Growth and mineral nutrition of two *Triglochin* species from saline wetlands: adaptation strategies to conditions of heterogeneous mineral supply

Andis Karlsons[1]*, Anita Osvalde[1], Gederts Ievinsh[2]

[1]Department of Plant Mineral Nutrition, Institute of Biology, University of Latvia, Miera 3, Salaspils LV-2169, Latvia
[2]Department of Plant Physiology, Faculty of Biology, University of Latvia, Kronvalda Bulv. 4, Riga LV-1586, Latvia

*Corresponding author, E-mail: andis.karlsons@email.lubi.edu.lv

Abstract

In addition to soil salinity and tidal regime, soil nutrient disbalance and ion toxicity affect plant growth in coastal wetlands. The aim of the present study was to examine the effect of soil mineral nutrient availability and salinity on growth, mineral nutrition, and proline content of two closely related wetland monocotyledonous species, *Triglochin maritimum* and *Triglochin palustre*. Growth of leaves of *T. maritimum* was lowest in natural soil and increased towards optimum conditions, while the opposite was true for *T. palustre*. Growth at gradually decreasing soil concentration of N resulted in directly proportional decrease in tissue concentration of N in both studied species. In general, root tissues of both species accumulated significantly higher concentrations of micronutrients in comparison to leaf tissues. This was more pronounced for *T. palustre*, where root concentration of Fe, Mn, Zn and Cu was directly proportional to the respective substrate concentrations. However, both species accumulated identical concentrations of Fe, Mn, Zn and Mo in leaves. It is evident that in highly heterogeneous soil conditions *T. maritimum* and *T. palustre* can effectively regulate internal ion concentration without any negative consequences for growth. Proline content increased from optimum to natural soil conditions both in leaf and root tissues of both studied species. In conditions of highly heterogeneous soil nutrient availability as well as fluctuating soil salinity, both *Triglochin* species possess several mechanisms of adaptive value, including salinity-induced leaf succulence, accumulation of Na in vacuoles with counterbalancing high concentration of proline in cytoplasm, and preferential accumulation of micronutrients in roots.

Key words: adaptation, heterogeneity, mineral nutrition, proline, salinity, *Triglochin maritimum*, *Triglochin palustre*, wetlands.

Introduction

Plants in saline wetlands are predominantly affected by changes in soil salinity and tidal regime. However, recent studies suggest that a number of edaphic factors should be reconsidered as important, including root oxygen availability, nutrient disbalance and toxicity of several ions (Silvestri et al. 2005). In non-tidal sea-affected wetlands, regular soil flooding by sea water results in both temporaly and spatially changing soil salt content, oxygen concentration, redox balance etc., leading to drastic changes in availability of mineral nutrients (Ievinsh 2006). As highly heterogeneous soil conditions are constantly maintained, plants native to saline coastal wetlands should possess adaptive mechanisms to cope with soil heterogeneity.

Two species of genus *Triglochin* L. (Juncaginaceae) are usually found in temperate wetlands. Triglochin palustre is a rather common species not associated exclusively with saline conditions (Nienartowicz, Wilkon-Michalska 1993) while occasionally located in coastal habitats. It is argued that *Triglochin palustre* is excluded from saline wetland habitats with low nitrogen concentration, high salinity and soil waterlogging (Mulder et al. 1996). However, provision

of exogenous nitrogen did not result in increased plant growth, suggesting limitation mainly by physical factors.

Triglochin maritimum is a perennial species distributed mainly along coasts while inland saline areas in Europe are also occupied by the species (Lambracht et al. 2007). In contrast to *T. palustre*, *T. maritimum* is a typical leaf-succulent euhalophyte (Breckle 2002) that accumulates inorganic ions and proline as a compatible solute (Stewart, Lee 1974; Jefferies et al. 1979). *T. maritimum* is characterized as an exceptional Na accumulator among monocotyledons, with a K/Na uptake ratio less than 1. The salinity tolerance mechanism is associated in part with accumulation of both Na and Cl in the vacuole (Jefferies 1973). *T. maritimum* is suggested to be more tolerant to salinity when flooded and vice versa (Rozema et al. 1985).

In natural conditions, competition for light is an important factor for growth of *T. maritimum* in conditions of a salt marsh (Mulder et al. 1996). Ability to tolerate high soil salinity may be adaptive for the species in a situation when the growth of neighboring species is inhibited by increased salinity or soil waterlodging. Another species of the genus, *T. bulbosa*, was not affected by up to 150 mol m^{-3} NaCl in conditions of hydroponic culture, while at 300 mol

m^{-3} NaCl, total dry biomass was reduced by 21% (Naidoo, Naidoo 2001). For this species, increase in substrate N was shown to significantly increase proline concentration both in roots and shoots, while shoot biomass accumulation and shoot N content was linearly correlated with the medium N concentration (Naidoo, Naidoo 2001).

The aim of the present study was to determine how the two closely related monocotyledonous plant species (*Triglochin maritimum* and *Triglochin palustre*), whitch have different ecological background, respond to changes in soil edaphic conditions, e.a., mineral nutrient availability and soil salinity. More specifically, it was asked to determine the mechanisms used by the two species to adapt to highly heterogeneous soil conditions of saline wetland soil. Shoot and root growth was used to determine possible limitation by these factors. Analysis of mineral constituents in both root and leaf tissues was used to assess possible strategies of mineral translocation and accumulation. Proline accumulation in adaptation to suboptimal conditions was considered.

Materials and methods

Soil samples from natural coastal habitats in Latvia with *T. maritimum* present were collected during the vegetation season of 2007. In total, 12 soil samples with three subsamples each were collected and analyzed separately for plant-available nutrient concentrations, Na, Cl, pH and electrical conductivity as described previously (Druva-Lūsīte et al. 2008).

For mineral nutrient availability experiments, three treatments with gradually changing mineral constituent levels were used (Table 1). As a control, nutrient levels optimal for the majority of crop species were used (Osvalde 2011). Based on the analysis of soil nutrient concentrations in coastal habitats with *T. maritimum*, a natural treatment mineral composition was established. A third treatment was an intermediate between the two former in relation to respective mineral nutrient concentrations.

Cultures of *T. maritimum* and *T. palustre* were established from seeds collected from wild populations in coastal habitats of Latvia. Seeds were individually sown in plastic pots (7 cm in diameter, 13 cm deep) filled with appropriate substrate that consisted of quartz sand plus mineral nutrients. A batch of 30 individual plants in three replicates per treatment was used. Plants were cultivated in a growth chamber, temperature 20 ± 2 °C. Illumination was provided by fluorescent lamps with 16-h photoperiod, photosynthetically active radiation of 120 μmol m^{-2} s^{-1}. Plants were watered when necessary with deionized water. The experiment was terminated one month after establishment.

For analysis of mineral constituents, plant material (leaves or roots) was oven-dried at 60 °C and finely ground using a ball mill. Samples were dry-ashed in concentrated HNO$_3$ vapours and re-dissolved in 3% HCl. Nutrient concentrations in extracts were measured by atomic absorption spectrophotometry (Ca, Mg, Fe, Cu, Zn, Mn), colorimetry (N, P, Mo, B) and flame photometry (K, Na) by the method of Rinkis et al. (1987) as described previously (Karlsons et al. 2008). Soil Cl was determined by AgNO$_3$ titration by the method of Patnaik (1997) as described earlier (Karlsons et al. 2008).

Separate experiments were performed to analyze the

Table 1. Soil mineral nutrient concentrations for *Triglochin maritimum* sites in natural conditions and in experimental treatments used in the present study (mg L^{-1}). Data are means from 12 samples in three replicates each ± SE

Indication	Mean value ± SE in natural conditions	Range in natural conditions	Coefficient of variation (%)	Natural soil (3)	Intermediate soil (2)	Optimal soil (1)
Nitrogen (N)	44 ± 6	16 ÷ 63	50	60	100	130
Phosphorus (P)	237 ± 35	116 ÷ 534	50	250	150	80
Potassium (K)	97 ± 20	17 ÷ 225	71	120	125	170
Calcium (Ca)	8798 ± 1207	4525 ÷ 13888	48	9000	5000	1100
Magnesium (Mg)	1834 ± 152	738 ÷ 2500	29	2200	1200	200
Sulphur (S)	357 ± 126	48 ÷ 1650	122	250	150	60
Iron (Fe)	1655 ± 368	380 ÷ 4050	77	1600	800	60
Manganese (Mn)	98 ± 26	13 ÷ 355	93	80	40	3.5
Zinc (Zn)	23 ± 7	6 ÷ 75	93	20	10	1.5
Copper (Cu)	2.5 ± 0.6	0.5 ÷ 6.5	73	2.5	1.5	0.7
Molybdenum (Mo)	0.040 ± 0.004	0.01 ÷ 0.06	32	0.05	0.03	0.03
Boron (B)	5 ± 1	0.4 ÷ 12.5	76	4.5	2.5	0.3
Sodium (Na)	955 ± 177	235 ÷ 1900	59	900	500	0
Chlorine (Cl)	1214 ± 217	325 ÷ 2225	62	1300	700	0
pH	7.2 ± 0.3	5.4 ÷ 8.5	12	–	–	–
EC	5.9 ± 1.0	1.6 ÷ 12.6	56	–	–	–

putative effect of increased soil salinity and relative substrate moisture on proline accumulation in leaf tissues of *Triglochin* species. First, seeds were sown in quartz sand supplemented with optimal concentrations of mineral nutrients (Table 1) plus different concentrations of NaCl (0, 50, 100 mM). Plants were watered with deionized water when needed. Leaf proline concentration was measured after one month. Second, seeds were sown in a commercial neutralized (pH 5.9 ± 0.3) peat substrate KKS-1 (Laflora, Latvia) with mineral nutrients (NPK 15-10-20). Plants were watered with different concentrations of NaCl (0, 100, 200, 400 mM). This treatment resulted in accumulation of extremely high concentrations of both Na and Cl in the substrate (more than 7 g L^{-1} and 5 g L^{-1}, for Na and Cl, respectively, in soil treated with 400 mM NaCl). Leaf proline concentration was measured after one month. Third, seeds were sown in quartz sand supplemented with optimal concentrations of mineral nutrients. Plants were watered with deionized water to provide a constant level of substrate moisture at 30, 60 and 85%. Leaf proline concentration was measured after one month.

Proline content in plant tissues was determined according to Bates et al. (1973) using the ninhydrin method. Briefy, 100 mg of fresh tissues were homogenized in sulphosalicylic acid. Ninhydrin and glacial acetic acid (2 mL each) were added to the extract followed by heating at 100 °C for 1 h. After extraction with toluene, free toluene was quantified spectrophotometrically at 528 nm. As a standard, L-proline was used. Five samples per treatment were analyzed.

Statistical analysis was performed by KaleidaGraph version 4.03 (Synergy Software). Differences between the means were determined by a Tukey-Kramer test, P < 0.05.

Results

The main differences between mineral constituent concentrations in soils, native for *T. maritimum*, in comparison to optimum concentrations considered for the majority of crop species, was relatively low nitrogen (46%) and potassium (71%) concentration (Table 1). In addition, concentration of several minerals was at relatively high level, including phosphorus (313%), sulphur (417%), copper (357%), and molybdenum (167%). Extremely high concentrations were noted for calcium (more than 8-fold), magnesium (11-fold), iron (more than 26-fold), manganese (more than 22-fold), boron (15-fold), and zinc (more than 13-fold). Also, high sodium and chlorine ion concentrations indicated a significant impact of saline water on soils. Due to the extreme spatial and temporal variability in mineral constituent concentrations in native soils, exceeding 90% in the case of Mn and Zn, and even 120% for S (Table 1), the concentration of the mineral of interest in the particular microhabitat could be even more different from the theoretical optimum level.

Linear growth of leaves for *T. maritimum* was lowest in natural soil and increased towards optimum conditions, while the opposite was true for *T. palustre* (Fig. 1A). Root elongation did not depend on soil mineral composition for *T. maritimum*, while it had a tendency to decrease towards optimum conditions for *T. palustre* (Fig. 1B). Leaf fresh mass of *T. maritimum* decreased with decreasing substrate N content and concomitant increase in NaCl level (Fig. 2A). However, difference in leaf dry mass was evident only between optimum and intermediate treatments (Fig. 3A). For *T. palustre*, mass of both leaves and roots did not
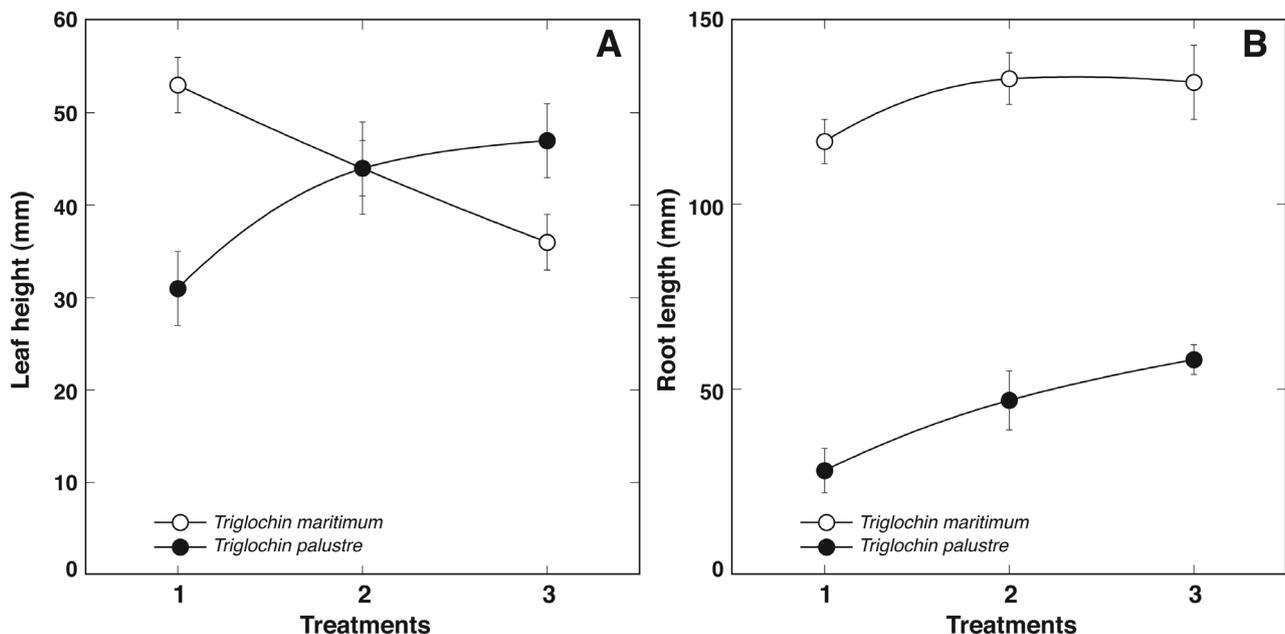

Fig. 1. Leaf height (A) and root length (B) in *Triglochin maritimum* and *Triglochin palustre* plants grown at different mineral nutrition treatments. Data are means from three replicates, 30 individual plants each ± SE.
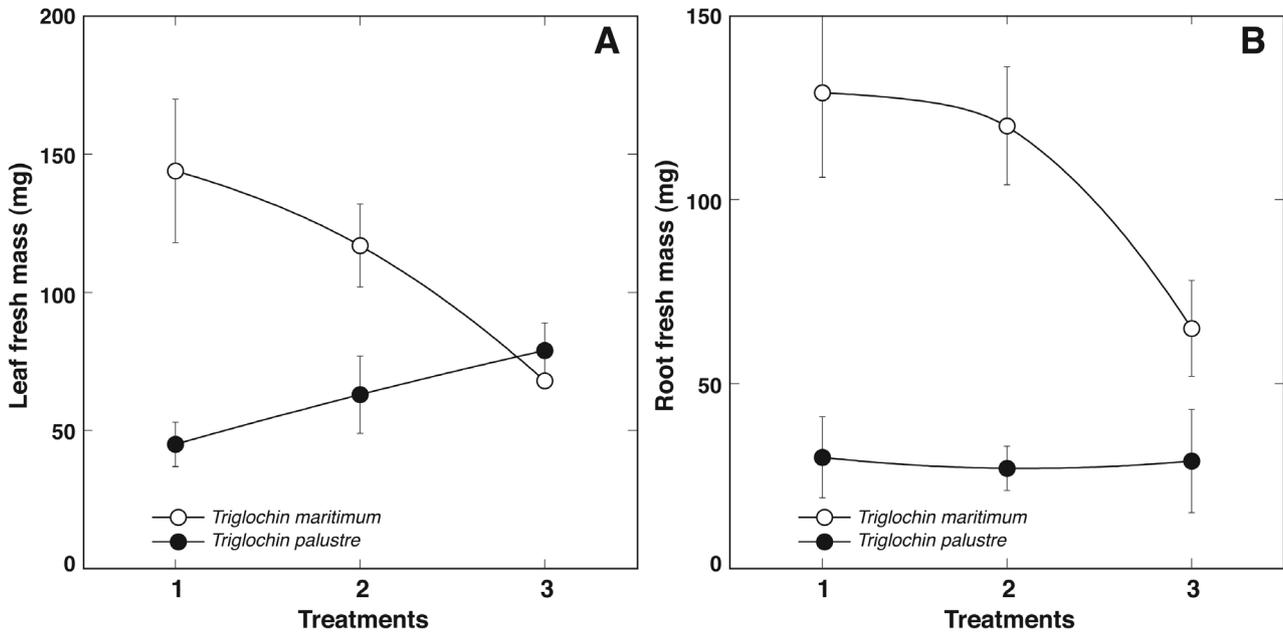
Fig. 2. Leaf fresh mass (A) and root fresh mass (B) of *Triglochin maritimum* and *Triglochin palustre* plants grown at different mineral nutrition treatments. Data are means from three replicates, 30 individual plants each ± SE.

differ between the treatments (Fig. 2). The degree of water content increased in *T. maritimum* leaves from optimum towards natural soil conditions, suggesting a salinity-induced increase in leaf succulence.

Growth at gradually decreasing soil concentration of N resulted in a directly proportional decrease in tissue concentration of N in both studied species (Table 2). Leaves of *T. maritimum* had significantly higher concentration of N in comparison to roots of *T. maritima* and both leaves

and roots of *T. palustre*. Increasing soil P concentration resulted in rather scattered and unpredictable tissue P concentration (Table 2). No significant changes were evident for K concentration in *T. palustre* and roots of *T. maritimum*, while in leaves of *T. maritimum* tissue concentration of K increased from optimum towards natural soil conditions (Table 2). Tissue Ca concentration did not change significantly in both leaves and roots of *T. palustre* (Table 2). However, in tissues of *T. maritimum*,
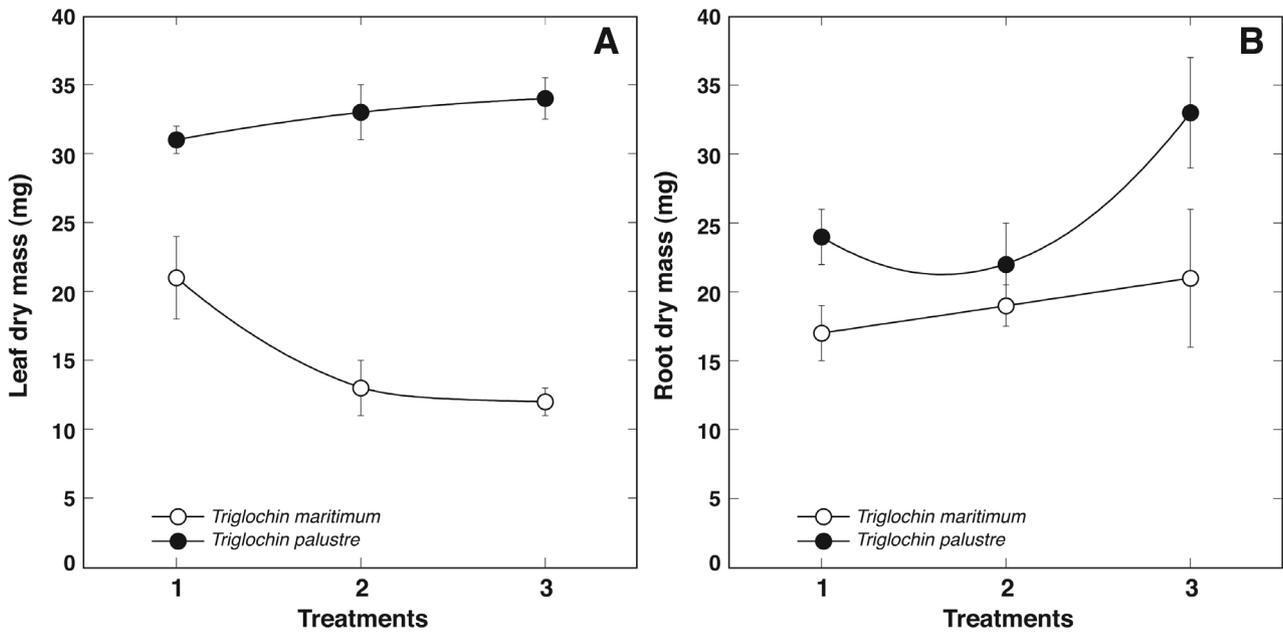

Fig. 3. Leaf dry mass (A) and root dry mass (B) of *Triglochin maritimum* and *Triglochin palustre* plants grown at different mineral nutrition treatments. Data are means from three replicates, 30 individual plants each ± SE.

Table 2. Mineral nutrient concentrations in root and leaf tissues of *Triglochin maritimum* and *Triglochin palustre* grown in different soils. Macronutrients (N, P, K, Ca, Mg, S) are expressed as % of dry mass; micronutrients (Fe, Mn, Zn, Cu, Mo) – as mg kg^{-1} dry mass; Na – as % of dry mass. Data are means from three independent measurements. Means with the same letter for every mineral are not significantly different from each other (Tukey-Kramer test, $P < 0.05$)

Mineral	Optimal soil (1)				Intermediate soil (2)				Natural soil (3)			
	Triglochin maritimum		*Triglochin palustre*		*Triglochin maritimum*		*Triglochin palustre*		*Triglochin maritimum*		*Triglochin palustre*	
	Leaves	Roots	Leaves	Roots	Leaves	Roots	Leaves	Roots	Leaves	Roots	Leaves	Roots
N	3.60 a	2.00 c	1.40 def	1.52 cde	2.80 b	0.96 efgh	1.36 defg	1.00 efgh	1.73 cd	0.56 h	0.75 h	0.42 h
P	0.31 cde	0.66 a	0.41 abcde	0.67 a	0.46 abcd	0.61 ab	0.34 bcde	0.21 de	0.48 abcd	0.51 abc	0.51 abc	0.13 e
K	2.85 c	1.50 f	3.00 c	2.44 cd	5.30 b	2.25 de	2.75 cd	2.46 cd	6.50 a	1.80 ef	3.00 c	1.39 f
Ca	0.81 d	0.32 efg	0.08 g	0.25 efg	1.10 c	0.42 e	0.15 fg	3.75 a	0.30 efg	0.38 ef	0.12 fg	1.64 b
Mg	0.08 c	0.06 cd	0.04 d	0.07 cd	0.08 c	0.05 cd	0.05 cd	0.07 cd	0.17 b	0.05 cd	0.21 a	0.15 b
S	0.45 a	0.21 c	0.41 ab	0.32 abc	0.43 a	0.20 c	0.37 ab	0.28 bc	0.38 ab	0.28 bc	0.36 ab	0.20 c
Fe	130 f	500 e	65 f	1780 c	100 f	1250 d	130 f	3800 b	375 e	1900 c	170 f	6944 a
Mn	85 g	140 fg	31 g	360 ef	220 fg	750 d	155 fg	1080 c	525 de	5250 a	240 fg	1694 b
Zn	37 g	80 e	42 g	134 cd	46 g	115 d	55 fg	225 b	75 ef	150 c	87 e	306 a
Cu	11.0 fg	12.5 defg	4.0 g	20.0 cd	14.0 cdef	22.5 bc	7.0 fg	28.0 b	17.5 cde	30.0 b	10.0 efg	47.0 a
Mo	1.88 f	1.38 f	1.75 f	3.00 e	3.50 de	2.88 e	3.13 de	6.50 c	8.75 b	3.75 d	3.50 de	9.72 a
Na	0.29 e	0.12 f	0.05 f	0.13 f	0.96 b	0.28 e	0.40 d	0.76 c	1.75 a	0.38 de	0.72 c	0.75 c

growth at intermediate soil nutrient supply resulted in an extreme increase of root Ca concentration. Both leaves and roots of *T. palustre* and leaves of *T. maritimum* had relatively high concentration of Mg in conditions of natural soil in comparison to optimum and intermediate treatments (Table 2). Tissue concentration of S did not change significantly with change in substrate mineral constituent concentration. However, it slightly decreased in leaves of both species and in roots of *T. palustre* from optimum to natural conditions.

In general, root tissues of both species accumulated significantly higher concentrations of micronutrients in comparison to leaf tissues (Table 2). This was more pronounced for *T. palustre*, where root concentration of Fe, Mn, Zn and Cu was directly proportional to the respective substrate concentrations. However, both species accumulated identical concentrations of Fe, Mn, Zn and Mo in leaves, with a tendency to increase with increasing
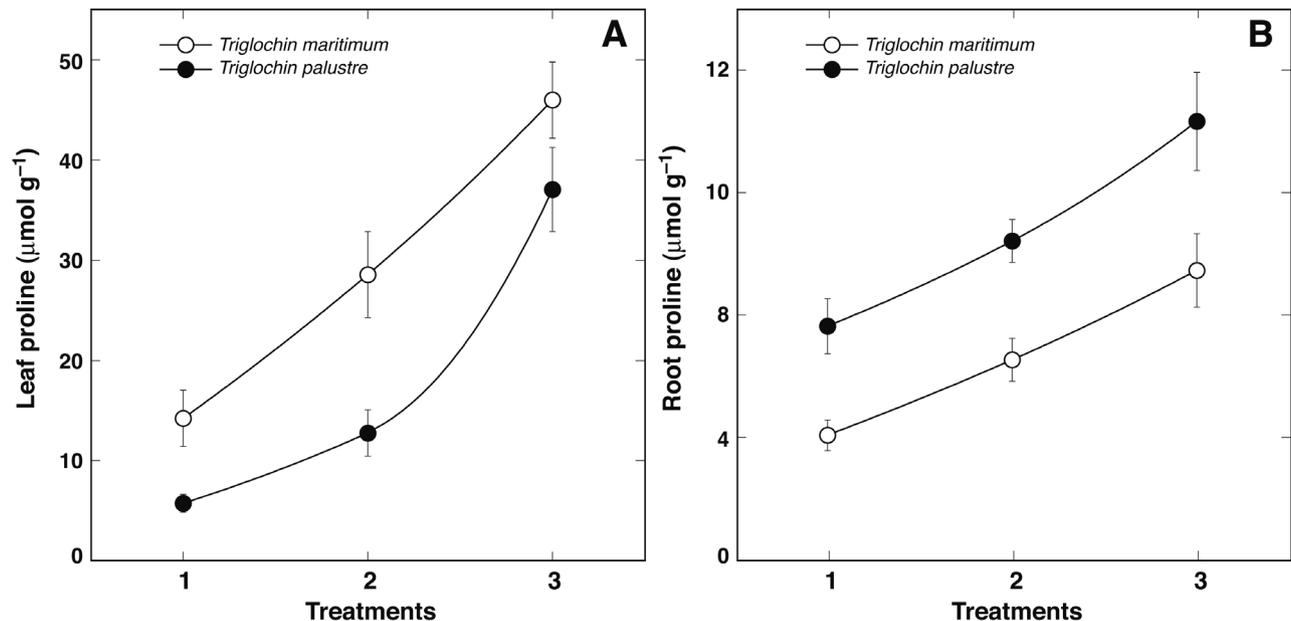

Fig. 4. Leaf (A) and root (B) proline concentration in *Triglochin maritimum* and *Triglochin palustre* plants grown at different mineral nutrition treatments. Data are means from five independent samples for each treatment ± SE.
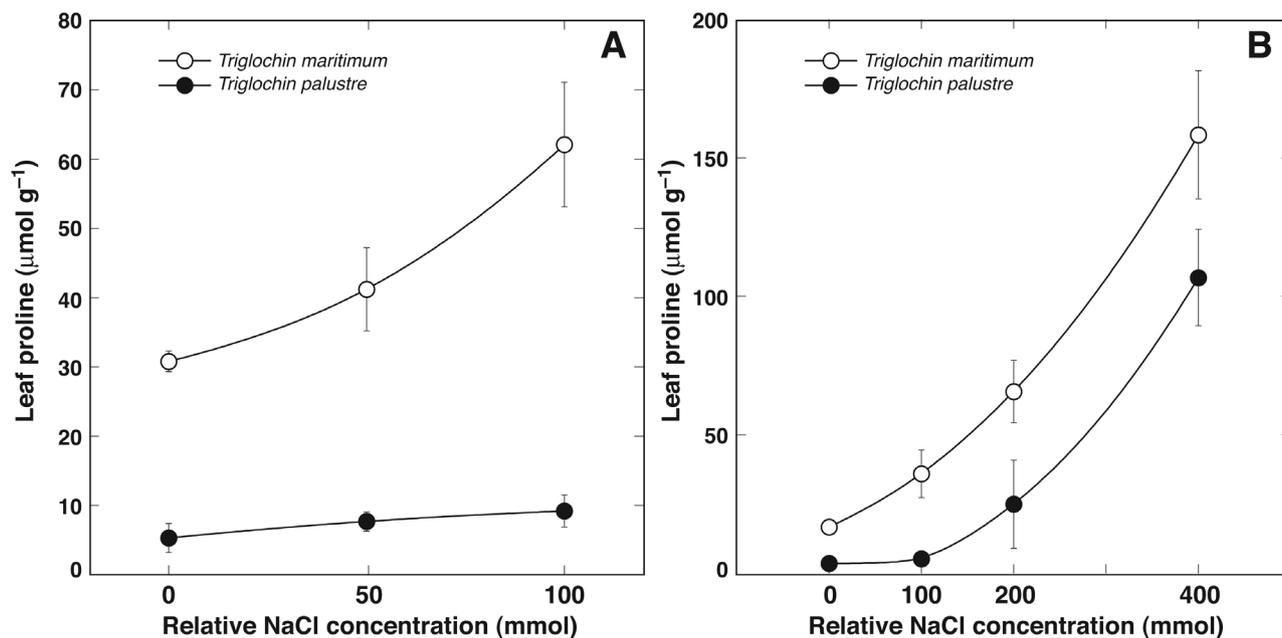
Fig. 5. Leaf proline concentration in dependence on NaCl concentration in soil (A) and in watering solution (B) for *Triglochin maritimum* and *Triglochin palustre* plants. Data are means from five independent samples for each treatment ± SE.

substrate concentrations for the respective mineral. In contrast to other elements leaves of *T. maritimum* had significantly higher Cu concentration in comparison to *T. palustre.*

For plants grown at different soil nutrient supply levels, there was a significant increase of proline concentration from optimum to natural conditions both in leaf and root tissues
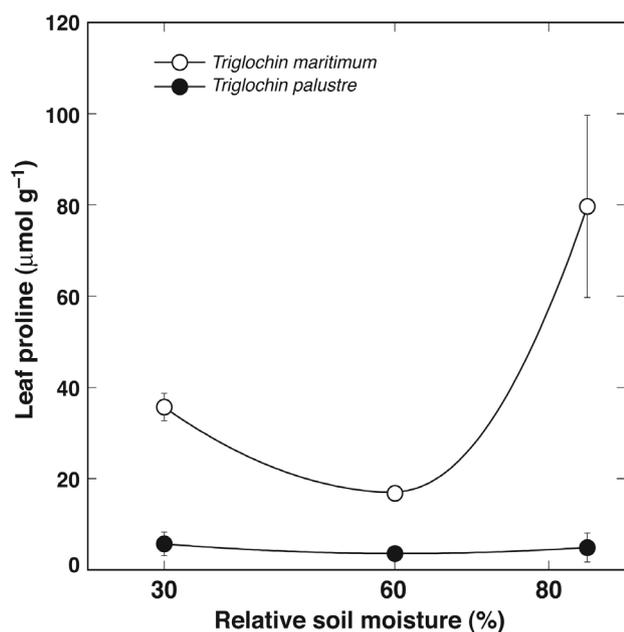

Fig. 6. Leaf proline concentration depending on soil moisture for *Triglochin maritimum* and *Triglochin palustre* plants grown at optimum mineral nutrition conditions. Data are means from five independent samples for each treatment ± SE.

of both studied species (Fig. 4). Leaves of *T. maritimum* had lower proline levels in comparison to *T. palustre*, while the opposite trend was evident for root tissues. A constant moderate soil NaCl level resulted in a tendency to have increased leaf proline concentrations in both species (Fig. 5A). However, the increase was not statistically significant and was not proportional to the tissue Na concentration. Leaf proline concentration increased in leaves of both species only when regular watering with NaCl solution in a high concentration resulted in extreme buildup in respective soil Na and Cl concentrations, (Fig. 5B). Both decreased (30%) and increased (85%) relative soil moisture resulted in significant increase in leaf proline concentration in *T. maritimum* in comparison to the control (60%) (Fig. 6). In *T. palustre* the change in proline concentration due to the change in relative soil moisture were not significant.

Discussion

Results from studies aimed at understanding of multiple interactions between mineral nutrients, mimicking natural conditions, are usually extremely difficult to interpret due to the complex relationship at both chemical and physiological levels. In the present study, an attempt was made to compare the effect of native mineral composition of wild species vs. gradual change towards a mineral supply optimal for the majority of crop species of humid and subhumid soils of temperate regions (Osvalde 2011). In the present study, soils native for *T. maritimum* were characterized by relatively low nitrogen and potassium concentration together with high or extremely high concentrations of other nutrients, as well as Na and Cl. Several of these minerals were clearly

in the zone of potential toxicity, especially regarding iron and manganese. As a result, in the present experimental system, low nitrogen content (with potentially growth-limiting effect) was accompanied by potentially toxic concentrations of several mineral constituents, including Na and Cl (again, with possible negative effect on plant growth). Consequently, due to this setup, it was not possible to discriminate between low nitrogen and high ion effects (especially, Na and Cl) in the present study. As a partial solution to the problem, further studies should include additional treatment with low nitrogen and potassium concentration without high NaCl.

It is evident, based on the present results, that in highly heterogeneous soil conditions monocotyledonous plants *T. maritimum* and *T. palustre* can effectively regulate internal ion concentrations without any evident negative consequences for plant growth and development.

Toxic concentrations of micronutrients in plant tissues are in the range from 20 (Cu) to 100 (Fe and Zn) and up to 300 (Mn) mg kg^{-1} (Macnicol, Beckett 1985). In the present study, these levels were clearly exceeded in all tissues of both studied species for Fe, as well as in roots of both species for Mn, Zn and Cu. Tolerance to toxic concentrations of heavy metals of micronutrient nature, including Cu and Zn, is associated with enhanced translocation and higher root accumulation (Hart et al. 1998; Osvalde, Paegle 2005; Osvalde, Paegle 2006). Equally low levels of micronutrients in leaf tissues of both wetland species of *Triglochin*, as revealed in the present study, indicate efficient protection of photosynthetic tissues from excess metal concentration through higher root accumulation. As an additional protective measure against heavy metal stress, accumulation of proline in leaf tissues has been described (Osvalde, Paegle 2005). Higher concentration of free proline was evident in tissues of both *Triglochin* species in natural soils in comparison to optimal conditions, and also as a result of elevated substrate salinity and changes in soil moisture.

For vegetable crops, a 10 mg L^{-1} concentration of Cu in substrate resulted in toxicity symptoms and decreased productivity (28 and 82% of control level), with leaf concentrations of Cu more than 15 and 35 mg kg^{-1}, for lettuce and radish, respectively (Osvalde, Paegle 2005). Similarly, a 20 mg L^{-1} concentration of Zn resulted in toxicity symptoms and inhibition of biomass production (30 and 75% of control level, for lettuce and radish, respectively), with leaf Zn concentrations reaching 1000 and 600 mg kg^{-1}, respectively (Osvalde, Paegle 2006). In the present study, maximum Cu and Zn concentrations in natural soil treatment were 2.5 and 20 mg L^{-1}, respectively, resulting in comparable leaf concentrations of Cu as in the study described above (Table 2). However, leaves of *Triglochin* species grown in natural soil accumulated significantly lower amounts of Zn, reaching only 75 and 87 mg kg^{-1}, for *T. maritimum* and *T. palustre*, respectively (Table 2). Most importantly, no apparent toxicity symptoms or decreased

dry matter production were evident (Fig. 3). Consequently, plants native to soils with extremely high potential toxic fluctuating concentrations of micronutrients have the ability to regulate tissue concentrations of these ions, in contrast to vegetable crop species.

Higher Fe and Mn concentration in roots of salt-marsh plants in comparison to shoots have been reported, suggesting a possible mechanism of adaptation through ion translocation (Rozema et al. 1985). In natural conditions, *T. maritimum* accumulated as much as 9.1 mg g^{-1} of Fe and 0.27 mg g^{-1} of Mn in roots and 0.10 mg g^{-1} of Fe and 0.08 mg g^{-1} of Mn in shoots (Rozema et al. 1985). A similar range of concentrations was achieved in the natural soil treatment in the present experiments for Fe, while considerably higher concentrations were found for Mn (Table 2). High root porosity, characteristic for waterlogged individuals of *T. maritimum*, could contribute to efficient oxidizing capacity of roots in conditions of a salt-marsh, leading to resistance against high soil Fe and Mn levels.

As a rule, leaves of *T. maritimum* accumulated higher levels of proline as a result of suboptimal conditions in comparison to *T. palustre* (Fig. 4 to 6) indicating higher putative protection against endogenous osmotic and oxidative stress (Hare, Cress 1997). Proline concentration as high as 113 µmol g^{-1} has been reported for *T. maritimum* in natural conditions (Stewart, Lee 1974). In laboratory conditions, with non-limiting nitrogen supply, even 330 µmol kg^{-1} was exceeded for this species (Stewart, Lee 1974). Therefore, it is possible to assume that low N content in natural soil treatment could be limiting for high salinity-dependent accumulation of proline. However, in the present study, treatment with 900 mg L^{-1} Na and 500 mg L^{-1} Cl together with 60 mg L^{-1} N resulted in a concentration of 46 µmol g^{-1} proline (Fig. 4A), while 41 µmol g^{-1} of proline accumulated when a concentration of NaCl (50 mM) was applied together with 130 mg L^{-1} N (Fig. 5A). Consequently, substrate N concentration was not limiting salinity-dependent accumulation of proline. Even at lower N supply, high substrate salinity resulted in accumulation of 162 µmol g^{-1} of proline in leaf tissues of *T. maritimum* (Fig. 5B).

It is evident from the present results that shoot linear growth of *T. palustre* is not limited by low nitrogen content or high soil salinity in contrast to *T. maritimum,* which is significantly inhibited (Fig. 1). However, similar to the present results, increased soil salinity (340 mM NaCl) did not result in decrease of shoot or root dry mass of *T. maritimum* within two months of treatment (Cooper 1982). In the same study, soil salinity induced increase in shoot Mn and Fe concentration of *T. maritimum*, but the effect was not statistically significant (Cooper 1982). Plants of *T. bulbosa* were not affected by up to 150 mol m^{-3} NaCl in conditions of hydroponic culture, while at 300 mol m^{-3} NaCl total dry biomass was reduced by 21% (Naidoo, Naidoo 2001). Consequently, different *Triglochin* species

show a relatively high level of resistance against increased substrate salinity.

In conditions of highly heterogeneous soil nutrient availability as well as fluctuating soil salinity, both *Triglochin* species possess several mechanisms of adaptive value. First, salinity-induced leaf succulence results in dilution of absorbed inorganic ions in *T. maritimum*. Second, accumulation of Na in vacuoles of photosynthetic cells with counterbalancing high concentration of proline or/and other compatible solutes in cytoplasm protects cytoplasmic constituents against ion toxicity and osmotic stress. Third, preferential accumulation of micronutrients in roots protects against metal toxicity in photosynthetic tissues.

Acknowledgements

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