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DISTRIBUTION OF THE HALOPHYTIC GRASS *Puccinellia limosa* (Schur.) Holomb. ON SALT AFFECTED SOILS IN SERBIA IN RELATION TO ITS MAIN ADAPTIVE RESPONSES TO SALINITY

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Abstract

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A survey on the presence of the halophytic grass *Puccinellia limosa* in numerous plant communities distributed on salt affected soils in Serbia indicated a general preference of this halophyte for moderately to highly salinized and very alkalinized soils, mainly of solonetz and sodic solonchak type. Responses to the salinity in *P. limosa* were studied by soil-plant relations, estimated through alterations in ions concentration, both in soil saturation extract and in root and shoot of plants collected in their typical community, the ass. *Puccinellietum limosae* (Rapcs.) Wend., found in the salt marsh situated in the middle Banat (Vojvodina, Serbia). Soil salt content gradually increased during the vegetation season of the plant, reaching a maximum of 0.64%, corresponding to EC_e of 25.1 mmhos/cm. Concentration of ions in root and shoot of *P. limosa* (μmol/g DW) significantly differed, whereas in the root the highest values had sodium (172.83 ± 94.86), potassium (147.26 ± 25.65) and calcium (139.66 ± 20.05), and in the shoot chlorides (186.68 ± 57.51), potassium (158.74 ± 50.2) and sodium (130.09 ± 58.84). The root/shoot ratio gradually increased during the investigated period, and was correlated with Na/K of the root, suggesting a significance of salt exclusion and control of transport of salts towards the shoot, operating at the root level. Statistical processing of data showed that factors assigned as age of the plant, corresponding to increasing soil salinity, and plant part (root and shoot), individually and mutually, had a significant effect on salt accumulation and related ions allocation in *P. limosa*.

Key words: halophytic communities, halophytic grass, plant–soil relations, salt tolerance

Introduction

Although salinity and sodicity are common phenomena for arid and semiarid regions of the world, salt-affected soils have been recorded in practically all the climatic regions, and in a wide range of altitudes. According to FAO Land and Plant Nutrition Management Service, the total world area under saline and soils is $397x10^6$ and $434x10^6$ ha, respectively, and of the almost $1500x10^6$ ha of dryland agriculture about 2% are salt-affected. In Serbia, there was estimated that about of 10% of the total agricultural land is exposed to salinity (Dajić, 2001).

Halophytes are considered a native flora of saline habitats, able to successfully grow in conditions of 2–6% salt (Strogonov, 1964), and capable to withstand even 20% salt in the soil. Although numerous similar cellular mechanisms are present in both halophytes and non-halophytes for growth in saline conditions (Binzel et al., 1989), the halophytic species seem to be more efficient in the utilization of different salt tolerance mechanisms. Mechanisms of salt tolerance are of two main types: those minimizing the entry of salt into the plant (or at least their accumulation in photosynthetic tissues), and those minimizing the concentration of salt in the cytoplasm (Dajic, 2006; Munns, 2002).

There are several ways of dealing with the problem of salinity, as indicated by Flowers, Yeo (1995), including direct use of halophytes, which refers to the relatively cheap method of domestication of salt-tolerant plants, compared with the modification of existing crops to grow in the niche of halophytes. For extremely salt-affected soils, the use of halophytes is recommended (O'Leary, 1994), since both soil reclamation and introduction of genetically modified crops, possibly adapted to such conditions, are time consuming and expensive. Many halophytes have a great potential for use in so called "saline agriculture", as oil seeds, food, fodder, fuel, fiber and other products. Halophytic grasses, including puccinellia, as distributed within grazing saline meadows and pastures are used mainly as forages (Peng et al., 2004; Robinson et al., 2004). Salt marshes in Europe are commonly grazed by sheep and cattle (Andersen et al., 1990; Jensen, 1985), whereas puccinellia-based pastures in South Australia are grazed by sheep (Edwards et al., 2002), and those of the Wadden Sea by livestock and geese (Bos et al., 2005). At low to moderate levels of salinity, plants such as *Puccinellia* ssp. have been reported to produce 4–10 t dry matter (DM) ha^{-1} $year^{-1}$ (Warren et al., 1994). In contrast to studies performed on salt tolerance in a range of species of the genus *Puccinellia* P a r l ., such as *P. maritima* (e.g. Leendertse et al., 1996), *P. distans* and *P. lemmoni* (Alshammary et al., 2004; Harivandi et al., 1982), *P. peisonis* (e.g. Stelzer, Lauchli, 1978), and *P. tenuiflora* (e.g. Peng et al., 2004; Shi et al., 2002), there is limited information on *P. limosa*, a species widespread on saline habitats of middle and south-east Europe. Therefore, a survey on distribution of sub-Pannonian species – the *P. limosa* – within various saline habitats in Serbia and the screening of basic responses of this halophyte to salinity was performed as grounds for the future research on use and quality of *P. limosa* as a forage.

Material and methods

A survey on distribution of the halophytic grass *Puccinellia limosa* on salt affected soils in Serbia was performed according to the available literature data (period 1979–2002), and our own research conducted in the 2000–2003 period in the region of the middle Banat (Vojvodina, Serbia). All used data were in the form of phyto-sociological tables according to the principles of Braun-Blanquet (1964). Soil and plant samples for evaluation of salt tolerance in *P. limosa* were collected in 2003 from the salt marsh situated near the village of Melenci (middle Banat, Vojvodina, Serbia) at the following geographic coordinates: 45°30'58.7" N, 20°18'16.2" E, and altitude 85.9 m a. s. l. Plant and soil samples were taken in the community previously characterized as *Puccinellietum limosae* Rapcs. Wendt (Dajić, 1996).

Soil performances

Soil samples of the layer of 0–20 cm were taken from micro-sites characterized by maximal coverage of the *Puccineliia limosa*, monthly, during the April–October period. The following parameters of soil salinity were measured: pH, EC_e (electrical conductivity of soil saturation extract), percentage of soil saturation, and concentration of ions in the soil saturation extract. Concentration of sodium, potassium, calcium and magnesium was determined by AAS, ammonium and nitrate ion by the distillation method, carbonates and bicarbonates by titration with 0.01 N H_2SO_4, chlorides and sulfates volumetrically with 0.01 $AgNO_3$ and $BaCl_2$, respectively, and phosphates using the colorimetric method. All values are expressed in meq/l. Soil analyses were performed according to the protocols proposed by Rhoades, Miyamoto (1990). Sodium adsorption ratio (SAR) and the total salt contents were calculated according to Kamphorst, Bolt (1976).

Plant analyses

Plant material was collected during the vegetation season (June–August). Ion concentrations in the root (after careful washing out of salts by distilled water) and shoot were analyzed in three individual samples (plants) by dry ashing and extraction with 0.01 N HCl, using the same methods as for the soil. Chlorides were extracted separately by hot solution of 1% KNO_3 and were determined by titration with 0.01 N $AgNO_3$. Ion concentration in plant material was expressed in μmol/g of dry weight. Root and shoot mass was weighted after drying at 60 C°. All analyses of plant material were performed according to the protocols proposed by Jones, Case (1990).

Data processing

All data were statistically processed using STATISTICA 5.0 software. Comparisons of means were carried out by the Duncan multiple range test, while alterations in ion content in root and shoot was conducted through unpaired Student's *t*-test and homogeneity of variances (*F*-test), where factors such as "plant age" and "plant part" (root and shoot) were used as categorical variables. Analysis of variance was performed as one way ANOVA and two-way MANOVA to estimate the effects of the single and common effects of analyzed factors, respectively.

Results

Distribution of Puccinellia limosa within different halophytic communities

Occurrence of the halophytic grass *P. limosa* was determined within the total of 21 plant communities of 4 classes, 7 orders and 11 alliances (data not showed). Most of the analyzed communities belong to typical halophytic vegetation, of the classes *Festuco-Puccinellietea* and *Thero-Salicornetea*, while the associations the *Halo-Agrostietum albae* and the *Trifolietum subterranei* were grouped within the class of moderately wet to wet meadows the *Molinio-Arrhenetheretea* and association *Bolboschoenetum maritimi continentale* into swamp vegetation of the class *Phragmitetea*.

Most of communities with *Puccinellia limosa* are developed on moderately to high salinized soils, such as solonchak and solonetz (Table 1), whereas communities such as the ass., *Halo-Agropyretum repentis* and *Halo-Agrostetum,* were determined on slightly salinized alluvium soil and slightly salinized solonetz meadow, respectively. Parameters, such as maximal abundance and frequency, indicated a general preference of *Puccinellia limosa* to sodic solonchak and to some lesser extent to the solonetz type of salt affected soils. The relatively high amplitude in soil salinity of vegetation with *P. limosa* is related to the ecological plasticity of the halophyte *P. limosa*, and its ability to adapt to a range of environmental conditions, namely the soil salinity and moisture of the habitat.

Plant–soil relations

The main characteristics of soil under the vegetation of *P. limosa,* monitored during the April–October period (Table 2), showed that among sodium salts the most presented were sulfates, followed by chlorides. High sodium concentration and related SAR and pH values are unfavorable, both for maintenance of the soil structure and for plant growth. According to all examined features, soil was characterized as sodic-sulfate solonchak, very alkalinized and highly salinized (Dajić, 1996).

Regarding seasonal alterations in soil salt content measured during the vegetation season of *P. limosa* (Table 2), a gradual increase in soil salinity was determined, ranging from 0.37 to 0.64% of the total salts. Low content of macro-nutrients, such as potassium, calcium and magnesium, compared with the high sodium concentration in the soil, is known as a limiting factor for development of plants other than halophytes (Dajic, 2006).

Seasonal dynamics of ion content in root and shoot of *P. limosa* (Table 3) showed that the concentration of accumulated salts increased gradually with soil salinity. In the root, the highest average concentration (μmol/g DW) had sodium (172.83 ± 94.86), calcium (139.66 ± 20.05), followed by potassium (147.26 ± 25.65) and chlorides (110.68 ± 60.33). In the shoot, the highest values had chlorides (186.68 ± 57.51), potassium (158.74 ± 50.2) and sodium (130.09 ± 58.84). The distribution of ion content between two parts of the plant was significantly different, especially in regards to chlorides, magnesium and potassium, and sodium at the beginning and at the end of the growing season of the *P. limosa*, respectively.

Analysis of variance showed that both the vegetation stage (corresponding to increased soil salinity) and the plant part, individually or mutually had a significant effect on the accumulation of particular ions (Table 4), especially of magnesium and chlorides. The effect of increased soil salinity during the vegetation season had a significant effect on the accumulation of sodium, whereas the ratio of salt uptake within the root and shoot differed highly for calcium and phosphates. For all investigated ions, both factors showed

T a b l e 1. Distribution of *Puccinellia limosa* on salt affected soils in Serbia.

Community	Maximal abundance	Frequency	Soil type	Reference
1	2.2	I	sodic-chlorine solonchak	Knežević, 1980, Kujundžić, 1980
2	1.1	II	solonetz	Vučković, 1985
3	1.2	IV	solonchak-like solonetz and highly alkaline solonchak	Knežević, 1981, Parabućski and Pekanović,1980
4	3.3	V	sodic- chlorine solonchak	Kujundžić, 1979
5	1.1	IV	solonchak	Vučković, 1985
6	+.2	II	slightly salinized alluvial soil	Vučković, 1985
7	1.1	II	meadow solonetz	Vučković, 1985
8	+	III	highly salinized solonetz	Vučković, 1985
9	+	II	solonetz	Vučković, 1985
10	4.5	V	sodic solonchak	Parabućski et al., 1971
11	+.1	III	solonetz	Knežević et al., 2000
12	4.5	V	solonetz, sodic solonchak	Vučković, 1985, Dajić,1996, current research
13	1.2	I	solonetz	Parabućski, 1979
14	2.2	IV	solonchak	Vučković, 1985
15	+	II	solonetz-solonchak	Vučković, 1985
16	2.2	IV	solonetz	Vučković, 1985
17	3.3	V	solonetz	Knežević et al., 2000
18	2.2	IV	solonchak	Vučković, 1985
19	2.2	V	solonetz	Knežević et al., 2000
20	2.2	V	solonchak-like solonetz	Knežević et al., 2002
21	1.2	II	solonetz	Parabućski,1979

1. *Agrosti-Caricetum distantis,* 2. *Artemisio-Festucetum pseudovinae pannonicum,* 3. *Bolboschoenetum maritimi continentale,* 4. *Camphorosmetum annuae,* 5. *Halo-Crypsidetum aculeatae,* 6. *Halo-Agropyretum repentis,* 7. *Halo-Agrostetum albae,* 8. *Halo-Atriplexetum hastatae,* 9. *Hordeetum hystricis,* 10. *Lepidio- Puccinellietum limosae,* 11. *Lepidio crassifolio – Festucetum pseudovinae,* 12. *Puccinelietum limosae,* 13. *Peucedano-asteretum punctati,* 14. *Pholiuro-plantaginetum tenuiflorae,* 15. *Plantagineto-festucetum pseudovinae,* 16. *Roriperetum kernerii,* 17. *Salicornieto- Suaedetum maritimae continentale,* 18. *Suaedetum maritimae,* 19. *Suaedetum pannonicae,* 20. *Salsoletum sodae,* 21. *Trifolietum subterranei*

T a b l e 2. General properties of soil and seasonal alterations of ions in the soil saturation extract.

Basic features of soil			
EC (mhos/cm)	18.9 ± 9.7		
pH	8.68 ± 0.56		
Saturation (%)	40.1 ± 2.5		
SAR	102.58 ± 13.24		
Total salt content (%)	0.4 ± 0.1		
Ion concentrations (meq/l)			
Na^+	136.2 ± 47.7		
SO_4^{2-}	78.2 ± 30.9		
Cl^-	51.1 ± 18.9		
CO_3^{2-}	4.8 ± 1.5		
HCO^{3-}	10.1 ± 4.1		
K^+	1.7 ± 0.6		
Ca^{2+}	2.5 ± 1.9		
Mg^{2+}	1.2 ± 0.5		
NH_4^+	0.1 ± 0.05		
PO_4^{3-}	0.7 ± 0.08		
NO_3^-	0.9 ± 0.04		
Soil parameters	**June**	**July**	**August**
EC (mhos/cm)	14.6	17.9	25.1
pH	8.6	8.8	9.1
Total salts (%)	0.37	0.55	0.64
Na^+	129.1	153.1	218.2
K^+	1.8	2.1	2.7
Ca^{2+}	1.6	2.4	6.3
Mg^{2+}	0.8	1.4	2.2
Cl^-	50.4	47.5	86.8
SO_4^{2-}	80.1	85.1	130.3
PO_4^{3-}	0.7	0.9	0.7

high regression coefficients, of R= 0.99 for factor "plant age", and R= 0.98 for differences in accumulated ions in two plant parts.

Alterations in Na/K content in the root and shoot showed that Na/K gradually increased in the root, whereas in the shoot, it rapidly increased at the end of the growing season (Fig.1). In the shoot, the Na/K ratio was significantly lower. The root/shoot ratio gradually increased during the vegetation season (Fig. 2). Increase in root biomass seemed to be correlated with Na/K ratio of the root (Fig. 3).

T a b l e 3. Ion concentration (μmol/g DW) in root and shoot of Puccinellia limosa (means and SD of N =3)

Month	**June**		**July**		**August**	
Ion conc.	Root	Shoot	Root	Shoot	Root	Shoot
Na^+	69.8 ± 24.2	78.9 ± 29.1	166.5 ± 33.9	105.3 ± 36.9 *	283.3 ± 54.7	206.2 ± 15.1 **
K^+	176.4 ± 42.1	124.4 ± 20.6*	123.4 ± 19.6	223.8 ± 41.1 **	142.1 ± 35.4	128.2 ± 27.4
Ca^{2+}	139.2 ± 43.5	58.9 ± 13.7**	157.8 ± 24.6	114.2 ± 26.4 *	122.0 ± 39.9	79.4 ± 14.6 **
Mg^{2+}	64.9 ± 21.5	41.9 ± 13.8**	83.2 ± 17.3	66.3 ± 9.7 *	142.9 ± 40.2	74.4 ± 28.9 **
Cl^-	37.7 ± 15.6	112.9 ± 33.4**	119.3 ± 41.4	214.0 ± 52.5 **	175.1 ± 30.1	233.8 ± 49.9 **
SO_4^{2-}	21.9 ± 3.5	23.6 ± 1.4	22.2 ± 3.6	15.6 ± 9.8	29.6 ± 8.5	26.7 ± 7.3
PO_4^{3-}	24.8 ± 2.4	37.8 ± 5.3*	25.6 ± 11.4	36.6 ± 4.1 **	27.7 ± 8.6	31.7 ± 94

Note: Means followed with * and ** indicating significant differences between root and shoot ion concentrations at p < 0.05, and p < 0.001, respectively

Discussion

Distribution of the plant community *Puccinellietum limosae* is supposed to be linked to the Pannonian plain, as it has been already recorded for Hungary, as well (Bodrogkozy, 1965). In addition to a previous statement that this region is a center of distribution of the association *Puccinellietum limosae* (Vučković, 1985), several communities with other puccinellia species have been found on saline soils throughout the Europe, including those of *P. maritima* on the salt marshes of Western Europe (e.g.

T a b l e 4. Analysis of variance (F- and p- levels) and summary effects of factors (MANOVA) for alterations in ion content during the vegetation season and plant part variables.

Factor	Plant age (1)		Plant part (2)	
Variable	F	p	F	p
Na^+	37.21413	< 0.0001	1.31965	n.s.
K^+	1.58265	n.s.	.37378	n.s.
Ca^{2+}	.02400	n.s.	73.89806	< 0.0001
Mg^{2+}	7.60375	< 0.001	7.45182	< 0.05
Cl^-	13.60433	< 0.001	7.48198	< 0.05
SO_4^{2-}	3.25866	n.s.	.73412	n.s.
PO_4^{3-}	.10298		37.03157	< 0.0001
Summary effects	Factor 1	Factor 2	All effects (1x 2)	
Wilk's lambda	.002199	.019704	.002192	
Rao's R	23.71259	58.04368	58.04368	
p-level	< 0.0001	< 0.0001	< 0.0001	

Adam, 1981; Dalby, 1985; Vevle, 1985), and of the *P. distans* and *P. convoluta* on continental saline habitats of the Central and East Europe (e.g. Hadač et al., 1983; Papastergiadou, Babalonas, 1996). Communities of the *P. palustris* (Beeftink, 1977; Ferari et al., 1985), and

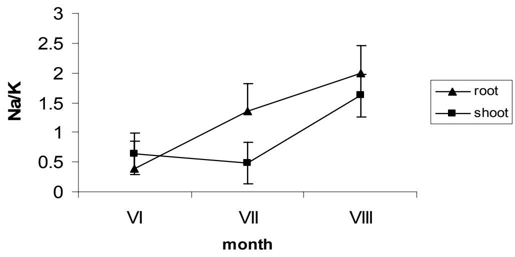

Fig. 1. Na/K ratio in root and shoot of the *P. limosa.*

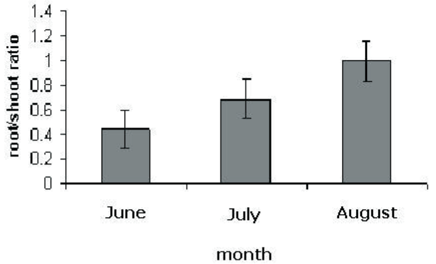

Fig. 2. Root/shoot ratio in *P. limosa*.

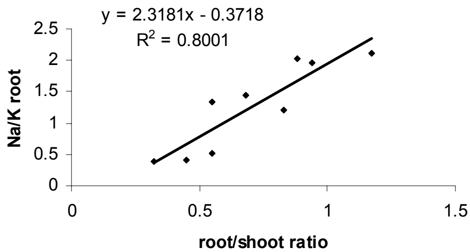

Fig. 3. Correlation between root/shoot ratio and Na/K in the root of *P. limosa.*

of a rare *P. fasciculata* (Haeck et al., 1985) are locally distributed on the European inland salines. In the Euro-Asian region different communities with the *P. hauptiana*, *P. scleroides*, *P. kulundensis* and *P. tenuissima* were registered (Lamanova, 1990).

According to the survey on distribution of the halophytic grass *P. limosa*, and an analysis of its abundance and frequency in a variety of communities of salt affected soils in Serbia, it could be concluded that this species preferably occupies sodic solonchak and solonetz soils, moderately to highly salinized and much alkalinized.

Halophyte *P. limosa* expresses a high ability for successful growth on soils containing even 0.6% of the total salts. Salt tolerance in *P. limosa* is related to several adaptive mechanisms, including the retention of salts in the root and salt exclusion, which is typical for glyco-halophytes and halophytic grasses (Dajic, 2006; Munns et al., 1983). The strategy of salt exclusion relies on the selective release of Na^+ into the xylem and its reabsorption from the xylem stream. The net accumulation of sodium ions in the plant is dependent on the balance between passive influx and active efflux. Re-absorption of sodium and other ions is performed by proton pumps on xylem parenchyma cells of the mature root regions, preventing transport and salt excess in above ground plant parts (Jeschke, 1983). It is thought that salt exclusion in the *Puccinellia* species could be also associated with a two-layer endoderm, being a kind of the physical barrier for ion transport towards shoot (Crawford, 1989). Significantly higher calcium content in the root, compared with the shoot in *P. limosa*, is related to an adsorption of calcium ions on membranes of root cells leading to reduced penetration of monovalent cations (Munns et al., 1983). A lower transport rate of calcium to the shoot was also evidenced for other salt tolerant grasses in conditions of increased salinity (Cramer et al., 1989). High calcium concentrations observed for the root may be explained by at least two roles of Ca^{2+} in salt tolerance: 1) a pivotal participation in salt stress signaling that controls ion homeostasis pathways (Yokoi et al., 2002), and 2) direct inhibitory effect on a Na^+ entry (e.g. Lazof, Bernstein, 1999). High concentrations of chlorides and sodium in the shoot of *P. limosa* are responsible for osmotic adjustment, as was found in other halophytes grown at high salinity (Dajić et al., 1998). The main sites for chloride accumulation in halophytic grasses are considered to be vacuoles of the leaf mesophylle and epidermis, together with the cells of the leaf sheath (Huang, van Steveninck, 1989). Different Na/Cl ratio in root and shoot, where much higher (Cl) was found in the shoot of *P. limosa*, has been considered a distinctive feature of the halophytic grasses (Waisel, 1972).

The stimulated root growth at increased salinity, and the higher salt content and higher Na/K ratio of the root compared with the shoot in *P. limosa*, was also reported for other halophytic grasses, such as *Sporobulus virginicus* (Marcum, Murdoch, 1992). The ability of *Puccinellia limosa* to maintain a relatively high potassium concentration in the shoot until the end of the vegetation season is an important feature of salt tolerance of this species. A similar ability was found for alkali grass (*P. distans*), suggesting its ability to regulate the uptake and distribution of ions by forming high concentration of (K^+) in the shoot, and a large (Na^+) gradient between the root and the shoot (Peng et al., 2004). Alkali grass consistently produced much higher root to shoot ratios at increasing salinity (Alshammary et al., 2004), which was also showed for *P. limosa* in our study, indicating the importance of salt retention in the root and controlled salt movement to photosynthetic organs, which are known to be more sensitive to salt stress (e.g. Blumwald et al., 2000).

Summarily, the main adaptive responses to salinity in the halophyte *P. limosa* are linked to the mechanisms such as: salt exclusion, salt retaining in the root and related high root capacity for calcium accumulation, followed by controlled transport rates of sodium to the shoot, the maintaining of shoot K/Na ratio and significance of chlorides and, to a lesser extent, of sodium ions for shoot osmotic adjustment.

Many plants capable of growing at high salt concentrations represent a feed resource for livestock. Even at high salinities, there are a range of halophytic grasses, including *P. limosa*, that will produce between 0.5 and 5 t of edible DM year^{-1} (Masters et al., 2007)**.** One of the primary determinants of livestock production in biosaline agriculture is the amount of edible biomass produced, and thus a study of salt tolerance in *P. limosa* should be extended to evaluation of its forage value.

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References

Adam, P., 1981: The vegetation of British salt marshes. New Phytol., 88: 143–196.
Alshammary, S.F., Qian, Y.L., Wallner, S.J., 2004: Growth response of four turfgrass species to salinity. Agric. Water Manag., 66: 97–111. doi:10.1016/j.agwat.2003.11.002
Andersen., H., Bakker, J.P., Brongers, M., Heydemann, B., Irmler, U., 1990: Long-term changes of salt-marsh communities by cattle grazing. Vegetatio, 89: 137–148. doi:10.1007/BF00032166
Beeftink, W.G., 1977: The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In Chapman, V.J. (ed.), Wet coastal ecosystems. Junk, Den Haag, p. 109–155.
Binzel, M.L., Hess, F.D., Bressan, R.A., Hassegawa, P.M., 1989: Mechanisms of adaptation to salinity in cultured glycophyte cells. In Cherry, J.H. (ed.), Biochemical and physiological mechanisms associated with environmental stress tolerance. Springer Verlag, Berlin, p. 139–157.
Blumwald, E., Aharon, G.S., Apse, M.P., 2000: Sodium transport in plant cells. Biochim. Biophys. Acta, 1465: 140–151. doi:10.1016/S0005-2736(00)00135-8
Bodrogközy, Gy., 1965: Ecology of the halophyllic vegetation of the Pannonicum IV. Investigations on the solonetz meadow soils of Orosháza. Acta Biol., 11: 3–4.
Bos, D, Loonen M.J.J., Stock, M., Hofeditz, F., van der Graaf, A.J., Bakker, J.P., 2005: Utilization of Wadden Sea salt marshes by geese in relation to livestock grazing. J. Nat. Conserv., 13: 1–15. doi:10.1016/j.jnc.2004.10.001
Braun Blanquet, J., 1964: Pflanzensoziologie. 3 Aufl., Wien, New York, 865 pp.
Cramer, G., Epstein, E., Lauchli, A., 1989: Na-Ca interactions in barley seedlings: relationship to ion transport and growth. Plant Cell Environ., 12: 551–558. doi:10.1111/j.1365-3040.1989.tb02128.x
Crawford, R.M.M., 1989: Studies in plant survival. Blackwell Scientific Publications, Oxford, London, 296 pp.
Dajić, Z., 1996: Ecological study of the halophytic community Puccinellietum limosae (Rapcs.) (in Serbian). Wend. PhD thesis. Faculty of Biology, University of Belgrade.
Dajić, Z., Stevanović B., Ajder, S., 1998: The role of ions in osmotic adjustment of several euhalophytes grown in natural habitat. Ekologija (Belgrade), 33: 169–174.

Dajić, Z., 2001: Analysis of flora grown on saline grasslands of Serbia (in Serbian). Archive for Agriculture Sciences, 62: 243–251.
Dajic, Z., 2006: Salt stress – salinity and tolerance mechanisms in plants. In Madhava Rao, K.V., Raghavendra, A.S., Reddy, K.J. (eds), Physiology and molecular biology of stress tolerance in plants. Springer, Berlin, p. 41–99. doi:10.1007/1-4020-4225-6_3
Dalby, D.H., 1985: Salt marsh vegetation in the Shetland Islands. Vegetatio, 61: 45–54.doi:10.1007/BF00039809
Edwards, N.J., Hocking Edwards, J.E., Sanders, D., Revell, D.K., 2002: Sheep production on puccinellia-based pastures in South Australia. Animal Production in Australia, 24: 293.
Ferari, C., Gerdol, R., Piccoli, F., 1985: The halophytic vegetation of the Po Delta (northern Italy). Vegetatio, 61: 5–14. doi:10.1007/BF00039805
Flowers, T.J., Yeo, A.R., 1995: Breeding for salinity resistance in crop plants: where next? Aust. J. Plant Physiol., 22: 875–884. doi:10.1071/PP9950875
Hadač, E., Rambousková, H., Valach, R., 1983: Notes of syntaxonomy and synecology of some ruderal plant communities in Praha-Holeshovice with special attention to winter-salted habitats. Preslia, 55: 63–81.
Haeck, J., van Tongeren., O., van der Maarel, E., 1985: Phytosociological amplitudes of some Dutch coastal species and their ecological interpretation. Vegetatio, 61: 77–85. doi:10.1007/BF00039812
Harivandi, M.A., Butler, J.D., Soltanpour, P.N., 1982: Effects of sea water concentrations on germination and ion accumulation in alkali grass (Puccinellia ssp.). Commun. Soil Sci. Plant Anal., 13: 507–517. doi:10.1080/00103628209367290
Huang, C.X., van Steveninck, R.F.M., 1989: maintenance of low Cl concentrations in mesophyll cells of leaf blades of barley seedlings exposed to salt stress. Plant Physiol., 90: 1440–1443. doi:10.1104/pp.90.4.1440PMid:16666949 PMCid:1061909
Jensen, A., 1985: The effect of cattle and sheep grazing on salt marsh vegetation at Skallingen, Denmark. Vegetatio, 60: 37–48. doi:10.1007/BF00053910
Jeschke, W.D., 1983: K^+-Na^+ exchange across the plasmalemma of meristematic root tissues. Zeitschrift für Pflanzenphysiologie, 94: 325–330.
Jones, J.B., Case, V.W., 1990: Sampling, handling and analyzing plant tissue samples. In Westerman, R.L. (eds), Soil testing and plant analyses. Soil Science Society of America Medison, Wisconsin, p. 389–427.
Kamphorst, A., Bolt, G.H., 1976: Saline and sodic soils. In Bolt, G.H., Bruggenwert M.G.M. (eds), Soil chemistry. A basic elements. Elsevier Scientific Publishing Company Amsterdam, Oxford, New York, p. 171–191. doi:10.1016/S0166-2481(08)70638-X
Knežević, A., 1980: Halophytic vegetation of a steppe-meadow type in the vicinity of Kruščić (in Serbian). Matica Srpska, 59: 101–129.
Knežević, A., 1981: The community Bolboschoenetum maritimi continentale Soo on the saline habitat in the vicinity of Kruscic (in Serbian). Matica Srpska, 60: 35-43.
Knežević, A., Boža, P., Butorac, B., Vučković, M., 2000: Lepidio crassifolio –Festucetum pseudovinae assoc. nova of the halobiome in Yugoslavia. Matica Srpska, 98: 45–51.
Knežević, A., Boža, P., Milošev, D., Anackov, G, 2002: Phytogeographical and ecological characteristics of the vegetation alliance Thero-Salicornion Br.-Bl. 33 EM. Tx.50 growing on continental salt-affected soils (Banat-Yugoslavia). Matica Srpska, 102: 35–44.
Kujundžić, M., 1979: About one halophytic community in Backa. The second Congress of the ecologists of Yugoslavia (in Serbian), 1: 597–604. Savez Društava Ekologa Jugoslavije, Zagreb.
Kujundžić, M., 1980: Halophytic vegetation in the vicinity of Ruski Krstur (in Serbian). Matica Srpska, 58: 99–112.
Lamanova, T.G, 1990: Puccinellia ssp. in the halophyte phytocoenoses in the Karasuk River valley (Novosibirsk Oblast, Russian SFSR, USSR) and their nutritive value. Rastitel'nye Resursy, 26: 400–409.
Lazof, D.B., Bernstein, N., 1999: The NaCl induced inhibition of shoot growth: the case for disturbed nutrition with special consideration of calcium. Advances in Botanical Research Incorporating Advances in Plant Pathology, 29: 113–189. doi:10.1016/S0065-2296(08)60311-0
Leendertse, P.C., Scholten, M.C.Th., van der Wal, J.T., 1996: Fate and effects of nutrients and heavy metals in experimental salt marsh ecosystems. Environ. Pollut., 94: 19–29. doi:10.1016/S0269-7491(96)00104-2
Marcum, K.B., Murdoch, C.L., 1992: Salt tolerance of the coastal salt marsh grass, Sporobulus virginicus (L.) K u n t h. New Phytol., 120: 281–288. doi:10.1111/j.1469-8137.1992.tb05665.x

Masters, D.G., Benes, S, E., Norman H.C., 2007: Biosaline agriculture for forage and livestock production. Agric. Ecosyst. Environ., 119: 234–248. doi:10.1016/j.agee.2006.08.003
Munns, R., Greenway, H., Kirst, G.O., 1983: Halotolerant eukaryotes. In Lange, O.L, Nobel, P.S., Osmond, C.B, Ziegler, H. (eds), Physiological plant ecology III. Responses to the Chemical and Biological Environment. Encycl. Plant Physiol. New Ser. Vol 12 C. Springer-Verlag, Berlin, p. 59–135.
Munns, R., 2002: Comparative physiology of salt and water stress. Plant Cell Environ., 25: 239–250. O'Leary, J.W., 1994: The agricultural use of native plants on problem soils. In Yeo, A.R, Flowers, T.J. (eds), Soil mineral stresses: approaches to crop improvement. Springer-Verlag, Berlin, p. 127–143.
Papastergiadou, E., Babalonas, D., 1996: Salt marshes and sand dune ecosystems in the North Aegean coastal areas. In Salman, A.H.P.M. et al. (eds), Coastal management and habitat conservation. Proceedings of the 4th EUCC Congress, Marathon, Greece, 2: 65–74.
Parabućski, S., 1979: Communities Peucedano-Asteretum punctati Soo i Trifolietum subterranei Slavnic on some localities in Bačka and their syn-taxonomic position (in Serbian). Matica Srpska, 56:17–43.
Parabućski, S., Janjatović, V., Andjelić, M., 1971: Plantago tenuifolia on saline habitats in vicinity of Novi Sad (in Serbian). Proceedings of the Faculty of Agriculture, University of Novi Sad.
Parabućski, S., Pekanović, V., 1980: Cirsium brachycephalum Jur. on some localities in Bačka (in Serbian). Matica Srpska, 58: 63–69.
Peng, Y.H., Zhu, Y.F., Mao, Y.Q, Wang, S.M., Su, W.A., Tang, Z.C., 2004: Alkali grass resists salt stress through high [K+] and an endodermis barrier to Na+. J. Exp Bot., 55: 939–949. doi:10.1093/jxb/erh071PMid:15020645
Rhoades, J.D., Miyamoto, S., 1990: Testing soils for salinity and sodicity. In Westerman, R.L. (eds), Soil testing and plant analyses. Soil Science Society of America Medison, Wisconsin, p. 299–333.
Robinson, P.H., Grattan, S.R, Getachew, G., Grieve, C.M., Poss, J.A, Suarez, D.L., Benes, S.E., 2004: Biomass accumulation and potential nutritive value of some forages irrigated with saline-sodic drainage water. Anim. Feed Sci. Technol., 111: 175–189. doi:10.1016/S0377-8401(03)00213-X
Shi, D.C., Yin, S.J., Yang, G.H., Zhao, K.F., 2002: Citric acid accumulation in an alkali-tolerant plant *Puccinellia tenuiflora* under alkaline stress. Acta Bot. Sin., 44: 537– 540.
Stelzer, R., Lauchli, A., 1978: Salt and flooding tolerance of Puccinellia peisonis. III.Distribution and localization of ions in the plant. Zeitschrift für Pflanzenphysiologie, 88: 437–448.
Strogonov, B.P., 1964: Physiological basis of salt tolerance in plants. New York, Academy of Science USSR & Davey & Co., 285 pp.
Vevle, O., 1985: The salt marsh vegetation at Vinjekilen Bamble, SE Norway, with special reference to the *Puccinellietum maritimae*. Vegetatio, 61: 55–63. doi:10.1007/BF00039810
Vučković, R., 1985: Phytocoenoses of the halophytic vegetation of the east Potamisje and their nutritive value (in Serbian). PhD Thesis, Faculty of Biology, University of Belgrade, p. 1–220.
Waisel, Y., 1972: Biology of halophytes. Academic Press, New York and London.
Warren, B.E., Casson, T., Ryall, D.H., 1994: Production from grazing sheep on revegetated saltland in Western Australia. In Squires, V.R., Ayoub, A.T. (eds), Halophytes as a resource for livestock and for rehabilitation of degraded lands. Kluwer Academic Publishers, Dordrecht, p. 263–265.
Yokoi, S., Bressan, R.A., Hassegawa, P.M., 2002: Salt stress tolerance of plants. JIRCAS Working Report, p. 25–33.