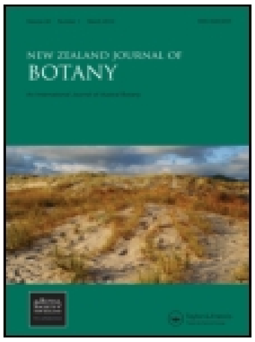

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Salt tolerance of salt marsh plants of Otago, New Zealand

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Abstract The salt tolerance of 31 species – 29 halophytes constituting a large proportion of the more important species in salt marshes of Otago, and 2 glycophytes – was examined in water culture. The effects of salinity on growth and survival were the main parameters measured. There were considerable differences between species; most could not grow in sea water (3.5% NaCl), although a small number could grow in hypersaline conditions of up to 7.5% NaCl. Some species had a salt requirement for maximum growth, the greatest being 1.5% NaCl, but most grew best in freshwater. No species required saline solutions to survive. In general, the salt tolerance of species decreased from the lower to the upper marsh, which generally parallels field salinities. There were, however, important differences between the shapes of the salt tolerance growth curves, these being related to habitat and, in particular, to the variability of salinity.

Keywords salt tolerance; halophytes; salinity; salt marsh; Otago

INTRODUCTION

Salt marshes, in New Zealand as elsewhere, afford a striking example of zonation in response to environmental variation. This zonation is most often described as a gradient of plant communities that change with marsh elevation. Chapman (1974), for instance, used a lower to upper salt marsh continuum as the basis for describing this zonation world-wide. At first sight, it appears that this zonation is simply related to a single variable in the environment, that is the tide. The tide however, consists of a number of inter-related environmental factors (Reed 1947), and it is difficult to determine the relative importance of these factors.

An understanding of how the species of the salt marsh respond to these various tidal factors can be extremely informative in determining the roles of each in controlling vegetation zonation. Such studies need to be carried out in laboratory experiments where suspected factors can be applied as treatments and the other correlated factors controlled. An experimental approach to understand salt marsh vegetation patterns was advocated by Chapman (1936) and Adams (1963) but has been avoided, probably because of the size of such a study. In most studies of salt tolerance, only a small proportion of the salt marsh flora has been examined (e.g., Clarke & Hannon 1970; Rozema 1976).

An unfortunate result of examining many species is that it is not feasible to include a range of suspected environmental factors, and often one particular factor needs to be chosen. In this study our hypothesis is that the factor controlling both growth and distribution of salt marsh plants in Otago is salinity, and salt tolerance was, therefore, the factor we chose to investigate and report on here. It is our intention to present in this paper only the patterns of salt tolerance. Correlations with environmental salinities and vegetation patterns are to be part of a separate paper.

METHODS

Growth Experiment

Features of salt tolerance were determined by growing selected species in solutions of different salinity. To allow statistical comparison the experiment was performed over two summers, the second being a repeat of the first except that additional information was obtained by adding salinities either to interpolate or extrapolate from the findings of the first.

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Plants of 29 salt marsh species were collected from the field. In addition, two glycophyte species *Triticum aestivum* and *Lolium perenne* were grown from commercial seed. The cultivars of each are unknown, but salt tolerant cultivars are generally not available in New Zealand. The plants were washed to remove any soil, divided, and kept in nurse water culture in the glasshouse with quarter strength Hewitt nutrient solution (Hewitt 1966), until all surviving plants showed visible growth and appeared healthy.

For each species, four size groups each of twelve selected plants of similar fresh weight were made up. Half of each group were randomly chosen and oven dried; this being the first harvest.

The remaining plants were grown in plastic buckets painted to reduce light transmission. There was one plant of each size-class per bucket, and they were held with pieces of closed cell plastic foam in holes in the lid. Six salinities were used in the first season: 0%, 0.25%, 0.5%, 1.5%, 3.5% (*c.* seawater concentration), and 5.0% added NaCl to a half-strength Hewitt nutrient solution. The cultures were aerated and glasshouse temperature extremes avoided. The arrangement of buckets was randomised. In the second season further salinities were added to provide more information.

The solutions were changed every 10 days, or more often if the plants were large, and the arrangement re-randomised. On completion, survival was noted, all plants were harvested and washed in fresh water. Those which had survived were divided into shoot and root. Dead plants were not measured because rot of roots made shoot/root measurements highly suspect. In the cases of all grasses, *Apium prostratum*, *Samolus repens*, and *Carex flagellifera*, shoot material was divided into green and non-green material. In the other species such a division was not always obvious. All plant material was oven dried. The time between harvests was different for each species, varying from five weeks for *Agrostis stolonifera* to twenty weeks for *Suaeda novae-zelandiae*. The ash content of the shoots was determined by combustion.

Plant dry weights were calculated and are the pooled total for the four plants whether they were live or dead. Some plant decay had taken place, but could not be avoided. However, in higher salinities this was probably slowed by the saline solutions. To compensate for salt uptake during growth, the change in ash content was subtracted and the dry weight calculated as organic accumulation. To compare growth at different salinities, a Duncan's New Multiple Range Test, $P = 0.05$, (Steel & Torrie 1960) was carried out on the log of the dry weight increase at each salinity, using the differences between the two experiments as the error. The following parameters were determined from the growth curves and the Duncan's test: salinity for maximum growth, half-growth salinity (that at which growth was half the maximum), salinity at which most plants died, and salinity at which significant growth ceased. The concept of half-growth salinity is a useful one as it neither emphasises growth in optimum conditions, nor does it use features of tolerance limits.

Survival Experiment

Thirteen species were chosen which showed little or no growth in 3.5% NaCl in the growth experiment. With three exceptions (*Triticum aestivum* and *Lolium perenne* were grown from seed, and *Plantago coronopus* from seed collected from a single plant grown in the glasshouse), plants of each species were collected from the same location as for the growth experiments and grown in garden soil in the glasshouse. This procedure was designed to obtain genetically similar material. When the plants were large enough, they were prepared and grown in water culture, as in the growth experiment, using half strength Hewitt solution and 3.5% NaCl. The number of plants surviving was noted every half week. The experiment was discontinued after all plants had died or when 32 weeks had elapsed.

RESULTS AND DISCUSSION

The measured growth parameters are shown in Fig. 1, and illustrate the range of responses to salinity. Using the different features, some interesting comparisons between species can be made.

The general pattern amongst the species is that the most salt tolerant are those of the lowermost salt marsh zones. There is a decrease in tolerance up the marsh, and into depressions in which fresh water tends to pond. Some species of such depressions and of lagoons (e.g., *Cotula coronopifolia*) are rather more tolerant than the others (e.g., *Isolepis cernua*). This pattern is found in regions of moderate to high rainfall, especially where evenly distributed throughout the year. A reversed pattern, where the more tolerant species occupy the higher zones, occurs in regions of low and highly seasonal rainfall, as a result of concentration of salt by evaporation in these infrequently inundated zones (Chapman 1974).

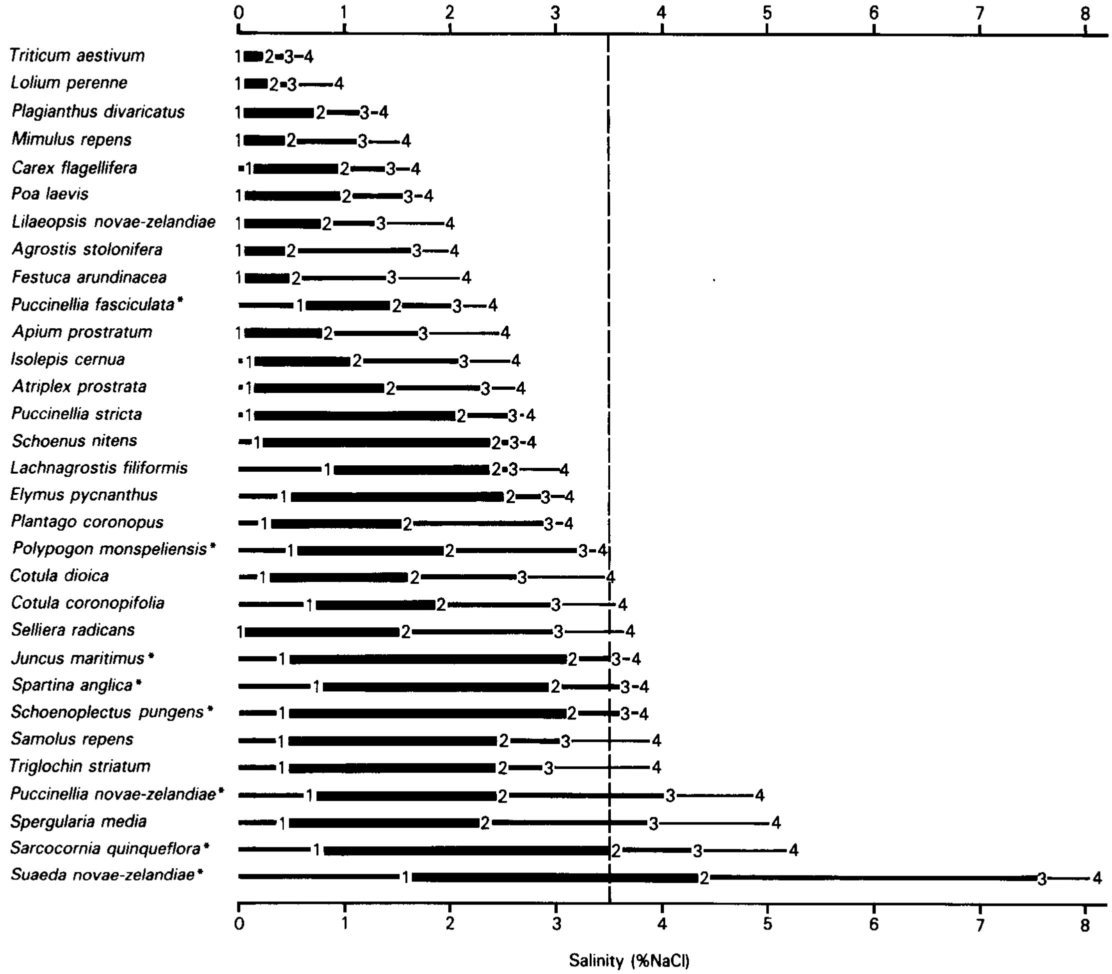

Fig. 1 Growth parameters of all species tested: 1 = salinity for maximum growth, 2 = half-growth salinity, 3 = salinity for death of plants, 4 = cessation of growth. The species have been arranged in an order based on cessation of growth. Asterisks indicate significant ($P = 0.05$) salt requirements for maximum growth. The thickness of the horizontal lines indicates the highest rates of growth and the vertical line, seawater salinity.

Experiments have shown that salt marsh halophytes do not require salt to survive. Barbour (1970) found that among the flowering plants, with the possible exception of some fully marine species, there were none with requirements of greater than 0.1% NaCl for survival. None of the species from Otago died in the nutrient solution without added salt.

There are two different kinds of response to increasing salinity. Glycophytes and a large proportion of halophytes grow best with no added salt. A smaller number of halophytes have improved growth with increasing salinity until a maximum is reached, and at greater salinities growth is depressed. As examples, Wallace & Romney (1972) found that all twelve species they examined grew best in fresh water. Barbour & Davis (1970) found this pattern in four out of five species, Taylor (1939) in five out of eight, and Clarke & Hannon (1970) in four out of eight species. In this study, 23 species grew best in fresh water, or had salt requirements that were small and not statistically significant (Fig. 1). The remaining eight had a significant (P=0.05) salt requirement for maximum growth as indicated by Duncan's test.

With one exception (*Suaeda novae-zelandiae*), the salinity of maximum growth is below 1% NaCl. Other studies have shown that most salinities for maximum growth are also below 1% NaCl. *Suaeda novae-zelandiae*, with a salinity of 1.5% NaCl for maximum growth is an exceptional species in other aspects of its response to salt as well (Fig. 1).

Further interesting comparisons can be made by examining the differences between the growth

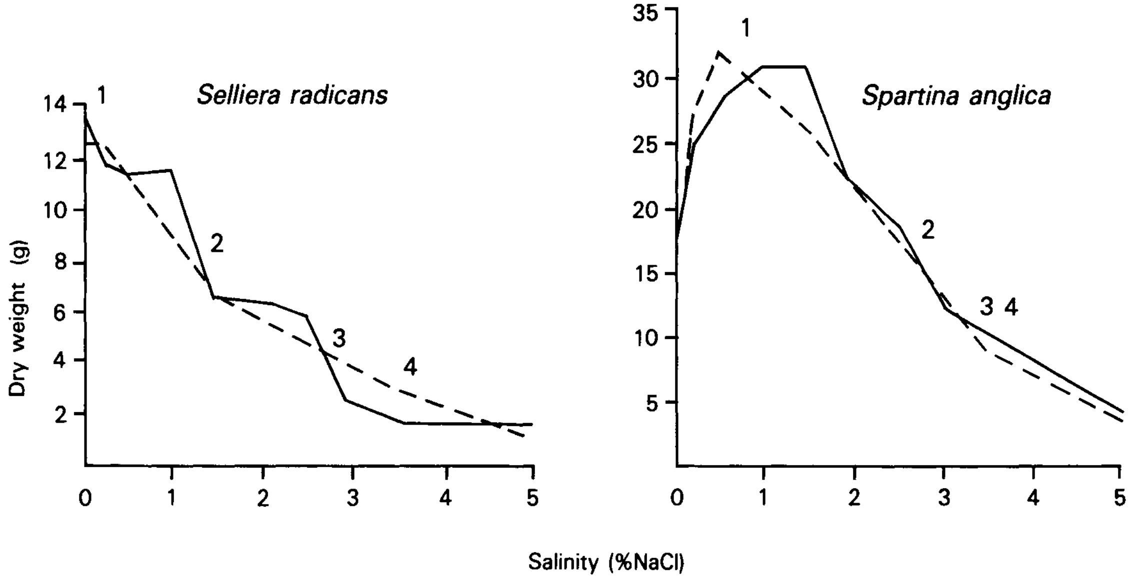

Fig. 2 Growth curves in water culture for *Selliera radicans* and *Spartina anglica* as examples of different responses. The vertical axis is dry weight for the second experiment only (solid line). The dotted line is for the first experiment, and has been adjusted so that both the starting dry weight and that at the half growth salinity correspond. Numbers are as for Fig. 1.

parameters in Fig. 1. The relation between salinity for maximum growth (1), half-growth salinity (2) and salinity for survival (3), indicates different growth curve shapes. This is further illustrated in Fig. 2 in which two species, *Selliera radicans* and *Spartina anglica*, which are close to each other on Fig. 1 (based essentially on salinity at which growth ceased – 4) have contrasting growth curves. In *Spartina anglica* there is a large difference between salinity for maximum growth and the half-growth salinity, indicating that there is only a gradual effect of salinity on growth over this range. Above the half-growth salinity however, the change is sudden, with plants dying in salinities not much greater. For *Selliera radicans*, salt has a greater effect on growth at salinities between that for maximum growth and the half-growth salinity. There is, however, no sudden change above the half-growth salinity. In other species such as *Agrostis stolonifera* (Fig. 1), the depression of growth at salinities hardly above that for maximum growth is even greater. However, the plants of this species are able to survive with little growth for a wide range of salinities above the half-growth salinity.

The survival experiment (Fig. 3) shows the same kind of differences between species. Although plants may be unable to grow during periods of high salinity, it is advantageous that they survive as long as possible. It might therefore be expected that species of sites subjected to occasional high salinities (e.g., sandy ridges) might be able to survive for longer in such salinities than those species of sites not subjected to such extremes (e.g., marsh depressions). To help answer this question, two parameters of field salinity are presented in Table 1; the mean monthly salinity and variation in monthly salinity. The more tolerant species are at the bottom of the table. The derivation of these values and more detailed numerical correlations are to be presented in a separate publication.

A number of interesting comparisons can be made. One is that of *Plantago coronopus*, a species of dry sandy areas, with *Triglochin striatum*, more commonly found in marsh depressions with ponded water. Although *Plantago coronopus* has a lower half-growth salinity and is killed by salinities that *Triglochin striatum* can survive (Fig. 1), it does have a percentage of plants surviving periods of high salinity (Fig. 3). It can be seen from Table 1 that although the habitat salinity of *Plantago coronopus* is lower than that of *Triglochin striatum*, it is subjected to greater salinity variation. A similar

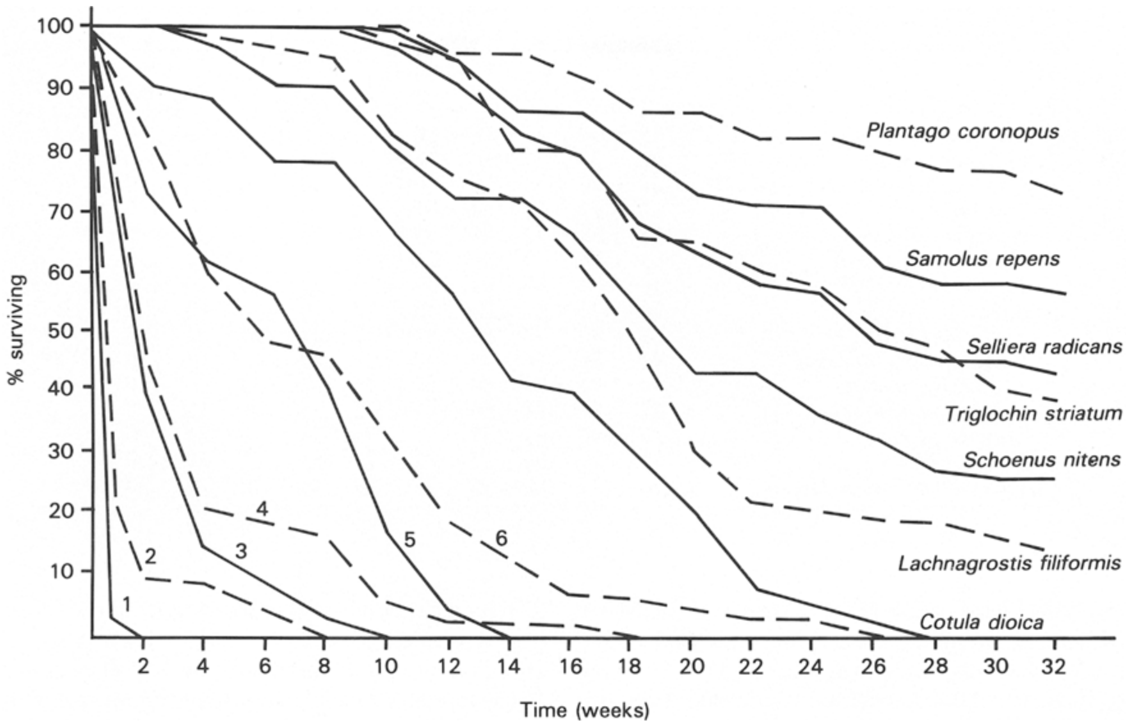

Fig. 3 Percentage survival with time of thirteen species grown in water culture with 3.5% NaCl. Numbered species are: 1 – *Triticum aestivum*, 2 – *Lolium perenne*, 3 – *Mimulus repens*, 4 – *Agrostis stolonifera*, 5 – *Festuca arundinacea*, 6 – *Isolepis cernua*.

Table 1 Monthly mean and variation in salinity for sites containing various species. Species order is as in Fig. 1.

	Soil salinity	
	Monthly mean	Variation
Plagianthus divaricatus	16.6	7.2
Mimulus repens	16.0	5.0
Carex flagellifera	18.0	8.0
Poa laevis	11.0	6.5
Agrostis stolonifera	13.7	5.0
Festuca arundinacea	17.0	7.0
Apium prostratum	22.5	7.8
Atriplex prostrata	19.0	5.0
Puccinellia stricta	28.5	9.0
Schoenus nitens	23.8	8.4
Plantago coronopus	19.0	12.0
Cotula dioica	17.5	8.5
Cotula coronopifolia	22.0	6.0
Selliera radicans	24.7	9.5
Juncus maritimus	28.7	9.0
Spartina anglica	27.7	7.5
Schoenus nitens	26.3	9.8
Samolus repens	30.8	10.7
Triglochin striatum	30.0	8.5
Puccinellia novae-zelandiae	25.0	12.0
Sarcocornia quinqueflora	30.5	12.5
Suaeda novae-zelandiae	30.0	19.3

comparison but among the less salt tolerant species is that of *Festuca arundinacea*, a species of dry marsh margins, and *Mimulus repens*, a species of wet brackish depressions and lagoons. Again, ability to survive long periods of high salinity in *Festuca arundinacea* is correlated with habitat salinity. Also, Table 1 shows that the growth curve differences between *Spartina anglica* and *Selliera radicans* in Fig. 2 are paralleled by differences in variability in habitat salinity. *Spartina anglica* grows in sites of high but relatively constant salinity below the lower marsh, and has a high half-growth salinity, but little growth at salinities above this. *Selliera radicans*, a species of the middle marsh, grows better at times of low salinity, which are probably more frequent in its variable salinity habitat.

Halophytes have various morphological, physiological, and anatomical adaptations to cope with the salt in their environments. These include succulence (e.g., Albert 1975), salt excretion (e.g., Anderson 1974), salt exclusion (e.g., McMillan 1974), and cellular mechanisms of tolerance (e.g., Greenway & Osmond 1972). Although not directly

Table 2 Live shoot dry weight as a percentage of total shoot dry weight against salinity. The species order is as in Fig. 1.

	Salinity (%NaCl)									
	0	0.25	0.5	1.0	1.5	2.0	2.5	3.0	3.5	5.0
Triticum aestivum	95	77	45	0	0	0	0	0	0	0
Lolium perenne	92	73	39	0	0	0	0	0	0	0
Carex flagellifera	67	60	55	39	0	0	0	0	0	0
Poa laevis	91	71	57	54	47	21	0	0	0	0
Agrostis stolonifera	95	88	72	53	35	9	0	0	0	0
Festuca arundinacea	93	74	35	29	22	7	0	0	0	0
Puccinellia fasciculata	79	82	98	93	49	27	20	9	0	0
Apium prostratum	90	72	64	53	45	12	0	0	0	0
Puccinellia stricta	81	90	78	83	81	67	43	21	0	0
Lachnagrostis filiformis	90	88	76	73	47	32	40	13	0	0
Elymus pycnanthus	85	94	92	84	67	65	57	31	0	0
Polypogon monspeliensis	87	87	88	66	41	35	18	19	15	0
Spartina anglica	79	90	99	87	71	75	71	59	59	0
Samolus repens	81	78	90	82	82	77	68	61	31	0
Puccinellia novae-zelandiae	70	77	80	85	77	79	84	76	71	39

examined here, some observations and measurements pertaining to these properties have been made. Salt excretion was observed in *Spartina anglica*, in which it was a feature, and *Samolus repens*, in which it appeared to take place only very slowly. The excretion structures in *Spartina* were described by Anderson (1974). *Atriplex prostrata* has bladder cells on the lower leaf surface in which salt may be stored (Osmond et al. 1969).

The ash content measurements give some indications of physiological aspects of tolerance. There was no suggestion of active salt exclusion of the kind described for various mangroves (McMillan 1974). Salt content increased with salinity but not at the same rate, and the rate of increase was generally greater in the less tolerant species. Low ash content was recorded in *Spartina anglica*, probably as a result of salt excretion. One peculiar and unexplained pattern was in *Suaeda novae-zelandiae* in which the ash content doubled from no added salt to 0.25% NaCl and rose only gradually with increased salinity. Succulence was a common feature amongst the Chenopodiaceae (*Atriplex prostrata, Suaeda novae-zelandiae, Sarcocornia quinqueflora*), but the degree of succulence varied with salinity only in *Selliera radicans*, the leaves becoming thicker with increasing salinity.

Premature death of leaves laden with salt has been suggested as a means of regulating salt content (e.g., Greenway & Thomas 1965). This is demonstrated in the live to total shoot ratios (Table 2) which show that the proportion of live to dead tissue parallels the growth performance (Fig. 1). However, this parallel extends to there being a lower live leaf proportion in low salinities for species with growth peaks at salinities above fresh water (e.g., *Spartina anglica*). Such an effect cannot be through accumulation of salt.

It has been suggested that the shoot to root ratio changes with salinity (e.g., Chatterton & McKell 1969). The measurements made here showed no evidence for this. It is interesting to note that the pattern obtained in halophytes by Clarke & Hannon (1970) largely disappeared when nutrient solution was added to the various salinities.

The salt tolerance of a number of species found within the Otago marshes have been examined in studies outside New Zealand. These can be compared with the results obtained in this study, but the comparisons must be treated with caution as genotypic differences may exist.

Clarke & Hannon (1970) examined *Sarcocornia quinqueflora*, under the name of *Arthrocnemum australasicum*. They found a growth peak at 20% seawater (0.7% NaCl) which is similar to the 1.0% NaCl found here. All their plants survived in 100% seawater (3.5% NaCl) and most in 150% seawater (5.2% NaCl), while very few surived in 200% seawater (7.0% NaCl). Although their plants performed slightly better, this pattern closely matches that of the Otago population examined here (Fig. 1).

The species described in New Zealand as *Triglochin striatum* is the same as the widespread

Triglochin striata (E. Edgar, pers. comm.), also examined in Australia by Clarke & Hannon (1970). They observed a salt requirement of 25% seawater (0.8% NaCl) for maximum growth, a value slightly higher than that for the Otago population. Only a small number of Australian plants survived 100% seawater (3.5% NaCl) which corresponds closely to the observations made for the species in Otago (Fig. 1).

Half-strength seawater (*c.* 1.8% NaCl) caused a considerable reduction in growth of plants of *Agrostis stolonifera* examined by Rozema & Blom (1977), a result similar to that obtained in this study. They also examined *Juncus gerardii*, a species found on the salt marsh at Aramoana, Otago, but not examined experimentally in this study, in which half-strength seawater (1.8% NaCl) caused very little reduction of growth. The study of Rozema (1976) included this last species, *Juncus bufonius*, and *Juncus maritumus*, all of which occur in Otago (although the *Juncus maritimus* is described as a different variety). He found that *Juncus maritimus* was very tolerant, with salinities up to seawater (*c.* 3.5% NaCl) having only a small effect on growth, while *Juncus bufonius* was found to have little salt tolerance. The tolerance of *Juncus maritimus* was verified by Clarke & Hannon (1970), theirs being the same variety (var. *australiensis*) as found in New Zealand. Maximum growth was in 20% seawater (0.7% NaCl) for their experiment and 0.5% NaCl for that undertaken here. Plants survived, but with much reduced growth in 100% seawater (3.5% NaCl), as they did in Otago plants (Fig. 1). Chapman (1936) cited an experiment which shows maximum growth of *Plantago coronopus* in 0.3% NaCl and equivalent growth in 0% and 0.5% NaCl, a pattern similar to that demonstrated here. Thus, in every case where it is possible to compare our results with those of other workers on samples of the same species overseas, the results are very similar.

One study performed within New Zealand, however, differs greatly with the results presented here. MacKay & Chapman (1954) measured salt tolerance of *Suaeda novae-zelandiae*, and found it to have very low tolerance (their plants died between 2% and 3% NaCl compared with 7.5% NaCl here). We cannot offer any reason for this difference.

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