The European Journal of Plant Science and Biotechnology ©2011 Global Science Books

Ammonium Nutrition Improves Salt Tolerance of *Spartina alterniflora*

Kamel Hessini[1*] • Cristina Cruz[2] • Mhemmed Gandour[3] • Ahmed Debez[3] • Hans-Werner Koyro[4] • Bernhard Huchzermeyer[5] • Chedly Abdelly[3]

[1] Laboratoire de Physiologie Moléculaire des Plantes, Centre de Biotechnologie à la Technopole de Borj Cedria, BP 901, 2050 Hammam-Lif, Tunisia
[2] Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Centro de Biologia Ambiental – CBA, Campo Grande, Bloco C-2, Piso 5, 1749-016 Lisboa, Portugal
[3] Laboratoire des Plantes Extrêmophiles, Centre de Biotechnologie à la Technopole de Borj-Cedria, BP 901, 2050 Hammam-Lif, Tunisia, Tunisia
[4] Institute of Plant Ecology, Justus Liebig-University of Giessen, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany
[5] Institute of Botany, Leibniz University of Hannover, Herrenhaeuser Str. 2, D-30419 Hannover, Germany

Corresponding author: *** hessini_kamel@yahoo.fr**

ABSTRACT

The effects of inorganic nitrogen (N) form on biomass allocation, photosynthesis, osmotic adjustment, and cell wall elasticity of *Spartina alterniflora* were studied in a greenhouse under natural light and with sandy soil in the presence or absence of 500 mM NaCl. Under non saline conditions ammonium nutrition enhanced dry matter production and leaf area by ca. 50% in comparison to nitrate-fed plants. Under saline conditions the enhancement was more pronounced. NH_4^+ nutrition improved photosynthesis, transpiration, and stomatal conductance, suggesting that *S. alterniflora* prefers ammonium as a nitrogen source. The addition of 500 $mol.m^{-3}$ NaCl significantly affected plant growth in both nitrate and mixed media, but had no impact when ammonium was supplied alone, suggesting a considerable advantage of NH_4^+ nutrition under saline conditions. As a whole, ammonium treatment seems to improve salt tolerance of *S. alterniflora* by decreasing the energetic cost, needed for osmotic adjustment and cell wall elasticity, to growth.

Keywords: cell wall elasticity, gas exchange, halophyte, osmotic adjustment, salinity

INTRODUCTION

Salinity is considered a significant factor affecting crop production and agricultural sustainability in arid and semi-arid region of the world, reducing the value and productivity of the affected land (Munns and Tester 2008; Mohamedin *et al*. 2010). Soil infertility is often due to the presence of large quantities of salt, and the introduction of plants capable of surviving under these conditions is highly interesting (Hessini *et al.* 2009a; Hamdia *et al*. 2010).

Because of their immobility, plants have evolved complex internal systems to adapt to the changing and often stressful environments. Of these systems, osmotic adjustment and cell wall elasticity (CWE) are two important physiological mechanisms of adaptation to internal and external constraints. Plants need to maintain internal water potential below that of soil to maintain turgor and sufficient water supply for growth. This requires the maintenance of low osmotic potentials, either by uptake of solutes from the soil or by synthesis of metabolically compatible solutes (Tester and Davenport 2003; Hessini *et al*. 2009b). Compatible solutes, such as soluble sugars and organic-N compounds, are known to accumulate under conditions of environmental stresses and to play a role in the process of osmotic adjustment in many crops (Hessini *et al.* 2009b).

The impact of N nutrition on salt tolerance has been analysed at different levels of N metabolism such as N uptake, assimilation and N (total N, proteins and amino acids) accumulation (Ehlting *et al*. 2007). It is thought that sufficient N supply helps to compensate and correct nutritional imbalances in salt-stressed plants (Gomez *et al.* 1996), as salt stress decreases the uptake of nutrients such as NO_3^- (Ehlting *et al*. 2007; Hessini *et al* 2009c).

Limited information is available on plant performance as a function of nitrogen source (nitrate or ammonium) upon exposure to salt stress. In a salt marsh of Barataria Bay (Louisiana), both yield and nutrient uptake of *S. alterniflora* were enhanced by increased ammonium supply (Patrick and Delaune 1976). Similar results in *S. alterniflora* fed with ammonium showed that the critical nitrogen concentration is a function of salinity and indicated that the internal nitrogen supply required for growth increases with salinity (Bradley and Morris 1992). Analysing growth rate and gas exchange, Lewis *et al.* (1989) suggested that ammonium-fed plants are more susceptible to salt. In different herbaceous species (*Pisum sativum*, *Helianthus anuus*, *Glycine max*), nitrate-supplied plants were less sensitive to salt stress compared with ammonium-supplied individuals with regard to mineral composition, growth and physiological parameters (Bourgeais-Chaillou *et al.* 1992; Ashraf and Sultana 2000; Frechilla *et al.* 2001).

Spartina alterniflora can be grown on saline soil in order to prevent erosion and to possibly forage production (Chung *et al.* 2004; Hessini *et al*. 2009b). We had previously demonstrated that ammonium treatment improved salt tolerance of this species at high salinity (500 mM NaCl) by increasing secretion activity of salt glands, thereby decreasing salt contents of leaves and avoiding toxic buildup of Na^+ in the leaf apoplasm (Hessini *et al*. 2009c). The purpose of the present work was to examine whether other physiological mechanisms may explain such an improvement.

MATERIALS AND METHODS

Plant material, growth conditions and stress imposition

Seeds of *Spartina alterniflora* Loisel from its native range (USA) were sown in five outdoor containers filled with a mixture of sandy soil and organic matter at the Experimental Station of Borj-Cedria Biotechnology Center (Tunisia) during the spring-summer

Received: 29 September, 2010. Accepted: 6 February, 2011.

Original Research Paper

Table 1 Variation of pH in different extract solutions during the experiment period.

NO_3^-/NH_4^+	0 (day)	10 (days)	20 (days)	30 (days)	40 (days)	50 (days)	60 (days)
0 mM NaCl							
100/0	6.25	6.55	6.65	6.95	6.80	7.05	7.2
0/100	6.26	5.89	6.43	6.75	6.50	6.55	6.8
500 mM NaCl							
100/0	6.07	6.62	7.09	6.95	7.21	6.90	7.05
0/100	6.05	5.95	6.71	6.50	6.50	6.90	6.60

season of 2005. The experimental station is located near the Mediterranean seashore, 35 km north-east of Tunis (10°10' E, 36°48' N; 10 m altitude). For the spring-summer period, the average daily temperature and cumulated rainfall were 20°C and 218 mm, respectively. About 200 plants were grown in each outdoor container (1 m^2) and were irrigated weekly with tap water. Uniform cuttings (25 cm height) were taken from these mother plants and were washed before individually transplanting into 4 L pots (one plant plug per pot) filled with sandy soil and weekly irrigated with modified Hewitt's solution (Hewitt 1966) [0.55 mM phosphorus (P), 1.45 mM potassium (K), 0.37 mM magnesium (Mg), 0.87 mM calcium (Ca), 10.0 µM boron (B), 1.0 µM manganese (Mn), 0.5 µM zinc (Zn), 0.5 µM copper (Cu), and 0.35 µM molybdenum (Mo)] under non-saline condition for the first month after transplanting. Iron (50 µM Fe-ethylenediaminetetraacetic acid, EDTA) was added separately. The base concentration of nitrogen was 0.5 mM-N. At this time, some plants performing poorly were replaced.

Thirty-day-old cuttings of *S. alterniflora* were then cultivated in a greenhouse under natural light, with an average temperature of 25/18°C day/night and a relative humidity of 65/90%. Four-fold diluted nutrient solution (250 mL per pot) providing macro- and micronutrients was incorporated in the irrigation system at three day-intervals, providing equal amounts of nutrients to each plant. The volume of irrigation water represented 100% of field capacity (FC), which was measured according to the technique of Bouyoucos (1983). Nitrogen (7.5 mM) was applied either as NO_3^- (100/0), NH_4^+ (0/100) or a mixture of NO_3^- and NH_4^+ (50/50) with or without 500 mM NaCl. Salt was added weekly in steps of 100 mM in order to avoid an osmotic shock. The medium containing NH_4^+ as the only N source was buffered with 0.33g $CaCO_3$ per Kg DW of soil (Cantera *et al.* 1999). The data about the culture solution pH are given in **Table 1**. Evaporation from the pots surface was reduced by enclosing all pots in plastic bags sealed at the base of the rhizome of each cutting.

Growth

The fresh (FW) and dry matter (DW) of shoots and roots of each plant were determined after counting the number of leaves and determining leaf surface area with portable area meter (LI-3000A). These measurements were performed between 9:00 and 10:00 AM. The dry matter weights were determined after drying shoots and roots for 72 h in a thermo-ventilated oven at 80°C. Measurements were performed on ten plants per treatment 60 days after beginning of treatment (DAT).

Gas exchange measurements

Gas exchange parameters were determined using a portable gas exchange system (Li-Cor 6200, Li-Cor Nebraska USA). Measurements were first performed under increasing light intensities (PAR from 0 to 2500 µmol m^{-2} s^{-1}) and showed that net CO_2 assimilation rate (*A*) was maximal at 2000 µmol m^{-2} s^{-1} (data not shown). Subsequently, measurement conditions were the following: 2000 µmol m^{-2} s^{-1} PAR (saturating light intensity), 350 µmol mol^{-1}; ambient CO_2 concentration; 29 ± 2°C leaf temperature. Measurements were carried out between 10:00 and 12:00, on leaves (10 replicates per each level of water logging) acclimated for 15 min to the leaf chamber conditions. The following parameters were registered at saturating light: net CO_2 assimilation rates (A), stomatal conductance (gs), transpiration rate (E), and transpiration efficiency (TE) as the ratio *A*/*E*. The gas exchange measurements were made at 58 DAT.

Leaf water potential and water content

Leaf water potential (Ψw) and water content (WC) were measured at 10:00 am on 7 to 10 fully expanded leaves per treatment at 60 DAT. Leaf water potential (Ψw) was measured using a pressure chamber (Soil Moisture Equipments Corp., Santa Barbara, CA, USA) (Scholander *et al.* 1965). Leaf WC was calculated as follows:

$$WC = [(FW - DW) / FW] \times 100 \qquad (1)$$

where FW corresponds to the leaf fresh weight, DW to the leaf dry weight (72 h at 80°C).

Osmotic potential and cell wall elasticity

The pressure chamber was also used to obtain pressure-volume curves from leaves of each treatment. Measurements were taken during 2 days between 56 and 58 DAT. Fully expanded leaves were removed by cutting under distilled water, and re-hydrated for 18 h at 4°C in a dark humid chamber. Pressure-volume curves were generated using the repeated pressurisation technique, with leaves weighed on a precision balance between measurements of pressure (Tyree and Hammel 1972). After establishing the balancing pressure, the chamber pressure was successively raised by 0.2 MPa increments. The elevated pressure was sustained for 10 min. After each sap collection, the chamber pressure was slowly reduced to the previous balance pressure. The new balance pressure was then determined. The pressurisation rate was about 0.025 MPa s^{-1}. Osmotic potential at full turgor (Ψs^{100}) and osmotic potential at zero turgor (Ψs^0) were determined according to Sinclair and Venables (1983) using the linear regression of Ψs^{-1} *versus* (1-RWC). The degree of osmotic adjustment (OA) was defined as the difference in Ψs^{100} between the control (Ψs_c^{100}) and the stressed plants (Ψs_s^{100}) (Martínez *et al.* 2004; 2007):

$$OA = \Psi s_c^{100} - \Psi s_s^{100} \qquad (2)$$

The cell wall elasticity (CWE) of leaf tissue was estimated through the determination of the elasticity module (ε) value. This parameter was determined according to Hessini *et al.* (2009b) as:

$$\varepsilon = (\Psi s^{100} - \Psi s^0)\,(1 - AWC)/(1 - RWC_0) \qquad (3)$$

where AWC is the apoplasmic water content and RWC_0 is the relative water content at zero turgor.

Statistical analysis

All data presented are mean values. The measurements were achieved on five replicates for shoot ionic content and ten replicates for biomass determination and water content. Statistical analyse (one-way ANOVA) test was carried out using the SPSS 16.0 software. In case of significant differences, means were compared by the Duncan's multiple range tests at $P < 0.05$.

RESULTS AND DISCUSSION

Plant growth and gas exchange

Plant growth was assessed by the whole plant dry weight (DW), the leaf area and leaf number (**Table 2**). Under non-saline conditions, the highest DW was registered in the medium containing both nitrate and ammonium, whereas the lowest DW was found for plants grown with nitrate as the only N source. Yet, growth was better under ammonium than nitrate supply, indicating that *S. alterniflora* is one of the scarce species preferring ammonium as nitrogen source. The beneficial effect of NH_4^+ over NO_3^- was also reported for some wetland and marine species (Thursby and Harlin 1984; Munzarova *et al.* 2006; Hessini *et al.* 2009c) as well as for plants colonising terrestrial habitats where NH_4^+-N form is prevailing (Munzarova *et al.* 2006; Dennis and Hans 2010).

Adding 500 mM NaCl to the different media led to a re-

Table 2 Effect of nitrogen ionic form and salinity on dry weight (DW, g.plant^{-1}), leaf area (cm^2. plant^{-1}), and leaf number in *Spartina alterniflora*.

NO_3^-/NH_4^+	DW (g.plant^{-1})	Leaf area (cm^2. plant^{-1})	Leaf number
0 mM NaCl			
100/0	2.82 ± 0.85 ab	152.64 ± 89.74 ab	12.57 ± 3.17 b
50/50	6.02 ± 1.07 c	359.81 ± 120.52 d	16.67 ± 0.72 c
0/100	4.57 ± 1.74 bc	221.48 ± 85.94 bc	13.43 ± 4.25 cb
500 mM NaCl			
100/0	2.35 ± 0.82 a	78.82 ± 17.34 a	8.25 ± 1.16 a
50/50	2.46± 0.87 a	142.78 ± 21.08 ab	7.1 ± 0.64 a
0/100	4.71 ± 0.94 bc	262.28 ± 41.59 c	16.75 ± 2.96 c

Lower case letters indicates differences ($P \leq 0.05$, Duncan test) between treatments

Table 3 Effect of nitrogen ionic form and salinity on photosynthesis (A, μmol CO_2 m^{-2} s^{-1}), transpiration rate (E, mmol H_2O m^{-2} s^{-1}) and stomatal conductance (gs, mmol H_2O m^{-2} s^{-1}) in *Spartina alterniflora*.

NO_3^-/NH_4^+	A	E	gs
0 mM NaCl			
100/0	12.48 ± 0.66 b	2.05 ± 0.26 b	153 ± 9.06 c
50/50	18.12 ± 0.79 c	2.21 ± 0.36 cb	213.13 ± 14.22 d
0/100	17.76 ± 0.94 c	2.55 ± 0.2 c	234.5 ± 3.58 e
500 mM NaCl			
100/0	8.02 ± 1.19 a	1.02 ± 0.21 a	75 ± 5.24 a
50/50	7.31± 0.61 a	1.26 ± 0.38 a	93.62 ± 6.47 b
0/100	16.92 ± 0.45 c	2.21 ± 0.06 cb	104 ± 4.94 b

Lower case letters indicates differences ($P \leq 0.05$, Duncan test) between treatments

duction of all growth parameters for both nitrate and mixed-treatments. Yet, no effect was observed on the growth of ammonium fed-plants; the application of an ammoniacal regime not only reduced the damamging (growth and photosyntitic parametres) effects of the salt treatment, but also slightly although not significantly increased plant dry matter accumulation (**Table 2**). This slight improvement was due to the increase in leaf area but not number of leaves (**Table 2**). These results are in agreement with some studies (Flores *et al.* 2001; Kant *et al.* 2007), while diverging from others (Speer and Kaiser 1994; Hessini *et al.* 2009c). Our findings have economical and ecological importance for at least two reasons: 1) the detrimental effects of salinity on *S. alterniflora* growth and productivity can be alleviated by partial or total substitution of NO_3^- by NH_4^+ in the root medium, and 2) when ammonium is added or substitutes to nitrate, the concentration of the latter in the plant tissues decreases. Vegetables with high NO_3^- concentrations loose commercial value, since when consumed in excess, NO_3^- may be harmful to human and animal health (Britto and Kronzucker 2002; Aly *et al.* 2010).

In order to ascertain whether the differences in growth between the three nitrogen regimes could be correlated with differences in carbon assimilations, photosynthetic rates were determined (**Table 3**). Except in ammonium fed-plant, for which the rate of photosynthesis and transpiration were not changed, salinity significantly reduced the two latter parameters in both nitrate and mixed-media. However, irrespective of the nitrogen form, the stomatal conductance was reduced by an average of 50%. This suggests that in spite of the large decrease of stomatal aperture, salt-treated plants in ammonium media were able to maintain a high photosynthetic and transpiration rate. This result is in agreement with previous findings on barley (Kant *et al.* 2007) and tomato (Flores *et al.* 2001; Horchani *et al.* 2010). On the other hand, the growth increase observed in the present study with the ammonium regime could be correlated with an increase in both photosynthesis per unit area and total leaf area available for photosynthesis. The beneficial effect of ammonium on total leaf area confirm our previous results (data unpublished) that showed that ammonium nutrition affected only slightly individual leaf area of *Beta macrocarpa*, but had no significant effect on the initiation rates of leaves.

Osmotic potential and cell wall elasticity

The effect of nitrogen form on the leaf water relations was also investigated. Irrespective of nitrogen form, the addition of 500 mM NaCl caused a reduction of water content, relative water content at turgor loss point and osmotic potential both at full turgor (Ψs^{100}) and at turgor-loss point (Ψs^0). However, this decrease was less pronounced in ammonium-fed plants than for the other treatments. The decrease of both osmotic potential at full turgor and at turgor-loss point (calculated from the pressure–RWC relationships) in salt stressed leaves compared with the control indicated an osmotic adjustment (**Table 4**). The role of the latter is to maintain growth capacity through turgor maintenance at lower external osmotic potentials (Gomes *et al.* 2010; Chen and Jiang 2010). However, the degree of osmotic adjustment was significantly affected by N-source; in fact, there is a close but negative corelation between the degree of osmotic adjustment and the NO_3^-/NH_4^+ ratio (**Fig. 1**), whereas there is a positive correlation for the growth parameter. This result indicated that there is an obvious correspondence between the degree of OA and the biomass production in *S. alterniflora* under our nitrogen treatments (**Fig. 1**). It seemed that the decrease of the osmotic adjustment by NH_4^+ in the salty medium led to positive effects on plant growth.

In addition to osmotic adjustment, the cell wall elasticity (CWE) is also considered one of the most important physiological mechanisms of adaptation to osmotic stress (Martínez *et al.* 2007; Hessini *et al.* 2009b; Singh *et al.* 2010). In our study, except in buffered ammonium medium, the addition of 500 mM NaCl induced a significant decrease in leaf cell elasticity (i.e., the bulk modulus of elasticity, ε_{max}, increased), which caused the turgor loss point to move to a higher RWC (**Table 4**). This result is in agreement with previous findings for olive tree (Karamanos 1984) and common bean plants (Stoyanov 2005; Sassi *et al.* 2010). An increase in ε_{max} (stiffness) is expected when the cell walls become more rigid or thicker. The greater stiffness of the cell wall, given an equal decrease in cell volume and will be responsible for the drop in water potential. Except in nitrate fed-plants, for which the apoplasmic water fraction was decreased, salinity significantly improved this parameter in both ammonium and mixed-media (**Table 4**). This change

Table 4 Effect of nitrogen ionic form and salinity on water content (WC), leaf water potential (Ψw), apoplastic water content (AWC), osmotic potential at full turgor (Ψs^{100}), osmotic potential at turgor loss point (Ψs^0), relative water content at turgor loss point (RWC_0),and bulk modulus of elasticity at full hydration (ϵ_{max}) in *Spartina alterniflora*.

Parameter	Treatments					
	NO_3NH_4		NO_3^-		NH_4^+	
	NaCl (mM)		NaCl (mM)		NaCl (mM)	
	0	500	0	500	0	500
WC (%)	80.01 ± 2.13 c	72.75 ± 2.30 a	79.28 ± 2.00 bc	73.10 ± 3.17a	78.71 ± 5.30 bc	75.04 ± 1.47ab
Ψw (MPa)	-0.70 ± 0.13 a	-2.50 ± 0.13 d	-1.70 ± 1.73 c	-4.50 ± 0.26 f	-1.12 ± 0.86 b	-3.70 ± 0.13 e
AWC (%)	44.15 ± 0.57 c	64.02 ± 0.95 e	80.31 ± 0.53 f	39.01 ± 2.93 b	27.22 ± 1.58 a	47.82 ± 2.12 d
Ψs^{100}	-2.00 ± 0.19 a	-2.55 ± 0.17 c	-1.73 ± 0.09 a	-2.60 ± 0.07 c	-2.03 ± 0.30 ab	-2.38 ± 0.36 bc
Ψs^0	-2.58 ± 0.35 a	-3.84 ± 0.18 cd	-3.57 ± 0.33 cb	-4.16 ± 0.18 d	-2.50 ± 0.1 a	-3.30 ± 0.16 b
RWC_0	87.00 ± 1.13 de	82.00 ± 4.06 bc	89.00 ± 0.65 e	80.00 ± 0.96 ab	85.00 ± 1.5 dc	78.50 ± 1.92 a
ε_{max}	2.49 ± 0.11 b	3.57 ± 0.13 d	3.29 ± 0.17 c	4.75 ± 0.18 e	2.28 ± 0.11 ab	2.23 ± 0.24 a

Values represent the mean ± SE. of 3 replicates per treatment. Different letters within indicates significant differences ($P \leq 0.05$, Duncan test) between treatments.

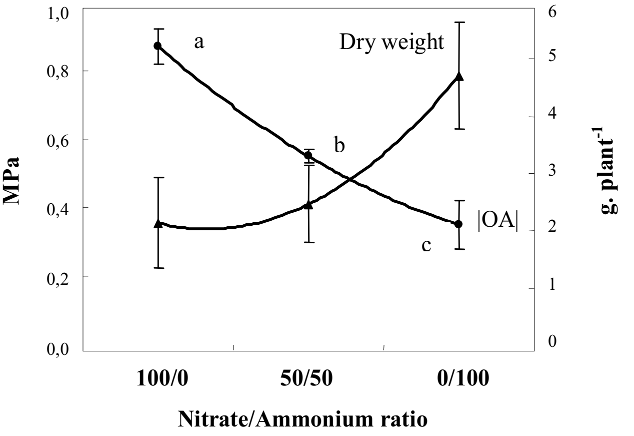

Fig. 1 Osmotic adjustment capacity and dry weight accumulation of salt-treated plants depending on nitrogen regime. Values are the means of five observations and bars are standard errors. Different letters on top of the symbols indicate statistically significant differences at $P<0.05$.

can contribute to passive concentration of solutes and thus to turgor maintenance in *S. alterniflora* plants grown on ammonium and mixed-media (Patakas and Noitsakis 1999). We concluded from our study of the cellular water relations that ammonium nutrition diverts the energetic cost, needed for osmotic adjustment and cell wall elasticity, to growth.

ACKNOWLEDGEMENTS

Authors would like to acknowledge the support of the COST action FA0901: Putting Halophytes to Work - From Genes to Ecosystems.

REFERENCES

Aly HA, Mansour AM, Abo-Salem OM, Abd-Ellah HF, Abdel-Naim AB (2010) Potential testicular toxicity of sodium nitrate in adult rats. *Food Chemistry Toxicology* **48 (2)**, 572-578

Ashraf M, Sultana R (2000) Combination effect of NaCl salinity and N-form on mineral composition of sunflower plants. *Biologia Plantarum* **43**, 615-619

Bouyoucos (1983) Les propriétés physiques du sol dépendent de sa texture et de sa structure. In: *Les Bases de la Production Végétale* (1st Edn), Collection Sciences et Techniques Agricoles, Bressuire, Québec, pp 67-87

Bradley PM, Morris JT (1992) Effect of salinity on the critical nitrogen concentration of *Spartina alterniflora* Loisel. *Aquatic Botany* **43 (2)**, 149-161

Britto DT, Kronzucker HJ (2002) NH_4 toxicity in higher plants: A critical review. *Journal of Plant Physiology* **159**, 567-584

Cantera R, Urdaniz A, Lerga J, Garcia-Mina J M (1999) Acidifying product as a source of stabilized ammonia nitrogen under greenhouse conditions. In: Bech J (Ed) *Soils with Mediterranean Type of Climate*, UB Publicaciones, Barcelona, pp 233-235

Chen H, Jiang J-G (2010) Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. *Environmental Review* **18**, 309-319

Chung CH, Zhuo RZ, Xu GW (2004) Creation of *Spartina* plantations for reclaiming Dongtai, China, tidal flats and offshore sands. *Ecological Engineering* **23**, 135-150

Dennis K, Hans B (2010) Nitrogen nutrition of *Canna indica*: Effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and N uptake rates. *Aquatic Botany* **92 (2)**, 142-148

Ehlting B, Dluzniewsk P, Dietrich H, Selle A, Teuber M, Hänsch R, Nehls U, Polle A, Schnitzler JP, Rennenberg H, Gessler A (2007) Interaction of nitrogen nutrition and salinity in grey poplar (*Populus tremula x alba*). *Plant Cell Environment* **30**, 796-811

Flores P, Carvajal M, Cerda A, Martines V (2001) Salinity and ammonium /nitrate interactions on tomato plant development, nutrition, and metabolites. *Journal of Plant Nutrition* **24**, 1561-1573

Frechilla S, Lasa B, Ibarretxe L, Lamsfus C, Aparicio-Tejo P (2001) Pea responses to saline stress is affected by the source of nitrogen nutrition (ammonium or nitrate). *Plant Growth Regulation* **35**, 171-179

Gomes FP, Oliva MA, Mielke MS, Almeida AAF, Aquino LA (2010) Osmotic adjustment, proline accumulation and cell membrane stability in leaves of *Cocos nucifera* submitted to drought stress. *Scientia Horticulturae* **126**, 379-384

Gomez I, Pedreno JN, Moral R, Iborra MR, Palacios G, Mataix J (1996) Salinity and nitrogen fertilization affecting the macronutrient content and yield of sweet pepper plants. *Journal of Plant Nutrition* **19**, 353-359

Hamdia MA, Shaddad MAK (2010) Salt tolerance of crop plants. *Journal of Stress Physiology and Biochemistry* **6 (3)**, 64-90

Hessini K, Gandour M, Megdich W, Soltani A, Abdely C (2009c) How does ammonium nutrition influence salt tolerance in *Spartina alterniflora* Loisel? Ashraf M, Ozturk M, Athar HR (Eds) *Salinity and Water Stress*, Springer Science + Business Media B.V, Germany, pp 91-96

Hessini K, Lachâal M, Cruz C, Soltani A (2009a) Role of ammonium to limit nitrate accumulation and to increase water economy in wild Swiss chard. *Journal of Plant Nutrition* **32**, 821-836

Hessini K, Martínez JP, Gandour M, Albouchi Ali, Soltani A, Abdelly C (2009b) Effect of water stress on growth, osmotic adjustment, cell wall elasticity and water-use efficiency in *Spartina alterniflora*. *Environmental and Experimental Botany* **67**, 312-319

Hewitt EJ (1966) Sand and water culture methods used in the study of plant nutrition. *Commonwealth Bureau of Horticulture Technical Communication* **22**, 431-446

Horchani F, Hajri R, Aschi-Smiti S (2010) Effect of ammonium or nitrate nutrition on photosynthesis, growth, and nitrogen assimilation in tomato plants. *Journal of Plant Nutrition and Soil Science* **173 (4)**, 610-617

Kant S, Kant P, Lips H, Barak S (2007) Partial substitution of NO_3^- by NH_4^+ fertilization increases ammonium assimilating enzyme activities and reduces the deleterious effects of salinity on the growth of barely. *Journal of Plant Physiology* **164**, 303-311

Karamanos AJ (1984) Ways of detecting adaptive responses of cultivated plants to drought. An agronomic approach. In: Margaris NS, Arianoutsou-Farragitakiand M, Oechel WC, (Eds) *Being Alive on Land. Tasks for Vegetation Science*, Junk Publisher, The Hague, pp 91-101

Lewis OAM, Leidi EO, Lips SH (1989) Effect of nitrogen source on growth response to salinity stress in maize and wheat. *New Phytologist* **111**, 155-60

Martínez JP, Lutts S, Schanck A, Bajji M, Kinet JM (2004) Is osmotic adjustment required for water stress resistance in the Mediterranean shrub *Atriplex halimus* L.? *Journal of Plant Physiology* **161**, 1041-1051

Martínez JP, Silva H, Ledent JF, Pinto M (2007) Effect of drought stress on the osmotic adjustment, cell wall elasticity and cell volume of six cultivars of common beans (*Phaseolus vulgaris* L.). *European Journal of Agronomy* **26**, 30-38

Mohamedin AAM, Awaad MS, Ahmed AR (2010) The negative role of soil salinity and waterlogging on crop productivity in the Northeastern Region of the Nile Delta, Egypt. *Research Journal of Agriculture and Biological Sciences* **6 (4)**, 378-385

Munns R, Tester M (2008) Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**, 651-681

Munzarova M, Lorenzen B, Brix H, Vojtiskova L, Votrubova O (2006) Effect of NH_4^+/NO_3^- availability on nitrate reductase activity and nitrogen accumulation in wetland helophytes *Phragmites australis* and *Glyceria maxima*. *Environmental and Experimental Botany* **55**, 49-60

Patakas A, Notsakis B (1999) Osmotic adjustment and partitioning of turgor responses to drought in grapevines leaves. *American Journal of Oenology and Viticulture* **50**, 76-80

Patrick WH, Delaune RD (1976) Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuarine and Coastal Marine Science* **4**, 59-64

Sassi S, Aydi S, Hessini K, Gonzalez EM, Arrese-Igor C, Abdelly C (2010) Long-term mannitol-induced osmotic stress leads to stomatal closure, carbohydrate accumulation and changes in leaf elasticity in *Phaselous vulgaris* leaves. *African Journal of Biotechnology* **9 (37)**, 6061-6069

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen ED (1965) Sap pressure in vascular plants. *Science* **148**, 339-346

Sinclair TR, Pinter JR, Kimball PJ, Adamsen BA, LaMorte FJ, Wall RL, Hunsaker GW, Adam DJ, Brooks N, Garcia TJ, Thompson RL, Leavitt T, Matthias S (2000) Leaf nitrogen concentration of wheat subjected to elevated [CO_2] and either water or N deficits. *Agriculture Ecosystems and Environment* **79**, 53-60

Singh P, Singh N, Sharma KD, Kuhad MS (2010) Plant water relations and osmotic adjustment in *Brassica* species under salinity stress. *Journal of American Science* **6 (6)**, 1-4

Speer M, Brune A, Kaiser WM (1994) Replacement of nitrate by ammonium as the nitrogen source increases the salt sensitivity of pea plant. I. Ion concentrations in roots and leaves. *Plant, Cell and Environment* **17**, 1215-1221

Speer M, Kaiser WM (1994) Replacement of nitrate by ammonium as the nitrogen source increases the salt sensitivity of pea plant. II. Inter- and intracellular solute compartmentation in leaflets. *Plant, Cell and Environment* **17**, 1223-1231

Stoyanov ZZ (2005) Effect of water stress on leaf water relations of young bean plants. *Central European Agriculture* **6**, 5-14

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. *Annals of Botany* **91**, 503-527

Thursby GB, Harlin MM (1984) Interaction of leaves and roots of *Ruppia maritima* in the uptake of phosphate, ammonia and nitrate. *Marine Biology* **83**, 61-67

Tyree MT, Hammel H (1972) The measurement of the turgor pressure and water relations of the plants to water by the pressure bomb technique. *Journal of Experimental Botany* **23**, 267-282