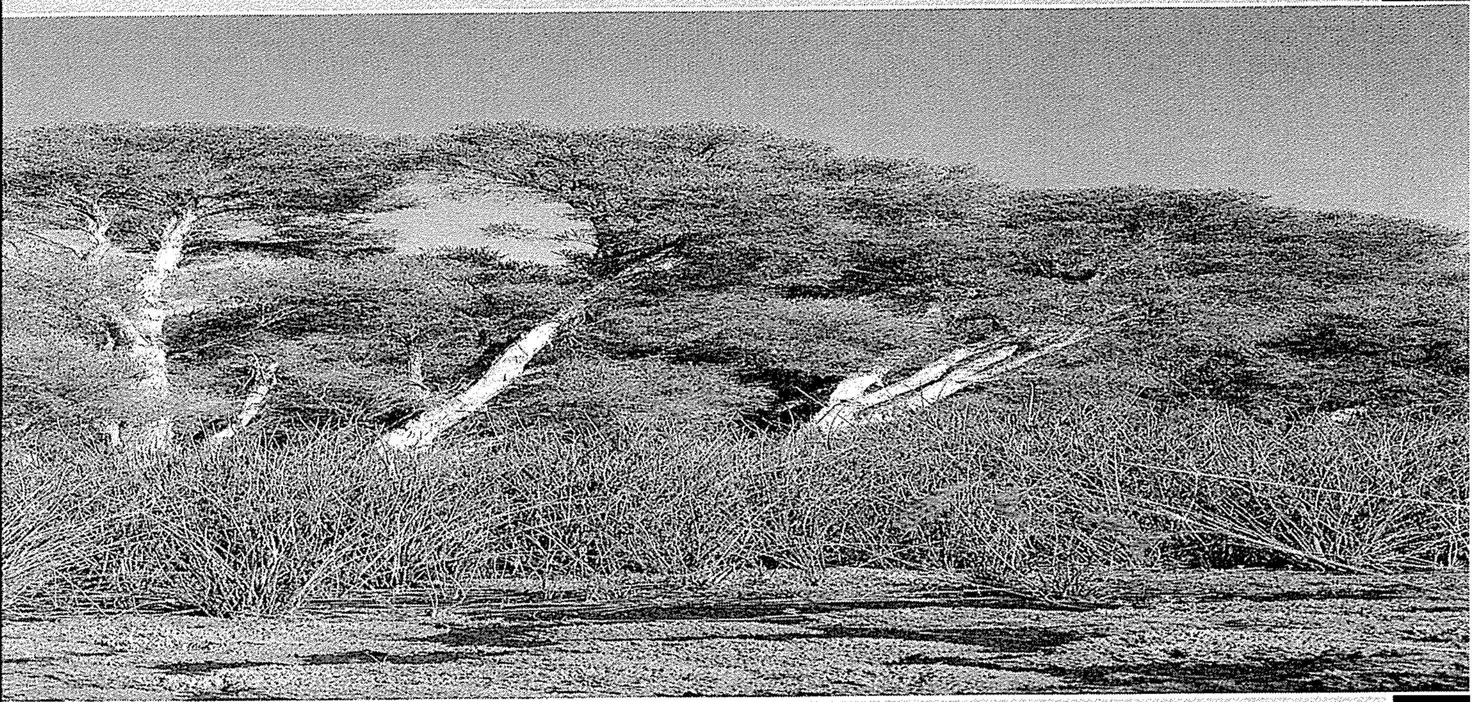
WETLANDS OF THE SWAN COASTAL PLAIN

Volume 4



The Effect of Altered Water Regimes on Wetland Plants

H. Froend, R. C. C. Farrell, C. F. Wilkins, C. C. Wilson and A. J. McComb

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Preface

The wetlands of the Swan Coastal Plain provide a habitat for many millions of animals and plants. Prior to European settlement the flora and fauna of these wetlands would have been as rich and diverse as the wetlands of Kakadu today. Many of the wetlands that once existed on the Swan Coastal Plain have been filled, drained, mined for peat or clay, or cleared of vegetation. As the urban and rural areas continue to expand and engulf more wetlands, the remaining wetlands become pressured by vegetation clearing, grazing, flooding, organic and metal contamination, nutrient enrichment and groundwater extraction. Clearly, there is a need to establish the extent of the wetland resource and develop strategies for wetland management.

Good management requires detailed information about the groundwater, the plants and the animals that live in these wetlands and the processes that bind them together. Good wetland management requires wetland boundary description, detailed information about surface and groundwater hydrology and the plants and animals that depend on them. Research provides information that enables managers to restore unhealthy wetlands and protect and conserve healthy ones.

Jeff Kite at the Water Authority of Western Australia, and the late Jenny Arnold, Bob Humphries and John Sutton at the Environmental Protection Authority and the Australian Water Resources Advisory Council (now Land and Water Resources Research and Development Corporation) have been instrumental in coordinating and funding five wetland research projects. The first of these projects commenced in 1988 and each project ran for at least 3 years and cost a total of $1.2 million in funding.

Research proposals for these projects were developed by Lloyd Townley and Jeff Turner at CSIRO Division of Water Resources, by Stuart Halse and Jim Lane at the Department of Conservation and Land Management in Woodvale in association with Rodney Vervest and Roger Jaensch of the Royal Australasian Ornithologists Union and Tony Ford at the Water Authority, by Jenny Davis and Arthur McComb at Murdoch University and Ron Rosich at the Water Authority. Other people that have been involved in coordinating these projects are Brian Kavanagh, Charlie Nicholson, Paul Lavery, Roy Stone and Karen Hillman.

Together with information on mapping and classification of wetlands by the V & C Semeniuk Research Group, initiated and coordinated by Alan Hill at the Water Authority, the results of this research form volumes 2 to 7 in this series Wetlands of the Swan Coastal Plain.

In order to encourage use of the information resulting from this research, volume 1 is a synthesis of information on wetlands of the Swan Coastal Plain and a tool for managers of wetlands.

Shirley Balla
July 1993

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Executive Summary

Objectives
The distribution, productivity and reproduction of emergent macrophytes (rushes and sedges) at eight wetlands on the Swan Coastal Plain were studied. The aim was to predict the consequences of altered water level regimes on the survival of individual species of common emergent plants and on the composition of emergent plant communities.

Wetland Water Regime
The wetlands on the Swan Coastal Plain are generally surface expressions of the shallow unconfined groundwater. The combination of successive years of below-average rainfall and the accelerated use of groundwater has resulted in concern being expressed within the community that the conservation value of wetlands is being compromised. A significant feature of these wetlands is the seasonal wet-dry cycle, maximum water levels occurring in September-October and minimum levels in March-April.

Wetland Vegetation
Highest species diversity was observed at shallow seasonal wetlands. A zonation of species and communities down the littoral gradient was evident at all wetlands. Peripheral wetland tree species occupied the highest elevations, and sedges and rushes typically occupied the lower elevations. The species of emergent macrophytes are adapted to both seasonal and long-term changes in water regime typical of a Mediterranean climate. They tolerate flooding and short periods of drought within each year, although the degree of tolerance varies between species. The fringing vegetation of all the wetlands studied was dominated by 1-3 species of sedge and or rush.

Vegetation Response to Water Regime
Changes in the quantity and quality of water being drained into wetlands is of concern. Increased quantity results in prolonged inundation of vegetation and corresponding decrease in dry period. Higher nutrient concentrations often increase macrophyte productivity but can have a detrimental affect when coupled with prolonged flooding, apparently because of increasing sediment anoxia.

Examination of changes in wetland vegetation with time, showed that emergent macrophyte communities are very dynamic, responding rapidly to both increases and decreases in water regime. The rate and magnitude of a change in plant distribution depends on the rate and magnitude of change in water regime. Emergent macrophyte vegetation is extremely dynamic, capable of responding rapidly to natural fluctuations in the environment, due to high productivity, rapid vegetative reproduction, high seed production, and tolerance of a wide range in water regimes. Wetland plant communities, in particular the emergent macrophytes, are not permanent or fixed entities, but are assemblages of species coexisting under a given set of environmental conditions. Therefore a given type and distribution of wetland vegetation will persist as long as a suitable environment persists. Changes in species distribution in response to water regime changes, reflect the dynamic and resilient nature of littoral communities and do not necessarily indicate degradation.

Although other factors have a secondary role in influencing community characteristics, water regime is the major determinant of distribution of emergent macrophytes. Depth, timing and duration of flooding and the length of the dry or exposed period are important parameters of water regime; which parameter is the most critical will depend on the elevation of the vegetation relative to water level.

The two most common species of emergent macrophyte are found in essentially the same water regimes. Both *Baumea articulata* (jointed twig rush) and *Typha orientalis* (bulrush) occur within the range of approximately 1.0 m above and 1.0 m below mean water depth. This range represents the maximum and minimum limits within which these species may survive. Experimental results and field observations indicated that optimum growth and reproduction is centred around (± 0.1 m) the point at which mean water level is at ground surface. However, there significant difference in the distribution of macrophytes relative to water regime both within and between wetlands.

Within a population, significant differences occurred in productivity, growth and reproductive phenology along a water regime gradient. Rates of productivity and reproduction (vegetative and sexual) varied seasonally as well as with water regime. At the high (drier) end of a species distribution the duration of the dry period and the minimum water level are the critical water regime parameters. At the lowest point of a species distribution, the duration and maximum depth of inundation are the most critical water regime parameters.

Differences in Vegetation Response Between Wetlands

Differences between wetlands in the distribution of a species were found to be due to the influence of several environmental factors other than water regime. Plants at nutrient-enriched wetlands generally had higher productivity, and longer periods of growth and flowering although, in combination with prolonged flooding, high nutrient concentrations lead to increased sediment anoxia and reduced plant vigour (or death). Sediment texture also had a significant influence on plant productivity. Productivity was lower on compacted coarse sand and heavy clays, compared to sandy peat or peat sediments. Interspecific interaction is likely at any point where two species are intermixed, and was often observed as a reduction in above-ground standing biomass and productivity of one species. Experimental results indicate that *Typha orientalis* is a superior competitor for rooting space and nutrients compared to *Baumea articulata*.

Plant Reproduction

Although rhizome extension and ramet production is the most common form of reproduction in emergent macrophyte species, seed germination and seedling establishment can be a significant form of recruitment during drawdown periods. If seasonal or long-term changes in water regime result in very shallow water depths or the exposure of open areas of sediment, seed stored within the seed bank from the previous year/s, or the preceding flowering event, will germinate. The larger, longer-lived species of wetland plants, such as the trees *Melaleuca preissiana, M. rhaphiophylla, Eucalyptus rudis* , also respond to changes in wetland water regime, however, their response is slower than emergent macrophytes and is hallmarked by episodic seedling recruitment events.

Implications for Management

The threat of lower wetland water regimes, due to groundwater abstraction for public and private use, is not necessarily a significant one for all wetlands. Relative to long-term variation in rainfall, groundwater abstraction has generally less impact on wetland water levels, although it would exacerbate the effects of a series of low rainfall years. Abstraction does not affect all wetlands equally because it produces localised rather than widespread effects.

A lowering of the water regime would most likely result in a gradual shift of the vegetation down-gradient. However, the exact nature of the vegetation response to a specific groundwater reduction, should only be determined by assessing the current vegetation distribution relative to water regime at the wetland in question. The plants will survive with minimal degradation, if the vegetation distribution occurs within the littoral water regime gradient (after groundwater level reduction) determined in this report.

The rate of wetland water regime reduction due to groundwater abstraction is also a critical factor with respect to vegetation survival. If permanent reduction in water levels is unavoidable, it should be gradual, over 2 or more years depending on the magnitude of the reduction. With respect to vegetation, the timing of seasonal drying of a wetland is not critical, indeed most species will survive permanent shallow inundation in some situations. Vegetative reproduction is not dependant on length and timing of the dry period, however. A favourable period is within the range November - June. Some seasonal wetlands have become permanent or semi-permanent and nutrient enriched as a result of clearing of catchments and urban drainage. This has the effect of reducing the area of fringing emergent macrophyte vegetation. If vegetation is to be preserved at these wetlands, drainage water may need to be diverted or flow reduced and nutrients filtered to allow seasonal drying and reduce sediment anoxia. Variation in water regime, which reflect seasonal and long-term climatic patterns, should be maintained, and artificial maintenance of water levels used only to mitigate the effects of abstraction.

1: Introduction

1.1 Wetlands and Groundwater of the Swan Coastal Plain

The abstraction of groundwater from the Swan Coastal Plain of Western Australia has increased significantly in recent years, providing increased security of water supplies for an expanding urban population. This abstraction has occurred at a time of reduced availability of surface water resources caused by below-average rainfall in the last ten years. The combination of successive years of below-average rainfall and accelerated use of groundwater resulted in community concern that because water table levels are being lowered, wetlands of significant conservation, education and landscape value may be drying up. This research project addresses the effect that continued or increasing use of groundwater may have on the survival of the emergent vegetation of wetland areas on the Swan Coastal Plain. It acknowledges that maintenance of the vegetation of certain wetlands is an appropriate purpose for the allocation of groundwater resources, and attempts to provide an objective basis for this allocation.

The importance of wetlands has been outlined in many studies (e.g. EPA, 1986), and wetland vegetation is central to wetland processes: it extracts nutrients from water and sediments, ameliorates effects of sediment transfer into wetlands, provides primary production for wetland ecosystems, provides a range of habitats for aquatic and terrestrial fauna (including migratory wading birds protected by international treaties) and may link conservation reserves. It also has high landscape value in urban areas. The conservation and management of wetlands in the Swan Coastal Plain is of particular significance since an estimated 75% have been lost due to landfill or drainage for agriculture, roads and playing fields, and use as sites for disposal of urban refuse (Riggert, 1966).

Water depth is the most important factor determining the survival and zonation of emergent vegetation in permanently flooded or waterlogged areas. The lower or deeper boundary at which a species is found is often determined by the tolerance of that species to water depth and light penetration, whilst the upper or shallower boundary is usually determined by how effectively the species competes against others that can tolerate the same moisture conditions. In seasonally waterlogged areas, species tolerance to desiccation also becomes important. This project primarily addresses effects of altered maximum and minimum water levels, but also recognises that changes in the duration of inundation is of prime importance in the survival and zonation of emergent vegetation. Other factors which may be relevant include nutrient availability, forms of physical disturbance, hydrologic history of a wetland, and competition with invasive species.

1.2 Significance of the Project

Water levels in wetlands on the Swan Coastal Plain have undergone marked changes since European settlement. Clearing for agriculture and urbanisation has led to increased runoff and elevated water table levels, whilst tapping of groundwater supplies for domestic use, for irrigation of market gardens and public open space and industry has led to lowered water table levels in some areas. Overlying these changes are the alterations caused by seasonal and annual changes in rainfall; of the many natural factors that affect groundwater levels in the Swan River Coastal Plain, rainfall is the most significant.

In June 1982 the Perth Urban Water Balance Study (PUWBS) was initiated in response to concern over lowered water tables in the Swan River Coastal Plain. The Water Authority of Western Australia (WAWA), in conjunction with the Centre for Water Research at The University of Western Australia (CWR), Geological Survey of Western Australia (GSWA) and the Environmental Protection Authority (EPA - formerly Department of Conservation and Environment) set out to address three objectives in the study: to identify areas where the unconfined groundwater resource may be at risk, to investigate the areas of greatest risk, and to identify groundwater management options for risk areas. One of the intensive studies carried out during the

PUWBS was a comprehensive wetlands review that compiled available hydrogeological, biological and surrounding landuse information on some 100 major wetlands in Perth. Of the eighteen conclusions reached by the PUWBS (PUWBS Executive Summary, 1987), Conclusion 6 noted that 'Urban wetlands are at risk due to hydrogeological changes associated with urban development'. Conclusion 13 noted that 'Effective on-going management of the (groundwater) resource requires comprehensive groundwater monitoring, criteria for environmental management and, because of the complexity of the groundwater system, a calibrated computer model'. Recommendation 5 of the PUWBS also noted that criteria needed to be developed for the water level and water quality tolerances of environmental features that rely upon groundwater for their viability. The research project described here is therefore directly relevant to the conclusions and recommendations of the PUWBS.

There is considerable public interest in wetland conservation throughout Australia (McComb and Lake, 1988, 1990) and notably in the Perth area. A recent study on water allocation in the Perth-Bunbury region (Western Australian Water Resources Council, 1987) recognises that, as a principle, wetland vegetation buffers should be preserved whenever possible. It notes that these wetlands are almost invariably expressions of the groundwater resource and are affected by pumping from the shallow, unconfined aquifer. It recognises that protection of ecosystem maintenance in important wetlands is an appropriate objective in the allocation of groundwater resources. But what water level changes are tolerable? Clearly, the work described here is relevant to management decisions concerning water use priorities. It was also hoped that certain changes in vegetation might be used as biological markers or predictors of water level changes, which will be of considerable management use when hard data are not available.

In addition, this research project addresses one of the two areas of highest priority for research determined at a Workshop of Biological Research Needs for the Management of Metropolitan Wetlands in November 1987, sponsored by the Western Australian Water Resources Council (McComb, 1988). The priority area identified was the need for research on changes in wetland water tables - groundwater extraction, flooding, relation of water table to fringing plants including *Typha*, and long-term past changes and predictions of future change due to climate. The workshop also pin-pointed the need for more biological and ecological information including species and habitat requirements as a high priority area for research. One of the key conditions in the Environmental Protection Authority (EPA) recommendations (EPA Bulletin 295) for the Gnangara Mound Groundwater Resources highlighted the requirement for management of water levels in wetlands.

This discussion of the significance of water allocation in the management of emergent wetland vegetation has concentrated on a local context, because this is where acute problems can be addressed definitively. However the work has broader significance, most directly for other areas of Australia where surface groundwater resources are used, and more generally where altered water levels may affect fringing vegetation (for example farm dams, reservoirs, Coastal Plain wetlands), as well as contribute to discussion of water resources allocation involving ecosystem function. The work also contributes to knowledge on the effects of flooding and drawdown on freshwater emergent plants; in particular there is a dearth of studies which have rigorously documented water level changes and presented these data to best represent the conditions experienced by the vegetation. Finally, the study is relevant to understanding the implications for wetlands of the changes in rainfall which may occur in response to man-induced alterations of the atmosphere.

Several species were chosen for examination in relation to water depth. All were chosen because they are perennial plants rooted in the sediments, and sufficiently common that their distribution could be studied in a range of wetlands. The key species were: *Baumea articulata, Baumea juncea, Typha orientalis, Schoenoplectus validus,* and *Melaleuca preissiana.*

All are common species. *B. articulata* occurs in relatively deep water, but *B. juncea* occurs in waterlogged 'fen' vegetation (McComb and McComb, 1967). *S. validus* usually fringes open water. *Typha* is of particular interest because it expands rapidly in disturbed areas. While most attention was to be given to these monocots, the paperbark *M. preissiana* was included because it is longer-lived and likely to indicate longer-term changes in water level.

There is a considerable literature on Northern Hemisphere species of freshwater emergent plants, particularly *Typha* spp., but most studies are concerned with morphology, phenology, biomass and productivity (e.g. Westlake, 1975; Bradbury and Grace, 1983, and references cited therein). Literature on the effect of altered water levels on emergent vegetation is far less comprehensive, simply because this is a relatively recent area of study (Gaudett, 1977; van der Valk and Davis, 1978, 1980; Yamasaki and Tange, 1981; Grace and Wetzel, 1982; Sjoberg and Danell, 1983; Rorslett, 1984; Hogeland and Killingbeck, 1985). In Australia, relevant literature is even sparser; for example the literature on *Typha* is confined to taxonomy, morphology, genetics, biomass and productivity (Finlayson *et al.*, 1983; Roberts and Ganf, 1986), and gas exchange (Sale and Orr, 1986). Therefore, it was felt that the proposed study would contribute significantly to current knowledge on the ecology of freshwater emergent plants, and provide baseline data on the response of Australian species to altered water levels.

1.3 Specific Aims of the Project

The general aim of the project was to predict the consequences of altered water regimes on the survival of individual species of common emergent plants and on the composition of emergent plant communities, in wetlands of the Swan Coastal Plain.

The specific aims of the project were to:

i Determine empirical relationships between the occurrence of common species of emergent plants and the water levels of different wetlands in which they occur.

ii If there is significant variability in these empirical relationships, determine the importance of other factors such as nutrient availability, sediment structure, light availability and competition in altering species response.

iii Test whether the empirical relationships are due to different tolerances to water level by using glasshouse experiments to examine directly the effects of different water levels on plant growth and seedling establishment.

iv Assess the importance of intra- and interspecific competition in controlling species survival at the shallower end of the water regime range by conducting glasshouse experiments to support field observations.

vi Use the data generated in the above investigations to provide recommendations to management.

2: Study Sites and Species

2.1 Selection of Wetlands for Study

The selection of eight wetlands for particular study was based on several criteria, including geomorphology, sediment type, amount and composition of remaining vegetation, history of water regime change and, trophic status, and collaborative, complementary work on wetlands already under study (Table 2.1). The general approach was to select a group of wetlands that depicted a range in the criteria so that variability in plant response between wetlands could be determined. Most of the wetlands chosen were of particular interest to the Water Authority of WA and Environmental Protection Authority as they are potentially affected by groundwater abstraction for private and public water supply (Water Authority of WA, 1986; 1991). Some of the wetlands selected were also affected by increasing groundwater and drainage input, that have resulted in rising water levels (Chapter 3). The characteristics of each study wetland are described below. Much of this information was obtained from Jenny Arnold's Perth Wetlands Resource Book (Environmental Protection Authority and Water Authority of WA, 1990).

Table 2.1: Characteristics of the 8 study wetlands. Arrows indicate current trends in lake levels and nutrient enrichment.

LAKE	G/WATER MOUND	GEOMORPH.	SEDIMENT	LAKE LEVEL TREND	NUTRIENT ENRICH.	SEDGE AREA (ha.) 1963	1987
Loch McNess	Gnangara	Spearwood	peat/sand	<>	<	114.5	118.7
Jandabup	Gnangara	Bassendean	sand	<<	<	23.4	181.9
Joondalup	Gnangara	Spearwood	peat/sand	<	>	127.3	70.1
Nowergup	Gnangara	Spearwood	peat/sand	<	>>	8.3	12.6
Herdsman	Gnangara	Spearwood	peat/sand	<>	>	-	-
Thomson	Jandakot	Spear./Bass.	peat-sand	>>	>	54	85.6
Banganup	Jandakot	Spear./Bass.	peat-sand	<	<	30.6	23.9
Forrestdale	Jandakot	Bassendean	clay/sand	<	<	0	20.4

Banganup Lake

Banganup Lake was selected for its extensive fringing vegetation which is comparatively undisturbed. The total area of the wetland is 37.5 ha. Of this total, 24.7 ha and 11.1 ha is sedgeland (*Baumea articulata*) and *Melaleuca preissiana/Eucalyptus rudis* woodland respectively. Consequently, the lake has little open water. Lying over the Jandakot groundwater mound, the lake is part of the Beeliar wetland chain (Fig. 2.1). The lake is a shallow oval basin with a sandy peat sediment. The water regime of this ephemeral lake has shown signs of becoming drier, although in recent years mean water level has increased gradually (Chapter 3). The lake will be affected by proposed increased groundwater abstraction to the east, but is currently unaffected by drainage.

Thomson Lake

The significant area of emergent macrophytes, and changing water and nutrient regimes were the major reasons for selecting Thomson Lake. The lake is a large (253.7 ha) shallow circular basin surrounded

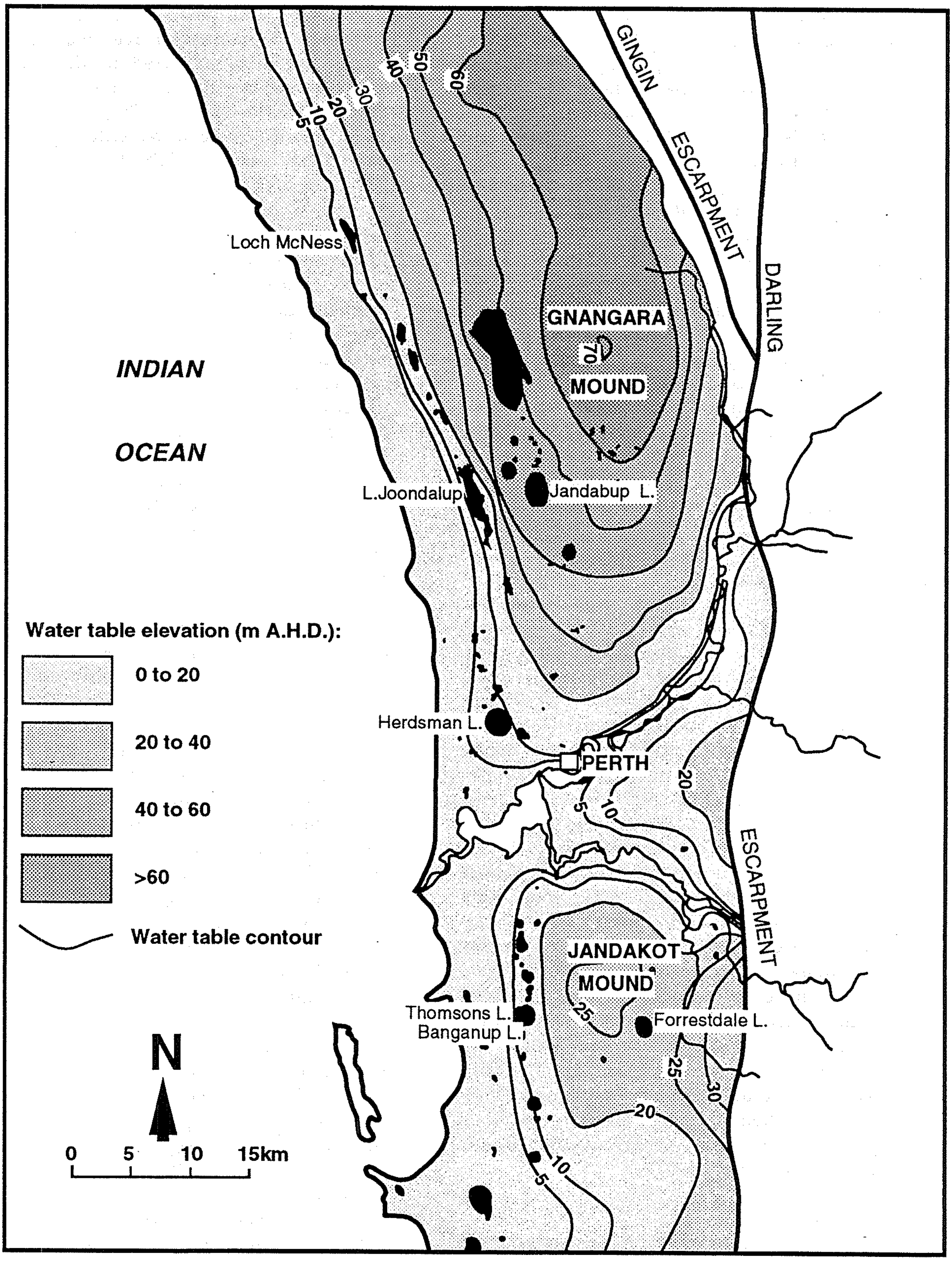


Figure 2.1: Location of the eight study wetlands on the Swan Coastal Plain, and position relative to the Gnangàra and Jandakot groundwater mounds.

by a ring of sand dunes. The extensive fringe of sedgeland (101.2 ha) is comprised of *Baumea articulata* and *Typha orientalis,* which is surrounded in part by *Melaleuca /E. rudis* woodland (1.3 ha). There has been a marked expansion of *Typha* since the mid-late 1970's, and this was of particular interest to the study of interspecific interactions (Chapters 4 and 7). Sediment structure is sandy peat similar to Banganup. Water levels have increased and decreased dramatically in the past with the lake changing from being seasonal to holding permanent water for several years. Currently, water levels are increasing gradually, with periods of drying occurring infrequently. Land use changes within the catchment have elevated nutrient concentrations as well as water levels (Davis and Rolls, 1987). The lake is currently affected by rural drainage and urban drainage will also impact on the lake in the near future.

Forrestdale Lake
The different sediment type and the extensive fringe of *Typha orientalis* were the major reasons for selecting this wetland. The total area of the wetland is 247 ha of which 10.7 ha is sedgeland (predominantly *Typha orientalis*) and 14.8 ha is fringing *Melaleuca* woodland. *Typha* has expanded from virtually no occurrence to its present distribution in the 16 years since 1976. The lake is a very shallow, flat-bottomed circular basin surrounded by a ring of low dunes. The sediment is generally a sand overlying alluvial clay, with relatively little organic matter. Rural drains and stormwater drains from urban areas enter the lake. Marked changes in water regime have occurred in recent years, after levels dropped rapidly since 1974, maximum levels have remained relatively constant (refer to Chapter 3). However, the lake is still seasonal. Due to the nearby septic tanks and rural and urban drainage entering the lake, nutrient levels have increased over recent years (Davis *et al.*, 1987).

Herdsman Lake
The lake was selected for its extensive area of *Typha orientalis.* The total area of the lake is 340 ha of which most is sedgeland. There is little remaining peripheral wetland vegetation due to past agricultural activities and present urban development. The lake is a shallow circular basin with sandy peat sediments, and has several urban drains entering it from an extensive area. Although water levels have varied in the past, the drainage water entering the lake has reduced this variability (refer to Chapter 3). Due to the urban drainage water entering the lake, nutrient levels are high (Davis and Rolls, 1987).

Joondalup Lake
Joondalup Lake was selected for its different geomorphology and sediment type, and extensive areas of remaining vegetation. The total area is 529 ha of which 79 ha is sedgeland and 64 ha is *Melaleuca/ Eucalyptus rudis* woodland. The sedgeland is generally composed of *Baumea articulata, Typha orientalis,* and *Schoenoplectus validus. Melaleuca rhaphiophylla* is the dominant fringing tree species (Congdon and McComb, 1976). More than 50% of the lake has a wide buffer of native vegetation although it has been altered in some areas by urban development and recreation. The width of fringing vegetation is relatively narrow due to the steep sides of the lake. The lake is a large relatively deep linear interbarrier depression, with sediments derived from limestone deposits. Urbanisation within the catchment has lead to increased surface flow and nutrient load into the lake (Congdon, 1981 and 1986; Davis and Rolls, 1987), resulting in problems with algal blooms and chironomid midges. Significant increases in water level have occurred in the past, but levels have dropped in recent years tending towards a seasonal regime (as it may have been originally). However, proposed urban development to the north of the lake is expected to raise water levels significantly.

Jandabup Lake
The extensive, relatively undisturbed emergent vegetation, low nutrient concentrations, and past, present and future changes in water regime, were the major reasons for selecting this wetland. The area of the wetland is 330 ha of which 134 ha is sedgeland. The sedgeland is dominated by *Baumea articulata* and *Leptocarpus* sp.. There are only a few remnants of the fringing tree vegetation remaining which are dominated by *Melaleuca* spp (refer to Chapter 4). The wetland is a shallow circular basin surrounded by sand ridges. Just

over half of the lake bed is covered with organic sediments, mostly diatomite, while the periphery is covered with sand (Allen, 1979). Lake levels have responded to catchment clearing, groundwater abstraction and climate trends, resulting in a distinct fall in levels during 1968-1984, since then levels have stabilised at a seasonal regime (Chapter 3). There is no surface drainage into the lake. Nutrient levels are relatively low, with no records of algal blooms (Davis and Rolls, 1987).

Nowergup Lake
Nowergup Lake was selected on the basis of its relatively intact fringing vegetation, sediment type, and potential response to nearby groundwater abstraction. The total area of the wetland is 54.3 ha of which 6.9 ha is sedgeland and 7.8 ha is fringing tree vegetation. The sedgeland is composed of *Baumea articulata* and *Typha orientalis*. *Melaleuca rhaphiophylla* is the dominant tree species. There has been a dramatic increase in the area covered by *Typha orientalis* since 1976. The lake is a small deep linear basin with similar sediments to Joondalup and McNess. Water level fluctuations are relatively low, however there is a trend towards lower levels (Chapter 3). Effluent from an adjacent piggery is the sole source of drainage into the lake, and has lead to high nutrient levels.

Loch McNess
This wetland was selected for its relatively constant water regime and large area of intact vegetation. The constant water regime enabled a comparison with other wetlands with a more dynamic water regime. The total area of the wetland is 255.3 ha, 149.3 ha of which is sedgeland and 56.6 ha is fringing tree vegetation. The sedgeland is composed of *Baumea articulata*, *Schoenoplectus validus*, *Typha orientalis*, and *Baumea juncea*. *Melaleuca rhaphiophylla* and *Eucalyptus rudis* dominate the fringing woodland. The lake is a linear depression with similar sediment to Nowergup and Joondalup. Water levels have remained fairly constant since records began, varying by less than 20 cm throughout the year (McComb and McComb, 1967). Loch McNess is the only wetland on the Swan Coastal Plain for which recorded water levels show no increasing or decreasing trend. The very low nutrient concentrations reflect the absence of surface drainage into the lake (Davis and Rolls, 1987).

2.2 Key Species

There have been few studies of the ecology of wetland vegetation on the Swan Coastal Plain. McComb and McComb's (1967) study of vegetation at Loch McNess and Congdon's (1981) study of marsh vegetation on the Blackwood River (although not on the Swan Coastal Plain) are some of few notable exceptions in which vegetation zonation and succession is described relative to water regime and other environmental parameters. Generally, descriptions of vegetation zonation have been an adjunct to alternative research objectives such as water quality and nutrient dynamics (e.g. Atkins *et al.* 1977; Congdon and McComb, 1981).

Nevertheless, sufficient information exists to enable dominant wetland plant species on the Swan Coastal Plain to be defined. With respect to the fringing emergent vegetation of wetlands, there are several dominant species of which one or more are found at every wetland. Most of these species are emergent macrophytes such as sedges and rushes belonging to the families Juncaceae, Typhaceae, Restionaceae and Cyperaceae. They typically inhabit open areas of the littoral zone forming dense stands around the waters edge but also occur as a sparse understorey in *Melaleuca* woodlands. Their mode of clonal growth through extension of the underground rhizome and formation of ramets, enables high productivity rates despite a changing environment. The fringing tree vegetation, occurring on higher ground, is typically composed of waterlogging-tolerant species mostly in the Myrtaceae but with one in the Proteaceae (1 species only).

Generally all species are adapted to seasonal waterlogging and/or inundation, and can be found at a range of wetland types, both lentic and lotic. This is supported by the relatively cosmopolitan distribution of wetland plant species (McComb and McComb, 1967). The key species of the Swan Coastal Plain are as follows (taxonomic descriptions are from Marchant *et al.*, 1987):

***Baumea articulata* (Cyperaceae)**
Common name: Jointed Twig Rush. *B. articulata* is a species common to many

wetlands on the Swan Coastal Plain. It is usually the dominant large emergent macrophyte and as such is an ecologically important species. It can tolerate deep inundation (>1m) for prolonged periods (>6 months) but generally has a wide tolerance range. Its distribution extends from just north of the Perth region to Fitzgerald River National Park. It is also found in all mainland states except Northern Territory. It is a perennial herb, up to 2.5 m high. Stems are terete (round in cross section), 6-13 mm in diameter, hollow and articulate (divided into segments). Leaves are similar and arise from the base of the plant. The inflorescence is a pendulous panicle (loose, irregular compound inflorescence) 0.2-0.4 m long. Flowers during September - December. There are six other species of *Baumea* recorded for the Swan Coastal Plain, all of which occur in wet depressions.

Baumea juncea **(Cyperaceae)**
Common name: Bare Twig Rush. *B. juncea* generally occurs under drier water regimes (waterlogging only) than *B. articulata*. It is less common and is rarely the dominant fringing emergent macrophyte species of a wetland. It is however, an ecologically important species at seasonal wetlands with a narrow range in water level. Distribution extends in near coast areas from Dongara to the Recherche Archipelago, and also SA, Vic, Tas and NSW. It is a perennial herb, up to 1.2 m high. Stems terete, 1-mm in diameter, usually 2 or 3 noded below the inflorescence, smooth. Leaves are reduced, 2-10 mm long, sheathing closely around the stem. Inflorescence spike-like, 10-60 mm long. Flowers during October-January.

Typha orientalis **(Typhaceae)**
Common name: Bulrush, Broadleaf Cumbungi. *T. orientalis* is a large emergent macrophyte and occurs at similar habitats to *B. articulata*. It is apparently introduced to Western Australia (native to the eastern states) where it is an aggressive coloniser of disturbed sites. However, it has dominated many wetlands and can be considered of ecological importance where native species have been lost or extensively disturbed (e.g. Herdsman Lake). It occurs mainly on the Swan Coastal Plain. Perennial herb, up to 4.5 m high. Stems 4-7 mm broad below the inflorescence. Leaves a sheath with blade 5-14 mm wide. Inflorescence with no separation or with a separation of up to 60 mm between the male and female portions, which are both cylindric, mature female portion usually chestnut brown. Flowers during November-January. Another species, *T. domingensis*, is considered native to WA and is sometimes found intermixed with *T. orientalis*. However, this species is less common on the Swan Coastal Plain and is the dominant *Typha* species in the northern part of the state.

Juncus pallidus **(Juncaceae)**
Common name: Pale Rush. *J. pallidus* is a medium to large emergent macrophyte that generally only occurs on waterlogged ground. It seldom forms large dense monospecific stands and tends to co-occur with other species of similar tolerance. Distribution extends from Dandaragan to east of Ravensthorpe, and it also occurs in SA, Vic, Tas and NSW. It is a perennial herb, up to 2m high. Stems arising singly along a creeping rhizome, terete, pale green, 2-7 mm broad, finely striate with a continuous pith. Leaves basal, reduced to a scale-like sheath, 120-230 mm long. Inflorescence a panicle, erect but appearing lateral, 25-185 mm long. Flowers during October-November. There are 11 other species of *Juncus* found on the Swan Coastal Plain which are associated with freshwater and brackish wetlands.

Schoenoplectus validus **(Cyperaceae)**
Common name: Lake Club-rush. This species is another large emergent macrophyte able to tolerate prolonged inundation. It forms dense stands and is also found intermixed with other large rushes such as *B. articulata* and *T. orientalis*. Occurs in winter-wet depressions and estuaries from Yanchep to the Blackwood River, and it also occurs in all other states. Perennial herb, up to 2 m high. Stems stout, terete, 3-8 mm broad, usually with fairly obvious longitudinal grooves. Leaves reduced to the sheath. Inflorescence resembling an irregularly compound umbel, terminal but appearing lateral, with numerous spikelets. Flowers December- January. Only two other species of Schoenoplectus, also associated with winter-wet depressions, occur in the state.

Lepidosperma longitudinale **(Cyperaceae)**
Common name: Pithy Sword-sedge. Can occur as the dominant sedge at some wetlands, particularly those that have a *Melaleuca* canopy over most of the littoral zone. Generally prefers waterlogged areas only,

with short periods of inundation. Distribution extends from Watheroo to the south coast, and occurs in all states except NT. Perennial herb, up to 2 m high. Stems 4-7 mm broad, convex on both surfaces, margins often compressed, acute, quite smooth. Leaves shorter and more compressed than the stems and often broader. Inflorescence is a panicle 90-300 mm long. Flowers during May-October. There are 16 other species of *Lepidosperma* which occur on the Swan Coastal Plain and Perth region.

Melaleuca rhaphiophylla **(Myrtaceae)**
Common name: Swamp Paperbark. *M. rhaphiophylla* is a common tree species which generally occurs at the drier end of the littoral zone. It is able to tolerate periodic inundation for several months of the year, but prefers waterlogged sites. It is of particular ecological significance as it provides habit for many waterbirds, and few fringing *M. rhaphiophylla* woodlands remain. Can be found near both fresh and saline water, but is less adapted to saline conditions. Distribution extends along the coast from Kalbarri to Fitzgerald River National Park and inland to York. Tree, up to 10 m high, bark stripping off in sheets. Leaves alternate widely spreading, petiole recurved, short, blade terete, 20-40 mm x 0.5-1 mm, apex pointed. Inflorescence is a spike, 10-40 mm. Flowers during September-January.

Melaleuca preissiana **(Myrtaceae)**
Common name: Modong, Moonah. *M. preissiana* tends to prefer only waterlogged soils and appears to be less tolerant of prolonged inundation than *M. rhaphiophylla*. There are few fringing *M. preissiana* woodlands remaining on the Swan Coastal Plain, and the species tends not to be intermixed with *M. rhaphiophylla*. Distribution extends along the coast from Eneabba to Fitzgerald River National Park, with scattered occurrences well inland. Tree, up to 10 m high, with whitish paper bark. Leaves alternate, spreading, shortly petiolate, blade narrowly elliptic, 9-14 x 1-2 mm, acute, indistinctly 3-veined. Inflorescence is an interrupted leafy spike, 20-70 mm long. Flowers during November-January.

Eucalyptus rudis **(Myrtaceae)**
Common name: Flooded Gum. *E. rudis* is a common species fringing winter-wet depressions and water courses throughout the Swan Coastal Plain. It is able to tolerate prolonged flooding but is usually found in waterlogged areas. Distribution extends from north of Geraldton to the south west corner of the state. Tree, 9-15 m high, short-trunked, widely spreading, bark dark grey and rough to the base of the lower branches, pale grey and smooth above. Juvenile leaves shortly petiolate, blade broadly ovate, slightly glaucous. Mature leaves alternate, petiole 14-28 mm long, blade isobilateral, pale green, narrowly ovate, 75-150 x 15-30 mm, intramarginal vein prominent, 1-2 mm from the margin, lateral veins prominent, at 40-50 degrees to the midrib. Inflorescence is an axillary umbel, 4-10 flowered. Flowers during April-November.

Banksia littoralis **(Proteaceae)**
Common name: Swamp Banksia. This is one of the few species of Proteaceae that is associated with winter-wet depressions. However, it is not tolerant of inundation and prefers areas subject to very short winter waterlogging or very shallow groundwater table. Distribution extends from Jurien Bay to east of Albany, in near-coastal areas. Tree, up to 12 m high, fire-tolerant. Leaves whorled or scattered, petiole 3-8 mm long, blade linear, 100-230 x 4-10 mm, usually toothed only towards the apex, recurved on the margins, teeth usually distant, 1 mm long. Inflorescence is a flower cone, subtended by a whorl of lateral branchlets, conspicuous, cylindric, 60-70 mm in diameter, axis 70-200 mm long. Flowers during March-July.

3: Water Regimes of Swan Coastal Plain Wetlands.

3.1 Origins of Wetland Water

The wetlands on the Swan Coastal Plain are typically shallow interdunal depressions in hydraulic connection with the shallow groundwater flow system. Changes in the surrounding groundwater levels therefore have a significant impact on wetland water levels. The shallow unconfined groundwater originates primarily from rain falling on the land surface and infiltrating the soil (Allen, 1981). Rainwater which exceeds the attractive forces of the soil and evapotranspiration, moves under gravity from the unsaturated zone to the saturated zone in the formation underlying the surface soils. The amount of this recharge is dependent on the amount and pattern of rainfall, the nature of the soil, moisture content of the unsaturated zone, interception by vegetation and the depth to the water table (upper limit of saturated zone). The groundwater moves down gradient towards discharge areas along the coast, and in low-lying areas occupied by wetlands.

The temperate, Mediterranean climate of the Swan Coastal Plain, with warm, dry summers and mild, wet winters is the principal factor determining groundwater and wetland water levels. Recharge of the shallow groundwater occurs mostly during April to October, and is accompanied by a rise in the water table of between 0.2 and 4.5 m, depending on location and climatic trends (Moncrieff, 1974). Although groundwater levels reflect cumulative rainfall, there is a lag of about 2-3 months between the maximum monthly rainfall and maximum wetland depth. Groundwater levels rise quickly after the start of the winter rains, and reach a peak in September-October. Levels decline during the summer months, reaching a low during March-April. Due to the hydraulic connectivity of wetlands to groundwater, wetland water levels follow similar seasonal trends.

As discussed above, lake levels and surrounding groundwater levels fluctuate seasonally, however the magnitude of the fluctuation is greater in the lake due to direct recharge from rainfall and direct discharge by evaporation and transpiration (Water Authority of WA, 1986). Before European settlement, very few wetlands (sumplands in particular) had any surface water inputs. Up to 95% of water loss from wetlands is due to evapotranspiration (Congdon, 1985).

3.2 Wetland Water Regimes

The term water regime is used to indicate that not only is the average water level important, but also the magnitude and time pattern of fluctuations in water levels. Climatic and aquifer conditions imply that wetlands of the Swan Coastal Plain are naturally adapted to seasonally fluctuating water levels, with maxima in late spring and minima in late summer or autumn. The seasonal range in levels is generally in the order of 0.7-1.5 m, and these fluctuations are superimposed on long-term variations due to periods (years) of below or above average rainfall.

The definition of 'normal' water regimes is fraught with difficulties. One approach is to take wetland water regimes during average rainfall years as the conditions to which the ecosystem has adapted. However, surface drainage into wetlands and land use changes within the catchment, alter the relationship between wetland water levels and rainfall. An indication of the range of natural fluctuations in lake levels can be obtained by calculating the frequency distribution of monthly lake levels (Water Resources Council, 1989). However, it is misleading to assume that the historic lake level records reflect the conditions to which the wetland ecosystems are adapted At best, the frequency distributions indicate the long-term range in water levels which may be tolerated by the biota. Rather than attempting to determine pristine water regimes through examination of historic lake levels, a more biologically-meaningful approach would be to observe current vegetation response to different water regimes, with the aim of maintaining or improving existing conservation values.

A parameter which is useful in characterising the water regime is the relationship between maximum lake level during winter-spring and the corresponding minimum level at the end of the subsequent summer. Regression analysis (Fig. 3.1) revealed there is a close correlation between the two, except for Loch McNess which has a relatively stable water level. The lower the slope of the regression line, the greater the rate of water level drawdown.

In order to interpret past and present wetland water regimes, the factors which affect water regime need to be highlighted. As discussed above, climate, recharge and vegetation cover are the key determinants of water regime, but, groundwater abstraction (public and private), surface drainage and land use have become more important with the advent of urbanisation. An example is Jandabup Lake (Fig. 3.2) on the Gnangara mound, which reflects a history of land use changes superimposed on changing rainfall patterns. Before the early 1960's the water level in Jandabup lake was up to 0.7 m lower than at present due to below average rainfall. After 1962, rain increased to above average, and combined with clearing within the catchment for pine plantation, water levels rose by up to 3.0 m. By the early 1970's rainfall had decreased and the pine plantation continued to mature, leading to a reduction in water levels. Groundwater abstraction for public and private supply also reduced water levels by about 0.15 m each (Water Authority of WA, 1986) during the period 1976 to 1985. The artificial maintenance of water levels by pumping bore water in to the lake, commenced in 1989. Thinning of the pine plantation to increase recharge and therefore lake water levels, began as a trial in 1987. A lag of 2-3 years is expected before lake levels will respond to pine thinning.

As indicated by the Jandabup Lake example, Perth and the Swan Coastal Plain have experienced long-term changes in rainfall (Fig. 3.3) which has been reflected in recorded wetland water regimes (refer below). During periods of above average rainfall (1930's, 50's and late 60's), mean wetland water levels have remained high (records available only for late 60's). During the last 15 years (since the early 1970's) however, rainfall has been below average and wetland water levels have lowered.

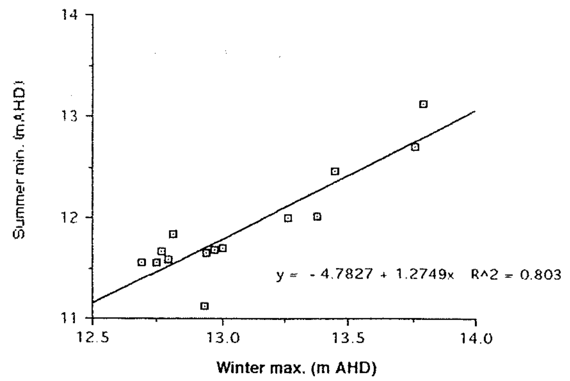
3.3 Water Regimes of Study Wetlands

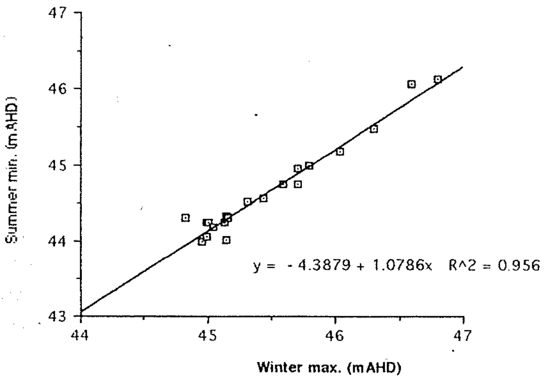
The water regimes of the eight study wetlands reflected differences in geomorphology, catchment land use and hydrology (Fig. 3.4). These wetlands can be separated into two general categories; circular shallow lakes or sumplands, and linear deeper lakes. The circular lakes are typically shallow (less than 2 m deep) with gentle sloping floors, and due to the surrounding shallow topography and groundwater gradient, are more susceptible to water table changes than the linear lakes. A fall in water level therefore exposes a wider fringe (littoral zone) than the same fall in a linear lake.

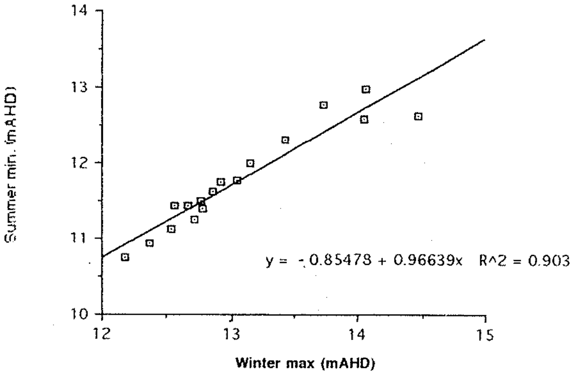
The annual mean water levels of all the lakes with longer records (Banganup, Thomson, Forrestdale, Joondalup and Jandabup), show a peak during the late 1960's when rainfall was above average (Fig. 3.4). All lakes except Herdsman and McNess show a decrease in annual mean water level from the early 1970's onwards, with stabilising or increasing water levels during the last 5 years. The decrease in lake levels since the 1970's correlates with lower rainfall during that period (Fig. 3.3) Herdsman and McNess have relatively stable to slightly increasing water levels over the period of records.

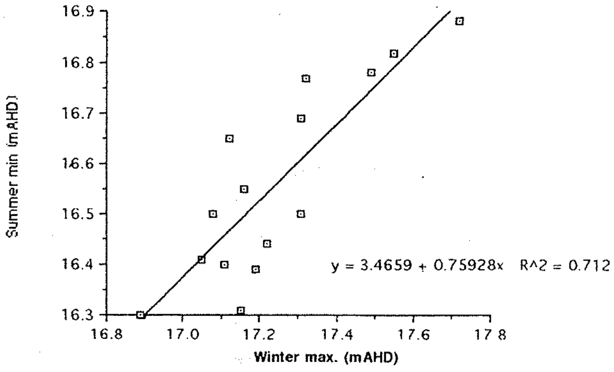
Banganup Lake water levels are determined solely by groundwater trends, as there are no significant surface water inputs. The lake is ephemeral with as little as 2 months of surface water per year (Fig. 3.4). Due to its broad, shallow geomorphology, the littoral zone of the lake is not inundated for extended periods each year. The lake bed (lowest point of the lake) is not significantly lower than the littoral zone. During the study period 1986-90 (3 years prior to, plus 2 years field work), 6 months was the longest period of surface water (1988), with water levels dropping to a metre below the lake bed during the drier months (Fig. 3.5). The seasonal range in water levels observed during this period was about 0.9 - 1.2 m, with summer levels 1 m below the lake bed and winter levels 0.2-0.5 m above. The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Banganup has experienced a wide range in water levels centred around lake bed level (Fig. 3.6).

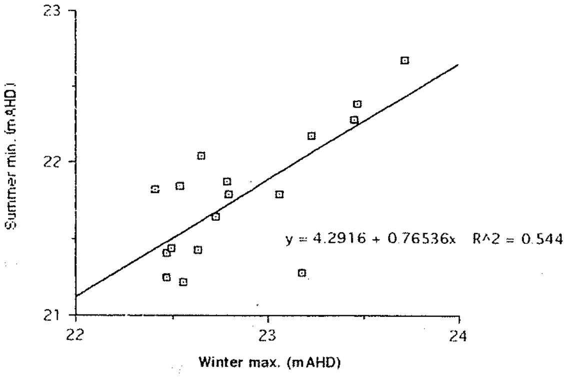
Thomson Lake water levels are influenced by surface water inputs via drains from the

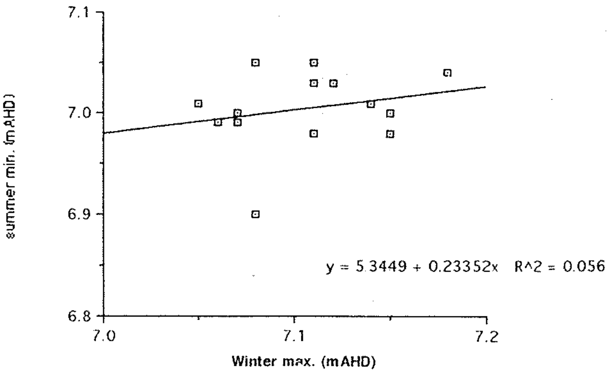

Banganup: Max winter level vs subsequent summer min. level


Jandabup: Max winter level vs next summer min. level


Thomson: Max winter level vs next summer min level


Nowergup: Max winter level vs next summer min level


Forrestdale: Max winter level vs next summer min. level


McNess: Max winter level vs next summer min level

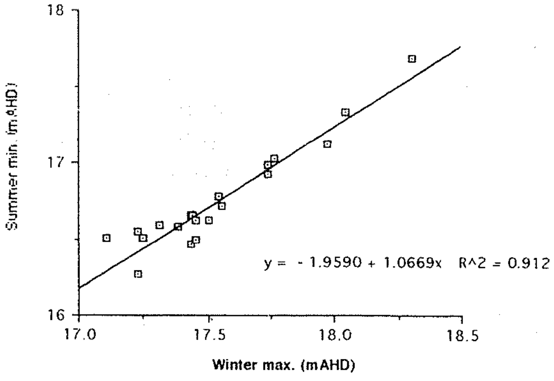

Joondalup: Max winter level vs next summer min level

Figure 3.1 Relationship between winter maximum lake level and subsequent summer minimum lake level at the study wetlands. Data taken from years in which monthly water level records were available.

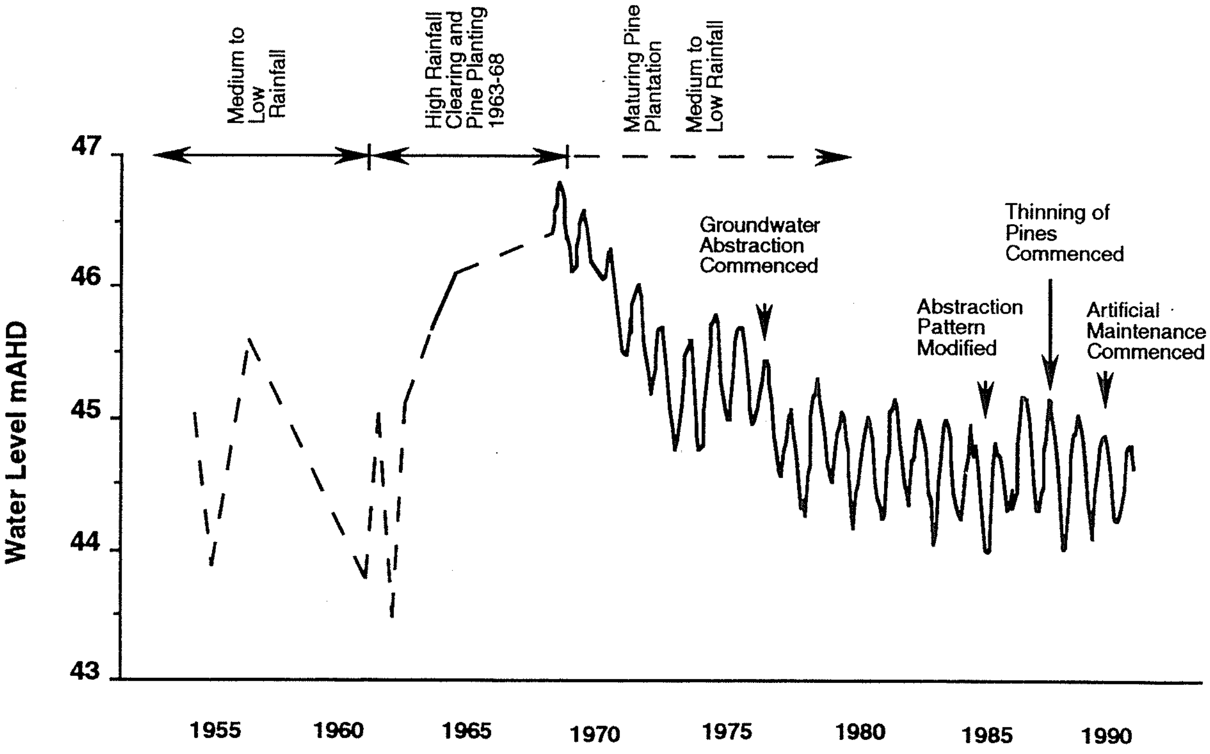


Figure 3.2: Hydrograph of Jandabup Lake depicting long-term and seasonal variation in lake levels.

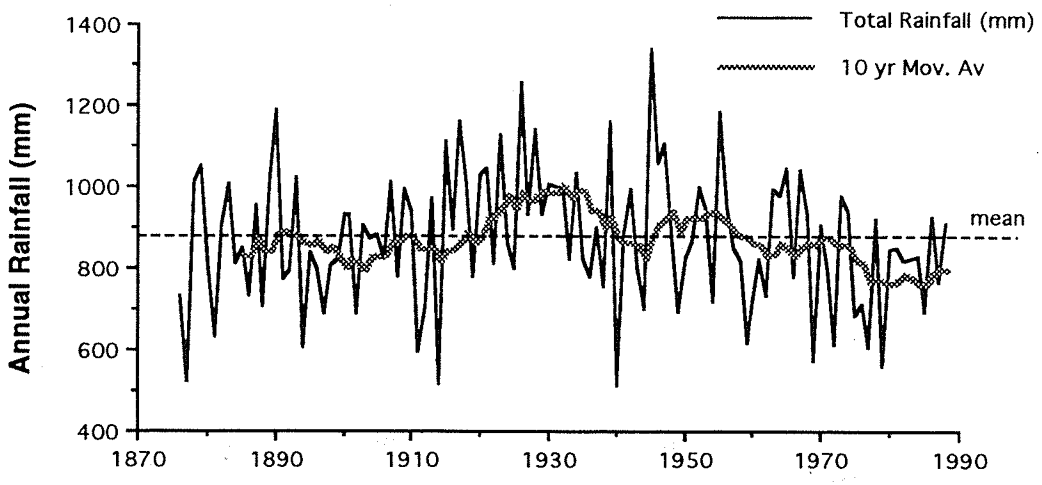


Figure 3.3: Perth annual rainfall since records began.

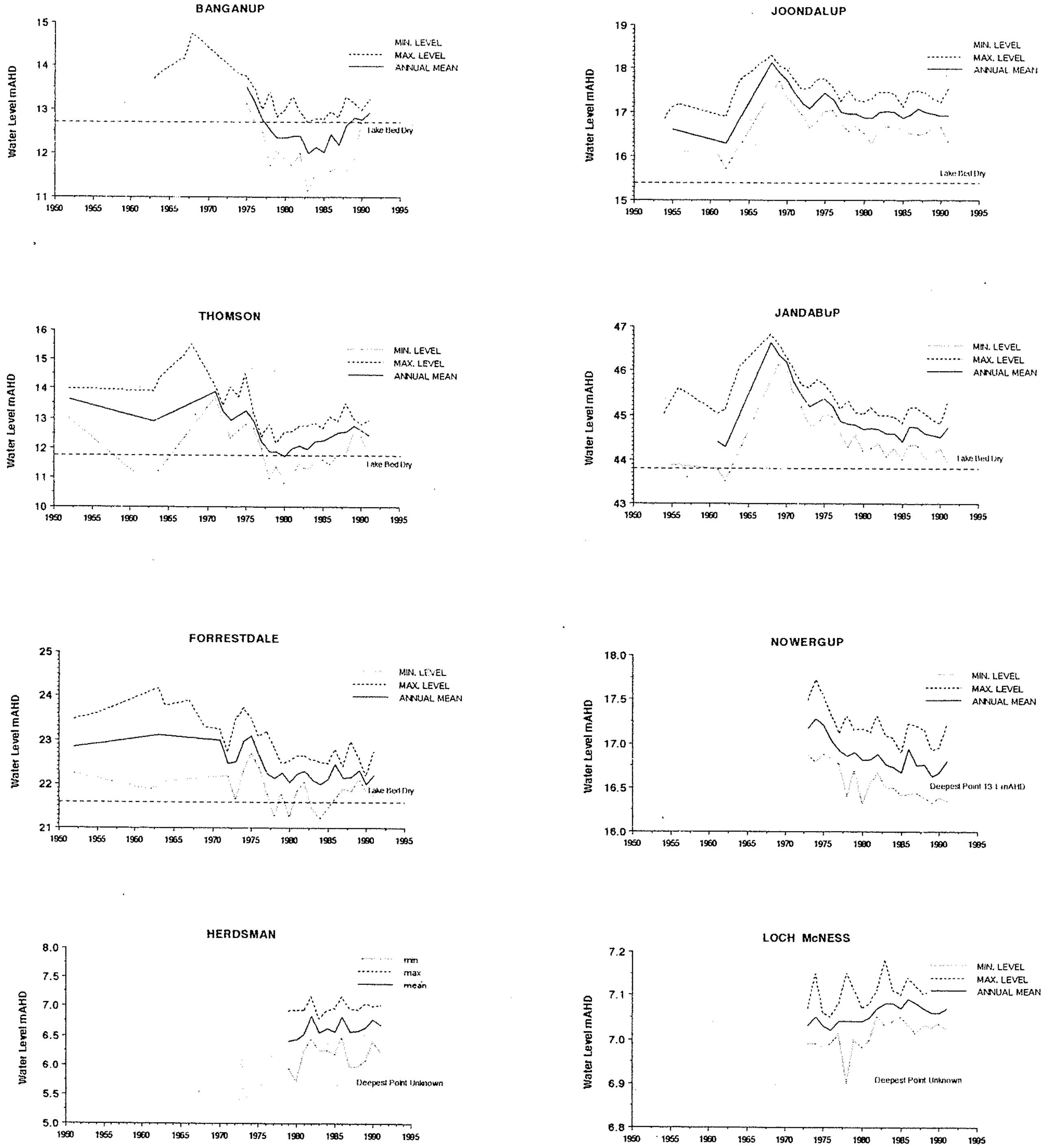


Figure 3.4: Minimum, maximum and annual mean lake levels of the study wetlands over the period records were available.

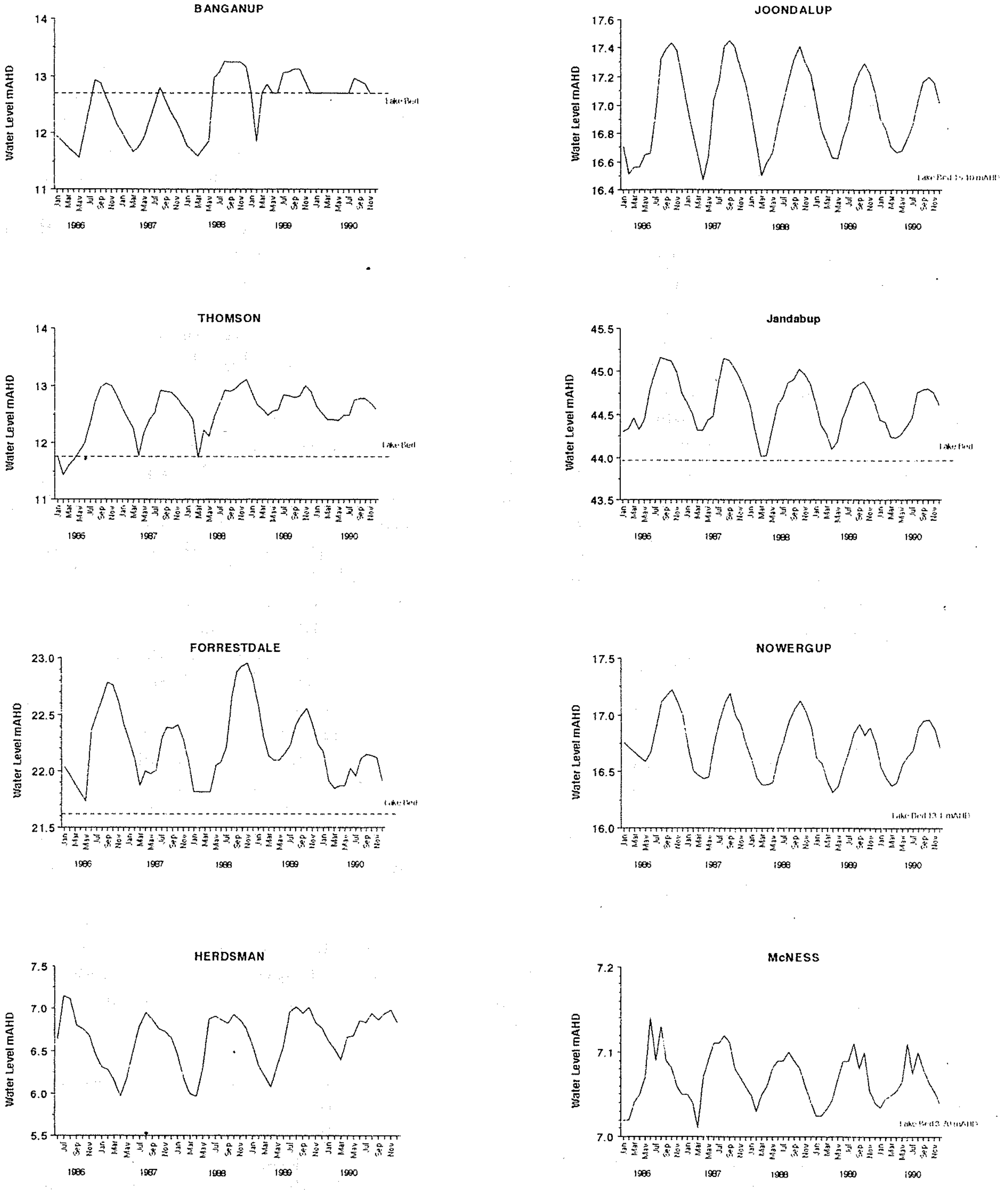


Figure 3.5: Monthly lake levels at the study wetlands during the study period 1986-90 (3 years prior to, plus 2 years field work)

surrounding semi-rural area, which increases the mean water level. The first 2 years of the study period reflect seasonal system with surface water for 10-11 months of the year, whereas the last 2 years of the study period have significantly higher minimum levels (increase of about 0.6-0.7 m) (Fig. 3.5). This increase in mean level during 1989 and 1990 relates to higher rainfall (just above long term average rainfall) (Fig. 3.3). It is possible that without surface inputs, Thomson Lake's water regime would be similar to Banganup. The lake is a large broad shallow basin with an extensive littoral zone which becomes dry for 2-4 months of the year (drier years only, e.g. 1986-87). The seasonal range during the study period was 0-1.2 m above lake bed during drier years, and 0.6-1.2 m during wetter years. The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Thomson has experienced a wide range in water levels centred on 0.1-1.0 m above the lake bed level (Fig. 3.6).

Forrestdale Lake is also a broad shallow basin with an extensive littoral zone that become dry for 3-8 months of the year. It has some surface water input via drains, but like Banganup and Thomson, is dominated by groundwater inputs. The seasonal range during the study period varied from 0.1-1.2 m above the lake bed, to 0.6-0.9 m above the lake bed, depending on rainfall (Fig. 3.5). The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Forrestdale Lake has experienced a wide range in water levels centred on 0.3-1.3 m above the lake bed level (Fig. 3.6).

Herdsman Lake has a long history of land use and disturbance. An extensive drainage network (inflows and outflows) regulates water level, but response to rainfall patterns is still evident. During 1989 and 1990, when rainfall increased, the range in water decreased by 0.7 m (ie. 0.7 m increase in minimum) (Fig. 3.5). The seasonal range during the study period varied from 1 to 0.7 m (the lake bed elevation is not known, and is artificial due to dredging). A frequency distribution of lake levels was not calculated due to the relatively short period of monthly recordings.

Joondalup lake is a linear, deep basin with relatively steep banks and narrow littoral zone, which is inundated for most of the year (9-11 months). It has significant surface water inputs from the surrounding urban area. The seasonal range during the study period was 1.0 - 2.0 m above the lake bed (Fig. 3.5). A slight decrease in the seasonal range was evident during 1989 and 1990 (1.3-1.8 m above lake bed). The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Joondalup Lake has experienced a narrower range in water levels centred on 1 2 to 2.2 m above the lake bed level (Fig. 3.6).

Jandabup Lake is another broad, shallow, ephemeral basin with an extensive littoral zone that is dry for approximately half of the year. As discussed earlier, a number of land use activities within the catchment have impacted on lake levels, however, the hydrology of the lake is still strongly determined by climate (via groundwater levels). The seasonal range during the study period was generally 0.1-1.2 m above the lake bed (Fig. 3.5). A slight decrease in the seasonal range was evident during 1989 and 1990. The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Jandabup Lake has experienced a wide range in water levels with one major peak centred around 0.5-1.5 m above lake bed, and a minor peak centred around 2-2.5 m above lake bed (Fig. 3.6). This minor peak represents the high lake levels during the late 1960's and early 70's, which were in response to above average rainfall and clearing in the catchment.

Nowergup Lake is a deep basin with relatively narrow margins and littoral zone, which are inundated for most of the year (9-11 months). It has some surface water inputs (from a piggery) but is predominantly groundwater driven. The seasonal range in water level during the study period was approximately 3.2 to 4.0 m above the lake bed (Fig. 3.5). The lake rarely dries out. The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Nowergup Lake has experienced a narrow range in water levels centred on 3.3 to 4.0 m above the lake bed level (Fig. 3.6).

Loch McNess is a deep linear basin with steep banks and a littoral zone of variable width, and is inundated virtually all of the year. The catchment is relatively pristine,

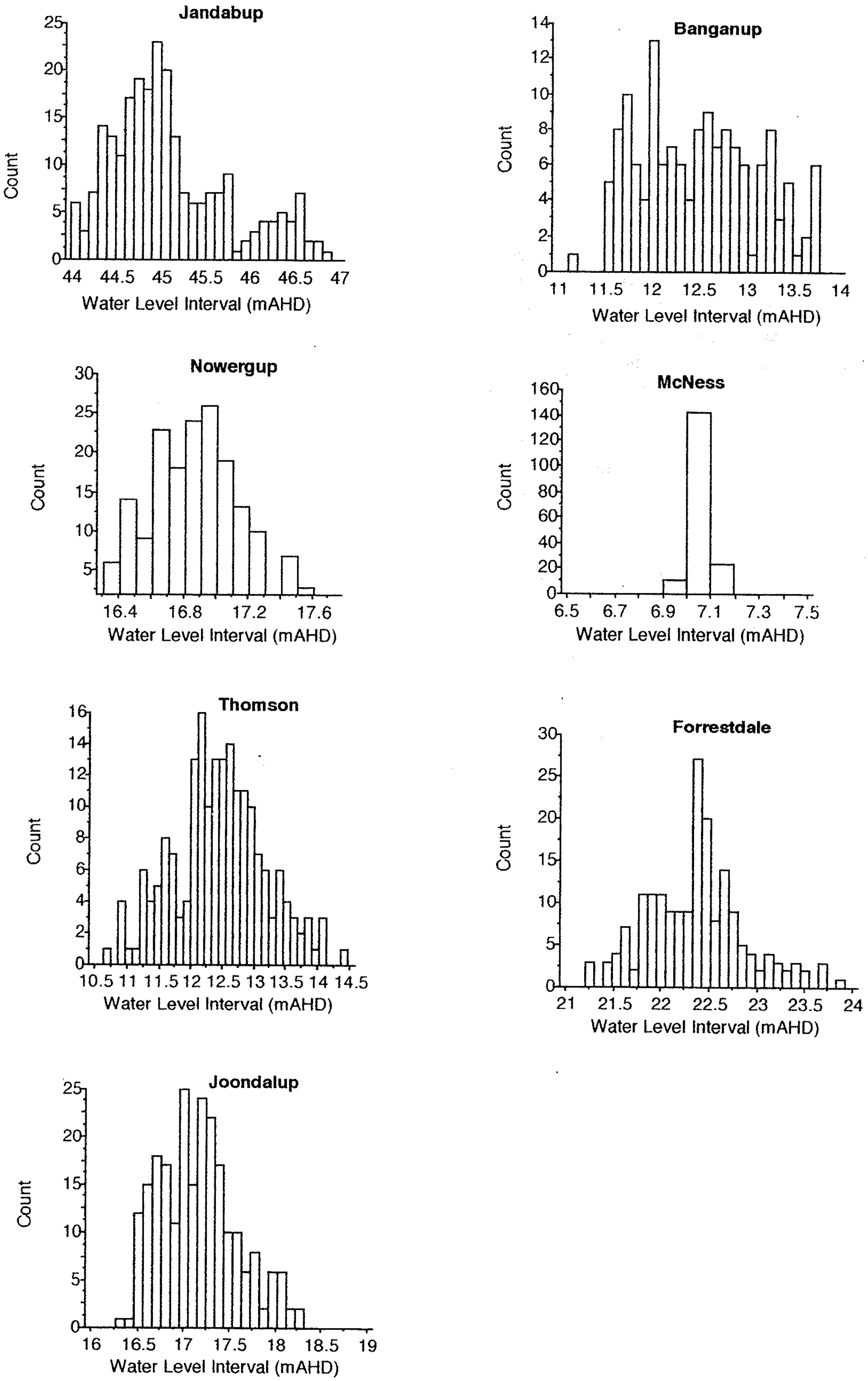


Figure 3.6: Frequency distribution of lake levels at the study wetlands during the period monthly lake level data were available.

and the lake receives no surface water inputs. The seasonal range in water level during the study period was very narrow, approximately 3.3 to 3.4 m above the lake bed (Fig. 3.5). The negligible variation in water level has lead to areas of extensive littoral vegetation despite the steep banks because of the formation of 'floating' mats of vegetation on deep peat calcareous deposits (McComb and McComb, 1967). Maximum water levels are controlled by caves in the coastal limestone acting as spillways (Allen, 1981). The water table contours rise steeply to the east of the lake so that lake levels are less susceptible to reductions in groundwater levels (Water Authority, 1986). This is also partially true for Joondalup Lake. The frequency distribution of monthly lake levels (since levels were recorded monthly) shows that Loch McNess has experienced an extremely narrow range in water levels centred on 3.3 m above the lake bed level (Fig. 3.6).

4: Emergent Macrophyte Response to Altered Water Regimes: Field Investigations

4.1 Introduction to Aquatic Plant Response to Inundation and Altered Water Regime

4.1.1 Structural and Physiological Adaptations to Waterlogging and Inundation

Arguably the single most important impact of water in the wetland environment is its role in determining gaseous diffusion (Armstrong, 1978). Water replaces air in interstitial soil spaces, and in flooded soils there are virtually no air spaces remaining. Due to the significantly lower rate of diffusion in water compared with air, oxygen supply to flooded sediments rapidly becomes limited. Consequently, wetland plants are exposed to lower soil oxygen availability and toxins resulting from anaerobiosis.

Virtually all wetland plants have some structural mechanisms to avoid root anoxia. The major strategy has been the evolution of air spaces (aerenchyma comprising a lacunal system) in roots and stems that allow the pressurised flow of oxygen from the aerial portions of the plant to the roots (Sorrell and Orr, 1992). The internal gas lacunal system is highly variable among freshwater angiosperm species, but is commonly extensive and constitutes a major portion (often exceeding 70%) of total plant volume. Some of the oxygen produced during photosynthesis, and from the atmosphere in emergent plants, is retained in the lacunal system and diffuses from the leaves through the petioles and stems to underground root and rhizome systems, where respiratory demands are high (Fig. 4.1) (Wetzel, 1988). In plants with well developed aerenchyma, the root cells no longer depend on diffusion of oxygen from the surrounding soil, the main source of root oxygen to terrestrial plants. The lacunal system is formed either by cell separation during maturation of the organs or by cell breakdown, and is not necessarily continuous throughout the stem and roots. However the thin cellular partitions within the aerenchyma are unlikely to impede internal gas diffusion significantly (Armstrong, 1975). The development of aerenchyma in plant roots appears to be stimulated by the plant hormone ethylene, the production of which is stimulated by flooded conditions.

The provision of oxygen to the roots and rhizomes via the stomata also has important implications for plant form and ecosystem function. The structure of the aerial portions of emergent wetland plants represents a compromise between the provision of a gas flow pathway to satisfy below-ground oxygen demands, and a requirement for structural rigidity which allows the leaves and stems to compete for light and space (Breen *et al*, 1988). Consequently, the aerial portions of wetland plants are low in bulk and high in fibre and function as organs that acquire carbon and oxygen from the atmosphere and 'pump' (pressurised ventilation) these to the underground organs. The tall persistent, fibrous aerial portions of wetland plants, in conjunction with dense clonal growth, confer a definite advantage in competition for light and space by exploiting all available site resources, and suppressing competitors by reducing available light.

The sufficiency of oxygen supply to the roots depends on root permeability (ie. how leaky the root is to oxygen, which can move out into the surrounding soil), the root respiration rate, the length of the diffusion pathway from the upper parts of the plant, and root porosity (the pore space volume). Models of gas diffusion show that, under most circumstances, root porosity is the overriding factor governing internal oxygen concentration (Armstrong, 1975). The magnitude of oxygen diffusion into the roots is apparently large enough not only to supply the roots but also to diffuse out and oxidise the adjacent anoxic soil (Sand-Jensen, Prahl and Stokholm, 1982; Carpenter, Elser and Olson, 1985; Barko and Smart, 1986). Plaques of hydrous iron oxides can form on the roots of wetland plants when in contact with reduced soil ferrous ions (Taylor, Crowder and Rodden, 1984; Crowder and Macfie, 1986). It has been suggested that oxygen diffusion from the roots is an important mechanism to moderate the toxic effects of soluble reduced ions such as manganese in anoxic soil (Mendelssohn and Postek, 1982; Chen *et al.*, 1980a and b). These ions tend to be oxidised and precipitated in the rhizosphere, which essentially detoxifies them. Oxygen released from the roots may also stimulate the degradation of organic matter in the sediment by permitting aerobic processes within an otherwise anaerobic environment.

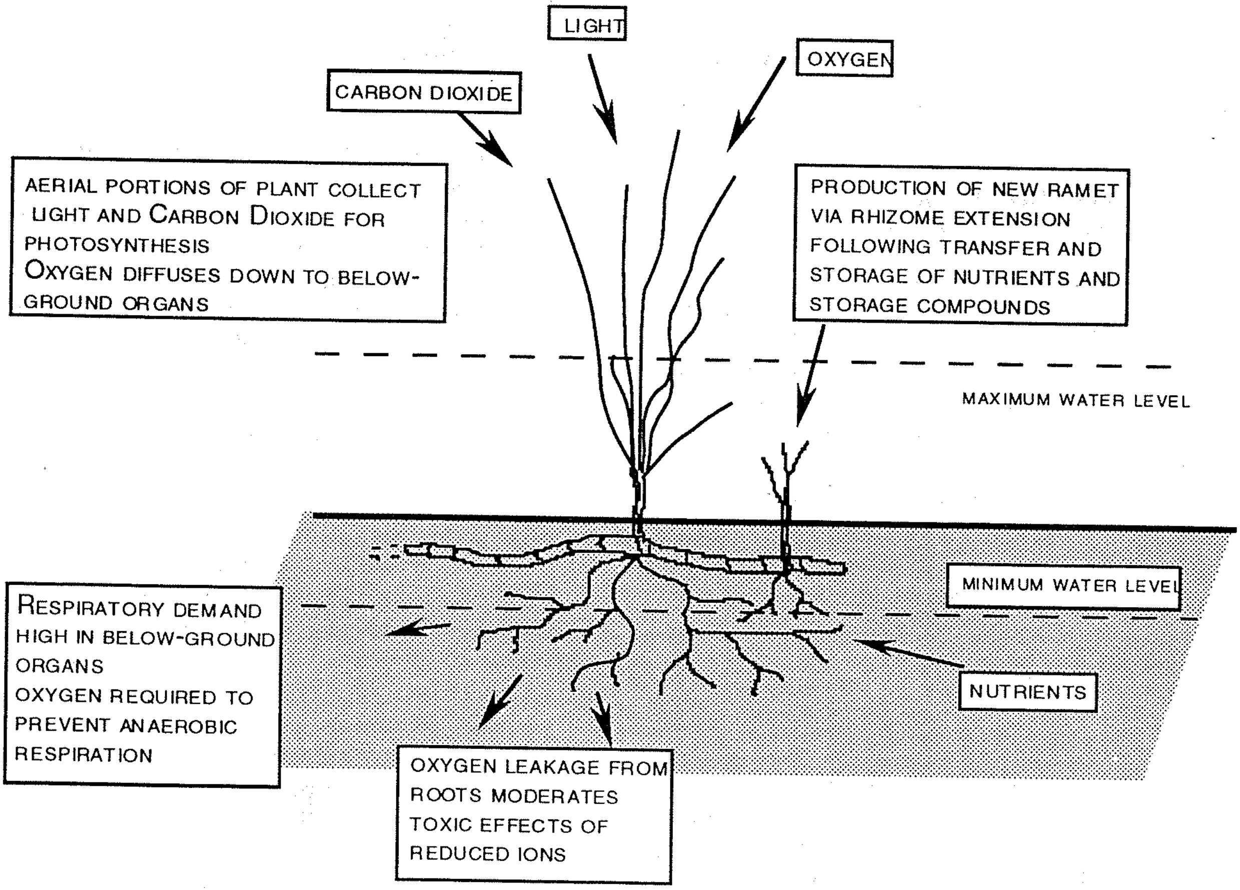


Figure 4.1: Schematic diagram showing the requirements and processes relevant to emergent macrophyte tolerance of inundation.

Among emergent angiosperms with an active transpiration-mediated root pressure system, nutrient absorption and translocation from the roots to the foliage are clearly operational (Wetzel, 1988). Practically no nutrients are absorbed from the water by the submersed portions of these plants. Most sediments of lakes contain significant amounts of organic matter and limited intrusion of dissolved oxygen from the overlying water. The intense bacterial metabolism rapidly produces anoxic, reducing conditions. Therefore, movement of oxygen from the atmosphere in emergent plants to the underground organs is essential to prevent anaerobic respiration of root and rhizome tissue and accumulation of toxic respiratory end products (eg. ethanol). Wetland emergent plants and submerged angiosperms often increase the volume of the lacunal system when sediments are more reducing along a littoral gradient (Armstrong, 1978). Yamasaki (1984) concluded that oxygen is the limiting factor for the distribution of *Zizania latifolia* and *Phragmites australis* along a water depth gradient, due to differences in the efficiency of oxygen diffusion of the species. Some aquatic plants have developed metabolic adaptations to cope with anaerobic rooting conditions such as non toxic end products (eg. malate) or releasing ethanol to the environment (Penhale and Wetzel, 1982; Sale and Wetzel, 1982).

Selection for survival in wetland environments favours long-lived plants of large size that are able to conserve nutrients and resources, and which possess specialised physiological adaptations to cope with anoxic soil conditions and the accumulation of toxic substances (Breen *et al.*, 1988). Over time, the vegetation develops into monospecific stands of stress-tolerant (*sensu* Grime, 1979) emergent macrophytes such as *Typha, Baumea* and *Juncus*. Their dense leaf canopy significantly reduces sub-canopy light levels and lowers the chances of seedling recruitment. Consequently, vegetative reproduction is the major means by which these species maintain or extend their position in the community. This phalanx growth form (Breen *et al.*, 1988) provides an effective barrier against encroachment by competing species, or neighbouring clones of the same species (Section 4.5 and Chapter 7). Seasonal cycles of vegetation growth are synchronised to permit rapid occupation of the available space by the developing leaf canopy, followed by the transfer of nutrients and storage compounds to, and accumulation within, underground rhizomes. These reserves can then be mobilised rapidly when they are required either for the re-establishment of aerial plant portions or production of new ramets and expansion of the phalanx.

Both vegetative and sexual reproduction are sensitive to environmental cues and stresses, and combine with morphological and physiological attributes to determine a plant's response to its environment. However, it has been argued that the true adaptation of a plant to an environment can be defined as its ability to undergo successful sexual reproduction in that environment (Solbrig, 1981). By this interpretation, growth and multiplication by purely vegetative means does not represent adaptation, rather it indicates tolerance of the environment stresses (Breen *et al.*, 1988). Consequently, a single species can display contrasting reproductive strategies when grown in different environments. The extreme variability of most aquatic environments selects for plants possessing a high degree of reproductive plasticity, favouring species with multiple regenerative adaptations (Grime, 1979). The optimum reproductive strategy therefore balances the options of both sexual and vegetative production. In this context, the stress tolerant competitive emergent macrophytes that dominate wetlands, reproduce principally by vegetative reproduction. Sexual reproduction occurs infrequently and both the habit and the structure of the plant community itself provide strong barriers to seedling recruitment. In order to extend their range, wetland plants employ a ruderal sexual reproductive stratagem in which inflorescences are elevated above the canopy level and large numbers of seed are produced by wind pollination and are subsequently wind dispersed (Breen *et al.*, 1988). However, clonal growth remains the major means by which emergent macrophytes maintain and extend their population. Although sexual reproduction can occur under certain conditions (Section 4.5 and Chapter 5), an assessment of the response of emergent macrophytes to different (spatial) or altered (temporal) water regimes, should consider both differences and changes in vegetative growth.

4.1.2 Wetland Plant Community Response to Altered Water Regime

The structural and physiological adaptations to inundation, discussed above, provide an insight to the mechanisms underlying wetland plant population and community response to altered water regimes. The tolerances of the component species to a changing environment will determine the nature of community response, be it a change in structure or composition in time or space. To determine the response to altered and different water regimes, changes in plant population and/or community characteristics over time and space (vegetation dynamics) should be monitored. Characteristics such as distribution, species composition, physiognomy, productivity, seedling recruitment, ramet production, and inflorescence and seed production, change with time (temporal variation) over a water regime gradient (spatial variation). The dynamic nature of these fringing emergent macrophyte communities is a cumulative response to a variable water regime.

Although other factors have a secondary role in influencing community characteristics, water regime is the principal abiotic determinant of the development of aquatic and semi-aquatic plant communities (Gosselink and Turner, 1978). There is much evidence that change in water levels results in changes in the distribution and composition of wetland vegetation (van der Valk and Bliss, 1971; Millar, 1973; van der Valk and Davis, 1976; Gaudet, 1977; Sjoberg and Danell, 1983; Meade and Blackstock, 1988). Despite this universally perceived significance of water depth, there are few detailed studies of growth rates at different water depths or even water depth tolerances of wetland species in the field or laboratory. The few experimental studies indicate that the water regime at which a plant grows has a significant impact on its productivity and seed production (Harms, 1973; Conner and Day, 1976; Keeley, 1979; van der Valk and Davis, 1980, Yamasaki and Tange, 1981; Liefers and Shay, 1981; Sjoberg and Danell, 1983). The impact of water depth on the distribution of wetland species is, in part, indirect. Work by Grace and Wetzel (1982) and Grace (1987) suggests that competitive exclusion at certain water depths is partly responsible for the water depths at which species are found.

With respect to water regime, regulation of vegetation composition and distribution is effected through the depth, timing and duration of flooding and the length of the dry or exposed period. The interplay between topography and hydrology has a significant influence on the distribution of communities, those species less tolerant of flooding being being more pronounced at higher elevations and those more tolerant of flooding but less tolerant of prolonged dry periods, occurring at the wetter end of the water gradient at lower elevations. Species occurring in the zone of periodic inundation have to be tolerant of the stress associated with inundation and exposure (Furness and Breen, 1980), and so this zone typically supports stress-tolerators and ruderals and has low species richness (Grime, 1979). This distinctive pattern of vegetation zonation is common to virtually all wetlands and is principally a response to the interaction of stresses imposed by both the degree and duration of inundation and the degree of exposure.

One of the simplest forms of wetland vegetation change is a shift in the distribution of a population or community along a water regime gradient. Long-term (between years rather than seasonal) changes in wetland water regime can result in changes in species distribution towards higher or lower elevations, depending on water regime trends. This change in distribution generally occurs via clonal growth, however expansion by mass recruitment of seedlings has also been observed if conditions are conducive (Howard-Williams, 1975; Merry and Slater, 1978; Chapter 5). A less extensive response would be a change in the value, location and timing of peak productivity within the current distribution. Prolonged drought and inundation often lead to the death of part or all of a species population, leading to the creation of open areas in an otherwise densely covered littoral zone. This often allows the establishment of seedlings of the same or different species (van der Valk and Davis, 1978; Smith and Kadlec, 1983; Keddy and Ellis, 1985; Parker and Leck, 1985; Galinato and van der Valk, 1986; Moore and Keddy, 1988). The establishment of new species alters the composition of the fringing vegetation, and may lead to dramatic changes if the new species is an aggressive coloniser such as *Typha* (Sharma and Gopal, 1978; Grace, 1987).

Very few studies have attempted to assess the relative importance of two or more variables simultaneously on the distribution of wetland species. An exception is the work of Walker and Coupland (1968), in which the relative importance of water regime and chemistry along environmental gradients was evaluated. Their results demonstrate that for most wetland species both water regime and water chemistry influence distribution, but the relative importance of each varies between species. Shay and Shay (1986) also concluded that water levels and chemistry coupled with life history features influence the distribution and successional role of emergent macrophytes.

In his review of vegetation dynamics of freshwater wetlands, van der Valk (1987) listed a number of generalisations which are relevant here:

1) aquatic and wetland species spread independently, each at its own rate;
2) aquatic plants with clonal growth often cover areas very rapidly;
3) wetland plant communities are not permanent or fixed entities, but are assemblages of species coexisting under a given set of environmental conditions;
4) a given type of wetland vegetation will persist as long as a suitable environment persists;
5) changes in water chemistry in a wetland are correlated with changes in the composition of the vegetation;
6) changes in water depth, caused either by water level fluctuations or sedimentation, are correlated with

changes in the type of wetland communities present;
7) different sequences of plant communities have been found in the same type of wetland at different sites;
8) zonational (spatial) patterns and successional patterns for a particular wetland need not be (and often are not) the same;
9) herbaceous wetland species adjust their population sizes to changes in environmental conditions from year to year; and
10) annual growth rates of perennial wetland species are influenced by environmental conditions, particularly water depth and water chemistry.

Van der Valk (1987) concluded that any assessment of vegetation change should consider the fact that community level changes are a collective reflection of population changes. Therefore, greater emphasis needs to be placed on life histories of wetland species if we are to understand and predict vegetation response to environmental changes. Furthermore, van der Valk stated that ultimately all vegetation change is a manifestation of population-level phenomena, ie. changes in the populations present at a site, changes in the age structure of the populations, and changes in the density and growth of the population due to changes in environmental conditions from year to year. This is supported by a number of studies which identify the importance of life history traits in determining wetland vegetation change due to an altered environment (van der Valk and Davis, 1980; Dickerman and Wetzel, 1985; Shay and Shay, 1986). Future research on the life histories of wetland species should pay particular attention to propagule dispersal, seed germination requirements, and growth and reproduction over the range of environmental conditions found in the field, particularly water depth (van der Valk, 1987).

4.2 Field Study Objectives

As highlighted in Chapter 1, one of the principle aims of this study was to determine emergent macrophyte distribution relative to current water regimes, and response to changes (temporal and spatial) in water regime. The approach taken in the field study involved the following steps:

a) Identify whether significant changes in species distribution occurs over time in response to long-term changes in water regime. This was done by examining aerial photographs from two different dates (approximately 24 years apart) and comparing the distribution and area of sedges and rushes. Photographs of each of the study wetlands (except Herdsman Lake, Section 4.3) was examined and trends related to water level records.

b) Determine the current distribution of selected species relative to water regime by documenting the patterns of vegetation zonation at the study wetlands. Emphasis was placed on recording the full range of each species relative to mean, maximum and minimum water depth and duration of inundation at each wetland. Variation in distribution within a wetland and between wetlands was examined.

c) Assess the relative importance of water regime in determining spatial and temporal variation in plant response within a population. This was done primarily by comparing phenology of reproduction and productivity, with gradients in water regime and other environmental factors such as nutrient and light availability, sediment type and competition.

This approach, in conjunction with glasshouse experiments (Chapters 5, 6 and 7), encompasses most of the considerations stipulated by van der Valk (1987) for further study on wetland plant response to water regimes (Section 4.1). This involved the response of selected species being determined by assessment of their life history traits and population dynamics, as well as simple description of species and/or community distribution.

4.3 Long-Term Changes in Emergent Macrophyte Distribution

Aerial photographs taken in 1963 (1961 for Loch McNess, 1969 for Nowergup Lake) and

1987 of all the study wetlands (except Herdsman Lake) where examined for the distribution and extent of fringing emergent macrophyte vegetation (irrespective of species). The areas of fringing vegetation were digitised into a Geographic Information System (ARC-INFO) so that maps could be rescaled and areas of vegetation calculated.

Differences in the extent of fringing vegetation between wetlands highlight the influence of geomorphology and water regime. Broad, shallow, flat-bottomed basins such as Thomson Lake, Jandabup Lake and Banganup Lake, had large areas of fringing vegetation occupying the wide littoral zone (Appendix 1). An exception to this rule is Forrestdale Lake which has a narrow fringe of vegetation relative to its size. This is probably due to a combination of the heavy clay sediment and a drier water regime (Section 4.5). Wetlands with steeper shores, and therefore a narrow littoral zone (Joondalup Lake, Nowergup Lake) had relatively narrow fringes of emergent vegetation.

Comparisons between the two dates showed some marked differences in sedge area and distribution (Table 2.1). Although these differences in area give an impression of the dynamic nature of macrophyte distribution, it should be noted that in some cases there has been significant fluctuation in distribution during the interval between photographs. The difference highlighted by comparing the photographs can therefore underestimate the extent of dynamic changes in emergent macrophyte distribution. For example, the area of fringing macrophytes recorded for 1963 at Thomson Lake was almost totally lost by the late 1960's due to increased water levels (Crook and Evans, 1981). Virtually all the area of emergent macrophytes seen in the 1987 photograph (85.6 ha at 1987), has returned since the mid 1970's, as water levels receded. The rapidity at which the area of vegetation re-established and expanded at Thomson Lake is partially due to the invasion of *Typha orientalis*, which was not present before the high water levels.

Jandabup Lake is another example of a wetland at which the distribution of emergent macrophytes has responded dramatically to changes in water level. The 1963 photograph shows a large area of very open and scattered submerged vegetation, and relatively small areas of emergent macrophytes. When the area of emergent macrophytes in 1963 and 1987 are compared, a dramatic increase is evident. This was primarily due to decreasing water levels since the mid 1970's (Chapter 3). Evidence of the 'old' distribution of *Baumea articulata* at Jandabup has enabled the estimation of rate of change (Chapter 4.5).

Forrestdale Lake showed a dramatic increase in macrophyte area due to the invasion of *Typha orientalis*. Previously (1963) the area of fringing macrophytes was relatively small and confined to a narrow strip beneath or close to remaining *Melaleuca* woodland. This made identification of the macrophytes in the 1963 photograph difficult, and their cover was assumed to be negligible.

Banganup Lake experienced a slight decrease in the already extensive area of macrophytes, due to disturbance. Changes in water regime over the interval were of a similar pattern to Thomson Lake but of a lower magnitude, and consequently, there has been comparatively less change in distribution and cover.

There has been a slight increase in the area of emergent macrophytes at Nowergup Lake from 1969-1987. Water levels during that period decreased (Chapter 3) and there has been considerable expansion of *Typha orientalis*.

Although Joondalup Lake is a large linear wetland, its relatively steep sides provide a narrow littoral zone on which fringing vegetation occur. Increases in water levels during the interval between photographs, lead to a decrease in overall macrophyte area. As with Forrestdale Lake, it was difficult to determine the extent of narrow macrophyte fringes beneath tree canopies. There was no significant change in macrophyte area at Loch McNess, apparently because of a relatively constant water regime.

4.4 Distribution of Vegetation Relative to Water Regime

4.4.1 Methods

At each wetland, 2-3 transects were established to determine the distribution of emergent macrophytes. The transects were located to represent the maximum range of the major species at each wetland. At most wetlands the major species were *Baumea articulata* and/or *Typha orientalis* and this is reflected in the selection of transect sites. Each transect was a 10 m wide belt transect, the length determined by the distribution of species along the elevational gradient. Elevation was determined at several points along each transect by Water Authority surveyors, so that the profile of each transect could be determined accurately (Fig. 4.2). Species composition and structure were recorded along each transect, starting from the fringing tree vegetation and extending down-gradient to the end of the emergent macrophyte distribution. The vegetation was classified according to the mapping notation and formulae used in Environmental Protection Authority Bulletin 266 (1990).

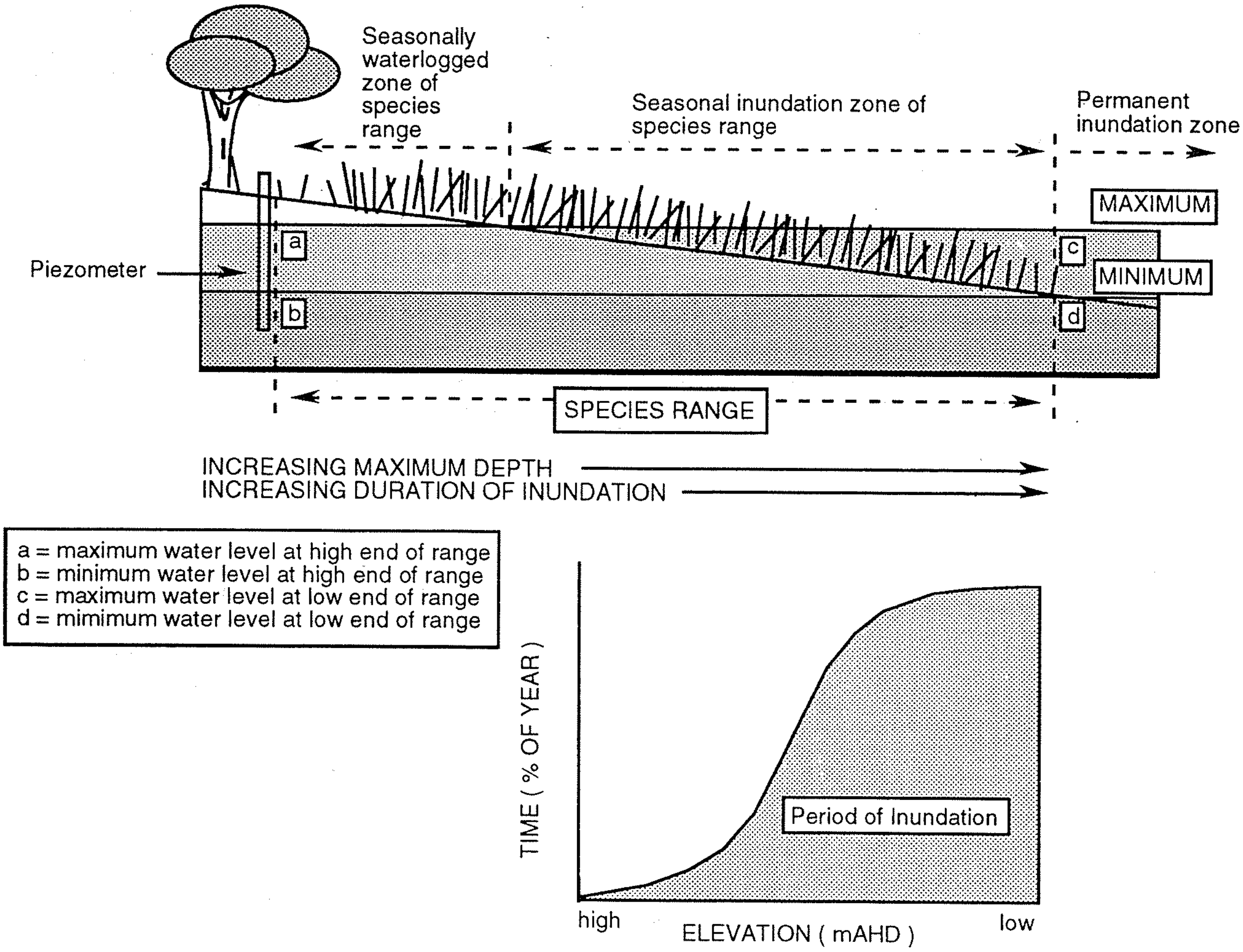


Figure 4.2: Relationships between emergent macrophyte distribution and water regime along the littoral gradient.

Accurate determination of the elevational gradient along each transect enabled monthly water levels (as recorded by the Water Authority of Western Australia) to be mapped against species distribution. As the distribution of the plants is likely to reflect previous as well as current water regimes, water levels were used from the 36 months prior to transect establishment (approximately 1987-89) were used. Maximum, minimum and mean levels within the 36 month period at each wetland were compared with species distribution along the transects. Maximum, minimum and mean water level were determined for the high and low ends of each species distribution at each transect (Fig. 4.2). At the high end of a species distribution, which often occurred in the seasonally waterlogged zone of a wetland, accurate determination of water (groundwater) level required the installation of a piezometer. Piezometers were monitored on a monthly basis and the records used to correct the levels determined from surface water records.

A species distribution relative to mean water level was determined by calculating the difference (metres) in elevation between the high and low ends of a species range, and the mean water level for the previous 36 months. This was done for each species of emergent macrophyte on each transect. Values from each wetland were combined to give an overall range for each species.

The range in duration of inundation for each species was determined by calculating the mean number of months per year (or % of year), over the previous 36 months, that the high and low end of a species range was inundated (water above sediment surface). Values from each wetland were combined to give an overall range for each species.

4.4.2 Results

Transect profile and vegetation descriptions

Banganup Lake
Two relatively short transects were established at Banganup Lake. A band of *Melaleuca preissiana* and *Eucalyptus rudis* woodland (8-12 m tall, 30-70 % cover) surrounded an area of *Baumea articulata* (1-2.5 m tall, >70% cover) (Appendix 2). The gradient along both transects was shallow except for the area of woodland at higher elevations. There was an obvious age structure to the population of *M. preissiana* with a dense stand of uniform-aged trees (Chapter 8) occurring over the high end of the *B. articulata* distribution. The *Baumea* beneath this canopy was sparse due to low-light conditions (Section 4.5).

Thomson Lake
Three transects were established at Thomson Lake. At higher elevations a woodland (10-14 m tall, 30-70% cover) of *Eucalyptus rudis* could be found, often with an understorey of Myrtaceous shrubs or sparse stand of *Baumea articulata*. No species of *Melaleuca* were present on the transects. The gradient was relatively shallow on all three transects, consequently the band of emergent macrophytes was broad and extended over 200 m (Appendix 2). Most of the area of emergent macrophytes was occupied by *Baumea articulata*, however *Typha orientalis* was found at the lower end of each transect. This is probably due to these open moist areas being the most susceptible to *Typha* colonisation during drawdown conditions (Chapter 5). Both species formed tall (>2 m), dense (> 70 % cover) stands. Individuals of *E. rudis* were found scattered amongst the *B. articulata*. The zone of overlapping *Baumea* and *Typha* was generally narrow, with *Typha* typically being the dominant species (Section 4.5 and Chapter 7). Areas of disturbance such as old fence lines, permitted the intrusion of *Typha* amongst dense stands of *Baumea*, indicating that the distribution of *Typha* also reflects pre-emption (by *Baumea*) rather than just tolerance of inundation.

Forrestdale Lake
Three transects were established at Forrestdale Lake. At higher elevations a woodland (<10 m tall, > 70 % cover) of *Melaleuca rhaphiophylla* occurred, with an understorey of Myrtaceous species or *Acacia* shrubs (Appendix 2). The dominant species of emergent macrophyte was *Typha orientalis* (1-2 m tall, >70% cover), with areas of *Baumea articulata* limited to scattered small stands (found on one transect only). The gradient was relatively low at all transects, however the width of the emergent macrophyte zone was narrow (50 - 75 m). This is probably due to the sediment type and dry water regime (Section 4.5). Peripheral sand dunes amongst the *Typha* supported stands of *M. rhaphiophylla* similar to areas of equivalent elevation.

Herdsman Lake
Two transects were established at Herdsman Lake. Due to the greatly modified nature of the lake basin and water regime, it was difficult to include a wide range in species distribution within a single transect. The short transects (<10 m) were located on the edge of dredged areas where a measurable range in water depth (elevation) could be determined. *Typha orientalis* was the only emergent macrophyte found on the transects, typically forming a dense (>70 % cover), tall (1.5-2.5 m) stand. The gradient of the transects was very steep (2 m drop over 8-10 m). Figures of the transects are not shown

because of the shortness and simplicity of vegetation.

Joondalup Lake
Three transects were established at Joondalup Lake. Being a deep linear lake, the banks were relatively steep, and this was reflected in the narrow (40 - 60 m) distribution of the emergent macrophytes. Due to the large size of this wetland, there was an obvious degree of variation in the vegetation zonation patterns. Generally, the peripheral tree vegetation consisted of *Melaleuca rhaphiophylla* and *Eucalyptus rudis* woodland (8-14 m tall, 30-70 % cover) (Appendix 2), with an understorey of *Acacia* . At one of the transects the *Melaleuca* woodland continued down-gradient to almost the end of the emergent macrophyte distribution, forming and open-mid dense canopy over the *Baumea articulata* (1-2 m tall, mid dense 30-70 % cover to dense > 70 % cover). Elsewhere, the *Baumea* occurred as a narrow, dense fringe beyond the tree line. *Typha orientalis* was also found on one of the transects, above, below (in elevation) and interspersed with *Baumea*. *Schoenoplectus validus* was also found in some areas, interspersed with *Typha*.

Jandabup Lake
Three transects were established at Jandabup Lake. All transects had a very shallow gradient, typical of the circular flat-bottomed basin wetlands. Peripheral sand dunes at the high end of the transects supported stands of tree vegetation such as open woodlands of *Eucalyptus rudis* and dense woodlands of *Melaleuca rhaphiophylla* (Appendix 2). Due to the shallow gradient, the distribution of the emergent macrophytes was not represented by distinct sequential zones but rather a mosaic. The species forming this mosaic included *Baumea articulata* (dominant), *Leptocarpus* sp., *Lepidosperma* sp and *B. juncea*. Some or all of these species occurred as both monospecific stands and intermixed. The height and density of *B. articulata* was variable, ranging from 1-2 m and <30 to >70% cover. Large areas of semi-decomposed dead *B. articulata* were found just down-gradient of the tree vegetation on two transects. These remains probably represent the distribution of *B. articulata* during a wetter period in the wetlands history (Section 4.5). Species more tolerant of drier conditions (ie. *Leptocarpus* sp and *Lepidosperma* sp.) currently occupy this area on both transects.

Nowergup Lake
Three transects were established at Nowergup Lake. The gradient varied considerably along the transects due to the very soft calcareous sediment on which the emergent macrophytes 'float' (Section 4.5). The gradient was steep down to where the sandy sediment ended and the calcareous sediment commenced (Appendix 2). A mound in the calcareous sediment, parallel with the sandy shoreline, changed the slope of the gradient. Woodlands of *Eucalyptus rudis* and *Melaleuca rhaphiophylla* with an *Acacia* understorey, occurred on the sandy sediment at the higher end of the gradient. On those transects were *Typha orientalis* occurred, *Baumea articulata* was limited to a narrow (<10 m) band just down-gradient of the fringing trees. Both *Typha* and *Baumea* were found to occur as a tall (>1m, >4m for *Typha*), dense (>70% cover) monospecific stand.

Loch McNess
Two transects were established at Loch McNess. Although the lake is large, there was little variation in the distribution of vegetation. This may reflect the relatively stable water regime. There were three major emergent macrophyte species, *Baumea articulata*, *Typha orientalis* and *Schoenoplectus validus*. (Appendix 2). All three species formed tall (>1 m), dense (>70 % cover) stands, and wide zones of overlapping distribution were also evident. *S. validus* appeared to occur only near the open water. The fringing tree vegetation was composed of *Eucalyptus rudis*, with very little *Melaleuca rhaphiophylla*. The elevational gradient and sediments were similar to Nowergup Lake.

Species distribution in relation to water regime
When comparing water regime with species distribution, it was necessary to compromise between acknowledging the importance of several water regime characteristics, and presenting relationships in a form simple enough for application. Mean water level over the preceding 36 months was the simplest water regime parameter to compare with species distribution. However, the importance of extreme levels (maximum, minimum and range) and duration of inundation could not be overlooked.

When comparing the overall range of the major emergent macrophytes relative to mean water level, distinct similarities are apparent (Fig. 4.3). The larger emergent macrophytes such as *Baumea articulata, Typha orientalis* and *Schoenoplectus validus*, were found to have similar overall ranges when their distributions from all the wetlands were combined. *Baumea articulata* was found between 1.3 m above and 1.1 m below mean water level, a slightly broader range (by approximately 0.2 m) than the other two large macrophytes. The overall range of *Baumea juncea* however, was considerably shorter than the other species (0.2 - 1.4 m above mean water level), and restricted to above mean water level. This reflects a lower tolerance towards inundation.

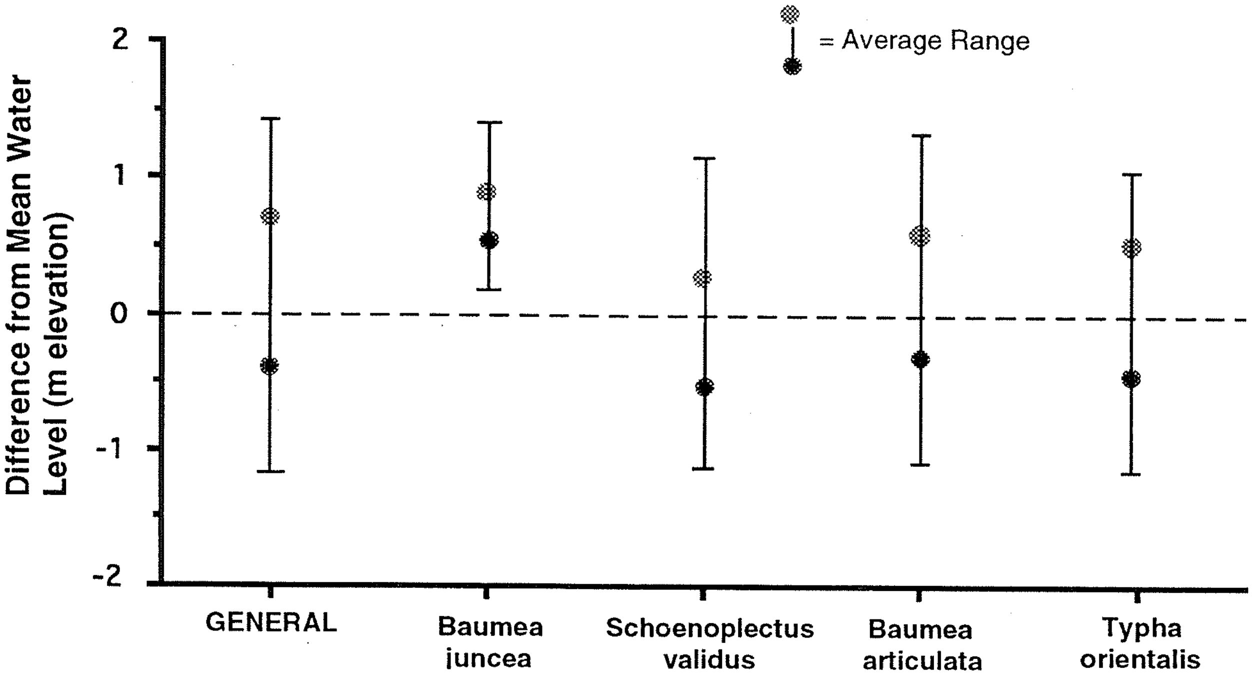


Figure 4.3: Elevation (distribution) range of major emergent macrophytes relative to mean water level. Data incorporates measurements taken at all study wetlands at which each species occurred. Average range is the average high and low point of a species distribution.

The average range (ie the difference in elevation between the average high and low extremes of distribution) relative to mean water level, reflects their most common distribution (Fig. 4.3). *Baumea articulata* and *Typha orientalis* have similar average ranges, with *T. orientalis* showing a slight shift towards lower elevations. *Schoenoplectus validus* however showed a significant shift towards lower (wetter) elevations. The average range of *Baumea juncea* was very short and reflected the limited distribution of this species on the study transects. The overall range in duration of inundation experienced by each of the major emergent macrophytes reflected the trends in elevation relative to mean water depth. *Baumea articulata, Typha orientalis* and *Schoenoplectus validus* had identical (0 - 12 months of the year) overall ranges in flooding duration, whereas *Baumea juncea* was observed to have a relatively short range (0 - 5 months) (Fig. 4.4). The average range for both *Baumea articulata* (0.5 - 9 months) and *Typha orientalis* (1 - 9.5 months) was broad compared to the other species. *Schoenoplectus validus* showed a shift towards the wetter end of its range (8 - 12 months), whereas *Baumea juncea* was more common at the dry end of its range (0 - 1 month).

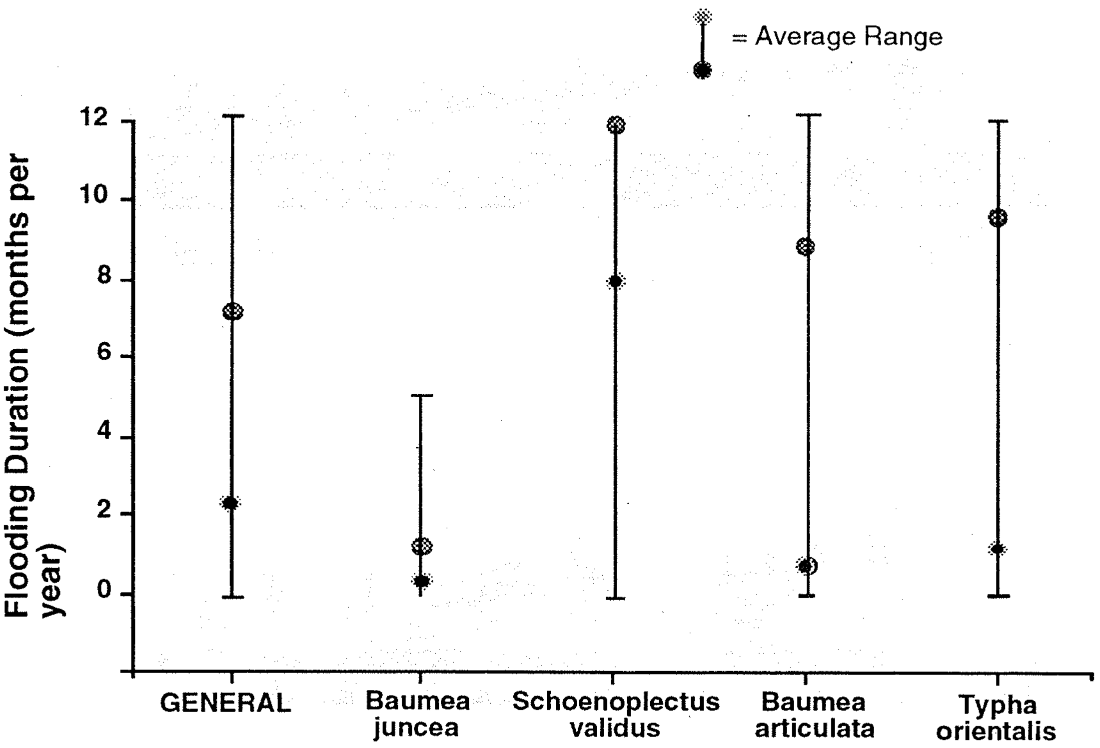


Figure 4.4: Range in months per year of inundation. Data incorporates measurements taken at all study wetlands at which each species occurred. Average range is the range in period of inundation between the average high and low point of a species distribution.

The average (all transects combined) maximum, minimum water levels and duration of inundation for the extremes in distribution of *Baumea articulata* and *Typha orientalis* are presented in Figure 4.5. *Typha orientalis* showed a slight tendency towards greater depths and longer periods of inundation, however this difference is not significant (Mann Whitney test, $p>0.05$ for all comparisons) given the variability between sites (see below). Both species were found at average maximum depths of less than 1m (0.78 m for *Baumea*, 0.95 m for *Typha*) and minimum depths of about 1m below sediment surface (-1.12 m for *Baumea*, -0.98 m for *Typha*). The range in duration of inundation was 5.8 - 74.2% of the year for *Baumea*, and 7.2 - 81.3% for *Typha*. These results demonstrate that within a stand of emergent macrophytes, there can be a significant difference in the water regime experienced by plants. This variability is dependent on the difference in elevation between the high and low end of a species distribution. Therefore, it is possible to have, within the same stand, plant growth limited by both drought and prolonged inundation (Section 4.5).

As *Baumea articulata* and *Typha orientalis* were the most common species of emergent macrophyte found on the transects, they were used for a more detailed assessment of the variability in distribution within and between wetlands. For both species, a significant degree of variability was observed between wetlands and, to a lesser extent, within wetlands. The distribution of each species relative to mean water depth varied from very narrow to broad ranges with no identifiable trends (Fig. 4.6). This indicates that any one transect will not give an accurate reflection of a species water regime tolerance. The factors which account for this variability are likely to be many and may include the pattern of seasonal drying, sediment structure, nutrient regime and interspecific competition. The influence of these factors on plant distribution and growth are discussed in Section 4.5 of this chapter.

Knowing the current distribution of a species relative to water regime, past or future distributions may be approximated assuming a similar relationship to mean water level. For example, at Jandabup Lake the high end

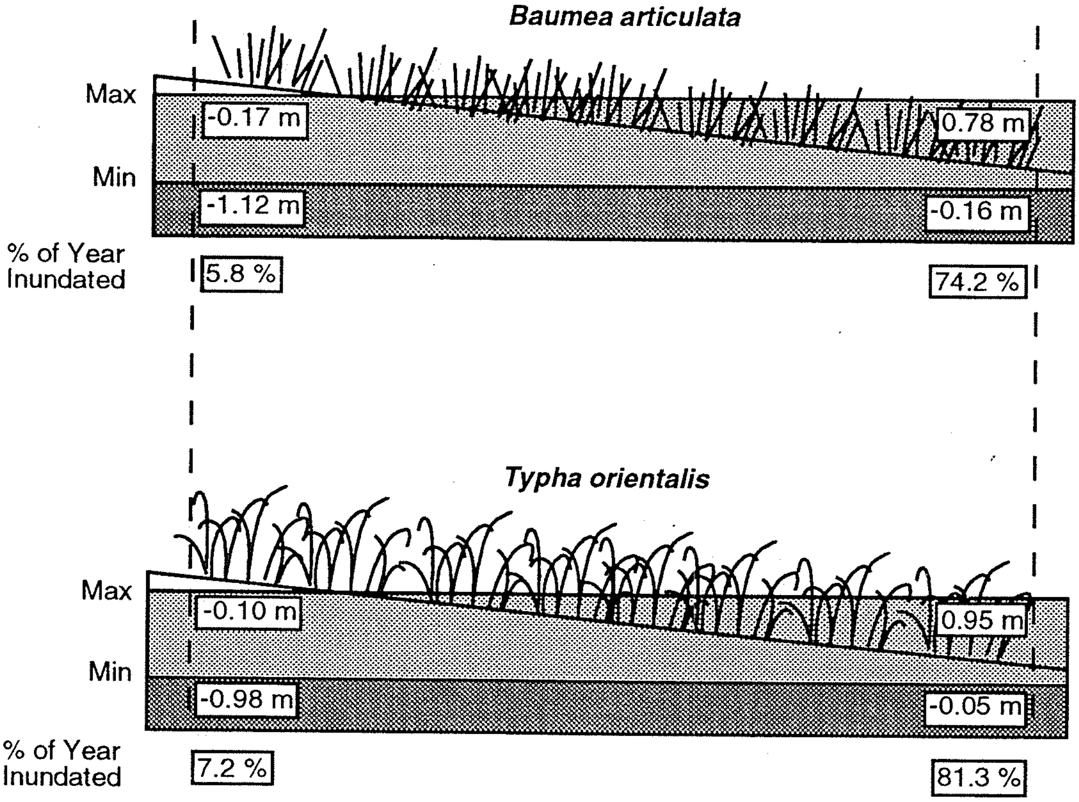


Figure 4.5: Average (all transects combined) maximum, minimum water levels and duration of inundation (% of the year) for the extremes in distribution of both *Baumea articulata* and *Typha orientalis*.

of the *Baumea articulata* distribution is 0.70 m above current (1990) mean water level, and on mean water level at the low end. Assuming this relationship is constant, the centre of *B. articulata* distribution in 1978 would have been 60m further upslope (Fig. 4.7). Indeed, remnants of dead *Baumea articulata* were found at elevations similar to the distribution predicted for 1978 when mean water levels were higher. However, it would be misleading to expect the current relationship between distribution and mean water level to remain constant. Other environmental factors, such as nutrient regime, may change over time and this is likely to influence this relationship (see Section 4.5). Furthermore, the broad shallow gradient at Jandabup and the steady reduction in mean water level, facilitates the use of such relationships as predictive tools. The formulation of distribution/water level relationships would be far more difficult for steep-sided wetlands with a variable water level history.

4.4.3 Discussion

Several conclusions can be drawn from these results with respect to emergent macrophyte distribution in relation to water regime. Firstly, aerial photography shows that the distribution of sedges and rushes is very dynamic, and alters with longer-term changes in water regime. Large rises in water level have lead to the demise of fringing vegetation at some wetlands, whereas gradual decreases have lead to considerable expansion and encroachment of fringing vegetation towards the centre of a wetland (down-gradient). In some cases the encroachment of emergent macrophytes, represents the plant community response to decreasing water levels after an extended period of above-average levels. Deeper wetlands with narrow littoral zones have relatively small changes in sedge area, whereas shallow wetlands with broad littoral zones experience large changes in sedge area. The rapidity at which emergent macrophytes can change their distribution is largely a function of their ability to undergo rapid rhizome extension and production of ramets. Populations of larger, longer-lived species which do not undergo clonal

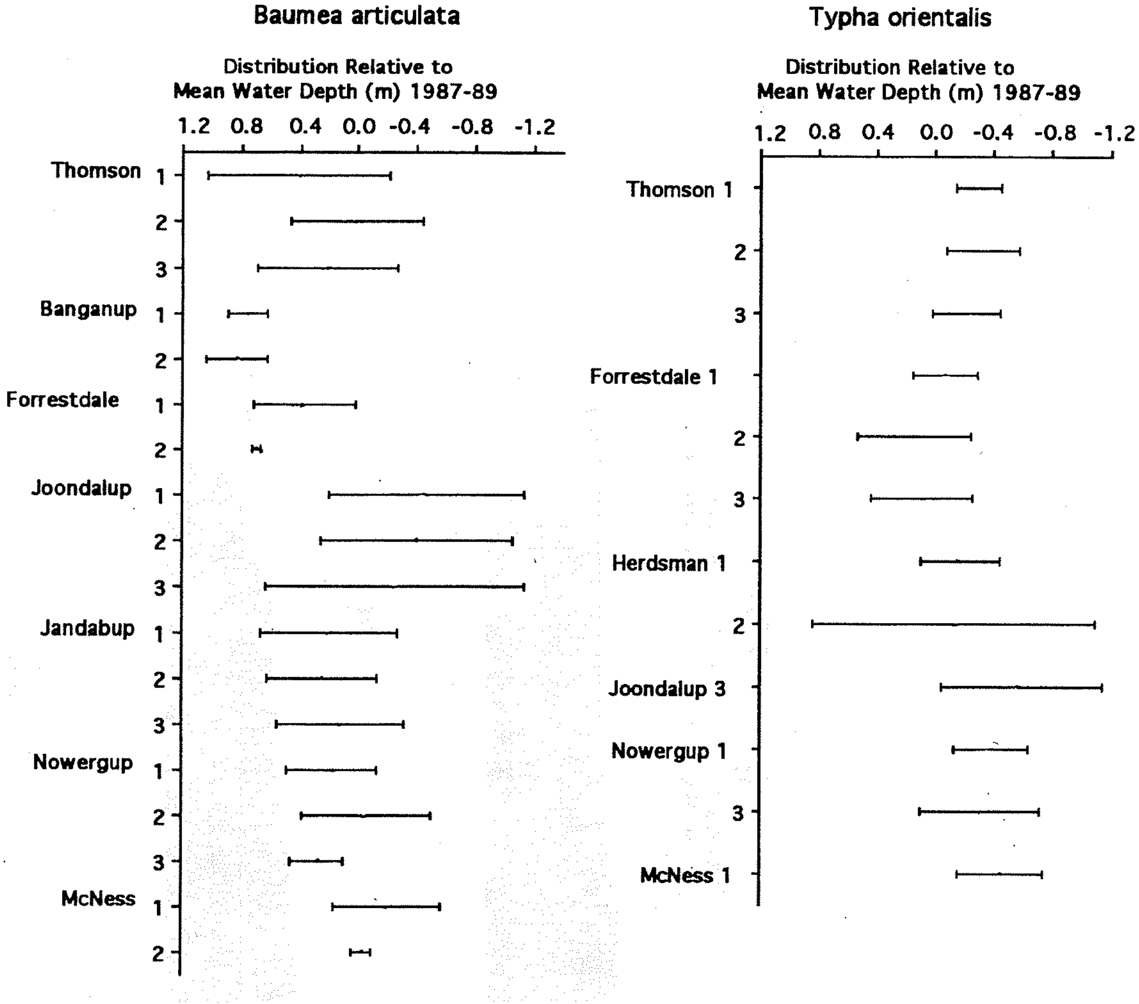


Figure 4.6: Distribution of *Baumea articulata* and *Typha orientalis* relative to mean water depth at all transects.

reproduction, such as *Melaleuca preissiana*, take a longer period of time to respond (ie. change distribution) to changes in water regime (Chapter 8).

All of the wetlands studied had distinct patterns of fringing vegetation zonation, typically an outer fringe of waterlogging-tolerant tree and shrub species surrounding an inner fringe of inundation-tolerant emergent macrophytes. The width and area of fringing vegetation (particularly emergent macrophytes) is primarily dependent on the geomorphology (slope of shoreline) and water regime of a wetland. Wetlands with steep littoral zones have relatively narrow fringes of emergent macrophytes, whereas wide fringes occur on littoral zones with shallow gradients. The most common species of emergent macrophyte at the study wetlands were *Baumea articulata* and *Typha orientalis*, whereas *Melaleuca rhaphiophylla*, *M. preissiana* and *Eucalyptus rudis* were the common fringing tree species.

Within a wetland, the water regime experienced by a plant may differ significantly depending on the elevation at which it occurs, and or even within a single stand of emergent macrophyte, there may be considerable variation in growth response along an elevational gradient (Section 4.5). It is a common misconception that the entire population of a species at a wetland experiences the same water regime. Individuals at the extremes of a population distribution may be stressed due to either prolonged drought or inundation, resulting in lower growth rates, poor reproduction or gradual extinction. The majority of a population, however, is likely to occur under conditions which have a nominal impact on growth.

Overall, there is significant variation in distribution relative to water regime between species and within species. Species of smaller growth form (*Baumea juncea*) are found at the drier end of a water regime

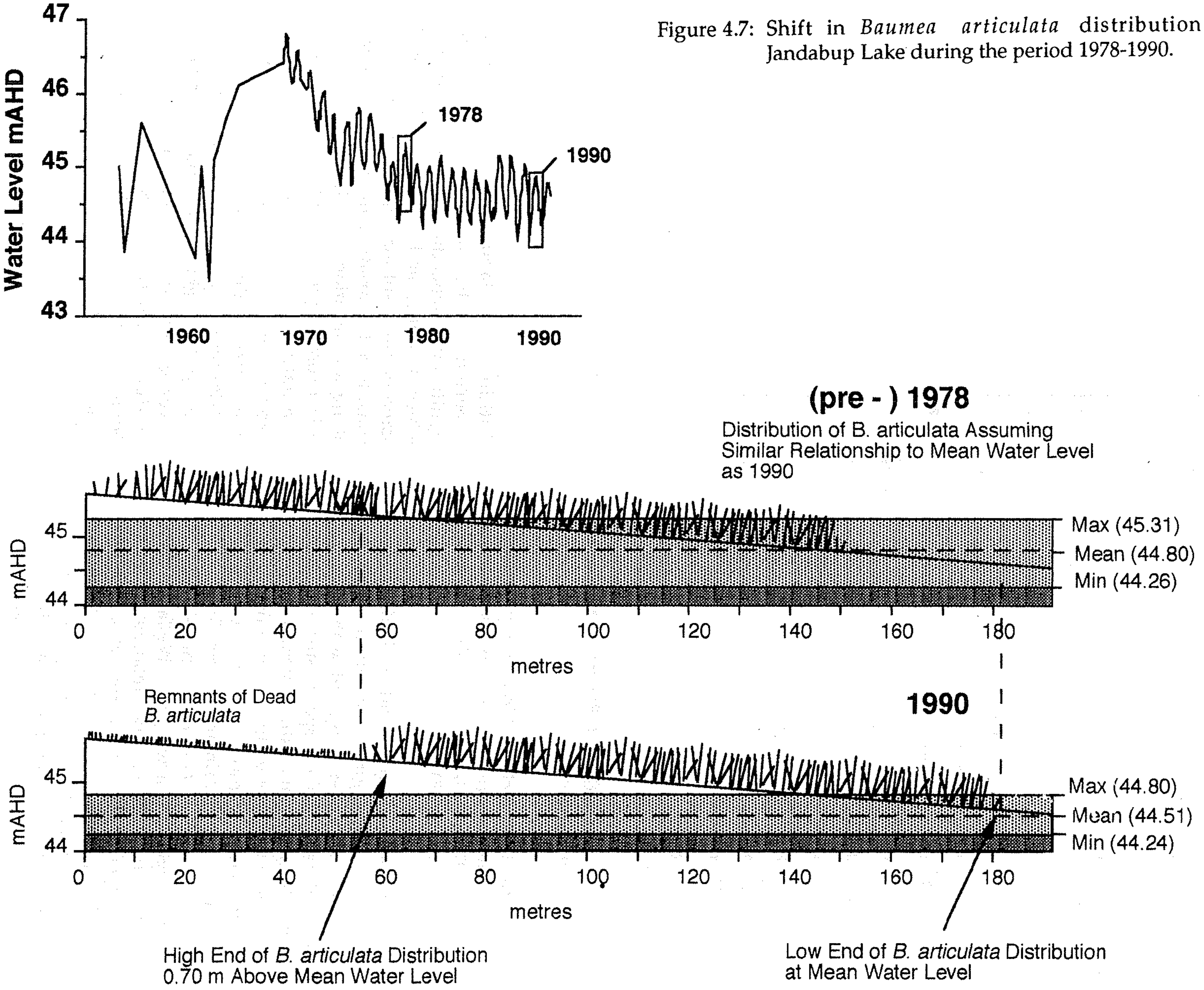


Figure 4.7: Shift in *Baumea articulata* distribution at Jandabup Lake during the period 1978-1990.

gradient, whereas larger species have a broader range extending to the wetter end of a gradient. A species does not always fully occupy its potential range (distribution in elevation relative to water regime) throughout a wetland due to the influence of factors other than water regime. Furthermore, a species of emergent macrophyte does not necessarily occupy the same range at different wetlands. The potential range of a species is generally greater than the range a species occupies at any one wetland. This is due to the influence of such factors as sediment structure, nutrient loads, light availability, disturbance and competition (Section 4.5).

Greater water depth implies longer duration of inundation of the root zone, however the length of inundation will vary between permanent and seasonal wetlands of similar maximum water depth. Emergent macrophytes were found to tolerate inundation from 0 - 12 months of the year, however the results do not allow us to determine whether these plants will tolerate the extremes for more than one growth season. Smaller species (ie. *Baumea juncea*) were found in areas that were flooded for no longer than 5 months.

With respect to species distribution, these results indicate the tolerance range of the major emergent macrophyte species. However, apart from large scale nonspecific changes detectable from aerial photography, these results give little indication of short (seasonal) and long-term (>1 year) temporal changes in plant response to water regime, nor is there any indication of spatial variation in plant response. These parameters are important if the true tolerance limits and population response are to be determined.

4.5 Spatial and Temporal Variation in Plant Population Response to Water Regime and other Environmental Factors.

4.5.1 *Methods*

Standing Biomass, Ramet and Inflorescence Density

Standing biomass (kg dry wt m^{-2}) of emergent macrophyte species was determine at selected points along transects at Banganup, Thomson, Forrestdale, Jandabup, Loch McNess and Nowergup Lakes. The above-ground live biomass within three 1 m^2 quadrats at each point was harvested in spring 1990. Samples were oven dried (70° C) and weighed. Maximum plant height, number of inflorescences and ramet density were also determined at the same locations.

Phenology and Productivity

Four lakes were selected for detailed examination of emergent macrophyte phenology and productivity. Jandabup Lake (drier, low nutrients) and Thomson Lake (wetter, higher nutrients) were selected as representative of populations of *Baumea articulata* under different water and nutrient regimes, whereas Forrestdale (drier, low nutrients) and Nowergup Lakes (wetter, higher nutrients) represented different conditions for *Typha orientalis*. Although a significant proportion of the vegetation at the paired lakes occurred at different water regimes, there was also overlap in distribution relative to water level. This also allowed comparison of vegetation at similar water regimes but different nutrient regimes by examining plants at corresponding points along the elevational gradient at each transect.

From winter 1990, the phenology of new ramet production, leaf growth, flowering and seed production was determined over 12 months at 14 day intervals at the paired lakes. New ramet production was taken as the time at which emergence of new ramets was first observed. Flowering was recorded when mature flowering inflorescences were first noticed until developing seed began to appear. In the case of *Typha*, this was judged by a change in inflorescence colour and firmness. Seed production was recorded from the time developing seed was observed until seed dehiscence. The period of leaf growth refers to the time over which significant new growth and leaf elongation on young and established ramets occurs.

The productivity of *Baumea articulata* and *Typha orientalis* at the paired lakes was determined over the period June 1990 to June

1991. Four sampling points (3 at Jandabup) were selected along one transect at each lake. At each sampling point, the above-ground growth of 3 groups (spaced 2-5 metres apart) of 4-8 ramets was determined by recording increments in leaf lengths every 14 days. All live, senescent and dead attached leaves on each ramet were measured to enable the tracing of individual leaves. In order to maintain a constant point from which to measure leaf lengths, heavy-gauge wire was strung at ground level between wooden stakes close to the ramets measured. The measurement of each leaf therefore was from the wire to the tip of the leaf. Samples of live leaves of various lengths from each species and each lake were collected, their length measured, oven dried (70° C) and weighed. Regressions between leaf length and dry weight were then used to convert the field leaf measurements to weights. Fortnightly dry weight increments were summed for each ramet, the area covered by each group determined, and the total dry weight increment of the group scaled up and expressed on a 1 m^2 basis. The fortnightly total dry weight increments of the 3 groups at each point were then averaged to give mean daily production for each time interval.

Sediment Nutrients and Texture

Sediment horizons, to a depth of up to 1 m, were described at the points used to measure standing biomass at the paired lakes. Using a corer or auger, sediment samples were taken at 10 cm intervals up to a depth of 30 cm, mixed together, and three bulk samples taken for carbon and texture analysis. Carbon (or organic matter) was determined by the loss-on-ignition method. Approximately 10g of dry sediment was placed in a porcelain crucible, oven dried at 100 ° C for 30 minutes, cooled in a desiccator and then weighed. The cooled soil was then heated to 700° C for 2 hours in a muffle furnace, cooled and reweighed.

Soil texture was determined using the Bouyoucos hydrometer method. Fifty grams of dry and sieved (2 mm) soil was placed in a 1 litre measuring cylinder along with 125 ml of 40g l^{-1} sodium hexametaphosphate solution and then made up to 1 litre with distilled water. The cylinders were shaken and left overnight to allow the sodium hexametaphosphate to disperse the clay particles fully. The cylinders were inverted five times the following day and hydrometer readings were taken at 40 seconds for the silt plus clay fraction and at 2 hours for the clay fraction. The sand fraction was then determined by subtraction.

Dissolved oxygen concentrations in water were measured fortnightly at the productivity sampling points (if inundated) at each of the paired lakes during Spring and early Summer only (ie when plants were flooded and growth rates were highest). Measurements were taken at the surface and bottom and then averaged. A Hanna Instruments Model HI8543 Dissolved Oxygen Meter was used.

Three sediment samples, taken at 0-20 cm depth, at each sampling point (see above) were collected every 14 days. Samples were kept in 250 ml plastic vials and frozen until analysis. Samples were air dried and analysed for total phosphorus (perchloric acid digestion, molybdate-ascorbic acid colorimetry) and total nitrogen (Kjeldahl digestion, Technicon AutoAnalyzer II method No. 334 - 74 N/B).

4.5.2 Results

Standing Biomass, Ramet and Inflorescence Density

Significant variation in standing above-ground biomass, ramet density, maximum plant (ramet) height and inflorescence density was observed along each of the transects studied (Fig. 4.8 - 4.11). Standing biomass and ramet density tended to be lowest at both the high (driest) and low (wettest) extremes of each species distribution on the transects. Patterns of change in standing biomass where similar to ramet density at all the transects. Thomson and Nowergup Lakes displayed the highest standing biomass with up to 4-5 kg dry weight m^{-2}, whereas Forrestdale and Jandabup Lakes had the lowest with 1-2 kg dry weight m^{-2}.

Where more than one species occurred on the same transect, distribution overlap was either narrow (2-5 m) with little difference in species biomass, or wide with the growth of one species being 'suppressed' (Fig. 4.8). At Jandabup Lake, although *Baumea articulata*

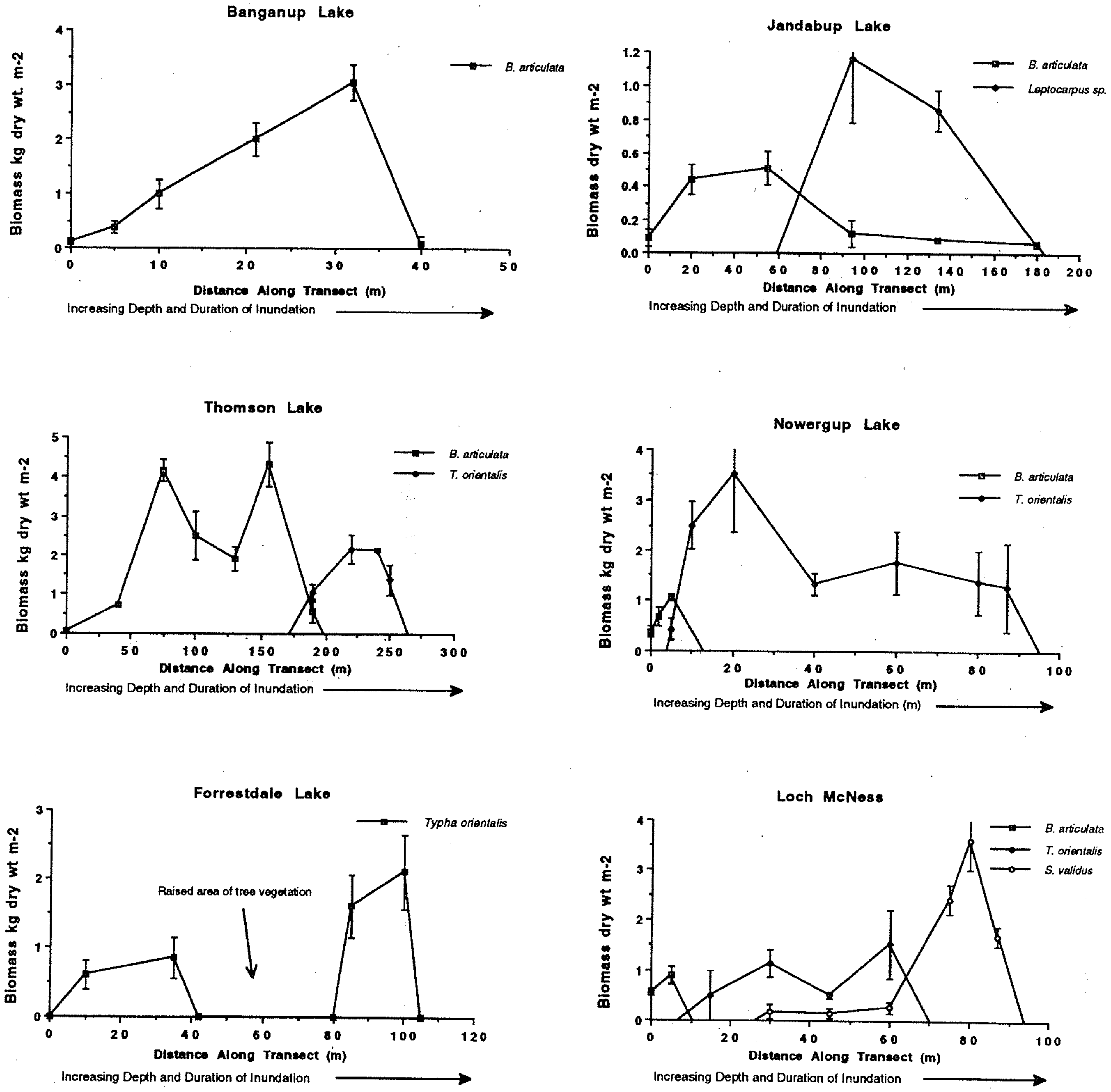


Figure 4.8: Variation in mean standing crop biomass (kg dry wt. m^{-2}) along the elevational (water regime) gradient of selected transects. Error bars are standard errors.

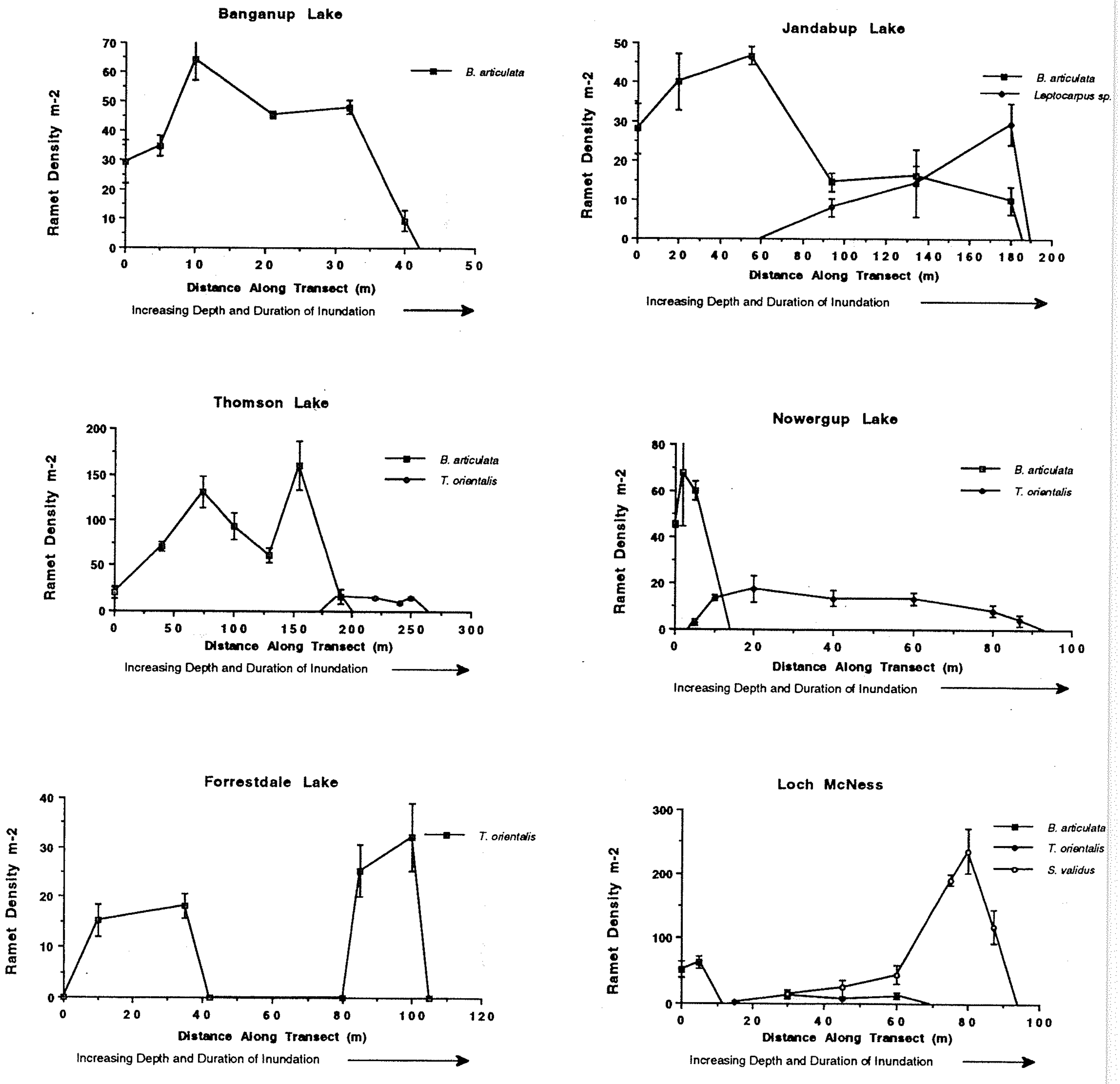


Figure 4.9: Variation in mean ramet density (m^{-2}) along the elevational (water regime) gradient of selected transects. Error bars are standard errors.

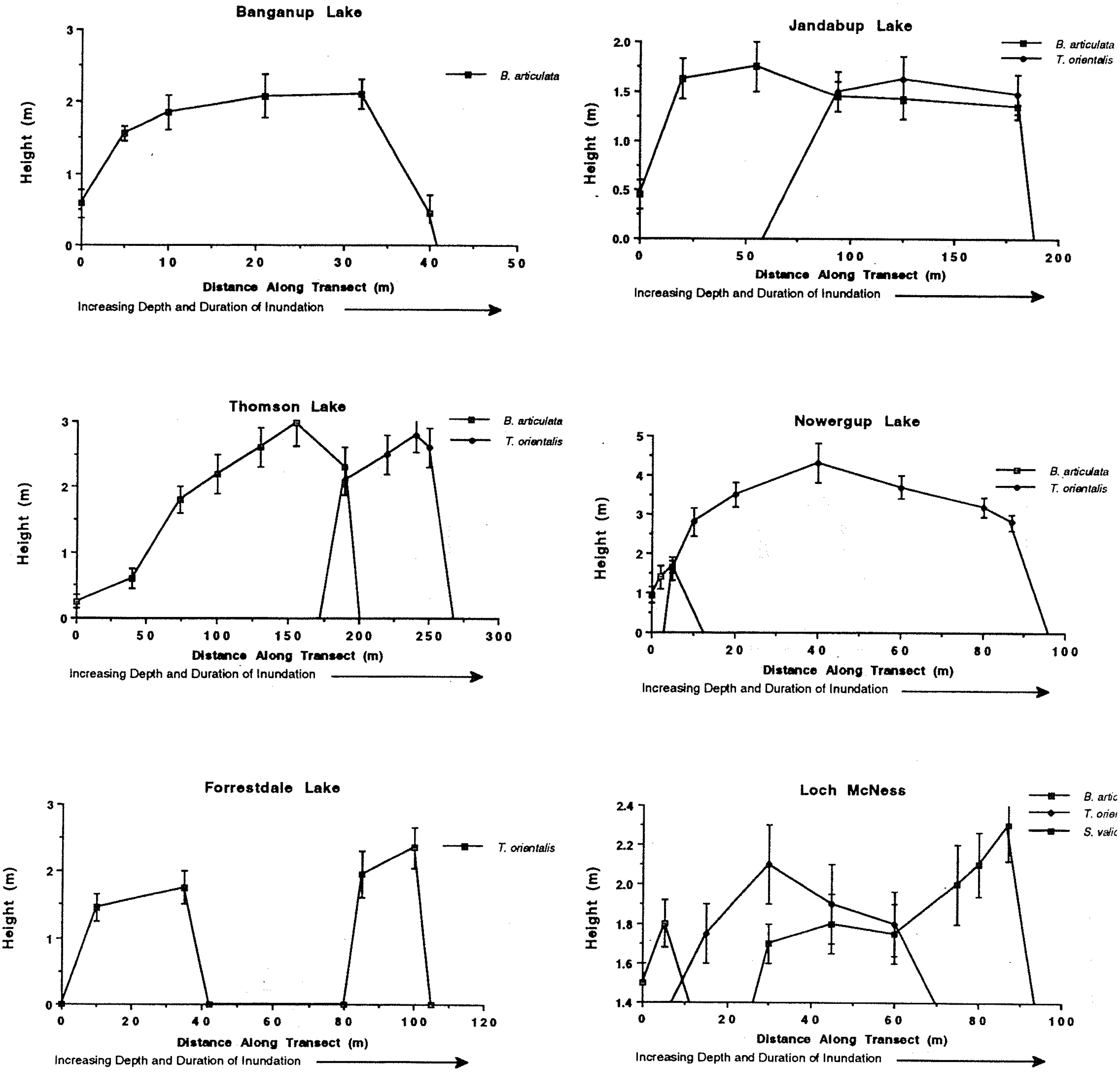


Figure 4.10: Variation in mean plant height (m) along the elevational (water regime) gradient of selected transects. Error bars are standard errors.

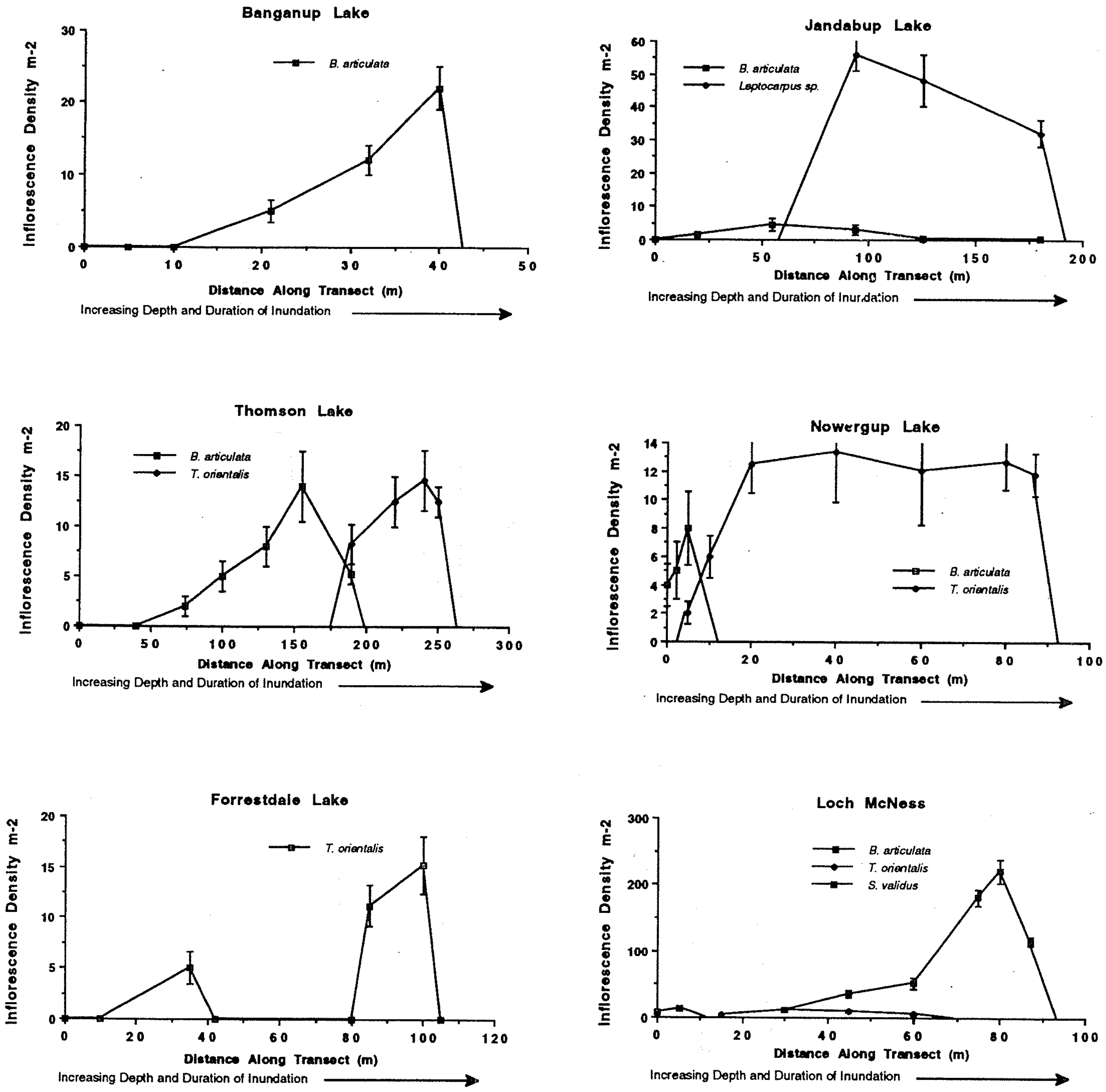


Figure 4.11: Variation in mean inflorescence density (m^{-2}) along the elevational (water regime) gradient of selected transects. Error bars are standard errors.

occurred over the whole transect, its standing biomass was reduced by 70 - 80% where it overlapped with *Leptocarpus* sp. Whereas at Loch McNess, the standing biomass of *Schoenoplectus validus* was reduced by up to 90% where it overlapped with *Typha orientalis*.

The density of *B. articulata* reached a maximum of approximately 150 ramets m^{-2} at Thomson Lake, but was usually found at densities of between 30 and 60 ramets m^{-2} (Fig. 4.9). *T. orientalis* was typically found at lower densities, between 10 and 20 ramets m^{-2} and up to 40. *S validus* occurred at only one transect but showed an extremely high ramet density of up to 250 ramets m^{-2}.

Maximum plant (ramet) height varied to a lesser degree than standing biomass, with heights of up to 4.5 m for *T. orientalis* and 3.0 m for *B. articulata* (Fig. 4.10). Most transects showed little variation in height over a species distribution, however a tendency towards peak height occurring at lower (wetter) elevations was observed at some transects (Thomson Lake and Loch McNess).

Inflorescence density varied significantly along the transects at most lakes (Fig. 4.11). Plants at the high (drier) end of the transects at Banganup, Thomson and Forrestdale Lakes did not flower during spring 1990. Inflorescence densities increased with increasing depth and duration of inundation at Banganup, Forrestdale and Thomson Lake and Loch McNess. This was not the case at Jandabup and Nowergup Lake where inflorescence density either decreased or remained constant with increasing depth.

Phenology and Productivity

There were differences in the phenology of new ramet production, leaf growth, flowering and seed production within and between wetlands. At Thomson Lake, *B. articulata* showed a significant shift in timing of emergence of new ramets along a water depth gradient (Fig. 4.12).

The onset of ramet emergence occurred during July at all depths except at the wetter end of the gradient where emergence commenced in September. However, there was greater variation in the time at which ramet emergence ceased, from October at the drier end of the gradient to February at the wetter end. The average period over which new ramets emerged was 4.5 - 5 months, with the driest end of the gradient having a period of only 3 months.

In comparison, *B. articulata* at Jandabup Lake showed a shorter period of new ramet production, except at the wettest end of the gradient (Fig. 4.13). Generally, ramet production commenced during July/August and ceased during September at the drier end of the gradient and December at the wetter end.

The period over which new ramets emerged ranged from 2 months at the dry end of the gradient to 5 months at the wettest end. At points of comparable mean water depths, the period of ramet production was generally shorter at Jandabup Lake than Thomson Lake. The long period of ramet emergence at deeper depths at Jandabup Lake was characterised by a low density of small ramets, and does not necessarily reflect higher productivity (refer to standing biomass Fig. 4.8).

Baumea articulata

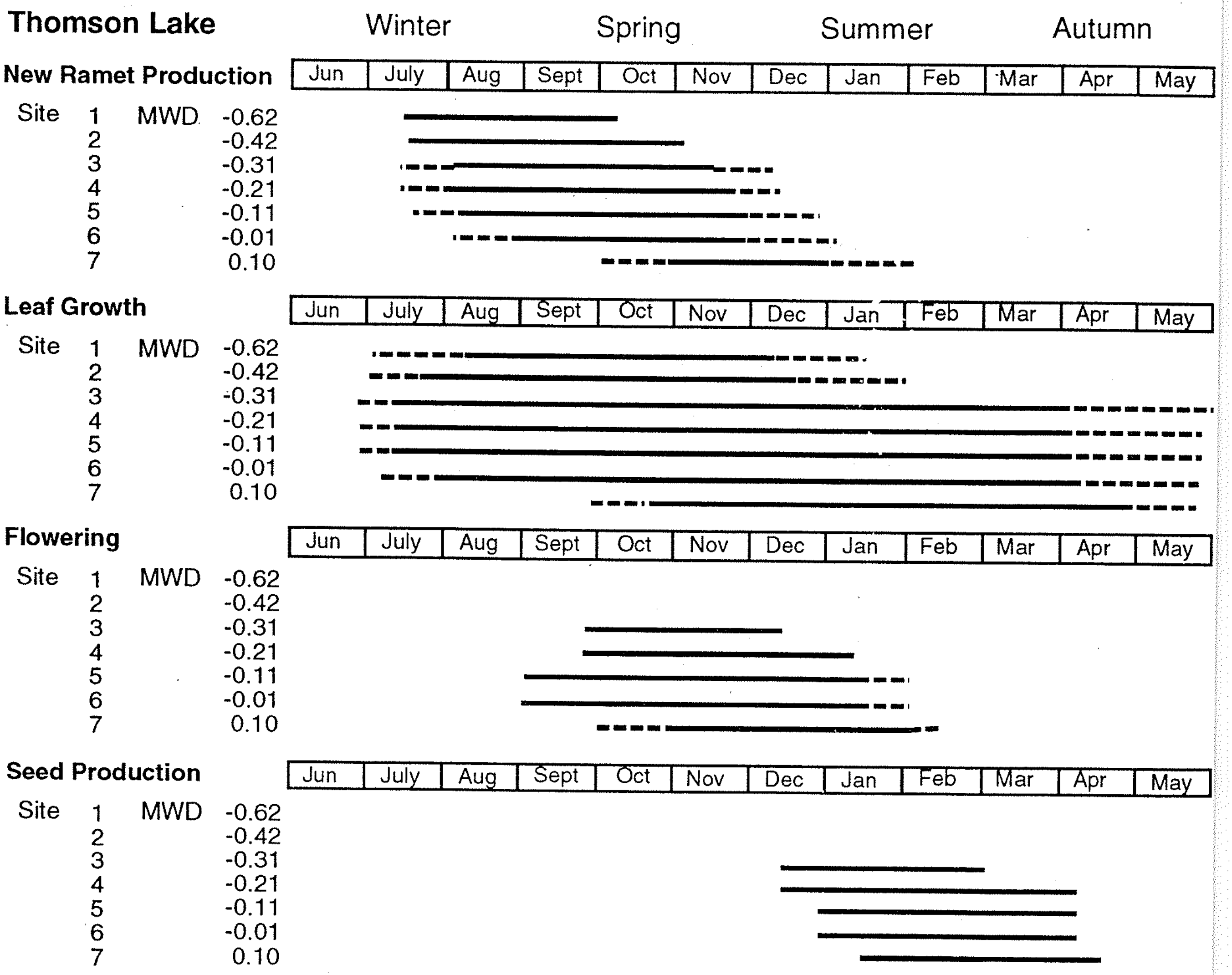


Figure 4.12: Phenology of *Baumea articulata* new ramet production, leaf growth, flowering and seed production at the sampling points on the Thomson Lake transect. MWD = Mean Water Depth.

The period of significant new leaf growth and elongation on young and established *B. articulata* ramets also differed within and between wetlands. At the driest end of the transect at Thomson Lake, leaf growth commenced during July and ceased during January, six months later (Fig. 4.12). Leaf production at the remaining points along the transect also commenced during July but ceased during the following May, representing almost continuous leaf growth throughout the year. One exception to this was at the wettest point of the transect where leaf growth commenced during September rather than July, representing only a 8 month period of leaf growth. *Baumea articulata* leaf growth at Jandabup Lake was generally over a shorter period compared to Thomson Lake (Fig. 4.13). Leaf growth phenology ranged from an August start and a mid-November finish (3 - 3.5 months) at the drier end of the gradient, to a mid July start and mid-February finish (6 - 7 months) at the wetter end. However, like Thomson Lake, the phenology of leaf growth was similar at most points along the water regime gradient.

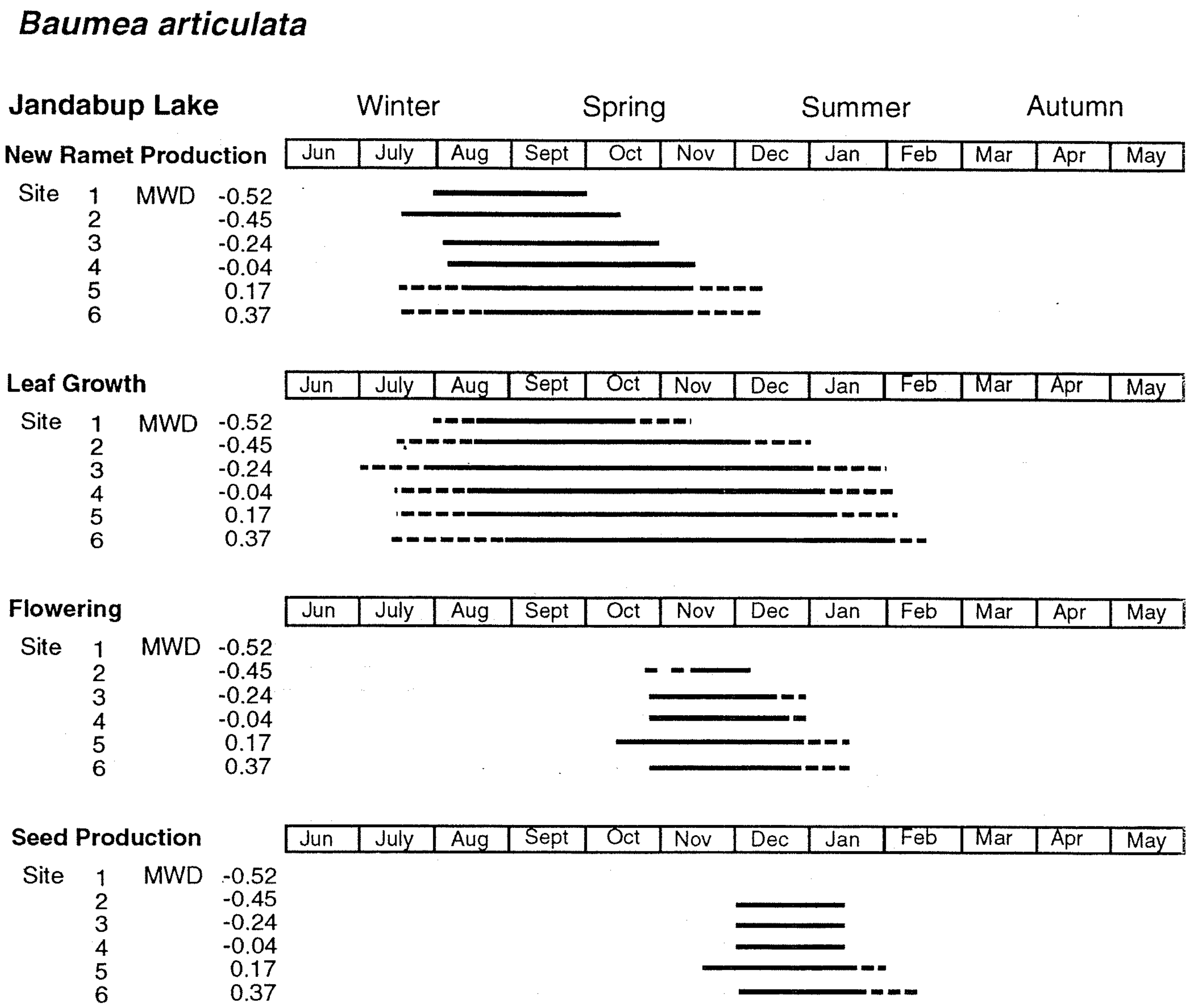


Figure 4.13: Phenology of *Baumea articulata* new ramet production, leaf growth, flowering and seed production at the sampling points on the Jandabup Lake transect. MWD = Mean Water Depth.

Flowering of *B. articulata* at Thomson Lake did not occur at the two driest points on the transect (Fig. 4.12). Flowering period generally increased with increasing water depth, from late September - mid-December (2 - 2.5 months) at the lower depths, to September - late January (4.5 - 5 months) at greater depths. At the greatest depth, however, flowering did not commence until October/early November (4 months). Flowering of *B. articulata* at Jandabup Lake was over a significantly shorter period compared to Thomson Lake (Fig. 4.13). Flowering did not occur at the driest point along the transect. The range in flowering phenology was from mid-October - early-December (1 - 1.5 months) at the drier end of the transect, to mid-October - mid-January at the wetter end (3 months).

Seed production phenology of *B. articulata* at Thomson Lake varied along the transect (Fig. 4.12). At the driest end, seed production commenced in mid-December and ceased at the end of February (2.5 months), whereas at the wetter end seed production commenced in mid-January and ended in mid-April (3 - 3.5 months). Seed production of *B. articulata* at Jandabup Lake was generally over a shorter period compared to Thomson Lake (Fig. 4.13). Seed production ranged from early-December - mid-January (1.5 months) at the drier end of the gradient, to mid-November - mid-

February (2 - 2.5 months) at the wetter end. In comparing the flowering and seed production phenology at both Thomson and Jandabup Lake, it appears that flowering and/or seed production takes longer at Thomson Lake. However, this may be due to more variability in phenology at any one point (spatial) because of the greater ramet and inflorescence density at Thomson Lake.

As with *B. articulata, T. orientalis* showed differences in new ramet production between and within wetlands. At Nowergup Lake, ramet production occurred over the majority of the year ranging from early August - late January (6 months) at the driest end of the transect, to early July - mid-May at the wetter end (10-11.5 months) (Fig. 4.14). Other than the driest point, there was little variation along the transect. New *T. orientalis* ramet production at Forrestdale Lake occurred over a significantly shorter period compared to Nowergup Lake (Fig. 4.15). The phenology of ramet emergence ranged from early August - mid-November (3.5 months) at the drier end of the gradient, to early August - mid-December at the wetter end (4.5 months).

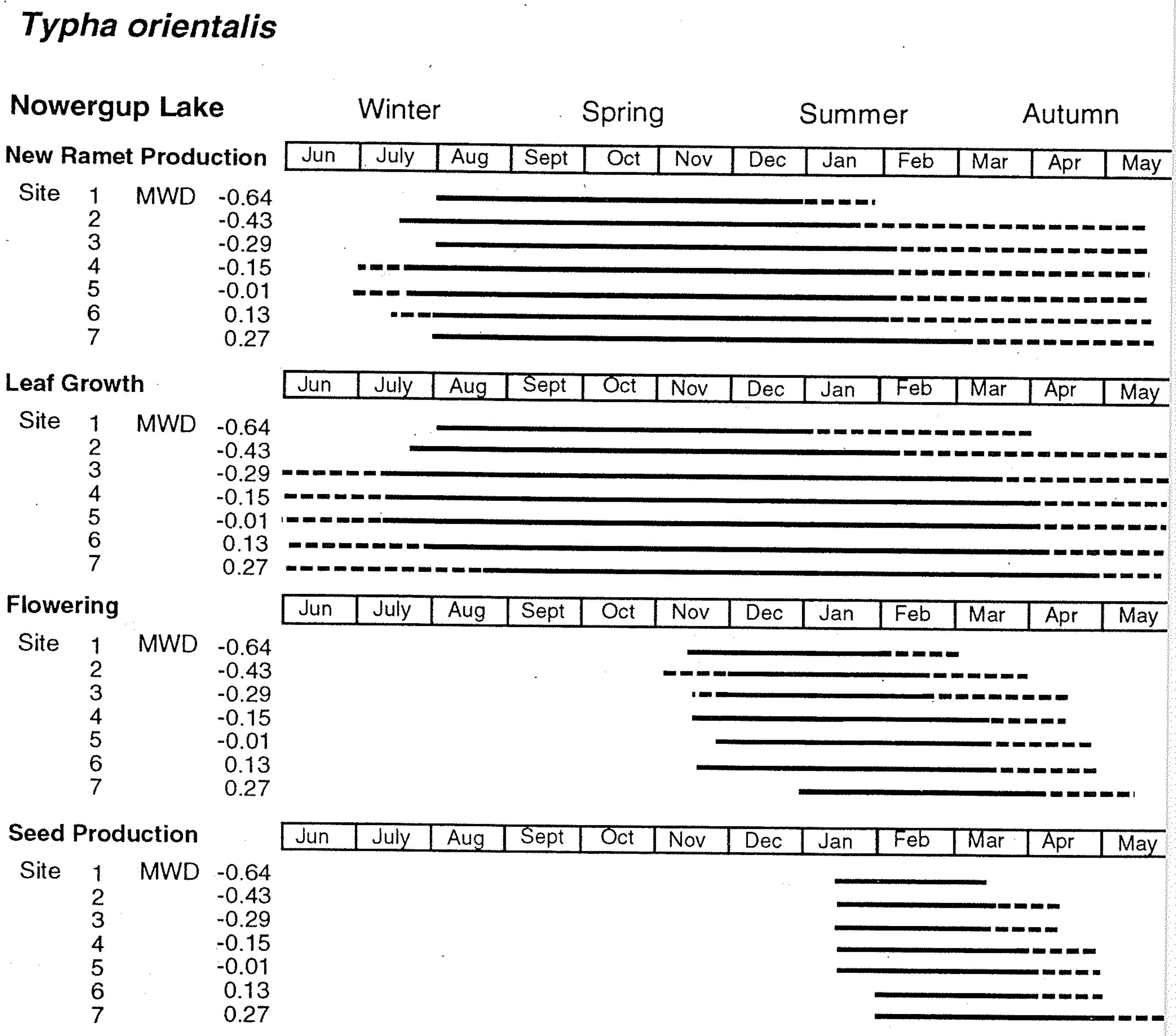


Figure 4.14: Phenology of *Typha orientalis* new ramet production, leaf growth, flowering and seed production at the sampling points on the Nowergup Lake transect. MWD = Mean Water Depth

The period of significant new leaf growth and elongation on young and established *T. orientalis* ramets at Nowergup Lake showed little variation along the water depth gradient, except for the points at the drier end (Fig. 4.14). Leaf growth phenology ranged from early August - late March at the driest end of the gradient, to all year long (although most growth occurred between mid July - mid April) at the wetter points on the gradient. Leaf growth of *T. orientalis* at Forrestdale Lake occurred over a significantly shorter period of time compared to Nowergup Lake (Fig. 4.15). Leaf growth phenology ranged from early August - mid December (4.5 months) at the drier end of the gradient, to mid July - late February (7 - 7.5 months) at the wetter end.

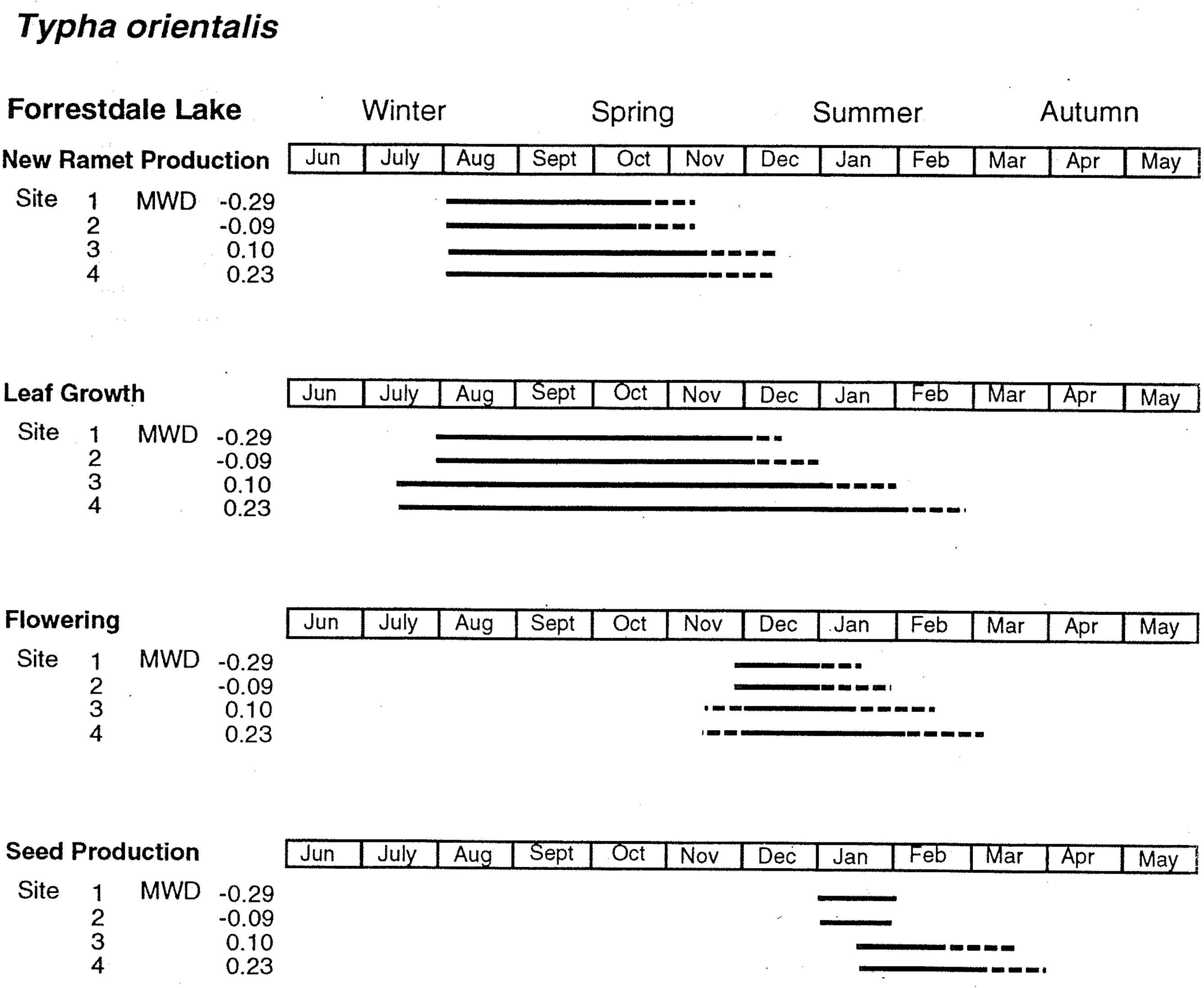


Figure 4.15: Phenology of *Typha orientalis* new ramet production, leaf growth, flowering and seed production at the sampling points on the Forrestdale Lake transect. MWD = Mean Water Depth

Flowering phenology of *T. orientalis* at Nowergup Lake ranged from mid November - late February (3.5 months) at the drier end of the gradient, to early January - mid May (4.5 months) at the wetter end (Fig. 4.14). At Forrestdale Lake, the period of flowering was significantly shorter and earlier in the year compared to Nowergup Lake (Fig. 4.15). Flowering phenology ranged from early December - mid January (1.5 months) at the drier end of the gradient, to mid November - early March (3 -3.5 months) at the wetter end.

Seed production of *T. orientalis* at Nowergup Lake ranged from mid January - mid March (2 months) at the drier end of the gradient, to early February - late May (4 months) at the wetter end (Fig. 4.14). Seed production of *T. orientalis* at Forrestdale Lake occurred over a significantly shorter period compared to Nowergup Lake (Fig. 4. 15). Seed production phenology ranged from early January - Late January (1 month) at the drier end of the gradient, to mid January - late March (2.5 months) at the wetter end.

The above-ground productivity (g dry weight m^{-2} d^{-1}) of *B. articulata* at Thomson Lake, which was measured at four points along the water regime gradient, varied spatially and temporally (Fig. 4.16). At the driest point (mean water depth of -0.52 m), productivity increased gradually during winter, rose steeply during September, and declined during summer, increasing again in the following May. The maximum mean productivity was 1.25 g dry weight m^{-2} d^{-1} during September. With increasing mean water depth, productivity increased to 5.7 g m^{-2} d^{-1} at -0.31 m mean water depth (MWD) and 4.2 g m^{-2} d^{-1} at -0.06 m MWD. The month during which peak productivity occurred also shifted from September to November. At the wettest point on the gradient (0.1 m MWD), the productivity decreased to a peak of 2.8 g m^{-2} d^{-1} in March. This represents a significant shift, along the water regime, in the timing of maximum productivity from one end of the species distribution to the other. Prolonged flooding, severe anoxic sediment conditions, and the co-occurrence of *T. orientalis* at the wettest end of the gradient, are likely reasons for the significant change in productivity phenology (refer below).

At Jandabup Lake, the above-ground productivity of *B. articulata* also varied along the water regime gradient, however the shift in timing of peak productivity was not as dramatic (Fig. 4.17). Productivity at Jandabup Lake was generally lower (maximum mean productivity of 1.4 - 2.1 g m^{-2} d^{-1} cf. 1.2 - 5.6 g m^{-2} d^{-1}) compared with Thomson Lake. At the driest end of the gradient (-0.45 m MWD), productivity increased during Spring, peaking during September (1.4 g m^{-2} d^{-1}), and decreased throughout Summer and Autumn. With increasing mean water depth (-0.14 m), productivity patterns were similar, however peak productivity (2.1 g m^{-2} d^{-1}) occurred during November. At the wettest end of the gradient (0.27 m MWD), productivity was only slightly lower but a 'plateau' of elevated productivity occurred from October to January, with peak productivity (1.2 g m^{-2} d^{-1}) occurring during October. This extended period of elevated productivity was not evident at the drier points on the gradient.

If the productivity at points of similar MWD at Thomson and Jandabup Lakes are compared (Fig. 4.18), a significant difference in the magnitude of productivity becomes evident. Minimum productivity levels at Thomson Lake were similar to the elevated levels at Jandabup Lake. Peak productivity at Thomson Lake was double that of Jandabup Lake and occurred during November at both lakes. However, at Thomson Lake, the productivity remained elevated during the summer months, whereas it decreases dramatically at Jandabup Lake with the onset of Summer. This may be due differences in sediment structure and nutrient concentration between these wetlands.

The maximum above-ground productivity of *T. orientalis*, particularly at Nowergup Lake, was considerably higher than *B. articulata*. The productivity of *T. orientalis* at Nowergup Lake varied both spatially and temporally, however there was no significant change in the timing of peak productivity (Fig. 4.19). At the driest point on the gradient (-0.08 m MWD), productivity increased during early spring, 'plateaued' during October - December (12.2 - 14.3 g m^{-2} d^{-1}), and gradually decreased over summer. A similar trend occurred at 0.27 m MWD but peak productivity was higher (18.8 - 19.1 g m^{-2} d^{-1}). Although productivity phenology was also similar at 0.41 m MWD, levels were greater with exceedingly high productivity (38.2 g m^{-2} d^{-1}) during December. At the wettest point on the gradient (0.48 m MWD), productivity phenology and magnitude was similar to 0.27 m MWD, with only a slight increase in peak productivity.

At Forrestdale Lake, *T. orientalis* productivity varied both in magnitude and phenology and was significantly lower compared with Nowergup Lake (Fig. 4.20). At the driest point on the gradient (-0.29 m MWD), productivity increased during Spring to a peak of 2.2 g m^{-2} d^{-1} (September - October), and decreased during late Spring. During January - April there was no live above-ground biomass and therefore

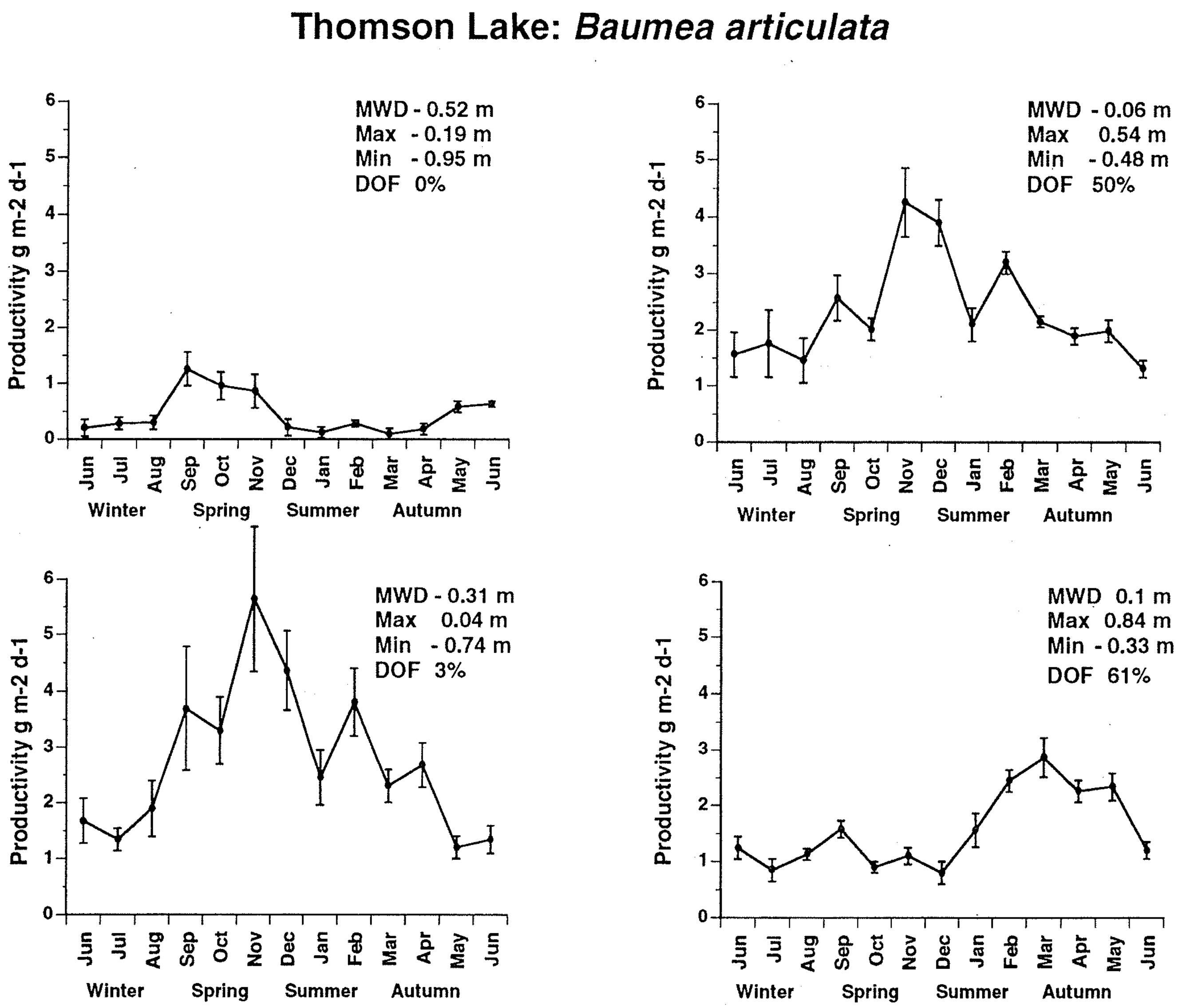


Figure 4.16: Seasonal variation in mean above-ground productivity (g dry wt. m^{-2} d^{-1}) of *Baumea articulata* at points of different water regime at Thomson Lake. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth, DOF = Duration Of Flooding (% of the year). Water regime parameters are for the period June 1989-June 1990 during which productivity was measured.

Jandabup Lake: *Baumea articulata*

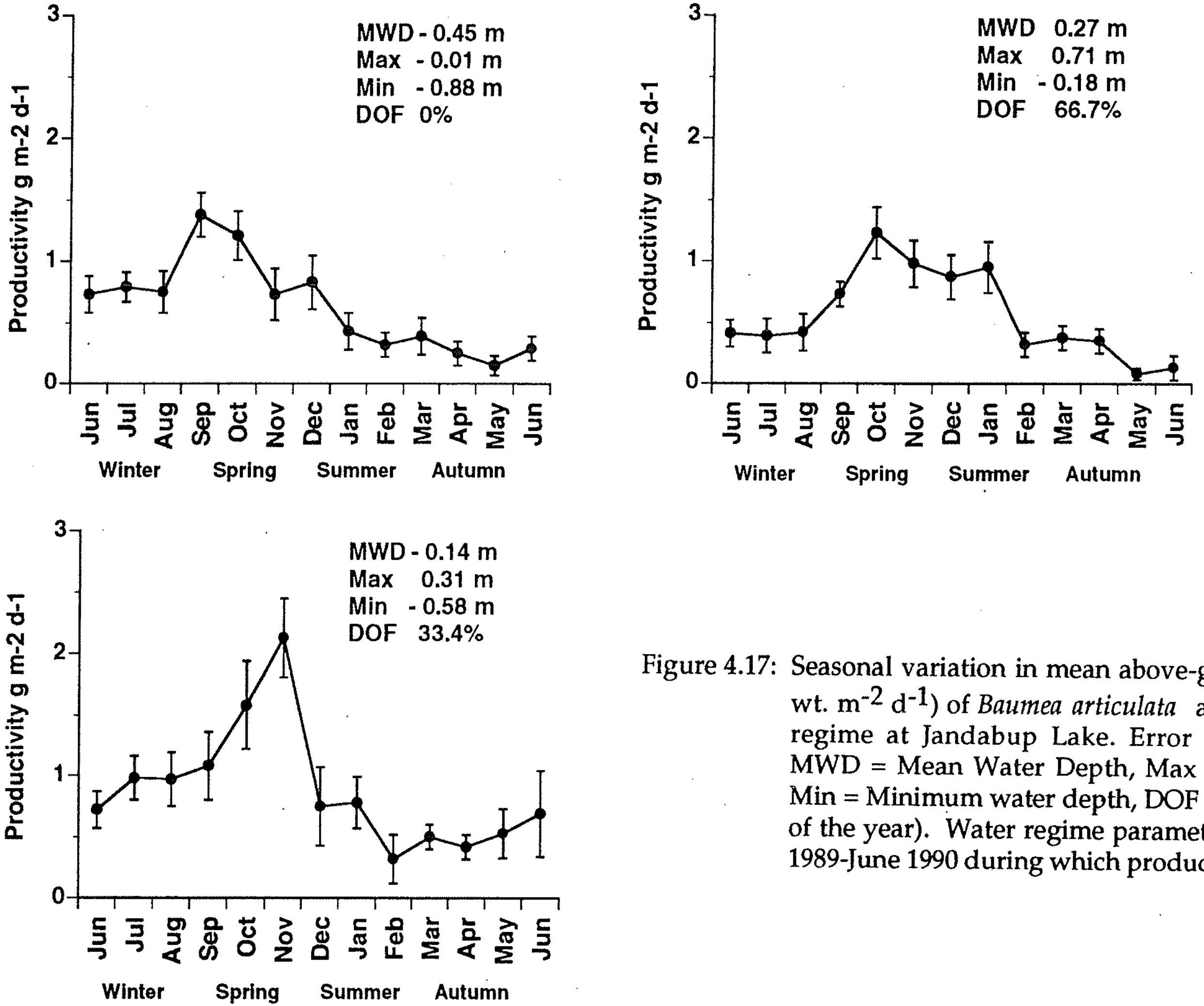


Figure 4.17: Seasonal variation in mean above-ground productivity (g dry wt. m^{-2} d^{-1}) of *Baumea articulata* at points of different water regime at Jandabup Lake. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth, DOF = Duration Of Flooding (% of the year). Water regime parameters are for the period June 1989-June 1990 during which productivity was measured.

Baumea articulata at Similar Mean Annual Depth

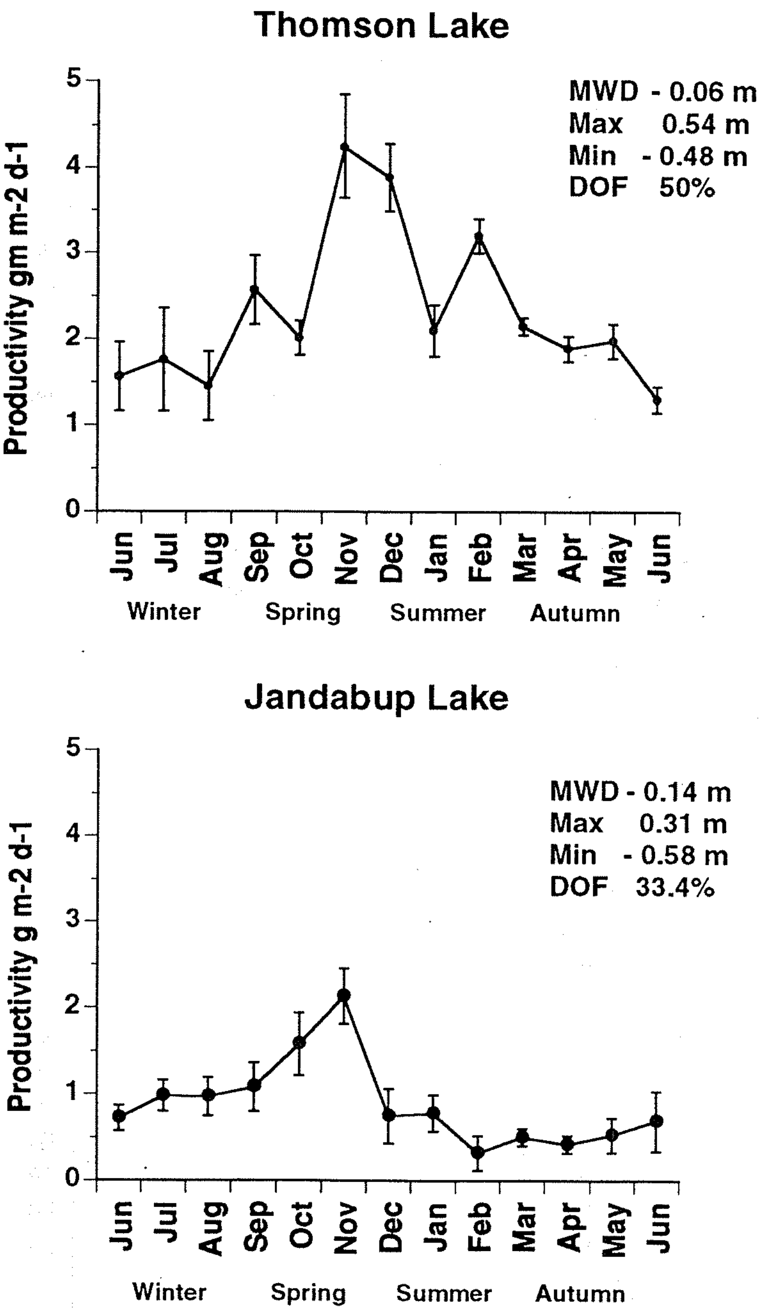


Figure 4.18: Seasonal variation in *Baumea articulata* productivity (g dry wt. m^{-2} d^{-1}) at points of similar water regime at Thomson and Jandabup Lakes. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth, DOF = Duration Of Flooding (% of the year). Water regime parameters are for the period June 1989-June 1990 during which productivity was measured.

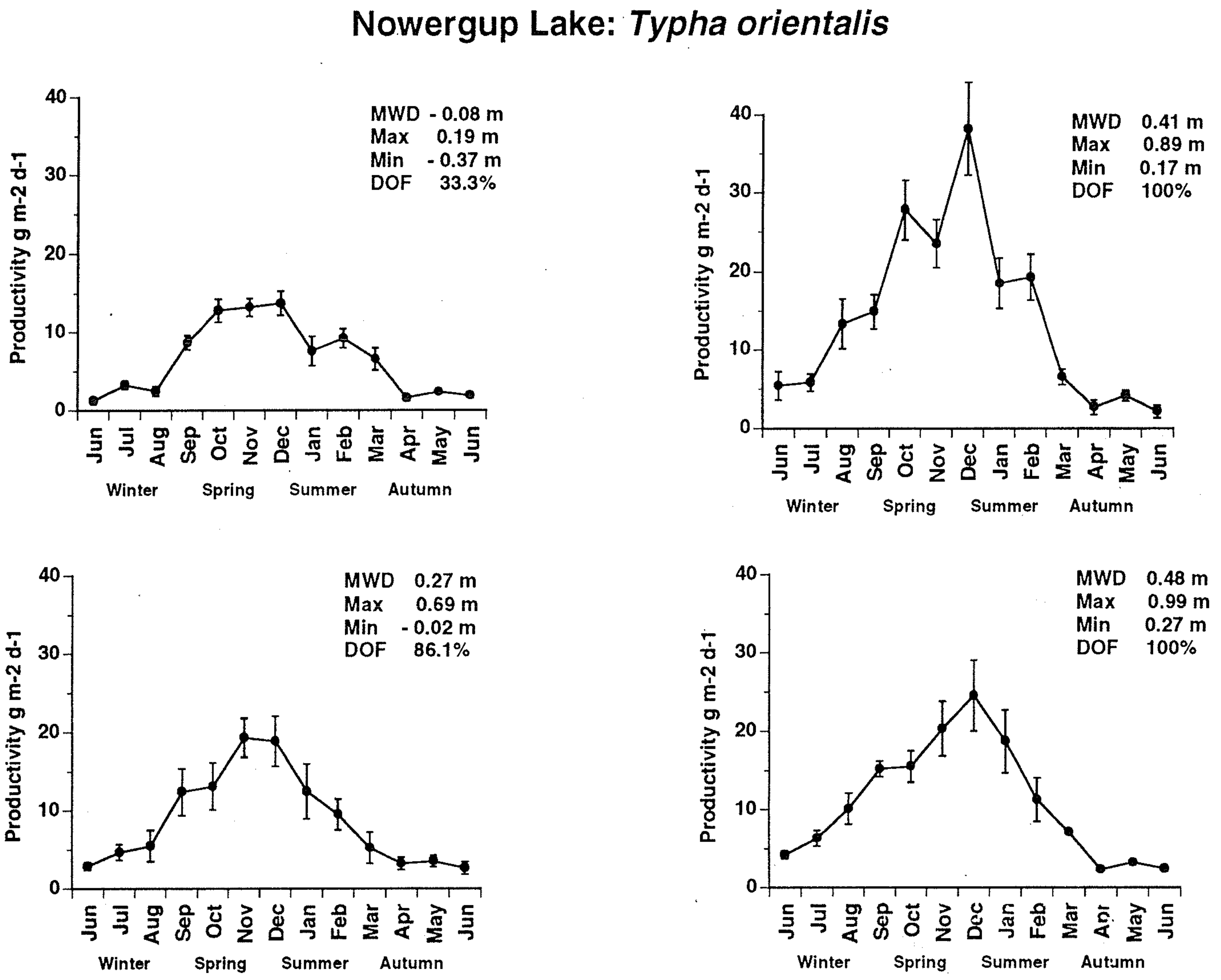


Figure 4.19: Seasonal variation in mean above-ground productivity (g dry wt. m^{-2} d^{-1}) of *Typha orientalis* at points of different water regime at Nowergup Lake. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth, DOF = Duration Of Flooding (% of the year). Water regime parameters are for the period June 1989-June 1990 during which productivity was measured.

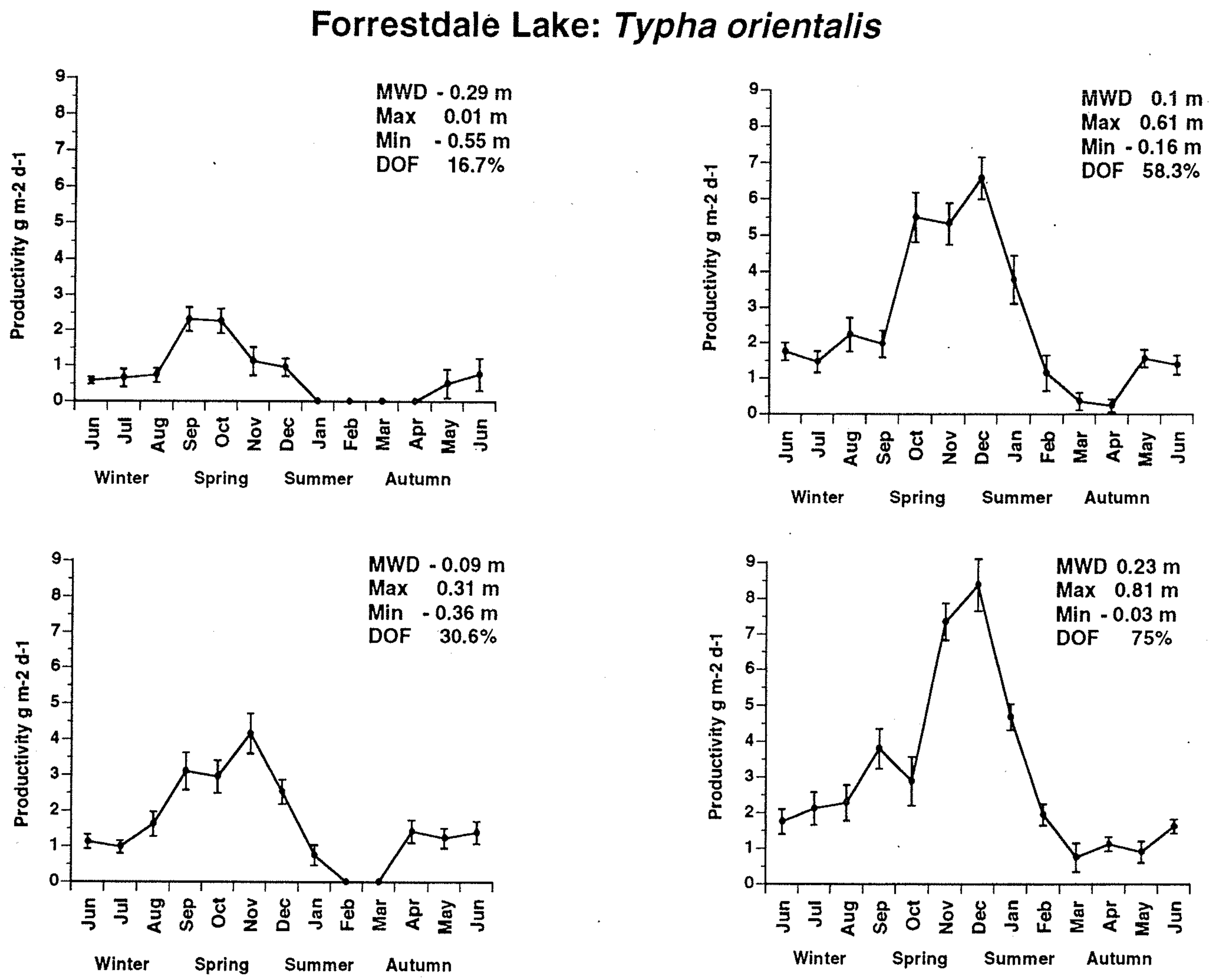

Forrestdale Lake: *Typha orientalis*

Figure 4.20: Seasonal variation in mean above-ground productivity (g dry wt. m^{-2} d^{-1}) of *Typha orientalis* at points of different water regime at Forrestdale Lake. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth, DOF = Duration Of Flooding (% of the year). Water regime parameters are for the period June 1989-June 1990 during which productivity was measured.

productivity was zero. With increasing MWD (-0.09 m), productivity increased during Spring to a peak of 4.1 g m^{-2} d^{-1} (November), then decreased rapidly during early summer. During February and March there was no live above-ground biomass. After new ramets emerged in April, productivity increased and 'plateaued during April - June. At 0.1 m MWD, productivity increased rapidly in early spring to a peak of 6.5 g m^{-2} d^{-1} in December, and then decreased rapidly to low levels in March - April of the following year. There was no period of zero productivity, unlike the drier points on the water regime. At the wettest point on the gradient (0.23 m MWD), productivity increased gradually during early Spring, increasing rapidly to a peak of 8.2 g m^{-2} d^{-1} in November - December, and decreased rapidly during summer. There was no period of zero productivity.

If the productivity at points of similar MWD at Nowergup and Forrestdale Lakes are compared (Fig. 4.21), a significant difference in the magnitude and phenology of productivity becomes evident. Minimum productivity levels at Nowergup Lake were similar to the elevated levels at Forrestdale Lake. Peak productivity at Nowergup Lake was over 3.3 times that of Forrestdale Lake, and occurred during October - December whereas peak productivity at Forrestdale Lake occurred during November. A period of no productivity (February and March) occurred at Forrestdale Lake but did not occur at Nowergup Lake, which had a productivity of 6.5 - 9 g m^{-2} d^{-1} during the same period.

Sediment Nutrients and Texture

Sediment profiles varied significantly within and between wetlands (Fig. 4.22 and 4.23). At Thomson Lake, the depth of peat increased along the water regime gradient, with little peat at the drier end and deep (>65 cm) peat at the wetter end. Coarse grey sand formed the base of the sediment at all sample points on the gradient. Sediment at Jandabup Lake however, had less peat and was dominated by coarse grey sand. The depth of peat/humus varied from 12-37 cm but was mixed with sand. Nowergup Lake varied from a sandy peat at the drier end of the gradient, to gelatinous grey calcareous silt at the wetter end. This calcareous silt was relatively unstable and contained dark bands of organic matter. Sediment at Forestdale Lake generally consisted of peaty sand over loam or clay, the heavy clay occurring at shallower depths at the wetter end of the gradient.

The texture analysis of sediment along each of the transects reflects the variation in sediment profiles (Fig. 4.24 and 4.25). All samples from all lakes had a high sand content and most variation was due to differences in silt and clay fraction. Thomson Lake had a higher clay fraction than Jandabup Lake, whereas Jandabup had no silt fraction. At Nowergup Lake, the silt fraction was several times greater than the clay fraction, whereas the reverse was true for Forrestdale Lake which had the highest clay fraction of all the lakes. It should be noted that the texture analysis does not reflect the texture of sediment at depths greater than 30 cm.

Percentage organic matter of the sediment, as determined by loss-on-ignition, varied significantly within and between wetlands (Fig. 4.26 and 4.27), and generally followed the trends observed in the sediment profiles. Significantly higher amounts of organic matter were found at Thomson Lake when compared with Jandabup Lake, and the proportion of organic matter increased dramatically at the wetter end of the Thomson Lake gradient. Organic matter remained at high (20-40%) levels over most of the gradient at Nowergup Lake, whereas levels remained low (<5%) at Forrestdale Lake.

Dissolved oxygen concentrations in water varied dramatically between lakes and, in some cases, along transects. At the driest points at each of the transects (except Nowergup Lake), surface water occurred for a relatively short time (< 2 months) and was very shallow, as a result dissolved oxygen (DO) readings proved unreliable and did not reflect sediment conditions. Thomson Lake showed the most dramatic difference in DO concentration along the transect or water regime gradient. The mean DO (% saturation) level at -0.06 m mean water depth (MWD) was 78% (range 63 - 123) whereas at 0.1 m MWD it was 38% (range 12 - 98). This significant reduction in DO at the wetter point was correlated with an increase

Typha orientalis at Similar Mean Annual Depth

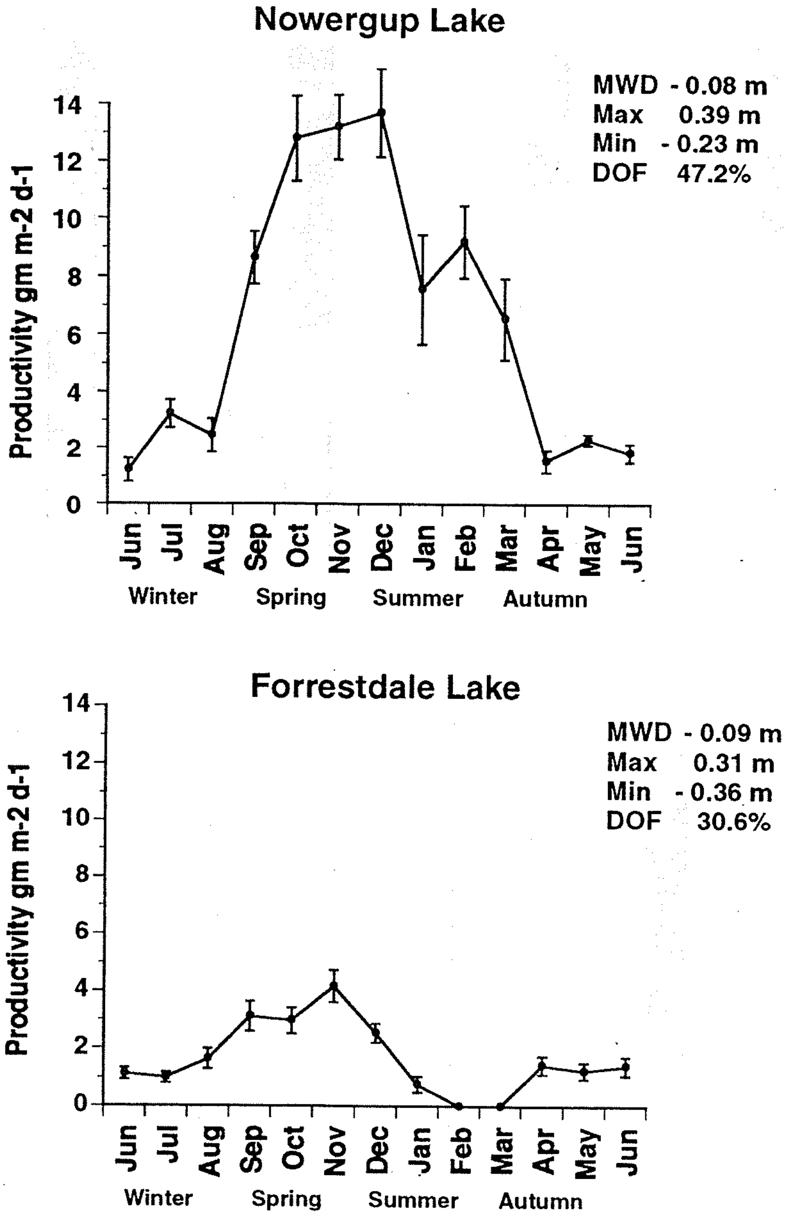


Figure 4.21: Seasonal variation in *Typha orientalis* productivity (g dry wt. m^{-2} d^{-1}) at points of similar water regime at Nowergup and Forrestdale Lakes. Error bars are standard errors. MWD = Mean Water Depth, Max = Maximum water depth, Min = Minimum water depth,

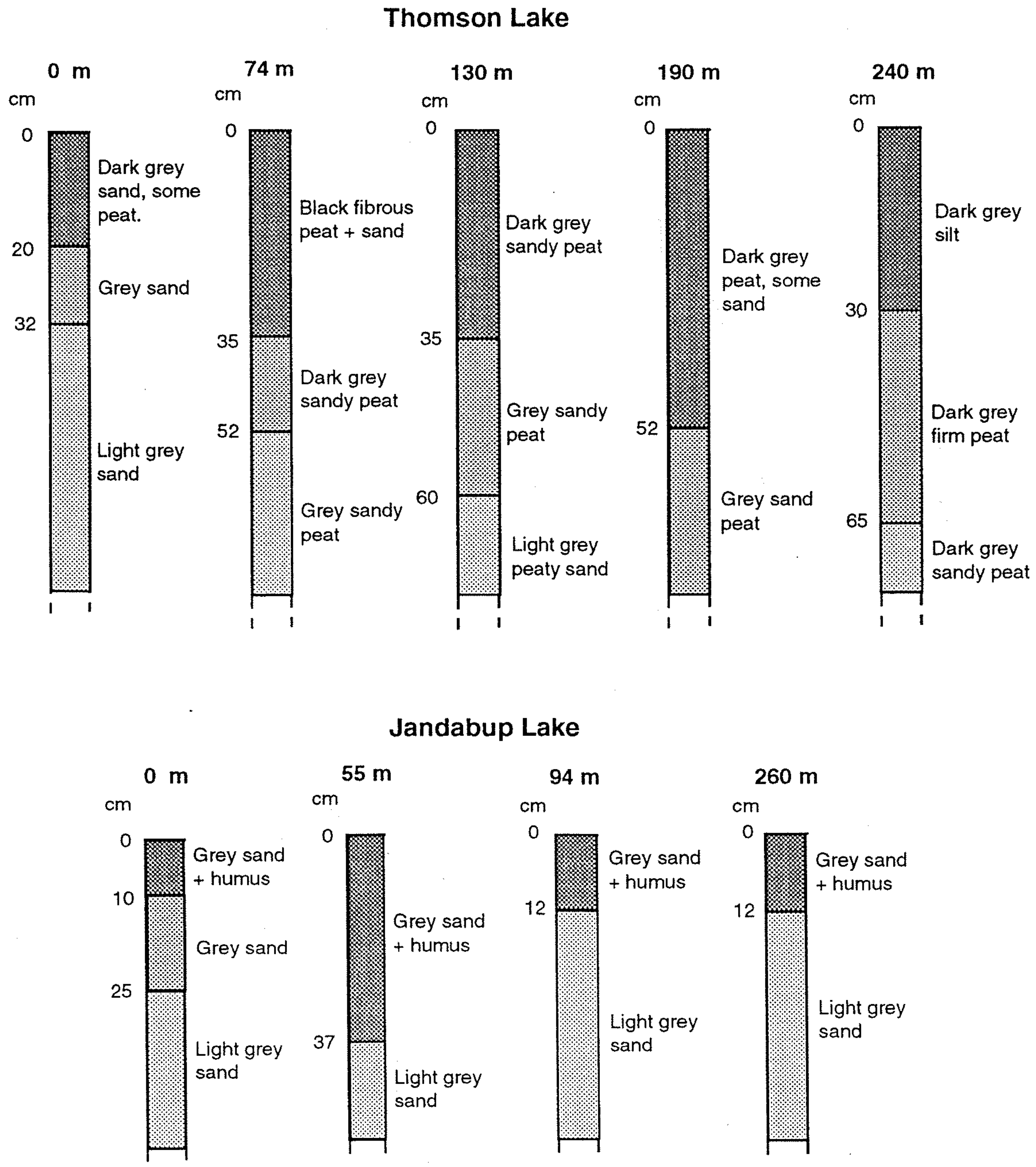
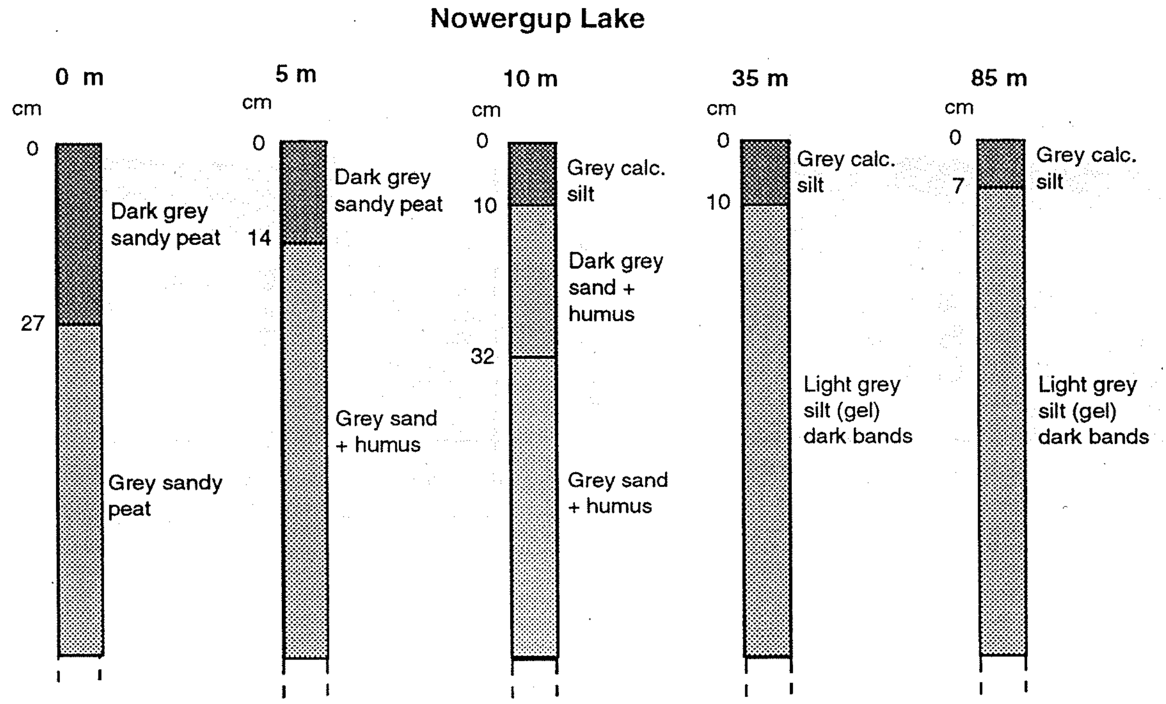


Figure 4.22: Sediment profiles at selected distances along the Thomson and Jandabup Lake transects. Elevation decreases and mean water depth increases with increasing distance along the transects.



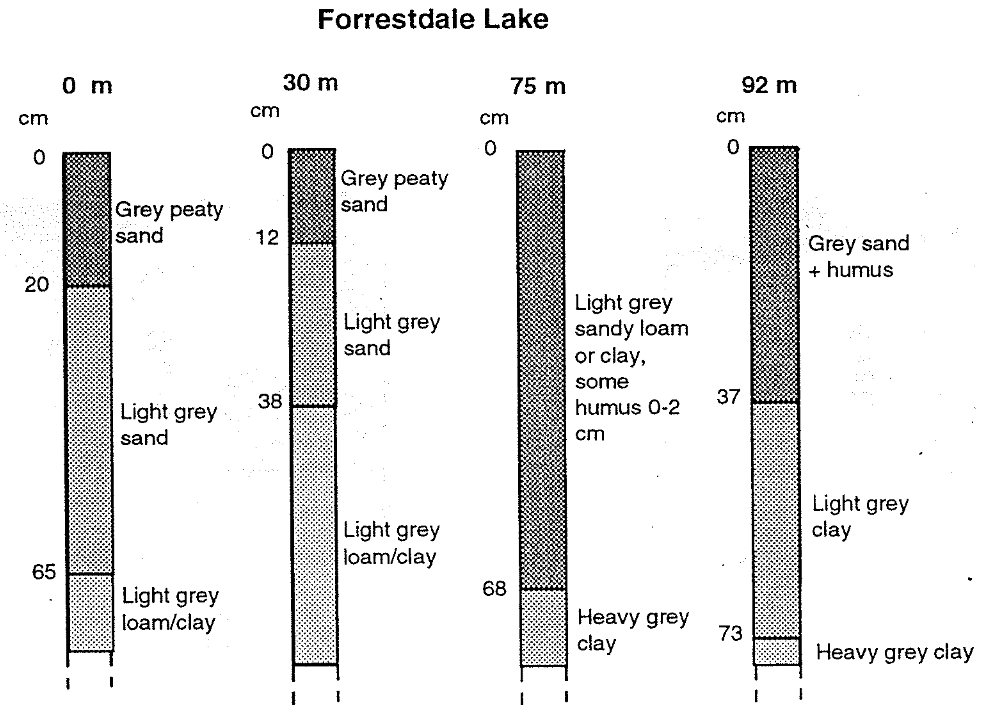


Figure 4.23: Sediment profiles at selected distances along the Nowergup and Forrestdale Lake transects. Elevation decreases and mean water depth increases with increasing distance along the transects.

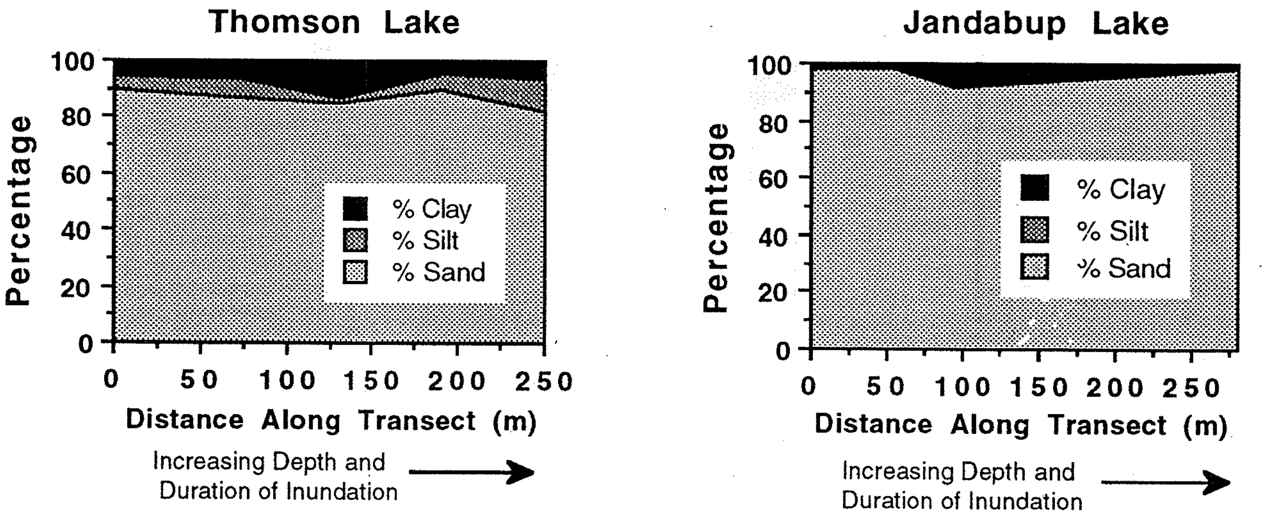


Figure 4.24: Variation in sediment sand, silt and clay fractions along the Thomson and Jandabup Lake transects.

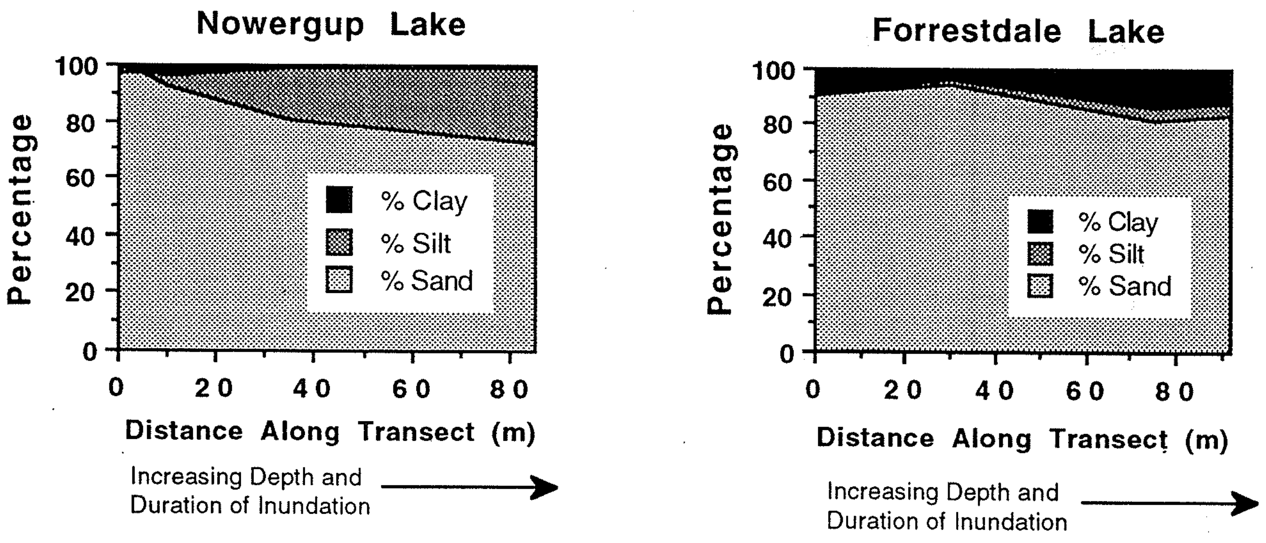


Figure 4.25: Variation in sediment sand, silt and clay fractions along the Nowergup and Forrestdale Lake transects.

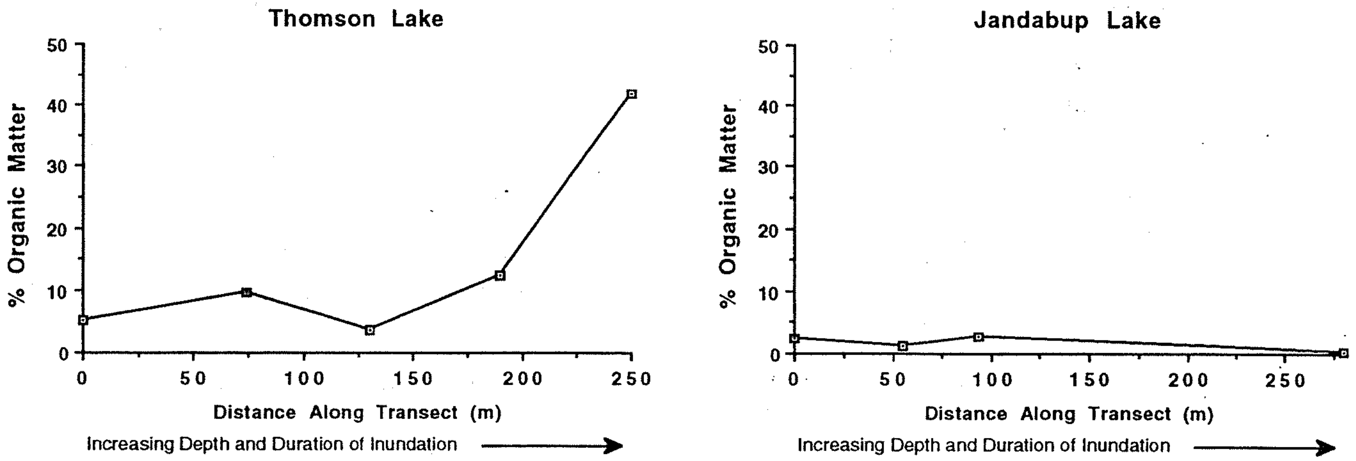


Figure 4.26: Variation in sediment % organic matter (% carbon) along the Thomson and Jandabup Lake transects.

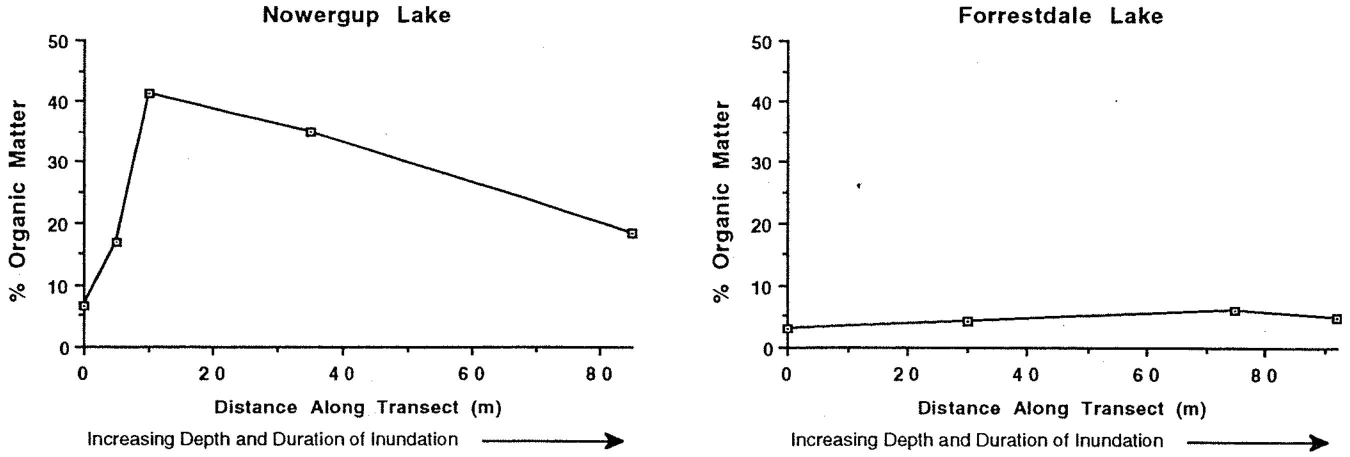


Figure 4.27: Variation in sediment % organic matter (% carbon) along the Nowergup and Forrestdale Lake transects.

in the proportion and depth of organic matter (see above). Biological oxidation of organic matter, especially by bacteria, chemical oxidation of organic compounds, and reduced wind-mixing of the water column due to dense vegetation, contribute to oxygen depletion. At Jandabup Lake, those sampling points that were inundated did not vary in DO concentration significantly and had a mean of 98% (range 86 - 131). Nowergup Lake varied from 83% (67 - 111) at -0.08m MWD to 74% (56 - 118) at 0.48 m MWD. Forrestdale Lake varied from 92% (83 - 110) at -0.09 m MWD to 81% (70-106) at 0.23 m MWD.

Sediment Total Kjeldahl Nitrogen (TKN) and Total Phosphorus (TP) varied both within and between lakes over time (Fig. 4.28 and 4.29). Both TKN and TP were significantly higher at Thomson Lake compared to Jandabup Lake (at similar mean water depth) and this is reflected in the differences in *B. articulata* productivity. Sediment TKN was 3 - 7 times greater at Thomson Lake, with significant variation between seasons. A significant decline in TKN was observed during late spring and early summer and may be due to increased decomposition, volatility and plant uptake (note increased productivity during this period). Sediment TP was 3 - 5 times greater at Thomson Lake.

Sediment TKN and TP were significantly higher at Nowergup Lake compared to Forrestdale Lake (at similar mean water depth) and this was reflected in *T. orientalis* productivity. There was nominal variation in nutrient concentration with time at both lakes. At Nowergup, TKN concentrations exceeded those at Forrestdale by approximately 9 times, and TP concentrations were approximately 3 - 6 times higher.

4.5.3 *Discussion*

As discussed previously (Section 4.4.3), altered water regime can induce a significant shift in the distribution of an emergent macrophyte population. However, as the above results indicate, productivity and growth phenology of plants within a population are also influenced by water regime. Due to differences in elevation, not all plants within a population experience the same water regime. Consequently, there is a degree of variability in plant growth and reproductive characteristics within a population and/or stand. Although these spatial or temporal differences or changes in growth are more subtle than differences or changes in distribution, they do allow more detailed assessment of population vigour and the processes which dictate distribution and survival.

With respect to standing biomass, ramet density and productivity, minimum values were usually observed at either extreme of a species distribution relative to elevation, ie. low productivity was observed both at the driest and the wettest points at which a species is found. At the driest point of a species distribution, factors such as water stress during summer, shading from fringing tree vegetation, slower rates of decomposition, lower nutrient concentrations and competition with 'dryland' species, limit the productivity and reproduction of plants at this point (Fig. 4.30). At the wettest point of a species distribution, prolonged inundation, anoxic sediment, increased light attenuation through the water column and competition with other emergent macrophytes, are the factors likely to limit growth.

Differences in growth and reproduction phenology were observed along transects (or water regime gradients) and between lakes. The emergence of new ramets and period of rapid leaf growth at the drier end of a gradient, generally commenced during late winter - early spring and ended during early summer. One may infer that water stress during the warmer summer months restricts growth at higher (drier) elevations. At some locations (eg. Thomson, Forrestdale and Nowergup Lakes), shading by overstorey tree species also reduces growth at the higher elevations. The reduced or absent inflorescence production observed at higher (drier) elevations on some transect gradients (Thomson, Jandabup and Forrestdale), signifies a possible lack of seedling recruitment under prolonged drawdown conditions. However, seed from previous flowering seasons (particularly *Baumea articulata* and most Cyperaceae), when conditions may have been more favourable, is stored within the surface sediment and this would negate any immediate effects of reduced seed set during the current season. Several years of little or no seed production

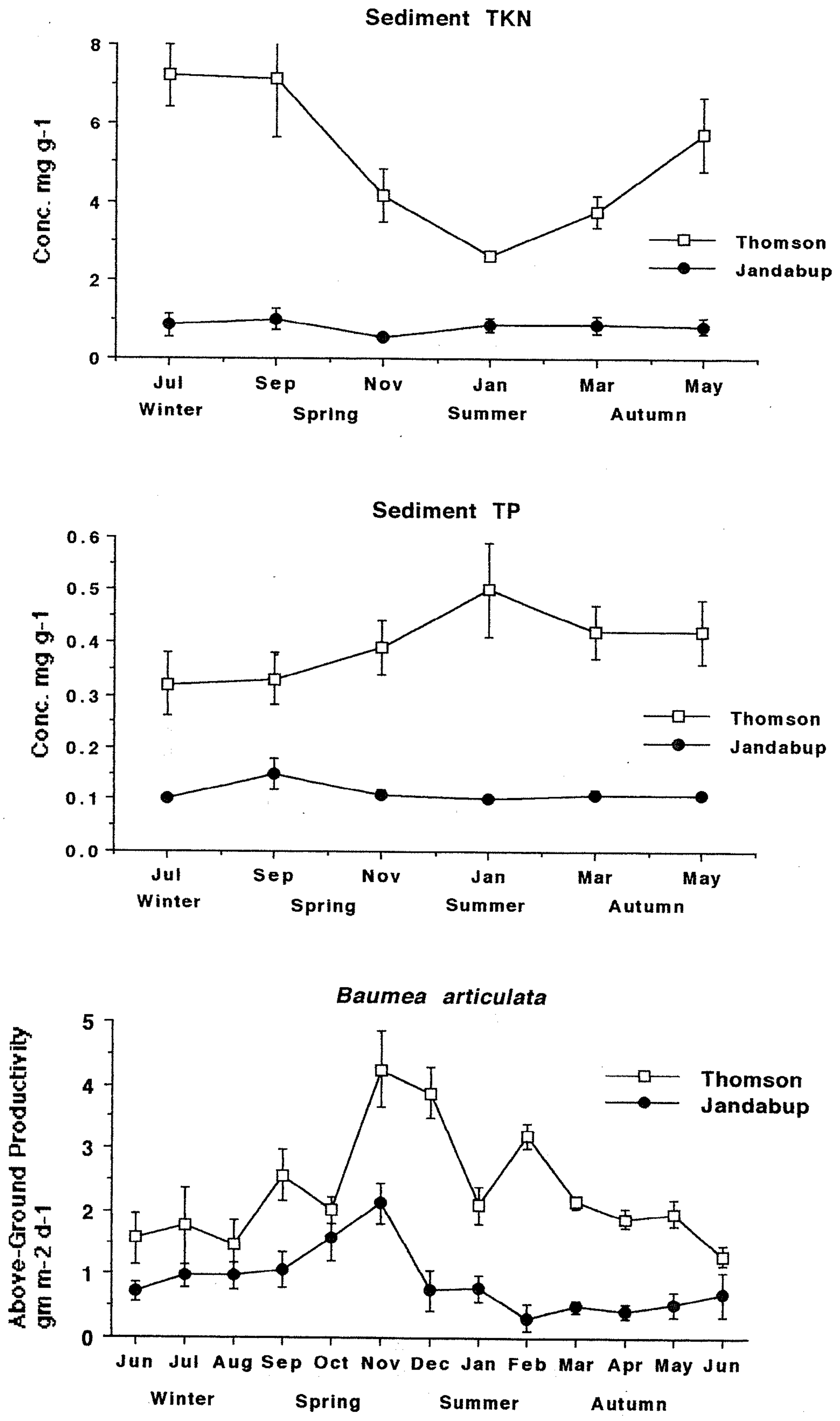


Figure 4.28: Seasonal variation in sediment Total Kjeldahl Nitrogen (TKN) and Total Phosphorus (TP) at points of similar water regime (see Fig. 4.19 for parameters) at the Thomson and Jandabup Lake transects. *Baumea articulata* above-ground productivity (g dry wt. m^{-2} d^{-1}) at the same points is also shown. Error bars are standard errors.

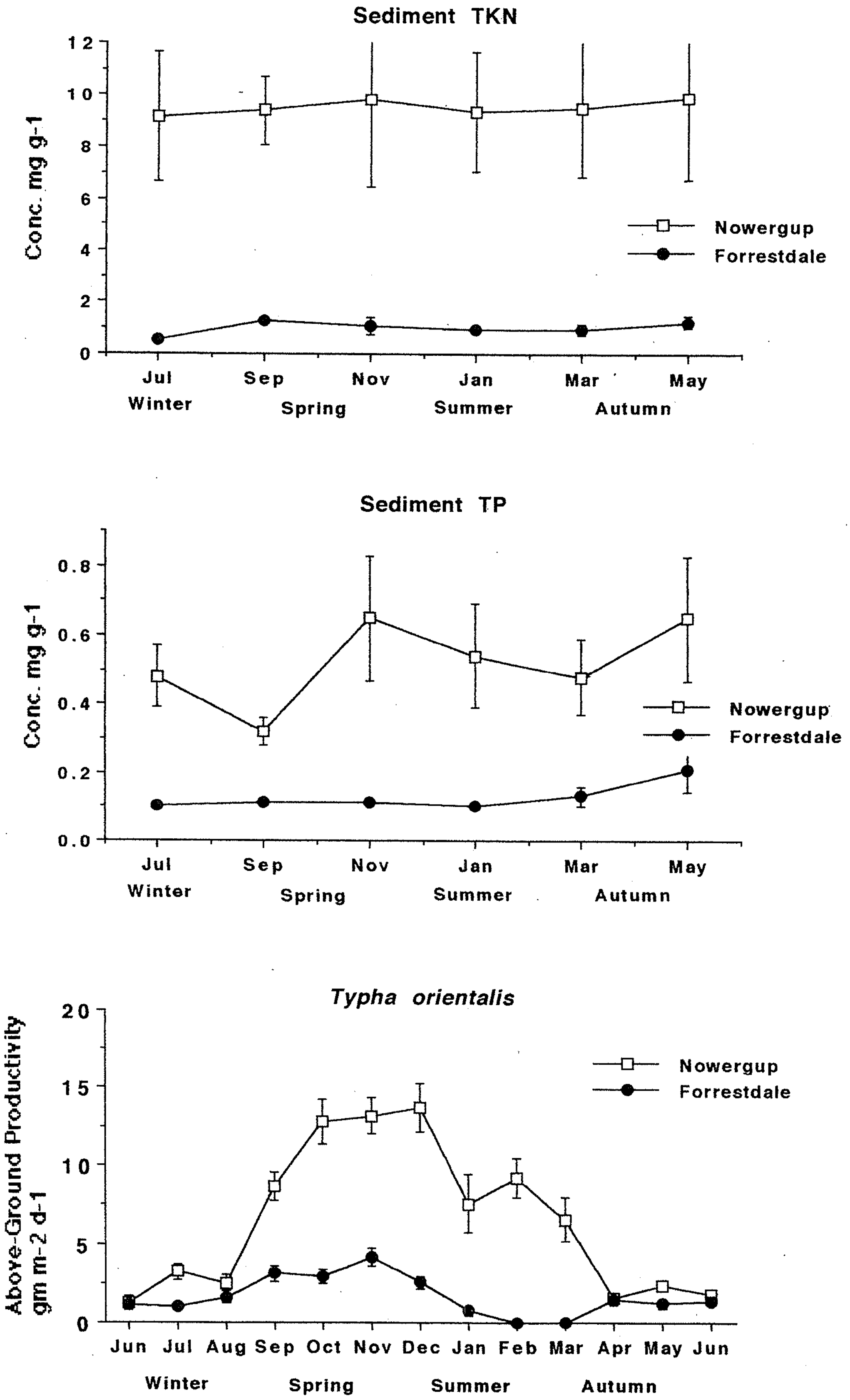
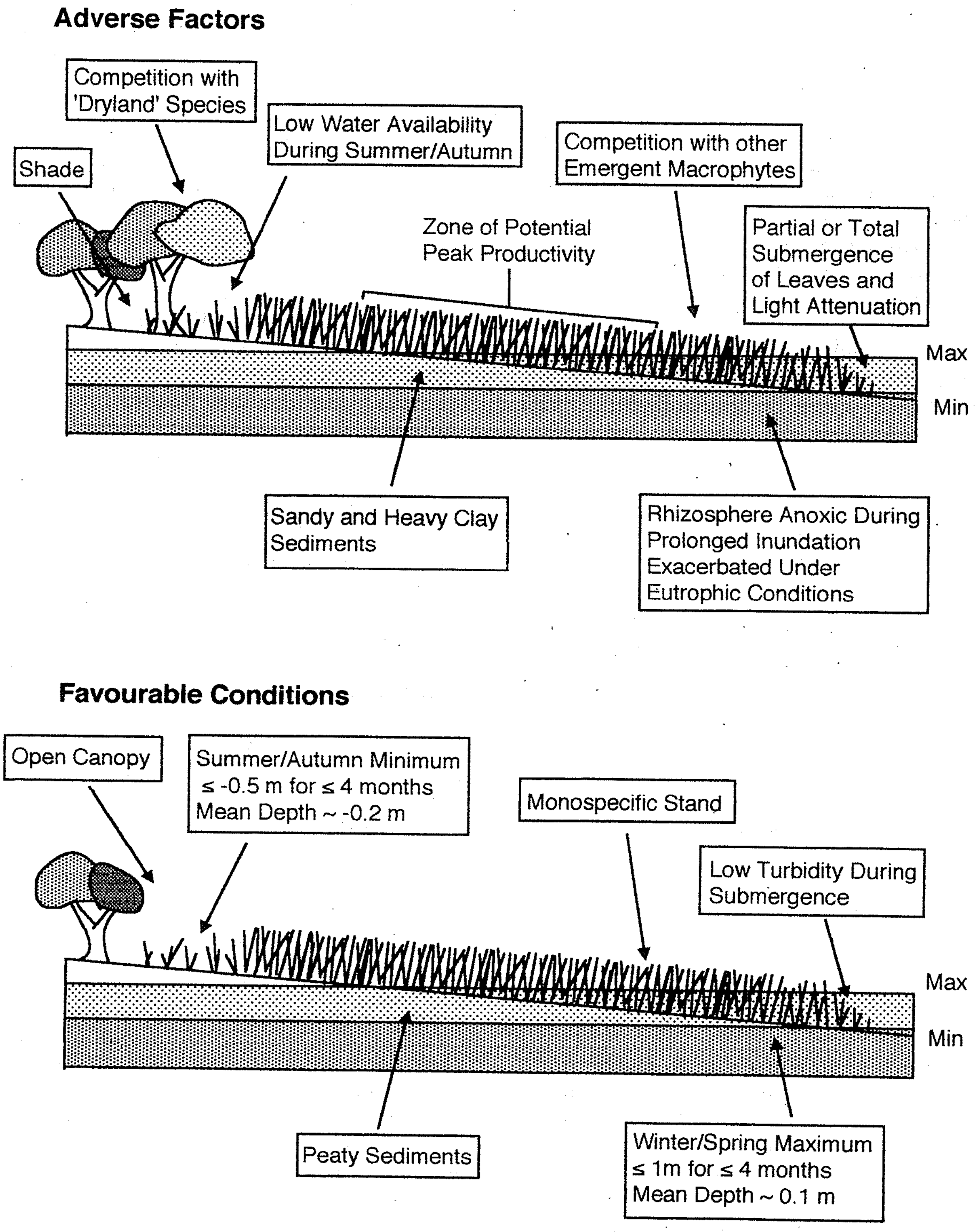


Figure 4.29: Seasonal variation in sediment Total Kjeldahl Nitrogen (TKN) and Total Phosphorus (TP) at points of similar water regime (see Fig. 4.19 for parameters) at the Nowergup and Forrestdale Lake transects. *Typha orientalis* above-ground productivity (g dry wt. m^{-2} d^{-1}) at the same points is also shown. Error bars are standard errors.



Adverse Factors

Favourable Conditions

Figure 4.30: Summary of the conditions which are adverse and favourable to emergent macrophyte survival and productivity.

however, may exhaust the sediment seed store, resulting in a reduced capacity for seedling recruitment.

Those wetlands with a higher nutrient status (Thomson and Nowergup Lakes) appeared to support a longer period (up to 12 months of the year) of above-ground growth than those wetlands with a lower nutrient regime (Jandabup and Forrestdale Lake). However, this relationship may be confounded somewhat by the fact that lower nutrient status lakes had a greater proportion of their species distribution at drier water regimes. Therefore, at some points along an elevation gradient, it is not possible to separate the effects of lower nutrient availability and drier water regime.

At all lakes, but particularly the *Baumea articulata* sites (Thomson and Jandabup Lakes), a significant shift in the timing of maximum productivity from late winter/early spring at the drier end of the gradient to late spring/early summer at the wetter end, was observed. This reflects the differences in seasonal water availability within a species distribution. However this temporal shift, as well as differences in productivity rates, may also be associated with factors other than water regime. For example, the 7 month (September vs March of the following year) difference in timing of peak *B. articulata* productivity at Thomson Lake, was due to a combination of prolonged flooding and elevated nutrient regime at the lowest (wettest) end of the species distribution. Under flooded conditions, high nutrient concentrations combined with peat sediments resulted in severe anaerobic conditions within the rhizosphere. Productivity, therefore, was low until mid-late summer when the lake dried and the sediment became oxygenated. This triggered a relatively uncharacteristic increase in productivity during late Summer and Autumn. Although this particular scenario was not observed at the other study wetlands, it is likely that it would occur elsewhere given similar conditions.

The measurement of productivity rates at selected points along water regime gradients at the paired lakes (Thomson, Jandabup and Nowergup, Forrestdale), allowed the comparison of plants at similar water regime but different nutrient and sediment conditions. At similar water levels but different sediment nutrient concentrations, both *B. articulata* and *Typha orientalis* productivity responded to a higher nutrient regime. This demonstrated that although two stands of the same species are experiencing similar water regimes, their productivity may vary significantly due to differences in nutrient regime and sediment type.

If annual mean productivity at each of the paired lakes is plotted against mean water depth (Fig. 4.31), the differences between lakes and species is emphasised. For *B. articulata*, productivity rates under low nutrient and sandy sediment condition (Jandabup Lake, see below), are relatively low with a narrow range in values. However, at Thomson Lake where nutrients levels are higher and the sediment has a greater peat and silt content, productivity rates are significantly higher and have a greater range. With increasing mean water depth, mean productivity values increase, reach a maximum value, and then decrease. Although high nutrient concentrations and peat sediments caused anoxic conditions and reduced productivity at the deepest mean water depth at Thomson Lake, mean productivity was still greater than at Jandabup Lake. The lower water holding capacity of the sandy sediment at Jandabup Lake may have a significant effect on water availability during the dry Summer and Autumn months.

The difference in mean productivity between the two *Typha orientalis* lakes was greater compared to the *Baumea articulata* lakes. Productivity under low nutrient and clay sediment conditions was relatively low at Forrestdale Lake but with a wide range in values. At Nowergup Lake however, productivity values were several times greater under the higher nutrient and calcareous silt sediment conditions. How the clay sediment at Forrestdale Lake may influenced productivity is uncertain, a possibility is that it may limit root and rhizome growth due to reduced penetrability. The heavy clay at depth (60-70 cm) may form an impermeable pan, implying that the depth of water-holding soil (solum depth) is limited, and that surface water is a more important water source than groundwater since capillary rise of groundwater through

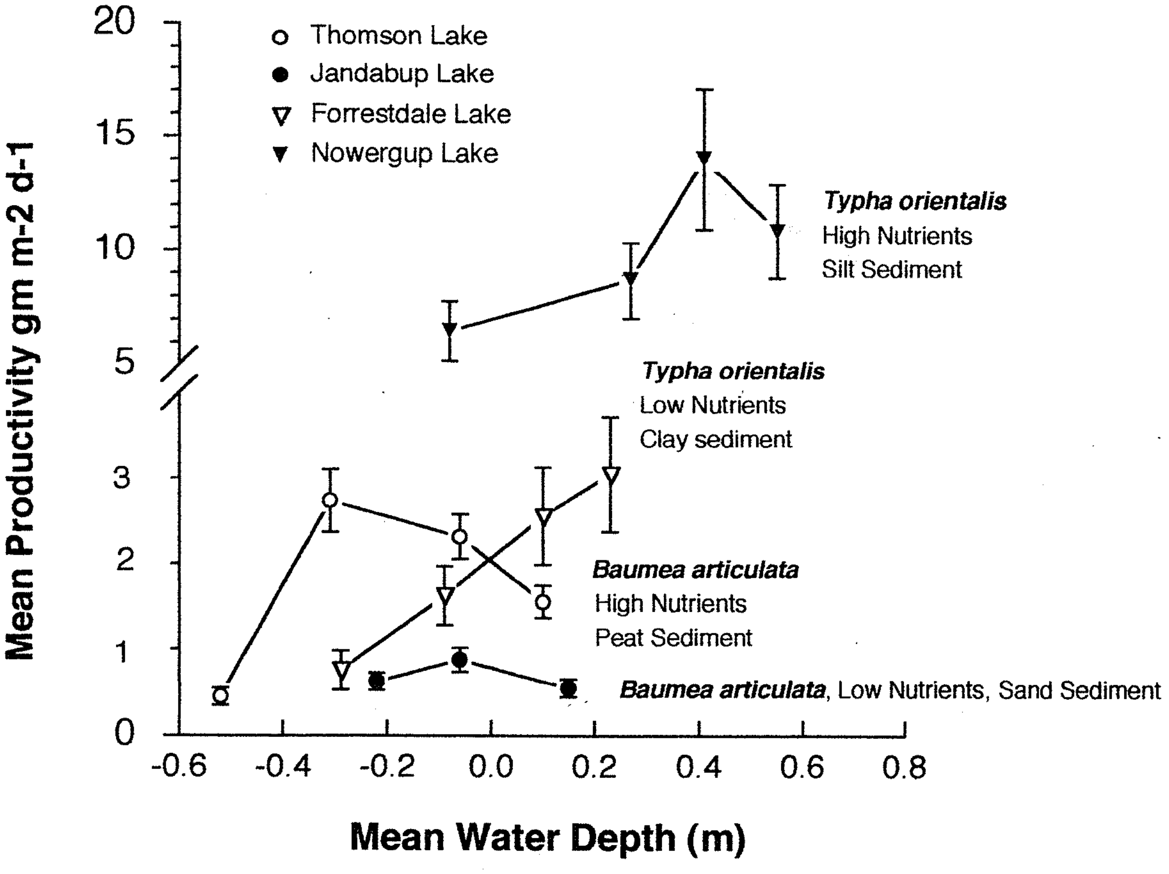
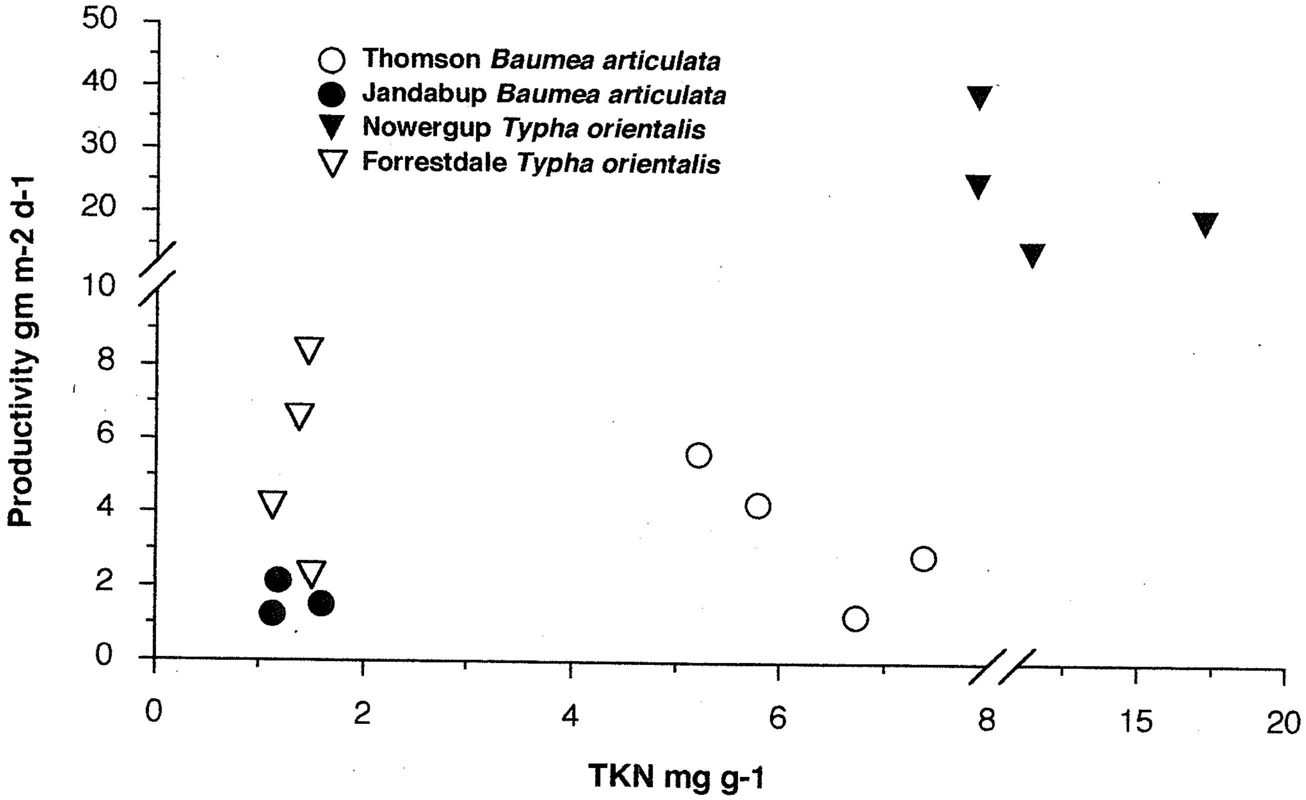


Figure 4.31: Comparison of mean above-ground productivity with mean water depth at the four paired study wetlands.

the unsaturated zone during summer, would be prevented by the clay pan.

Differences in response to nutrient regime are emphasised when mean above-ground productivity is plotted against sediment TKN and TP concentration (Fig. 4. 32). The *Baumea articulata* sites at Jandabup Lake varied little in productivity and nutrient concentration. Although the *Typha orientalis* sites at Forrestdale Lake also had low sediment nutrient concentrations, productivity values differed significantly. This implies that factors other than nutrient concentration, such as water regime and sediment type, were responsible for the observed variation in productivity. Although the *B. articulata* productivity values at Thomson Lake increased with higher nutrient concentrations, there was considerable variation, probably due to shading (drier end of gradient) and the anoxic sediment (wetter end) discussed above. Most of the productivity sites at Nowergup Lake (*T. orientalis*) had similar (or only slightly greater) nutrient concentrations to Thomson Lake (*B. articulata*), however productivity at Nowergup was approximately 6 - 10 times greater. This difference may be due to other factors such as sediment composition but it does suggest that *T. orientalis* has a greater response to elevated nutrient regimes. This is of particular interest when considering the invasive nature of *Typha* , particularly at disturbed wetlands with an elevated trophic status. Higher productivity represents faster vegetative expansion, resulting in the colonising of open areas and the shading and exclusion of other species.

Although two stands (or populations) of the same or different species may have a similar distribution relative to water regime, there can be considerable variation in productivity and reproductive phenology within and between stands. This is generally a reflection of the variability in abiotic (water regime, nutrients, sediment etc) and biotic (competition) factors along an elevational gradient and between wetlands. Consequently, a species 'preferred' (based on productivity and reproduction) water regime in the field, represents the interaction of a number of environmental factors.



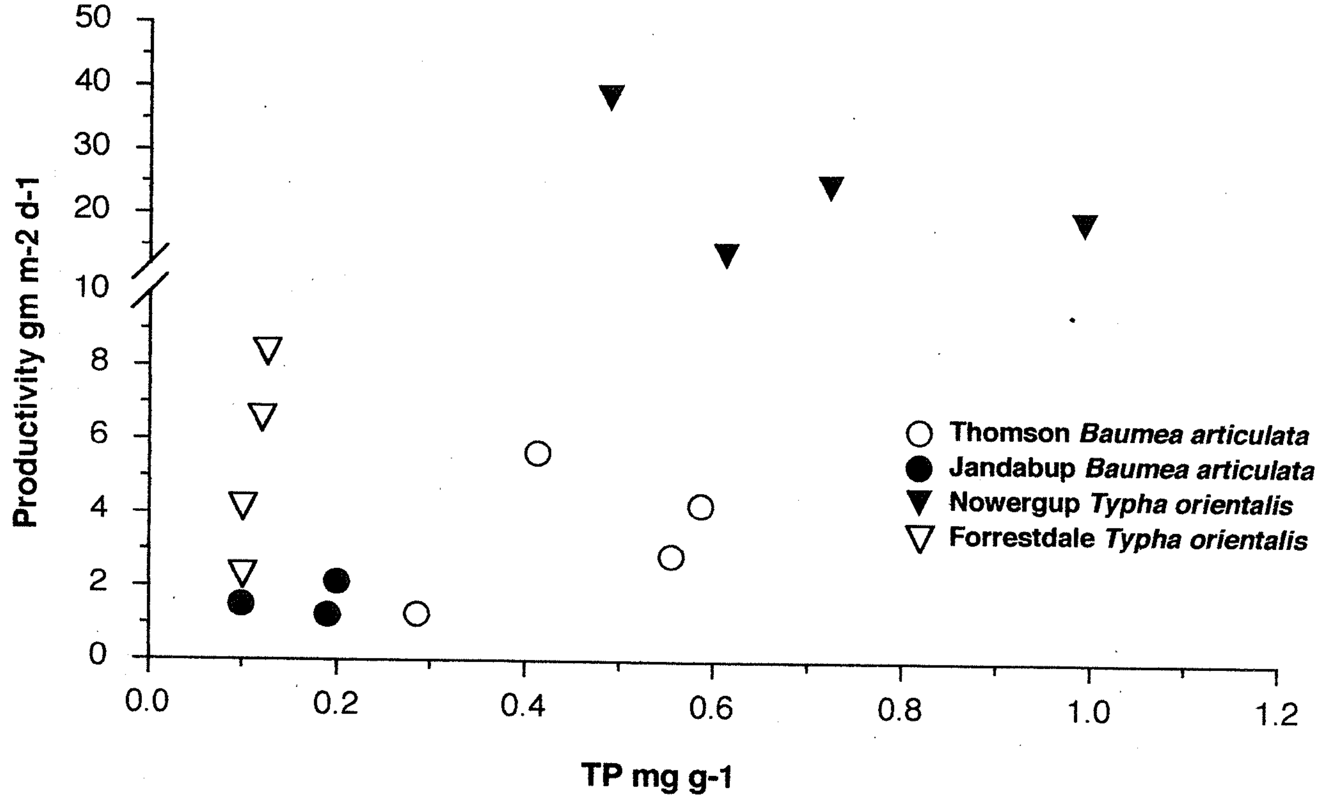


Figure 4.32: Comparison of mean above-ground productivity with mean sediment Total Kjeldahl Nitrogen (TKN) and Total Phosphorus (TP) concentration at the four paired study wetlands.

5: Seedling Recruitment of Emergent Macrophytes

5.1 Introduction

The mechanisms that determine the zonation of wetland vegetation along water regime gradients cannot be understood by describing only the distributions of adult plants. Seed germination, or recruitment patterns, of emergent macrophytes may play a significant role in the replacement of individuals in existing populations, and the colonising of new sites. The frequency, however, at which this occurs is dependent upon the vigour of the parental population, the seed germination and seedling establishment biology of the species, and environmental factors such as light availability, sediment type, oxygen concentrations, temperature and water regime. Given the predominantly clonal nature of growth in these species (Chapter 4), seedling recruitment may only become significant in the demography of a macrophyte population when:

a) the water regime is reduced sufficiently (magnitude and duration) during natural or artificial drawdown to permit germination and seedling establishment on exposed sediment (van der Valk, 1978; Moore and Keddy, 1988);

b) severe drawdown or flooding kills the parental population, and subsequently, conditions permit germination of seeds within the sediment seed bank (van der Valk, 1978; Galinato and van der Valk, 1986; van der Valk, 1986);

c) the biology of a species is indicative of an invasive species with high seed production, wide dispersal, and high germinability and viability (Sharma and Gopal, 1978; Bonnewell *et al.*, 1983).

Little is known about the seed germination and seedling recruitment biology of the fringing wetland plant species indigenous to the Swan Coastal Plain. However, a significant amount of research has been conducted on species of similar ecological function in the northern hemisphere (see above). With respect to seedling recruitment, three types of species are found in wetland seed banks: emergent species which germinate on exposed mud flats or in very shallow water; submersed and free-floating species whose dormant seeds can survive on exposed mud flats for a year and which germinate when there is standing water; and mud flat species which are ephemerals whose seeds can only germinate on exposed mud flats during periods when no standing water exists in the wetland (van der Valk, 1978). When the wetland refloods, these species are eliminated from the visible wetland flora. The species studied in this chapter are included in the first type, and are typically classed as emergent or drawdown species. Germination requirements can significantly influence the distribution of adults in the field, by controlling recruitment of species after disturbance. Moore and Keddy (1988) have shown that only two water level states (flooded or unflooded) are necessary to predict vegetation changes after disturbance (prolonged drawdown). After disturbance, high shoreline species will be the primary colonisers if unflooded conditions exist, while low shoreline species will colonise the disturbed habitat if flooded conditions exist. Other factors such as sediment characteristics may also determine the species which will become established. These factors are particularly significant in wetland vegetation of high species richness with a diverse seed bank. Most of the wetlands on the Swan Coastal Plain support fringing emergent vegetation of low species diversity with apparently similar requirements for germination (Chapter 4).

Although mature stands of emergent macrophyte species generally produce seed each year, seedling recruitment is not a common occurrence. By determining the germinability and viability of seed, and the composition of the sediment seed bank, an impression of the potential for seedling recruitment can be gained. This chapter aims to determine these parameters for a number of emergent macrophytes of the Swan Coastal Plain.

5.2 Methods

A number of experiments were conducted to determine viability and germinability of seeds collected from selected wetland plant species. The germination of wetland plant species from seed within the sediment seed store, and the ability of selected species to germinate while submerged, was also investigated. The species used in each experiment were dependent on seed availability. The following is a list of all the experiments conducted;

(i) an examination of the germinability of seed under natural light conditions and diurnal temperature within the glasshouse
(ii) an examination of the germinability of seed at a number of constant temperatures and 12 hours light/12 hours dark
(iii) the effects of different seed treatments on germination
(iv) an investigation of seed viability using the technique of tetrazolium staining
(v) an examination of the germinability of seed with *in-vitro* culture techniques
(vi) the germinability of submerged seed
(vii) an investigation of the species of wetland plants germinating from sediment collected from a number of Swan Coastal Plain wetlands: under submerged and non-submerged conditions

5.2.1 Glasshouse Germination

The seeds of eleven species were allowed to germinate under glasshouse conditions of diurnal temperatures and natural light between 3.7.90 and 4.9.90. The species collection sites and dates of collection are shown in Table 5.1.

Table 5.1: Glasshouse germination experiment seed sources and collection dates.

	Experiment Date					
	July 1990		**February 1991**		**September 1991**	
Species	**Site**	**Date**	**Site**	**Date**	**Site**	**Date**
Schoenoplectus validus	Goollelal	4.6.90	Perth	7.1.91	Perth	7.1.91
			Perth	4.2.91	Perth	4.2.91
					Perth	8.3.91
					Perth	5.4.91
					Perth	29.4.91
Baumea articulata	Banganup	21.2.90	Banganup	4.2.91	Thomson	4.2.91
			Thomson	4.2.91	Thomson	4.3.91
					Banganup	4.2.91
					Banganup	7.3.91
Lepidosperma longitudinale	Rivervale	28.2.89				
Isolepis prolifera	AMC Capel	10.4.90				
Juncus pallidus	AMC Capel					
Leptocarpus	AMC Capel		AMC Capel	21.11.90	AMC Capel	19.12.90
	Jandabup	4.6.90	AMC Capel	19.12.90	AMC Capel	21.11.90
Typha domingensis	AMC Capel					
Typha orientalis	Forrestdale	1990				
Eleocharis acuta	Wellard	14.3.90	Wellard	14.12.90	Wellard	14.12.90
					Wellard	8.2.91
Bolboschoenus caldwellii	Wellard	14.3.90	Wellard	17.12.90	Wellard	14.12.90
			Wellard	14.12.90	Wellard	17.12.90
			Wellard	11.1.91	Wellard	11.1.90
Baumea juncea	Lake Clifton	5.2.90				

Seeds were removed from their main seed capsules but had no seed coats or dispersal appendages removed. All species, except *Leptocarpus* aff *tenax* (**Lt**), *Juncus pallidus* (**Jp**), *Typha orientalis* (**To**) and *T. domingensis* (**Td**) (due to their small size) were rinsed in a surface sterilant (1% aqueous sodium hypochlorite) and then rinsed in distilled water. Two replicates of 100 seeds were used for each species, and the seed were placed in sterile 9 cm Petri dishes on filter paper (Whatman No. 1) separated from the floor of the dish by pieces of sponge. Each dish was kept moist with an anti-fungal solution (Previcur) throughout the duration of the experiment. The Petri dish lid was replaced to prevent evaporation and decrease the number of fungal spores invading the dish.

Seeds were checked three times a week or more if germination rates were high. Germinated seeds were recorded and removed from the petri dish. Seeds which were attacked by fungi were also recorded and then removed to lessen the contamination of other seeds. The maximum and minimum temperature for the glasshouse was recorded for the length of the trial.

The experiment was repeated for *Isolepis prolifera* (**Ip**), **Jp** and **To** because rapid germination made interpretation of the first experiment difficult.

5.2.2 *Constant Temperature Experiment*

This experiment was conducted to determine whether the species had a optimum temperature for germination. Two trials used three different temperature-controlled cabinets set at 15, 20 and 25°C, and 12/12 photoperiod.

Eleven species were used for the first trial (Murdoch University), in which all seed were from the same sources as the glasshouse experiment. However, the germination of six species was uncharacteristically poor, and the experiment was repeated (University of WA) for these species. The seed sources for these species however were different (Table 5.2)

Table 5.2: Seed sources for the constant temperature experiments.

Family	Species	Collection Site	Collection Date
Juncaceae	*Juncus articulata*(Ja)	AMC Capel	19.12.90
Juncaceae	*Juncus pallidus* (Jp)	AMC Capel	19.12.90
Restionaceae	*Leptocarpus* (Lt)	AMC Capel	21.11.90
Cyperaceae	*Eleocharis acuta* (Ea)	Wellard Alcoa	14.12.90
Cyperaceae	*Isolepis prolifera* (Ip)	AMC Capel	17.1.90
Cyperaceae	*Bolboschoenus caldwellii* (Bc)	Wellard Alcoa	17.12.90

Both growth cabinet trials had two replicates at each temperature, each replicate with twenty seeds. Seeds were treated the same as those in the glasshouse experiment and the Petri dishes set up in an identical manner. Distilled water was used in the bottom of the Petri dishes until fungal growth was apparent, then anti-fungal solution was applied.

5.2.3 *Seed Pretreatments: Leaching, Boiling and Scarification Experiments*

Three experiments were conducted to examine if germinability was improved by the pretreatments of scarification, leaching or boiling. The species used were those which demonstrated poor germination in the glasshouse experiment, and have a large seed size. It was not practicable to do these tests on small seeds.

Scarification

The scarification experiment involved rubbing each seed with fine sandpaper for approximately one minute to remove some of the seed coat. The species used in this trial were **Ea**, *Lepidosperma longitudinale* (**Ll**), *Schoenoplectus validus* (**Sv**), *Baumea articulata* (**Ba**) and *Baumea juncea* (**Bj**). Two replicates of twenty seeds for each species were used, and the seeds were placed in petri dishes as described above in the glasshouse experiment. The petri dishes were placed in a growth cabinet (20°C) between 4.9.90 and 23.11.90. The seeds were checked and recorded as described for the other germination experiments.

Leaching
The leaching experiment involved the same species, number of seeds, replicates and procedure as the scarification experiment. The seeds were leached prior to germinating in the growth cabinet. Leaching entailed placing each replicate in a gauze bag and suspending in beakers of distilled water. Species were kept in separate beakers. The beakers remained at room temperature and the water replaced every 24 hours for 14 days (19.9.90 to 23.11.90).

Boiling
The boiling trial used seeds from only two species **Ba** and **Bj**. Two replicates, each containing ten seeds, were placed in gauze bags and boiled for one minute in water. They were then placed in petri dishes in a 20°C growth cabinet and monitored as above (7.11.90 to 14.12.90).

5.2.4 *Viability Tests*

The species selected for viability testing were those which displayed poor germination, and have a large seed size. It was not practical to do these tests on small seeds.

Tetrazolium Test
The tetrazolium test was used to determine the percentage of viable seed in some species. Tetrazolium stains the tissue of the seed pink and the intensity of the pink colouration can be used to distinguish between healthy, aged, weak, damaged and dead tissue. The test is best used on large seeds.

Twenty seeds were selected from each of the following species **Bc**, **Sv**, **Bj** and **Ba**. The seeds were soaked in distilled water for 20 hours to aid sectioning. Seeds were bisected longitudinally through the embryo, to allow the stain to come in contact with the embryo. Water was removed from the petri dish and replaced with 0.5% w/v tetrazolium solution. Enough solution was used to cover the seeds and they were allowed to stand for 16 hours in the fume cupboard at room temperature. The following day the stain was removed from the Petri dish and replaced with distilled water to prevent the seeds from drying.

The seed halves were examined for signs of viability, characterised by a pink stain, while dead areas of the seed remain colourless. The intensity of the stain indicates the health of the tissue. The results were expressed as a percentage of viable seeds.
The test was repeated using **To**, **Ba**, **Bj**, **Ll** and **Bc**. The method was identical to the prior test except for the duration of imbibing of seeds in distilled water being 72 hours and a 1% w/v tetrazolium solution was used.

***In-vitro* Germination**
Seeds of seven species were given to Kingsley Dixon and Kathy Meney at Kings Park to determine viability through the use of *in-vitro* culture techniques. The tests were conducted on fresh seed (Table 5.3)

Table 5.3: Seed sources for *in-vitro* germination tests

Family	**Species**	**Collection Site**	**Collection Date**
Cyperaceae	Baumea articulata (Ba)	Banganup	4.2.91
Cyperaceae	Baumea juncea (Bj)	Lake Clifton	5.2.90
Cyperaceae	Schoenoplectus validus (Sv)	Perth	4.2.91
Cyperaceae	Eleocharis acuta (Ea)	Wellard Alcoa	14.12.90
Cyperaceae	Bolboschoenus caldwellii (Bc)	Wellard Alcoa	11.1.91
Cyperaceae	Isolepis prolifera (Ip)	AMC Capel	17.1.91
Restionaceae	Leptocarpus(Lt)	AMC Capel	21.11.90

The species chosen were those which had shown little or no germination in previous experiments. The numbers of seed used in each culture technique depended on the seed availability and ease of extraction (Table 5.4).

Table 5.4: Number of seed used in each culture technique

	No. of embryos tested		
	embryo	embryo + endosperm	whole seed
B. caldwellii	50	50	50
E. acuta	50	50	50
I. prolifera	21	-	50
Leptocarpus sp.	35	-	50
S. validus	50	50	50
B. juncea	50	-	50
B. articulata	50	-	50

Ll was not tested as seeds were not available at the time. For comparison, **Ip** and **Bc** were included, which had displayed high germination in previous trials.

All seed batches were treated similarly as described in Meney and Dixon (1988). Seeds were sterilised by agitating for 1 min in 1% hypochlorite and then rinsing in distilled water. Seeds were then placed in 1% hypochlorite with a drop of Tween 80 and vacuum sterilised for a total of 15 minutes (alternating vacuum pressure 5 min on, 5 min off, 5 min on). Seeds were transferred to a laminar flow cabinet and double rinsed in sterile distilled water. Seeds were then placed in sterile petri dishes in distilled water and left to imbibe 1-2 hours before extraction.

Extracted embryos were cultured on filter paper bridges placed in polypropylene tubes containing 10 ml of embryo media. Media composition was as follows:

2.2g/L MS powder (Sigma) (Half-strength Murashige and Skoog, 1962)
100µm EDTA iron solution
500µm meso-inositol
60µm sucrose (60mm conc.)
3µm thiamine HCl
2.5 µm pyridoxine HCl
4µm niacin
8gL^{-1} agar (solid media only)
pH 6.0

Media was autoclaved at 121°C and 100 kpa for 20 min. It was then transferred to a laminar flow cabinet and 3µm GA$_3$ and 1µm zeatin added to the cooled solution. Media was then dispensed into sterilised tubes.

Extracted embryos and whole seed of each species were cultured on embryo media and incubated in the dark until germination. Germinated embryos were maintained under 16 hr light and 8 hr dark conditions. Two week old plantlets were subcultured onto shoot proliferation media containing BAP (see embryo media described above, minus growth hormones with added agar). Plantlets were subcultured every 28 to 42 days onto alternating concentrations of BAP at 0.2µm and 5µm.

5.2.5 *Submerged Germination Experiments*

Seeded Experiment
This trial was conducted to determine the germinability of seeds subjected to submergence. The species investigated, were **Ja**, **Jp**, **Ip**, **Ea**, **Bc** and **Lt**. Those species which did not germinate, or had very poor germination, in the glasshouse experiment, were not included in this experiment. The two species of *Typha* were also not included as their ability to germinate under water has been previously documented. Seeds were germinated in one litre plastic containers (18cm diameter) containing 2kg of washed white quartzite sand and one teaspoon (4g approx.) of Osmocote slow release fertilizer. The sand was saturated with tap water. Twenty seeds of each species (for the two species of *Juncus*, a liberal sprinkling of seed was used, the seed being minute) were sown on the soil surface, with one species per container. There were two replicates of each species per depth. Containers were transferred to plastic tanks (100cm x 50.5cm x35cm) and submerged with tap water to a depth of either 5cm or 20cm above the level of the sand. Germination, seedling vigour (healthy or stressed in appearance) and mean seedling height was monitored on a daily basis. Temperature was monitored every second day and dissolved oxygen was monitored on a weekly basis.

Seed Bank Experiment

Submerged
This experiment was conducted to ascertain whether seeds of emergent macrophytes within wetland sediment were capable of germinating and growing under submerged conditions.
Sediments were collected from four sites at Banganup (**Ba** stand) and Forrestdale (**To** stand) lakes along transects starting at the tree line on the lake boundary and progressing toward the lake centre (refer to Chapter 2). Sediments were collected mid March of 1991 and stored in plastic bags to prevent desiccation until the beginning of the experiment in the first week of April. The sediment samples were then transferred to one litre plastic containers (18cm diameter, 10cm depth) and saturated with tap water. The containers were transferred to plastic tanks (100cm x 50.5cm x 35cm) and submerged with tap water to a depth of either 5cm or 20cm. There were two replicates for each sediment sample and for each depth. Tanks were covered with sheets of glass to reduce potential contamination with algae and pathogens. Germination, seedling vigour (healthy or stressed in appearance) and mean seedling height was monitored on a weekly basis for the first month and thereafter, on a monthly basis. Temperature, pH and dissolved oxygen were monitored monthly.

Non-Submerged
This experiment was conducted to ascertain the germinability of seed present in lake sediments under non-submerged conditions. Sediments were collected from a number of lakes located on the Swan Coastal Plain between August 1990 and February 1991. Sediment was transferred to seedling trays (34.5cm x 28.5cm). Trays were placed in a glasshouse and watered with tap water twice daily by an automatic sprinkler system. Germination and plant growth was monitored bimonthly.

5.2.6 *Field Seedlings of* **Baumea articulata**

Seedlings of **Ba** were found in the field at Banganup Lake during the spring of 1990. It was evident that seedlings only occurred on the open sediment where ample light was available. Three 5x5m plots, and one 2x2m exclosure plot were established to monitor seedling survival over the coming summer. The exclosure plot was fenced with chicken wire to prevent grazing. The plots were monitored monthly.

5.3 Results

5.3.1 *Glasshouse Germination*

Germination of seeds from each species could be classified into two groups, those that displayed high germination rates, and those that did not (Fig. 5.1). Four of the eleven species of seed examined in this experiment did not germinate; Ba, **Bj**, **Ll** and **Lt**. Both **Ea** and **Sv** displayed poor germination. **To, Td, Ip, Bc** and **Jp** had high total % germination.

Jp, Ip, To and **Td** germinated early in the experiment and displayed rapid germination rates, with the exception of **To** (Fig. 5.1). **Td, Sv** and **Ea** did not germinate until 10-20 days later than the other species, and of these only **Td** had a high germination rate. Temperatures in the glasshouse ranged from daily maxima of 20-40 °C to nightly minima of 5-20 C (Fig. 5.1). The average maximum temperature in the glasshouse for the first experiment was higher and the average minimum temperate lower than for the repeat experiments.

5.3.2 *Constant Temperature Germination*

Four of the eleven species examined in this experiment germinated, **Ip, Jp, Td** and **To** (Fig. 5.2). **Bc, Sv** and **Ea** which germinated in the glasshouse, did not germinate in this experiment, even though the same seed source was used. The constant temperature experiment, however, was conducted later in the year. A possible explanation is that the viability of the seed of these species drops rapidly after harvest.

Of the species that germinated, **To** (especially) and **Td** showed reduced germination rates c.f. the glasshouse results (Fig. 5.2). There was negligible difference in germination rates between the temperatures for **To** and **Td**. Ja and **Jp** both had high germination rate, with Ja displaying a much slower rate of germination in the 15 °C treatment. There was no difference however, in total % germination. Highest germination rate for **Ip** was in the 20 °C treatment, but after a slow start.

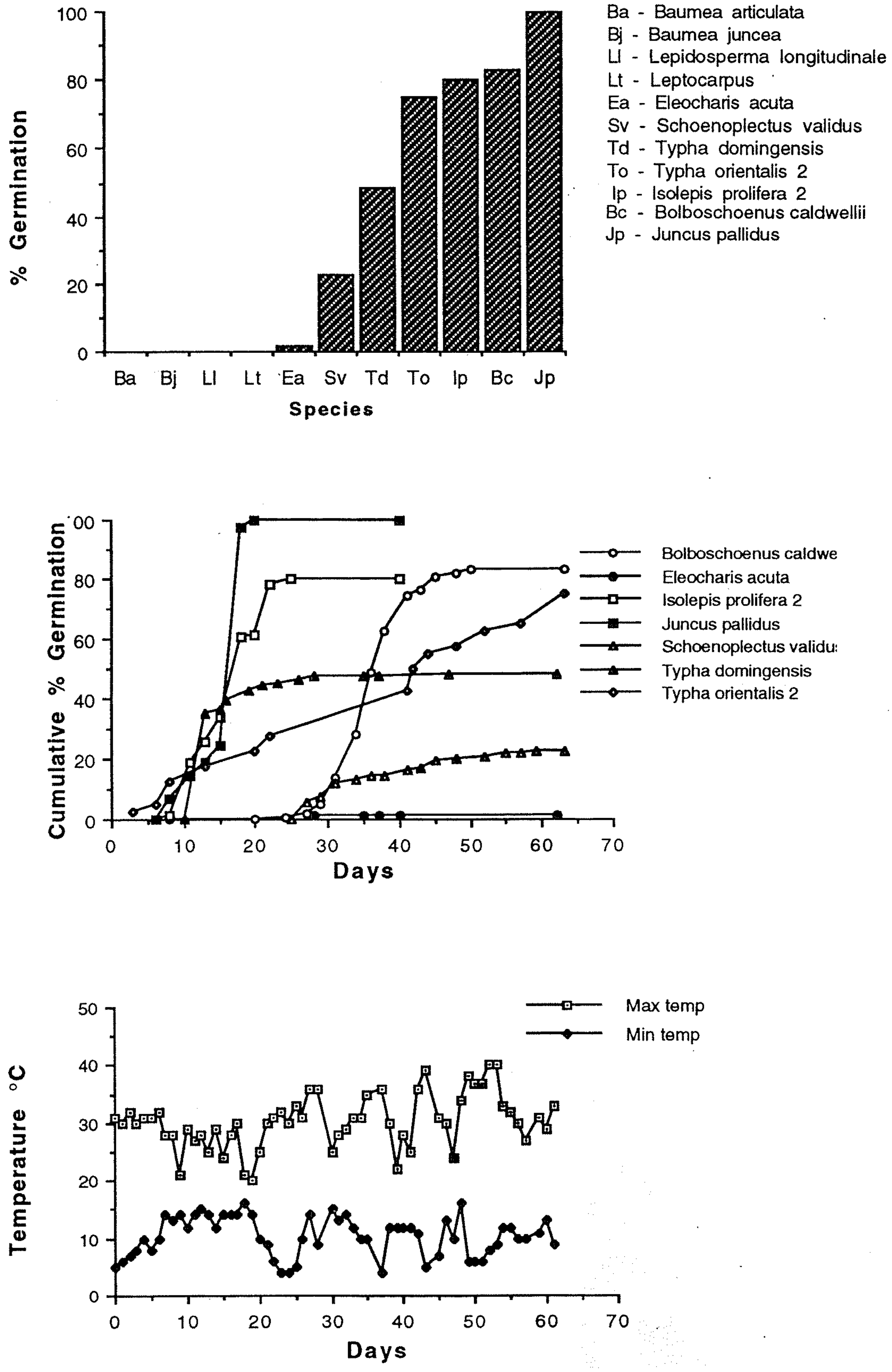


Figure 5.1: Percent germination and cumulative percent germination of the species tested in the glasshouse germination. Maximum and minimum glasshouse temperatures are also shown.

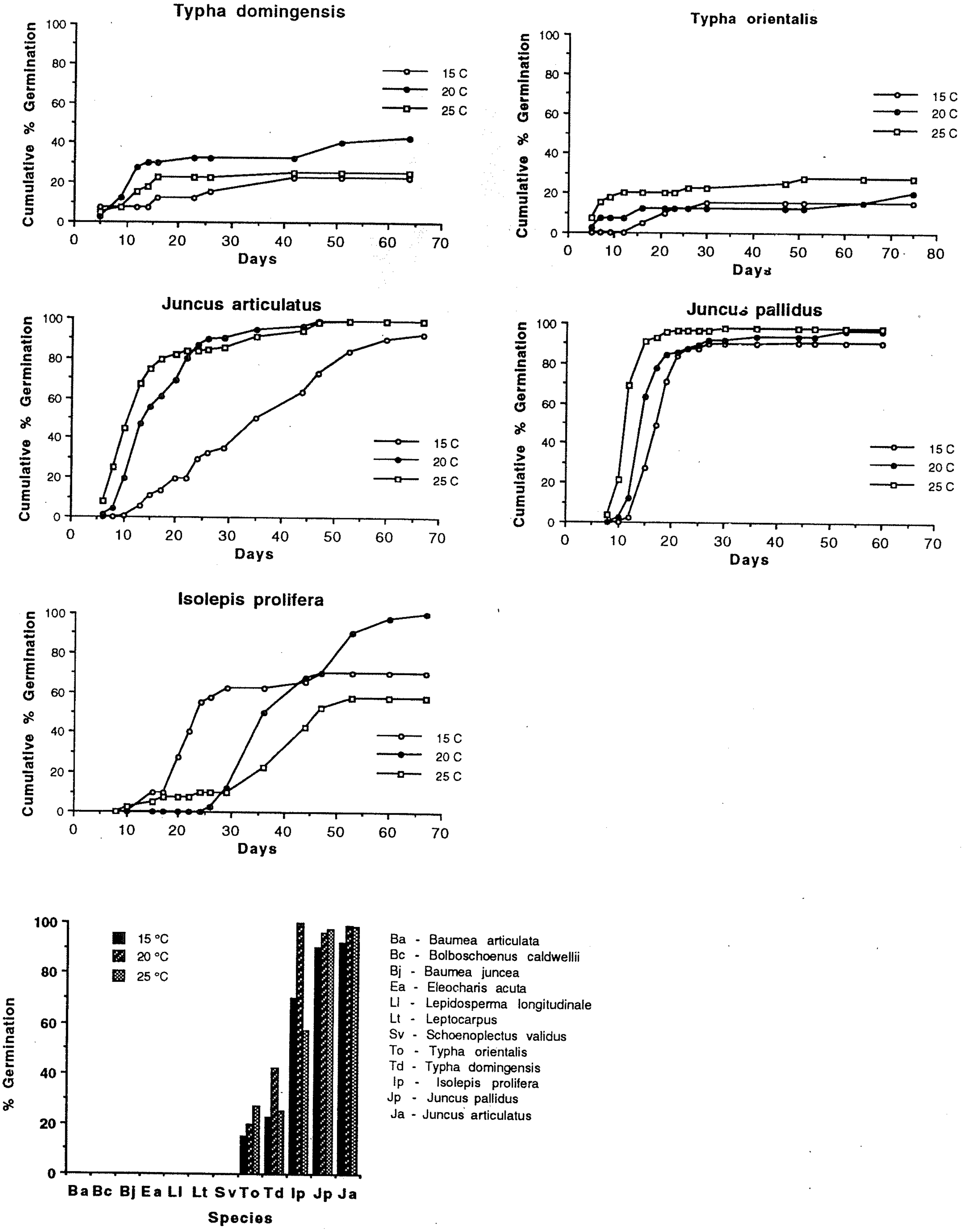


Figure 5.2: Percent germination and cumulative percent germination of the species in the constant temperature experiment (15, 20 and 25 °C).

5.3.3 Seed Pretreatment

None of the species included in the scarification, leaching or boiling treatments germinated. If leaching or gradual breakdown of the outer seed coat (test) is required before germination in these species, then the process is prolonged and was not well simulated in these trials.

5.3.4 Viability Tests

Tetrazolium Test

Tetrazolium staining showed high viability for **Sv**, **To** and **Bc** (1% tetrazolium only), with the remaining species examined having % viabilities of < 20 (Table 5.5). Increasing the duration of imbibition and the percentage of tetrazolium in the solution resulted in a higher viability score for **Bc** but not for **Bj**. **Ll** showed no seed viability, which explains this species poor performance in the germination experiments. Although no germination was recorded in the previous experiments for **Ba** and **Bj**, up to 20% and 15% respectively of the seed is viable. This indicates certain requirements for dormancy to be broken in these species. However, the technique was thought to be too subjective, and the *in vitro* culture technique was relied upon.

In-vitro *Germination*

The *in vitro* results supported the tetrazolium findings, though percentage germination was generally higher than in the tetrazolium seeds (Table 5.6). All species, other than **Lt**, which did not germinate in the glasshouse experiment, had viability between 32 and 85%. A comparison of these species with a good germinant, **Bc**, showed comparable levels of seed viability. The lack of data for **Ip** and **Lt** were because of small seed size, making embryo extraction difficult. The 'multiplication rate' describes the number of viable shoots that can be taken from a specimen every 4-5 weeks so as to increase the stock of plants.

5.3.5 Submerged Germination

Seeded

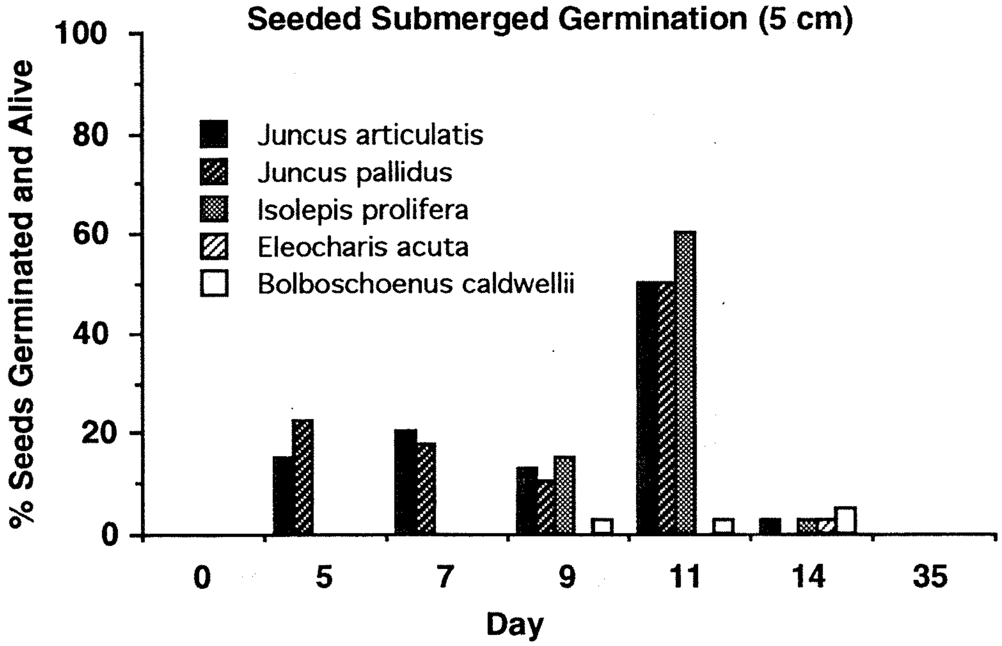
The seed of all species with the exception of **Lt** germinated. Germination was most successful for the two *Juncus* species (Fig. 5.3) with all seeds germinating within fourteen days for both levels of submergence, except **Bc** (20). For both *Juncus* species, germination commenced on the sixth day at each level of submergence. The rate of germination was initially greater at 5cm but by day 9, the rate was similar for both depths. **Ip** achieved 78% germination at 5cm and 100% germination at 20cm . The rate of germination of **Ip** seed was greater at 20cm (80% germination at day nine) than at 5cm (15% at day 9 and 75% at day 11). **Ea** was slow to germinate (14 days) and performed poorly with only 2.5% of seed germinating at 5cm submergence and no seed germinating at the 20cm depth. **Bc** germinated at both depths, with maximum germination(12.5%) at 20cm submergence. The rate of germination was much faster at 5cm (first germination at day 9) than at 20cm (first germination at day 27).

Table 5.5 Percentage viability of seeds using the Tetrazolium Staining Technique.

Species	% Tetrazolium	No. of Seeds Examined	No. of Viable Seeds	% Viability
S. validus	0.5	18	14	77.8
B. caldwellii	0.5	20	2	10
B. articulata	0.5	16	3	18.8
B. juncea	0.5	13	2	15.4
B. juncea	1.0	40	1	2.5
L. longitudinale	1.0	40	0	0
T. orientalis	1.0	40	28	70
B. caldwellii	1.0	40	20	50
B. articulata	1.0	40	8	20

Table 5.6 Percentage germination of seeds, embryos or embryos and endosperms using the *In-vitro* Culture Technique.

	Percentage Germination (% ±S.E)			
Species	**Embryo**	**Embryo+ Endosperm**	**Whole Seed**	**Multiplication Rate**
B. articulata	32	28	0	1.5
B. juncea	80	72	0	1.5
B. caldwellii	80(±20)	100(±0)	0	1
E. acuta	42(±5)	90(±6)	0	4-6
S. validus	85(±3)	95(±5)	0	<1
I. prolifera	55(±15)	-	32	5-6
Leptocarpus	0	-	0	-



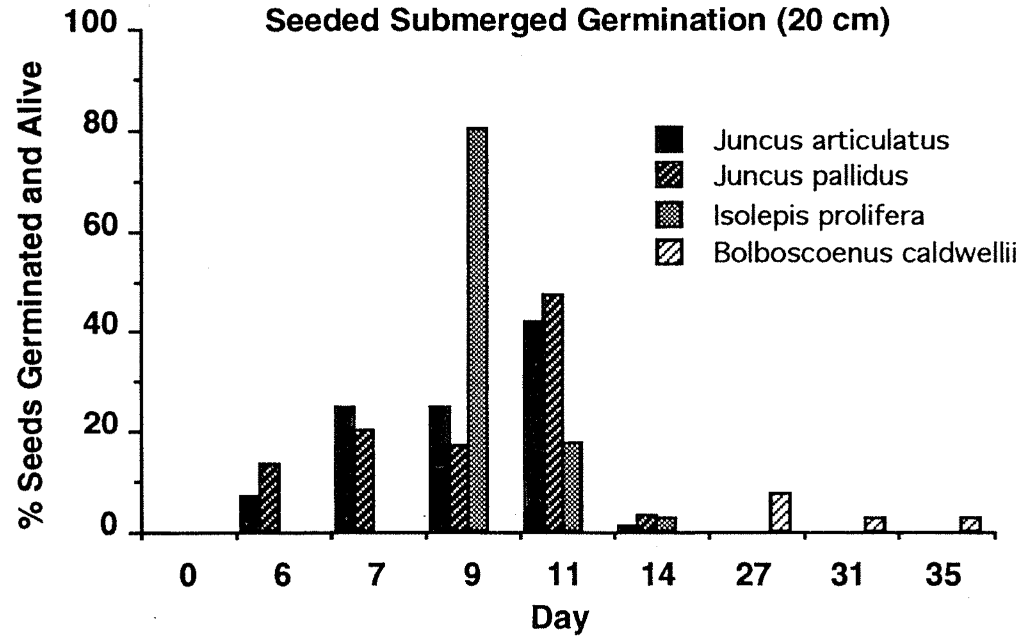
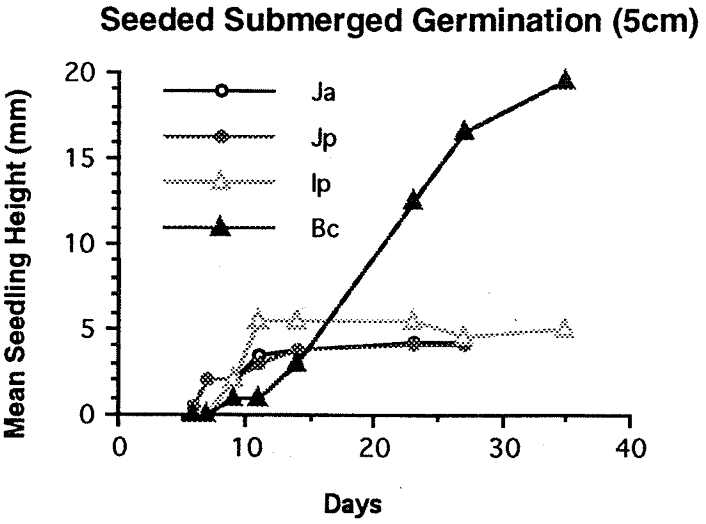


Figure 5.3: Percentage of seeds (seeded submerged germination experiment) that germinated and survived over 35 days of inundation at 5 cm and 20 cm depths.

By day 14 at 5cm and day 11 at 20cm, seedlings began to die. By day 35 all seedlings had died, with the exception of **Bc** which died 1 week later. Therefore, although the species germinated while submerged, under these artificial conditions, none of the species could become established and survive.

This is supported by the fact that no seedlings grew above the surface of the water (i.e. greater than 5cm) within the 35 days of the experiment. The rate of growth for those seedlings germinated under 5 cm of water was greatest for **Bc**, followed by **Ip** (Fig. 5.4). Ja and **Jp** displayed similar rates of growth. The pattern of growth was the same at 20cm.



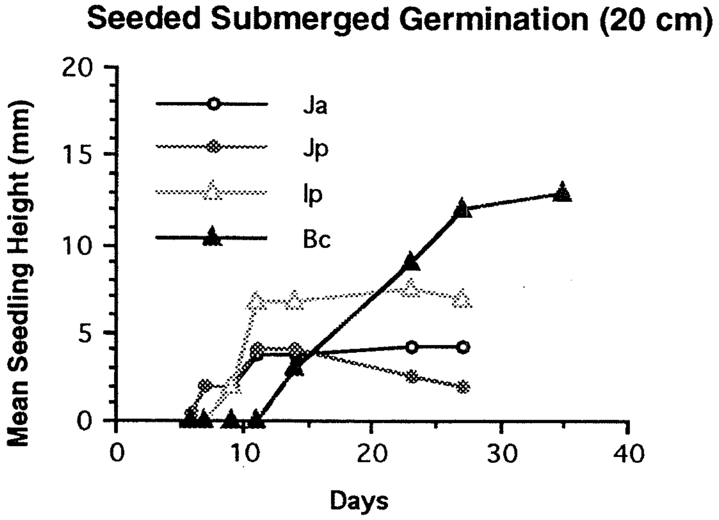


Figure 5.4: Mean seedling height over 35 days (seeded submerged germination experiment) at 5 cm and 20 cm inundation.

Ip achieved a greater mean height (7mm) at 20 cm submergence than at 5 cm submergence (5.5mm). This situation was reversed for **Bc** (19.5mm at 5cm depth and 12.5mm at 20 cm depth), although this may be attributed to the delay in germination and hence shorter growing period for those seedlings germinating at 20cm submergence. Both *Juncus* species had the same mean height at both depths, although towards the end of the experiment, the height of **Jp** declined slightly in the 20cm submerged seedlings. This is probably attributable to the overall decline in the health status of the seedlings at the later stages of the experiment.

This experiment was conducted in the open during summer. Water temperature was always above 20° C and was usually closer to 30° C, and high temperatures may have contributed to the poor germination in some species. The concentration of dissolved oxygen in both depth treatments remained similar throughout the experiment (7-10 mg/l).

The experiment was discontinued at day 35, because of problems with epiphytic algae. Algal blooms proved to be impossible to control, and algae essentially smothered seedlings.

Seed Bank

Submerged

To was the only emergent macrophyte species to germinate from the collected lake sediments. The Forrestdale Lake sediment produced many **To** seedlings, with densities up to 45 $0.1m^{-2}$, with negligible variation between collection sites. The Banganup sediment, however, did not produce any **Ba** seedlings, but did produce 2 **To** seedlings, even though **To** does not occur there; this indicates that **To** seeds from neighbouring Thomson Lake can disperse to Banganup. A species of *Chara* and a number of weed species germinated and grew with varied success. These plants although not included in this study, are worthy of mention as a reminder of the ever present problem of weed invasion threatening metropolitan wetlands.

The growth of **To** germinating from sediment collected from Forrestdale Lake is shown in Figure 5.5. Seedling growth varied little between the positions along the transect at which the sediment samples were taken. This implies there was no significant variation in seed bank content within the stand. There was no germination evident until after a period of 133 days submergence for those sediments collected from between 0 (lake edge) and 25 metres (towards open water) along the transect. Sediment collected at the 50 metre mark had no germinating *Typha* until after 168 days of submergence.

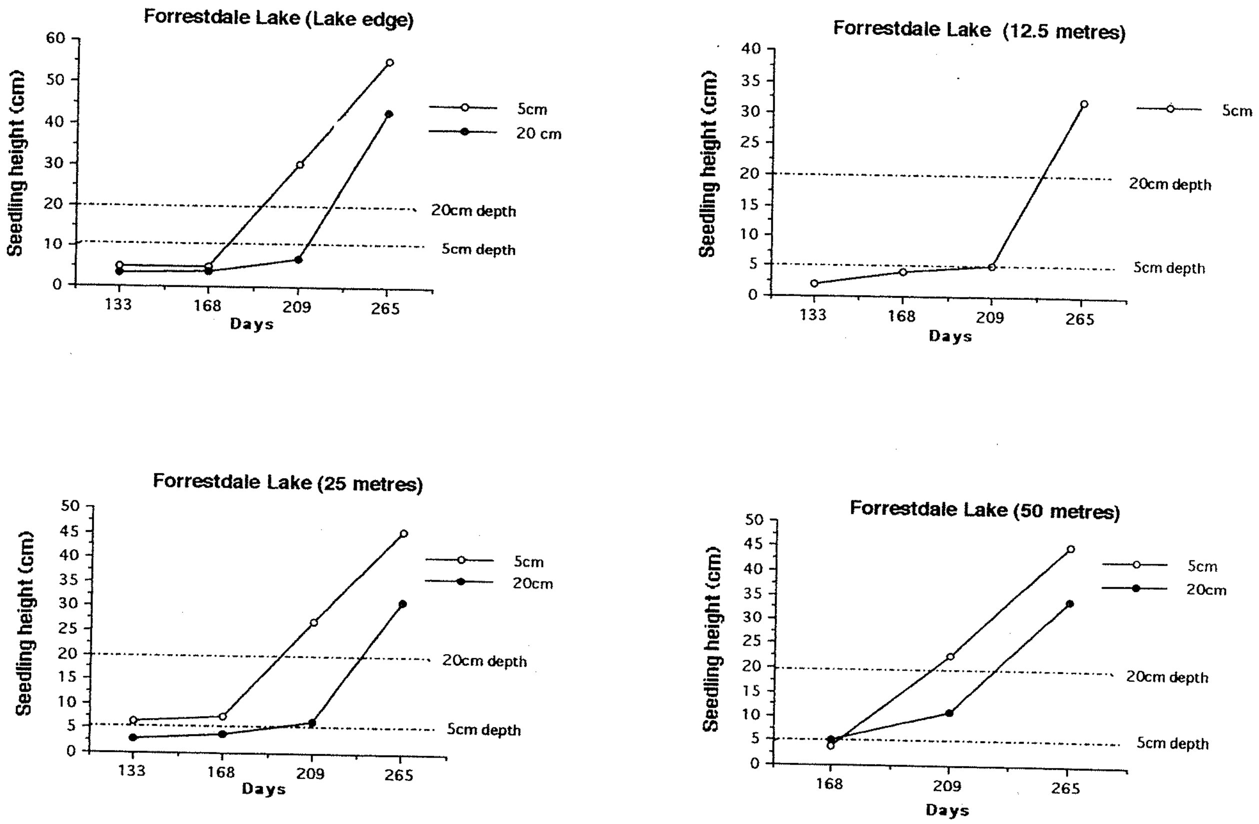


Figure 5.5: Seedling height of *Typha orientalis* that germinated from field sediment submerged by 5 cm and 20 cm. Each graph represents sediment collected from different points along the parent plants distribution (along a transect) at Forrestdale Lake. No seedlings emerged in the 20 cm trial of the 12.5 m sample.

There was no germinating *Typha* in sediment collected at 12.5 metres subjected to 20cm submergence. This may be due to a poor supply of viable seed in these particular replicates. *Typha* germinating from Forrestdale Lake sediment grew well under both depths of submergence, and in all cases grew above the surface of the water. The rate of growth was generally greater in those sediments subjected to 5 cm of submergence than those subjected to 20 cm. The two **To** recorded in the Banganup sediment, germinated at day 209 and at the end of the experiment (56 days later) the plants had leaves between 11.5 cm and 25 cm long.

Water temperature during this experiment varied between a minimum of 14 °C and a maximum of 40 °C. Variation between treatments and replicates was however, small. The dissolved oxygen content of the water varied considerably, from 7 - 16 mg/l. Algae were rarely a problem in the Lake Banganup trials, possibly because of the low pH and tannins.

Non Submerged

The results of the non-submerged seed bank trial gave a valuable indication of the potential for seed germination at a number of Swan Coastal Plain wetlands. All of the major emergent macrophyte species were represented in the seedlings that emerged during the experiment (Table 5.7). Generally, those species which were present in the field as mature stands, were present in the respective seed bank. Of particular note, **Ba** germinated from all the sediments taken from wetlands at which it was present in mature form. This demonstrates that this species is present as germinable seed within sediments (although at low densities), however the mechanism required to trigger germination is not clear.

Forrestdale Lake sediments contained seeds of *Melaleuca preissiana* (**Mp**), **To** (high densities) and **Jp**, which was not evident as a mature form in the field (refer to Chapter 4). **Ba**, **Lt**, *Lepidosperma* sp., and **Jp** were present in the Jandabup sediments, which represents the majority of the species at that wetland. Banganup Lake sediments contained **Ba** and **Jp** seeds, **Ba** at relatively high densities. **Ba**, **To**, **Jp** and a species of *Cyperus* were present in the Nowergup Lake sediments, **To** and *Cyperus* sp. at particularly high densities. Loch McNess sediments contained **Sv**, **To**, **Ll**, *Cyperus* sp and *Eucalyptus rudis*. **Sv**, **To** and **Ba** were at high densities.

5.3.6 *Survival of Seedlings of* **Baumea articulata** *in the Field*

All the seedlings of **Ba** found at Banganup Lake were eliminated during the following summer, except those in the exclosure. This indicates that grazing of seedlings on the dry lake bed plays an important role in determining establishment success. None of the seedlings within the exclosure died, implying that sufficient moisture was available during the summer months. This is supported by the high water holding capacity of Banganup Lake sediments (Chapter 4). The exclosure seedlings grew to heights (30-55 cm) sufficient to maintain leaf area above the water surface during the following winter. Rhizome extension and subsequent ramet production did not occur until the summer one year after germination.

5.4 Discussion

The results of the germination experiments and viability tests have given a valuable insight to the potential of emergent macrophyte populations to produce viable germinants, and the requirements for germination. Although most emergent macrophytes predominantly reproduce vegetatively once established, the production and dispersal of viable seed is an important process which enables the colonisation of near or distant open areas. During periods of severe or prolonged drawdown, and subsequent exposure of sediment, seedling germination would play a significant role in the colonising of new sites. Where drawdown led to the death of the fringing vegetation, seed of high longevity within the sediment seed store may be the only avenue to re-establishment of a species. The seed bank trials (submerged and unsubmerged) confirmed that most of the major emergent macrophytes do germinate readily in field sediment. High seedling density was observed for **To**, **Ba**, **Sv**, **Lt**, and **Jp** in the sampled sediment.

There were large differences in the germinability of the species tested. Generally the very small seeded species (**Jp**, **Ja**, **To**, **Td**, **Ip**) had high germination rates (>>50%) whereas the larger seeded species (with the exception of **Bc**) displayed poor or no germination. However, all the species (except **Lt**, where the seed was probably attacked by pathogens) which did not germinate (particularly **Ba**, **Bj**) were shown to have viable seed (at least 30%). This demonstrates that these species have particular germination requirements which

Table 5.7: Seedling Densities in the field seed bank experiment.

		Seedlings 0.1 m-2				
		17-Apr	1-Jun	23-Jul	22-Oct	12-Dec
Site	**Species**					
Forrestdale 1	*Melaleuca preissianna*	0	0	0	2	2
Forrestdale 2	*Melaleuca preissianna*	0	0	0	1	3
Forrestdale 3	*Typha orientalis*		20	24	10	19
	Juncus pallidus				2	3
Jandabup 1	*Baumea articulata*	3	5	6	2	2
	Leptocarpus sp.	1	3	3	3	9
	Lepidosperma sp.	0	0	0	7	8
Jandabup 1	*Leptocarpus sp.*	2	8	10	14	23
	Baumea articulata				1	3
	Juncus pallidus				2	1
Jandabup 2	*Baumea articulata*	3	7	18	5	7
	Leptocarpus sp.	2	8	12	11	65
	Lepidosperma sp.				2	8
Jandabup 2	*Leptocarpus sp.*	7	12	17	21	75
	Juncus pallidus	1	1	1	3	23
Banganup 1	*Baumea articulata*	4	8	8	10	9
	Juncus pallidus				1	1
Banganup 2	*Baumea articulata*	2	3	3	2	2
Banganup 3	*Baumea articulata*	2	3	3	2	1
	Juncus pallidus	1	1	1	1	1
Banganup 4	*Baumea articulata*	4	4	3	2	2
	Juncus pallidus	1	1	1	1	1
Banganup 5	*Baumea articulata*	4	5	5	4	3
	Juncus pallidus	1	1	1	1	1
Nowergup 1	*Cyperus sp.*			1	1	4
	Juncus pallidus				1	1
Nowergup 2	*Cyperus sp.*	12	13	16	26	50
	Baumea articulata	1	1	1	3	4
Nowergup 3	*Cyperus sp.*	3	3	3	5	11
	Typha orientalis	11	13	13	0	
Loch McNess 1	*Baumea articulata*	16	19	19	9	9
	Typha orientalis	5	5	5	7	10
	Lepidosperma	1	1	1	2	2
	Cyperus sp.					10
Loch McNess 2	*Schoenoplectus validus*	4	6	6	9	30
	Typha orientalis	5	6	6		
Loch McNess 3	*Schoenoplectus validus*	6	4	4	3	6
	Typha orientalis	5	55	50		
	Cyperus sp.		5	5	6	7
Loch McNess 1 Post fire	*Eucalyptus rudis*				2	2
	Baumea articulata					1
Loch McNess 2 Post Fire	*Typha orientalis*				1	2
	Schoenoplectus validus			2	2	2
	Cyperus sp.				3	5
Loch McNess 3 Post Fire	*Typha orientalis*				4	4
	Schoenoplectus validus				15	36

were not met in the germination and pretreatment trials.

The germination of **Ba** in the seed bank trials may provide some insight as to what these requirements are. Given that the seed bank trials were conducted under glasshouse conditions, one may suggest that a combination of higher temperatures, and a moist sediment with a high organic content and low pH, promotes germination in this species. In addition, the large size of **Ba** seeds and their hard testas may indicate good longevity, and that the seed morphology is an adaptation to prolonged burial in peaty sediments. Germination would occur only once the low pH of these soils breaks down the hard outer testa, and the sediment is exposed but moisture and ample light is available. Such a trait may be best described as a seed phase which promotes the species resilience at the parental site if the 'adult' population becomes severely disturbed, rather than an invasive seed form.

To on the other hand, has a seed phase which best represents an invasive competitor. This species produces extremely large numbers of seeds which can be dispersed large distances because of its large pappus which facilitates wind dispersal. The seed generally has high germinability, with no special requirements. The seed is also capable of germinating while submerged. Once established, the seedlings grow rapidly and reproduce vegetatively after the first year. These traits enable **To** to quickly establish a large number of seedlings at suitable sites, far from the parental stand.

With respect to the importance of seed biology in determining species response to altered water levels, it is clear that seed germination is only significant under certain conditions. Normally, vegetative growth is the dominant mode of population expansion and replacement (Chapter 4). Although seed is produced, seed germination and/or seedling survival is suppressed by shading by established stands, submergence, grazing and desiccation. The impact of these factors varies between species. Seedlings become established in areas of open ground where ample light is available, and when the water regime provides shallow or waterlogged conditions during periods of higher temperatures. Early growth requires water levels sufficiently low to prevent submergence. These conditions are usually present in truly ephemeral wetlands (seasonal variation), or at lower water regimes during a low rainfall period (short-term variation). The timing of seed release relative to water level may be crucial for those species which have seed of poor longevity (ie less than 1 year). Species with good seed longevity are not dependent upon the success of this timing, as viable seed will be stored in the sediment seed bank awaiting suitable germination conditions.

6: Emergent Macrophyte Response to Different Water Depths; Experimental Conditions

6.1 Introduction

In the field, differences may be found in emergent macrophyte species distributions relative to water regime (Chapter 4), but the causes of these differences may not be straightforward. Relationships in the field between productivity, water regime, nutrient availability and sediment parameters, provide valuable indications of what may underly (or explain) the interaction between wetland plants and the environment. However, these field observations may be fortuitous correlations, and experimentation under more controlled conditions is required to test specific hypotheses developed from these relationships.

On the to Swan Coastal Plain, there are distinct differences in field distribution between species relative to water regime (Chapter 4). The most significant differences exist between species of greater stature (>1m) and productivity (*Baumea articulata, Typha orientalis, Juncus pallidus, Schoenoplectus validus*) and species of smaller stature (<1m) and lower productivity (*Baumea juncea, Juncus articulata, Eleocharis acuta, Isolepis prolifera*). Larger species, that tend to occupy the wetter end of the water regime gradient in the field, maintain leaf area above a wide range in water levels, allowing gaseous exchange between the atmosphere and below-ground organs. Smaller species, that generally occupy the drier end of the water regime gradient, do not have sufficient height to maintain leaf area above deep water levels. Of course, differences in root and rhizome anatomy and physiology, are also likely to contribute to the differences in tolerance between the two groups of species.

However, other factors such as light availability, interspecific competition, sediment chemistry and structure, nutrient concentrations, grazing and disturbance, also influence species distribution and productivity, resulting in complex mosaics of species and suppressed or enhanced productivity along a moisture gradient. To elucidate the differences in species response to water depth and changes in a species productivity along a water depth gradient, additional influences need to be eliminated or controlled.

The principal objective of this experiment was to identify the water depth preference of a number of Swan Coastal Plain emergent macrophytes, and identify particular growth habits and life history traits that determine tolerance to prolonged flooding or drought. This information would then be of value in interpreting the patterns of species distribution in the field.

6.2 Methods

6.2.1 Collection and Establishment of Species Studied

Plants (ramets) of nine species were collected from wetlands on the Swan Coastal Plain beginning in September and October 1989 (Table 6.1).

Table 6.1: The collection site and date of each of the species studied.

Species	Collection Site	Collection Date
Baumea articulata	Lake Banganup	13.10.89
Typha orientalis	Lake Forrestdale	13.10.89
Lepidosperma longitudinale	Murdoch Swamp	18.9.89
Baumea juncea	Lake Clifton	18.9.89
Eleocharis acuta	Wellard - Alcoa	18.9.89
Juncus pallidus	Capel - AMC	2.10.89
Juncus articulata	Capel - AMC	2.10.89
Isolepis prolifera	Capel - AMC	2.10.89
Schoenoplectus validus	Capel - Westralian Sands	2.10.89

The same day as collection, the young ramets were trimmed to approximately 10cm of rhizome and 30-35cm of leaves to lower transpiration. Five ramets of each species were set aside for biomass analysis (see below), and the remainder planted in 9L (28cm x 24cm) black plastic pots containing washed white quartzite sand (20cm depth). The pots were placed in a pool (oval swimming pool 7.2m x 3.5m) containing water to a depth of 20cm and allowed to establish for 6 months. A fertilizer spike (Selleys) was pushed into the sand of each pot, and were renewed at 3-4 monthly intervals.

6.2.2 *Experimental Design*

The objective was to expose plants of each species, over a full seasonal cycle (13 months), to different water depths ranging from 100 cm below (-) to 75 cm above (+) the soil surface. The treatments simulating flooding were levels of water 0.25 m, 0.5 m and 0.75 m above the surface of the sand in the pots. The control for the flooding treatments was 0 m, where the water is level with the sand surface of the pot. Because of their smaller size, the treatments for *Isolepis prolifera, Juncus articulata* and *Eleocharis acuta* had depths at 0.1 m, 0.25 m and 0.5 m. The treatments simulating drought were water levels of 0.5 m and 1.0 m below the sand surface in the pots. The control for the drought treatments was also 0 m, where the water is level with the surface of the sand in the pots. There were five replicates per species per treatment except in the drought treatments where, due to lack of space in the containers, five species were randomly chosen in each treatment to have four replicates.

At the commencement of the experiment, a stage with step-wise levels in the oval pool was constructed to support the flooding treatment plants at the desired height from the pool floor (Fig. 6.1). The stage had three levels 0.8 m, 0.55 m and 0.3 m from the base of the pool and faced north to minimize shading. The 0.75 m plants were placed on the floor of the pool, and a separate shelf was constructed to support the 0.1 m plants.

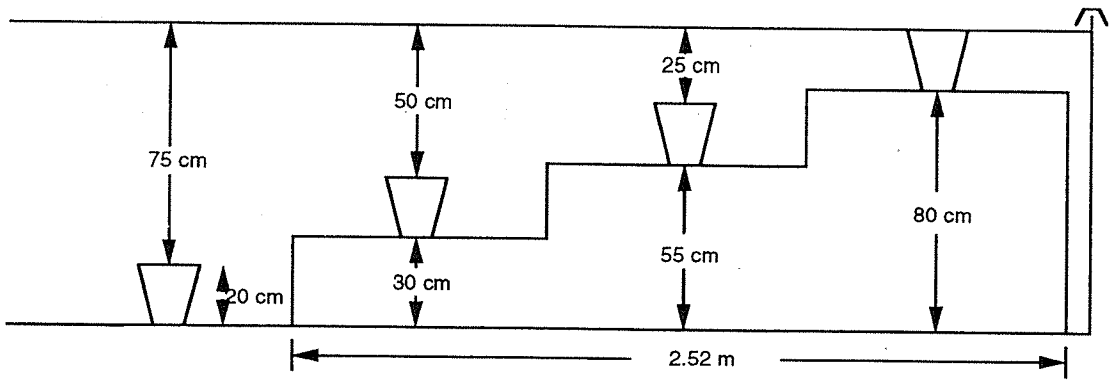
Once construction of the stage was completed, plants in the flooding treatments were gradually increased in depth, using 0.25 m increments with a fortnightly interval between water depth increases. Once all the plants were at their appropriate levels, the water level in the pool was maintained at the soil surface of the 0 m pots, and monitoring of all the flooding treatment plants commenced (see below). All plants were positioned randomly within each level.

For the drought treatments, the potted plants intended for the - 0.5 m, and - 1.0 m treatments were removed from the pool and placed in grey PVC tubs (Fig. 6.1) filled with 5 cm of water and left for 2 weeks. The drought control (-0 m) plants were randomly placed into similar PVC tubs with the water level maintained at the soil surface for the remainder of the experiment. The following fortnight the water was drained from the pots of the -0.5 m and -1.0 m plants, and were hand watered for a further 2 weeks. This was to ensure gradual drying phase. The plants were then transplanted to specially constructed tubs of which the dimensions were 1.2 m long, 0.5 m wide and 0.6 m (-0.5 m treatment) or 1.1 m (-1.0 m treatment) high. Each tub was partitioned into spaces 20 cm x 25 cm with corrugated plastic sheet and each partition was filled to the desired height (0.5 m and 1.0 m) from the base of tub with washed white sand. Around the base of each tub, holes (4mm diameter) were drilled every 10cm to allow water to pass into the tub. The tubs were placed in trays (140 cm x 65 cm x 10cm) which were filled with water, and checked regularly. One plant (ramet) was transplanted into each partition (randomly selected), and a fertilizer spike pushed into the soil next to each plant. The plants received supplementary hand watering for a further fortnight, after which monitoring commenced.

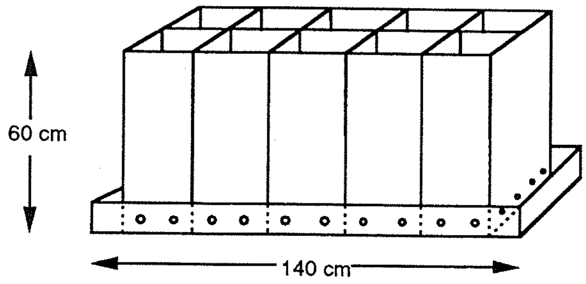
6.2.3 *Monitoring of Plant Growth*

For 13 months, all plants were monitored each fortnight for i) the number of green, senesced and dead 'leaves' (photosynthetic above-ground organs), ii) the length of the longest and shortest leaf, iii) the number of inflorescences and their flowering stage, and iv) the number of ramets in each pot. All leaves that were at least half (in length) brown were considered senescent. Although the leaves of each plant were trimmed at the time of collection from the field, the plants had produced significant above-ground growth before monitoring commenced. At the commencement of the experiment each plant

Flooding Treatments (Pool)



Drought Treatment Tub (0.5 m)



Drought Treatment Control (-0 m) Tub

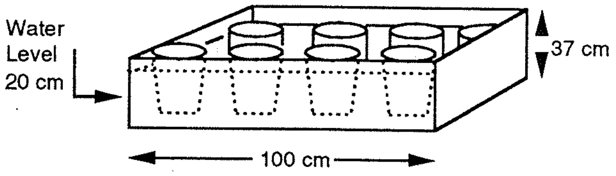


Figure 6.1: Design of the pool flooding treatments and the containers used for the drought treatments and control. The tub used for the 1.0 m drought treatment was identical to the 0.5 m tub shown except that the total height of the tub was 120 cm.

consisted of a single ramet, however with time, virtually all plants underwent rhizome extension resulting in the production of one or more additional ramets. Flowering stages recorded were flower bud, flower, immature seed, mature seed, and dehisced.

Initial biomass of five spare plants of each species was determined by dividing each plant into 'leaves' (photosynthetic aboveground organs), leaf bases (portion of leaves and/or stem beneath soil surface), rhizomes and roots. The length of each leaf was also measured to determine leaf length vs weight regressions. All material was dried at 70°C for approximately one week before dry weights were measured. This was not performed for *Lepidosperma longitudinale* due to the lack of vigorous plants of this species, however, separate plants were harvested at the end of the trial that were thought to approximate the size of the original transplants. At the end of the experiment, the biomass of each plant was measured using the same method.

6.2.4 Monitoring of Physical Parameters

Light levels (above and below water), dissolved oxygen (pool only), water (pool only) and air temperature, and pH (pool only) were measured each fortnight. Light levels were taken at each level within the pool (ie at the soil surface of a randomly chosen pot in each level) to determine the attenuation of light with depth. Temperature, pH and dissolved oxygen were also monitored this way to determine if there was any stratification in these parameters. Due to the nature of the tub treatments, below water measurements were not applicable.

Water nutrient concentrations were determined half way through the experiment and included measurement of total nitrogen, total phosphorus, ammonia, nitrate and orthophosphate. Samples were taken from the surface and bottom of the pool, from the interstitial water in randomly selected pots on each pool level, from the trays of each drought treatment tub, and from the interstitial water in randomly selected pots of drought control plants. The interstitial water samples were taken with a syringe, whereas water was collected from the bottom of the pool with a bilge pump and hose. All samples were initially filtered through silk to remove any large particles, and subsamples for ammonia, nitrate and orthophosphate determination were filtered through GF/C filter paper before being placed in 'whirlpaks' (NASCO) and frozen until analysis.

6.3 Results

6.3.1 Physical Parameters

There was significant light attenuation with increasing water depth. The submerged fraction of the leaf and/or stem area of those plants in the deeper pool treatments (i.e. +0.5 m and +0.75 m) receiving on average less than 20% of the ambient light (Fig 6.2).

There was no significant stratification in dissolved oxygen levels, pH or temperature. Pool dissolved oxygen concentrations were predominantly within the range 40 - 160 % saturation, with peaks of 170 % during the winter months. Water pH was generally between 6.2 and 7.5, with peaks of 9.5 during summer and 8.7 during early autumn. Air temperature varied between 12 °C in winter and 35 °C in summer. Water temperature fluctuated between 9 °C in winter and 26 °C in summer. The drought control tubs did not differ significantly from the flooded controls in dissolved oxygen concentration, pH or temperature.

With respect to open water and interstitial water nutrient concentrations, there were no significant trends with increasing water depth in the pool treatments, or with increasing depth to water table in the drought treatments (Fig. 6.3). High concentrations of orthophosphate (up to 95 $\mu g\ l^{-1}$) were found in the interstitial water compared to open water (5 $\mu g\ l^{-1}$) in the pool treatments, and this is attributed to the fertilizer spike. Orthophosphate was particularly high in the drought treatment perhaps due to concentrating effects of lack of water movement and evapotranspiration. Organic phosphorus was present in high concentrations in the open pool water due to algal blooms which were prevalent both in the pool and the drought tub trays. Total phosphorus reflected the sum of orthophosphate and organic phosphate trends. Concentrations of ammonia and nitrate were low except in the drought interstitial (NH4) and the water in the tray

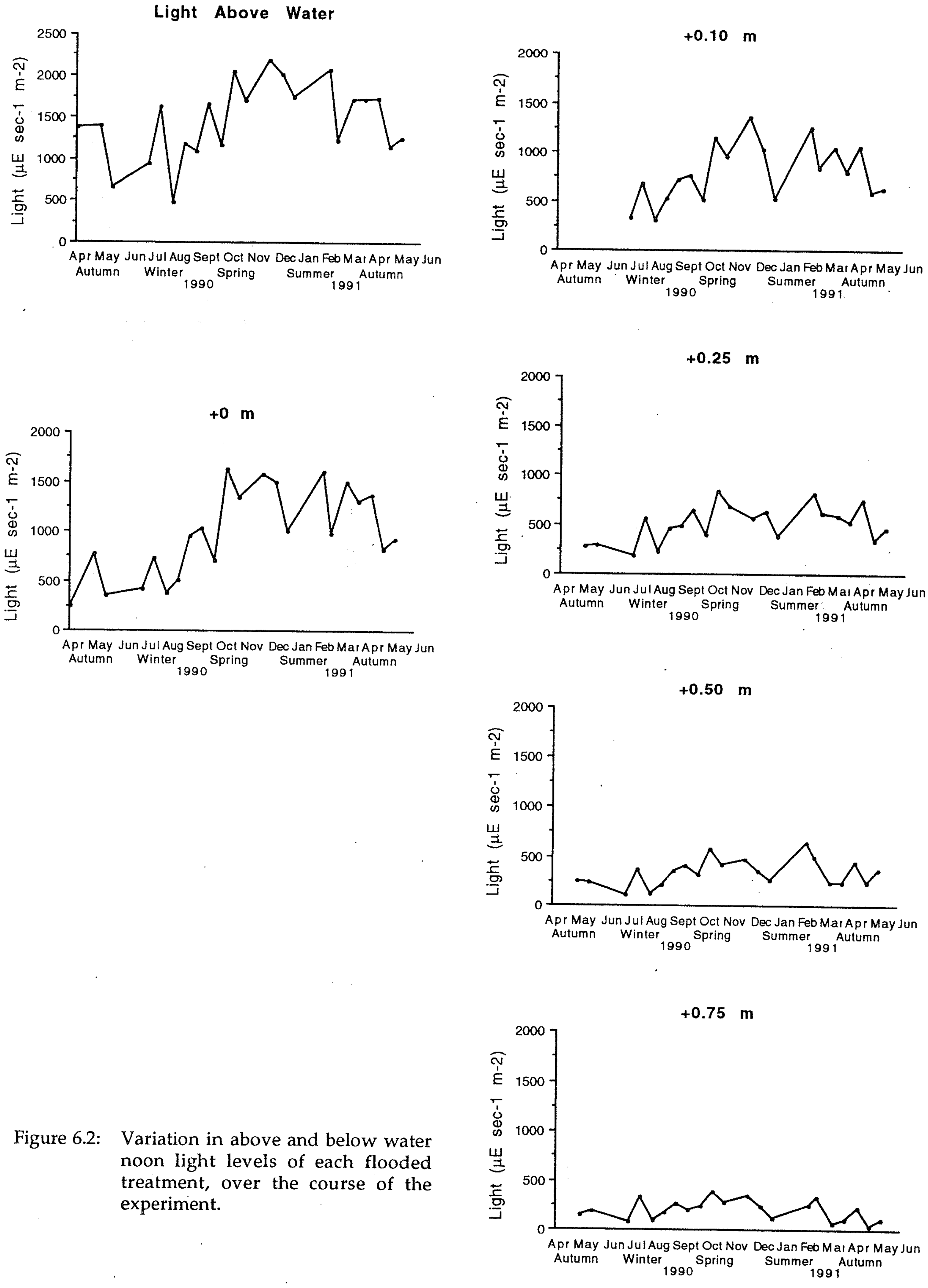
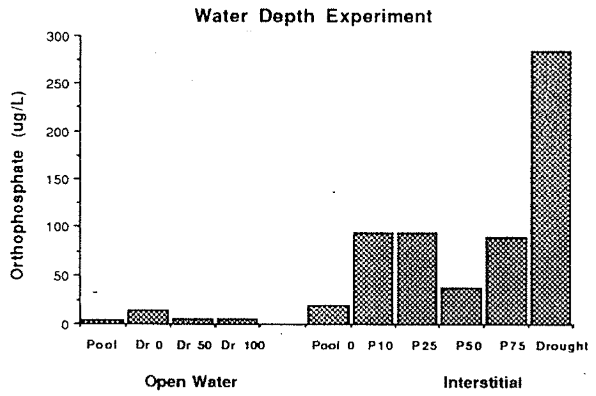
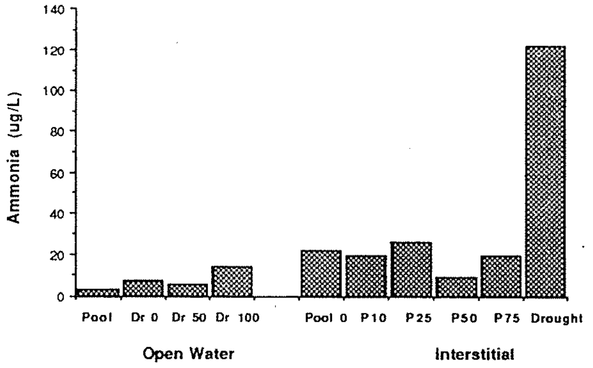
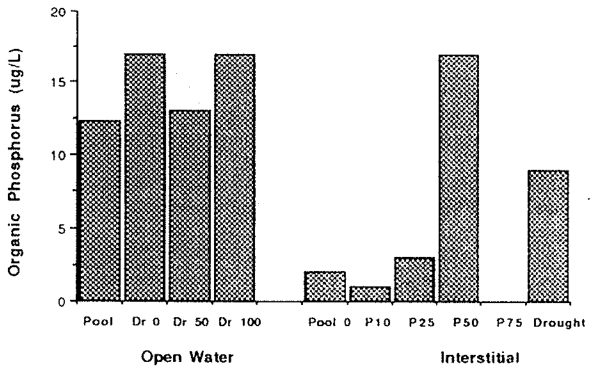
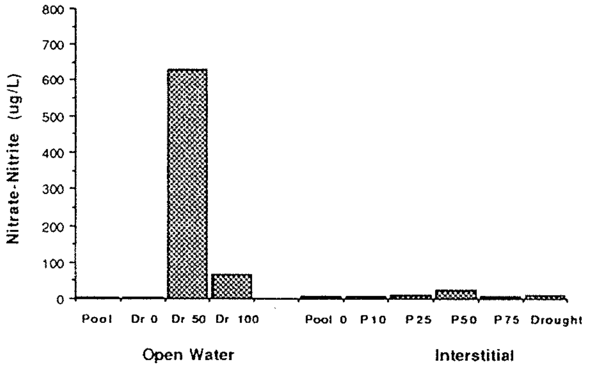


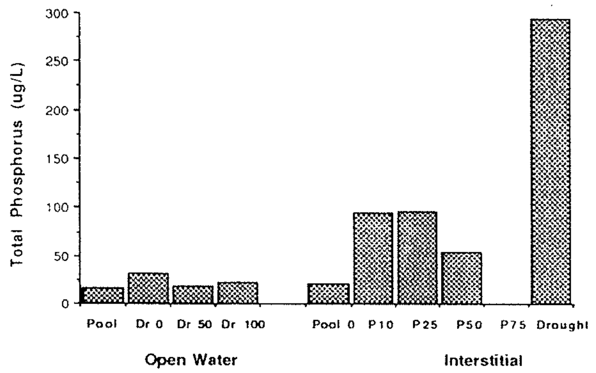
Figure 6.2: Variation in above and below water noon light levels of each flooded treatment, over the course of the experiment.

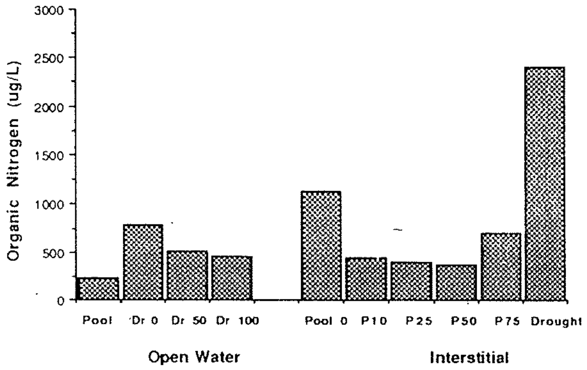












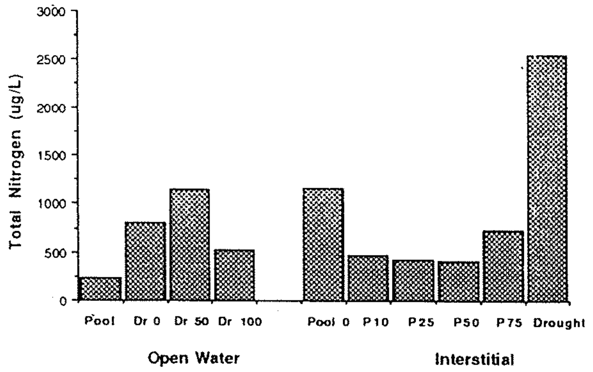


Figure 6.3: Open water and interstitial water nutrient concentrations of each treatment.

of the -0.5 m drought treatment (NO3). Organic and total nitrogen were higher, particularly in the drought control interstitial, once again likely due to concentrating effects.

6.3.2 Phenology of Leaf Production

Examples of phenology of leaf production patterns are presented in Appendix 3. All the quantities discussed below are expressed as average per pot. As the plants (ramets) became established and grew during the course of the experiment, the production of additional ramets (through rhizome extension) was common. The growth parameters therefore represent the sum of all ramets within a pot. True seasonal patterns of growth were sometimes masked by continued poor establishment of some plants. The notes on the response of the different species has been grouped into size classes.

Large Species

Baumea articulata (**Ba**) maintained a high percentage (approximately 50 - 80%) of alive leaves throughout the experiment in almost all treatments. The flooding treatment control (+0) plants showed increased senescence during the spring and summer months, but returned to a high proportion of live leaves in the following autumn. If one refers to the number of leaves, it is clear that this decrease in proportion of living leaves during the growth season/s is mostly a reflection of increased senescent leaves at the time of new leaf production. The remaining flooding treatments displayed a similar trend during spring but did not recover during the following autumn. Growth patterns in the drought treatment control (-0) plants were similar to the flooding controls, with a pronounced decrease in the proportion of living leaves in spring and summer; this was reflected in a decrease in the number of living leaves. In both the flooding and drought treatments, the percentage of attached dead and senescent leaves generally increased as the plants became more established during the experiment.

Typha orientalis (**To**) displayed a high proportion of attached dead leaves in all treatments, the proportion of living leaves being low compared to **Ba**. Lowest proportions occurred in winter in all treatments (except +0.75 m). A subsequent increase in proportion of living leaves was evident during spring and summer, and a second decline during late summer and autumn, indicating a seasonal cycle in senescence. This was most evident in the -0.5 m and -1.0 m drought treatments which suggests water stress during late summer and autumn. The exceptions to this pattern were the +0.5 m and +0.75 m flooding treatments which maintained a low number (and %) of alive leaves throughout the experiment. The small % of senescent leaves, and large % of dead leaves in all treatments throughout the experiment suggests a rapid senescence and turn-over of leaf material, and persistence of dead leaves.

Schoenoplectus validus (**Sv**) generally had a high percentage of alive leaves (60-80%) but showed increased leaf mortality in spring and summer in all flooding treatments. A subsequent increase in proportion of living leaves occurred during autumn, except in the drought treatments which declined further. This pronounced seasonal response was not evident in the flooding and drought controls. Senescent and dead leaf patterns indicated rapid turn-over with persistent dead leaves. The drought treatments showed the most significant reduction in turn-over of leaf material during late summer and autumn, probably due to water stress.

Medium Species

Juncus pallidus (**Jp**) showed an increase in proportion of living leaves during late winter and spring in all treatments, followed by a decrease in late summer. Leaf production increased again in the following autumn. The -1.0 m drought treatment however maintained a high proportion of alive leaves throughout the experiment, with an increase to 60% in autumn. Variations in leaf numbers also indicate a sharp increase in the number of alive leaves in autumn. The drought treatment control (-0) displayed a dramatic seasonal pattern in leaf production and senescence, in contrast to the flooding treatment control. The high proportion (40-50%) of persistent dead leaves and the small % of senescent leaves (5-15%) indicates rapid senescence.

Baumea juncea (**Bj**) maintained a very high proportion of living leaves (60-80%) with little seasonal variation in the controls (-0 and +0) and +0.25 m flooding treatment, but decreased in the drought treatments and the deeper flooding treatments. An increase in leaf mortality (40-45%) occurred from mid-spring to the end of summer under flooded conditions, with recovery in the following autumn. Whereas increased leaf mortality (30-40%) in the drought treatments occurred in summer and autumn with no perceived recovery. This reduction in leaf turn-over in the drought treatments appears to be in response to water stress, although the reduction in new leaf production was not as pronounced as other species. However, total leaf number increased steadily in almost all treatments.

Lepidosperma longitudinale (**Ll**) displayed an increase in the proportion of alive leaves over the course of the experiment in all treatments except in the +0.75 m flooding treatment where rapid decrease occurred in autumn. The increase in proportion of living leaves was greatest in the controls and the drought treatments (30-75% at -1.0 m). This is supported by a rapid increase in live leaf numbers in these trials, indicating a preference for drier conditions.

Small Species

Juncus articulatus (**Ja**) displayed a very high proportion (50-90%) of alive leaves in most treatments. Increased leaf senescence occurred during winter and spring in the flooded treatments (+0.1, +0.25 and +0.5 m), with pronounced leaf mortality in the +0.5 m treatment. The +0.5 m treatment recovered slightly during spring and summer but declined again in the following autumn. In the drought treatments there was a slight decline in proportion of living leaves during late summer/autumn in the 0 m and -0.5 m treatments, and a more pronounced decline in the -1.0 m treatment. Increases in live leaf numbers over the course of the experiment was greatest in the drought control and -0.5 m treatments, indicating a preference for 'drier' conditions.

Eleocharis acuta (**Ea**) exhibited a decline in proportion of living leaves with increased flooding, minimum levels occurring in winter/spring. The highest proportions were evident in the control (+0 and -0 m) and +0.1 m treatments, whereas the +0.5 m flooding treatment had the lowest levels (20%) with only marginal recovery in summer and autumn. Minimum new leaf production was during summer/early autumn in the drought treatments, probably due to water stress, with some recovery during late autumn. Seasonal trends were evident in all the trials. Leaf numbers increased the most in the control treatments (+0 and -0 m).

Isolepis prolifera (**Ip**) maintained a high proportion of alive leaves (40-60%) in the control (+0 and -0 m) treatments, with lowest levels occurring in spring and recovery during summer and autumn. With increased flooding however, leaf mortality increased dramatically to where, for example, all plants were dead by late summer/autumn in the +0.25 m and +0.5 m treatments. The drought treatments exhibited an increase in live leaves during summer followed by a decrease (especially -1.0 m) during the following autumn. Increases in leaf numbers, particularly during late summer, were most evident in the control (+0 and -0) and drought treatments (-0.5 and -1.0 m), indicating a preference for waterlogged to 'drier' conditions.

6.3.3 Flowering Phenology

All but two species, *Baumea articulata* and *Typha orientalis*, flowered during the course of the experiment (Fig. 6.4). Flowering patterns were not clear during the first six months, but as the plants became more established, trends in flowering behaviour became apparent. Virtually all species flowered, set seed and dehisced during November- May.

Sv flowered during summer and set seed during late summer-autumn. Seed set was slower in the +0.5 and +0.75 m flooding treatments with dehiscence starting up to 2 months later than in the other treatments. The flooding control and the +0.25 m treatments were the only plants to flower and set seed during the first 6 months of the experiment

Bj set seed twice during the experiment in all but the drought control and -0.5 m treatments. Seed set was identified in all plants, however dehiscence was not evident. The +0.75 m plants had an uncharacteristically long seed set period. There were no identifying trends in flowering phenology between the experimental treatments.

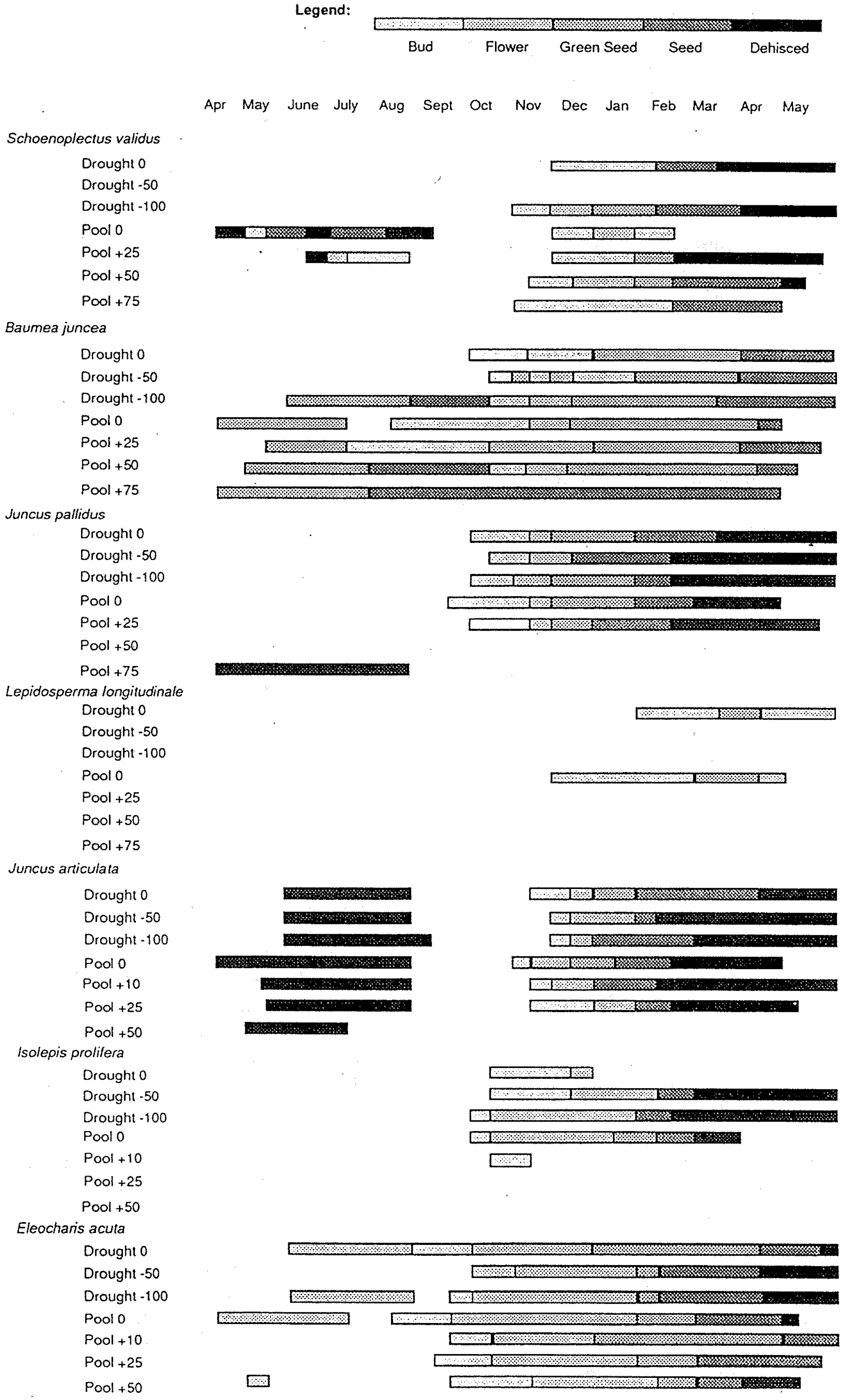


Figure 6.4: Flowering and seed production phenology of each species in each treatment.

Jp did not flower during the first 6 months of the experiment, except for the +0.75 m treatment which included plants which were flowering before the experiment commenced. The 'deeper' flooding treatments (+0.5 and +0.75 m) did not flower once inundated. The remaining treatments displayed a distinctive flowering pattern from flower budding (October) to seed dehiscence (March-May).

Ll exhibited very poor flowering, the flooding and drought control treatments being the only plants that flowered. Seed set and dehiscence was not observed.

Capsules dehisced in **Ja** treatments during the first six months, probably because of flowering before the start of the experiment. However, during the latter part of the experiment, all treatments except +0.5 m exhibited the full flowering sequence from flower buds (November) to dehiscence (February-May). There were no identifiable trends between treatments other than the absence of flowering in the deepest flooding treatment.

Ip did not flower in the 2 deepest treatments (+0.25 and +0.5 m). Seed set and dehiscence was observed only in the drought -0.5 and -1.0 m treatments and the flooding control (+0 m). The drought control (-0 m) flowered but did not set seed.

Ea had an extended flowering period in all treatments (June-February). Seed set also occurred in all treatments, and no significant trends were observed between treatments.

6.3.4 Above- and Below-Ground Biomass

Large Species

The difference between the initial plant biomass at the start of the experiment and the final biomass was calculated for each species in all treatments (Fig. 6.5). With respect to total biomass, all large species (**Ba**, **To** and **Sv**) showed a maximum biomass increment in the control treatments (+0 and -0 m). Biomass generally decreased with increasing or decreasing water depth. All species exhibited lowest biomass in the -1.0 m treatment, with the exception of **Sv** which was lowest in the +0.75 m treatment.

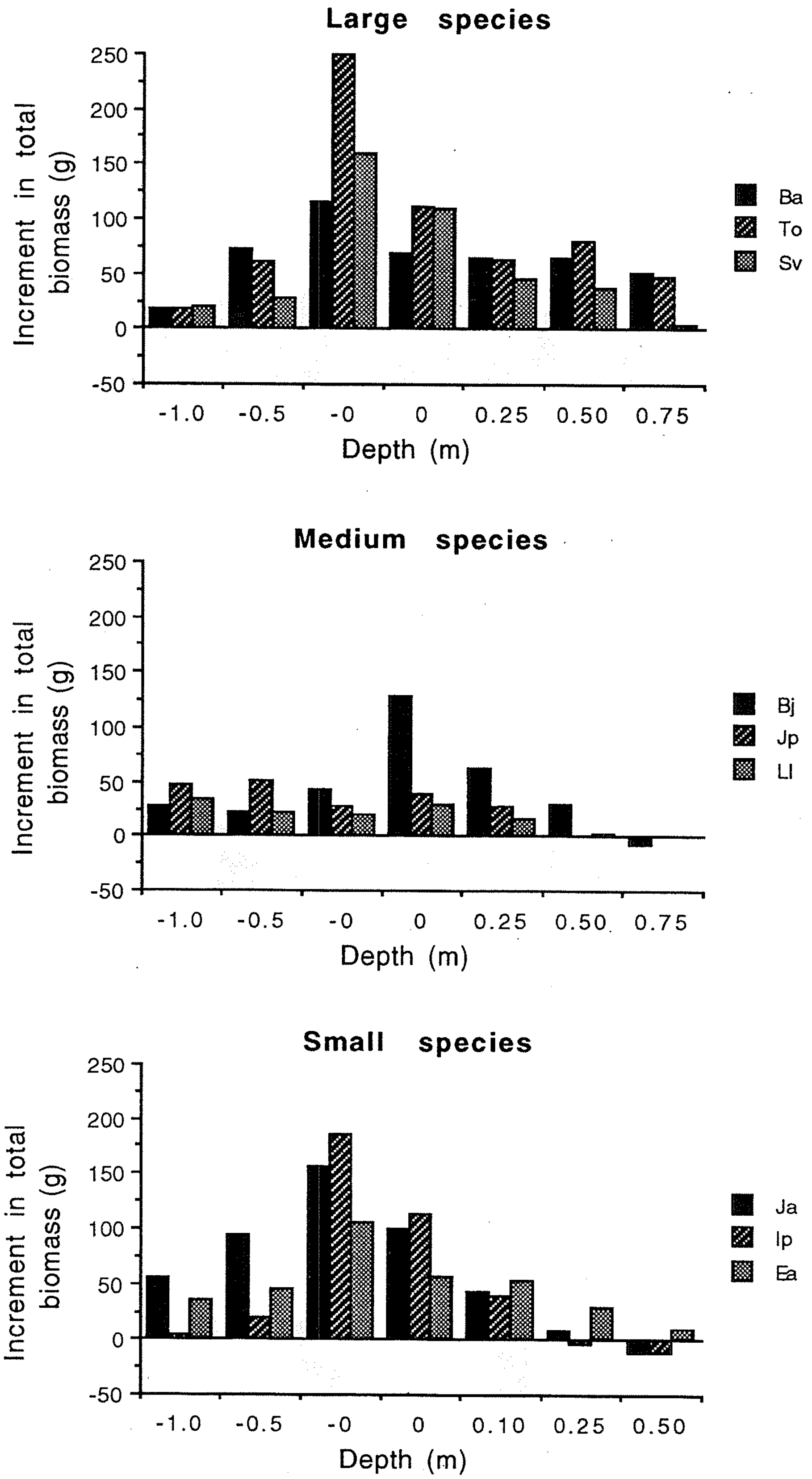
Root biomass generally represented the largest fraction (in weight) of the total biomass in all treatments with the exception of the -1.0 m treatment, and the -0.5 m and +0.75 m treatments for **Sv** (Fig. 6.6). The biomass of the below-ground components (roots, rhizome and below ground stem) was greatest in the control treatments (+0 and -0 m) for all large species, and was responsible for most of the variation between treatments. Furthermore, the above-ground:below-ground ratio was lowest for all 3 species in the control treatments, and increased with increasing and decreasing water depth (Fig 6.7). For **Ba** the ratio increased particularly in the deepest treatment (+0.75 m). Although following similar trends, **To** showed minimal variation between treatments.

There were no significant trends in large species leaf biomass along the water depth gradient (Fig. 6.6). **To** showed highest leaf biomass in the drought control treatment (-0 m), whereas **Ba** exhibited highest leaf biomass in the drought control and +0.75 m treatments. Increases in leaf biomass at greater depth could be interpreted as an adaptation to maintain sufficient leaf area above water level. The taller stature (longer leaves) of these species facilitated survival at greater depths.

Medium Species

Bj displayed greatest biomass increase (final minus initial biomass) in the +0 m treatment with decreasing biomass with increasing and decreasing water level (Fig. 6.5) **Jp** and **Ll** had maximum biomass increment in the drought treatments, however variation in biomass was minimal compared to other species. All three species had poor biomass in the +0.5 and +0.75 m treatments, with **Bj** showing a decrement from initial biomass.

Below-ground biomass again generally represented the greatest proportion of total biomass in all treatments (Fig. 6.8). **Bj** root and rhizome biomass variation along the water level gradient was similar to the large species; maximum biomass occurring in the control, and decreasing biomass with increasing and decreasing water level. **Jp** and **Ll** root and rhizome biomass in the drought treatments (-0.5 and -1.0 m) was equal to, if not greater than, the flooding control,


Large species

Medium species

Small species

Figure 6.5: Mean increment (over 13 months) in total biomass for the large, medium and small species in each treatment.

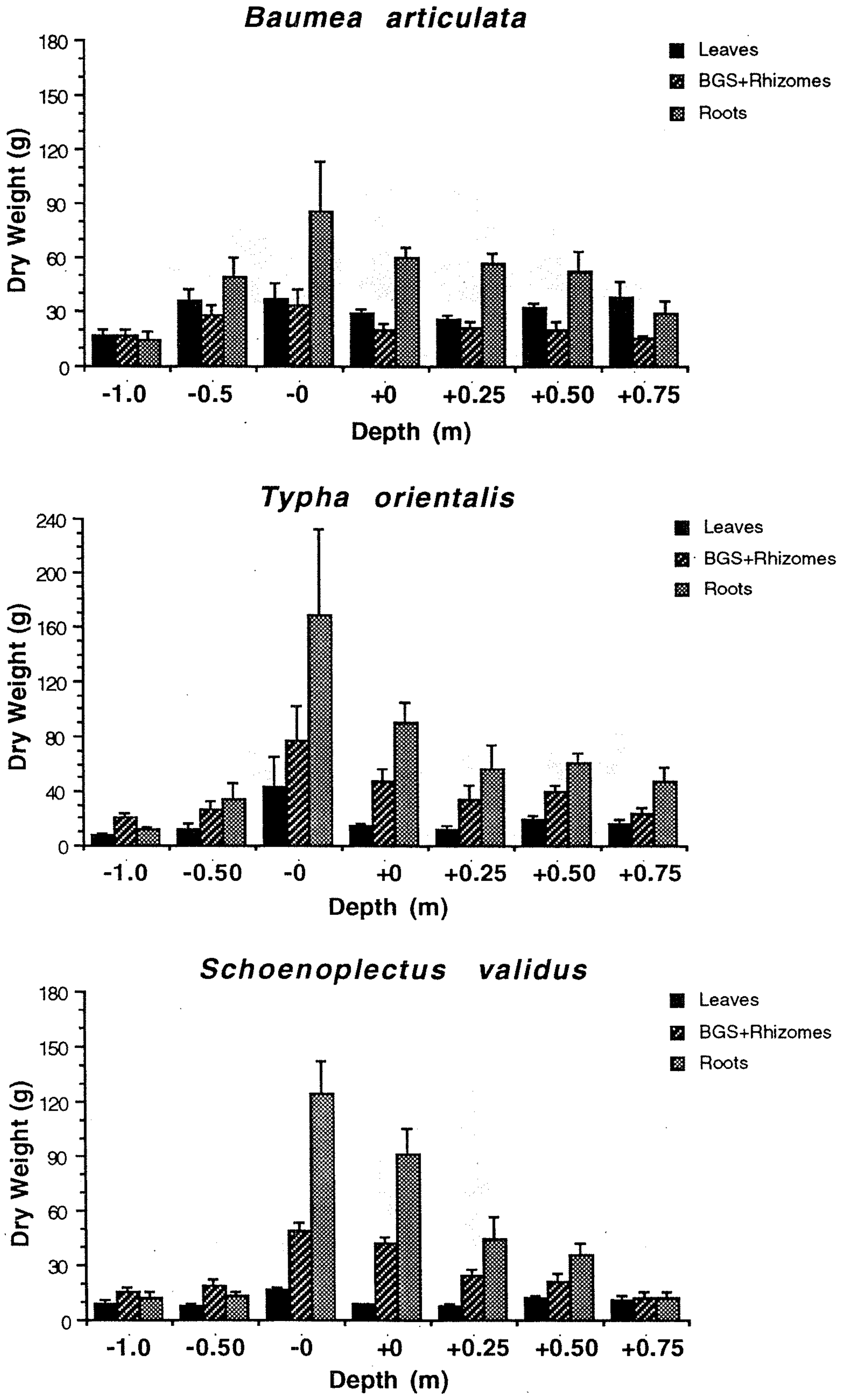


Figure 6.6: Final mean leaf, below ground stem (BGS) + Rhizome, and root biomass of the three large species in each of the treatments. Error bars shown are standard errors.

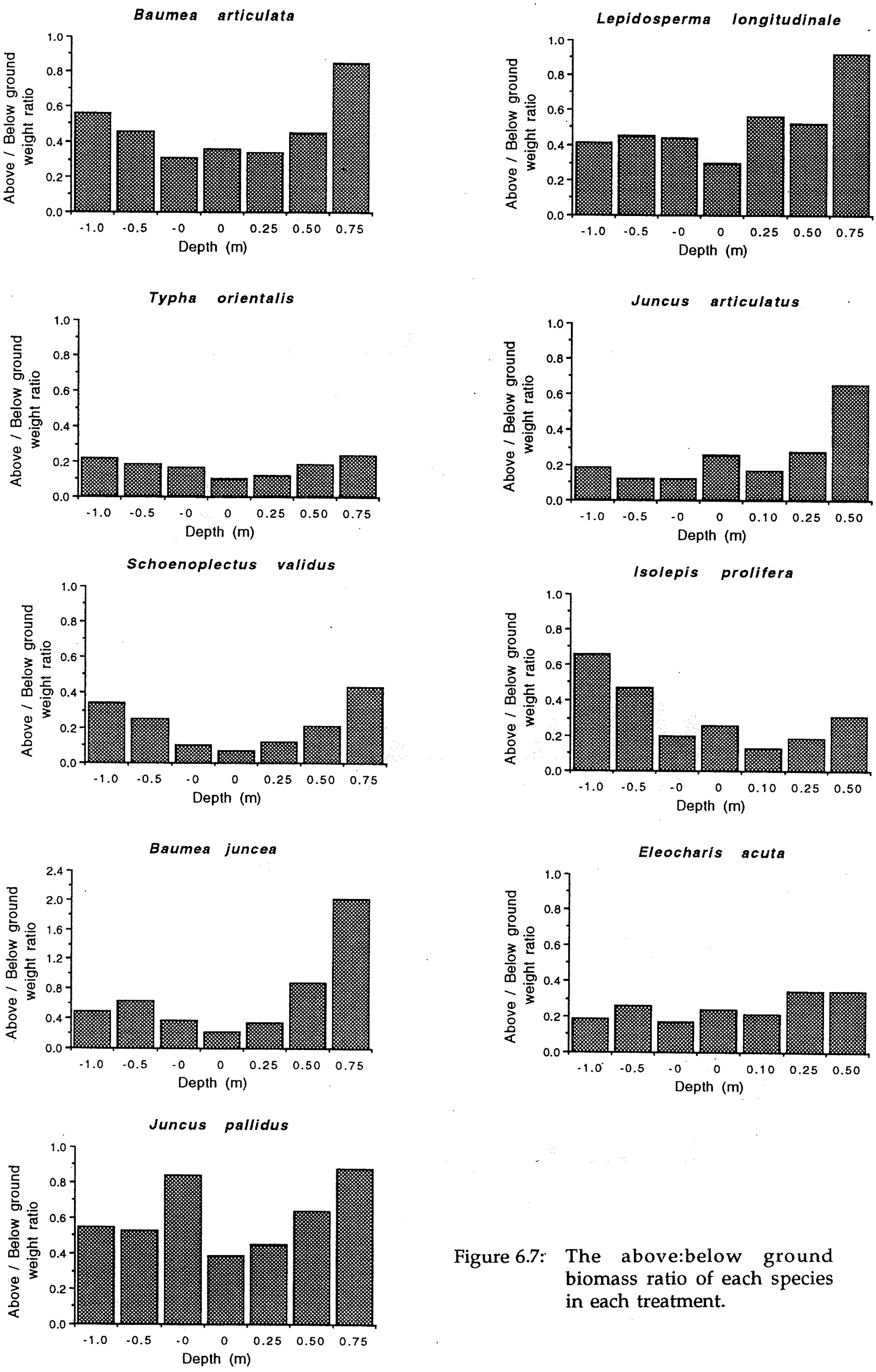


Figure 6.7: The above:below ground biomass ratio of each species in each treatment.

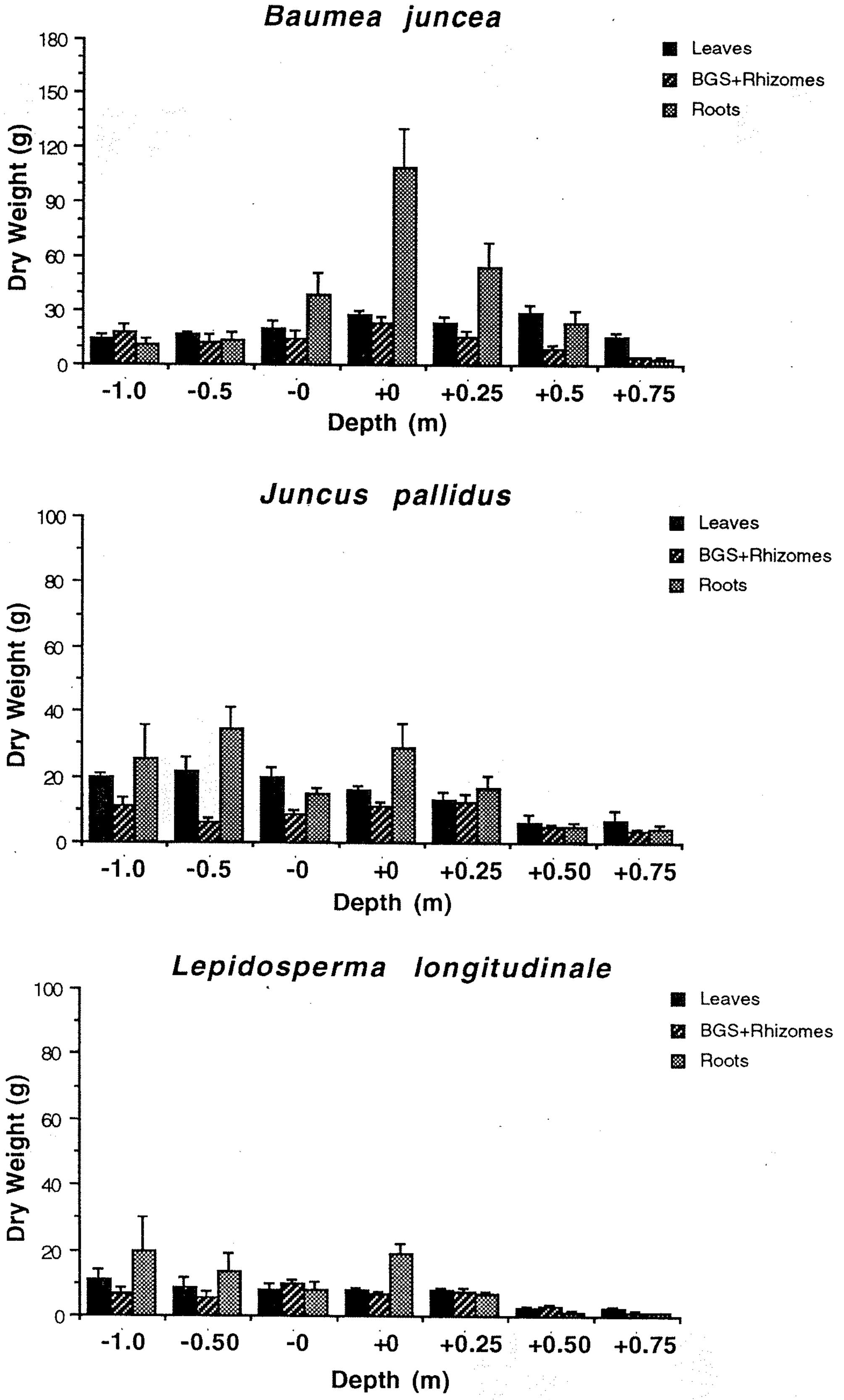


Figure 6.8: Final mean leaf, below ground stem (BGS) + Rhizome, and root biomass of the three medium species in each of the treatments. Error bars shown are standard errors.

whereas below-ground biomass was very poor in the +0.5 and +0.75 m treatments. This indicates a preference for drier conditions. The above:below-ground ratio for **Bj** was lowest in the +0 m treatment and increased with decreasing and (especially) increasing water level (Fig. 6.7). The ratios for **Jp** and **Ll** were variable but both increased with increasing water level.

Leaf biomass of **Bj** increased with increasing water level, except for the +0.75 m treatment which decreased dramatically (Fig. 6.8). Both **Ll** and **Jp** showed decreasing leaf biomass with increasing water level.

Small Species

All three small species (**Ja**, **Ip** and **Ea**) displayed a similar trend in biomass increment to the large species, although biomass in the deeper treatments (+0.25 and +0.50 m) was significantly lower (Fig. 6.5). **Ja** had a high total biomass increment in the drought treatments, increasing in the controls (-0 and +0 m) and decreasing rapidly in the flooding treatments, with a decrement in the +0.50 m treatment. **Ip** had relatively poor total biomass in all treatments other than the controls, indicating a distinct preference for waterlogged conditions only. **Ea** also had greatest biomass in the controls, with biomass decreasing with increasing and decreasing water level.

Below-ground biomass, particularly roots, represented the greatest proportion of total biomass in all three species (Fig. 6.9). **Ja** and especially **Ip** displayed dramatic increases in root biomass in the control treatments. Both above and below-ground biomass of all three species was poor in the flooding treatments. **Ja**, which indicated a preference for the drier end of the water level gradient, had the highest above:below-ground biomass ratio in the +0.50 m treatment (Fig. 6.7). **Ip** displayed the exact opposite trend, whereas no clear trend in the ratio could be identified for **Ea**.

All three small species had very poor leaf biomass in the +0.50 m flooding treatment , but generally increased to 0 m then decreased with depth (Fig. 6.9).

6.3.5 *Leaf Morphology*

An examination of leaf morphology provides an insight into the adaptations of some species to greater water depth. Increases in leaf length and a corresponding reduction in leaf number at increasing water depth, suggest a plasticity in leaf morphology correlated with maintenance of surface area above a high water level. More resources are required per leaf from an increasingly limited photosynthetic potential. The large species, **Ba**, **Sv** and to a lesser extent **To**, displayed decreasing leaf number (Fig. 6.10) and increasing mean leaf length (Fig. 6.11) with increasing water level. In medium species, all species showed decreasing leaf number and weight (Figs. 6.9 and 6.10), but only **Bj** had increasing leaf length with increasing water depth. Only **Ja** in the small species group displayed similar trends in both leaf number and leaf weight (Fig. 6.9).

6.4 Discussion

As indicated in the results of field investigations, there are distinctive differences in the growth response between species, and between different positions on a water regime gradient within a species. Under the more controlled conditions in the glasshouse, these differences become clearer and allow further interpretation of the field results.

Virtually all species showed peak total biomass at waterlogged conditions, i.e. with the water level at the soil surface. However, the species differed greatly in the response to lower and/or higher water levels. As a result, preferences towards drier or wetter water regimes could be identified.

The larger species, **Ba To** and **Sv**, tended to tolerate deeper water than did other species. This, in part, is due to their larger growth habit and greater productivity, resulting in greater leaf area exposed above water depth. The greater this leaf area, the greater the potential for internal transfer of gases and oxygenation of below-ground organs. Inefficient gaseous transfer would result in anaerobic conditions in the below-ground organs and the rhizosphere. In **Ba**, the decrease in total biomass with increasing water depth, concurrent with increased investment in leaves compared to below-ground organs, is connected with increased leaf length maintaining leaf area above the

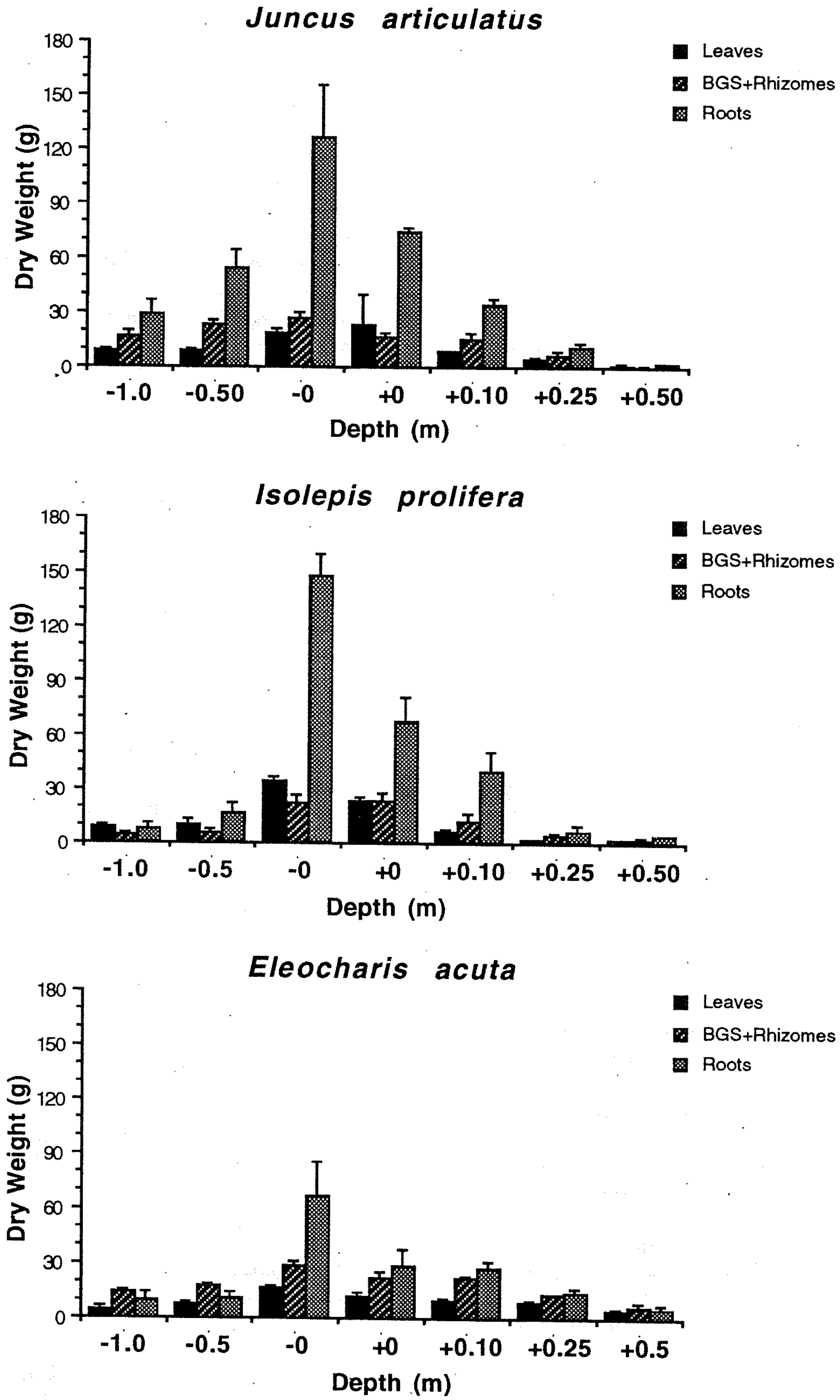


Figure 6.9: Final mean leaf, below ground stem (BGS) + Rhizome, and root biomass of the three small species in each of the treatments. Error bars shown are standard errors.

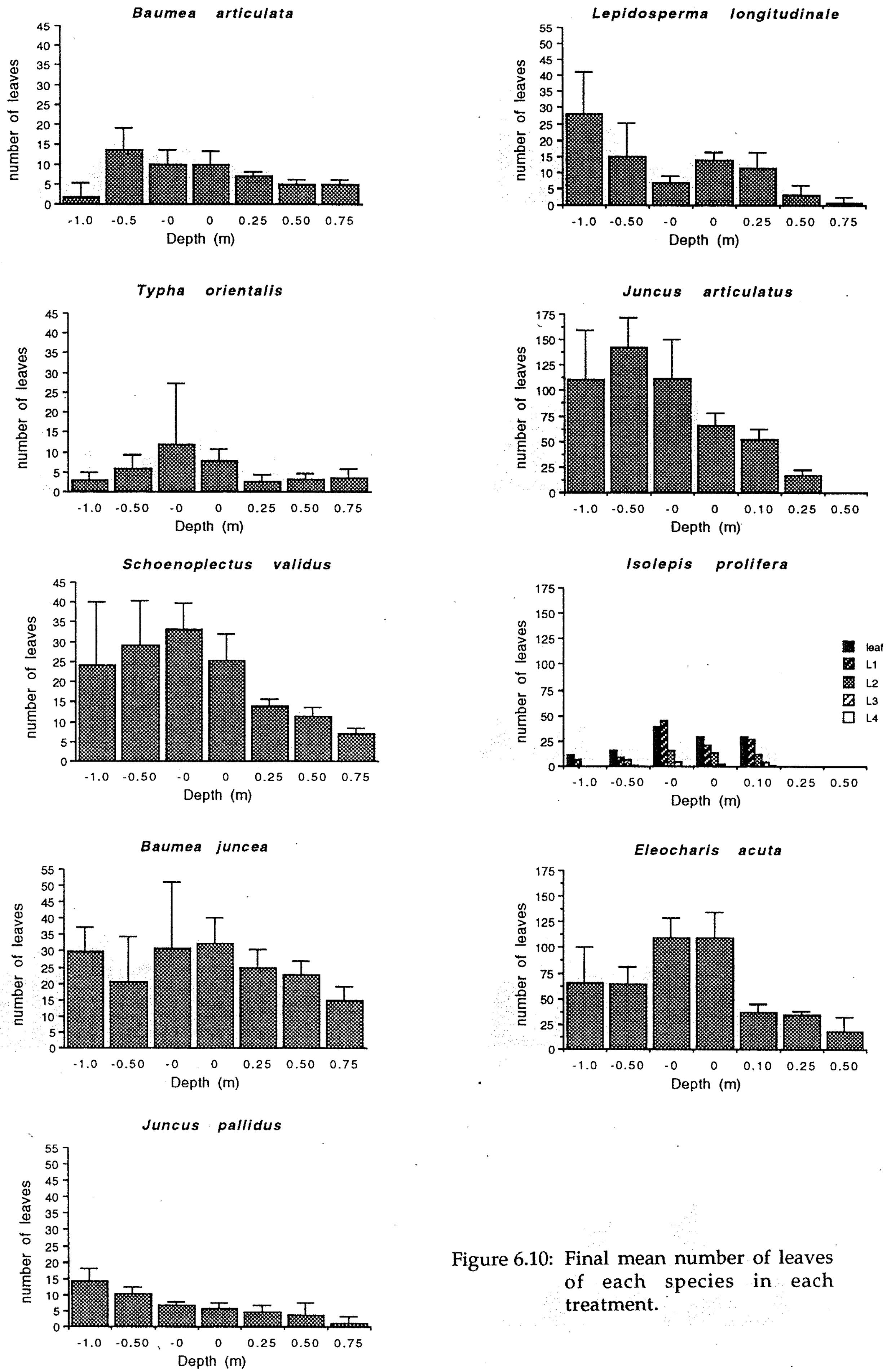


Figure 6.10: Final mean number of leaves of each species in each treatment.

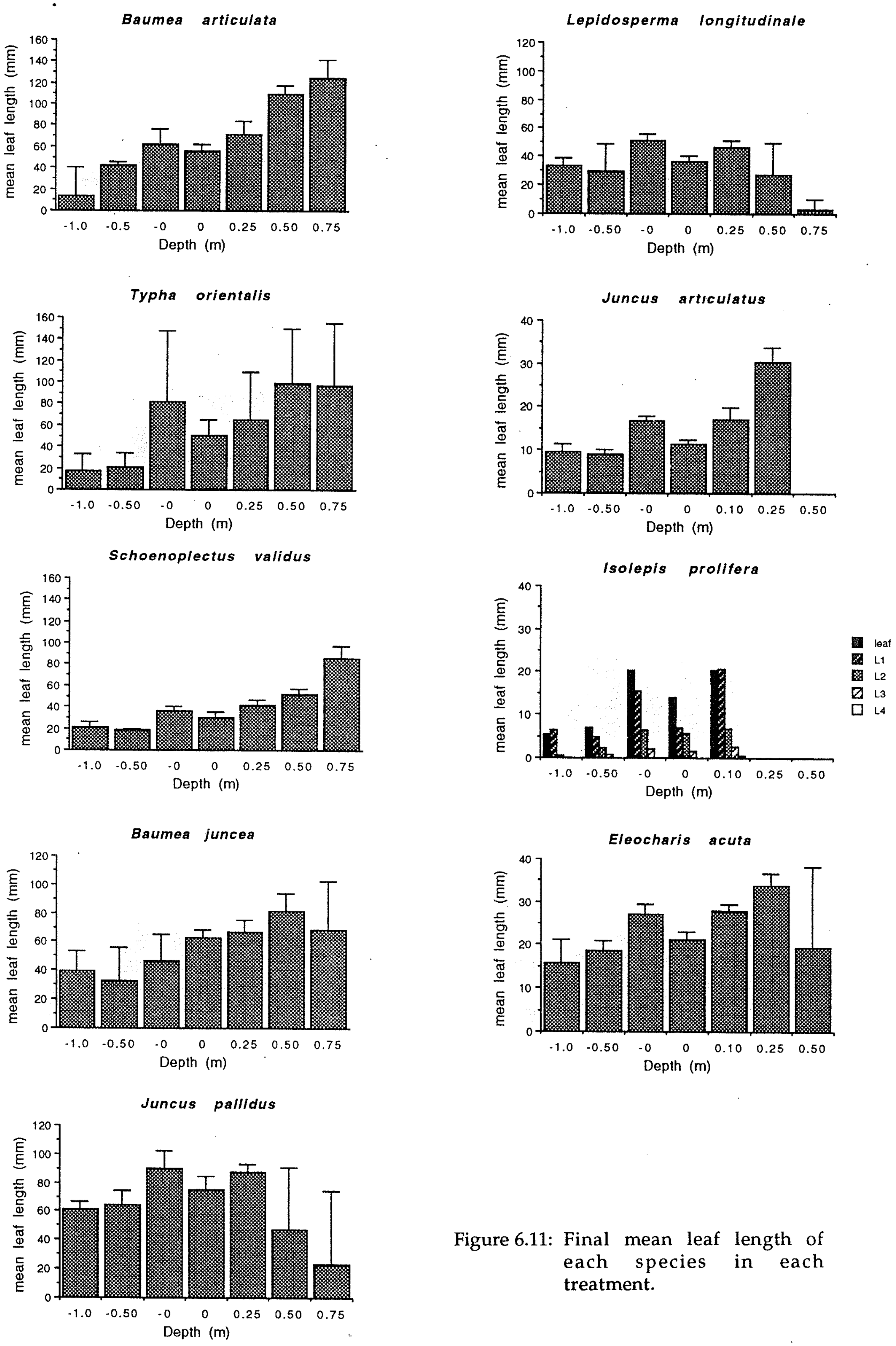


Figure 6.11: Final mean leaf length of each species in each treatment.

water level. This was less evident in **To** and **Sv**.

With respect to the two most common species of emergent macrophyte on the Swan Coastal Plain, **Ba** and **To**, their tolerance range appeared to be similar. The productivity of **To**, however, was greater than **Ba** in all but the drought treatments and the +0.75m treatment. This indicates a vegetative growth advantage to **To** under conducive conditions, whereas this advantage is curtailed under less favourable conditions. Below-ground organs (rhizome and roots) represented a greater proportion of total biomass in **To** compared with **Ba**. This reflects the seasonal senescence of above-ground biomass in **To**, and the necessity for greater below-ground storage of photosynthesis products. On the other hand, **Ba** had a higher leaf biomass than **To**.

Below-ground biomass of all species, represented the greatest (by weight) proportion of total biomass. Root growth was curtailed by both increasing and decreasing water depth due to either less demand for water and nutrients (flooding treatments) or unfavourable conditions. However below-ground biomass at the deeper end of the water depth gradient was generally greater than other species, suggesting maintenance of an aerobic rhizosphere in the larger species.

Of the medium species, **Bj** showed similar trends to the large species, with higher relative investment in leaves at greater water depths. Leaf number and mean length also increased with increasing water depth. However total biomass was very low (a decrement relative to initial biomass) in the +0.75 m treatment. This indicates that **Bj** is capable of growing under shallow inundation conditions but its growth is severely limited in deeper water. The other remaining medium species, **Jp** and **Ll**, did not follow a similar trend, and appeared to have an equally wide tolerance range but preferred drier conditions. Both species had very poor growth during the course of the experiment at the deeper water levels. All three medium species displayed pronounced decreases in below-ground biomass with increasing depth, indicating unfavourable conditions for root and rhizome development.

The small species (**Ja**, **Ip**, **Ea**) again showed peak total biomass at 0 water depth (waterlogged soil), and generally had little tolerance of inundation. Their small growth habit prevents them from maintaining sufficient leaf area above water at even moderate depths (>0.20 m). As a result, below ground productivity decreases rapidly with increasing water depth. With respect to the drier end of the gradient, **Ja** appeared to tolerate the +0.50 and +0.75 m treatments better than **Ip** and **Ea**. **Ea** and especially **Ip** displayed a relatively narrow tolerance range (0 to +0.10 m), with very poor below-ground biomass at both ends of the gradient.

Flowering patterns became established only during the last 9 months of the experiment. Generally the flowering phenology of the plants changed with increasing depth. Of those species that displayed a better tolerance of inundation, flowering at the deeper treatments (+0.50 m and +0.75 m) was more protracted, with seed set taking significantly longer than in the drier treatments. Some of the medium species and all of the small species either had very poor seed set and/or aborted seed, or did not flower at the deeper water levels. Protracted seed set or lack of flowering at greater water depth indicates that most if not all plant resources are required for survival rather than the 'luxury' of inflorescence production.

This experiment was designed to test the performance of the species under different constant water depths, rather than their response to a seasonally fluctuating water level or the change from an established water regime to another. However, all species showed seasonal growth patterns despite constant water levels, which were pronounced in the more 'stressful' treatments (-1.0 and +0.75 m). There is thus a coinciding seasonality of growth, a response to changes in daylength and temperature, which is modified in magnitude (and to a lesser extent, timing) by water depth. Generally, the differences observed along transects in the field can be interpreted as due primarily to water depth, and modified by other factors along the gradient. The small species, and to some extent **Ll** and **Sv**, showed stress in winter-spring in the flooding treatments and in summer-autumn in the drought treatments. Increased number of senescent and/or dead leaves and a reduction in the rate of alive leaf growth were the common indicators of stress.

7: Inter- and Intraspecific Interactions under Experimental Conditions; Growth and Reproduction of *Typha orientalis* and *Baumea articulata* at Different Densities

7.1 Introduction

Wetland environments are characterised by several environmental stresses to which plants must be adapted. The structural and physiological adaptations these plants undergo enable them to compete for limited resources in a continually changing environment. Several wetland species have characteristics that give them a competitive advantage over other wetland plants. Under certain conditions these species are able to invade other wetlands and exclude species native to the area. *Typha orientalis* is considered to have characteristics enabling it to become established in wetlands of the south-west, where it has previously been unknown (Brock and Pen, 1984). The competitive advantage of *Typha* lies with a high productivity and fecundity, and an ability to exclude other competitors through its growth form. It also produces large numbers of seed with a high percentage of viability. Furthermore, it forms tall, dense canopies that shade competitors and extensive underground networks of bulky rhizome-mats preventing other species from establishing.

In the last decade, managers have witnessed its establishment and expansion in coastal and inland wetlands on the Swan Coastal Plain (Zedler *et al.*, 1990). In both inland and tidal wetlands the expanse of *T. orientalis* occurs at the expense of native species, with total replacement occurring over large areas (Pen, 1983; Brock and Pen, 1984; Watkins and McNee, 1985; Bartle *et al.*, 1986; Zedler *et al.*, 1990). With respect to tidal marshes, *T. orientalis* was found to have a narrow establishment niche, invading only following salinity reduction and after disturbance disrupts the native vegetation (Zedler, 1990). Its dominance of freshwater lakes has been attributed to colonisation following cultivation (Benger Swamp), other severe disturbances to wetland soils (Herdsman Lake), or disturbance of native vegetation through alterations in water regime (Chapter 4). *Typha orientalis* is considered detrimental not only to wetlands but it also blocks water courses, invades farm dams and causes serious weed problems in aerially-sown rice (Cary *et al.*, 1983), and while it is thought to be beneficial as a habitat for wildlife, its rapid growth can reduce the area of open water, restricting bird use (Murkin *et al.*, 1982). It does however, play an important role in stabilising wetlands and it has potential use in the treatment of wastewater (Finlayson and Mitchell, 1983).

The most common emergent macrophyte in the southwest, *Baumea articulata*, is an important component of many ephemeral peat wetlands, and is one of the native species affected by *T. orientalis* invasion. The distribution of these two species in the field is often explained by water regime or other abiotic factors (Chapter 4), but the relative importance of interspecific competition in determining species survival and distribution is poorly understood. Although indications as to the outcome of competition are evident in the field (Chapter 4), experimental validation of the nature of interactions is required. Field observations suggest that *B. articulata* vegetative growth is suppressed by the presence of *T. orientalis* in zones of overlapping distribution. The aim of the work described here was to determine whether the growth of *B. articulata* is suppressed by *T. orientalis* under controlled conditions, and interpret the results in light of field observations.

7.2 Methods

7.2.1 Establishment of Ramets and Experimental Design

Ramets of *Typha orientalis* and *Baumea articulata* were collected in November 1990 from Forrestdale and Banganup lakes respectively, and were transplanted into white quartz sand contained in 9L (28cm x 24cm) black plastic pots. The same day as collection, the young ramets were trimmed to approximately 10cm of rhizome and 30-35cm of leaves to lower transpiration loss. Between intraspecific treatments and within the interspecific treatment, the ramets used were approximately the same fresh weight (± 20 g). The experimental design employed was as outlined by Underwood (1990) and involved the investigation of intra- and interspecific interactions between two species. This includes two initial intraspecific densities for each species, and an interspecific treatment with both species at the same density;

	Ramet Density (per pot)				
Baumea articulata	2	4	2	0	0
Typha orientalis	0	0	2	4	2

This design enabled the comparison of growth at two different initial densities for each species, and the relative growth of each species in a interspecific treatment of similar density. The densities refer to the number of ramets per pot. There were six replicates (pots) of each treatment. The pots were positioned in PVC tubs (100cm x 50.5cm x 35cm) and submerged to approximately 7 cm above the soil surface. Plants were maintained in the open under this regime for a period of eleven weeks, to allow acclimatisation and establishment.

7.2.2 *Monitoring of Plant Growth*

After the initial establishment period, the plants were measured every two weeks, with the number of ramets, inflorescences, and green, senescent and dead leaves being recorded. All leaves that were at least half (in length) brown were considered senescent. Although the leaves of each plant were trimmed at the time of collection from the field, the plants had produced significant above-ground growth before monitoring commenced. In some cases the plant had undergone rhizome extension during the establishment phase resulting in an increase the number of ramets. The length of each individual green and senescent leaf was measured to the nearest 0.5cm.

In November 1991, all plants were harvested. The lengths of approximately 70 leaves from each of the five treatments were recorded (70 from each species in the interspecific treatment) for determination of length vs weight regression. These leaves were individually bagged for drying. The remaining green and senescent leaves were separated from the dead leaves, and all leaves were then bagged for drying. Below ground material was washed free of soil and separated into roots, rhizomes and leaf bases (portion of leaves and/or stem beneath soil surface). In the case of the interspecific treatment (2T/2B), the roots of each species were separated as far as practicable, the remaining roots being bulked. All harvested material was oven dried at 70^{o}C and then weighed. The weight of the bulked roots of the 2T/2B treatment was assigned to each species on a percentage basis, according to the weight of the separated below ground biomass of the species.

7.2.3 *Monitoring of Physical Parameters*

Nutrients were supplied on a regular basis with 'Aquasol' soluble fertilizer (Hortico Australia Pty Ltd) at a rate of 40g (dissolved in 10 litres of water) for each tub. Nutrients were supplied on average, every 14 days during summer and autumn, and every 35 days during winter and spring. This was done to maintain a moderate-high nutrient regime. Water samples were taken to ascertain the concentrations of total nitrogen, total phosphorus, ammonia, nitrate and orthophosphate. All samples were initially filtered through silk to remove any large particles, and subsamples for ammonia, nitrate and orthophosphate determination were filtered through GF/C filter paper before being placed in 'whirlpaks' (NASCO) and frozen until analysis. Water temperature, pH and dissolved oxygen were monitored on a monthly basis.

7.3 Results

7.3.1 *Physical Parameters*

All treatments displayed similar temperature fluctuations, from 28 °C in autumn to 12 °C in winter. There no significant differences in dissolved oxygen concentration between treatments, which ranged seasonally from 5 - 12 mg/l. There were no trends in pH, which fluctuated between 5.5 and 7.6.

Nutrient concentrations in all treatments were generally high (Fig. 7.1). Occasional algal blooms in the tub water resulted in lower levels of NO_3 and high values for Organic N. There was little variation between treatments in concentrations of TN

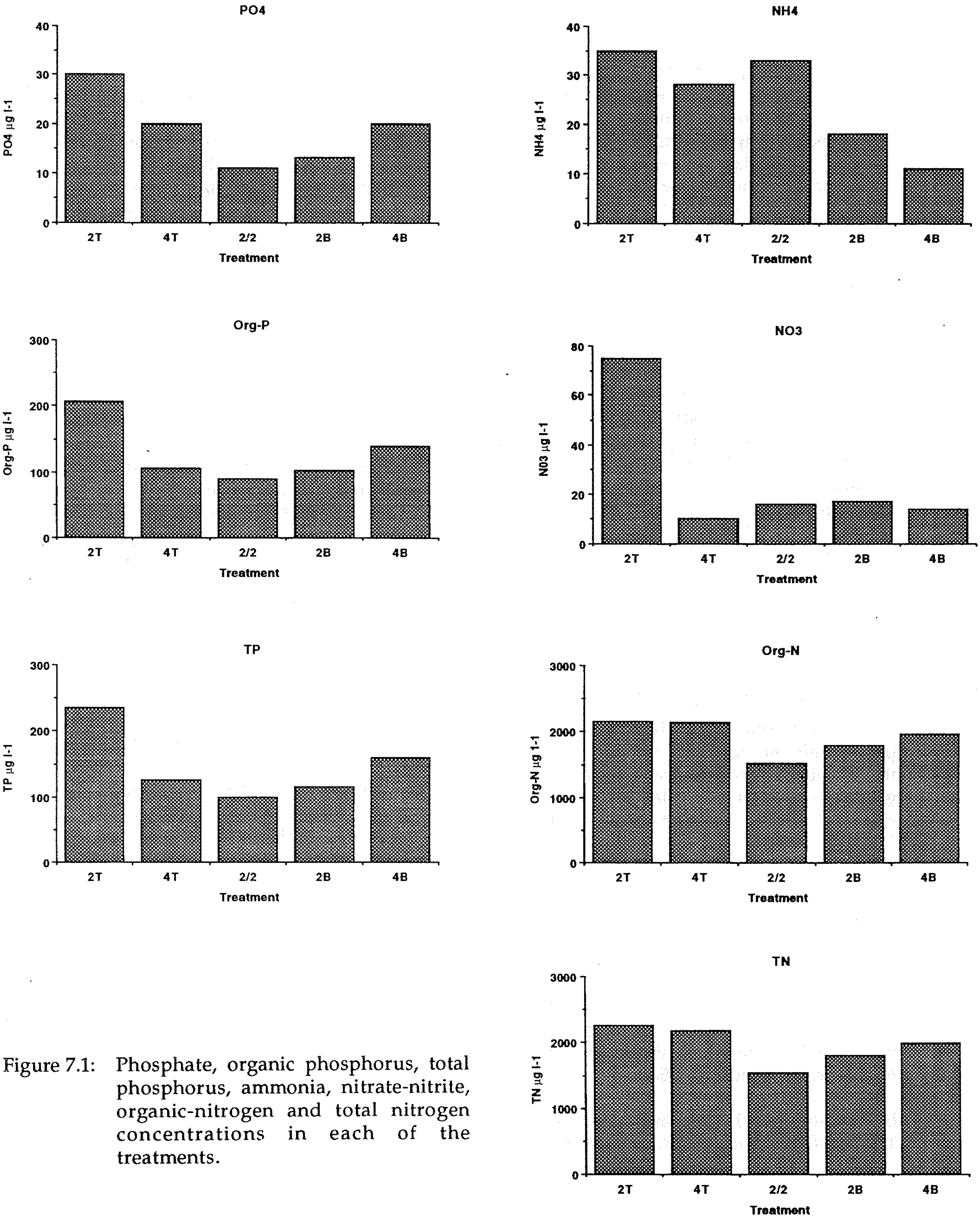


Figure 7.1: Phosphate, organic phosphorus, total phosphorus, ammonia, nitrate-nitrite, organic-nitrogen and total nitrogen concentrations in each of the treatments.

and Org-N. The 2T treatment appeared to have the highest levels of PO_4, Org-P, TP and NO_3.

7.3.2 Phenology of Leaf Production

Baumea articulata: The average number of alive leaves per ramet generally increased in *Baumea articulata* during the course of the experiment in all treatments (Fig. 7.2). The number of alive leaves was greatest in the 2B treatment, followed by 4B and 2T/2B. The production of *B. articulata* leaves in the 2T/2B treatment was approximately half of that in the 2B treatment. There appeared to be no winter senescent phase in *B. articulata.* The number of senescent and dead leaves remained very low during the experiment, with little difference between treatments. The proportion of dead and senescent leaves appeared to be higher in the 2T/2B treatment, however this difference became less significant as the experiment progressed (Fig. 7.3). The density of ramets in each treatment gradually increased during the experiment with the 4B treatment displaying the greatest rate of increase (Fig. 7.4). Ramet numbers were highest in the 4B treatment (up to 12 ramets per pot), and lowest in the 2T/2B treatment (6 ramets) where the number of ramets plateaued for several months during late autumn and winter. The number of ramets in the 2B treatment were approximately half of the 4B treatment.

The average live above-ground biomass per pot, calculated from the leaf length vs leaf weight regressions, increased steadily in all three treatments with no perceptible seasonal fluctuation (Fig. 7.5). The 2B and 4B treatments had similar biomass per pot, however the 2T/2B treatment had a significantly lower biomass throughout the experiment, down to 26% of the intraspecific treatments by mid-spring. When expressed as average above-ground biomass per ramet the higher density 4B treatment is significantly lower than the 2B treatment, and similar to the 2T/2B treatment (Fig. 7.6). This is supported by comparing leaf number with ramet number (Fig. 7.2 and 7.4 respectively).

The *B. articulata* in the 2B, 4B and 2T/ 2B treatments flowered during the course of the experiment, the 2B and 2T/2B treatments started flowering during August, however the 4B treatment flowered during mid-September (Fig. 7.7). The maximum number of inflorescences was the same for the 2B and 4B treatments, however the 2T/2B treatment had only 30 % of the other treatments.

Typha orientalis: *Typha orientalis* displayed a distinctive seasonal pattern in leaf production in all treatments (Fig. 7.2). Leaf number increased from the start of the experiment, decreased during winter, and increased again in the following spring. The number of alive, senescent and dead leaves remained approximately the same in all three treatments. The number and proportion of senescent leaves in *T. orientalis* was significantly higher than *B. articulata* (Fig. 7.2 and 7.3). Ramet numbers were virtually the same in all three treatments (Fig. 7.4). The 4T treatment maintained the highest number of ramets in the early phase of the experiment (autumn), however the remaining treatments equalled the ramet numbers in the 4T treatment after a surge in ramet production during early winter. Ramet numbers plateaued during the following spring.

The 2T treatment had the highest average live above-ground biomass per pot by the end of the experiment (Fig. 7.5). All treatments increased gradually in biomass during autumn, decreased during late winter, and increased dramatically during the following spring. This reflects the more seasonal pattern in productivity of *T. orientalis.* The dramatic increase in biomass towards the end of the experiment was probably due to the compounding effect of an increase in the number of ramets. Trends in average above-ground biomass per ramet were similar in all three treatments. By the end of the experiment, the 2T treatment had significantly higher biomass than the 4T and 2T/2B treatments which were similar. All *T. orientalis* in the 2T, 4T and 2T/2B treatments started flowering during October (Fig. 7.7). The 2T and 4T had similar maximum number of inflorescences, however the 2T/2B treatment had 2.5 times the number of inflorescences as the other treatments.

Baumea articulata vs Typha orientalis: In comparison with *T. orientalis* biomass in the 2T/2B treatment (Fig. 7.8), *B. articulata* average biomass per pot remained significantly lower during the first half of the experiment (autumn) but increased above *T. orientalis* during the end of winter when

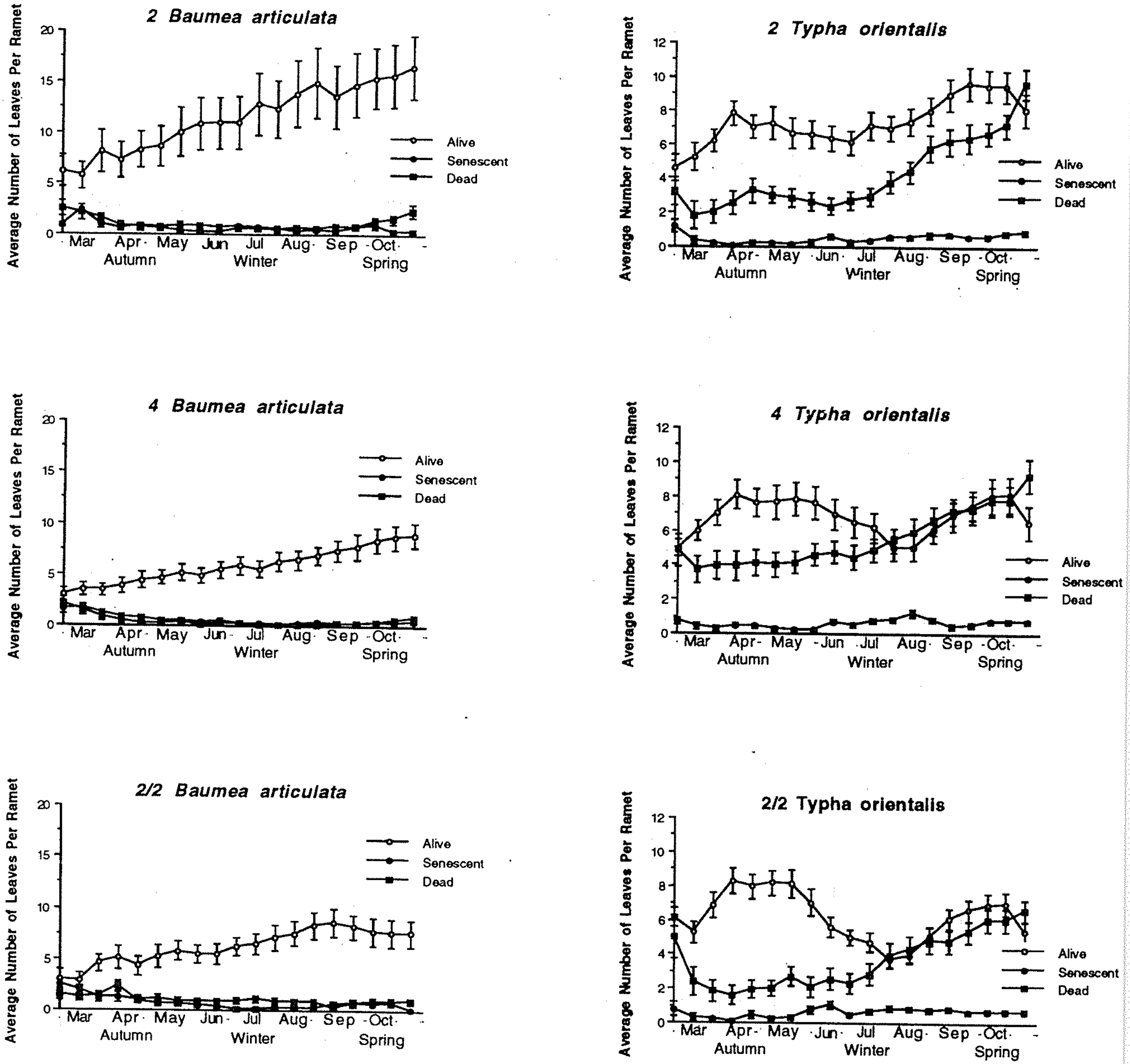


Figure 7.2: Average number of live, senescent and attached dead leaves per ramet in each of the treatments over the course of the experiment. Error bars shown are standard errors.

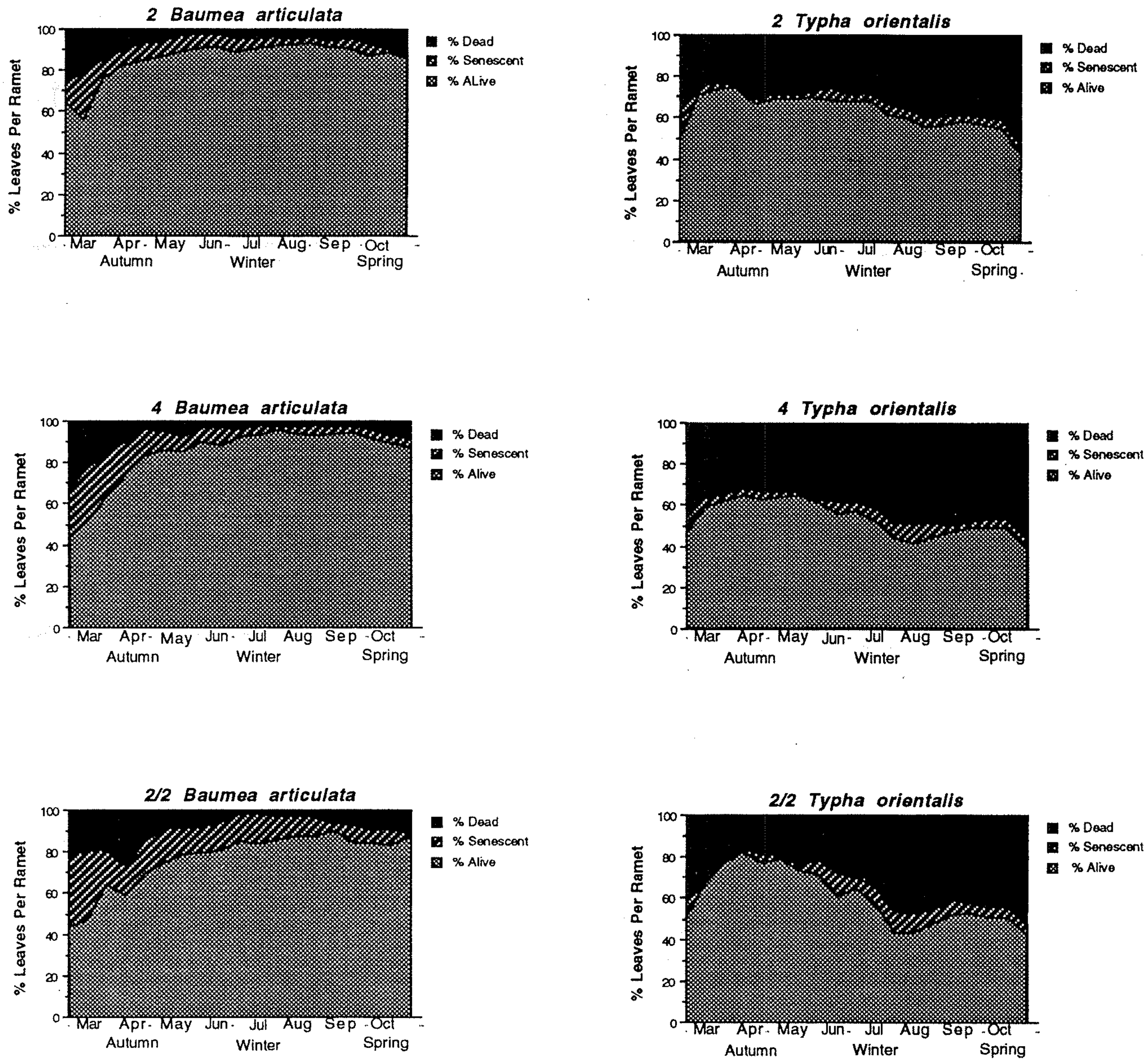


Figure 7.3: Percentage live, senescent and attached dead leaves per ramet in each of the treatments over the course of the experiment. Error bars shown are standard errors.

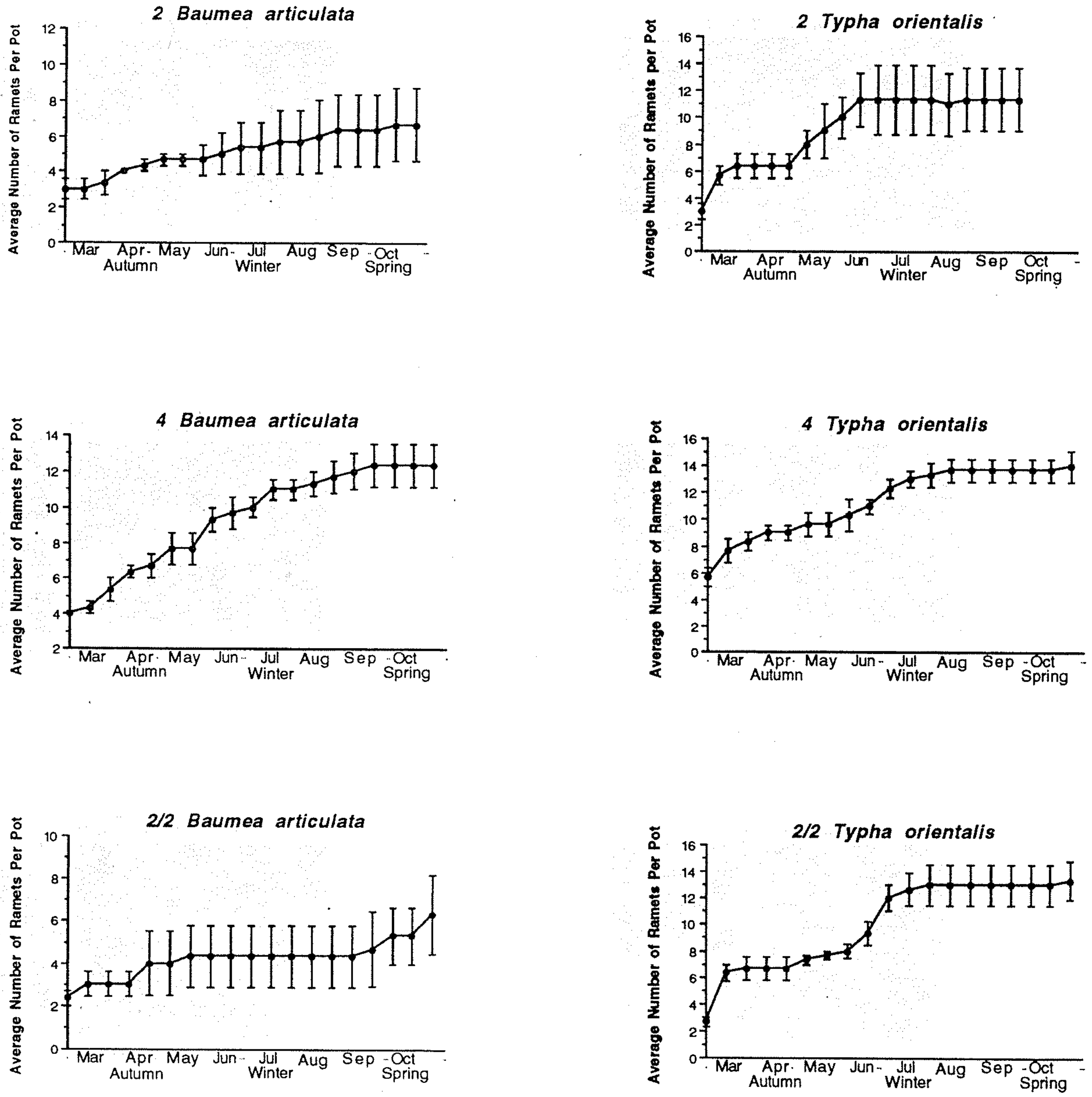
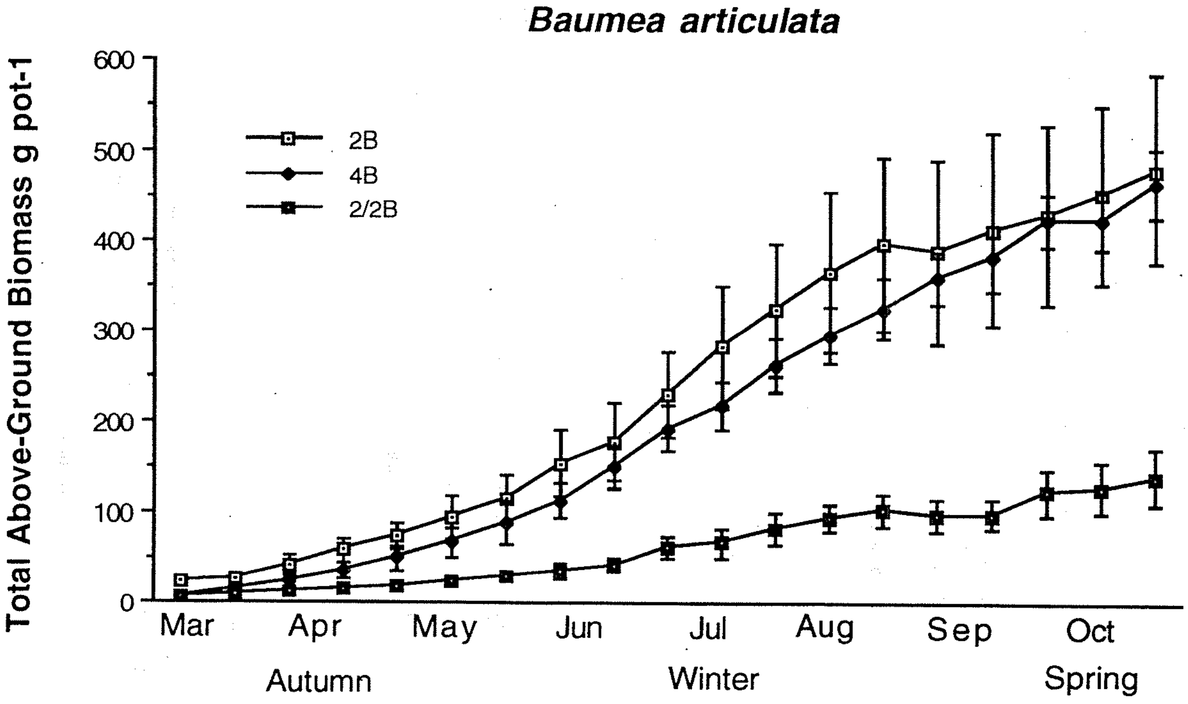


Figure 7.4: Average number of ramets per pot in each of the treatments over the course of the experiment. Error bars shown are standard errors.



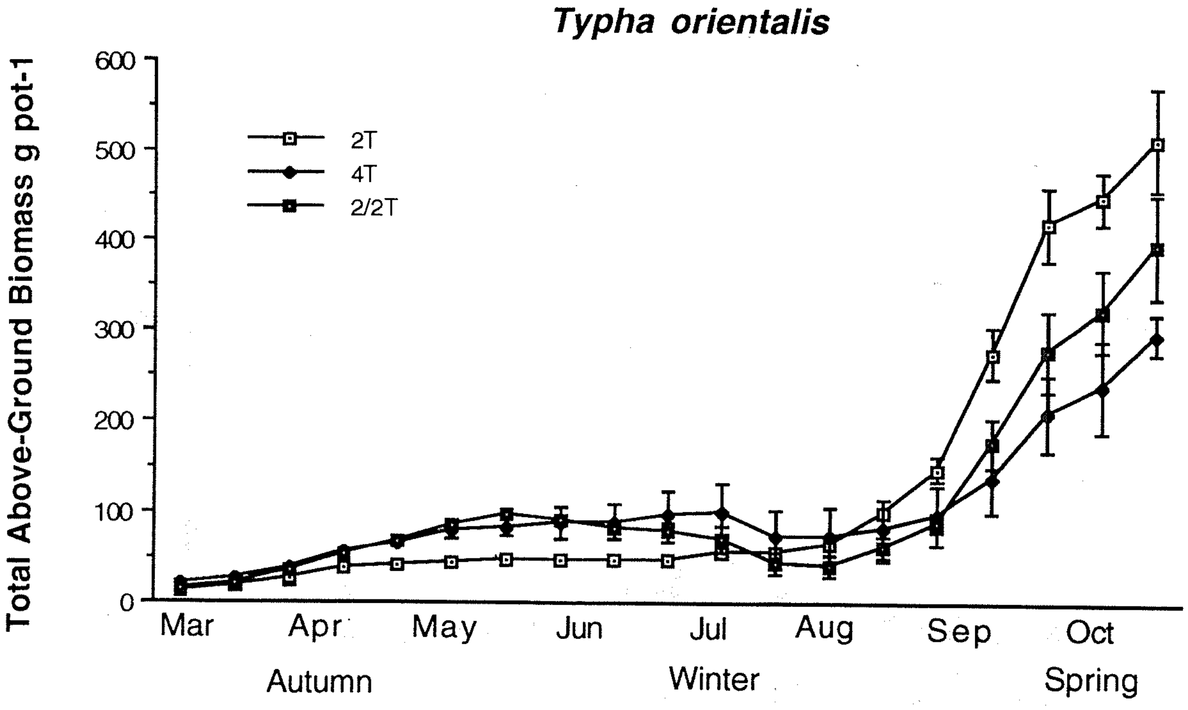
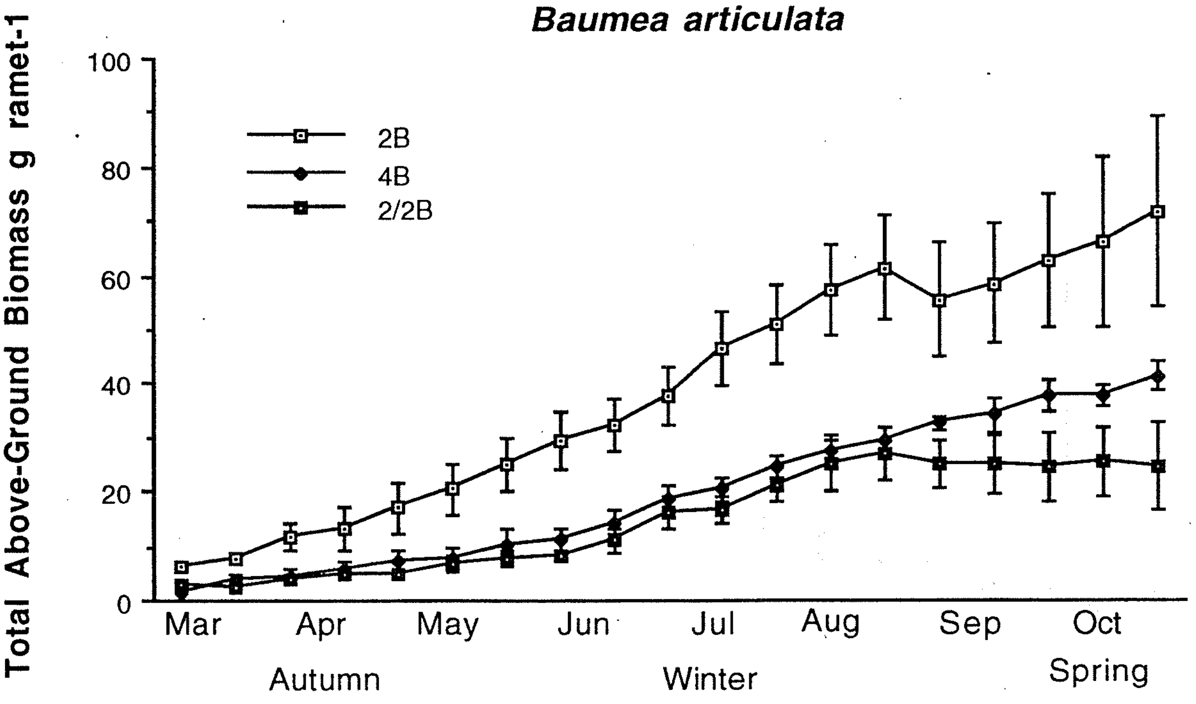


Figure 7.5: Mean total *Baumea articulata* and *Typha orientalis* above-ground biomass per pot in each treatment over the course of the experiment. Error bars shown are standard errors.



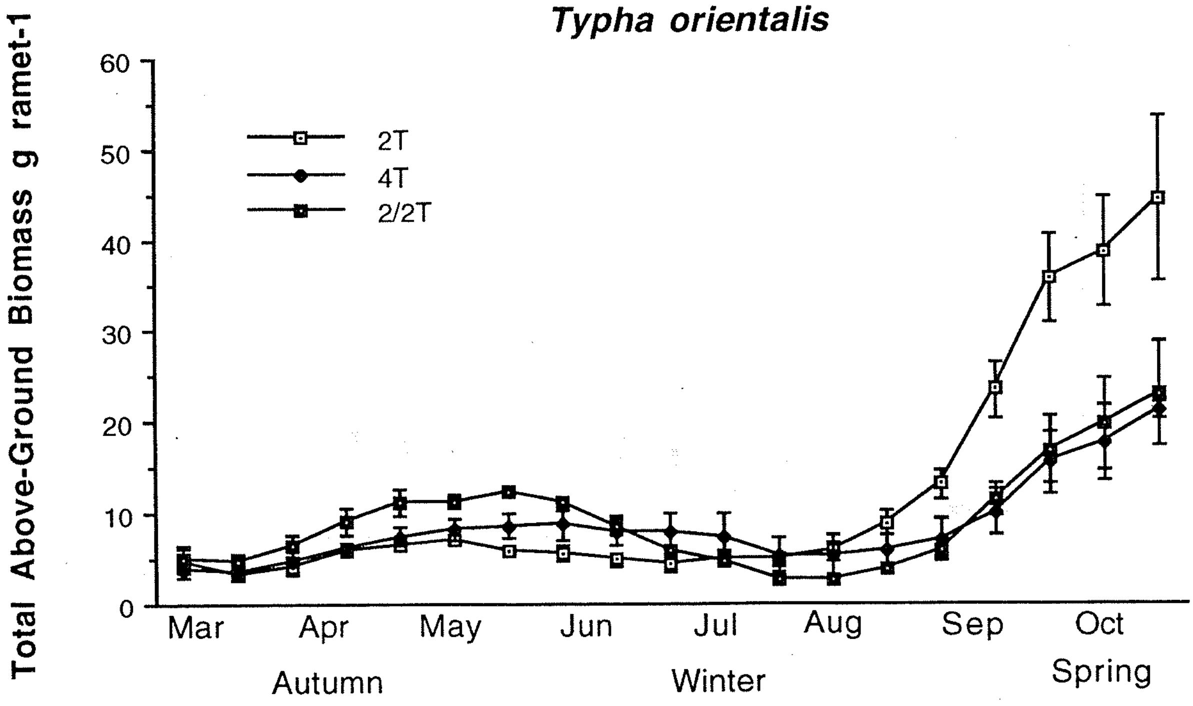


Figure 7.6: Mean total *Baumea articulata* and *Typha orientalis* above-ground biomass per ramet in each treatment over the course of the experiment. Error bars shown are standard errors.

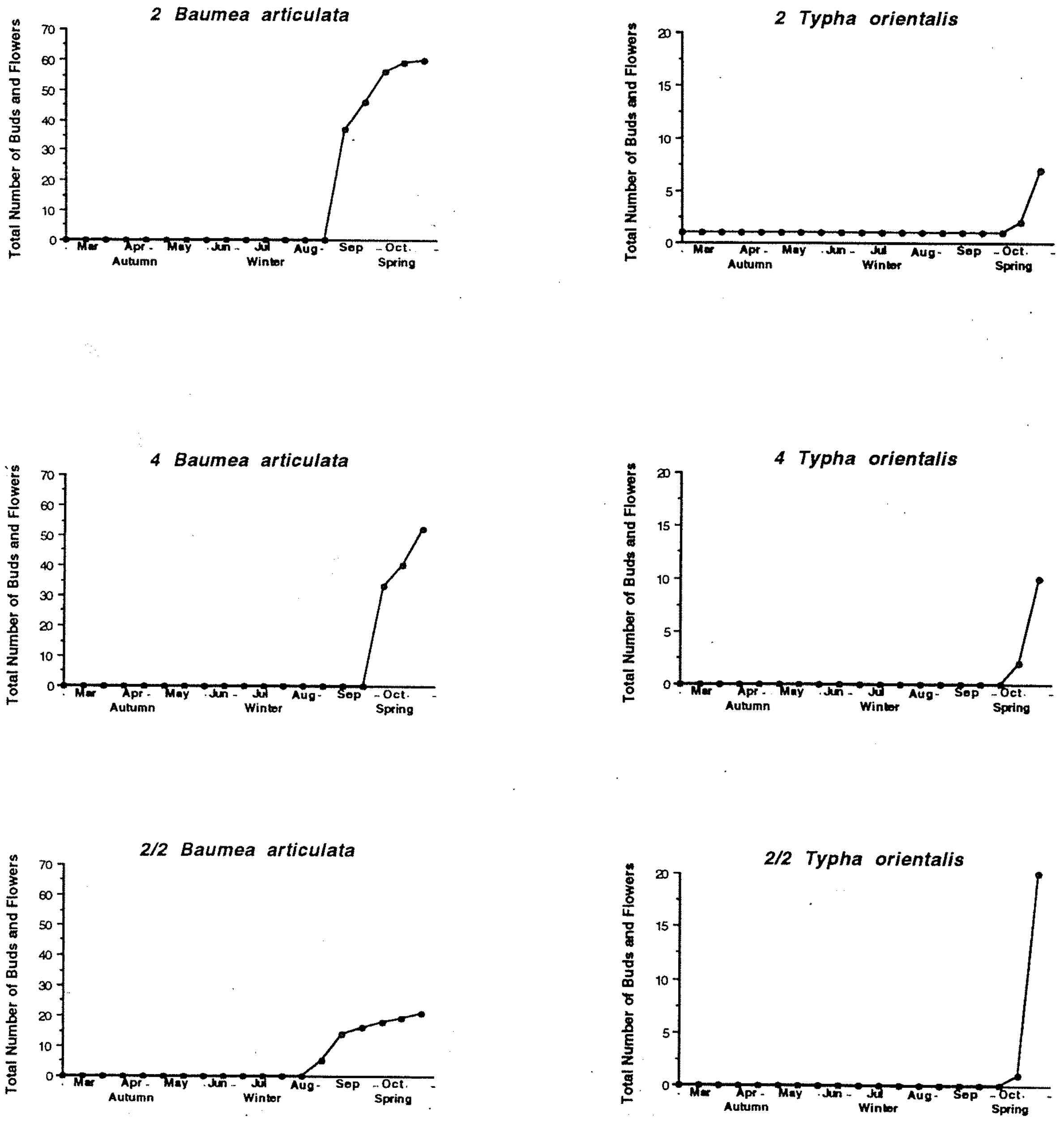


Figure 7.7: Total number of flower buds and flowers in each treatment over the course of the experiment. Error bars shown are standard errors.

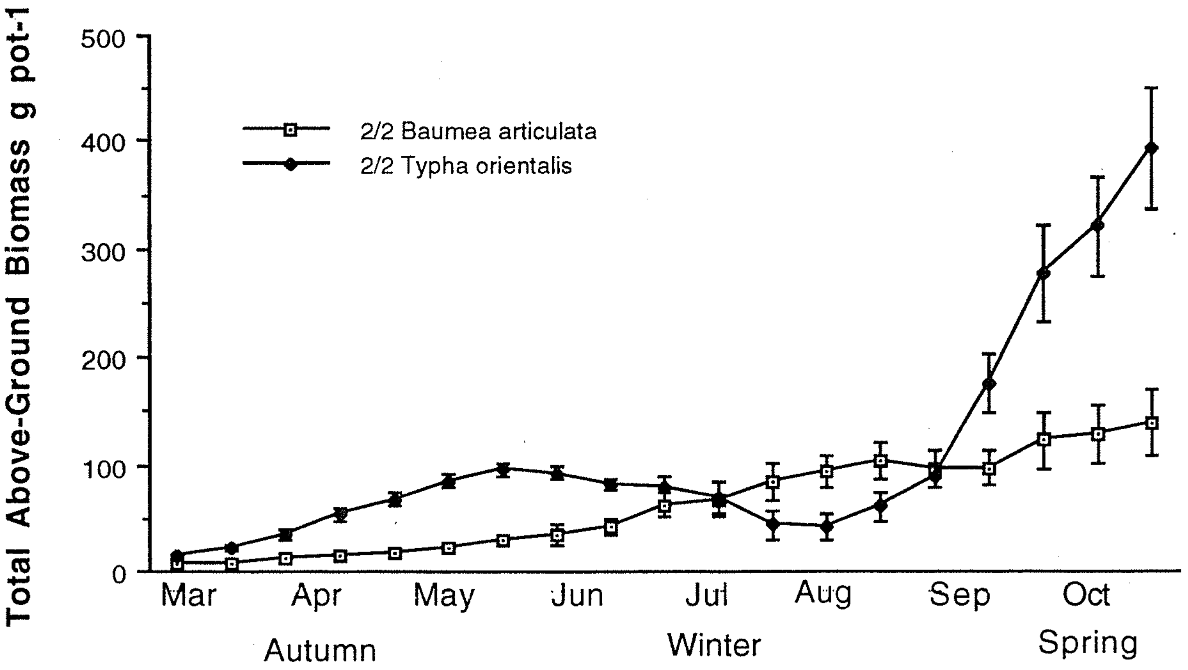


Figure 7.8: Mean total *Baumea articulata* and *Typha orientalis* above-ground biomass per pot in the mixed treatment over the course of the experiment.

many of the leaves became senescent in *T. orientalis* . Biomass of *T. orientalis*, however, increased dramatically during early spring to over 2.5 times that of *B. articulata*. *B. articulata* alive leaf biomass per ramet was lower than *T. orientalis* during autumn but increased to over 5 times that of *T. orientalis* by the end of winter (Fig. 7.9). However the biomass of T. *orientalis* increased to equal that of *B. articulata* by mid-spring. It should be noted that the leaf biomass of *B. articulata* increased rapidly during the phase of *T. orientalis* leaf senescence, and that *T. orientalis* had a significantly greater number of ramets. In comparison with the intraspecific treatments, the number of *B. articulata* inflorescences was reduced, whereas the number of *T. orientalis* flowers increased.

7.3.3 *Above and Below Ground Final Biomass*

Baumea articulata: The final biomass harvest at the end of the experiment was significantly different between the intraspecific and interspecific treatments. The average leaf biomass per pot of the 2B and 4B treatments were similar, and both were significantly greater than the 2T/2B treatment (Fig. 7.10). The same trend also applied to leaf base and rhizome biomass. Root biomass of the 2T/2B treatment was no different to the intraspecific treatments. Relative yield (RY) was calculated as average total biomass per pot in 4B treatment divided by average total biomass per pot in 2B treatment. For *B. articulata* intraspecific interactions the RY = 0.96. This slight reduction in the 4B treatment however was not significant ($p>0.05$). Thus, *B. articulata* grew equally well at both densities, two ramets producing as much biomass as four ramets, even though the final number of ramets differed. Apparently, the experiment continued long enough so that resources, rather than starting density, determined final biomass. The below-ground : above-ground biomass ratios (per pot) (B:A) were the same for both treatments (0.48 for both 2B and 4B). This indicates no difference in carbon allocation patterns.

Typha orientalis: There was no significant difference between the three treatments in respect to leaf, leaf base, rhizome and root biomass (Fig. 7.9). For *T. orientalis*

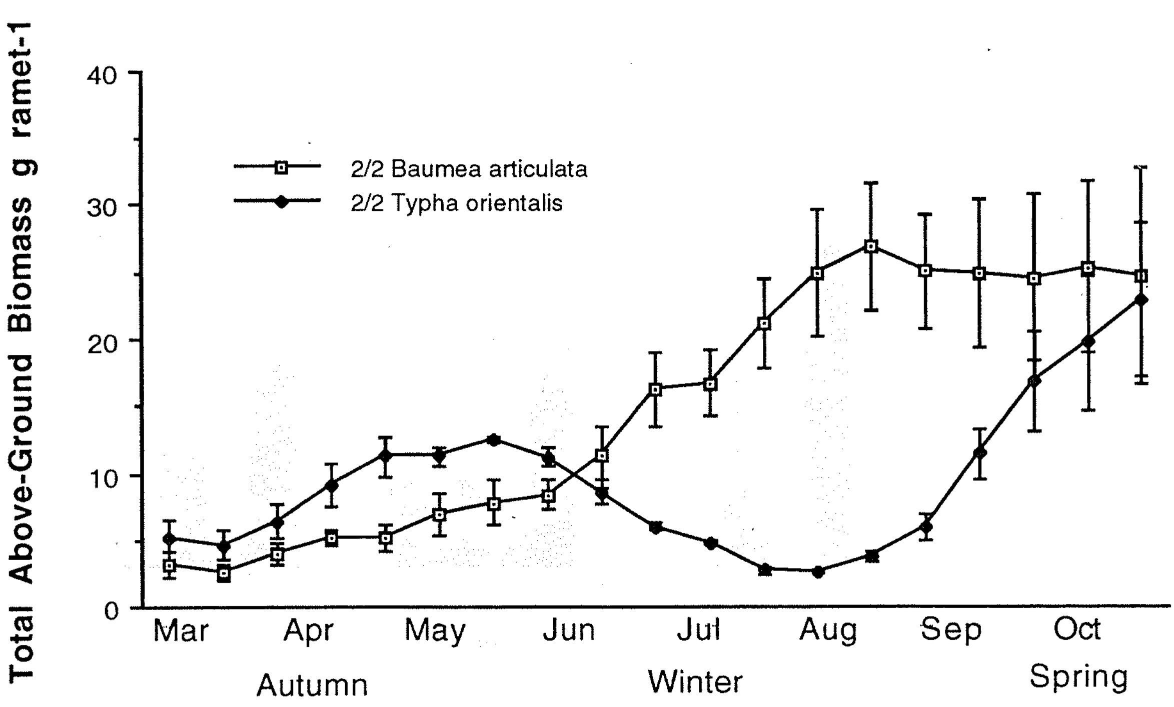


Figure 7.9: Mean total *Baumea articulata* and *Typha orientalis* above-ground biomass per ramet in the mixed treatment over the course of the experiment.

intraspecific interactions the RY = 0.82, the difference was not significant ($p>0.05$). The B:A ratios were similar (0.84 for 2T and 0.99 for 4T) and indicate a far greater proportion of biomass in the below-ground structures.

Baumea articulata vs Typha orientalis: Although the average leaf biomass of *B. articulata* appeared lower, there was no significant difference between the species (Fig. 7.11). However, the below-ground biomass (leaf base, rhizome and root) of *B. articulata* was significantly lower than *T. orientalis*. The RY (2/2T divided by 2T) for *T. orientalis* was 0.72 (non-significant reduction), whereas the RY for *B. articulata* was 0.32, representing a significant ($p<0.01$) drop in yield in the interspecific treatment. The B:A ratio for *B. articulata* in the 2T/2B treatment was 0.61, which indicates a shift in carbon allocation towards below-ground structures compared with the intraspecific treatments. The B:A ratio for *T. orientalis* was 1.07, which also represents an slight increase in below-ground allocation.

7.4 Discussion

7.4.1 Intraspecific Interactions

The growth habit of both *Typha orientalis* and *Baumea articulata* is such that these species typically form dense monospecific stands in nature. The density of ramets in these stands is variable but > 50 ramets m^{-2} is not uncommon. It can be assumed, therefore, that these species are able to proliferate under higher degrees of intraspecific interactions. A critical factor in this tolerance is that, by definition, each ramet is a clone produced by rhizome extension of a parent plant, and that all the ramets produced within one (or more) year may still remain 'connected' to the parent plant/s via the rhizome. This implies the potential for translocation of water, nutrients and gases between ramets, and indeed this has been demonstrated (Chapter 4). This exchange of resources may imply a more uniform response of the population to factors limiting growth. Each ramet does not become an independent individual (ie a true ramet) until the rhizome connecting it to the parent plant/s has senesced during the following year. The actual pattern, both temporal and spatial, of rhizome extension and subsequent formation of 'true' ramets however, is poorly understood.

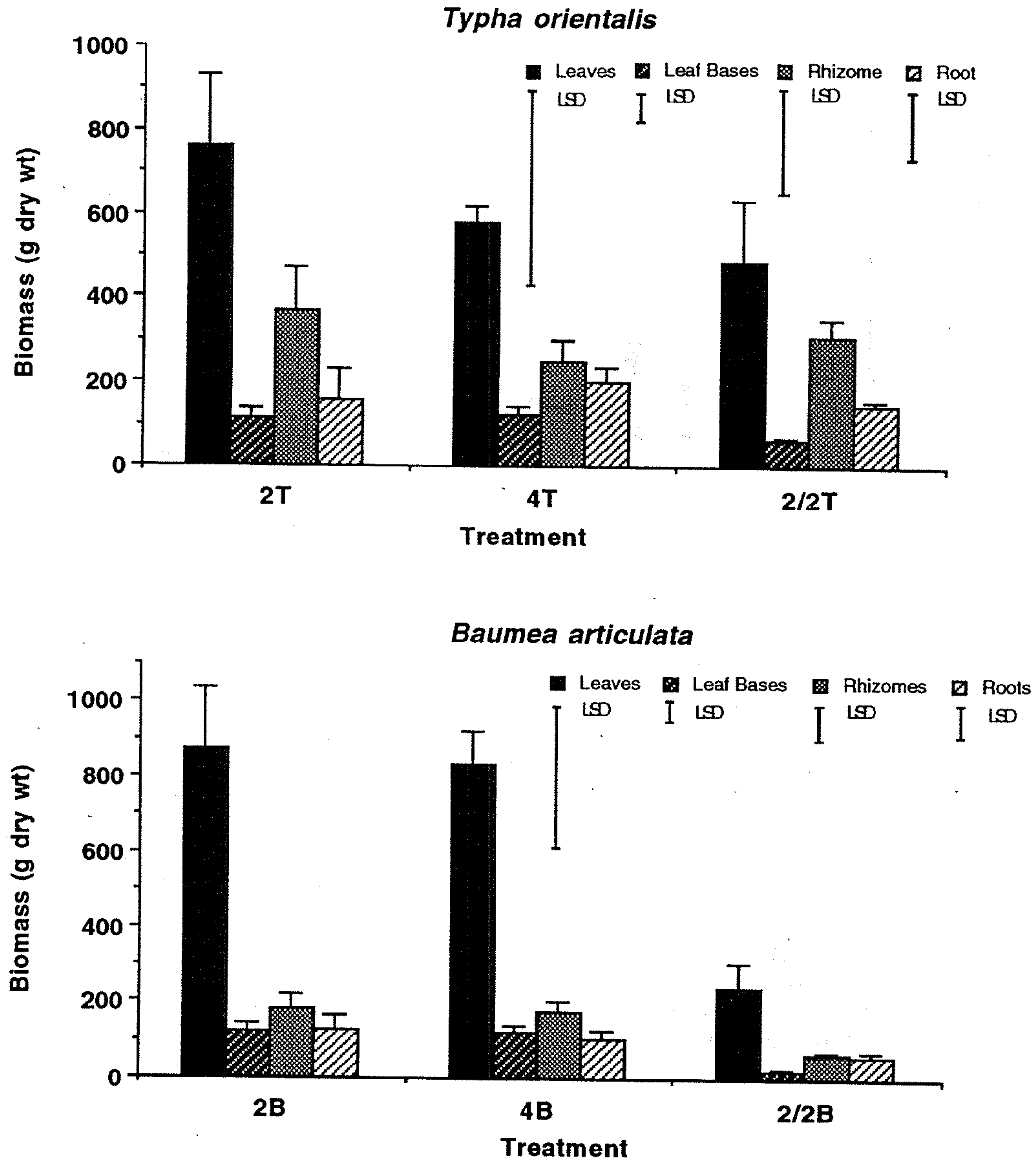


Figure 7.10: Final leaf, leaf base, rhizome and root biomass of *Baumea articulata* and *Typha orientalis* in each treatment. Error bars shown are standard errors. LSD = Least Significant Difference as determined by ANOVA ($p < 0.05$).

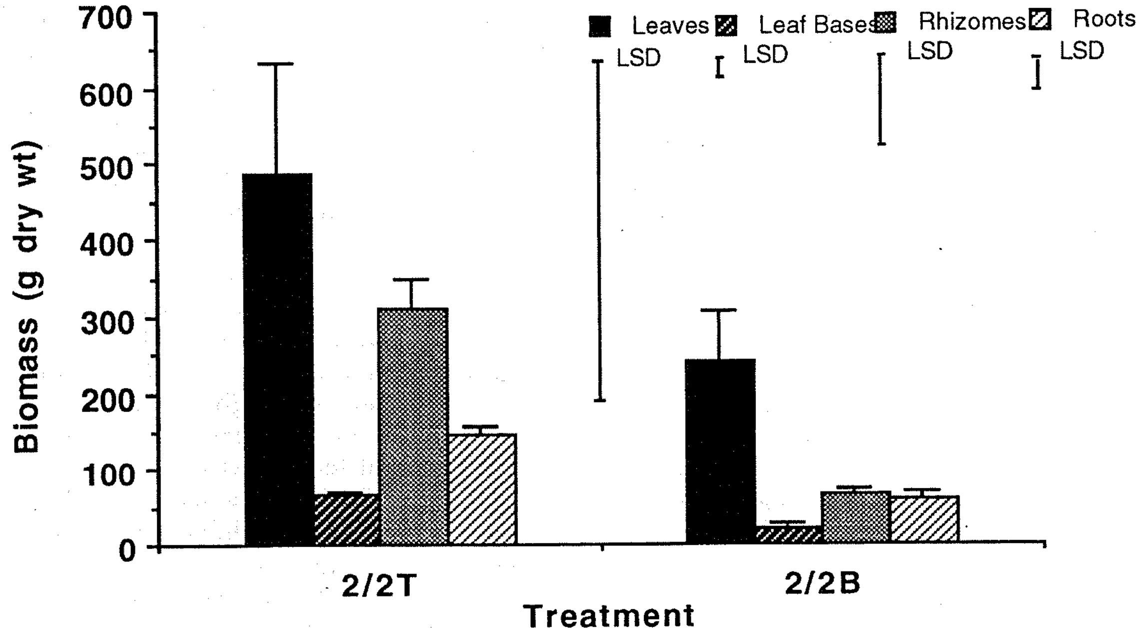


Figure 7.11: Final leaf, leaf base, rhizome and root biomass of *Baumea articulata* and *Typha orientalis* in the mixed treatment. Error bars shown are standard errors. LSD = Least Significant Difference as determined by ANOVA ($p < 0.05$).

Given the clonal nature of growth of these species, it is not surprising that there was little evidence of reduced growth due to intraspecific interactions. With respect to both species, doubling the initial density had no effect on total above-ground biomass production per unit area. *B. articulata* 4B treatment had a higher average number of ramets, probably due to the higher number of parental ramets to start with c.f. the 2B treatment. However the 4B treatment had a lower (c.f 2B) average above-ground biomass per ramet. It appears that, for *B. articulata*, the above-ground biomass per ramet was reduced to accommodate the higher number of ramets produced within the confines of the spatial and nutrient resources available. This absence of a reduction in ramet production with increasing density is reflected by the fact that both density treatments (2B and 4B) had the same increase (300%) in ramet number.

There was no significant difference in the total biomass or the different biomass components between the 2B and 4B treatments. Leaf, leaf base, rhizome and root biomass were similar on an area basis. However, the difference in above-ground biomass per ramet would also extend to the below-ground biomass components as well.

T. orientalis responded differently, as the 4T treatment produced the same average number of ramets as the 2T treatment, with no significant difference in average above-ground biomass per ramet. The percentage increase in ramet number in the 2T treatment (600%) was almost twice that of the 4T treatment (320%). This implies that the above-ground biomass per ramet was not compromised, rather, the rate of ramet production during the early phase of the experiment was reduced in the 4T treatment. The 2T treatments had a higher rate of ramet production probably due to the greater spatial and nutrient resources (per ramet) available. However, as numbers increased, ramet production in both treatments plateaued at comparable densities.

There was no significant difference in the total (final) biomass, or the different biomass components (leaves, leaf bases, rhizomes and roots), on an area (per pot) basis between the

2T and 4T treatments. It is likely that this similarity extends to below-ground biomass per ramet.

The slight evidence of intraspecific interactions in both species may become more pronounced under less controlled conditions. Water level fluctuations, particularly prolonged exposure to the extremes of drought and inundation, may induce greater interspecific competition for resources. Low nutrient availability and poor sediment structure may also be factors that exacerbate competition. Greater intraspecific interaction may be expressed as poor growth per ramet, low ramet densities, and poor sexual reproductive effort. Seasonal variation in the availability of water, nutrients and possibly space could determine change in the intensity of interactions, both intraspecific and interspecific.

7.4.2 Interspecific Interactions

There was a significant reduction in growth of *B. articulata* in the 2T/2B treatment when compared with the 2B treatment. On a per area basis, the above-ground biomass of *B. articulata* in the interspecific treatment was significantly less throughout the experiment than the intraspecific treatment of similar monospecific density (2B). When expressed as above-ground biomass per ramet, *B. articulata* in the 2T/2B treatment remained lower than the 2B treatment, however, weights were similar to the 4B treatment. The reason for this similarity was due to the combination of very low above-ground biomass and low ramet number, rather than higher biomass but very high ramet number (4B). Therefore, it appears that *B. articulata* above-ground expression to interaction with *T. orientalis* is to substantially reduce biomass rather than reduce ramet production. This reduction in *B. articulata* growth was extended to below-ground organs as well. There were significant reductions in leaf base and rhizome biomass in the interspecific treatment. Unlike the 2B treatment, ramet production of *B. articulata* in the 2T/2B treatment ceased from late autumn to spring.

In contrast, T. *orientalis* showed no significant reduction in biomass in the 2T/ 2B treatment cf the 2T treatment. Close to the end of the experiment, when growth rates increased, alive above-ground biomass per unit area in the 2T/2B treatment decreased slightly, and this reduction became more evident when expressed on a per ramet basis. Ramet production was also similar to the 2T treatment. Furthermore, total (final) biomass and the different biomass components, remained the same. It appears, therefore, that *T. orientalis* was not affected, in terms of growth, by interspecific interaction with *B. articulata*.

In comparing the two species, it is clear that the growth of *T. orientalis* was significantly greater than *B. articulata*. The alive above-ground biomass of *T. orientalis* per unit area was higher throughout most of the experiment, except during late winter when the seasonal leaf senescence of *T. orientalis* occurred. During this senescence phase *B. articulata* showed a slight increase in rate of above-ground growth. However, at the onset of spring, above-ground biomass of *T. orientalis* rapidly overtook *B. articulata*. The number of *T. orientalis* ramets was consistently greater (up to 3 times as many) than in *B. articulata*. On a per ramet basis, above-ground biomass of *B. articulata* was significantly greater from mid-winter to mid-spring, however, even though *T. orientalis* had considerably more ramets, its biomass per ramet equalled that of *B. articulata* by the end of spring. The increase in above-ground growth of *B. articulata* during winter suggests that it may be responding to an increase in resource availability as leaf growth of *T. orientalis* is reduced. Light availability may have increased as a greater proportion of the broad strap-like leaves of *T. orientalis* became senescent. Once leaf growth of *T. orientalis* increased dramatically during spring, however, there was a reduction and subsequent levelling of *B. articulata* leaf growth.

Flower production in *B. articulata* was significantly reduced in the interspecific treatment. This appears to be a response to lower resource availability, a trait commonly seen in the field (Chapter 4). Resource partitioning in this situation is balanced in favour of maintaining vegetative growth rather than the 'luxury' of producing many inflorescences. However, a completely different strategy was displayed by *T. orientalis* which dramatically increased its flower production in the interspecific treatment. It appears that in a interspecific competitive situation, *T. orientalis* is able to

a) maintain vegetative growth at similar rates to the intraspecific treatments, and b) increase the production of inflorescences (by approximately 250%). This increase in flower production may be solely due to the presence of *B. articulata*, rather than a response just to higher plant density and reduced resource availability. A strategy such as this is typical of competitive-ruderal species (Grime, 1979), which have rapid lateral growth rates, high seed production, litter accumulation, shading canopy of leaves, and well defined peaks of leaf production coinciding with period(s) of maximum potential productivity.

Below-ground biomass of *T. orientalis* was significantly greater than *B. articulata* in the interspecific treatment. Even though above-ground biomass production by *T. orientalis* was subdued during winter, ramet production of this species increased dramatically during early-mid winter. Rhizome extension and subsequent ramet production in *B. articulata* did not increase from the end of autumn to the beginning of spring. It appears that *T. orientalis* significantly reduced *B. articulata* below-ground growth by limiting space and/or nutrient availability. A distinct advantage of *T. orientalis* is its ability to rapidly reproduce vegetatively and expand into open areas if conditions are ideal. Its large, rapidly extending rhizomes are capable of forming a dense subsurface 'mat' of growth which potentially excludes competitors (Finlayson *et. al*, 1983).

There are several characteristics evident from this and previous research (Grace and Wetzel, 1982; Finlayson *et al*, 1983; Grace and Harrison, 1986), that give *T. orientalis* a competitive edge relative to *B. articulata*. Firstly, exclusion mechanisms in established monospecific stands, exhibited by both species, are typically attributed to the dense tangle of rhizomes limiting the rooting space available to colonisers, and the tall dense canopy (especially *T. orientalis*). Accumulation of dead organic matter also aids the exclusion of other species. It is uncommon to see seedlings of either species establishing in dense stands. Growth in these stands is exclusively via rhizomatous expansion. The clonal growth pattern, and distribution of resources between attached ramets, lessens the impact of both intraspecific and interspecific interactions at such high densities. This probably enables the persistence of *B. articulata*, albeit at low densities and poor growth, amongst *T. orientalis* in zones of overlapping distribution (Chapter 4). The seasonal relaxation of *T. orientalis* growth in the winter could also act to prevent complete displacement of *B. articulata*.

When sparse stands of *B. articulata* or open areas are colonised by *T. orientalis*, the establishment and suppression mechanisms of the competitive-ruderal nature of *T. orientalis* becomes a distinct advantage. The most common situation in which interspecific interaction and co-habitation will occur is when the low density leading edge or perimeter of stands of each species meet on relatively open ground. Depending on the environmental parameters, both species will grow and produce new ramets, with *T. orientalis* typically becoming the dominant species. Alternatively, seedlings of *T. orientalis* may emerge within relatively open stands of *B. articulata* and spread via ramet production. In this situation, *T. orientalis* tends to become less dominant (Chapter 3). Seed production and viability in *T. orientalis* is extremely high (Chapter 3; Prunster, 1941; Krattinger, 1975) and will germinate readily in open areas of high light intensity, and can also germinate and establish under 20 cm of water (Chapter 3; Sharma and Gopal, 1979; Yeo, 1964). *B. articulata*, however, has a comparatively small but viable seed set and germination rates are very low (Chapter 4). Once *T. orientalis* seedlings have established, rapid rhizomatous growth begins within the first year with the rate of spread dependant on the substrate space available under favourable conditions. Flowering may also commence at the end of the first year, furthering the potential for new germinants. Given further expansion by *T. orientalis*, tall, dense spring growth results in canopy dominance during the summer and early autumn, ensuring replacement of carbohydrate reserves which allow spring growth and canopy dominance next season (Finlayson *et. al*, 1983). The vegetative growth rates of *B. articulata*, however, are lower and therefore takes considerably longer to form a dense canopy (Chapter 4).

As with intraspecific interactions, the intensity of interspecific interactions between *T. orientalis* and *B. articulata* in the field is likely to vary both spatially and temporally. Changes in nutrient availability, water regime, sediment structure, and light availability over a spatial gradient and in time, would influence the nature and outcome of interactions between the two species. Of particular interest is the effect of water regime, and the factors that vary with it, and how these determine the intensity and degree of competitive displacement. Previous work has indicated that morphological and physiological differences between species are responsible for different outcomes along a water regime gradient (Grace and Wetzel, 1981; Grace and Wetzel, 1982; Grace, 1985). Better competitors at the shallow end of the gradient had greater leaf area to maintain shading, whereas the better competitors at the deeper end of the gradient had taller leaves and larger rhizome storage. At intermediate depths, the species were able to coexist.

In monospecific stands both *T. orientalis* and *B. articulata* have similar water regime ranges (Chapter 4). However, where they co-occur, *T. orientalis* is typically lower on the elevational gradient. This is not necessarily the outcome of changes in competitive ability with water regime. Given the ephemeral nature of many of the Swan Coastal Plain wetlands, exposed sediment or shallow water near the leading edge of a *B. articulata* stand during the drier seasons, provide ideal conditions for *T. orientalis* invasion. The density of existing *B. articulata* stands prohibits seedling establishment, whereas establishment higher on the gradient above *B. articulata* is limited by the threat of desiccation and or shading by fringing tree vegetation. Once established at lower elevations, *T. orientalis* may expand further down gradient or invade the existing *B. articulata* stand.

8: Response of *Melaleuca preissiana* Populations to Altered Water Regimes

8.1 Introduction

The response of fringing tree populations to altered water regimes is of great relevance to the management and conservation of wetland vegetation. As described in Chapter 4, tree species such as *Melaleuca preissiana, M. rhaphiophylla, Eucalyptus rudis* and *Banksia littoralis* are integral components of wetland vegetation on the Swan Coastal Plain. Clearing near the shores of wetlands has resulted in the loss or severe degradation of fringing tree vegetation at most wetlands. The future survival of remaining tree vegetation is especially dependent on wetland water regimes. Dramatic changes in water levels, such as flooding at Yangebup Lake, can lead to the death of fringing tree species, and reduce the potential for further natural recruitment.

Unlike sedge and rush vegetation, tree species seldom reproduce vegetatively; the production of viable seed, and the establishment of seedlings, are crucial for the long-term survival and viability of tree populations. Recruitment will occur naturally under suitable conditions, and large scale or mass recruitment generally occurs when there is a temporary or long-term change in prevailing conditions, eg. a disturbance such as fire, or a moderate change in water regime. The potential for seedling recruitment should be maintained if fringing tree populations are to be preserved.

Banganup Lake has one of the most significant populations of *Melaleuca preissiana* on the Swan Coastal Plain. Located on the Jandakot groundwater mound, it is part of the Beeliar wetland chain. The lake is a shallow depression in the centre of 253.7 hectares of bushland that was leased to the University of Western Australia in 1970 as a marsupial breeding station. This area is surrounded by a high wire mesh fence inside which grazing pressure is monitored and kangaroos culled. This marsupial reserve has preserved the banksia woodland catchment area of Lake Banganup and there are no artificial drainage lines or industrial effluent inflow. The lake is seasonally dry in summer with little recharge of groundwater after rainfall ceases. Generally, recharge occurs until November each year (Clay 1989, pers comm.).

Lake Banganup has an area of 33 ha and is largely covered by dense stands of *Baumea articulata*. It has fringing vegetation of extensive bands of *M. preissiana* mixed with some *Eucalyptus rudis, Banksia littoralis* and *M. teretifolia*. At higher elevation there is a surrounding woodland of predominantly *B. menziesii* and *B. attenuata* with some *Allocasuarina fraseriana* and *Eucalyptus marginata*. Mixed with this woodland, at slightly lower elevations, are *B ericifolia* and a few old *M. preissiana* trees.

The predominant fringing tree species at Banganup, *Melaleuca preissiana* Schau (common name moonah), has a tree form that is typically 9-13 m high. It occurs on the Swan Coastal Plain and valleys in the Darling Scarp, bordering watercourses and winter wet depressions, 1-2 m above depressions where water may lie for several months of the year. The species distribution extends around the coast of WA from Eneabba to Fitzgerald River National Park, with scattered occurrences well inland. It flowers from November to January (Marchant et al.1987).

In March 1977 the Banganup Lake reserve including the lake was subjected to a bushfire in which the current stands of *M. preissiana* survived (pers comm. B. Clay 1989). Since the fire there has been mass recruitment of *M. preissiana* in a band close to the north, northeast and eastern margin of the lake.
This study investigated:

- the age structure and distribution of the *M. preissiana* population at Banganup Lake
- the relationship between the distribution of *M. preissiana* and water level regimes.
- the water regime, and other factors, required by this species for establishment.
- the water regime required for the continued survival of the mature stands of this species.

8.2 Methods

8.2.1 Establishment of Field Transects

The distribution of *Melaleuca preissiana* at Banganup Lake was mapped to determine the best locations for field study (Figure 8.1). Two transects were established during the summer of 1989 to document the position of *M. preissiana* relative to the elevational gradient extending away (at right angles) from the wetland centre. Transect 1 (87m) was established on the eastern side of the lake and transect two (50m) was on the northern side of the lake running in a north-south direction (Fig. 8.1). Trees within one metre either side of the transect line were included in the transect. The diameter at breast height, vigour (dead, low vigour, diseased etc), and height of each *M. preissiana* tree was recorded along each transect. Changes in community structure and composition were also noted as were evidence of recruitment of *M. preissiana* .

8.2.2 Determination of Age Structure of **Melaleuca preissiana** *Population*

Two spatially distinctive age groups became apparent from the mapping of *M. preissiana* distribution (Figure 8.1). To establish the age of the apparently younger band of *M. preissiana* close to the lake edge, four saplings (two from transect one and two from transect two) were felled in 1989 and six saplings (three from transect one and three from transect two) were felled in 1992.

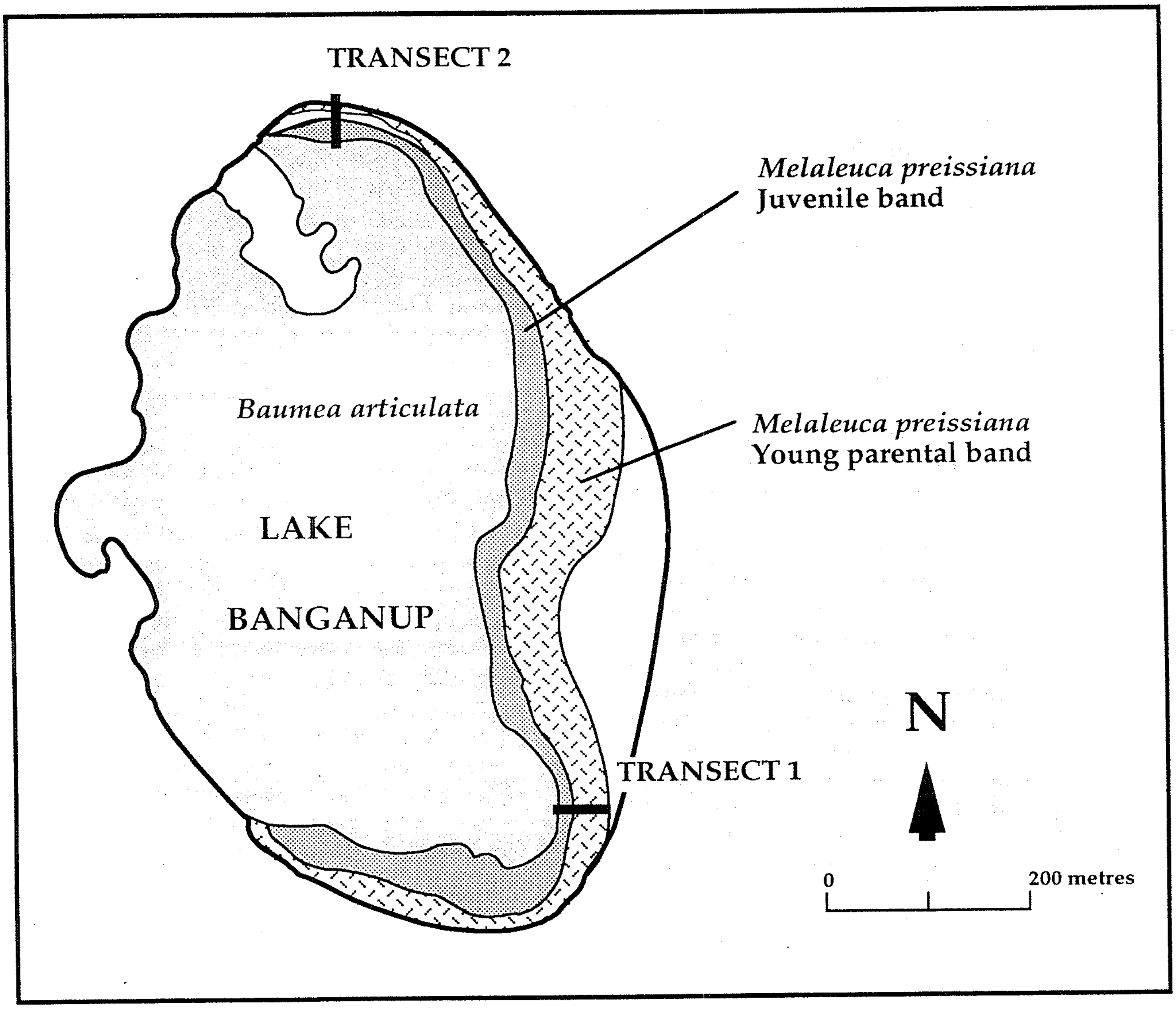


Figure 8.1: Distribution of juvenile and young parental*Melaleuca preissiana* and the location of the study transects at Banganup Lake.

Whole trunk cross sections were taken for analysis of tree ring structure. For each section, the cross-sectional surface was sanded smooth and then planed using a Norris Pattern Panel Plane (38 cm length). Planing continued until the vessels showed clear and dark. Final surface finish was performed with a Norris Pattern Mitre Plane (15 cm length).

In July 1991, to establish the age of *M. preissiana* trees in the second band from the lake edge (referred to in this report as the young parental trees), tree coring was performed on selected trees on transect 2. Sampling procedures followed the standard techniques as described by Stokes and Smiley (1968), Ferguson (1970) and Fritts (1976). Trees were cored at or near the standard sampling height of 1.3 m, taking into consideration any visible fire scarring. Cores of 25 mm triangular section were collected from 11 trees. The cores were cut with a specially adapted electric chainsaw with a 25 mm wide chain bar. The end of the chain bar is the major cutting surface, and the angle and position of the three 'cuts' required to extract a core, is controlled by a cutting guide that is attached to the tree. The cores were sanded and planed as for the whole trunk cross sections.

8.2.3 Melaleuca preissiana *Seedling Establishment Trials*

Germinability of seeds

Fruits were collected in June 1991 from four old parental *M. preissiana* trees in the vicinity of transect 2. The fruits were dried in a drying oven (45°C) for 24 hours to release the seeds.
The seeds and chaff were placed in distilled water overnight to imbibe water after which time the chaff was recognisable and subsequently removed.
Percentage germinability was determined by noting the number of germinated seeds from the total placed in petri dishes on filter paper (dampened with a solution of distilled water and Previcur fungicide). These dishes were kept at room temperature (approximately 18°C) and the number of germinants counted after three weeks.

Field trial sites and sections of plots

The apparent mass recruitment of *M. preissiana* trees (juvenile band), and the possibility of germination being linked to water regimes and fire events, determined the experimental design of the field trials. Four sites ranging from the lowest level near the lake (13.1 mAHD, highest soil moisture level) to a higher elevation under the parental *M. preissiana* trees (14.0 mAHD, lowest soil moisture level) were established along transect 2 (Fig. 8.2).

Site A:	cleared area (represent conditions after fire) of the lakebed vegetation (*Baumea articulata*) adjacent to juvenile band of *M. preissiana*. Wettest conditions.
Site B:	under the canopy of the juvenile *M. preissiana* . There was no open plot at this site. Shaded and wet conditions.
Site C:	clear area between the juvenile band and the supposed parental band of *M. preissiana*. Open and drier conditions.
Site D:	under the canopy of the supposed young parental band of *M. preissiana* trees. Shaded and driest conditions.

At all four sites, a 2 x 1 m exclosure plot of one metre high bird wire (except for site B due to insufficient space) and a 2 x 1 m open plot were established to determine if predation of germinants is of significance (Fig. 8.2). Each plot was divided into four sections of three treatments and a control;

- a control section not sown with seed and no clearing of litter.
- a section cleared of litter, with 0.45g of scattered *M. preissiana* seeds and chaff.
- a section that has been subjected to burning of litter to form an ash bed, with 0.45g of scattered *M. preissiana* seeds and chaff (after ash became cool).
- a section with litter intact, and 0.45g of *M. preissiana* seeds and chaff scattered thereon. This was done in an attempt to establish if allelopathy could be a factor in the inhibition of seedling germination.

The trial was established during late summer/autumn 1990, a time when seed fall and fires naturally occur. Seed was sown on the trial plots, rather than assess *in situ* seed germination, so that the experiment could commence with a seed bank of known seed quantity and composition. Germinants were counted fortnightly for 6 months, and then every 3 months for a further 6 months.

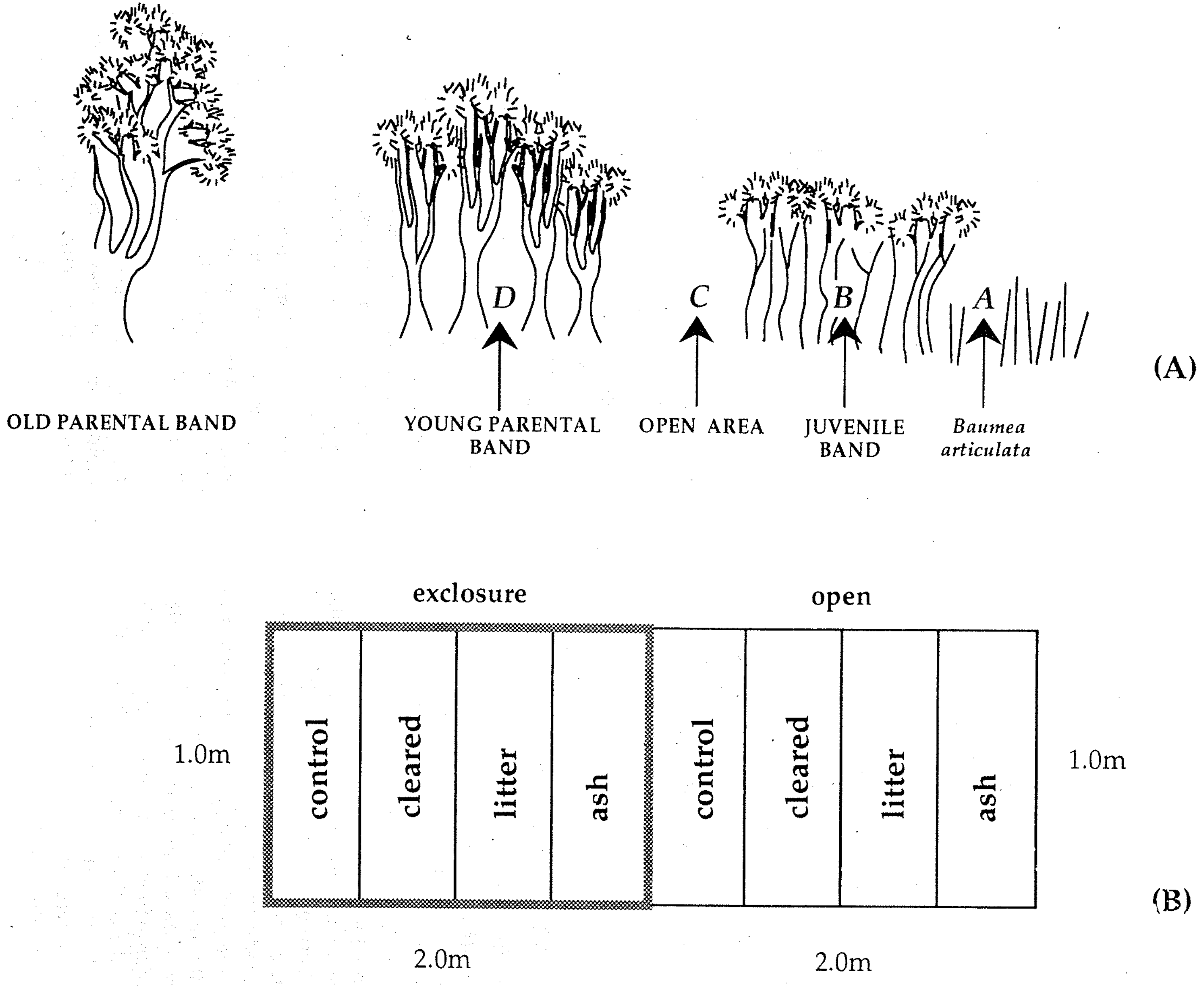


Figure 8.2: Location of the field germination plots relative to the different-age stands (A), and the design of the plots.

8.3 Results

8.3.1 Distribution of Melaleuca preissiana *along Elevational Gradient*

Transect 1 (87 m) had a shallower elevational gradient than transect 2 (50 m), and consequently the width of the littoral zone (area of inundation and waterlogging) was greater (Fig. 8.3 cf. Fig. 8.4). Starting from the highest point on the transect, large (referred to as old parental) individuals of *M. preissiana* were found scattered amongst *Eucalyptus rudis* and *Banksia littoralis* with a dense understorey of *Kunzea ericifolia* and *Astartea fasicularis* (Fig. 3). These old parental *M. preissiana* trees were up to 1.7 m DBH and 15 m in height, but few in number, and occurred at an elevation of 18m or more and must have established at a time of considerably higher groundwater and presumably higher rainfall levels. Further down gradient, the younger (smaller DBH and height) *M. preissiana* (young parentals) formed a dense closed canopy forest over most of the transect. The height and DBH of the these trees was relatively uniform. Several dead trees and trees of poor vigour were found in this stand, all of which were relatively small in stature. Due to shading by the overstorey, the understorey was comprised of a sparse cover of *Lepidosperma longitudinale*. Adjacent to the young parental *M. preissiana* was a relatively narrow stand of younger *M. preissiana* (juvenile band). *Baumea articulata* occurred in the open area beyond the transect, and as a sparse understorey to the juvenile *M. preissiana* and the low limits of the young parental *M. preissiana*.

Transect 2 had a steeper elevational gradient and narrower stands of young parental and juvenile *M. preissiana* (Fig. 8.4). At the highest point on the transect, old parental *M. preissiana* of large stature were once again found scattered amongst *Eucalyptus rudis* and *Banksia littoralis* with an understorey of *Astartea fasicularis* . The band of young parental *M. preissiana* also formed a dense closed canopy but was much narrower in width compared to Transect 1. No dead or low-vigour trees were found in the young parental band, even though variation in height led to some trees being shaded by the canopy formed by taller trees. The narrowness of the band may allow more light to penetrate from the sides. An open area separated the young parental trees from the juvenile *M. preissiana* which also formed a narrow band. *Baumea articulata* occurred in the open area beyond the transect.

8.3.2 Age Structure of Melaleuca preissiana *Population*

The 1989 cross sections of the juvenile trees at Transect 1 and 2 and the 1991 cores of the young parental trees at Transect 2 revealed that DBH could not be correlated with age (Table 8.1). The DBH of the juvenile trees felled in 1989 ranged from 3.7cm to 9.2cm with all the trees being approximately 12 years old. The DBH of the juvenile trees felled in 1992 ranged from 6 to 8.5 with all the trees being 15 years old. The Banganup Lake reserve caretaker Mr B. Clay confirmed that the juvenile band of *M. preissiana* had germinated after a severe fire during March 1977 which had burnt or scorched the canopy of the young parental trees and the *B. articulata* of the lakebed. The DBH of the young parental trees on Transect 2 ranged from 19.6cm to 39.8cm with the 1991 cores indicating an age of approximately 60-66 years (Table 8.1). As an approximately 66 year old tree has a DBH of 20-40cm then an old parental tree with a DBH of 1.7m, may be approximately 200 years old or more.

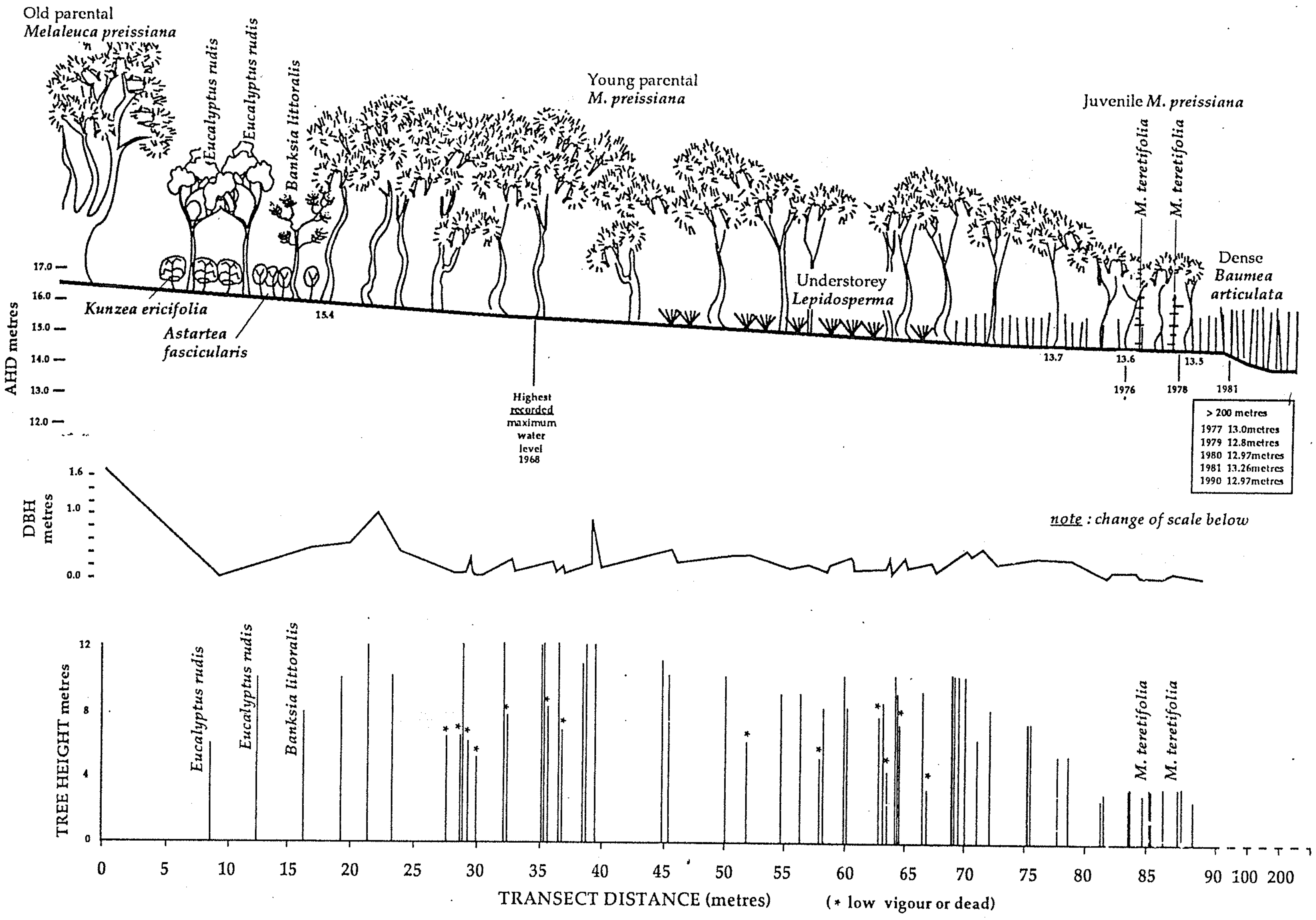


Figure 8.3: Profile diagram of transect 1 depicting elevational gradient, position of different-aged stands, change in tree diameter at breast height (DBH) and tree height, and location of maximum water levels during relevant years.

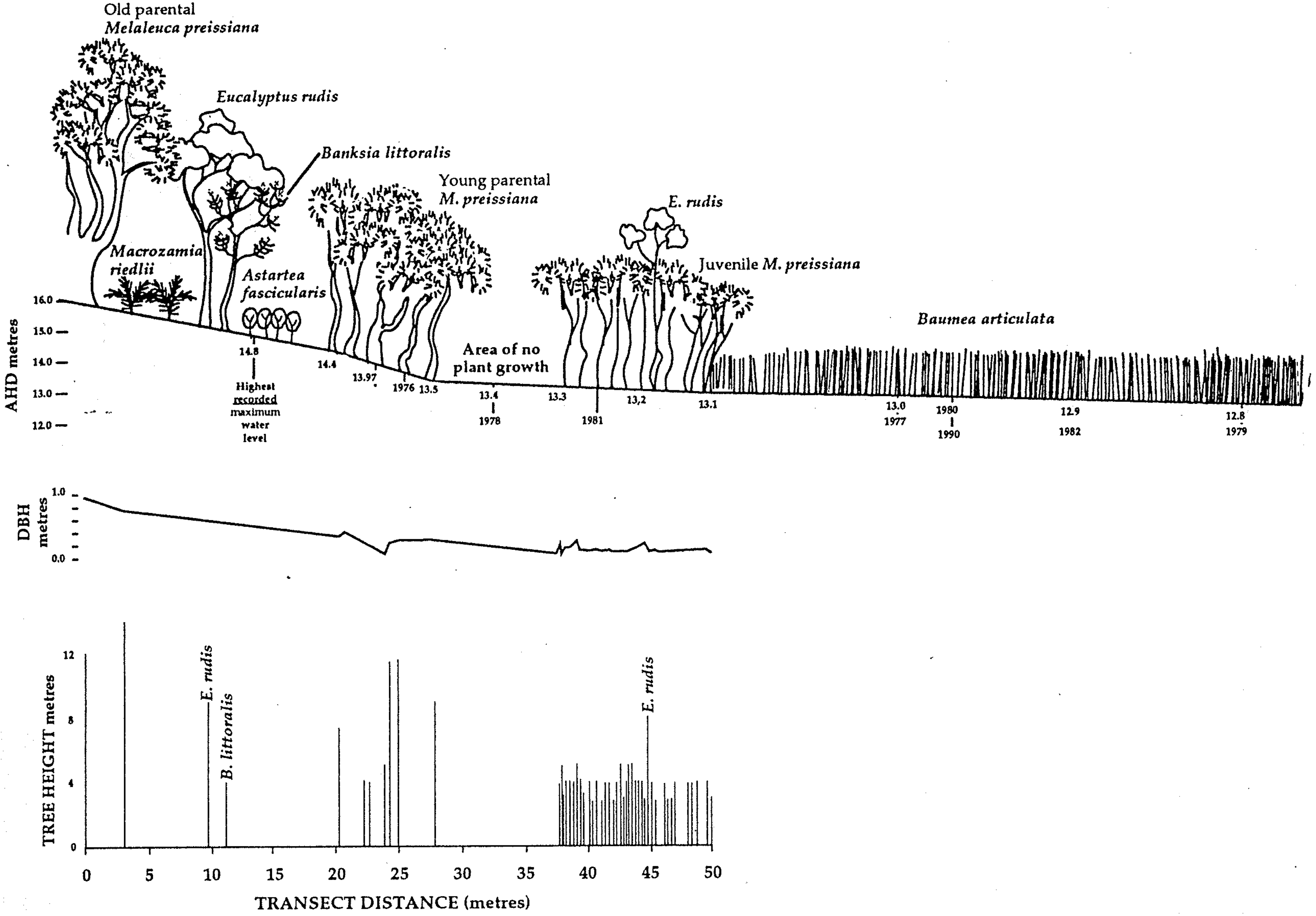


Figure 8.4: Profile diagram of transect 2 depicting elevational gradient, position of different-aged stands, change in tree diameter at breast height (DBH) and tree height, and location of maximum water levels during relevant years.

Table 8.1: Number of annual rings determined from cross sections and tree cores of *Melaleuca preissiana* trees and saplings at Banganup Lake.

Cross sections of 1989 felled saplings from juvenile band.

Tree no.	No. rings	DBH cm
T1.1	12	8
T1.2	10	4
T2.1	12	8
T2.2	12	6

Cross sections of 1992 felled saplings from juvenile band.

T1.1	15	7
T1.2	15	7
T1.3	15	7.5
T2.1	15	6.5
T2.2	15	6
T2.3	15	8.5
T1.4 recent juvenile	8	3

1991 Tree core approximate annual ring number of young parental band

YP.1	67, 69 base	28
YP.2	60	39.8
YP.3	60	23.4
YP.4	66	19.6
YP.5	65	-
BL.1	61	-
BL.2	Not to centre	-
BL.3	66	-
BL.4	61	-
BL.5	66	-
BL.6	66, 70 base	-

DBH = diameter at breast height. The recent juvenile was sampled, for comparison, from an elevation just above the juvenile band. 'Not to centre' refers to a misaligned core that did not go through the centre of the trunk.

Apart from the three well established age groups outlined above, very little recruitment was evident on the transects and elsewhere. Notable exceptions were young saplings of apparent uniform age that had established in the open area between the young parental and juvenile trees adjacent to Transect 2. One whole trunk section from these saplings was examined in 1992 and estimated at 8 years old with a trunk diameter of 3 cm. However these saplings were very sparse and did not represent a mass recruitment such as the juvenile band, but rather, can be considered as 'background' recruitment.

8.3.3 *Relationship between Water Regime, Age and Distribution*

The highest recorded water level (1968) reached well into the young parental stand of *M. preissiana* on Transect 1 (Fig. 8.3). Subsequent maximum water levels have either reached the area of the juvenile *M. preissiana* or have not reached any part of the transect. The juvenile *M. preissiana* was centred on the 1976 and 1978 maximum water levels. The highest recorded water level reached well beyond the young parental band on Transect 2 (Fig. 8.4). Subsequent maximum water levels have reached beyond the juvenile M. *preissiana* and up to the lower limit of the young parental band. The 1976 and 1978 maximum water levels reached just above the juvenile trees.

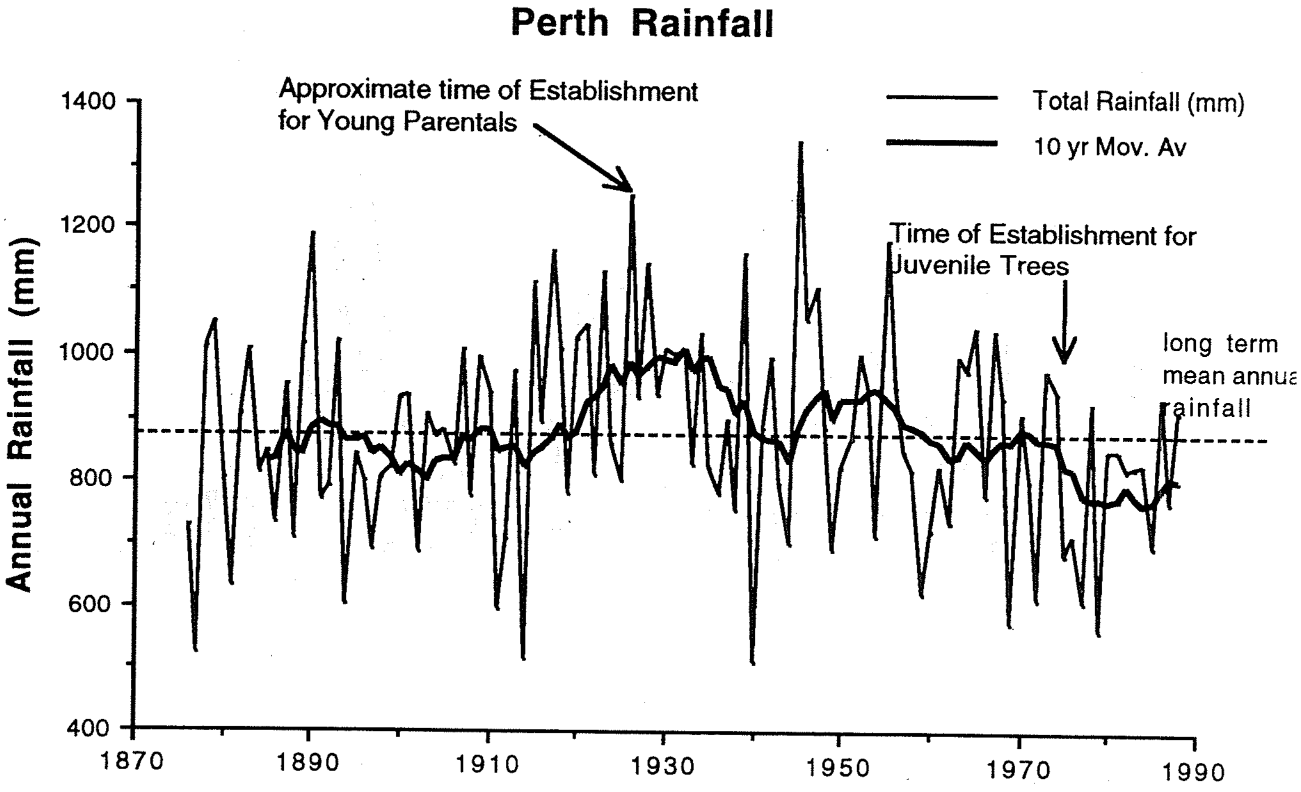


Figure 8.5: Perth annual rainfall showing estimated times at which young parental and juvenile *Melaleuca preissiana* established at Banganup Lake.

The young parental band established approximately 60-65 years ago (1925-30) when the rainfall was significantly higher (Fig. 8.5). Clearing for rural development occurred in Jandakot from 1890 onwards when the Jandakot Agricultural area was first established (Berson, 1978). This clearing combined with the high rainfall in the 1920s would have elevated the lake levels. Seddon (1972) noted that between 1894 and 1926 there was an increase in rainfall and a rise in water table on the Swan Coastal Plain which flooded market gardens and killed paperbarks.

The juvenile *M. preissiana* trees established in 1977 after a protracted period of declining lake levels and rainfall, leading to their establishment at a lower elevation. The fire that occurred in March 1977 would have provided an ash bed of high nutrient availability for the seed that would have fallen from the open fruit desiccated by the fire (Fig. 8.6). Average rainfall and moderate water levels ensured amble moisture availability for germination during late winter/spring 1977 without submerging the seedlings. Rainfall and water levels during the following year (1978) were greater, however the seedlings were not submerged and inundation occurred for 1 month only. This subsequent year of high water availability without prolonged inundation seems critical in allowing the seedlings to become established and attain sufficient height to avoid submergence.

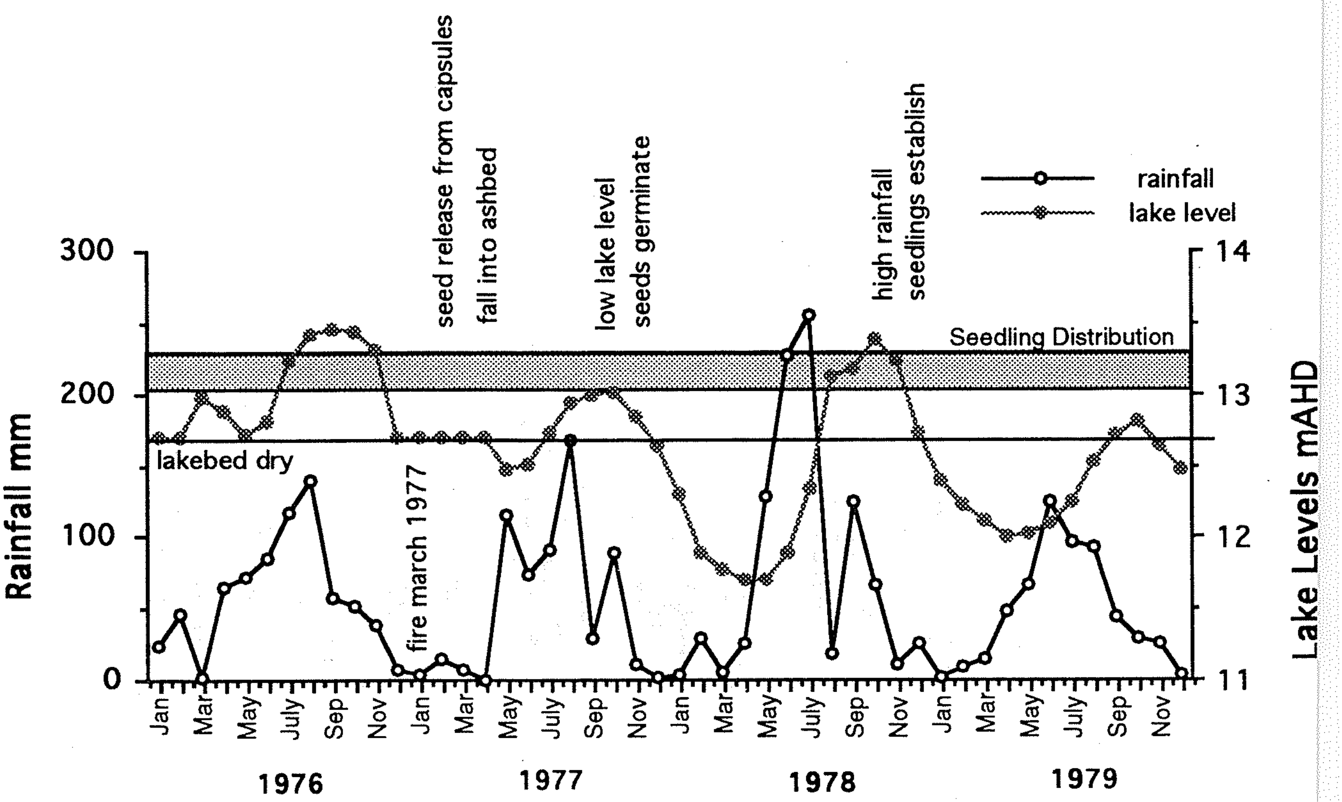


Figure 8.6: Comparison of rainfall and lake levels with sequence of events which lead to the establishment of the juvenile *Melaleuca preissiana* at Banganup Lake.

Further monitoring of lake vegetation in 1992 has revealed no further recruitment of bands of juvenile *M. preissiana* trees since these transects were established.

8.3.4 Seedling Establishment Trials

Germinability

There was 90 % germinability of the seeds collected from parental trees in 1991 and used for the field trials.

1991 Seedling Establishment Field Trial

There was no seed germination in Plot A or B due to rising water levels scattering the seed and submerging the plot treatments. There was no seedling establishment after water levels receded.

Seeds started to germinate in August at both site D and C, 2-4 weeks after being sown. Seeds germinated at the higher elevation site D beneath the young parental trees but were generally not as abundant as at the lower elevation site C (Fig. 8.7 cf. Fig. 8.8). The seedlings at site D survived for approximately 2 months (both exclosure and open plots) but not after the rain ceased in October 1990. The difference in elevation between the two sites (D and C) is approximately 50 cm, and although soil moisture was not determined, the surface soil at site C was visibly moist for a greater part of the year than site D. Seedlings at site C

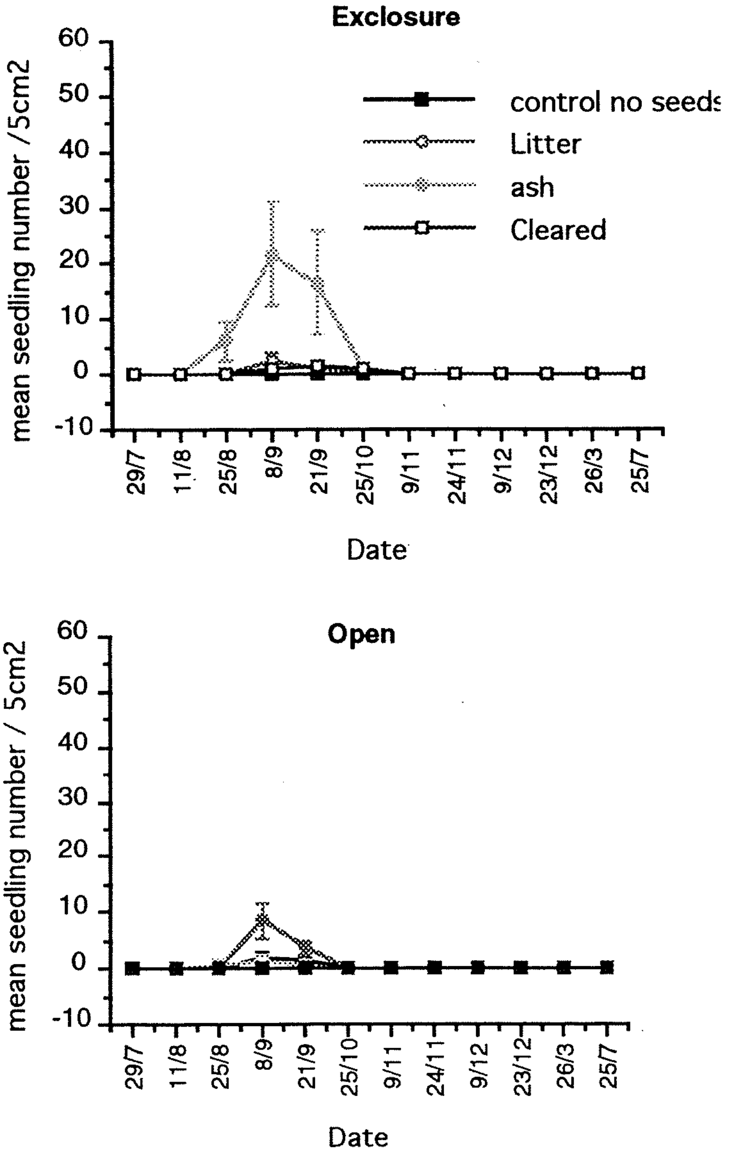


Figure 8.7: Mean seedling density in each of the treatments in the exclosure and open halves of seedling plot D.

open plots survived for a longer period (approximately 4 months) but no live seedlings were found at the end of the 1990/91 summer. Although seedling density was significantly reduced in the exclosure plots by the end of summer, seedlings survived until the end of the experiment. A visit to the sites during the winter of 1992 showed that these seedlings were still alive. These results indicate that grazing is a significant factor in seedling establishment and that the intensity increases (or selectivity decreases) over the summer months. Reductions in seedling densities in the exclosure plots however, indicate that soil moisture and light availability also have significant influence on the potential of seedlings to survive and become established.

At sites D and C, more seed germinated in the ash treatment than the other treatments or control (Fig. 8.7 and 8.8). At the drier, shaded site D, the seedlings in the ash treatment had a relatively low density (mean of up to 22 seedlings 5 cm^{-2} for the exclosure, 10 seedlings 5 cm^{-2} for the open plots). The open, moist site C had significantly higher seedling densities in the ash treatment (up to 48 seedlings 5 cm^{-2}). The seedlings in the ash bed were 10cm tall in Plot C after a years growth.

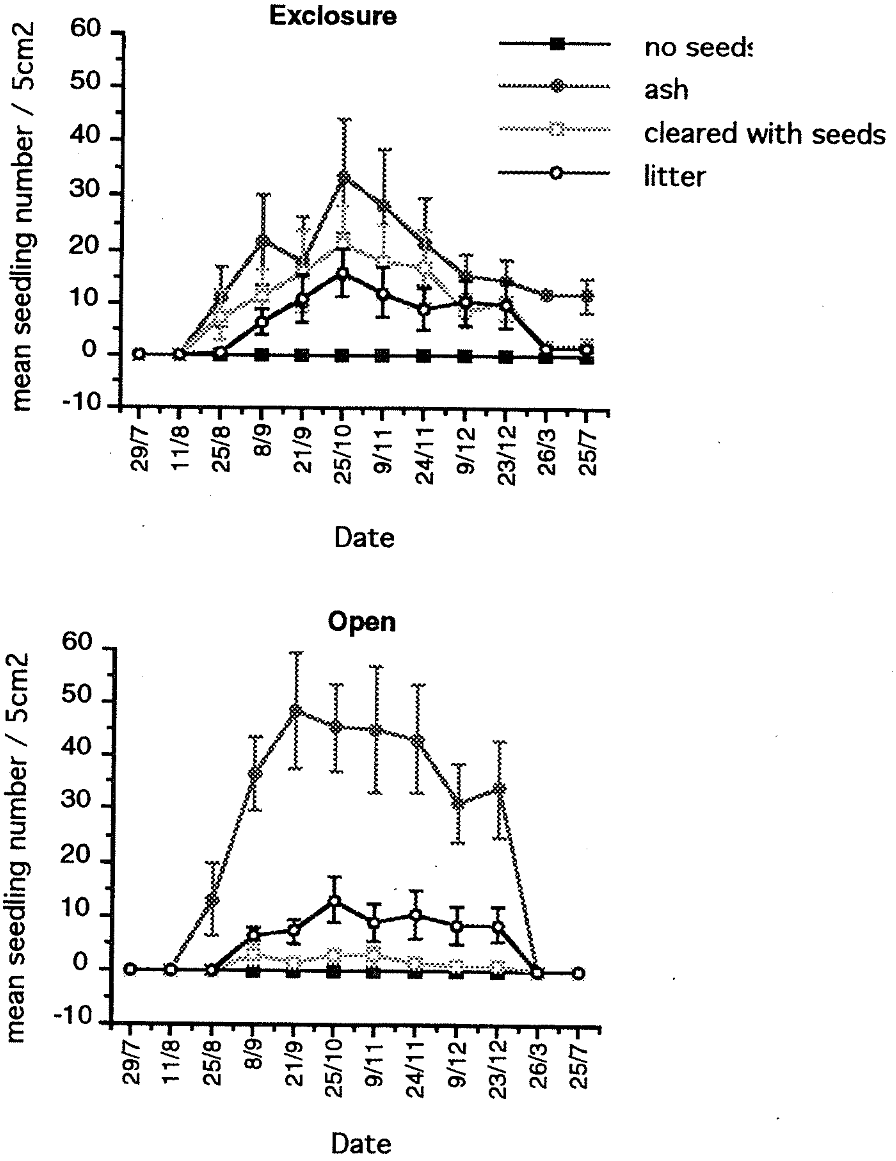


Figure 8.8: Mean seedling density in each of the treatments in the exclosure and open halves of seedling plot C.

The litter and cleared treatments at site D had no germination (open plot litter) or very low densities (< 3 seedlings 5 cm^{-2}, litter and cleared in exclosure, cleared in open plot) (Fig. 8.7). The litter and cleared treatments at site C however, had significantly greater seedling densities (Fig. 8.8). Seedling longevity was also greater at site C, with a proportion (approximately 3 seedlings 5 cm^{-2}) of the exclosure litter and cleared seedlings surviving after the end of the experiment. Therefore, allelopathy does not appear to exclude germination in field trials in plots under the parental trees or in the sections spread with *M. preissiana* leaf litter in the open area plots.

The unsown control plots at each site showed no germination. This suggests that there was no viable seed in the soil seed bank, or that the viable seed is naturally at very low densities. Low densities can be attributable to high seed mortality in the canopy and/or soil, or facultative flowering and seed set of parental trees (ie flowers and sets seed when conditions are conducive rather than each year) coupled with short seed longevity.

8.4 Discussion

The field observations and experimental results discussed in this chapter suggest that recruitment of *Melaleuca preissiana* does not occur frequently. The very structured nature of the age distribution of the Banganup Lake population implies that recruitment is episodic rather than a common occurrence. The greater longevity and different growth habit of this tree species, compared with the emergent sedges and rushes, is associated with lower rates of productivity, and sexual and vegetative reproduction. The relatively longer life and larger size of individuals dictates a low rate of replacement of parental stock. Therefore, species response (such as changes in distribution, productivity and reproduction) to a changing environment (altered water regime) occurs over a much greater period of time. The very structured sequence of *M. preissiana* ages down the elevational gradient at Banganup Lake represents the species response, in recruitment, to long-term change in water level measured over decades. In contrast, the vegetative reproduction of emergent sedges and rushes enables a more rapid response to a changing environment by altering distribution and productivity to suit the new conditions over months or years. Although the rate of response and the mechanisms employed are different, the response in spatial distribution is similar.

Rapid changes in environmental conditions, such as rapid and prolonged drawdown or flooding, will result in severe degradation of the vegetation if the species are unable to respond (alter distribution by reproduction etc) within the period the change occurs. For *M. preissiana*, and other fringing tree species, the slower response in population distribution and growth, is somewhat compensated for by greater plasticity of the individual, eg. alter root system distribution to 'follow' a declining water table. This is demonstrated by the persistence of old parental trees high on the elevational gradient at Banganup, despite decreasing water levels over the decades. However, if the changes are too rapid for the individuals to adapt to, then local extinction will occur at that point on the water regime gradient, or possibly the whole wetland.

The correlation between the time of establishment of the juvenile trees and the 1977 fire, provided an insight to the type of event/s that lead to successful mass seedling recruitment. The fire was followed by more than 2 years of at least average rainfall that provided sufficient soil moisture during seedling establishment, but did not elevate lake levels to the point where seedlings became inundated (for more than a month) or submerged. The fire scorched the canopy, drying and opening the fruits, and releasing the seed during early autumn. Burning of *Baumea articulata* would have reduced competition for light and provided a nutrient-rich ashbed upon which the *M. preissiana* seed would have fallen and germinated. The position along the elevational gradient where the most seeds germinated and seedlings survived, would have been determined predominantly by the water level regime at the time. The fire, therefore, may be viewed as playing a secondary role in ensuring greater light and nutrient availability, which enabled higher growth rates, seedling density and percentage survival.

This scenario is partially supported by the results of the field seedling establishment experiment. Although the effects of water availability and canopy shade could not be completely separated, soil moisture did appear to be the more significant factor in determining density and survival of seedlings. The higher nutrient availability in the ashbed treatments resulted in higher seedling densities than the unburnt treatments, irrespective of soil moisture regime. However, the ashbed did not appear to influence seedling survival. Clearing of the litter as apposed to burning it, resulted in lower seedling densities, indicating the beneficial effect of an ashbed.

The combination of conducive water regime and fire may have facilitated the mass recruitment of the young parental band 60-66 years ago as the rainfall, and presumably lake levels, were higher at that time. The relatively even age of the young parentals certainly suggests that they established as an earlier mass recruitment. Whether fire played a role in this event is difficult to determine. Fire was reported by Padovan (pers. comm 1992) to be a regular occurrence in the Jandakot area in summer in the 1940s-50s when fuel loads of litter accumulated to high levels (approximately every 6 years). Cores from the old parental trees could not be examined for fire scars as the coring equipment was unable to extract cores of sufficient length.

As discussed above, the temporal scale over which the response of *M. preissiana* populations to altered water regimes occurs, is in the order of decades. Changes in distribution are slow and essentially episodic in nature, and are the result of 'opportunities' for successful mass recruitment. Rapid, prolonged changes of high magnitude would be particularly detrimental to the survival of local populations of M. *preissiana* because conditions suitable for recruitment do not occur frequently enough to compensate for mortality or to change distribution to where conditions are more favourable. When such changes are beyond the adaptability of individuals, part or all of a population may be lost, depending on the population's distribution relative to the altered water regime. More opportunities for recruitment are likely to present themselves over the time taken for gradual changes (temporal and spatial) in water regime to occur. However, it may be that, irrespective of the rate of change, the population will remain viable in the long term, as long as the parental trees are able to survive and favourable conditions for seedling establishment remain at some part of the of the water regime gradient accessible to propagules.

9. Conclusions and Management Implications

Because of different land uses within wetland catchments of Swan Coastal Plain, human impacts on to water regime vary in magnitude and duration. Groundwater abstraction has the potential to reduce wetland water levels, whereas clearing of vegetation and urbanization have the opposite effect. This report is concerned with the response of wetland vegetation to changes in water regime, and the conclusions drawn from this study are discussed below under the primary research phases outlined in previous chapters.

9.1 Dynamics of Wetland Vegetation

There can be considerable variation in the water regime scenario between wetlands. In attempting to elucidate the response of emergent macrophytes to different water regimes, this report firstly documents and analyses the variability in species distribution within and between wetlands. Spatial differences in plant distribution between wetlands were identified as well as changes in species distribution over time within a wetland.

The Cause of Change

The temporal and spatial variation in vegetation attributes reflect the complexity of vegetation/environment interactions. Wetland plant communities, in particular the emergent macrophytes, are not permanent or fixed entities, but are assemblages of species coexisting under a given set of environmental conditions. It follows that a given type and distribution of wetland vegetation will persist as long as a suitable environment persists. Many of the changes experienced by the communities, such as altered water and nutrient regimes, are associated with urban and semi-rural development. In some cases the vegetation has been able to tolerate these changes with negligible compromise of conservation values. However, with further demand for developed land, the health of remaining wetland vegetation at an increasing number of outer-urban wetlands has become threatened.

Response to Short-Term Change

The impact of land-use changes on wetland plant communities depends on their species composition and the magnitude, rapidity and duration of the changes. The species are adapted to the seasonal and long-term changes in water regime which are typical of a Mediterranean climate. Emergent macrophyte vegetation is capable of responding rapidly to natural fluctuations in the environment, due to high productivity, rapid vegetative reproduction, high seed production, and tolerance of a wide range of water regimes. Seasonal changes in water level are, by definition, of short duration and therefore seldom have a detrimental effect as wetland communities are tolerant of, if not favoured by, these conditions. However, if the magnitude of the seasonal change is such that a site is inundated throughout the year, there can be a reduction in vegetation vigour due to prolonged sediment anoxia and reduced photosynthesis in deep water. In the reverse situation, a shift or reduction in range may result in no surface water and deeper groundwater levels, in which case plant water stress may develop during the summer months. The phenomenon of seasonal change implies that water levels revert back to a previous regime in the following year; where changes occur for more than a year, the potential impact on wetland vegetation is increased.

Response to Long-Term Change

Wetland plant community response to prolonged or long-term changes in water regime is characterised by a gradual shift (over 2 or more years) in distribution relative to elevation and mean water level. Under 'pristine' conditions on the Swan Coastal Plain, long-term changes in water regime due to altered rainfall and subsequently groundwater patterns, resulted in a gradual redistribution of plant species around a wetland rather than the loss or severe degradation of vegetation. Changes in species distribution in response to altered water regime is a reflection of the dynamic and resilient nature of littoral communities and should not necessarily be considered as 'degradation'. With the advent of European settlement, factors such as artificial surface water inputs, drainage, catchment clearing and groundwater abstraction have significantly altered seasonal and long-term water regime patterns. In many cases the regimes have been permanently altered and this has resulted in the loss, degradation and/or redistribution of vegetation. The fringing communities we see today reflect not only long-term changes (particularly in rainfall) within an undisturbed environment, but also the more rapid changes induced by human activities. Vegetation response to the cumulative affect of these changes may be in the form of a change in the position and timing of maximum productivity or a small shift in distribution only, or it may be a degradation of the community structure and local extinction of a species. In some wetlands extensive clearing of the immediate surrounds precludes the long-term adjustment of plant communities which usually follow increased water levels. It is only when significant disturbance of communities and reduction of species diversity occurs primarily through man's modification of the environment, that the result can be regarded as degradation.

Differences in Rate of Response

Not all species of wetland plant respond to changes in water regimes at the same rate. The larger, longer-lived species of wetland plants, such as the trees *Melaleuca preissiana, M. rhaphiophylla,* and *Eucalyptus rudis* , also respond to changes in wetland water regime, but their response is slower than that of emergent macrophytes and is hallmarked by episodic seedling recruitment events. Fringing tree species rarely or never reproduce vegetatively, and parent plants may grow for several years before flowering and setting seed. Conditions which favour seed germination and seedling recruitment may only occur periodically, for example under drawdown conditions on open areas of moist sediment, after fire when the cover is reduced and a nutrient-rich ashbed is present, when water levels are high enough to carry fallen seed to open areas with full sunlight, or a combination or sequence of these events. Once seeds germinate at a point on a elevational (water regime) gradient, the small, relatively slow-growing seedlings will survive only if they are not totally submerged the following year. This slower population response necessitates a broad physiological tolerance of changes in water regime. This is apparently the case for *M. preissiana* , which occurs over a wide range of water regimes.

9.2 Population Response to Water Regime

Characterization of the water regime requirements of emergent macrophyte species was the second phase of the study. Significant spatial and temporal variation in plant productivity and reproduction was found within populations, and was compared to the underlying water regime spatial gradient. The empirical relationships derived from field studies were then assessed by glasshouse experiments to examine directly the effects of different water levels on plant growth.

Water regime is the major determinant of distribution of emergent macrophytes, although other factors have a secondary role in influencing community characteristics. Depth, timing and duration of flooding and the length of the dry or exposed period are important parameters of water regime; which parameter is the most critical will depend on the elevation of the vegetation relative to water level.

Concept of a Preferred Water Regime

With respect to emergent macrophytes, maximum productivity and reproduction occurs when water levels are close to or at the sediment surface (within approximately ± 0.1 m from surface), other factors being equal. Experimental results suggest that such water levels could remain constant during all seasons without any detrimental impact on plant growth or survival. Conceptually, reduction in productivity and reproduction occurs only if water levels increase or decrease from this 'ideal' regime. Although plants may survive and reproduce at significantly wetter or drier regimes, their potential productivity is not achieved. If the water regime is changed to the point where the physiological tolerance of a species is reached, growth is significantly reduced and reproduction is unlikely.

As we have seen, wetland water levels are seldom constant, changing both seasonally and over the long-term (2 or more years), so that few emergent macrophyte communities experience the 'ideal' water regime discussed above. Seasonal variation in wetland water level may be 1 metre or more, whereas water levels may vary by 2 or more metres over the long-term. It was found, however, that plants located near the contour where mean lake level met the sediment surface, displayed the highest productivity and reproduction rates. This contour band is where seasonal water level range is an approximately equal distance above and below the sediment surface, and can be thought to represent a 'balanced' wet-dry cycle. Because this area seems important in defining plant behaviour it is appropriate to name it, and we suggest the 'optimum water regime zone'. The size of the zone would naturally depend on the littoral gradient. The duration of the wet and dry periods are not necessarily equal and depends on the timing and rate of groundwater rise, surface water inputs and evaporation.

It is important to note that, other factors being equal, the distribution of a emergent macrophyte species is generally greater than the area near the mean water level contour. Although the productivity of a species may be greatest at or near this contour, most species are able to tolerate 'wetter' and 'drier' water regimes. Within a single stand or population of *Baumea articulata* for example, plants or ramets at either end of the species distribution on the gradient will be experiencing different water regimes.

Response to a 'Dry' Water Regime
At the high (drier) end of a species distribution the duration of the dry period and the minimum water level are critical water regime parameters. If the minimum water level is too low for capillary rise of water to reach the roots of emergent macrophytes (water table > 0.8 - 1.0 m below the sediment surface), summer water stress and subsequent reduction in productivity becomes evident (Chapter 4). The length of time at which groundwater remains at or near this level is most critical. If the wetland water regime changed so that groundwater did not exceed this level for more than 3 -4 months each year, most species of emergent macrophyte would not survive for longer than 1 - 2 years (Chapter 4). This would result in the death of plants at the higher end of the species distribution, and a shift of the high end to a more favourable water regime further down-gradient. Such shifts in distribution may occur within 2 years due to the rapid vegetative expansion of these macrophytes.

Response to a 'Wet' Water Regime
At the lowest point of a species distribution, the duration and maximum depth of inundation are the most critical water regime parameters. The period of inundation increases with increasing maximum depth, and in some cases macrophytes are partially submerged for 12 months of the year. The impact of prolonged or permanent inundation on emergent macrophytes is very variable and depends on the species in question and other environmental variables (see below). On the Swan Coastal Plain, very few rushes and sedges have been observed to be permanently inundated by water over 1.0 m deep. Under a permanent inundation regime, maximum water levels may be higher than 1.0 m, however seasonal variation in water level usually results in the minimum being less than 0.1-0.2 m. In most cases, the low end of a species distribution is seldom permanently inundated, as even there a period of 'drying' (water level at or < 0.2 m below sediment surface) usually occurs during late summer/autumn. Inundation of the plant rhizosphere results in the depletion of oxygen within the sediment due to the low rate of oxygen diffusion in water. However, biological oxidation of organic material and chemical oxidation of organic compounds within the sediment exacerbate this oxygen depletion. Oxygen input via the atmosphere and as a by-product of photosynthesis may balance oxygen depletion. The greater the proportion of a plants leaf or stem area that is inundated, the lower the potential to diffuse oxygen down to the roots and rhizome. Although prolonged inundation reduces productivity, significant reduction in vigour and possibly death only occurs if the plants are permanently inundated by a minimum water level above 0.5 m (under oligotrophic-eutrophic conditions). Under such conditions, the low end of a species distribution shifts up-gradient to a position where the water regime is more favourable.

Differences Between Species
Significant differences were observed in the distribution of emergent macrophyte species relative to water regime within and particularly between wetlands. The difference between species in the field appeared to be due to a combination of factors such as different inundation tolerances, water quality, sediment type, and interspecific interactions. However, experimental results

(Chapter 6) supported the species distributions observed in the field, suggesting that field distributions are primarily due to water regime tolerance. The larger species such as *Baumea articulata, Typha orientalis,* and *Schoenoplectus validus* are more tolerant of deep, prolonged inundation, presumably because of their more extensive rhizome and root structure and their tall stature, allowing them to maintain a larger leaf area above water. Medium-stature species such as *B. juncea, Juncus pallidus* and *Lepidosperma longitudinale* were found in the experiment to be less tolerant of inundation, occurring mainly at shallow depths (< 0.5 m) where they tolerate longer dry periods. The small-stature species such as *Juncus articulatus, Isolepis prolifera* and *Eleocharis acuta* favour very shallow depths (< 0.25 m) or waterlogged conditions, no doubt because their height does not allow sufficient leaf area to be maintained above high water levels.

Phenology of Growth and Reproduction

Water regime also induced more subtle differences within and between wetlands such as differences in the phenology of growth and reproduction. There was generally a shift in the timing of ramet emergence, leaf elongation, flowering and seed production along the gradient of the littoral zone. This shift was more prominent along the wide littoral zone of shallow gradient wetlands. The period over which growth and reproduction occurred was significantly shorter in wetlands of lower nutrient status. In the case of *Typha orientalis,* an early summer/autumn period of above-ground biomass senescence occurred in a wetland of low nutrient status, but was absent at a wetland of higher nutrient status, where there was higher above-ground productivity.

Importance of Seedling Recruitment

Although rhizome extension and ramet production is the most common form of reproduction in emergent macrophyte species, seed germination and seedling establishment can be a significant form of recruitment during drawdown periods. If seasonal or long-term changes in water regime result in very shallow water or the exposure of open sediment, seed stored within the seed bank (usually from the previous year/s or the preceding flowering event), may germinate if conditions permit. A prolonged period of drawdown (> 3 months) is required to allow the germination and establishment of seedlings without total submergence. Furthermore, shallow water levels are required during the following year to allow the growing seedling to maintain leaf area above water level. Germination of seed and survival of seedlings only occurs in open areas that are not shaded. Experimental results indicate that *Typha orientalis* is the only species of those studied which is able to germinate and become established while submerged by up to 0.2 m of water. This has important implications for *Typha* invasion and management.

9.3 Factors Influencing Response to Water Regime

Variation in plant response between and within wetlands cannot be attributed to water regime alone. Therefore, the third phase of the study assessed the significance of sediment nutrient concentration, sediment texture and interspecific interactions in influencing plant response to water regime. Field results suggest that all three factors can be important.

Sediment Nutrient Concentration

Higher sediment nutrient concentrations where correlated with significantly higher emergent macrophyte productivity. *Typha orientalis* displayed a higher productivity apparently in response to elevated nutrient concentrations, than did *Baumea articulata.* The relationship between higher nutrient concentrations and increased productivity occurred irrespective of water regime, resulting in significant differences in species behaviour between wetlands of different nutrient status. A higher nutrient status was associated with a reduction in productivity (or increased senescence) at the lower point of a species distribution, only when coupled with prolonged inundation and severe sediment anoxia.

Sediment Structure

Sediment structure was also related to plant productivity. Productivity was lower on compacted, coarse sand and heavy clays, compared to sandy peat or peat sediments. Lower water holding capacity during dry spells at higher elevations and low organic matter content of sandy soils, are suggested as the causes of reduced productivity. Reduced rhizome and root penetration, high soil matric potential during summer, and reduced capillary rise from shallow groundwater, may be reasons for lower productivity on heavy clay sediments.

Interspecific Interactions

Interspecific interactions occurred at any point where two species were intermixed, but were most common at either the lowest or highest contours of a species distribution. In the field, the outcomes of interspecific interactions were observed as a reduction in above-ground standing biomass and productivity of one species. At the high end of a species distribution, shading by shrub or tree species was common. When comparing *Baumea articulata* and *Typha orientalis,* experimental results indicate than *Typha* is a superior competitor for rooting space and nutrients. *Baumea* below-ground biomass was significantly reduced in the presence of *Typha,* but no reduction was observed under high densities of *Baumea* alone. It is concluded that interspecific interactions may lead to a lower productivity and vigour of plants in a mixed stand, compared to a monospecific stand at a similar water regime.

9.4 Management Implications

The final phase of the study was the analysis of the research results in a management context.

Impact of Groundwater Abstraction

The dynamic nature of fringing emergent macrophyte vegetation implies considerable resilience to changes in water regime; this dynamic behaviour is demonstrated by large changes in fringing vegetation following altered water levels. The perceived threat of lower wetland water regimes, resulting from groundwater abstraction for public and private use, is not necessarily a significant one for all wetlands.

The rate at which water regime is reduced due to groundwater abstraction is a critical factor with respect to vegetation survival. Rapid (within 1 year), permanent reduction of mean water level does not permit gradual distribution and productivity changes, and is likely to result in degradation of the vegetation. If a permanent reduction in water level is unavoidable, it should be gradual, over 2 or more years depending on the magnitude of the reduction. The timing of seasonal drying of a wetland is not critical for vegetation, indeed most species will survive permanent, shallow inundation. Vegetative reproduction does not depend on length and timing of the dry period, but a favourable period is within the range November - June.

The minimum water regime requirements for survival of the most common species is waterlogged sediment, with the groundwater capillary fringe within 1.0 m of the sediment surface during the driest months. Those wetlands which already have a water regime similar to this are at the greatest risk of significant degradation after groundwater abstraction. Seasonal wetlands with a moderate period (< 7 months) of shallow (< 0.5 m) inundation, support the largest areas and most diverse fringing plant communities. A lowering of the water regime would most likely result in a gradual shift of the vegetation down-gradient. Predicting the response of vegetation to a specific groundwater reduction in a particular wetland can only be determined by assessing the current vegetation distribution relative to water regime at the wetland in question. The plants will survive with minimal degradation if the vegetation distribution occurs within the littoral water regime gradient (after groundwater level reduction) determined in this report (Chapter 4).

Impact of Increased Flow into Wetlands

While groundwater abstraction may lower the water regime of wetlands, catchment clearing and urbanisation often results in elevated water regimes, resulting in the mitigation of both effects at some wetlands. However, some seasonal wetlands have become permanent or semi-permanent due to runoff entering the water body and elevated groundwater levels. In most cases this has the effect of reducing the area of fringing emergent macrophyte vegetation.

Fringing tree populations, which typically occur at higher elevations than emergent macrophytes, can also be adversely affected by elevated water levels. Prolonged flooding (> 2 years) can lead to severe degradation of these populations and possibly local extinction. Their dependence on seedling establishment for recruitment results in a slow rate of change in population distribution relative to water regime. Although this study provides some indication of the water regime requirements of *Melaleuca preissiana,* further research on this and other tree species is required to determine their flooding tolerance and reproduction rates.

If vegetation is to be preserved at wetlands affected by increased inflow, drainage water may need to be diverted or flow reduced to allow seasonal drying to promote vegetation growth and reproduction. High nutrient levels in drainage water entering permanent wetlands poses a particular management problem as the cumulative effect of nutrient enrichment and prolonged flooding often results in severe degradation of the vegetation.

Influence of Climatic Pattern
Relative to long-term variation in rainfall, groundwater abstraction has generally less impact on wetland water levels, although it would exacerbate the effects of a series of low rainfall years. Abstraction does not affect all wetlands equally because it produces localised rather than widespread effects. Most of the significant changes in wetland vegetation distribution observed on the Swan Coastal Plain have been caused by long-term cyclic patterns in rainfall. High lake levels observed in the late 1960's reflected the above average rainfall of the time exacerbated by clearing and urbanization of wetland catchments. Water levels decreased as rainfall dropped below average during the late 1970's and early-mid 1980's. This rainfall pattern has occurred in the past and is likely to continue in the future and should be an important consideration in the management of wetland water levels.

Artificial Maintenance of Water Levels
Natural variation (seasonal and long-term) in water regime should be maintained, and artificial maintenance of water levels used only to mitigate the effects of abstraction or increased artificial inflow. This would allow rainfall patterns to determine the variability in water depth. However, alterations to rainfall patterns as suggested by models of climatic change, need to be considered.

Water regime criteria developed for the management of artificial maintenance should include a period of late summer-autumn drying, the timing of which is probably more critical to macroinvertebrates (Balla and Davis, 1992) than to vegetation. The distribution, vigour and composition of wetland vegetation should be considered as biological indicators of required water regime, of the outer extent of a wetland, and of the success of water regime management.

Implications for Damplands
Generally, species composition is the same at seasonal and permanent wetlands, although not all the major species will be present at any one wetland. However, the structure and extent of the vegetation relative to the wetland basin can be very different. Some seasonal wetlands and damplands do not have a distinct fringe of vegetation and may support macrophyte, shrub and tree species over the entire basin. The response of this type of vegetation to altered water regimes was not covered in this study, but some aspects would be similar, such as emergent macrophyte distribution, productivity and survival relative to water depth. These damplands are characterized by a relatively dry water regime, with only waterlogged soil or a short period (generally < 2 months) of shallow (< 20 cm) surface water. Therefore, a relatively small reduction in water level due to groundwater abstraction could induce summer water stress of emergent macrophytes. Further research is required on the impact of drawdown on damplands to determine quantitative water regime criteria.

Invasion of Typha orientalis
Typha orientalis is often considered an introduced, invasive aquatic weed that replaces native species of emergent macrophyte, presents a fire hazard, chokes drainage channels, and encroaches on waderbird habitat.

At the wetlands included in this study, *Typha orientalis* had the same distribution relative to water regime as *Baumea articulata* (and other larger native emergent macrophytes), suggesting that these species can and do occupy the same habitat niche. *Typha* can colonize a wetland via airborne seed, or seed floating down drainage channels. Generally the seedlings can only establish on bare, open (unshaded) sediment that is either moist or inundated by at most 20 cm of water. Given the wide distribution of *Typha* on the Swan Coastal Plain, there is significant potential for any wetland to become colonized. Dense, vigorous stands of *Baumea* are unlikely to allow the establishment of *Typha* seedlings.

Once established, *Typha* is capable of rapid vegetative reproduction. Disturbed, nutrient-enriched wetlands or sparse stands of native species are quickly invaded. At some wetlands *Typha* is the only emergent macrophyte present in significant numbers, and represents valuable fauna habitat (eg. Herdsman Lake).

The best means of controlling *Typha* invasion is the retention of existing dense, vigorous populations of *Baumea* by maintaining a favourable water regime and limiting the import of nutrients. Control of *Typha* by altering water regime (eg. increasing maximum depth and duration of flooding) is also likely to have a deleterious effect on the native species present. This method would only be applicable in disturbed wetlands where *Typha* is the only remaining species. Cutting the stems underwater during the growing season is a control method practiced in the Northern Hemisphere, but is only practical for small areas and would need to be repeated each year. Further research on the applicability of the cutting technique is required.

The Setting of Water Regime Criteria

The field studies showed that there are two aspects from which wetland plant water regime requirements can be viewed: 1) the water regime required to maintain current vegetation distribution, composition and vigour through vegetative reproduction; and 2) the water regime required to promote seedling germination and recruitment. The regimes at many seasonal wetlands support both processes, but successful seedling recruitment is rarely an annual event as the required water regime, sediment and light conditions may occur infrequently. Although vegetative reproduction is the major mode of population maintenance, in order to foster genetic diversity within macrophyte populations, management should propose water regimes which permit periodic seedling recruitment. This is especially important for fringing tree species which reproduce only through seedling recruitment.

Given the variability in macrophyte distribution and productivity observed in this study, it is suggested that wetland water regime criteria are set for individual wetlands or groups of similar wetlands. Sufficient scope should be incorporated in the criteria to allow for seasonal and long-term fluctuation in water regime and future revision should situations change.

At those wetlands where the threat of water level reduction is significant, emphasis should be placed on the setting of minimum water level criteria to suit the most drought-susceptible species. Parameters that should be considered are absolute minimum, preferred minimum, and maximum frequency and duration of any breach of the preferred minimum.

The criteria for wetlands experiencing elevated water levels should emphasize maximum limits which favour the most flooding-intolerant species. Of increasing concern are fringing tree species. Although equally tolerant of waterlogging as some sedges and rushes, they are less resilient due to their slow recruitment, as this limits the rate at which the distribution of the population can adjust to a changing water regime.

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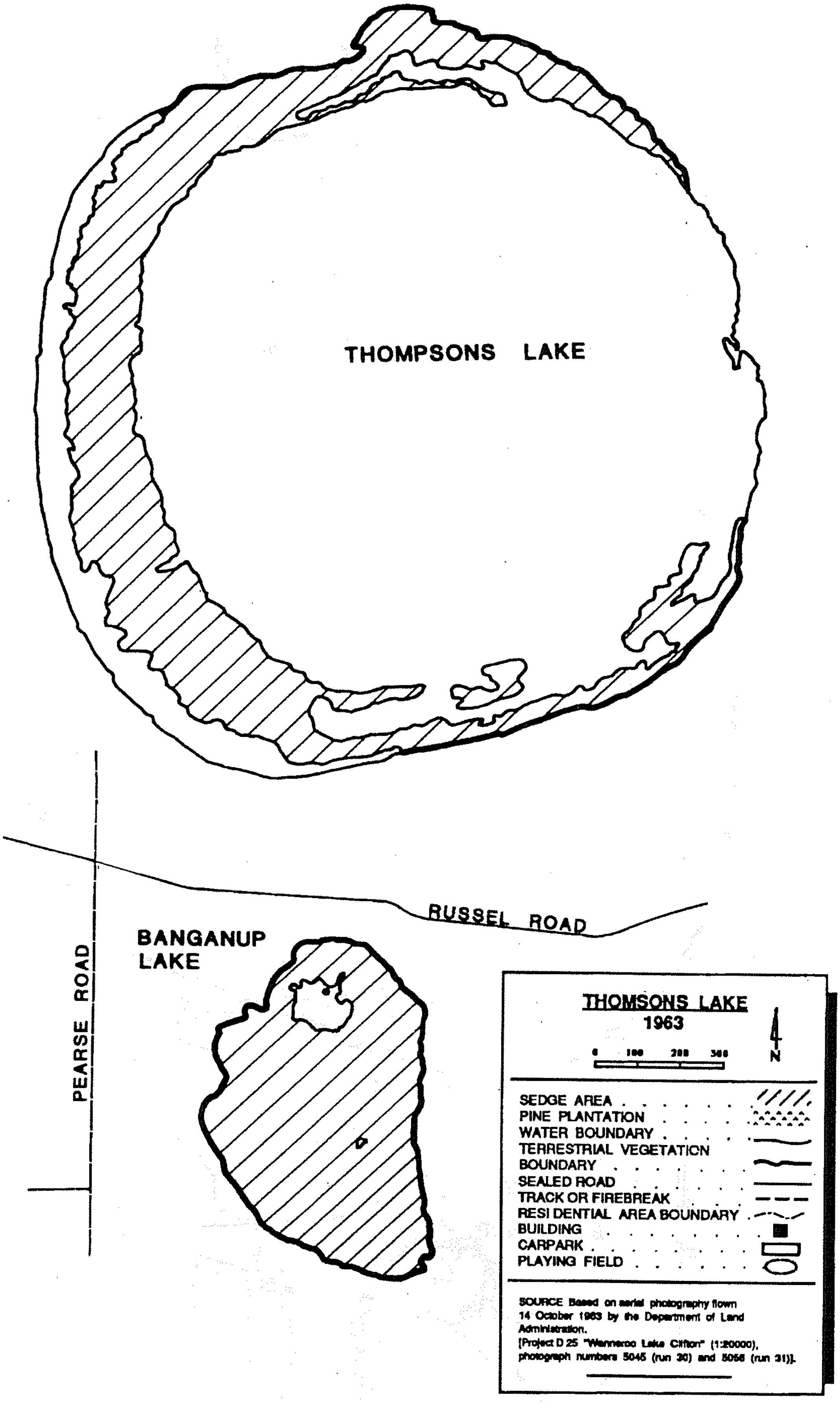
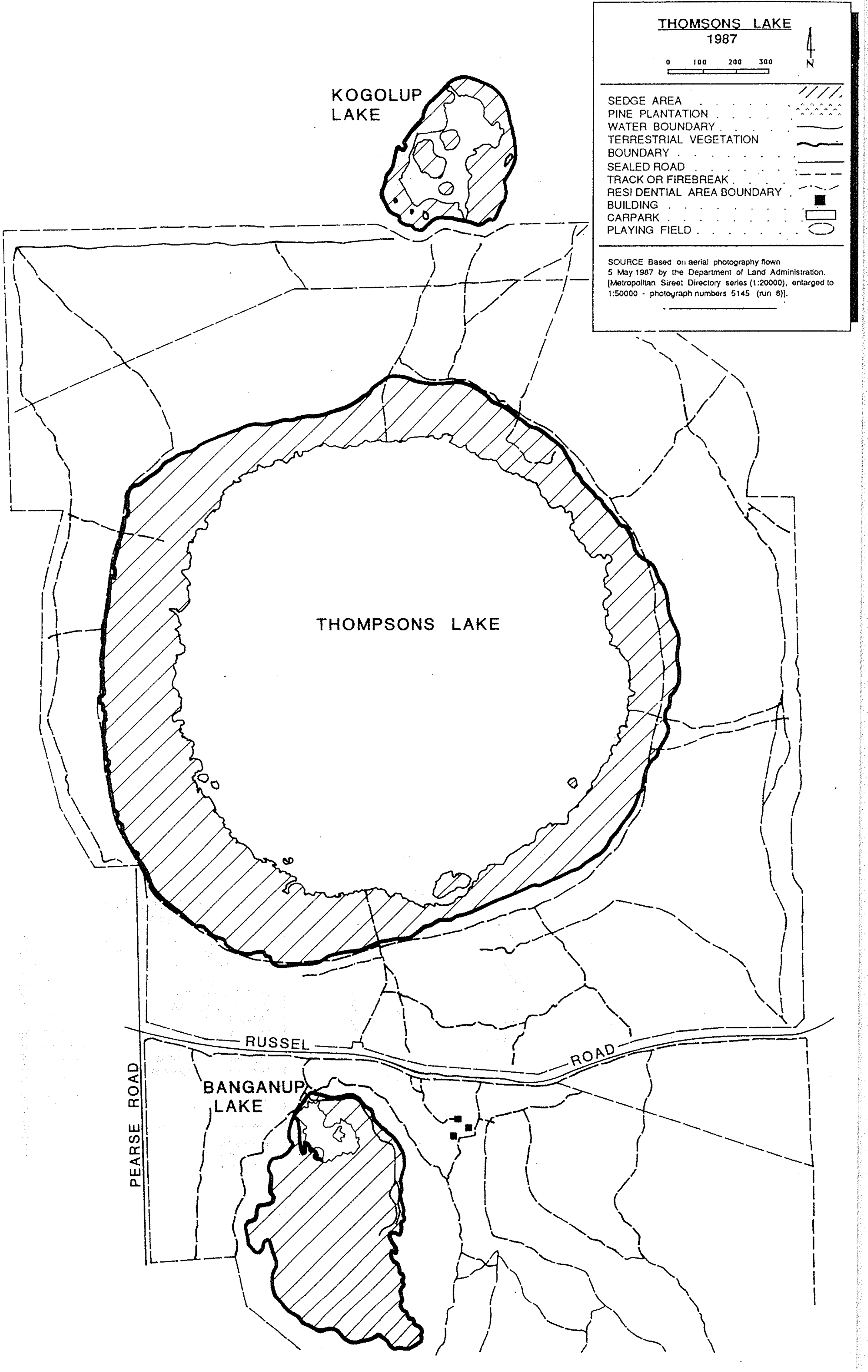
APPENDIX 1

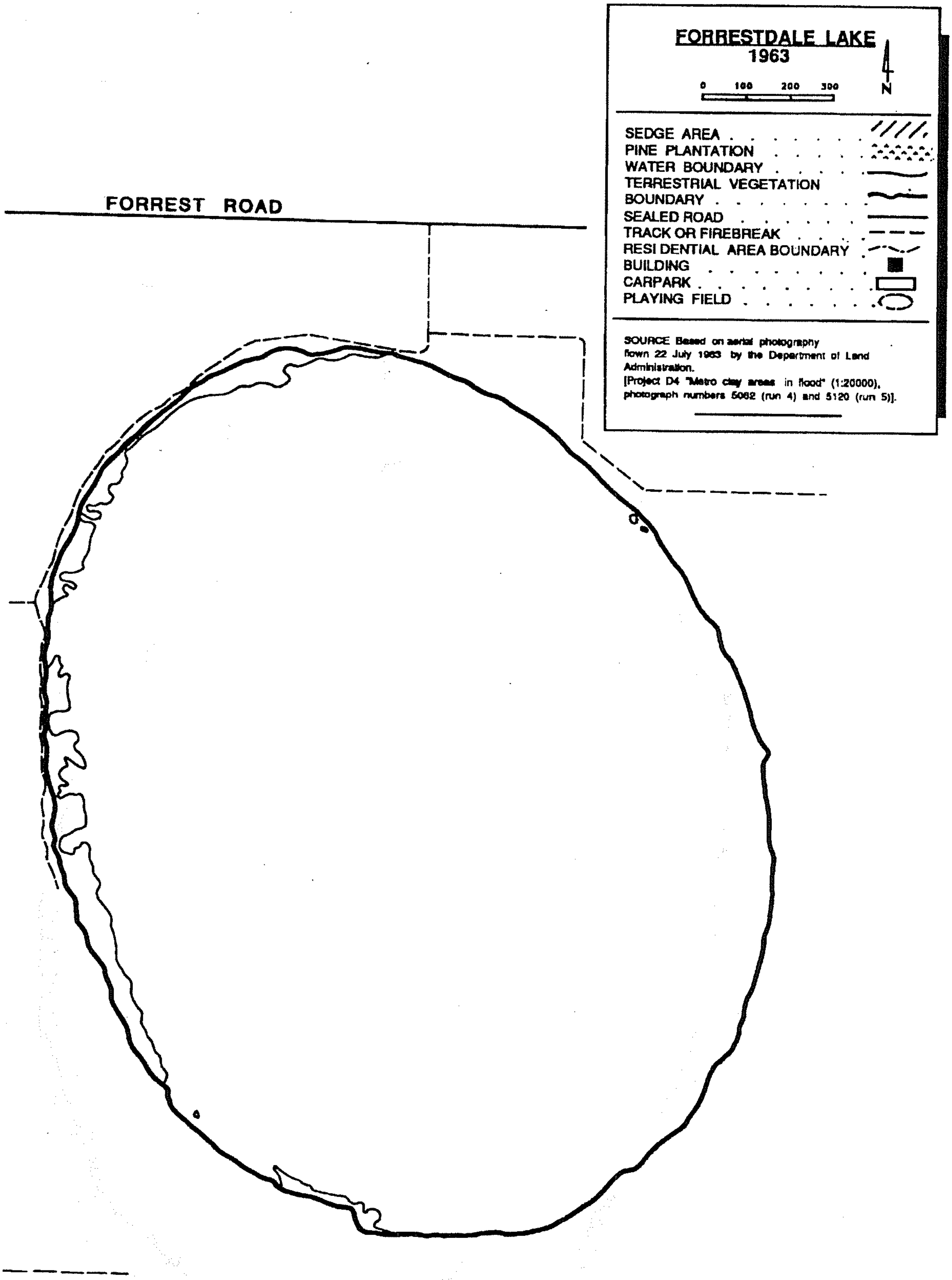
Maps of the emergent macrophyte distribution in 1963 (1969 for Nowergup Lake)
and 1987 at 7 of the study wetlands



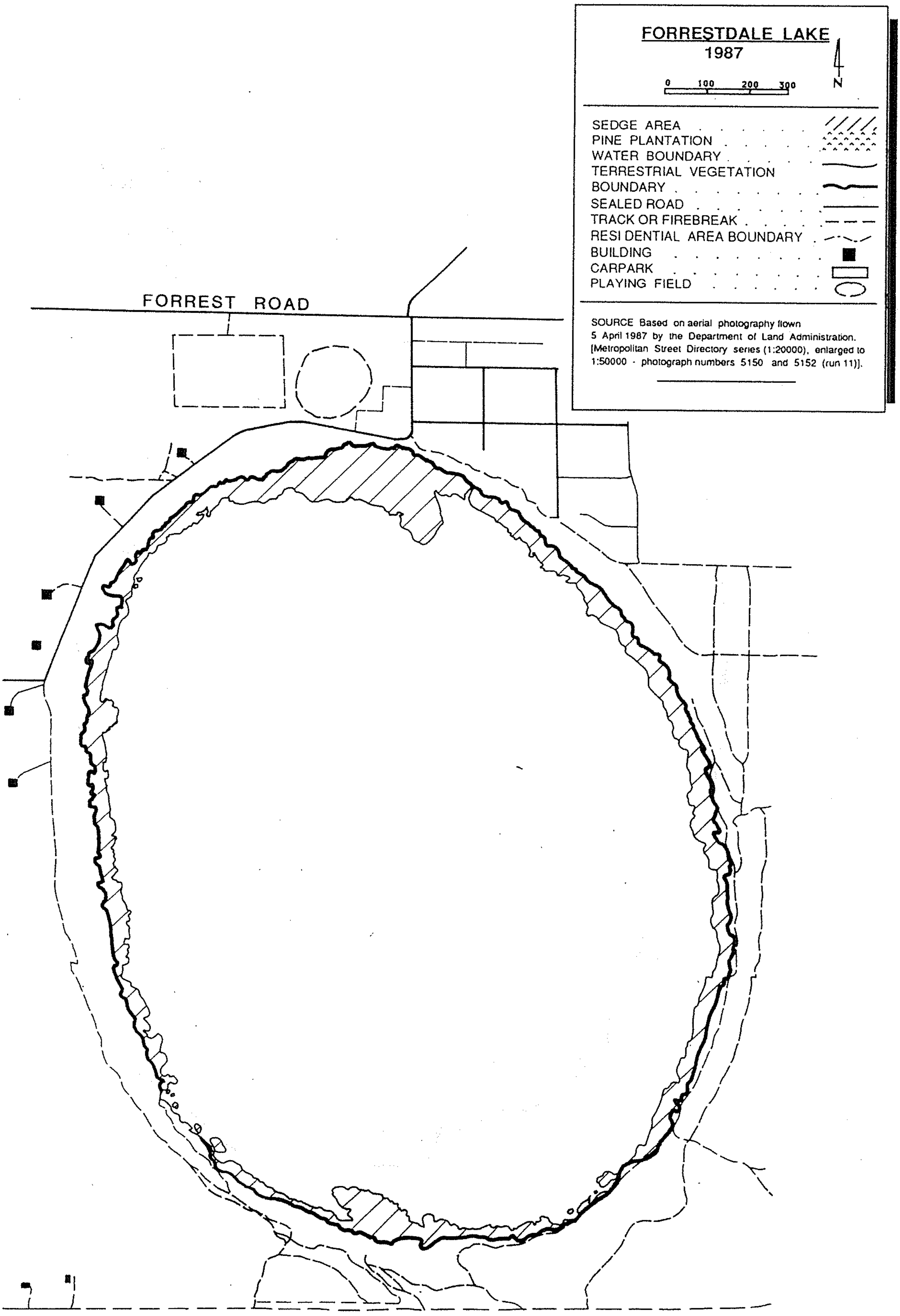
SOURCE Based on aerial photography flown 14 October 1963 by the Department of Land Administration.
[Project D 25 "Wanneroo Lake Clifton" (1:20000), photograph numbers 5045 (run 30) and 5056 (run 31)].



SOURCE Based on aerial photography flown 5 May 1987 by the Department of Land Administration. [Metropolitan Street Directory series (1:20000), enlarged to 1:50000 - photograph numbers 5145 (run 8)].

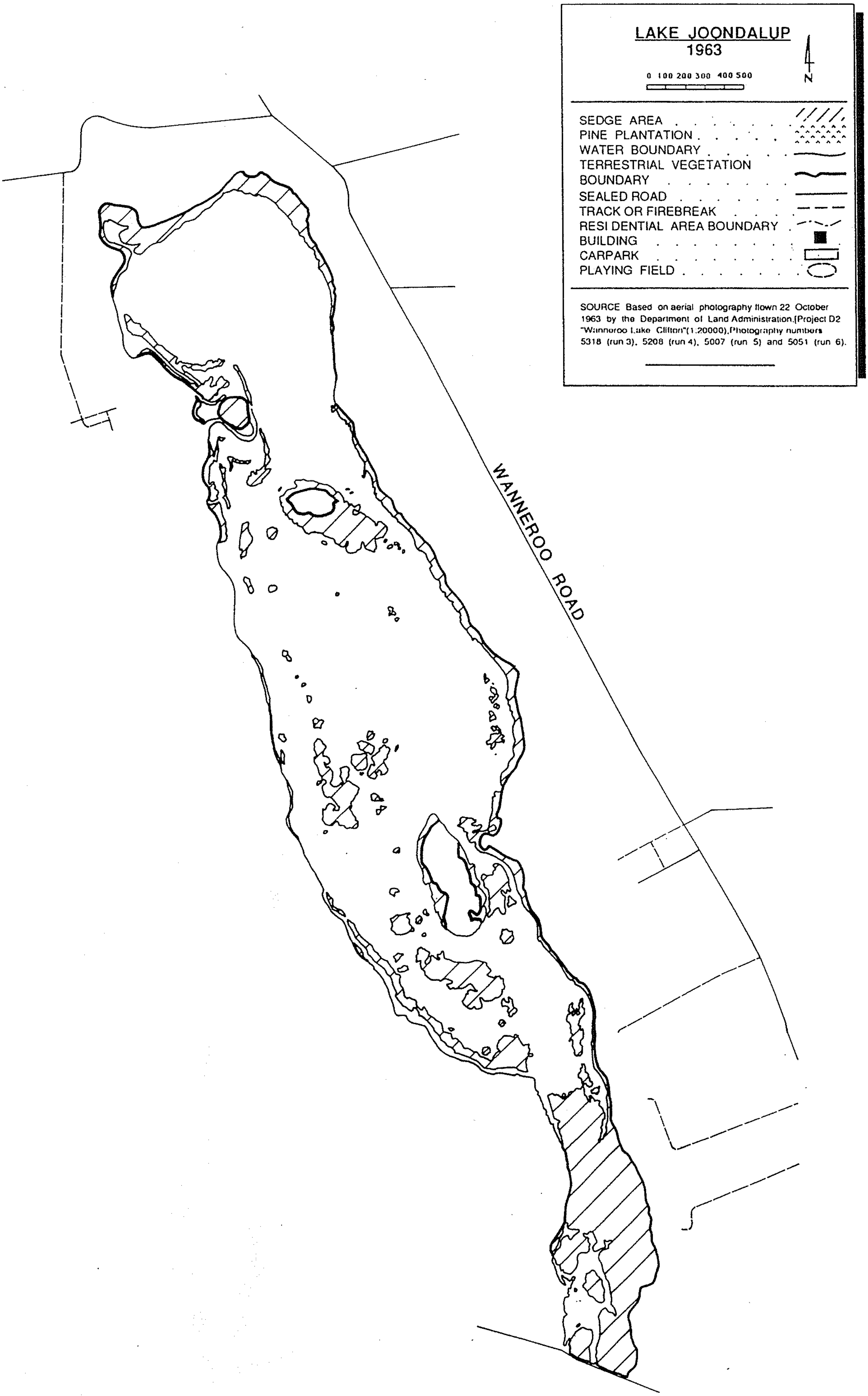


SOURCE Based on aerial photography flown 22 July 1963 by the Department of Land Administration.
[Project D4 "Metro clay areas in flood" (1:20000), photograph numbers 5062 (run 4) and 5120 (run 5)].

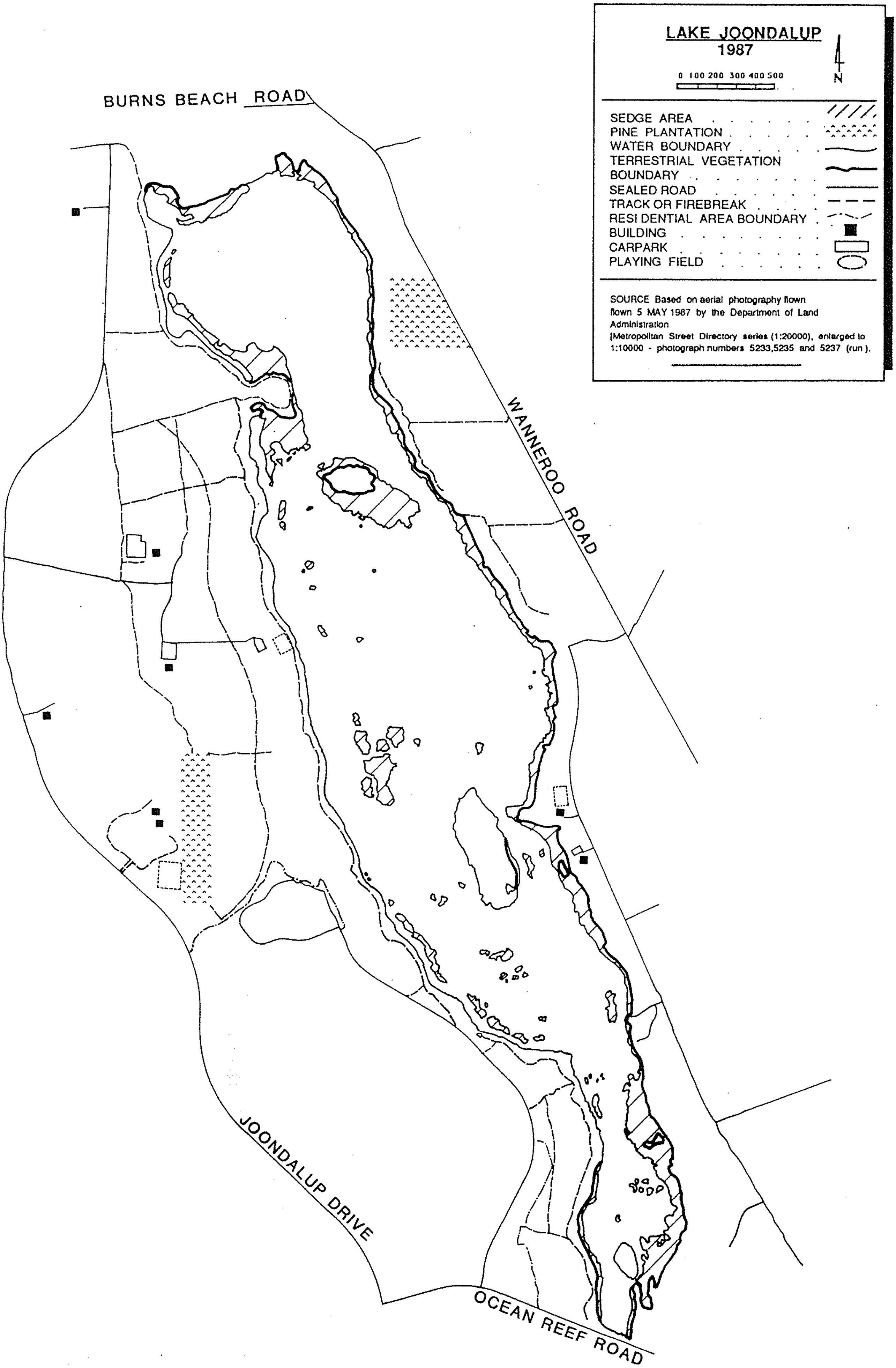


FORRESTDALE LAKE
1987

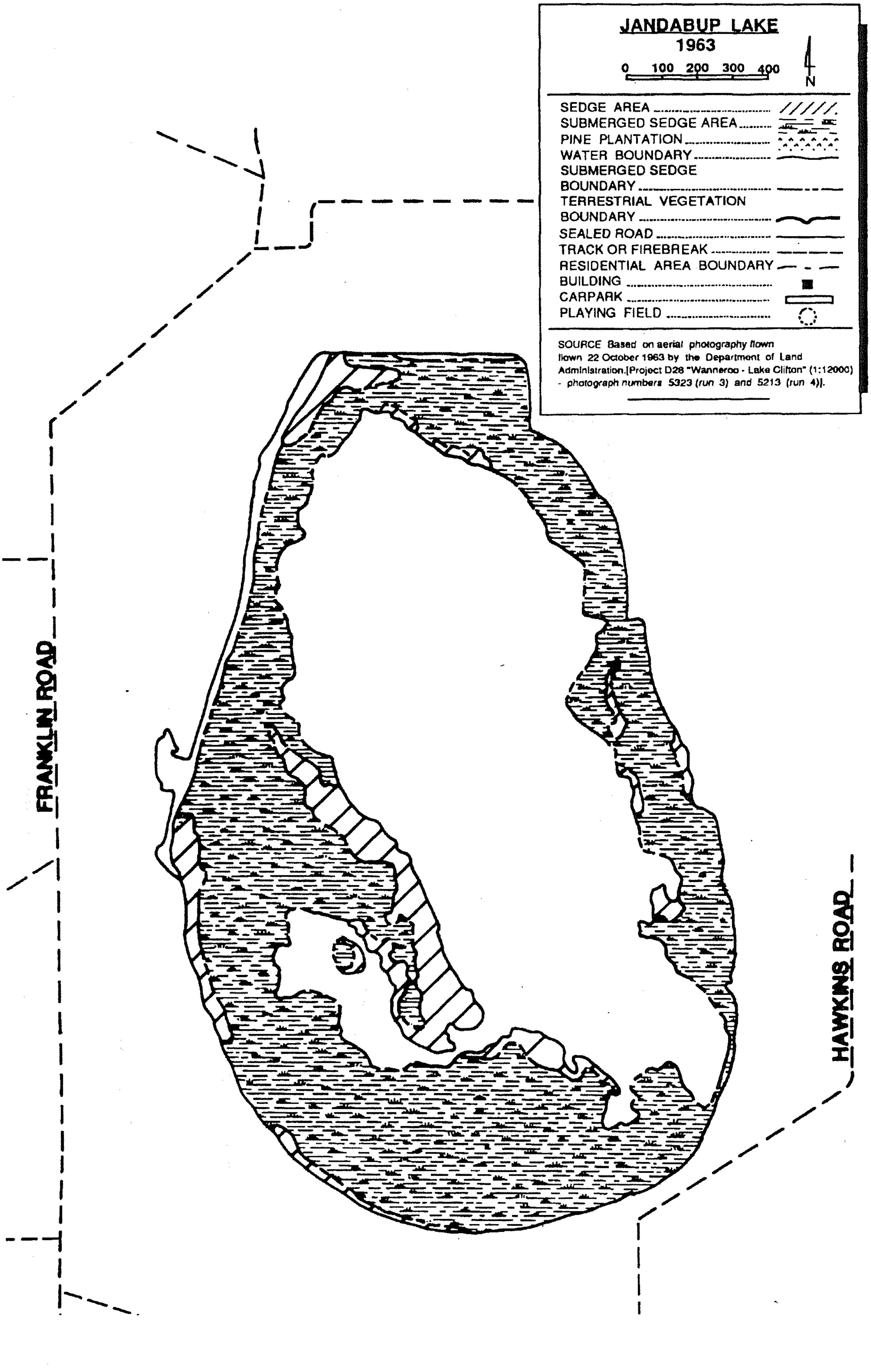
SOURCE Based on aerial photography flown 5 April 1987 by the Department of Land Administration. [Metropolitan Street Directory series (1:20000), enlarged to 1:50000 - photograph numbers 5150 and 5152 (run 11)].



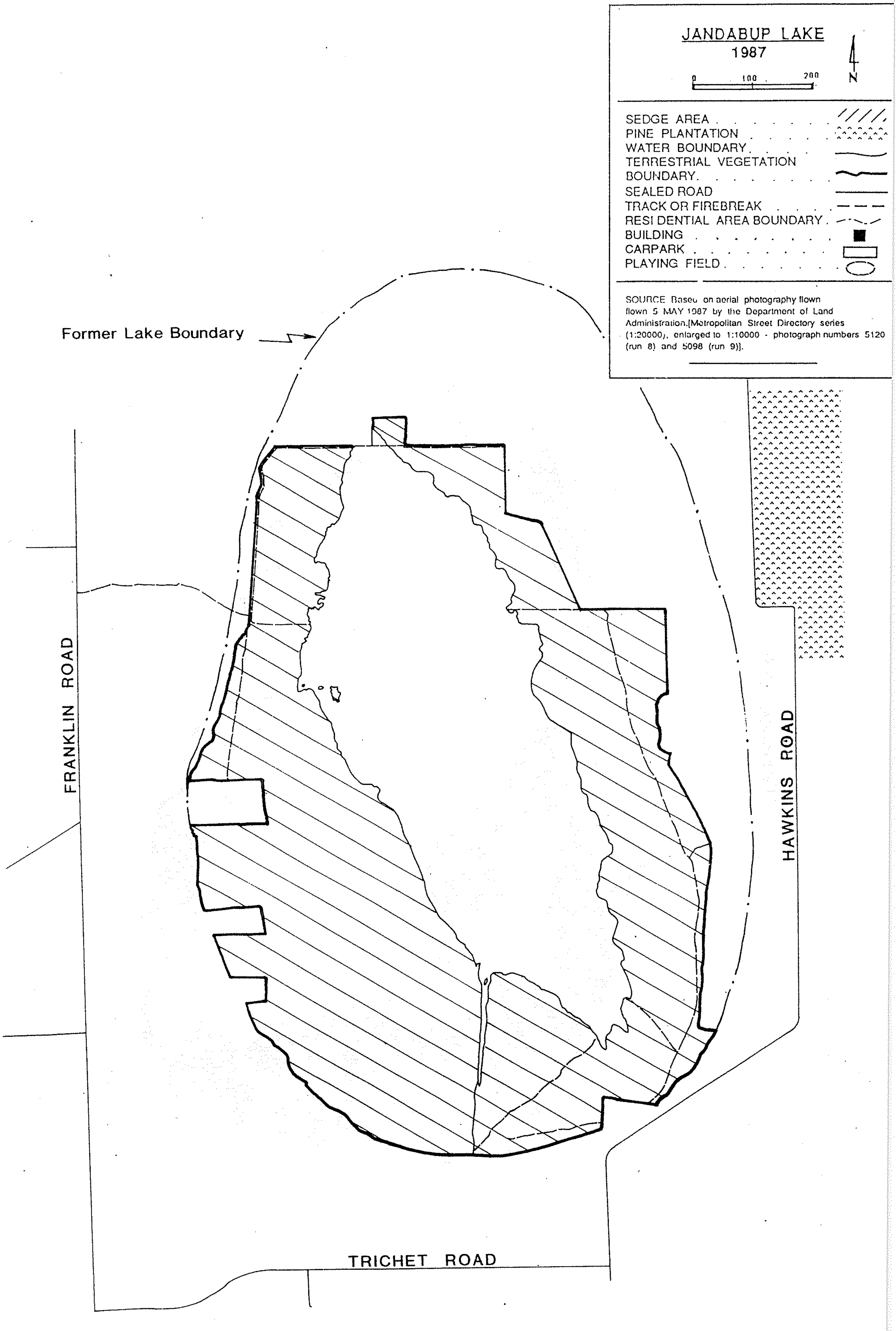
SOURCE Based on aerial photography flown 22 October 1963 by the Department of Land Administration.[Project D2 "Wanneroo Lake Clifton"(1:20000).Photography numbers 5318 (run 3), 5208 (run 4), 5007 (run 5) and 5051 (run 6).



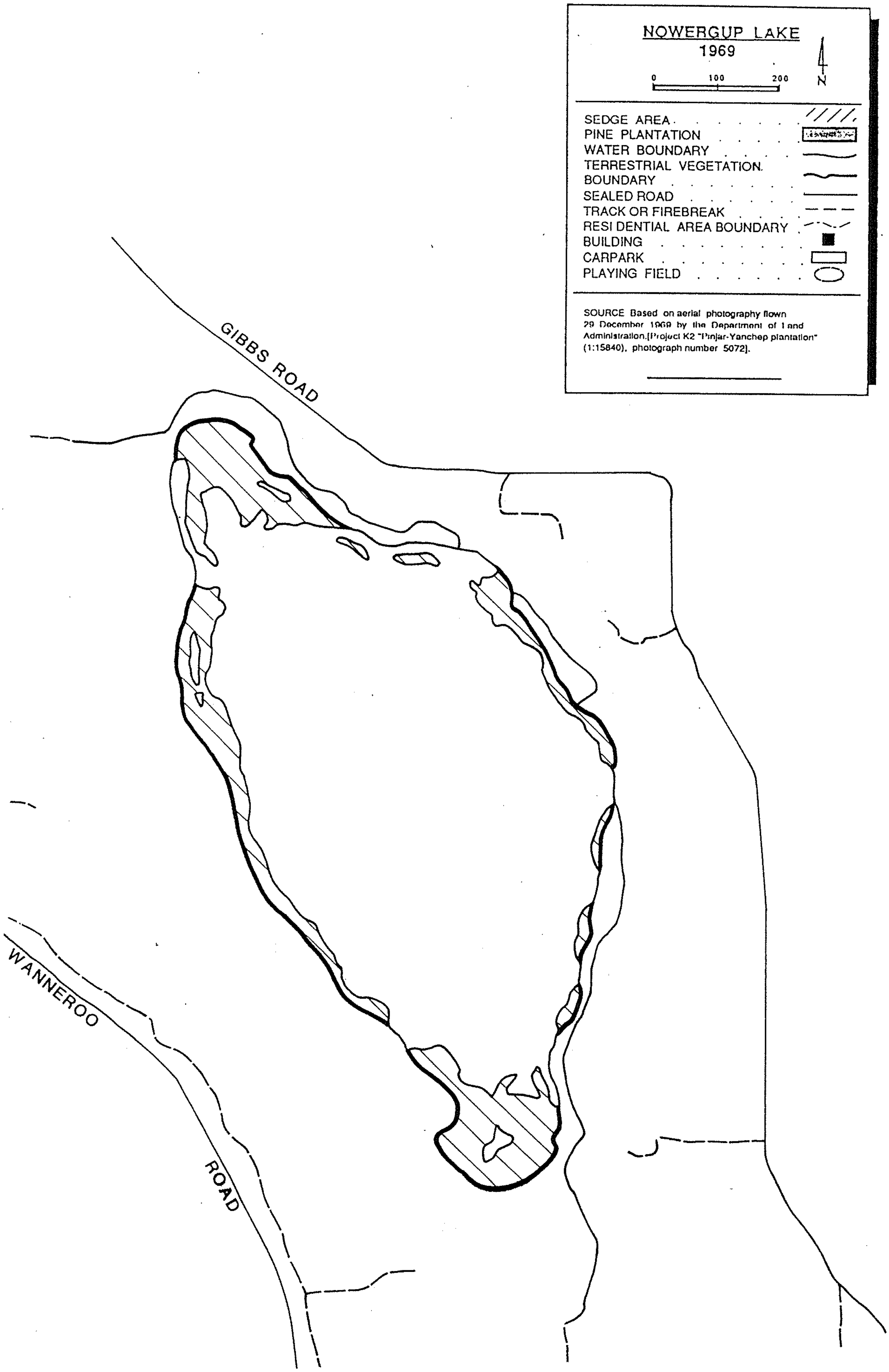
SOURCE Based on aerial photography flown flown 5 MAY 1987 by the Department of Land Administration [Metropolitan Street Directory series (1:20000), enlarged to 1:10000 - photograph numbers 5233,5235 and 5237 (run).



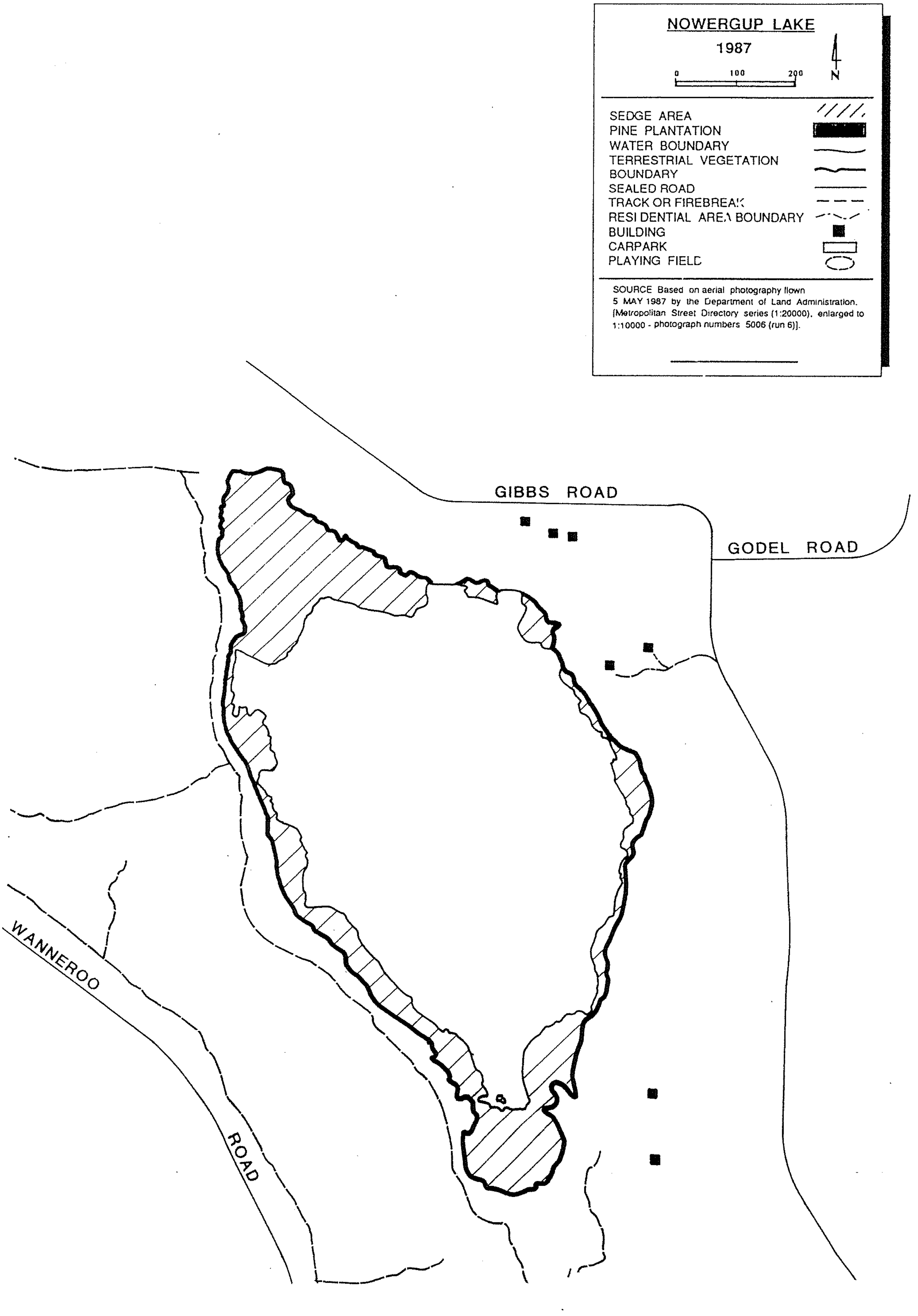
SOURCE Based on aerial photography flown flown 22 October 1963 by the Department of Land Administration.[Project D28 "Wanneroo - Lake Clifton" (1:12000) - *photograph numbers* 5323 (*run* 3) and 5213 (*run* 4)].


JANDABUP LAKE
1987

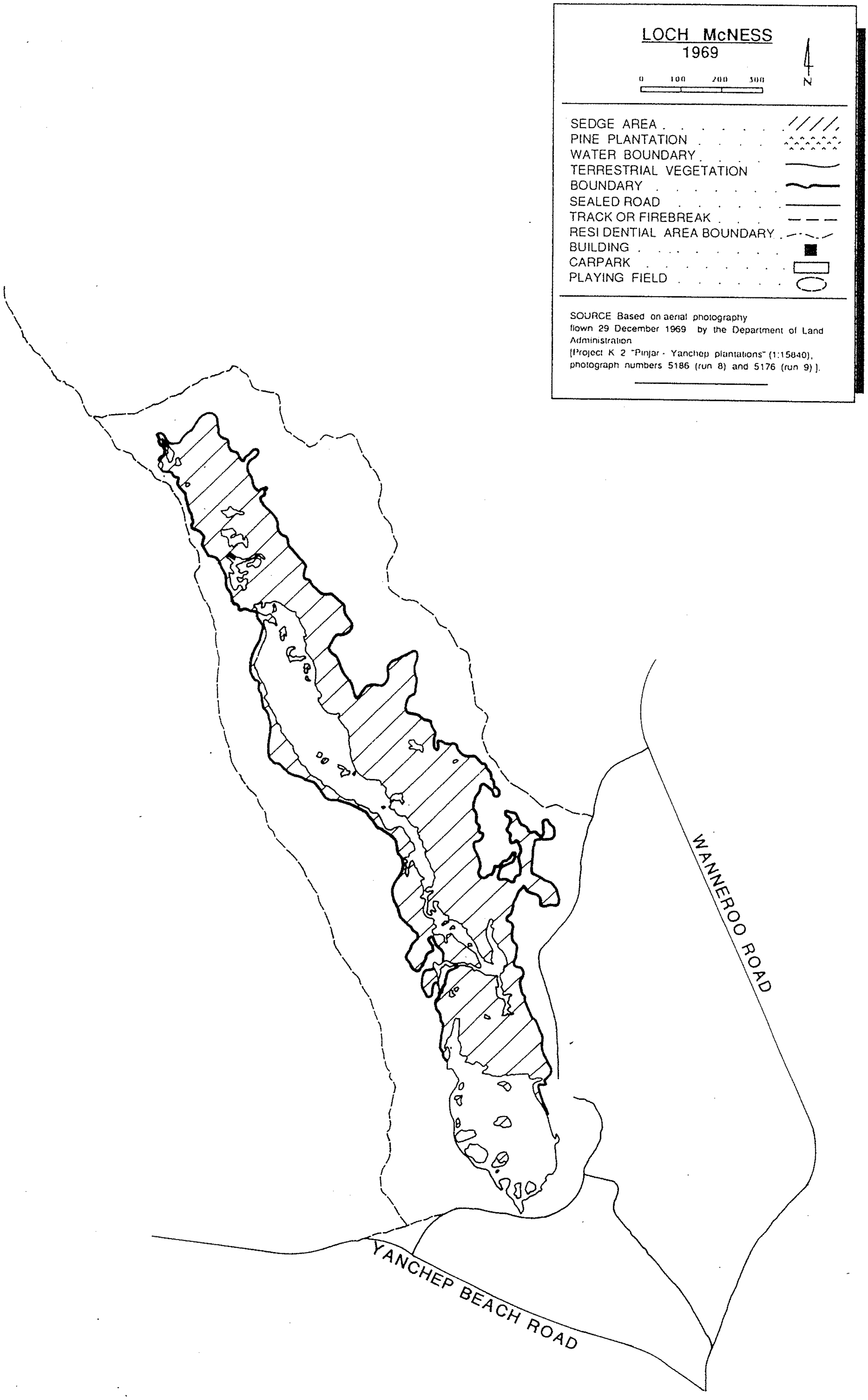
SOURCE Based on aerial photography flown flown 5 MAY 1987 by the Department of Land Administration.[Metropolitan Street Directory series (1:20000), enlarged to 1:10000 - photograph numbers 5120 (run 8) and 5098 (run 9)].



SOURCE Based on aerial photography flown 29 December 1969 by the Department of Land Administration.[Project K2 "Pinjar-Yanchep plantation" (1:15840), photograph number 5072].

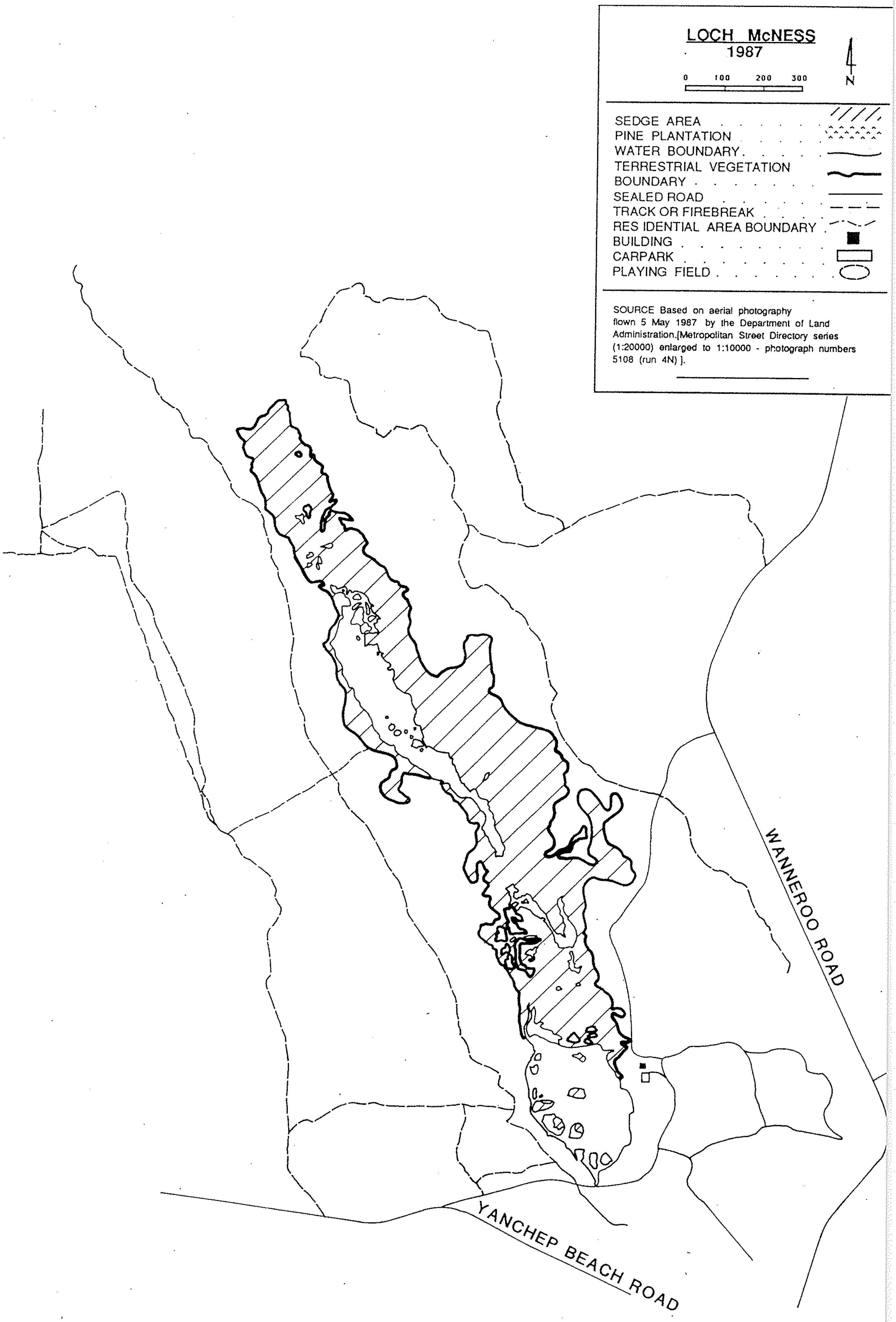


SOURCE Based on aerial photography flown 5 MAY 1987 by the Department of Land Administration. [Metropolitan Street Directory series (1:20000), enlarged to 1:10000 - photograph numbers 5006 (run 6)].



LOCH McNESS
1969

SOURCE Based on aerial photography flown 29 December 1969 by the Department of Land Administration
[Project K 2 "Pinjar - Yanchep plantations" (1:15840), photograph numbers 5186 (run 8) and 5176 (run 9)].

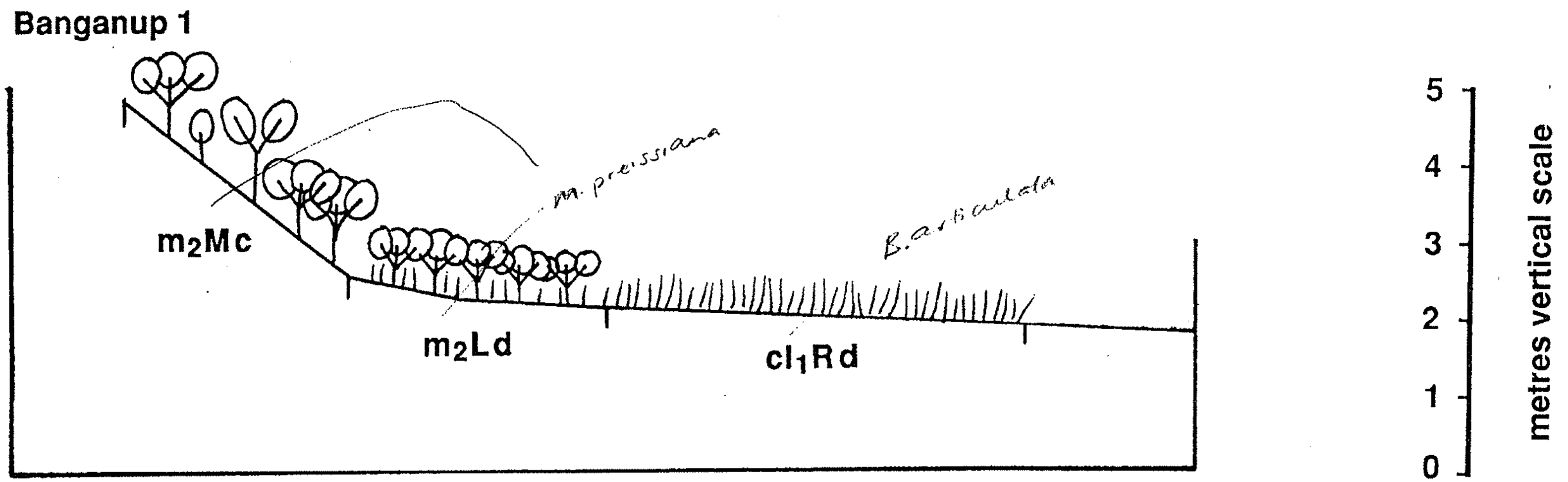


LOCH McNESS
1987

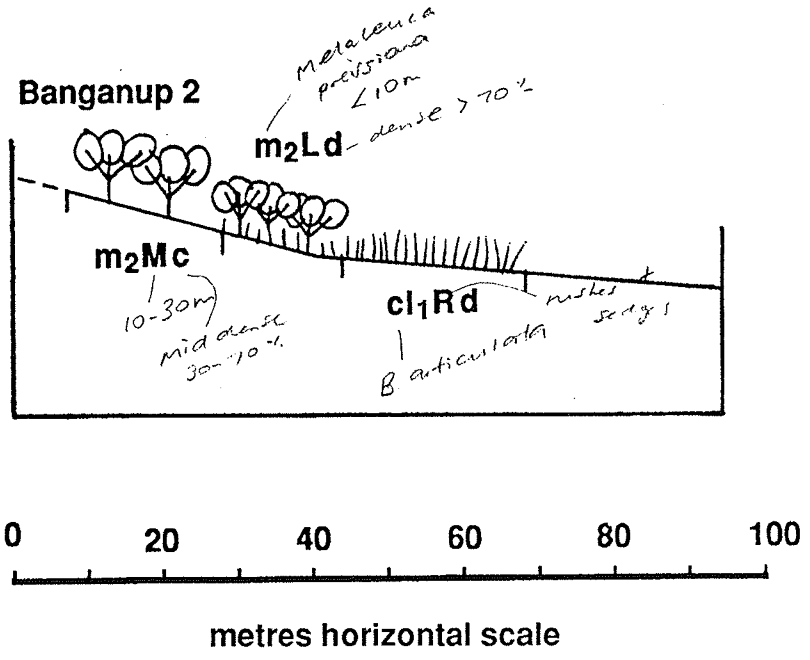
SOURCE Based on aerial photography flown 5 May 1987 by the Department of Land Administration.[Metropolitan Street Directory series (1:20000) enlarged to 1:10000 - photograph numbers 5108 (run 4N)].

APPENDIX 2

Profile diagrams and vegetation association descriptions of the transects at each of the study wetlands.



Vegetation not drawn to scale



Species	
a	*Acacia*
cl$_1$	*Baumea articulata*
e$_1$	*Eucalyptus rudis*
l$_1$	*Leptocarpus*
l$_2$	*Lepidosperma sp.*
m$_1$	*Melaleuca rhaphiophylla*
m$_2$	*Melaleuca preissiana*
m$_4$	*Melaleuca teretifolia*
s	*Schoenoplectus validus*
t	*Typha orientalis*
r	*Regelia*

Physiognomy of Dominant Stratum	
t	Tall trees > 30m tall
M	Medium trees 10-30m tall
L	Low trees < 10m tall
S	Shrubs > 1m tall
Z	Dwarf shrubs < 1m tall
R	Rushes and sedges > 1m tall
V	Rushes and sedges < 1m tall
G	Bunch grasses
F	Forbs
L	Lichens and mosses
C	Succulents

Canopy Cover	
d	Dense cover > 70% foliage cover
c	Mid dense 30-70%foliage cover
i	Incomplete canopy-open, not touching
r	Rare but conspicuous foliage cover < 10%
b	Vegetation largely absent
p	Scattered groups - no definite foliage cover

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m_4	*Melaleuca teretifolia*
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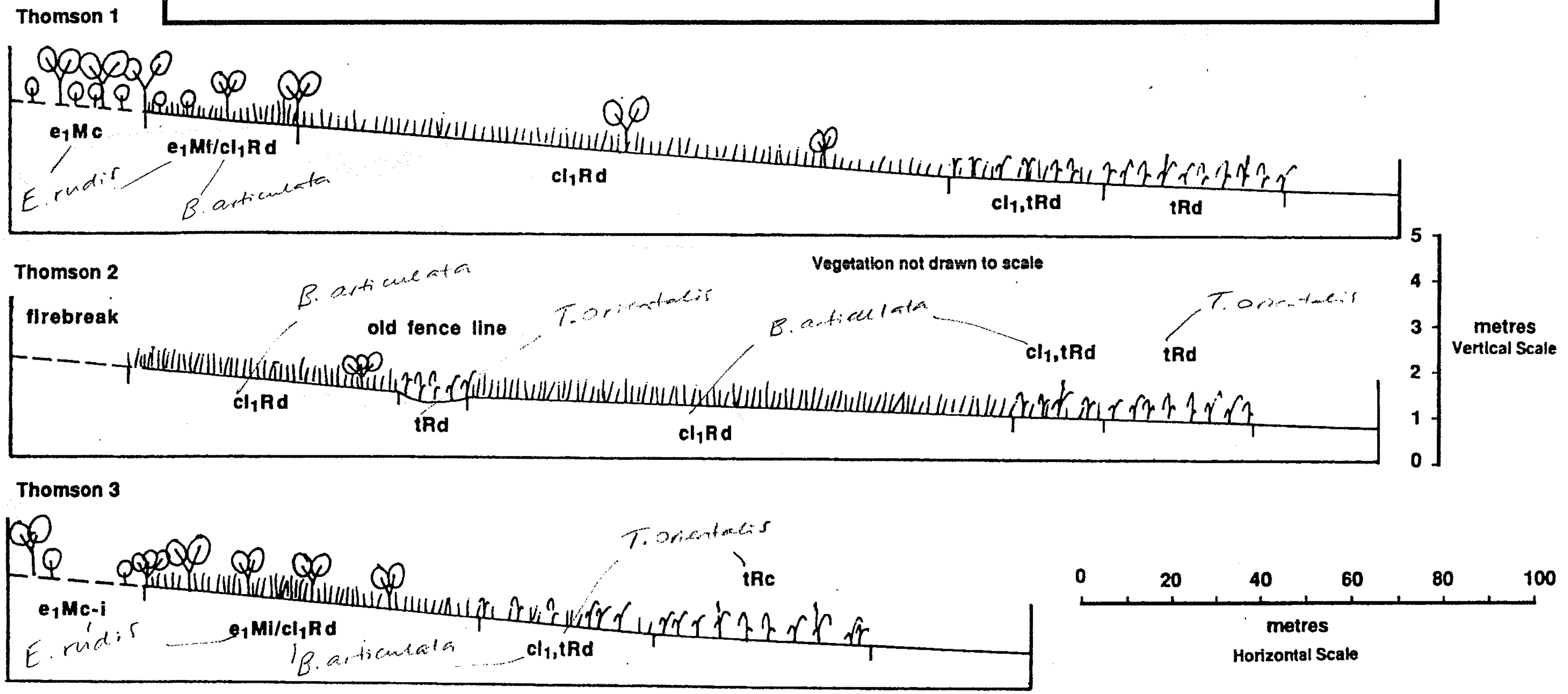

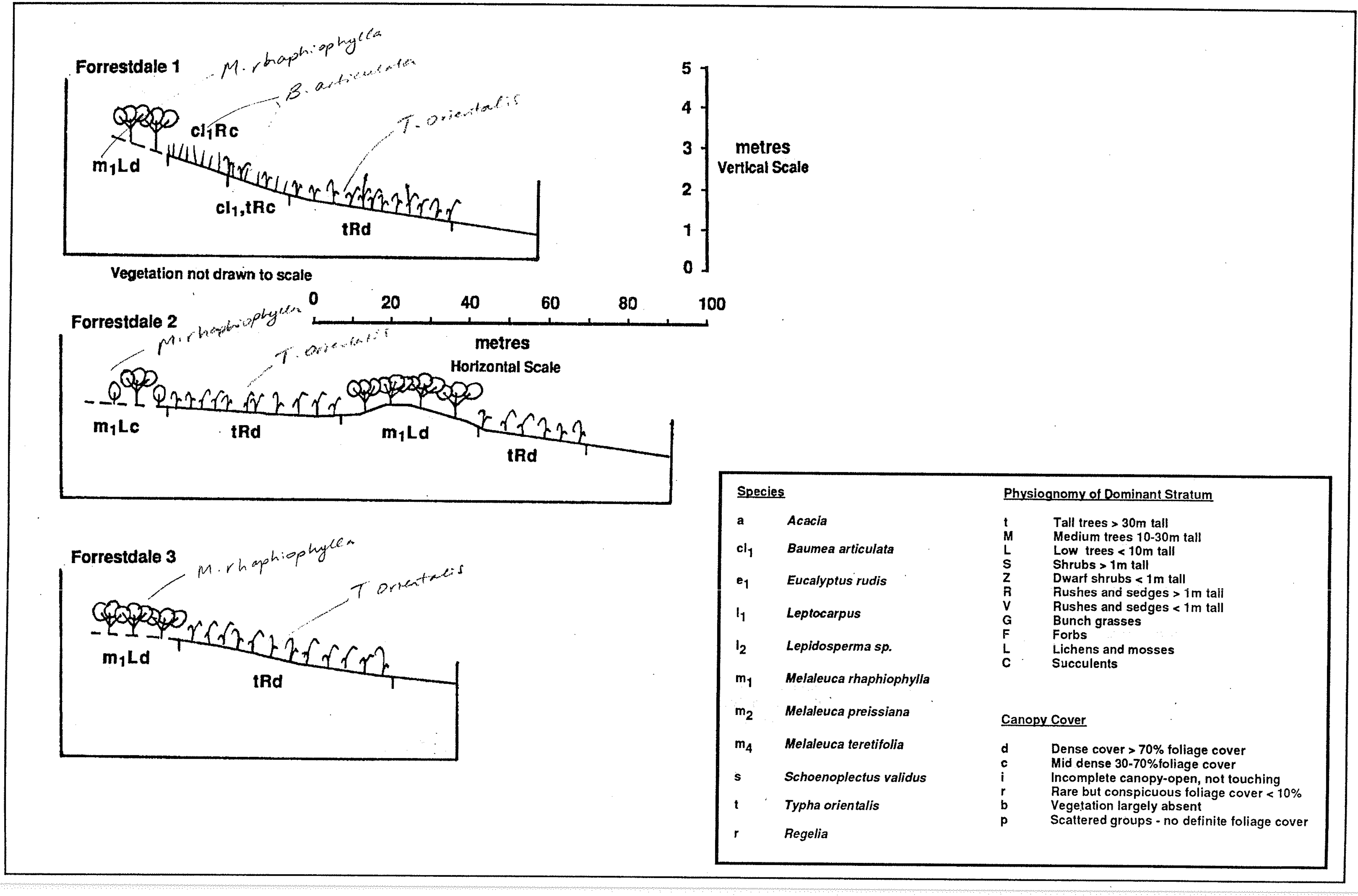

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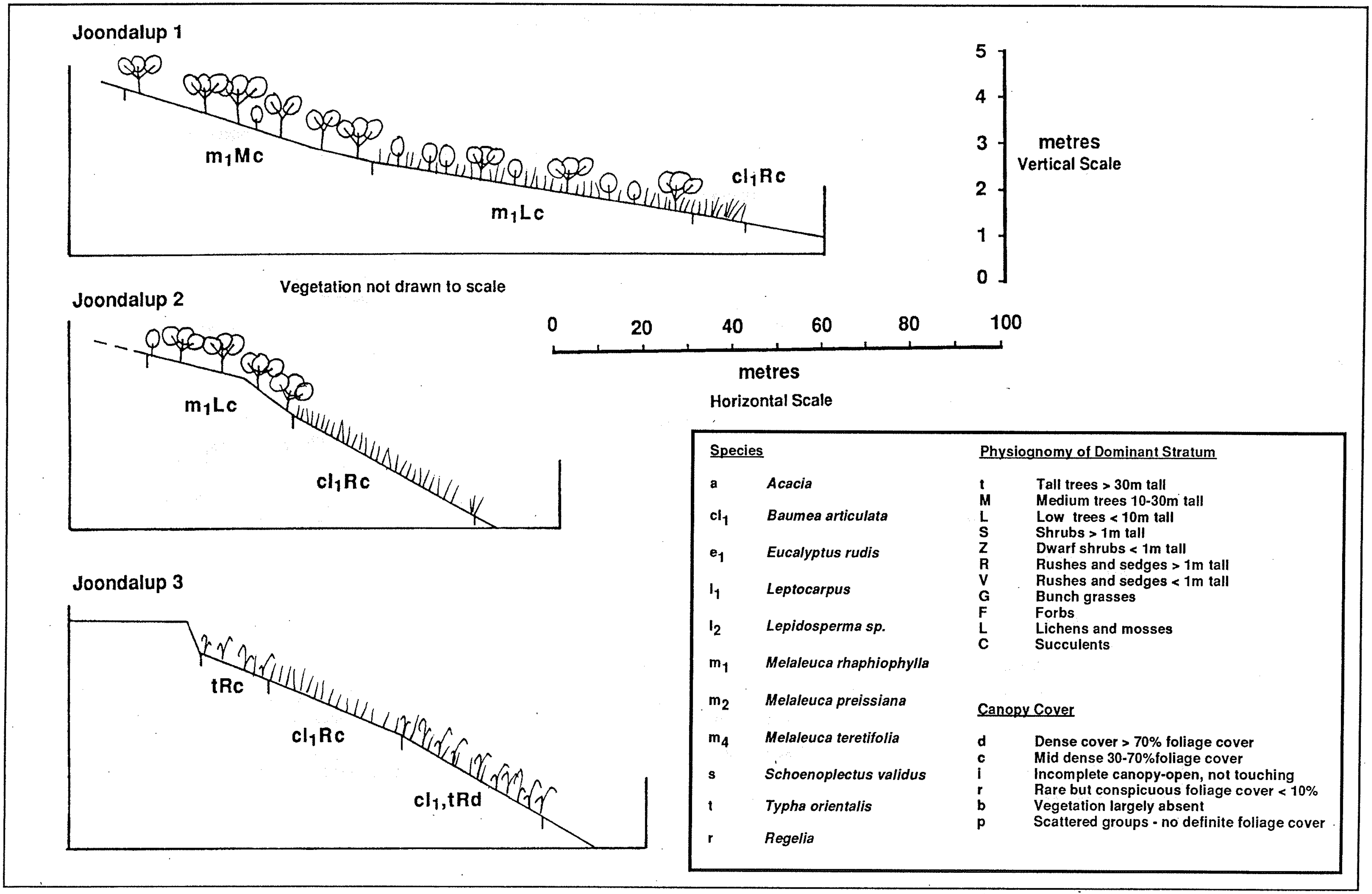

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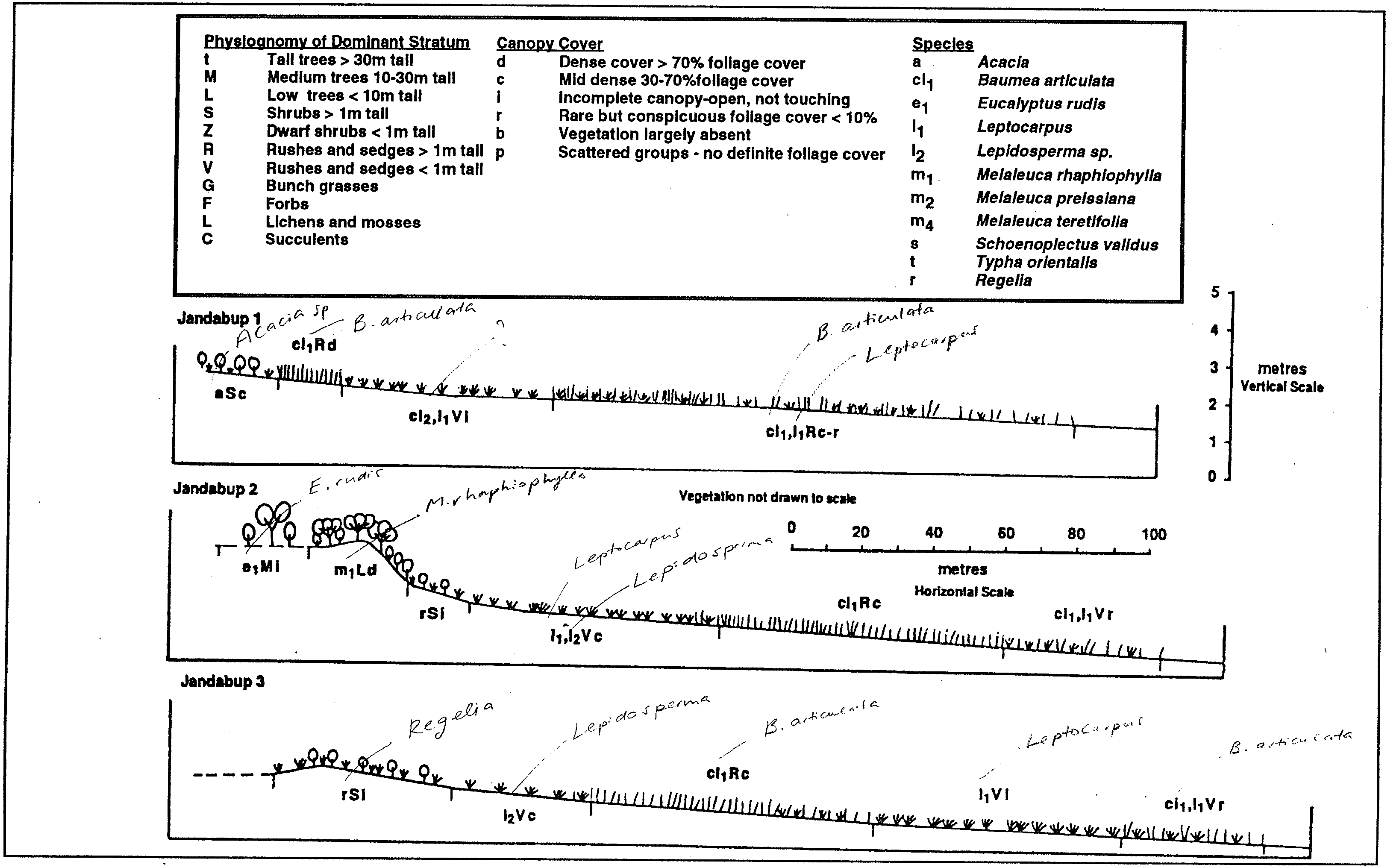
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l2 Lepidosperma sp.
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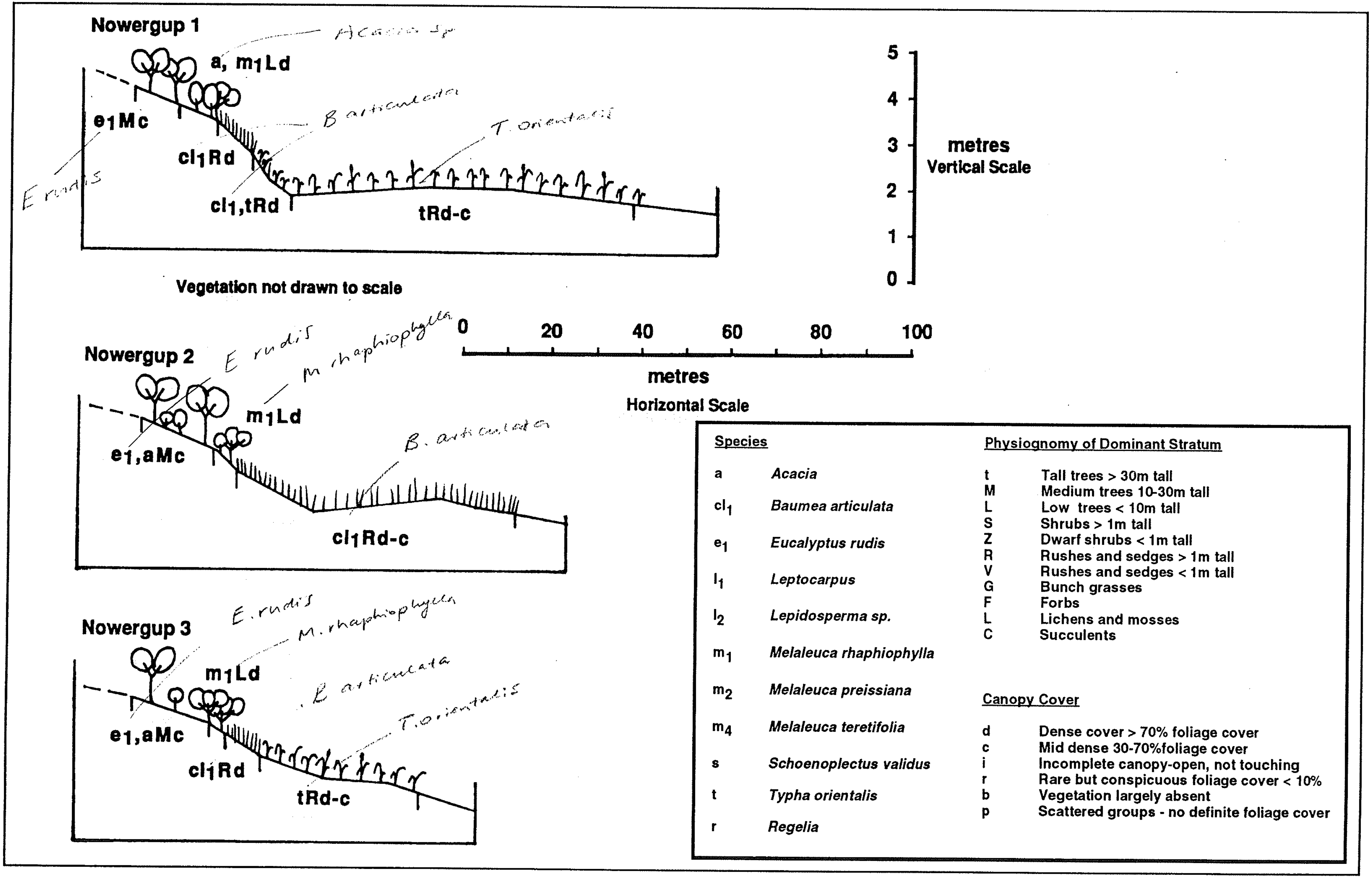
m2 Melaleuca preissiana
m4 Melaleuca teretifolia
s Schoenoplectus validus
t Typha orientalis
r Regelia
Jandabup 1
Acacia sp
B. articulata
cl1Rd
aSc
cl2,l1Vi
B. articulata
Leptocarpus
cl1,l1Rc-r
5
4
3
2
1
0
metres
Vertical Scale
Jandabup 2
E. rudis
M. rhaphiophylla
e1Mi
m1Ld
rSi
Leptocarpus
Lepidosperma
l1,l2Vc
Vegetation not drawn to scale
0
20
40
60
80
100
metres
Horizontal Scale
cl1Rc
cl1,l1Vr
Jandabup 3
Regelia
Lepidosperma
B. articulata
Leptocarpus
B. articulata
rSi
l2Vc
cl1Rc
l1Vi
cl1,l1Vr



Vegetation not drawn to scale

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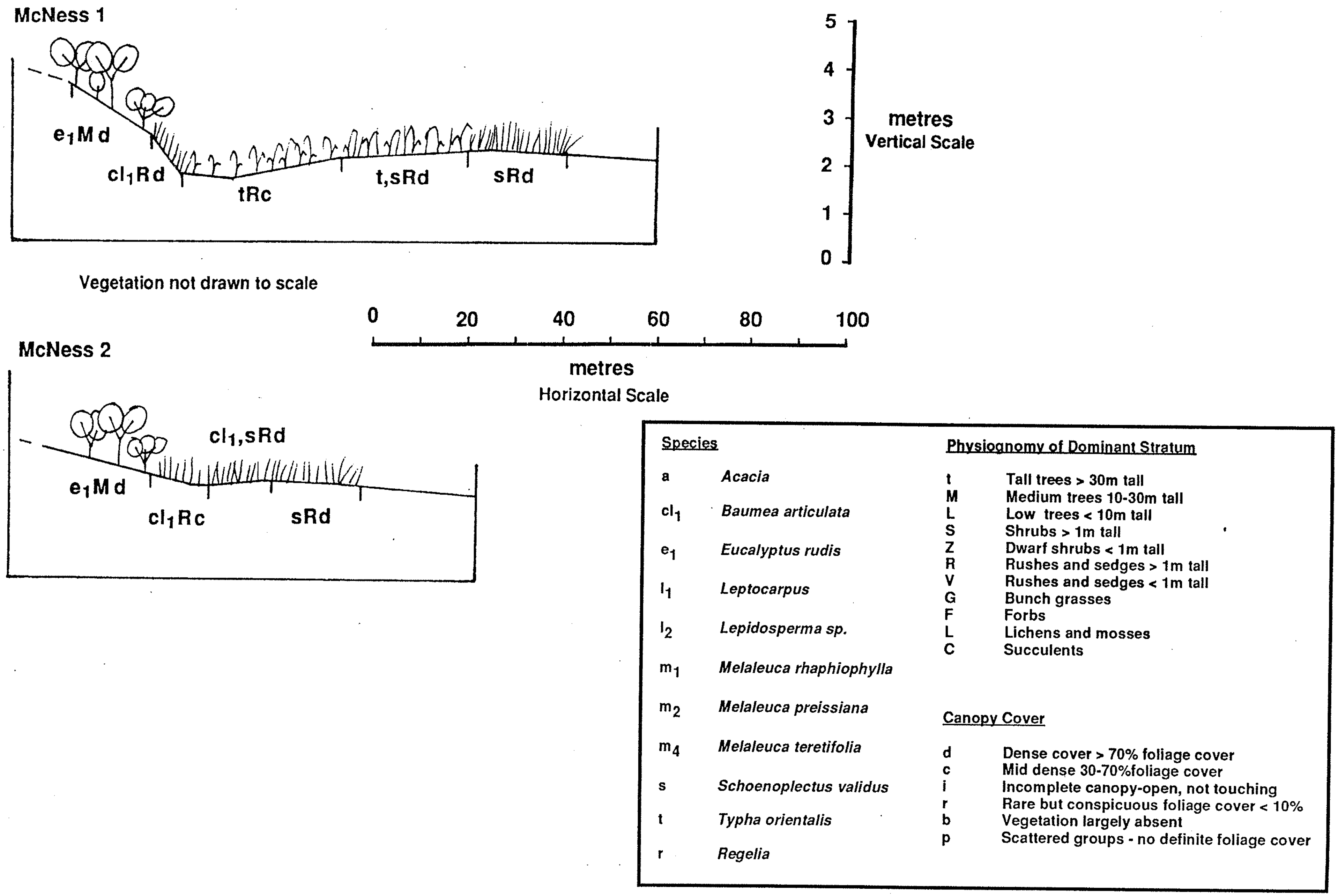

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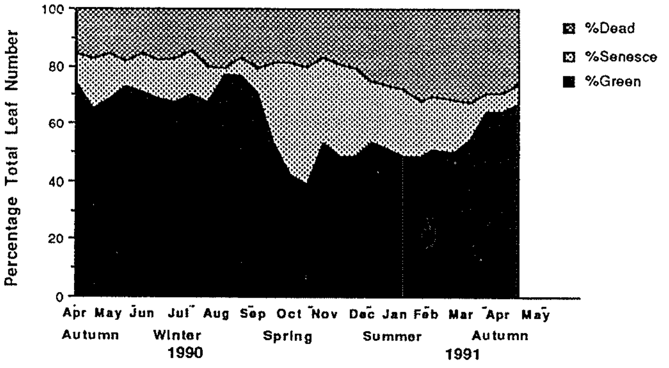
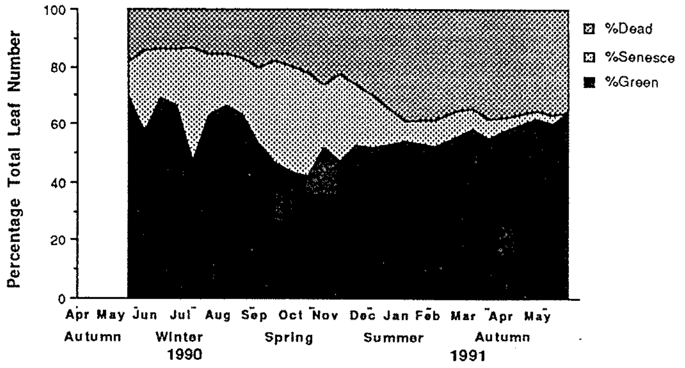
APPENDIX 3

Percentage Dead, senescent and live leaves, total number of leaves, difference in percentage live leaves from control treatment, and difference in total number of leaves from control treatment of each species in each treatment over the course of the water depth experiment.

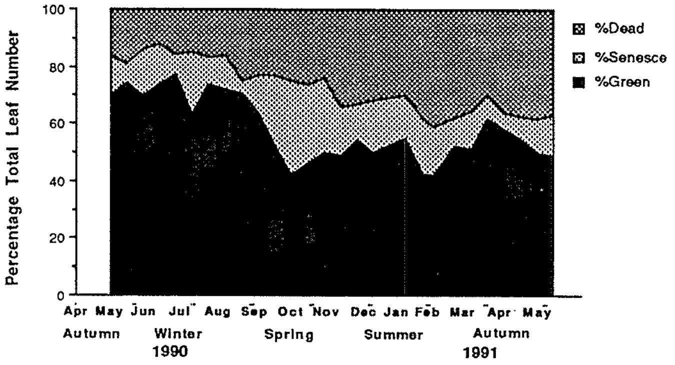
Ba Pool 0



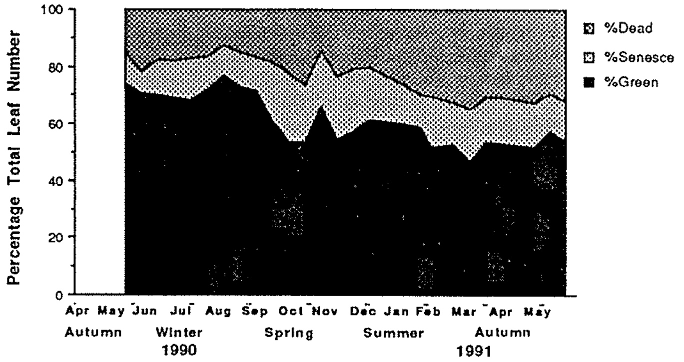
Ba Drought 0



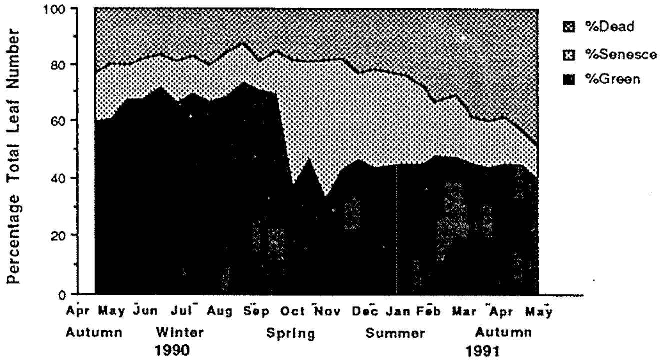
Ba Pool +25



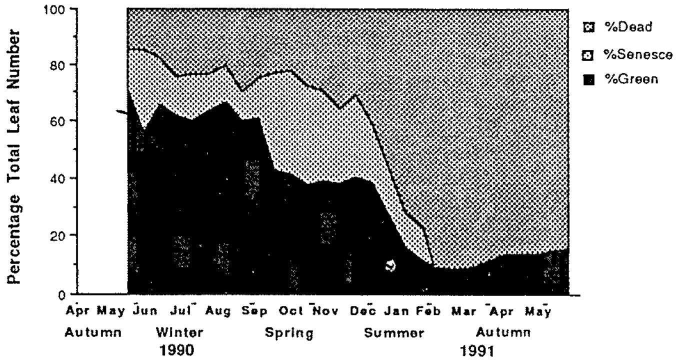
Ba Drought -50



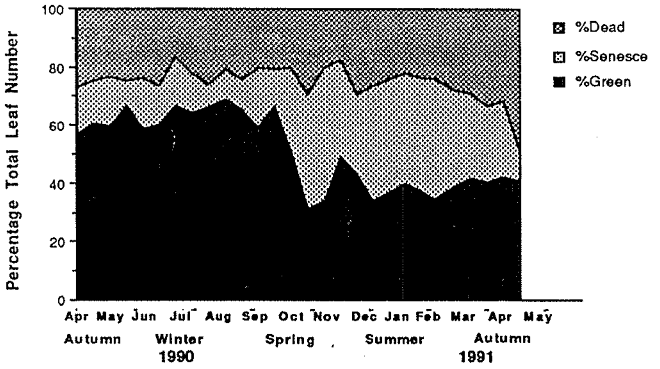
Ba Pool +50

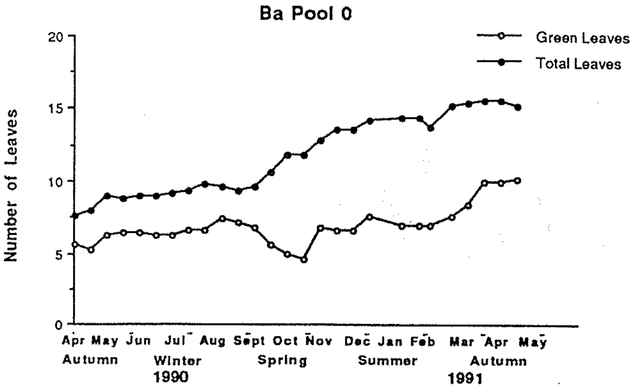


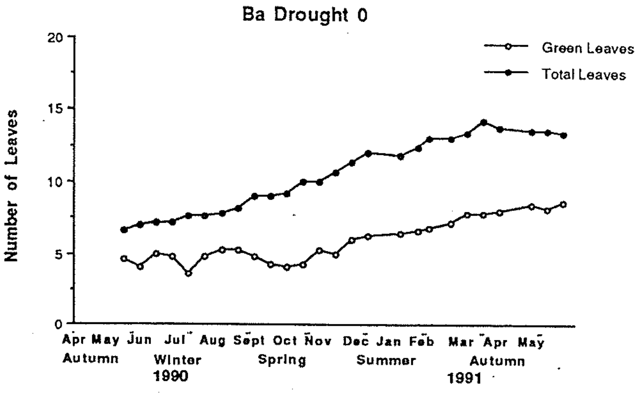
Ba Drought -100

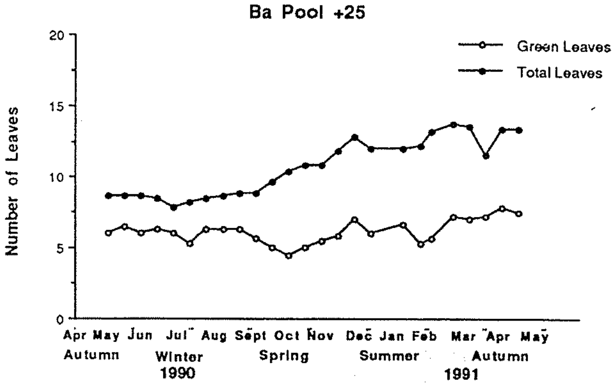


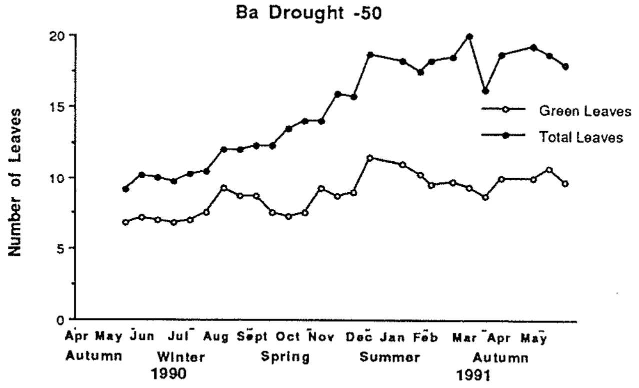
Ba Pool +75

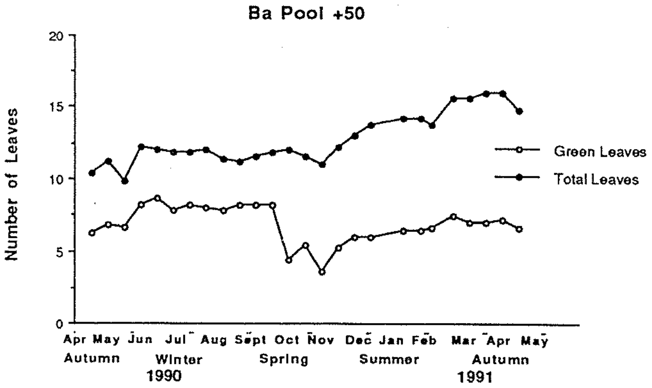


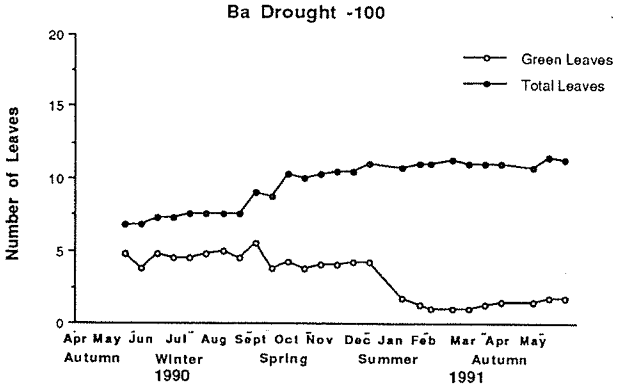

Ba Pool 0

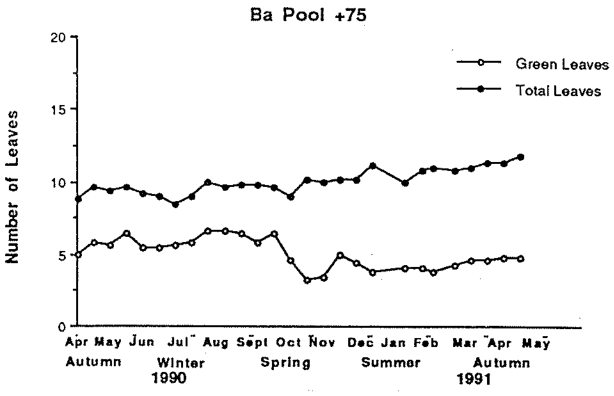

Ba Drought 0

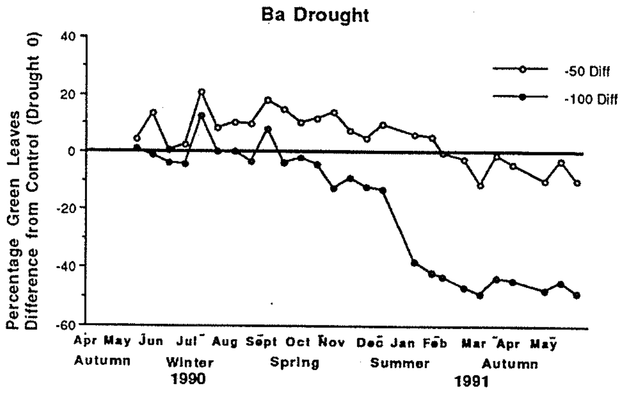

Ba Pool +25

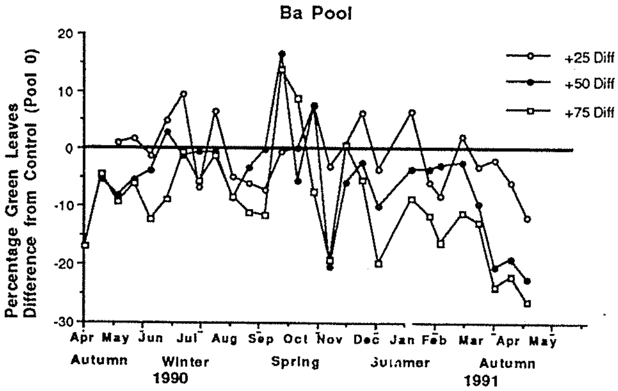

Ba Drought -50

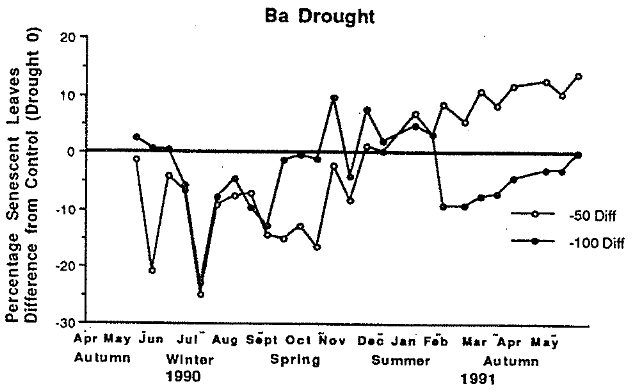

Ba Pool +50

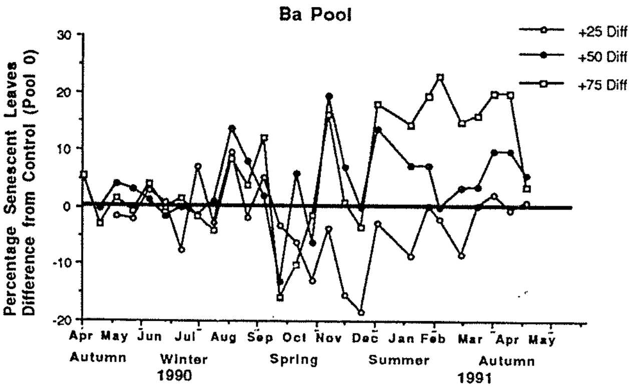

Ba Drought -100

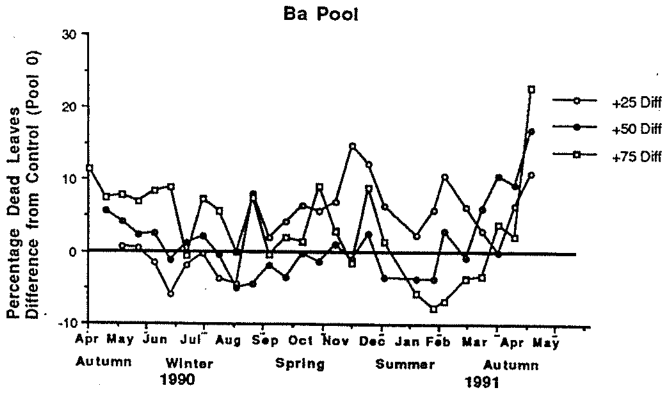

Ba Pool +75

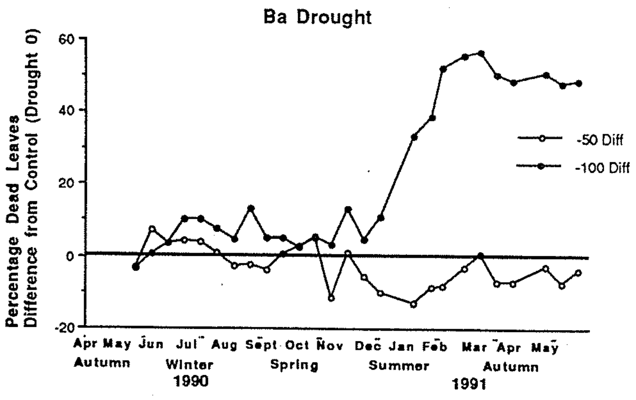

Ba Drought
Percentage Green Leaves Difference from Control (Drought 0)
40
20
0
-20
-40
-60
-50 Diff
-100 Diff
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

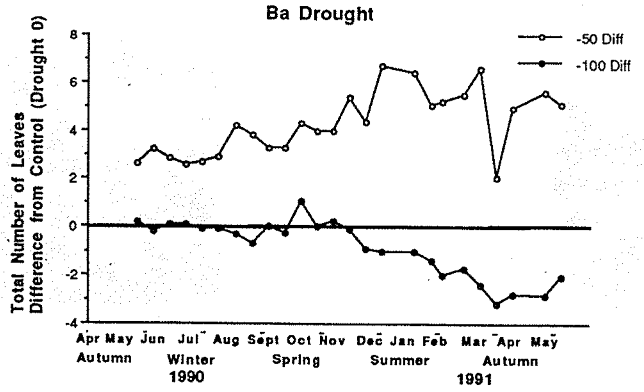

Ba Pool
Percentage Green Leaves Difference from Control (Pool 0)
20
10
0
-10
-20
-30
+25 Diff
+50 Diff
+75 Diff
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

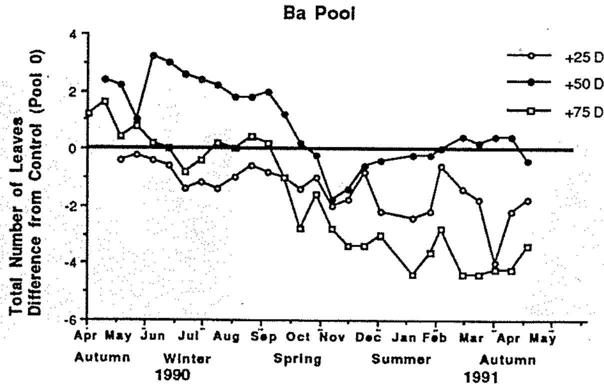

Ba Drought
Percentage Senescent Leaves Difference from Control (Drought 0)
20
10
0
-10
-20
-30
-50 Diff
-100 Diff
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

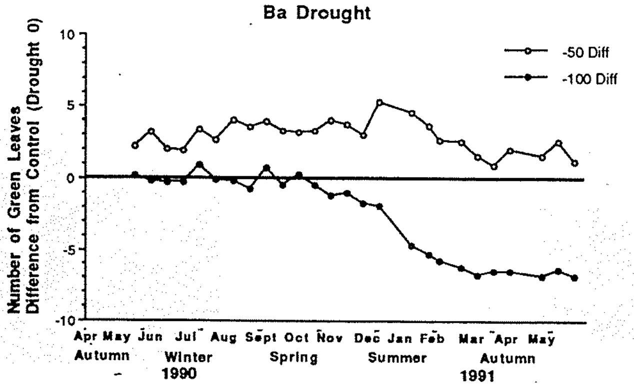

Ba Pool
Percentage Senescent Leaves Difference from Control (Pool 0)
30
20
10
0
-10
-20
+25 Diff
+50 Diff
+75 Diff
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

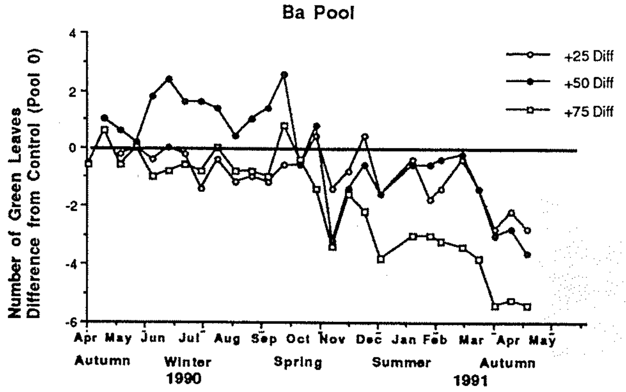

Ba Pool
Percentage Dead Leaves Difference from Control (Pool 0)
30
20
10
0
-10
+25 Diff
+50 Diff
+75 Diff
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

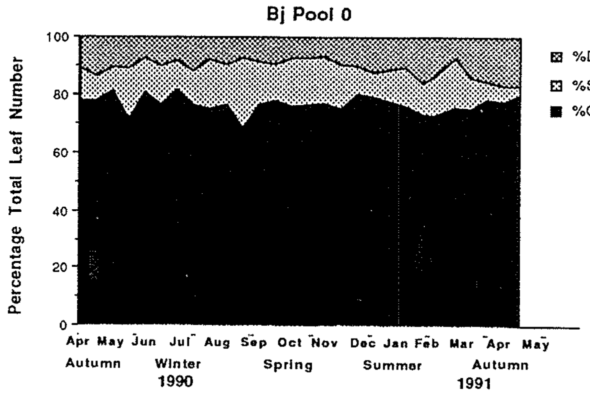

Ba Drought
Percentage Dead Leaves Difference from Control (Drought 0)
60
40
20
0
-20
-50 Diff
-100 Diff
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn Winter Spring Summer Autumn
1990
1991

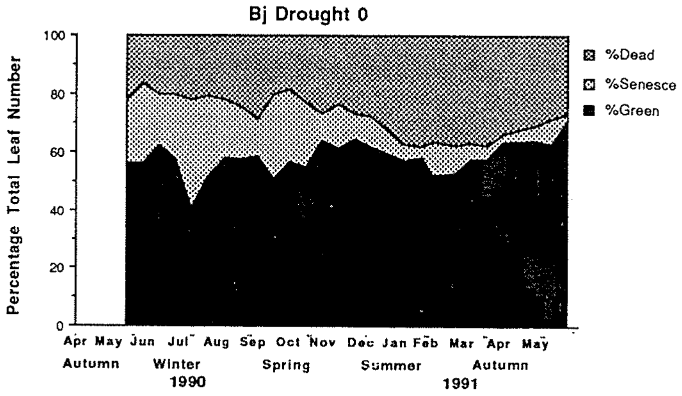

Ba Drought
-50 Diff
-100 Diff
Total Number of Leaves
Difference from Control (Drought 0)
8
6
4
2
0
-2
-4
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

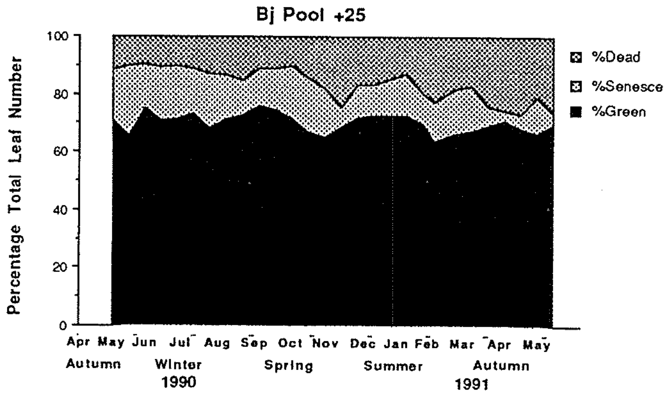

Ba Pool
+25 Diff
+50 Diff
+75 Diff
Total Number of Leaves
Difference from Control (Pool 0)
4
2
0
-2
-4
-6
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

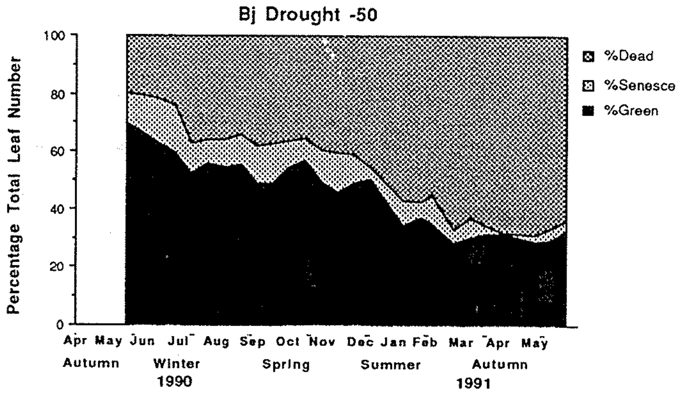

Ba Drought
-50 Diff
-100 Diff
Number of Green Leaves
Difference from Control (Drought 0)
10
5
0
-5
-10
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

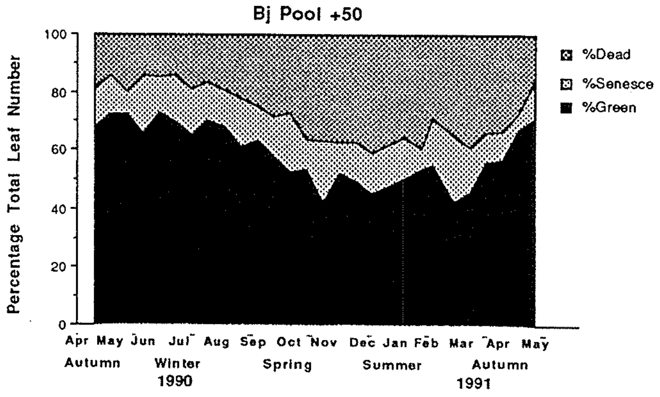

Ba Pool
+25 Diff
+50 Diff
+75 Diff
Number of Green Leaves
Difference from Control (Pool 0)
4
2
0
-2
-4
-6
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

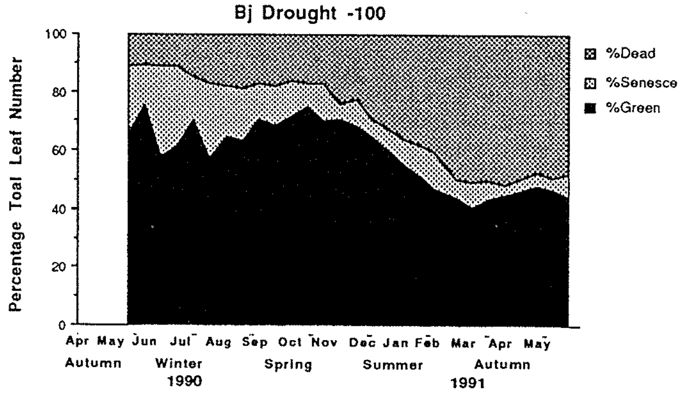

Bj Pool 0

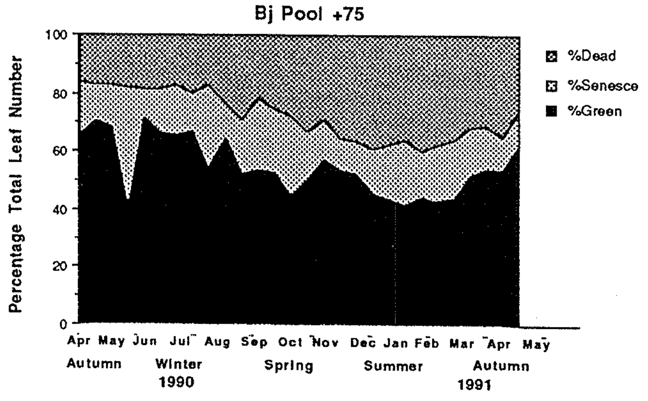

Bj Drought 0


Bj Pool +25

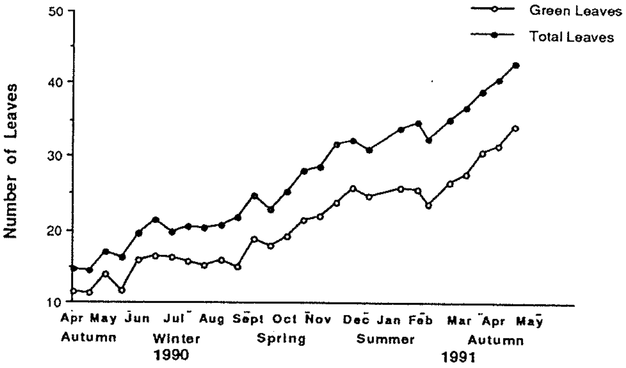

Bj Drought -50


Bj Pool +50

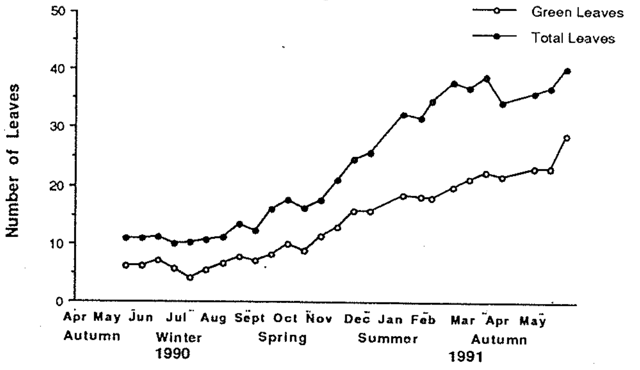

Bj Drought -100


Bj Pool +75

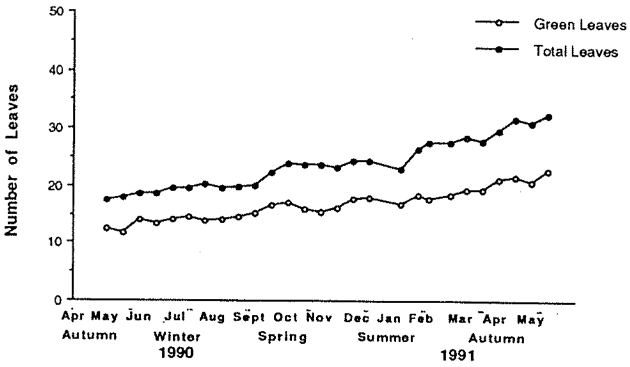
Bj Pool 0



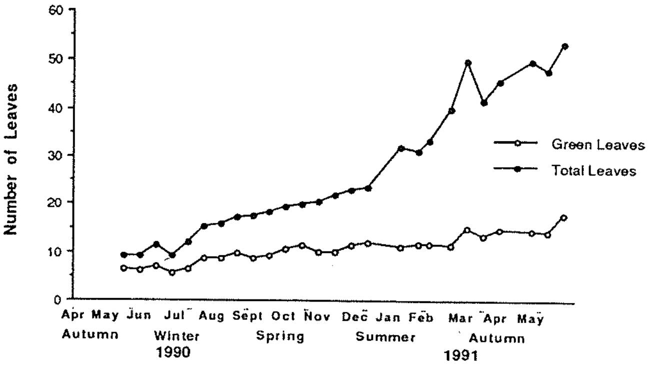
Bj Drought 0



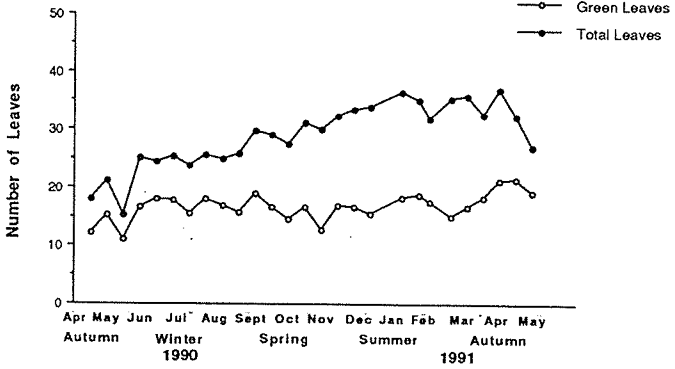
Bj Pool +25



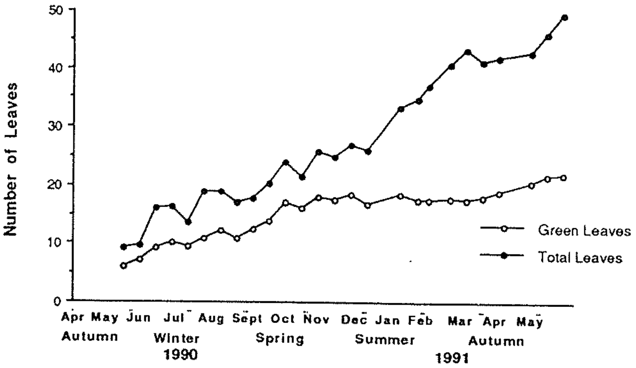
Bj Drought -50



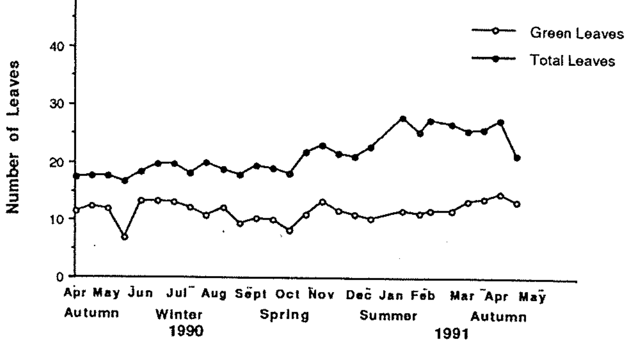
Bj Pool +50

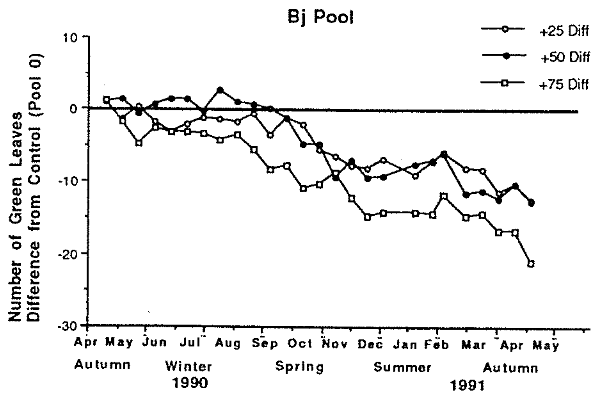


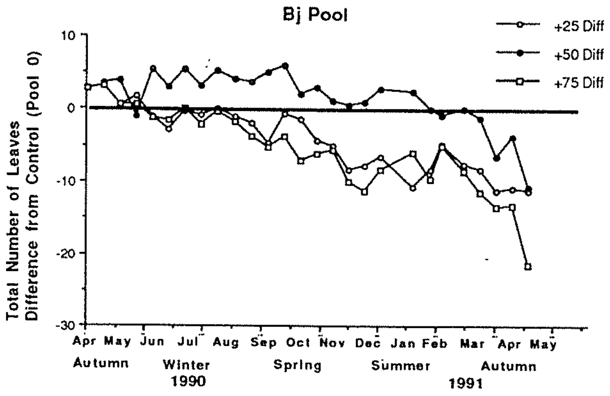
Bj Drought -100

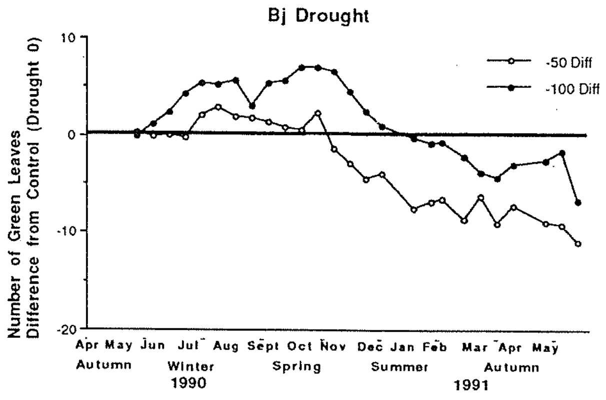


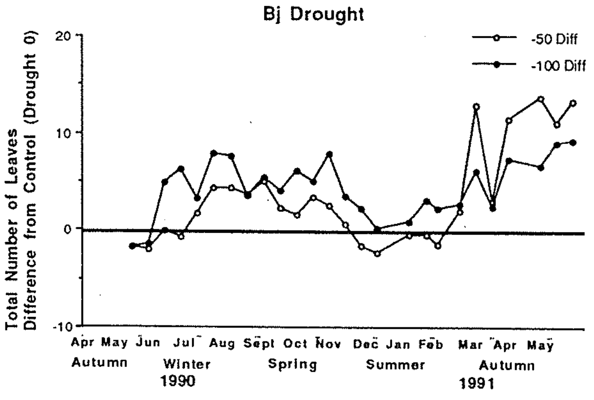
Bj Pool +75

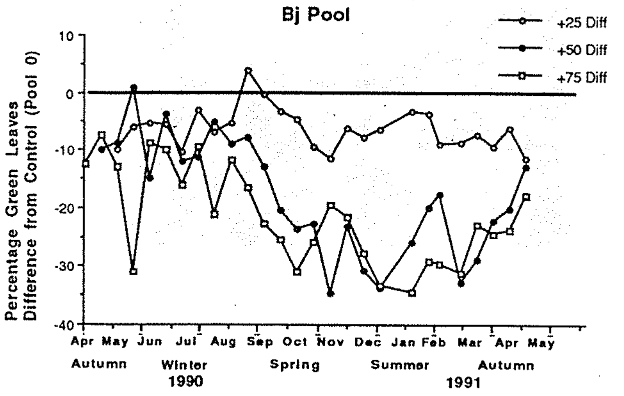


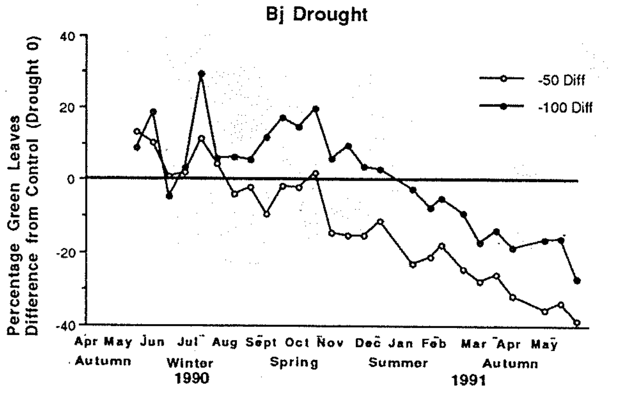

Bj Pool
+25 Diff
+50 Diff
+75 Diff
Number of Green Leaves
Difference from Control (Pool 0)
10
0
-10
-20
-30
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

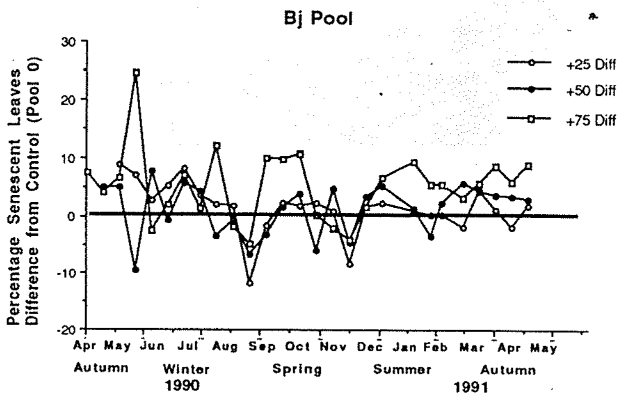

Bj Pool
+25 Diff
+50 Diff
+75 Diff
Total Number of Leaves
Difference from Control (Pool 0)
10
0
-10
-20
-30
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991

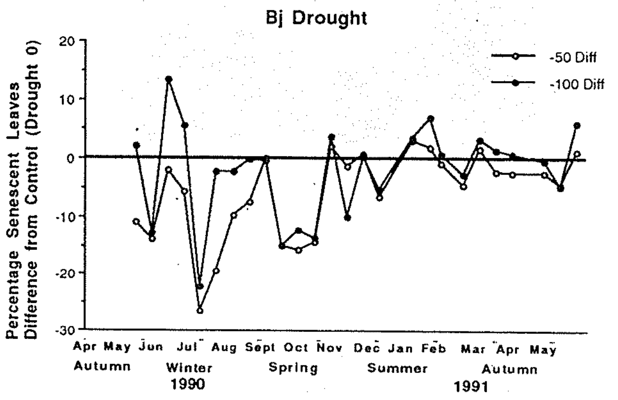

Bj Drought
-50 Diff
-100 Diff
Number of Green Leaves
Difference from Control (Drought 0)
10
0
-10
-20
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991


Bj Drought
-50 Diff
-100 Diff
Total Number of Leaves
Difference from Control (Drought 0)
20
10
0
-10
Apr May Jun Jul Aug Sept Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991


Bj Pool


Bj Drought


Bj Pool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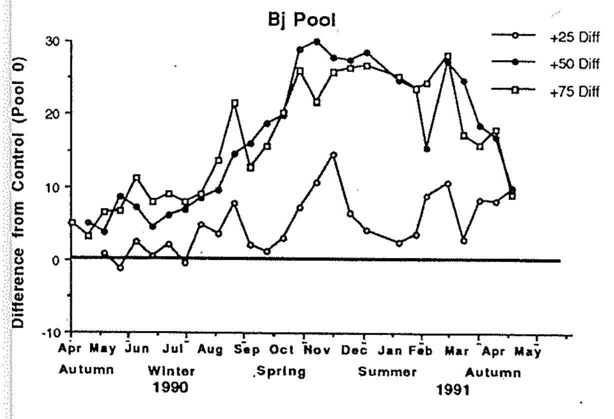
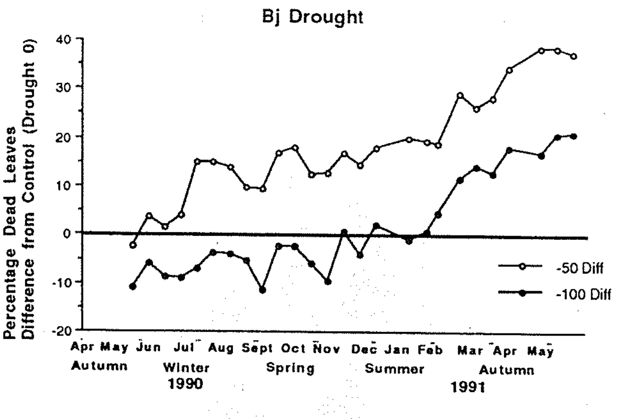
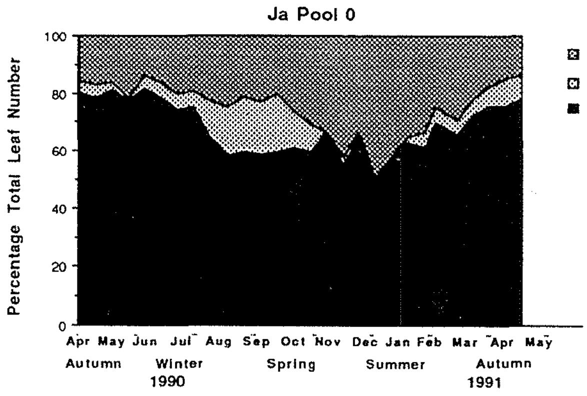
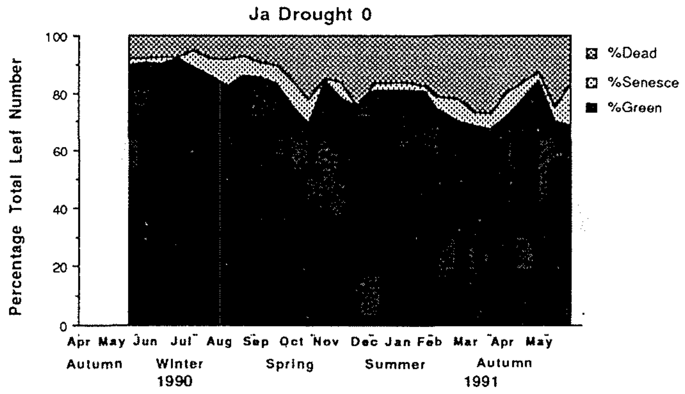
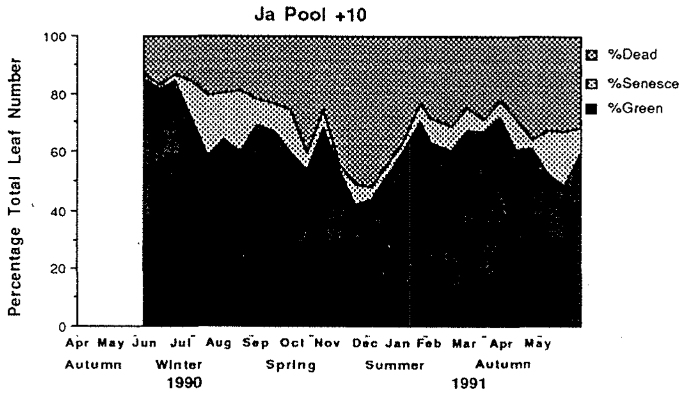
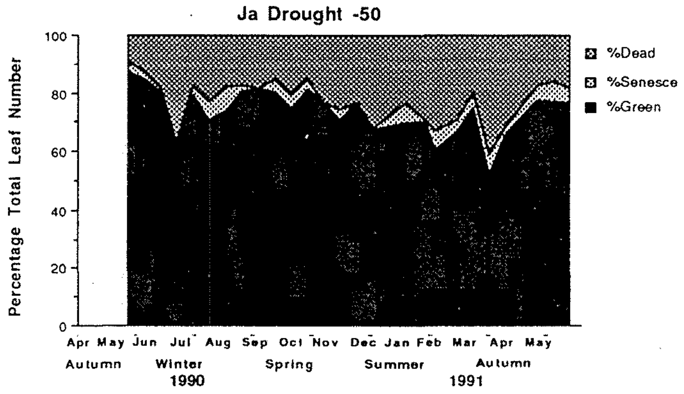

Bj Pool

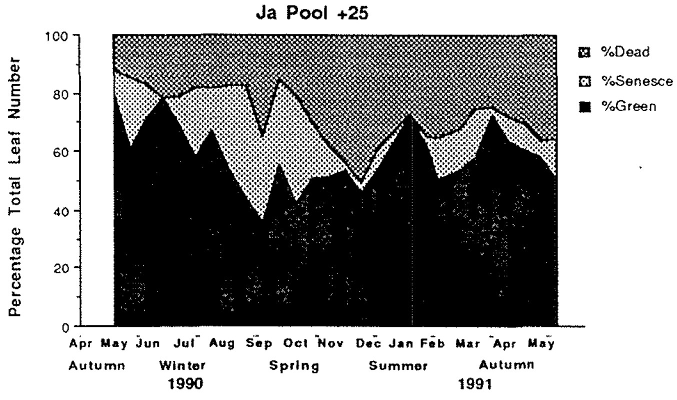

Bj Drought

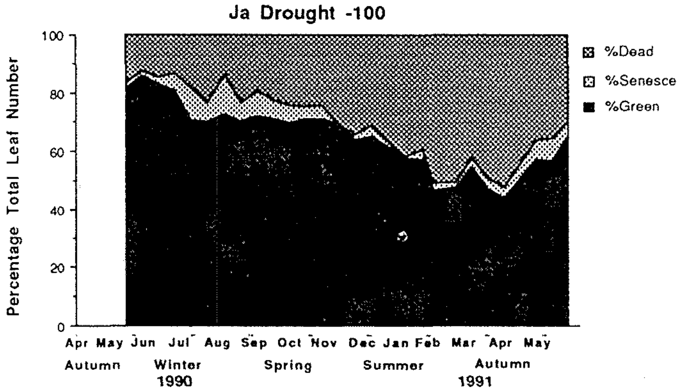

Ja Pool 0

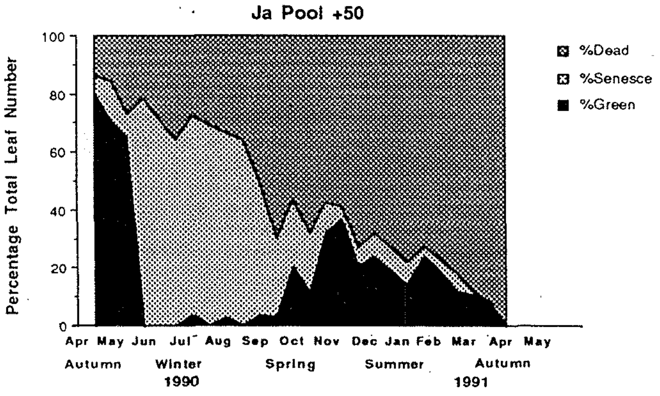

Ja Drought 0

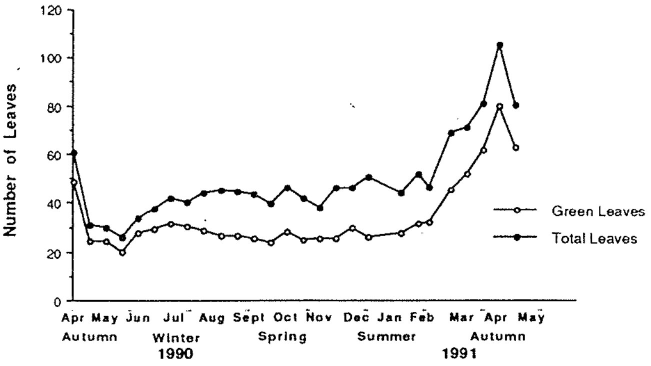

Ja Pool +10


Ja Drought -50

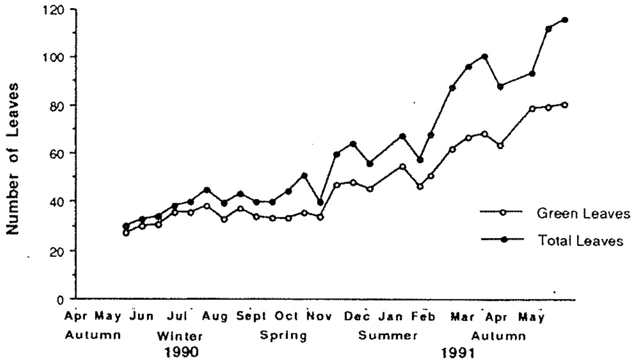

Ja Pool +25


Ja Drought -100

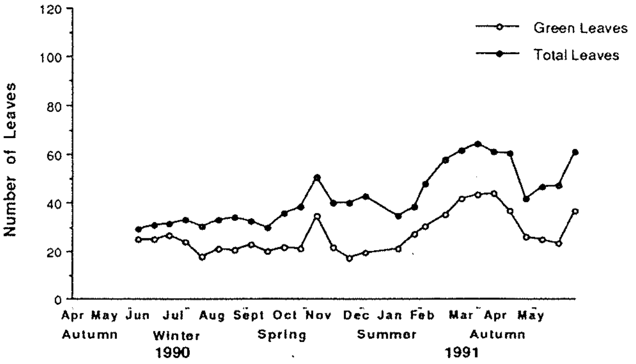

Ja Pool +50



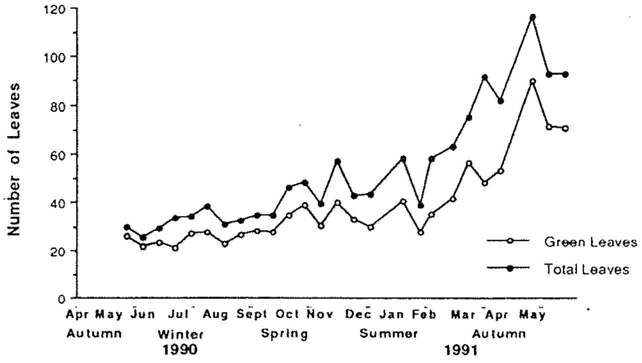
Ja Pool 0



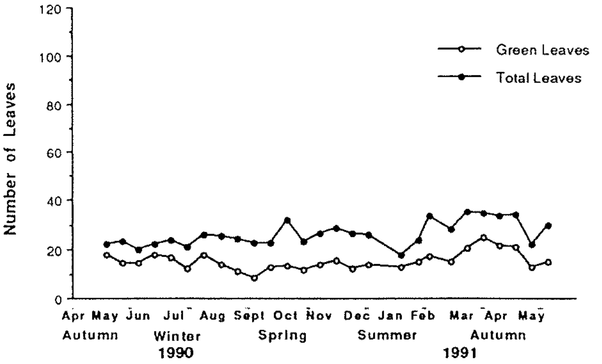
Ja Drought 0



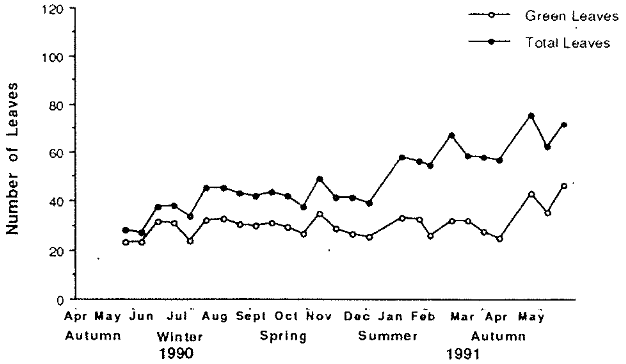
Ja Pool +10



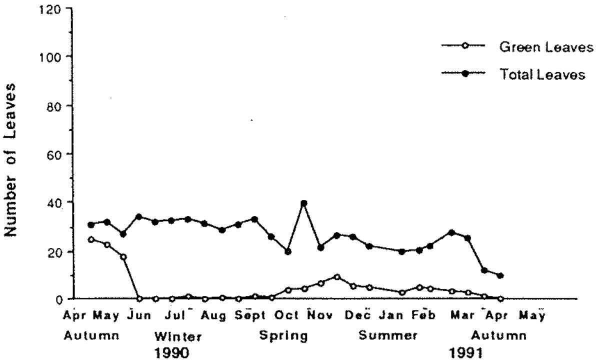
Ja Drought -50



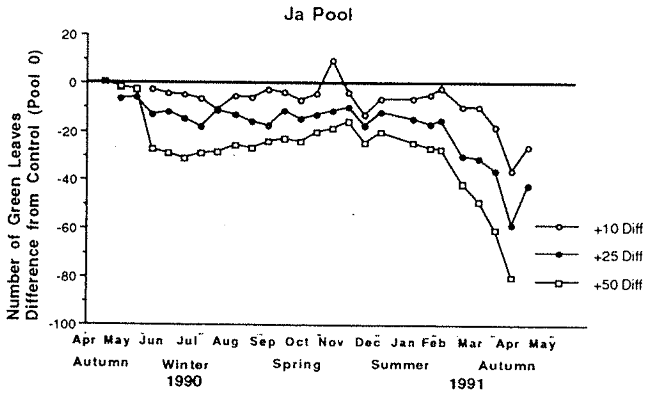
Ja Pool +25

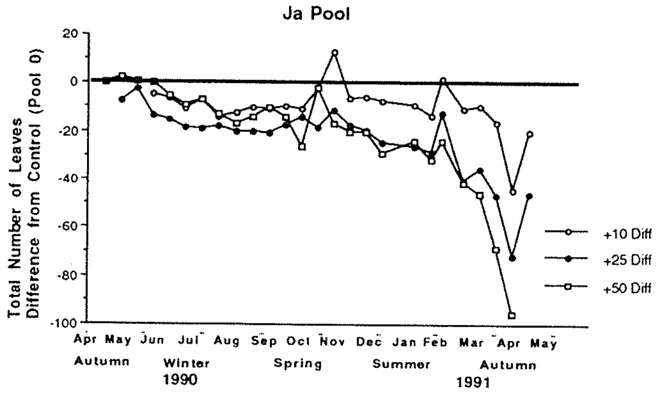


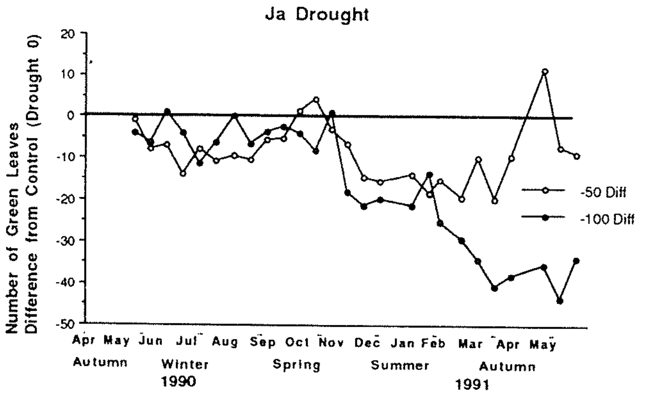
Ja Drought -100

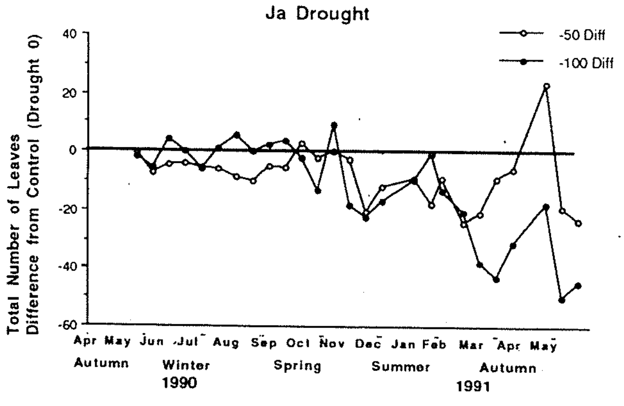


Ja Pool +50


Ja Pool
Number of Green Leaves
Difference from Control (Pool 0)
20
0
-20
-40
-60
-80
-100
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991
+10 Diff
+25 Diff
+50 Diff


Ja Pool
Total Number of Leaves
Difference from Control (Pool 0)
20
0
-20
-40
-60
-80
-100
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991
+10 Diff
+25 Diff
+50 Diff


Ja Drought
Number of Green Leaves
Difference from Control (Drought 0)
20
10
0
-10
-20
-30
-40
-50
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
Autumn
Winter
1990
Spring
Summer
Autumn
1991
-50 Diff
-100 Diff


Ja Drought
-50 Diff
-100 Diff
Total Number of Leaves
Difference from Control (Drought 0)
40
20
0
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-60
Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May
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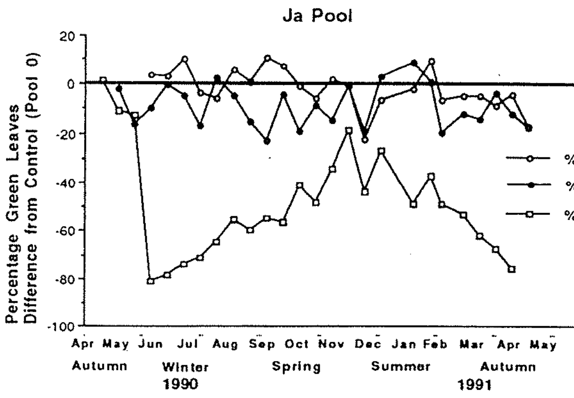
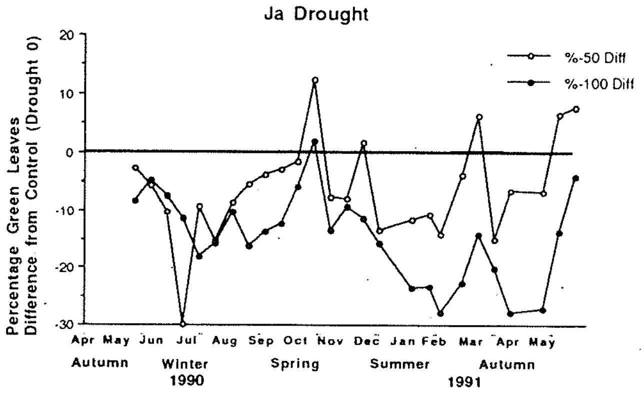
Winter
1990
Spring
Summer
Autumn
1991


Ja Pool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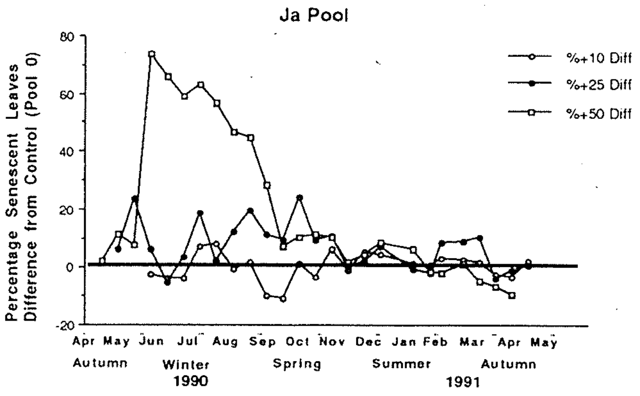
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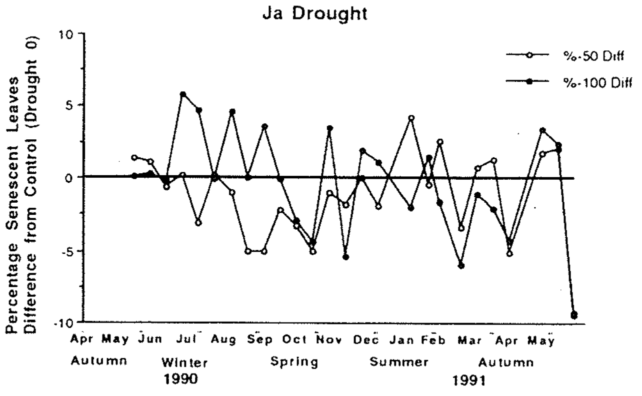
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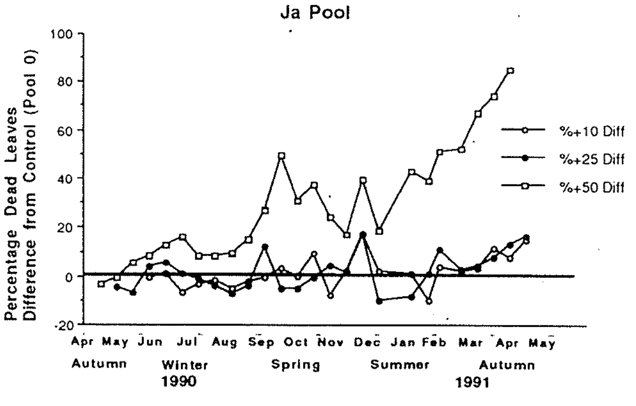
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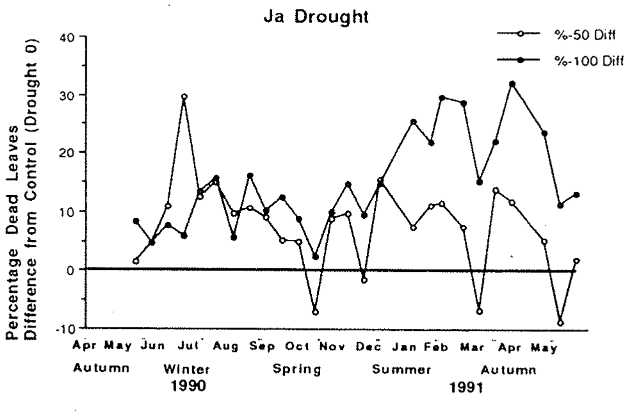
Ja Drought

Water Authority
of Western Australia

EPA

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