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GROWTH OF THREE MEADOW SPECIES ALONG A SALINITY GRADIENT IN AN INLAND SALINE HABITAT: TRANSPLANT EXPERIMENT

ABSTRACT: The mechanisms of vegetation zonation were determined in order to provide an advice for restoration of natural saline habitats. Field experiments were conducted to examine the response of mature plants to different edaphic conditions. Three dominant species *Salicornia europaea* L., *Puccinellia distans* (L.) Parl. and *Elymus repens* (L.) Golud, characteristic of distinct zones along the salinity gradient (EC_e 28.5–2.3 m Scm^{-1}) were studied. Results from a 2-year reciprocal transplant experiment demonstrated that species were restricted to every zone mostly by a salinity level. The obligatory halophyte *S. europaea* had optimal growth conditions at its home site. This is an opposite result to the one known from inland salt marshes of North America. A distinct growth limitation of transplants was observed in the *P. distans* and *E. repens* zones of lower salinity. Fewer individuals and lower above-ground biomass were recorded in the *P. distans* zone, whereas in the *E. repens* zone all seedlings died in the second year of observations. The glycophyte *E. repens* from the less saline site (*ca* 2.3 mS cm^{-1}) was strongly inhibited in the most saline *S. europaea* zone (15.8–28.5 mS cm^{-1}). Compared to the control transplants in the *S. europaea* zone it had shorter new shoots, fewer and shorter shoots, lower above-ground biomass and biomass of rhizomes. The *P. distans* transplants were markedly limited in the *E. repens* zone of lower salinity. Fewer and shorter new shoots, flowering shoots, lower above-ground biomass and biomass of grasses' roots were noted in the transplants of this zone. Since *P. distans* was found in non-saline areas outside the investigated meadow this effect could not result from the salinity level but from *E. repens* interaction. The obtained results suggest that for restoration of natural saline habitats the most important is to keep or rebuild the original salinity level of soils. As the second point the control of strong competitors by cutting or grazing should be considered.

KEY WORDS: halophytes, soil salinity, transplant experiment, zonation

1. INTRODUCTION

Vegetation zonation in coastal and inland saline habitats has been noted in a number of studies (Chapman 1974, Ungar 1974, Bertness and Ellison 1987, Adam 1990). Early works identified the importance of physiological tolerance in structuring the distribution of plants along physical gradivents (Whittaker 1956, Hutchinson 1957, Chapman 1974). More recent studies have focused on the role of biotic interactions (Ungar 1998), impact of parasites (Pennings and Callaway 1996) and herbivores (Miller *et al.* 1996), management by grazing and cutting (Bakker 1989, Bakker and de Vries 1992, Kiehl *et al.* 1996). In coastal ecosystems field experiments have indicated that environmental variation, disturbance and interspecific interactions are all important factors in the formation of vegetation zones (Snow and Vince 1984, Bertness and Ellison 1987). Relatively fewer studies have been done on inland saline systems (Ungar *et al.* 1979, Kenkel *et al.* 1991, Keiffer *et al.* 1994). However, in general the best competitors are believed to dominate the least stressful regions along physical gradients and to displace more poorly competing species to more stressful habitats (Ungar *et al.* 1979, Keiffer *et al.* 1994).

In inland saline habitats in Central Europe very often three vegetation zones are observed along the salinity gradient (Wilkoń-Michalska 1963, Piernik *et al.* 1996, Westhus *et al.* 1997, Brandes 1999). The most saline places are taken by *Puccinellio distantis association Salicornietum brachystachyae* dominated by annual *Salicornia europaea*. The next zone is often formed by *Puccinellio-Spergularietum salinae* where *Puccinellia distans* is the most dominant species. The third zone is relatively often dominated by the *Elymus repens* community. In Poland such zonation in natural saline places in surroundings of salty springs, connected with cechstein rock salt, were described in the Kujawy region in Central Poland (Szulczewski 1954, Wilkoń-Michalska 1963, 1970). In the second half of the 20th century many saline places became impoverished both in area and in species richness as a consequence of changes in the ground water level (meliorations) or activity of salt springs. Actually patches dominated by *S. europaea* (*Puccinellio distantis-Salicornietum brachystachyae*) occur only in the industry area next to soda factories. Nevertheless, there is still a chance to restore this community and the vegetation zonation in natural places, especially that inland saline habitats are designated as prior ones in Europe and included in the NATURA 2000 network. Mechanisms of vegetation zonation should be recognised to make a proper scenario for restoration. Therefore, as a first step in this direction, a transplant experiment was carried out to determine whether site conditions restrict each dominant species to its usual zone of occurrence.

2. METHODS

2.1. Study area

The research was done in the Kujawy region in Central Poland (between 52–53° N and 18–20° E) on the saline meadow in the vicinity of the soda factory in Janikowo (Fig.1). The factory has been working since 1957. Wastes of soda production are collected in open sediment traps next to the factory (Abramski and Sobolewski 1977). As a result of inappropriate tightening of sediment traps' bottoms, wastes infiltrate into the soil, causing soil alkalisation and salinity (Cieśla and Dąbkowska-Naskręt 1984, Czerwiński *et al.*1984). For the experiment the largest meadow with the distinct zonation pattern was selected. The meadow was isolated from the border of the setting tank by a road. On one side it was surrounded by a ditch, on the other side it bordered with an arable field located slightly higher. The middle part of the meadow was located lower and slightly sloping up towards borders. Three vegetation zones were distinguished along the salinity gradient: *Salicornia europaea*, *Puccinellia distans* and *Elymus repens* zone.

2.2. Data collection

In each zone 15 vegetated soil-blocks (25×25×25 cm) were randomly dug out in May. Five of those blocks were randomly replanted at the same site to serve as controls. The remaining 10 blocks were transplanted to the other two zones, five at each site. To minimise the effects of between-species competition, a 20-cm zone around each transplant was cleared every four weeks from May to the end of October during two growing seasons of the experiment. In order to monitor the growth of plants *in situ*, five 25×25 cm areas were designated in each garden.

Growth and development of *P. distans* and *E. repens* transplants were recorded at the beginning of August in each of the two observation years by measuring the number of shoots, number of flowering shoots, number of new shoots and for 50 randomly selected individuals – shoots' height and new shoots' height. For *S. europea* transplants, measurements were taken at the beginning

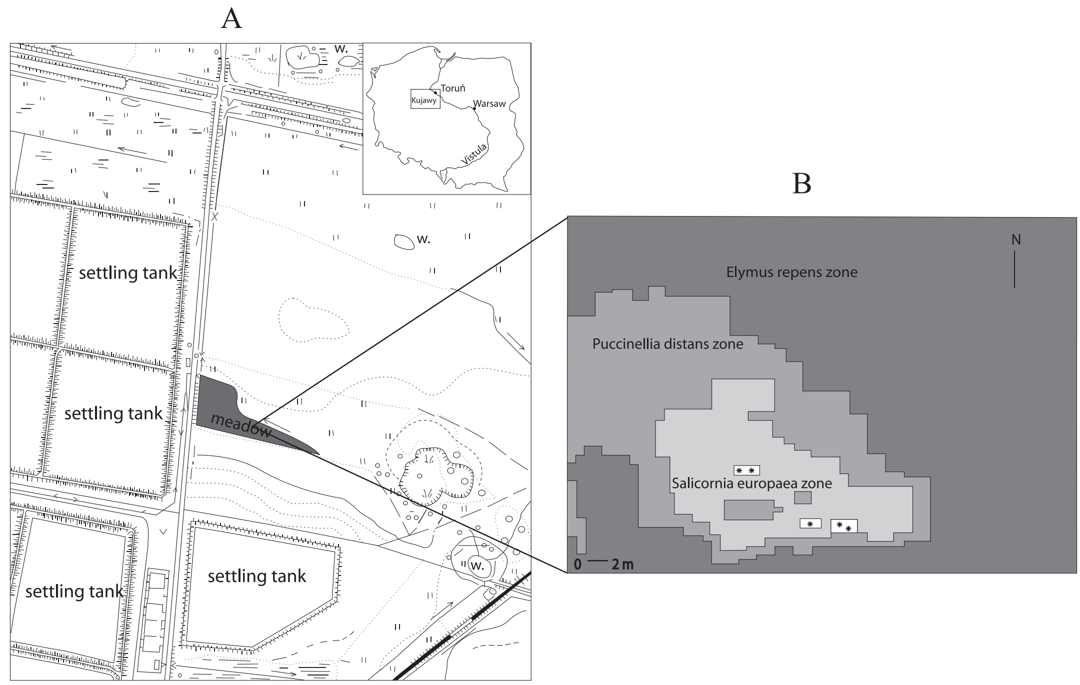

Fig. 1. Location of the study area: A – saline meadow close to the setting tanks of soda factory in Janikowo (Kujawy Region), B – distribution of three vegetation zones on an area of *ca* 1020 m^2. * – single individuals of *Salicornia europaea*, other signs according to standard topographical map.

of September. On each transplant the number of individuals was counted and for 50 randomly selected individuals the height of main shoots, the number of the first order and second order lateral shoots, and the number of 'ears' was recorded.

In the second season after transplantion, *E. repens* and *P. distans* transplants were dug out again at the beginning of August and *S. europaea* at the beginning of September. Above- and below-ground dry biomass of the species was determined.

During the experiment, soil samples (0–25 cm) were taken in each vegetation zone and their properties were determined. The moisture content of the soil was determined by weighting the samples before and after drying at 105°C. The air-dried samples were sieved through a 1.02 mm mesh, after which the following parameters were estimated: the organic matter content by deflagration at 550° C, total nitrogen by the Kjehdahl's method and electrical conductivity of saturated extracts (EC_e) by a conductivity meter. EC_e is the main measure of soil salinity in soil science. In the soluble extracts (1:5, soil to distilled water) the following parameters were analysed: pH by the potentiometric method, EC by a conductivity meter, Ca^{2+}, K^+, Na^+ by the photo-flame method, Mg^{2+} by the atomic absorption spectrophotometer, HCO_3^- with 0.01 n H_2SO_4 using methyl orange indicator, SO_4^{2-} by the nephelometric method, Cl^- with 0.1 n $AgNO_3$ using $K_2Cr_2O_7$ indicator were determined. The content of anions and cations are given in percentages (g 100^{-1} g dry soil). Total dissolved salts were calculated by summing up anions and cations. Furthermore, the Ca^{2+}:Na^+ ratio and Cl^- concentrations (%) in the soil water were calculated.

Statistically significant differences between means of the measured parameters of the transplanted species were assessed by ANOVA, using the BMDP package for calculations (Dixon 1992).

The nomenclature followed Tutin *et al.* (1964–1980).

3. RESULTS

The vegetation zones where transplant experiments were done distinctly differed in soil properties. The highest differences were related to Cl^- concentration, EC_e and the

Table 1. Selected soil properties (0–25 cm level) in three vegetation zones of the saline meadow under study in the period of transplant experiment (I – first, II – second year of study). moist – moisture (%), EC_e – electrical conductivity of saturated extract (mS cm^{-1}), EC – electrical conductivity of 1:5 water extract (mS cm^{-1}), org.mat. – organic matter (%), N_{tot} – total nitrogen (%), sum.salt. – total sum of salts (%), con. Cl^- – chloride concentration in the soil water (%), contents of anion and cations in %.

Property	*Salicornia europaea* zone		*Puccinellia distans* zone		*Elymus repens* zone	
	I	II	I	II	I	II
moist	21.9	18.9	19.0	23.3	21.5	29.5
EC_e	15.8	28.5	8.1	11.8	2.3	2.3
EC	4.1	n.o.	3.0	n.o.	2.2	n.o.
pH	7.2	6.9	7.1	7.1	7.1	7.0
org.mat.	3.1	3.01	3.0	2.53	3.2	3.92
N_{tot}	0.07	0.07	0.78	0.07	0.12	0.14
Cl^-	0.26	0.62	0.11	0.18	0.02	0.01
SO_4^{2-}	0.35	0.50	0.52	0.52	0.50	0.59
HCO_3^-	0.017	0.021	0.017	0.019	0.023	0.021
Na^+	0.076	0.155	0.040	0.054	0.006	0.003
Ca^{2+}	0.18	0.30	0.10	0.18	0.09	0.11
K^+	0.0009	0.0013	0.0009	0.0006	0.0021	0.0036
Mg^{2+}	0.002	0.006	0.039	0.054	0.001	0.002
sum.salt.	0.88	1.60	0.83	1.00	0.65	0.74
con. Cl^-	1.16	3.30	0.59	0.76	0.08	0.02
$Ca^{2+}:Na^+$	2.3	1.9	2.6	3.3	15.0	33.6

$Ca^{2+}:Na^+$ ratio (Table 1). The highest salinity occurred in the *S. europaea* zone of EC_e 28.5 mS cm^{-1} and Cl^- concentration 3.30%. The salinity in the *P. distans* zone was almost twice as low, with EC_e reaching 8.1 and 11.8 mS cm^{-1} respectively in both years of investigation and Cl^- concentration of 0.59 and 0.76%. In the *E. repens* zone EC_e amounted to 2.3 mS cm^{-1} and Cl^- concentration to 0.08%. In that zone the highest $Ca^{2+}:Na^+$ ratio (over 15) was observed. According to Jackson's scale of soil salinity (Jackson 1958) *S. europaea* zone represented extremely saline soils (EC_e over 16 mS cm^{-1}), *P. distans* zone strongly saline soils (EC_e 8–16 mS cm^{-1}) and *E. repens* zone slightly saline soils (EC_e 2–4 mS cm^{-1}).

3.1. Effects of transplanting

Comparison between the control transplants and *in situ* replicates demonstrated some significant differences in the growth of plants. For *S. europaea* a higher number of the second order lateral shoots was noted at the replanted sites in the first year of experiment (Table 2). In the second year the population of this species had higher main shoots than on in situ replicates. For *P. distans* and *E. repens* shorter new shoots and for *E. repens* more new shoots and at the same time less last year's shoots were observed for transplanted blocks as compared to undisturbed sites in the first year. In the second year the flowering shoots of transplants of *P. distans* and *E.repens* were shorter. For *P. distans* more flowering shoots and for *E. repens* more shoots were produced in the transplants. Differences in above-ground biomass were observed only in the case of *E. repens* with biomass being lower at transplanted sites than in situ (Fig. 2).

However, the above effects of transplantation were not significant in the interpretation of the experiments' results as all transplanted blocks were related to the replanted controls.

3.2. Effects of site conditions

Growth of *S. europaea* was significantly inhibited both in the *P. distans* zone as well as in the *E. repens* zone (Table 2, Fig. 2). After two years in the *P. distans* zone fewer individuals and lower above-ground biomass of transplants were observed as compared

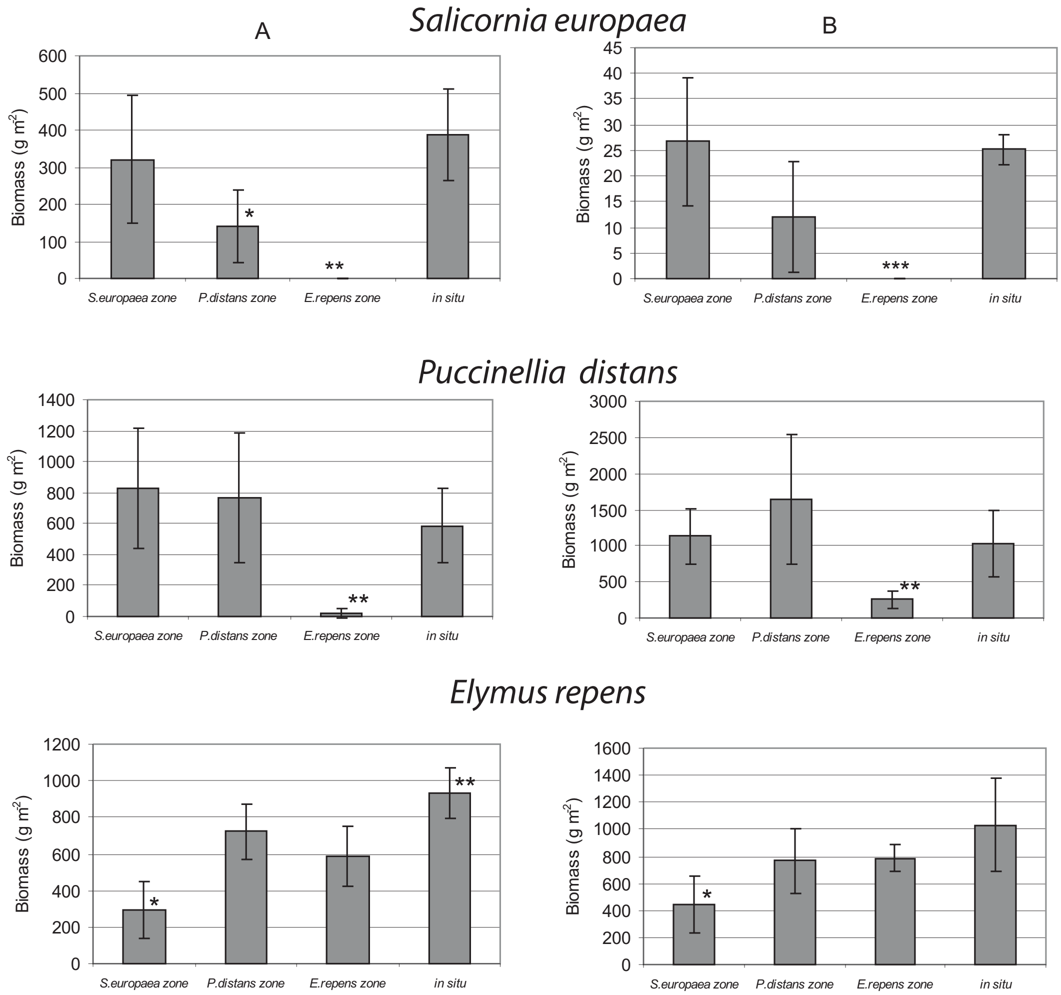

Fig. 2. Above-ground (A) and below-ground (B) dry biomass (mean ± SD, n = 5) after two growing seasons of three meadow species transplanted to two alien sites and replanted at their home sites. In situ – plants undisturbed at their home sites. Asterisks denoted a significance level of differences between means in relation to transplants at their home sites: * $P<0.05$, ** $P<0.01$, *** $P<0.001$ (ANOVA). Below-ground biomass: roots in the case of *S. europaea*, roots of grasses in the case of P. distans and rhizomes in the case of *E. repens*.

to the control garden. In the *E. repens* zone during the first growing season transplants were significantly shorter, with fewer first order lateral shoots and fewer 'ears'. However, they had more second order lateral shoots than replanted controls. In the second year, *S. europaea* seedlings that were present on the transplants in spring died, but species from the surroundings did not invade the transplants.

Puccinellia distans grew quite well in the *S. europaea* zone and after two growing seasons only shorter shoots were observed in comparison to the control replanted at the original site (Table 2, Fig. 2).

On the other hand the growth of *P. distans* was significantly inhibited in the *E. repens* zone where in the second year of observation lower above-ground biomass and lower biomass of grasses' roots were measured (Fig. 2). Apart from that, the remaining growth measures were also significantly different from the control. Significantly fewer flowering shoots and fewer new shoots were produced in the transplants. Shoots were shorter than at the home site (Table 2).

Table 2. The response after one (I) and two (II) growing seasons of three species of salt marsh plants transplanted to three vegetation zones and replanted at their home sites. Number of individuals, number of flowering shoots and number of new shoots are means ± SD for plot: 0.25 × 0.25 cm (n = 5). Number of first order lateral shoots, number of second order lateral shoots, number of 'ears', height of main shoots, height of shoots, height of new shoots are means ± SD for individuals in each treatment. Results for plants replanted at their home sites are in italics, and values for plants undisturbed at their home sites (*in situ*) are shown. Asterisks denote a significance level of differences between means in relation to transplants at the home sites: * *P* <0.05, ** *P* <0.01, *** *P*<0.001 (ANOVA).

	I				II			
	Salicornia europaea zone	*Puccinellia distans* zone	*Elymus repens* zone	*in situ*	*Salicornia europaea* zone	*Puccinellia distans* zone	*Elymus repens* zone	*in situ*
Salicornia europaea								
number of individuals	*746.6 ± 109.9*	582.0 ± 201.6	479.2 ± 128.5	738.0 ± 82.8	*390.8 ± 143.7*	**172.0** ± 111.3*	–	640.0 ± 166.2
height of main shoots (cm)	*7.4 ± 2.8*	8.0 ± 1.4	**5.1** ± 1.2*	7.5 ± 0.6	*7.5 ± 0.5*	8.8 ± 1.9	–	**5.9** ± 1.3*
number of first order lateral shoots	*3.0 ± 0.2*	4.4 ± 1.5	**1.4** ± 0.6**	2.5 ± 1.6	*1.6± 0.9*	3.1 ± 1.6	–	1.3 ± 0.9
number of second order lateral shoots	*0*	**0.97** ± 0.6**	**0.24** ± 0.3*	**0.05** ± 0.08*	*0.13± 0.06*	0.29 ± 0.3	–	0.10 ± 0.06
number of 'ears'	*4.0 ± 0.2*	5.7 ± 2.1	**2.4** ± 0.9*	3.5 ± 1.7	*2.8 ± 0.9*	4.4 ± 1.9	–	2.4 ± 0.9
Puccinellia distans								
number of flowering shoots	51.4 ± 26.4	*82.8 ± 37.9*	55.0 ± 15.3	101.4 ± 65.5	135.2 ± 61.5	*155.6 ± 73.1*	**0.2** ± 0.4**	**48,20** ± 10,73*
height of shoots (cm)	**31.7** ± 4.4**	*40.91 ± 1.6*	39.2 ± 4.1	42.7 ± 5.7	**17.9** ± 2.8*	*27.7 ± 6.0*	**7.6** ± 17.1*	**35.08** ± 3.76*
number of new shoots	299.4 ± 65.4	*235.2 ± 43.8*	232.4 ± 84.5	246.0 ± 72.9	339.8 ± 207.8	*253.8 ± 80.3*	**44.4** ± 41.2***	231.6 ± 97.17
height of new shoots (cm)	**9.3** ± 1.4*	*11.2 ± 0.3*	11.0 ± 1.8	**17.7** ± 1.3 ***	10.5 ± 3.7	*11.1 ± 4.3*	8.8 ± 1.1	15.50 ± 1.62
Elymus repens								
number of flowering shoots	1.6 ± 0.9	0.6 ± 0.9	*0.4 ± 0.9*	4.8 ± 4.8	8.2 ± 7.9	**23.8** ± 7.1***	*5.6 ± 2.9*	1.80 ± 2.68
number of shoots	32.6 ± 12.1	14.0 ± 7.2	*16.0 ± 13.8*	**99.6** ± 25.0***	**23.0** ± 16.7**	79.6 ± 11.0	*82.6 ± 28.4*	**47.00** ± 14.97*
height of shoots (cm)	45.7 ± 5.9	43.6 ± 3.2	*36.7 ± 8.8*	48.4 ± 10.1	**21.2** ± 12.2*	41.5 ± 7.5	*35.5 ± 3.0*	**46.31** ± 8.41*
number of new shoots	106.4 ± 28.6	178.8 ± 57.4	*149.4 ± 31.8*	**56.8** ± 20.5***	21.8 ± 21.3	90.8 ± 20.5	*54.4 ± 31.3*	54.00 ± 27.7
height of new shoot (cm)	**9.6** ± 1.7***	18.3 ± 3.4	*17.3 ± 1.5*	**21.1** ± 2.0*	**9.5** ± 6.1**	19.7 ± 2.1	*24.4 ± 4.6*	24.09 ± 4.27

Growth of *E. repens* was significantly inhibited in the *S. europaea* zone. At the beginning of the second year of observations one of the five transplanted populations died. At the end of the experiment fewer shoots, shorter shoots and shorter new shoots were observed as compared to the control (Table 2). Above-ground biomass and biomass of rhizomes was significantly lower as well (Fig. 2). In the *P. distans* zone *E. repens* transplants grew well and no growth limitations were observed. Even more flowering shoots were produced in the transplants than at the home sites.

4. DISCUSSION AND CONCLUSIONS

The transplant experiments demonstrated a direct effect of physical factors on species distribution. An obligatory halophyte *S. europaea* had optimal growth conditions at its home site. A distinct growth limitation of transplants was observed in the *P. distans* and *E. repens* zones of lower salinity. At the same time no penetration of neighbouring species into transplants was noted. In similar experiments, Wilkoń-Michalska (1976) observed the growth of *S. europaea* transplanted to the *Potentillo-Festucetum arundinaceae* association on a meadow next to the soda factory in Inowrocław during three growing seasons. *Salicornia europaea* seedlings died in the fourth season. Growth limitation of *S. europaea* on less saline areas was also discovered in inland salt marshes in North America (Ungar *et al.* 1979, Keiffer *et al.* 1994). However, in that study area the *S. europaea* zone occurred at the far end of the salinity gradient because of interspecific competition. Biomass and survival rate of transplants in the neighbouring zones of slightly lower salinity was higher than at the home site (Ungar *et al.* 1979, Ungar 1987). Such effect was not observed in the current study.

The occurrence of *P. distans* was limited on the one hand by the salinity level in the *S. europaea* zone and on the other hand by interaction with *E. repens*. Even *P. distans* transplants in the *S. europaea* zone were not limited during the observation period but this perennial grass is known to be a stronger competitor as compared to annual glasswort of which distribution very often depends on free space available (Ellison 1987). And thus, we can expect the growth limitation of *P. distans* in the most saline *S. europaea* zone in a longer period than the two years monitored.

On the other hand *P. distans* was markedly limited in the *E. repens* zone of lower soil salinity. Since *P. distans* was found in nonsaline areas outside the investigated meadows this effect could not be the result of the salinity level but of allelopathic interaction of *E. repens* (Beyschlag *et al.* 1996). Apart from that, underground competition could take place as *E. repens* rhizomes penetrated transplanted blocks. However, biomass of rhizomes was rather small.

Results of *E. repens* transplantation demonstrated that the distribution of this species in the meadow was strongly related to the soil salinity level. Transplants in the *S. europaea* zone were significantly inhibited. Limitation of growth in the *P. distans* zone was not observed after two growing seasons. However, Beyschlag *et al.* (1996) and Ryel *et al.* (1996) reported strong competitive ability of *E. repens* against *P. distans,* limited only by the available soil level for roots, mowing and salinity. Therefore inhibition of *E. repens* in the *P. distans* zone could be expected in the longer run.

After the experiment, it could be concluded that species zonation depends mostly on soil salinity and in the case of *P. distans* and *E. repens* on biotic interactions as well. Nevertheless biotic factors seem to be more important in coastal marshes (Ungar *et al.* 1979, Snow and Vince 1984, Bertness and Ellison 1987, Ungar 1987). The main limiting factor for the distribution of halophytes in inland saline habitats seems to be the salinity level. Therefore, the most important conclusion from this research for restoration is that the chance to keep a high salinity level at each naturally saline place has to be assessed first and original water conditions should be rebuilt if possible. The second issue is to control the expansion of strong competitors by cutting or grazing (Wilkoń-Michalska 1970, Bakker 1989). When the salinity level is high enough this expansion is naturally limited by physical stress. To demonstrate for inland saline habitats the relationship between a cause and effect for the distribution of other than *S. europaea*, *P. distans* and *E. repens* plant species, more similar experiments on other meadows or greenhouse experiments are needed.

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