THE ECOLOGY OF SALT LAKE HYDROPHYTES:

THE SYNECOLOGY OF SALINE ECOSYSTEMS AND THE AUTECOLOGY OF THE GENUS *RUPPIA* L. IN THE SOUTH-EAST OF SOUTH AUSTRALIA

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"For there are some plants which cannot live except in wet; and again these are distinguished from one another by their fondness for different kinds of wetness; so that some grow in marshes, others in lakes, others in rivers, others even in the sea ..."

Theophrastus (370-c. 285 B.C.)
'Enquiry into Plants'

CONTENTS

SUMMARY

The nature and distribution of submerged and emergent macrophytes in relation to salinity, to the temporary or permanent nature of the aquatic habitats and to the tolerance of fluctuating environments was investigated in a series of saline ecosystems in the Coorong and Robe/Beachport areas of the south-east of South Australia. A synecological survey of the floral relationships in a range of saline habitats was followed by an autecological study of *Ruppia* L., a genus of submerged halophytes.

Only two genera of angiosperms occur above a salinity of 4 °/oo TDS: *Ruppia* is found in waters from 3 to 230 °/oo TDS and *Lepilaena* Drumm. ex Harvey from 3 to 50 °/oo TDS. Both occur in permanent and ephemeral habitats, in pure and mixed stands and in the understorey of emergent salt marsh communities.

The plant associations of a salt marsh, a saline lake and a fresh lake were compared by means of morphometric and vegetation maps and quadrat and biomass sampling. For the Lake Eliza Salt Marsh community twelve plant associations were delimited by species composition, and mapping of these associations shows that their distribution is related to small increases in elevation, which total 0.5 m height above the lake level over 500 m distance from the shore.

Annual and perennial growth forms of *Ruppia* were observed and the genetic or ecological bases of these growth form differences were examined further. A systematic survey indicated the presence of three species, two annuals, *Ruppia tuberosa* Davis and Tomlinson and *Ruppia polycarpa* Mason, and one perennial, *Ruppia megacarpa* Mason, none of which has previously been recognised in South Australia. Both annual species have asexual perennating organs (turions), structures that have not been recorded for this genus outside Australia.

Transplantation, germination and salinity experiments were used to examine the differences between annual and perennial growth forms. The wide salinity tolerance of all three species was confirmed. Under experimental conditions annual and perennial growth forms did not alter in alternate habitats. Decrease in salinity had a positive effect on the germination of the perennial *R. megacarpa* whereas increase in salinity and the wetting and drying of seeds broke the dormancy of the annual *R. tuberosa* seeds.

Explanations advanced to explain the ability of this species to withstand harsh and fluctuating environments were examined by analyses of life cycles, reproductive patterns and osmoregulatory mechanisms of the three species of *Ruppia*.

DECLARATION

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

Margaret A Brock.

Name : MARGARET ANNE BROCK Course : Ph.D

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SECTION I

INTRODUCTION AND LITERATURE SURVEY

CHAPTER 1. INTRODUCTION

Studies of inland saline waters of Australia have centred on their chemical and physical properties and faunas; autotrophs have generally been neglected. Hussainy (1969), Yezdani (1970), Timms (1973) and Walker (1973) have considered aspects of the phytoplankton, but little attention has been paid to the macrophytes. Yet littoral macrophytes are of considerable importance in the fixation of energy in many aquatic ecosystems (Wetzel 1975). The ecological work of Higginson (1967) in the Tuggerah Lakes of New South Wales and the study of the vegetation history of some Victorian lakes (Yezdani 1970) are the principal Australian contributions in this field.

'Aquatic macrophyte' or 'hydrophyte' are terms loosely applied to any aquatic multicellular plant and cover angiosperms and macroscopic algae and a few pteridophytes and bryophytes. The salt tolerant hydrophytes are termed 'halophytes'. Most aquatic plants may be divided into three life form categories: submerged rooted, emergent rooted and free floating (Sculthorpe 1967; Hutchinson 1975). These divisions are not mutually exclusive; e.g. rooted plants may have floating leaves, or environmental fluctuations may cause a plant's life form to change from submerged to emergent.

This study concentrates particularly on the aquatic angiosperms, a group which shows little species diversity in either freshwater or marine situations. Few freshwater species can tolerate saline conditions or fluctuations of salinity, and among the marine angiosperms only very few can withstand hypersaline or brackish waters. While estuaries have salinity gradients in which species from freshwater and marine origins can be studied, a range of saline lakes, such as that provided by the series selected in the south-east of South Australia (Figure 1.1),

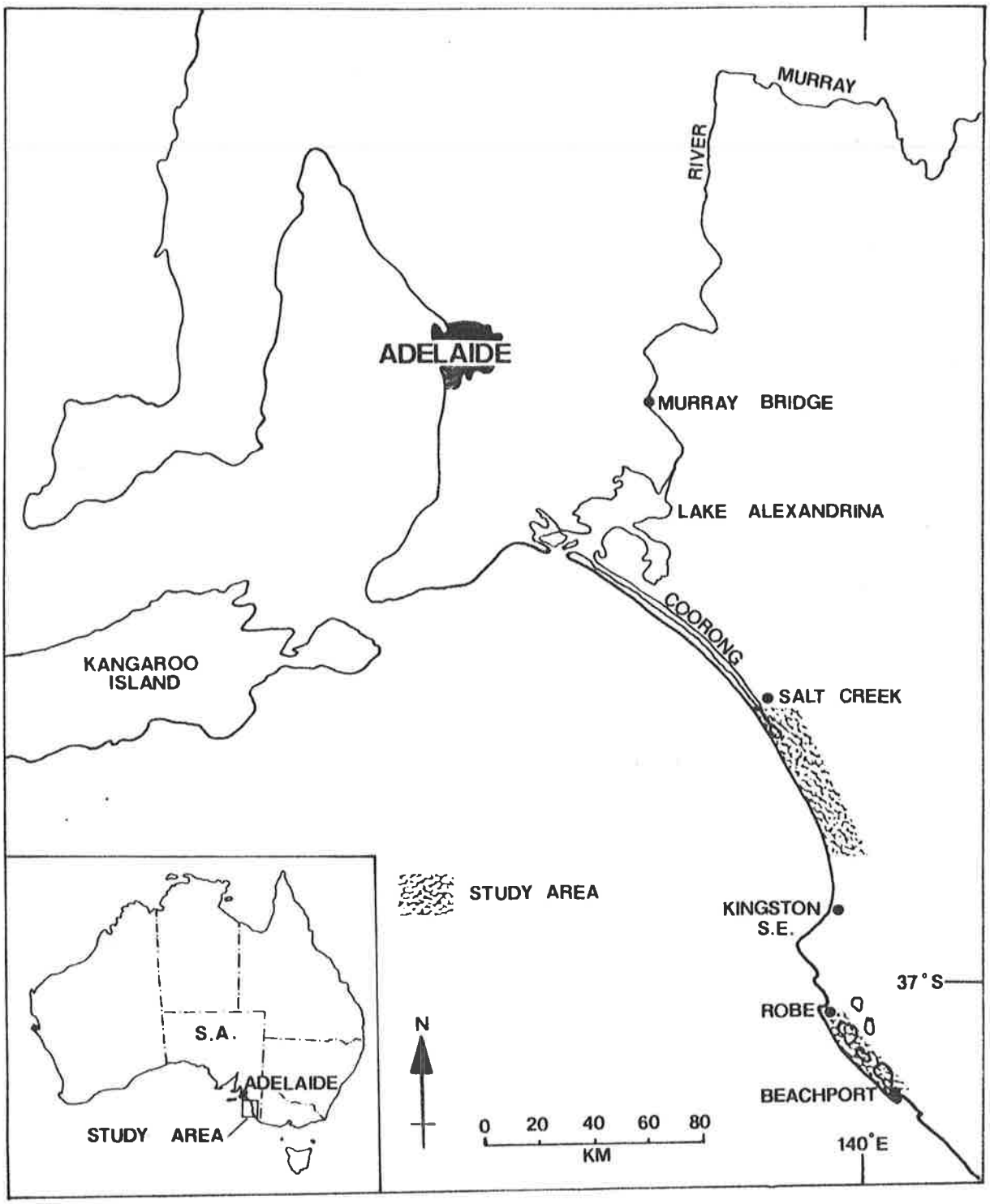


Figure 1.1 The location of study areas in the south-east of South Australia.

provides an ideal opportunity to study salinity tolerance and fluctuations on a wider scale.

The nature and distribution of submerged and emergent macrophytes in relation to their tolerance of fluctuating environments and salinity are investigated in this study. Particular attention is given to the submerged genus *Ruppia* L.

Such a study provides information on the role of macrophytes in saline lakes, and on the responses of plants to salinity in undisturbed and agriculturally modified situations. An understanding of the diversity, distribution and interrelationships of halophytes in a range of saline ecosystems subject to wide environmental fluctuations will provide a basis for more effective assessment of such ecosystems.

The need for research on the response and tolerance of plants to salinity has been heightened by continued exploitation of soil and water resources. Drainage and cultivation have resulted in increased salinities on existing agricultural land and have led to expansion of marginal agriculture into naturally saline areas. Thus physiological work on structural and functional adaptations for salinity tolerance is necessary as well as ecological work on the interrelationships of halophytes within their biotic and physical environments. Concomitantly, research on the variability in salinity tolerance found in wild and cultivated species may elucidate the roles of genetic and environmental components in conferring such tolerances (Chapman 1960, 1974; Poljakoff-Mayber and Gale (1975).

Studies on salinity stress and tolerance of terrestrial and salt marsh (semi-aquatic) halophytes have been reviewed by Poljakoff-Mayber and Gale 1975). An understanding of the physiological effects of salinity fluctuations on fully aquatic halophytes aids research on the breeding and maintenance of salt tolerant plants.

Manipulation of potentially economic plants may thus be explored in saline environments. Extrapolation from information on individual species and specific ecosystems can serve as an indication of tolerances and adaptations of other organisms and environments.

The series of saline ecosystems selected has been studied from two viewpoints: synecological and autecological (*sensu* Dansereau 1957). First, studies of the whole communities provide a general description for each ecosystem by determining species composition and distribution and the empirical biotic relationships and environmental interactions. Second, an investigation of the genus *Ruppia*, a single element within the total ecosystem enables the examination of one biotic component in varying environments.

The synecological study permits an overview of each saline ecosystem, and allows direct comparisons. However, the delimitation of boundaries of the physical and biotic factors involved is subjective, rather than objective, and consequently the trends observed are qualitative, or at best, semi-quantitative. Other limitations are imposed by problems of sampling such complex and variable ecosystems.

The autecological study enables precise and quantitative study of the parameters which appeared, from the synecological study, to be important factors in determining the plant-ecosystem relationships, e.g. life cycles, reproductive patterns, dormancy and salinity tolerance.

The necessity for considering the total ecosystem, as well as its individual parts, is reinforced as individual factors seldom act in isolation although they may have a major influence in a particular system. Examination of the nature of a range of saline communities, combined with detailed studies of the vascular hydrophyte *Ruppia*, maximized the advantages of these two approaches while minimizing the disadvantages.

CHAPTER 2 PREVIOUS STUDIES

Although little comparative work on the macrophytes of salt lakes has been published, a survey of research on saline ecosystems, vascular hydrophytes and the aquatic biology of the south-east of South Australia provides a background to this study.

2.1 Saline ecosystems

High salinities and wide fluctuations in several environmental parameters cause biological stress; low biotic diversity results (Williams 1970, 1978). The virtual absence of macrophytes in saline waters (Williams 1969), the shallow completely mixed nature of salt lakes (Cole 1968; Scudder 1969) and the ionic similarity of Australian salt lakes to sea water (*cf.* Williams and Buckney 1976b), mean that such ecosystems are suitable locations for the study of the concepts of ecological energetics (Williams 1969) and maturity (*sensu* Margalef 1968, Williams 1970). Bayly and Williams (1973) and Williams (1978) have summarized the physical, chemical and biological work done in Australia.

Lake ecosystems in Australia span a full range of salinity from fresh water to saturated salt solutions; most are shallow (<5 m) and many are part of endorheic drainage systems, with great fluctuations of water level, salinity and temperature. Many of the salt lakes are ephemeral, with an annual dry season of up to nine months, while others (e.g. Lake Eyre) may exist for many years either as dry salt pans or as semi-permanent lakes. Permanent lakes of high salinity are less common, but have been described from Victoria and South Australia (Bayly and Williams 1966, 1973; Williams 1978).

Seasonal salinity fluctuations are generally greater in lakes of higher mean salinity. Salinity maxima tend to vary from year to

year, particularly in temporary lakes where marked water level changes followed by complete drying and deposition of a salt crust are involved. As these lakes refill, salinity increases until the water level is above the salt crust, and then decreases until evaporation exceeds precipitation (Hussainy 1969).

Salinity fluctuations are greatest in ephemeral, hypersaline shallow lake systems whereas fluctuations in permanent saline lakes are comparatively small and salinity maxima less extreme (Bayly and Williams 1973).

Surface water temperatures are highest in shallow hypersaline lakes, and where maxima may exceed 40°C, diurnal and seasonal fluctuations of over 20°C may occur. Deeper bodies of water may have seasonal temperature variations of up to 15°C, but diurnal differences are usually less extreme than in shallow water. Shallow lakes show no persistent thermal stratification, whereas the permanent deeper lakes often stratify in summer and are isothermal in winter (Williams 1978). Considerable turbulence and complete mixing are common features of Australian saline lakes, and are most pronounced in the shallow, temporary waters which are exposed to stirring by wind and have easily suspended sediments. Wind induced turbidity at times results in Secchi disc readings of less than 0.1 metre. Only one saline meromictic lake has been reported in Australia, West Basin Lake in western Victoria (Timms 1972).

Australian saline lakes characteristically have high pH values and show a marked ionic homogeneity with a general pattern of ionic dominance $Na > Mg > Ca > K : Cl > SO_4 \geqslant HCO_3 + CO_3$. Most lakes are NaCl dominated with the same order of ionic dominance as sea water, and ionic proportions remain constant in lakes over wide salinity and geographical ranges (Williams and Buckney 1976a,b). A small group of carbonate dominant lakes in Victoria is an exception (Bayly 1969; Walker 1973; Williams 1978).

The availability of nutrients, carbon dioxide and oxygen may affect primary productivity. The solubility of oxygen in water decreases with increasing salt content (Kinne and Kinne 1962); therefore the degree of mixing and the depth and surface area of lakes will largely determine oxygen concentration and hence the distribution and abundance of the biota at high salinities. High levels of dissolved carbon dioxide are often inversely related to the oxygen concentration (Bayly and Williams 1973) and whereas a high carbon dioxide level may limit the fauna, it can result in enhanced photosynthesis. In a range of saline ecosystems, plant nutrient concentrations (phosphate and nitrate) have been found to be high compared with those of freshwater systems (Jenkin 1932; Hutchinson 1957; Talling and Talling 1965; Hussainy 1969; Milbrink 1977). Thus while oxygen concentration and temperature may limit the biota in saline situations, the availability of carbon dioxide, phosphate and nitrate is not likely to limit plant growth.

An inverse relationship between biotic diversity and salinity has been demonstrated for the fauna of the salt lakes of western Victoria. Endemic species predominated and some otherwise cosmopolitan salt lake species were not recorded (Williams 1978). Initial investigations of lakes in the south-east of South Australia (including some of those considered in this study) were made by Bayly and Williams (1966) and were followed by studies of the fauna by Bayly (1970). Permanent lakes examined in more detail included a carbonate-bicarbonate dominated lake, Lake Werowrap (maximum 57 parts per thousand total dissolved solutes ($^{o}/_{oo}$ TDS)) (Walker 1973), and three deeper maar lakes covering a wide salinity range, Lakes Purrumbete (fresh), Bullenmerri (maximum 9$^{o}/_{oo}$ TDS) and Gnotuk (maximum 60$^{o}/_{oo}$ TDS) (Timms 1973, 1976). Detailed studies of the ecology and physiology of *Parartemia zietziana* Sayce (Crustacea: Anostraca) occurring in shallow lakes have been

provided by Geddes (1973) and Marchant (1976). Studies of other animal species are summarised by Bayly and Williams (1973) and Williams (1978).

Data on secondary production in salt lakes have suggested high standing crops (Williams 1964). Paterson and Walker (1974) estimated secondary production in a low salinity lake and Marchant and Williams (1977) in hypersaline systems: the former found a low primary to secondary production ratio, the latter demonstrated a high efficiency of conversion. Marchant and Williams suggested that input of allochthonous material may be the major energy source. However, primary production in each case was estimated from phytoplankton production only, and no estimates of macrophytic or periphytic production were made for these ecosystems. Data from the saline Borax Lake, California, show that periphyton production may be particularly important, even when macrophyte production is low (Wetzel 1964).

In Australia, studies of botanical diversity and primary production have been undertaken largely as adjuncts to the work mentioned previously. Phytoplankton production is reported to be high at low salinities and conversely low in high salinities (Hammer 1970; Hammer *et al.* 1973; Walker 1973; Marchant and Williams 1977), a result which is inconsistent with the high nutrient levels of saline lakes. The estimates of Hammer *et al.* (1973) were made from short term experiments and those of Walker (1973) were made on a carbonate-bicarbonate lake, ionically atypical for Australia, yet a type of lake known to be highly productive elsewhere (Walker 1975). Hussainy's (1969) estimates of planktonic chlorophyll *a* showed little correlation with salinity. Wetzel (1964) included phytoplankton, periphyton and macrophytes in his study and suggested that the non-planktonic communities may be an important component of the biomass. As yet, periphyton and macrophytes have not been considered in detail in Australian salt lakes.

In the permanent Victorian salt lakes studied, the macrophytic species recorded include *Ruppia maritima* L., *Lepilaena preissii* (Lehm.) F. Muell., *Potamogeton pectinatus* L. and *Enteromorpha* sp. (Willis 1964; Yezdani 1970; Timms 1973). Yezdani (1970) recorded *Ruppia* as the most halotolerant species in salinities up to $56^{o}/_{oo}$ TDS. The emergent semi-aquatic halophytes occurring in the eulittoral zone of lakes have been considered only briefly; Willis (1964) gave a species list for the lakes of the basaltic plains of western Victoria. No information is available on the role of the allochthonous sources of nutrients provided by annual flooding or by connection of these peripheral habitats with the lakes.

2.2 Vascular hydrophytes

The major studies on hydrophytes in marine, freshwater or inland saline waters in which the geographical distribution, species composition and other aspects of macrophyte biology were considered have been collated by Arber (1920), Sculthorpe (1967) and Hutchinson (1975). The ecology of emergent halophytes in salt marshes has been extensively reviewed by Chapman (1960, 1974), Waisel (1972) and Reimold and Queen (1974).

Arber's (1920) early work on water plants described adaptations to the submerged environment. Photosynthetic adaptations, the development of heterophylly in different environmental conditions, and respiratory adaptations, such as lacunae and aerenchyma, were discussed more recently by Sculthorpe (1967) and Hutchinson (1975). In addition, aspects of the life history, including mechanisms of sexual reproduction, seed dormancy and germination and asexual reproduction by rhizomes and perennating organs, were emphasised by these authors.

Factors influencing the differential distribution of plants within and between lakes have been studied principally in fresh waters in the

northern hemisphere (*cf.* Pearsall 1920, 1926; Spence 1967). The vertical and horizontal distribution of species within ecosystems has been attributed variously to the effects of substrate, turbulence, depth, light penetration and other associated environmental parameters as discussed extensively by Hutchinson (1975).

A series of workers in Wisconsin, U.S.A. (Denniston 1922; Rickett 1921, 1924; Wilson 1935, 1937, 1941; Potzger and van Engel 1942; Swindale and Curtis 1957), and in the Netherlands (den Hartog and Segal 1964), used phytosociological and quantitative analyses to study the interrelationships between plants and environmental factors in hydrophyte communities. Difficulties in defining communities along gradients using such approaches were outlined by Whittaker (1962). Modified techniques have been applied more recently to the analyses of semi-aquatic and salt marsh vegetation (Howard-Williams 1972, 1975; Howard-Williams and Walker 1974; Lee 1977).

Halophytes of saline and brackish inland waters are poorly documented, as previous work has been concerned mainly with marine and estuarine angiosperms. The only genus common to inland saline waters and some estuaries is *Ruppia*. This is a cosmopolitan taxon with salinity tolerance up to $100^{o}/_{oo}$ TDS (Wood and Baas Becking 1937), but it does not require specifically waters of marine origin (den Hartog and Segal 1964). Recent European studies of *Ruppia* communities in a variety of isolated or marine-connected ponds on the Camargue and on Corsica (France) and on Texel (The Netherlands) have described the distribution and community structure in relation to salinity and salinity fluctuations (Verhoeven 1975, 1978, 1979; Verhoeven and van Vierssen 1978a,b).

Studies of angiosperms in Australian inland and coastal waters are not extensive. Ferguson Wood (1959a,b) described the *Zostera* and *Ruppia* communities of Lake Macquarie, New South Wales. Higginson (1965,

1967) followed with a more detailed account of submerged angiosperms in the marine connected Tuggerah lakes system; he considered both the plants and the chemical and physical environment, particularly the sediments. Congdon (1977) and Congdon and McComb (1979a, 1979b in press), reported on studies of the Blackwood River Estuary in Western Australia, concentrating on the productivity and light dependence of *Ruppia*. Work on Australian inland salt lakes is even less extensive. Yezdani (1970) presented a species list in his study of the vegetation history of a series of hypersaline and slightly to moderately saline lakes in western Victoria. He reported *Ruppia* sp. as the only submerged angiosperm occurring throughout the salinity range from fresh to 60°/oo TDS and as the only submerged species recorded over 30°/oo TDS. Species of *Lepilaena* Drumm. ex Harvey occurred up to 30°/oo TDS, *Myriophyllum elatinoides* Gaudich. and *Myriophyllum verrucosum* Lindl. up to 9°/oo TDS and *Potamogeton pectinatus* and *Myriophyllum muelleri* Sond. up to 3°/oo TDS. The most salt tolerant emergent and semi-aquatic species were *Triglochin striatum* Ruiz & Pavon, *Suaeda australis* (R.Br.) Moq., *Salicornia australasica* (Moq) Eichl. (1963) [possibly refers to *Sarcocornia quinqueflora* (Bunge ex Ung-Steinb.) Scott] and *Cotula coronopifolia* L. which were reported in root-water salinities of up to 60°/oo TDS. *Ruppia* sp. and *Lepilaena* sp. have been reported at salinities above that of sea water (35°/oo TDS) in the Coorong, South Australia (Lucas and Womersley 1971; Womersley in Noye 1974) and a new species of *Ruppia*, *R. tuberosa* Davis & Tomlinson, has been described from a salinity of over 100°/oo TDS in Western Australia (Davis and Tomlinson 1974).

Research into the physiology of plant salt tolerance in both aquatic and terrestrial environments is relevant to the study of aquatic halophytes. The early work in the field was summarised by Bernstein and Hayward (1958) and Waisel (1972), whereas Reimold and Queen (1974),

Stroganov (1974), Flowers (1975), Poljakoff-Mayber and Gale (1975) and Flowers, Troke and Yeo (1977) have reviewed more recent work. Studies of water regulation in halophytes has mainly concerned salt marsh and terrestrial (crop) species; little attention has yet been paid to submerged aquatic plants.

Halophytes must maintain turgor without inhibition of cellular processes by accumulation of excess ions. Chloride, sodium and potassium ions are abundant in most saline environments and hence much of the research into halophytes has concerned the maintenance of turgor and the exclusion or accumulation of these ions (Cram 1976; Hellebust 1976; Flowers, Troke and Yeo 1977). Extensive work on the salt marsh species *Suaeda maritima* (L.) Dum. has contributed to the knowledge of salt tolerance of this species. Plants growing in the field were able to tolerate higher concentrations of sodium chloride than those in sand culture (Flowers 1972; Yeo 1975; Ernst 1978). *In vitro* callus tissue cultures (Hedenström and Breckle 1974) and subcellular cytoplasmic enzymes (Ernst 1978) tolerated lower concentrations of sodium chloride than the whole plant. This suggests the presence of regulatory mechanisms which maintain the salt concentration in the cytoplasm at levels suitable for metabolic activity. Jefferies (1973) presented data to support this for *Triglochin maritima* L. Exclusion of inorganic ions from the cytoplasm by maintenance of osmotic pressure with organic solutes has been suggested as a mechanism for salt tolerance (see Hellebust 1976; Flowers, Troke and Yeo 1977; Ernst 1978). Proline levels in some halophytes were found to increase in plants grown at increasing levels of salinity (Stewart and Lee 1974; Calvalieri and Huang 1979) and data suggest that betaine accumulates in several salt resistant species (Storey and Wyn Jones 1977).

Most studies of aquatic primary productivity estimate phytoplanktonic and photosynthetic bacterial production and assume that macrophyte

production forms a relatively insignificant proportion of total production by photosynthesis. Wetzel (1964) commented that, while this assumption is generally valid for marine areas and many deep lakes, the benthic macrophytes are important in marshes and in many rivers, ponds and shallow lake systems. The assessment of macrophytic production is difficult and methods need to be developed further.

Biomass and productivity estimation are generally based on the levels of chlorophyll, oxygen evolution and C_{14} accumulations. The limitations of these techniques are summarized and discussed by Wetzel (1964) and Vollenweider (1974).

In one of the first productivity studies to cover all photosynthetic components, Wetzel (1964) used C_{14} techniques to provide an estimate of total annual mean primary production of 1057.3 mg $C/m^2/day$ (385.9 $g/m^2/yr$) in Borax Lake, California with 7% produced by macrophytes, 24% by phytoplankton and 69% by periphyton. The only macrophyte present was *Ruppia maritima*.

Other estimates of productivity of members of this genus, based on biomass measurements indicate wide variability with season, type of ecosystem and species; Verhoeven (1978) recorded a winter maximum standing crop of 8.5 g/m^2 and a summer maximum of 131.9 g/m^2 for *Ruppia cirrhosa* (Petagna) Grande, in shallow brackish waters on Texel, the Netherlands, whereas Congdon and McComb (1979b, in press) recorded minimum and maximum values of 81 and 503 g/m^2 for *Ruppia* sp. in the Blackwood River Estuary in Western Australia.

Variability is also reported in the growth forms of *Ruppia*. The taxonomic status of forms within the genus requires clarification as a consequence; Australian material has been referred previously to *R. maritima* or *R. spiralis* L. ex Dum. (or more correctly *R. cirrhosa*). The taxonomic status of the genus is considered in Chapter 8.

2.3 Inland aquatic ecosystems of south-eastern South Australia

A series of lakes occurs between stranded beach dune ridges along the south-eastern coast of the State (see Figure 2.1). These dunes are composed of unconsolidated Tertiary and Quaternary sands and lithified dune limestones. The interdune depressions are poorly drained naturally as they are on spongy peats and grey black clays overlying limestone, or on sandy soils overlying clay (M. Williams 1974). The Robe/Beachport lakes and the Coorong (a series of lagoons, with a single marine connection and associated salt pan lakes to the south) have formed in the interdunal hollow behind the most recently emerged dunes of the Robe and Woakwine series. The fresh water seeps and volcanic crater lakes of the Mount Gambier region are the only other major lakes in the south-eastern part of the State.

The dune systems parallel the existing shoreline and were stranded by Pleistocene sea-level oscillations (Tindale 1959; Sprigg 1959). The lagoonal deposits in the interdunal depressions subsequently were modified by gentle regional upwarping (Hossfeld 1950; Sprigg 1952).

The land has a slight south-east to north-west tilt with natural drainage westwards to a dune ridge and then to the north-east with a natural outflow into Salt Creek and the Coorong (Figure 2.1). Underground drainage is continuous: it is below surface in summer, but reaches the surface in winter. Permanent springs are present in some low-lying areas. Large areas of these wetlands have been artificially drained in the last 100 years in order to improve their agricultural potential (see M. Williams 1974; Jones 1978). The Coorong and the Robe/Beachport lake ecosystems, although not directly subjected to drainage, have been affected indirectly by changes in groundwater levels.

Precipitation in the area increases southwards (Figure 2.2) grading from 450 mm *per annum* at the mouth of the River Murray to 500 mm at Salt Creek on the South Lagoon of the Coorong, 625 mm at Robe and

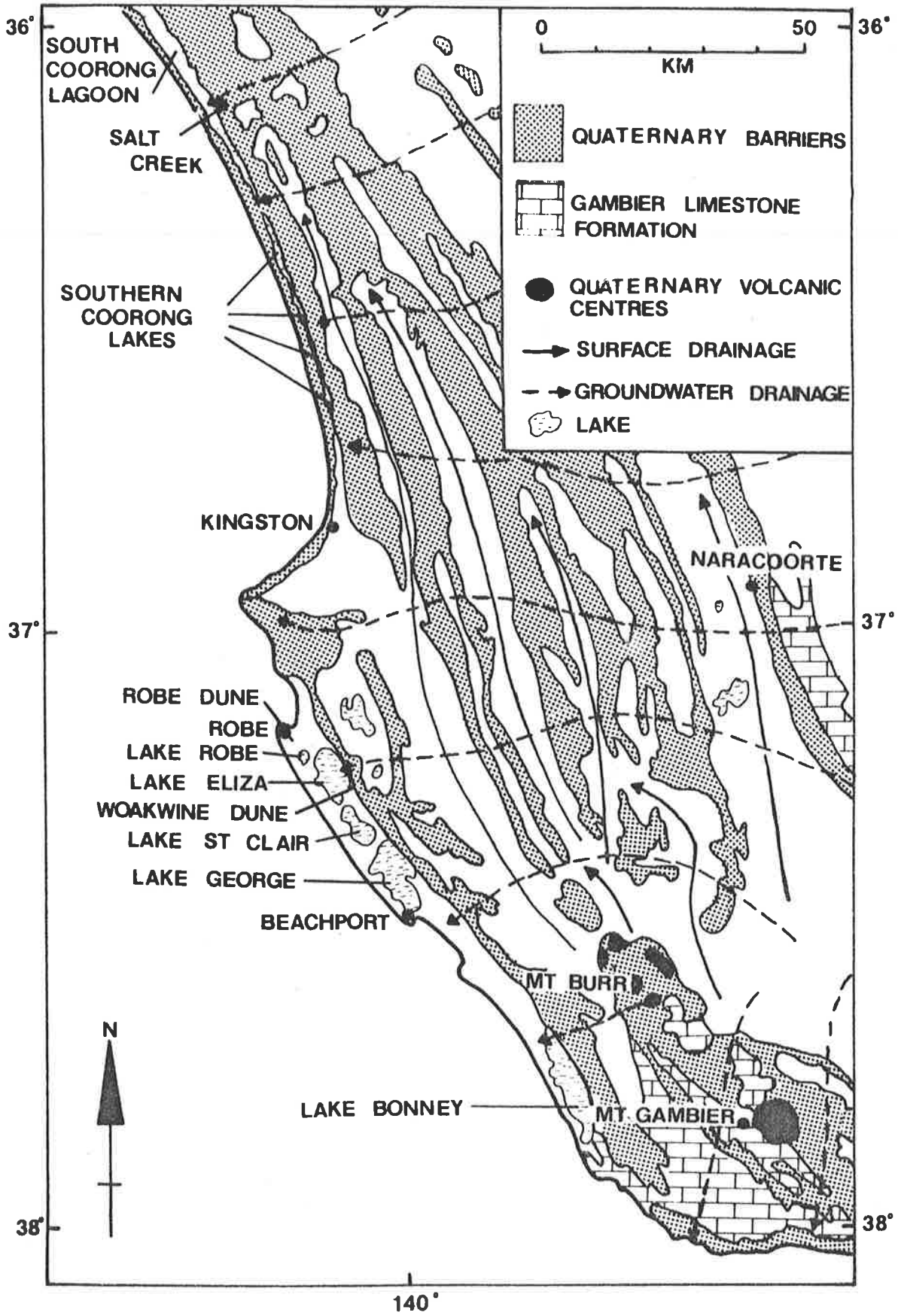


Figure 2.1 The physiography and geology of the south-east of South Australia (after Gilbertson and Foale, 1977).

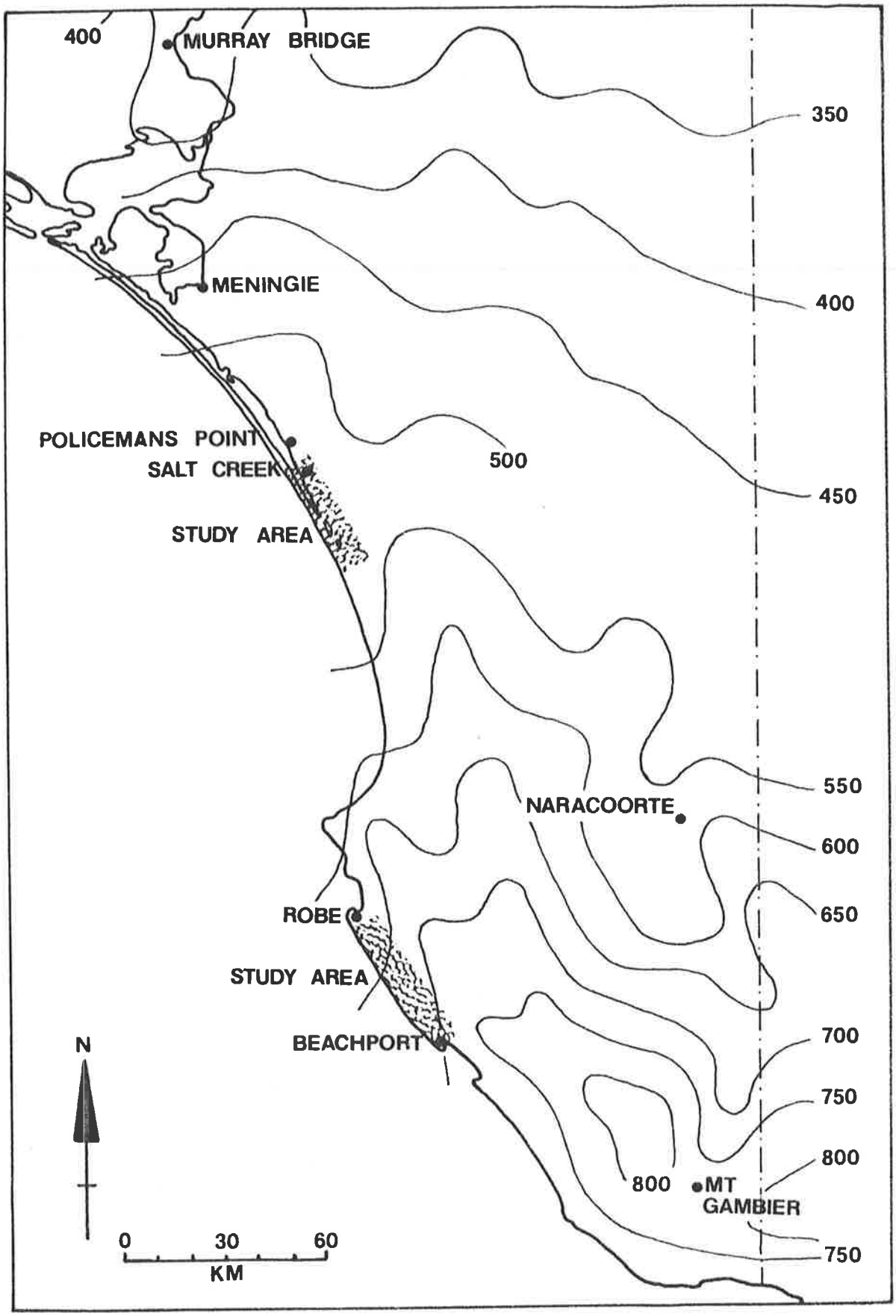


Figure 2.2 Annual precipitation isohyets for the south-east of South Australia. Data provided by the Bureau of Meteorology for the 50 years to 1973 (after Gilbertson and Foale, 1977).

800 mm around Mount Gambier. However, evaporation generally exceeds precipitation throughout the area and the climate is classified as mesothermal (for classification see Jätzold 1961) with a marked summer drought. Precipitation occurs on an average of 138 days per year (at Policemans Point on the Coorong) with a marked winter peak and a dry summer (Meteorological Bureau data). Air temperatures show seasonal extremes from below freezing to above 40°C.

Sea level oscillations and the associated geological history of the Coorong were described by von der Borch (1962, Ch. 2 in Noye 1974) from studies of sediment cores from the area. He postulated that a sea level similar to the present existed 120,000 years ago and formed the landward Coorong shore. A subsequent retreat followed by a rise in sea level 80,000 years ago resulted in the formation of the Younghusband Peninsula; a further retreat and rise of waters inundated the Coorong with oceanic water. Further isolation of the Coorong occurred with the build-up of the Younghusband Peninsula as a barrier; the lagoonal area became increasingly hypersaline and cut-off lagoons became sequentially stranded from the south. The most recent sediments of these restricted and hypersaline habitats are organic-rich calcite and aragonite ($CaCO_3$) muds with a sparse fauna (von der Borch 1965).

Current ecological conditions are important in the geomorphological evolution of these lakes. Salinity changes may control the vegetation which traps sediments on lagoon shores (Bird 1967). Where low salinities occur, reed-swamp communities often predominate, while salt marshes usually become established in more saline situations.

Water levels of the ephemeral lagoons are controlled largely by evaporation and while this influences the level of the Coorong proper, fluctuations also occur with varying wind conditions, seiche movements, tidal influences and the opening of the barrage at the mouth of the

River Murray; such changes may exceed one metre. Input of water is from rainfall, backflow from the River Murray and the sea, and from freshwater seeps on the sides of dunes, where fresh water lies above saline water in the aquifer (Noye 1974). Salt Creek has not functioned as an input channel since the drainage schemes were instigated.

Hydrological studies of the Coorong (Noye 1970) showed a salinity gradient which increases southwards. In winter the North Lagoon may be diluted with water from the River Murray. The permanently hypersaline South Lagoon which is often isolated from the North Lagoon in summer, may increase in salinity to over 90^{o}/oo TDS. Seasonal fluctuations in salinity from nearly fresh to six times sea water are recorded for the series of ephemeral lakes to the South. These pans now appear to be cut off from the Coorong proper by shifting dunes.

The Robe/Beachport lake series lies between the Woakwine and Robe ranges, two dunes of aeolian calcarenite which are probably marine in origin, having been isolated from the sea by coastal dune emergence (Hossfeld 1950; Sprigg 1952; Bird 1967). Lakes Eliza, St. Clair and Robe (and the associated smaller coastal lakes) are shallow with natural catchment areas in the surrounding dunes. They are often hypersaline and show fluctuations in salinity and water level; Lake St. Clair and Lake Eliza are slightly below sea level (Jack 1921). The deeper hypersaline Lake George which now receives water from the man-made Drain M, is connected to the sea by an artificial channel (Jones 1978). Several small, fresh, brackish or saline permanent lakes lie between these larger lakes and the sea.

Evaporation causes the shallow closed lakes to become hypersaline and to form salt pans intermittently. The salts are thought to be of marine origin and date from residual sea water as a result of lowered ocean levels and dune emergence (Bayly and Williams 1966). An

alternative explanation is that the salts are derived from seawater by atmospheric precipitation (Jack 1921). Bayly and Williams (1966) reported a strong parallel in the ionic composition of these lakes and seawater (see Table 2.1). However, the calcium concentration of these lakes is higher than in other inland saline situations with atmospherically derived salts, and, as calcium is not readily transported atmospherically (Bayly 1964), it appears that the marine origin is more likely (Bayly and Williams 1966). The calcareous dunes may be an alternative calcium source (Hossfeld 1950).

While wide seasonal fluctuations in salinity are reported for these lakes (Bayly and Williams 1966; Bayly 1970) there is no evidence to suggest that the relative ionic proportions change throughout the year.

The faunal composition of the Robe/Beachport lakes was cursorily examined by Bayly and Williams (1966) and Bayly (1970). Most of the organisms in the coastal lakes of the south-east are non-marine in origin, and thus are classed as athalassic (Bayly and Williams 1973). Bayly (1970) suggested that most marine forms are incapable of sustaining and perpetuating themselves in closed systems and, where present, are generally short lived. Thus the dominant faunal groups are of freshwater lineage (insects, amphipods, calanoid and cyclopoid copepods, ostracods and rotifers); a small group of these is of marine or brackish descent (harpacticoid copepods and the cyclopoid copepod *Halicyclops ambiguus* Kiefer) (Bayly and Williams 1966).

Bayly (1970) noted the absence of Anostraca from the area, but *Parartemia* sp. has been recorded recently from several localities in the Coorong area (Geddes and Brock in Gilbertson and Foale 1977, Geddes pers. comm.).

Records of animals of terrestrial or semi-terrestrial origin, now secondarily adapted to saline aquatic habitats, are also noteworthy,

TABLE 2.1. Mean proportions of major ions in seawater and in waters of saline lakes of South Australia. All values are given as equivalent percentage of total cations or anions.

Water	Na^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}	HCO_3^-	Na^+/Cl^-
Seawater	77.1	1.6	17.7	3.5	90.3	9.3	0.4	0.85
Beachport-Robe series*	76.5	1.9	18.9	2.7	87.0	12.5	0.6	0.88
Beachport-Robe lakes†	78.8	1.5	18.0	1.5	91.8	8.0	0.5	0.86
Coorong (8 sites)	71.3	1.9	22.7	4.0	96.6	3.1	0.4	0.74

*Omitting the single saturated water.

†Calculated from Jack (1921, p.74). Mean data for four lakes: samples taken May 27, 1920.

Data from Bayly and Williams (1976) and Williams and Buckney (1976b).

e.g. the isopod *Haloniscus searlei* Chilton and possibly the gastropod *Coxiella striata* Reeve (Bayly and Williams 1966). The hypothesis currently accepted is that this gastropod has evolved from marine littoral → semi-terrestrial → athalassic saline supra-littoral → athalassic saline habitats with no freshwater intermediate (Bayly and Williams 1966).

The only species of fish recorded, *Taeniomembras microstomus* Gunther, in the marine family Atherinidae, is euryhaline (Bayly and Williams 1966; Lui 1969); the identity of this species has been doubted (Bayly 1970).

The aquatic floras of these lakes have not been catalogued. The terrestrial vegetation from the south-east of South Australia has been classified into plant alliances (Specht 1972) and described in these terms by Specht, Roe and Broughton (1974), and Jones (1978). The vegetation of the southern Coorong region has been considered recently by Alcock and Symon, and Mowling and Taylor (in Gilbertson and Foale 1977).

Thirteen plant alliances covering the natural grasslands, heath swamplands and forests of the area are recognized for the wetlands of the South-East (Specht *et al.* 1974). The dominant vegetation surrounding saline lakes in the Little Dip Conservation Park and Beachport areas is low open forest or scrub of the *Melaleuca halmaturorum* F. Muell. ex Miq. alliance, with an understorey of herbs. Some of the fresher lakes are surrounded by low open *Eucalyptus ovata* Labill. alliances with wet heath understorey. Closed associations of *Leptospermum pubescens* Lamk. and *Leptospermum juniperinum* Sm. and *Melaleuca* spp. dominate in some coastal areas, and heath alliances of species of *Melaleuca*, *Hakea*, *Xanthorrhea*, *Banksia*, *Leptospermum* and *Casuarina* are also typical. Closed grassland/sedgeland communities of *Phragmites australis* (Cav.) Trin ex Steud., *Typha*, *Scirpus* and *Machaerina*

surround swamps and coastal flats, and *Gahnia* tussocks often occupy the slightly elevated flats nearby.

Salt marshes and aquatic plant communities have not been considered extensively and further studies are needed. Osborn and Wood (1923) commented on edaphic and climatic factors in relation to aridity and the halophytic nature of the vegetation in succession from mangroves to salt marsh. The only early study including an aquatic plant list was that of Eardley (1943). Crocker (1944) considered only terrestrial plants in his discussions of soil and vegetation relationships in the south-east. A species list for the northern Coorong was given by L. Williams and Cleland (1960) and vegetation relationships of the dunes between Robe and Naracoorte were analysed by Welbourn and Lange (1968). However, wetland vegetation was not considered in either study.

In discussing the submerged plant life of the Coorong, Womersley (in Noye 1974) summarised the short-term studies of Delroy, Macrow and Sorrel (1965) and Lucas and Womersley (1971). *Ruppia*, the principal angiosperm, was reported to be an important bird food; ducks fed on tubers, rhizomes and seeds when available, and swans ate the leaves as well (Delroy *et al.* 1965; Verhoeven 1978). Both *Ruppia* and *Lepilaena*, the only other angiosperm recorded, are more common in ephemeral lakes than in the Coorong itself. *Lamprothamnium papulosum* (Wallr.) J.Gr. (Characeae) has also been recorded as a bird food in this area (Delroy *et al.* 1965). Other algae include *Cladophora* and *Enteromorpha* (of freshwater lineage) and the marine green alga *Acetabularia peniculus* (R.Br.) Solms-Laubach (Womersley in Noye 1974).

Little work has been done on the plants of ephemeral or permanent lakes of the south-east. The only report is the preliminary survey of Geddes and Brock (in Gilbertson and Foale 1977) on the occurrence of *Ruppia* in the ephemeral lagoons south of the permanent Coorong basins.

SECTION II

SYNECOLOGICAL SURVEY OF THE SOUTH EAST OF SOUTH AUSTRALIA

CHAPTER 3. STUDY SITES AND ENVIRONMENTAL VARIABLES: SELECTION AND DESCRIPTION

3.1 Selection of determinants and sites

Selection of those determinants likely to influence species distribution and composition was based on the hypothesis that it is fluctuating or variable factors which cause localised floral differences. Since ephemerality, water depth and salinity were the most obvious factors which varied between and within lakes, these were the factors used in the selection of study sites. The south-east of South Australia was selected as the general region for investigation as the lakes there provide the necessary range of conditions in reasonable proximity to one another in an area accessible from Adelaide. The desert salt pans of the northern areas of the State were considered unsuitable for limited term studies as they are all ephemeral and may remain dry for several seasons.

The study sites fall geographically into two areas: the Coorong and the Robe/Beachport lakes (Figure 1.1, 3.1). A permanent location on the Coorong South Lagoon, subject to considerable salinity and depth fluctuation, was selected as a permanent hypersaline habitat for study, and several of the temporary Coorong lagoons were selected as ephemeral habitats (Figure 3.2). A second series of lakes of varying size, permanence, depth and salinity were chosen from the Robe/Beachport area (Figure 3.3). Three of these, a permanent fresh lake, a permanent saline lake, and an ephemerally wet salt marsh (Figure 3.4) were selected for extensive study. Details of the locations, size and characteristics of sites are summarized in Table 3.1. Plates 3.1 to 3.6 show some of the sampling sites. Photos of the ephemeral salt pan lake, Pipeclay Lake (Plate 3.1), the hypersaline temporary lagoon, Brineshrimp Lake (Plate 3.2) and the brackish roadside pool, Blue-Green

TABLE 3.1. Main sampling sites; names, numbers, areas, characteristics and locations. Numbers, names or their abbreviations will be used for reference in the text. Names marked * have been assigned for the purpose of this study as names have not been given for these sites on published maps. P = permanent, E = ephemeral. Characteristics of lakes not sampled regularly are to be found in Appendix I.

No.	Lake Name	Abbreviation	Approx. area (ha)	Characteristics	Grid Reference 1:250,000 series	Grid Reference 1:50,000 series	Bayly (1970) Lake No.
	Coorong Series				Naracoorte sheet	Santo sheet	
*1	Pipeclay Lake	(PL)	5	E shallow saline-hypersaline	268539	780000	
2	Flax Point	(FP)		P hypersaline	266539	774984	
*3	Mikes Lake	(ML)	<2.5	E brackish-saline	272529	827897	
						Tilley Swamp sheet	
*4	Blue-Green Algal Pool	(BGAP)	<2.5	E brackish	280507	917658	
*5	Brine Shrimp Lake	(BL)	100	E shallow saline-hypersaline	282501	938600	
	Robe/Beachport Series				Penola sheet	Robe sheet	
6	Lake Robe	(LR)	250	P shallow saline	284409	940813	10
						Beachport sheet	
*7	Fresh Dip Lake	(FDL)	2.5	P fresh	286404	947758	
*8	Little Dip Lake	(LDL)	2.5	P saline	286404	954754	10B
*9	Lake Eliza Salt Marsh	(LESM)		E seasonally inundated salt marsh	286404	955755	
*10	Erringtons Hole Lake	(EH)	3	P brackish	286401	956730	
*11	Lake Eliza Cut-Off	(LEC)	28	P hypersaline	287402	962740	11
12	Beachport Salt Lake	(B/p SL)	2.5	P hypersaline	304377	114510	17

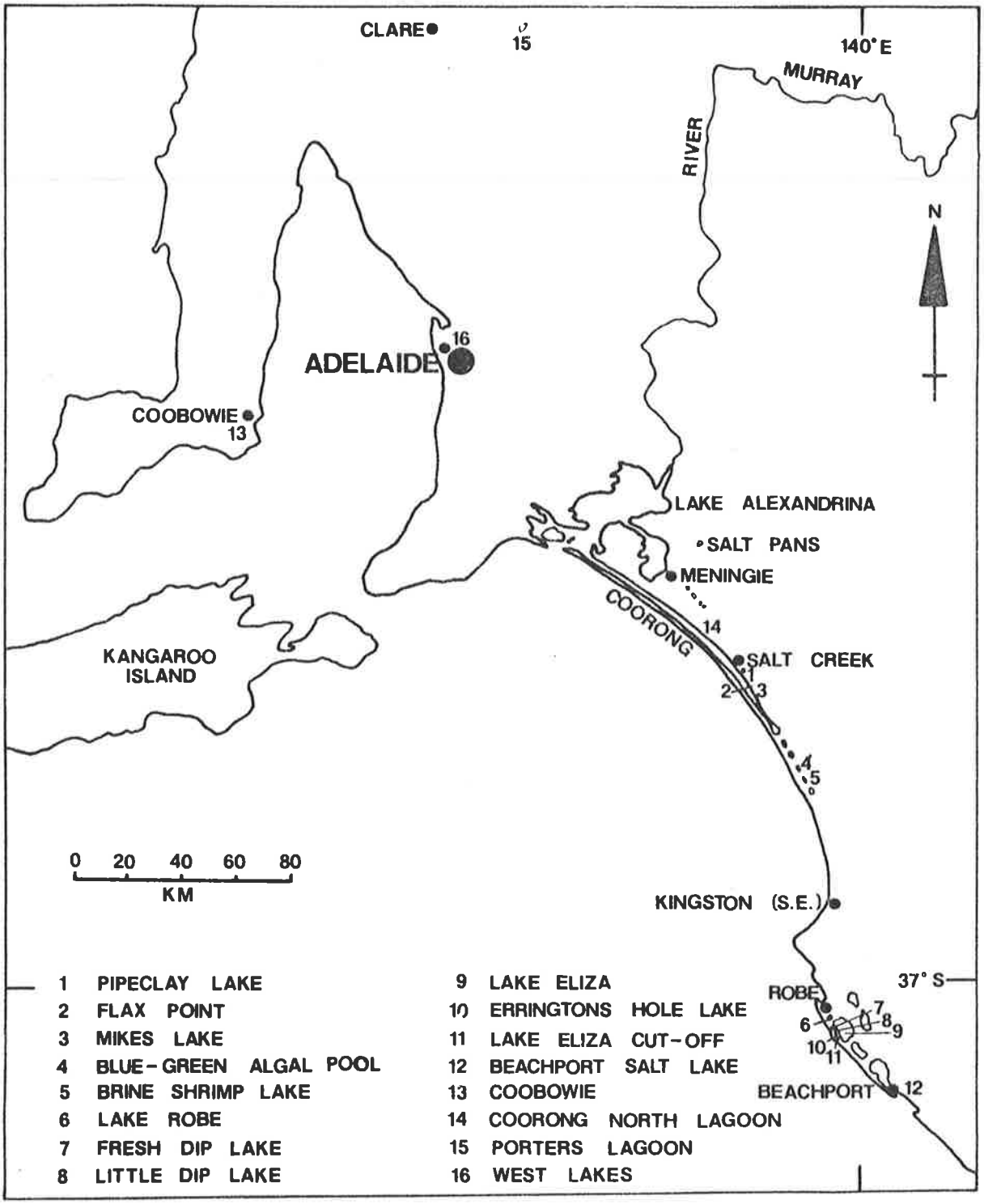


Figure 3.1 The location of sites sampled in the south-east of South Australia.

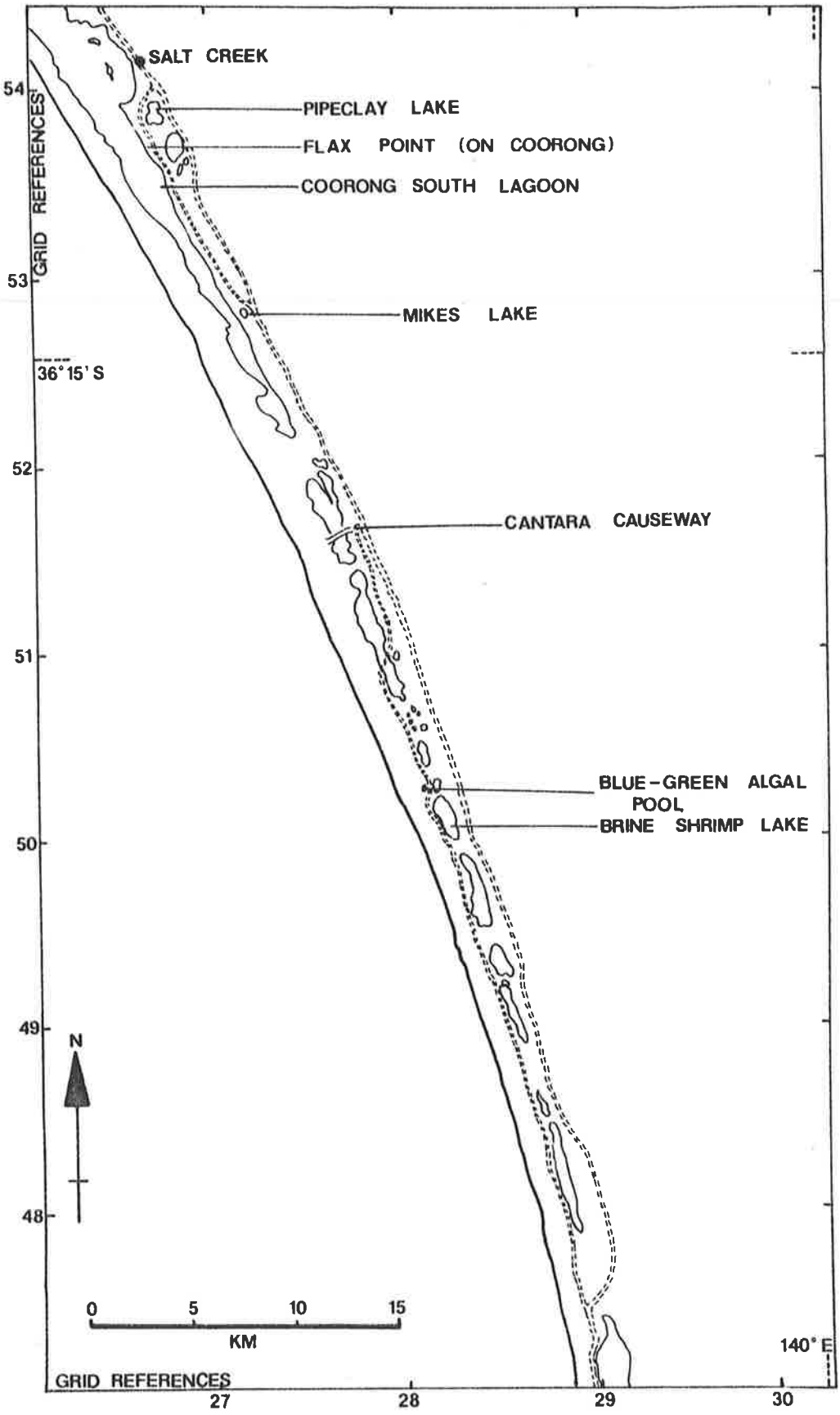


Figure 3.2 Sampling sites in the Coorong Lake series (Australia 1:250,000 Series, Naracoorte Sheet).

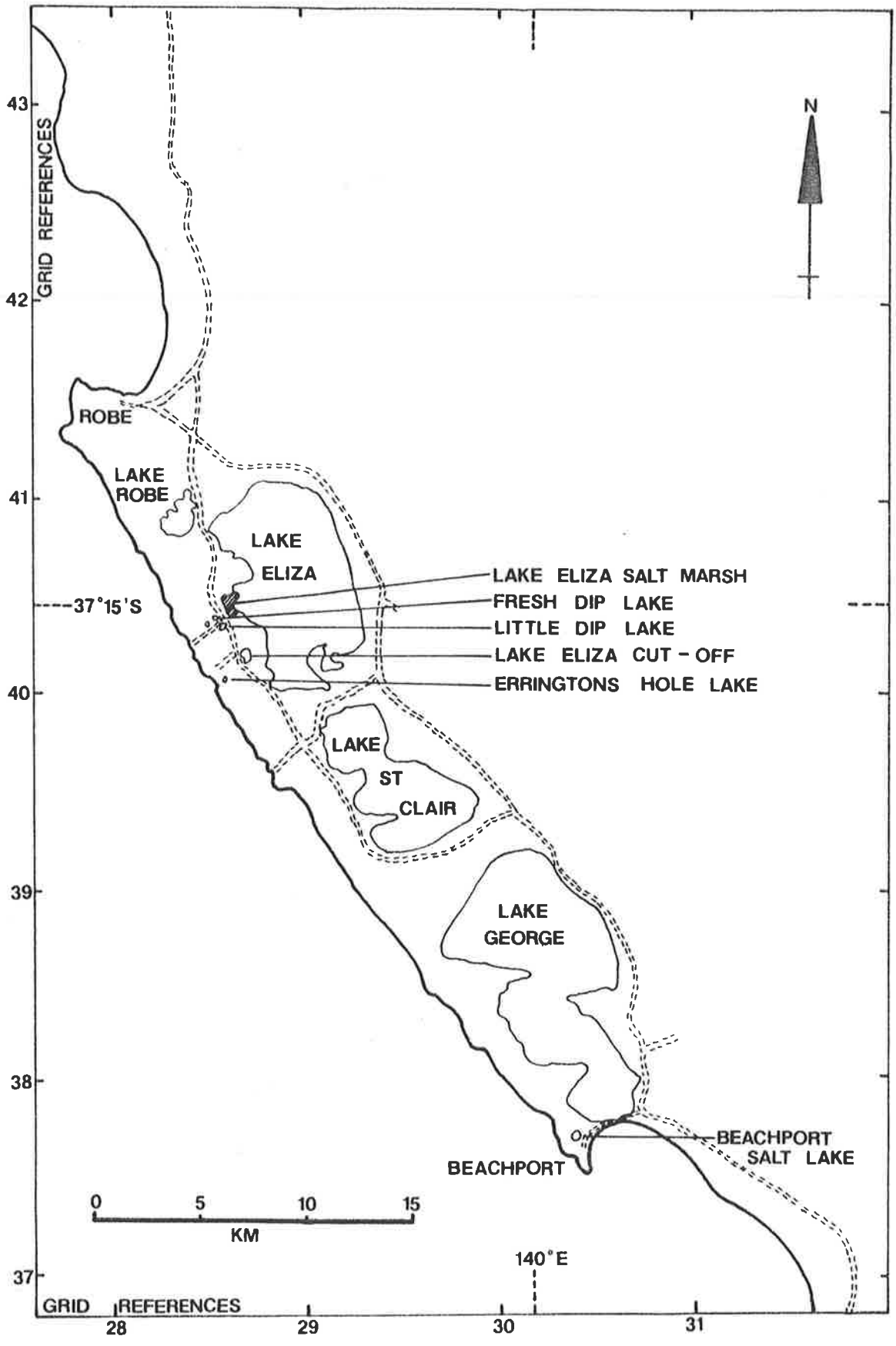


Figure 3.3 Sampling sites in the Robe/Beachport Lakes series (Australia 1:250,000 Series, Penola Sheet).

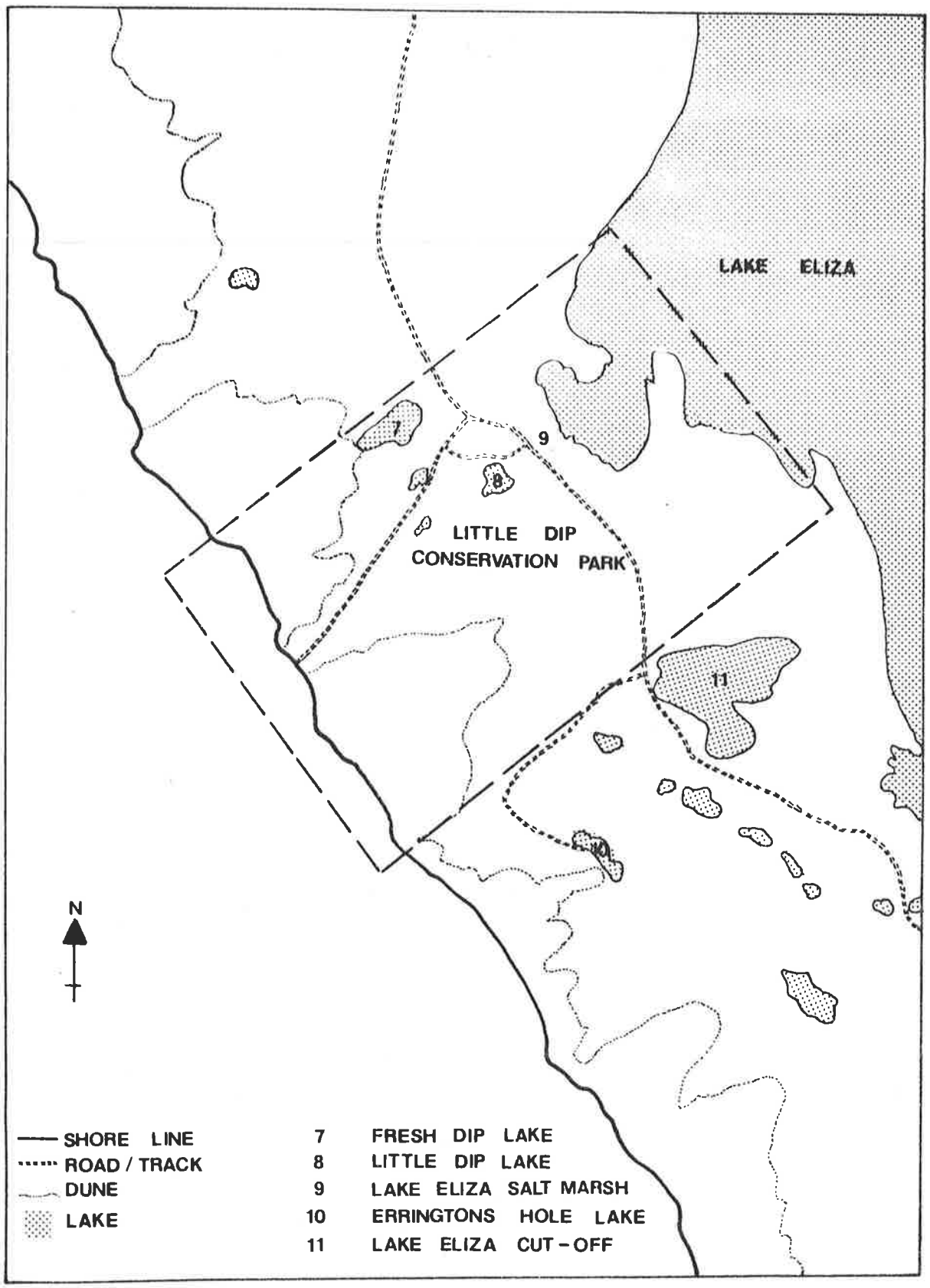


Figure 3.4 The major study sites in the Little Dip Conservation Park (from aerial photographs 60/5062 1951 and 1/43/30 1969, Department of Lands, South Australian Government).

Plate 3.1 Pipeclay Lake: an ephemeral salt pan (wet phase).

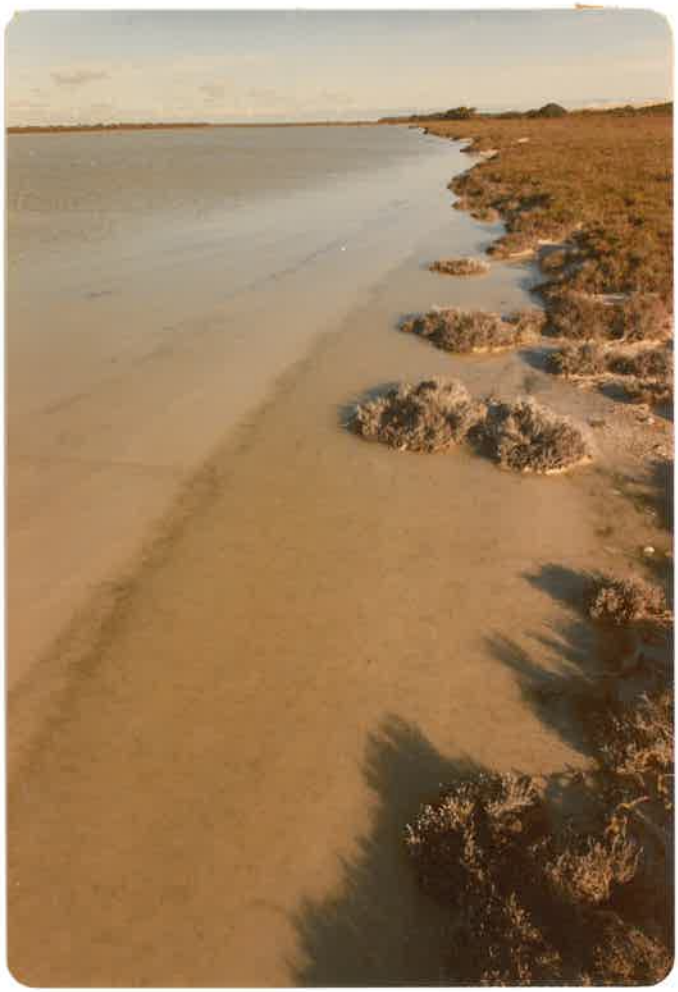


Plate 3.2 Brineshrimp Lake: a hypersaline temporary lagoon (wet phase).

Plate 3.3 Blue-Green Algal Pool: a brackish roadside pool (wet phase).

Plate 3.4 Lake Eliza Salt Marsh: the cracked mud surface is typical of the ephemeral sites in summer.

Plate 3.5 Little Dip Lake: a saline permanent lake.

Plate 3.6 Fresh Dip Lake: a fresh permanent lake.

Algal Pool (Plate 3.3) were taken in winter. The dry cracked mud surface shown in Plate 3.4 is characteristic of these lakes in their dry season. A saline permanent lake, Little Dip Lake and a fresh permanent lake, Fresh Dip Lake are shown in Plates 3.5 and 3.6 respectively.

The ternary diagrams (Figure 3.5) show the ranges of several environmental parameters (mean salinity, degree of permanence, depth and seasonal salinity fluctuation) in the lakes selected for study. Data from which these diagrams are constructed are presented in Chapter 5. The aquatic phases of the sites selected vary in duration from five to twelve months. Maximum salinities range from 3 to 180$^{o}/_{oo}$ TDS, and the sites have absolute seasonal salinity fluctuations varying from less than 2$^{o}/_{oo}$ TDS in the fresh lake to over 100$^{o}/_{oo}$ TDS in the hypersaline sites. Depth fluctuations are most significant to submerged plants when the morphometry of the basin is such that small changes in depth expose or submerge large areas of the eulittoral plant habitats.

3.2 Salinity terminology

The terminology applied to saline waters in this study is related to the classification of brackish and saline waters according to the Venice system adopted at the Symposium on the Classification of Brackish Waters (Venice 1958).

The Venice classification is too strict to apply to many of the variable waters since salinity fluctuations, in 8 of the 12 ecosystems considered, span at least two of the major categories, and another spans the (mixo)polyhaline and (mixo)mesohaline groupings. This leaves only three sites, two hypersaline and one oligohaline, that fit discretely into these categories (compare Table 3.2 with Table 5.1). The arbitrary boundary of 3$^{o}/_{oo}$ TDS between fresh and saline waters

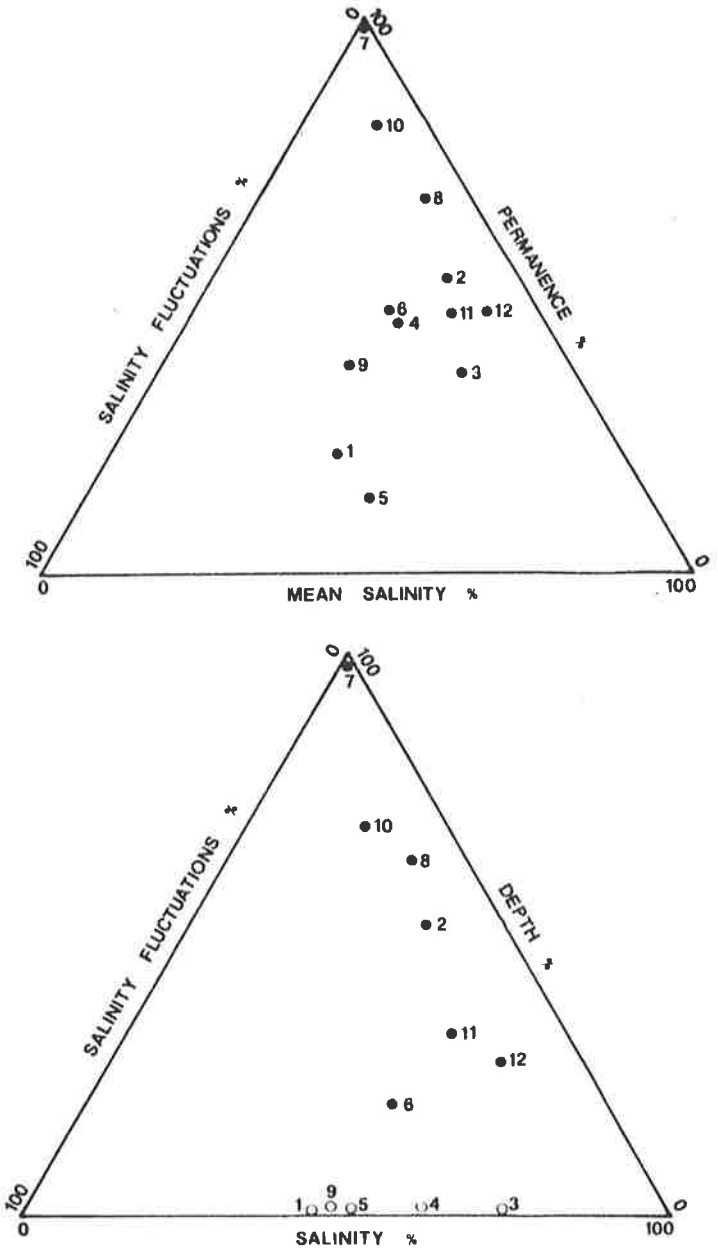


Figure 3.5. Ternary diagrams plot the relative ranges of parameters in the study sites. Percentages for each parameter have been calculated as follows:

$$\% \text{ Permanence} = \frac{\text{no. months aquatic}}{12} \%$$

$$\% \text{ Salinity fluctuation} = \frac{\text{max. salinity - min. salinity}}{\text{max. salinity range recorded in any lake}} \%$$

$$\% \text{ Mean Salinity} = \frac{\text{mean salinity for a lake}}{\text{max. figure for mean salinity in any one lake}} \%$$

$$\% \text{ Depth} = \frac{\text{max. depth (m) of a lake}}{\text{max. depth recorded in any lake}} \%$$

sites are indicated by site numbers
in the first diagram all sites are represented by •
in the second diagram temporary sites o and permanent •

TABLE 3.2. A comparison between the classification of water salinity used in this study and the Venice classification (Venice 1958).

Classification used		Venice classification	
Terms	Salinity °/oo TDS	Salinity °/oo TDS	Terms
Hypersaline	>40	>40	Hyperhaline
Saline	30-40	30-40	Euhaline
Moderately saline	25-30	0.5-30	Mixohaline
		>30 <adjacent euryhaline sea	Mixoeuhaline
Slightly saline	15-25	18-30	(Mixo)polyhaline
Brackish	3-15	5-18	(Mixo)mesohaline
Fresh	<3	0.5-5	(Mixo)oligohaline
		<0.5	Limnetic

(Williams 1966) is a useful division for the purposes of this study. Salinities above sea water ($35^{o}/_{oo}$ TDS) are referred to as hypersaline; those between $3^{o}/_{oo}$ TDS and $35^{o}/_{oo}$ TDS as saline, with the terms brackish and slightly or moderately saline used to modify these.

3.3 Details of sites

The general characteristics of the twelve main study sites are outlined in Table 3.1. Details for other sites examined are presented in Appendix I. Names, numbers and name abbreviations have been given to each site; where names were unavailable from published maps the lakes have been named arbitrarily (Table 3.1). The lake numbers and name abbreviation (in brackets after lake names in this section) are used to refer to these sites throughout the text.

Pipeclay Lake (1, PL), Plate 3.1: temporary hypersaline shallow lagoon with large salinity and eulittoral zone water level fluctuations, approximately 1.0 x 0.4 km, located 5 km east of the South Lagoon of the Coorong in the Coorong National Park just south of Salt Creek. The surface is a white dolomitic mudstone of dolomite, magnesite, aragonite and calcite (von der Borch 1965, Warren pers. comm. 1978). The lake refills annually following winter rains and evaporates to a dry, cracked pipeclay pan by late spring, leaving a central salt crust. Salinities from 13 to over $200^{o}/_{oo}$ TDS were recorded with wide seasonal and short term fluctuations.

Salinity is often low in side-pools immediately after rain, while extremely high salinities may be recorded in pools in areas where salt crusts have formed. Floral and faunal remains and propagules may be found stranded in the pipeclay or salt crust. Halophytic plants border the lake and give way to mallee scrub vegetation.

Flax Point (2, FP): permanent, hypersaline, large eulittoral zone fluctuations, located on the South Lagoon of the Coorong in the Coorong National Park. An extensive eulittoral zone, exposed seasonally by evaporative and wind-induced water level fluctuations, extends to 150 m. Rotting mats of detritus, characteristic of the Coorong, mark previous water levels. These mats are comprised of *Cladophora*, *Lamprothamnium*, *Acetabularia* and *Ruppia* together with faunal remains (e.g. large mats of cast skins of Ephydridae). Algae and angiosperms were found growing in the Coorong waters in the sulphide-rich substrate of skeletal grainstone composed of calcite and aragonite, but beds of these macrophytes were neither dense nor extensive at this site. Salinities ranging from 37 to 90$^{o}/_{oo}$ TDS reflected seasonal evaporation and precipitation with a minimal influence from the North Lagoon marine-estuarine connection. The surrounding vegetation was halophytic and wind-stunted and showed an eastward succession to mallee scrub as exposure decreased.

Mikes Lake (3, ML): temporary, brackish to saline pool, dimensions approximately 0.5 x 0.14 km, separated from the eastern Coorong shore of the South Lagoon by less than 1 km. Like Pipeclay Lake, this site refills after winter rains and remains wet during winter and early spring. Salinity fluctuated from 12 to 33$^{o}/_{oo}$ TDS and the maximum depth was 0.3 m over the study period. During its aquatic phase, rich floral and faunal growth occurred; macrophytic algae including *Enteromorpha* and *Lamprothamnium* and the angiosperms *Ruppia* and *Lepilaena* grew through a mat of blue-green algae. The fauna was dominated by copepods, ostracods and amphipods. In the dry phase, the dolomitic mudstone substrate was covered by a dried (rather than decayed (*cf.* Flax Point)) organic layer of plant and animal debris stranded as the water level retreated; a mat of blue-green algae is usually the main component and leaves a black sulphide-rich

organic layer in the sediment below. A mallee vegetation dominated by *Melaleuca halmaturorum*, *Leucopogon parviflorus* (Andr.) Lindl. with salt tolerant shrubs forming an understorey, lines the shore.

Blue-Green Algal Pool (4, BGAP), Plate 3.3: temporary brackish roadside ditch, approximate dimensions 0.1 x 0.5 km, located behind the coastal dune system south of the permanent Coorong waters. In its annual aquatic phase from July to October, it reached depths of up to 0.6 m. A prolific ephemeral biota consisting largely of blue-green algae, macrophytic algae, *Ruppia*, *Lepilaena* and various animals was present. When the pool dried, a detrital crust with seeds, plant propagules, and presumably resistant stages of some animals, was left on the surface. The extreme spring and summer temperatures caused rapid evaporation resulting in drying and desiccation rather than decay of these organic components (*cf.* Mikes Lake, Flax Point). Salinities from 8 to 35^{o}/oo TDS were recorded, with most macrophyte growth occurring when salinities were less than 20^{o}/oo TDS. The organically-rich substrate of this roadside pool is a skeletal wackestone of calcite and aragonite which contrasts with the saline organically-poor skeletal wackestone of the salt pan less than 20 m away on the other side of the road.

Brine Shrimp Lake (5, BL), Plate 3.2: large, temporary, hypersaline, shallow (to 0.1 m) turbid lagoon, approximately 5 x 0.5 km in dimensions. It is one of the ephemeral lagoons which were part of the Coorong water body at times of higher sea level and has a flat and shallow morphometry which shows similarities to Pipeclay Lake. An extensive salt crust forms over the skeletal wackestone base in the dry season. Salinities recorded ranged from 13 to 150^{o}/oo TDS but are probably much higher just prior to drying. Plant and animal growth was limited to the annual, four-month aquatic phase of the lake. Desiccated propagules stranded in the salt crust, or in the cracked and dried clay pan in summer, regenerate in the following wet season.

The surrounding trees and shrubs have been cleared, leaving the lake periphery covered with halophytic species intermingled with introduced grasses. The area has been grazed in recent years.

Lake Robe (6, LR): large, permanent, hypersaline, shallow (to 1.0 m) lake approximately 5 x 1 km in dimensions. This lake, located south of Robe, is wind mixed and has a milky appearance from the easily suspended sediments of the calcite mudstone pan. Outcrops of ancient marine shell deposits form beaches around the lake. Evaporation causes salinity to rise over summer and the lake is then diluted by late autumn and winter rains: 20°/oo TDS and 136°/oo TDS were the extremes recorded. Although submerged macrophytes were not prolific, *Ruppia*, *Lepilaena* and *Lamprothamnium* grew in sparse patches. Stands of these macrophytes were more abundant in an ephemeral side pool which was connected to Lake Robe in winter. It is possible that this pool is innoculated annually with fauna and flora from the permanent lake. However, it is also likely that desiccated propagules withstand the drying, and germinate in the following season. A halophytic understorey surrounded by *Melaleuca halmaturorum* encloses the lake.

Fresh Dip Lake (7, FDL), Plate 3.6: permanent, fresh (to slightly brackish) lake, maximum depth 4.5 m, dimensions approximately 0.4 x 0.22 km, situated between Lake Eliza and the Robe coastal dune, just north of the Little Dip road in the Little Dip Conservation Park. Its western shore is formed by an unstabilized dune while the other shores are bounded by reed beds which begin a succession to *Eucalyptus* or *Melaleuca* associations. No extensive eulittoral zone was present and most areas under 1 m were colonized by emergent reeds. The substrate is a skeletal grainstone with a high percentage of organic material and sand. Salinity and depth fluctuations were minimal with salinity values from 2.1 to 3.3 °/oo TDS recorded. The variety of submerged macrophytes is greater than in the saline sites. The lake is fed by

fresh water run-off from the surrounding dunes and vegetation, and possibly from fresh water seeps at the base of the dune.

Little Dip Lake (8, LDL), Plate 3.5: permanent saline lake, maximum depth 3.5 m, dimensions approximately 0.25 x 0.22 km, located to the south of the Little Dip Road in the Little Dip Conservation Park. Like Fresh Dip Lake, it is located between the parallel dunes to the west of Lake Eliza but it does not border the coastal dune. The lake, enclosed by *Melaleuca* and *Leucopogon* scrub, has reeds at the water's edge in deeper areas and a beach of low halophytic herbs on the south-eastern side. The general basin depth was 2 m and large shallower areas occurred on the periphery. The salinity fluctuated from 18 to 39^{o}/oo TDS parallelling seasonal depth fluctuations. An eulittoral zone is consequently exposed seasonally on the south-eastern and eastern shores. A macrophytic flora of large *Ruppia* clumps and charophytes cover the permanent basin, while mixed carpets of *Ruppia*, charophytes and *Lepilaena* recolonize the eulittoral zone annually. The substrate is a calcitic mudstone similar to that of Lake Robe. This lake is of comparable size to the nearby Fresh Dip Lake and is subject to similar environmental conditions, thus providing a situation in which the effects of salinity on the nature and composition of hydrophytes can be contrasted.

Lake Eliza Salt Marsh (9, LESM), Plates 5.1 to 5.10: ephemerally wet salt marsh extending over 0.5 km from the western shore of Lake Eliza towards Little Dip and Fresh Dip Lakes in the Little Dip Conservation Park. Lake Eliza, a large hypersaline lake lying below sea level, acts as a collecting basin for ground water draining from the east (see Figure 2.1). A complex of halophytic plants form various associations within the salt marsh community. This vegetation gives way intermittently to a series of shallow pools which are either ephemeral and dry seasonally or are permanent, possibly fed by springs

from the water table. The seasonally inundated salt marsh vegetation stabilizes a deep (over 2 m) layer of soft calcitic mud; the upper surfaces of this are anaerobic and sulphide-rich. Both submerged and emergent macrophytes were studied at this site. Some of the submerged macrophyte species, found as dominants at other sites, occurred in isolated pools or as ephemeral members of the wet underlayers of the salt marsh community. Water level and salinities fluctuated seasonally; the salt marsh was inundated by 0.03 - 0.1 m of water in winter and most areas except the permanent pools dried in summer.

Erringtons Hole Lake (10, EH): permanent, brackish lake, dimensions approximately 0.3 x 0.15 km, located behind the beach dune of the Robe system to the south of the Little Dip Conservation Park. The lake, comprising three basins, is filling gradually as the mobile dune moves eastwards. The northern basin was colonized by *Melaleuca*, *Leptospermum* and marsh species; the middle basin had dense peripheral vegetation with large areas of *Phragmites australis* and reeds extending into the water; *Phragmites* and reeds also had colonized a central island of the deeper southern basin. This basin was bordered by *Melaleuca*, *Leptospermum* and reeds on the eastern shore and was bound to the west by a beach formed from the moving sand-spit. A sharp break in slope occurs where the sand dune meets the grey, sulphide-rich skeletal grainstone muds of the lake bottom; a band of *Ruppia* clumps grows along this break in slope. Salinities from 5 to 20°/oo TDS were recorded and a general increase in salinity and drop in water level were noted over the sampling period. The lake is fed by run-off and possibly from fresh water seepage at the base of the dune.

Lake Eliza Cut-Off (11, LEC): a permanent, hypersaline lake, depth over 1 m, located to the south-west of Lake Eliza. The salinity fluctuated from 44 to 116°/oo TDS. The lake is surrounded by dense *Leptospermum*, *Melaleuca* and *Olearia* scrub with *Phragmites australis* and

reeds lining the water's edge. No submerged macrophytes were recorded during the study period.

Beachport Salt Lake (12,B/pSL): permanent, hypersaline lake, approximate dimensions 0.2 x 0.15 km. This site, located behind the coastal dune at Beachport, has a shallow beach area to the south and a deeper basin on the northern side. Seasonal depth fluctuations of up to 0.5 m expose a eulittoral zone on the southern beach in summer. The northern basin is over 2 m deep. The substrate is a halite-gypsum evaporite formed by evaporation under extremely hypersaline conditions. Salinities ranging from 57 to 115°/oo TDS were recorded.

3.4 The major study area: Little Dip Conservation Park

The interrelationships of hydrophytes in the plant associations of various habitats were examined extensively in the three ecosystems provided by Fresh Dip Lake, Little Dip Lake and the Lake Eliza Salt Marsh, all in close proximity to one another, and thus under similar macro-environmental conditions.

A variety of macrophytes occurs in Fresh Dip Lake, but species diversity decreases in the saline Little Dip Lake. A complex community of emergent halophytes occupies niches on the Lake Eliza Salt Marsh with various combinations of plant species forming associations on the marsh and in the permanent or temporary pools. The submerged hydrophytes *Ruppia*, *Lepilaena* and *Lamprothamnium* occur in all three ecosystems in different associations: as mono- or co-dominants in the lakes and pools, or as sparse occurrences in the understorey of complex halophytic stands. Thus, as well as comparison of species composition and diversity between ecosystems, an opportunity to consider the life strategies of these genera in a variety of niches and habitats is provided.

CHAPTER 4. METHODS

4.1 General sampling methods

Field sampling and observations took place at intervals of one to four months from May 1975 to November 1978 (Table 4.1). Changes in the aquatic vegetation and physical parameters were recorded and water samples were collected for salinity estimation. Other parameters were examined less regularly.

The general site descriptions presented in Chapter 3 are based on qualitative observations supported by quantitative measurements of biotic and non-biotic factors. Permanence was recorded as the number of months a lake basin contained water, excluding brief periods when water remained on the surface after rain. Initial depths, and subsequent changes in water levels, were measured from depth poles or estimated where exact determination was not possible. The mean maximum depth of the Coorong at Flax Point is approximately 1.5 metres (Noye 1974). Vertical water level fluctuations were calculated from this reference depth and from the minimum level at the end of summer; wind and seiche movements made exact determination of seasonal fluctuations difficult. The extent of the eulittoral zone is a biologically important indicator of water level fluctuation.

Climatic data on precipitation, air temperature and humidity were extracted from Meteorological Bureau records for Policemans Point, Robe and Beachport from 1973 to 1978; rainfall data have been examined for correlation with lake salinity and depth.

Salinity estimates were made from measurements of conductivity, from which total dissolved solutes (TDS) in parts per thousand ($^{o}/_{oo}$) were calculated. Water samples were collected in clean plastic screw-topped bottles and analysed in the laboratory. Initially samples from various depths were tested, but as the greatest variation between

TABLE 4.1. Sampling frequency.

Year & Month / Site	1975												1976												1977												1978											
	A	M	J	J	A	S	O	N	D				J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
1	X					XX		X					X			X			X	X	X				X	X	X				X		X				X			X	X	X	X	X		X			
2	X				X	X	X		X				X			X			X	X	X				X	X	X				X		X				X			X	X	X	X	X		X			
3					X	X	X		X				X			X			X	X	X				X	X	X				X		X				X			X	X	X	X	X		X			
4						XX		X					X			X			X	X	X				X	X	X				X		X				X			X	X	X	X	X		X			
5						XX		X					X			X			X	X	X				X	X	X				X		X				X			X			X	X		X			
6	X		X		X	X		X					X			X			X	X	X				X	X	X				X		X				X			X			X	X		X			
7						X		X					X			X			X	X	X				X	X	X				X		X				X			X			X	X		X			
8	X		X		X	X		X					X			X			X	X	X				X	X	X				X		X				X			X			X	X		X			
9	X		X		X	X		X					X			X			X	X	X				X						X				X								X	X		X			
10						X	X		X				X						X	X					X						X				X								X	X					
11	X					X	X		X				X						X	X					X		X				X		X										X	X					
12									X				X						X	X					X		X				X		X				X			X			X	X		X			

X - site sampled

samples from one site was less than 5% of the mean salinity value (insignificant when compared with seasonal fluctuations), subsequent samples were taken at half the depth, at a site where littoral influences and sheltering were minimal. Conductance (K) was measured in millisiemens using a CDM3 Conductivity Meter and readings were corrected for temperature (K_{25^oC}). A good correlation between specific conductance and concentration of total dissolved solutes is obtained below 150 millisiemens for a wide range of Australian saline waters (Williams 1966). This relationship is described by the equation $cK = T$ where K is the conductivity, T the total dissolved solutes and c is a coefficient determined by the ionic composition, salinity and temperature (Edmondson 1956; Anderson 1958). The coefficient c is given by $c = \frac{3.4\ K_{18}}{10^6} + 0.666$ for a wide range of Australian saline waters dominated by sodium chloride (Williams 1966), and thus $T = \left[\frac{3.4\ K_{18}}{10^6} + 0.666\right] K_T$ where $K_{18} = \frac{K_T}{(1 + 0.025(t-18))}$. The major source of unreliability of conductivity as an estimate of total dissolved solutes for saline lakes over $50^o/_{oo}$ is ionic variability (Hem 1959). This is of little relevance in most Australian saline waters as their ionic proportions are comparatively stable (Bayly and Williams 1966; Williams 1966; Williams and Buckney 1976a,b).

Salinity is largely a measure of the inorganic solutes present; the measurement of total dissolved solutes includes organic and inorganic solutes. The relationship of inorganic solutes to total dissolved solutes was calculated for a series of Victorian and South Australian lakes by Williams (1966). He found the average ratio of inorganic to total dissolved solutes to be 0.91 with 50% of values falling between 0.87 and 0.93 and 100% between 0.84 and 0.99. Buckney and Tyler (1976) estimated salinities for Tasmanian saline waters from the equation $\log S = 0.921 \log K_{18} - 0.047$, but this equation is only applicable to fresh and brackish waters.

In this study, conductivity was used to calculate total dissolved solutes (Williams 1966), and these values were used as estimates of salinity. No estimate of the dissolved organic solutes has been made. The data are presented either as K_{25^oC} in millisiemens or as total dissolved solutes in parts per thousand (TDS $^o/_{oo}$). Some readings are above 150 millisiemens, the maximum at which the conductivity/TDS relationship is reputed to be reliable. These high readings are unimportant in terms of the floral components of the ecosystems as macroscopic plants only occasionally occur above this salinity. Salinity recorded as >150 millisiemens was therefore considered sufficient.

Water and air temperatures were measured with a mercury in glass thermometer graded from 0 - 50 degrees Celsius. In October 1976, a diurnal temperature profile for Little Dip Lake was recorded at 0.25 metre in water of 0.5 metre depth at a distance 10 metres from shore. As routine visits to sites were brief and at irregular times of day, no regular temperature monitoring could be undertaken. The relationships of air temperature to water temperature, for various seasons and sites can be related to the mean daily minimum and maximum air temperatures.

Dissolved oxygen was measured in several of the lakes in October 1976. Measurements were made with a YSI Model 51B oxygen meter. Spot readings were taken at the bottom and on the surface within the plant communities. A 24 hour oxygen profile was taken for Little Dip Lake as previously described for the temperature profile. This was used as a reference for comparison of spot readings.

Water level fluctuations were measured by reference to standards. Metal depth poles were installed at most sites in July 1975 and measurements made from the top of the pole to the water surface; this avoided discrepancies in readings due to movement of the soft bottom muds. Some estimation and recalculation of these data were necessary

as poles were positioned at the time of the highest water level for the entire study and water in some sites has not reached these levels again. Some poles were therefore replaced at the inner edge of the eulittoral zone and recalibrated with the old markers. Several poles disappeared during the study and other wooden depth poles had their tops shot off by vandals. However, a reasonably reliable record of water level fluctuation was obtained. Additionally, the presence or absence of water in a lake basin was noted at every visit and the horizontal area of exposed lake basin estimated. This was recorded as horizontal distance from high water mark to the existing lake level.

Sediment samples were analysed on a Siemen's Type S X-ray Diffractometer (J. Warren, Flinders University) and mineral composition, percentage of organic matter and substrate type were recorded. Substrate salinities were measured at various sites but were found not to differ greatly from the salinities of the overlying waters.

Some pH readings were taken in the laboratory on a Metrohm Herisau E488 pH meter (equipment was not available for field trips). All readings fell between 7.5 and 9.0. This agrees with reported values for similar lakes (Williams and Buckney 1976a).

Light penetration was measured using a Secchi disc or a quantum metre (Li-cor Ll-185 Quantum/Radiometer/Photometer). These instruments (particularly the quantum meter) were not available for all field trips. As changes in light penetration may be short-term, spot readings are of limited use for seasonal comparisons within lakes; however, they may be useful for comparisons between lakes.

Collections of aquatic and terrestrial plants (with reproductive parts if present) were pressed and mounted for identification. Aquatic, and some semi-aquatic, halophytic species required special treatment: submerged aquatic plants were floated directly onto mounting sheets and oven-dried to minimize disintegration of fragile material by excessive

handling; semi-succulent halophytes were frozen or boiled briefly before pressing and oven-drying. Specimens of aquatic angiosperms and algae were also preserved in 4% formaldehyde or 70% alcohol; wet rather than dry preserved material is more suitable for dissection, drawing and measurement. Preservation in formaldehyde minimized shrinkage and decreased fragility. Identifications were made using the works of Black (1943-1957), Eichler (1965), Wood (1972), Aston (1973) and Jessop (1978). Determination of the identity of some species and confirmation of the identity of others were made with assistance from The State Herbarium of South Australia. Plant lists and the occurrence of submerged aquatic species in relation to depth and salinity are tabulated for each site (Table 5.6, Figure 5.5).

4.2 Particular sampling methods for three localities in the Little Dip Conservation Park: Little Dip Lake, Fresh Dip Lake and Lake Eliza Salt Marsh

Observations of three ecosystems in the Little Dip Conservation Park, namely Little Dip Lake, Fresh Dip Lake and Lake Eliza Salt Marsh, were more frequent and intensive than at other study sites, and it is therefore appropriate to describe separately the methods specific to these localities. Application of these methods provided a comprehensive description of these areas.

Morphometric maps were prepared using automatic and dumpy levels, a theodolite, siting staff, depth staff and dinghy. Measurements were made in April 1976 (autumn) and November 1977 (spring). Hydrographic charts of Little Dip Lake and Fresh Dip Lake were constructed by first plotting the surface outline. Measurements were then made at intervals along a series of transects from a base point; spot readings between transects were taken and interpolated; depths were measured with either a depth staff or graduated line and weight. Contours were plotted from

these data. The morphometric survey of the Lake Eliza Salt Marsh was made by recording heights along a transect line from the terrestrial vegetation near the road to the water line.

These surveys were referenced to each other and to a locally established temporary bench mark which was referenced to sea level at Little Dip Beach 2.00 p.m. (Central Summer Time) on November 20th, 1977. It was not possible to refer the survey to a permanent bench mark.

Plant lists were compiled as indicated in Section 4.1. Qualitative estimates were made of the relative abundance of aquatic or semi-aquatic species in each association. For Little Dip Lake and Fresh Dip Lake the nature of the vegetation and the water depth were recorded along several linear transects to give a representative sample of vegetation changes with depth and aspect. Spot recordings were made between transect lines. For the Lake Eliza Salt Marsh vegetation, changes with height and distance from the lake shore were recorded along a linear transect through the salt marsh and along sectional profiles taken perpendicular to the initial survey line through the various plant associations. Species present, growth forms and the relative abundance of plants were recorded. Seasonal and inter-habitat comparisons of the ecosystems were made from these data.

Vegetation maps were compiled by superimposing vegetation data on morphometric maps. Vegetation-depth profiles were constructed for the conditions in Little Dip Lake in April 1976 and November 1977, in Fresh Dip Lake in November 1977 and in Lake Eliza Salt Marsh in April 1976.

Species association and community composition were analysed from samples taken from the three ecosystems. These samples also allowed qualitative estimates of species cover and density to be made. Examination of the biomass and life cycle of *Ruppia* populations was made for comparison between the ecosystems.

Vegetation data for Fresh Dip Lake and Little Dip Lake were obtained using several sampling methods: Ekman grab samples were analysed for species association in deeper areas and a Tvärminne enclosed quantitative sampler (Figure 4.1) and a galvanized steel frame (0.5 x 0.5 m) were used to collect quadrat data at random (FDL) and along transects (LDL) to a water depth of one metre. Samples were either preserved in formalin (4%) or frozen to prevent decay before processing in the laboratory.

The metal quadrat frame yielded comparative samples from various *Ruppia* populations but was unreliable as an estimate of standing crop. This was because material inside the frame was harvested with a spade or by hand and the amount of root material collected depended largely on the thickness and age of the rhizome mat and on the depth from which it was feasible to extract material. Sampling became extremely difficult in depths greater than 0.5 m. The enclosed quantitative sampler (0.185 m in diameter Tvärminne design, Figure 4.1) had the advantage of enclosing the entire sample (hydrophytes, sediments, fauna and water) while the sample was extracted. A bag could be attached to the sampler and this enabled sampling in taller vegetation. The bottom metal plate cut the vegetation at the required substratum level (0.01, 0.05 or 0.08 m). A metal spade with the same curvature as the cylinder was used to loosen the vegetation from inside the sampler. In dense submerged vegetation with strong rhizomes or root mats, the cutting plate was not always efficient and material was then extracted by hand with the aid of a shovel. This apparatus provided more reliable samples for estimate of biomass, but operating difficulties were again encountered in deeper water.

Biomass samples were sorted and wet and dry weights obtained for each taxon. The *Ruppia* material from selected samples was further

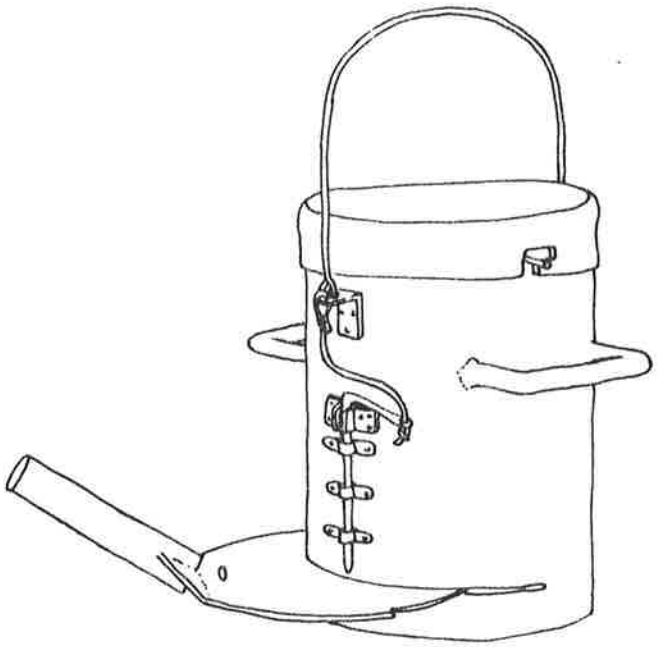


Figure 4.1 The Tvärminne sampler: diameter 18.5 cm (Finnish IBP-PM Group, 1969).

sorted into roots, rhizomes, leaves and reproductive material for analysis of the life strategies of the two forms of *Ruppia* found (see Chapter 9).

Samples from the shallow eulittoral zone were taken with the Tvärminne sampler to 0.01 m, a depth which in this case included all rhizomes and roots. In deeper water samples also were taken to 0.01 m below the sediment surface even though this depth did not include all underground parts. Although samples without underground parts are inadequate for accurate estimates of total biomass, they are useful for comparisons within and between lakes. However, the assumption that above-ground parts are proportional to below-ground parts depends on plant age and growth form as well as on the species involved. Some difficulty was experienced in sorting dead and decaying matter and categorizing underground material into species. Doubtful material was dried, weighed and recorded separately.

In the examination of the semi-aquatic plant community of the Lake Eliza Salt Marsh, phytosociological methods were employed even though such methods are often more applicable to terrestrial than aquatic conditions. However the rationale behind their use is just as applicable to an investigation of submerged plant communities.

Most phytosociological analyses are based on the assumption that the vegetation can be broken into discrete units which in turn can be structured into a classification. As this classification is arbitrary and natural vegetation forms a continuum (Whittaker 1962), the distinguishing of discrete vegetation units as selected homogeneous areas is artificial, but nevertheless often useful. This approach was applied to the complex salt marsh community of Lake Eliza.

The terms 'community' and 'association' are used here in the sense of the Braun-Blanquet system of the Zurich-Montpellier school of phytosociology (see Becker 1957). An 'association' is the fundamental

unit of vegetation, distinguished by a characteristic floristic composition. The plant 'community' of a particular habitat is the total assemblage of species competing for light, space, nutrients and other environmental factors. Thus, the Lake Eliza Salt Marsh is a community which can be analysed in terms of various plant associations. Definitions and analyses of plant associations should reflect the characteristics of the vegetation (e.g. species composition, abundance, dominance etc.) while retaining information that reflects the totality of the community and its temporal changes in habitat.

The size of a quadrat used for phytosociological sampling must be appropriate to the vegetation being studied and will depend on growth form and homogeneity of the vegetation. Because large variation in growth form is found within each salt marsh association, an optimal quadrat size for a small species such as *Triglochin striatum* will be too small to detect larger plants such as *Sarcocornia quinqueflora*. If a larger quadrat size is used, the frequency of the smaller species will be 100% and distibutional changes of these species will go undetected.

The optimal quadrat size for examination of vegetation associations also depends on the homogeneity of the area. Commonly it can be estimated as an area slightly exceeding the 'minimal area' as calculated by plotting species number against quadrat area (Poore 1955) (see Figure 4.2a), or as defined by Shimwell (1971, quoted in Chapman 1976): "the smallest area which provides enough environmental space for a particular stand (association) to develop its true characteristics of species complement and structure". From the series of species-area curves for the Lake Eliza Salt Marsh associations (Figure 4.2b) the minimal area was estimated as 0.025 m^2 or less, except for the *Suaeda-Wilsonia-Sarcocornia* Association where it was 0.1 m^2.

The number of quadrats required depends on the purposes of sampling: for biomass, density and cover estimates the total area

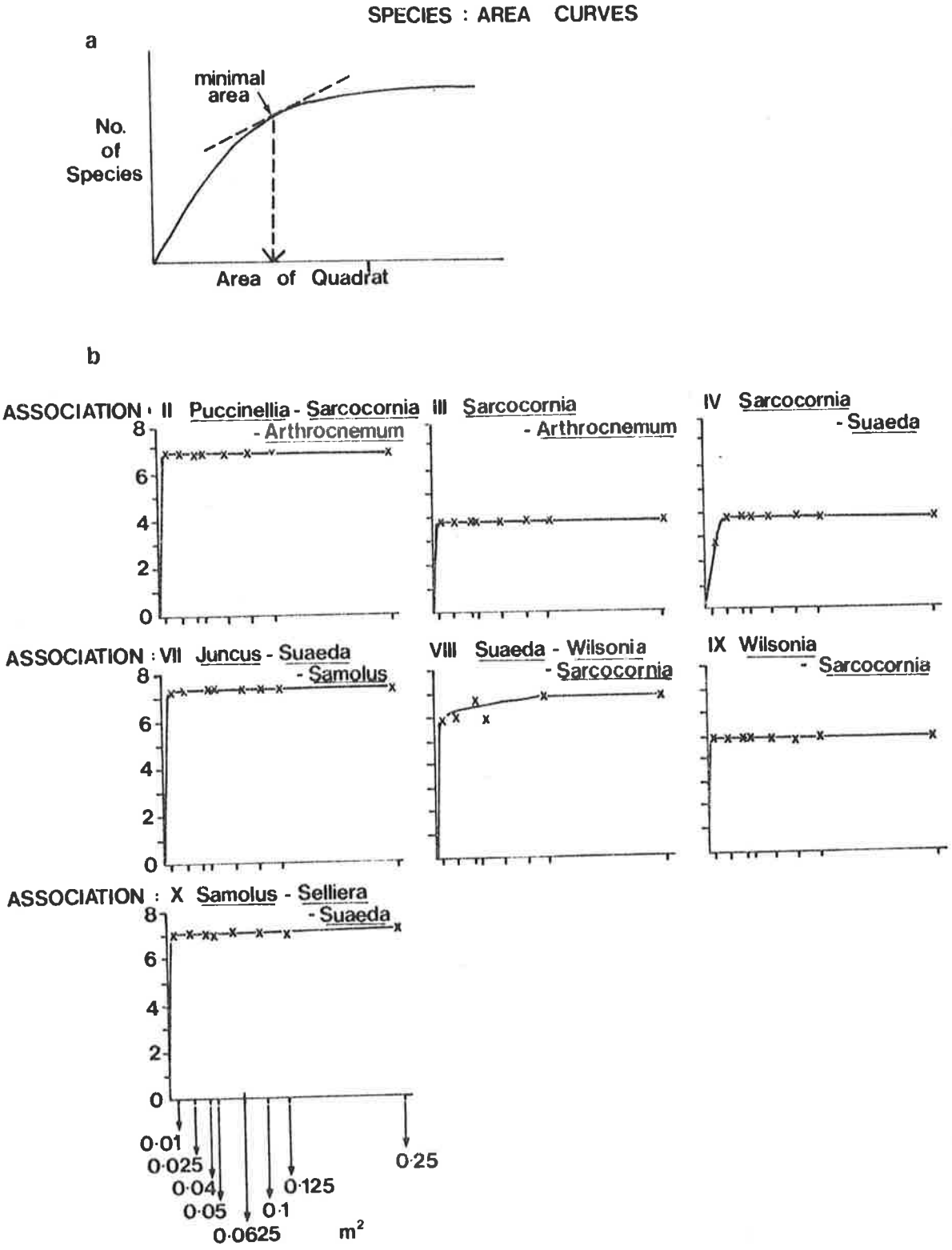
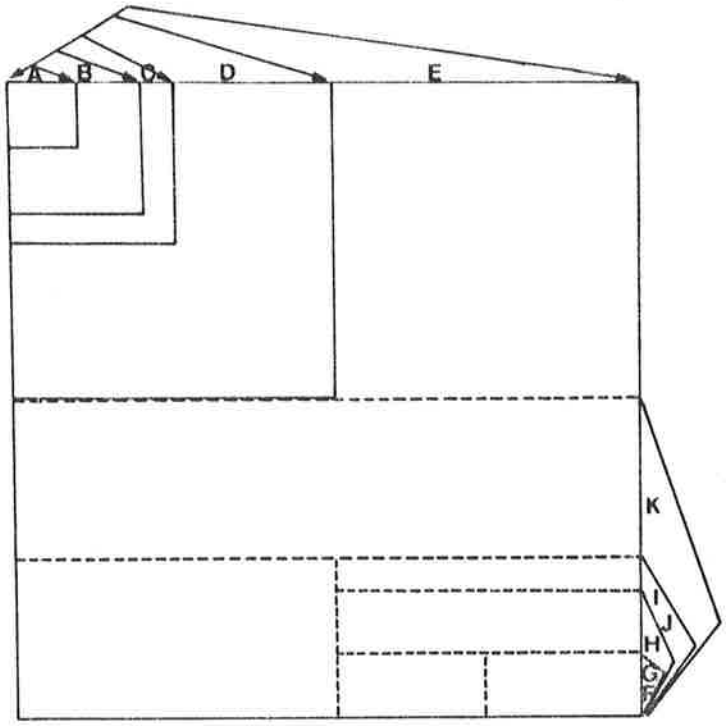


Figure 4.2 Minimal area of quadrats as determined from species: area curves.
a. Minimal area (after Shimwell, 1971)
b. Species area curves for Lake Eliza Salt Marsh Associations.



No.	Dimensions (metres)	Area (sq. metres)
A	0·10 x 1·00	0·01
B	0·20 x 0·20	0·04
C	0·25 x 0·25	0·0625
D	0·50 x 0·50	0·25
E	1·00 x 1·00	1·00
F	0·10 x 0·25	0·025
G	0·10 x 0·50	0·05
H	0·20 x 0·50	0·10
I	0·25 x 0·50	0·125
J	0·25 x 1·00	0·25
K	0·50 x 1·00	0·50

Figure 4.3 The nested quadrat design used for sampling series of quadrats with areas from 0.05 m^2 to 1.0 m^2.

sampled is the important parameter; for frequency sampling, the actual number of quadrats is more important. The minimum number of quadrats, or area to be sampled, was calculated from a plot of cumulative mean or variance of species number against the number of quadrats by determining the position on the curve where fluctuations levelled out. Alternatively, a selected percentage of the total area may be sampled. However, a balance between accuracy and feasibility must be considered; the number of samples that would be required for reliable biomass estimation on Lake Eliza Salt Marsh, could not be justified in terms of vegetation destruction.

Floristic measures used in the phytosociological analyses include frequency, cover and density. The importance of a species in an association can be estimated from changes in the frequency of occurrence of both dominant and minor species. Frequency was scored by presence or absence of a species in a quadrat. However, this measure depends on the use of a suitable quadrat size and the presence of identifiable material. The problems of dealing with dead material and the difficulty of defining and distinguishing single plants are eliminated with this method. As already discussed, the optimal quadrat size is not empirically the same for all species, but must be the same for any one species in all associations (Hyder *et al.* 1965). The larger species *Sarcocornia*, *Suaeda* or *Juncus*, may require a larger quadrat size than *Triglochin* or *Ruppia*. In comparisons of species composition between different vegetation types, where optimal quadrat sizes for species differ, this technique may be of limited use (Walker 1970).

Cover is an estimate of the proportion of ground occupied by the perpendicular projection of the individuals of a species (Greig-Smith 1964). This has been estimated visually for associations on the salt marsh; records have been made using the percentage cover classes of

Braun-Blanquet (1932) (Table 4.2).

The measurement of cover by line intercept (see Walker 1970), wheel point (Tidmarsh and Havenga 1955) or variable plot (Hyder and Sneva 1960) methods was considered, but the irregularities of growth form, the amount of dead material and the scale of sampling required, made measurement unsatisfactory.

Estimation of density (number per unit area (Greig-Smith 1964)) was difficult because of the problems in distinguishing a unit of area relevant to all species. Bias is introduced by different growth forms (bushes, clumps, tufts or single tillers) and when individuals cannot be distinguished because of vegetative growth. Subjective estimates of density were made where considered relevant but, in general, this parameter was not measured.

In the actual sampling programme on the Lake Eliza Salt Marsh an area 150 m wide and spanning 500 m from the low water line to the terrestrial associations near the road was selected as representative of the salt marsh community. Within this, homogeneous areas were delimited as plant associations on the basis of their similarity of floristic composition. These associations were then sampled intensively to generate quantitative data to test the initial subjective delimitation. Multiple series of quadrats were taken in each association. Each initial quadrat was thrown at random and a series of four quadrats taken systematically around this point. A quadrat falling in the transition zone between associations was excluded and the quadrat rethrown. Transition from one association to another was examined using data from quadrats placed sequentially at intervals along a transect line running through an association. Presence or absence of species was recorded in quadrats of from 0.05 to 1.0 m^2 within a nested quadrat (see Figure 4.3). This protocol was designed to determine optimum quadrat size and shape for associations and individual species,

TABLE 4.2. Cover classification of Braun-Blanquet (1932).

Class	% Cover
+	<1
1	1-5
2	6-25
3	26-50
4	51-75
5	76-100

and to calculate the percentage of quadrats in an association for which each species was recorded. Estimation of the percentage area of quadrats occupied by vegetation and a description of the growth form of each species was made using the larger quadrats (0.5 m and 1.0 m sides).

In September 1975, several quadrats (0.5 m^2) were selected at random in each major association: these quadrats were harvested to ground level and samples were frozen prior to sorting and weighing in the laboratory. One quadrat from each association sampled was analysed for total biomass including the below-ground parts (root and rhizome mats). In April 1976 this sampling procedure was repeated using the series of nested quadrats (Figure 4.3).

One square metre of vegetation in total was sampled for each of the three major associations. Pooled results are presented as biomass per square metre. Surface water samples were collected for conductivity determination in each association. Biomass samples were sorted into species in the laboratory and wet and dry weights (105^{o}C) obtained. Again, underground parts caused problems in both harvesting and sorting, as it was difficult to harvest all root material in a given quadrat and impossible to remove it while attached to recognizable plant parts. The best solution to the problem of identification of these parts was to use a predetermined ratio of above-ground to below-ground parts for each species and to apportion the underground biomass appropriately. Data showing this ratio are presented for one association in Table 4.3. In this sample more than 50% of plant material was below the ground surface. The difference between 69% for wet weight and 57% for dry weight may reflect water held by roots and soil not removed in sorting. Similar large ratios of below-ground to above-ground parts occurred in all associations and these ratios varied with species. Major differences need closer examination if the total biomass of an area

TABLE 4.3. Relationship of above-ground and below-ground parts for plant Association IX from Lake Eliza Salt Marsh (biomass g/m^2 in September 1975).

Association IX (*Wilsonia-Sarcocornia*)	Wet Weight		Dry Weight	
	g/m^2	% T	g/m^2	% T
Total sample (T)	16692	100	1896	100
Above-ground parts (A)	5104	31	812	43
Below-ground parts (B)	11588	69	1084	57
Ratio A : B	0.44		0.75	

is to be considered. The establishment of a ratio of above-ground to below-ground parts for each species by harvesting a representative sample of whole individuals of each species may facilitate this.

Sampling within an association was carried out using a number of quadrat sizes and the data pooled to give above-ground biomass per square metre. Sub-sampling in the laboratory verified the unreliability of estimates by such methods. The use of both small quadrat sizes in the field, and sub-sampling in the laboratory, introduced considerable bias; species frequencies were highly variable for species with clumped or tufted growth forms, whereas frequencies usually remained constant for smaller, uniformly distributed species. Thus routine sub-sampling was not feasible. Data from one association are presented in Table 4.4.

Variation in species biomass was expected to decrease with the larger quadrat size, and while this was so for several small uniformly distributed species (*Samolus*, *Selliera* and *Wilsonia*) and for the miscellaneous unidentified material, other species did not follow this trend. Of the larger species, *Suaeda* has a bushy growth form, *Juncus* grows in clumps and *Sarcocornia*, although distributed evenly in some associations, grows in patches in associations containing many species; *Puccinellia*, *Triglochin*, *Cladophora* and *Lamprothamnium* are small and patchily distributed throughout the quadrats. The erratic and high variability in biomass for all these species was possibly due to sampling bias caused by the non-homogeneous distribution of plants resulting from growth form or a combination of low frequency and small growth form.

Similar results were obtained for other associations, indicating that biomass estimates must be made from many more samples if they and, more particularly, species frequency estimates are to be reliable. The large sample areas required for effective study of primary production and the detection of vegetation changes in response to environmental

TABLE 4.4. Variation of biomass within a sample: Association VII (*Juncus-Suaeda-Samolus*).

Quadrat/Subsample size / Species	2x 0.25 m^2	0.0625 m^2			0.04 m^2		0.01 m^2			Average
	%	%	%	%	%	%	%	%	%	% in 0.84 m^2
Sarcocornia quinqueflora	45.9	26.5	39.4	20.9	12.0	31.1	28.1	30.8	31.8	37.4
Suaeda australis	6.8	7.1	5.7	27.0	56.6	11.9	13.6	5.6	11.0	9.5
Puccinellia stricta	0	0.5	2.3	0.7	0	0	0	0	0	0.3
Triglochin striatum	0.5	2.0	3.4	1.6	1.8	2.1	1.0	1.0	1.7	1.2
Algae (*Cladophora*, *Lamprothamnium*)	0.1	1.0	0	0.2	0	1.5	0	0	0	0.5
Samolus repens	7.1	14.0	14.7	8.1	10.3	7.5	25.2	14.1	6.9	9.5
Selliera radicans	4.2	18.0	14.9	19.7	10.5	20.1	11.7	30.8	14.5	9.2
Juncus kraussii	21.1	3.0	0.9	0	0.6	1.0	6.8	0	0	13.2
Wilsonia backhousei	0.7	9.0	2.0	4.8	2.0	8.1	5.8	1.9	7.5	3.5
Unidentified parts	13.2	18.4	17.5	16.9	7.1	16.6	7.7	15.9	26.6	14.8

total harvested = 1 m^2 in 4 x 0.25 m^2 plots

total sorted = 0.84 m^2

change, were not justified in terms of the destruction of the salt marsh or the time available for this study.

Transplantation and recolonization experiments were conducted in sites where quadrats had been harvested previously. Areas in the *Wilsonia-Sarcocornia* Association and in the *Suaeda-Juncus-Samolus* Association were permanently marked for subsequent observation. Two adjacent quadrats were set out in September 1975; one harvested to surface level only, and the other to a depth of 0.15 m. These quadrats were examined every four months for recolonization and seasonal changes.

A quadrat from the *Suaeda-Juncus-Samolus* Association which surrounds a sterile pool was transplanted into a sterile permanent pool in September 1975, and was observed seasonally for changes in species abundance, composition and for evidence of growth.

4.3 Comparison of species composition and vegetation associations of the three ecosystems

Vegetation associations within Little Dip Lake, Fresh Dip Lake and Lake Eliza Salt Marsh were compared and, where possible, the distribution and species composition of particular associations within each ecosystem were related to the variation in environmental parameters.

Species of the genera *Ruppia* and *Lepilaena* are common to the three ecosystems. Both are submerged hydrophytes that occur in different associations of the three systems. Their growth form, occurrence, relative abundance and species association were examined from different habitats in each ecosystem, and comparisons from quadrat presence/absence, biomass and life cycle data were made.

A series of samples taken with the Tvärminne biomass sampler in these associations was used to compare the growth forms and relationships of *Ruppia*.

CHAPTER 5. SYNECOLOGICAL RESULTS: DATA AND INTERPRETATION

5.1 All sites

1. General descriptions

The salinity, permanence, water movements and dimensions of study sites are indicated in Table 5.1. Maximum annual salinity ranged within a lake from 1.2°/oo TDS in Fresh Dip Lake to 217°/oo TDS in Pipeclay Lake; correspondingly extreme maximum salinities (3.3°/oo TDS and 230°/oo TDS) occurred in these lakes. In general, the less saline lakes have smaller annual salinity ranges than do lakes of higher overall salinity.

Of the ephemeral lakes, three are hypersaline and two saline (*cf.* Table 3.2). The permanent lakes, which range from fresh to hypersaline, showed marked differences (1-100 metres) in the horizontal extent of the eulittoral zone exposed when vertical water fluctuations were lowest. The ephemeral habitats created by the temporary lakes and the eulittoral zones of permanent lakes are controlled largely by the interaction of catchment topography, lake morphometry and climatic parameters.

2. Environmental data

Climatic data are presented for Policemans Point (Coorong) and Robe (Table 5.2). As the Robe weather station is subject to significant marine influences, data from this station may not be representative of all sites in the region. Nevertheless they provide a general idea of the north-south precipitation gradient and overall climatic conditions for the region.

The climate is characterised by a marked summer and early autumn drought followed by winter and early spring rains, with mild winter temperatures. Diurnal temperature ranges can be wide, with

TABLE 5.1. Characteristics of the study sites, May 1975 - November 1978: salinity, permanence, water movements and dimensions.

	Salinity (‰ TDS)			Permanence months/yr	Water Movements (m) (maximum)			Dimensions (km) (approximate)	
	Max.	Min.	Maximum annual range (over 3 yrs)	Number of months wet (av. 3 yrs)	Depth	Fluctuations		Length	Width
						Vertical	Horizontal eulittoral		
Coorong series									
1. PL	230	13	217	5	0.25	0.25	lake width	1	0.4
2. FP	90	37	43	12	2.0	0.75	100m	20	1.5 (Sth Lagoon)
3. ML	33	12	21	3	0.3	0.3	lake width	0.5	0.14
4. BGAP	35	9	26	3	0.6	0.6	" "	0.1	0.05
5. BL	150	13	137	4	0.1	0.1	" "	5	0.5
Robe/Beachport series									
6. LR	135	20	116	12	1.0	0.4	35m	5	1.0
7. FDL	3.3	2.1	1.2	12	4.5	0.3	1m	0.4	0.22
8. LDL	39	18	21	12	3.5	0.5	15-20m	0.25	0.22
9. LEP	105	6	99	6	0.1	0.1	600m	>2	1.0
10. EH	20	5.6	14	12	2.0	0.4	12m	0.3	0.15
11. LEC	116	44	72	12	2.0	0.3	2m	0.7	0.7
12. B/pSL	108	64	44	12	2.0	0.5	70m	0.2	0.15

TABLE 5.2. Climatic data for Policemans Point and Robe.
Source: South Australian Meteorological Bureau
(50 year averages).

Climatic feature	Policemans Point (Coorong)	Robe
Annual average precipitation (mm)	500	630
Raindays (mean number)	138	151
Highest monthly rainfall (mm)	73 (August)	104 (July)
Lowest monthly rainfall (mm)	20 (March)	20 (Feb.)
Mean annual daily maximum temp. (^{o}C)	19.0	18.2
Mean annual daily minimum temp. (^{o}C)	10.8	10.9
Smallest monthly temperature range	not recorded	5.5 July
Largest monthly temperature range	not recorded	9.1 January
Humidity 9.00 a.m.	not recorded	83% June 64% January
3.00 p.m.	not recorded	75% June 58% January

air temperatures ranging from below freezing to 15-20°C daily in winter, and from 12->40°C in summer. Monthly temperature ranges (Table 5.2) indicate differences between mean monthly maxima and minima.

Monthly precipitation records for Policemans Point, Robe and Beachport from 1974 to 1978 (Figure 5.1) show the extent of deviation from average conditions. Rainfall was above average in 1974 and 1975, below average in 1976 and 1977, and above average in 1978. The study sites have thus been studied in wet and dry years.

The rainfall is extremely variable and unreliable with wide monthly fluctuations. Precipitation and evaporation largely determine salinity and depth fluctuations (compare Figure 5.1 and Figures 5.2, 5.3 and 5.5).

Salinities (TDS $^{o}/_{oo}$) are graphed for the Robe/Beachport lakes (Figure 5.2) and for the Coorong lake series (Figure 5.3). The readings of conductivity at 25°C (K_{25}) and estimates of total dissolved solutes calculated from these are presented in Appendix II. Wide variation between lakes and fluctuation within lakes are apparent. The tendency for the Coorong series to be ephemeral (except for the hypersaline Flax Point), and the Robe/Beachport series to be permanent (except the Lake Eliza Salt Marsh) probably reflects the higher rainfall of the southern series and differences in lake basin origins.

The ephemeral Coorong lakes are always dry from the end of December to March, and some have been dry from October to June. Sites 1 and 5 are hypersaline lakes, while lakes 3 and 4 are brackish to moderately saline. The Robe/Beachport permanent lakes range from fresh (site 7) through brackish (site 10) to saline (sites 8 and 9) and hypersaline (sites 6, 11 and 12).

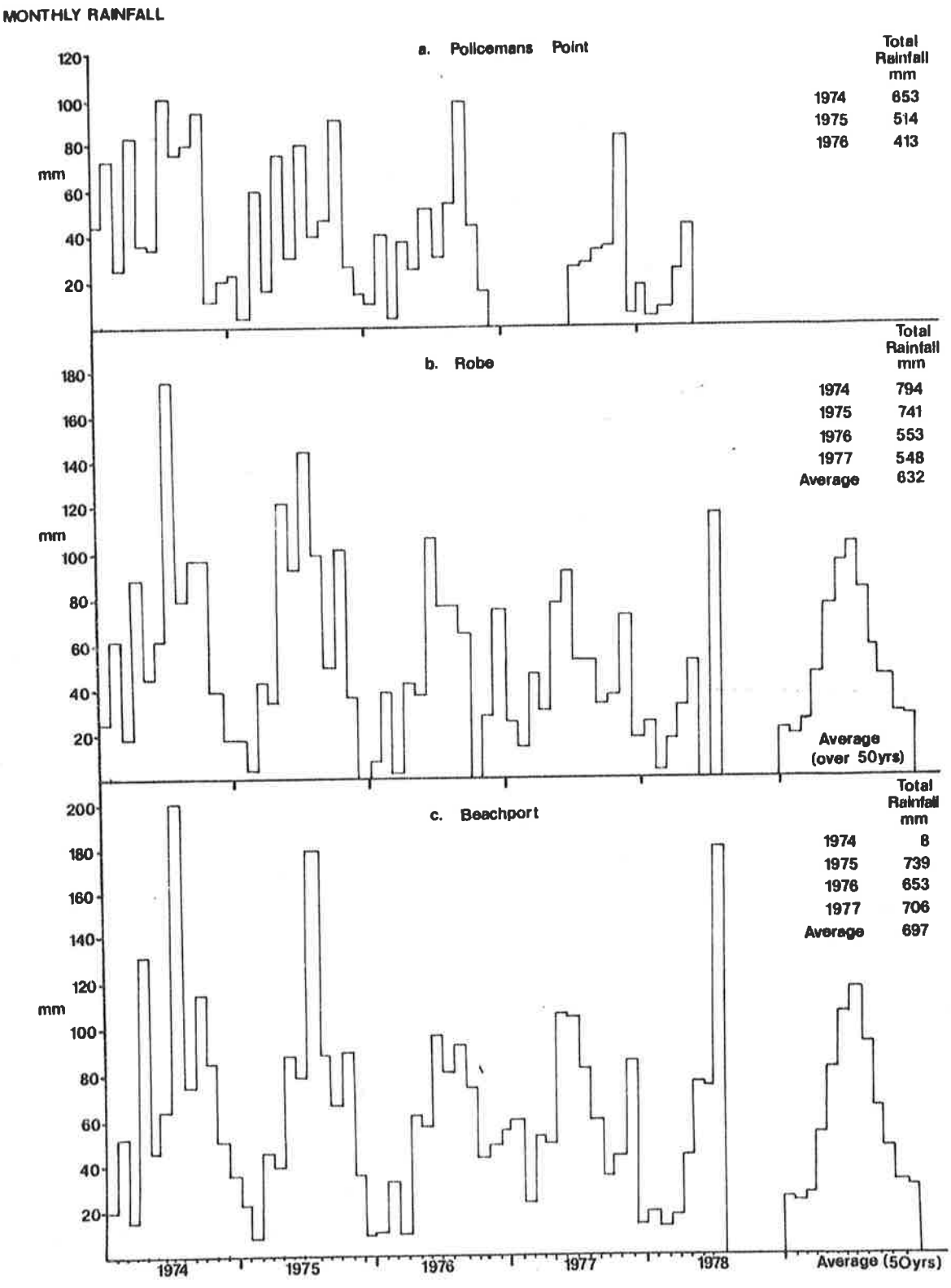


Figure 5.1 Monthly precipitation for 1974 to 1978
a. Policemans Point
b. Robe
c. Beachport
(Data from the South Australian Bureau of Meteorology).

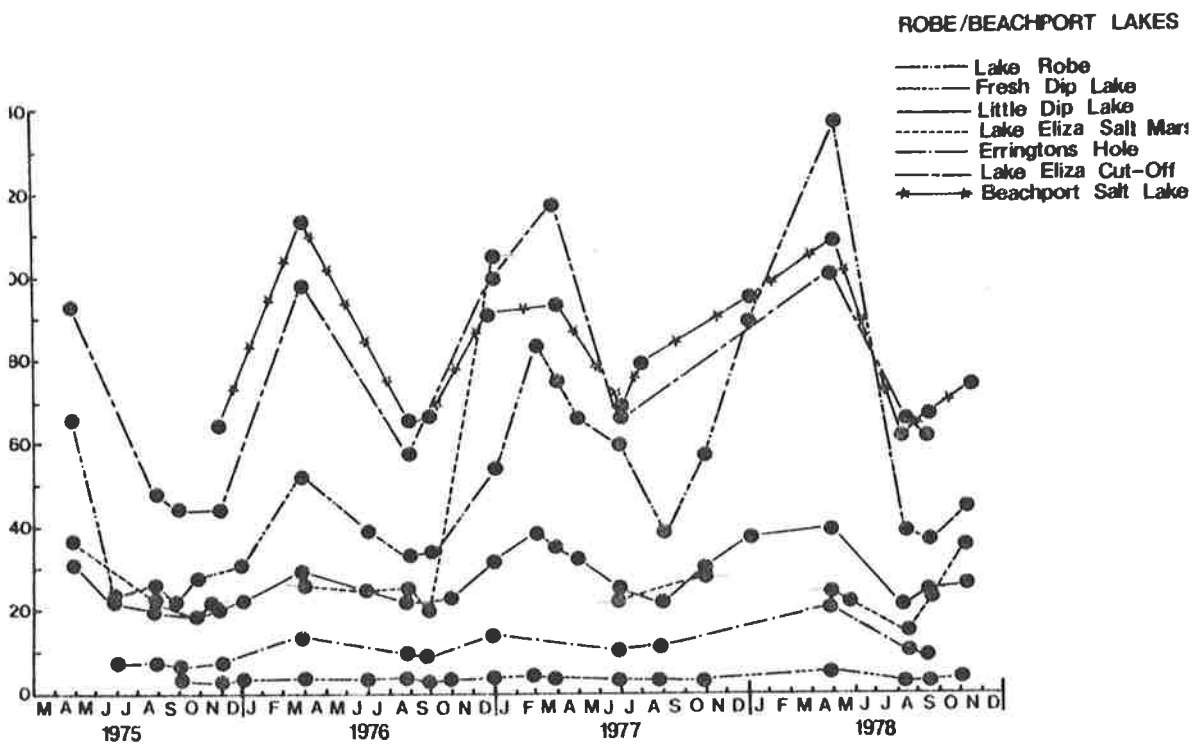


Figure 5.2 Salinity in the Robe/Beachport Lakes 1975 to 1978.

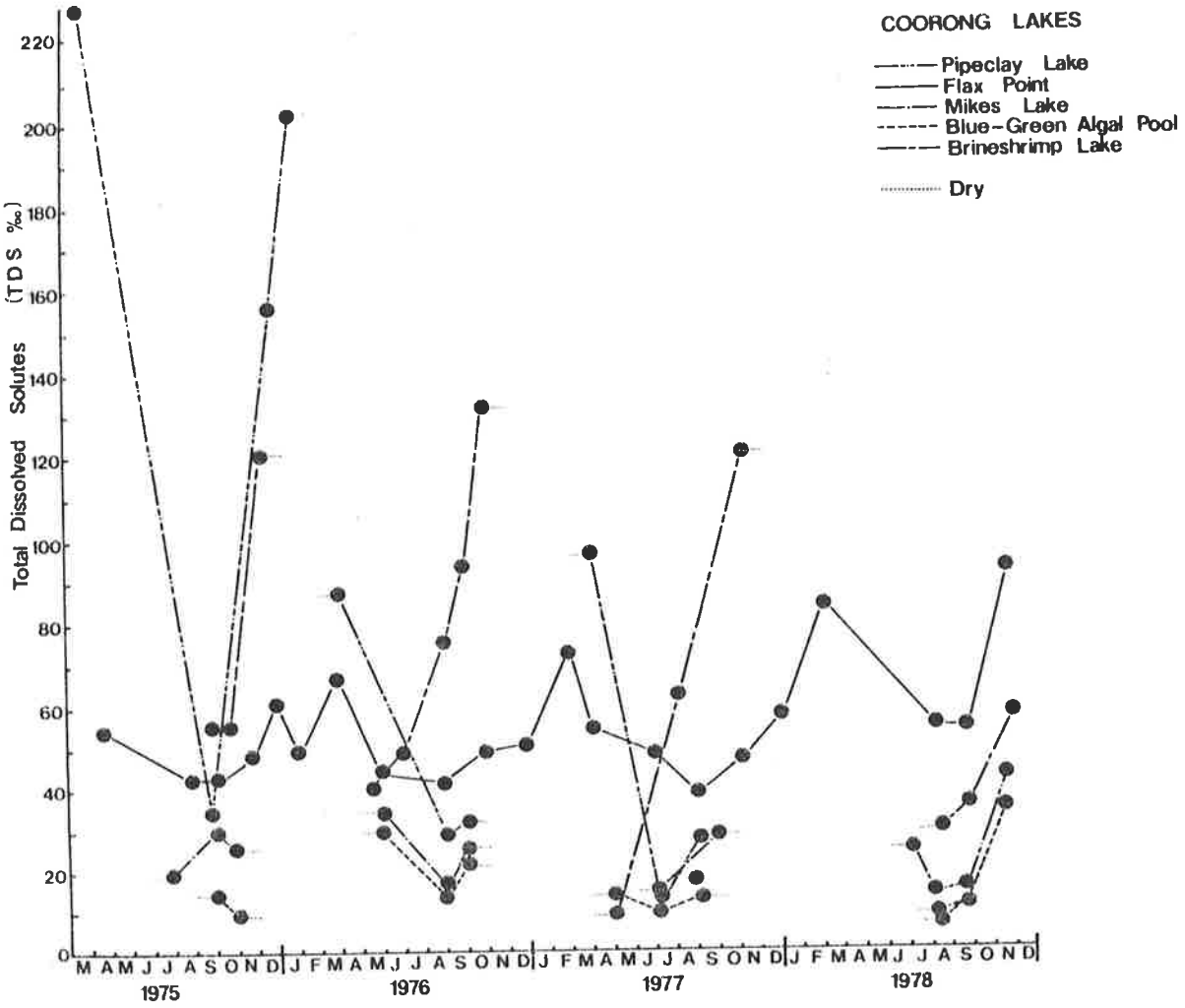


Figure 5.3 Salinity in the Coorong Lakes 1975 to 1978.

Data on the chemical composition of lakes in these series have been extracted from the literature and are summarised in Appendix III. The homogeneity of the data strongly suggests that biotic and abiotic differences between lakes are not due to major differences in ionic proportions.

Data on depth and salinity fluctuations and on the vegetation for each site are presented in Figure 5.5. The correlation of rainfall with these parameters indicates that precipitation and evaporation are generally the determinants of the rate of depth decrease and salinity increase. However, groundwater input from both saline and fresh aquifers may help to regulate the levels of the Coorong, Fresh Dip Lake, and the permanent pools on the Lake Eliza Salt Marsh; wind action and seiches also affect water level in the Coorong.

An oxygen profile was recorded for Little Dip Lake over a 32-hour period in mid-October 1976. The results, coverted to % saturation values at the appropriate salinity, altitude and temperature, are plotted in Figure 5.4. This profile was recorded in an area without dense macrophytic vegetation, but within 10 metres of low (10-30 mm) beds of *Lamprothamnium papulosum*. Dissolved oxygen was above 100% saturation during daylight hours after an initial post-dawn lag. Oxygen concentration decreased from midday to a minimum saturation level of 50% at dawn. The drop in oxygen levels during daylight hours may be a result of increased dispersal of oxygen throughout the lake by turbulence.

Spot readings were taken in various communities of Little Dip Lake and other lakes (Table 5.3). In Little Dip Lake, near-saturation levels were recorded outside the vegetation beds between 1000 and 1100 hours. In 0.5 m deep water, oxygen saturation values varied from 93% to 104% from the bottom to the surface. Within *Lepilaena cylindrocarpa*-dominated communities, oxygen levels were greater than

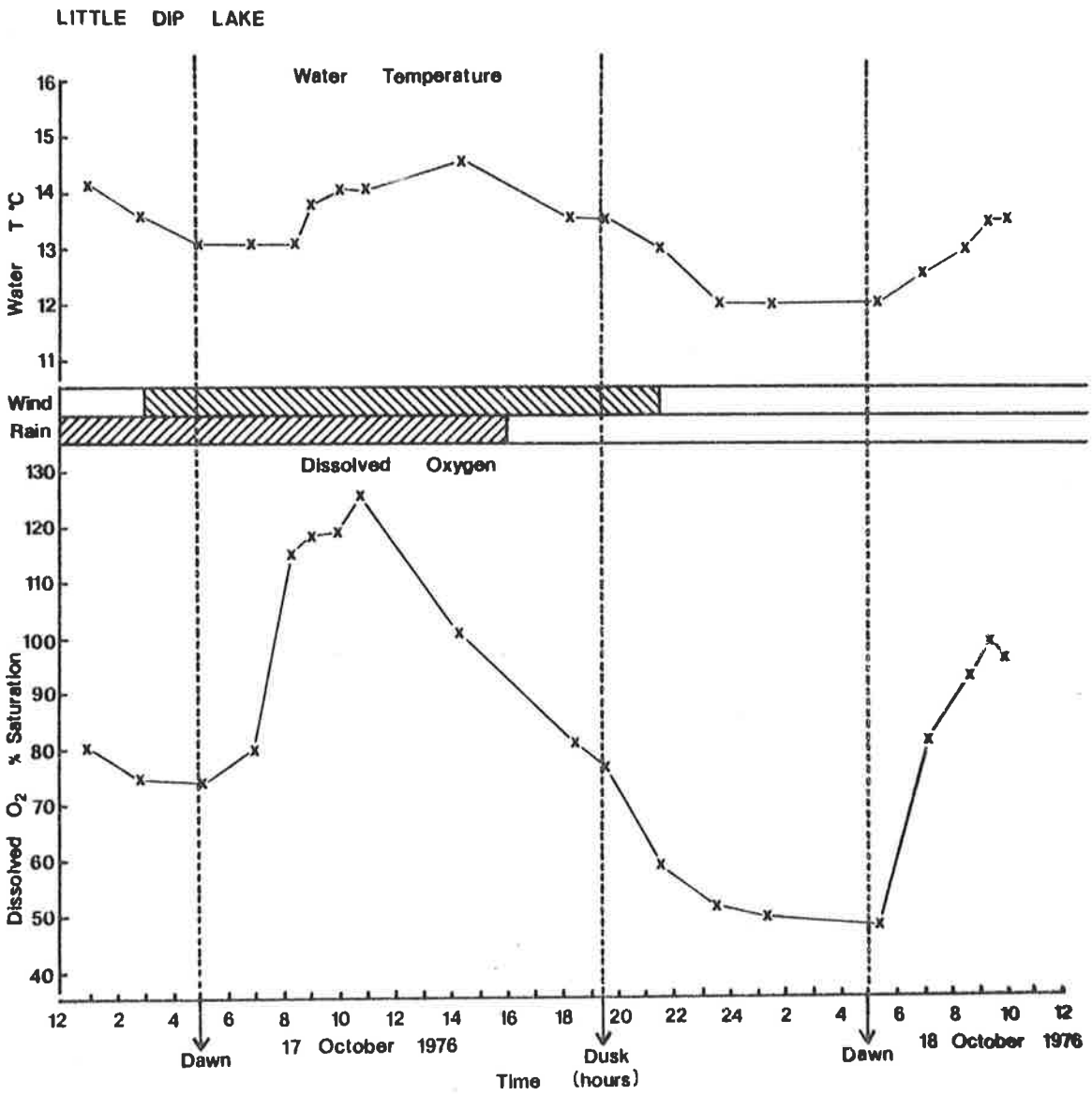


Figure 5.4 32 hour temperature and oxygen profile for Little Dip Lake taken in spring 1976. Oxygen and temperature probes were located at a depth of 0.25 m in 0.5 m of water, 30 m from the shore.

Table 5.3 Spot readings of oxygen and temperature (18 October 1976)

Site	Probe location	Time hr	Water depth cm	Reading depth cm	T°C	Diss. O_2 ppm	O_2 sat. %
Little Dip Lake (diurnal profile conditions)	30m from shore no vegetation	1000	50	b 0	14.25	9.7	93
				25	14.25	10.2	99
				s 50	14.50	10.6	104
	Lamprothamnium bed	1030	15	b 0	15.00	8.6	85
				s 15	15.10	9.4	93
	Ruppia E/*Lepilaena*	1040	15	0	15.00	7.8	77
				15	15.50	9.2	92
	Lepilaena/Ruppia E	1050	10-15	0	16.00	10.9	110
				7	16.00	11.1	112
				13	16.25	11.2	114
	Ruppia P clump	1100	60	0	14.00	6.6	62
				20	14.00	6.9	66
				40	14.40	7.6	74
				60	14.50	7.5	74
Fresh Dip Lake	*Myriophyllum/ Potamogeton*	1130	60	0	15.25	10.0	100
				20	15.25	9.8	98
				40	15.25	9.8	98
				60	15.25	10.8	108
	Myriophyllum	1145	25	0	17.50	12.2	127
				12	17.50	12.6	131
				25	18.00	13.2	139
Brineshrimp Lake		1400	5-10	5	17.50	6.7	70
		1405	10	5	18.00	6.7	71
Blue-Green Algal Pool	*Lepilaena/Ruppia* E	1500	20	10	21.00	10.8	121
	water (no vegetation)	1510		10	21.00	10.2	125
Mikes Lake	water/algae	1600	10	5	20.00	10.3	113
	Lepilaena/Ruppia E	1600	10	5	20.00	10.4	114

b = bottom
s = surface

100% saturation over the 0.15 m depth. In adjacent waters of the same depth, oxygen concentration varied from 85-93% in a *Lamprothamnium*-dominated area, and from 77-92% in an ephemeral *Ruppia* and *Lepilaena*-dominated area. Oxygen concentrations in perennial *Ruppia* clumps in 0.6 m of water in Little Dip Lake varied from 62-74%. This variation may reflect differences in the metabolic activities of the various communities. In October, the perennial *Ruppia* clumps had not yet begun their active growth phase, whilst plants of the eulittoral zone (*Lepilaena*, *Ruppia* and *Lamprothamnium*) were already producing flowers or fruiting bodies.

In the plant communities of Fresh Dip Lake (*Myriophyllum* and *Potamogeton*), and the ephemeral Blue-Green Algal Pool and Mikes Lake (*Lepilaena* and *Ruppia*), oxygen saturation values were at least 98% at all depths. The lower values for Brineshrimp Lake may reflect the paucity of photosynthetic activity in this shallow, turbid, wind-stirred lake (Table 5.3). From these data it appears that oxygen is not limiting in these systems.

A 32-hour water temperature profile for Little Dip Lake, recorded at 0.25 m depth in 0.5 m of water, reflects changes in water temperature with diurnal fluctuations in air temperature (Table 5.4). Changes in surface water temperature in response to air temperature would be expected to be more rapid than changes at depth. In the shallower lakes the water temperatures follow air temperatures closely, and readings above 40^{o}C were recorded in summer.

Temperature differences from surface to bottom (0.6 m) were at most 0.5^{o}C (Table 5.3). These are less than temperature variations recorded in different plant associations in the same locality. No temperature records were made in the deeper areas of lakes.

Light penetration was estimated for all sites with a Secchi disc: results varied with the lake and climatic conditions. The

shallow, ephemeral lakes with easily-suspended sediments often had Secchi readings of less than 0.05 m. Flax Point had extremely variable readings related to prevailing conditions rather than seasonal trends. The Secchi disc was still visible at maximum depth in Mikes Lake (0.10 m) and Blue-Green Algal Pool (0.20 m) even when the water was pigmented by decaying plants. Both Little Dip Lake and Fresh Dip Lake, the deeper sites, gave Secchi readings at maximum depths (3.5 and 4.5 m respectively) in November, 1977. Although readings were not taken regularly at these depths, light penetration did not appear to be limiting in these locations or in other sites in the Robe/ Beachport series.

Readings of photosynthetically active radiation (PAR), made with a quantum meter for various areas in two locations, indicate considerable light attenuation by depth and vegetation. Light readings and the percentage of the surface light remaining at each position are presented in Table 5.4. The percentages of surface light have been calculated in preference to extinction coefficients as the latter are unreliable in water less than one metre in depth (Wetzel 1975).

The high light and temperature conditions in shallow unshaded areas may facilitate early germination and growth of plants in the ephemeral lakes and in the eulittoral zones of permanent locations. Later in the season the higher light intensities and temperatures of these sites may lead to senescence of vegetation before the salt-pans dry completely.

The attenuation of light by existing vegetation mats could reduce establishment of seedlings; whereas parts of established plants which are nearer the surface may photosynthesize and translocate their products to roots or rhizomes, seedlings may not have sufficient light to photosynthesize and establish themselves.

Table 5.4 Light readings (microeinsteins) and light penetration with depth and macrophyte shading in Beachport Salt Lake and Little Dip Lake in January 1978 (summer)

	Beachport Salt Lake 1200 hrs		Little Dip Lake 1400 hrs	
	microeinsteins	% surface light	microeinsteins	% surface light
Water surface	2300	100	2500	100
0.05 m unshaded	1700	74	1500	65
0.05 m shaded by *Ruppia*			900	36
0.3 m unshaded	1350	59	1300	52
0.3 m shaded by *Ruppia*			250	10
0.6 m unshaded	1200	52	1150	50
0.6 m shaded by *Ruppia*			60	2

Sediments from each site were analysed: depositional environments, particle and sediment types, and the percentages of various minerals were determined for each sample. The results are presented in Table 5.5. Both Pipeclay and Mikes Lake lie on dolomitic mudstones precipitated in a hypersaline environment within the basin. The dominance of micritic aggregates, which readily break down on contact with water, probably accounts for the turbid appearance of these lakes. Lake Robe, Little Dip Lake (eulittoral zone) and the pools of the Lake Eliza Salt Marsh also have high proportions of weakly-cemented micritic aggregates. The Calcite Mudstones found in these sites were all deposited under brackish to saline conditions with little allochthonous input. The Lake Eliza Salt Marsh sediment has tubular, encrusted angiosperm fibres which also occur in the sample from the eulittoral zone of Little Dip Lake. These tubular crusts could form by aerial drying of the angiosperm fragments in eulittoral zones and temporary habitats.

Both permanent and eulittoral samples from Little Dip Lake comprise micritic aggregates mixed with shell and organic fractions. The Calcitic Wackestone sediments of the permanent habitat differed from the eulittoral sediments in having a higher proportion of unbroken shells and organic matter. No allochthonous deposits occur in Little Dip Lake.

Skeletal Grainstone is the sediment type of the three locations most influenced by the coastal dune. Flax Point is composed of 90% sand (both skeletal fragments and quartz); marine shells, whole and fragmented, are also prevalent. Most of the sediment has been transported to this site, probably from the surrounding dunes. Fresh Dip Lake and Erringtons Hole Lake have large proportions of skeletal sand grains, again probably of dunal origin. All three depositional environments are brackish to saline in origin even though the latter two are presently fresh or brackish.

Table 5.5 Analysis of sediments from each site (X-ray diffractometer): depositional environment particle and sediment types and mineral composition (%)

Lake/depositional environment	Micritic aggregates %	Particles			Biotic origin				Mineralogy	Sediment type
		Quartz sand grains %	Gypsum %	Halite %	Organics %	Whole shells %	Living shells %	Skeletal shell and sand grains %		
Pipeclay Lake restricted, hypersaline	95				5				calcite-dolomite with minor halite	Dolomitic Mudstone
Flax Point brackish, saline		5			3-5	3-5		85	calcite aragonite	Skeletal Grainstone
Mikes Lake hypersaline	85-90				10-15		<3		dolomite	Dolomitic Mudstone
Blue-Green Algal Pool hypersaline	30-35	20-25			30-40	<5		10-15	calcite aragonite	Skeletal Wackestone
Brineshrimp Lake hypersaline	15-20				5			70-75	calcite and aragonite calcarenite sand	Skeletal Wackestone
Lake Robe brackish, saline	80-85				15-20	<2		<5	calcite	Calcitic Mudstone
Fresh Dip Lake brackish, saline		3-5			50-55			40-45	calcite aragonite	Skeletal Grainstone
Little Dip Lake (eulittoral zone) brackish, saline	60-70				<3			30-40	calcitic aggregates coarse sand	Calcitic Mudstone
Little Dip Lake (Permanent) brackish, hypersaline	40-50				40-50		10-15		calcite aragonite	Calcitic Wackestone
Lake Eliza Salt Marsh(pool) brackish, saline	70-80			<10	20-30				calcite	Calcitic Mudstone
Erringtons Hole Lake brackish, saline		5-7			<10			80-85	calcite	Skeletal Grainstone
Beachport Salt Lake hypersaline			5-10	65-70	5-10			20-25	halite gypsum	Halite-gypsum Evaporite

The southern Coorong locations, Blue-Green Algal Pool and Brineshrimp Lake, have formed on Skeletal Wackestone deposited under hypersaline conditions. These sediments consist of dolomite and aragonite micritic aggregates deposited within the lakes, together with calcarenite transported from surrounding dunes. The high levels of organic matter and shell fragments in Blue-Green Algal Pool reflect the less saline and more productive nature of this lake.

Beachport Salt Lake is the only location with halite-gypsum evaporite sediments, formed by the evaporation of lake water which deposited first gypsum, then halite. The deposition of gypsum in preference to calcium carbonate (normally deposited first) may indicate deposition under extremely hypersaline conditions (usually $>180^{o}/_{oo}$ TDS). Sand grains, possibly wind-transported from nearby dunes are also part of this sediment.

In summary, the Coorong lagoonal lakes have formed on Dolomitic Mudstone or Skeletal Wackestone, whereas Calcitic Mudstone and Wackestone are more common in the southern region. Skeletal Grainstone is the sediment-type of the dune-influenced sites. The only uniquely hypersaline sediment is the Halite-gypsum Evaporite of Beachport Salt Lake.

3. Vegetation data

Species lists, divided into three habitat groupings for each site, are presented in Table 5.6. Plants were identified only to genus or family when fruiting material was not available. Submerged aquatic plants were recorded on each field trip. Lists of the emergent aquatic and salt marsh plants of the flats around lakes, and the common species of the surrounding terrestrial vegetation are included for background information: the lists of emergent macrophytes are comprehensive only for Lake Eliza Salt Marsh and Brineshrimp Lake. The Lake Eliza Salt Marsh is the only site for which the emergent community is considered

Table 5.6 Plant lists for each study site

a. submerged aquatic species
b. emergent aquatic and salt marsh species
c. common terrestrial species

* marks introduced species
collection numbers and authorities for all plant names are listed in Appendix IV

1. PIPECLAY LAKE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia tuberosa

Emergent aquatic and salt marsh species

Acaena anserinifolia
Brachycome exilis
Centrolepis polygyna
Cotula vulgaris
Distichlis distichophylla
Gahnia filum
Hemichroa pentandra
Hydrocotyle medicaginoides
Juncus kraussii
Myosotis australis
Samolus repens
Sarcocornia quinqueflora
Senecio glossanthus
Sporobolus virginicus
Suaeda australis
Threlkeldia diffusa
Triglochin mucronatum
Wilsonia humilis

Common terrestrial species

Acacia pycnantha
A. sophorae
Atriplex paludosa
Clematis microphylla
**Echium lycopsis*
Eucalyptus diversifolia
E. fasciculosa
Leucopogon parviflorus
**Lycium ferocissimum*
Muehlenbeckia adpressa
Olearia axillaris
Tetragonia amplexicoma

2. FLAX POINT, COORONG

Submerged aquatic species

Angiosperms:

Ruppia tuberosa

Macro-algae:

Acetabularia peniculus
Lamprothamnium papulosum
Cladophora sp.

Common salt marsh and terrestrial species (rocky peninsula and back from beach)

Acaena anserinifolia
Arthrocnemum
Cakile maritima
Carpobrotus rossii
Cotula vulgaris
Dianella revoluta
Euphorbia paralias
Frankenia sp.
Hordeum marinum
Muehlenbeckia adpressa
Sarcocornia quinqueflora
Sporobolus virginicus
Stackhousia spathulata
Tetragonia amplexicoma

Table 5.6 continued

3. MIKES LAKE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia tuberosa

Macro-algae:

Lamprothamnium papulosum
Cladophora sp.
Enteromorpha sp.

Micro-algae:

Calothrix sp.
Hydrocoleum sp.
Nostoc sp.
Vaucheria sp.

Emergent aquatic and salt marsh species

Arthrocnemum sp.
Juncus kraussii
Samolus repens
Sarcocornia quinqueflora
Sporobolus virginicus
Suaeda australis
Wilsonia backhousei

Common terrestrial species

Acacia pycnantha
A. sophorae
Clematis microphylla
Eucalyptus diversifolia
E. fasciculosa
Leucopogon parviflorus
Melaleuca halmaturorum
Amyema melaleucae

4. BLUE-GREEN ALGAL POOL

Submerged aquatic species

Angiosperms:
Lepilaena cylindrocarpa
Ruppia polycarpa
Macro-algae:
Lamprothamnium papulosum
Micro-algae:
Calothrix sp.
Hydrocoleum sp.
Nostoc sp.
Vaucheria sp.

Emergent aquatic and salt marsh species

Arthrocnemum sp.
Cotula vulgaris
Sarcocornia quinqueflora
Suaeda australis
Thelkeldia diffusa
Wilsonia backhousei

Common terrestrial species

Acacia pycnantha
A. sophorae
Leucopogon parviflorus
Melaleuca halmaturorum
Muehlenbeckia adpressa
Tetragonia amplexicoma

5. BRINESHRIMP LAKE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia tuberosa

Emergent aquatic and salt marsh species

Agropyron scabrum
**Anagallis arvensis*
**Arenaria serpyllifolia*
**Avena sativa*
Arthrocnemum sp.
Brachycome exilis
B. goniocarpa
**Bromus rubens*
**Bupleurum semicompositum*
Centrolepis polygyna
Cotula vulgaris
Cyperus laevigatus
**Echium lycopsis*
Frankenia pauciflora
Gahnia filum
Galium murale
Hemichroa pentandra
Hydrocotyle pilifera
Juncus bufonius
**Koeleria phleoides*
**Parapholis incurva*
Poa fax
**Polypogon maritimus*
Pomaderris paniculosa
Puccinellia stricta
Pultenaea prostrata
Samolus repens
Sarcocornia quinqueflora
Scirpus antarcticus
S. nodosus
Sebaea albidiflora
S. ovata
Selenothamnus squamatus
Senecio glossanthus
**Sonchus oleraceus*
Stipa teretifolia
Triglochin centrocarpum
T. mucronatum
**Vulpia myuros*
Wilsonia backhousei

Table 5.6 continued

6. LAKE ROBE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia polycarpa
R. tuberosa

Macro-algae:

Lamprothamnium papulosum
Cladophora sp.

Emergent aquatic and salt marsh species

Arthrocnemum sp.
Samolus repens
Sarcocornia quinqueflora
Selliera radicans
Wilsonia backhousei

Common terrestrial species

Melaleuca halmaturorum
Tetragonia amplexicoma

7. FRESH DIP LAKE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Myriophyllum propinquum
Potamogeton pectinatus
Ruppia polycarpa

Macro-algae:

Chara vulgaris
Cladophora sp.

Emergent aquatic and salt marsh species

Gahnia trifida
Lepidosperma canescens
L. longitudinale
Machaerina juncea
Scirpus nodosus

Common terrestrial species

Acacia pycnantha
A. sophorae
Cassytha sp.
Clematis microphylla
Eucalyptus diversifolia
Euphorbia paralias
Leptospermum pubescens
Leucopogon parviflorus
Melaleuca halmaturorum
Muehlenbeckia adpressa
Stackhousia spathulata
Tetragonia amplexicoma

8. LITTLE DIP LAKE

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia megacarpa
R. tuberosa

Macro-algae:

Lamprothamnium papulosum
Cladophora sp.

Emergent aquatic and salt marsh species

Arthrocnemum sp.
Gahnia filum
Hemichroa pentandra
Juncus kraussii
Samolus repens
Sarcocornia quinqueflora
Selliera radicans
Wilsonia backhousei

Common terrestrial species

Acacia pycnantha
A. sophorae
Clematis microphylla
Eucalyptus diversifolia
Leucopogon parviflorus
Melaleuca halmaturorum
Tetragonia amplexicoma

Table 5.6 continued

9. LAKE ELIZA SALT MARSH

Submerged aquatic species

Angiosperms:

Lepilaena cylindrocarpa
Ruppia megacarpa
R. tuberosa

Macro-algae:

Lamprothamnium papulosum
Cladophora sp.

Cyanophyta

Emergent aquatic and salt marsh species

Agrostis aemula
Amyema melaleucae
Arthrocnemum sp.
**Bromus diandrus*
Cotula vulgaris
Frankenia pauciflora
Gahnia filum
G. trifida
Hemichroa pentandra
Hordeum marinum
Juncus kraussii
Leptocarpus brownii
Machaerina juncea
Puccinellia stricta
Rhagodia baccata
Samolus repens
Sarcocornia quinqueflora
Scirpus inundatus
Selliera radicans
**Senecio vulgaris*
**Serrafalcus hordeaceus*
Suaeda australis
Triglochin mucronatum
T. striatum
Wilsonia backhousei

Common terrestrial species

Acacia sophorae
Melaleuca halmaturorum
M. lanceolata
Tetragonia amplexicoma

10. ERRINGTONS HOLE LAKE

Submerged aquatic species

Angiosperms:

Ruppia megacarpa

Macro-algae:

Lamprothamnium papulosum

Emergent aquatic and salt marsh species

Cotula vulgaris
Lepidosperma gladiatum
Machaerina tetragona
M. juncea
Samolus repens
Scirpus nodosus

Common terrestrial species

Acacia sophorae
A. pycnantha
Acaena anserinifolia
Clematis microphylla
Euphorbia paralias
Leptospermum pubescens
Leucopogon parviflorus
Melaleuca sp.
Olearia axillaris
Senecio lautus
Tetragonia amplexicoma

11. LAKE ELIZA CUT-OFF

Submerged aquatic species

none observed

Emergent aquatic and salt marsh species

Juncus kraussii
Phragmites australis
Scirpus maritimus
S. nodosus

Common terrestrial species

Acacia pycnantha
A. sophorae
Leptospermum pubescens
Leucopogon parviflorus
Melaleuca halmaturorum

12. BEACHPORT SALT LAKE

Submerged aquatic species

Angiosperms:

Ruppia tuberosa

Common terrestrial species

Clematis microphylla
Dianella revoluta
Leptospermum pubescens
**Lycium ferocissimum*
Melaleuca halmaturorum
Muehlenbeckia adpressa
Olearia axillaris
Sarcocornia quinqueflora
Scaveola sp.
Tetragonia amplexicoma

further. Introduced species are marked with an asterisk. A full list of plant collections are records (including authorities for all names) is presented in Appendix IV.

The occurrence and reproductive state of submerged hydrophytes in relation to seasonal changes of depth and salinity in each lake are shown in Figure 5.5. Data for both algae and angiosperms are presented, although accurate information on the reproductive times of the algae were not always available. Generic names are used except when two forms of *Ruppia* from ephemeral and permanent habitats are distinguished as Forms E and P respectively, and when algae could be identified only to family. This eliminated discrepancies caused by difficulties in the identification of species when reproductive stages were unavailable. The monocotyledons *Ruppia*, *Lepilaena* and *Potamogeton pectinatus* are extremely similar in vegetative form and hence, where possible, comparison of the 1975 collections with material collected subsequently was made to validate initial identifications.

Ruppia and *Lepilaena* were the only two genera of angiosperms found over wide salinity and depth ranges. The only location which had neither genus was Lake Eliza Cutoff; at that location no submerged angiosperms or macrophytic algae were recorded. *Ruppia* occurred in all other sites, and *Lepilaena* in all but Flax Point, Erringtons Hole Lake and Beachport Salt Lake. Fresh Dip Lake was the only location where other submerged angiosperms (*Myriophyllum propinquum* and *Potamogeton pectinatus*) were present (Figure 5.5).

Macrophytic algae of the Characeae (*Lamprothamnium* or *Chara*) were present in all but three hypersaline sites (Pipeclay Lake, Brineshrimp Lake and Beachport Salt Lake) and in the brackish dune-lake (Erringtons Hole). The absence of macrophytic algae in the three hypersaline sites may be attributed to maximum salinity levels above the tolerance limits for these species, while their absence in Erringtons Hole is possibly

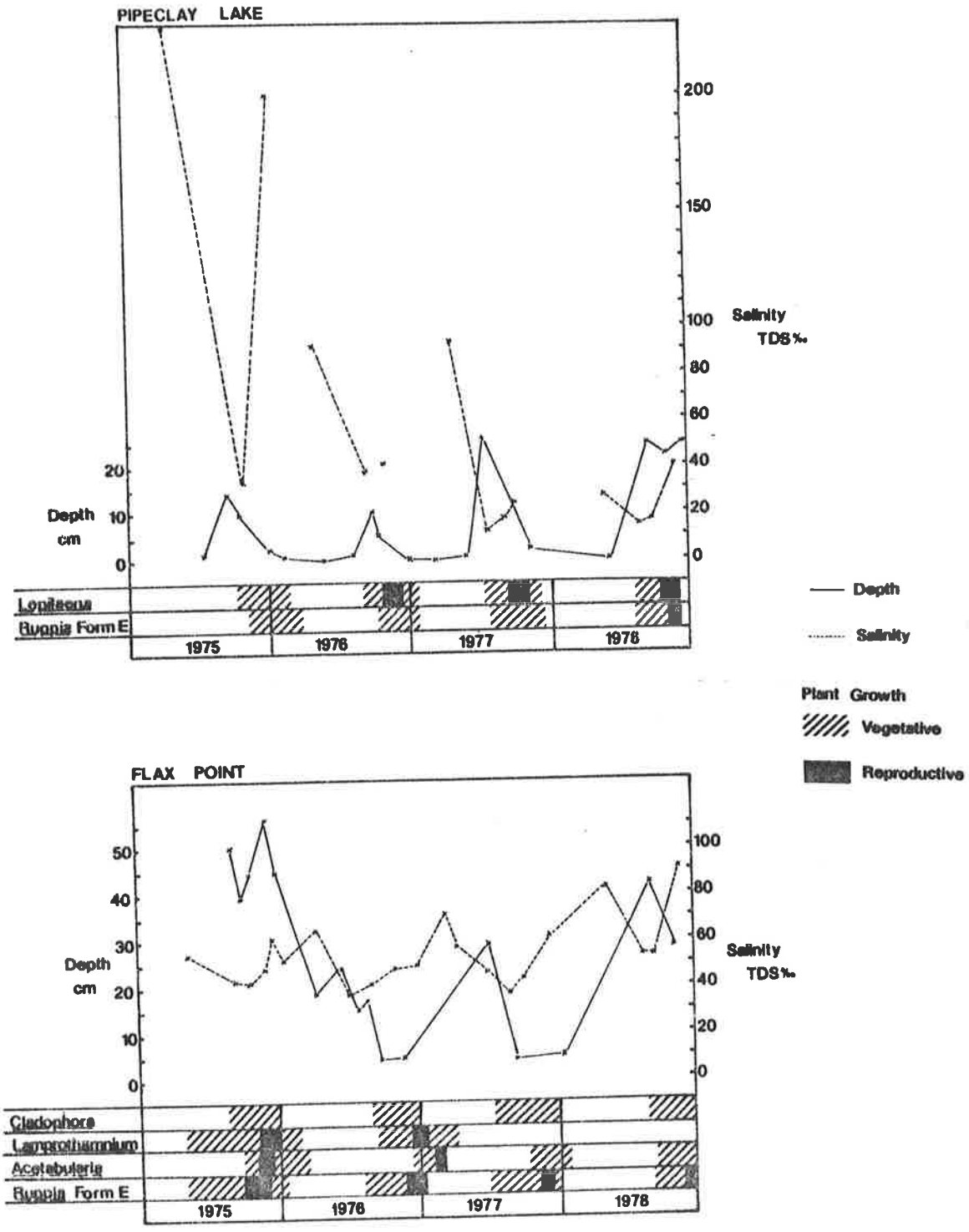


Figure 5.5 Salinity, depth and plant occurrence in the eleven study sites containing macrophytes.

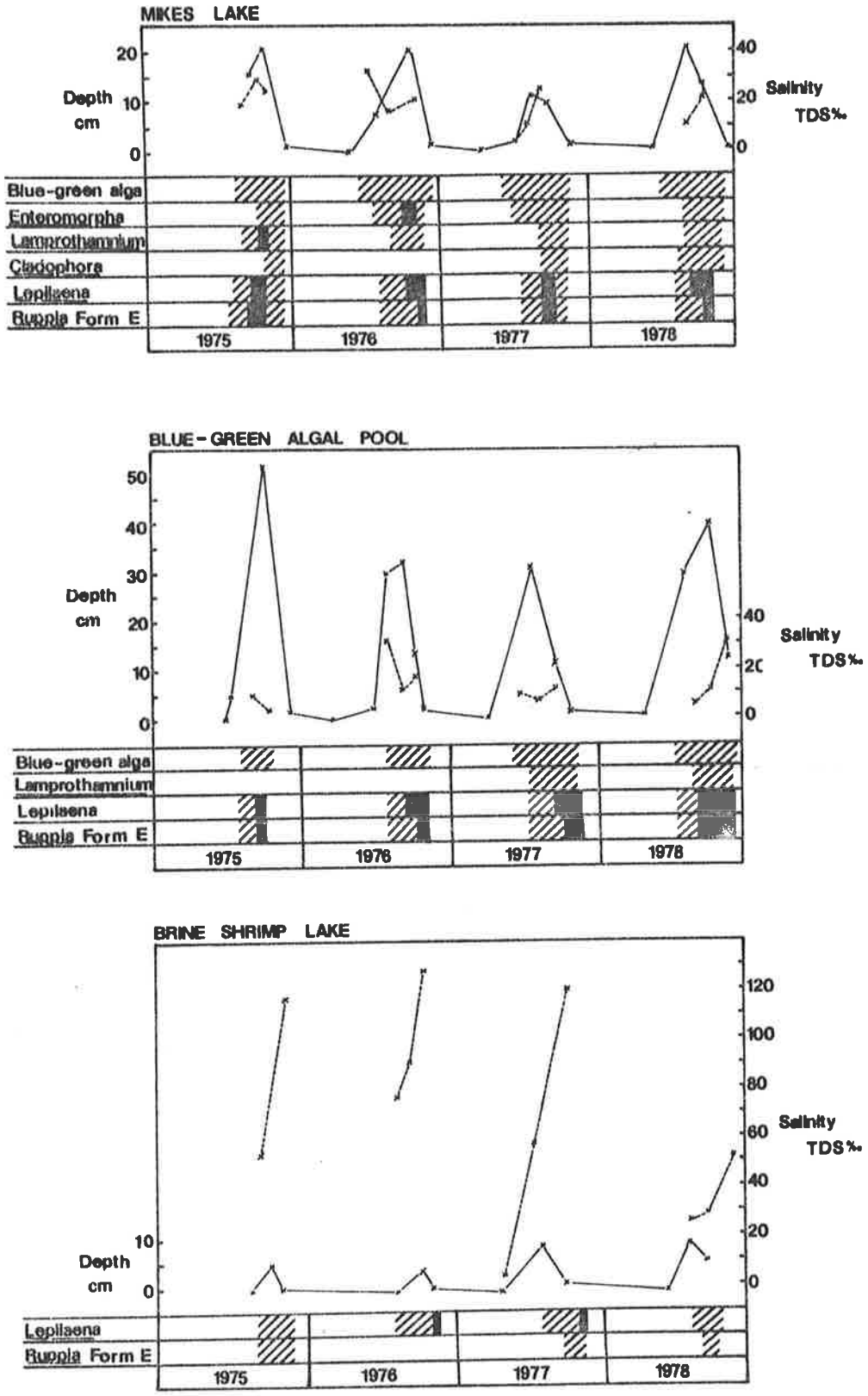
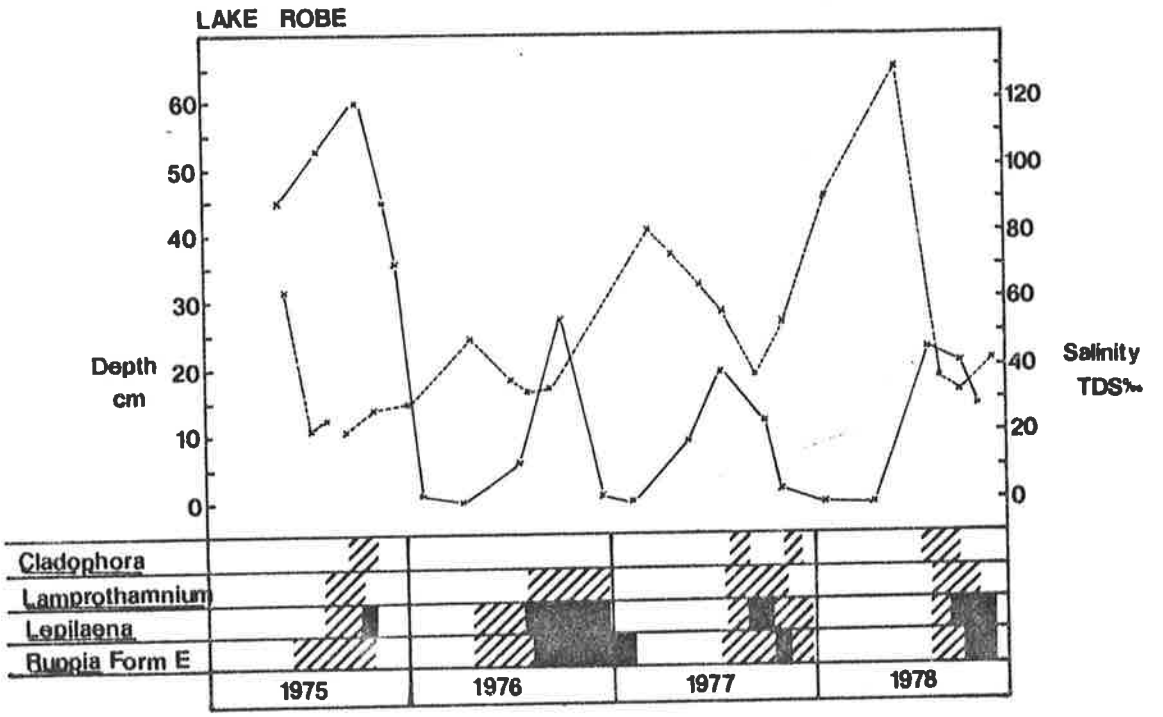


Figure 5.5 continued



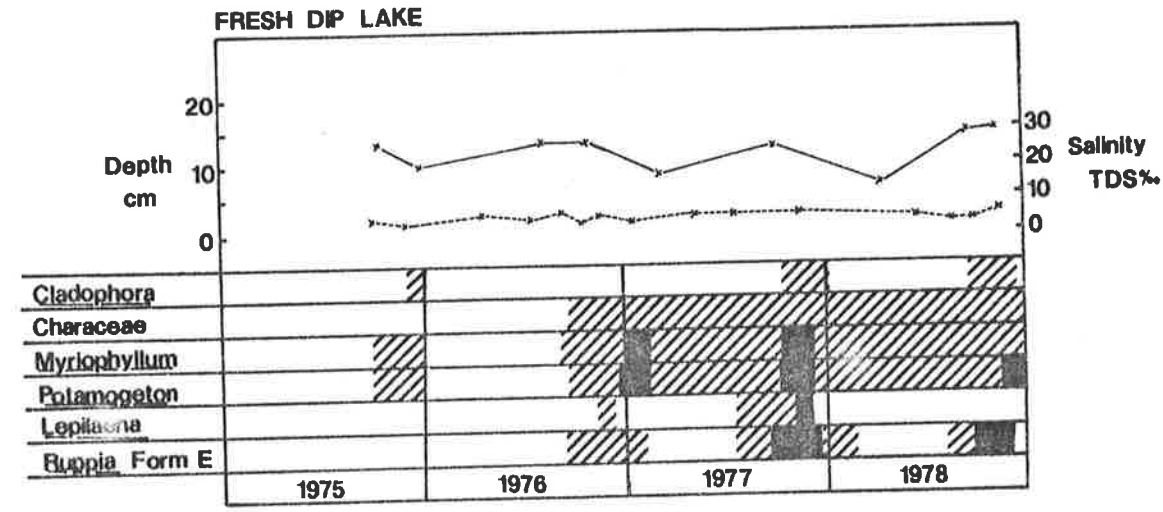


Figure 5.5 continued

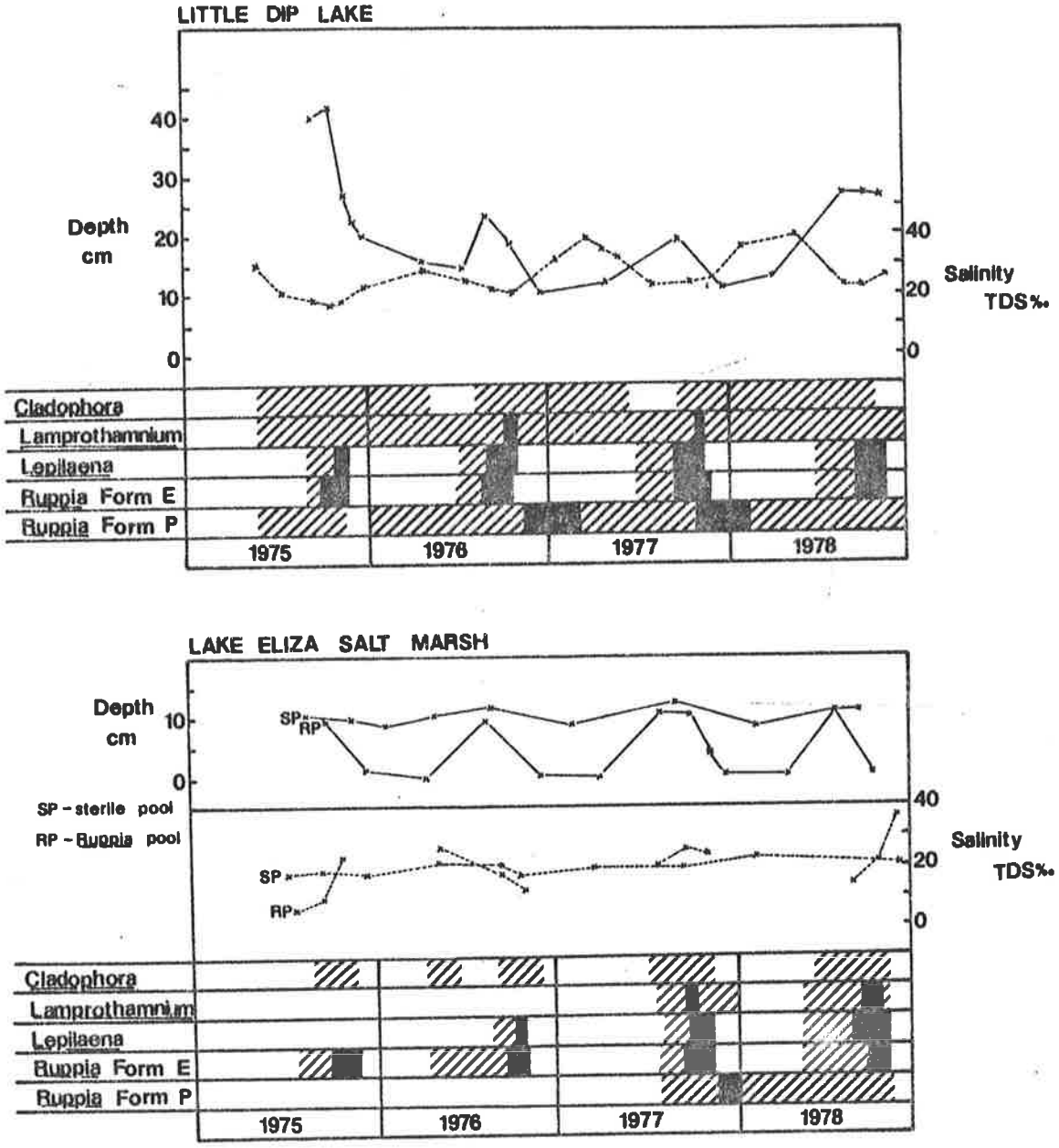


Figure 5.5 continued

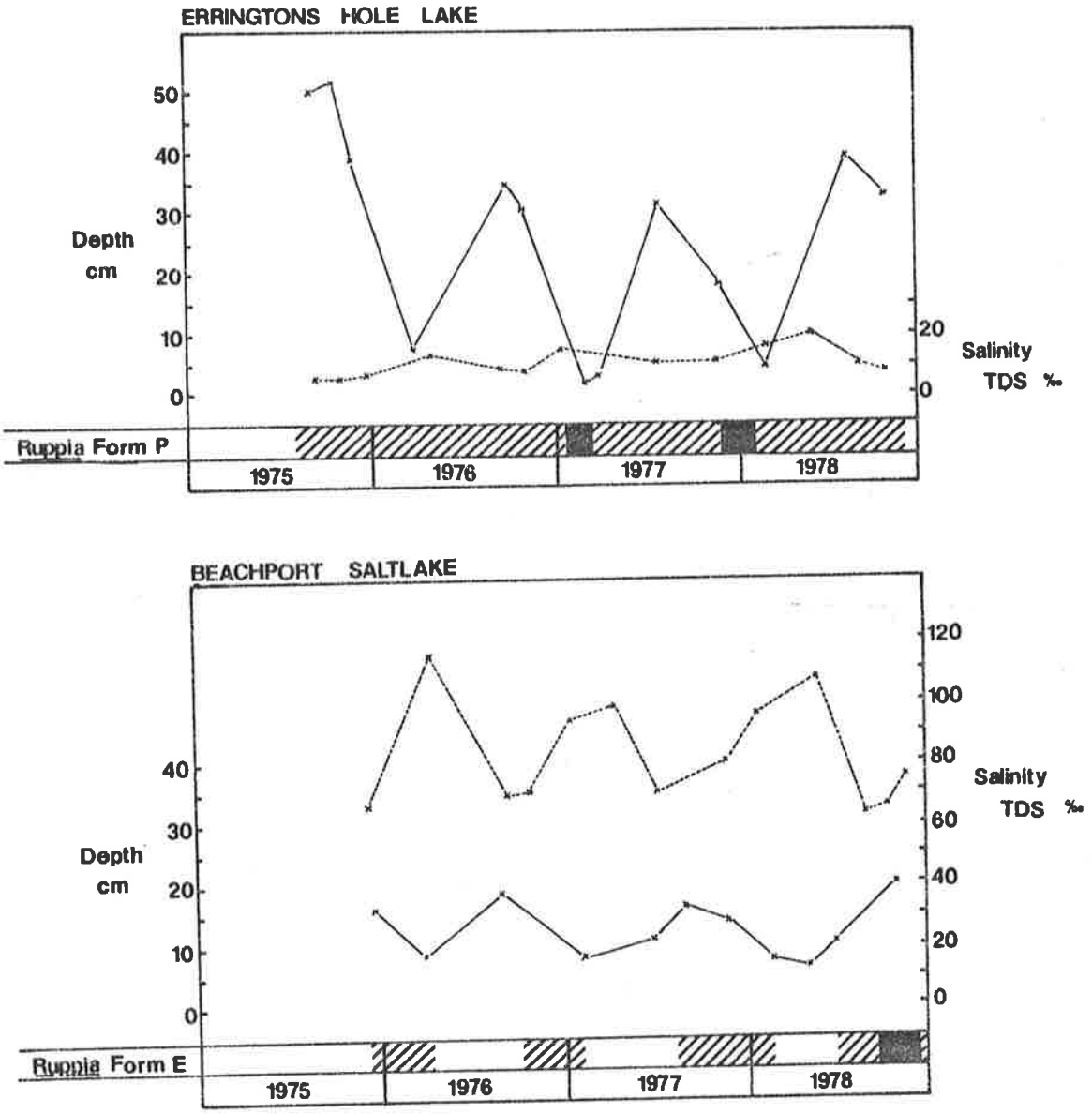


Figure 5.5 continued

due to the drifting of sand into potential habitats. Insufficient sampling of the deeper areas of Erringtons Hole may also account for the apparent absence. Fresh Dip Lake, which is similar to Erringtons Hole Lake in sediment type and morphological characters, had dense beds of charophytes covering the deeper areas of its basin. *Cladophora*, a green filamentous alga, was also absent from these three hypersaline sites, and from Blue-Green Algal Pool, but was present in other localities. *Acetabularia peniculus*, generally a marine species, was recorded at Flax Point. Another green alga, *Enteromorpha*, was recorded in Mikes Lake adjacent to the Coorong. Blue-green algae were recorded where dominant, but have not been identified. Phytoplankton occurrence has not been recorded.

The growth of hydrophytes in ephemeral lakes is related to depth and salinity. In all ephemeral sites the basins fill quickly after winter rains and seed germination is rapid (Figure 5.5). The decrease in depth and increase in salinity later in summer result in plant senescence or stranding on the salt crust. Both *Ruppia* and *Lepilaena* have dormant seeds which can withstand the harsh desiccating summer conditions. *Ruppia* also produces vegetative perennating organs (turions) on the rhizomes. In the most hypersaline sites (Pipeclay, Brineshrimp and Beachport Salt Lake), *Ruppia* did not flower in all years (*cf*. Figure 5.5), and plant growth in the subsequent growing seasons was from turions. Prolific seeds and turions were produced by the *Ruppia* populations in 1978. The roles of these forms of reproduction are examined further in Chapter 9. *Lepilaena* flowers at the same time as, or earlier than, *Ruppia*, and produces prolific numbers of seeds. Plant remains, including seeds and turions, were extensive in the salt and mud crusts left in summer.

The eulittoral zone of permanent sites provides seasonal, wet habitats in which these plants act as annuals. The extensive eulittoral

zones of Little Dip Lake and Lake Robe support prolific mixed stands of *Ruppia* and *Lepilaena* during the 4-6 month wet phase. An ephemeral side pool connected to Lake Robe in spring supports a more dense macrophytic growth than the permanent lake. Similarly, the eulittoral zone of Little Dip Lake is more prolific, in its short growing season, than the permanent *Ruppia* beds.

The permanent sites of Flax Point and Beachport Salt Lake provide similar temporary habitats for *Ruppia*, but *Lepilaena* is absent. *Ruppia* beds at Flax Point were rarely extensive, and plant growth was not perennial even in the permanent areas. On the permanently wet beach of Beachport Salt Lake *Ruppia* died back in summer, leaving a brown root stock around which turions germinated in the following season. Increases in salinity or temperature may have caused this browning and die-back. Fresh Dip Lake shows the same phenomenon with *Ruppia* beds, which, although still covered with water, die back in summer after flowering. However, turions were not observed in these beds; propagation must be by rhizome growth or from seeds at this site.

Little Dip Lake, Erringtons Hole Lake and Lake Eliza Salt Marsh differ from all other localities in having a robust form of *Ruppia* present perennially. This *Ruppia* (Form P) grows in clumps in deeper water in the first two locations, and on the edges of a permanent pool in the salt marsh. It occurs in Little Dip Lake surrounded by *Lamprothamnium* but, unlike the annual form, did not occur with *Lepilaena*. The delicate Form E occurs in temporary habitats, whereas *Ruppia* Form P grows in permanent water of both Little Dip Lake and Lake Eliza Salt Marsh. The two forms appear disjunct with respect to flowering times.

5.2 Little Dip Conservation Park

1. Little Dip Lake and Fresh Dip Lake

Contour maps which plot the lake basin morphometry for Little Dip Lake (Figure 5.6) and Fresh Dip Lake (Figure 5.10) are used as bases for the consideration of the general environmental and vegetation data presented in Section 5.1. Little Dip Lake (Figure 5.6) has a maximum depth of 3.3 metres and a general basin depth of between 0.5 and 1.5 metres, depending on fluctuations in water level. The shallow beach on the south-eastern shore is a significant temporary habitat since a large area above the 0.25 m contour is exposed in summer. Fresh Dip Lake (Figure 5.10) is a deeper lake with a maximum depth of 4.5 metres with a general basin depth between 1 and 4.25 metres.

Vegetation maps, constructed for Little Dip Lake, can be superimposed on the map of lake morphometry (Figure 5.6). Vegetation was mapped in April 1976 (Figure 5.8) and in November 1977 (Figure 5.7) to illustrate vegetational change with season. Beds of the charophyte *Lamprothamnium papulosum* were recorded at all depths of the lake basin but their distribution was discontinuous. A band of perennial *Ruppia* (Form P) occurred between 0.5 and 1.0 metre contours. *Cladophora* sp. occurred sporadically, and was often trapped in the perennial *Ruppia* beds. The northern, western and southern shores were bordered by the reed beds composed mainly of *Gahnia filum* and *Juncus kraussii*. The spring vegetation (Figure 5.7) followed the same basic pattern, but an ephemeral community of *Ruppia* (Form E) and *Lepilaena cylindrocarpa* occurred on the south-eastern beach together with a low carpet of the charophyte. Vegetation changes with depth are illustrated on profile diagrams (Figure 5.9).

The distribution of vegetation in Fresh Dip Lake is shown in Figure 5.11. The lake basin was covered with *Chara vulgaris* and was bordered (except for the western dune shore) by dense reed beds of

Figure 5.6 Little Dip Lake: morphometric map

Figure 5.7 Little Dip Lake: vegetation map for September - November 1977

Figure 5.8 Little Dip Lake: vegetation map for April 1976

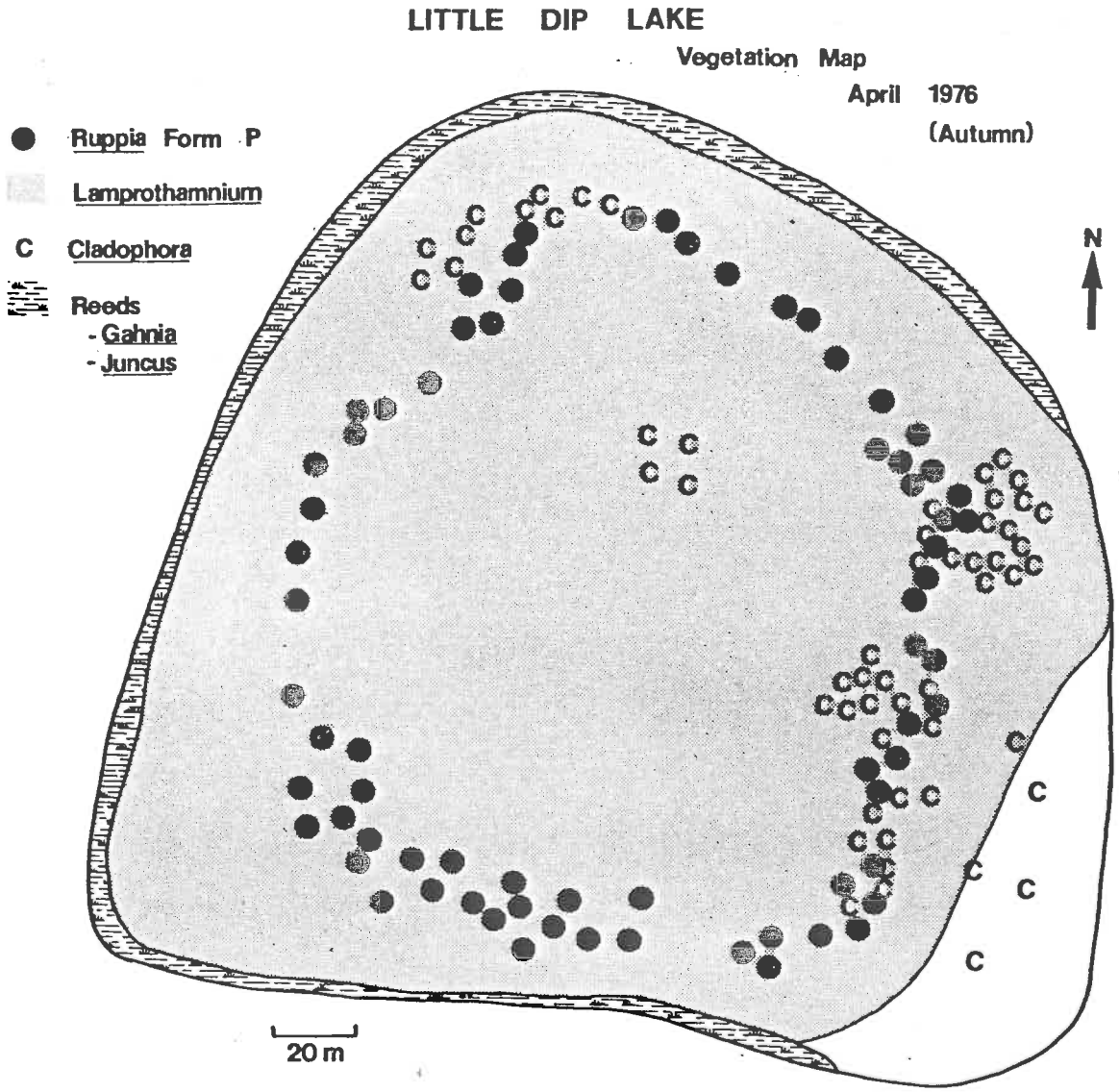

LITTLE DIP LAKE
Vegetation Map
April 1976
(Autumn)
Ruppia Form P
Lamprothamnium
C Cladophora
Reeds
- Gahnia
- Juncus
N
20 m

Figure 5.8

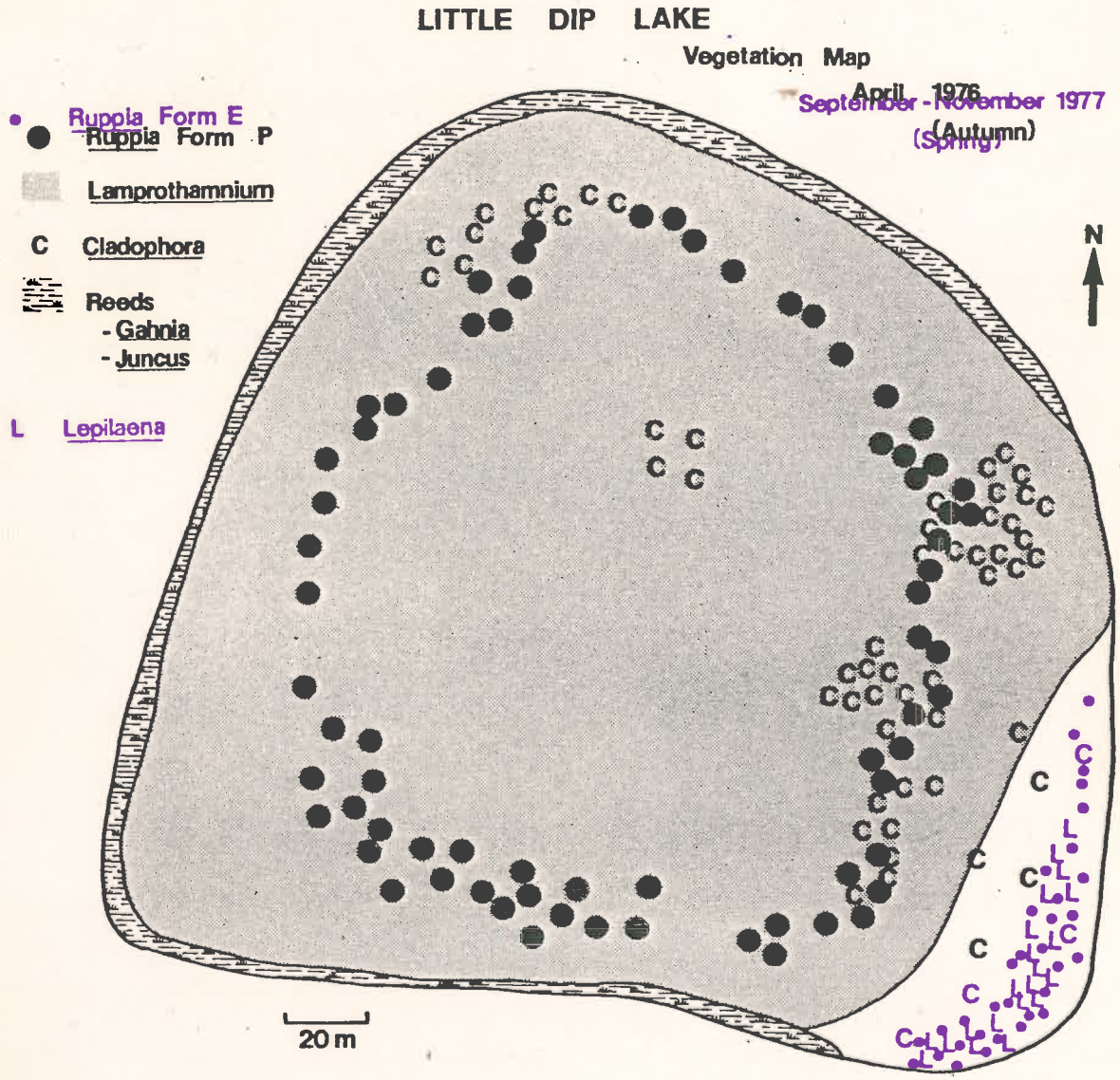


Figure 5.7

Figure 5.8

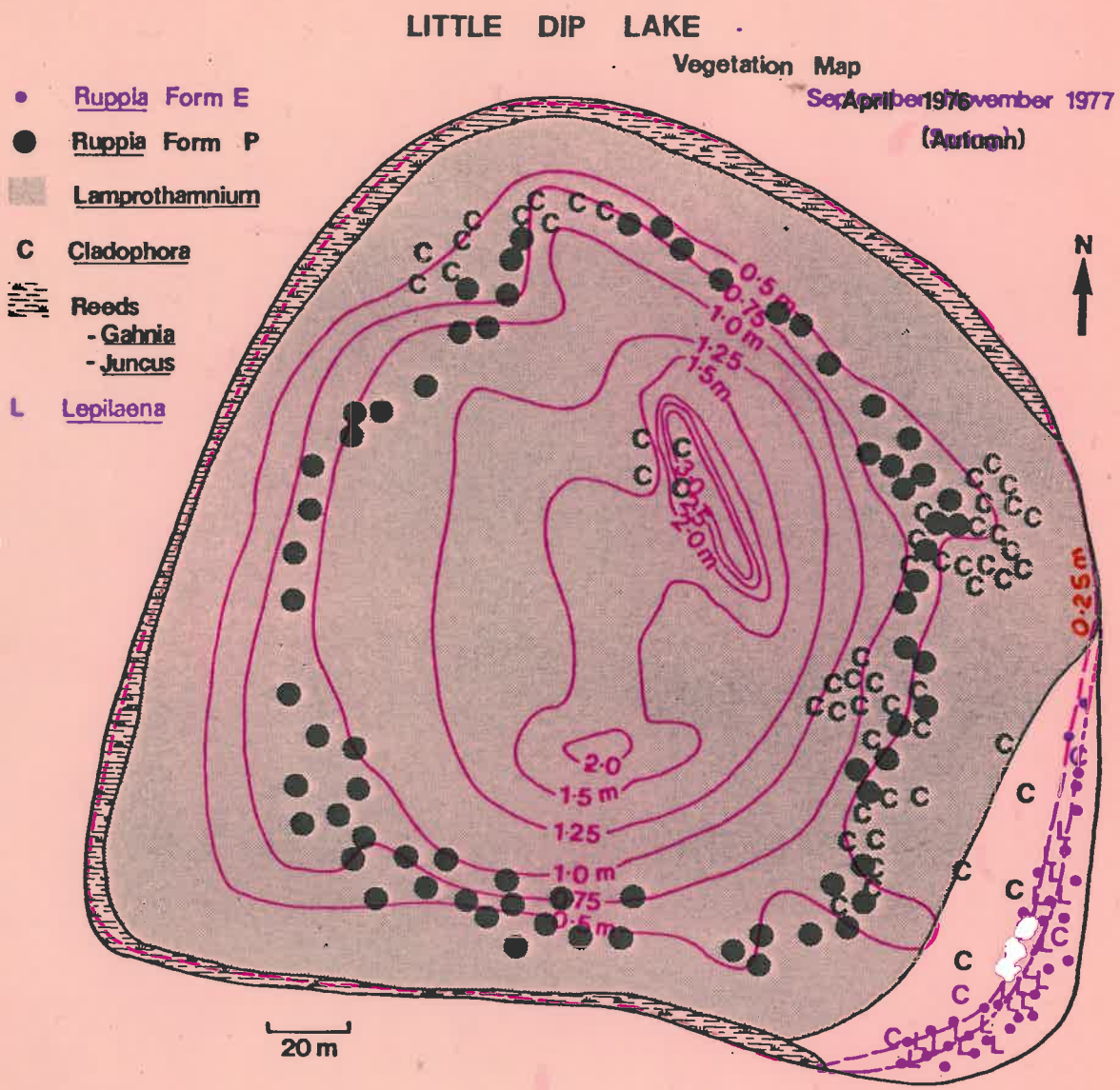


Figure 5.6

Figure 5.7

Figure 5.8

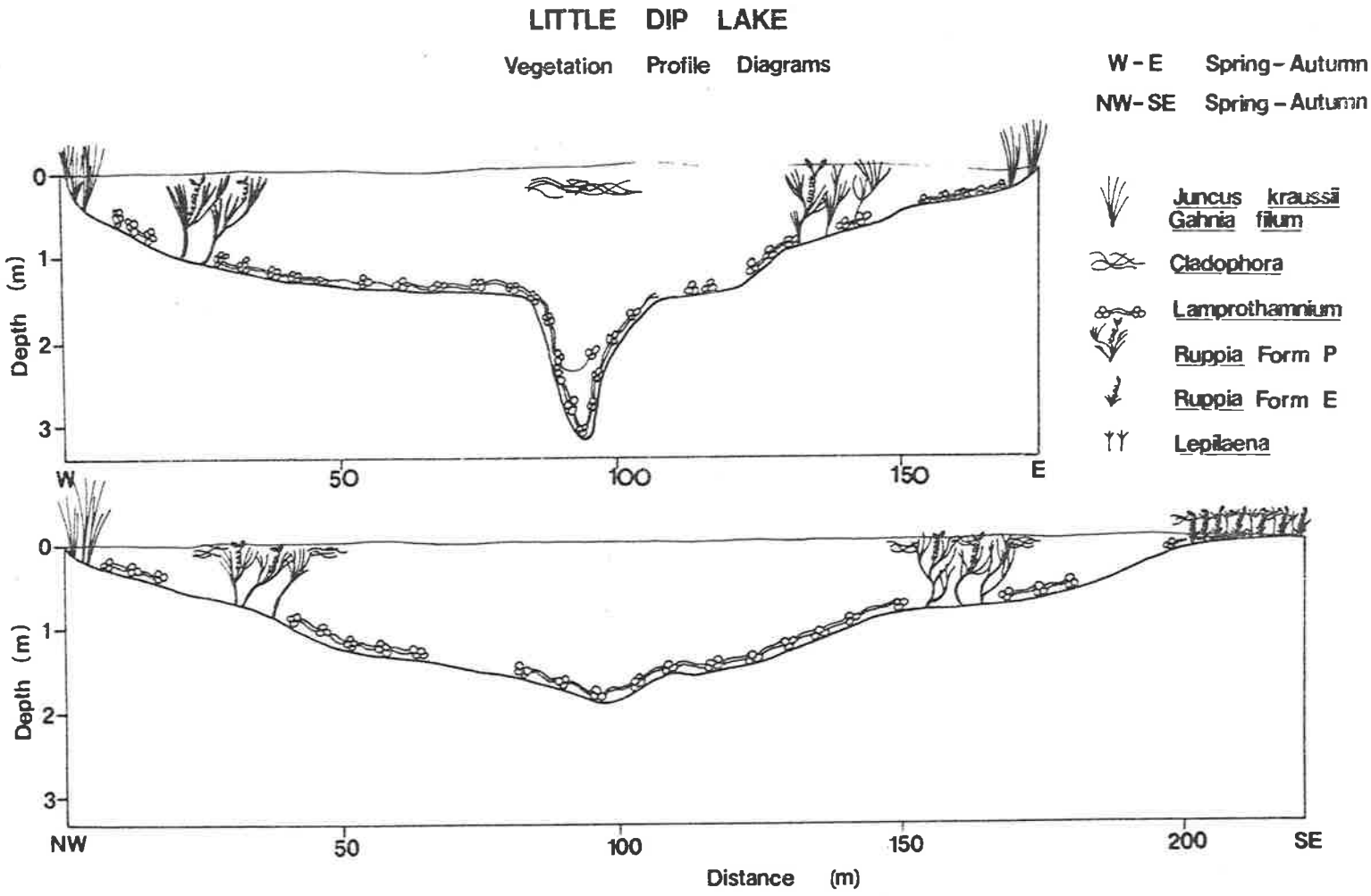


Figure 5.9 Little Dip Lake: profile diagrams taken along W → E and NW → SW transects across the lake.

Gahnia trifida, *Lepidosperma canescens*, *Lepidosperma longitudinale*, *Machaerina juncea* and *Scirpus nodosus*. *Myriophyllum propinquum* occurred around the interface of reeds and open water. *Potamogeton pectinatus* occurred sporadically with the *Myriophyllum*. *Ruppia* was abundant along the dune interface and occurred in patches with *Myriophyllum* elsewhere in the lake. *Lepilaena cylindrocarpa* was found in small localized areas together with *Cladophora* sp.

Profile diagrams of vegetation change with depth (Figure 5.12) shows that all species except *Chara vulgaris* were concentrated in the shallower regions.

Plant associations within Little Dip Lake and Fresh Dip Lake were analysed by quadrat and biomass sampling. Species frequency was estimated as the percentage of quadrats in which a species occurred and cover was estimated as the percentage of a quadrat occupied by a species; thirty 0.25 m^2 quadrats were examined in each association. Biomass estimates are for one square metre of vegetation only, harvested in 4 x 0.25 m^2 blocks from the densest area of each *Ruppia* dominated association. Data are presented in Table 5.7.

Ruppia Form E and *Lepilaena cylindrocarpa* were dominants in terms of frequency, cover and biomass in the eulittoral zone of Little Dip Lake (Table 5.7). *Ruppia* Form P is the dominant species in terms of cover and biomass in the permanent *Ruppia* habitat, but because of its clumped growth form and discontinuous distribution it was only recorded in 50% of the quadrats examined. Similarly, the frequency values of *Lamprothamnium papulosum* across the lake basin indicate its patchy distribution.

The bed of Fresh Dip Lake is covered by *Chara vulgaris*; this species has both 100% frequency and a complete cover estimate (Table 5.7). *Ruppia* occurs only occasionally in this ecosystem (Figure 5.11). However on the dune/water interface *Ruppia* occurs with *Myriophyllum*

Figure 5.10 Fresh Dip Lake: morphometric map

Figure 5.11 Fresh Dip Lake: vegetation map for November 1977

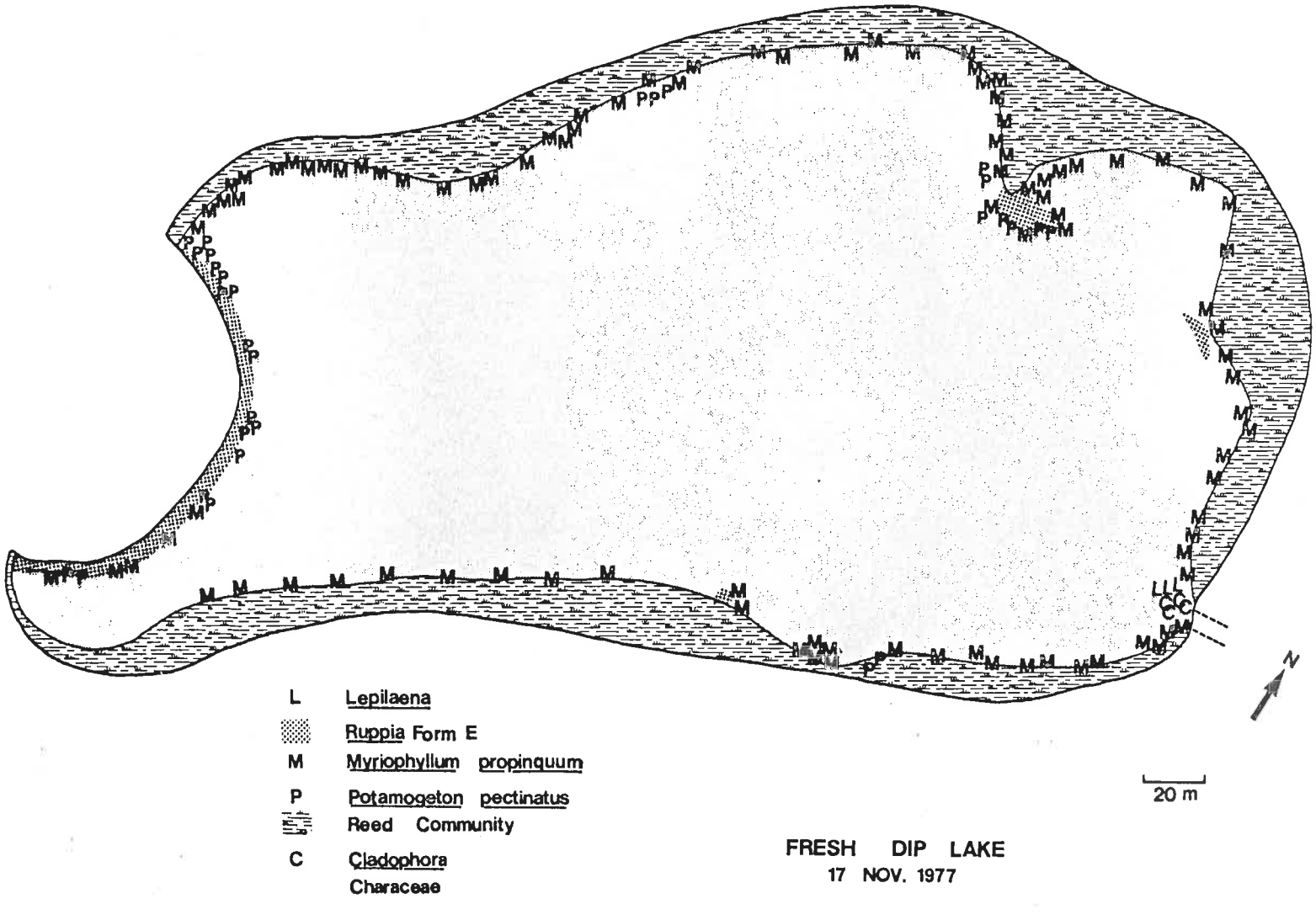

L Lepilaena
Ruppia Form E
M Myriophyllum propinquum
P Potamogeton pectinatus
Reed Community
C Cladophora
Characeae
20 m
FRESH DIP LAKE
17 NOV. 1977

Figure 5.11

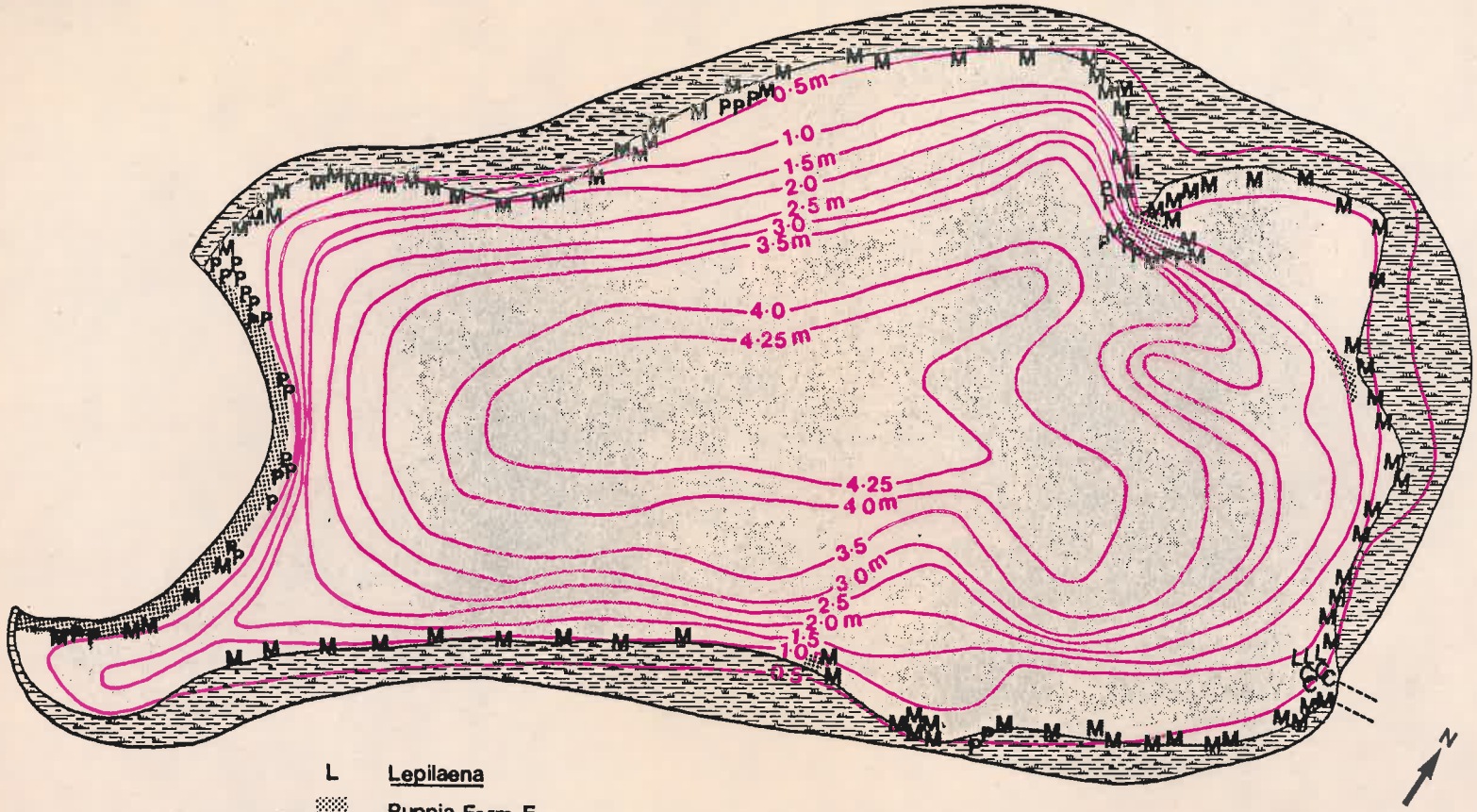


Figure 5.10

Figure 5.11

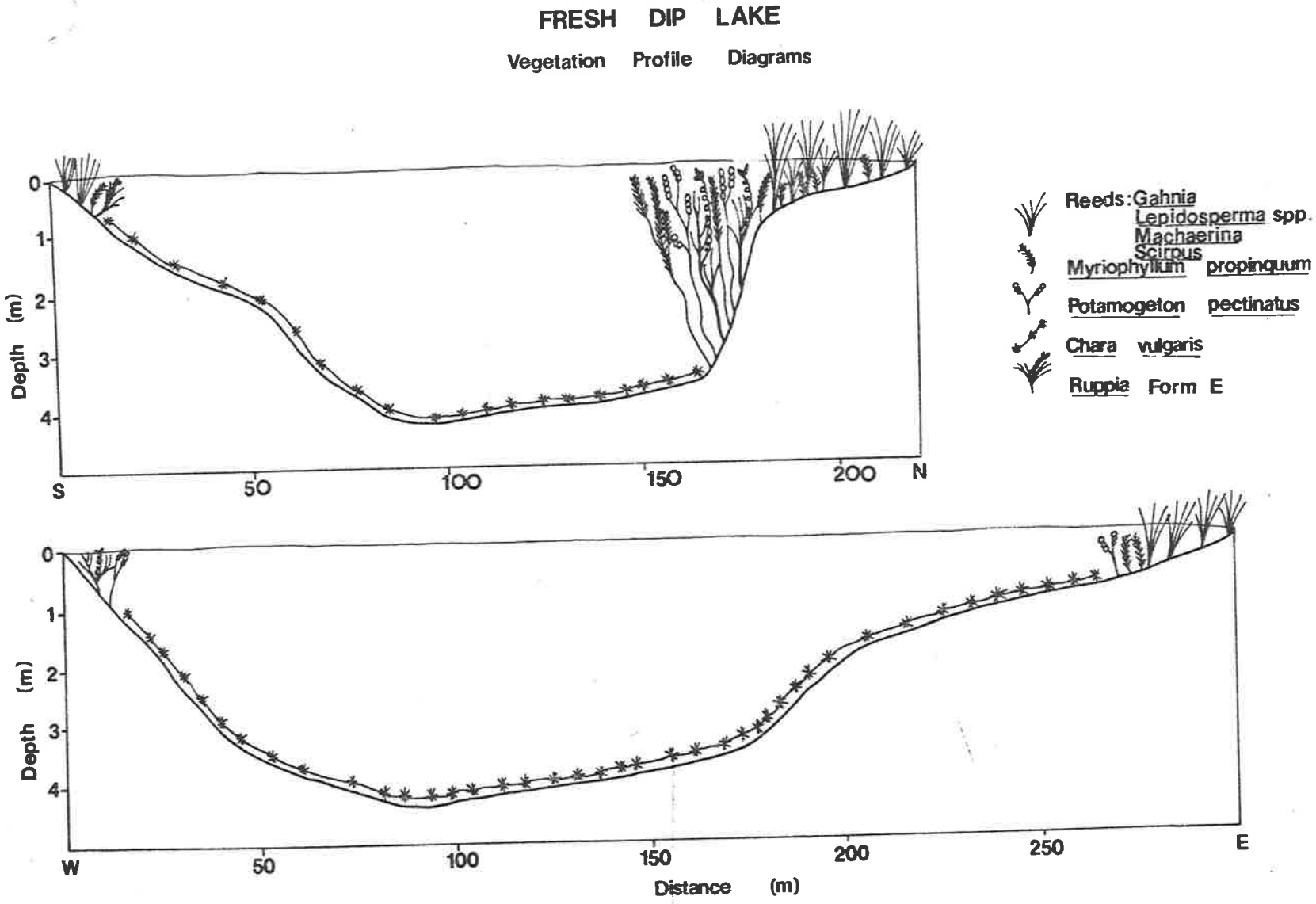


Figure 5.12 Fresh Dip Lake: profile diagrams taken along N → S and E → W transects across the lake.

Table 5.7 Frequency, cover and biomass for submerged species in plant associations in Little Dip Lake and Fresh Dip Lake in November 1977 (growing season)

Plant association	Frequency % quadrats	Cover class*	Biomass dry weight g/m^2
LITTLE DIP LAKE			
a. Eulittoral zone (0-0.25m)			Total 11.7
Ruppia Form E	80	5	3.3
Lepilaena cylindrocarpa	85	5	6.0
Lamprothamnium papulosum	50	4	1.4
Cladophora sp.	10	3	
b. 0.25-0.4 m			
Lamprothamnium papulosum	30	4	
Cladophora sp.	5	2	
c. *Ruppia* Form P clumps 0.4-1.5m			Total 410.3
Ruppia Form P	50	5	282.5
Lamprothamnium papulosum	15	2	10.8
Cladophora sp.	15	2	107.0
d. >1.5 m			
Lamprothamnium papulosum	70	5	
Cladophora sp.	10	2	
FRESH DIP LAKE			
a. Dune face (0-1.5 m)			Total 213.9
Ruppia Form E	60	5	143.3
Potamogeton pectinatus	20	3	56.0
Myriophyllum propinquum	10	3	14.6
b. Edge of reed beds (0-1.5 m)			
Ruppia Form E	5	2	
Potamogeton pectinatus	20	4	
Myriophyllum propinquum	50	4	
Lepilaena cylindrocarpa	2	1	
Chara vulgaris	10	1	
Reeds	60	5	
c. Lake bottom >2 m			
Chara vulgaris	100	5	

* Classification after Braun-Blanquet (1932) (see Table 4.4)

and *Potamogeton* and is locally dominant, having 60% frequency score and high cover estimate. Elsewhere *Ruppia* occurs only occasionally along the reed/water interface (Table 5.7).

The total plant biomass of the eulittoral zone of Little Dip Lake is only 2.9% of that in the perennial *Ruppia* association, and the biomass of *Ruppia* Form E is only 1.2% of that of *Ruppia* Form P. The biomass differences between annual and perennial forms may have been exaggerated because November is towards the end of the annual growing season. In Fresh Dip Lake the annual *Ruppia* Form E population was growing in 1 metre of water, a comparable depth to the perennial *Ruppia* habitat of Little Dip Lake. The biomass of *Ruppia* Form E in Fresh Dip Lake is 43 times greater than *Ruppia* Form E from Little Dip Lake and is half of the biomass of the perennial *Ruppia* Form P from Little Dip Lake. Water depth and salinity could account for these differences. Further analysis of the variation in biomass of *Ruppia* associations is discussed in Section 9.4.

2. Lake Eliza Salt Marsh: vegetation survey

Delimitation of associations

Twelve plant associations are described for the study area on Lake Eliza Salt Marsh; delimitation was on the basis of floristic composition and visual homogeneity within associations. The characteristic species composition of each association is outlined in Table 5.8 and Plates 5.1 to 5.10 illustrate the associations. These photographs were taken in August 1978 during the annual wet phase of the marsh.

Association I, the true littoral area of Lake Eliza, is distinguished by its paucity of vegetation. Associations II, III and IV have *Sarcocornia quinqueflora* and *Arthrocnemum* sp. as dominants, but are distinguished by the associated species: an herbaceous layer of

Table 5.8 Species composition of the twelve plant associations on the Lake Eliza Salt Marsh

* occasional occurrence

Plant Association	Characteristic Species
I Lake Eliza	*Ruppia* Form E
II *Arthrocnemum-Sarcocornia-Puccinellia*	*Arthrocnemum* sp. *Sarcocornia quinqueflora* *Puccinellia stricta* *Senecio vulgaris* *Cotula vulgaris* *Agrostis aemula* *Triglochin striatum* *Suaeda australis* * Blue-green alga *
III *Sarcocornia-Arthrocnemum*	*Sarcocornia quinqueflora* *Arthrocnemum* sp. *Puccinellia stricta* Blue-green alga * *Ruppia* Form E *
IV *Sarcocornia-Suaeda*	*Sarcocornia quinqueflora* *Suaeda australis* *Arthrocnemum* sp. *Puccinellia stricta* * Blue-green alga *
V Sterile pool	Sulphur bacteria *Ruppia* Form P * (edges)
VI *Ruppia* pool	*Ruppia* Form E *Lepilaena cylindrocarpa* *Ruppia* Form P *
VII *Juncus-Samolus-Suaeda*	*Samolus repens* *Suaeda australis* *Juncus kraussii* *Selliera radicans* *Triglochin striatum* *Cladophora* sp. *Sarcocornia quinqueflora* *Gahnia filum* *Wilsonia backhousei* *Ruppia* Form E * *Puccinellia stricta* *Lepilaena cylindrocarpa* *Frankenia pauciflora* *
VIII *Suaeda-Wilsonia-Sarcocornia*	*Suaeda australis* *Sarcocornia quinqueflora* *Wilsonia backhousei* *Triglochin striatum* *Samolus repens* *Cladophora* sp. *Selliera radicans* *Juncus kraussii* * *Puccinellia stricta* * *Frankenia pauciflora* *
IX *Wilsonia-Sarcocornia*	*Wilsonia backhousei* *Sarcocornia quinqueflora* *Triglochin striatum* *Ruppia* Form E *Lepilaena cylindrocarpa* *Lamprothamnium papulosum* *Cladophora* sp. *Samolus repens* * *Selliera radicans* *
X *Samolus-Selliera-Suaeda*	*Samolus repens* *Selliera radicans* *Suaeda australis* *Wilsonia backhousei* *Triglochin striatum* *Cladophora* sp. *Lamprothamnium papulosum* *Sarcocornia quinqueflora*
XI *Melaleuca-Samolus*	*Melaleuca halmaturorum* *Samolus repens* *Selliera radicans* *Tetragonia amplexicoma* *Amyema melaleucae* *
XII *Selliera-Gahnia*	*Selliera radicans* *Gahnia trifida* *G. filum*

Plates 5.1 to 5.10 Lake Eliza Salt Marsh Associations

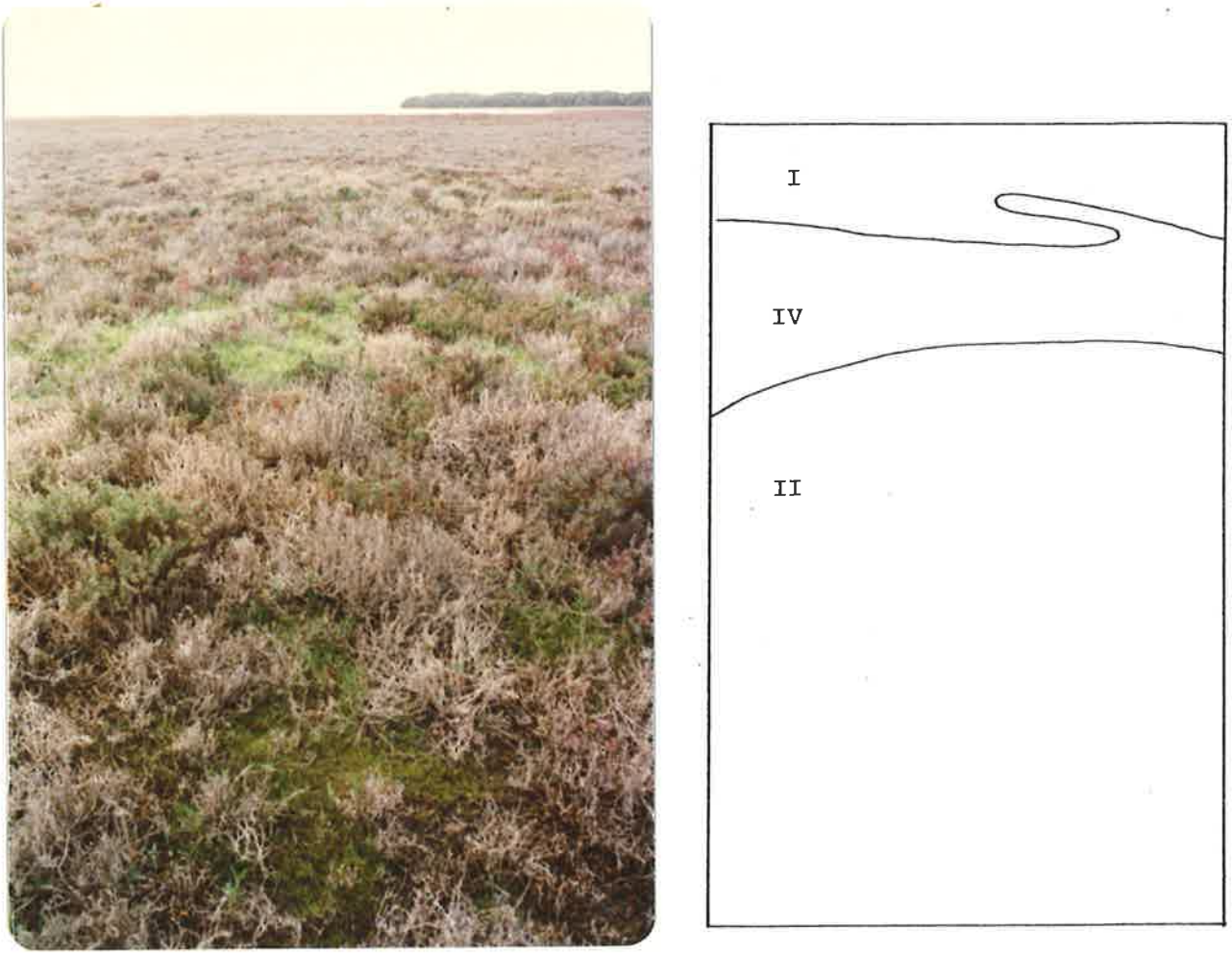


Plate 5.1 Associations I Lake Eliza, II *Arthrocnemum-Sarcocornia-Puccinellia* and IV *Sarcocornia-Suaeda*.

Plate 5.2 Association III *Sarcocornia-Arthrocnemum*.

Plate 5.3 The Sterile Pool (V) and *Ruppia* Pool (VI) Associations surrounded by Association VII, *Juncus-Samolus-Suaeda*. The transplant (VII) (foreground) was placed in the sterile pool in September 1975.

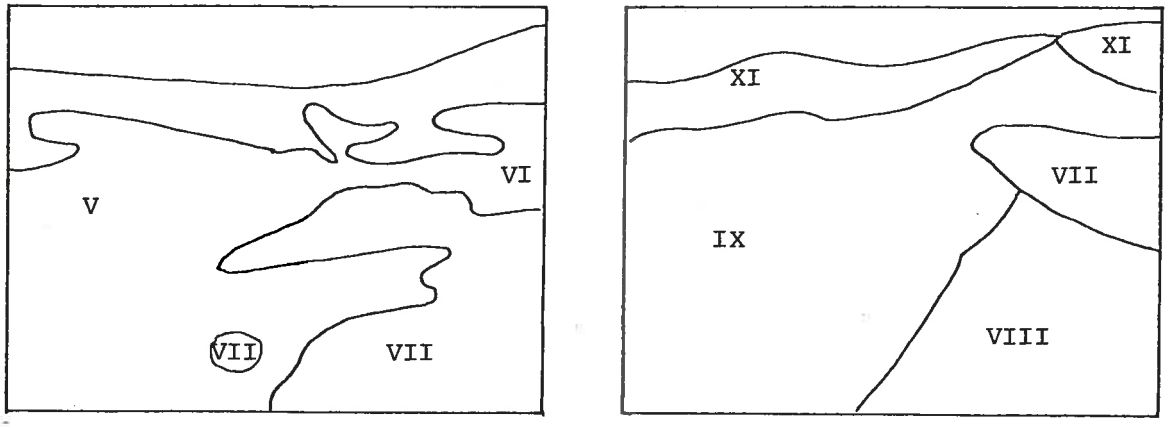


Plate 5.4

Plate 5.4 Associations VII *Juncus-Samolus-Suaeda*, VIII *Suaeda-Wilsonia-Sarcocornia*, IX *Wilsonia-Sarcocornia*, and XI *Melaleuca-Samolus*.

Plate 5.5 Sulphur bacteria in a sterile pool.

Plate 5.6 *Ruppia* Form P growing on the interface between a sterile pool (V) and a *Ruppia* pool (VI).

Plate 5.7 *Ruppia* Form E in a *Ruppia* pool (VI) with a *Sarcocornia* succession towards its periphery.

Plate 5.8 *Lepilaena cylindrocarp* in the underlayers of the *Wilsonia-Sarcocornia* Association (IX).

Plate 5.9 The *Wilsonia-Sarcocornia* Association showing the pools of charophytes.

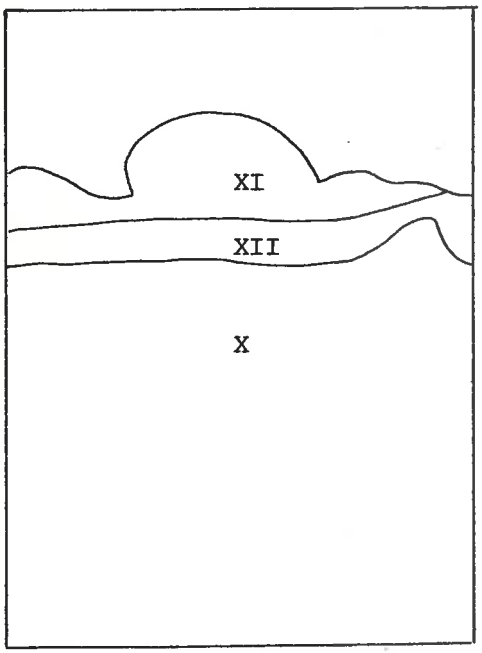


Plate 5.10 Associations X *Samolus-Selliera-Suaeda*, XI *Melaleuca-Samolus* and XII *Selliera-Gahnia*.

Puccinellia stricta, *Senecio vulgaris*, *Cotula vulgaris*, *Agrostis aemula* and *Triglochin striatum* characterize Association II; the bushy *Suaeda australis* distinguishes Association IV (Plate 5.1); bare substrate occurs between the *Arthrocnemum* and *Sarcocornia* in Association III (Plate 5.2).

Pools isolated from the surrounding vegetation are of two distinct types: the 'sterile' pools (Association V) are permanent and devoid of vegetation; the *Ruppia* pools (Association VI) are ephemeral and covered with a mat of *Ruppia* Form E in the wet season (Plates 5.3,5.5,5.6,5.7). The spring-fed sterile pools, which are often situated in the tops of mounds of the *Juncus-Samolus-Suaeda* Association (VII), are sometimes colonized by a surface mat of sulphur bacteria (Plate 5.5). The *Juncus-Samolus-Suaeda* Association (VII) forms a sharp interface with the pool (Plate 5.3) in contrast to the gradual succession from the *Sarcocornia-Arthrocnemum* (Association III) into the *Ruppia* pools (Association VI) (Plate 5.7). *Ruppia* pools rely on precipitation and as this is exceeded by evaporation they remain as cracked and dry salt pans for over six months of the year. The annual *Ruppia* (Form E) completes its life cycle in the short wet period, while the robust perennial, *Ruppia* (Form P), similar to that found in the deeper areas of Little Dip Lake was found growing on the permanent wet interface between a sterile and a *Ruppia* pool (Plates 5.3 and 5.6).

The progression from the pool area to the terrestrial vegetation is shown in Plate 5.4. The *Juncus-Samolus-Suaeda* Association (VII) surrounding the sterile pools gives way to a *Suaeda-Wilsonia-Sarcocornia* Association (VIII) with a lower growth form and with *Suaeda australis* as the visual dominant. Adjacent to this is the low *Wilsonia-Sarcocornia* Association (IX, Plate 5.4). The submerged macrophytes *Ruppia* (Form E), *Lepilaena cylindrocarpa* and *Lamprothamnium papulosum* are found in the underlayers of this association: Plate 5.8 shows *Lepilaena* in the

water below the emergent species *Wilsonia backhousei* and *Sarcocornia quinqueflora*; Plate 5.9 shows a charophyte-filled pool that occurs in Association IX in the wet season.

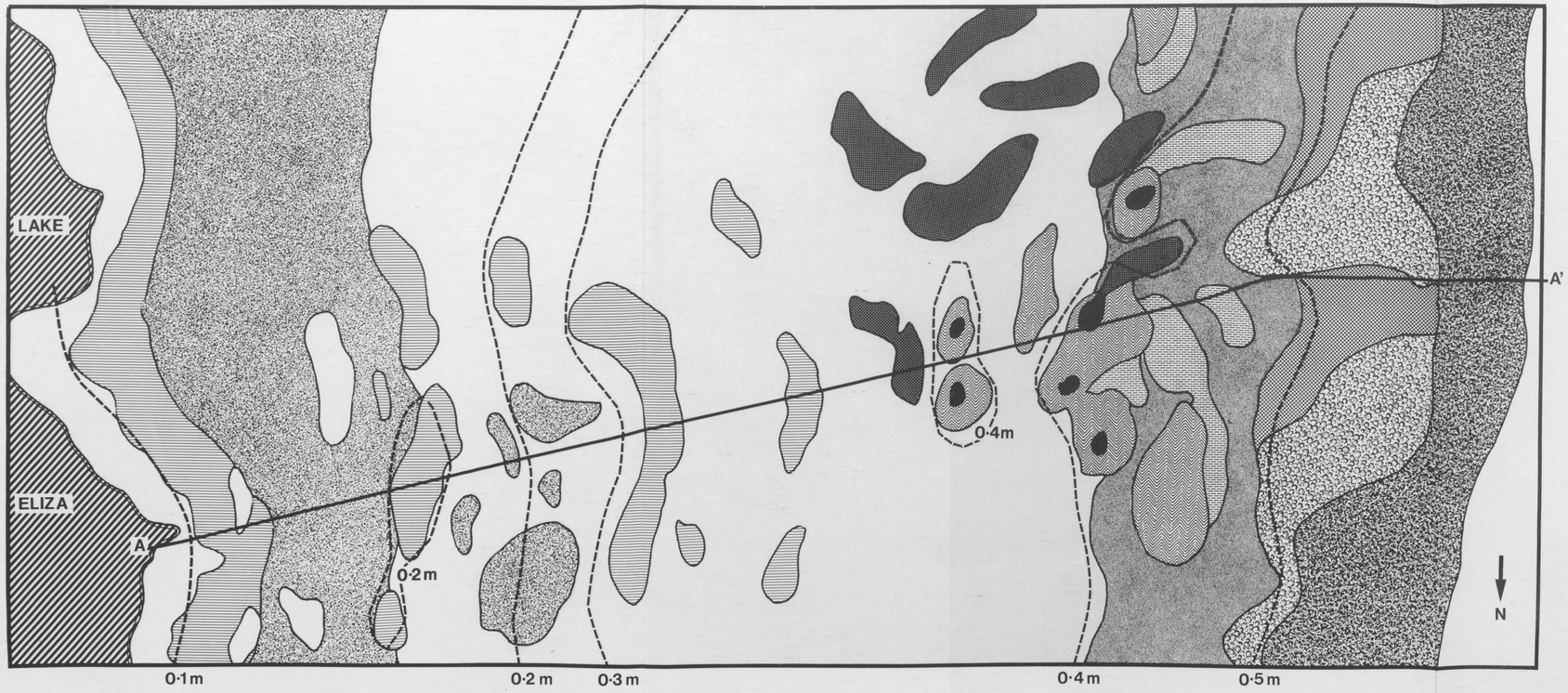
Associations X, XI and XII are located on slightly higher ground inland from Association IX (Plate 5.10). The lush *Samolus-Selliera-Suaeda* Association (X) gives way to the *Melaleuca-Samolus* Association (XI) with the *Selliera-Gahnia* Association (XII) on the higher areas. Figure 5.13 shows the relative positions of the associations.

The vegetation map, superimposed on a morphometric map of the salt marsh (Figure 5.13), incorporates survey data collected in April 1976 and vegetation data collected for associations from 1975 to 1978. The precision of mapping is high in the area 30 metres either side of the survey line, but decreases with distance from this transect where data have been interpolated from field observations.

The profile diagram (included in Figure 5.13) gives an indication of vegetation change with height above the lake level. A rise of up to 0.5 m above the lake level (a.l.l.) occurs over the 500 metre transect. All twelve associations are seasonally inundated with water and are considered as part of the eulittoral area of the Lake Eliza basin.

Plant associations tend to follow the height contours. The only associations occurring below 0.1 m a.l.l. are the Lake Eliza Association (I) and the *Sarcocornia-Arthrocnemum* Association (II). Association II with its annual herbaceous understorey occurs in a band between 0.1 m and 0.2 m a.l.l. and in isolated patches to an elevation of 0.25 m. The occurrence of Association IV is also related to height. The *Suaeda australis* which distinguishes IV from Associations II and III tends to occur in areas higher than the surrounding *Arthrocnemum* and *Sarcocornia* based associations. It occurs in a narrow band 0.1 and 0.2 m a.l.l. near the lake shore, and in patches between 0.2 and 0.4 m a.l.l. The limited occurrence of this association on elevated mounds

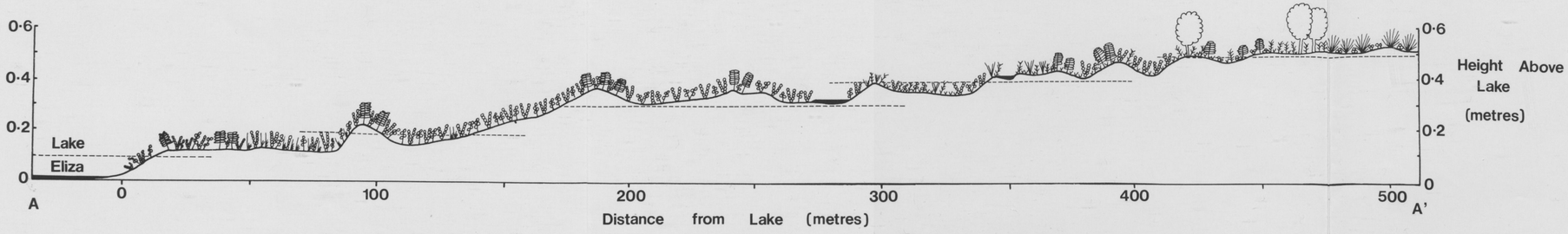
Figure 5.13 The Lake Eliza Salt Marsh: a map of vegetation associations and height contours and a profile diagram of height and vegetation changes with distance from the lake shore.
Erratum in key - for *Puccinella* read *Puccinellia*.



ASSOCIATION

- I Lake Eliza
- II Arthrocnemum – Sarcocornia – Puccinella
- III Sarcocornia – Arthrocnemum
- IV Sarcocornia – Suaeda
- V Sterile Pool
- VI Ruppia Pool
- VII Juncus – Samolus – Suaeda
- VIII Suaeda – Wilsonia – Sarcocornia
- IX Wilsonia – Sarcocornia
- X Samolus – Selliera – Suaeda
- XI Melaleuca – Samolus
- XII Gahnia – Selliera

- Sarcocornia quinqueflora
- Arthrocnemum sp
- Puccinella stricta
- Suaeda australis
- Juncus kraussii
- Selliera radicans
- Samolus repens
- Wilsonia backhousei
- Gahnia trifida
- Melaleuca halmaturorum
- Pool or Lake



can be seen by comparison of the areas on the vegetation map with the profile diagram.

The distribution of permanent sterile pools (V) and the ephemeral *Ruppia* pools (VI) with respect to elevation and the surrounding associations is noteworthy as the permanent pools occur at levels above those of the ephemeral pools. The permanent pools are generally located above the 0.4 m contour and occur in the centre of localized mounds covered with the *Juncus-Samolus-Selliera* Association (VII) that occurs between 0.35 and 0.45 m a.l.l. *Ruppia* pools (VI) are more widespread, occurring between 0.3 and 0.5 m a.l.l. surrounded by the *Sarcocornia* based *Arthrocnemum-Sarcocornia* (III) and *Wilsonia-Sarcocornia* (IX) associations.

The *Suaeda-Wilsonia-Sarcocornia* Association (VIII) and *Wilsonia-Sarcocornia* Association (IX) located between 0.4 and 0.5 m a.l.l. are also approximately distributed in relation to elevation; Association VIII (with *Suaeda australis*) occurs on the mounds, and Association IX in the hollows. The *Samolus-Selliera-Suaeda* Association (X) is restricted to areas between 0.45 and 0.5 m a.l.l. with the *Melaleuca-Samolus* (XI) and *Gahnia-Selliera* (XII) associations occupying areas above 0.5 m a.l.l.

A summary of the data generated by examination of quadrats for species frequency is presented for September 1975 (Table 5.9). Data for spring, rather than autumn, are graphed as they show species association during the growing season, and thus include the annuals.

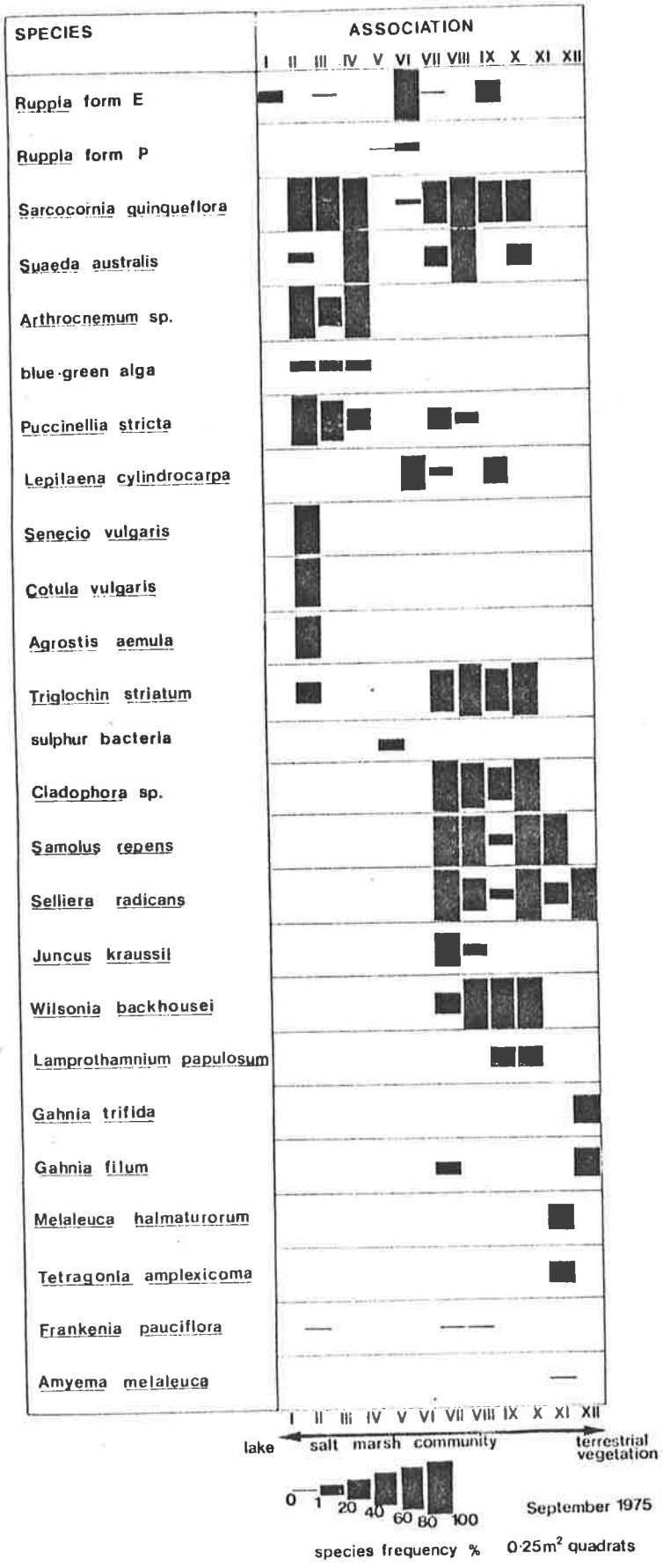
These data substantiate the associations and groupings outlined in the initial descriptions and mapping. However it should be noted that visual dominants, by which associations were characterized, are not always the frequency dominants. The comparative importance of species with small growth form is apparent from these data.

As shown in Table 5.9 some species are unique to particular associations, while others generally occur throughout the community

Table 5.9

LAKE ELIZA SALT MARSH

SPECIES FREQUENCY IN PLANT ASSOCIATIONS



with different species frequencies in the various associations. The common occurrence of species in particular groupings of associations indicates that associations can also be grouped. Among the twelve associations, two such groups related in a general way to height above the lake level are distinguished: Associations II, III and IV form one natural group and Associations VII, VIII, IX and X form another. The Lake Eliza littoral zone (I) and the *Ruppia* pools (VI) have *Ruppia* Form E in common, but the *Ruppia* pool is distinguished by the presence of *Lepilaena* and localized patches of the perennial *Ruppia* Form P and *Sarcocornia*. Associations XI and XII both have terrestrial species together with a reduced number of salt marsh species. The sterile pool (V) is unique in its lack of flora, except for sulphur bacteria and *Ruppia* Form P on the edge of one pool.

The first grouping, Associations II, III and IV, have *Sarcocornia quinqueflora*, *Arthrocnemum* sp., *Puccinellia stricta* and blue-green algae as common elements (Table 5.9). *Sarcocornia* has an 80-100% presence score in all three associations, while *Arthrocnemum* has 80-100% frequency in II and IV and 60-80% in III. Blue-green algae occur with a frequency of less than 20% on mud surfaces devoid of other vegetation. *Arthrocnemum* and blue-green algae do not occur elsewhere on the marsh. *Puccinellia* has a frequency of 100% in Association II where it is the visually dominant species of the annual herbaceous layer. Lower frequencies are recorded for Associations III and IV. The annual herbaceous understorey of Association II comprises species unique to this association; *Cotula vulgaris*, *Senecio vulgaris* and *Agrostis aemula* are recorded with high frequencies in the growing season. *Triglochin striatum* is also common in II, but is absent in III and IV. *Suaeda australis* occurs occasionally in Association II, but is a co-dominant (with 100% frequency) with *Sarcocornia* and *Arthrocnemum* in Association IV.

The second grouping of associations (VII, VIII, IX and X) have six species in common (Table 5.9). Only one of these, *Sarcocornia quinqueflora*, occurs throughout the previous group. *Triglochin striatum* has frequencies between 75 and 100% for all four associations. *Cladophora* sp. occurs only in this grouping; it has frequencies of 80%-100% in Associations VII, VIII and X, and 60%-80% in Association IX, but it did not generally form dense mats (*cf.* Little Dip Lake). *Wilsonia backhousei* occurs in 40% of quadrats in Association VII and has 100% frequency in Associations VIII, IX and X. This species forms the basis of the understorey of these three associations yet it does not occur outside this grouping of associations. *Samolus repens* and *Selliera radicans* occur similarly in the four associations. Both have frequencies of 100% in Associations VII and X and 20% in Association IX. *Samolus* has a 100% frequency in Association VIII where *Selliera* occurs in 60% of quadrats.

Suaeda australis occurs in Associations VII, VIII and X but not in IX. It is a dominant with 100% frequency in Association VIII and has 20%-40% occurrence in the other two associations. *Ruppia* Form E and *Lepilaena cylindrocarpa* occur as occasional submerged aquatics in the wet underlayers of Association VII. Both of these species and *Lamprothamnium papulosum* are found in similar habitats in 40%-60% of the quadrats of Association IX. The charophyte also occurs in Association X but not elsewhere on the marsh. *Juncus kraussii* is found with *Gahnia filum* in Association VII and also occurs with low frequency in Association VIII. The grass *Puccinellia stricta*, which was a dominant in the first grouping of associations, occurs with 20%-40% frequency in VII and VIII. *Frankenia pauciflora* was recorded infrequently.

Melaleuca halmaturorum, *Tetragonia amplexicoma* and *Amyema melaleucae* are unique to Association XI where they occur with *Samolus repens* and *Selliera radicans*. Association XII alone contains *Gahnia trifida* which co-exists with *Gahnia filum* and *Selliera radicans*.

Relationships of individual species vary in different associations of this large community. *Ruppia* Form E and *Lepilaena cylindrocarpa* occur as co-dominants in the *Ruppia* pools yet are occasionally recorded in the underlayers of more complex communities. *Sarcocornia quinqueflora* is the one species common to all major associations below 0.5 m a.l.l. *Suaeda australis* occurs in both groupings of associations, generally growing on higher elevations. As discussed, other species may be unique to a particular association or localized to a grouping of associations.

Spring and autumn data on species in each association are tabulated from 0.25 m^2 quadrat data (Table 5.10b and c). Trends in frequency can be extracted from this table for each association. As anticipated, a general paucity of annual species was recorded in autumn; plant parts from previous seasons contributed the few records of annuals. In autumn no *Ruppia* Form E occurred in Lake Eliza or in any association except VI; *Ruppia* Form E was germinating in the *Ruppia* pools (VI). The frequency of the perennial *Ruppia* Form P remained constant in both seasons. Algal frequencies *(Cladophora* and *Lamprothamnium)* were also reduced in April. The higher frequency of the perennial species *Triglochin striatum* in autumn in some associations, may be due to its spread into vacant niches, left by annual species.

A comparison of data in Figures 5.10a and 5.10b shows the significant effect of quadrat size in the determination of frequencies for each species. For example, a small quadrat may detect fine differences in the smaller species, whereas it may give an inadequate representation of the species with larger growth form (see Chapter 4).

The growth form and interaction of a species with other members of the same species may influence the reliability of quadrat estimates. As a measure of this, sociability of species within associations was estimated (Table 5.11a). Species such as *Ruppia* Form E, *Sarcocornia*,

Table 5.10 The effect of quadrat size and seasonality on species frequency in plant associations of the Lake Eliza Salt Marsh

a. species frequency in 0.1 sq m quadrats in spring (Sept 1975)
b. species frequency in 0.25 sq m quadrats in spring (Sept 1975)
c. species frequency in 0.25 sq m quadrats in autumn (April 1976)

Frequency class	% quadrats
1	0 - 20
2	20 - 40
3	40 - 60
4	60 - 80
5	80 -100

Species \ Association	a. Sept 1975 0.1 sq m quadrat											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Ruppia Form E	1		5			5			1			
Ruppia Form P						1						
Sarcocornia quinqueflora		3	5	3		1	2	5	2	3		
Suaeda australis				1			1	2		2		
Arthrocnemum sp.		4	1	3								
Blue-green alga												
Puccinellia stricta		1	1	1			1					
Lepilaena cylindrocarpa												
Senecio vulgaris		2										
Cotula vulgaris		3										
Agrostis aemula		3										
Triglochin striatum		1					2	5	2	4		
Sulphur bacteria					1							
Cladophora sp.												
Samolus repens							4	3		3	4	
Selliera radicans							2	2		5	1	4
Juncus kraussii							2					
Wilsonia backhousei							2	5	5	4		
Lamprothamnium papulosum									4	2		
Gahnia filum												
G. trifida												2
Melaleuca halmaturorum											4	

Species \ Association	b. Sept 1975 0.25 sq m quadrats											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Ruppia Form E	2		1			5	1		3			
Ruppia Form P						1						
Sarcocornia quinqueflora		5	5	5		1	4	5	4	4		
Suaeda australis		2		5			2	5		2		
Arthrocnemum sp.		5	3	5								
Blue-green alga		1	1	1								
Puccinellia stricta		5	4	2			2	1				
Lepilaena cylindrocarpa						4	1		3			
Senecio vulgaris		5										
Cotula vulgaris		5										
Agrostis aemula		4										
Triglochin striatum		2					4	5	4	5		
Sulphur bacteria					1							
Cladophora sp.							5	4	3	5		
Samolus repens							5	5	1	5	5	
Selliera radicans							5	3	1	5	2	5
Juncus kraussii							3	1				
Wilsonia backhousei							2	5	5	5		
Lamprothamnium papulosum									2	2		
Gahnia filum							1					1
G. trifida												3
Melaleuca halmaturorum											4	

Species \ Association	c. April 1976 0.25 sq m quadrats											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Ruppia Form E						3						
Ruppia Form P						1						
Sarcocornia quinqueflora		5	5	4			5	5	4	2		
Suaeda australis		1		4				4	4	1		
Arthrocnemum sp.		4	4	4								
Blue-green alga		1		1								
Puccinellia stricta		3		2				3				
Lepilaena cylindrocarpa												
Senecio vulgaris												
Cotula vulgaris												
Agrostis aemula												
Triglochin striatum							5	5		5		
Sulphur bacteria												
Cladophora sp.						2	2	4	5	3		
Samolus repens							5	4		5	5	
Selliera radicans							5	3		5		5
Juncus kraussii							2	1				
Wilsonia backhousei							3	5	5	5		
Lamprothamnium papulosum									1			
Gahnia filum							1					1
G. trifida											3	3
Melaleuca halmaturorum												

Table 5.11 Cover and sociability estimates for species in plant associations of the Lake Eliza Salt Marsh

a. Sociability
b. Cover

Sociability Class
1 occurs singly
2 tufts
3 patches
4 extensive patches - carpets
5 crowded, pure stands

% Cover Class
+ <1
1 1-5
2 6-25
3 26-50
4 51-75
5 76-100

Species	a. Sociability												b. Cover											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Ruppia Form E	3		2			4					3		2		1			3			1			
Ruppia Form P						3												1						
Sarcocornia quinqueflora		3	4	3		1	3	3	2	2				3	4	4		1	2	2	3	2		
Suaeda australis				1			1	2		2						2			2	3		2		
Arthrocnemum sp.		2	2	1										3	3	2								
Blue-green alga			4	1											2	3								
Puccinellia stricta		2	2	2			1	1						1	1	2			+	1				
Lepilaena cylindrocarpa						4	2		3									1	1		1			
Senecio vulgaris		2												1										
Cotula vulgaris		1												1										
Agrostis aemula		1												1										
Triglochin striatum		1					1	1	1	1				1					1	1	1	1		
Sulphur bacteria					5												1							
Cladophora sp																								
Samolus repens							4	3	1	4	5								3	2	+	4	5	
Selliera radicans							4	3	5	5		3							3	2	5	5		3
Juncus kraussii							2												2					
Wilsonia backhousei							2	4	5	3									1	4	4	2		
Lamprothamnium papulosum									3	2											1	1		
Gahnia filum								2				2							1					
G. trifida												2												3
Melaleuca halmaturorum											4												5	

blue-green algae, *Lepilaena*, *Samolus* and *Wilsonia* have different sociability ratings in different associations. They may occur singly or in tufts where they are not dominant, or may form carpets or pure stands. The quadrat sampling methods employed were not designed to detect such differences.

Cover estimates, made by visual estimation of the percentage of a quadrat occupied by any one species, are presented in Table 5.11b. The total cover for one association often totals more than 100% because species overlap one another. Cover gives an indication of the density of the association and reflects the growth forms. It may also be related to sociability for some small species which have their highest cover percentages when they are in pure stands or carpets, e.g. *Samolus repens*, *Wilsonia backhousei*.

Biomass data are summarized in Table 5.12. As a limited number of samples was taken, the reliability of these estimates is low (see Chapter 4). However, comparison of biomass from particular associations can be made and the distribution of plant matter between species within associations can be examined. Figures for dry weight g/m^2 and percentage of total dry weight are presented for above ground parts sampled in September 1975 and April 1976. Some general trends were detected. The smallest mean total dry weight (g/m^2) was obtained for the monospecific stand of *Ruppia* (Association VI); the considerable drop in biomass from September (499 g/m^2) to April (32 g/m^2) reflected the ephemeral nature of the pool and its vegetation. *Ruppia* was germinating in this pool in April 1976 soon after it had been inundated by rainwater.

In September 1975 the total biomass per square metre was slightly less in associations near the shore than in landward associations. In general, the order of magnitude of biomass estimates for associations was Association VI<II<III=VII<IX (samples in Associations I-V were not taken in April 1976, so season confirmation of this trend cannot be made).

Table 5.12 Biomass of plant associations - breakdown into species for spring (September) and autumn (April) presented as dry weight (DW g/m^2 105°C) and percentage in each association

Association	September 1975												April 1976					
	II		III		VI		VII		IX		IX		VI		VII		IX		X	
Species									without roots		with roots									
	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%	DW g/m^2	%
Ruppia Form E					499.0	100.0							32.4	100.0						
Sarcocornia quinqueflora	139.2	18.9	20.8	2.6			17.6	2.2	99.2	12.2	128.0	6.8			467.5	37.4	46.5	7.0	52.1	8.8
Suaeda australis							128.0	15.7							119.3	9.5	7.2	1.0		
Arthrocnemum	409.0	55.7	709.6	86.2																
Puccinellia stricta	12.1	1.6	92.0	11.8											2.9	0.3				
Senecio vulgaris	2.5	0.3																		
Cotula vulgaris	2.0	0.3																		
Agrostis aemula	3.1	0.4																		
Triglochin striatum	27.2	3.7					4.0	0.5	0.4	0.1	12.0	0.6			14.2	1.2			11.5	0.9
Algae									8.4	1.0					4.4	0.5	19.5	3.0	1.3	0.1
Samolus repens							186.4	22.9							116.1	9.5	1.5	0.2	128.1	10.0
Selliera radicans							44.0	5.4							120.9	9.7			36.2	2.9
Juncus kraussii							66.0	7.9							163.9	13.2				
Wilsonia backhousei							193.6	23.8	702.0	86.7	1336.0	70.5			4.3	3.5	625.0	88.0	443.0	36.0
Extras, roots etc.	140.0	19.5					175.6	21.6			420.0	22.1			185.0	14.8	8.7	1.0	92.0	7.4
Total	735		822		499		814		968		1896		32.4		1238		708		1203	

In April the biomass of Association VII was greater than that of IX or X and it was also greater than the September value for Association VII. This may be attributed mainly to the values for *Sarcocornia* which were 2.2% of the total in September and 37% in April; the 1975-76 growth had not occurred by September but probably contributed to the April measurement. Association IX had a smaller biomass in April, perhaps attributed to a general decrease in all species. The higher biomass of Association X may reflect a general increase in biomass of species at higher elevations.

If data for samples with and without roots are compared for Association IX (see Table 5.12) the contribution of below ground material can be estimated. Approximately 50% of the material harvested was below the surface. 52% of *Wilsonia backhousei* and 77% of *Sarcocornia quinqueflora* are above the marsh surface.

Table 5.13 gives the breakdown of biomass for Associations VII, IX and X. Wet weights, dry weights (g/m^2), dry weight:wet weight (%) and dry weight:total weight (%) are presented for each association. Dry weight of roots, unidentifiable material and dead parts and the percentages of these are also included. Table 5.14 presents similar data itemized for individual species for a sample of two associations. If this sampling programme was to be continued, indices of above ground: below ground parts and dry weight:wet weight could be used to make estimates more accurate.

Transplantation and recolonization trials were set up in September 1975 and April 1976 when biomass was harvested. The harvested plots were observed at intervals of four months. Material from within a 0.25 m^2 quadrat harvested from Association VII was transplanted into a sterile pool as a trial to investigate the paucity of vegetation in this habitat. Results are summarized in Tables 5.15 and 5.16.

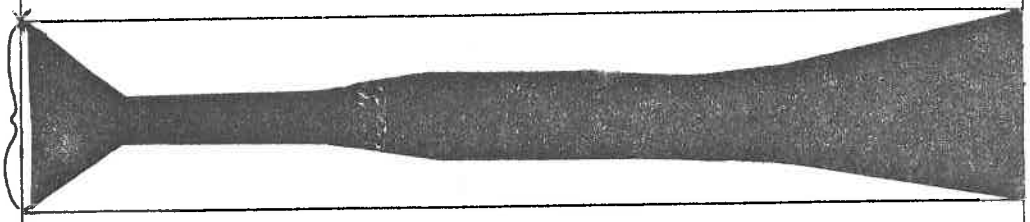
Table 5.13 The relationship of dry weight of plant parts (g/m^2 105^{o}C) to wet weight of plant parts in associations (VII, IX, X) in April 1976

	Wet Wt. g/m^2	Dry Wt. g/m^2	% Dry Wt./ Wet Wt.	Dry Wt. Roots+ Extras g/m^2	Roots + Extras/ Dry Wt. %	Dead Material g.	Dead/ Total Dry Wt. %
Association VII	4140	1238	30.0	177	14.0	202	16.0
Association IX	3108	698	22.6	12	1.7	not separated	not separated
Association X	4913	1203	24.4	128	10.6	121.	13.4

Table 5.14 The relationship of dry weight (DW g/m^2 105°C) to wet weight (WW g/m^2) for individual species in two associations (VII and IX).

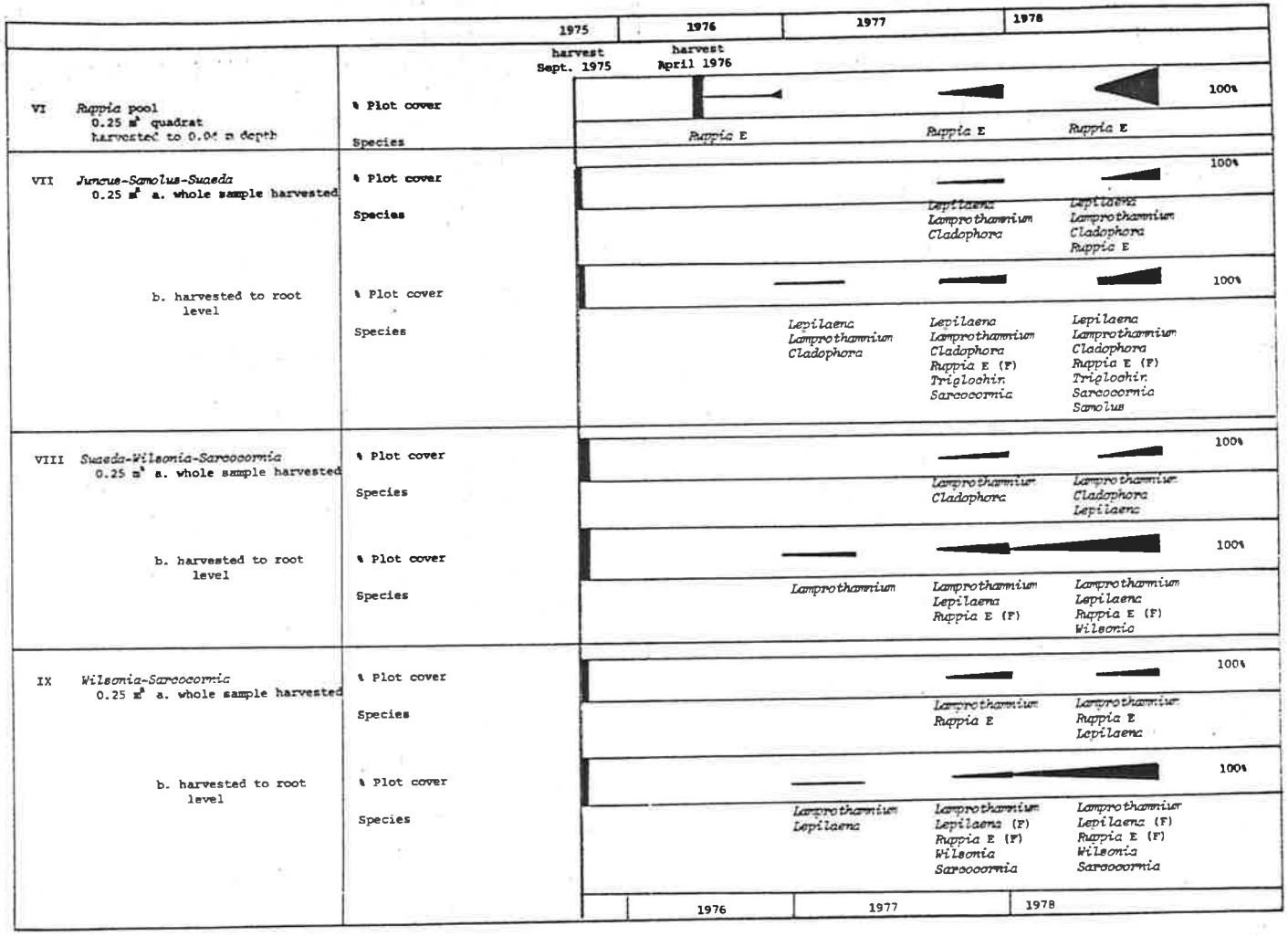
April 1976 Species		VII *Juncus-Samolus-Suaeda*					IX *Wilsonia-Sarcocornia*			
		WW g/m^2	DW g/m^2	DW/T %	DW/WW %	Dead %	WW g/m^2	DW g/m^2	DW/T %	DW/WW %
Sarcocornia quinqueflora	live	1317.0	336.7	26.9	25.5	27.9	146.8	46.5	7	32
	dead	262.0	130.0	10.5	50.0					
Suaeda australis		510.0	119.3	9.5	15.7		20.7	7.1	1	35
Puccinellia stricta		6.1	2.9	0.3	47.0					
Triglochin striatum		84.2	14.4	1.2	17.1					
Lamprothamnium Cladophora		16.9	4.4	0.5	26.0		109.0	19.6	3	18
Samolus repens	live	185.0	87.3	7.0	47.0	25.4	2.6	1.4	0.2	55
	dead	55.1	29.8	2.5						
Selliera radicans	live	570.0	89.7	7.2	15.7					
	dead	128.3	31.2	2.5						
Juncus kraussii		253.2	1.6	13.2	64.4	25.8				
Wilsonia backhousei		203.4	43.0	3.5	21.0		277.5	625.0	88	23
Extras		549.0	185.0	14.8	33.5		26.5	8.7	1	33
Total		4140	1238		30		3080	708		23

Table 5.15 Regrowth of plants in a quadrat following transplantation from Association VII (*Juncus-Samolus-Suaeda*) into a sterile pool (Association V).

September Transplant 1975	1976	1977	1978
Quadrat Regrowth 100%			
	edges decline → growth increase	edges stabilized	→ regrowth
Species condition: Growth increase	no species	*Triglochin* *Samolus*	*Triglochin* *Samolus* *Sarcocornia*	*Samolus* (F) *Triglochin* (F) *Sarcocornia*
Growth stable	*Triglochin* *Samolus*	*Sarcocornia*	*Wilsonia*	*Wilsonia* *Suaeda* *Juncus*
Growth decrease	*Sarcocornia* *Cladophora* *Ruppia* *Lepilaena* *Suaeda* *Juncus* *Wilsonia*	*Cladophora* *Ruppia* *Lepilaena* *Suaeda* *Juncus* *Wilsonia*	*Cladophora* *Ruppia* *Lepilaena* *Juncus*	*Cladophora* *Ruppia* *Lepilaena*

F - flowering

Table 5.16 Regeneration and recolonization of vegetation in cleared quadrats from plant associations of the Lake Eliza Salt Marsh community



F - flowering

Growth of some of the transplanted vegetation resumed within twelve months and *Samolus* and *Triglochin* became the dominant species. These species flowered in the third year after transplant (Plate 5.3, Figure 5.15). The underlayers of *Ruppia*, *Lepilaena* and *Lamprothamnium* gradually declined; *Sarcocornia*, *Suaeda*, *Juncus* and *Wilsonia* did not show growth until the third year. This evidence suggests that plant growth is possible in the sterile pools. This micro-environment may be inhibitory to colonization by aquatic species and may not be conducive to plant propagation from seed or perennating organs even though vegetative growth, once established, can be maintained. Alternatively the regrowth of the transplant may have been dependent on the transfer of an island of sediments with the plants. The vegetative spread of *Ruppia* Form P along the interface between sterile and *Ruppia* pools also suggests that this environment is amenable to colonization. The reason why the plants of the association bordering the pools (VII) do not encroach these pools needs further investigation.

Recolonization following harvesting was slower in the plots harvested completely than in those harvested to root level only (Table 5.15). Aquatic submerged species were usually the colonizers. *Lamprothamnium*, normally absent from Association VII, was one of the colonizing species in this association: this species may play a role in primary succession on the marsh. Regeneration from root and rhizome mats began two wet seasons after harvesting. Thus regeneration after damage, although slow, seems possible.

CHAPTER 6. DISCUSSION OF SYNECOLOGICAL RESULTS

The presence or absence of hydrophyte species in the study habitats was influenced by fluctuations in salinity as well as by water level and maximum salinity: other environmental parameters had a greater effect on plant distribution within each ecosystem than on plant occurrence. The ephemeral or permanent nature of each habitat, which is determined by water level fluctuations and lake-basin morphometry, had a major effect on the species of hydrophytes present.

The occurrence of submerged macrophytes in relation to salinity and the ephemerality of the aquatic habitats is summarized in Figure 6.1. In brackish, saline and hypersaline waters the diversity of submerged macrophytes was low: above a salinity of 4 °/oo TDS only two genera of angiosperms, *Ruppia* and *Lepilaena*, were present and the algae were limited to *Lamprothamnium*, *Enteromorpha* and *Cladophora* and in one ecosystem *Acetabularia*. Only *Ruppia*, *Lepilaena* and *Lamprothamnium* tolerated ranges of salinity from less than 4 °/oo TDS to over 60 °/oo TDS, and only *Ruppia* grew actively in waters over 100 °/oo TDS. *Ruppia* was recorded in waters up to 230 °/oo TDS in another salt pan in the south-east of South Australia, although at this salinity the plants were obviously under physiological stress.

All but one of these taxa are halophytic members of mainly freshwater plant groups. The occurrence of the marine *Acetabularia peniculus* suggests that plants of both marine and freshwater origin can occur in these salt lake ecosystems.

In general a greater species diversity was found for emergent macrophytes than for submerged macrophytes; reeds of various species occurred around both fresh and saline permanent lakes, and a variety of species formed emergent salt marsh communities on the edges of ephemeral salt pans and on the shallow beach areas of permanent saline lakes.

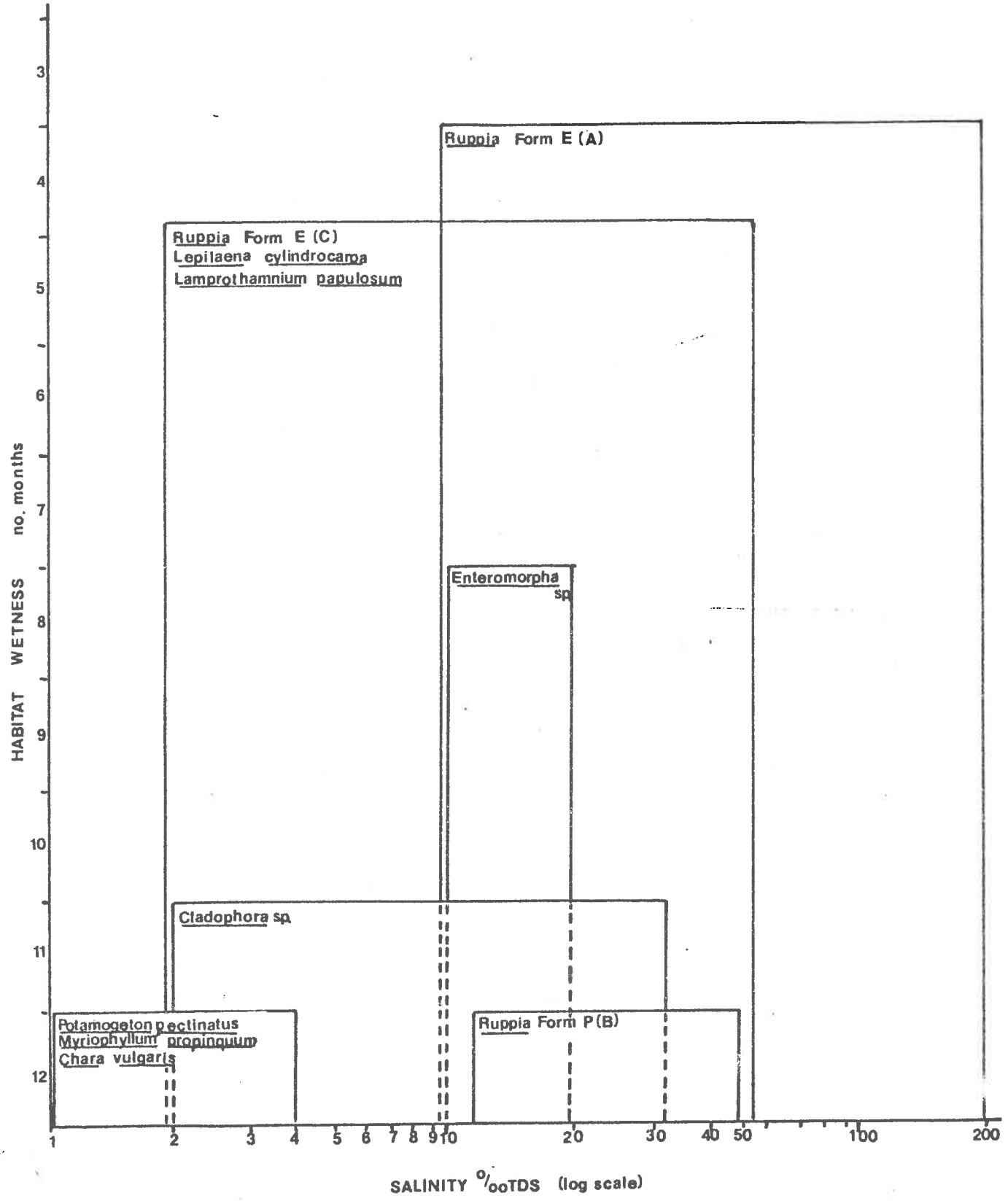


Figure 6.1 Occurrence of submerged macrophytes in relation to salinity and the ephemerality of habitats.

The submerged plant communities of permanent aquatic ecosystems are less variable than those of ephemeral lakes and eulittoral zones as the environmental conditions are more constant and perennial species can establish themselves. As submerged species must recolonize ephemeral habitats in each wet phase species with annual life cycles are favoured. *Ruppia, Lepilaena* and *Lamprothamnium* were the only submerged macrophytes which exhibited annual life cycles and could thus occur in ephemeral salt pans or the eulittoral zones of permanent lakes.

Aquatic angiosperms can withstand the dry and desiccating conditions of ephemeral habitats as dormant seeds: *Ruppia* and *Lepilaena* both produce prolific numbers of seeds which lie dormant on the salt crust over summer. Most vegetative parts of plants cannot withstand desiccation in these harsh environments. However, in Australian ephemeral ecosystems, *Ruppia* often produces swollen turions at the junction of leaf bases and rhizomes. These perennating organs become detached from the parent-plant, remain viable in the salt crust during the dry phase and germinate when the lakes refill. This contrasts with reports of the behaviour of members of this genus in ephemeral habitats in Europe where propagation is solely from seed as no vegetative parts survive drying (Verhoeven 1979). The structure and function of the perennating organs of *Ruppia* are considered in Chapter 9. The charophyte *Lamprothamnium papulosum* survives desiccation by forming resistant oospores which remain in the salt and mud crust until suitable conditions for germination occur.

The present submerged and emergent vegetation found in the lakes studied may reflect previous water regimes within the lakes. Information about the environmental conditions under which sediments were deposited is provided by the analysis of lake sediments (Table 5.5). Deposition of sediments of the ephemeral lakes of the Coorong and some

of the hypersaline Robe-Beachport lakes took place under highly saline conditions indicating a long history of hypersaline conditions. However, Flax Point on the Coorong (now hypersaline) and most of the permanent sites of the Robe-Beachport series have sediments which were deposited under brackish to saline conditions. The least saline lake, Fresh Dip Lake, was probably saline at some stage. The saline Little Dip Lake may have had a fresh water phase in its history as evidenced by shells of freshwater species of ostracods found in the sediments (de Deckker pers. comm. 1979). These changes possibly were caused by movements of the water table which altered the relative position of fresh and saline aquifers with respect to the lake basins.

Water table levels have direct or indirect effects on the water regimes of the saline permanent Little Dip Lake, the fresh permanent Fresh Dip Lake and the hypersaline Lake Eliza and its peripheral salt marsh. When surveyed in November 1977 all three ecosystems were within 0.5 m altitude of each other and all were within 0.5 m altitude of the sea level. Fresh Dip Lake is fed by rain which percolates through the surrounding dunes and it probably also fills by seepage from a freshwater lens entering on the south western dune shore. Lake Eliza is just below sea level at most times of the year and the ground water table meets the marsh surface in permanent pools which appear to be spring fed. Large areas of the marsh are stabilized by vegetation or covered by an impermeable layer that forms the Lake Eliza salt pan. However even when the surface is cracked and dry in summer, the underlying sediments are fluid indicating that the water table is not far below the marsh surface.

Comparisons of the vegetation associations of fresh and saline permanent lakes, and of permanent and temporary lakes can be made by consideration of the Fresh Dip Lake, Little Dip Lake and Lake Eliza

Salt Marsh ecosystems. Many of the submerged and emergent species are common to the various permanent and temporary aquatic habitats even though they occur in different associations.

The least saline lake, Fresh Dip Lake, has a greater diversity of both submerged and emergent plants than the permanent saline Little Dip Lake. The basins of both lakes are covered by beds of charophytes: the fresh lake has a dense low bed of *Chara vulgaris* and *Lamprothamnium papulosum* whereas the saline lake has a less dense cover of *L. papulosum* alone. Similarly there are more angiosperm species in the fresh lake than in the saline lake. *Myriophyllum propinquum* and *Potamogeton pectinatus* are the dominant fresh-lake-submerged angiosperms with isolated patches of *Ruppia* sp. and *Lepilaena* sp. *Ruppia* is locally dominant along the dune face. Five species of reeds (*Lepidosperma canescens, L. longitudinale, Machaerina juncea, Gahnia trifida* and *Scirpus nodosus*) comprise the emergent aquatic plant association which typically gives way to stands of the terrestrial *Leptospermum pubescens* followed by a *Eucalyptus diversifolia* association. In contrast, the saline Little Dip Lake is bordered by only two emergent reeds, *Juncus kraussii* and *Gahnia filum*, and only one species of submerged angiosperm, a perennial form of *Ruppia* (Form P), occurs in the permanent areas of the lake.

On the south eastern shore of Little Dip Lake, a shallow beach area forms an extensive eulittoral zone in which three submerged aquatic species, *Ruppia* (Form E), *Lepilaena cylindrocarpa* and *Lamprothamnium papulosum* grow annually. All complete their life cycles in the few months in which their habitats are wet. Higher up the beach a narrow band of emergent salt marsh species gives way to the *Melaleuca halmaturorum* association which typically surrounds saline aquatic ecosystems in the area. The salt marsh species in general order of dominance with distance from the permanent water

include *Arthrocnemum* sp., *Sarcocornia quinqueflora*, *Wilsonia backhousei*, *Samolus repens* and *Selliera radicans*. These salt marsh species also occur in the salt marsh community adjacent to Lake Eliza.

In general, the salt marsh community of Lake Eliza typifies Australian salt marsh communities: the primary zonation based on *Arthrocnemum* and *Sarcocornia* is common to coastal and inland salt lakes as well as to mangroves and desert salt pans. The complex of species associations delineated on this marsh provides further evidence to suggest that the species present occur in different species combinations and frequencies in response to both the general environmental conditions and to specific micro-environmental factors, in this case height above the water table.

The complexity of this emergent salt marsh community, which has twelve plant associations, contrasts with the relatively simple association of species in the other aquatic ecosystems studied. Within this community the diversity of species in each emergent plant association increased with elevation (a rise of 0.5 m over a distance of 500 m). The species occurrence of submerged and emergent species with height and distance from the lake shore is summarized in Figure 6.2. Submerged aquatic species *Ruppia*, *Lepilaena* and *Lamprothamnium* occurred in pools on the marsh or in the seasonally wet understorey of emergent associations. Most emergent and submerged species occurred in more than one association, in each case in different frequencies and associated with different species. The ubiquitous *Sarcocornia quinqueflora* was a member of eight associations. *Suaeda australis*, *Arthrocnemum* sp., *Triglochin striatum*, *Wilsonia backhousei*, *Puccinellia stricta*, *Selliera radicans* and *Samolus repens* all occurred in several associations and were common to similar salt marsh areas in the region (*cf.* Little Dip Lake) and elsewhere in Australia (Wood 1937; Clarke and Hannon 1967).

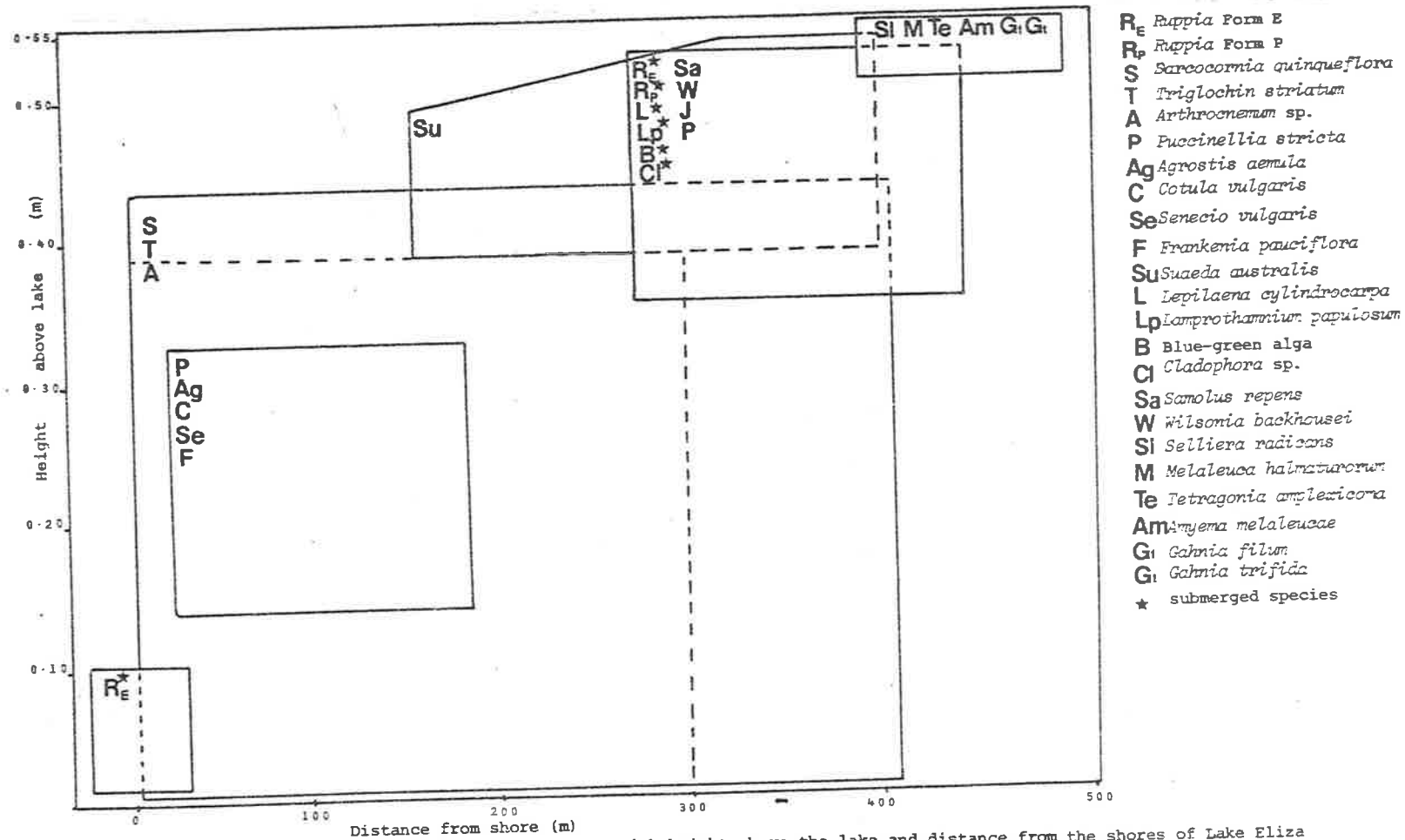


Figure 6.2 Generalized diagram of species occurrence with height above the lake and distance from the shores of Lake Eliza

Previous work on Australian coastal saline marsh communities has been confined to the southern coastal areas as these habitats are replaced by mangroves elsewhere (Chapman 1974). Studies of the salt marsh communities behind the coastal mangroves are provided by Sauer (1965) and Clarke and Hannon (1967, 1969, 1971). Where the mangroves (*Avicennia marina* (Forst.) Vierh) are not in pure stands they may be intermingled with *Arthrocnemum*. A zonation through *Sarcocornia*, *Suaeda australis*, *Triglochin striatum* and *Samolus repens* to *Sporobolus virginicus* (L.) Kunth followed by *Juncus maritimus* Lamk. var *australiensis* Buch. and *Baumea juncea* (R. Br.) Palla forms behind the frontal mangrove zone (Clarke and Hannon 1967).

Many of these genera are also present around inland salt lakes and desert salt pans. The pioneer stages of the salt marsh zonation with *Arthrocnemum* and *Sarcocornia* are similar in most Australian marsh ecosystems but the later stages of zonation differ with the type of ecosystem and the geographic area. In South Australian arid ecosystems *Sporobolus virginicus*, *Juncus maritimus* var *australiensis* (= J. kraussi and *Cyperus vaginatus* R.Br. form the later stages of zonation with *Atriplex paludosa* R.Br. dominating the final community. In less saline, more humid, areas *Melaleuca halmaturorum* and *Wilsonia backhousei* may be the primary colonists followed by a *Suaeda*, *Sarcocornia* and *Samolus* association and then *Sporobolus* and *Selliera radicans* (Wood 1937; Chapman 1974). In Victorian salt marsh communities the primary zonation of *Arthrocnemum* is usually succeeded by bare ground, or *Mesembryanthemum australe* Ait. or *Frankenia pauciflora* which leads to *Melaleuca ericifolia* Smith scrubland and finally *Eucalyptus viminalis* Labill. woodland (Chapman 1974).

Species of many of these genera occur in European (Lee 1977) and American (Ungar 1974) salt marshes. *Triglochin*, *Puccinellia*, *Distichlis*, *Suaeda* and *Salicornia* (Australian material has only recently been placed in the closely related *Sarcocornia*) are

cosmopolitan members of most salt marsh communities. A comparison of most saline ecosystems throughout the world shows that estuaries, inland permanent salt lakes, ephemeral salt pans, inland salt marshes, coastal mangrove communities and some desert saline areas all have fluctuating environments and high water salinities, and they have similarities in species composition and productivity.

Lakes with water salinities between 2 and 6 °/oo TDS often contain species which cannot tolerate water salinities above 10 °/oo TDS. *Potamogeton pectinatus*, *Ruppia maritima* and *Chara* spp. are reported in such lakes in the United States of America (Ungar 1974) and show a remarkable similarity to the species composition of the Australian Fresh Dip Lake. In the American studies *Potamogeton pectinatus* is reported to withstand salinities of 13 °/oo TDS.

Marine sea grasses often occur in estuarine areas, but the halophyte *Ruppia* is usually the dominant species in these fluctuating environments. *Ruppia* has been reported in Australian estuarine areas by Congdon (1977) and Congdon and McComb (1979a) in the Blackwood River Estuary of Western Australia and by Higginson (1967) in the Tuggerah Lakes system in New South Wales.

Ruppia also occurs as the dominant species in permanent inland salt lakes in America (Wetzel 1964; Ungar 1974), Europe (Verhoeven 1979) and England (Lee 1977) irrespective of whether lakes are evaporation pans or associated with salt deposits or marine incursions. In most lakes of high salinity *Ruppia* is the only submerged angiosperm present (e.g. Borax Lake, Wetzel 1964). Ungar (1974) reports that it can tolerate salinities up to 74 °/oo TDS.

Standing crop estimates from the study sites and from saline ecosystems elsewhere allow comparisons of plant productivity in a variety of habitats. In this study standing crop was estimated by measurement of the above-ground parts from a dense area of each plant association in November 1977 (g/m^2 dry weight 105°C). As the total

area sampled was small in each case, only general comparisons can be made. Standing crop estimates of 410, 213 and 11.7 g/m^2 were obtained respectively from a perennial *Ruppia* (Form P) bed in Little Dip Lake (0.6 m) and annual *Ruppia* (Form E) beds in Fresh Dip Lake (0.6 m) and the eulittoral zone of Little Dip Lake (0.1 m). The maximum value of 213 g/m^2 for the annual *Ruppia* in Fresh Dip Lake is half the maximum value of 410 g/m^2 for the perennial growing at a similar depth in the saline Little Dip Lake, yet it is twenty times greater than the maximum value of 11.7 g/m^2 for the annual from the shallow eulittoral zone of the same saline lake. In Little Dip Lake the standing crop of the annual is only 3% of that of the perennial. Crop density measurements in *Ruppia* associations in permanent and temporary habitats in other salt lakes and salt marsh communities gave estimates between 3 and 500 g/m^2 dry weight. These values are low when compared to the standing crop estimates for the emergent salt marsh associations: these estimates ranged from 32 g/m^2 (dry season) to 499 g/m^2 for a *Ruppia* pool association to nearly 2000 g/m^2 in more complex associations of emergent salt marsh species. Further analyses of the differences in biomass of annual and perennial populations of *Ruppia* are reported in Chapter 9.

These estimates fall within the ranges for similar plant associations elsewhere. Westlake (1975) reports biomass yields in a freshwater lake: species such as *Chara* or *Myriophyllum* have crop densities of from 400 to 700 g/m^2 dry weight and the emergent reed species from 3000 to 10,000 g/m^2. Submerged marine associations have crop densities between 3,000 and 6,000 g/m^2 (Westlake 1975).

Ruppia is the only cosmopolitan genus which shows a wide tolerance of salinity and habitat variability. Biomass estimates for *Ruppia* in an estuary in Western Australia ranged seasonally from 8 to 503 g/m^2 (Congdon and McComb 1979a). In brackish and inland shallow habitats in Europe, Verhoeven (1978) recorded biomass ranging

from 8.5 g/m^2 in winter to 132 g/m^2 in summer for *Ruppia cirrhosa*.

The occurrence of submerged macrophytes on the salt marsh and in permanent and temporary lakes can be contrasted. On the Lake Eliza Salt Marsh the annual *Ruppia* Form E occurred both in monospecific stands and with patches of *Lepilaena cylindrocarpa* in ephemeral pools and in the lake proper. These species and *Lamprothamnium papulosum* also occurred in the ephemerally wet understorey of several emergent plant associations on the salt marsh. The perennial *Ruppia* Form P was present at the edge of a permanent spring-fed pool. *Ruppia* Form E, *Lepilaena* and *Lamprothamnium* were observed to act as colonizing species in areas which had been cleared or damaged. These submerged species covered such areas within 12-18 months of disturbance and emergent species tended to regrow in the areas after this pioneer colonization. Similarly these species recolonized the eulittoral zone of Little Dip Lake annually. The presence of *Ruppia*, *Lepilaena* and *Lamprothamnium* in fresh and saline permanent lakes and in ephemeral salt lake eulittoral zones, salt marsh pools and underlayers of salt marsh associations is indicative of the wide range of environmental conditions that these species can tolerate. The distinct annual and perennial forms of *Ruppia* (Form E and Form P respectively) are related to the temporary or permanent wetness of the habitats in Little Dip Lake and Lake Eliza Salt Marsh. In Fresh Dip Lake the *Ruppia* acted as an annual even though its habitat was permanently aquatic and its leaf widths were wider than annual *Ruppia* plants from saline locations. The growth form, life cycle type, salinity range, type of ecosystem and species associations for *Ruppia* from the study sites are summarized in Table 6.1 and are considered further in Section 3.

Table 6.1 Summary of the occurrence of the submerged angiosperm *Ruppia* in the study sites: type of ecosystem, salinity, life cycle type, growth form and species association.

Type of Ecosystem	Salinity Category	Locality	Life Cycle type	Growth Form	Association
Aquatic					
1. Permanent	Fresh slightly brackish (2-5°/oo TDS)	Fresh Dip Lake	Annual	Large	monospecific patches surrounded by *Potamogeton pectinatus*
	Brackish (5-20°/ooTDS)	Erringtons Hole	Perennial	Large robust	monospecific association
	Saline (20-40°/oo TDS)	Little Dip Lake	*Annual	Small delicate	co-dominant with *Lepilaena* sp.
		Little Dip Lake	Perennial	Large robust	monospecific patches surrounded by *Lamprothamnium*
	Hypersaline (>40°/oo TDS)	Flax Point	*Annual	Small delicate	monospecific association
		Lake Robe	*Annual	Small delicate	co-dominant with *Lepilaena* sp.
		Beachport Salt Lake	*Annual	Small delicate	monospecific association
2. Temporary	Brackish	Blue-Green Algal Pool	Annual	Small delicate	co-dominant with *Lepilaena* sp.
	Saline	Mikes Lake	Annual	Small delicate	co-dominant with *Lepilaena* sp.
	Hypersaline	Pipeclay Lake	Annual	Small delicate	co-dominant with *Lepilaena* sp.
		Brineshrimp Lake	Annual	Small delicate	co-dominant with *Lepilaena* sp.
Semi-Aquatic					
1. Permanent	Saline	Lake Eliza Salt Marsh permanent pool	Perennial	Large robust	submerged at edge of pool bordered by *Samolus-Suaeda* association
2. Temporary	Saline	Lake Eliza Salt Marsh ephemeral pool	Annual	Small delicate	monospecific association in pools, occasional in underlayers of *Wilsonia-Sarcocornia*, *Sarcocornia-Suaeda* and *Samolus-Suaeda* associations

* edges ephemeral with seasonal water level changes

SECTION III

AUTECOLOGICAL STUDY OF THE GENUS *RUPPIA*

CHAPTER 7. OBJECTIVES

The general ecological character of the halophyte communities occupying permanent and temporary habitats in a range of saline ecosystems is described in Section 2. The evidence presented suggests that the wide variability of environmental factors, such as salinity, water depth and its permanence, limits the distribution and diversity of plant communities: once water salinity exceeds 4°/oo TDS the macrophytes are restricted to two genera of angiosperms, *Ruppia* and *Lepilaena*, and a few species of algae. It is of interest now to explore the nature of adaptations evolved by plants in response to their uncertain environments, and for this purpose the angiosperm *Ruppia* is selected as the focus of the studies in Section 3.

Ruppia inhabits virtually the entire range of environments considered in the synecological study. Over this range it is represented by two forms which are distinctive in growth form, life history and habitat. An annual growth form (Form E), typically small and delicate, occurs most commonly in temporary (but occasionally in permanent) waters 0.1 - 0.4 m deep with salinities up to 180°/oo TDS. A perennial growth form (Form P), typically large (to 2.5 m) and robust, occurs only in permanent waters. It has been recorded in water up to 3 m deep with salinities between 3 and 45°/oo TDS. *Ruppia* is present continuously whether actively growing or dormant: the plant persists in permanent waters whereas it withstands drought as seeds or perennating organs in temporary habitats.

The two forms of *Ruppia* were investigated from both taxonomic and ecological standpoints to determine whether differences in form were due to species differences, or to wide phenotypic variation which may be expressed under conditions of fluctuation and stress.

A review was made of the taxonomic history and nomenclatural status of the genus *Ruppia* both in Australia and elsewhere. Local material was then examined to determine whether one, two, or more species were represented. Field data, including observations of distribution, habitat and morphology of individuals and populations, and laboratory data, including data on cytology, anatomy, physiology and palynology, were used to select suitable taxonomic criteria.

Ecological investigations were made independently: comparative studies of the reproductive biology, life history and of physiological requirements and tolerances were made to elucidate the apparent distinctions between the two forms in relation to their habitats.

CHAPTER 8. SYSTEMATIC STUDIES

8.1 Previous studies

1. Taxa of *Ruppia*

The genus *Ruppia* in the monogeneric family Ruppiaceae was previously included in the Potamogetonaceae (Hutchinson 1959; Takhtajan 1967). The Potamogetonaceae, *sensu lato*, has been divided into five or six families: Potamogetonaceae, Posidoniaceae, Zosteraceae, Ruppiaceae, Zannichelliaceae and sometimes Cymodoceaceae (Engler and Gilg, 1964) However, not all authors accept this division and similarities in the floral morphology of *Ruppia* and *Potamogeton*, reported by Gamerro (1968) and Posluszny and Sattler (1974a), have led to further re-examination of relationships within the larger context of the Alismatales (Helobiae). Evolutionary trends within the group have been postulated using evidence from floral development (Uhl 1947; Singh 1964, 1965; Posluszny and Sattler 1973, 1974a, b; Posluszny and Tomlinson 1977). A close relationship between *Potamogeton* and *Ruppia* was suggested by Davis and Tomlinson (1974) who described perennating organs and sessile fruiting carpels of an Australian species of *Ruppia*, *R. tuberosa* Davis and Tomlinson; these structures parallel the perennating organs and sessile fruit of many species of *Potamogeton*. Problems of interpreting such similarities as indicative of evolutionary relationships within the group of families, or as examples of convergence, are outside the scope of this study.

In spite of uncertainties at familial and specific levels, *Ruppia* is clearly distinguished by its characteristic flowers and fruits. Vegetatively it may be confused with the aquatic monocotyledon *Potamogeton pectinatus* and with species of *Lepilaena* of the families Potamogetonaceae and Zannichelliaceae respectively. *Ruppia* often grows in association with these in Australia.

Ruppia is cosmopolitan in distribution, with records from Africa (Obermeyer 1966), North and South America (Fernald and Wiegand 1914; Gamerro 1968), Asia (Miki 1935), Europe (Reese 1962; den Hartog 1971), New Zealand (Mason 1967) and Australia (Aston 1973; Davis and Tomlinson 1974).

Ruppia is a submerged, rooted, aquatic monocotyledon found in fresh to hypersaline water of depth 0.1 to over 3 m. Long filiform or narrow linear sessile leaves with basal sheaths without ligules are borne alternately from nodes on the rhizome or elevated stems; leaves and stems branch alternately in the same plane. Basal sheaths, with two small auricles above, broaden below to enclose developing inflorescences until peduncles elongate and elevate the flowers for pollination, either at the surface or in the water body. The inflorescence is a terminal spike of two bisexual flowers borne one above the other on opposite sides of the peduncle. Each sessile flower consists of two anthers, one above and one below the 2-19 free carpels; no perianth is present. Anthers contain two bilocular thecae which dehisce longitudinally at anthesis. Each carpel has one pendulous ovule and a sessile peltate stigma; the carpel base, sessile at first, may elongate during fruiting to form a long stalk or podogyne. Drupaceous fruits, usually with podogynes, develop on peduncles before falling from the plant; decay of the exocarp leaves a hardened, often sculptured, endocarp with an operculum marked by weaker tissue at one end. Figures 8.1 - 8.3 illustrate these generic characters together with specific variations. A glossary of terms used to describe the morphological characters of this genus is presented in Appendix V.

Opinions on the number of species of *Ruppia* present in countries from which it has been described fall into two general groups:

those which consider *Ruppia* to have one widely distributed and variable species, *R. maritima* L., with variation at a varietal or sub-specific level (Ascherson and Graebner 1907; Fernald and Wiegand 1914; McCann 1945; Phillips 1958; van Ooststroom and Reichgelt 1964; Mayer 1969); and those which distinguish at least two species (Hagström 1911; Setchell 1924, 1946; Luther 1947; Reese 1962; Mason 1967; den Hartog 1971). Separation of species generally has been based on peduncle length and structure after anthesis. In Europe two species are described, *R. maritima* with short straight peduncles, and *R. cirrhosa* (Petagna) Grande, with long spiralling peduncles. *R. cirrhosa* replaces the incorrect, later name *Ruppia spiralis* L. ex Dum. (see Gamerro 1968). Setchell (1924, 1946) found the two European forms to be constant and intersterile and Reese (1962, 1963) also supported the distinction on morphological and cytological grounds. He found that for *R. maritima* 2n = 20, and for *R. cirrhosa* (syn. *R. spiralis*) 2n = 40. Den Hartog (1971) re-examined the two species and considered them separate, at least in the Netherlands.

Additional species of more localized distribution have been described from other continents. Those considered to be good species by den Hartog (1971), from literature examination, included *R. occidentalis* Watson from north-western U.S.A. and Canada (Watson 1890), *R. truncatifolia* Miki from Japan (Miki 1935), and *R. megacarpa* Mason and *R. polycarpa* Mason from New Zealand (Mason 1967).

Australian material has previously been referred to *Ruppia maritima* or *Ruppia cirrhosa* (incorrectly designated *R. spiralis*). Thompson (1961) recognized both species while Aston (1973), recognizing the variability and world-wide taxonomic uncertainty within the genus, placed all material under the oldest name *R. maritima* pending revision of the genus. The spirally coiled peduncles of most Australian material (Sutton 1919; Thompson 1961; Eichler 1965;

Aston 1973) key it to *R. cirrhosa* (syn. *R. spiralis*) rather than *R. maritima* in the British Flora(Clapham, Tutin and Warburg 1962). However, such keys, designed for use elsewhere are inadequate for identification of Australian species as demonstrated by the fact that in other important characters Australian material differs from *R. cirrhosa* (syn. *R. spiralis*).

An Australian species, *Ruppia tuberosa* Davis & Tomlinson, was described from a hypersaline habitat in Western Australia (Davis and Tomlinson 1974). It was distinguished on the basis of two morphological characters not described for other species; the occurrence of individually sessile fruiting carpels and the development of swollen shoots forming overwintering buds. Lucas and Womersley (1971) and Aston (1973) have described similar perennating organs in specimens from south eastern Australia. Jessop (1978) suggested that some South Australian material may be *R. tuberosa*. Unfortunately Davis and Tomlinson (1974) have described *R. tuberosa* from a narrow range of localities. A full examination of its life cycle and distribution is necessary to establish its distribution and variability.

The only other species described from the Australasian region are from New Zealand, namely *R. polycarpa* and *R. megacarpa*, separated by Mason (1967) on morphological, cytological and ecological grounds. Their occurrence in Australia has not been considered prior to this study.

2. Taxonomic criteria

Wide variation in the size and growth form of the leaves, stems, flowers and fruit occurs in the genus *Ruppia*. Species have been defined by a variety of characters including leaf width, leaf apex, peduncle length, carpel number and shape and size of fruit and podogynes. Characters which are not subject to wide genetic variability or environmental modification, and thus remain constant

throughout the range of the taxon, are the most useful taxonomically (Davis and Heywood 1963). The environmental constancy of characters is particularly important in a genus such as *Ruppia* where morphological variation is associated with fluctuating environments. Morphological forms which are characteristic of a species are not always easily separated from responses to environmental gradients (Bradshaw 1965; Heywood 1968).

The difficulties of species definition within *Ruppia* have arisen because characters useful in one geographic area do not separate species adequately in other parts of the distribution range; fruit size and shape, distinguishing features of the New Zealand *R. polycarpa* and *R. megacarpa* (Mason 1967) have been reported to be affected by salinity in other species (Mayer 1969). Similarly, the shape of the leaf apices, considered useful to distinguish *R. cirrhosa* and *R. maritima* (Reese 1962), is affected by age and by treatment of material in some areas (Mason 1967; den Hartog 1971).

If variation in the structure or behaviour of an organism falls into discrete classes which cannot logically be subdivided further, it is a valid basis for taxonomic separation (Sokal and Sneath 1963). In practice, bimodal distributions of character states may also be useful. A combination of characters related to the morphology and anatomy of the plant is probably most useful for separating material from one area. However, such a combination of characters may not apply in other areas, and may be difficult to apply retrospectively to descriptions from the literature and to herbarium specimens in which the appropriate vegetative and reproductive characters are absent or inadequately preserved. Thus characters used at species or generic levels must be critically evaluated if taxa are to be soundly circumscribed. Characteristics of the habit, vegetative and reproductive parts and chromosome number have been used by various authors in the

classification of *Ruppia*.

Plant form and height is determined by leaf length, stem elevation into the water and by branching patterns. Leaf length accounts for plant height in forms in which stems do not elongate and in which leaves arise from nodes on the rhizome. In New Zealand, the species that maintains a creeping rhizomatous habit (*R. polycarpa*) has longer leaves than the species with lengthened stems (*R. megacarpa*). When stems raise nodes into the water the stems contribute to the height. Prolific branching, with leaves crowded distally on branches, and the production of shoots and roots from elevated nodes, are associated with the taller *R. megacarpa* (Mason 1967).

Asexual reproduction by lateral growth of rhizomes is a characteristic of the genus; the modification of the rhizome and leaf bases as perennating organs has not been reported for *Ruppia* outside Australia.

Species have been separated by leaf width in Europe (den Hartog 1971) and in New Zealand (Mason 1967). Leaf cross-sectional dimensions recorded as width:breadth ratios by Mason (1967) have been used as taxonomic characters.

The size and shape of the two lacunae found on either side of the vascular bundle, and the number of parenchyma cells between the lacunae and epidermis also were considered distinctive characteristics by Hagström (1911) and Mason (1967). Mason (1967) and Ogden (1974) stated that the number of lacunae varies along the stem, but that leaves are more constant in having two lacunae on either side of the central vascular bundle. Den Hartog (1971) doubted the reliability of using differences in epidermal cell width as he found no clear distinction between size classes. The shape of leaf apices was used to differentiate species in German (Reese 1962), New Zealand

(Mason 1967) and Dutch (den Hartog 1971) material. This character can be used only for young and undamaged material. Leaf colour and leaf sheath swelling, used by some authors, are only useful for fresh material.

Reproductive characters are often stated as less subject to environmental influence than vegetative ones. Small changes in reproductive organs may cause infertility or incompatibility within a group, whereas vegetative changes, irrespective of their advantages, are unlikely to result in reproductive isolation. Floral and fruit characteristics are the most frequently used taxonomic characters in *Ruppia*.

In Europe *R. maritima* has been distinguished from *R. cirrhosa* by the length and degree of coiling of the peduncle (Reese 1962; den Hartog 1971). These features are related to the pollination mechanisms of the two species. *R. maritima* with consistently short straight peduncles is fertilized under water. *R. cirrhosa*, with long spiralling peduncles, is fertilized at the surface. The spiralling was postulated to provide a means of adaptation to variable water depth (den Hartog 1971). Similar long spiralling peduncles are characteristic of most Australian and New Zealand forms. Mason (1967) found that a peduncular swelling at the inflorescence base is specific for *R. polycarpa* in New Zealand.

Anthers are 'french roll' and 'kidney' shaped in the European *R. maritima* and *R. cirrhosa* respectively (Reese 1962; Schwanitz 1967). Mature anthers must be examined to record this character state (den Hartog 1971). Differences in pollen shape have been interpreted by Schwanitz (1967) as developmental rather than taxonomic.

There are generally four carpels per flower in European material. Rare variants with two to ten carpels were recorded by Roze (1894). New Zealand species can be separated by carpel number: *R. megacarpa* has four, with variation from two to six: *R. polycarpa*

usually has more than eight but ranges from two to sixteen (Mason 1967). Fallen or aborted carpels must be taken into account if this character is recorded from fruiting material.

Fruit size was used to separate species in New Zealand (Mason 1967). Fernald and Wiegand (1914) also used fruit size and shape as distinguishing characters in American material. Mayer (1969) accounted for size differences by endocarp thickness and indicated that this was influenced by salinity. His evidence, however, only accounts for the small differences found between varieties of *R. maritima* in North America. Differences in the shape of fruit are attributed to the degree of swelling of the fruit by den Hartog (1971). The length of the stylar beak relative to fruit length and shape of the perforation, or window on each side of the endocarp, have been used to separate species in New Zealand (Mason 1967). Den Hartog (1971) also considered perforation shape to separate species in the Netherlands. The ratio of podogyne length to peduncle length was used by Reese (1962) to separate *R. cirrhosa* from *R. maritima*. However, den Hartog (1971) rejected podogyne length because of its variability. The shape of podogyne attachment to the fruit is distinctive in New Zealand species (Mason 1967). The lack of a podogyne distinguishes the Western Australian species *R. tuberosa* (Davis and Tomlinson 1974); sessile or subsessile fruits have not been recorded outside Australia.

Different chromosome numbers are reported and provide a further basis for species distinction. The cytotaxonomic study of *Ruppia* by Reese (1962) indicated that European *R. maritima* has 2n = 20 and *R. cirrhosa* 2n = 40. New Zealand material is not polyploid, but chromosome numbers differ: *R. polycarpa* 2n = 18 and *R. megacarpa* 2n = 20 (J.B. Hair cited in Mason 1967).

In summary, *Ruppia* species cannot be distinguished reliably on the basis of one or a few morphological characters. Fruiting,

flowering and vegetative characters together with chromosome number and information on the life cycle, environmental tolerances and distribution are needed to delimit taxa. It is essential to examine material from all life cycle stages. Consequently, herbarium collections often do not provide sufficient information for determination of the species: the material described in this thesis is based on field collections over several growing season from 1975 - 1978, supplemented by examination of specimens in The State Herbarium of South Australia.

8.2 *Ruppia* in the south-east of South Australia

1. Introduction

Three taxa of *Ruppia* occur in the saline ecosystems in the south-east of South Australia. Two of these taxa (A and C) generally grow in ephemeral habitats and have annual life cycles: the growth form of these taxa has been designated Form E in Section 2. The other taxon (B) grows in permanent habitats and has a perennial life cycle: this growth form is referred to as Form P in Section 2. Descriptions of these three taxa follow: Taxon A is described from the ephemeral habitat in the eulittoral zone of Little Dip Lake (Figure 8.1), Taxon B from a habitat in the permanent water of Little Dip Lake (Figure 8.2), and Taxon C from an ephemeral roadside habitat, Blue-Green Algal Pool (Figure 8.3). The character states which distinguish material of the three taxa in these locations are summarized in Table 8.1.

The distribution of the taxa and the ranges of their distinguishing character states in the south-east of South Australia were determined from an examination of populations of *Ruppia* in all study sites and from populations outside the study areas. A close examination of particular characters was undertaken to establish the reliability of using these characters taxonomically and hence to

Figure 8.1 *Ruppia* Taxon A

a habit showing growth and flowering from rhizome (x 1)

b growth by rhizomes from perennating organs (x 3)

c turion type I (swollen rhizome) dried (x 8)

d turion type II sprouting (x 8)

e turion type I (swollen leaf base) (x 8)

f turion type I sprouting (x 8)

g turion type I dried (x 8)

h leaf apices (x 20)

i junction of leaf sheath and blade (x 8)

j germinating seed (x 8)

k mature endocarp (x 8)

l fertilized carpel (x 8)

m inflorescence with developing fruit (x 8)

n TS anther (lower) (x 8)

o TS anther (uppermost) (x 8)

p carpels with sessile peltate stigma (x 20)

q inflorescence (before anthesis) (x 8)

r inflorescence in swollen basal sheath (x 3)

s inflorescence side view (x 3)

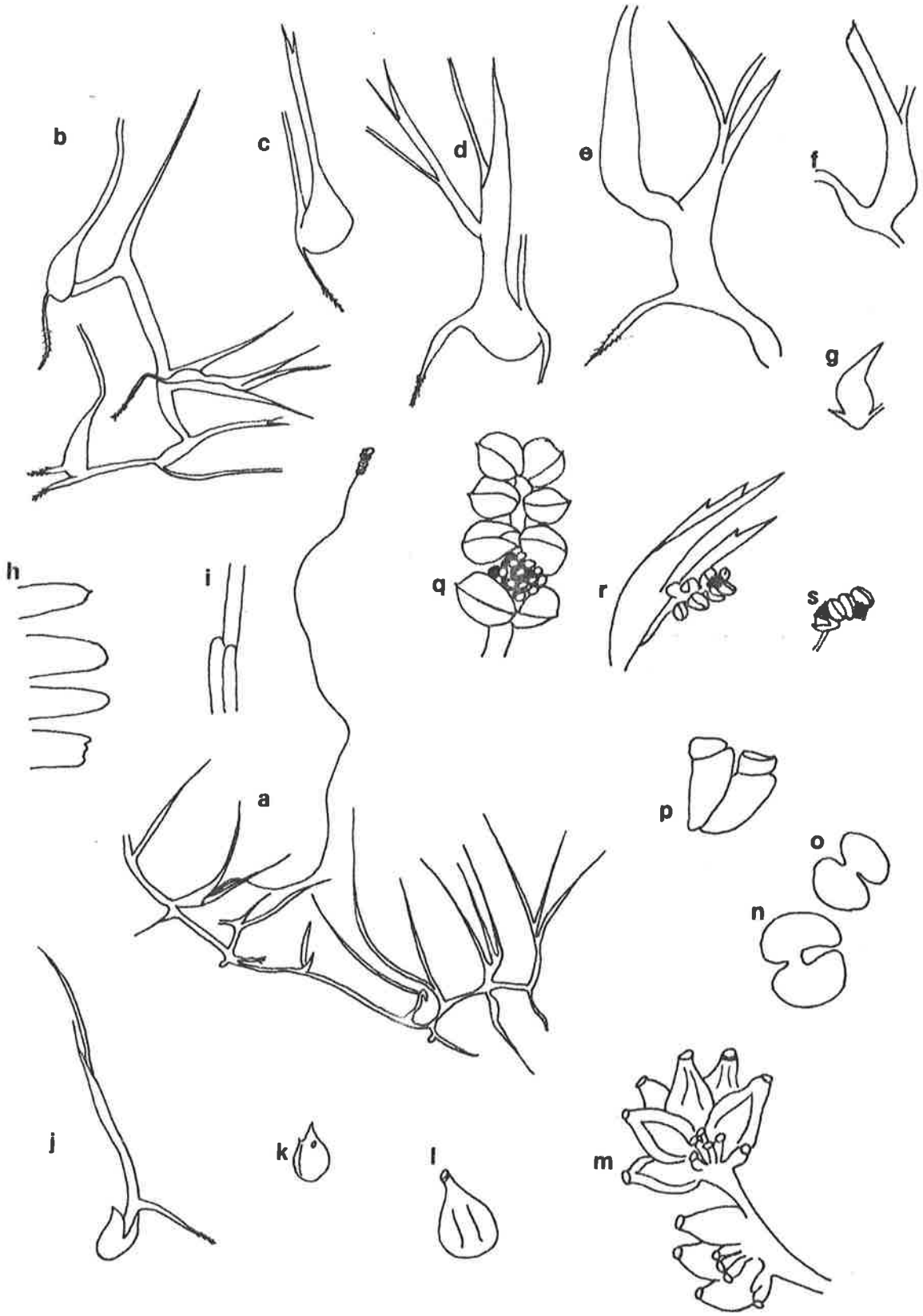

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Figure 8.2 *Ruppia* Taxon B

a habit showing branching (x 0.4)

b junction of leaf sheath and blade (flattened) (x 6.4)

c leaf apices (x 16)

d germinating seedling (x 6.4)

e mature endocarp with tapered persistent podogyne (x 6.4)

f immature fruit - exocarp with tapered persistent podogyne (x 6.4)

g TS anther (x 16)

h,i carpels with sessile peltate stigma (x 16)

j inflorescence before anthesis (x 6.4)

k upper branch with terminal inflorescence enclosed in extended sheath (x 2.5)


a
b
c
d
e
f
g
h
i
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k

Figure 8.3 *Ruppia* Taxon C

a habit showing growth from rhizome and branching (x 2/3)

b leaf apices (x 20)

c perennating organ (type I), swollen leaf base (x 8)

d immature fruit - exocarp with straight slender podogyne
endocarp visible through exocarp (x 8)

e mature fruit - endocarp with persistent straight slender podogyne (x 8)

f fruit developing in inflorescence (x 8)

g fertilized carpels after anthesis before podogyne elongation (x 8)

h inflorescence before anthesis (x 8)

i inflorescence before anthesis side view (x 3)

j carpels with sessile peltate stigma (x 20)

k inflorescence in leaf sheath (x 3)

l TS anther (uppermost) (x 20)

m TS anther (lower) (x 20)


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determine the validity of the division into species. Further evidence is provided from chromosome studies which examined the possibilities of polyploidy, hybridization and chromosome number differences. Transplantation experiments in the field and laboratory were designed to examine the viability and stability of the three taxa under differing environmental conditions (see Chapter 9). A map of the distribution of the taxa A, B and C in South Australia was compiled from field collections and data from herbarium material from The State Herbarium of South Australia (Figure 8.4).

2. Descriptions

Ruppia Taxon A (Figure 8.1)

Submerged plants in water 0.02-0.4 m depth, occur in the eulittoral zone of Little Dip Lake when wet; annual growth from seeds or perennating organs with rapid rhizomatous spread; plants individual, not clumped. Stems present as slender rhizomes; elevated stems usually lacking or, where present, branching never extensive. Leaves 20-150 mm arising from rhizomes; blades 0.18-0.5 mm wide x 0.05-0.15 mm thick, often flattened in transverse section; width:thickness ratio 3.5; apices rounded, obtuse to acute finely serrulate, occasionally truncate or bidentate in older or damaged material (Figure 8.1h); epidermal cells 19 x 14.5 x 22 µm length (longitudinal) x width (tangential) x breadth (radial); 2 circular lacunae on either side of the vascular bundle separated from the epidermis by 1 (occasionally 2) mesophyll cells approximately 50 µm in diameter. Inflorescence (Figure 8.1q,r,s) before anthesis 4.5-6 mm long x 1.8-2.5 mm broad; flowers with anthers oriented perpendicular to the inflorescence axis; peduncle elongate, elevates inflorescence to surface for pollination, usually retracted spirally in fruit; fruiting inflorescence a dense spike (Figure 8.1m) without a swelling below the lower flower. Flowers with clusters of 6-19 (usually >8) carpels.

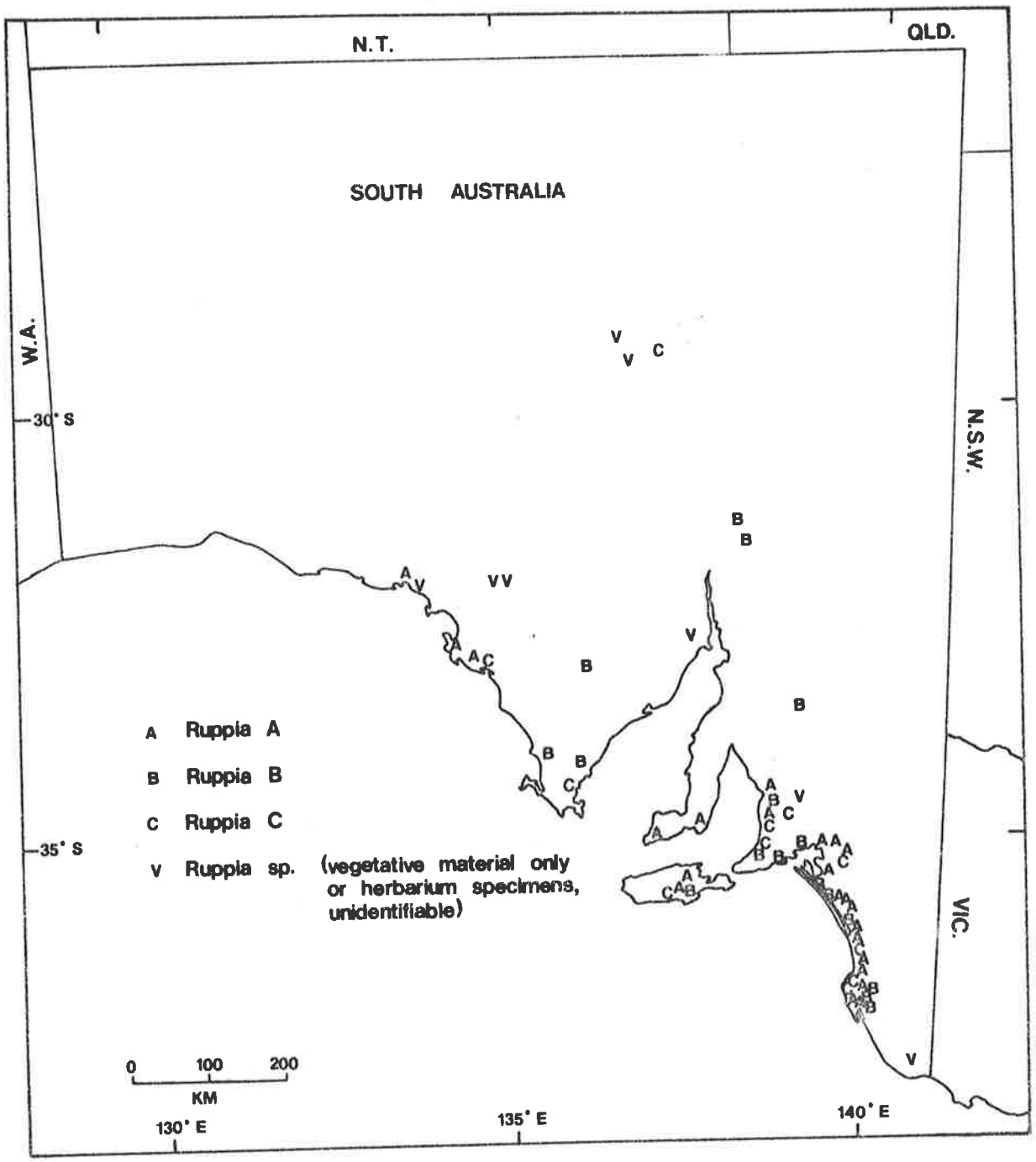

Figure 8.4 Sites of *Ruppia* collections from South Australia

Carpels sessile or subsessile in fruit (podogyne < 2 mm, not persistent after exocarp decays) (Figure 8.1 l,m, Plate 8.2). Fruit (Figure 8.1k), pyriform, nearly symmetric, 1.6 (1.3-2.3) mm length x 0.9 (0.7-1.5) mm width x 0.7 (0.6-0.9) mm breadth; l:w:b ratio 2.3:1.3:1; endocarp, sessile with very short stylar beak (<0.2 mm), longitudinal opercular ridge and an ovate perforation (window) on each side of the endocarp (Figure 8.1k, Plate 8.1). Habitat (eulittoral zone) wet midwinter to early summer (June to November or December); salinity 19-24°/oo TDS. Flowering time spring (September to November); flowers prolific. Reproduction: sexual by seeds, asexual by perennating organs and rhizomes; seeds and perennating organs dormant in the dry eulittoral zone sediments from late spring to late autumn (November - May). Occurs in mixed stands with *Lepilaena cylindrocarpa* or occasionally alone, stands often surrounded by areas of the charophyte *Lamprothamnium papulosum*.

Ruppia Taxon B (Figure 8.2)

Submerged, perennial plants often in clumps in water of 0.5-2.5 m depth in Little Dip Lake. Stems elevated and branched up to 2 m long or as strong, lateral, spreading rhizomes; elevated stems slender, sometimes zig-zag in one plane. Leaves 20-250 mm in length, arising from elevated stems or rhizomes; blades 0.4-1.0 mm wide, 0.3-0.7 mm thick, concavo-convex in transverse section, width:thickness ratio 1.5; apices bidentate or truncate, obtuse in young material Figure 8.2); epidermal cells 11.5 x 12 x 20 µm length (longitudinal) x width (tangential) x breadth (radial); 2 elliptical lacunae on either side of the vascular bundle separated from the epidermis by 2 or in places 3 mesophyll cells, 30 µm diameter. Inflorescence (Figure 8.2j,k) before anthesis 5.0-5.5 mm long x 1.5-2.0 mm broad; lower anther of the lower flower at 45° to axis, upper anther perpendicular, peduncle elongate often to >1 m,

elevating inflorescence to surface for pollination, often spirally retracted in fruit; the fruiting inflorescence umbellate due to the elongation of the individual podogyne (stalk) of each fruiting carpel; a swelling of the peduncle below the lower flower present in some material. Flowers with clusters of 2-6 usually 4, carpels. Carpels each with a base elongating in fruit to form a stout podogyne 20-40 mm long x 0.3-0.4 mm wide with the attachment to the fruit tapering to a width of 0.8 mm (Figure 8.2e,f, Plate 8.4). Fruit turbinate with a swollen base, asymmetric with a marked convex side (Plate 8.3) 3.1 (2.8-4.6) mm length (excluding stylar beak) x 2.3 (1.9-3.1) mm width x 1.8 (1.5-2.0) mm breadth; l:w:b ratio 1.7:1.3:1; podogyne persistent after the exocarp has decayed in mature and fallen fruit; endocarp with a longitudinal opercular ridge and a deltate perforation on each side of the endocarp; terminal stylar beak 0.9-17 mm long. Habitat permanently wet, salinity 19-46^{o}/oo TDS; flowering and fruiting late spring to early autumn (November - March), flowering not prolific; seeds viable (laboratory germination) but field germination has not been recorded. Reproduction mainly asexual by the spread of rhizomes in the spring growing season after a winter quiescent period; plants may produce roots and shoots from nodes on the stem. Occurs in clumps often surrounded by carpets of *Lamprothamnium papulosum* and *Cladophora* sp.

Ruppia Taxon C (Figure 8.3)

Submerged plants rooted in water 0.1-0.4 m deep in an ephemeral roadside pool (Blue-Green Algal Pool); annual growth from seed or perennating organs with horizontal rhizomatous growth and vertical extension by branching. Stems present as slender rhizomes or elevated stems from which branching initiates. Leaves 50-150 mm long from branches or rhizomes; blades 0.1-0.35 mm wide x 0.05-0.18 mm thick often flattened in transverse section; width:thickness ratio 2:1; apices rounded acute to obtuse occasionally truncate or

bidentate in older or damaged material (Figure 8.3b) epidermal cells 18 x 13 x 16 µm length (longitudinal) x width (tangential) x breadth (radial); 2 elliptical lacunae on either side of the vascular bundle separated from the epidermis by one mesophyll cell approximately 25 µm in diameter. Inflorescence (Figure 8.3h,i) before anthesis 2.4-3.7 mm long 1.4-1.7 mm broad; flowers with anthers oriented perpendicular to inflorescence axis; peduncle elongate elevating inflorescence to surface for pollination, usually retracted spirally in fruit; fruiting inflorescence umbellate with individual carpel stalks (podogynes) without a swelling below the lower flower. Flowers with clusters of 4-10 (av. 6.9) carpels. Carpels, each with a base elongating in fruit to form a slender podogyne 10-20 mm long 0.05-0.10mm wide, with a straight (non-tapered) attachment to the endocarp (Plate 8.8). Fruit pyriform slightly asymmetric 1.8 (1.5-2.4) mm length, 1.0 (0.8-1.4) mm width, 0.5 (0.3-0.7) mm breadth excluding stylar beak and podogyne; l:w:b ratio 3.9:2.1:1; endocarp surface often rough or barbed with a narrow elliptical perforation on each side; podogyne usually remains attached to endocarp; terminal stylar beak very short $<$0.2 mm (Plate 8.7, Figure 8.3d,e). Habitat (ephemeral pool) wet midwinter to early summer (June to November); salinity 9-35^{o}/oo TDS, flowering time spring (September to November); flowers prolific. Reproduction sexual by seed, asexual by perennating organs and rhizomes; seeds and perennating organs remain dormant throughout the dry season from late spring to late autumn. Occurs in pure stands or mixed stands with *Lepilaena cylindrocarpa*.

3. Methods and Data

Fifty seven characters (most of which have been considered in previous studies) were examined by the following methods. Data obtained are tabulated for each site in Appendix VI. The characters which appeared, from initial descriptions and the results generated,

Plates 8.1 to 8.8 Scanning electron micrographs of fruit of *Ruppia* showing endocarp and podogyne (fruit stalk) attachments.

Plate 8.1 *Ruppia* A endocarp, Little Dip Lake, fruit length 1.2 mm

Plate 8.2 *Ruppia* A, Little Dip Lake, showing sessile base of fruiting carpel

Plate 8.3 *Ruppia* B endocarp, Little Dip Lake, fruit length 2.4 mm

Plate 8.4 *Ruppia* B, Little Dip Lake, showing tapered stout fruit stalk attachment

Plate 8.5 *Ruppia* B endocarp, Porters Lagoon, fruit length 2.6 mm

Plate 8.6 *Ruppia* B, Porters Lagoon, showing tapered stout fruit stalk attachment similar to fruit of *Ruppia* B from Little Dip Lake (Plate 8.4)

Plate 8.8 *Ruppia* C endocarp, Blue-Green Algal Pool, fruit length 1.4 mm

Plate 8.7 *Ruppia* C, Blue-Green Algal Pool, showing slender straight attachment of fruit stalk to endocarp

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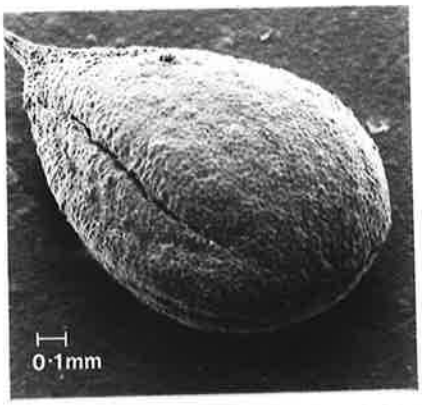

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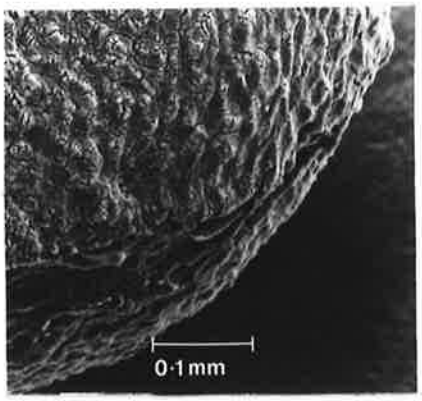

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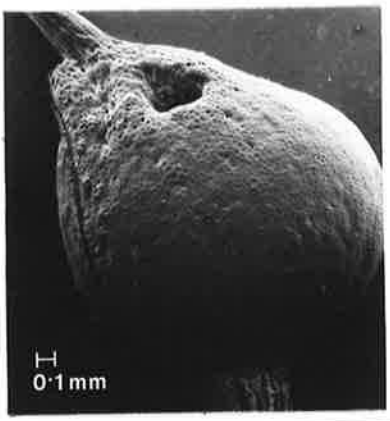

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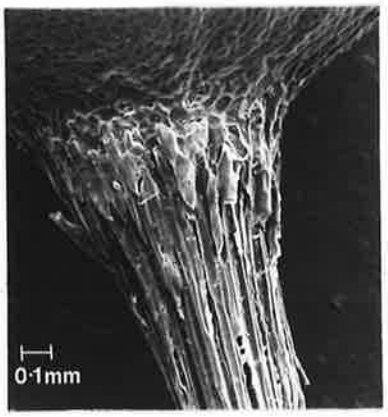

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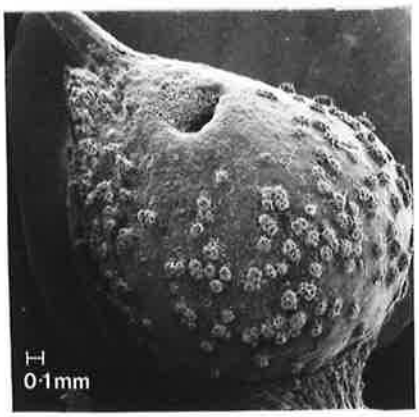

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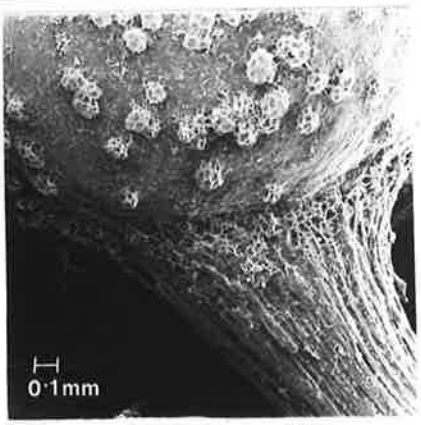

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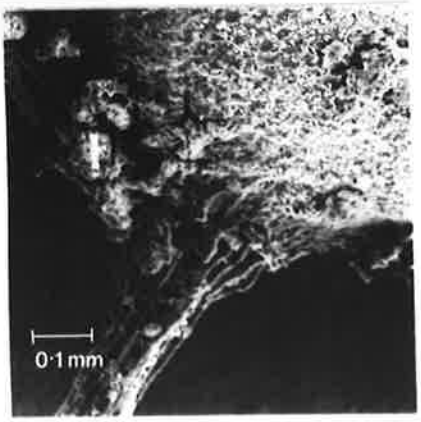

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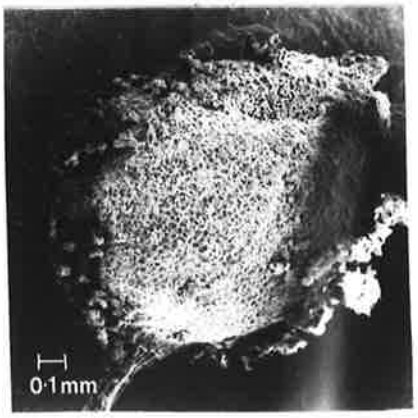

to be useful for species distinction, are examined in detail: measurements for characters examined quantitively are in Appendix VII; means, standard errors, numbers of observations and ranges are presented for each character.

Morphological measurements

Most measurements were made on fresh or formalin-fixed material. The only dried specimens examined were from The State Herbarium of South Australia and parts were rehydrated in water if measurements were necessary.

The shape of leaf apices from each site was described according to the shape diagrams of Radford *et al* (1974 p135). Several tips were examined on each of at least 10 plants per stand, of several stands within each habitat. Plants of varying age and size were scored and, where present, shoots were included. Leaf width and thickness were measured from whole leaves and transverse sections. Measurements were taken 70-100 mm from the leaf base or, where leaves were shorter, at the midpoint. Blades of varying age were examined from each of several plants in several stands within a habitat. Analysis of variance was used to examine variation in leaf width in relation to locality and plant form. Maximum leaf length was ascertained for each site from measurements within and between stands at each site.

The number of cells separating the lacunae (of stems and leaves) from the epidermal cells, the shape of the lacunae and the dimensions of epidermal cells were recorded from hand and microtome sections. Freehand sections were difficult to obtain as most leaves and stems are small and fragile. Limited success was obtained using the method of Ogden (1974) but delicate material tended to disintegrate under the pressure of the blade. An Ames microtome cryostat was used to cut frozen sections of stems and leaves.

Sections 30 µm in thickness were cut and taken up onto clean cold albumen coated slides. Sections were flattened and fixed to the slides by gentle thawing of the underside of the slide, and then stored below 0°C until staining. Individual sections were stained with aniline sulphate and haemotoxylin 1:7, rinsed carefully with water and mounted in glycerine jelly: staining and mounting were carried out under a dissecting microscope. The inability to obtain whole sections from some material may have been due to the collapse and fracturing of cells around the large lacunae during sectioning. Wax embedding might overcome this problem. Results are presented in Appendix VIII. Measurements are in micrometres and represent the mean of 10 measurements from at least two leaves or stems.

These results show that epidermal cells of Taxon B tend to be smaller and shorter than cells of Taxon A. The number of cells between the epidermis and lacunae varies within plant populations and sometimes within a plant. In general, Taxon B has 2 or 3 cells while Taxa A and C have one, occasionally two. This character is unreliable as the variation between populations of A and C overlap the ranges of B. The sizes of the lacunae are related to the diameters of the leaves.

The dimensions of the inflorescence and the number of carpels for upper and lower flowers of each inflorescence were recorded from stands at each site (Appendix VII). The inflorescence measurements vary according to the stage of development of each specimen; length measurements may be biased by elongation of the axis between the two flowers of an inflorescence after anthesis. Where possible, measurements were made on mature flowers just before anthesis. Means, ranges, standard errors and the number of observations are presented (Appendix VII). Carpel number has been analysed by analysis of variance. The shape of the thecae, the form of the peduncle, the position of flowers, and the swelling of floral sheaths and peduncles

were recorded for samples from each habitat. Time and abundance of flowering were recorded also.

Exocarp and endocarp were examined where available and if necessary the exocarp was removed to reveal the endocarp with its stylar beak and podogyne. Length (excluding beak and podogyne), width and breadth of endocarp and beak length were measured (Appendix VII). Shape, symmetry and podogyne characters of the fruiting carpels were assessed subjectively from a wide range of material. Data on fruit lengths were analysed by analysis of variance.

Features of the habit and habitat of *Ruppia* were recorded in the field and laboratory.

Differences in pollen shape and size for *Ruppia maritima* and *Ruppia spiralis* were thought to be specific by Reese (1962). Pollen examined in this study was prepared by staining with gentian violet and aniline oil (Radford *et al* 1974). Preliminary examination of size and shape of pollen from South Australian material suggested differences between the taxa A and B, and C (Appendix IXa). Pollen of Taxon A was generally elongate, dumbell shaped (Figure 8.5-1) and longer than the squat, elliptical or dumbell shapes (Figure 8.5-2, 4) of Taxon B pollen; pollen of Taxon C was elongate and boomerang-shaped at maturity (Figure 8.5-3).

Mean lengths of pollen grains were analysed for three habitats using Student's "T" test for comparison of means. Variation between habitats, between plants, and between mature and immature anthers from the same plant and anthers of the same flower were tested. Results are presented in Appendix IXb. There were significant differences in pollen grain lengths between habitats; no significant difference occurred between plants from the same habitat when pollen grains from anthers at the same stage of maturity were scored. Significant differences between mean pollen lengths of immature and

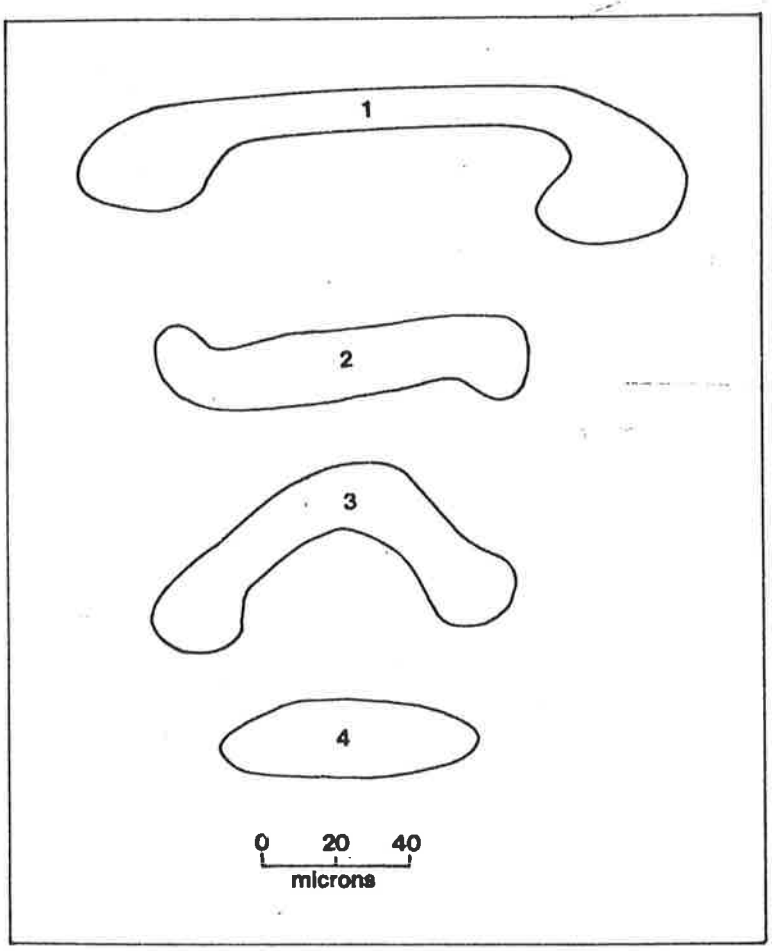

Figure 8.5 Pollen grain shape in *Ruppia*
1 dumbell, elongate
2 dumpy
3 boomerang
4 elliptic

mature anthers were obtained for two sites. No significant difference was recorded for pollen of Taxon C from Lake Robe but this material may all have been immature as no dehisced thecae were found. Differences between pollen grains within an anther, or between anthers from the same flower, were not significant. The variation within and between anthers may be attributed to the age of the pollen. Developmental changes probably occur suddenly with all grains maturing simultaneously rather than gradually and sequentially, or alternatively full development may not occur until immediately before anthesis and thus mature pollen would be difficult to obtain from intact thecae. These observations confirm those of Schwanitz (1967) who found differences in *Ruppia* pollen in Europe to be developmental, with pollen maturing immediately before anthesis.

The differences in pollen grain shape between Taxon B and the annual taxa, A and C, may reflect the later flowering times of B (see Appendix IX) as material was collected in November 1977, which is late in the flowering period of A and C yet early for B. Alternatively, the developmental regime of pollen of A and C may be such that pollen matures well before anthesis, whereas in B it matures immediately before anthesis. Systematic examination of pollen changes at short intervals throughout a flowering season in each habitat would be necessary to test these hypotheses.

Chromosome numbers

Studies were carried out to determine whether the chromosome numbers of the three taxa of *Ruppia* differ: any differences would give an indication of the genetic basis and evolutionaay history of the variation observed. As polyploidy has been recorded in this genus in Europe, but not in the species in New Zealand (see Section 8.2), the possibility of it occurring within the genus in South Australia warranted further examination. Polyploidy may have occurred, by the doubling of the chromosome number in a single species or by the

doubling of the chromosome number following hybridization (Dobzhansky 1970).

Ruppia collected and fixed in the field included germinating seeds and perennating organs of A from Little Dip Lake, rhizomes with growing shoots of B from Little Dip Lake and young flowers of A, B and C from various locations. Although only actively growing material was collected and fixation took place at various times of the day, no mitotic material was isolated from these collections.

Laboratory germinated material included: seeds of A from Little Dip Lake, seeds of B from Little Dip Lake and Porters Lagoon (north of Adelaide), seeds of C from Blue-Green Algal Pool and perennating organs of A from Beachport Salt Lake and Waltowa Swamp (26 km from Wellington). Laboratory grown material was more suitable as the time lag between collection and processing was eliminated and sampling of material at intervals during a 24 hour period allowed the determination of the optimal time for cell division. The optimal time for division was between 0730 and 1000 hours.

Developing anthers and root and stem meristems were suitable as potential areas of cell division. Squashes made of cells of stem meristems from the base of the sheath near the endocarp or perennating organ were the most successful. Attempts to obtain and fix the meiotic cells of developing anthers were unsuccessful, possibly because division is complete at a stage when the flowers can scarcely be distinguished in the leaf axils. Root tip preparations of both field and laboratory material failed to yield dividing cells.

A variety of methods of pretreatment, fixation, hydrolysis and staining were used on both field and laboratory material. Material was pretreated with various mitotic inhibitors (including saturated aqueous solutions of α-bromonapthalene, 0.002 M 8-hydroxyquinoline,

0.2% colchicine, indol acetic acid, and cold (4°C overnight)) and the lengths of time used for fixation and hydrolysis were varied.

Vegetative material from roots and shoots was fixed in a mixture of alcohol:acetic acid (3:1) for periods from 12 to 24 hours. Flowering material was fixed for varying times in a mixture of alcohol:acetic acid:chloroform (3:1:4).

Hydrolysis with 1N HCl was found to be the most satisfactory procedure, although a direct fixation hydrolysis technique with 5N HCl followed by staining with toluidine blue was also used with some success. Various stains, including toluidine blue, aceto-orcein, feulgen (leuco basic fuchsin) and a haemotoxylin ferric chloride and iodine stain, were used. The most successful method for obtaining chromosome squash preparations is outlined in Appendix X.

Chromosome numbers were determined for the three forms A, B and C. Although some overlapping of chromosomes occurred in most cells examined, a chromosome number of 2n = 20 was counted in several cells of each form. Thus polyploidy is not evident. Camera lucida drawings of chromosomes for each are presented (Figures 8.6, 8.7, 8.8). This chromosome number is consistent with the basic diploid number 2n = 20 found for the European material (Reese 1962) and for *R. megacarpa* from New Zealand (Mason 1967). The 2n = 18 recorded for *R. polycarpa* in New Zealand (Mason 1967) could have occurred by reduction in the basic chromosome number (2n = 20). Detailed karyotype studies of both Australian and New Zealand material could elucidate this further.

Transplantation experiments

The stability of growth form differences in *Ruppia* in different habitats was examined by field and laboratory transplantation experiments. If the observed differences are constant for each form, then they should be maintained in all habitats. However,

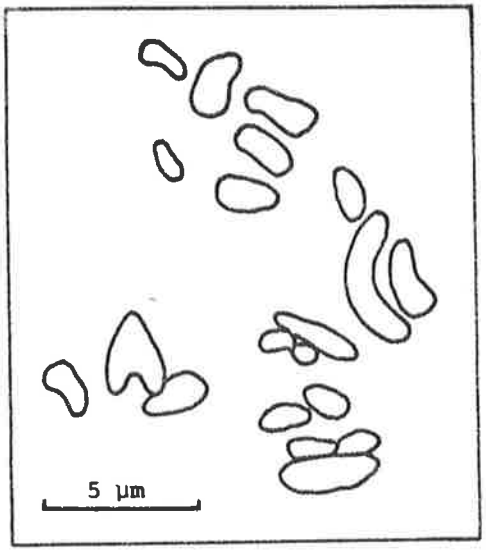

Figure 8.6

Chromosomes from a mitotic cell of *Ruppia* Taxon A, Little Dip Lake
2n = 20 (possibly 18)

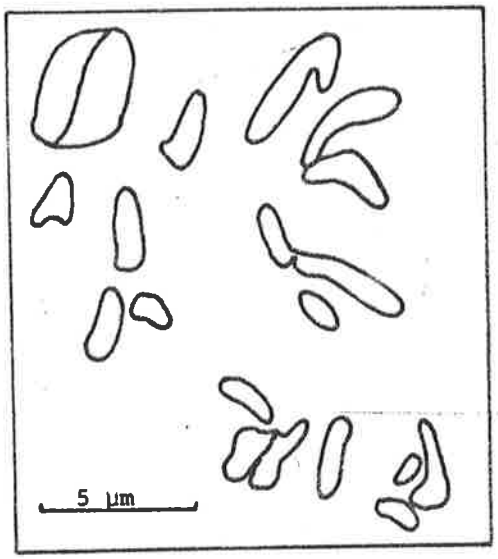

Figure 8.7

Chromosomes from a mitotic cell of *Ruppia* Taxon B, Little Dip Lake
2n = 20 (possibly 18 or 22)

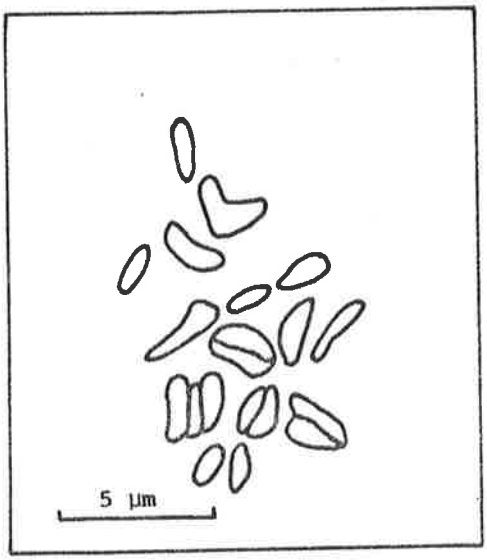

Figure 8.8

Chromosomes from a mitotic cell of *Ruppia* Taxon C, Blue-Green Algal Pool
2n = 20 (possibly 16 or 18)

Figures 8.6, 8.7 and 8.8 Camera lucida drawings of mitotic cells of *Ruppia*

if growth form is a response to environmental conditions such as the ephemeral or permanent nature of the habitat or salinity, then the growth forms of A, B and C should change under different environmental regimes. One field trial and eight laboratory trials were conducted to examine these alternatives. These experiments are described and discussed in Chapter 9 (Section 9.2, Table 9.2).

There is no evidence to suggest that the growth forms of *Ruppia* A, B and C change with habitat. Although the results of the field trial were not definitive, they indicated that *Ruppia* A and *Ruppia* B would not grow in alternative habitats. In the laboratory, the annuals, A and C did not grow perennially under permanently submerged conditions and the perennial, B, failed to regenerate after the dry phase of the ephemeral cycle.

8.3 Analysis of taxonomic characters

A set of characters most likely to be useful for the separation of species of *Ruppia* in South Australia, was chosen as a result of the preceding examination of the South Australian material and the literature. Table 8.1 lists the characters by which taxa A, B and C were initially distinguished, and the characteristics examined for each taxon in each habitat are tabulated in Appendices XI and XII. To show differences between taxa, quantifiable variables (leaf width and breadth, fruit dimensions, carpel number and inflorescence dimensions) together with qualitative morphological differences of podogyne, fruit and perennating organs and some parameters related to habit and habitat (growth form, flowering time and abundance, depth and permanence) were analysed. The constancy of these differences was used as a guide to the validity of the taxa A, B and C.

Table 8.1 Comparison of taxa A, B and C from 3 localities in the south-east of South Australia

	Taxon A (LDL)			Taxon B (LDL)			Taxon C (BGAP)		
Habitat	saline temporary waters 19-24 °/oo TDS up to 0.4 m deep			saline permanent waters 19-46 °/oo TDS 0.5-3.0m deep			saline temporary waters 9-35 °/oo TDS 0.1-0.3 deep		
Habit	-delicate annual, stems absent or very short - height mainly due to leaves from rhizomes -not clumped -growing season June-November -flowering September-November			-robust perennial, stems branching to 1.5-2.0 m -clumped -present 12 months -flowering November-March			-annual growth with stems branched or growth from rhizomes -not clumped -growing season June-November -flowering September-November		
Leaves: WxB (mm)	0.18-0.5x0.05-0.15			0.5-1.0 x 0.3-0.7			0.1-0.35x0.05-0.18		
W:B	3.5			1.5			2.1		
Flowers: Carpels	6-19 usually >8			2-6 usually 4			4-10 average 7		
Fruit:	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE
length	1.3-2.3	1.6	0.04	2.8-4.6	3.1	0.04	1.5-2.4	1.8	0.03
width	0.7-1.5	0.9	0.02	1.9-3.1	2.5	0.04	0.8-1.4	1.0	0.02
breadth	0.6-0.9	0.7	0.02	1.5-2.0	1.8	0.03	0.3-0.7	0.5	0.02
podogynes	sessile-subsessile non persistent <2 mm			stout tapering persistent 10-40 mm			thin straight persistent 10-20 mm		
shape	pyriform			asymmetrical turbinate			pyriform		
beak	<0.2 mm			0.9-1.7 mm			<0.2 mm		
endocarp perforations	2, narrow elliptic			2, deltate			2, narrow elliptic		
Reproductive potential	seeds asexual perennating organs of two kinds a) swollen stem bases b) swollen rhizomes rhizomes			seeds (not seen germinating in the field) no perennating organs rhizomes			seeds asexual perennating organs of one kind a) swollen stem bases at junction with rhizome rhizomes		

From the twelve quantitative characters measured for *Ruppia* from each site (Appendix XII), eight were selected for further analyses. The matrix of scatter diagrams (Figure 8.9) shows the variation in each character and the relationship of this to the variation of each of the other seven characters. Each point represents the mean values for two characters in one habitat. These values and their standard errors are presented in Appendix XII. The presence or absence and state of the podogyne (fruit stalk), divides the material into three distinct groups which correspond to the taxa A, B and C. These podogyne characteristics are represented on the scatter diagrams (Figure 8.9): podogyne absent characterizes Taxon A; podogyne present, stout 10-40 mm in length with a tapered attachment to the endocarp, characterizes Taxon B; and podogyne present, slender 10-30 mm in length with a straight attachment to the endocarp, characterizes Taxon C (Plates 8.1 - 8.8).

Scatter diagrams for characters measured from individual plants were constructed for a limited number of plants. Combinations of unrelated characters such as vegetative and fruiting characters were difficult to score, as mature fruits usually had fallen from the parent plant. Figure 8.10 shows a plot of fruit length against leaf width, with habitat permanence (shown by symbols for each locality). Material scored was from Blue-Green Algal Pool, (C), Little Dip Lake, (A, B), and Porters Lagoon, (B). This scatter diagram shows a discontinuity between two taxa only; B is separated from A and C by these characters, but A and C are not separated from one another. Three characteristics of the fruit, (length, width and podogyne features) from 14 habitats are plotted in Figure 8.11. The ranges of fruit length and width for A and B are discrete taken separately, but are overlapped by the range of C. Podogyne form, however, divides the material distinctly into the three categories corresponding to A, B and C.

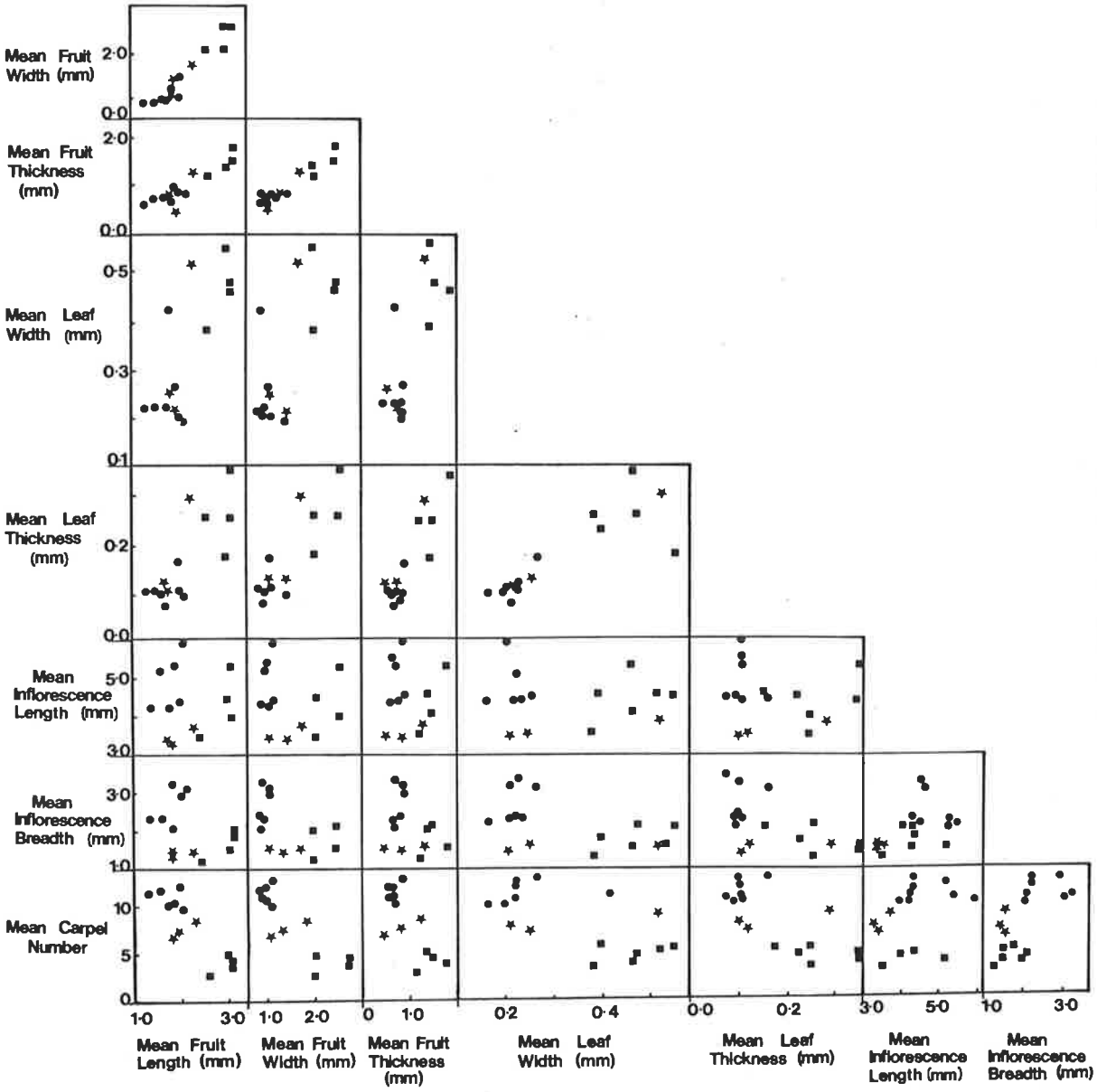

Figure 8.9 Matrix of scatter diagrams of characters of *Ruppia* in the south-east of South Australia. Mean values are plotted for each character at each location, standard errors for each mean are presented in Appendix VII.

A ● Fruit sessile or subsessile - podogyne 1-2 mm not persistent

B ■ Podogyne 10-40 mm stout, persistent tapered attachment to endocarp

C ★ Podogyne 10-30 mm slender, persistent straight attachment to endocarp

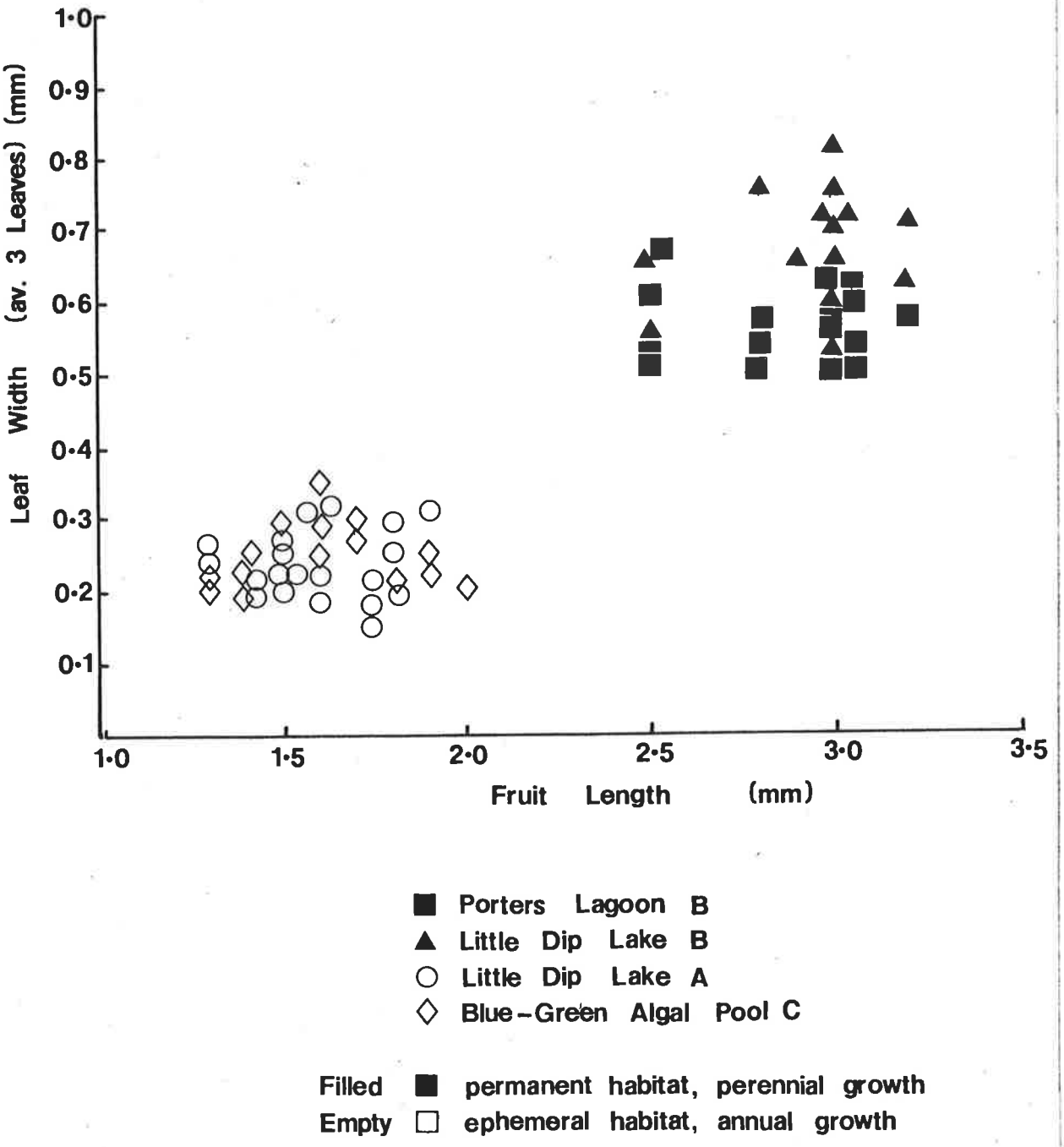

Figure 8.10 Leaf width, fruit length, habitat and habit characters for individual plants from three locations

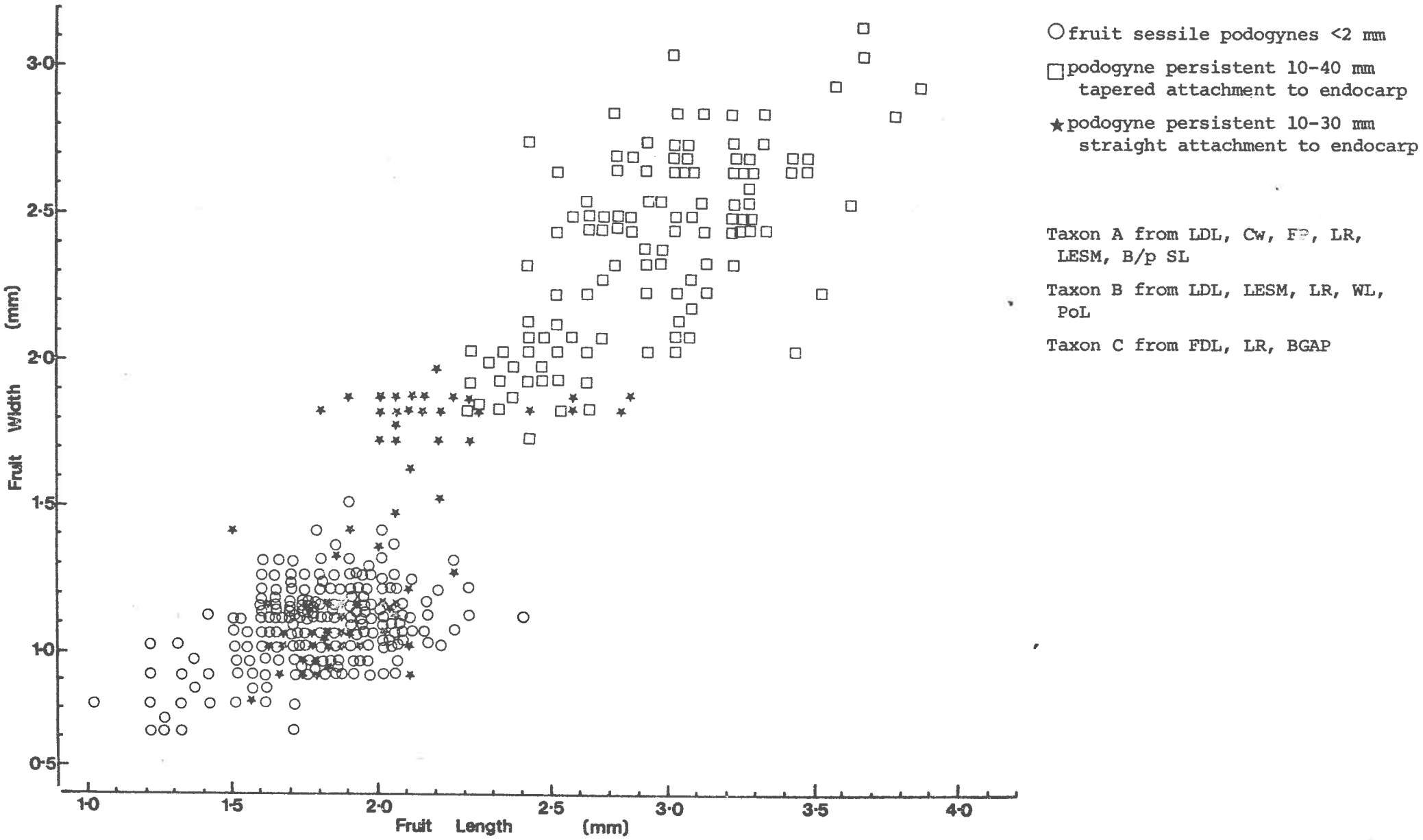

Figure 8.11 Fruit length, fruit width and podogyne characters plotted for *Ruppia* from ten localities:

The quantitative characters most likely to separate the three proposed taxa were selected from the matrix of scatter diagrams (Figure 8.9). Graphs of carpel number, leaf width, and fruit length, width and breadth are plotted for each location and also for each taxon (Figures 8.12, 8.13, 8.14, 8.15, 8.16). Differences between sites and between taxa can be compared in each figure. The sample numbers for fruits and carpels are small for some localities as a result of the scarcity of flowering material. Carpel number clearly separates A, B and C: fruit measurements show a similar trend although the ranges of A and C overlap. The ranges of A, B and C for the leaf width all overlap, even though three groups are evident. Carpel number, fruit length and leaf width were chosen for statistical analyses.

For each of these three characters an Anova table was constructed and an analysis of variance carried out on differences between sites and between forms (Tables 8.2, 8.3, 8.4). The F values indicate a significant difference between sites and between taxa for each of these three characters.

Localization of this variation was made using the New Multiple Range Test of Duncan (Li 1964 p270) to rank and compare the differences between treatment means. This test works on a principle similar to the principle of least significant difference (LSD) using the value shortest significant range (SSR). This value is calculated from the formula $SSR = \sqrt{2}t_{0.025} \times s_{\bar{y}}$, where $s_{\bar{y}}$, the standard error of the mean ($s_{\bar{y}} = \sqrt{s^2/n}$), and $\sqrt{2}t_{0.025}$ (or $\sqrt{2}t_{0.005}$) the significant studentized range, are read from tables at 5% or 1% levels of significance (Appendix tables 8a, 8b in Li 1964). Values are read for g, (the number of means in the group to be compared) and v_2 (the number of degrees of freedom of the error mean square as calculated for the Anova).

Table 8.2 Statistical Analysis of Data on Carpel Number

a) Anova Tables

Differences between sites

Source of Variation	df	SS	MS	F
among sites (treatments)	15	4232.7	282.2	*1 80.0
within locations (error)	403	1420.9	3.5	
total	418	5653.6		

*1 $F_{0.05\ (15,\ 120)} = 1.75$

$F_{0.01\ (15,\ 120)} = 2.19$

$F_{0.001\ (15,\ 120)} = 2.78$

$\therefore P<0.001$. There is a significant added variance component due to differences in carpel number between sites

Differences between A, B, C

Source of Variation	df	SS	MS	F
among A, B, C	2	3778.3	1889.2	*2 438.6
within A, B, C	393	1692.7	4.3	
total	395	5471.0		

*2 $F_{0.05\ (2,\ 120)} = 3.07$

$F_{0.01\ (2,\ 120)} = 4.79$

$F_{0.001\ (2,\ 120)} = 7.32$

$\therefore P<0.001$. There is a significant added variance component due to differences in carpel number between forms A, B, C.

b) Multiple Range Test

Site	Taxon	$\bar{x}$ *	Salinity (°/oo TDS) range for plant habitats
B/p SL	A	12.85	64-108
LDL	A	11.98	19-24
LESM	A	11.80	6-25
Cw	A	10.53	>38
LR	A	10.47	20-50
FP	A	9.96	37-90
ML	A	9.60	12-33
LR	C	6.50	20-50
FDL	C	6.42	2.1-3.3
BGAP	C	6.09	9-35
WL	B	4.96	>38
CNL	B	5.58	≡38
PL	B	4.11	12-29
LDL	B	3.32	18-39
LESM	B	2.84	20-24

Form	n	$\bar{x}$
A	177	11.08
B	101	6.31
C	118	4.07

There is no significant difference between means

* for values of n see Appendix VII.

Table 8.3 Statistical Analysis of Fruit Length Measurements

a) Anova Tables

Differences between sites

Source of Variation	df	SS	MS	F
among sites (treatments)	12	84.28	7.02	*1 148.85
within locations (error)	246	11.61	0.05	
total	258	95.89		

*1 $F_{0.05\ (13,\ 120)} = 1.80$

$F_{0.01\ (13,\ 120)} = 2.30$

$F_{0.001\ (13,\ 120)} = 2.90$

$\therefore P < 0.001$. There is a significant added variance component due to differences in fruit length between sites

Differences between A, B, C

Source of Variation	df	SS	MS	F
among A, B and C	2	72.15	36.08	*2 393.19
within A, B and C	257	23.58	0.09	
total	259	95.74		

*2 $F_{0.05\ (2,\ 120)} = 3.07$

$F_{0.01\ (2,\ 120)} = 4.79$

$F_{0.001\ (2,\ 120)} = 7.32$

$\therefore P < 0.001$. There is a significant added variance component due to differences in fruit length between A, B, C

b) Multiple Range Test

Site	Taxon	$\bar{x}$ *
PoL	B	3.12
LDL	B	3.09
LR	B	3.03
LESM	B	2.59
FDL	C	2.26
FP	A	2.02
B/p SL	A	1.95
LR	C	1.89
BGAP	C	1.83
Cw	A	1.79
LR	A	1.71
LDL	A	1.55
LESM	A	1.25

Form	$\bar{x}$
B	2.96
C	1.98
A	1.75

The differences between means are all significant

* for values of n see Appendix VII

Table 8.4 Statistical Analysis of Leaf Width Measurements

a) Anova Tables

Differences between sites

Source of Variation	df	SS	MS	F
among sites (treatments)	18	8.91	0.05	*1 116.05
within locations (error)	445	1.90	0.004	
total	463	10.81		

*1 $F_{0.05\ (18,\ 120)} = 1.75$

$F_{0.01\ (18,\ 120)} = 2.19$

$F_{0.001\ (18,\ 120)} = 2.78$

$\therefore P<0.001$, There is a significant added variance component due to differences in leaf width between sites

Differences between A, B, C

Source of Variation	df	SS	MS	F
among A, B and C	2	5.61	2.80	*2 246.82
within A, B and C	441	5.01	0.01	
total	443	10.62		

*2 $F_{0.05\ (2,\ 120)} = 3.07$

$F_{0.01\ (2,\ 120)} = 4.79$

$F_{0.001\ (2,\ 120)} = 7.39$

$\therefore P<0.001$, There is a significant added variance component due to differences in leaf width between A, B, C

b) Multiple Range Test

Site	Taxon	$\bar{x}$ *
PoL	B	0.55
WL	B	0.55
CNL	B	0.53
FDL	C	0.52
LDL	B	0.46
Cw	A	0.42
EH	B	0.39
LESM	B	0.38
B/p SL	A	0.26
BGAP	C	0.22
LDL	A	0.22
LR	A	0.20
LR	C	0.21
PL	A	0.20
FP	A	0.20
BL	A	0.19
ML	A	0.16

Form	$\bar{x}$
B	0.48
C	0.35
A	0.23

Significant differences occur between all means

* for values of n see Appendix VII

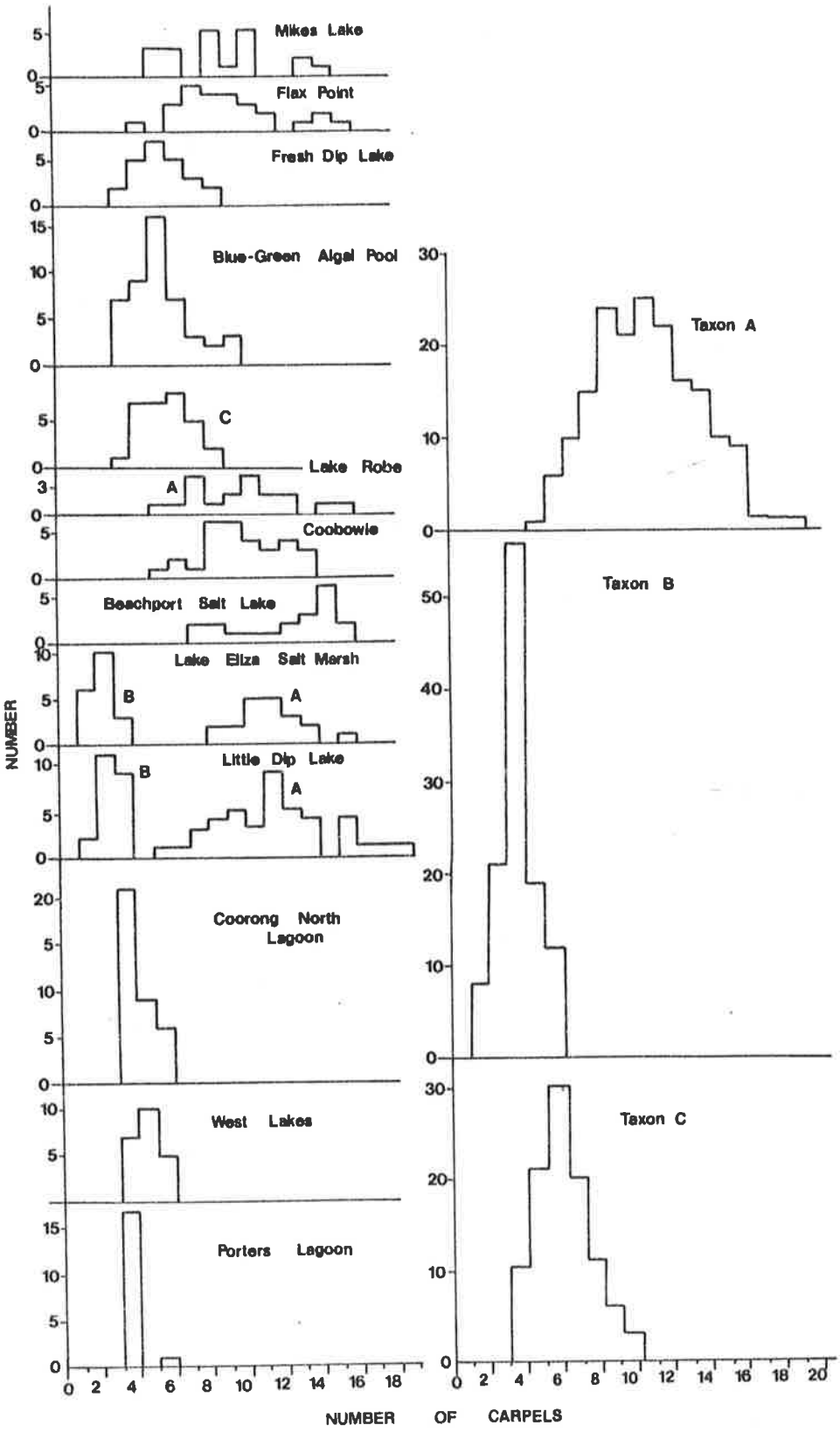

Figure 8.12 Histograms of the number of carpels per flower for sites in the south-east of South Australia and for the three taxa A, B and C.

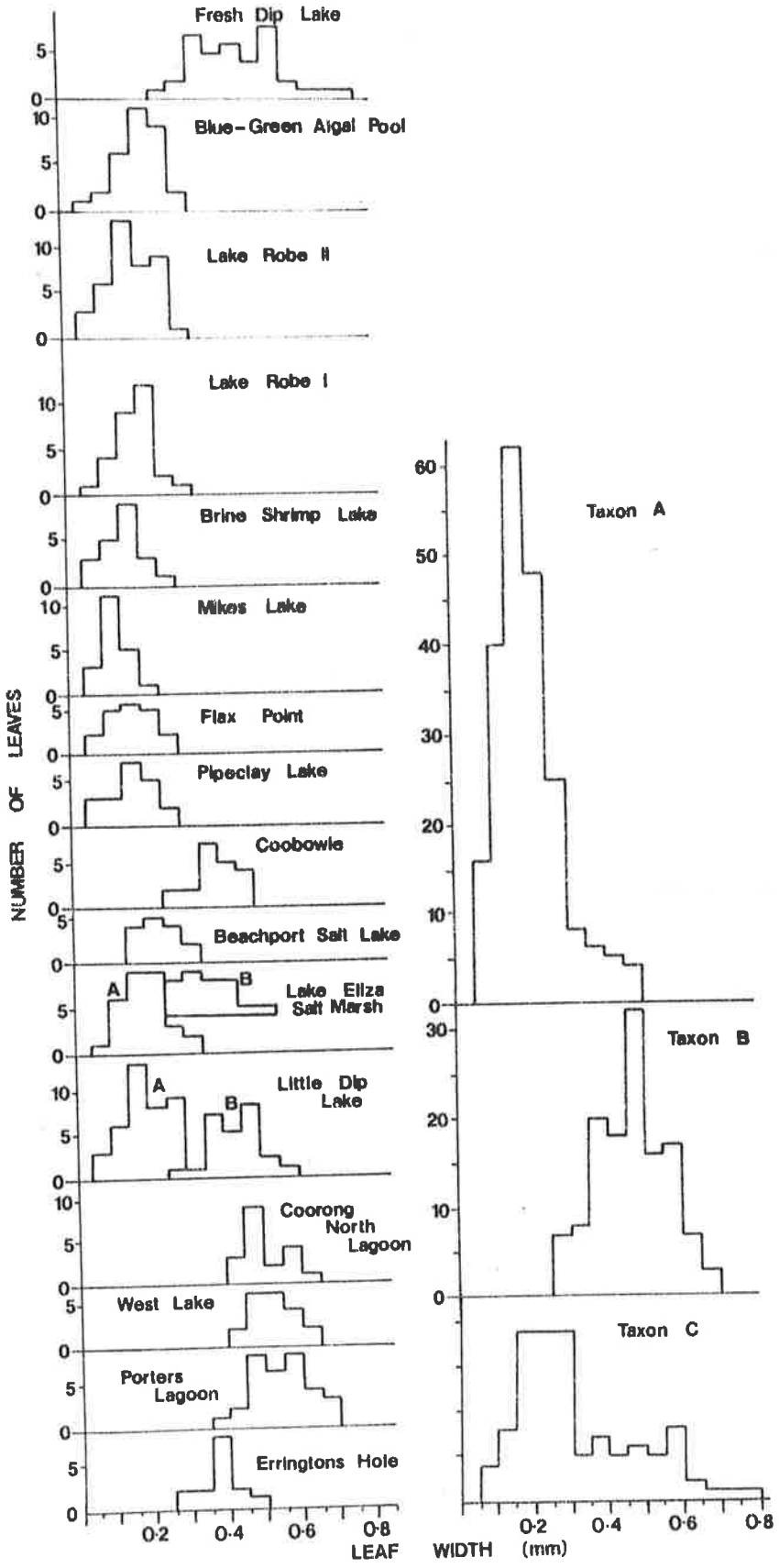

Figure 8.13 Histograms of the leaf width of plants from sites in the south-east of South Australia and for the three taxa A, B and C.

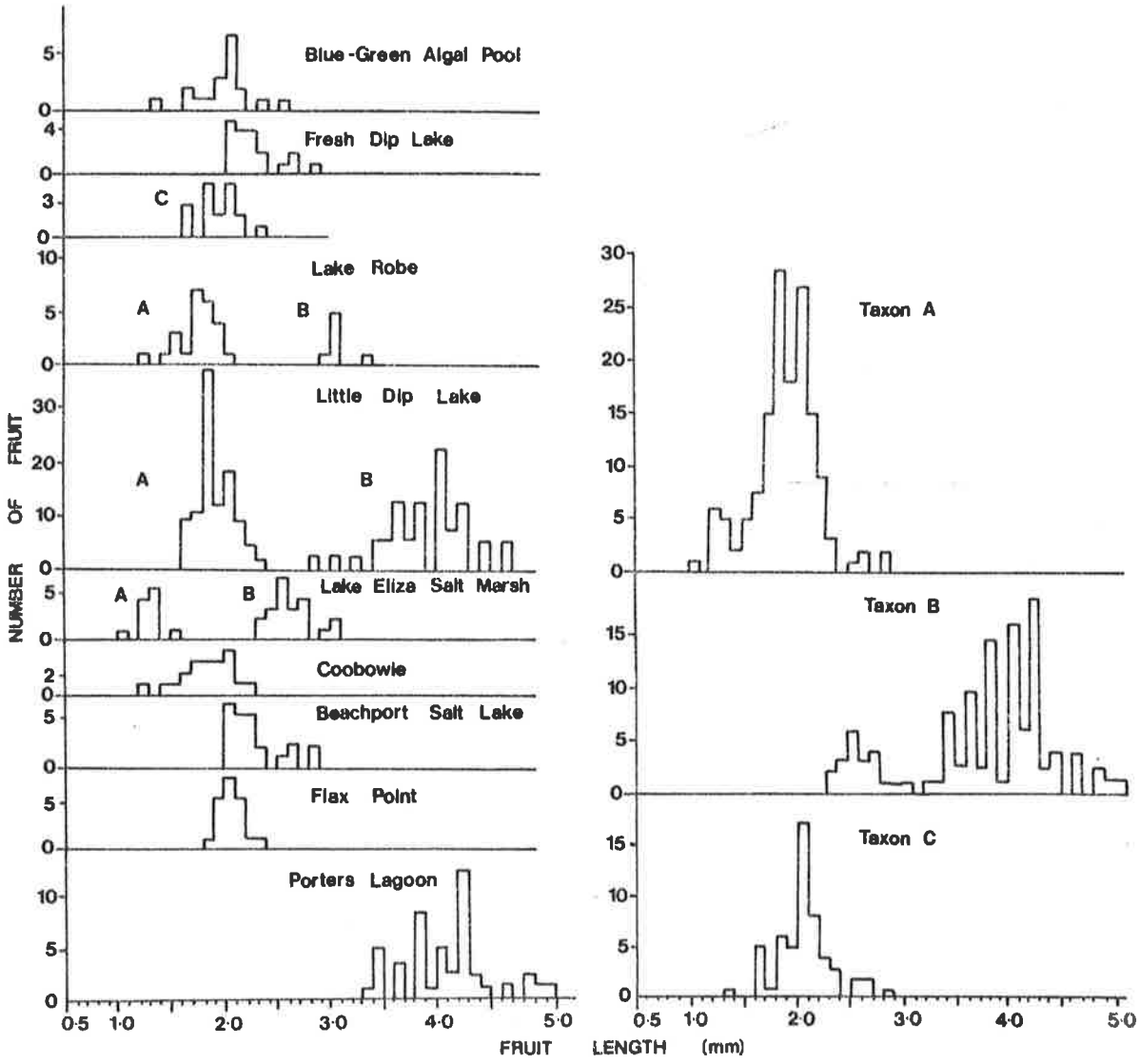

Figure 8.14 Histograms of the length of the fruits from plants from sites in the south-east of South Australia and for the three taxa A, B and C.

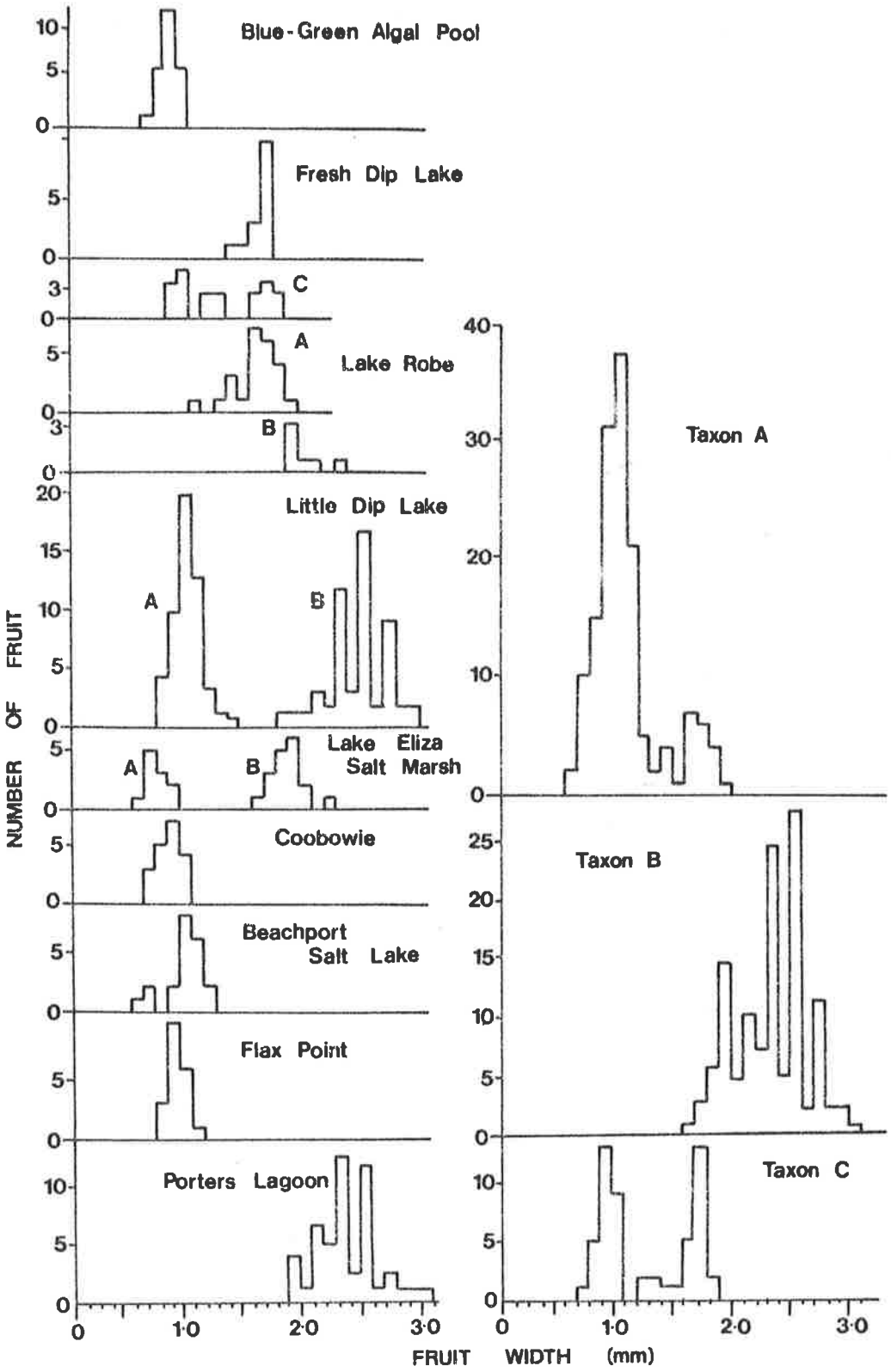

Figure 8.15 Histograms of the width of fruit from plants from sites in the south-east of South Australia and for the three taxa A, B and C.

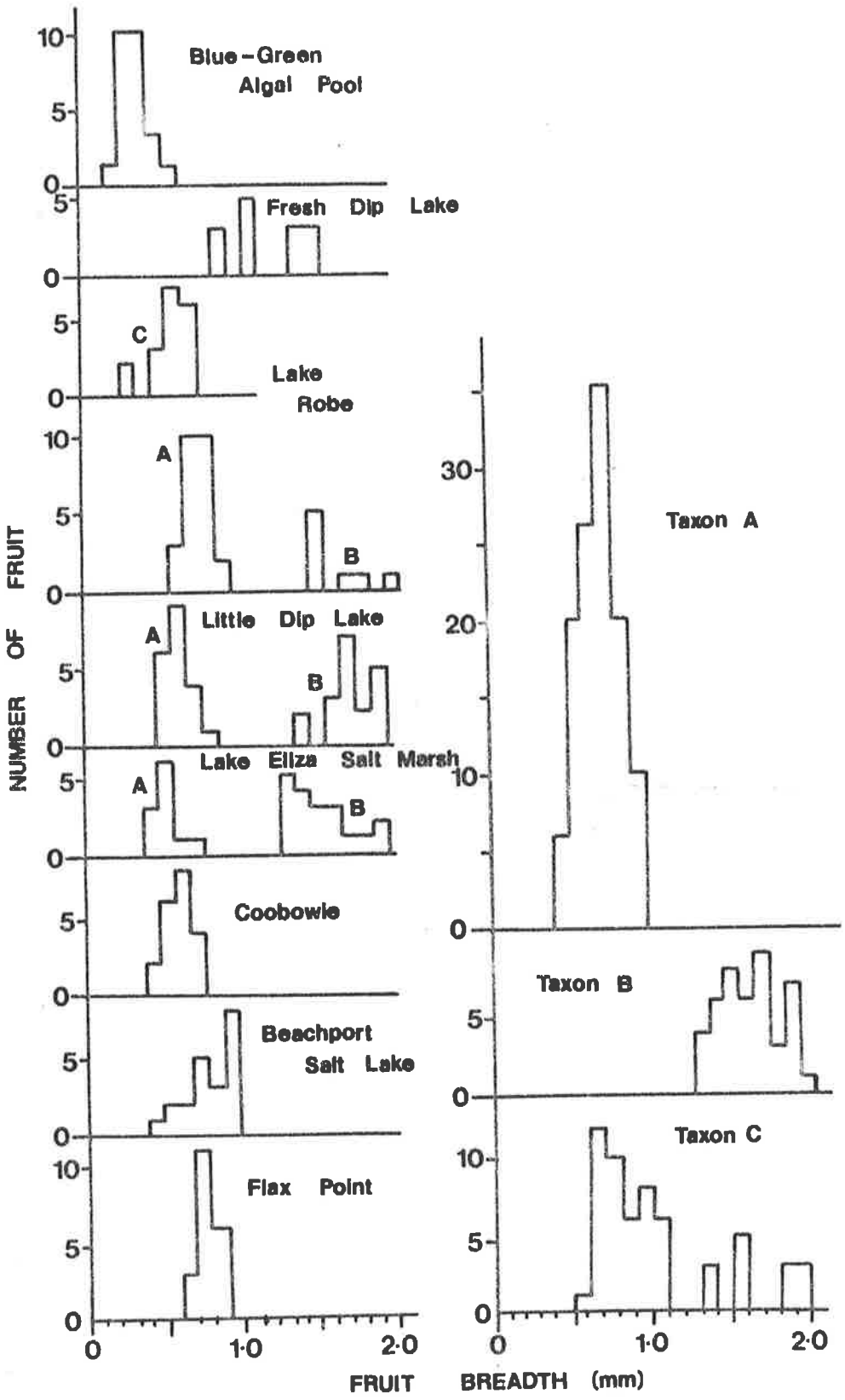

Figure 8.16 Histograms of the breadth of fruit from plants from sites in the south-east of South Australia and for the three taxa A, B and C.

Means (for sites and for taxa) were ranked according to their magnitude and the standard error of each mean calculated (from the formula $s_{\bar{y}} = \sqrt{s^2/n}$ where s^2 is the error mean square and n the number of observations). As the sample sizes were unequal, it was assumed that $n \equiv n_o$ where $n_o = \frac{1}{k-1}\left[\sum^{k} n_i - \sum^{k} n_i^2 / \sum^{k} n_i\right]$ (Sokal and Rohlf 1969) where k is the number of treatments and n the number of scores for each sample. The shortest significant range (SSR), for each of the k-1 comparisons to be made, was therefore calculated as the product of the standard error of the mean and the significant studentized range for the number of means being compared. The difference between a pair of the ranked means was considered significant if it exceeded the corresponding SSR value for that number of comparisons. In this way differences between sites and between taxa were localized for carpel number, fruit length and leaf width. In Tables 8.2, 8.3, and 8.4 the ranked means are aggregated into groups (marked by bars). There are no significant differences between means within each of these groups.

For carpel number, significant differences are evident between A and B, B and C, and A and C. The variation between sites supports these divisions; significant differences were recorded when each site for A was compared with each site for B and C, and when sites for B were compared with C. No significant differences occur between the three sites for Taxon C. The seven sites for Taxon A fall into three groups with considerable overlap and a similar situation occurs for the five sites for Taxon B (Table 8.2, Figure 8.12). It may be postulated that the differences within groups A and B are due to variation of environmental parameters between habitats: for example salinity increase may stimulate small increases in the number of carpels (salinity ranges for the plant habitats are presented in Table 8.2). Another source of variation could be the small sample sizes for some sites. However, this analysis indicates that the

differences between the groups A, B and C are significant when sites are grouped, thus taking the variation between sites into account.

Analysis of fruit length data also supports the division into three groups as differences between A and C, B and C, and A and C are significant (Table 8.3). There is no overlap between A and B or B and C, but there is some overlap between A and C and again some variation between sites for each taxon. The fruit lengths of A and B from Lake Eliza Salt Marsh and of C from Fresh Dip Lake are significantly different from all other sites and from each other. The fruits of A and B from the salt marsh are significantly smaller than the fruits of these taxa from other sites. These differences seem to be related to environmental factors such as the short wet cycle in habitats with A or the shallow depth of locations with B (Table 5.1), although the small sample size may have biased these results. Fruits of C from Fresh Dip Lake are longer than from other sites, possibly attributable to the fresh water in this habitat. Although the analysis of fruit length again supports the same three groupings, this character is more variable than carpel number (Table 8.3, Figure 8.14).

Significant differences in leaf width between the three taxa, A, B and C are observed, notwithstanding some variation between sites (Table 8.4, Figure 8.13). Groups of sites for A and B are separate, except for the Coobowie site (Cw), which has plants with wider leaves than other sites of A. However, these measurements were made on leaves from only one collection. Further collections are needed to substantiate the observation that the leaves are wider and the plant form more robust at this site than at the localities of A in the South-East. Leaf width of C is more variable than for A or B; leaf widths of C overlap with both A and B. The leaves of material from the fresh site (FDL) are consistently wider than

the leaves from the other two sites for C. Examination of material from a wider selection of habitats is necessary to determine the effects of salinity on leaf width in all of these forms.

The subdivision of *Ruppia* in the south-east of South Australia into three taxa is supported by the analyses of carpel number, fruit length and leaf width. Taxon A is distinguished from B and C by its greater carpel number per flower, smaller fruit and narrower leaves and by the sessile individual fruiting carpels. Taxon B is distinguished from A and C by the small number of carpels per flower, robust and wider leaves and larger fruiting carpels with a stout persistent podogyne with a tapered attachment to the endocarp. Taxon C is intermediate between, but distinct from, A and B in carpel number, leaf width and fruit length. It is also distinguished by the slender persistent podogyne with a straight attachment to the endocarp. Fruit dimensions and leaf width are more variable in group C than in either A or B. The greater variability within C can possibly be explained by the wider range of habitats in which it occurs; it is found in both permanent and ephemeral habitats of varying depth and in salinities ranging from fresh to hypersaline.

A and C share some characters which are absent in B. Perennating organs are found in A and C,both of which grow in ephemeral and permanent habitats and are always annuals. B is a robust perennial found in permanent waters: perennating organs have never been recorded for this taxon. In addition a greater overlap of fruit length and leaf width occurs between A and C than between A and B,or C and B. Flowering times for A and C are similar (August to November) and distinct from B (usually November to March). In Little Dip Lake and Lake Eliza Salt Marsh,where A and B grow sympatrically, reproductive isolation occurs as the flowering times do not overlap.

On the basis of the above findings there is a strong argument for the designation of the three taxa of *Ruppia* as separate species. *Ruppia* B is easier to identify in the field than *Ruppia* A and *Ruppia* C as it has distinguishing vegetative characters which separate it from the other two. Species A and C are vegetatively similar and often occupy similar habitats; thus flowering and fruiting material are needed for reliable identification.

The most reliable taxonomic criteria for distinguishing the three species are carpel number and podogyne characters. Fruit dimensions and leaf width are useful but as their ranges overlap (particularly A and C) they should not be relied upon without the support of other distinguishing characters. The wider leaves of A from Coobowie and C from Fresh Dip Lake indicate that this character may be influenced by the environment. However, the need for a vegetative character for field identification may necessitate the use of this character. Although leaf tips of A and C are generally rounded, obtuse or acute, whereas tips of B are bidentate or truncate, this character does vary with the condition of the plant. Obtuse or rounded tips are found on new shoots of B and truncate or bidentate tips are often found on old or damaged tips of A and C. The formation of truncate and bidentate tips by decay and breakage of the upper portions of the leaf blades has been observed in both A and B. Leaf tip shape should therefore be used only as a population character.

8.4 Nomenclature

The names applicable to these three species can only be ascertained by comparison with the type specimens; if the characteristics of one taxon or specimen fall within the accepted ranges of a species, then that name could be correctly applied to the taxon. The characteristics of described species have been tabulated from literature (Appendix XIII) and specimens have been examined where

possible: *Ruppia polycarpa* and *Ruppia megacarpa* from the DSIR Herbarium (CHR) Christchurch New Zealand (specimens now donated to AD) and *Ruppia maritima* and *Ruppia cirrhosa* from collections made on the island of Texel, the Netherlands. Australian specimens from outside the study area have been examined and extend the ranges of the species described. These include specimens from The State Herbarium of South Australia (AD) and field collections for South Australia (Figure 8.4), specimens from the National Herbarium in Sydney (NSW) for New South Wales, from Herbarium Australiense (CANB) for the Australian Capital Territory, Northern Territory and parts of New South Wales, the Western Australian Herbarium (PERTH) and University of Western Australia Herbarium (UWA) for Western Australia, the National Herbarium of Victoria (MEL) for Victoria. Limited field collections from Victoria and Western Australia have also been examined. Unfortunately the only herbarium specimen of *Ruppia tuberosa*, the species described from Western Australia, is the type specimen and this has been mislaid from the Herbarium of the University of Florida (FLAS). The species has not been seen again at the type locality, Shark Bay, Western Australia which has been devoid of *Ruppia* in its growing seasons in 1978 and 1979 when collections were sought.

The names previously applied to *Ruppia* in South Australia are *Ruppia maritima* and *Ruppia spiralis* (syn. *R. cirrhosa*). Examination of specimens suggests that these names are not valid for any of the taxa proposed. *Ruppia maritima* is characterized by short (<5 cm), non spiralled peduncles which bear flowers that are fertilized underwater. All the south-eastern South Australian specimens examined have long (>10 cm) peduncles which are usually spirally coiled and bear flowers which are fertilized at the water surface. *Ruppia cirrhosa* is a polyploid with 2n = 40 (*R. maritima* 2n = 20), has four carpels per flower, and fruit with a mean length of 2.6 mm. Specimens from the taxa A, B and C have 2n = 20. *Ruppia* A and *Ruppia* C have more than

four carpels per flower and *Ruppia* B has fruits which are larger and more asymmetrical than the fruits of *Ruppia cirrhosa*.

Ruppia tuberosa has characteristics in common with *Ruppia* A while *Ruppia megacarpa* and *Ruppia polycarpa*, described from New Zealand, show similarities to *Ruppia* B and *Ruppia* C respectively. These comparisons are drawn in Table 8.5.

The ranges in variability of some characters described for *Ruppia tuberosa* are narrower than those observed in *Ruppia* A (e.g. carpel number, leaf width, salinity range; see Table 8.5). However, the ranges of *R. tuberosa* are spanned by those of *Ruppia* A with no discontinuities. It is probable that *R. tuberosa* was described from an extreme of its range, as the type collections were made over only part of the life cycle from only one location in one growing season.

The characteristic features of *Ruppia megacarpa* in New Zealand are for the main part shown by *Ruppia* B; for example the branched, often zig-zag growth form, crowding of leaves at the shoot tips and the ability to form roots from stem nodes are characteristic of these species but are not found in other described species. The average fruit length is greater for *Ruppia megacarpa* than for *Ruppia* B but the range overlaps with that characteristic of *Ruppia* B. Salinity tolerances are probably also greater for the Australian species: *R. megacarpa* is generally found in saline estuarine waters of New Zealand (Mason pers. comm.) whereas *Ruppia* B is found in brackish to hypersaline waters. There are no clear discontinuities in the characters used to distinguish these species.

Ruppia polycarpa is unusual in that it is the only species described that grows in fresh as well as brackish waters (Mason 1967). *Ruppia* C also grows in fresh water as well as in saline and hypersaline waters. *Ruppia polycarpa* and *Ruppia* C have many other features in common: the fruit stalk, fruit size, shape and perforation shape and the growth form are all closely similar. Carpel number is more

Table 8.5 Comparison of *Ruppia* species A, B and C with the described species *R. tuberosa*, *R. megacarpa* and *R. polycarpa*

	Ruppia A	*R. tuberosa* Davis & Tomlinson (1974)	*Ruppia* B	*R. megacarpa* Mason (1967)	*Ruppia* C	*R. polycarpa* Mason (1967)
Habitat	13-230 °/oo TDS ephemeral or permanent up to 0.5 m	92-132 °/oo TDS 0.08-0.65 m	5-46 °/oo TDS permanent 0.5 - 3.0 m	Saline coastal	2-66 °/oo TDS ephemeral or permanent up to 0.5 m	Fresh to brackish
Leaves apex	rounded to acute occasionally truncate	rounded occasionally bidentate	truncate to bidentate occasionally rounded when young	bidentate	obtuse to acute occasionally truncate	obtuse
width mm	0.23 (0.1-0.5)	up to 0.3	0.48 (0.25-0.6)	0.3 - 0.7	0.35 (0.1-0.8)	0.3 - 0.4
Peduncles swelling below lower flower	absent	-	absent	absent	absent	present
Carpels per flower	2-19 (av. 11)	>4 up to 12	2-7 (usually 4)	4 (4-6)	4-11 (av 6)	2-16 usually 8
Fruit length mm	1.8 (1.2-2.5)	-	3.0 (2.1-4.6)	4-5	2.0 (1.5-2.8)	1.7-2.7
fruit stalk mm	sessile sub-sessile <3	sessile	stout tapered persistent 10-40	stout tapered	slender persistent straight attachment 10-30	slender straight attachment
Endocarp shape	pyriform	flask shaped	turbinate asymmetric deltate	asymmetric	pyriform	less asymmetric
perforation	narrow elliptic	-	0.9 - 2.0	triangular	narrow elliptic	longitudinal
beak mm	<0.2	not pronounced		1.5	<0.3	0.25
Reproduction	perennating organs rhizomes seeds	perennating organs rhizomes seeds	rhizomes seeds	rhizomes seeds	perennating organs rhizomes seeds	rhizomes seeds
Chromosome number	20	-	20	20	20	18
Habit	growth from rhizomes	tufts from rhizomes	branched zig-zag stems, clumped leaves occasionally	branched zig-zag stems, clumped leaves occasionally	growth from rhizome and branching	growth from rhizome and branching (not common)

variable in *R. polycarpa* than in *Ruppia* C and leaf widths are more variable in *Ruppia* C than in *R. polycarpa*, but for both characters the ranges are continuous. The peduncular swelling below the lower flower in *R. polycarpa* is not characteristic of *Ruppia* C and has only been recorded sporadically in any Australian material. The perennating organs produced by *Ruppia* C in some of its habitats have never been recorded for the New Zealand species. The development of perennating organs could be associated with the ephemerality of habitats in Australia. If so, the absence of such overwintering buds in New Zealand, where all habitats are permanent, is not surprising as there would be little adaptive advantage in having such organs in permanent habitats where plants reproduce successfully by rhizomes and seeds. A chromosome number of 2n = 18 was reported for *R. polycarpa* whereas chromosome counts of 2n = 20 were made for *Ruppia* C. The possibility of chromosome number reduction by translocation and loss, or other genetic processes could have caused this. This difference cannot be reconciled without karyotype studies of chromosome number and structure in a range of habitats of the two species. Apart from chromosome number differences and the absence of a peduncular swelling in *Ruppia* C, species specific characters for *R. polycarpa* are consistent with those of *Ruppia* C.

The three taxa described from the south-east of South Australia are covered by descriptions of established species and thus it is proposed that the names *Ruppia tuberosa* for *Ruppia* A, *Ruppia megacarpa* for *Ruppia* B and *Ruppia polycarpa* for *Ruppia* C be accepted.

A key for the identification of these species in South Australia is presented. Specimens from all sites examined are located in The State Herbarium of South Australia (AD). Duplicates of some specimens are located in the National Herbarium (NSW) in

Sydney and the herbarium of the Botany Division DSIR Christchurch New Zealand (CHR).

8.5 Key to *Ruppia* in the south-east of South Australia

0 Fruiting peduncle elongated, usually >10 cm and spirally coiled; flowers fertilized at the surface 1

0* Fruiting peduncle <5, cm not spirally coiled; flowers fertilized underwater ..... *Ruppia maritima* L. group

1 Carpel number usually 4 (2-7); mature fruit turbinate, asymmetrical, 3.0 (2.1-4.6) mm in length, 2.3 (1.5-3.1) mm in width, 1.5 (1.0-2.5) mm in breadth; individual fruit stalked, stalks persistent, stout, 10-40 mm long, tapered attachment to the fruit; stylar beak of fruit 0.9-2.0 mm long, oblique; (flowering time usually November to March; leaves 0.48 (0.25-0.6) mm wide; leaf tips truncate to bidentate (obtuse when young); branched habit, to 2.5 m; permanent brackish to hypersaline waters, 0.5-3 m deep ..... *Ruppia megacarpa* Mason = *Ruppia* B

1* Carpel number usually >6 (4-19); mature fruit pyriform, smaller than in 1; individual fruit sessile or subsessile or with a slender persistent stalk with a straight attachment to the fruit; stylar beak of fruit <0.3 mm; flowering time usually September to November; leaves generally <0.35 mm wide (0.1-0.8 mm); leaf tips rounded to acute (occasionally truncate or bidentate in old

or damaged material); leaves from rhizome, sometimes branched to 0.5 m; ephemeral or permanent habitats, fresh to hypersaline waters to 0.6 m deep 2

2 Carpel number 4-19 (mean no. 11) usually >8; individual fruit sessile or subsessile, fruit stalk if present <0.3 mm, never persistent in mature fruit; fruit 1.8 (1.2-2.5) mm in length, 1.1 (0.7-1.9) mm in width, 0.7 (0.4-1.2) mm breadth; leaf width 0.23 (0.1-0.5) mm; growth mainly from rhizome; branching, if present, not prolific; water salinity 13->230 °/oo TDS ..... *Ruppia tuberosa* Davis & Tomlinson = *Ruppia* A

2* Carpel number 4-11 (mean no. 6); individual fruit with a slender stalk 10-30 mm long, stalk persistent with a straight attachment to the fruit; fruit 2.0 (1.5-2.8) mm in length, 1.4 (0.8-1.9) mm in width; 0.8 (0.3-1.6) mm in breadth; leaf width variable 0.1-0.8 (mean 0.35) mm, usually <4 mm; branched habit or growth from rhizome; water salinity 2-66 °/oo TDS ..... *Ruppia polycarpa* Mason = *Ruppia* C

CHAPTER 9. ECOLOGICAL STUDIES

9.1 Introduction

The systematic study (Chapter 8) demonstrated that the annual form of *Ruppia* included two species, *viz.* *R. tuberosa* and *R. polycarpa* whereas the perennial form was a single species, *R. megacarpa*. The sympatric populations of the annual *R. tuberosa* and the perennial *R. megacarpa* in Little Dip Lake were subjected to detailed ecological study. Since the third species, *R. polycarpa*, was not recorded from this ecosystem, the population in Blue-Green Algal Pool was used for comparison.

The autecological investigation of *Ruppia* included studies of the population biology, physiology and life histories of the three species. The permanence and stability of the annual and perennial growth forms with fluctuations of environmental factors were assessed by field and laboratory growth trials. Annual and perennial growth forms were compared by a more detailed examination of the effects of variation of environmental parameters (salinity, habitat wetness, photoperiod and some aspects of temperature) on physiological processes such as breakage of dormancy, growth and osmoregulation. The population dynamics have been examined through studies of the life cycles and reproductive regimes of the three species.

9.2 Growth experiments

Field and laboratory growth experiments were conducted to examine the stability of growth form under varying conditions such as permanent or fluctuating inundation, or salinity differences.

1. Field transplantation trial

A field transplantation trial was established in Little Dip Lake in January 1977. Part of the eulittoral zone on the south-eastern beach, a habitat for *R. tuberosa*, and a section of permanent water in the zone where *R. megacarpa* occurs, were selected as experimental

sites. The temporary site was dry at this time and the permanent site was covered by 0.4 m of water. Each site was prepared by clearing a 2m x 1m plot of all plant parts and the top one centimetre of sediments including most of the plant propagules and rhizomes. Experimental plots were marked with stakes placed outside the cleared area to prevent shading by the aggregation of windblown and epiphytic filamentous algae or localized nutrient increase from bird droppings. At each cleared site, two 0.5m x 0.5m plots 0.3 m apart were seeded with material collected from temporary and permanent habitats. For each habitat a control plot (0.5m x 0.5m) was selected outside the region of trampling. Seeds collected with an Ekman grab from around *R. megacarpa* clumps were mixed with sediment and spread, 0.01 m deep, in a 0.4 x 0.5m section of the *R. megacarpa* plot at each site. Rhizomes with four or five nodes were cut and planted in the remaining 0.5 x 0.1m blocks adjacent to the seeded plots. Two 0.5m x 0.5m blocks of dried sediment 0.01 m deep, containing *R. tuberosa* seeds and perennating organs, were excavated from the eulittoral zone and planted in the remaining experimental plots in each habitat. The majority of seeds and perennating organs from both habitats were probably from the 1976-77 season, but viable material from previous years also may have been present. Similar samples were germinated in the laboratory to check the viability of seeds.

Plots were examined in March, July, September and November 1977 and in January 1978. Those in the temporary habitat were replanted in March 1977 after disturbance by vandals. The temporary habitat was inundated from July to November 1977 by 0.05-0.2 m of water.

Results are presented in Table 9.1. No seed or rhizome growth of *R. megacarpa* was recorded in either experimental plot. Rhizome growth occurred in the control plot of the permanent habitat in November 1977. No growth of *R. tuberosa* occurred in the experimental plot of the permanent habitat. Growth of *R. tuberosa* from seed and perennating organs was recorded in the experimental plot of the temporary habitat in

Table 9.1 Field transplantation trial: growth of *R. tuberosa* and *R. megacarpa* in temporary and permanent habitats in Little Dip Lake in 1977

Species	Material	Temporary Habitat		Permanent Habitat	
		Experimental Plot	Control Plot	Experimental Plot	Control Plot
R. tuberosa	seeds	+	+	-	-
	turions	+	+	-	-
R. megacarpa	seeds	-	-	-	-
	rhizomes	-	-	-	+

\+ growth

\- no growth

July and September 1977. More prolific growth occurred in the control plot of the temporary habitat and flowering of *R. tuberosa* was recorded in these temporary habitats in September (spring).

Thus although neither *R. tuberosa* nor *R. megacarpa* grew in alternate habitats no definitive conclusions can be drawn as these species did not grow in the experimental plots of the permanent habitat. Since no seed germination of *R. megacarpa* was recorded in the field (1975-1978) it is postulated that the germination requirements of this species were not satisfied in either habitat throughout this period. Sediment disturbance may have altered conditions and prevented seed or rhizome growth in the experimental plots of the permanent habitat, while the relatively stable sediments around the existing *R. megacarpa* clumps (in the control) provided suitable conditions for rhizome growth.

2. Laboratory growth trials

Eight laboratory trials were set up to test growth responses under different conditions and to propagate material for physiological studies. The experimental conditions and results of the trials are summarized in Table 9.2. More detailed discussion of salinity trials and of requirements for germination are given in Section 9.3.

Table 9.2 Laboratory growth trials: experimental conditions and results

Trial No.	Date	Field conditions: Material: Origin	Species	Type	Habitat	Laboratory conditions: Water: Salinity °/oo TDS	Origin	Sediment Origin	Temp °C	Light	Day length	Location of trial	Results and Comments
1	4.76	LDL LR EH FP LESM LESM	M T M T T M	v v v v v v	p e p p e p	29 51 13 66 22 25	Coorong 66 °/oo TDS diluted with rain water	Collection site mixed with washed sand	A	D	N	1 x 1 x 1 m plastic lined bins roof of Dept	- tanks disturbed and moved Dec 76 - all material except LESM A declined without regrowth, LESM A germinated then declined - discontinued July 77
2	11.76	PoL	M	s	p	dry	rewet by rain 3.77, 2.78	Collection site	A	D	N	0.25x0.2x0.08m plastic dishes roof	- half seeds stored dry 18°C for 12 months. First half germinated May 77, second half germinated March 78 flowered Sept 78
	1.77	LDL	M	s	p	distilled water		none	A	D	N	laboratory shelf	germination March 77 rewet Feb. 78 germination March 78
3	12.76 1.77	All sites	T,M,P	v	p,e	habitat 1.77	lakewater and salty rainwater	Collection sites				plastic dishes roof of Dept	ephemeral trials - germination July 77 permanent trial - shoots from nodes Nov 77
4	1.77	BGAP	P	t,s	e	<1	distilled water	Collection site	A	D	N	0.5x0.5x1.0m tank	BGAP - germinated 7.77 flowered 9.77, germinated Nov 77, flowered Jan 78
		LDL	M	v,s	p	dry	rain	"	A	D	N	plastic dishes	LDL B - no growth
5	4.77	LDL LDL PoL	T M M	s s s	e p p	10 19 32 46 64 84	NaCl + nutrient solution (Gerloff's) + distilled water	washed sand	20°C day 10°C night	fluoro/ growlux light bank	12hr L 12hr D	constant temp room aquarium tanks	initial growth followed by decline of all material, general trend of earlier decline in higher salinities
6	7.77	Ephemeral sites All sites	T,P T,M,P	sl v,f	e v,f,p	from field sites	levels maintained with distilled water	Collection site	A	D 52% D from 12.77	N	plastic trays	Ephemeral - growth in all trials, flowering in some Ephemeral - growth→flowering from seeds and turions Permanent - growth→decline
7	12.77	LDL LDL B/p SL LR BGAP	M M T T P	Rh s t sl s	p p p e e	6 12 25	Coorong salts + distilled water	washed sand	A	52% D	N	1.0x1.5m diameter fibreglass tanks	LDL B rh - decline LDL B s - germination 6°/oo 12 °/oo - decline B/p SL - germination 6 °/oo, 12 °/oo, 25°/oo - decline LR - decline after initial growth BGAP - no germination
8	12.77	B/p SL LDL	T M	t Rh	p p	10 19 32 46 64 84	LDL water diluted	washed sand	A	52% D or light bank	N	aquarium tanks roof	replicates under light bank - decline (burning) - outside trial - rhizomes - declined in all salinities - turions - germination, decline after initial growth in all salinities

M - *R. megacarpa* P - *R. polycarpa* T - *R. tuberosa* p - permanent e - ephemeral v - vegetative material
s - seeds t - turions sl - seedlings Rh - rhizomes f - flowering A - ambient temperature
D - daylight N - normal day length

Trials were designed to propagate plants from vegetative material to determine suitable growth conditions, and to follow through the life cycle of *Ruppia* transplanted from various habitats (Trials 1, 3, 6; Table 9.2). All material in Trial 1 showed a gradual decline in condition. *R. tuberosa* from the Lake Eliza Salt Marsh showed some new growth but even this declined after several weeks. Coorong water was possibly not suitable as a plant growth medium. In Trial 3, samples collected from ephemeral habitats were left dry until rainwater covered the dry sediments in May 1977. Germination and growth of *R. tuberosa* occurred in these trays. Growth of the perennial *R. megacarpa* by new shoots and by roots from stem nodes occurred in late spring 1977 and summer 1977-78. Flowering was not recorded in these trials. Seedlings and mature plants were set up in July and September 1977 (Trial 6) under similar conditions to Trial 3. Flowering was recorded for *R. tuberosa* from many of the ephemeral sites and vegetative growth of *R. megacarpa* was maintained. *Ruppia* from Fresh Dip Lake, which was kept under permanent conditions grew, flowered, then senesced without setting fruit. This parallels the 1977-78 field situation where fruit did not set on plants in Fresh Dip Lake.

These trials confirmed that *Ruppia* can be propagated, at least for short periods, in the laboratory under simulated field conditions, and that normal growth sequences are maintained under these conditions.

Responses of seeds, perennating organs and rhizomes to various conditions were tested in Trials 2 and 7. Germination of *R. megacarpa* seeds from Porters Lagoon was tested in Trial 2. These seeds were collected from permanent habitats and were allowed to dry in the trial plots. Half these seeds were rewet by rain in March 1977 and the other half in February 1978 after dry storage at 18^{o}C. In each trial over 50% of the seeds germinated, and the 1978 plants were grown until they flowered. It is not known whether any of the seeds collected were produced prior to the 1976-77 season, so the possibility of a long

term dormancy of seeds could not be explored. These results show that seeds from *R. megacarpa* at Porters Lagoon are viable for over 12 months and that germination can occur after the type of desiccation experienced in ephemeral habitats.

Germination and growth of the three species of *Ruppia* under permanent conditions of varying salinity were tested in Trial 7. Growth of *R. tuberosa* from perennating organs occurred in all three trial salinities, and germination of *R. megacarpa* seeds was recorded in the two lower salinities. Growth from rhizomes of *R. megacarpa* gradually deteriorated; seeds of *R. polycarpa* failed to germinate. Seedlings of *R. tuberosa* transplanted from Lake Robe grew for a short time and then died back. The paucity of plant growth under these conditions may again parallel the situation in Trial 1 where salts from the Coorong were used.

The stability of growth form of *Ruppia* transplanted from ephemeral lakes to permanent conditions, and of perennial *Ruppia* under ephemeral conditions was tested (Trial 4) to confirm the results of the field trial. Dried mats of the annual *R. polycarpa* from Blue-Green Algal Pool, and submerged vegetative and seed material of the perennial *R. megacarpa* from Little Dip Lake, were transplanted in July 1977. The dried material from Blue-Green Algal Pool was set up in distilled water 1 m deep; *R. polycarpa* grew, flowered and produced fruit between July and October. It died back in November, but further germination and subsequent growth and flowering occurred from January to March 1978. This second generation may have grown from seeds produced in October 1977 or possibly from dormant seeds from the original sediment mat. Only one generation grew in the control trial before drying occurred. *R. polycarpa* maintained its small growth form and annual life cycle even under permanent conditions.

Shoots, rhizomes and seeds of *R. megacarpa* were allowed to dry; no growth occurred subsequent to rewetting. Controls in permanent

water grew shoots from both rhizomes and stem nodes in November 1977. These results support the hypothesis that *R. megacarpa* does not regenerate after drying.

The propagation and maintenance of *Ruppia* under varied salinities was examined (Trials 5, 7, 8). Seeds of *R. tuberosa* and *R. megacarpa* and shoots from perennating organs and rhizomes (respectively) were transplanted. Initial growth was followed by senescence in all cases; senescence occurred first in the higher salinities.

Water from individual collection sites or from Little Dip Lake (Trials 3, 6, 8) appeared to be a more suitable medium for propagation of *Ruppia* than either Coorong water (Trials 1 and 7) or the artificial Gerloff's Solution (Gerloff and Krombholz 1966) plus sodium chloride (Trial 5).

In summary, these trials showed that under laboratory conditions the annual form *R. polycarpa* maintained its annual life cycle and delicate growth form when permanently submerged. Vegetative parts (rhizomes) of *R. megacarpa* failed to regenerate following drying. Germination of some *R. megacarpa* seeds after drying was recorded in the laboratory and these seedlings were more robust than seedlings of the annual species.

These preliminary trials suggested that rewetting stimulates growth of annual *Ruppia* in ephemeral habitats, and that decrease in salinity stimulates germination and growth of *R. megacarpa*. These hypotheses are tested in the germination trial (Section 9.3.1).

9.3 Physiological experiments

1. Germination and Dormancy

Field observations suggested that the annual species of *Ruppia* were propagated from seeds and perennating organs and the perennial species regenerated mainly by rhizomes even though viable seeds were produced. No germination of the seeds of *R. megacarpa*

was recorded in the field and this confirmed the observations of Higginson (1967) and Congdon (pers. comm. 1978) who rarely saw germination of seeds from perennial populations in New South Wales and Western Australia respectively. Preliminary investigations of Higginson (1967) suggested that cold treatment, salinity decrease and seed coat breakage enhanced germination of *Ruppia* in the Tuggerah Lakes (coastal New South Wales).

Dormancy of seeds and perennating organs limits the time and place of plant growth by predetermination of the environmental conditions under which growth will occur; advantageous conditions are thus probable while detrimental conditions are avoided (Leopold and Kriedmann 1975). Dormancy can be imposed and maintained by properties of the seed coat, by the immaturity or physiological state of the embryo, or by a combination of these factors (Villiers in Kozlowski 1972). Most aquatic angiosperms have dormant seeds and Sculthorpe (1967) suggested that this is largely due to either the mechanical constriction of the embryo in a tightly sealed endocarp or the impermeability of the endocarp.

It appeared that the breakage of dormancy was important in the propagation of both annual and perennial forms from seed and this postulate was examined further by laboratory trials. Some of the environmental factors previously reported to affect seed dormancy, e.g. photoperiod, water salinity, drying and diurnal temperature ranges, were tested using the annual *R. tuberosa* and the perennial *R. megacarpa* from Little Dip Lake.

A large scale factorial experiment and a series of supplementary trials were established to examine the factors affecting dormancy breakage in *Ruppia* seeds. In all trials it was assumed that seeds were collected from statistically normal populations. Seed viability was tested with 1% 2,3,5 triphenyl tetrazolium hydrochloride (Lakon 1949) and viability was estimated to be greater than 60% for *R. megacarpa* and 30% for *R. tuberosa*. The lower viability for *R. tuberosa* is likely

to be caused by the inclusion of relatively large numbers of empty seed cases which were more easily detected and removed from the *R. megacarpa* seeds. To ensure their maturity, all seeds were collected from sediments rather than from their parent plants, thus the age of seeds could not be accurately determined.

Germination Trials

Trials designed to test the after-ripening requirements of seeds were started concurrently with the factorial experiment and continued for 20 months from March 1977 to October 1978. Germination was recorded in the first growing season for seeds of all three species (Tables 9.3 and 9.4). In the second growing season over 40% of the initial number of seeds of *R. megacarpa* germinated after either permanently wet or dry and rewet conditions (Table 9.3). Seeds of *R. tuberosa* from Little Dip Lake sediments also germinated in the second season but the germination percentage was low (Table 9.4). The germination of *R. polycarpa* in the second season could not be directly related to the initial seed bank as seeds which set after the first laboratory generation had not been removed. As the initial number of seeds of annual *Ruppia* present in the sediments was not known, accurate germination percentages for the annual species were not available. However the necessity for an extended after-ripening period for a proportion of the seeds is suggested from these data.

Anaerobic muds were examined as potential inhibitors of germination in *R. megacarpa* seeds. Laboratory trials tested germination of seeds with and without the anaerobic sediments (Table 9.5). Seeds were placed in distilled water, saline water (LDL), or with sediments in saline water or under ephemeral conditions. All trials were diluted by periodic rainfall. Seeds without sediments germinated in distilled water, but not in saline water. A similar result was recorded in the subsequent growing season after the water level was renewed with distilled water. Seeds within the sediments germinated in both trials after

Table 9.3 Germination of seeds of perennial *Ruppia megacarpa* in successive growing seasons

		Little Dip Lake	Porters Lagoon
Germination % of initial no. of seeds	Feb 77	40	35
	March 78	42	50
Conditions		distilled H_2O window ledge in laboratory no sediments permanently wet	lake water diluted by rain roof, Zoology Dept. gravel substrate dried after March 77 rewet by rain Feb. 78

Table 9.4 Germination of seeds of the annuals *Ruppia tuberosa* and *Ruppia polycarpa* in successive growing seasons

Date	*R. tuberosa* Little Dip Lake	*R. polycarpa* Blue-Green Algal Pool
Feb. 77	Trial commenced	Trial commenced
July 77	↓	Seed germination
Sept. 77	Seed germination	Flowering, seeds set
Jan. 78	↓	Seed germination
Sept. 78	Seed germination (low %)	

Table 9.5 Germination of seeds of *Ruppia megacarpa* with and without anaerobic mud sediments

Date	Seeds only		Seeds and sediments	
	Distilled H_2O	Saline H_2O	dry, rewet	permanent 10cm H_2O
Feb. 77	Trial commenced	Trial commenced		
March 77	Germination	↓		
Feb. 78	↓	↓	Trial commenced	Trial commenced
March 78	Germination	↓	↓	↓
Aug. 78	↓	↓	Germination	Germination
water addition	retopped Feb. 78		rain April - July 78	

seasonal rain diluted the overlying water. Thus seeds of the perennial *R. megacarpa* germinated with or without sediments but did not germinate unless salinity decreased.

Factorial experiment

A factorial experiment was designed to test parameters affecting seed dormancy and to detect synergistic effects. The factorial experimental design enabled the examination of independent, as well as combined, effects as equal number of observations for each set of variables were included.

Materials and methods

Seeds from the annual *R. tuberosa* and the perennial *R. megacarpa* population from Little Dip Lake were collected and kept in sediments from their respective habitats in January 1977. *R. tuberosa* seeds (E_1) were collected from the dried salt- and vegetation-crust and were stored at 18°C. *R. megacarpa* (E_o) seeds, collected with an Ekman grab from around *R. megacarpa* clumps in 0.5 - 2.0 m of water, were washed gently from the muds with a mixture of sea water and distilled water adjusted to the salinity of Little Dip Lake. These E_o seeds were stored at 18°C in water from Little Dip Lake, or outdoors under normal diurnal temperature and light.

Germination dishes were prepared by lining sterile plastic petri dishes (5 cm diameter) with two Whatman No.1 filter papers. Twenty seeds per dish were spaced with maximum distance between them to minimize any possible inhibitory or stimulatory effects of substances produced by germinating seeds.

Five parameters, cold treatment (*a*), seed coat breakage (*b*), water salinity (*c*), light (*d*) and species (*e*), were tested, each at two levels (Table 9.6), except parameter *b* which was tested at one level only for E_o seeds as insufficient seeds were available. The E_o seeds

Table 9.6 Treatments for each parameter tested in the germination trial

Parameter	Level	Treatment
a Cold pretreatment	A	4 - 20°C daily, 14 days
	A_o	4°C, 7 days
control	A_1	no cold treatment
b Seed coat breakage	B	wet/dry (two cycles wetting with distilled H_2O)
	B_o	mechanical breakage (shaking with sandpaper)
control	B_1	no seed coat breakage
c Salinity	C	distilled water
	C_o	water conductivity 25 mS. (19°/oo TDS) (LDL:distilled, 1:1)
control	C_1	water conductivity 50 mS. (42°/oo TDS) (LDL water)
d Light (8 Growlux fluoro tubes)	D	16 hrs light : 8 hrs dark
	D_o	8 hrs light :16 hrs dark
controls	D_1	24 hrs light : 0 hrs dark
	D_2	0 hrs light :24 hrs dark
e Species	E_1	ephemeral habitat, annual, LDL, small seed *(R. tuberosa)*
	E_o	permanent habitat, perennial, LDL, large seed *(R. megacarpa)*
	E_2	perennial, Porters Lagoon *(R. megacarpa)* roof tanks
	E_3	annual, Blue-Green Algal Pool *(R. polycarpa)* roof tanks

were subjected to the wet/dry seed coat breakage treatment (B) and this was compared with a control in which no seed coat breakage occurred (B_1). Treatments and the experimental design are set out in Table 9.6 and Figure 9.1 respectively.

The trials were conducted with three replicates in a constant temperature room at 18-20°C; they were checked for germination daily and watered when required. The trial was run in March and April 1977 and was discontinued after 8 weeks. 80 seeds were under each treatment combination giving a total of 1280 seeds for E_1 and 640 seeds for E_o. E_1 and E_o were analysed to compare species.

Controls were run simultaneously. General controls under simulated field conditions with normal day length (*d*), salinity fluctuations, (*c*), diurnal temperatures (*a*) and seed coat breakage (*b*) were set up outside with E_o and E_1 seeds in sediments from their habitats. Similar controls were set up for E_o in the laboratory without mud and in distilled water (Table 9.7). Controls for the factorial experiment had no cold treatment (A_1), no seed coat breakage (B_1), highly saline water (50 mS.) (C_1) and 24 hours light (D_1) or dark (D_2) (see Table 9.6).

Results

The total number of germinations per treatment combination and the percentage germination for *R. megacarpa* (E_o) and *R. tuberosa* (E_1) are tabulated for the factorial treatments and controls in Table 9.7.

The controls which compared cold (A_o) with no cold (A_1) both showed approximately 30% germination for *R. tuberosa* and no germination for *R. megacarpa*. The similarity of results with and without cold suggests that cold treatment did not affect germination significantly. The germination percentage for *R. tuberosa* without any mechanical seed coat breakage, (B_1), is probably not representative as the seed stock from which seeds were extracted was collected dry and seeds had probably already undergone the wet/dry regime in the field. There was 24% germination of *R. tuberosa* in the high salinity control (C_1)

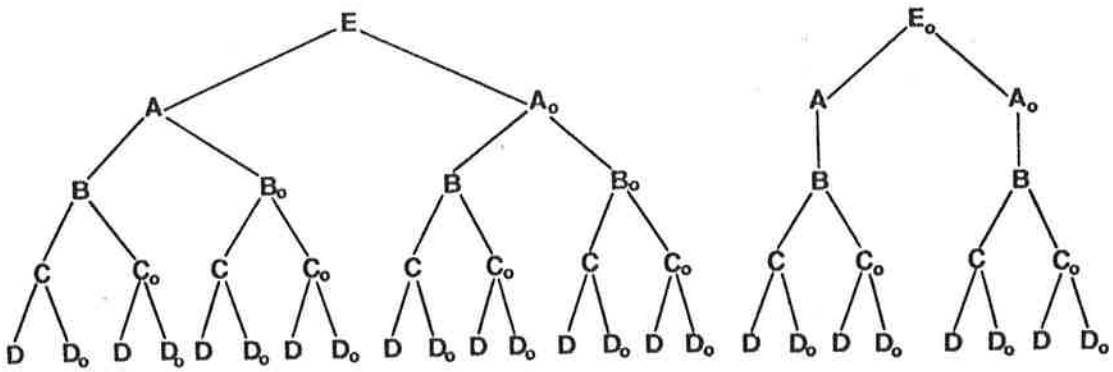

Figure 9.1 Factorial experimental design used in the germination trial.

Table 9.7 Results of germination trials

I. Factorial Trial

Treatment				Seed Type			
				E_1 (*R. tuberosa* LDL)		E_0 (*R. megacarpa* LDL)	
A/A_o	B/B_o	C/C_o	D/D_o	No. seeds germinated	% Total	No. seeds germinated	% Total
A	B_o	C_o	D_o	4	2.9		
A_o	B	C_o	D_o	22	15.8	2	1.1
A_o	B_o	C	D_o	1	0.7		
A_o	B_o	C_o	D	5	3.6		
A	B	C_o	D_o	21	15.1	7	3.7
A	B_o	C	D_o	2	1.4		
A	B_o	C_o	D	3	2.2		
A_o	B	C	D_o	13	9.4	57	29.8
A_o	B	C_o	D	22	15.8	0	0
A_o	B_o	C	D	0	0		
A	B	C	D_o	8	5.8	47	24.0
A	B	C_o	D	15	10.8	4	2.1
A_o	B	C	D	10	7.2	36	18.9
A	B_o	C	D	1	0.7		
A	B	C	D	7	5.0	38	19.9
A_o	B_o	C_o	D_o	5	3.6		
					100%		100%
Total seeds germinated				139		191	
Total No. seeds				1280		640	
% Germinated/Total				10.9		29.8	

II. Control Trials Treatment	E_1 *R. tuberosa* No. seeds germinated	% Total	E_0 *R. megacarpa* No. seeds germinated	% Total
A_o (cold) $B_1C_1D_o$	40/120	33	0	0
$B_1C_1D_1$				
A (no cold) $B_1C_1D_2$	36/120	30	0	0
B_1 no mechanical breakage ≡B for E_1	76/320	23.75	0	0
C_1 (high salinity) light : dark	76/320	23.75	0	0
D_1 24 : 0	25/80	31.25	0	0
D_2 0 : 24	23/80	28.75	0	0
D^2 16 : 8	13/80	16.25	0	0
D_o 8 : 16	15/80	18.75	0	0

Table 9.8 Germination of *R. tuberosa* seeds under various treatment combinations: analysis of variance

R. tuberosa seeds (LDL)

Replicates \ Treatment	$AB_oC_oD_o$	$A_oBC_oD_o$	$A_oB_oCD_o$	$A_oB_oC_oD$	ABC_oD_o	AB_oCD_o	AB_oC_oD	A_oBCD_o	A_oBC_oD	A_oB_oCD	$ABCD_o$	ABC_oD	A_oBCD	AB_oCD	$ABCD$	$A_oB_oC_oD_o$	Total
I	1	4	1	0	4	0	2	2	5	0	3	2	3	0	2	1	30
II	1	6	0	3	6	0	0	6	9	0	3	4	2	0	4	1	45
III	0	9	0	2	6	2	1	3	3	0	1	5	4	1	1	1	39
IV	2	3	0	0	5	0	0	2	5	0	1	4	1	0	0	2	25
Total	4	22	1	5	21	2	3	13	22	0	8	15	10	1	7	5	139

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
Trial replicates (4)	3	15.05	5.02	F(3,45) = 2.91 $0.05<F<0.25$
a	1	4.52	4.52	F(1,45) = 2.63 NS
b	1	147.02	147.02	F(1,45) = 85.48 S
c	1	47.27	47.27	F(1,45) = 27.48 S
d	1	2.64	2.64	F(1,45) = 1.53 NS
ab	1	3.50	3.50	F(1,45) = 2.03 NS
ac	1	0.39	0.39	F(1,45) = 0.23 NS
ad	1	0.02	0.02	F(1,45) = 0.01 NS
bc	1	13.14	13.14	F(1,45) = 7.63 S
bd	1	0.77	0.77	F(1,45) = 0.45 NS
cd	1	0.02	0.02	F(1,45) = 0.01 NS
abc	1	0.39	0.39	F(1,45) = 0.23 NS
abd	1	0.14	0.14	F(1,45) = 0.08 NS
bcd	1	0.14	0.14	F(1,45) = 0.08 NS
acd	1	1.27	1.27	F(1,45) = 0.74 NS
abcd	1	0.77	0.77	F(1,45) = 0.45 NS
Treatments (16)	15	222.00	14.80	
Error	45	77.70	1.72	
Total	63	314.75		

NS-not significant
S-significant

Table 9.9 Germination of *R. megacarpa* seeds under various treatment combinations: analysis of variance

R. megacarpa seeds (LDL)

Replicates \ Treatment	AC_oD_o	A_oCD_o	A_oC_oD	ACD_o	AC_oD	A_oCD	ACD	$A_oC_oD_o$	Total
I	3	18	0	15	2	14	8	1	61
II	1	12	0	9	0	11	9	0	42
III	2	13	0	11	2	4	16	0	48
IV	1	14	0	12	0	7	5	1	40
Total	7	57	0	47	4	36	38	2	191

b treatment for all seeds was B, wet/dry x 2

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F
No. replicates (4)	3	33.63	2.8	F(3,21) = 0.43 NS
a	1	0.03	0.03	F(1,21) = 0.0046 NS
c	1	850.80	850.80	F(1,21) = 130.69 S
d	1	38.30	38.30	F(1,21) = 5.88 NS at 0.025
ac	1	9.00	9.00	F(1,21) = 1.38 NS
ad	1	3.80	3.80	F(1,21) = 0.58 NS
cd	1	19.50	19.50	F(1,21) = 0.81 NS
acd	1	5.30	5.30	F(1,21) = 0.63 NS
Treatments (8)	7	926.70	132.39	
Error	21	136.60	6.51	
Total	31	1096.9		

NS - not significant
S - significant

Table 9.10 2 x 2 Contingency tables and χ^2 analysis of independent treatments

G - germinated
NG - not germinated

E_1 *R. tuberosa*

	G	NG	
A	61	579	640
A_0	78	562	640
	139	141	1280

χ^2 = 2.33
P> 0.1
not significant

	G	NG	
B	118	522	640
B_0	21	619	640
	139	1141	1280

χ^2 = 75.94
P<0.005
significant

	G	NG	
C	42	598	640
C_0	97	543	640
	139	1141	1280

χ^2 = 24.41
P<0.005
significant

	G	NG	
D	63	577	640
D_0	76	564	640
	139	1141	1280

χ^2 = 1.36
P>0.1
not significant

E_0 *R. megacarpa*

	G	NG	
A	96	224	320
A_0	95	225	320
	191	449	640

χ^2 = 0.0075
P> 0.5
Not significant

	G	NG	
C	178	142	320
C_0	13	307	320
	191	449	640

χ^2 = 203.17
P<0.005
significant

	G	NG	
D	78	242	320
D_0	113	207	320
	191	449	640

χ^2 = 9.14
P<0.005
significant

Table 9.11 Contingency table and χ^2 analysis for treatment combinations of seed coat breakage (*b*) and salinity (*c*) for *R. tuberosa*

		C	C_0	
B	G	38	80	640
	NG	282	240	
B_0	G	4	17	640
	NG	316	303	
		640	640	1280

χ^2 values for C and C_0 in the presence of B χ^2 = 18.33 P<0.005
C and C_0 in the presence of B_0 χ^2 = 8.32 P<0.005
B and B_0 in the presence of C χ^2 = 29.46 P<0.005
B and B_0 in the presence of C_0 χ^2 = 48.22 P<0.005

compared with no germination for *R. megacarpa* seeds. This confirms and extends the results of the distilled water and salinity treatments (C_o and C_1) which suggest that *R. tuberosa* seeds germinate in saline water whereas *R. megacarpa* seeds germinate in fresh water. The higher germination rate for *R. tuberosa* with 24 hours light or 24 hours dark (D_1 or D_2) than with either diurnal regime (D or D_o) may indicate that disturbance (i.e. physical movement of seed trays from dark to light) may lower germination.

Germination did not occur in seeds of the perennial species from Little Dip Lake (E_o) or Porters Lagoon (E_4) when subject to no seed coat breakage (B_1), salinity of 50 mS. (C_1), 24 hours light (D_1) or 24 hours dark (D_2). This may indicate that one of these factors has a dominating inhibitory effect. Lack of seed coat breakage and high salinity are the most likely factors as the opposing treatments produced a significant percentage of germination in the main trial.

Analysis of results

The results were subjected to an analysis of variance to examine the significance of the individual treatments and their interactions on germination. F values with a probability of 1% or less are accepted as highly significant and probabilities between 1 and 2.5% as significant. Probabilities between 2.5 and 5% are considered to be of doubtful significance because of the relatively small sample sizes. The analysis of variance tables for *R. tuberosa* and *R. megacarpa* are presented in Tables 9.8 and 9.9 respectively. These analyses indicated highly significant effects of salinity (*c*) for both species and for seed coat breakage (*b*) for *R. tuberosa*. An F value with a probability of 2.5% was obtained for photoperiod (*d*) for *R. megacarpa* seeds. This factor needs further examination. The only interaction with a significant F value was seed coat breakage and salinity (*bc*) for *R. tuberosa*. The factors *b* and *c* and their interaction *bc* must be examined more closely to determine whether these effects are significant independently as well as in combination.

The null hypothesis that the percentage germination of seeds is independent of the level of a parameter is re-examined for each factor by chi-square test. The total number of germinations for each level are tabulated separately for each parameter and are presented in 2 x 2 contingency tables (Table 9.10). The null hypothesis is accepted for parameter *a* (cold treatment) for *R. megacarpa* and *R. tuberosa* and for parameter *d* (light) for *R. tuberosa*. Significant chi-square values for the parameters *b* (seed coat breakage) and *c* (salinity) for *R. tuberosa* seeds and for *c* for *R. megacarpa* seeds confirm that these factors are significant, as indicated by the analysis of variance. A significant value is also obtained for *d* for *R. megacarpa*. The null hypothesis is rejected for these parameters.

Thus salinity (*c*) has a positive effect on the germination of *R. tuberosa* seeds and a negative effect on the germination of *R. megacarpa* seeds. Seed coat breakage (*b*) by wetting and drying has a positive effect on germination of *R. tuberosa* seeds, and the shorter photoperiod (*d*) has a positive effect on the germination of E_o seeds. As previously stated, no conclusions can be drawn from factor *d* as deviations are not as highly significant as for other parameters. Twenty four hour light and twenty four hour dark treatments produced no germination in *R. megacarpa* but parallel trials for *R. tuberosa* both yielded higher germination percentages than either diurnal regime (Table 9.7 II).

The synergistic effect of salinity and seed coat breakage (*bc*) was analysed further for *R. tuberosa* by testing the independence of these characters. A contingency table of the germination of seeds under each treatment combination of seed coat breakage and salinity (*b* and *c*) was constructed, and the two treatments levels for each parameter were compared by chi-square at each level of the other factor (Table 9.11).

Table 9.12 Germination percentage of seeds of *R. megacarpa* and *R. tuberosa* at different levels of salinity: data expressed as percentage germination

Species \ Salinity °/oo TDS	0	19	42
R. megacarpa	27.8	2.0	0
R. tuberosa	1.2	6.6	23.8

In each case the null hypothesis that the two factors are independent is rejected. Thus the differential effects of C and C_o and B and B_o are significant irrespective of the level of the other factor present. The significance of the *bc* interaction in the analysis of variance is probably due to the numerical differences in the values of *b* and *c* even though individually they are always very significant.

Discussion

Salinity and seed coat breakage by wetting and drying stimulate germination of the small seeds of *R. tuberosa* (E_1). A further increase in salinity from 19 to 42 °/oo TDS in the control trials increases this germination percentage (Table 9.12). The seeds of *R. megacarpa* respond to salinity in an opposite way, with high germination levels in distilled water but apparent inhibition in saline waters (Table 9.12).

Higher germination percentages for seeds which have undergone seed coat breakage by wetting and drying rather than mechanical breakage are recorded for *R. tuberosa* seeds. All trials for *R. megacarpa* underwent this wetting and drying treatment and 30% of seeds germinated. Supplementary trials showed that seeds of *R. megacarpa* germinated in lower salinities with or without drying. This indicates that the main factor controlling germination is salinity rather than seed coat breakage.

These trends can be used to interpret field observations on dormancy and to account for differences in the life cycles of the two growth forms of *Ruppia*. The wetting and drying of seeds and substrate in the ephemeral habitats is likely to bring about seed coat breakage and to make seeds permeable to water. Imbibition of water by the seed initiates the development of enzyme systems which are thought to induce embryo growth (Leopold and Kriedmann 1975). In ephemeral habitats where aquatic plants have short annual life cycles, the seed coat

breakage during the dry season may prove advantageous as seeds are ready to germinate when the habitats are rewet; plants thereby maximize their use of the short wet phase for growth. Seed coat breakage by drying would be rare in permanent habitats of the perennial *Ruppia*.

The differential effects of salinity on the germination of seeds of the annual and perennial forms may also reflect differences in the life cycle strategies of the two forms. The strong correlation of low salinity with germination of seeds of the perennial is consistent with the lack of seed germination records from permanent saline habitats and the failure of *R. megacarpa* to germinate or establish when transplanted to temporary (more saline) habitats (Table 9.1). The seeds of the perennial *R. megacarpa* remain dormant in permanent relatively stable environments conducive to vegetative growth and rhizomatous spread. Germination is most likely after heavy rain when the waters will dilute and conditions are conducive to germination and seedling growth. Thus the potential for propagation by seeds is conserved until a disturbance such as salinity decrease within the habitat results in seed germination.

Whereas salinity is usually inhibitory or toxic to seed germination (Mayer and Poljakoff-Mayber 1963) the annual species *R. tuberosa* clearly shows the opposite trend (Table 9.12). This positive response of seed germination of the annual *R. tuberosa* to high salinity is probably an opportunistic strategy which enables this species to survive in ephemeral, unpredictable and extremely saline conditions. The ability to germinate in highly saline water rather than in fresh water would protect seeds from germinating prematurely when the first rains leave temporary fresh pools on salt pan surfaces for short periods before the lakes refill. Germination would be stimulated when salinity increased as the salts in ephemeral lake basins dissolved as the lakes refill. This would enable annual species to utilize to a

maximum the short growing season. The effects of saline water on the processes of germination in this halophytic plant need more detailed examination to substantiate and understand the physiological basis for seed germination under saline conditions.

2. Salinity

The effects of salinity were compared by relating data on salinity tolerance (Table 5.5) and the effects of salinity on growth (Table 9.2 Trials 5, 7, 8) and germination (Section 9.3.1) to habitat characters (Table 5.1) and fruit size (Table 8.10) for each species. These data are collated in Table 9.13.

Species of *Ruppia* have been recorded regularly in salinities from 2.1 to >108 °/oo TDS in the field sites, and on occasions plants have been recorded in salinities up to 230 °/oo TDS in salt pans of the Coorong region and on the Yorke Peninsula. In these extreme salinities there was little active plant growth: this is likely to be the result of increased temperature and salinity and decreased depth resulting from high evaporation. Many of the *Ruppia* populations in extreme salinities remained vegetative; those that did flower in water above 50 °/oo TDS were identified as *R. tuberosa*. Laboratory trials supported the view that senescence of plant growth was induced by higher salinities (Table 9.2).

Salinity tolerance ranges for the three species in the study sites can be estimated from Table 9.13: *R. tuberosa* grew over the salinity range from 10-108 °/oo TDS; *R. polycarpa* grew in salinities from 2-50 °/oo TDS; *R. megacarpa* grew in salinities from 12-50 °/oo TDS. Seasonal salinity variation within individual habitats was also high; ranges of 30 °/oo TDS were recorded for *R. megacarpa* and *R. polycarpa* and a range of over 50 °/oo TDS was recorded for *R. tuberosa* in the study sites (over 100 °/oo TDS in other areas).

Table 9.13 Comparison of seed length with habitat salinity, depth and permanence for *R. megacarpa*, *R. polycarpa* and *R. tuberosa*

Species	Location	Mean Endocarp Length (Table 8.10)	Habitat (Table 5.1)		
			Salinity Range °/oo TDS	Depth (m)	Permanence no. months wet
R. megacarpa	Porters Lagoon	3.12	12 - 29	0.4-2.0	12
	Little Dip Lake	3.09	18 - 39	0.4-2.5	12
	Lake Robe	3.03	20 - 50	0.2-1.0	12
	Lake Eliza Salt Marsh	2.59	20 - 24	0.1-0.2	12
R. polycarpa	Fresh Dip Lake	2.26	2.1-3.3	0.3-3.0	12
	Lake Robe	1.89	20 - 50	0.2-0.5	8-12
	Blue-Green Algal Pool	field 1.83	9 - 35	0.0-0.5	4-6
		lab 2.18	<1.0	0.15-1.0	12
R. tuberosa	Flax Point	2.02	37 - 90	0.2-0.5	12
	Beachport Salt Lake	1.95	64 - 108	0.1-0.6	12
	Coobowie	1.79	>38	0.1-0.5	12
	Lake Robe	1.71	20 - 50	0.0-0.4	4-7
	Little Dip Lake	1.55	19 - 24	0.0-0.3	4-12
	Lake Eliza Salt Marsh	1.25	10 - 25	0.0-0.2	4-5

No general correlation of seed size with salinity is apparent (Table 9.13). However seed size of each species does appear to increase with increases in the duration of the wet phases of the habitats. Correlations of seed size with salinity can be hypothesized within each annual species but not within the perennial species. Seed size increased with decrease in habitat salinity for the three *R. polycarpa* populations whereas there was a general increase in seed size with increase in salinity for the six habitats of *R. tuberosa*. The only laboratory trial which grew to set mature fruit supported this for *R. polycarpa; R. polycarpa* from Blue-Green Algal Pool was grown in a tank of permanent water of salinity <1 °/oo TDS and fruit produced from these plants had a mean endocarp length of 2.18 mm (n = 20 SE = 0.18) which was larger than the field mean endocarp lengths of 1.83 mm (n = 25 SE = 0.03) for seeds produced in salinities from 9 to 35 °/oo TDS. Seed character differences between species were greater than differences between populations of one species. These correlations of seed size with salinity need to be examined extensively both in the field and laboratory to establish the significance of these initial observations.

3. Osmoregulation

Ruppia occurs in a wider range of salinity than any other angiosperm. In the field sites studied *R. tuberosa* occurred over a range of 98 °/oo TDS, *R. megacarpa* over a range of 38 °/oo TDS and *R. polycarpa* over a range of 48 °/oo TDS. A plant completely submerged in saline water must either tolerate the high level of solutes in the medium or possess osmoregulatory mechanisms that enable it to reduce the effect of such high salinities. The actual range of salinities that individual plants will experience in

one habitat is possibly as important as the maximum salinity or range of salinities that the species can withstand as it indicates the physiological tolerance of cells of the individual organism. Populations of *Ruppia* are known to withstand fluctuations of over 50 $^{o}/_{oo}$ TDS in some study sites. Information on the methods and mechanisms that enable a physiological system to function while submerged in high and variable salinities can be explored through an examination of the osmoregulatory mechanisms of *Ruppia*. Previous studies of osmoregulatory mechanisms in halophytes have dealt mainly with emergent salt marsh or crop species (see Section 2.2).

Preliminary trials investigated the osmotic potential of the cells of *Ruppia* from various habitats and the values obtained were compared with the osmotic potentials of waters from these habitats.

Actively growing shoots of *Ruppia* were collected to minimize bias due to the age of the material. Plant 'sap' was collected with a capillary tube after extraction by grinding in a mortar and pestel in the field. As evaporation of fluid during this process may have been considerable, a mechanical tissue grinder was used in the field when available. Samples were frozen on dry ice and transported to the laboratory for osmotic measurements. Some samples were frozen whole, then ground and centrifuged in the laboratory. The osmotic fluid was extremely difficult to extract from the plants and as a result measurements for samples of *R. megacarpa* are not available.

Measurements of freezing point depression were made on a Halbmikro Osmometer (Knauer) and results are presented in Table 9.14. The relationship between the osmotic potential of the plant sap, water salinity and the osmotic potential of water samples is shown in Figure 9.2.

Table 9.14 Measurements of the osmotic potential of the sap of *Ruppia* plants and of the lake water from their habitats: measurements in milliosmols made by the freezing point depression method on a Halbmikro Osmometer (Knauer) in September 1977

Location	Species	Osmotic Potential milliosmols				Water Salinity °/oo TDS
		Ruppia		Water (habitat)		
		$\bar{x}$	SD	$\bar{x}$	SD	
Fresh Dip Lake	*R. polycarpa*	480	4.0	65	6.1	2
Blue-Green Algal Pool	*R. polycarpa*	564	13.9	403	1.5	12
Little Dip Lake	*R. tuberosa*	1198	50.0	685	5.0	21
Lake North of Salt Creek	*R. tuberosa*	1200	50.0	950	8.5	33
Coorong, Flax Point	*R. tuberosa*	1541	38.8	1330	15.3	38

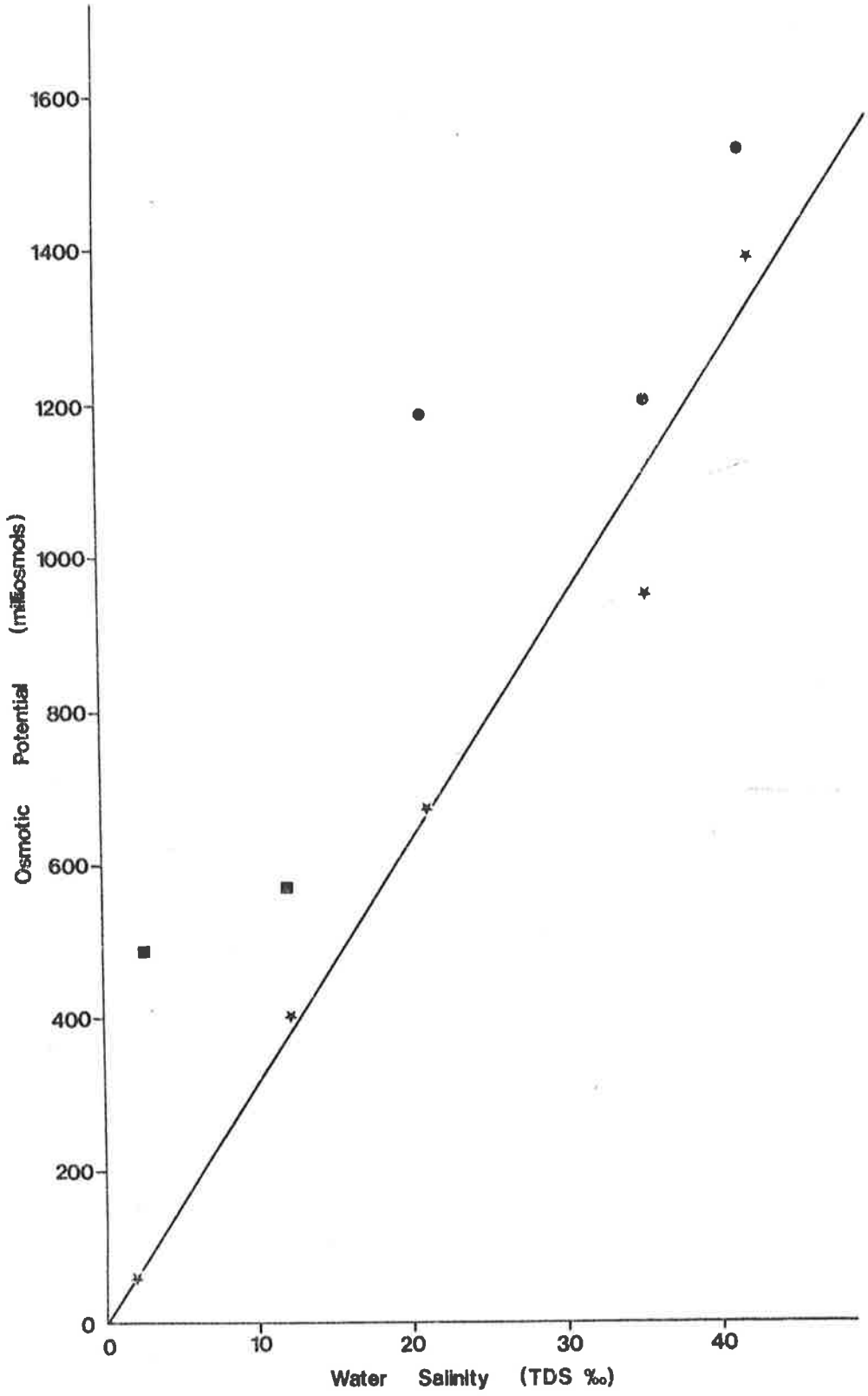

Figure 9.2 Changes in the osmotic potential of plant sap and habitat water with salinity increase: *R. tuberosa* ● , *R. polycarpa* ■ , water samples are represented by ★ at these locations: the line of best fit shows the increase in osmotic potential of the water with increase in salinity.

The osmotic potentials of plant fluids in all cases were greater than the osmotic potentials of water from the plant habitats. Evaporation during extraction of plant fluids may have exaggerated the differences between plants and their habitat water. However these results indicate that in a less saline environment the osmotic potential of the plant fluid decreases but remains at a level well above that of the surrounding medium. The value of 480 milliosmols for *Ruppia* in water of only 65 milliosmols suggests that there may be a lower limit to the osmotic potential of the plant fluid. Samples measured from plants from waters of higher salinities had osmotic potentials relatively closer to those of the external media.

The observation that the osmotic potential of the plant fluid is higher than that of the environment in all salinities tested implied that solutes must accumulate in the plant fluids (vacuolar, cytoplasmic and intercellular fluids were not separated).

Previous work indicates that, in halophytes, metabolic regulation is necessary to maintain lower levels of salts in the cytoplasm than in the external medium, as enzyme structure and function and many cell and organelle processes are impaired at high levels of sodium chloride (Ernst in Freysen and Woldendorp 1978). This regulation may be achieved in halophytes by excluding salts from metabolic sites, by compartmentation and possibly by the storage of ions. Selective accumulation of salts in vacuoles by the maintenance of an osmotic equilibrium between cytoplasm and vacuole has been proposed as an osmoregulatory mechanism (Wyn Jones *et al* 1977a; Ernst 1978). Accumulation of proline (Stewart and Lee 1974; Calvalieri and Huang 1979), glycerol (Ben-Amotz and Avron 1973) and betaine (Storey and Wyn Jones 1977; Wyn Jones *et al* 1977b) are reported to achieve this regulation in some species.

It has been postulated that amino acid accumulation may function as a salt tolerance mechanism by adjusting the osmotic potential of the cytoplasm to counterbalance high vacuolar solute levels induced by high external salinities (Stewart and Lee 1974; Treichel 1975; Storey and Wyn Jones 1977). As the halotolerant genus *Ruppia* occurs over a much wider range of salinity than any angiosperm species previously used for osmoregulatory studies, it provides an opportunity to examine solute accumulation over an extended salinity range. Consequently assays for proline were made in a series of samples of *Ruppia* from habitats of widely differing salinity levels and with wide seasonal salinity fluctuation. Plants of different age and species were assayed.

Materials and methods

Samples of *R. megacarpa*, *R. tuberosa* and *R. polycarpa* were taken from a number of field sites in the south-east of South Australia in August, September and November 1978. Growing shoots of uniform age were collected and frozen immediately on dry ice. Roots, rhizomes and other material were excluded from samples. The frozen samples were stored at -20°C within 24 hours of collection. Samples were freeze dried, weighed, ground and stored at 4°C in sealed bags.

Samples of 20 - 50 mg of ground tissue were weighed for each determination of free proline. Proline estimation followed the method of Faber and Aspinall (1977) modified from that of Troll and Lindsley (1955) and Singh *et al* (1973). Quantitative assays of proline were made by reading the optical density of acidic solutions of proline and ninhydrin. Other interfering amino acids (lysine, ornithine and hydroxylysine) were removed by shaking with Permutit resin.

Each sample of ground tissue was homogenized with approximately 1.5 g of Permutit resin (Folin Decalso-F) and 5 ml of M.C.W. (methanol: chloroform:water 12:5:3 by volume) until no large segments of plant material remained. The mixture was decanted into a centrifuge tube

together with a further 10 ml of M.C.W. which was used to rinse all traces of tissue from the homogenizer. Eight ml of water was added to each tube and tubes were centrifuged at 2000 r.p.m. for five minutes. The upper aqueous layer of each tube was transferred to a boiling tube and 5 ml of glacial acetic acid and 5 ml of ninhydrin reagent added (ninhydrin reagent: 125 g ninhydrin + 3 ml glacial acetic acid + 2 ml 5M orthophosphoric acid per sample dissolved over gentle heat <70^{o}C, within two hours of use). Tubes (with boiling chips added and marbles on top to prevent evaporation) were boiled for 45 minutes in a water bath and then cooled to room temperature. Ten ml of toluene (crystallizable) was added to each tube and shaken vigorously. Layers were allowed to separate for 30 minutes and optical densities were read at 520 nm. A series of standards with known amounts of proline were measured to establish a standard curve.

The proline concentration was determined from the standard curve and calculated on a dry weight basis from the equation $x = \frac{y-b}{m} \times \frac{D}{W}$ (where x = µg proline/g dry wt., y = optical density, b = y intercept for lowest dilution in toluene, m = slope of line for lowest dilution in toluene, D = dilution factor, W = initial weight of plant material). Proline determinations are reported in the literature in units of either mg proline per gram dry weight or as µmoles proline per gram fresh weight. For *Ruppia* this conversion can be made on the basis that dry weight is estimated as 15% of fresh weight (Chapter 5). Therefore 1 mg proline/g dry wt. = $\frac{15}{100} \times \frac{1}{115.5}$ mmoles/g fresh wt. (MW proline = 115.5), = 1.3 µmoles proline/g fresh wt.

Twenty eight samples comprising *Ruppia* of three species (from 10 sites collected on three occasions) and two samples of *Lepilaena cylindrocarpa* were assayed. Three proline determinations were made from each sample.

Results and discussion

The data (in mg/g dry weight and µmoles/g fresh weight) together with means and standard errors are presented in Appendix XIV. Proline concentrations are plotted against the salinity of the habitat water for each sampling time (Figure 9.3) and these data are separated for individual species (Figures 9.4, 9.5, 9.6). Changes in salinity and proline concentration throughout the growing season (August - November 1978) are plotted in Figure 9.7. Germination of *R. polycarpa* and *R. tuberosa* occurred in July and *R. megacarpa* began to shoot from rhizomes in August.

Although trends vary with stage in the growing season and species, a general increase in the proline concentration of tissue occurs with increase in habitat salinity for each sampling time (Figure 9.3). This finding is consistent with the observation that many halophytes, including *Ruppia*, accumulate proline when subjected to high salinities (Stewart and Lee 1974). However, the *Ruppia* analysed by Stewart and Lee was grown only in water salinities of up to 12 °/oo TDS (200 mM NaCl) whereas in the present study, the *Ruppia* tested was collected from waters with salinity concentrations from brackish to over 70 °/oo TDS (>1200 mM NaCl). For *R. maritima* Stewart and Lee reported that proline increased from 1 to 5 µmoles/g fresh weight with salinity increase from 0-9 °/oo TDS (0-150 mM NaCl): the material tested in this study had proline concentrations which increased from 0.6 to 5.0 mg dry weight (= 0.8-6.5 µmoles/g fresh weight) over the same salinity range, and proline levels generally continued to increase with increase in salinity. The highest proline level recorded was 47.7 mg proline/g dry weight (62 µmoles/g fresh weight) for *R. tuberosa* growing in water with a salinity of 65 °/oo TDS. This value is very similar to the highest values obtained by Cavalieri and Huang (1979) for *Limonium carolinianum* (Walt.) Britt. and

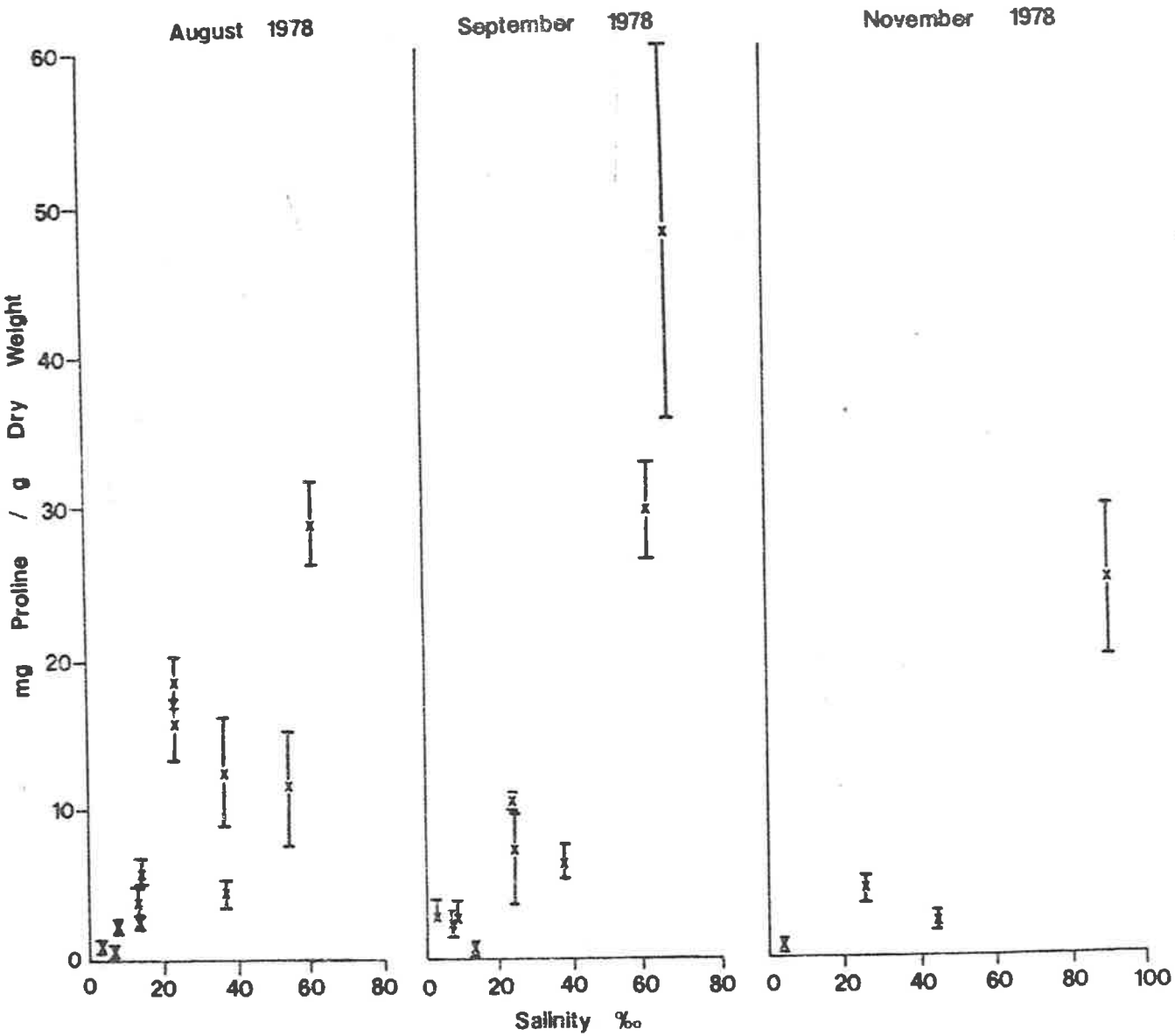

Figure 9.3 Proline concentration in *Ruppia* plotted against the salinity of water from the habitats: values for August, September and November 1978. Mean values with upper and lower standard errors are plotted for each sample (data in Appendix XIV).

Juncus roemerianus Scheele (60-70 μmoles/g fresh weight) grown in growth chambers at NaCl concentration of >800 mM (>55 °/oo TDS). However, Stewart and Lee (1974) recorded higher values for the halophytes *Triglochin maritima* L. (>300 μmoles/g fresh weight) and *Puccinellia maritima* (Huds.) Parl. (80 μmoles/g fresh weight). The values for all of these halophytes are considerably higher than the highest record of 24.1 mg/g dry weight (31.3 μmoles/g fresh weight) for specimens of barley grown under conditions of stress imposed by NaCl (Singh *et al* 1972).

The species *R. tuberosa* and *R. megacarpa* show increased proline content with increase in salinity (Figure 9.4, 9.5). Little information is available for *R. polycarpa* (Figure 9.6) as sites had similar salinities. The high values for *R. tuberosa* probably reflect the higher salinity tolerance of this species.

Studies of proline content and salinity change throughout the growing season (Figure 9.7) suggest that, although salinity increased over the period studied at all four sites for *R. tuberosa*, at three of the four sites the proline content of *R. tuberosa* reached a maximum and then declined. Flax Point was the only site in which proline levels continued to increase in November. Plants at this permanently aquatic site may not have reached their maximum growth by this collection date. Data for *R. megacarpa* and *R. polycarpa*, although limited, also show a decline in proline concentration later in the growing season. This decline may be related to a decrease in metabolic activity as the plant passes its maximum photosynthetic activity. A similar decrease in proline content was shown in *Triglochin maritima* by Stewart and Lee (1974). This is consistent with the hypothesis that proline functions as a source of solute for intracellular osmotic adjustment rather than as a stress response to decreased protein synthesis and breakdown.

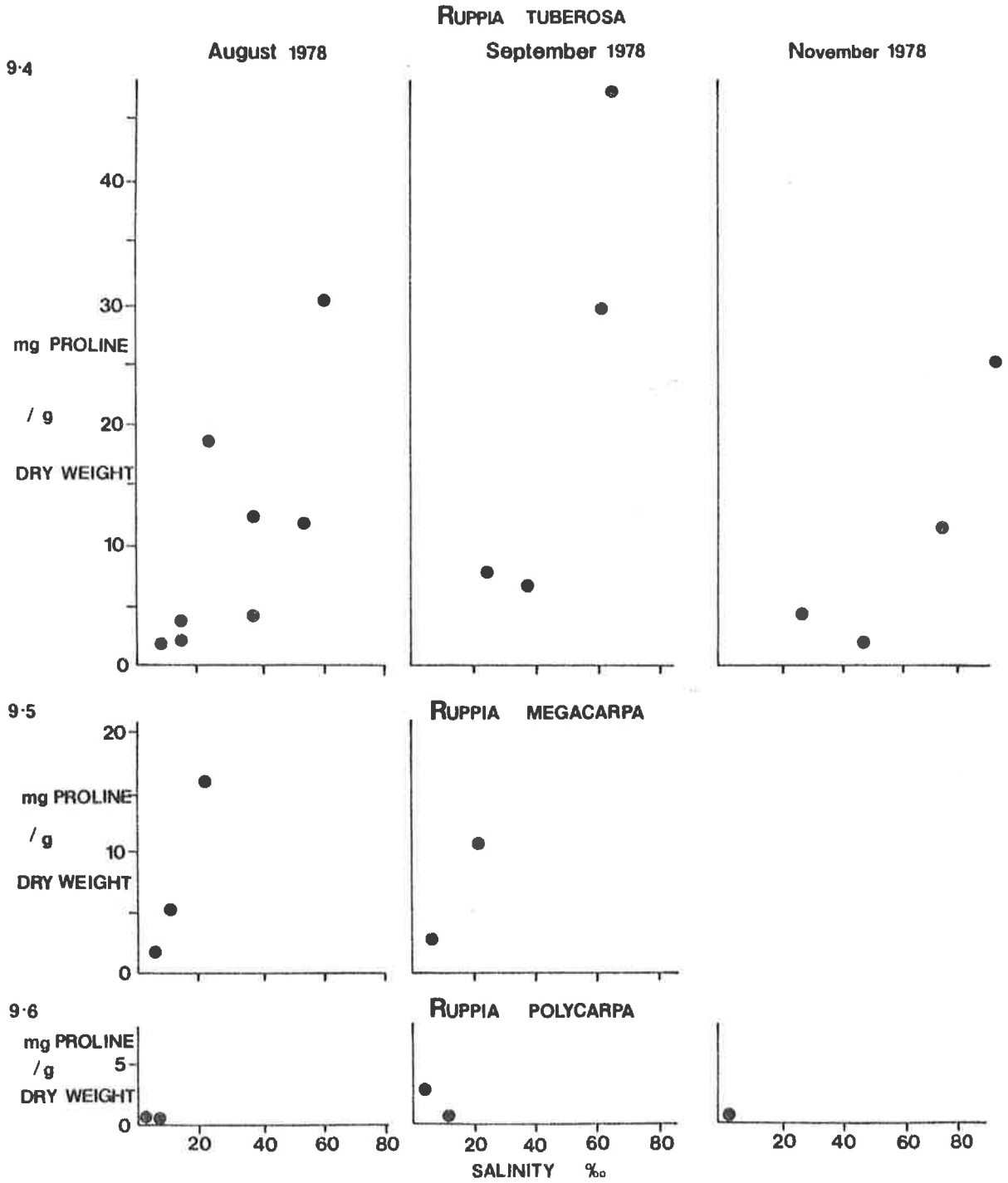

Figure 9.4 Proline concentration in *R. tuberosa* plotted against the salinity of water from the habitats: values for August, September and November 1978.

Figure 9.5 Proline concentration in *R. megacarpa* plotted against the salinity of water from the habitats: values for August, September and November 1978.

Figure 9.6 Proline concentration in *R. polycarpa* plotted against the salinity of water from the habitats: values for August, September and November 1978.

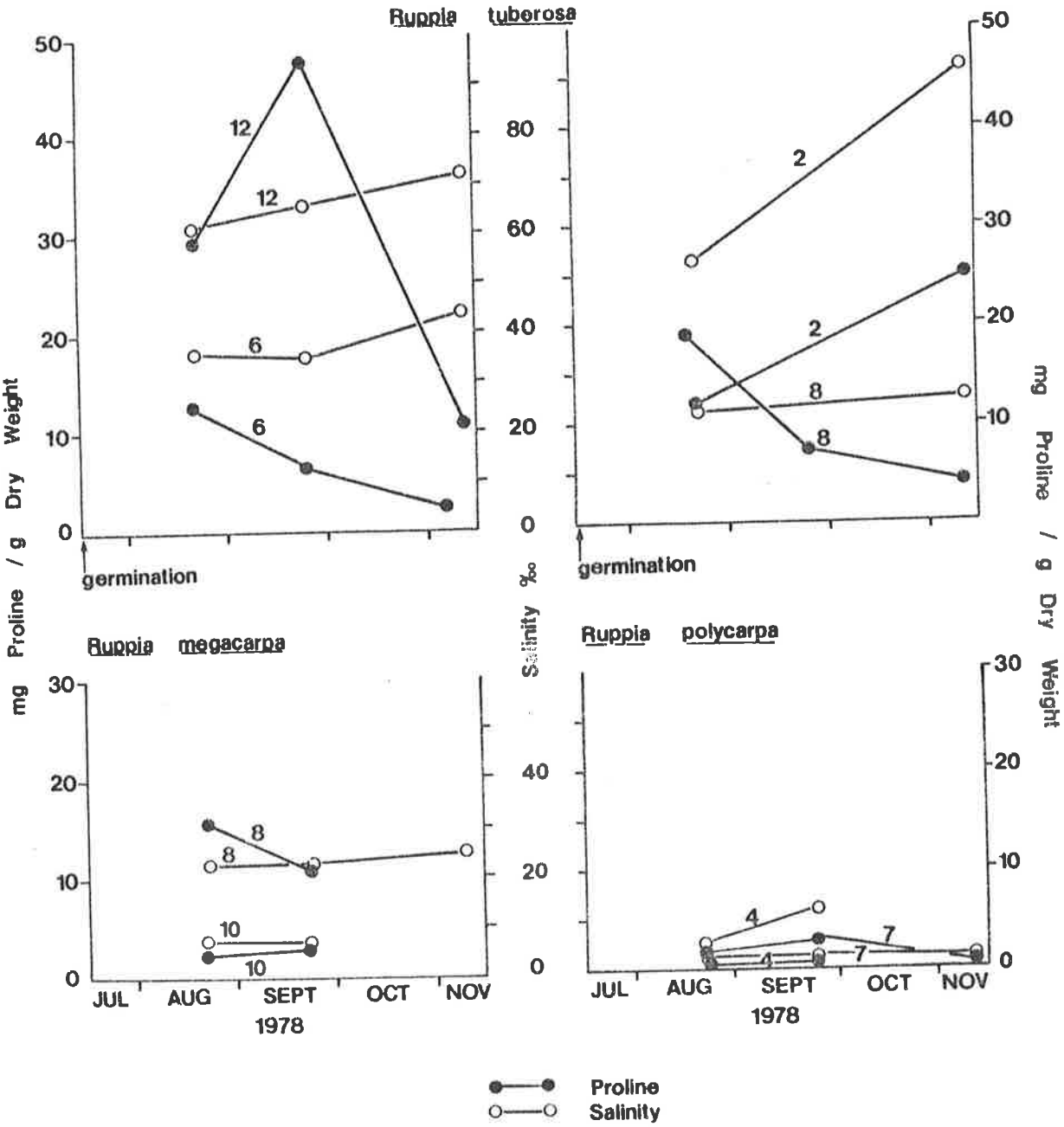

Figure 9.7 Changes in water salinity and proline concentration throughout the growing season for *Ruppia* of each species within each habitat

●——● Proline
○——○ Salinity

Habitats-
2 Flax Point
4 Blue-Green Algal Pool
6 Lake Robe
7 Fresh Dip Lake
8 Little Dip Lake
10 Erringtons Hole
12 Beachport Salt Lake

The contribution of proline to the cytoplasmic osmotic potential can be assessed by comparing the concentration of proline (converted from μmoles/g fresh weight to a mM concentration) with the concentration of solutes (mM) in the water from the habitat. If free proline is restricted to the cytoplasm, as suggested by Stewart and Lee (1974), Flowers *et al* (1977) and Wrench *et al* (1977), and if the cytoplasm is estimated to occupy 10% of the total cell volume, the concentration of proline in the cytoplasm of *Ruppia* accounts for 30-50% of the solute concentration of the external habitat in waters of higher salinities. Thus proline makes a significant contribution to the cytoplasmic solute potential and would function in helping to exclude the vacuolar salts from entering the cell. It is possible that other amino acids accumulate in the cytoplasm with the same effect. The amino acid betaine also has been shown to have an osmoregulatory role in some halophytes and crop species (Storey and Wyn Jones 1978a, b; Wyn Jones and Storey 1978a, b). Although assays for the presence of betaine in *Ruppia* were not undertaken in this study, work in this area may serve to elucidate further the role of amino acids as mechanisms for salt tolerance.

Alternatively the role of proline may not be entirely osmoregulatory. It has also been suggested that proline may associate with enzymes in such a way that serves as protection for the enzyme in the cytoplasm (Bar-Nun and Poljakoff-Mayber 1977; Schobert 1977; Wrench *et al* 1977).

9.4 Population dynamics: life cycle patterns

Both annual and perennial forms of *Ruppia* have continuous life cycles; annuals are present as dormant organs (seeds or turions) between their active growth phases, and the perennials maintain their vegetative plant structure throughout periods of quiescence. Growth

experiments (Section 9.2) gave no indication that these life cycle types are reversible in the alternate habitats.

Confirmation of these results was sought through investigation of the life cycles of the sympatric annual and perennial populations of *R. tuberosa* and *R. megacarpa* in Little Dip Lake and of *R. polycarpa* from Blue-Green Algal Pool.

Methods

Life cycles were followed by measuring seasonal changes in the standing crop of annual and perennial *Ruppia* populations. Samples were taken with a Tvärminne sampler (Figure 4.1) at different depths and locations. Macroscopic organic matter (plants and animals) was sorted from inorganic and microscopic parts; living plant parts were separated from the macroscopic fraction and then *Ruppia* plants were removed. These plants were partitioned into roots, rhizomes, leaves and reproductive parts to estimate seasonal changes in the relative weights of parts of annual and perennial populations.

Samples were selected from the densest part of each population. All samples were sorted, dried to constant weight at 105^{o}C, cooled in a desiccator and weighed. Mean dry weights are given for replicas and all weights are in grams dry weight per square metre (DWg/m^{2}). Where dry summer samples from the eulittoral zone were sorted for seeds and turions, subsamples of 25% of each sample were processed.

Profiles of standing crop with depth and distance from the shore were constructed to detect changes in total macroscopic organic matter (plant and animals), total macrophyte parts and *Ruppia* (Figure 9.8). Data for these profiles were obtained by systematic sampling at 0.05 m depth intervals (from 0 - 0.75 m depth) along a transect through both *R. tuberosa* and *R. megacarpa* habitats in Little Dip Lake in November 1977. For inter-ecosystem comparisons *Ruppia* samples from other localities were taken, also in November 1977.

Results

1. Dry weight of *Ruppia* compared with total plant parts and total organic matter.

The values for dry weights of macroscopic organic matter, live macrophytes and *Ruppia* are presented in Table 9.15. Comparisons of the dry weights of *Ruppia* with macrophytes and total organic matter can be made within and between ecosystems for the one perennial and two annual species. The dominant animal species associated with *Ruppia* in these habitats was the benthic gastropod *Coxiella striata* (Reeve); the gastropod *Physastra gibbosa* Gould was sometimes found. Not all macroscopic organic material was live; many of the shells for example were empty. Plant species associated with the annual species of *Ruppia (R. tuberosa* and *R. polycarpa)* in ephemeral habitats included *Lamprothamnium papulosum* and *Lepilaena cylindrocarpa* and a mat-producing blue-green alga. *Lamprothamnium papulosum* and *Cladophora* sp. occurred with both annual and perennial *Ruppia* species in permanently wet habitats of varying salinity and depth. Perennial *R. megacarpa* clumps are generally monospecific, but may be surrounded or shaded by these other species, whereas the annual *Ruppia* species grow in mixed associations of species. *Potamogeton pectinatus* and *Myriophyllum propinquum* are found in association with the annual *R. polycarpa* in Fresh Dip Lake, but not in localities with higher salinities. In the more saline situations *Ruppia* comprises a high percentage of the total plant standing crop, which increases with increasing depth. The dry weight of *Ruppia* per square metre is generally higher for perennial than for annual forms; depth differences may contribute to this effect.

Table 9.15 Standing crop and species composition at particular depth and salinities within lakes in November 1977: dry weights of *Ruppia*, total plant parts and total organic matter.

Site	*Ruppia* species	Depth m	Salinity °/oo TDS	Total *Ruppia* g/m^2	Total plant parts g/m^2	Total macro-scopic organic matter g/m^2	*Ruppia*/ plant parts %	*Ruppia*/ total organic parts %	Other species
LDL	*R. tuberosa*	0.0	dry	3.3	11.5	223.2	29	1.5	*Coxiella striata* *Physastra* sp. *Lamprothamnium papulosum* *Lepilaena cylindrocarpa*
LDL	*R. megacarpa*	0.65	23.3	282.5	410.3	528.3	93	72.0	*Coxiella striata* *Cladophora* sp.
EH	*R. megacarpa*	0.25	9.4	17.7	21.4	31.6	82	56.0	*Cladophora* sp.
LESM	*R. megacarpa*	0.15	23.0	48.4	66.9	182.7	72	27.0	*Coxiella striata*
LESM	*R. tuberosa*	0.0	dry	1.0	1.0	101.2	100	1.0	*Coxiella striata*
LR	*R. tuberosa*	0.25	42.4	5.9	5.9	380.0	100	1.5	*Coxiella striata* *Lepilaena cylindrocarpa*
B/p SL	*R. tuberosa*	0.3	55.7	107.0	116.3	116.3	92	92.0	-
BGAP	*R. polycarpa*	0.0	dry	2.3	25.0	210.0	9	1.0	*Lepilaena cylindrocarpa* *Lamprothamnium papulosum* *Coxiella striata* blue-green alga
FDL	*R. polycarpa*	0.5	3.2	143.3	213.9	357.2	67	40.0	*Lamprothamnium papulosum* *Potamogeton pectinatus* *Myriophyllum propinquum*

Table 9.16 Percentage of total dry weight allocated to roots, rhizomes, leaves and reproductive parts for the perennial species, *R. megacarpa*, and the annual species, *R. tuberosa* and *R. polycarpa* in November 1977

Site	Species	% Total *Ruppia*								
		Leaves and Elevated Stems	Rhizomes	Roots	Flowers	Fruit	Turions I	Turions II	Dried Material Undifferentiated	Total
LDL	*R. tuberosa*	-	-	-	-	11.4	34.5	54.1	-	100
LDL	*R. megacarpa*	68.4	19.6	10.9	-	1.1	-	-	-	100
EH	*R. megacarpa*	51.4	23.3	25.3	-	-	-	-	-	100
LR	*R. tuberosa*	19.7	43.9		-	1*	5.4	31.0	-	100
B/p SL	*R. tuberosa*	16.4	37.5	22.1	-	-	4.0	20.0	-	100
LESM	*R. megacarpa*	51.2	24.4	22.5	1.9		-	-	-	100
LESM	*R. tuberosa*	-	-	-	-	-	-	-	100	100
FDL	*R. polycarpa*	64.7	15.4	9.2	10.7		-	-	-	100
BGAP	*R. polycarpa*	-	-	-	-	95.0	5.0	-	-	100

* estimate

2. Dry weights of roots, rhizomes, leaves and reproductive parts in annual and perennial *Ruppia* populations

Variations in the dry weights of plant portions of the three *Ruppia* species are shown in Table 9.16. During the dry phase of ephemeral habitats, seeds and turions of two structural types (see Section 9.5) were the only live parts present. In late spring (November), leaves comprised 50% and rhizomes 20% of the dry weight of the *R. megacarpa* plants, while the proportions found in the annual *R. tuberosa* from habitats which were still wet were less than 20% for leaves, approximately 40% for rhizomes and over 20% for turions. These annual *R. tuberosa* plants had passed their most active photosynthetic stage and were producing turions. At this time the annual *R. polycarpa* from the permanent habitat in Fresh Dip Lake was flowering prolifically with no sign of senescence; this population regressed in January 1978.

3. Changes in the structure of *R. tuberosa* and *R. megacarpa* populations along a transect in water of increasing depth

Figure 9.8 shows changes in *Ruppia*, total plant matter and total organic matter along a transect through ephemeral and permanent plant habitats in Little Dip Lake. The occurrence of other species is also recorded. Dry weight data extend to a depth of 0.75 m but plant occurrence was recorded to the centre of the lake. The *R. tuberosa* habitat was partially dry at the time of the survey and samples in this zone were taken at 0.05 and 0.1 m height above the water level. The *R. tuberosa* populations extended to 0.2 m depth. No *Ruppia* occurred between 0.2 and 0.25 m. Patches of *R. megacarpa* were located at 0.25, 0.35 and 0.45 m with a more extensive dense band between 0.55 and 0.75 m. The differences in dry weights of the two forms are marked: differences in the amount of organic matter per plant unit, rather than the density of plants are reflected.

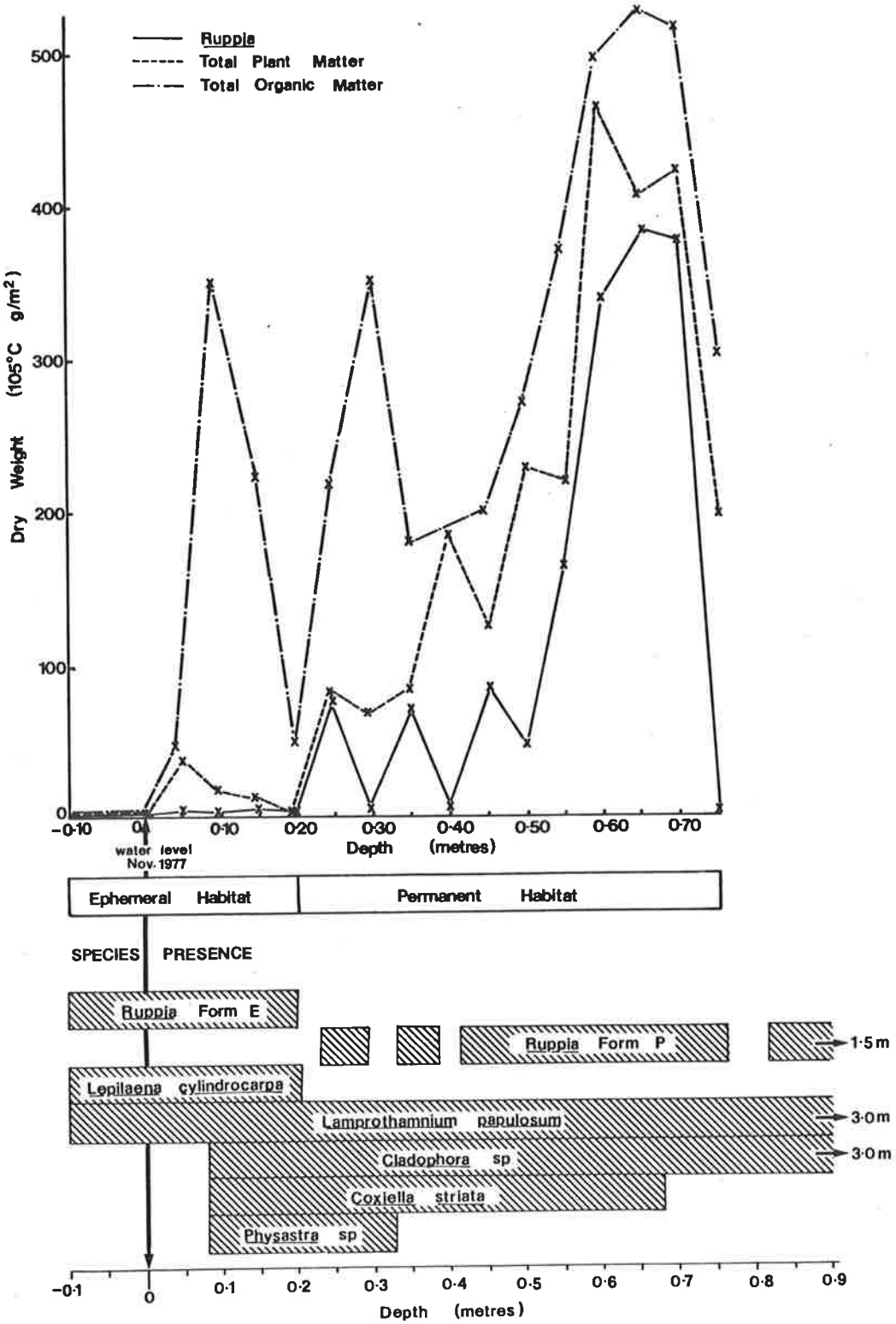

Figure 9.8 Profile of standing crop and species occurrence with depth and distance from the shore through ephemeral and permanent plant habitats in Little Dip Lake

The graph of total plant matter (Figure 9.8) indicates that the percentage of dry weight of other plant species increased where the dry weight of *Ruppia* is low. *Lepilaena cylindrocarpa* and *Lamprothamnium papulosum* occur throughout the *R. tuberosa* habitat; both *Cladophora* and *Lamprothamnium* occur from 0.1 m to the centre of the lake.

4. Seasonal changes of total dry weight of *Ruppia* and of the proportions of parts for the three species

Seasonal changes in the dry weight of *Ruppia* are plotted for the 13 months from November 1977 to November 1978 in Figure 9.9a,b,c. The aquatic regimes of these habitats are indicated on the abscissa. The dry weight of plant parts as a percentage of the total *Ruppia* present is also presented.

The annual populations died off as the habitats dried leaving seeds and dormant turions alive over the dry phase (November to June). The perennial population had a quiescient period over winter (April to September) and then increased to a summer peak of organic matter. Senescence and decay of many of the older plant parts in the perennial populations occurred during this period. The minimum total dry weight of *Ruppia* per square metre for the *R. megacarpa* population was greater than the maximum for either annual species. As mid-winter figures for *R. megacarpa* are not available, only a general comparison of the differences in organic matter between the annual and perennial life cycles can be made. The minimum dry weight for *R. megacarpa* was 103 g/m^2 in September and the maximum was 383 g/m^2 in November, whereas *R. tuberosa* and *R. polycarpa* had minima of 4.2 g/m^2 and 1.6 g/m^2 respectively from November to June and maxima of 60 g/m^2 and 88 g/m^2 respectively in September. The similarities in magnitude and timing of these maximum and minimum figures for the annual forms are emphasized when contrasted with the greater weights and

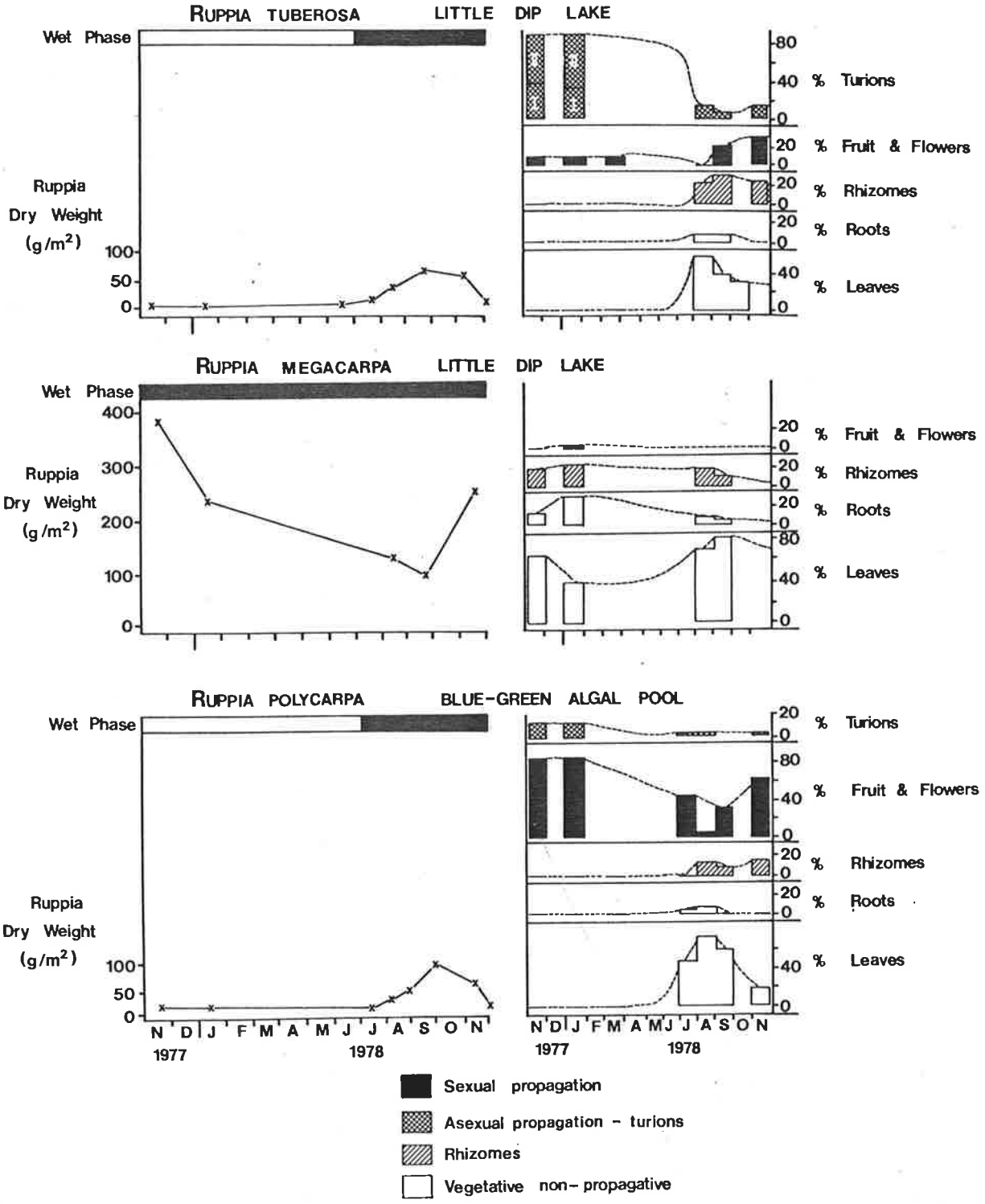

Figure 9.9 Seasonal changes in the standing crop of *Ruppia* and the percentage of dry weight allocated to roots, rhizomes, leaves and reproductive parts: a. *R. tuberosa* (LDL) b. *R. megacarpa* (LDL) c. *R. polycarpa* (BGAP)

differences in timing of growth phases of the perennial *R. megacarpa*. Both the annual species reached their growth peak in September (spring), two months after germination whereas the perennial had not commenced its annual growth phase at this time. By November, when the annual populations had set seed and their habitats were nearly dry, the perennial population was actively growing, both by production of new shoots from old stems and new rhizomatous spread at the edge of old *Ruppia* clumps. Seasonal increases in temperature, light, water depth or decrease in salinity may stimulate these growth phases. The annual populations show a more immediate response to such factors since the shallow habitats refill and warm quickly whereas a time lag and buffering of these effects occurs in the perennial habitats.

Discussion

Although these data are sufficient for comparisons of life cycle strategies, extensive biomass sampling within these populations is necessary for detailed studies of the energetics of the populations. The comparisons of annual and perennial life strategies by estimates of the live organic matter produced may be biased by inclusion or exclusion of parts of the perennial plants which are visually difficult to classify as dead or alive. This source of error is less marked in annual populations.

Partitioning of *Ruppia* into plant parts reveals differences between annual and perennial forms as well as seasonal differences within each life cycle. In the perennial species the leaves and above-ground stems constitute over 40% of the plant matter throughout the year and may comprise up to 80% of the total. Rhizomes constantly make up 10 to 20% of the total, and roots between 5 and 30%. The function of rhizomes for storage and propagation is important in the perennial species. The low percentage dry weight of flowers and fruits is consistent with the observation that reproduction is mainly asexual, by spread of rhizomes.

Both annual species show a proliferation of leaves during the short growing season. The maximum contribution of roots is less than 7% by dry weight and occurs in the early growth phases. Rhizome growth replaces this as the growing season progresses. The proportion of the dry weight of parts that function reproductively is much higher in the two annual forms than in the perennial. Even when vegetative growth of the annuals is at its maximum, the percentage of dry weight accounted for by reproductive parts is higher than at any stage of the life cycle of the perennial. During the dry period of seven months, all surviving parts of the annuals are reproductive. The differences in reproductive strategies for the three species and their roles in propagation are examined more extensively in Section 9.5.

9.5 Reproductive biology

Both annual and perennial species of *Ruppia* propagate sexually and asexually. The predominant method of reproduction for the perennial species, *R. megacarpa*, is asexual, by rhizomes and rooting from stem nodes: a limited number of viable seeds supplement this vegetative spread. On the other hand, the annual species, *R. tuberosa* and *R. polycarpa*, flower and fruit prolifically and produce large numbers of asexual turions, and also spread laterally by rhizomes.

1. Seeds

Seeds of the perennial species differ in size shape and podogyne characters (Section 8.4) as well as in their physiological requirements for breaking dormancy (Section 9.3).

2. Vegetative spread by rhizomes and shoots from nodes

The perennial species, *R. megacarpa*, conforms to pattern of reproduction found in many aquatic angiosperms. Most propagation occurs by the lateral spread of starch-filled rhizomes. The limited number of seeds produced may be dormant for long periods

before germination (Sculthope 1967: Hutchinson 1975). Regeneration from mechanically broken plant fragments is common in *R. megacarpa* and has been recorded in other aquatic species (Spencer and Lekic 1974; Hutchinson 1975).

The lateral spread of the annual species *R. tuberosa* and *R. polycarpa* by rhizomes is important in the short growing season. The development of asexual perennating organs (turions) may be associated with the rhizomes in these species.

3. Asexual perennating organs (turions)

Turions function as organs of perennation (overwintering buds) in some temperate aquatic species where vegetative parts senesce. In Australia, turions produced by the annual species of *Ruppia* enable the plants to withstand an extended dry summer. No turions have been recorded for the perennial *R. megacarpa*. Turions formed by *R. polycarpa* and *R. tuberosa* detach from the parent plants and disperse; these plants may thus act as 'asexual annuals' (Hutchinson 1975). Both seeds and turions of *R. polycarpa* and *R. tuberosa* survive drying and propagate these species in the subsequent annual wet phase.

Turions of two types were recorded (type I Plate 9.1, type II Plate 9.2). In *R. tuberosa*, turions occur prolifically in all localities and both structural types may occur on the same plant. However, only type I turions were recorded in *R. polycarpa* in the two ephemeral habitats (BGAP and LR) and no turions were recorded in the permanent habitat (FDL). Turions have not been observed in *R. polycarpa* in New Zealand (Mason 1967; Mason pers. comm. 1978).

Seeds and both types of turions germinated simultaneously shortly after the habitats refilled with water. Turions were produced in several field sites where no flowering was recorded in the 1976-77 and 1977-78 seasons. Two of these sites, Beachport Salt Lake and Pipeclay Lake, produced seeds as well as turions in the 1978-79 season when salinities did not reach the extreme levels of the previous season.

A similar situation, in which more than one structural type of turion occurs, has been recorded in the aquatic genus *Potamogeton* where five structural types of turions have been noted (Hutchinson 1975). These turions were produced from the rhizome or were modifications of buds borne on stems.

Turions have not been recorded for populations of *Ruppia* outside Australia and no distinction between types of turions has previously been made within this genus. Lucas and Womersley (1971) described yellow-white swellings at the junction of leaves and rhizomes, whereas Aston (1973) referred to small brown turions about 3 mm long, enveloped in a sheath of reduced leaf-like bracts produced at the tips of the rhizomes. Davis and Tomlinson (1974) considered that each turion, formed at a leaf base, consisted of a single short internode with leaf and root primordia, surrounded by cortical parenchyma cells enclosed by leaf sheaths.

Type I turions (Plate 9.1) are similar to the turions described by Davis and Tomlinson (1974). Those described by Aston (1973) appear to be structually similar to these, but were described as being produced on rhizome tips rather than at the junction of the leaf blades and the rhizome; this positioning is similar to that of the type II turions found in this study. The description of yellow-white swellings (Lucas and Womersley 1971) conforms with the appearance of type II turions (Plate 9.2) except that the turions were described by Lucas and Womersley as occurring at leaf bases, whereas type II turions were observed at rhizome tips in this study.

Confusion between turions (particularly type II) and galls, formed as a pathological response to the fungus *Tetramyxa parasitica* Goebel, is possible as both structures appear as white swellings on the rhizome. Galls of this fungus have been recorded on *Ruppia* in Europe (den Hartog 1963). Galls formed by this organism occurred on *Ruppia*

from Lake Eliza Salt Marsh and from Beachport Salt Lake where both types of turions occur. Galls were identified by C. den Hartog (pers. comm. 1977).

Anatomical studies were conducted to elucidate differences in the structure of the turions.

Methods

Type I and II turions were collected from populations of *R. tuberosa* at Beachport Salt Lake, Lake Robe and Little Dip Lake. Specimens for sectioning were preserved in 4% formalin and transferred to F.A.A. (formalin:acetic acid:alcohol, 2:1:25) for 24 hours. Specimens were embedded in wax (Paraplast) and sectioned with a Cambridge Rocking Arm microtome by methods outlined in Johansen (1940). Serial sections were made in both transverse and longitudinal planes and were stained with Safranin and Fast Green (see Johansen 1940). Specimens for examination with the Scanning Electron Microscope were collected from dry lake sediments and oven-dried (105^{o}C) before spatter coating with gold.

Results and interpretation

Scanning electron micrographs (Plates 9.1 and 9.2) show the external differences between type I and II turions. Type I organs are asymmetrical, 1 - 2.5 mm long, and have a hardened brown outer layer enclosing a swollen area from which shoots and roots emerge when growth is stimulated. These organs are formed at nodes on the rhizome and the enclosing tissues appear to be modified from the leaf bases at each node along a section of the rhizome. When dry and detached from the plant, pieces of the rhizome may remain attached as basal extensions of these organs. Type II turions are symmetrical, spherical and cream in colour and are 1.5 - 3.0 mm long, and were observed to form at rhizome tips.

The photomicrographs (Plates 9.3 to 9.20) show transverse and longitudinal sections taken through turions of type I and II. The location of these sections are shown in Plates 9.1b and 9.2b. Plates 9.3 to 9.8 are transverse sections and 9.9 to 9.11 longitudinal sections through type I turions: Plates 9.12 to 9.18 are transverse sections and 9.19 and 9.20 longitudinal sections through type II turions. Plates 9.3 to 9.6 are representative of the serial sections taken from the apex to the base of type I turions. Plates 9.12 to 9.17 are representative of the serial sections from apex to base of type II turions. The sections of type I turions are described in the legend to Plates 9.3 to 9.11 and the sections of type II turions are described in the legend to Plates 9.12 to 9.20.

Discussion

Turions of type I and II are both structures containing dormant meristematic areas which can be stimulated to resume growth by favourable environmental conditions. Meristematic vascular traces are located in both turion types. Type I turions consist of modified hardened leaves, originating from the old leaf base. These leaves enclose a central vascular area in the position of the previous basal meristem which would have marked the connection between the growing stem, leaves and the rhizome. The dormant meristematic area of type II turions is embedded in swollen leaf structures with numerous enlarged starch-filled cells. The central vascular area resembles that of the rhizome and connects with vascular areas of the stem and leaf initials.

One of the major structural differences between the two types of turions is the location of the swelling, and the nature of the outer protective coating. The outside layer of cells of the enclosing leaves in type I turions are modified and scale-like. These leaves protect and enclose the enlarged region of starch-filled cortical parenchyma cells of the stem. The enclosing leaves of type II turions

Plate 9.1 Turion type I

a. Scanning Electron Micrograph

b. Position of sections shown in Plates 9.2 to 9.11

Plate 9.2 Turion type II

a. Scanning Electron Micrograph

b. Position of sections shown in Plates 9.12 to 9.20

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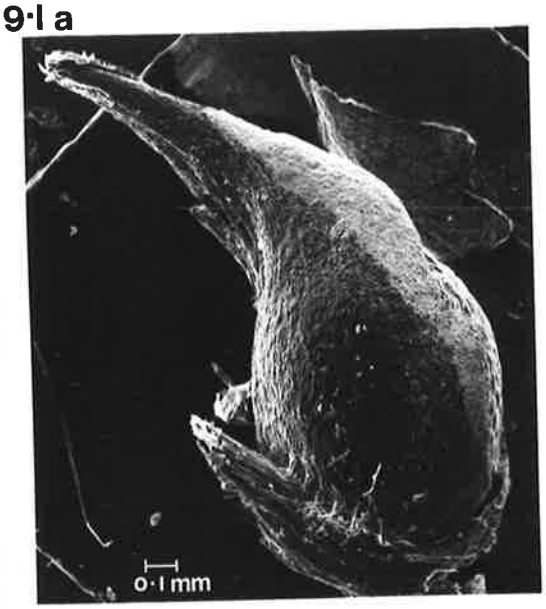
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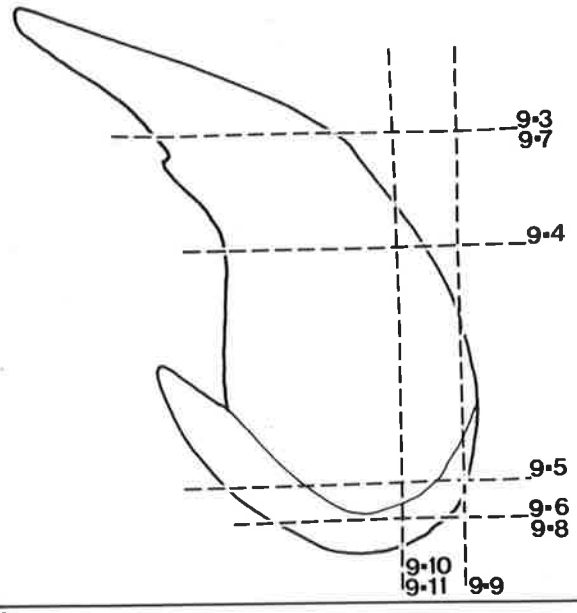
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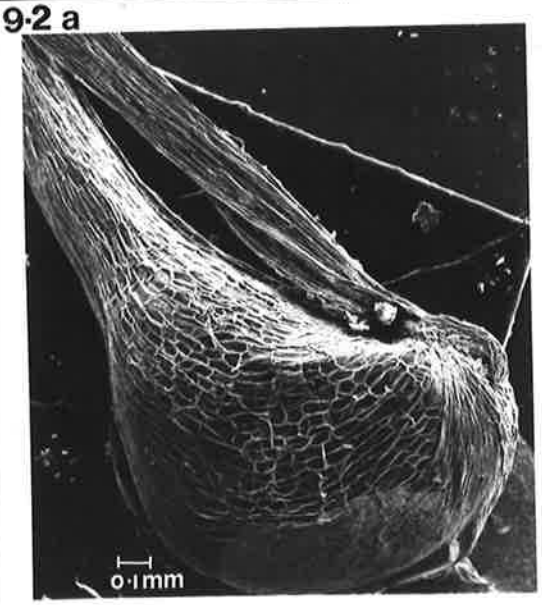
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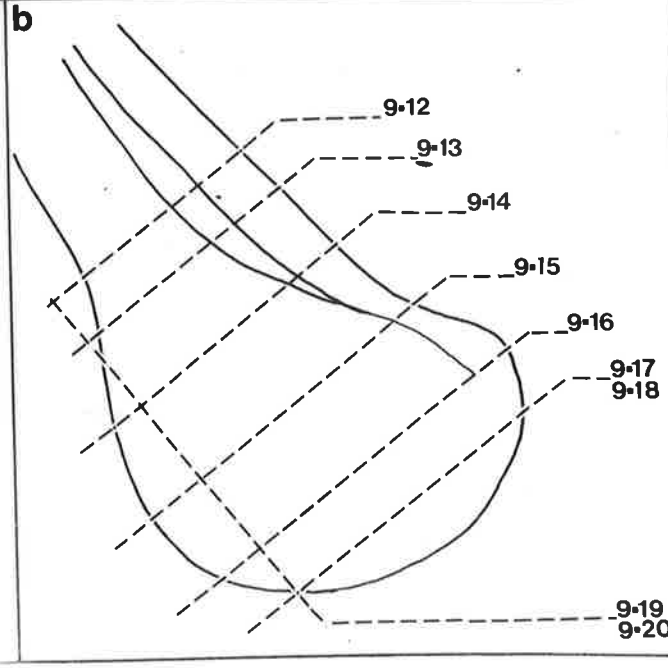
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Plates 9.3 to 9.11 Type I turions

Plates 9.3 to 9.8 are transverse sections and 9.9 to 9.11 longitudinal sections through type I turions. Plates 9.3 to 9.6 are representative of the serial sections taken from the apex to the base of type I turions.

Type I turions are composed of a central region of starch-filled cells (ST) surrounded by leaf-like structures (SL) (Plates 9.3 to 9.7). The outer cells of these leaves have thickened walls and seem to be modified as a protective layer of scales (SL) (Plate 9.7). The region of starch-filled cells broadens from the apex to the base of the turion (Plates 9.3 and 9.6) and a central vascular region (V) is visible in the basal sections (Plates 9.5, 9.6). This vascular trace is small and not extensively developed (Plate 9.8) suggesting that it may be a dormant meristematic region. Transverse sections nearer the base show an area of cells oriented longitudinally (LOC) (Plate 9.6); these are part of the rhizome. The central vascular area (V) of the stem cortex is continuous with vascular tissue (V) within this longitudinal series of cells (Plate 9.6) suggesting that the vascular tissues of stem, leaf base and rhizome are connected. The longitudinal sections confirm the above deductions (Plates 9.9, 9.10, 9.11) and also show connection of vascular areas lying perpendicular to one another.

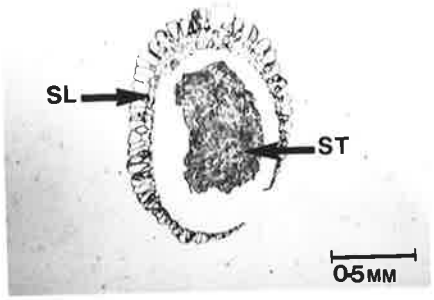
ST - starch-filled cells

SL - scale-like leaf

V - vascular region

LOC - longitudinally oriented cells

9·3



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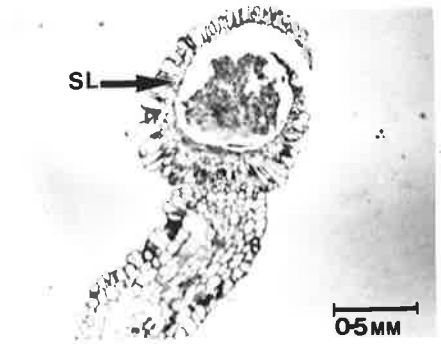

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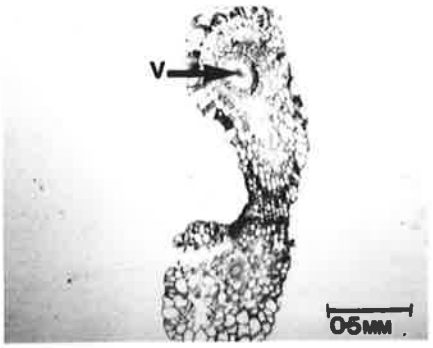

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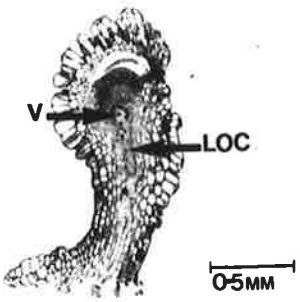

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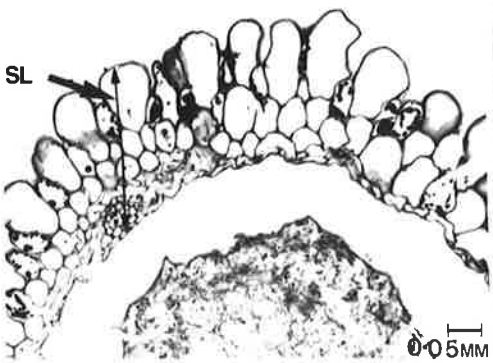

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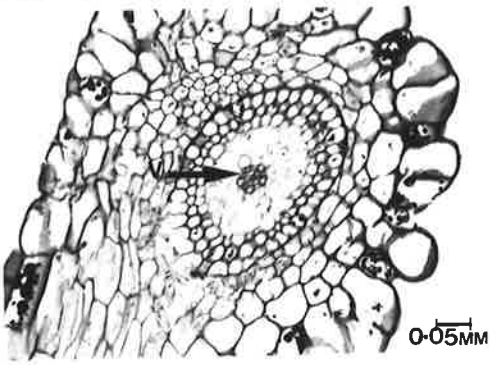

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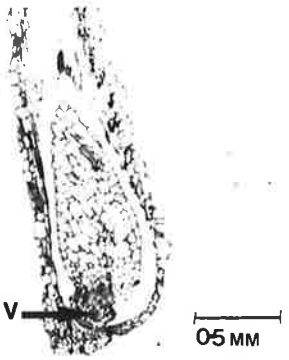

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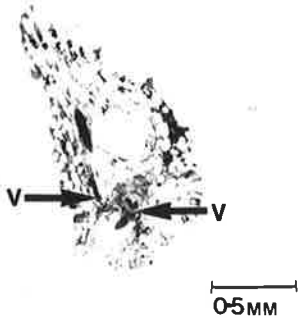

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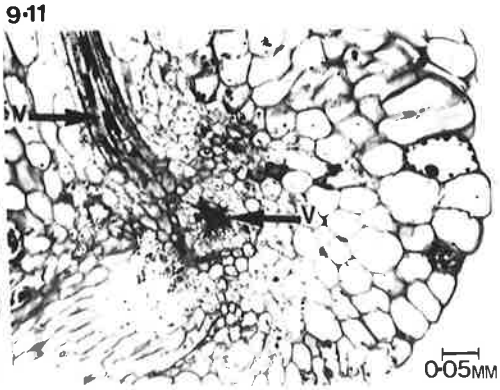

Plates 9.12 to 9.20 Type II turions

Plates 9.12 to 9.18 are transverse sections and 9.19 and 9.20 longitudinal sections through type II turions. Plates 9.12 to 9.17 are representative of the serial sections from apex to base of type II turions. The sections 9.14 to 9.18 show a split in the turion; this is an artefact introduced during the wax embedding.

In type II turions a region of swollen starch-filled cells (ST) surrounded by two leaf-like structures (L) can be seen in the transverse sections near the apex (Plates 9.12, 9.13). However the enclosing leaf-like structures do not have the modified scale-like cells present in type I turions (Plate 9.7). Plates 9.12 to 9.15 show that in type II turions both the number and size of the parenchyma cells of the inner leaf increase further from the apex (SwL). The inner leaf becomes even thicker and is continuous with the central cortex in lower sections (Plates 9.14 to 9.17). In Plate 9.14 two vascular traces (V) can be seen in the central region; one of these can be followed to the central stem and the other to the enclosing leaf sheaths (Plates 9.13, 9.14). Closer to the base (Plates 9.16 to 9.18) cells are oriented longitudinally and another area of vascular tissue is visible: this probably connects the vascular initials in the stem and leaf areas with vascular tissue of the rhizome. Longitudinal sections (Plates 9.19, 9.20) show a transversely oriented vascular trace (TOC): this is the vascular system of the rhizome seen in longitudinal orientation (LOC) in Plates 9.15 to 9.18.

ST	starch-filled cells	LOC	longitudinally oriented cells (in TS)
L	leaf-like structures		
SwL	swollen leaf	TOC	transversely oriented cells (in LS)
V	vascular region		

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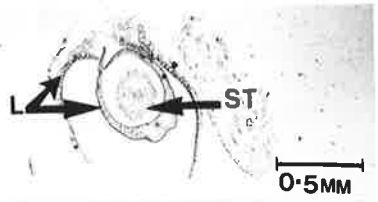

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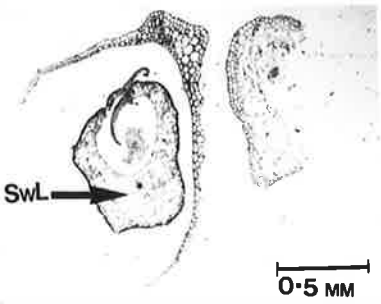

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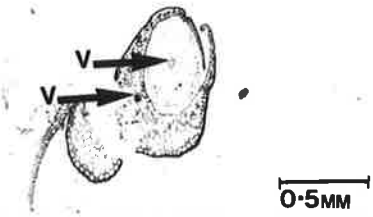

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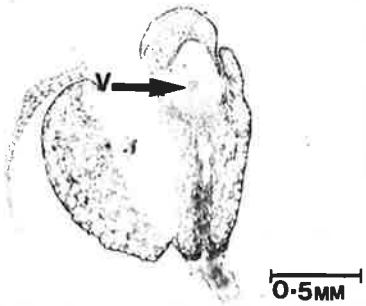

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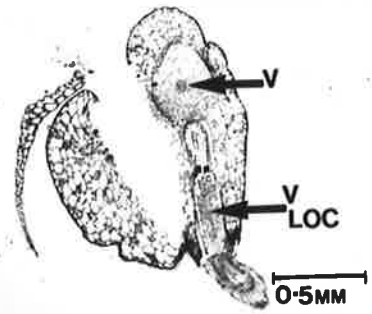

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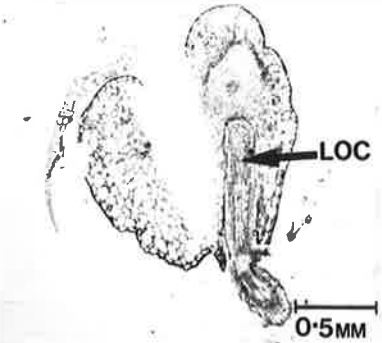

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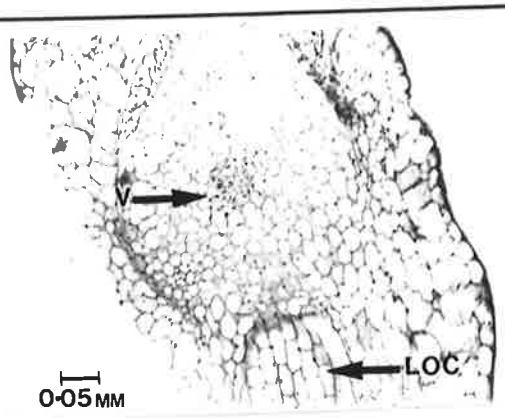

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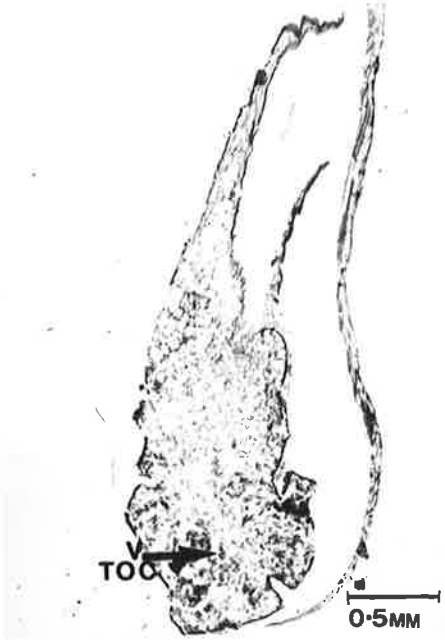

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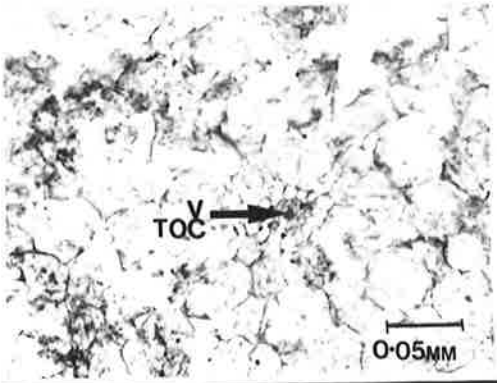


do not have modified outer cells, but have a waxy non-cellular layer on the outside of the extensive region of starch-filled leaf parenchyma.

The observation that type II turions internally resemble rhizomes and are found at rhizome tips, suggests that the apical meristem and undeveloped leaf primordia have been modified to form a swollen protected bud.

The occurrence of type II turions on *R. tuberosa* but not on *R. polycarpa* could be explained by differences in the habitat of these species. After initial rhizomatous growth, stems of *R. polycarpa* elevate and branch into the water and thus apical meristems around which turions can form will not be present at rhizome tips in the sediments. Alternatively, apical meristems are present at the many rhizome tips of *R. tuberosa* as this plant spreads laterally through the sediments without branching into the water; turions often form at these locations. The smaller number of type I turions produced by *R. polycarpa* can be explained similarly; more nodes of *R. polycarpa* are elevated into the water leaving only a few basal nodes around which turions form in the sediments. The many basal nodes of *R. tuberosa* enable many type I turions to form.

4. Reproductive patterns

Introduction

Seeds, turions and rhizomes all function as mechanisms of regeneration in *Ruppia*. Such a variety of propagative mechanisms often accounts for habitat differences between species (Grime 1979). The type of reproductive pattern that has evolved in a particular species may be related to the accessory functions of seeds and turions as units of dispersal and perennation, and, for seeds, as a source of genetic variability (Harper 1977). An analysis of the allocation of both resources and time to various reproductive (both sexual and asexual) and non-reproductive functions in the life cycles of species of *Ruppia*

can be used to examine how each species has achieved a compromise of these functions in various habitats.

Although no similar study has been conducted for aquatic plants, comparable methods have been used to examine life cycle patterns of terrestrial plants. Previous studies have examined reproductive strategies by partitioning the plant material produced in a generation into categories by measurements of dry weights. Hickman and Pitelka (1975) found that there was a good correlation between estimates of energy allocation made by measurement of dry weight with those based on calorific determinations. It has been postulated that reproductive effort may be fixed and constant in a constant environment and may be variable and subject to environmental stress in fluctuating environments (Harper 1967). Life cycle strategies have been examined for annual species (*Senecio vulgaris* L., Harper and Ogden 1970; species of *Polygonum* L., Hickman 1975, 1977) and for perennial species (*Taraxacum officinale* Weber, Gadgil and Solbrig 1972; the composite *Solidago* L., Abrahamson and Gadgil 1973; *Tussilago farfara* L. by Ogden 1974). Annual and perennial strategies of species of *Lupinus* L. were compared by Pitelka (1977) and strategies of a crop species of *Medicago* L. and stoloniferous species of *Trifolium* L. were considered by Turkington and Cavers (1978). All these studies substantiate the ideas that the proportion of energy allocated to reproduction is higher in annual than in perennial species. Studies have generally considered annuals and perennials in laboratory or field situations: Pitelka (1977) combined both approaches.

Data have been analysed variously in terms of plant strategies in stable and fluctuating or in competitive and harsh environments. The interpretation of the reproductive patterns in terms of r- and K-selection (MacArthur and Wilson 1967) have been made by many workers (see Harper 1977): r-selection is characterized by the combination of early maturity, many small young, a short life and a large reproductive

effort, whereas K-selection is characterized by a combination of late maturity, few large young, a long life and a small reproductive effort. These terms are used either as labels for these combinations of traits or as explanations of why those traits are found together (Stearns 1976).

No previous studies have included asexual perennating organs as part of the reproductive effort nor have they considered reproductive patterns in aquatic plants. Hence the populations of the aquatic angiosperm *Ruppia* provide the opportunity to study a variety of reproductive patterns in two annual and one perennial species.

Methods, results and interpretation

First, the proportion of the total plant dry weight devoted to reproduction in annual and perennial forms was examined; second, the allocation of this reproductive effort between asexual and sexual reproductive structures was compared for annual and perennial life patterns and for individual species; and third, the size, weight and numbers of each type of propagule were compared for each group.

Figures 9.10, 9.11 and 9.12 show the percentage allocation of dry weight to plant parts for the three *Ruppia* species. Figures 9.10 and 9.12 represent the life cycles of the annual species *R. tuberosa* and *R. polycarpa* from Little Dip Lake and Blue-Green Algal Pool respectively and Figure 9.11 represents the perennial *R. megacarpa* from Little Dip Lake. These figures were compiled from data collected and sorted as described in the discussion of life cycles (Section 9.4). The total dry weights (105^{o}C) of *Ruppia* were compared on a seasonal and population basis in the previous section (Figure 9.9). In Figures 9.10, 9.11 and 9.12 plant parts are considered as a percentage of each total sample.

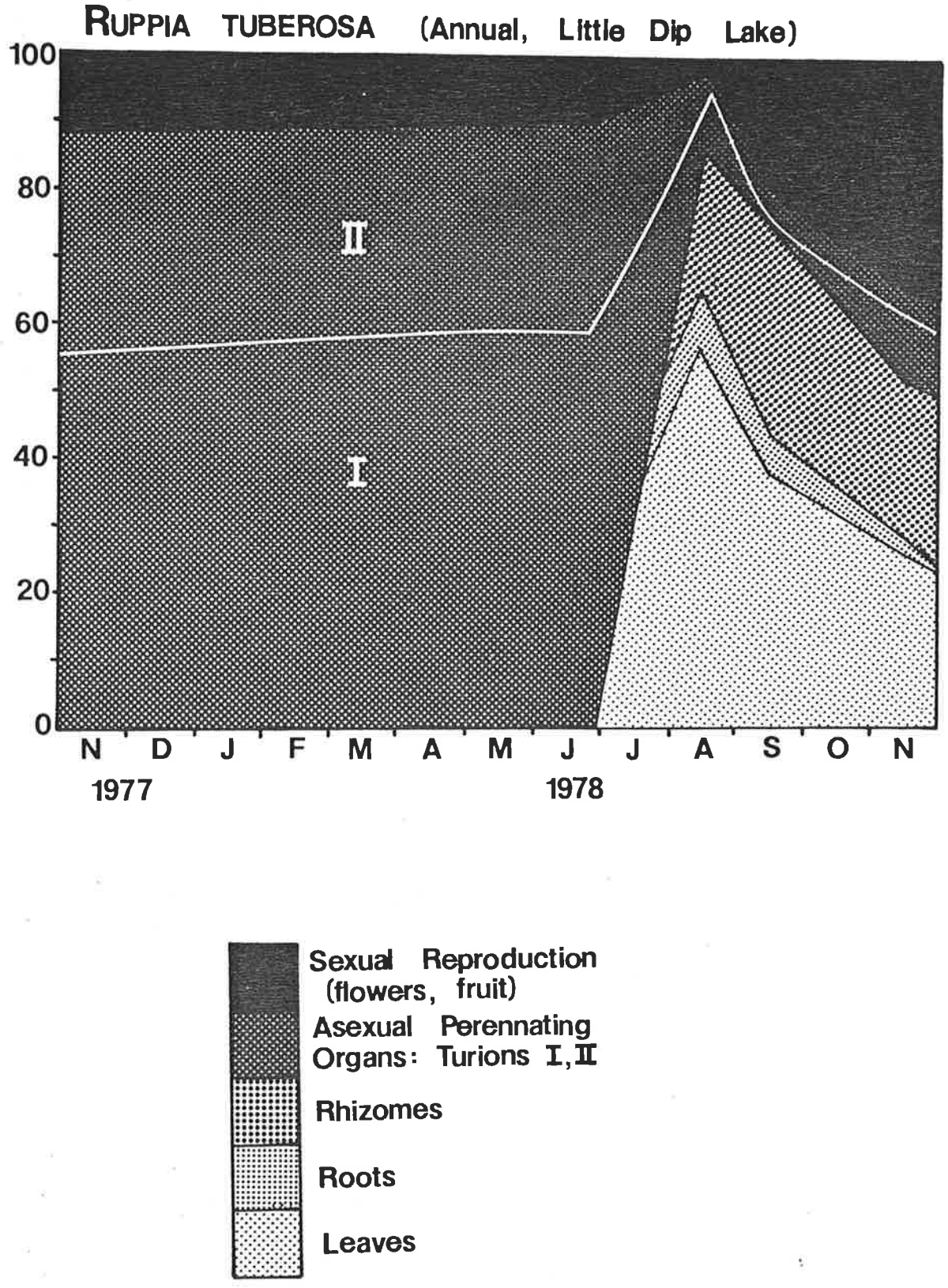
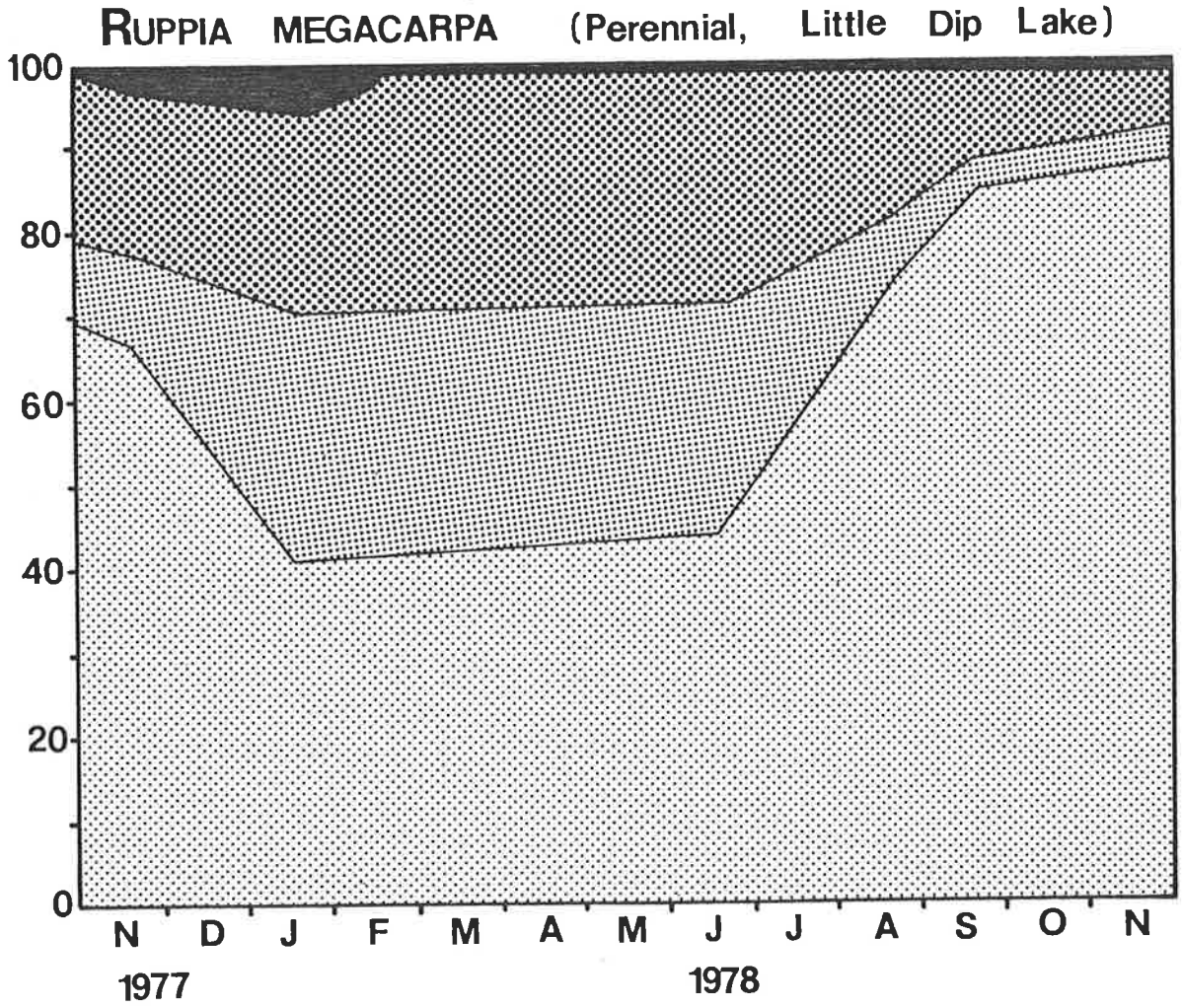


Figure 9.10 Percentage allocation of the dry weight of *R. tuberosa* to various plant parts over a thirteen month period.



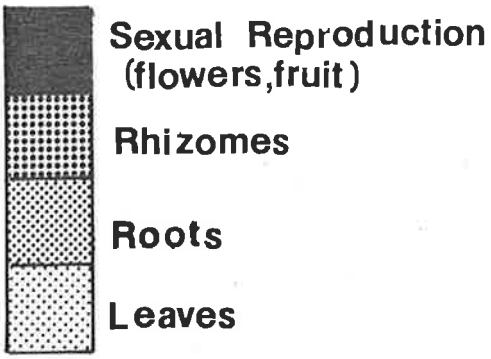


Figure 9.11 Percentage allocation of the dry weight of *R. megacarpa* to various plant parts over a thirteen month period.

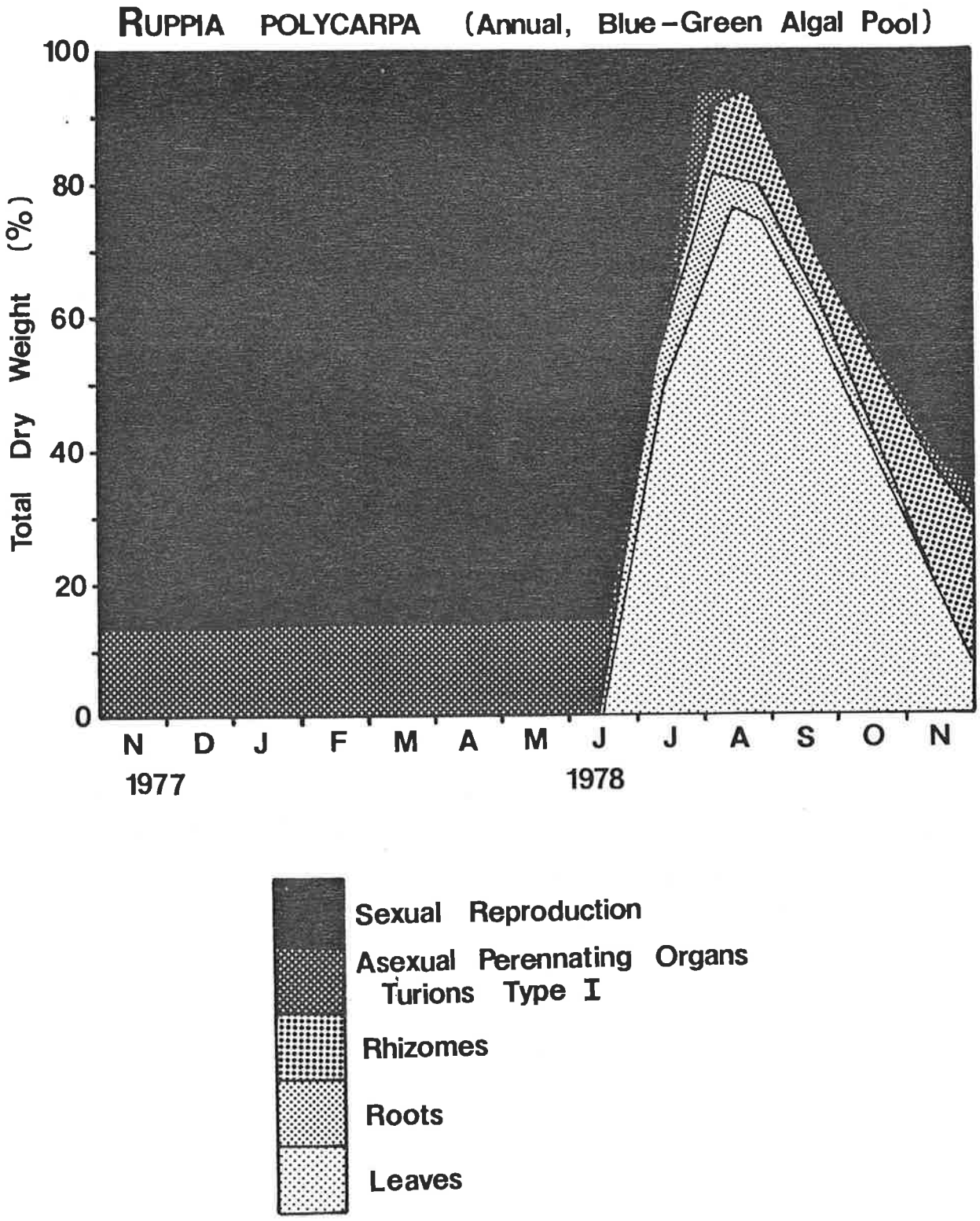


Figure 9.12 Percentage allocation of the dry weight of *R. polycarpa* to various plant parts over a thirteen month period.

The allocation of dry weight to reproduction differed greatly between annual and perennial species. In the perennial, a very small percentage of the total dry weight of live parts was allocated to sexual reproductive parts in any season (Figure 9.11). A maximum of 4.5% was devoted to seeds and floral parts in summer (January). The rhizomes, structures important in asexual reproduction, comprised between 10% and 30% of the live organic matter of the perennial plants. The proportion of dry weight in rhizomes decreased in the growing season, perhaps indicating a mobilization of starch reserves as plants began to grow actively and photosynthesis increased. Alternatively, this decrease could simply reflect the increase in the proportion of leaves compared with the more static rhizome stock.

The percentage of the total dry weight represented by reproductive structures was much higher in all seasons for the two annual species (Figures 9.10, 9.12). In the short active growing phase, when production of photosynthetic material reached a peak (57% for *R. tuberosa* 76% for *R. polycarpa*) and rhizomes and roots also reached their annual maxima, seeds and asexual propagules reached their annual minima of 14% for *R. tuberosa* and 5% for *R. polycarpa*. At all other stages, reproductive organs, both asexual and sexual, comprised a much higher percentage of the total live parts. In the eight months from November to July, when the habitats were dry, 100% of the live material for these annual species was reproductive. Rhizomes also functioned in the spread of these plants, but they could not survive desiccation. Rhizomes comprised up to 37% of the total dry weight during the growing season.

The two annual species are remarkably similar in the proportion of reproductive parts at the different stages of their life cycles (Figures 9.10, 9.12). In the dry phase, 100% of parts were reproductive for both species. This dropped to 13.2% for *R. tuberosa* and 6.3%

for *R. polycarpa* early in the growing season, then increased to 24% and 31% respectively when total weight of *Ruppia* was at its maximum, and increased further to 46% and 62% respectively in November before the habitats dried. The magnitude of the observed differences between *R. tuberosa* and *R. polycarpa* was similar to the variation between samples from within each population. This contrasts with the marked difference between these species and the perennial *R. megacarpa*.

Notwithstanding the general similarities of total reproductive effort for *R. tuberosa* and *R. polycarpa*, they differ in their division of reproductive parts into sexual (seeds) and asexual (turions) propagules. Of the total reproductive parts in the dry season 11.4% were seeds and 88.6% were turions in *R. tuberosa*, whereas 86% were seeds and 14% turions in *R. polycarpa*. The type of asexual bud also differed; only type I turions were present for *R. polycarpa* whereas both types I and II were recorded for *R. tuberosa* (39% type I and 61% type II). Although the two annual species produce both seeds and turions these data suggest that *R. tuberosa* relies on asexual propagation from turions to a greater extent than does *R. polycarpa*. Both seeds and asexual organs germinated simultaneously in the *R. tuberosa* population from Little Dip Lake and the *R. polycarpa* population from Blue-Green Algal Pool.

An alternative way of examining reproductive effort is by considering the number of reproductive units produced. The number of seeds produced by a plant will be determined by the weight of a plant, the proportion of its weight allocated to seeds and the average weight of each seed (Harper 1977). The number of asexual reproductive units (turions) will be determined by the same variables and thus an estimate of the total number of reproductive units can be made. Asexual reproductive units can only be considered in this way if they become

independent of the parent plant. Spread by rhizomes is not assessable, as potentially every rhizome is totipotent and could be stimulated to spread and become independent of the parent plant. Estimates of the number of reproductive propagules were based on counts of seeds and turions separated from the samples sorted for dry weight determinations. Estimates of propagules per plant were not possible as individuals were impossible to distinguish in the perennial populations because of rhizomatous spread. Further estimates of seed numbers were made from the number of flowers produced. From these figures the number of reproductive units per square metre was calculated. Samples were taken from the densest part of each population. Differences in the standing crops of these annual and perennial species are discussed in Section 9.4 (Figure 9.9).

Estimates of the number of viable seeds and turions per square metre are presented for two populations of *R. tuberosa* and of *R. megacarpa* and one of *R. polycarpa* (Table 9.17). Differences between annual and perennial growth forms, the three species and between the two populations of *R. tuberosa* were examined. The number of generations represented by the propagule bank was difficult to determine: seed cases which had already germinated were removed (73% of total for *R. polycarpa* and 50% for *R. tuberosa*), few *R. megacarpa* seeds showed signs of either previous germination or non-viability; all turions appeared to be intact. It was assumed that non-viability of seeds and turions would affect samples equally and that even where differences in viability between seeds and turions occurred, this would not affect the magnitude of the differences between the groups being compared. As it was not possible to determine the age of seeds or turions, the numbers predicted are for the total bank of reproductive units rather than those produced per plant or per generation. There will always be more than one generation present in situations where a long period of dormancy is required for maturity. Germination of proportions of the

same seed bank in successive years is suggested from evidence presented for the perennial *R. megacarpa* but not for the annual species. Thus the estimates of seed number for the perennial species would be inflated as they would include more than one generation; whereas estimates for the annuals would largely be based on the production for one generation, supplemented by minor proportions of older seeds which did not germinate in previous seasons.

These estimates (Table 9.17a) show that the total number of reproductive units per square metre was similar for annual populations: the estimate for *R. polycarpa* was 3394 and for the two *R. tuberosa* populations 3980 and 3119. These data contrast with the estimate of 372 seeds per square metre for *R. megacarpa*. Comparisons of seed numbers show that the *R. polycarpa* estimate included more seeds than either *R. tuberosa* or *R. megacarpa*. Other seed number differences were not considered to be of sufficient magnitude to be significant when sampling bias and the inability to distinguish generations were taken into account.

The potential seed production in one generation was estimated from the number of flowers per plant or sample and the number of carpels per flower (Table 9.17b). These estimates cannot take into account fertilization and development, viability or dispersal. It was assumed that only half the carpels would develop to maturity. These calculations suggest that the two annual species could each produce over 10,000 seeds per square metre in a growing season whereas the perennial could produce less than 500 seeds (Table 9.17b). These estimates, although considerably in excess of the actual numbers of seeds found, support the initial observations that annual plants produce many more reproductive units than perennial plants.

The evidence presented for *Ruppia* is consistent with the hypothesis that species in variable habitats produce many small seeds whereas species in more stable, mature habitats produce a smaller

Table 9.17 Estimates of the number of plant propagules produced by annual and perennial *Ruppia* populations.
a. estimate based on seeds and turions in the sediments
b. estimate of seed production based on flowers produced per plant or sample

a.

*Species	Location		No. /subs		No. viable /subs		No. viable /Tvs	No. viable /m^2
R. tuberosa	LDL	seeds	24	(22%)	(50%)	12	54	507
		turions type I	15		(100%)	15	68	632
		turions type II	47		(100%)	47	213	1980
		Total						3119
	Lake Robe	seeds	36	(100%)	(50%)	18	18	167
		turions type I	230		(100%)	230	230	2139
		turions type II	180		(100%)	180	180	1674
		Total						3980
R. megacarpa	LDL	seeds	40			40	40	372
		turions	0			0	0	0
		Total						372
R. polycarpa	BGAP	seeds	264		(27%)	72	313	2910
		turions type I	12		(100%)	12	52	484
		Total						3394

b.

*Species	No. /fl.	carpels mature (estimate)	No.fl. /infl.	No. infl. /50 pl. or tillers	No. infl. /pl. or tiller	est-imated No.pl. /Tvs	No.pl. /m^2	No. seeds /m^2
R. tuberosa (LDL)	6-19 (10)	5	2	25	0.5	500	4650	11600
R. megacarpa (LDL)	2-4 (4)	2	2	167 seeds	3.3 seeds	15	140	466
R. polycarpa (BGAP)	4-11 (6)	3	2	37	0.74	500	4650	10300

* Sample no. of material used for estimates a. seeds & turions b. flowers

R. tuberosa	LDL	37-8A-11/77	8A-9/78
R. megacarpa	LDL	10-8B-11/77	8B-1/78
R. polycarpa	BGAP	4-4C-11/77	4C-9/78
R. tuberosa	Lake Robe	52-6A-11/77	

Tvs = Tvarminne sampler = 0.11 sq m

subs = subsample

wt = weight

fl = flower

infl = inflorescence = 2 flowers

pl = plant

number of larger seeds (Salisbury 1942).

Discussion

The reproductive strategies analysed for the three species of *Ruppia* can be interpreted through the principle of strategic allocation. This principle as quoted by Harper (1977) states "that organisms under natural selection optimize the partitioning of the limited time and energy in a way that maximizes fitness", and this hypothesis has been developed and used to discuss the reproductive strategies of many groups of plants and animals (Cody 1966; Harper 1967; Harper and Odgen 1970; Odgen 1974). Harper (1977) further stated that this principle depends on the idea that structures or activities of organisms are alternatives. Thus organisms which recolonize fluctuating ephemeral habitats each year, for example the two annual *Ruppia* species, may depend on a high fecundity to maximize the chance of leaving descendents, whereas in a more stable habitat, such as that of the perennial *R. megacarpa*, fitness may be maximized by vegetative vigour. The reproductive strategy of the annual species *R. tuberosa* and *R. polycarpa* can be described as monocarpic (Harper 1977) or semelparous (Stearns 1976) as they reproduce only once and produce large numbers of reproductive units. In contrast, the perennial species *R. megacarpa* has a polycarpic (Harper 1977) or iteroparous (Stearns 1976) reproductive strategy as it reproduces more than once, over several seasons of the prolonged life cycle, but produces smaller numbers of seeds on each occasion.

The life cycles of the annual *Ruppia* species, *R. tuberosa* and *R. polycarpa* with their monocarpic reproductive patterns, rapid development of the plants, early maturity and a large amount of energy allocated to producing large numbers of small propagules, appear suitable for interpretation as an example of r-selection.

The life cycle of the perennial *R. megacarpa*, with its polycarpic reproductive pattern, slow development of plants, late maturity and the small amount of energy allocated to producing a small number of large propagules, appears suitable for interpretation as an example of K-selection. However more extensive consideration of the predictability of environmental fluctuations in these habitats would be necessary before the basic assumptions behind the theories of r- and K-selection could be satisfied. Theories of r- and K-selection also imply the presence or absence of competition for which only qualitative evidence is available. As the data are consistent with the concepts of semelparity and iteroparity it is more appropriate to interpret them in this way.

CHAPTER 10 CONCLUSIONS

This study shows that both environmental fluctuations and maximum salinity levels are important in determining the macrophyte flora in saline environments. Most submerged hydrophytes are unable to tolerate waters with a salinity above 4 °/oo TDS and emergent halophytes, although more diverse, are separated from the much larger group of non-halophytic species by their tolerance of high root water salinities. The adaptability of the small group of halophytes which does occur at salinities above 4 °/oo TDS is determined by the ability to survive a variety of harsh and fluctuating conditions. The variation within the genus *Ruppia* is an example of how one halophyte has adapted to these conditions. Even though extrapolation from this example to other biotic systems must be made with caution, a knowledge of the variation, life history and physiology of this genus contributes to the knowledge of submerged aquatic halophytes.

The systematic and ecological assessment of the variation observed within the genus *Ruppia* in south-eastern South Australia revealed major taxonomic differences; these are related to habitat preferences. Interactions between the genotype and the environment are expressed in the life cycles of annual and perennial populations adapted, respectively, to ephemeral and permanent habitats. Systematic examination of this genus in South Australia indicated that the differences between annual and perennial forms were indeed of species rank and that the variation within the annual forms allowed a further division into species. Thus, three species, one perennial and two annual, occur in the saline ecosystems studied. All three occur sympatrically in Lake Robe, and the perennial and one annual species are found in both Little Dip Lake and the Lake Eliza Salt Marsh.

Although the three species of *Ruppia* are not new, none of them previously has been reported from South Australia. All South Australian material - in fact all Australian material - has been described to date as *Ruppia maritima* or *R. spiralis* (= *R. cirrhosa*). These names have been applied incorrectly to the three taxa present in the study area and to most Australian material. The robust perennial species of *Ruppia* is identified as *R. megacarpa*, and the delicate annual species as *R. polycarpa* and *R. tuberosa*. These species are distinguished by differences in characters such as carpel number, fruit size, sessile or stalked fruit, the shape of the fruit stalk attachment and leaf width. *R. megacarpa* and *R. polycarpa* were described from New Zealand, and *R. tuberosa* was described from Western Australia. Most of the specimens of this genus located in The State Herbarium of South Australia belong to these three species. The only exceptions to this are several herbarium specimens from central Australia; these specimens fit into the *R. maritima* group as all have short peduncles and are fertilized underwater. Specimens belonging to this group have been collected recently in western New South Wales (S. Jacobs pers. comm. 1979). All material collected from Victoria, New South Wales and Western Australia and specimens examined from herbaria in New South Wales, Australian Capital Territory, Victoria and Western Australia are placed in one of the four species, *R. tuberosa*, *R. polycarpa*, *R. megacarpa* or *R. maritima*. Very few specimens are *R. maritima* and none of the Australian specimens conform to the species description for *R. cirrhosa* (*R. spiralis*).

The occurrence in South Australia of the two species described from New Zealand and the one from Western Australia has wide biogeographical implications. The presence of *R. megacarpa* and *R. polycarpa* outside New Zealand suggests that they are temperate species with a wide distribution, at least in the Southern Hemisphere. Recent records

of these species from New South Wales, Victoria and Western Australia extend their known distribution in the temperate southern areas of Australia. Similarly the widespread occurrence of *R. tuberosa* in South Australia, together with recent isolated records of the species on Rottnest Island, Western Australia and in Swan Bay, on the western side of Port Phillip Bay in Victoria extend the recorded distribution of this species across southern Australia.

In South Australia *R. polycarpa* and *R. tuberosa* are similar in life cycle, growth form and habitat preference and thereby show closer affinities to each other than either does to *R. megacarpa*. *R. megacarpa* is similar to the majority of Northern Hemisphere species in its perennial life cycle, larger growth form and permanently aquatic habitat.

From the limited numbers of records of plants from the *R. maritima* group it appears that this species is confined to the central and northern areas of Australia. It may be speculated that *R. maritima* occupies northern permanent water holes and springs as a relict species of past climates in Australia, and that *R. megacarpa*, *R. tuberosa* and *R. polycarpa* form a group of temperate climate species that have evolved in response to fluctuating environments. An extensive examination of the distribution and biology of the *R. maritima* group and the distribution of *R. tuberosa*, *R. megacarpa* and *R. polycarpa* throughout Australia are necessary before a complete revision of the genus in Australia can allow further biogeographical speculation.

Turions produced by both *R. polycarpa* and *R. tuberosa* in Australia provide the only records of perennating organs within this genus: Verhoeven (1979) and others state that vegetative material of *Ruppia* in Europe does not resist desiccation. In South Australian ecosystems, large numbers of turions of two structural types form on

R. tuberosa, and a smaller number of only one type form on *R. polycarpa*. In both species a swelling around a meristematic area at the junction of the leaf sheath and rhizome is enclosed in resistant leaves and detaches to form a turion: in *R. tuberosa* a swelling at the extremity of a rhizome, presumably around the apical meristem, may form a starch-filled turion which becomes detached from the decaying plant. Both structures serve as perennating organs and germinate when conditions are favourable. All records of turions were from ephemeral or very shallow saline habitats. Turions have never been recorded for *R. polycarpa* in New Zealand where habitats for this species are always permanent (Mason pers. comm. 1979). This suggests that turions only occur in ephemeral habitats. These observations have important taxonomic implications for the genus and family as the presence of turions in the Potamogetonaceae and their absence in Ruppiaceae have been considered as basic differences between these closely related families (Davis and Tomlinson 1974). The two structural types of turions described for *Ruppia* in this study parallel the many types of turions found in the Potamogetonaceae (Hutchinson 1975). A detailed examination of other differences (e.g. floral morphology by Uhl 1947) in Australian material may lead to further consideration of the close relationships of these families.

Of the submerged angiosperms *Ruppia* has the widest tolerance of both absolute concentration and range of salinity. The osmoregulatory mechanisms that enable members of this group to survive in both fresh and extremely hypersaline waters provide further insight into mechanisms of salinity tolerance. The cellular fluids of all three species of *Ruppia* were found to be hypertonic to the surrounding water: these concentrations of solutes would normally be damaging to metabolic enzymes. It has been suggested that the accumulation of certain amino acids, e.g. proline, in the cytoplasm of halophytes and water-stressed

plants may function as a salt tolerance mechanism by counter-balancing the high solute concentration of the vacuolar fluids (see Chapter 9). The investigation of proline concentration in *Ruppia* shows that the levels of proline increase with increase in habitat salinity. This supports the idea that these plants can survive and photosynthesize in a range of environments at least partially by osmotic adjustment of proline levels in the cytoplasm.

The ecological variation of *Ruppia* in different habitats has been considered in terms of life cycle patterns. The annual species, *R. tuberosa* and *R. polycarpa*, synchronize their life cycle stages to the wet and dry phases of their ephemeral habitats; many seeds and turions lie dormant in the dry lake sediments during the summer. The perennial life cycle of *R. megacarpa* gives this species an advantage in deeper permanent and more stable habitats where annual recolonization by seeds would be a competitive disadvantage. Evidence from trans-plantation experiments does not indicate that these annual or perennial strategies are reversible in the alternate habitats, at least in the subsequent generation.

Differences between the annual and perennial populations of *Ruppia* were also evident from seed germination: dormancy breakage is stimulated by fresh water in the perennial *R. megacarpa* whereas the presence of saline water and alternate wetting and drying stimulate germination of seeds of the annual *R. tuberosa*. These observations are consistent with the life cycle patterns of the two species. The seasonal drying of the ephemeral habitat breaks dormancy and thus seeds can germinate as soon as habitats refill: the plants can thus maximize their use of the short growing season to complete their life cycles. The germination of the *R. tuberosa* seeds in response to high salinity also allows the plant life cycle to proceed in ephemeral, unpredictable

and highly saline environments. The correlation of low salinity with germination of the *R. megacarpa* seeds may also be advantageous for this species as, in general, seeds lie dormant in the lake sediments until a major decrease in salinity occurs.

The reproductive patterns of the annual and perennial forms of *Ruppia* are also adaptive in the ephemeral and permanent environments. *R. megacarpa* does not flower and fruit prolifically, seeds rarely germinate in the field and reproduction is asexual by growth from rhizomes and rooting at stem nodes. This strategy is advantageous in a stable permanent habitat where competition for space appears to be more important than the ability to recolonize from dormant propagules. In contrast, both annual species flower and fruit prolifically by producing many more flowers per plant and more seeds per flower than the perennial species. In general, seeds of the annuals germinate after one dry season. Many turions are produced by the annuals and these resist desiccation and remain viable to propagate the species asexually. Thus the large number of asexual and sexual reproductive units produced enables the annual species to recolonize their habitats each wet season.

In summary, the annual species, *R. tuberosa* and *R. polycarpa*, occupy ephemeral habitats which are subject to wide environmental fluctuations whereas the perennial, *R. megacarpa*, occupies permanent habitats which in comparison are stable, constant and predictable. Even though fluctuations in ephemeral habitats are seasonally predictable the timing and length of the wet phase is not predictable. In these temporary habitats annual recolonization from seeds or turions is necessary and consequently population size may vary with the availability of the reservoir of reproductive units as well as with environmental conditions. Rapid development of the plants, early and prolific

reproduction and the allocation of large proportions of the plant's resources to production of a large number of small reproductive units (seeds and turions) are characteristic of these populations; the reproductive patterns of the annual species are semelparous (monocarpic). In contrast the perennial has an iteroparous (polycarpic) reproductive pattern as it produces only small numbers of larger seeds in each year and devotes most of its energy to vegetative growth.

APPENDICES

APPENDIX I. Characteristics of sites not sampled regularly.

Lake Name	Abbreviation	Area (ha)	Characteristics	Grid Reference 1:250,000 Series	Bayly (1970) Lake No.
Lake Eliza	(LE)	3824	large shallow salt lake	Penola sheet 28-40-	10A
Lake Fellmongery	(LF)	26	permanent fresh-brackish	282415	10C
Lakes just past 'Karinya'					
- west of road	(wKL)	<2.5	permanent	287401	14
- east of road	(eKL)	8	permanent	286401	15
Lake St. Clair	(LSC)	2225	shallow salt lake	29-39-	
Coorong Policemans Pt	(PP)		permanent (Coorong proper)	Naracoorte sheet 261548	
Coorong North Lagoon	(CNL)		permanent (Coorong proper)		
Lake north of Meningie	(NM)	<2	temporary roadside saline pool	Barker sheet 242618	
Coobowie	(Cw)	<2	permanent marine saline/ hypersaline lagoon		
Porters Lagoon east of Clare	(PoL)		permanent saline lake	Burra sheet 185818	
West Lakes Adelaide	(WL)		permanent estuarine	Adelaide sheet 151695	

APPENDIX II Lake conductivities ($K_{25}°_C$ millisiemen) and salinity (°/oo TDS) 1975 - 1978

Site	Date	1975								1976										1977										1978											
		A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
1	K_{25}	230						49		203	d			110				41		46	d	50			113			17		41	d	d		41		21		23		57							
	TDS	212						34		156	d			92				28		31	d	33			95			11		27	d	d		27		13		14		41							
2	K_{25}		73			59		59	60	61				85		52	59				65	68	92	77			66		55	80		80	102		72		72		109							
	TDS		54			42		42	43	43				66		37	41				47	50	73	59			48		38	61		61	84		53		53		91							
3	K_{25}					29		44	38	d		d			48	26	38	d				d	d	d			19		41	d		d	d		12		18		d							
	TDS					19		29	25	d		d			33	16	25	d				d	d	d			12		27	d		d	d		7		11		d							
4	K_{25}						21	15		d		d				21	33	d				d	d	d		21	16		20	d		d	d		10		20		48							
	TDS						13	9		d		d				13	21	d				d	d	d		13	10		12	d		d	d		6		12		33							
5	K_{25}						75	74	150	d		d			67	94	106	170				d	d	d		21			81	266		d	d		44		52		d							
	TDS						56	55	122	d		d			49	75	88	132				d	d	d		13			62	120		d	d		29		36		d							
6	K_{25}		85	33		39	35	31	40	44				69		55	47	48				73	101	93	85	68		55	75		107	147		53		51		61							
	TDS		66	21		26	23	20	27	29				51		39	32	33				54	83	74	66	58		38	56		89	136		36		35		45							
7	K_{25}							3.9		3.6	3.8			5.0			4.8	3.8	4.0			4.0	5.6	4.8			4.4		3.8	3.9			4.6		4.1		4.1		4.5							
	TDS							2.3		2.1	2.2			2.9			2.8	2.2	2.3			2.3	3.3	2.8			2.6		2.2	2.2			2.6		2.4		2.4		2.6							
8	K_{25}		45	33		29		28	29	34				42		36	34	33	35			46	54	51	45	36		33	41		51	55		36		36		40							
	TDS		30	21		19		18	19	22				29		24	22	21	23			32	38	35	31	24		21	28		36	39		24		24		25							
9	K_{25}		52	11		76	26	25						37				35	30			121	d	d	d	31		37			d	39		22		32		50							
	TDS		36	6		57	22	19						25				24	19			105	d	d	d	20		25			d	24		13		20		35							
10	K_{25}					10	9		10					21			13	9				22				16		17				31		13		13									
	TDS					6	6		6					13			8	8				14				10		10				20		8		8									
11	K_{25}		111			65	61		61					120			76					112		131										84		80									
	TDS		94			47	44		44					104			57					95		116										65		61									
12	K_{25}								82					128			83	85				109		111			79			98	113	126		80		85		92							
	TDS								63					113			64	66				91		94			67			80	95	108		61		65		73							

d - dry

APPENDIX III Lake chemistry of South Australian salt lakes: data extracted from Bayly and Williams (1966), B, and Williams and Buckney (1976), A.

Locality/ Locality Group		No. of Localities	Na	K	Ca	Mg	Cl	SO_4	$HCO_3 + CO_3$	pH	Salinity °/oo TDS
Seawater			77.1	1.6	3.5	17.7	90.3	9.3	0.4		
Beachport/Robe Series	B	8	74.7 (64.3-77.3)	2.0 (1.6-2.7)	2.6 (0.2-3.7)	20.7 (17.2-32.7)	86.4 (80.1-92.9)	13.1 (6.6-19.6)	0.5 (0.2-0.9)		
Coorong S.A.	A	8	71.3 (68.3-72.9)	1.9 (1.6-2.2)	4.0 (3.6-4.3)	22.7 (19.6-25.6)	96.6 (95.7-98.0)	3.1 (1.0-4.0)	0.4 (0.1-0.6)		
S.E. Salt Lakes	A	5	82.1 (80.2-84.3)	1.8 (1.1-2.5)	2.0 (0.3-6.9)	14.2 (9.5-17.3)	95.6 (91.4-97.7)	3.4 (2.3-3.7)	0.9 (0.1-3.5)		
No.											
2 Flax Point	A	1	69.0	2.2	3.9	24.9	97.1	2.6	0.3		49.3
6 Robe	B	1	73.9	1.9	2.2	21.9	92.9	6.6	0.5	7.4	112.5
12 Beachport Salt Lake	B	1	76.5	2.0	3.1	18.4	87.4	12.3	0.3	7.6	124.9
11 Lake Eliza Cutoff	B	1	76.3	1.9	2.4	19.4	84.5	15.3	0.2	7.4	159.2

APPENDIX IV Plant list from saline lakes, and surrounds, of the Coorong and south-east of South Australia

Records from personal collections and from a survey of the Coorong by the Nature Conservation Society in 1975, Alcock and Symon (1975)

* introduced species

lm = lake margin
sm = saline marsh
sf = samphire flats

	Location	Collection No.
ANGIOSPERMAE		
Aizoaceae		
Carpobrotus rossii (Haw.) Schwantes	Wood's Well	06-775
	Pipeclay Lake	78-975
Tetragonia amplexicoma (Miq.)Hook.f.	Pipeclay Lake	10-775
	Lake Eliza Salt Marsh	61-775
	Pipeclay Lake	74-975
	Flax Point	79-975
Amaranthaceae		
Hemichroa pentandra R.Br.	Lake Eliza Salt Marsh	46-775
	Pipeclay Lake	223-1275
Apiaceae (Umbelliferae)		
Apium prostratum Labill.ex Vent.	Coorong sf	A5122
**Bupleurum semicompositum* L.	" sm	S10517
Hydrocotyle capillaris F.Muell.ex Klatt.	" sm	S10520
H. medicaginoides Turcz.	" lm	S10474
H. pilifera Turcz.	" sm	S10494
Asteraceae (Compositae)		
Brachycome exilis Sond.	Coorong lm	S10472
	sm	S10501
	sf	A5119
B. goniocarpa Sond. & F.Muell.ex Sond.	Coorong sm	S10509
		S10515
Cotula vulgaris Levyns	Lake Eliza Salt Marsh	117-975
	"	118-975
	"	120-975
	"	122-975
	Coorong Nat. Park	166-1075
	Coorong lm	S10471
	sm	S10487
**Hypochoeris glabra* L.	Coorong sm	S10514
**Inula graveolens* (L.) Desf.	Coorong sf	A5102
Olearia axillaris (DC.)F.Muell. ex Benth.	Erringtons Hole	200-1075

	Location	Collection No.
Senecio glossanthus (Sond.) Belcher	Coorong lm	S10479
	" sm	S10496
S. lautus Forst.f.ex Willd.	Erringtons Hole	147-975
* *S. vulgaris* L.	Lake Eliza Salt	123-975
	Marsh	139-975
* *Sonchus oleraceus* L.	Coorong sm	S10502
Boraginaceae		
Cynoglossum australe R.Br.	Coorong sf	A5105
* *Echium lycopsis* L.	Brineshrimp Lake	978
	Coorong sm	S10521
	" sf	A5106
Myosotis australis R.Br.	" lm	S10480
Brassicaceae		
Cakile maritima Scop.	Erringtons Hole	10-978
Hymenolobus procumbens (L.) Nuttall ex Schinz & Thell.	Coorong lm	S10470
	" sm	S10490
Caryophyllaceae		
* *Arenaria serpyllifolia* L.	Brineshrimp Lake	
	Coorong sm	S10511
* *Sagina apetala* Ard.	" sf	A5024
Centrolepidaceae		
Centrolepis polygyna (R.Br.) Hieron.	" lm	S10475
	" sm	S10519
Chenopodiaceae		
Arthrocnemum Moq.	Lake Eliza Salt	140,114-975
	Marsh	235,236, 237-1275
	Cantara	22-775
	Yorke Peninsula	69-775
	Mikes Lake	94-975
	Brineshrimp Lake	162-1075
	Lake Robe	102-975
	Coorong sm	S10482, S10484
		S10491, S10500
Atriplex paludosa R.Br.	Pipeclay Lake	13-775
Maireana oppositifolia (F.Muell.) P.G.Wilson	Coorong sm	S10497
Rhagodia baccata (Labill.) Moq.	Lake Eliza Salt	
	Marsh	142-975
Sarcocornia quinqueflora (Bunge ex Ung-Steinb.) Scott	Pipeclay Lake	11-775
	Flax Point	18-775
	Cantara	21-775
	Little Dip Lake	29-775
	"	31-775
	Mikes Lake	90-975
	Lake Robe	100-975
	Lake Eliza Salt	113-975
	Marsh	140-975
		241,229,234,242-1275

	Location	Collection No.
Suaeda australis (R.Br.)Moq.	Wood's Well	04,07-775
	Pipeclay Lake	14-775
	"	222-1275
	Coorong sf	A5103
Threlkeldia diffusa R.Br.	Pipeclay Lake	187-1075
Convolvulaceae		
Wilsonia backhousei Hook.f.	Lake Eliza Salt Marsh	48-775
		128-975
	"	228-1275
	Brineshrimp Lake	171-1075
	Porters Lagoon	181-1075
	Blue-Green Algal Pool	195-1075
W. humilis R.Br.	Yorke Peninsula	67-775
	Pipeclay Lake	220-1275
Cyperaceae		
Cyperus laevigatus L.	Brineshrimp Lake	7-1078
Gahnia filum (Labill.) F.Muell.	Karinya	62-775
	Lake Eliza Salt Marsh	127-975
		129-975
		350-878
	Pipeclay Lake	189-975
	Coorong sm	S10526
G. trifida Labill.	Lake Eliza Salt Marsh	340-177
	Fresh Dip Lake	-1177
	Coorong sf	A5101
Lepidosperma canescens Boeck.	Fresh Dip Lake	341-177
L. longitudinale Labill.	Fresh Dip Lake	342-177
		-1177
L. gladiatum Labill.	Erringtons Hole	156-975
Machaerina juncea (R.Br.)Koyama	Lake Eliza Salt Marsh	130-975
	Erringtons Hole	150-975
	Fresh Dip Lake	-1177
M. tetragona (Labill.) Koyama	Erringtons Hole	144-975
Scirpus antarcticus L.	Coorong sm	S10518
S. inundatus (R.Br.) Poir.	Lake Eliza Salt Marsh	227-1275
S. maritimus L.	Lake Eliza Cutoff	249-1275
S. nodosus Rottb.	Wood's Well Coorong	1-775
	Karinya	64-775
	Erringtons Hole	149-975
		158-975
	Lake Eliza Cutoff	250-1275
	Coorong sm	S10503
Epacridaceae		
Leucopogon parviflorus (Andr.)Lindl.	Lake Eliza Cutoff	160-975
	Little Dip Lake	-978
	Fresh Dip Lake	-978
	Coorong	-978

	Location	Collection No.
Euphorbiaceae		
Adriana klotzschii (F.Muell.)Mueller-Arg.	Coorong sf	A5115
Beyeria leschenaultii (DC.)Baill.	" sf	A5116
* *Euphorbia paralias* L.	Erringtons Hole	148-975
	Flax Point	
Fabaceae (Papilionaceae)		
**Medicago polymorpha* var *vulgaris*(Benth.) Shinners	Coorong sf	A5107
Pultenea prostrata Benth.ex Hook.f.	" sm	S10525
Frankeniaceae		
Frankenia pauciflora DC.	Lake Eliza Salt Marsh	138-975
	"	205-1075
	"	244-1275
	"	345-188
	Coorong sm	S10483
	" sf	A5104
	Southern Coorong	163-1075
Frankenia L. sp.	Coorong-Wood's Well	03-775
	Flax Point	19-775
	"	80-975
	Cantara	22A-975
Gentianaceae		
Sebaea albidiflora F.Muell.	Coorong lm	S10478
	" sm	S10512
S. ovata (Labill.)R.Br.	" lm	S10477
	" sm	S10513
Goodeniaceae		
Scaveola L. sp.	Beachport Salt Lake	-1178
Selliera radicans Cav.	Lake Eliza Salt Marsh	51-775
		346-177
Haloragaceae		
Myriophyllum muelleri Sond.	Kangaroo Island	-378
M. propinquum A.Cunn.	Fresh Dip Lake	
Juncaceae		
* *Juncus acutus* L.	Coorong lm	S10481
J. bufonius L.	" sm	S10492
	" sf	A5123
	Beachport Salt Lake	-1178
J. kraussii Hochst.	Mikes Lake	24-775
	"	92-975
	Little Dip Lake	34-775
	Pipeclay Lake	190-1075
	Lake Eliza Cutoff	253-1275
	Lake Eliza Salt Marsh	49, 57-775
		125-975
		233-1275
		343-177

	Location	Collection No.
Juncaginaceae		
Triglochin centrocarpum Hook.	Coorong lm	S10476
	" sm	S10493
T. mucronatum R.Br.	Lake Eliza Salt Marsh	121-975
	"	137-975
	"	206-1075
	Coorong lm	S10473
	" sm	S10485
T. striatum Riuz & Pavon	Lake Eliza Salt Marsh	133-975
		230,232-1275
Lauraceae		
Cassytha L.	Fresh Dip Lake	11-78
Liliaceae		
Dianella revoluta R.Br.	Beachport Salt Lake	11-78
Loranthaceae		
Amyema melaleucae (Lehm.ex Miq.)Tiegh.	Coorong sm	S10524
	Lake Eliza Salt Marsh	
Mimosaceae		
Acacia pycnantha Benth.	Coorong	
	Little Dip Lake	
A. sophorae (Labill.)R.Br.ex Ait.	Coorong-Pipeclay Lake	16-775
	Little Dip Lake	
Myrtaceae		
Eucalyptus diversifolia Bonpl.	Pipeclay Lake, Fresh Dip Lake, Little Dip Lake	
E. fasciculosa F.Muell.	Coorong	
Leptospermum pubescens Lamk.	Erringtons Hole	153-975
	Lake Eliza Cutoff	251,252-1275
*Melaleuca halmaturorum*F.Muell.ex Miq.	Mikes Lake	88-975
	Lake Eliza Salt Marsh	59,60-775
	Erringtons Hole	199-1075
M. lanceolata Otto	Lake Eliza Salt Marsh	
Poaceae (Gramineae)		
Agropyron scabrum (Labill.)Beauv.	Coorong sm	S10508
	" sf	A5110
Agrostis aemula R.Br.	Lake Eliza Salt Marsh	239-1275
	"	344-177
A. billardieri R.Br.	Coorong sf	A5109
* *Avena barbata* Pott ex Link	" sm	S10507
	" sf	A5111
* *A. sativa* L.	Brineshrimp Lake	
* *Bromus diandrus* Roth.	Lake Eliza Salt Marsh	245-1275
* *B. rubens* L.	Coorong sm	S10505
	" sf	A5105
* *Catapodium rigidum*(L.)Hubb.ex Dony.	" sf	A5114
Distichlis distichophylla (Labill.) Fassett	" sf	A5094

	Location	Collection No.
Hordeum marinum Huds.	Lake Eliza Salt Marsh	243-1275
**Koeleria phleoides* (Vill.) Pers.	Coorong sm	S10510
* *Parapholis incurva* (L.) Hubbard	" sm	S10489
Phragmites australis (Cav.) Trin. ex Steud.	Lake Alexandrina	-1175
	Lake Eliza Cutoff	248-1275
Poa fax Willis & Court	Coorong sm	S10495
* *Polypogon maritimus* Willd.	" sm	S10504
Puccinellia stricta (Hook.f.) C.Blom.	Lake Eliza Salt Marsh	42-775
	"	116,135-975
	"	204-1075
	" 231, 233,	240-1275
	Coorong	164,165-1075
	" sm	S10486
* *Serrafalcus hordeaceus* (L.) Gren. & Godr. ≡*Bromus mollis* L. ≡*B. hordeaceus*	Lake Eliza Salt Marsh	246-1275
	Coorong sf	A5122
Sporobolus virginicus (L.) Kunth	Pipeclay Lake	15-775
	Flax Point	19-775
	"	85-975
	Mikes Lake	25-775
Stipa L. sp.	Coorong sm	S10508
	" sf	A5100
	" sf	A5113
* *Vulpia myuros* (L.) Gmel.	" sm	S10506
Polygonaceae		
Muehlenbeckia adpressa (Labill.) Meisn.	Fresh Dip Lake	-978
	Pipeclay Lake	-1178
Potamogetonaceae		
Potamogeton pectinatus L.		7-1178
Primulaceae		
* *Anagallis arvensis* L.	Coorong sm	S10516
	" sf	A5020
Samolus repens (Forst. & Forst.f.) Pers.	Pipeclay Lake	12-775
	"	186-1075
	Little Dip Lake	30,32,33-775
	Lake Eliza Salt Marsh	38-775
	"	109,124,159-975
Ranunculaceae		
Clematis microphylla DC.	Little Dip Lake	-978
	Fresh Dip Lake	-978
	Pipeclay Lake	-1178
Restionaceae		
Leptocarpus brownii Hook.f.	Lake Eliza Salt Marsh	132-975
		58-775
Rhamnaceae		
Pomaderris paniculosa F.Muell. ex Reisseck	Coorong sm	S10522
	" sf	A5117
Rosaceae		
Acaena anserinifolia (Forst. & Forst.f.) Druce	Pipeclay Lake	169-1075
	Erringtons Hole	-1177

	Location	Collection No.
Rubiaceae		
Galium murale (L.)All.	Coorong sm	S10510
Ruppiaceae		
Ruppia megacarpa Mason	Erringtons Hole	154-975
	Little Dip Lake	247-1275
	Lake Eliza Salt Marsh	10-1178
	Porters Lagoon	19-1176, 30-17
	Coorong North Lagoon	14-1278
	Lake Hamilton Eyre Peninsula	20-1276
	Willochra Creek	21-1276
	Kangaroo Island (Murray Lagoon)	23-1276
	West Lakes Adelaide	18-1176
	Policemans Point	31-177
R. polycarpa Mason	Fresh Dip Lake	7-177 7-1178
	Lake Robe	6-1078
	Blue-Green Algal Pool	4-978
R. tuberosa Davis and Tomlinson	Lake Robe	202-1075
	"	6-978
	"	6-1178
	Little Dip Lake	8-778
	"	8-1178
	Mikes Lake	3-978
	Coobowie Yorke Peninsula	13-1178
	"	13-1278
	"	15-1278
	Brineshrimp Lake	224-1275
	Pipeclay Lake	1-978
	Beachport Salt Lake	12-1178
	Lake Eliza Salt Marsh	9-978
	"	9-1178
	Flax Point, Coorong	192-1075
Scrophulariaceae		
* *Parentucella latifolia* (L.)Car.in Parl	Coorong sf	A5125
* *Verbascum virgatum* Stokes in Withering	" sf	A5096
Solanaceae		
* *Lycium ferocissimum* Miers	Pipeclay Lake	-1178
	Beachport Salt Lake	-1178
Stackhousiaceae		
Stackhousia spathulata Sieb.ex Spreng.	Coorong sf	A5083
	Fresh Dip Lake	-1178
S. monogyna Labill.	Coorong sf	A5093
Zannichelliaceae		
Lepilaena cylindrocarpa (Koern.ex Walp.)Benth.	Coorong sm	S10523
	Blue-Green Algal Pool, Pipeclay Lake, Mikes Lake, Brineshrimp Lake, Lake Robe, Fresh Dip Lake, Little Dip Lake, Lake Eliza Saltmarsh	

ALGAE	Location
CHLOROPHYTA	
Characeae	
Chara vulgaris L.	Fresh Dip Lake
Lamprothamnium papulosum(Wallr.)J.Gr.	Little Dip Lake, Mikes Lake, Lake Robe, Fresh Dip Lake
Cladophoraceae	
Cladophora Kuetzing	Flax Point, Mikes Lake, Little Dip Lake, Lake Eliza Salt Marsh
Dasycladaceae	
Acetabularia peniculus(R.Br.)Solms-Laubach	Flax Point,
Ulvaceae	
Enteromorpha Link in C.G.Nees	Mikes Lake
CHRYSOPHYTA	
Vaucheria Decandalle	Blue-Green Algal Pool, Mikes Lake
CYANOPHYTA	
Calothrix C.Agardh	Blue-Green Algal Pool, Mikes Lake
Hydrocoleum Kuetzing	Blue-Green Algal Pool, Mikes Lake
PHAEOPHYTA	
Nostoc Vaucher	Coorong

APPENDIX V Glossary of terms used in the description of *Ruppia*

beak	a hardened terminal extension of the endocarp formed around the stylar canal
carpel	ovule-bearing organ, sessile before fertilization with the carpel base often elongating in fruit
elevated stem	an elongated often branched stem which vertically supports the leaves in the water
flower	a cluster of carpels with two bilocular anthers one above and one below the carpels
fruiting carpel	one fruit developed from one carpel consisting of an outer fleshy exocarp which decays on maturity leaving the hardened black endocarp which surrounds the embryo
inflorescence	a terminal spike of only 2 flowers borne on opposite sides of the peduncle
peduncle	inflorescence stalk, often elongate and spiral
perennating organs	overwintering buds formed from stem bases surrounded by leaves or from the underground rhizomes
podogyne	elongate stalk of an individual fruiting carpel
rhizome	horizontal stems which spread the plant laterally, partially or wholly submerged in the sediments

Key to abbreviations used in Appendices VI, XI, XIII

Leaf apex	T	truncate
	B	bidentate
	R	rounded
	A	acuminate
	O	obtuse
Lacunae shape	E	elliptical
	C	circular
Theca shape	K	kidney shaped
	Ro	rounded
Thecae, longitudinal slit for dehiscence	S	sunken
	Ri	ridged
Inflorescence location	bs	basal sheaths
	tes	terminal elevated sheaths
	t	terminal
Flower sheath	sw	swollen
	nsw	not swollen
Pollination	su	at the water surface
	uw	underwater
Pollen shape	ed	elongated dumbell
	sd	stout dumbell
	eb	elongated bent (boomerang shape)
	el	elliptical
Peduncle form	sp	spiral
	st	straight
Abundance, flowering, branching etc.	p	prolific
	c	common
	oc	occasional
	u	uncommon
	r	rare
Fruit shape	py	pyriform
	asy	asymmetric
	sy	symmetric
	tu	turbinate
Stylar beak	sh	short
	ex	extended
Colour of endocarp	bl	black
Podogyne	ss	subsessile, sessile
	th	thin
	st	stout
	sr	straight attachment
	ta	tapered attachment
	nta	not tapered " (straight)
Fruit Sculpturing	M	many
	v	variable
	sm	smooth
	ba	barbed
	ro	rough
Endocarp window	nel	narrow elliptic
	el	elliptic
	de	deltate
Habit	an	annual
	pe	perennial
Associations	ms	monospecific
	cd	co-dominant
	L	*Lepilaena*
	Ch	charophytes
	Cl	*Cladophora*
	Sms	salt marsh species
	Al	other algae
	Pot	*Potamogeton*
Habitat	perm	permanent
	temp	temporary
	hysal	hypersaline
	sal	saline
	br	brackish
	fr	fresh
Months	J F M Ap My Ju Jl A S O N D	
	→	grading to, ranging to
	oc	occasionally
	irr	irregularly
	✓	character present
	X	character absent
	-	data not available

Location abbreviations and numbers see Table 3.1

APPENDIX VI Characters examined for three forms of *Ruppia* from 18 habitats

Character	Locality	Taxon A								Taxon C			Taxon B					
		LDL	LESM	PL	FP	ML	BL	LR	B/p SL	Cw	BGAP	LR	FDL	LDL	LESM	EH	PoL	WL	CNL
INFLORESCENCE																			
	mean length (mm)	5.2	4.3	-	6.0	4.3	-	4.3	4.4	5.4	3.4	3.3	3.7	5.3	3.5	4.5	4.0	4.5	4.4
	mean width (mm)	2.3	2.3	-	3.1	2.1	-	3.3	3.0	2.1	1.5	1.4	1.5	1.5	1.2	1.8	2.1	2.0	1.5
	mean number of carpels	12	12	-	10	10	-	10	13	11	7	7	8	4	3	5	4	5	5
	thecae and thecal slit shape	K, Ri	K, Ri	-	K, Ri	K, Ri	-	K S	K S	K S	K S	K S	K S	K S	K S	K S	K S	K S	K S
	location	bs	bs	-	bs	bs	-	bs	bs	bs oc tes	bs oc tes	bs oc t	bs p tes	tes	tes	tes	tes	tes	tes
	pollination	su	su	-	su	su	-	su	su	su	su	su	su	su	su	su	su	su	su
	pollen shape	ed	ed	-	ed	ed	-	ed eb	-	-	eb	-	e or eb	sd	sd	-	-	-	-
	peduncle length (cm)	10 - 100	10 - 50	-	10 - 100	10-100	-	10 - 100	10 - 70	10 - 70	10 - 100	10-50	10-100	50-150	10-100	10-100	10-100	10-100	10-100
	peduncle form	sp	sp	-	sp	sp	-	sp	sp	sp	sp	sp	sp	sp	sp	sp	sp	sp	sp
	sheath subtending flower	sw	sw	-	sw	sw	-	sw	sw	sw	sw	sw	sw	sw	sw	sw	sw	sw	sw
	peduncle swelling below inflorescence	X	X	-	x	X	-	X	X	X	X	X	X	oc	X	X	X	X	X
	flowering abundance	c	p	-	p	c	-	p	p	c	pr	c	c	oc	c	u	c	c	oc-c
	flowering time	A, S-N	S-N	-	O-N	S-N	-	S-N	S-N	O-N	S-N	S-N	O-N	N-M	S-F	J	O-N	N-	N-
FRUIT																			
	mean length (mm)	1.6	1.3	-	2.0	1.7	2.1	1.7	2.0	1.8	1.8	1.9	2.3	3.1	2.6	-	3.1	3.0	-
	mean width (mm)	0.9	0.9	-	1.0	-	1.4	0.9	1.1	1.0	1.0	1.4	1.8	2.5	2.0	-	2.5	2.0	-
	mean thickness (mm)	0.7	0.6	-	0.8	-	0.8	0.7	0.8	0.7	0.5	0.7	1.3	1.8	1.2	-	1.5	1.4	-
	ratio L:W:T	2.3:1.3:1	2.1:1.4:1	-	2,5:1.3:1	-	2.6:1.8:1	2.3:1.3:1	2.3:1.3:1	2.7:1.4:1	3.9:2.1:1	2.6:1.9:1	1.8:1.4:1	1.7:1.3:1	2.1:1.3:1	-	2.1:1.6:1	2.1:1.4:1	-
	shape	py	py	-	py	py	py	py	py	asym py	asym py	asym py	asym py	asym tu	asym tu	-	asym tu	asym tu	-
	stylar beak (mm)	sh <0.3	sh <0.1	-	sh <0.3	sh <0.1	sh <0.2	sh <0.3	sh <0.2	sh <0.1	sh <0.1	sh <0.2	sh <0.2	0.9 - 1.7	1.0 - 1.5	-	1-2	1-2	-
	podogyne shape	ss th	ss th	-	ss th	ss th	ss th	ss th	ss th	ss th	th sr	th sr	th	st ta	st ta	-	st ta	st ta	-
	podogyne length (mm)	1.2	1	-	1	1	1	1-2	1-2	1-3	10-20	10 - 20	10 - 30	10 - 30	20 - 30	-	20 - 30	20 - 40	-
	number of carpels developed	M	M	-	M	M	M	M	M	M	M	M	1-5	1-3	1-3	-	1-4	1-4	-
	endocarp colour	bl	bl	-	bl	bl	bl	bl	bl	bl	bl	bl	bl	bl	bl	-	bl	bl	-
	thickness (mm)	0.1 - 1.1	0.1	-	-	-	-	0.1	-	-	-	-	-	0.23-0.3	0.2	-	-	-	-
	sculpturing	sm	sm	-	sm	sm	sm	sm	sm	sm	ba	ba	sm	sm	ro	-	ro	ro or sm	-
	window	nel	nel	-	el	el	el	el	el	el	nel	el	el	de	de	-	de	de	-
LEAF																			
	apex shape	R→A oc T	R oc T	R oc T	R→A	R→A	R oc T	R oc T	A oc T	A→O oc T	A oc T	A→ O	A oc T	T→B oc R	T oc O	T→B oc R	T→B	T→B	T→B
	mean width (mm)	0.22	0.22	0.21	0.20	0.16	0.19	0.22	0.26	0.42	0.25	0.21	0.52	0.46	0.38	0.39	0.47	0.55	0.52
	mean thickness (mm)	0.10	0.10	0.08	0.10	0.09	0.09	0.08	0.16	0.10	0.12	0.10	0.29	0.35	0.25	0.22	0.25	0.15	0.35
	ratio W:T	2.2	2.2	2.6	2.0	1.8	2.1	2.7	1.7	4.2	2.1	2.1	1.8	1.3	1.8	1.7	1.9	3.5	1.5
	epidermal cells mean length (µm)	19.0	23.0	12.5	17.5	17.5	13.8	19.0	13.8	-	17.6	-	35.0	11.5	13.1	15.0	13.8	12.5	-
	mean width (µm)	14.5	14.5	10.9	14.4	12.8	12.4	16.0	10.8	-	13.3	-	21.0	17.0	13.4	15.0	12.5	12.5	-
	mean breadth (µm)	22.0	18.0	15.0	19.0	14.0	12.0	18.0	18.0	-	16.0	-	63.0	20.0	17.0	13.0	62.0	25.0	-
	number of cells lacunae→epidermis	1	1	1	1	1 (oc 2)	1 (oc 2)	1 (oc 2)	1 (oc 2)	-	1	-	1	2 or 3	2	2	1	1	-
	mesophyll cells mean diameter (µm)	25	24	23	23	24	15	25	13	-	25	-	50	25	24	40	-	-	-
	lacunae shape	C	E	C→E	C	C	C	E	C	-	E	-	E	E	E	E	C	E	-
	maximum leaf length (cm)	15	5	5	5	5	5	10	15	15	15	10	25	25	15	20	25	25	-
STEMS																			
	maximum length, elevated stem (cm)	1-2	1	1-2	1-2	1	1	2	2-3	5	7	3	40	50	10	50-100	50-100	50-150	50-150
	zig-zag form	X	X	X	X	X	X	X	X	X	X	X	X	✓	-	✓	✓	✓	✓
ROOTS																			
	from rhizome	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	from stem nodes	X	X	X	X	X	X	X	X	X	X	X	X	✓	-	✓	✓	✓	✓
VEGETATIVE REPRODUCTION																			
	rhizomes	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	perennating organs I	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	X	X	X	X	X	X	X
	perennating organs II	✓	✓	✓	✓	-	-	✓	✓	-	-	-	X	X	X	X	X	X	X
HABIT	branching	r	r	r	r	r	r	r	r	oc	C	oc	c	c	c	c	c	c	c
	annual/perennial	an	an	an	an	an	an	an	an	-	an	an	an	pe	pe	pe	pe	pe	pe
	maximum plant height (cm)	15	5	5	15	10	5	10	15	30	30	15	50	200	20	100	150	150	>150
	leaf crowding at terminal shoot	X	X	X	X	X	X	X	X	X	X	X	X	✓	-	✓	✓	✓	✓
	creeping grass-like habit	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	oc	✓	✓	✓	✓	✓
	clumping	X	X	X	X	X	X	X	X	X	X	X	X	✓	✓	✓	✓	✓	✓	-
PLANT ASSOCIATIONS		cd, L Ch	oc Sms ms/pools	cd L	ms Ch Al	cd L Ch	cd L	cd L Ch	ms	ms	cd L Ch	cd L	ms Pot or Cl	ms Ch Cl	ms	ms	cd L	ms Al	-
HABITAT																			
	salinity range °/oo TDS	19 - 24	20 - 25	23-230	37 - 94	13 - 33	13-150	20 - 66	64 - 105	-	9 - 35	20-66	2.1 - 3.3	19-46	19-22	5.6 - 20	12-30	35-37	-
	permanence	temp	temp	temp	perm	temp	temp	perm	perm	perm	temp	perm	perm	perm	perm	perm	perm	perm	perm
	depth range (m)	0 - 0.3	0.02-0.15	0-0.15	0.15-0.30	0.15-0.25	0.15-0.25	0-0.25	0.2-0.3	→0.4	0 - 0.6	0 - 0.25	3.5	1 - 2.5	0.05 - 0.20	1.0 - 2.5	2.0	1.5 - 4.0	>1.5
	type	sal	salt marsh	hysal	hysal	br-sal	hysal	hysal	hysal	hysal	br-sal	hysal	fresh	sal	sal	sal	hysal	hysal	hysal
CHROMOSOME NUMBER		16 - 20	16 - 20	-	-	-	-	-	16-20	-	16-20	-	-	16-20	-	-	16-20	-	-

APPENDIX VII Quantitative measurements (mean, standard error, number and range) of 12 characters of *Ruppia*

a. *Ruppia* Taxon A (9 localities)
b. *Ruppia* Taxon B (6 localities)
c. *Ruppia* Taxon C (3 localities)

a. *Ruppia* Taxon A

Character \ Locality	8. Little Dip Lake				9 Lake Eliza Salt Marsh				1 Pipeclay Lake				2 Flax Point				3 Mikes Lake				5 Brineshrimp Lake				6 Lake Robe				12 Beachport Salt Lake				Coobowie			
	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range
LEAF																																				
width (mm)	0.22	0.01	30	0.10-0.35	0.22	0.01	30	0.10-0.35	0.21	0.05	20	0.10-0.30	0.20	0.01	20	0.10-0.30	0.16	0.05	34	0.10-0.50	0.19	0.01	21	0.10-0.30	0.22	0.01	30	0.10-0.35	0.26	0.01	15	0.20-0.35	0.42	0.01	20	0.30-0.50
thickness (mm)	0.10	0.06	10	0.05-0.20	0.10	0.01	10	0.06-0.16	0.08	0.03	10	0.04-0.14	0.10	0.01	10	0.05-0.15	0.09	0.01	10	0.05-0.15	0.09	0.01	10	0.07-0.14	0.07	0.01	10	0.05-0.10	0.16	0.02	10	0.10-0.20	0.10	0.01	10	0.05-0.15
EPIDERMAL CELLS																																				
length (µm)	19	0.29	20		23	0.31	20		12.5	0.20	20		17.5	0.22	20		17.5	0.25	20		13.6	0.22	20		19	0.09	20		13.8	0.22	20		not available			
breadth (µm)	14	0.20	20		14	0.22	20		10.9	0.11	20		14.4	0.16	20		12.8	0.16	20		12.4	0.13	20		16	0.16	20		10.6	0.20	20		not available			
thickness (µm)	22	0.49	20		18	0.47	20		15.0	0.36	20		19.0	0.27	20		14.0	0.25	20		12.0	0.25	20		18	0.27	20		18.0	0.36	20		not available			
MESOPHYLL CELLS																																				
diameter (µm)	25	0.31	20		24	0.35	20		23.0	0.35	20		23.0	0.30	20		24.0	0.31	20		15.0	0.27	20		25	0.34	20		13.0	0.49	20		not available			
INFLORESCENCE																																				
length (mm)	5.2	0.35	15	4 - 6	4.3	0.36	10	3.6- 5.6	no flowers recorded				6.0	0.38	13	3.6 -8.3	4.3	0.35	10	3.5 -4.8	no flowers recorded				4.3	0.39	15	2.8 -5.0	4.4	0.35	10	2.7 -5.2	5.4	0.40	10	4.0 -6.0
breadth (mm)	2.3	0.25	15	2 - 2.5	2.3	0.30	10	1.6- 2.6					3.1	0.42	13	2.9 -4.3	2.1	0.30	10	1.4 -2.6					3.3	0.28	15	1.9 -4.0	3.0	0.25	10	2.0 -4.1	2.1	0.31	10	1.5 -3.0
carpel no. (av.)	11.98	0.46	42	6 - 19	11.8	0.39	20	9.0 - 13					9.96	0.54	26	4.0-16.0	9.6	0.60	20	7.0 -15.0					10.4	0.61	19	6.0 -15.0	12.6	0.61	20	8.0 -16.0	10.53	0.39	30	6.0 -14.0
FRUIT																																				
length (mm)	1.55	0.04	21	1.3 - 2.3	1.25	0.04	11	1.0 - 1.5	no fruit recorded				2.02	0.03	20	1.5 -2.5	no fruit available				2.1		1		1.71	0.04	25	1.2 -2.0	1.95	0.06	20	1.4 -2.3	1.79	0.06	20	1.5 -2.4
width (mm)	0.93	0.02	20	0.7 - 1.5	0.85	0.09	11	0.7 - 1.0					1.03	0.02	20	0.9 -1.2					1.4		1		0.93	0.02	20	0.7 -1.2	1.09	0.03	20	0.7 -1.0	0.95	0.02	20	0.8 -1.1
breadth (mm)	0.70	0.20	20	0.6 - 0.9	0.60	0.08	11	0.5 - 0.8					0.81	0.01	20	0.7 -0.9					0.8		1		0.74	0.02	20	0.7 -0.9	0.84	0.03	20	0.5 -0.8	0.67	0.02	20	0.5 -0.8

APPENDIX VII

b. *Ruppia* Taxon B

Character \ Locality	8 Little Dip Lake				9 Lake Eliza Salt Marsh				10 Erringtons Hole				Porters Lagoon				West Lakes				Coorong N. Lagoon			
	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range
LEAF																								
width (mm)	0.46	0.02	24	0.30-0.60	0.38	0.02	24	0.25-0.45	0.39	0.02	15	0.30-0.51	0.47	0.02	30	0.40-0.52	0.55	0.02	21	0.40-0.60	0.52	0.01	20	0.45-0.65
thickness (mm)	0.35	0.11	10	0.30-0.40	0.25	0.07	10	0.20-0.30	0.22	0.02	10	0.20-0.24	0.25	0.04	10	0.20-0.40	0.15	0.02	10	0.10-0.22	0.35	0.04	10	0.30-0.40
EPIDERMAL CELLS																								
length (µm)	11	0.22	20		13	0.34	20		5	0.27	20		13	0.27	20		12	0.09	20		not available			
breadth (µm)	17	0.25	20		13	0.31	20		5	0.29	20		12	0.20	20		12	0.11	20		not available			
thickness (µm)	20	0.40	20		17	0.45	20		3	0.38	20		62	0.65	20		25	0.36	20		not available			
MESOPHYLL CELLS																								
diameter (µm)	25	0.34	20		24	0.35	20		0	0.49	20		55	0.63	20		28	0.31	20		not available			
INFLORESCENCE																								
length (mm)	5.3	0.41	15	5.0 -5.5	3.5	0.31	10	2.6 -4.3	4.5	0.36	4	3.7 -5.0	4.0	0.30	10	3.1 -5.0	4.5	0.34	8	4.0 -5.0	4.4	0.40	10	4.0 -5.0
breadth (mm)	1.5	0.21	15	1.2 -1.7	1.2	0.20	10	1.0 -1.4	1.8	0.20	4	1.4 -2.1	2.1	0.11	10	1.3 -4.0	2.0	0.21	8	1.8 -2.2	1.5	0.25	10	1.0 -1.6
carpel no. (av.)	3.7	0.38	22	2.0 -4.0	2.8	0.17	18	2.0 -4.0	5.0	1.20	4	3.0 -7.0	4.1	0.11	18	4.0 -6.0	4.9	0.75	23	4.0 -6.0	4.6	0.13	36	4.0 -6.0
FRUIT																								
length (mm)	3.1	0.04	20	2.8 -4.6	2.6	0.04	21	2.3 -3.0	fruit not available				3.1	0.06	30	2.5 -3.6	3.0	0.10	5	2.1 -3.2	fruit not available			
width (mm)	2.5	0.04	20	1.9 -3.1	2.0	0.03	21	1.7 -2.6					2.5	0.04	30	2.0 -3.2	2.0	0.10	5	1.5 -2.4				
breadth (mm)	1.8	0.03	20	1.5 -2.0	1.2	0.05	21	1.4 -2.0					1.5	0.06	30	1.5 -2.5	1.4	0.10	5	1.0 -2.0				

APPENDIX VII

c. *Ruppia* Taxon C

Character \ Locality	4 Blue-Green Algal Pool				6 Lake Robe				7 Fresh Dip Lake			
	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range
LEAF												
width (mm)	0.25	0.01	30	0.10-0.35	0.21	0.01	20	0.20-0.25	0.52	0.02	35	0.20-0.80
thickness (mm)	0.12	0.01	10	0.05-0.18	0.10	0.01	10	0.05-0.12	0.29	0.03	10	0.20-0.50
EPIDERMAL CELLS												
length (µm)	17	0.27	20		data not available				35	0.36	20	
breadth (µm)	13	0.11	20		data not available				21	0.34	20	
thickness (µm)	16	0.47	20		data not available				63	0.78	20	
MESOPHYLL CELLS												
deameter (µm)	25	0.36	20		data not available				50	0.63	20	
INFLORESCENCE												
length (mm)	3.4	0.36	14	2.4 -3.7	3.3	0.32	10	2.8 -3.7	3.7	0.31	10	3.0 -4.3
breadth (mm)	1.5	0.21	14	1.1 -1.7	1.4	0.32	10	1.2 -1.6	1.5	0.21	10	1.0 -1.7
carpel no. (av.)	6.89	0.52	47	4.0 -10.	7.3	0.45	30	4.0 -9.0	8.41	0.83	34	4.0 -11.0
FRUIT												
length (mm)	1.83	0.03	25	1.5 -2.4	1.89	0.05	20	1.6 -2.3	2.26	0.06	20	2.0 -2.8
width (mm)	1.01	0.02	25	0.8 -1.4	1.39	0.08	20	1.0 -1.9	1.76	0.02	20	1.5 -1.8
breadth (mm)	0.47	0.02	25	0.3 -0.7	0.72	0.04	20	0.4 -1.2	1.29	0.04	20	1.0 -1.6

APPENDIX VIII Leaf cell characters: microscopic measurements of leaf cell length and width (LS), cell diameters and lacunae characters (TS) for *Ruppia* A, B and C from various field sites. Measurements in micrometres (μm) n = 20 for each mean

Taxon	Locality	Longitudinal Sections				Transverse Sections									
		Cell diameters (LS)				Cell diameters (TS)				Epidermis to Lacuna	Lacunae (TS)				
		Length		Width		Epidermis		Mesophyll			Length		Width		Ratio
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	No. cells	$\bar{x}$	SE	$\bar{x}$	SE	L:W
A	LDL	19.0	0.3	14.5	0.2	30	0.5	25	0.3	1	81	0.3	80	0.3	1.0
	LESM	23.0	0.3	14.5	0.2	17	0.5	24	0.3	1	100	0.4	62	0.2	1.6
	PL	12.5	0.2	10.9	0.1	15	0.4	23	0.4	1	50	0.3	37	0.2	1.3
	FP	17.5	0.2	14.4	0.2	19	0.3	23	0.3	1	100	0.5	63	0.4	1.6
	ML	17.5	0.2	12.8	0.2	14	0.3	24	0.3	1 or 2	56	0.3	44	0.5	1.3
	BL	13.8	0.2	12.4	0.1	12	0.3	15	0.3	1 or 2	54	0.7	32	0.5	1.7
	LR	19.0	0.1	16.0	0.2	18	0.3	25	0.3	1	128	0.9	52	0.5	2.5
	B/p SL	13.8	0.2	10.7	0.2	18	0.4	13	1.0	1 or 2	1	0.5	52	0.4	1.1
B	LDL	11.5	0.2	17.0	0.3	18	0.4	25	0.4	2 or 3	125	0.7	100	6.5	1.3
	LESM	13.1	0.3	13.4	0.3	18	0.5	24	0.4	2	116	0.6	83	0.5	1.4
	EH	15.0	0.3	15.0	0.3	13	0.4	40	0.5	2	137	0.8	81	1.3	1.7
	PoL	13.8	0.3	12.5	0.2	62	0.7	55	0.6	1	87	0.3	70	1.3	1.2
	WL	12.5	0.1	12.5	0.1	25	0.4	28	0.3	1	150	0.8	62	0.5	1.2
C	BGAP	17.6	0.3	13.3	0.1	16	0.5	25	0.4	1	88	0.5	50	0.3	1.8
	FDL	35.0	0.4	21.0	0.3	63	0.8	50	0.6	1	335	2.3	263	3.6	1.3

APPENDIX IX Pollen grain length, width and shape for pollen of *Ruppia* from taxa A, B and C

a. length and width and shape for study sites

Taxon	Locality	Shape (see Figure 8.5)	Length (µm)			Width (µm)		
			$\bar{x}$	SE	n	$\bar{x}$	SE	n
A	LDL	1	143	3.2	10	23	0.5	10
	LESM	1	143	3.4	10	22	0.4	10
	FP	1	119	3.0	10	23	0.5	10
	ML	1	152	4.2	10	22	0.4	10
	LR	1, 3	94	3.8	10	18	0.6	10
B	LDL	2	97	2.0	10	21	0.4	10
	LESM	2	80	1.8	10	18	0.4	10
	EH	4	48	1.7	10	21	0.4	10
	PL	4	68	1.2	10	23	0.7	10
	WL	4	86	1.3	10	19	0.7	10
C	BGAP	3	67	1.4	10	21	0.4	10
	LR	3	62	1.7	10	20	0.5	10
	FDL	4, 3	71	1.5	10	16	0.9	10

APPENDIX IX b. variation of pollen with plant age and habitat

Taxon	Locality	Specimen No.	Shape	M	P	A	Length (µm) $\bar{x}$ n=10	SE	Width (µm) $\bar{x}$ n=10	SE	Comparison	t	DF	Sig.
A	LR	6-978	2, 4	i	1		27	1.0	15	0.6	iP_1 vs iP_2	7.5	12	S
			2	i	2		26	0.6	18	0.7	mP_1 vs mP_2	1.0	12	NS
			3	m	1		56	1.1	19	0.6	m within flower variation	1.9	12	NS
			1, 3	m	2	a	94	4.1	18	0.6	m vs i	21.49	19	S
			1, 3	m		b	90	1.0	19	0.6				
C	LR	6-1078	3	i	1		59	1.8	19	0.3	iP_1 vs iP_2	1.1	15	NS
			3	i	2		64	1.9	19	0.4	mP_1 vs mP_2	2.0	12	NS
			3	m	1		60	1.7	20	0.5	m within flower var.	1.9	12	NS
			3	m	2	a	62	1.0	19	0.4	m vs i	0.29	29	NS
			3	m		b	61	0.6	19	0.4				
C	FDL	7-978	4	m	1		12	0.5	8	0.4	m vs i	30.4	12	S
			3	m	2	a	71	1.5	17	0.9	m within flower variation	2.0	12	NS
			3	m		b	69	1.0	16	0.8				

M = Maturity m = mature
i = immature

P = Plant number

A = Anther number

Sig. = Significance S - significant at 0.05 level
NS - not significant at 0.05 level

APPENDIX X Method for preparing chromosome squash preparations of *Ruppia*

1. Pretreat material at 4°C overnight.

2. Fix material 3-24 hours in glacial acetic acid:alcohol 1:3.

3. Wash in distilled water for 6-8 minutes with at least 2 changes.

4. Hydrolyse in 1N HCl for 6-10 minutes at 60°C (6 minutes optimal).

5. Wash in distilled water 1-2 minutes.

*6. Stain 10-20 minutes in freshly mixed haematoxylin stain with reagents added in the following proportions and order

5% alcoholic haematoxylin	2.5
10% ferric chloride	1
Verhoeffs iodine (iodine 2g, potassium iodide 4g, water 100 ml)	1

7. Wash well in distilled water 1-2 minutes (2 changes).

8. Differentiate in 45% acetic acid at 60°C for 2 minutes.

9. Wash in distilled water.

10. Store in 10% absolute alcohol if necessary.

11. Squash in 45% acetic acid or absolute alcohol.

12. Mount permanent slides in Euparal or Xam.

* alternatively stain 2-3 hours in leuco-basic fuchsin and follow Feulgen Squash Method of Darlington and La Cour (1947).

APPENDIX XI Summary of characters examined for *Ruppia* taxa A, B and C (For key to abbreviations see Appendix VI)

Character	A (average of 9 habitats)	B (average of 6 habitats)	C (average of 3 habitats)
INFLORESCENCE			
mean length (mm)	4.5	4.4	3.5
mean width (mm)	2.5	1.7	1.5
mean number of carpels	11.1	4.1	6.3
thecae and thecal slit shape	K Ri or S	K S	K S
location	bs or tes	tes	bs oc tes
pollination	su	su	su
pollen shape	ed oc eb	sd	eb or e
peduncle length (cm)	>10	>10	>10
peduncle form	sp	sp	sp
sheath subtending flower	sw	sw	sw
peduncle swelling below inflorescence	X	oc	X
flowering abundance	c,→pr	oc→uc→c	c→pr
flowering time	A→N	S→M us N→M	S→N
FRUIT			
mean length (mm)	1.8	3.0	2.0
mean width (mm)	1.1	2.3	1.4
mean thickness (mm)	0.7	1.5	0.8
ratio L:W:T	2.6:1.6:1	2.5:1.5:1	2.5:1.7:1
shape	py	asy tu	asy py
stylar beak (mm)	sh<0.3	0.9-2.0	sh<0.2
podogyne shape	ss th	st ta	th sr
podogyne length (mm)	1-3	10-40	10-30
no. of carpels developed	M	1-4	1-M
endocarp colour	bl	bl	bl
thickness (mm)	0.1-1.1	0.2-0.3	-
sculpturing	sm	sm→ro	ba
window	nel→el	de	nel→el
LEAF			
apex shape	R→A oc T	T→B oc R	A oc O or T
mean width (mm)	0.23	0.48	0.35
mean thickness (mm)	0.10	0.26	0.17
ratio W/T	2.3	1.8	2.1
epidermal cells mean length(µm)	17	13	15
mean width (µm)	13	14	17
mean breadth (µm)	17	28	40
number of cells lacunae→epidermis	1 oc 2	1, 2 or 3	1
mesophyll cells mean diameter (µm)	22	34	38
lacunae shape	C or E	E or C	E
maximum leaf length (cm)	5-15	15-25	10-25
STEMS			
maximum length, elevated stem (cm)	1-3	10-150	3-7
zig-zag form	X	✓	X
ROOTS			
from rhizome	✓	✓	✓
from stem nodes	x	✓	X
VEGETATIVE REPRODUCTION			
rhizomes	✓	✓	✓
perennating organs I	✓	X	✓
perennating organs II	✓	X	-
HABIT branching	r	c	oc→c
annual/perennial	an	pe	an
maximum plant height (cm)	5-30	20-200	15-50
leaf crowding at terminal shoot	X	✓	X
creeping grass-like habit	✓	✓	✓
clumping	X	✓	X
PLANT ASSOCIATIONS	cd, ms	ms	cd, ms
HABITAT			
salinity range °/oo TDS	13-230	5-46	2-66
permanence	temp	perm	perm or temp
depth range (m)	0→0.4	0.4→3.0	0→0.25(0.60)
LOCATION NUMBERS (see Table 3.1)	1,2,3,5,6A,8A,9A,12,13	8B,9B,10,PL, CNL,WL	4, $6A_{II}$, 7
CHROMOSOME NUMBER	20	20	20

APPENDIX XII Summary of 12 measured characters of *Ruppia* for taxa A, B and C

Character	A				B				C			
	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range	$\bar{x}$	SE	n	Range
LEAF												
width (mm)	0.23	0.01	230	0.10-0.50	0.48	0.01	129	0.25-0.60	0.35	0.02	85	0.10-0.80
thickness (mm)	0.10	0.01	90	0.05-0.20	0.26	0.06	60	0.10-0.40	0.17	0.05	30	0.05-0.50
EPIDERMAL CELLS												
length (µm)	17	0.30	10	12 - 23	13	0.25	100	11 - 15	25	1.80	40	17 - 35
breadth (µm)	13	0.40	10	10 - 16	14	0.30	100	12 - 17	17	1.50	40	13 - 21
thickness (µm)	17	0.60	10	12 - 22	28	2.50	100	13 - 62	40	3.00	40	16 - 63
MESOPHYLL CELLS												
diameter (µm)	22	0.50	160	13 - 25	34	0.60	100	24 - 55	38	2.50	40	25 - 50
INFLORESCENCE												
length (mm)	4.5	0.40	83	3.3 -6.0	4.4	0.40	57	2.6 -5.5	3.5	0.04	34	2.4 -4.3
breadth (mm)	2.5	0.40	83	1.9 -4.3	1.7	0.25	57	1.0 -4.0	1.5	0.06	34	1.0 -1.7
carpel no. (av.)	11.1	0.21	177	4.0 -19.0	4.1	0.09	118	2.0 -7.0	6.3	0.15	101	4.0 -11.0
FRUIT												
length (mm)	1.8	0.03	117	1.2 -2.5	3.0	0.04	78	2.1 -4.6	2.0	0.04	65	1.5 -2.8
width (mm)	1.1	0.03	117	0.7 -1.9	2.3	0.04	78	1.5 -3.1	1.4	0.08	65	0.8 -1.9
breadth (mm)	0.7	0.04	117	0.4 -1.2	1.5	0.06	78	1.0 -2.5	0.8	0.04	65	0.3 -1.8

APPENDIX XIII Tabulation of characters of described species of *Ruppia*. (For key to abbreviations see Appendix VI).

Character / Species	*R. megacarpa*	*R. polycarpa*	*R. tuberosa*	*R. cirrhosa*	*R. maritima*	*R. occidentalis*	*R. truncatifolia*
INFLORESCENCE							
mean length (mm)	-	-	-	-	-	-	-
mean width (mm)	-	-	-	-	-	-	-
mean no. carpels	4 (oc 5,6)	8 (2-16)	4-12	4	4	2-8	-
theca shape	oblong	oblong	-	K	Ro	oblong	-
location	tes	bs	bs	-	-	-	-
pollination	su	su	su	su	uw	su	su
pollen shape	-	-	-	-	-	-	-
peduncle length (cm)	>7	>7	>7	>7	<5	>7	>7
peduncle form	sp	sp	sp	sp	st	sp	sp
sheath subtending flower	sw (v)	sw (v)	sw	sw	nsw	-	-
peduncle swelling below inflorescence	nsw	sw	-	-	-	-	-
flowering abundance	-	-	-	-	-	-	-
flowering time	-	-	-	-	-	-	-
FRUIT							
mean length (mm)	4-5	2 (1.7-2.5)	2.0-2.5	2.6	2.2	3-4	-
mean width (mm)	-	-	-	1.7	1.5	-	-
mean thickness (mm)	-	-	-	-	-	-	-
ratio L:W:T	-	-	-	-	-	-	-
shape	asym	py	py	sym	sw asym	sym py	-
stylar beak (mm)	→1.5	0.25	sh	-	-	-	-
podogyne shape	st ta	th sr	ss	v	v	-	-
podogyne length (mm)	-	-	-	-	-	-	-
no. carpels developed	-	-	→12	-	-	-	-
endocarp colour	bl	bl	bl	bl	bl	bl	bl
thickness (mm)	1	0.2-0.3	-	-	-	-	-
sculpturing	ro	sm	-	-	-	-	-
window	de	el	-	nel	el	-	-
LEAF							
apex shape	B	O	R oc B	R→T	irr A	R→T	T
mean width (mm)	0.3-0.7	0.3-0.4	0.3	1.0	→0.5	≤0.3	0.3-0.7
mean thickness (mm)	-	-	-	-	-	-	-
ratio W/T	1.5	1.2	-	> 2	-	-	-
colour	br olive gr	dark gr	dark gr	dark gr	light gr	-	-
epidermal cells							
mean length (µm)	-	-	60	16 - 19	12.5-16	-	-
mean width (µm)	-	-	30	-	-	-	-
mean breadth (µm)	-	-	-	-	-	-	-
no. cells lacunae → epidermis	2	1	-	2	-	3	2 or 3
mesophyll cells mean diameter (µm)	-	-	-	-	-	-	-
lacunae shape	-	-	-	-	-	-	-
maximum leaf length(cm)	-	-	-	-	-	-	-
STEMS							
max.length, elevated stem (cm)	-	-	-	-	-	-	-
zig-zag form	✓	x	-	-	-	-	-
ROOTS							
from rhizome	✓	✓	✓	✓	-	-	-
from stem nodes	✓	x	-	-	-	-	-
VEGETATIVE REPRODUCTION							
rhizomes	✓	✓	✓	✓	✓	✓	✓
perennating organs I	x	x	x	x	x	x	x
perennating organs II	x	x	x	x	x	x	x
HABIT							
branching	c	r	-	-	-	-	-
annual/perennial	pe	pe	pe	pe	pe	pe	pe
max. plant height (cm)	> 50	< 50	-	-	-	-	-
leaf crowding at term.shoot	✓	x	-	-	-	-	-
creeping grass-like habit	x	✓	-	-	-	-	-
clumping	-	-	-	-	-	-	-
HABITAT							
salinity range °/oo TDS	coastal saline	br→fr	92 - 132	1.89-64	0.32-12	-	-
permanence	perm	perm	perm	perm	perm	perm	perm
depth range (m)	-	-	0.08-0.65	-	-	-	-
LOCATION	NZ	NZ	WA	Europe	Europe	N. America	Asia
CHROMOSOME NO.	2n=20	2n=18	-	2n=40	2n=20	-	-
Reference	Mason 1967	Mason 1967	Davis&Tomlinson 1974	Reese 1962, den Hartog 1971		Mason 1967	Mason 1967

APPENDIX XIV Measurements of proline concentration in *Ruppia*.

	Species	mg proline/ dry weight n = 3 $\bar{x}$	S.E.	µmoles proline/g fresh weight	Location Date 1978	Salinity °/oo TDS
1	*R. tuberosa*	4.14	0.57	5.4	PL -19.8	13.1
2	*R. tuberosa*	12.10	2.73	15.7	FP - 18.8	53.8
3	*R. tuberosa*	25.20	2.93	32.8	FP -11.11	90.9
4	*Lepilaena*	1.44	0.21	1.9	ML -25.9	7.2
5	*R. tuberosa*	2.23	0.44	2.9	ML -25.9	7.2
6	*R. polycarpa*	0.61	0.08	0.8	BGAP -19.8	5.6
7	*R. polycarpa*	0.83	0.03	1.1	BGAP -25.9	12.0
8	*R. tuberosa*	4.47	0.47	5.8	LR -20.8	36.0
9	*R. tuberosa*	12.69	2.17	16.5	LR -20.8	36.0
10	*R. tuberosa*	6.47	0.70	8.4	LR -24.9	35.1
11	*R. tuberosa*	2.26	0.16	2.9	LR -11.11	44.5
12	*R. polycarpa*	1.05	0.12	1.4	FDL -20.8	2.4
13	*R. polycarpa**	2.06	0.43	2.7	FDL -20.8	2.4
14	*R. polycarpa*	3.10	0.59	4.0	FDL -24.9	2.4
15	*R. polycarpa*	0.76	0.10	1.0	FDL -12.11	2.6
16	*R. megacarpa*	15.95	1.34	20.7	LDL -20.8	23.2
17	*R. megacarpa*	10.61	0.23	13.8	LDL -24.9	23.2
18	*Lepilaena*	6.80	0.55	8.8	LDL -24.9	23.5
19	*R. tuberosa*	18.53	0.86	24.1	LDL -20.8	23.2
20	*R. tuberosa*	7.41	1.85	9.6	LDL -24.9	23.5
21	*R. tuberosa*	4.65	0.54	6.0	LDL -11.11	25.0
22	*R. tuberosa*	2.61	0.29	3.4	LEP -20.8	13.5
23	*R. megacarpa*	5.65	0.73	7.3	LEP -20.8	13.5
24	*R. megacarpa*	2.32	0.28	3.0	EH -20.8	7.9
25	*R. megacarpa*	2.80	0.33	3.6	EH -24.9	7.6
26	*R. tuberosa*	29.21	4.06	38.0	B/p SL-20.8	61.3
27	*R. tuberosa*	47.72	6.42	62.0	B/p SL-24.9	65.4
28	*R. tuberosa*	11.81	0.87	15.4	B/p SL-12.11	72.7

1 mg proline/g dry weight ≡ 1.3 µmoles/g fresh weight

* rhizomes

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