

3. The ecology of halophytes in the south-east of South Australia

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Introduction

The nature and distribution of submerged and emergent macrophytes in relation to salinity and the temporary or permanent nature of the aquatic habitats, and to their 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 (Fig. 3.1). This investigation took place over three and a half years (1975 to 1978).

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. This paper summarizes some of the findings of the general survey and then concentrates on the study of *Ruppia*. Data to support the statements in this paper are to be found in the full report of the study (Brock 1979).

Plant occurrence in relation to environmental parameters was considered in a series of twelve lakes which ranged in salinity from fresh to hypersaline, in depth from a few centimetres to four metres, and in permanence from twelve months wet to five months wet/seven months dry per year. Seven of the lakes were permanent and five temporary (Fig. 3.2). Four of the permanent lakes had extensive eulittoral zones which formed temporary plant habitats within permanent lake ecosystems. Fig. 3.3 shows the location of the main study sites (1-12) and some additional locations sampled.

The synecological survey

The interrelationships of the submerged and

emergent angiosperms were considered in detail in three ecosystems: a fresh permanent lake, a saline permanent lake with a large eulittoral zone, and an extensive salt marsh community on the shores of Lake Eliza (Fig. 3.3, sites 7, 8, 9). This analysis of plant communities dealt chiefly with the angiosperms and only considered macroalgae secondarily. The presence of submerged species in relation to depth and salinity was monitored for all study sites and representative data are presented here for the three ecosystems indicated above (Fig. 3.4).

The only genera of submerged angiosperms that occurred above 4‰ total dissolved solids (TDS) were *Ruppia* (3-230‰ TDS) and *Lepilaena* (3-50‰ TDS). Both *Ruppia* and *Lepilaena* are monocotyledons and live only in submerged aquatic situations. Both taxa occur in a wide range of ecosystems including ephemeral lakes, and in both permanent water and eulittoral zones of permanent saline and fresh lakes. They also may occur in pure or mixed stands, in shallow and deeper waters, and as occasionals in the understorey of emergent salt marsh plant associations.

Some macroalgae also occur over wide salinity ranges; the charophyte *Lamprothamnium papulosum* (Wallr.) J. Gr., the filamentous alga *Enteromorpha* sp., and species of blue-green algae are found in some ecosystems. *Lamprothamnium papulosum* is the macroalga which occurs over the widest range of salinities. The occurrence of the marine alga *Acetabularia peniculus* (R.Br.) Solms-Laubach in the hypersaline Coorong is an interesting record as this species is usually confined to marine situations.

The angiosperms *Myriophyllum propinquum* A.

Cunn. and *Potamogeton pectinatus* L. and the alga *Chara vulgaris* L. represent the group of freshwater species and these occur near the limits of their salinity tolerance at 4‰ TDS.

Emergent salt tolerant plants are greater in diversity than the submerged halophytes. On the salt marsh which extends for 500 m from the shores of Lake Eliza, over twenty species of emergent plants occur. These species occur variously in twelve plant associations distinguished by species composition and species frequency. In general, the twelve plant associations were related to a gradient of height increase above the lake level: a rise of 0.5 m over a distance of 500 m was sufficient to alter

species composition to form different plant associations. Many of the species found on this salt marsh are common to other salt marsh areas in Australia and the genera are common to salt marsh, mangrove and arid ecosystems in Australia and elsewhere in the world. These emergent plant associations are considered further in Brock (1979).

The synecological survey has provided some information on the ranges and tolerances of salt lake hydrophytes. The occurrence of the same three submerged plants, *Ruppia*, *Lepilaena* and *Lamprothamnium* in salt marsh pools, in the understorey of complex emergent salt marsh vegetation, in ephemeral lakes, and in permanent saline and fresh lakes

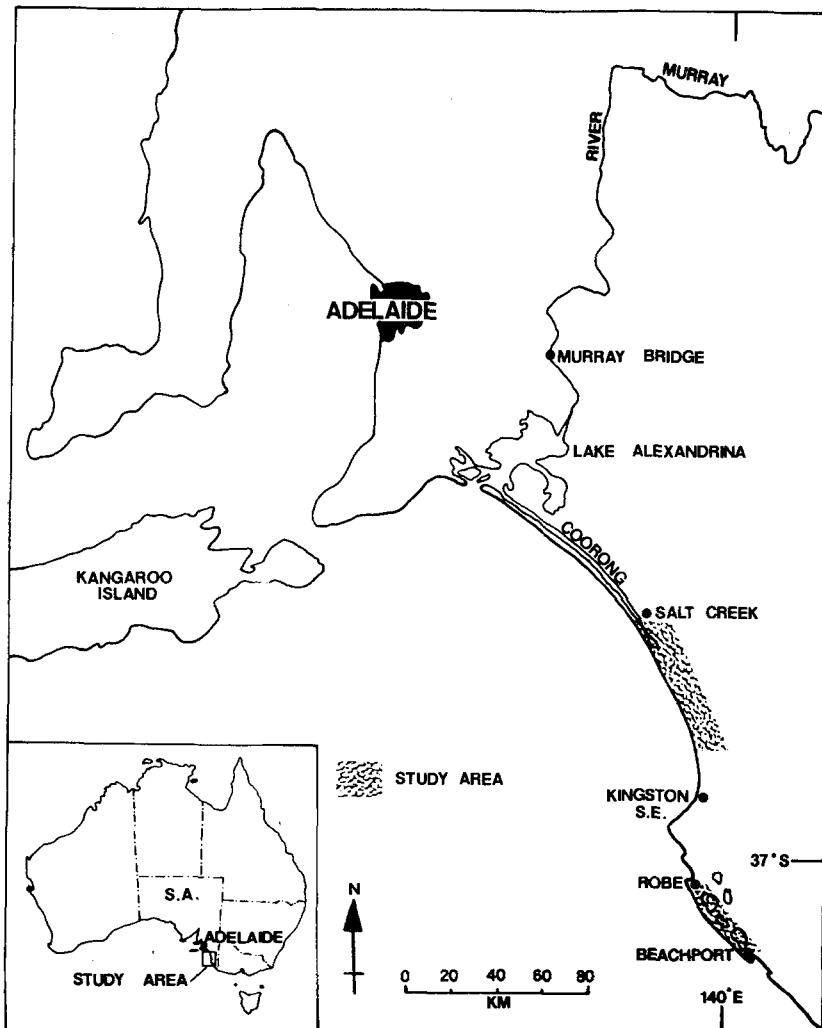


Fig. 3.1 The location of study areas in the south-east of South Australia.

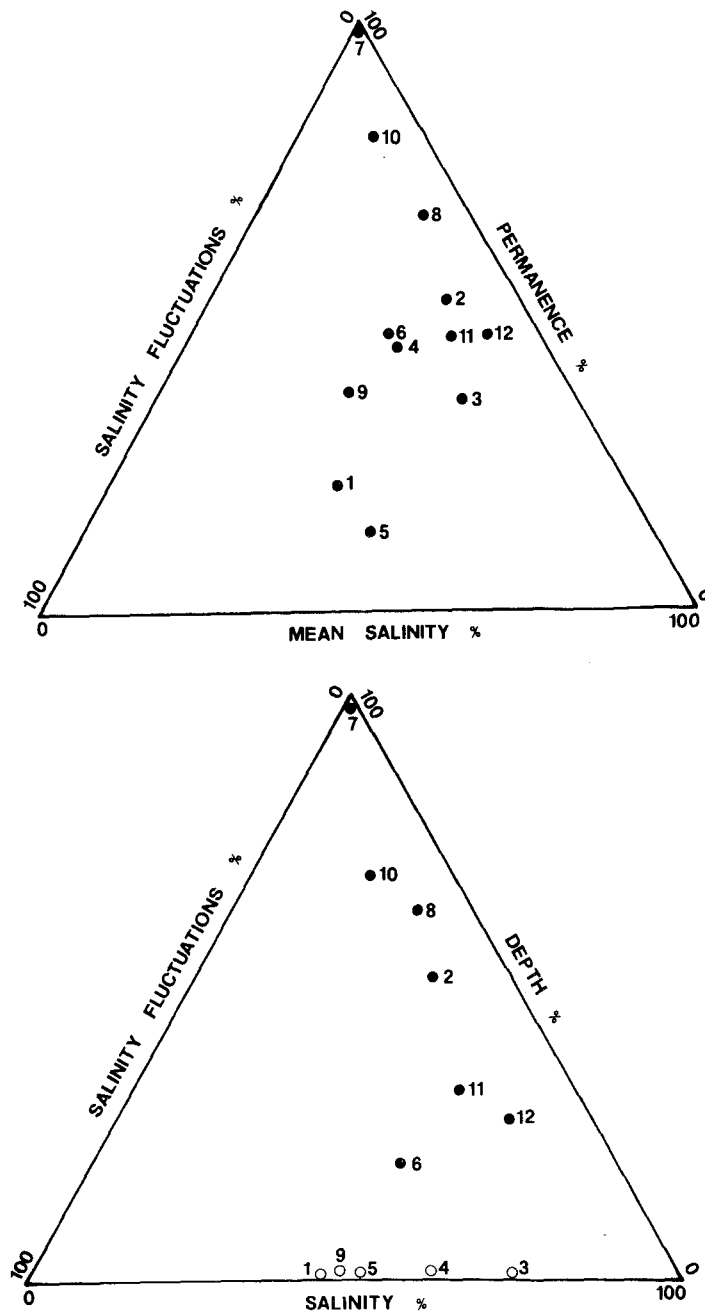


Fig. 3.2 Ternary diagrams plot the relative ranges of parameters in the study sites. Percentages for each parameter have been calculated as follows:

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

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

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

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

sites are indicated by site numbers

in the first diagram all sites are represented by ●

in the second diagram temporary sites ○ and permanent ●

provides further evidence that these are the three halophytic species with the widest tolerance of salinity, salinity fluctuation, and permanence of habitat. In these study areas fluctuations of environmental parameters (e.g. salinity, water level) have at least as great an effect on the macrophyte flora as the maximum level of salinity.

Autecology of *Ruppia*

The genus *Ruppia* was chosen to examine the ability of a small group of halophytes to survive

harsh and fluctuating conditions. This genus occurs over the whole range of habitats studied. Diversity of growth form, life cycle and reproductive strategy may enable these plants to tolerate such conditions.

During the field survey it was noted that two distinct growth forms of *Ruppia* (one annual, the other perennial) occurred in these habitats. The annual growth form is represented by a small delicate plant which grows, flowers and fruits prolifically in shallow water from a few centimetres to 0.4 metres deep during the short growing season from July to November. In general this form is associated with temporary habitats, but it can also

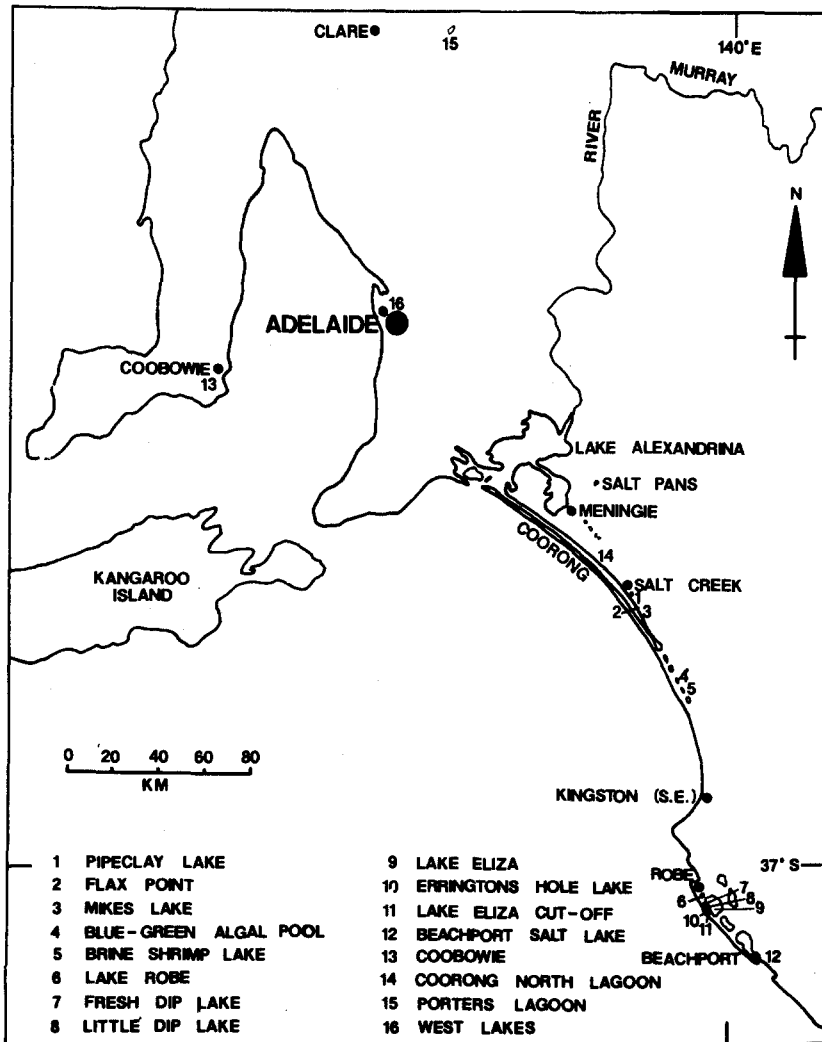


Fig. 3.3 The location of sites sampled in the south-east of South Australia.

be found in shallow permanent waters. The perennial growth form typical of this genus elsewhere in the world occurs in permanent and deeper habitats; it is more robust, has branches to 1.5 to 2 m long, and grows in clumps.

The annual and perennial forms occur sympatrically in several ecosystems. Both forms occur in a permanent saline lake, the annual in the eulittoral

zone and the perennial in a band between 0.5 and 1.5 m in depth; both also occur in a salt marsh community, the annual in temporary pools and in the ephemerally wet understorey of the salt marsh associations and the perennial in a small band on the edge of a permanent shallow spring fed pool.

The life cycles of these annual and perennial forms of *Ruppia* are not synchronized. The peren-

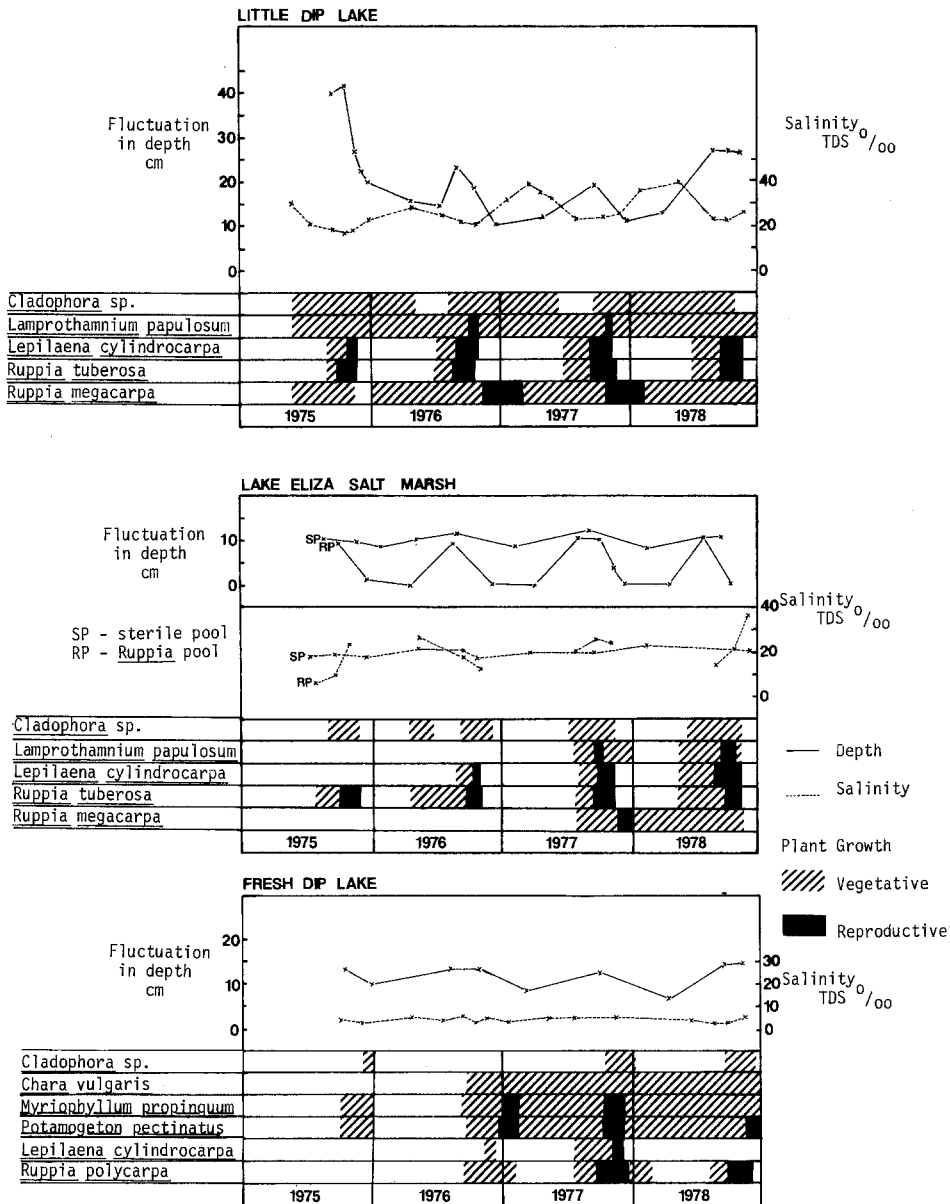


Fig. 3.4 Salinity, depth fluctuation and plant occurrence in three study sites.
Ruppia Form E - annual growth form
Ruppia Form P - perennial growth form

nial resumes growth after winter by lateral growth of the rhizomes and flowering occurs between December and March. Flowers are not prolific and the seeds although viable (laboratory trials), are not numerous and have not been observed to germinate in the field. The reproductive patterns of the annuals are more regular and extensive. The annual plants flower and fruit prolifically from September to November and fruit has set and fallen from the plants before the habitats dry in November or December. As well as large numbers of seeds these annual plants produce a prolific number of asexual perennating organs (turions). Thus many reproductive units, both seeds and turions, can survive the harsh and desiccating conditions in a salt crust over summer.

These annual and perennial growth forms were examined further to discover whether genetic or environmental differences were determinants of this variation. A systematic and an ecological assessment of the variation was thus attempted and this indicated that major taxonomic differences, which could also be related to habitat, existed within the genus in the south-east of South Australia.

The systematic examination of this genus in

South Australia indicated that the differences between the annual and perennial categories were of species rank and that the variation within the annual category allowed a further division into species (Table 3.1). Thus three species, one perennial and two annual occur in the ecosystems studied. All three occur sympatrically in lake Robe and the perennial and one annual species are found on Lake Eliza Salt Marsh and in Little Dip Lake.

Although the three species of *Ruppia* are not new, none of them has been reported in South Australia in the past. Previously all South Australian material – in fact all Australian material – has been referred to as *Ruppia maritima* L. or *Ruppia spiralis* L. ex Dum. (= *R. cirrhosa* (Petagna) Grande, the correct name). These names are incorrectly applied to the three taxa from this study and to most of the Australian material. The robust perennial species fits within the ranges described for *Ruppia megacarpa* Mason and the delicate annual species fit within the descriptions of *R. polycarpa* Mason and *R. tuberosa* Davis & Tomlinson (Table 3.2). These species are differentiated by a variety of characters including carpel number, fruit size, sessile or stalked fruit, shape of the fruit stalk attachment, and leaf width. *R. polycarpa* and *R. megacarpa* are species described first from New Zealand (Mason 1967) whereas *R. tuberosa* was described first from Western Australia (Davis & Tomlinson 1974).

The occurrence in South Australia of the two species described from New Zealand and the species described from Western Australia has wide biogeographical implications. The presence of *R. megacarpa* and *R. polycarpa* outside New Zealand leads to the consideration of them as temperate species with a much wider distribution, at least in the southern hemisphere. Recent records of these species from New South Wales, Victoria and Western Australia confirm their distribution over the temperate areas of Australia. Similarly, the widespread occurrence of *R. tuberosa* in South Australia together with recent isolated records of the species in Western Australia and Victoria extends the recorded distribution of this species across southern Australia.

In South Australia the annuals *R. polycarpa* and *R. tuberosa* are similar in life cycle, growth form and habitat, and thereby show closer affinities to each other than either does to *R. megacarpa*.

Table 3.1 The characteristics of three taxa of *Ruppia* in the south-east of South Australia.

	TAXON A	TAXON B	TAXON C
Habitat	temporary or permanent	permanent	temporary or permanent
Carpel No. \bar{x} range	11 2–19	4 2–7	6 4–11
Fruit stalk (podogyne)	absent or 1 mm	stout, tapered 10–25 mm	thin, straight 10–20 mm
Leaf tip	round	blunt	obtuse-rounded
Leaf width \bar{x} (mm) range	0.23 0.1–0.5	0.48 0.25–0.6	0.35 0.1–0.8
Fruit length \bar{x} (mm) range	1.8 1.2–2.5	3.0 2.1–4.6	2.0 1.5–2.8
Reproduction	seed turions rhizomes	seed – rhizomes	seed turions rhizomes
Habit	not branched	branched	rarely branched
Life cycle pattern	annual	perennial	annual

Table 3.2 Comparison of Taxa A, B and C with described species of *Ruppia*.

	TAXON A	<i>R. tuberosa</i>	TAXON B	<i>R. megacarpa</i>	TAXON C	<i>R. polycarpa</i>
Habitat	temporary or permanent	temporary or permanent	permanent	permanent	temporary or permanent	permanent
Carpel No. \bar{x}	11		4	4	6	
range	2-19	5-12	4-6	4-11	4-11	2-16
Fruit stalk (podogyne)	absent	absent	stout, tapered	stout, tapered	thin, straight	thin, straight
Leaf tip	round	round	blunt	blunt	obtuse	obtuse
Leaf width \bar{x} (mm)	0.23		0.48		0.35	
range	0.1-0.5	0.3	0.25-0.6	0.3-0.7	0.1-0.8	0.3-0.4
Fruit length \bar{x} (mm)	1.8	-	3.0	-	2.0	-
range	1.2-2.5	-	2.1-4.6	4.0-5.0	1.5-2.8	1.7-2.7
Reproduction	seed turions rhizomes	seed turions rhizomes	seed - rhizomes	seed - rhizomes	seed turions rhizomes	seed - rhizomes
Habit	not branched	not branched	branched	branched	rarely branched	rarely branched

R. megacarpa is similar to the majority of the northern hemisphere species in its perennial life cycle, larger growth form, and permanent habitat.

It is possible that the three species common in South Australia form a group of temperate climate species that have evolved in response to the unpredictable and fluctuating environments of the saline aquatic ecosystems in the southern areas of Australia and New Zealand. An extensive examination of the distribution and biology of the Australian *Ruppia* must be completed before a revision of the genus in Australia can enable further biogeographical speculation.

Turions produced by *Ruppia* in Australia provide the only records of asexual perennating organs within this genus. Turions have previously been reported by Lucas & Womersley (1971) in South Australia, Aston (1973) in Victoria, and Davis & Tomlinson (1974) in Western Australia. Prior to the present study no distinction between types of turions had been reported. In South Australian ecosystems large numbers of turions of two structural types form on *R. tuberosa*, and smaller number of only one type form on *R. polycarpa*. Serial sections of these organs elucidated their structure. In both species a swelling around a meristematic area at the junction of the leaf sheath and rhizome is enclosed by scale-like leaves and

detaches to form a turion (type I). These structures may form at each node along a length of rhizome. A second structural type of turion occurs only in *R. tuberosa*. This is a swelling at the extremity of a rhizome (presumably around the apical meristem) which may form a starch filled turion (type II) 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 its habitats are permanent. This suggests that turions only form in ephemeral habitats.

The ecological variation expressed by this genus 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 fit in with the wet and dry phases of their ephemeral habitats; many seeds and turions lie dormant in the dry lake sediments during summer. The perennial life cycle pattern of *R. megacarpa* may give these plants an advantage in deeper permanent more stable habitats, in which annual recolonization by seeds would be a disadvantage in competition with established perennial plants. Evidence from transplantation experiments does not indicate that these annual or perennial strate-

gies are reversible in the alternate habitats, at least in the subsequent generations.

Basic differences between the annual and perennial populations of *Ruppia* were also evident from seed germination trials: dormancy breakage is stimulated by fresh water in the perennial *R. megacarpa*, whereas saline water and seed coat breakage by wetting and drying have a positive effect on the 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 allows dormancy breakage to occur and seeds germinate as soon as habitats refill: thus the whole of the short wet phase forms the growing season and the chances of completion of the life cycles are maximized. The positive response of *R. tuberosa* seeds to salinity can also be considered as opportunistic as this 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 be advantageous for this species; in general seeds lie dormant in the lake sediments and a major decrease in salinity is necessary before germination occurs. This perennial species is prolific in more stable permanent habitats conducive to vegetative growth, and thus the potential to propagate by seed is conserved until a habitat disturbance such as decrease in salinity stimulates germination.

Seeds, turions and rhizomes all function as mechanisms of regeneration in *Ruppia* and such a variety of propagative mechanisms has often been said to account for the ecological differences between species (Grime 1979). The type of reproductive pattern that has evolved for 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.

Life cycle patterns in terrestrial species have been examined by comparing the allocations of plant material (dry weights) for various functions (e.g. Hickman & Pitelka 1975). Such techniques have been used for terrestrial annual species (Harper &

Ogden 1970; Hickman, 1975, 1977), and for perennial species (Gadgil & Solbrig 1972; Abrahamson & Gadgil 1973; Ogden 1974). The life cycle patterns of annuals and perennials have been compared to substantiate the idea that a higher proportion of energy is allocated to reproduction in annual species than in perennial species (Pitelka 1977; Turkington & Cavers 1978).

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

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 efforts between asexual and sexual reproductive structures was compared for annual and perennial life patterns and for individual species; and third, the numbers of each type of propagule were compared for each species. Speculations on the roles of various methods of regeneration in the life cycles of each species under harsh or relatively conducive conditions have been made from these data (Brock 1979).

It was found that the proportion of the plants' energy allocated to reproduction was much greater in all seasons for the two annuals *R. polycarpa* and *R. tuberosa* than for the perennial *R. megacarpa*. During the 7–8 month dry season, 100% of the live parts of the annuals are reproductive. These include both turions and seeds. Rhizomes could not survive desiccation unless modified as turions. The minimum percentages of the total dry weight found in reproductive structures of these annual species (14% for *R. tuberosa*, 5% for *R. polycarpa*) occurred in the growing season, when vegetative growth was at its peak. In contrast, the maximum allocation of the perennial to sexual reproduction was less than 5% of the total dry weight in any season. Turions did not form on the perennial and the asexual reproduction by rhizomatous spread could not be assessed in this way as only a small proportion of the rhizomes (10–30% total dry weight) were reproductive.

The two annual species were remarkably similar in the proportion of their dry weight allocated to reproduction. However, differences did occur in the

distribution of this reproductive effort between asexual and sexual reproductive structures. In the dry season, 11% of the reproductive organs of *R. tuberosa* are seeds and 89% turions, whereas for *R. polycarpa* 86% of the reproductive organs are seeds and 14% turions. Of the two types of turions occurring in *R. tuberosa*, 39% are the structural type formed at the junction of leaf base and rhizome (type I), and 61% are formed as rhizome swellings at the apical meristem of the rhizome (type II). All turions in *R. polycarpa* were of type I structure. Thus *R. polycarpa* relies mainly on seeds for reproduction, and *R. tuberosa* mainly on turions.

An alternative way of examining reproductive effort is by considering the number of reproductive propagules produced. Harper (1977) suggests that the number of seeds produced will be determined by plant weight, the proportion of weight allocated to seeds and the average weight of each seed. I suggest that the number of asexual reproductive units will be determined by the same variables. An estimate of the total number of propagules will include both sexual and asexual units providing each propagule becomes independent from the parent plant. Thus seeds and turions can be included, but spread by rhizomes still attached to the parent plant is not assessable in this way as potentially every rhizome would be reproductive.

Estimates of the number of viable propagules per square metre (see Brock 1979) showed remarkable similarities between the annual populations and differences from the perennial population. Estimates of between 3 000 and 4 000 propagules per square metre for each of the two annual *R. tuberosa* populations and for the annual *R. polycarpa* population provided a marked contrast to the estimate of 370 seeds per square metre for the perennial *R. megacarpa*. The sample of *R. polycarpa* contained many more seeds than the samples of *R. tuberosa* or *R. megacarpa*. The inability to distinguish generations and the bias of the inaccuracy of subsampling were counteracted by confirmation of these estimates by calculating the potential seed production based on the number of flowers per plant (in *Ruppia* 1 inflorescence has 2 flowers) and the number of carpels per flower. These calculations suggested that each annual species could produce over 10 000 seeds per square metre in one growing season, whereas the perennial would produce less than 500 seeds. Such estimates, although unrealistic

when the actual number of seeds found is considered, support the observation that the annual species produce large numbers of reproductive units, whereas the perennial produces only a few.

In summary, the perennial populations of *R. megacarpa* live in permanent environments which can be considered stable, constant and predictable when compared with the ephemeral, fluctuating environments of the annual populations. Even though fluctuations 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 a reservoir of reproductive units as well as with environmental conditions.

The reproductive patterns of the two annual species can be described as monocarpic (*sensu* Harper 1977) or semelparous (*sensu* Stearns 1976) because of their characteristics of rapid development of plants, early and prolific reproduction which occurs only once, and the allocation of large proportions of the plants' resources to reproduction. In contrast, the reproductive pattern of the perennial is polycarpic (*sensu* Harper 1977) or iteroparous (*sensu* Stearns 1976); it reproduces annually but only produces small numbers of seeds in each year, and it devotes most of its energy to vegetative growth. In this perennial, the ability to use resources and maintain its space in the habitat are more important than the ability to recolonize and reproduce prolifically.

Finally, an examination of the osmoregulatory mechanisms of the members of this genus was carried out to look further at mechanisms of salt tolerance. *Ruppia* is the genus of submerged angiosperms with the widest tolerance of both level and fluctuation of salinity. The osmoregulatory mechanisms that enable the members of this group to survive in both fresh and extremely hypersaline waters provides further insight into the mechanisms of salinity tolerance. The cellular fluids of all three species of *Ruppia* were hypertonic to the surrounding water: such high concentrations would normally be damaging to metabolic enzymes. It has been suggested (Stewart & Lee 1974; Storey & Wyn Jones 1977) that the accumulation of certain amino acids, e.g. proline, in the cytoplasm of halophytes and water stressed crop plants may function as a salt tolerance mechanism by counterbalancing the

high solute concentration of the vacuolar fluids. The investigation of proline concentration in *Ruppia* showed that the levels of proline increase drastically with increase in habitat salinity (Brock 1979). This strongly supports the idea that plants can survive and photosynthesize in a range of environments by osmotic adjustment of proline levels in the cytoplasm.

Thus osmoregulatory mechanisms, and life cycle and reproductive patterns enable species of the submerged aquatic halophyte *Ruppia* to survive in a range of harsh and fluctuating environments.

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