THE AUTECOLOGY OF *TYPHA* SPP. IN SOUTH-EASTERN AUSTRALIA

by

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"The method employed I would gladly explain,
   While I have it so clear in my head,
If I had but the time and you had but the brain -
   But much yet remains to be said.

In one moment I've seen what has hitherto been
   Enveloped in absloute mystery,
And without extra charge I will give you at large
   A lesson in Natural History".

Fit the Fifth: The Beaver's Lesson
from The Hunting of the Snark
Lewis Carroll

DECLARATION

To the best of my knowledge and belief, this thesis contains no material previously submitted for a degree or any other award, in any university by any person, or any material previously published or written by another person, except where due reference is made in the text

Jane Roberts

SUMMARY

The thesis is an autecological study of Typha spp., a freshwater emergent macrophyte common in south-eastern Australia. Typha forms dense stands, frequently monospecific, in natural and man-made habitats. There are two morphologically similar species endemic to Australia, the narrow-leafed T. domingensis and the broad-leafed T. orientalis. Their physiological and habitat differences have not been investigated. The ecology of emergents in Australia is little known and has relied on overseas work. Annual production of dry matter and aspects of the germination ecology of Typha have been quite well-studied in North America, Europe and India. However it cannot be assumed that studies done in mid-latitude regions of the northern hemisphere can be usefully applied to lower latitude warmer regions such as Australia. This study attempts to understand the ecology of Typha in Australian conditions. It is uses four component niches (Grubb 1977) as a framework, life form, phenology, habitat and regeneration.

For the life form niche, annual aboveground production of T. orientalis was estimated from changes in standing crop using Smalley's method, modified to account for mortality and within stand variability. Standing crop changes in the year suggested an annual cycle of spring growth and autumn die-back but demographic data showed that growth and production continued all year round. Aboveground production of T. orientalis was above the published range for Typha spp. This was probably due to the relatively mild climate of western New South Wales. Whole plant production was estimated after making a correction for rhizome mortality and translocation. Most of annual production went to the canopy, either directly as leaves or indirectly as starch storage. Thus the leaf was key to aboveground growth and the rhizome to production. Less than 2% of the yearly total was allocated to reproductive structures, peduncle and

seeds.

For the phenology niche, shoot life cycle was monitored in permanent quadrats over one year and included T. domingensis and T. orientalis at two sites. The species were similar in terms of the timing of shoot recruitment, canopy development and seasonal mortality, but differed in reproductive allocation and life cycle. There were two unplanned treatments, a 3-4 month summer drought and grazing. Summer drought advanced shoot death and seed dispersal, and postponed shoot recruitment until conditions improved. The effects of grazing were herbivore specific with waterfowl having the greatest impact, probably because they grazed more frequently and their manner of grazing was more destructive. The result was a shoot population with a completely different age structure.

Water is the key factor in the distribution of emergents yet the role of water in the ecology of emergents has been little investigated. The warm dry climate of south-east Australia means water is a transient characteristic of the habitat and regeneration niches. The study of water in the habitat niche was in two parts. The first was a field study which correlated an observed height gradient of Typha with substrate water availability. A static definition of water availability was used, matric potential, and the primary importance of water as opposed to other substrate resources was determined by soil analyses. The presence of Typha was not indicative of resource adequacy because the clonal habit allowed resource sharing between ramets. Thus the probable range for R*, the equilibrium resource level for T. domingensis in a semi-natural field situation in South Australia, was between -0.13 and -0.006 MPa, levels which are close to Field Capacity and adequate for species from other habitats. The second part of this study sought to understand reasons for this limitation. The relationship between resource availability, transpiration and growth was investigated in a lysimeter experiment using

isolated ramets of T. domingensis and solutions of polyethylene glycol to give a controlled water potential for substrate. Experimentally determined R* values were lower than field values, -0.7 MPa, probably because of differences in canopy size and connected versus isolated ramets. A hypothesis put forward to explain why R* values close to Field Capacity were limiting for Typha spp. was based on a number of anatomical and morphological characteristics.

Three types of factors were considered for the regeneration niche, water availability, light and seed characteristics, and eight seed types were used from sites in south-east Australia. The two principal components of water availability, matric and osmotic potential, were investigated separately using polyethylene glycol and sodium chloride solutions. Surprisingly, Typha was relatively unaffected by dry conditions, with almost maximal germination and seedling survival as low as -1.0 MPa. Salt sensitivity in young seedlings was removed by nutrients. Germination was light dependent. In general sense, seeds and seedlings had similar responses regardless of provenance and variations in seed characteristics, but their responses were not uniform.

Finally, the four niches are brought together and the significance of key characteristics discussed in relation to whole plant ecology.

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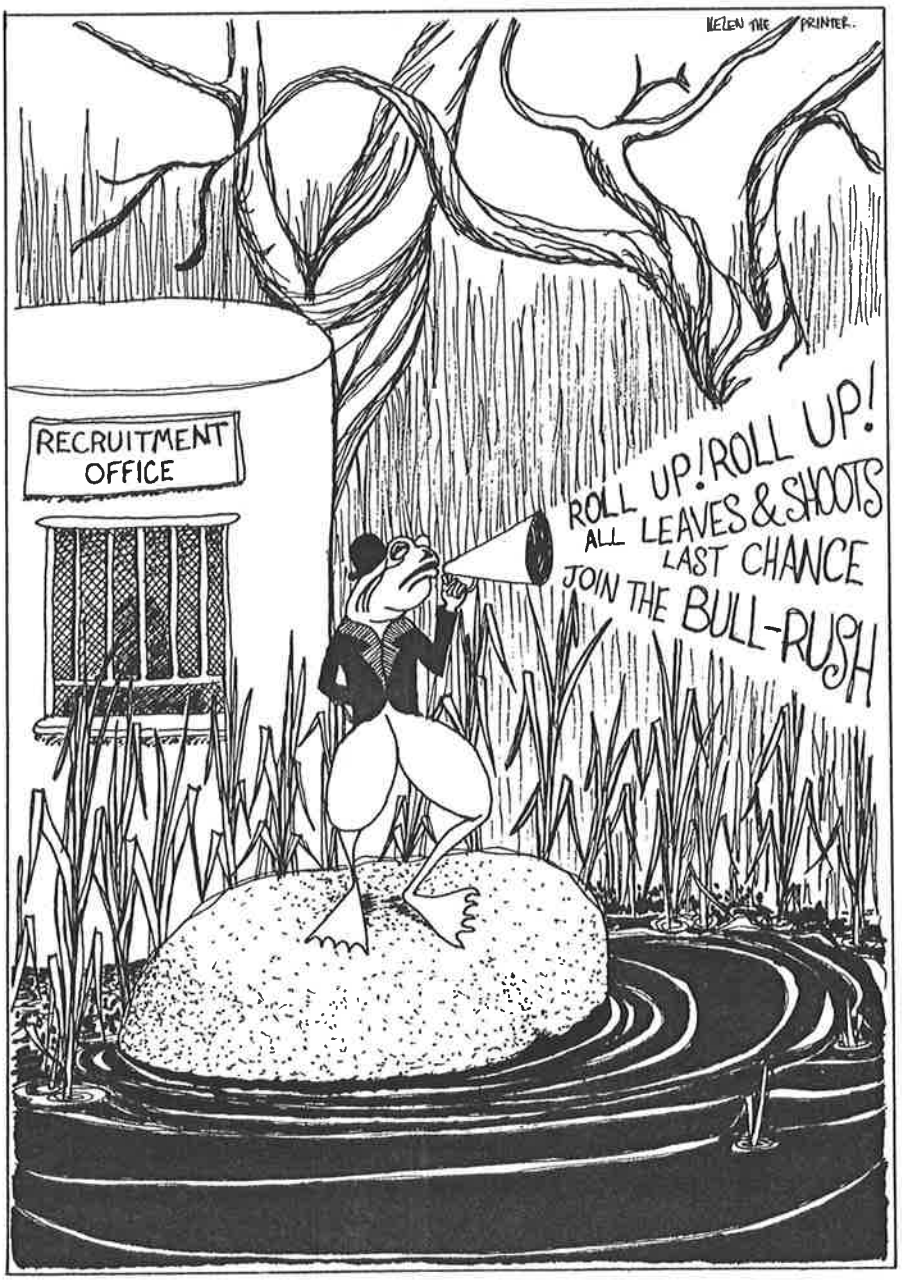
HELEN THE PRINTER.
RECRUITMENT OFFICE
ROLL UP! ROLL UP!
ALL LEAVES & SHOOTS
LAST CHANCE
JOIN THE BULL-RUSH

Chapter One

INTRODUCTION TO THE STUDY

1.1 Rationale for the study

In comparison with other continents, Australia is depauperate in wetlands (Note: terms used in this study are defined in Table 1.1). Maps in Gore (1983) and Paijmans et al. (1985) show that wetlands cover only a small part of the continent. This is thought to be due to a combination of climatic and topographic factors which makes most of Australia unsuitable for wetlands, especially permanent ones (Campbell 1983).

Possibly because of their relative rarity, wetlands have received little scientific attention. In 1965, authors reviewing tropical freshwater systems were frustrated by the almost complete absence of relevant Australian studies (Walker and Gregory 1965). This situation was slow to change. In 1975 CSIRO Division of Land Use Research published a series of technical memoranda summarising and reviewing wetland literature for individual states (e.g. Smith 1975) which showed that published work on wetlands was descriptive rather than investigative. A strong bias towards "recreational organisms", waterbirds and fish, was evident which reflects the contribution of enthusiastic amateurs to wetland ecology.

Since then the number of wetland studies has increased. This has been due to a growing perception of wetlands as part of our natural resource and to the need to understand this resource when resolving conflicts of interest. Concern at the extent of wetland loss and irreversible change (Goodrick 1970, Tyler 1976, DEP 1983) has prompted - belatedly - regional surveys (Kirkpatrick and Harwood 1983), regional assessments (Jones 1978), discussion of different classification systems (Goodrick 1984,

Pressey 1986) and national compilations (Paijmans et al. 1985) as well as documentary studies on large wetlands or wetland areas such as Maquarie Marshes in New South Wales (Knights 1980, Paijmans 1981), the Barmah Forest of Victoria (Dexter 1978, Chesterfield 1986) and the South-East region of South Australia (Jones 1978, DEP 1983). Awareness of the recreational importance of duck shooting has resulted in a specific type of wetland research directed towards conservation and management of recreational species of waterbirds and classification and assessment of wetlands as duck habitats (Lavery 1975).

Concurrent with this development of wetland science, there have been three landmarks in the study of wetland plants. These are the publication of illustrated regional aquatic flora (Aston 1973, Sainty and Jacobs 1981), a review of introduced and indigenous aquatic weeds (Mitchell 1978a) and a synthesis of available literature on wetland vegetation (Briggs 1981). The review by Mitchell (1978a) included a useful introduction to macrophyte ecology in an Australian context. However understanding of macrophyte community and species dynamics is still poor (Briggs 1981). This is probably because there have been only a few field-based wetland studies (e.g. Briggs et al. 1985, Briggs and Maher 1985) and because of a tendency to consider Australian species as ecological equivalents of overseas species. Mitchell (1978b) cautioned against uncritical use of overseas data in Australia. His argument, that there are gross environmental differences which could have an ecological significance, means there is a strong case for studying Australian species within local conditions (Mitchell 1978b). As yet this question of ecological equivalence has received little attention. Possibly the most important developments in aquatic plant research have been in the use of wetland systems to treat wastewater (Finlayson and Chick 1983, Cary and Weerts 1984, Chambers 1984).

The purpose of this study was to fill these gaps by undertaking an autecological study of a species important in Australian wetland ecology. The taxon chosen for study was Typha spp.

1.2 Typha: an introduction

Typha is an emergent macrophyte. It is a herbaceous perennial, with a rhizomatous habit, found in water approximately 0-2 m deep. The genus comprises about 10 species (Cook et al. 1974) with a cosmopolitan distribution. Two species are native to Australia, T. orientalis Presl., a tetraploid species 2n = 60 native to south-west Pacific, and T. domingensis Persl. a diploid species widespread in tropical and warm temperate zones (Briggs and Johnson 1968). There is no evidence of hybridisation (Briggs and Johnson 1968, Finlayson et al. 1985) even though they grow in similar habitats, sometimes adjacent. A third and introduced species T. latifolia is also present in Australia but has a limited distribution (Finlayson et al. 1983).

Species are morphologically similar. The Australian species are difficult to distinguish in the field but can be separated using three measurements of the inflorescence (Finlayson et al. 1985). Where two species are sympatric, typically one is broad-leafed and the other narrow-leafed such as T. elephantina and T. angustata in India (Sharma and Gopal 1980) and T. orientalis and T. domingensis in Australia. Sympatric pairs differ subtly in rhizome biology (Marsh 1962, Sharma and Gopal 1977, Grace and Wetzel 1982a), resource allocation (Grace and Wetzel 1982b) and reproductive biology (Krattinger 1975, Sharma and Gopal 1980).

These differences have have been studied only in USA (Grace and Wetzel 1981a, 1981b, 1982a). Their results cannot be uncritically extrapolated to Australia because it appears that tolerance traits are not consistent with leaf type between continents. In India the broad-leafed species

grows vigorously in drier and more saline habitats (Sharma and Gopal 1977) but in USA it is the two narrow-leafed species which are more characteristic of unstable or saline habitats (Smith 1967). In Australia T. domingensis may be more tolerant of desiccation and/or salinity than T. orientalis. It is more frequently found in inland seasonally dry sites (Briggs and Johnson 1968) and, at least in Victoria, in less acidic conditions, mean pH = 7.8 compared to 6.1 for T. orientalis (Barson 1984).

As with many rhizomatous emergents, the clonal habit of Typha means that genotypes can only be identified by specialist mapping techniques. In Switzerland, iso-electric focussing of pollen proteins showed that genotypes of T. latifolia did not form discrete clumps within the stand but intergraded (Krattinger 1983). This kind of mapping may define individual genotypes but it cannot identify physiological individuals, the size and number of which are determined by rhizome longevity. This has been variously estimated as one year (Gustafson 1976) and two to three years (Krattinger 1983).

One characteristic of Typha that is frequently mentioned is plasticity. This is more often physiological than morphological. Populations originating from different climates have different photosynthetic characteristics which were retained when transplanted to uniform conditions (McNaughton 1966a). Similarly, enzymes from ramets of different provenances had different thermal sensitivites (McNaughton 1966b, McNaughton 1969) and thermal stabilities (Liu et al. 1978). Summaries of variations found in North American species are given by Mashburn et al. (1978) and Sharitz et al. (1980). Some natural variation could be expected in Typha because of its wide distribution and nuisance status. One of the "ideal" weed characteristics is tolerance and plasticity (Baker 1974).

Up to 1980, literature on Typha spp. in Australia consisted of a taxonomic revision (Briggs and Johnson 1968) and early observational studies on germination and control in irrigation channels (Prunster 1940, 1941). The biology of Typha spp. with reference to Australia was recently reviewed (Finlayson et al. 1983) but relied heavily on overseas work where it has been much studied particularly in USA, Europe, India and Africa. The extensive literature on Typha, both scientific and anecdotal, covers taxonomy, production and germination.

Within Australia Typha has many "hats". It is a common type of wetland vegetation throughout coastal and southern inland Australia (Briggs 1981) and is a habitat and refuge for waterfowl (Braithwaite and Frith 1969, Fjeldsa 1985). It is a nuisance plant in farm dams and irrigation works (Mitchell 1978a, Finlayson et al. 1983) and recognised as a wetland invader in Western Australia. It can rapidly colonise isolated man-made waterbodies, even in central Australia (Finlayson et al. 1983, Symon 1984). It is also one of several emergent species being investigated for treating wastewater (Finlayson and Chick 1983). This variety of "hats" makes it a challenging plant.

One way of focussing an autecological study is to describe the species niche, where the niche is the total relationship of that species to its environment, both physico-chemical and biotic. As such it can be completely defined by four component niches (Grubb 1977), life form, phenological, habitat and regeneration niche. These are discussed below with reference to emergent macrophytes and to Typha as appropriate.

1.3 The four niches

The life form niche, which includes size, annual productivity and 3-dimensional pattern (sic Grubb 1977), and the phenological niche, which is the pattern of seasonal development, both describe growth. The habitat niche is the physico-chemical limits tolerated by the mature plant, thus

it is the plant's position on a number of overlapping gradients. This definition refers only to the fundamental niche. The regeneration niche includes elements of the other niches and summarises conditions that must be met to ensure successful replacement.

The two outstanding growth characteristics of large emergents is high annual production and formation of dense often monospecific stands. Comparisons with other plant communities show that swamps and marshes have a mean annual (aboveground) production of 2000 g dry weight m^{-2} y^{-1} compared with 500 for temperate grasslands or 1500 for "raingreen" forests (Lieth 1975). These estimates are based on data from cool temperate zones, usually latitudes higher than 40°, where the growing season is well-defined (Bradbury and Grace 1983). At lower latitudes, where the growing season is longer or even continuous, production may be even higher. There is already some evidence for this, namely the few studies done in the tropics and subtropics (e.g. Howard-Williams and Lenton 1974, Thompson *et al.* 1979) which show high standing crops and turnover. Put together, these studies show an inverse correlation between latitude and maximum biomass in widely distributed taxa such as *Spartina*, *Carex* and *Phragmites australis* (Keefe 1972, Gorham 1974, Westlake 1982).

Typha is similar to these other emergents, with annual aboveground production estimates ranging from 500-2000 g dry weight m^{-2} y^{-1} (Keefe 1972, Westlake 1975, Bradbury and Grace 1983). Maximum seasonal biomass is strongly influenced by latitude-related factors (Figure 1.1: references in Appendix 1). All references to *Typha* at latitudes of 40° and higher, regardless of species, report a seasonal growth pattern with a spring flush, autumn die-back and winter inactivity (e.g. Penfound 1956, Bernard and Fitz 1979, Mason and Bryant 1975). At latitudes lower than 40°, this seasonality is not so apparent. Some populations show year-Bnd growth whilst others retain a strongly seasonal pattern (Sharma

and Gopal 1977, Ramirez and Anazco 1982). As mainland Australia lies between 10°-40°S, it was possible that, as suggested by Mitchell (1978b), the Australian species could differ from species of higher latitudes in terms of production and phenology.

Emergents are slightly unusual in the plant world as biotic interactions have little importance in limiting their distribution. Therefore the realised niche approaches the fundamental niche. The only effective competitors recorded are other emergents (Buttery and Lambert 1965, Fiala and Kvet 1971, Yamasaki and Tange 1981, Grace and Wetzel 1982a). Herbivory is not thought to be important. Although it may be intense enough to alter biomass allocations within the plant, this effect is usually localised (van der Toorn and Mook 1982, Boar and Crook 1985). Consequently herbivory has not been considered a factor in wetland plant distribution. This traditional view has recently been challenged by case histories of dramatic change due to herbivory, all of which involve introduced herbivores, such as cattle in Australia (Chesterfield 1986) or muskrats in Sweden (Danell 1979).

The most obvious feature of the habitat niche is vertical distribution with respect to water depth, evident as well-defined boundaries and referred to as zonation (Hutchinson 1975). Boundaries are obvious because pronounced changes in life form, size and biomass accompany species replacements (Mandossian and McIntyre 1960, van der Valk and Bliss 1971). Extensive field experiments on zonation patterns in the rocky inter-tidal zone have shown that species' upper limit tends to be set by physical constraints and lower limits by biotic interactions (Connell 1985). Zonation is thus a vertical sequence of truncated distributions. No comparable work has been done for wetland zonation, but it is commonly accepted that water is a physical constraint, either as depth and/or duration of inundation (Thompson 1985) which is the principal factor

controlling life form distribution (Hutchinson 1975) and community dynamics (Hejny 1971). Water table position is identified as the primary environmental gradient in wetlands whenever it is included in multivariate analyses (Walker and Coupland 1968, Howard-Williams and Walker 1974, Bernard et al. 1983, Clarkson 1984).

Physiological experiments investigating the environmental limits of aquatic plants are lacking (Spence 1982). There is some evidence that the lower limit of emergents is defined by their capacity for rhizome ventilation, i.e. oxygen limitation (Yamasaki 1984). The upper limit has received even less investigative attention. This is probably a question of perspective. In aquatic plant ecology, the emphasis has been on understanding adaptations to the aquatic environment (Sculthorpe 1967, Hutchinson 1975, Thompson 1985) rather than understanding landwards limitations.

The regeneration niche is "an expression of the requirements for a high chance of success in the replacement of one mature individual of the next generation" (Grubb 1977). In long-lived terrestrial communities with a closed canopy, such as clonal perennial herbs, within-site regeneration by seed is unlikely. Regeneration occurs away from the parent and the regeneration niche is typically disturbance-related (Silvertown 1982). This may also apply to large emergents such as Typha which are potentially long-lived and have dense canopies. The status of Typha as a nuisance plant and its extension into arid and semi-arid Australia shows that seed regeneration does occur (Finlayson et al. 1983, Symon 1984).

The regeneration niche includes all processes from seed production to seedling establishment (Grubb 1977) thus it involves two generations, the parent and the new individual. Regeneration sites can be deduced from seedling occurrence. Seedlings of emergents are most abundant on mudflats following a drop in water level (Howard-Williams 1975, Linde et al. 1976,

Gaudet 1977, Kaul 1985) and the mudflat has been accepted as the regeneration site in theoretical and empirical discussions of wetland succession (Kadlec 1962, Harris and Marshall 1963, van der Valk 1981). It appears to be favourable growing conditions as irradiance and nutrients are unlikely to be limiting, but water availability is not assured. In inland south-eastern Australia the climate is warm with a pre-dominantly winter rainfall (Paijmans et al. 1985). Consequently mudflats are likely to dry out during warmer months. Thus in the regeneration niche, as in the habitat niche, water may have an important role.

1.4 Study aims and organisation

The two themes recurring through the above discussion of the niche were growth and water. Study aims were set by combining these with the four component niches. These were:

1. To measure annual production
2. To describe growth phenology
3. To measure growth in water-limiting conditions
4. To determine the importance of water in the regeneration niche.

The species studied were the two Australian endemics. The introduced species was not considered.

Results are presented in the same order as study aims. With one exception, the investigation of each aim is contained within one chapter. Because a wide range of field and experimental approaches was used, methods and analytical techniques are given in each chapter where relevant. Two methods, use of thermistor psychrometer and measurements relating to polyethylene glycol, are given in appendices.

Standard parametric and non-parametric statistical analyses used in the study follow Snedecor and Cochrane (1967), Parker (1973) and Sokal and Rohlf (1981). Statistical programmes from the BIOM package (F. J.

Rohlf 1984) are shown by their acronym after reference to the type of analysis, for example factorial analysis of variance (FACTAN). Statistical and data conventions are set out below.

CL = Confidence limits

Calculated using correction for small (less than 30) samples with t set at 95% for n-1 degrees of freedom (Parker 1973)

V* = Coefficient of variation

Calculated using the correction for small (less than 30) samples, and expressed as a proportion (Sokal and Rohlf 1981)

nd = no data, not recorded

The results of analyses of variance are tabulated with the significance level of the calculated sample variance ratio, Fs (Sokal and Rohlf 1981) indicated by an asterisk, as follows:

NS = not significant (in statistical tests)

* = $0.01 < p < 0.05$

** = $0.001 < p < 0.01$

*** = $p < 0.001$

Table 1.1
Terminology

The usage of some common terms is set out below

WETLAND
waterbodies which are primarily lentic, whether permanent or not, with a plant assemblage which includes macrophytes, woody species and/or phytoplankton. As used here, it refers mainly to inland waterbodies whilst including saltmarshes but excluding estuaries.

WETLAND and/or AQUATIC VEGETATION
includes woody and non-woody species but excludes phytoplankton, epiphytes and other aquatic photosynthetic micro-organisms.

MACROPHYTES
vascular and non-vascular herb-like aquatic plants thereby excluding shrub and tree species.

EMERGENTS
macrophytes growing and reproducing when partially immersed, that is with leaves projecting out and above the water surface and root systems in water-logged sediment or forming a floating mat. Although tolerant of temporary immersion, their primary carbon source is atmospheric carbon dioxide. Large emergents are those in deeper water, with a shoot height of approximately 1 m or more.

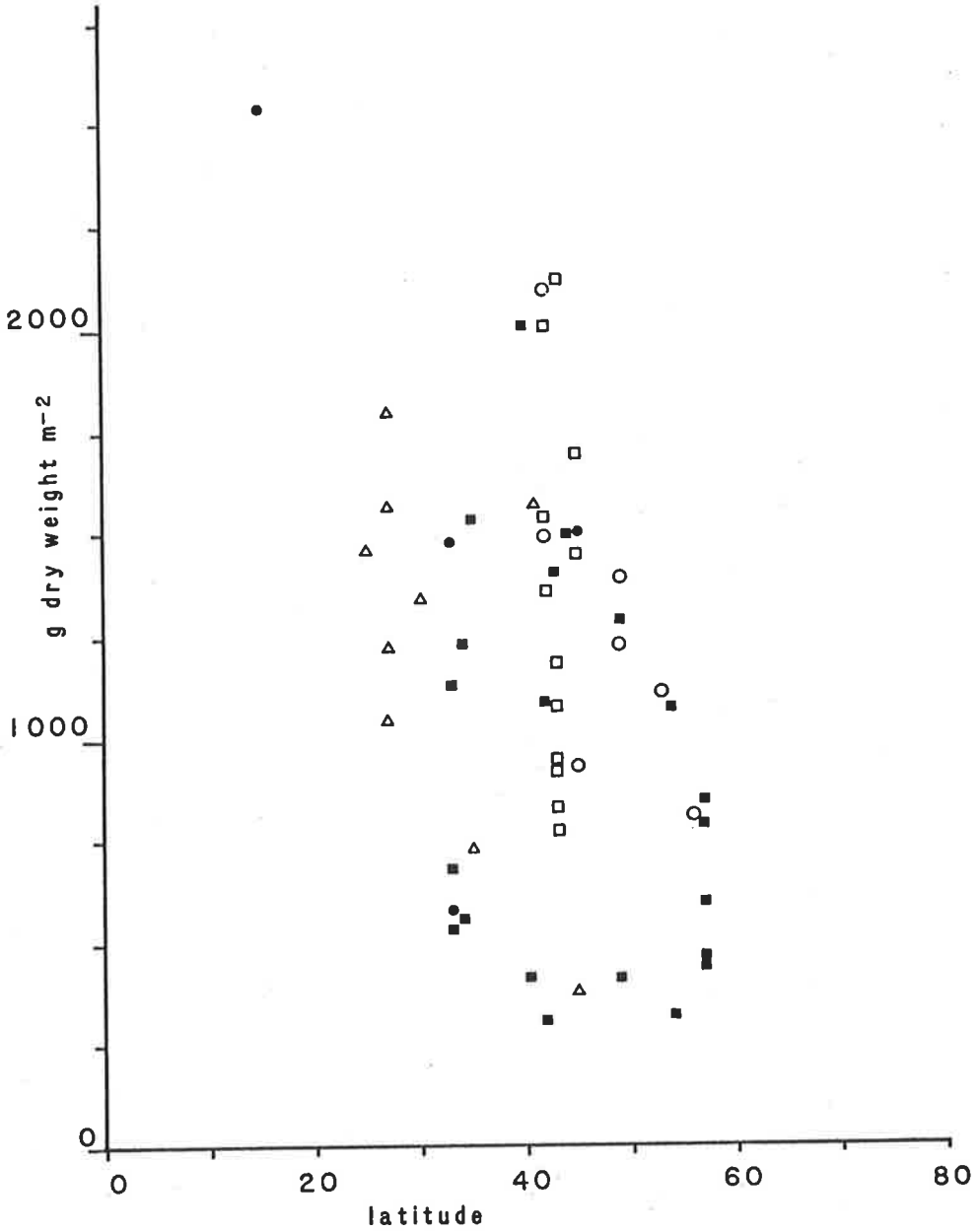

Figure 1.1
Latitudinal variation in standing crop

Maximum aboveground standing crop, as grams dry weight m^{-2}, of Typha spp., as a function of latitude.
Linear regression significant (alpha <0.005).
Predicted maximum standing crop for 34°S = 1299.9 g m^{-2}

Key
- ■ T. latifolia
- □ T. glauca including "hybrid"
- ○ T. angustifolia
- ● T. domingensis
- △ T. spp. (unspecified)

Chapter Two

ANNUAL PRODUCTION OF *T. ORIENTALIS*

INTRODUCTION

2.1 Study aims

The term, annual production, is used here to refer to all carbonaceous matter "deposited" above or below ground by the plant (Linthurst and Reimold 1978) and is expressed as g dry weight m^{-2} y^{-1}. It is assumed to measure approximately the difference between carbon fixed and carbon used. This difference can be measured more accurately by gas exchange techniques at the leaf surface but is likely to involve much extrapolation in order to understand whole plant, long-term resource allocation patterns. Measurements made over 24 hours must be repeated throughout the year under varying climatic and age conditions (e.g. Gustafson 1976). For these reasons the more conventional harvesting approach was used.

Study aims were to estimate annual and seasonal production of *Typha* and to determine resource allocation patterns.

2.2 Production methods: limitations

One of the earliest and simplest methods, and one still used, was to define the maximum and minimum standing crop by repeated harvests during the year, and assume the difference between them was equivalent to annual production. This is known as the max-min method (Westlake 1975). It assumes there has been no mortality before maximum standing crop and no production afterwards (Matthews and Westlake 1969). These assumptions have been frequently stated but rarely tested and the size of the error (if any) has not been systematically investigated. Instead, other methods of estimating production from sequential estimates of standing crop have

been developed. These fall into two main categories (described below) according to whether standing crop is measured directly by harvesting or estimated indirectly. Standing crop is usually sorted into live, dead and (sometimes) litter, referred to as fractions. The number of fractions is sometimes associated with accuracy and precision.

Methods of calculating production from direct estimates of standing crop are often referred to by their proponents' names, e.g. Milner and Hughes', Smalley's, Wiegert-Evans' or Lomnicki's modification. Milner and Hughes' method uses changes in live standing crop only and therefore reduces to max-min method (Kirby and Gosselink 1976). Smalley's method uses live and dead standing crop and corrects for mortality in live standing crop but not for losses from dead standing crop (Kirby and Gosselink 1976, Linthurst and Reimold 1978). Wiegert-Evans' method corrects for losses from dead standing crop by measuring instantaneous loss rates using paired plots or litter bags (Kirby and Gosselink 1976, Linthurst and Reimold 1978, Groenendijk 1984). Lomnicki's modification of Wiegert-Evans' method uses paired plots to measure the rate at which dead material is produced (Shew et al. 1981). Direct methods also include the so-called "mortality" methods which estimate production from dead material only (Linthurst and Reimold 1978, Hopkinson et al. 1980).

Indirect estimates of standing crop use shoot demographic and weight (Mason and Bryant 1975) or shoot height:weight relationships (Lieffers 1983). Production can be corrected for shoot mortality before maximum standing crop (e.g. Mason and Bryant 1975), but these methods are not always sensitive to production later in the season. The use of mean values is justifiable only if recruitment and mortality are known to be single events. Where shoot life cycle is unknown, this may need to be established by detailed demography of shoots and leaves (e.g. Hardisky 1980, Pierce 1983). The subsequent growth analysis can then be based on

hierarchical concepts of modularity and metamerism (Harper 1978, Harper and Bell 1979, White 1984).

Several studies have assessed different production methods by comparing estimates. Most of these have been on saltmarsh species and as these have a growth form and habitat comparable to freshwater emergents, their results are relevant to Typha. Nearly all concluded that max-min, Smalley's and mortality methods underestimate whereas detailed demographic methods or comprehensive harvesting methods give more reliable estimates (Kirby and Gosselink 1976, Linthurst and Reimold 1978, Hardisky 1980, Hopkinson et al. 1980, Shew et al. 1981, Pierce 1983, Groenendijk 1984). The cost of increased reliability is increased effort. Wiegert-Evans' method requires 2-6 times more field hours than Smalley's method (Hopkinson et al. 1980, Groenendijk 1984) but it is not known if it is 2-6 times more reliable. Some authors take a pragmatic approach, recommending Smalley's method with short sampling intervals (Linthurst and Reimold 1978, Groenendijk 1984) although "short" is not defined. Sampling intervals used in these comparisons were typically four weeks (Kirby and Gosselink 1976, Shew et al. 1981, Birch and Cooley 1982, Pierce 1983) and sometimes eight (Linthurst and Reimold 1978, Hardisky 1980). These seem long for communities with a potentially rapid turnover.

Problems associated with these methods and often mentioned when production is estimated from successive harvests are losses, "fluctuations" and "negative production". Interpretation shows the problems are actually stand variability, losses from live and dead standing crop and a calculation effect.

The first problem is one of precision. Within-site variability is rarely accounted for. Calculations based on changes in mean standing crop assume all changes are significant. Reviews of production methods rarely discuss within-stand variability (Keefe 1972, Westlake 1975, 1982,

Bradbury and Grace 1983) probably because few original authors address this problem. Monospecific stands appear homogeneous (Hardisky 1980, Groenendijk 1984) but homogeneity is not always evident in standing crop data. Coefficients of variation for saltmarsh species range from <5% to 20% (Kirby and Gosselink 1976, Pierce 1983, Groenendijk 1984). Data can be smoothed using polynomial regression and this tends to give a lower estimate of annual production (Kirby and Gosselink 1976, Cramer et al. 1981, Groenendijk 1984). These lower estimates have been rejected, because variations were thought to be real (Kirby and Gosselink 1976), because fitted curves did not adequately represent fluctuations (see below) in the primary data (Cramer et al. 1981) and because not all variability was accounted for (Groenendijk 1984) even though coefficients of determination were greater than 0.97.

The words fluctuation and variation as used in production ecology refer to up-down changes over short periods such as from harvest to harvest. Kirby and Gosselink (1976) concluded that such fluctuations were "real" because two sites fluctuated in the same way at the same time, whereas Groenendijk (1984) argued that fluctuations were a sampling problem.

The second main problem, losses from standing crop, affects accuracy. Failure to account for mortality in live standing crop or losses from dead standing crop means each standing crop fraction is underestimated. Losses from live standing crop may be due to grazing or mortality. Grazing is rarely important for freshwater emergents (Keefe 1972, Westlake 1975, 1982, Bradbury and Grace 1983) perhaps because they are inaccessible to large herbivores, which are pre-dominantly terrestrial (Thompson 1985). Field work is simpler if grazing losses do not have to be measured so most studies accept shoot mortality as the principal loss from live standing crop (Westlake 1982, Bradbury and Grace 1983).

Emergents with seasonal growth lose 2-20% of annual production before maximum standing crop (Westlake 1975). In harvest methods, this loss is measured by changes in dead standing crop. Losses from dead standing crop, sometimes referred to as litterfall, can be caused by strong water movements such as tidal action which can flush out significant amounts of material (Kirby and Gosselink 1976, Linthurst and Reimold 1978). This type of loss is unlikely in non-tidal or lentic wetlands. Losses from dead standing crop can be measured as in Wiegert-Evans' method or Lomnicki's modification as described above. Errors due to not measuring litterfall may be overcome by reducing the sampling interval (Linthurst and Reimold 1978).

Translocation is a different kind of loss. In rhizomatous plants such as most emergents, the rhizome is both carbon source and sink yet few studies consider this, probably because of the considerable practical difficulties of harvesting underground material (Bradbury and Grace 1983). Whigham and Simpson (1978) suggested underground biomass could be estimated from aboveground biomass and tried to establish a species specific ratio. This approach is too simple for it assumes the ratio remains constant. In some species, growth above and below ground do not follow the same seasonal cycles and in Zizaniopsis miliacea the cycles are off-set by two months (Birch and Cooley 1982).

Negative production has been frequently reported (Kirby and Gosselink 1976, Shew et al. 1981, Groenendijk 1984). It occurs when the sum of changes in live and dead standing crops is negative (the calculation is explained below in 2.4 and Table 2.1) and may last 5-6 months (Kirby and Gosselink 1976, Shew et al. 1981). Because it occurs at times of high mortality (Linthurst and Reimold 1978), negative production has been attributed to losses from dead standing crop (Kirby and Gosselink 1976, Groenendijk 1984) and to translocation into the rhizome (Birch and Cooley

1982). Negative production means production is underestimated but by an unknown amount. There have been no suggestions as to how to cope with negative production.

2.3 Growth hierarchies

In production ecology, plant growth is measured by changes in weight. In contrast, the population biologist sees plants as a series of repeated structural units and measures growth as changes in their number. These structural units have been loosely referred to as modules (e.g. Harper and Bell 1978, Silvertown 1982) but may be modules or metamers (White 1984). A module is the product of a single apical meristem and may comprise a set of metamers, whereas a metamer is a repeatable unit such as a node. In Typha, as in most plants, a module comprises many metamers so the terms are not equivalent. In this study, modules are the basic unit for the demographic approach to plant growth. The usefulness of this approach when studying clonal plants is discussed below (3.3).

The demographic approach has three advantages. It can be applied simultaneously to different organisational levels such as shoot and leaf (e.g. Carpenter 1980). The dynamics of these levels reveal growth processes within a stand which a production estimate conceals, thus making it invaluable for determing turnover. Finally, it can be used with module or metamer dry weights to give an indirect estimate (2.2) of production (e.g. Pierce 1983, Thompson et al. 1979).

2.4 Study approach

Characteristics of the study organism and field site together determine which methods are appropriate and what modifications may be necessary. A production study of Typha shouldd consider the problems discussed above (2.2). Previously published studies have shown that mortality, variation and translocation were all likely to be important

but gave little indication as to how much or under what circumstances. Although over 50 measurements of maximum standing crop have been published (Figure 1.1), there are less than 20 estimates of production, of which only four have attempted to correct for mortality (e.g. Howard-Williams and Lenton 1975, Mason and Bryant 1975, van der Valk and Davis 1978, Bernard and Fitz 1979). The highest estimate of mortality losses before maximum standing crop was 23% of annual aboveground production (Mason and Bryant 1975). This was for T. angustifolia in a temperate climate at 53°N where the growing season is well-defined.

Standing crop variation within stands is high. For example, the coefficient of variation for T. latifolia in southern USA was usually 20-30% but reached 50% at times (Boyd and Hess 1970). In addition, there is considerable variation between sites as shown by the range from a single latitude, for example 42° and 43° (Figure 1.1). This is most likely due to site differences in the major nutrients phosphorus and nitrogen (Boyd and Hess 1970, Graneli 1985).

Starch stored in the rhizome is apparently essential to Typha in cool temperate zones. In Wisconsin, aboveground production of T. latifolia in spring was 304 g m^{-2} greater than could be accounted for by photosynthetic rate, and a carbon budget showed rhizome reserves accounted for 15% of aboveground matter produced during the year (Gustafson 1976). A seasonal cycle of starch concentrations decreasing suddenly and rapidly in spring then increasing again in summer after flowering is frequently reported for T. latifolia in cooler parts of North America (Linde et al. 1976, Kausch et al. 1981, Biesboer 1984). The importance of rhizome reserves in warm areas has not been established. The only data available, for coastal Chile at 40°S, show a strong seasonal increase then decrease (Ramirez and Anazco 1982). Starch concentrations were not measured, so it is not clear whether this

decrease was due to starch utilisation or rhizome mortality. The latter seems unlikely as there is evidence of a latitudinal gradient in Typha (McNaughton 1975) with over-winter rhizome mortality decreasing as the growing season lengthens. In colder areas of North America, it reaches 40% for T. latifolia (Grace and Wetzel 1981c).

The study area near Griffith, western New South Wales, is at 34°S, which is a lower latitude than most production studies (Figure 1.1). The area has mild winters (Butler 1979) and an earlier study measuring leaf lengths (CSIRO 1980) found T. domingensis did not die back completely during the colder months. This indicated the growing season was likely to be long or even continuous.

The production method had to take account of stand variability, standing crop losses through mortality, litterfall and translocation, and an extended growing season. The method chosen was Smalley's. Its principal limitations, failure to adequately measure dead standing crop and failure to account for stand variability, were overcome by using a short sampling interval, and statistical procedures as described below (2.5). Thus its advantages, ease of calculation and low sampling effort, were maintained. As a cross-check with previous studies, annual production was also calculated by max-min method, and as an internal cross-check, by an indirect method. For this, standing crop was estimated from shoot height:weight relationship and population census, and the accuracy of this estimate assessed by comparing estimated with actual (harvested) standing crop.

Shoot and leaf demographic data were used to help interpretation of dry weight data and production estimates. These were collected from a permanent quadrat established within the harvest area. Shoot height and demography from this quadrat were compared with harvested quadrats to give a measure of stand variability. In addition, growth of two shoots

was monitored intensively to clarify the relationship between shoot and leaf dynamics. Leaf dynamics in the permanent quadrat were used to calculate a dead leaf retention index to determine periods of high litterfall. Time limitations meant only one species was studied, T. orientalis.

METHODS

2.5 Methods

Site description

Griffith, 34°18'S 146°04'E altitude 125 m, in western New South Wales is on the riverine plains and within the Murrumbidgee Irrigation Areas (MIA). The climate is warm and dry (Butler 1979). Mean daily maxima for January and July are 32°C and 15°C and mean daily minima are 16°C and 3°C. Mean annual rainfall is 404 mm, uniformly distributed throughout the year but erratic within a season. Mean annual evaporation (US Class A Evaporation Pan) is 1889 mm with monthly maxima of 287 mm for January and 46 mm for June. The windiest time of the year is spring and summer (records held at Centre for Irrigation Research, CSIRO, Griffith). Weather records for 1980-81 were obtained from NSW Department of Agriculture at Leeton.

The study site was approximately 12 km west of Griffith (GR CC 997048 on "Koorongal" 1:100,000 topographic map, Department of Mines and Energy) where Mirrool Creek flows under Brogden's Road. Mirrool Creek is the main drainage channel and natural outlet from the MIA. It is typically bordered with Typha spp. The study site on "Kyeema" was a flat area covered with T. orientalis, approximately 100 m wide and 500 m long. Sheep occasionally grazed the adjacent paddock but did not enter the stand which was dense. The stand was usually burned in winter to destroy

habitat for "bald coots" which damage the rice crop, but had not been burned in winter 1979 (Vic Browne of "Kyeema" pers. comm. 1981). Thus at the start of the study the canopy was two growing seasons old. The site flooded when water levels rose in Mirrool Creek, either in response to rain or to synchronised release from rice fields.

Water in the Main Drain (Mirrool Creek) is turbid, high in gilvin and slightly saline. Mean conductivity in the irrigation period is 985 μS cm^{-1} s^{-1} with sodium and chloride the dominant anion and cation. Although water coming into the MIA is low in nitrogen and phosphorus, water in the Main Drain is slightly enriched, probably by fertiliser leachates (CSIRO 1980). Soils were fine dark silt.

Soil sampling

Duplicate soil samples taken from 0 cm and 20 cm in June 1981, were dried at 110°C and stored in a desiccator. Organic matter was estimated gravimetrically after 3 hours combustion in a muffle furnace at 550°C. Total nitrogen, as KN, was measured by Kjeldahl technique and soluble reactive phosphorus or SRP was measured colorimetrically using ascorbic acid, ammonium molybdate method (Murphy and Riley 1962) after overnight leaching in 5% cold HCl. Nutrient analyses of single samples were done by Australian Mineral Development Laboratories (AMDEL), Frewville, South Australia. Results are given as mg KN or SRP g^{-1} dry weight soil.

Field work: production

For the direct method, shoots of *T. orientalis* were cut at ground level every two weeks from 9 June 1980 to 12 June 1981. No harvests were done on 8 December 1980 or 16 February 1981 when the site flooded as this would have required a change in field technique which could have affected results. Harvest quadrats were 1 m by 1 m, randomly located within the stand and at least 10 m from the edge and from previously harvested

quadrats. Five replicates were used because this was the most that could be harvested, processed and prepared for drying ovens in one day.

Only standing shoots were harvested. Shoots rotted through at the base or which had fallen over were excluded. Harvests were sorted into three fractions, live, dead and burned shoots, then dried separately in a forced draught oven for 3-4 days at 75°C. Fresh and dry weights of each fraction and of individual reproductive structures (inflorescence and peduncle) were measured. Shoots were classed live when at least half (subjective assessment) the leaf area was green rather than brown, but with two exceptions: shoots damaged by rodents but with vigorous new growth were classed live, and green shoots which were soft or limp to handle were classed dead.

Data for underground standing crop were supplied by Mitchell and Chick (pers. comm.). Harvests were done at monthly intervals in a pure stand of T. orientalis beside Mirrool Creek at Gum Creek Road, approximately 14 km south of Griffith. Five randomly placed quadrats, each 1 x 1 m, were subsampled twice to 25 cm depth using metal corers. The surface area of each corer was one sixteenth of quadrat area. Preliminary harvests had shown this to be the appropriate sampling depth. Harvested material was washed, sorted into live root, rhizome and leaf fractions, and dried in a forced draught oven at 75°C for 7 days. Dead material was not measured.

Data organisation and analysis

Standing crop data were used in two forms, primary and derived. Primary data are the mean of five replicates and the coefficient of variation was used to calculate annual V* for each primary fraction.

Derived data were got by fitting a splined regression to primary replicates, thereby accounting for variation between and within harvests. In splined regression a chain of cubic polynomials is calculated. Neighbouring functions meet at knots. Because the number of knots

determines the degrees of freedom and hence width of the confidence limits and degree of fit (Parsons and Hunt 1981, Hunt 1982), it is better to have as few knots as possible and to position them close to inflexions (Parsons and Hunt 1981). Four to five knots may overfit (Hunt and Evans 1980) so three knots were used. The program used was HUNTXY, a shortened modified version (N. A. Walker, University of Sydney, 1984) version of HUNT (R. Hunt, University of Sheffield, no date). This program accepts sequential replicates, fits curves to primary data and gives a derived standing crop for each harvest date with standard errors and 95% confidence limits. Data are log normal transformed.

Annual production was calculated either by Smalley' method or by max-min method using primary and derived data. For Smalley's method, production between harvest dates is estimated from changes in live and dead standing crop, and these are summed to give annual production. The calculation for each harvest interval (Table 2.1) follows published descriptions (Linthurst and Reimold 1978, Groenendijk 1984). Mortality is the difference between production and net increase in standing crop expressed as a percentage of production.

Whole plant production is the sum of belowground and aboveground production corrected for translocation. This was estimated from maximum and minimum rhizome standing crop assuming starch concentrations of 45% and 7% (Gustafson 1976) then converting net change in starch load to equivalent dry weight using the factor 0.645 (Penning de Vries et al. 1974).

To establish whether all changes in mean standing crop were real as assumed in Smalley's method, sequential harvests were tested for significant differences by one-way analysis of variance. Homogeneity of variances was tested by F_{MAX} test. The effect of sampling frequency was determined by calculating annual production using both types of data as

if harvested at 4, 6 and 8 week intervals.

Production: indirect method

For the indirect estimate of production, shoots for height:weight relationship were harvested near the permanent quadrat and measured and dried as described above. Harvests were timed so as to cover a range of heights but were not extended beyond midsummer because height:weight relationships change once leaf loss and translocation begin (Ho 1979). Regression analysis was used to describe shoot height:weight relationship. A number of standard models were tried, and the one with the highest coefficient of determination was used.

The weight increase of individual shoots in the permanent quadrat (see below) was calculated from height changes and annual production was the sum of these. This estimate of aboveground production in the stand was therefore corrected for shoot mortality before maximum standing crop and production afterwards.

The accuracy of this method was assessed by two comparisons. The first compared indirect estimate of standing crop in the permanent quadrat with its harvest of 29 June 1981, done just after the study ended. The second compared direct estimates of live standing crop for 15 quadrats, harvested at three times in spring, with indirect estimates for the same quadrats, using demographic and height data of harvested shoots.

Demography and phenology

Demographic data for harvested shoots was collected at each fortnightly harvest for each replicate quadrat. The following measurements were made: height to tip of tallest green leaf of each live shoot; numbers of live, dead and burned shoots.

The permanent quadrat was 100 m west of the harvested area. It measured 2 m by 0.5 m. The first census was on 27 May 1980 and the last

on 3 June 1981. On average, quadrats were visited every 2-3 weeks. Water depths were measured when possible. Shoots and leaves were labelled with indelible waterproof ink. At each visit shoot height was measured to tip of tallest green leaf and a census was made of live and dead leaves. Shoots were classed dead when they had no live leaves. Leaves were classed dead when less than 50% of surface area was green.

The dead leaf retention index to define periods of high litterfall was the ratio of observed to expected number of dead leaves in the canopy. The number expected was the number observed at the beginning of the previous month plus the number dying in the interval.

Population characteristics of the permanent quadrat were compared with harvested shoots as follows: shoot density was compared with mean density by special application of the t-test (Sokal and Rohlf 1981) and mean shoot heights were compared by one-way analysis of variance after testing for homogeneity of variances with F_{MAX} test.

Two shoots were randomly selected for intensive monitoring. For this, leaf length was measured from leaf tip to ground for all live leaves at each census. This was set up as part of the phenology study and a total of eleven shoots were monitored in this way.

RESULTS

2.6 Results

Field notes

Spring weather was warmer and drier than usual. Mean daily temperatures at Leeton, 50 Km south-east of Griffith, for September to January, were 2 to 4.8°C higher than the long-term mean. Rainfall over the same period was 1355 mm compared to the long-term mean of 179.5 mm. Downpours of more than 25 mm or rain within a 24 hour period occurred in

late August, early December and twice in February. For most of the study period the harvested area was under shallow water, 5-10 cm deep, or else the substrate was saturated as indicated by soft muds underfoot. The ground firmed up at the end of November, in January and at the end of March. The site flooded (briefly) three times, in June 1980 to 30 cm, in December 1980 to 80 cm and in February 1981 to 100 cm. Water depths in the permanent quadrat were consistently 10-15 cm shallower than in the harvested area. Lots of litter was noted in early March and May.

Soils

Mean organic matter was 23.9% ($s = 0.8143$, $n = 4$) at 0 cm and 8.7% ($s = 0.8723$, $n = 4$) at 20 cm. Nutrient concentrations at 0 and 20 cm respectively ($n = 1$) were 7.0 and 0.8 mg KN g^{-1} soil, and 0.30 and 0.10 mg SRP g^{-1} soil.

Standing crop: direct estimate

Standing crops of all three fractions, live, dead and burned shoots, were quite variable. Live standing crop had the highest mean V* 0.35. For dead standing crop mean V* was 0.27 and for burned standing crop it was 0.24. (Primary standing crop data in Appendix 2.)

Live standing crop was low during winter, 142-252 g m^{-2}, increased rapidly from September reaching 1306 g m^{-2} at the end of November and remained at this level until late January (Figure 2.1 a). The low value for mid December was not significantly different from preceding or subsequent harvests. Dead standing crop also had a seasonal pattern but with the maximum in late summer and early autumn (Figure 2.1 a). In winter, spring and early summer, it varied between 902 and 1379 g m^{-2}, then increased at the end of summer as live shoots died off reaching the maximum of 2509 g m^{-2} at the end of April.

The standing crop of burned shoots was roughly constant in the first six months then decreased in the next six (Figure 2.1 b). Mean standing crop from June to November 1980, 744 g m^{-2}, was significantly higher (p

= 0.001) than for January to June 1981, 531 g m^{-2}, which suggested the burned material fraction was decreasing with time. However statistical tests showed this was not so as the regression coefficient was not significantly different from zero.

Total aboveground standing crop was the most variable. It increased between September and November as live standing crop increased and decreased in May-June as dead standing crop decreased (Figure 2.1 b). The maximum, 3278 g m^{-2} at the end of November, coincided with maximum live standing crop but was almost equalled at the end of April, 3227 g m^{-2}, when dead standing crop reached its maximum. The net increase in aboveground standing crop from June 1980 to June 1981 was 324 g m^{-2} including burned shoots and 710 g m^{-2} excluding burned shoots.

Live reproductive structures averaged 6% of live standing crop from November to March, range 0-16.4%. After emerging, inflorescence weight continued to increase whilst height hardly changed (Figure 2.2). Mean dry weight of inflorescences in early November when still completely sheathed by leaves was 11.63 g. Inflorescence maximum weight of nearly 60 g was reached in early January (mean = 57.4 g, n = 25, January-March).

Fitting a splined regression to primary data dampened fluctuations and clearly showed how the decrease in live standing crop was followed by an increase in dead standing crop (Figure 2.3). The decrease was 1553 g m^{-2} and the increase was 1245 g m^{-2}, a difference of 308 g m^{-2}.
Live standing crop had the same seasonal cycle as primary data but the midsummer peak was shorter and higher, 1613 g m^{-2} in mid December. Fluctuations evident in dead standing crop from June to November were smoothed to an increase from the beginning of June to the end of August, then a decrease until the end of November. Maximum dead standing crop was 2283 g m^{-2} at the end of April. Derived data showed a net annual increase in live plus dead standing crop of 791 g m^{-2} to June 1981.

Underground standing crop at Gum Creek Road

Live underground standing crop had a seasonal cycle which was offset from aboveground standing crop by 3-4 months (Figure 2.4), with the maximum 3562 g m^{-2} in April and the minimum in October. In 1979 the October minimum was 678 g m^{-2} and in 1980 it was 1254 g m^{-2}, a net increase of 576 g m^{-2}. As most of the underground biomass was rhizome, changes in rhizome biomass determined the seasonal pattern. Throughout the year live standing crop was greater underground than aboveground. Because their seasonal cycles were off-set, the below:above rato was not constant but ranged from 1.3 in January to 28.8 in July. (Original data are in Appendix 3.)

The seasonal cycle and values of aboveground standing crop at Gum Creek Road and Brogden's Road were very similar (Figures 2.1 a and 2.4). At Gum Creek Road, maximum live standing crop in January 1980 was 1208 g m^{-2} and minimum in June 1980 was 63 g m^{-2}, which was very similar to Brogden's Road in 1980-81. Because of this and the similarity in site and location, it was assumed that underground production from Gum Creek Road would give a reasonable estimate for the site at Brogden's Road.

Standing crop: indirect estimate

Of the 74 shoots used to establish height:weight relationships, 64 were vegetative with a height range of 259-2345 mm. This was shorter than shoots in the permanent quadrat, 2453 mm, and in harvested quadrats, 3066 mm. Shoots were harvested on 13 August (12 shoots), 10 September (30 shoots), 14 October (22 shoots). Shoots harvested on 9 December (10 shoots) were all reproductive with a height range of 2110-2786 mm.

The dry weight of vegetative shoots increased exponentially with height (Figure 2.5 a). The highest coefficient of determination, r^2 = 0.8916, was given by an exponential first order polynomial for log normal transformed data, compared to 0.8468 and 0.8802 for exponential and power

curves. High coefficients are usual for this kind of data (Hutchings 1975). The dry weight of reproductive shoots increased linearly with height (Figure 2.5 b). Regression details are in Table 2.2.

Despite the high coefficients of determination, indirect estimates of standing crop were not accurate. Comparisons with harvests showed that the indirect method was an overestimate. The indirect estimate for the permanent quadrat on 29 June 1981 was 213.4 g which was nearly 50% more the harvest on the same day, 147.5 g. Comparison of indirect estimates with live standing crop of 15 quadrats harvested on 5 September, 13 October and 27 November (Figure 2.6) also showed that the height:weight relationship overestimated. A linear regresion was significant. The regression coefficient of 0.4942 meant there was a consistent error of almost 100% (Table 2.3).

Annual production: direct estimate

Annual aboveground production estimated by the max-min method was 1175 g m^{-2}. Annual aboveground production calculated by Smalley's method data was 3824 g m^{-2} using primary data and 2026 g m^{-2} using derived data. Estimates of mortality before maximum standing crop and production afterwards depended on whether primary or derived data were used. For primary data, mortality was 1777 g m^{-2} or 50% of production to date but for derived data it was only 225 g m^{-2} or 13% of production. Production after the seasonal maximum was 934 g m^{-2} or 24% of annual total for primary data, and 406 g m^{-2} or 20% for derived data.

Underground production at Gum Creek Road in 1979-80 was 2884 g m^{-2} y^{-1} estimated by the max-min method. The translocation correction which was the April to October decrease in rhizome biomass converted to canopy equivalent, was 839 g m^{-2}.

Annual production for the whole plant at Gum Creek Road was 2802 g m^{-2} if estimated by max-min method. Whole plant production was 4071 g

m^{-2} y^{-1} when estimated as the sum of underground and aboveground production corrected for translocation, 2884 + 2026 - 839 g m^{-2} y^{-1}. Reproductive production was only 75 g m^{-2} y^{-1}, calculated by multiplying mean density (1.3 shoots m^{-2}) by mean weight at maturity (57.4 g).

Comparison of sequential harvests showed that out of 25 possible changes in standing crop, only 11 live and 3 dead were significant ($p = 0.10$). By increasing the probability of a Type I error from 0.10 to 0.75, the number of significant differences rose to 25 for live and 24 for dead which was almost the entire primary data set. Thus production of T. orientalis estimated with primary data was equivalent to a 75% probability of falsely identifying two harvest means as different when they were statistically indistinguishable.

Halving the sampling frequency reduced annual production by almost 50% when estimated with primary data (Table 2.4). Production calculated with derived data was much less sensitive. Halving the frequency reduced production by less than 10%.

There were five instances of negative production. In the primary data set they were scattered through the year whereas with derived data they were clustered between January and April (not shown).

Annual production: indirect estimate

Annual aboveground production estimated by applying the vegetative and reproductive height:weight relationships for vegetative and reproductive shoots to height and census data from the permanent quadrat was 1570 g m^{-2}.

Demography of harvested shoots

In the harvested quadrats, mean density of live shoots fluctuated between a maximum of 33.4 m^{-2} in June 1980 and a minimum of 11.6 m^{-2}

in February 1981 (Figure 2.7). These fluctuations and their large standard deviations make it difficult to detect periods of recruitment or mortality. Mean density of reproductive shoots during summer was 1.30 or 7% of live shoots. Dead shoot dynamics are easier to distinguish but again there is considerable variability (Figure 2.7). Shoot mortality, indicated by an increase in number, occurred in July-August, January-February and March-April. Shoot loss, indicated by decreasing numbers, was erratic between September and January. Density did not change smoothly with time implying recruitment and mortality were continuous or that the stand was variable.

Mean density of burned shoots from June to November (not shown), 44.0 shoots m^{-2}, was significantly higher ($p < 0.001$) than from January to June 1981, 28.4 shoots m^{-2}. This was similar to trends in burned standing crop. The increase in burned shoots at the start of the study is attributed to increasing care in the field. Some burned shoots were inconspicuous muddy stumps less than 15 cm high.

Height frequency distributions for six dates through the year show a unimodal travelling peak from June to November (Figure 2.8) indicating a single or synchronised recruitment period. There were additions to the smallest height classes in midsummer which indicates recruitment at this time. In November there were no shoots in the two smallest height classes but by January these contained 7% of shoot population.

The travelling peak shows that shoot growth was not confined to spring and summer. In June 1980, 90% of live shoots were less than 1500 mm tall, and the modal height class was 0-500 mm with 37% of live population. By early September, only 8% of live shoots were in 0-500 mm height class, and the modal height class was 1501-2000 mm with 35% of live shoots. Height distribution in June 1981 was similar to that of June 1980 with 38% of live population in height class 0-500 mm. Mean height of

inflorescences was 1990 mm (n = 45, s = 203.1048). The shortest viable inflorescence was 1771 mm. An inflorescence measuring 1375 mm was aborted.

Permanent quadrat

Population trends were clearer than in harvested quadrats. Live shoot density was fairly stable from the beginning of July to the end of December with 30-32 shoots in the quadrat, i.e. 30-32 shoots m^{-2} (Figure 2.9 a). At the beginning of January, density began to increase and reached 47 at the beginning of March then declined to 28 in mid-May. After an initial increase in June 1980, dead shoot density remained stable until late December (Figure 2.9 a) then fell to the lowest of the year, 20. After this density increased, slowly in January and February then rapidly in March, April and May, reaching the maximum of 56 at the beginning of June.

The cumulative plot of shoot recruits and deaths shows recruitment extended from January to June (Figure 2.9 b). This was also the main mortality period. At other times of the year, recruitment and mortality were low, almost negligible. Thus the stability evident in shoot density between July and December was real.

Comparison of shoot heights showed the same seasonal trends in the permanent quadrat as in the harvested quadrats (Figure 2.8) but mean shoot height was significantly shorter ($p < 0.01$) in September to January. Live shoot density in the permanent quadrat was significantly higher than in harvested quadrats ($p < 0.05$) but the number of reproductive shoots was similar, 2 in the permanent quadrat compared to a mean of 1.3 m^{-2} in the harvested quadrats (not tested).

The number of live leaves in the quadrat (Figure 2.10) fluctuated between 64 and 104 during June and July then increased from early August to 211 in early November which was the highest for the year. Numbers

decreased during November and were roughly stable at 153-179 during December, January and February. From the beginning of March, numbers again decreased and reached the lowest value in May, 60. The gap between recruitment and mortality was widest in spring indicating a net gain in leaf number after being relatively constant in winter.

The cumulative plot showed leaf recruitment and mortality were continuous except for a short period of two consecutive sampling dates in late spring-early summer. These events were not synchronised. Mortality was zero 21-28 October and recruitment was zero 2-10 December. Slopes of the cumulative plots show recruitment and mortality were highest (subjective assessment) at the same time, late January to early March, a time when leaf populations appeared roughly stable.

The dead leaf retention index was lowest, 0.75, at the beginning of January and March (Figure 2.11), implying that leaf fall was highest in December, January and February. (February was not recorded separately).

The two T. orientalis shoots chosen for intensive leaf monitoring were both grazed in August and do not show the growth pattern of Typha shoots as well as ungrazed shoots. All shoots showed the same growth pattern, regardless of species, so results for a vegetative T. domingensis shoot from Bringagee Road are used instead (Figure 2.12). The diagram shows leaf height for all live leaves between June 1980 and January 1981, with leaves coded D to P in order of age and appearance. The growth pattern has three important characteristics. Each leaf grows to its own maximum height and eventually dies after a variable period which is longer in spring and summer than winter. Each successive leaf grows taller and faster than the preceding one, thus shoot height is determined by a sequence of leaves. The last few leaves M N O and P do not fit these generalisations because the shoot was droughted after November (3.7 Height). The maximum extension rate for this shoot was 76 mm day^{-1} in

mid-November for leaves L and M. Maximum extension rates in winter were much lower, 2-5 mm day^{-1} for leaves E and F in June and July, but did not fall to zero.

DISCUSSION

2.7 Stand variability

Although the stand of T. orientalis at Brogden's Road was monospecific it was not homogeneous. Mean live standing crop had high coefficients of variations, there was difficulty in statistically distinguishing between successive harvests, and shoots in the permanent quadrat were both shorter and denser than in harvested quadrats. This variability obscured seasonal trends described simply as the mean of five randomly located, fortnightly replicates. Interpretation of seasonal trends was made possible by fitting a splined regression to standing crop data and by reference to demography in the permanent quadrat.

Accounting for stand variability clarified the problem of negative production. In this study, two types of negative production were evident. One was apparent even when derived data were used so was not due to variability. It occurred in late summer and early autumn and masked production from new shoots. This was interpreted as the result of downward translocation from leaves prior to senescence. A maximum estimate of this is given by the difference between dead standing crop increase and live standing crop decrease, 308 g m^{-2}. The second type of negative production occurred at other times of the year but only with primary data. It was interpreted as due to variability.

The importance of accounting for variability when estimating production from standing crop changes is shown by the difference between estimates using primary and fitted data, 3824 and 2026 g m^{-2} y^{-1}. Primary data gives the higher estimate because all changes in mean values are treated as real and because of the way Smalley's method treats

negative production. An apparent increase in mean standing crop is counted positively as production but an apparent decrease is not counted negatively and instead is set to zero (Table 2.1). A sequence of statistically indistinguishable fluctuations thus leads to a compounded overestimate. If the number of sampling intervals is high, production will be overestimated more frequently. Thus the sensitivity of Smalley's method to sampling frequency is another aspect of the effect of stand variability on production.

The usefulness of the indirect method was also limited by variability. Annual production estimated by the indirect method, 1570 g m^{-2}, differed from the direct method in that it referred to a small area of the Brogden's Road stand, defined by 74 shoots and one quadrat with no replication, whereas harvested shoots came from a more extensive area. Thus in order to give valid estimates, the indirect method must be accurate, precise and be based on correct assumptions. This was not so.

First, the vegetative shoot height:weight regression did not give precise enough estimates of shoot weight from height. The regression fitted the data well and passed close to the origin without being forced, which seldom happens (Hutchings 1975, Hardisky 1980, Lieffers 1983). Despite this, the error associated with weight prediction was high. The estimate for a shoot 2000 mm tall was 42.16 g, with 99% confidence limits of 26.76 and 66.35 g.

Second, regressions specific to one time and place were used at another time and place. Some studies have reported that time and place variations alter height:weight relationships. Regressions for herbaceous perennials such as Mercurialis perennis (Hutchings 1975) and Spartina alterniflora (Hardisky 1980) are time specific, changing with season or month. This is probably due to changes in the number of live and dead leaves per shoot (Hardisky 1980). This could equally apply to T.

orientalis which accumulates leaves during spring (Figures 2.10 and 2.12). In addition, height:weight regressions reflect site quality. In Canada, shoots of T. latifolia from five ox-bow lakes differing in water quality and history differed in density, height and height:weight relationships (Lieffers 1983). In this study, shoots used for the regressions came from an area which did not flood as deeply as the harvested part of Brogden's Road stand. Finally, the vegetative regression was used beyond its upper limit of 2345 mm. These limitations were not evident at the time and may have been the source of the almost 100% discrepancy between harvested and predicted standing crop.

Third, the indirect method assumed shoot weight was equivalent to production. This is unlikely to be true as leaf loss may be substantial. In Spartina alterniflora leaf loss from live shoots was 31% of annual production (Hardisky 1980). In T. orientalis, leaf mortality and litterfall were virtually continuous (Figures 2.10 and 2.11) but without weight measurements for individual leaves, production cannot be corrected.

2.8 Estimates of production

Four estimates were used to estimate annual aboveground production. The max-min method assumes no mortality before maximum standing crop and no production afterwards. The demographic data showed both these assumptions were false, so 1175 g m^{-2} y^{-1} was an underestimate. Smalley's method using primary data assumes stand homogeneity. Both standing crop data and demographic data showed this was false. The effect of variability was compounded by sampling frequency (Table 2.4), and ironically the frequency chosen to best estimate dead standing crop gave the grossest error.

The indirect method assumed height:weight relationships remained constant and that shoot weight was equivalent to production. However

there are several instances when such assumptions are likely to be false, most of which were relevant to this study. Comparisons between estimated and measured standing crop (see above, Standing crop: indirect estimate and Figure 2.6) showed the indirect method overestimated by nearly 100%. This suggests the indirect production estimate of 1570 g m^{-2} y^{-1} for the permanent quadrat was probably closer to 700-800 g m^{-2} y^{-1}, which is less than the max-min estimate. This is very low and could be partly accounted for by stand variability as shoots in the permanent quadrat were shorter. The exponential character of height:weight relationship means small height differences between tall shoots can result in large weight differences (Figure 2.5 a).

Smalley's method using derived data was accepted as the most reliable estimate. It does not assume stand homogeneity but instead accounts for variability. Seasonal trends in derived standing crop were corroborated by shoot and leaf demography from the permanent quadrat. The method was not sensitive to new shoot production during old shoot mortality or to translocation but these errors were corrected as described above (2.7) to give a final estimate of 2334 g m^{-2} y^{-1}. Using this revised estimate, whole plant production was corrected from 4071 to 4379 g m^{-2} y^{-1}.

2.9 Annual production

Aboveground standing crop of *T. orientalis* at Griffith was not high compared with other *Typha* spp. (Figure 1.1) but maximum standing crops from the Griffith area, 1306 g m^{-2} at Brogden's Road in 1980-81 and 1208 g m^{-2} at Gum Creek Road in 1979-80, were close to 1300 g m^{-2}, the value predicted for 34°S by regression of standing crop and latitude (not shown). Maximum underground standing crop, 3562 g m^{-2}, was within the upper range reported in production reviews (Keefe 1972, Bradbury and Grace 1983). Maximum total standing crop of 3810 g m^{-2} was close to that reported for *T. domingensis* in Malawi, 4400 g m^{-2}

(Westlake 1975).

In contrast, annual production of T. orientalis was 2334 g m^{-2} which was high compared to data reported for Typha spp. with one exception: a record of 2297 g m^{-2} for T. glauca in Iowa, USA (van der Valk and Davis 1978). Both these are above the probable range of 2000 g m^{-2} suggested for temperate zone freshwater emergents (Bradbury and Grace 1983).

The possibility that high production was a species characteristic was discounted. Claims that Typha spp. have exceptionally high photosynthetic rates are frequently based on measurements using isolated plants or plant parts in non-natural situations. In fact maximum carbon assimilation rate for T. orientalis communities is comparable to well-irrigated crops (Sale and Orr 1986). High production indicates growing conditions were more favourable at Griffith than at sites used in production reviews. In general, all wetlands are resource rich as they have abundant irradiance, nutrients and water (Keefe 1972, Bradbury and Grace 1983). Thus a highly productive wetland site must be exceptionally rich in these resources or else have a more favourable climate.

Soil analyses showed that concentrations of available phosphorus at Brogden's Road site, 0.10-0.30 mg SRP g^{-1} were similar to other Typha dominated wetlands, for example 0.05-0.20 in Wisconsin (Klopatek 1978) and 0.14-0.46 near Ottawa (Bayly and O'Neill 1972). In contrast nitrogen concentrations of 0.8-7.0 mg KN g^{-1} were lower than two Typha wetlands in North America, 13.6-23.4 (Auclair 1977, Klopatek 1978) but similar to Lake Chilwa, Malawi at 3.0 (Howard-Williams and Lenton 1975). Lower values for warmer climates could be due to faster rates of de-nitrification. Plant growth in wetlands is more likely to be nitrogen limited than phosphorus (Barko and Smart 1979, Graneli 1985). Thus it appears unlikely that soil nutrients, specifically nitrogen, could account for high production.

Field trials show that nutrient supplements increase not just production but also the standing crop of emergents (Graneli 1985) and that nitrogen supplements lead to a larger canopy and a shift in the above:below ratio (Boar and Crook 1985, Neeley and Davis 1985, Ulrich and Burton 1985). However, aboveground standing crop of T. orientalis was not exceptionally high and in fact was close to the value predicted for Griffith.

Together these points indicate that high production at Griffith was due to latitude-related factors, a non-specific phrase referring to temperature, irradiance and daylength collectively. Of these temperature was probably the most important. Most metabolic reactions are markedly influenced by temperature (Nobel 1974) and curtailed by sub-freezing temperatures. At Norman Oklahoma, 35°N, late frosts in March killed off all aerial shoots of T. latifolia (Penfound 1956). Leaf recruitment (Figure 2.10) and leaf extension diagrams (Figure 2.12) show that temperatures did not become limiting at Griffith nor was there any evidence of winter related mortality in shoots (Figure 2.9 b).

High production for T. glauca in Iowa (see above) was nearly double the average for the region. Factors contributing to this were polluted waters rich in nitrogen and phosphorus, and removal of all standing litter in the previous year which lengthened the growing season by allowing the soil to warm up more quickly (van der Valk and Davis 1978).

2.10 Production in context

The resource allocation pattern indicated by dry weight was as follows. Nearly half (53%) of total production was canopy but approximately one third (36%) was due to starch storage. At the end of the study a large percentage (28%) of canopy production was still standing. Underground production was two thirds (66%) of whole plant production. Of this 80% was lost during winter and only 20% accumulated

within the ground. Reproductive structures were only 3.2% of aboveground production and only 1.7% of whole plant production. This is not unusual for herbaceous perennials (Silvertown 1982) and is similar to T. latifolia (Grace and Wetzel 1982a).

Canopy production increased in each season after midsummer emergence from 8% in autumn to 13% in winter then 52% of annual total in spring. This exponential increase mirrors the increase in shoot height and the height:weight relationship. It is also evident within seasons, for example September accounted for 17% of spring production, October for 31% and November for 52%. Only 27% of annual total occurred in summer, the time of flowering and initiation of new shoots.

An annual production of 4379 g m^{-2} represents a considerable carbon input. Not all of this becomes "available" as litter within the year. In the Griffith conditions, 576 g m^{-2} accumulated underground or approximately 20% of underground production, and 710 g m^{-2} was retained aboveground or 28% of canopy production, making a total of 1286 g m^{-2} of nearly 30% of annual total. A high retention rate has been observed elsewhere (e.g. Ogden 1981) but may be related to the burning regime at Brogden's Road. In Iowa only 64% of standing dead T. glauca material present in October 975 had fallen by October 1976 (Davis and van der Valk 1983). Burned stumps of T. orientalis reproductive shoots seemed particularly resistant to decomposition.

2.11 Growth: phenology and demography

Each data set and each organisational level showed a slightly different growth phenology. At the whole stand level, aboveground standing crop (Figure 2.1 a) showed strongely seasonal changes indicating growth in spring, with autumn a time of die back, and summer and winter as periods of quiescence. Production data (2.8) showed growth was not confined to spring. Shoot demography showed that growth, as indicated by

an increase in shoot numbers or shoot recruitment (Figure 2.9) occurred in summer and autumn. The key to these contrasts is the way these growth hierarchies inter-connect, leaf to shoot and shoot to stand.

The leaf to shoot relationship is characterised by the fact that the shoot comprises leaves only, with no aboveground stem. Internodes between leaves are highly compressed and are underground on the rhizome crown. Thus leaf numbers directly affect shoot size. Leaf numbers were never constant. Recruitment was virtually continuous (Figure 2.10) therefore each shoot was producing new leaf matter constantly from emergence to flowering and/or death. Continuous leaf recruitment combined with a growth pattern where leaves are successively taller means shoot height continuously increases, even if only marginally as in winter (Figure 2.12). Dead and "superseded" leaves accumulating on the shoot explain why weight is a non-linear function of shoot height (Figure 2.5 a) and why it is variable.

The shoot to stand relationship was different. Changes in shoot numbers occurred within a limited period between January and June leaving a six month period of relative constancy. Because older shoots are so much taller and heavier than newly emerging shoots (Figure 2.5 a) the generation changeover in January-June has dramatic effects on live standing crop. Conversely, because newly emerging shoots were short and had short leaves, leaf recruitment in autumn meant production was only a small contribution to annual total. Production increased through the seasons from autumn to spring as shoots and leaves increased in height.

Leaf demography is thus the key to understanding growth in *T. orientalis*. The only period when leaf recruitment ceased was between shoot generations (Figure 2.10). Production did not cease, as the plant switched from vegetative to reproductive growth. Seasonal changes in underground standing crop cannot be correlated with demography as

individual ramets were not tagged. Nonetheless, high over-winter survival of T. orientalis shoots suggests ramet survival was also high.

The process of downward translocation began before flowering and before maximum standing crop. The 3-5 month lag between peak aboveground standing crop and peak belowground standing crop in T. orientalis was longer than the 1-4 months lag for T. angustifolia in Chile, 40°S (Ramirez and Anazco 1983). Duration of peak standing crop and lag time may help to determine underground production.

Table 2.1
Production per harvest interval by Smalley's method

Change in standing crop		
L (live)	D (dead)	P (production)
L is positive	D is positive	P = L + D
L is positive	D is negative	P = L
L is negative	D is negative	P = 0
L is negative	D is positive	P = L + D

If this last term is negative, then P is set to zero

Table 2.2
Height:weight relationships for shoots of T. orientalis

Vegetative data fitted a first order polynomial for log normal transformed data of the form $y = \exp(a + bx)$.
Data for reproductive shoots fitted a linear regression.
x = shoot height in mm
y = shoot weight in g

Vegetative shoots

$y = \exp(-0.109120 + 0.001925x)$
99% confidence limits of regression coefficient = +/- 0.000227
Coefficient of determination $r^2 = 0.8916$
Regression significant: $p < 0.001$

Reproductive shoots

?? delete

$y = 263.125 + 0.1513x$
~~$\exp(-0.109120 + 0.001925x)$~~
99% confidence limits of regression coefficient = +/- 0.070597
Coefficient of determination $r^2 = 0.7532$
Regression significant: $p = 0.001$

Table 2.3
Live standing crop: comparison of direct and indirect estimates

Data are harvested quadrats from three dates, each with five replicates.
y = harvested standing crop g m^{-2}
x = estimated standing crop g m^{-2}

$y = 156.0181 + 0.4942x$

Coefficient of determination: $r^2 = 0.9851$
Regression significant: $p < 0.01$

Table 2.4
Sampling frequency and production estimates

The effect of sampling frequency on two estimates of annual production

Harvest interval (days)	Harvests per year	Production aboveground g m^{-2} y^{-1}
Primary data		
14	26	3824
28	13	2066
56	7	1075
Derived data		
14	26	2071
28	13	2001
56	7	1957

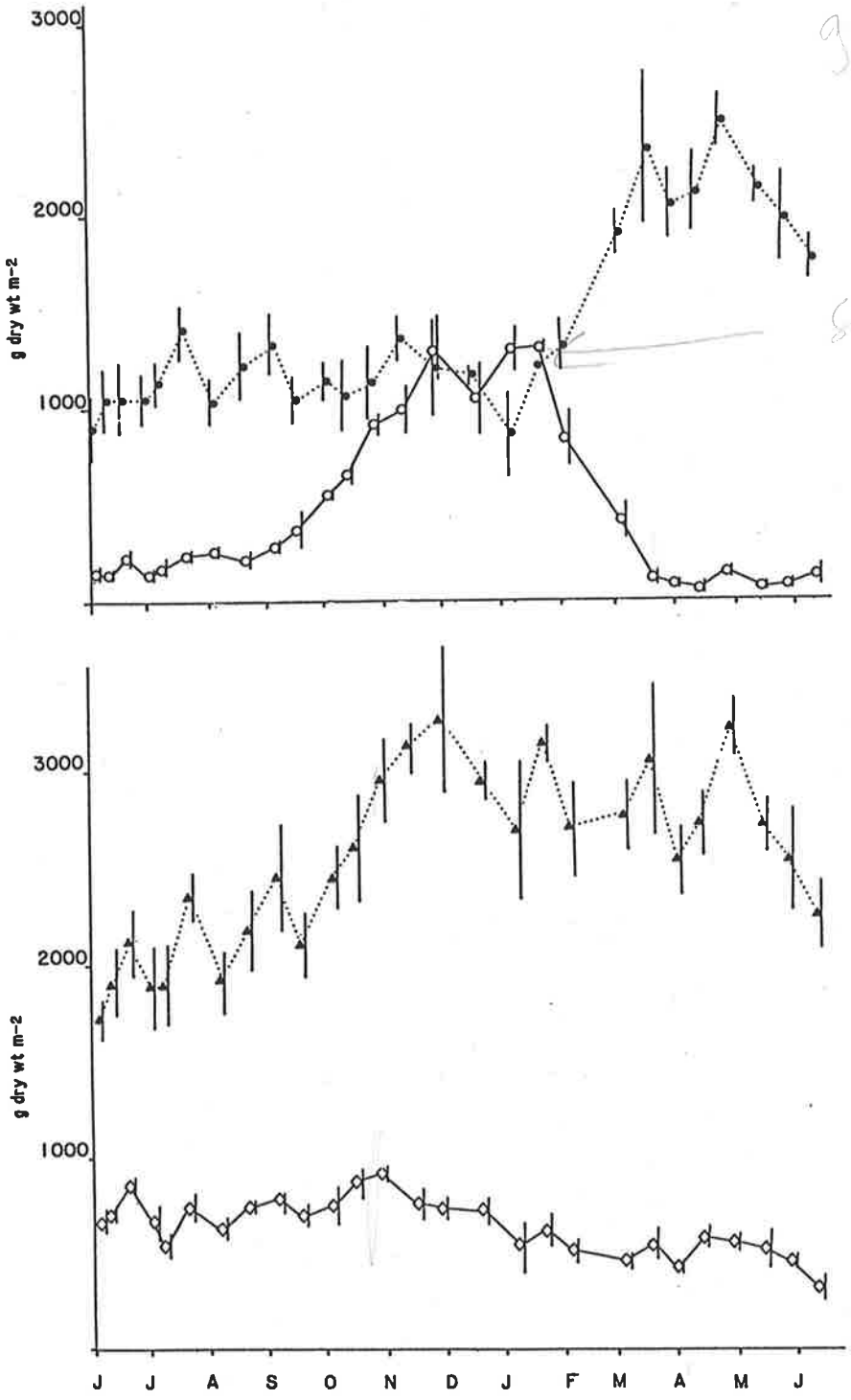

Figure 2.1
Aboveground standing crop: primary data

Seasonal changes in mean (n = 5) standing crop of T. orientalis as g dry weight m^{-2}, Mirrool Creek at Brogden's Road, near Griffith, New South Wales, June 1980 to June 1981. Data are mean (n = 5) with one standard error.

(a) Live (o–) and dead (•··) standing crop
(b) Burned (◇–) and total (▲··) standing crop

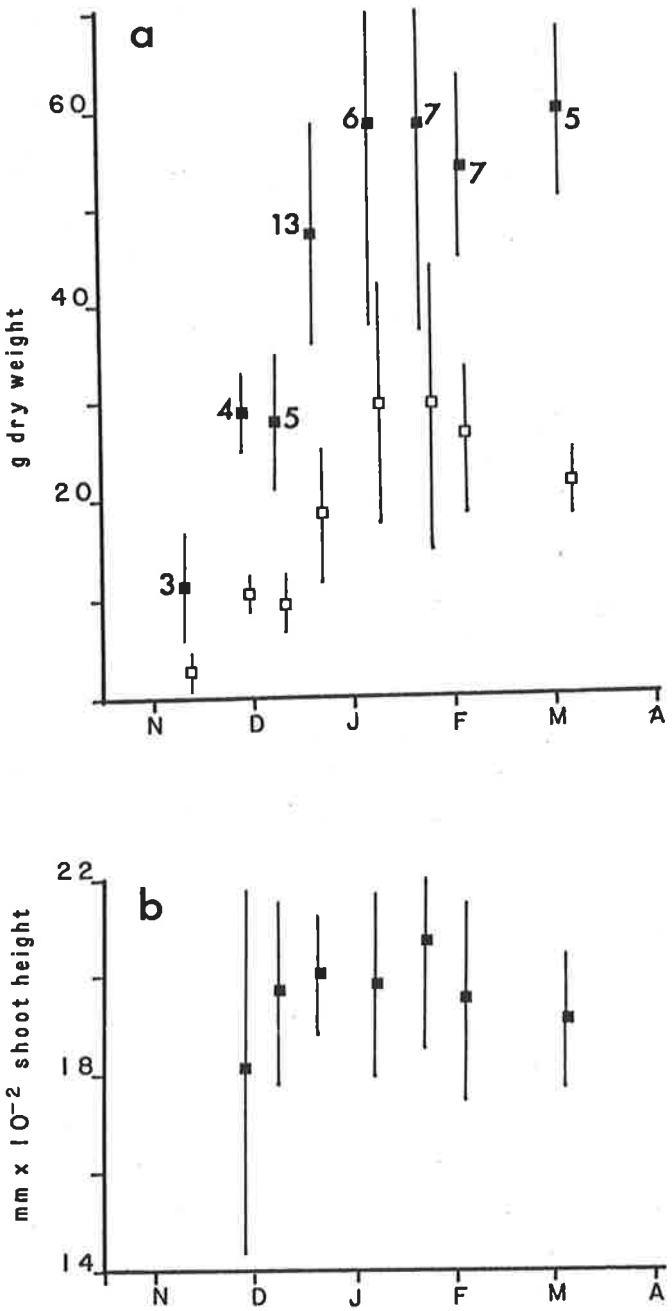

Figure 2.2
Growth of reproductive structures

Growth of reproductive structures of T. orientalis at Brogden's Road, Griffith. Dry weight and height of inflorescence and peduncle measured at fortnightly intervals from flowering in November to beginning of die-back in March. In mid-November, structures were entirely sheathed by leaves, and their height was not measured. Data are mean +/- one standard deviation. Sample size is shown on the first diagram.

(a) Dry weight in g, inflorescence (□) inflorescence and peduncle (■).

(b) Height to tip above male inflorescence, in mm.

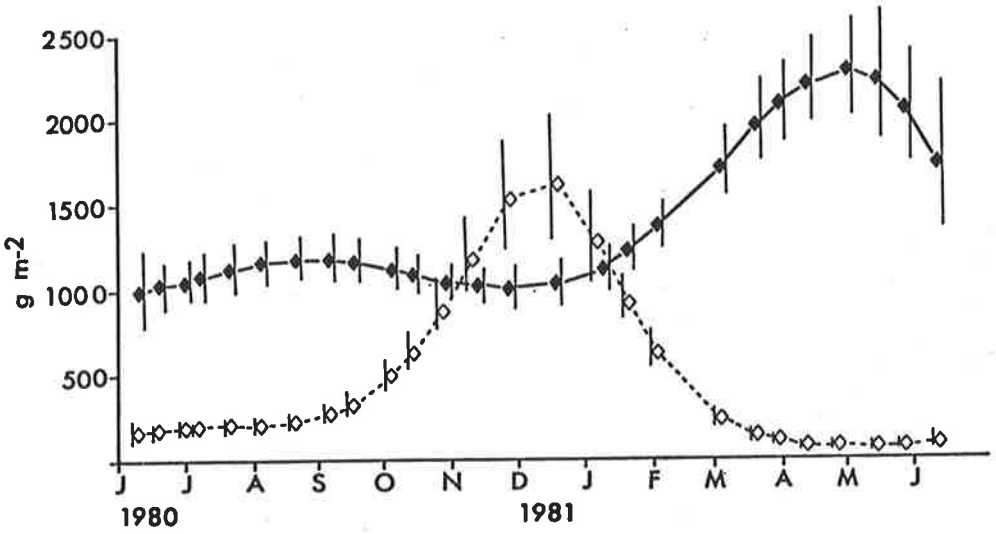

Figure 2.3
Seasonal changes in aboveground standing crop: derived data

Seasonal changes in aboveground standing crop, as g dry weight m^{-2}, of T. orientalis at Brogden's Road, Griffith, using derived data with 95% confidence limits. Points derived from fitting spline function to primary data (see text) for live (◇) and dead (◆) standing crop.

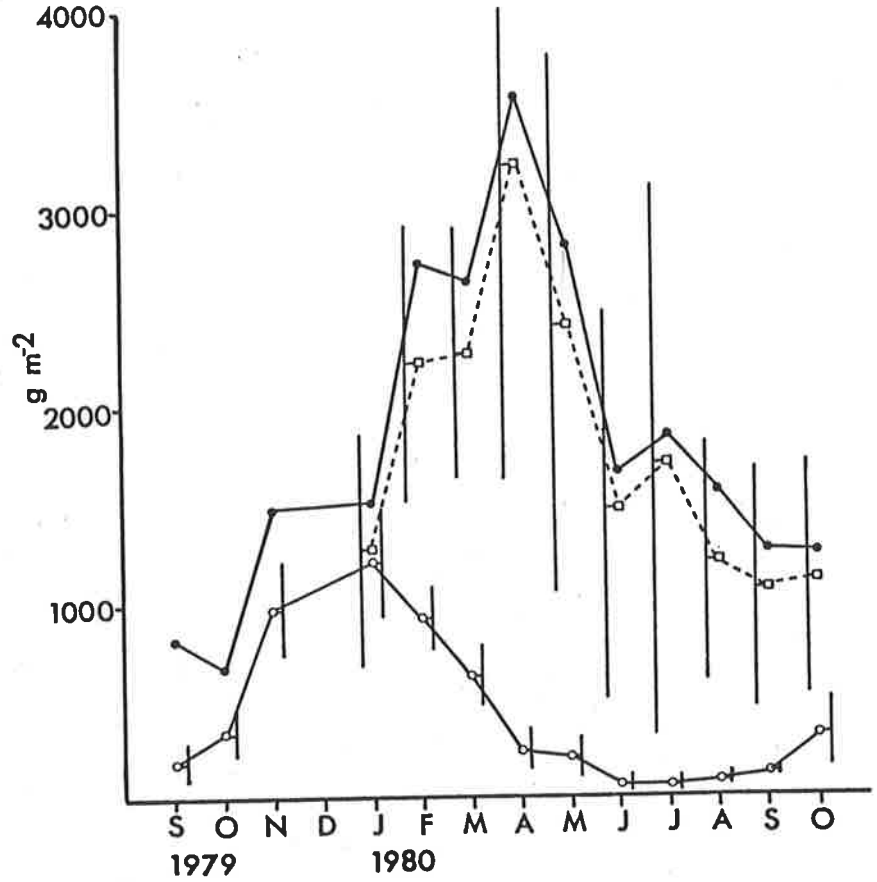

Figure 2.4
Standing crop of T. orientalis 1979-80

Seasonal changes in mean live standing crop with one standard deviation of T. orientalis, in g dry weight m^{-2}, at Gum Creek Road, Mirrool Creek, near Griffith, New South Wales, from September 1979 to October 1980.

Key
- o Aboveground
- • Roots and rhizomes
- ▫ Rhizomes only

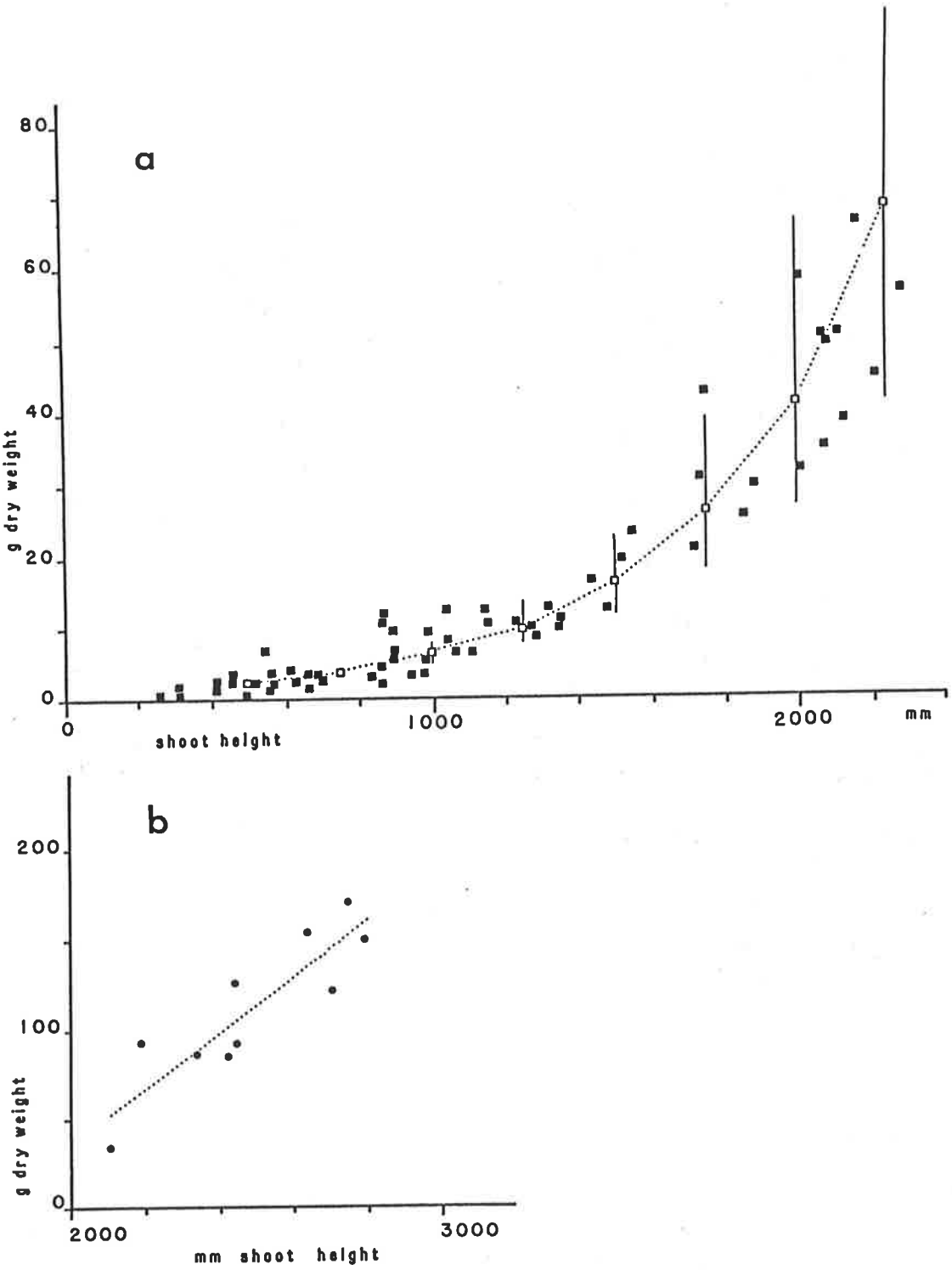

Figure 2.5
Height:weight relationships

Height:weight relationship for T. orientalis shoots, harvested near the permanent quadrat at Brogden's Road, Griffith, New South Wales. Fitted regression shown by dotted line, details in Table 2.2.

(a) Vegetative shoots
Primary data (▪), regression (▫) with 99% confidence limits.

(b) Reproductive shoots

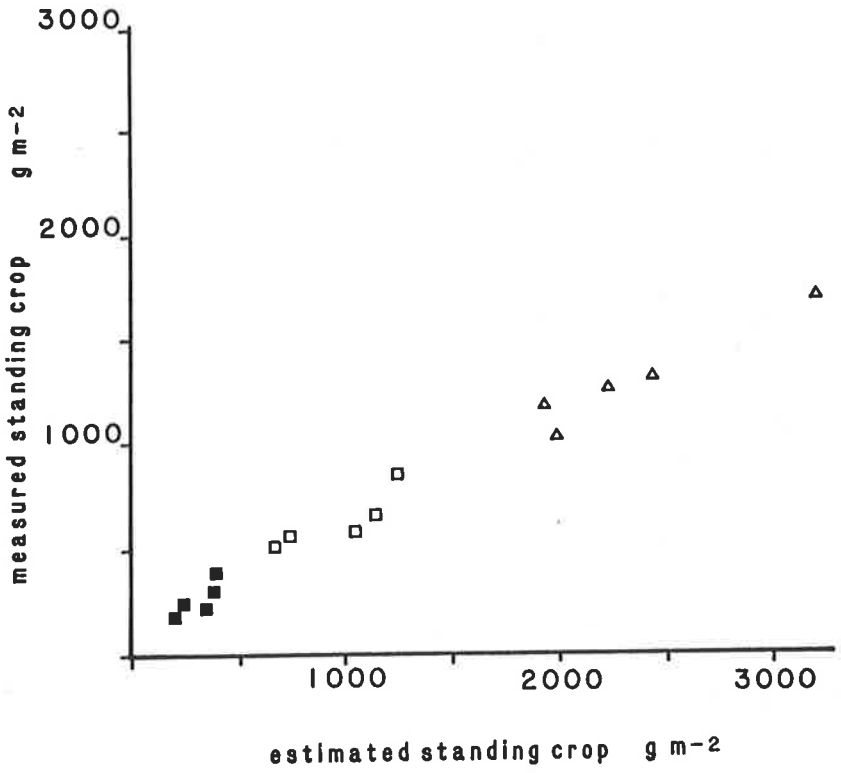

Figure 2.6
Validation of indirect method

Validation of indirect method of estimating aboveground standing crop, using regression to compare indirect estimates with harvests done on three dates in spring 1980. Regression details in Table 2.3.

Key
■ 5 September
□ 13 October
△ 27 November

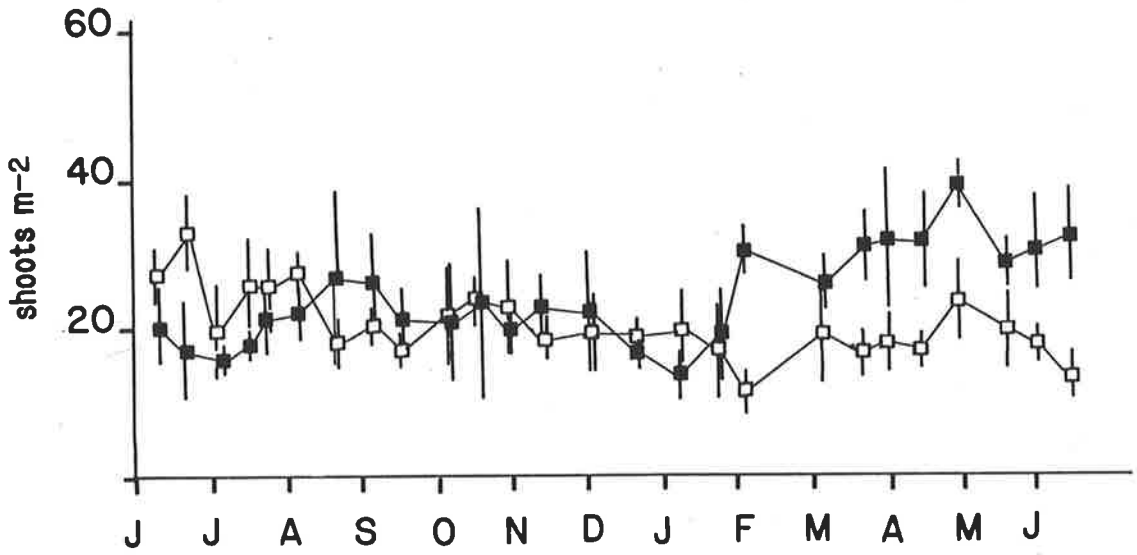

Figure 2.7
Demography of harvested shoots: density

Demography of harvested shoots of T. orientalis, June 1980 to June 1981, showing density changes of live (□) and dead (■) shoots.

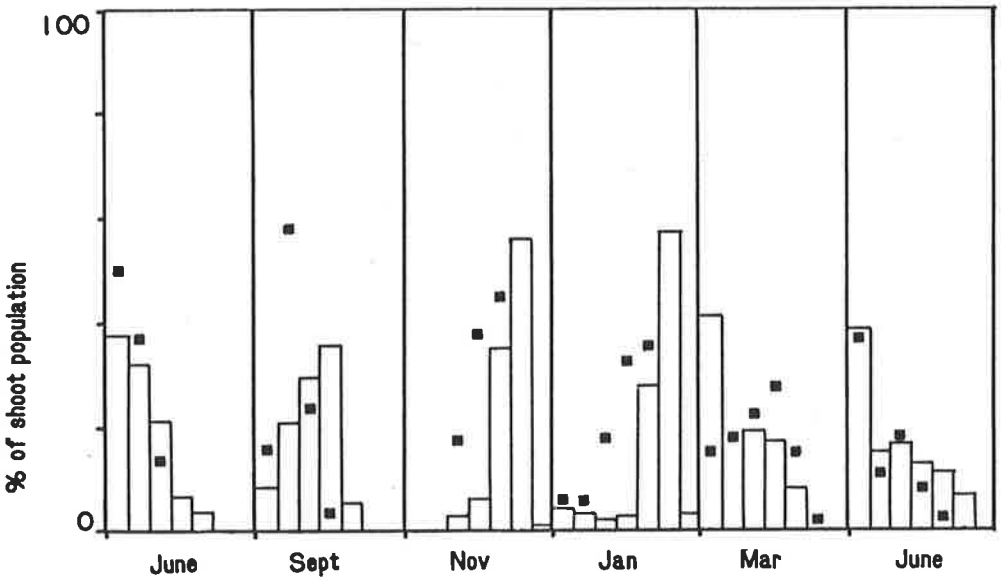

Figure 2.8
Shoot demography: population structure by height class

Population structure of T. orientalis shoots, at 2-3 monthly intervals from June 1980 to June 1981, based on height class. The number of shoots per height class shown as a mean (n = 5) percentage of live population. Height classes are equal sizes, in increments of 500 mm. Harvested shoots shown by histograms, shoots in permanent quadrat indicated by (■).

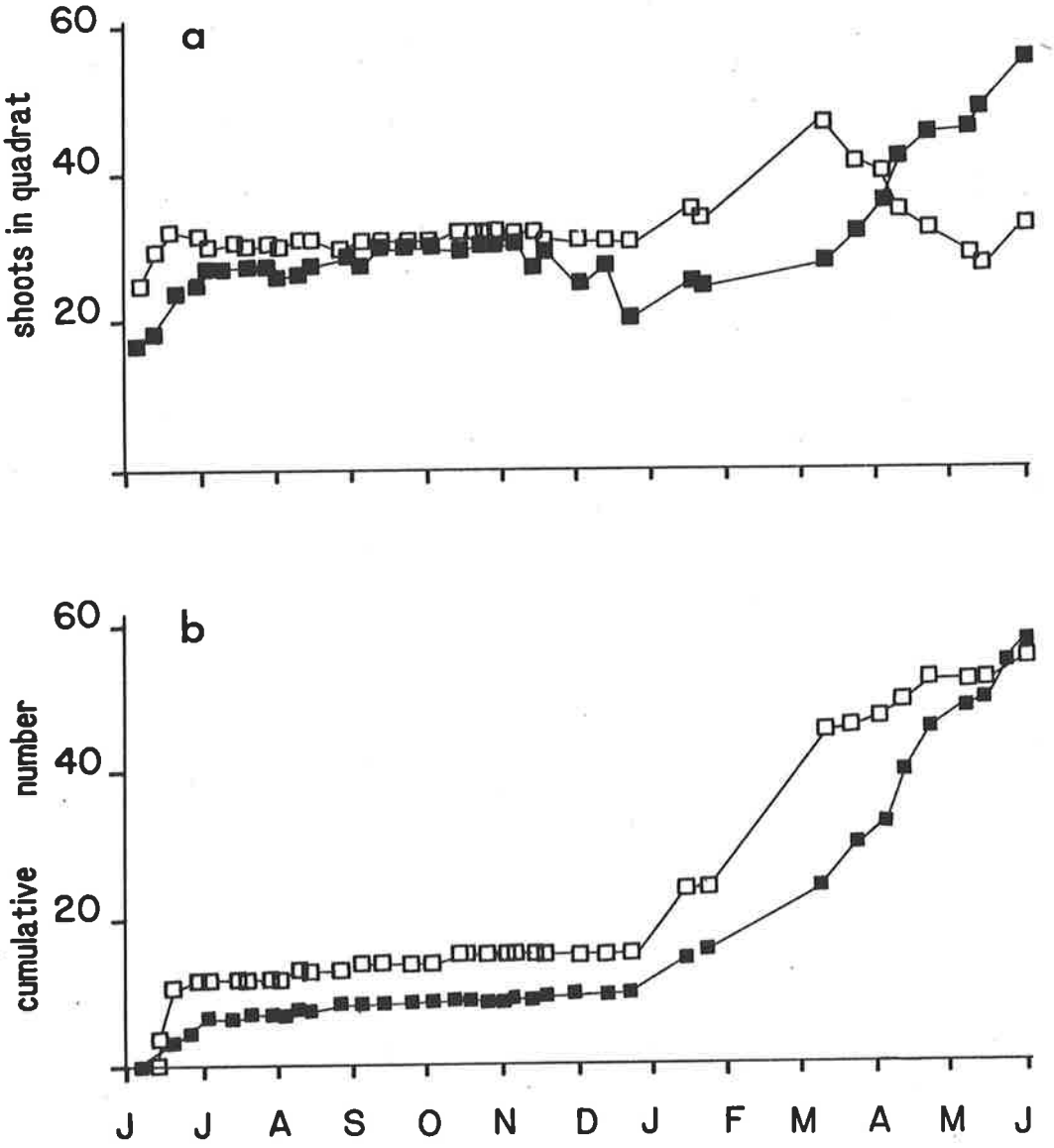

Figure 2.9
Shoot demography

Demography of T. orientalis shoots in the permanent quadrat from June 1980 to June 1981.

(a) Density: number of live (□) and dead (■) shoots present
(b) Flux: cumulative number recruited (□) and dying (■)

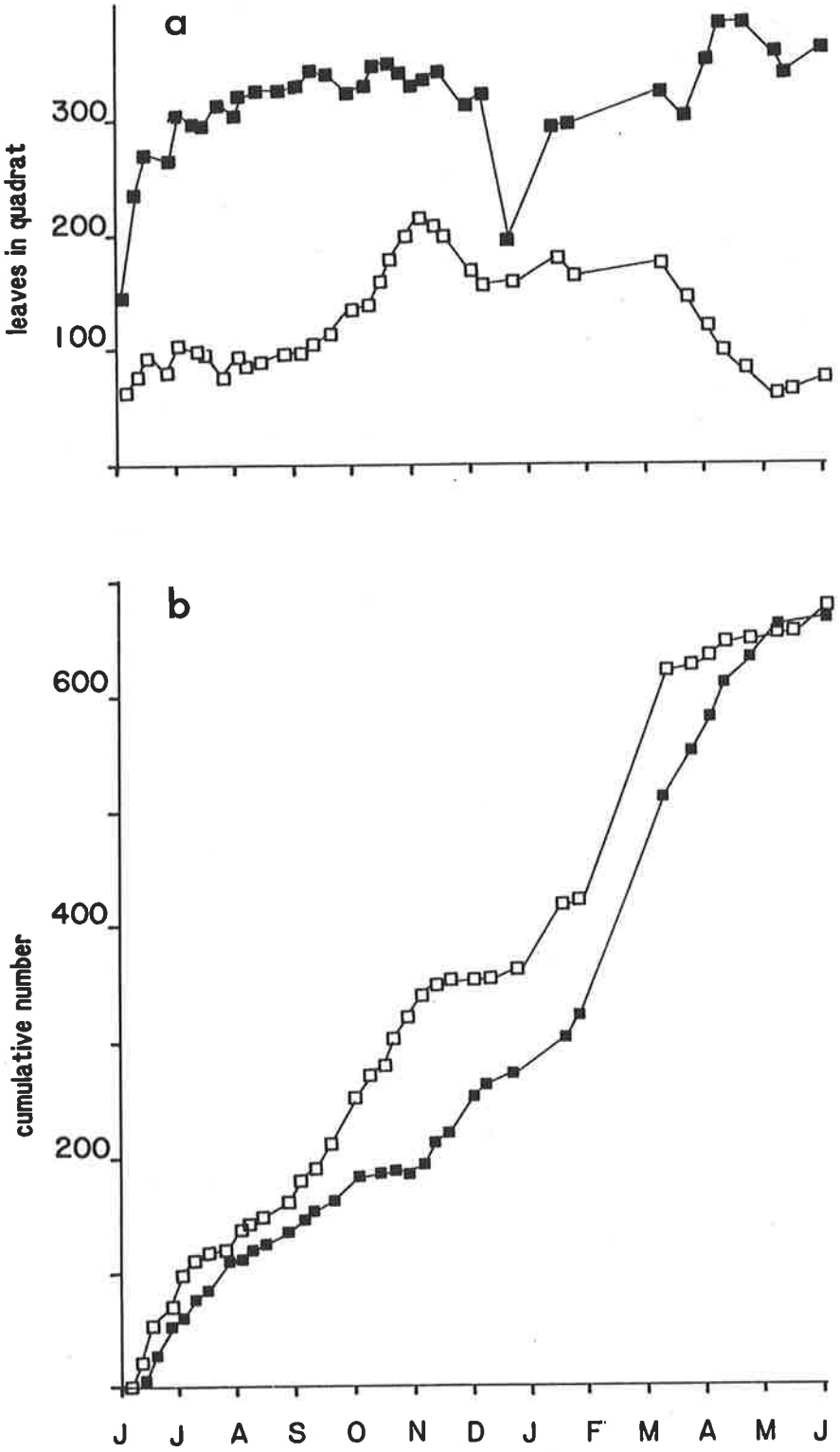

Figure 2.10
Leaf demography

Demography of T. orientalis leaves in the permanent quadrat from June 1980 to June 1981.

(a) Density: number of live (□) and dead (■) leaves present
(b) Flux: cumulative number of leaves recruited (□) and dying (■)

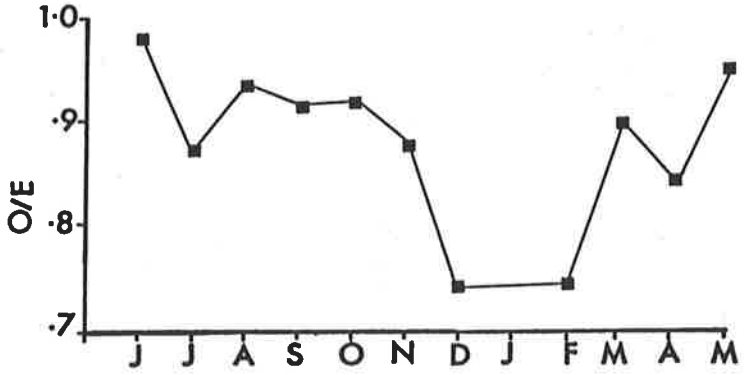

Figure 2.11
Dead leaf retention index

Seasonal changes in loss of dead leaves from canopy of T. orientalis at Brogden's Road indicated by O:E, the dead leaf retention index. The Observed:Expected number of dead leaves is calculated for the beginning of each month from July 1980 to June 1981. Quadrat was not read in February 1981.

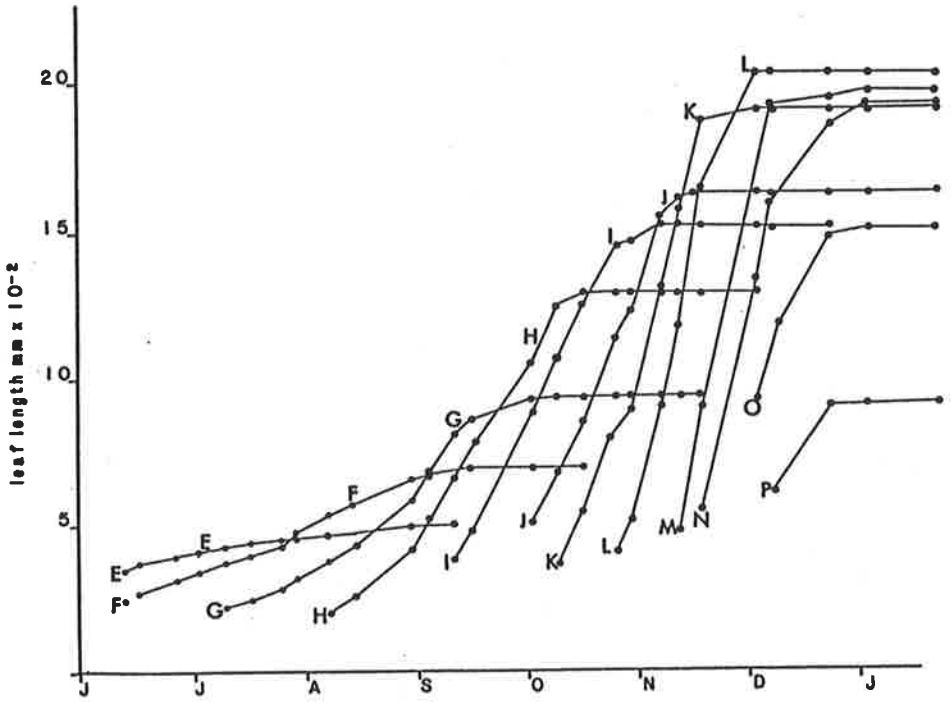

Figure 2.12
Growth within a shoot

Sequential growth within a shoot shown by changes in leaf length for all leaves on a shoot from June 1980 to the end of recruitment in January 1981. Data are for an ungrazed T. domingensis shoot from Bringagee Road, a site described in the next chapter. Each leaf was measured from first appearance until death. Leaves are coded E to P in order of appearance. The outer enveloppe, which is a sequence of truncated curves delineating the height of the tallest leaves E to L in succession, gives shoot height.

Chapter 3

PHENOLOGY IN SOUTH-EAST AUSTRALIA

INTRODUCTION

3.1 Background and aims

Phenology is the study of seasonal timing of events in the life cycle (Rathcke and Lacey 1985) and includes both vegetative and reproductive events. If it is accepted that a plant's life history is the result of natural selection, then phenology is the key to understanding a species in relation to its environment. The premise that events such as pollination, dispersal and germination are temporally optimised (e.g. Rathcke and Lacey 1985) means community and evolutionary biologists have placed great emphasis on interpreting events in the reproductive life cycle. Consequently reproductive phenology has become a statistical science. Parametric and non-parametric frequency analysis are used to compare populations etc. and events are described by distribution statistics such as mean, mode, location, synchrony and skew (Rathcke and Lacey 1985). Population sizes need not be large but sampling at 2-3 day intervals is essential to statistically describe the distribution of short events such as anthesis.

Events in the vegetative life cycle are not so distinct. They are generally less critical to survival with the obvious exception of establishment (6.1), the transition from heterotrophy to autotrophy before seed reserves are exhausted. Studies of vegetative phenology usually focus on processes important in community dynamics such as the timing of canopy development (Al-Mufti et al. 1977). Defining the beginning and end of a process such as canopy dominance is difficult so studies of vegetative phenology tend to be descriptive (e.g. Kunii and Maeda 1982) or investigative (Grace and Wetzel 1981a, 1981c, 1982a). The

emphasis on life cycle events means quantitative phenology is close to population biology. Special points to consider when doing a population study of clonal plants are discussed below (3.3).

Phenological data presented in the production study (Chapter 2) were collected from one quadrat in a stand of T. orientalis and therefore give no indication of inter- or intra-specific variability. Intra-specific variations are likely to be small and probably due to resource differences between sites (Brown et al. 1985), whereas inter-specific variations may be important isolating mechanisms.

Variations in species' vegetative and reproductive life cycle are known for Typha. In India T. elephantina grows in March-August then flowers whereas the sympatric T. angustata grows and flowers all year round (Sharma and Gopal 1977). Of three Typha spp. distributed across a latitudinal range of 26-49°N in North America, one flowers at a set time regardless of origin whereas flowering time of the other two follows a north-south gradient (McNaughton 1966a). In Australia no life cycle differences, vegetative or reproductive, have yet been recognised at species level (Briggs and Johnson 1968, Aston 1973, Sainty and Jacobs 1981). This could be due to the difficulty of distinguishing species in the field. There is obviously some confusion as one aquatic flora reports "Plants flower most of the year but less commonly in the colder months" and the other "Flowering and fruiting spikes present (Sept-) Nov-Mar (-April)".

The aim of this study was to describe vegetative and reproductive phenology of Typha spp. for the Griffith area of New South Wales. The possibility of inter-specific differences meant both T. domingensis and T. orientalis were included. Site-related variations were considered by including sites of different water depths but chance events during the year (see below) meant summer drought and grazing had to be recognised as

treatments. Thus the two subsidiary aims, retrospectively defined, were to describe the effects of summer drought and grazing on Typha spp. These were discussed earlier in general terms (1.3) and it was pointed out that water level was of primary importance in determining the distribution of wetland plants and that grazing was unlikely to be significant except when herbivores were introduced. These are discussed more fully below.

3.2 Water and grazing

Water

Water levels in a wetland change in response to broad climatic, hydrologic and geomorphologic influences, and thus are characteristic of a wetland or region. Water level changes, here referred to as water regime, include an array of characteristics such as duration, timing as in seasonality, frequency, direction as in up or down, magnitude as in vertical change, and rate of change.

Water levels in natural wetlands are rarely stable but constantly change, slowly or fast, seasonally, stochastically and even randomly (Hejny 1971, Segal 1971, Tallis 1983, Gopal 1986). Wetland ecologists have been slow in coming to grips with this dynamic component. As yet there is no universal model which can be used to define critical features of water regime. This means the norm is poorly defined, therefore departure from normality can only be assessed by changes in the vegetation. These can be classed as major or minor. A major change would be a shift in species composition whereas a minor change would be a change in species vigour or reproductive output without affecting survival of the individual. This is a distinction of convenience, as major and minor intergrade over an extended time scale.

There are many examples of species shifts. Mostly these show the difficulty of assessing vegetation change, the importance of time scale and the need for a theoretical framework involving succession. An unusual

drying out of Lake Chilwa in Malawi and Lake Naivaisha in Kenya provided a transient niche for short-lived and poorly competitive species (Howard-Williams 1975, Gaudet 1977). Periodic drying out may even be necessary to ensure the long-term presence of certain species (Keddy and Reznicek 1982). Conversely in wetlands where fluctuating water levels are common, such as shallow marshes of North America, periodic drying out does not change the community (van der Valk and Davis 1976a) which has been selected by this periodic disturbance in the same way that fire "selects" a community.

Minor changes describe processes such as competition, invasion and die-back, and may explain co-existence. At Eagle Lake, Iowa USA, the presence of four species of emergents, described as "polydominant", was attributed to irregular dry spells (van der Valk and Davis 1980) which affected species vegetative and reproductive vigour differentially.

Grazing

The impact of grazing on the individual depends on how much and what parts are removed. The most usual kind of grazing is defoliation. In terrestrial plants, defoliation temporarily reduces root activity and nutrient uptake, and repeated defoliation may lead to root mortality (Crawley 1983). There are two types of herbivory, parasitic which slows down the plant's growth rate, and predatory which directly reduces the probability of survival (Crawley 1983). Leaf feeding is parasitic whereas virus introduction via sap-suckers is predatory. This distinction excludes ancillary effects such as trampling. Grazing can alter recruitment and survival patterns so that the impact of grazing on a population is frequently obvious as an altered age structure typified by the lack of younger age groups (Silvertown 1982).

The quantity of material removed by grazing is sometimes used as an index of grazing intensity. It may be measured by comparing standing crop

or production in grazed and ungrazed areas. The preconception (1.3) that grazing is unimportant in wetlands means estimates of grazing intensity have only recently become available for emergents. These show that grazing intensity is high, but perhaps because the studies were done to demonstrate the importance of wetlands to wildlife. In Utah, the activity of geese, coots and muskrats had a grazing intensity of 47.5% for aboveground T. latifolia (Smith and Kadlec 1985) and on coastal saltmarshes of North Carolina, snow geese had a grazing intensity of 58% on belowground biomass of Scirpus robustus (Smith and Odum 1981). A problem with this approach is that grazing may alter growth patterns.

Possibly more important than the quantity removed, is the part selected. Choice of species or plant part is determined by factors such as availability, taste and nutritive value, specifically nitrogen content. Again there are few studies of food preferences in macrophytes perhaps because low species diversity, typical of macrophyte communities (e.g. Rice and Westoby 1983), makes identification of target species less important than identification of target communities.

3.3 Clonal growth

The unit of information in population biology and demography studies is the individual. The significance of the clonal habit, especially when the plant is rhizomatous and therefore partly hidden underground, is the difficulty of identifying an individual. This can be be overcome if a species has a visual genetic marker or is easily dug up, factors which have probably contributed to the popularity of Trifolium repens and sand dune species for population biology studies. Typha does not have a visual genetic marker nor is it easily dug up.

The alternative is to by-pass the plant as an individual and consider its component parts i.e. treat the individual as a population of parts. This is the modular approach to growth championed by Harper (e.g. Harper

1977, 1979, Harper and Bell 1978) which was used as an alternative approach in the production study (2.3). Advantages of the modular approach for classical plant growth experiments have been overstated (Bazzazz and Harper 1977, Hunt 1978) but it is invaluable for field studies of rhizomatous plants. The unit of study is usually the ramet, which comprises shoot and rhizome, and its demography is now basic to ecological studies of clonal plants (e.g. Silvertown 1982, Bell 1984). The main disadvantage is that data analysis is limited to techniques, mainly non-parametric, which do not have independence as a basic assumption. Consequently much population analysis is graphical or uses simple statistical tests. Techniques for analysing grouped, dependent, proportional data are still being developed, e.g. the proportional death rates model of Bartlett and Noble (1985).

Another consequence of the clonal habit relevant to demography is the lack of density-dependent mortality. Changes in shoot density-weight relationships in thinning populations of 9 clonal species, mainly cool temperate wetland species, did not conform to the -3/2 law (Hutchings 1979), allegedly the universal law describing self-thinning due to resource competition (Silvertown 1982). This claim was indirectly supported by studies of underground "adaptive architecture" in clonal plants (Bell and Tomlinson 1980). In many species, ramet branching patterns are thought to have been naturally selected so that modules are spaced to minimise inter-module competition. This view is not fully accepted (e.g. Harper 1985). Regular branching patterns which have been theoretically described may not occur in a naturally heterogeneous world (Cook 1985). Instances of density-related reductions in ramet weight are known (Pitelka 1984). The question will probably be clarified by recognising that clonal growth encompasses a variety of growth forms with different ecological and physiological implications. This recognition and

classification process has begun. Lovett Doust (1981) saw two strategies in Ranunculus repens. One was "guerilla" characterised by an advancing, invasive edge of widely spaced ramets and the other was "phalanx", a tightly packed, monospecific, slowly advancing formation.

A third consequence is due to stand longevity. Clonal herbs may be several centuries old (Silvertown 1982, Cook 1985). Plants such as Pteridium aquilinum and Carex arenaria show a change of vigour from oldest to youngest parts of the stand with up to five demographically distinct phases (e.g. Noble et al. 1979).

3.4 Study approach

A demographic approach with permanent quadrats was chosen. This gave continuity with the production study (Chapter 2). Emphasis was on shoots rather than leaves because shoots are the visual part of the ramet and therefore the natural sub-sampling unit for the whole plant. The relationship between leaf and shoot was clarified earlier (2.11). Demographic analysis may be by age or size. Analysis by age assumes time is the critical factor but population trends such as reproduction and mortality are frequently size-related (Kirkpatrick 1984). Genetic differences, habitat micro-heterogeneity and competition mean plants of similar age are not necessarily of similar size, even if they are the same genotype. Therefore analysis was by age and size, with size defined by shoot height. Stand age was considered because rhizomes from the middle of an established stand of T. orientalis were shorter than colonising rhizomes, had larger crowns and seemed to have fewer live shoots along the connected ramets (Appendix 4).

The time requirement for surveying, marking and locating shoots and leaves was high. Quadrats were sampled as frequently as possible but the rigorous sampling required for statistical analysis of reproductive events was not feasible. Study sites were chosen for ease of access and

because they gave appropriate combinations of species, age and water depth.

METHODS

3.5 Methods

Field sites

Two study areas were chosen, one at Bringagee Road and the other at Lake Wyangan. The Bringagee Road site was 25 km west of Griffith, just beyond the irrigation area (GR CC853107, 1:100,000 "Koorongal" topographic map, Dept of Mines and Energy, 1972) where a small creek lined with sparse blackbox *Eucalyptus largiflorens* passed under the road. There were clumps of *T. domingensis* and *T. orientalis*, 7-15 m diameter, in the creek bed and on ground adjacent to the creek. The soil was a heavy grey clay. When visited the previous summer the creek had water. Conductivity of creek water in September 1980 was 900 $\mu S\ cm^{-1}$. There were three study sites here, shallow *T. domingensis*, shallow *T. orientalis* and deep *T. orientalis*. Shallow sites were 1-2 m above the creek bed and the deep site was in the deepest part. Water here was 75 cm deep in May 1980.

Lake Wyangan, 5 km northwest of Griffith (GR DC097116, 1:100,000 "Griffith" topographic map, Dept of Mines and Energy 1970) was a canegrass swamp and was mined for gypsum (G. Bischard, pers. comm. 1980). Now it is permanently flooded. A dense fringe of emergents, mainly *T. domingensis* and *T. orientalis* reach 3-4 m in summer. Waterfowl are abundant. From 1977-79 conductivity of lake water averaged 1366 $\mu S\ cm^{-1}$, pH 8.9 and the dominant ions were sodium and chloride (CSIRO 1980). There was one site at Lake Wyangan, deep *T. domingensis*, in an area of 30-50 cm deep silt. In May 1980, water depth in the quadrats was approximately 10 cm but was expected to be deeper in summer.

Rectangular quadrats, 2 x 0.5 m, were set up with metal posts and wire

in May-June 1980 as in the production study (2.5: Demography and phenology). Quadrats were in pairs, separated by 2-3 m, and referred to as Centre and Edge because of their positions. Centre quadrats were within the stand whereas Edge quadrats had their long face parallel to stand edge and included as few shoots from previous season as possible. This gave a total of eight quadrats, 2 species x 2 depths x 2 ages. In addition, there was one extra T. orientalis quadrat at Bringagee Road, aligned at right angles to the stand edge and referred to as Colonising quadrat as well as the permanent quadrat from the production study at Brogden's Road (Chapter 2).

This 2 x 2 x 2 study design was subsequently modified for two reasons. First, all green shoots from the deep T. orientalis quadrats were grazed in August 1980 and there were no live shoots in this quadrat until March 1981. Monitoring was discontinued in September 1980 and data from the permanent quadrat at Brogden's Road used instead. Second, the Bringagee Road site dried out completely in summer and re-flooded in autumn (details in 3.6) whereas at Lake Wyangan and Brogden's Road, ground in the quadrats remained saturated. The original treatment designation of deep and shallow became inappropriate so were amended to summer wet and summer dry water regime, referred to as Wet and Dry. This was recorded in the field by presence of free water in each quadrat. Final study design is summarised in Table 3.1.

A census was done in each quadrat at 2-3 week intervals from 27 May 1980 to 3 June 1981 as described previously (2.5: Demography and phenology). Shoot positions were plotted onto a quadrat map which was useful for finding small shoots and confirming losses. By late spring T. orientalis shoots at Bringagee Road were too tall and brittle to measure without causing damage. Consequently shoot heights from November to March were only measured intermittently when assistance was available. There

was no difficulty distinguishing new shoots from seedlings. New shoots are rigid cones of overlapping leaves which open to show leaves approximately triangular in shape, thick, stiff and dull green. Seedling leaves are almost linear, thin, soft and vivid green.

After the study finished, the depth distribution of rhizomes was charted by digging a 25 cm deep trench along the long face of permanent quadrats and mapping the intercepts. High water tables and heavy clays meant only three quadrats were dug, two at Bringagee Road and one at Brogden's Road. At the same time, single soil samples were collected from below the coarse litter layer and at 20 cm depth. These were analysed for organic matter, Kjeldahl nitrogen and soluble reactive phosphorus as described above (2.5: Soil sampling).

Data organisation and analysis

Shoots present at the first census were of two types, shorter vigorous ones and taller, yellowing ones assumed to be two age groups. An attempt was made to distinguish these on the basis of height but it proved impossible to be consistent so these are treated as one group called pre-Winter shoots. Because their age was unknown, mortality for this group is presented as a depletion curve (Harper 1977, Silvertown 1982) whereas mortality for shoots of known age is shown on a survival curve.

A cohort was all shoots emerging in one calendar month. This was the most convenient time unit. "Natural" cohorts as recognised by Dickerman and Wetzel (1985) could only be defined by pooling quadrat data but results and treatments indicated this would lead to an information loss. Only cohorts with 5 or more shoots are graphed or statistically analysed.

The numbers of leaves were high and variable. Seasonal variations in recruitment and mortality are standardised and monthly totals given as a proportion of the yearly total, p(yT) with mean coefficient of variation V* as an index of temporal variability between quadrats. Leaf recruitment

rate is the number of leaves recruited per shoot per day, expressed per 100 shoots as leaves shoot 10^2 d^{-1}.

Grazing frequency was the number of visits on which recent grazing was noted or deduced from data analysis. Two levels were recognised, total defoliation when whole shoots disappeared, and partial defoliation when part of the shoot disappeared. Initially disappearances were regarded as human errors but after carefully re-checking data records and specifically searching for missing leaves and shoots using quadrat maps, it became apparent these losses were due to animal activity. This was later confirmed by finding marked leaves nearby.

Statistical analysis was made awkward by wide variations in sample sizes and lack of real replication so most analysis is graphical. Chi-squared analysis was used to determine if partial grazing affected shoot survival. For this monthly cohorts were sub-divided into grazed and ungrazed and the proportion alive on successive months compared.

RESULTS

3.6 General results

Soils

Soil analyses (Table 3.2) showed that nitrogen and phosphorus concentrations were higher at Lake Wyangan and Brogden's Road than at Bringagee Road, probably because the first two receive drainage water from irrigated crops. Organic matter was also higher. Soils at Bringagee Road showed no evidence of surface litter accumulation as might be expected for a productive plant like Typha.

Trench excavation of T. domingensis quadrats at Bringagee Road showed a coarse but well-defined litter layer, 2-3 cm deep, overlying a heavy grey clay of uniform colour and texture. Most rhizomes (80%), dead and

alive, were 6-9 cm below organic layer (not shown). Rhizomes were not obviously succulent but were shrunken, except for one at 14-15 cm. At Brogden's Road the substrate was sloppy organic silt. Rhizomes were larger (no measurements taken), succulent and deeper within the soil, range 6-33 cm with 60% in 14-20 cm depth range. Rhizome depth was not established at Lake Wyangan.

Water regime

The table summarising water regime by presence-absence of free water (Table 3.1) does not fully convey the differences between Wet and Dry sites. Although there was no free water of any depth for much of the year at Lake Wyangan, the Wet T. domingensis site, the substrate remained saturated at all times. Water levels were highest over summer, reaching a maximum depth of 35 cm in January, in response to irrigation over-flow. At Brogden's Road, the Wet T. orientalis site, the situation was similar with the quadrat being saturated for most of the year although lacking free water for some of that time. In summer it alternately flooded and firmed up (2,6) but did not reach the stage of cracking or hard muds. In contrast, the Dry sites at Bringagee Road dried out for an extended period in summer. This was because the creek level fell in spring, rose again, then rapidly dried out during summer. By January the ground in all quadrats was hard and remained so until reflooded in autumn. The T. domingensis quadrats were on slightly higher ground than T. orientalis quadrats and so flooded later (Figure 3.1) and not so deeply. Thus T. domingensis quadrats flooded in August to 10 cm, in November to 25 cm and in April to 25 cm. In comparison T. orientalis quadrats were flooded almost continuously during winter, in October-November to 30 cm then in March to 15 cm and in April to 35 cm. Autumn flooding at Bringagee and Brogden's Road was a response to rice field releases.

3.7 Shoot demography

Density

The eight quadrats differed in shoot density. When first surveyed in May-June 1980, live shoot density ranged from 9 to 42 shoots quadrat^{-1} and tended to be higher in T. domingensis quadrats than in T. orientalis quadrats, 20-42 compared to 9-25 shoots quadrat^{-1} (Table 3.3).

There was no uniform response during the year (Figure 3.2). In general Centre and Edge pairs tracked each other. Dry quadrats at Bringagee Road showed a density decrease in February-March (Figure 3.2 b, d) reaching zero in T. domingensis Centre quadrat. This decrease was followed by a rapid increase in March-April. Centre Wet quadrats of both species had a population peak in February-March (Figure 3.2 a, c). Shoot populations in T. orientalis quadrats were stable in winter-spring (Figure 3.2 c, d, e).

In most quadrats live shoot density in June 1980 was similar to June 1981 (Table 3.3) with the ratio of Final:Initial density being close to unity. The exceptions were the two T. domingensis Centre quadrats where density showed a net increase at Lake Wyangan with F/I = 1.55 and a net decrease at Bringagee Road with F/I = 0.59.

The density of dead shoots in June 1980 (Table 3.3) ranged from 0-33 shoots quadrat^{-1} and was highest in the two established stands, 18-33 shoots quadrat^{-1} at Lake Wyangan and Brogdens' Road. All quadrats showed an accumulation of standing dead material with dead shoot density in June 1981 exceeding June 1980.

Recruitment

The number of shoots recruited during the year (Table 3.4) ranged from 15 to 133 quadrat^{-1} and was higher in T. domingensis quadrats, 34-133 than in T. orientalis quadrats, 15-45 shoots quadrat^{-1}. The number of shoots recruited during the year was equal to or greater than the initial shoot density (Table 3.4). For most quadrats this replacement ratio was 1.2-1.8 except for the two T. domingensis Centre quadrats. At Lake Wyangan this ratio was 6.65 indicating a high turnover during the year,

and at Bringagee Road it was 1.0.

The timing of shoot recruitment differed between quadrats (Figure 3.3). In the T. domingensis quadrats at Lake Wyangan shoot recruitment occurred in all seasons whereas in other quadrats there was little to no recruitment in spring. The Centre quadrat at Lake Wyangan had two recruitment peaks, one in August-September and one in January-February, compared to single peaks in summer-autumn in other quadrats. In the T. orientalis Wet quadrat at Brogden's Road recruitment extended over six months from January to June-July whereas at Bringagee Road recruitment of T. domingensis and T. orientalis was concentrated in one month, March or April shortly after re-flooding (Figures 3.1 and 3.3). This was the time of maximum recruitment rates in Dry quadrats (Table 3.4). In Wet quadrats, maximum recruitment rates were earlier, in January.

Mortality

Depletion curves (Figure 3.4) show that most Pre-Winter shoots, 192 out of 196 present at the start of the study, died during the year regardless of species or water regime. The four exceptions which survived longer than a year were all from the same T. domingensis Edge quadrat at Lake Wyangan. All quadrats showed some mortality in early winter. It was most evident in Centre quadrats because these had a higher proportion of previous season shoots than Edge quadrats. In the two Centre T. domingensis quadrats mortality was fairly constant from midwinter onwards but in T. orientalis quadrats mortality was low in spring. Nearly all depletion curves became steeper from December-January showing that mortality was concentrated in summer-autumn.

Cohort survival showed the same trends as depletion curves but without early winter mortality (Figure 3.5). There was persistent mortality during spring in T. domingensis quadrats at Lake Wyangan which contrasted with high survival in T. orientalis populations. Heavy mortality in

August-September for June and July cohorts of T. domingensis quadrats at Bringagee Road (Figure 3.5) was due to cattle trampling in August. Shoot death was strongly seasonal for both species and was concentrated in the months following December. The majority of shoots recruited between June and December were dead by June of the following year. Exceptions to this were all in the same quadrat, T. domingensis Edge Wet (Figure 3.5 b).

Cohorts at Dry sites died earlier than cohorts from Wet sites and this was more obvious for T. domingensis than T. orientalis. The June to September cohorts of Dry T. domingensis at Bringagee Road were completely dead by the beginning of February whereas similar aged cohorts at Lake Wyangan survived to May, June or longer (Figure 3.5). Pre-Winter and June cohorts at the Dry T. orientalis site at Bringagee Road were all dead by April and May whereas at the Wet site they survived until June or beyond (Figure 3.4 b and 3.5 e-h).

Both species had an inverse relationship between size and over-winter survival (Figure 3.6) with the same critical height class, 1001-1200 mm. Shoots less than 1200 mm tall at the beginning of winter had a high probability of successfully over-wintering, with p = 1.0 and only occasionally less. No shoots taller than 1200 mm survived winter.

Height

Mean height of each cohort and pre-Winter shoots at the beginning of each month is shown in Figure 3.7. The tallest was T. orientalis at Bringagee Road where in midsummer cohorts were at least 2.5 m and the shortest was T. domingensis Edge at Bringagee Road where midsummer heights were 1.0-1.5 m. All other populations were 1.0-2.0 m in midsummer. Heights of T. domingensis in Lake Wyangan quadrats were not typical for the lake as elsewhere Typha spp. reached 4 m (pers obs.). The exceptional shortness of this site only became obvious in August-September when spring growth began.

Shoot growth as indicated by changes in shoot height was slow in winter then rapid in spring reaching maximum height in midsummer when growth generally ceased. This was the same growth pattern described by intensive leaf monitoring in the production study (Figure 2.12). Pre-Winter shoots decreased in height during early winter due to the loss of tall senescing shoots from the previous season. Shoots recruited between summer and winter grew rapidly at first but by the beginning of winter had not reached the heights of cohorts in midsummer (Figure 3.7). Shoots of both species had high absolute growth rates. Winter cohorts from all sites except T. domingensis Dry quadrats averaged 18-37 mm d^{-1} in September and October, and autumn rates were equally high.

Growth of T. domingensis shoots in Dry quadrats at Bringagee Road (Figure 3.7 c, d) was a little different from other quadrats. In the Centre quadrat, mean height for June and July cohorts did not have a complete sigmoidal shape but appeared truncated, dying off before reaching maximum height. In the Edge quadrat, pre-Winter shoots and July and August cohorts reached a height plateau two months earlier than other quadrats, in October. After the site re-flooded, the youngest cohort had a growth spurt in November-December.

Population structure

By midsummer the largest age group in most quadrats was the initial pre-Winter shoots which was 0.6-0.9 of live population (Table 3.5). The exception was the T. domingensis Centre quadrat at Lake Wyangan where the midsummer population was younger and the largest age group was shoots recruited after winter, 0.4 of live population.

Population structure of Pre-Winter shoots, based on height classes of 200 mm, is shown for two consecutive years (Figure 3.8) for all quadrats. Only two quadrats, both Centre Wet, were the same (not tested) in June 1980 and June 1981 (Figure 3.8 a, e). Other quadrats, mainly at Bringagee

Road, had similar shaped distributions but located at different heights indicating temporal displacement with recruitment apparently earlier in 1981 (Figure 3.8 b-d, f, g) and this is further evidence of year to year variations in growing conditions at this site. In June 1980, senescing shoots of T. domingensis were in the 2401-2600 mm height class so were 0.5-1.0 m taller than midsummer cohorts of the following growing season (Figure 3.7 c and d, Figure 3.8 c and d).

A noticeable feature of these height distributions was the differences between quadrats, ranging from bell-shaped to bi-modal. These would have been due to site history factors such as grazing, water regime etc. An additional factor was the time period over which recruitment occurred. The bell-shaped distribution evident in June 1981 populations of T. domingensis at Bringagee Road (Figure 3.8 d) resulted from intense recruitment, 5 recruits in 8 days then 24 recruits in the following 7 days (Table 3.4). These differences clearly illustrates the difficulty of separating pre-Winter shoots into age groups using height as a criteria (3.5).

3.8 Reproductive growth

Description

Typha shoots changed in appearance before flowering, due to the rapid recruitment of increasingly narrower leaves. These formed a cylinder up to 1 m tall around the immature inflorescence thus protecting it. After emergence, peduncles were soft and pliable then hardened. This lignification process is reflected in weight changes (Figure 2.2). At Lake Wyangan eleven inflorescences matured successfully even though bent at right angles to normal orientation by high winds in late November. Once emerged, peduncles extended rapidly. Rates of 50-70 mm day^{-1} over a 7-10 day period were recorded in early November from all quadrats.

T. domingensis and T. orientalis had similar flowering times with

anthesis from mid-November to early or mid-December. The overlap between peak flowering period, the time when 75-100% flowering shoots were in anthesis, and the duration of anthesis (Table 3.6) shows that flowering was fairly well sychronised within quadrats and within T. orientalis stand at Bringagee Road. During anthesis, inflorescences were attractive to pollen-feeding Rice Beetles (Dicranolaius sp.) with up to 12 beetles observed on one inflorescence at once. In 1980 dispersal began in autumn after peduncles died (Figure 3.9 a).

Seedlings were rare in all quadrats. At Brogden's Road, there were extensive mats of dense seedlings at the edges of Typha clumps in June and July (Figure 3.9 b) but none grew more than 5 cm or survived more than 3 weeks.

Comparisons

Phenological data were collected too infrequently, and population sizes were too small for statistical analyses, so comparisons of phases in the reproductive cycle are graphical. Reproductive cycles began at virtually the same time, as shown by the pre-flowering habit change in late October. Successive phases, shown by colour changes and infloresence swellings (not shown), were gradually separated as each T. domingensis phase lasted slightly longer and thus started slightly later. This is evident in the first-last records of anthesis (Table 3.6) and duration of seed dispersal at Wet sites (Figure 3.9). Dispersal of seeds formed before the study lasted two months in winter for T. orientalis and six months in winter-spring for T. domingensis, June-July versus June-December (Figure 3.9 a). Seedlings were mainly observed during dispersal period (Figure 3.9 b), June to December at Lake Wyangan and June-July at Bringagee Road. Seedlings at Bringagee Road in December and March were found after the site had flooded.

Height class structure of quadrat populations in mid-October, before

the habit change was apparent, showed that successfully flowering shoots were the tallest in each quadrat (Figure 3.10), indicating ramets had to reach a critical minimum size before flowering. This minimum size differed between species being height class 10 for T. domingensis and nearly double 18 for T. orientalis, equivalent to 901-1000 mm height and 1701-1800 mm respectively. The proportion of the shoot population which flowered, p(R), was higher in T. orientalis quadrats but the actual number of flowering shoots was higher in T. domingensis quadrats (Table 3.7). In both species and in seven out of eight quadrats, at least 50% of reproductive shoots was recruited before June, p(pre) >0.05 (Table 3.7), and all were recruited before the end of winter, p(post) = 0. In the eighth and exceptional quadrat, T. domingensis Centre at Lake Wyangan, reproductive shoots were recruited much later, p (post) = 0.2917. The difference in the number of reproductive shoots reported in Table 3.7 and shown in Figure 3.10, is due to the failure of some shoots to properly develop and set seed. This was most obvious in T. domingensis Dry site at Bringagee Road (Table 3.7).

The effect of a different summer water regime on reproductive phenology was only evident in dispersal. In quadrats with dry summer, dispersal began 1-3 months earlier than in wet summer quadrats (Figure 3.9 a).

3.9 Leaf demography

The number of leaves recruited during the year varied 10-fold between quadrats (Table 3.8). More leaves were recruited in T. domingensis quadrats than in T. orientalis quadrats, 179-1059 compared to 139-435. This was not reflected in the number of live leaves shoot^{-1} (Table 3.9) which tended to be higher on T. orientalis shoots and highest at Bringagee Road.

Most quadrats showed temporal variation in the timing of leaf

recruitment (Figure 3.11). Peaks in the Dry quadrats and in T. domingensis Wet Centre quadrat coincided with shoot recruitment peaks (Figures 3.11 and Table 3.3). This was because an emerging shoot was a tight conical cap which rapidly opened. Thus 4-5 leaves, all small, were recorded at once. Leaf recruitment in Dry quadrats was negligible to zero once quadrats dried up (Figure 3.11 b, d). Temporal variations were dampened in T. orientalis and V* for 12 months lower, 0.4631 (Table 3.8). Small troughs occurred in late winter, during the spring generation gap (c.f. Figure 2.10) and in autumn. Small peaks in spring and late summer coincided with shoot recruitment.

Leaf recruitment per shoot is shown for just one age group, the Pre-Winter shoots. All quadrats had low recruitment rates in winter, increasing in spring then falling to negligible levels in December and zero in January (Figure 3.12). However quadrats differed as to when maximum and minimum rates occurred. T. domingensis quadrats tended to peak in August-September, with the exception of the Edge quadrat at Bringagee Road (Figure 3.12 b). In T. orientalis quadrats recruitment peaked later in October. This was associated with the pre-flowering habit change (3.8). Flowering was the end of a growth cycle, with no further leaf recruitment. The Colonising T. orientalis quadrat had the highest recruitment rate, 21 leaves 100 shoots day^{-1} (Figure 3.12 c, d). This was 2-3 times the recruitment rate of T. domingensis quadrats at Bringagee Road. Recruitment rates for winter cohorts (not shown) had the same seasonal trends, reaching almost zero in January. The late spring growth spurt in T. domingensis Edge quadrat was even more pronounced with a November recruitment rate of 14 compared to 5 and 2 in the preceding months.

The seasonal pattern of leaf deaths also varied between quadrats (Figure 3.13). Strong seasonal trends with peaks in December-January

followed by troughs in February (presumably because most leaves were now dead) and sometimes March, was typical of Dry quadrats (Figure 3.13 b, d). In contrast, two Wet quadrats, T. domingensis Edge and T. orientalis Centre, showed little temporal variation and V* was correspondingly lower (Table 3.8). In the third Wet quadrat, T. domingensis Centre, leaf deaths increased from spring onwards and peaked in February (Figure 3.13 a).

The leaf death rate for December for shoots of two age groups, Pre-Winter and Winter shoots (Table 3.9) was 2-4 times higher in Dry quadrats than in Wet, but this was not evident in spring (not shown).

3.10 Grazing

Identification

Herbivores were identified as follows. At the deep water site at Bringagee Road and at Lake Wyangan numbered leaves were found floating near quadrats. In August and September bird scats of coarse green fibrous material, similar to Typha, were found near quadrats at Lake Wyangan. These quadrats were always covered with prints of birds' feet. In addition, an Eastern swamphen Porphyrio porphyrio was seen pulling a Typha rhizome out of soft mud at Lake Wyangan and eating it on 12 August, 18 March and 14 May. From these observations it was concluded that shoot and leaf disappearance at these sites was due to grazing by waterfowl. The diet of swamphens consists mainly of "tender young reed stems" (Reader's Digest 1976).

Herbivores were easily identified at other sites by tracks and behaviour. At Bringagee Road foraging cattle ate portions of younger leaves and knocked over shoots in June and August 1980. T. domingensis quadrats were more affected as cattle trampled through them in August 1980. Protective fences put up around quadrats in September were knocked down by cattle in May 1981. At Brogden's Road shoots were grazed in a distinctive manner, being eaten in from one side to the soft inner

tissues, 7-10 cm above ground. Rodent footprints and droppings were found near shoots grazed this way in June, July and September 1980 and March 1981. This form of grazing killed off upper portions.

Incidence and impact

The highest incidence of grazing was at Lake Wyangan. In the Centre quadrat, grazing was recorded on more than half the visits (Table 3.10). Brogden's Road had the next highest incidence and Bringagee Road the least. Grazing was most persistent at Lake Wyangan where it occurred throughout the year. At Brogden's Road, grazing was mainly in winter, and at Bringagee Road a fence excluded cattle from September to May.

Total defoliation, the removal of a whole shoots, was most frequently recorded at Lake Wyangan in the Centre quadrat (Table 3.10) where the number of shoots lost was 37 or more than 1/4 of yearly recruits. On a monthly basis, this was 71% of deaths in October, 33% in November, 71% in February, 45% in March and 40% in May. In other quadrats totally defoliated shoots numbered 0-5, which was never more than 1/10 of yearly recruits. Shoots selected were predominantly young but not always short. At Lake Wyangan, 100% of defoliation losses in October, 100% in January, 60% in February, 82% in March and 100% in May were less than two months old. Heights ranged from 15-1806 mm with the majority taller than 600 mm (Table 3.10).

Records for partial defoliation are incomplete. The method used did not distinguish between recent, not so recent and repeated grazing in all quadrats so total numbers are not shown. The number of shoots affected in Lake Wyangan quadrats was high, particularly in the Centre quadrat where 10% of live shoots in July, October and December and 39% in March lost one or more leaves. In the Edge quadrat, the maximum was 12% in November.

Partial grazing reduced shoot survival in the Centre quadrat at Lake Wyangan. Shoots of winter and spring cohorts which had been partially

grazed had significantly fewer survivors in November to February period than ungrazed shoots. In the Edge quadrat, there was no association between partial defoliation and survival.

In the Edge T. domingensis quadrat at Bringagee Road, shoots damaged by grazing and/or trampling, had lower survival than undamaged shoots. No such association could be demonstrated for other quadrats at Bringagee Road because the numbers damaged were too few for statistical tests. Grazing had little impact on T. orientalis shoots at Brogden's Road. Although rodent grazing meant the upper part of a shoot died, shoots re-grew at the base from the rhizome crown. The number affected by rodents was small, 12 in winter 1980 and one in autumn 1981. Their survival was not significantly reduced.

DISCUSSION

3.11 The annual cycle

The aim was to describe vegetative and reproductive life cycle of Typha spp. using a population biology approach. The study was structured so as to account for some natural variation and the two factors considered, stand age and water depth, were chosen because of their relevance to Typha as a rhizomatous herb and as a wetland species. This 2 x 2 x 2 study design was disrupted because of the loss of two deep water T. orientalis quadrats at Bringagee Road and because remaining quadrats were subjected to varying types of grazing. Grazing was particularly intense at Lake Wyangan, in the T. domingensis Wet quadrats. This meant the number of quadrats that could be considered relatively undisturbed by summer drought or grazing, was reduced from 4 to 1, the T. orientalis quadrat at Brogden's Road. Shoot phenology of this quadrat was presented earlier (Chapter 2) within a production context and in relation to growth hierarchies. The annual shoot cycle, described demographically below, is based mainly on this quadrat but includes results from other quadrats as

appropriate.

One of the original treatments was stand age. In retrospect it is apparent that Centre and Edge quadrats were not an appropriate way to investigate stand age at Griffith as the distance between pairs was too short. A distance of only 2-3 m is probably equivalent to only a few years growth (see below) and therefore insufficient to distinguish age phases within a stand. Age differences between stands were probably greater with stands at Bringagee Road being younger than at other sites. Here Typha was in discrete clumps which is unusual and suggested establishment was very recent. When visited two years after the study ended, the clumps had extended and coalesced. In addition, a younger site would have less time to accumulate organic matter in the soil, or dead shoots and leaves in the stand. These characteristics were evident in Bringagee Road quadrats (Tables 3.2, 3.3, 3.8). Therefore stand age is not discussed as a treatment and Centre and Edge quadrats are counted as replicates.

Vegetative cycle

Except in heavily grazed quadrats, the main period of shoot recruitment lasted from midsummer to midwinter (Figure 3.3). This was also the main period of shoot mortality (Figures 3.4, 3.5). Unfortunately the study began and ended in June which was halfway through the annual cycle so typical shoot longevity cannot be quantified. It appeared however that most shoots had a maximum life-span of one year, although theoretically eighteen months was possible. There was some indication that T. domingensis shoots lived longer than T. orientalis shoots.

Shoots recruited before winter had high mortality in T. orientalis stand at Brogden's Road where 18 out of 39 recruits were dead by June. The probability of surviving over winter was apparently size related. Shoots up to 1200 mm tall had a survival probability close to 1.0 whereas

for taller shoots it was zero (Figure 3.6). After winter mortality rate dropped almost to zero except in grazed or trampled quadrats.

This sequence of early mortality (summer-winter) followed by a period of high survival (winter-spring) then senescence (summer-autumn) describes a Deevey Type III survivorship curve. This is typical for seedlings of polycarpic perennials (Silvertown 1982) where early mortality is often density dependent, i.e. due to competition for resources. There are arguments (3.3) for believing that early ramet mortality in clonal herbs is not due to density dependent factors but although frequently reported (e.g. Bernard and Gorham 1978, Lovett Doust 1981, Dickerman and Wetzel 1985) reasons are not given.

The explanation is probably a combination of generation replacement and internal competition. Generation replacement (Cook 1985) is a one-for-one replacement which assumes no juvenile mortality. Monocarpic flowering stimulates a bud to develop and this acts as a resource sink for the senescing shoot. However if more than one is stimulated, buds would compete for apical dominance and for parental resources. Field excavated Typha ramets usually have only one active shoot per rhizome crown (Appendix 4) but ramets cultivated for a few months often have two to three shoots.

A sequence of flowering or death, then bud stimulation and internal competiton could eventually result in one-for-one replacement after some juvenile mortality. This was the situation for T. orientalis at Brogden's Road. In contrast, quadrats with a large generation gap had minimal juvenile mortality (Figure 3.5). Constant population size is a characteristic of clonal plants (Cook 1985) which means the carrying capacity of the habitat has been reached and has not changed. In this study, five quadrats had relatively constant June population size in 1980 and 1981 (Table 3.3) but a replacement ratio higher than unity (Table

3.4). Factors common to these five were species and disturbance, in common, being predominantly T. orientalis and wetter or less severely grazed.

Size-related mortality over winter has been reported for wetland clonal species but again no explanation has been given. Age may be a factor but is not a complete explanation. In the probability diagram (Figure 3.6) the tallest shoots included reproductive shoots and were therefore from the previous growing season, the shortest shoots were obviously new recruits and therefore from the current growing season but the age of the intermediate sized shoots, e.g. 1200-2200 mm was indeterminate. The difficulty of equating shoot height with age is apparent in the population height structure for T. orientalis in June 1981 (Figure 3.8 d). Eleven shoots recruited between 9-27 March and therefore of similar age had a height range of 1582 to 2477 mm. Although difficult to explain, it does seem that size as height is the factor. Both species had the same cut-off point, 1200 mm, which was similar to the cut-off point for T. latifolia in Michigan, 1060 mm (Dickerman and Wetzel 1985).

Reproductive cycle

The reproductive cycle began in late spring to early summer when both species flowered, and lasted to early winter or early spring, depending on species, when dispersal was completed. Anthesis began between 12-18 November for T. orientalis and 14-28 November for T. domingensis, days 316-322 and 318-332 of the year (Table 3.6). Allowing for seasonal shift between hemispheres, these dates are similar to T. latifolia from Austin, Texas at 30°N, days 132-142 (McNaughton 1966a).

Flowering was synchronised (Table 3.6) within quadrats and within T. orientalis at Bringagee Road, but less so for T. domingensis. Synchronous flowering is common in wind-pollinated species where it is usually a

response to unambiguous environmental cues (Rathcke and Lacey 1985) such as photoperiod and temperature. The significance of dispersal timing is discussed in relation to germination ecology (7.2).

Although flowering phenology may be set by environmental cues, the probability of flowering was clearly related to shoot size. No shoots below a critical minimum height flowered, compared to most shoots above that height (Figure 3.10). A minimum critical size for flowering, whether measured as shoot height or rosette diameter, has been reported for other clonal herbs (Bradbury 1981, Pitelka et al. 1985) as well as T. latifolia (Dickerman and Wetzel 1985). The usual interpretation is that flowering is "costly", and is only possible if sufficient resources are available. Grace and Wetzel (1981c) argued that flowering must depend on rhizome storage because it occurred so rapidly. The growth rate of peduncles was exceptionally fast (3.8).

The timing of reproductive life cycle gave clear evidence of species differences. The broad-leafed T. orientalis flowered earlier than the narrow-leafed T. domingensis yet its critical minimum size was almost double. This suggests that T. orientalis was more effective at resource capture. This is supported by species differences in the timing of leaf recruitment (Figure 3.12) and leaf recruitment rates (Figure 3.13).

Species differences in critical minimum size and timing of canopy development have parallels with sympatric species of North America. Cultivated ramets of T. angustifolia require 10 days less growing time to reach flowering than T. latifolia (McNaughton 1966a) and in the field it flowers at smaller weights (Grace and Wetzel 1982a) thus allocating a greater percentage of biomass to sexual reproduction (Grace and Wetzel 1982a). Despite this its canopy develops later than T. latifolia.

3.12 The water treatment

The three sites had different summer water regimes as defined earlier

(3.2). Lake Wyangan quadrats were under water continuously in December, January and February, the Brogden Road quadrat flooded intermittently over this period, and the Bringagee Road quadrats were completely dry (Figure 3.1). There were also differences within sites, with T. domingensis quadrats at Bringagee Road having a drier water regime than T. orientalis quadrats. However grazing meant not all inter-site differences could be attributed to water regime.

In Wet sites, shoot recruitment coincided with and slightly preceded, shoot senescence. This generation overlap was evident as large density peaks in February-March (Figure 3.2 a, c). The summer Dry water regime created a gap between shoot generations. Generation overlap was minimal in most Dry quadrats and zero in the quadrat with zero live density in late March (Figure 3.2 b). Recruitment began in early summer, close to flowering as in Wet quadrats but was not maintained. It stopped when the site dried out in January and was not resumed until March-April after re-flooding (Figure 3.3) thus creating large density troughs. Leaf mortality rates for December (Table 3.8) indicate mortality began earlier in Dry quadrats. This was evident in the earlier death of Dry cohorts compared to similar aged cohorts in Wet quadrats (Figures 3.4 and 3.5).

Reproductive life cycle was not much affected by the dry summer but this was probably a question of timing as the dry months occurred after flowering. Seed set and viability may have been affected but these were not measured. Dispersal was advanced because of earlier shoot death. Seeds only dispersed after peduncles had died.

At Bringagee Road, quadrat differences in trough size are probably due to water regime rather than species. The T. orientalis quadrats dried out in December at the same time as T. domingensis quadrats but re-flooded in March rather than April, giving a 3 month as opposed to a 4 month dry summer. This extra month prolonged the period of mortality with no

recruitment, creating a larger generation gap in T. domingensis quadrats.

There were other species differences at Bringagee Road. November and December cohorts survived 3 months longer in T. orientalis quadrat than in T. domingensis quadrat (Figure 3.5 d, h). Mean shoot height in midsummer was similar to the previous season for T. orientalis (Figure 3.7, Figure 3.8 f) whereas T. domingensis shoots were 0.5-1.0 m shorter. These differences are consistent with T. domingensis having a drier water regime in summer but spring conditions must also be included. Cohorts in T. domingensis Edge quadrat almost stopped growing in spring (Figure 3.7) but the youngest cohort recruited in August showed a height increase after the site re-flooded in November (Figures 3.12 b, 3.13 b).

When quadrats re-flooded, Dry quadrats responded quickly showing that rhizome buds survived a 3-4 month summer drought quite well despite their relatively shallow position in the substrate (3.6). There was a difference in the post-drought recovery with T. orientalis quadrats recovering better than T. domingensis quadrats. Shoots of T. domingensis did not have the rapid height increase of T. orientalis shoots (Figure 3.7) and T. domingensis quadrats had a lower replacement ratio (Tables 3.3, 3.4). Again, this was probably due to differences in water regime than species. The significance of drought duration and timing are discussed in the last chapter (7.2).

3.13 The grazing treatment

Lake Wyangan quadrats were demographically distinct from other quadrats. Shoots were recruited in all seasons and there was mortality throughout the year. The Centre quadrat was further distinguished by a relatively young midsummer age structure, huge density changes and high shoot and leaf recruitment. These characteristics can be attributed to grazing. They were not apparent in other grazed quadrats because grazing at Lake Wyangan was much more severe. The incidence was higher,

continuous, and more shoots were affected. In addition, the grazing action of waterfowl, the herbivores at Lake Wyangan, was potentially more destructive.

In terrestrial plants, defoliation temporarily affects root growth and nutrient uptake, and repeated defoliation may lead to root mortality (Crawley 1983). Leaf feeders typically have least effect on plant survivorship because this type of grazing is parasitic rather than predatory (Crawley 1983). The three herbivores in this study, waterfowl, rodents and cattle, were all leaf feeders but had quite different grazing action, specifically the cutting position relative to water level. Rodents grazed 7-10 cm above wet muds, cattle grazed leaves above the water, but waterfowl cut shoots and leaves at the water or mud surface. This would allow water to enter the plant with the result that the ventilation pathway between root and leaf would be blocked. This can lead to complete de-oxygenation of tissues below the blockage in as little as eight hours (Sale and Wetzel 1983), resulting in tissue death in meristems, roots and rhizome. It is for this reason that cutting below waterlevel is sometimes recommended as mechanical control for Typha (e.g. Finlayson et al. 1983). Thus in wetland plants such as Typha, the usual effect of leaf feeding are likely to be compounded if grazed by waterfowl as leaf feeding becomes predatory than parasitic (3.2).

The consequence of internal tissue damage is lower yield (Sale and Wetzel 1983) and the consequence of shoot death or removal is bud development, eventually. Thus the combined effects of persistent grazing, partial and total, such as at Lake Wyangan is less biomass, early shoot mortality, continuous recruitment and a youthful shoot population. This is in contrast with the more usual effect of grazing, absence of younger age groups (3.2), and is only apparent because of using demography of plant parts. A similar effect has been reported for Spartina alterniflora

in USA. In grazed areas shoots are shorter, denser and reach maturity earlier (Stanholtzer 1974). A critical reproductive size of only 900 mm for T. domingensis means shoots can flower when relatively young, e.g. six weeks (Table 3.7). It is questionable whether T. orientalis with a criticial minimum size of 1700 mm could recover as quickly, despite its more rapid spring growth.

There was a distinct preference for young shoots. In general, young shoots are thought to be more palatable to herbivores because their lignin content is lower than old ones so their nitrogen concentrations are relatively higher (Mooney and Gulmon 1982, Smith and Kadlec 1985). Nitrogen concentration in leaves of T. domingensis and T. orientalis were not measured in this study but in two month old shoots of T. angustifolia it was 10-20 mg g^{-1} (Mason and Bryant 1976) and the percentage protein content of North American Typha was 2.6-6.8% (McNaughton 1966a). This is lower than the palatable and important flood-plain plant Cynodon dactylon which has a protein content of 6-18% (Furness and Breen 1986).

Table 3.1
Quadrat organisation

The table shows location of quadrats and sites according to species and water regime and the total number of quadrats in each category. Centre and Edge are explained in the text.

Treatment	- Species -		Total
	T. domingensis	T.orientalis	
Wet	Lake Wyangan Centre + Edge	Brogden's Road Centre	= 3
Dry	Bringagee Road Centre + Edge	Bringagee Road Centre + Edge + Colonising	= 5
Total	= 4	= 4	= 8

Table 3.2
Soil analyses

Organic matter is the combustible percentage of dry soil, OM as %
Nutrients concentrations are given as mg g^{-1} dry soil
Nitrogen is Kjeldahl nitrogen KN
Phosphorus is soluble reactive phosphorus SRP

Site and depth	Organic %	Nitrogen KN	Phosphorus SRP
Lake Wyangan			
0 cm	22.7	4.4	0.20
10 cm	22.3	5.9	0.20
Brogden's Road			
0 cm	23.9	7.0	0.30
20 cm	8.7	0.8	0.10
Bringagee Road			
0 cm	8.4	1.0	0.15
20 cm	7.5	0.6	<0.05

Table 3.3
Demographic details

Density of shoots m^{-2}

	Live shoots			Dead shoots	
	I	F	F/I	I	F
T. domingensis					
Wet C	20	31	1.55	33	74
Wet E	32	37	1.16	0	28
Dry C	34	20	0.59	6	24
Dry E	42	34	0.81	5	46
T. orientalis					
Wet C	25	23	0.92	18	56
Dry C	18	17	0.94	2	17
Dry E	14	13	0.93	1	21
Dry Col	9	8	0.89	0	15

KEY
I = Initial density, June 1980
F = Final density, June 1981

Table 3.4
Recruitment details

	Recruitment		Maximum recruitment		
	No.	RR	No.	Period	Rate
T. domingensis					
Wet C	133	6.65	21	9 Jan-21 Jan	1.75
Wet E	54	1.69	4	16 Jan-23 Jan	0.57
Dry C	34	1.0	6	9 Apr-16 Apr	0.86
Dry E	51	1.21	32	9 Apr-16 Apr	3.43
T. orientalis					
Wet C	45	1.80	22	23 Jan-10 Mar	0.48
Dry C	27	1.50	16	9 Mar-27 Mar	0.89
Dry E	23	1.64	12	9 Mar-22 Mar	0.92
Dry Col	15	1.67	6	9 Mar-22 Mar	0.46

KEY
Recruitment
No. = number recruited June 1980-June 1981
RR = Replacement ratio (Number recruited/Initial density)
Maximum recruitment
No. = Number recruited during period of highest recruitment
Period = Period of maximum recruitment
Rate = Maximum rate as shoots day^{-1}

Table 3.5
Population age structure

Midsummer populations 18-23 December 1980

		Number	p(pre)	p(W)	p(post)
T. domingensis					
Wet	C	58	0.1724	0.3448	0.4310
Wet	E	47	0.5957	0.2340	0.1702
Dry	C	21	0.8571	0.0952	0.0476
Dry	E	39	0.6667	0.1795	0.0256
T. orientalis					
Wet	C	29	0.9310	0.0345	0.0345
Dry	C	13	0.8462	0.1538	0.00
Dry	E	21	0.7143	0.2857	0.00
Dry	Col	13	0.6154	0.00	0.3846

KEY
p(pre) = proportion recruited before winter
p(W) = proportion recruited during winter, June-August
p(post) = proporion recruited after winter

Table 3.6
Synchronisation of anthesis

Peak is the period when most (as a percentage of all) flowering shoots are in anthesis
Duration is defined by census intervals which give the first and last records of anthesis

			-Peak-	-Duration-	
		%	period	First	Last
T. domingensis					
Wet	C	40	14 Nov-28 Nov	14 Nov-28 Nov	4 Dec-18 Dec
Wet	E	nc	4 Dec-18 Dec	4 Dec-18 Dec	18 Dec
Dry	C	43	23 Dec-7 Jan	3 Dec-9 Dec	23 Dec-7 Jan
Dry	E	50	18 Nov-3 Dec	12 Nov-3 Dec	23 Dec
T. orientalis					
Wet	C	nc	17 Nov-2 Dec	17 Nov-2 Dec	2 Dec-10 Dec
Dry	C	89	12 Nov-18 Nov	12 Nov-18 Nov	5 Dec
Dry	E	50	19 Nov	12 Nov-19 Nov	19 Nov-5 Dec
Dry	Col	88	12 Nov-18 Nov	12 Nov-18 Nov	18 Nov-3 Dec

KEY
nc = not calculated (sample too small)

Table 3.7
Reproduction demography and recruitment times of reproductive shoots

		p(R)	Number	p(pre)	p(W)	p(post)	Failures
T. domingensis							
Wet	C	0.3636	24	0.0833	0.6250	0.2917	4
Wet	E	0.0196	3	1.0	0.0	0.0	2
Dry	C	0.1250	12	0.8333	0.1667	0.0	8
Dry	E	0.3158	15	1.0	0.0	0.0	3
T.orientalis							
Wet	C	0.0667	3	0.6667	0.3333	0.00	1
Dry	C	0.6429	9	0.5556	0.4444	0.00	0
Dry	E	0.7619	16	0.7500	0.2500	0.00	0
Dry	Col	0.8889	8	0.8750	0.1250	0.00	0

KEY
p(R) = reproductive proportion of live population
p(pre) = shoots recruited before June
p(W) = shoots recruited June-August inclusive
p(post) = shoots recruited September onwards
Failure = flowering shoots which did not set seed

Table 3.8
Leaf demography

Table shows initial live and dead leaves per quadrat, the number recruited/dying during the year, and leaf mortality in December 1980 for two cohorts, pre-Winter and Winter. Mortality is number of leaves dying per 100 shoots day^{-1}.

		---Recruits---			---Deaths---			--Mortality--	
		I	R	V*	I	M	V*	preW	W
T. domingensis									
Wet	C	69	1059	1.0123	290	1115	0.7480	2.31	6.07
Wet	E	257	457	0.6210	63	779	0.3803	4.65	5.38
Dry	C	250	179	0.9532	122	406	0.9532	10.08	14.29
Dry	E	320	391	0.6801	95	744	1.0902	9.14	10.20
T. orientalis									
Wet	C	607	435	0.4631	248	619	0.4631	4.58	2.63
Dry	C	92	264	0.5808	92	334	1.0901	8.66	12.12
Dry	E	176	253	1.0780	23	409	1.0780	10.96	11.30
Dry	Col	124	139	0.9718	17	263	0.5342	10.88	-

KEY
I = initial number of live/dead leaves in June 1980
R = number recruited June 1980 to June 1981
M = number of leaf deaths June 1980 to June 1981
V* = seasonality (see text)

Table 3.9
Leaf density per shoot

Table shows maximum and minimum mean number of live leaves shoot^{-1} with month of occurrence for shoots of two age groups, preWinter shoots and Winter cohorts

	--Minimum--				--Maximum--			
	PreWinter		Winter		preWinter		Winter	
	No	month	No	Month	No	month	No	month
T. domingensis								
Wet C	1.83	Aug	2.00	July	5.29	Oct	8.04	Nov
Wet E	3.57	Aug	2.20	July	5.62	Nov	7.00	Dec
Dry C	3.25	July	2.50	July	7.26	Dec	5.40	Dec
Dry E	5.18	Aug	3.57	Aug	7.52	Oct	7.43	Dec
T. orientalis								
Wet C	2.44	June	3.45	Sept	6.63	Nov	7.60	Nov
Dry C	4.38	July	4.33	July	10.43	Nov	10.14	Nov
Dry E	4.36	Aug	3.00	Aug	11.77	Nov	10.25	Nov
Dry Col	4.13	July	-	-	11.43	Nov	-	-

Table 3.10
Grazing details

	Incidence		Total defoliation No	p(T)	>600 mm
T. domingensis					
Wet C	16/29	0.5317	37	0.2782	23
Wet E	10/28	0.3571	5	0.0926	1
Dry C	1/39	0.0256	2	0.0588	0
Dry E	4/31	0.1290	0	0.00	0
T. orientalis					
Wet C	10/36	0.2778	1	0.00	0
Dry C	0/37	0.00	2	0.0741	0
Dry E	4/31	0.1290	1	0.0435	0
Dry Col	3/33	0.0909	0	0.00	0

KEY
Incidence = (Visits when grazing recorded)/(Total visits)
No = number of shoots lost by total defoliation
p(T) = number of shoots lost as proportion of annual recruits
>600 mm = number of shoots taller than 600 mm

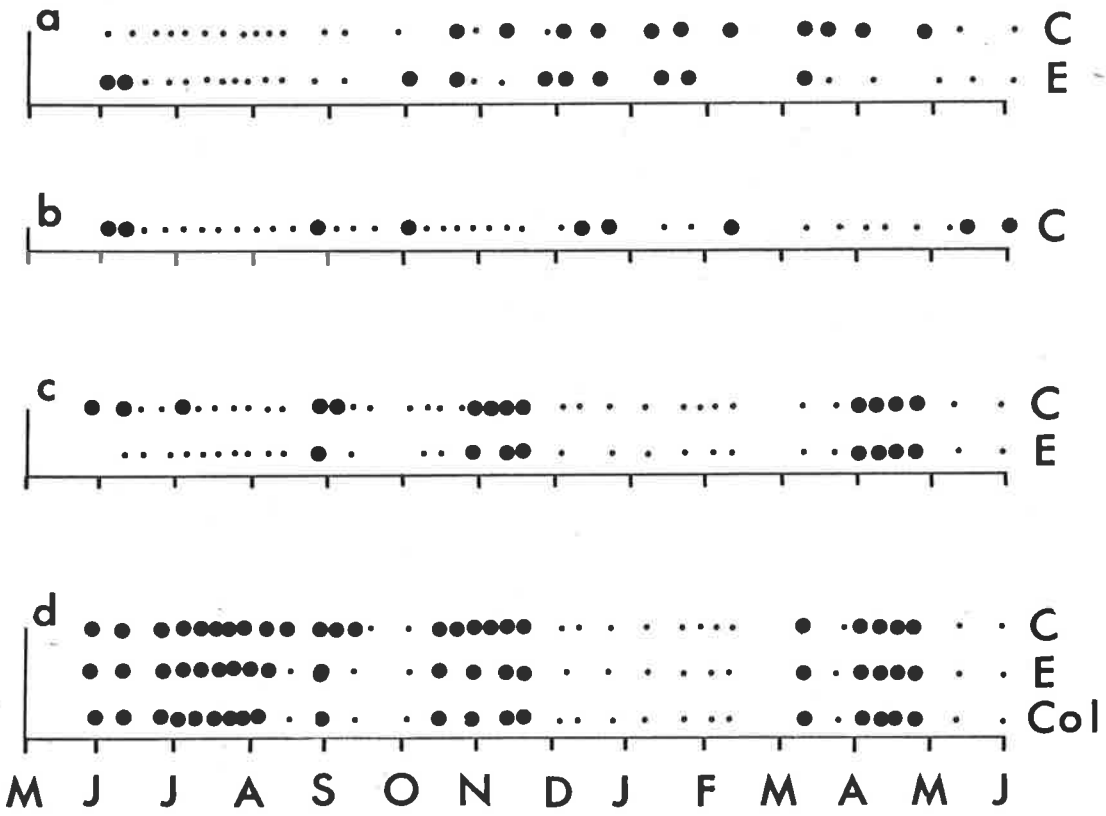

Figure 3.1
Water regime at four sites

Water regime of the four sites defined by presence-absence of free water from end of May 1980 to June 1981, showing Centre and Edge quadrats (C and E) at each site. Sites are in Wet-Dry sequence.

(a) T. domingensis. Wet. Lake Wyangan
(b) T. orientalis. Wet. Brogden's Road
(c) T. domingensis. Dry. Bringagee Road
(d) T. orientalis. Dry. Bringagee Road

Key
● Free water present
· No free water

Figure 3.2
Shoot density

Changes in density of live shoots of T. domingensis and T. orientalis in Centre (C) and Edge (E) quadrats from May 1980 to June 1981. Results are presented in site sequence.

(a) T. domingensis. Wet. Lake Wyangan
(b) T. domingensis. Dry. Bringagee Road
(c) T. orientalis. Wet. Brogden's Road
(d) T. orientalis. Dry. Bringagee Road
(e) T. orientalis. Colonising. Dry. Bringagee Road

Key
Symbols given here are in consistent use throughout this chapter unless otherwise stated.
- • T. domingensis
- ▪ T. orientalis
- ▲ Colonising
- ▪-▪ Wet
- •-• Dry

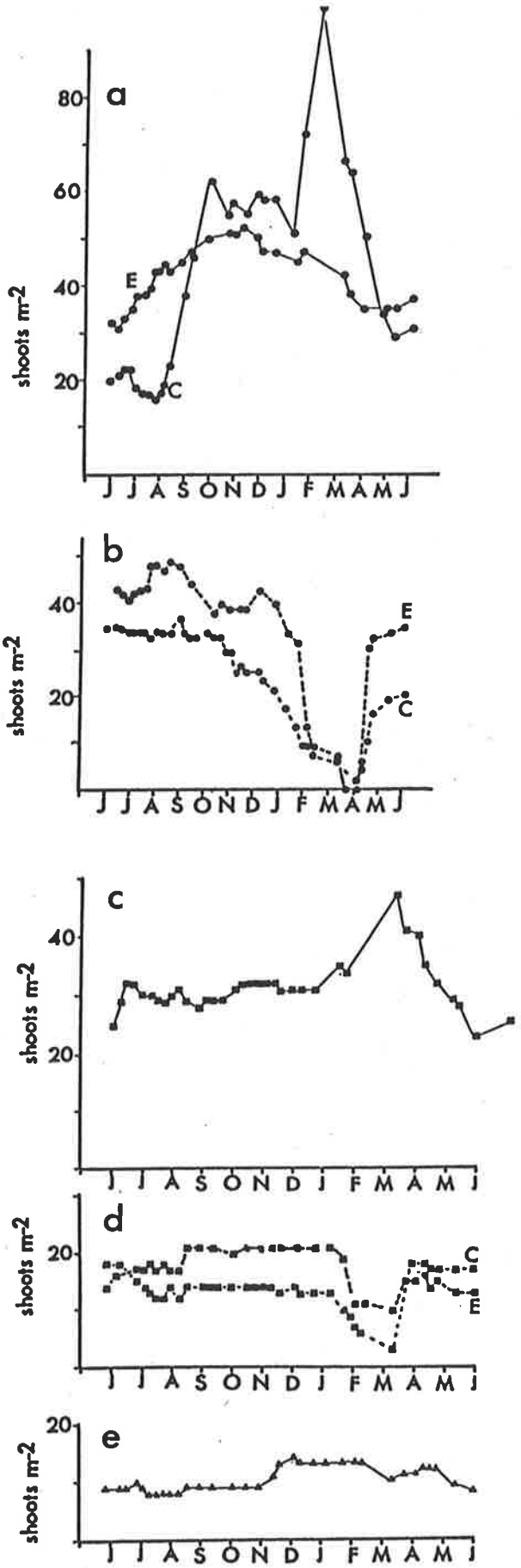

Figure 3.2
Shoot density

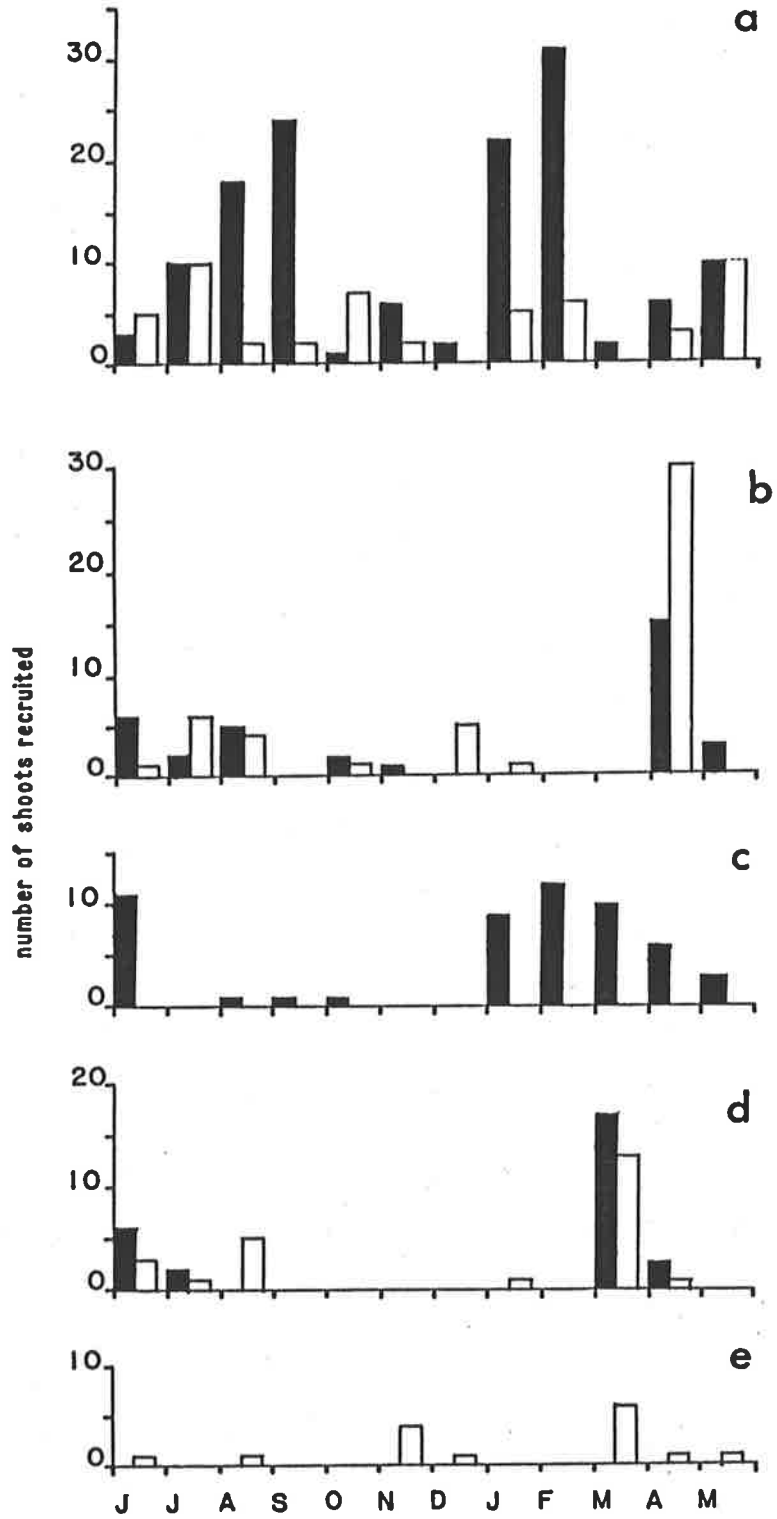

Figure 3.3
Shoot recruitment

Number of shoots recruited per quadrat in each month from June 1980 to May 1981. Centre quadrats shown by solid bars, Edge quadrats by hollow bars. Results are given in site sequence.

(a) T. domingensis. Wet. Lake Wyangan
(b) T. domingensis. Dry. Bringagee Road
(c) T. orientalis. Wet. Brogden's Road
(d) T. orientalis. Dry. Bringagee Road
(e) T. orientalis. Colonising. Dry. Bringagee Road

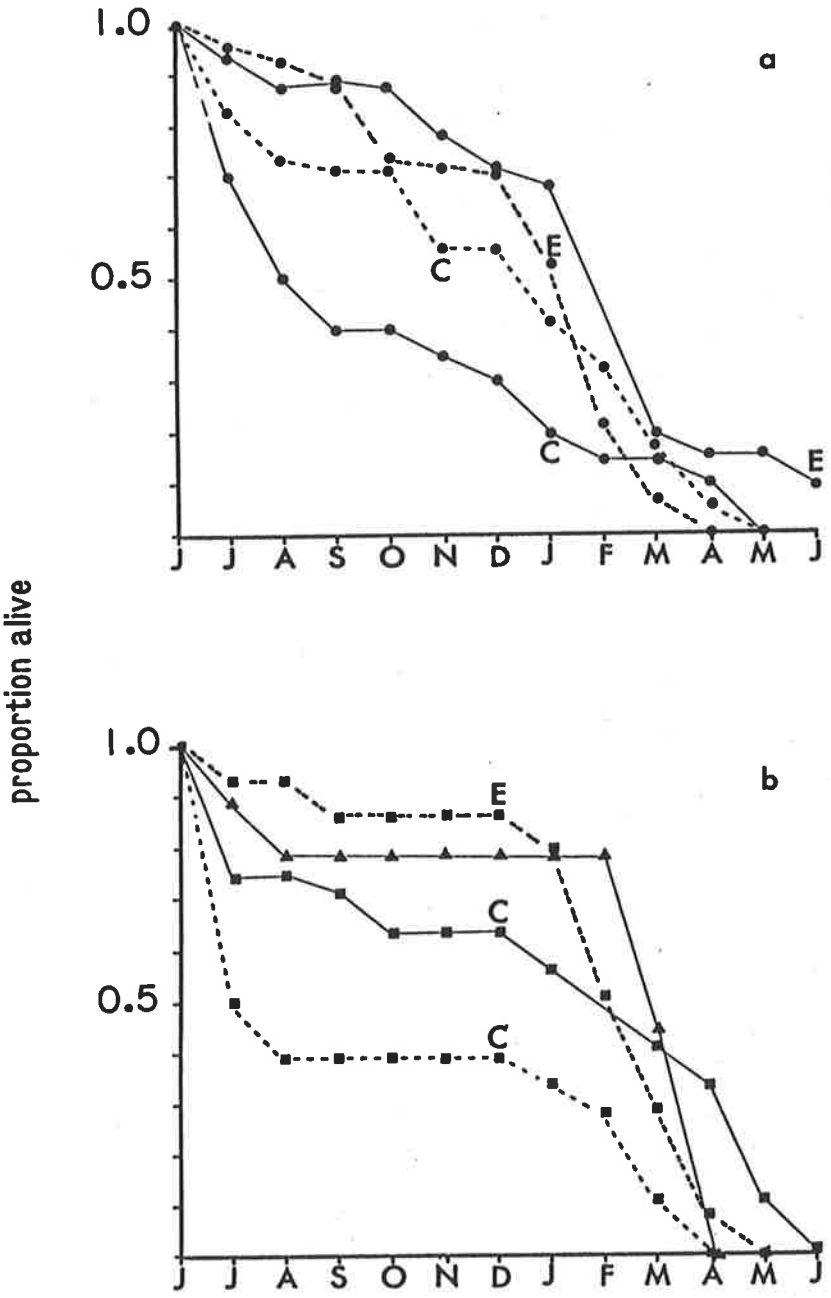

Figure 3.4
Shoot survival; depletion curves

Depletion curves for shoots present at first census showing the proportion alive at the beginning of each month from June 1980 to June 1981. Results presented in species sequence, symbols as for Figure 3.2.

(a) T. domingensis: Lake Wyangan and Bringagee Road
(b) T. orientalis: Brogden's Road and Bringagee Road

Figure 3.5
Shoot survival; survival curves

Survival curves for monthly cohorts showing proportion surviving at the beginning of each month for each quadrat, from June 1980 to June 1981. A cohort is all shoots recruited within a calendar month, minimum size five. Month of recruitment shown for cohorts alive at the end of study. Results given in site sequence, Centre quadrats on the left (a, c, e, f), Edge and Colonising quadrats on the right (b, d, g, and h).

(a and b) T. domingensis. Wet. Lake Wyangan
(c and d) T. domingensis. Dry. Bringagee Road
(e) T. orientalis. Wet. Brogden's Road
(f and g) T. orientalis. Dry. Bringagee Road
(h) T. orientalis. Colonising. Dry. Bringagee Road

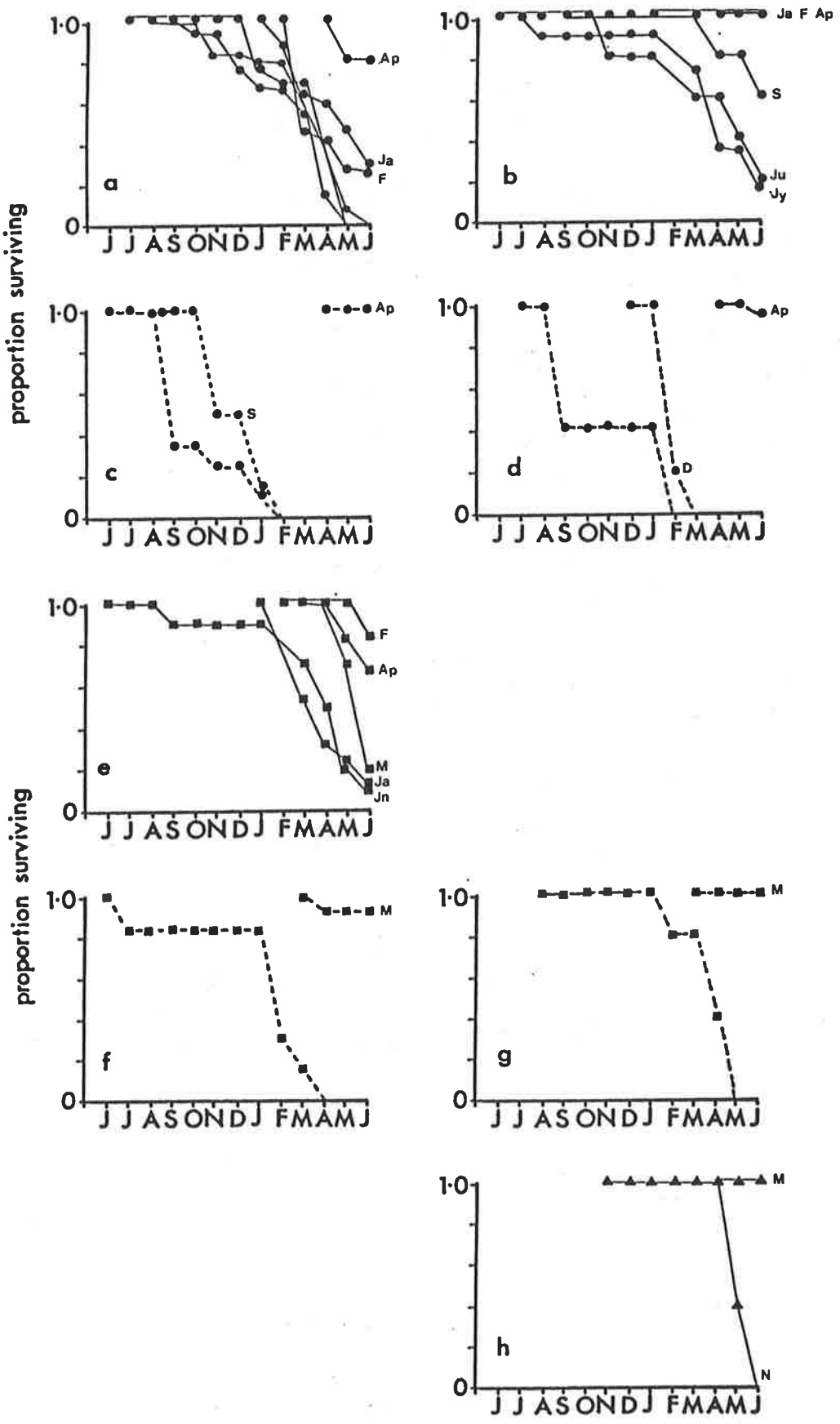

Figure 3.5
Shoot survival; survival curves

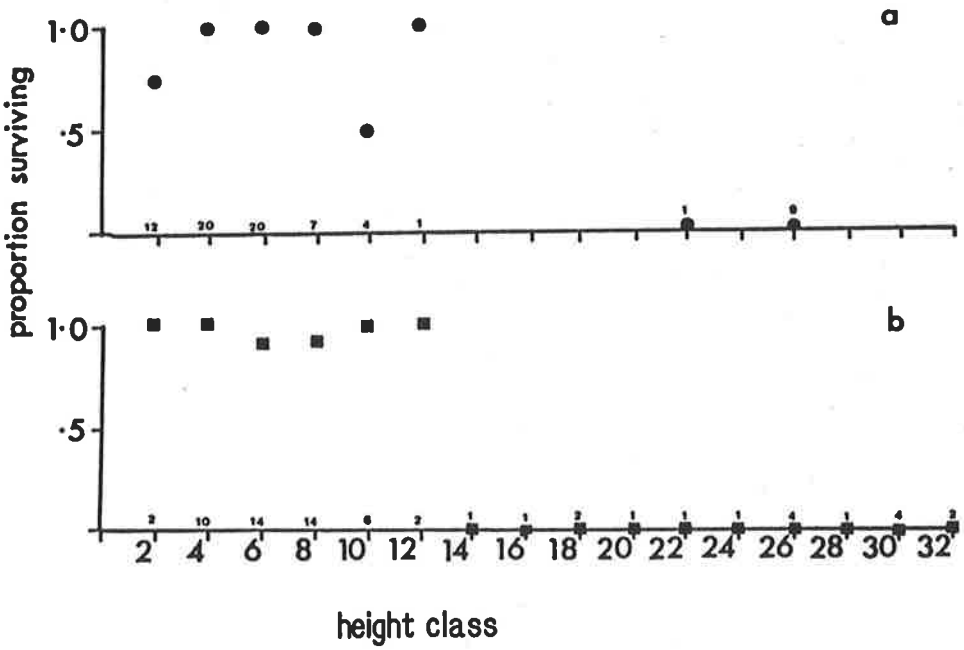

Figure 3.6
Overwinter survival

Overwinter survival of pre-Winter shoots of T. domingensis and T. orientalis by height class, as a proportion. Initial sample size for each height class is also shown. Height classes in increments of 200 mm, thus 2 = 0-200 mm, 4 = 201-400 mm etc. Results in species order.

(a) T. domingensis, Bringagee Road only

(b) T. orientalis, Bringagee Road and Brogden's Road combined

Figure 3.7
Shoot height

Mean cohort height in metres at the beginning of each month from June 1980 to June 1981 for all cohorts in each quadrat. A cohort is all shoots recruited within a calendar month, minimum size five. The pre-Winter cohort is distinguished by a dashed line. Results are given in site sequence with Centre quadrats on the left (a, c, e, f), and Edge and Colonising quadrats on the right (b, d, g and h).

(a and b) T. domingensis. Wet. Lake Wyangan
(c and d) T. domingensis. Dry. Bringagee Road
(e) T. orientalis. Wet. Brogden's Road
(f and g) T. orientalis. Dry. Bringagee Road
(h) T. orientalis. Colonising. Dry. Bringagee Road

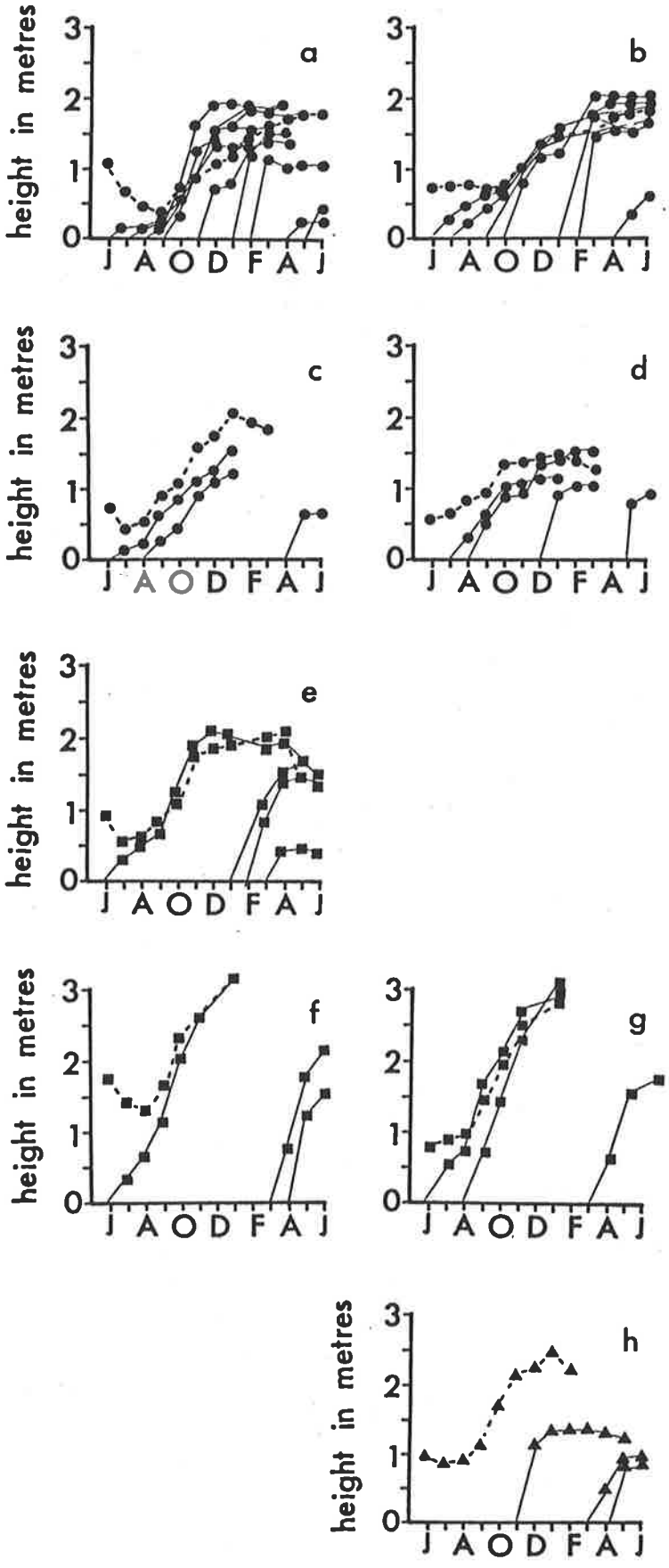

Figure 3.7
Shoot height

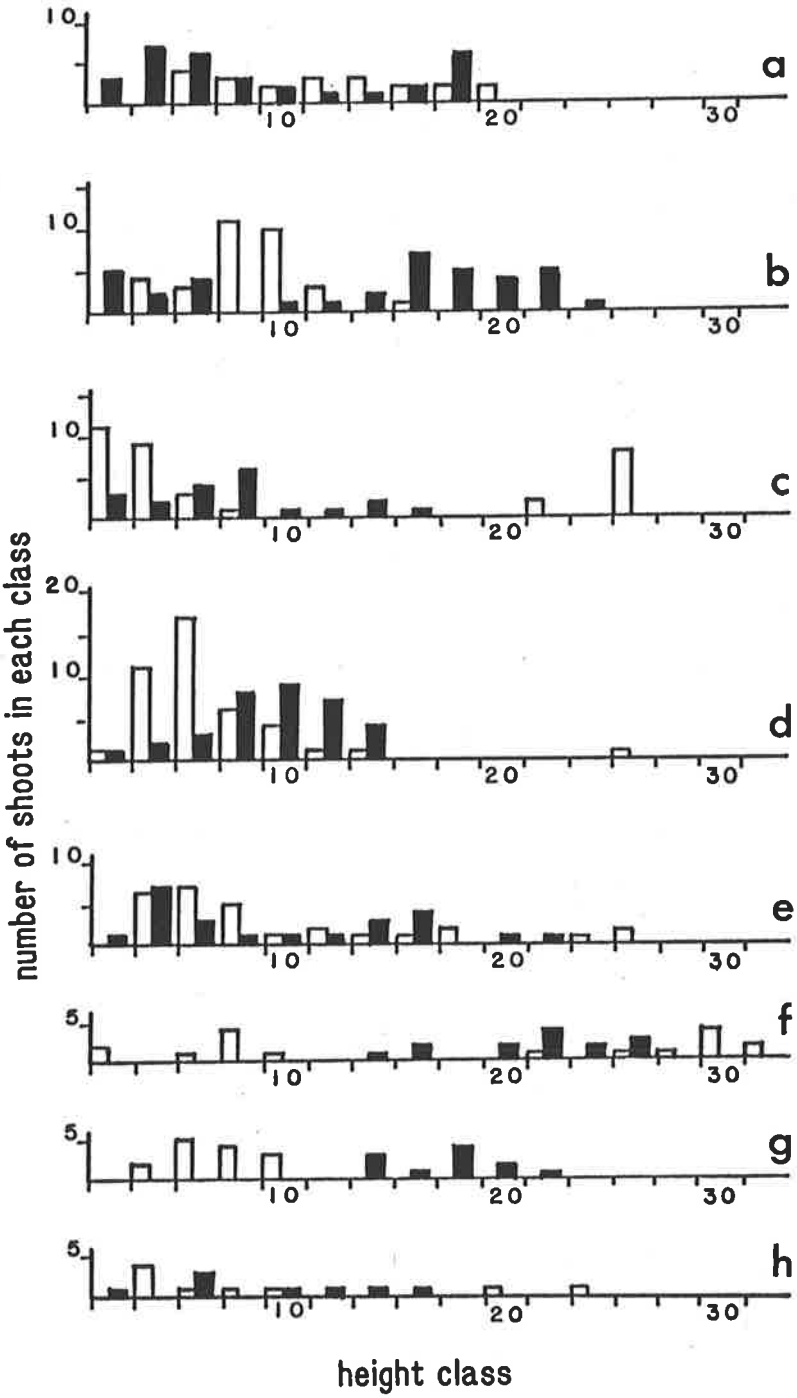

Figure 3.8
Shoots: population structure

Structure of shoot population in each quadrat by height class, June 1980 (hollow bars) and June 1981 (solid bars). Height class increments are 200 mm, thus 10 = 1001-1200 mm etc. Results in site sequence.

(a and b) T. domingensis. Wet. Lake Wyangan
(c and d) T. domingensis. Dry. Bringagee Road
(e) T. orientalis. Wet. Brogden's Road
(f and g) T. orientalis. Dry. Bringagee Road
(h) T. orientalis. Colonising. Dry. Bringagee Road

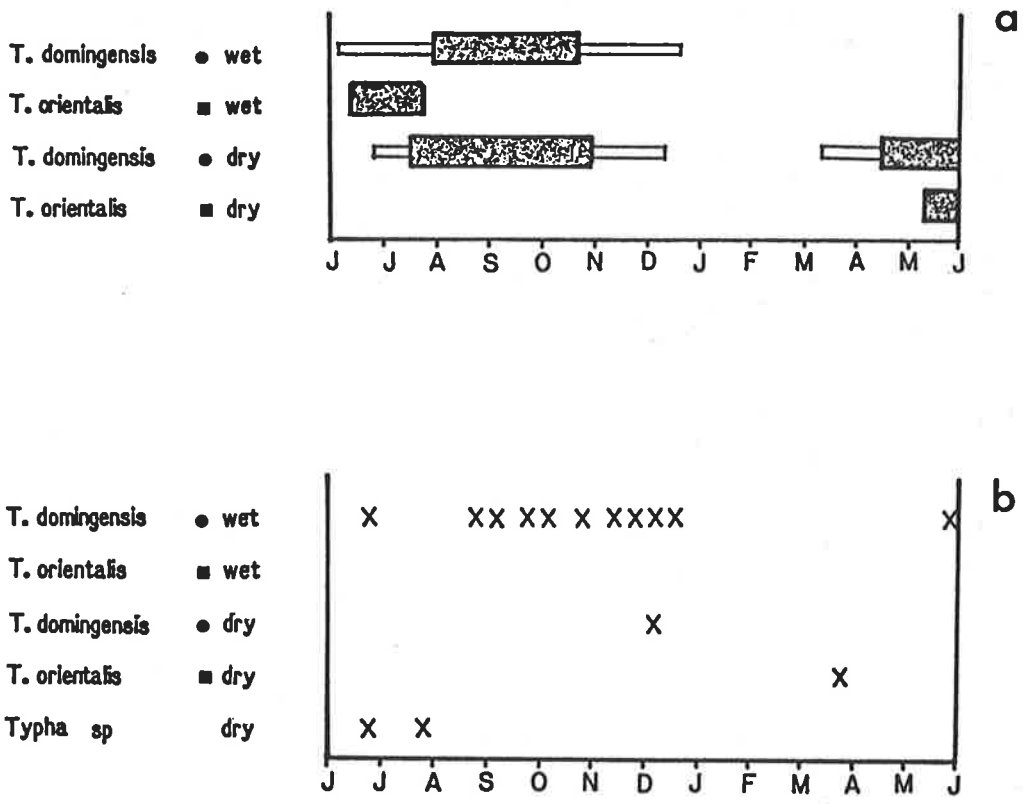

Figure 3.9
Reproduction phenology

(a) Seed dispersal
Timing of seed dispersal at four sites. Data from Centre, Edge and Colonising quadrats combined, where appropriate, to give dispersal characteristics for each site. Duration of dispersal period from time of first record to completion shown by bar length. Peak dispersal when 75-100% flowering shoots were dispersing shown by wide, shaded section of bar. Sites in water regime sequence, Wet then Dry.

(b) Seedling occurrence
Presence of live seedlings at each site based on data from Centre, Edge and Colonising quadrats combined where possible. Sites in water regime sequence, Wet then Dry. Typha spp. refers to seedlings found at Bringagee Road but not in quadrats.

Figure 3.10
Shoots: October population structure

Structure of quadrat populations in mid-October 1980 before the pre-flowering habit change, by height class. Shoots which later flowered indicated by solid bars, shoots remaining vegetative by hollow bars. Height classes in increments of 100 mm, thus 5 = 401-500 mm. Results in site sequence.

(a and b) T. domingensis. Centre and Edge. Wet. Lake Wyangan
(c and d) T. domingensis. Centre and Edge. Dry. Bringagee Road
(e) T. orientalis. Centre. Wet. Brogden's Road
(f and g) T. orientalis. Centre and Edge. Dry. Bringagee Road
(h) T. orientalis. Colonising. Dry. Bringagee Road

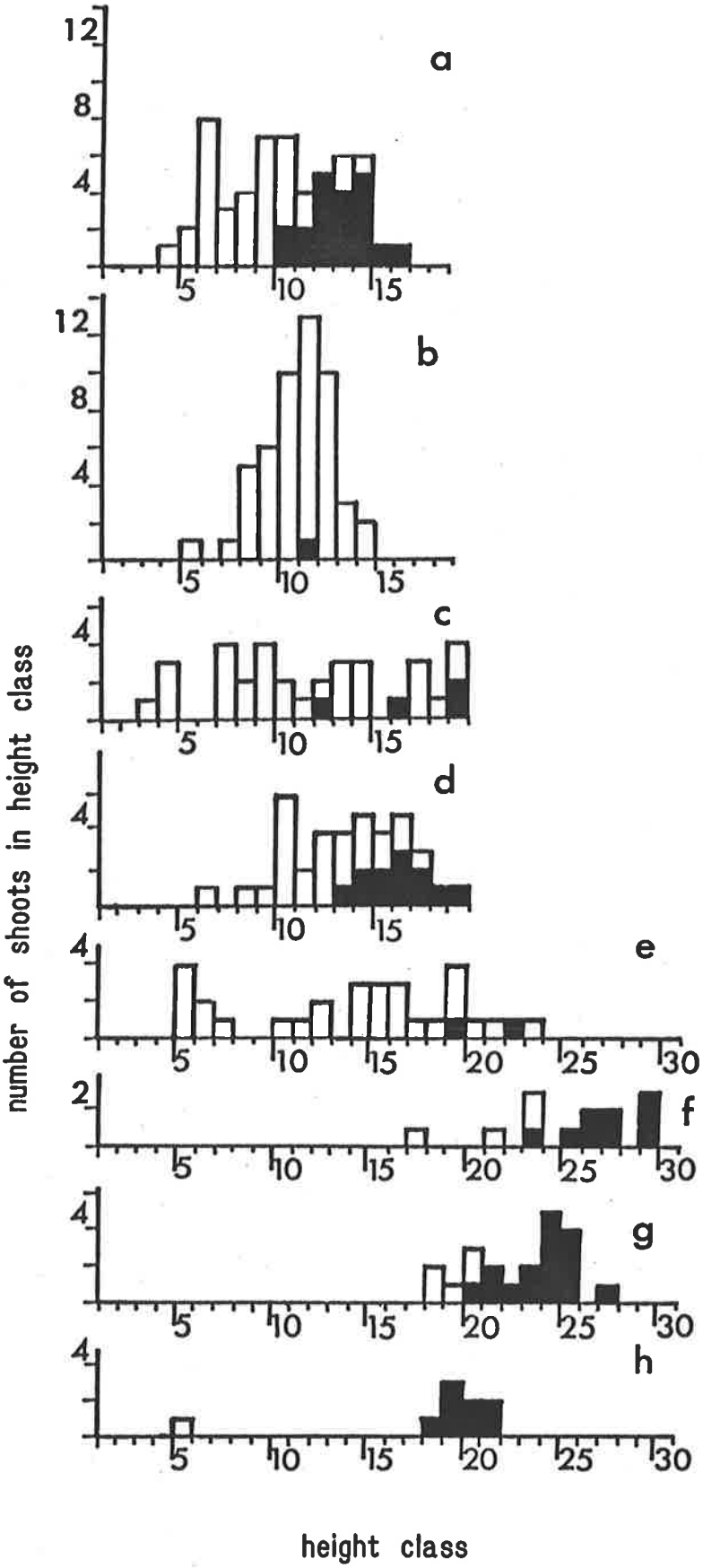

Figure 3.10
Shoots: October population structure

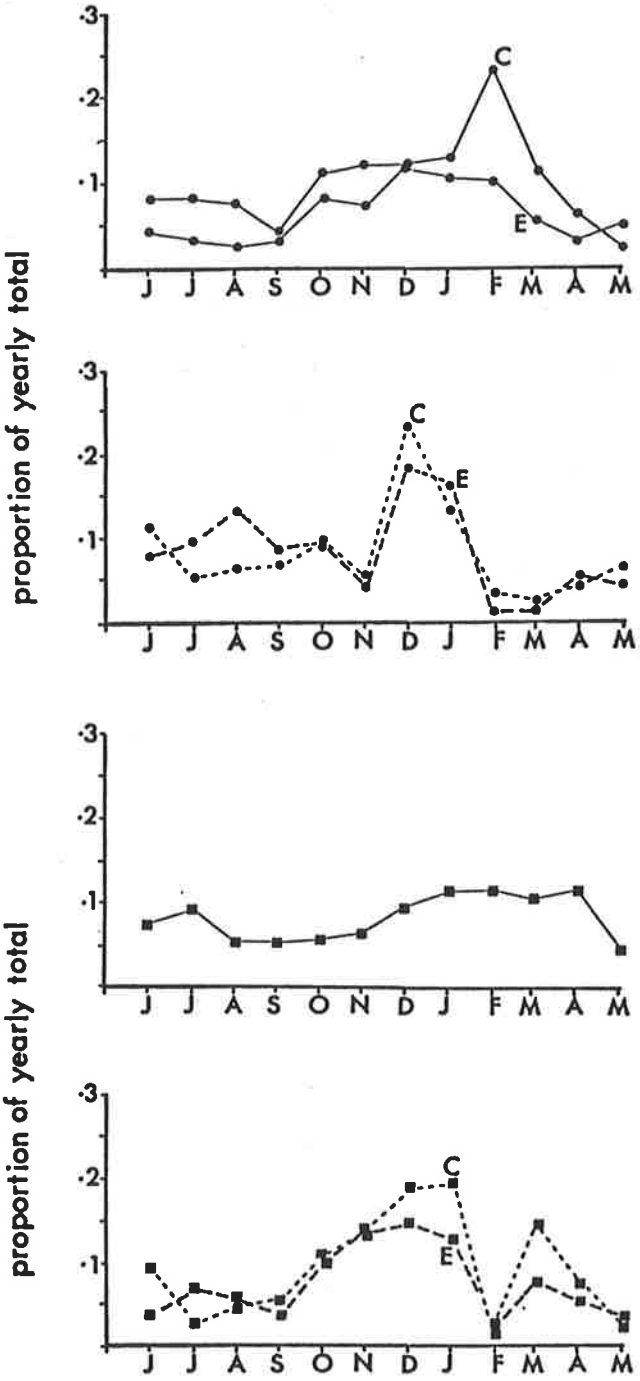

Figure 3.11
Leaf recruitment: phenology

Temporal variation in leaf recruitment to pre-Winter shoots from June 1980 to January 1981, shown as a monthly proportion of the yearly total p(yt) for each quadrat. Data for T. orientalis Colonising quadrat were very similar to T. orientalis Centre and Edge quadrats from Bringagee Road, so are not shown. Results in site sequence.

(a) T. domingensis. Wet. Lake Wyangan
(b) T. domingensis. Dry. Bringagee Road
(c) T. orientalis. Wet. Brogden's Road
(d) T. orientalis. Dry. Bringagee Road

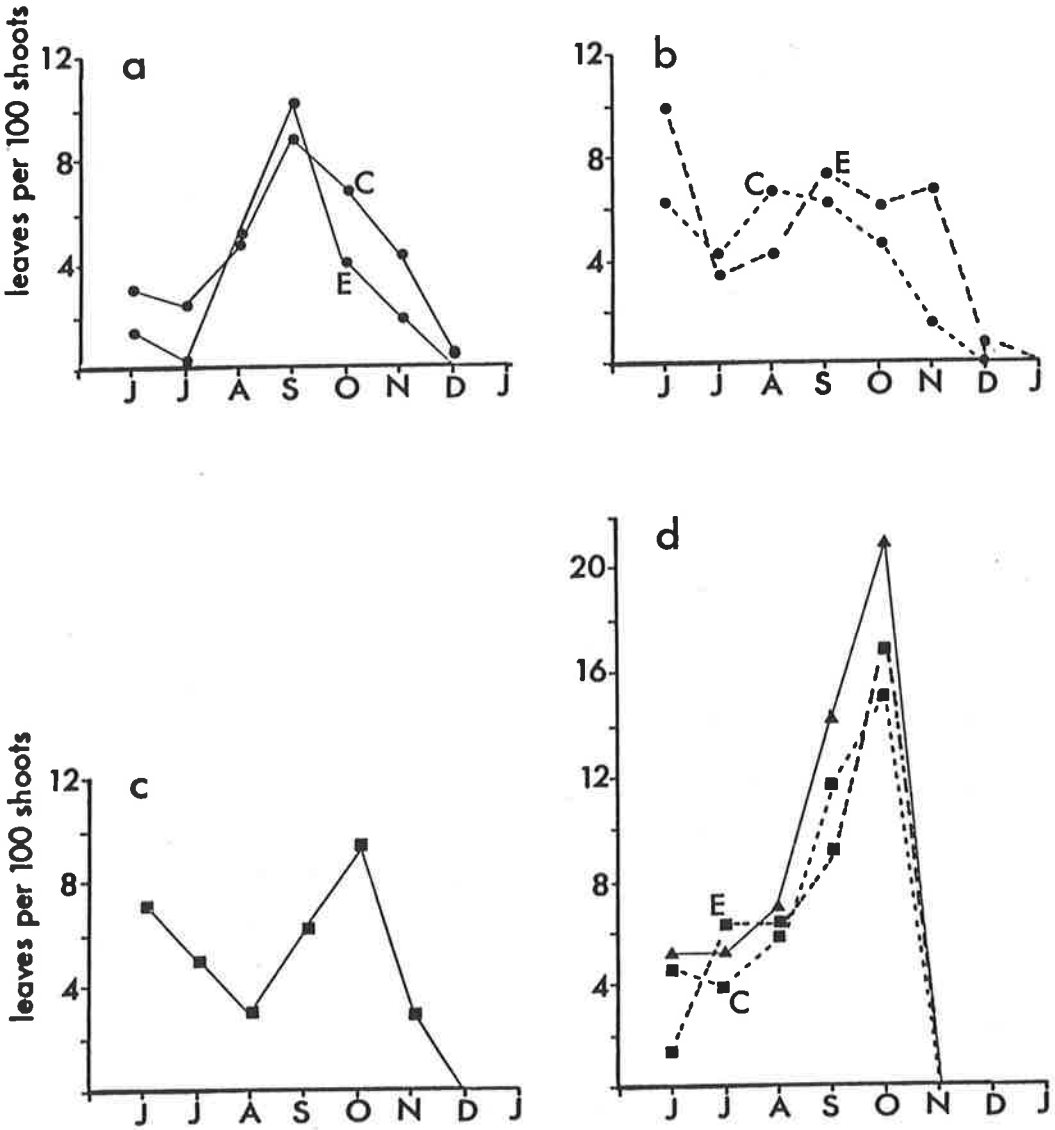

Figure 3.12
Leaf recruitment rate

Monthly variations in leaf recruitment rate to pre-Winter shoots from June 1980 to January 1981 for each quadrat. Recruitment rate is number of leaves recruited to 100 live shoots per day. Results are in site sequence and include Colonising quadrat (▲).

(a) T. domingensis. Centre and Edge. Wet. Lake Wyangan
(b) T. domingensis. Centre and Edge. Dry. Bringagee Road
(c) T. orientalis. Centre. Wet. Brogden's Road
(d) T. orientalis. Centre, Edge and Colonising. Dry. Bringagee Road

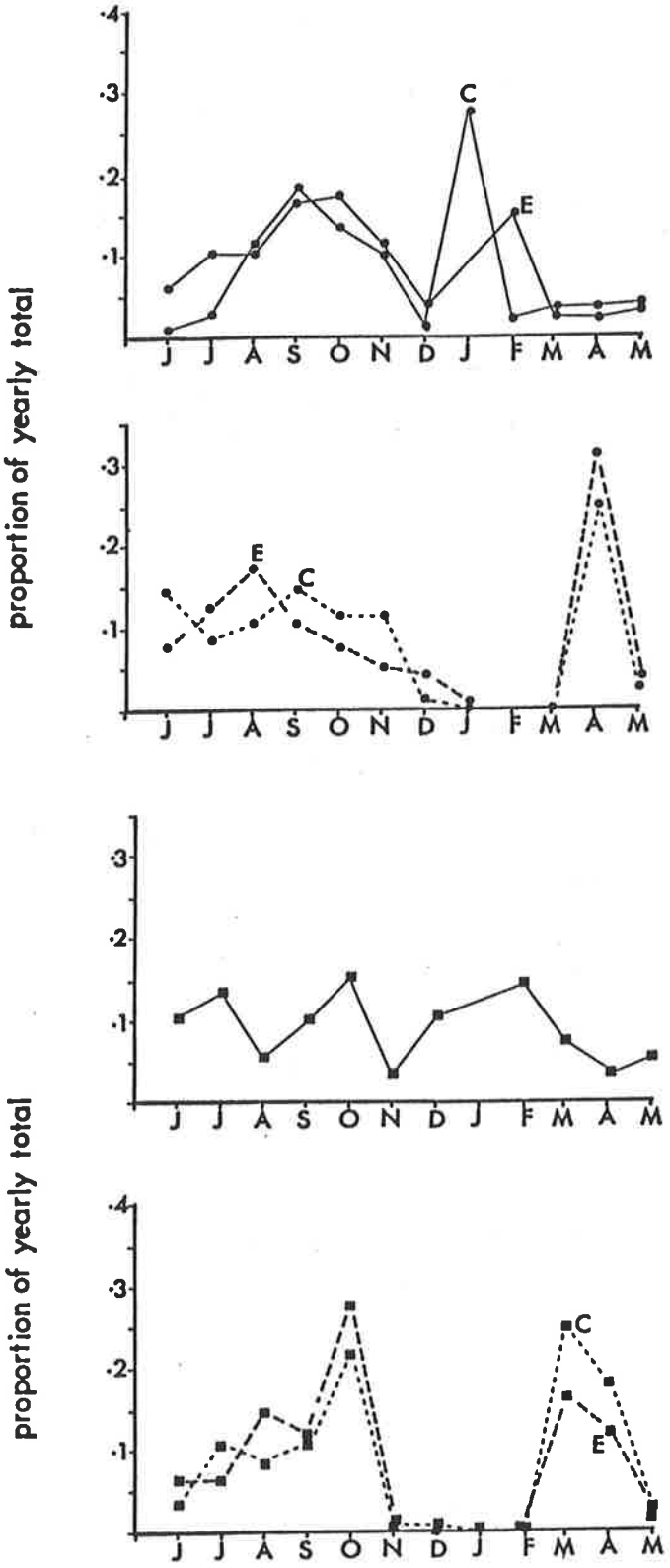

Figure 3.13
Leaf mortality: phenology

Temporal variations in leaf mortality shown by expressing the number of leaves dying each month from June 1980 to May 1981 as a proportion of the total for each quadrat. Data for T. orientalis Colonising quadrat were very similar to T. orientalis Centre and Edge quadrats at Bringagee Road, so are not shown.

(a) T. domingensis. Centre and Edge. Wet. Lake Wyangan
(b) T. domingensis. Centre and Edge. Dry. Bringagee Road
(c) T. orientalis. Centre. Wet. Brogden's Road
(d) T. orientalis. Centre and Edge. Dry. Bringagee Road

Chapter Four

GROWTH ON A NATURAL WATER GRADIENT

INTRODUCTION

4.1 Background and aims to gradient study

The factor most likely to limit upward distribution of emergents was identified (1.3) as water. Water is an essential resource and insufficient water causes reduced growth or even mortality. The previous study found that shoot growth of T. domingensis was restricted when there was no free water in spring, and that leaf mortality increased after sites dried up in summer (3.11). These show high quantities of substrate water are necessary for shoot growth and survival in Typha spp.

The relationship between growth and water availability has been described for Typha (Grace and Wetzel 1981a, 1982a) and other freshwater emergents (Thomas and Stewart 1969, Yamasaki and Tange 1981) using distance, as depth to water table or height above water level, to approximate water availability. Typically there is a position of maximum biomass along a water gradient, with biomass decreasing away from this optimum towards deeper water and towards drier conditions. For Typha spp. in North America this optimum is 50 cm below water level (Grace and Wetzel 1981a) and for Phragmites australis in Japan it is 0-15 cm above (Yamasaki and Tange 1981). Distance is a qualitative measure of water which is useful for comparing species performance within a site (e.g. Yamasaki and Tange 1981) but not between sites or plants. For this, water availability must be measured quantitatively so that the distribution of Typha can be put into a broader perspective. Thus the first aim of the study was to correlate growth of Typha with water availability. The second was to define resource levels that are growth limiting for Typha. In the terminology of Tilman (1982), these are the resource levels below

R*, the resource equilibrium level where a population is stable and growth equals mortality.

The approach chosen was a natural water gradient and the perfect site was envisaged as a Typha covered slope rising imperceptibly out of a permanent waterbody thus giving a wide water gradient. A field study was preferred as this would give continuity with previous work. For the same reason, growth was measured in terms of shoot and leaf demography.

The choice of a natural gradient had important implications. First, the study was correlative rather than manipulative therefore it was necessary to establish that the primary resource gradient was water and not nitrogen or phosphorus which are the other essential resources most likely to limit plant growth. Second, natural water gradients are complex rather than simple. The transition from terrestrial to water-logged soils is accompanied by physical changes which in turn affect chemical characteristics. Soil physical characteristics do not change smoothly down a water gradient as sometimes assumed (e.g. Byer 1969) but alter abruptly at the land-water interface (Yamasaki and Tange 1981). This is evident in plant response (e.g. Grace 1985). Measuring this complex of environmental change is not easy so a pragmatic approach was taken which treats water availability as an integrative factor (e.g. Keddy 1984). Third, defining growth in terms of shoot and leaf demography assumes ramets are physiologically discrete. However physiological independence cannot be assumed. It varies according to species (Ashmun et al. 1982), resource supply (Hartnett and Bazzaz 1983) and generation. In Carex arenaria there is a decreasing water potential from young to old shoots. Water movement occurs principally in one direction from young to old with virtually no translocation from old to young (Tietema and van der Aa 1981). Therefore it was necessary to establish whether translocation was continuous between Typha ramets.

4.2 Water availability

The relationship between plant growth and soil water is determined by soil water availability, water collecting ability of the plant and transpiration which is driven by environmental conditions. The study design using a natural gradient assumed water collecting ability and environmental conditions were constant. Typha's root system is discussed below (4.3).

Slavik (1974) recognised two types of definitions and concepts of soil water availability, "static", an instantaneous description of the water potential gradient from soil to plant and "dynamic", a more complex concept describing rate of water movement to roots, the quantity of water present in the rhizosphere, uptake rate and the total uptake area. Opinion is divided as to whether to account for the rate of water movement or not. There is an unacknowledged pragmatic element in these opinions as it is difficult to measure dynamic components accurately (see below).Some definitions are circular with water availability defined in terms of plant response, for example Permanent Wilting Point as the lower limit of soil water store and a proposal to re-define the lower limit of the soil water store as the point "when crops reach their maximum vegetative size without stress and then grow on stored soil water until plants are visibly severely distressed" (Ritchie 1981). Circularity makes species comparisons difficult as it becomes impossible to separate soil from plant factors.

The most commonly used concept is a static one, the unused fraction of the soil water store (e.g. Benecke and van der Ploeg 1981, Greacen and Gardner 1982) where the soil water store is the quantity of water present in a given soil between an upper limit, Field Capacity, and a lower limit, Permanent Wilting Point. This definition is accepted generally but specific applications are not uniform. Permanent Wilting Point is usually

set at -1.5 MPa. Field Capacity which is the water content of a thoroughly wetted soil after draining for 2 days (Marshall and Holmes 1979) may be set at -10 kPa (Benecke and van der Ploeg 1981) or -100 kPa (Greacen and Gardner 1982). This is not a problem when working with terrestrial species as it represents only a small fraction of the total but it could be important for emergents.

The most appropriate measure of soil water availability is one that is dynamic, i.e. includes rate of water movement but excludes plant absorption factors. Flux density, which is the product of water potential gradient per unit distance and soil hydraulic conductivity, is preferred by workers who believe availability is limited by movement (Passioura 1982). Although this is the most appropriate measure, it is also the most difficult to estimate. Measurement of hydraulic conductivity requires considerable care when handling samples and great caution in the laboratory (Marshall and Holmes 1979) otherwise errors involving several orders of magnitude result (Ritchie 1981, Passioura 1982). Whilst recognising that water movement is important, a static definition was used, the fraction of soil water store still available. This was a pragmatic choice, determined by the effort, difficulty and lack of equipment for measuring hydraulic conductivity.

For this it was necessary to measure soil water content and soil matric potential in the field. In sub-saturated non-saline soils, matric potential is equivalent to water potential. A study on a natural water gradient could expect a wide range of matric potentials. There is a range of commonly used techniques, each appropriate to specific conditions. Thus gypsum blocks are effective in dry soil over the range -0.05 to -1.5 MPa whilst tensiometers are limited to wet soils in the range 0 to -0.08 MPa (Kramer 1983). Vapour equilibration techniques using thermocouple psychrometers or hygrometers measure total water potential over a wide

range but temperature sensitivity particularly in wetter soils limits their field use to dry soils with negligible salt content (Marshall and Holmes 1979). The filter paper method (Hamblin 1981) has an operating range from 0 to approximately -10 MPa, is easy to use and does not require access to specialised equipment. The operating principle is simple. The weight of water taken up by a standard filter paper in equilibrium contact with soil, expressed as a fraction of filter paper weight, is a function of soil matric potential.

4.3 Roots of Typha

The most important characteristics of a root system are function and architecture which includes rooting depth. Characteristics may be modified by plant-soil interactions for as soil dries out, there is an increase in mechanical impedance and a possible loss of contact with the soil water pathway. For convenience this study assumed that function and architecture were constant across the gradient.

Roots of Typha arise adventitiously from the shoot base and only rarely from along the rhizome (pers. obs., Weaver and Himmel 1930) thus the upper limit of the rooting zone is set by the position of the rhizome crown. This has ecological significance. In India the broad-leafed species T. elephantina has rhizomes deep within the substrate at 0.5-1.5 m and roots even deeper whilst the narrow-leafed species T. angustata has shallower rhizomes at 0-0.25 m and roots only down to 0.7 m. It is the broad-leafed species which grows "luxuriantly" in drier areas (Sharma and Gopal 1977). In most Typha species, the roots are fairly shallow and within 0.5 m of the surface (Table 4.1). Shallowness may be a consequence of an annual shoot life cycle with the root system being replaced each season. The rooting depth of annual crops such as corn and sorghum is 2 m (Kramer 1983).

Like most emergents Typha has two types of roots, soil roots and water

roots (Weaver and Himmel 1930). Water roots are formed only when the substrate is under water or in very moist conditions (Weaver and Himmel 1930) and are thought to be a response to anaerobiosis (Dean 1933) as they are absent from aerated cultures. Ramets in conditions dry enough to significantly reduce growth have no water roots (Weaver and Himmel 1930). In the field, water roots are evident in spring (pers. obs.) which suggests a feeding role. Soil roots spread out and down in a hemispherical shape (Weaver and Himmel 1930). Root growth of Typha, whether measured as length, diameter or biomass, is thought to depend on substrate type (Dean 1933, Merezhko et al. 1979) but this may simply be a response to nutrient levels or mechanical impedance. Nitrogen-fixing activity has been reported in the rhizosphere of T. latifolia (Biesboer 1984).

METHODS

4.4 Methods

The study had three parts, a transect study and a zone study both done in the field, and a dye study. The transect was only a preliminary survey of the site to sample spatial distribution for suitability but the data are included because they contribute to study aims. The zone study used areas of comparable height as treatments to sample for temporal changes in plant growth and soil water. The dye study was a brief laboratory trial to determine whether there was inter-ramet continuity in the transpiration stream.

Site description

The perfect site (4.1) proved hard to find in the Adelaide area where Typha occurs mainly in drainage channels or farm dams, sites which are

grazed or else have steep slopes with abrupt gradients. The chosen site, henceforward referred to as the Strathmont site, was near Strathmont Centre in a paddock cropped by South Australian Department of Agriculture. A flat, not incised, natural drainage line in the paddock was overgrown with T. domingensis, forming a stand approximately 400 m long and 3-20 m wide. Water flow in summer was supplemented by drainage from the grounds and buildings of Hillcrest Hospital (Figure 4.1).

Field work

For the transect study, one 10 m transect was laid out on 15 November 1982 from paddock to creek at the widest part of the stand. At 1 m intervals, surface soil samples were collected by coring and the height of the four closest shoots measured. Soils were analysed for water content, matric potential, soil water conductivity and pH.

For the zone study, four zones with shoots of similar height were recognised (subjectively) and marked out with fluorescent surveyors' tape. Zones were numbered consecutively with increasing height. There was an area with no Typha shoots, Zone 0, as close to Zone 1 as possible. Zones were irregular strips parallel to the creek and up to 5 m wide and 10 m long. Zone 4 was in the creek, Zones 2 and 3 were on eastern side and Zones 0 and 1 on the western side straddled the transect (Figure 4.1). Cattle broke through the protective electric fence erected voluntarily by the Department of Agriculture and grazed shoots between 21 March and 7 April. Shortly afterwards, part of the site was excavated by backhoe to 30 cm by Public Buildings Department for drain maintenance.

Sampling was done at fortnightly intervals from 6 January to 21 March for plants and 18 January to 7 April for soils. Rain disrupted sampling in early March. The following measurements were made on Typha shoots. Shoot height in mm was length to the tip of the tallest green leaf, and green leaf length was length to the green tip on the same leaf. The

number and identity of live and dead green leaves on each shoot was recorded. Sample size was 50 shoots in each zone except Zone 4 where the number was reduced to 35 because high winds in January caused lodging. Shoots in this zone were too tall and dense to measure in the field so were measured on shoots harvested in December from a 0.5 x 0.5 quadrat in the creek. The harvest was oven dried to give total standing crop. Midday irradiance was measured above and within the canopy in Zones 4 and 1 to indicate relative canopy density using a Li-Cor quantum meter and sensor (Lambda Instrument Company, Nebraska, USA).

Rhizome depth was the distance from soil surface to widest part of rhizome crown in mm. For this blocks of earth 20 cm deep were cut from around four live shoots in each zone in April.

Water availability and conductivity were monitored in soil samples collected by coring with a hand auger, diameter 7 cm. The maximum depth was 40 cm but this was restricted to 30 cm in Zone 0 because the C horizon was closer to the surface. In Zone 4, only surface samples were collected because of the difficulty of sampling under water. There were three replicates. Cores were cut into segments corresponding to 10 cm depths, slit vertically and a Whatman 42 filterpaper inserted in two places. The core segment was then wrapped in industrial aluminium foil to prevent water loss and placed in polystyrene containers to minimise temperature effects.

Soils were collected for chemical analysis on 16 February, dried at 105°C, ground in a ceramic mortar and pestle and stored in a desiccator until used. Soils were described from observations made during routine sampling and analysis.

Data organisation

Plant growth was mean shoot height and mean and modal number of green leaves shoot^{-1}. Tissue death was indicated by the length of the brown

tip which was the difference between mean height and mean green length. The critical reproductive height for T. domingensis was 900 mm, taken from the previous study at Griffith (3.10). Shoot survivorship was the proportion of marked shoots alive at the end of the study. Leaf survival was expressed as mean daily percentage depletion rate. This was the regression coefficient of percentage of the original leaf population alive on successive sampling days. Leaf recruitment was the number of new leaves day^{-1} for 100 shoots.

Sample analysis

Soil water content was estimated gravimetrically after drying for 3-4 days at 105°C as (Fresh-Dry)/(Dry) x 100. Each field replicate was subsampled twice and data are mean (n = 6) percentage. Soil matric potential was estimated from fractional water content of a Whatman 42 filter paper (Hamblin 1981). The calibration curve was provided by Dr E. L. Greacen, CSIRO Division of Soils, Glen Osmond, South Australia (pers. comm. 1983). Filter papers had at least three hours to equilibrate. In the laboratory wet and dry filter papers were weighed in clean tared glass Petri dishes to minimise errors due to atmospheric water uptake or release. Each field replicate was subsampled twice. Data are mean matric potential (n = 6) expressed as MegaPascals.

The resistance of soil water extracts was measured with a Philips Universal Measuring Bridge, Model Philisco E11, calibrated with fresh sodium chloride standards. Readings were converted to their reciprocal, conductivity, and corrected for dilution using water content to give in situ soil water conductivity. Data are mean conductivity (n = 6) in $\mu S\ cm^{-1}\ s^{-1}$. Extracts were prepared by shaking approximately 20 g fresh soil in 50 ml of de-ionised water. This sample size was more convenient in the laboratory than 1:5. The extract was gravity filtered and left

covered overnight in the same laboratory as the measuring bridge so that machine and solutions were thermally equilibrated. Laboratory temperatures were 20-23°C.

The pH of transect soils was measured on a 1:5 soil water extract using a Radiometer 29 pH meter. Extracts were prepared by shaking 20 g of air dry soil in 100 ml of distilled water for 1 hour, then filtering through a Whatman Number 1 filter paper.

Organic carbon was estimated by dichromate oxidation following Walkley-Black procedure and using a correction factor of 1.33 (Allison 1965). Chloride interference was eliminated by adding Ag_2SO_4. Titrations were done amperometrically on a Metrohm Herisau Multi Dosimat E415. Dry soils did not respond to HCl so were not pre-treated further for bicarbonate. Two extracts were prepared from one field replicate and each extract was analysed twice. Final value is the mean (n = 4) percentage organic carbon.

Analysis for nitrogen as Kjeldahl nitrogen KN was done by AMDEL as described earlier (2.5). The concentration of soluble reactive phosphorus SRP in soil extracts was measured using the ascorbic acid/ammonium molybdate method (Murphy and Riley 1962). Extracts were prepared by shaking approximately 0.5 g dry soil for 30 minutes in 2/1000 N H_2SO_4. For nutrient analyses, three field replicates were used with no laboratory replication. Final values are mean (n = 3) mg nutrient g^{-1} dry soil.

Sodium and potassium concentrations of 1:5 extracts were determined by flame photometry using a Corning 400 flame photometer. Extracts were prepared by shaking soil in glass distilled water for 1 hour, allowing this to settle overnight then centrifuging and gravity filtering through Whatman 44 filterpaper. Only one extract was prepared for each field replicate. Data are mean (n = 3) weight expressed as mg Na+ or K+ g^{-1}

dry soil.

A sample of creek water taken on 16 February was analysed for major ions by Engineering and Water Supply Department, Bolivar Laboratories, Adelaide.

Data analysis

Analysis of variance (FACTAN) was used to test for significant differences between zones in shoot height and depth to rhizome crown, and Bartlett's test for homogeneity of variances (HOMOV). Proportions of reproductive shoots, surviving shoots and surviving leaves were compared using chi-squared statistic. Regression statistics for leaf depletion rates were tested for significance and compared following Sokal and Rohlf (1981). Differences between zones in the number of live leaves $shoot^{-1}$ were analysed by frequency analysis using Kolmogorov-Smirnov test for goodness of fit with a hypothesis extrinsic to the data. For all analyses, alpha was 0.05.

Correlations between soil chemical characteristics were established using multiple linear regression program (MULREG). Organic carbon was the dependent variable because it reflected plant growth, and Kjeldahl nitrogen, soluble reactive phosphorus, sodium and potassium, were independent variables.

Dye translocation study

Three ramets of T. domingensis from Strathmont field site were cultivated in nutrient solution for six weeks prior to use. Each ramet had two generations, parent and daughter. The trimmed roots of a donor ramet, either parent or daughter, were immersed in the dye, basic cleared fuchsin (Tietema and van der Aa 1981). Receiver ramets were water stressed by leaving their roots exposed to the air. After 24 hours hand cut sections were taken from leaf and rhizome of donor and receiver

ramets. Pink colouration of vascular bundles was taken as evidence of translocation.

RESULTS

4.5 Results

Weather

The six months preceding the study were dry with below average rain. Weather during January and February continued dry and hot and culminated in the extreme conditions of 16 February 1983 (Ash Wednesday). March was cooler with above average rainfall. Rain was particularly heavy on 3-4 March, 43 mm (Bureau of Meteorology).

Transect study

On 15 November, surface soil water availability where Typha was found ranged from 20-224% and from -0.001 to -0.59 MPa (Figure 4.3). The pH range was 5.05-7.55 which is within the range reported for Typha (Segadas-Vianna 1951). The reading for the 6 m mark seems low compared to adjacent values on the transect. The conductivity of soil water extracts ranged from 165 to 3000 $\mu S\ cm^{-1}$. Soil conditions where no Typha was growing were similar to soils with Typha, 35% water content, pH 7.3 and conductivity 300 $\mu S\ cm^{-1}$, except for matric potential which was lower, -0.70 MPa.

Shoot height decreased with decreasing water availability and the shape of the response depended on how this was estimated (Figure 4.3). A normal plot of height v water availability showed that shoot height range was approximately halved, from 2500-2800 mm to 1150-1600 mm, as water content was approximately halved, from 224 to 98%, but the equivalent in matric potential was a thirty-fold decrease, from -0.001 to -0.03 MPa,

MPa. Decreases below 70% and -0.04 MPa had very little effect on shoot height.

Zone study

Typha grew vigorously in the centre of the creek, equivalent to Zone 4. Mean height of live harvested shoots was 2506 mm. Live standing crop was 2615 g m^{-2} and total aboveground standing crop was 3590 g m^{-2}. The December canopy was so dense that the midday irradiance of 2100 μE m^{-2} s^{-1} above the canopy was reduced to 1.5 μE m^{-2} s^{-1} at 0.5 m above the ground. In comparison, Zone 1 canopy was much less dense and irradiance at ground level was 1500-2000 μE m^{-2} s^{-1}. Mean shoot height in January ranged from 598 to 2506 mm in Zones 1 to 4 (Table 4.2) and zones were significantly different. A decrease from 598 mm in January to 548 mm in March in Zone 1 was not significant.

The height decrease from creek to paddock meant the proportion of shoots reaching reproductive size (900 mm) decreased from 1.00 in Zones 3 and 4 to only 0.07 and 0.60 in Zones 1 and 2. Consequently the reproductive proportion also decreased from Zone 4 to Zone 1, from 0.31 to 0.00 with no significant differences between Zones 4, 3 and 2 (Table 4.2).

Shoot survival during the study period was high in Zones 4, 3 and 2 with 94-96% of marked shoots still alive on 21 March (Table 4.2). Survival in Zone 1 was lower at 84% but not significantly different and was irregular with the number of live shoots increasing between 1 and 10 March. This was not an error but was due to "resurrections". Five shoots with only dead leaves on 1 March had 1-3 green leaves $shoot^{-1}$ on 10 March.

The number of live leaves $shoot^{-1}$ was highest in Zone 4 where the mean and modal number in January was 7.44 and 6. This was twice as high as in Zone 1. In Zones 2, 3 and 4, mean live leaves $shoot^{-1}$ decreased from January onwards and was significantly lower at the end of the study. However Zone 1 showed no significant change (Table 4.2).

The number of leaves recruited in Zone 1 was 106 which was 5-6 times more than in Zones 2, 3 or 4. Daily recruitment rate (Table 4.3) decreased from January in all zones but increased in Zones 1 and 4 after the beginning of March. In Zone 4 this was due to a growth spurt on one shoot with 5 new leaves or 36% of total. Recruitment rates in Zone 1 were consistently higher than in other zones and increased by 1-2 orders of magnitude after 1 March. High leaf recruitment in late summer was not typical for Typha unless actively recruiting (2.11, 3.9).

Daily mortality rate for leaves in each sampling interval ranged from 1.33 to 8.33 leaves per 100 tagged shoots d^{-1} (Table 4.4). These were within the range for December shoots at Griffith (Table 3.9) with no consistent difference between zones. Zonal differences become apparent when data are expressed as a mean percentage depletion rate. In Zone 4 the depletion rate for leaves tagged in January was 0.5040% day^{-1} (not shown). This was significantly higher than depletion rates for Zones 2 and 3, 0.3460% and 0.3299% day^{-1}, but lower than Zone 1, 0.6115% day^{-1}. Depletion rates in Zones 2 and 3 were not significantly different. (All regressions were significant and had correlation coefficients greater than -0.8900.)

Rhizome crowns were 22 to 126 mm below the surface with no significant difference between zones.

Soil water

Results are presented and discussed in Appendix 5. Determination of moisture characteristic was unsuccessful possibly because of changing conductivity characteristics and/or sample storage methods. The percentage soil water content and matric potential were used as estimates of soil water availability.

There was an increase in soil water from Zone 0 to Zone 4 which was

most noticeable in surface soils, 0-10 cm (Figures 4.4, 4.5). Thus in January the water content of surface soils in Zones 0 and 1 was 18-52% and matric potentials were -0.20 to -0.57 MPa compared to 77-530% and -0.001 to -0.12 MPa in Zones 2, 3 and 4. Below 10 cm there was less difference between zones and at the bottom of the profile differences were negligible. At 30-40 cm soil water in Zones 1, 2 and 3 was 35%, 41% and 39% and -0.02, -0.04 and -0.003 MPa.

Soils in Zone 4 were under water at all times and were thus above Field Capacity (not shown). Matric potential was measured once, -0.0012 MPa, which was probably outside the resolution of the method. Changes in water content from 419-573% do not represent trends but show the difficulty of sampling consistently when soils were under water.

In contrast to constant conditions in Zone 4, there was considerable temporal change in Zones 0-3, again most obviously in surface soils. Zones 0 and 1 dried out from 20 January to 16 February during which time surface matric potentials decreased by a factor of 10 to -7.0 and -3.5 MPa. Surface drying resulted in an abrupt change in soil water down the profile. After rain at the beginning of March the profile wetted up, reaching 37-73% and -0.003 and -0.025 MPa in 0-10 cm layer, and 28-45% and -0.003 to -0.007 MPa below 10 cm.

Zones 2 and 3 did not dry out but instead wetted up and on 21 March resembled a saturated sponge. Between 20 January and 16 February, the water content of surface soils increased from 77% to 229% in Zone 2 and from 265% to 522% in Zone 3. It is not clear when this wetting began but it appeared to have been recent. The January subsurface water content in Zone 2 was 30-41% which was similar to Zones 0 and 1 on the same date whereas surface water content was much higher. This was interpreted as a recent wetting front with limited infiltration, and was presumably due to increased garden watering in the hot dry summer. Because the creek was

overgrown with Typha, water spread out on the eastern side into Zones 2 and 3. The blocked creek was the reason for excavation in April.

Soil water conductivity data were not used to estimate in situ osmotic potential. Readings made on an extract obtained by dilution are likely to be overestimated as dilution brings more compounds into solution than were present originally (Slavik 1974). Thus conductivity data can only indicate spatial and temporal differences.

Conductivity was consistently higher in Zone 3 than in Zones 0 to 2 (Figure 4.6). Zone 3 was also the wettest zone and therefore least likely to be affected by dilution overestimations. This coincidence of wetness and conductivity implicated creek water which was saline (see below). Conductivity increased down the profile to form a wedge sitting at or above the bottom. In early February, conductivity of this wedge in 20-30 cm layer of Zone 3 reached 13,000 $\mu S\ cm^{-1}$ which was 3-5 times higher than other zones on the same date. This wedge was also present in Zone 2 but was less well developed. In Zones 0-2 conductivity increased in surface soils during January and February which was consistent with concentrating effects of soil drying but could have been due to dilution (see above). Conductivity decreased after 16 February in all zones. This coincided with March rains.

Soil characteristics and analysis

Soil characteristics changed from Zone 0 to Zone 4 and from top to bottom of profiles (Figure 4.7). In Zones 0 and 1 the surface soil was a crumbling brown loam, in Zones 2 and 3 it was fibrous and peat-like overlying silt and in Zone 4 it was fine black silt with abundant roots. Bottom soil in Zones 0-3 was a heavy sticky red clay which occurred at increasingly greater depths closer to the creek. Thus in Zone 0 it was found at 20-30 cm and occasionally in 10-20 cm layer whereas in Zone 3 it was only at 30-40 cm. Zones 2 and 3 had a distinctive transitional layer

of dark brown silty clay with none of the sticky characteristics of the red clay below.

Soil organic carbon OC increased from Zone 0 to Zone 4 in surface soils, 32-146 mg g^{-1} dry soil, and decreased with depth down the profile to <10 mg g^{-1} dry soil in the red clay layer of all zones (Fig 4.8 a). High OC in surface of Zones 2 and 3 corresponded with fibrous character (Figure 4.7).

Concentrations of Kjeldahl nitrogen KN and soluble reactive phosphorus SRP also increased from Zone 0 to Zone 4 and decreased down the profile (Figures 4.8 b, 4.8 c). Surface concentrations of KN were 2.0 mg g^{-1} in Zone 0 and 4.8-8.0 mg g^{-1} in Zones 1-4, and SRP concentrations were 0.81 mg g^{-1} in Zone 0 and 1.5-3.9 mg g^{-1} in Zones 1-4. Sodium and potassium had the same distribution (Figures 4.8 d, e) reaching 199.6 and 5.8 mg g^{-1} respectively in Zone 4.

Similar distributions meant chemical characteristics were highly correlated with each other with the exception of potassium (Table 4.5). Together KN, SRP, sodium and potassium accounted for 96% of variation in organic carbon. Phosphorus had the highest standard partial regression coefficient and was the only significant partial regression coefficient.

Organic carbon was highly correlated with soil water content ($r = 0.9053$, $n = 16$) but not with matric potential ($r = -0.1357$, $n = 15$).

Creek water

Creek water sampled on 16 February had a pH of 8.3 and was dominated by sodium and chloride ions, 415 and 680 mg l^{-1} respectively. These were assumed to originate from bore water used in the hospital grounds. Phosphorus and potassium levels were low, 0.041 and 5 mg l^{-1}.

Water availability and plant growth

Growth of Typha, as indicated by mean shoot height, the proportion

flowering and the number of leaves shoot^{-1}, was lowest in Zone 1 (Figures 4.9 a, b). Height decreased with decreasing water availability and a linear regression of height and $\log_{10}$ water availability in January was significant. The regression coefficient for soil water content was two times greater than for matric potential, -1631.8 $\log_{10}$ height compared to -765.1 $\log_{10}$ height (differences significant at 0.05). The proportion flowering (Figure 4.9 a) and canopy size (Figure 4.9 b) showed a stepped response. Decreases in water availability from 77 to 265% or from -0.0023 to -0.1238 MPa (Zone 3 to 2) had less effect than from 77 to 52% or -0.1238 to -0.2007 MPa (Zone 2 to 1).

Length of the brown tip on tallest leaf per shoot was 135-186 mm in Zone 1 or 0.25-0.30 of total leaf length. In Zones 2 and 3 it was shorter, 24-59 mm and 54-125 mm and never more than 0.08 of leaf length. Zone 4 shoots were too tall to measure. In Zone 1 brown tip length decreased after March rains from 177 mm on 15 February to 136 mm on 21 March. Brown tip length cannot actually decrease as tissues do not revive. This decrease was due to turnover in the leaf population. Leaves which were tallest in March were not the same individuals as in February, and had less necrosis. Brown tip length increased in Zones 2 and 3 (not shown). This was consistent with low leaf recruitment (Table 4.3) and with being the season for die-back and senescence (3.11).

Dye translocation study

Pink colouration was evident in vascular bundles of rhizomes and leaves of all donor and receiver ramets. This showed that basic fuchsin had been taken up by roots and translocated between ramet generations, from daughter to parent, from parent to daughter and from daughter to daughter via the parent. The translocation distances in this last example were 265 mm and 245 mm, giving a total of 510 mm. The dye showed preferred pathways. In leaves, central vascular bundles were more heavily

stained than lateral ones, and stained adaxial bundles outnumbered abaxial ones. The dye also showed transverse connections between vascular bundles in the leaf. These were only seen at diaphragms. In the rhizome, vascular bundles in the pith were more heavily stained than in the cortex.

DISCUSSION

4.6 The resource gradient

The study premise was that water was the limiting resource gradient at Strathmont and that growth across the gradient was in response to this limitation. Soil analyses confirmed a strong water gradient between Zones 0 and 4 but found that soil characteristics were strongly correlated with each other and with water. Thus nutrients and salinity could also explain observed differences between zones. The correlation between OC and water was considered a summary of past and present root growth. OC and nutrients were correlated because the majority of soil nitrogen and 10-85% of total phosphorus is organic (Alexander 1977). The correlation between OC and sodium was probably due to the correlation between OC and water and was due to the dominance of sodium in creek water.

Soil nutrients KN and SRP in the top soil layers at Strathmont were greater than at the T. domingensis site at Bringagee Road where shoots reached 2401-2600 mm height class in 1979-80 (Figure 3.10). Therefore nutrient concentrations per se at Strathmont were unlikely to be limiting. This may not be true for nutrient availability which is water dependent. Conversion of nutrients from organic to inorganic forms suitable for uptake is dependent on microbial activity and is therefore a water sensitive process. In addition, nutrients can only be taken up when in solution. This requirement for water confirms the importance of water

as the primary and driving resource.

In January and February the conductivity of the wedge reached 8900-13,000 $\mu S\ cm^{-1}$ equivalent to 90-140 mM NaCl. Although this is sufficient to significantly reduce growth of T. domingensis (Hocking 1981) it is unlikely that conductivity is the explanation for shoots in Zone 3 being shorter than in Zone 4. These high conductivity levels were reached in summer, after the main growing season, and were probably not so high during spring. The conductivity wedge disappeared after March rains (Figure 4.6) which showed its temporary nature and it is likely that winter rains would flush the profile in a similar way. Accumulation of saline water was probably a result of summer irrigation ponding above the sticky red clay layer.

The Strathmont site could therefore be accepted as a water gradient in which zones had different water regimes. In Zone 4, water regime was constant with soils always above Field Capacity. Water availability in Zones 2 and 3 was initially lower than Zone 4 but surface soils wetted up and eventually reached Field Capacity. Zones 0 and 1 had an even lower level of resource availability. Wetting up did not begin until March, at least two months later than Zones 2 and 3, by which time matric potentials in surface soils of Zones 0 and 1 and in subsurface soils of Zone 0 had reached -1.5 MPa, recognised as the Permanent Wilting Point.

Species absence from a given site, such as the lack of Typha from Zone 0, may be due to lack of propagules or unsuitable growing conditions. Lack of propagules is discounted as a factor because mature Typha was within 10 m of Zone 0. This distance cannot be considered an obstacle to Typha which has wind dispersed seeds and is renowned for its colonising ability. In one growing season the plant can advance 3 m (Finlayson et al. 1983). Unsuitable growing conditions may be competitive exclusion, herbivory or insufficient resources. There was no evidence of

grazing in Zone 0 or adjacent zones. The only competitors present were scattered Rumex crispus L. and Polygonum aviculare L. but their cover seemed too sparse to effectively outcompete young Typha shoots with access to carbohydrate and nutrient storage in the rhizome. Thus the absence of Typha from Zone 0 was due to insufficient resources, namely water. Shrivelled dead rhizomes and rhizome crowns in surface soils indicated that growth had been possible there in the past and showed its absence was only temporary.

4.7 Water availability and growth of Typha

The soil depth available to Typha roots at Strathmont was less than 0.5 m (Figure 4.7) and although shallow this was unlikely to be limiting as roots of Typha are typically shallow (4.3). Rhizome crown position and a hemispherically shaped root system (Weaver and Himmel 1930) mean the top 10 cm was the most important layer for soil water and plant growth. Surface soils in Zones 2 and 3 were a fibrous tangle of roots.

Decreases in resource availability in surface soils were accompanied by a corresponding decrease in shoot height and canopy size as the number of live leaves shoot^{-1} (Figure 4.9). These decreases were evident when soil water availability was close to Field Capacity. The height difference between Zones 4 and 3, 890 mm, was significant yet corresponded to a relatively small drop in resource availability.

Module dynamics did not show the same clear trend between zones as did shoot height. The death rate of shoots and leaves was higher in Zone 1 than in Zone 4 which was consistent with lower resource levels but results from Zones 2 and 3 did not fit between Zones 1 and 4. Although shoot survival was similar to Zone 4, leaf depletion rate was significantly lower. This inconsistency is attributed to the wetting water regime in Zones 2 and 3 where improvement in resource availability postponed senescence. A similar effect was evident in Zone 1 where a

sudden increase in resource levels at the beginning of March resulted in a burst of leaf recruitment, 5 shoot resurrections and a decrease in brown tip length. In the previous study T. domingensis showed a similar response (3.12).

There were two instances where shoot height was apparently independent of water availability, both associated with Zone 1. First, shoots were present and growing in Zone 1 in February at resource levels which were similar or lower than resource levels in Zone 0 in January where there was no growth (Figure 4.10). This was particularly clear from the matric potential data. Typha was present on 16 February in Zone 1 at -3.32 MPa yet absent from Zone 0 where on 20 January matric potential was -0.58 MPa. Second, transect results showed no height decrease with decreasing water over the range 15-35% or -0.1 to -0.6 MPa (Figure 4.3). Usually such a response indicates another essential resource was limiting but the most likely candidates, nitrogen and phosphorus, were apparently adequate.

These inconsistencies can be explained by assuming that shoots were physiologically integrated and that shoots in Zone 1 were supplied from parent ramets. The dye study showed translocation was possible between generations and over a distance of 0.5 m. Although this does not prove translocation occurred at Strathmont or could happen over distances up to 5 m, the explanation fits both examples cited above and is consistent with the literature. Physiological integration between ramets is now well documented (e.g. Callaghan 1984, Pitelka and Ashmun 1985). Although beneficial to a receiver ramet when the plant is growing on a steep resource gradient, there is a cost to the donor ramet which is evident as reduced biomass (e.g. Salzman and Parker 1985).

Physiological integration means that growth and module dynamics in Zone 1 were not a response to soil water in that zone. It is also

possible that Zone 2 shoots were subsidised from Zone 3 (Figure 4.1) and that in a confined gradient such as at Strathmont none of the zones were truly separated. Thus Zone 2 shoots were probably subsidised from Zone 3 which could explain the disproportionately large height differences between Zones 4 and 3. Thus the relationship between shoot height etc and soil water (Figure 4.9) at Strathmont was for connected ramets.

The second aim of the study was to define limiting resource levels and R*, the equilibrium level for T. domingensis. The simplest definitions of limiting resource levels are given by Zone 0 with no Typha shoots. Thus January water conditions of 16% and -0.57 MPa at 0-10 cm, and 26% and -0.21 MPa at 10-20 cm were below R*.

The definition of R* (Tilman 1982) is the resource level below which existing plants die and new individuals cannot establish. In the absence of individuals, R* can be defined via the modular approach as the leaf population shoot^{-1}. This was stable in Zone 1 (Table 4.2) therefore resource levels must have been close to R*. However Zone 1 was probably subsidised which makes Zone 1 conditions unsuitable for independent growth and therefore below R*. January conditions in Zone 1 can also be used to define limiting conditions. These were 52% and -0.20 MPa at 0-10 cm and 25-80% and -0.02 to -0.06 MPa at 10-20 cm. Another definition of resource levels below R* comes from the November transect data. Shoots showing independence of water availability were in soils as wet as 50% and -0.13 MPa (Figure 4.3). Questions of connectedness and subsidy make it impossible to define R* more precisely but a lower limit can be set by putting these data together. For surface soils R* is wetter than 52% and -0.13 MPa.

4.8 Typha in context

It is difficult to compare these results for T. domingensis with other emergents because of the way availability has been measured (4.1). The

problem is not merely one of incompatible units, distance versus water potential, but of assumptions. Vertical distance disregards the importance of slope and assumes a position 30 cm above water level is twice as dry as one 15 cm above. Moreover it is not clear how much isolated pots with surfaces 10 cm above the water level as used for Scirpus maritimus (Lieffers and Shay 1981) resemble field sites with a 60 cm drop over 2 m (Grace and Wetzel 1981a).

In addition, studies of emergents on a water gradient have been concerned with establishing the depth for maximum growth (e.g. Grace and Wetzel 1981a, Thomas and Stewart 1969) or response across a gradient (e.g. Lieffers and Shay 1981, Yamasaki and Tange 1981) rather than tolerance limits. In Scirpus maritimus a shift towards sexual reproduction with increasing water depth was interpreted as a survival mechanism to flooding (Lieffers and Shay 1981). T. domingensis showed a similar shift but it is more likely this was a response to resource availability rather than a survival strategy. The high cost of flowering was discussed earlier (3.11).

An equilibrium resource level above 52% or -0.13 MPa for T. domingensis is close to Field Capacity (4.2). This seems high but is consistent with results from Bringagee Road where December drying after November flooding was associated with increased leaf mortality (3.12). R* values cannot be precise because of ramet connectedness (see above) and because factors determining R* are dynamic (Chapter 5). These R* values represent water levels adequate for terrestrial or flood-plain plants. Amongst terrestrial plants, for example, seedlings of three West Australian arid zone annuals do not survive at -1.5 MPa (Mott and McComb 1975); dawn water potentials of two Eucalyptus spp. in Victoria were never higher than -1.67 MPa in three years (Myers and Neales 1984). On the Pongolo flood-plain Cynodon dactylon continued to grow even after

soil moisture was below -1.5 MPa (Furness and Breen 1986).

Table 4.1
Root characteristics of Typha

Details from ramets of T.latifolia cultivated for 35 days (Weaver and Himmel 1930)

	SOIL WATER TREATMENTS			
	Saturated	Drained	Moist	Dry
Water roots	Present	Present	Absent	Absent
Soil root:				
Branching	No	Profuse	Regular	Dense
Max length (cm)	28	40-47	40-53	-
Max width (cm)	15	-	16-35	-
In top 7-9 cm	Yes	Yes	No	No

Table 4.2
Plant growth

	Zone 1	Zone 2	Zone 3	Zone 4
SHOOTS				
Mean height in mm				
18 January	598	881	1616	2506
21 March	548	906	1618	nd
Demography				
Initial pop	50	49	49	35
p(T)	0.0652	0.5918	1.0000	1.0000
p(R)	0.0000	0.1630	0.2449	0.3143
p(L)	0.8400	0.9600	0.9600	0.9440
GREEN LEAVES				
Initial pop	158	297	311	262
p(L)	0.5127	0.7407	0.7556	0.6183
Recruits	101	14	14	14
Leaves shoot^{-1}, mean				
18 January	3.33	6.06	6.35	7.23
21 March	3.70	4.79	4.98	5.09
Leaves shoot^{-1}, mode				
18 January	3	5	5	5
21 March	2	4	4	5
RHIZOMES				
Mean depth in mm	41.00	84.75	75.75	47.00

KEY
nd = no data
p(L) = proportion alive on 21 March
p(R) = proportion reproductive
p(T) = proportion taller than 900 mm

Table 4.3
Leaf recruitment rate

Mean numbers of leaves recruited shoot^{-1} day^{-1} x 10^2
Zones 2, 3 and 4 were not sampled on 1 March because of rain

	Period ending					
	18 Jan	1 Feb	15 Feb	1 Mar	10 Mar	21 Mar
Zone 4	0.95	0.61	0.41	-	0	1.52
Zone 3	1.46	0.17	0.44	-	0	0
Zone 2	nd	1.09	0.32	-	0.39	0.40
Zone 1	3.78	1.98	0.79	0.16	8.20	6.46

Table 4.4
Leaf mortality rate

Mean number of leaves dying shoot^{-1} d^{-1} x 10^2

	Period ending					
	18 Jan	1 Feb	15 Feb	1Mar	10 Mar	21 Mar
Zone 4	3.34	5.92	3.06	-	3.35	5.71
Zone 3	1.76	7.68	1.44	-	1.33	3.13
Zone 2	nd	8.33	4.43	-	1.38	4.18
Zone 1	6.33	2.18	2.36	6.52	3.68	3.32

Table 4.5
Soil analysis

Multiple linear regression (MULREG)
Dependent variable, as % dry weight soil
y = Organic carbon (OC)
Independent variables as mg g^{-1} dry weight soil
x1 = Kjeldahl nitrogen (KN)
x2 = Soluble reactive phosphorus (SRP)
x4 = Potassium (K)

Multiple correlation coefficient, r = 0.9797
Coefficient of multiple determination, r^2 = 0.9597

Correlation matrix

	OC	KN	SRP	Na	K
OC	-				
KN	0.9352	-			
SRP	0.9521	0.8770	-		
Na	0.9282	0.8786	0.9009	-	
K	0.5293	0.4466	0.6525	0.5496	-

Anova table

Source of Variation	df	SS	MS	Fs	Significance
Explained	4	32885.02	8221.26	47.66	***
Unexplained	8	1380.07	172.51		

Significance table
T-test of partial regression coefficients,
using n-k-1 = 8 degrees of freedom

Variable	Ts	Significance
KN	1.7391	NS
SRP	2.5719	*
Na	1.1755	NS
K	0.7844	NS

Prediction equation
y = 14.7859 + 6.1584x1 +19.7916x2 + 0.1816x3 -2.5181x4

Table 4.6
Soil nutrients at Strathmont field site

Comparisons with other study sites
Nutrient concentrations as mg nutrient g^{-1} dry soil

	Nitrogen		Phosphorus	
	0-10 cm	10-20 cm	0-10 cm	10-20 cm
Strathmont				
Zone 4	7.33	nd	3.910	nd
Zone 3	8.03	4.03	3.032	3.700
Zone 2	6.63	2.47	2.440	0.315
Zone 1	4.80	1.63	1.490	0.171
Zone 0	2.03	0.87	0.805	0.157
Brogden's Rd	7.00	0.80	0.300	0.100
Bringagee Rd	1.00	0.60	0.150	<0.05

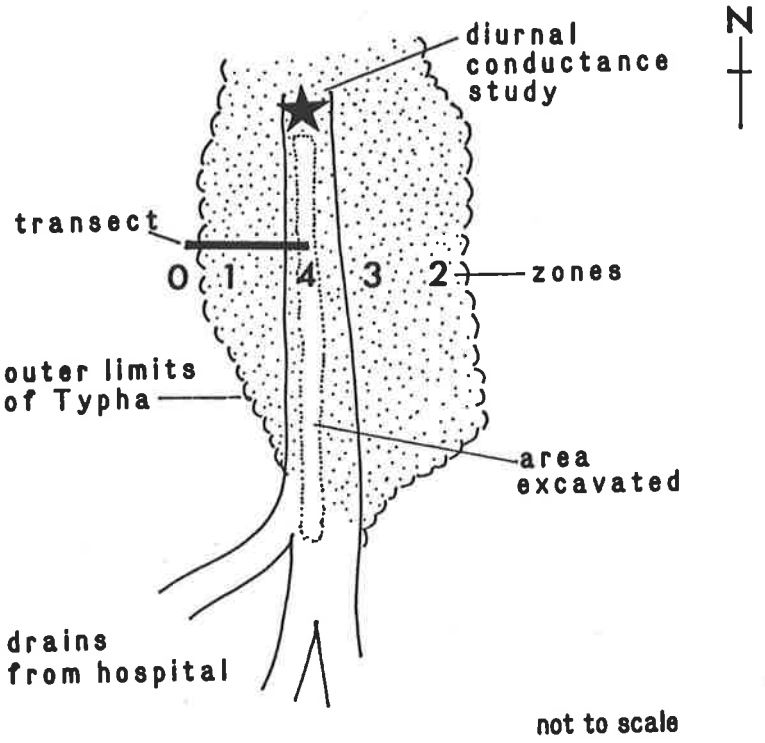

Figure 4.1
Strathmont study site

Schematic map (not to scale) of study site near Strathmont Centre, Adelaide, showing position of transect and Zones 0-4 for the gradient study (Chapter 4), location of diurnal stomatal conductance study (Chapter 5), and area of drain excavated in April 1983. Water draining from grounds of Hillcrest Hospital flows northwards. Before drain clearance, a continuous stand of T. domingensis straddled the creek, extending out into the paddock and ponding flow.

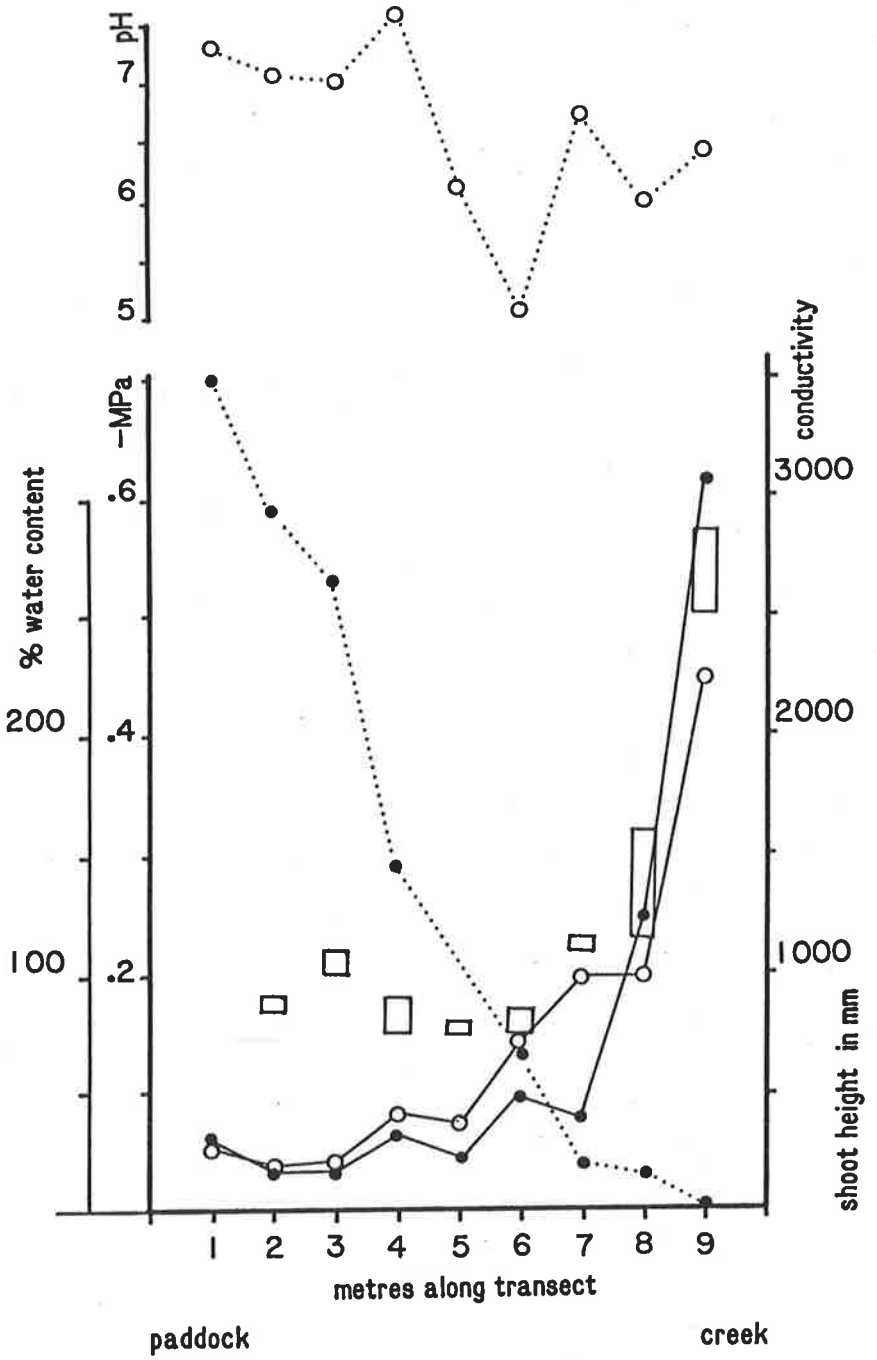

Figure 4.2
Transect at Strathmont

Changes in shoot height and soil characteristics at one metre intervals from paddock at 0 m towards creek at 10 m, on 15 November 1982. Shoot height in mm is the range for four shoots closest to the soil sample, shown by hollow bar. Soil samples taken from surface layer, 0-10 cm.

Key
●—● Soil water content, as % dry weight
●····● Soil water potential in -MPa
o—o Conductivity of soil extract, in $\mu S\ cm^{-1}$
o····o pH of soil extract

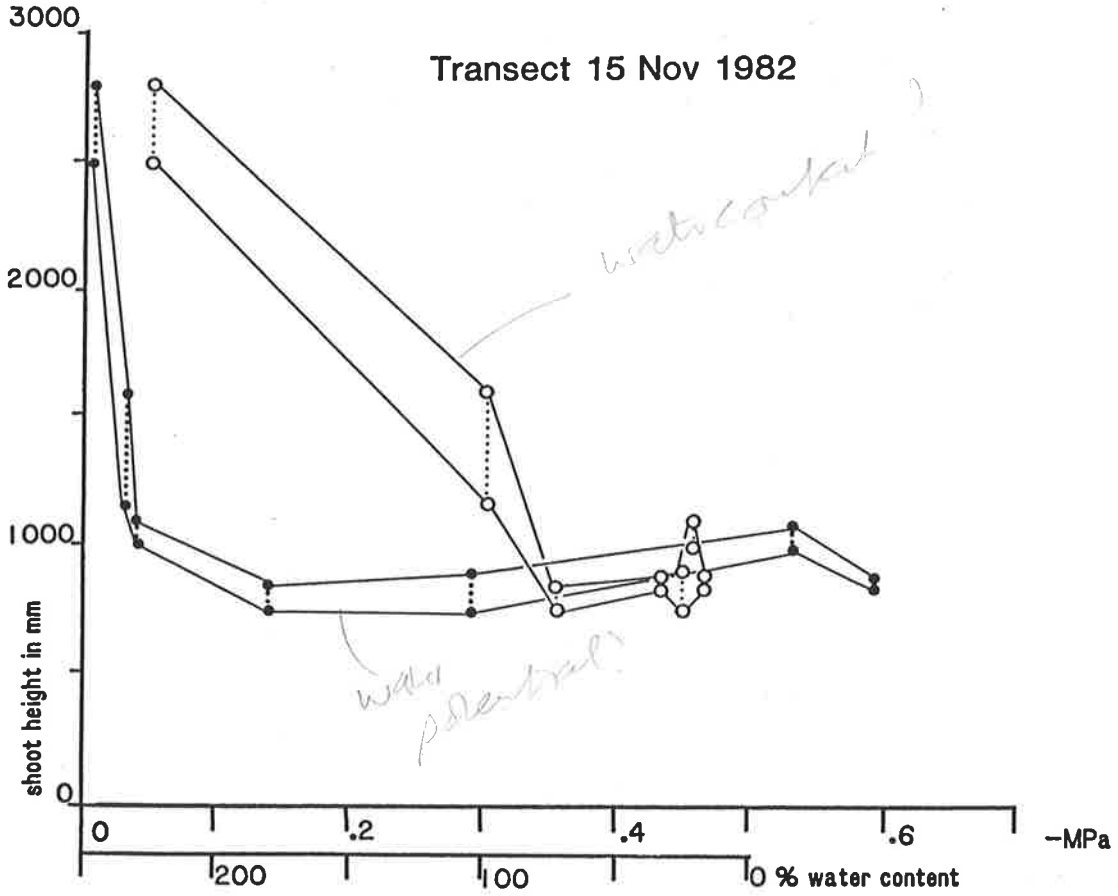

Figure 4.3
Transect: shoot height v water availability

Shoot height as a function of soil water availability measured two ways. Height is height range of four shoots closest to sampling point.

● Soil water content as % of soil dry weight
o Soil water potential in -MPa

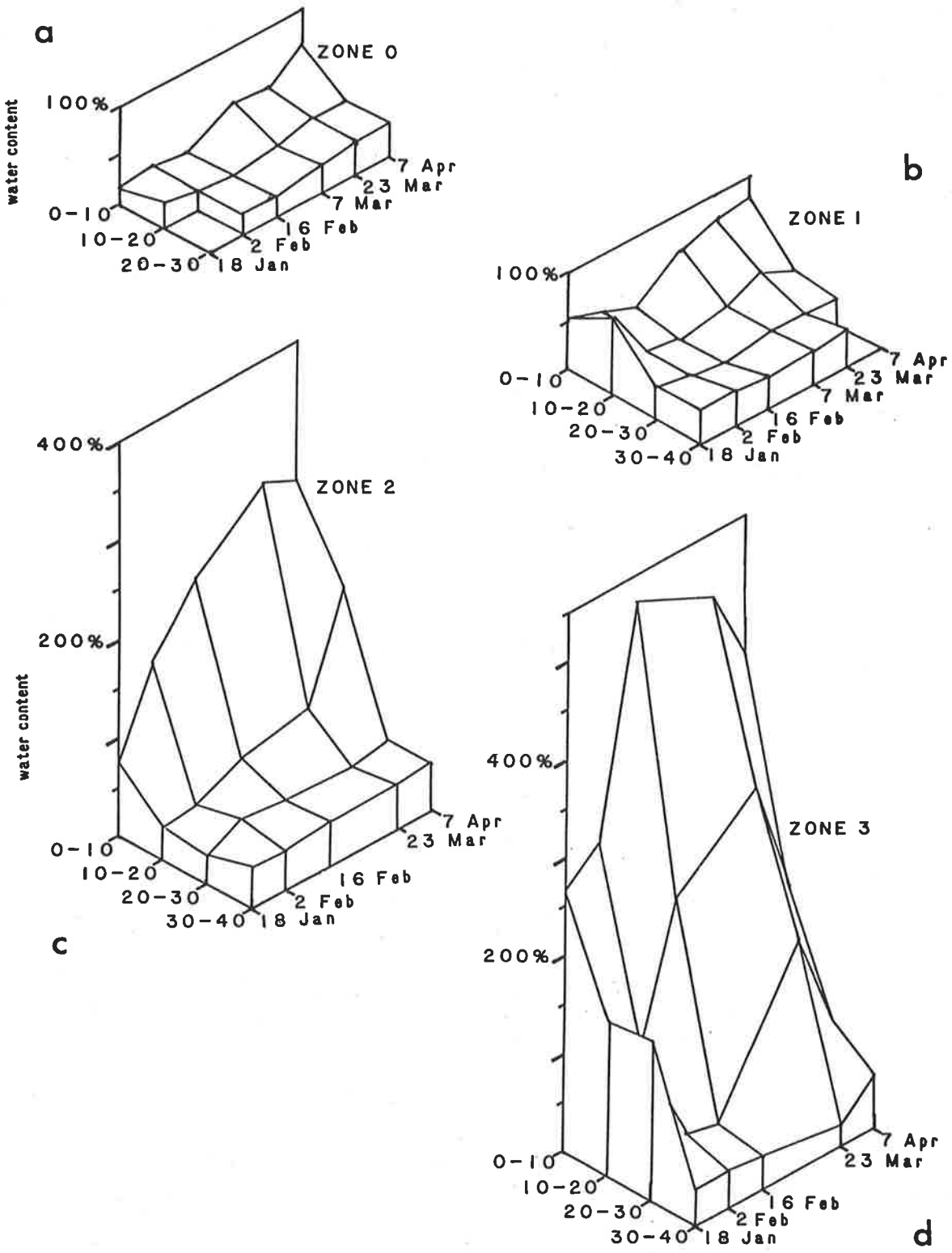

Figure 4.4
Gradient: soil water content

Spatial and temporal changes in water availability as percentage water content of dry soil for Zones 0-3 (a-d) from 18 January to 7 April 1983. Data are mean values (n = 6) plotted linearly on a vertical axis of increasing "wetness". Soil profile in 10 cm deep sections. No 30-40 cm samples were taken from Zone 0 throughout the study, and none from 30-40 cm depth from Zone 1 on 7 April.

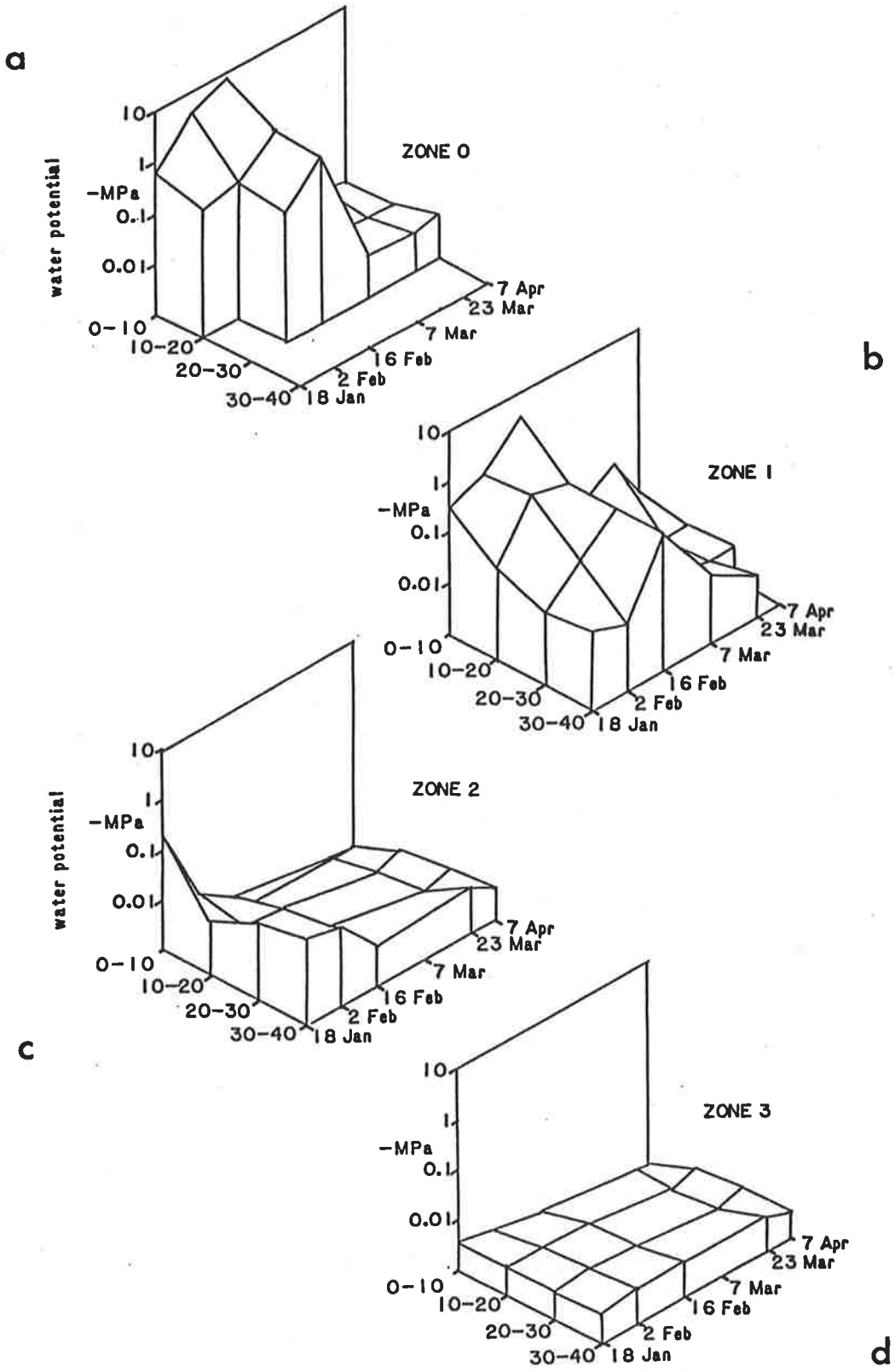

Figure 4.5
Gradient: water (matric) potential

Spatial and temporal changes in water availability as water (matric) potential in -MPa from 18 January to 7 April 1983 for Zones 0-3 (a-d). Mean matric potential (n = 6) is plotted on a logarithmic vertical scale of increasing "dryness".

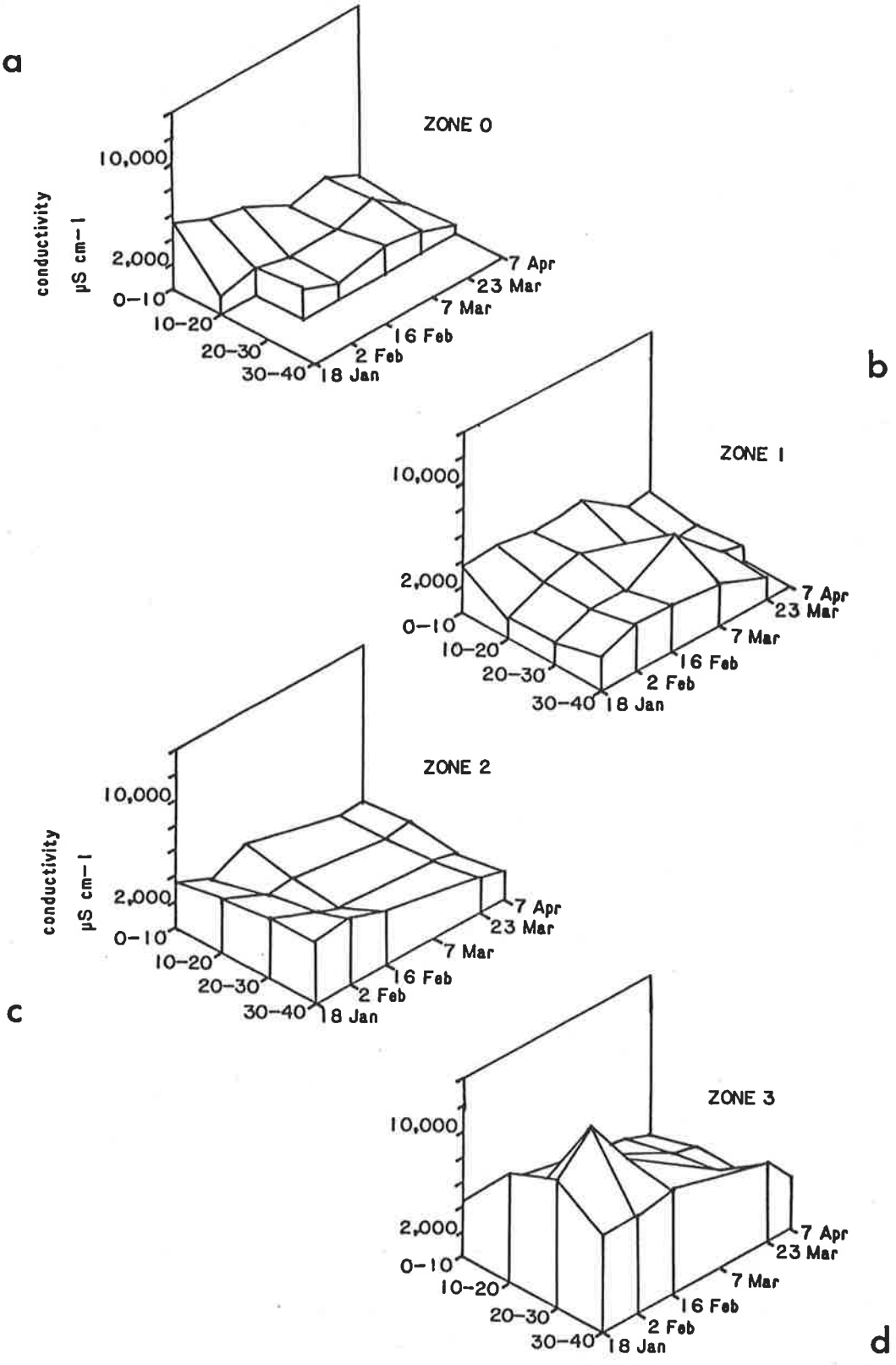

Figure 4.6
Gradient study: soil water conductivity

Spatial and temporal changes in soil water conductivity in $\mu S\ cm^{-1}$ from 18 January to 7 April 1983 for Zones 0-3 (a-d). Mean conductivity (n = 6) plotted on a linear vertical scale. Results for Zone 3 are partly obscured by a conductivity peak at 20-30 cm on 2 February.

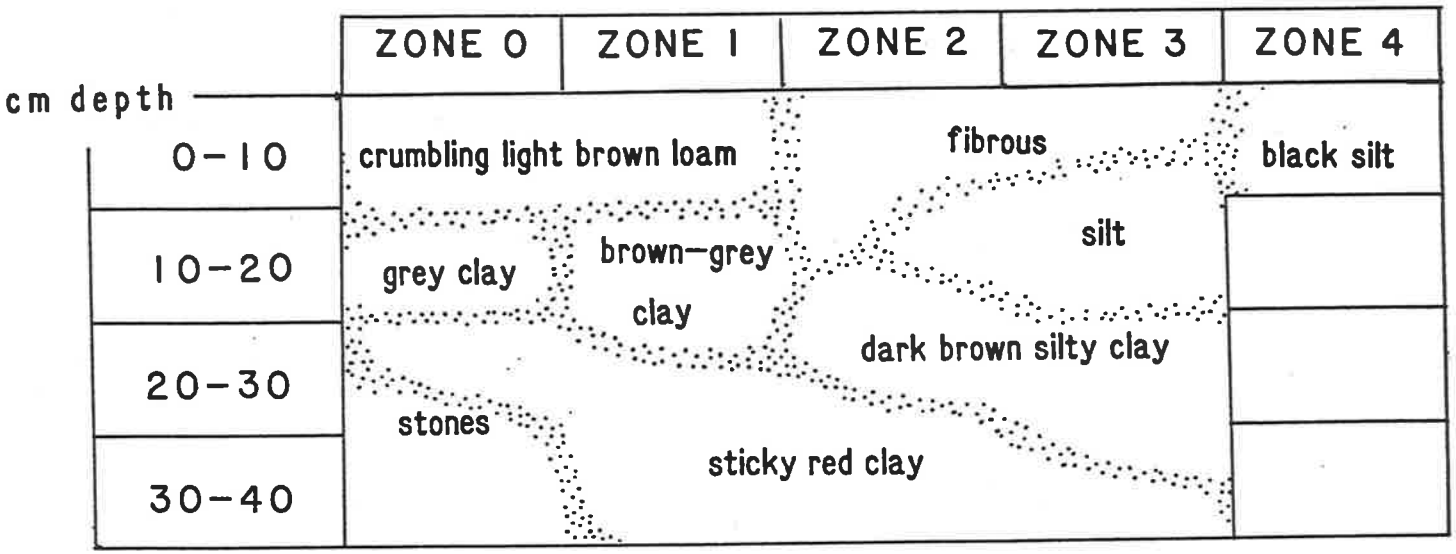

Figure 4.7
Gradient study: soil characteristics

Changes in soil characteristics from Zone 0 to Zone 4 and down the profile, based on observations made during field sampling and sample processing.

Figure 4.8
Gradient study: soil minerals

Mean concentration of five minerals across the gradient from Zone 0 to 4 and down the profile. Sample sizes etc in text.

(a) Organic carbon, as % dry weight
(b) Kjeldahl nitrogen, mg g^{-1} dry soil
(c) Soluble reactive phosphorus, mg g^{-1} dry soil
(d) Sodium, mg g^{-1} dry soil
(e) Potassium, mg g^{-1} dry soil

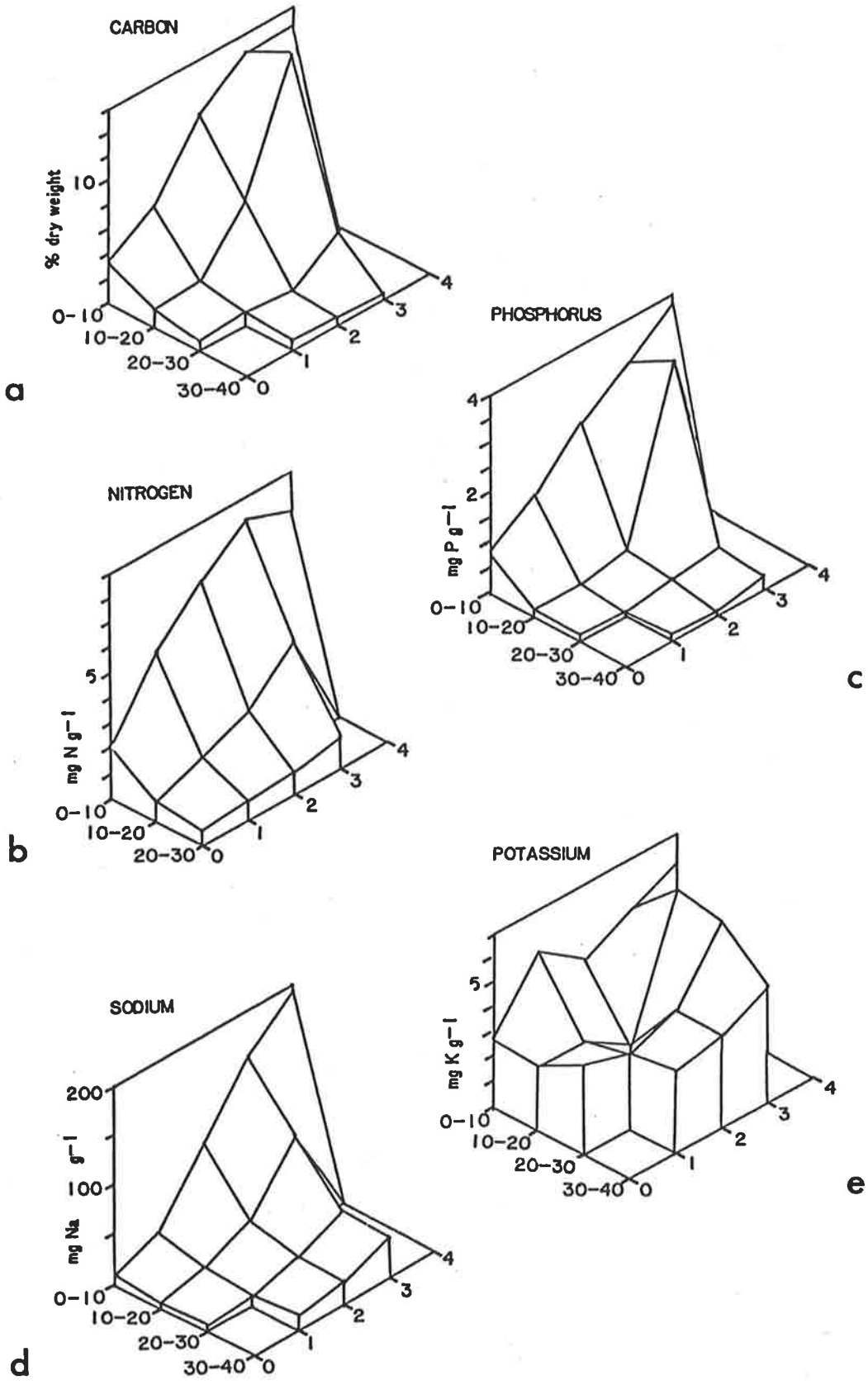

Figure 4.8
Gradient study: soil minerals

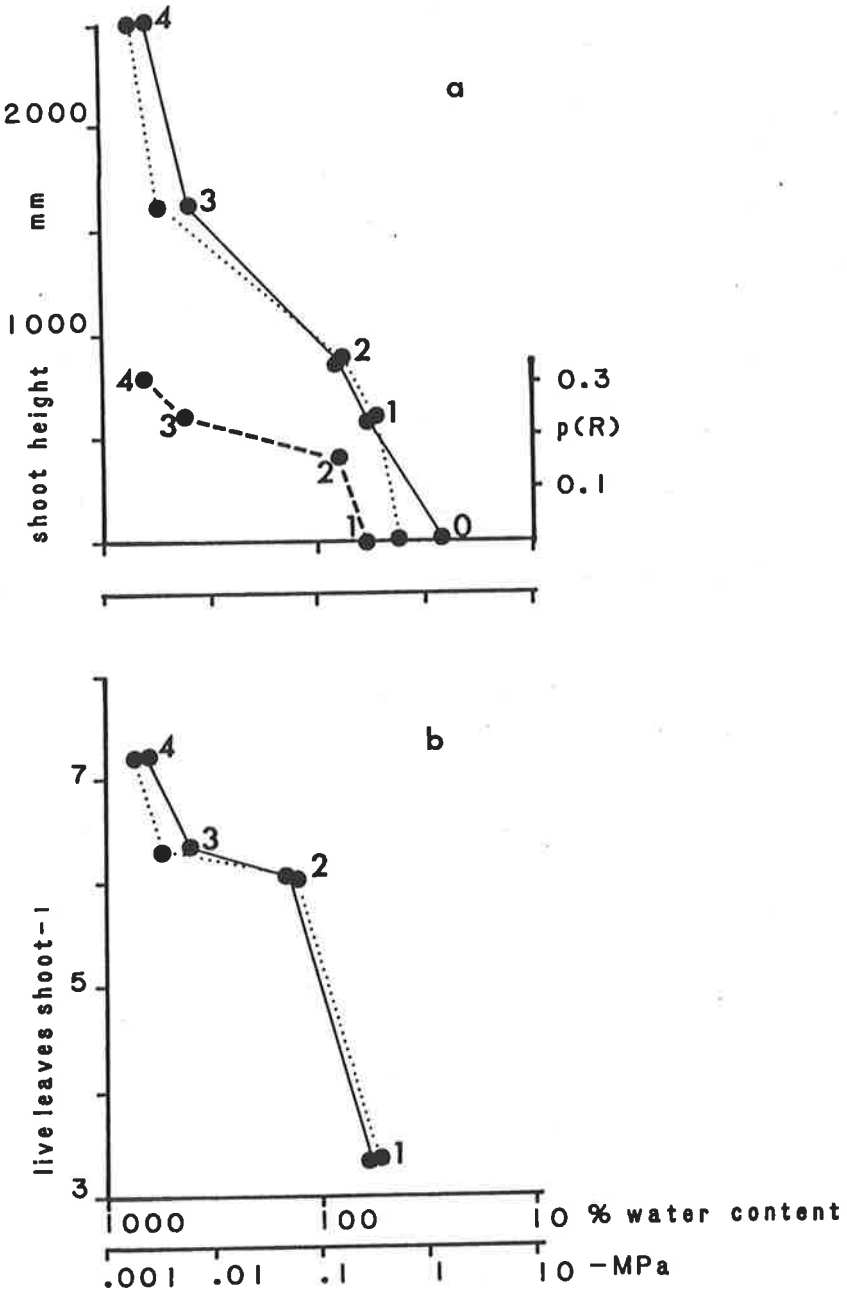

Figure 4.9
Gradient study: growth v water availability

Growth of T. domingensis in relation to water availability in 0-10 cm layer of Zones 0-4. Indices of plant growth were mean shoot height in mm, the proportion of live shoots that flowered p(R) and mean number of live leaves per shoot. Water availability is percentage water content and matric potential, plotted logarithmically but at different scales.

(a) Shoot growth
(b) Leaf growth
●--● p(R)
●—● Water content, as % of dry soil
●···● Water potential, as MPa

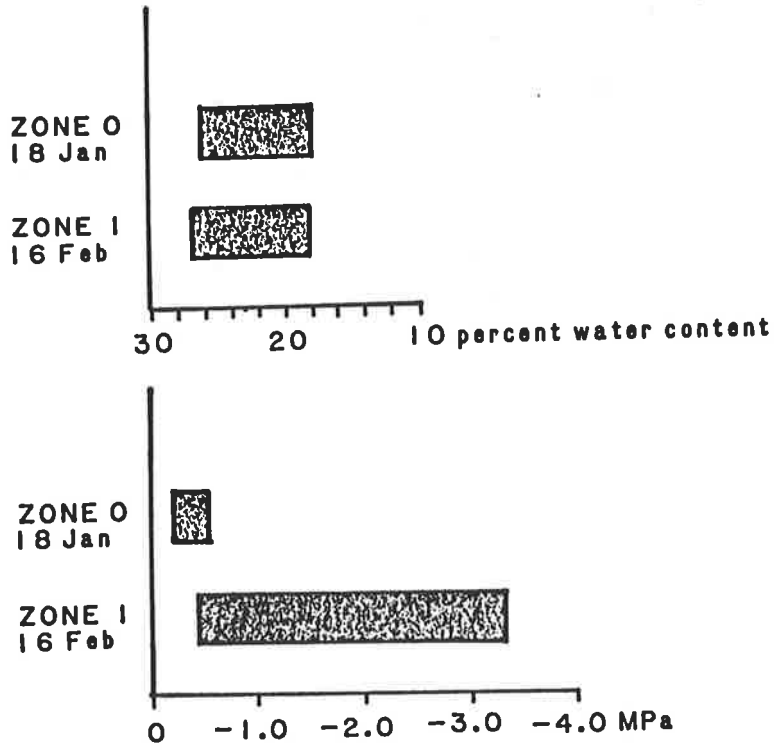

Figure 4.10
Water availability in Zones 0 and 1

Range of water availability (n = 6) in surface soils (0-10 cm) in Zones 0 and 1 on 18 January and 16 February 1983 respectively.

(a) Water content as % dry soil
(b) Matric potential as -MPa

Chapter Five

WATER AND GROWTH

INTRODUCTION

5.1 Study aims

The gradient study showed that Typha domingensis shoots reached heights of 2 m and flowered only in areas where soil water was close to Field Capacity. The equilibrium resource level was probably above -0.13 MPa which was higher than most terrestrial plants and at least one flood-plain species (4.8).

In mesophytes mechanisms of adaptation to water deficit can conveniently be described as escape, tolerance of low water status or tolerance of dry conditions by maintaining high water status (Turner 1986). The first includes timing life cycle to avoid dry conditions and rapid "opportunistic" growth. (This is not relevant to understanding R* in T. domingensis so is not considered further.) The second includes osmotic regulation and resilience of cells and membranes to degradation and denaturation. The third includes reducing water loss and maintaining or increasing water uptake. The second represents rather extreme adaptations whereas the third describes baseline adaptations for maintaining a positive water balance on land and are found in most mesophyte species. Attention is focussed on this third category as Typha appears to have a R* higher than most mesophytes.

The first aim was to confirm the gradient study by measuring growth in controlled water conditions, unaffected by connectedness. The second aim was to interpret growth in terms of factors affecting plant water balance, namely uptake and transpiration.

5.2 Uptake, transpiration and *Typha*

Plant characteristics which determine water uptake are root architecture, the proportion of the root surface effective in uptake, and hydraulic resistance. Root architecture refers to length, surface area, degree of branching and volume of soil occupied.

Plant characteristics which determine transpiration are leaf size, shape, orientation and surface characteristics, such as hairs and waxiness. These increase the thickness of the boundary layer and reduce leaf heat load. Most important are stomates which directly regulate leaf resistance to water vapour by opening and closing.

Stomates affect leaf resistance to water vapour, not just because of their opening-closing actions, but because they vary in pore depth and diameter, density and distribution. Deep or sunken pores increase diffusion distance thereby increasing resistance (Nobel 1974). Leaf conductance tends to increase with increasing number of stomates and significant positive correlations between conductance and density have been found (e.g. Reich 1984). This is equivalent to correlating conductance with the proportion of leaf area occupied by open stomates, known as pore area. Stomatal density affects transpiration because diffusion from a leaf surface is higher for a given surface area with many-small stomates than few-large (Ceulemans *et al.* 1978). Stomatal distribution is important because an amphistomatous leaf, i.e. one with stomates on both surfaces, should have a higher transpiration rate per leaf than a similar leaf with stomates on only one surface, epistomatous or hypostomatous. Amphistomaty does not correlate well with water availability but is advantageous to plants of open, full sun environments with high photosynthetic capacity (Mott *et al.* 1982).

Water uptake can be increased either by continuous root growth "in search of water" (Larcher 1980) or by osmotic adjustment (Turner 1986),

thus more of the soil water present becomes available. A set water supply will last longer if the transpiring surface is reduced by leaf rolling, abscission or death, or if water loss is reduced by stomatal closure. This is discussed below (5.3). High Root:Shoot ratios are not always indicative of drought tolerance or characteristic of desert vegetation, possibly because woody material is included (Cowan 1981), but ratio changes can be informative of a species response. Root:Canopy ratio is more appropriate for understanding plant responses to water deficit as this directly reflects the absorbing and transpiring surfaces. The Root:Canopy ratio for a mature mallee in semi-arid western New South Wales is 4.3 (Cowan 1981) whereas for experimentally grown Typha seedlings and mature field populations, it was less than one for most of the year (Table 5.1).

Although the root system of Typha is bulky and extensive (Weaver and Himmel 1930, Dean 1933), it is shallow (Table 4.1) so the plant is dependent on surface and shallow soil water. It is not known whether the plant can osmoregulate. The minimum root water potential for water plants, thought to be -1.0 MPa (Larcher 1980), would suggest not. Minimum root potential for crop plants is -1.0 to -2.0 MPa, and at least -6.0 MPa for xerophytes. Typha leaves do not have bulliform cells so do not roll, neither do they wilt like herbaceous Dicots (pers. obs.). Thus their only mechanisms for increasing uptake or making it more effective are root growth and canopy reduction.

The leaves and stems of emergents are sometimes said to have a xeromorphic nature (Jones and Muthuri 1984). However the function is not water conservation but preventing entry of unoxidised iron which is believed to occur when transpiration rates are high. Describing the leaves of emergents as xeromorphic ignores surface features of xerophytes and hydrophytes. For example, unlike xerophytes, leaves of Typha are

large, with an acute-to-vertical leaf orientation which is very effective in energy interception (Jones 1983). The leaves of emergents are glossy and lack surface features such as hairs which increase surface roughness and boundary layer resistance.

Stomatal responses of freshwater emergents have been little documented. There is a possibility they are not sensitive to water deficit as in some aquatics the stomates apparently do not respond to abscissic acid (ABA) the drought messenger (Dorffling et al. 1977) and in others droughting promotes very little increase in ABA (Milborrow 1981). On the other hand species such as Cyperus papyrus may be very sensitive. A decrease in conductance when ray water potential fell below -0.5 MPa was interpreted as a feed-forward response to vapour pressure deficit rather than a feed-back response to tissue water potential (Jones and Muthuri 1984). The response of Typha is unknown. Conductance measurements show that stomates of T. latifolia do not close completely at night (Sale and Wetzel 1983) which could explain its significant nocturnal transpiration (Otis 1914).

The transpiration capacity of leaves is highest in swamp and floating-leafed plants (Larcher 1980). Maximum transpiration rates for hydrophytes in their natural habitat are 180-400 $\mu g\ mm^{-2}\ h^{-1}$, references not cited (Larcher 1980) which is not much higher than for herbaceous dicotyledons in sunny habitats, 170-250 $\mu g\ mm^{-2}\ h^{-1}$. High transpiration rates for emergents may be a habitat rather than a plant factor. Unlimited water supply means leaves of wetland plants are less likely to suffer loss of turgor than are mesophyte leaves, so transpiration is unlikely to be restricted by stomatal closure. Well-watered emergents in warm-hot environments of Death Valley, California and western New South Wales show no evidence of reduced conductance or transpiration (Pearcy et al. 1974, Sale and Orr 1986). The

transpiration rate of well-watered mesophytes equals and exceeds emergents (Table 5.2).

In free-floating and floating-leaved aquatic plants, stomates are confined to the upper surface, i.e. epistomatous (Kaul 1976, Willmer 1983). Leaves of emergents are thought to be amphistomatous to some degree (Mott et al. 1982). Monographs on Monocots (e.g. Dahlgren and Clifford 1982) classify stomates by arrangement of guard and subsidiary cells and do not consider size, frequency or inter-leaf distribution. The stomates of T. latifolia have been described as "abundant on both sides of the leaves" (Otis 1914).

5.3 Transpiration and growth

Transpiration is connected to growth, not just because water is essential for metabolic processes, but because water loss and carbon gain have the same leaf-air pathway. Thus maximum conductance and photosynthetic capacity are linearly correlated amongst plants with the same biochemical pathway (Cowan 1981). There is debate as to the importance of stomatal regulation to growth but at the whole plant level there is no doubt that reducing leaf water loss whether by stomatal regulation or leaf loss has a cost in terms of reduced growth and production (Turner 1986).

The relationship between plant growth and transpiration is described in two reciprocally related ways. The transpiration coefficient k is the quantity of water transpired ("used": Kramer 1983) per unit plant growth usually dry weight. It varies between species, particularly between different photosynthetic systems. Typical values are 50-100 for CAM plants, 220-350 for C4 plants and 500-800 for herbaceous C3 plants (Larcher 1980). Water use efficiency WUE is the quantity of dry matter produced per unit water transpired. This can be measured at different

temporal and spatial scales such as the canopy of whole plants and stands over weeks and seasons versus gas exchange over hours and days. Larcher (1980) suggests "water use efficiency of productivity" (g dry matter l^{-1} H_2O) for the former and "water use efficiency of photosynthesis" (mg CO_2 g H_2O) for the latter. In practice, transpiration coefficients tend to be used to measure water-growth relationships at a coarser scale and WUE at a finer scale.

Conductance and assimilation are higher for swamp than other C3 communities (Cowan 1981). Because they have unlimited water, emergents might be expected to have high k values and low WUE, but the evidence shows the opposite. A two year study in Poland found that k = 275-565 for T. angustifolia and T. latifolia (Bernatowicz et al. 1976). In Griffith, Australia, T. orientalis had a WUE of 7.86-6.42 which was similar to glasshouse tomatoes (Sale and Orr 1986) and higher than sorghum (Ritchie 1974). No explanation for these conservative values was given but it seems probable they are a consequence of transpirational cooling making photosynthesis more efficient.

To many physiologists, transpiration is the cost or unavoidable curse of CO_2 fixation with no physiological benefits (e.g. Milburn 1979, Kramer 1983). Leaves in full sun rarely suffer thermal injury as a result of stomatal closure (Kramer 1983) and the possibility that plants might benefit from transpiration by cooling is hardly mentioned. However if the emphasis is shifted from survival to growth it becomes apparent that high transpiration in warm to hot environments can benefit emergents by increasing net photosynthesis. The thermal optima for net photosynthesis is not high for emergents being 30°C and 15-25°C respectively for P. australis and T. orientalis (Pearcy et al. 1976, Sale and Orr 1986). In Death Valley, California, the midday leaf temperature of P. australis was 36.8°C which was 5.7°C below air temperature whereas adjacent desert

shrubs had leaf temperatures within -0.9 and +1.4°C of air temperature (Pearcy et al. 1976).

5.4 Study approach

The most accurate method for determining the relationship between growth and water loss is to measure net carbon assimilation and water vapour loss using gas exchange techniques. These can be applied to plant communities in situ (e.g. Sale and Orr 1986) but are rarely used for extended periods. Such techniques were not available and a simpler approach, lysimetry, was used. This has the advantages of not requiring specialist equipment and being suitable for long-term experiments. Although conceptually simple, rates obtained by lysimetry cannot be extrapolated to canopies of natural stands because canopy micro-climate of isolated plants or lysimeters is influenced by advection effects and not representative of large natural stands. This is also true for small stands of plants, such as a farm dam in a paddock (Linacre 1976) and is not just a scaling effect. No attempt was made to overcome micro-climate differences between lysimeters and natural stands as the aim was to compare treatments rather than predict transpiration of natural stands.

In droughting experiments, water availability in pots is maintained at constant level by daily replacement of evapotranspiration losses. In this experiment lysimeters were sealed so the only water loss was transpiration. Substrate water potential was controlled by filling lysimeters with polyethylene glycol, henceforward referred to as PEG. Solutions of PEG are frequently used to control water potential in growth studies. Its use is somewhat controversial (6.3), with claims that it is taken up by plants and that the oxygen content is abnormally low. The problem of uptake can be overcome by using polymers with a molecular weight greater than 6000 and ensuring no roots are damaged. Low oxygen in

the rhizosphere is unlikely to be a problem for emergents as in wetlands the substrate is normally anaerobic.

The relationship between growth and transpiration and the effect of different treatments were compared by the transpiration coefficient, k. Usually this is calculated with growth as dry weight of live material present in the canopy. In this study leaf surface area was also used produced because indirect estimates of dry weight were not successful. Transpiration ratios were calculated for net and total production. Absorption and transpiration capacity were not specifically measured but approximated by dry weight, surface area and leaf characteristics (see below) and their inter-relationship expressed by a Root:Canopy ratio.

Some background studies were done on Typha stomates. Diurnal changes in stomatal conductance were measured in the field to establish whether stomates of well-watered Typha closed during the day. Stomatal size and density were measured, and distribution between leaves and surfaces compared to establish the potential for transpiration. Stomatal behaviour in relation to leaf water potential was not studied because the problem of using soft-tissued aerenchymatous leaves in a pressure bomb was not overcome.

METHODS

5.5 Methods for PEG study

Vegetative T. domingensis was collected from Strathmont on 21 November 1983. The plant was not yet in flower but new rhizomes were developing. All mud was washed away, and plants trimmed to single ramets. The shoot was trimmed to a datum line marked by masking tape (Figure 5.1). Pre-existing roots, unavoidably damaged by digging, were removed. To

force new root growth and to test for viability, ramets were grown for one week in nutrient solutions. Previous experience had shown not all ramets re-grow after cutting and immersion. Ramets were size matched between treatments by visual estimate of crown diameter and rhizome. This trimming, growing and matching procedure resulted in 3 sizes, small, medium and large referred to as S M and L. There were three treatments, Control, High and Low (see below). By the beginning of the experiment, two ramets had developed daughter ramets and one was about to, therefore these were not ramets in the strict sense of being one module. For this reason plant material in this experiment is referred to as a clone regardless of whether it had one ramet or two.

For the experiment, clones were sealed into plastic bags which could be opened and re-sealed to change solutions and accomodate new lateral shoots as necessary. These plastic bags were lysimeters. Each lysimeter had a sealed tube for daily re-filling (Figure 5.1). Industrial weight aluminium foil was wrapped around each lysimeter as insulation. Hoagland's nutrient solution (Appendix 6) and PEG were mixed to give 1/4 strength nutrient concentration and water potentials of 0, -0.1 MPa and -0.65 MPa for Control, High and Low treatments respectively. These levels were chosen to represent that part of the Strathmont transect where growth was apparently independent of decreasing surface matric potential (Figure 4.3 b). The water potential of PEG 20,000 solutions was estimated from its concentration using a regression model (Appendix 7). Fresh solutions were given on Day 9 and Day 20. Clones were grown outside but received direct sunlight only in the afternoon. The experiment was done over 30 days in midsummer from 14 December (Day 0) to 13 January 1984 (Day 30).

Experimental procedure

Lysimeters were watered to weight in the morning at the same time and additional water given on hot days. After Day 6 lysimeters were re-watered daily. Bags were palpated to mix water with solution already present. Length from datum line to tip of all green leaves was measured every 3-4 days. Clone fresh weight was measured on Days 0 and 30 as well as when solutions were changed on Days 9 and 20. At the end of the experiment, clones were harvested for dry weight, water content and leaf weight v area calibration. Initial and final water potential of PEG solutions was read on a Wescor 5100B vapour pressure osmometer (Wescor Inc., USA). On Day 28, the diurnal course of water loss and changes in transpiration rate were followed by weighing at approximately 60 minute intervals from 0945 to 1930 hours, Central Standard Time.

Data organisation

Growth indices were the change in clone fresh weight and green leaf area, and mean relative growth rate. Leaf area was estimated from leaf length (see below). Leaf recruitment and mortality were the numbers of leaves recruited or dying $clone^{-1} \times 10^2\ day^{-1}$. Mean relative growth rate of the canopy in $mm^{-2}\ mm^{-2}\ d^{-1}$ was the regression coefficient of a linear regression of $\log_{10}$ clone surface area (all leaves, both surfaces) in mm^{-2} v time in days. Although relative growth rate usually refers to dry weight it can be used in a wider sense (Hunt 1982). Final harvest was dried for 3 days at 75°C to give dry weight and percentage water content of rhizomes, roots and leaves, calculated as (Fresh-Dry)/(Fresh) x 100. The Root:Canopy ratio was the ratio of dry weight in g of live material.

Leaf surface area was calculated from calibration curve of leaf length v leaf area, based on green leaves from final harvest (n = 37). These

were photocopied and length and area measured using a HI-PAD digitiser (Houston Instruments, supplied by Applied Data Control Pty. Ltd.) and program DIGIT3 (Patrick Hone, Botany Department, University of Adelaide). Measurements were corrected for operator error using a correction factor of 1.0376 estimated from measurements of known areas. Area measurements were doubled to give both adaxial and abaxial surfaces.

The quantity of water lost from one clone in 24 hours was daily water loss as g H_2O $clone^{-1}$ d^{-1}. From this was calculated a mean daily transpiration rate, expressed as μg H_2O mm^{-2} d^{-1}, using interpolated clone leaf area. This was the sum of two surfaces and thus assumed adaxial and abaxial surfaces transpired equally,. Transpiration rate during the diurnal on Day 28 was an hourly rate, μg H_2O mm^{-2} h^{-1}. The transpiration ratio was the quantity in g of water transpired in 30 days divided by the quantity of leaf material produced, first as dry weight in g and then as leaf area (two sides) in mm^{-2}.

The effect of environmental conditions on transpiration was shown by plotting mean daily transpiration rate as the dependent variable and daily evaporation as the independent variable. The rationale for this was that instantaneous transpiration flux E is the product of leaf vapour pressure deficit or lvpd and stomatal conductance or g, normally expressed as E = lvpd x g. This can be re-expressed as g = E/lvpd. Thus the regression coefficient gives a mean daily stomatal response. Data used for this excludes dates on which solutions were changed and data from Days 1-6 when lysimeters were read every 1-2 days. Records of daily evaporation in mm from a Class A pan with birdguard were obtained from the Adelaide Regional Office of the Meteorological Bureau. The same environmental factors affect evaporation from a free water surface as from a leaf surface therefore daily evaporation was a reasonable integration of vapour pressure deficit.

Data analysis

Regressions were tested for significance and regression coefficients were compared following Sokal and Rohlf (1981) with alpha set to 0.05. Analysis of variance was used to compare water content of Low treatment rhizomes and roots with Control and High treatments (pooled) and Cochrane's test was used for homogeneity of variances.

5.6 Methods for stomatal studies

Strathmont diurnal

Diurnal resistance of T. domingensis at the Strathmont field site was measured from before sunrise to after sunset on 7 March 1984 using an automatic diffusion porometer, Delta-T Mark 3 (Delta-T Devices, Cambridge, England). Resistances were measured on the adaxial surface, 10 cm from tip. Sample comprised the youngest and oldest green leaf on eleven shoots, total 22 leaves. Shoots were well-established vigorous shoots at least 1900 mm tall in the centre of the creek at Strathmont, with no indication of senescence (Figure 4.1). The leaf tip was used as it is the flattest part of a Typha leaf and fitted the porometer cup better than the almost triangular lower portions. A count:resistance calibration was done before each run using the calibration plate supplied by manufacturers. Resistance was converted to conductance g, as cm^{-1} s^{-1}. Environmental measurements made during the day were irradiance measured with a Li-Cor quantum meter and sensor (Lambda Instrument Company, Nebraska, USA) held horizontally, and temperature and relative humidity using the porometer. Run time to calibrate porometer, take readings and environmental measurements was 30-45 minutes.

Stomatal measurements

Stomatal impressions were made by painting clear nail polish onto Typha leaves. When set the impression was removed by pressing clear

sellotape on top and peeling tape and varnish off together. This was mounted on a glass slide and viewed directly under the microscope. Sellotape provided a firm backing which prevented the nail varnish from distorting.

Impressions were made of adaxial and abaxial surfaces, 15 cm from the tip. The sample was nine green leaves from one vegetative shoot 2 m tall in St. Peter's River Park, Adelaide. The two youngest leaves were shorter than the third youngest so were presumably not fully extended. Camera lucida drawings were made of ten open stomates, randomly selected from each surface. Stomatal index was the total number of stomates as a percentage of all epidermal cells (Willmer 1983) in a field of view 140 x 140 μm, replicated 7 times. A stomate was the stomatal complex of pore and guard cells. Stomatal density was the number of stomates mm^{-2}.

Stomatal dimensions were measured on camera lucida drawings using Vernier calipers. Dimensions were external and internal length along the line of maximum length, and maximum external and internal width at right angles to length line. Stomatal pore area was calculated assuming an ellipse as internal length x internal width x 0.785 (Rawson and Craven 1975). Leaf pore area was stomatal density x pore area and expressed as a percentage of leaf surface. All measurements were made in the intercostal area which occupies 65% of leaf surface and final estimates of density and pore area are corrected for this.

Data analysis

Differences in stomatal index and density between leaf surfaces and leaves of different ages were tested by two-way analysis of variance (FACTAN) and variances were tested for homogeneity using Cochrane's test.

5.7 Results: PEG study

Weather

There was a cool period in the middle of the study when daily evaporation was less than 6 mm, Days 16, 17, 18, 19 and 20. Days of highest evaporation were Days 5, 6, 14 and 30 when evaporation exceeded 10 mm (Figure 5.2). Evaporation for the 24 hour period of the diurnal on Day 28 was 9.2 mm.

Water potentials in lysimeters remained close to treatment despite transpirational loss. Calculations of changes in PEG concentrations showed that the water potential in High treatment lysimeters before re-watering was within the range -0.0067 to -0.0108 MPa except on Days 5 and 30 for High (S) clone when they fell to -0.0151 MPa and -0.0127 MPa. In Low treatment lysimeters, minimum water potential was never lower than -0.7025 MPa except on Day 5 when it fell to -0.8320 MPa and Days 21 and 22 when Low (L) fell to -0.7996 and -0.7625 MPa. Osmometer readings confirmed PEG concentrations were fairly consistent (not shown). For example the osmolality of Low treatment solutions ranged from 259-264 mOsm for initials to 234-274 mOsm for final solutions. Low values for Day 5 were partly due to transpiration losses in dry conditions (Figure 5.2) and partly due to the fact that ramets were not re-watered on Day 4.

Calibrations

Leaf area (sum of two sides) in mm^{-2} and leaf length in mm were linearly related (Figure 5.3 a). The regression was significant (alpha <0.001) and passed close to the origin. Leaf area and dry weight were also linearly related (Figure 5.3 b) but although the regression was significant (alpha <0.001) with a high coefficient of determination (r^2 = 0.9497), it did not pass through the origin. The intercept on the x-axis was equivalent to 16,980 mm^{-2} which meant leaf areas less than this had negative weight. This affected transpiration ratios based on

weight (see below).

Plant growth

During pre-conditioning, the trimmed shoot died back in most Control and High clones and a daughter ramet developed either during the experiment or during the pre-conditioning period. M sized clones in Control and High treatments died during the experiment which meant these treatments had only two replicates. Shoots were shorter than field populations. At the end of the experiment the height range for each treatment was 608-915 mm for Control, 664-690 mm for High and 495-656 mm for Low (not shown).

Leaf area of Control and High treatment clones steadily increased during the study (Figure 5.4) and final leaf area was 2.62 and 1.89 times initial (not shown). In the Low treatment, leaf area increased then decreased thus final leaf area was only 1.07 times the initial. This includes Low (S) clone which had a net decrease. The three Low treatment clones had synchronous reponses with decreases on Days 2-6 and 23-27, and maximum area on Days 20-23.

Total leaf area produced was highest in Control treatment but individuals in Control and High treatments were very similar (Table 5.3). Canopy turnover as indicated by the ratio of Total:Net leaf area production was lowest in Control treatment and highest in Low treatment, 1.14 and 3.70. Large differences between treatments in initial leaf area (Figure 5.4) were canopy re-growth during pre-conditioning rather than differences in clone size.

Initial fresh weights (not shown) of M clones which died were lower than surviving clones, 30-38 g compared to 57-127 g suggesting capacity to re-grow was linked to size. Between Day 0 and Day 30 fresh weight of Control clones increased by 7-29 g whereas Low clones decreased by 9-26

g. In the High treatment, one clone increased by 14 g and one decreased by 8 g.

Mean relative growth rate based on leaf area in Control and High treatments was similar, 0.0149 and 0.0166 mm^{-2} mm^{-2} d^{-1} but was 7-8 times lower in the Low treatment, 0.0022 mm^{-2} mm^{-2} d^{-1} (Table 5.4). The high growth rate of the High (L) clone was probably the result of shoot opening. The coefficient of regression of log_{10} leaf area v time for Low (S) and Low (M) clones was not significantly different from zero showing these clones had no net growth over 30 days.

The total dry weight of roots and leaves, the proportion of this alive p(Live) and the percentage water content of live material is shown in Table 5.5. Roots of Low treatment clones had the highest total standing crop but the lowest proportion alive and the lowest water content. The same trends were evident in leaf standing crop and p(Live) but were not so clear for water content. An inappropriate weighing technique, paper bags, was used for 6 out 7 samples. These took up moisture from the air whereas the glass vials used for other samples did not. Root and rhizome water content was significantly lower in Low treatment clones than in Control and High clones. Mean Root:Canopy ratios increased from 0.08 to 0.19 with decreasing water potential (Table 5.5) and were lower than field and cultured populations (Table 5.1).

There was a net increase of 3-7 leaves $clone^{-1}$ in Control and High treatments but a decrease of 1-2 leaves for Low clones (Table 5.6). Mean recruitment rate was 16.67-36.67 leaves $clone^{-1}$ in Control and High treatments which was 6-8 times higher than in Low treatment, 3.33-6.67. Leaf mortality rates showed an odd distribution being highest for Control and lowest for High treatments. Leaf deaths in Low treatment occurred between Days 2-6 and 23-27, coincident with times when canopy area was reduced and below average water potentials. In other treatments, leaf

deaths had only a slight effect on canopy size and only in the early part of the study. Thus in the Control treatment, leaf deaths between Days 0-2 and 2-6 resulted in a decrease in leaf area whereas deaths on Days 9-13, 17-20 and 20-23 had no obvious effect (Figure 5.4).

Water use

During the diurnal on Day 28-29, hourly transpiration rates for Control and High treatment clones increased rapidly after midday reaching maximum of 214-366 $\mu g\ mm^{-2}\ h^{-1}$ between 1330-1430 hours, then decreased during the afternoon (Figure 5.5). There was no obvious stomatal closure during the middle of the day in Control and High treatments. In Low (S) and Low (M) clones, the highest transpiration rates of 19 and 49 $\mu g\ mm^{-2}\ h^{-1}$ were reached earlier at 1230-1330 hours and 1145-1230 hours respectively. The response of the Low (L) clone was different. Between 0945 and 1330 hours, transpiration increased in the same way as for Control and High clones although at a lower rate, reaching a maximum of 144 $\mu g\ mm^{-2}\ h^{-1}$ at 1230-1330 hours. It then decreased sharply indicating stomatal action (Figure 5.5).

The quantity of water transpired over 30 days decreased with decreasing water potential and ranged from 3194.1 g for Control (L) to 171.3 g for Low (S) (Table 5.7). Daily water loss ranged from 323.5-3.34 g H_2O $clone^{-1}\ d^{-1}$ from live clones compared to 0.13-2.31 g for the two dead M clones. Daily transpiration rates showed the same pattern ranging from 2547 $\mu g\ H_2O\ mm^{-2}\ d^{-1}$ for Control (L) clone on Day 29-30 to 95 $\mu g\ H_2O\ mm^{-2}\ d^{-1}$ for Low (L) clone on Day 23-24.

Transpiration ratios based on weight were only calculated for Control and High clones. The indirect method gave a negative weight for Low clones, and therefore a negative estimate of net and total production. Transpiration ratios for net Production ranged from 638-2091 and were

therefore much higher than Typha in Poland (5.3). Ratios for net production were higher than for total. Transpiration ratios based on area and net production were similar in Control and High clones but higher in Low treatment clones. Mean ratios for total area produced were similar in all three treatments (Table 5.7).

Transpiration increased linearly with increasing evaporation. Only one clone, High (S), is given as an example (Figure 5.6 a). Mean daily stomatal response, as shown by the regression coefficients (5.5), showed a 3-fold and significant increase from Low (S) to High (S) clones, from 72.7960 to 208.4294 (Table 5.8). Regression coefficients were not significant for two clones, Low (M) and Low (L). A scattergram of transpiration v evaporation for Low (L) revealed two trends, transpiration increasing as evaporation increased and transpiration constant, which corresponded to different time periods, Days 6-21 and Days 22-30 (Figure 5.6 b).

Because of this, transpiration v evaporation data for these time periods were analysed separately. In Control and High treatments, regressions were significant for both time periods (not shown). There was a tendency for regression coefficients for the second time period, Days 22-30, to be higher but the difference was not significant. This was not so for Low treatment clones (Table 5.9). Regression coefficients for S, M and L clones were similar for the first time period, range 60.6-73.6. During the second time period, Days 22-30, all regression coefficients were lower, and coefficients for M and L clones were not significantly different from zero.

5.8 Results: Stomatal studies

Strathmont diurnal

Weather on 7 March was sunny and still except for a small cloud patch

which shaded the sun for 10 minutes in mid-morning and evening breezes from 1700 hours. Irradiance increased sharply after sunrise and reached its maximum of 1800 $\mu E\ m^{-2}\ s^{-1}$ just before midday. During the first set of readings at 0555 hours irradiance increased from 0.5 to 80 $\mu E\ m^{-2}\ s^{-1}$, and during the last run at 1855 hours it decreased from 14 to 0.2 $\mu E\ m^{-2}\ s^{-1}$. Sunlight reached leaf tips at 0630 hours between first and second runs. Temperature at the beginning of the first run was 18.7°C, reached a maximum of 32.0°C at 1445 hours and at the end of the last run was 16.0°C. Relative humidity decreased from 57% at 0545 hours and was lowest after midday, 22-27%.

The leaf population did not have a uniform response. Three responses were recognised based on the number of peaks evident in a plot of diurnal conductance, one, two-plus and none. In responses with one and two-plus peaks, stomates were closed at dawn and rapidly opened as irradiance increased. In no-peak response stomates were already partly open at dawn and did not open much wider during the day (Figure 5.7). The number of leaves in each response type was 5, 10 and 6 respectively thus the majority of leaves (15 out of 21) had one or two-plus conductance peaks. All leaves with no-peak response were old, 6/6. In contrast, leaves with one and two-plus peaks were pre-dominantly young, 4/5 and 6/10 respectively. Thus these responses correspond to an age gradient.

Stomatal measurements

Stomatal indices for adaxial and abaxial surfaces were similar, 11.06-15.64 and 9.53-14.99 respectively. The three oldest and two youngest leaves had lowest indices. Stomatal density was the same on adaxial and abaxial surfaces, mean = 296 and 299 stomates mm^{-2}, V* = 0.1620 and 0.1886. This was similar to another shoot from the same site, 273 stomates mm^{-2}. Within the intercostal area stomatal density was 456

and 460 stomates mm^{-2}. Mean external stomatal length on adaxial and abaxial surfaces was 21.08 and 21.45 μm and mean internal width was 5.24 μm on both surfaces. Open pore area was similar on both surfaces, 61.9 and 59.6 μm^{-2} giving a leaf pore area of 1.85 and 1.77% including costal region.

DISCUSSION

5.9 Interpretation of results

Analysis and interpretation was limited by the small number of replicates and treatments. Results for Control clones were consistent (Tables 5.4 and 5.7) whereas results for High clones were variable. This was probably due to the different phenology of High (L) clone which had no functional canopy at the beginning of the experiment (Figure 5.4) but later produced two daughter ramets. Low replication meant the role of clone size as S M or L could not be statistically confirmed.

Ramet number was important in demographic data. Variations in leaf recruitment rates amongst Control and High treatment clones (Table 5.6) virtually disappear if expressed per ramet rather than per clone. The highest recruitment rates, 33.33-36.67 leaves $clone^{-1} \times 10^2\ d^{-1}$, were for clones with two functional ramets, such as parent and daughter or two daughters. This is equivalent to a recruitment rate of 16.67-18.33 leaves $ramet^{-1}\ d^{-1}$ which is similar to High (S) clone with only one ramet (Table 5.6). Ramet numbers also explained variations amongst Low treatment clones (Table 5.6). The Low (L) clone had two ramets, thus recruitment rate for all Low clones was 3.33 leaves $ramet^{-1}\ d^{-1}$, five times slower than in Control and High treatment.

Leaf mortality per clone was also affected by ramet number. On newly

opened shoots the outermost leaves are rapidly deciduous after the shoot opens and thus make an important contribution to the number of dead leaves. Clones affected in this way were Control (S), Control (L), and High (L). In Low (L) the daughter ramet was recruited on Day 30, too late to contribute to mortality rates. Mortality in Control (L) which had two daughter ramets was further boosted by complete die back of the original shoot. In comparison, leaf mortality in Low treatment was for one ramet only yet was marginally higher than in Control and High treatments.

There was no evidence to suggest that the observed effects were due to PEG toxicity. Reports of PEG entering plants are typically associated with small PEG polymers or damaged root systems. When PEG uptake does occur it has a dramatic response. Azolla spp. became necrotic and died within 24 hours of exposure to PEG 1000 (Zimmerman 1985). In Solanaceous plants and kidney beans, PEG appears on the leaf surface and petioles as a "white efflorescence" (Lagerwerff et al. 1961, Yaniv and Werker 1983). Leaves of Typha were not analysed for PEG content because care was taken to initiate new roots before exposing the plant to PEG and to use a large polymer, PEG 20,000. There was no evidence of white secretions.

Transpiration v evaporation plots showed a marked change in stomatal response in Low (M) and Low (L) clones from Day 22 onwards (Figure 5.7 and Table 5.9), just after solutions were changed on Day 20. However the fresh solution was probably not the reason for the aberrant behaviour of Low (M) and (L) clones because all Low clones were given solutions made from the same PEG and nutrient stock. On the other hand, all Low clones had similar and synchronised leaf responses over Days 20-23, 23-27 and 27-30 with a sequence of no growth, mortality then growth which looked very like shock and recovery (Figure 5.4). The osmolality of solutions used for Days 9-20 and Days 20-30 was similar.

An explanation for these inconsistencies is that in the days preceding

Day 20 transpiration exceeded absorption in Low clones and that the two largest failed to rehydrate adequately. Calculations of changes in PEG due to transpiration losses showed the water potential of PEG on Days 20-21 and 21-22 was 0.06-0.09 MPa lower in the Low (L) clone than on other days even though these were not as dry as Days 5-8 (Figure 5.2). The different effect of Days 5-8 compared to Days 20-22 can be explained by canopy size. By Days 20-23, leaf area in Low treatment clones was 40-50% higher than on Day 6 (Figure 5.4) which would have greatly increased transpiration clone^{-1}. The Low (S) clone was not so affected because of its lower leaf area.

5.10 Transpiration in T. domingensis

Comparison with published values shows that stomates of T. domingensis with a density of 296-299 stomates mm^{-2} and measuring 21 µm long and 5.25 µm wide, are denser and smaller than equivalent plant groups. Published values for terrestrial Monocots, mainly crop species, range from 26-175 stomates mm^{-2} (Milburn 1979, Jones 1983, Willmer 1983). In free-floating and floating-leafed aquatics, stomatal density ranges from 70-170 mm^{-2} (Kaul 1976). In the emergent Sparganium spp., the other genus in Typhales, it is 110-250 mm^{-2} (Kaul 1976) and in Carex aquatilis it is only 48.5 mm^{-2} (Standley 1986).

Stomatal measurements are reported even less frequently than density. Typical lengths for Monocots, mainly crop species, given in monographs are 24-70 µm long (Willmer 1983) with 6 µm accepted as standard width (Milburn 1979, Willmer 1983). The pore area of T. domingensis, 1.85-1.77%, was not exceptionally high but is at the top of the reported range, 2.0-2.1%, if re-calculated using the standard width of 6 µm 2.0-2.1% (Milburn 1979, Wilmer 1983).

This combination of stomatal characteristics is significant when

considering transpiration. Many-small is the combination giving less resistance to water vapour for a given pore area. In T. domingensis this pore area is relatively large and occurs equally on both sides of the leaf. These characteristics add up to a leaf with low resistance to water vapour and a high transpiration potential. In addition the leaf lacks surface roughness and stomatal depth is shallow, only 10 µm deep, not sunken and with only a slight lip (pers. obs.).

It is not known if all emergents have these characteristics. Juncus roemerianus, a saltmarsh species, is partly similar in that stomates are not recessed and leaves have no surface roughness but differs in that the sub-stomatal cavity is lined with protective cells (Eleuterius 1976). Stomatal density of Carex aquatilis is much lower but unfortunately sizes were not reported (Standley 1986). The plant is highly variable, with amphistomatous and epistomatous populations with adaxial:abaxial ratios ranging from 0.5 to 44.0. These differences have not been correlated with habitat differences. The habitat of Carex aquatilis is freshwater marshes but the plant is described as "Although generally terrestrial, plants may also be emergent" (Standley 1986).

The stomates of T. domingensis had a typical mesophyte response for hot sunny weather, with rapid opening at dawn and partial to complete closure during the day (Figure 5.7). Thus even in a well-watered environment, individual leaves apparently have a water deficit. Without further experimentation it is impossible to determine whether this was an uptake problem or stomatal sensitivity such as the feed-forward response of Cyperus papyrus (Jones and Muthuri 1984). However when transpiration rates are high, water supply may become limiting because the size of the root system in Typha is small relative to canopy (Tables 5.1 and 5.5).

Some species have a distinct loss of stomatal mobility with age and this appeared to be true for T. domingensis (Figure 5.7). In savanna

grasses, leaf ageing means increasing lack of control over leaf water balance as old leaves transpire uncontrollably until withered (Larcher 1980). The effect of leaf age on plant water balance obviously depends on leaf population age structure and phenology of canopy development. For Typha, midsummer is the most vulnerable time being the season of lowest leaf recruitment (Figure 3.12), oldest shoots and leaves and highest water stress.

Further evidence of mesophyte-like behaviour in Typha stomates is that unlike some aquatic species (5.2) they do respond to the "drought messenger" ABA. Exogenous application to T. domingensis clones was followed by a marked decrease in conductance and assimilation 12 minutes later (Dr. Brian Loveys, CSIRO, pers. comm. 1984).

In the diurnal study, maximum transpiration rates of 214-366 μg mm^{-2} h^{-1} were within the range for emergents and well-watered mesophytes (Table 5.2) and thus not high expected for a warm dry climate or from stomatal features. This was because calculation of the transpiration rate treated water loss from both surfaces as equal (5.5). In fact, this is most unlikely even when stomatal density is identical. Positive correlations between conductance and density (e.g. Reich 1984) are established under constant laboratory conditions. These do not apply in the field where each leaf surface has a very different micro-environment. Moreover, adaxial and abaxial stomates do not always have identical responses (Mott and O'Leary 1984). The variability and magnitude of inter-surface differences is indicated by conductance ratios (Table 5.10) which show that conductance of exposed adaxial surfaces may be three times greater than shaded abaxial surfaces. This means adaxial transpiration could be under-estimated by as much as 50% giving maximum rates of 320-550 μg mm^{-2} h^{-1} for Day 28 of diurnal (Figure 5.5). This is relatively high for a leaf surface (Table 5.2).

Typha forms dense natural stands with high maximum standing crop (4.5) which intercepts nearly all incoming irradiance because of its leaf orientation and high projected foliage area. Midsummer estimates of leaf area index for broad-leafed Typha species from USA and Australia are 7.64 and 6.8 (Gustafson 1976, Sale and Orr 1986). The range for temperate crops is 2-10 (Hunt 1982). LAI values are based on one surface only but Typha is equally amphistomatous. Thus whilst stomatal measurements show that Typha has a potentially high transpiration rate per unit leaf surface area and measured rates are probably high if calculated appropriately, amphistomaty means transpiration must be high when calculated on a whole leaf basis, and because Typha has a medium sized LAI, transpiration rate ramet^{-1} must also be high.

5.11 Water potential and plant growth

Water potential in High treatment lysimeters fell below -0.010 MPa on only three days, thus this treatment was higher than the water potential commonly used to define Field Capacity, -10 and -100 kPa (4.2). It was also within the matric potential range for unrestricted transpiration thought to lie between -0.010 and -0.05/0.10 MPa (Benecke and van der Ploeg 1981). Therefore it is not surprising that Control and High treatment clones were so similar in growth responses and transpiration coefficients (Tables 5.4, 5.6 and 5.7).

In Low treatment lysimeters, water potentials were set at -0.65 MPa and fell below -0.70 MPa on only three days. Low water potential had a greater effect on canopy growth than on canopy mortality. Growth in Control and High treatments was very similar with an RGR 7-8 times greater than Low treatments clones and a leaf recruitment rate 5 times greater (Tables 5.4 and 5.6 but see above, 5.9). In contrast leaf area turnover was 3 times less and leaf mortality was approximately the same.

As anticipated, Root:Canopy ratio increased with decreasing water availability but only when net production was used. This is consistent with changes in R:C ratios observed when seedlings of T. orientalis are grown on a decreasing resource gradient (Table 5.7). Unlike xerophytes where R:C shifts are caused by an increased root system and leaf abscission, this change in T. domingensis was caused by lack of canopy growth rather than abscission.

Contrary to expectations and early work on T. latifolia (Table 4.1) live root system was not larger at lower water potentials. However total root standing crop suggests that root production was higher in Low treatments and survival was lower (Table 5.5). Low oxygen in PEG solutions was not expected to be a problem (5.4) because emergents oxygenate the rhizosphere. However for this to be effective, stomates must be open. Hourly transpiration rates (Figure 5.7) and non-significant regression coefficients (Table 5.8) show this was unlikely in Low treatment clones thus rhizosphere hypoxia probably contributed to low survival.

In the field, a situation of decreasing water availability and decreasing substrate oxygen would not arise. Transpiration can continue even if roots are experimentally killed (Weatherly 1982) thus dead roots may have a minor role in absorption. Re-calculating R:C ratios using total root standing crop and live canopy gives means of 0.2754, 0.3345 and 10.2266 for Control, High and Low treatments respectively. These show the same trend as T. orientalis seedlings grown on a decreasing nutrient resource and are closer to field R:C values (Table 5.1).

Leaf area in Low treatment clones showed increases then decreases, and leaf recruitment and mortality were nearly equal. Interpreting these as oscillations around a mean suggests that -0.65 MPa was close to equilibrium resource levels. This is lower than probable R* set in the

gradient study.

5.12 Water as a limiting resource

The canopy of Typha has architectural characteristics which mean each ramet has a potentially high transpiration rate thus water will have to flow rapidly into the shoot if the plant is to maintain a positive water balance. This is only possible at high water potentials. Consideration of the diffusive properties of soil water led Passioura (1982) to the conclusion that a dense root system was essential if water was to be extracted rapidly from soils with matric potentials below -0.1 MPa. Similarly Benecke and van der Ploeg (1981) believe that only at matric potentials higher than -0.05/0.10 MPa is transpiration unrestricted. Typha does not have an extensive root system. Instead its roots are small relative to the canopy therefore the quantity of water that can be delivered to the shoot is not large. In fact the actual quantity supplied appears to be marginal even for well-watered shoots as shown by stomatal closure during the day (Figure 5.8).

The quantity of water lost by transpiration is roughly the product of leaf surface area and transpiration rate. Because of this, the water balance of a ramet in water conditions just adequate to maintain a positive water balance will become negative if either factor increases. Thus there is an inverse relationship between supply and leaf area. This means when supply is fixed and the environment is uniform, a larger ramet will become resource limited before a smaller one, as for example Low (L) clone in the diurnal study (Figure 5.5) or Low (M) and (L) clones versus Low (S) (Table 5.9). Shoot height and therefore canopy size explain why R* values for the gradient and lysimeter studies are different.

Similarly there is an inverse relationship between supply and transpiration rate, which although regulated by stomates is largely

determined by environmental conditions. An increase in transpiration rate means that a shoot of a given canopy size will be resource limited at a higher resource level or that a particular water supply will support a smaller canopy size. Thus in warmer and drier climates, the transition from abundant to R* will be shorter than in cool moist ones. In Africa Typha is described as "a reliable indicator of prolonged waterlogging in the root zone" (Thompson 1985). Given the high evaporative demand of the semi-arid Adelaide climate, it is perhaps not surprising that the perfect site for the gradient study could not be found.

An imbalance in plant water status is probably maintained because the plant fails to re-hydrate overnight. Slow overnight re-hydration was noticed in Cynodon dactylon which only reached saturation levels towards 6 a.m. (Furness and Breen 1986). This was attributed to shallow root system and low soil water hydraulic conductivity as at other times the plant showed rapid and opportunistic uptake in response to dew and mist. Low water content in T. domingensis roots and rhizomes in Low treatment clones indicated a net water loss and inability to rehydrate at -0.7 MPa.

In addition natural stands may be "leaky". Otis (1914) reported significant transpiration losses overnight from floating lysimeters of T. latifolia and Sale and Wetzel (1983) reported that stomates of T. latifolia did not close at night. The study showed a loss of function in old stomates and in summer, an ageing leaf population would mean uncontrolled water loss. The 30 day water loss from dead M clones was small but showed that dead leaves are potential leaks.

Table 5.1
Root to canopy ratios

Table 5.1 a

Mature clones of T. angustifolia near Kiev, USSR, field populations
Date of harvest not given (Merezhko et al. 1980)

	--- WATER DEPTH ---				
	35 cm	50 cm	70 cm	135 cm	150 cm
R:C =	0.50	0.49	0.46	0.23	0.32

Table 5.1 b

Mature clones, field populations
T. orientalis at Griffith

	MONTH OF HARVEST								
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
R:C =	0.54	0.62	1.36	1.96	2.93	2.27	4.60	1.48	0.48

Table 5.1.c

The effect of nutrient supplements on R:C ratios of cultivated seedlings
Calculated from data in Tables I and II (Cary and Weerts 1984)

	NUTRIENT SUPPLEMENTS in mg l^{-1}			
	Nitrogen N			
	0.02	0.20	2.0	20.0
R:C =	0.9545	0.9722	0.6481	0.3341
	Phosphorus $PO_4.P$			
	0.01	0.10	1.0	10.0
R:C =	0.5324	0.4545	0.2981	0.2571

Table 5.2
Transpiration rates of well-watered plants

All transpiration rates are expressed as $\mu g\ H_2O\ mm^{-2}\ h^{-1}$
and are maximum values or the maximum range

EMERGENT	E	REF	OTHERS	E	REF
Typha latifolia	119-213	a	Sunflower	600	A
Phragmites australis	600-840	b	Corn	300	A
Phragmites australis	150	c	Populus deltoides	30-310	B
Juncus roemerianus	150-350	d	Vigna unguiculata	432	C
Cyperus papyrus	290-360	e	Zebrina pendula	1080	D

REFERENCES and locality

a Otis 1914
Wisconsin, USA

b Pearcy et al. 1974
Death Valley, California, USA

c Larcher 1980
Netherlands

d Giurgevich and Dunn 1978
coastal Georgia, USA

e Jones and Muthuri 1984
Kenya

A Kaufman and Hall 1974

B Regehr et al. 1974

C Osonubi 1985

D Jarvis and McNaughton 1986

Table 5.3
Leaf area produced

Table shows production as leaf area in mm^{-2} for clones for each treatment

Treatment		Net	Total	Total/Net	Mean (sd)
Control	S	43,410	47,361	1.09	1.14
	L	85,066	101,406	1.19	(0.0707)
High	S	34,859	45,496	1.31	1.23
	L	41,503	47,155	1.14	(0.1202)
Low	S	-3,772	8258	nc	
	M	1823	8463	4.64	3.70
	L	6,698	18,483	2.76	(1.3294)

KEY
nc = not calculated, data incomplete
Net = difference between final and initial area, live
Total = difference betweeen final and initial live and dead area

Table 5.4
Mean relative growth rate of clones

RGR of leaf area as mm^{-2} mm^{-2} d^{-1}
showing mean and standard deviation

Treatment		RGR	Significance	Mean (sd)
Control	S	0.0149	***	0.0149
	L	0.0149	***	(0.0)
High	S	0.0099	***	0.0166
	L	0.0233	***	(0.0095)
Low	S	0.0035	NS	0.0022
	M	-0.0008	NS	(0.0026)
	L	0.0039	*	

Table 5.5
Harvest data

Dry weight in g, and percentage water content

Treatment		Total	Mean (sd)	p(live)	Mean (sd)	%WC	Mean (sd)
ROOTS							
Control	S	0.39	0.9200	0.2051	0.2819	96.7	94.65
	L	1.45	(0.7495)	0.3586	(0.1085)	92.6	(2.8991)
High	S	0.54	0.5050	0.5185	0.4295	91.4	92.00
	L	0.47	(0.0495)	0.3404	(0.1259)	92.6	(0.8485)
Low	S	1.22	1.5767	0.0388	0.0197	81.7	84.37
	M	0.93	(0.8809)	0.0105	(0.0166)	80.3	(5.8731)
	L	2.58		0.0097		91.1	
LEAVES							
Control	S	1.56		0.9412	0.8145	91.1	e
	L	7.39		0.6878	(0.1792)	89.8	e
High	S	0.62		0.6157	0.4057	88.0	e
	L	5.01		0.1956	(0.2971)	93.0	e
Low	S	2.91		0.0481	0.0460	95.8	e
	M	4.14		0.0121	(0.0329)	98.6	e
	L	9.51		0.0778		85.5	

ROOT:CANOPY RATIOS (live tissue)			
Control	S	0.0544	0.0784
	L	0.1024	(0.0339)
High	S	0.1035	0.1309
	L	0.1582	(0.0386)
Low	S	0.3371	0.1890
	M	0.1960	(0.2147)
	L	0.0338	

KEY
e = water content data possibly in error (see text)
Total = live and dead material, in g
p(Live) = the proportion of total that was alive at harvest
%WC = percentage water content

Table 5.6
Leaf demography

Recruitment (R) and mortality (M) rates
Number of leaves recruited/dying clone^{-1} x 10^2 d^{-1}
Change refers to the difference between final and initial

Treatment		Change	R rate	Mean (sd)	M rate	Mean (sd)
Control	S	7	33.33	35.00	10.00	16.50
	L	4	36.67	(2.3617)	23.33	(9.1924)
High	S	3	16.67	26.67	6.67	6.67
	L	5	36.67	(14.1421)	6.67	(0.00)
Low	S	-2	3.33		10.00	
	M	-2	3.33	4.44	10.00	10.00
	L	-1	6.67	(1.9283)	10.00	(0.00)

Table 5.7
Transpiration ratios

Tables show mean transpiration ratio k calculated for net and total production using estimated dry weight and leaf area.
E is total water transpired in 30 days in g, estimated dry weight in g and leaf area in mm^{-2} of adaxial and abaxial surfaces

Table 5.7 a

DRY WEIGHT: k = g H_2O g^{-1} dry material

Treatment		E	NET production g	k	mean	TOTAL production g	k	mean
Control	S	1164.32	1.15	1012	1046	2.06	565	718
Control	L	3194.08	2.96	1079		3.67	870	
High	S	1631.19	0.78	2091	1365	1.24	1315	918
High	L	682.51	1.07	638		1.31	521	
Low	S	171.30	-ve	-	-	-ve	-	
Low	M	204.74	-ve	-		-ve	-	
Low	L	393.60	-ve	-		-ve	-	

Table 5.7 b

LEAF AREA: k = g H_2O mm^{-2} leaf area

Treatment		E	NET production area	k	mean	TOTAL production area	k	mean
Control	S	1164.32	43,410	0.0268	0.0322	47,361	0.0246	0.0281
Control	L	3194.08	85,066	0.0375		101,406	0.0315	
High	S	1631.19	34,859	0.0468	0.0316	45,496	0.0359	0.0252
High	L	682.51	41,503	0.0164		47,155	0.0145	
Low	S	171.30	-3,772	-ve		8,258	0.0207	
Low	M	204.74	1,823	0.1123	0.0856	8,463	0.0242	0.0221
Low	L	393.60	6,698	0.0588		18,483	0.0213	

Table 5.8
Transpiration rate and evaporation

Regression analysis for all days
y = Mean daily transpiration in $\mu g\ H_2O\ mm^{-2}\ d^{-1}$ ($x10^{-3}$)
x = Evaporation in mm for 24 hours

Control	S	y = 50.8037 + 122.8068x	r = 0.6819 Fs = 15.64 ***
Control	L	y = 132.1405 + 172.6386x	r = 0.6966 Fs = 16.97 ***
High	S	y = -472.2974 + 208.4294x	r = 0.8604 Fs = 48.65 ***
High	L	y = -222.0999 + 151.1990x	r = 0.8216 Fs = 39.46 ***
Low	S	y = -56.1324 + 72.7960x	r = 0.6217 Fs = 11.97 **
Low	M	y = 48.4272 + 43.8523x	r = 0.5634 Fs = 0.18 NS
Low	L	y = 141.9695 + 36.5565x	r = 0.2295 Fs = 1.06 NS

Comparison matrix
Pairwise comparison of regression coefficients

		TREATMENT				
		---CONTROL---		---HIGH---		-LOW-
TREATMENT		Small	Large	Small	Large	Small
Control	S	-				
Control	L	NS	-			
High	S	NS	NS	-		
High	L	NS	NS	NS	-	
Low	S	NS	*	***	*	-

Table 5.9
Transpiration at different time periods

Mean daily transpiration rate as a function of evaporation.
Regression details, for x = evaporation in mm

	DAYS 6-21		DAYS 22-30	
Small				
	y = -86.5936 + 73.2095x		y = 59.9539 + 62.9742x	
	r = 0.5938		r = 0.7248	
	n = 12		n = 9	
	Fs = 7.75	*	Fs = 7.75	*
Medium				
	y = -3.35395 + 60.5945x		y = 154.3333 + 18.3986x	
	r = 0.8162		r = 0.5476	
	n = 12		n = 9	
	Fs = 18.00	*	Fs = 0.18	NS
Large				
	y = 98.6061 + 73.5655x		y = 97.9792 + 2.8217x	
	r = 0.8162		r = 0.2055	
	n = 12		n = 9	
	Fs = 19.95	**	Fs = 0.31	NS

Pairwise comparison of regression coefficients

Day 6-21				
Small	v	Medium	Fs = 0.1339	NS
Medium	v	Large	Fs = 0.1080	NS
Small clone				
Days 7-21	v	22-30	Fs = 0.0061	NS

Table 5.10
Conductance ratio

Conductance ratio = adaxial conductance/abaxial conductance
Leaf sequence is from the oldest A to the youngest G

	LEAF SEQUENCE						
	-A-	-B-	-C-	-D-	-E-	-F-	-G-
Ratio =	1.41	1.68	3.16	2.54	1.64	1.37	1.36

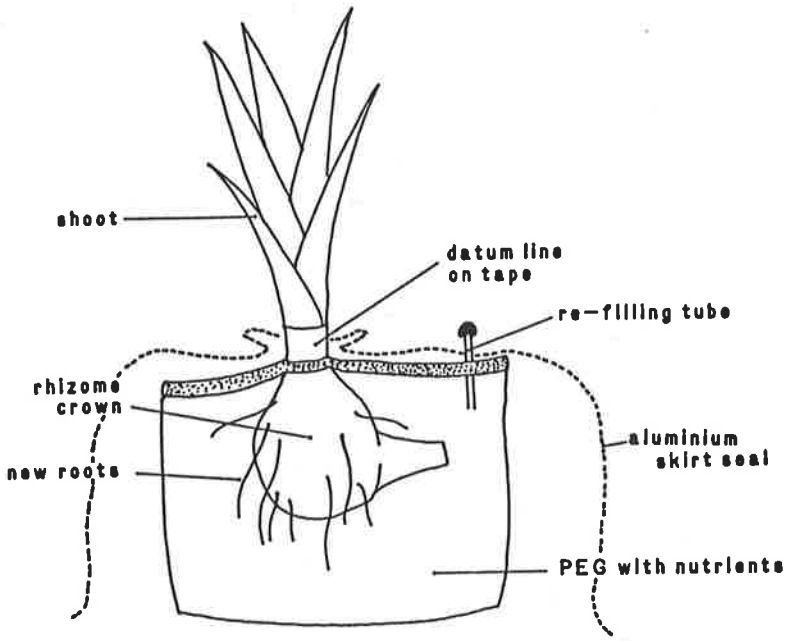

Figure 5.1
Lysimeter

A strong plastic bag containing treatment solution and one pre-conditioned T. domingensis clone (see text) comprising shoot, rhizome crown and rhizome, is sealed along the top, and around the shoot and the capped re-filling tube with tape. A datum line on masking tape round the shoot base is the reference point for leaf measurements. The lysimeter is insulated by a skirt of aluminium foil which also stops light reaching the rhizome, thus ensuring that photosynthesis only occurs in the leaves.

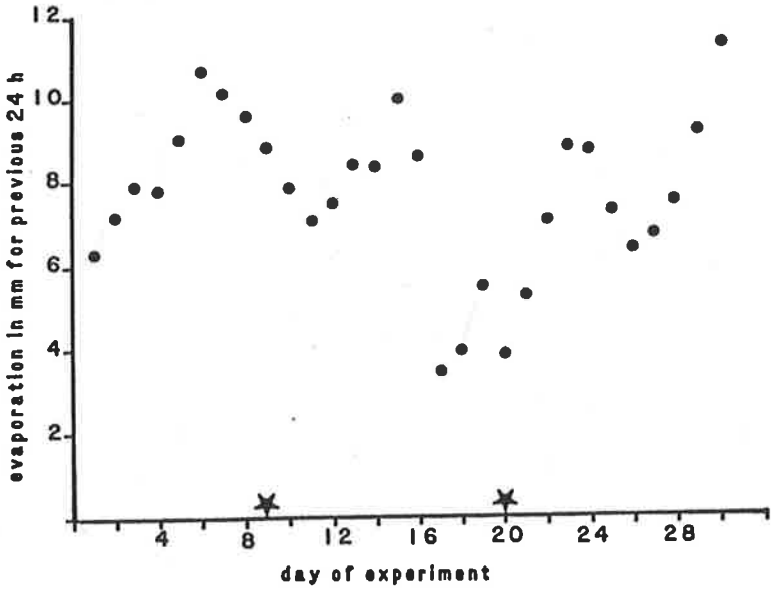

Figure 5.2
Environmental conditions

Daily evaporation as mm of water lost in previous 24 hours from Class A pan with birdguard at Kent Town, Adelaide, 1.5 km away (Adelaide Regional Office of the Meteorological Bureau) from Day 1 to Day 30, 15 December 1983 to 13 January 1984. Days when treatment solutions were completely changed are indicated by ✶.

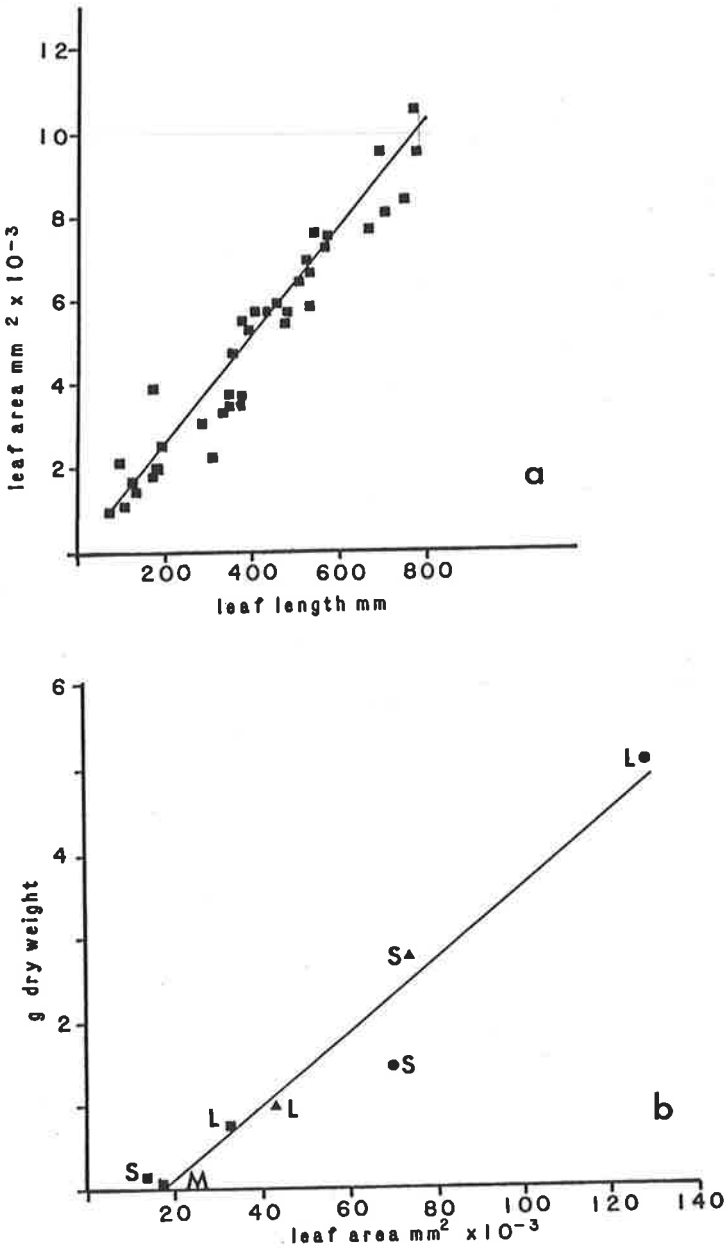

Figure 5.3
Calibration of growth measurements

(a) Leaf: length and area
Adaxial and abaxial leaf surface area in mm^{-2} as a linear function of leaf length in mm. Leaves were cut at the datum line at the end of the experiment. Results from different clones are combined (n = 37).

(b) Shoot: leaf area and weight
Shoot dry weight in g and area in mm^{-2}. Leaf area is sum of both surfaces for all leaves in a clone. Symbols showing clone classification based on rhizome size and water potential treatment.

Key
S M L Size class: Small, Medium and Large
● ▲ ■ Treatment: Control, High, and Low water potential

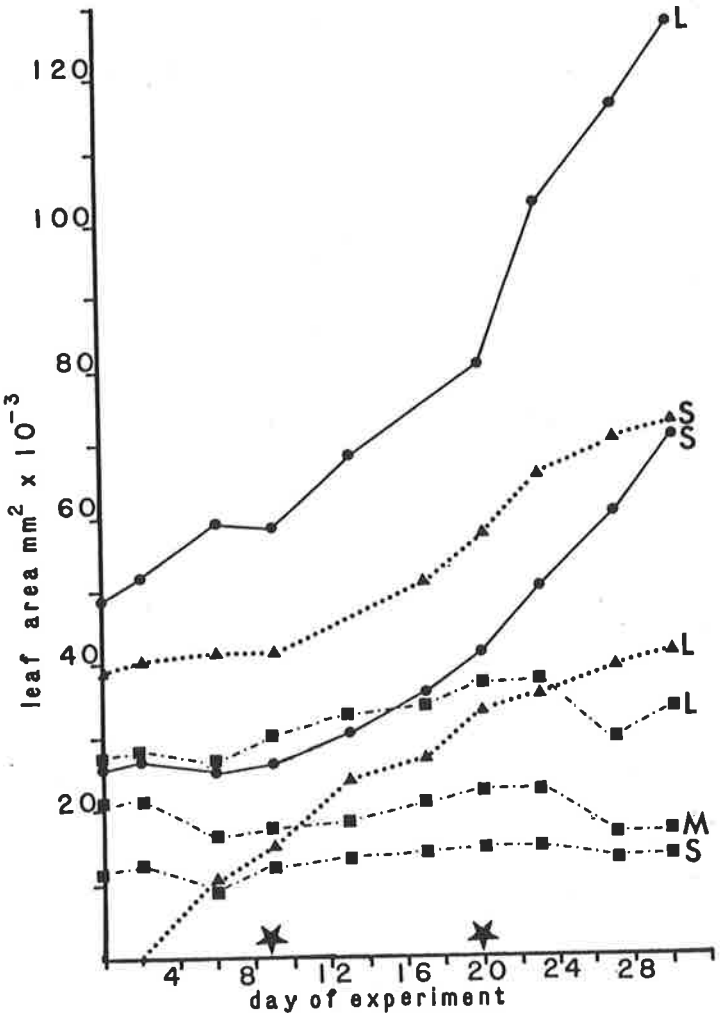

Figure 5.4
Growth and water potential

Growth in three water potential treatments based on leaf area in mm^2 per clone. Leaf length measurements made every 3-4 days were converted to leaf area using length:area relationship for individual leaves.

Key

SML	Size class: Small, Medium, Large
•—▲..■-·	Treatment: Control, High, Low water potential
★	Solutions completely changed, Days 9 and 20

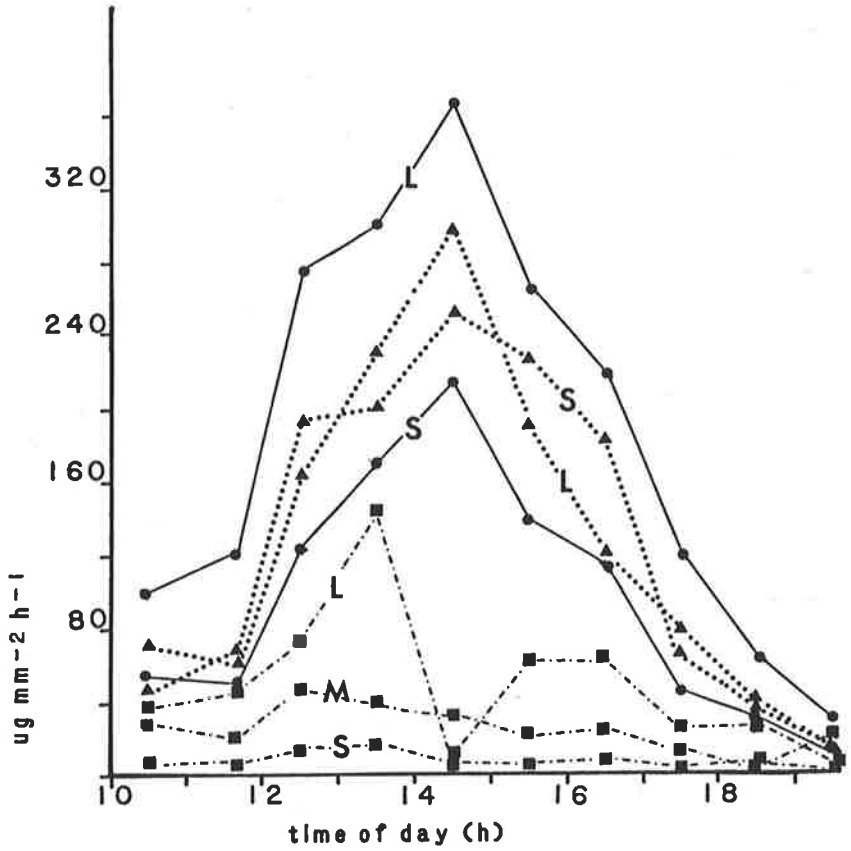

Figure 5.5
Diurnal changes in transpiration

Transpiration rate, in μg H_2O mm^{-2} h^{-1}, of experimental clones on Day 28 of experiment, 11 January 1984 from 0930-1930 hours.

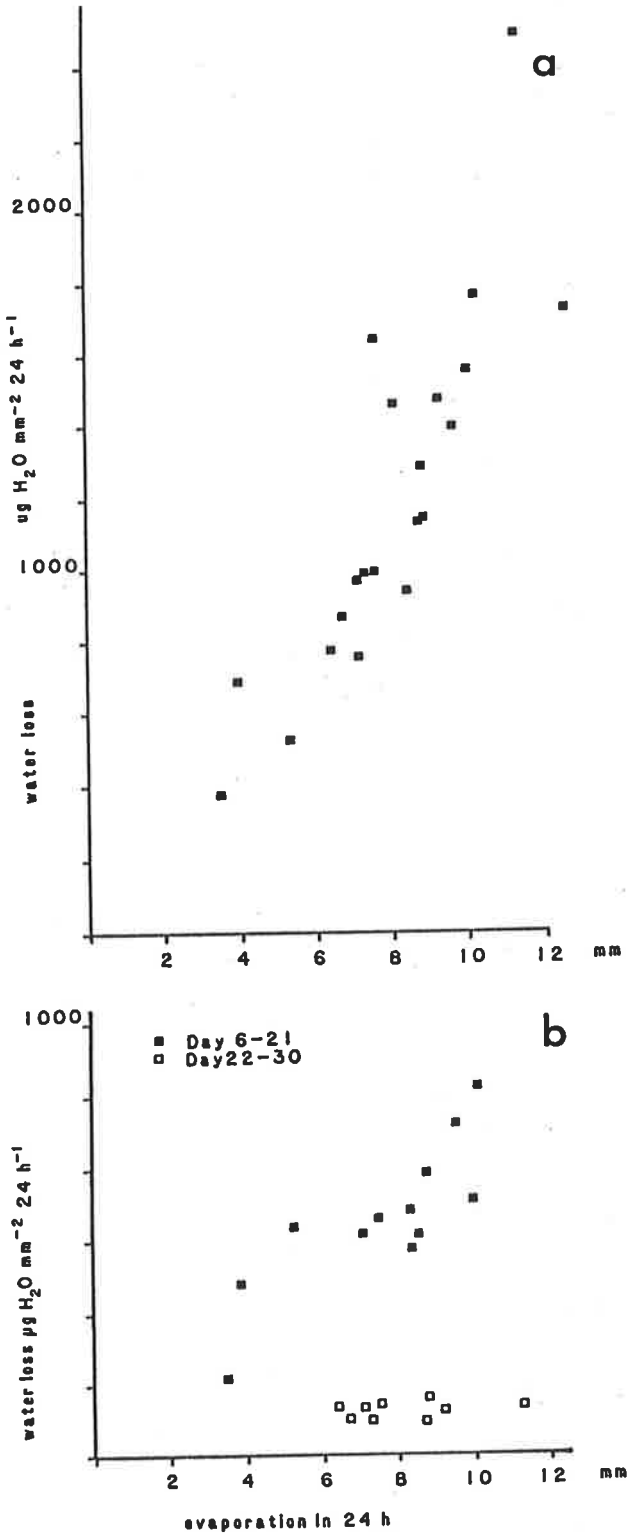

Figure 5.6
Evaporation and water loss

Water loss from T. domingensis clones, as mean daily transpiration in $\mu g\ H_2O\ mm^{-2}\ 24\ h^{-1}$, as a function of ambient conditions, mm evaporation in 24 hours.

(a) Linear response for High (S), the Small clone in High water potential treatment, for Days 6-30.

(b) Two contrasting responses for Low (L), the Large clone in Low water potential treatment, from different time periods.

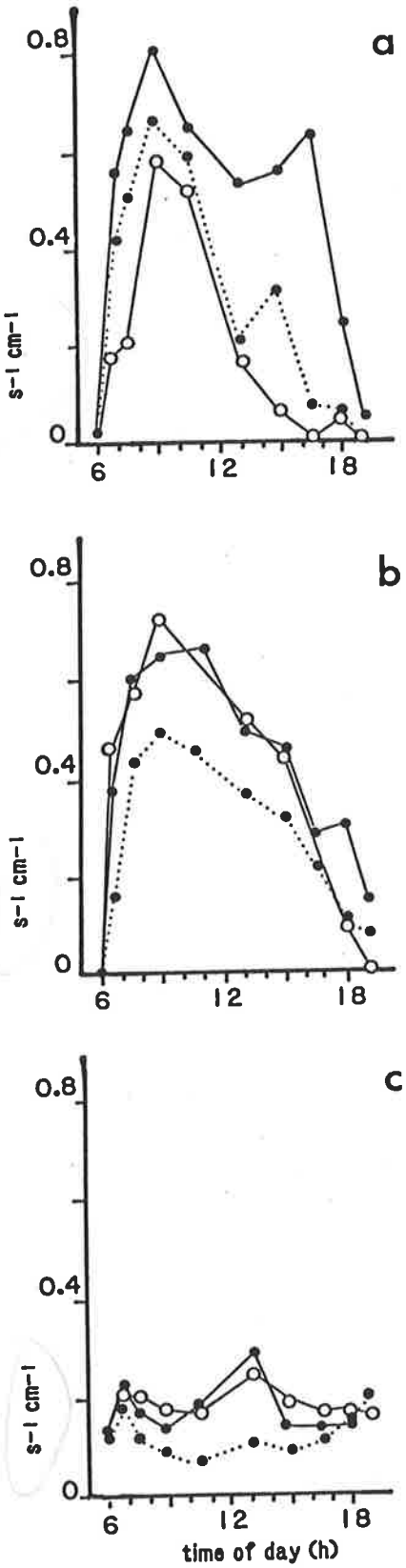

Figure 5.7
Diurnal conductance

Diurnal conductance of 21 T. domingensis leaves in $(s^{-1}\ cm^{-1}$ on 11 shoots in well-watered conditions at Strathmont, 7 March 1984, showing three individuals for each response type: (a) two-plus peaks, (b) one peak, (c) no peak.

Chapter Six

WATER AND GERMINATION

INTRODUCTION

6.1 Perspective

The regeneration niche comprises six stages (Grubb 1977), from flowering, pollination and seed set (on the parent) to dispersal, germination and establishment of the new individual. The entire sequence from flowering to establishment can be written as a transition matrix, but because this requires copious data, only one or two stages, recognised as critical, are usually studied. The life cycle of most perennials is characterised by a Deevey Type III survivorship curve (Silvertown 1982). This means germination and establishment are periods of highest mortality, and are critical stages in the life cycle. Establishment is the phase "when seedlings have expanded a photosynthetic surface and are theoretically capable of pursuing an existence independent of their seed reserves" (Harper 1977, p.132).

Germination has been extensively studied as a physiological process of dormancy release but the probability that a dispersed seed will become an established seedling is determined by a range of factors of which dormancy release is just one. Some factors are "hazards" (Harper 1977) such as predation, competition, unfavourable seed orientation and unsuitable patches in a micro-heterogeneous environment. A viable seedling means all conditions for a successful transition from seed to seedling have been met presumably because the seed was in a "safe site" (Harper 1977). The term "safe site" is unfortunate because it emphasises a spatial dimension at the expense of a temporal one.

Non-hazard factors are seed size, composition, capacity to remain viable through time and variability. Size expresses indirectly the

quantity of cotyledonary reserves available. These are an environmental buffer for seedlings (Silvertown 1982). The benefit of large reserves in sub-optimal conditions has been demonstrated for terrestrial plants by comparing performance in shaded and unshaded situations (Gross 1984) and for wetland plants along a water gradient (Keddy and Constabel 1986). Seed size is usually expressed as weight. It has a wide range covering 10 orders of magnitude from 10^{-6} g to 10^{4} g (Silvertown 1982). Chemical composition is another form of environmental buffering. The nutrient content of Australian Proteaceous seeds is 2-3 times higher than non-Proteaceous species including legumes (Pate et al. 1986). Long viability is an essential characteristic for species dependent on its seed bank, as occurs when germination conditions are irregular or widely separated in time and space. Thus longevity is another kind of environmental buffering. Usually intra-population variability is an expression of natural variation. The few known instances of extreme intra-population variation such as seed and germination dimorphism in Atriplex and Salicornia (Silvertown 1984) represent different "options". Inter-population differences are interpreted as ecotypic variations.

The typical safe site for Typha is a mudflat or an area exposed by falling water levels (1.3). In warm climates with predominantly winter rainfall such as much of south-east Australia, these can be expected to dry out rapidly thus water availability to seed and seedling is likely to be a hazard. Falling water levels mean ions are increasingly concentrated in the remaining waterbody and soil water. For example, conductivity in Lake Merrimajeel, western New South Wales, increased six-fold in five month drying-out period from 373 $\mu mho\ cm^{-1}$ in September 1977 to 2510 $\mu mho\ cm^{-1}$ in February 1978, (S. V. Briggs, 1987, pers. comm.). Therefore another hazard is salinity, particularly in endorheic and high conductivity wetlands. This can affect the regeneration niche and

subsequent vegetation dynamics of wetlands. The failure of T. domingensis to colonise the exposed floor of Lake Chilwa, Malawi, was attributed to high sodium content in residual water. Conductivity reached 12,000 μmho cm^{-1} during the drying phase which was shown to inhibit germination and establishment (Howard-Williams 1975).

Salinity inhibits germination either because an osmotic potential prevents water uptake or because ions entering the seed interfere with cellular processes. Sodium chloride and gypsum are recognised as inhibitory whereas nitrate stimulates germination (Koller and Hadas 1982). The inhibitory effect can be reversed by returning seeds to freshwater but recovery tends to be poor for seeds previously immersed in highly saline solutions (Bewley and Black 1982). Germination is probably more sensitive to salinity than are subsequent growth stages (Bewley and Black 1982). Populations vary in salt tolerance with seeds from mother plants in saline habitats being more salt tolerant than seeds of non-saline provenance.

This overview shows that the regeneration niche is a complex interaction of environmental and plant factors, and that an investigation of it must consider more than water availability. The following sections present studies on the regeneration niche of Typha (6.2), water as it relates to germination with a summary of techniques (6.3) and specific aims and experimental approach (6.4).

6.2 Typha: literature review

The extensive literature on the regeneration niche is mostly on germination of the cool temperate species T. latifolia. Studies of Australian species are limited to temperature effects (Priinster 1941).

Flowering, pollination and fertilisation have been described for sympatric species in Switzerland and USA (Marsh 1962, Krattinger 1975). The male inflorescence is above the female and most pollination is by

gravity thus self-pollination is dominant except in windy conditions with at least 50% of flowers setting seed (Krattinger 1975). Seed number per inflorescence is typically more than 200,000. Seeds are small and light (Finlayson et al. 1983). The fruit has basal hairs giving it a pappus-like appearance. Propagules may fall next to the parent or be dispersed by wind. At Lake Chilwa, Malawi, at the end of the dry season "large clouds of seed may be seen blowing around the lake and swamps" (Howard-Williams 1975). Despite current sceptism (Silvertown 1982) about the efficacy of long-distance dispersal, Typha seeds travel large distances. The presence of T. domingensis at Purni Bore, 60 km east of Dalhousie Springs, central Australia, prompted the following comment: "The two species of Cyperus and Typha now occur about almost all bores and springs in Central Australia where free water is available and obviously have efficient methods of dispersal" (Symon 1984).

Seeds of Typha spp. stored dry will maintain viability for $5^{1/2}$ but not $12^{1/2}$ years (Prunster 1941). This is relatively short. Water content is the most critical factor affecting long-term seed viability (Mayer and Poljakoff-Mayber 1975) so it is likely that longevity of wet stored seeds, such as wetland muds, will be even shorter. Longevity has not been questioned in seed bank studies of wetlands (McIntyre 1985, van der Valk and Davis 1976b). The seed coat is approximately 15 μm thick and extremely resistant to concentrated H_2SO_4 which was thought to be the reason germination was difficult (Marsh 1962). This is a minority view as most studies report Typha seeds germinate profusely and rapidly.

Typha seeds have aleurone grains (Sifton 1959), a generalised term for protein bodies (Bewley and Black 1978). These swell in response to water uptake and their expansion forces off the cap (Sifton 1959). The protruding primary root is "weak" (Boyd 1932). The extending hypocotyl arches lifting the seed then the "plumule" (Boyd 1932) emerges from a

basal slit in the hypocotyl sheath. Leaves develop on a short axis giving the young seedling a tufted appearance (Boyd 1932, Sharma and Gopal 1978). Experimental studies of environmental factors affecting germination and establishment are presented below.

Oxygen Germination is highest in hypoxic conditions of 2.3-4.3 mg oxygen l^{-1} and is completely inhibited in anoxic or oxygen-rich environments (Morinaga 1926a, Bonnewell et al. 1983). Oxygen requirements of seedlings have not been studied except indirectly as submersion (see Water regime below). Typha seedlings do not produce a long vertical leaf through the water to air, described as a snorkel (Bewley and Black 1978, p.133) as does Oryza sativa.

Temperature Alternating temperatures were once thought to be essential for germination (Morinaga 1926b). This was disputed (Prunster 1941, Sifton 1959) and now most germination studies of Typha are done at constant temperatures. Germination increases with increasing temperature with an optimum of 20-25°C is indicated for Australian species (Figure 6.1). The optimum temperature for North American species is higher, up to 30° and 35°C (Sifton 1959, Bonnewell et al. 1983). The critical minimum temperature, near 15°C, is similar in all studies (Sifton 1959, Bonnewell et al. 1983, Figure 6.1). Stratification improves germination according to some experiments (Galinato and van der Valk 1986) but not all (Bonnewell et al. 1983) and is frequently a pre-treatment for cool temperate species.

Light Light requirement, intensity, duration and quality have all been studied. Germination is increased in presence of light (e.g. Galinato and van der Valk 1986) and light is sometimes described as obligatory with germination in the dark being close to zero (Sifton 1959, Gopal and Sharma 1983, Bonnewell et al. 1983). Light has much less stimulatory effect on germination of Australian species (Prunster 1941) which have up

to 45% germination in the dark.

Germination in Typha is phytochrome controlled (Bonnewell et al. 1983). Factors which alter the P_R (inactive) to P_{FR} (active) ratio, such as light:dark duration and light quality, affect germination because these affect synthesis, reversion and destruction of phytochrome. In T. latifolia one red light exposure of 12 hours or 4 exposures each 30 minutes long in a 12 hour period give a 63-65% germination whereas one exposure of 2 hours results in only 7% germination (Bonnewell et al. 1983). The inhibitory effect of blue light (Sifton 1959, Gopal and Sharma 1983) is presumably due to slightly higher absorption of P_{FR} in the blue part of the spectrum (Nobel 1974).

Salinity The germination responses of two species, T. latifolia on the Washington steppes and T. domingensis in Lake Chilwa, Malawi, to sodium salinity have been studied to test hypotheses of regeneration processes (Choudhuri 1968, Howard-Williams 1975). Germination of T. latifolia was only 10% at an osmotic potential of 4.50 atmospheres, approximately equivalent to 0.1 molal NaCl or -0.46 MPa. Germination of T. domingensis was only 22% in 108.7 m mol Na+, equivalent to approximately 0.1 molal Na+. Unfortunately these species cannot be ranked for salinity sensitivity because the experiments were not comparable. Seeds of T. latifolia were in pure NaCl whereas T. domingensis seeds were in a mixture of NaCl and Na_2CO_3 plus nutrients. The effect of sodium on T. latifolia was anion specific with NaCl being slightly less inhibitory than Na_2SO_4 and much less than Na_2CO_3 (Choudhuri 1968).

Sodium concentrations of 108.7 m mol dm^{-3} or more inhibited root growth in T. domingensis seedlings which were mostly dead at the end of 20 days (Howard-Williams 1975). Seeds of T. angustifolia and T. latifolia survived 4 months immersion in 2% NaCl and maintained viability (McMillan 1959). Seedlings from a salt flat in Nebraska, presumed to be salt

tolerant, germinated in 1% NaCl but did not survive when concentrations were increased to 2% (McMillan 1959).

Water The different components of water regime discussed earlier (3.2) have not been systematically investigated. Early studies documented recruitment flushes after drawdown but lacked details of subsequent environmental changes and vegetation dynamics (Kadlec 1962, Harris and Marshall 1963). Vertical distance to water table has been used to approximate water availability in studies of germination and seedling survival (Grace 1985, Keddy and Constabel 1985, Keddy and Ellis 1985) and seedling growth in constant and fluctuating conditions (Bedish 1967, Sharma and Gopal 1979). Seedlings can survive to 160 days in 20 cm water (Grace 1985) but have high mortality if subjected to 40-50 cm flood or 25-50 cm drawdown (Sharma and Gopal 1979).

Biotic factors A number of biotic factors have been experimentally shown to reduce germination, survival and growth but their importance in field situations is unknown. For example, tubificid worms active enough to re-deposit 3 mm sediment over seeds will significantly reduce germination and seedling survival of T. latifolia and T. domingensis (Grace 1984) but it is not known whether this activity level is normal for tubificids. Allelopathy has been an issue. Concentrated samples of leaf extracts inhibit germination (McNaughton 1968, Grace 1983) yet natural swamp waters do not (McNaughton 1968, Sharma and Gopal 1978).

Seedlings of T. latifolia and T. domingensis differ in competitive ability with the outcome dependent on water depth (Grace 1985). Competitive interaction with other mudflat seedlings is unknown and in drawdown situations is usually complicated by changes in water level (Howard-Williams 1975, van der Valk and Davis 1979).

6.3 Water and germination

Water is essential for germination. Only when a seed is adequately

hydrated can metabolic machinery be hydrolysed. The amount of water required for hydration is "minute" (Koller and Hadas 1982), probably 2-3 times seed dry weight (Bewley and Black 1978) but represents a huge change in seed water status. Dry seeds have an enormous matric and very little osmotic potential. Seed water potential before imbibition may be -100 MPa or lower rising to -1 MPa at germination (Bewley and Black 1978).

Water uptake occurs in three phases referred to as initial, transition and growth (Koller and Hadas 1982) or imbibition, lag and germination (Bewley and Black 1978). The initial phase is one of rapid uptake and is accompanied by rapid leakage of cellular contents until membrane function is re-established. In some species this may occur within 20 minutes. Opinion is divided as to whether this phase is entirely physical (Bewley and Black 1978) or not (Koller and Hadas 1982). In the transition phase, water uptake gradually becomes negligible. Seeds are metabolically active and remain in this phase until released by an environmental stimulus or increased water uptake in response to metabolically prompted decrease in seed water potential (Bewley and Black 1978). In the growth phase, water uptake is again rapid and leads to radicle protrusion.

The level of hydration reached is determined by the quantity of water entering the seed. This can be simply described as Flow = (Water potential gradient)/(Resistance) where water potential gradient is the difference between seed and soil, and resistance includes hydraulic conductivity of soil and seed, and the degree of soil-seed contact (Bewley and Black 1978). The lowest water content at which a seed can germinate is its critical hydration level (Koller and Hadas 1982). This is a species or cultivar attribute (Bewley and Black 1978, Koller and Hadas 1982). The only data available for wetland species are for rice, -0.79 MPa (Koller and Hadas 1982). The critical water potential for

germination is lower than that at which radicle extension occurs (Bewley and Black 1982).

Many field studies (Lazenby 1955, Grace 1985, Keddy and Ellis 1985) have related germination to water table position. This approach is useful for species comparison or gradient analysis but replication and manipulation become difficult. The limitations of using distance to approximate water availability were discussed earlier (4.1). Techniques available for maintaining a constant and controlled water potential in laboratory experiments include sintered glass plates (Harper and Benton 1966), soils calibrated for water content and water potential, atmospheres of controlled humidity and solutions of known water potential.

Solutions have an advantage in that they are easy to prepare and reproduce. More importantly, the effects of water availability and salt can be investigated by the same method giving experimental uniformity. The use of iso-osmotic solutions of different composition means osmotic effects can be distinguished from specific ionic effects. Substances used are dextran, mannitol and polyethylene glycol or as PEG. Mannitol and dextran are less commonly used because they are taken up and affect cell function (Slatyer 1961). In contrast, PEG is widely used in experiments on plant growth (Zimmerman 1985), seed germination (Kaufman 1969, Sharma 1976) and tissue culture (Bressan et al. 1981). PEG is an inert non-ionic long chain polymer (Steuter et al. 1981) previously known as Carbowax. Due to its colloidal-like properties the water potential of large PEG polymers is almost entirely matric with only a small osmotic component (Steuter et al. 1981). This makes it especially useful as a comparison with osmotic potential but its use to give controlled water (matric) potential is not straightforward. A review of PEG follows.

The water potential of PEG solutions increases (becomes less negative)

with increasing PEG concentration and changes with temperature (Michel and Kaufman 1973) and polymer size (Steuter et al. 1981). In addition, estimates of water potential vary according to method used, freezing point depression, vapour pressure osmometry or thermocouple psychrometry (Michel and Kaufman 1973, Steuter et al. 1981, Michel 1983). Differences between methods are least noticeable when concentrations are low and when large polymers are used such as PEG 20,000 (Steuter et al. 1981). No explanation for this has been put forward but the surface-air properties of PEG solutions may be a factor (Michel and Kaufman 1973). Vapour pressure osmometry has been singled out as being "in error" (Michel and Kaufman 1973, Michel 1983) but the error seems small, 0.04 MPa at 0.1 molal for PEG 8000 (Michel 1983). Steuter et al. (1981) were not prepared to favour one method over another.

Some workers have reported a synergistic effect between PEG and nutrients (Michel and Kaufman 1973) and between PEG and NaCl (Lagerwerff et al. 1961, Michel 1983). The water potential of a mixed solution was more negative than the sum of the pure solutions. No reason has been given as to why an "inert" polymer should interact with simple salts although it may be due to the "possible existence of cation-active polyoxonium ions" (Steuter et al. 1981). Despite these problems, PEG continues to be used (e.g. Bressan et al. 1981, Zimmerman 1985).

There have been several reports of PEG entering plants and having toxic effects (Lagerwerff et al. 1961, Lesham 1966, Lawlor 1970, Janes 1974). In nearly all of these, small PEG polymers were used or else roots were damaged (e.g. Emmert 1974, Lesham 1970, Lawlor 1970, Yaniv and Werker 1983). The importance of polymer size and root integrity in facilitating entry of PEG has been demonstrated (Carpita et al. 1979, Lawlor 1970). Plasmolysis and cytorrhysis showed that polymers with narrow diameters such as PEG 400-600 readily pass through cell walls and

membranes whereas large polymers such as PEG 6000 do not and intermediate ones such as PEG 4000 do sometimes (Carpita et al. 1979). Intact roots have low permeability to polymers with molecular weights of 1000 or more but damaged or cut roots are readily permeable to polymers as large as PEG 4000 (Lawlor 1970). Thus plants with intact roots should not take up PEG polymers larger than 6000. Inexplicable plant damage and necrosis (Lawlor 1970) is probably due to hypoxic conditions around roots (Mexal et al. 1975). The oxygen content of PEG solutions is inversely related to concentration and large polymers are more hypoxic than smaller ones.

6.4 Aims and approach to the study

The aim was to investigate water as a factor in the regeneration niche of Typha. Obviously this must also include salinity effects and variability (6.1 and 6.2). Thus specific aims were to determine the critical hydration level for Typha spp., to compare matric and osmotic effects and to determine if there was evidence of population variation either in germination responses or seed characteristics known to affect germination and/or establishment.

Time constraints meant only germination studies could be done so it was decided to also record early seedling survival and growth. Radicle protrusion is frequently used as a definition of germination and as an indication that growth has begun. This is not always an appropriate index because it is usually due to cell elongation rather than mitotic division and protein synthesis (Bewley and Black 1978). In species with epigeal germination such as Typha, extension of the hypocotyl may be the first sign of growth. In this study leaf presence, which appears after the hypocotyl has extended (6.2), was selected as unambiguous evidence for growth.

Experiments were done in the laboratory rather than in the field. Typha seeds are small (Finlayson et al. 1983) and although their location

may be marked in the field, such marking advertises the experimental area. The field site available at the beginning of this study was on public land and could not be guaranteed to stay free of disturbance. A laboratory study had the advantage that conditions could be reproduced.

The study is in three parts. The first is a series of germination experiments. The aims of these were firstly to determine the critical hydration level, response to water availability and comparison of matric v osmotic effects using T. domingensis; and secondly to determine response to water availability, the ameliorating effect of nutrients on salt sensitivity, responses to light intensity (irradiance) and duration (photoperiod), using seed from a number of sources. The salt-nutrients experiment was included because natural waters include ions other than Na+ and Cl- and these, particularly nitrate and calcium, have a role in mitigating adverse effects of NaCl on cell membranes. Nutrients were used as a non-specific ion source. Germination responses to irradiance and photoperiod were studied to ensure experimental settings did not favour one population over another. These results are included because they contribute to the study of the regeneration niche and variability.

PEG was used for matric potential and the initial step was to calibrate solutions and determine the most appropriate polymer for use. NaCl was used for osmotic potential as this is the salt most typical of saline waters in Australia (Bayly and Williams 1973). Variation was assessed using seeds collected opportunistically in south-east Australia.

The second part attempts to identify the nature and significance of inter-population variation. First, site characteristics known to affect seed characteristics, and seed characteristics known to affect seedling success are presented. Then a causal relationship is sought between site and seed characteristics, and between seed characteristics and seedling response using regression analysis. In the third part multi-variate

analysis is used to define population groups with similar seed and seedling responses.

For the first part, an experimental design was required which would measure responses, variations and interactions. Consequently, experiments were designed as multi-level factorial experiments to be analysed by analysis of variance (FACTAN and MCPAIR). This meant there was an emphasis on replication rather than on sample size. As the study progressed, replication was increased in an attempt to reduce variability and so conform to assumptions of homogeneity of variance.

METHODS

6.5 Germination experiments

Seeds

Seeds, henceforward referred to as ecotypes, were collected from eight sites in south-east Australia (Figure 6.2). Six were *T. domingensis*, of which four came from South Australia (LP M P S) and two from Lake Wyangan, New South Wales (LWN and LWS). Two were *T. orientalis* indicated by pre-fix "TO". Site locations and acronyms are given in Table 6.1 and site details are given below (6.9: Seed and site characteristics). Inflorescences were stored in the dark for up to nine months before separating viable seeds from accessory structures and infertile seeds. Separation technique was similar to that used by Sharma and Gopal (1978). A handful of fruits was shaken and soaked in tap water for 15-30 minutes. Heavier seeds sank to the bottom and were assumed to be the viable ones. These were air-dried overnight then stored in the dark.

Experimental procedure

Experiments were done in growth cabinets. Seeds were germinated in clear plastic 1.5 ml or 4.0 ml autoanalyser vials containing approximately 1 ml or 3 ml of treatment solution. Capped vials were

grouped into clear plastic beakers with screw-on lids. All beakers were on the same shelf in a growth cabinet except for irradiance experiments. Experiments ran for 8-10 days. Changing the number of seeds in a vial was not considered important as previous trials had shown no detectable difference in germination between 1 and 25 seeds $vial^{-1}$. In some experiments it was impossible to harvest and process all treatments in one day so "rolling" replication was used. This meant replication was staggered with a complete replicate starting on successive days.

Solutions of PEG, NaCl (AR grade) and Hoagland's nutrient medium (Appendix 6) were made using de-ionised water. Water potentials of pure and mixed PEG solutions were estimated from calibration curves using a vapour pressure osmometer (methods and results in Appendix 7). The water potential of NaCl solutions was taken from published tables (Lang 1967). Sodium chloride concentrations are molal for High Salt treatments but elsewhere are molar. Space restrictions and a diminishing seed supply meant less than eight ecotypes were used for some experiments. Experiments are not in chronological order. Details of each experiment are given below.

Growth cabinet conditions were as follows except when varied as a treatment: temperature was 20-22°C, irradiance was 220 $\mu E\ m^{-2}\ s^{-1}$ except for the photoperiod experiment which was done in a different growth cabinet at 250 $\mu E\ m^{-2}\ s^{-1}$, and light:dark cycle was 16:8 hours. Lights were Sylvania cool white light and photon flux in 400-700 nm range was measured with Li-Cor quantum meter and quantum sensor (Lambda Instrument Company, Nebraska, USA).

Data organisation

Germination was rupture of the testa by the protruding radicle. Green seedlings were counted as live, brown or white seedlings as dead. For most experiments there are three data sets, germination, survival and

growth, each expressed as a proportion. Germination is the proportion of seeds that germinate or become seedlings, p(g): survival is the proportion of seedlings that survive to the end of the experiment, p(s): growth is the proportion of seedlings that survive and develop a first leaf, p(L). To save multiple labels on diagrams, axes are labelled only "p". Results are presented using aggregated data for graphs, and using means with standard deviation for tables. Details of replicates and sample sizes are given below (Experimental details).

Data analysis

Experiments were analysed in two ways. The first was factorial analysis of variance (FACTAN) with Bartlett's test for homogeneity of variances. Multiple a posteriori comparisons were done using an experimental error of 0.05 (MCPAIR). All data were arcsin transformed prior to analysis.

The second used GLM (Generalised Linear Modelling) to fit a linear model to the data. Data were aggregated and transformed to log odds ratio, log(p)/(1-p), and the fit assessed from the scaled deviance and degrees of freedom. Output is a table showing the estimate, its standard error and ratio of (estimate)/(standard error) for each level tested where level is treatment such as ecotype or interaction such as ecotype x irradiance. This ratio is approximately normally distributed and its significance can be assessed with reference to a normal approximation of Z statistic. Separate models were fitted to germination, survival and growth data.

Experimental details

PEG bioassay

Three PEG polymers were compared, PEG 6000, PEG 10,000 and PEG 20,000, at concentrations of 0.1 to 0.4 molal PEG. The control was de-ionised

water with no PEG. This gave a water potential range from 0 to -1.71 MPa. One ecotype was used LP which is T. domingensis from Little Para River, South Australia. There were 4 replicates of 15 seeds. Only germination was recorded.

Matric potential

Solutions of PEG 20,000 were made up with nutrients to give four matric potentials -0.6, -0.84, -1.11 and -1.4 MPa with 0 MPa as control. Final nutrient concentration was 1/4 H. All eight ecotypes were used. There were ten replicates of 4-6 seeds. Germination and survival were recorded but not leaf growth.

Osmotic potential

Treatment solutions were 0.05-0.4 molal NaCl, equivalent to -0.23 to -1.87 MPa (Lang 1967), with a control of 0 molal NaCl. Because there was a catastrophic decrease in seedling survival between control and 0.05 molal NaCl, the experiment was repeated using lower NaCl concentrations, 1-75 mM NaCl. These are referred to as High and Low Salt treatments. This experiment complements the matric potential experiment, done at the same time as PEG bioassay, therefore the same ecotype was used, LP. For the High Salt experiment there were 8 replicates of 15 seeds, and for the Low Salt experiment there were 7 replicates of 15 seeds. Germination, survival and leaf growth were recorded.

Salt and nutrients

Nutrients were added to salt solutions to give final concentrations of 50 mM NaCl with 1/4, 1/8, 1/16 etc to 1/256 of Hoagland's nutrient medium (Appendix 6). Fungal growth developed in three middle-range treatments, 1/8, 1/16 and 1/32, so these were discarded. Fortuitously their loss did not affect results. Six ecotypes were used, five T. domingensis (LP LWN LWS M S) and one T. orientalis (TOT). There were seven replicates of

10-15 seeds. Germination, survival and leaf growth were recorded.

Irradiance

A gradient of five irradiance levels from 15 to 220 $\mu E\ m^{-2}\ s^{-1}$ was set up in one growth cabinet by covering shelves with clear plastic. The growth cabinet was ventilated and temperature was not affected. Dark treatments were imposed by covering beakers of seeds with light-excluding covers. Irradiances were read after beakers and shelf covers were in place. For the dark treatment care was taken to cover beakers 2-3 minutes after putting dry seeds into solutions. Treatment solutions were 1/4 H with a plus/minus salt treatment of 0 and 50 mM NaCl. All eight ecotypes were used. There were nine replicates of 4-6 seeds each. Germination, survival and leaf growth were recorded.

Photoperiod

Five daylengths ranging from 8 to 16 hours were achieved in one growth cabinet by manually covering beakers with light-excluding covers. As with irradiance experiment, treatment solutions were 1/4 H with a plus/minus salt treatment of 0 and 50 mM NaCl. Beaker covers reduced space available and only four ecotypes were tested, three *T. domingensis* (LWN M P) and one *T. orientalis* (TOT).

6.6 Site and seed characteristics

Site characteristics were conductivity and latitude. Conductivity was measured in the field or determined from published reports of water quality (CSIRO 1980, Glatz 1985). Some localities did not have precise information. Conductivity for Parachilna, South Australia was a catchment mean (Glatz 1985). Data for Scottsfield, Tasmania was provided by Dr R Shiel, Botany Department, University of Adelaide (pers. comm. 1986). Latitude to closest 15' and expressed as decimal for analysis was read from 1:50,000 topographic maps.

Species were identified by inflorescence morphology and colour following Aston (1973), Finlayson *et al.* (1983) and experience. Only one inflorescence was used for each ecotype. Seeds were weighed on an electronic balance, reading to 10 µg in separate groups of 7-30 seeds. Mean seed weight was the regression coefficient of seed number and total weight and sample size was 14-18 for each ecotype. Water content was standardised by storing material for 8 days in desiccator with fresh silica gel before weighing.

Nitrogen and carbon concentrations were determined using a Hewlett-Packard CHN analyser, Model 185 (Hewlett-Packard Australia Pty Ltd, Blackburn, Victoria). This converts sample elements to oxidation states at high temperature in the presence of an oxidant. The output was calibrated against cystine provided by the manufacturer. Samples were weighed on a Cahn Electrobalance, Model G (Ventron Instruments, Paramount, California, USA). Results are mean (n = 5) mg N or C g^{-1} seed dry weight.

Sodium and potassium concentrations were measured using a Corning 400 flame photometer calibrated with fresh solutions of 0.5, 0.25, 0.10 and 0 mMolar NaCl and KCl. Seeds were hard to grind so the testa was broken naturally by allowing 0.03-0.10 g dry seeds to imbibe for 48 hours in 3 ml of 10 mM HNO_3. Samples were digested for 2 hours at 90°C and solutions made up to 20 ml before reading. Ionic concentrations are given as mean (n = 3) mg Na^+ or K^+ g^{-1} seed dry weight.

Data analysis

Seed weight of *T. domingensis* ecotypes was compared by calculating minimum significant distance using T'-method with an experimental error rate of 0.05. Ecotype differences in seed composition were compared by analysis of variance (FACTAN) and *a posteriori* multiple pair-wise comparisons done using T-method with alpha = 0.05 (MCPAIR). Homogeneity

of variances was tested using F_{MAX} and Bartlett's method (HOMOV). Correlation and multiple linear regression (MULREG) were used to establish whether variation in seed characteristics correlated with variations in site characteristics.

6.7 Ecotypic variation

Data analysis

Multiple linear regression (MULREG) was used to determine whether variations in physiological response could be explained by seed characteristics. The independent variables were N, Na and K concentrations and seed weight as an indication of size. The dependent variable was physiological response as germination, survival or leaf development. These were standardised relative to control of each experiment as (C-T)/(C), where C = control and T = mean response to treatment. Anova was used to determine the significance of regressions with alpha set at 0.05 and the size of standard partial regression coefficients or beta-prime gave the relative importance of each independent variable (Sokal and Rohlf 1981).

Multi-variate analysis was used to cluster ecotypes first by similarity of seed characteristics (n = 4) and then by similarity in seedling responses (n = 15). These were selected from graphs as likely to give best discrimination between ecotypes. A polythetic agglomerative hierarchical numerical classification procedure was used as being less likely to misclassify than monothetic or divisive procedures (Greig-Smith 1983). The program was FUSE, part of NTP or Numerical Taxonomy Package (Belbin et al. 1984, available 1985 from CSIRO Division of Water and Land Resources). The fusion strategy used was Furthest Neighbour and the initial matrix of distances between seed characteristics and physiological responses was constructed using Czekanowski's coefficient of similarity and the program ASO, also part of NTP. Characteristics were

standardised as described above for multiple linear regression then transformed so that all values fell between 1.0 and 8.0

RESULTS

6.8 Germination experiments

Analysis

Statistical analysis was a problem. It proved impossible to do a factorial anova using all the data from an experiment. The variance was unacceptably heterogeneous despite trying all transformation options available on BIOM package. This heterogeneity originated from uniform germination responses to the extreme treatments such as complete darkness, highest salt and controls, where variance was zero. A contributing factor was that many of the results were outside the range 0.2 and 0.8. The arcsin transformation fails to correct values in this range for heterogeneous variance (Austin et al. 1984). As an alternative, factorial analyses were done at a lower level by analysing each ecotype separately but it was still necessary to delete the extreme treatments from some analyses. Multiple lower level factorials are not satisfactory because one interactive term is lost. Moreover presentation is clumsy.

The second analysis using GLM to fit a linear model to transformed data is appropriate for binomial data with very high and very low probabilities, and has the advantage of fitting data to a flexible rather than a fixed model (Austin et al. 1984). This approach was also unsuccessful and for the same reason. Treatments with a variance of zero had exceptionally high standard errors. This affected the deviance calculation and generated ludicrous results. The most extreme treatments, such as 0 and -1.4 MPa, were not significantly different from each other but were from intermediate treatments. Results of these analyses are not presented.

PEG Bioassay

In control solutions of de-ionised water with no PEG and a water potential of 0 MPa, germination of T. domingensis seeds from Little Para River, South Australia was high with p(g) > 0.95 (Figure 6.3). Germination remained high down to -0.8 MPa in all three polymers but tended to decrease at water potentials below -0.8 MPa. This effect was polymer specific with the smallest polymer PEG 6000 having more effect on germination than the largest PEG 20,000. Thus at -1.71 MPa in PEG 6000 p(g) = 0.33 compared to p(g) = 0.97 at -1.55 MPa in PEG 20,000.

The polymer chosen for the matric potential experiment was PEG 20,000. Reasons for this choice are given elsewhere (6.11).

Matric potential

The eight ecotypes had similar germination and survival responses with only minor variations (Figure 6.4). As with the PEG bioassay experiment, germination was little affected by matric potentials of 0 to -0.6 MPa or -0.84 MPa, then decreased rapidly and was zero at -1.4 MPa. Thus the critical hydration level for all ecotypes was between -1.1 and -1.4 MPa. Ecotypes differed in how much water potentials below -0.84 MPa affected germination. At -1.11 MPa, germination for LWN LWS P TOG was fairly low with p(g) <0.25, whilst for TOT and M it was fairly high with p(g) >0.75. The control value for TOT p(g) = 0.68 is low compared to controls for other ecotypes (Figure 6.4) and low compared to controls for TOT in other experiments. It is therefore accepted as an experimental error.

Seedling survival was high for all ecotypes with p(s) >0.85 at water potentials from 0 to -1.11 MPa, but P (Parachilna) had zero survival at -1.11 MPa. There are no survival data for -1.4 MPa because no seeds germinated.

Osmotic potential

In the High salt treatment, germination between 0 and -1.35 MPa was high with p(g) >0.9 (Figure 6.5 a). Germination decreased at lower water potentials and at -1.82 MPa p(g) = 0.30. Survival in control solutions was high, p(s) >0.95 but in salt solutions survival was very low with p(s) <0.15 in -0.2 to -1.82 MPa and slightly erratic. None of these survivors developped leaves whereas p(L) = 0.50 in control (not shown).

Results for Low Salt experiment are presented as two graphs to emphasise there are two ranges, 1-10 and 10-75 mM NaCl (Figure 6.5 b, c). Germination was high in all treatments (not shown). Survival and leaf growth were erratic with a decrease at 2.5 mM NaCl and again at 10 mM NaCl when p(s) and p(L) reached zero. There was no leaf growth in 10-75 mM NaCl (Figure 6.5 c). Reasonable survival p(s) = 0.73 at 25 mM NaCl contradicts survival at 10 mM NaCl and is attributed to an error in preparation of treatment solutions.

Salt and nutrients

Germination of ecotypes was high in all treatments with p(g) = 0.94-1.0, with no perceivable trend corresponding to decreasing nutrient concentration (not shown). Survival was little affected by a decrease in nutrient concentrations from 1/4 to 1/64 H. Survival response to dilutions less than 1/64 H varied slightly between ecotypes (Figure 6.6 a-f). For most, survival was lower at 1/128 H and even lower at 1/256 H. The exception was TOT, T. orientalis from Tasmania, which had maximal survival even in the most dilute nutrient treatment (Figure 6.6 f).

Similarly, leaf growth was initially high then decreased with no leaf growth at all in 1/256 H. Again, response shape differed between ecotypes. Whereas for most ecotypes p(L) decreased sharply between 1/64 and 1/128 H, TOT differed being the one most affected by nutrient dilution with p(L) = 0.27 at 1/64 H and p(L) = 0 at 1/128 H. Least

affected were the two Lake Wyangan ecotypes, LWN and LWS, with p(L) = 0.16-0.20 at 1/128 H.

One-way analyses of variance of treatment effects within an ecotype confirmed the trends described above (Table 6.2). Survival of four ecotypes, LWN LWS M and S, was significantly reduced in 1/256 H. Leaf growth of five ecotypes, LP LWN LWS M and S, was significantly reduced at 1/128 H whereas for TOT, 1/64 was the critical dilution.

Irradiance

Germination response to irradiance was similar for all ecotypes (Figure 6.7) and took the form of a rectangular hyperbola. Germination in the dark was typically close to zero, increased rapidly at low irradiances of 15-50 $\mu E\ m^{-2}\ s^{-1}$ then peaked well below 220 $\mu E\ m^{-2}\ s^{-1}$, the highest treatment. For all ecotypes highest germination was near the maximum possible with p(g) close to 1.0. Maximal germination was reached at irradiances as low as 15-50 $\mu E\ m^{-2}\ s^{-1}$ (Figure 6.7) with the exception of TOT seeds which reached maximum germination at higher irradiances, 50-90 $\mu E\ m^{-2}\ s^{-1}$.

Survival of germinated seeds (not shown) was consistently high with $p(s) > 0.95$ for all ecotypes x irradiance x salt treatments, except at 15 $\mu E\ m^{-2}\ s^{-1}$ in 50 mM NaCl where survival tended to be slightly lower, $p(s) > 0.81$.

All ecotypes showed the same growth response with p(L) increasing in response to increasing irradiance (Figure 6.7) but response shape differed between ecotypes. Within the tested range of 15 to 220 $\mu E\ m^{-2}\ s^{-1}$, some showed a linear increase with no clear asymptote (LP and S) whereas others reached peak growth at 50 $\mu E\ m^{-2}\ s^{-1}$ (TOG and TOT). Leaf growth was much lower in P seeds than other ecotypes. Germination, survival and leaf growth were slsightly lower in 50 mM NaCl than in 0 mM NaCl but the effect was small and not significant (Table

6.3).

Photoperiod

Increasing daylength from 8 to 16 hours did not increase germination (Figure 6.8) except for P seeds (Table 6.4). The proportion of live seedlings with leaves increased with increasing daylength and this was most noticeable in P seeds and least evident in LWN seeds. Leaf growth was not affected by 50 mM NaCl (Table 6.4). As in the Irradiance experiment, P seedlings showed least growth with p(L) = 0.62 at 16 hours compared to p(L) = 0.61-70 at 8 hours for other ecotypes.

6.9 Site and seed characteristics

Sites where seeds were collected covered a latitudinal range of 10° from Parachilna in South Australia to Scottsfield, Tasmania (Table 6.1). Site conductivity ranged from 120 $\mu S\ cm^{-1}$ for Scottsfield, Tasmania to 3700 $\mu S\ cm^{-1}$ for Marne River and 5510 $\mu S\ cm^{-1}$ for Parachilna in South Australia. Assuming all ecotypes flowered at the end of October, inflorescences were collected 2-10 months after flowering.

Seed characteristics are summarised in Table 6.5. Seeds of T. domingensis were lighter, 24.4-35.6 μg, than T. orientalis seeds. T. domingensis seeds collected in South Australia were significantly lighter than LWN seeds from New South Wales.

Nitrogen content was 21-36 mg N g $seed^{-1}$ dry weight and was significantly lower in TOT seeds than all others, 21.4 compared to 28.2-36.5. Approximately half seed weight was carbon, 425-539 mg g^{-1} seed dry weight with no significant differences between ecotypes.

Sodium concentration ranged from 0.11 to 0.34 mg Na g^{-1} seed dry weight. M seeds had significantly higher Na+ concentrations than other seeds except S seeds. Potassium concentrations were 10-100 times higher than sodium with a range of 2.00 to 3.06 mg K+ seed g^{-1} dry weight.

Concentration of potassium was significantly higher in S seeds than in other ecotypes and significantly lower in TOT and LWS seeds.

The possibility that site characteristics could influence seed size, that size and other seed characteristics could be correlated, and that seed characteristics could influence seedling reponse was investigated using regression techniques. Conductivity, latitude and maturation time explained 94% of variation in seed weight (Table 6.6) but anova and standard partial regression coefficients showed that only one of these was significant, conductivity (Figure 6.9 a). Seed sodium concentration was positively and significantly correlated with habitat conductivity, $r^2 = 0.5819$ with alpha <0.05 (Figure 6.9 b). Concentrations of N, Na and K tended to decrease as seed size decreased but correlation coefficients of -0.6260, -0.3971 and -0.6040 were not significant.

Of the six multiple regressions done testing seedling response against seed characteristics, only one was significant, leaf growth at 1/64 H in 50 mM NaCl (Table 6.7). Standard partial regression coefficients showed response to this treatment was positively associated with seed size and to a lesser extent was negatively associated with nitrogen concentration. Sodium concentration was least important. Although the coefficient of determination for growth in 1/128 H was also high it was not significant. The sample size of six to eight ecotypes was small in relation to the number of independent variables (four) which reduced the degrees of freedom to 3 or 1, depending on the number of ecotypes tested.

6.10 Ecotypic variation

The numerical classification clustering ecotypes by similarity in seed characteristics shows three groups (Figure 6.10 a). TOT is separated from other ecotypes at the highest level and comprises a group of its own; the remaining group of seven can be divided into two with LWN, LWS and TOG in one group and LP M S and P in the other. This last group is characterised

by repeated fusions at short distances, or chaining. Thus seed characteristics tend to be clinal rather than discretely distributed with the result that the group is not homogeneous or pristinely defined.

Based on seed characteristics presented above (and see Table 6.5), the distinctive features of these three groups are as follows. The first group (TOT) has the largest seed, 48.9 μg and lowest concentrations of N and K, 21.4 and 2.00 mg g^{-1} dry seed. The second group (TOG LWS and LWN) has seeds of intermediate size, 30.3-37.6 μg and intermediate Na and K concentrations, 0.1427-0.1969 and 2.06-2.74 mg g^{-1} dry seed. The third group (LP M P and S) has the smallest seeds, 24.4-27.4 μg, and highest K+ concentration with 2.60-3.06 mg K+ g^{-1} seed. These groups correspond with provenance, Tasmania, Griffith area of New South Wales, and South Australia.

The dendrogram resulting from clustering ecotypes by similarities in seedling response shows two distinct groups (Figure 6.10 b) corresponding to species. One group comprises TOT and TOG, both *T. orientalis*, and the remaining six ecotypes, all *T. domingensis*, are in the other. There is an indication that the *T. domingensis* group could be broken into two groups, again, corresponding to regional provenance.

DISCUSSION

6.11 PEG bioassay

The three PEG polymers tested were all thought to be too large to pass through cell walls and membranes. Average molecular diameter of the smallest polymer, PEG 6000, is 5.2 nm which is larger than the pore diameter of cells in roots hairs, 3.5 nm or palisade parenchyma, 4.5 nm (Carpita *et al.* 1979). However the three polymers did not elicit the same response in *T. domingensis* seeds (Figure 6.3). At high PEG

concentrations, survival decreased most sharply in PEG 6000 and least in PEG 20,000, showing the smallest polymer had the greatest effect. Although the diameter of the average PEG 6000 molecule is apparently too large to pass through cell pores, uptake cannot be discounted completely. Molecular weight is only an average value therefore it is likely some molecules will be small enough to pass through cell pores. These will be more numerous in the smallest polymer and at highest concentrations.

An alternative explanation is that the correspondence between polymer effect and polymer size was fortuituous and was caused by differences in the manufacturing process. A number of catalysts polymerise ethylene oxide and different techniques are used to manufacture large and small polymers (Bailey and Koleske 1976). The three polymers used came from different suppliers.

An elimination process was used to select the most appropriate PEG polymer. PEG 6000 was discounted because of its obvious adverse effect on survival, and because the wide range of values published for its regression coefficient, 1.24 to 2.0 (Appendix 7, Table A7.1) suggested a certain variability. Although PEG 10,000 and PEG 20,000 had very similar effects on T. domingensis (Figure 6.3), PEG 20,000 was chosen because of its slightly higher survival rates and because its regression coefficient of 1.827 was more consistent with the published value of 2.1 (Table A7.1). There were no published values for PEG 10,000 to use as an independent check.

6.12 Water, salinity and light

Water potential

Species differences in critical hydration level have been interpreted as having an adaptive significance. Germination of native Australian grasses was limited to moister conditions than introduced species (Watt 1982). This was interpreted as showing that native species would be better adapted to their environment and that germination in wetter conditions meant seedlings would have a higher probability of

establishment (Watt 1982). A similar argument was put forward in relation to shrubs of the semi-arid zone (Sharma 1976).

The critical hydration point for all Typha ecotypes, between -1.11 and -1.42 MPa (Figure 6.4), was lower than crop species such as carrots, lettuce and citrus with a critical hydration point between -0.5 MPa and -1.0 MPa (Kaufman 1969, Hegarty 1977) or rice at -0.79 MPa. However it is similar to shrubs and grasses of semi-arid Australia, -1.0 to -1.5 MPa (Sharma 1976, Watt 1982) which is close to the Permanent Wilting Point.

This low critical hydration point means Typha seeds can germinate over a wide range in soil moisture and contrasts markedly with the narrow range tolerated by adult plants where R* is close to Field Capacity (4.7). The adaptive value of this response for a wetland plant is not obvious. It is likely this has not been positively selected but is associated with another character which is. This would mean low critical hydration point is a neutral character.

Germination of T. domingensis was high over a water potential range from 0 to -0.84 MPa and showed only a slight tailing off at the lowest water potentials used. This response was the same whether water potential was matric or osmotic. Usually a decrease in matric potential has a greater inhibitory effect on germination than an equivalent or larger decrease in osmotic potential (Koller and Hadas 1982). This differential effect is caused by the drying out process. As water recedes first from large then from smaller pores, soil hydraulic conductivity decreases and eventually the contact between seed and soil water is broken.

Matric and osmotic potentials were both solutions which meant perfect contact between seed and soil water in all treatments. The contrast between seedling survival in High Salt and its control or PEG 20,000 shows water uptake was accompanied by salt influx. This is not surprising as cellular membranes of seeds are initially leaky and membrane integrity

is only restored by imbibition (Bewley and Black 1979, 1982). Presumably this is the reason germination is more salt sensitive than subsequent seedling growth.

Salinity

These results show T. domingensis is salt sensitive when compared with halophytes. Germination of Puccinellia nuttalliana and Crithmum maritimum is highest in solutions without NaCl and decreases with increasing salt concentration to 34% at approximately -0.27 molal NaCl or 35% at 0.12 molar NaCl respectively (Macke and Ungar 1971, Marchioni-Ortu and Bocchieri 1984). Unfortunately both studies define germination as emergence of coleoptile with no reference to seedling viability.

As pointed out earlier (6.2) apparently "small" differences in experimental procedure affect germination and survival. Germination in Typha, and therefore interpretation of NaCl response, is altered by pre-treatments and treatments such as whether seeds have been stratified or not (Galinato and van der Valk 1986), which sodium salt is used (Choudhuri 1968), and whether saline solutions are pure (Choudhuri 1968, Galinato and van der Valk 1986) or include other ions (Howard-Williams 1975) and if so which ones. The toxic effect of 50 mM NaCl was completely lost when nutrients were present at 1/4 H concentrations. Germination, survival and leaf growth, although consistently lower in 50 mM NaCl, were statistically indistinguishable from 1/4 H and 0 mM NaCl (Tables 6.4 and 6.5).

Excess sodium chloride is thought to affect either membrane or enzyme function (Greenway and Munns 1980). Salt-induced impairment of membrane function means ion selection, sodium extrusion and prevention of solute leakage from cytoplasm are disrupted. Such membranes are described as "leaky". Because normal membrane function is largely dependent on adequate supplies of calcium in the cell environment (Kirkby and Pilbeam

1985), much recent research on salinity effects at the cellular level has focussed on the mitigating effects of calcium and Na:Ca molar ratio. The critical Na:Ca above which fresh weight of beans is reduced is 17:1 (Greenway and Munns 1980). Other studies have emphasised the importance of nitrogen, usually as nitrate, in mitigating salt effects. Thus the following sequence could be presented using $Na:NO_3$ ratio.

Survival and growth of Typha seedlings were significantly reduced when nutrients were 1/256 and 1/128 H respectively. This was equivalent to Na:Ca molar ratio of 2560:1 and 1280:1. Although higher than critical values for beans, these ratios should not be interpreted as evidence for salinity tolerance. Typha shows an ontogenetic shift which can be described as a shrinking habitat niche because the critical Na:Ca ratio decreases as the plant grows. Thus for 8 day old T. domingensis seedlings the critical ratio for survival was 2560:1 and for growth was 1280:1. With slightly older T. domingensis seedlings from Malawi, root growth was reduced at 21 days when Na:Ca ratio was 954 to 477:1 but not when it was 191:1 or less (Howard-Williams 1975). Growth of mature T. domingensis ramets from Lake Wyangan in New South Wales was severely reduced at 125:1 and slightly reduced at 6:1 (Hocking 1981).

Light

The experiments using irradiance and photoperiod were done to ensure growth cabinets settings for water potential experiments had not unduly favoured one ecotype over another. Previous measurements of germination response to light had used illuminance (Sharma and Gopal 1983) which is not appropriate when considering growth.

The irradiance experiment showed that a light:dark cycle of 16:8 hours and an incident irradiance of 220 $\mu E\ m^{-2}\ s^{-1}$ was unlikely to introduce bias because peak germination occurred below this. This was not so for leaf growth where only TOG and TOT showed a clear peak below 220

$\mu E\ m^{-2}\ s^{-1}$. With the exception of P seeds, the remainder were obviously close to optimum irradiance as p(L) values were greater than 0.8. The photoperiod experiment was done at slightly higher irradiance. Comparison with the irradiance experiment shows this extra light energy increased leaf growth, particularly in the case of P seedlings where p(L) was doubled (Figures 6.6, 6.7).

For most seeds with a positive light requirement, germination is a function of total light energy received. This can be calculated as the product of intensity and duration (Mayer and Poljakoff-Mayber 1975) or irradiance x photoperiod. For all Typha ecotypes, germination was near maximal at 50-90 $\mu E\ m^{-2}\ s^{-1}$ in 16 hours light (Figure 6.6), equivalent to 100-180 $\mu E\ m^{-2}\ s^{-1}$ in 8 hours light. Total energy in the photoperiod experiment, with 250 $\mu E\ m^{-2}\ s^{-1}$ for 8 to 16 hours light, was well above this which explains why increasing photoperiod had no significant effect on germination (Table 6.4).

As for salinity, an ontogenetic shift is indicated, but with threshold energy totals for maximum leaf growth being generally higher and more variable than for maximal germination. For TOT seeds, near maximal leaf growth occurred at 50 $\mu E\ m^{-2}\ s^{-1}$ in 16 hours light (Figure 6.6). As this was lower than all treatments in photoperiod experiment, photoperiod was not significant. In contrast, for LWN M and P ecotypes, near maximal leaf growth occurred at 150-220 $\mu E\ m^{-2}\ s^{-1}$ in 16 hours light (Figure 6.6), equivalent to 300+ $\mu E\ m^{-2}\ s^{-1}$ over 8 hours. This was between 8 and 16 hours light, so photoperiod was significant for these ecotypes (Table 6.7). Total energy thresholds make it possible to predict whether increasing photoperiod will significantly affect leaf growth of the four untested ecotypes. Thus TOG, with an irradiance response similar to TOT, is unlikely to be affected, whereas LWS, with an irradiance response similar to LWN, probably will.

6.13 Seed characteristics and variability

Seed size varied between ecotypes and a species difference was indicated with narrow-leafed species having lighter seeds than broad-leafed species (Table 6.5). A similar difference has been described for sympatric North American species. Seeds of the narrow-leafed T. angustifolia are lighter, with a mean weight of 34.9 µg and a range of 23.9-50.7 µg, than seeds of the broad-leafed T. latifolia, with a mean weight of 62.37 µg and a range of 46.9-96.5 µg (Marsh 1962).

Intra-specific variations in seed weight have been attributed to harvest time and habitat differences in moisture, temperature and photoperiod (Cavers and Steel 1984, Benjamin and Hardwick 1986). Harvest time was not a relevant factor here (Table 6.6) probably because seeds were already mature when collected. Reproductive structures of T. orientalis showed little weight gain from January onwards (Figure 2.2) and most seeds used in this study were collected later than this (Table 6.1). Seed size was inversely and significantly related to habitat conductivity (Table 6.6) which in turn was correlated with seed sodium content (Figure 6.9 b). This suggests that in saline habitats it is not only vegetative biomass that is reduced (Hocking 1981) but also the individual units of reproductive biomass.

Species differences in seed composition are often interpreted as adaptive strategies to the habitat. Proteaceous seeds are particularly rich in nitrogen, with a mean concentration of 95 mg N g^{-1} dry weight embryo compared to 40 mg for non-Proteaceous species (Pate et al. 1986). These values are not strictly comparable with Typha results presented here as this study included both testa and embryo in the analysis. Nitrogen concentrations for Typha seeds, 21-36 mg g^{-1} dry weight, were slightly lower than for 9 Grevillea spp. and two strand-line plants in Western Australia, 28.8-45.2 and 36.5-46.0 mg N g^{-1} seed dry weight

(Hocking 1982, 1986). This was not unexpected as the germination niche of Typha is unlikely to be oligotrophic and a maternal care strategy of high nitrogen concentration would not be critical. Although concentrations are similar, the difference in seed size means the nitrogen load available to Typha seedlings is 500-1000 times smaller.

Some species in saline habitats exclude Na+ and Cl- from the seed. Seeds of Cakile maritima have only 0.17-0.47 mg Na^+ g^{-1} seed which is 360 times less than the leaves and 74 times less than the silicule (Hocking 1982). Although sodium concentrations in Typha seeds were comparable, ranging from 0.1105 to 0.3365 mg Na^+ g^{-1} seed (Table 6.5), the correlation between habitat and sodium concentration shows this was a direct environmental response and not ion exclusion. This is consistent with Typha as a freshwater plant.

Clustering ecotypes by similarities in seed characteristics showed two groups (Figure 6.10 a), TOT and the rest, with the rest dividing into two further groups. Size appeared to be the principal characteristic determining cluster shape, however geographical distribution was also implicated.

The exact basis for the clustering cannot be determined because there is an interdepence between factors. Collecting sites can be ranked according to conductivity whether low, medium or high (Table 6.1) and this roughly corresponds with the three provenance areas of Tasmania, New South Wales and South Australia. Conversely, the three regions differ in seed size, which is correlated with habitat conductivity (Table 6.6). Species distribution is a further complicating factor. T. domingensis which has smaller seeds is believed to be more typical of inland habitats than T. orientalis (Briggs and Johnson 1968) and inland waters in South Australia are more likely to be brackish and ephemeral than irrigation waters of New South Wales or Tasmania (Peck et al. 1983).

6.14 Ecotypic variation

An assessment of ecotypic variation in Typha is limited by the smallness of the data base, only eight ecotypes comprising two T. orientalis and six T. domingensis, two from the same lake in New South Wales. This compares unfavourably with 33 sites used by McNaughton (1966). In addition intra-population variation was not considered. Thus ecotypic differences can be tentatively identified only at a coarse scale as any evidence of clinal variations is likely to be obscured by other environmental gradients acting as noise.

Seeds came from a wide area of south-east Australia (Figure 6.2). This included a range in climate from semi-arid to temperate, and site conditions from fresh to brackish. It probably also included a range in water regime from permanently wet to ephemeral but this was not included (Table 6.1) because information was incomplete. For example, LWN and LWS came from Lake Wyangan, sites which are known to be wet throughout the year, whereas the site for ecotype P in the Flinders Ranges is probably ephemeral. The two most extreme site conditions, represented by TOT and P seeds, are opposite in terms of latitude, climate and conductivity, as well as species (Figure 6.2, Table 6.1).

As a group, Typha seeds and seedlings had clear well-defined germination, survival and growth responses to experimental conditions (6.12). However group response was not uniform and it is these non-uniform responses that will be discussed here. Problems with analyses meant ecotypes were not statistically compared so responses different from the main population trend have been identified from graphs and tables.

Distinctive germination responses were the higher irradiance requirements for germination of TOT seeds, and the positive response of P seeds to increasing photoperiod. Distinctive survival responses were the

lower survival of P seedlings to water potentials of -0.84 MPa and below, and the higher survival of TOT seedlings in 50 mM NaCl at the most dilute nutrient concentrations tested. Distinctive growth responses were the persistently low level of leaf development of P seedlings in all experiments and treatments, the greater requirement of TOT seedlings for nutrients in 50 mM NaCl, and lower irradiance levels required by TOT and TOG to reach near maximal leaf development. Thus P and TOT seedlings consistently differed from other ecotypes which suggests these variations are associated with some axis between the extremes described above.

In contrast the dendrogram for physiological responses (Figure 6.10 b) emphasised a taxonomic separation. The T. orientalis ecotypes, TOT and TOG, were grouped together but separate from the remaining group which was entirely T. domingensis. Despite being as distinctive as TOT (see above), P was not separated from other ecotypes and instead was virtually indistinguishable from LP. This taxonomic separation may be a product of the program and of the responses used in analysis. The program calculates missing values by extrapolation so it is possible the dendrogram is an overemphasised trend in existing data. The TOG ecotype was only used in two experiments, water potential and irradiance or only 6 out of 15 characters in the analysis (Appendix 8). The distinctive trend in these experiments is similarity in the irradiance response of TOT and TOG which, if extrapolated, would account for their linkage in the dendrogram. Analysis did not separate P ecotypes from remaining ecotypes, which were all T. domingensis, because characteristics used did not include all the distinctive ones.

The coincidence between ecotypes with the most distinctive responses and those from the most extreme sites makes it impossible to ascertain the relative importance of species or population differences, and climatic or habitat gradients, and the interaction of these with seed

characteristics. The possibility that variations in seed characteristics could account for variations in seedling response was shown to be statistically unlikely as only one out of six tested was significant (Table 6.7). The raw data indicated the contrary. Thus the ecotype with the least seed nitrogen (TOT) had least leaf growth in salt-stress conditions; and the ecotype with the lowest seed weight (P) had lowest levels of leaf development whereas the largest seed (TOT) had consistently high levels of leaf development. Resolution of this question of whether seed characteristics influence seedling response and eventually their success, requires a larger and better structured data base, and the inclusion of other characteristics such as site nutrient status and seed calcium content.

For experimentally-induced differences, evident in 8 day old seedlings, to have biological significance they must reflect the probability of establishment. For plants such as Typha with small seeds and small reserves, the period after germination and before establishment must be a race against time. Ecotypes with relatively larger seeds, such as TOT, may be at an advantage.

However the significance of this is difficult to assess because, ultimately, it is a question of converting a probability to a real number. From an evolutionary perspective, the establishment of only one seedling constitutes a "success". When seed numbers are high, as for Typha, ecotype differences in probability may become meaningless if all probabilities convert to a number greater than one. Although p(L) may be relevant in a competitive situation such as a germination flush on a mudflat, other growth information is needed to predict or interpret the long-term. Competitive success does not necessarily correlate with seed size and may instead be determined by environment changes such as position along a water gradient (Grace 1985). Assuming seed size is

relevant to establishment, it is unlikely to be made effective because of the large distance between localities of the largest and smallest ecotypes.

Table 6.1
Collecting details

Table showing locality, collecting date and site conductivity

Acronym & locality		Lat	Date	Cond
T. domingensis				
LP	Little Para River SA	34.25	Dec 81	1560
LWN	Lake Wyangan NSW, north	34.75	Apr 81	1370
LWS	Lake Wyangan NSW, south	34.75	Apr 81	1370
M	River Marne, SA	34.75	Aug 83	3700
P	Parachilna, SA	31.00	Jun 83	5510
S	Strathmont, SA	34.25	Jun 83	2000
T. orientalis				
TOG	Griffith NSW	34.75	July 80	900
TOT	Scottsfield Tas	41.25	Jun 82	120

KEY
Cond = Conductivity in $\mu S\ cm^{-1}$
Lat = Latitude in °S expressed as decimal for regression

Table 6.2
Salinity and nutrient levels

Comparison of survival p(s) and leaf growth p(L) of six Typha ecotypes in 50 mM NaCl in serially diluted nutrients. Data are mean of seven replicates with standard deviation in brackets on line below. Analysis is treatment comparison within an ecotype (one-way anova, alph <0.05). Data underlined are significantly different from other data within a row.

Ecotype	1/4 H	1/64 H	1/128 H	1/256 H
Survival				
LP	1.0	1.0	1.0	0.8714
	0	0	0	0.1704
LWN	1.0	0.9711	0.8857	0.6552
	0	0.0496	0.1069	0.1541
LWS	0.9857	1.0	0.9286	0.7260
	0.0378	0	0.0756	0.1503
M	0.9760	0.9857	0.9270	0.7448
	0.0411	0.0378	0.0764	0.3108
S	1.0	0.9762	0.9597	0.5120
	0	0	0.0344	0.0315
TOT	1.0	1.0	0.9870	0.9881
	0	0	0.0344	0.0315
Growth				
LP	0.7639	0.8583	0.0469	0
	0.3279	0.1413	0.0626	-
LWN	0.8391	0.7908	0.1824	0
	0.1469	0.1618	0.1884	-
LWS	0.8894	0.9000	0.1599	0
	0.1470	0.1155	0.1493	-
M	0.8781	0.9297	0.0582	0
	0.1524	0.0918	0.0748	-
S	0.8719	0.7652	0	0
	0.1306	0.1231	-	-
TOT	0.9491	0.2598	0	0
	0.0709	0.1361	-	-

Table 6.3
Leaf growth, irradiance and NaCl

Comparison of leaf growth
in 0 mM and 50 mM NaCl, with 1/4 H nutrients.

ANOVA Table: Model I
Ecotype x NaCl at 220 $\mu E\ m^{-2}\ s^{-1}$

Source of variation	Degrees of freedom	Fs	Significance
Ecotype	7,128	20.02	***
NaCl	1,128	0.0787	NS
Ecotype x NaCl	7,128	0.9725	NS

Table 6.4
Ecotype, photoperiod and salt

Table shows the effects of 8 v 16 hours photoperiod in 0 v 50 mM NaCl on germination p(g) and leaf growth p(L) for each ecotype 1/4 H.
Comparisons were done by two-way analysis of variance.

	Response p(g)		Response p(L)	
Ecotype	Photoperiod	NaCl	Photoperiod	NaCl
LWN	NS	NS	***	NS
M	-	-	***	NS
P	**	NS	***	NS
TOT	NS	NS	NS	NS

Table 6.5

Seed characteristics

Table shows seed weight in µg and chemical compositon as concentration of nitrogen, carbon, sodium and potassium as mg g^{-1} seed dry weight. Mean values are on first line with standard error of regression coefficient for seed weight and standard deviation of element concentration on following line.

Seed	Weight	N	C	Na	K
LP	26.2	31.50	510.2	0.1105	2.60
	1.2657	4.597	131.557	0.0531	0.2038
LWN	35.6	36.48	457.92	0.1427	2.66
	2.0306	3.647	44.461	0.0520	0.1065
LWS	30.3	28.16	454.52	0.1674	2.06
	1.2774	7.882	107.628	0.0608	0.0957
M	27.4	31.44	514.12	0.3365	2.87
	1.8514	3.366	30.535	0.0203	0.1258
P	24.4	32.82	478.80	0.2804	2.72
	0.9264	4.651	71.128	0.0717	0.0732
S	26.2	29.60	539.10	0.2185	3.06
	1.3891	2.601	15.042	0.0305	0.1249
TOG	37.6	29.28	484.12	0.1969	2.74
	n.a.	4.826	58.314	0.0368	0.2504
TOT	48.9	21.38	425.52	0.1565	2.00
	1.4572	3.749	82.562	0.0381	0.0711

Table 6.6
The influence of habitat characteristics and collection time on seed size

Multiple linear regression (MULREG)

Dependent variable is seed weight
y = weight in μg
Independent variables
x1 = habitat conductivity, $\log_{10}$ of $\mu S\ cm^{-1}$
x2 = latitude to nearest 15′
x3 = collecting date, months since October

ANOVA Table

Source of variation	Degrees of freedom	Fs	Significance
Explained:			
x1 + x2 + x3	3	19.74	**
x1	1	18.63	*
x2	1	2.32	NS
x3	1	4.88	NS
Unexplained	4		

Coefficient of multiple determination
$r^2 = 0.9367$

Standard partial regression coefficients

Variable	Beta-prime
x1	-1.38
x2	-0.49
x3	0.29

Table 6.7 a
Seed characteristics and physiological responses

Table shows the result of six multiple linear regressions where the dependent variable is treatment effect of eight ecotypes, standardised to control (see text).
Independent variables are seed characteristics, nitrogen, sodium, potassium and size as weight

Treatment effect	Result	Significance
Germination		
at -1.11 MPa	r^2 = 0.3909	NS
Survival		
at 90 μE m^{-2} s^{-1}		
in 0 mM NaCl	r^2 = 0.8343	NS
at 1/256 H in 50 mM NaCl	r^2 = 0.4706	NS
Growth		
at 1/4 H in 50 mM NaCl	r^2 = 0.4953	NS
at 1/64 H in 50 mM NaCl	r^2 = 0.9997	*
at 1/128 H in 50 mM NaCl	r^2 = 0.9273	NS

Table 6.7 b

Table gives statistical details of the only significant response v seed characteristic.

y = p(L) at 1/64 H in 50 mM NaCl
Independent variables are seed characteristics
x1 = nitrogen as % dry weight
x2 = sodium
x3 = potassium
x4 = size as μg

Anova table

Source of variation	Degrees of freedom	Fs	Significance
Explained	4	878.40	*
x1	1	617.04	*
x2	1	114.91	NS
x3	1	302.16	NS
x4	1	1112.23	*
Unexplained	1		

Standard partial regression coefficients or beta-prime

x1	-0.6064
x2	-0.2210
x3	0.4939
x4	0.8078

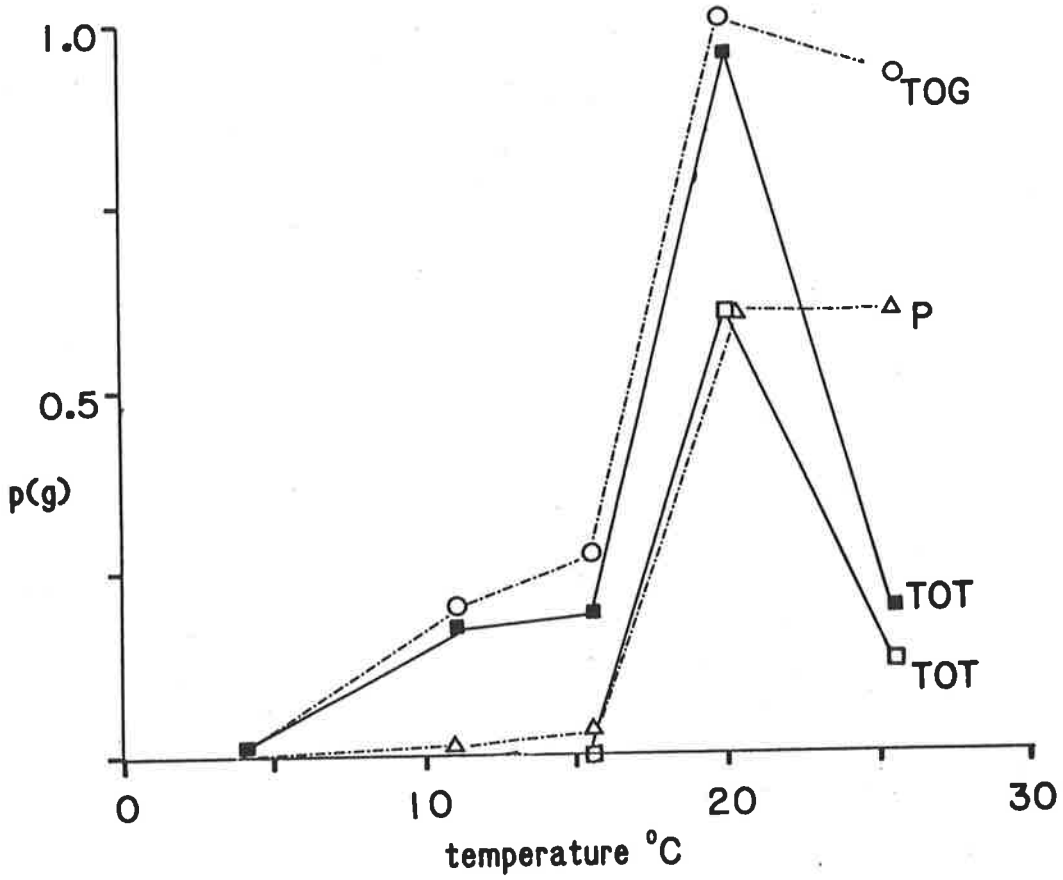

Figure 6.1
Temperature and germination of Australian Typha spp.

Germination response of Australian Typha spp. to temperatures ranging from 4-26°C (class experiments, Botany Department, University of Adelaide, 1983 and 1985). Data are proportion germinating, p, and n = 196-440. Seeds were from contrasting climates, a cool-mild area in north-east Tasmania (TOT), and warm-hot inland areas of mainland Australia (TOG and P). Further details in Table 6.1 and Figure 6.2.

Key
■ □ TOT = T. orientalis, Tasmania (1983 and 1985)
○ TOG = T. orientalis, Griffith, New South Wales
△ P = T. domingensis, Parachilna, South Australia
— Cool-mild climate
-·- Warm-hot climate

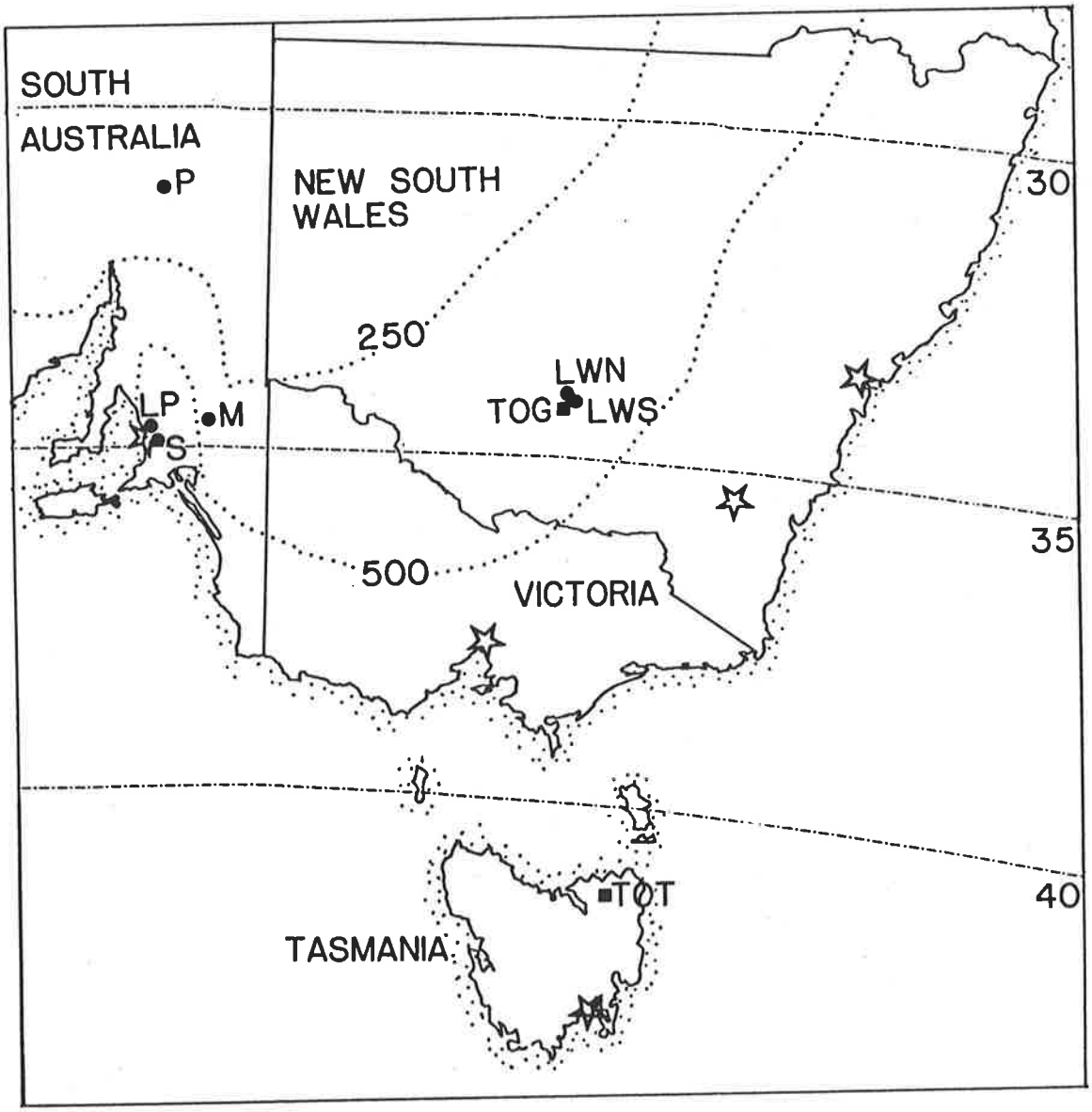

Figure 6.2
Seed provenance

Map of south-eastern Australia with every 5° latitude showing provenance of seeds used in germination experiments. Acronyms are explained in Table 6.1. Dotted lines show 250 and 500 mm isohyets for mean rainfall, hollow stars show state capitals.

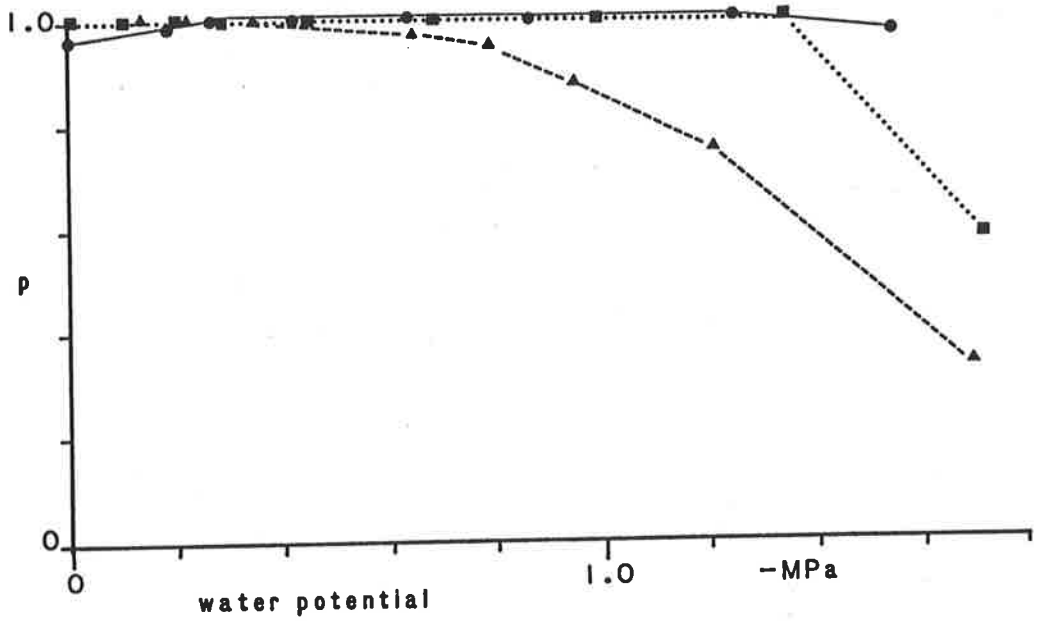

Figure 6.3
PEG bioassay

Germination of T. domingensis (LP seeds) in three PEG polymers, in concentrations of 0-0.4 molal, equivalent to water potentials of 0 to -1.71 MPa. Data as proportion, p.

Key
●—● PEG 6000
■··■ PEG 10,000
▲--▲ PEG 20,000

Figure 6.4
Matric potential

Germination and seedling survival of eight Typha ecotypes in matric potentials of 0 to -1.4 MPa. Data are proportion, p. Acronyms listed in Table 6.1.

Key
•—• p(g)
o----o p(s)

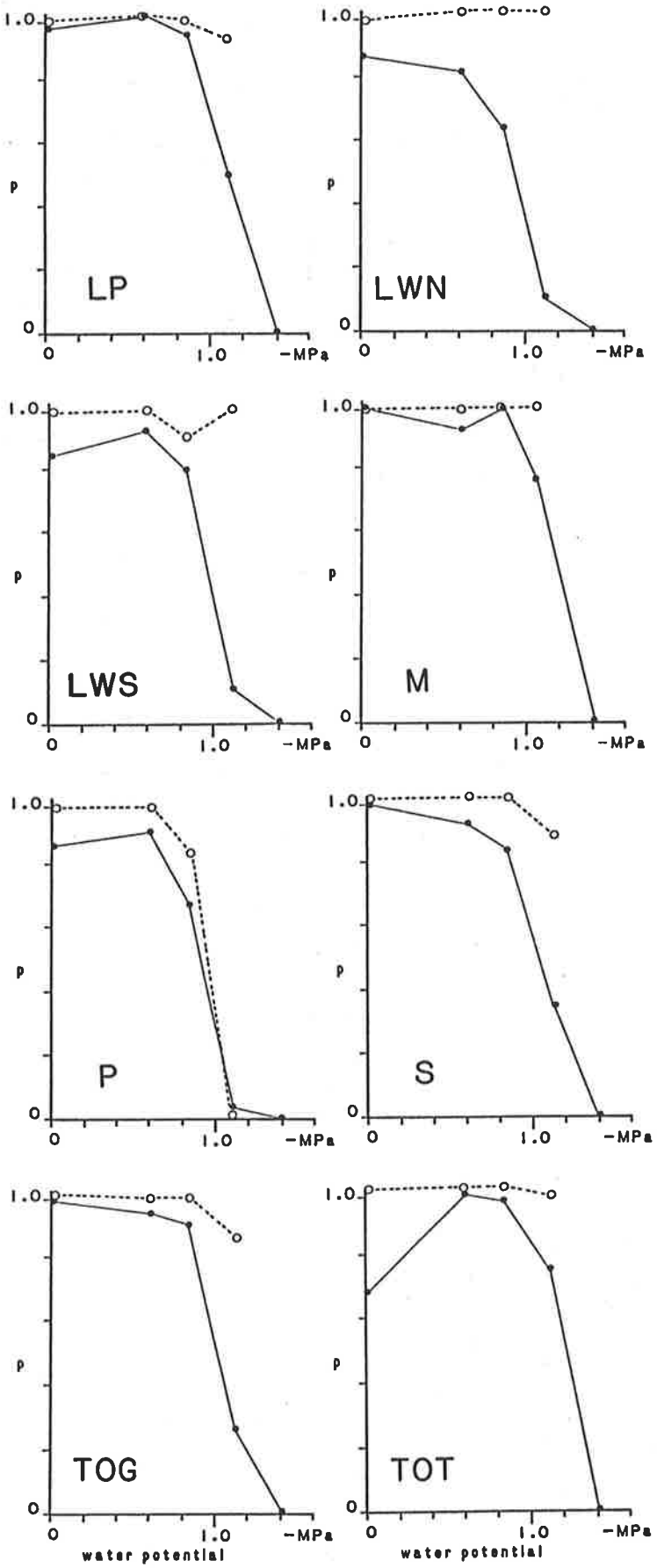

Figure 6.4
Matric potential

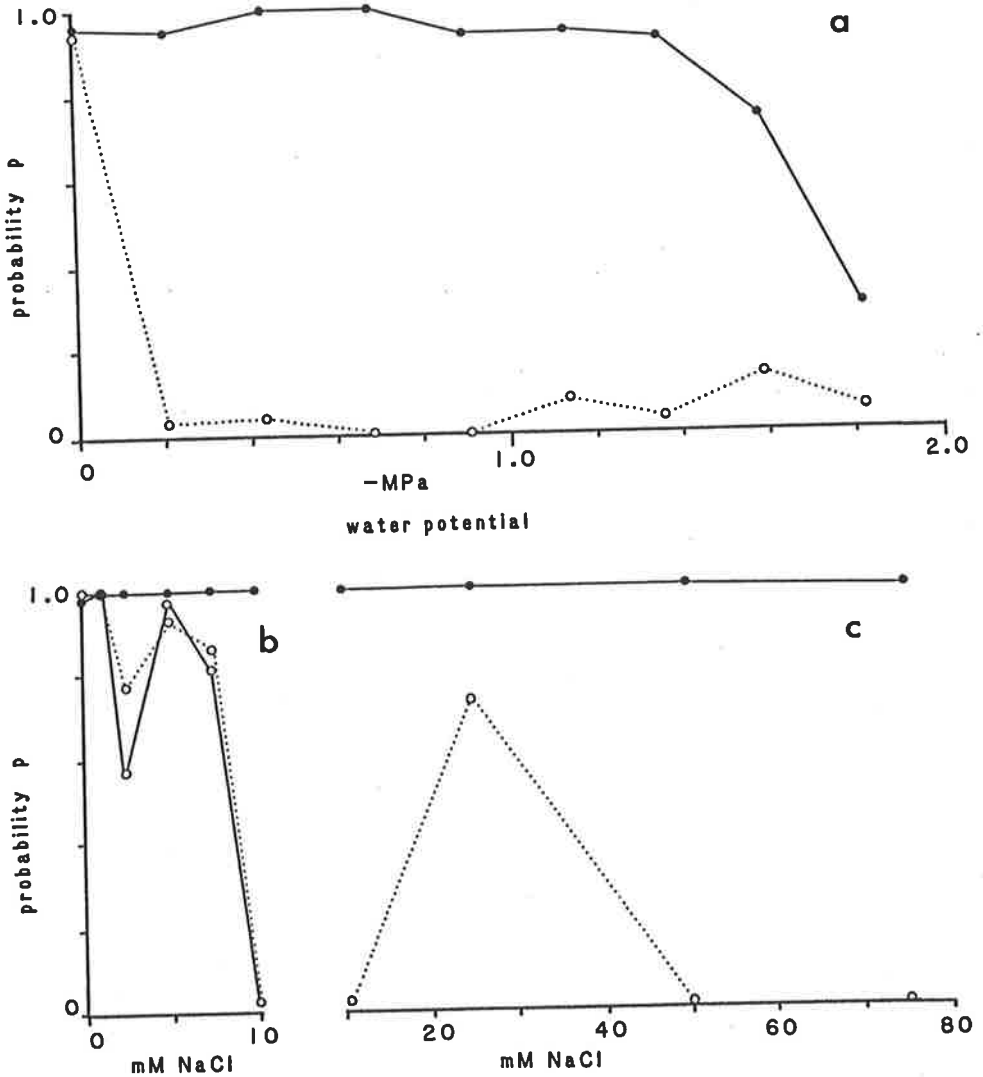

Figure 6.5
Osmotic potential

Germination, survival and leaf growth of T. domingensis (LP seeds) in High (0-0.4 molal) and Low (0-75 mM) pure NaCl. Data as proportion, p.

(a) High salt. Concentrations as water (osmotic) potential

(b) and (c) Low salt. Two concentrations ranges, 0-10 and 10-75 mM NaCl.

Key
●—● p(g)
o····o p(s)
o—o p(L)

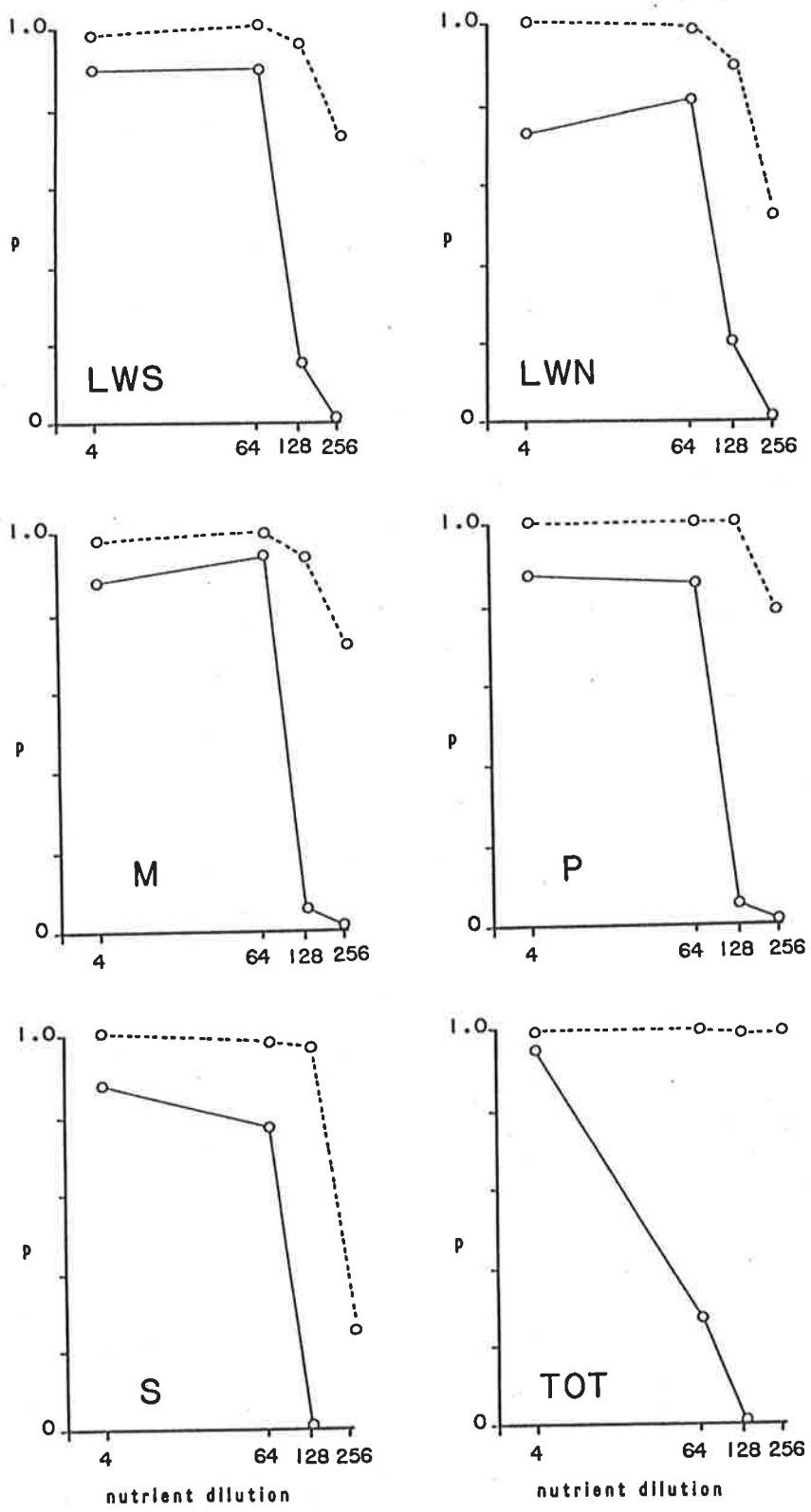

Figure 6.6
Salt and nutrients

Survival and leaf growth of six ecotypes in salt with nutrients present. Salt concentrations constant at 50 mM NaCl and nutrients diluted to 1/4 to 1/256 Hoagland's complete nutrient medium. Data are a proportion, p. Acronyms listed in Table 6.1.

Key
o----o p(s)
o——o p(L)

Figure 6.7
Irradiance

Germination and leaf growth of eight ecotypes in constant photoperiod of 16:8 hours light:dark at 20-22°C, but with irradiances varying from 0 to 220 $\mu E\ m^{-2}\ s^{-1}$. Data are a proportion, p. Acronyms in Table 6.1.

Key
●——● p(g)
○——○ p(L)

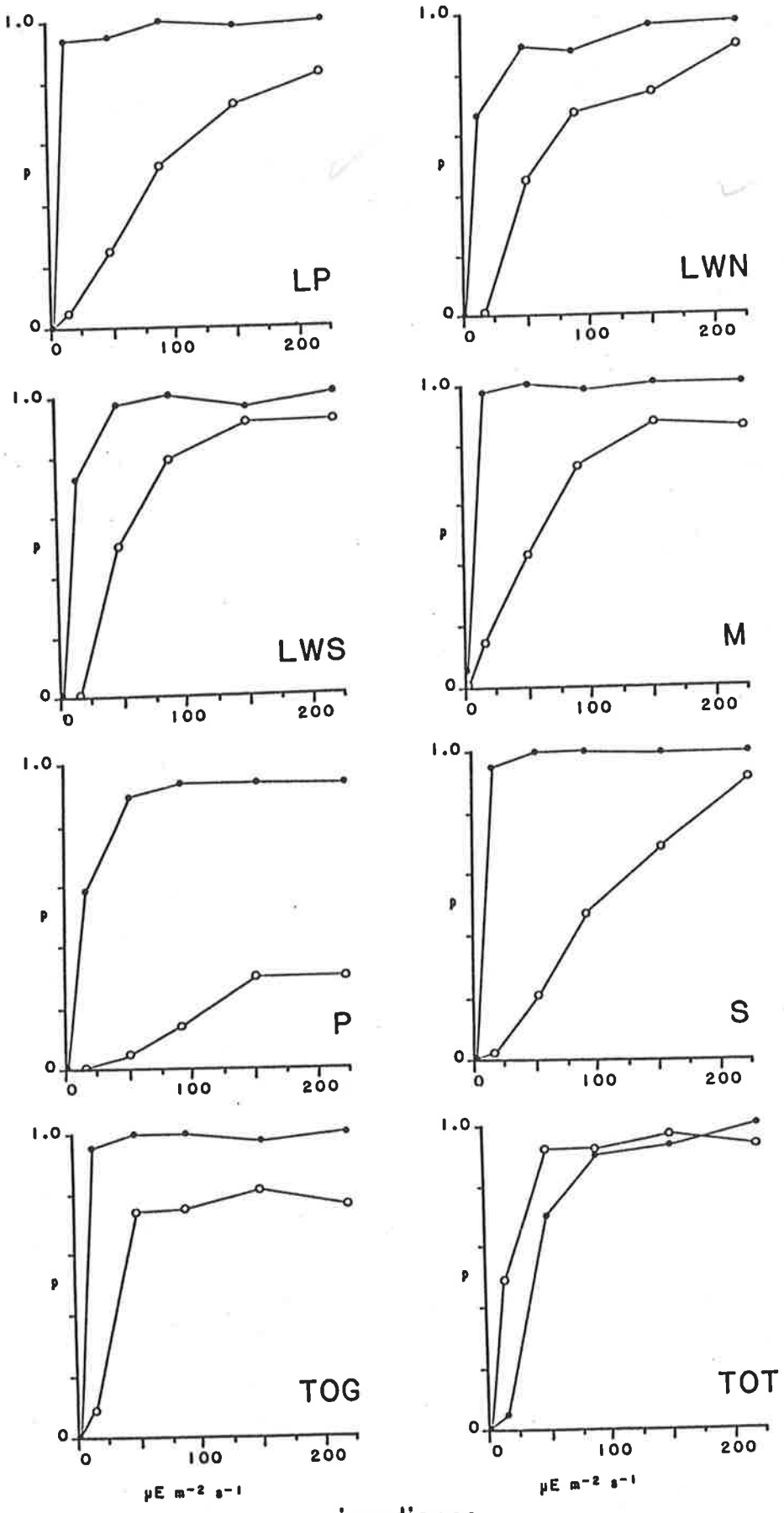

Figure 6.7
Irradiance

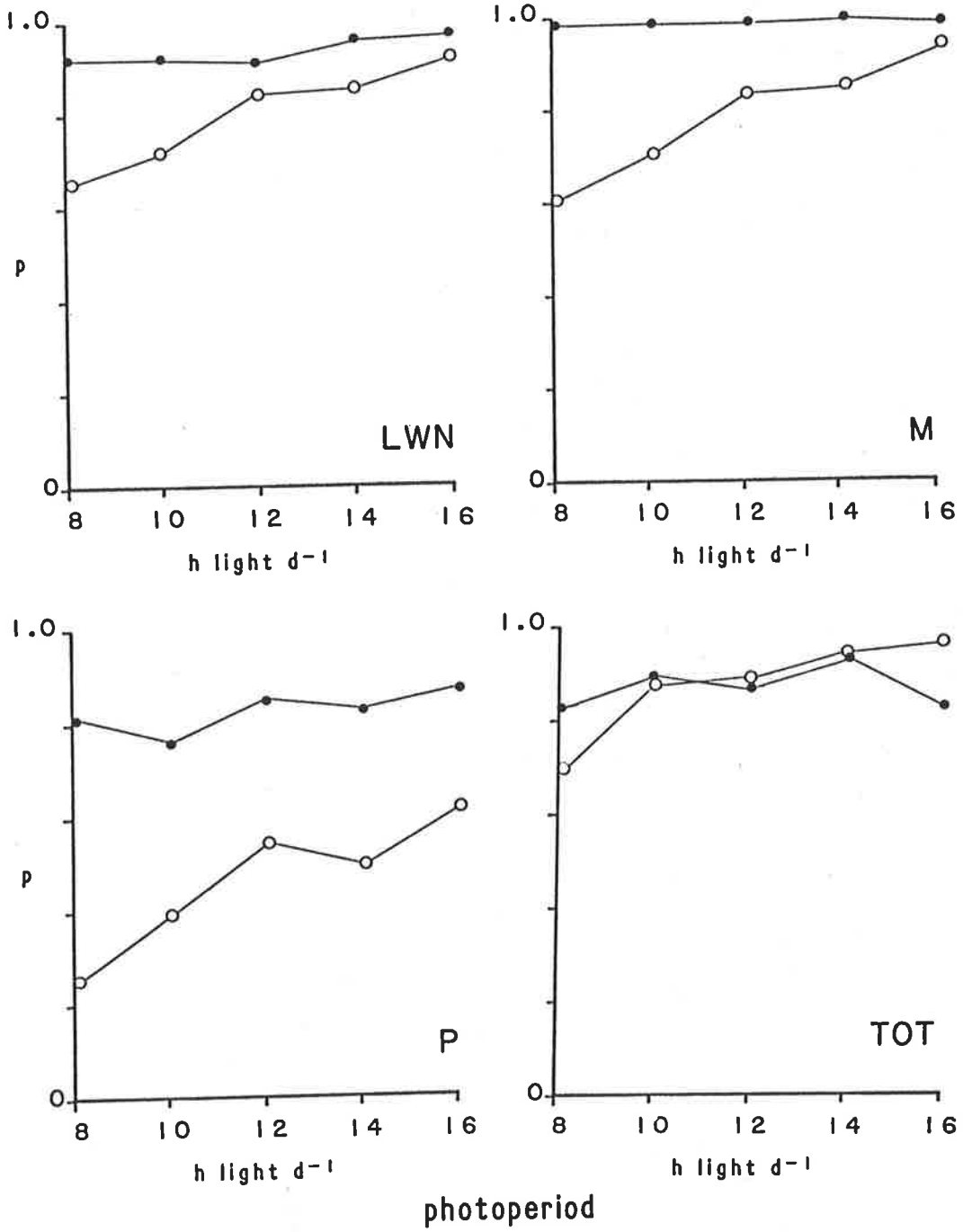

Figure 6.8
Photoperiod

Germination and leaf growth of four ecotypes in constant irradiance of 250 μE m^{-2} s^{-1} and 20-22°C, with variable light:dark periods ranging from 8:16 to 16:8 hours. Data are a proportion, p. Acronyms in Table 6.1.

Key
p(g)
p(L)

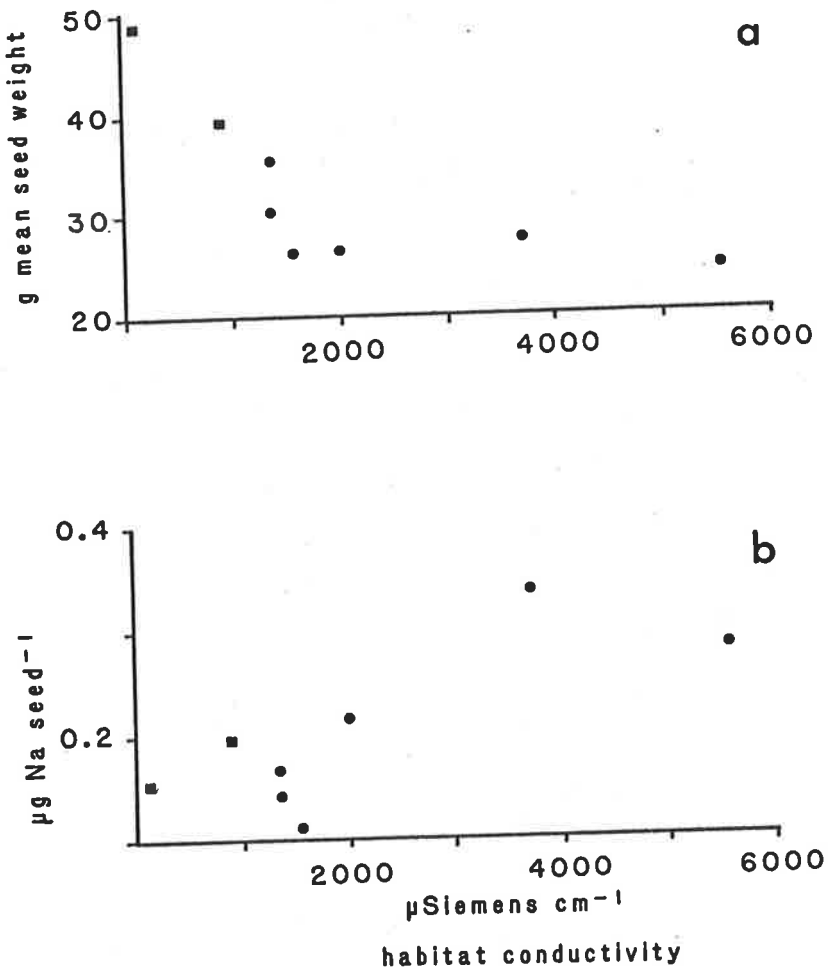

Figure 6.9
Site and seed characteristics

The effect of habitat conductivity on two seed characteristics for six T. domingensis ecotypes (•) and two T. orientalis ecotypes (▪).

(a) Mean seed weight, in µg

(b) Mean sodium concentration, in µg Na^+ $seed^{-1}$

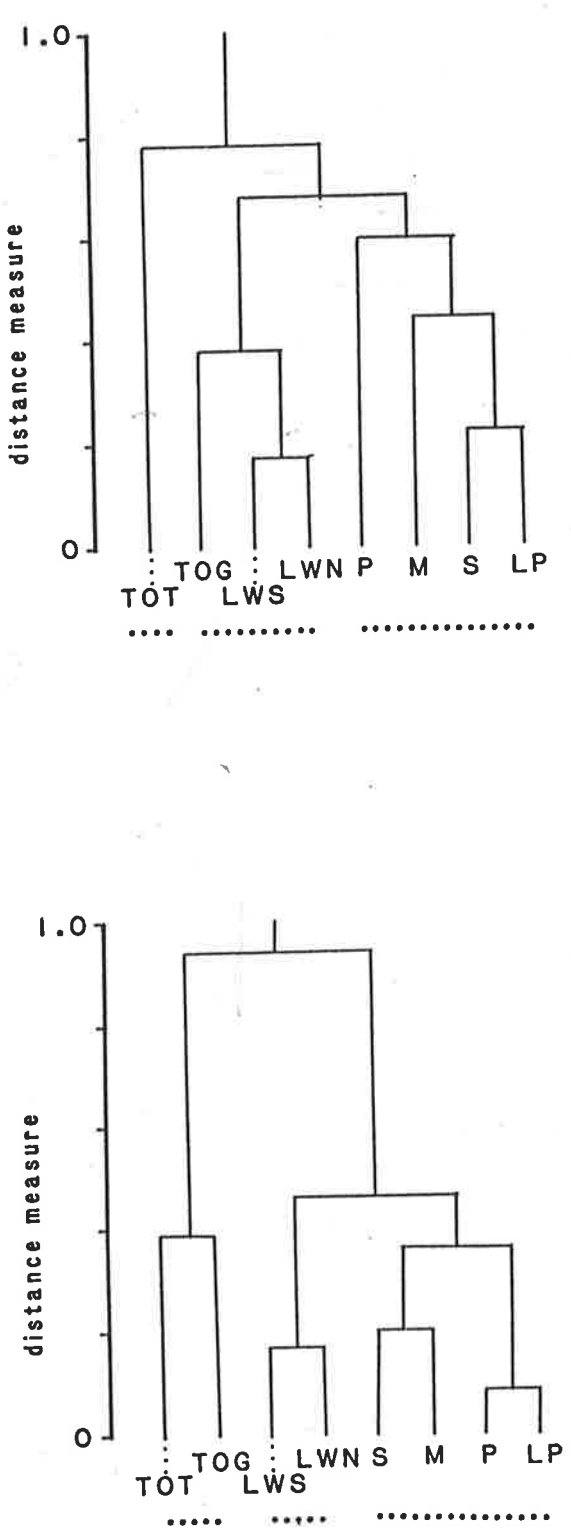

Figure 6.10
Ecotype classification

Dendrograms showing results of numerical classification of eight Typha ecotypes based on four seed characteristics, and fifteen seedling responses (listed in Appendix 8). Possible groupings are indicated by dotted underlining.

(a) Seed characteristics

(b) Seedling characteristics

Chapter Seven

CONCLUSION

7.1 Introduction

Four component niches were used as a framework to study the ecology of Typha. The success of re-combining them depends on how well the components were defined originally and how completely the study defined each component. Limitations of the originals are that definitions given by Grubb (1977) describe a fundamental niche, thus taking little account of competition and herbivory, and that the study investigated only one phase of the regeneration niche and only one environmental gradient in the habitat niche. For reasons presented earlier and discussed below, these gaps are unlikely to seriously distort the synthesis presented below.

This chapter is organised in the following way. First, results pertaining to each component niche are briefly summarised and significant features discussed (7.2). Second, the components are brought together, and the niche and its "emergent" properties considered (7.3). According to hierarchy theory, a higher level of organisation, in this case the re-combined niche, has characteristics which are not evident at lower levels of organisation. These are usually described as "emergent" properties, but this term is not used here because of overlap with emergent macrophyte.Third, the niche and its characteristics are placed in context (7.4) by considering the "hats" mentioned earlier (1.2), Typha as a competitive species, as a weed and as an emergent macrophyte.

7.2 The four niches

Life form niche

Annual aboveground production of T. orientalis at Griffith, New South Wales was high compared to emergents from cool temperate zones. This was

attributed to climate, specifically a long growing season and mild winter. This extended growing period meant that at Griffith, where tissue production continued throughout winter, aboveground production for autumn and winter was 21% of annual total. The reasonable agreement between estimated aboveground production from April to September, 714 g m^{-2}, and the translocation correction of 839 g m^{-2} (2.8) suggests production over this period was largely due to rhizome starch reserves. This makes the rhizome a key factor in production timing and quantity.

Underground biomass and production were also towards the top of the range of published values for cool temperate areas (2.9). Most underground biomass in T. orientalis is rhizome (Figure 2.4) which indicates a large carbohydrate store. At Gum Creek Road in 1979-80 T. orientalis "used" only 80% of the previous season's production leaving 20% or 576 g m^{-2} underground, whereas in Wisconsin the "unused" underground biomass was only 107 g m^{-2} (Gustafson 1976). Consideration of McNaughton's (1975) suggestion that there is a north-south gradient in ramet mortality, suggests that a larger excess may be typical of warmer climates.

Annual production was estimated for only one species, T. orientalis but it seems T. domingensis is comparable. Two sets of data, standing crop in favourable conditions at Strathmont (4.5) and shoot phenology near Griffith (3.11), indicated this was so.

Phenological niche

Vegetative and reproductive phenology of T. domingensis and T. orientalis shoots were similar with none of the gross differences reported for sympatric species in India (1.2). Shoots recruited early during the recruitment period suffered considerable mortality before winter and their over-winter survival was size dependent. Shoots

recruited later had little mortality, unless droughted or grazed, until seasonal die-back in the following year. Both species flowered in late spring-early summer.

All shoot populations studied were disturbed to some degree, either by drought and/or grazing. The level of disturbance was consistently higher in T. domingensis quadrats, making it difficult to detect fine differences between species in their vegetative life cycle. Disturbance did not mask, or perhaps even emphasised, species differences in reproductive life cycle. These are discussed below (7.4).

Seasonality in the vegetative life cycle was evident in the relatively undisturbed conditions of Brogden's Road, with shoots being recruited predominantly in summer-autumn, the stand developing during winter-spring to maximum size in early summer and then senescing. This pattern suggests recruitment and growth were controlled by seasonal changes in temperature, photoperiod and/or irradiance. In heavily grazed quadrats, shoot recruitment and growth occurred throughout the year so were independent of seasonal controls. This independence means that in Typha the effects of canopy removal are minimised. Seasonality in the vegetative life cycle was due to synchronised population responses rather than regulatory control.

In general, decreasing daylength and falling temperatures trigger an increase in underground biomass and in starch accumulation. This was apparently true for Typha. North American T. domingensis and T. latifolia allocate more biomass to underground structures at low temperatures than at high, 7°C and 21°C (McNaughton 1966a). Seedlings of T. orientalis show a similar response (Sale and Orr, in prep.). In mature stands the switch from downwards to upwards translocation and vice versa occurs in March-April and September-October (Figure 2.4). This coincides with the equinoxes, further implicating photoperiodism. Thus in contrast with

shoot and leaf recruitment, the timing of underground growth is probably fixed.

The reproductive cycle also shows a combination of seasonally fixed and flexible events. Although flowering is probably a photoperiod response (McNaughton 1966a) and therefore fixed, the timing of subsequent phases, namely ripening and dispersal, are typically determined by plant vigour and/or site conditions rather than by seasonal cues (Rathcke and Lacey 1985) and are therefore more flexible. This was true for Typha where flowering was fairly synchronised but dispersal was disrupted by summer drought (Table 3.6, Figure 3.9). Implications of this are discussed below.

One distinctive feature of the vegetative life cycle of Typha spp. at Griffith was that shoots initiated in the latter part of one growing season matured then died during the next, giving a maximum life-span of one to one-and-a-half years. Comparison with other plants shows this was a short retention of plant parts. Rapid turnover is advantageous to competitive species and is characteristic of invasive species (Grime 1981) while slow turnover is an efficient strategy in environments which are resource poor or with a limited growing season (Miller and Stoner 1979). The environment of wetland plants, excluding acid bogs which are not a typical habitat for Typha spp. (Segadas-Vianna 1951, Finlayson et al. 1983), is generally resource rich (Bradbury and Grace 1983). In wetland plants, there is a rough correlation between shoot longevity and length of growing season. Shoot life-span for equatorial species such as Lepironia articulata in Malayasia and Cyperus papyrus in Africa is 3-7 months (Ikusima 1978, Thompson et al. 1979) whereas tillers of the sub-antarctic sedge Uncinnia meridensis in South Georgia live for five years (Callaghan 1984). T. orientalis with an intermediate distribution at 34°S has intermediate longevity. Continuous leaf production is

advantageous because it means the canopy can be rapidly re-established after leaf loss by herbivory, and because it allows a rapid response to patchy resource availability (Jonasson and Chapin 1985). Both these were evident in Typha, in the recovery from grazing and in the belated growth spurt of the August cohort of T. domingensis at Bringagee Road (Figure 3.7, 3.12).

Habitat niche

The water limit of the habitat niche was established by estimating R*, the equilibrium resource level, or point of no growth (Chapters 4 and 5). Although field estimates were affected by variable water regimes and ramet connectedness, it was clear that R* for T. domingensis at Strathmont was close to Field Capacity and thus considerably higher than for terrestrial or even flood-plain species.

This high R* was explained by interpreting Typha's canopy and leaf characteristics in terms of demand-supply, stomatal number, distribution and canopy area. The combination of many-small, amphistomaty and medium-high LAI indicated a potentially high demand for water. In contrast the root system being shallow, seasonally renewed and small relative to canopy size, indicated a potentially small ability to supply. This was confirmed by midday stomatal closure in autumn, in conditions of apparently unlimited water availability (Figure 5.7).

An experiment determined using lysimeters and isolated ramets gave a lower estimate of R*, close to -0.65 MPa. The discrepancy between these two estimates was attributed to differences in demand, i.e. in leaf surface area. Even in relatively dry conditions of Zone 1, field ramets were taller than experimental ones so had a larger transpiring surface.

This highlights a problem of using R* to define boundaries for the habitat niche when the resource is water. This conceptual approach is based on the premise that resource availability affects growth and

ultimately determines size. In the case of water, this is too simplistic for it ignores interactions between size and climate. Size determines the rate of resource utilisation and therefore the rate of resource depletion in the environment. This means R* is influenced by the rate of resource replenishment. Thus R* is partly defined by those soil characteristics which affect water movement, specifically hydraulic conductivity. Climate also affects the rate of resource utilisation. Leaf vapour pressure deficit increases as relative humidity falls and temperature rises. Consequently R* for Typha at Griffith or Adelaide, both with warm dry summers, will be at higher soil water potentials than for equivalent sized Typha in cooler or more humid climates. Finally, because of the influence of canopy size, R* is likely to be higher in nutrient-rich sites than in nutrient-poor ones.

Because R* is dynamic, estimates of R* need a context of plant size, soil type and nutrient status, and climate. Compared to terrestrial soils, swamp soils are relatively uniform. They tend to be depositional zones, characterised by fine particle size, usually silts, high organic matter and nutrients, and a lack of structure. This relative uniformity means soil characteristics can be omitted when comparing wetland plants.

Clearly an R* near Field Capacity means growth of Typha domingensis is not water limited as long there is free water above the substrate. However when the water table falls below ground level, and the water potential below Field Capacity, growth will be resource limited. It is possible that growth of T. orientalis at Brogden's Road was affected in this way as substrate condition was described as "firmed up at the end of November, in January and the end of March" (2.6).

The exact impact of water potentials below R* depends on factors similar to those that describe water regime (3.2), specifically timing and duration. The effects of timing are best assessed by considering

whether the life cycle stage in question is fixed or flexible, for example flowering or shoot recruitment, or critical for survival, for example rhizome re-charge. If the water table falls below soil level in spring, canopy growth should be reduced as this is the main period for canopy development. Presumably this was the reason T. domingensis shoots at Bringagee Road were not as tall in 1980-81 as in 1979-80 (Figure 3.8, 3.12). If the water table falls below soil level in summer, then the plant should be rapidly affected because not only is summer the time of highest water demand in terms of temperature and evaporation rates, but canopy area is at its maximum and leaves are senescing and losing stomatal mobility. This was certainly so at Bringagee Road. Within a month of water levels dropping below soil level, leaf mortality was higher than in still wet quadrats (Table 3.8, 3.12).

Duration interacts with timing. At Bringagee Road, although leaf mortality increased almost immediately sites dried, the canopy did not die until nearly 4 months later (Figure 3.2). As far as could be determined from Final:Initial density and replacement ratios (Tables 3.3, 3.4 and Figure 3.7), T. orientalis ramets made a complete recovery after being "dry" for 3 months for there was no evidence of ramet mortality or impaired growth. In contrast, T. domingensis ramets made an incomplete recovery after 4 months drought. Thus survival threshold for underground ramets in summer at Griffith was 3-4 months.

The cause of this mortality was assumed to be desiccation or desiccation-associated. Dead leaves are thought to be permeable to gas vapour (Sale and Wetzel 1983) and therefore can act as a pathway for water. It is unlikely water could be lost directly from the rhizome, for although it does not have a true epidermis, it does have a layer of ground parenchyma modified into protective tissue by suberisation (Esau 1965). In rhizomes of healthy T. domingensis from Strathmont this layer

was 3-5 cells deep and 100-200 μm thick (pers. obs.).

If drought-induced canopy death occurs during the six month period of downward translocation, then a long-term effect of drought may be reduced reserves and carbohydrate starvation. In the T. domingensis quadrats at Bringagee Road, there was a dry spell over summer, from December to March inclusive, and in spring, September-October (Figure 3.1), leaving only one month of normal "functioning" during the period of rhizome re-charge. This could explain why fewer shoots emerged in T. domingensis quadrats and why rhizomes had a shrunken appearance in June 1981 (3.6). It was unfortunate ramets were not excavated and analysed for carbohydrate content at the end of this study.

Regeneration niche

Experiments showed Typha seeds could germinate and survive to 8 days in a range of conditions, including high to low water availability, low irradiances, and fresh to almost saline water provided nutrients were present. This apparent lack of specific requirements means Typha seeds should germinate in a variety of aquatic and terrestrial situations. When these experimentally determined tolerances are considered in conjunction with more specific requirements reported in the literature, namely hypoxia and a high red:far red ratio (6.2), it becomes apparent this is not quite true. For example, Typha seeds falling down cracks into (terrestrial) soil or through water into unconcolidated muds are unlikely to germinate because of unfavourable conditions. The sub-soil light climate is characterised by low intensity with a low red-far red ratio (Bliss and Smith 1985), whilst bottom waters and benthic muds are generally anoxic (Howard-Williams and Gaudet 1985). Optimal germination conditions of hypoxia with white light or high red-far red ratios, are possible in unshaded shallow waters and most likely on saturated muds. In cooler climates, the regeneration site is furter defined by minimum

temperature requirement of 15°C (Figure 6.1) but this is probably not significant in warm temperate or semi-arid areas. Mean daily maxima for July and August at Griffith, where Typha seedlings were recorded during winter (Figure 3.9 b), are 15 and 17°C (Butler 1979).

So far only the germinating environment has been considered. The regeneration niche becomes more complex when establishment and subsequent phases are considered. Critical factors as deduced from p(L) data and from the literature (6.2) are water level, water regime and salinity. In terms of establishment, the regeneration niche has to be a fresh to brackish, shallow to mud, fairly stable environment.

Much germination work is reductionist, with a tendency to comprehend germination only as a list of physiological responses. To counteract this, Angevine and Chabot (1979) adopted an evolutionary perspective. Their premise was that germination means the plant has "bet its life" on a high probability of successful establishment, therefore germination requirements are really a set of environmental cuing mechanisms which have been naturally selected. An array of correlated seed and germination characteristics constitutes a syndrome (Angevine and Chabot 1979). Many plants within a habitat type are likely to share a syndrome.

Typha's particular combination of physiological characteristics, namely ready germinability and relative paucity of environmental controls, and seed characteristics, namely smallness, dispersability and low reserves, means it fits the "spatial disperser syndrome" (Angevine and Chabot 1979). This is one of two strategies recognised as a means of avoiding biotic stress, usually competition, by increasing the probability that seeds will germinate in a competition-free space or "gap". (The other avoidance strategy is the "temporal disperser syndrome", characterised by seed longevity and a viable seed bank ready to take advantage of temporally created gaps.)

Further evidence for a germination strategy of Typha adapted to spatial gaps comes from total energy requirements for establishment. This has not been commented on in the literature (6.2) but was demonstrated, and an ontogenetic shift indicated. Total energy required for max p(L) in 8 day old seedlings was 300 $\mu E\ m^{-2}\ s^{-1}$ at 8 hours (6.12), levels which are not likely to be attained at ground level in the parent stand where most seeds fall. In midsummer, the canopy of T. domingensis was so thick that irradiance at ground level was only 0.07% of 2100 $\mu E\ m^{-2}\ s^{-1}$, the above canopy irradiance at midday (4.5). At the time when seeds begin to disperse, shoots are shorter and less leafy so a greater proportion of above canopy irradiance is likely to penetrate the stand. However, this seasonal reduction in canopy size coincides with a lower irradiances and shorter daylenths, so it is still unlikely the seedling's light requirements will be met within the parent stand. No irradiance measurements were made in Typha stands in winter but mean daily radiation flux in winter in Adelaide is 3-4 times lower than in summer (Schwerdtfeger 1976) and incident midday irradiance is 2-3 times lower (Oliver 1981).

The sensitivity of Typha seeds to temperatures greater than 15°C, to white light of low intensity and short duration, plus their relatively short life-span, means that Typha seeds are not well-suited to form long-term seed-banks in warm climates, and this re-inforces their dependence on spatial gaps. In addition, laboratory experiments (not reported elsewhere) showed more than 50% germination in the dark after only one hour imbibition in 100 $\mu E\ m^{-2}\ s^{-1}$ laboratory light. This means seeds dispersing into shallow or clear water must be buried almost immediately in dark, anoxic muds if they are to enter the seed-bank. Thus a Typha seed-bank is probably dependent on frequent and often replenishment.

Because the occurrence of gaps, whether spatial or temporal, is unpredictable, the spatial disperser syndrome can only be an effective strategy if the parent plant produces large numbers of seeds, which Typha does. A single inflorescence comprises a few hundred thousand flowers, giving an estimated seed load for T. orientalis and T. domingensis of 6 x 10^6 fruits m^{-2} and 17 x 10^6 fruits m^{-2} (Prunster 1941) of which approximately 50% are viable (pers. obs.). Although only a small fraction of this disperses, the numbers involved are so large that this fraction is still a sizeable seed rain on the landscape.

7.3 Synthesis

When combining these four niches it is useful to recall their significance and meaning. The life form and phenological niches describe size, by its spatial and temporal distribution. This indirectly describes status within the community because size is a crude index of space occupancy which in turn is a crude index of resource capture. The habitat niche describes environmental conditions where the species is found. The regeneration niche describes how it is maintained.

Typha is an herbaceous rhizomatous perennial. Two plant parts, rhizome and canopy, dominate biomass and production. The remaining parts, roots and reproductive structures, are relatively insignificant. Although biomass and production allocation are imperfect indices of plant strategy (Harper 1977), canopy and rhizome are accepted as keys to understanding Typha, partly because they so clearly dominate biomass and production, and partly because they explain many characteristics in the four niches.

Canopy

The possibility that life form may be a factor contributing to high production in wetland plants such as Typha is generally overlooked and explanations are sought elsewhere, namely unlimited resources (Bradbury

and Grace 1983). In Typha aboveground production is almost entirely leaves. A large canopy has a specific array of benefits and costs. The benefits are that the total amount of light energy intercepted is high and that competition is eliminated by occupying space and pre-empting resources particularly light energy. The principal cost is a high water demand.

Although shoots have a relatively short life span with an annual turnover, the overlap between generations means a canopy is maintained throughout the year. Effectively, the plant is an evergreen. This is true in the contrasting conditions of warm temperate Griffith and cool temperate North America although here the pre-winter canopy is typically small, for example only 4 cm high in Ottawa (Bayly and O'Neill 1972). The new canopy is established when growing conditions are deteriorating and is maintained over the most unfavourable growing period. Consequently when spring comes, the plant already has a canopy with which to take advantage of improved growing conditions. Curiously, one Typha species appears to lack this evergreen habit. In England 53°N (Mason and Bryant 1976) and in coastal Chile 40°S (Ramirez and Anazco 1982), the canopy of T. angustifolia is apparently established in spring.

The habitat niche for Typha is partly defined by its large canopy size. Towards the boundaries of its range, resource limitation means less canopy is produced and can be maintained. This in turn reduces the effectiveness of its competitive mechanism.

Rhizome

Buds are arranged in two rows at 180° to each other on the rhizome crown. Growth is sympodial although it looks monopodial. Factors determining which bud develops and whether it becomes an extended or short rhizome have not been determined. No distinctive angular branching pattern (c.f. Bell 1984) was evident in ramets of T. orientalis from Gum Creek Road or T. domingensis at Strathmont. From observations made during the production and phenology studies, it appears that direction of ramet

growth is linear but is modified by natural obstacles. Thus in mature stands ramets were often twisted around and occasionally through each other and tended to be short, and mostly crown whereas in younger stands or at the advancing edge, rhizomes tended to be longer and of more slender proportions (Appendix 4). Cross-sections show that of the two rhizome tissues, pith and cortex, the pith occupies a greater volume but is proportionally smaller in young and colonising ramets. The pith contains amyloplasts which are densely packed with carbohydrate granules.

The rhizome functions as an underground bud and carbohydrate reserve. Underground buds make the plant more secure from predation or damage and thus make the plant resilient. This was evident in the response to grazing at Lake Wyangan, and in its persistence despite repeated disturbance.

In warm dry climates where water availability may be limited from time to time, the rhizome appears to have an additional function in relation to water balance. The gradient study (Chapter 4) implied intra-ramet water transport, and a re-growth experiment (see below) implied a minor role as a water store adequate to initiate shoot and root growth. For the re-growth experiment, ramets were potted into soils of different water potentials at two temperatures. After one month it was clear that re-growth was a function of temperature alone. At 21-22°C, 22 out of 25 ramets re-grew compared to only 2 out of 25 at 11-12°C. There was no association between water potential and dry weight of leaves and/or roots.

This result was intriguing so the quantity, distribution and availability of rhizome water were investigated. The lacunate cortex had a higher water content (as percentage of fresh tissue weight) than the pith, 81-92% compared to 61-73%, but because of its greater volume and density, most rhizome water was in the pith. Desiccation treatments

reducing ramets to 80% of initial fresh weight showed water loss was from the cortex with the pith showing no significant change. This was presumably due to protection. Staining with Sudan IV shows the endodermis is thickly suberised with only a few passage cells, 11 out of 500 inspected in T. domingensis, and that bundles around the vascular tissue are highly lignified (pers. obs.). Desiccation trials were done to establish a critical hydration limit but rhizome variability in size, shape and physiological condition made it difficult to establish experimental controls. Results were inconclusive and this area of work was discontinued.

Most studies of resource sharing between ramets have been done in relation to light or after defoliation and have monitored the movement of photosynthate (Pitelka and Ashmun 1985). Water sharing has been studied only incidentally, for example in steep salinity gradients (Salzman and Parker 1985). The gradient study (Chapter 4) did not demonstrate that water was relayed between ramets in the field but this interpretation was consistent with results and may also explain the discrepancy between field and laboratory determined R* values.

7.4 Hats

The competitor

For one species to be successful at the expense of others, it must either be more efficient in its use of available resources or exclude others from those resources. There is insufficient physiological data available on emergents to compare Typha with other species, although obviously there is a great range in efficiency, from C4 for a few species such as Cyperus papyrus to C3 for Typha and most other emergents. Studies of competition between emergents have focussed on space occupancy as the exclusion mechanism (Buttery and Lambert 1965, Fiala and Kvet 1971). The principal characteristic of the life form and phenological niche of Typha

was large size and constancy, characteristics that favour resource pre-emption by space occupancy. Aboveground, the density of Typha stands and their medium-high LAI means irradiance levels below the canopy are low (7.2 Regeneration niche). If other species are present, they are only in trace amounts (Segadas-Vianna 1951) and, like Typha seedlings (Sharma and Gopal 1978), are clustered in spots of higher irradiance such as at stand edges and in areas disturbed by lodging or grazing. Belowground competition is harder to demonstrate but has been linked to differences in underground biomass and rhizome position (Fiala and Kvet 1971).

The present distribution of Typha in Australia is in farm dams, drains, wetlands and on river margins where it is usually monospecific. This makes it difficult to judge with confidence which species, if any, are being or have been excluded. Generalised zonation patterns for wetlands in south-eastern Australia (Briggs 1981) show an overlap between Typha and floating-leaved, floating and emergent herblands at the "wetter" end of the water gradient. Species cited for the emergent herbland are only "shortly" emergent such as Myriophyllum spp., Triglochin procera, Polygonum spp.. These do not project above the water as much as tall emergents (Table 1.1) and must therefore be susceptible to being shaded out by them. At the "drier" end of its habitat niche, Typha overlaps with other emergents, principally Phragmites australis grassland or "Eleocharis" sedgeland (Briggs 1981). In Western Australia, Typha appears to be replacing Baumea.

For a plant to outcompete Typha, it would have to have a similar and overlapping habitat niche but be more effective at resource capture, notably irradiance. It would therefore have to be an emergent, presumably taller or larger. In Czechoslovakia, the ability of Phragmites australis to invade stands of Typha has been attributerd to its greater height, deeper rhizomes and earlier canopy development (Fiala and Kvet 1971). In

south-east Australia there are few species of emergents taller than Typha (Aston 1972, Briggs 1981, Sainty and Jacobs 1981), so the number of potential competitors is small. In other parts of the world the diversity of emergents is greater, for example, in Africa emergents growing as tall or taller than Typha include Cyperus papyrus, Phragmites spp., Cladium spp., Echinochloa spp. (Thompson 1985). It may be that displacement of established Typha by another emergent is only likely if the habitat is disturbed in some way, such as grazing or altered water regime. This allows secondary characteristics already present to come into play, such as palatability of Typha spp. versus the unpalatability of Juncus ingens (Chesterfield 1986). It is interesting that the Great Cumbung Swamp in south-western New South Wales appeared to have more Phragmites than Typha (common name cumbungi) when visited in March 1980.

The weed

The definition of "weediness" has been a discussion point for weed scientists over many years (Baker 1974, Radosevich and Holt 1984). Anthropomorphic definitions such as "a plant out of place" were converted into ecological terms by Baker (1974) out of which a list of 12 "ideal weed" characteristics was distilled. This was first published in 1965 but is still used (Baker 1974, Radosevich and Holt 1984) because it has proved valuable in discussions of weediness. It is based on terrestrial plants and is used here as a way of examining Typha for weedy qualities on the assumption that weediness is universal and that characteristics which make a plant a weed in a terrestrial habitat will be equally true in an aquatic one.

The "ideal weed" characteristics fall into four ecological categories, reproduction ecology which includes three phases namely seed dispersal, germination and establishment, regeneration, persistence and competitive ability (Table 7.1). It is unlikely one species will have all twelve

(Baker 1974) and conversely, the presence of one characteristic does not turn a plant into a weed. "Weediness" is an array of characteristics, or a syndrome.

Typha has eight positive characteristics (Table 7.1) scattered in all four categories. This array of "ideal weed" characteristics shows it is pre-adapted to being a weed. The plant is well suited to colonise new sites. Agricultural development, such as dams and irrigation works, involve a change in only one gradient in the habitat niche, namely the provision of permanent or semi-permanent water. Such development is frequently in areas where neither temperature nor irradiance are limiting for Typha. Thus all four niches are relatively unrestricted, which explains why Typha is so often a weed in irrigation areas in semi-arid climates such as Australia and India.

Sympatric species

Sympatric pairs of Typha were briefly reviewed in the Introduction (1.2). They lack obvious physiological differences and are most easily distinguished in the field by morphological criteria, leaf width, giving broad-leafed and narrow-leafed species. In USA, broad-leafed species are linked with stable environments and narrow-leafed species with unstable, saline or marginal habitats (Smith 1967). Broad-leafed and narrow-leafed species in USA have been described as "clumpers" and "runners" (Marsh 1962) which has obvious parallels with phalanx and guerilla strategies described for Ranunculus repens (Lovett Doust 1981).

Sympatric pairs in the USA differ in the timing of canopy development, in their response to depleted sunlight, in their resource allocation and in some aspects of reproduction biology (Grace and Wetzel 1981 a, b. 1982 a, b). The broad-leafed species develops earlier and has a higher leaf surface area per ramet. It allocates less than 5% of total standing crop to reproductive structures compared to 20% in the narrow-leafed species.

Associated with this is a difference in ramet size, with the broad-leafed species tending to be heavier. Broad-leafed species have seeds which are larger but fewer per inflorescence, and have a larger critical size (Table 7.2 a).

This study was not designed to elucidate differences between T. orientalis and T. domingensis but data, principally on reproductive biology, suggest the Australian species are separated in the same ways as the North American species. Thus the broad-leafed species T. orientalis has larger but fewer seeds per inflorescence, disperses sooner and has a larger critical size for flowering (Table 7.2 b). Differences in canopy development could not be positively established because grazing and water regime "treatments" although leaf recruitment data indicated that the canopy of T. orientalis developed earlier and faster (Figure 3.12).

The emergent macrophyte

The purpose of this section is to explore which niche characteristics are specific to Typha and which are typical of emergent macrophytes. The functional-physiological definition of emergents proposed in the Introduction (Table 1.1) was plants growing rooted in a flooded substrate, in water 0 to nearly 2 m deep, with leaves projecting above the water surface. As pointed out previously, this could include terrestrial species which, although sometimes found in shallow waters, are not adapted to growing in water and are merely tolerant of temporary submersion. For the following synthesis, the term "emergent" is narrowed to exclude these and here refers to only those species which grow in water at least 50 cm deep.

Two regional floras (Sainty and Jacobs 1981, Leach and Osborne 1985) were used to compile a list of 45 emergents in the Australasian region. Introduced and naturalised species were excluded as well as plants of decumbent life form such as Myriophyllum which are sometimes described as

emergent because terminal flowering spikes are above the water. Relevant taxonomic, life form and leaf arrangement characteristics were derived from descriptions in the monographs. Emergents were "creeping" if they had stolons, short or long rhizomes, or were so described. Leaf arrangement was "basal" if projecting leaves were radical as in Typha and some Cyperus spp., "graminoid" if cauline as in Phragmites spp. and "culm" if reduced to relatively short basal sheaths or absent as in Eleocharis spp.

Tabulation of these characteristics (Table 7.3) shows emergents share many taxonomic, life cycle and canopy characteristics. Nearly all are Monocots, predominantly from one evolutionary line, the super-order Commeliniflorae (Dahlgren et al. 1985) which includes Juncaceae, Cyperaceae and Poaceae. The majority are perennials, of "creeping" habit and mostly with a rhizome. Leaf arrangement is typically basal. Although originating from a different evolutionary line, viz the super-order Bromelliflorae, Typha's perennial, rhizomatous, creeping habit and basal leaf arrangement make it a "typical" emergent.

In Typha the regeneration niche and the habitat niche have different spatial dimensions. The regeneration niche is confined to mudflats and shallow waters, whereas the habitat niche stretches to include land well above and well below the water-line. Niche expansion is presumably due to rhizomes and ramet integration in Typha, which together give it its creeping habit. It seems likely niche expansion is characteristic of many emergents. Not only do most have a creeping habit and a similar habitat niche, as defined by the term emergent above, but many typically have safe sites on mudflats (6.1), on moist earth or in shallow water (McIntyre 1985).

A notable exception is the North American annual, Zizania aquatica, which successfully establishes in water at least 32 cm deep (Thomas and

Stewart 1969). Presumably the larger seeds of this plant, which mean more reserves, give it the capacity to establish in deeper water than can small-seeded Typha and thus free it from the creeping or perennial habit. The environmental strategy represented by Z. aquatica, large seeds and annual habit, although not common amongst emergents, is an effective strategy in the cultivated situation, being characteristic of several weeds of Australian rice-fields (McIntyre 1985).

Although Typha shares life cycle, habit, leaf arrangement and seed size characteristics with many other emergents, it differs from them in certain morphological and anatomical details. From the limited information available, it appears the root system of Typha is relatively small and rhizomes are relatively shallow. (The very deep-seated rhizomes of T. elephantina are an exception.) Typha rhizomes are not as deep as rhizomes of Phragmites australis (Fiala and Kvet 1971, pers. obs. Little Para River 1985), and roots of T. latifolia grow half as deep as roots of Scirpus validus, 28 cm compared to 59 cm (Weaver and Himmel 1930).

Differences between Typha and other emergents are most obvious when the canopy is considered. A great range in canopy size could be expected with laminate leaf arrangements whether radical such as Typha or cauline such as Phragmites having higher biomass and surface area than species with culms or few terete leaves such as Scirpus, Eleocharis or Baumea. Compilations of standing crop data show this is true with Typha and Phragmites consistently at the top of the recorded range (Keefe 1972, Bradbury and Grace 1983). An exception is Cyperus papyrus which because of its height and large umbel has an effective leaf area 10 times greater than Typha (Howard-Williams and Gaudet 1985).

In terms of stomatal characteristics, it is difficult to determine how typical Typha is because there are few data. What is apparent is the diversity amongst emergents. Some are amphistomatous, for example members

of Juncaginaceae, Cladium mariscus, Eriophorum vaginatum and Phragmites australis (Metcalfe 1971, Haslam 1972, Tomlinson 1982), some are mainly epistomatous, for example Machaerina and Butomus umbellatus (Metcalfe 1971, Tomlinson 1982) and some are hyperstomatous for example Cyperus papyrus (Jones and Muthuri 1984) or even variable as in Carex aquatilis (Standley 1986). There are even fewer data on stomatal size and density, and it is impossible to determine whether the small-many combination found in Typha is widespread amongst emergents. Phragmites australis is probably similar with stomates described as "abundant", being 470-700 mm^{-2} (Haslam 1972), whereas Sparganium sp. and C. aquatilis apparently differ (5.10).

Diversity is also apparent in stomatal morphology. Several emergents have features which lower or minimise the diffusion rate of water vapour. Thus stomates may be sunken as in Lepironia and Cladium mariscus, or protected by over-arching papillae as in Lepironia and Eriophorum vaginatum or have thickened protective walls on cells lining the sub-stomatal cavity as in E. vaginatum and Juncus roemerianus (Metcalfe 1971, Eleuterius 1976). It is not clear from descriptions in monographs whether these features are absent from other emergents or simply not described (Metcalfe 1960, 1971, Tomlinson 1982) but it does appear that the simple shallow stomates of Typha differs are not typical.

The supply-demand characteristics used to explain the high R* for T. domingensis (Chapter 5), help to distinguish it from other emergents. It should follow that in comparison with other emergents Typha is a relatively "wet" emergent. Field observations in Australia tend to support this. Where Typha and Phragmites are found together, such as on the banks of the Little Para River, SA and along Mirrool Creek, NSW, they tend to form zones with Typha towards water and Phragmites towards land (pers. obs.). In central Africa, Typha is recognised as a reliable

indicator of prolonged flooding in the root zone (Thompson 1985).

This lack of morphological uniformity amongst emergents emphasises they are not a coherent group despite occupying such a specific habitat. This diversity is beginning to be appreciated. Research into using emergents for biological wastewater treatment has found it useful to do trials to identify appropriate species and shown not all species have same effects (Finalyson and Chick 1983). Wherever more than one species has been studied, non-uniform responses have been observed. This has been well-demonstrated in seed-bank studies (Keddy and Ellis 1985, Keddy and Constabel 1986, Galinato and van der Valk 1986). Amongst established plants it is evident in their response to draw-down whether in Canadian wetlands or Lake Chad (van der Valk and Davis 1980, Thompson 1985) and in zonation sequences. The swamps of the Nile are an extensive emergent habitat and the typical sequence from open water to permanent then seasonal swamp, has as dominants Cyperus papyrus, then Phragmites karka and Typha domingensis, and Echinochloa pyramidalis (Thompson 1985). Zonation of large emergents is not so apparent in south-east Australia where there are fewer taxa and the habitat is spatially restricted.

Physiological features related to root survival and growth in anaerobic sediments are common to all emergents (Crawford 1983, Thompson 1985) but it is obvious from this brief survey that different character syndromes exist within the general umbrella of "emergent macrophyte". It is also apparent that whilst Typha is fairly representative of emergents, it has a distinctive combination of features. These are expressed in its "hats", namely its competitive and weedy nature, and its position towards the "wet" end of the water gradient in the habitat niche.

Table 7.1
Ideal weed characteristics and Typha spp.

These ideal characteristics are grouped into four ecological categories but otherwise follow Baker (1974) verbatim.

Characteristic	Present	Comment and reference
REPRODUCTION BIOLOGY		
1. Germination requirements fulfilled in many environments	No	Germination requirements for hypoxia are specific (Chapter 6)
2. Discontinuous germination (internally controlled)	Yes	Germination discontinuous, because of external controls, namely temperature and the availability of mudflats (Chapters 3 and 6)
Great longevity of seed	No	Seed longevity relatively short (Chapter 6)
3. Rapid growth through vegetative phase to flowering	No	Seedlings show rapid growth in first year but do not flower until second year (Yeo 1964)
4. Continuous seed production for as long as growing conditions permit	No	Flowering time restricted to once per year and is shorter than growing season
5. Self-compatible but not completely autogamous or apomictic	Yes	(Krattinger 1975)
6. When cross-pollinated, unspecialised visitors or wind utilised	Yes	(Krattinger 1975) Wind
7. Very high seed output in favourable conditions	Yes	Chapter 6
8. Produces some seed in wide range of environmental conditions: tolerant and plastic	Yes	T. domingensis mainly ? Chapters 3 and 6
9. Has adaptations for short-and long-distance dispersal	Yes	Seed has pappus thus may fall immediately or drift with wind. Possible role of water birds (Chapter 6).

Table 7 (continued)

Characteristic	Present	Comment and reference
REGENERATION		
10. If a perennial, has vigorous reproduction or regeneration from fragments	Yes	Rhizome fragments observed to establish in Lake Wyangan. Fragments from drain dredging are capable of re-establishing if left wet (pers. obs.)
PERSISTENCE		
11. If a perennial, has brittleness so not easily drawn from the ground	Yes	Brittleness not a characteristic, but excavation is difficult unless substrate is exceptionally soft and unconsolidated
COMPETITIVE ABILITY		
12. Has ability to compete interspecifically by special means (rosette, choking growth allelochemics)	Yes	Dense canopy backed by rhizome (7.4)

Table 7.2
Differences in reproductive biology of sympatric species

a) ex-Australasia

	Broad-Leafed	Narrow-Leafed	References
Seed dimension in mm			
length	1.412	0.958	
width	0.299	0.238	Marsh (1962)
Seed weight in µg			
mean	62.37	34.39	
range	46.9-96.5	23.9-50.7	Marsh (1962)
Seed number per inflorescence x 10^3			
	-	600	Howard-Williams (1975)
(fertile)	250	60-100	Linde et al. (1976)
	200	-	van der Valk and Davis (1978)
	222	-	(Yeo 1964)
Ramet: critical size for reproduction			
weight g	40-49	10-19	Grace and Wetzel (1982a)

b) Australasian species

Seed weight in µg			
range	37.6-48.9	24.4-35.6	This study (Table 6.5)
Seed number per inflorescence, x 10^3			
	336	682	Prunster (1941)
Dispersal time			
	June-July	June-Dec	This study (Figure 3.9 a)
Ramet: critical size for reproduction			
mm	17-1800	9-1000	This study (Figure 3.10)

Table 7.3
Characteristics of emergents

Characteristics of 45 Australasian emergents listed in two regional aquatic plant guides

a) Taxonomy and life cycle

	Monocot	Dicot
Annual	1	3
Perennial/Annual	2	2
Perennial	33	4
creepers	18	2
Total	36	9

b) Leaf type of perennial Monocots

Leaf type	Number
Basal	16
Graminoid	5
Culm	8
Unknown/unspecified	4
Total	33

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Appendix 1
Production of Typha spp

Summary of published data of maximum standing crop and annual production for Typha spp showing species, location and latitude.

	Reference	Species	Location	Lat	MSC	NAPP	Method
1	Ramirez and Anazco (1983)	angustifolia	Chile	40	2501	1985	M-M
2	Bernard and Fitz (1979)	glauca	New York USA	42	1361	1309	SxW M-M
3	Boyd (1970)	latifolia	S.Carolina USA	33	684	-	
4	Boyd (1971)	latifolia	S.Carolina	"	1132	-	
			"	"	530	-	
5	Bray et al (1959)	hybrid	Minneapolis USA	45	1440	-	
		"		"	1680	-	
6	Gustafson (1976)	latifolia	Wisconsin USA	43	1400	1356	M-M
7	Sharma and Gopal (1977)	elephantina	India	27	1049	975	M-M
		"	"	"	1791	1699	M-M
		"	"	"	1230	987	M-M
		angustata	India	25	1458	1458	M-M
		"	"	27	1565	1565	M-M
8	Davis and van der Valk (1983)	glauca	Iowa USA	42	2000	-	
9	Mason and Bryant (1975)	angustifolia	England	53	1118	1445	SxW M-M*
10	Andersen (1976)	angustifolia	Denmark	56	807	-	
11	Klopatek and Stearns (1978)	latifolia	Wisconsin USA	44	1494	1465	M-M
12	van Dyke (1972)	glauca	Iowa USA	42	1531	-	
13	Boyd and Hess (1970)	latifolia	Mississippi USA	34	1225	-	
	"	"	Georgia USA	34	561	-	
14	Jervis (1969)	sp	New Jersey USA	41	1566	1551	M-M
15	Penfound (1956)	latifolia	Oklahoma USA	35	1527	1527	M-M
16	Whigham et al (1978)	latifolia	New Jersey USA	40	1200	-	
17	van der Valk and Davis (1978)	glauca	Iowa USA	43	1180	-	
		"	"	"	2106	2297	SxW
18	van der Valk and Bliss (1971)	latifolia	Alberta Canada	54	322	-	
19	van der Valk and Davis (1980)	glauca	Iowa USA	43	834	-	
		"	"	"	1075	-	
		"	"	"	956	-	
	"	"	"	"	772	-	
	"	"	"	"	920	-	

East Europe ??

Appendix 1 (continued)

	Reference	Species	Location	Lat	MSC	NAPP	Method
20	Lieffers (1983)	latifolia	Alberta Canada	57	848	-	
	"	"	"	"	787	-	
	"	"	"	"	595	-	
	"	"	"	"	456	-	
	"	"	"	"	433	-	
21	**Grace and Wetzel (1981a)**	**latifolia**	**Michigan USA**	**42**	**309**	**-**	
	"	"	"	"	1088	-	
	"	angustifolia	"	"	2098	-	
	"	"	"	"	1487	-	
22	Whigham and Simpson (1976)	sp	New Jersey USA	40	-	1320	NS
23	Pearsall and Gorham (1956)	latifolia	England	54	1070	-	
24	Kvet and Husak (1978)	latifolia	Czecho-	49	1287	-	
		angustifolia	slovakia	"	1221	-	
	"	"	"	"	1389	-	
25	Howard-Williams and Lenton (1975)	domingensis	Malawi	15	2537	1580	M-M*
26	Polisini and Boyd (1972)	domingensis	S.Carolina	33	1483	-	
		latifolia	USA	33	574	-	
27	Auclair (1979)	angustifolia	Quebec Canada	45	1504	-	
28	Auclair (1977)	angustifolia	"	"	936	-	
29	McNaughton (1966)	latifolia	N.Dakota	49	404	-	
		sp	S.Dakota	45	378	-	
	"	latifolia	Nebraska	41	416	-	
	"	sp	Oklahoma	35	730	-	
	"	sp	Texas USA	30	1336	-	

KEY

MSC	Maximum standing crop as g dry weight m^{-2}
NAPP	Annual net aerial primary production as g dry weight m^{-2}
Lat	Latitude as °N or S
M-M	Maximum-Minimum
SxW	Shoot weight x shoot height
*	Mortality factor
NS	Not stated

Appendix 2
Aboveground standing crop of Typha orientalis

Total aboveground standing crop and its three fractions.
Harvests done at fortnightly intervals.
Mirrool Creek, near Griffith, New South Wales
1980-1981

Mean of 5 replicates (with standard error)
Data are g dry weight m^{-2}

Date		Total	Live	Dead	Burnt
June	9	1913.6 (193.5)	158.9 (11.9)	1047.5 (166.5)	707.1 (56.6)
	19	2108.2 (176.2)	217.5 (28.4)	1050.2 (192.6)	840.5 (34.6)
July	1	1866.0 (207.1)	141.7 (14.4)	1062.6 (137.8)	661.7 (77.2)
	7	1869.1 (190.8)	175.1 (19.9)	1152.0 (135.7)	541.1 (72.2)
	21	2388.9 (177.5)	231.3 (39.4)	1403.9 (164.5)	753.6 (66.1)
Aug	4	1907.3 (151.4)	251.9 (13.8)	1027.1 (102.2)	628.3 (50.3)
	20	2192.3 (213.6)	215.4 (37.2)	1223.2 (193.1)	753.7 (30.2)
Sept	5	2443.3 (279.9)	290.5 (33.2)	1355.4 (174.1)	797.4 (82.3)
	15	2107.7 (154.6)	372.9 (92.1)	1028.3 (122.5)	700.5 (59.7)
Oct	3	2466.4 (177.4)	560.8 (12.1)	1147.2 (109.2)	758.4 (96.6)
	13	2613.5 (272.5)	658.8 (58.2)	1066.5 (202.9)	888.2 (97.5)
	27	2971.6 (241.4)	911.8 (54.7)	1131.8 (193.8)	928.6 (49.1)
Nov	10	3159.3 (161.1)	996.0 (116.4)	1378.9 (104.6)	784.4 (92.2)
	27	3277.9 (378.2)	1306.4 (143.2)	1219.4 (255.2)	752.0 (84.7)
Dec	19	2947.2 (80.1)	1033.0 (197.1)	1127.5 (29.9)	741.6 (81.1)
Jan	6	2695.1 (354.3)	1308.5 (116.1)	869.4 (218.8)	517.2 (97.5)
	20	3148.8 (106.6)	1316.6 (24.1)	1217.9 (124.7)	614.3 (51.6)
Feb	2	2706.3 (251.7)	830.4 (128.9)	1338.9 (122.2)	537.0 (56.3)
Mar	3	2786.5 (188.9)	416.9 (106.7)	1915.2 (118.3)	454.4 (37.5)
	20	3069.1 (402.7)	129.2 (46.5)	2365.5 (403.3)	574.4 (113.1)
	30	2555.3 (182.7)	82.1 (17.5)	2047.7 (169.9)	425.5 (32.5)
Apr	13	2769.8 (199.1)	59.4 (20.17)	2111.9 (209.7)	597.5 (58.0)
	27	3226.8 (139.4)	145.4 (31.66)	2509.4 (153.8)	572.0 (42.3)
May	15	2738.9 (151.5)	49.0 (0.97)	2154.7 (102.8)	535.2 (103.2)
	28	2549.7 (286.8)	75.7 (21.5)	1999.7 (239.9)	474.3 (53.9)
June	12	2237.9 (149.5)	122.1 (40.4)	1787.8 (122.1)	328.0 (70.9)

Appendix 3
Total standing crop

Live belowground and aboveground standing crop
of T. orientalis harvested at monthly intervals,
September 1979 to October 1980
from Gum Creek Road, near Griffith, New South Wales.

Standing crop are mean (n = 5) g dry weight m^{-2}

Date	Rhizome	Roots	Total below	Above-ground	Total	Ratio Below:Above
Sept	499.7	311.4	811.1	197.5	1008.6	4.17
Oct	-	-	677.4	344.2	1021.6	1.97
Nov	-	-	1493.3	979.2	2472.5	1.53
Jan	1274.9	266.4	1531.3	1208.0	2749.3	1.28
Feb	2227.2	499.0	2726.2	932.5	3658.7	2.92
Mar	2261.8	386.2	2648.0	622.2	3270.2	4.26
Apr	3224.0	337.6	3561.6	248.0	3809.6	14.36
May	2407.7	409.3	2817.0	209.1	3026.1	13.47
June	1494.1	185.3	1742.6	63.2	1679.4	27.57
July	1705.1	146.2	1851.3	64.4	1915.7	28.75
Aug	1216.5	371.4	1587.9	80.8	1668.7	19.65
Sept	1078.4	192.0	1270.4	129.8	1400.2	9.79
Oct	1101.0	153.0	1254.0	315.6	1569.6	3.97

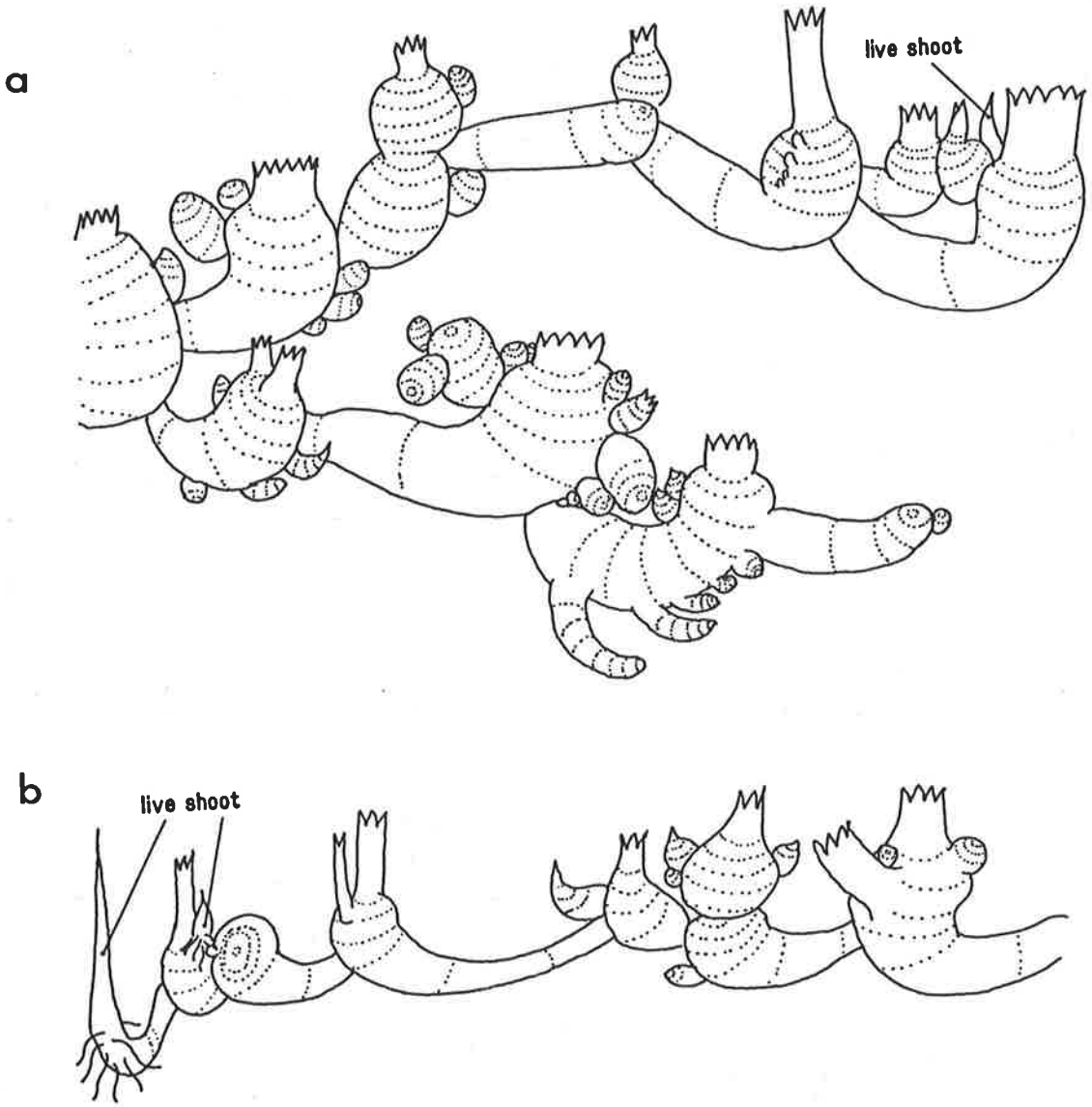
Unpublished data
Courtesy of Dr D.S.Mitchell and Mr A.J.Chick
Centre for Irrigation Research
Griffith
New South Wales

Appendix 4
Rhizomes of Typha orientalis

Diagram of rhizomes of T. orientalis excavated from Gum Creek Road near Griffith, New South Wales in May 1980.

(a) Rhizome from middle of dense stand

(b) Rhizome from colonising edge under willow tree



Appendix 5
Soil Moisture Characteristic

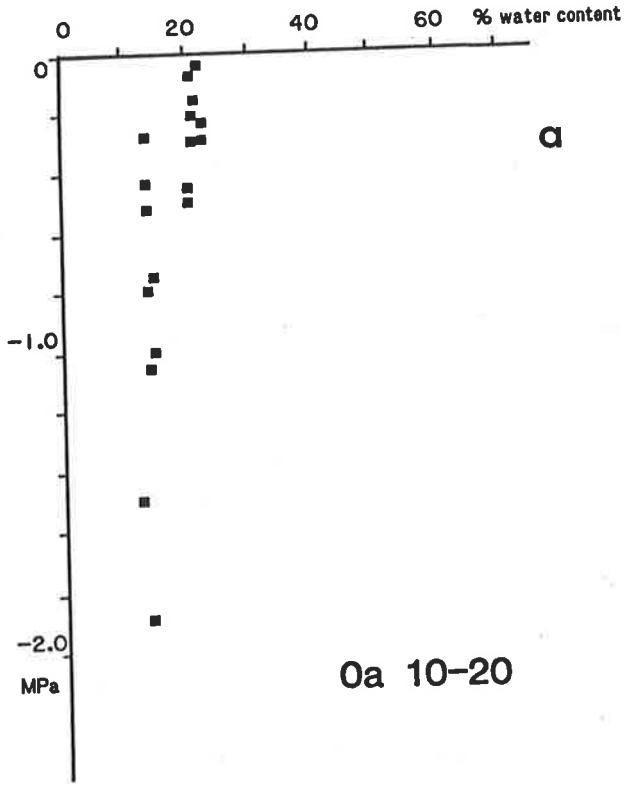
The Strathmont site had large horizontal and vertical gradients in physical and chemical factors which affect the soil moisture characteristic. Therefore each zone x depth (n = 15) was considered an individual soil type.

Sample processing
Soil samples were stored frozen. Before use, samples were thawed and left sealed in their original containers for 24-48 hours in basement laboratory to thermally equilibrate. In order to acheive a range of values, samples were used fresh and lightly air dried overnight. Each sample was divided into two parts, each 1-5 g fresh weight. One part was used for water potential and the other for gravimetric water content. Great care was taken to minimise the possibility of water loss from samples. Operating time for cleaning and setting up 12 probes with new samples and taking initial weights was 20 minutes.

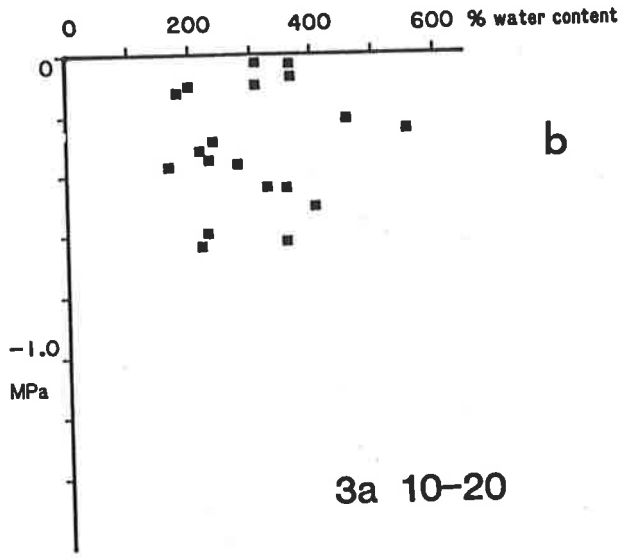
Machine operation
Water potential was determined on a 12 probe SMI thermistor psychrometer fitted with a 12 track Rikadenki recorder. The machine was housed in a basement laboratory thermostatically controlled to 20°C in the Department of Civil Engineering, University of Adelaide. There was no operating manual for this machine so one was written. Probes were individually calibrated once a month using fresh sodium chloride solutions following tables of Lang (1967). Glass distilled water was used for 0 MPa. Chart output was linear function of water potential over the range tested, 0 to -2.24 MPa. All correlations were greater than 0.9800 (n = 8) with very little drift between calibrations. Drop size was a constant 8 µl, administered with a Gilson Micrometer Syringe. Run time was 6-8 hours. Chart readings were made 6 hours after starting up.

Output
In contrast to the calibration curves, the 15 soil moisture characteristics all showed wide scatter with very little trend. Data plots from Zones 0 and 1 had a wide range of water potential over a narrow range of water content e.g. Zone 0 at 10-20 cm (Figure 5.2 a) whereas others, typically from Zone 3, had an almost complete scatter, e.g. Zone 3 at 10-20 cm (Figure A5.2 b).

Interpretation
Two sources of scatter were variable salinity and storage. The thermistor psychrometer measures total soil water potential, i.e. the sum of matric and osmotic effects. In saline soils, the osmotic component may dominate the matric component. Nonetheless, the moisture characteristic of a soil of given salinity should have a definable shape unless the salinity content changes. At Strathmont, the salinity content of soils changed during the summer. Irrigation water appeared to accumulate above the red clay layer. Thus water content v water potential relationship for the wettest soils was not constant which would explain why there was more scatter in Zone 3 data than in Zones 0 and 1. Alternatively, results for all zones could have been affected by storage method. Ice expansion during freezing can alter soil structure and may not be uniform in effect (Marshall and Holmes 1979).



0a 10–20



3a 10–20

Appendix 6
Hoagland's nutrient medium

Recipe used in Botany Department, University of Adelaide

KNO_3	5 mM
$Ca(NO_3)_2\ 4H_2O$	5 mM
$MgSO_4\ 7H_2O$	2 mM
KH_2PO_4	1 mM

One litre of above nutrient medium also contains:
1 ml of stock micronutrient
1 ml of stock Fe EDTA solution

Stock micronutrient solution
One litre:
2.86 g H_3BO_3
1.81 g MnCl2 $4H_2O$
0.22 g $ZnSO_4\ 7H_2O$
0.08 g $CuSO_4\ 5H_2O$
0.025 g $Na_2MoO_4\ 2H_2O$

Stock Fe EDTA solution
One litre:
5 mg l^{-1}

Appendix 7
Water potential of pure and mixed PEG solutions

Method
Solutions of pure PEG were made up using de-ionised water to give a range of concentrations from 0.1 to 0.45 molal PEG. Three polymers were used, PEG 6000, PEG 10,000 and PEG 20,000. These were supplied by BDH Chemicals, Poole, England; Merck-Schuchardt, Munich, West Germany; Sigma Chemicals, St Louis, USA. Mixed solutions were PEG with NaCl, and PEG with nutrients, in volumteric ratios of 1:1, 1:4, 1:9, 4:1 and 9:1, and nutrients with NaCl in 1:1. Mixed solutions were prepared from stock solutions of 0.185 molal PEG 20,000, 0.65 molar NaCl and four times normal strength Hoagland's nutrient solution (Appendix 6).

The osmolality of pure and mixed solutions was measured using a Wescor 5100 B vapour pressure osmometer (Wescor Inc. USA), thermally equilibrated to 20°C for 2-3 hours before use and calibrated with fresh sodium chloride solutions. For pure solutions, mean osmolality readings ($n = 5$) were converted to water potential using NaCl v water potential tables of Lang (1967). Osmolality readings were not converted to water potential for mixed solutions.

For pure solutions, power models of the form $y = ax^b$ were fitted to $\log_{10}$ $\log_{10}$ transformed data. Regression coefficients of three polymers were compared using F test (Sokal and Rohlf 1981). For mixed solutions, an E:O ratio was calculated with E as theoretically expected osmolality for mixture and O as measured osmolality. Ratios <0.95 or >1.05 were considered different.

Results
The water potential of pure solutions of each polymer decreased curvilinearly with increasing PEG concentration (not shown). Coefficients of determination were all high, $r^2 = 0.96$-0.99 (Table A7.1). Regression coefficients for PEG 6000 and PEG 10,000 were significantly different from each other but indistinguishable from PEG 20,00 which was intermediate.

Coefficients of regression and intercepts for PEG 20,000 were similar to published values (Table A7.2) and show a narrow range. In contrast, coefficients of regression for PEG 6000 had a much wider range, 1.24-2.00, with intercepts varying by up to two orders of magnitude.

The NaCl and nutrient mixture was within 2% of expected value. Mixtures with PEG were within 5% of expected value only when PEG was very dilute (Figure A7.1). Osmolalities of PEG:NaCl mixtures were higher than expected whereas PEG:nutrients were lower. There was no sign of discolouration or precipitation.

Comment
Although calibrations of PEG 6000 and PEG 20,000 were within or close to their published range it was obvious that PEG 6000 was generally more variable than PEG 20,000. No published data were available for PEG 10,000 so it could not be assessed in the same way.

Mixtures of PEG with NaCl and PEG with nutrients were different from expected whereas mixtures of NaCl with nutrients were not. This showed

there had been an interaction between PEG and NaCl or nutrients. However, the mixtures changed in opposite ways which implied that interactions were solution specific. The water potential of PEG with NaCl was higher than expected, i.e. osmsolality had increased, whereas PEG with nutrients was lower, i.e. decreased osmolality. As osmolality can only increase if there has been an increase in the number of particles in solution this shows that in a PEG plus NaCl solution where NaCl is ionised, PEG molecules must have split. Conversely osmolality can only decrease if there is a decrease in the number of particles in solution indicating that in PEG plus nutrient mixes there has been some bonding.

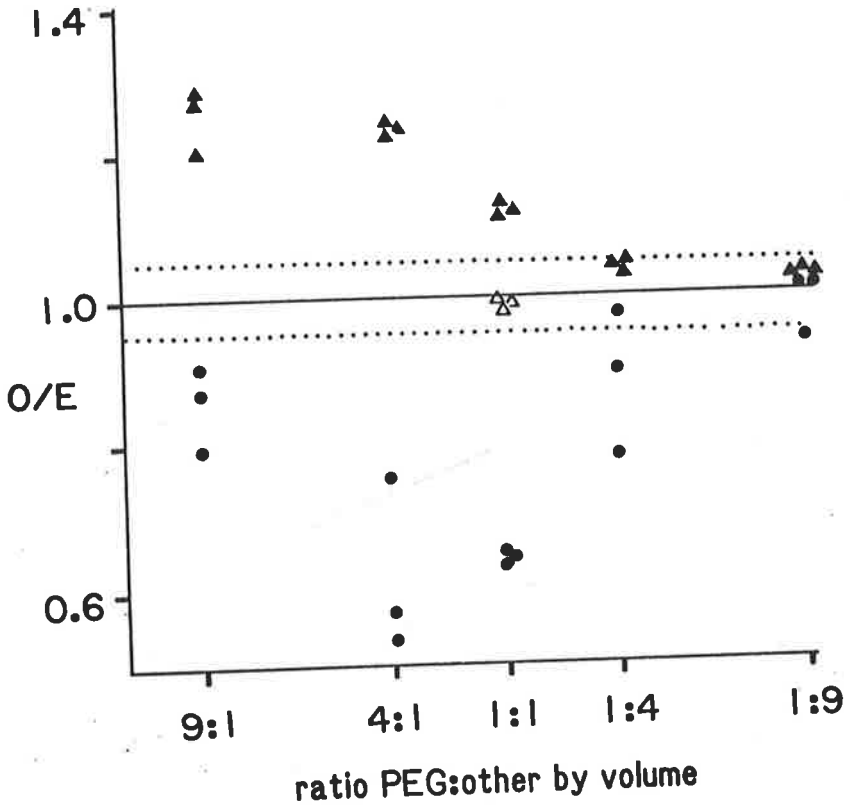


Figure A7.1
Water potential of PEG mixtures

The effect of PEG on water potential of solutions of PEG with other substances shown by comparing expected water potential with observed, and by varying the quantity of PEG present. Observed and expected water potential are presented as a ratio, O/E. Values <0.85 and >1.15 are considered significantly altered (not tested), mixtures prepared from stock solutions made up in proportions ranging from 9:1 to 1:9 (PEG:other) by volume. Expected water potential is calculated from water potential of pure stock solutions, with corrections for volume. Observed water potential is measured by vapour pressure osmometry, n = 3.

Key
▲ PEG and NaCl
● PEG and nutrient solution
△ NaCl and nutrient solution

Table A7.1
Water potential of PEG polymers

Power models for PEG determined by vapour pressure osmometry at 22°C
Independent variable x = concentration of PEG in g kg^{-1} water
Dependent variable y = water potential (negative) in MPa

PEG 6000
$y = 0.00017x^{1.317}$
$r^2 = 0.99$

PEG 10,000
$y = 0.0001x^{2.011}$
$r^2 = 0.99$

PEG 20,000
$y = 0.000025x^{1.827}$
$r^2 = 0.96$

Table A7.2
Published determinations of water potential of PEG concentrations

PEG 6000
$y = 0.000045x^{1.768}$
22°C
Regression calculated from author's model for another temperature
Thermocouple osmometry (Michel and Kaufman 1969)

$y = 0.00001x^{2.0}$
$r^2 = 0.99$
23°C
Freezing point depression (Steuter et al. 1981)

$y = 001x^{1.24}$
$r^2 = 0.88$
23°C
Vapour pressure deficit (Steuter et al. 1981)

PEG 20,000
$y = 0.00001x^{2.1}$
$r^2 = 0.99$
23°C
Freezing point depression (Steuter et al. 1981)

$y = 0.000041x^{1.9}$
$r^2 = 0.92$
23°C
Vapour pressure deficit (Steuter et al. 1981)

Appendix 8
Character sets for numerical classification

No	Response	Treatment
1. Matric potential: treatment compared with 0 MPa		
	p(g)	-1.11 MPa
	p(g)	-0.84 MPa
2. Salt and nutrients: treatment compared with 1/4 H		
	p(s)	1/256 H
	p(L)	1/64 H
	p(L)	1/128 H
3. Irradiance: treatment compared with 0 mM NaCl, 220 $\mu E\ m^{-2}\ s^{-1}$		
	p(g)	15 $\mu E\ m^{-2}\ s^{-1}$
	p(L)	50 $\mu E\ m^{-2}\ s^{-1}$
	p(L)	90 $\mu E\ m^{-2}\ s^{-1}$
4. Irradiance: treatment compared with 0 mM NaCl, 1/4 H, at 220 $\mu E\ m^{-2}\ s^{-1}$		
	p(g)	50 mM NaCl
	p(L)	50 mM NaCl
5. Irradiance: treatment compared with 0 mM NaCl, 1/4 H, at 50 $\mu E\ m^{-2}\ s^{-1}$		
	p(L)	50 mM NaCl
6. Photoperiod: treatment compared with 0 mM NaCl, 16 hours		
	p(g)	8 hours
	p(L)	8 hours
7. Photoperiod: treatment compared with 50 mM NaCl, 16 hours		
	p(g)	8 hours
	p(L)	8 hours

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Roberts, J., and Ganf, G.G., (1986) Annual production of *Typha orientalis* Presl. in inland Australia.
Australian Journal of Marine and Freshwater Research, v. 37 (5), pp. 659-668.

CORRECTIONS AND AMENDMENTS in response to examiners' reports

Page 6 and Fig. 1.1.
Figure 1.1. shows maximum seasonal biomass (MSC) as g m^{-2} for several sites per degree latitude. This therefore includes sites recognised as untypical or unsuitable for *Typha*.
The highest MSC for each degree latitude does appear to decrease with increasing distance from the equator. The trend would be clearer if only these were plotted, instead of all MSC values.

Page 6
For "year-Bnd" read "year-round"

Page 16 line 26
Correct "shouldd" to "should".

Pages 18 and 24
Eleven shoots were monitored intensively as part of the phenology study because this was the maximum that could be done routinely. By chance, all except two were grazed and these were used to describe a general pattern of shoot growth by increase in height and leaf number (Fig. 2.12). There was nothing to suggest that these two shoots were atypical of *Typha* populations in the eight quadrats.

Page 24 line 26
Correct "1355" to "135.5"

Page 27 line 9
For "Rato" read "Ratio"

Page 27 line 6
The difficulties of separating live from dead fine roots from silt mean that root biomass was underestimated. Nonetheless the sheer size of the rhizomes and the volume of space they occupied in the soil make it highly unlikely that root biomass could exceed rhizome biomass for this species at this site.

Page 28, Figs. 2.2.a and 2.5.b.
There is no discrepancy between these figures, as the former refers to reproductive structures, i.e. inflorescence and peduncle and the latter to whole reproductive shoots, i.e. inflorescence, peduncle and leaves.

Page 28.
January 20th biomass for derived data (Fig. 2.3), at 915.3 g m^{-2} compared to 1306.6 g m^{-2} for the primary data is not half as suggested. Suspicions that the derived data underestimate "real summer production" would be easier to discuss if based on theory and data (see 2.7, 2.8 and 2.9) rather than two graphs.

Page 25.
The crux of using an indirect estimate of annual production, such as mean height x weight x density is that it ignores turnover and treats biomass as production (see also 2.2).

Page 37 line 13
Refers to growing conditions and last line to soil nutrients, which are a subset of growing conditions.

Table 2.1
Delete "exp (etc.)" under Reproductive Shoots.

Page 44 Lines 20, 21
"Norm" and "normality" should be replaced by "typical sequence of conditions" and "these"

Page. 46
I am not aware of the "classic" work of Gaefskaya (no reference supplied) nor have I seen it cited.

Page 56.
The inverse relationship between size and over-winter survival refers to the fact that short shoots survive whereas tall ones do not.

Page 65 line 19
For "from midsummer to midwinter" read "January to July inclusive", and "Fig. 3.3" to "Fig. 3.3c"

Page 71 line 20
Correct "effect" to "effects"

Page 81
The critical height class on Page 56 refers to the probability of over-winter survival, whereas on Page 81 it refers to probability of becoming reproductive.

Page 89.
Regressions of KN and SRP should have Organic Carbon as the independent variable. This will be changed for publication.

Page 91
The hypothesis that the decrease in shoot height with increasing distance from wetland edge has not been tested previously, nor measured.

Page 91 lines 24-27
Delete sentences "Conversion of nutrients....." and "In addition, nutrients ....."

Fig. 4.3.
Labels should be amended so that solid circles refer to water potential, and hollow to water content.

Page 102
Correct units for "k" are unit weight per unit weight, gm gm^{-1} or kg kg^{-1}

Page 105 line 7
Delete "produced".

Page 107 line 18
Correct "mm^{-2} mm^{-2} d^{-1}" to "mm^2 mm^{-2} d^{-1}". Also on Page 113, line 4 and line 5. Tables 5.4, 5.7. Fig. 5.4.

Page 109 line 19
Correct "cm^{-1} s^{-1}" to "cm s^{-1}". Also on Fig. 5.7.

Page 108 line 11
Insert after "....transpired equally" "This assumption was made as a first approximation, based on stomatal counts for both surfaces, see pages 115-117.

Page 112 & 114
The usage of "clone" and "treatment" is clearly set out on Page 106.

Page 112 3rd para.
The text says that the huge variation in leaf area evident on Day 0 at the start of the study do not correspond with clone size, defined by visual estimate of rhizome size page 106. I consider this a fair statement.

Page 124 line 16
Correct "Figure 5.8" to "Figure 5.7".

Page 140 line 13
Data were arcsin transformed prior to analysis because they were as proportions (Page 140 line 1).

Page 145.
The initial response to the problem of treatments with zero or 100% response, and therefore with a variance of zero, was to do an ANOVA with a reduced data set, using only those treatments with variances greater than zero. These treatments were not the same for all ecotypes, making comparison between ecotypes even more selective. Presentation of analyses done in this way would have involved many tables per experiment, and would have been cumbersome and inelegant. The advice of a statistician was sought. He suggested GLM.

Page 147 line 7
Correct "developped" to "developed".

Page 148 line 28
Correct "slsightly" to "slightly".

Page 148 lines 24-27
The four ecotypes referred to in the text (LP and S, then TOG and TOT) are given as examples to clarify the statement.

Page 156 lines 19, 23
Correct "Figure 6.6" to "Figure 6.7"

Pages 157-159 and Table 6.6.
Seed size is a species specific character, which may vary in response to environmental conditions. The assumption in treating both species in one analysis is that both vary in some way. This assumption was forced onto the analysis by the smallness of the data set.

Page 158 line 20
Correct "interdepence" to "inter-dependence"

Page 160
Ecotype is used as a convenience in writing to avoid cumbersome sentences with "species and ecotype". This stretching of the term should have been more explicitly acknowledged in Methods 6.5 Seeds (Page 138 line 13).

Page 163
Correct "re-combined" to "combined"

Page 165 lines 13-14.
The statement about factors controlling shoot recruitment and growth is stating the obvious but is not superfluous because it is a necessary pre-cursor to the following sentence. A subsequent statement, referring indirectly to irradiance (page 173) is in the context of establishing new individuals from seed, not vegetative re-growth.

Page 168 line 19.
The comparison is between wetland soils and terrestrial soils, and at this level of generalisation the characteristics considered are both physical and chemical.

Page 178 lines 4-5
The text reads "as tall or taller than *Typha*"

Page 179 and Table 7.1
The table is used here not as a definition of a weed but to explore "weediness" in ecological terms, using an accepted approach. The four ecological groupings, as far as I can tell, are original. As pointed out by one examiner, the usefulness of the system may be limited when applied to submerged aquatic weeds, which would have few positive scores (Examiner's report). If so, this is a matter of scientific interest.