Salinity and Nutrients; Growth and Water Use of Aquatic Macrophytes Under Controlled and Natural Conditions

by

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Summary

Both salinity and eutrophication are regarded as significant threats to freshwater habitats. This research addresses several issues related to these critical problems. The first was to evaluate the potential for nutrient load to alter plant performance under saline conditions. In *Bolboschoenus medianus,* salinity was found to reduce the relative growth rate (RGR), whilst higher nutrient loads generally increased the RGR. The benefits of higher nutrient loads however diminished as salinities increased, suggesting a limited potential for nutrients to improve plant performance. Responses to nutrient load and salinity were specific; with nutrient load increasing the RGR via an increase in the leaf area ratio (LAR), and salinity reducing the RGR via a reduction in the net assimilation rate (NAR). Reductions in NAR in response to salinity were associated with lower rates of photosynthesis. Increases in LAR in response to higher nutrient loads were associated with a shift in biomass allocation from roots to leaves. A prominent response of *B. medianus* to higher salinities was a change in biomass allocation from culms to tubers.

The second objective was to determine if species with contrasting RGRs would demonstrate differential responses to salinity-nutrient regimes, as predicted by the plant strategy model of Grime. To explore this, the influence of salinity-nutrient regimes on the performance of *Typha domingensis* and *Baumea arthrophylla*, with putative high and low RGRs, respectively was tested. As anticipated *B. arthrophylla* was found to have a considerably lower RGR compared to *T. domingensis*. As predicted by Grimes' model the RGR of *B. arthrophylla* was unaffected by nutrient load regardless of salinity, whilst the RGR of *T. domingensis* was increased by higher nutrient loads. In both species productivity was reduced by salinity. The decline in RGR in response to salinity was however steeper in *T. domingensis* than *B. arthrophylla* at the higher nutrient loads, demonstrating a greater sensitivity to salinity, and again a limited capacity for nutrients to enhance growth as salinities increase. As found in *B. medianus*, the response to nutrient load and salinity were specific in *T. domingensis*; with LAR increasing in response to higher nutrient loads and NAR declining in response to salinity. In *B. arthrophylla,* growth analysis did not clearly

demonstrate specificity in responses to salinity and nutrient load. LAR was reduced by salinity and unaffected by nutrient load, however, NAR was reduced by both salinity and the high nutrient load. Despite this, specificity to salinity and nutrient load in *B. arthrophylla* was demonstrated, since most other measured parameters were affected by salinity but unaffected by nutrient load. As observed in *B. medianus*, *B. arthrophylla* responded to increasing salinity by a shift in biomass allocation from stems to rhizomes.

The third aspect of this research was to assess the influence of saline ground water on soil and surface water salinities within ephemeral wetlands. Salinities were monitored within three sites at Bool Lagoon; a major wetland in the lower south east of South Australia. Substantial changes in surface water, and soil salinities in the 0-15 cm depth class, occurred in response to drawdown at all sites, even where the salinity of the ground water was only 3 dS m^{-1}. Salinities in the 15-30 cm were more stable. The presence of a fresh water lens over saline ground water (18 dS m^{-1}) appeared to minimise the impact of ground water on soil salinities. Soil and surface water salinities were considerably higher at a site isolated from the main wetland system with a ground water salinity of 15 dS m^{-1}, and demonstrated the significance of drawdown duration and flushing on the salt balance.

The water balance of wetlands was considered an essential factor influencing salinities within wetlands systems. Therefore rates of evaporation for two morphologically distinct macrophytes, *T. domingensis* and *B. arthrophylla*, were estimated using the Penman-Monteith equation and compared to open water. This permitted the potential impact of vegetation, vegetation type and salinity on the water balance of wetlands to be evaluated. Canopy transpiration differed between vegetation types and between sites. Differences were driven primarily by differences in leaf area indices (LAIs) rather than by differences in vegetation height or stomatal resistance. Although lower LAIs yielded lower rates of canopy transpiration, it also increased the penetration of solar radiation to the water body below the canopy. Consequently, differences in canopy transpiration were less apparent when total water loss; the sum of canopy transpiration and evaporation of water below the canopy, were compared. Water loss from vegetation was found to be strongly influenced by VPD, whilst

evaporation from open water was determined primarily by net radiation. As such, differences in rates of water loss from open water and vegetation varied depending on climatic conditions. Calculations based on meteorological conditions in February '97, when the mean vapour pressure deficit was high, indicated that under these conditions water loss from *T. domingensis* or *B. arthrophylla* canopies were greater than open water when the LAI was greater than 3. When water loss below the canopy is also considered, then water loss from these stands exceeded open water when the LAI was greater than 0.5. The findings highlight the importance of water loss below the canopy in evaluating the impact of vegetation on the water balance.

Declaration

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

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Table A. Glossary of symbols and units.

Symbol	Meaning	Units
	Leaf gas exchange characteristics	
	Assimilation	μmol CO_2 m^{-2} s^{-1}
g_s	Stomatal conductance	mmol m^{-2} s^{-1}
r_s	Stomatal resistance	s m^{-1}
I	Irradiance	μmol m^{-2} s^{-1}
C_i	Intercellular CO_2 concentration	ppm
C_a	Ambient concentration of CO_2	ppm
	Photosynthesis vs Irradiance Parameters	
P_{max}	Light saturated rate of photosynthesis	μmol CO_2 m^{-2} s^{-1}
I_k	Irradiance at which photosynthesis saturates	μmol m^{-2} s^{-1}
R	Dark respiration rate	μmol CO_2 m^{-2} s^{-1}
α	Alpha: initial slope of photosynthesis versus irradiance response	μmol CO_2 (μmol Irradiance)$^{-1}$
	Water use efficiency	
WUE	Water use efficiency	
$\Delta‰$	Carbon isotope discrimination	‰
$\delta^{13}‰$	Isotopic composition of carbon	‰
	Growth analysis	
RGR	Relative growth rate	mg g^{-1} d^{-1}
NAR	Net assimilation rate	g m^{-2} d^{-1}
LAR	Leaf area ratio	m^2 kg^{-1}
SLA	Specific leaf area	m^2 kg^{-1}
RWR	Root weight ratio	g g^{-1}
LWR	Leaf weight ratio	g g^{-1}
	Evapotranspiration	
E	Evapotranspiration; flux density of water vapour in air	L m^{-2} h^{-1} L m^{-2} d^{-12}
VPD	Vapour pressure deficit	kPa
r_l or r_s	Leaf (stomatal) resistance to water vapour	s m^{-1}
r_c	Canopy resistance to water vapour loss	s m^{-1}
r_a	Aerodynamic resistance	s m^{-1}
E_c	Canopy transpiration	L m^{-2}
E_w	Evaporation of water below the canopy	L m^{-2}
E_{total}	Total evapotranspiration (E_c + E_w)	L m^{-2}
LAI	Leaf area index	m^2 m^{-2}
$\mathcal{K}$	Light extinction coefficient in canopy	nil
α	Albedo	nil

Chapter 1. Introduction

1.1 Crucial issues for southern Australian wetlands

Despite the extent and magnitude of salinisation in wetland systems the potential impact that elevated salinities may have on freshwater macrophytes has received inadequate attention (Hart *et al.* 1991). It is however apparent that many freshwater macrophytes are quite sensitive to salinity. James and Hart (1993) found growth to be impaired at 2000 mg NaCl L^{-1} in four common freshwater macrophytes representing a range of growth forms. Moreover, field studies suggest that once salinities approach 4000 mg L^{-1} most freshwater macrophytes are absent (Brock 1981; Brock and Lane 1983; Brock and Shiel 1983; Hart *et al.* 1991).

This research was initiated to facilitate a broader understanding of the responses of aquatic macrophytes to salinity. In particular the role of nutrients in the response of aquatic vegetation to salinity is examined, since nutrient addition has been demonstrated to enhance productivity under saline conditions in a number of crop or salt marsh species. This is of significance as nutrient loads into wetlands are inherently variable on both temporal and spatial scales (Brett 1989). As such, high nutrient loads may be coupled with high salinities as found in a number of wetlands associated with the Murray River (Goonan *et al.* 1992). The variable nature of nutrient loads within wetlands will be exacerbated by eutrophication, considered nationally as a serious threat to freshwater habitats (Cullen 1986; SOTEAC 1996).

It is recognised that salinity within wetlands is strongly influenced by the hydrological characteristics of the wetland and will therefore be subject to dynamic fluctuations both spatially and temporally. Hatton and Evans (1997) claim that the significance of ground water in wetlands systems is poorly understood. Whilst changes in surface water salinities over time have been documented for a large number of southern Australian wetlands by Brock (1981) and Brock and Lane (1983), the work of Froend *et al.* (1987) and Mensforth (1996), are possibly the only instances where soil salinities have been measured within seasonally ephemeral wetlands and the influence of saline ground water discussed.

Southern Australia predominantly experiences a Mediterranean climate where evaporation exceeds precipitation over summer, causing water levels within many wetlands to drawdown. Where a shallow saline ground water table is present, the drying of the soil surface will promote the capillary rise of saline ground water and hence the expression of salts at the sediment surface. The influence of aquatic vegetation on the water balance of wetlands may therefore play a critical role in the process of salinisation. The impact of vegetation on the water balance remains equivocal, with reports indicating both exacerbation and inhibition of water loss by aquatic macrophytes. As demands on water resources escalate there exists a need to define more clearly the water requirements of natural ecosystems, and hence water use by aquatic vegetation.

The following review provides background information related to these issues. A number of terms are frequently used in quantifying salinity, electrical conductivity (EC) expressed as dS m^{-1}, total soluble salts (TSS) expressed in mg L^{-1}, and molar concentrations of NaCl. Conversion from dS m^{-1} to mg L^{-1} is achieved by multiplying conductivity values in dS m^{-1} by 640 (Ghassemi *et al.* 1995). Where molar concentrations of NaCl have been approximated from mg L^{-1} (TSS) reported in the literature the assumption was made that all salts were present as NaCl, and as such are approximations. Total dissolved solids (TDS, mg L^{-1}) is also used to define salinity and refers to the residual weight following evaporation of a known volume of water which has been filtered to remove particulate matter (Peck *et al.* 1983). Total dissolved solids however closely approximates total soluble solids (TSS = 1.05 TDS) and the units are generally interchanged without adjustment.

1.2 The salinisation of freshwater habitats

At a national level increasing salinity is recognised as a significant threat to freshwater habitats (SOTEAC 1996; de Jong 1997). Salinisation of water resources is not however a problem isolated to Australia; Argentina, China, Commonwealth of Independent States, India, Iran, Iraq, South Africa, Thailand, and the United States of America are also plagued by land and water salinisation (Ghassemi *et al.* 1995). Globally 76.6 Mha of cultivated land is salinised as a consequence of human impacts (Ghassemi *et al.* 1995). In Australia the states most affected

by salinity are Victoria, Western Australia and South Australia with 150 000 ha, 1.6 Mha and 400 000 ha affected by dryland salinity, respectively (SOTEAC 1996). Substantial areas of irrigated land are also affected by salinity.

Current and historical agricultural practices are regarded as the prime causative agents for salinity increases within Australia (Peck *et al.* 1983). The replacement of deep rooted native vegetation with pasture crops which have lower evapotranspiration losses has increased aquifer recharge, causing saline ground water tables to rise (Wood 1924). Where the water table is shallow and saline, evaporation of water from the soil surface will result in the capillary rise of saline ground water, with the subsequent expression of subsurface salts at the sediment surface (Peck *et al.* 1983; WPODSIA 1982). Where poor quality irrigation water is used additional salts may be introduced into the soil and ground water. In most instances salts present in the ground water originate from past or present oceanic influences (Flowers and Yeo 1986). As such, the principle ions concerned are those dominant in sea water; Na and Cl (Flowers and Yeo 1986).

The depth of a saline water table which will result in soil salinisation is referred to as the critical depth (Ghassemi *et al.* 1995). The critical depth for a range of soil types varies from 0.9 to 2 m for irrigated land, and from 1.6 to 6.3 m for dryland areas (Peck 1978). For irrigated soils the water table depth can be shallower than in dryland areas, as accumulated salts will be leached from the soil more regularly. In the major irrigation regions of Victoria the ground water table has risen over the last 50 years such that it now lies only a metre below the surface (Hart *et al.* 1990,1991). Ground water salinities in these regions range from 2000 mg L^{-1} to 10000 mg L^{-1} (Hart *et al.* 1990,1991).

Rising water tables not only result in land salinisation, but directly and indirectly increase salinities within rivers and wetlands. Directly, the increased volume and pressurisation of aquifers can increase seepage of saline ground water into watercourses (Peck *et al.* 1983; Ghassemi *et al.* 1995). Indirectly, salinities within wetlands can increase due to surface runoff from salinised land. The Wimmera river near Jeparit Victoria now experiences salinities of

7000-8000 mg L^{-1} highlighting the compounding salinity problem within our water systems (Hart *et al.* 1991). In south-western Australia many rivers with high annual run-off have average salinities in excess of 2000 mg L^{-1} (Ghassemi *et al.* 1995). Water courses in the upper south east of South Australia have surface water salinities which vary from 1000 mg L^{-1} to 4000 mg L^{-1} under moderate water flows. Salinities exceed these levels when flows are low at the end of winter, as salinities are then more strongly influenced by ground water inflow. Flushing at the beginning of flow periods also increases salinities (USEDSFMPPSC 1993).

Salinisation of watercourses may be compounded by strategies aimed at alleviating land salinisation. In particular the drainage of saline ground water into river systems has been proposed (Hart *et al.* 1990). James and Hart (1993) suggest that such practices could increase the salinity of natural freshwater wetlands to around 5000 mg L^{-1} (the criteria for saline waters set by the Australian Water Research Council) exceeding the upper limits of tolerance of many freshwater macrophytes (Hart *et al.* 1991).

The direct impact of rising saline ground water tables on wetlands will be dependant on the degree of interaction the wetland has with the ground water. Most wetlands have some form of interchange with ground water. The exception being perched wetlands where the wetland sits well above the level of the ground water and receives only surface water (Mitsch and Gosselink 1993). In wetlands where ground water is intercepted, the nature of the interchange may vary. Some wetlands may both intercept ground water and discharge it as surface flow (springs/seeps), whilst others may only intercept it (Mitsch and Gosselink 1993). In these systems water quality will be influenced by the quality of both ground water and surface water inputs. Paijmans *et al.* (1985) suggests that significant ground water flows into wetland systems in Australia is restricted to the discharge zones of major basins such as the Murray Basin, the Great Artesian Basin and the Perth coastal plain systems. Ground water seepage into wetlands will occur when the aquifer is sufficiently pressurised and there exists a suitable connection to the surface (Paijmans *et al.* 1985).

In the absence of direct ground water discharge the presence of a shallow ground water table

may increase salt loads into wetlands systems. In summer when evaporation exceeds precipitation water levels fall. If drawdown events are sufficient to promote the capillary rise of saline ground water salts will accumulate at the sediment surface (Froend *et al.* 1987). Wetlands may also become salinised via surface water flow from saline catchments. Whilst inflow salinities may be marginal, evaporation of surface water over summer will increase salt concentrations.

If salts entering the system via ground water discharge, or surface water inflows, are not periodically leached from the system, salts will accumulate over time. Salts may be leached from the system laterally via surface flow, or vertically via ground water recharge. In ground water discharge zones the hydraulic gradient may not permit the transmittance of surface water away as ground water (Paijmans *et al.* 1985), hindering the leaching of salts into the ground water table. Under these conditions surface flow will be the prime mechanisms by which salts are removed from the system.

Salinity not only affects natural freshwater systems but may also be encountered in constructed wetlands. The ability of wetlands to remove pollutants and excess nutrients from waste waters is well documented (Bavor and Mitchell 1994). As such, the construction of artificial wetlands to treat local effluent and storm water discharges is increasing in popularity. Within Adelaide a number of artificial wetlands have been constructed over the last 20 years to manage storm water discharges, or to treat local effluent. Salinity may be encountered by such wetlands when the sediments are naturally saline, when they intercept saline ground water, or when saline effluent enters the wetland for purification. Within Adelaide a number of wetlands have been created within coastal regions which overlie shallow, highly saline ground water; Greenfields, The Barker Inlet, Magazine Creek and Range wetlands.

1.3 The impact of salinity on plant performance

It should be noted that the physiological bases underlying salinity imposed growth reductions have been developed primarily from crop research, as such there is an inevitable bias within this review towards these genera.

The deleterious impact of non-lethal levels of NaCl on plant performance is ultimately characterised by reductions in above and below ground biomass, coupled with reductions in crop yield/reproductive effort. Concentrations of NaCl which do not cause chlorosis, leaf burn or necrosis are classified as non-toxic (Downton 1977; Schwarz and Gale 1981). Above ground biomass tends to be reduced to a greater extent than below ground biomass, resulting in lower above ground to below ground ratios (Greenway and Munns 1980; Munns and Termaat 1986). Reductions in above ground biomass have been associated with an increased rate of leaf senescence, and reductions in both plant height and leaf size. The extent to which plant productivity is reduced relative to a non-salinised control is often used as an index of a species' sensitivity/tolerance to salinity. Salinity tolerance differs dramatically between genotypes, species and even varieties.

Despite attempts to elucidate a principle mechanism to explain differential salinity tolerances of species, it is apparent that no one factor is responsible. In contrast, susceptibility to salinity appears to be mediated by three main mechanisms; a low external water potential, ion toxicity and nutrient imbalance. The relative impact of each will vary for individual species, hence a species may demonstrate greater tolerance via a particular suite of physiological and morphological characters.

1.3.1 Low external water potential

Under saline conditions the external water potential is lowered, imposing a water deficit which can reduce cell turgor and hence cell expansion. As plant growth is a function of both cell division and cell expansion a reduction in the rate of cell expansion will ultimately reduce growth. The capacity of plants to restore turgor appears to be variable. For some plants growth upon exposure to salinity is restricted by a loss of turgor, yet for others turgor is rapidly regained (Munns 1993). However, even in those plants in which turgor is regained growth fails to fully recover (Munns 1993). This phenomenon has been demonstrated by Theil *et al.* (1988), Cramer and Bowman (1991) and Yeo *et al.* (1991). As reviewed by Munns (1993) all cases displayed a rapid but transient reduction in leaf elongation rates when plants were

exposed to salinities exceeding 50 mM NaCl. This transient reduction is attributed to a reduction in cell turgor. Although the rate of leaf elongation recovers within hours (via osmotic adjustment), it is incomplete, remaining slightly lower than the original rate. This effect can not be explained by a reduction in turgor, since turgor has been restored. Experiments in which root pressurisation techniques have been employed to maintain shoot turgor of salinised plants also demonstrate similar growth reductions (Munns and Termaat 1986; Passioura 1988).

These effects are not considered to be salt specific, as they can be produced with other osmoticum, and occur prior to high foliar ion concentration being reached (Munns 1993). Munns (1993) concludes that these changes are mediated by root signal(s), possibly phytohormones, sent to the shoot in response to low external water potential at the root. A considerable body of work implicates the involvement of ABA in this message (Munns and Cramer 1996).

1.3.2 Ion toxicity

1.3.2.1 NaCl uptake

Na and Cl may enter the shoot via apoplastic or symplastic pathways (Pitman 1977). In developing regions of the roots where the casparian strip is incomplete apoplastic uptake may occur (Pitman 1977). As the cytoplasm is negatively charged with respect to the apoplast, and intracellular Na concentrations generally lower, Na may enter the symplasm passively down its electrochemical gradient (Cheeseman 1988). However, access into the cell is dictated by the selective permeability of transmembrane transport systems. In the absence of a specific Na channel symplastic uptake must occur via other transport systems, although these mechanisms remain ill defined.

As the uptake of NaCl into the xylem is poorly regulated in most glycophytes, the concentration of Na and Cl in leaf tissues will increase over time, in proportion to the external concentration. The rate of Na delivery to the leaf is considered a product of the xylem concentration and the transpiration rate (Yeo and Flower 1986), however, transpiration rates have not been directly linked to Na accumulation in wheat (Nicolas *et al.* 1993) or rice (Yeo *et al.* 1985a).

Retranslocation of Na and Cl from the xylem or leaf tissue has been found in a number of species. This may potentially obscure direct relationships between transpiration and ion accumulation (Lessani and Marschner 1978; Jacoby 1979; Jeschke and Wolf 1988; Matoh *et al.* 1988). Despite this, a gradient in ion concentration with leaf age does exist (Yeo *et al.* 1985ab; Yeo *et al.* 1991). Yeo and Flowers (1986) claim that Na is preferentially delivered to older leaves, thereby protecting developing leaves. Furthermore, ions which are delivered to expanding leaves are diluted through growth, as a result concentrations increase more slowly than in fully expanded leaves (Schachtman and Munns 1992). Once fully expanded ion concentrations increase rapidly to toxic levels causing premature senescence (Yeo and Flowers 1986; Munns 1993; Schachtman and Munns 1992).

1.3.2.2 Vacuolar compartmentation

In order to protect sensitive cytoplasmic enzymes, Na and Cl are primarily stored in the vacuole (Greenway and Munns 1980). Na appears to be sequestered in the vacuole via a Na/H antiporter in the tonoplast. Salinity induced vacuolar alkalinisation resulting from the activation of this transport system, has been detected in barley roots (Martinez and Läuchli 1993), carrot cells (Reuveni 1993), sunflower roots (Ballesteros *et al.* 1997), and the herb *Plantago* (Staal *et al.* 1991) Amiloride which is known to block Na/H transport systems in animals also inhibited this transport system in sugar beet tonoplast vesicles (Blumwald *et al.* 1987). As such, there exists substantial evidence for a Na/H antiporter in the tonoplast and it is likely the vacuole functions as a significant sink for Na in some species. Greenway and Munns (1980) have speculated that species highly sensitive to NaCl may lack the capacity to sequester ions into the vacuole. This has been demonstrated in *Plantago* where Na/H anitport activity at the tonoplast was found in *P. maritimus*, a salt tolerant species, and not in *P. media*, a salt sensitive species (Staal *et al.* 1991).

1.3.2.3 Organic osmotica

Compartmentation of Na and Cl into the vacuole will increase its osmotic potential, necessitating osmotic adjustment of the cytoplasm. In glycophytes this is achieved with non-toxic organic compounds such as sucrose, and nitrogen based compounds (Greenway and Munns, 1980). In

halophytes; organic acids, nitrogen compounds and carbohydrates are used (Flowers *et al.* 1977). Glycinebetaine and proline are the two principle nitrogen based osmoticants found in plants. The contribution of glycinebetaine in osmotic adjustment is more convincing than proline, which tends to accumulate only under severe stress (Greenway and Munns 1980). The accumulation of glycinebetaine in the chloroplasts of spinach was able to explain 36% of the osmotic potential (Robinson and Jones 1986). In *Spartina alterniflora* (a salt marsh grass), whilst both glycinebetaine and proline increased in response to salinity, the concentration of glycinebetaine rather than proline was sufficient to account for osmotic adjustment (Cavalieri 1983). Beta aldehyde dehydrogenase (BADH) is an enzyme which gives rise to glycinebetaine. BADH mRNA has been shown to respond rapidly to changes in external NaCl concentration in sugar beet (McCue and Hanson 1992). This indicates that the production of glycinebetaine responds directly to salinity.

A number of higher plants from broad taxonomical groups have been found to accumulate glycinebetaine as an osmoticum in response to salinity stress (Story *et al.* 1977; Weigel *et al.* 1986; Robinson and Jones 1986; Hanson and Wyse 1982). The highest concentrations are however found in halophytes. In glycophytes, the level of glycinebetaine present is to some extent reflective of a species sensitivity to NaCl; tolerant species having higher concentrations and very sensitive species having none (Story *et al.* 1977).

1.3.2.4 Toxicity

Although under saline conditions ions taken up by the plant are compartmentalised within vacuoles their sink capacity will eventually be exhausted. Ions will then become concentrated in the cytoplasm or the cell wall. Concentrations within these two compartments will increase rapidly given their small volumes. Where apoplastic transport occurs, concentrations in the leaf apoplast will increase more rapidly than in the cytoplasm. This will result in loss of cell turgor, with cellular desiccation and death ensuing. Alternatively, symplastic transport will cause cytoplasmic concentrations in the leaf to increase faster than apoplastic concentrations, resulting in toxicity and cell death. This ultimately reduces leaf longevity (Oertli 1968; Yeo and Flowers 1986; Greenway and Munns 1980). Unless the emergence of new leaves matches the rate of

leaf loss the photosynthetic area will decline, reducing the supply of photosynthates. Growth will be restricted further and death will ultimately ensue (Munns and Termaat 1986; Munns 1993).

1.3.3 Nutrient imbalance

Salinity can adversely effect plant performance by interfering with nutrient uptake and transport processes (Lynch *et al.* 1987). Evidence from agricultural species and salt marsh species suggest that nutrient addition under saline conditions can enhance performance. Specifically, the significance of Ca, K and N in the response of vegetation to salinity has been demonstrated and is detailed below. It is important to note that whilst positive responses to nutrient addition are reported in crop species, reviews by Feigin (1985) and Mass and Hoffman (1977) indicate that sensitivity to salinity is also increased. Consequently, as salinity increases the benefits of nutrient addition diminish.

1.3.3.1 Calcium

Ca plays several important roles in plants. It is essential in cell division, cell wall development, and it also acts as a secondary messenger (Marschner 1995). Under saline conditions, where the concentration of Ca is not also increased, plant productivity has been found to be compromised by Ca deficiencies (Maas and Grieve 1987; Muhammed *et al.* 1987), and impaired ion selectivity (Epstein 1961; LaHaye and Epstein 1969). Ca deficiency is primarily observed in young leaves and is characterised by rolled and bleached leaves (Maas and Grieve 1987). Calcium deficiencies occur first in developing leaves as calcium is not readily translocated within the plant (Mass and Grieve 1987).

Impaired ion selectivity is induced by the perturbation of membrane bound Ca by Na (LaHaye and Epstein 1969; Cramer *et al.* 1985; Lynch and Läuchli 1988; Zidan *et al.* 1991). Impaired membrane selectivity under saline conditions results in a greater influx of Na, escalating the rate at which toxicity is reached (LaHaye and Epstein 1969; Lynch and Läuchli 1988). Reduced membrane selectivity has also been demonstrated to result in an increased leakage of K in some plants, which may also potentially impair performance (Epstein 1961; LaHaye and Epstein 1969).

Additional calcium is thought to improve plant performance under saline conditions by reducing Na uptake and K leakage, resulting in a lower Na/K ratio. The Na/K ratio is important in plant tolerance to salinity (Greenway and Munns 1980). Secondly, supplemental Ca prevents Ca deficiencies, thereby improving plant performance. The positive effects of additional calcium on plant growth under saline conditions has been documented for barley seedlings (Cramer *et al.* 1990), cotton seedlings (Kent and Laüchli 1985; Cramer *et al.* 1987), wheat plants (Hawkins and Lewis 1993ab), bean plants (LaHaye and Epstein 1969), corn plants (Maas and Grieve 1987), and rice plants (Muhammed *et al.* 1987; Grieve and Fujiyama 1987). Whilst the requirement for Ca under saline conditions will vary between species, studies of bean and rice suggest that a ratio of 17-18 is sufficient to minimise the effects of salinity directly related to Ca.

The literature provides strong evidence that the normal functions of Ca are perturbed by increasing the Na/Ca ratio, yet this may not be relevant under field conditions. Greenway and Munns (1980) claim that in saline soils, the average Na/Ca is 6 with a range of 4 to 24. However, in salinity experiments where Ca is not also added in addition to that contained in the base nutrient solution, the Na/Ca ratio will be considerably higher than that found under field conditions. This is likely to increase plant sensitivity to salinity.

1.3.3.2 Potassium

Plants require K to maintain cell turgor and hence cell expansion, and as a cofactor for many enzymes. *Invitro* synthesis of stromal proteins requires K concentrations between 50-150 mM, and a low Na/K ratio, reflecting the importance of K in metabolic processes (Ball *et al.* 1987). The importance of K in protein synthesis has been used to explain photosynthetic reductions occurring at low foliar K concentrations in the halophyte *Avicennia marina* (Ball *et al.* 1987) and in tomato leaves (Spencer and Possingham 1960). Quantum yield reductions resulting from foliar K deficiency were associated with lower concentrations of the D1 protein, an integral component of PS II (Ball *et al.* 1987).

Exposure to NaCl has been found to result in reduced foliar K concentrations in *Avicennia* (Ball

et al. 1987), barley (Storey and Wyn Jones 1978), and rice (Bohra and Doerffling 1993). Low K concentrations are thought to arise by Na competing with K for uptake sites on the plasma membrane (Epstein 1961). Intracellular K is also reduced by increased membrane permeability. This can be remedied at least partially by additional calcium as previously discussed. In addition, the release of K from stellar cells into the xylem may be suppressed by salinity in some species (Lynch and Läuchli 1984).

Using tobacco cell cultures Watad *et al.* (1991) found that NaCl adapted cells had intracellular K concentration 3.5 times greater than unadapted cells at 160 mM NaCl, suggesting that tolerance was in part mediated by increased intracellular K concentrations. The ameliorative effect of enhanced K nutrition, in plants subjected to saline conditions has been demonstrated in rice (Bohra and Doerffling 1993), barley (Helal *et al.* 1975) and Indian mustard (Garg *et al.* 1993). Bohra and Doerffling (1993) have shown K additions of 50 and 75 mg kg^{-1} soil, to increase yield and potential photosynthetic activity in a sensitive rice variety (IR28) grown at salinities of 5395 mg L^{-1}. K fertilisation also increased the K content, and lowered the Na content in rice straw, thus increasing the K/Na ratio. The importance of K nutrition is also indicated by a more salt tolerant rice variety (Pokkali) maintaining higher K concentration in straw tissue under saline conditions than the sensitive variety (IR28). In barley plants Helal *et al.* (1975) found 10 mM K significantly increased dry matter production of roots and shoots at 60 mM NaCl. No K effect was however obtained at 120 mM NaCl. However, high Na/Ca ratios may have influenced these findings. Under saline conditions, enhancing N, K and P fertility of the soil improved growth and yield in Indian Mustard. Higher K/Na ratios were again associated with improved productivity.

1.3.3.3 Nitrogen

Nitrogen assimilation is not only essential for plant growth and development but also in adaptation to salinity stress (Muhammad *et al.* 1984). Glycinebetaine and proline, metabolites of nitrogen assimilation contain 12% nitrogen (Cavalieri 1983), and often accumulate in plants under saline conditions (Storey *et al.* 1977). For plants which use glycinebetaine or proline in adaptation to saline conditions, the demand for N may increase significantly. In *Spartina*

alterniflora the concentration of nitrogen required to maintain growth (the critical nitrogen content) was found to increase under saline conditions (Bradley and Morris 1992). This may be associated with the production of glycinebetaine and proline which is stimulated by salinity in this species (Cavalieri 1983).

Salinity had been found to inhibit the uptake of NO_3 and/or NH_4 in barley (Muhammad *et al.* 1984; Helal *et al.* 1975), wheat (Hawkins and Lewis 1993a), citrus trees (Lea-Cox and Syvertsen 1993) and *Spartina alterniflora* (Bradley and Morris 1991). Where the requirement for nitrogen is increased by salinity or the uptake of nitrogen is competitively inhibited by salinity, increased productivity may be anticipated by nitrogen addition.

Field studies have found growth of *Spartina alterniflora* to be enhanced by N application (Broome *et al.* 1975; Buresh *et al.* 1980; Gallagher 1975). Garg *et al.* (1993) have shown that improving the soil fertility of Indian mustard (6, 4 and 2 g m^{-2} N, P_2O_5 and K_20, respectively) significantly lessened growth and seed yield reductions produced by salinity (50-150 mM). Under glasshouse conditions, nitrogen applications of 25 to 100 mg L^{-1} ($CO(NO_3)_2$) enhanced dry matter production of ryegrass throughout a range of salinities between 100 mg NaCl L^{-1} and 6000 mg NaCl L^{-1} (Mehanni and West 1992). Nitrogen applications of 200 mg L^{-1} elicited further small increases at all salinities, excluding 1520 mg NaCl L^{-1}, where productivity declined. Significant decreases in production resulted from N applications of 800 mg L^{-1}. Under field conditions, nitrogen fertilisation of 1.5 g m^{-2} also improved pasture yield across a range of salinities between 100 to 3000 mg L^{-1}. Although nitrogen addition did not lower the threshold at which salinity caused yield reductions it did reduce the extent of yield reduction (Mehanni and West 1992).

Growth response to N fertilisation can also be dependant on P supply. Yield of *S. alterniflora* in the field responded poorly to nitrogen application in the absence of additional P (Broome *et al.* 1975). During the first year of N fertilisation a maximal yield of approximately 10 metric tonnes ha^{-1} was achieve by N and P fertilisations of 33.6 g m^{-2} yr^{-1} and 7.4 g m^{-2} yr^{-1}, respectively (Broome *et al.* 1975). Yield failed to increase with N additions above this, possibly as P was not also increased. Interestingly, the response to subsequent fertilisation the following year was

considerably greater. Furthermore, the response to N and P fertilisation was linear, showing no evidence of saturation at 67.2 g N m^{-2} yr^{-1} (Broome *et al.* 1975).

1.3.4 Integrating the effects of salinity on plant performance

Relative growth rate is defined as the increase in biomass over time, per unit of initial biomass (Hunt 1982). It is a function of both the leaf area ratio (LAR), and the net assimilation rate (NAR). LAR represents the proportion of photosynthetic tissue relative to total plant biomass, whilst NAR represents the rate of biomass increase per unit leaf area (Hunt 1982). From this relationship growth may be reduced by salinity, via a reduction in the leaf area ratio, or a reduction in the net assimilation rate.

Salinity can reduce leaf expansion, resulting in smaller leaves, and can increase the rate of leaf senescence, reducing the total number of leaves. Consequently LAR may be reduced and hence growth. NAR is determined by both the rate of CO_2 assimilation and the respiration rate. The impact of salinity on either of these processes will ultimately influence NAR.

Maintenance respiration is described as the respiration at zero growth, that is the cost of resynthesising degraded biomass (Shwarz and Gale 1981). The greater the maintenance respiration the smaller the amount of carbon available for growth. It has been proposed that salinity will increase maintenance respiration by increasing the demand for compartmentation, secretion and repair processes (Greenway and Munns 1980; Schwarz and Gale 1981). At salinities which were not toxic, Schwarz and Gale (1981) found that maintenance respiration increased with increasing salinity in three out of four species examined. Salinities which produced symptoms of toxicity resulted in a decline in maintenance respiration. In *Xanthium* a salt tolerant species, increased maintenance respiration induced by salinity was able to explain 24% of the growth reduction (Schwarz and Gale 1981). Reductions in photosynthesis was able to explain the remaining growth reduction (Schwarz and Gale 1981).

Reductions in net photosynthesis under saline conditions have been reported for: glycophytes, ie rice (*Oryza sativa*) (Yeo *et al.* 1985b), bean (*Phaseolus vulgaris*) (Seeman and Crictchley 1985),

grapevine (*Vitus vinifera*) (Downton 1977), lemon tree (*Citrus lemon*) (Walker *et al.* 1993), and tupelo gum (*Nyssa aquaticum*) (Pezeshki 1987): and for salt tolerant/halophytic species, ie mangroves (*Avicennia marina, Aegiceras corniculatum*) (Ball and Farquhar 1984), alligator weed (*Alternanthera philoxeroides*) (Longstreth *et al.* 1984), and a marsh grass (*Spartina patens*) (Pezeshki and DeLaune 1993). Reductions in photosynthesis may be mediated by effects on the biochemical apparatus and via stomatal limitation of CO_2. Reduced stomatal conductance is frequently induced by salinity, and is considered to be mediated by ABA in response to a water deficit perceived at the root (Munns and Sharp 1993). Reductions in stomatal conductance can limit the flux of CO_2 into the leaf, leading to a decline in photosynthesis. Munns (1993) has also proposed that lower rates of photosynthesis may arise from feedback inhibition in response to the accumulation of carbohydrates in leaves. Carbohydrates are thought to accumulate in leaves of salinised plants as their utilisation is blocked by salinity (Munns 1993).

1.4 Salinity and freshwater macrophytes

The influence of salinity on freshwater macrophytes has previously been reviewed by Hart *et al.* (1991). This review summarises the findings of Hart *et al.* (1991) and includes additional reports from both Australian and overseas studies. The impact of salinity on flood tolerant trees is not discussed, but has been examined by Hart *et al.* (1991).

The surface water salinities over which freshwater macrophytes have been observed in the field, and the findings of experimentally imposed salinities are summarised in Table 1.1 and 1.2, respectively. As discussed by Hart *et al.* (1991), field surveys carried out by Brock and colleagues in the south-east of South Australia and the south-west of Western Australia, indicate that macrophyte species more commonly associated with freshwater habitats tend to be absent from sites with salinities in excess of 4000 mg L^{-1} (Brock 1981; Brock and Shiel 1983; Brock and Lane 1983). Sites with higher salinities were found to have lower species diversity, and once salinities exceeded 10 000 mg L^{-1} only halophytic species were recorded. Sites with salinities greater than 1000 mg L^{-1} excluded a number of aquatic species.

Of the species experimentally tested (Table 1.2) the most tolerant is *Phragmites*. As *Phragmites*

communus seeds were sourced from a salt mine, high tolerance may be associated with the evolution of tolerance mechanisms. Matoh *et al.* (1988) demonstrated that *P. communus* has the capacity to retranslocate Na from the shoot to the root, thus maintaining low foliar Na concentrations despite high external salinities. Whether this mechanism operates in other aquatic vegetation is unknown.

It should be noted that salinity tolerance indicated from field observations, and salinity experiments will be influenced by a number of auxiliary factors. The capacity to osmotically adjust, and hence tolerance to salinity, is influenced by the rate at which salinities are increased. It is apparent from Table 1.2 that experimental protocols for increasing salinities vary widely between researchers and may influence observed tolerances. In the field the rate at which salinity increases is also variable (Brock and Lane 1983). Increased sensitivity to salinity is demonstrated when the Na/Ca ratio is high. However the Na/Ca ratio has not been directly considered in salinity experiments on fresh water macrophytes, and high Na/Ca ratios may increase sensitivity. Note that where seawater or sea salts have been used to increase salinities high Na/Ca ratios are avoided. The duration of exposure to salinity will also influence tolerance. Munns (1993) and Yeo *et al.* (1991) claim that ion toxicity does not manifest in the short term, suggesting that tolerance may decrease in time. James and Hart (1993) did not observe any salinity effects until 22 days after salinisation, hence experiments of brief duration are likely to underestimate sensitivity to salinity. As surface water salinities may be quite disparate from soil salinities, salinity tolerance may not correlate with surface water salinities in deep rooted aquatic vegetation. Lissner and Schierup (1997) found that surface water salinities did not generally reflect the salinity levels *Phragmites australis* stands were exposed to; as soil water salinities declined significantly with depth in many instances.

Where morphological responses to salinity have been measured, they are typically characterised by reductions in leaf/stem height and number, and a decline in sexual and asexual reproduction. There exists however a poor understanding of the physiological responses of aquatic vegetation to salinity (Hart *et al.* 1991). It is unclear whether reduced growth is mediated primarily via effects on photosynthesis or respiration, or on leaf production, extension or senescence.

James and Hart (1993) examined the response of *Eleaocharis acuta, Myriophyllum crispatum*, *Potamogeton tricarinatus* and *Triglochin procerum* to elevated NaCl ranging from 0 to 7000 mg L^{-1}. Leaf senescence was most pronounced in the two most sensitive species; *M. crispatum* and *P. tricarinatus*. Further investigations by Warwick and Bailey (1997) found growth reductions at 6000 mg L^{-1} NaCl in *P. tricarinatus* to be associated with an increased rate of leaf senescence, coupled with a decline in leaf production. In *T. procerum* growth was reduced at 6000 mg L^{-1} but was not attributed to changes in leaf production or loss, however the size of individual leaves were reduce. *Amphibromus fluitans* was unaffected by the salinity levels examined, and also did not demonstrate any change in leaf production or loss in response to salinity level.

Whilst it is generally accepted that increased leaf senescence associated with salinity can be attributed to toxic levels of Na or Cl this was not evident in *P. tricarinatus*. Although the addition of NaCl increased foliar Na and Cl concentrations, increasing NaCl above 2000 mg L^{-1} did not elicit any further increases. Consequently, reduced growth, which was only evident at 6000 mg L^{-1}, could not be attributed to foliar Na and Cl concentration. As K concentrations did decline substantially with increased levels of NaCl, leaf loss was attributed to high Na/K ratios. It should be noted that differences in ion concentrations may have been demonstrated if examined in terms of leaf water content, which is considered more indicative of physiological concentrations. However, even this may not be informative, as sensitivity to foliar ion concentrations will be determined by the capacity for vacuolar compartmentation.

Differential sensitivity to salinity may be demonstrated at different life stages (Zedler *et al.* 1990; Lissner and Schierup 1997). Whilst seed germination generally declines with increasing salinity, there does not appear to be any relationship between salinity tolerance, at seedling and adult life stages, and germination success under saline conditions. Rozema (1975) found that differences in the salt tolerance of a number of halophytic and glycophytic species were not reflected in the sensitivity of germination to salinity. Consequently, even though tolerance is demonstrated at other life stages, establishment in saline regions may be prevented due to the sensitivity of germination. Conversely, tolerance of germination to salinity does not imply

tolerance at other life stages. Zedler *et al.* (1990) found that both *Juncus kraussii* and *Typha orientalis* seeds germinated at 5000 mg L^{-1}, however *Juncus* proved more tolerant to salinity at both the seedling and adult life stages. In contrast *Phragmites australis* demonstrated a higher sensitivity to salinity in both seed germination and seedling development compared to *Spartina patens* (Wijte and Gallagher 1996ab). As discussed by Zedler *et al.* (1990), the establishment of a species in a saline region may be dependant on periods of low salinity which permit germination and seedling establishment.

In environments where salinity is spatially heterogeneous, connections between ramets can prove beneficial to plant growth (Evans and Whitney 1992; Hester *et al.* 1994). Evans and Whitney (1992) demonstrated that in *Hydrocotyle bonarienis* (a sand dune perennial), ramets which were connected to other ramets grown under non-saline conditions, were able to proliferate despite localised salt exposure, and did not demonstrate any visible effects of salinity. In contrast, where the connection between ramets was severed high mortality was demonstrated under saline conditions. A similar response has also been observed in *Spartina patens* by Hester *et al.* (1994).

1.5 The impact of vegetation on water loss from wetlands

1.5.1 Evaporation

Evaporation has been defined as the rate at which water is transformed to water vapour from land or water surfaces, and is commonly expressed in mm day^{-1} or its equivalent L m^{-2} d^{-1} (Shuttleworth 1993). Transpiration is the portion of total evaporative loss which enters the atmosphere via vegetation (Shuttleworth 1993). Evaporation is controlled by two main processes, the energy available to drive the vaporisation of water, and the gradient in vapour pressure between the evaporative surface and the atmosphere.

Approximately 2.5 million joules are required to evaporate 1 kg of water, this energy is termed the latent heat of vaporisation and is derived from the absorption of solar radiation (Shuttleworth 1993). In plant canopies the absorption of solar radiation is determined by; the leaf area index (LAI), the extinction coefficient (K) and the albedo (α). The leaf area index is

used to quantify the leafiness of vegetation, and is defined as the leaf surface area (one sided) overlying a unit area of land (Watson 1947). The extinction of light through plant canopies is dependant on the structural characteristic of the canopy (Monteith 1976; Monteith and Unsworth 1990). In canopies where leaf orientation is predominantly horizontal, little light is transmitted to lower layers in the canopy. Such canopies have high extinction coefficients. In contrast, canopies with vertically orientated leaves have low extinction coefficients, and a greater portion of light is transmitted through the canopy (Monteith and Unsworth 1990). The albedo represents the portion of intercepted radiation which is reflected and not absorbed (Jones 1983).

Although energy may be available to transform water into water vapour, evaporation will only occur if a vapour pressure deficit exists. The saturation vapour pressure represents the vapour pressure at which the air can no longer hold water. As temperatures increase the saturation vapour pressure increases, and hence the potential for evaporation. When the saturation vapour pressure is reached, the rate of evaporation is balanced by the rate of condensation, and there is no net loss of water (Shuttleworth 1993). The rate at which water vapour can move away from the evaporating surface, and hence the maintenance of a water vapour deficit will also determine rates of evaporation.

Water vapour is lost to the atmosphere via either molecular or turbulent diffusion (Jones 1983). In molecular diffusion water vapour movement is controlled by the rapid and random motions of air molecules. In turbulent diffusion the movement of wind is restricted through contact with vegetation, soil or water surfaces, causing pockets of air to be transported away from the evaporative surface. Turbulent diffusion will also occur in the absence of wind due to turbulence produced by convective heat exchange (Fitter and Haye 1987). Turbulent diffusion is considered to be the most important process determining the exchange of air at the evaporative surface with that higher in the atmosphere.

In vegetation transpiration is dependant on the resistance to water vapour loss offered by stomata and the vapour pressure deficit (VPD) between the sub stomatal pore, which is

considered to be saturated with water vapour, and the air surrounding the leaf. The potential for stomatal resistance to influence water loss from plant canopies will be determined by the extent to which the air surrounding the leaves is coupled to the atmosphere (Schulze 1993 Jarvis and McNaughton 1986). A relatively still layer of air exists at the leaf surface called the boundary layer. Water vapour must diffuse through this layer before reaching the bulk air which is subject to turbulent diffusion and as is therefore well mixed.

1.5.2 Aerodynamic resistance

Aerodynamic resistance (r_a) in plant canopies represents the ease by which water loss from the leaf surface is transferred to the bulk air (Monteith 1995). Aerodynamic resistance is inversely proportional to wind speed and vegetation height. As aerodynamic resistance declines, the VPD at the leaf surface approximates that of the atmosphere, and the vegetation is considered to be closely coupled to the atmosphere (Jarvis and McNaughton 1986). In such instances, the resistance offered by stomata will strongly influence water loss from the canopy (Jarvis and McNaughton 1986; Jones 1983). Consequently, the sensitivity of stomata to changes in VPD will be an important factor in determining rates of water loss.

In canopies with high aerodynamic resistance, evaporation is not driven by atmospheric VPD, but by an equilibrium VPD that develops within the canopy (Jarvis and McNaughton 1986). Such canopies are considered to be decoupled from the atmosphere, and net radiation tends to drive transpiration (Jones 1983; Jarvis and McNaughton 1986). This occurs as the air is poorly mixed, and leaf temperatures increase more in response to radiation than leaves of canopies with low aerodynamic resistance. High leaf temperatures will increase the vapour pressure within leaves, creating a strong gradient for transpiration. Closure of stomata in canopies which are decoupled from the atmosphere does not result in a significant change in transpiration, due to feedback effects (Jarvis and McNaughton 1986; Jones 1983). Transpiration remains reasonably constant under these conditions, as increases in stomatal resistance reduces heat loss through transpiration, resulting in an increase in sensible heat, and inturn, the VPD at the leaf surface. Consequently, the resultant increase in VPD will tend to offset any reduction in transpiration produced by stomatal closure.

1.5.3 Canopy resistance

The resistance to water loss from plant canopies is the mean stomatal resistances of all the leaves within the plant canopy, divided by the leaf area index (LAI) (Jarvis 1981). Due to variability in stomatal resistance between leaves, the estimate of canopy resistance is problematic. Stomatal resistance between the upper and lower layers of a canopy can be quite disparate, with lower resistances occurring in the upper canopy layers. This has been attributed to the extinction of light through different layers in the canopy (Saugier and Katerji 1991). Differences in leaf age will also contribute to variability in stomatal resistance within plant canopies (Jarvis 1981). Resolution of canopy resistance has been attempted by weighting the stomatal resistance of different layers within the canopy by their contribution to the total LAI (Roberts *et al.* 1980; Sauger and Katerji 1991; Abtew *et al.* 1995). Due to the inherent difficulties associated with the determination of canopy resistance it has often been approximated by dividing the LAI by the minimal stomatal resistance (Saugier and Katerji 1991). This considerably underestimates canopy resistance and the estimate has been improved by multiplying the minimum stomatal resistance by .5 to compensate for the portion of leaves not fully active in transpiration (Sziecz and Long 1969; Allen *et al.* 1989).

Whilst stomatal resistance within plant canopies may be highly variable, stomatal resistance of individual leaves also vary in response to light, water availability, VPD, temperature and CO_2 concentration (Willmer 1983). Consequently, stomatal resistance and therefore canopy resistance will vary on diel, daily and seasonal time scales as light, temperature, VPD and water availability change.

It is apparent from the preceding discussion that a number of plant parameters influence evapotranspiration. The absorption of solar radiation is determined by the LAI, the albedo and the light extinction coefficient of vegetation. Canopy resistance is governed by the LAI and stomatal resistance, while aerodynamic resistance is altered by vegetation height.

1.5.4 Water loss from aquatic vegetation

The influence of aquatic vegetation on water loss from wetlands remains controversial. In the past, research has supported the supposition that aquatic plants can "rob" wetlands of water; with reports indicating that water loss from vegetated (E) water bodies can exceed that from open water (E_O) by up to 300%. These high estimates are considered to be unrealistic, since they have been obtained when small and or isolated stands of vegetation within lysimeter systems have been studied. Such errors arise as heat is transferred from non vegetated surfaces to the periphery of the stand, causing an accelerated rate of water loss (Idso 1979; Anderson and Idso 1987; van Bavel *et al.* 1963; Linacre 1976). The greater the peripheral area of the stand to its total area, the more inflated E/E_O estimates will be (Anderson and Idso 1987). This phenomenon has been referred to as the "oasis effect" (Anderson and Idso 1987). Where this phenomenon has been addressed more conservative estimates of E/E_O are reported. Water loss from vegetated surfaces, however, are still reported to exceed open water by 40% and greater (Anderson and Idso 1987; Idso and Anderson 1988; DeBusk *et al.* 1983).

Linacre *et al.* (1970) has presented theoretical evidence which suggests that evaporation from a vegetated water body can potentially be greater than from an open water body. If water loss from aquatic vegetation is not restricted by stomata, then evaporation will be governed by the absorption of solar radiation and the aerodynamic resistance of vegetation . The albedo, or proportion of radiation reflected by open water is considered to be lower than that of vegetated surfaces. Water loss from an open water body will therefore be greater, since it absorbs more solar radiation. Counteracting this, however, is aerodynamic resistance. Aerodynamic resistance is lower for vegetated surfaces than for open water, due to the enhanced turbulence created by vegetation. Using typical albedo and aerodynamic resistance values for vegetated and open water bodies, Linacre *et al.* (1970) calculated that evaporation from a vegetated surface could potentially exceed that of an open water body by 30%, providing stomata did not restrict water loss.

As aquatic plants may differ in both canopy and aerodynamic resistance, it is possible that some species may inhibit water loss, whilst others may exacerbate it. Idso (1981) predicted that E/E_O

estimates could be shifted above or below unity, purely by differential resistances of stomata to water loss. A study by Koch and Rawlik (1993) in a subtropical wetland found *Typha domingensis* to have considerably lower stomatal resistances and higher rates of transpiration than *Cladium jamaicense* in winter and spring. Anderson and Idso (1987) found stomatal conductance of *Typha latifolia* to differ considerably to water hyacinth. This indicates that stomatal behaviour can differ in aquatic species and potentially rates of water loss.

Differences in evapotranspiration between species may also arise from differences in LAIs, since this not only influences canopy resistance, but the interception of solar radiation. Snyder and Boyd (1987) report peak leaf area indices of 30 and 6, for *Eichhornia crassipes* and *Typha latifolia,* respectively, when grown under high nutrient regimes. This indicates that large differences in LAIs can potentially exist between species. As many aquatic plants die back over winter, large temporal changes in LAIs are likely to occur. Both the magnitude and timing of changes in LAIs will influence water loss on a seasonal basis. Peaks in LAIs which coincide with peaks in evaporative demand will result in higher seasonal rates of water loss than if they occur when evaporative demand is low. Seasonal growth patterns may also be coupled with changes in vegetation height and hence aerodynamic resistance. To accurately evaluate the influence of aquatic vegetation, or the significance of species composition on water balances in wetlands requires an understanding of how these variables change over time.

The response of stomata and the leaf area index (LAI) to environmental factors such as salinity, drought or nutrient levels may also alter rates of water loss. Higher nutrient levels have been shown to increase the LAI, and have been correlated with higher rates of transpiration in a number of aquatic macrophytes (Koch and Rawlik 1993; Debusk *et al.* 1983; Snyder and Boyd 1987). In contrast, salinity has been found to reduce rates of evapotranspiration in *Typha domingensis* (Glenn *et al.* 1995). The response of stomata to meteorological conditions can also vary between species, yielding different rates of water loss. Stomatal conductance was found to increase with falling vapour pressure in *T. domingensis* whilst temperature was found to be the best predictor of stomatal resistance in *C. jamaicense* (Koch and Rawlik 1993).

Evidence such as that outlined above indicates that species composition, climatic factors, nutrient availability, salinity or soil water potential may alter water fluxes in wetlands. Wetlands dominated by vegetation exhibiting high rates of water loss, may experience more extended and pronounced drawdown events than those dominated by vegetation with lower rates of water loss. The influence of vegetation on the water balance is of particularly importance in Mediterranean wetlands where water supply is limited over summer; since it influences the integrity of the system, not only from a hydrological perspective, but more significantly in terms of salinisation.

As transpiration can influence rhizosphere salinities, species with different transpiration rates may experience salinity differently. It has been proposed that the exclusion of salt from the transpiration stream can cause a localised accumulation of salt around the rhizosphere (Passioura *et al.* 1992). This occurs when the rate of transpiration and hence salt accumulation is greater than the rate at which salt diffuses back into the bulk sediment (Passioura *et al.* 1992). Consequently, species exhibiting high rates of transpiration may incur salinities within the rhizosphere which limit productivity earlier than those with low rates of water loss.

Not only is the total amount of water used by aquatic vegetation of interest, but how much carbon is gained for a given loss of water; that is the water use efficiency of vegetation. For two species which exhibit similar transpiration losses, the species for which this water loss results in a greater gain in carbon may be more suited to water stressed conditions. Despite the apparent implications of water use by aquatic macrophytes in Mediterranean climates few field based studies exist in which they have been determined.

1.6 General outline of research

A broad description of each component of work undertaken, and the principle hypotheses or objectives examined are outlined. The underlying rational, and specific hypotheses or objectives are detailed in the introduction of each chapter.

The influence of different salinity-nutrient regimes on plant performance was initially examined

in the emergent sedge *Bolboschoenus medianus,* in a controlled outdoor pond experiment. The central hypothesis was that higher nutrient loads would moderate growth reductions imposed by salinity, but that the benefits of higher nutrient loads would diminish as salinities increased. *B. medianus* was selected as it is a prevalent species in south eastern Australia. Furthermore, it was anticipated that it would demonstrate both a tolerance to salinity and a marked response to nutrient load.

A subsequent pond experiment was conducted to examine the influence of different salinity-nutrient regimes on *Typha domingensis* and *Baumea arthrophylla* with putative high and low RGRs, respectively. Based on plant strategy theories developed by Grime (1977) it was hypothesised that differential responses to salinity-nutrient regimes would be demonstrated in species with contrasting RGRs. It was hypothesised that *B. arthrophylla* would have a low RGR and be unresponsive to nutrient load, whilst *T. domingensis* would have a high RGR and demonstrate a marked response to nutrient load. *B. arthrophylla,* whilst being unresponsive to nutrient load would demonstrate a greater tolerance to salinity than *T. domingensis*. *T. domingensis* and *B. arthrophylla* were examined as they were considered to have characteristics attributed to species with high and low RGRs, respectively, and again due to their prevalence in southern Australian wetlands.

In both pond experiments performance was assessed using a variety of physiological and morphological parameters. Growth analysis was also used to evaluate performance, since this enabled the underlying mechanisms governing changes in RGR to be identified. Responses to salinity were evaluated against the bi-phasic model proposed by Munns and Termaat (1986) to explain salinity imposed growth reductions.

The extent and nature of seasonal changes in both soil and surface water salinities were examined in regions underlain by shallow ground water differing in salinity within Bool Lagoon, a large wetland in the south east of South Australia. To establish the potential influence of vegetation, vegetation type, and salinity, on the water balance, evapotranspiration of *T. domingensis* and *B. arthrophylla* stands in regions differing in ground water salinity were

estimated using the Penman-Monteith equation. *T. domingensis* and *B. arthrophylla* were examined since pond experiments indicated that evapotranspiration in *T. domingensis* would be considerably higher than *B. arthrophylla.* Furthermore, these species provided a link between pond and field observations.

Table 1.1. Surface water salinity ranges over which aquatic macrophytes have been found in the field.

Species	Salinity mg L^{-1}	Reference
Acacia stenophylla	230-2500	Goonan *et al.* (1992)
Azolla filiculoides	280-4400	Goonan *et al.* (1992)
Azolla sp.	700	Goonan *et al.* (1992)
Bolboschoenus caldwelli	700-25000	Goonan *et al.* (1992)
Ceratophyllum demersum	280	Goonan *et al.* (1992)
Cotula coronopifolia	5000	Brock and Shiel (1983)
Crassula helmsii	3000-10000	Brock and Shiel (1983)
Crassula natans	500-2000	Brock and Lane (1983)
Cyperus gymnocaulus	230-25000	Goonan *et al.* (1992)
Eragrostis sp.	450	Goonan *et al.* (1992)
Eucalyptus camaldulensus	360-2200	Goonan *et al.* (1992)
Eucalyptus largiflorins	230-2500	Goonan *et al.* (1992)
Lemna minor	3000-7000	Brock and Lane (1983)
Lepilaena preissii	6500-150000	Brock and Shiel (1983) Brock and Lane (1983)
Lepilaena australis	3000-11000	Brock and Shiel (1983)
Lepilaena bilocularis	3000-15000	Brock and Shiel (1983) Brock and Lane (1983)
Lepilaena cylindrocarpa	3000-10300	Brock and Shiel (1983) Brock and Lane (1983)
Muehlenbeckia florulenta	450-4400	Goonan *et al.* (1992)
Myoporum acuminatum	360-700	Goonan *et al.* (1992)
Myriophyllum sp.	3000-4000	Brock and Shiel (1983)
Myriophyllum sp.	280	Goonan *et al.* (1992)
Pachycornia sp.	25000	Goonan *et al.* (1992)
Paspalum sp.	6700	Goonan *et al.* (1992)
Paspalum vaginatus	450-7100	Goonan *et al.* (1992)
Phragmites australis	9-30000	Lissner and Schierup (1997)
Phragmites australis	280-2200	Goonan *et al.* (1992)
Potamogeton pectinatus	1000-6000	Brock and Lane (1983)
Ruppia maritma	500-3000	Brock and Shiel (1983) Brock and Lane (1983)
Ruppia megacarpa	11000-150000	Brock and Shiel (1983) Brock and Lane (1983)
Ruppia tuberosa	12000-160000	Brock and Shiel (1983) Brock and Lane (1983)
Ruppia polycarpa	3000-125000	Brock and Shiel (1983) Brock and Lane (1983)
Schoenoplectus validus	280-700	Goonan *et al.* (1992)
Suaeda australis	25000	Goonan *et al.* (1992)
Triglochin procerum	500-10000	Brock and Shiel (1983) Brock and Lane (1983)
Typha sp.	280-2200	Goonan *et al.* (1992)
Typha domingensis Pers.	5000-8000	Glenn *et al.* (1995)
Typha angustifolia L.	0-8000	Whigham *et al.* (1989)
Vallisneria spiralus	280-700	Goonan *et al.* (1992)

Table 1.2. Responses of freshwater macrophytes to experimentally imposed salinities. Responses are classified in terms of biomass reduction (BR); visual symptoms (VS) ie leaf burn/wilting/chlorosis; reduced growth (RG) ie reduced number leaves/shoots/leaf elongation rate; and mortality (M). The salinity level at which these responses have been observed are also indicated.

Salinity mg L^{-1}	Rate of increase mg L^{-1}	Growth conditions	Duration (weeks)	Species	Response to salinity mg L^{-1}	Reference
0-30000 seawater	over 6 weeks	glasshouse marsh sediment	c. 30	*Phragmites australis*	BR 15000	Hellings & Gallagher 1992
0-50000 sea salts	nil	greenhouse hydroponic	6	*Phragmites australis*	RG 10000 M 88% 22500 (seedling) M 25% 22500 (adult)	Lissner & Schierup 1997
0-29220 NaCl	11690 $week^{-1}$	glasshouse hydroponic	6	*Phragmites communis* (sourced from salt mine)	VS 17530 BR 29220	Matoh *et al.* 1988
29-5800 NaCl	14 day^{-1}	glasshouse hydroponic	8	*Typha domingensis*	BR VS 5800	Hocking 1981
1100-15000 NaCl	nil	glasshouse sand/vermiculite	c. 10	*Typha domingensis* Pers.	BR by 50% 3500 BR by 90% 6000 M 75% 15000	Glenn *et al.* 1995
0- 17530 NaCl	584 day^{-1}	glasshouse hydroponic	not stated	*Typha latifolia*	VS 4675 BR 5800	Anderson 1977
1660-16650 seawater	nil	glasshouse hydroponic	4	*Pistia stratiotes* L. *Eichornia crassipes* (Mart.) Solms *Hydrilla verticullata* Loyle *Myriophyllum spicatum* L. *Najas quadalupensis* (Spreng.) Magnus *Vallisneria americana* Michx *Azolla caroliniana* Willd *Salvinia rotundifolia* Willd. *Lemna minor* L	BR 830 M 2500 BR 830 M 3300 BR 6600 M 10000 BR 10000 M 16650 BR 10000 M 13320 BR 6660 M 13320 BR 3330 BR 6666 BR 10000	Haller *et al.* 1974
0-7000 NaCl	nil	glasshouse wetland Soil	c. 10	*Potamogeton tricarinatus* *Myriophyllium crispatum* *Eleacharis acuta* *Triglochin procerum*	M 44% 5000 M 48% 7000 M nil 7000 M nil 7000 RG 1000 all species	James & Hart 1993
58-8700 NaCl	not stated	glasshouse hydroponic	8	*Cyperus involucratus*	BR 4090 Necrosis 8700	Hocking 1985
0-12000 sea salts	1000 day^{-1} to 6000 then 2000 day^{-1} to 12000	outside tanks river sediment at 50% (H) or 8% (L) actinic light	c.4	*Hydrilla verticulata* (L.f.) *Myriophyllum spicatum* L. *Potamogeton perfoliatus* L. var. *Vallisneria americana* Mitchx.	BR 2000 H 4000 L BR 12000 H >L BR 4000 H >L BR 12000 H >L	Twilley & Barko 1990
0-9400 seawater	gradual	glasshouse marsh soil	c. 6	*Sagittarius lancifolia* *Panicum hemitomon* *Leersia oryzoides*	VS 4790 RG 2400 all species	M^{c}Kee & Mendelssohn 1989
300-12000 sea salts	nil	growth chamber		*Panicum hemitomon* Shultz.	tissue necrosis 12000	Pezeshki *et al.* 1987
c.80 & 400 NaCl	nil	outdoor ponds river sediment	8	*Potamogeton lucens* *Potamogeton nodosa* *Potamogeton perfoliatus* *Ranunculus circinatus*	BR 400 BR 400 BR 400 nil effect on biomass	van den Brink & van der Velde 1993
0-6000 NaCl	nil	greenhouse sediment	c.9	*Potamogenton tricrinatus* *Triglochin procerum* *Amphibromis fluitans*	BR 6000 BR 6000 nil effect on biomass	Warwick & Bailey 1997
	gradual 500 $week^{-1}$ 2000-6000			*Potamogenton tricrinatus* *Triglochin procerum* *Amphibromis fluitans*	nil effect on biomass	

Chapter 2. The influence of salinity and nutrient load on morphology, biomass allocation, and gas exchange characteristics in the emergent sedge *Bolboschoenus medianus*

2.1 Introduction

The deleterious impact of salinity on plant performance is thought to be mediated by three main mechanisms; a low external water potential, ion toxicity and nutrient imbalance. A bi-phasic model has been used by Munns and Termaat (1986) to differentiate between osmotic effects, which are evident in the short term, and ion toxicity effects, which ensue later. In the first phase growth is reduced by a low soil water potential. It is believed that the roots sense changes in soil conditions and produce chemical signals, the most convincing being ABA, which mediate reductions in leaf expansion. As shoot growth is more inhibited than root growth the root weight ratio (RWR; root weight to total plant weight) increases, whilst the leaf weight ratio (LWR; leaf weight to total plant weight) declines. Consequently the leaf to root ratio is reduced. This response is not considered to be a salt specific effect as other osmotica produce similar effects.

In the second phase, growth is reduced by ion specific effects. Specific ion effects are manifest in the long term by premature leaf senescence. This occurs in mature leaves when the capacity of the vacuole to sequester Na and Cl ions is exhausted, and salts accumulate either in the cytoplasm, inhibiting cellular metabolism, or in the cell wall, inducing cellular desiccation. If the rate of leaf senescence is greater than the rate of leaf production, the leaf area declines and growth is further compromised.

Changes in photosynthetic capacity are also commonly associated with salinity induced growth reductions. Reductions in photosynthetic capacity have been attributed to both stomatal closure, which limits CO_2 supply, and to a reduced biochemical capacity for CO_2 fixation. In addition, salinity can also reduce growth by impairing nutrient uptake and transport processes resulting in nutrient deficiencies (Lynch *et al.* 1987). Research directed at

crop species and salt marsh species indicate that nutrient addition can ameliorate, at least to some extent, growth reductions imposed by salinity (Feigin 1985; Mehanni and West 1992; Garg *et al.* 1993; Broome *et al.* 1975; Bohra and Doerffling 1993; Cramer and Nowak 1992; Helal *et al.* 1975). Improved performance by nutrient addition has been associated with higher rates of photosynthesis, lower Na/K ratios, higher levels of amino acids, and an increased synthesis of glycinebetaine (see Chapter 1). Whilst nutrient addition can increase the yield of many crop species it also frequently increases their sensitivity to salinity (Mass and Hoffman 1977; Feigin 1985). This implies that increased productivity achieved by fertilisation at low salinity will decline at higher salinities.

Whilst the relevance of salinity-nutrient interactions is clear for agricultural crops where soil fertilisation is a common practice, it also has considerable implications in the context of natural wetlands. Nutrient loads into wetlands are characterised by considerable spatial and temporal variability (Brett 1989). Furthermore, anthropogenic perturbations of nutrient fluxes into wetlands can result in nutrient loads being increased well above natural levels. Consequently, substantial variability in the response of aquatic macrophytes to salinity may be manifest if plant performance is influenced by nutrient load.

Chapin (1980) reports that vegetation from fertile habitats are characterised by high RGRs which are sensitive to nutrient supply. As many aquatic macrophytes have high RGRs, nutrient deficiencies imposed by salinity may exert a strong influence on performance. As such, the response to nutrient load under saline conditions may be quite marked.

A common response of fast growing species to high nutrient levels is a decrease in the root weight ratio (RWR), and an increase in the leaf weight ratio (LWR) (Chapin 1980; Chapin *et al.* 1987). A response opposite to that induced by salinity. Increased nutrient levels may therefore enhance performance, not only by preventing nutrient deficiencies, but by minimising reductions in leaf area which are commonly observed under saline conditions.

However, as salinities increase higher nutrient loads may compromise plant water relations, because the transpiring surface is increased (higher LWR) whilst root biomass is reduced (lower RWR). Thus the capacity to supply water to the shoot declines whilst the transpirational demand increases. The capacity to respond to enhanced nutrient supply by shifting biomass allocation away from the root to the shoots will therefore diminish as salinities increase. Furthermore, stomatal limitation of photosynthesis may become more pronounced as salinities increase and water conservation becomes more critical . Under these conditions, an enhanced biochemical capacity for photosynthesis, achieved at higher nutrient loads, may not be realised due to stomatal limitation of photosynthesis. The benefits associated with higher nutrient loads may therefore diminish as salinities increase, and growth becomes more constrained by osmotic and ion toxicity effects.

In Australia increasing salinities within streams and wetlands has highlighted the need to further examine the impact of salinity on freshwater macrophytes (Hart *et al.* 1991). Whilst the response of a number of aquatic macrophytes to salinity has been examined, the influence of nutrient load has not previously been addressed.

This experiment characterises the response of *Bolboschoenus medianus* (V. Cook) SojáK (formerly *Scirpus medianus*) to NaCl salinity and the interaction between nutrient load and salinity. The Na/Ca ratio was maintained at less than 15 as this is considered sufficient to avoid salinity effects directly related to Ca (LaHaye and Epstein 1969; Greenway and Munns 1980). In addition, this ratio lies within the range commonly found in saline soils (Greenway and Munns 1980).

B. medianus was considered a key species to examine due to its prevalence in wetlands of south eastern Australia. Furthermore, many species of *Bolboschoenus* and *Scirpus* tolerate brackish conditions (Ewing 1986; Zákravsky and Hroudová 1996) suggesting that *B. medianus* may be tolerant to salinity. *B. medianus* was also considered to have a high RGR which would be responsive to changes in nutrient load.

A variety of performance indices were used to characterise the response of *B. medianus* to different salinity-nutrient regimes, and to identify the mechanisms underlying changes in growth. These included morphological measurements, rates of leaf production and senescence, gas exchange parameters, carbon isotope discrimination, biomass, biomass allocation patterns and growth analysis.

Growth analysis involves the measurement of relative growth rate (RGR), net assimilation rate (NAR) and the leaf area ratio (LAR). RGR is considered a more accurate means of assessing plant performance as it take into account differences in initial biomass (Hunt, 1982). NAR is an index of the net photosynthetic capacity per unit leaf area and reflects the balance between gross photosynthesis and whole plant respiration (Hunt 1982; Harper 1977). LAR is broadly the ratio of photosynthetic to respiring tissue and is a function of the leaf weight ratio (LWR) and the specific leaf area (SLA) (Harper 1977). The LWR is analogous to the percentage of total biomass allocated to leaves, whilst the SLA is the ratio of leaf area to leaf weight. As such, the SLA represents the cost in terms of biomass of producing a given leaf area.

As RGR is a function of NAR and LAR the physiological processes underlying changes in RGR can be evaluated. Whilst several experiments have utilised growth analysis to understand the physiological basis for growth reductions imposed by salinity (Crammer and Nowak 1992; He and Cramer 1993; Shennan *et al.* 1987; Curtis and Läuchli 1986), the benefits of nutrient addition under saline conditions has only been evaluated in this way for Ca (Cramer *et al.* 1990). This experiment evaluates several hypotheses related to the impact of salinity on plant performance, the influence of nutrient loads, and the interaction between nutrient load and salinity.

Response to increasing salinity

- In accordance to the model proposed by Munns and Termaat (1986) the response of *B. medianus* to increasing salinity will be characterised by lower LWRs and higher RWRs, in response to both hormonal induced signals (short term osmotic effects) and to an

increased rate of leaf senescence (long term ion specific effects). As such, both the leaf to root ratio and LAR will decline with increasing salinity. Furthermore, NAR will decline in response to salinity and will be associated with lower rates of photosynthesis. However, as implied by the model of Munns and Termaat (1986) the dominant response will be a reduction in LAR.

Response to higher nutrient loads

- The response of *B. medianus* to higher nutrient loads will be characterised by higher LWRs, and lower RWRs. These changes will cause both the leaf to root ratio and LAR to increase. In addition, rates of photosynthesis will increase, yielding higher NAR. As such, RGR will increase at higher nutrient loads via increases in both LAR and NAR.

Salinity x nutrient interaction

- As ion toxicity and osmotic influences on growth are exacerbated at higher salinities, increases in LAR and NAR at higher nutrient loads will diminish, causing RGRs to converge.

2.2 Materials and methods

2.2.1 Species description

Bolboschoenus medianus (V. Cook) SojáK (Cyperaceae) is an emergent perennial native to Australia. *B. medianus* can grow to c. 1 m in height and forms dense stands via rhizomes. Plants commonly die back in winter (May-June, Blanch 1997) and re shoot from tubers in spring (Sainty and Jacobs 1994).

2.2.2 Experimental design

The experiment consisted of two phases, establishment under non-saline conditions at three nutrient loadings (30, 100 and 350 g N m^{-2} yr^{-1}); and the subsequent response to NaCl salinity (control, 4.5, 9 and 13 dS m^{-1}) under these nutrient loadings, utilising a full factorial design.

The establishment phase lasted c. 8 weeks (23rd Sept to 18th Nov 1994). The duration of the salinity phase was c. 9 weeks (18th Nov 1994 to 17th-21st Jan 1995).

The first phase of the experiment was instituted to prevent harvest trauma increasing the plants susceptibility to salinity. The bi-phasic nature of the experiment was also considered to reflect natural conditions where salinity is often experienced or exacerbated temporally; salinities often being lower at the end of winter and highest at the end of summer. Given this, there may exist periods of low salinity where available nutrients can be utilised to a greater extent. This may ultimately influence plant performance under saline conditions.

Rational for selected salinity and nutrient treatments

It has been proposed that secondary salinisation processes may increase salinities within aquatic systems from values less than 500 mg L^{-1} (0.73 dS m^{-1}) to 10 000 mg L^{-1} (c. 14.7 dS m^{-1}) (Hart *et al.* 1990, 1991). As such, the salinity levels examined encompass potential salinities arising from increasing salinisation of fresh aquatic systems.

Nitrogen loadings into freshwater marshes are on average around 22 g N m^{-2} yr^{-1} but may increase to around 600 g N m^{-2} yr^{-1} as a result eutrophication (Mitsch and Gooselink 1993; Horne and Goldman 1994). However, these estimates do not consider nutrient cycling within sediments and hence provide only a rough guide. However, they do place the loadings examined in this study in some context, with 30 and 100 g N m^{-2} yr^{-1} being considered within the potential range for natural wetlands, and 350 g N m^{-2} yr^{-1} representing a possible loading arising from eutrophication.

2.2.3 Collection

Newly shooted *B. medianus* tubers were collected from Greenfields, Adelaide, South Australia (34° 48′ S, 138° 36′ E), a local artificial wetland. One hundred and seventeen plants were selected for uniformity, having one tuber and a single culm c. 15 cm tall, bearing 4 to 5 leaves. Root biomass was poorly developed at the time of collection. Fresh weights were obtained on the 20th Sept 1994.

2.2.4 *Experimental treatments*

Nutrient loadings

Nutrients were supplied by Osmocote Plus® (8-9 months), a slow release, complete nutrient fertiliser. The amount of Osmocote Plus® required to achieve the desired nutrient loading was calculated from the release rate of the product at 21°C provided by Osmocote® (% of product released = (0.365 x days) - 0.522).

Using pots with a top surface area of 0.055 m^{-2} the amount of Osmocote Plus® added to each pot to achieve loadings of 30, 100 and 350 g N m^{-2} yr^{-1} were 8.3 g, 28 g, and 97 g, respectively. Whilst calculated in terms of nitrogen, loadings of 30, 100 and 350 g N m^{-2} yr^{-1} are expressed as low, moderate and high nutrient loads, respectively since they represent loadings of N, P and K plus micronutrients and not just N. The nutrient composition of Osmocote Plus® is provided in Appendix A.

Plants were potted in non-perforated plastic potting bags containing c. 9 L of low nutrient sandy loam mixed with the required amount of Osmocote Plus® and topped with c. 3 L of grey cracking clay. The final soil depth was c. 17 cm. Plants were grown in two outdoor ponds at the University of Adelaide. Prior to salinisation nutrient treatments were distributed evenly within each pond and flooded 5 cm above the sediment surface. Prior to imposing salinity treatments seven plants from each nutrient load were randomly selected for harvest.

Salinity treatments.

In order to isolate different salinity treatments, plants allocated to each salinity-nutrient treatment were placed in clear rigid PVC chambers. Chambers were constructed as dual units to minimise cost, the dimensions of each compartment was 60 cm x 60 cm x 57 cm high. All joins were sealed with a non-toxic silicon sealant.

To avoid pseudoreplication the 8 replicates of each treatment were split between two chambers. These were placed in different ponds and occupied different positions within each

pond. Chambers were semi-emersed within the pond to minimise temperature variations. To permit the free movement of ions between the sediment and external solution numerous holes were pierced in the sides of the pots close to the base.

NaCl and $CaSO_4$ were added to the chamber water in daily increment of 10 mM and 0.66 mM, respectively until final conductivities were reached. To ensure NaCl and Ca concentrations were maintained, and no contamination from other chambers occurred, EC readings (TPS LC81 conductivity meter) and Ca concentrations were monitored twice weekly and weekly, respectively. Water loss from evaporation was replaced daily as needed. Conductivities were maintained at 4.5, 9 and 13 dS m^{-1} above control chambers. Conductivities of control chambers varied from 1-1.8 dS m^{-1} depending of nutrient treatment. Na concentrations determined by flame photometry (Corning 400) were c. 15 (control) 45 , 90 and 130 mM Na, respectively. Ca concentrations were determined colorimetricaly using the method of Golterman (1969). The addition of NaCl and $CaSO_4$ was required to maintain concentrations at the desired levels. The Na/Ca ratio across all treatments ranged from 5 to 11, well below the level considered to influence plant performance under saline conditions. The variation in Na/Ca ratios were incurred due to additional Ca released from Osmocote Plus®.

2.2.5 Morphological measurements

The total number of leaves and culms, and culm height were measured every 7-14 days. Leaves were considered living if greater than 50% of their length was green. The height of the 4th emerged culm was measured from the sediment surface to the last node. Harvested plants were separated into leaves, culms, seed heads, roots, rhizomes and tubers. Dry weights were obtained after drying at 70°C until a constant weight.

2.2.6 Growth analysis

The relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were determined using the following formulae (Harper 1977):

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{\Delta T} \qquad (mg\ g^{-1}\ d^{-1}) \qquad (2.1)$$

$$NAR = \frac{(W_2 - W_1)}{(\Delta T)} \times \frac{\ln(LA_2) - \ln(LA_1)}{(LA_2 - LA_1)} \qquad (g\ m^{-2}\ d^{-1}) \qquad (2.2)$$

$$LAR = \frac{(LA_1 - LA_2)}{(W_2 - W_1)} \times \frac{(\ln W_2 - \ln W_1)}{(\ln LA_2 - \ln LA_1)} \qquad (m^2\ kg^{-1}) \qquad (2.3)$$

W_1, W_2, represents plant dry weight (kg) at time 1 and 2 respectively. LA and ΔT represent change in time (days) and leaf area (m^2), respectively.

The initial dry weights of plants were determined using the relationship between fresh and dry weight, where dry weight = (fresh weight x 0.9281) + 2.18 (r^2 =0.93, n = 21, $P < .0001$). Seven plants from each nutrient load were harvested prior to imposing salinity treatments and their mean RGR calculated. To calculate RGR during the salinity phase of the experiment dry weight prior to salinisation was determined from equation 2.4 using mean RGRs at each nutrient load.

$$W_2 = \exp(RGR \times \Delta T) + \ln(W_1) \qquad (2.4)$$

Total leaf area was determined from the relationship between leaf dry weight and leaf area (Fig. 2.1). This was obtained by determining the area (DeltaT area meter) of 5-7 fresh leaves, representing a range of size and age classes, from 6 plants in each nutrient-salinity treatment and subsequently obtaining there dry weights. As the relationship did not visibly differ between treatments the regression obtained using all the data was used in calculating leaf area. Leaf dry weight of plants prior to imposing salinity treatments was calculated from the percentage of total biomass allocated to leaves under each nutrient regime as determined from harvested plants.

2.2.7 Leaf gas exchange measurements

Gas exchange measurements were performed prior to harvesting using a closed-system infra-red gas analyser (IRGA, Li6200, LiCor, NE, USA). As environmental variables influence photosynthesis it is necessary under field conditions to make comparisons between treatments close in time. Because of these constraints not all treatments could be measured at one time. Gas exchange characteristics were therefore compared between control and 13.5 dS m^{-1}, at each nutrient load on separate days. In addition, the effects of nutrients on CO_2 gas exchange characteristics were examined for plants grown at 13.5 dS m^{-1}. Measurements were performed on the youngest fully expanded leaf of culms 3-5.

The conductance to water loss measured within the leaf chamber represents the combined resistances of the boundary layer and stomata. As the boundary layer within the leaf chamber can differ substantially to that in the natural environment it is necessary to account for this when determining stomatal conductance. Boundary layer conductance was measured with a wet filter paper replica of a standard leaf which was used by the LiCor program to calculate stomatal conductance.

Assimilation versus light response relationships can provide information on a number of photosynthetic parameters. These include: alpha (α), an index of photosynthetic efficiency, determined from the initial slope of the light versus irradiance response; P_{max}, the maximal rate of photosynthesis; I_k, the light intensity at which photosynthesis saturates and R, dark respiration. Assimilation versus light response relationships were obtained with the use of shade cloth. Curves were fitted using a hyperbolic tangent function (equation 2.5;Jassby and Platt 1976).

$$P_{gross} = P_{max} \tanh\left(\frac{I}{I_k}\right) + R \qquad (2.5)$$

where P_{gross} is gross photosynthesis.

P_{max}, I_k and R were solved by minimising the sum of squares of differences between modelled values and real values. Alpha (α) was derived by dividing P_{max} by I_k. Correlation coefficients were determined from regressions between modelled data and real data.

2.2.8 Carbon isotope discrimination

At the final harvest the 4th and 5th youngest leaves from culms 3-5 were collected for carbon isotope discrimination. Leaves were oven dried at c. 70°C until a constant weight and ground to powder in a mill (Labtechnics LM1). The isotopic composition of carbon and percent nitrogen of leaf samples were determined by mass spectrometery by the CSIRO Department of Water Resources. Carbon isotope discrimination (Δ ‰) was calculate using equation 2.6.

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \qquad (2.6)$$

where δ_a and δ_p represent the carbon isotopic composition with respect to PBD of the air and the plant, respectively (Farquhar *et al.* 1989). A value of .008 was used for δ_a (Farquhar *et al.* 1989).

2.2.9 Statistical analysis

Statistical analyses were carried out using the statistical software package JMP® (version 3). A single ANOVA was used to identify significant nutrient effects prior to salinisation. Where ANOVA was significant, differences between means were identified using a Tukey Kramer test at $P<.05$. Following salinisation a two way ANOVA was used to identify significant nutrient and salinity effects and significant salinity x nutrient interactions. Normality was determined with a Shapiro-Wilk test and homogeneity of variance with an O'Brian and Brown-Forsythe tests.

2.3 Results

2.3.1 The influence of nutrient load on plant performance prior to salinisation

Leaf and culm number, and the height of culm 4 were significantly reduced at the high nutrient load (Table 2.1). The biomass of all tissues, excluding tubers, were reduced at the high nutrient load, but only the reduction in root biomass was statistically significant (Table 2.2). Although nutrient load had no statistically significant effect on total plant biomass, RGR was significantly lower at the high nutrient load (Table 2.2). The statistical significance of RGR compared to total biomass can be attributed to the lower variance associated with mean RGR, in which initial differences in biomass are removed. Lower productivity evident at the high nutrient load may be due to high nutrient concentrations lowering the soil osmotic potential or to nutrient toxicity.

For all nutrient loads, plant biomass was preferentially allocated to above-ground parts (64-70%), and was evenly partitioned between leaves and stems (Table 2.3). Biomass of below-ground parts was allocated predominantly to roots and tubers. The allocation of biomass to the roots declined with increasing nutrient load, significantly increasing the above ground to root ratio (Table 2.2). The reduction in root biomass was associated with increased biomass allocation to leaves and culms at the moderate nutrient load and to tubers at the high nutrient load (Table 2.3). The shift in biomass allocation from roots to shoots at the moderate nutrient load is consistent with the hypothesis of Chapin *et al.* (1987) that biomass allocation will shift to acquire the most limiting resource. The shift in biomass allocation from roots to tubers at the high nutrient load is not however consistent with this hypothesis, and proposes that carbohydrate storage was triggered due to a stress signal or because shoot growth was inhibited.

2.3.2 The influence of salinity and nutrient load on plant performance

2.3.2.1 Height

The maximum height of culm 4 was 1 m (Fig. 2.2). This was reached in the control at the moderate and high nutrient load but was 20 cm lower at the low nutrient load. The height

reached in culm four at 4.5 and 9 dS m^{-1} was 75 cm and 65 cm, respectively, for all nutrient loads. At 13 dS m^{-1} culm height did not exceed 50 cm at the low or moderate nutrient load and was reduced by a further 10 cm at the high nutrient load. The rate of culm extension was reduced by all salinity levels, and at 13 dS m^{-1} culm extension ceased 23 days following salinisation at the low and moderate nutrient load.

2.3.2.2 Leaf and culm number

Leaf and culm number pot^{-1} were reduced with increasing salinity at all nutrient loads (Figs. 2.3, 2.4). Reductions imposed by salinity were evident earlier as salinities increased (Figs. 2.3, 2.4). At the highest salinity level, reductions were evident 20 days after salinisation at the low and moderate nutrient load, and at 30 days at the high nutrient load (Fig. 2.3). At 4.5 dS m^{-1} reductions were not evident until at least 44 days following salinisation. James and Hart (1993) also found the effects of salinity became apparent earlier as salinities increased in four freshwater macrophytes. Similarly at the highest salinity of 7000 mg L^{-1} (10.9 dS m^{-1}) they found no visible effects until 22 days after salinisation.

The extent to which salinity reduced leaf or culm number differed for each nutrient load (Figs. 2.3, 2.4). At 4.5 dS m^{-1} the number of leaves was unaffected at the high nutrient load but was reduced at both the low and moderate nutrient load (Fig. 2.3). At 9 dS m^{-1} the number of leaves and culms were reduced to a greater extent at both the moderate and high nutrient load than at the low nutrient load (Fig. 2.3 and 2.4). At 13 dS m^{-1} the reduction in the number of leaves was similar at all nutrient loads, whilst the number of culms was less affected at the high nutrient load compared to the low or moderate nutrient load.

Despite differential sensitivities to salinity at each nutrient load, the number of leaves and culms at the moderate and high nutrient load were considerably greater than at the low nutrient load, across all salinity treatments by the end of the experimental period (Figs. 2.5, 2.6). At the high nutrient load, the time taken for the number of leaves and culms to increase above that achieved at the low nutrient load, was greater compared to the moderate nutrient load (Figs. 2.5 and 2.6). Although leaf and culm numbers were generally greater at the high

nutrient load than at the moderate nutrient load, this was only reached after c. 17 weeks of growth.

2.3.2.3 LAI

At the end of the experimental period the maximum leaf area (one sided) per m^{-2} of soil surface for the control was 13.2, 10.3 and 5 at high, moderate and low nutrient loads, respectively (Fig. 2.7a). As salinities increased LAIs declined. LAIs declined more severely in response to salinity at the higher nutrient loads, hence differences between nutrient loads diminished. At 4.5 dS m^{-1} LAIs were 9.9, 8.4 and 4.3 at high, moderate and low nutrient loads, respectively and 5.6, 5.1 and 3.7 at 9 dS m^{-1}, respectively. At 13 dS m^{-1} the LAI was c. 4 at both the moderate and high nutrient loads and 2.6 at the low nutrient load.

Differences in LAIs between the moderate and high nutrient loads were not always reflected in differences in the numbers of leaves pot^{-1} at the end of the experiment (Fig. 2.7b). LAIs at the high nutrient load were considerably greater in comparison to LAIs at the moderate nutrient load at salinities less than 9 dS m^{-1}, but did not differ at 9 or 13 dS m^{-1}. In contrast, the number of leaves pot^{-1} were greater at the high nutrient load than at the moderate nutrient load across all salinities. This suggests that at 9 and 13 dS m^{-1} the average area of individual leaves were smaller at the high nutrient load than at the moderate nutrient load.

2.3.2.4 Rates of leaf production and senescence in culm four

Reduction in leaf number may arise from lower rates of leaf production, increased rates of senescence, or both. Leaf production in culm four was reduced by salinity within 20 days of salinisation (Fig. 2.8). Leaf production declined over time as culms reached maturity. Consequently, differences in rates of leaf production between salinity levels tended to converge over time. Rates of leaf senescence were low and were unaffected by treatment conditions. Although leaf production in the control was clearly enhanced at the high nutrient load, comparisons between nutrient loads are likely to be confounded by differences in culm age. As growth was reduced at the high nutrient load prior to salinisation, the fourth culm would be younger at the high nutrient load compared to the low or moderate nutrient loads.

Increased rates of leaf senescence due to salt toxicity is considered a major long term factor leading to reduced above ground biomass in salinised plants (Munns 1993). Rates of leaf emergence and senescence presented here indicate that lower rates of leaf production, rather than increased rates of senescence, were responsible for the lower numbers of leaves in salinised *B. medianus* plants.

2.3.2.5 Biomass

Plant biomass was reduced by increasing salinity at all nutrient loads (Fig. 2.9). Biomass was reduced relative to the control; by 10%, 16%, and 37% at 4.5, 9 and 13 dS m^{-1}, respectively at the low nutrient load; by 27%, 48% and 54% at the moderate nutrient load; and by 21%, 54% and 58%, respectively at the high nutrient load.

Higher nutrient loads increased biomass at low salinities, however the decline in biomass as salinities increased was also greater, reflecting a greater sensitivity to salinity at the higher nutrient loads. Biomass was increased at the moderate and high nutrient loads compared to the low nutrient load by 73% and 48%, respectively in the control, and by 39% and 29%, respectively at 4.5 dS m^{-1}. At 9 dS m^{-1} biomass was not altered at the moderate nutrient load compared to the low nutrient load and was reduced by 18% at the high nutrient load. At 13 dS m^{-1} biomass was increased by 25% at the moderate nutrient load compared to the low nutrient load and was not altered by the high nutrient load. These effects were reflected in a two-way ANOVA, where salinity, nutrients and the interaction of these factors were significant (Table 2.4). The interaction between nutrients and salinity resulted from the increased sensitivity of biomass to salinity at the higher nutrient loads.

The results indicate that the moderate nutrient load was beneficial at all salinities excluding 9 dS m^{-1}, whilst the high nutrient load enhanced growth only at salinities less than 9 dS m^{-1}. Biomass at the moderate nutrient load exceeded that attained at the high nutrient load at all salinity levels excluding 4.5 dS m^{-1} where biomass was equivalent. As such, the moderate nutrient load can be considered optimal.

2.3.2.6 Biomass allocation

Biomass allocation patterns changed over time. Prior to salinisation biomass was preferentially allocated above-ground after c. 8 weeks of growth, with above to below-ground ratios of 1.8 to 2.4 (Table 2.2). After c. 17 weeks of growth biomass allocation in controls had shifted away from above-ground parts, with above to below-ground ratios of 0.8 to 1.2 (Table 2.5). The change can be attributed to a shift in biomass allocation away from leaves to tubers (Table 2.6). Prior to salinisation, after c. 8 weeks growth tubers represented 12-20% of the total biomass and leaves 30-36% (Table 2.3). After c. 17 weeks this allocation pattern was reversed with tubers representing 37-43% of the total biomass and leaves only 12-22 % (Table 2.6). It may be concluded that assimilates are initially directed to leaves to maximise light interception. In the longer term assimilates are stored in the tuber, ensuring sufficient reserves to meet respiratory demands during winter dormancy and to initiate spring growth.

Biomass allocation patterns changed in response to salinity and to nutrient load (Table 2.6). In response to salinity biomass was shifted predominantly away from culms to tubers regardless of nutrient load (Fig. 2.10a). At the high nutrient load and 13 dS m^{-1} biomass was also shifted from leaves to tubers (Table 2.6). Changes in culm biomass were mediated primarily via changes in culm height rather than culm number. Correlations between mean culm biomass and mean culm height, and mean culm number produced correlation coefficients of 0.9 ($P<.0001$, $n=12$) and 0.54 ($P<.006$, $n=12$), respectively. Carbohydrate storage induced by salinity may reflect a stress response strategy which ensures sufficient reserves are accumulated over the growth season to meet respiratory demands through winter dormancy. Alternatively assimilates may be simply redirected as utilisation by the shoot is blocked.

Changes in carbon allocation patterns in response to increasing salinity, resulted in lower above-ground to below-ground, and above-ground to root ratios (Table 2.5). In contrast the leaf to root ratio was only reduced at the high nutrient load and 13 dS m^{-1} (Table 2.5). Lower above-ground to root ratios in response to salinity or drought is commonly observed and is

considered to improve plant water relations. Lower shoot biomass reduces the surface area from which water is lost, and increased root biomass enhances water supply to the shoot. In *B. medianus* higher above-ground to root ratios with increasing salinity are unlikely to improve plant water relations as they arise from reductions in stem biomass, and not from reductions of leaf biomass or from increases in root biomass.

In response to increased nutrient loads biomass allocation was shifted away from roots to leaves (Table 2.6, Fig. 2.10b). Increased biomass allocation to the tubers evident after c. 8 weeks at the high nutrient load was no longer apparent in control plants. Changes in carbon allocation patterns in response to nutrient load resulted in leaf to root ratios increasing with increasing nutrient loads. It is likely that these changes may compromise plant water relations under more saline conditions and may thereby limit the benefits of higher nutrient loads. The reduction in leaf biomass at 13 dS m^{-1} and the high nutrient load suggests that the supply of water to the shoots may have been insufficient to meet transpiration losses associated with a higher leaf area.

2.3.2.7 Growth analysis

RGR was calculated over the salinity phase of the experiment as it provides an evaluation of performance which is independent of initial differences in biomass. A two-way analysis of variance identified significant nutrient and salinity effects and a significant salinity x nutrient interaction (Table 2.4). RGR over the salinity phase of the experiment, declined with increasing salinities, and was increased by higher nutrient loads at all salinities, excluding 9 dS m^{-1}, where nutrient load did not affect RGR (Fig. 2.11). Increases in RGR at higher nutrient loads were smaller at 13 dS m^{-1} than at the control or 4.5 dS m^{-1}, suggesting that the benefits of nutrients were generally weakened with increasing salinity.

As RGRs were greatest at the high nutrient load, the lower biomass at this load can be attributed to the initial reduction in growth prior to salinisation. It is likely therefore that in time the biomass of plants grown at the high nutrient load would exceed that achieved at the low and moderate nutrient loads, provided the growth season was sufficiently long. Plant

biomass over a longer growth period can be predicted from equation 2.4, assuming RGR does not change. At control, 4.5, 9 and 13 dS m^{-1} the biomass of plants grown at the high nutrient load would reach that achieved at the moderate nutrient load after a further 9, 6 46 and 50 days of growth, respectively. As the growth season may continue until May, more than 90 days longer, the potential for the high nutrient load to increase plant biomass above the moderate nutrient load does exist even at 13 dS m^{-1}.

The physiological processes underlying changes in RGR can be assessed by evaluating changes in NAR and LAR (Fig. 2.11). Reductions in NAR with increasing salinity under each nutrient load paralleled reductions in RGR (Fig. 2.11c). NAR was unaffected by nutrient load at all salinities excluding 9 dS m^{-1}, where NAR was considerably greater at the low nutrient load. LAR was increased substantially with increasing nutrient loads (Fig. 2.11b) and was only affected by salinity at the high nutrient load and 13 dS m^{-1}.

For all nutrient loads RGR was positively correlated with NAR; with correlation coefficients of 0.86 or greater (Fig. 2.12). The decline in RGRs as salinities increased are therefore correlated with reductions in NAR. No correlation was evident between RGR and LAR (Fig. 2.13) suggesting that NAR was the dominant factor associated with salinity induced reductions in RGR. However, a two-way analysis of variance found salinity to significantly influence both NAR and LAR (Table 2.4). As the interaction between nutrients and salinity was significant for LAR it is not possible to identify the levels of salinity at which significance lies. The influence of salinity on LAR however is likely to be attributed to the reduction in LAR at the high nutrient load and 13 dS m^{-1} (Fig. 2.11b). This response would also explain the significant interaction term for LAR. The reduction in NAR may be considered the main factor determining changes in RGR in response to salinity. This is supported by the higher F value for NAR compared to LAR and by linear regressions between RGR and NAR.

In contrast, a two-way analysis of variance demonstrated that nutrient load significantly increased LAR but did not affect NAR (Table 2.4). Enhanced RGR at higher nutrient loads

may therefore be attributed to LAR and not NAR. LAR is a function of the leaf weight ratio (LWR) and the specific leaf area (SLA) (Harper 1977). The SLA is represented here by the slope of the regression between leaf area and leaf weight (Fig. 2.1). As this regression did not differ between nutrient loads (Fig. 2.1), the SLA did not contribute to changes in LAR. In contrast, the LWR increased considerably at higher nutrient loads, indicating that increases in LAR at higher nutrient loads were achieved purely by a greater allocation of biomass to the leaves.

2.3.2.8 Leaf gas exchange characteristics

Reduction in NAR in response to salinity may arise from lower rates of photosynthesis due to reductions in the biochemical capacity for photosynthesis, or to stomatal closure limiting CO_2 diffusion. Alternatively reductions in the NAR may be associated with increased respiration rates. Maximum rates of photosynthesis were recorded at c. 2000 µmol m^{-2} s^{-1} for all treatment conditions (Fig. 2.14). Although curves were fitted to photosynthesis vs irradiance responses using a hyperbolic tangent function (Jassby and Platt 1976), both variability within the data set and insufficient measurements between light intensities of 1500 and 2000 µmol m^{-2} s^{-1} yielded estimates of photosynthetic parameters which were considered unreliable, and are therefore not reported in some instances. Salinities of 13 dS m^{-1} significantly reduced maximum rates of photosynthesis (c. 50%) compared to controls at all nutrient loads (Table 2.7). Consequently, the reduction in NAR at 13 dS m^{-1} can be attributed at least in part to lower rates of photosynthesis.

The intercellular CO_2 concentration (C_i) reflects the balance between CO_2 supply via stomata and the biochemical demand for CO_2. Where lower rates of photosynthesis are associated with relatively lower C_i it indicates that the biochemical demand for CO_2 is greater than supply and that photosynthesis is restricted by stomatal conductance (g_s) (Farquhar and Sharkey 1982; Seeman and Critchley 1985). Farquhar and Sharkey (1982) however point out that this does not imply that limitation by stomata is the primary cause for lower rates of assimilation. Assimilation may also saturate at lower values of C_i, consequently the limitation imposed by stomata may actually be lessened. Where lower rates of

photosynthesis are associated with relatively higher C_i, the supply of CO_2 exceeds demand and photosynthesis is not limited by g_S. In such cases the biochemical capacity for photosynthesis is the dominant mechanism by which photosynthesis is reduced (Farquhar and Sharkey 1982).

Reductions in photosynthesis at 13 dS m^{-1} were associated with large reductions in g_S (Table 2.7). As such, CO_2 limitation may contribute to lower rates of assimilation at 13 dS m^{-1}. This should be reflected in the intercellular CO_2 concentrations. The ratio of C_i to ambient CO_2 (C_a), was used to standardise for fluctuation in chamber CO_2 concentrations between measurements. Salinity did not induce a significant change in C_i/C_a compared to controls regardless of nutrient load. This suggests that lower rates of photosynthesis are primarily due to a lower biochemical capacity rather than to stomatal limitation. It is however unclear whether g_S declined in response to salinity, and was followed by a decline in the biochemical capacity, or if g_S declined in response to a lower biochemical capacity.

At 13 dS m^{-1} maximum rates of photosynthesis were significantly increased at the high nutrient load compared to the low or moderate nutrient loads (Table 2.8, Fig. 2.15). Maximum rates of photosynthesis were also slightly higher at the moderate nutrient load compared to the low nutrient load but differences were not statistically significant. Differences in photosynthetic rates were not apparent at light intensities less than c. 1200 μmol m^{-2} s^{-1}, indicating that the benefits of a higher photosynthetic capacity can only be exploited at high light intensities (Fig. 2.15). Indeed, both I_k and P_{max} are considerably greater at the high nutrient load compared to the lower nutrient loads (Table 2.9). Although rates of photosynthesis at each nutrient load presented in Table 2.7 are not directly comparable, as they were sampled on different days, the same trends are demonstrated across nutrient loads. Higher rates of photosynthesis at the high nutrient load were associated with both lower C_i/C_a and higher g_S, indicating that the biochemical capacity for CO_2 fixation was greater.

2.3.2.9 Water use efficiency

As lower C_i values indicate that the demand for CO_2 is relatively greater than supply via stomata, it also implies that water loss via stomata is reduced relative to assimilation. As such, a reduction in C_i represents an increase in water use efficiency (WUE) (Farquhar *et al.* 1989). The isotopic composition of leaf carbon provides an integrated record of C_i values over time (Farquhar *et al.* 1989). Where C_i is low, discrimination against C^{13} by rubisco is less, and the isotopic composition becomes more enriched in C^{13} (less negative) relative to a standard. Carbon isotope discrimination refers to the extent to which the isotopic composition in plant material deviates from the source air. Due to discrimination against C^{13} in photosynthesis the abundance of C^{13} in air is higher compared to plant material, but as WUE increases C_i is lowered, discrimination declines and the isotopic composition of plant material more closely resembles that of the source air (Farquhar *et al.* 1989).

Although instantaneous measurements revealed that 13 dS m^{-1} imposed only small reductions in C_i/C_a carbon isotope discrimination was reduced by 2 to 3 ‰ at both the low and moderate nutrient loads (Table 2.10). In the control discrimination was lower at the high nutrient load compared to the low and moderate nutrient loads and no further decrease occurred in response to 13 dS m^{-1}. The discrepancy between instantaneous measurement of C_i/C_a and carbon isotope discrimination may arise due to changes in C_i over time. It may be speculated that salinity reduced g_s, initially lowering C_i, but over time the biochemical capacity declined and C_i increased. Alternatively differences in C_i between control and 13 dS m^{-1} may occur at times other than that measured. Lower C_i/C_a values at the high nutrient load are however reflected to some extent in carbon isotope discrimination, being c. 1‰ lower than values at the low nutrient load.

2.3.2.10 Leaf nitrogen

Leaf nitrogen concentration increased at the higher nutrient loads, both in the control and at 13 dS m^{-1} (Table 2.10). Consequently, higher rates of photosynthesis at the high nutrient load may have been mediated by higher chlorophyll or rubisco concentrations. Improved leaf nitrogen content at the moderate nutrient load however failed to increase rates of photosynthesis. Although photosynthesis declined at 13 dS m^{-1} the nitrogen content of leaves

was increased. Whilst this may imply that factors other than nitrogen were involved in reducing the biochemical capacity, salinity may also divert nitrogen away from photosynthesis to the production of nitrogen based organic solutes (ie. glycinebetaine) to achieve osmotic adjustment. As such, less nitrogen may be available for photosynthesis.

2.4 Discussion

2.4.1 The influence of salinity on plant performance

The results clearly demonstrate that the salinity treatments imposed significantly reduced plant growth. Reductions in growth were reflected in lower numbers of leaves, lower LAIs, fewer and shorter culms and lower rates of photosynthesis. These effects were manifest in reductions in total biomass and reductions in RGR. Despite this, considerable growth was still achieved at 13 dS m^{-1}, regardless of nutrient load. As many freshwater macrophytes fail to persist at salinities of c. 6 dS m^{-1} (4000 mg L^{-1}, Brock 1981) *B. medianus* may be considered moderately salt tolerant.

Reduced growth of *B. medianus* in response to salinity, did not conform to that predicted by the bi-phasic model proposed by Munns and Termaat (1986). In *B. medianus*, salinity did not reduce biomass allocation to leaves (LWR), nor increase biomass allocation to roots (RWR), hence the leaf to root ratio was not decreased. Furthermore, salinity did not increase rates of leaf senescence. Consequently, lower RGRs imposed by salinity were not correlated with LAR but were strongly correlated with NAR. Although at the high nutrient load and 13 dS m^{-1} the LWR declined and hence LAR.

Similarly in barley, lower RGRs imposed by salinity were correlated with NAR and not LAR (Crammer *et al.* 1990; Crammer and Nowak 1992). Considerable variability in the response of growth parameters to salinity is however apparent. Curtis and Läuchli (1986) found reductions in RGR in kenaf (a fibre crop) to be correlated with both lower LAR and NAR. The correlation with NAR was however greater than with LAR (Crammer *et al.* 1990). Shennan *et al.* (1987) found LAR and not NAR to decline in response to increasing salinity in

Aster tripolium, a maritime halophyte. For *Brassica carinatus* the reduction in RGR imposed by salinity was associated with a reduction in NAR, during the early stages of growth, whilst in *Brassica napus* lower RGR was associated with a lower LAR, in the later stages of growth (He and Cramer 1993).

The findings of this experiment and of others indicate that salinity can substantially reduce growth without reducing LAR via osmotic or ion toxicity effects. Although NAR primarily mediated reductions in RGR, this does not exclude a hormonal influence on growth rate, which in contrast to that commonly observed may exert an equivalent influence on both roots and shoots. Whilst ion toxicity effects may have contributed to lower rates of photosynthesis, premature leaf senescence was not observed. Although it is acknowledged that higher levels of salinity may induce these effects, it seems unlikely given the duration of the experiment that they would become apparent over a longer time in *B. medianus*. In contrast to *B. medianus* rice is highly sensitive to salinity, and increased leaf senescence does occur within weeks at a low external Na concentrations (Yeo *et al.* 1991). Furthermore, James and Hart (1993) and Warwick and Bailey (1997) found an increased rate of leaf loss in three aquatic macrophytes; *Potamogeton tricarinatus*, *Eleocharis acuta* and *Myriophyllum crispatum*. However, *Triglochin procerum and Amphibromus fluitans* did not incur any change in leaf number in response to salinity although leaf size declined (Warwick and Bailey 1997).

Whilst changes in the RWR and shoot to root ratio are frequently induced by a water deficit or by salinity this response was not observed in *B. medianus*. Similarly Hocking (1981, 1985) found the shoot to root ratio to be insensitive to salinity in both *Cyperus involucratus* and *T. domingensis*. Experiments where the RWR has been found to be responsive to water or salinity stress have frequently been performed on seedlings. As demonstrated in this experiment ontological changes in carbon allocation patterns do occur, and it may be argued that root development is more sensitive to environmental cues early in development. Aquatic vegetation is adapted to water logged conditions and may therefore have root systems which are less responsive to water deficits. It is interesting to note that in rice and *Lemna*, both freshwater macrophytes, ABA stimulated growth in shoot tissue rather than inhibited it

(Munns and Cramer 1996). Root signals may hence play a lesser or different role in the response of aquatic vegetation to drought or salinity. It may also be proposed that the RWR in *B. medianus* is insensitive to salinity as the tuber acts as an alternate sink for assimilates.

Lower rates of photosynthesis in *B. medianus* at 13 dS m^{-1} were correlated with reductions in NAR imposed by salinity. Inhibition of photosynthesis has been observed for many species in response to salinity. Reductions have been attributed to both stomatal limitation and to effects on the biochemical capacity for photosynthesis (non-stomatal effects.) Both stomatal and non-stomatal reductions in photosynthesis have been reported in bean (Seeman and Critchley 1985), grapevines (Downton 1977) and both *Spartina* and *Scirpus* (Pearcy and Ustin 1984) In all cases, non-stomatal effects were found to be the dominant factor associated with lower assimilation. Similarly, Farquhar and Sharkey (1982) found that where water stress reduced assimilation it was, in most instances, due predominantly to a lower biochemical capacity rather than to stomatal limitation. A review by Farquhar and Sharkey (1982) on stomatal conductance and photosynthesis concluded that ABA applied to cut stems, and changes in humidity were the only instances where photosynthesis was primarily reduced by stomatal conductance. ABA does not itself affect rates of photosynthesis (Munns and Cramer 1996). As ABA is involved in the response to salinity, stomatal conductance may be reduced and limit photosynthesis. Furthermore, responsiveness of stomata can be retarded by salinity and lead to transient limitation by stomata (Farquhar and Sharkey 1982).

In *B. medianus*, lower rates of assimilation observed at 13 dS m^{-1} were not associated with large reductions in C_i/C_a, reductions can therefore be attributed to a lower biochemical capacity rather than to stomatal limitation. Reductions in the biochemical capacity for photosynthesis under saline conditions are considered to arise from either a lower concentration of rubisco, a lower efficiency of rubisco, or a reduced capacity to regenerate rubisco. In bean plants, high cytoplasmic chloride concentrations within chloroplasts were associated with lower rubisco efficiency, indicating salt-specific effects (Seeman and Critchley 1985). In mangroves, lower rates of photosynthesis at high salinity has been associated with low cytosolic K concentrations which inhibited the synthesis of the D1

protein; an integral constituent of PSII (Ball *et al.* 1987). In barley, salt induced Mn deficiency was found to reduce photosynthesis (Crammer and Nowak 1992).

It has also been proposed that reductions in the biochemical capacity for photosynthesis, arise not from direct effects of salinity on the photosynthetic apparatus, but due to altered source-sink relationships (Munns and Termaat 1986; Munns *et al.* 1982; Rawson and Munns 1984). Under saline conditions, carbohydrates and starches have been found to accumulate in leaves, proposing that the capacity to utilise these products is blocked (Munns *et al.* 1982). Munns (1993) and others have suggested that this may result in down regulation of photosynthesis as a feedback response.

In *B. medianus* the cause for reduced biochemical capacity at 13 dS m^{-1} remains speculative. It is possible that the biochemical capacity was impaired directly by ionic effects or was down regulated, due either to altered source sink relationships, or in response to lower g_s imposed by salinity. The later proposal is to some extent supported by the discrepancy between carbon isotope discrimination (representing a long term integrated value of C_i) and instantaneous measurements of C_i/C_a performed at the end of the experimental period. At 13 dS m^{-1} carbon isotope discrimination declined, indicating a reduction in C_i, however this was not reflected in instantaneous measurement C_i/C_a. Furthermore, stomatal limitation of photosynthesis in response to water stress has been found to cause feedback inhibition of biochemical reactions (Sharkey and Seeman 1989; Vassey and Sharkey 1989).

In *B. medianus*, biomass allocation to the tubers increased with increasing salinity. This may suggest that growth was reduced by an inability to utilise assimilates. If this is so then an altered source-sink relationship may have induced a reduction in the photosynthetic capacity. However, a high correlation exists between the allocation of biomass to culms and tubers suggesting that the increase in allocation to tubers is not induced by a general reduction in growth, but specifically to changes in biomass allocation between culms and tubers. Blanch *et al.* (in press) also found a strong correlation between biomass allocation of tubers and culms in the response of this species to changes in water levels. In response to increased

flooding depth, biomass allocation to the tubers declined whilst allocation to the culms increased. It is interesting to note that under similar water levels, allocation to the tubers reported by Blanch *et al.* (in press) was considerably greater than that of the control plants in this experiment. In fact allocation patterns described by Blanch *et al.* (in press) for *B. medianus* reflected those of plants at 13 dS m^{-1} in this experiment. As this experiment was carried out early in the growth season (September to January) whilst that of Blanch *et al.* (in press) was carried out late in the growth season (February to April), seasonal responses may explain these differences. It may be hypothesised that investment in culms late in the season is curtailed because the cost of production is less likely to be recovered, given the time remaining in which growth is possible. Consequently, biomass is more wisely invested in tubers thereby maximising growth the subsequent season. As such, there may exist environmental cues such as day length which trigger changes in carbon allocation.

The change in biomass allocation induced by salinity, was not specific to salinity as it was evident at the pre salinity harvest, in response to the high nutrient load. The similarity between high salinity and the high nutrient load during early growth is most likely a high (more negative) soil osmotic potential. At the high nutrient load the osmotic potential would decline (become less negative) over time as nutrient uptake increased with plant growth. This would explain the loss of this response over time. It is tempting to speculate that osmotic stress triggers a shift in biomass allocation away from culms to tubers.

Changes in biomass allocation patterns in response to salinity in *B. medianus* has several advantages. Firstly, increased biomass allocation to tubers will ensure sufficient reserves are acquired to sustain respiration over winter or over prolonged or more severe stress. Secondly, increased biomass allocation to tubers will minimise reductions in tuber biomass and reduce the impact of salinity on growth the subsequent year. In addition, reductions in culm height rather than culm number, associated with increased biomass allocation to tubers, has advantages in maintaining the occupation of space, thereby retarding the invasion of other species. Maximising culm number in preference to height may also maintain a mechanism by which more favourable soil conditions are located. Investment in taller culms may be

considered the most dispensable, since it is not directly involved in resource capture unless flooding occurs. However, reductions in culm height may compromise success if salinity is associated with or followed by significant increases in water level. As demonstrate by Blanch *et al.* (in press) in *B. medianus* and by Cooling (1996) in *Villarsia reniformis* R. Br. flooding will shift biomass away from tubers to culms. As such, responses to salinity and flooding are antagonistic. Plasticity between culms and tubers may be under selective pressure in environments with stochastic changes in both the level and availability of water. Whilst increased ethylene concentration is considered to induce stem elongation in flooded plants (Jackson 1993) the mechanism mediating changes in response to salinity has not been identified.

2.4.2 The influence of nutrient load on plant performance

The number of leaves and culms, and LAIs increased at the higher nutrient loads compared to the low nutrient load, across all salinities by the end of the experimental period. However, the influence of nutrient load on these parameters declined as salinities increased. Differences between the moderate and high nutrient load were marginal and took longer to manifest, compared to differences between either of these loads, and the low nutrient load. The high nutrient load increased culm numbers above that achieved at the moderate nutrient load at 13 dS m^{-1}, but this was also associated with a greater reduction in culm height. Whilst the number of leaves pot^{-1} at the end of the experimental period was greater at the high nutrient load compared to the moderate nutrient load across all salinities, this was not reflected in LAIs, which were only greater at the high nutrient load at salinities less than 9 dS m^{-1}.

Although higher nutrient loads enhanced the RGR of *B. medianus* at all salinity levels, excluding 9 dS m^{-1}, the benefits diminished as salinites increased. In the control, the moderate and high nutrient loads increased the RGR above that achieved at the low nutrient load by 6.4 and 11.7 mg g^{-1} d^{-1}, respectively, whilst at 13 dS m^{-1} the RGR was increased by 4 and 7.5 mg g^{-1} d^{-1}, respectively.

Although the high nutrient load increased RGRs, it did not yield a greater biomass than the moderate nutrient load after c. 17 weeks growth, regardless of salinity. At higher salinities however the effect was more pronounced. This resulted from the initial inhibition of growth prior to salinisation. As such it highlights the prolonged impact of even small and transient reductions in growth. Furthermore, it demonstrates that high nutrient loads at the time of establishment when nutrient uptake capacity is limited may compromise plant growth, and that recovery from this is slowed in the presence of salinity. Despite this, it was calculated that by the end of the growth season, biomass would exceed that reached at the moderate nutrient load, provided RGRs did not change.

Increased RGR at higher nutrient loads was associated with significantly higher LAR and not NAR. Increased LAR at the higher nutrient loads was mediated by a higher LWR and not via changes in the SLA. Changes in LWR were associated with a change in biomass allocation away from roots to leaves. This response supports the hypothesis of Chapin *et al.* (1987) that the allocation of biomass will shift to acquire the most limiting resource in order to optimally utilise available resources. At higher nutrient loads, nutrients are readily available and less biomass needs to be invested in roots permitting more assimilates to be directed toward light interception. Whilst the RWR was insensitive to the salinity levels examined (excluding 13 dS m^{-1} at the high nutrient load) the response to the imposed nutrient loads was marked. This may be because the signal inducing changes in the RWR in response to nutrients differ. The role of ABA in inducing changes in the RWR in response to nitrogen deficiency has not been substantiated and it is thought that cytokinins or sucrose may be involved (Munns and Cramer 1996; van der Werf and Nagel 1996).

Whilst higher LWRs mediated increased growth at higher nutrient loads this declined at the high nutrient load at 13 dS m^{-1}, causing the shoot to root ratio to decline. This suggests that the capacity to meet the transpiration demands of a higher leaf area was compromised by this level of salinity. The benefits of higher nutrient loads which are associated with a shift in carbon allocation to leaves may therefore diminish further at higher salinities than those examined, since the capacity to supply sufficient water to the shoots will become increasingly

more compromised. Despite high shoot to root ratios, wilting was not induced by 13 dS m^{-1}, indicating that water loss was sufficiently curtailed by reductions in stomatal conductance. However, the capacity to increase the leaf to root ratio in response to high nutrient loads, even at 13 dS m^{-1} without a compensatory reduction in stomatal conductance, suggests that hydraulic resistance must be low.

Rates of photosynthesis were significantly greater at the high nutrient load and tended toward higher rates at the moderate nutrient load, however NAR was not influenced by nutrient load at any level of salinity. Several explanations for this are possible. Increased rates of photosynthesis at higher nutrient loads will only be realised at high light intensity (Fig. 2.15). However, leaf numbers are increased by high nutrient loads increasing the extinction of light through the canopy. As such, less leaves receive full irradiance and achieve higher rates of photosynthesis. Although potential rates of photosynthesis may not be realised, the metabolic cost incurred in achieving a higher biochemical capacity can be considerable. For nitrogen, on which most of the components of photosynthesis depend, the cost of absorption, translocation and assimilation represents c. 20-50% of the total plant carbon expenditure (Chapin *et al.* 1987). Ten percent of this is incurred by root growth in the acquisition of nitrogen (Chapin *et al.* 1987). Although the costs of absorption are reduced under high nutrient loads the cost will still be between 10-40%. Furthermore, leaf respiration can increase with high leaf nitrogen content (Chapin *et al.* 1987). Consequently, if photosynthesis is limited by light or stomatal conductance the benefits of a greater biochemical capacity are reduced relative to the costs (Chapin *et al.* 1987). It may be proposed that the failure of NAR to respond to nutrient addition, despite higher rates of photosynthesis at least at the high nutrient load, is due on the one hand to the increased extinction of light which limits photosynthesis, and on the other to increased respiratory costs associated with the translocation and assimilation of nutrients.

Although nutrient loads clearly enhanced growth, the benefits were reduced at higher salinities. This is consistent with the observation in crop species that increased soil fertility

increases productivity but also increases sensitivity to salinity. This suggests that the potential for nutrients to enhance plant performance will diminish as salinities increase.

It is clear that a high level of co-ordination prevails between specific structural and functional tissues in *B. medianus*. There exists a high degree of co-ordination between the growth of tubers and stems, and between root and leaves, the former being sensitive to salinity/water stress and water level, and the later being sensitive to nutrient status. Locally *B. medianus* has been successfully established in both a constructed wetland used to treat effluent, and in coastal salt affected wetlands constructed to treat stormwater. Furthermore, *B. medianus* persists in the river and wetland systems of the Murray-Darling river system where it experiences fluctuations in both water level and water availability (Walker *et al.* 1994; Blanch *et al.*, in press). It is proposed that relatively discrete responses to distinct environmental conditions demonstrated by *B. medianus* may mediate its success across broad environmental gradients.

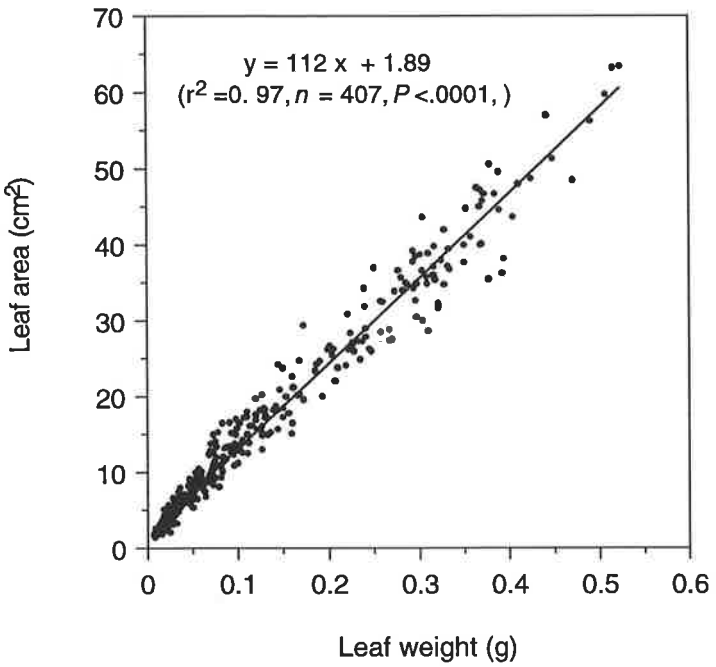


Figure 2.1. Leaf area as a function of leaf weight for all salinity-nutrient treatments.

Table 2.1. Number of leaves and shoots per pot, and height of culm four at each nutrient load prior to salinisation. Data are means ± se (n= 39). Letters represent means which are significantly different (P<.05) across nutrient treatments.

	Nutrient Load		
	Low	Moderate	High
Leaves pot^{-1}	63.1 ± 2.1^{a}	63.3 ± 2.7^{a}	38.9 ± 2.3^{b}
Culms pot^{-1}	8.5 ± 0.3^{a}	9.0 ± 0.4^{a}	6.2 ± 0.3^{b}
Height culm four cm	27.5 ± 1.5^{a}	26.0 ± 1.4^{a}	19.0 ± 1.4^{b}

Table 2.2. RGR (mg g d^{-1}), plant biomass (g) and above to below ground, and above-ground to root ratios at each nutrient load prior to salinisation. Data are means ± se (n=7). Letters represent means which are significantly different (P<.05) across nutrient treatments.

	Nutrient Load		
	Low	Moderate	High
RGR	28.9 ± 1.1^{a}	29.5 ± 1.9^{a}	22.4 ± 2.2^{b}
Total Biomass	31.5 ± 1.8^{a}	31.2 ± 4.3^{a}	22.4 ± 4.2^{a}
Above-ground	20.2 ± 1.2^{a}	21.9 ± 2.9^{a}	14.3 ± 2.7^{a}
Leaves	10.6 ± 0.6^{a}	11.3 ± 1.8^{a}	7.9 ± 1.6^{a}
Stems	9.3 ± 0.5 ^{a}	10.4 ± 1.6^{a}	6.7 ± 1.5^{a}
Below-ground	11.4 ± 0.9^{a}	9.3 ± 1.4^{a}	8.0 ± 1.6^{a}
Tubers	4.6 ± 0.4^{a}	3.8 ± 0.6^{a}	4.3 ± 0.9^{a}
Rhizomes	2.0 ± 0.2^{a}	1.8 ± 0.3 ^{a}	1.5 ± 0.3^{a}
Roots	4.8 ± 0.5^{a}	3.6 ± 0.6^{ab}	2.2 ± 0.5^{b}
Above : Below	1.8 ± 0.1^{a}	2.4 ± 0.1^{b}	1.8 ± 0.1^{a}
Above : Root	4.4 ± 0.4^{a}	6.3 ± 0.5^{b}	6.8 ± 0.4^{b}

Table 2.3. Biomass allocation as a percentage of total biomass at each nutrient load prior to salinisation. Data are means ± se (n= 7).

	Nutrient Load		
	Low	Moderate	High
%Above-ground	64.1 ± 1.7	70.4 ± 1.0	63.9 ± 1.3
%Leaves	33.6 ± 1.3	36.4 ± 0.6	34.1 ± 0.8
%Stems	29.5 ± 0.3	33.3 ± 0.5	28.9 ± 0.6
%Below-ground	35.9 ± 1.7	29.6 ± 1	36.0 ± 1.3
%Tubers	14.5 ± 1.0	12.1 ± 0.4	19.7 ± 1.7
%Rhizomes	6.3 ± 0.6	5.9 ± 0.2	6.6 ± 0.4
%Roots	15.1 ± 1.1	11.6 ± 0.8	9.7 ± 0.7

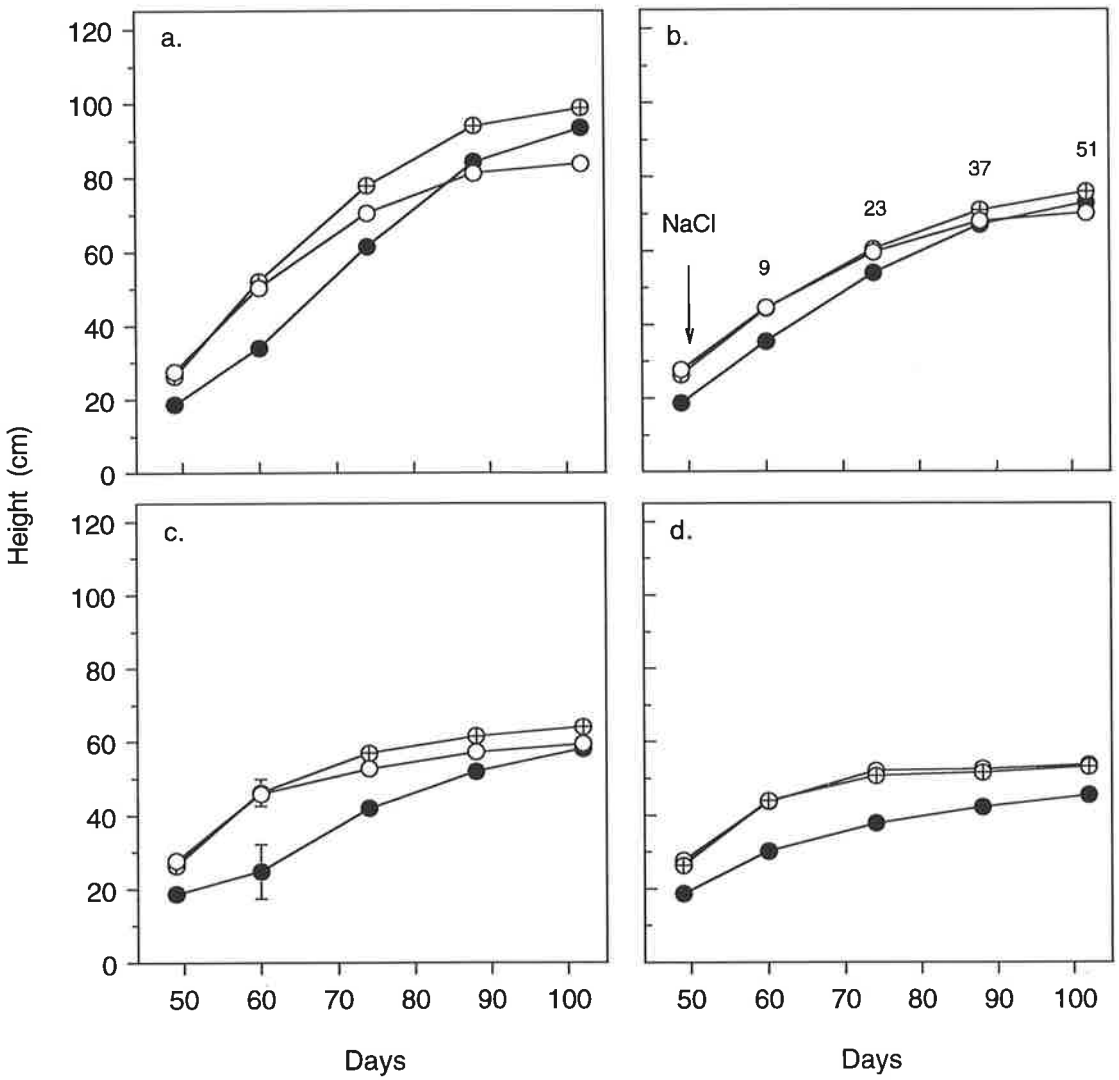


Figure 2.2. Change in height over time at low (open circles), moderate (hatched circles) and high nutrient loads (filled circles); a. control, b. 4.5 dS m^{-1}, c. 9 dS m^{-1} and d. 13 dS m^{-1}. Data are means, bars represent se (n = 8). The arrow in b. represents the time at which salinisation commenced, and numbers above symbols are days after salinisation.

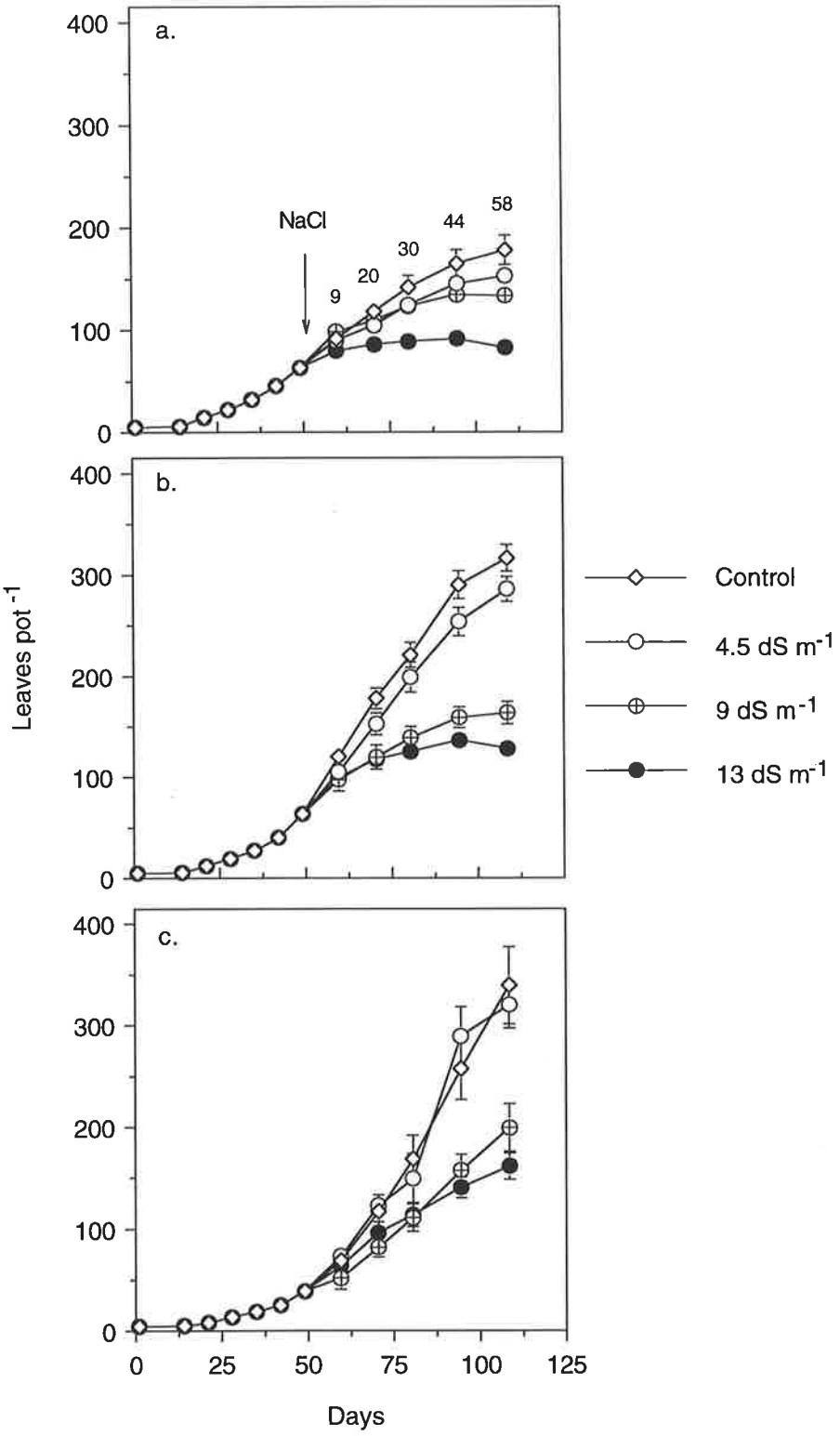


Figure 2.3. Leaves per pot^{-1} over time at each salinity level; a. low, b. moderate, and c. high nutrient loads. Data are means, bars represent se (n=8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days after salinisation.

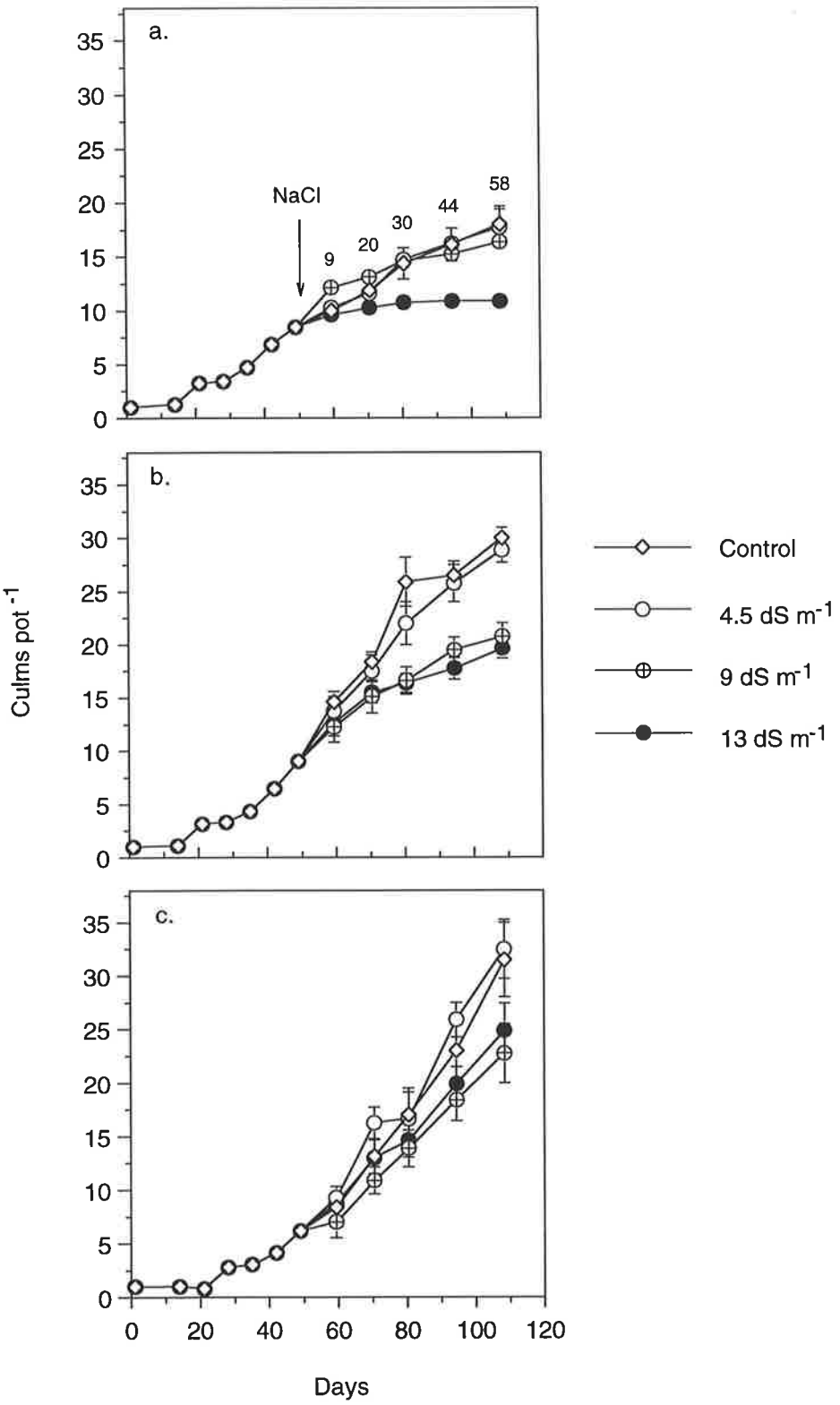


Figure 2.4. Culms pot^{-1} over time at each salinity level; a. low, b. moderate, and c. high nutrient loads. Data are means, bars represent se (n=8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

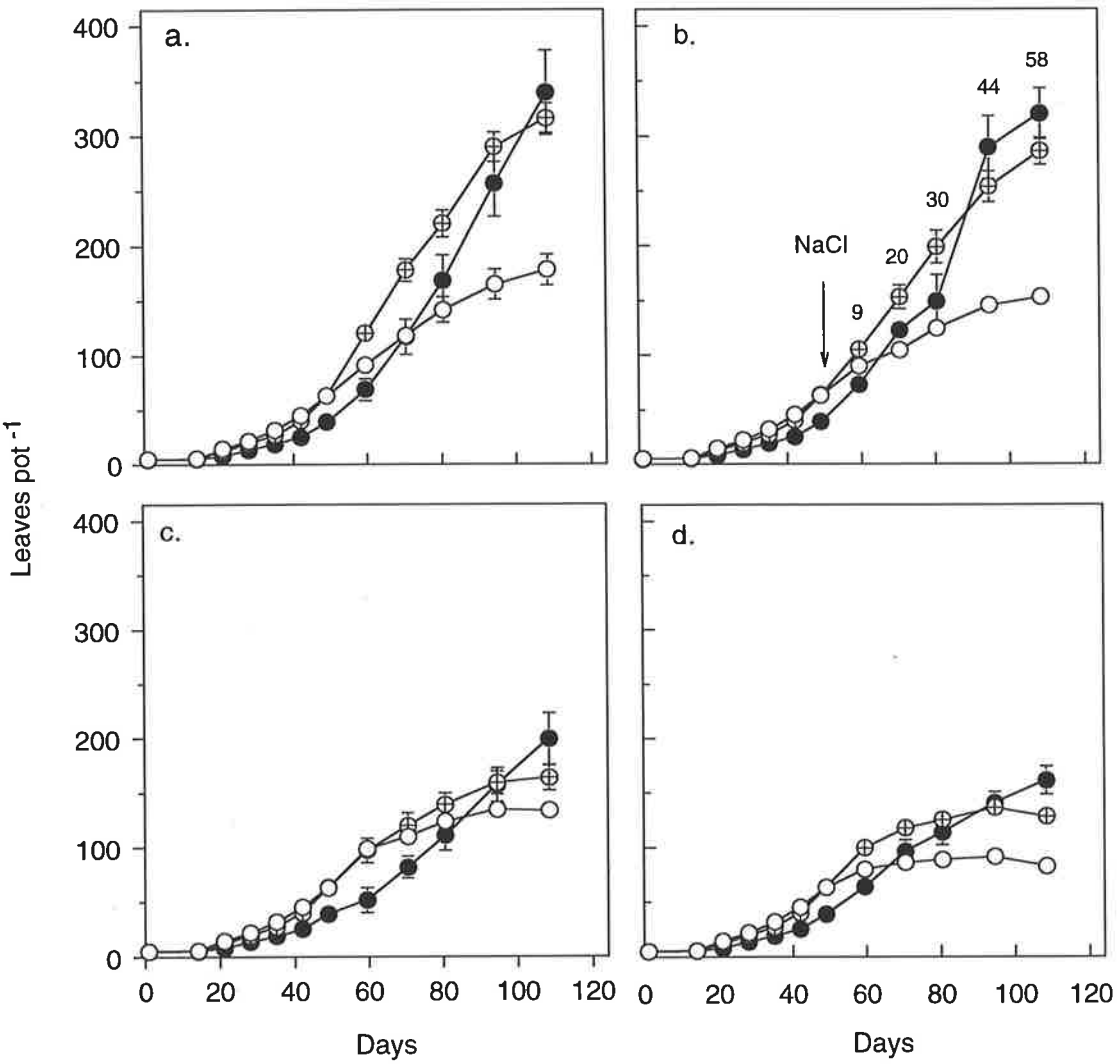


Figure 2.5. Leaves pot^{-1} over time at low (open circles), moderate (hatched circles) and high (filled circle) nutrient loads; a. control, b. 4.5 d S m^{-1}, c. 9 dS m^{-1} and d. 13 dS m^{-1}. Data are means, bars represent se (n=8). The arrow in b. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

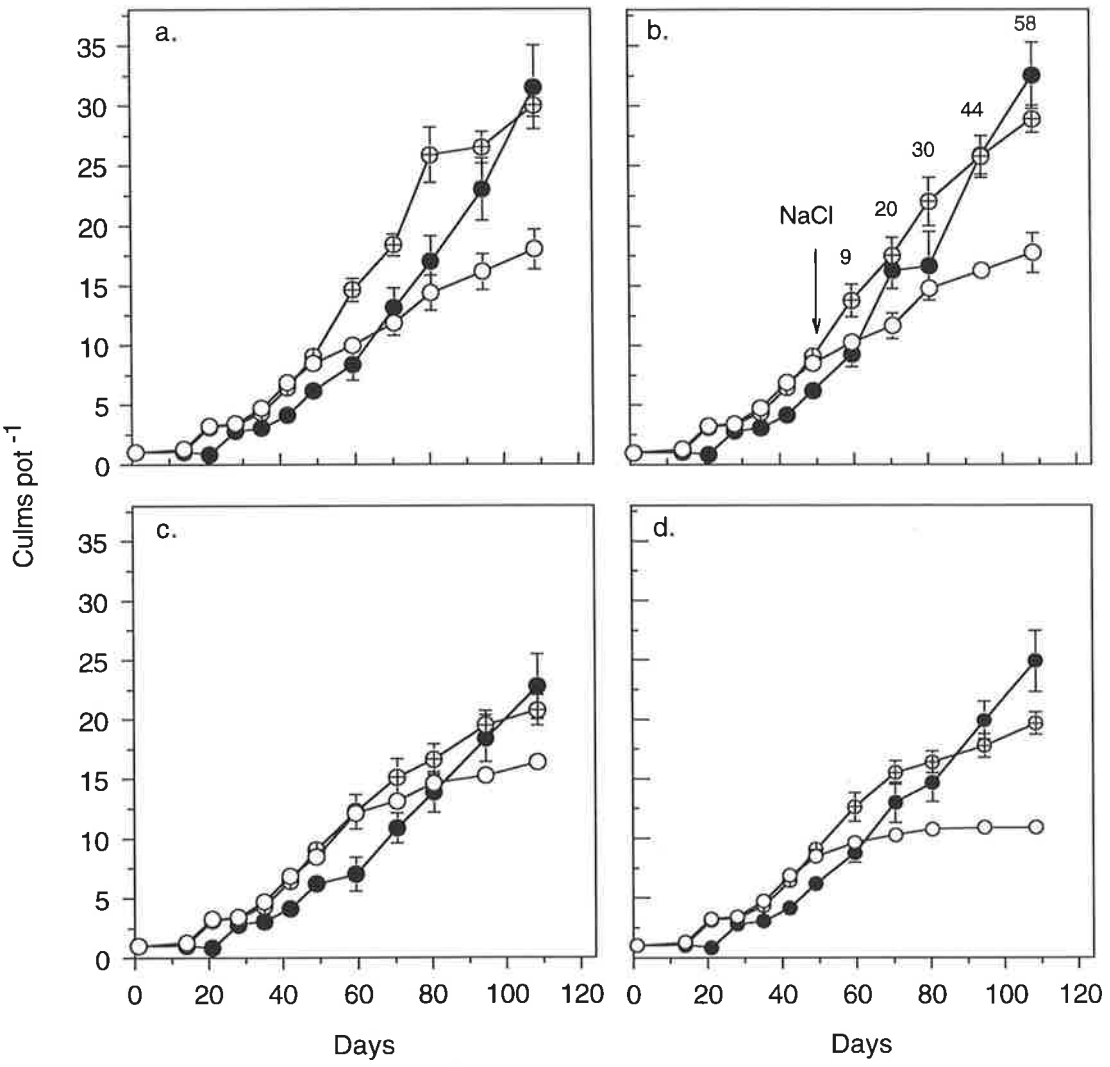


Figure 2.6. Culms pot^{-1} over time at low (open circles), moderate (hatched circles) and high (filled circles) nutrient loads; a. control, b. 4.5 d S m^{-1}, c. 9 dS m^{-1} and d. 13 dS m^{-1}. Data are means, bars represent se (n=8). The arrow in b. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

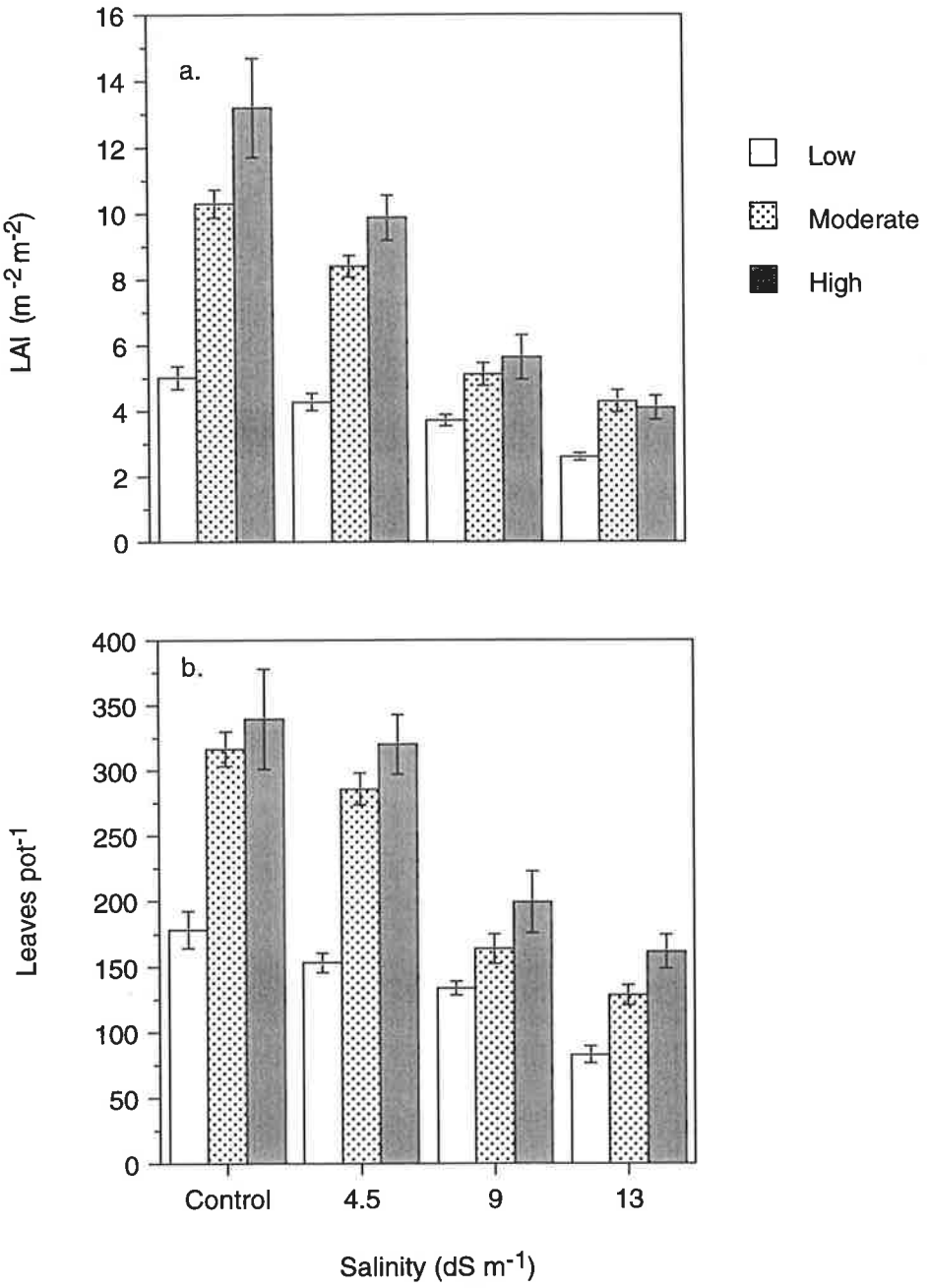


Figure 2.7. LAI (a.) and leaves pot^{-1}(b.) as a function of salinity for each nutrient load (low, moderate and high). Data are means, bars represent se (n=8).

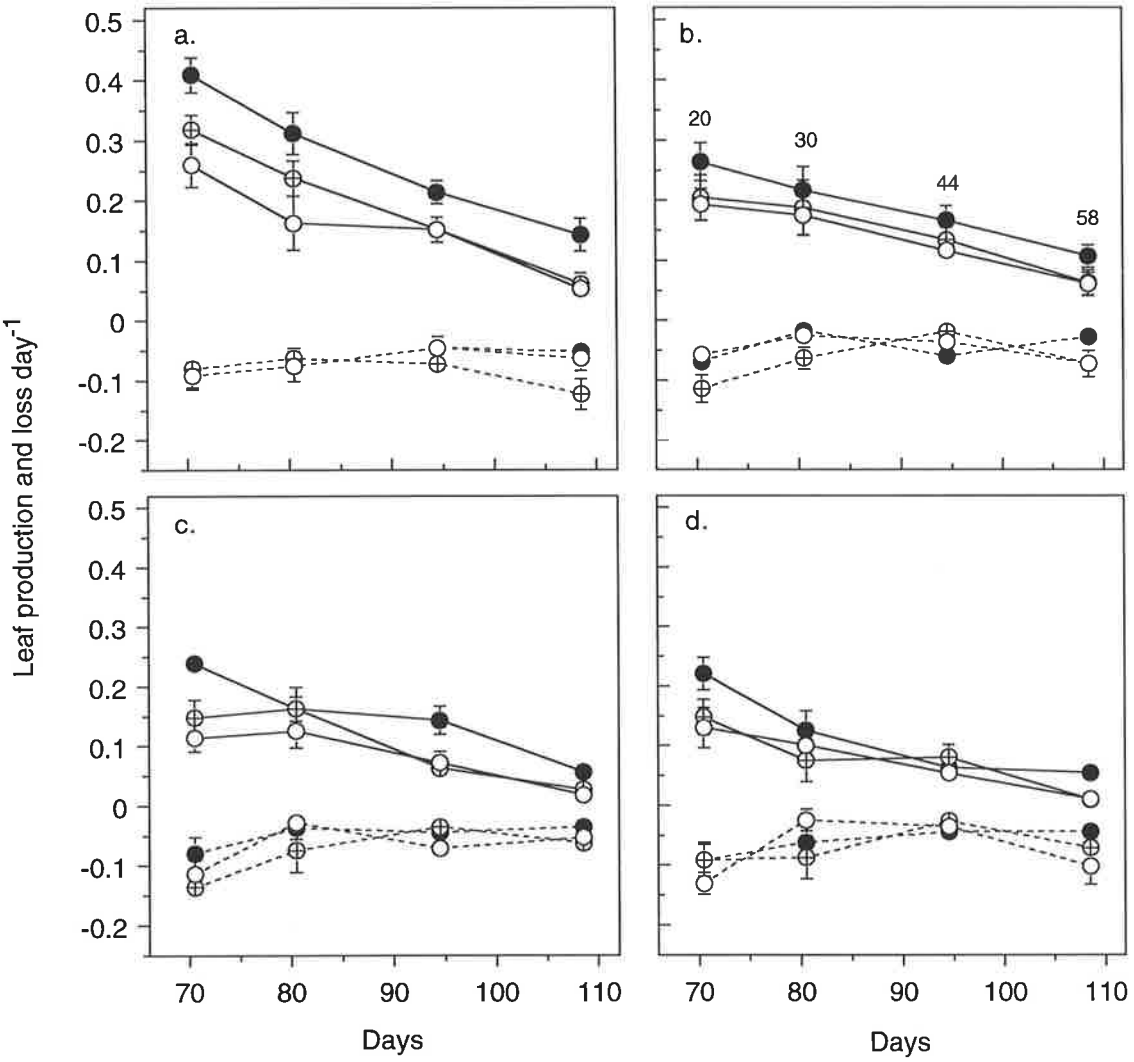


Figure 2.8. Leaf production (solid lines) and loss (broken lines) day^{-1} for culm 4 at low (open circles), moderate (hatched circles) and high (filled circles) nutrient loads; a. control, b. 4.5 dS m^{-1}, c. 9 dS m^{-1} and d. 13 dS m^{-1}. Bars represent se (n = 6-8). Numbers above symbols in b. are days following salinisation.

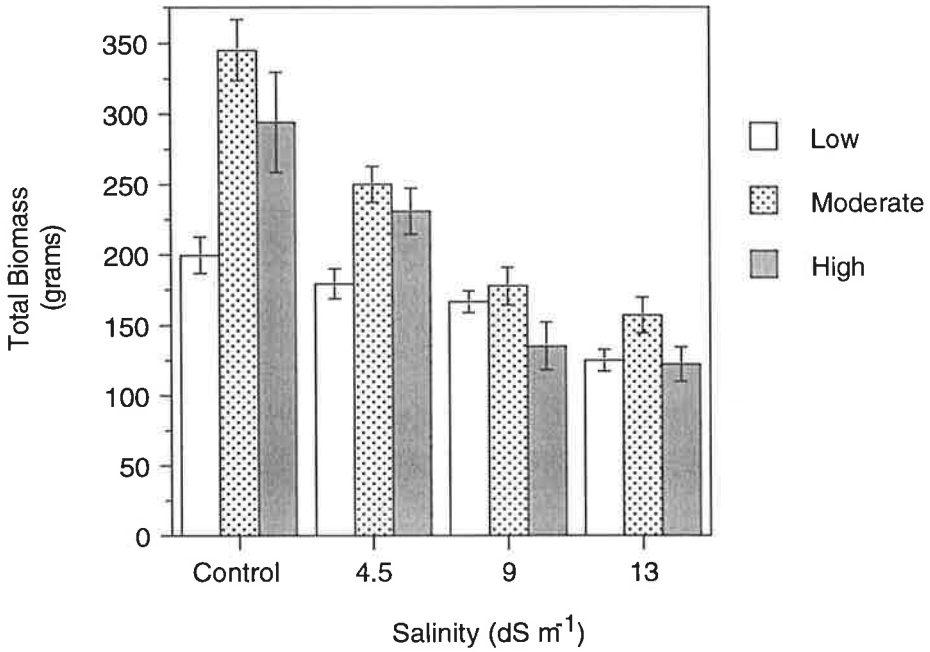


Figure 2.9. Total biomsss at each salinity level and nutrient load (low, moderate and high). Bars represent se (n= 8).

Table 2.4. Results of two-way analysis of variance for growth parameters. NB. the factor pond was not significant for any variable. Nutrient load df =2, 96; salinity df = 3, 96; interaction df = 6, 96; ns indicates no significant difference.

Source of Variation	*F*	*P*
Total Biomass		
Nutrient load	15.3	<.001
Salinity	45.6	<.001
Nutrient load x salinity	4.1	.001
RGR		
Nutrient load	37.6	<.001
Salinity	44.5	<.001
Nutrient load x salinity	2.5	.027
NAR		
Nutrient load	0.60	ns
Salinity	21.0	<.001
Nutrient load x salinity	2.1	ns
LAR		
Nutrient load	217.2	<.001
Salinity	8.1	<.001
Nutrient load x salinity	4.1	.001

Table 2.5. Ratios of above to below-ground biomass, above-ground to root biomass and leaf to root biomass at each salinity-nutrient treatment. Data are means ± se (n = 8).

	Salinity	Nutrient Load		
	dS m^{-1}	Low	Moderate	High
Above: Below	Control	0.78 ± .03	0.85 ± .04	1.21 ± .03
	4.5	0.66 ± .05	0.77 ± .03	1.05 ± .04
	9	0.53 ± .02	0.60 ± .04	0.93 ± .05
	13	0.48 ± .01	0.55 ± .02	0.65 ± .03
Above : Root	Control	2.87 ± .24	5.73 ± .33	10.17 ± .34
	4.5	2.99 ± .31	5.67 ± .35	8.98 ± .31
	9	2.94 ± .11	5.86 ± .60	9.32 ± .89
	13	2.43 ± .14	5.17 ± .35	6.31 ± .61
Leaf : Root	Control	0.82 ± .08	1.85 ± .11	4.12 ± .16
	4.5	.089 ± .08	2.17 ± .16	3.67 ± .10
	9	0.93 ± .04	2.24 ± .12	4.06 ± .41
	13	0.76 ± .05	1.99 ± .14	2.68 ± .27

Table 2.6. Biomass allocation as a percentage of total biomass at each salinity-nutrient treatment. Data are means ± se (n = 8).

	Salinity	Nutrient Load		
	dS m^{-1}	Low	Moderate	High
%Above-ground	Control	43.8 ± 1.9	45.9 ± 1.1	54.78 ± 0.6
	4.5	39.3 ± 1.9	43.4 ± 0.8	51.17 ± 0.9
	9	34.6 ± 0.8	37.5 ± 1.4	47.91 ± 1.6
	13	32.7 ± 0.5	35.5 ± 0.7	39.29 ± 1.2
%Leaves	Control	12.4 ± 0.5	14.9 ± 0.6	22.18 ± 0.4
	4.5	11.7 ± 0.4	16.5 ± 0.6	20.95 ± 0.4
	9	11.0 ± 0.9	14.3 ± 0.6	20.80 ± 0.7
	13	10.2 ± 0.4	13.7 ± 0.6	16.62 ± 0.5
%Stems	Control	29.6 ± 0.7	31.0 ± 0.7	32.6 ± 0.4
	4.5	26.2 ± 1.1	26.8 ± 0.4	30.1 ± 0.6
	9	23.2 ± 0.6	23.0 ± 0.8	27.1 ± 0.9
	13	22.1 ± 0.4	21.8 ± 05	22.7 ± 0.7
%Seed Heads	Control	4.1 ± 1	0	0
	4.5	3.2 ± 1	0.1 ± 0.1	0.1 ± 0.1
	9	1.1 ± 0.6	0.4 ± 0.2	0
	13	1.1 ± 0.6	0.1 ± 0.1	0
%Below-ground	Control	56.2 ± 0.9	54.1 ± 1.1	45.2 ± 0.6
	4.5	60.7 ± 1.9	56.5 ± 0.8	48.8 ± 0.9
	9	65.4 ± 0.8	62.5 ± 1.4	52.1 ± 1.6
	13	67.3 ± 0.5	64.5 ± 0.7	60.7 ± 1.2
%Tubers	Control	37.9 ± 1.0	43.0 ± 1.3	36.7 ± 0.75
	4.5	44.3 ± 1.3	45.5 ± 1.1	40.3 ± 1.0
	9	50.9 ± 0.7	52.7 ± 1.0	43.5 ± 1.7
	13	50.2 ± 0.7	53.7 ± 0.5	51.1 ± 1.1
%Rhizomes	Control	2.53 ± 0.2	3.0 ± .16	3.1 ± 0.1
	4.5	2.66 ± 0.1	3.2 ± 1.5	2.8 ± 0.2
	9	2.74 ± 0.2	3.0 ± 0.22	3.2 ± 0.2
	13	3.39 ± 0.3	3.8 ± 0.16	3.1 ± 0.2
%Roots	Control	15.8 ± 1.0	8.2 ± 0.5	5.4 ± 0.2
	4.5	13.7 ± 0.9	7.9 ± 0.6	5.7 ± 0.2
	9	11.8 ± 0.3	6.8 ± 0.6	5.4 ± 0.4
	13	13.7 ± 0.7	7.0 ± 0.3	6.5 ± 0.5

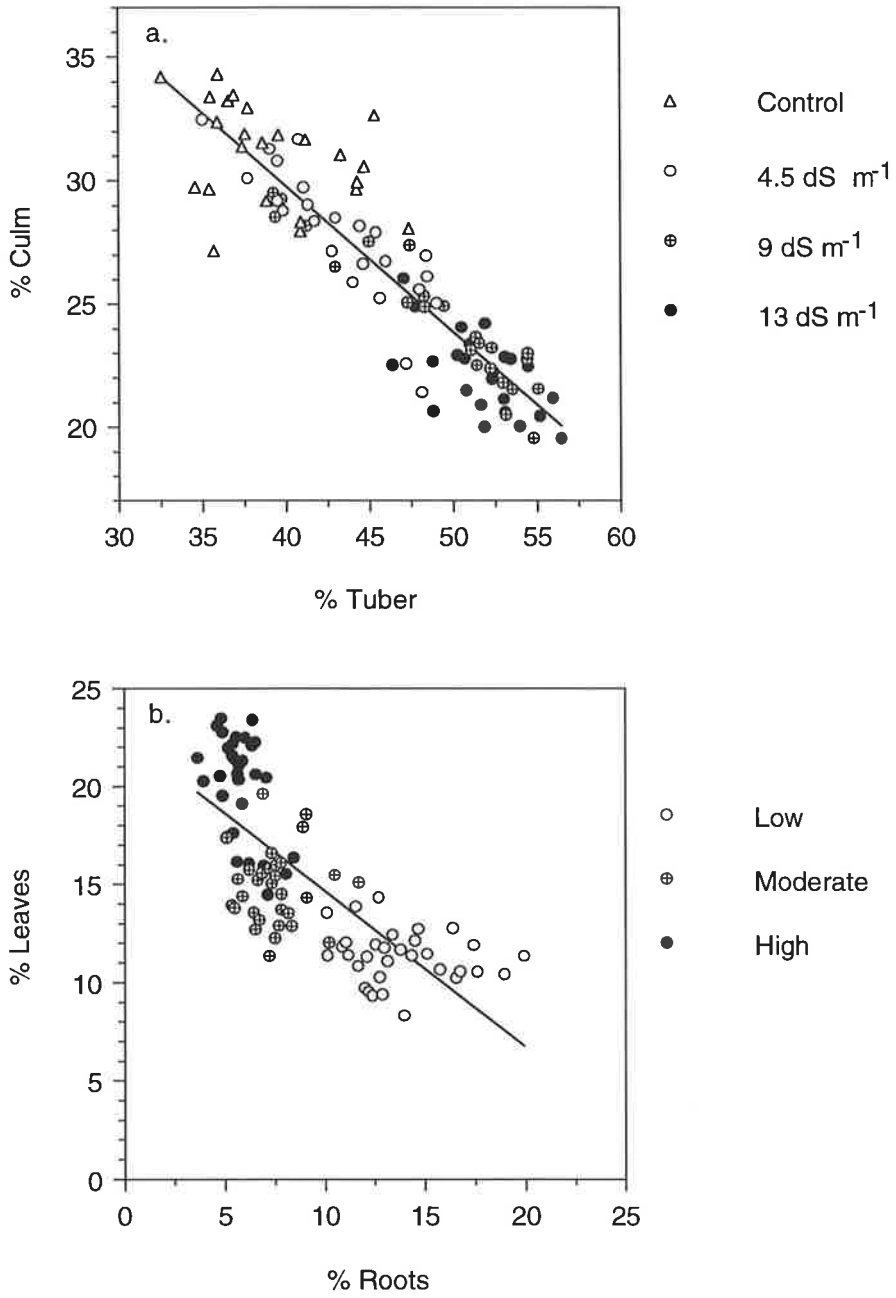


Figure 2.10. Relationships between percent culm biomass and percent tuber biomass in response to salinity (a.), and percent leaf biomass and percent root biomass in response to nutrient load (b.). NB. The origin of the axes in a. do not begin at zero.

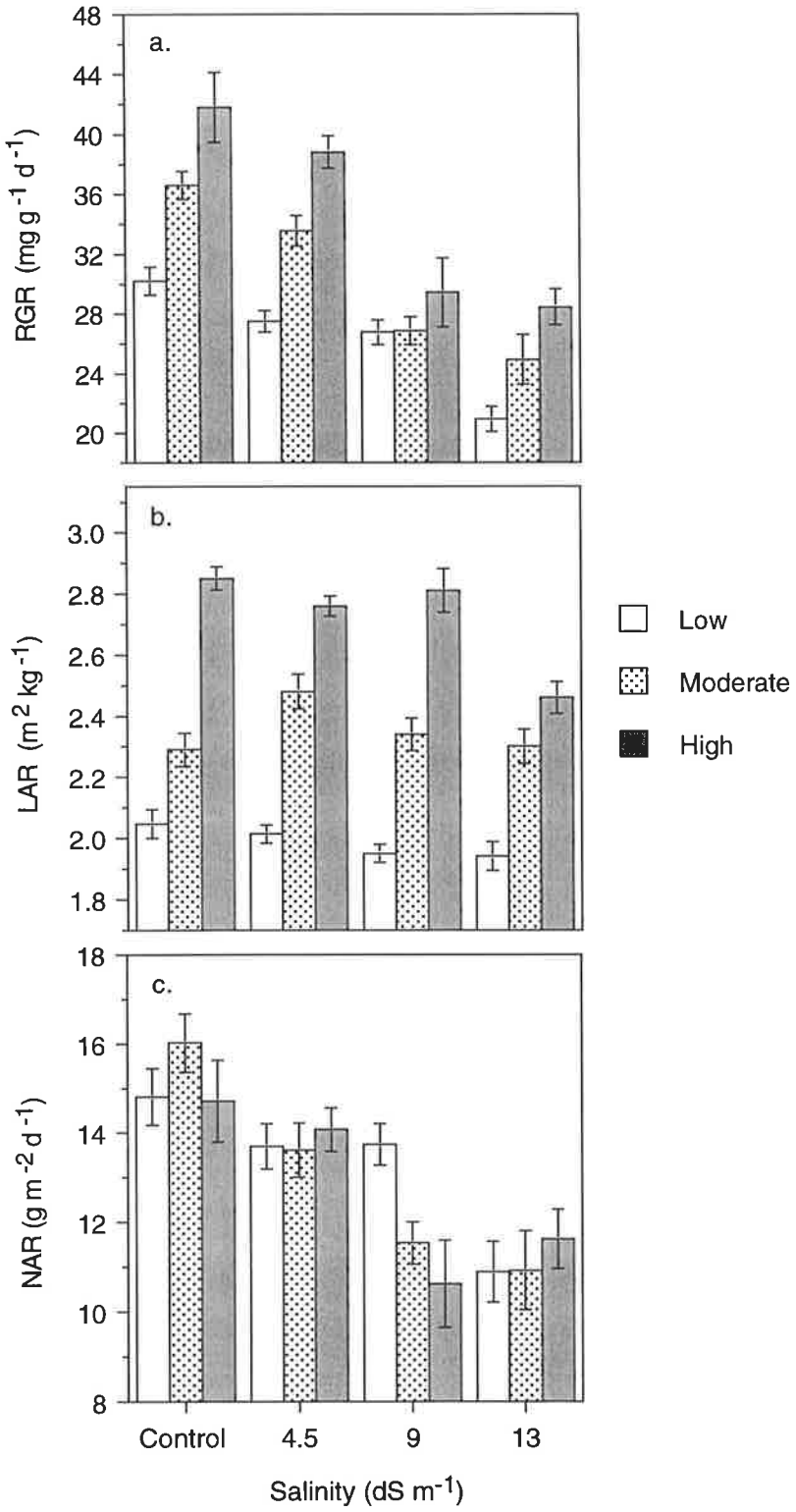


Figure 2.11. Growth parameters;a. RGR, b. LAR and c. NAR in response to salinity at each nutrient load (low, moderate and high). Data are means, bars represent se (n=8). NB. The origin of the y axis in a.,b. and c. does not begin at zero.

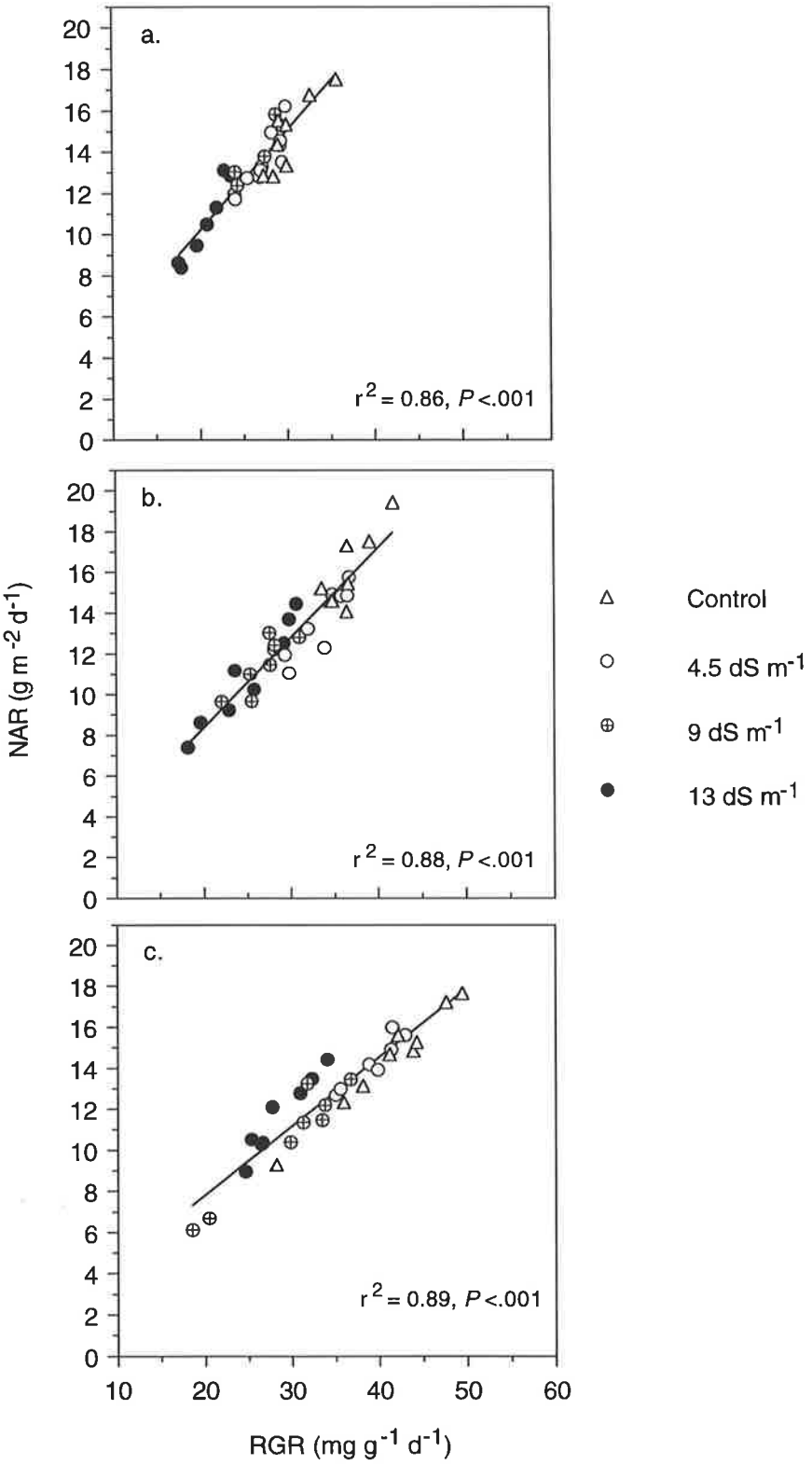


Figure 2.12. NAR as a function of RGR in response to salinity; a. low, b. moderate, and c. high nutrient loads (*n*=32). NB. The origin of the x axis does not begin at zero.

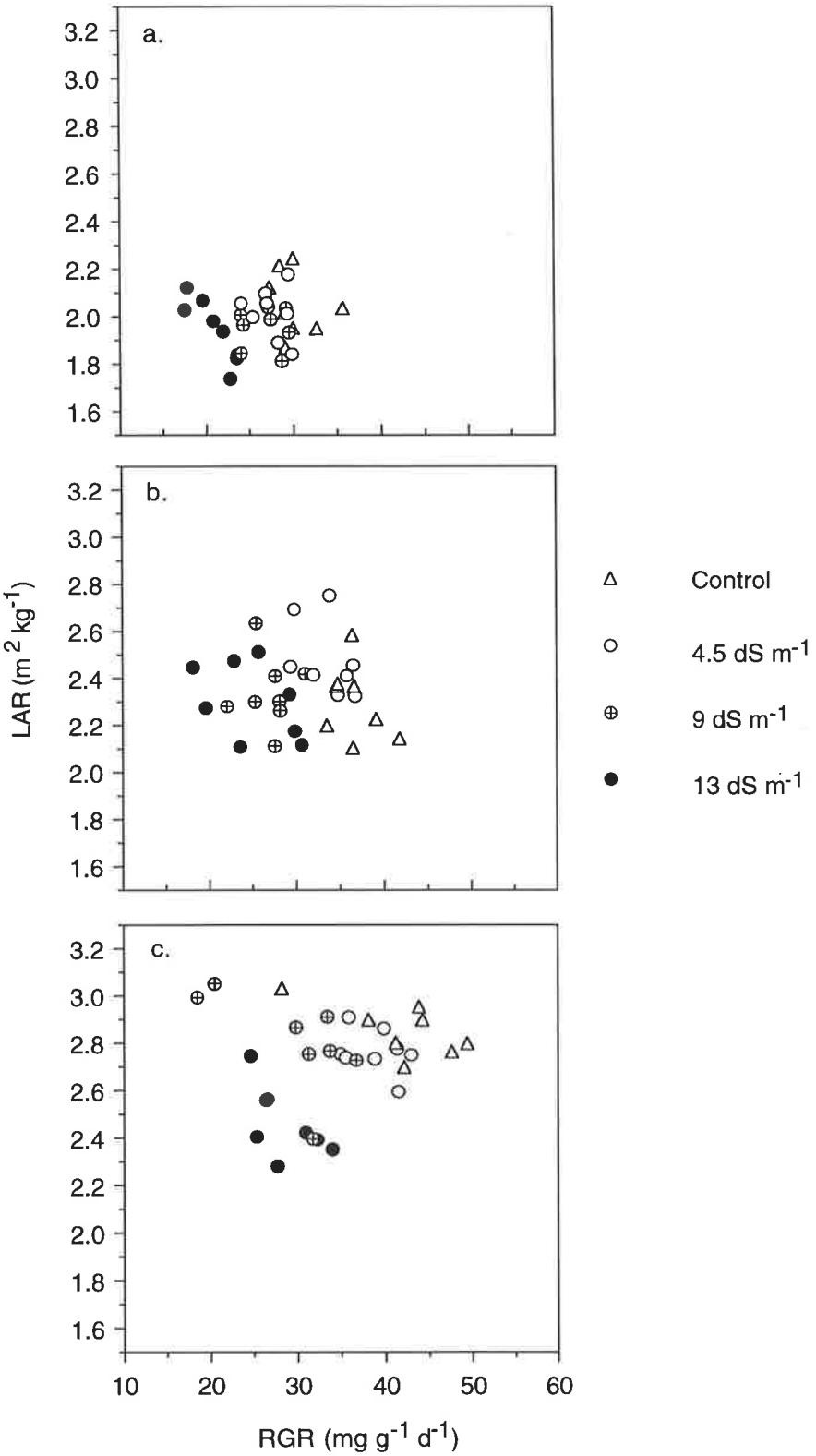


Figure 2.13. LAR as a function of RGR in response to salinity; a. low, b. moderate and c. high nutrient loads (n=32). NB. The origin of the axes do not begin at zero.

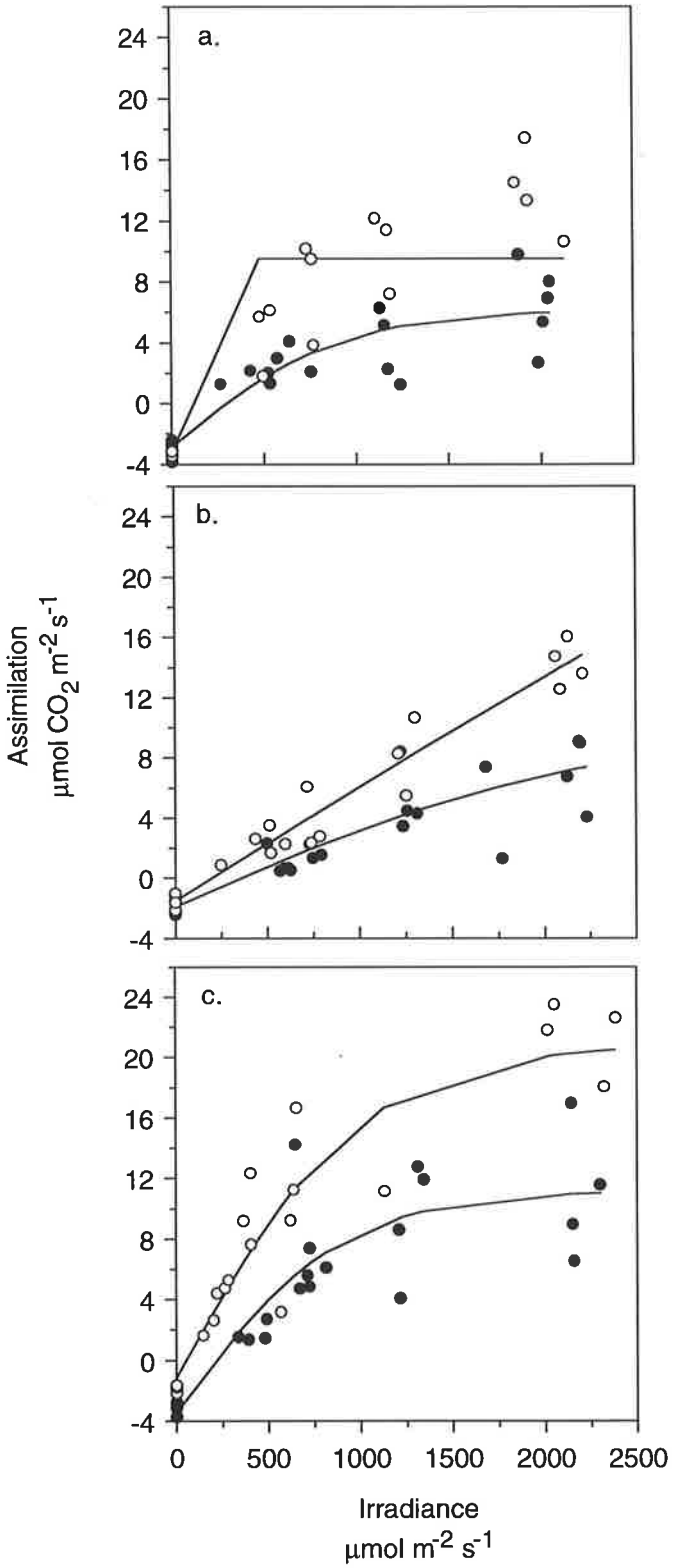


Figure 2.14. Assimilation as a function of irradiance at control (open circles) and 13 dS m^{-1} (filled circles); a. low, b. moderate and c. high nutrient loads. Curves were fitted using a hyperbolic tangent function.

Table 2.7. The effect of salinity on leaf gas exchange characteristics at maximum irradiance at each nutrient load. Data are means ± se (n =4). Different letters represent means at each nutrient load which were significantly different (P<.05). The symbol ‡ indicates that a Wilcoxin/Kruskal Wallace non-parametric test was used due to non-normality which could not be corrected by transformation.

Nutrient Load	Salinity dS m^{-1}	Irradiance µmol m^{-2} s^{-1}	Assimilation µmol CO_2 m^{-2} s^{-1}	Conductance mmol m^{-2} s^{-1}	C_i/C_a
Low	Control	1956 ± 57^a	14.0 ± 1.4^a	339 ± 53^a	0.74 ± .02^a
	13	2018 ± 14^a	5.8 ± 1.1^b	102 ± 12^b	0.67 ± .02^a
Moderate	Control	2118 ± 32^a	14.2 ± 0.7^a	236 ± 20 ^{a}	0.65 ± .02^{a‡}
	13	2183 ± 22^a	7.2 ± 1.2^b	95 ± 15^b	0.61 ± .04^a
High	Control	2190 ± 93^a	21.5 ± 1.2^a	351 ± 47^a	0.63 ± .03^a
	13	2185 ± 37^a	11.0 ± 2.2^b	146 ± 35^b	0.59 ± .01^a

Table 2.8. The effect of nutrient load on leaf gas exchange characteristics at maximum irradiance at 13 dS m^{-1}. Data are means ± se (n = 4-5). Different letters represent means which were significantly different (P<.05).

Nutrient Load	Irradiance µmol m^{-2} s^{-1}	Assimilation µmol CO_2 m^{-2} s^{-1}	Conductance mmol m^{-2} s^{-1}	C_i/C_a
Low	1971 ± 24^a	7.2 ± 1.0^a	151 ± 20^a	0.70 ± .02^a
Moderate	1987 ± 46^a	9.5 ± 0.6^a	156± 15^a	0.64 ± .01^{ab}
High	1985 ± 40^a	15.2 ± 1.5^b	242 ± 37^a	0.61 ± .02^b

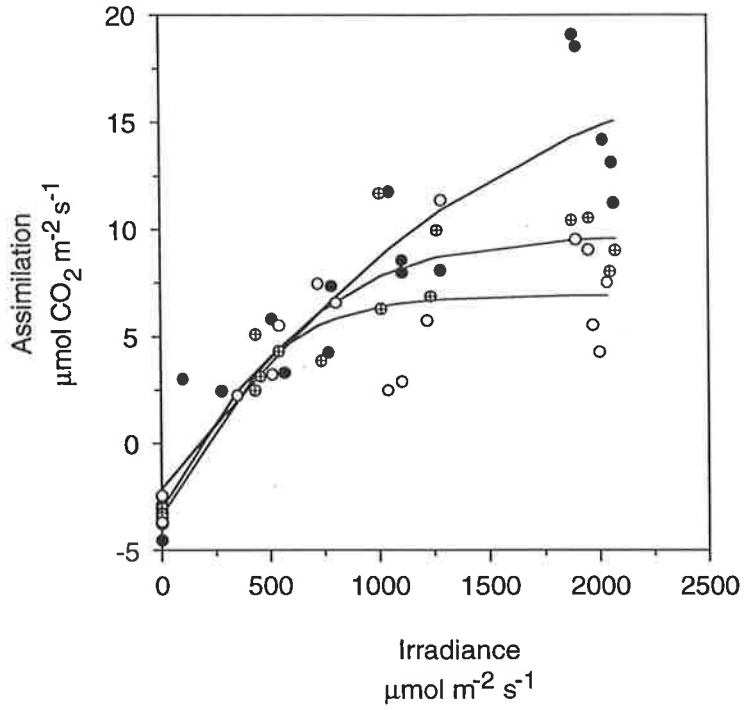


Figure 2.15. Assimilation as a function of irradiance at 13 dS m^{-1} and low (open circle), moderate (hatched circles), and high (filled circles) nutrient loads. Curves were fitted using a hyperbolic tangent function.

Table 2.9. The influence of nutrient load on photosynthesis vs irradiance paramaters at 13 dS m^{-1}.

		Nutrient Load		
Parameter		Low	Moderate	High
P_{max}	µmol CO_2 m^{-2} s^{-1}	9.97	13.08	20.60
I_k	µmol m^{-2} s^{-1}	566	792	1720
R	µmol CO_2 m^{-2} s^{-1}	-3.03	-3.35	-2.11
α	µmol CO_2(µmol Irradiance)$^{-1}$	0.018	0.016	0.012
r^2		0.67	0.92	0.86

Table 2.10. Carbon isotope discrimination (Δ), isotopic composition of CO_2 ($\delta^{13}C$) and percent nitrogen in leaves of plants grown at each nutrient load and at control or 13 dS m^{-1}. Data are means ± se (n = 4-5).

Nutrient Load	Salinity dS m^{-1}	Δ ‰	$\delta^{13}C$ ‰	Nitrogen %
Low	Control	25.39 ± 0.19	-32.56 ± 0.36	1.47 ± .035
	13	22.88 ± 0.22	-30.19 ± 0.47	1.7 ± .06
Moderate	Control	25.35 ± 0.28	-32.53 ± 0.60	1.78 ± .026
	13	22.28 ± 0.28	-29.63 ± 0.61	2.44 ± .08
High	Control	22.91 ± 0.12	-30.22 ± 0.23	2.68 ± .042
	13	21.76 ± 1.0	-29.13 ± 1.92	3.01 ± .06

Chapter 3. The influence of salinity-nutrient regimes on the performance of two aquatic macrophytes, *T. domingensis* and *B. arthrophylla*, with contrasting relative growth rates.

3.1 Introduction

In environments where resources are not limiting but competition is high, Grime (1974, 1977) claims that plant strategies have been selected for which maximise resource capture and growth. These *competitive* strategies include a rapid growth rate, high phenotypic plasticity and high biomass/leaf turnover. In contrast, where resources are chronically scarce *stress tolerant* strategies have evolved which permit species to endure resource limitation. Traits characteristic of a *stress tolerant* strategy include low growth rates, low phenotypic plasticity, extensive and long lived root systems, extended leaf longevity, and the conservation of carbon, mineral nutrients and water.

The absence of species with high RGRs in infertile habitats has evoked the hypothesis of a trade-off between high RGR and stress tolerance (Grime 1977). Support for this hypothesis has been found in the response of species with high and low RGRs to nutrient availability. Productivity in species with high RGRs has been found to be more sensitive to nutrient supply than species with low RGRs (Chapin 1980; Shipley and Keddy 1988). Generalisation of this hypothesis to other types of resource limitation, or the interaction of stress factors has however received limited attention (Crick and Grime 1987; Lambers and Poorter 1992).

If the trade-off hypothesis can be generalised to other types of stress such as salinity, disparate responses to various salinity-nutrient regimes may be exhibited in species with contrasting RGRs. At low salinities productivity may be considerably enhanced by high nutrient loads in species with high RGRs as demonstrated in *B. medianus* (Chapter 2). However, as species with high RGRs are also more sensitive to stress, productivity may decline to a greater extent as salinities increase compared to species with low RGRs. As such, the potential for higher nutrient loads to enhance performance of species with high

RGRs will decline as salinities increase as demonstrated in *B. medianus* (Chapter 2). In contrast, species with inherently low RGRs may be less affected by nutrient load or salinity level.

It has been proposed that in unfavourable habitats, where species with low RGR tend to dominate, the alleviation of a limiting resource/or stress factor with sufficient frequency will give species with high RGRs a competitive edge and enhance their success in such environments (Goldberg and Novoplansky 1997). Similarly in regions where the soil is both saline and infertile, and dominated by species with low RGRs, nutrient enrichment may enhance the competitive ability of species with high RGRs and lead to invasion.

Whilst the success of species with low RGRs in unfavourable habitats is evident by their dominance in such areas, it is argued that a low RGR *per se* does not explain success in unfavourable habitats. Rather it is the mechanisms which underlie low RGRs that yield enhanced tolerance (Poorter and Remkes 1990; Lambers and Poorter 1992). Growth analysis has been used by Poorter and Remkes (1990) to elucidate mechanisms associated with variation in RGR among 24 wild plant species. Under optimal growth conditions inherent low RGRs were found to be highly correlated with lower LARs. Lower LARs were mediated by both a lower LWR and SLA. The SLA was however of greater significance in determining RGR than LWR. A literature review by Poorter (1989) also supports the importance of LAR in determining RGR; a 10% increase in RGR was correlated with a 7.5% increase in LAR but only a 2.4% increase in NAR. It may therefore be proposed, that a lower LAR has adaptive value in unproductive habitats and has thus been selected for, whilst in fertile habitats a higher LAR is adaptive. In fertile environments competition for light is of greater importance than competition for nutrients; hence success will be determined by the capacity to capture light (Grime 1977; Chapin 1980). This is clearly facilitated by a large investment of biomass in leaves and a low cost of leaf production. In contrast, in infertile habitats light is less limiting but the capture and conservation of nutrients is important (Grime 1977; Chapin 1980). To enhance nutrient capture resources are preferentially allocated to roots rather than leaves, lowering LAR, whilst the conservation of captured resources is

achieved by increased longevity of both roots and leaves. Increased longevity of leaves necessitates protection against biotic and abiotic stress and hence a greater cost of production (Poorter and Remkes 1990; Lambers and Poorter 1992; Chapin 1980). This will tend to lower the SLA reducing LAR and hence RGR.

Whilst species with high RGRs demonstrate a high degree of morphological plasticity and can lower LAR in response to soil infertility, their absence from such habitats suggest that a lower LAR *per se* does not explain the differential success of species with high and low RGRs in unproductive habitats. Reductions in LAR in response to low soil fertility in species with high RGRs arise from reductions in the LWR, whilst the SLA is unresponsive to nutrient supply (Lambers and Poorter 1992). It has therefore been speculated that it is the SLA which is most reflective of tolerance to infertile habitats due to its relationship with increased leaf longevity (Chapin 1980; Lambers and Poorter 1992).

In arid environments nutrient supply is linked with water availability (Noy-Meir 1973), hence traits which permit tolerance may also be associated with the conservation of water as well as nutrients. As the effects of salinity on plant performance are due in part to a high soil osmotic potential (more negative) which imposes a physiological drought, water use characteristics may also be significant in the response to salinity.

The LAI in conjunction with stomatal behaviour reflects the potential for water loss from plant canopies. Stem or shoot height may also modify canopy transpiration by altering aerodynamic resistance. Whilst these characters reflect the potential for water loss from plant canopies, carbon isotopes provide some index of how efficiently water is used in the acquisition of carbon. Species which use water efficiently and have a lower demand for water may be more successful in both saline and arid habitats. The observation that water availability in arid and semi arid vegetation is correlated with LAIs suggest that this may be a significant trait determining water loss from vegetation (Hatton and Evans 1997).

Whilst water use characteristics of vegetation have been extensively examined, the extent to which species with contrasting RGRs differ in water use characteristics has received considerably less attention. Poorter and Farquhar (1994) examined transpiration and water use efficiency in 24 wild species with variable RGRs and found no correlation between RGR and transpiration per unit leaf area, or water use efficiency; measured via instantaneous measurements of C_i/C_a, or via carbon isotope discrimination of leaves. However, experiments of Poorter and Farquhar (1994) were carried out under optimal growth conditions in which no water stress was incurred. As such, it is uncertain if species with contrasting RGRs differ in the plasticity of these traits in response to water stress. Although Poorter and Farquhar (1994) did not find a correlation between transpiration per unit leaf area they did observe a strong positive correlation between RGR and transpiration per unit root weight, indicating quite different water demands of fast and slow growing species. This clearly has implication in water limited and saline environments, however the relative capacities of fast and slow-growing species to reduce the demand for water in response to water stress remains speculative.

This experiment evaluates the response of two aquatic macrophytes, *Typha domingensis* and *Baumea arthrophylla*, to different salinity (control, 50 and 100 mM NaCl) and nutrient regimes (low and high nutrient loads) utilising a complete factorial design. *Typha domingensis* has many features of a competitive strategy, having a putative high RGR, high carbon turnover and high phenotypic plasticity. Both high rates of primary production and carbon turnover have been demonstrated in *Typha orientalis* (Roberts and Ganf 1986). These competitive characteristics are highlighted by the invasive nature of *Typha* spp (Zedler *et al.* 1990) and their colonisation of channels where nutrient inputs tend to be high. In contrast, *B. arthrophylla* has characteristics of a stress tolerant strategy with slow growth, long lived stems and evergreen habit (Rea 1992; Cooling 1996). Furthermore, Froend and McComb (1994) found productivity of *Typha orientalis* to be significantly enhanced at nutrient enriched sites whilst *Baumea articulata* was less responsive to nutrient enrichment. As such, differential responses of *T. domingensis* and *B. arthrophylla* to nutrient availability may also be anticipated.

The response of each species to different salinity-nutrient regimes was assessed via a range of performance indices, both morphological and physiological in nature. Growth analysis was used to evaluate the mechanisms underlying changes in RGR in response to these regimes, and to identify differences between species which may explain differential responses where they were observed. To evaluate the role of water conservation, in explaining differences in RGR and tolerance to salinity; LAIs, stomatal conductance and WUE were measured. Leaf demography was also measured due to the significance of rates of leaf loss on nutrient conservation and salinity tolerance.

Objectives and hypotheses

The primary objective of this work was to determine if *T. domingensis* and *B. arthrophylla* would demonstrate differential responses to salinity-nutrient regimes as predicted by their putative RGRs and growth strategies. It was hypothesised that *T. domingensis* would have a high RGR and demonstrate a marked response to nutrient load, whilst *B. arthrophylla* would have a low RGR and be unresponsive to nutrient load. Furthermore, it was predicted that *B. arthrophylla*, with a low RGR would be more resilient to salinity than *T. domingensis.*

The response to both salinity and nutrient load was also characterised. Responses to salinity were evaluated against the bi-phasic model of Munns and Termaat (1986). Based on this model it was predicted that the response to salinity would be characterised by a reduction in the LWR and an increase in the RWR, resulting from hormonal signals (osmotic effects) and an increased rate of leaf loss (ion toxicity effects). These responses would be manifest in a reduction in LAR and a lower leaf to root ratio. Rates of photosynthesis would also decline in response to salinity, lowering NAR, however the dominant response would be a reduction in LAR. In response to nutrient load it was predicted that growth would be enhanced by the higher nutrient load in *T. domingensis*. However, this effect would diminish as salinities increased. In contrast, *B. arthrophylla* would be either unaffected by nutrient load, or would experience symptoms of nutrient toxicity as growth became more constrained at higher salinities.

The underlying mechanisms associated with a low RGR which may impart greater tolerance to low nutrient levels or salinity were investigated. It was hypothesised that a greater tolerance to low nutrient loads would be associated with a lower SLA and LWR, yielding a low RGR. In addition, a low SLA would be coupled with increased leaf longevity. The water use characteristics of each species were examined to identify it these parameters differed between *T. domingensis* and *B. arthrophylla*, the extent to which they were altered by salinity in each species, and if they conferred greater tolerance to salinity. It was hypothesised that *B. arthrophylla*, having a low RGR would be more conservative in its water use compared to *T. domingensis*. This would be reflected in lower LAIs, stomatal conductance, height and WUE. Moreover, salinity would reduce water use, and increase water use efficiency in both species, but *B. arthrophylla* would be more conservative in its water use and hence more tolerant to salinity.

3.2 Materials and methods

3.2.1 Species description

Both *Typha domingensis* (Pers.) Steudel (Typhaceae) and *Baumea arthrophylla* (Nees) Boeckeler (Cyperaceae) are emergent rhizomatous perennials native to Australia. Both species are distributed widely throughout Australia. *B. arthrophylla* has slender cylindrical photosynthetic stems 1-2 m in height. *T. domingensis* has long leaves with stems usually 2 m in height (Jessop and Toelken 1986).

3.2.2 Experimental design

A full factorial design was used to examine the response of each species to three levels of salinity, control (15 mM), 50 and 100 mM NaCl, and two nutrient loads based on nitrogen; 30 g N m^{-2} yr^{-1} (low nutrient load) and 150 g N m^{-2} yr^{-1} (high nutrient load). Eight plants of each species were randomly allocated to each salinity-nutrient treatment. Plants were established (1st December 1995) under each nutrient load for c. 3 weeks until growth was evident before salinity treatments were imposed on the 25th December 1995. *T. domingensis*

plants were harvested between the 4th and 6th of April 1996. Due to the slow growth of *B. arthrophylla* the experimental phase was extended for a further month to increase the likelihood of a nutrient response. *B. arthrophylla* plants were harvested between the 2nd and 4th of May 1996. The duration of the experimental period lasted c. 18 weeks and c. 22 weeks for *T. domingensis* and *B. arthrophylla*, respectively with c. 15 and c. 19 weeks exposure to the salinity treatments, respectively.

3.2.3 Collection

Ramets; consisting of a single shoot and associated rhizome, were harvested from established stands of each species. *B. arthrophylla* was collected from Bool Lagoon, South Australia (37° 08´ S, 140° 41´ E) and *T. domingensis* from the Little Para River, Carrisbrook Reserve, Adelaide, South Australia (34° 45´ S, 138° 40´ E). Ramets of *T. domingensis* were established in sand saturated with water, and ramets of *B. arthrophylla* in water prior to the experiment. Establishment of *T. domingensis* ramets in water had proven unsuccessful with rhizomes becoming necrotic, possibly due to anoxia. Ramets which produced new buds and roots indicating viability were selected for the experiment. Fresh weights of ramets were obtained on the 30th of November 1995 prior to planting.

3.2.4 Experimental treatments

Nutrient loads

Nutrients were supplied with both Osmocote Plus® to provide a base load of N, P and K plus trace nutrients, and Osmocote® containing only N, P and K. The composition of both Osmocote Plus® and Osmocote® are detailed in Appendix A. Loadings were calculated in terms of nitrogen. A loading of 30 g N m^{-2} yr^{-1} was supplied with Osmocote Plus® to both the high and low nutrient treatments. An additional loading of 120 g N m^{-2} yr^{-1} was supplied with Osmocote® to the high nutrient treatment only to achieve a total nitrogen loading of 150 g N m^{-2} yr^{-1}.

The amount of Osmocote® required to achieve the desired loadings were based on the release rate of the product at 21 °C provided by Osmocote® (section 2.2.4). Using potting bags with

a top surface area of 0.055 m^2, 8.3 g of Osmocote Plus® was required per pot to achieve a loading of 30 g N m^{-2} yr^{-1}. For the high nutrient load an additional 29.2 g of Osmocote® was required per pot to increase the load by 120 g N m^{-2} yr^{-1} to a total of 150 g N m^{-2} yr^{-1}. Plants were potted in plastic potting bags containing c. 9 L of low nutrient sandy loam mixed with the required amount of Osmocote® and topped with c. 3 L of cracking clay.

Salinity treatments

PVC chambers semi-emersed in two outdoor ponds were used to isolate salinity treatments. Plants of each species were placed in separate chambers, and replicates of each treatment divided between two chambers to avoid pseudoreplication. Numerous holes were pierced at the base of pots to permit the free exchange of ions. Water levels were maintained at 5 cm above the sediment surface. NaCl and $CaSO_4$ were added as per section 2.2.4. Salinity levels were monitored twice weekly by measuring Na concentrations of the chamber water by flame photometry (Corning 400). This was considered to provide a more direct measurement of NaCl salinity than provided by conductivity measurements. Ca concentrations were monitored weekly using the method of Golterman (1969) and evaporative water losses replaced daily as required. Na concentrations were maintained at 10-15 mM (control), 50 mM and 100 mM which produced conductivities of c. 1.5-2, 6.7 and 12 dS m^{-1}, respectively. Na/Ca ratios ranged from 11 to 14 at 50 and 100 mM NaCl and from 7 to 15 in controls. Lower Na/Ca ratios were incurred in the controls at the beginning of the experiment as Ca concentrations were initially higher, presumable due a lower rate of plant uptake. As Ca concentrations declined $CaSO_4$ was added to maintain the Na/Ca ratio below 15. In both the 50 mM and 100 mM NaCl treatments the addition of NaCl and $CaSO_4$ was required to maintain concentration at the desired level.

3.2.5 Morphological measurements

The total number of leaves and shoots for *T. domingensis*, and stems for *B. arthrophylla* were measured regularly throughout the experimental period. The height of *T. domingensis* shoots were measured from the sediment surface to the tip of the longest leaf. For *B. arthrophylla* the height of the tallest stem per pot was measured. Harvested *T. domingensis* plants were

separated into leaves, stems, rhizomes and roots. Leaves were removed at the point at which they separated from the stem. *B. arthrophylla* plants were separated into stems, stem bases, rhizomes and roots. Stem bases in *B. arthrophylla* were defined as the section of a stem enclosed within the sheath of an older stem as well as the enclosing section itself. Plant material was dried at c. 70°C until a constant weight.

3.2.6 Growth analysis

The relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) were determined using the formulae presented in section 2.2.6. The initial dry weight of plants were determined from relationships between fresh and dry weight for *T. domingensis* (equation 3.1) and *B. arthrophylla* (equation 3.2).

$$\text{dry weight (g)} = .08278\ (\text{fresh weight (g)}) - 0.0713 \quad (r^2 = 0.95,\ n = 19,\ P < .0001) \qquad (3.1)$$

$$\text{dry weight (g)} = .2563\ (\text{fresh weight (g)}) - 0.1752 \quad (r^2 = 0.91,\ n = 19,\ P < .0001) \qquad (3.2)$$

The leaf area (one- sided) of *T. domingensis* plants was derived from the relationship between leaf dry weight and leaf area (Fig. 3.1b). This relationship was established by measuring the area (Delta T leaf area meter) of 3 to 4 fresh leaves representing a range of size and age classes from each plant. The dry weight of leaves were subsequently obtained and regressed against leaf area. As the relationship did not visibly differ between treatments the regression describing the whole data set was used in determining leaf area. Leaf dry weight of initial plants was estimated from the relationship between total dry weight and leaf dry weight determined for similar sized ramets (equation 3.3)

$$\text{leaf dry weight (g)} = 0.282\ \text{dry weight (g)} - .0177 \quad (r^2 = 0.81,\ n = 19,\ P < .0001) \qquad (3.3)$$

The area of *B. arthrophylla* stems was derived from the relationship between stem area and stem dry weight (Fig. 3.1a). Stem area was calculated from equation 3.4 which describes the surface area of an elliptical cone. The surface area obtained from equation 3.4 was divided by

two to derive a one-sided stem area. The length and basal radii of three to four stems per pot were measured, and the area of each stem calculated from equation 3.4 and regressed against stem dry weight (Fig. 3.1a.). The initial area of stems was determined from the relationship between stems height and stem area (equation 3.5). The relationship between total dry weight and stem dry weight (as used for *T. domingensis)* was not used as the correlation was weak.

$$\text{surface area } (cm^2) = \frac{\pi(r_1 + r_2)}{2} \times H \qquad (3.4)$$

Where H is stem height (cm) and r_1 and r_2 are maximum and minimum radii at the base of the stem (cm).

$$\text{stem area } cm^2 \text{ (one-sided)} = 0.00531\ H^2 + 1.64\ (r^2 = 0.94,\ n = 143,\ P<.001) \qquad (3.5)$$

3.2.7 Leaf gas exchange measurements

An open system infrared gas analyser (Ciras-1, PPSystems, UK) was used to measure gas exchange parameters in both *T. domingensis* and *B. arthrophylla*. Measurements in *T. domingensis* were obtained under maximal ambient light intensities on young fully expanded leaves. However, variable weather conditions and cloud cover made measurement under ambient conditions difficult to obtain. Consequently, measurements on *B. arthrophylla* were carried out within laboratory conditions with a mercury vapour light at similar irradiances under which measurement for *T. domingensis* were obtained. Individual measurements on *B. arthrophylla* stems were obtained on 2 young but mature stems. Blu tac® was used to ensure seals were achieved around protruding stems. Seals were checked by breathing around the chamber and observing for an increase in CO_2 supply.

3.2.8 Carbon isotope discrimination and percent nitrogen

Carbon isotope discrimination and percent nitrogen were determined for whole young stems of *B. arthrophylla*. For *T. domingensis* material was obtained from the top third of young fully expanded leaves which correlated to regions where rates of photosynthesis were measured. Carbon isotope discrimination measured in leaves of *T. domingensis* under

different salinities in the field did not differ along the length of leaves (Appendix A). The percent nitrogen in leaves did however vary along the length of leaves, being highest in the top sections (Appendix A). However, the percent nitrogen in the top third of leaves are most closely related to measurements of photosynthesis. Material was prepared and analysed as per section 2.2.8.

3.3 Results

3.3.1 B. arthrophylla

3.3.1.1 Morphology

Maximum stem height was not affected by nutrient load regardless of salinity (Fig. 3.2). At the end of the experimental period maximum stem height was c. 75 cm in control plants at both nutrient loads. Stem height was largely unaffected by 50 mM NaCl but was reduced by 100 mM NaCl. Stem height at 100 mM NaCl failed to increase 79 days after salinisation commenced, attaining a maximum height of c. 60 cm at both nutrient loads. The effect of 100 mM NaCl on stem height was apparent 39 and 79 days after salinisation, at the low and high nutrient loads, respectively.

Nutrient load did not influence final stem numbers per pot regardless of salinity (Fig. 3.3). However, the number of stems per pot were lower at 50 mM NaCl relative to that of control plants at the high nutrient load only, reflecting a greater sensitivity. At 100 mM NaCl the number of stems per pot were reduced relative to control plants by 30% and 42% at low and high nutrient loads, respectively. Reductions in the number of stems per pot were evident after 39 days of salinisation at the high nutrient load, and at 66 days at the low nutrient load.

Lower numbers of stems per pot with increasing salinity resulted from a lower rate of stem production, rather than an increased rate of senescence (Fig. 3.4). Stem production in *B. arthrophylla* increased over time in an erratic fashion, tending to increase rapidly and then either stabilise at a higher rate or decline slightly. Stem production was reduced at 50 and 100 mM NaCl at the higher nutrient loads, whilst at the low nutrient load stem production was only clearly reduced at 100 mM NaCl, thus reflecting patterns in stem number per pot

across treatments. Over c. 20 weeks the average number of stems lost per pot across all experimental treatments was one or less. As such, nutrient retention would be expected to be high and hence the dependence on nutrient supply low.

3.3.1.2 Biomass and biomass allocation

Biomass was reduced by 50 mM NaCl relative to control plants by c. 6% and 25% at low and high nutrient loads, respectively (Table 3.1, Fig. 3.5a). At 100 mM NaCl biomass was reduced by 43% and 46% at low and high nutrient loads, respectively. A two-way ANOVA found total biomass in *B. arthrophylla* to be significantly reduced by salinity but unaffected by nutrient load (Table 3.2). Despite differential sensitivities to 50 mM NaCl at each nutrient load the interaction between nutrient load and salinity was not significant.

At 100 mM NaCl the percent of total biomass allocated to above-ground tissue was reduced by c. 10%, whilst allocation to the rhizomes was increased by c. 10 %, at both nutrient loads (Table 3.1). A linear regression between percent rhizomes and percent stems produced a correlation coefficient of 0.81, reflecting the strength of the relationship (Fig. 3.6). The shift in biomass allocation from stems to rhizomes at 100 mM NaCl resulted in a reduction in the above to below-ground ratio of 30-40% (Table 3.3).

Biomass allocation to roots (analogous to RWR) was reduced slightly by the high nutrient load, in control and 50 mM NaCl but not at 100 mM NaCl (Table 3.1). Salinity reduced the RWR at the low nutrient load but not at the high nutrient load. At the low nutrient load the RWR declined at 100 mM NaCl to values recorded for high nutrient plants. Hence the effect of nutrients on the RWR was absent at 100 mM NaCl. The reduction in the RWR at the high nutrient load, at salinities less than 100 mM NaCl, resulted in higher above-ground to root, and stem to root ratios compared to low nutrient plants (Table 3.3). The decline in the RWR at 100 mM NaCl at the low nutrient load, caused the above-ground to root and stem to root ratios to increase relative to control values.

3.3.1.3 Growth analysis

Mean maximal RGRs of 20 mg g d^{-1} and 18.6 mg g d^{-1} were recorded in control plants of *B. arthrophylla* at the low and high nutrient load, respectively (Fig. 3.7). RGR was unaffected at 50 mM NaCl at the low nutrient load but declined slightly at the high nutrient load. At 100 mM NaCl RGR declined to c. 14 mg g d^{-1} at both nutrient loads, representing a decline from the control of 6 (30%) and 4.5 mg g d^{-1} (24%) at low and high nutrient loads, respectively. The decline in RGR at 50 mM NaCl was correlated with a decline in NAR at the high nutrient load (Fig 3.7c). At the low nutrient load NAR also declined slightly but was compensated by an increase in LAR (Fig 3.7b), consequently RGR did not alter. The reduction in RGR at 100 mM NaCl, when compared to the control, was associated with a decline in LAR and NAR at both nutrient loads. LAR was reduced by similar amounts at each nutrient load (0.23 m^2 kg^{-1}, 15%) whilst NAR was reduced more at the high nutrient load (2.3 g m^{-2} d^{-1}, 17%) compared to the low nutrient load (1.1 g m^{-2} d^{-1}, 8.9%).

The reduction in LAR at 100 mM NaCl can be attributed to changes in biomass allocation away from stems to rhizomes thereby reducing the LWR (analogous to biomass allocation to stems). Changes in the SLA were not apparent from the regression of stem area and stem dry weight (Fig. 3.1a). The decline in NAR at 100 mM NaCl may be attributed to a reduction in photosynthesis or an increase in respiration. Furthermore, the decline in NAR may not be independent of the decline in LAR. As LAR declines respiration increases relative to photosynthesis which itself may elicit a reduction in NAR. RGRs were lower at the high nutrient load compared to the low nutrient load, in both the control and 50 mM NaCl treatments, and were associated with lower NAR and not LAR (Fig. 3.7).

The influence of salinity, nutrient load, and the interaction of these factors, on the growth parameters; RGR, NAR and LAR, were evaluated using a two-way ANOVA (Table 3.2). RGR was found to be significantly reduced by salinity but unaffected by nutrient load. As both LAR and NAR were significantly reduced by salinity the decline in RGR in response to salinity can be attributed to reductions in both LAR and NAR. Although NAR was significantly reduced at the high nutrient load it did not result in a significant reduction in

RGR. There was no significant interaction between nutrient load and salinity for any of the growth parameters examined.

3.3.1.4 Leaf gas exchange characteristics

Nutrient load did not influence gas exchange parameters (Tables 3.4, 3.5) or carbon isotope discrimination values (Tables 3.6, 3.7). This was despite a significant increase in nitrogen content of stems at the high nutrient load (Tables 3.7, 3.8). Rates of photosynthesis were however significantly reduced by 100 mM NaCl (Tables 3.4, 3.5). Lower rates of photosynthesis were associated with lower g_s and C_i/C_a values (Table 3.4). Whilst this may suggest that the biochemical demand for CO_2 is greater than supply, it is not possible to conclude that stomatal limitation is the primary cause for lower rates of photosynthesis, since photosynthesis may also saturate at lower values of C_i. Consequently, stomatal limitation of photosynthesis may in fact be less (Farquhar and Sharkey 1982). As carbon isotope discrimination values were not significantly reduced by any of the imposed treatments a lower biochemical capacity may be the primary mechanism for lower rates of photosynthesis in response to salinity (Tables 3.6, 3.7).

The reduction in NAR in response to salinity can be attributed at least in part to a reduction in photosynthetic capacity. Whilst NAR was significantly reduced at the high nutrient load this was not reflected in rates of photosynthesis. As the percent nitrogen in stems was greater (Table 3.8) the cost associated with nitrogen uptake and translocation may have increased rates of respiration and lowered NAR.

3.3.1.5 Water use characteristics

Nutrient load did not substantially influence LAIs (Fig. 3.8a), g_s (Table 3.5) or vegetation height (Fig. 3.2). As such, nutrient load did not alter the potential for water loss from *B. arthrophylla* canopies. In contrast, 100 mM NaCl reduced both the LAI (c. 50 %) and g_s (> 60%), considerably reducing the potential for water loss from the canopy. At 50 mM NaCl the effect of salinity on the LAI was marginal. As maximal stem height was also reduced, aerodynamic resistance may be increased and reduce canopy transpiration further. Carbon

isotope discrimination in *B. arthrophylla* was around 21‰ and was not significantly influenced by nutrient load or 100 mM NaCl indicating that water use efficiency was not altered (Tables 3.6, 3.8). Although a two-way analysis of variance found C_i/C_a to be significantly reduced by salinity (Table 3.5) it was marginal (P= .037) and may not be biologically significant as suggested by carbon isotope values.

3.3.2 T. domingensis

3.3.2.1 Morphology

Maximum shoot height was influenced by both nutrient load and salinity (Fig. 3.9). Maximum shoot height was increased at the high nutrient load by 44%, 17% and 15% at control, 50 and 100 mM NaCl, respectively. At the low nutrient load, maximal shoot height was not affected at 50 mM NaCl, but was reduced by 9% at 100 mM NaCl. Maximum shoot height was more sensitive to salinity at the high nutrient load; being reduced by 10% at 50 mM NaCl and by 26% at 100 mM NaCl. Reductions in maximum shoot height were evident within 25 days of salinisation at 100 mM NaCl, and within 39 days at 50 mM NaCl.

At the low nutrient load, the number of shoots per pot in control plants was only slightly less than that produced at the high nutrient load (Fig. 3.10). However, the number of shoots per pot was reduced by salinity at the low nutrient load but not at the high nutrient load. At the low nutrient load the number of shoots per pot was reduced by c. 1 and 1.7 at 50 and 100 mM NaCl, respectively. Reductions in the number of shoots per pot at the low nutrient load were evident 25 days following salinisation, and the number of shoots failed to increase after 52 days of salinisation.

The number of leaves per pot was increased at the high nutrient load compared to the low nutrient load by 63%, 90% and 47% at control, 50 and 100 mM NaCl, respectively (Fig. 3.11). At 50 mM NaCl the number of leaves per pot was reduced slightly at the low nutrient load but was not reduced at the high nutrient load. The numbers of leaves per pot was reduced at 100 mM NaCl compared to control plants by 21% and 11 % at low and high nutrient loads, respectively. Maximum numbers of leaves per pot was reached after c. 64

days growth at the low nutrient load (Fig 3.11). At the high nutrient load the number of leaves increased up to 91 days in both control and 50 mM NaCl, whilst at 100 mM NaCl leaf numbers increased throughout the experimental period. Consequently, differences in leaf number between 100 mM NaCl and both control and 50 mM NaCl diminished after 91 days at the high nutrient load.

Differences in the number of leaves per pot across treatments can be attributed to different rates of leaf production, rather than to different rates of leaf loss (Fig. 3.12). Rates of leaf production peaked after 50 days of growth in all treatments excluding 100 mM NaCl at the high nutrient load, in which production peaked two weeks earlier. Following this peak rates of leaf production declined slowly over time. Differences in rates of leaf production between treatments were evident 25 days following salinisation and diminished over time. Rates of production were generally greater at the high nutrient load regardless of salinity. At the low nutrient load leaf production was not reduced at 50 mM NaCl but was reduced at 100 mM NaCl for a short period. At the high nutrient load leaf production was reduced transiently compared to the control at 50 mM NaCl, but for c. 7 weeks at 100 mM NaCl. Rates of leaf loss varied over time from c. 1 to 3 leaves per week but varied little between treatments.

3.3.2.2 Biomass and biomass allocation

Biomass was increased at the high nutrient load compared to the low nutrient load by 129%, 96% and 63% at control, 50 and 100 mM NaCl, respectively (Table 3.9, Fig. 3.5b). At the low nutrient load biomass was reduced by 2% and 34% at 50 and 100 mM NaCl, respectively. Reductions in biomass were greater at the high nutrient load, reflecting a greater sensitivity to salinity with reductions of 16% and 53% at 50 and 100 mM NaCl, respectively. A two-way ANOVA found total plant biomass to be significantly influenced by both nutrient load and salinity (Table 3.2). The greater sensitivity to salinity at the high nutrient load compared to the low nutrient load produced a significant interaction between nutrients and salinity (Table 3.2).

In response to the higher nutrient load biomass allocation was shifted from below-ground tissues (10-17%), predominantly roots, to leaves and stems (Table 3.9). The change in biomass allocation in response to nutrients yielded higher above-ground to below-ground, above-ground to root and leaf to root ratios (Table 3.3). The greatest increase was however in the above-ground to root ratio and not the leaf to root ratio, reflecting the reallocation of biomass from roots to both leaves and stems. Salinity did not strongly influence biomass allocation patterns. However, there was a tendency for biomass allocation to the roots to be reduced slightly.

3.3.2.3 Growth analysis

A two-way ANOVA found RGR to be significantly reduced by salinity and significantly increased by the higher nutrient load (Table 3.2). However, the interaction of these factors was not significant. Mean maximal RGRs of 40.7 mg g d^{-1} and 35.3 mg g d^{-1} were recorded for *T. domingensis* in control plants at the high and low nutrient loads, respectively (Fig. 3.13). RGR declined with increasing salinity, however the decline was greater at the high nutrient load than at the low nutrient load indicating a greater sensitivity to salinity at the high nutrient load. Consequently, whilst RGR was increased by the high nutrient load differences in RGRs were minimal at 100 mM NaCl. The decline in RGR in response to salinity was associated with a significant reduction in NAR whilst LAR was unaffected by salinity (Fig. 3.13). The greater sensitivity to salinity at the higher nutrient load arose from a steeper reduction in NAR as salinity increased. NAR was reduced at 100 mM NaCl relative to the control by 4.9 mg g^{-1} d^{-1} (c. 15%) and 6.8 g m^{-2} d^{-1} (20%) at the low and high nutrient loads, respectively and yielded reductions in RGRs of 4.2 mg g^{-1} d^{-1} (12%) and 7.9 mg g^{-1} d^{-1} (19.5%), respectively.

The increase in RGR at the higher nutrient load was associated with a significant increase in LAR and not NAR (Fig. 3.13). An increase in LAR of 2 m^2 kg^{-1} (c. 20%) in response to the high nutrient load at salinities less than 100 mM NaCl increased RGR by c. 5 mg g^{-1} d^{-1} (c. 15%). However, at 100 mM NaCl an increase in LAR of 1.9 m^2 kg^{-1} (17%) only increased the RGR by 1.6 mg g d^{-1} (c. 5%) due to a large reduction in NAR. The increase in LAR

induced at the higher nutrient load can be attributed to an increase in the LWR, arising from the shift in biomass allocation from the roots to the leaves. The regression between leaf area and leaf weight was not influenced by nutrient load, and hence the SLA did not contribute to the increases in LAR. Whilst NAR was not significantly affected by nutrient load it was slightly but consistently reduced at the higher nutrient load.

3.3.2.4 Leaf gas exchange characteristics

Photosynthesis in *T. domingensis* was reduced at 100 mM NaCl at the high nutrient load (21 vs. 13.9), but not at the low nutrient load (19.2 vs. 15.7) (Table 3.10). However, rates of photosynthesis at the high nutrient load at 100 mM NaCl were more variable, and comparisons between nutrient loads at control and 100 mM NaCl did not demonstrate any differences in photosynthetic rates or other gas exchanges parameters.

The reduction in photosynthesis at the high nutrient load at 100 mM NaCl was associated with a reduction in g_S but not in C_i/C_a, suggesting biochemical limitation of photosynthesis rather than stomatal limitation (Table 3.10). Statistically, carbon isotope discrimination was significantly reduced by salinity (Tables 3.6, 3.8), however, the level of significance was marginal, and reductions may be of little biological significance. Leaf nitrogen contents were significantly increased by the high nutrient load and by 100 mM NaCl but did not yield higher rates of photosynthesis or increase NAR (Tables 3.7, 3.8). High foliar nitrogen contents can increase respiration and may offset higher rates of photosynthesis. Alternatively, increased nitrogen content in leaves may not be associated with higher concentrations of chlorophyll or rubisco.

Although there is some evidence that photosynthesis was reduced by salinity at the high nutrient load there was no effect of salinity at the low nutrient load. As such, the reduction in NAR with increasing salinity at the low nutrient load can not be explained by lower rates of photosynthesis. At the high nutrient load at least some of the reduction in NAR may result from lower rates of photosynthesis. However, the effect of salinity on rates of photosynthesis

may have been obscured by restricting measurements to the youngest fully expanded leaf which may be less affected by salinity than older leaves.

3.3.2.5 Water use characteristics

Whilst the LAI was only marginally reduced at 50 mM NaCl it was reduced at 100 mM NaCl by 31% and 52% at the low and high nutrient loads, respectively (Fig. 3.8). The LAI was more sensitive to salinity at the high nutrient load, consequently the influence of nutrient load on the LAI declined as salinity increased. The high nutrient load increased LAIs compared to the low nutrient load by 192%, 155% and 107% at control, 50 and 100 mM NaCl, respectively (Fig. 3.8). Stomatal conductance was not significantly influenced by nutrient load but was reduced at 100 mM NaCl at the high nutrient load, but not at the low nutrient load (Table 3.10). Although shoot height was increased by the high nutrient load it was also more sensitive to salinity. Shoot height was reduced at 100 mM NaCl by 11 cm and 44 cm at the low and high nutrient loads, respectively indicating a potentially higher aerodynamic resistance to water loss in response to salinity. In contrast, shoot height was increased by the high nutrient load by 52 cm and 19 cm, at control and 100 mM NaCl, respectively indicating a potentially lower aerodynamic resistance to water loss. LAIs and shoot height data suggest that water loss from *T. domingensis* canopies may potentially be reduced by salinity but increased substantially by high nutrient loads even at 100 mM NaCl.

Carbon isotope discrimination in *T. domingensis* was significantly decreased from 24 ‰ at the low nutrient load in control plants, to c. 22.5‰ at the high nutrient load, in both control and 100 mM NaCl treated plants, indicating an increased water use efficiency in response to the high nutrient load (Table 3.6, 3.7). Salinity elicited a marginally significant decreased in carbon isotope discrimination. Changes in carbon isotope discrimination were not however reflected in instantaneous values of C_i/C_a.

3.4 Discussion

3.4.1 The response to nutrient load

As predicted the RGR of *T. domingensis* (40.76 mg g^{-1} d^{-1}) was considerably higher compared to *B. arthrophylla* (18.6 mg g^{-1} d^{-1}) under optimal conditions of high nutrient load and control salinities. Furthermore, the response of *T. domingensis* and *B. arthrophylla* to nutrient load was characteristic of species with high and low RGRs, respectively. In control plants the RGR of *T. domingensis* was significantly increased by the high nutrient load, whilst the RGR in *B. arthrophylla* was not affected by the nutrient loads examined.

In *T. domingensis* increased RGR in response to the high nutrient load was mediated by an increase in LAR whilst NAR was unaffected by nutrient load. The increase in LAR at the high nutrient load resulted from changes in biomass allocation, predominantly away from roots to leaves. There was no evidence of a change in the SLA in response to nutrient load. These findings are consistent with the responses to nutrient supply commonly observed in species with inherent high RGRs (Chapin 1980; Lambers and Poorter 1992).

3.4.2 Mechanisms underlying low RGRs.

The success of species with low RGRs in infertile habitats is not considered a function of low RGRs *per se*, but due to the underlying mechanisms which give rise to low RGRs. In contrast to the findings of Poorter and Remkes (1990) the lower RGR of *B. arthrophylla* under optimal conditions (high nutrient load and control salinities) was not associated with a lower LAR but with a lower NAR. LAR in *B. arthrophylla* (1.5 m^2 kg^{-1}) was slightly higher compared to *T. domingensis* (1.26 m^2 kg^{-1}). However, NAR in *B. arthrophylla* was only 12.3 g m^{-2} d^{-1}, whilst in *T. domingensis* it was 32.4 g m^{-2} d^{-1}. Similarly Garnier (1992) found differences in RGR in congeneric annual and perennial grass species to arise from differences in NAR and SLA and not to differences in LWR.

A low SLA is of adaptive significance in infertile habitats because it is usually associated with enhanced protection from biotic and abiotic factors which promote leaf longevity and

hence the retention of nutrients (Chapin 1980; Lambers and Poorter 1992). Although leaf longevity in *B. arthrophylla* was clearly greater than in *T. domingensis,* this was not reflected in the SLA. The SLA represented by the slopes of leaf area to leaf weight relationships were 4.1 and 3.6 m^2 kg^{-1} for *T. domingensis* and *B. arthrophylla*, respectively. Although these differences indicate that more biomass (c. 13%) must be allocated to leaves to achieve the same LAR differences are small. Jones (1988) measured a SLA of 13.9 in *Cyperus papyrus* and 3.8 in *T. domingensis*, indicating that differences in SLA can potentially be large.

Although NAR differed considerably between *T. domingensis* and *B. arthrophylla* differences in rates of photosynthesis per until leaf area were not apparent. A review by Lambers and Poorter (1992) also indicate that photosynthesis per unit leaf area does not generally differ between species with contrasting RGRs, provided species with similar life forms are compared. As rates of photosynthesis did not differ between *T. domingensis* and *B. arthrophylla* differences in NAR must be produced by different respiration rates.

Species with low RGRs generally demonstrate a greater investment in roots and hence nutrient capture compared to species with high RGRs (Lambers and Poorter 1992). However, this was not observed in *B. arthrophylla* and *T. domingensis*. The RWR in *B. arthrophylla* was in fact less than *T. domingensis*. As root weight is considered a poor indicator of function, inferring functional differences from root weight measurements are problematic. Physical differences in root structure between *T. domingensis* and *B. arthrophylla* roots highlight the difficulties in such comparisons. *T. domingensis* roots are thick with minimal investment in structural tissue, whilst *B. arthrophylla* roots are fine and fibrous in nature. Root weight is therefore unlikely to reflect absorptive capacity. As roots are generally long lived in species with low RGRs, differences in RWR may become apparent over a longer time frame.

Differences between species were also characterised by different rates and patterns of leaf production. Rates of leaf/stem production in *B. arthrophylla* were generally lower than *T. domingensis*. However, in *T. domingensis* rates of leaf production peaked and then steadily

declined. In *B. arthrophylla* leaf production fluctuated but generally increased throughout the experimental period. Rates of leaf loss were considerably greater in *T. domingensis* compared to *B. arthrophylla*. Furthermore, *T. domingensis* experiences seasonal die back with the senescence of above ground tissue whilst *B. arthrophylla* retains above ground biomass throughout the year. These factors suggest that nutrient loss from *T. domingensis* will be considerably greater than *B. arthrophylla*. As such, growth is more dependant on nutrient supply in *T. domingensis* than *B. arthrophylla*.

Although leaf longevity was substantially greater in *B. arthrophylla* than *T. domingensis*, differences in the SLA were not apparent and therefore failed to explain differences in RGR. The lower RGR of *B. arthrophylla* compared to *T. domingensis* was attributed to a lower NAR. As rates of photosynthesis per unit leaf did not differ between species, differences in NAR and hence RGR must be attributed to higher respiration rates. The ecological significance of a high respiration rate is speculative, but may be associated with the synthesis of chemical compounds which confer greater resistance to stress, and which promote leaf longevity.

Whilst *T. domingensis* was more sensitive to nutrient supply compared to *B. arthrophylla* the RGR of *T. domingensis* at low nutrient load was still substantially higher than *B. arthrophylla*. Although species with high inherant RGRs, demonstrate a greater sensitivity to low soil fertility, RGRs frequently remain higher than species with low inherant RGRs, even under infertile conditions (Poorter and Lambers 1992; Chapin 1980). Consequently, the absence of species with high inherant RGRs from infertile environments, suggests that higher RGRs, measured in relatively short experiments may not be predictive of success.

3.4.3 The response to salinity

In *B. arthrophylla* salinity imposed growth reductions were characterised by reductions in stem number and stem height resulting in lower LAIs. Salinity also induced changes in biomass allocation away from stems to rhizomes and reduced rates of photosynthesis and g_S. In *T. domingensis* growth reductions imposed by salinity were associated with reductions in

the number of leaves and height of shoots. However, biomass allocation patterns were largely unaffected by salinity and lower rates of photosynthesis were not consistently observed. In both species the effects of salinity were manifest in reductions in total biomass and RGRs.

In both species RGR declined in response to salinity, however the underlying mechanisms differed. For *T. domingensis* the decline in RGR in response to salinity was associated with lower NAR and not LAR, whilst in *B. arthrophylla* reductions were associated with both NAR and LAR. Reductions in NAR in response to salinity in *B. arthrophylla* can be attributed in part to lower rates of photosynthesis. However, in *T. domingensis* lower rates of photosynthesis were not evident in low nutrient plants at 100 mM NaCl, and were variable at the high nutrient load. Although differences in rates of photosynthesis may be apparent in older leaves it is also likely that increased respiration may be the primary cause for lower NAR. Shwarz and Gale (1981) found that increased respiration rates under saline conditions can contribute substantially to growth reductions.

In contrast to the model proposed by Munns and Termaat (1986) salinity did not increase the rate of leaf senescence, or increase the RWR, or decrease the leaf to root ratio in either *T. domingensis* or *B. arthrophylla*. Furthermore, the decline in RGR imposed by salinity was not associated with a reduction in LAR but in NAR. Although the reduction in RGR in *B. arthrophylla* was associated with both lower NAR and LAR the reduction in LAR did not arise from increased rates of stem loss, or from a shift in biomass allocation from stems to roots, but from a shift in biomass allocation from stems to rhizomes. As such, the response of either *T. domingensis* or *B. arthrophylla* to salinity does not conform to the model proposed by Munns and Termaat (1986).

In *B. arthrophylla* the shift in biomass allocation away from stems to rhizomes at 100 mM NaCl may be of adaptive significance in saline or water limited environments since it reduces water loss by decreasing the LAI. It also maintains sites for new growth when conditions are more favourable, and provides a mechanism whereby more suitable sites can be located. As

such, biomass allocation to the rhizome may be considered a low risk investment in carbon with considerable gains.

3.4.4 The influence of nutrient load on the response to salinity.

Nutrient load did not influence the response of *B. arthrophylla* to salinity. Although NAR was significantly reduced at the high nutrient load it did not influence the RGR. In contrast, nutrient load increased the RGR of *T. domingensis* by 5 mg g^{-1} d^{-1} at control and 50 mM NaCl but elicited only a marginal increase in RGR at 100 mM NaCl. These results imply that at salinities less than 100 mM NaCl the success of *T. domingensis* in saline environments will be enhanced by higher nutrient loads whilst that of *B. arthrophylla* will not. This may have considerable implications for the relative competitive abilities of each species and ultimately for community structure.

3.4.5 Differential sensitivities of T. domingensis and B. arthrophylla to salinity

The effects of 100 mM NaCl on the number and height of stems in *B. arthrophylla*, and on numbers of leaves and height of shoots in *T. domingensis*, as well as rates of leaf production were generally evident after c. 3 weeks following salinisation in *T. domingensis*, and after c. 5 weeks in *B. arthrophylla*. Although this may suggest that *B. arthrophylla* is less sensitive to salinity, the delayed response to salinity may simply result from a slower growth rate, whereby the effects of salinity take longer to manifest.

RGR in *B. arthrophylla* declined at 100 mM NaCl by 6 mg g^{-1} d^{-1} (30%) and 4.5 mg g^{-1} d^{-1} (24%) at low and high nutrient loads, respectively whilst in *T. domingensis* RGR declined by 4.2 mg g^{-1} d^{-1} (12%) and 7.9 mg g^{-1} d^{-1} (19.5%), respectively. Differential sensitivity to salinity will consequently depend on nutrient load, and whether comparisons are based on absolute reductions in RGR or as a percentage of control values. Under high nutrient loads *T. domingensis* may be considered more sensitive since RGR is reduced more in absolute terms compared to *B. arthrophylla*, diminishing differences in RGRs. Differences in RGR between *T. domingensis* and *B. arthrophylla* were reduced at the high nutrient load from 22 mg g^{-1} d^{-1} in the control to 18.6 mg g^{-1} d^{-1} at 100 mM NaCl. The greater sensitivity of *T. domingensis* to

salinity at the high nutrient load was absent at the low nutrient load, with both species experiencing similar reductions in RGR.

The findings demonstrate that the benefits conferred by the high nutrient loads diminish as salinities increase in *T. domingensis*. The greater sensitivity to salinity at the high nutrient load was not associated with a reduction in LAR but NAR. As such, the response of *T. domingensis* to salinity and nutrient load are specific, with NAR being influenced by salinity and LAR by nutrient load. Specificity of plant responses has also been reported in tomato plants, where LAR responded to nutrient availability whilst the shoot to root ratio decreased in response to water stress (Coleman and Schneider 1996).

3.4.6 Water use characteristics

As salinity imposes a physiological drought by increasing the soil osmotic potential (ie more negative), water use characteristics either inherent or induced by salinity may enhance success under saline conditions. Nutrient load may also alter water use characteristics and influence performance under saline conditions.

In *T. domingensis* WUE as determined from carbon isotope discrimination was increased (lower discrimination values) significantly by nutrient load and weakly by salinity. In contrast, neither nutrient load or salinity influenced carbon isotope discrimination in *B. arthrophylla*. Instantaneous values of C_i/C_a however, were not consistent with carbon isotope discrimination values, failing to reflect increased WUE in *T. domingensis* whilst indicating increase WUE in *B. arthrophylla*.

Discrepancies between instantaneous values of C_i/C_a and carbon isotope discrimination may arise for a number of reasons. Firstly, if photosynthesis saturates at a lower value of C_i stomatal limitation of photosynthesis may in fact be reduced (Farquhar and Sharkey 1982). As such, discrimination against C^{13} may not be reduced even though C_i/C_a is lower. Secondly, carbon isotope discrimination reflects an integrated value of discrimination over time, however it will be dominated by values when most CO_2 fixation occurs. Consequently,

changes in C_i/C_a with leaf age and in response to environmental conditions may produce discrepancies with instantaneous values.

Although WUE, as determined from carbon isotope discrimination values was more responsive to salinity and nutrient load in *T. domingensis*, discrimination values were always lower in *B. arthrophylla* regardless of treatment conditions. Differences between species were greatest at the low nutrient load, with discrimination values of 24.00 ‰ and 21.24‰ in *T. domingensis* and *B. arthrophylla*, respectively. At the high nutrient load discrimination declined in *T. domingensis* but not in *B. arthrophylla*, hence differences between species were smaller (c. 1.0 ‰). The data indicates that water use efficiency, as represented by carbon isotope discrimination is greater in *B. arthrophylla* compared to *T. domingensis* across the range of salinity-nutrient regimes examined.

Conductance to water loss from plant canopies is influenced by the LAI and by g_S, whilst aerodynamic resistance is influenced by vegetation height. In *B. arthrophylla* salinity reduced the LAI, g_S and height of stems whilst nutrient load did not influence any of these parameters. As such, potential rates of water loss were reduced by salinity and were unaffected by nutrient load. In *T. domingensis* salinity reduced the LAI and shoot height whilst g_S was only reduced at the high nutrient load. Nutrient load increased the LAI and height at all salinities, however these effects diminished as salinities increased. Consequently, potential rates of water loss in *T. domingensis* were reduced by salinity and increased by nutrient load. At 100 mM NaCl, increased water loss associated with higher LAIs at the high nutrient load, may be offset by lower g_S.

Despite changes in height and LAIs in *T. domingensis* in response to nutrient load and salinity, neither vegetation height or LAIs were as low as those measured in *B. arthrophylla* under any nutrient-salinity regime. LAIs varied in *T. domingensis* from 8 at the high nutrient load and control salinities, to 2 at the low nutrient load and 100 mM NaCl, whilst in *B. arthrophylla* LAIs varied from 1.3 to 0.6 across these treatments (Fig. 3.8). Height in *T. domingensis* varied from 171 cm at the high nutrient load and control salinities, to 108 cm at

the low nutrient load and high salinities, whilst in *B. arthrophylla* height varied from 75 cm to 59 cm across these treatments (Figs. 3.2, 3.9). Based on LAIs and vegetation height *B. arthrophylla* can be considered to be more conservative in its water use. It should be noted that differences in LAIs between species may simply be an artefact of different RGR, hence LAIs may be higher in established stands of *B. arthrophylla* than measured in this experiment.

Although RGR in *T. domingensis* may be considered more sensitive to salinity under high nutrient loads, RGRs under all treatment conditions were considerably greater in *T. domingensis* than *B. arthrophylla*. Consequently, the greater water conservation characteristics of *B. arthrophylla* do not confer any advantage over *T. domingensis* in the range of salinities examined. However, the growth season of *B. arthrophylla* is likely to be longer, and on an annual basis productivity may be similar between species. Furthermore, it remains speculative if under high salinities than examined, whether the greater water conservation characteristics of *B. arthrophylla* will confer any advantage over *T. domingensis*, or if *T. domingensis* is able to adjust its morphology and physiology to reduce water loss at higher salinities.

It is evident that *B. arthrophylla* has many traits which may be considered adaptive to infertile and water limited (and hence saline) environments which are not evident in *T. domingensis*. These include increased leaf longevity, a greater conservation of water and water use efficiency, and the preferential allocation of biomass to rhizomes in response to salinity. Despite these traits performance in terms of RGR was substantially lower. Whilst these traits do not result in a higher RGR, they may permit survival or continued growth under greater levels of nutrient limitation or salinity than examined in this experiment.

At salinities less that 100 mM NaCl higher nutrient loads strongly influenced the performance of *T. domingensis* but not *B. arthrophylla*. As salinities increased the benefits of higher nutrient loads diminished in *T. domingensis* and differences in RGR between species

declined. This indicates that at 100 mM NaCl and greater the competitive ability of *T. domingensis* will be reduced irrespective of nutrient load.

Whilst this experiment examines responses under static regimes the importance of fluctuations in environmental conditions in determining the success of species, and in turn community assemblages has become more recognised. The two-phase resource dynamic hypothesis of Goldberg and Novoplansky (1997) emphasises the importance of temporal variability in resource supply. It has been proposed that the differential success of species with high and low RGRs is dependant on the frequency of nutrient pulses (Goldberg and Novoplansky 1997). Where nutrient pulses occur with sufficient frequency species with high RGRs will dominate. As the interpulse period increases the ability to tolerate prolonged soil infertility becomes more important, favouring species with low RGRs. In addition, whether responses during pulse periods are correlated negatively, or positively with performance during interpulse periods is also considered a factor determining success during interpulse periods. The response of vegetation to different salinity-nutrient regimes may therefore elicit different outcomes under field conditions, where nutrient supply and salinities fluctuate in a dynamic manner both seasonally and inter-annually.

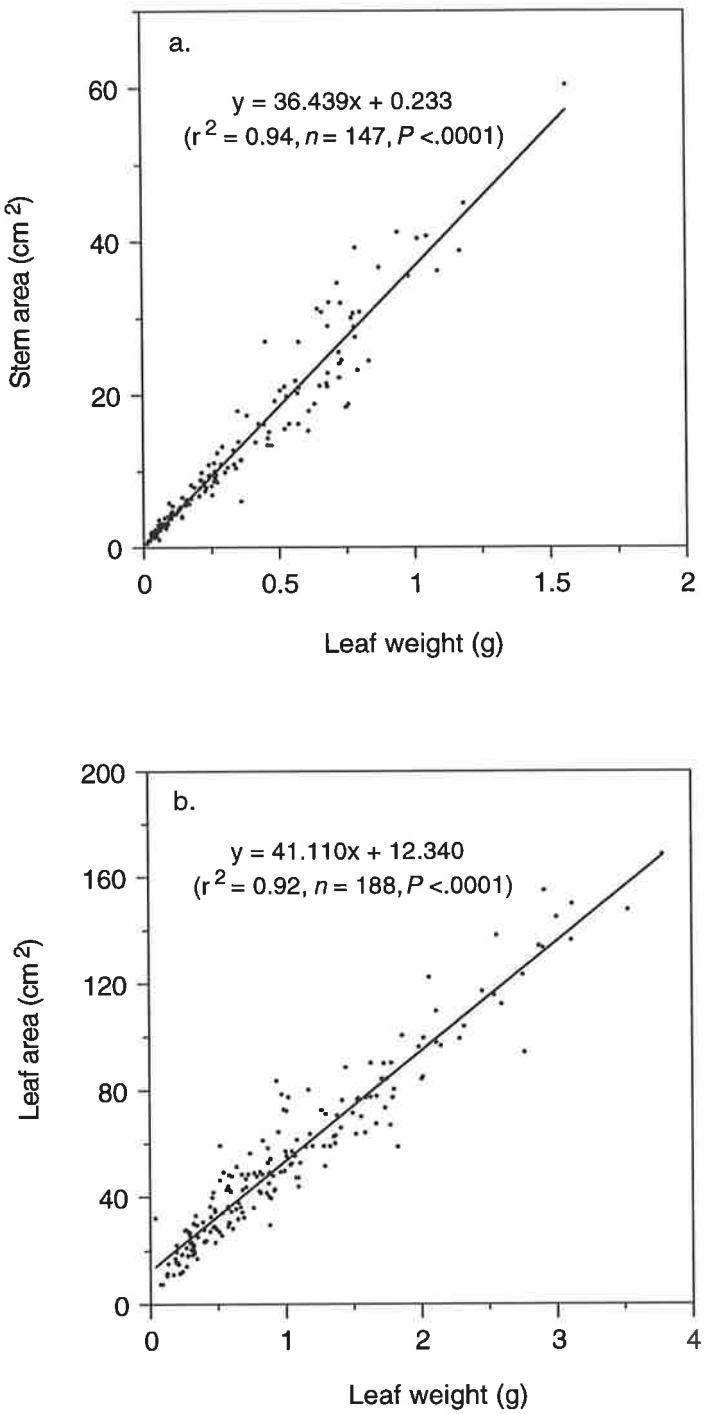


Figure 3.1. Leaf area as a function of leaf weight for all salinity-nutrient treatments; a. *B. arthrophylla* and b. *T. domingensis*.

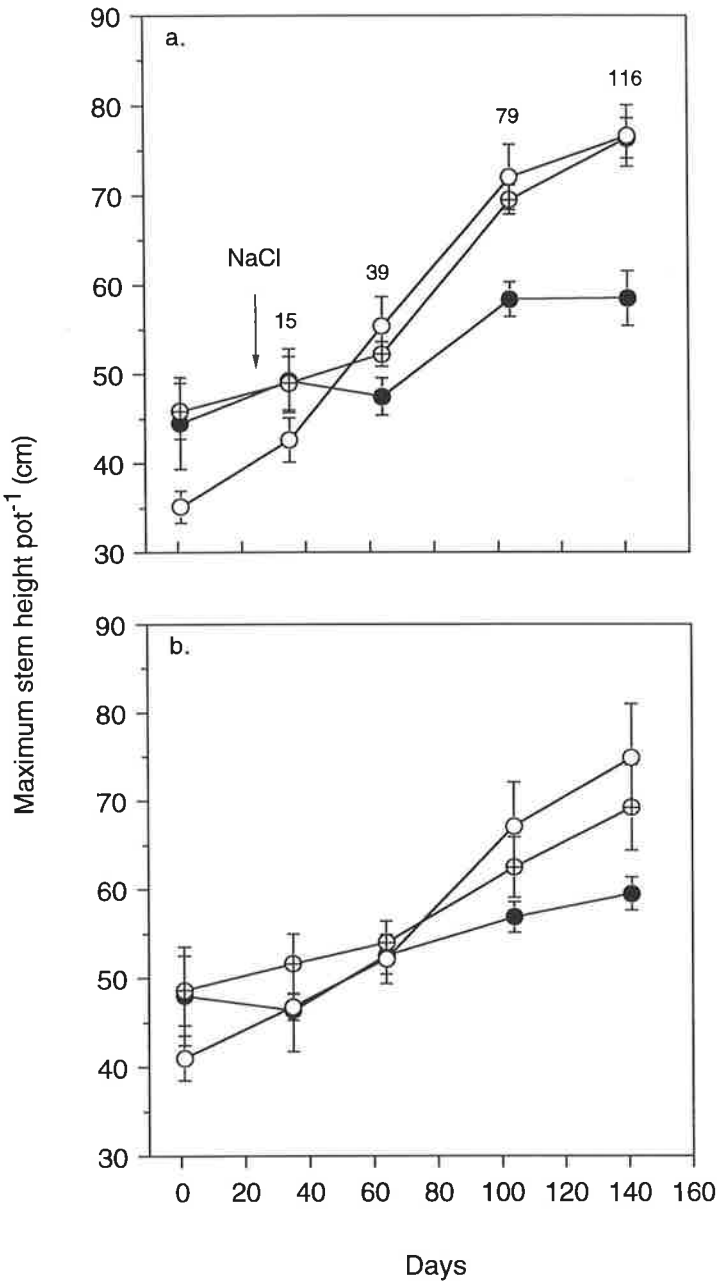


Figure 3.2. Maximum stem height pot^{-1} (cm) as a function of time in *B. arthrophylla* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles); a. low nutrient load and b. high nutrient load. Data are means, bars represent se (n=8). The arrow in a. represents the time at which salinity treatments commenced, and numbers above symbols are days following salinisation. NB. The origin of the y axis in a. and b. does not begin at zero.

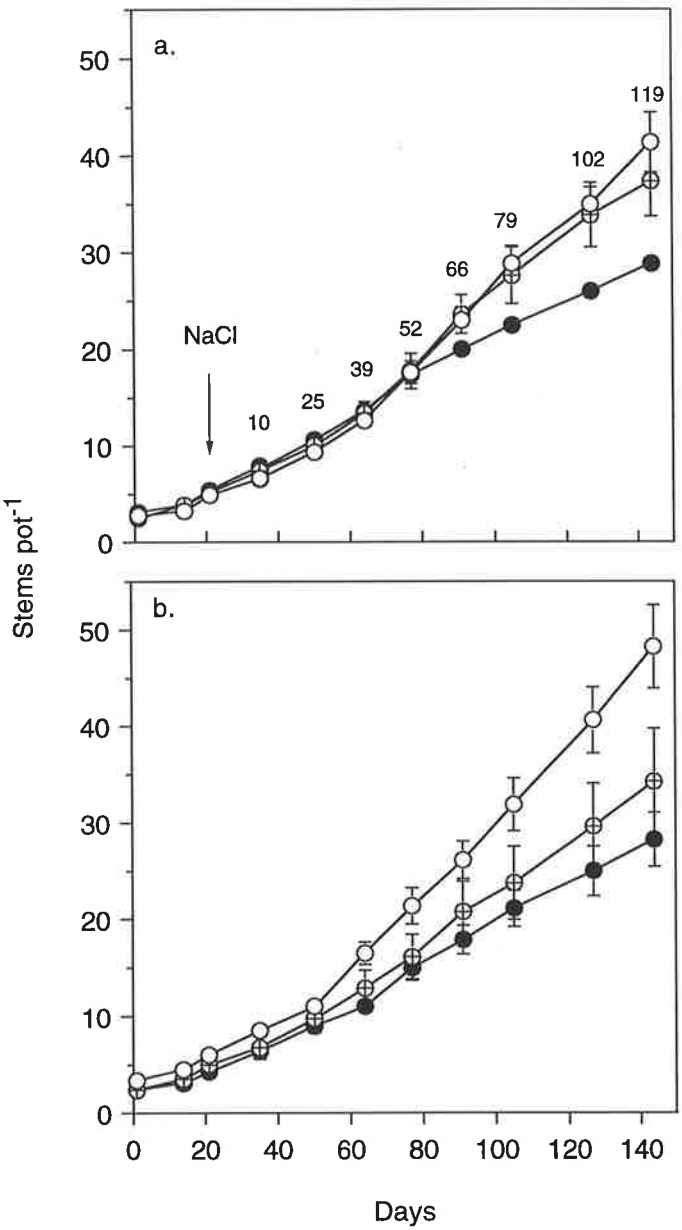


Figure 3.3. Number of stems pot $^{-1}$ as a function of time for *B. arthrophylla* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles);a. low nutrient load and b. high nutrient load. The data are means, bars represent se (n=8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

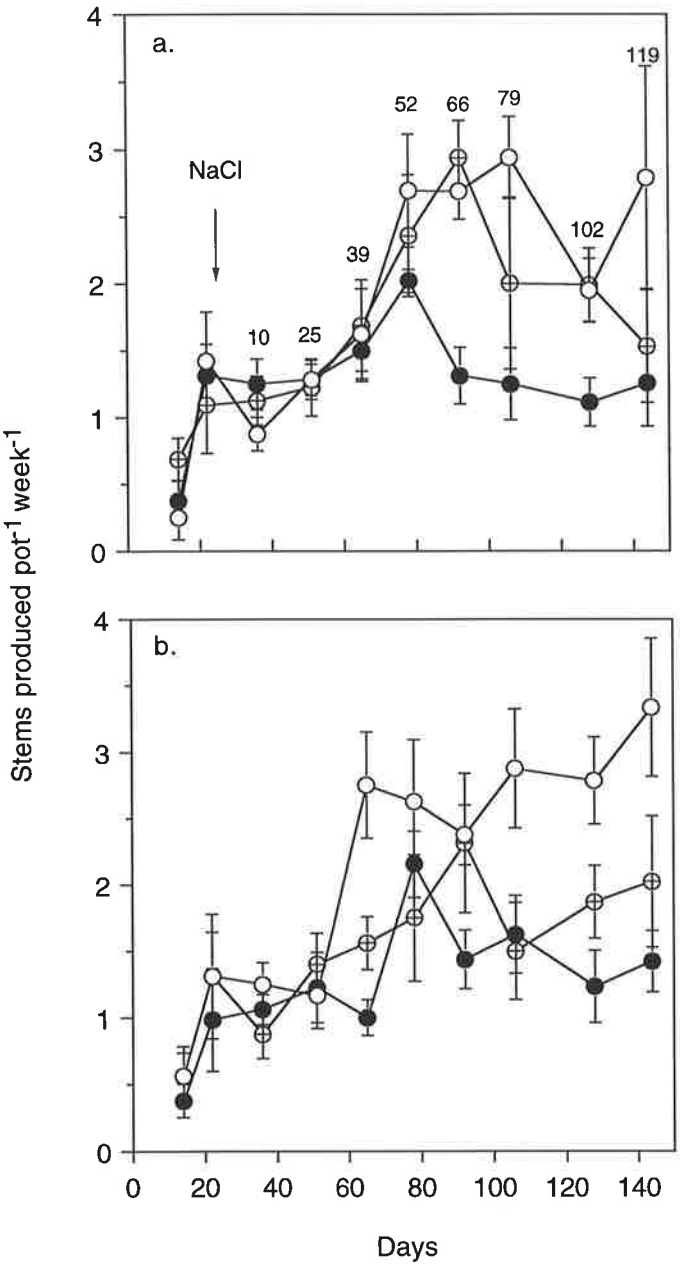


Figure 3.4. Stem production pot $^{-1}$ week^{-1} for *B. arthrophylla* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles); a. low nutrient load and b. high nutrient load. Data are means, bars represent se (n=8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

Table 3.1. Biomass (g) and biomass allocation as a percentage of total biomass in *B. arthrophylla* at each salinity-nutrient treatment. Data are means ± se (n =8).

		Biomass (g)		Percentage of Total	
	Salinity	Nutrient Load		Nutrient Load	
	mM NaCl	Low	High	Low	High
Total biomass	Control	35.8 ± 2.2	38.9 ± 5.0		
	50	33.4 ± 3.5	29.2 ± 5.3		
	100	20.4 ± 1.5	21.0 ± 1.8		
Above-ground	Control	23.4 ± 1.3	27.4 ± 3.9	65.7 ± 1.1	68.3 ± 2.9
	50	21.6 ± 2.4	20.1 ± 3.8	64.2 ± 1.8	67.3 ± 2.8
	100	11.5 ± 0.7	12.3 ± 1.4	56.9 ± 1.9	57.5 ± 2.4
Stems	Control	16.9 ± 1.0	20.2 ± 3.0	47.3 ± 1.1	49.8 ± 2.9
	50	15.9 ± 1.8	14.9 ± 2.8	47.2 ± 1.4	50.2 ± 2.7
	100	8.3 ± 0.5	8.9 ± 1.0	40.9 ± 1.6	41.5 ± 1.6
Stem bases	Control	6.5 ± 0.3	7.2 ± 1.0	18.4 ± 0.5	18.4 ± 0.5
	50	5.7 ± 0.6	5.2 ± 1.0	17.0 ± 0.6	17.1 ± 8
	100	3.2 ± 0.2	3.4 ± 0.4	16.0 ± 0.8	16.0 ± 1.0
Below-ground	Control	12.4 ± 1.0	11.5 ± 1.3	34.3 ± 11	31.7 ± 2.9
	50	11.8 ± 1.2	9.1 ± 1.5	35.7 ± 1.8	32.7 ± 2.8
	100	8.9 ± 0.9	8.7 ± 0.5	43.0 ± 1.9	42.5 ± 2.4
Rhizomes	Control	8.2 ± 0.7	8.5 ± 0.9	22.8 ± 1.1	24.3 ± 3.3
	50	8.7 ± 0.8	7.1 ± 1.2	26.2 ± 1.0	25.8 ± 2.7
	100	7.6 ± 0.8	7.2 ± 0.4	36.8 ± 2.0	35.2 ± 2.0
Roots	Control	4.1 ± 0.5	3.0 ± 0.4	11.4 ± 11	7.5 ± 0.6
	50	3.1 ± 0.5	2.0 ± 0.4	9.5 ± 1.0	7.0 ± 1.0
	100	1.3 ± 0.1	1.5 ± 0.2	6.3 ± 0.4	7.2 ± 0.8

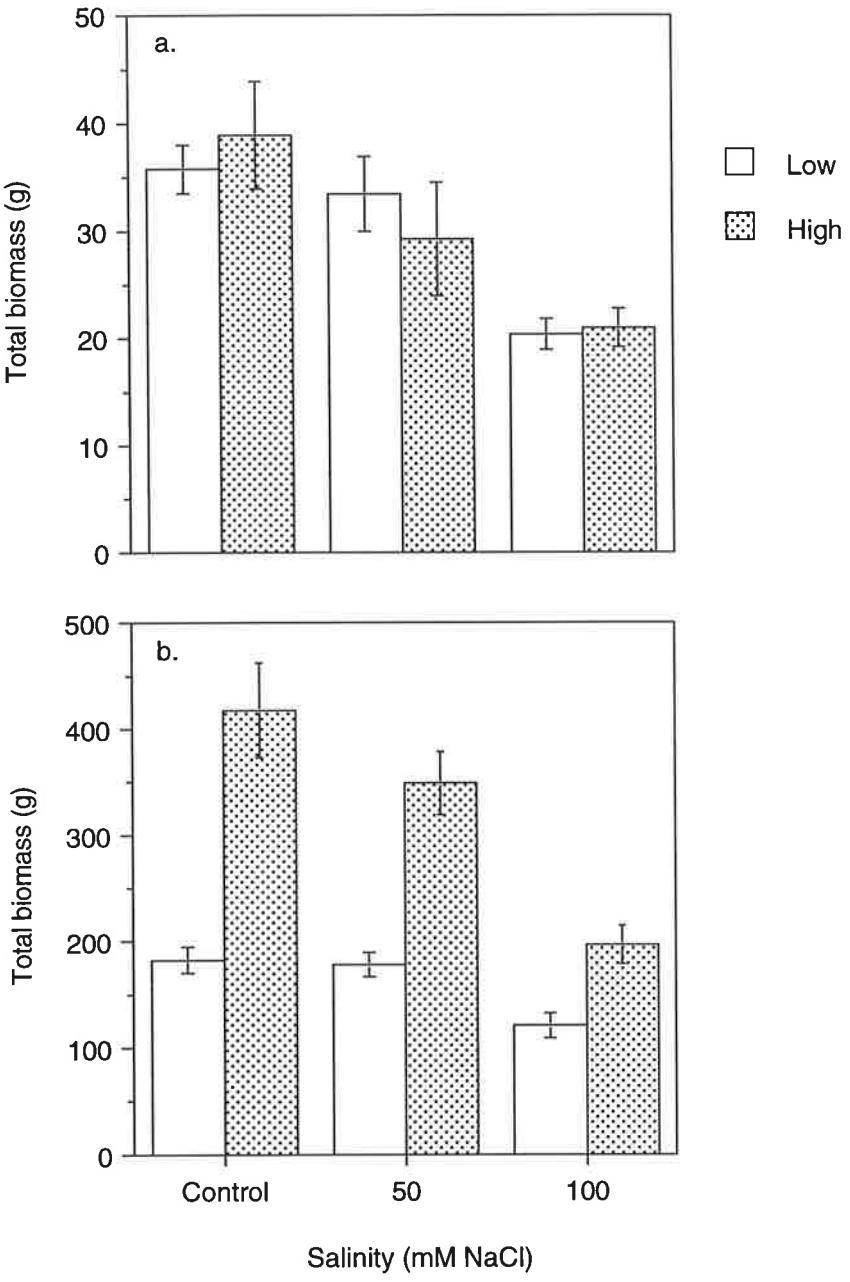


Figure 3.5. Total biomass as a function of salinity at low and high nutrient loads; a. *B. arthrophylla* and b. *T. domingensis.* Data are means, bars represent se (n=8).

Table 3.2. Results of a two-way analysis of variance for total biomass, RGR, NAR and LAR for *T. domingensis* and *B. arthrophylla*. NB. the factor pond was not significant for any variable. Nutrient load df 1, 48; salinity df 2, 48; interaction df 2, 48.

Source of Variation	*T. domingensis*		*B. arthrophylla*	
	F	*P*	F	*P*
Total biomass				
Nutrient load	64.1	<.0001	.003	ns
Salinity	17.9	<.0001	11.9	<.0001
Nutrient load x salinity	5.3	.008	.58	ns
RGR				
Nutrient load	12..1	.0012	3.2	ns
Salinity	10.4	.0002	18.5	<.0001
Nutrient load x salinity	1.0	ns	1.1	ns
NAR				
Nutrient load	3.1	ns	8.5	.0055
Salinity	9.6	.0004	6.9	.0026
Nutrient load x salinity	0.2	ns	1.4	ns
LAR				
Nutrient load	57.2	.0001	0.4	ns
Salinity	0.45	ns	7.4	.0018
Nutrient load x salinity	0.19	ns	0.9	ns

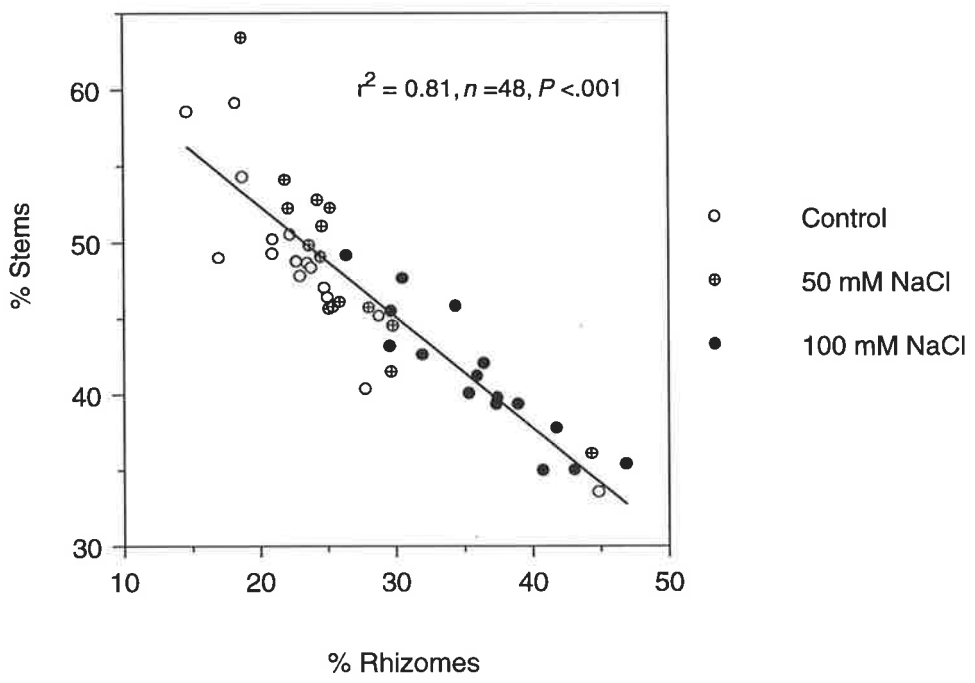


Figure 3.6. Relationship between percent stem biomass and percent rhizome biomass in response to salinity for *B. arthrophylla*. NB. The origin of the axes do not begin at zero.

Table 3.3. Ratios of above to below-ground biomass, above-ground to root biomass, and leaf/stem to root biomass, in *T. domingensis* and *B. arthrophylla* at each salinity-nutrient treatment. Data are means ± se (n =8).

		B. arthrophylla		*T. domingensis*	
	Salinity	Nutrient Load		Nutrient Load	
	mM NaCl	Low	High	Low	High
Above:Below	Control	1.94 ± 0.09	2.3 ± 0.26	1.80 ± 0.08	4.44 ± 0.20
	50	1.85 ± 0.16	2.2 ± 0.24	2.60 ± 0.27	4.64 ± 0.32
	100	1.36 ± 0.11	1.4 ± 0.14	2.46 ± 0.22	5.13 ± 0.43
Above:Root	Control	6.12 ± 0.54	9.4 ± 0.61	2.48 ± 0.14	7.09 ± 0.60
	50	7.8 ± 1.4	11.0 ± 1.6	4.15 ± 0.61	6.97 ± 0.47
	100	9.4 ± 0.71	8.6 ± 1.0	3.73 ± 0.39	8.87 ± 0.55
Leaf:Root	Control	4.39 ± 0..37	6.84 ± 0.45	0.85 ± 0.05	2.51 ± 0..29
	50	5.69 ± 1.0	8.32 ± 1.35	1.33 ± 0.20	2.56 ± 0.19
	100	6.76 ± 0.57	6.20 ± 0.70	1.20 ± 0.10	3.11 ± 0.18

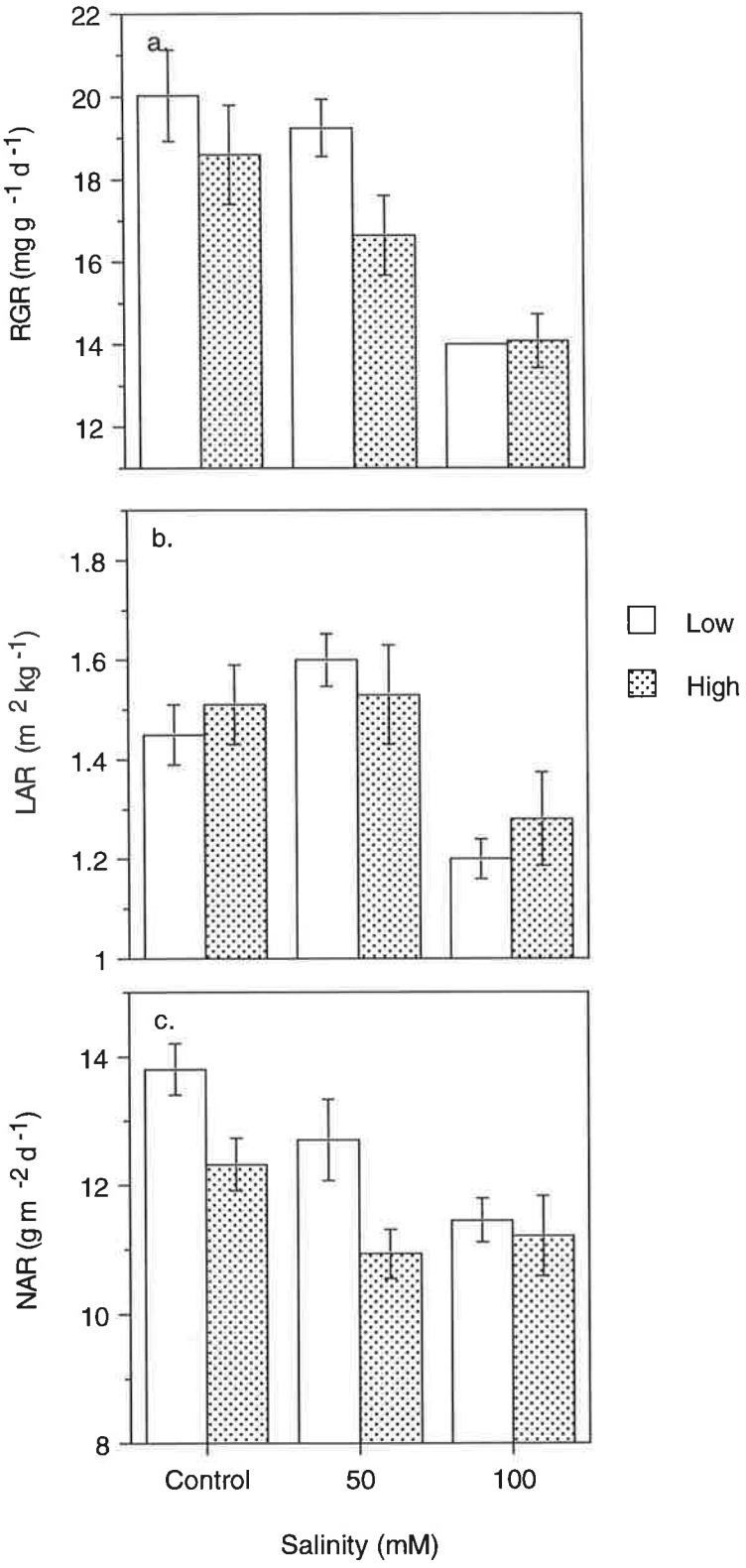


Figure 3.7. Growth parameters for *B. arthrophylla*; a. RGR, b. LAR, and c. NAR as a function of salinity at low and high nutrient loads. Data are means, bars represent se (n=8). NB. The origin of the y axis in a., b. and c. does not begin at zero.

Table 3.4. Irradiance and gas exchange characteristics of *B. arthrophylla* stems at various salinity-nutrient treatments. Data are means ± se (*n*=3-4).

Nutrient Load	Salinity mM NaCl	Irradiance μmol m^{-2} s^{-1}	Assimilation μmol CO_2 m^{-2} s^{-1}	Conductance mmol m^{-2} s^{-1}	C_i/C_a
Low	Control	1610 ± 115	19.8 ± 1.3	394 ± 38	0.624 ± .05
Low	100	1390 ± 80	11.3 ± 1.8	129 ± 19	0.516 ± .04
High	Control	1643 ± 88	23.0 ± 1.6	655 ± 160	0.647 ± .04
High	100	1570 ± 111	13.5 ± 1.3	168 ± 39	0.516 ± .06

Table 3.5. Results of two-way analysis of variance for irradiance and leaf gas exchange variables of *B. arthrophylla* stems. Arcsine square root transformations were performed on C_i/C_a data. Degrees of freedom for nutrient load, salinity and interaction terms were 1,12.

Source of Variation	F	*P*
Irradiance (μmol m^{-2} s^{-1})		
Nutrient load	1.13	ns
Salinity	2.16	ns
Nutrient load x salinity	0.54	ns
Assimilation (μmol CO_2 m^{-2} s^{-1})		
Nutrient load	2.9	ns
Salinity	34.4	0.0002
Nutrient load x salinity	.09	ns
Conductance (mmol m^{-2} s^{-1})		
Nutrient load	2.00	ns
Salinity	12.54	0.006
Nutrient load x salinity	1.08	ns
C_i/C_a		
Nutrient load	0.055	ns
Salinity	5.9	.037
Nutrient load x salinity	0.055	ns

Table 3.6. Carbon isotope discrimination (Δ) and isotopic composition of CO_2 ($\delta^{13}C$), in top sections of *T. domingensis* leaves and whole *B. arthrophylla* stems. Data are means ± se (n =3).

Nutrient Load	Salinity	*T. domingensis*		*B. arthropylla*	
	mM NaCl	Δ ‰	$\delta^{13}C$ ‰	Δ ‰	$\delta^{13}C$ ‰
Low	Control	24.00 ± 0.27	-31.25 ± 0.25	21.24 ± 0.35	-28.64 ± 0.33
	100	22.80 ± 0.37	-30.12 ± 0.36	20.29 ± 0.22	-27.73 ± 0.21
High	Control	22.63 ± 0.26	-29.95 ± 0.25	20.68 ± 0.24	-28.10 ± 0.23
	100	22.51 ± 0.17	-29.84 ± 0.16	20.79 ± 0.38	-28.20 ± 0.36

Table 3.7. Results of a two-way analysis of variance for carbon isotope discrimination and percentage nitrogen for *T. domingensis* and *B. arthrophylla*. An arcsine square root transformation was performed on percentage nitrogen data. The degrees of freedom for nutrient load, salinity and interaction term were 1, 11.

Source of Variation	*T. domingensis*		*B. arthrophylla*	
	F	*P*	F	*P*
Δ				
Nutrient load	8.68	.018	0.12	ns
Salinity	5.44	.047	1.87	ns
Nutrient load x salinity	3.69	ns	2.96	ns
% Nitrogen				
Nutrient load	37.4	.0003	71.15	<.0001
Salinity	12.24	.008	7.44	ns
Nutrient load x salinity	0.77	ns	4.95	ns

Table 3.8. Percentage of nitrogen in top sections of *T. domingensis* leaves and whole stems of *B. arthrophylla*. Data are means ± se (n =3).

Nutrient Load	Salinity	% Nitrogen	
	mM NaCl	*T. domingensis*	*B. arthrophylla*
Low	Control	1.66 ± 0.06	1.13 ± 0.03
	100	2.17 ± 0.15	1.60 ± 0.12
High	Control	2.51 ± 0.17	2.24 ± 0.14
	100	2.86 ± 0.09	2.30 ± 0.13

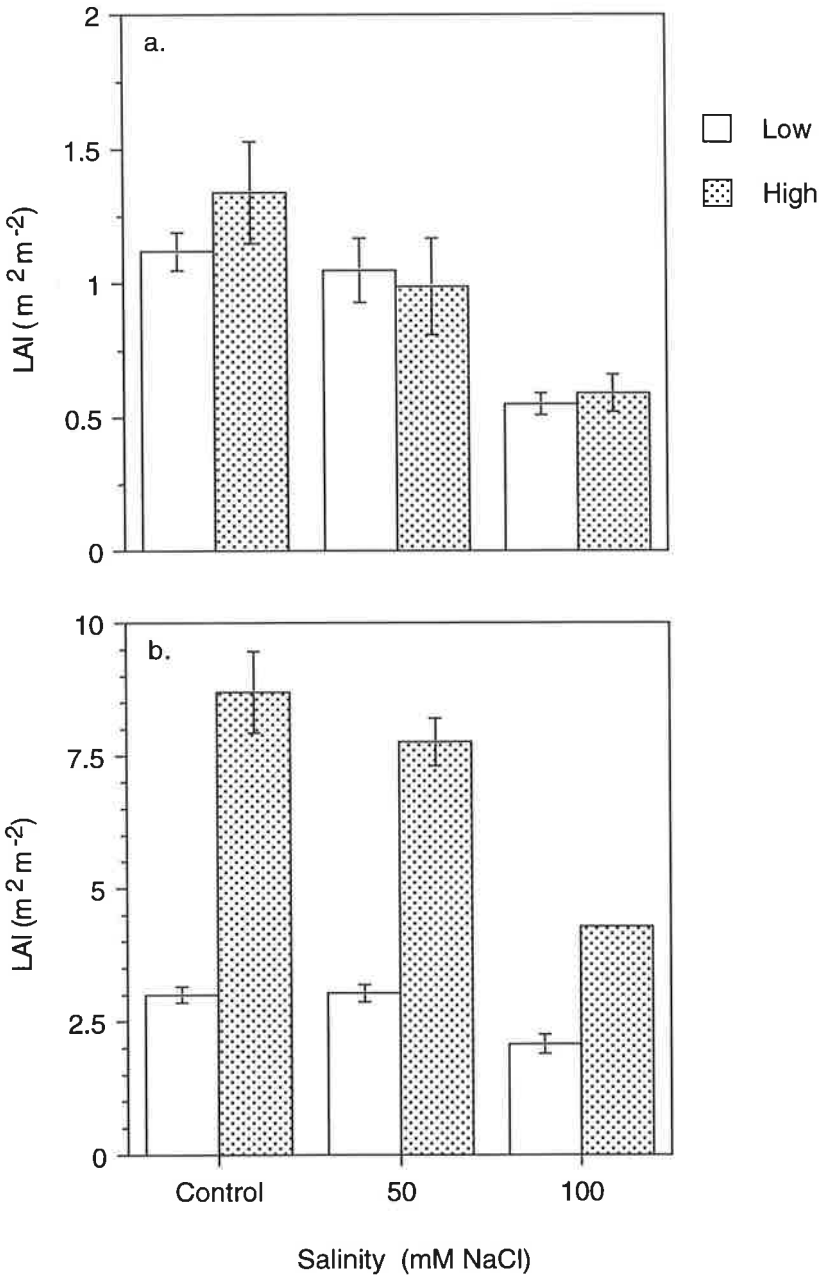


Figure 3.8. LAIs as a function of salinity at low and high nutrient loads; a. *B. arthrophylla* and b. *T. domingensis*. Data are means, bars represent se (*n* =8).

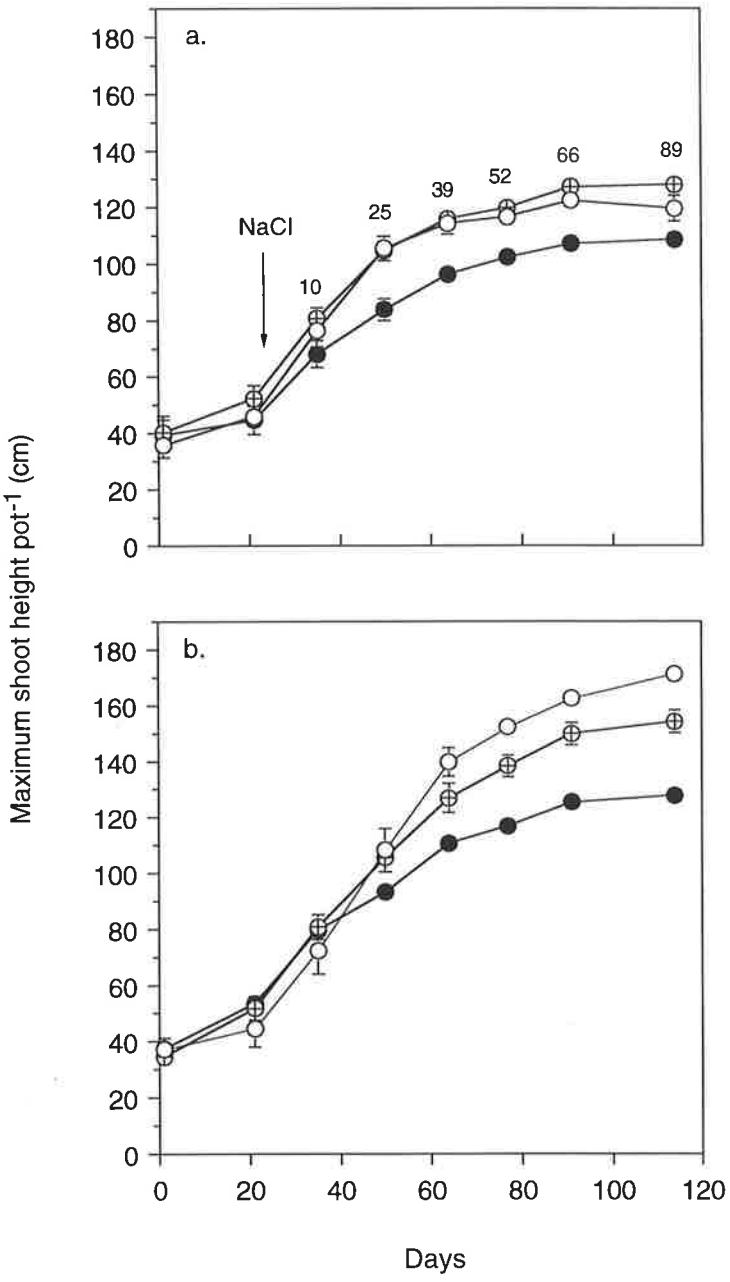


Figure 3.9. Maximum shoot height pot $^{-1}$ over time for *T. domingensis* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles); a. low nutrient load and b. high nutrient load. Data are means, bars represent se (*n* =8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days following salinsation.

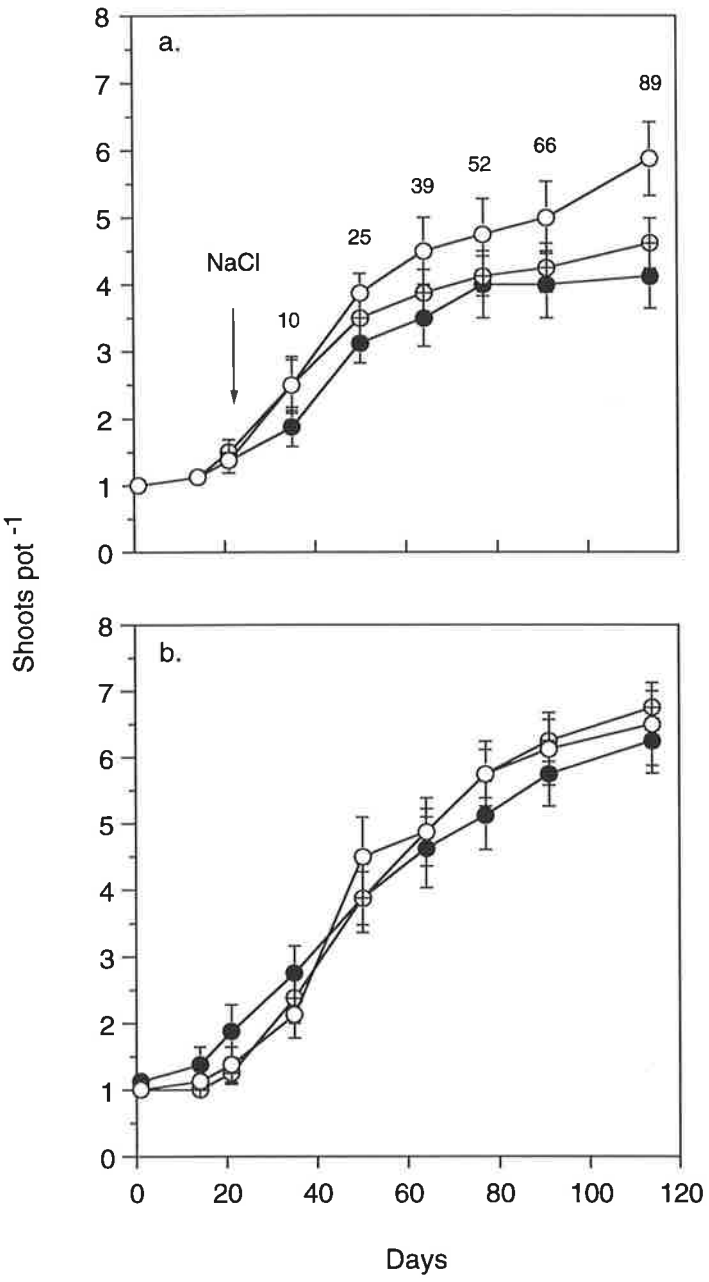


Figure 3.10. Shoots pot $^{-1}$ over time for *T. domingensis* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles); a. low nutrient load and b. high nutrient load. Data are means, bars represent se (n =8). The arrow in a. represents the time at which salinisation commenced, and numbers above symbols are days following salinisation.

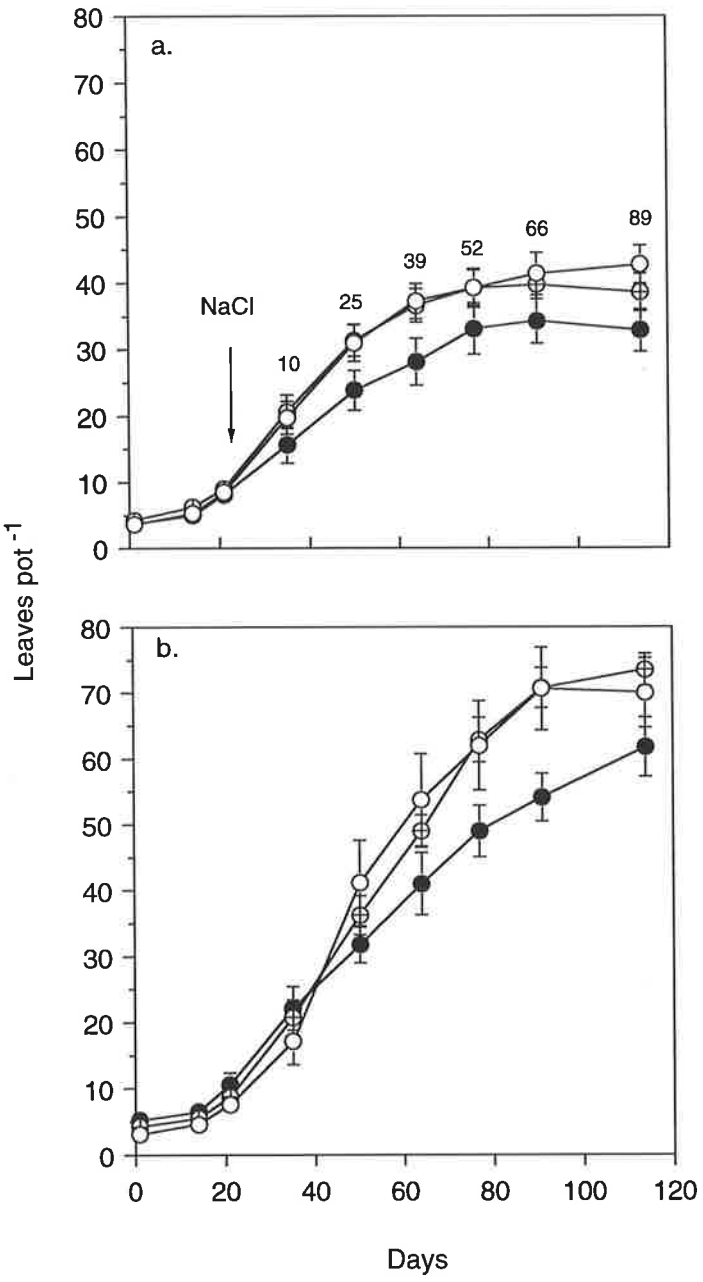


Figure 3.11. Number of leaves pot^{-1} over time for *T. domingensis* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles); a. low nutrient load and b. high nutrient load. Data are means, bars represent se (n=8). The arrow in a. indicates the time at which salinity treatments commenced, and numbers above symbols are days following salinisation.

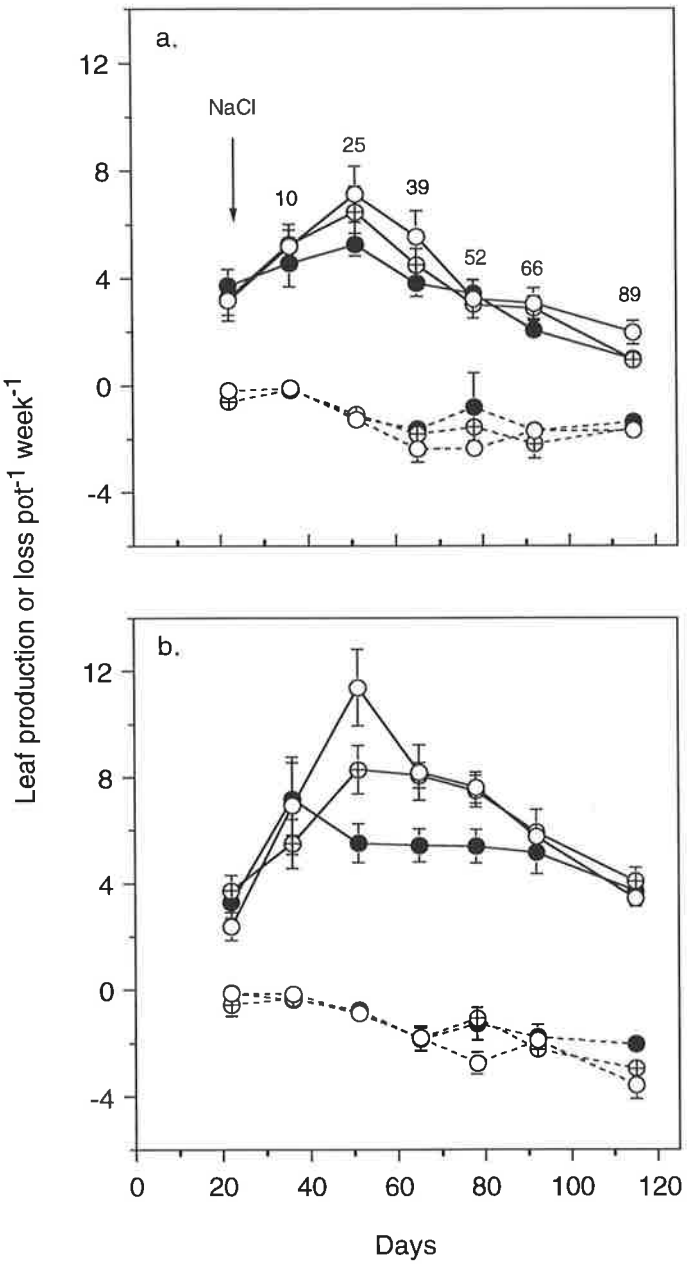


Figure 3.12. Rates of leaf production (solid line) and senescense (broken line) pot^{-1} $week^{-1}$ over time for *T. domingensis* at control (open circles), 50 mM (hatched circles) and 100 mM NaCl (filled circles);a. low nutrient load and b. high nutrient load. Data are means, bars represent se (n=8). The arrow in a. represents the time at which salinity treatments commenced, and the numbers above symbols are days following salinisation.

Table 3.9. Biomass (g) and biomass allocation as a percentage of total biomass in *T. domingensis* at each salinity-nutrient treatment. Data are means ± se (n =8).

		Biomass (g)		Percentage of Total	
	Salinity	Nutrient Load		Nutrient Load	
	mM NaCl	Low	High	Low	High
Total biomass	Control	182.3 ± 12	417.5 ± 45		
	50	177.8 ± 11	348.8 ± 30		
	100	120.8 ± 12	196.7 ± 18		
Above-ground	Control	116.8 ± 7	339.8 ± 36	64.1 ± 0.9	81.4 ± 0.68
	50	125.9 ± 7	284.2 ± 22	71.2 ± 1.9	81.9 ± 1.0
	100	84.9 ± 9	163.7 ± 15	70.14 ± 2.3	83.1 ± 1.2
Leaves	Control	39.9 ± 2.1	116.2 ± 10.4	22.0 ± 0.5	28.5 ± 1.1
	50	40.2 ± 2.1	103.5 ± 6.1	22.8 ± 0.8	30.1 ± 0.7
	100	27.3 ± 2.4	56.9 ± 4.5	22.8 ± .05	29.3 ± 1.0
Stems	Control	76.9 ± 5.6	223.7 ± 26	42.1 ± 1.0	52.9 ± 0.9
	50	85.7 ± 5.4	180.7 ± 16	48.4 ± 1.4	51.8 ± 0.1
	100	57.5 ± 7.0	106.7 ± 11	47.3 ± 2.2	53.8 ± 1.7
Below-ground	Control	65.5 ± 5.2	77.7 ± 8.8	35.8 ± 1.0	18.5 ± 0.7
	50	51.9 ± 5.5	64.5 ± 8.4	28.8 ± 1.9	18.1 ± 1.0
	100	35.9 ± 4.0	33.0 ± 3.4	29.8 ± 2.3	16.9 ± 1.2
Rhizomes	Control	17.0 ± 1.2	26.3 ± 2.6	9.5 ± 0.8	6.6 ± 0.6
	50	17.1 ± 1.5	21.3 ± 2.6	9.7 ± 0.8	6.0 ± 0.4
	100	11.3 ± 1.0	13.7 ± 1.9	9.6 ± .07	7.2 ± 1.2
Roots	Control	48.5 ± 4.5	51.3 ± 6.7	26.3 ± 1.2	11.9 ± 0.8
	50	34.8 ± 4.9	43.2 ± 6.1	19.0 ± 1.9	12.1 ± 0.7
	100	24.6 ± 3.4	19.3 ± 2.6	22.3 ± 2.1	9.6 ± 0.6

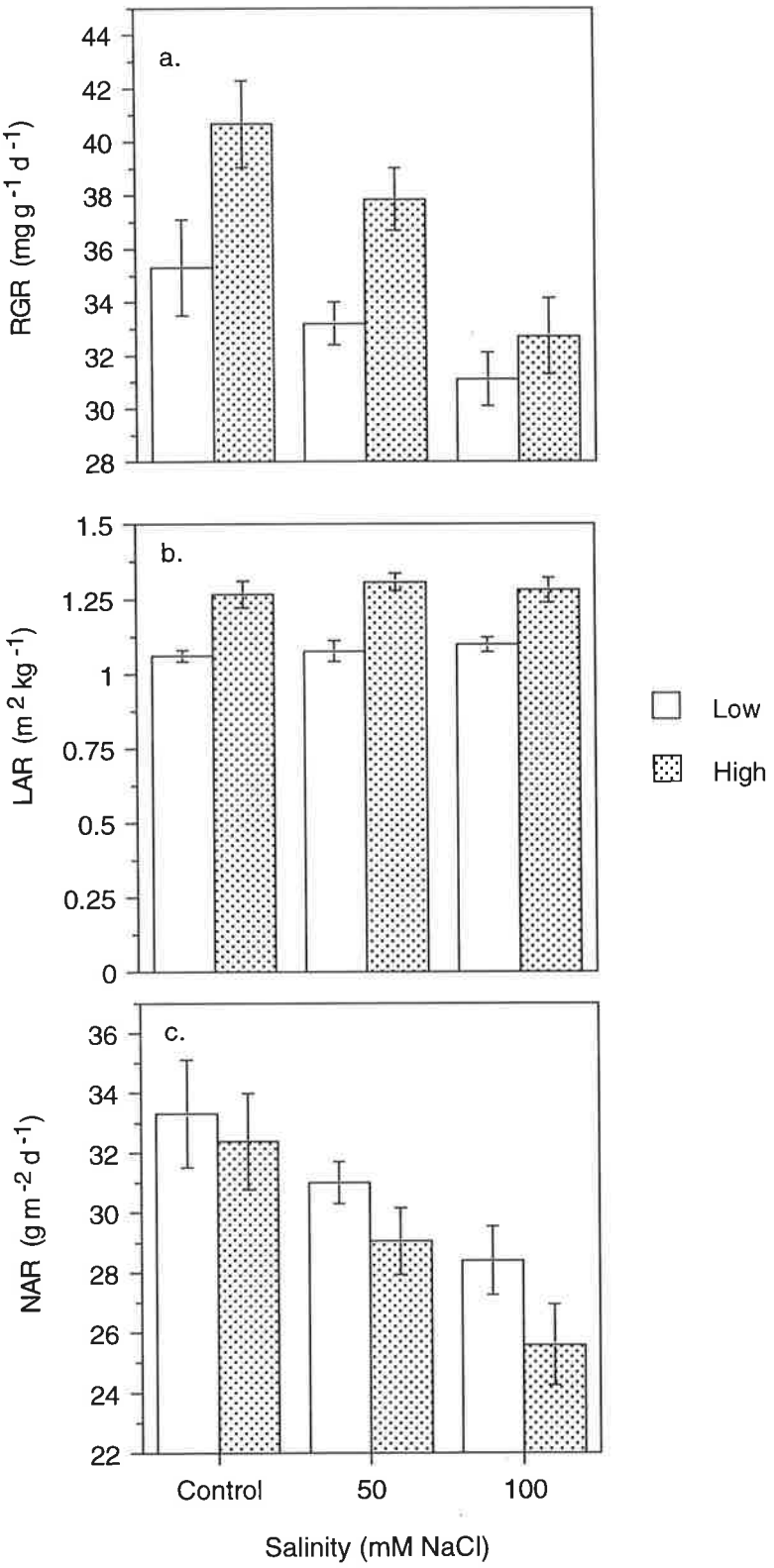


Figure 3.13. Growth parameters; a. RGR, b. LAR and c. NAR as a function of salinity for *T. domingensis* at low and high nutrient load. Data are means, bars represent se (n = 8). NB. The origin of the y axis in a. and c. does not begin at zero.

Table 3.10. Irradiance and gas exchange characteristics of *T. domingensis* leaves at various salinity-nutrient treatments. Arcsine square root transformations were performed on C_i/C_a data. Data are means ± se (n =8); ns indicates no significant difference; *** significance at $P<.001$ and ‡ indicates that a Welch Anova was used due to unequal variances. Each pair of measurements were sampled on different days and represent an individual set of measurements.

Nutrient Load	Salinity mM	Irradiance μmol m^{-2} s^{-1}	Assimilation μmol CO_2 m^{-2} s^{-1}	Conductance mmol m^{-2} s^{-1}	C_i/C_a
Low	Control	1528 ± 17	20.6 ± 1.0	275 ± 12	0.49 ± 0.05
Low	100	1523 ± 13 ns	22.0 ± 0.7 ns	294 ± 20 ns	0.50 ± 0.06 ns
High	Control	1261 ± 58	21.0 ± 1.0	310 ± 38	0.46 ± 0.09
High	100	1325 ± 57 ns	13.9 ± 2.0 ***	140 ± 17 ***	0.42 ± 0.07 ns
Low	Control	1420 ± 29	19.3 ± 1.2	401 ± 37	0.61 ± 0.01
High	Control	1480 ± 17 ns	21.2 ± 0.4 ns	507 ± 35 ns	0.59 ± 0.06 ns ‡
Low	100	1513 ± 12	19.2 ± 1.0	264 ± 72	0.51 ± 0.02
High	100	1524 ± 12 ns	15.7 ± 1.9 ns	213 ± 34 ns	0.51 ± 0.01 ns

Chapter 4. Salinity; growth and water use in *T. domingensis* and *B. arthrophylla* under natural conditions

4.1 Introduction

Southern Australian wetlands are characterised by seasonal fluctuations in water levels, with peaks occurring in winter and troughs in summer (Paijmans *et al.* 1985). In winter regional ground water recharge may cause saline ground water to rise and encroach the root zone of vegetation. In summer the evaporation of surface water results in the concentration of dissolved salts and hence increases in salinity. In the absence of surface water the capillary rise of saline ground water results in the accumulation of salts in the soil profile. The salinity and depth of ground water, the extent and duration of drawdown, and the magnitude of flushing events all influence salinisation. As such, salinity will rarely be static but subject to dynamic fluctuations both seasonally and inter-annually.

Whilst the threat of salinity on fresh water systems is well recognised (Hart *et al* 1991, 1990; de Jong 1997) studies of salt fluxes in wetlands systems have focused primarily on flood plains, particularly of the Lower River Murray, (Jolly *et al.* 1993; Thorburn *et al.* 1993; Thorburn *et al.* 1995; Mensforth 1994) rather than on swamps. The notable exceptions being the work of Mensforth (1996) and Froend *et al.* (1987) where soil salinities were measured within ephemeral swamps. From these studies it is evident that soil salinities within ephemeral swamps may vary both spatially and temporally. In salt marshes, variability in soil salinities over time and with soil depth have also been demonstrated (Whigham *et al.* 1989; Lissner and Schierup 1997).

Salinity fluctuations within wetland systems which intercept saline ground water are strongly influenced by the hydrological regime. Consequently, the impact of vegetation on the water balance may be considerable. Where evapotranspiration (E) is exacerbated by vegetation, drawdown will be imposed earlier. In regions affected by salinity this will promote salt accumulation and shorten the period favourable for growth.

The literature (1.5.4) suggests that the contribution of vegetation to the water balance may be influenced by vegetation type, and the response of vegetation to environmental conditions. The vegetation parameters which may influence evapotranspiration (E) include; the leaf area index (LAI), vegetation height, stomatal resistance (r_S), albedo and the light extinction coefficient of the canopy($\mathcal{K}$). In pond experiments both the height and LAI of *T. domingensis* were significantly greater than *B. arthrophylla*, under optimal conditions of high nutrients and low salinity. Under favourable conditions *T. domingensis* may therefore use more water than *B. arthrophylla*. In pond experiments the LAI and height of vegetation were reduced by salinity. These changes were more pronounced in *T. domingensis* than *B. arthrophylla* indicating that differences in transpiration between species, evident under favourable conditions, may be reduced at higher salinities. However, the extent to which LAIs from pond experiments reflect those occurring under natural conditions is uncertain. It is also unclear the degree to which differences in these parameters translate to difference in rates of transpiration. Furthermore, the contribution of vegetation to the water balance will be determined by the extent to which seasonal changes in LAI, height and r_S are coupled to peaks in evaporative demand. Layered upon this is the degree to which soil salinities vary seasonally and the manner in which vegetation respond to these changes.

Water loss from vegetation not only has implications for the salt and water balance of wetlands, but the capacity to minimise water loss will be significant in the tolerance of vegetation to salinity. Plant productivity in saline environments will also be governed by water use efficiency (WUE), that is how closely water loss is coupled to CO_2 assimilation. In environments where salinity levels fluctuate, the capacity of vegetation to respond to the speed and magnitude of these changes will influence survival and productivity. Furthermore, the extent to which periods of high salinity coincide with seasonal growth patterns may be a factor governing success in such environments. As such, the performance of vegetation under static salinity regimes imposed in pond experiments may differ under variable salinity regimes .

As demands on water resources escalate the water requirements of natural systems must be better understood to ensure their integrity is preserved. Central to achieving this is an understanding of the dynamics of salt fluxes in wetlands, the influence of vegetation on E, and the impact that salinisation may have on plant performance and E. This research attempts to provide some insight into each of these processes.

The specific objectives of this study were:

- To assess the nature and extent of seasonal variation in soil salinities in wetland regions influenced by ground water differing in salinity.

- To establish whether E or WUE differs in two morphologically distinct macrophytes, *T. domingensis* and *B. arthrophylla*, under conditions of low salinity.

- To evaluate the impact that saline ground water may have on plant performance, E and WUE in *B. arthrophylla* and *T. domingensis*.

- To identify the underlying mechanisms which gives rise to different rates of E where they exist.

4.2 Site description

Bool Lagoon is a 2690 ha wetland situated 15 km south of Naracoorte in the south east of South Australia (37° 08' S,140° 41' E; Fig. 4.1) (ANCA 1996). Bool Lagoon represents one of the largest and most important wetland areas remaining in the south east of South Australia, where most wetlands have been lost or extensively altered by drainage or development. Moreover, Bool Lagoon is recognised at an international level by its classification under the Ramsar Convention. It is currently utilised as both a conservation park and as a game reserve (ANCA 1996).

Bool lagoon consists of three interconnecting basins, with a total maximum capacity of 31 000 ML, a mean water depth of 1 m, and a maximum depth of 1.5 m. The hydrological regime of the wetland has been regulated since the 1960s to impound water and control flooding of low lying agricultural land. Floodwaters from a 1215 km^2 catchment are diverted into the wetland through the Mosquito Creek channel, whilst the discharge of water from the wetland is manipulated via a regulated outlet channel (Drain M) (Fig. 4.1). Annual rainfall is approximately 600 mm and average annual evaporation approximately 1400 mm, with peaks in January and February (ANCA 1996)

Bool Lagoon was selected as a study site since it supported established stands of both species of interest, and was known to have regions which differed in ground water salinity. Moreover Bool Lagoon is considered a window of the ground water table (pers com. Fred Stadter; SE Drainage Board 1997). As such, ground water salinities, and changes in ground water level have the potential to strongly influence soil salinities, and hence plant performance. Exceptionally slow ground water flows in the region (.001-.01 m day^{-1}; Stadter and Stewart 1991) suggest that ground water levels will rise with ground water recharge in winter. Hence saline ground water may encroach the root zone of vegetation over winter-spring when ground water levels are high. Elevation of the ground water table above the floor of the lagoon, and in low-lying hollows in winter have been reported (ANAC 1996). Furthermore, during drawdown ground water will remain shallow, and the capillary rise of saline ground water will increase soil salinities.

4.3 Material and methods

4.3.1 Selection of study sites, plot sizes and measurements

Two sites within Bool Lagoon referred to as TB3 and TB18 were selected in September '96, based on contrasting ground water salinities; 3 and 18 dS m^{-1}, respectively, and the presence of established stands of *T. domingensis* and *B. arthrophylla* (Fig. 4.1). The juxtaposition of *B. arthrophylla* and *T. domingensis* at both of these sites permitted the water use and performance characteristics of these species to be compared under both fresh and saline

conditions. A third site referred to as T15 was selected in December '96 (Fig. 4.1). This site differed from the TB3 and TB18 sites by its isolation from the main wetland system, having been created by the excavation of land for road construction. The site was monitored as it supported a stand of *T. domingensis* subjected to both saline surface water (10 dS m^{-1}) and ground water (15 dS m^{-1}). As such, there existed no zone in which salinity could be avoided. The hydrological isolation of the T15 site from the main wetland system also suggested that complete drawdown would occur during summer, permitting the consequences of capillary rise of saline ground water to be measured. *B. arthrophylla* was absent from this site and it was not possible to locate a stand of *B. arthrophylla* under similar conditions.

Single plots 30 m x 12 m were established within stands of *B. arthrophylla* at both the TB3 and TB18 sites. Within stands of *T. domingensis* a 30 m x 12 m plot was established at the TB3 site, while at both the TB18 and T15 sites the extent of the stands only permitted 20 m x 12 m plots.

Leaf area indices and soil salinities were monitored within these plots every 6 to 8 weeks between September '96 and April '97. The salinity of surface water when present, and the salinity and depth of ground water were also monitored at these times. Leaf gas exchange characteristics were measured in both species at each site in February, March and April '97. Carbon isotopes were measured on samples collected in December '96 and March '97.

4.3.2 Ground water salinity and depth

The depth to ground water was estimated at 1, 6 and 11 m from the landward edge of each plot. Estimates were derived from the depth to ground water within piezometers and the elevation profiles within plots, and between plots and piezometers. Data collected in September '96 were obtained during the initial survey of a number of potential sites, at this time permanent plots had not been established and piezometers had not been installed. Therefore surface water depths, and depths to ground water are not available for this time.

4.3.3 Soil salinities

To determine soil salinities three soil cores were obtained using hand augers within stands of each vegetation type at each site. Two depth intervals were sampled, 0-15 cm and 15-30 cm. Soil samples were collected in glass jars and sealed with electrical tape to prevent water loss. Soils samples were weighed before and after drying at 105°C to determine gravimetric water content. Dried samples were ground with a mortar and pestle and passed through a 2 mm sieve. Soil conductivities were measured on extracts of 1 part soil to five parts deionised water after two hours of shaking. The salinities of soils in the field were calculated from soil moisture contents and conductivities of 1:5 extracts.

4.3.4 Root profiles

To determine the vertical distribution of roots within these zones three root samples were taken from each vegetation type at each site, at both 0-15 cm and 15-30 cm depths. A single root replicate consisted of two soil cores taken proximal to shoots. Soil was washed from roots cores using a high pressure hose and a 1 mm mesh sieve. Roots were separated from organic debris and the roots of other species, dried at 70°C and weighed. It was not possible however to separate fine roots from fine debris. The fine root mass was therefore qualitatively assessed on a scale of 1 to 3, with 1 indicating a minimal fine root mass, 2 moderate and 3 large. However, the qualitative assessment of fine roots did not differ from root biomass; with a large root biomass being associated with a large quantity of fine roots.

4.3.5 Leaf area indices (LAIs) and leaf area duration (LAD)

A non-destructive means of determining the leaf area index was developed to permit repeated sampling within established plots over the duration of the study. For *T. domingensis* a relationship between shoot basal diameter and leaf area was established from plants harvested adjacent to each site. The leaf area of each shoot was measured by removing the leaves and passing them through a leaf area meter (Delta T). Leaf area measurements were carried out on live leaves in which senescent sections had been removed. A leaf was classified as living if more than 50% of its length was green.

To asses if the relationship between leaf area and basal diameter (BD) changed over time, measurements were obtained at each sampling period until April '97. The relationship did not alter over time, and the data from each collection period was therefore pooled. The relationship did however differ between the TB3 site and the saline sites (ie TB18 and T15). Consequently, regressions were determined separately for the TB3 and saline sites.

A regression predicting the leaf area of *T. domingensis* shoots from either the TB18 or T15 sites was determined by pooling the data from these two sites. For the TB3 site a regression was derived using data from the TB3 site, and data from shoots at the saline sites in which the basal diameter was less than 2 cm. This was done as few shoots collected from the TB3 site had basal diameters less than 2 cm, resulting in insufficient data points in this region. It is apparent from the relationships (Fig. 4.2a) that differences between the TB3 and saline sites would be lost when basal diameters are less the 2 cm, as such the approach taken would seem justified. The relationship between leaf area and basal diameter for the TB3 and saline sites are described by equations 4.1 and 4.2, respectively.

$$\text{Leaf area } (cm^2)\ shoot^{-1} = 1.62 + 107\ (BD^2)\ (r^2=.89,\ df_{1,\ 89},\ P<.001) \quad (4.1)$$

$$\text{Leaf area } (cm^2)\ shoot^{-1} = 11.9 + 65\ (BD^2)\ (r^2=.87,\ df_{1,\ 65},\ P<.001) \quad (4.2)$$

For *B. arthrophylla* a relationship between stem height (H) and stem area was established (Fig. 4.2b). The area of a stem was calculated using the formula for the surface area of an elliptical cone (equation 3.4, section 3.2.6). The calculated surface area was divided by two to obtained a one sided leaf area. As the relationship between stem height and stem area, did not differ, either between sites or over time, the entire data set was used in deriving the relationship. The relationship is described by equation 4.3.

$$\text{Stem area } (cm^2) = 2.88 + .0034\ (H^2)\ (r^2=.79,\ df_{1,\ 667}\ P<.0001) \quad (4.3)$$

To calculate the LAI for each species at each site the basal diameter of every *T. domingensis* shoot, and the height of every *B. arthrophylla* stem was measured within a number of

quadrats (25 cm x 25 cm). The appropriate equations were then applied to derive the area of each shoot or stem within a quadrat. These were then summed and divided by the quadrat area to obtain the LAI of a single quadrat.

During the initial survey of sites in September '96 quadrats were placed only where vegetation was present, as such non-vegetated areas were not accounted for, and the data therefore represent maximum rather than average LAIs of each plot. The sampling approach was subsequently changed to obtain an unbiased estimate of the LAI of each plot. This was achieved by placing quadrats at either 3, 6 or 9 m into a plot at a number of evenly spaced points along its length.

Large variability in LAIs between replicate quadrats was found at the TB3 site. This was incurred as the size of the quadrat chosen resulted in some quadrats having *T. domingensis* absent, and others having many large shoots. To resolve some of this variance data from two successively sampled quadrats were combined, effectively increasing the quadrat size. This was carried out for both species at all sites after the September '96 sampling period. Insufficient quadrats were sampled in September '96 to combine quadrats.

Leaf area duration (LAD) is the LAI integrated over time and is derived from equation 4.4 (Harper 1977).

$$LAD = \tfrac{1}{2}(LAI_n + LAI_{n+1})(t_{n+1} - t_n) \qquad (4.4)$$

where LAI_n is the LAI at time n, LAI_{n+1} is the LAI at a subsequent time, and $(t_{n+1} - t_n)$ is the time interval (days) between estimates of LAI. The LAD was calculated for each sampling interval and summed to derive the LAD over the entire sampling period.

4.3.6 Leaf gas exchange characteristics

The conductance of leaves/stems to water vapour, and rates of photosynthesis were determined for each species at each site using a closed-system infrared gas analyser (IRGA,

Li6200, LiCor, NE, USA). At each site 6-8 readings were obtained on leaves of *T. domingensis* and stems of *B. arthrophylla*, at approximately two hourly intervals throughout the day in February '97 and March '97, and less frequently in April '97. Due to logistical reasons measurements were taken at each site on different days.

Boundary layer conductance was measured with filter paper replicas approximating the variety of leaf dimensions which would be enclosed in the chamber. The boundary layer conductance of leaves or stems between 0.5 and 1 cm wide was 2.9 mol m^{-2} s^{-1} whilst those with widths between 1 to 2 cm was 1.9 mol m^{-2} s^{-1}. Abtew *et al.* (1995) using a similar Licor system and chamber obtained a value of 2.26 mol m^{-2} s^{-1} for *T. domingensis*. As the width of healthy leaves of this species lie between 1-2 cm values are comparable. Appropriate boundary layer conductance for each measurement was used by the Licor program to derive stomatal conductance values.

Stomatal conductance has been demonstrated to vary both between leaves and along the length of single leaves in *T. domingensis* (Abtew *et al.* 1995). Abtew *et al.* (1995) found the mean conductance of a *T. domingensis* shoot to be represented by readings taken on either the apical aspect of outer leaves, or the basal section of the second leaf. To derive mean canopy resistance values for computation of the Penman-Monteith equation, measurements were obtained on the apical region of healthy outer leaves of *T. domingensis* Additional readings were obtained on the apical aspect of the inner most mature leaf to assess maximum photosynthetic rates under different conditions, and to assess variation with leaf age.

Readings were taken on the upper third of 3 to 4 randomly selected green stems of *B. arthrophylla*. Stems were carefully sealed within the chamber to avoid tissue damage. To ensure no leakage occurred around protruding stems, readings were restricted to the upper third of the stem where stem diameters were smaller. In addition blu tack® was used around the gasket to facilitate a seal. This approach was checked by breathing around the sealed chamber and observing for an increase in CO_2 concentration.

4.3.7 Carbon isotope discrimination

Whole stems of *B. arthrophylla* and young fully expanded leaves of *T. domingensis* were collected in December '96 and March '97 from each site for carbon isotope determination. Leaf samples were washed in deionised water and wiped dry to remove any debris. Leaves of *T. domingensis* were divided into thirds to identify if carbon isotope discrimination differed along their length (Appendix A). All samples were dried at c. 70°C until a constant weight. Carbon isotope determination were carried out as previously described (2.2.8).

4.3.8 Estimates of evapotranspiration using the Penman-Monteith equation.

Whilst a number of alternative methods of deriving rates of evapotranspiration exist, the Penman-Monteith equation was considered the most appropriate for both logistic and economic reasons, but also because it permits the mechanisms driving differences in evapotranspiration to be identified. In addition, this approach had already been applied to stands of *T. domingensis* and validated against a large scale lysimeters (Abtew *et al.* 1995; Abtew and Obeysekera 1995).

The Penman-Monteith equation is a mathematical model based on meteorological variables, physical processes and plant resistance factors, which predicts water loss from vegetated surfaces. The equation evolved from the work of Penman, who in 1948 developed a model, based on meteorological variables and physical processes, to calculate evaporation from a free water surface, or from well watered crops which completely covered the soil. The Penman equation however did not account for vegetation parameters which may alter water loss. Monteith in 1965 addressed this by incorporating stomatal and boundary layer resistances into this model forming the Penman-Monteith Equation.

The Penman-Monteith equation (4.5) is now regarded as the most developed model of evaporation, and its accuracy in predicting water loss from closed canopies has been extensively validated (Allen *et al.* 1989). The equation however assumes that all radiation available for evaporation is accessible to the plant canopy, and is therefore only directly applicable to closed canopies. For sparse canopies water loss will occur from both the soil

and the vegetation and it therefore necessary to account for losses from each of these components (Fig. 4.3).

Meteorological variables

A weather station (Measurement Engineering) was installed within the wetland (Fig. 4.1) to measure; solar radiation, barometric pressure, air temperature, air humidity and wind speed. A data logger was programmed to scan all variables every 5 seconds and record averages at 15 minute intervals.

The Penman-Monteith equation:

$$\lambda ET_0 = \frac{\Delta\left(R_n - G\right) + \rho c_p \left(e_s - e_a\right)\frac{1}{r_a}}{\Delta + \gamma\left(1 + \frac{r_c}{r_a}\right)} \qquad (4.5)$$

where

λET_0 = latent heat flux of evapotranspiration (MJ m^{-2} s^{-1})

Rn = net radiation flux at surface (MJ m^{-2} s^{-1})

G = soil heat flux (MJ m^{-2} s^{-1})

ρ = atmospheric density (kg m^{-3})

cp = specific heat of moist air (1.013X10^{-3} MJ kg^{-1} $°C^{-1}$)

e_s = saturation vapour pressure (kPa)

e_a = water vapour pressure of air (kPa)

r_c = canopy resistance (s m^{-1})

Δ = slope of vapour pressure curve (kPa $°C^{-1}$)

γ = the psychometric constant (kPa $°C^{-1}$)

λ = latent heat of vaporisation of water (MJ kg^{-1})

r_a = aerodynamic resistance (s m^{-1})

Atmospheric density (ρ), the slope of the vapour pressure curve (Δ), the saturation vapour pressure (e_S), the latent heat of vaporisation of water (λ) and the psychometric constant (γ) were derived from the following formulae (Smith *et al.* 1991; Shuttleworth 1993).

$$\rho = 3.486 \times \left(\frac{P}{275 + T} \right) \tag{4.6}$$

$$\Delta = \frac{4098 e_s}{(273.3 + T)^2} \tag{4.7}$$

$$e_s = 0.61078 \exp\left(\frac{17.269T}{237.16 + T} \right) \tag{4.8}$$

$$\lambda = 2.501 - (.0024T) \tag{4.9}$$

$$\gamma = 0.001628 \times \left(\frac{P}{\lambda} \right) \tag{4.10}$$

$$e_a = \left(\frac{RH}{100} \right) \times e_s \tag{4.11}$$

where T is air temperature in °C, P is atmospheric pressure in kPa and RH is relative humidity. The daily soil heat flux is considered to be negligible and can normally be neglected (Smith *et al.* 1991).

Net radiation

The net radiation (MJ m^{-2} s^{-1}) received by a surface is the net flux of both shortwave (.3-3.0 μm) and longwave (3-100 μm) radiation (Shuttleworth 1993) (equation 4.12).

$$Rnet = Rsnet + Rlnet \tag{4.12}$$

where Rnet is net radiation, Rsnet is net shortwave radiation and Rlnet is net longwave radiation.

Net shortwave radiation

Net shortwave radiation (MJ m^{-2} s^{-1}) received by a surface is the total shortwave radiation incident at the surface, minus that portion which is reflected by the surface (Equation 4.13).

$$Rsnet = Rs(1-\alpha) \quad (4.13)$$

where Rsnet is net shortwave radiation (MJ m^{-2} s^{-1}), Rs is the total shortwave radiation (MJ m^{-2} s^{-1}) and α is the reflection coefficient or albedo of the surface.

The fraction of radiation which is reflected by a surface is termed the reflection coefficient or albedo. The albedo differs for soil, water and types of vegetation. An albedo of 0.17 determined by Abtew and Obeysekera (1995) for *T. domingensis* was used for both vegetation types. The albedo for open water is .08 (Shuttleworth 1993) (Fig. 4.3).

Net long-wave radiation

Net long-wave radiation (MJ m^{-2} s^{-1}) is the net exchange of longwave radiation emitted by the sky and the ground/vegetation. It is derived by subtracting the outward longwave radiant flux (L_o) emitted by the surface (ground/vegetation) from the incoming longwave radiation flux (L_i) emitted by the sky (Equation 4.14). In most instances ground temperature is higher than atmospheric and there is a net loss of thermal radiation from the ground (Shuttleworth 1993).

$$L_n = (L_i - L_o) \quad (4.14)$$

where L_n is net longwave radiation (MJ m^{-2} s^{-1}), L_i in incoming longwave radiation and L_o is outward longwave radiation.

Net long-wave radiation (L_n) was estimated from equation 4.15 (Shuttleworth 1993)

$$Ln = - f\varepsilon' \sigma (T + 273.2)^4 \quad (4.15)$$

Where f is adjustment for cloud cover, ε' is the net emissivity between the atmosphere and the ground, σ is the Stefan-Boltzmann constant (5.67 x 10^{-8} W m^{-2} K^{-4}), and T_a is the air temperature (K). No adjustment for cloud cover was made in this study. Net emissivity (ε')was derived using equation 4.16.

$$\varepsilon' = 0.261\exp(-7.77 \times 10^{-4}T^2) - .02 \qquad (4.16)$$

where T is air temperature in °C

Canopy and Aerodynamic Resistance

Canopy resistance (r_c) is the average daily bulk stomatal resistance (s m^{-1}), determined by the resistance offered by stomata to water loss and the leaf area index. (equation 4.17; Allen *et al.* 1989).

$$r_c = \frac{r_l}{0.5LAI} \qquad (4.17)$$

where r_l is the average minimum day time stomatal resistance of a single leaf (s m^{-1}) and LAI is the leaf area index (m^2 m^{-2}). The factor 0.5 has been suggested as a correction factor to account for the leaf area which is fully active in transpiration (Allen *et al.* 1989). However, in this study the method of Abtew *et al.* (1995) was followed and a correction factor of 0.5 was not used since leaf/stem stomatal resistance measurement were considered to represent an average (rather than a minimum) for each vegetation type.

Canopy aerodynamic resistance(r_a) reflects the extent to which air above the canopy is mixed, and hence the transference of water vapour from the plant to the atmosphere. Aerodynamic resistance of a canopy is principally a function of wind speed and plant height. Estimates of aerodynamic resistance were calculated from equation 4.18 (Abtew *et al.* 1995).

$$r_a = \frac{\ln\left(\frac{Z-d}{Z_o}\right)\ln\left(\frac{Z_h-d}{Z_{oh}}\right)}{k^2 x U_z} \quad (4.18)$$

where

r_a = aerodynamic resistance (s m^{-1})

Z = wind speed measurement height (m)

Z_o = aerodynamic roughness (m)

Z_{oh} = air temperature and humidity measurement height (m)

d = zero displacement height (m)

K = von Karman constant for turbulent diffusion (0.41)

U_z = wind speed (m s^{-1}) at height Z over site .

Displacement height (d) and aerodynamic roughness (Z_O) were estimated using equations 4.19 and 4.20 (Abtew and Obeysekera 1995).

$$d = .85F_cH \quad (4.19)$$

where d is the zero displacement height (m), F_c is the fraction of ground covered by vegetation and H is vegetation height (m).

$$Z_o = .13(H\text{-}d) \quad (4.20)$$

Where Z_o is the aerodynamic roughness (m), H is the average vegetation height (m) and d is the zero displacement height (m).

Partitioning water losses between vegetation and underlying soil or water

In a stand of vegetation water is lost (E) both from the canopy (E_C) through stomata and from the ground/water body below the canopy (E_W) (Fig. 4.3). In a closed canopy where little or no radiation reaches the ground, water loss may be entirely attributed to the vegetation.

However, as the penetration of radiation to the ground increases, water loss from the ground/waterbody will constitute a greater portion of the total loss.

The approach taken here has been to partition water loss from a vegetated stand, between that lost from the vegetation itself (E_C), and that lost from the underlying waterbody or soil surface(E_W) . The sum of these losses being the total loss from the stand (E_{total}) (Fig. 4.3). By comparing total losses from vegetated stands to those which may occur from an open water body (E_O) the influence of vegetation on water fluxes may be better understood (Fig. 4.3).

The major factors altering water losses from vegetation, water surfaces or soil surfaces are; net radiation, albedo, aerodynamic resistance and canopy resistance (Fig. 4.3). The amount of radiation received by leaves within a canopy varies according to the position of leaves within the canopy, the orientation of leaves and the structure of the canopy. Generally radiation received by different horizontal layers in a canopy declines exponentially with depth in a manner predicted by Beer's Law (Monsi and Saeki 1953). The amount of radiation intercepted by the canopy is described by equation 4.21 and is based on the model of Monsi and Saeki (1953). The remaining radiation will be received by the ground or waterbody below the canopy (equation 4.22).

$$Rnet_{canopy} = Rs(1-\alpha)(1-e^{(-\mathcal{K}LAI)})+Rlnet(1-e^{(-\mathcal{K}LAI)}) \qquad (4.21)$$

$$Rnet_{water/soil} = Rs(1-\alpha)(e^{(-\mathcal{K}LAI)})+Rlnet(e^{(-\mathcal{K}LAI)}) \qquad (4.22)$$

where $Rnet_{canopy}$ and $Rnet_{water/soil}$ are the net radiation (MJ m^{-2} s^{-1}) intercepted by the canopy and water/soil below the canopy, respectively. $\mathcal{K}$ is the extinction coefficient of the vegetation and LAI is the leaf area index. An extinction coefficient of 0.6 was used.

Aerodynamic resistance of a free water surface (R_{aw}) was estimated from equation 4.23 (Shuttleworth 1993).

$$R_{aw} = \frac{4.72\left(\ln\left(Z_m / Z_o\right)\right)}{1+.536U_2} \qquad (4.23)$$

where R_{aw} is the aerodynamic resistance of a free water surface, Z_m is the height (m) at which meteorological variables were measured and Z_o is the aerodynamic roughness (m). For a free water surface Z_o is given as .00137 (Shuttleworth 1993). The canopy resistance term is obsolete is calculating evaporation from water or soil.

The water surface from which evaporation can take place below the canopy, may be reduced by the area occupied by plant stems. To account for this mean stem/shoot densities and basal diameters for each species at each site was used to calculate the water surface area occupied by plant stems. As the area occupied by stems/shoots was less than 5% water loss below the canopy was considered to occur from the entire water surface.

4.3.9 Statistical analysis

Data analysis was carried the out using the statistical software package JMP® (Version 3). A single ANOVA was used to analyse all data unless stated otherwise. Heteroscedasticity was determined using O'Brians test. Non-homogeneous data was transformed where possible or analysed using a Kruskal-Wallis non-parametric test. Tukey-kramer pairwise comparisons were performed on homogeneous or transformed data to identify which group means were significantly different at an alpha value of 0.05. For data in which heteroscedasticity could not be resolved a Tukey-type non-parametric multiple comparison was performed to identify group means which were significantly different (Zar 1984). The specific statistical treatment of the different data sets are described.

Soil

In both January and April '97 a log transformation ($\log_{10}(x+1)$) was required to resolve heteroscedasticity and a single ANOVA performed. Although this approach in analysis has been taken it is acknowledged that the two soil depths (0-15 cm and 15-30 cm) are not independent of each other, being partitioned from the same soil core. As such, the results

should be viewed with some caution. As sampling was repeated over time it was felt that the collection of extra cores to achieve independent samples would have been too destructive.

LAI

A square root transformation was performed on data obtained in December '96 to resolve heteroscedasticity. In April '97, heteroscedasticity could not be resolved, and the data was analysed using a Kruskal-Wallis non-parametric test, and differences between group means were identified using a Tukey-type non-parametric multiple comparison.

Morphology

Log transformation (log 10 (x+1)) was required to resolve heteroscedasticity in leaf width data in March and April '97. Heteroscedasticity was unresolvable for the number of leaves shoot^{-1} in both January and March '97. A Welch ANOVA was therefore used. Pairwise comparisons were made using a Tukey-kramer test at increased alpha value of .01.

4.4 Results

4.4.1 Salinity

4.4.1.1 Surface water

Surface water conductivities were less than 1.5 dS m^{-1} at both the TB3 and TB18 sites in September '96 (Table 4.1) when water levels were at their peak. By March '97 surface water was only present in patches at the basin of both the TB3 and TB18 sites, sediments however remained fully saturated with water. The salinity of the residual surface water at these sites had more than doubled exceeding 4 dS m^{-1}. In April '97 the salinity measured in a small pool of water at the TB18 site was c.7 dS m^{-1} representing a further substantial increase. Surface water conductivities were highest at the T15 site with a conductivity of 10 dS m^{-1} being recorded in December '96 at peak water level. By January '97 surface water had evaporated, however a surface water salinity of 18 dS m^{-1} was measured following rainfall.

4.4.1.2 Ground water

Ground water salinities (Table 4.1) were lowest at the TB3 site ranging from 2.9-3.6 dS m^{-1} over the study period, and were highest at the TB18 site ranging from 15.1-18.4 dS m^{-1}. Ground water salinities at the T15 site varied between 10.2 and 15 dS m^{-1}. Variation in ground water salinity over the duration of the study was marginal at the TB3 site (.6 dS m^{-1}), but considerable at both the TB18 (3.4 dS m^{-1}) and T15 sites (6.3 dS m^{-1}). Peaks in ground water salinities occurred in September and December '96 at the saline sites, declining to a stable level by March '97. The decline in ground water salinity may be attributed to the recharge of ground water with fresh surface water.

At the TB18 and TB3 sites the depth of surface water within plots approximated the depth to ground water (Table 4.1), and regressions between surface water and ground water depth produced correlation coefficients of 0.99. Consequently, ground water and surface water at these sites were not spatially separated, with surface water representing a continuum of the ground water. At the TB18 site ground water salinities were high (18-15 dS m^{-1}) whilst surface water salinities were low (1.2-6.9 dS m^{-1}). Therefore, whilst surface water and ground water were not spatially separate at the TB18 site, there was a distinct separation of ground water and surface water in terms of salinity. A permanent piezometer was not installed at the T15 site until January '97 by which time no surface water remained. Because of this conclusions regarding the connection between surface water and ground water was not possible at this site. However, the unsaturated nature of the soils (Table 4.2) throughout the period of study suggest that the ground water and surface water may have been spatially separated (Table 4.2).

Within piezometers the water level fell by c. 60 cm at both the TB18 and TB3 sites over a period of c. 20 weeks, between December '96 and April '97 (Table 4.1). As the exit gates of Bool Lagoon were closed throughout this time, and considering low ground water flows in this region (.001-.01 m day^{-1}), the loss of water can be attributed purely to evapotranspiration. Fifty percent of the drop in ground water occurred over six weeks, between measurements

made in December '96 and January '97. These months therefore represent a period of high evaporative demand.

4.4.1.3 Soil

As the depth to ground water remained shallow throughout the study period (Table 4.1) it had the capacity to directly or indirectly influence soil salinities. The influence of ground water on soil water salinity was evaluated for two depth classes; 0-15 cm and 15-30 cm, at each site over the study period (Table 4.2). Soil water salinities were derived from soil moisture contents and conductivities of 1:5 extracts. As the conductivities of 1:5 extracts are standardised in terms of soil water content they reflect the salt load held in the soil. As such they provide insight into the movement of salt in the system. Conductivities of the soil water however represent in situ salinities which are influenced by both the soil water content, and the salt load of the soil.

In September '96 and December '96, soil water conductivities of the 0-15 cm profile was c. 6 dS m^{-1}, at both the TB3 and TB18 sites (Table 4.2). At the TB3 site, conductivities did not differ significantly with depth at either of these sampling periods. At the TB18 site however, the conductivity of the 15-30 cm profile (13.6 dS m^{-1} and 10.7 dS m^{-1} in September and December '96, respectively), was significantly greater than the 0-15 cm profile, and was also greater than either profile at the TB3 site. After this time soil water conductivities did not differ significantly with soil depth, at either the TB3 or TB18 sites, or between these sites.

Lower conductivities of the 0-15 cm profile at both the TB18 and TB3 sites, compared to the 15-30 cm profile at the TB18 site, can be attributed to a combination of lower salt loads and to higher water contents. The higher conductivity of the 15-30 cm profile at the TB18 site, compared to the same profile at the TB3 site, appears to be due to a higher salt load, since 1:5 extracts were considerably higher, whilst soil water contents were similar.

Soil water conductivities of the 0-15 cm depth class, at both the TB3 and TB18 sites (c. 6 dS m^{-1}), remained stable between September '96 and January '97, after which conductivities

began to increase. The total increase in salinity, between September '96 and April '97, was c.6 dS m^{-1} and 8 dS m^{-1} at the TB3 and TB18 sites, respectively. A similar increase can also be found in surface water salinities, with an increase of c. 6 dS m^{-1} over this same period at the TB18 site. As such, increases in soil water salinity may have arisen from the evaporation of surface water concentrating dissolved salts already present in the surface water .

Soil water conductivities of the 15-30 cm depth profile, at the TB18 site, peaked at c. 13.5 dS m^{-1} in September '96, and again in April '97. Between this time the conductivity declined to 9.3 dS m^{-1} in March. The fall in conductivities may be due to salt contained in this profile reaching some level of equilibrium with fresh surface water. Alternatively it may be associated with falling water levels. As the water level falls the soil profile previously in direct contact with saline ground water may freshen as fresh surface water is drawn down into this zone. The relief however appears to be transient, with soil water salinities increasing once more in March '97. Again this may reflect the impact of surface water evaporation.

Soil water salinities were always significantly greater at the T15 site, compared to the TB3 or TB18 sites, regardless of depth class. This resulted predominantly from higher salt loads but also due to lower water contents. Soil water conductivities were not significantly different between depth classes at the T15 site until March '97, when the conductivity of the 0-15 cm profile (56 dS m^{-1}) doubled that of the 15-30 cm profile (23 dS m^{-1}). Conductivities of the 15-30 cm profile also increased over time but more slowly than the 0-15 cm profile. Increases in soil conductivities over time at this site, arose from an increase in the salt load, and from a decline in soil water content for the 0-15 cm profile. Water content did not appear to contribute to salinity increases over time in the 15-30 cm profile . As surface water was absent after January '97, and soils become drier at this site, the capillary rise of saline ground water to the surface sediments would have contributed to the increased salt load observed between March and April '97.

4.4.2 Plant responses

4.4.2.1 Root profiles

At the TB3 and TB18 sites, the root biomass of both species was greatest in the 0-15 cm profile, representing 70-80% of the total root biomass between 0-30 cm (Table 4.3). Root biomass did not differ significantly between the TB3 and TB18 sites, at either depth class for either species. At the T15 site the root biomass of *T. domingensis* in the 0-15 cm profile was less than half that recorded at either the TB3 or TB18 sites. However, the biomass of the 15-30 cm profile did not differ significantly between sites. Consequently, the distribution of roots at the T15 site was shifted towards the deeper profile, and root biomass did not differ significantly with soil depth. Both higher soil moisture contents, and lower conductivities of the 15-30 cm soil profile, are likely to be driving the shift in rooting depth at the T15 site. The root biomass of *T. domingensis* was c. two times greater than *B. arthrophylla* at both sites.

The root profile data indicate that roots were present in the two soil profiles examined. Soil water conductivities of either of these profiles may potentially influence plant performance. As the majority of roots were located in the 0-15 cm zone, it is possible that roots in the 15-30 cm profile may not strongly influence plant performance, however it is not possible to evaluate the functional importance of roots based on biomass.

4.4.2.2 Leaf area indices

Comparisons between sites

At the TB3 site, the leaf area index (LAI) of *T. domingensis* increased rapidly from less than 1 in September '96 to a peak of 5.9 in January '97, and declined as rapidly to 1 in April '97 (Table 4.4, Fig. 4.4). At the TB18 site, the LAI of *T. domingensis* did not increase substantially until January '96, when soil salinities had fallen to those recorded at the TB3 site. A peak LAI of 2 was reached by March '97, which then declined rapidly to less than 0.5 in April '97. At the T15 site, the LAI was very low throughout the study, reaching a peak in March '97 of 0.5, and declined to almost zero by April '97. LAIs of *T. domingensis* at the TB18 and T15 sites peaked two months later, and were significantly lower in December '96,

January '96 and March '97, compared to the TB3 site. Differences in the LAI of *T. domingensis* at the TB18 and T15 sites were not statistically significant.

At both the TB3 and TB18 sites, LAIs for *B. arthrophylla* increased slowly over time, reaching a peak over January and March '97 of c. 3 and 1.4, respectively before declining slightly in April '97 (Table 4.4, Fig. 4.4). The LAI of *B. arthrophylla* at the TB18 site, was significantly less than the TB3 site in March '97 and April '97.

Comparisons between Species

Changes in LAIs over time (Table 4.4, Fig. 4.4) illustrate that the growth season for *T. domingensis* extended from the end of September '96, when shoots began to emerge, to the end April '97, when dieback was almost complete, a period of c. 7 months. In contrast, *B. arthrophylla* is able to maintain a viable aboveground biomass over winter. The higher LAI of *B. arthrophylla* compared to *T. domingensis*, in both September '96 and April '97, reflect this.

Comparisons between *B. arthrophylla* and *T. domingensis* at the TB3 site, indicate that the LAI of *T. domingensis* was significantly greater than *B. arthrophylla*, in December '96 and January '97, comparable to *B. arthrophylla* in March '97, and significantly less than *B. arthrophylla* in September '96 and April '97, when *T. domingensis* was emerging from or receding into winter dormancy (Table 4.4). The lower maximal LAI of *B. arthrophylla* compared to *T. domingensis* at the TB3 site, is compensated in part by its capacity to retain a viable LAI over a longer time. Whilst the LAI of both species was lower at the TB18 site compared to the TB3 site, the reduction was greater in *T. domingensis* than in *B. arthrophylla,* hence difference in LAIs present under more optimal conditions at the TB3 site were absent.

Growth Period

The active growth period can be assessed from the period over which LAI increase. Whilst interpretation is less clear, as September values represent maximal LAI rather than averages for the sites, it is evident that the duration of growth did not differ substantially between

species (Table 4.4, Fig. 4.4). At the TB3 site, growth in *T. domingensis* was initiated earlier but also ceased earlier than in *B. arthrophylla*. At the more saline sites, the initiation of growth was delayed in *T. domingensis*, and growth patterns followed that of *B. arthrophylla*.

4.4.2.3 Leaf area duration

LAD calculated over the study period (220 days) was greatest at the TB3 site, intermediate at the TB18 site, and lowest at the T15 site (Table 4.5). Over the study period, the LAD of *T. domingensis* was considerably greater than *B. arthrophylla* at the TB3 site, but was slightly less at the TB18 site. The results of the study represent the LAD of *T. domingensis* on an annual basis, since measurements extended from the emergence of new shoots in September '96 to almost complete senescence in April '97. However, the LAI of *B. arthrophylla* extends throughout the year. To obtain estimates of annual LAD for *B. arthrophylla*, it was assumed that the LAI would decline over winter to values recorded in September '96, at the same rate at which increases were observed. If this prediction is correct, and it may be considered an underestimate, then on an annual basis the LAD of *B. arthrophylla* will be comparable to *T. domingensis* at the TB3 site, and considerably exceed *T. domingensis* at the TB18 site.

4.4.2.4. T. domingensis shoot density

Changes in LAIs can be mediated via changes in shoot density, or via changes in the morphological characteristics of individual shoots. The number of *T. domingensis* shoots (Table 4.6) increased from 27 m^{-2}, in December '96 at all sites, to peaks of 35, 58 and 42 m^{-2} at the TB3, TB18 and T15 sites, respectively. Peak shoot densities coincided with peaks in LAIs, occurring 2 months later at both the TB18 and T15 sites. Although there is a distinct trend towards higher shoot densities at the saline sites, differences were not statistically significant. In April '97, the almost complete senescence of shoots at the T15 site, resulted in shoot densities being significantly lower than either the TB3 or TB18 sites.

4.4.2.5. T. domingensis shoot morphology

Maximum shoot height and leaf width were reached by December '96 at all sites, and remained relatively stable until April '97, when shoot senescence resulted in a decline in shoot height at all sites (Table 4.6). Maximum shoot height was c. 2 m at the TB3 site, and c.1 m at both the TB18 and T15 sites, respectively. Leaf width at the TB3 site (c.1.6 cm) was twice that measured at either the TB18 or T15 sites. Differences in shoot height and leaf width, between the TB3 site and both the TB18 and T15 sites, were significant at each sampling period. These parameters did not however differ significantly between the TB18 and T15 sites.

The average number of leaves shoot^{-1} varied over time and between sites (Table 4.6). The maximum number of leaves per shoot at each site were 7, 6 and 5 at the TB3, TB18 and T15 sites, respectively. At the TB3 site, the greatest number of leaves shoot^{-1} occurred over December '96 and January '97, whilst at the TB18 site peaks occurred over January '96 and March '97. The delay in leaf production at the TB18 site, resulted in the number of leaves per shoot being significantly greater at the TB3 site compared to the TB18 site, in September '96 and December '96. After this time the number of leaves per shoot did not differ significantly between these two sites. At the T15 site, the number of leaves per shoot was greatest in September '96 and December '97, declining slowly thereafter. The number of leaves per shoot at the T15 site was significantly less than the TB18 site, in January '97 and March '97, and significantly less than the TB3 site, at all sampling periods excluding April '97.

Whilst seasonal changes in LAIs are reflected in changes in shoot density, differences in LAIs between sites are governed by changes in the morphology of individual shoots. High LAIs at the TB3 site were associated with leaves which were both longer and wider than those at the TB18 or T15 sites. The number of leaves per shoot did not appear to contribute to differences in LAIs between the TB3 and TB18 site. The number of leaves per shoot were however associated with lower LAIs at the T15 site.

4.4.2.6. B. arthrophylla stem density

The mean density of *B. arthrophylla* stems (Table 4.6) increased between December '96 and January '97, from 954 to 1286 m^{-2} at the TB3 site, and from 617 to 957 m^{-2} at the TB18 site. Stem densities remained relatively constant at the TB3 site for the remainder of the study, but declined slowly thereafter at the TB18 site to 635 m^{-2} in April '97. Standard deviations at the TB18 site were twice that of the TB3 site and reflect the patchiness of the stand at this site. Although stem densities were always greater at the TB3 site compared to the TB18 site, differences were not statistically significant between these sites until April '97, when stem densities at the TB18 site had declined.

4.4.2.7. B. arthrophylla stem height

At both sites the mean height of stems doubled between September '96 and March '97, from 42 cm to 81 cm at the TB3 site, and from 31 to 65 cm at the TB18 site (Table 4.6). By April '97 the mean stem height had declined by 10 cm at both sites. Stem height at the TB3 site was significantly greater than at the TB18 site at all sampling periods. Seasonal changes in LAIs in *B. arthrophylla*, and differences between sites, were determined by both stem density and stem height.

4.4.2.8 Leaf gas exchange characteristics

4.4.2.8.1 Stomatal Conductance (g_S)

Whilst the LAI is a major factor determining canopy water loss, the influence of the LAI will be modified by stomatal conductance (g_S). Stomatal conductance (g_S) is reported in molar units, as most physiological studies use these units. To facilitate comparisons with the literature on evapotranspiration, in which units of r_S are commonly used, stomatal r_S are also provided (Appendix A).

Comparisons across sites

In February '97, between 1000 and 1600 hrs, stomatal conductance (g_S) measured on outer *T. domingensis* leaves, was highest at the TB18 site (770-500 mmol m^{-2} s^{-1}), followed by the TB3 site (400-300 mmol m^{-2} s^{-1}), and lowest at the T15 site (260-180 mmol m^{-2} s^{-1}) (Fig.4.5).

In *B. arthrophylla* g_S was also higher at the TB18 (1150-560 mmol m^{-2} s^{-1}) site compared to the TB3 site (670-350 mmol m^{-2} s^{-1}) (Fig. 4.5).

Stomatal conductance recorded in March '97 decreased in both species at the TB18 site, but did not differ at the TB3 or T15 sites to those recorded in February '97. Despite lower g_S at the TB18 site, g_S in *T. domingensis* remained higher compared to the TB3 or T15 sites. By April '97, g_S in *T. domingensis* had declined to c.200 mmol m^{-2} s^{-1} at both the TB3 and TB18 sites. In *B. arthrophylla* g_S did not differ between sites in March '97 or April '97.

Comparisons between species

Stomatal conductance was generally similar between species (Fig. 4.5). Differences between *T. domingensis* and *B. arthrophylla* were only observed in the morning and around 1700 hrs prior to April '97, when g_S was higher in *B. arthrophylla*. In April '97, g_S in *T. domingensis* decreased substantially, and g_S was generally higher in *B. arthrophylla*.

Diurnal patterns

In February '97 and March '97 at both the TB3 and TB18 sites g_S in both species varied depending on the time of day that measurements were taken (Fig. 4.5). Values of g_S were higher in the morning and declined throughout the day. In *B. arthrophylla*, g_S tended to increase again slightly after 1600. At the T15 site where g_S was lowest, diurnal changes were absent. In contrast, at the TB18 site where g_S was high, diurnal variation in g_S was greatest.

Comparisons between inner and outer leaves in T. domingensis.

In *T. domingensis* g_S varied between inner and outer leaves (Fig. 4.5). In February '97, inner leaves were c. 50% and 25% higher than outer leaves at the TB18 and TB3 sites, respectively. In March '97, differences between inner and outer leaves at the TB3 site were no longer distinguishable, as g_S of inner leaves had decreased. At the TB18 site differences between inner and outer leaves, although smaller persisted in March '97, but were absent by April '97. At the T15 site differences between inner and outer leaves were not evident at any sampling time.

For *T. domingensis* g_S varied over time, both throughout the day and between sampling periods. Stomatal conductance in *T. domingensis* also varied between leaves and between sites. At the T15 site where salinities were high g_S was lowest throughout the study. At both the TB18 and TB3 sites g_S declined to those values measured at the T15 site in April '97 when dieback was pronounced. Associated with low g_S, both in response to salinity, and with shoot senescence, was loss of variability in g_S between leaves and over the day. In contrast, where g_S was high considerable variability existed between leaves and over the day. Whilst g_S in *B. arthrophylla* varied over the day, it varied less between sampling periods, declining only a small amount in April '97.

4.4.2.8.2 Photosynthesis

LAIs indicate that the productivity of both *T. domingensis* and *B. arthrophylla* were reduced at the TB18 and T15 sites compared to the TB3 site (Fig. 4.4). Impaired CO_2 assimilation, due to either stomatal closure, or to damage of the photosynthetic apparatus may explain these differences. Lower LAIs in *B. arthrophylla* compared to *T. domingensis* may arise from differences in photosynthetic capacity, respiration rates, or carbon allocation patterns.

In *T. domingensis*, rates of photosynthesis between 1000 and 1600 hrs in February '97, were highest at the TB18 site (23-20 μmol CO_2 m^{-2} s^{-1}), followed by the TB3 site (18-15 μmol CO_2 m^{-2} s^{-1}) and lowest at the T15 site (13-8 μmol CO_2 m^{-2} s^{-1}) (Fig. 4.6). In *B. arthrophylla* rates of photosynthesis were also higher at the TB18 site (25-20 μmol CO_2 m^{-2} s^{-1}) compared to the TB3 site (18-15 μmol CO_2 m^{-2} s^{-1}) in February '97 (Fig. 4.6). Rates of photosynthesis in March '97 did not alter at the TB3 site for either species, but declined slightly in both at the TB18 site. Consequently, differences in photosynthetic rates were absent between the TB3 and TB18 sites, for both species in March '97. Rates of photosynthesis at the T15 site did not alter in March '97, remaining c. 30% lower than either the TB18 or TB3 sites.

Photosynthesis did not differ substantially between species at either site in February '97 or March '97 (Fig. 4.6). By April '97, rates of photosynthesis declined at both the TB3 and

TB18 sites, ranging from 14-7 μmol CO_2 m^{-2} s^{-1} in *T. domingensis*, and from 18-12 μmol CO_2 m^{-2} s^{-1} in *B. arthrophylla*. At this time rates of photosynthesis tended to higher in *B. arthrophylla* than *T. domingensis*

Differences observed in g_S between inner and outer leaves were also reflected in rates of photosynthesis, with inner leaves demonstrating higher photosynthetic rates than outer leaves (Fig. 4.6). Diurnal changes in photosynthesis were less apparent than diurnal changes in g_S, but crudely followed the same patterns.

Low productivity at the T15 site can be attributed at least in part to lower rates of photosynthesis. Lower LAIs at the TB18 site were not reflected in rates of photosynthesis, being higher than recorded at the TB3 site. As such, factors other than the supply of assimilates must be responsible. Rates of photosynthesis did not differ substantially between species at either site prior to April '97. Consequently, differences in LAIs between species at the TB3 site can also not be explained in terms of photosynthetic capacity, again implicating other factors.

4.4.2.9 Water use efficiency

4.4.2.9.1 Stomatal conductance vs assimilation

The extent to which changes in g_S are coupled to changes in assimilation is often considered to reflect water use efficiency. Where a small change in g_S elicits a large change in assimilation the two variables are tightly coupled and water use efficiency is high.

For both species g_S was only tightly coupled to assimilation when g_S was low. As g_S increased beyond 400-500 mmol m^{-2} s^{-1} the relationship weakened, and increases in assimilation in response to higher g_S were marginal. Consequently, the relationship was best described using a logarithmic equation (Figs. 4.7, 4.8). The relationship implies that water use efficiency would be low at high g_S, since increased water loss at higher g_S yields only a minimal increase in assimilation. Conversely, WUE would be high when g_S is low, as water loss is tightly coupled to assimilation.

As the relationship between g_S and assimilation for each site conform well to the curve produced using the whole data set, it can be proposed that the relationship did not differ between sites. Instead differences between sites and changes over time are reflected in the portion of the curve that values extended over (Figs. 4.7, 4.8).

For *T. domingensis* the steepest portion of the curve was between g_S values of c.100 and 300 mmol m^{-2} s^{-1}. In this region WUE would be greatest. As g_S in *T. domingensis* at the T15 site rarely exceeded 250 mmol m^{-2} s^{-1}, WUE can be considered to be higher at this site compared to the other sites (Fig. 4.7). Values of g_S above 500 mmol m^{-2} s^{-1} were only weakly coupled to photosynthesis yielding a low WUE. This was also found by Jones (1988) in *T. domingensis* with departure from linearity at g_S values in excess of 400 mmol m^{-2} s^{-1}. At the TB18 site, most g_S values exceeded 500 mmol m^{-2} s^{-1} in February '97, indicating lower WUE at this site. Conductance values and hence WUE at the TB3 site were intermediate between the TB18 and T15 in February '97 (Fig. 4.7). In March '97 g_S values declined slightly at the TB18 site, which may have improved WUE. By April '97 data from the TB18 and TB3 sites were confined to the lower and steeper portion of the curve, indicating increased WUE.

The relationship between g_S and assimilation in *B. arthrophylla* did not differ substantially from *T. domingensis* (Fig. 4.8). In *B. arthrophylla*, data for each site did not occupy distinct portions of the curve, however values of g_S and assimilation tended to be higher at the TB18 site than the TB3 site in February '97. Maximal g_S in *B. arthrophylla* declined between sampling periods, also suggesting an increase in WUE over time.

4.4.2.9.2 Carbon isotope discrimination

Whilst g_S versus assimilation relationships provide some insight into WUE, they do not represented WUE integrated over time, as represented by carbon isotope discrimination. Discrimination in *T. domingensis* was significantly lower at the T15 site in December '97 and March '97 (18.1‰ and 19.3 ‰, respectively) compared to the TB3 (20.4 ‰ and 20.8‰) and TB18 (20.2 ‰ and 21.4‰) sites (Table 4.7). This suggests a comparatively higher WUE at

this site, which is consistent with the data presented in section 4.4.5a. Discrimination did not differ between the TB3 and TB18 site, in *T. domingensis* or *B. arthrophylla* at either sampling period.

At the TB3 site discrimination values were significantly higher (c. 1.2 ‰) in *T. domingensis* than *B. arthrophylla* indicating lower WUE. Differences between species were not statistically significant at the TB18 site, due to high variability in *B. arthrophylla*, but demonstrated the same trend. Higher variability in *B. arthrophylla* at the TB18 site may reflect the heterogenous soil salinities at this site. Differences in carbon isotope discrimination between species were not however reflected in g_S versus assimilation responses.

4.4.3 Evapotranspiration

4.4.3.1 Canopy transpiration (E_C)

Differences in LAIs, stomatal resistance (r_S) and vegetation height, both between species and between sites suggest that rates of canopy transpiration (E_C) may also differ. Estimates of E_C in February '97 were calculated for each species at each site, using mean LAIs and heights measured in late January '97 (Table 4.8). Hourly rates of E_C (Fig. 4.9) calculated using r_S values obtained at each measurement period in February '97, did not differ from values derived using mean daily r_S for either species regardless of site (Table 4.8, Fig. 4.9). Daily variation in r_S was therefore not sufficient to influence rates of E_C. As such, it was considered valid to use mean daily r_S to examine patterns in water loss over a longer time frame.

Comparisons across sites.

At the T15 site where soil salinities were high throughout the whole study period, the LAI and mean shoot height of *T. domingensis* were greatly reduced, and mean daily r_S increased in comparison to the TB3 site in February '97 (Table 4.8). This reduced daily and cumulative estimates of E_C (Table 4.9, Fig. 4. 10). Cumulative estimates of E_C over February '97 were reduced to 25 L m^{-2} (Table 4.9); 206 L m^{-2} less than for *T. domingensis* at the TB3 site.

Whilst all vegetation parameters influencing E_C were reduced at the T15 site, the prime factor responsible for this reduction was the LAI.

The reduction in height alone would increase aerodynamic resistance (r_a) by only 14%, reducing E_C for *T. domingensis* at the TB3 site by only 10 L m^{-2} (5%). The capacity of stomata to reduce E_C in response to a water deficit also appears to be limited. Increasing r_S in *T. domingensis* at the TB3 site to 200 s m^{-1} measured at the T15 site, would decrease E_C by only 25 L m^{-2}. However, lowering the LAI from 5.9 to .36, whilst maintaining r_S at 126 s m^{-1}, would reduce E_C by 195 L m^{-2}. This suggests that changes in r_S and height altered rates of E_C to a limited extent compared to that achieved by changing the LAI.

At the TB18 site, E_C for *T. domingensis* was considerably lower compared to the TB3 site, whilst E_C for *B. arthrophylla* was only marginally lower (Table 4.9, Fig. 4. 10). As r_S was lower in both species at the TB18 site compared to the TB3 site, lower estimates of E_C can be attributed to changes in the LAI. As previously discussed, differences in vegetation height exerts a minimal effect on E_C under the conditions that estimates were calculated.

Comparisons between species

Differences in E_C between *T. domingensis* and *B. arthrophylla* were only evident at the TB3 site (Fig. 4. 10, Table 4.9). In February '97 E_C for *T. domingensis* was 53 L m^{-2} greater than for *B. arthrophylla*. As the r_S was lower in *B. arthrophylla*, differences in E_C between species can be attributed to differences in the LAI.

The data indicates that differences in E_C, both between species and between sites, can be attributed to differences in LAIs. Using a logarithmic fit 98% of the variation in E_C is explained by changes in LAIs (Fig. 4.11). In contrast regressions between E_C and r_S, or height produced correlation coefficients of less than 0.35, with either linear or logarithmic fits.

4.4.3.2 Water loss below the canopy

When E_{total}; the sum of water loss from the canopy (E_C) and water below the canopy (E_W) is examined, differences between species and between sites are considerably smaller (Fig. 4.10, Table 4.9). The can be attributed to contribution of water loss below the canopy (E_W). As the LAI is reduced, the extinction of light through the canopy declines and the flux of solar radiation to the water body below the canopy increases. Consequently, whilst low LAIs reduce E_C, E_W is increased (Fig. 4.11, Table 4.9). In *T. domingensis* at the TB3 site, where the LAI was greatest (5.9), E_W was only 37 L m^{-2}. In contrast, at the T15 site where the LAI was lowest (0.36), 164 L m^{-2} was lost from the water body below the canopy. Differential contributions of E_W to E_{total} as the LAI varies, appears to minimises differences in E_{total}. This is illustrated in Fig. 4.11, where E_{total} plateaus earlier and more severely than E_C. An increase in the LAI from 1.5 to 5.9 only increased E_{total} by 13%, whilst E_C was increased by 59%.

4.4.3.3 The influence of climatic conditions.

Daily rates of E_O (open water) in February '97 varied from less than 1 L m^{-2} day^{-1} to c. 9 L m^{-2} day^{-1} (Fig. 4.10). This variability is reflected in daily changes in mean solar radiation (Fig. 4.12). Estimates of E_C also demonstrated large daily fluctuations, however the pattern differed to that of E_O, following more closely changes in VPD (Fig. 4.12). Linear regressions were used to assess the influence of mean daily VPD and solar radiation on E_O and E_C at each site (Table 4.10). Regressions verified that E_O was influenced more by solar radiation than VPD, with r^2 values of 0.79 and 0.46, respectively (Table 4.10). In contrast, E_C was controlled primarily by VPD (r^2 0.69- 0.95) rather than by solar radiation (r^2 0.18-0.30). These results arise from differences in boundary layer resistance (r_a) between vegetation (less than 100, Table 4.8) and open water (182 ± 31). Similarly, Jones (1983) found E_C for a forest canopy with a low r_a to be more influenced by VPD, than a short grass canopy with a high r_a. In contrast, E_C for the short grass canopy was influenced more by solar radiation than was the forest canopy.

As the environmental parameters controlling E_C differ to that of E_O, differences between E_C and E_O will vary from day to day as environmental conditions change. This is clearly seen in Fig. 4.10. On days where both solar radiation and VPD are low (day 8, Fig. 4.12) E_C is close to E_O (Fig. 4.10a, c, e), whilst when both solar radiation and VPD are high (day 20, Fig. 4.12), E_C for *T. domingensis* at the TB3 site exceeded E_O by c.100% (Fig. 4.10a).

4.4.3.4 The influence of LAIs

Differences between E_O and E_C were also influenced by the LAI. The relationship between LAIs, and the ratio of E_C to E_O for February '97 (Fig. 4.11), indicates that E_C was lower than E_O when LAIs were less than 3.0. At the highest LAI (5.9) E_C exceeded E_O by 27%. However, these comparisons do not consider water loss below the canopy. When E_{total} is compared to E_O, the presence of vegetation was found to increase water loss above E_O at a LAI of only 0.5 (Fig. 4.11). LAIs of 1.5 increased E_{total} above E_O by 31%. At the maximum LAI of 5.9, E_{total} was increased above E_O by 48%. Increasing the LAI from 1.5 to 5.9, a 3.8 fold increase, increased E_{total}:E_O by only 17%. This suggests that whilst the presence of vegetation will considerably increase the demand for water, the LAI of the stand will not greatly influence total water loss. This is due to changes in water loss below the canopy as the LAI varies.

4.4.3.5 E_{net} vs E_{total}

Estimates of E for *T. domingensis* made by others (Abtew *et al.* 1995; Abtew and Obeysekera 1995; Allen *et al.* 1992) assume that the canopy intercepts all solar radiation. However, even for dense stands where the LAI is high, sufficient light may penetrate the canopy to cause the evaporation of water below the canopy. Estimates of E for *T. domingensis* at the TB3 site were calculated assuming all radiation is intercepted by the canopy (E_{net}). Comparisons of these estimates with E_{total} (Fig. 4.13), indicate that whilst the relationship is close to unity failure to partition E between that lost from the canopy, and that lost from water below the canopy, results in an underestimation when E_{total} is high, and an overestimation when E_{total} is low (Fig. 4.13).

4.4.3.6 Potential error associated with estimates of evapotranspiration.

Canopy resistance

Szeicz and Long (1969) have suggested that r_c be calculated by dividing the minimal r_s by one half the LAI. This model has been developed, as it has been proposed that most of the radiation is absorbed by the upper half of the canopy, and as such only half the canopy is considered active in heat and vapour exchange from a fully developed crop. Whilst the correction term of .5 was not used in this study the approach is considered valid for two reasons. Firstly, the amount of radiation intercepted by the canopy, and hence active in heat and vapour exchange was calculated based on formulae of Monsi and Saeki (1953), a function of the extinction coefficient and the LAI. Secondly, measurement of r_s were made in an attempt to reflect the mean r_s of the canopy and therefore do not represent minimum values (Abtew *et al.* 1995). Mean canopy resistance for *T. domingensis* was calculated by Abtew *et al.* (1995) to be 50 s m^{-1} using a LAI of 1.8. In this study, at the TB18 site where the LAI was similar (1.5), canopy resistance was also c. 50 s m^{-1}. High correlations were obtained by Abtew *et al.* (1995) between estimates of evapotranspiration using the Penman-Monteith equation, and that measured by a lysimeter, thus validating estimates of canopy resistance. Error in estimates of E_c associated with the variance in canopy resistance ranged from 1% at the T15 site to 11% for *T. domingensis* at the TB18 site.

Ra

In deriving aerodynamic resistance an estimate of the fractional cover (F_c) of vegetation is required. A value of .75 as used by Abtew *et al.* (1995) was considered appropriate for both vegetation types at the TB3 site. An F_c value of .75 was also used at the more saline sites, however it is recognised that F_c would have been lower at these sites. To identify the potential error associated with this, the effect of a lower F_c estimate on r_a, and consequently E_c was evaluated. Varying the F_c estimate from 0.75 to 0.25 at the TB18 site altered r_a by 2%, and did not alter E_c in either species. Under the conditions examined it is apparent that no error can be attributed to applying the same F_c values as used at the TB3 site.

Extinction coefficient in canopy (K)

Although the validity of the K value selected in this work may be debated, the value does lies within the upper range measured for rice of .45-.6 (Uchijima 1976). K values of .7 have be measured for maize and barely and .43 for ryegrass (Monteith and Unsworth 1990). As such it is considered a reasonable estimate.

It is acknowledged that assuming equivalent K values for *T. domingensis* and *B. arthrophylla*, may obscure differences in rates of evapotranspiration between them. To evaluate the extent to which variance in K values may alter estimates of evapotranspiration, values were recalculated using a K value of 0.4 rather than 0.6, for each species at the TB3 site, where differences between species were evident. Values of E_C for February '97 were; 231 and 185 L m^{-2} for *T. domingensis* and *B. arthrophylla*, respectively when K was 0.6; and 220 and 166 L m^{-2}, respectively when K was 0.4. Values of E_{total} for February '97 were; 268 and 250 L m^{-2} for *T. domingensis* and *B. arthrophylla*, respectively when K was 0.6; and 271 and 257 L m^{-2}, respectively when K was 0.4. The effect of changing the K value from 0.4 to 0.6 altered estimates of E_C by 4-10% and altered E_{total} by 1-4%. As such, errors associated with assuming equivalent K values were small, and were not sufficient to obscure differences between species. Furthermore, as *B. arthrophylla* stems are more vertical than *T domingensis* leaves, if differences do exist it is more likely that K will be higher in *T. domingensis* than *B. arthrophylla*, enhancing differences between species.

4.5. Discussion

4.5.1 Salinity

This study demonstrates that within the sites examined at Bool Lagoon, surface water salinities can differ considerably from soil salinities, and soil salinities can vary over relatively small changes in depth. Both surface water and soil salinities were influenced by drawdown. Soil salinities increased even when drawdown was not substantial enough to cause the soil to dry (ie at the TB3 and TB18 sites). It is significant to note that considerable increases were observed in both surface water (1.4->4 dS m^{-1}) and soil salinities (6-12 dS m^{-}

^{1}) at the TB3 site, where surface water salinities were initially low and ground water salinities only c. 3 dS m^{-1}. As such, even relatively fresh systems are susceptible to increases in salinity, and it is likely that the magnitude of these increases will be considerably greater under more pronounced drawdown events. Where the capillary rise of saline ground water occurs, increases in salinity can be large and rapid as clearly illustrated at the T15 site. Where salt accumulation from the capillary rise of saline ground water occurs, it is evident that the 0-15 cm profile is the most vulnerable, whilst salinity in the 15-30 cm profile is more stable. This is similar to the general pattern of salt accumulation in the sediment profile observed by others in regions underlain by shallow, saline ground water (Mensforth 1996; Thorburn *et al.* 1993). The shift in root biomass at the T15 site, toward the deeper soil profile where salinities were lower and soil moisture higher, has also been observed in the response of *M. halmaturorum* to increased salinities in the surface soil profile (Mensforth 1996).

Between January and March '97 soil salinities did not differ between the TB3 and TB18 site, despite large differences in ground water salinities. The presence of a freshwater lens overlying saline ground water at the TB18 site may have minimised the impact of saline ground water on soil salinities. The presence of a fresh water lens would provide a hydrological head and minimise up welling of saline ground water. A large body of fresh surface water would also minimise drawdown events, and hence the capillary rise of saline ground water. In September '96 and December '96, salinities within the 15-30 cm profile were higher at the TB18 site compared to the TB3 site. This may be attributed to either the leaching of surface salts back down the soil profile, or alternatively to direct contact with saline ground water.

Although salts deposited at the surface soil layers over summer may be leached back down the soil profile to the ground water it is uncertain to what extent this restores the salt balance. As the input of freshwater into the system will tend to be associated with regional ground water recharge, ground water levels will rise at the same time that fresh surface water enters the system. The leaching of surface salts down the soil profile may therefore be obstructed by rising ground water. The freshening of the soil profile will hence be dependant on the net

balance between the tendency for ground water to rise, and the hydrological head produced by the overlying fresh water body. Where the leaching of salt back down the soil profile is obstructed by rising ground water, the freshening of the soil profile may be limited to the salinity of the ground water. Moreover, the flow of surface water through the wetland may represent an important mechanism which prevents salinities from increasing. Indeed Paijmans *et al.* (1985) points out that all types of swamps, whether receiving ground water or not depend on surface runoff events to both supply nutrients and to flush out wastes. If surface flows are inadequate, accumulated salts which have been diluted in the surface water will be deposited back into the sediments as water is lost in evaporation. As such, any salt entering the system via surface flow or ground water discharge will not be removed, and the salt load will increase over time. The significance of surface flows are reflected in a survey by Goonan *et al.* (1992) of wetlands associated with the River Murray. Wetlands connected to the River Murray had salinities less than 1000 mg L^{-1} (c. 1.6 dS $m^{-1)}$ whilst those isolated from the river had salinities in excess of this.

The sites examined within Bool Lagoon can be broadly categorised in terms of salinity as predominantly fresh, unstable and chronically saline. The TB3 site can be considered to represent a system which is predominantly fresh with low surface and ground water salinities. Salinity may only inhibit plant growth at this site when seasonal drawdown is prolonged. The TB18 site, where ground water salinity is high, but is overlain by fresh surface water, will experience an unstable salinity regime, governed by changes in ground water level and by both the magnitude and persistence of the freshwater lens. The period favourable for plant growth at this site may potentially be constricted by high salinity in the 15-30 cm profile at the beginning of the growth season, when ground water levels are elevated, and then by salt accumulation in the 0-15 cm profile associated with drawdown. The impact of drawdown on salt accumulation in surface sediments will be dependant on the duration of drawdown and the salinity of the ground water. At the T15 site surface water salinities, ground water salinities, and soil salinities were chronically high and plant growth was severely inhibited. As ground water salinities were lower at the T15 site compared to the TB18 site, the

importance of drawdown duration, flushing, and the presence of a hydrological head of surface water, in preventing excessive salt accumulation in surface sediments is apparent.

4.5.2 Plant performance

The performance of *T. domingensis* at the T15 site was clearly correlated with high soil salinities at this site. The response of vegetation at this site reflected the responses to salinity observed in controlled pond experiments, with reductions in LAIs, vegetation height, photosynthesis and stomatal conductance.

Shoot density was not reduced by salinity but tended to increase. Similarly in pond experiments shoot density was not decreased by salinity at the high nutrient load, although reduction were observed at the low nutrient load. In *T. angustifolia* Whigham *et al.* (1989) found shoot density to increase by more than 50% in response to high salinity in a coastal marsh. In *Typha* spp. it would seem that whilst salinity reduced the size of individual shoots, the capacity for vegetative reproduction is not impaired and may be stimulated. Although flowering was observed at the TB3 site in *T. domingensis*, flowering did not occur at either the TB18 or T15 sites, indicating a suppression of sexual reproduction in response to salinity. Reproductive shoots in *T. angustifolia* have also been found to decline in response to high salinity (Whigham *et al.* 1989). *B. arthrophylla* did not flower at either the TB3 site or the TB18 site.

At the T15 site *T. domingensis* persisted at salinities in excess of 17 dS m^{-1}, a level which is at the very upper limits of tolerance reported by Glenn *et al.* (1995) for this species. Glenn *et al* (1995) found *T. domingensis* Pers. absent from regions where the salinities of standing water exceed 8000 mg l^{-1} (12.5 dS m^{-1}) in a coastal desert marsh in Mexico. Although soil salinities may have been higher than the salinity of standing water, glasshouse experiments were consistent with field observations, with growth being negligible at 9000 mg L^{-1} (14 dS m^{-1}) and 75% mortality occurring at 15000 mg L^{-1} (23.4 dS m^{-1}) (Glenn *et al.* 1995).

Although the performance of *T. domingensis* was correlated with high salinities at the T15 site, the influence of salinity on the performance of *T. domingensis* and *B. arthrophylla* at the TB18 site is equivocal. Soil salinities measured over the study were only significantly greater than the TB3 site, in the 15-30 cm profile, and only in September and December '96. However, the decline in salinity within this zone did correlate with increased growth.

Both *T. domingensis* and *B. arthrophylla* at the TB18 site demonstrated short term responses indicative of non-salinised plants. Rates of photosynthesis and g_S measured in February and January '97, were considerably higher than measured at the TB3 site. As growth was initiated later at the TB18 site, and as rates of photosynthesis and stomatal conductance (g_S) were observed to decline with leaf age in *T. domingensis*, differences between sites may simply reflect differences in shoot age. Although short term performance characteristics were not reduced at the TB18 site, morphological characteristics did reflect those of salinised plants, with reductions in height and LAIs. The lack of concordance between short term performance characteristics and morphology suggest that growth was inhibited by some factor other than the supply of assimilates.

Measurements of residual surface water at this site in previous years when the system had been kept drier were around 14 dS m^{-1}, twice that measured in this study and indicate that soil salinities may have been considerably higher in previous years. The response of vegetation may therefore reflect previously higher salinities. This may be mediated by high NaCl levels in rhizomes and root which influence growth the following season. As salinity can increase Na concentrations in rhizome and root tissue (Lissner and Schierup 1997; Hocking 1981), it is probable that there will be a direct carry over effect of salinities from one growth season to the next. Growth may also be affected by reduced carbohydrate reserves as a consequence of impaired growth in previous years. It is also not known the extent to which high salinities during the initiation of summer growth may trigger changes in growth patterns. Whigham *et al.* (1989) suggests that consecutive years of high salinity may exert an accumulative effect on production in *T. angustifolia*. In contrast to this study, rapid recovery during years of low salinity were also noted. Whilst factors other than salinity may have contributed to lower

LAIs at the TB18 site, it is unlikely to be related to nutrient regime. The TB3 and TB18 site are within 4-5 km of each other and therefore experience similar surface water quality. Soil cores (10-25 cm depth) obtained in 1991 by Brownlow (1997) did not reveal any major differences in %N or $\%P_2O_5$ in areas proximal to the TB3 (.72 %N and .13 $\%P_2O_5$) or TB18 sites (.61 %N and .13 $\%P_2O_5$).

Both the LAI and LAD provide an index of the relative performance of each species at each site. At the TB3 site *T. domingensis* had a high LAI which was maintained over a relatively short time period whilst *B. arthrophylla* had a lower LAI which persisted over a greater time span. The peak LAI of *T. domingensis* was 44.7% higher compared to *B. arthrophylla*. However, the LAD of *T. domingensis* over the 220 days of the study was only 29.6% higher than *B. arthrophylla* and differences were absent on an annual basis. Comparable estimates of LAD may not represent similar levels of productivity as rates of photosynthesis will decline over winter in *B. arthrophylla*, due to lower air temperatures and lower levels of irradiance. However, the maintenance of stems over an annual cycle in *B. arthrophylla* may be significant in the retention of nutrients, thereby enhancing tolerance to periods of low nutrient supply. The maintenance of an intact canopy may also protect against the invasion of other species. This may be of particular significance in *B. arthrophylla*, which due to its low RGR will compete poorly for the capture of space.

At the TB18 site, LAIs and LAD were reduced in both species compared to the TB3 site. Reductions were however more pronounced in *T. domingensis*. Whilst the peak LAI of *T. domingensis* at the TB18 site was 33% higher than *B. arthrophylla,* the LAD over the study was greater in *B. arthrophylla* than *T. domingensis*. Annual predictions indicate that the LAD will be 44% greater in *B. arthrophylla*. It is evident that at the TB18 site the performance of *T. domingensis* is compromised to a greater extent than *B. arthrophylla*.

4.5.3 Water use efficiency

Both the g_S versus assimilation relationship, and carbon isotope discrimination indicated a greater water use efficiency in *T. domingensis* at the T15 site compared to either the TB3 or

TB18 sites. However, differences in water use efficiency between species and between the TB3 and TB18 site were more ambiguous.

In both *T. domingensis* and *B. arthrophylla* g_S and assimilation were not tightly coupled when g_S exceeded 400-500 mmols m^{-2} s^{-1}, indicating low water use efficiency. Jones (1988) also found the relationship between g_S and assimilation to become non-linear at higher values of g_S in *T. domingensis* . Similarly in *Typha latifolia* Knapp and Yavitt (1995) report a weak relationship between g_S and assimilation compared to that observed in terrestrial species (Yoshie 1986).

At the TB3 and TB18 sites g_S operated within a range which did not limit photosynthesis. Knapp and Yavitt (1995) also found assimilation in *T. latifolia* not to be limited by stomatal g_S under typical field conditions. Where g_S operates within a range which does not influence assimilation it is unlikely that discrimination will be affected. However, such changes will substantially alter water loss and hence WUE. Consequently, carbon isotope discrimination values may not always reflect WUE.

The validity of carbon isotope discrimination in representing WUE may also be compromised if respiratory CO_2 is refixed in photosynthesis, as this uncouples the relationship between g_S, photosynthesis and C_i, on which the interpretation of carbon isotope discrimination rests. Knapp and Yavitt (1995) report CO_2 concentrations in aerenchyma of *T. latifolia* leaves to be 18 times ambient in the morning. They suggest that the failure of assimilation to increase in response to higher ambient CO_2 concentrations in *T. latifolia,* as typically observed in C_3 plants, may arise from the utilisation of this internal source of CO_2 (Knapp and Yavitt 1995). Where CO_2, which has already undergone discrimination in photosynthesis is refixed, carbon isotope discrimination will be higher, falsely indicating a lower water use efficiency. Given these complications carbon isotope discrimination can not be considered a reliable index of WUE in aquatic vegetation.

4.5.4 Evapotranspiration

In wetland systems where shallow, saline ground water is present, the persistence of fresh surface water is essential to prevent the accumulation of salts in the surface sediments, as previously discussed. Although changes in the hydrological regime are a necessary component of wetland dynamics, the integrity of wetlands influenced by salinity will be dependant on the extent and duration of drawdown, and on the magnitude of flushing events. Ensuring the integrity of salinity prone wetland systems will therefore be dependant on a sound understanding of their hydrology. In order to achieve this the impact of vegetation on evapotranspiration must be assessed.

Factors controlling E_C.

Cumulative estimates of evapotranspiration from the canopy (E_C) for February '97 differed between vegetation types and between sites. Differences were driven primarily by differences in LAIs, rather than by changes in vegetation height or r_S. Similarly Sala *et al.* (1996) found the LAI rather than transpiration per unit leaf, to be a key variable controlling water use in well watered riparian stands. In this study differences in E_C between species were only evident at the TB3 site, where the LAI of *T. domingensis* was greater than *B. arthrophylla*. Differences in E_C between sites reflected differences in LAIs, being greatest at the TB3 site followed by the TB18 site, and lowest at the T15 site. For *T. domingensis* the LAI varied from 5.9 at the TB3 site, to 0.36 at the T15 site in response to salinity, and the mean daily E_C in February '96, varied from 8.24 to .88 L m^{-2} d^{-1}, respectively. Glenn *et al.* (1995) also found salinity to reduce E in *T. domingensis*. However, estimates were not derived under natural conditions and the mechanisms underlying changes in E were not determined.

LAIs of *T. domingensis* under field conditions have previously been reported and reflect the variability measured in this study; 1.8 (Abtew *et al.* 1995, Florida Everglades) , 4.8 (Jones 1988, Kenya), and 3 to 5.8 (Koch and Rawlik 1993, Florida Everglades). LAIs for *B. arthrophylla* have not been reported previously, however the LAI of *Juncus roemerianus* with

a somewhat similar morphology varied annually from a minimum of 2 in winter to a maximum of 4 in summer (Giurgevich and Dunn 1982).

Mean daily stomatal resistances measured in this study ranged from 60-200 s m^{-1}, with high resistances only being demonstrated under considerable salinity stress, or when die back was pronounced. Low stomatal resistances (c. 90 s m^{-1}) for *T. domingensis* have also been reported by Koch and Rawlik (1993) and Abtew *et al* (1995). Although r_S were not reported, g_S for *T. latifolia* is also high and comparable to *T. domingensis* at the TB3 and TB18 sites (Knapp and Yavitt 1995). Körner *et al* (1979) reported r_S for the genus *Carex* of 60-100 s m^{-1}. Minimum and maximum r_S for several salt marsh species have been reported: *Juncus roemarianus* 156 and 455 s m^{-1};*Spartina alterniflora* (tall form) 217 and 909 s m^{-1}; and *Spartina alterniflora* (short form) 250 to 1660 s m^{-1}, respectively (Giurgevich and Dunn 1982). These results suggest that salt marsh plants have greater stomatal control. Stomatal resistance in *Melaleuca halmaturorum* (a salt tolerant tree) is also high and can vary from a minimum of 150 s m^{-1} to over 2000 s m^{-1}, depending on the site characteristics, time of year and time of day (Mensforth 1996). These considerably higher r_S values suggest that more salt tolerant species have a greater potential to lower E_C via r_S than demonstrated in *T. domingensis* in response to salinity. At a LAI of 5.9 a r_S of 1000 s m^{-1} rather than 126 s m^{-1}, measured in this study for *T. domingensis*, would reduced E by 115 L m^{-2} (57%).

Despite greater control of water loss via stomata in *M. halmaturorum*, differences in E_C between sites differing in ground water salinity were correlated with LAIs, which varied from 1.1 to 2.4, rather than with stomatal resistance which was generally high at all sites (Mensforth 1996). Although comparisons are confounded somewhat by different climatic and site conditions, Mensforth (1996) points out that differences in E_C between species are reflected somewhat in differences in LAIs. Under similar ground water salinities (33-55 dS m^{-1}), average daily E_C for *Atriplex nummularila* with a LAI of .34, was 0.2 m^{-2} day^{-1} (Slavich *et al.* 1996), whilst in *M. halmaturorum* with a LAI of 1.2, E_C was 1.4 L m^{-2} day^{-1}. Thorburn *et al.* (1993) also notes that differences in E_C between *Eucalyptus camadulensis* and *Eucalyptus largiflorens* were due in part to difference in LAIs.

The significance of water loss below the canopy

In assessing water loss from aquatic vegetation it is apparent that E_W (water below the canopy) can contribute significantly to E_{total}. The contribution of E_W is determined by both the LAI, and by the extinction coefficient ($\mathcal{K}$). Jones (1988) claims that when the LAI is 2 or less that wet soil evaporation may contribute 50% to the total loss. In this study, E below the canopy in *T. domingensis* at the TB18 site, where the LAI was c.1.5 contributed 45% to the total, supporting this claim.

Whilst Jones (1988) claims that at a LAI of 4, only 5% of E_{total} can be attributed to water loss below the canopy, the contribution will also be influenced by the $\mathcal{K}$ value of the canopy. In the application of the Penman-Monteith equation to dense canopies it is assumed that all the radiation is intercepted by the canopy. It is clear from this work that even when the canopy may be considered dense, such as in *T. domingensis* or *B. arthrophylla* stands at the TB3 site, that even at a relatively high $\mathcal{K}$ value of 0.6 there will be some contribution to E_{total} by E_W. In *T. domingensis* E_W still contributed 20% to E_{total} at a LAI of 5.9. In canopies with higher $\mathcal{K}$ values the contribution of E below the canopy would become insignificant at much lower LAI. As many species of emergent macrophytes have vertically orientated leaves, it is likely that E_W will contribute to water loss from vegetated stands even for dense canopies with high LAIs. Rates of water loss from understorey vegetation can account for 20% (Robert *et al.* 1980) and up to 50% of forest transpiration (Tan and Black 1976), demonstrating the potential for water loss below the canopy.

Estimates of E in which all the radiation is considered to be intercepted by the canopy tend to overestimate when E_{total} is high, and to underestimate when E_{total} is low. Abtew *et al.* (1995) compared E from a *T. domingensis* canopy using the Penman-Monteith equation, to values of E obtained from a large scale lysimeter. Estimates of E using the Penman-Monteith equation assumed all radiation was intercepted by the canopy. Comparisons of daily estimates of E calculated using the Penman-Monteith equation closely matched values of E measured by the lysimeter, with a correlation coefficient of .80. However, computed values

of E tended to overestimate when the measured E was high, and underestimate when the measured E was low. Abtew *et al.* (1995) suggest that the use of a single height value for the whole period produced these discrepancies. A more likely explanation is the failure to partition water loss, between that lost from the canopy, and that lost from the water below the canopy, as demonstrated in this study (Fig. 4.13). Errors however will be reduced when E is calculated over a longer time frame, since errors will tend to cancel each other. The errors observed by Abtew *et al.* 1995 on a daily time scale were lost when weekly means were used (Abtew and Obeysekera 1995).

The significance of climatic conditions

As E_O and E_C are differentially influenced by solar radiation and VPD, the ratios between E_{canopy} or E_{total} and E_O will vary as the environmental conditions change. Where VPD is high, E_{canopy} will tend to exceed E_O. The variability of estimates of E from vegetated water bodies to E_O reported in the literature may in part be attributed to differences in the environmental conditions under which measurements were made. Van der weert and Kamerling (1974) have also reported that the ratio between E from vegetated water bodies and open water is strongly influenced by climatic conditions; the ratio increasing as VPD increased and decreasing as solar radiation increased.

In summer water loss from vegetated water bodies may be anticipated to be high in southern Australia, due to high solar radiation and high VPD. Although the Florida Everglades is considered a highly evaporative environment, mean solar radiation and VPD for February '97 at Bool Lagoon exceeded that recorded in the Florida Everglades by Abtew and Oberysekera (1995). In the Florida Everglades the maximum mean monthly solar radiation and VPD were 21.97 MJ m^{-2} d^{-1} and 0.97 kPa, respectively in April. At Bool Lagoon, mean monthly solar radiation and VPD in February '97, were 24.6 MJ m^{-2} d^{-1} and 1.13 kPa, respectively (Table 4.11). These climatic conditions resulted in rates of evapotranspiration from *T. domingensis* stands (LAI of 1.8) in the Florida Everglades of 5.6 L m^{-2} d^{-1}. For *T. domingensis* at the TB18 site (LAI 1.5) E_{total} was 8.5 L m^{-2} d^{-1} indicating higher E.

As differences between E_C and E_O vary from day to day, long term estimates are more indicative of the influence of vegetation on the water balance. Calculations based on meteorological conditions in February '97 when mean VPD was high, indicated that under these conditions, E_C from both *T. domingensis* and *B. arthrophylla* canopies will exceed E_O when the LAI is greater than 3. Moreover E_{total} will exceed E_O when the LAI is greater than only 0.5. At the highest LAI of 5.9, E_C exceeded E_O by 28% whilst E_{total} exceeded E_O by 48%. These values are consistent with values reported by others where advective effects were avoided. Based on theoretical principles and selected meteorological conditions, Linacre *et al.* (1970) concluded that E_C could exceed E_O by 30%, provided stomata did not offer any resistance to water loss. Estimates of water loss from stands of hydrophytes in a lysimeter (representing E_{total} rather than just E_C), surrounded by native vegetation exceeded E_O by 40% (Young and Blaney 1942). Similarly E for water hyacinth on a lake within a stand of similar vegetation was 44% greater than E_O (van der Weert and Kamerling 1974). However, water loss from isolated stands of hydrophytes where advective effects operate are considerable higher. Lysimeter studies by Allen *et al.* (1992) found water loss from narrow stands of *Typha* and *Scirpus* to exceed that of alfalfa by 60% and 80%, respectively.

It is proposed that water loss from vegetated water bodies would only be lower than E_O if stomata offered sufficient resistance to water loss to increase r_a below that of open water. At the highest LAI in this study (5.9), r_S would need to have been c. 550 s m^{-1} to reduce cumulative estimates of E_{total} in February to that of E_O. As the LAI declined, the r_S required to achieve an E_{total}:E_O of unity declined, at a LAI of 1.5 a r_S of 250 s m^{-1} was required. Consequently, for vegetation not to increase water loss above E_O, r_S must increase as the LAI increases. The data provided in this study does not indicate that high r_S occur concurrently with high LAIs. In *T. domingensis*, high r_S were only observed when the LAI was also low; at the T15 site, and when dieback occurred at the other sites. The maximal mean daily r_S measured was 200 s m^{-1} in *T. domingensis* , a value three time lower than that required to keep E_{total} equal to E_O at a LAI of 5.9. Given this, it is questionable whether *T. domingensis* would be able to achieve these resistances.

Not all aquatic vegetation will increase water loss. Anderson and Idso (1987) found species with planate floating leaves had E/E_O ratios less than unity, and proposed that this was due to both high r_a and r_s. Debusk *et al.* (1983) also found *Lemna minor* L. to reduce water loss compared to open water. Furthermore, increasing the LAI did not increase E. This was attributed to the growth habit of *Lemna minor* which forms thin mats over water bodies rather than increasing the aerial extent of leaf tissue.

Whilst the presence of vegetation increased E_{total} above open water, high LAIs did not exacerbate this much further. The situation will differ however when the water level falls below the leaf litter layer or soil, since the absorption of solar radiation by water below the canopy will be reduced, and hence water loss below the canopy. The extent to which evaporation is reduced once water levels drop below the sediment surface may however be debated. Rates of evaporative discharge from bare soil can be between 1-5 L m^{-2} day^{-1} even where the water table is at a depth of 1 m (Thorburn *et al.* 1992). Where water loss below the canopy is negligible, water loss will be primarily governed by E_C which is strongly influenced by LAIs. Consequently, differences between species and sites will become more important. Even water loss from canopies will however plateau as LAIs increase due to increased self shading from solar radiation (Debusk *et al.* 1983) as observed in this study. Sala *et al.* (1996) also report that whilst the LAI is a controlling factor for canopy transpiration in *Tamarix ramosisima* (saltcedar) E_C does not increase linearly with stand density; increasing cover by 50% only increased E_C by 33%.

4.5.5 Summary

This study demonstrates that surface water and soil salinities can be quite disparate, and that both increase substantially in response to drawdown. Furthermore, soil salinities may vary over small changes in soil depth. In assessing the extent of salinisation within wetlands consideration must therefore be given to this potential variability. Whilst seasonal changes in salinity in response to drawdown have been demonstrated, marked changes in salinity from year to year may also occur. During this study, drawdown at the TB3 and TB18 sites was insufficient to dry the soil and induce in the capillary rise of saline ground water. In previous

years water levels have been considerably lower and drawdown events more pronounced. At the TB18 site where ground water salinities were high, this would have yielded substantially higher salinities than measured in this study. Salinities in residual surface water in previous years of c. 14 dS m^{-1} support this.

At the TB18 site morphological characteristics of both *T. domingensis* and *B. arthrophylla* reflected that of salinised plants, with reductions in LAIs and height. These responses were however inconsistent with photosynthesis and g_s, short term responses, which were not reduced. As salinities at the TB18 site were only significantly higher in September and December '96, the influence of salinity on performance is equivocal. It is speculated that the morphological responses of both *T. domingensis* and *B. arthrophylla* at the TB18 site may result from higher salinities in previous years, or that high salinities at the initiation of growth strongly influences plant morphology. In contrast, at the T15 site where soil salinities were high throughout the study, both leaf gas exchange characteristics and morphological attributes were reflective of salt stressed plants.

As demonstrated in this study, drawdown can substantially increase both soil and surface water salinities. As such, the impact of vegetation on the water balance will ultimately influence salinity. Although evapotranspiration from the canopy of *T. domingensis* and *B. arthrophylla* stands differed at the TB3 site, differences were small when water loss below the canopy was taken into account. When water loss below the canopy was considered the presence of vegetation increased water loss above that of an open water body when the LAI was greater than 0.5.

The influence of vegetation on the water balance varied with changes in climatic conditions. Water loss from the plant canopies examined were strongly influenced by VPD, whilst evaporation from open water was influenced more by solar radiation than by VPD. Consequently, when VPD was high water loss was exacerbated by vegetation.

As demands on water resources increase there exists a need to define more clearly the water requirements of natural systems. To ensure sufficient water is allocated to protect natural systems, it is evident that consideration must be given to the influence of vegetation on the water balance, and the effects of drawdown on surface water and soil salinities.

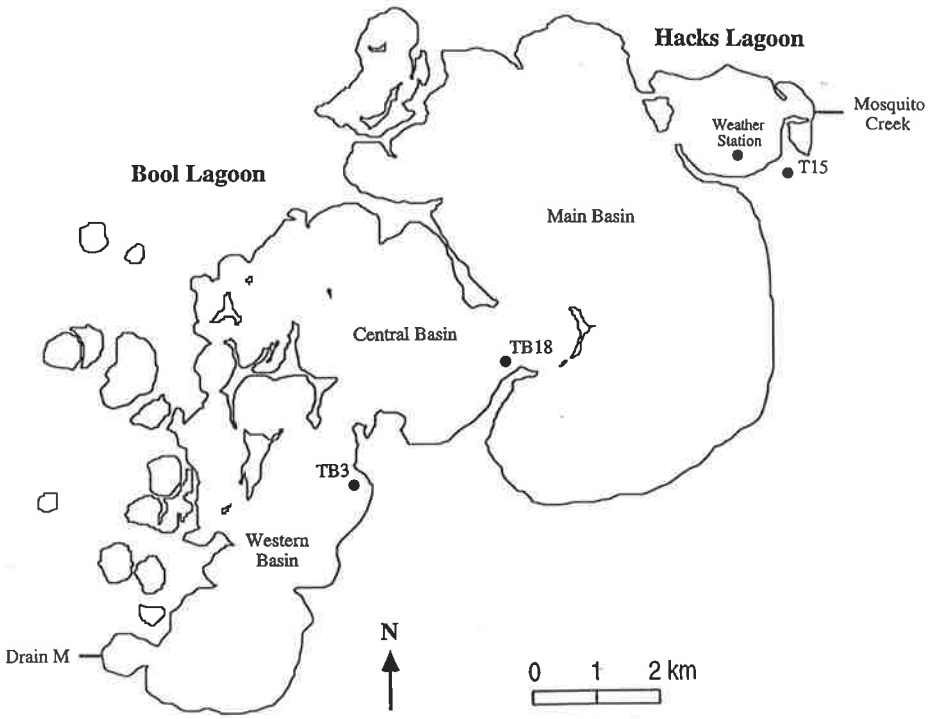


Figure 4.1. Bool Lagoon: Main, Central and Western basins and Hacks Lagoon in the South East of South Australia (37°08'S 140°41'E). Solid circles indicate the location of the study sites; T15, TB18, TB3, and the location of the weather station.

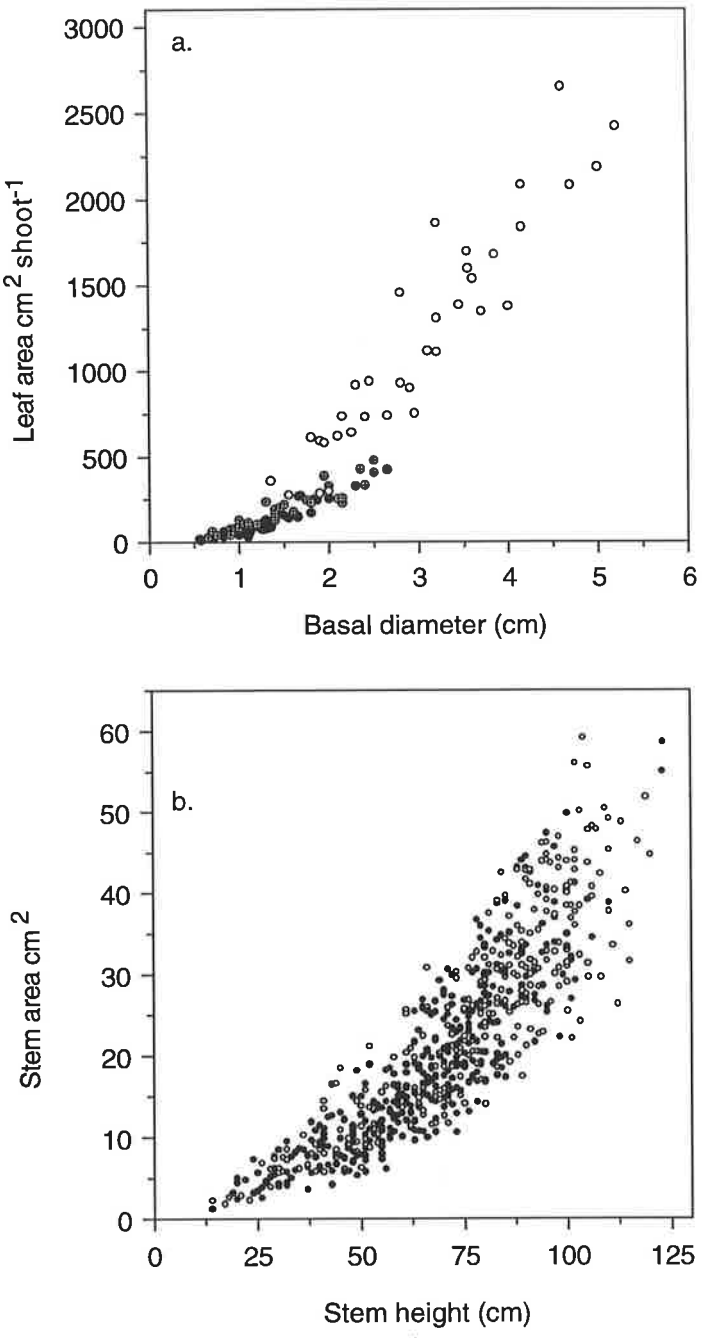


Figure 4.2. Relationships between; a. leaf area and basal diameter for *T. domingensis*; b. stem area and stem height for *B. arthrophylla*. TB3 (open circles), TB18 (hatched circles) and T15 (filled circles).

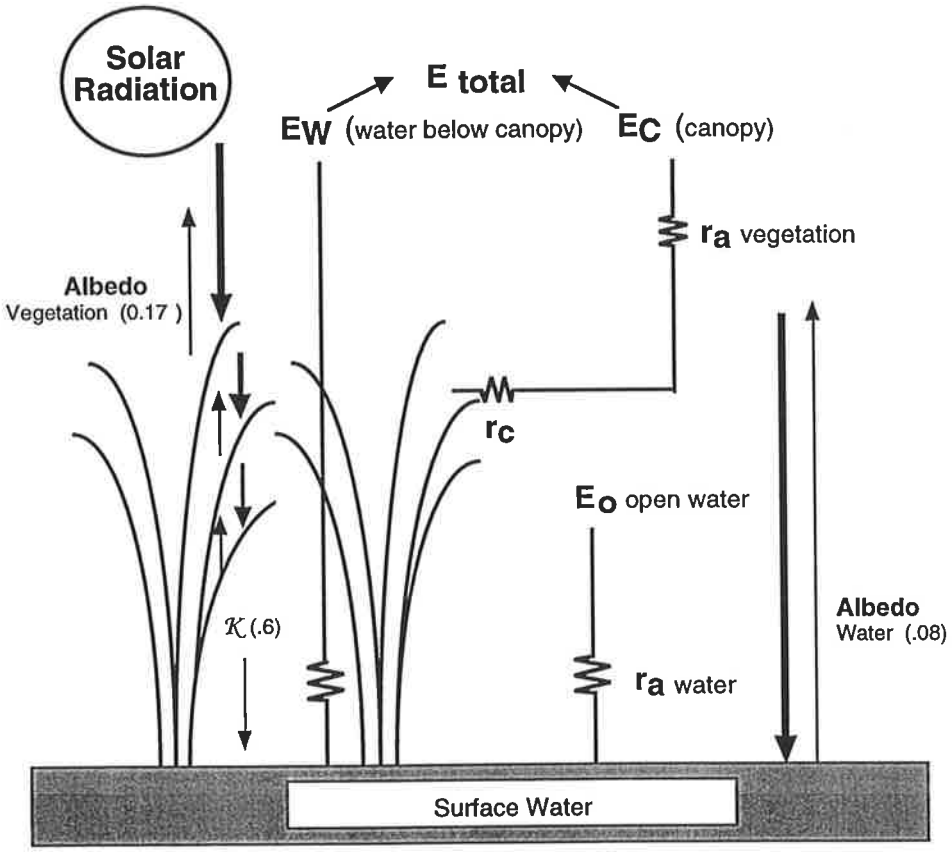


Figure 4.3. Components of evapotranspiration (E) from vegetated water bodies (E_{total}) and open water (E_o). E_{total} is the sum of water loss from the canopy (E_c) and water below the canopy (E_w); r_a and r_c are aerodynamic and canopy resistances to water loss, respectively; $\mathcal{K}$ is the light extinction coefficient. The albedo is the portion of solar radiation which is reflected and not absorbed.

Table 4.1. Electrical conductivity (dS m^{-1}) and depth of surface water (SW), and depth to ground water (GW) over time at each site. The depth of ground water within each stand was approximated from the depth of ground water within piezometers, and elevation profiles within stands, and between stands and piezometers. The depth of SW and depth to GW is given at 1, 6 and 11 m from the landward edge of each plot. nd indicates that no surface water was present although the soil may have been wet.

	Site	SW	GW	GW depth in piezometer	Depth of SW (cm)		Depth to GW (cm)	
		dS m^{-1}	dS m^{-1}	cm	*T. domingensis*	*B. arthrophylla*	*T. domingensis*	*B. arthrophylla*
September '96	TB3	1.4	3.2					
(17th-20th)	TB18	1.2	18.4					
	T15							
December '96	TB3	1.7	2.9	- 8	6, 31, 36	38, 46, 48	+7, +32, +37	+39, +47, +49
(2nd-9th)	TB18	1.1	17.2	+13	32, 39, 44	35, 39, 46	+30, +37, +42	+33, +37, +44
	T15	10.0	15		20, 43, 29			
January '97	TB3	3.1	3.0	- 40	nd *wet*, 2, 9	14, 17, 21	-25, 0, +5	+12, +15, +19
(20th-27th)	TB18	1.7	16.0	- 17	3, 9, 17	10, 15, 19	0, +7, +12	+8, +13, +17
	T15	18.3	8.7	- 48	nd *dry*	nd *dry*	-57, -34, -48	
March '97	TB3	4.7	3.4	- 56	nd *wet*	nd *wet*	-41, -16, -9	-4, -1, +3
(8th-15th)	TB18	4.1	15.2	- 40	nd *wet*	nd *wet*	-23, -17, -9	-16, -11, -7
	T15	ND	10.2	- 69	nd *dry*	nd *dry*	-78, -55, -69	
April '97	TB3	ND	3.6	-68	nd *wet*	nd *wet*	-53, -28, -21	-19, -11, -9
(23rd-26th)	TB18	6.95	15.1	-49	nd *wet*	nd *wet*	-32,-25, -20	-29, -25, -18
	T15	ND	10.2	-63	nd *dry*	nd *dry*	-72, -39, -63	

Table 4.2. Electrical conductivity (dS m^{-1}) of soil water and 1:5 soil extracts, and water content of soil, at 0-15 cm and 15-30 cm depths over time at each site. Data are means ± SD. Letters represent means across sites and depth classes which were significantly different ($P<.05$) at each sampling period, nd indicates no data.

	Site	*n*	EC Soil Water dS m^{-1}		EC 1:5 Soil Extract dS m^{-1}		Soil Water Content ml g^{-1} dry wt	
		0-15,15-30	0-15 cm	15-30 cm	0-15 cm	15-30 cm	0-15cm	15-30cm
September 96	TB3	6,6	6.18 ± 0.55[a]	8.00 ± 1.62[a]	1.32 ± 0.27	1.09 ± 0.34	1.06 ± .21	0.66 ± .05
17th-20th	TB18	6,6	5.94 ± 2.4[a]	13.60 ± 5.4[b]	1.42 ± 0.30	1.93 ± 0.56	1.20 ± .19	0.71 ± .05
	T15	3,3	nd	nd	nd	nd	nd	nd
December 96	TB3	6,5	5.09 ± 0.54[a]	6.10 ± 0.87[a]	1.10 ± 0.3	0.90 ± 0.18	1.08 ± .29	0.73 ± .11
2nd-9th	TB18	6,5	6.51 ± 2.26[a]	10.70 ± 1.46[b]	1.50 ± 0.31	1.74 ± 0.27	1.21 ± .28	0.82 ± .13
	T15	3,3	17.68 ± 1.38[c]	17.25 ± 1.6[c]	2.24 ± 0.35	2.03 ± 0.29	0.63 ± .07	0.59 ± .07
January 97	TB3	6,4	6.60 ± 0.97[a]	6.62 ± 0.70[a]	1.45 ± 0.38	0.88 ± 0.24	1.11 ± .28	0.65 ± .1
20th-27th	TB18	6,6	7.38 ± 2.10[a]	11.40 ± 4.67[a]	1.58 ± 0.36	1.70 ± 0.65	1.13 ± .34	0.75 ± .06
	T15	3,3	23.94 ± 2.8[b]	19.55 ± 3.78[b]	3.26 ± 0.57	2.32 ± 0.44	0.68 ± .04	0.59 ± .02
March 97	TB3	6,6	8.03 ± 0.92[a]	6.90 ± 0.72[a]	1.85 ± 0.45	1.08 ± 0.25	1.16 ± .30	0.78 ± .11
6th-13th	TB18	6,6	8.89 ± 2.72[a]	9.33 ± 2.15[a]	2.72 ± 0.54	1.71 ± 0.24	1.56 ± .17	0.98 ± .10
	T15	3,3	56.28 ± 6.04 [b]	23.00 ± 2.57[c]	5.34 ± 1.32	2.54 ± 0.11	0.47 ± .11	0.55 ± .04
April 97	TB3	6,6	12.34 ± 3.8[a]	8.95 ± 0.8[a]	2.9 ± 1.5	1.5 ± 0.34	1.12 ± .28	0.92 ± .16
23rd-26th	TB18	6,6	14.03 ± 4.4[a]	13.55 ± 2.7[a]	4.4 ± 1.2	2.5 ± 0.5	1.63 ± .28	0.81 ± .03
	T15	3,3	74.98 ± 21[b]	28.16 ± 3.1[c]	5.7 ± 0.1	3.1 ± 0.25	0.40 ± .13	0.54 ± .06

Table 4.3. Root dry weight (mg) at 0-15 cm and 15-30 cm depths, and percent of total root weight between 0 and 30 cm in each depth class, for each species at each site in April 1997. Data are means ± SD (n =3). Letters indicate means which were signficantly different (P<.05) between sites and depth classes for each species .

Soil Profile	Site	*T. domingensis*		*B. arthrophylla*	
		Dry Wt mg	% Total (0-30 cm)	Dry Wt mg	% Total (0-30 cm)
0-15 cm	TB3	440 ± 45^{a}	79.2	268 ± 61^{a}	80.6
	TB18	334 ± 156^{ab}	75.6	193 ± 63^{a}	79.4
	T15	177 ± 80^{bc}	67.9		
15-30 cm	TB3	116 ± 22^{bc}	20.8	65 ± 8^{b}	19.4
	TB18	108 ± 53^{c}	24.4	50 ± 19^{b}	20.6
	T15	83 ± 49^{c}	32.1		

Table 4.4. LAIs ($m^2 m^{-2}$) for *T. domingensis* and *B. arthrophylla* over time at each site. Data are means ± SD, *n* in parenthesis. LAIs in September represent maximal values (see 4.3.5). Different letters represent means which are significantly different ($P < .05$) between sites and species at each sampling time, nd indicates no data.

Site	Species	September '96 17th-20th	December '96 2nd-9th	January '97 20th-27th	March '97 6th-13th	April '97 22nd-25th
TB3	*T. domingensis*	0.73 ± 0.46^{ac} (5)	3.79 ± 1.52^{a} (6)	5.88 ± 2.21^{a} (5)	3.48 ± 0.92^{a} (5)	1.05 ± 0.92^{a} (11)
	B. arthrophylla	1.47 ± 0.42^{b} (5)	1.70 ± 1.3^{b} (6)	2.95 ± 0.50^{b} (4)	3.25 ± 1.17^{a} (5)	2.78 ± 0.61^{b} (11)
TB18	*T. domingensis*	0.27 ± 0.17^{c} (5)	0.46 ± 0.15^{c} (7)	1.49 ± 0.75^{bc} (5)	2.09 ± 1.0^{ab} (4)	0.46 ± 0.30^{ac} (12)
	B. arthrophylla	0.95 ± 0.31^{ab} (5)	1.05 ± 0.89^{bc} (5)	1.35 ± 1.21^{bc} (5)	1.40 ± 1.26^{b} (6)	0.97 ± 0.71^{a} (11)
T15	*T. domingensis*	nd	0.23 ± 0.11^{c} (7)	0.36 ± 0.12^{c} (5)	0.55 ± 0.21^{b} (5)	0.02 ± 0.03^{c} (12)

Table 4.5. LAD over the study and predicted annual LAD for each species at each site.

Site	Species	LAD (over 220 days)	Predicted Annual LAD
TB3	*T. domingensis*	740	740
	B. arthrophylla	521	782
TB18	*T. domingensis*	225	225
	B. arthrophylla	256	401
T15	*T. domingensis*	67.3	67

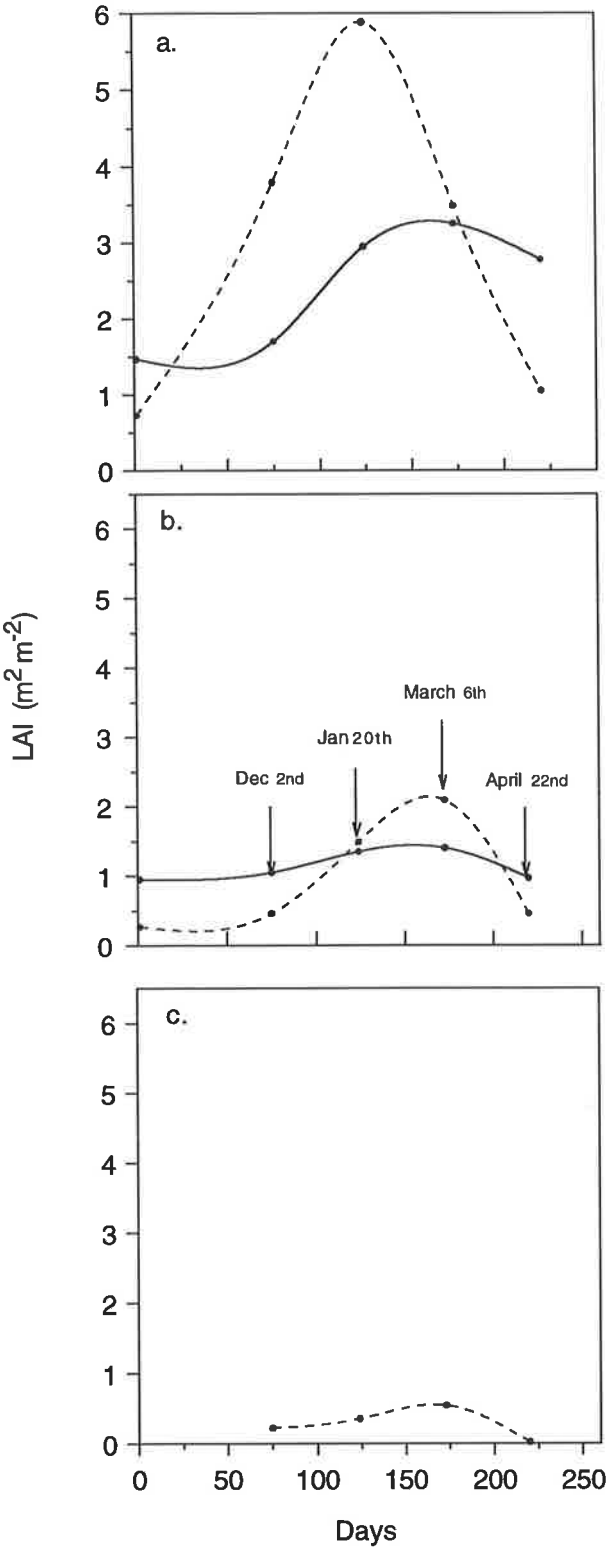


Figure 4.4. LAIs over time from Sept 17th '96 for *T. domingensis* (dashed line) and *B. arthrophylla* (solid line) at each site; a.TB3,b.TB18 and c.T15.

Table 4.6. Number of shoots m^{-2}, height of shoots, number of leaves $shoot^{-1}$, and width of longest leaf $shoot^{-1}$, for *T. domingensis* or *B. arthrophylla* at each site over time . Data are means ± SD, *n* in parenthesis. Letters represent means which were significantly different ($P<.05$) between sites at each sampling period for each species, ns indicates no significant difference.

Species	Site	September 17th-20th	December 2nd-9th	January 20th-27th	March 6th-13th	April 22nd-25th
T. domingensis Shoots m^{-2}	TB3	35 ± 17 (5)	27 ± 15 (6)	35 ± 16 (5)	30 ± 7 (5)	29 ± 10.3[a] (11)
	TB18	48 ± 26 (5)	26 ± 20 (7)	48 ± 14 (5)	58 ± 19 (4)	39 ± 19.8[a] (12)
	T15		26 ± 18 (7)	26 ± 10 (5)	42 ± 23 (5)	4 ± 5.5[b] (11)
		ns	ns	ns	ns	
B. arthrophylla Stems m^{-2}	TB3	1697 ± 596 (5)	954 ± 371 (6)	1286 ± 256 (4)	1243 ± 371 (5)	1237± 260[a] (11)
	TB18	1286 ± 276 (5)	617 ± 553 (5)	957 ± 733 (5)	785 ± 610 (6)	635 ± 385[b] (11)
		ns	ns	ns	ns	
T. domingensis Height cm	TB3	101 ± 25 (11)[a]	243 ± 44 (19)[a]	258 ± 24 (22)[a]	229 ± 48 (19)[a]	143 ± 30 (38)[a]
	TB18	66 ± 25 (15)[b]	104 ± 26 (24)[b]	104 ± 29 (30)[b]	103 ± 28 (29)[b]	60 ± 24 (58)[b]
	T15		119 ± 20 (20)[b]	93 ± 25 (16)[b]	91 ± 13 (25)[b]	29 ± 13 (7)[c]
B. arthrophylla Height cm	TB3[a]	42 ± 16 (316)[a]	70 ± 18 (771)[a]	74 ± 17 (643)[a]	81 ± 16 (777)[a]	73 ± 17 (1702)[a]
	TB18	31 ± 11 (271)[b]	62 ± 15 (386)[b]	55 ± 14 (598)[b]	65 ± 15 (675)[b]	57 ± 19 (890)[b]
T. domingensis Leaves $shoot^{-1}$	TB3	4.7 ± 1.3[a] (11)	6.9 ± 1.4[a] (19)	6.2 ± .66[a] (22)	4.7 ± 1.4[ab] (19)	2.7 ± 1.3 (38)
	TB18	3.3 ± 1.2[b] (15)	4.2 ± 1.7[b] (24)	5.4 ± 1.6[a] (30)	5.8 ± 1.8[a] (29)	3.0 ± 1.1 (58)
	T15		4.6 ± 1.3[b] (20)	4.4 ± 1.3[b] (16)	3.6 ± 0.8[b] (25)	2.7 ± 0.7 (7)
						ns
T. domingensis Leaf width cm	TB3	1.23 ± .28[a] (11)	1.60 ± 0.35[a] (19)	1.69 ± 0.26[a] (22)	1.58 ± 0.29[a] (19)	1.29 ± 0.36[a] (38)
	TB18	0.67 ± .23[b] (15)	0.72 ± 0.24[b] (24)	0.73 ± 0.23[b] (30)	0.75 ± 0.19[b] (29)	0.61 ± 0.25[b] (58)
	T15		0.60 ± 0.10[b] (20)	0.57 ± 0.13[c] (16)	0.65 ± 0.09[b] (25)	0.51 ± .07[b] (7)

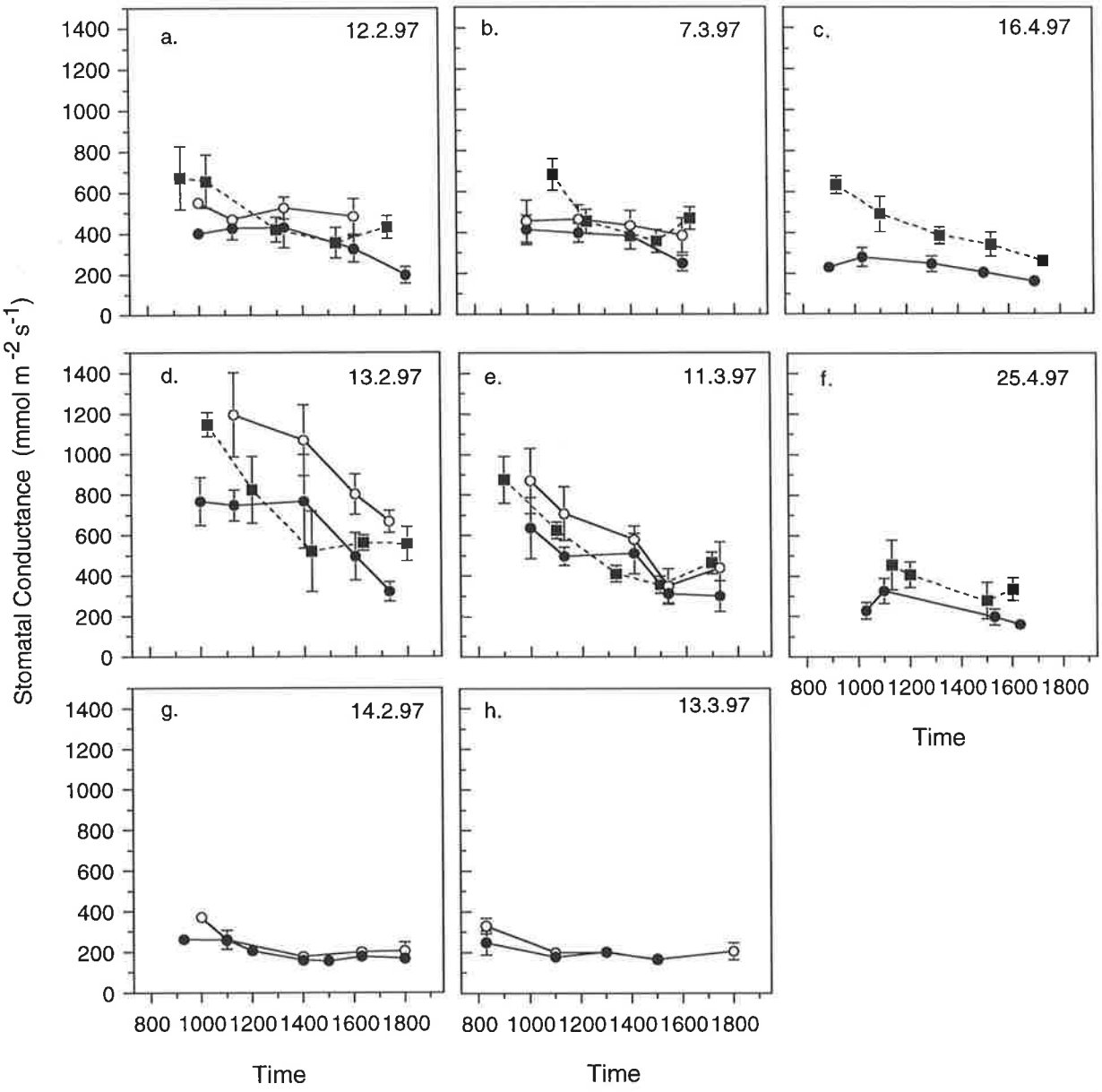


Figure 4.5. Daily changes in stomatal conductance in *T. domingensis* (circles) and *B. arthrophylla* (squares) at each sampling period at each site; TB3 (a.,b.,c.); TB18 (d.,e.,f.) and T15 (g.,h.). Open circles are readings taken on inner leaves of *T. domingensis* and closed circles are readings taken on outer leaves. Bars represent SD (n=6-8), inner leaves of *T. domingensis* (n=4-5).

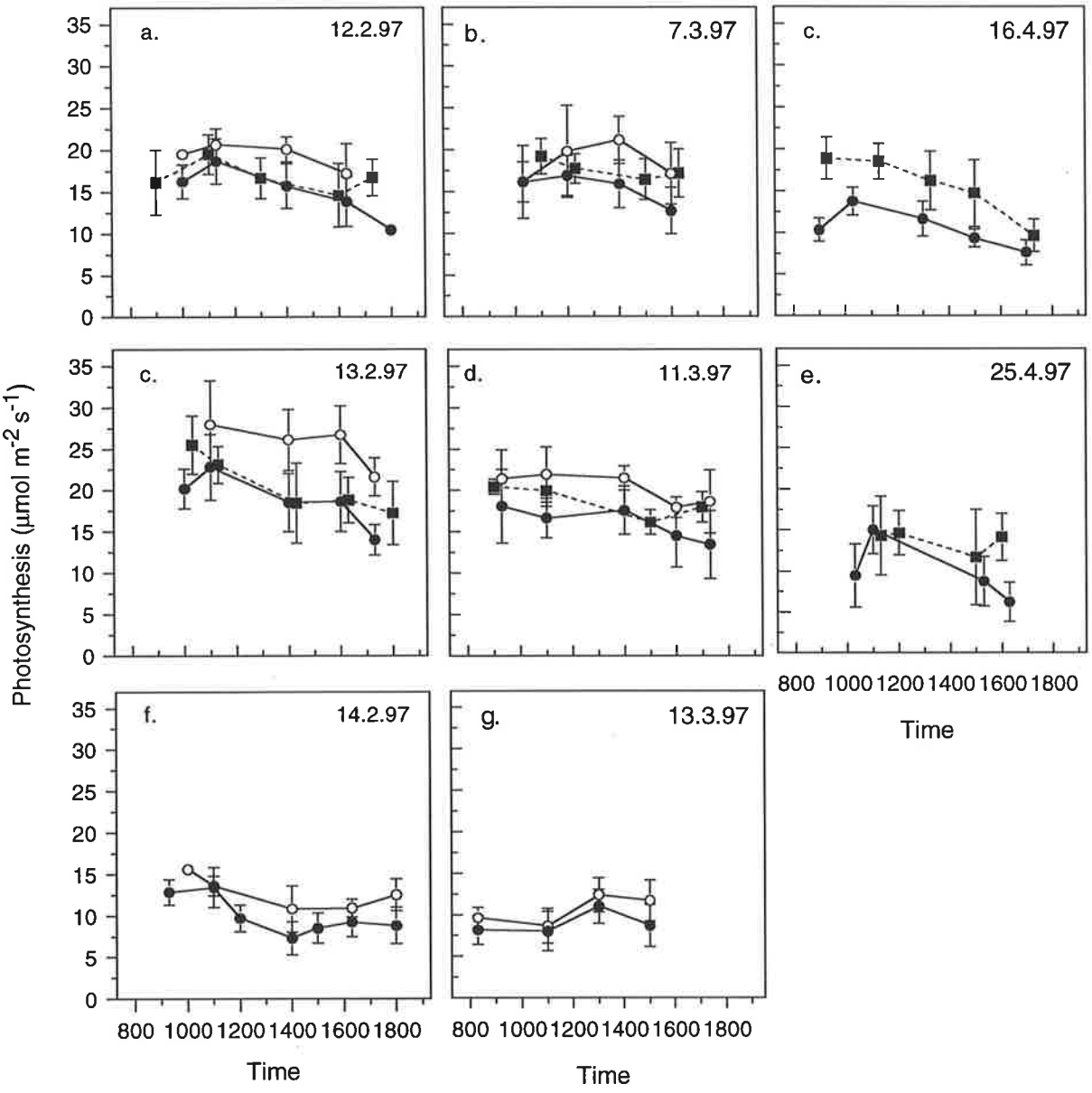


Figure 4.6. Daily changes in rates of photosynthesis in *T. domingensis* (circles) and *B. arthrophylla* (squares) at each sampling period at each site; TB3 (a.,b.,c.); TB18 (d.,e.,f.) and T15 (g.,h.). Open circles are readings taken on inner leaves of *T. domingensis* and closed circles are readings taken on outer leaves. Bars represent SD (n =6-8), inner leaves of *T. domingensis* (n =4-5).

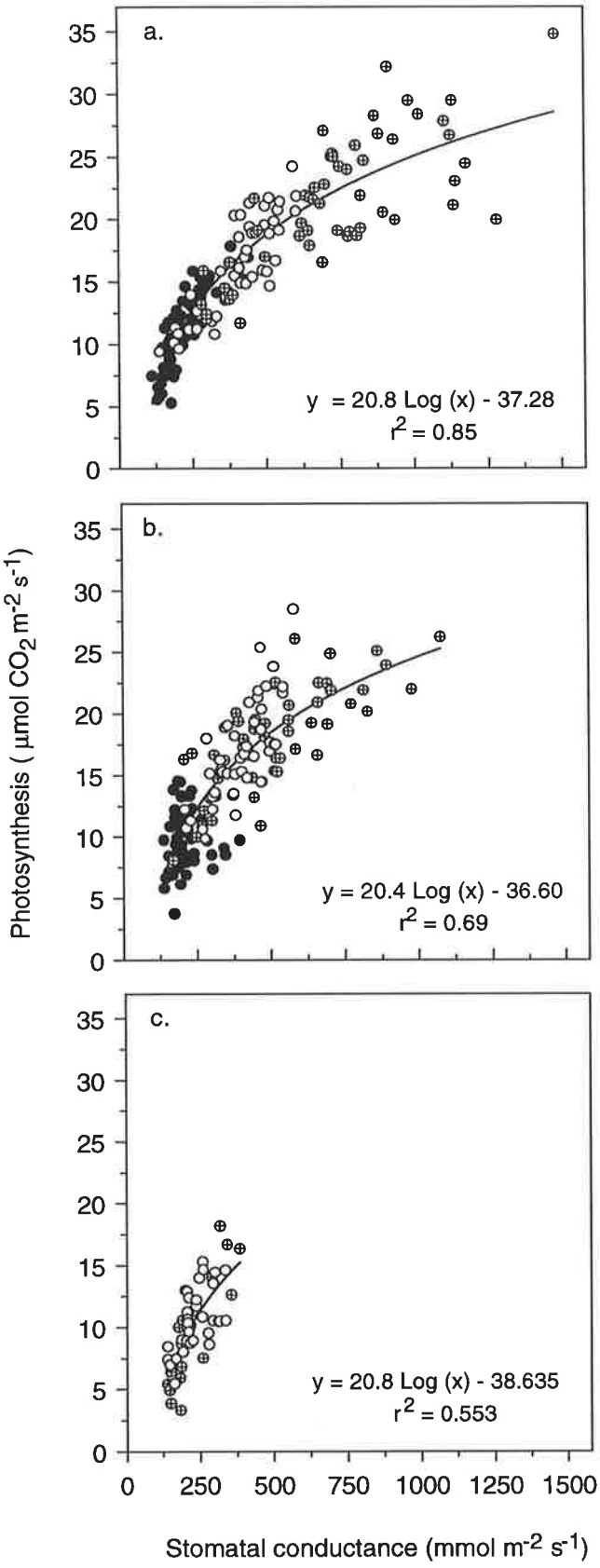


Figure 4.7. Photosynthesis as a function of stomatal conductance for *T. domingensis* at the TB3 (open circles), TB18 (hatched circles) and T15 (filled circles) sites; a. February, b. March and c. April '97.

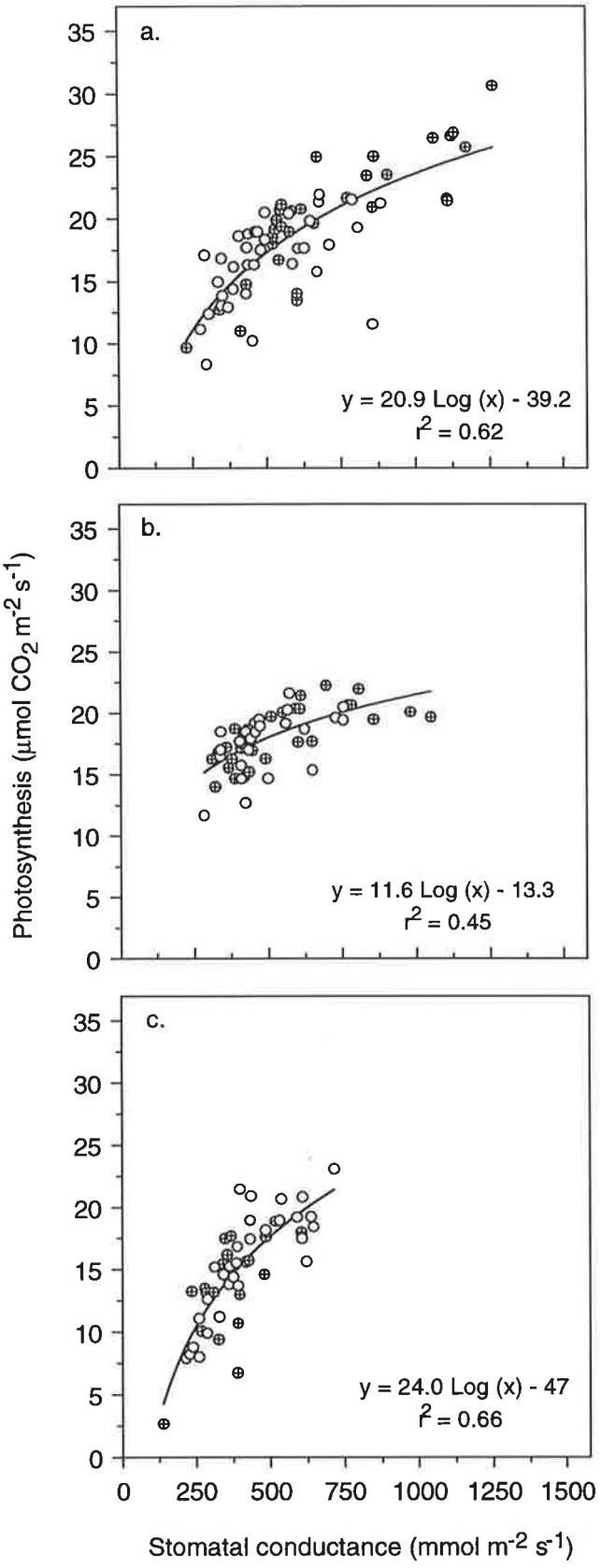


Figure 4.8. Photosynthesis as a function of stomatal conductance in *B. arthrophylla* at the TB3 (open circles) and TB18 (hatched circles) sites; a. February, b. March and c. April '97.

Table 4.7. Carbon isotope discrimination (Δ ‰) and isotopic composition of C (δ^{13}C ‰) of *T. domingensis* leaves and *B. arthrophylla* stems, at each site in December '96 and March '97. Data are means ± SD (n =3). Different letters represents means which were significantly different (P<.05) across species and sites at each sampling period.

Site	Species	December '96		March '97	
		Δ‰	δ^{13}C ‰	Δ‰	δ^{13}C ‰
TB3	*T. domingensis*	20.37 ± 0.35^{a}	-27.8 ± 0.34	20.8 ± 0.72^{a}	-28.21 ± 0.68
	B. arthrophylla	19.09 ± 0.13^{bc}	-26.59 ± 0.12	18.77 ± 0.30^{b}	-26.28 ± 0.29
TB18	*T. domingensis*	20.17 ± 0.27^{a}	-27.61 ± 0.26	21.43 ± 0.07^{a}	-28.82 ± 0.06
	B. arthrophylla	19.5 ± 0.65^{ab}	-26.97 ± 0.62	20.46 ± 1.47^{ab}	-27.89 ± 1.4
T15	*T. domingensis*	18.08 ± 0.36^{c}	-25.62 ± 0.34	19.28 ± 0.19^{b}	-26.77 ± 0.18

Table 4.8. Canopy characteristics used in calculating E_C, and aerodynamic resistance (r_a) for February '97. Values are means ± SD, *n* in parenthesis.

	TB3		TB18		T15
	T. domingensis	*B. arthrophylla*	*T. domingensis*	*B. arthrophylla*	*T. domingensis*
LAI	5.9 ± 2 (5)	2.9 ± 5 (4)	1.49 ± 0.7 (5)	1.35 ± 1.2 (5)	0.36 ± .01 (5)
r_s s m^{-1}	126 ± 49 (5)	86 ± 22 (5)	75 ± 31 (5)	61 ± 18 (5)	202 ± 41 (6)
r_c s m^{-1}	21 ± 8 (5)	30 ± 8 (5)	50 ± 21 (5)	45 ± 13 (5)	562 ± 114 (6)
Height m	2.5 ± 0.2 (22)	0.74 ± 0.2 (643)	1 ± 0.3 (30)	0.55 ± 0.1 (598)	0.93 ± 0.2 (16)
r_a s m^{-1}	83.9 ± 35 (28)	96.3 ± 41 (28)	95.5 ± 41 (28)	96.4 ± 41 (28)	95.7 ± 41 (28)

Table 4.9. Cumulative (L m^{-2}) and mean daily (L m^{-2} day^{-1}) (in parenthesis) estimates of; E_C, E_W and E_{total} for each species at each site for February '97.

	TB3		TB18		T15
	T. domingensis	*B. arthrophylla*	*T. domingensis*	*B. arthrophylla*	*T. domingensis*
E_C	231 (8.24 ± 3.6)	185 (6.61 ± 2.9)	145 (5.18 ± 2.31)	146 (5.21 ± 2.35)	25 (0.88 ± 0.49)
E_W	37 (1.34 ± 0.62)	65 (2.31 ± 0.79)	93 (3.32 ± 1.19)	98 (3.51 ± 1.26)	164 (5.86 ± 2.09)
E_{total}	268 (9.58 ± 4.12)	250 (8.90 ± 3.69)	238 (8.50 ± 3.4)	244 (8.74 ± 3.5)	189 (6.75 ± 2.5)

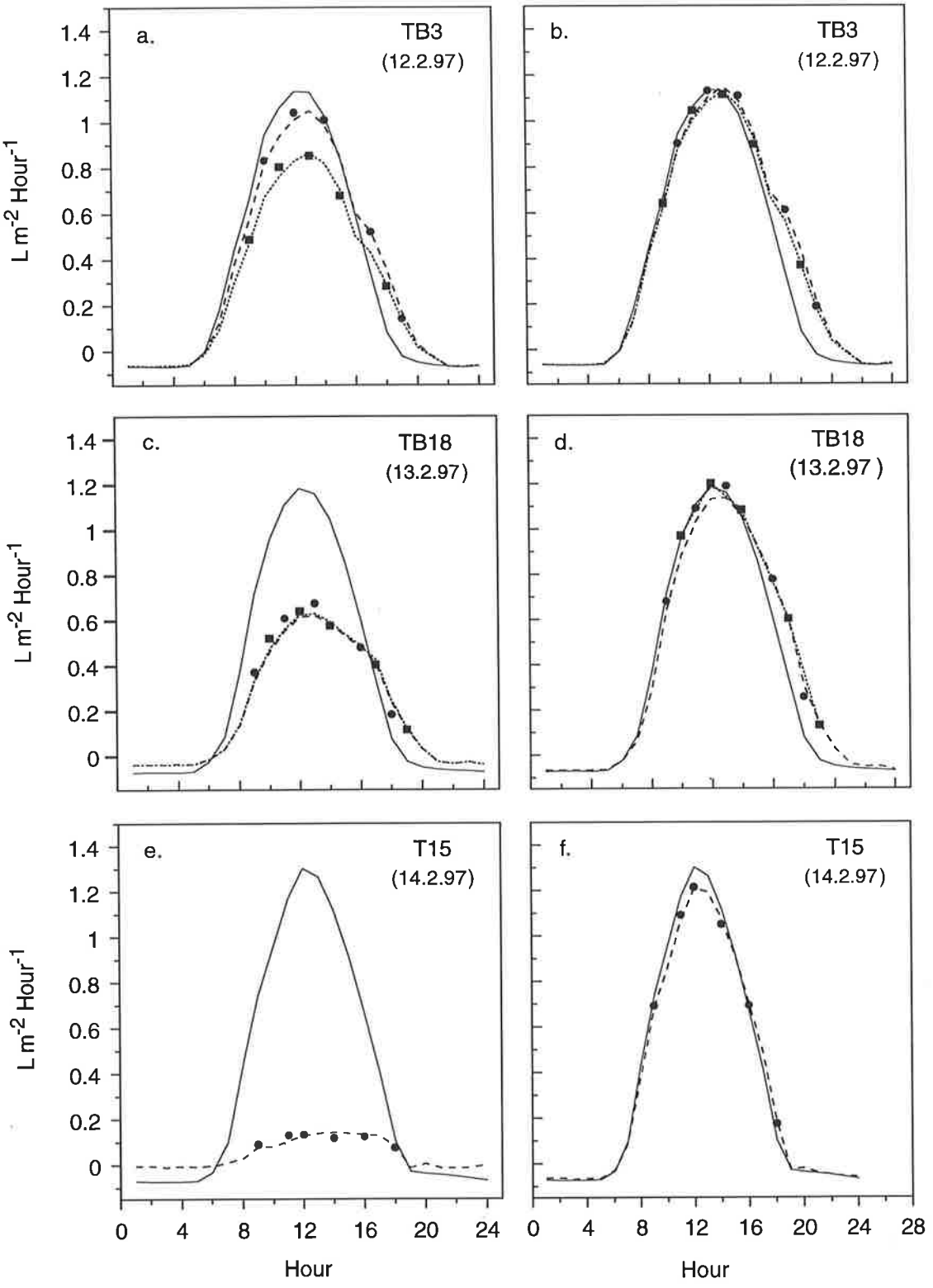


Figure 4.9. Hourly estimates of E_c (a.,c.,e.) and E_{total} (b.,d.,f.) calculated using mean daily stomatal resistances for *B. arthrophylla* (dotted line) and *T. domingensis* (dashed line) at each site; TB3 (a,b.), TB18 (c.,d.) and T15 (e.,f.). Filled circles and squares represent rates estimated using mean stomatal resistances at each measurement period for *T. domingensis* and *B. arthrophylla*, respectively. Rates are compared to E_0 (solid line) in all graphs.

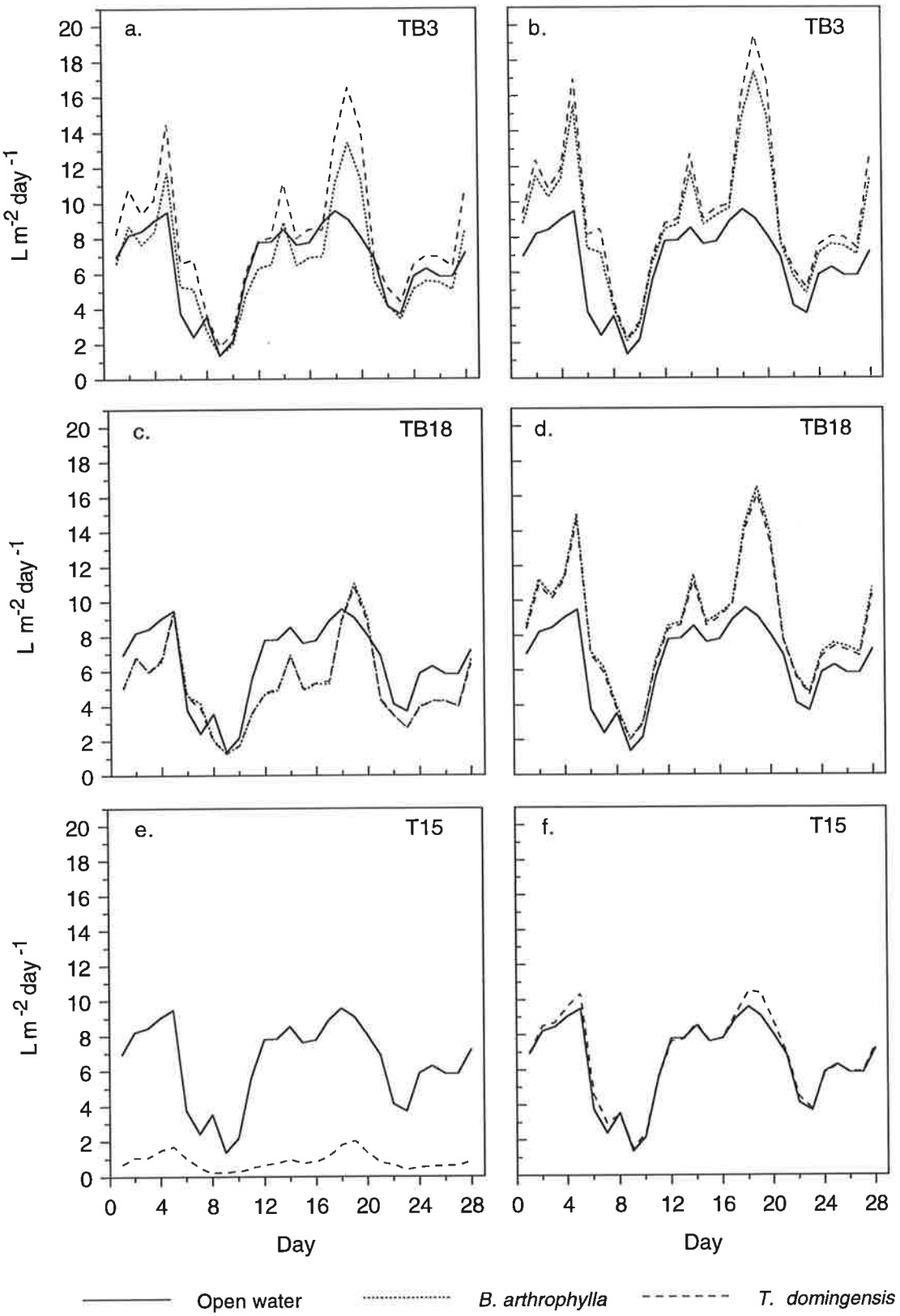
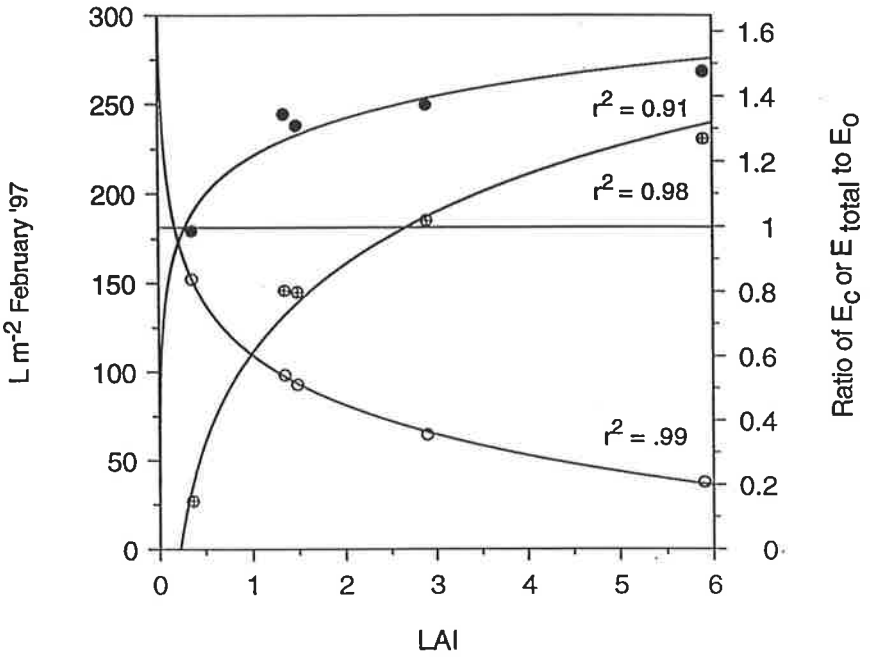


Figure 4.10. Estimates of E_c (a.,c.,e.) and E_{total} (b.,d.,f.) over February '97 for each species, at each site; TB3 (a.,b.), TB18 (c.,d.) and T15 (e.,f.). Values are compared to E_o in all graphs.



$E_C = 166.2 \log (x) + 110.5$

$E_{total} = 77.1 \log (x) + 220.5$

$E_W = -95.1 \log (x) + 110.06$

$E_C:E_O = 0.39 \log (x) + 1.21$

$E_{total}:E_O = 0.907 \log (x) + 0.61$

Figure 4.11. Estimates of E_C (hatched circles), E_W (open circles), and E_{total} (filled circles) calculated for February '97, and ratios of E_C or E total to E_O as a function of LAI. E_O (181 L m^{-2}) is represented by the horizontal line.

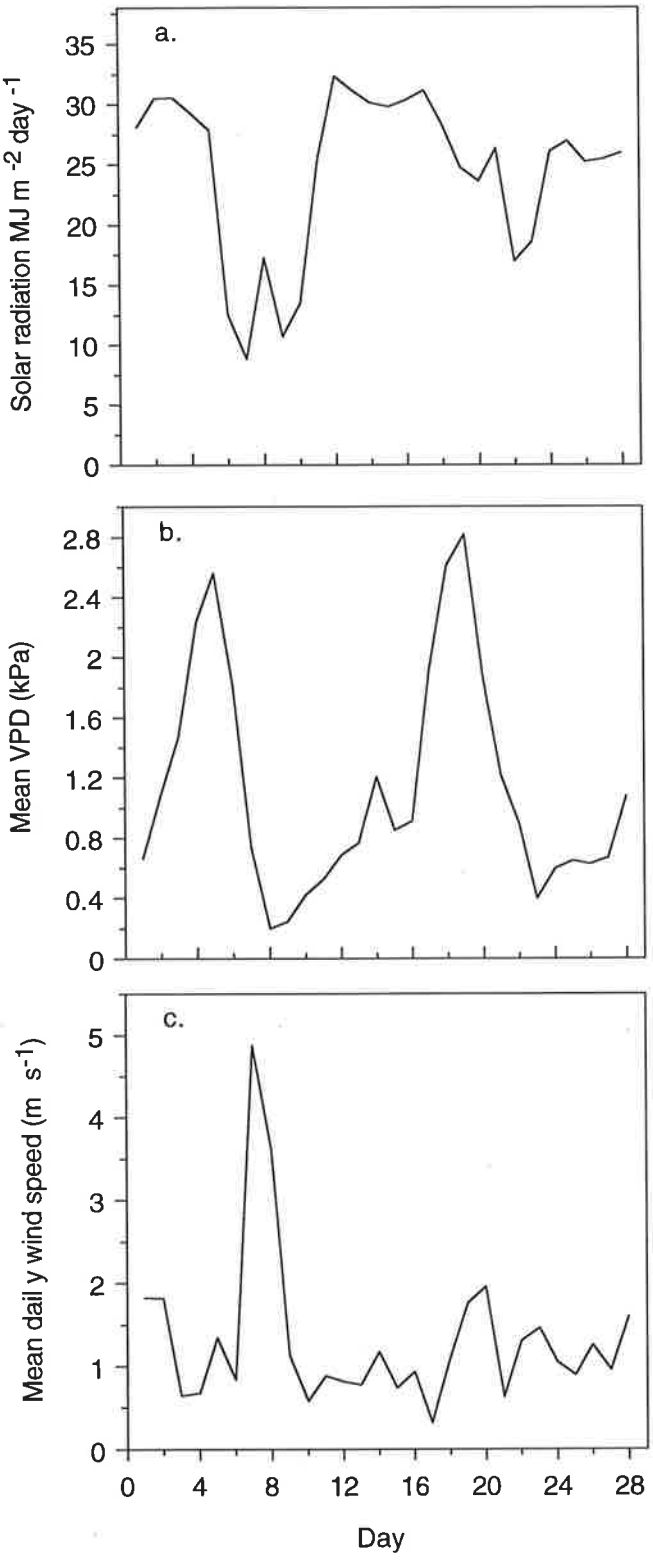


Figure 4.12. Meteorological variables influencing E in February '97; a. solar radiation b. VPD c. wind speed.

Table 4.10. Correlation coefficients for linear regressions between meteorological variables (VPD and solar radiation), and daily estimates of E from open water (E_o), and from plant canopies at each site. E_c *T. domingensis* (TE_c) and E_c *B. arthrophylla* (BE_c). All correlations were significant at $P<.001$ (n =28).

		TB3		TB18		T15
	E_o	TE_c	BE_c	TE_c	BE_c	TE_c
VPD (kPa)	0.457	0.69	0.71	0.75	0.75	0.94
Solar radiation (MJ m^{-2} d^{-1})	0.795	0.28	0.30	0.26	0.24	0.18

Table 4.11. Climatic conditions in February '97 and E for open water (E_o). Values are daily averages ± SD (n=28).

Climatic Variable	
Solar radiation (MJ m^{-2} d^{-1})	24.56 ± 6.77
VPD (kPa)	1.13 ± 0.74
Air temperature (°C)	21.38 ± 4.34
Relative humidity (%)	69.22 ± 12.79
Wind speed (m s^{-1})	1.32 ± 0.94
E_o (L m^{-2} d^{-1})	6.84 ± 2.4

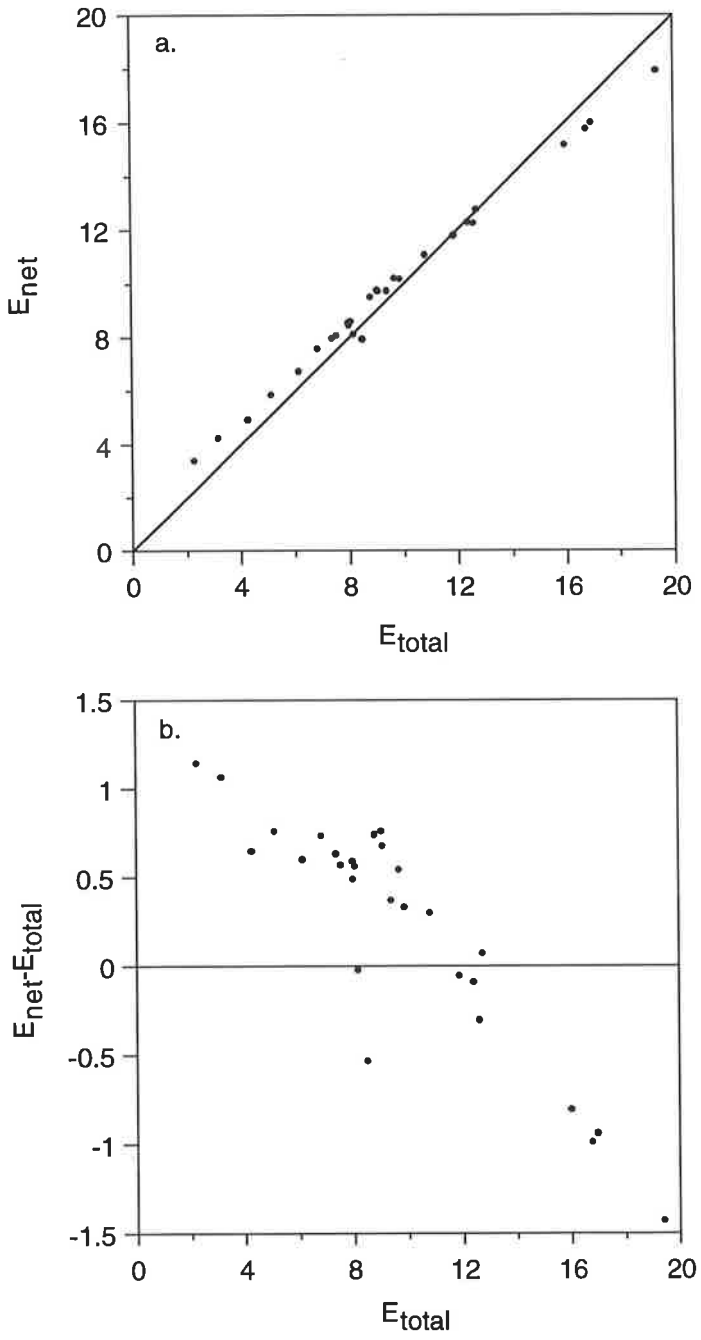


Figure 4.13. E_{net} as a function of E_{total} (a.), and differences between E_{net} and E_{total} as a function of E_{total} (b.).

Chapter 5. Discussion

5.1 Salinity and growth

The three species examined in this work; *B. medianus*, *T. domingensis* and *B. arthrophylla*, can all be regarded as moderately salt tolerant since growth continued at salinities of 100 mM NaCl (5800 mg L^{-1}) and greater. At 50 mM NaCl (2900 mg L^{-1}) the effect of salinity was marginal in all species, indicating a relatively high threshold before the impact of salinity is evident. Whilst the influence of salinity on the performance of *B. medianus* and *B. arthrophylla* has not previously been reported the response of *T. domingensis* has been experimentally evaluated by Hocking (1981) and Glenn *et al.* (1995). Similar to this work Hocking (1981) found 50 mM NaCl did not significantly reduce growth. At 100 mM NaCl Hocking (1981) found growth to be severely reduced with leaf curling and necrosis evident. Glenn *et al.* (1995) found growth to be reduced by 50% at 3500 mg L^{-1} (c. 60 mM) and by 90% at 9000 mg L^{-1} (c. 154 mM). In the pond experiments detailed in this work biomass was reduced by only 53% at 100 mM NaCl and no visual symptoms of toxicity were apparent. The greater sensitivity to salinity demonstrated in *T. domingensis* by Hocking (1981) and Glenn *et al.* (1995) may have been evoked by high Na/Ca ratios, since no additional calcium was added in either experiment.

In all species examined in this work, reductions in plant growth imposed by salinity were characterised by reductions in plant height, leaf number and LAIs. In *B. medianus* culm number was also reduced by salinity, whilst in *T. domingensis* it was only reduced by salinity when the nutrient load was also low. Salinity did not elicit a substantial change in the ratio of leaf biomass to root biomass in any of the species examined. Nor was there an increase in the rate of leaf senescence in response to salinity. In contrast, Hocking (1981) observed increased leaf loss in *T. domingensis* at 100 mM NaCl. Pronounced leaf loss in response to salinity has also been documented for other aquatic species (James and Hart 1993).

In all species the reduction in RGR imposed by salinity was associated with a reduction in NAR. In both *B. medianus* and *B. arthrophylla* this was clearly associated with lower rates of

photosynthesis. However, in *T. domingensis* the direct effect of salinity on photosynthesis was more ambiguous, as photosynthesis was only reduced by salinity when the nutrient load was also high. Only in *B. arthrophylla* was the reduction in RGR associated with a reduction in LAR. The reduction in LAR in *B. arthrophylla* being induced by a shift in biomass allocation from stems to rhizomes rather than to roots as is commonly observed. A similar and more definitive shift in biomass allocation was observed in *B. medianus,* with biomass shifting from stems to tubers with increasing salinity. In *B. medianus*, as the stems are not the major photosynthetic tissue as is the case in *B. arthrophylla* the response did not affect LAR.

5.2 The Munns and Termaat salinity response model

The responses of the species examined to the experimentally imposed salinities did not conform to the biphasic model proposed by Munns and Termaat (1986). The biphasic model of Munns and Termaat (1986) implies that salinity reduces growth primarily via reductions in LAR. This is implied since shoot growth, and by implication leaf area, is considered to be more inhibited than root growth. This is induced in the short term in response to a hormonal signal from the root to the shoot in response to low soil osmotic potential, and in the long term due to an accelerated rate of leaf loss resulting from ion toxicity. In the species examined the leaf to root ratio did not generally decline, and the rate of leaf senescence did not increase. The only instance where the leaf to root ratio declined was in *B. medianus* at the high nutrient load in response to 13 dS m^{-1}. Hence the two major factors which are considered to mediate salinity imposed growth reduction were not evident in the species examined. Indeed, the decline in RGR in response to salinity was correlated with NAR and not LAR as would be predicted under the model of Munns and Termaat (1986).

The model of Munns and Termaat (1986) does suggest that sensitivity to salinity is related to the speed at which toxicity is reached, in more sensitive species ion toxicity is reached sooner than in more tolerant species. Hence leaf senescence manifests later in more tolerant species. The responses of the species examined reflect this, being relatively tolerant and failing to demonstrate an increased rate of leaf senescence. In contrast, sensitivity to salinity in species such an *Potamogeton tricarinatus* and *Myriophyllum crispatum* has been clearly associated

with leaf loss (James and Hart 1993; Warwick and Bailey 1997). Whether an increased rate of leaf loss in these species is associated with ion toxicity remains speculative.

The failure of the shoot to root ratio to decrease in response to increasing salinity has also been demonstrated in *T. domingensis* and *Cyperus involucratus* by Hocking (1981, 1985). In *Cyperus involucratus* the shoot to root ratio was unresponsive to a range of salinities between 1 and 100 mM NaCl (r^2 0.005) (Hocking 1985). However, the shoot to root ratio did decline at 150 mM NaCl causing the correlation coefficient to increase to 0.30. Similarly in *B. medianus* at the high nutrient load, the leaf to root ratio declined at c. 130 mM NaCl and not at 45 or 90 mM NaCl. Carbon allocation patterns in response to salinity has not frequently been reported in aquatic macrophytes and it is hence difficult to make general conclusions. The responses described in this work and by Hocking (1981, 1985) do however suggest that quite high salinities are required to induce changes in the leaf to root ratio. As aquatic vegetation is adapted to water logged conditions their root systems may be less responsive to low soil water potentials. As the plants examined did not demonstrate any evidence of wilting there does not appear to be any adverse affects associated with this insensitivity, possibly as there is little internal resistance to water flow. It may be speculated that the failure of root biomass to increase in response to increasing salinity, is because survival is not as dependant on accessing a water source, since the rhizome will permit survival over unfavourable periods. This is consistent with increased biomass allocation to rhizomes in response to salinity, suggesting preparation for dormancy.

5.3 Nutrients and growth

Growth in both *B. medianus* and *T. domingensis* was highly sensitive to nutrient load, whilst growth in *B. arthrophylla* did not respond to the nutrient loads examined. Both *T. domingensis* and *B. medianus* demonstrated higher RGRs (41.8 and 40.67 mg g day^{-1}, respectively) under optimal conditions compared to *B. arthrophylla* (20.0 mg g day^{-1};Table 5.1). This is consistent with the hypothesis, that the performance of species with high RGRs is more dependant on nutrient supply than species with low RGRs (Chapin 1980).

Whilst nutrient load strongly influenced plant performance in both *B. medianus* and *T. domingensis*, increased RGRs achieved at higher nutrient loads diminished as salinities increased. This is consistent with responses to nutrient supply observed in crop species, where nutrient addition generally enhances growth but also increases sensitivity to salinity (Feigin 1985).

In both *B. medianus* and *T. domingensis* higher nutrient loads elicited a strong shift in biomass allocation away from the roots to shoots, particularly to the leaves yielding greater numbers of leaves, higher LAIs and higher leaf to root ratios. Consequently, LAR was significantly increased at the high nutrient loads and was correlated with higher RGRs. Increased RGRs in response to nutrient load was not however associated with increases in NAR.

Photosynthesis was relatively insensitive to nutrient load in the species examined. In *T. domingensis* and *B. arthrophylla* there was no effect of nutrient load on photosynthesis. In *B. medianus*, photosynthesis at 13 dS m^{-1} was significantly increased at the high nutrient load but not at the moderate nutrient load (comparisons between nutrient loads were not made in non-salinised plants).

It has been proposed that there exists an optimal LAI at which nitrogen use efficiency is maximised at the level of the canopy (Anten *et al.* 1995). High LAIs whilst increasing light interception, and potentially carbon gain, may lower the nitrogen concentration and photosynthesis per unit leaf, and increases in carbon gain may not be realised (Anten *et al.* 1995). There will therefore exist an optimal LAI where light interception is maximised without compromising photosynthesis per unit leaf. So it is not surprising that we see generally no change in photosynthesis per unit leaf in response to nutrient load, and rather large changes in LAI, and consequently why it is LAR and not NAR that dominated the response to nutrient load. Lawlor (1995) also reports that leaf area is much more responsive to environmental conditions than photosynthesis per unit leaf area, and that photosynthesis per unit leaf area rarely explains variation in crop production.

Although higher rates of photosynthesis were observed in *B. medianus* at the high nutrient load at 13 dS m^{-1} it did not increase NAR. This can be rationalised if salinity prevented the optimal LAI from being achieved; hence canopy photosynthesis would not be increased in proportion to the costs associated with achieving high leaf nitrogen concentrations.

5.4 Growth analysis; comparisons between species, and with other studies

Although *B. medianus* and *T. domingensis* may generally be considered fast growing species RGRs calculated in this study were considerably lower compared to RGRs reported for a range of species (Poorter and Remkes 1990; Cramer *et al.* 1990; He and Cramer 1993; Shennan *et al.* 1987). A literature review by Lambers and Poorter (1992) found RGR to vary between 18 and 386 mg g day^{-1}, with a mean of 158, indicating that values obtained in this work are generally low (Table 5.1). As discussed by Poorter and Remkes (1990) large plants tend to have lower RGRs due to a greater investment in structural tissue or due to self shading. A greater investment in structural tissue would result in lower values of LAR whilst self shading would reduce NAR. LAR values reported by Lambers and Poorter (1992) varied between 2 and 65, with a mean of 18, whilst NAR varied from 2 to 25, with a mean of 10. In the species examined in this work, LAR varied from 1 to 2.8, whilst NAR varied from 11 to 33 (Table 5.1). The comparatively lower RGRs obtained in this work therefore arise from lower estimates of LAR rather than NAR. This can be attributed to the use of plants with tubers or rhizomes, and hence a large investment in structural tissue compared to many herbaceous seedlings on which most growth analysis work has been conducted. Furthermore, the SLA is generally low compared to values reported by Lambers and Poorter (1992), indicating that the leaves of the species examined have a greater investment in structural tissue, which will also contribute to lower LARs (Table 5.1). Values reported in this work are however within the range reported for several aquatic macrophytes in the field: *Cyperus papyrus*, 13.9;*Cyperus latifolius*, 7.2; and *T. domingensis*, 3.8 (Jones 1988).

Lower RGRs observed in *B. arthrophylla* can be attributed to lower NARs when compared with *T. domingensis*, but to lower LARs when compared with *B. medianus* (Table 5.1). If

compared with *B. medianus*, lower RGRs observed in *B. arthrophylla* are consistent with the proposition that low RGRs arise from low SLAs. The rational being that slow growing species have longer lived leaves which necessitate a greater investment in structural tissue, yielding a lower leaf area per unit of leaf weight (Lambers and Poorter 1992). This is clearly apparent between *B. medianus* and *B. arthrophylla* with the SLA of *B. medianus* being almost three times that of *B. arthrophylla*.

Whilst the SLA is lower in *B. arthrophylla* compared to *T. domingensis*, differences are small, and it is differences in NAR rather than SLA that drive differences in RGR. As rates of photosynthesis did not differ between *B. arthrophylla* and *T. domingensis* under experimental or field conditions, differences in RGR must be attributed to differences in respiration. Although *T. domingensis* has a lower SLA compared to *B. medianus* which reduces LAR this was compensated by a higher NAR. Again rates of photosynthesis appear unable to explain differences in NAR and respiration must therefore determine differences in RGR.

The ecological significance of elevated respiration rates is unclear, but it may be associated with the cost of synthesising compounds which promote longevity and tolerance to adverse environmental conditions. For example, the cost of synthesising glycinebetaine and proline in *Spartina alterniflora* is considered to reduce its competitive ability at low salinity, but enhances tolerance at high salinity (Cavalieri 1983). As suggested by Goldberg and Novoplansky (1997) the success of species with low RGRs relative to species with high RGRs is determined by the duration of periods of resource limitation; where longer periods of resource limitation will favour species with low RGR.

5.5 The centralised whole plant stress response model

It has been hypothesised that there exists a centralised whole plant response to low soil-resource availability (Chapin 1991; Coleman and Schneider 1996). This has been generated due to the similarity of plant responses to both soil infertility and to water deficits which are characterised by reductions in stomatal conductance, photosynthesis, growth rate, and

decreased leaf and shoot growth relative to root growth, yielding low shoot to root ratios. These responses are indeed similar to those typically produced by salinity. Furthermore, in all instances the involvement of ABA has been implicated. Whilst the centralised whole plant stress response model implies a uniform response to soil resource limitation, the responses of the species examined in this work demonstrate, in contrast, a specificity in response to nutrient load and salinity. In both *B. medianus* and *T. domingensis* the response to salinity was associated with a change in NAR, whilst the response to nutrient load elicited a change in LAR. In *B. arthrophylla* NAR was influenced by both salinity and nutrient load. Specificity in response to nutrient load and salinity are expressed in *B. arthrophylla* by the failure of biomass, RGR or morphological characteristics to respond to nutrient load. Salinity, in contrast elicited strong changes in all these parameters. In both *B. medianus* and *B. arthrophylla* salinity induced a change in carbon allocation from stems to rhizomes/tubers which was not induced in response to nutrient load. In *B. medianus* salinity also elicited a reduction in plant height whilst low nutrient load did not. Specificity in plant responses to nutrient load and water deficits has also been demonstrated in tomato plants (Coleman and Schneider 1996). The role of ABA in the putative centralised whole plant stress response is also equivocal. Mutant tomato plants deficient in ABA demonstrated a weaker change in LAR in response to low nitrogen than wild-type plants, a response opposite to that anticipated (Coleman and Schneider 1996).

5.6 Spatial and temporal variability in salinity

Pond experiments carried out in this work examined responses to stable salinity levels, yet this may rarely occur in the field. Field studies carried out in this work demonstrate that salinities within wetland systems can vary on rather small temporal and spatial scales. At all sites examined salinity increased over time in response to drawdown. Even where surface water and ground water salinities were initially low (1.5 and 3 dS m^{-1}, respectively) both surface water and soil salinities increased substantially in response to drawdown. At all sites the salinity of surface water was always lower than soil salinities. Furthermore, at the sites where the ground water was saline soil salinity at times varied with depth. Changes in soil salinity with depth indicated that saline ground water may potentially increase soil salinities

within deeper soil profiles (15-30 cm) in winter-spring; due to elevated ground water tables or the leaching of salt back down the soil profile. In summer however, saline ground water may increase salinities within the surface soil profiles (0-15 cm) via the capillary rise of saline ground water.

Where saline, shallow ground water was present increases in soil salinities were minimised by the presence of an overlying lens of fresh surface water. The presence of a fresh water lens was considered to minimise increases in soil salinities by; providing a hydrological head of fresh water which minimised ground water up welling; and by minimising drawdown and hence the capillary rise of saline ground water.

The response of *T. domingensis* to salinity at the T15 site where salinities were chronically high, reflected that observed in pond experiments. However, the at the TB18 site where soil salinities were only significantly higher than the TB3 site in September and December '96, in the 15-30 cm profile only, the influence of salinity on performance is ambiguous. Both *T. domingensis* and *B. arthrophylla* demonstrated short term responses representative of non-salinised plants, with high rates of photosynthesis and high g_S. However, morphological characteristics of both species reflected that of salinised plants, with substantial reductions in height and LAIs. Whether the morphological responses observed at the TB18 site are the result of high salinities in previous years, or if high external salinities at the initiation of new growth, or residual salts in rhizomes exert strong influences on growth characteristics remains speculative.

A history of high salinities at this site may also induce morphological changes which become less plastic over time. As suggested by Goldberg and Novoplansky (1997), where resources are supplied in pulse events success during interpulse periods, when resources are limited will depend on the capacity to tolerate periods of resource limitation. Success during interpulse periods is also considered to be dependant on how responses during pulse periods influence tolerance to interpulse periods. Periods of low salinity may stimulate increases in leaf area, which may increase susceptibility to salinity under saline conditions, by increasing the

demand for water. Consequently, where salinity is chronically variable a more conservative and less responsive leaf area may prove adaptive.

The inherent variability of salinity both spatially and temporally suggests that vegetation may experience salinity differently, depending on rooting depth and timing of growth. For example, floating or shallowly rooted vegetation will experience salinities associated with surface water which will generally be lower than soil salinities. However, as the system dries out the greatest increases in salinity will be at the sediment surface. Tolerance will therefore depend on the capacity to complete the life cycle prior to drawdown, and for seeds to tolerate exposure to high salinities without germination being affected. As the rooting depth increases, the influence of soil salinities in the deeper profile will more strongly influence performance. Whilst salinities in deeper soil profiles may be high when the ground water is saline, increases in salinity associated with drawdown will be less pronounced. Roots located deeper in the soil profile may therefore permit access to relatively less saline water during drawdown. Where roots proliferate both at the sediment surface, permitting access to fresh surface water when present, and in deeper soil profiles, permitting access to alternative water sources as surface soil profiles become more saline, greater resilience to salinity may be demonstrated. The capacity to exploit zones of lower salinities is considered an important mechanisms which facilitates the survival of *M. halmaturorum* in highly saline environments (Mensforth 1996). Species such as *Phragmites*, in which rooting depth can reach 1 m (Adcock and Ganf 1994) will also have the potential to avoid high salinities by greater access to zones of lower salinities. Lissner and Schierup (1997) found the salt tolerance of *Phragmites australis* in a coastal marsh to be correlated with soil salinities rather than surface water salinities, which tended to be higher. In this work the shift in root biomass towards the deeper soil profile at the T15 site, where salinities were lower and water content higher, also demonstrates plant responses to zones differing in salinity.

As a number of aquatic macrophytes have been demonstrated to share water resources between connecting ramets this represents a further strategy of avoiding salinity (Evans and Whitney 1992; Hester *et al.* 1994). This will be of particular benefit where soil salinities are

laterally heterogenous as demonstrated at the TB18 site. High salinities may also be avoided if growth can be completed before salinity increases to levels which limit productivity. The rapid growth of *T. domingensis* compared to *B. arthrophylla* at the TB3 site in which peak productivity was reached in January and March, respectively, suggests that *T. domingensis* is more likely to be able to escape high salinities associated with drawdown than *B. arthrophylla*.

5.7 The contribution of vegetation to the water balance

As demonstrated drawdown can result in large and rapid increases in both soil and surface water salinities. Consequently, in salinity prone wetlands the impact of vegetation on the water balance will be of critical importance in determining the extent of drawdown and hence increases in salinity .

Water loss from both *B. arthrophylla* and *T. domingensis* canopies (E_C) was found to be strongly influenced by the LAI, rather than by aerodynamic or stomatal resistance. As such, differences in E_C between species and between sites were attributed to differences in LAIs. LAIs at the TB3 site where salinities were low, were greater in *T. domingensis* than *B. arthrophylla*. At the two sites influenced by saline ground water, LAIs were reduced and differences between species were absent.

LAIs measured under field conditions for *T. domingensis* were generally lower than that measured in controlled pond experiments, whilst the converse was true for *B. arthrophylla*. For *T. domingensis* the maximal LAI attained in pond experiments was c. 8.5, whilst in the field the maximum was c. 6. Higher LAIs attained under experimental conditions may have been due to either higher nutrient levels than present in the field, or as light interception was increased due to edge effects. In pond experiments the peripheral surface area was greater than the total area, increasing light interception, whilst in the field edge effects are small and light capture will be lower. For *B. arthrophylla* the maximal LAI under experimental conditions was c. 1.3 whilst in the field it was 3.25. Lower LAIs under experimental conditions are most likely associated with the slow growth of *B. arthrophylla*.

Whilst LAIs strongly influenced E_c, the effect of LAIs on total rates of water loss (E_{total}) was considerably less. Where LAIs were reduced the penetration of light below the canopy was increased, enhancing evaporation of water below the canopy. Consequently, whilst low LAIs reduced canopy transpiration it increased water loss below the canopy.

When water loss below the canopy is considered, then LAIs greater than 0.5 were found to increase water loss above open water. At a LAI of c. 1.5 total water loss from stands of either species was found to be c. 35% greater than open water. Increases in the LAI above this elicited relatively small increases in rates of water loss. The finding indicates that the presence of either *T. domingensis* or *B. arthrophylla* stands will increase water loss and hence the rate of drawdown. As discussed by Bernatowicz *et al.* (1976) the influence of vegetation will however depend on the area covered by vegetation, and the influence of the vegetation types present on the water balance. Where the wetland has large areas of deep open water, increased water loss by vegetation may be insignificant. The influence of emergent macrophytes on the water balance of four Mazurian lakes was calculated by Bernatowicz *et al.* (1976) based on rates of water loss from each type of vegetation dominating the lakes, the area covered by them, and rates of evaporation among plants. In three of the four lakes examined water loss was 17 to 27% greater than open water, whilst in only one was it reduced by 8% .

In this study water loss from vegetation and open water were found to be differentially influenced by climatic conditions, with evapotranspiration from vegetation being influenced more by VPD than was open water. As such, E from vegetation tended to exceed open water when VPD was high. The influence of the species examined on water loss will therefore be greatest in summer when VPD is maximal. In regions in which VPD is low the impact of vegetation will be less pronounced.

It is proposed that for vegetation to reduce water loss below that of open water would require a high LAI, and a high light extinction coefficient; such that the canopy intercepts all

incoming solar radiation, preventing water loss below the canopy. Furthermore, the resistance to water loss by the canopy would also need to be high, requiring high stomatal resistances. The species examined in this work demonstrated low stomatal resistance when LAIs were high, hence it is unlikely that in these species water loss will be reduced below open water. However, higher resistances are reported for a number of salt marsh species which can also achieve high LAI (Giurgevich and Dunn 1982), suggesting that water loss may be lower than open water in other species.

5.8 Ecological implications of elevated nutrients and salinities

The findings of this work have a number of implications in predicting the influence of increased nutrient inputs and salinities on aquatic flora. For species with high RGRs nutrient load will moderate the impact of salinity. This implies that variable responses to salinity will be demonstrated in wetlands differing in nutrient status. However, as salinities increase the influence of nutrient load also diminishes.

Differential responses of species with high and low RGRs to nutrient load, indicates that at low salinities high nutrient loads will favour species with high RGRs. However, as the influence of nutrient load diminishes at higher salinities, species with higher RGRs will become less competitive.

Salinity and nutrient regimes within wetlands demonstrate spatial and temporal variability which is compounded by anthropomorphic perturbations in flow regime and nutrient inputs. The frequency of these changes may dictate community structure (Goldberg and Novoplansky 1997). Even in regions where salinities are normally prohibitive to less tolerant species, periods of low salinity, if of sufficient frequency may permit persistence. Rhizomes and tubers by enabling dormancy during period unfavourable for growth will also facilitate persistence. The invasion of *Typha orientalis* in salt marshes dominated by the more salt tolerant *Juncus krausii* has been attributed in part to increased freshwater inputs arising from stormwater drainage (Zedler *et al.* 1990). As implied by this work, nutrient pulses carried in storm water events may also favour the persistence of *Typha orientalis.*

This work demonstrates that considerable disparities may exist between surface water and soil salinities. Moreover soil salinities may vary both laterally and with soil depth. Both surface water and soil salinities are subject to pronounced seasonal variation imposed by drawdown and interactions with shallow saline ground water. The success of aquatic vegetation will therefore be influenced not only by the upper limits of salinity tolerance at each life stage but by:

- The extent to which zones differing in salinity can be exploited.
- The capacity to complete the life cycle before salinities become prohibitive to growth.
- The capacity to share water sources between connecting ramets.
- The ability of the rhizome to support dormancy during periods unfavourable for growth.

Consequently, differential tolerances between species not apparent under experiment conditions may be expressed under field conditions. Clearly further field based research exploring the dynamics of salt fluxes within wetlands and the response of vegetation to these changes is needed.

As greater demands are placed on water resources the water requirements of natural systems must be more clearly defined. This work demonstrates that consideration must be given to:

- The impact of drawdown on salt accumulation in regions underlain by shallow saline ground water
- The significance of surface flows in leaching accumulated salts from wetlands systems
- The influence of ground water seepage into wetlands
- The potential for ground water recharge to leach salts back down the soil profile.

It has been demonstrated that vegetation has the potential to substantially enhance water loss at times when water is most limiting. The impact of vegetation on the water balance must therefore be considered to ensure that sufficient water is allocated to support vegetation and prevent increases in salinity.

Table 5.1. Summary of growth parameters for each species examined in this work and for herbaceous C_3 species reported by Lambers and Poorter (1992), mean values are in parenthesis.

Growth Parameter	*B. medianus*	*T. domingensis*	*B. arthrophylla*	C_3 Herbs
RGR mg g day^{-1}	42-22	42-32	20-15	386-19 (158)
NAR g m^{-2} day^{-1}	16-11	33-26	14-11	65-2 (18)
LAR m^{-2} kg^{-1}	2.8-2.0	1.3-1.0	1.6-1.3	25-2 (10)
SLA m^{-2} kg^{-1}	11.2	4.1	3.6	131-10 (34)
LWR g g^{-1}	0.22-0.10	0.30-0.22	0.50-0.41	0.81-0.26 (0.53)
RWR g g^{-1}	0.16-.054	0.26-0.096	0.11-0.062	0.38-0.22 (0.29)

Appendix A

Table A.1. Composition of Osmocote® and Osmocote Plus®.

Osmocote®	
Nitrogen	18%
Ammoniacal nitrogen	10.5%
Nitrate nitrogen	7.5%
Phosphorous	4.8%
Potassium	8.3%
Sulphur	4.2%

Osmocote Plus®	
Nitrogen	16%
Ammoniacal nitrogen	8%
Nitrate nitrogen	8%
Phosphorous	3.5%
Potassium	10%
Sulphur	3.6%
Calcium	2.0%
Magnesium	1.2%
Iron	0.15%
Manganese	0.06%
Copper	0.05%
Molybdenum	0.02%
Boron	0.02%
Zinc	0.015%

Table A.2. Percent nitrogen and carbon isotope discrimination in top, middle and bottom sections of *T. domingensis* leaves from each site in December 1996. Data are means ± SD.

	TB3	TB18	T15
%N			
Top	2.48 ± 0.15	1.74 ± 0.46	2.36 ± 0.15
Middle	1.37 ± 0.16	1.78 ± 0.21	2.01 ± 0.25
Bottom	0.79 ± 0.15	1.57 ± 0.84	1.03 ± 0.12
Δ ‰			
Top	20.11 ± 0.36	20.07 ± 0.26	18.28 ± 0.27
Middle	20.39 ± 0.30	20.00 ± 0.27	18.02 ± 0.30
Bottom	20.61 ± 0.46	20.43 ± 0.41	17.94 ± 0.65

Table A.3. Daily changes in stomatal resistance (s m^{-1}) in February 1997, for outer (T.O) and inner (T.I) *T. domingensis* leaves, and *B. arthrophylla* stems (B) at each site. Data are means ± SD.

	TB3			TB18			T15	
Time	T. O	T.I	B	T .O	T.I	B	T .O	T.I
0900			63.4 ± 15.1					
0930								
1000	101.8 ± 7.2	74.16 ± 4.3		53.9 ± 8.2			153.7 ± 16.2	
1030			64.5 ± 16.6			35.0 ± 1.16		
1100				54.0 ± 5.5	34.1 ± 5.6			
1130	95.3 ± 11.7	85.5± 6.2				50.3 ± 11.7	156.5 ± 29	111 ± 21.4
1200								
1230							195 ± 26.6	152.8 ± 10.6
1300			96.2 ± 14.5					
1330	98.0 ± 30.0	76.0 ± 7.9		56.3 ± 20.7	37.8 ± 6.9			
1400								
1430						76.2 ± 25.1	249.4 ± 34	227.5 ± 40.0
1500			115.5 ± 22.7					
1530							259.9 ± 55	
1600	125 ± 24.5	83.8 ± 14.5		83.2 ± 19.0	49.7 ± 6.4			
1630								196.7± 22.7
1700							220. ± 18.2	
1730			93.8 ± 13.0	126.7 ± 17.1	60.3 ± 4.9	70.35 ± 4.7		
1800								
1830	211 ± 47.6					73.5 ± 13.0	240 ± 41.2	198.9 ± 42

Table A.4. Daily changes in stomatal resistance (s m^{-1}) in March 1997, for outer (T.O) and inner (T.I) *T. domingensis* leaves, and *B. arthrophylla* stems (B) at each site. Data are means ± SD.

	TB3			TB18			T15	
Time	T. O	T.I	B	T .O	T.I	B	T .O	T.I
0830							174.4 ± 5.9	127.8 ± 3.9
0900						47.9 ± 5.7		
0930				67.2 ± 14.8	48.6 ± 9.3		207.2 ± 1.3	191.0 ± 3.9
1000	100.2 ± 18.8	94.1 ± 28.9						
1030			59.8 ± 6.9				234.7 ± 1.7	209.9 ± 2.5
1100						65.4 ± 3.9	197.1 ± 1.5	196 ± 1.4
1130	101.9 ± 12.3	87.9 ± 13.6		82.0 ± 7.5	59.3 ± 13.1			
1200			88.5 ± 10.0					
1230								
1300							204.0 ± 2.4	206.3 ± 2.0
1330						98.8 ± 9.2		
1400	105.8 ± 18.5	93.3 ± 15.3		80.3 ± 13.6	69.8 ± 8.0			
1430								
1500			113.1 ± 17.0			113.6 ± 13.2	253.4 ± 1.7	250.1 ± 2.1
1530								
1600	163.2 ± 24.2	107.5 ± 21.9		131.9 ± 22.5	120 ± 32.0			
1630			86.4 ± 9.5					
1700						88.3 ± 9.6		
1730				145.0 ± 49	103.2 ± 46			

Table A.5. Daily changes in stomatal resistance (s m^{-1}) in April 1997, for outer (T.O) *T. domingensis* leaves and *B. arthrophylla* stems (B) at the TB3 and TB18 sites. Data are means ± SD.

	TB3		TB18	
Time	T.O	B	T.O	B
0830				
0900	185.0 ± 22.9			
0930		66.4 ± 4.3		
1000				
1030	151.6 ± 28.2		186.0 ± 30.6	
1100		86.5 ± 16.4		97.4 ± 20.3
1130			131.5 ± 30.6	
1200				
1230				104.2 ± 18.1
1300	169.0 ± 28.6			
1330		106.7 ± 11.7		
1400				
1430				
1500	202.5 ± 13.8			168.4 ± 76.8
1530		124.1 ± 25.8	217.1 ± 41.3	
1600				
1630				127.3 ± 22.6
1700	266.9 ± 37.0		262.8 ± 32.4	
1730		167.2 ± 20.7		

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