is important, because if a continuous or patchy supply is maintained, potential competitors can coexist. The classification of resources according to the way they vary spatially and temporally, and on scales relevant to the species under study, is an important aspect of competition studies (Keddy 1990).

Fluctuating water levels indirectly influence the supply of space and sediment nutrients, the resources that emergent macrophytes first compete for. For example, space is resupplied when plants die, either naturally or from hydrological disturbances such as continuous inundation or extreme fluctuations. Flooding and exposure of the substrate, together with particular plant traits, affects the oxygen status of sediment and thereby the availability of nutrients. Although emergent plants do not compete for gaseous carbon and oxygen, their supply is directly affected by changing water levels. Competition for dissolved carbon and oxygen may take place between submerged plants and/or fleshy leafed emergents such as *Triglochin*. Variation in the timing and amplitude of water level changes also means that resource supply rates are variable. ✶Although the time lag is not known, supply rates temporally relate to seasonal changes in water level and spatially are continuous; continually low where inundation is permanent, and continually high in shallow sites that become exposed.

As the supply ratio of key resources change, so too do the competitive abilities of plants (Tilman 1988). Tilman proposed that the superior competitor for the resource, which has been reduced or which is limiting, will dominate. For an emergent like *Baumea* and to a lesser extent *Triglochin*, access to gaseous C and 0_2, will decrease across a depth gradient, and the relative availability of sediment nutrients will change. In deep water, *Triglochin* was shown to increase both the accumulation and allocation of mass to its leaves, wheras *Baumea* increased only the allocation of mass to its stems. These responses reflect adaptation to a C and/or O_2 deficit. In shallow water, where these gases are abundant, belowground resources (space and nutrients) are more likely to become limiting sooner. Although the proportional accumulation and allocation of biomass and nutrients are generally not correlated (Abrahamson and Caswell 1982, Konings *et al.* 1989), the accumulation and allocation of nutrients can also indicate limitation and interaction. In sites with low nutrient levels, plants respond by having a greater belowground mass (Gallagher 1974, 1975, Barko and Smart 1978, Smart and Barko 1978) and higher tissue nutrient concentrations (Graneli and Solander 1988, Konings *et al.* 1989). As essential resources (ie. not substitutable, an increase in one does not overcome limitation in another), nitrogen, phosphorus, sodium and potassium concentrations in the tissues of both species, were examined as another measure of interspecific competition. From the accumulation and allocation of nutrients and biomass, the tissues experiencing stress and the site of competition can be determined. Even though *Triglochin* may be able to utilize C, N and P from the water, the primary source of C for both species, as emergents, is from the air, while the primary source of N and P is from the sediment. Changes in the C:N and C:P ratios would confirm the difference between allocation to aboveground parts, to overcome C limitation and to belowground parts to overcome N or P limitation.

Measuring final outcome alone is not sufficient for an understanding of the processess behind vegetation change. Demographic, growth and morphological data can help to identify when interactions take place and the importance of specific plant traits. To determine the influence of competition on the known responses to depth, it was necessary to sample the plants on a number of levels. For example, changes in growth rates, translate into changes in mass, which in turn, translate into changes in recruitment and thereby population structure. Traits of individual shoots that have been related to competitive ability include above and belowground biomass (Gaudet and Keddy 1988) and morphology (Lovett Doust 1981, Schmid and Harper 1985). At the level of the population, plant architecture (Werner 1977, Yen and Myerscough 1989, Yamasaki 1990) and the timing of life-history events (Buttery *et al.* 1965, Werner 1977, Grace and Wetzel 1981a, Yamasaki and Tange 1981, Spitters and Aerts 1983, Yamasaki 1990) have explained species segregation or coexistence. The role of these factors also were considered.

Competition is usually assessed by pairwise experiments, although the attempt to identify multiple interactions has begun (Fowler 1981, Silander and Antonovics 1982, Keddy 1990). Transplant/removal experiments conducted *in situ*, are some of the best methods, but a more controlled approach, employed here, was the Reciprocal Replacement Series (RSS) (de Wit 1960; reviewed by Hall 1974 & Harper 1977). Used in agriculture to assess crop performance in the presence of other crops, invading weeds or pasture species, it is a substitutive design where density is held constant and proportions varied. Comparing monocultures with mixtures which are at different densities, however, is basically invalid (Debenedictis 1977, Inouye and Schaffer 1981, Jolliffe *et al.* 1984, Firbank and Watkinson 1985, Connolly 1986, Snaydon 1991). Snaydon (1991), showed that the likelihood of interactions being found when none exist, decreases as the starting density increases. Of the indices used to measure interaction (Connolly 1986, Wilson 1988), the Relative Yield Total and the Relative Crowding Coefficient were found to give the most consistent results, across a range of densities (Snaydon 1991).

The experimental design in this study eliminated many of the concerns about density. In the agricultural context, the initial density of seeds/seedlings of the colonizer/original species is clearly relevant. However, for interactions between adults as populations which are at carrying capacity, there *is only one* density for each species. RRS experiments on annual crops typically run for weeks to months, over the important stages of seedling establishment, but perennial species require the generation of at least one shoot module to pass, for interactions at the scale of natural populations to occur. Because the outcome will change as water levels change, a longer experiment also allows the effects of seasons and the sum effect of the annual cycle to be measured. In addition, the interaction can be measured as growth and reproduction over time, whereas short-term experiments usually just measure the outcome (survivorship and yield). RSS experiments are also useful for showing the effects of different treatments on the outcome of competition (Firbank and Watkinson 1990). To see if interactions were produced or modified by water regime, the experiment was replicated at two depths.

The RSS experiment was set up to investigate competitive interactions between *Triglochin* and *Baumea*, and the influence of water regime upon them. Information about individual performance, provided by the monocultures, added to the results of abiotic responses (as presented so far). An aim of this Chapter was to assess the relative contribution of abiotic and biotic factors, re the demise of *Baumea* stands in Bool Lagoon. The hypothesis was that water regime had a greater influence on distribution patterns than interspecific competition. Other aims were to determine whether interspecific competition was experienced above or belowground and to investigate the influence of traits, such as above and belowground biomass, plant architecture and the timing of life-history events, on the final outcome.

6.2 METHODS

Experimental Design

A Reciprocal Replacement Series experiment was set up with adult material. This design sought to mimic what looked to be happening in the field. The densities chosen were designed to simulate natural populations and the observed interaction between single or several *Triglochin* plants and established stands of *Baumea*. There were three treatments, planted into 30x30x30 cm crates, at the ratios 75T:25B, 50T:50B and 25T:75B (Appendix 6.1). The controls or monocultures consisted of four ramets of *Triglochin* which was equivalent to field densities and eight ramets of *Baumea*, which was less than in natural stands, because *Baumea* was known to recruit many new shoots when transplanted. For mixtures, one ramet of *Triglochin* was considered equivalent to two of *Baumea* on the basis of total dry weight and shoot bud number. Each treatment and control were replicated four times for a total of 20 crates at each depth. To see if any interaction was produced or modified by water regime, the experiment was replicated at two depths; 10 (0-20) and 60 (50-70) cm, termed 'shallow' and 'deep' (Figure 6.1). Based on previous results, these were within their depth limits. The shallow treatment approaches the upper limit of *Triglochin* and the deep treatment the lower limit of *Baumea*. Crates were lined with heavy duty, plastic garbage bags and filled with lagoon mud, predominantly black clay from the Main basin. The experiment ran for 20 months, which allowed populations to reach the carrying capacity of the crates, so that maximum contact with neighbours could take place and for at least one generation of shoots to pass. The length of the experiment was also designed to allow life-history and demography to match that in natural stands.

Field

Ramets of *Baumea* were dug from healthy and monspecific stands adjacent to the outlet channel in May-87. These were potted and left at 10 cm depth for 5 weeks, after which the best performing ramets were selected. Because *Baumea* transplants are less reliable than *Triglochin*, this method ensured a high survival rate. *Triglochin* ramets were dug from the Main basin and along with *Baumea* planted directly into crates in Jun-87. Crates were arranged in a segregated block design on the banks of the outlet channel at depths of 10 and 60 cm. This design prevented abovground interaction between different treatments, and was necessary for reasons of space and ease of taking records.

Measurements

The original ramets were tagged O1, O2, O3 etc when the crates were put in place on 6-Jun-87. The first measurements were taken in 7-Jul-87, when all new shoots were tagged. As with other studies, the tag was placed on the second youngest leaf or stem, so that recruitment within the shoot could be followed. The recruitment of new shoots (flowering and vegetative) and the photosynthetic height of all stems and leaves were recorded 15 times, at @35 day intervals from 7-Jun-87 to 6-Feb-89. On the last recording date, all measured stems and leaves were clipped at the sediment. A hose was used to wash sediment from the remaining belowground plant. This was done over a coarse grid to retain all live material that had snapped off. Tags were kept in place so that belowground shoot development could be examined later. Complete rinsing and separation of tissue types took place in Adelaide, where samples could be kept in a cool room during processing.

Shoots, rhizomes, roots and tubers were dried in a fan-forced oven at 60 C° for 48-72 hours. The individual dry weights of stems and leaves were used to produce regression equations for the conversion of height data into biomass. A sample of each dried tissue, from all crates, was taken for nutrient analysis. The tissue chosen looked healthy and was in the young to mature stage. The exception was *Triglochin* leaf which was all mature. Several grams of each sample were ground (mesh size 0.1 mm). The concentrations of total phosphorus, total nitrogen, sodium and potassium were determined on subsamples from each population. Total P (mg g^{-1} dwt) was determined by persulphate digestion followed by the addition of ammonium molybdate and ascorbic acid. An autoanalyser was used to determine total N (mg g^{-1} dwt). Samples were digested with a kjeltab and sulphuric acid, which broke down all N (except triple bonded) to ammonium sulphate. Na^+ and K^+ (uM g^{-1} dwt) were determined by flame-photometry.

Analysis: Plant Growth and Demography

Regression equations for each species at each depth (SAS 1985) were used to convert heights and diameters (*Triglochin* only) to biomass.

Baumea

shallow: $g\ dwt = (1.739*10^{-4}) * (height^2 + 0.1831)$

deep: $g\ dwt = (7.300*10^{-7}) * (height^3 + 0.5382)$

Triglochin

shallow: $g\ dwt = (2.741*10^{-3} * height) + (2.852*10^{-4} * width^3) + 8.194*10^{-3}$

deep: $g\ dwt = (1.271*10^{-4} * height^2) + (0.1386 * width) - 0.9596$

Demographic data were collated using the relational database RBase in combination with a program written in BASIC. All consecutive measurements of leaves and stems were entered. The gross and absolute (net) increase and decrease in height, biomass, shoot, stem and leaf density, as well as total values, were calculated for each time interval (see Appendix 5.1 for equations). Data is presented as the mean and standard deviation of four replicates, either on a m^{-2} or $shoot^{-1}$ basis. For comparison of monocultures, most data was presented on a m^{-2} basis and for comparison of growth in mixture, data was on a $shoot^{-1}$ basis. The latter was calculated separately for each record, by dividing population data by the number of shoots, present for each record. Relative growth rates of shoot tissue, were not calculated, as the morphological difference between species were considered too great for them to be meaningful.

Linear regressions were fitted to cumulative increases and decreases in stem and leaf densities (the progressive sum of gross increases and decreases respectively). These equations gave the overall rates of change (e.g. stems d^{-1}). The inverse of this rate (days $stem^{-1}$) gives the number of days for the addition of a new stem.

The shared occupation of aboveground space can lead to indirect competition, where one species shades or physically interferes with another. The potential for aboveground interaction was investigated by frequency distributions of stem and leaf heights. Results led to the distribution of *Baumea* stem heights from single populations at both depths, being compared over time to see how *Baumea* might affect *Triglochin*.

The quickest way to assess pairwise interaction was to draw up replacement diagrams which summarize the whole experiment. Final biomass data as well as the cumulative recruitment of shoots, stems and leaves per initial ramet were used for these. Two indices of interaction were calculated. The Relative Yield Total (RYT), is the sum of each species yield in mixture as a proportion of yield in monoculture. If RYT=1, the two species are said to share the same resources. If RYT>1, they partially share the same resources and if RYT>1.5 there is no overlap of resource use and no competition. The Relative Crowding Coefficient (RCC) is an index of the competitive ability of species A relative to B. It is calculated for each species separately and is the yield of one species divided by the yield of the other in a 50:50 mixture. For each species in mixture, a RCC of 1 indicates similar competitive abilities but if the RCC of species A is > 1 and for species B<1, then A is the superior competitor. Snaydon (1991) recommended taking the $\log_{10}$ of the RCC, to make values symmetrical around zero. A negative or positive value would then indicate inferior or superior competitive abilities, respectively.

Because the outcome at 20 months may differ from the outcome at earlier stages, it was important to follow up the first conclusions with alternative approaches. The leaf recruitment rate and leaf extension rates (gross increase in leaf densities and total leaf height) on a per shoot basis, gave a common measure of performance, and were employed to see if population interactions extended to the level of the shoot. This data was compared by 2-way AOV's (Statistix 1987), where factors, depth and mixture had two (shallow and deep) and four levels (monoculture, 75%, 50%, 25%), respectively. Analyses were conducted every second record, so that samples were independent. In addition, replacement ratios at each record, calculated for the total number of *Triglochin* leaves and the total *Triglochin* leaf height per population, were plotted in three dimensions.

Analysis: Plant Nutrient Levels

To compare the nutrient status of each species, the concentrations of N, P, Na^+ and K^+, in each tissue were compared by 1-way AOV's. To determine the effect of depth and a different neighbour on nutrient levels in each tissue, data were analysed by 2-way AOV's. The factors, depth and mixture had two levels each (shallow v deep and monoculture v 50:50 mixture). This analysis isolates the factor, or combination of factors, that explain the variation in the measured responses. N:P ratios were calculated for each tissue and for each species as a whole. The total nutrient levels in the whole plant were calculated on a per m^{-2} basis. To investigate if the results for biomass data extended to the amount and distribution of major nutrients, the proportional allocation of nutrients and biomass were illustrated in bar charts. This mean data could not be statistically verified, as the nutrient data could not be matched exactly to each set of biomass data. For each tissue in both species, the effect of depth (shallow v deep) and mixture (monoculture v 50:50 mixture) on the ratios of carbon (g; 47 % of dry-weight mass, Adcock 1991) to N or P (g), were compared by 1-way AOV. Due to the small sample sizes (n=3-4), probabilities less than 0.01 were considered significant.

6.3 RESULTS

6.3.1 Water regime

The 50 cm relative difference between treatments was maintained. However, when the outlet gates were closed soon after crates were put in place, depths rose to 40 and 90 cm and remained there for 10 weeks. Instead of fishing them out, plants experienced the natural fall in water level over the next six months. In the second year, levels were kept constant by moving crates before these changes took place. A short sudden fall in water level on the 5th to last record was unavoidable.

6.3.2 Monocultures

Biomass

The final total biomass *of Baumea* populations, was significantly less in deep water (Table 6.1). This reflected decreases in all tissue types, but mostly in rhizomes and roots, which led to the below:aboveground ratio falling to below one. The root:shoot ratio calculated for total shoot mass in shallow water (0.79) was greater than recorded in natural stands (Table 3.5), while the smaller value in deep water (0.15) was considered very low, as similar values were found for plants showing no growth (Appendix 4.3). As the significance of this ratio is the amount of photosynthetic relative to nutrient acquiring tissue, it was recalculated using green shoot tissue only and not including the shoot bases which were belowground. This increased the value in shallow water to 1.13, which was considered indicative of healthy stands, but in deep water there was little change and the value of 0.17, although apparently sufficient for long term survival, signified a vulnerable plant. Rhizomes had a greater mass than roots in *Baumea* populations. The small decrease in the root:rhizome ratio from shallow to deep water, showed that root mass declined more rapidly than rhizome mass. Nutrient acquisition was thus more adversely affected, at least in the short term, than storage and vegetative reproduction. Ramets in deep water had a greater total mass which was mostly held in shoots, whereas in shallow water, mass was mostly held in rhizomes.

Triglochin showed much smaller differences between shallow and deep treatments (Table 6.1). Total biomass was slightly reduced in deep water but not significantly so. This was because a large increase in shoot tissue was offset by a decrease in the total belowground mass, due mostly to a major decrease in tuber mass. These reallocations meant the below:aboveground ratio fell markedly between the two treatments, although at both depths the majority of tissue was still held belowground. The decline in root:shoot ratios, was due to an increase in shoot mass and not a decrease in root mass. Because the root:rhizome ratio did not change, reallocations had taken place without either tissue suffering. *Triglochin* ramets had a greater mass in deep water. Figure 6.2 illustrates the relative allocation of tissues at the two depths.

Recruitment

Partitioning the biomass data into shoot, stem and leaf densities, further differentiated the species (Table 6.2). *Baumea* had far fewer shoots and stems in deep water compared with shallow, and approximately half the photosynthetic height. The number of shoots and stems recruited per initial shoot were approximately four times higher in shallow water. The % survivorship showed high mortality rates for shoots and stems at both depths. The highest values were attained by shoots in shallow water. For *Triglochin*, there were also fewer shoots and leaves in deep water as well as fewer tubers (Table 6.2), but the final photosynthetic height was much greater. There were virtually no shoots recruited in deep water, but in shallow water, a mean of 2.44 new shoots were produced for each shoot planted. Leaf recruitment in shallow water was almost double that in deep. In contrast to *Baumea*, shoot survivorship was high and the lowest values were in shallow water. Depth had no effect on leaf survivorship. The low rates were due to short life-spans and fast turnover rates.

Cumulative changes

Figures 6.3 and 6.4, illustrate the cumulative increases and decreases in *Baumea* stem and *Triglochin* leaf numbers (per crate population). The production of *Baumea* stems exceeded that of *Triglochin* leaves in shallow water, but in deep water it was the reverse situation (Figures 6.3a & 6.3b). In shallow water, *Baumea* stems emerged and died at a rate of 0.63 and 0.37 d^{-1} respectively, whereas in deep water, stem death closely corresponded to stem birth (0.12 v 0.11 d^{-1}) (Figure 6.4a; Table 6.3). This was also the situation for *Triglochin* populations whose leaves had birth and death rates of 0.46 v 0.43 d^{-1} in shallow water and 0.22 v 0.21 d^{-1} in deep water, respectively (Figure 6.4b, Table 6.3). Because these values average population growth over 20 months, seasonal differences may have been cancelled out, and it was important to look at the gross and net changes that took place. The negative values for some intercepts, resulted from analysing data from the first record (day 36) instead of when the experiment began (day 0).

Growth rates: Recruitment

In deep water, *Baumea* had initially faster rates of shoot and stem recruitment (Figures 6.5a & 6.5b). These dropped off after about 3 months, to low steady rates, with no obvious pattern. In shallow water, shoot recruitment rose in autumn (Mar-May) and winter (Jun-Aug), seasons previously identified as major periods of recruitment (Chapter 4). After initially high rates, stem recruitment was more or less constant (Figure 6.5b). The recruitment of *Triglochin* shoots and leaves was greater in shallow water, but at both depths occurred throughout the year (Figures 6.6a & 6.6b). The shoots to emerge in shallow water, were small with thin leaves. This contrasted with natural stands, where new shoots were large with terete leaves and emerged only in autumn. In shallow water, higher rates of leaf recruitment in autumn, compared well with natural stands (Figure 5.14). Because this was not found in deep populations, it may reflect the addition of new shoots. Recruitment at both depths fell to a minimum in Jun-88.

Growth rates: Biomass

In shallow water but not deep, *Baumea*'s gross rate of aboveground biomass accumulation (g d^{-1} m^{-2}) increased in spring of each year and was least in autumn and winter (Figure 6.7a). In deep water, populations grew at a slow but steadily increasing rate. *Triglochin* also exhibited spring growth (Figure 6.7b), but at both depths. The larger response in spring-87, when the unexpected flooding took place, contrasted with the smaller response in spring-88, when water levels were stable. The decrease in the 5th to last point, was due to a sudden drop in water levels, when the outlet gate was opened. The magnitude of this change, could not be experienced in shallow water (10 cm). On a per shoot basis, both species accumulated shoot mass faster in deep water, leading to taller and broader shoots (Figures 6.8a & 6.8b). In shallow water, *Baumea* shoots exhibited the same seasonal pattern as the population. Deep shoots grew fastest in autumn and spring, and finished up with a much higher growth rates than shallow shoots. Because there was little change in the density of *Triglochin* shoots, the rates of biomass accumulation per shoot had the same pattern as populations.

When the absolute rate of biomass accumulation (g d^{-1} m^{-2}) was considered, it was shown that the timing of *Baumea*'s growth in deep and shallow water was different (Figure 6.9a). In deep water, growth preceeded that in shallow water. Shallow populations experience negative growth rates in late summer/autumn, but this pattern was not evident in deep populations, where growth was mainly positive. For *Triglochin*, absolute growth rates at the beginning of the study (following the increase in depth), increased. With the exception of spring, they were othwerwise around zero, and similar at both depths (Figure 6.9b). In shallow water, the increase in *Triglochin*'s total aboveground biomass, reached and remained at a relatively constant level after the first 6 months (Figure 6.10a). *Baumea*'s did not plateau until the last 4 months. In deep water, *Triglochin* populations exhibited the same pattern, but with higher masses, whereas *Baumea*'s aboveground biomass continued to accumulate (Figure 6.10b). By the final record, *Baumea* had a greater shoot mass than *Triglochin*.

Frequency distribution

In shallow water, on the final sampling date, *Baumea* stem heights were normally distributed and *Triglochin* leaf heights were skewed to smaller size classes (Figure 6.11a). *Baumea* thus had not only more stems, but taller stems as well. Although *Baumea* stems were again taller than *Triglochin* leaves in deep water (Figure 6.11b), they were not normally distributed, but showed considerable inequality. Whereas *Triglochin* was represented in all classes between 0 and 100 cm, there were only a few *Baumea* stems shorter than 100 cm. This reflected the need for all photosynthetic parts to reach similar heights as determined by water depth.

Because of *Baumea*'s seasonal response (Figures 6.7a & 6.9a), it was apparent that the distribution of stem heights would change with time. *Triglochin*'s seasonality under constant depths was not as distinct, and changes in heights for this species mainly reflect changes in water level. In shallow water, on the first record, *Baumea* had just 2 stems, both less than 11 cm in height (Figure 6.12). By 17-Jan-88, the population was comprised of 115 stems, between 0-90 cm in height. Once the population had established, a pattern of normally distributed stem heights emerged. This tended toward being skewed to the left during autumn, winter and spring-88, when there were high levels of recruitment (range: 11-16 & 13-25 stems in the 0-10 & 11-20 cm size class), and to the right in summer-88, when there were fewer new stems produced (range: 2-6 & 4-11 stems in the 0-10 & 11-20 cm size class). In deep water, the population developed into a stand of unevenly distributed stem heights (Figure 6.13), with not all size classes consistently represented.

To conclude these results for monoculture populations, Figure 6.14 summarizes the species individual responses to different water regimes. Data from previous Chapters were incorporated. To simplify the effects of changing water levels, four constant depths, and changes between these, were considered. Although *Triglochin*, cannot establish in exposed or deep conditions, it can survive in those habitats as a mature plant. With increasing depth, the increase in shoot mass is offset by a decrease in tuber mass and number. As with *Baumea*, rhizome length decreases and rhizome diameter increases. Shoot density is

Baumea performs best at elevations 35 cm higher than *Triglochin* (48.00 v 47.65 AHDm).

highest at medium water depth, while the proportion of shoots in flower, increases with depth. The vegetative shoot buds of *Baumea*, can be stimulated to grow under exposed and shallow conditions, but they will not establish at depths greater than 80 cm. Once established in shallow conditions, they can withstand moderate flooding, but not to depths of 140 cm. In shallow water, the high density of shorter shoots are supported by an equal amount of belowground mass, whereas, in deeper water, there are fewer but taller and broader shoots, which have a smaller belowground mass. Flowering is restricted to shallow water.

Their optimal performance (in terms of total biomass & shoot densities) under the natural ✶ Lagoon water regime, is compared in Figure 6.15. *Baumea* performs best at elevations about 25 cm higher than *Triglochin* (47.90 v 47.65 AHDm). At elevations ca. 48.20 AHDm, where *Baumea*'s performance is average, the population would be exposed for @ five months of the year, and inundated to no more than @ 60 cm, for the rest of the year. It performs best at 48.0, where it is exposed for @ three months of the year, and performs worst at 47.70 when it is continuously inundated at depths between 20-120 cm. In contrast, *Triglochin* performs worst at the shallow end of the gradient (48.30), where a wet/dry cycle exists. Its performance gets better as elevation decreases, and is best in the deepest parts of the Lagoons (47.65). *Triglochin* survives a wider amplitude of hydrological conditions than *Baumea*.

6.3.3 Mixtures

Replacement Ratios: Final Biomass

In mixture, *Baumea's* total mass was in proportion to the initial planting density, whereas *Triglochin*'s mass was depressed in shallow water and boosted in deep (Figures 6.16a & 6.16b). This asymmetric interaction produced a Relative Yield Total of less than one in shallow water and greater than one in deep water (Table 6.4). The Relative Crowding Coefficient indicated the superior competitor was *Baumea* in shallow water (Table 6.5). Although *Triglochin* dominated in deep water, this was not the result of competition.

The production of *Triglochin* shoot and root mass in shallow water was reduced in the presence of *Baumea* (Figures 6.17a & 6.17b). Rhizomes did not show this pattern (Figures 6.17c). Due to slow rhizome growth in this species, the final amounts are probably more a reflection of inital masses. In deep mixtures, *Baumea* showed no sign of being affected by *Triglochin*, whereas, all *Triglochin* tissue types perfomed better (Figures 6.17d-f). These results extended to the cumulative number of shoots, stems and leaves recruited per initial shoot (Figures 6.18a-d). Recruitment of *Baumea* shoots and stems was unaffected by the presence of *Triglochin* at either depth, whereas the number of shoots and leaves produced by each original *Triglochin* shoot decreased in shallow and increased in deep mixtures.

The increase in *Triglochin*'s yield in deep mixtures, may be due to the release of space, from both the poor growth of *Baumea* and the decrease in its own density. This suggests a belowground interaction, which would explain the results from shallow mixtures. To examine this idea, absolute values of root and rhizome mass were portrayed (Figures 6.19a-d). In shallow water, *Triglochin* and *Baumea* monocultures had similar root masses, but in the 50T:50B treatment, *Baumea* had the greater root mass. In the deep monocultures and mixtures, *Baumea* had very little root compared with *Triglochin*. In terms of rhizome, both species had a similar mass in the deep monocultures, but *Triglochin* had the greater mass in mixture. *Baumea* had the greater amount of rhizome in shallow water. The difference in tuber mass between shallow and deep monocultures was smaller in mixtures, due to disproportionate changes in shallow water (decreases) and deep (increases) (Figure 6.20).

Replacement Ratios: Demography

To trace back when interactions began to take affect, the replacement ratios for the number of leaves and their total height in shallow and deep *Triglochin* populations were calculated. As a proportion of the monoculture, the number of leaves in the shallow 75T:25B mixture fell immediately and continued to decline (Figure 6.21a). However, in the 25T:75B mixture, the proportion did not fall below 0.25 until the final few months. These changes were due to the effect of continuous shoot and leaf recruitment in the monocultures and lack of shoot recruitment in mixtures. In deep water where recruitment was minimal in all treatments, the initial increase in leaf number, in all mixtures, was a response to deep water that was maintained from there on (Figure 6.21b).

The absolute numbers of shoots of both species recruited in each treatment, showed that at the ratio 25B:75T, new *Triglochin* shoots were rare, but still emerging by the end of the study (Figures 6.22a-d). In contrast, at ratios of 50B:50T and 75B:25T, *Triglochin* stopped recruiting new shoots after one year. This shows that *Baumea* does not exert a negative effect on *Triglochin* until it has reached a particular density and this was a density achieved in shallow water after the growth of 4 ramets for 12 months (@ 44 shoots m^{-2}).

In terms of total leaf height, the initial increase in mixed shallow populations in the first six months (Figure 6.23a) resulted from the unexpected flooding. When conditions returned to the constant shallow depth, the heights as proportions steadily fell. This also reflected the low but continuous recruitment in the monocultures, which had the effect of gradually reducing mixture proportions. Only when the water level changed as in the beginning, was the interaction reversed. When submerged in deep water the positive response was immediate and was maintained in the 75T:25B and 50T:50B mixtures (Figure 6.23b). The slower response from the 25T:75B mixture may be due to the higher numbers of *Baumea* neighbours that *Triglochin* was in contact with. This showed as did Figures 6.21a and 6.21b that the longer the experiment runs, the stronger the interaction.

Individual Shoot Data

To compare performance in mixture, rates of leaf recruitment and extension were calculated on a per shoot basis. The mean stem recruitment rates for *Baumea* shoots, in shallow and deep water are shown in Figures 6.24a and 6.24b. Significant differences among mixtures were uncommon and not related to particular times of the year or to particular ratios. This was also the situation for leaf recruitment rates for *Triglochin* shoots at both depths (Figures 6.24c & 6.24d), as well as the extension rates for both species (data not shown). The presence of weak differences may be due to the variation associated with mixtures which had only a few shoots. Overall it was apparent that once shoots were established, the growth of their constituent stems and leaves in mixture was similar to that in monocultures. Also on a per shoot basis, the final number of leaves, stems, biomass, height and mean leaf diameter (Table 6.6) showed significant increases with depth, but no effect of mixture or evidence of interaction.

Flowering

The flowering of *Baumea* shoots was almost completely suppressed in deep water (Table 6.7). Depth had less effect on *Triglochin,* although fewer shoots flowered in shallow water. The proportion of shoots that flowered, increased in shallow *Triglochin* mixtures, but was unaffected in shallow *Baumea* and deep *Triglochin* mixtures.

6.3.4 Nutrient Concentrations

Absolute Values

In the monoculture populations, and in both shallow and deep water, *Triglochin* tissues generally had higher concentrations of N and P (Table 6.8). In the shoots, at both depths, however, there were similar amounts of P, and in the shoots and roots in deep water, there were similar amounts of N (due to increases in *Baumea* values, Appendix 6.2). Na^+ and K^+ values were significantly greater in all *Triglochin* tissues, at both depths (Table 6.8).

For *Triglochin,* the only significant interaction between depth and mixture, was for N levels in the roots (Table 6.9). Depth and mixture, also independently affected P levels in the roots and tubers. The rhizomes experienced a decrease in N and P in mixture, and N in deep water. Aboveground, the only affect of depth and/or mixture, was a small increase in shoot P levels in deep water.

For *Baumea,* the only significant interaction between depth and mixture was for N levels in the shoots (Table 6.9). Mixture had a weak ($P=0.03$) effect on P in the roots, otherwise differences were due to depth. In deep water, there were higher concentrations of N and P in the roots, and P in the shoots.

Na^+ concentrations in *Triglochin* roots and shoots, were unaffected by depth and/or mixture (Table 6.10). K^+ concentrations, however, decreased with depth, and in the roots, decreased in mixture. In contrast, both Na^+ and K^+ levels in *Baumea* shoots resulted from a significant interaction between depth and mixture. There was a weak affect of mixture on K^+ levels in the roots, whereas depth alone, affected both root Na^+ and K^+.

To expand on the result that the majority of responses from *Triglochin* were related to mixture, nutrient concentrations in all treatments for this species were illustrated (Figures 6.25a-c & 6.26a-c). In shallow water, there was a steady increase in the N and decrease in the P levels of *Triglochin* roots (Figures 6.25a & 6.26a) as the proportion of *Baumea* increased. As shown earlier, concentrations in the shoots did not significantly vary with depth or mixture (Figures 6.25b & 6.26b). The increase in rhizome N of deep plants was an artifact of the data, because levels fell in the 25% mixture (Figure 6.25c). The level of P in the rhizomes of shallow plants increased with the proportion of *Baumea* (Figure 6.26c).

Nutrient Allocation v Biomass Allocation

To investigate if the asymmetric interaction identified from biomass data extended to nutrients, the proportional allocation of N, P and biomass was illustrated (Figures 6.27 to 6.30). The distribution of N and biomass in *Baumea*, was similar in shallow and deep monocultures and shallow mixtures (Figures 6.27a & 6.27b), but in deep mixtures, more N and biomass was allocated belowground (Figure 6.27b). In shallow water, more biomass relative to P was allocated to the root, whereas more P relative to biomass was allocated to the rhizome (Figures 6.28a & 6.28b). As with N, more P and biomass were allocated to belowground tissues in deep water (Figure 6.28b).

In contrast to *Baumea*, there were marked differences in both the allocation of biomass and nutrients within monoculture and mixture populations of *Triglochin* (Figures 6.29 & 6.30).

In shallow water monocultures, most N, P and biomass were concentrated in the roots, but in mixture, N and P had been reallocated to rhizomes, and biomass had been reallocated to tubers (Figures 6.29a & 6.30a). In deep water, mixture had no effect on the distribution of N, P or biomass (Figures 6.29b, 6.30b). As in shallow water, there was more biomass relative to N allocated to tubers, a finding also made for P in shallow water, but not deep.

The tissue ratios of N to P in both species (Table 6.11), were slightly lower than those recorded in emergents with similar morphologies (*Scirpus lacustris* 3.0-7.7, *Glyceria maxima* 4.2-10.1, Dykyjova 1978). *Triglochin*'s shallow mixture response was illustrated by a significantly higher N:P ratio in the roots (6.22 v other tissues mean range 1.84-2.63). In *Baumea* the highest and most variable ratios were also found in the roots, but the response was to depth and not mixture, with higher values in shallow water (mean range: 5.07-6.51 v other tissues range: 2.70-2.79). The final total amount of N and P held in *Triglochin* was similar between monoculture plants at both depths and plants from deep mixtures. Plants from shallow mixtures, however, had accumulated far fewer of these nutrients (Table 6.12). In contrast *Baumea* held less P and N in both deep water and mixture. The combination of these factors had the effect of producing low levels of these nutrients in *Baumea*. The effect of depth on the amount of nutrients held in the stand (g m^{-2}), may be a contributing factor to the wide range of values recorded in the literature (e.g. *Scirpus lacustris* 17.6-52.9 N, 3.8-11.1 P, *Glyceria maxima* 6.6-49.1 N, 0.9-8.5 P, Dykyjova 1978).

With the exception of a decrease in the C:P ratio in the roots of shallow *Baumea* populations (Table 6.13), depth did not affect the ratios of C:N or C:P in any other tissue or in either species (Appendix 6.2). In mixture, the C:P ratio in the roots of shallow *Triglochin* populations, increased. Mixture also affected the ratios in *Baumea* rhizomes (C:N increased in shallow water; C:N & C:P decreased in deep water).

6.4 DISCUSSION

6.4.1 Monoculture Data

The monoculture data added to the information base about the effect of water regime on individual performance. At constant, shallow depths, the cumulative rate at which *Baumea* recruited stems and accumulated shoot mass was greater than *Triglochin*, but the reverse was true in deep water. *Baumea*'s total biomass was adversely affected in constant deep water, but *Triglochin*'s did not change significantly. Sexual reproduction was greater in shallow water for *Baumea* and in deep for *Triglochin*. These data reflect three major responses to growth in deep water; a decrease in shoot, stem and leaf recruitment in both species, high mortality of *Baumea* shoots and the ability of *Triglochin* to compensate by allocating tissue from tubers to shoots. These responses identify their different relative positions on a depth gradient, where maximum growth and productivity are achieved.

6.4.2 Competitive Interactions and the Influence of Water Regime

Final Outcome

The final outcome at both depths was an asymmetric interaction, which was competitive in shallow water but not deep. In mixture, *Baumea* was dominant in shallow water and *Triglochin* in deep. These results were due to changes made by *Triglochin*, but not *Baumea*, which at both depths was unaffected by the presence of *Triglochin*. In shallow water, *Triglochin* was adversely affected, with its final total biomass, root, shoot and tuber mass and the recruitment rates of shoots, stems and leaves per intital shoot, all depressed. In deep mixtures, *Triglochin*'s performance was better than in monocultures and the responses were immediate and maintained. Its recruitment, total yield and yield of individual tissues were enhanced, and this was because intraspecific effects had limited monoculture plants. The additional space was not only due to the decrease in *Triglochin*'s initial planting density (4, 3, 2, 1), but to the poor performance from *Baumea* which held most tissue aboveground. This defines *Triglochin* as a plant which requires a large amount of belowground space. The deep water response, pointed to the interaction in shallow water, taking place belowground.

The major difference in biomass allocation was the concentration of *Triglochin* tissue belowground and *Baumea* tissue aboveground. *Triglochin* changed its allocation pattern in shallow mixtures, but *Baumea* did not. The majority of mass in *Triglochin* monocultures was allocated to roots but in mixture, root mass and allocation to roots fell. This identified roots as the tissue that was experiencing competition and because roots are major sites of nutrient uptake, it implies competition for sediment resources. This was not the situation in deep water, because *Triglochin* roots were not influenced by mixture. Conversely, it was *Baumea* which changed its allocation pattern, reallocating mass to shoots in the monocultures and to rhizomes in mixture. This suggested compensation for a limiting resource; however, because yield was in proportion to initial densities, this response had redressed the imbalance, and overall the plant was not adversely affected.

Reallocations of N and P supported biomass data. Because *Triglochin*'s shoot N, P, Na^+ and K^+ did not change with depth or mixture, this tissue is not directly involved in any interaction. In shallow monocultures, *Triglochin* allocated most N, P and biomass to the roots, but in mixture, N and P had been reallocated to rhizomes and biomass to tubers. The decline in root mass and root P levels in mixture, implied it could not overcome P limitation. K^+ levels in roots also fell in mixture. The increase in rhizome P, with increasing *Baumea* may reflect a strategy to conserve P by moving it to an organ which does not experience the same competitive effects as roots. Graneli and Solander (1988) suggested that when P was limiting, its uptake and storage was part of the competitive interaction. In deep water, there was virtually no effect of mixture on N, P or biomass distribution. For all treatments, more biomass relative to N and P (except P in deep plants) was allocated to tubers, identifying their primary role as a carbohydrate store, rather than a nutrient store.

Unlike *Triglochin, Baumea* responded more to depth than mixture, increasing root N, P, Na^+ and K^+, and shoot N, changes that can be interpreted as accumulations in smaller amounts of tissue. Both depth and mixture influenced shoot Na^+ and K^+ and also N, concentrations of which increased with depth, but decreased in mixture. The allocation of nutrients and biomass in monocultures was unaffected by depth or mixture in shallow water, but in deep mixtures, more nutrients and biomass were reallocated belowground, but again, because mixture yields were in proportion to planting densities, these changes had overcome any limitation. Because Na^+ and K^+ are less labile than N and P, the fact that they too respond to growth in mixture suggests interaction is being experienced at other physiological levels within both species.

Recruitment and Reproduction

The effect of depth and mixture on the recruitment of *Triglochin* shoots did not extend to the growth of a shoot's constituent leaves. Mixture had no effect at either depth on leaf recruitment rate, leaf extension rate, the number of leaves, biomass or height per shoot. However, in shallow water there was some evidence that proportionally more *Triglochin* flowered in mixtures, suggesting that it may compensate for the loss of vegetative growth by redirecting resources into seed production. This requires verification, as if *Triglochin* is prompted into extra sexual production under those conditions, this may be a further mechanism that is facilitating its spread.

The vegetative shoots which did emerge in shallow monocultures were of two types, small or robust. Most were the small type, which had narrow thin leaves, emerged throughout the year and had variable survivorship. This contrasted with the robust shoots in natural stands (Figure 5.4), which emerged only during autumn and had 100% survivorship. The small shoots were similar to the lateral shoots photographed from potted ramets (Figure 4.8). Autumn recruitment may be restricted to buds that terminate rhizomes, and which produce the long-lived shoots with leathery terete leaves, that were followed in the demographic study. The lateral buds, which produce smaller shoots, may, given the appropriate stimulus (eg. transplanting/cutting), emerge at any time.

Growth Rates

The major difference in species growth was that under constant depths, *Baumea* had a much more distinct seasonal response than *Triglochin*, which responded to water levels as they changed. For example, at the start of the study, the rapid increase in *Triglochin*'s leaf extension rate and rate of biomass accumulation gave it a temporal height advantage over *Baumea*, which did not have this reaction. Several studies have shown that the species which gains a height advantage early in the growing season is the stronger competitor (*Glyceria maxima* v *Phragmites communis* Buttery *et al*, 1965, *Typha latifolia* v *T. angustifolia* Grace and Wetzel 1981a, *Zizania latifolia* v *Miscanthus sacchariflorus* and *Phragmites australis* Yamasaki and Tange 1981, *Miscanthus sacchariflorus* v *Phragmites australis* Yamasaki 1990). However, shading or light limitation is unlikely to be important in *Triglochin*'s replacement of *Baumea*, because when water levels fall, *Triglochin* loses any gain it had made (although it presumably keeps the additional resources by translocation). In contrast, *Baumea* grew gradually into populations with densities similar to those in the field. Once resources and space were captured, they were secured within the stand, the biomass of which was maintained irrespective of depth. In summary, *Triglochin* preceeded and exceeded the growth rates of *Baumea* in the first year when water levels fluctuated but in the second year when depth was constant *Baumea* had the temporal edge in growth and higher rates.

Triglochin shoots at both depths exhibited the same growth cycle and similar rates. The influence of depth on the timing of growth in *Baumea* did not appear to affect *Triglochin*. Rates reached maximum values in spring, in shallow water, and in winter/spring, in deep water. Over the course of the experiment, *Baumea* shoots in deep water grew at steadily faster rates, suggesting that given time and space, they were able to slowly adapt to those conditions. Such adaptation, may over time, alter the competitive outcome.

Nutrient Allocation

Triglochin had higher concentrations of N, P, Na^+ and K^+ than *Baumea*, which, given the positive correlation between leaf N and photosynthetic capacity (Field and Mooney 1986, Tilman 1986b, Sage and Pearcy 1987), suggests *Triglochin* has a higher maximum growth rate. The negative correlation found between leaf longevity and soil fertility (Jonasson 1989) further identifies *Triglochin* as a species adapted to higher nutrient levels than *Baumea*. There was, nevertheless, no evidence of this in terms of absolute growth rate of shoot tissue (cm d^{-1}, g d^{-1}) nor in total production per unit area, which was more a function of water

★ The inference of nutrient limitation from tissue concentrations and ratios was not intended to suggest that P levels were below the level where growth rate decreases (the critical concentration). *Triglochin*'s reduced capacity to accumulate P in shallow mixtures (in the whole plant but particularly in the roots) meant there was insufficient P to match and make use of its N reserves. Plants adjust their growth and allocation so as to be equally limited by all essential resources (Tilman 1982). In this case, *Triglochin* did not do this and was thus 'limited' by P.

depth.

✶ The low range of whole plant N:P ratios (*Triglochin*: 1.88-2.43, *Baumea*: 2.04-2.49) indicated N was more likely to limit growth than P. Crate populations contrasted with natural populations (Rea 1985), where P was more likely to limit growth. Although lagoon sediment was used in the experiment, the plants had reached the carrying capacity of the crates, and had N requirements beyond that which was available. Other authors have proposed that N is the nutrient most likely to limit the growth of emergent macrophytes because of the large requirement for structural tissue (Barko and Smart 1979, Graneli and Solander 1988). Nevertheless, in shallow *Triglochin* plants, it was P that was clearly the limiting nutrient. The only evidence for N limitation, (*Baumea* rhizomes in shallow water) was not supported by changes in overall biomass. The similarity in N:P ratios, despite depth and mixture effects and interactions, shows how compensations have redressed imbalances.

6.4.3 Below v Aboveground Competition

Aboveground

Although plant architecture was not examined quantitatively, the possibility of plant to plant contact was considered high, given the rosette habit of *Triglochin* and the tall attenuate habit of *Baumea*. Plants with contrasting morphologies can either coexist through resource differentiation (Watson and Cook 1982, Dickerman and Wetzel 1985, Yen and Myerscough 1989) or be segregated by competitive displacement (Clatworthy and Harper 1962, Grace and Wetzel 1981a). Their lack of natural coexistence suggests the latter occurs. The spread of *Triglochin* parallels that described for teasel, a biennial with a broad-leaved rosette (Werner 1977) which causes openings in the vegetation of old-field pastures when it invades. This enables its seedlings to establish and the plant to fully colonize, and implies indirect competition or physical interference, a scenario that may be happening in the Lagoons.

In shallow water, the relatively uniform structure of *Baumea* stands and their high densities meant greater neighbour contact. As *Triglochin* leaves were recruited continuously, they would always have to contend with a dense stand of *Baumea* stems which occupy all strata. Light limitation might be expected to inhibit the growth of newly emerged shoots. However, due to parental support, new shoots may not photosynthesize for some weeks after emerging (*Phragmites*, Graneli and Solander 1988) and thus low light levels at this time are immaterial. Also as new shoots were not even emerging this suggests the inhibition must have occurred belowground. This inhibition may partly depend on the relative timing of shoot emergence. The demographic study identified autumn as the major recruitment period for both species. In the monocultures, it began slightly earlier for *Baumea*, and this may explain the lack of new *Triglochin* shoots in mixture. In contrast, *Baumea*'s variable structure in deep stands reflected high mortality rates, the continuous attempt to replace dead shoots and the need for all stems to reach a minimum emergent height. Only some size classes were represented; short stems attempting to grow tall and tall stems that had attained the necessary height. The spatial placement of aboveground *Baumea* was therefore patchy and offered little opposition to *Triglochin*.

The requirement for plants to maintain gaseous C supply is clearly affected by water depth, and the consequences are altered patterns of biomass allocation and architecture, traits which Goldberg (1987) considered were more important than physiology in determining the effect which plants have on resources. In shallow water where C supply is unrestricted, *Baumea*'s allocation patterns are such that they adversely affect resource supply to *Triglochin*, but in deep water the reallocations made to overcome the C deficit do not have this effect. In deep water, the smaller C:P ratio in *Baumea* roots, indicates it is C or photosynthesis limited. Other indications that C limitation is more important for *Baumea* than *Triglochin*, comes from the life-span of their photosynthetic organs, which reflects an adaptation to minimize C loss. Unlike long life-spans (*Baumea* stems), short life-spans (*Triglochin* leaves) mean the species is less likely to be limited by C. This was also borne out by constant C:N and C:P ratios. Low loss rates are also a mechanism for nutrient conservation in infertile habitats (Berendse *et al.* 1987) and are correlated to low maximum growth rates (Grime 1977, Bazzaz 1979, Chapin 1980, Chapin *et al.* 1986 and 1987, Shipley and Keddy 1988), although this was not the case for *Baumea*.

Belowground

The finding that belowgound competition was operating in shallow water (affecting *Triglochin*), and perhaps in deep water (affecting *Baumea*), is supported by much of the literature. Fitter & Setters (1988) found competition for belowground resources was more important than competition for light. Wilson (1988) concluded that it was root not shoot competition which determined competitive intensity and resource use. Williams (1987) found the successional replacement of one seagrass by another was a function of belowground competition for nutrients rather than competition for light. Competition for sediment nutrients and competition for belowground space are not unrelated, because an increase in space should theoretically provide greater access to nutrients. Their effects were not distinguished, though, in two studies comparing the removal of belowground and aboveground biomass. Removing belowground biomass had a significantly greater effect, increasing total biomass, growth rate and fecundity (Snaydon and Howe 1986) and altering allocation to asexual and sexual reproduction and the timing of flowering (McConnaughay and Bazzaz 1991). Different rooting depths were also found to be a major type of niche differentiation (Berendse 1982) and Wilson (1988) stressed the need for experimental studies to provide large belowground space so as natural rooting profiles could develop. When the plants were harvested, it was noticed that the roots of both species in shallow populations (but not deep), were entwined, which supports the finding that this tissue is the site of competition.

6.4.4 Conclusion

The results of the RSS experiment and the literature, together point to the asymmetric interaction between *Triglochin* and *Baumea* in shallow water, resulting from indirect competition for space and/or sediment nutrients rather than indirect aboveground competition for light. The unrestricted supply of photosynthetic and respiratory gases in shallow water allows *Baumea* to produce a large biomass, much of which is belowground, exploiting resources at the expense of *Triglochin*. Such preemption of above and belowground space is believed to lead to dominance (Grime 1979). This had the effect of not only reducing *Triglochin*'s root yield, but root concentrations of major nutrients and the recruitment of new shoots. This scenario supports the theory that when abundant soil resources leads to a dense sward of vegetation, the resulting competitive outcome is not due to competition for light (Tilman 1988), but to competition for soil nutrients produced by many overlapping resource depletion zones (Campbell and Grime 1992). Grimes CSR model is also supported by the finding that *Baumea* was most competitive where it was most productive and least competitive where the stress of deep water had reduced its biomass.

In conclusion, the relative allocation to belowground (sediment resource acquisition) and aboveground (C acquisition) parts under different water regimes, led to the outcome being a combination of both biotic and abiotic effects. At high elevations, where shallow depths and a pronounced wet/dry cycle prevail, competition between *Triglochin* and *Baumea* occurs, and *Baumea* is the superior competitor. At low elevations, where deep depths and permanent inundation prevail, biotic interactions are minimized and it is under these conditions, where *Triglochin* performs best and *Baumea* rather poorly, that a change in species composition would occur. This change, would be the result of *Baumea* passively retreating and *Triglochin* passively taking it's place.

This scenario is illustrated in Figure 6.31. The potential niche of these species, is based on a performance axis, gaged from population growth and reproduction (above and belowground biomass & shoot density m^{-2}), and a water regime axis, which represents exponentially increasing depth and duration of inundation and decreasing frequency of drawdown. The effects of interspecific interactions will depend on the water regime. At one extreme of the range of hydrological conditions in the 1980's, *Baumea* can maintain its position by outcompeting *Triglochin*. Today, this compares with a narrow zone around the Lagoon shoreline, but historically, these conditions once existed throughout the main body of the basins. At the other extreme of the 1980's water regime, *Triglochin*'s performance is enhanced at a time when *Baumea*'s is severely limited. Consequently, *Triglochin* can expand its distribution into a habitat it thrives in and without having to contend with competitive affects. Extrapolation of these responses, illustrates how *Baumea* tolerates a relatively narrow range of water regimes, whereas *Triglochin* has a much wider amplitude.

Predictions about how changes in the water regime will influence distribution patterns can be made from this model. Any further increases in depth, will hasten the rate at which *Baumea* is lost. Although the changes have occurred due to a mean depth increase of 46-57 cm (Table 2.1), *Baumea* populations cannot simply be restored by reversing this increase alone. The ponding of water in spring and summer, which prolongs inundation at deeper depths, and reduces the frequency and duration of drawdown, must also be changed. The original range of maximum depths in Hacks Lagoon (0-110 cm), where both species once occurred, together with results from experiment 1 Chapter 4, show that *Baumea* can tolerate deep water, but for short durations only (4 weeks). The present range of maximum depths in Hacks Lagoon (76-142 cm) and in the Western basins (61-127 cm), excludes the possibility of drawdown. For present *Baumea* stands to be maintained, this event would need to occur more frequently and for longer intervals.

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CHAPTER TWO: THE HYDROLOGICAL ENVIRONMENT AND VEGETATION OF THE STUDY SITE AND REGION

Figures 2.1 - 2.11

Tables 2.1 - 2.3

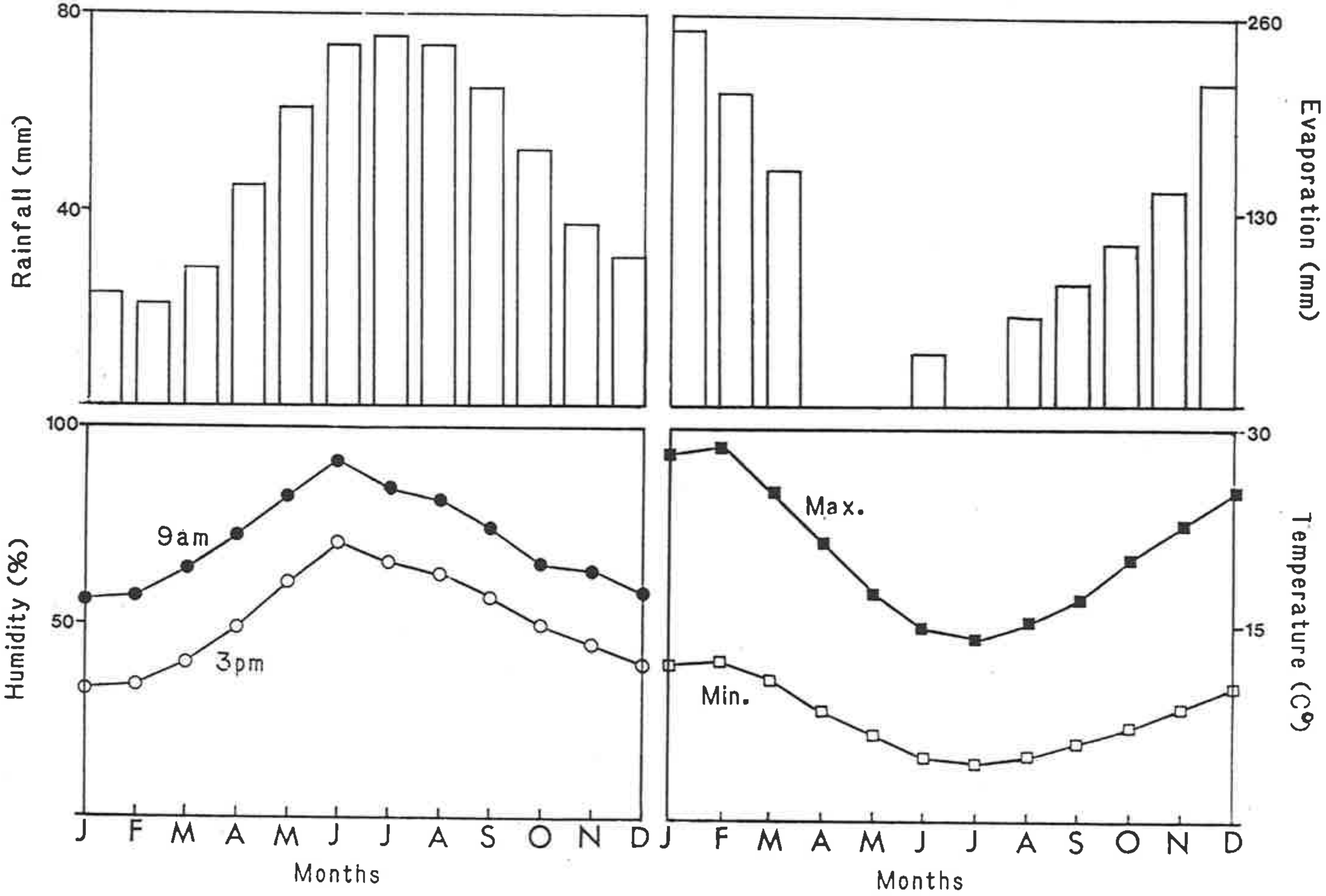


Figure 2.1
The mean monthly rainfall, evaporation, humidity and temperature of the Bool Lagoon Region. Data taken at Struan, 8 kilometres away, by the Bureau of Meteorology.

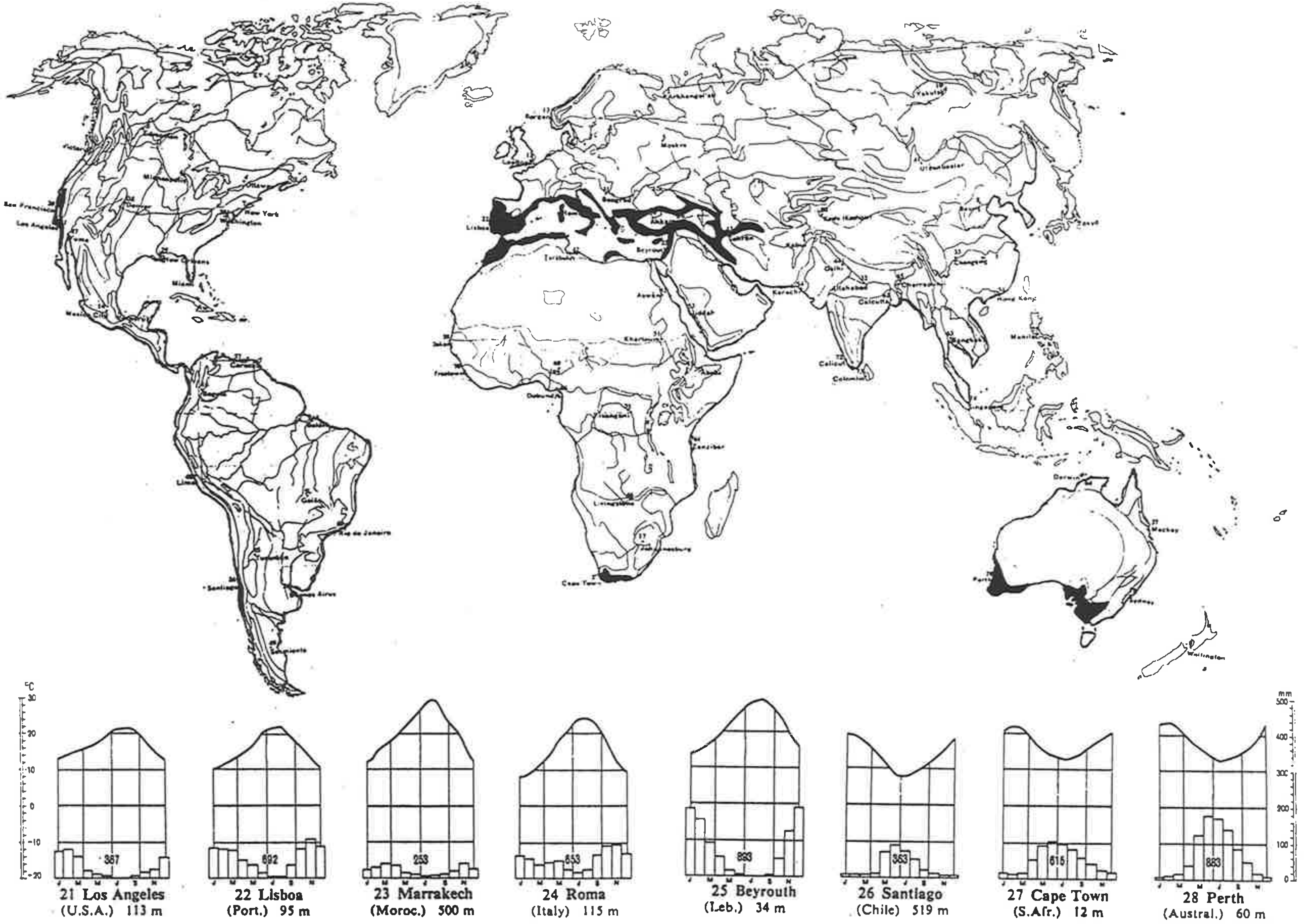


Figure 2.2

Regions of the world that share the Mediterranean climate (warm to hot dry summers and cool to cold wet winter) of the South-east of South Australia.

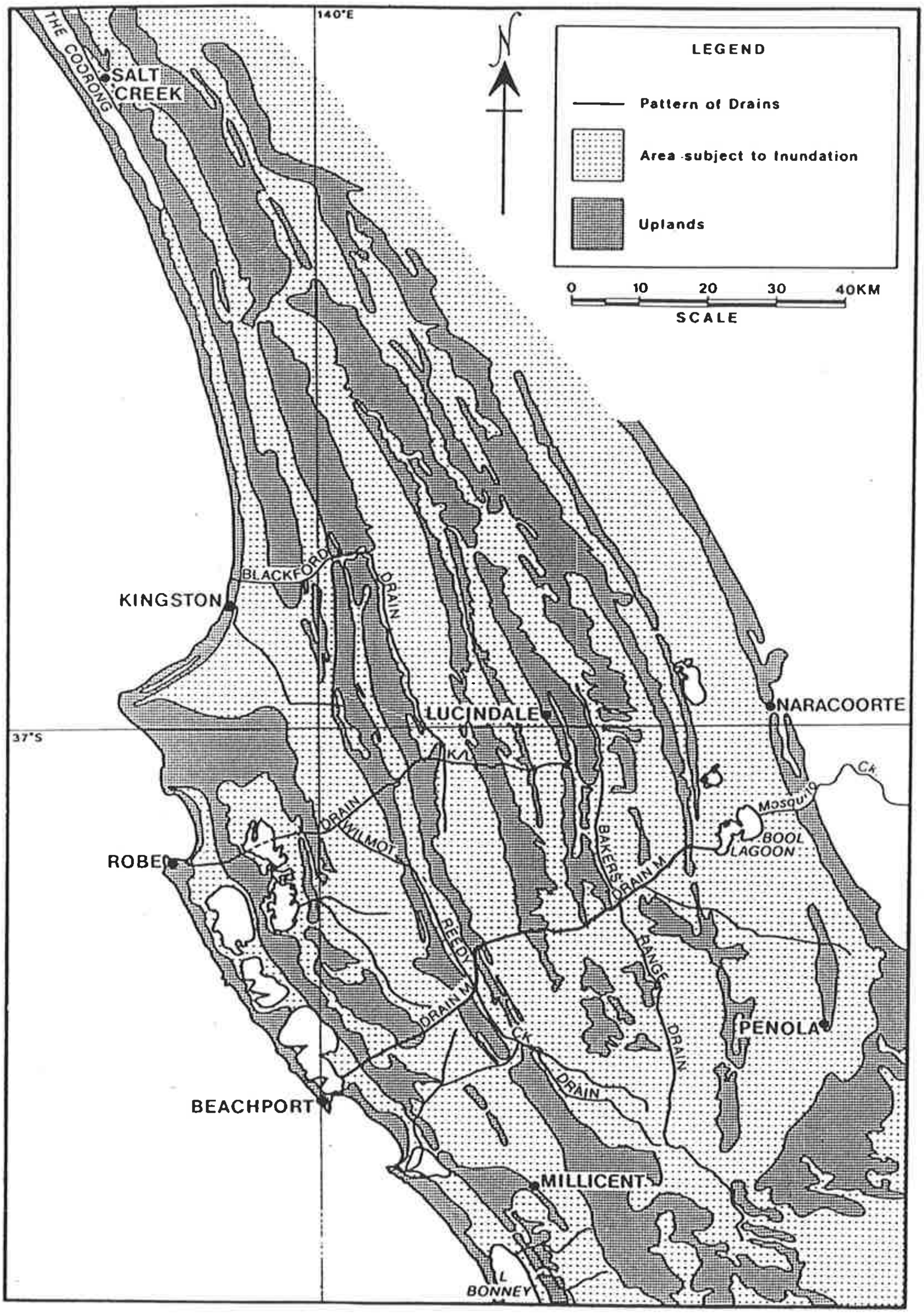


Figure 2.3
A map of the South-east of South Australia, showing the dune ranges and the area subject to inundation. Bool Lagoon is situated in the east of the region. The major drains of the extensive drainage network are shown.

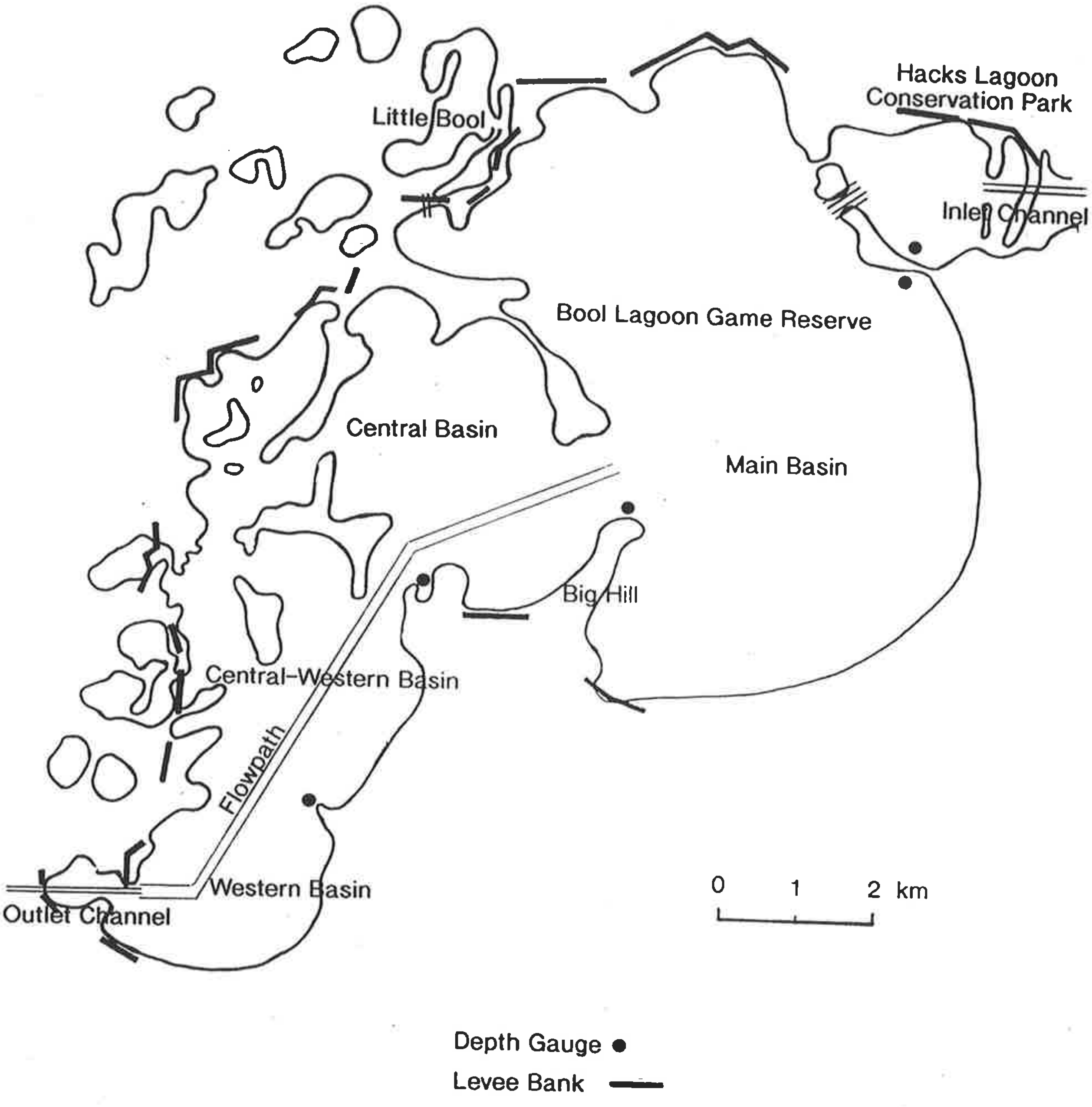


Figure 2.4
A map of Hacks Lagoon Conservation Park and Bool Lagoon Game Reserve. The location of the inlet and outlet channels, depth gauges, levee banks and the flowpath are shown.

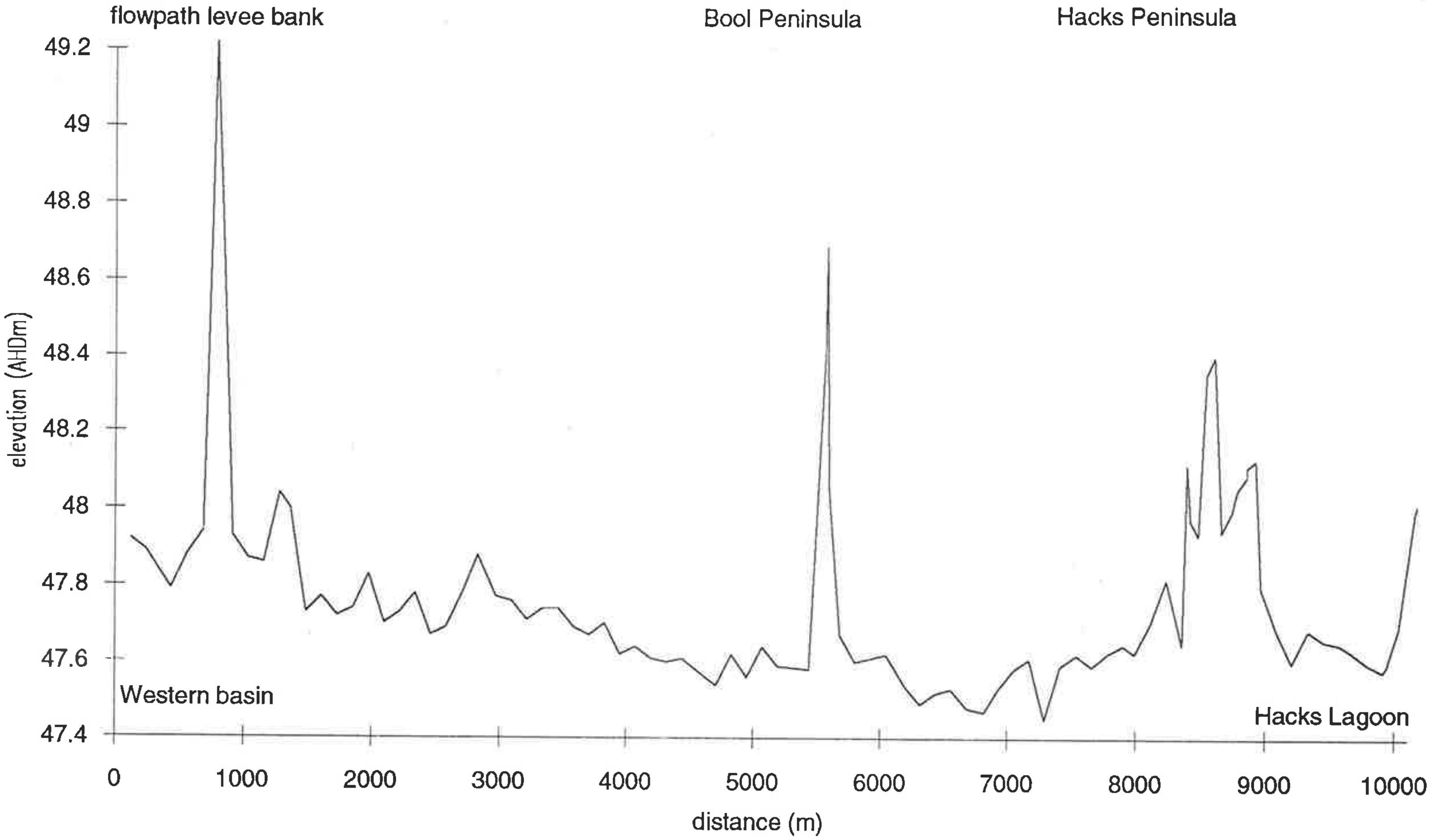


Figure 2.5
The elevation of the Lagoon floor along a 10 km transect from the West basin to Hacks Lagoon. The transect was surveyed in 1960 and traversed three raised areas (see Figure 2.8 for their location).

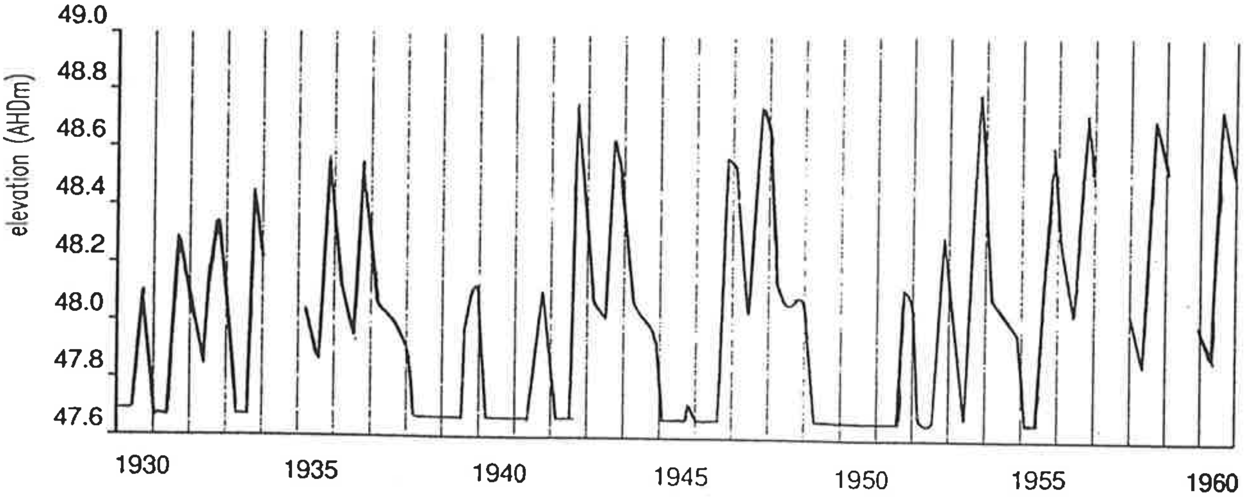


Figure 2.6
Simulated water levels in Hacks and Bool Lagoon between 1930 and 1960 (Department of Environment and Planning unpublished). Data came from monthly flow records in Mosquito Creek at Struan, 8 km's upstream of the Lagoons.

o/

decade	1930-39	1940-49	1950-59	1980-89	Results of 1-way AOV F	Results of 1-way AOV P
mean maximum water level (AHDm)						
x	48.28	48.22	48.17	48.74	3.41	0.029
sd	0.30	0.42	0.58	0.33		
mean maximum depth in Hacks Lagoon (m)						
x	0.63	0.57	0.52	1.09		
sd	0.30	0.42	0.58	0.33		
mean maximum depth in the Western Basins (m)						
x	0.48	0.42	0.37	0.94		
sd	0.30	0.42	0.58	0.33		
no. winters lagoon was dry in each decade						
total	5	6	4	2		

Table 2.1 were

These

This data was calculated from Figure 2.6. The mean maximum water level in the decade s of the 1930's, 40's, 50's and 80's are shown and compared by 1-way AOV. The mean maximum depths were calculated on the basis that the mean floor level of Hacks Lagoon and the Western basin system, were 47.65 and 47.80 AHDm,respectively.

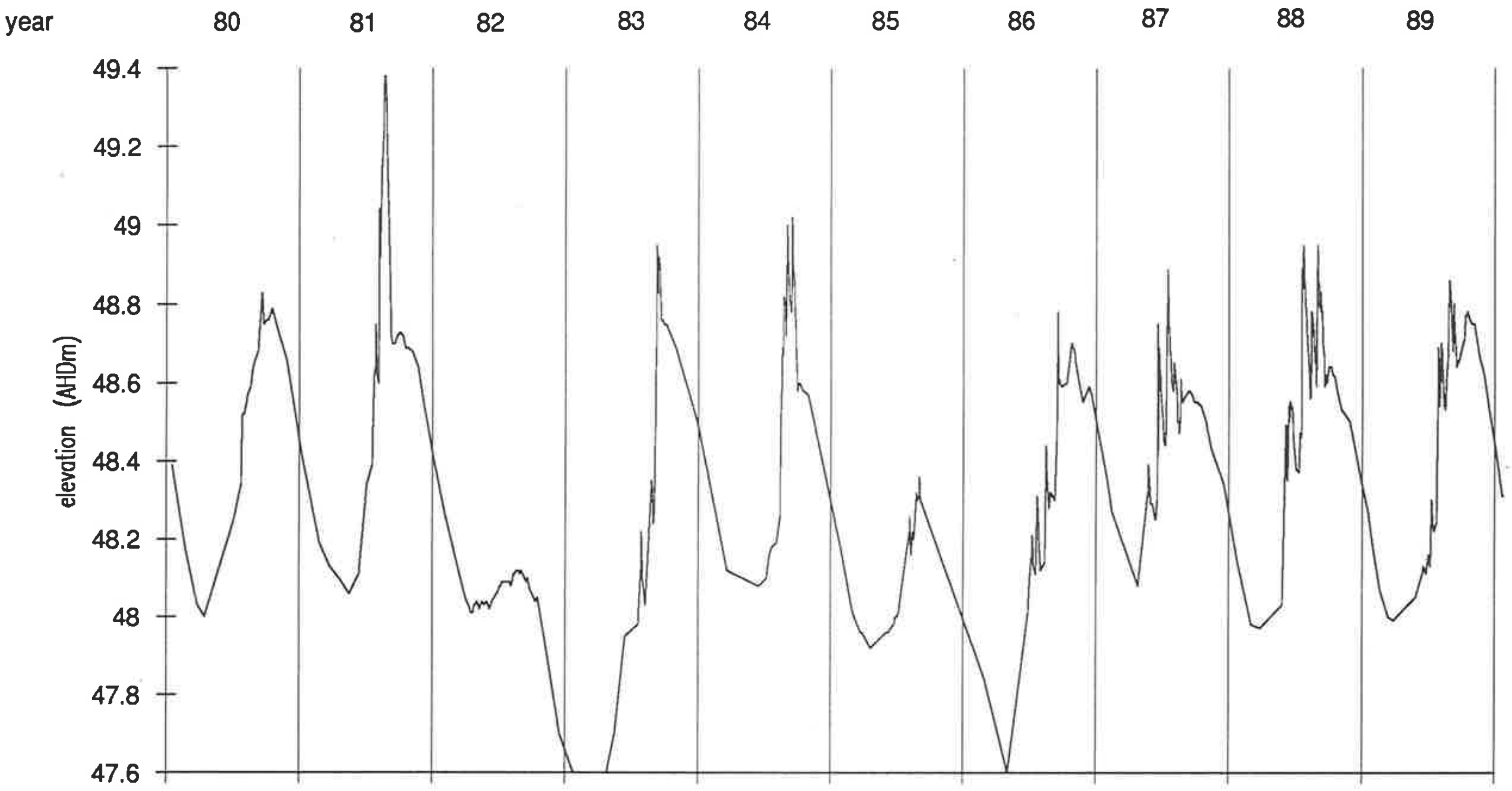


Figure 2.7
Water level in Hacks Lagoon from 1980 to 1989.

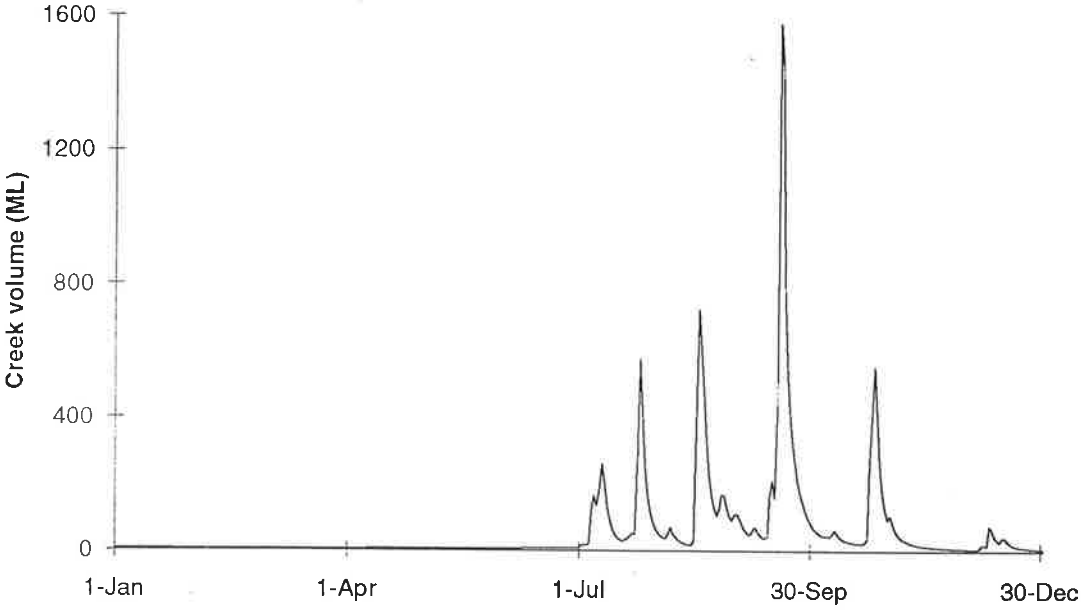


Figure 2.8
Daily volume of Mosquito Creek in 1986 at Struan (8 km's upstream from the lagoons).

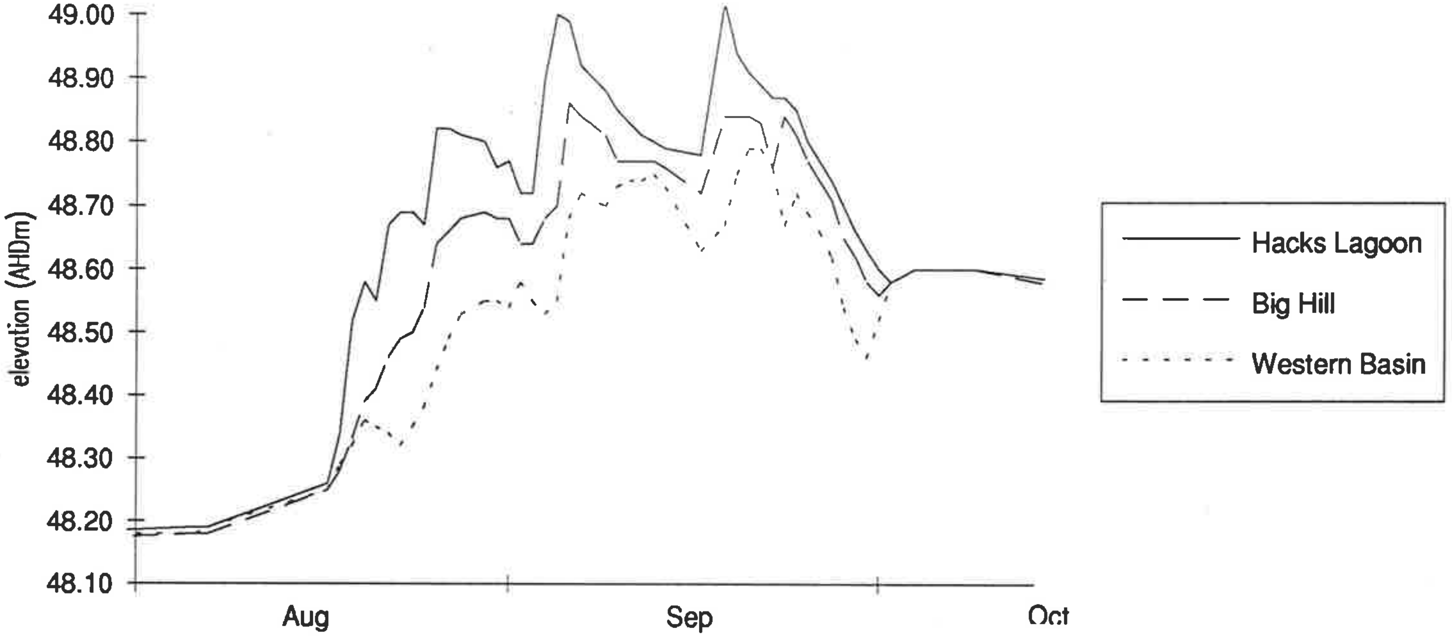
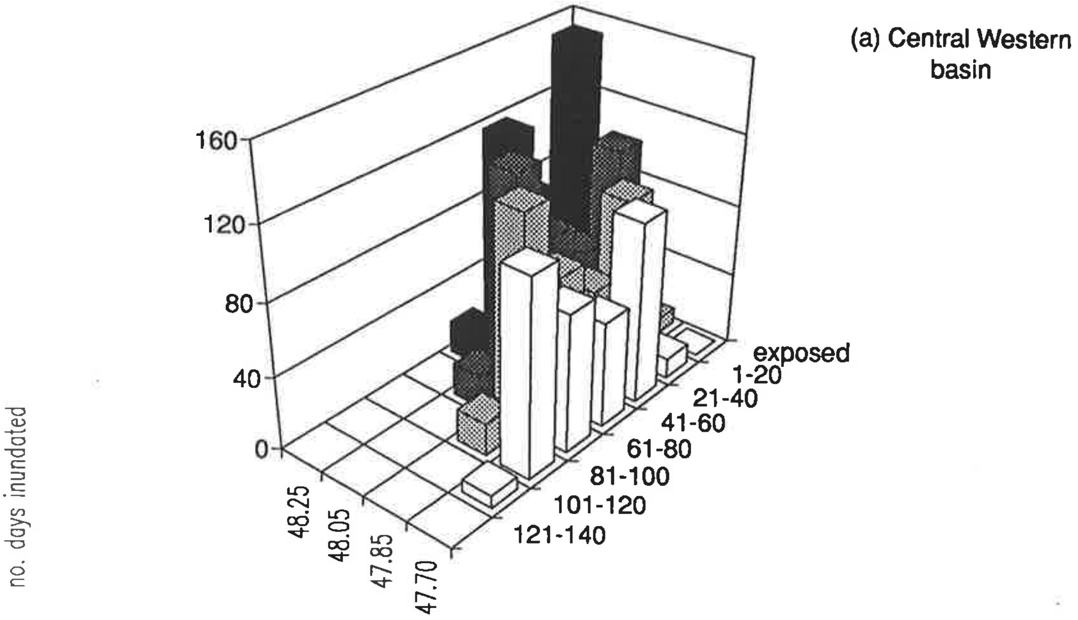


Figure 2.9
An example of the water levels in Hacks Lagoon (near inlet), at Big Hill and in the Western Basin (near outlet), before, during and after flooding. (Aug-winter, Sep/Oct-spring).


(a) Central Western basin

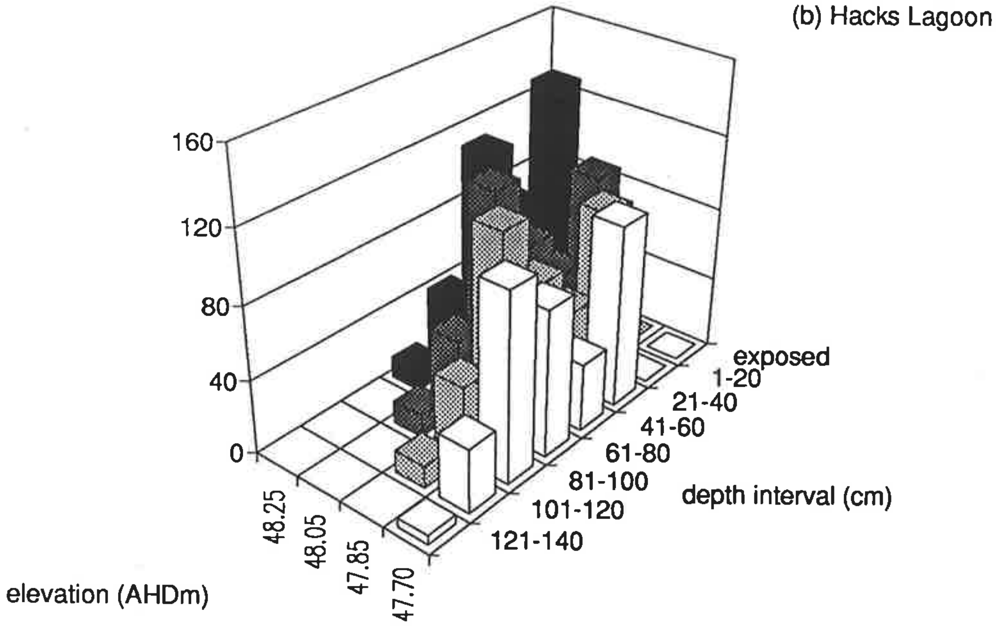

(b) Hacks Lagoon

Figure 2.10
Comparison of the water regime (Apr-88-Apr-89) at 4 elevations in the Central Western basin and Hacks Lagoon.

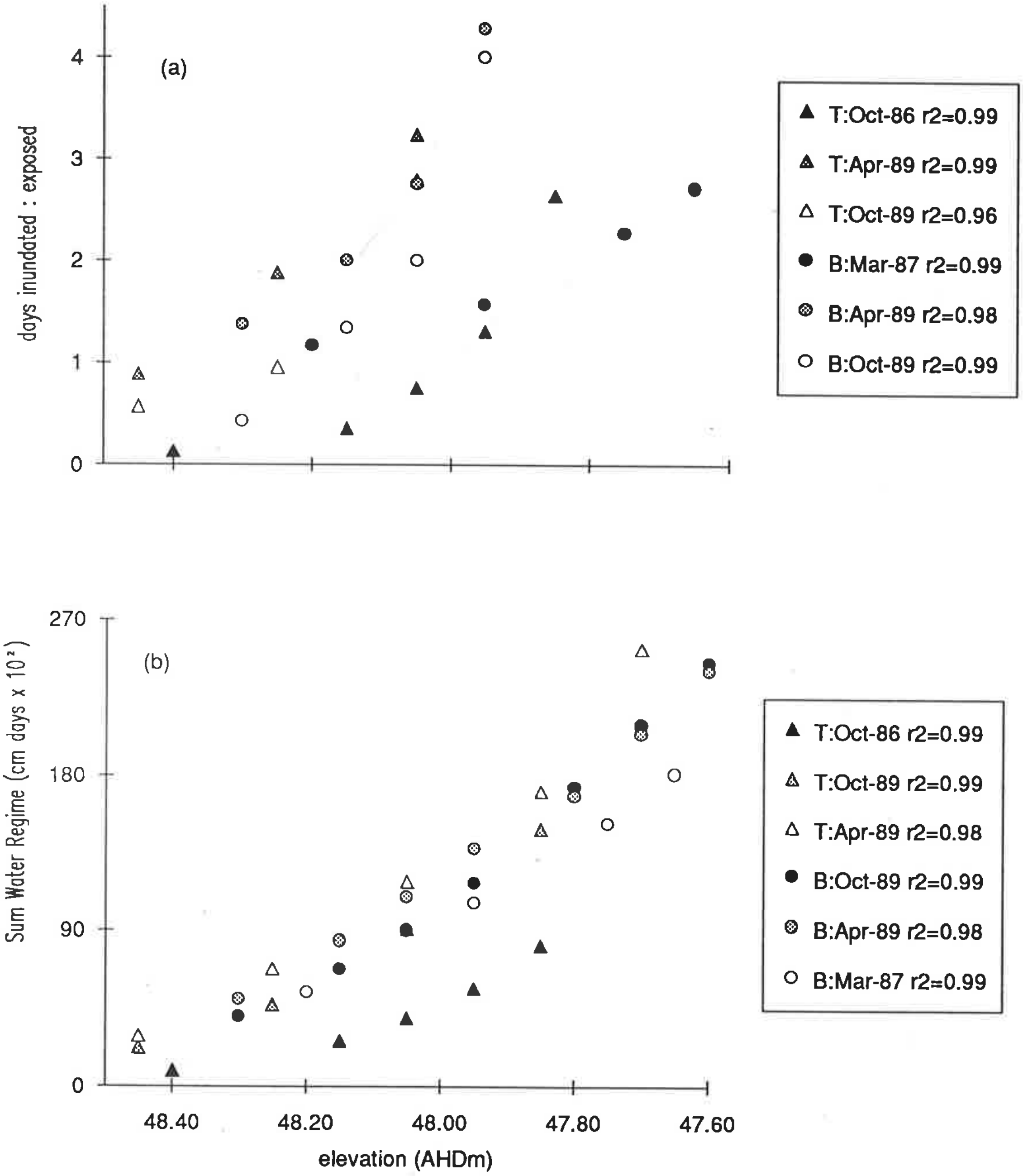


Figure 2.11
The relationship between elevation and indices of the lagoons' water regime, calculated for each harvest site: (a) the ratio of days inundated to exposed and (b) the sum depth and duration of inundation over the 360 days prior to harvests. *Baumea* (B) and *Triglochin* (T) harvests came from the Central Basin and Hacks Lagoon, respectively. The r^2 values from exponential equations fitted to each data set are shown.

	1960	1989	
	mean ± sd	range	flowpath
West basin	47.88 ± 0.06	47.89-48.03	
		47.80-47.88	47.65
Central-west basin	47.80 ± 0.11	47.71-47.92	47.60
Central basin	47.64 ± 0.07		
Main basin	47.57 ± 0.06	47.66-47.70	
Hacks Lagoon	47.62 ± 0.04	47.65-47.68	

Table 2.2
The elevation of the floor of each basin in 1960 (mean ± sd) and 1989 (range). The flowpath did not exist in 1960.

month	upstream	downstream
J	0.23	0.02
F	0.07	0.00
M	0.05	0.00
A	0.05	0.00
M	7.00	0.00
J	25.4	4.14
J	31.0	6.80
A	7.92	4.64
S	0.92	0.03
O	0.24	0.03
N	0.09	0.01
D	0.14	0.01

Table 2.3
The instantaneous maximum monthly flow rate (cumecs) in 1987, upstream (Mosquito Creek at Struan) and downstream (Bool Lagoon outlet channel), of Hacks and Bool Lagoon.

CHAPTER THREE: INDIVIDUAL RESPONSES TO DEPTH AND WATER REGIME

Figures 3.1 - 3.7

Tables 3.1 - 3.8

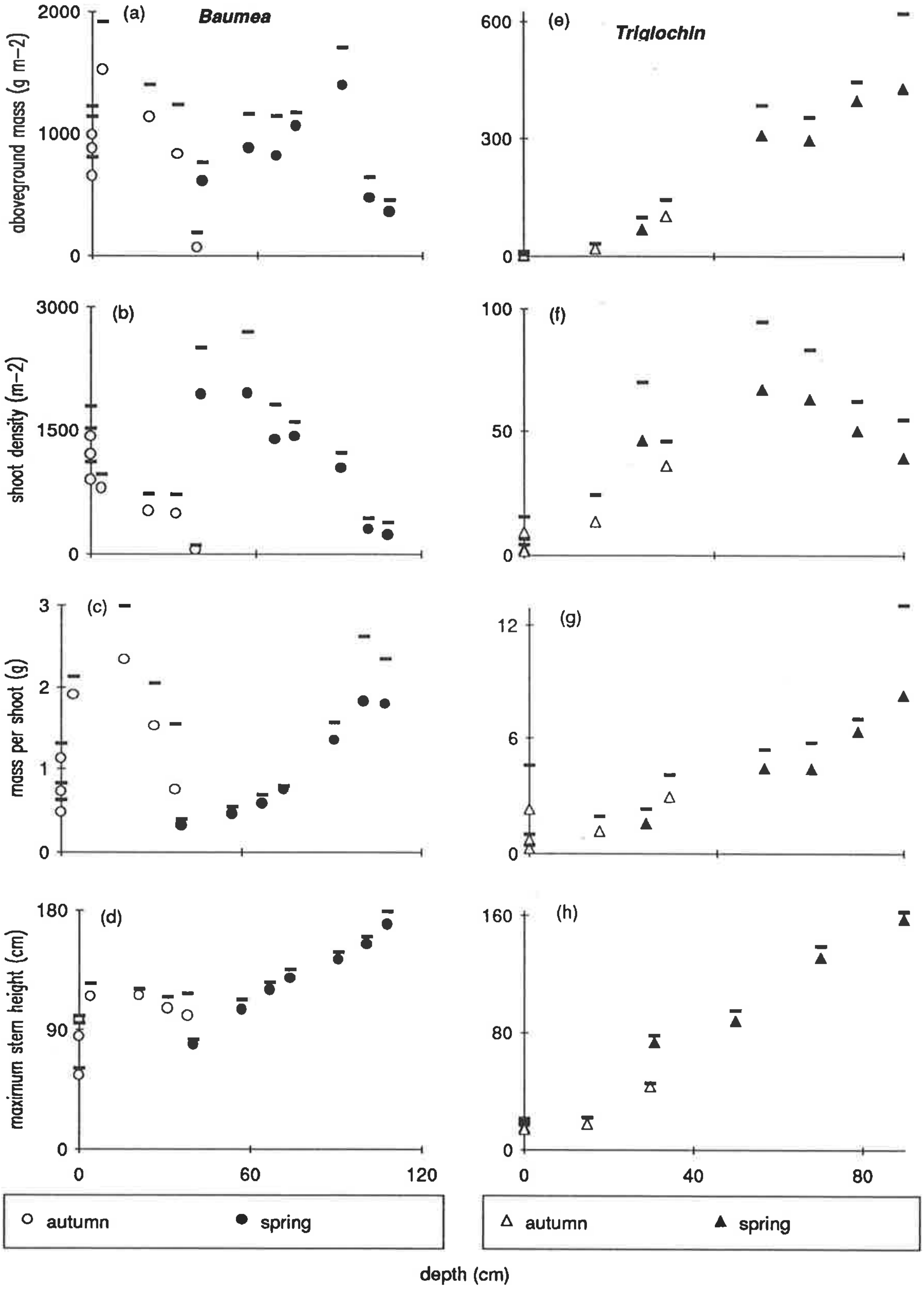


Figure 3.1
The relationship between depth and aboveground characteristics of *Baumea* (a-d) and *Triglochin* (e-h). The r^2 values of significant linear correlations for seasonal data are shown in Table 3.1.

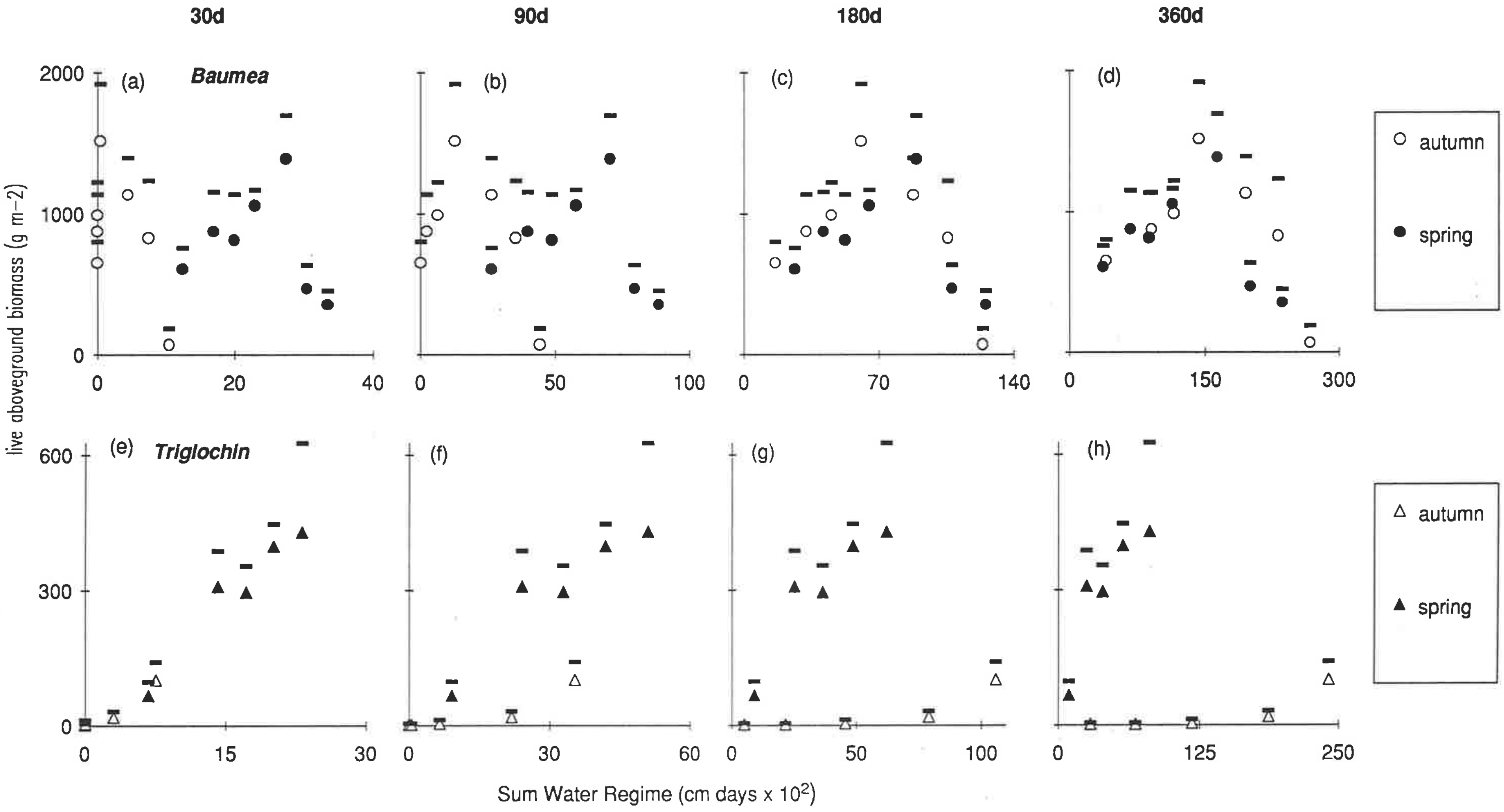


Figure 3.2
The relationship between live aboveground biomass (g m-2; mean +sd; *Baumea*, a-d; *Triglochin*, e-h) and the Sum Water Regime, for the 30, 90, 180 and 360 days prior to spring and autumn harvests. See text for explanation of this index and Table 3.1 for associated regression statistics.

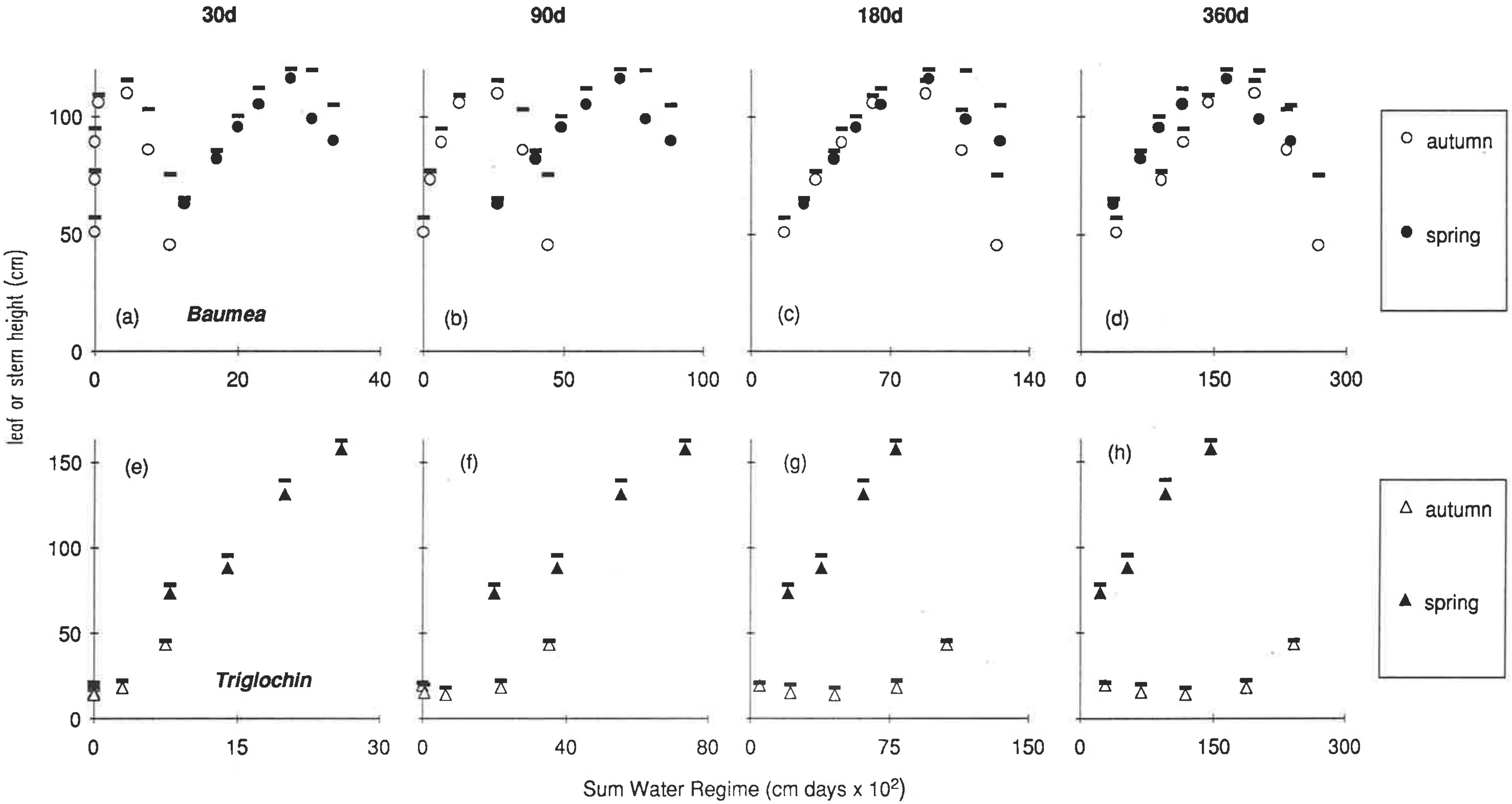


Figure 3.3
The relationship between the mean height of *Baumea* stems (a-d) and maximum height of *Triglochin* leaves (e-h), and the Sum Water Regime, for the 30, 90, 180 and 360 days prior to spring and autumn harvests. See text for explanation of Sum Water Regime and Table 3.1 for associated regression statistics.

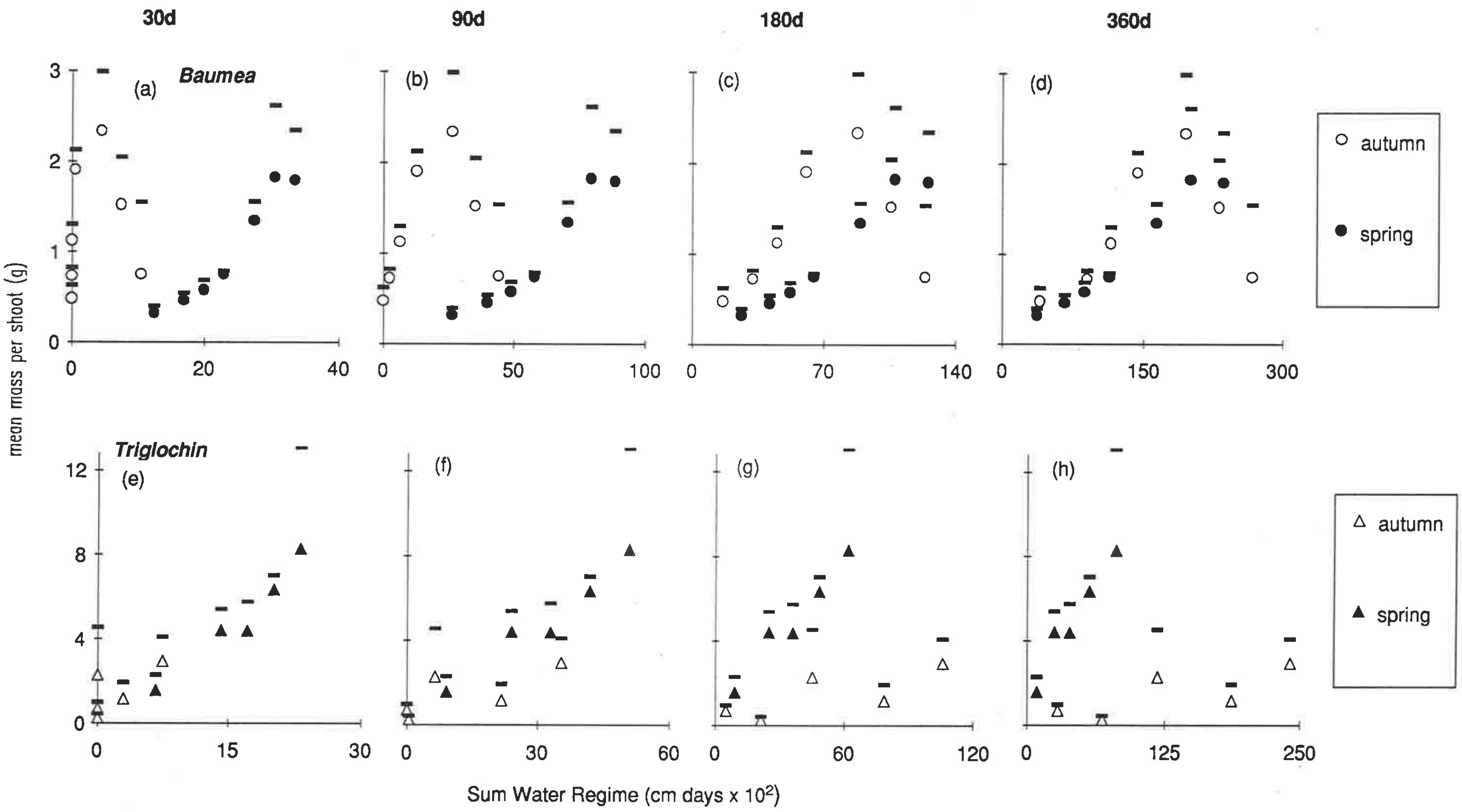


Figure 3.4
The relationship between the mean mass per shoot (g, mean +sd; *Baumea*, a-d, *Triglochin* e-h) and the Sum Water Regime, for the 30, 90, 180, and 360 days prior to spring and autumn harvests. See text for explanation of Sum Water Regime and Table 3.1 for associated regression statistics.

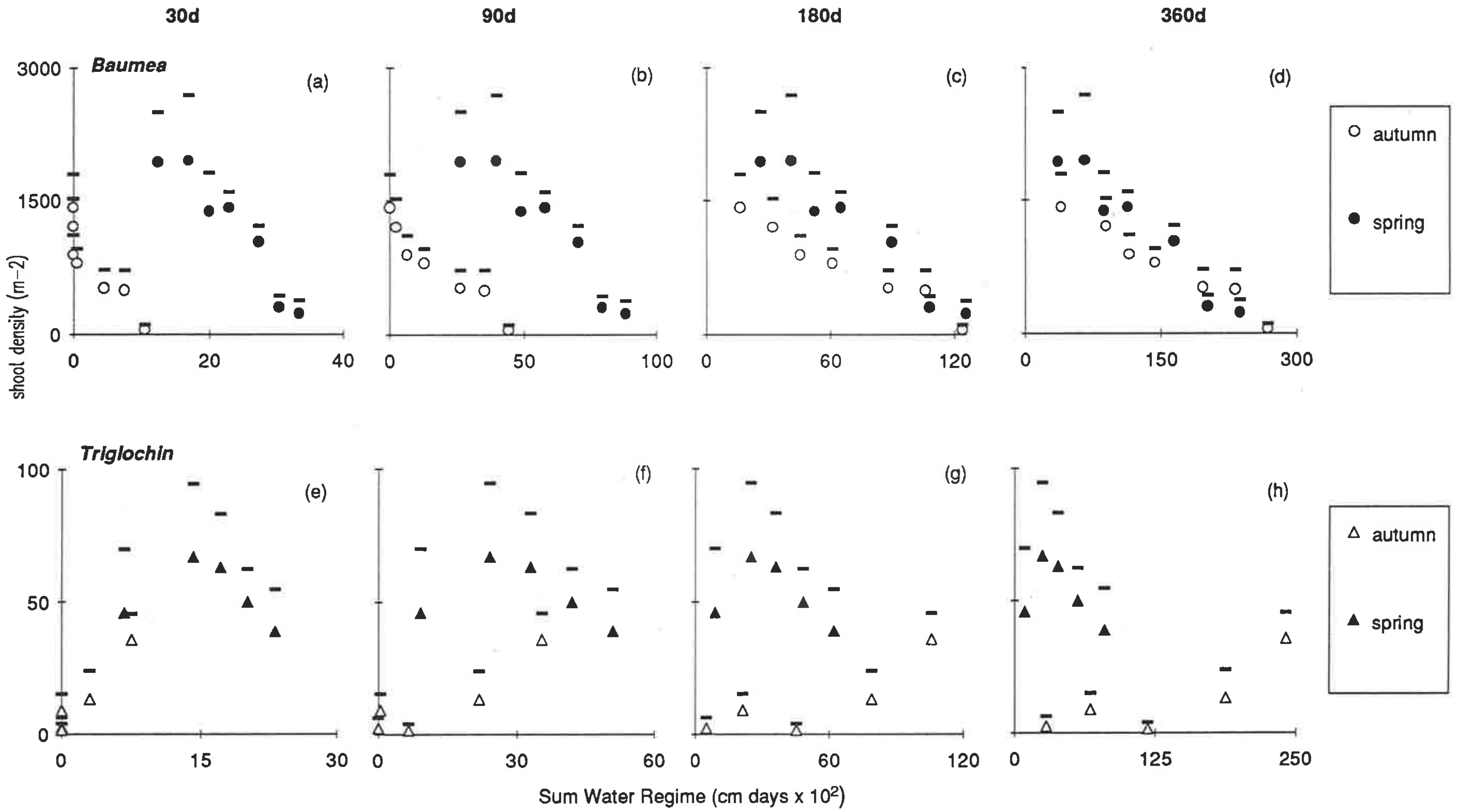


Figure 3.5
The relationship between shoot densities (mean +sd; *Baumea* a-d, *Triglochin* e-h) and the Sum Water Regime, for the 30, 90, 180 and 360 days prior to spring and autumn harvests. See text for explanation of Sum Water Regime and Table 3.1 for associated regression statistics.

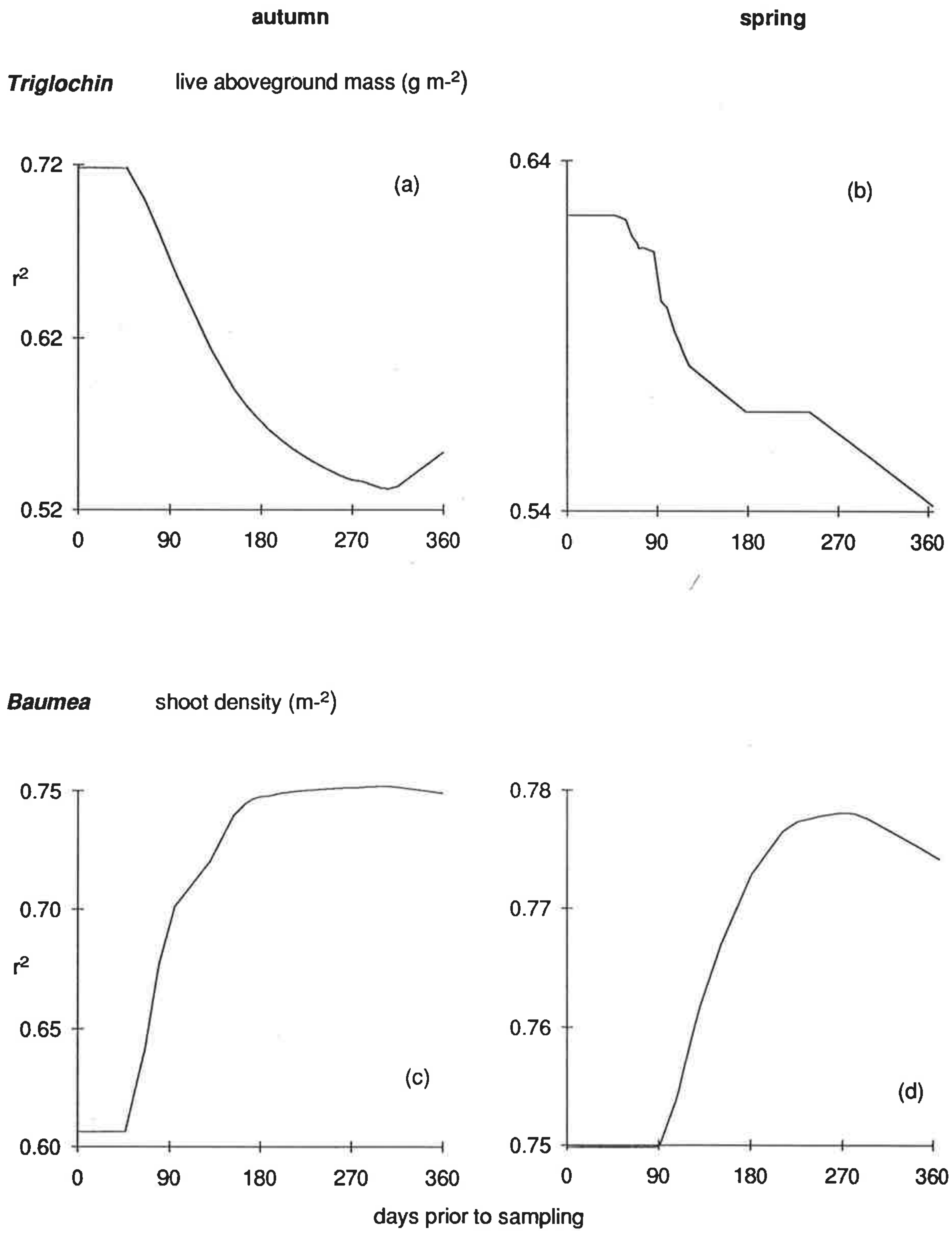


Figure 3.6

The r^2 values of linear regressions of *Triglochin*'s live aboveground mass (a & b) and *Baumea*'s shoot density (c & d) versus the Sum Water Regime calculated for each water level record, for the 360 days prior to sampling in autumn and spring..

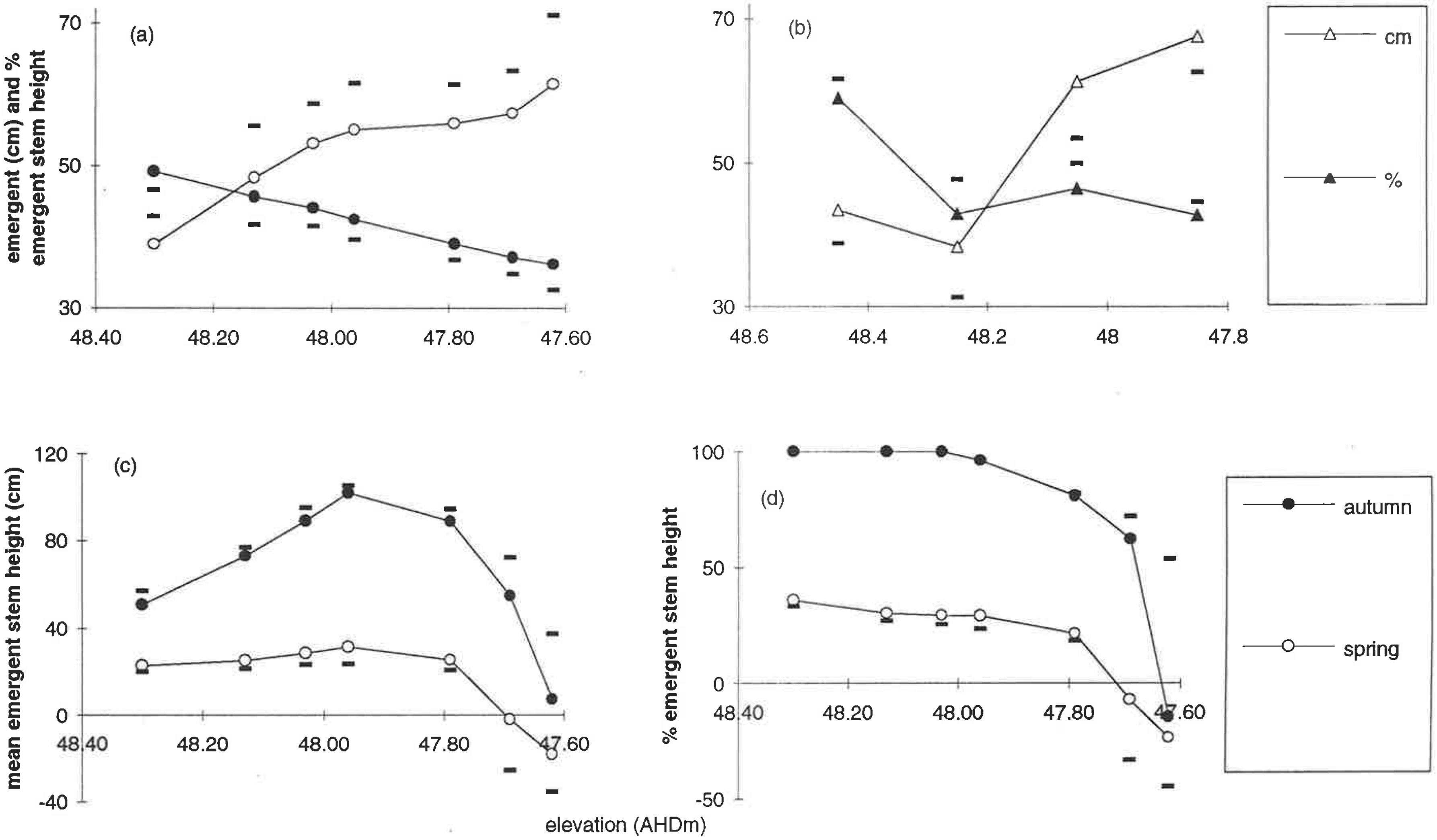


Figure 3.7
The emergent height and % emergent height (mean +one sd) of the tallest *Baumea* stems (a) and *Triglochin* leaves (b) across a spring elevation gradient. The emergent height (c) and the percent emergent height (d) (mean +one sd) of all *Baumea* stems in the population across an elevation gradient in autumn and spring

		autumn data	spring data	combined data	related figure
		depth (cm)			
Baumea					
shoot density (m^{-2})		0.64	0.69	0.02	3.1b
mass per shoot (g)		0.04	0.70	0.01	3.1c
maximum stem height (cm)		0.21	0.91	0.80	3.1d
Triglochin					
live aboveground biomass (gm^{-2})		0.73	0.62	0.83	3.1e
mass per shoot (g)		0.65	0.51	0.71	3.1g
maximum leaf height (cm)		0.78	0.94	0.95	3.1h
	days before harvest	**Sum Water Regime (cm days x 10^2)**			
Baumea					
shoot density (m^{-2})	30	0.61	0.75	0.01	3.5a
	90	0.70	0.75	0.09	3.5b
	180	0.75	0.77	0.58	3.5c
	360	0.75	0.77	0.69	3.5b
Triglochin					
live aboveground biomass (gm^{-2})	30	0.72	0.62	0.85	3.2e
	90	0.66	0.60	0.62	3.2f
	180	0.57	0.57	0.01	3.2g
	360	0.55	0.54	0.06	3.2h
maximum stem height (cm)	30	0.85	0.94	0.96	3.3e
	90	0.69	0.94	0.86	3.3f
	180	0.56	0.95	0.06	3.3g
	360	0.54	0.95	0.003	3.3h
mass per shoot (g)	30	0.69	0.51	0.72	3.4e
	90	0.61	0.52	0.61	3.4f
	180	0.51	0.52	0.02	3.4g
	360	0.50	0.52	0.04	3.4h

Table 3.1
The r^2 values of linear regressions (all significant, except where $r^2<0.06$) of aboveground plant characteristics versus (a) depth and versus (b) the Sum Water Regime, calculated for the 30, 90, 180 and 360 days prior to harvests. See text for explanation of Sum Water Regime and related Figures for the plotted data.

		Baumea						
elevation (AHDm)		48.30	48.13	48.03	47.96	47.79	47.69	47.62
stem density (m^{-2})								
autumn	x	2454	1696	1567	1613	971	913	129
	sd	631	456	460	467	277	427	142
	V*	26	27	29	29	29	47	110
spring	x	2660	2440	1580	1565	1345	470	385
	sd	651	712	527	104	285	183	303
	V*	24	29	33	7	21	39	79

		Triglochin					
elevation (AHDm)		48.45	48.40	48.25	48.05	47.95	47.85
leaf density (m^{-2})							
autumn	x	9		23	28		35
	sd	14		15	23		18
	V*	149		65	81		51
spring	x		208		269	218	179
	sd		126		68	88	84
	V*		60		25	40	47

Table 3.2
Triglochin leaf and *Baumea* stem densities (m^{-2}) across an elevation gradient in spring and autumn. Data are the mean, standard deviation and coefficient of variation.

Baumea

elevation (AHDm)		48.30	48.13	48.03	47.96	47.79	47.69	47.62
stems per shoot								
autumn	x	1.7	1.4	1.8	2.0	2.0	1.9	2.7
	sd	0.2	0.1	0.2	0.5	0.4	0.3	0.8
spring	x	1.4	1.3	1.1	1.1	1.3	1.6	1.6
	sd	0.3	0.3	0.1	0.1	0.1	0.3	0.2
groups with significantly different means		ab	a	ab	b	bc	c	d

2-way AOV	F	P
season	104.6	< 0.000
elevation	10.3	< 0.000
interaction	4.7	< 0.000

Triglochin

elevation (AHDm)		48.45	48.40	48.25	48.05	47.95	47.85	P
leaves per shoot								
autumn	x			2.7	2.3		3.5	ns
	sd			0.8	0.5		1.7	
spring	x		4.5		4.4	4.3	4.5	ns
	sd		1.0		0.6	0.9	0.4	

1-way AOV: autumn v spring	
F	P
19.3	< 0.000

Table 3.3
The number of leaves or stems per shoot (mean & sd) across elevation gradients in autumn and spring. Results of 2-way AOV on *Baumea* data and 1-way AOV on *Triglochin* data are shown.

		Baumea							*Triglochin*			
elevation (AHDm)		48.30	48.13	48.03	47.96	47.79	47.69	47.62	48.45	48.25	48.05	47.85
depth (cm)		40	57	67	74	91	101	108	30	50	70	90
mass (g)	x	0.47	0.59	0.72	0.77	1.18	1.47	1.83	1.63	2.27	5.30	7.88
	sd	0.16	0.16	0.14	0.17	0.22	0.42	0.39	0.25	0.58	1.64	1.35
height (cm)	x	78.9	105.3	120.1	129.0	142.9	154.4	169.5	73.5	88.3	131.3	157.6
	sd	4.0	7.2	5.6	6.6	5.5	5.9	9.7	4.8	7.1	7.9	4.9
basal diameter (cm)	x	0.40	0.78	1.02	1.18	1.58	1.70	1.82	1.66	1.79	2.63	3.54
	sd	0.05	0.09	0.20	0.17	0.30	0.43	0.41	0.28	0.39	0.42	0.32
height per unit mass (cm g-1)	x	186.4	193.0	174.1	176.7	125.6	111.5	93.3	46.3	40.7	26.9	20.6
	sd	56.0	51.2	41.6	39.1	23.5	23.3	23.3	8.6	7.7	7.6	3.5
height : diameter	x	126.9	108.7	95.7	97.3	73.4	62.6	55.2	45.9	51.6	51.2	44.9
	sd	n/a							9.5	11.4	8.6	4.3
fresh : dry weight	x	2.3	2.3	2.8	2.2	2.6	3.0	2.4	8.6	8.5	10.1	11.5
	sd	0.5	0.3	0.3	0.1	0.3	0.9	0.9	0.7	0.6	0.7	0.8

Table 3.4
Morphological characteristics (mean & sd) of the tallest *Baumea* stems and *Triglochin* leaves (n=10) across a depth/elevation gradient in spring.

	Baumea					***Triglochin***	
elevation (AHDm)	48.20	47.95	47.75			48.20	47.70
depth (cm)	5	30	50			0	50
biomass (g m-^{2})				F	P		
total live	1961	2188	3393	5.4	0.028	1060	4040
total live and dead	3998	4964	5180	1.9	0.202		
dead aboveground	983	1595	371	7.4	0.013		
dead belowground	1054	1182	1415	2.4	0.148		
live aboveground	323	355	1699	12.1	0.003	72	445
live belowground	1638	1832	1657	0.6	0.584	988	3595
live root	112	153	435	63.3	0.000	210	1201
live rhizome	1526	1679	1259	2.9	0.104	244	1550
live tuber						534	844
rhizome morphology							
live rhizome length (cm m-^{2})	14428	8700	3263	15.3	0.002	165	679
live rhizome (cm g-1)	9.38	5.14	2.71	22.7	0.001	0.68	0.44
ratios							
live below : aboveground	5.67	5.19	1.06	47.0	0.000	13.78	8.07
root : shoot	0.38	0.43	0.29	1.9	0.204	2.93	2.70
root : rhizome	0.07	0.09	0.36	24.3	0.000	0.84	0.88
mass per ramet (g dwt)							
root	0.10	0.18	0.78	32.4	0.000	7.01	34.32
rhizome	1.44	1.98	2.21	5.2	0.031	8.12	44.28
tuber						17.8	24.1

Table 3.5
A comparison between the belowground characteristics of *Baumea* and *Triglochin* across an elevation gradient in spring. The significance levels (F statistic and probability) from 1-way AOV's for *Baumea* data are shown. *Baumea* data are means (n=4) and *Triglochin* data are from one sample.

elevation (AHDm)	48.20	47.95	47.75		F	P
depth (cm)	5	30	50			
no. live rhizome pieces	1056	794	300		21.6	< 0.001
total no. expended shoots	8400	4561	1721		9.24	0.006
no. live and dead long shoots	4058	1501	645		34.6	< 0.001
no. live and dead short shoots	4342	3060	1076		10.9	0.005
proportion long shoots	0.50	0.34	0.37		4.18	0.057
elevation (AHDm)	48.15	47.90	47.65	47.60		
depth (cm)	0	25	50	55		
rhizome crown diameter (mm)						
long shoots	5.25	5.28	6.31	6.88	7.76	< 0.001
	n=23	44	48	12		
short shoots	4.58	3.75	5.12	6.00	6.69	< 0.001
	n=46	26	34	6		
oldest shoot (origin unknown)	6.66	6.61	7.00	9.14	6.40	< 0.001
	n=24	9	14	7		
rhizome length (cm)	6.25	7.43	10.83	14.05	6.51	< 0.001
	n=11	7	12	19		

Table 3.6

Rhizome characteristics (m^{-2}) of *Baumea* across elevation gradients in autumn-87. Data are means (n=4) and the results (F statistic and probability level) of 1-way AOV's.

elevation (AHDm)	48.40	48.15	48.05	47.95	47.85	r^2	F	P
depth (cm)	25	50	60	70	80			
vegetative shoot density (m^{-2})	46	67	63	50	39			
flowering shoot density (m^{-2})	1	16	11	20	25	0.61	36.7	<0.000
proportion of shoots in flower	0.02	0.26	0.21	0.42	0.67	0.63	38.6	<0.000
no. fruit/inflorescence	50	86	120	154	167	0.62	97.4	<0.000
seed density (m^{-2})	300	5718	6474	13824	25092	0.65	43.4	<0.000
mass per vegetative shoot (g)	1.59	4.42	4.40	6.37	8.29	0.51	24.0	<0.000
mass per flowering shoot (g)	1.59	4.98	5.16	8.06	12.87	0.64	41.0	<0.000
mass per seed (mg)		1.73	2.17	2.20	1.52			
proportion of live aboveground mass held in inflorescence (m^{-2})	0.02	0.09	0.12	0.22	0.31	0.66	45.0	<0.000

Table 3.7
Aboveground characteristics of a flowering *Triglochin* population across a spring depth/elevation gradient. Data are means (n=5) and where linear regressions were significant and r^2>0.50, results of regression analysis (F statistic and probability) are shown.

elevation	mean no. seedlings (m^{-2})		% seedling survival	proportion of seedlings in adult population
(AHDm)	May-86	Aug-86	Aug-86	Aug-86
47.97	3	0	0	0
47.95	3	0	0	0
47.93	0	0	0	0
47.96	0	0	0	0
47.96	3	0	0	0
47.92	1	0	0	0
47.92	2	0	0	0
47.90	2	0	0	0
47.90	4	0	0	0
47.90	4	0	0	0
47.88	8	0	0	0
47.86	26	0	0	0
47.83	66	0	0	0
47.81	64	0	0	0
47.83	57	0	0	0
47.85	51	2	3.9	0.06
47.82	42	0	0	0
47.77	47	1	2.1	0.04
47.66	134	3	2.2	0.07
47.66	233	1	0.4	0.04
47.67	422	2	0.5	0.05
47.64	303	5	1.7	0.11
47.64	228	4	1.8	0.13
47.68	259	2	0.8	0.07
47.68	188	4	2.1	0.11
47.65	266	8	3.0	0.21
47.68	172	9	5.2	0.22
47.66	126	15	11.9	0.30
47.63	109	13	11.9	0.30
47.60	131	5	3.8	0.20

Table 3.8
The number of *Triglochin* seedlings (m^{-2}) on 5-May-86 and 1-Aug-86 and their survivorship and contribution to the population across an elevation gradient (47.97-47.60 AHDm).

CHAPTER FOUR: THE ACCUMULATION AND ALLOCATION OF BIOMASS

Figures 4.1 - 4.12

Tables 4.1 - 4.11

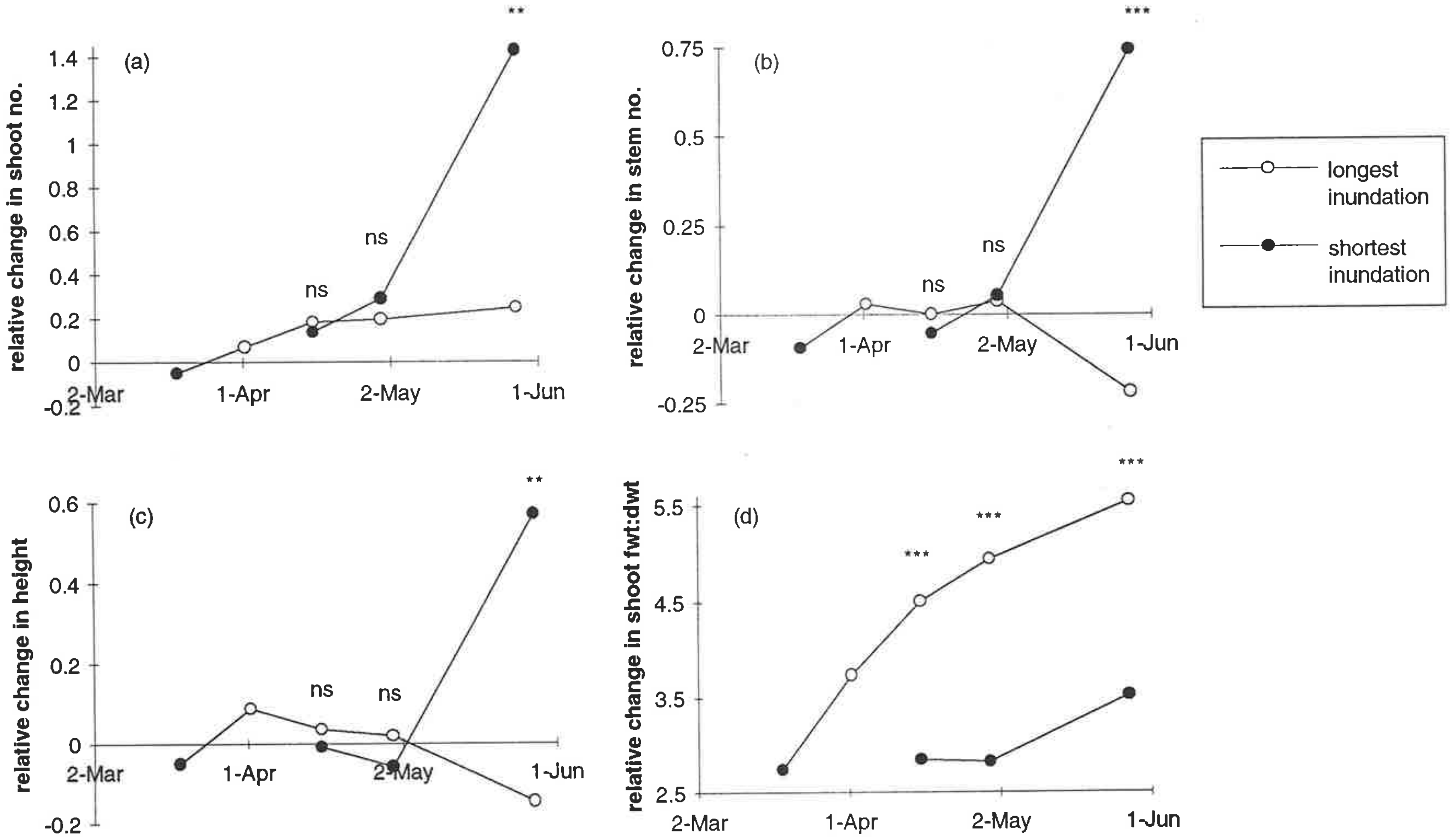


Figure 4.1
The relative change in the number of (a) shoots, (b) stems, (c) stem height and (d) stem fresh to dry weight ratio of *Baumea* ramets over 12 weeks growth. The longest inundation was 12 weeks at 80 cm depth and the shortest, 2-4 weeks at 80 cm followed by 8-10 weeks at 10 cm depth. Data are mean values (n=4-8) and associated significance levels of 1-way AOV's comparing the two treatments at 6, 8 and 12 weeks. (***= P<0.01, **=P<0.025, ns=P>0.05)

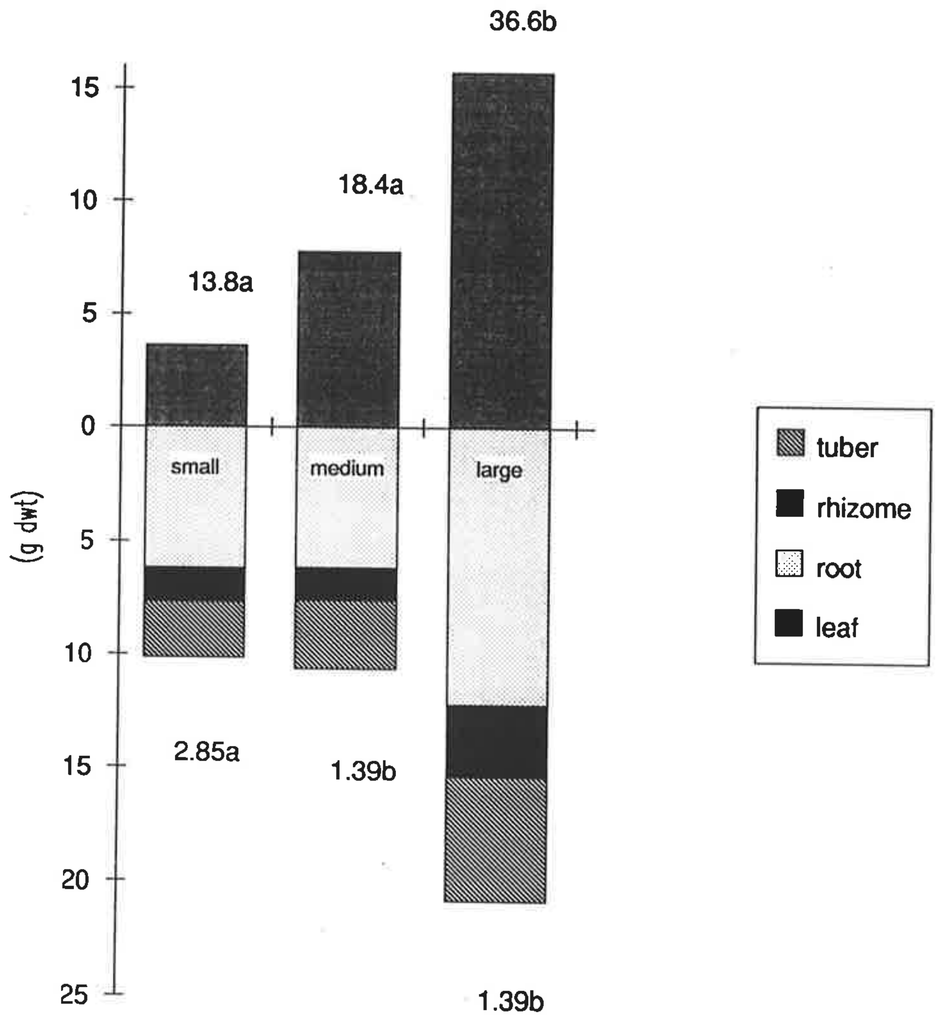


Figure 4.2
The allocation of biomass within 8 month old ramets of *Triglochin* after 4 months growth in small (10x10x10 cm), medium (15x15x15 cm) and large (22x22x22 cm) pots. The total mean mass of plants are written above and the below : aboveground ratio is written below. Different letters denote significantly different groups, identified from 1-way AOV with planned comparisons.

Figure 4.3
An example of root and rhizome growth on a ramet of *Baumea*, after 12 months at 0 cm.

Figure 4.4
An example of root and rhizome growth on a ramet of *Baumea*, after 12 months at 50 cm.


1
7
6
4
3
5
2
1
2

Figure 4.5
An example of root, rhizome and tuber growth on a ramet of *Triglochin*, after 12 months at 0 cm.

Figure 4.6
An example of root, rhizome and tuber growth on a seedling of *Triglochin*, after 12 months at 0 cm.

Figure 4.7
Examples of the distal and lateral origin of *Triglochin* shoots, recruited by ramets at 0 cm.


0.A.1


0.5.2

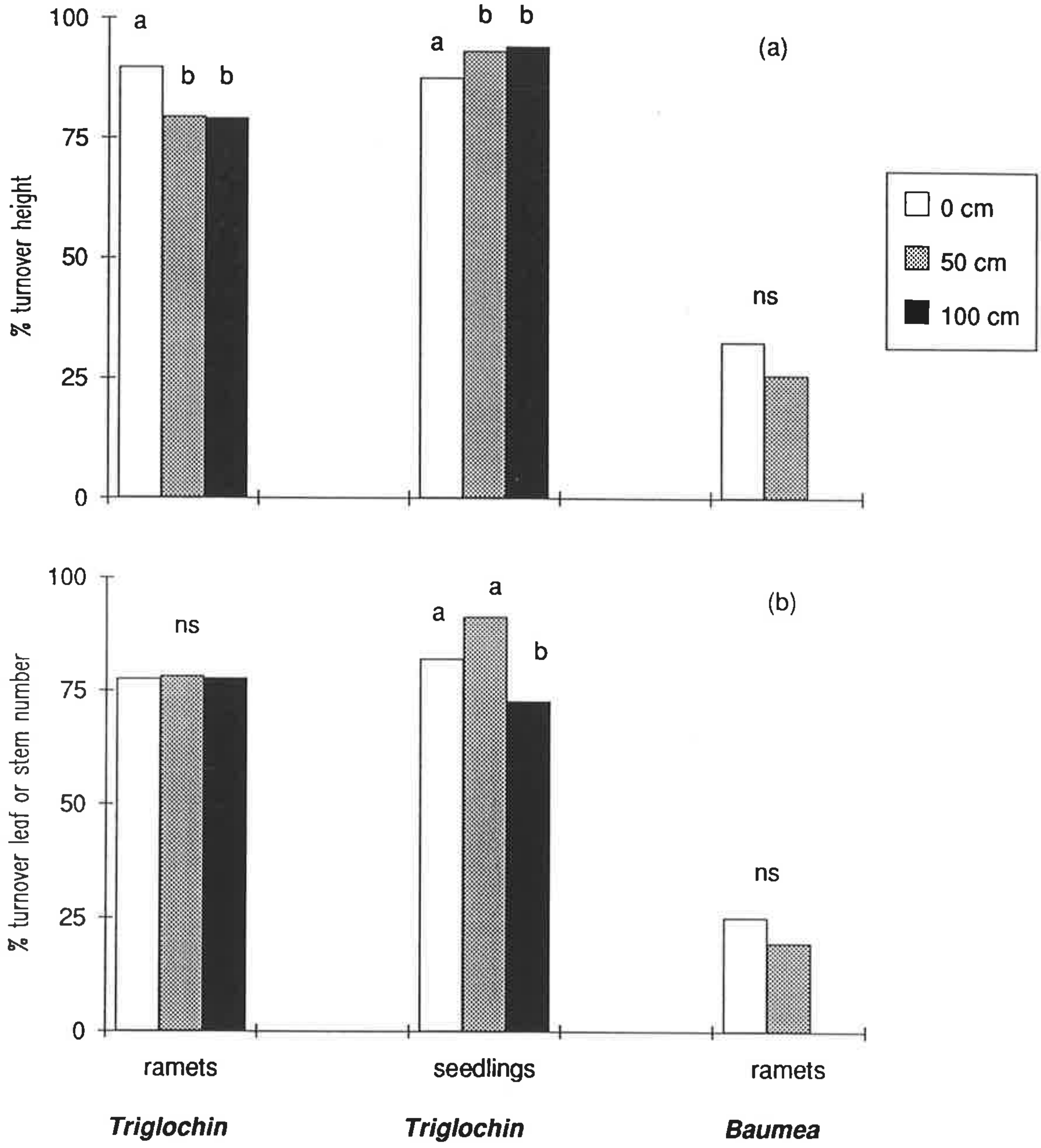


Figure 4.8
The percent turnover of (a) photosynthetic height and (b) stem or leaf number after 12 months growth at constant depths (0, 50, 100 cm). Results of 1-way AOV's and planned comparisons are shown as letters that delineate different or not significantly different (ns) groups.

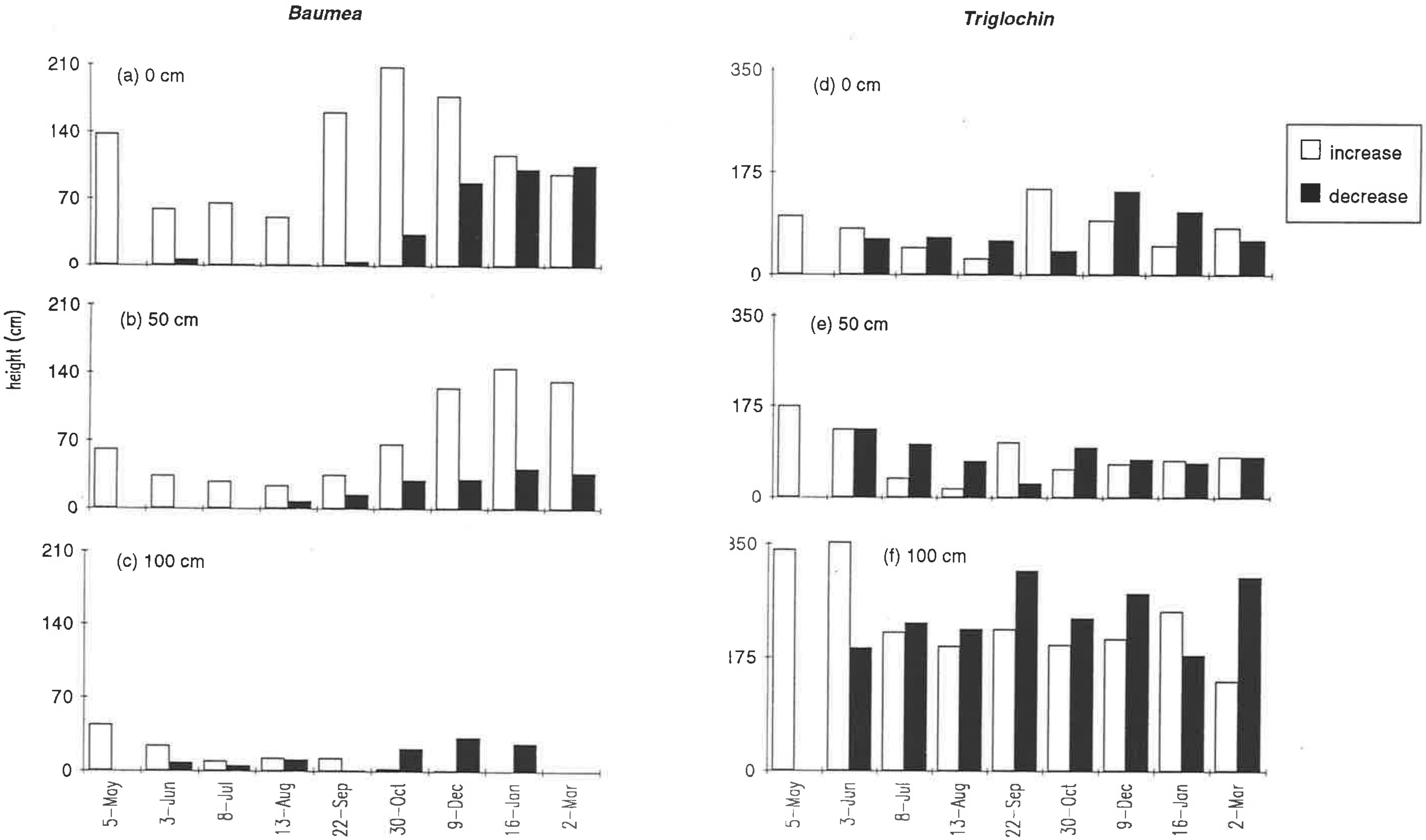


Figure 4.9
The absolute increase and decrease in the photosynthetic height of (a-c) *Baumea* stems per ramet and (d-f) *Triglochin* leaves per seedling, for each sampling interval.

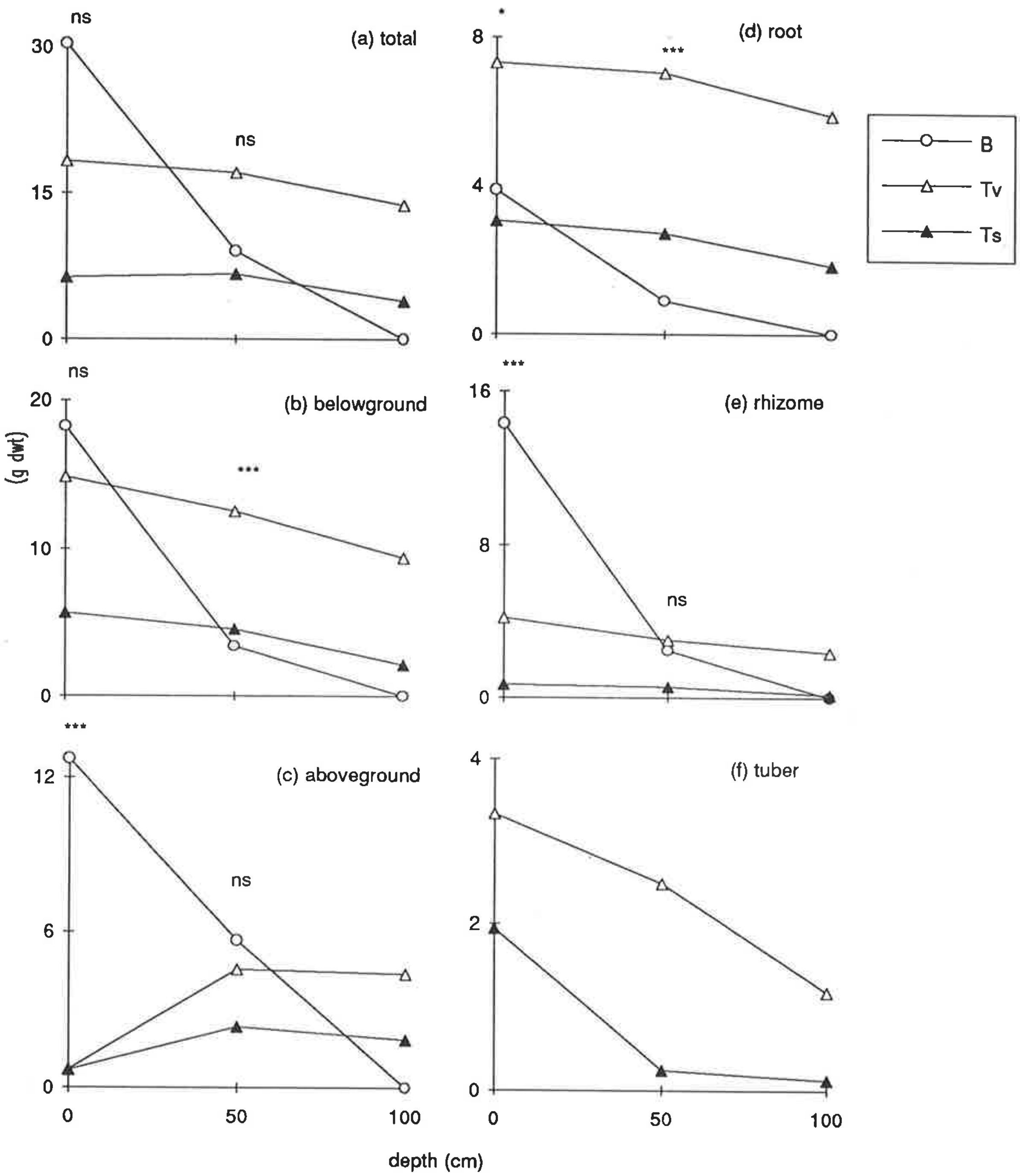
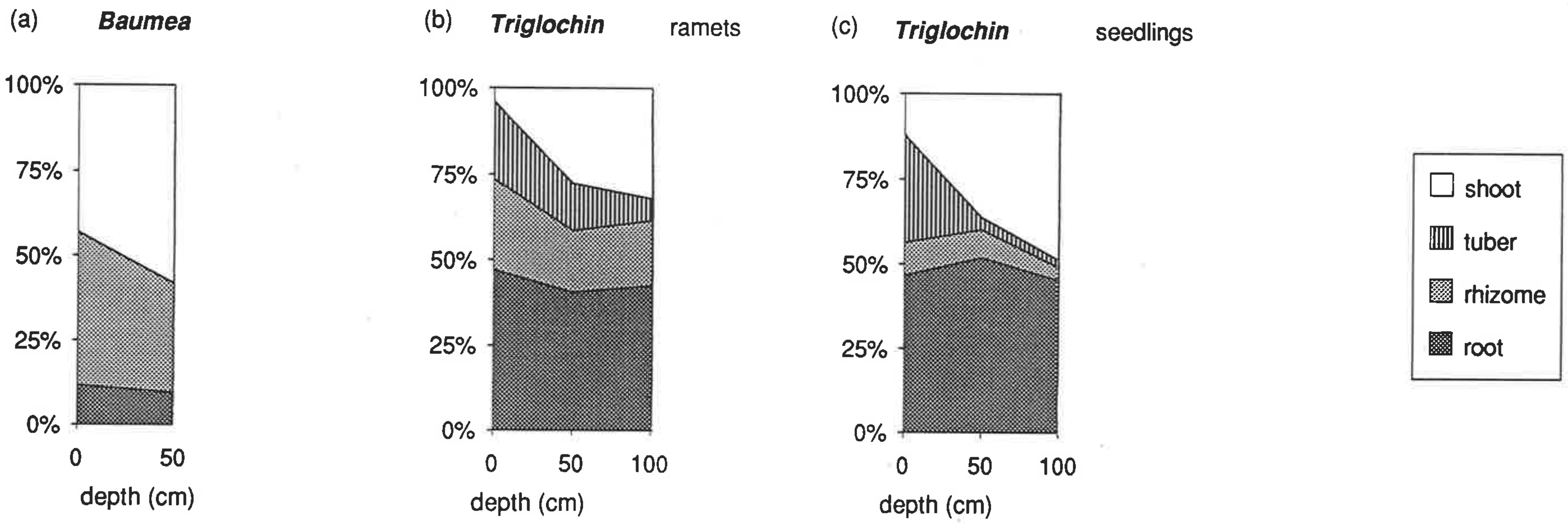


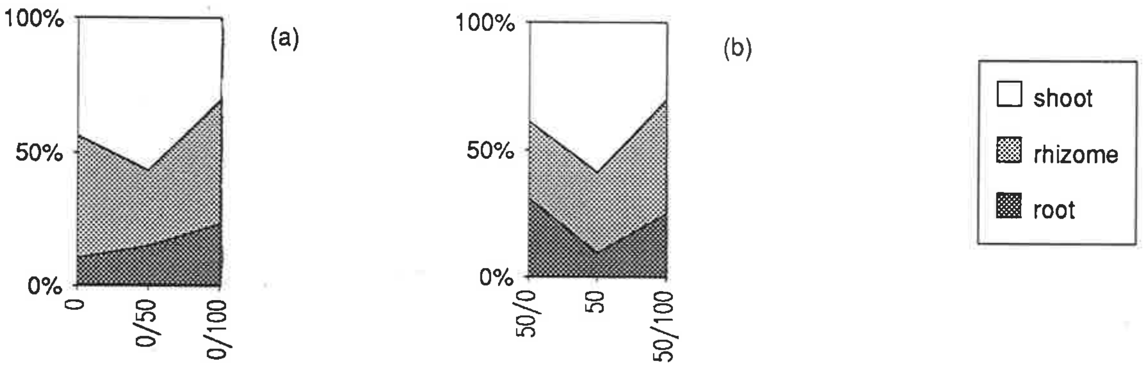
Figure 4.10
The final mean (a) total, (b) belowground, (c) aboveground, (d) root, (e) rhizome and (f) tuber mass of *Triglochin* (Tv) and *Baumea* (B) ramets and *Triglochin* seedlings (Ts) after 12 months growth at constant depths. The significance levels between *Baumea* and *Triglochin* ramets at 0 and 50 cm, are shown above the relevant data. (***=P<0.01, *=P<0.05, ns=P>0.05)



source of variation	shoot	root	rhizome	shoot	root	rhizome	tuber	shoot	root	rhizome	tuber
among groups	**	ns	ns	***	ns	ns	ns	***	ns	ns	***
0 v 50 & 100 cm				***	ns	ns	*	***	ns	ns	***
50 v 100 cm				ns	ns	ns	ns	ns	ns	ns	ns

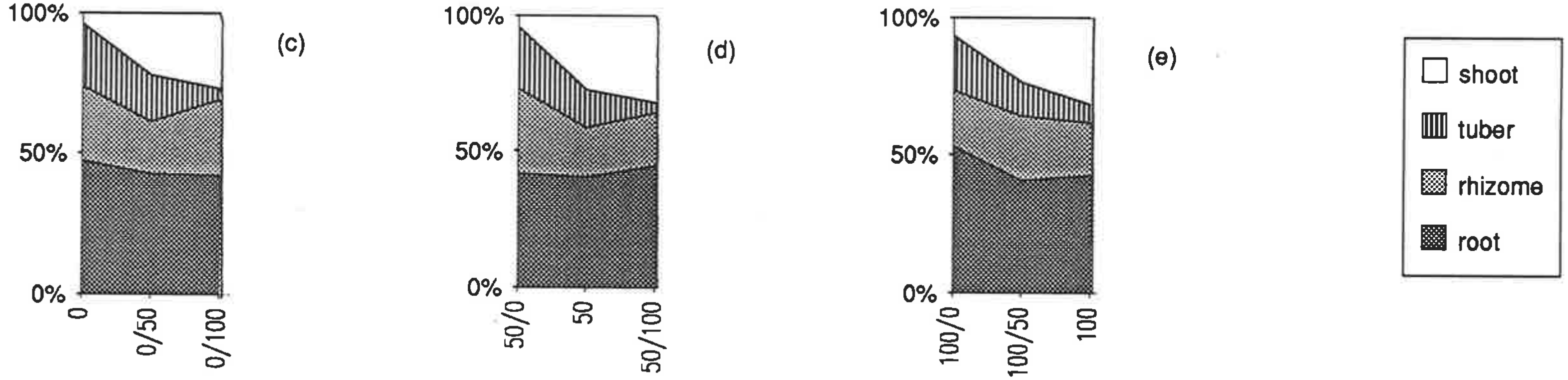
Figure 4.11
The final percent allocation of biomass within ramets of (a) *Baumea* and (b) *Triglochin* and (c) seedlings of *Triglochin,* grown at constant depths for 12 months. The significance of 1-way AOV's and planned comparisons which compare the allocation of each tissue at the three depths is shown below the relevant data. (***=P<0.01, *=P<0.05, ns=P>0.05)

Baumea



source of variation	shoot	root	rhizome	shoot	root	rhizome
among treatments	***	***	***	**	***	ns
0 v 50 & 100 cm	ns	ns	***	ns	*	ns
50 v 100 cm	***	*	***	***	***	***

Triglochin



source of variation	shoot	root	rhizome	tuber	shoot	root	rhizome	tuber	shoot	root	rhizome	tuber
among treatments	***	ns	ns	**	***	ns	*	*	***	*	ns	**
0 v 50 & 100 cm	***	ns	ns	*	***	ns	***	**	***	*	ns	***
50 v 100 cm	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns

Figure 4.12
The final percent allocation of biomass within *Baumea* (a, b) and *Triglochin* (c-e) ramets, submerged or emerged (±50, ±100 cm) at 9 months and harvested at 12 months. The significance of 1-way AOV's and planned comparisons which compare the allocation of each tissue at the three depths is shown below the relevant data. (***=P<0.01, *=P<0.05, ns=P>0.05)

	treatment	x	sd	P	source of variation
root (g dwt)	initial	8.3	4.3	**	among groups
	T1	2.1	0.5	***	initial v treatments
	T2	2.4	0.8	ns	treatment 1 v 2
root : shoot	initial	0.27	0.13	*	among groups
	T1	0.08	0.03	***	initial v treatments
	T2	0.13	0.08	ns	treatment 1 v 2
% root allocation	initial	0.11	0.03	**	among groups
	T1	0.05	0.01	***	initial v treatments
	T2	0.06	0.03	ns	treatment 1 v 2

Table 4.1
Final root characteristics (mean & sd) of *Baumea* ramets in experiment 1. The initial represents ramets harvested at the start, and treatments 1 and 2 (T1, T2) represent pots inundated for a short (2-4 weeks) and long (12 weeks) period, respectively. Significance levels of 1-way AOV's and unplanned comparisons are shown. (***=P<0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

	pot size (cm)			
	small (10x10x10)	medium (15x15x15)	large (22x22x22)	P
leaf length (cm)	62.7	63.3	62.0	ns
leaf diameter (cm)	1.25	1.50	1.50	ns
mass per leaf (g dwt)	5.57	7.70	6.98	ns
no. leaves per shoot	6.67	6.50	7.67	ns
yield per shoot (g dwt)	6.76	9.74	6.19	ns
no. leaves per pot	6.67a	10.3b	23.0c	***
no. new shoots per pot	0.0a	0.67b	2.0c	***
yield per pot (g dwt)	6.76a	13.4a	18.6b	*
no. tubers per pot	6.67a	7.33a	18.7b	*
mass per tuber (g dwt)	0.39	0.41	0.28	ns

Table 4.2
The influence of pot size on the growth of *Triglochin* shoots (n=3) over 4 months. The significance levels of 1-way AOV's are shown. Different groups, identified from planned comparisons, are denoted by different letters. (ns=P<0.10, **=P<0.05, ***=P<0.01)

	initial 3-Mar-87	9 months 8-Dec-87	survivorship %	9 months 8-Dec-87	12 months 3-Mar-88	survivorship %
depth (cm)						
Baumea						
0	16	16	100	8	8	100
50	16	12	75	8	8	100
100	12	7	58	4	0	0
Triglochin	- vegetative ramets					
0	12	12	100	4	4	100
50	12	12	100	4	4	100
100	12	12	100	4	4	100
Triglochin	- seedlings					
0	16	14	88	10	10	100
50	16	4	25	4	4	100
100	12	3	25	3	3	100

Table 4.3
The initial and final number of *Triglochin* and *Baumea* ramets and percent survivorship, following inundation at constant depths for 9 and 12 months

aboveground characteristics after 9 months (per ramet)

depth (cm)	final height (cm)	stem no.	shoot no.
0	678 ***	13.3 ***	5.3 ***
50	323 ***	6.0 ***	2.0 ***
100	68 ***	1.6 ***	1.0 ns

final biomasses after 12 months (g dwt ramet)

depth (cm)	total	belowground	aboveground shoot	root	rhizome	root : shoot	below : above
0	30.32 ***	18.25 ***	12.71 ***	3.88 ***	14.31 ***	0.28 ns	1.34 ns
50	9.04	3.39	5.65	0.91	2.48	0.17	0.87
100	0	0	0	0	0	0	0

Table 4.4
The influence of constant depths (0, 50, 100 cm) on *Baumea* ramets: aboveground characteristics after 9 months and final biomasses after 12 months. Data are mean values for each treatment and significance levels from 1-way AOV's and planned comparisons. See Appendix 4.2 for experimental design and arrangement of source of variation tables. (***=P< 0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

aboveground characteristics after 9 months (per ramet)

depth (cm)	final height (cm)	leaf no.	shoot no.
vegetative ramets			
0	171 ***	5.4 ns	1.2 ns
50	255 ***	5.1 ns	1.3 ns
100	342 ***	4.3 ns	1.1 ns
seedlings			
0	73 ***	4.4 **	1.1 ns
50	172 *	3.8 **	1.0 ns
100	35 ***	2.0 ns	1.0 ns

final biomasses after 12 months (g dwt ramet)

	total	belowground	aboveground shoot	root	rhizome	tuber	no. tubers	mean tuber mass	root : shoot	below : above
vegetative ramets										
0	18.32 ns	14.85 ns	0.71 ***	7.32 ns	4.20 ns	3.33 ns	6.25 ns	0.54 ns	12.13 ***	25.10 ***
50	17.08 ns	12.55 ns	4.53 ***	7.03 ns	3.03 ns	2.49 ns	5.00 ns	0.44 ns	1.63 ***	2.97 ***
100	13.79 ns	9.42 ns	4.37 ns	5.88 ns	2.36 ns	1.17 ns	4.00 ns	0.24 ns	1.41 ns	2.23 ns
seedlings										
0	6.37 ns	5.69 ns	0.68 ***	3.06 ns	0.69 ns	1.94 **	5.30 **	0.36 *	5.22 ***	10.05 ***
50	6.72 ns	4.56 ns	2.33 ***	2.72 ns	0.57 ns	0.24 ***	6.50 ns	0.09	1.17 ***	1.99 ***
100	3.99 ns	2.14 ns	1.85 ns	1.87 ns	0.16 ns	0.12 ns	0.50 ***		0.96 ns	1.10 ns

Table 4.5
The influence of constant depths (0, 50, 100 cm) on *Triglochin* ramets: aboveground characteristics after 9 months and final biomasses after 12 months. Data are mean values for each treatment and significance levels from 1-way AOV's and planned comparisons. See Appendix 4.2 for experimental design and arrangement of source of variation tables. (***=P< 0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

aboveground characteristics after 9 months (per ramet)

original depth & change in depth (cm)	final height (cm)	stem no.	shoot no.
0	733 ***	15.9 *	7.0 ns
0/50	1207 ns	21.3 ns	9.0 ns
0/100	411 ***	10.0 ***	7.3 ns
50/0	510 ***	12.3 ***	4.5 ***
50	486 ns	7.3 ***	2.3 ***
50/100	107 ***	2.5 *	1.5 ns

final biomasses after 12 months (g dwt ramet)

original depth & change in depth (cm)	total	belowground	aboveground shoot	root	rhizome	root : shoot	below : above
0	30.32 ***	18.25 ***	12.71 ***	3.88 ns	14.31 ***	0.28 ns	1.34 ***
0/50	23.34 ***	9.28 ***	11.96 ***	3.16 ns	6.13 ***	0.27 ns	0.78 ns
0/100	7.80 ***	5.15 *	2.72 ***	1.57 ns	3.59 ns	1.13 ns	3.24 ***
50/0	17.41 ns	12.17 ***	8.07 *	5.68 ***	6.49 *	0.84 ***	1.64 **
50	9.04 **	3.39 ***	5.65 *	0.91 ***	2.48 ***	0.17 ***	0.87 ns
50/100	5.40 ns	4.31 ns	2.34 ns	1.39 ns	2.53 ns	0.39 ***	4.42 ***

Table 4.6
The influence of rapid changes in depth (±50, ±100 cm) on the final biomass (g dwt) of *Baumea* ramets after 12 months growth. Data are mean values for each treatment and significance levels from 1-way AOV's and planned comparisons. See Appendix 4.2 for experimental design and arrangement of source of variation tables. (***=P< 0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

aboveground characteristics after 9 months (per ramet)

original depth & change in depth	final height (cm)	leaf no.	shoot no.
vegetative ramets			
0	76 ***	5.8 ns	1.3 ns
0/50	214 ***	4.5 ns	1.0 ns
0/100	435 ***	5.8 ns	1.5 ns
50/0	87 ***	7.5 ns	2.0 ns
50	202 ***	4.0 ns	1.0 ns
50/100	428 ***	5.0 ns	1.3 ns
100/0	110 ***	6.3 *	1.5 ns
100/50	230 ***	4.5 ***	1.0 ns
100	365 **	4.5 ns	1.0 ns
seedlings			
0	85 ***	5.1 *	1.1 ns
0/100	262	3.5	1.0

final biomasses after 12 months (g dwt ramet)

original depth & change in depth	total	belowground	aboveground shoot	root	rhizome	tuber	no. tubers	mean tuber mass	root : shoot	below : above
vegetative ramets										
0	18.32 ns	14.85 ns	0.71 ***	7.32 ns	4.20 ns	3.33 ns	6.25 ns	0.54 **	12.13 ***	25.10 ***
0/50	13.59 ns	10.70 ns	2.90 ***	5.73 ns	2.55 ns	2.42 ***	7.75 ns	0.28 ***	2.07 ***	3.80 ***
0/100	10.97 ns	8.12 ns	2.85 ns	4.76 ns	2.79 ns	0.57 ns	2.50 ns	0.21 ns	1.57 ns	2.76 ns
50/0	19.34 ns	17.09 ns	0.87 ***	7.32 ns	5.33 ns	4.44 ***	8.00 ns	0.59 ns	21.80 ***	15.86 ***
50	17.08 ns	12.55 ***	4.53 ***	7.03 ns	3.03 ns	2.49 ***	5.00 ns	0.44 ns	1.63 ***	2.97 ***
50/100	16.45 ns	11.18 ns	5.27 ns	7.33 ns	3.24 ns	0.61 ns	3.50 ns	0.25 ns	1.39 ns	2.12 ns
100/0	13.02 ns	12.16 ns	0.86 ***	6.87 ns	2.65 ns	2.64 ns	8.50 ns	0.36 ns	8.76 ***	15.09 ***
100/50	15.36 ns	11.63 ns	3.72 ***	6.25 ns	3.58 ns	1.81 ns	5.00 ns	0.34 ns	1.78 ***	3.41 ***
100	13.79 ns	9.42 ns	4.37 ns	5.88 ns	2.36 ns	1.17 ns	4.00 ns	0.24 ns	1.41 ns	2.23 ns
seedlings										
0	6.37 ns	5.69 ns	0.68 ***	3.06 ns	0.69 ns	1.94 *	5.30 ***	0.36 *	5.22 ns	10.05 ns
0/100	5.32	3.88	1.44	3.04	0.21	0.63	3.67	0.17	2.18	2.78

Table 4.7
The influence of rapid changes in depth (±50, ±100 cm) on the final biomass (g dwt) of *Triglochin* ramets after 12 months growth. Data are mean values for each treatment and significance levels from 1-way AOV's and planned comparisons. See Appendix 4.2 for experimental design and arrangement of source of variation tables. (***=P< 0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

		5-May	6-Jun	12-Aug	21-Sep	29-Oct	8-Dec	17-Jan	3-Mar	total
0 cm										
long	x	1.8	0.3	0.5	0.8	0.1	0.1	1.3	4.1	8.9
	sd	1.0	0.7	0.9	0.8	0.3	0.3	1.1	3.6	4.1
short	x	0.1	0.3	0.0	0.3	0.3	0.3	0.5	2.1	3.8
	sd	0.3	0.7	0.0	0.7	0.7	0.4	0.7	2.6	2.8
50 cm										
long	x	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.5
	sd	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.0
short	x	0.4	0.0	0.0	0.3	0.1	0.0	0.4	0.5	1.6
	sd	0.7	0.0	0.0	0.4	0.3	0.0	1.0	1.0	2.1

Table 4.8
The number of long and short shoots per *Baumea* ramet (mean & sd; n=8), that emerged in each time interval over 12 months, at constant depths (0, 50 cm).

		total no. shoots per ramet		
		emerged	yet to emerge	total
0 cm	x	12.6	9.6	22.3
	sd	5.2	3.8	6.9
50 cm	x	3.1	2.1	5.3
	sd	1.7	1.8	3.2

Table 4.9
The total number of *Baumea* shoots per ramet (mean & sd; n=8), divided into shoots that had emerged and shoots that were yet to emerge, after 12 months growth at constant depths (0, 50 cm).

		5-May	6-Jun	12-Aug	21-Sep	29-Oct	8-Dec	17-Jan
0 cm	x	4.1	4.0	1.0	3.8	3.0	3.0	1.4
	sd	1.1	1.0	0.7	1.0	0.0	0.8	0.9
	n	19	4	4	8	3	3	14
50 cm	x	1.7			1.5	2.0		0.3
	sd	1.5			0.5	0.0		0.5
	n	11			2	1		3

Table 4.10
The number of shoots (mean & sd, sample size) that had developed from *Baumea* shoots recruited on each record over 12 months at constant depths (0, 50 cm).

		emerged	yet to emerge	total
0 cm	x	589	824	1413
	sd	295	394	507
50 cm	x	91	173	264
	sd	49	177	194

Table 4.11
The total length (mean & sd; n=8) of *Baumea* rhizomes (mm per ramet) preceding shoots that had emerged and shoots that were yet to emerge, after 12 months growth at constant depths (0, 50 cm).

CHAPTER FIVE: *IN SITU* PLANT DEMOGRAPHY

Figures 5.1 - 5.26

Tables 5.1 - 5.8

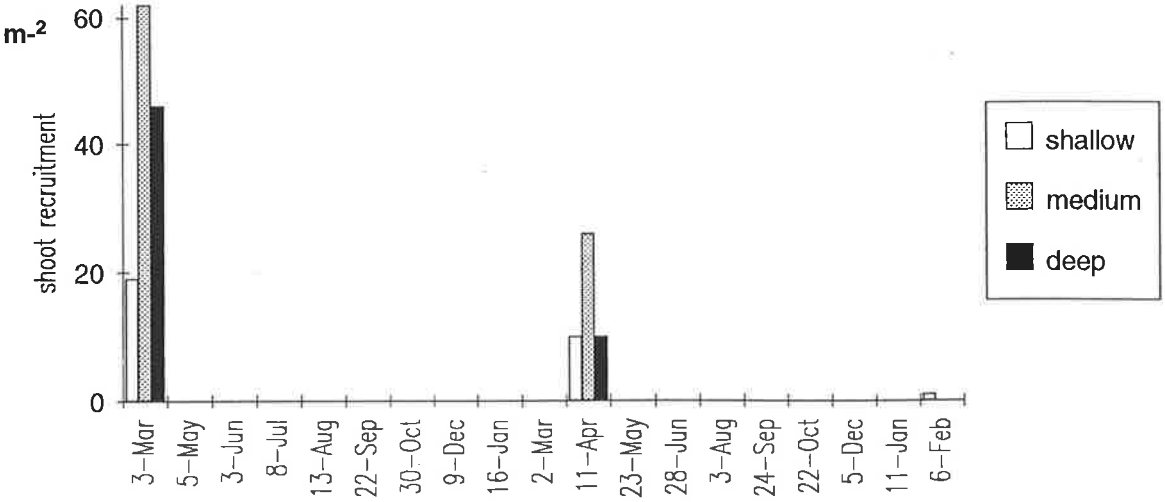


Figure 5.4
The number of *Triglochin* shoots recorded at the start of the demographic study and their recruitment throughout the study, at the three elevations.

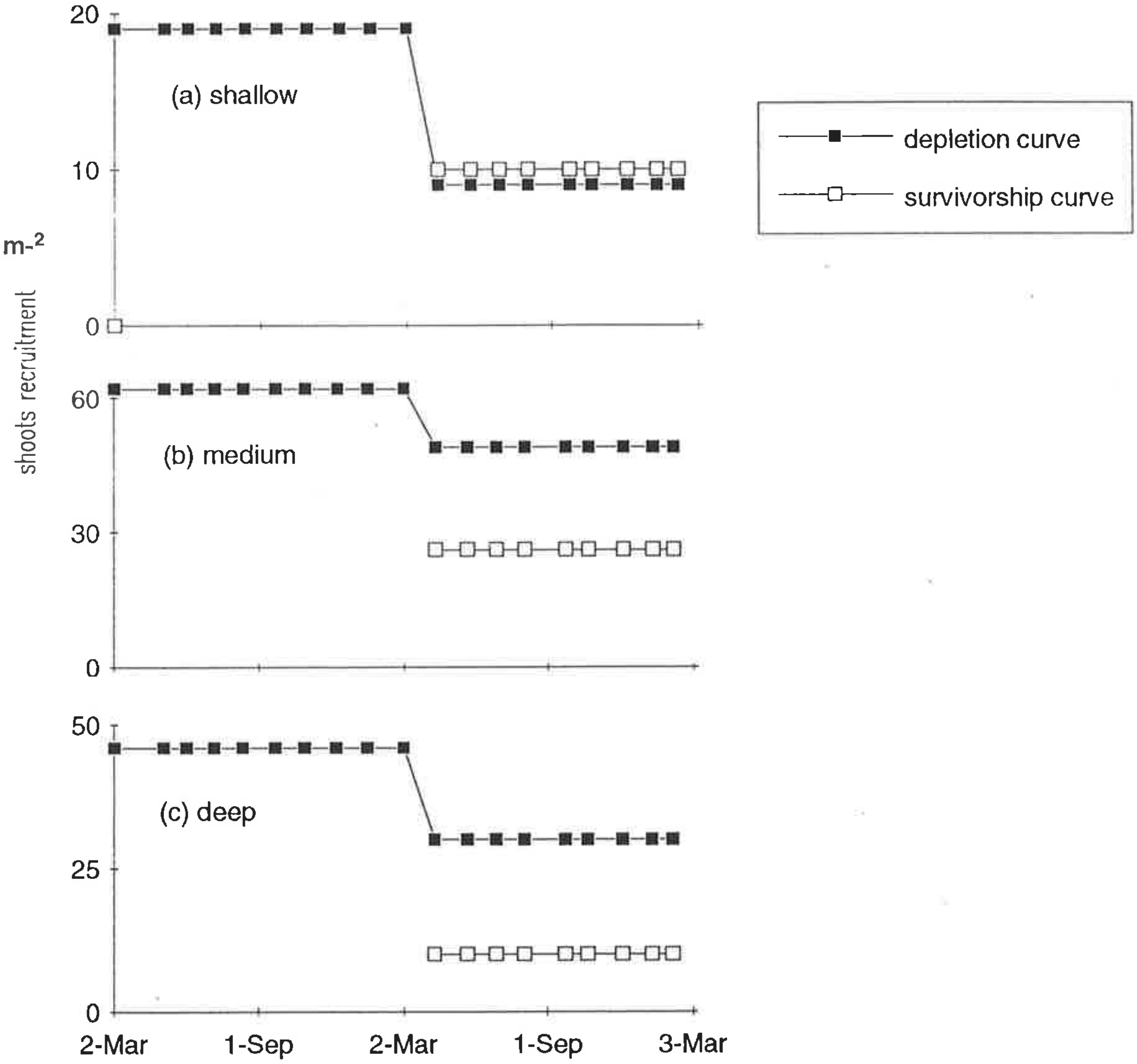


Figure 5.5
Depletion and survivorship curves for *Triglochin* shoots recorded at (a) shallow, (b) medium and (c) deep elevations over 2 years.

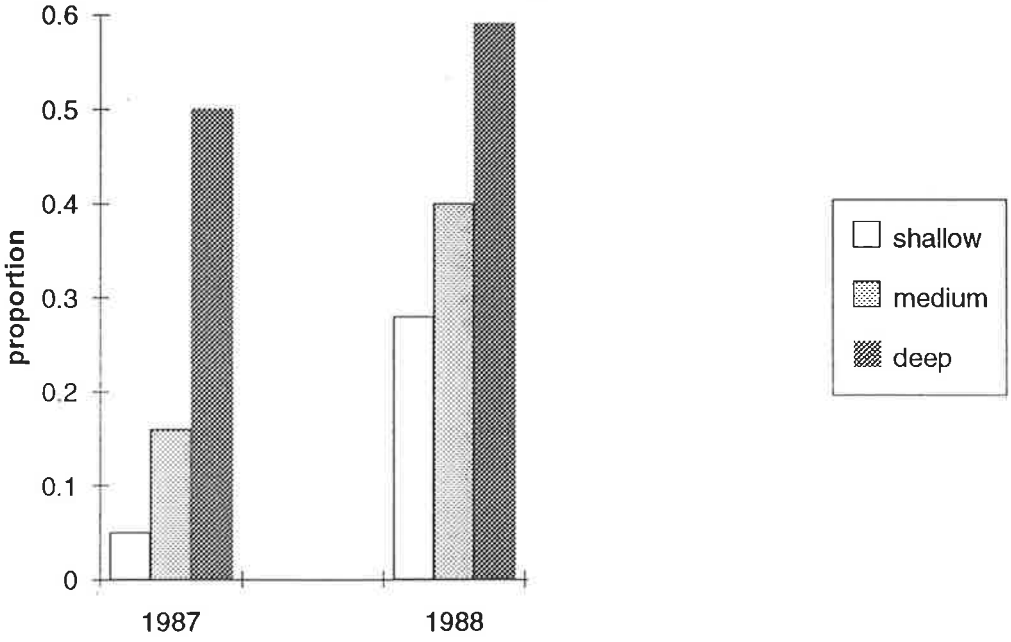
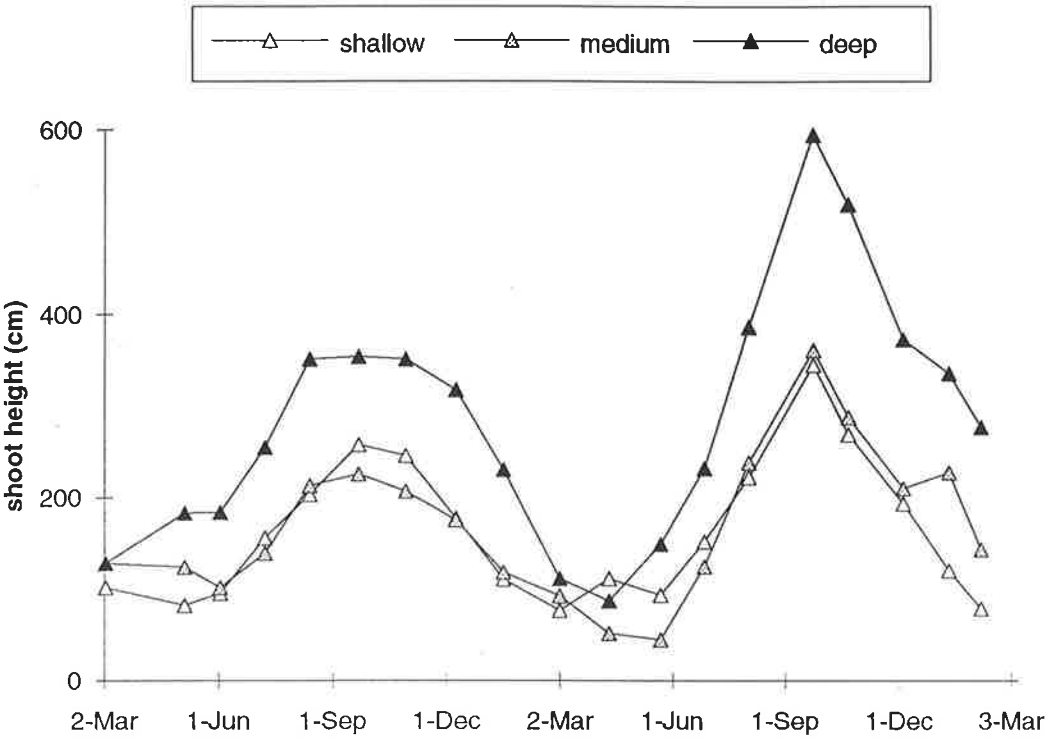


Figure 5.6
The proportion of *Triglochin* shoots that flowered in 1987 and 1988 at three elevations in Hacks Lagoon.



record no. season	2 aut	4 win	7 spr	9 sum	11 aut	13 win	16 spr	18 sum
between depths	***	***	***	***	***	***	***	***
D v S & M	***	***	***	***	***	***	***	***
S v M	ns	ns	ns	ns	ns	ns	ns	***

Figure 5.7
Mean height of *Triglochin* shoots at three elevations (shallow (S), medium (M), deep (D)) over 2 years. Significance levels of 1-way AOV's with planned comparisons are shown for records which represent the four seasons. (***=P<0.001, ns=P>0.05)

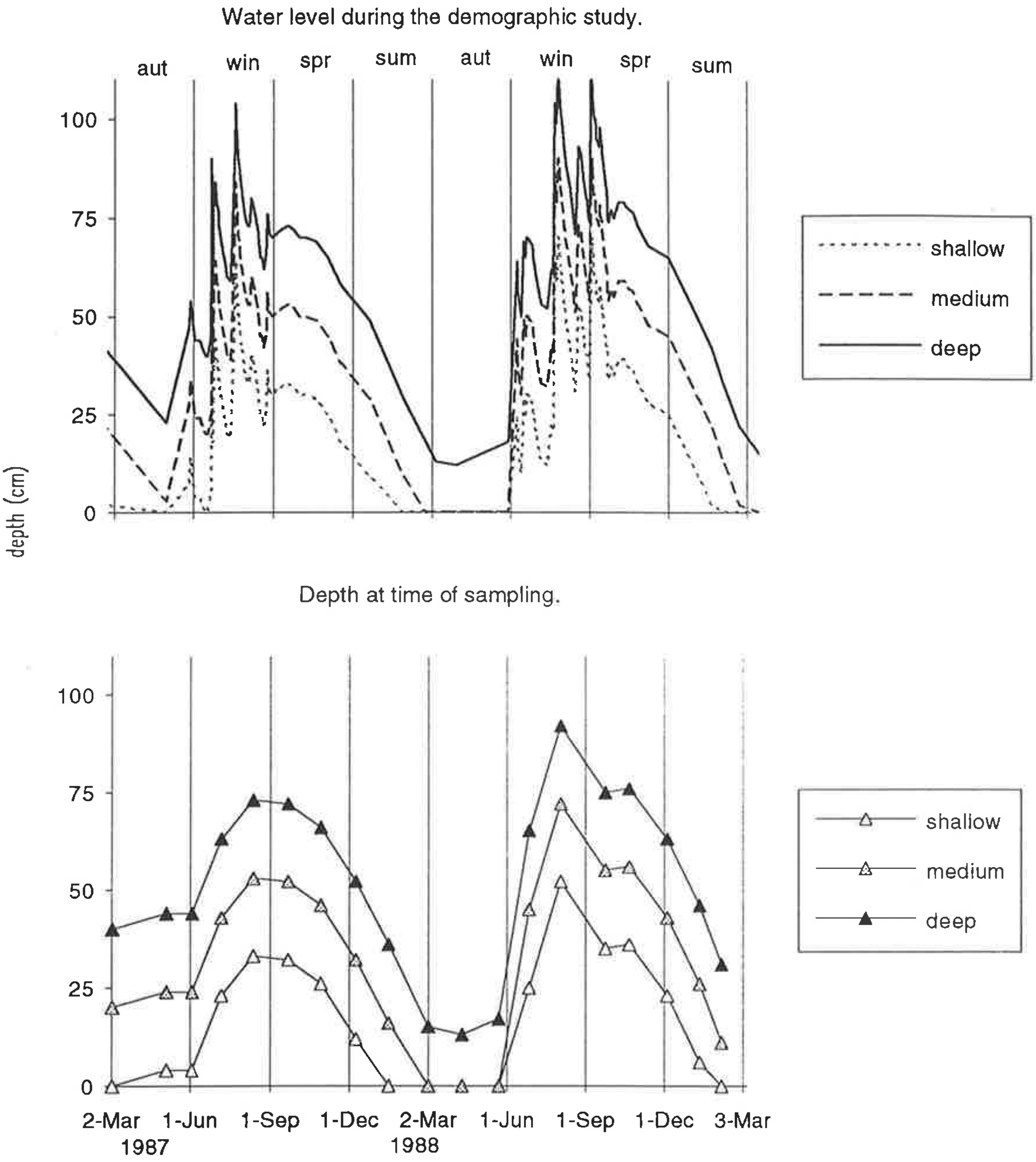
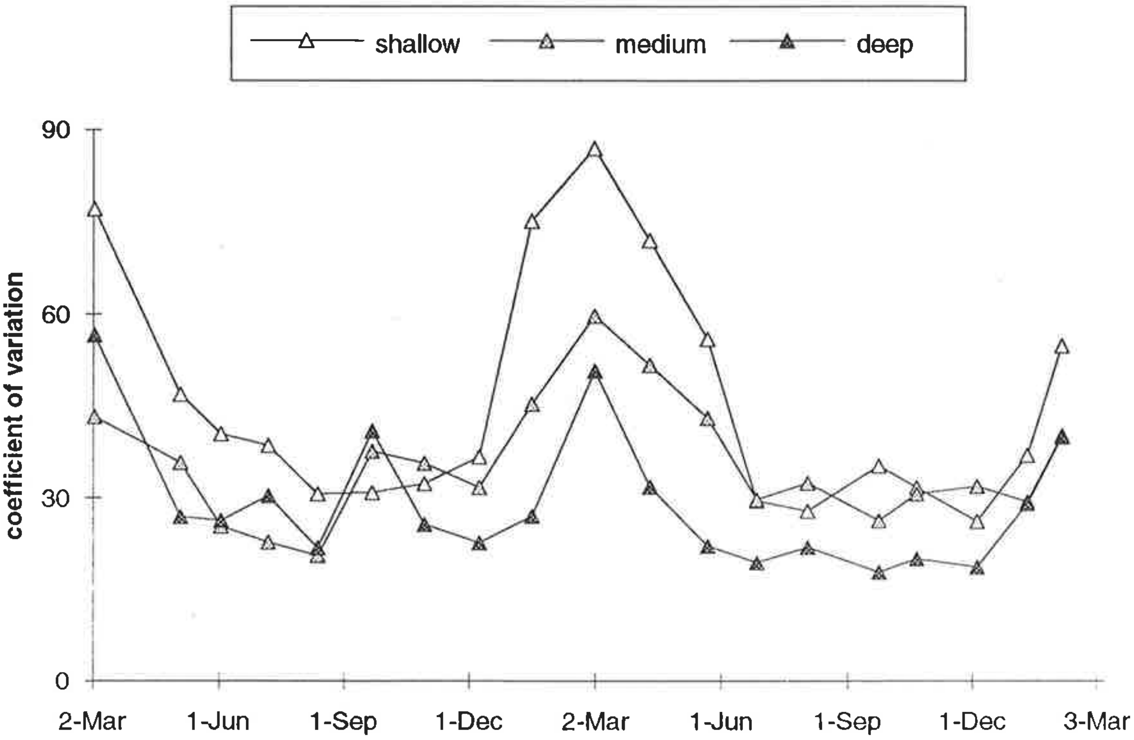
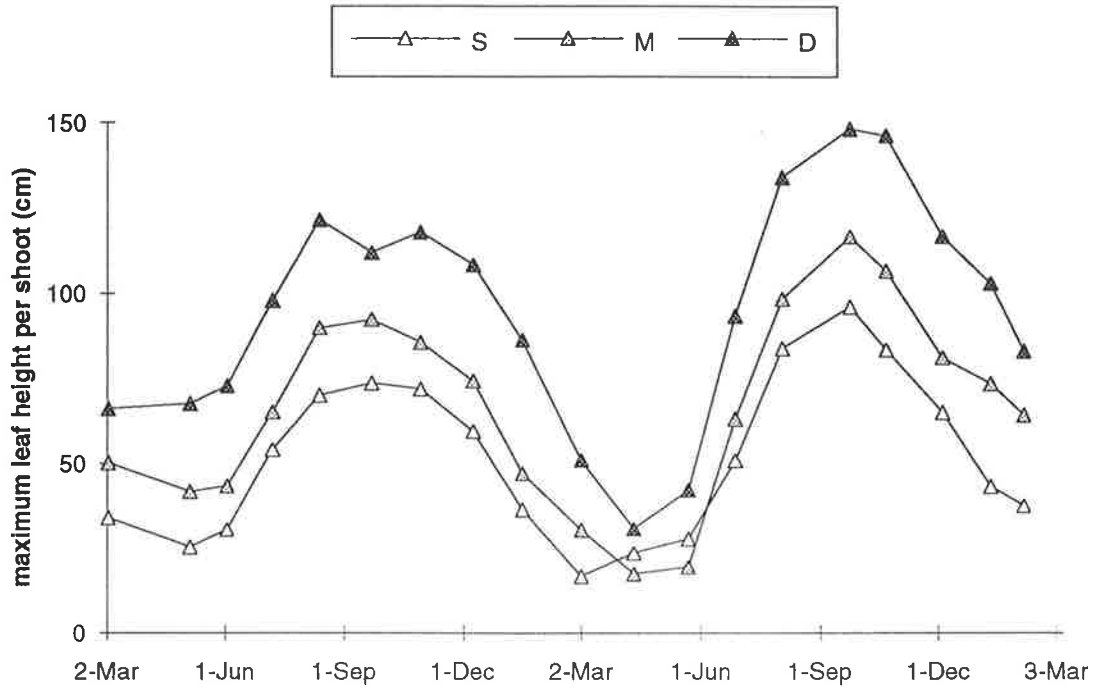


Figure 5.8
The water level and the depth at time of sampling, during the demographic study of *Triglochin* in Hacks Lagoon. Grid lines demarcate the seasons.



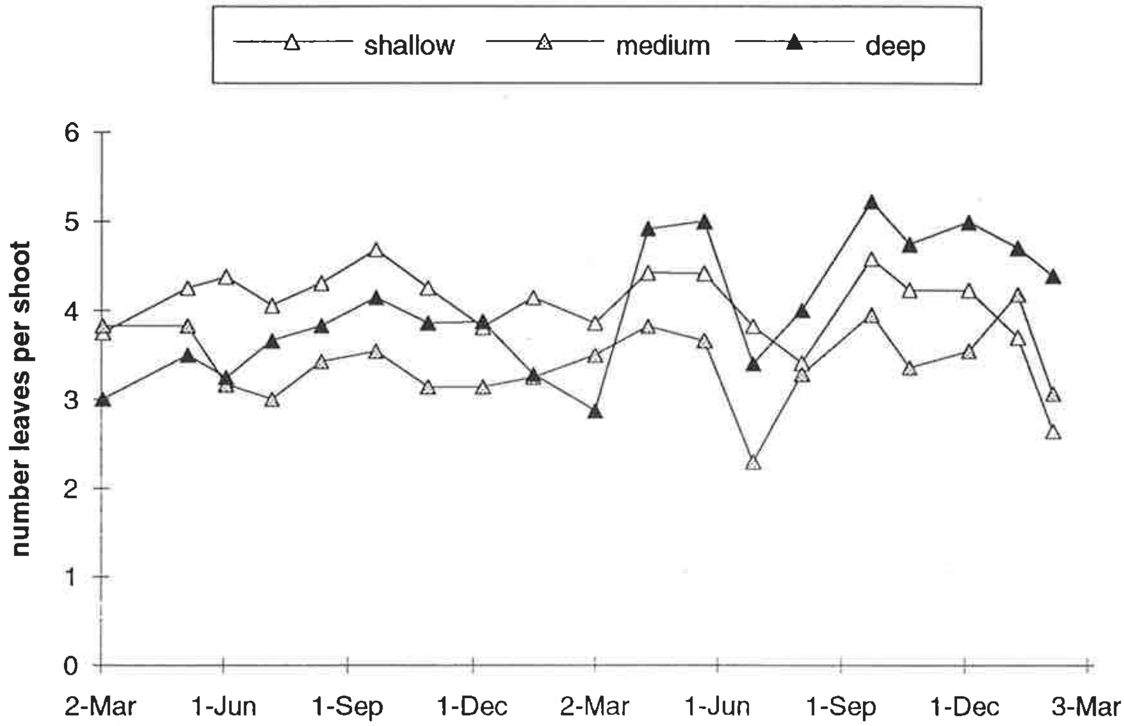
	range	mean (sd)	n
shallow	26.2 - 86.9	45.6 (19.1)	16-17
medium	20.5 - 59.8	35.4 (10.0)	6-46
deep	17.8 - 56.6	28.9 (10.9)	4-26

Figure 5.9
The coefficient of variation for *Triglochin* shoot heights in populations at three elevations (shallow, medium, deep) . The range and mean for each elevation are shown below.



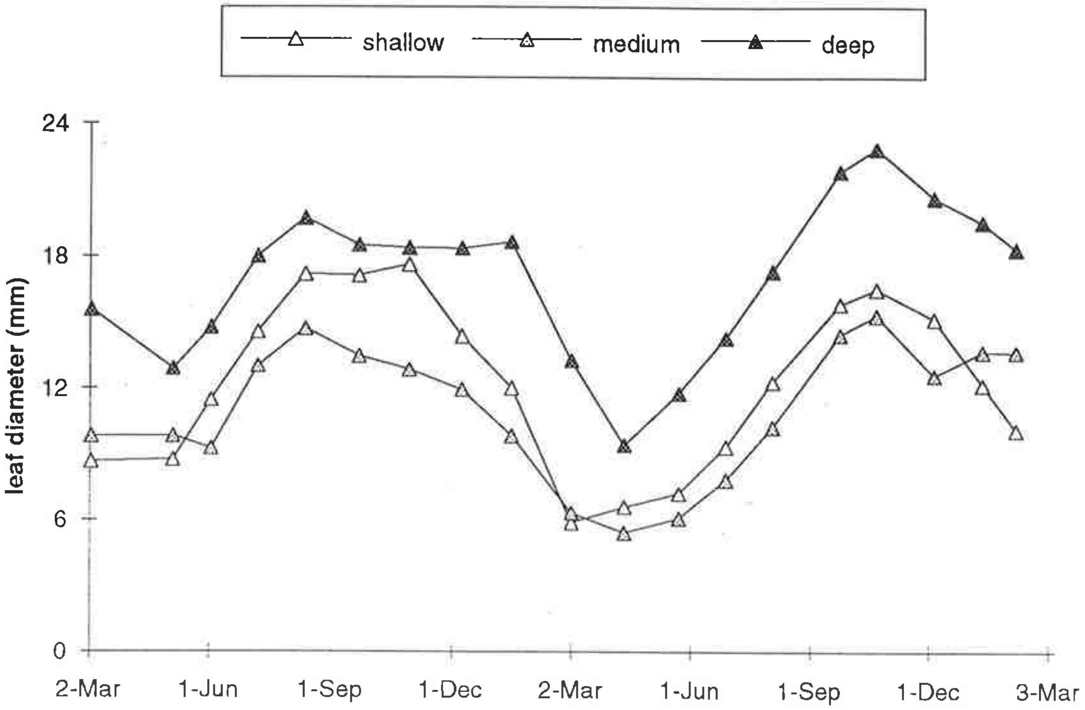
record no.	2	4	7	9	11	13	16	18
season	aut	win	spr	sum	aut	win	spr	sum
between depths	***	***	***	***	***	***	***	***
D v S & M	***	***	***	***	***	***	***	***
S v M	***	***	***	*	ns	***	***	***

Figure 5.10
Mean height of the tallest leaf per *Triglochin* shoot at three elevations (shallow (S), medium (M), deep (D)), over 2 years. Significance levels of 1-way AOV's with planned comparisons are shown for records which represent the four seasons. (***=P<0.001, *=P<0.05, ns=P>0.05)



	range	n
shallow	2.6 - 4.7	7-17
medium	2.3 - 4.2	6-58
deep	2.9 - 5.2	4-15

Figure 5.11
The mean number of leaves per *Triglochin* shoot at three elevations, over 2 years. The range of mean values at each site are shown below.



record no. season	2 aut	4 win	7 spr	9 sum	11 aut	13 win	16 spr	18 sum
between depths	***	ns	***	***	***	***	***	***
D v S & M	***	ns	ns	***	***	***	**	***
S v M	ns	ns	***	ns	ns	ns	ns	ns

Figure 5.12
The mean diameter of the tallest leaf per *Triglochin* shoot at three elevations (shallow (S), medium (M), deep (D)), over 2 years. Significance levels of 1-way AOV's with planned comparisons are shown for records which represent the four seasons. (***=P<0.001, **=P<0.025, ns=P>0.05)

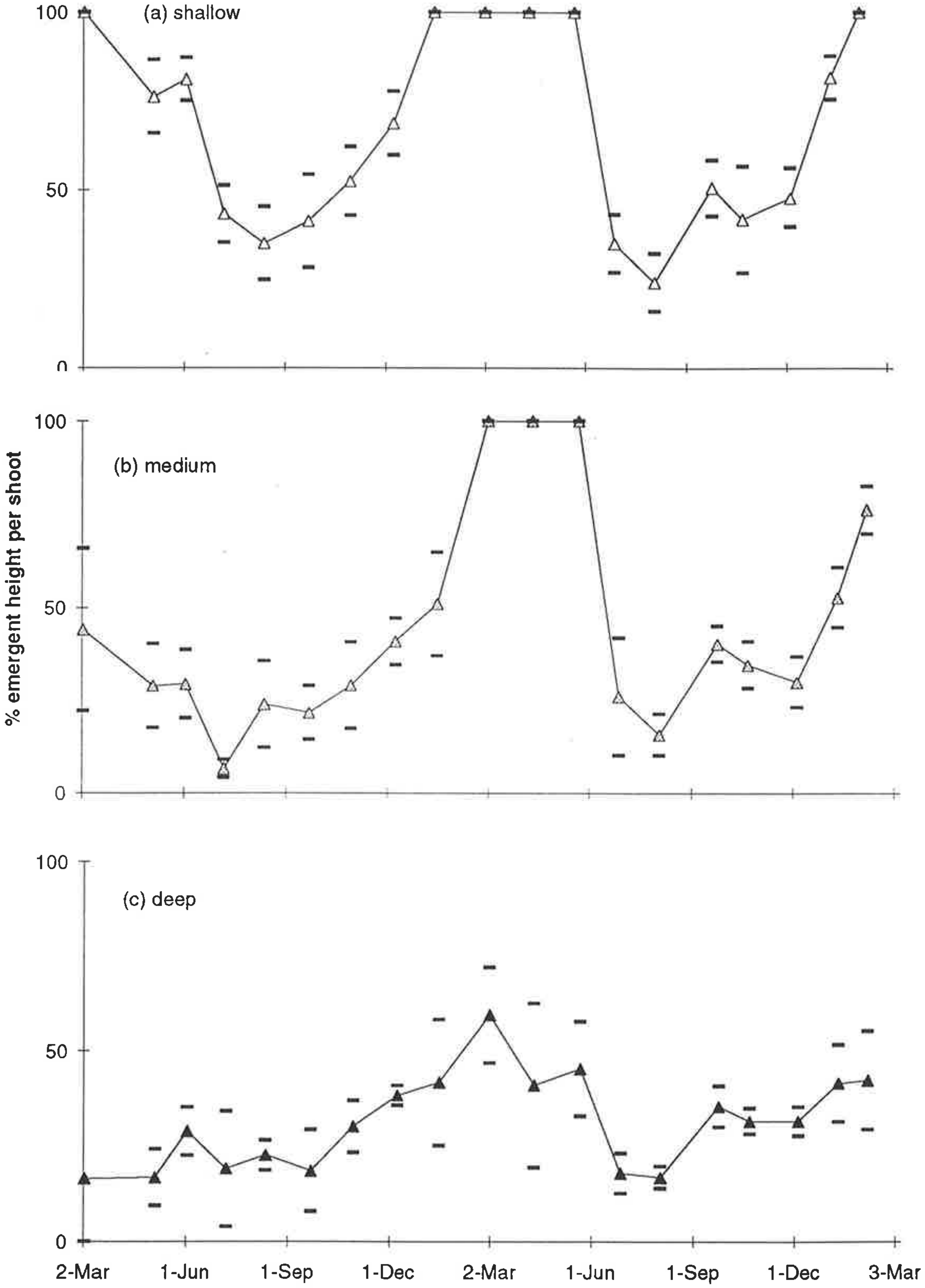
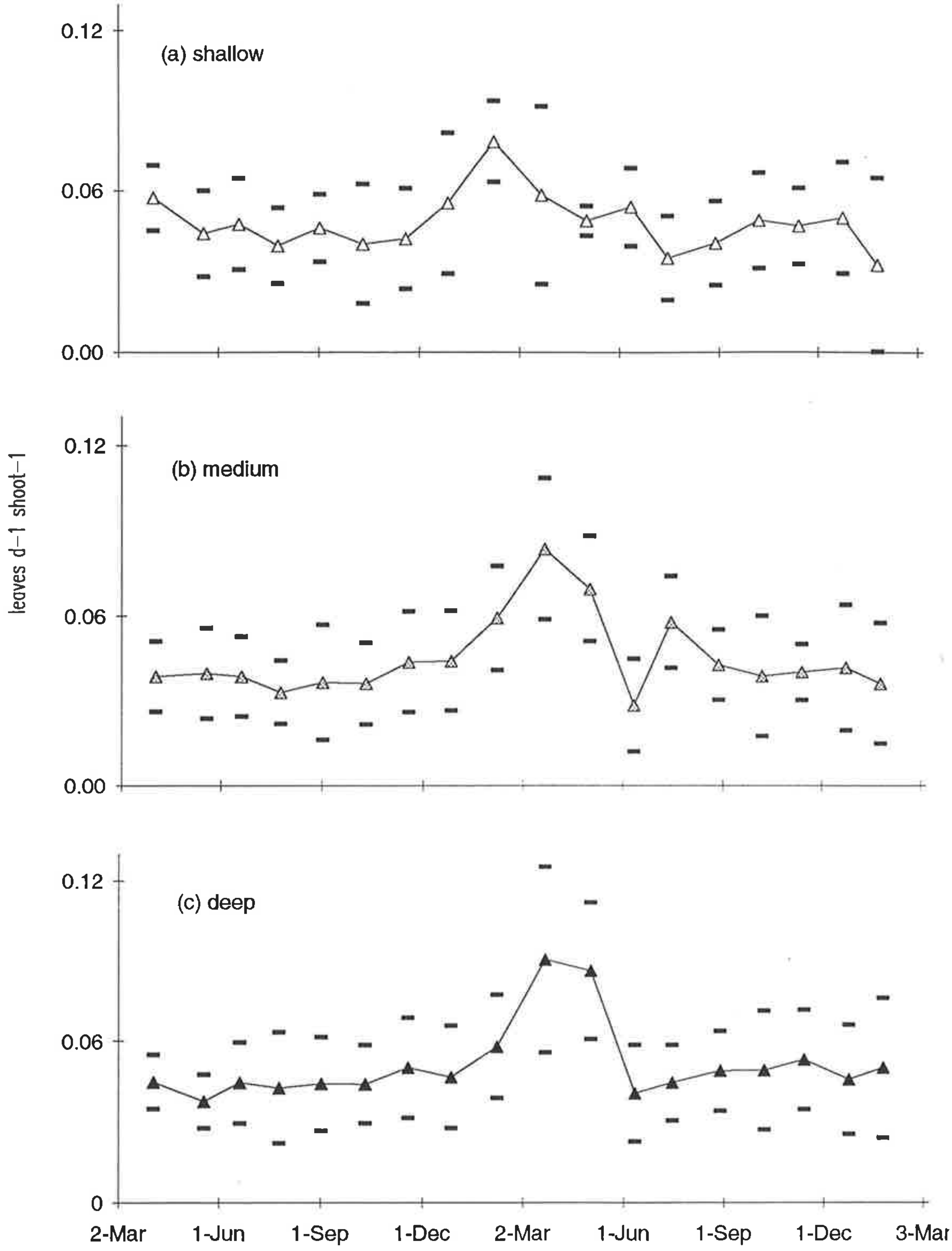


Figure 5.13
The percent emergent height (mean ± sd) of *Triglochin* shoots at (a) shallow, (b) medium and (c) deep elevations, over 2 years.



record no.	1	4	6	8	10	14	16	18
season	aut	win	spr	sum	aut	win	spr	sum
between depths	***	ns	ns	ns	*	ns	ns	ns
S v D & M	ns	ns	ns	ns	***	ns	ns	ns
D v M	ns	ns	ns	ns	ns	ns	ns	ns

Figure 5.14
The leaf recruitment rates (leaves d-1 shoot-1; mean ± sd) of *Triglochin* at three elevations (shallow (S), medium (M), deep(D)), over 2 years. Significance levels of 1-way AOV's are shown for records which represent the four seasons. (***=P<0.001, *=P<0.05, ns=P>0.05)

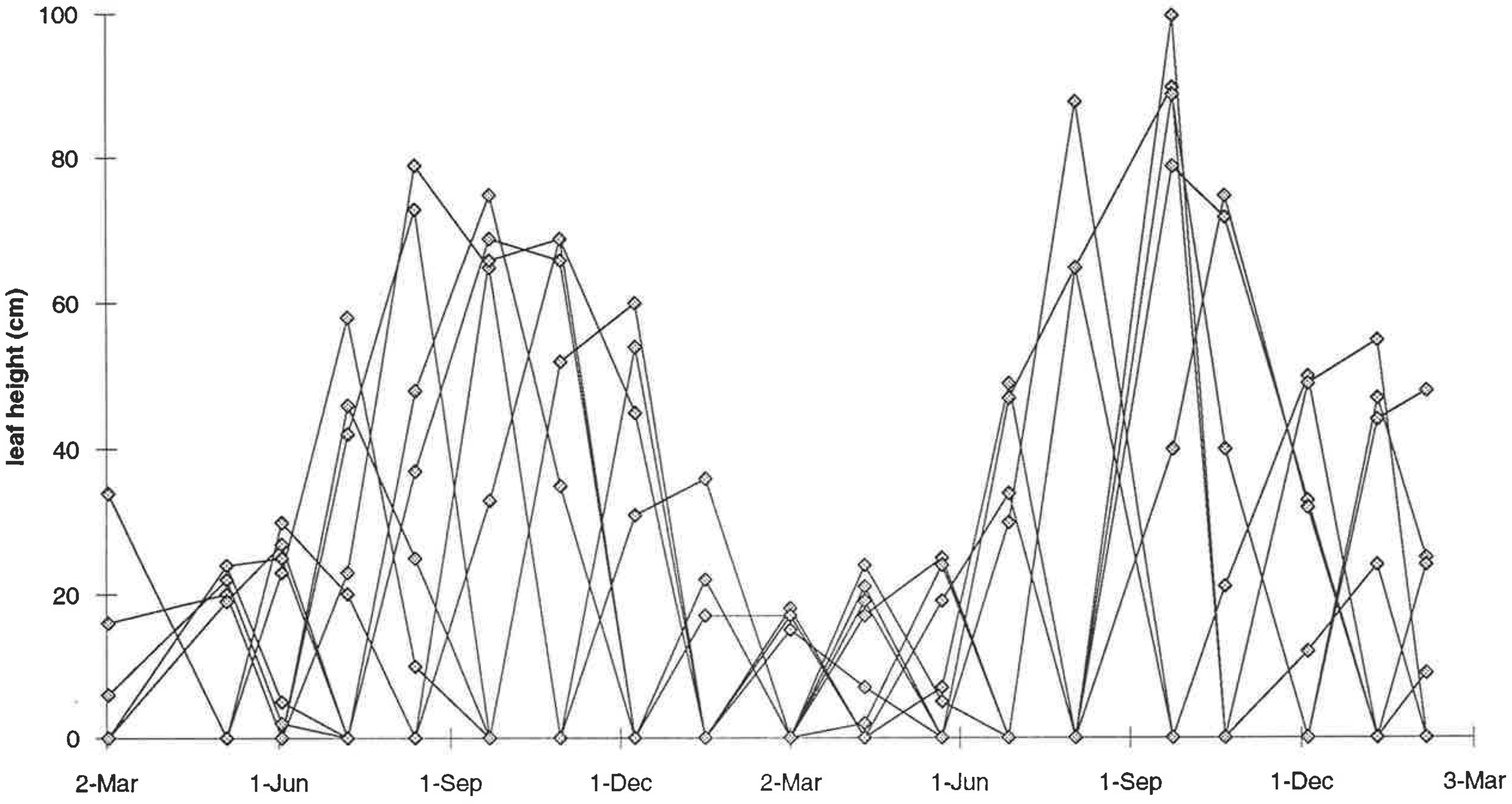


Figure 5.15

The pattern of leaf growth within a single *Triglochin* shoot at the shallowest elevation. Symbols represent measurements and lines extrapolated from, or to the x axis, represent leaf natality and mortality, respectively.

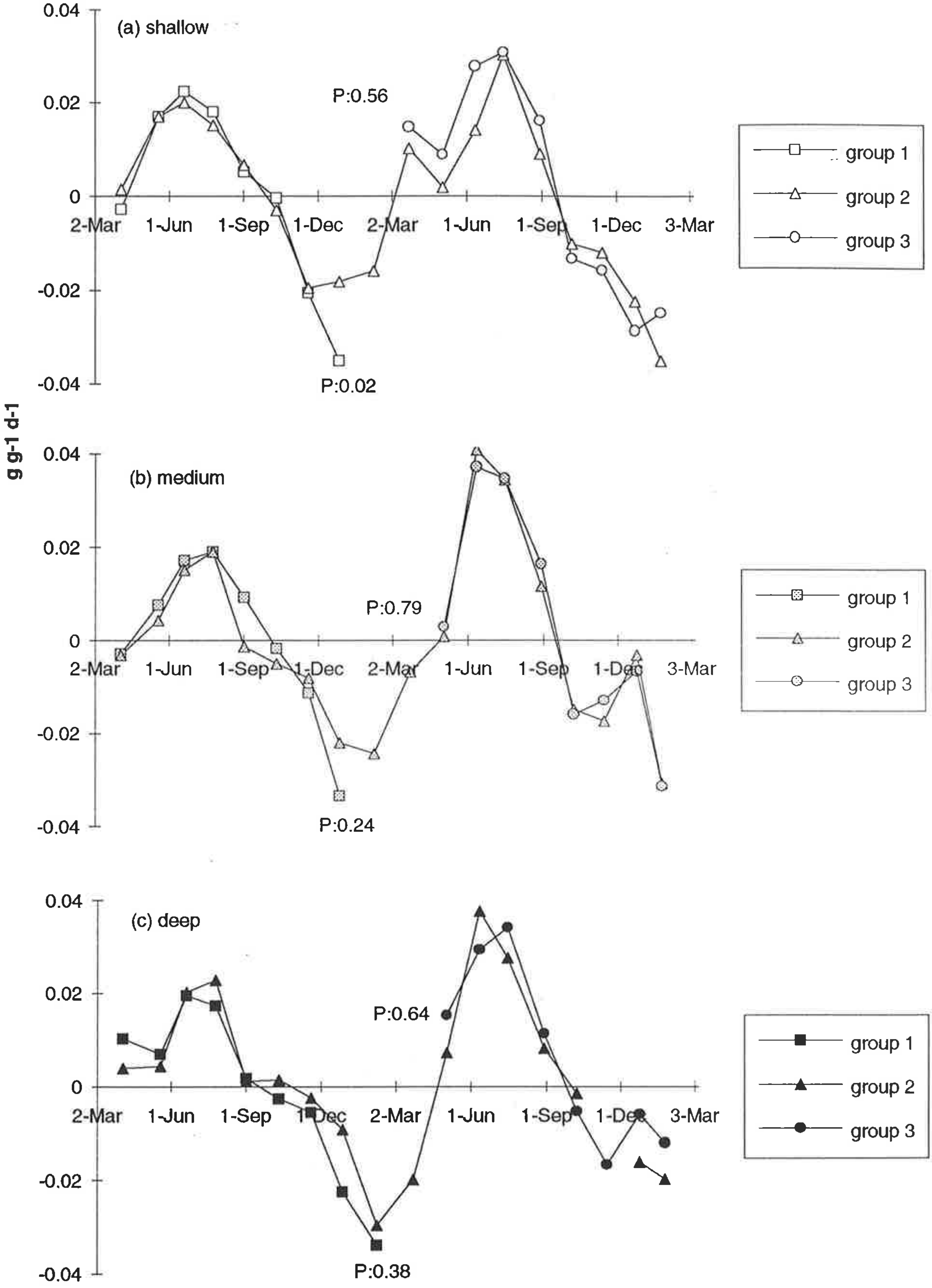
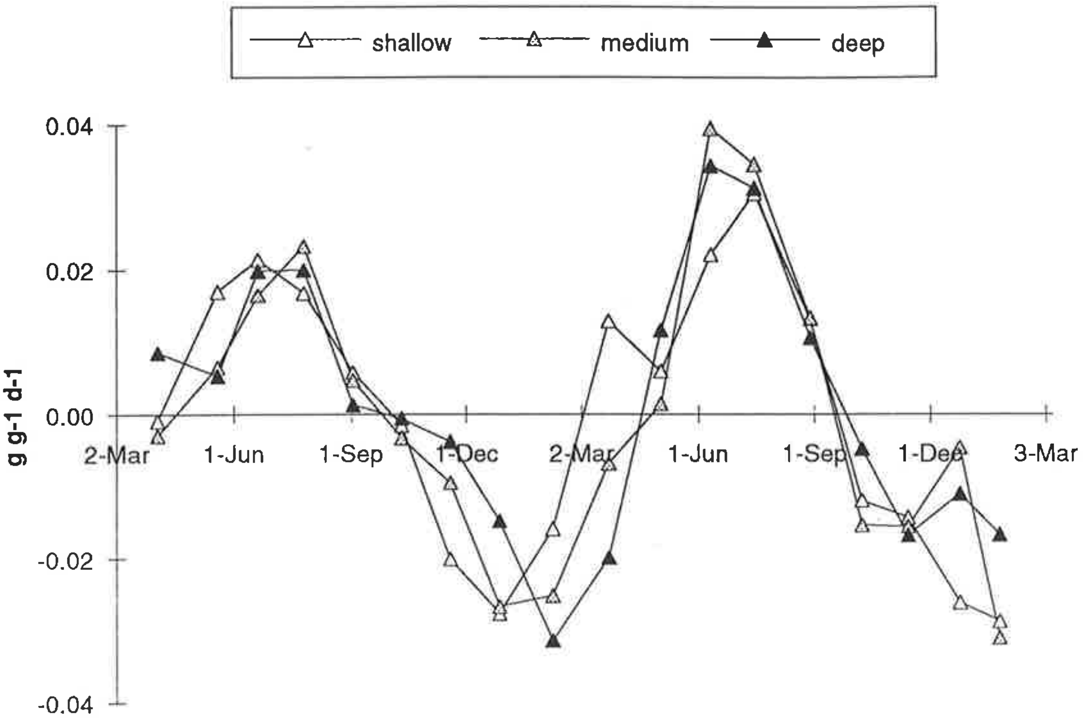


Figure 5.16
The relative growth rates (g g-1 d-1) of the three groups of *Triglochin* shoots at each elevation. Significance levels of 1-way AOV's comparing groups prior to their death or after their emergence are shown (e.g. (a) shallow, record 8 & 10: (b) medium, record 8 & 11; (c) deep, record 9 & 11).



record no.	2	4	6	8	10	13	16	18
season	aut	win	spr	sum	aut	win	spr	sum
between depths	*	ns	ns	ns	***	ns	ns	ns
S v D & M	***	ns	ns	ns	***	ns	ns	ns
M v D	ns	ns	ns	ns	ns	ns	ns	ns

Figure 5.17
The mean relative growth rate (g g-1 d-1) of *Triglochin* shoots from three elevations (shallow (S), medium (M), deep (D)), over 2 years. Significance levels of 1-way AOV's with planned comparisons are shown for records which represent the four seasons.(***=$P<0.001$, *=$P<0.05$, ns=$P>0.05$)

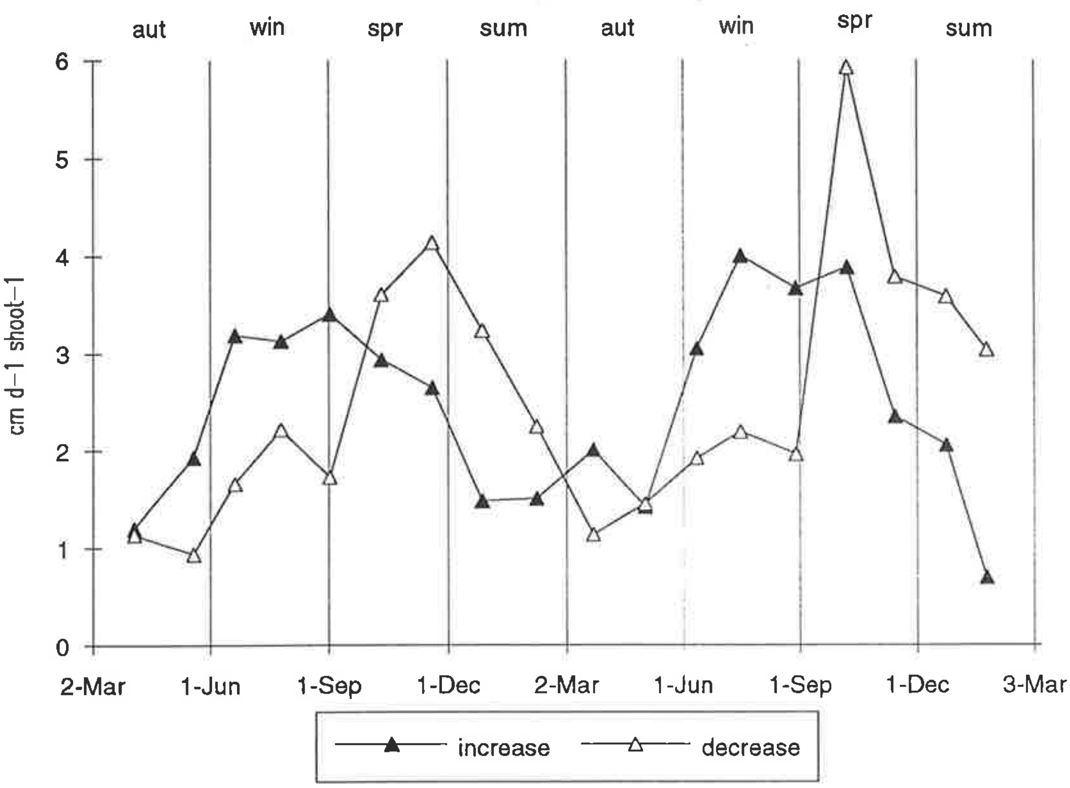


Figure 5.18
The gross rate of increase and decrease (mean, cm d-1 shoot-1) in the height of *Triglochin* shoots at the shallow elevation, over 2 years.

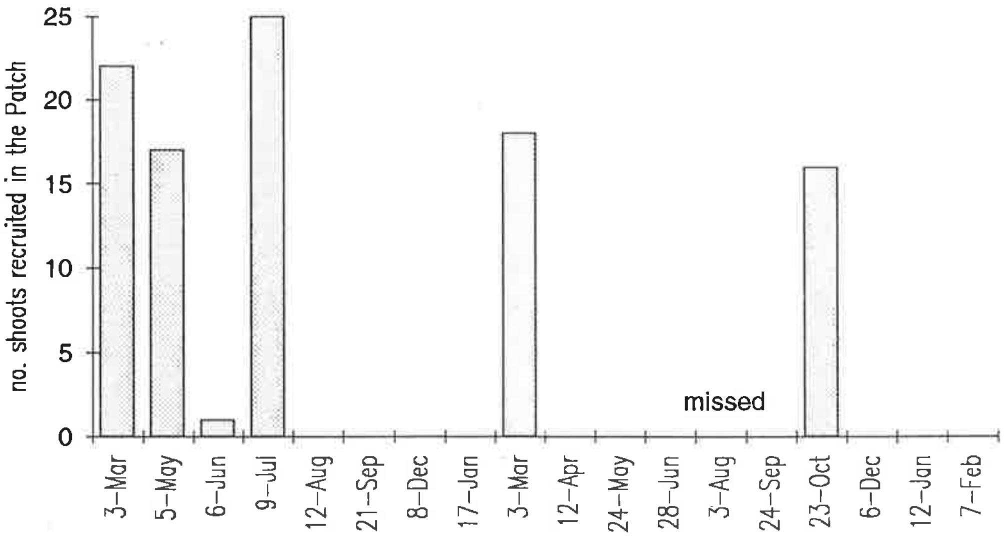


Figure 5.19

The number of *Baumea* shoots recorded at the start of the study at the Patch and the recruitment of new shoots thereafter. Three records were missed during high winter water levels in 1988.

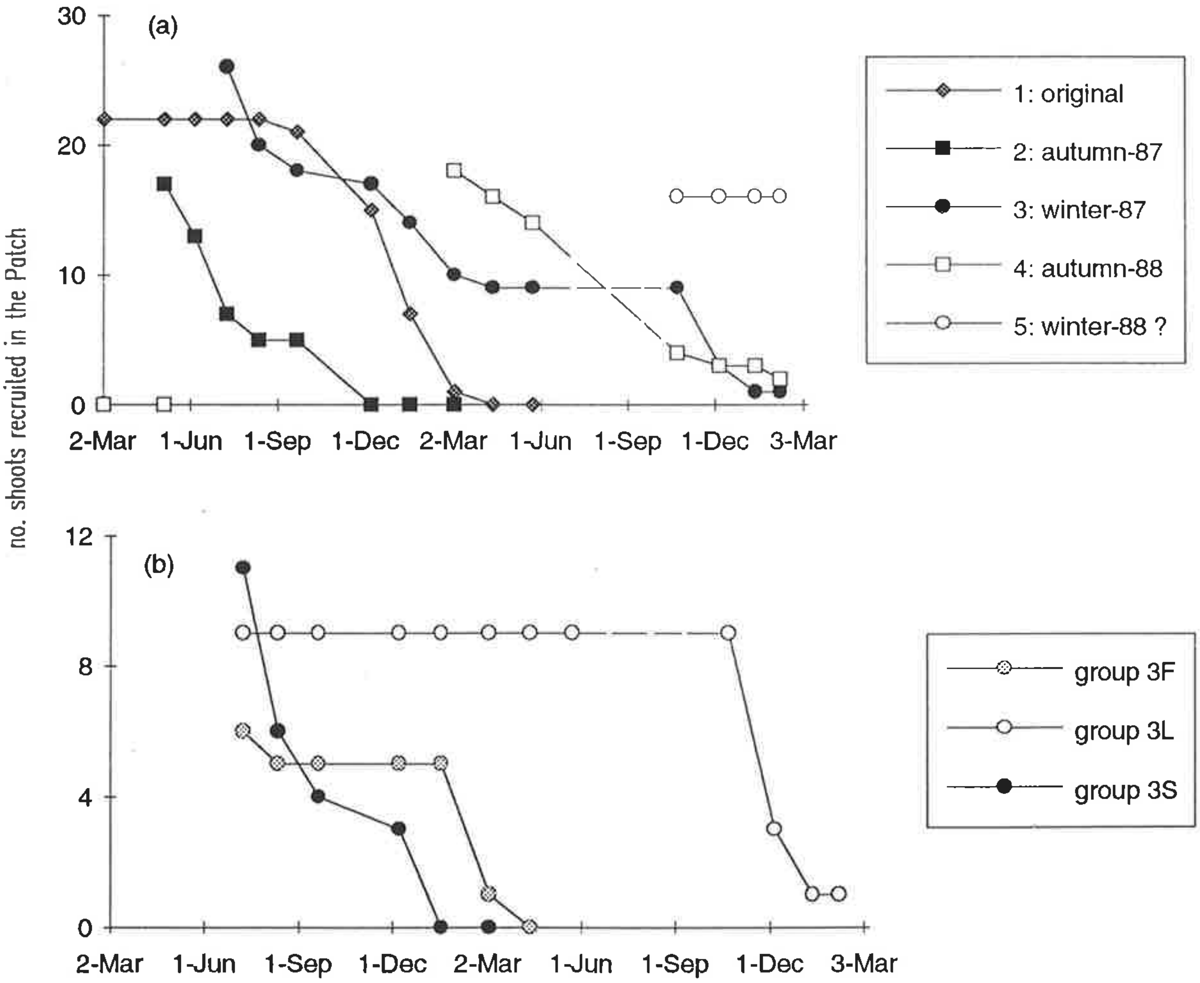


Figure 5.20

Depletion and survivorship curves for (a) all groups of *Baumea* shoots recorded at the Patch, and (b) group 3 divided into shoots that flowered (3F), long-lived (3L) and short-lived shoots (3S). Where records were missed, lines are dotted.

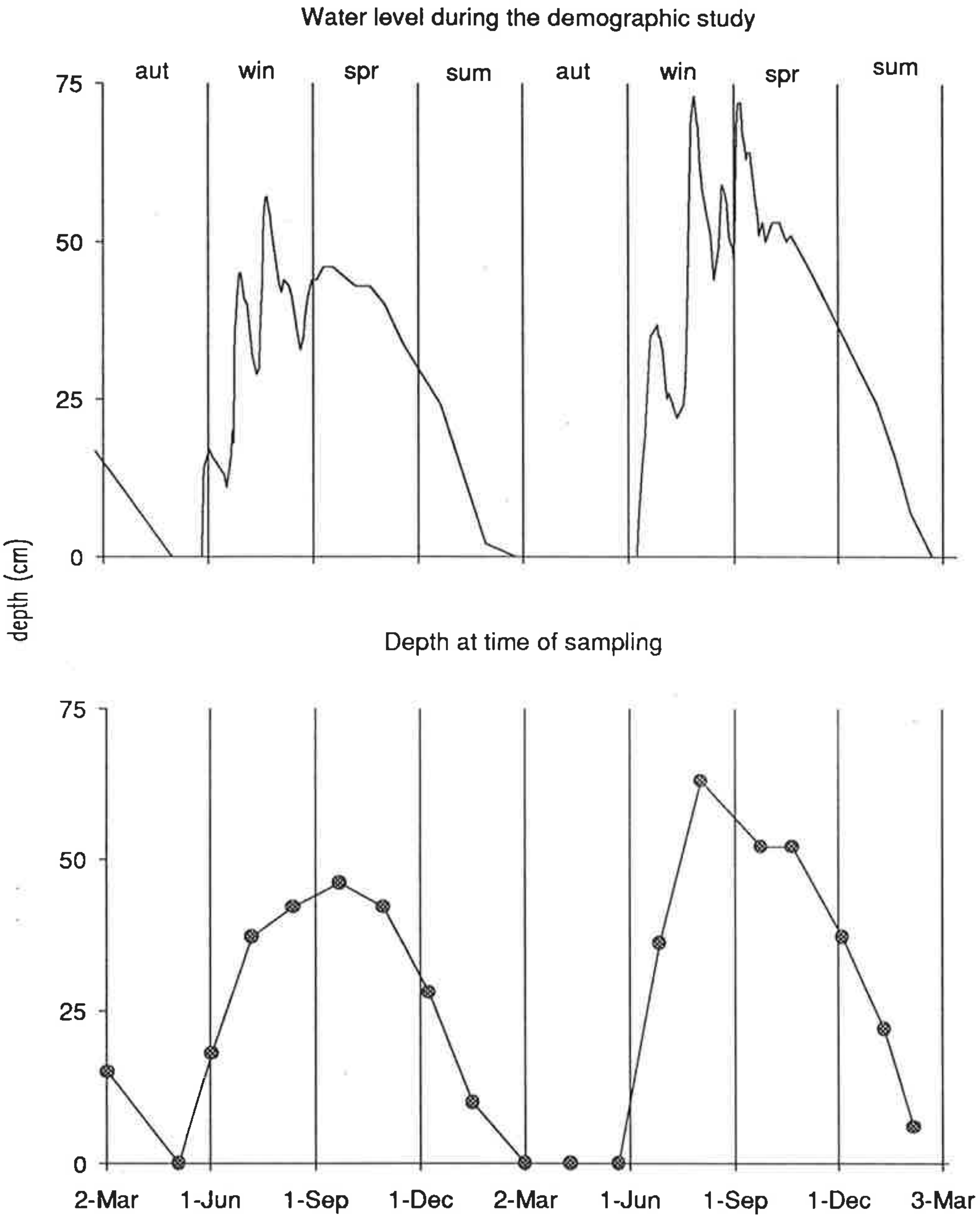


Figure 5.21
The water level and depth at time of sampling, during the demographic study of *Baumea* in the Central-Western basin. Grid lines demarcate the seasons.

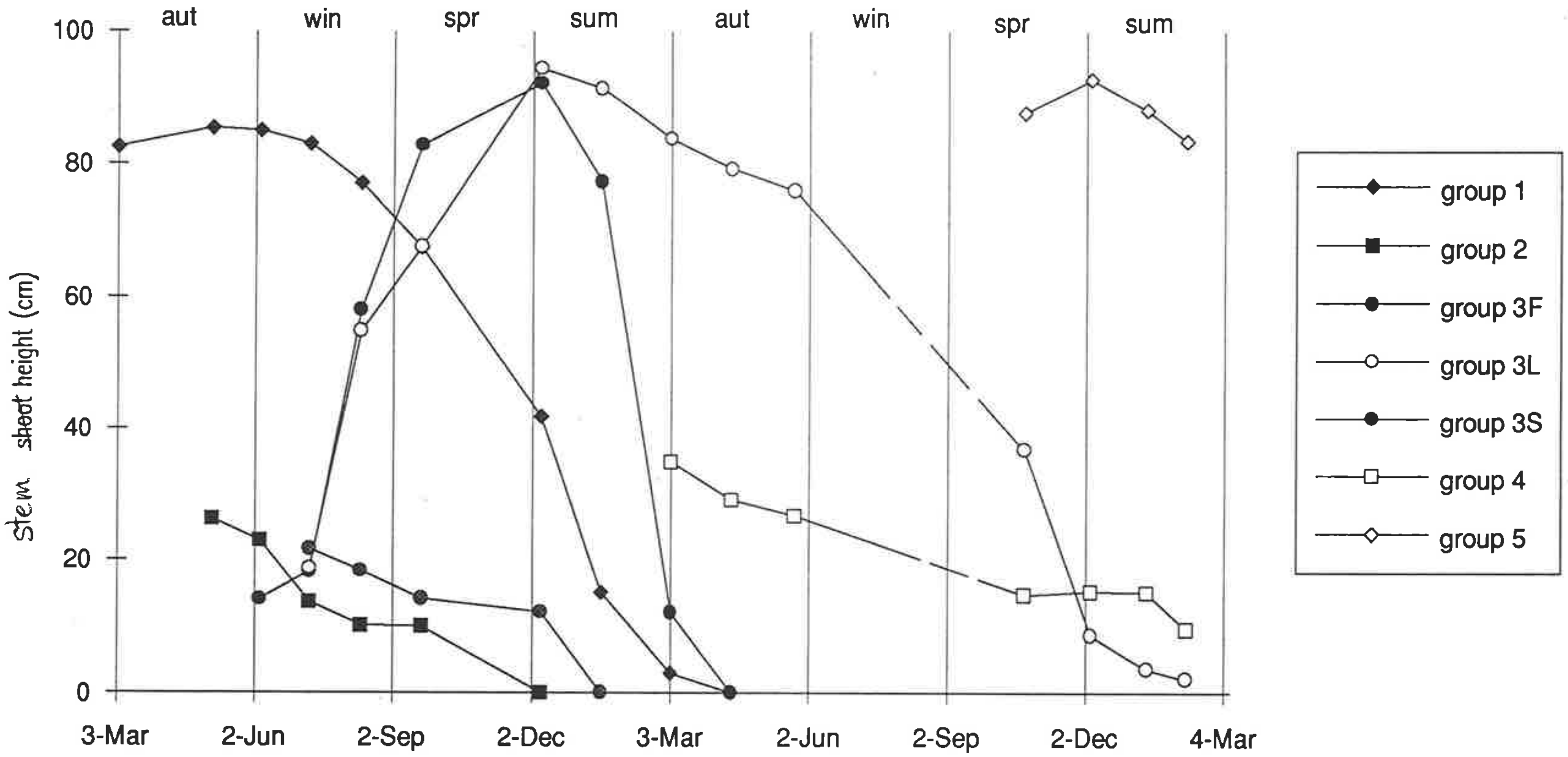


Figure 5.22
The mean maximum height of *Baumea* stems for each recorded group of shoots at the Patch. Gridlines demarcate the seasons and dotted lines indicate where records were missed.

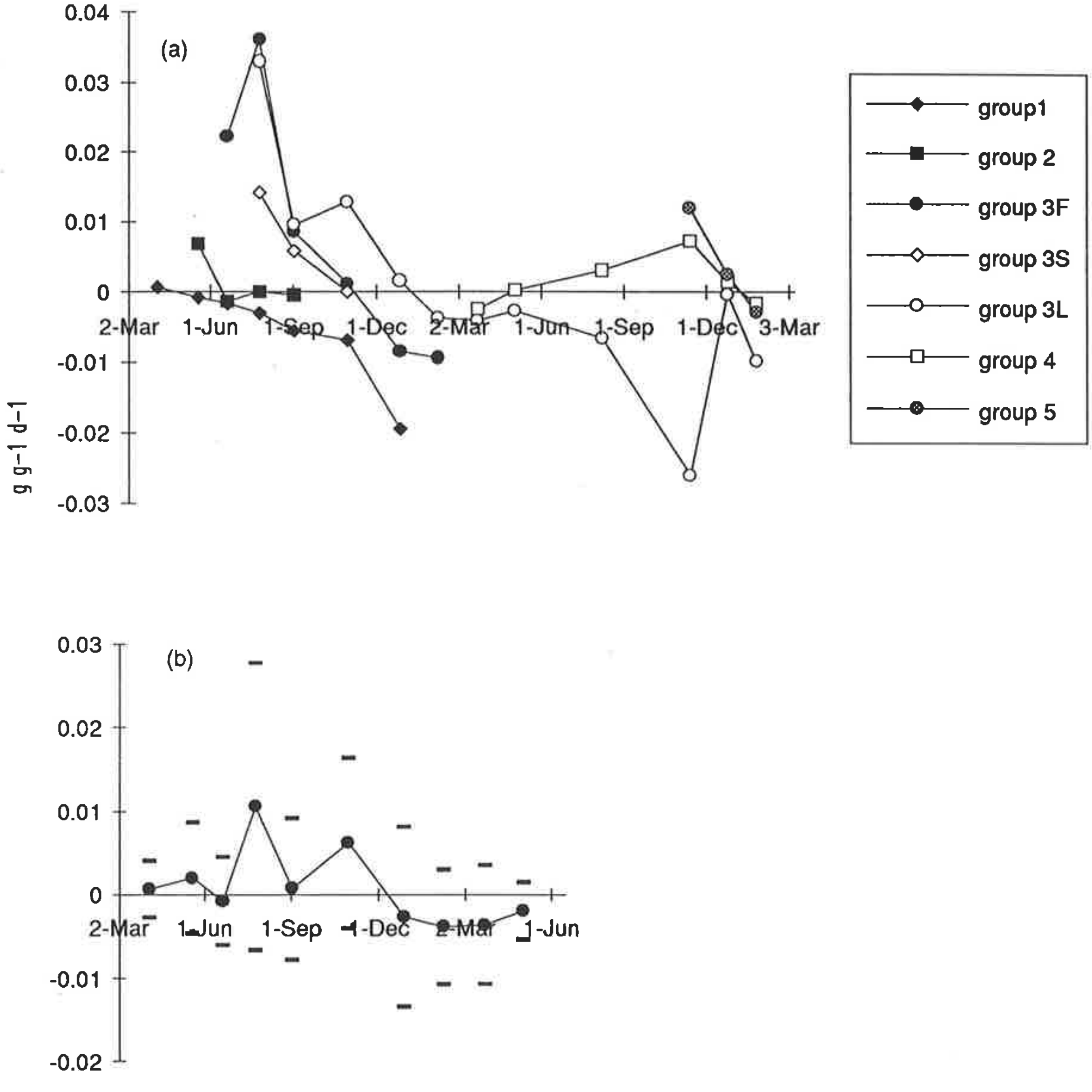


Figure 5.23
Relative growth rates (g g-1 d-1) of *Baumea* shoots: (a) mean value for each shoot cohort and (b) combined shoot data (mean ± sd).

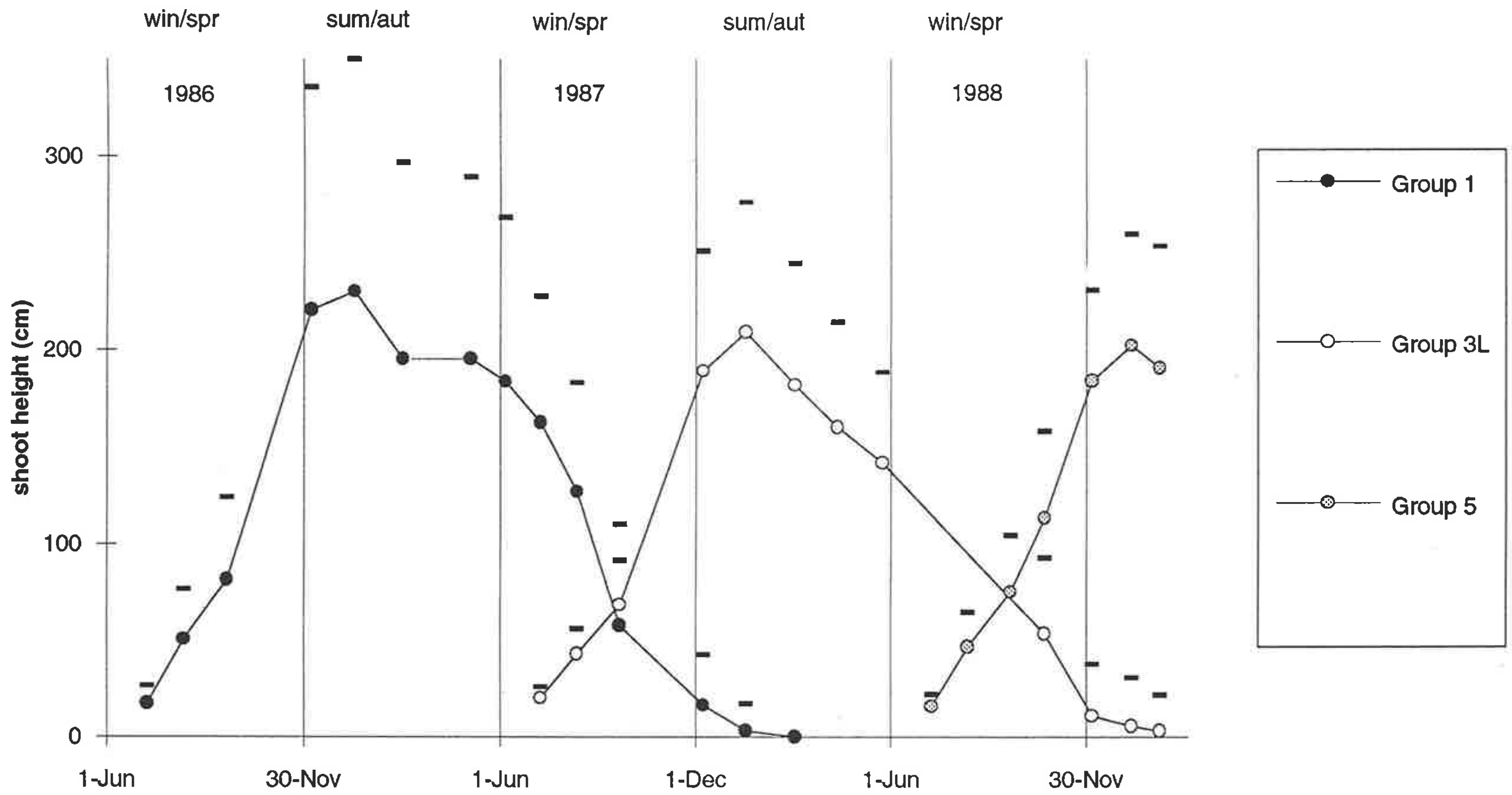


Figure 5.24
The heights (mean +sd) of *Baumea* shoots from groups 1 (original shoots), group 3L (long-lived shoots from win-87 cohort) and group 3 (last recorded group). The first 5 and 3 points for groups 1 and 3, respectively, were calculated from the RGR of group 3 shoots.

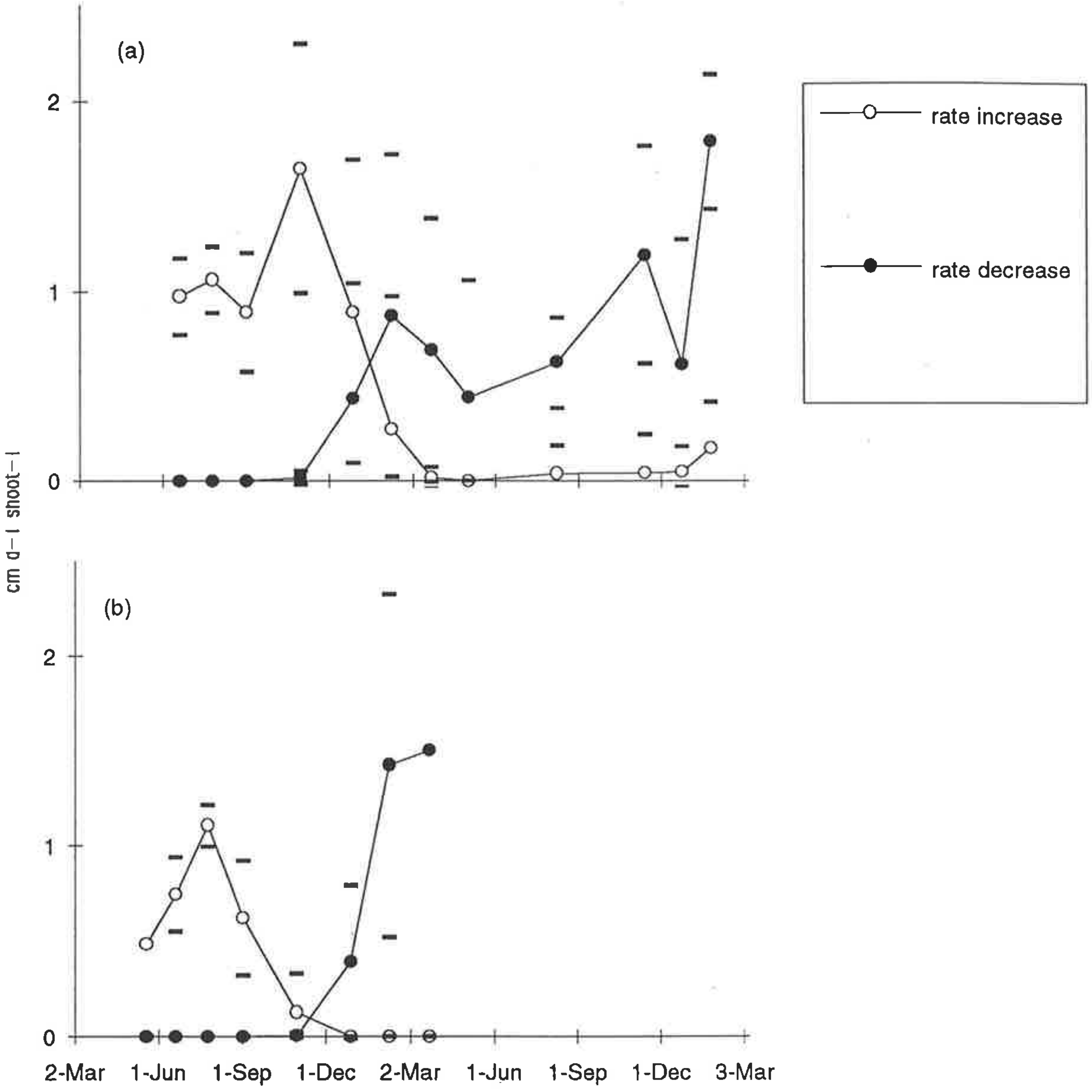


Figure 5.25
The gross rate of increase and decrease (mean ± sd, cm d-1 shoot-1) in the height of *Baumea*'s (a) long-lived shoots and (b) flowering shoots from group 3.

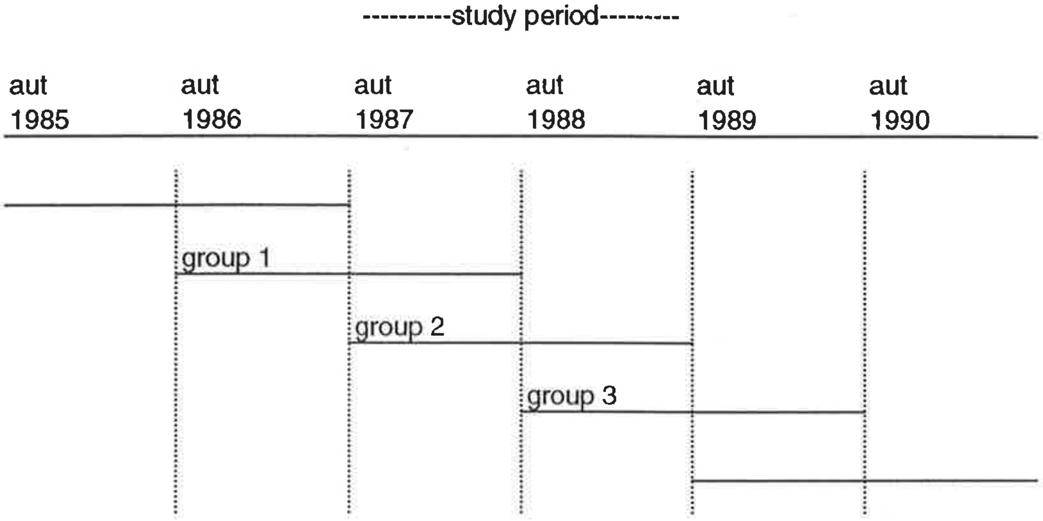


Figure 5.26
The proposed pattern of shoot growth in shallow *Triglochin* populations. Overlapping cohorts would have two year life-spans and simultaneous natality and mortality in late summer/early autumn each year. The study period where populations were monitored is shown. Groups 1 to 3 would represent 3 cohorts.

	1987		1988		1987	1988
	total no. shoots	no. flowered	total no. shoots	no. flowered	proportion that flowered	
shallow						
group 1	10	0	-	-	0	-
group 2	9	1	9	2	0.11	0.22
group 3	-	-	9	3	-	0.33
medium						
group 1	10	3	-	-	0.30	-
group 2	15	1	5	3	0.07	0.60
group 3	-	-	5	1	-	0.20
deep						
group 1	2	1	-	-	0.50	-
group 2	6	3	7	4	0.50	0.57
group 3	-	-	10	6	-	0.60

Table 5.1
The number and proportion of *Triglochin* shoots that flowered in each group of shoots in 1987 and 1988, at the three elevations.

	length of flowering stalk (cm)		length of inflorescence (cm)	
	1987	1988	1987	1988
shallow	69	100	13	14
		98		19
		108		17
		95		20
		116		16
x (sd)		103 (9)		17 (2)
medium	95	120	19	20
		118		18
		100		20
x (sd)		113 (11)		19 (1)
deep	130	154	20	34
	125	148	25	28
	120	145	20	22
	135	160	25	26
		155		15
		146		28
		173		23
		135		25
		155		20
		132		22
		148		28
x (sd)	128 (6)	150 (11)	23 (3)	25 (5)

Table 5.2
The maximum length (cm, mean & sd) of *Triglochin* flowering stalks and inflorescences in 1987 and 1988. at the three elevations.

		flowering		vegetative		significance
	month	x	sd	x	sd	P
shallow	May	48.4	15.1	111.7	50.8	*
	Jun	100.2	38.3	173.0	25.9	***
	Aug	161.0	34.8	248.3	52.0	***
medium	May	67.3	15.6	44.0	19.6	ns
	Jun	174.3	20.2	121.6	30.6	***
	Aug	295.5	58.7	213.9	59.9	ns
deep	May	157.4	21.1	142.1	40.3	ns
	Jun	242.1	44.7	219.9	44.8	ns
	Aug	409.5	94.2	339.4	32.1	ns

Table 5.3
Total shoot height (cm, mean & sd) of flowering and vegetative *Triglochin* shoots at the three elevations in the months leading up to flowering. T-tests were used to test the difference between means. ($P>0.05$ = ns, $P<0.01$ = ***, $P<0.05$ = *)

	season	aut 1987	win	spr	sum		aut 1988	win	spr	sum
x	group 1	121.6	151.4	253.4	53.4	group 2	111.3	215.4	246.7	127.3
sd		89.0	42.2	47.6	43.6		71.1	77.4	114.8	56.5
x	group 2	76.7	162.7	236.9	110.9	group 3	50.7	227.7	284.6	116.1
sd		59.9	81.4	112.5	63.4		15.4	52.7	59.0	37.0
P		0.27	0.72	0.69	0.05		0.02	0.70	0.38	0.63

Table 5.4
Comparison of the mid season *Triglochin* shoot heights (cm, mean & sd) of group 1 versus group 2 in 1987 and group 2 versus group 3 in 1988. The significance (P) of two-sample t-tests for each comparison are given.

	season	aut 1987	win	spr	sum		aut 1988	win	spr	sum
x	group 1	4.56	5.44	3.00	0.33	group 2	6.11	3.00	3.44	2.44
sd		0.88	0.53	1.00	0.71		1.54	1.22	0.88	1.13
x	group 2	4.86	4.75	3.33	5.56	group 3	7.10	3.70	3.40	2.90
sd		0.38	1.16	1.22	1.01		1.20	1.06	0.70	1.10
P		0.41	0.13	0.54	0.00		0.13	0.20	0.90	0.39

Table 5.5
Comparison of the number of leaves (mean & sd) recruited per *Triglochin* shoot within each season: group1 versus group 2 in 1987 and group 2 versus group 3 in 1988. The significance (P) of two-sample t-tests for each comparison are given.

date	1987								1988									1989
	Apr	May	Jun	Jul	Sep	Oct	Nov	Dec	Feb	Mar	May	Jun	Jul	Aug	Oct	Nov	Dec	Jan
elevation																		
shallow	18.3	25.0	24.0	28.4	23.9	26.1	25.9	23.5	13.4	19.7	20.6	20.2	30.0	26.0	22.8	23.9	24.0	20.1
medium	29.2	26.1	28.8	32.6	32.9	31.3	26.1	27.0	18.6	12.8	15.6	32.1	19.0	26.0	25.8	27.1	25.3	24.1
deep	22.3	27.2	28.0	27.3	26.3	26.0	22.4	24.5	19.3	9.6	12.0	27.2	27.0	19.5	22.2	17.7	23.1	19.5

Table 5.6
Triglochin's mean plastochrone interval (days leaf-1 shoot-1) at the three elevations throughout the study. As the inverse of leaf recruitment rates, the same significance levels in Figure 5.14 apply.

(a)

group no.	1	2	3	4	5
season emerged	win-86	aut-87	win-87	aut-88	win-88
number of shoots sampled	22	17	26	18	16
Life-history					
survivorship (high @ 100%, medium @ 50%, low <10 %)	high	low	medium	low	
mean maximum life-span (months)	18	3	17	3	
range of life-spans (months)		1 - 7	1 - 19	1 - 12	
Size					
maximum shoot height (cm)	208 (101)	30 (12)	189 (120)	36 (13)	257 (80)
range of shoot heights (cm)	98 - 396	14 - 63	17 - 527	17 - 58	148 - 387
maximum shoot biomass (g)	3.21 (1.52)	0.55 (0.17)	3.12 (1.26)	0.55 (0.20)	3.27 (0.94)
mean no. stems/shoot	2.8 (0.9)	1.1 (0.2)	2.4 (1.3)	1.0 (0.0)	3.0 (0.6)
range of no. stems/shoot	2 - 4	1 - 2	1 - 6	1 - 3	2 - 3
Growth					
maximum relative growth rate (mg g-1 d-1)	0.6 (3.3)	6.7 (8.4)	28.1 (11.7)	7.2 (9.1)	11.8 (5.6)

(b)

flowered (3F)	long-lived (3L)	short-lived (3S)
win-87	win-87	win-87
5	10	11
high	high	low
8	17	3
8 - 9	15 - 19	1 - 6
93 (25)	254 (84)	31 (11)
54 - 118	108 - 362	17 - 53
1.50 (0.43)	3.38 (1.09)	0.65 (0.23)
1.0 (0.0)	3.1 (1.0)	1.0 (0.0)
1	1 - 6	1
36.0 (5.5)	33.0 (6.6)	14.1 (9.4)

Table 5.7
Summary of the major demographic characteristics (range, mean & sd) of groups of *Baumea* shoots at the Patch: (a) groups 1 to 5 and (b) group 3 divided into shoots that flowered (3F), and short (3S) and long-lived shoots (3L).

		Triglochin			***Baumea***	
		depth			cohort	
		shallow	medium	deep	aut	win
		biomass production				
1987	x	2.36	2.64	3.07	1.00	1.08
	sd	0.38	0.24	0.39	0.00	0.10
1988	x	1.92	2.26	2.34		
	sd	0.30	0.11	0.34		
		leaf production				
1987	x	6.74	7.24	7.44	1.00	1.00
1988	x	7.35	8.43	8.40		

Table 5.8
The production to biomass (maximum) ratios for biomass produced per shoot and number of leaves or stems produced per shoot. *Triglochin* shoots were from shallow, medium and deep sites and *Baumea* shoots were the long-lived shoots from autumn and winter cohorts

CHAPTER SIX: SPECIES INTERACTION: DEMOGRAPHY AND RESOURCE ALLOCATION

Figures 6.1 - 6.31

Tables 6.1 - 6.13

Figure 6.1
The Reciprocal Replacement Series after 12 months growth. The experiment was set up at two depths (10(0-20) & 60(50-70) cm). Monocultures of *Baumea* are in the foreground.

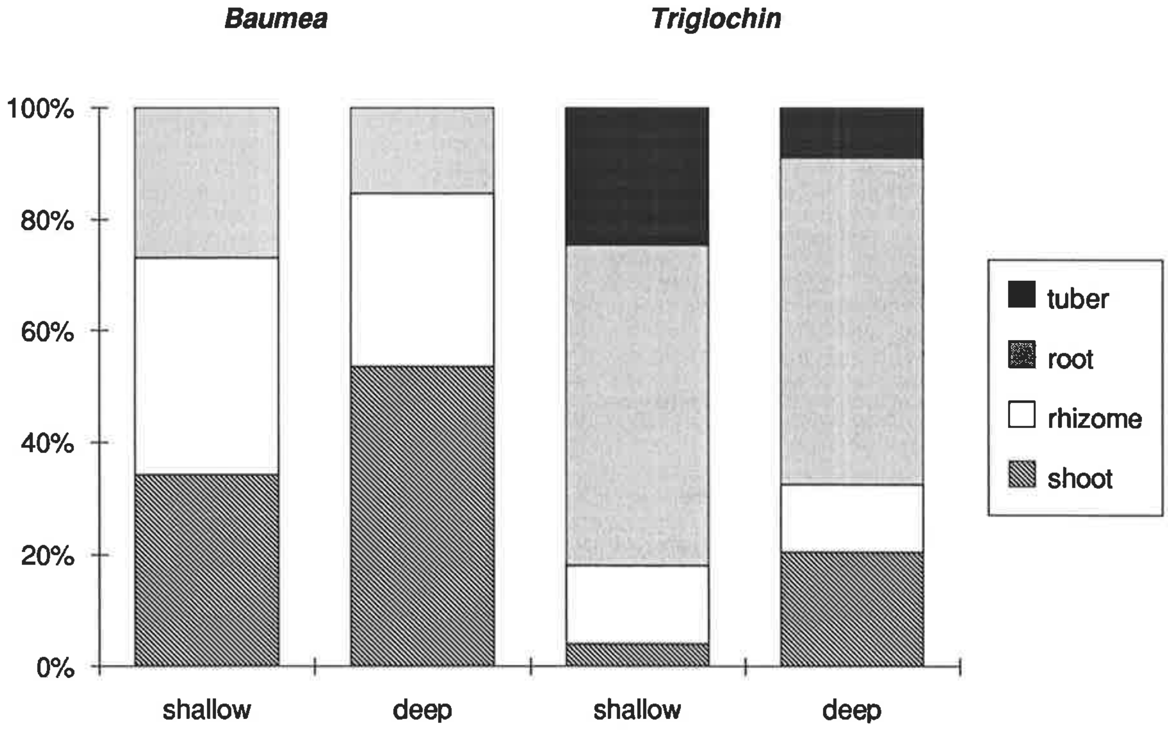


Figure 6.2
Biomass allocation in monoculture populations of *Baumea* and *Triglochin*, in shallow and deep water.

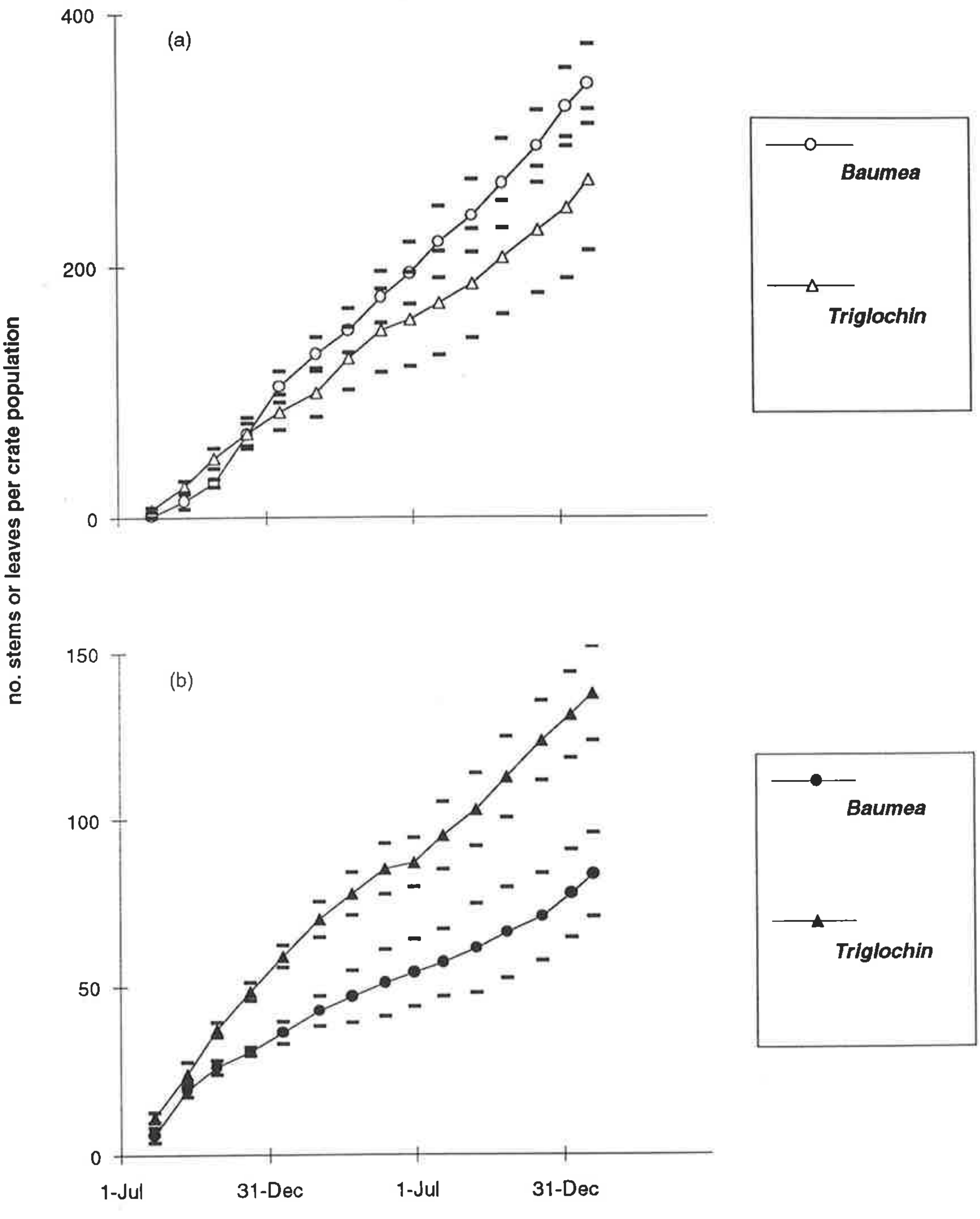


Figure 6.3
The cumulative increase in the number of *Baumea* stems and *Triglochin* leaves in monoculture populations, in (a) shallow and (b) deep water.

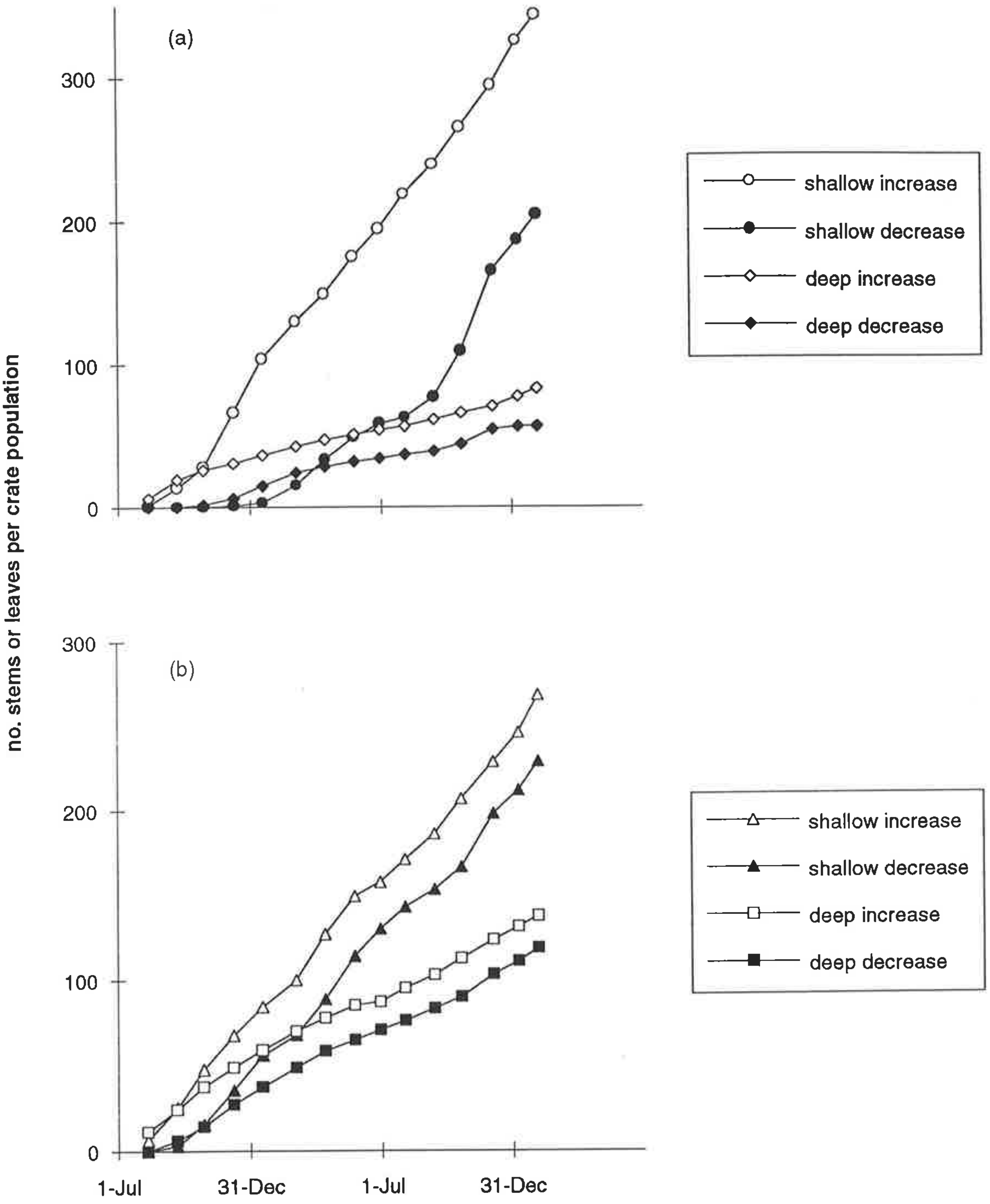


Figure 6.4
The cumulative increase and decrease in the number of (a) *Baumea* stems and (b) *Triglochin* leaves, in shallow and deep water monocultures.

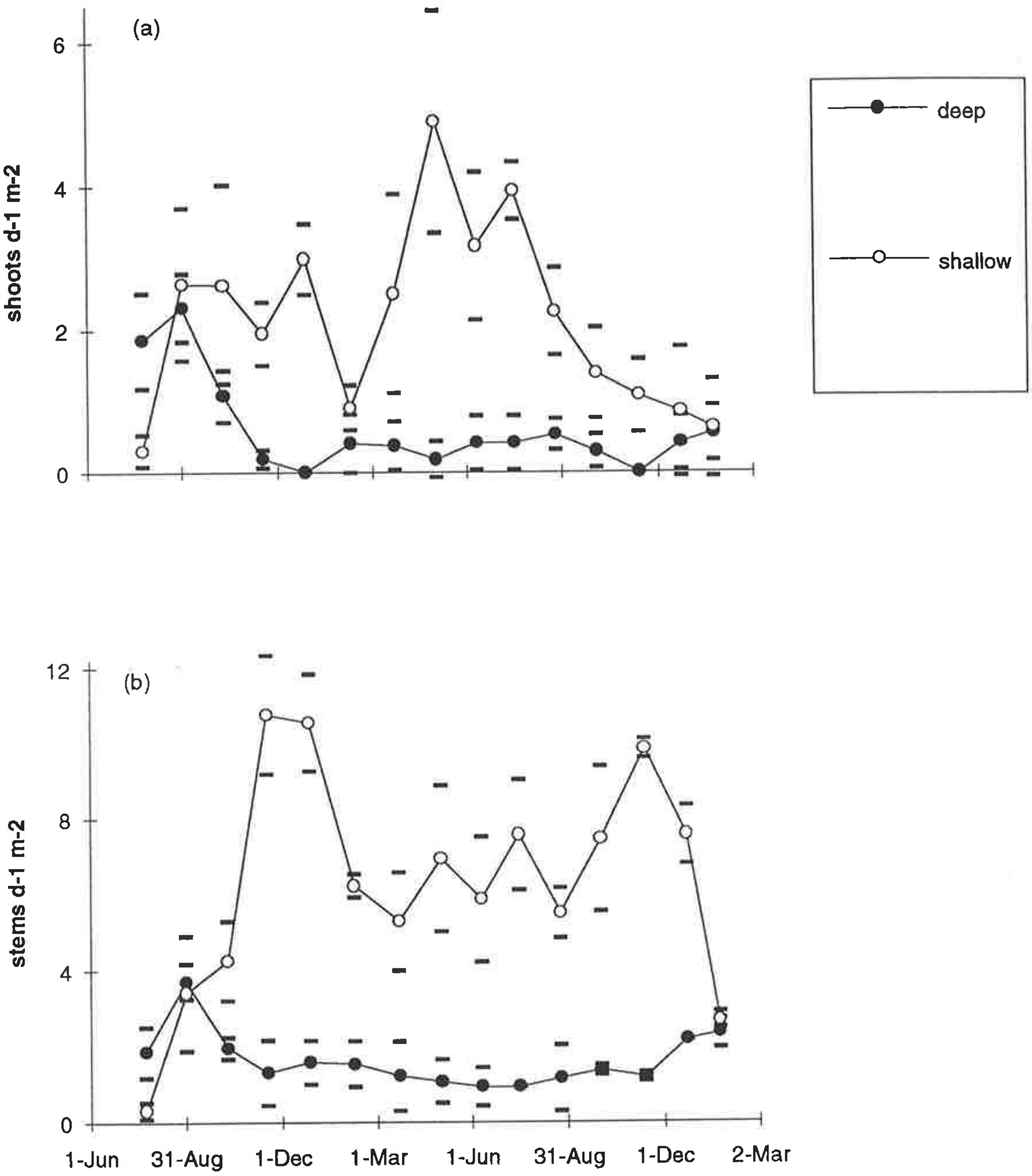


Figure 6.5
Baumea's gross rate of (a) shoot and (b) stem recruitment (mean ± sd; m^{-2}) in shallow and deep monocultures.

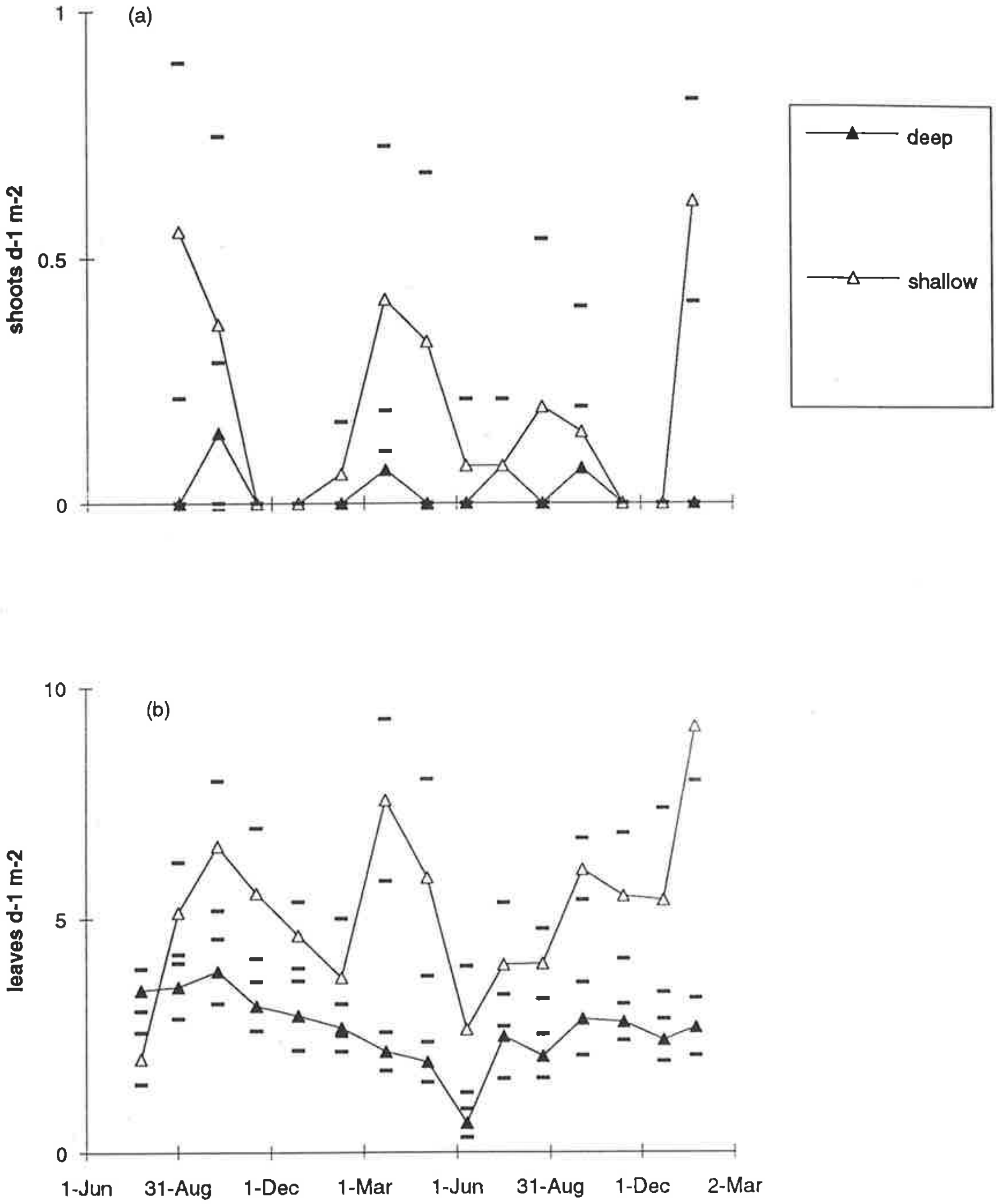


Figure 6.6
Triglochin's gross rate of (a) shoot and (b) leaf recruitment (mean ± sd; m-^{2}) in shallow and deep monocultures.

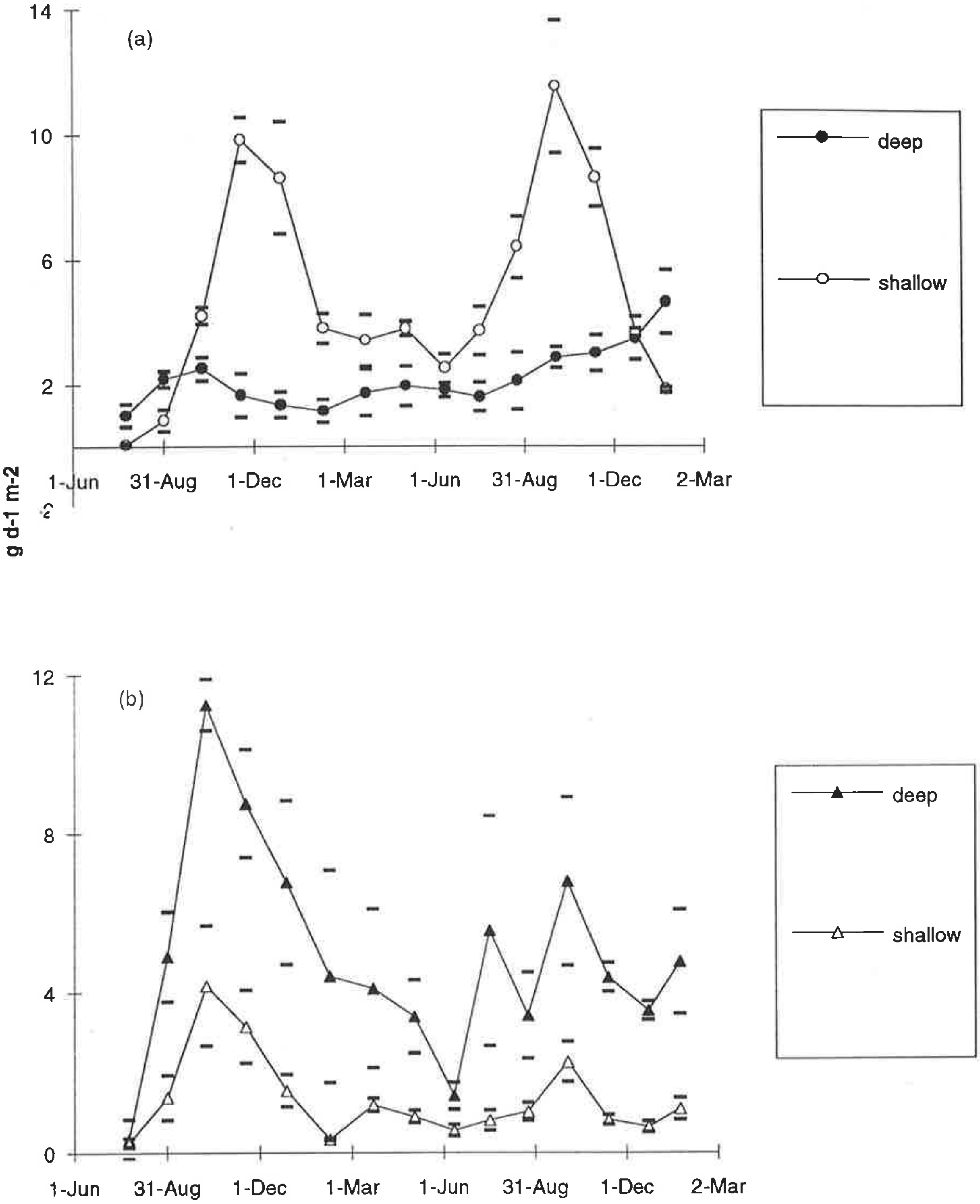


Figure 6.7
The gross rate (mean ± sd) of shoot mass accumulation per m-^{2} (g d-1 m-^{2}) in (a) *Baumea* and (b) *Triglochin* monocultures, in shallow and deep water.

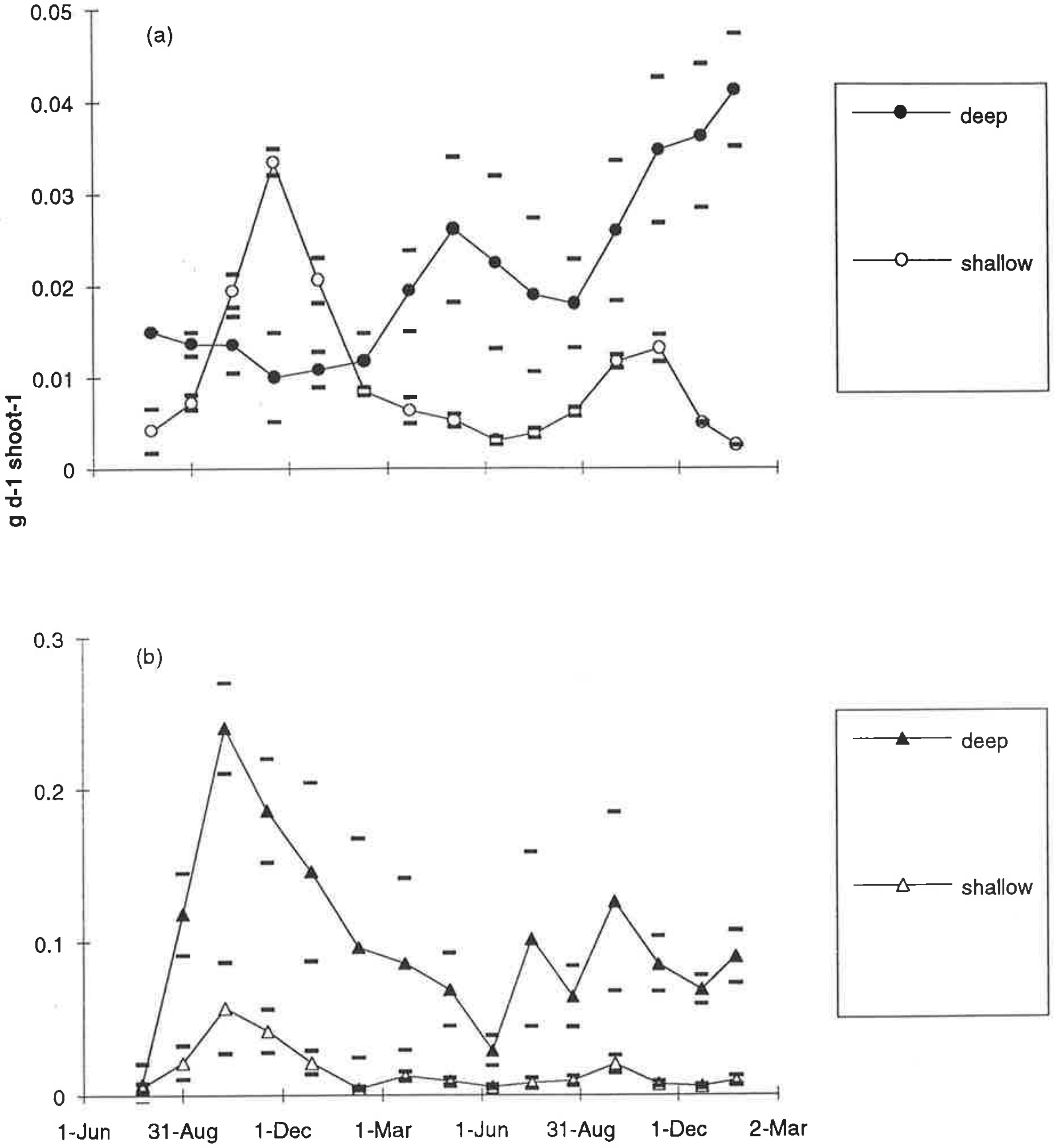


Figure 6.8
The gross rate (mean ± sd) of shoot mass accumulation per shoot (g d-1 shoot-1), for (a) *Baumea* and (b) *Triglochin* monocultures, in shallow and deep water.

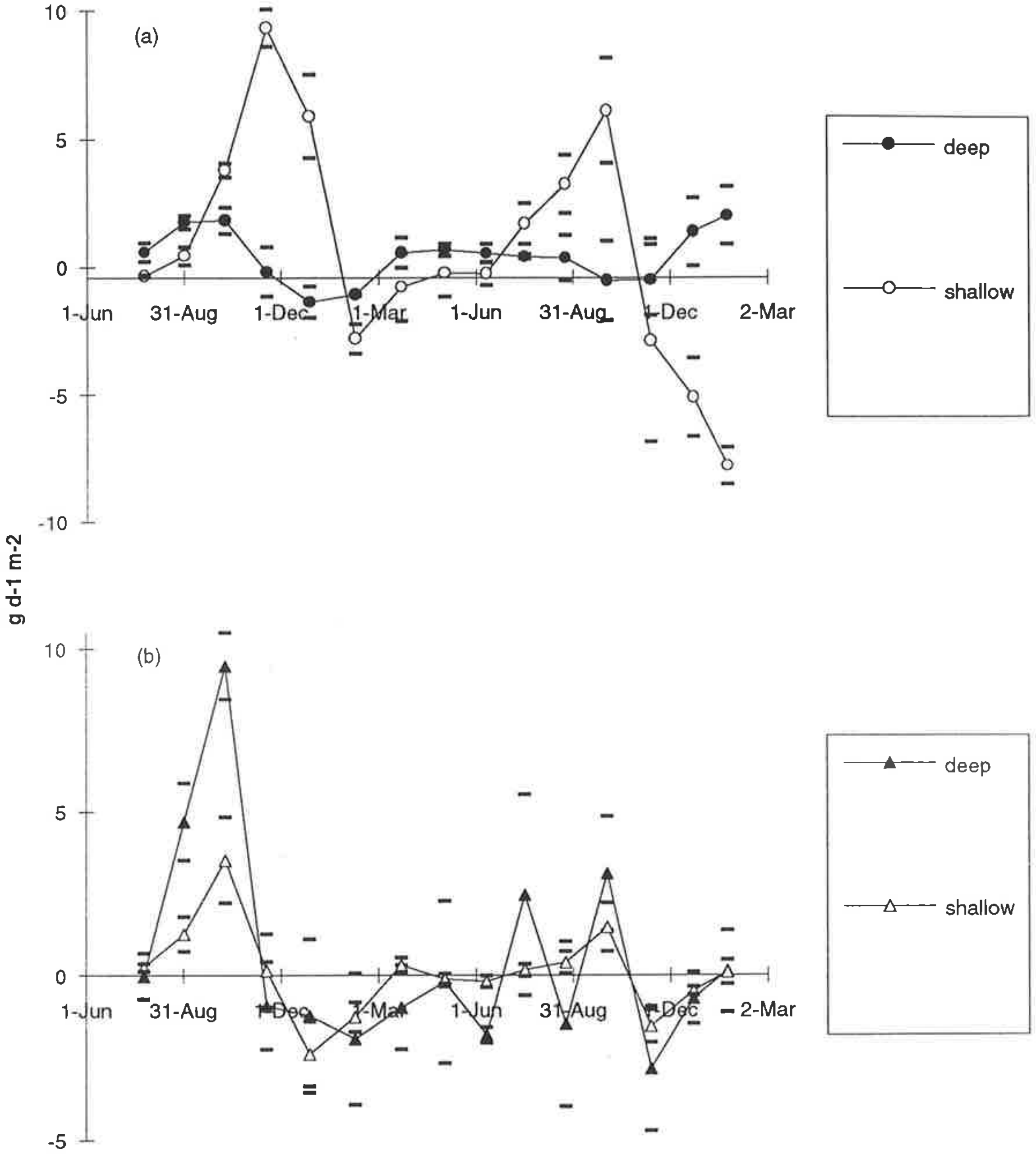


Figure 6.9
The net rate of shoot mass accumulation (mean ± sd; g d-1 m-2), for (a) *Baumea* and (b) *Triglochin* monocultures in shallow and deep water.

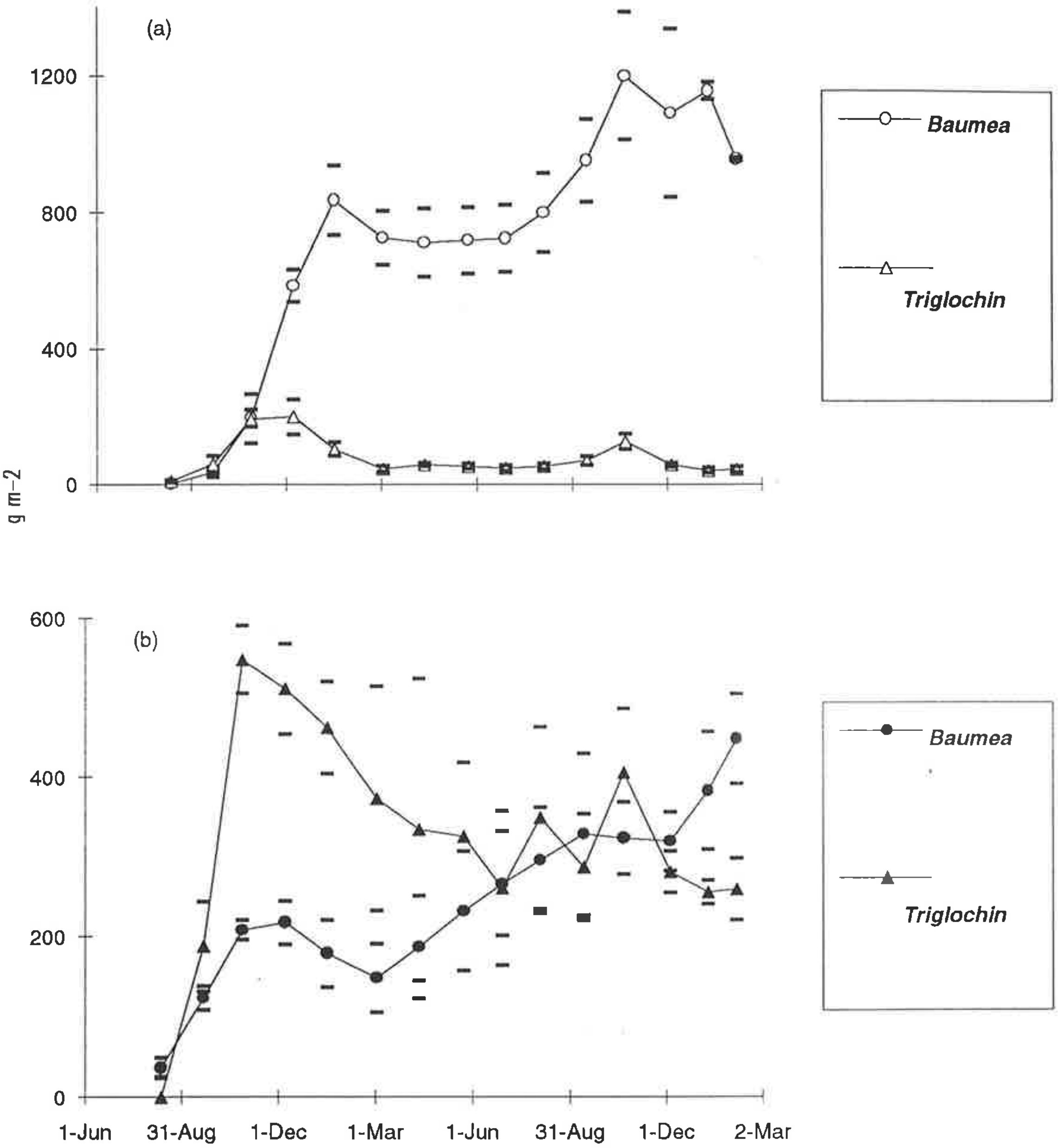


Figure 6.10
The total shoot (aboveground) mass (g m^{-2}) of *Baumea* and *Triglochin,* monocultures in (a) shallow and (b) deep water

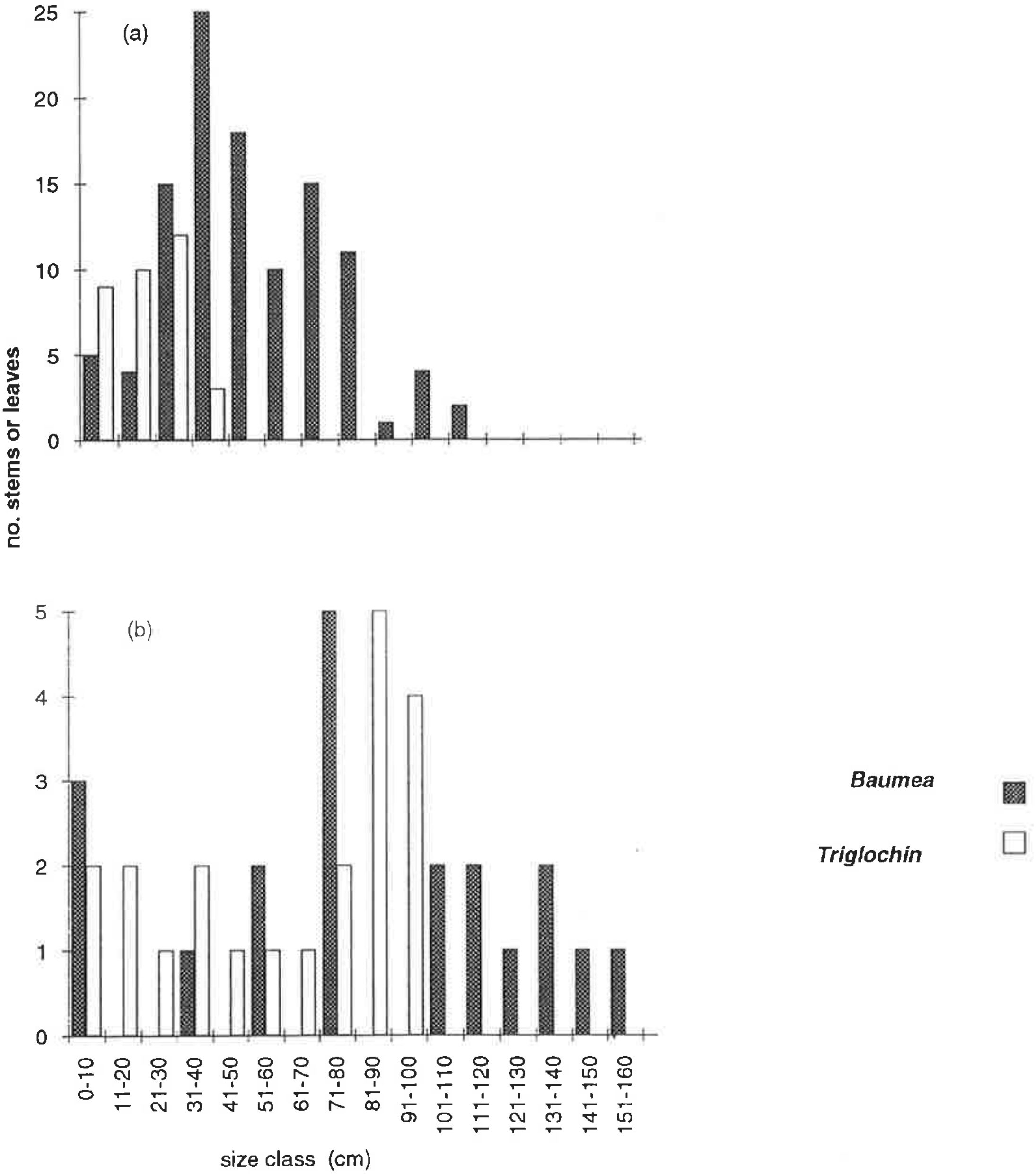


Figure 6.11
Frequency distributions of the heights of *Baumea* stems and *Triglochin* leaves (mean no. per population) in (a) shallow and (b) deep monocultures.

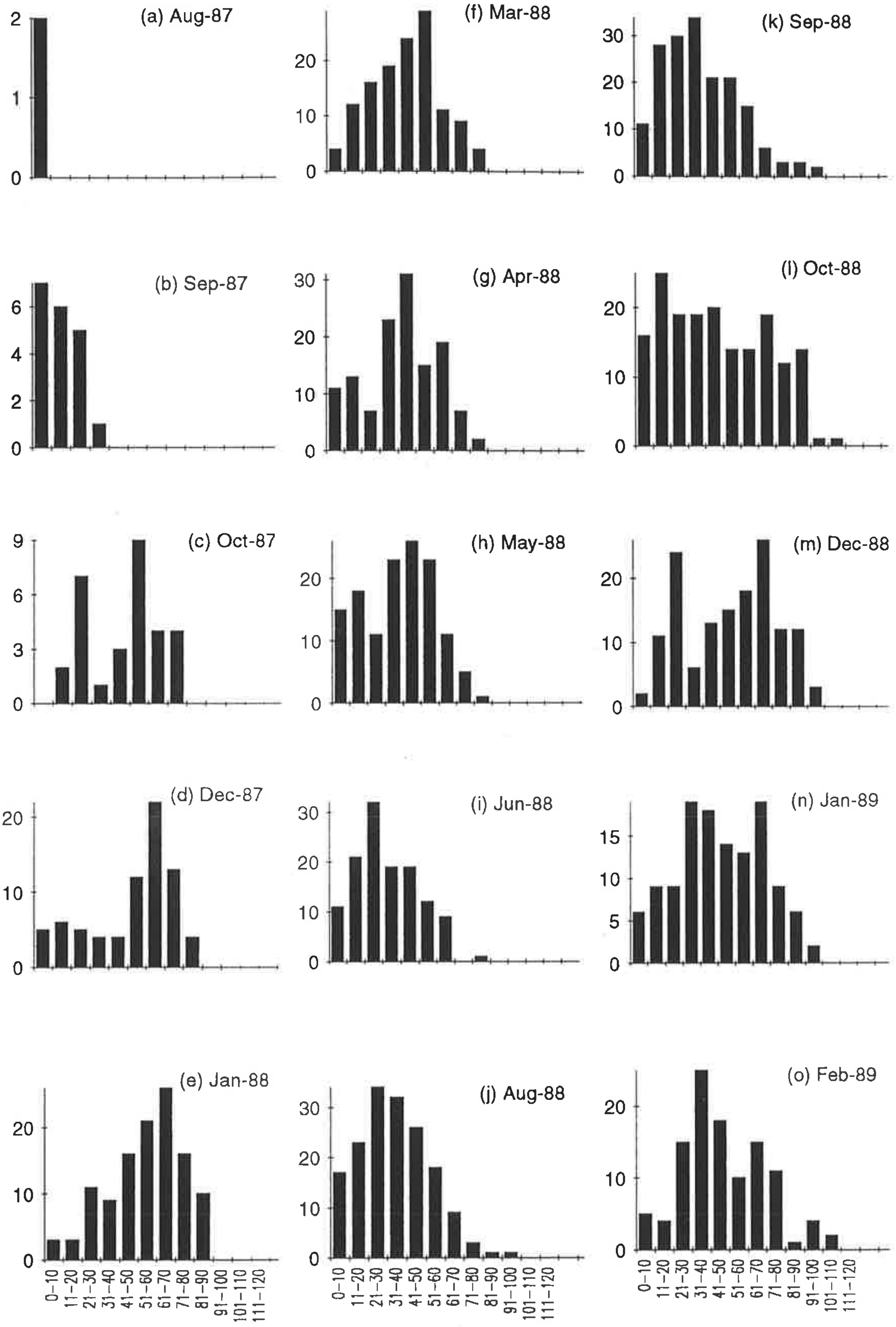


Figure 6.12
Frequency distributions of *Baumea* stem heights in one of the shallow monoculture populations. (a) to (o) represent the development of the population over the course of the experiment.

good

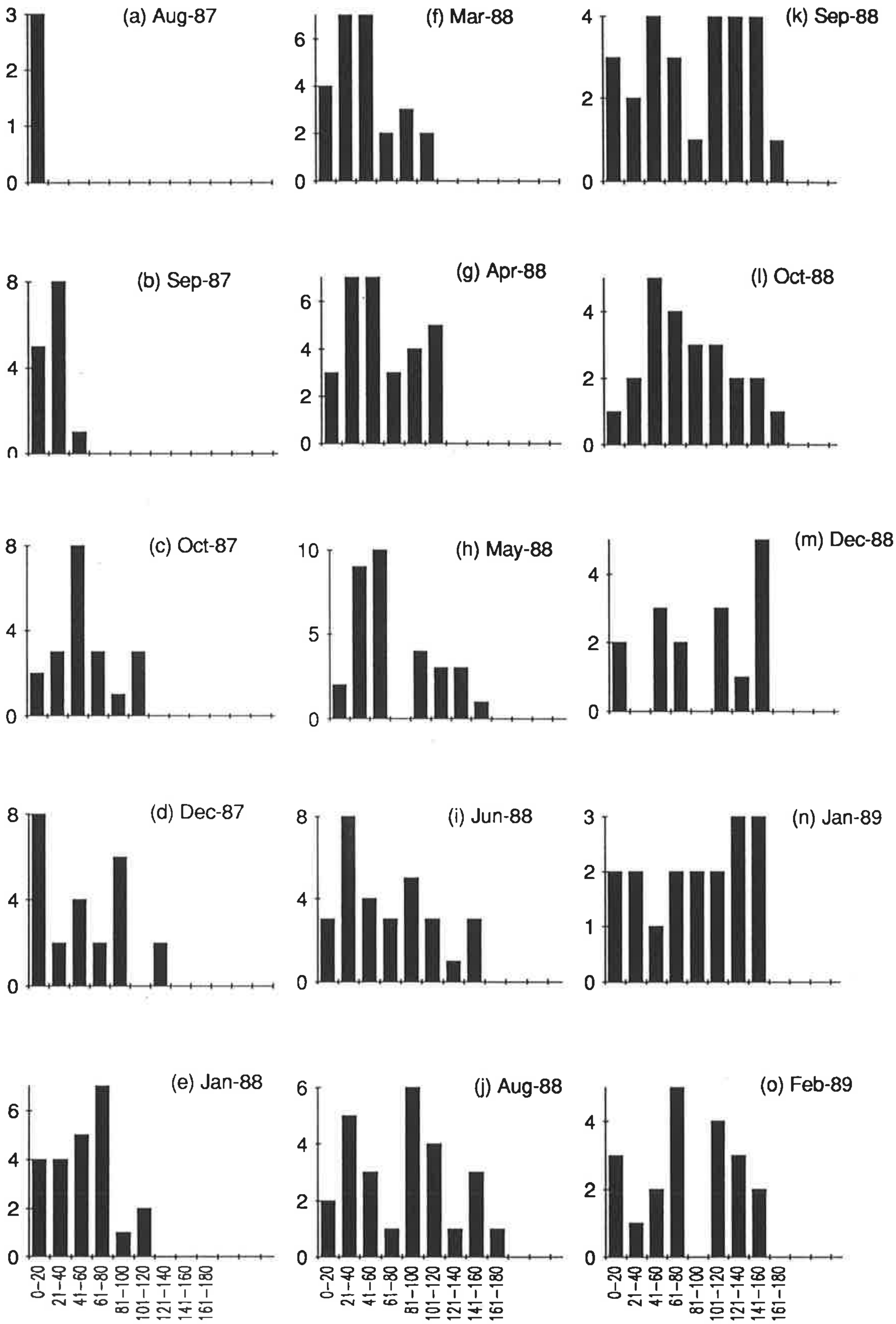


Figure 6.13
Frequency distributions of *Baumea* stem heights in one of the deep monoculture populations. (a) to (o) represent the development of the population over the course of the experiment.

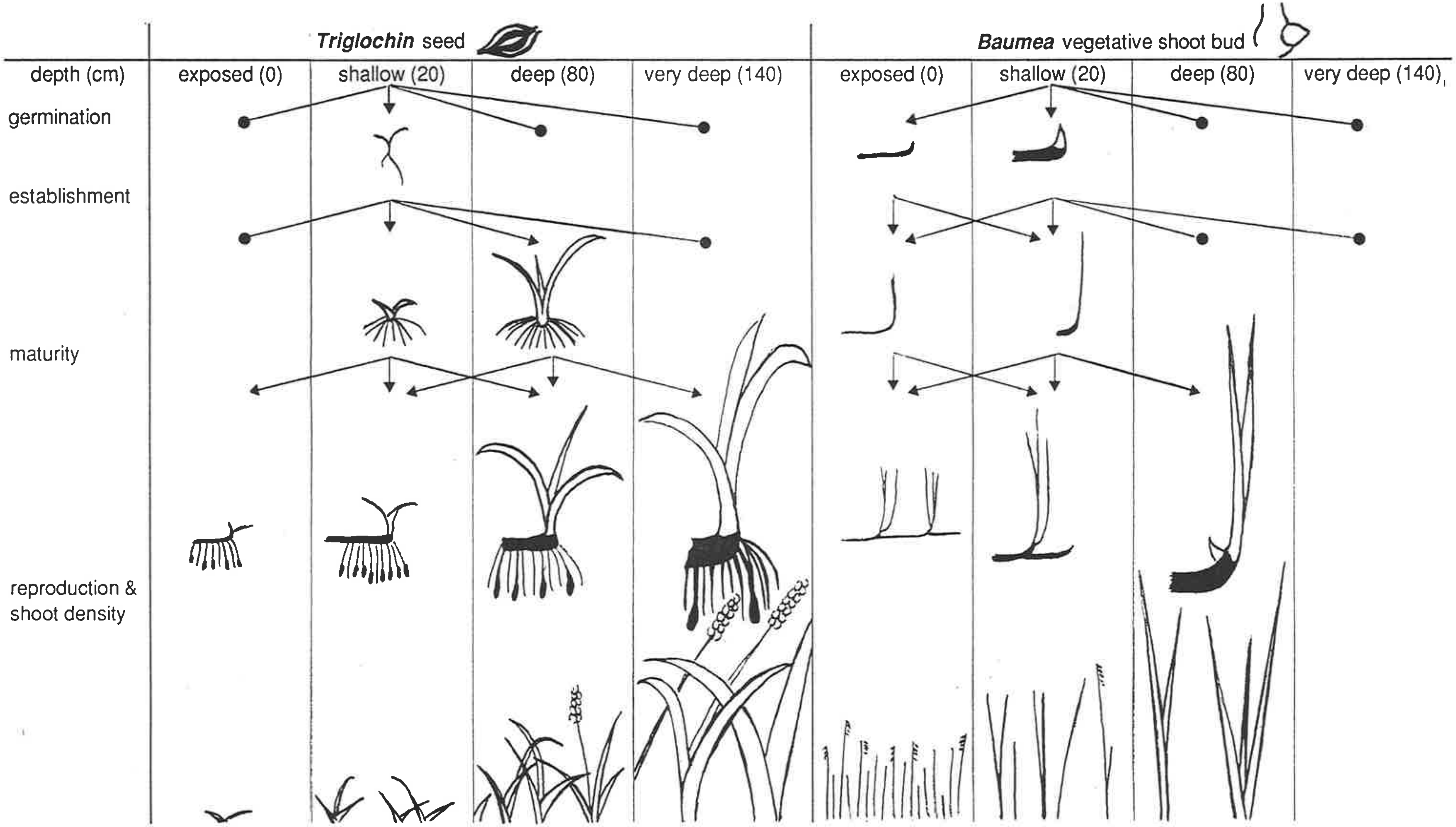


Figure 6.14
A summary of the individual responses of *Triglochin* and *Baumea* to water regime. The influence of four depths and the changes between them were considered with regard to growth and population structure. Arrows represent the ability of the plant to pass from one stage to another (germination, establishment, reproductive maturity), whereas circles indicate the plant does not survive.

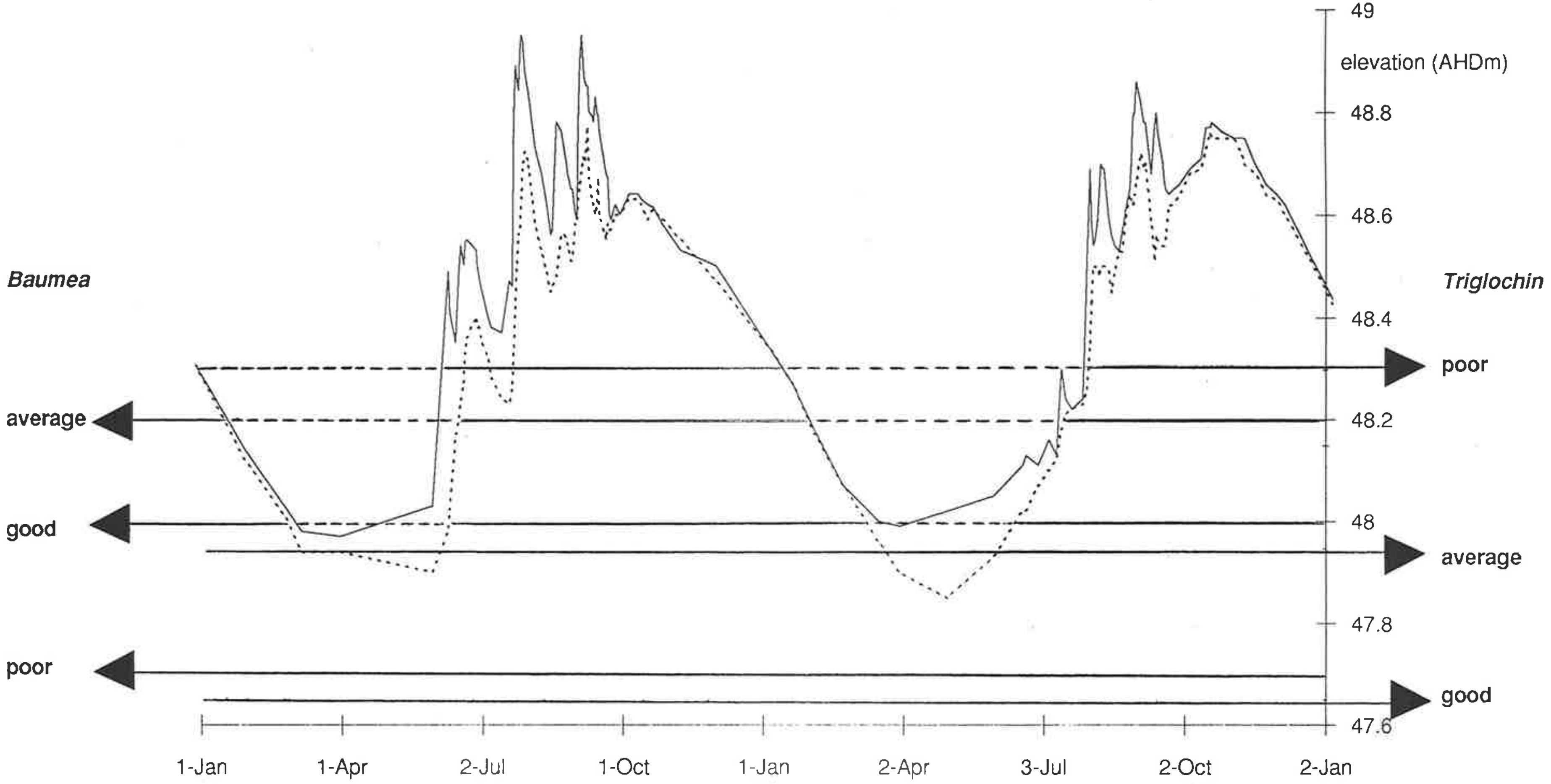


Figure 6.15
The mean elevations where the performance of *Baumea* and *Triglochin* is poor, average or good (performance is based on total biomass and shoot density m-^{2}). *Baumea* is compared to the water level in the Western Basin (dotted line) and *Triglochin* to the water level in Hacks Lagoon (solid line). The water levels, which are from 1988 and 1989, are typical of the present Lagoon water regime. When sites were inundated or exposed, elevations are drawn as solid or dashed lines, respectively.

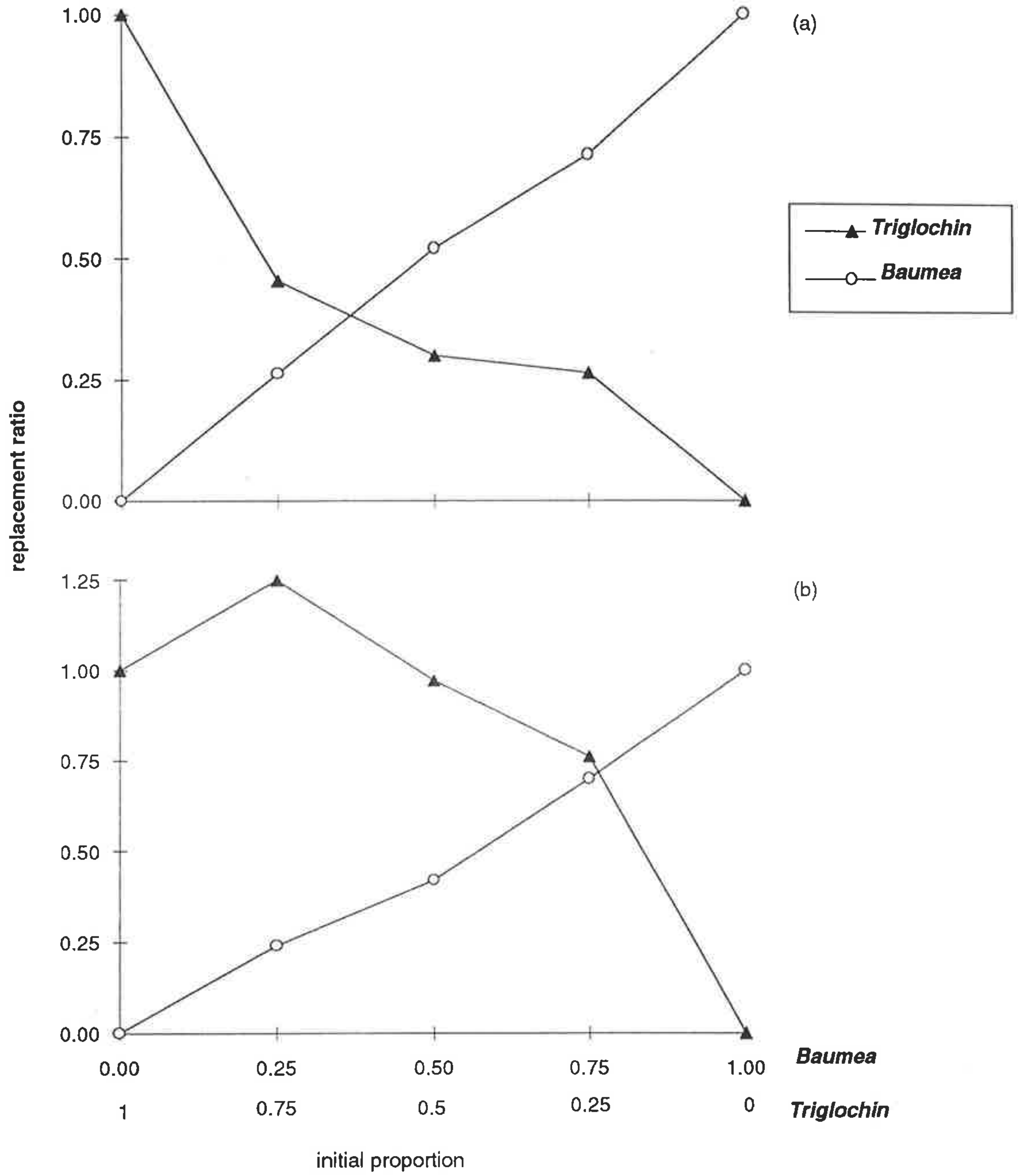


Figure 6.16
The final total biomass of *Baumea* and *Triglochin* in mixture, calculated as replacement ratios (yield in mixture/yield in monoculture), in (a) shallow and (b) deep water.

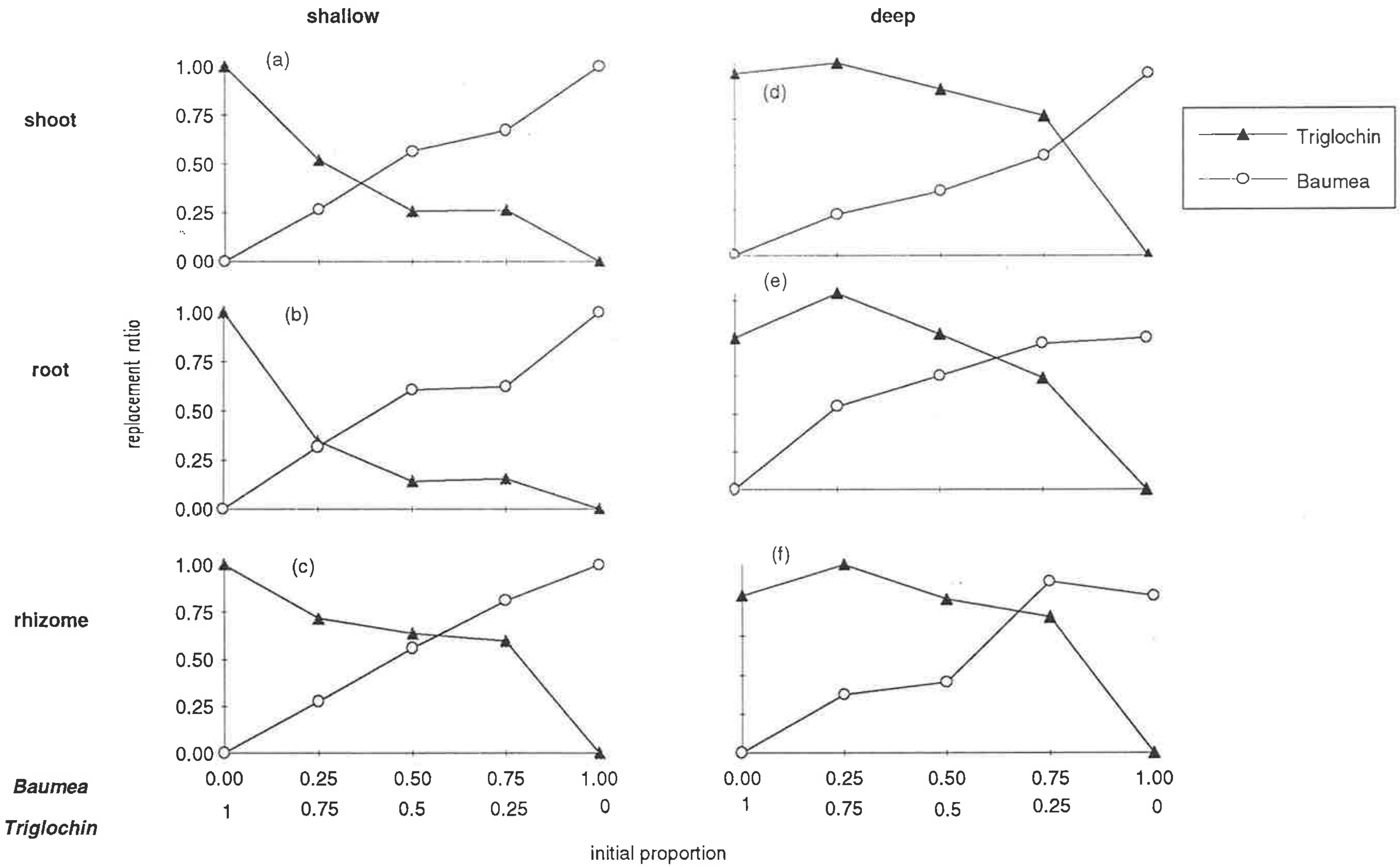


Figure 6.17
The final shoot, root and rhizome biomass of *Baumea* and *Triglochin*, calculated as replacement ratios (yield in mixture/yield in monoculture), in shallow (a-c) and deep (d-f) water.

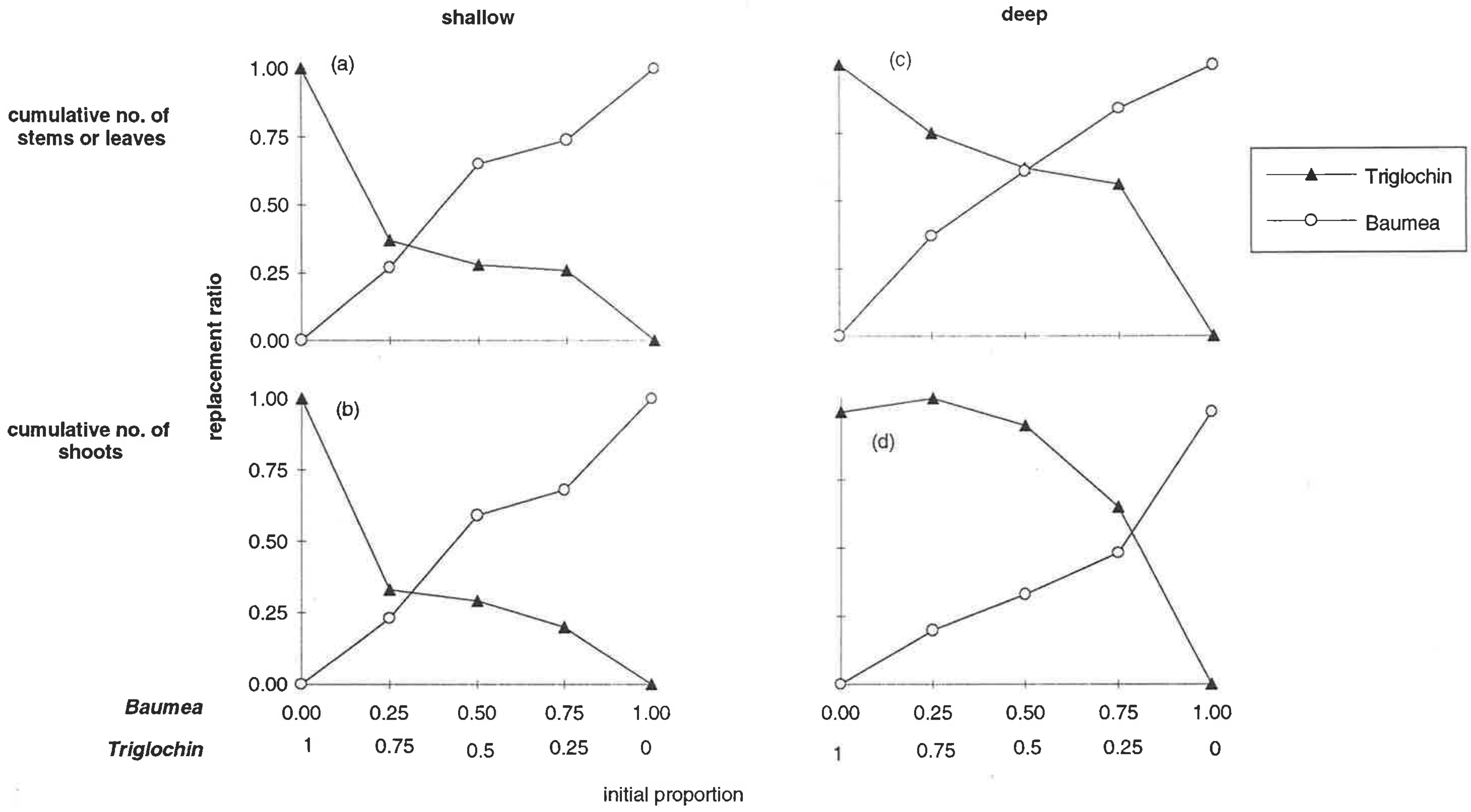


Figure 6.18
The cumulative number of stems, leaves and shoots produced per initial shoot of *Baumea* and *Triglochin*, calculated as replacement ratios (no. in mixture/no. in monoculture) in (a, b) shallow and (c, d) deep water.

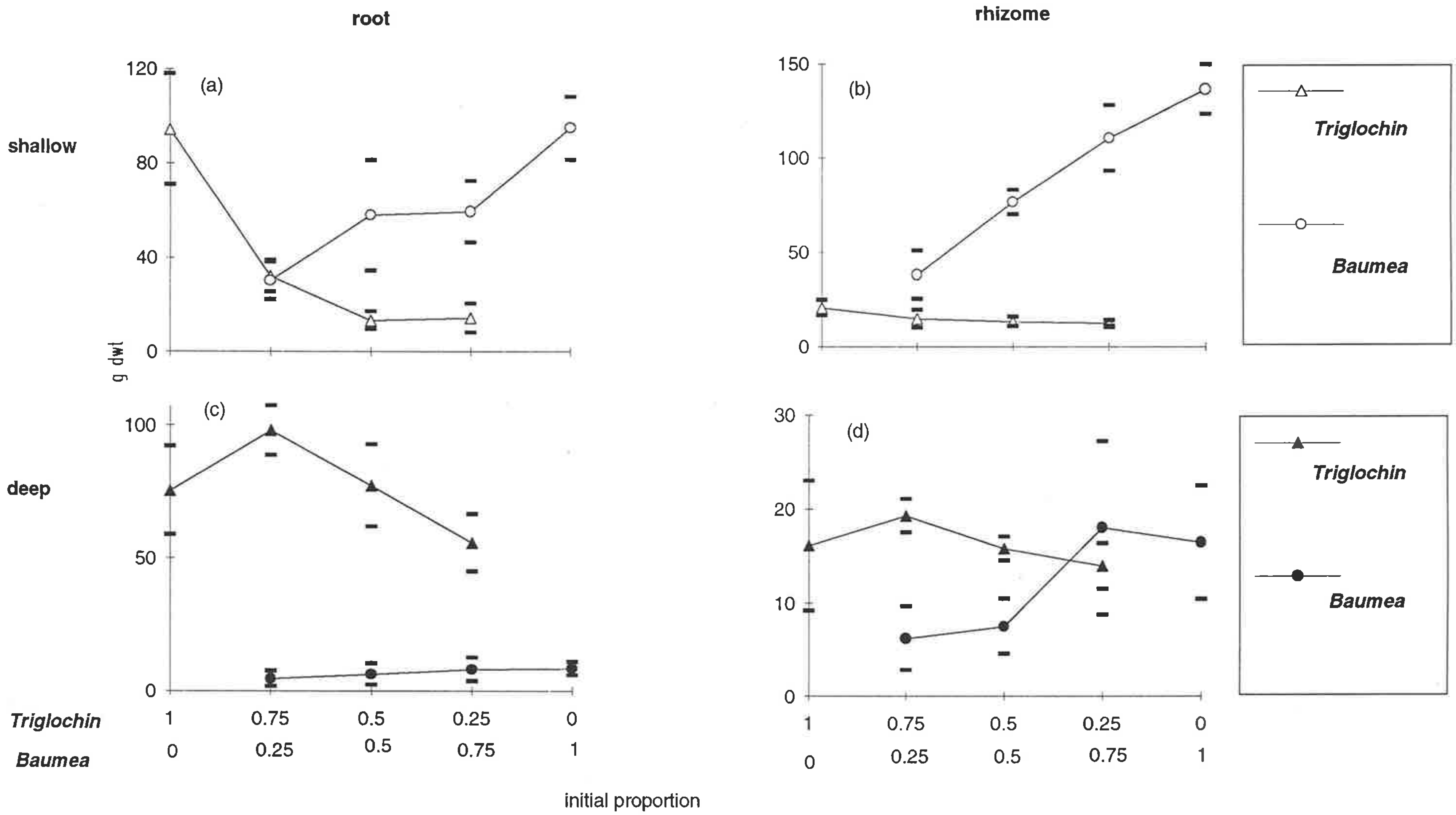


Figure 6.19
The final root and rhizome mass in *Baumea* and *Triglochin* mixtures and monocultures, in (a,b) shallow and (c, d) deep water.

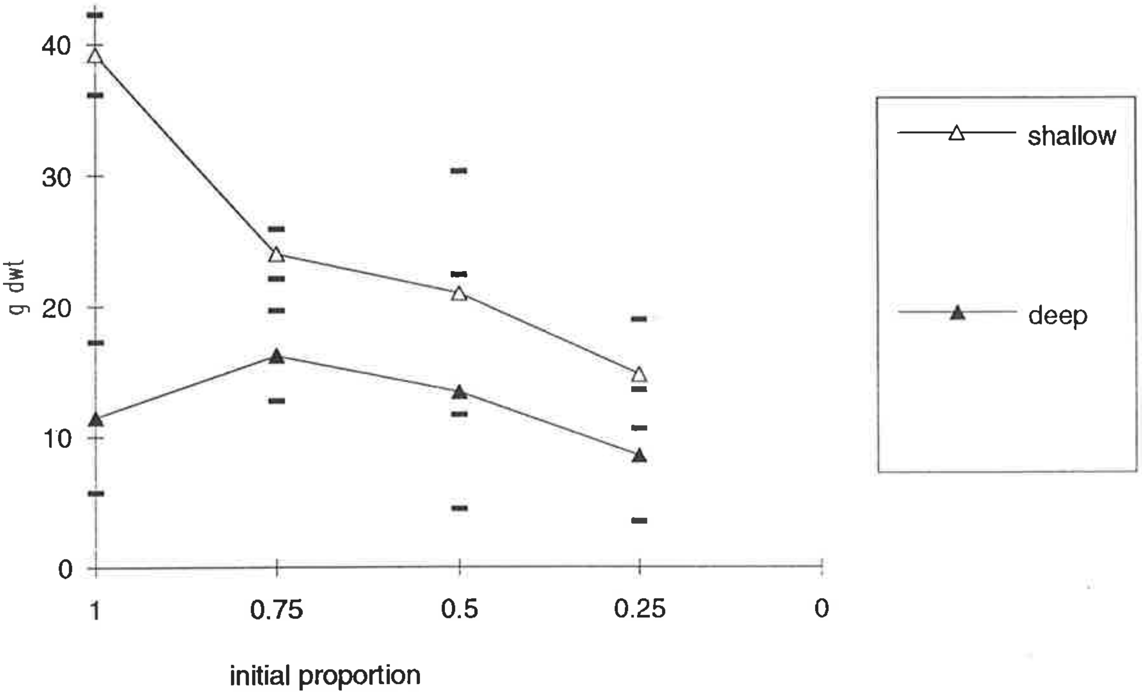
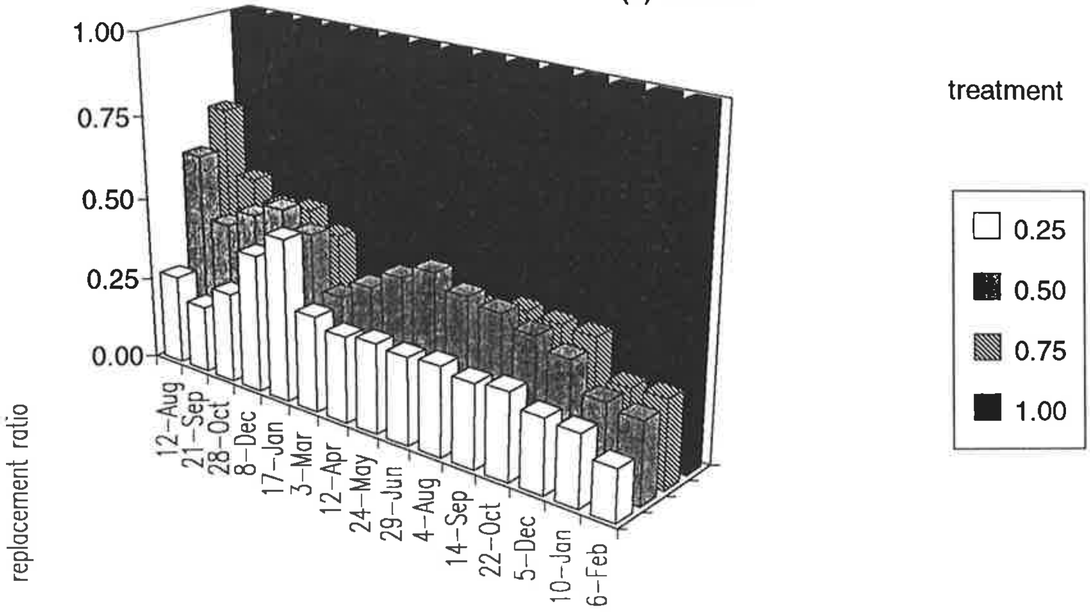


Figure 6.20
The final tuber mass (mean ± sd) in *Triglochin* mixtures and monocultures, in shallow and deep water.

(a) shallow



(b) deep

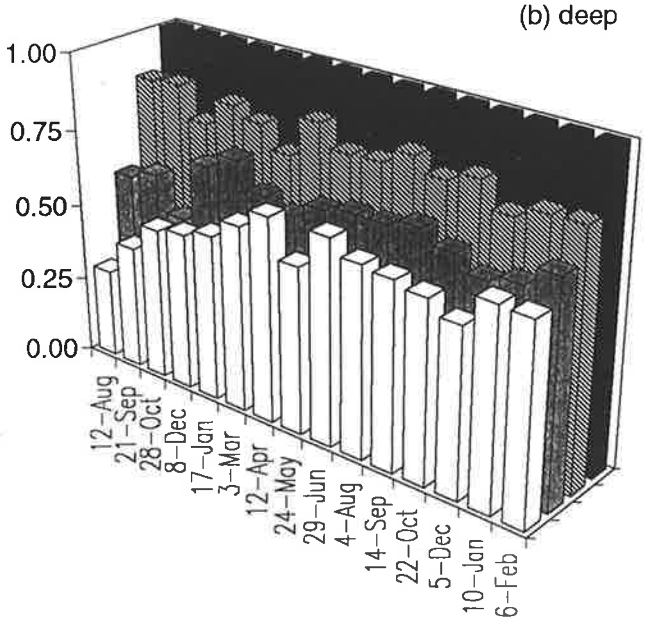


Figure 6.21
The replacement ratios, calculated for each record, for the number of *Triglochin* leaves per treatment in (a) shallow and (b) deep water.

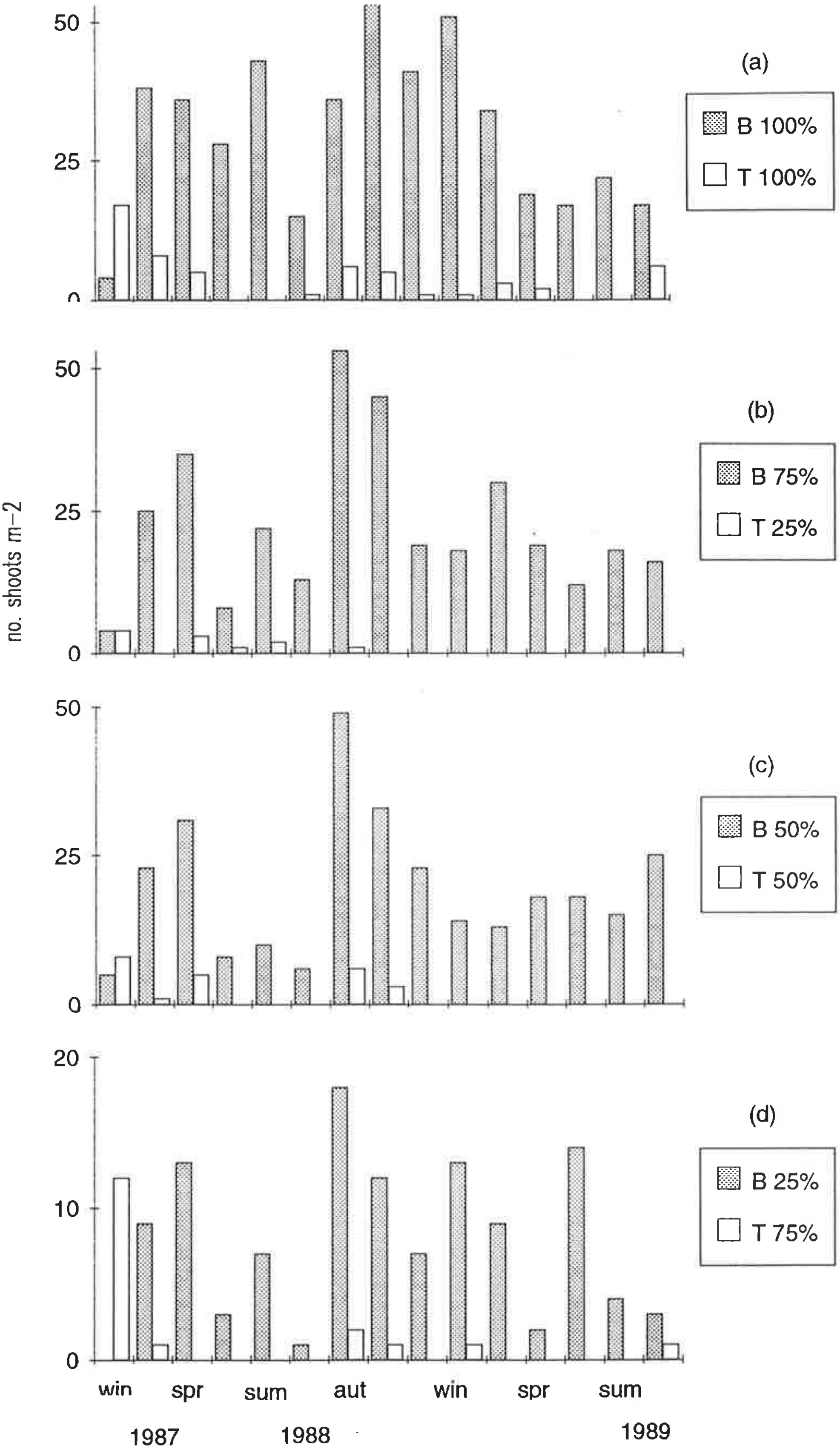
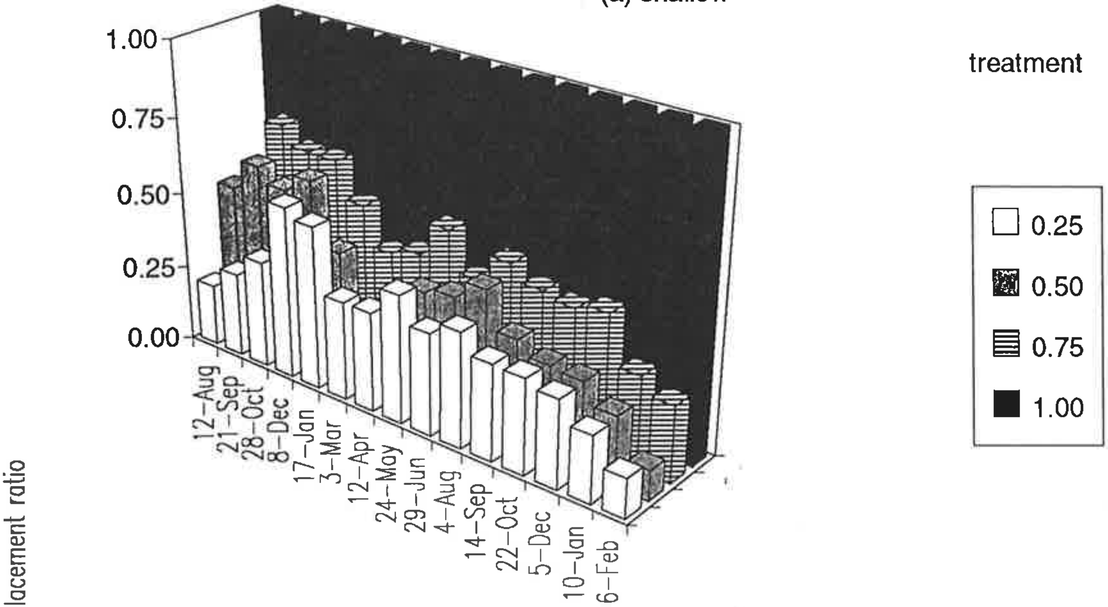


Figure 6.22
The mean number of new *Baumea* (B) and *Triglochin* (T) shoots (m-^{2}), recorded on each sampling date, in (a) monocultures and (b-d) mixtures.

(a) shallow



(b) deep

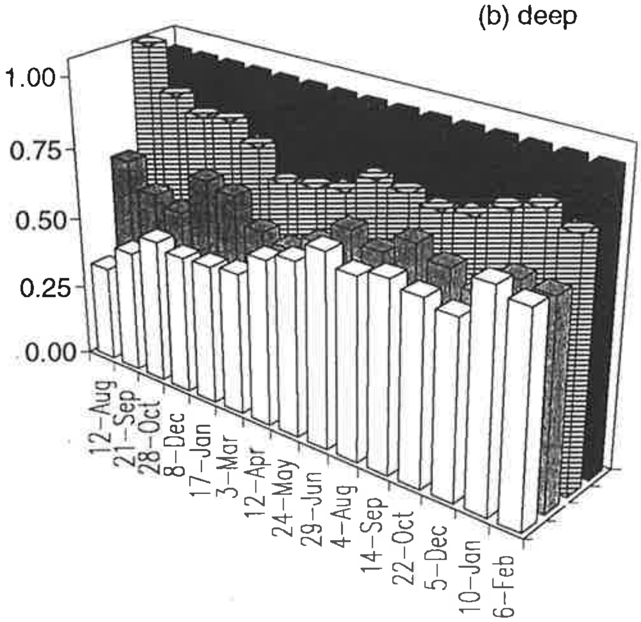


Figure 6.23
The replacement ratios, calculated for each record, for *Triglochin*'s total leaf height per treatment in (a) shallow and (b) deep water.

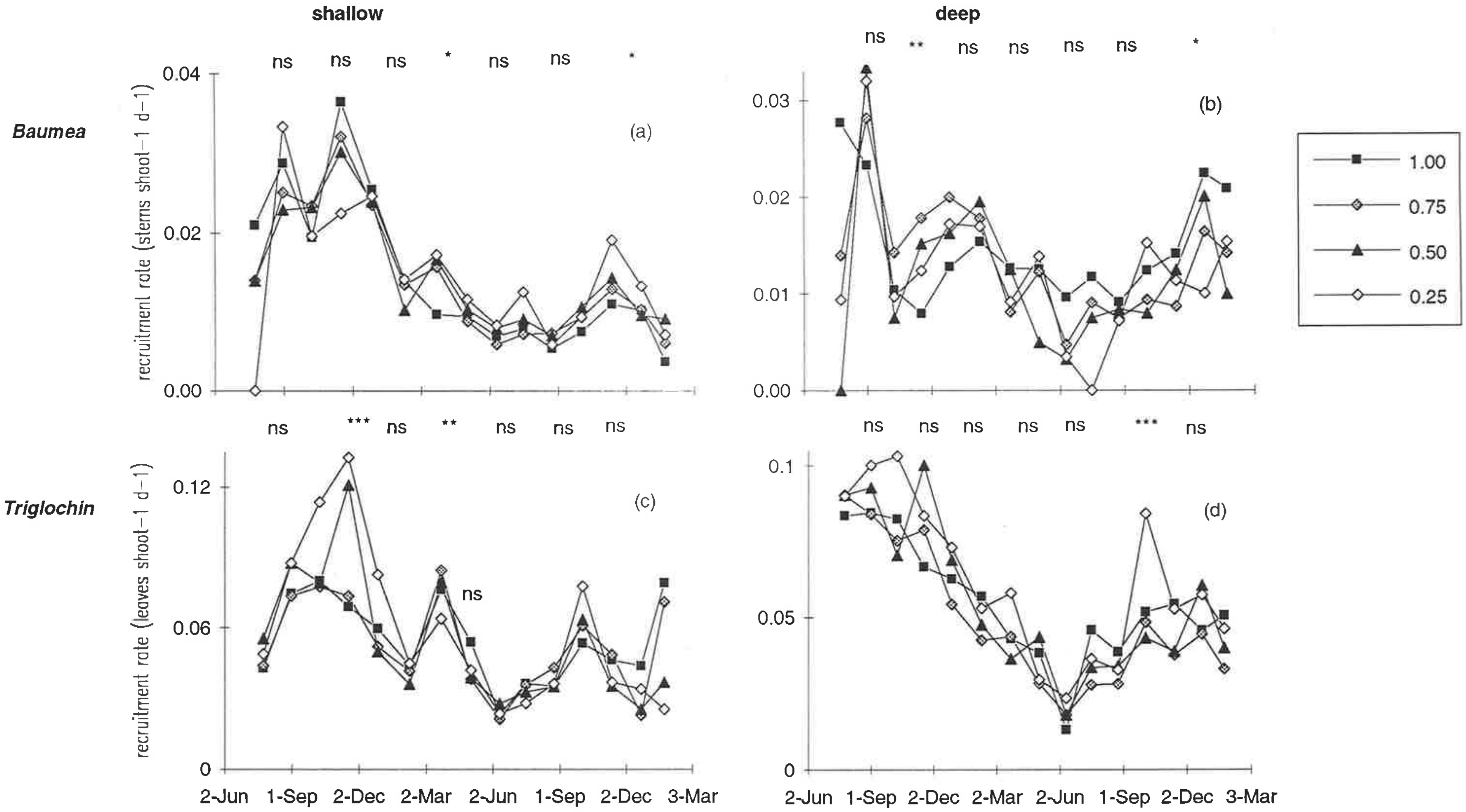


Figure 6.24

Comparison of the recruitment rate of *Baumea* stems (a & b) and *Triglochin* leaves (c & d) per shoot, in monoculture (1.0) and mixtures (0.25-0.75). Results of 1-way AOV's for every second record are shown above the relevant data (***=P<0.01, **=P<0.025, *=P<0.05, ns=P>0.05)

Figure 6.25

Figure 6.26

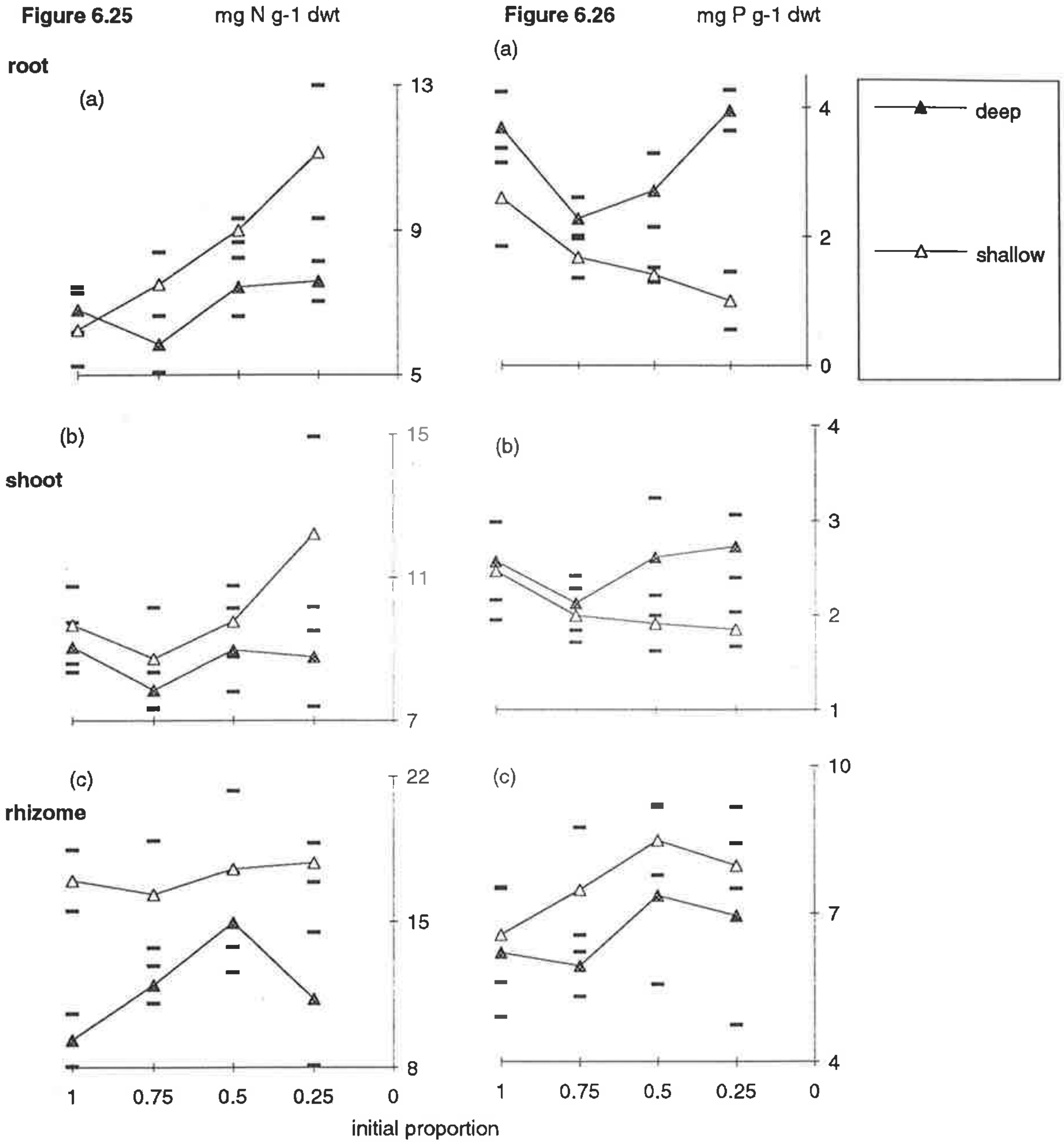


Figure 6.25 & 6.26
The concentrations of N (Figure 6.25) and P (Figure 6.26) in the tissues of *Triglochin*, in monocultures and mixtures, in shallow and deep water.

Figure 6.27

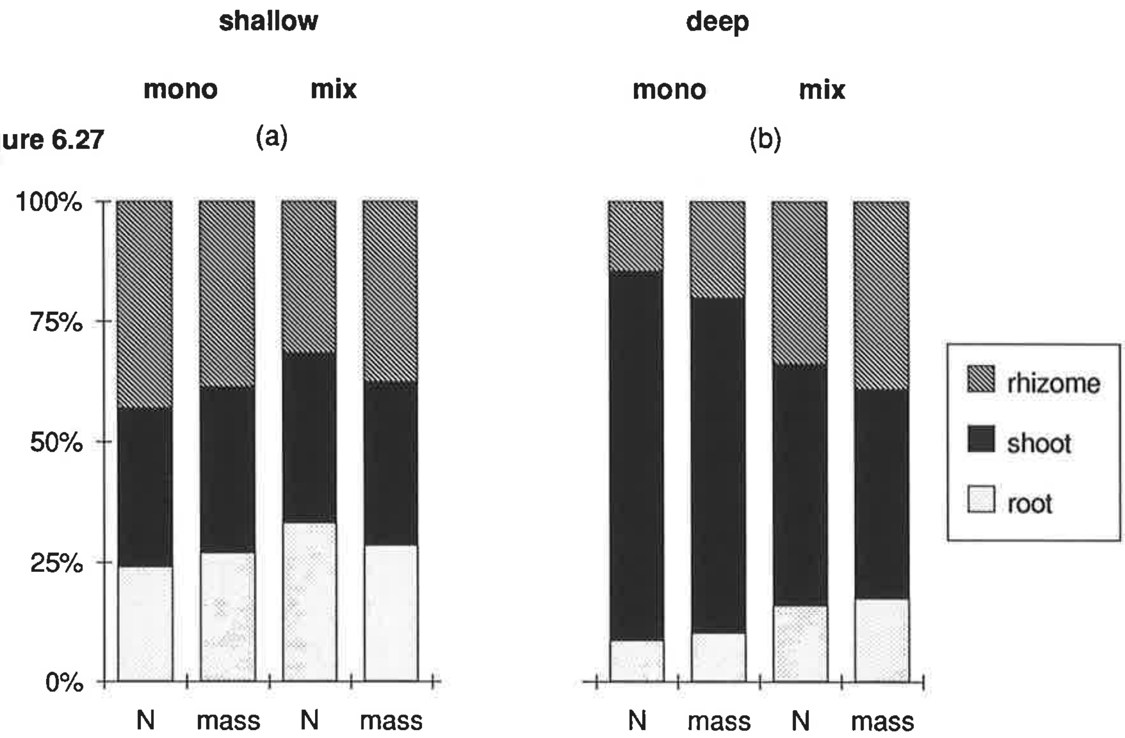


Figure 6.28

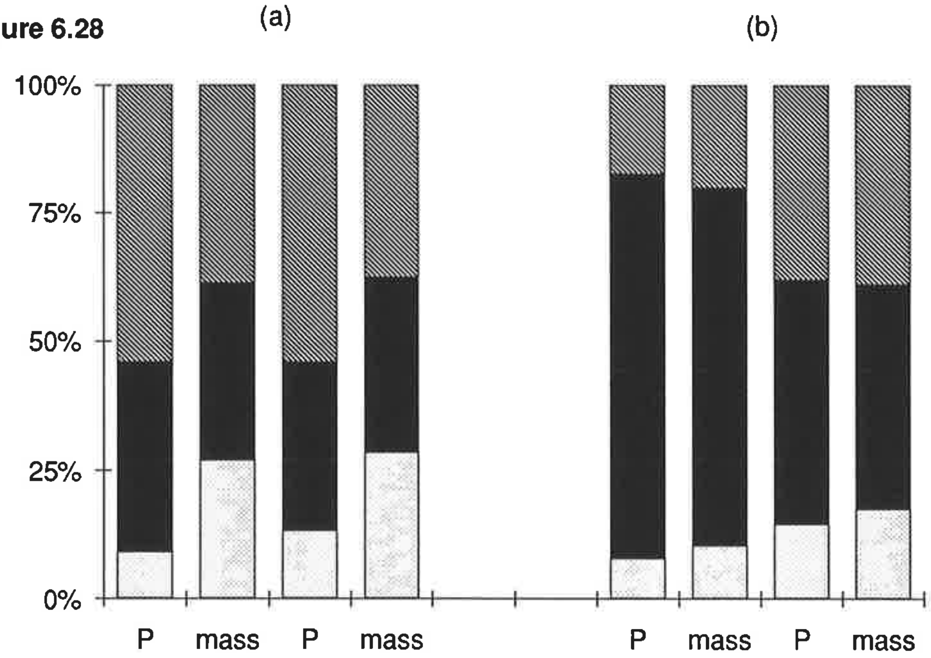


Figure 6.27 & 6.28
The percent distribution of N and mass (Figure 6.27) and P and mass (Figure 6.28) in the tissues of *Baumea*, in (a) shallow and (b) deep water and in monoculture or mixture (50:50).

Figure 6.29

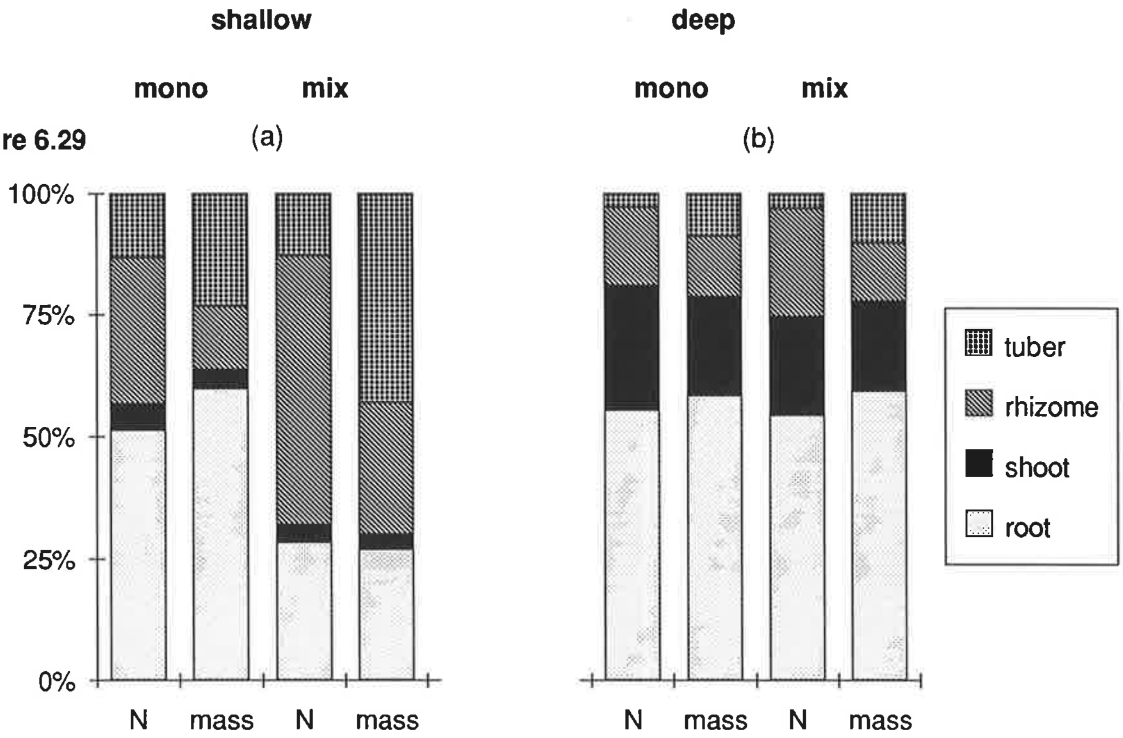


Figure 6.30

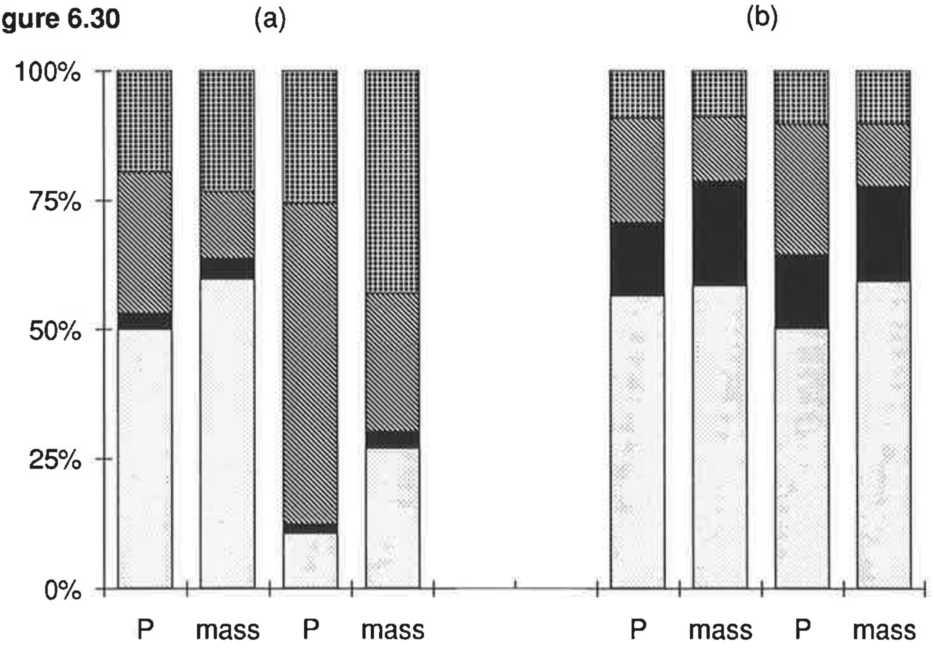


Figure 6.29 & 6.30
The percent distribution of N and mass (Figure 6.29) and P and mass (Figure 6.30) in the tissues of *Triglochin*, in (a) shallow and (b) deep water.

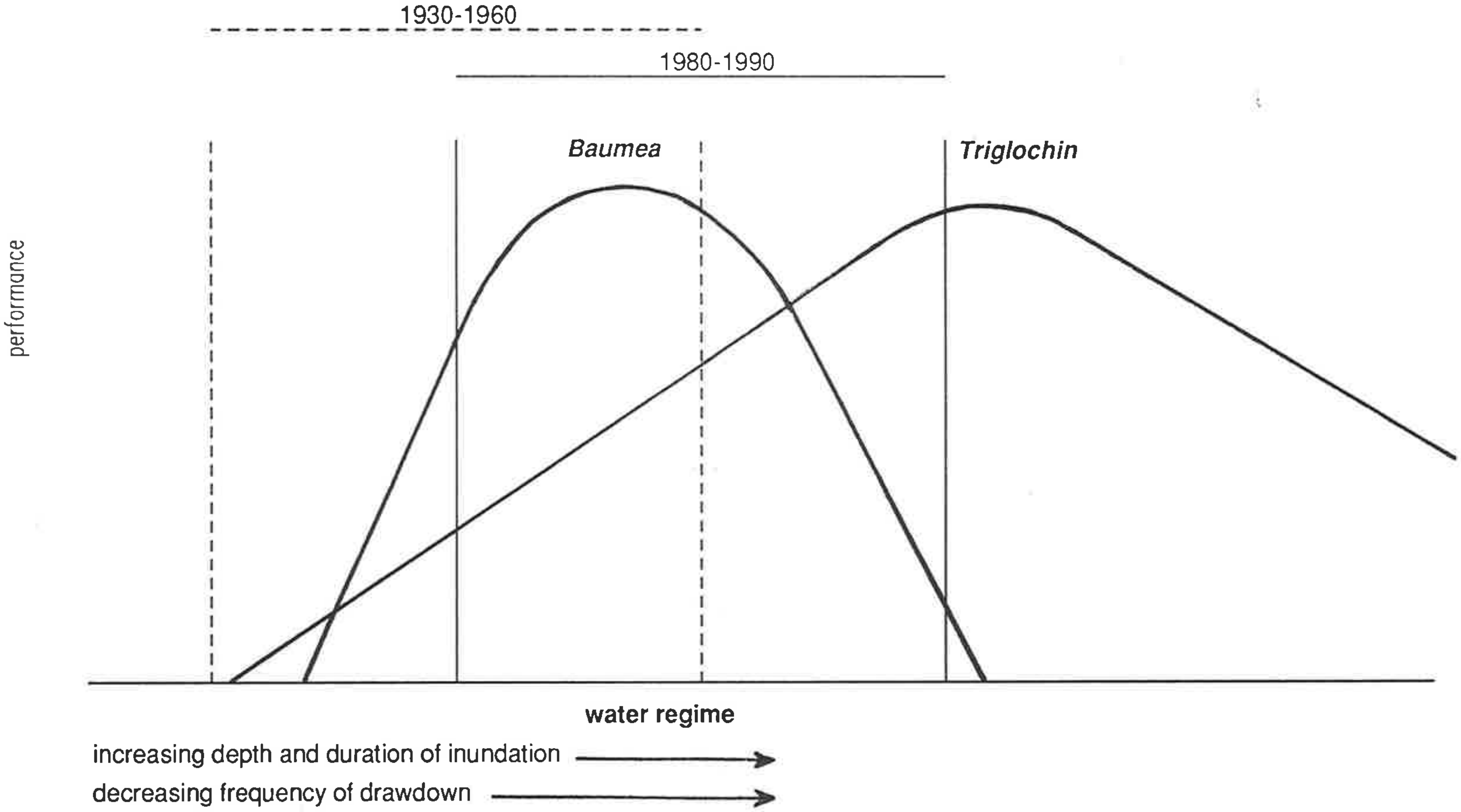


Figure 6.31
The performance of *Baumea* and *Triglochin*, across a theoretical water regime gradient. Performance was based on the population characteristics of total biomass and shoot density. The water regimes corresponding to the periods between 1930-1960 and 1980-1990, are shown.

biomass characteristics (m^{-2})		***Baumea***		***Triglochin***	
		shallow	deep	shallow	deep
biomass	total	3908 (1.3)	903 (157)	1801 (236)	1435 (331)
	aboveground (green shoot)	930 (62)	536 (103)	40.7 (9.2)	248 (61.1)
	belowground	2978 (63.5)	368 (76)	1766 (239)	1188 (283)
	rhizome	1515 (148)	183 (67.1)	227 (45)	179 (77)
	root	1054 (149)	93.1 (28.7)	1047 (263)	838 (186)
	shoot base (belowground)	408 (64)	91.6 (26.7)	34.1 (9.1)	43.6 (7.5)
	tuber			435 (34)	127 (64)
ratios	below : aboveground	3.22 (0.28)	0.90 (0.26)	50.5 (11.3)	4.92 (0.98)
	root : shoot (total shoot)	0.79 (0.11)	0.15 (0.04)	14.8 (2.4)	2.90 (0.26)
	root : shoot (green shoot only)	1.13 (0.08)	0.17 (0.04)	30.2 (10.2)	3.43 (0.38)
	root : rhizome	0.71 (0.17)	0.52 (0.08)	4.26 (1.10)	5.62 (2.65)
mass per shoot	total	5.46 (0.13)	7.39 (1.29)	17.9 (4.5)	27.1 (2.3)
	shoot	1.87 (0.04)	5.14 (0.94)	0.69 (0.15)	5.52 (0.84)
	rhizome	2.11 (0.16)	1.50 (0.55)	2.06 (0.70)	3.25 (0.96)
	root	1.48 (0.24)	0.76 (0.24)	10.6 (3.9)	15.9 (1.6)
	tuber			4.23 (1.39)	2.43 (1.39)

Table 6.1
Final biomass characteristics (g m^{-2}, mean & sd) of monocultures of *Triglochin* and *Baumea* after 20 months growth in shallow (10 cm) and deep (60 cm) water.

demographic characteristics (m^{-2})		***Baumea***		***Triglochin***	
		shallow	deep	shallow	deep
final	no. shoots	728 (39)	111 (9.1)	122 (30.4)	52.8 (9.2)
	no. leaves or stems	1422 (167)	293 (13.9)	436 (99.5)	292 (13.9)
	total height (cm)	67582 (2733)	27619 (2781)	7138 (1449)	14771 (2177)
	no. tubers			881 (60.4)	280 (55.9)
cumulative	no. shoots	1366 (78)	341 (27.7)	153 (41.1)	55.6 (7.9)
	no. leaves or stems	3694 (350)	767 (301)	2980 (619)	1530 (157)
	total height (cm)	206663 (18393)	78181 (9003)	90244 (10965)	137092 (17283)
% survivorship	shoot	53.3 (0.2)	32.7 (3.0)	80.7 (5.1)	95.0 (8.7)
	leaves or stems	38.4 (0.9)	32.4 (5.7)	14.6 (0.8)	14.0 (0.07)
recruitment (per initial shoot)	shoot	15.4 (0.9)	3.8 (0.3)	2.44 (0.92)	0.25 (0.18)
	leaves or stems	41.6 (3.9)	10.4 (1.6)	67.1 (13.9)	34.4 (3.5)

Table 6.2
Final demographic characteristics (g m^{-2}, mean & sd) of monocultures of *Triglochin* and *Baumea* after 20 months growth in shallow (10 cm) and deep (60 cm) water.

cumulative		linear equation	r^2	cumulative rates		related figures
				stems d-1 or leaves d-1	days stem-1 or days leaf-1	
increase in no. stems or leaves						
shallow	***Baumea***	$y = -29.8 + 0.634x$	0.996	0.63	1.58	2a
	Triglochin	$y = -6.83 + 0.459x$	0.997	0.46	2.18	2a
deep	***Baumea***	$y = 9.75 + 0.123x$	0.993	0.12	8.7	2b
	Triglochin	$y = 11.70 + 0.217x$	0.989	0.22	4.61	2b
decrease in no. stems or leaves						
Baumea	**shallow**	$y = -53.22 + 0.373x$	0.862	0.37	2.68	3a
	deep	$y = -7.22 + 0.114x$	0.981	0.11	8.77	3a
Triglochin	**shallow**	$y = -28.43 + 0.431x$	0.994	0.43	2.32	3b
	deep	$y = -6.65 + 0.213x$	0.994	0.21	4.69	3b

Table 6.3

Equations, r^2 values and rates from linear regressions of the cumulative increase and decrease in the number of *Triglochin* leaves and *Baumea* stems at shallow and deep sites. See related figures for plotted data. (y = cumulative no. of stems or leaves & x = time in days)

		shallow						**deep**					
		initial proportions					related figure	initial proportions					related figure
Triglochin		1.00	0.75	0.50	0.25	0.00		1.00	0.75	0.50	0.25	0.00	
Baumea		0.00	0.25	0.50	0.75	1.00		0.00	0.25	0.50	0.75	1.00	
		Relative Yield Totals						Relative Yield Totals					
dwt-biomass													
total	x	1.00	0.72	0.82	0.98	1.00	14a	1.00	1.51	1.34	1.49	1.00	14b
	sd		0.07	0.10	0.13				0.21	0.24	0.38		
shoot	x	1.00	0.76	0.81	0.93	1.00	15a	1.00	1.26	1.27	1.38	1.00	15d
	sd		0.22	0.08	0.09				0.15	0.19	0.22		
root	x	1.00	0.64	0.75	0.78	1.00	15b	1.00	1.87	1.78	1.71	1.00	15e
	sd		0.05	0.25	0.19				0.26	0.58	0.56		
rhizome	x	1.00	0.99	1.19	1.41	1.00	15c	1.00	1.52	1.40	2.01	1.00	15f
	sd		0.24	0.09	0.20				0.22	0.21	0.58		
cumulative no.													
stems or leaves per shoot	x	1.00	0.64	0.90	1.00	1.00	16a	1.00	1.12	1.22	1.39	1.00	16c
	sd		0.09	0.03	0.21				0.21	0.19	0.38		
shoots per shoot	x	1.00	0.56	0.83	0.88	1.00	16b	1.00	1.25	1.28	1.08	1.00	16d
	sd		0.09	0.15	0.15				0.22	0.26	0.21		

Table 6.4
The Relative Yield Totals (mean & sd) for the dry weight biomass of *Baumea* and *Triglochin* tissues and the cumulative number of stems, leaves and shoots recruited per initial shoot, in shallow and deep water. See related figures.

		shallow					**deep**				
		B/T	Log10	**T/B**	Log10	related figure	**B/T**	Log10	**T/B**	Log10	related figure
dwt-biomass											
total	x	1.99	0.30	0.65	-0.19	17a	0.37	-0.43	3.36	0.53	17b
	sd	0.96		0.31			0.19		1.35		
shoot	x	2.44	0.39	0.45	-0.34	18a	0.39	-0.41	3.23	0.51	18d
	sd	0.77		0.15			0.17		1.54		
root	x	4.79	0.68	0.27	-0.57	18b	0.74	-0.13	2.11	0.32	18e
	sd	2.37		0.14			0.55		1.14		
rhizome	x	0.94	-0.03	1.16	0.06	18c	0.43	-0.37	2.84	0.45	18f
	sd	0.26		0.36			0.19		1.19		
cumulative no.											
stems or leaves per shoot	x	2.27	0.36	0.45	-0.35	19a	0.98	-0.01	1.06	0.03	19c
	sd	0.30		0.06			0.18		0.19		
shoots per shoot	x	2.21	0.34	0.53	-0.28	19b	0.37	-0.43	2.99	0.48	19d
	sd	0.87		0.20			0.11		0.95		

Table 6.5
The Relative Crowding Coefficient (mean & sd) for *Baumea* relative to *Triglochin* (B/T) and *Triglochin* relative to *Baumea* (T/B), or the dry-weight biomass of tissues, and the cumulative number of stems, leaves and shoots recruited per initial shoot for 50:50 mixtures. The Log10 of means are included. Refer to related figures.

ratio and depth		no. stems	height (cm)	biomass (g dwt)	no. leaves	height (cm)	biomass (g dwt)	diameter (mm)
		Baumea			***Triglochin***			
shallow								
100T	x				3.60	58.5	0.34	4.69
	sd				1.10	29.8	0.24	1.57
25B : 75T	x	2.42	94.2	1.23	3.08	49.1	0.42	5.86
	sd	0.84	49.1	0.87	1.14	22.6	0.30	3.28
50B : 50T	x	2.04	81.9	1.05	2.33	26.2	0.15	3.64
	sd	0.77	45.0	0.97	1.05	15.7	0.14	2.13
75B : 25T	x	2.17	86.7	1.03	3.11	39.8	0.24	4.73
	sd	0.82	47.6	0.84	1.52	24.2	0.17	2.17
100B	x	2.21	94.3	1.08				
	sd	0.92	51.5	0.82				
deep								
100T	x				4.20	254.2	4.03	8.70
	sd				0.75	77.8	3.33	2.56
25B : 75T	x	2.58	205.7	2.31	4.00	287.8	5.87	10.46
	sd	0.86	96.9	1.91	1.27	134.8	3.64	4.34
50B : 50T	x	2.45	208.7	3.38	4.58	313.2	6.96	11.19
	sd	0.74	129.2	3.19	1.11	121.6	4.94	4.94
75B : 25T	x	2.47	206.8	2.78	4.90	378.4	6.79	11.44
	sd	0.93	111.0	2.25	1.37	119.2	4.08	3.33
100B	x	2.61	244.2	5.17				
	sd	1.15	160.4	4.41				
significance								
depth		***	***	***	***	***	***	***
mixture		ns	ns	ns	ns	ns	ns	ns
depth x mixture		ns	ns	*	ns	ns	ns	ns

Table 6.6
The height, biomass, number of leaves or stems and leaf diameter (mean & sd) per shoot of *Triglochin* and *Baumea,* in controls and mixtures and in shallow and deep water. The results of 2-way AOV's (factors: depth, mixture) for each characteristic are shown. (***=P < 0.01, *=P < 0.05,

initial proportion	total number of flowering shoots				% of population that flowered			
	1.00	0.75	0.50	0.25	1.00	0.75	0.50	0.25
Baumea								
shallow								
x	14.25	6.25	5.75	3.25	0.128	0.075	0.073	0.087
sd	4.09	0.83	4.32	5.07	0.031	0.012	0.042	0.137
deep								
x	0.250	0.250	0.250	0.000	0.021	0.007	0.018	0.000
sd	0.433	0.433	0.433	0.000	0.036	0.011	0.031	0.000
Triglochin								
shallow								
x	0.500	0.250	0.500	0.750	0.026	0.050	0.148	0.375
sd	0.866	0.433	0.500	0.829	0.046	0.087	0.207	0.415
deep								
x	1.000	0.500	1.000	1.000	0.183	0.083	0.217	0.288
sd	1.000	0.866	0.707	0.707	0.185	0.144	0.136	0.188

Table 6.7
The absolute and proportional number of shoots that flowered (mean & sd) in monoculture (1.0) and mixture (0.75, 0.50, 0.25) crate populations.

depth	nutrient	shoot	root	rhizome
shallow	N	0.002	0.024	<0.001
	P	0.990	<0.001	<0.001
deep	N	0.252	0.260	0.004
	P	0.051	0.006	<0.001
shallow	Na+	<0.001	<0.001	<0.001
	K+	<0.001	<0.001	<0.001
deep	Na+	<0.001	<0.001	<0.001
	K+	0.002	<0.001	<0.001

Table 6.8
The probability levels of 1-way AOV's comparing the concentrations of N and P (mg g-1 dwt) and Na+ and K+ (µM g-1 dwt) (see Table 6.9) in the tissues of *Triglochin* and *Baumea,* in shallow and deep water.

		P (mg g-1 dwt)				N (mg g-1 dwt)				Na+ (µM g-1 dwt)				K+ (µM g-1 dwt)				Na+ : K+			
		root	shoot	rhizome	tuber	root	shoot	rhizome	tuber	root	shoot	rhizome	tuber	root	shoot	rhizome	tuber	root	shoot	rhizome	tuber
SHALLOW																					
Triglochin																					
pure	x	2.60	2.37	6.57	2.60	6.25	9.66	16.97	4.12	717.1	793.4	175.7	119.6	568.4	732.4	227.7	311.3	1.23	1.13	0.78	0.40
	sd	0.78	0.48	0.96	0.57	1.02	1.07	1.47	1.86	303.0	137.6	44.1	45.4	146.7	187.5	25.2	48.7	0.25	0.29	0.19	0.19
mixed	x	1.44	1.97	8.48	2.18	8.99	9.77	17.51	2.56	573.6	756.1	143.4	92.6	381.0	729.6	213.7	261.0	1.50	1.06	0.68	0.36
	sd	0.18	0.34	0.72	0.43	0.33	1.00	3.76	0.18	142.9	140.7	49.8	56.4	75.6	82.3	16.9	45.9	0.17	0.31	0.24	0.25
Baumea																					
pure	x	0.74	2.37	3.07		4.83	5.22	6.02		137.2	272.3	239.0		49.3	140.0	172.3		2.86	2.03	1.49	
	sd	0.13	0.44	0.48		0.10	1.42	0.65		22.6	14.7	31.0		9.3	32.4	44.1		0.68	0.43	0.55	
mixed	x	0.89	1.83	2.73		4.51	4.05	3.27		162.3	472.2	230.5		65.4	154.5	217.0		2.47	3.15	1.13	
	sd	0.24	0.25	0.30		0.80	0.22	0.67		56.9	241.9	9.2		10.7	56.8	79.2		0.64	1.24	0.37	
DEEP																					
Triglochin																					
pure	x	3.69	2.67	6.21	3.89	6.80	9.04	9.30	2.28	632.6	915.3	208.0	105.6	412.1	601.5	233.8	321.8	1.56	1.56	0.90	0.34
	sd	0.55	0.51	1.30	0.55	0.62	0.70	1.28	0.69	179.5	179.7	47.3	27.6	78.8	107.3	29.0	86.8	0.46	0.34	0.20	0.12
mixed	x	2.82	2.60	6.95	3.35	7.43	8.96	14.94	2.46	641.3	910.4	167.1	110.4	371.8	592.5	172.4	260.0	1.74	1.62	1.06	0.46
	sd	0.71	0.50	2.21	0.67	0.81	1.17	2.39	0.79	82.9	200.4	65.4	42.0	65.1	126.3	60.7	101.7	0.13	0.56	0.47	0.20
Baumea																					
pure	x	2.23	3.16	2.53		6.23	8.05	5.29		208.0	583.0	334.0		87.0	461.5	227.0		2.39	1.28	1.85	
	sd	1.24	0.41	0.79		0.69	1.39	1.25		32.8	39.9	36.8		10.0	75.4	135.8		0.28	0.16	1.27	
mixed	x	1.99	2.59	2.33		5.37	6.75	5.09		207.6	304.5	289.3		117.4	270.4	72.5		2.16	1.20	4.82	
	sd	0.26	1.13	1.66		0.61	2.12	0.34		29.1	175.4	121.0		57.3	162.6	51.6		1.05	0.38	1.65	

Table 6.9
Final concentrations (mean & sd) of major nutrients in the tissues of *Baumea* and *Triglochin*, in shallow and deep water and in monoculture and mixture (50:50).

	source of variation	shoot	root	rhizome	tuber
Triglochin					
P	depth	0.004	<0.001	0.161	<0.001
	mixture	0.275	<0.001	0.002	0.012
	depth x mixture	0.180	0.943	0.513	0.752
N	depth	0.178	0.196	0.001	0.093
	mixture	0.979	0.001	0.026	0.223
	depth x mixture	0.859	0.014	0.058	0.129
Baumea					
P	depth	<0.001	0.004	0.280	
	mixture	0.936	0.030	0.584	
	depth x mixture	0.463	0.952	0.483	
N	depth	0.195	0.003	0.003	
	mixture	0.003	0.081	0.116	
	depth x mixture	0.008	0.392	0.930	
Triglochin					
Na+	depth	0.105	0.967		
	mixture	0.648	0.205		
	depth x mixture	0.807	0.493		
K+	depth	0.008	0.070		
	mixture	0.492	0.003		
	depth x mixture	0.530	0.054		
Baumea					
Na+	depth	0.346	<0.001		
	mixture	0.137	0.391		
	depth x mixture	<0.001	0.375		
K+	depth	<0.001	<0.001		
	mixture	0.019	0.050		
	depth x mixture	0.008	0.533		

Table 6.10
The probability levels of 2-way AOV's comparing the influence of depth and mixture on the concentrations of N and P (mg g-1 dwt) and Na+ and K+ (µM g-1 dwt) in the tissues of *Triglochin* and *Baumea*.

	root		shoot		rhizome		tuber		total	
	shallow	**deep**	**shallow**	**deep**	**shallow**	**deep**	**shallow**	**deep**	**shallow**	**deep**
Triglochin										
monoculture	2.40	1.84	4.07	3.38	2.58	1.50	1.59	0.59	2.34	1.88
mixture	6.22	2.63	4.96	3.44	2.06	2.15	1.17	0.73	2.33	2.43
Baumea										
monoculture	6.51	2.79	2.20	2.55	1.96	2.09			2.46	2.49
mixture	5.07	2.70	2.21	2.60	1.20	2.18			2.04	2.46

Table 6.11
The N:P ratios within each tissue and in the plant as a whole, in monocultures and mixtures (50:50) and in shallow and deep water.

	N g m^{-2}		P g m^{-2}	
	shallow	**deep**	**shallow**	**deep**
Triglochin				
monoculture	12.76	10.28	5.44	5.47
mixture	4.61	11.74	1.98	4.83
Baumea				
monoculture	21.19	6.60	8.61	2.65
mixture	8.73	3.00	4.27	1.22

Table 6.12
The total amount of nitrogen and phosphorus (g) held in the whole plant on a m^{-2} basis, in monocultures and mixture (50:50) and in shallow and deep water.

	C:P	C:N
Baumea	**monoculture**	
	root	shoot
shallow	634.3	90.1
deep	210.3	58.4
probability level	0.018	0.048
Triglochin	**shallow**	
	root	
monoculture	180.6	
mixture	325.4	
probability level	0.087	
Baumea	**shallow**	
	rhizome	rhizome
monoculture		78.0
mixture		144.0
probability level		0.013
Baumea	**deep**	
	rhizome	rhizome
monoculture	186.0	89.1
mixture	84.2	38.6
probability level	0.076	0.070

Table 6.13
The significant results of 1-way AOV's (where probability level<0.1), which compared the ratios (means, n=3-4) of C:N and C:P in the tissues of *Baumea* and *Triglochin*, between shallow and deep monocultures, and monocultures and mixtures (50:50) in shallow and deep water.

APPENDICES

data presented from each harvest	aboveground characteristics		belowground characteristics	*Baumea* vegetative reproduction	*Triglochin* sexual reproduction & aboveground characteristics
Baumea					
season	spring	autumn	autumn	autumn	
date	29-Oct-89	15-Apr-89	3-Mar-87	5-May-87	
elevation of water level (AHDm)	48.70	48.00	48.25	48.10	
sampled water depths (cm) and elevations	40 (48.30) 57 (48.13) 67 (48.03) 74 (47.96) 91 (47.79) 101 (47.69) 108 (47.62)	0 (48.30) 0 (48.13) 0 (48.03) 4 (47.96) 21 (47.79) 31 (47.69) 38 (47.62)	5 (48.20) 30 (47.95) 50 (47.75)	0 (48.15) 25 (47.90) 50 (47.65) 55 (47.60)	
quadrat size	20 x 20 cm	20 x 20 cm	20 x 20 cm	25 x 25 cm	
no. of replicates	5	6	4	1	
Triglochin					
date	29-Oct-89	15-Apr-89	3-Mar-87		23-Oct-86
elevation of water level (AHDm)	48.75	48.00	48.20		48.65
sampled water depths (cm) and elevations	30 (48.45) 50 (48.25) 70 (48.05) 90 (47.85)	0 (48.45) 0 (48.25) 0 (48.05) 15 (47.85) 30 (47.70)	0 (48.20) 25 (47.95) 50 (47.70)		25 (48.40) 50 (48.15) 60 (48.05) 70 (47.95) 80 (47.85)
quadrat size	-	1.0 x 0.2 m	1.0 x 0.2 m		1.0 x 0.2 m
no. of replicates	10	5	1		5

Appendix 3.1
The date, season, elevation, depths, quadrat size and number of replicates for harvests of each species. The data presented from each harvest is shown.

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treatment		initial depth		final depth	no. replicates at 9 & 12 months (9/12)		
		1987 3-Mar	8-Dec	1988 3-Mar	*Baumea*	*Triglochin*	
						ramet	seedling
1) Constant depth for 9 months							
exposed (0 cm)	0	0		0	16/8	12/4	16/8
inundated (50 cm)	50	50		50	16/8	12/4	16/8
inundated (100 cm)	100	100		100	12/4	12/4	12/4
2) Constant depth for 9 months followed by a sudden change in depth kept for 3 months.							
Submergence from 0 cm							
exposed (0 cm)	0	0		0	8	4	8
exposed (0 cm) + 50 cm	0/50			50	4	4	4
exposed (0 cm) + 100 cm	0/100			100	4	4	4
Submergence/emergence from 50 cm							
inundated (50 cm) - 50 cm	50/0			0	4	4	8
inundated (50 cm)	50	50		50	8	4	8
inundated (50 cm) + 50 cm	50/100			100	8	4	8
Emergence from 100 cm							
inundated (100 cm) - 100 cm	100/0			0	4	4	4
inundated (100 cm) - 50 cm	100/50			50	4	4	4
inundated (100 cm)	100	100		100	4	4	4

Appendix 4.1
The design of experiment 3: 1) the influence of constant depth and 2) the influence of rapid changes in depth on the growth of *Triglochin* and *Baumea* ramets. The treatments, their initial and final depth, replicate number and duration of inundation are shown.

treatment	sample size			source of variation
	Baumea	***Triglochin***		
		ramet	seedling	
1) Constant depth				
variable = aboveground characteristics af 9 months: total green height, stem or leaf #, shoot #				
exposed (0 cm)	16	12	14	among treatments (depth)
inundated (50 cm)	12	12	4	exposed v inundated
inundated (100 cm)	7	12	3	inundated at 50 v 100 cm
variable = final biomasses after 12 months				
exposed (0 cm)	8	4	10	among treatments (depth)
inundated (50 cm)	8	4	3	exposed v inundated
inundated (100 cm)	0	4	2	inundated at 50 v 100 cm
Results in Table	4.3	4.4	4.4	
2) Constant depth for 9 months then sudden change in depth, kept for another 3 months				
variable = aboveground characteristics af 12 months: total green height, stem or leaf #, shoot #				
variable = final biomasses after 12 months				
0	8	3	10	among treatments (depth)
0 /50	4	4		exposed v inundated
0/100	4	4	4	inundated to 50 v to 100 cm
50/0	4	4		among treatments (depth)
50	8	4		exposed to 0 cm v inundated
50/100	8	4		inundated at 50 v to 100 cm
100/0	0	4		among treatments (depth)
100/50	0	4		exposed to 0 cm v inundated
100	0	4		inundated at 100 cm v to 50 cm
Results in Table	4.5	4.6	4.6	

Appendix 4.2
The analyses undertaken for experiment 3. 1) the influence of constant depth and 2) the influence of rapid changes in depth. The treatments, sample size and source of variation tables for 1-way AOV's and planned comparisons on the aboveground characteristics of *Baumea* and *Triglochin* (at 9 & 12 months) and the final biomasses (after 12 months). Refer to listed tables for results.

		biomass (g dwt)			% allocation		
characteristic		x	sd	P	x	sd	P
total	initial	71.2	41.0	ns			
	T1	51.0	23.9	ns			
	T2	45.4	16.2	ns			
aboveground	initial	30.8	17.0	ns	0.46	0.09	ns
	T1	32.1	17.6	ns	0.61	0.05	ns
	T2	23.8	12.2	ns	0.52	0.09	ns
belowground	initial	40.4	25.1	ns	0.54	0.09	ns
	T1	18.9	7.0	ns	0.39	0.05	ns
	T2	20.4	4.1	ns	0.48	0.09	ns
shoot-base	initial	17.2	10.7	ns	0.24	0.02	ns
	T1	11.8	4.9	ns	0.24	0.05	ns
	T2	11.4	2.8	ns	0.28	0.07	ns
root	initial	8.3	4.3	**	0.11	0.03	**
	T1	2.1	0.5	***	0.05	0.01	***
	T2	2.4	0.8	ns	0.06	0.03	ns
rhizome	initial	14.9	10.8	ns	0.18	0.07	ns
	T1	4.9	1.8	ns	0.10	0.02	ns
	T2	6.1	2.0	ns	0.14	0.03	ns
below : above	initial	1.27	0.47	ns			
	T1	0.64	0.14	ns			
	T2	0.86	0.49	ns			
root : rhizome	initial	0.68	0.18	ns			
	T1	0.46	0.07	ns			
	T2	0.47	0.26	ns			
root : shoot	initial	0.27	0.13	*			
	T1	0.08	0.03	***			
	T2	0.13	0.08	ns			

Appendix 4.3
The final biomass and its allocation (mean & sd) of potted *Baumea* ramets in experiment 1. The initial represents pots harvested at the start and treatments 1 and 2 (T1, T2) represent pots inundated for a short (2-4) weeks) and long (12 weeks) period respectively. Significance levels of 1-way AOV's and unplanned comparisons between the initial and treatments and between treatments are shown.

Leaf recruitment rate, (leaves d^{-1} $shoot^{-1}$),

$$LRR = \frac{CL_2 - C_{L1}}{t_2 - t_1}$$

where CL is the cumulative increase in the number of leaves per shoot at consecutive records: time (t) 2 and 1.

Relative growth rates ($g\ g^{-1}\ d^{-1}$),

$$RGR = \frac{LnW_2 - LnW_1}{t_2 - t_1}$$

where W is the aboveground biomass per shoot (or m^{-2}) at consecutive records: time (t) 2 and 1.

Absolute Growth Rate ($cm\ d^{-1}$),

$$AGR = \frac{H_2 - H_1}{t_2 - t_1}$$

where H is the total leaf height per shoot (or m^{-2}) at consecutive records: time (t) 2 and 1.

The components of AGR ($cm\ d^{-1}$),

$$\text{Increase in height} = \frac{CIH_2 - CIH_1}{t_2 - t_1}$$

$$\text{Decrease in height} = \frac{CDH_2 - CDH_1}{t_2 - t_1}$$

where CIH and CDH are the cumulative increase and decrease in height per shoot (or m^{-2}), respectively, at consecutive records: time (t) 2 and 1.

Appendix 5.1
The equations used for gross, net (absolute) and relative growth rates.

	control **Baumea**	treatments ----------------------mixtures----------------------			control ***Triglochin***
replacement ratios	100:0	75:25	50:50	25:75	0:100
ramet planting densities *(Baumea : Triglochin)*	8:0	6:1	4:2	2:3	0:4
no. crates - shallow (10 cm) - deep (60 cm)	4 4	4 4	4 4	4 4	4 4

Appendix 6.1
The design of the Reciprocal Replacement Series experiment between *Triglochin* and *Baumea*.

	C:P				C:N			
	root	rhizome	tuber	shoot	root	rhizome	tuber	shoot
(a)								
Triglochin								
shallow	180.6	71.6	192.1	197.2	75.2	27.7	121.1	48.4
deep	127.6	75.5	120.4	176.1	69.1	50.4	205.7	52.1
probability level	ns	ns	ns	ns	ns	ns	ns	ns
Baumea								
shallow	634.3	153.1		198.2	97.4	78.0		90.1
deep	210.3	186.0		148.7	75.3	89.1		58.4
probability level	0.018	ns		ns	ns	ns		0.048
(b)								
Triglochin		**shallow**						
monoculture	180.6	71.6	192.1	197.2	75.2	27.7	121.1	48.4
mixture	325.4	55.4	215.3	238.9	52.3	26.8	183.4	48.1
probability level	0.087	ns	ns	ns	ns	ns	ns	ns
Baumea								
monoculture	634.3	153.1		198.2	97.4	78.0		90.1
mixture	527.8	172.4		256.4	104.1	144.0		116.2
probability level	ns	ns		ns	ns	0.013		ns
Triglochin		**deep**						
monoculture	127.6	75.5	120.4	176.1	69.1	50.4	205.7	52.1
mixture	166.6	67.6	187.1	180.4	63.3	31.5	254.8	52.5
probability level	ns	ns	ns	ns	ns	ns	ns	ns
Baumea								
monoculture	210.3	186.0		148.7	75.3	89.1		58.4
mixture	184.4	84.2		181.2	68.3	38.6		69.6
probability level	ns	0.076		ns	ns	0.070		ns

Appendix 6.2
A comparison of the C to N and C to P ratios (means, n=3-4) in the tissues of *Baumea* and *Triglochin*, in a) shallow and deep water monocultures and b) monocultures and mixtures (50:50) in shallow and deep water. The results of 1-way AOV's (ns>0.1, probability level given if <0.1) are shown.