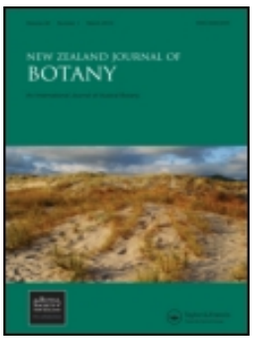

New Zealand Journal of Botany

ISSN: 0028-825X (Print) 1175-8643 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzb20

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To cite this article: C. B. Watkins , J. M. A. Brown & F. I. Dromgoole (1988) Salt-tolerance of the coastal plant, Tetragonia trigyna Banks et Sol. ex Hook. (climbing New Zealand spinach), New Zealand Journal of Botany, 26:1, 153-162, DOI: 10.1080/0028825X.1988.10410107

To link to this article: http://dx.doi.org/10.1080/0028825X.1988.10410107

New Zealand Journal of Botany, 1988, Vol. 26: 153–162
0028–825X/88/2601–153$2.50/0

Salt-tolerance of the coastal plant, *Tetragonia trigyna* Banks et Sol. ex Hook. (climbing New Zealand spinach)

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Abstract A field and laboratory study of the salt tolerance of *Tetragonia trigyna* has been carried out. The mineral element composition of the soil in native sand dune and cliff habitats of the plant showed that the concentrations of extractable sodium, chloride, potassium, magnesium, calcium, phosphorus, and total nitrogen varied, probably reflecting differences in exposure, leaching, and ageing processes. Sodium and chloride ion concentrations were lower than those found in fully saline soils and never exceeded those of the predominant cation, calcium. However, *T. trigyna* accumulated sodium and chloride ions, particularly in its leaves, in high amounts relative to those of potassium, calcium, magnesium, and total phosphorus. Such accumulations of sodium and chloride are a noted halophytic attribute but it is suggested that these may also aid survival in low soil moisture conditions. Total nitrogen concentrations were often comparable with those found in cultivated pasture plants despite low concentrations in some soils.

The growth response of *T. trigyna* to NaCl in water culture was similar to that of a salt-tolerant nonhalophyte or marginal halophyte; plant fresh weights were not stimulated by any NaCl concentration and were only severely inhibited above 150 mM whereas dry weights declined rapidly above 20 mM. However, *T. trigyna* showed several adaptations which could aid survival under saline conditions. The water content of leaves and stems increased, the growth of leaves and roots was less sensitive to salt stress than that of stems, and leaf areas were relatively less depressed than were leaf numbers. Also, the plant responded to increasing NaCl concentrations by accumulating sodium and chloride ions in its leaves to levels typical of those of halophytes. It is suggested that *T. trigyna* is a marginal halophyte rather than a salt-tolerant glycophyte.

Keywords ecophysiology; sand dune; cliff; sodium chloride; growth; semihalophyte; *Tetragonia trigyna*

INTRODUCTION

Under saline conditions, the growth of halophytes is generally stimulated and accompanied by accumulations of sodium, and chloride ions, particularly in the leaves (Waisel 1972, Flowers 1975, Flowers et al. 1977). In contrast, glycophyte growth is readily depressed by the presence of these ions, or any increased concentrations of them, in leaf tissues (Greenway & Munns 1980). Between these extremes are a range of plant growth responses to salinity (Greenway & Munns 1980), a study of which might yield further information on physiological attributes relating to survival under saline conditions. Plants from above the tidal range in coastal habitats are a potential source of these intermediate responses since the combined effect of salt spray and physiography can result in highly variable localised salinities (Boyce 1954; van der Valk 1974). Ecological and physiological information on the salt-tolerance of strand vegetation is meagre (Chapman 1974), and even less is known about that of sand dune and cliff species.

Tetragonia trigyna Banks et Sol. ex Hook. (climbing New Zealand spinach) is an edible perennial herb which has a common but discontinuous distribution throughout the New Zealand coastline (Allan 1961; Fig 1). Within this

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Received 30 September 1986; accepted 23 December 1986

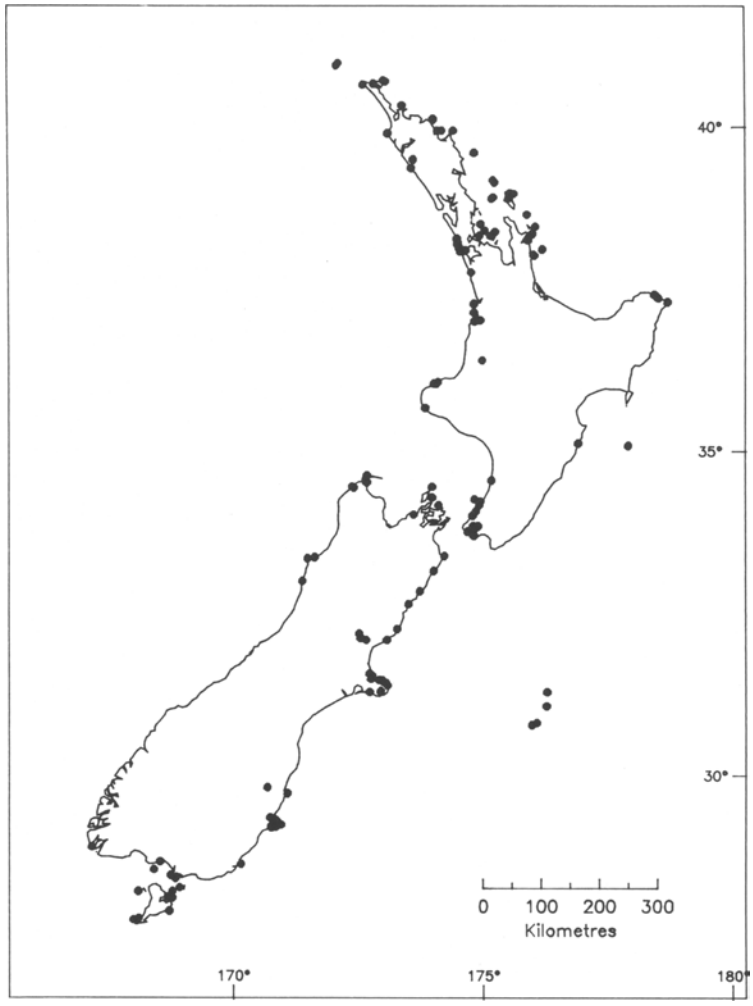

Fig. 1 Distribution map of *Tetragonia trigyna* on the main islands of New Zealand based on herbarium records.

environment, *T. trigyna* has a wide ecological range. It grows predominantly on sand dunes where it can extend inland from the strand, but also grows on cliffs and other open communities, particularly grasslands. Herbarium records indicate that on rare occasions *T. trigyna* has been found inland (e.g., as a roadside hedge CHR 159540). Whilst *T. trigyna* is not restricted to saline habitats, it can survive inundation by seawater or grow on previously marine-flooded areas (Lush 1948). Also, *T. trigyna* is closely related to the commercially grown *T. tetragonioides* (syn. *T. expansa*) or New Zealand spinach which is resistant to extreme salt stress under special conditions of cultivation (Mudie 1974).

This paper presents a field and laboratory study on the salt tolerance of *T. trigyna*. Information on the mineral element compositions of leaves and associated soils of this plant growing in its environment were obtained and its salt tolerance under glasshouse conditions examined.

MATERIAL AND METHODS

Field Investigation

Field investigations were carried out at Piha and Karekare, adjacent beaches on the west coast near Auckland. Sites (1 m × 1 m) were chosen to represent the range of habitats, from strand to cliff,

of *T. trigyna* at these locations. At each site, both plant material and soil were analysed.

Description of sites

Site 1 (Piha): An "island" of vegetation situated 10 to 15 m from the extreme high water tide. Other species present were: *Spinifex hirsutus*, *Sonchus oleraceus*, and *Calystegia soldanella.*

Site 2 (Piha): A sand flat protected from direct exposure to wind but within reach of storm waves. Only *T. trigyna* was present. The site was covered with dead *Lupinus arboreus* which had apparently died as a result of recent inundation by seawater.

Site 3 (Piha): Top of a dune ridge behind foredunes and exposed to the prevailing westerly wind. *T. trigyna* was intermingled with *Muehlenbeckia complexa* in a dense ground cover. Small plants of *Lotus subbiflorus* were growing under the *M. complexa* and *T. trigyna.*

Site 4 (Piha): Situated at the rear of the sand dunes under a large tree of *Metrosideros excelsa.* Only *T. trigyna* was present.

Site 5 (Karekare): A cliff site, directly exposed to the prevailing westerly wind although some shelter was afforded to *T. trigyna* by a rocky ridge. No other species were present.

Sampling and treatment of plant material

A whole plant was collected from each site in the morning, sealed in a plastic bag and quickly transferred to the laboratory. Plants were then separated into leaves, stems and roots. Dead or senescent tissue was removed and the plant parts were then washed, blotted dry, weighed and oven dried at 85°C to constant weight. The dry material was milled to a fine powder suitable for analysis.

Sampling and treatment of soils

Five soil cores, 20 cm deep and 4 cm diameter, were collected from within each site using a calibrated soil borer. The sampling was random within a grid pattern which divided each site into 100 equal squares. Squares were located by random numbers (0–9) in the x and y direction and soil cores collected. These cores were divided into subsamples of 0–5 and 5–20 cm, and sealed in plastic bags. Preliminary investigations showed that a depth of 20 cm included most of the root system of *T. trigyna* and that the largest proportion of the root biomass was in the top 5 cm.

In the laboratory, stones and organic material were removed, with a 2 mm sieve, from the samples which were then weighed and air dried at 30°C to constant weight.

Analytical methods

Triplicate samples of powdered plant material (100 mg) were digested in a sulphuric acid : hydrogen peroxide (42:35 v/v) mixture to which lithium sulphate and selenium had been added to allow quantitative determination of nitrogen (Allen et al. 1974). Sodium, potassium, calcium, and magnesium were measured on the digestate by atomic absorption spectrophotometry (Southern Analytical A3000). Nitrogen was estimated by titration with HCl after alkaline distillation. Chloride was measured on water extracts (90°C, 90 min) of further samples by potentiometric titration with silver nitrate using a K601 mercury/mercurous sulphate reference electrode and a P4011 silver billet electrode (Radiometer, Copenhagen). Soil samples (100 g) were extracted with ammonium acetate (pH7) (Allen et al. 1974) prior to sodium, potassium, calcium and magnesium analysis by atomic absorption spectrophotometry. Chloride in the soils was measured on water extracts (as for plant material), after soils were shaken in deionised water for 20 minutes. Available phosphorus was estimated according to Truog (1930), and nitrogen was estimated by titration, as above, after Kjeldahl digestion.

Laboratory Study

Plant material

Vegetative propagules from runners of low-salt plants were used as the initial plant material. Plants, collected from Piha, were cut into segments (approximately 5 mm long) bearing 2–5 leaves, and induced to form roots by planting in river sand in a mist room. After 5–6 weeks the rooted segments were transferred to darkened 15 l aquarium tanks, and supported so that their roots were in constantly aerated Hoagland's solution, prepared as in Hewitt (1966) except that iron was supplied as FeEDTA (Steiner & van Winden 1970). After 10–12 weeks, nodal segments cut from stems of these plants were induced to form roots as before, and returned to Hoagland's solution for two weeks prior to experimentation. The average sodium concentration of leaves from these plants was 0.47 $nmol.g^{-1}$ dry weight after this procedure.

Growth experiments

Two experiments are reported here: Experiment 1, Hoagland's solution plus 10, 20, 40, 60, and 100 mM NaCl; and Experiment 2, Hoagland's solution plus

60, 150, and 300 mM NaCl. Twenty plants, each with fresh weight within the range of 0.8–1.2 g per treatment, were transferred to Hoagland's nutrient solution. Salinisation to the required NaCl concentrations was begun by the addition of no more than 50 mM NaCl per day. The solutions were changed weekly throughout the experiments and deionised water was added at 1 to 2 day intervals to compensate for losses due to evaporation and transpiration. The pH was maintained at 5.5 throughout the experiments. The mean day/night temperatures and relative humidites were 23°C/22°C and 80%/72% during Experiment 1 and 24°C/22°C and 86%/72% during Experiment 2.

Six weeks after salinisation was begun, plants were harvested, washed thoroughly in deionized water, and blotted dry. Leaves, stems and roots were separated and weighed. Leaf areas were calculated gravimetrically. The plant parts were then dried at 85°C to constant weight and milled to a fine powder prior to extraction and analysis.

Analytical methods

Samples were wet-washed or extracted with deionised water and analysed as already described. Nitrate and phosphorus were determined colorimetrically on a chloride-free extract by the phenoldisulphonic acid method (Johnson & Ulrich 1959) and by the phosphomolybdenum-blue complex method (Allen et al. 1974), respectively.

RESULTS

Field Investigations

Tables 1 and 2 show the element composition of soil and plant material at five sites on which *T. trigyna* was found growing at Piha and Karekare. Although the data presented were collected on only one sampling date per site, monthly analyses at three other sites from April to September (unpubl. data), indicate that these values are representative of the element compositions found at these sites.

Soils

Sodium and chloride concentrations greater than 0.25 mmol 100 g^{-1} dried soil were measured in only two sites (Table 1): the cliff site (Site 5) and under *M. excelsa* (Site 4). Although Site 5 was selected some distance from the shoreline, the concentrations of sodium and chloride were probably higher than at closer sites due to interception of wind-blown salt spray by *M. excelsa* and subsequent washing down of the salt from the leaves.

The concentrations of the other elements varied between sites but calcium was always the predominant cation (Table 1). No consistent pattern between the relative proportions of the cations was observed. Phosphorus levels were consistently low, never exceeding 0.10 mmol 100 g^{-1} dried soil, while total nitrogen levels ranged from 0.52 to 8.42 mmol 100 g^{-1} dried soil between the sites.

Plant material

Sodium concentrations were higher in the leaves than in any other plant part, and the accompanying anion was chloride (Table 2). The sodium concentrations in the leaves were also greater than those of any other cation, frequently ten times (Table 2). Highest sodium and chloride concentrations were found in leaves from the cliff site (Site 5) and under *M. excelsa* (Site 4), and thus reflected relatively higher soil concentrations of these ions (Table 1).

The concentrations of potassium, calcium, and magnesium in the leaves were relatively constant in the various sites (Table 2) despite variation in the soil content of these elements (Table 1). Although there were low concentrations of total nitrogen at some sites, particularly those with little organic matter, the concentrations of total nitrogen in the leaves were occasionally greater than 2 mmol g^{-1} dry weight.

Laboratory Study

Growth response

At harvest, the growth of *T. trigyna*, expressed on a fresh weight basis, was not significantly stimulated by any NaCl addition (Table 3). The fresh weight was still 83% of that of non-salinised plants at 150 mM NaCl, and severe inhibition occurred only at 300 mM. Dry weight growth was also not stimulated at any NaCl concentration but, in contrast to fresh weight, declined above 20 mM.

Leaf areas were reduced by NaCl (Table 3) but were still 72% of non-salinised plants at 150 mM. Leaf number (Table 3) declined markedly above 60 mM NaCl and was only 50% of that of the non-salinised plants at 150 mM. This was possibly due to inhibition of lateral shoot development by NaCl which was observed, particularly at concentrations of 100 mM and above, but not measured.

The relatively small reduction of the leaf areas of plants was reflected in a differential depression by NaCl of the growth of plant parts in the order: stems>roots>leaves (Table 4). For example, at 100 mM NaCl, the dry weight of stems, roots, and

Table 1 Mean soil moisture, extractable element, and total nitrogen concentrations in the soils from Piha and Karekare. All concentrations are expressed as mmol 100 g^{-1} dried soil (± s.e.).

	Soil depth (cm)	Site no. 1	2	3	4	5
% moisture	0–5	3.56±1.23	8.31±4.37	7.73±1.92	6.37±1.53	1.63±0.76
	5–20	3.26±1.30	4.03±0.98	2.96±0.67	2.28±0.68	2.09±0.98
Na	0–5	0.18±0.02	0.20±0.03	0.24±0.01	1.71±0.47	0.78±0.21
	5–20	0.08±0.03	0.09±0.02	0.16±0.01	1.17±0.29	0.64±0.22
Cl	0–5	0.14±0.03	0.07±0.01	0.12±0.03	1.60±0.39	0.76±0.30
	5–20	0.03±0.01	0.04±0.01	0.06±0.01	1.03±0.60	0.64±0.28
K	0–5	0.06±0.02	0.10±0.01	0.09±0.01	0.42±0.06	0.19±0.01
	5–20	0.05±0.01	0.06±0.01	0.04±0.01	0.32±0.06	0.16±0.01
Ca	0–5	1.05±0.22	1.17±0.05	2.57±0.34	3.77±0.52	1.35±0.25
	5–20	1.03±0.28	0.48±0.04	0.80±0.08	3.38±0.33	0.51±0.02
Mg	0–5	0.26±0.09	0.57±0.12	0.88±0.23	1.52±0.47	0.43±0.11
	5–20	0.26±0.05	0.33±0.04	0.32±0.20	0.90±0.21	0.40±0.11
P	0–5	0.03±0.01	0.07±0.01	0.08±0.01	0.09±0.02	0.03±0.00
	5–20	0.02±0.00	0.05±0.01	0.05±0.01	0.08±0.01	0.03±0.00
Total N	0–5	1.86±0.26	8.42±0.22	3.15±0.38	0.52±0.06	0.71±0.06
	5–20	0.85±0.03	5.06±0.20	1.97±0.36	0.59±0.06	0.46±0.03

Each parameter was determined on five soil cores samples. Sampling dates (1976): Sites 1–4, 13 December; Site 5, 1 December.

Table 2 Element concentratins (mmol g^{-1} dry weight) in *Tetragonia trigyna* at Piha and Karekare*,†.

		Site no. 1	2	3	4	5
leaves	Na	2.24	3.22	2.73	4.40	4.04
stem		0.90	1.49	0.93	1.26	1.28
root		0.94	0.58	0.65	1.03	0.91
leaves	Cl	1.69	2.87	1.94	3.71	3.60
stem		0.73	1.27	0.61	0.99	0.91
root		0.67	0.52	0.55	0.96	0.87
leaves	K	0.33	0.25	0.22	0.24	0.27
	Ca	0.23	0.12	0.23	0.20	0.20
	Mg	0.25	0.18	0.27	0.29	0.24
	Total P	0.08	0.10	0.09	0.09	0.06
	Total N	2.11	1.59	2.23	1.32	1.12

* Sampling dates (1976): Sites 1–4, 13 December; Site 5, 1 December.

† Each value is the mean of 3 analyses of bulked plant tissue.

leaves was depressed by 61%, 36%, and 17% respectively. Shoot weights (leaves and stems) were depressed similarly to those of the roots and, therefore, there was no significant difference between treatments on the root to shoot ratios.

Water content

A significant increase in the fresh to dry weight ratio occurred for all plant parts under saline conditions (Table 5). For example, at 100 mM NaCl, the increase in relative water content (ratio of water to dry weight) was less marked in the stems than in both leaves and roots which increased over 30%. However, since leaves make a major contribution to the total plant weight and their tissue growth is less inhibited by salinisation, the relative water content of whole plants increased by some 38% in the 100 mM NaCl treatment.

Leaf morphology

The leaves of *T. trigyna*, whilst lower in number and greater in individual size, also became thicker as a result of salinisation (Table 6). The most obvious visual effect was an increase in prominence of the dense bladder-like trichomes in the abaxial surfaces. However, as shown in Table 6, the major contribution to increased leaf thickness came from increase in the width of the mesophyll layers. Leaf width increased progressively with NaCl concentration up to at least 150 mM but was reduced below the maximum recorded by the 300 mM NaCl addition.

Table 3 Fresh weight, dry weight and leaf areas of *Tetragonia trigyna* grown for six weeks on Hoagland's solution with various NaCl concentrations. Data from two separate experiments are given for each parameter.

NaCl concentration mM	Fresh weight g plant^{-1}		Dry weight g plant^{-1}		Leaf area cm^2 plant^{-1}		Leaf number	
0	20.65 ab	18.84 ab	2.22 a	2.00 a	268 a	223 a	112 a	93 a
10	20.85 ab		2.19 a		260 a		109 a	
20	22.77 a		2.12 ab		239 ab		98 ab	
40	21.08 ab		1.84 bc		235 ab		82 b	
60	20.48 ab	17.98 ab	1.68 cd	1.45 b	234 ab	192 ab	85 b	69 b
100	18.39 b		1.48 d		198 b		51 c	
150		15.56 b		1.13 c		160 b		46 c
300		7.26 c		0.64 d		69 c		21 d

Values indicated by the same letter in a column do not differ significantly at $P<0.05$ (Duncan's Multiple Range Test).

Table 4 Dry weight of plant organs of *Tetragonia trigyna* grown for six weeks on Hoagland's solution with various NaCl concentrations. Data from two separate experiments are given for each parameter.

NaCl concentration mM	Leaves g		Stems g		Roots g	
0	1.19 a	1.08 a	0.67 a	0.59 a	0.36 a	0.33 a
10	1.14 ab		0.68 a		0.37 a	
20	1.20 a		0.55 b		0.37 a	
40	1.10 ab		0.43 b		0.31 b	
60	1.09 ab	0.99 a	0.30 c	0.22 b	0.29 bc	0.24 b
100	0.99 b		0.26 c		0.23 c	
150		0.79 b		0.13 c		0.21 b
300		0.47 c		0.06 d		0.11 c

Values indicated by the same letter in a column do not differ significantly at $P<0.05$ (Duncan's Multiple Range Test).

Table 5 Fresh to dry weight ratios of the plant parts of *Tetragonia trigyna* grown for six weeks on Hoagland's solution with various NaCl concentrations. Data from two separate experiments are given for each parameter.

NaCl concentration mM	Leaves		Stems		Roots		Whole plant	
0	11.10 a	10.84 a	6.43 a	7.34 a	8.87 a	8.48 a	9.30 a	9.42 a
10	11.28 a		6.76 ab		8.61 ab		9.52 a	
20	13.06 b		6.93 b		8.24 b		10.72 b	
40	13.79 bc		7.06 b		9.13 a		11.46 c	
60	14.11 c	13.51 b	7.67 c	8.64 b	10.91 c	11.36 b	12.19 d	12.36 b
100	14.38 c		7.72 c		11.53 d		12.86 e	
150		15.09 c		8.89 b		11.82 b		13.77 c
300		12.25 d		6.66 c		10.12 c		11.34 d

Values indicated by the same letter in a column do not differ significantly at $P<0.05$ (Duncan's Multiple Range Test).

Table 6 Width of cell layers in leaves of *Tetragonia trigyna* grown for six weeks on Hoagland's solution with various NaCl concentrations. Each value is the mean of two leaves taken from the fifth node from the apex.

NaCl concentration mM	Cuticle µm	Pallisade Mesophyll µm	Paren-chyma mesophyll µm	Trichome layer µm	Total leaf width µm
0	30	150	200	115	495
60	50	210	270	190	720
150	95	520	370	160	1145
300	100	380	285	175	940

Element composition

At NaCl concentrations up to 150 mM there was an increase in the concentrations of sodium and chloride (dry weight basis) in all plant parts (leaves>stems>roots: Fig. 2). Between 150 and 300 mM NaCl, the concentrations of both ions increased either slowly (roots) or were depressed (leaves and stems). However, when data were recalculated on a "plant water" basis, the leaf concentrations of sodium and chloride were 476 and 451 mmol l^{-1}, respectively, at 300 mM, and 409 and 364 mmol l^{-1}, respectively, at 150 mM NaCl.

Potassium concentrations declined with increasing salinity, being high in non-salinised plant parts (Fig. 2). The concentrations of other elements in the leaves were also altered by increasing salinity (Table 7). Although the absolute values for the individual elements in the two experiments varied in both the non-salinised plants and those grown at 60 mM NaCl, the trends were consistent. The concentrations of calcium, magnesium, nitrate, and total nitrogen were depressed by salinisation. The concentration of total phosphorus increased in the leaves above 40 mM NaCl and only declined at 150 mM and 300 mM NaCl.

The same patterns were generally found in stems and roots with increasing salinity (unpubl. data) except in three respects: magnesium did not decline in the roots, total nitrogen in stems was unaffected, and the concentrations of total phosphorus in the stems and roots increased steadily.

DISCUSSION

Halophytes are plants which complete their life cycle in a high salt environment (Flowers 1975). Such an environment is commonly regarded as having salt concentrations in the soil solution greater than 0.5% or about 85 mM (Waisel 1972, Chapman 1974). Thus, it has been generally concluded (MacDonald & Barbour 1974) that plants in coastal habitats above high tide are not halophytes, although in some habitats, e.g., cliffs, they may be regarded as salt-tolerant.

T. trigyna would appear to fit this latter category as it seems unlikely that NaCl concentrations greater than 0.5% were reached in the soils of Piha and Karekare. Even at those sites (4 and 5) with the highest salt concentrations, sodium and chloride were well below that commonly found in salt marsh soils (usually greater than 10 mmol $100g^{-1}$ dry weight (Tsuda 1961, Waisel 1972)). The concentrations of sodium and chloride in the soil are similar to those generally found in other sand dune environments (e.g., Boyce 1954, Tsuda 1961). The ion retention capacity of dune sand is very low (van der Valk 1974) and salts are leached quickly through the upper 60 cm of soil (Boyce 1954).

In the glasshouse, the growth of *T. trigyna* was not stimulated by NaCl as found in halophytes *sensu stricto* (Flowers et al. 1977). Growth still occurred at 300 mM NaCl, but was greatly inhibited, and its response was therefore similar to that of salt-tolerant non-halophytes or marginal halophytes shown by Greenway & Munns (1980). However, *T. trigyna* responded to increasing NaCl concentrations by accumulating sodium and chloride ions in its leaves to levels found typically in halophytes, i.e., generally in the range 2–6 mmol g^{-1} dry weight (Waisel 1972, Flowers 1975, Grouzis et al. 1977, Zid & Boukhris 1977). In contrast, sodium and chloride concentrations in glycophytes are relatively low under saline conditions (e.g., Greenway 1973, Tal & Shannon 1983). In halophytes, usually more than 90% of the sodium is in the shoot and at least 80% of this is in the leaves (Flowers 1975): calculations based on Fig. 2 and

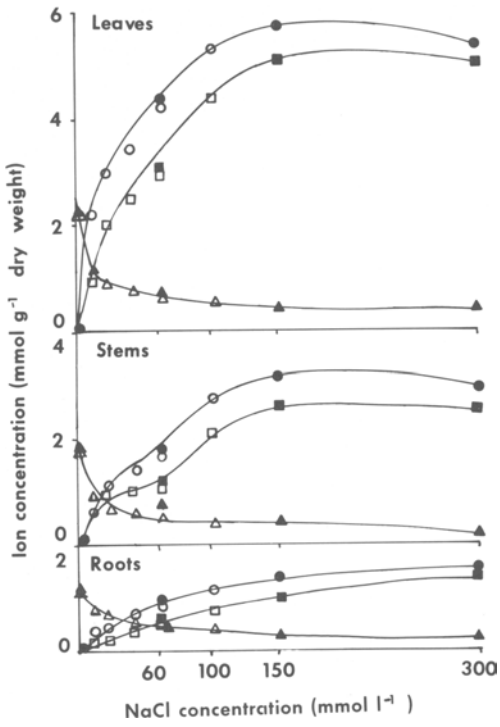

Fig. 2 Effect of NaCl concentration on the levels of sodium (circles), chloride (squares), and potassium (triangles), in plant organs of *Tetragonia trigyna* grown in Hoaglands solution. Experiment 1 (open symbols) and Experiment 2 (closed symbols).

Table 4 showed that at all NaCl concentrations, more than 95% of the total sodium content of the plant was contained in the shoot. Thus, the high sodium and chloride uptake and accumulation of these ions in the shoots clearly indicate the halophytic nature of *T. trigyna*.

The accumulation of sodium and chloride ions in the leaves of *T. trigyna* also appears to be an important feature of this plant in its natural habitat, even though the soil content of these ions seems low. Similar levels of sodium and chloride have been measured in some sand beach, sand dune and cliff plants (Winter et al. 1976), although these concentrations are lower than the values of about 6 mmol g^{-1} dry weight found more frequently in plants of highly saline soils (Waisel 1972, Winter et al. 1976). The lower levels measured in field plants relative to salt-marsh halophytes, and the demonstrated capacity of *T. trigyna* to accumulate these ions in water culture, probably reflects the low soil concentrations of NaCl rather than an inability to accumulate sodium and chloride to high concentrations.

Accumulation of sodium and chloride in the leaves of *T. trigyna* may be an adaptation which provides this plant with considerable flexibility to survive both fluctuating NaCl concentrations in its environment and water stress due to low soil moisture. High sodium and chloride levels in halophyte leaves are ascribed to uptake systems with a high capacity for these ions, and linked with adjustment to unfavourable water potentials (Flowers et al. 1977). Such potentials can result from either high salt levels in the soil solution or low soil moisture. Some xerophytes are also capable of accumulating high levels of sodium and chloride in their leaves, e.g., *Atriplex vesicaria* (Black 1960).

Under non-saline conditions *T. trigyna* also accumulated other ions, particularly potassium and nitrate. Accumulation of potassium is characteristic of halophytes (Flowers 1975) and indicates a high constitutive capacity for ion uptake. Black (1960) regarded "excess" potassium concentrations under non-saline conditions as substituting for sodium, and as being osmoregulatory in character rather than nutritional. Also, high concentrations of nitrate in *T. trigyna* under non-saline conditions indicate that a substantial amount of this ion remained unmetabolised and was probably an important counter ion. Similar concentrations of nitrate occur in the halophytes *Atriplex hastata* (Black 1960) and *Salicornia europaea* (Austenfeld 1974).

The concentrations of potassium, calcium, magnesium, nitrate, and total nitrogen were depressed by salinisation, although at NaCl levels up to 150 mM, potassium and calcium concentrations were relatively constant after an initial decline. These levels probably constitute basic and minimal concentrations of these ions in the tissues for satisfactory growth to occur. Concentrations of nitrogen were still high under saline conditions, being close to the range of 1.78–2.5 mmol g^{-1} dry weight commonly measured in cultivated pasture crops (El-Ghonemy et al. 1977). Such concentrations were also found in field plants growing in low soil nitrogen, suggesting that *T. trigyna* is well adapted to low available soil nitrogen conditions. It is notable that this adaptation is also common in halophytes (Caldwell 1974).

Several features of the growth response of *T. trigyna* to NaCl may also be adaptations to saline conditions. Firstly, the growth of leaves and roots

Table 7 Element composition (mmol g^{-1} dry weight) of leaves of *Tetragonia trigyna* grown for six weeks on Hoagland's solution with various NaCl concentrations. Data from two separate experiments are given for each parameter.

NaCl concentration mM	Ca		Mg		NO_3		Total N		Total P	
0	0.47	0.55	0.35	0.37	0.86	0.94	2.78	2.93	0.21	0.27
10	0.43		0.25		0.46		2.60		0.19	
20	0.27		0.25		0.33		2.19		0.20	
40	0.23		0.20		0.27		2.17		0.28	
60	0.20	0.27	0.16	0.24	0.25	0.25	1.17	2.39	0.30	0.39
100	0.20		0.15		0.24		1.96		0.26	
150		0.23		0.12		0.21		1.60		0.23
300		0.12		0.08		0.13		1.67		0.11
LSD (P<0.05)	0.03	0.04	0.02	0.02	0.04	0.04	0.16	0.21	0.02	0.02

was much less sensitive to salt stress than that of stems. Similar differential depression of individual plant parts has been shown in *Tamarix ramosissima* (Kleinkopf & Wallace 1974) and *Atriplex halimus* (Zid & Boukhris 1977), but it is difficult to ascertain if this effect is a general one as leaves and stems are rarely separated. Secondly, while both total leaf areas and leaf numbers declined in increasing NaCl concentrations, leaf areas were relatively less depressed. Glycophytes such as *Phaseolus vulgaris* L. have fewer and smaller leaves when exposed to saline conditions (Ayoub & Ishab 1974, Wignarajah et al. 1975). In contrast, the leaf areas of halophytes are usually greater, either because of more intensive sprouting of lateral leaf buds (Williams 1960, Gale & Poljakoff-Mayber 1970) or because of larger individual leaves (Waisel 1972). The response of *T. trigyna* to NaCl appears to be intermediate between these extremes.

An increased water content, especially in the leaves and stems, when NaCl is added to a nutrient solution is well known in both glycophytes and halophytes, and is usually regarded as a mechanism by which high concentrations of salt in the cells can be prevented by dilution (Waisel 1972, Jennings 1976). Although the width of the mesophyll cell layers increased, an expansion of the bladder-like trichomes under saline conditions suggests a possible role for them in the salt tolerance of *T. trigyna*. The trichomes are similar to those of *Atriplex* species (Osmond et al. 1969, Troughton & Card 1974) and *Haliomione portulacoides* (Baumeister & Kloos 1974). In these species the bladders contain about half the total salt in the leaf.

Thus, this study shows that *T. trigyna* possesses several mechanisms that might aid survival under high salt conditions. It is not a halophyte by ecological definition (Flowers 1975) and no growth stimulation occurred in the presence of NaCl. However, the halophytic attribute of accumulating sodium and chloride strongly suggests that *T. trigyna* is a marginal halophyte rather than a salt-tolerant glycophyte. In its native environment the range of salinity encountered is likely to be variable, and the ability to survive short periods of high salt condtions resulting from salt spray or even inundation by seawater may be crucial.

ACKNOWLEDGMENTS

We would like to thank the curators and keepers of the following herbaria for locality records of *T. trigyna*: AK, AKU, CANU, CHR, LINC, WELT, WELTU, NZFRI, WAI, MPN, Plant Health and Diagnostic Station, MAF (Lynfield).

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