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AIRBORNE AND SOILBORNE SALINITY AND THE DISTRIBUTION OF COASTAL AND INLAND SPECIES OF THE GENUS ELYTRIGIA

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SUMMARY

Salt-spray was estimated along a gradient in a coastal beach and dune system on the Island of Schiermonnikoog by analyzing the chemical composition of rain. The annual airborne input of NaCl on the beach amounts to 1460 kg NaCl/ha.year, which decreases to 150 kg NaCl/ha.year at a distance of 2 km landinwards.

Elytrigia junceiformis (foredunes), *E. pungens* (salt-marshes) and *E. repens* (inland sites) were compared in their response to varied levels of salinity in the rooting medium and of airborne salinity. *E. pungens* was most resistent, *E. junceiformis* intermediate and *E. repens* the most sensitive to high soil salinity, while *E. junceiformis* was most resistent to salt-spray, with *E. repens* being more sensitive. Resistence to salt-spray in these species seems to be based on exclusion of foliar ion uptake. The role of the leaf structure and the epicuticular wax layer is discussed.

1. INTRODUCTION

The ecology and physiology of plant species in coastal vegetations, have been thoroughly studied and widely reviewed (WAISEL 1972, FLOWERS et al. 1977, ALBERT 1982). The major part of halophyte studies deals with effects of salt absorbed via the root system, while effects of airborne salt and foliar ion uptake are less well-known. Measurements of the distribution of airborne salt are relatively scarce and although the unfavourable effects of salt-spray on plants and trees near coasts are well-known, only a few detailed studies on the effects of salt spray on wild-plant growth have been published (OOSTINGS & BILLINGS 1942, BOYCE 1954, EDLIN 1957).

OOSTING & BILLINGS (1942) concluded that the zonation of coastal species could be explained by differential tolerance to wind-borne salt. Other authors emphasize that apart from negative effects of NaCl to plant growth, sea water minerals form a significant input in the mineral cycles of coastal ecosystems (CLAYTON 1972).

Within the genus *Elytrigia*, three species commonly occur in Western Europe. *Elytrigia junceiformis* A. D. Löve colonizes and stabilizes embryo dunes. *E. pungens* (Pers.) Tutin inhabits upper levels of saltmarshes, while *E. repens* (L) Desv. (nomenclature follows HEUKELS & VAN OOSTSTROOM 1977) is an inland species from ruderal sites. It is expected that not only variation in the species response

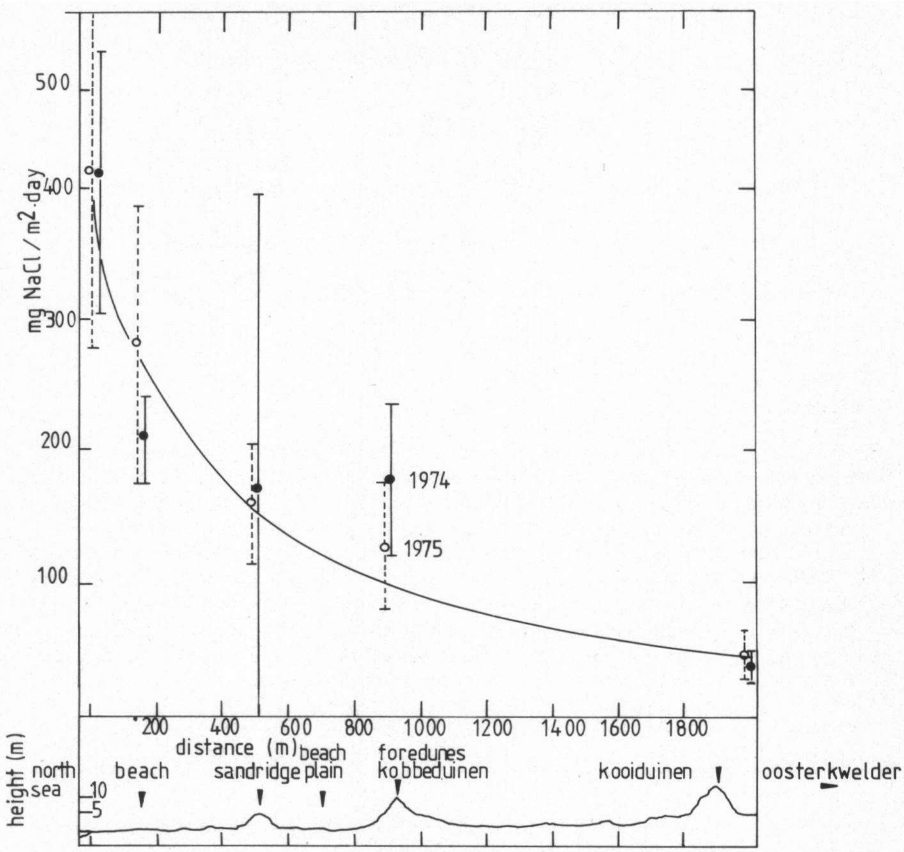

Fig. 1. Salt-spray collected in raingauges in relation to distance from the North Sea on the Island of Schiermonnikoog. Average values of week samples in the period May–October 1974 and 1975, with bars representing the standard error of the mean. Below a schematized geomorphological profilel of the gradient.

to soil salinity but also differential adaptation to salt-spray contributes to the understanding of the differences in the habitat preference of the three *Elytrigia* species.

The aim of the present paper is twofold: to report measurements of salt-spray in the habitats of the *Elytrigia* species, and to consider possible causes of the differences in the habitats by comparing the effects of airborne and soilborne salinity in greenhouse experiments.

2. MATERIAL AND METHODS

2.1. Salt-spray

Salt-spray was estimated analysing both the amount of precipitation and the chemical composition of the rainfall catch in special chemical raingauges (catch area 400 cm^2). The raingauges were installed at a height of 1.5 m above the soil surface along a transect ranging from the North sea beach to a dune valley as indicated in *fig. 1*. Salt-spray data reported here refer to measurements made from May–October in 1974 and 1975. Precipitation in the gauges was collected weekly, except in the case of storms, when collection took place daily or more frequently in order to relate the chemical composition of the precipitation to these meteorological factors.

2.2. Plant growth

Caryopses of *Elytrigia junceiformis* (foredunes), *E. pungens* (upper levels in saltmarshes) were collected on the Island of Schiermonnikoog (53°19′, 6°12′) and those of *E. repens* Desv. from a ruderal site near the Free University, Amsterdam. They were stored dry (20 °C) and then germinated on moist filter paper (20 °C, 12 h light, 12 h dark). The seedlings were transplanted in plastic trays (30 × 30 × 15 cm^3) filled with 2700 g Norh Sea dune sand mixed with 700 g commercial garden soil (Calceolaria No. 1) (ROZEMA et al. 1982) and were irrigated with 0.1 strength Hoagland solution (HOAGLAND & ARNON 1950).

2.3. Airborne salt

Salt-spray was produced using a commercial indoor plant sprayer filled with North Sea water collected near Egmond aan Zee (ROZEMA et al. 1982). It was applied every two days for 2½ months, to such an extent, that 450 mg NaCl per m^2 per day was deposited, which is about twice the salt spray level measured on the foredunes of Schiermonnikoog (*fig. 1.*). Soil salinization was avoided by covering the soil surface with three layers of filter paper during the spray treatment. Control plants were sprayed with distilled water.

2.4. Soil-borne salt

The effects of soil salinity were studied in aerated hydroculture with 0.25 strength Hoagland's solution with NaCl (0, 150, and 300 mM NaCl) added stepwise during two weeks to avoid an osmotic shock. Thirty plants were used per treatment. For measurements of the mean relative growth rate $\bar{R}$, 10 plants were harvested after two weeks (t_1); the remaining plants were harvested after another four weeks of growth (t_2). Chemical analysis was according to methods described elsewhere (ROZEMA et al. 1982). Epicuticular wax was removed from the shoot by immersion of 4 g fresh leaves in 25 ml chloroform for 10 s. The extract thus obtained was filtered and evaporated to dryness and the remaining wax was weighed (BAKER 1974).

3. RESULTS

3.1. Salt-spray

Measurements of the deposition of sea salt in raingauges sampled in the period May to October 1974 and 1975 on the Island of Schiermonnikoog are summar-

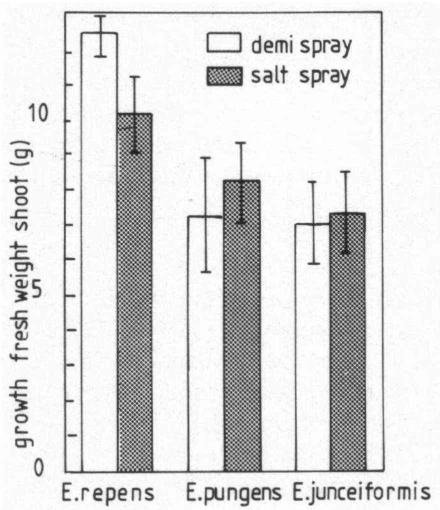

Fig. 2. Effect of salt-spray on the shoot growth of seedlings of three *Elytrigia* species. Average values of 15 replicates with standard error of the mean.

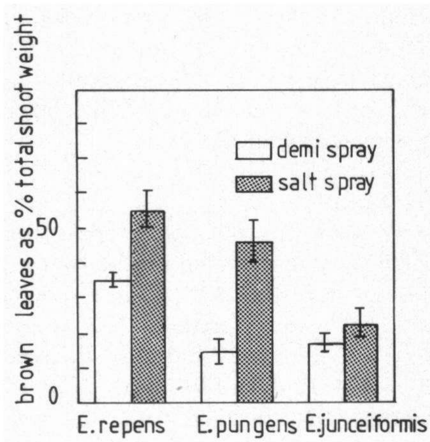

Fig. 3. Effect of salt-spray on the percentage of brown leaves expressed as a percentage of the total fresh weight (g) of the leaves. Average values of 15 replicates with standard error of the mean.

ized in *fig. 1*, which gives mean values over 19 intervals of 7 days with the standard error of the mean. There is a steep gradient in the deposition of sea salt, with high values (400–200 mg NaCl/m^2.day, which equals 1460–730 kg NaCl/ha.year) on the beach and the foredunes, the habitat of *Elytrigia junceiformis*. The salt marsh Oosterkwelder, the habitat of *Elytrigia pungens*, is located on the eastern part of the Island of Schiermonnikoog 2–3 km from the North Sea. There is considerable seasonal variation in the salt-spray levels as indicated by the standard error of the mean. The seasonal variation is particularly marked at the post on the beach, where the salt spray level could be enhanced by a factor of four during periods of storms. During storms the slope of the salt-spray gradient from the sea to the land was steeper than usual. As storms and storm-surges along the North Sea coastline prevail in the winter, the values presented in *fig. 1* underestimate salt-spray on a yearly basis. On the other hand, the above values from the period May to October refer to the time of active growth of coastal vegetation, and are thus more relevant from an ecological point of view.

3.2. EFFECTS OF SALT-SPRAY ON PLANT GROWTH

Differences in the effect of salt-spray on shoot growth are relatively small between the species (*fig. 2*); salt-spray reduces the fresh weight of the shoots of the inland species *Elytrigia repens* somewhat more, relative to the other species. Analysis of the leaves revealed however, that more than 50 percent of the salt

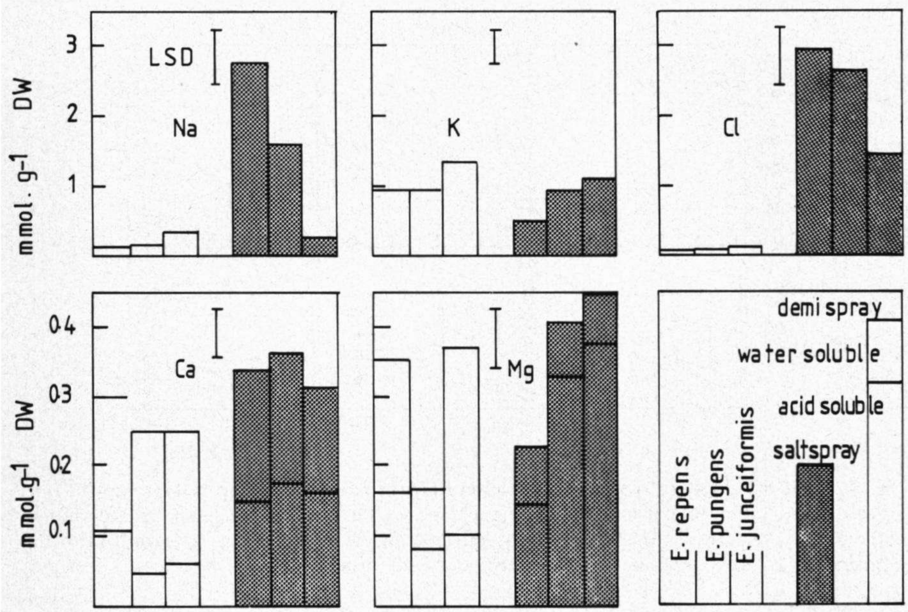

Fig. 4. Effect of salt-spray on the concentration of Na^+, Cl^-, K^+, Ca^{2+} and Mg^{2+} in the shoot of three *Elytrigia* species. Average values of 5 replicates.

sprayed *Elytrigia repens* shoot consisted of dead leaves, while the percentage of dead leaves on control plants was 35 percent. The percentage of dead leaves from the control plants of *E. junceiformis* was lower and did not increase under salt-spray (*fig. 3*). The percentage of dead leaves in *E. pungens* increased from 14 (control plants) to 45 percent in salt-sprayed plants. From *fig. 3* it may also be concluded that the inland species has a higher growth rate compared to the coastal species. The relatively high percentage of dead leaves on *E. repens* control plants further suggests a high leaf turn-over rate. Obviously the longevity of *E. repens* leaves is even more reduced by salt-spray compared to *E. junceiformis*. There are significant differences between the species in the concentration of the mineral elements Na^+, K^+ and Cl^-, which, to a lesser extent, also holds for Mg^{2+} and Ca^{2+} (*fig. 4*). The low Na^+ content of the control shoots of all three species is similar, but under the influence of salt-spray, the inland species accumulates up to 2.76 mmol $Na^+ . g^{-1}$DW, while there was no such significant increase in *E. junceiformis*, *E. pungens* taking in an intermediate position. *E. repens* and *E. pungens* absorbed more Cl^- than *E. junceiformis* under salt-spray. The K^+ level in the shoots of the inland species seems to be more depressed by salt-spray than in both coastal species.

Application of salt-spray enhances Ca^{2+} and Mg^{2+} concentrations in the leaves, and this effect is mainly based on an increase of the acid-soluble fraction of Mg^{2+}.

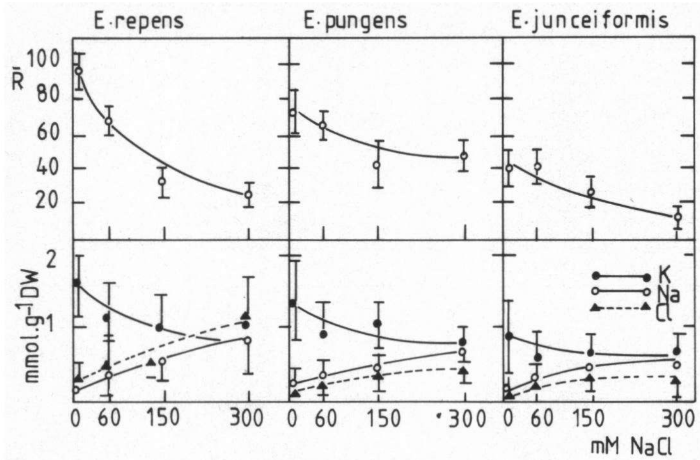

Fig. 5. Effect of salinity in the nutrient solution (mM NaCl) on the mean relative growth rate $mg.g^{-1}.day^{-1}$ (of the total plant) of three *Elytrigia* species. Below Na^+, Cl^- and K^+ concentration of the shoot as influenced by increased salinity of the rooting medium. Average values of 10 (growth) or 5 (mineral elements) replicates with standard error of the mean.

3.3. Effects of salinity of the rooting medium on plant growth

There is a marked difference between the species in their growth on hydroculture with salinity increased to 300 mM NaCl (*fig. 5*). The mean relative growth rate (R) of *E. repens* is higher than that of *E. junceiformis*, *E. pungens* being intermediate. At 300 mM NaCl the $\bar{R}$ of *E. pungens* is the least reduced (67 percent of the control (0 mM NaCl)), relative to a reduction of 27 percent and 40 percent in *E. repens* and *E. junceiformis* respectively. The percentage of dead leaves in the control and sprayed plants never exceeded 10 percent of the shoot fresh weight in any of the three species in the hydroculture experiment at harvest time (*fig. 3*).

Taking into account the salinity of the rooting medium, the salt marsh species *E. pungens* is most resistent, the inland species *E. repens* relatively salt sensitive and *E. junceiformis* from the embryo dunes has an intermediate position.

The shoot tissue concentration of methylated quaternary ammonium com-

Table 1. Shoot tissue concentration of dry weight of methylated quaternary ammonium compounds, expressed as glycine betaine equivalents (μmol/g dry weight) of three *Elytrigia* species under increased salinity of the rooting medium and under salt-spray. Average values of four replicates with standard error of the mean.

Species	Salinity rooting medium (mM NaCl)		Demi spray	Salt-spray
	0	300		
Elytrigia repens	82.0 ± 8.9	112.8 ± 7.9	94.5 ± 4.7	93.9 ± 8.6
Elytrigia pungens	80.2 ± 10.4	127.0 ± 4.3	97.1 ± 6.7	105.2 ± 9.8
Elytrigia junceiformis	54.6 ± 13.2	149.8 ± 7.2	123.1 ± 10.4	112.4 ± 10.8

Table 2. Transpiration rates mg H_2O/g fresh leaf. min of three *Elytrigia* species as influenced by increased salinity of the nutrient solution. Average values of four replicates with standard error of the mean.

Species	Salinity (mM NaCl)	
	0	300
Elytrigia repens	2.03 ± 0.09	0.42 ± 0.06
Elytrigia pungens	1.54 ± 0.12	0.38 ± 0.04
Elytrigia junceiformis	1.54 ± 0.06	0.33 ± 0.02

Table 3. Total amount of epicuticular wax (μg cm^2 leaf surface) of three *Elytrigia* species with increased salinity of the rooting medium and exposed to salt-spray. Average values of four replicates with standard error of the mean.

Species	Hydroculture salinity (mM NaCl)				Potculture control	saltspray
	0	60	150	300		
Elytrigia repens	18.0 ± 3.1	20.1 ± 2.4	22.2 ± 2.8	19.8 ± 3.0	25.3 ± 2.8	23.9 ± 1.8
Elytrigia pungens	20.6 ± 4.1	28.2 ± 3.5	43.0 ± 5.2	66.9 ± 5.4	64.7 ± 2.6	71.2 ± 2.1
Elytrigia junceiformis	61.2 ± 5.1	65.9 ± 4.8	59.6 ± 5.2	73.5 ± 4.5	49.5 ± 2.3	57.4 ± 3.1

pounds increases under salt stress in all three *Elytrigia* species (*table 1*) when salt is absorbed from the rooting medium, but not when sprayed on the shoot At 0 mM NaCl water loss through transpiration is highest in *E. repens* and relatively low in *E. junceiformis*, but the degree of depression of the transpiration rate to 20 percent under 300 mM NaCl salt stress is the same in all three (*table 2*). The amount of epicuticular wax, expressed as μg wax/cm^2 leaf surface, was highest in *E. junceiformis* in the hydroculture salinity experiment. The amount of epicuticular wax on *E. junceiformis* did not increase with increasing salinity, contrary to *E. pungens*, where the amount of epicuticular wax was higher at high salinity, while the colour of the leaves changed from bright green on 0 mM NaCl to greyish green at 300 mM NaCl (*table 3*). The amount of leaf wax was relatively low in *E. repens* and was not influenced by increased salinity, while both coastal *Elytrigia* species had more wax on their leaves than the inland species.

4. DISCUSSION

Chemical analysis of rainwater and salt spray collected weekly during six months in the summer showed a sharp NaCl gradient in the raingauges in a seaside – land transect over 2 km length. Similar steep gradients were reported by BOYCE (1954), ETHERINGTON (1967), SLOET VAN OLDRUITENBORGH & HEERES (1969),

Table 4. Airborne and soilborne salinity in the habitats of three *Elytrigia* species.

	E. repens	*E. pungens*	*E. junceiformis*
Airborne salinity kg NaCl/ha.year	50*	150*	1500*
Soilborne salinity (mM NaCl in the soil moisture)	6***	280**	40**

Rounded off values from *fig. 1*, this paper (*), ROZEMA et al. 1982 (**), ROZEMA 1978 (***).

VAN DER VALK (1974), TSUNOGAI (1975) and VERMEULEN (1977). Measuring the distribution of air-borne salt in Wales, EDWARDS & CLAXTON (1964) found deposition of salt on the windward side of a hedgerow to be four times the amount on the leeward side. In a larger scale survey of salt-spray along the coast of North-Holland VERMEULEN (1977) measured 66 mg Cl^{-}/m^{2}.day 1 km inland, which roughly equals to 375 kg NaCl/ha.year. He also measured a very steep decrease between 1 and 2 km from the sea, comparable to *fig. 1* of the present paper, and a more gradual decrease further away, with at 50 km from the North Sea deposits of some 50 kg NaCl/ha.year. Measurements of the sea spray in the immediate vicinity of foredunes on the US West coast by VAN DER VALK (1974) amounted to 2350 kg NaCl/ha.year, which is higher than the estimation of 1460 kg NaCl/ha.year relating to the Dutch Waddencoast in the present paper. Our salt-spray measurements imply that salt-spray deposition is highest in the habitat of *Elytrigia junceiformis* (foredunes), and that there is a lower level of seaspray in the salt-marsh habitat (*E. pungens*), while salt-spray is lowest in inland sites (*E. repens*).

BOYCE (1954) has described zonation of coastal vegetation, as the "salt spray community" and it is reasonable to expect that this zonation is the expression of differential sensitivity of plant species to injurious effects of aerosol salt. Other authors indicate that salt spray forms an important input into the mineral cycle of otherwise nutrient-poor sand dunes and other coastal soils (CLAYTON 1972). ETHERINGTON (1967) could show that potassium was not deficient in soils of the Welsh coast due to the incoming salt-spray and the same holds for all micronutrients. ROZEMA et al. (1982) showed that the growth of salt-tolerant Chenopodiaceae, amongst which was *Salsola kali*, was enhanced by seawater spray.

The differences in the distribution of the three *Elytrigia* species compared in this study cannot completely be ascribed to differences in sensitivity to soil salinity. The soil salinity (280 mM NaCl) is much higher than that (40 mM NaCl) of the foredune habitat of *E. junceiformis* and that (6 mM NaCl) of the inland sites habitat of *E. repens* (*table 4*). The relatively high resistence of *E. pungens* to increased soil salinity is in accordance with the high soil salinity of the natural habitat. *E. junceiformis* is less resistent to soil salinity, but at 300 mM NaCl 40% of the growth at 0 mM NaCl was achieved, reflecting considerable salinity resistence. This was already recognized by BENECKE (1930), who noticed that *Ammophila arenaria* from higher dunes with roots in contact with a fresh water lense, was less resistent to soil salinity than *E. junceiformis*.

In the present paper *E. junceiformis* showed to be better adapted than the other species to an abiotic factor operating in addition to soil salinity in the foredune habitat, that is to airborne salt. A strongly reduced uptake of Na^+ and Cl^- was shown in the leaves of the salt-spray resistent *E. junceiformis*, to a lesser extent in *E. pungens* and the least in *E. repens*.

This finding is in accordance with the low "Na^+ retention capacity" in addition to a smaller contact angle of seawater droplets with the leaf surface reported for spray zone populations of *Agrostis stolonifera* (AHMAD & WAINWRIGHT 1976). The degree of reduction in the transpiration rate induced by increased salinity of the rooting medium (300 mM NaCl), which probably reflects stomatal closure, was about the same in the three species and does therefore not help to clarify the observed difference in foliar ion uptake. Probably it is not so much the amount of epicuticular wax as the structural composition of the wax layer as suggested by AHMAD & WAINWRIGHT (1976), reporting the presence of upright flakes of wax which is of importance in salt-spray adapted populations of *Agrostis stolonifera*. In conclusion, it appears that the occurrence of the three *Elytrigia* species from three different habitats can reasonably well be explained on the basis of two abiotic factors operating in combination: soil salinity and salt-spray. Both contribute to the exclusion of the sensitive *E. repens* from coastal sites, while it must be salt-spray that prevents *E. pungens* from entering the foredune habitat, which should otherwise be possible on the basis of its high resistence to soil salinity. On the other hand, *E. junceiformis* is well adapted to salt-spray and sufficiently well to the low soil salinity prevailing in its natural habitat, but is less sensitive to soil salinities occurring in salt marshes, providing a competitive advantage to the rapidly growing *E. pungens*.

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