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Effects of seasonal changes of soil salinity and soil nitrogen on the N-metabolism of the halophyte *Arthrocnemum fruticosum* (L.) Moq.

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Summary The N-metabolism of *Arthrocnemum fruticosum* (L.)Moq., growing in a saline area north-east of the Dead Sea in Jordan, was studied over its vegetative growth period from March to September 1981. Plant and soil samples were taken at monthly intervals. Water content, Na^+, K^+, Cl^-, NH_4^+, NO_2^- and NO_3^- concentrations were determined in the soil extracts, and the same determinations plus ash weight, soluble carbohydrates, proline, proteins and *in vivo* nitrate reductase in the plant roots and shoots.

Soil humidity decreased and salinity increased from March to August, with re-wetting occurring in late July. K^+ and Cl^- were much lower in the soils than Na^+. Plant relative dry weight increased during summer due to the absorption of Na^+ in addition to increased organic dry weight. The uptake of Na^+ was not balanced by a similar uptake of Cl^-.

Ammonium and nitrate decreased in soil and plants in parallel with increasing salinity. Nitrite was only found in the roots and always in very low quantities. Proline was found only in March. The total soluble carbohydrates in the roots showed a short increase in June when the sodium in the plants also increased. It was concluded that carbohydrates may be used to balance osmotic shocks, but that another compatible compound is necessary to maintain long-term osmotic equilibrium.

The nitrate reductase activity, measured *in vivo*, and the soluble protein changed roughly in parallel with the internal nitrate from May to August, suggesting that nitrogen uptake and reduction in the plant is inhibited during summer when the soil is dry and very saline. This could be a direct effect of drought and/or salinity on the plants, or an indirect one *via* an inhibition of nitrifying bacteria.

Introduction

Millions of hectares of arable land are too saline for agriculture, and hundreds of thousands of hectares more of previously agriculturally productive land are lost annually for food production due to salinization[20]. The fact that such soils cannot sustain food crops does not exclude vegetation with halophytic plants, which are well-adapted to the salt- and water-stress which prevent the growth of most crops. Growth of all plants is dependent on an adequate supply of minerals. Quantitatively one of the most important is nitrogen. Therefore, study

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of the nitrogen uptake and metabolism under saline conditions may provide valuable information about the survival strategy of halophytes.

Nitrogen, which is available to plants, is produced mainly by the mineralization of organic matter by several species of soil micro-organisms. The effects of NaCl on N mineralization is not yet extensively investigated[29], but there are indications that ammonification is less affected by salt than nitrification[22].

In a previous paper on the same study area and in the same period of time as the studies reported here, we showed that there was a relationship between soil salinity, soil-nitrogen concentration and the activity of nitrifying organisms[24]. Nitrate is taken up from the soil by higher plants in an active process[9], after which it is reduced by nitrate reductase (NR*) and nitrite reductase (NiR) to ammonium. Ammonium is subsequently incorporated into amino acids by the reductive amination of glutamic acid and further transaminations[25].

The effects of salinity on NR are complex and work published in this field is sometimes contradictory. Generally *in vivo* activity may be either stimulated[5, 31], not affected[27], or inhibited[16, 17, 28]. The effects of NaCl on nitrite reductase have been less studied, but it seems to be less affected than NR[17]. The *in vitro* activity of glutamate synthase was reduced by NaCl in the glycophyte Phaseolus as well as in the halophyte Suaeda[8].

The present paper reports on a study of the effects of soil salinity on the nitrogen metabolism of the halophyte *Arthrocnemum fruticosum* near the Dead Sea in Jordan, from germination of the plants to flowering. The salinity of the soil was followed throughout the season and related to the mineral nitrogen concentration of soil and plants, and to some plant parameters. Nitrate reductase activity (*in vivo*) was chosen as an indicator of nitrate reduction rate, and total soluble protein as an indicator of N-incorporation. Soluble carbohydrates and proline were determined as indicators of osmotic stress[3].

Materials and methods

Description of study area and collection procedure

Arthrocnemum fruticosum (L.)Moq. was collected from an area north-east of the shore of the Dead Sea in Jordan. In winter, lasting approximately from December to March, the mean monthly precipitation is *ca* 15 mm; there is no summer precipitation[1]. The mean daily temperature ranges from *ca* 20°C in January to *ca* 40°C in August[1], but in the middle of the day temperatures of 50°C at ground level are common[24]. The soil is a relatively coarse sandy loam with low water-holding capacity, and solid rock is close to the surface. The top layer consists of a hard crust of fine silt and clay of *ca* 1 cm thick[30]. Since the area is surrounded on three

* Abbreviations: NR = nitrate reductase; NiR = nitrite reductase.

sides by roads on raised embankments and on the fourth by a sandy bank, drainage is poor and in winter the whole area easily becomes water-logged and changes from a dry desert to a muddy salt marsh. Plants were collected at monthly intervals from the earliest seedling stage in March until the flowering stage in September 1981. *In vivo* nitrate reductase activity was determined in the field. Each of the composite plant and soil samples was a mixture of at least four sub-samples collected at randomly determined sampling sites. The soil and plant samples were put in polyethylene bags, which were then closed airtight and brought to the lab for analysis.

Drying, ashing and extraction

Plant and soil samples were dried in an oven at 110°C for 24 hours. Water loss was calculated and expressed as a fraction of the fresh weight. Dried plant samples were ashed in porcelain crucibles on a Bunsen burner for up to 8 hours, until no more loss of weight occurred. Weight loss, representing the organic fraction, was expressed as a fraction of the dry weight before ashing.

Ten grams of fresh shoots or roots were cut in small pieces, homogenized and shaken with 100 ml of distilled water for three hours. The concentrations of Na^+, K^+, Cl^-, NO_2^-, NO_3^-, NH_4^+ and soluble proteins were determined in this aqueous extract. Soils were extracted similarly, using 10 grams of fresh soil in 100 ml distilled water. The same determinations, except for protein, were done on these extracts.

The ash of the plant roots and shoots was shaken with 25 ml distilled water. Na^+, K^+ and Cl^- were determined in this extract.

For the determination of the soluble carbohydrates in the plants, 1 gram of fresh roots or shoots was homogenized and extracted in 20 ml of 95% (v/v) ethanol for three hours.

Sodium, potassium and chloride determinations

Sodium and potassium were determined in plant, ash and soil extracts by flame photometry after dilution to suitable concentrations. Chloride was determined by a colorimetric method as follows: one ml of reagent A (0.25 *M* ferric ammonium sulfate in 9.0 *N* HNO_3) and one ml of reagent B (saturated solution of mercuric thiocyanate) were added to 10 ml diluted plant, ash or soil extract and vigorously shaken after each addition for 20 seconds on a Vortex mixer. After 10 minutes the absorbance at 460 nm was measured in a Spectronic 20 spectrophotometer.

Inorganic nitrogen determination

Ammonium was determined with a Philips ammonia electrode in a strongly alkaline solution. Nitrate was also determined with this electrode, after reducing it to ammonia with Devarda's alloy at room temperature overnight (modified from [32]). This method resulted in a 99–100% recovery of the nitrate as ammonia.

Nitrite was determined with 1% (w/v) sulfanilamide in 1 *N* HCl and 0.01% (w/v) N-(1-naphthyl)-ethylenediamine dihydrochloride in distilled water, according to Snell and Snell [35]. Ammonium, nitrite and nitrate were expressed in μg N/g fresh plant or soil.

Soluble protein and carbohydrate determinations

Protein was determined in the aqueous plant extracts with the Folin phenol reagent [23]. Soluble carbohydrates were determined in the alcoholic plant extracts with the anthrone reagent [10], using glucose as a standard.

Nitrate reductase in vivo

Essentially the method of Jaworski [19] was used to determine the *in vivo* NR activity. Preliminary experiments, however, resulted in the following adapted procedure: Plants were collected and the roots and the green parts of the shoots were cut into small pieces in the field. The amount of sample was measured as a volume, using small test tubes with calibrations, corresponding to *ca* 1.0 g for the shoots and *ca* 0.5 g for the roots. The plant pieces were put into twelve test tubes per sample. Each test tube was wrapped in aluminum foil. Five ml of an

assay medium were added to each test tube. The assay medium contained 865 ml K-phosphate buffer (0.1 *M* K_2HPO_4 and 0.1 *M* KH_2PO_4; pH = 7.5); 95 ml KNO_3 0.6 *M*; 30 ml n-propanol, 100% and 10 ml chloramphenicol, 0.05% (w/v) per liter. The test tubes were closed with a rubber stopper and incubated in a waterbath at *ca* 30°C, kept at that temperature by adding cold or warm water from thermos flasks. No N_2 was bubbled through and no vacuum infiltration was applied.

After 0, 30, 60 and 90 minutes incubation, three tubes were boiled in a 100°C waterbath for 5 minutes and stoppered again. After all the tubes had been treated like this, they were brought back to the lab for the nitrite determination. One ml samples were taken from each test tube and filtered through a millipore filter (pore size 0.22 μm) to remove debris. Two ml reagent A (1% w/v sulfanilamide in 1 *N* HCl) and two ml reagent B (0.1% w/v N-(1-naphthyl) ethylenediamine dihydrochloride in distilled water) were added to the filtrate and mixed well. After 30 minutes the absorbance at 540 nm was measured in a Spectronic 20 spectrophotometer. Nitrate reductase activity was expressed as μg N (in the form of NO_2^- produced per hour per gram fresh weight of shoots or roots.

Proline

Proline was determined according to Bates *et al.*[7]. All determinations were done in triplicate.

Results

Water content of the soil

The water content of the vegetated soil expressed as the percentage of water in fresh soil was *ca* 36% in the top layer and *ca* 30% at 5 cm depth during the months of March, April and May, but dropped sharply to *ca* 5% and 10% respectively for the two layers in June, July and August. In the soil without plants the water content in the top layer was *ca* 12% in the first three months, whereas at a depth of 5 cm it was *ca* 13% at that time. Again a sharp decline was observed in June and values of 5% in the top layer and 9 to 5% at 5 cm depth were observed in June and July. In August the water content at 5 cm had risen again to 9% in the soil carrying plants, and to 16.5% in the bare soils (Table 1).

Table 1. Moisture percentage in the soils

	Moisture percentage					
Soil samples	March	April	May	June	July	August
A0	36	36	30	6	4	2
A5	32.5	30	20	10	6	9
B0	12	12	12	5	5	5
B5	16	13	13	9	5	16.5

A: vegetated soils; B: bare soils. 0: at the surface of the soil; 5: at 5 cm depth in the soil.

Salinity of the soil

The sodium concentration, expressed as mg/g fresh soil, increased in the surface of the soil from below the limit of detection in March to 380 mg/g in August. This increase was rather regular, with the exception of July, when an unexpected low value (20 mg/g soil) was found (Figure 1, A0). A similar pattern was observed in the surface of the soils without plant cover (Figure 1, B0). At 5 cm below the surface the increase with time of sodium in the soil was less clear, but nevertheless present, both with and without plants (Figure 1, A5 and B5). Potassium concentrations were always low; in many cases below the limit of detection with our method. Chloride concentrations were also low in these soils and, except in August, there was no clear increase with time.

Fresh, dry and ash weights of the plants

During the growth of the plants from tiny seedlings of less than 0.2 g fresh weight in March to grown plants of more than 2 grams in August, the relative dry weight (dry weight in g/g fresh weight) increased from 0.20 to 0.85 in the root and from 0.08 to 0.25 in the shoot. Of this dry weight the relative ash weight (ash weight in g/g dry weight) remained approximately constant at 0.2 (Table 2).

Salinity of the plants

The sodium concentration, expressed as mg/g fresh plants, were low in both shoots and roots in March and April (*ca* 1 mg/g). In May there was a marked increase of Na^+ in the shoots, followed in June by a similar increase in the roots (to *ca* 17 mg/g). In July both roots and shoots still contained high Na^+ concentrations (21 mg/g and 15 mg/g respectively), but the root concentration of Na^+ declined clearly in the August samples (7 mg/g), whereas the shoot concentration remained high at 16 mg/g (Figure 2a). The chloride concentrations in both roots and shoots fluctuated around 7 mg/g fresh weight from March to August (Figure 2b). If these analyses were expressed per gram of plant ash, the situation was quite different: the sodium concentration of both shoots and roots fluctuated irregularly around a value of about 150 mg/g ash, without any increase or decrease with time (Figure 3a). Chloride on the other hand showed a high concentration especially in the root in March (460 mg/g ash), followed by a decrease to less than 100 mg/g ash in August. In March and April the chloride concentration of the root was higher than that of the shoot. From May onwards the reverse was true (Figure 3b).

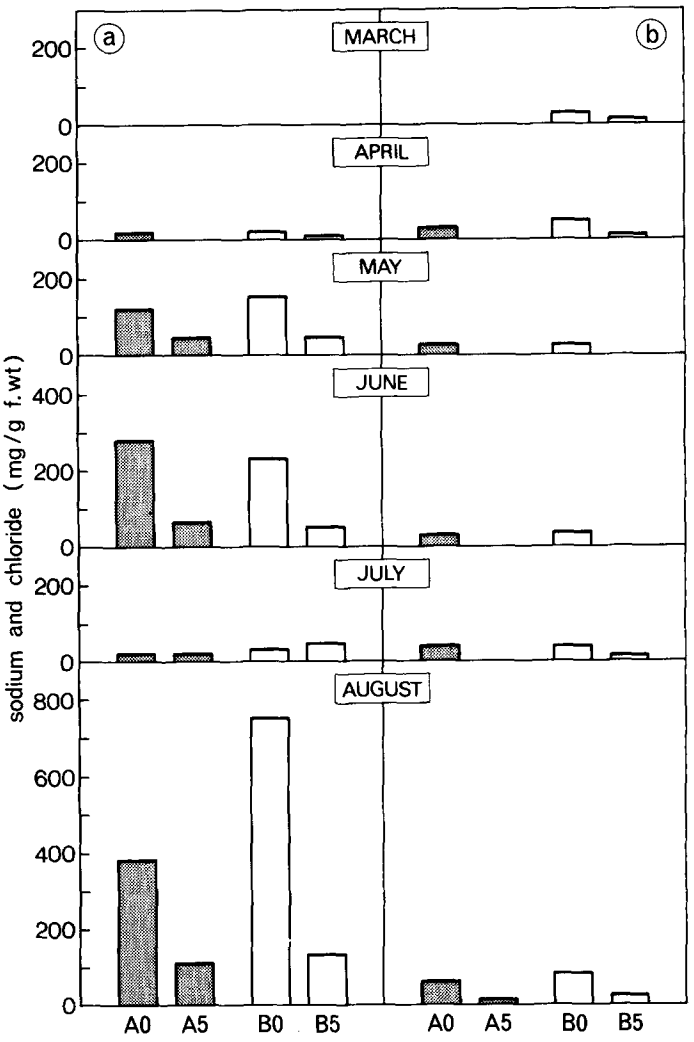

Fig. 1. Salinity of the soil. a.: sodium; b.: chloride; A: vegetated soil; B: bare soil, 0: at the surface; 5: at 5 cm depth.

Ammonium and nitrate in the soils

Ammonium in the surface soils decreased from about 19 μg N/g soil in April to 1 μg N/g in August (March was not determined. Figure 4a, A0). There were similar changes in the soils without plant cover (Figure 4a, B0). At 5 cm below the surface, where the bulk of the roots was found, ammonium was very low throughout the whole period (Figure 4a, A5). In the soils without plant cover ammonium at 5 cm below the surface was lower than in the surface layer, but usually somewhat higher than in the soils with plants (Figure 4a, B5).

Table 2. Fresh, dry and ash weights, water contents and organic matter of the plants

Month	Dry weight (g/g f.wt)		Ash weight (g/g d.wt)		Humidity (g/g f.wt)		Org. matter (g/g d.wt)	
	R	S	R	S	R	S	R	S
March	0.20	0.08	0.32	0.40	0.80	0.92	0.68	0.60
April	0.40	0.11	0.16	0.47	0.60	0.90	0.84	0.53
May	0.48	0.13	0.18	0.46	0.52	0.87	0.82	0.54
June	0.70	0.20	0.23	0.47	0.30	0.80	0.77	0.53
July	0.77	0.22	0.22	0.42	0.23	0.78	0.78	0.58
August	0.85	0.25	0.20	0.38	0.15	0.75	0.81	0.63

Determinations were done as described in the text. R: roots; S: shoots.

Nitrate in the surface soils with plants increased from March to April, but decreased again in May. After that it stayed more or less constant at 15 μg N/g soil (Figure 4b, A0). At 5 cm depth the nitrate concentration decreased steeply from March to April and stayed afterwards on very low values (Figure 4b, A5). In the soils without plant cover the nitrate concentration in both the surface layer and

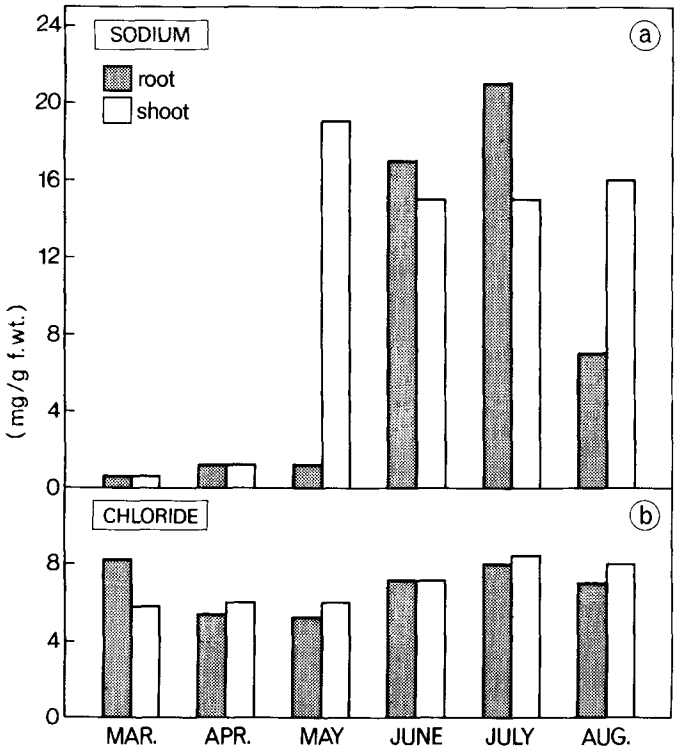

Fig. 2. Salinity of the plants. a: sodium; b: chloride.

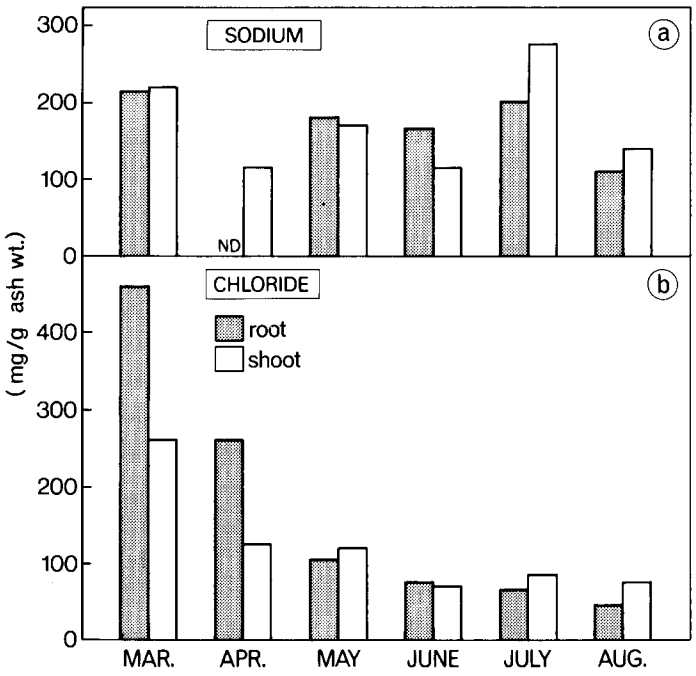

Fig. 3. Salinity of the ash of the plants. a: sodium; b: chloride.

at 5 cm depth was low (Figures 4b, B0 and 4b, B5). In July all values of ammonium and nitrate were zero.

Ammonium and nitrate in the plants

Ammonium in shoots and especially roots decreased from March (25 μg N/g and 50 μg N/g respectively) to April (*ca* 12 μg N/g), after which it remained at 10 to 15 μg N/g in the roots, but gradually declined to 1 μg N/g in the shoots, in July. In August there was a slight increase again to 20 μg N/g in the roots and 15 μg N/g in the shoots (Figure 5a).

Nitrate showed a similar pattern, but more extreme. From 90 μg N/g nitrate in the roots in March, it declined to *ca* 5 μg N/g in April and *ca* 1 μg N/g in July, after which it suddenly soared up to 50 μg N/g in August. In the shoot the nitrate went down first from 30 μg N/g in March to *ca* 2 μg N/g in June and then up again to 75 μg N/g in August (Figure 5b). Nitrite was found only in the roots and always in quantities less than 1 μg N/g fresh weight (not shown).

Total soluble carbohydrates and proline

The total soluble carbohydrate concentration was less than 1 μg/g fresh weight in both the shoots and the roots during the first months

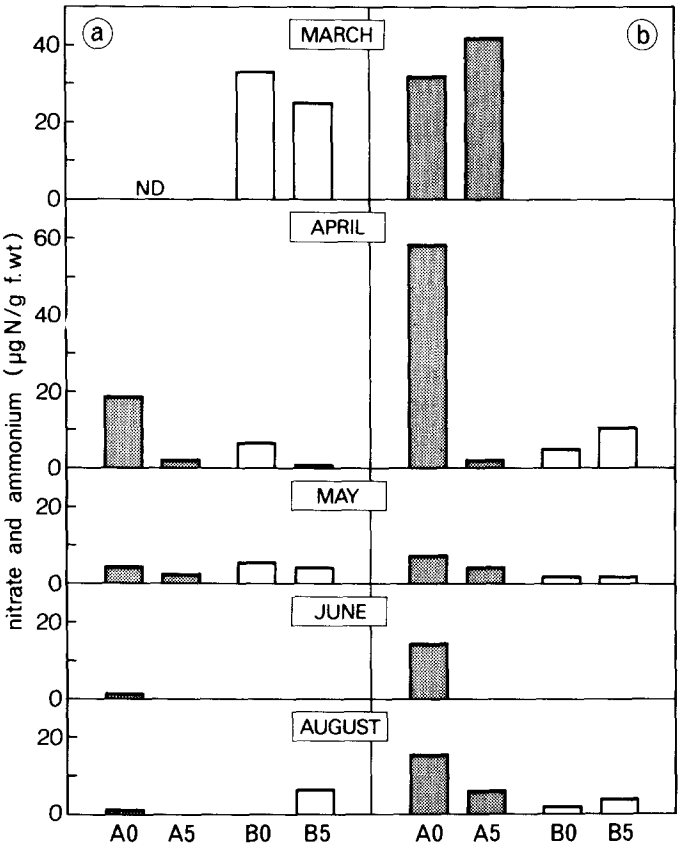

Fig. 4. Inorganic N in the soil. a: ammonium; b: nitrate; A: vegetated soils; B: bare soils; 0: at the surface of the soil; 5: at 5 cm depth in the soil. In July all values were zero.

of the growing season (March–May). In June there was a small increase in the roots to *ca* 3 µg/g which steadily declined again to about 1 µg/g in August. There was no change in the soluble carbohydrate concentration of the shoots (Figure 6a). Proline was found only in March (1.4 µ*M*/g fresh weight) and only in the shoots of the plants.

Nitrate reductase activity

In the roots, *in vivo* nitrate reductase activity was only found in March (1.5 µg N/h · g) and April 1.6 µg N/h · g), and from May on no more NRa could be found. The NRa in the shoots increased from March to April from 0.2 to 0.9 µg N/h · g and thereafter it gradually decreased until it reached a value of 0.1 µg N/h · g in July. In August there was a small increase again to *ca* 0.3 µg N/h · g (Figure 6b).

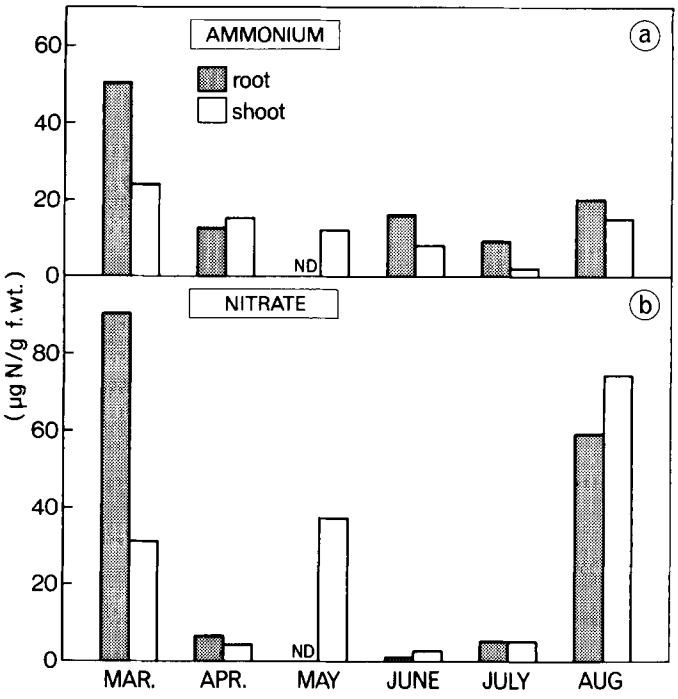

Fig. 5. Inorganic N in the plants. a: ammonium; b: nitrate.

Soluble proteins

The soluble proteins of the roots did not change appreciably from April to July and fluctuated around 0.5 mg/g fresh weight. In August there was an increase to *ca* 1.75 mg/g. The soluble proteins in the shoots showed larger fluctuations, increasing from 0.8 mg/g in March to 3.7 mg/g in April, after which there was a decline in May and June to 0.4 mg/g, followed again by an increase in July and August to 1.4 mg/g fresh weight (Figure 6c).

Discussion

The water content of the vegetated soil during March, April and May was around 30% and in the bare soil about 12% in the same period. In June there was a sudden drop of water content in both soils and the same low values were found in July. In August the water content at 5 cm depth increased in both soils, indicating a re-wetting of the soil some time after the July sampling, but before the August sampling. The re-wetting effect showed up in virtually all other determinations, as well as in the activity of the soil organisms[24]. The

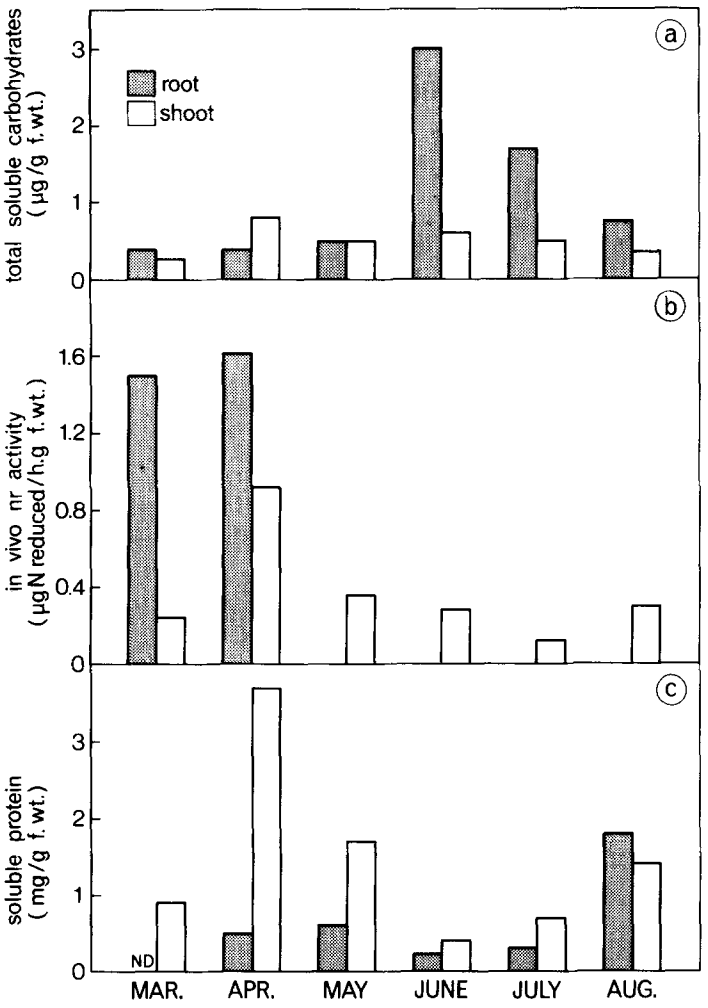

Fig. 6. Organic components in the plants. a: total soluble carbohydrates; b: in vivo nitrate reductase; c: soluble proteins.

salinity, expressed as Na^+, increased throughout the season, except for a sudden drop in July. The sodium concentration in the plants rose abruptly in May–June, coresponding to the drop in soil humidity. In summer, the chloride concentration in both shoots and roots was much lower than the sodium concentration, indicating that Na^+ and Cl^- are not taken up stoichiometrically upon increasing soil salinity. This means that another negative ion balances the positive sodium. Since the increase in ash weight was caused almost completely by the Na^+, this counterion must be organic. Soluble oxalate may act as such a counterion in *Salicornia europaea*[6]. This might be the case in the

closely related *A. fruticosum* as well, but oxalate was not determined in our experiments. In August the root Na^+ concentration and to a lesser extent also the Cl^- concentration, declined markedly. In a previous paper[24] we showed that soil bacterial activity increased dramatically in the same period and simultaneously the nitrate in the soil went up, but not the ammonium.

The *in vivo* nitrate reductase activity in the shoot rose from March to April and then gradually declined to a low value in July. In August there was a slight increase again. It appears, therefore, that external conditions had an effect on the N-metabolism of the plants. A gradually drying soil led to an increase in salinity and an inhibition of the nitrifying bacteria[24]. Increasing salinity has been found to retard ammonification, but not to suppress it completely[22]. Nitrification on the other hand can be completely inhibited by a salinity of 0.44% NaCl[22]. A similar inhibition of nitrification by salinity was observed by other authors[12, 15, 33, 38]. Therefore, less ammonium was oxidized to nitrate in May–June, and ammonium in the soil increased (Figure 4a and ref. 24). Re-wetting led to a temporary increase of humidity and a decrease of salinity, followed by a rapid increase in bacterial growth[24], causing oxidation of ammonium to nitrate. As a result the ammonium in the soil decreased and the nitrate increased. Higher soil nitrate leads to higher plant nitrate, both in the shoots and in the roots. And although the *in vivo* NRa of the shoots increased only slightly in August, it caused a clear increase in soluble protein in the plant. Barley plants subjected to osmotic stress have been shown to slow down the synthesis of proteins, and after 40 hours even a decrease of protein in the leaves and roots could be observed[34]. Nilsen and Müller[26] showed that *Lotus scoparius*, a drought-deciduous species, decreased its growth although no change in protein concentration could be found. Nitrate accumulated in this plant because nitrate uptake was less reduced by water-stress than the nitrate reduction. Hall and Flowers[14] isolated an amino acid incorporating microsomal fraction from the leaves of the halophyte *Suaeda maritima*, grown in saline conditions. They showed that the protein synthesis in this fraction was as much inhibited by NaCl as in a similar fraction from plants grown under non-saline conditions. This indicates that in both halophytes and non-halophytes the salt is kept separated from the enzymes, *e.g.* by storage in the vacuoles[11]. In our experiments there was a clear increase of protein content per gram fresh weight of the shoot in July–August after an initial decrease from April to July. This parallelled roughly the *in vivo* nitrate reductase activity in the shoot. It is not clear if the NRa was influenced directly by the decreasing humidity or the

increasing salinity of the soil, or by the diminished nitrate concentration in the soil and plants caused by an inhibition of nitrification by soil salinity[24], or both.

Huber[18] studied the effects of NaCl on the protein metabolism of *Pennisetum typhoides*. It was found that protein synthesis was inhibited by NaCl, but that the enzymes leucine-arylamidase, glutamine synthetase and Δ-pyrroline-5-carboxylate reductase were promoted. He explained these results in terms of a metabolic pathway shifting in the direction of proline production *via* glutamate. Proline is known to accumulate in many plants under water stress[36], and is supposed to accumulate in the cytoplasm in order to balance the osmotic potential of the accumulated NaCl in the vacuole[11]. Other organic compounds such as pipecolic acid and 5-hydroxy pipecolic acid[13], methylated ammonium compounds such as glycine betaine[37] and homobetaine[21], glutamine, Δ'-acetyl ornithine, asparagine[3], sugar alcohols such as sorbitol[2] and other soluble carbohydrates[4] may have a similar function. In our experiments proline was measurable in the shoots of the field plants only in March, when no salt or water stress was present, indicating that proline does not play a role in the osmotic regulation in this plant. The total soluble carbohydrates were relatively low in March, April and May, but showed a sudden 6-fold increase in the roots in June, the month in which salinity increased abruptly. However, the salinity remained high throughout June, July and even August, but the carbohydrate concentration decreased gradually again to its original low level. Apparently, these carbohydrates are not maintained as compatible compounds over a longer period. Other osmotically active compounds take over this task and glycine betaine may be a good candidate, since this was found to be abundantly present in the Chenopodiaceae[36], the family to which Arthrocnemum belongs to as well.

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