The effect of salinity on the growth of some New Zealand sand dune species

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SUMMARY

Soil salinity affects many coastal communities, but it is not clear to what extent salinity is involved in the distribution of sand dune vegetation. Twenty-nine species (including nine exotic species) found on New Zealand sand dunes were used in a study of root-salinity tolerance. Six concentrations of salt were added to plants grown in water culture; growth rates and the percentage of live material were measured.

About half the species were more intolerant of root-salinity than the glycophytic control (wheat). These were mainly native New Zealand herbs and grasses and the introduced species *Silene gallica* and *Lupinus arboreus*. Tolerant species included the native species *Desmoschoenus spiralis* and *Scirpoides nodosa*. Most tolerant exotic species were grasses; *Elymus farctus* was the most salt tolerant species tested, and possibly in Barbour's 'facultative halophyte' category.

Species scores from the first vegetation gradient of an ordination of field data from four dune systems were plotted against results from this study. For some species, root-salinity tolerance correlated with their field position. However, there was little correlation with distributions on West Coast dunes, with some glycophytes growing in the semi-fixed dunes. This was attributable to the high rainfall. On the dry east coast, however, species were more tolerant and their distribution more closely linked to their salinity tolerance.

New Zealand dunes contain a mixture of root-salinity tolerant species and root-salinity intolerant species. It is suggested that root-salinity is only one of a complex of environmental factors important on dunes.

Key-words: New Zealand, ordination, root salinity, sand dune vegetation.

INTRODUCTION

Soil salinity is one of the important determinants of zonation in salt marshes (Evans 1953; Partridge & Wilson 1988) and on cliffs (Goldsmith 1973; Wilson & Cullen 1986), but it is unclear to what extent coastal sand dune vegetation is controlled by it.

Sand dune vegetation has often been considered non-halophytic (Rozema *et al.* 1985; Kearney 1904; Tansley 1939). The supply of salt from salt spray and high tides is intermittent, and because sand is a porous medium rain quickly leaches away salt (Etherington

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1967). However, rain leaching is less effective in dry summer weather (Berger & Heurteaux 1985) and in arid regions (Hayward & Wadleigh 1949). Salinity may also be high in dune hollows, up to 3–5% NaCl, though more normally around 1% (Salisbury 1952).

Barbour *et al.* (1985) suggested that dune species are less tolerant of salinity than salt marsh species, but more tolerant than glycophytes, however, few experimental results are available, and none on native New Zealand dune species. Sykes & Wilson (1988) investigated the effect of salt spray on aerial plant parts. This study measured the responses of a large number of species, both native to New Zealand and introduced, to different levels of root salinity (salinity in the rooting medium). This represents the first survey of the root-salinity tolerance of a dune flora.

MATERIALS AND METHODS

Plants were either collected from the field or germinated from seed and propagated in the greenhouse. *Desmoschoenus spiralis*, the native sand-binder, was collected from the field twice, as mature plants and as seedlings. The nomenclature follows Allan (1961) for native dicotyledons, Moore & Edgar (1976) for native monocotyledons except Cheeseman (1925) for Poaceae, changes in Connor & Edgar (1987), Clapham *et al.* (1981) for adventive species, except where indicated.

Twenty-nine species including nine introduced species (Table 1) were grown in nurse water culture before being transferred for the experiment to $\frac{1}{4}$-strength Hewitt's (1966) solution, in 2·5-litre plastic pots. The pots were aerated three times daily for 4 h at a time. Four (except in the case of the largest species such as *D. spiralis*, for which three) individual plants were placed in each pot, supported in an opaque top by non-absorbent plastic foam. Each pot of four plants represented one harvest and was carefully matched in plant size and vigour with all other treatments and harvests for that species. The pots were allocated to treatments at random. There were two to seven replicates set in a randomized block design, re-randomized at intervals.

All species were grown in salinity (NaCl) concentrations of 1·00%, 0·75%, 0·50%, 0·25% and control (0%), plus either 2% (*Ammophila arenaria, Bromus diandrus, Carex pumila, Cyperus ustulatus, Desmoschoenus spiralis, Elymus farctus, Lupinus arboreus, Phormium tenax, Scirpoides nodosa* and *Senecio elegans* L.) or 1·5% (all others). The latter choice was made on the field distribution of the species.

The glasshouse was lit by 400 W mercury vapour lights at a density of 1 light m^{-2} which gave an extra 32 W m^{-2} light intensity at pot level. There was no additional heating. Air vents were set to open if temperatures exceeded 15°C. The mean daily temperature during the experiment was 15·1°C. The minimum temperature was 10°C and the maximum 34°C. The mean daily relative humidity was 81·9% ranging from 50 to 100%.

A first harvest (of complete pots) was taken 7 days after salt was added and a second 32 days later. A longer period of continuous salinity would have had different effects, but would have been inappropriate in view of the transient nature of dune salinity (Donnelly & Pammenter 1983). At each harvest, plants were removed from their pots, rinsed, divided into root, stem, leaf and dead material, and oven dried at 95°C for 48 h. The results were calculated on mean weight per plant.

RESULTS AND DISCUSSION

Wheat, and the definitions of 'halophyte'

Triticum aestivum (wheat) was included as a species not found on coastal dunes, though not particularly sensitive to salt (Francois *et al.* 1986; Partridge & Wilson 1987). It tolerated salt

Table 1. Relative growth rates (RGR week^{-1}) of a range of species when grown in six different concentrations of salt. Within species, salinities with the same letter have a RGR which is not significantly different ($P=0.05$)

Species		Salt treatments (%)					
		0·0	0·25	0·50	0·75	1·00	1·5 or 2·0
Acaena anserinifolia	E	0·414a	0·281a	0·069b	0·056b	−0·007b	−0·008b
Ammophila arenaria	I	0·242a	0·221a	0·126ab	0·054b	0·130ab	−0·001b
Austrofestuca littoralis	N	0·088a	0·115a	0·103a	0·037a	0·059a	0·026a
Bromus diandrus	I	0·425a	0·429a	0·326a	0·142b	0·056b	−0·033b
Carex pumila	N	0·168a	0·080ab	0·077ab	0·102ab	0·049ab	−0·010b
Centella uniflora	E	0·301a	0·169ab	0·119abc	−0·064c	−0·075c	−0·007bc
Colobanthus muelleri	E	0·128a	−0·003ab	−0·059ab	−0·025ab	−0·055ab	−0·133b
Coprosma acerosa	E	0·264a	0·232a	0·176ab	0·072ab	−0·013b	0·005b
Craspedia uniflora	E	0·123a	0·061a	0·050a	0·022a	0·085a	0·023a
Cyperus ustulatus	E	0·367a	0·292ab	0·257ab	0·174bc	0·156bc	0·022c
Desmoschoenus spiralis (m)	E	0·040a	−0·006a	−0·006a	0·001a	0·021a	−0·006a
Desmoschoenus spiralis (s)	E	0·061a	0·112a	0·062a	0·011a	0·022a	0·049a
Elymus farctus	I	0·177ab	0·203ab	0·224ab	0·282b	0·106ab	0·068a
Gnaphalium audax	E	0·520a	0·158b	0·088b	−0·033b	−0·020b	−0·014b
Gnaphalium luteo-album	N	0·452a	0·460a	0·402a	0·313ab	0·174bc	0·056c
Gunnera albocarpa	E	0·009a	−0·059a	0·046a	0·026a	0·011a	−0·033a
Holcus lanatus	I	0·407ab	0·450a	0·296ab	0·249bc	0·103c	0·091c
Hydrocotyle novae-zelandiae	E	0·245a	0·184ab	0·133ab	0·067ab	0·015b	0·018b
Lachnagrostis lyallii	N	0·265a	0·061b	0·024b	−0·001b	−0·016b	0·099ab
Lagenifera pumila	E	0·194a	0·119ab	−0·010b	0·048ab	−0·037b	−0·026b
Lagurus ovatus	I	0·468a	0·504a	0·401a	0·340a	0·135b	0·038b
Lupinus arboreus	I	0·497a	0·454a	0·221b	0·049bc	0·005c	−0·050c
Phormium tenax	E	0·237a	0·105ab	0·186ab	0·058ab	−0·001b	−0·017b
Plantago triandra	E	0·222a	0·138ab	0·152ab	0·136ab	0·014b	0·019b
Poa pusilla	E	0·246a	0·047b	0·017b	0·044b	0·041b	−0·001b
Scirpoides nodosa	N	0·264a	0·256a	0·181a	0·225a	0·181a	0·019b
Senecio elegans	I	0·467a	0·462a	0·327ab	0·321ab	0·178b	−0·117c
Silene gallica	I	0·577a	0·537a	0·286b	0·146bc	0·054c	−0·041c
Triticum aestivum	I	0·608a	0·580a	0·482b	0·260c	0·148d	−0·020c
Wahlenbergia congesta	E	0·258a	0·113ab	0·025b	0·063b	−0·026b	0·002b

Significant effects ($P<0.05$): Sp, Tr, Sp × Tr.
Error M.S: 0·008512 (226 d.f.).
The status of the species is indicated by the code: I = Introduced; N = Native; E = Endemic to New Zealand. See text for which species were grown in 1·5% or 2·0% salt concentrations.
m = mature plants; a = seedlings.
For statistical effects: Sp = species; Tr = salt treatment.

more successfully than many dune species and was unaffected by very low levels of salt, but there was a significant reduction in the relative growth rate (RGR) at 0·5% salt (Table 1). Some plants were alive in 1% salt but in 1·5% nearly all died (Table 2). These results are similar to those obtained by Francois *et al.* (1986) and Partridge & Wilson (1988).

Table 2. Live material weight as a percentage of the total plant weight in a range of species when grown in six different concentrations of salt. For each species salinities with the same letter have a percentage live which is not significantly different ($P=0.05$). Format as for Table 1

Species		Salt treatments (%)					
		0·0	0·25	0·50	0·75	1·00	1·5 or 2·0
Acaena anserinifolia	E	98·5a	68·2a	0·0b	0·0b	0·0b	0·0b
Ammophila arenaria	I	92·0a	84·1a	81·2a	80·0a	72·4a	32·0b
Austrofestuca littoralis	N	82·4a	78·6a	71·7a	67·6a	64·2a	47·5a
Bromus diandrus	I	97·4a	94·8a	84·5ab	45·7b	5·5c	0·0c
Carex pumila	N	96·3a	91·9a	90·7a	83·7a	68·5a	32·9b
Centella uniflora	E	94·0a	57·4a	60·7a	0·0b	0·0b	0·0b
Colobanthus muelleri	E	66·4a	4·8b	0·0b	0·0b	0·0b	0·0b
Coprosma acerosa	E	100·0a	90·6ab	92·7ab	60·9bc	36·3cd	0·0d
Craspedia uniflora	E	77·8a	63·2ab	57·7ab	28·0bc	25·2bc	0·0c
Cyperus ustulatus	E	99·0a	94·6a	83·8a	80·1a	76·5a	32·0b
Desmoschoenus spiralis (m)	E	30·1a	25·7a	31·4a	9·1a	18·3a	17·5a
Desmoschoenus spiralis (s)	E	84·0a	77·7a	51·2a	57·0a	47·6a	4·6b
Elymus farctus	I	85·8a	92·0a	88·8a	88·3a	74·7a	63·0a
Gnaphalium audax	E	89·8a	60·5ab	45·6b	0·0c	0·0c	0·0c
Gnaphalium luteo-album	N	98·1a	98·2a	97·8a	96·5a	85·2a	0·0b
Gunnera albocarpa	E	55·4a	0·0b	0·0b	0·0b	0·0b	0·0b
Holcus lanatus	I	97·4a	88·6a	76·4ab	72·3ab	28·8b	0·0c
Hydrocotyle novae-zelandiae	E	96·1a	97·2a	91·6a	79·3a	23·3a	0·0b
Lachnagrostis lyallii	N	86·9a	35·8b	16·4b	5·0b	6·9b	7·0b
Lagenifera pumila	E	94·6a	90·9a	43·3b	46·3b	25·7bc	0·0c
Lagurus ovatus	I	96·9a	98·0a	93·7ab	81·7ab	57·2b	0·0c
Lupinus arboreus	I	96·4a	87·2a	37·0b	0·0b	0·0b	0·0b
Phormium tenax	E	97·5a	86·9a	87·4a	70·5ab	39·1bc	9·7c
Plantago triandra	E	91·8a	83·5a	79·3a	54·5ab	29·8bc	0·0c
Poa pusilla	E	94·0a	48·1b	24·8bc	25·1bc	4·8c	9·0bc
Scirpoides nodosa	N	98·4a	86·9a	95·0a	97·8a	97·0a	77·4a
Senecio elegans	I	99·1a	99·8a	99·6a	99·2a	90·5a	13·0b
Silene gallica	I	100·0a	98·4a	72·7a	27·8b	27·3b	0·0b
Triticum aestivum	I	95·6a	88·8a	86·6a	61·9b	34·6c	1·5d
Wahlenbergia congesta	E	94·7a	31·7b	11·8bc	0·0c	0·0c	0·0c

Significant effects ($P<0.05$): Sp, Tr, Sp × Tr.
Error M.S: 0·067750 (227 d.f.).

It is relatively easy to identify the extreme halophyte or extreme non-halophyte (glycophyte) but the boundary between the two is problematic (Chapman 1960). 'Glycophyte' has been defined as a plant that can tolerate up to 0·5% NaCl and 'halophyte' as a plant that can tolerate greater than 0·5% NaCl at any stage in its life cycle (Stocker 1928; Chapman 1942). Barbour (1970) defined an 'obligate halophyte' as a plant that requires more than 0·1% salt in the medium, although he found none. He considered a 'facultative halophyte' to be one which had optimal growth at moderate salinity. Barbour implied that no dune species were facultative halophytes. 'Intolerant halophytes' were those that showed optimal growth at low salinity. Partridge & Wilson (1988), in view of the tolerance of *T. aestivum*, suggested that the criterion for a halophyte should be survival at 1·0% over
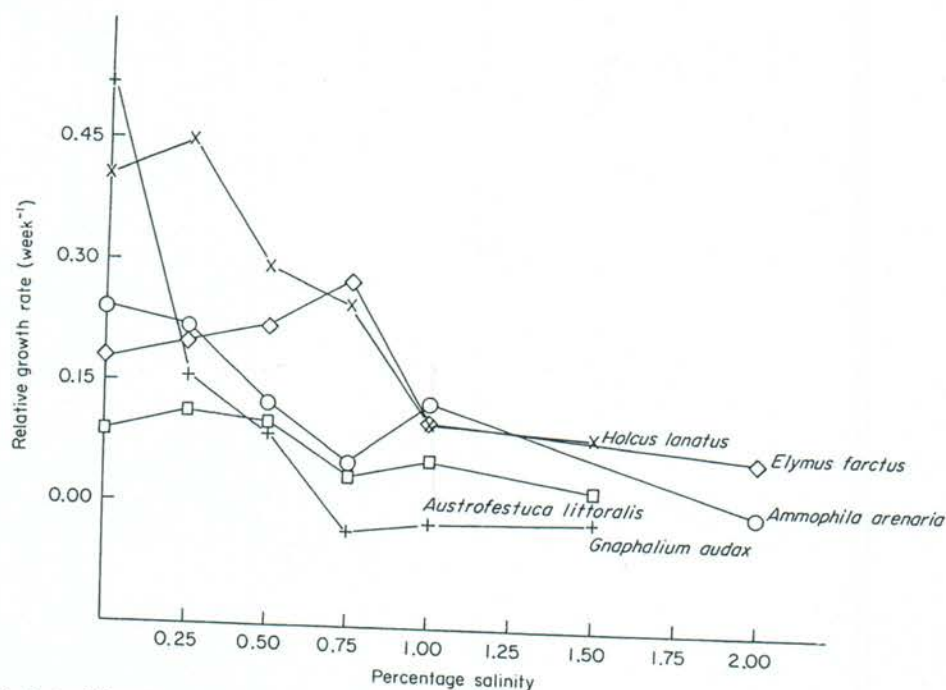
Fig. 1. Plots of the relative growth rate week⁻¹ against the percentage salinity for five of the experimental species based on the mean weight of four individual plants at each harvest. (×) *Holcus lanatus*, (◇) *Elymus farctus*, (○) *Ammophila arenaria*, (⊓) *Austrofestuca littoralis*, (+) *Gnaphalium audax*.
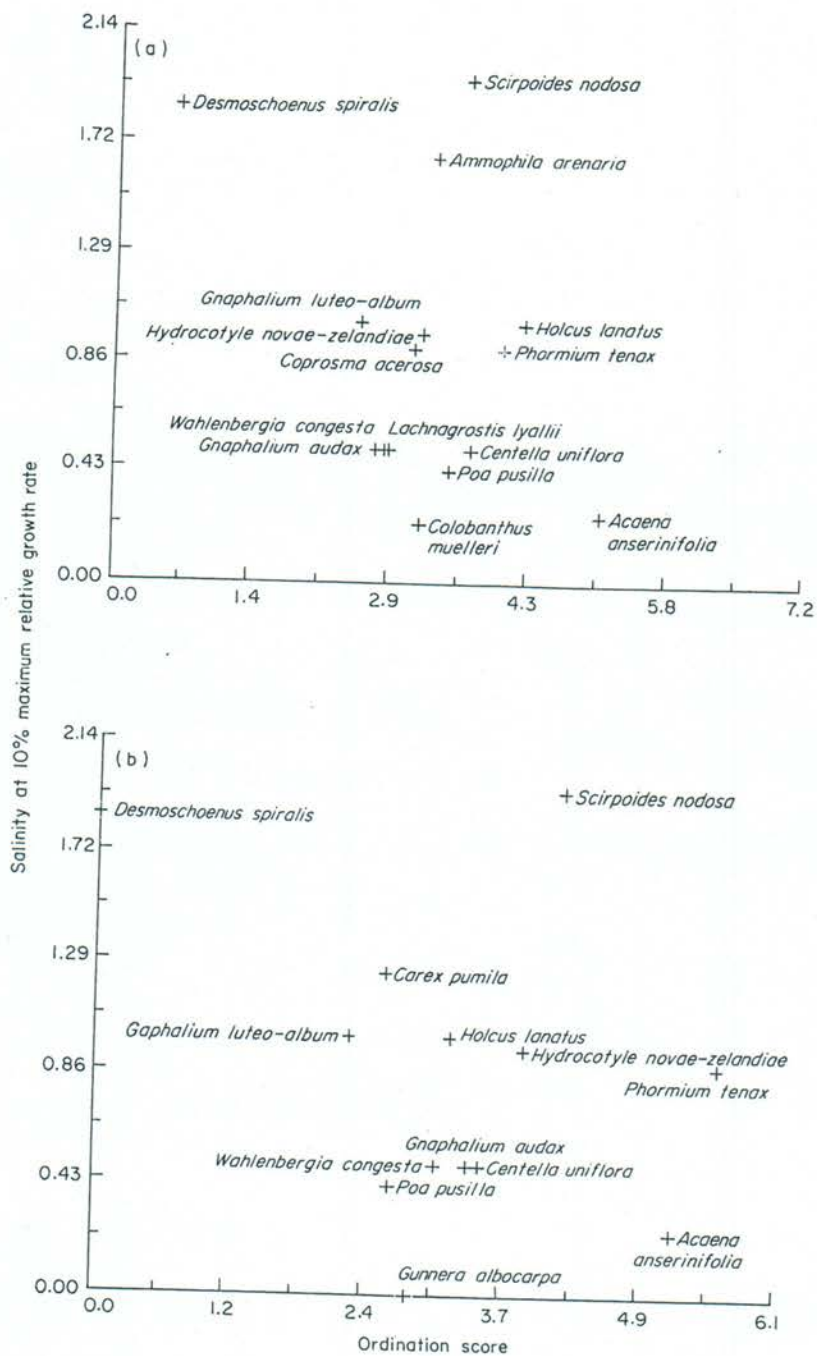
long periods. If this criterion is adopted for the dune plants tested, then many can only be classed as glycophytes.

Effects of salinity on dune species: RGR and live material

There was a general decrease in RGR with increased salinity (Table 1), though species differed significantly ($P = 0.05$) in their response. The percentage of live material (Table 2) generally decreased with increasing salinity, though again species differed in their response.

The most important variate for long-term survival is RGR. By this criterion, typical dune species were affected least by increased salinity. For example, the RGR of the exotic species *Elymus farctus* in 1% salt was still 78% of that in the control (Fig. 1). It was not significantly affected until a 2% salt level was reached, and the amount of live material was little affected (Table 2). This confirms the conclusion of Rozema *et al.* (1983) that *E. farctus* has 'considerable salinity resistance'. Benecke (1930) reports its cultivation in 6–7% salt, but in the present experiment some plants died in 2% salt. The period of inundation is probably the key to its survival in high salt concentrations. Tansley (1939) and Chapman (1964) suggested it can tolerate only short periods of inundation. There was an indication in the present experiment that the growth rate was maximal at 0·75% salt, though the difference from 0% was not significant. However, this would be the first indication of a salt requirement for *E. farctus*, which would put it in the facultative halophyte category of Barbour (1970).

Ammophila arenaria showed somewhat less tolerance to salt (Fig. 1). The plants all remained alive up to a concentration of 1%, with the proportion of live material being
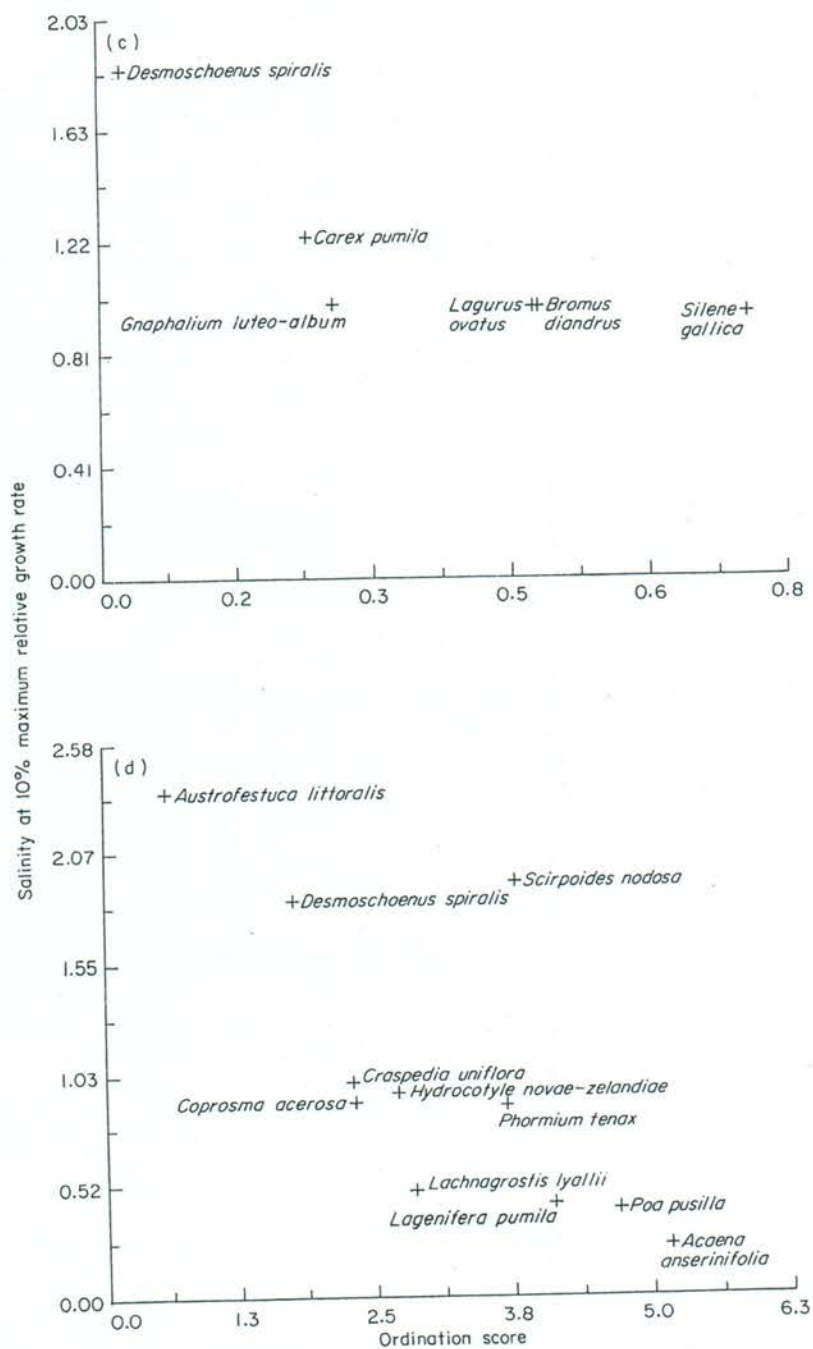
Salinity at 10% maximum relative growth rate

(a)

2.14
1.72
1.29
0.86
0.43
0.00

+Desmoschoenus spiralis   +Scirpoides nodosa

+Ammophila arenaria

Gnaphalium luteo-album
+
Hydrocotyle novae-zelandiae+   +Holcus lanatus
+   ÷Phormium tenax
Coprosma acerosa

Wahlenbergia congesta Lachnagrostis lyallii
Gnaphalium audax +++   +Centella uniflora
+Poa pusilla

+Colobanthus   +Acaena
muelleri   anserinifolia

0.0   1.4   2.9   4.3   5.8   7.2

(b)

2.14
1.72
1.29
0.86
0.43
0.00

+Desmoschoenus spiralis   +Scirpoides nodosa

+Carex pumila

Gaphalium luteo-album+   +Holcus lanatus
+Hydrocotyle novae-zelandiae
+
Phormium tenax

Gnaphalium audax
Wahlenbergia congesta+   ++Centella uniflora
+Poa pusilla

+Acaena
anserinifolia

Gunnera albocarpa
+

0.0   1.2   2.4   3.7   4.9   6.1

Ordination score

Fig. 2. Plots of the percentage salinity at which the growth rate was reduced to 10% of the maximum against ordination scores from four dune systems in southern New Zealand. Only those experimental species recorded at each of the four sites are used in each plot. (a) Cole Creek, West Coast, $r = -0.380$; (b) Ship Creek, West Coast, $r = -0.328$; (c) Kaitorete Spit, Canterbury, $r = -0.789$; (d) Mason Bay, Stewart Island, $r = -0.718$.

little affected. This confirms earlier studies of Benecke (1930), Salisbury (1952), Chapman (1964) and Seneca (1972).

The results from this study confirm the halophytic status of the latter two species, even using the restrictive Partridge & Wilson (1988) criterion.

About half the species in this study can, on the latter criterion, be classed as glycophytes in that they were no more tolerant than *T. aestivum*. These species were the native forbs *Acaena anserinifolia*, *Centella uniflora*, *Colobanthus muelleri*, *Gnaphalium audax*, *Gunnera albocarpa*, *Hydrocotyle novae-zelandiae*, *Lagenifera pumila* and *Wahlenbergia congesta*; the native grasses *Lachnagrostis lyallii* and *Poa pusilla*; and the native shrub *Coprosma acerosa*. Of the exotic species, *Lupinus arboreus*, and *Silene gallica* were the most glycophytic. Most of these species were intolerant of even low levels of salt, for example RGR in *G. audax* (Fig. 1) was much reduced in 0·25% salt and all the plants died in 0·75% salt.

Native species which can be classed as halophytic are the forbs *Craspedia pedicellata* var. *uniflora*, *Gnaphalium luteo-album* and *Plantago triandra*, cyperads *Cyperus ustulatus*, *Carex pumila*, *Scirpoides nodosa* and *Desmoschoenus spiralis*, the grass *Austrofestuca littoralis*, and *Phormium tenax*. Exotic halophytes were *Senecio elegans* L., and the grasses *Ammophila arenaria*, *Bromus diandrus*, *Elymus farctus*, *Holcus lanatus* and *Lagurus ovatus*. The most salt tolerant native species proved to be *Desmoschoenus spiralis*, *Austrofestuca littoralis*, *Cyperus ustulatus*, *Carex pumila* and *Scirpoides nodosa* (e.g. *A. littoralis* Fig. 1); in all of these, some plants survived in 2% salt.

The native sand-binder *D. spiralis* was tolerant of 2% salt; growth was reduced, but plants were still alive. It seemed more tolerant of root-salinity than the exotic *Am. arenaria* with which it often competes. Seedlings may be marginally less tolerant to higher concentrations than mature plants. Salinities greater than 1% prevented flowering.

The exotic halophytes were all grasses except for *S. elegans*, a species of South African dunes (Lubke 1983). Moderate levels of salinity seemed to affect this species little, and it remained quite healthy in 1% salt. At higher concentrations there was chlorosis, though plants survived through the experimental period. It had somewhat fleshy, succulent leaves. Succulence has been considered as a mechanism for salt tolerance in dune plants (Boyce 1951).

Members of the grass family (Poaceae) are among the dominant families of halophytic vegetation (Waisel 1972) and most of the exotic grasses sampled in this study are halophytic. Cliff ecotypes of *Holcus lanatus* have been reported as salt tolerant (Chapman 1964; Watt 1983). It seems that dune populations of *H. lanatus* are also salt tolerant (Fig. 1). Two other grasses, *Bromus diandrus* and *Lagurus ovatus*, are both weedy annuals and this, coupled with moderate salt tolerance, must be advantageous in the sand dune environment.

Correlation with field position

We (in preparation) sampled four dune systems in southern New Zealand for vegetation distribution. The first vegetation gradient (axis) from ordination of each site could be interpreted as proximity to the sea, an environmental complex involving salt, exposure, wind etc. The species scores from these ordinations have been plotted against results from this study (Fig. 2) using the salinity at which the growth rate was reduced to 10% of maximum as the tolerance criterion.

At Cole Creek, on the West Coast of the South Island, fifteen of the experimental species were recorded. There was no significant correlation between salt tolerance and

field position ($r = -0.380$, $P > 0.05$). Some salt-tolerant species such as *D. spiralis* occur at the front dune ridge. Others such as *Sc. nodosa*, a species common in dune slacks (Sykes & Wilson 1987), were found further from the sea than would be expected from their salt tolerance. We suggest that tolerance of sand burial may limit this species' distribution. *Am. arenaria* was not found as close to the sea as might be expected, probably because it had only recently invaded the dune system. Many species, particularly native herbs, occurred closer to the sea than their tolerance to root-salinity would suggest. Some of these, however, (for example the herbs *Wahlenbergia congesta* and *Lagenifera pumila*) are restricted almost entirely in their distribution to coastal areas. It may be that in areas of high rainfall such as this (3455 mm year^{-1} at Haast), soil salinity is rarely a problem. None of these species were recorded on the drier east coast sample site.

At Ship Creek, 2 km south of Cole Creek, the correlation was also non-significant ($r = -0.328$). *Sc. nodosa* was again found well to the rear, along the scrub edge.

Mason Bay, on Stewart Island, has an extensive and very mobile system of dunes. Eleven of the experimental species occurred and their salt tolerance showed a significant correlation with field position ($r = -0.718$, $P < 0.05$). Those species shown to be root-salinity tolerant were found in the most exposed areas.

At Kaitorete Spit, Canterbury, the tolerance/field-position correlation was high ($r = -0.789$) but, because only six experimental species were found there, this was non-significant ($P > 0.05$). However, most of the species found there do seem to have root-salinity responses which correspond fairly well to their site position. Sykes & Wilson (1988) also noted that salt-spray tolerance correlated with species distributions at this site. Rainfall is low (515 mm year^{-1}) with extended dry periods. It must be presumed that intermittent high soil salinities occur as a result of high tides or storms with subsequent summer droughts. Berger & Heurteaux (1985) reported a 25-fold increase from winter to summer soil salinity on sand dunes in the Camargue.

New Zealand sand dunes contain both species intolerant of salt and species tolerant of salt. The classification into halophytic and non-halophytic is often arbitrary but even the most restrictive criterion gives a fairly even distribution of the experimental species into each category. This suggests that whilst root-salinity is important for dune species it is only one of a complex of environmental factors that determines whether a species can survive in the dune environment, and that determines the chorology of those that can.

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