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Drought Adaptation Confers Short-Term but Not Long-Term Salt Tolerance in Cocksfoot, *Dactylis glomerata*

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Abstract: The effects of different levels of NaCl (0, 50, 100 and 150 mM) on growth, water relations, ions accumulation and nitrogen assimilation in two varieties of *Dactylis glomerata*, i.e., Hispanica from a semi-arid area and Frontier from a temperate climate, were studied in a greenhouse in hydroponic culture. Salinity induced a significant decrease in the growth of both varieties; however, their responses to NaCl stress were different. Based on weight and photosynthesis, Hispanica was found initially to be more resistant to salinity than Frontier. However, over a longer period of salinity treatments, Frontier displayed higher salt tolerance, especially at 50 mM NaCl concentration. The initial resistance to salinity of Hispanica, compared to Frontier, appeared to be related with a greater decrease in transpiration and water potential due to salinity, while there was no change in relative water content, suggesting better osmotic adjustment. In contrast, Frontier demonstrated more exclusion of Na^+ and Cl^- from the xylem stream and a higher K^+/Na^+ ratio, leading to a less harmful effect of salinity in the shoot, manifesting itself in better growth of this variety over the longer term. The results support the hypothesis that growth response to salinity has two phases. The first phase of growth reduction is mostly due to water (osmotic) stress, with the drought adapted variety, Hispanica, exhibiting higher tolerance. In the second phase, when toxic effects of accumulated Na^+ and Cl^- in tissues caused growth retardation, Frontier proved to have the higher resistance to salinity.

Key words: Salinity, xylem sap, *Dactylis glomerata*, water relation, ion accumulation

INTRODUCTION

The responses of plants to salt stress have long been investigated, since a better knowledge of the effect of NaCl on plants is critical for land management in saline areas (Munns, 2002, 2005). Salinity can inhibit plant growth by a range of mechanisms, including low external water potential, ion toxicity and interference with the uptake of nutrients, particularly K^+ (Munns, 1993; Tester and Davenport, 2003). The degree to which each of these factors affects growth depends on the plant genotype and environmental conditions. In saline soil, salt induced water deficit is one of the major constraints for plant growth. However, long-term salt effects are very different to those of short-term ones. Munns (1993) proposed a biphasic model of growth response to salinity. According to this model, growth is first reduced by a decrease in the soil water potential. This phase of growth reduction is a water stress effect and may be regulated by inhibitory signals from the roots. Plants, growing in arid or semi-arid lands, with greater risk for drought stress may exhibit more tolerance to salt stress in this phase, for example because of the accumulation of osmo-protectants in their tissues (Huang and Redmann, 1995; Munns, 2005). In the second phase, the concentration of toxic ions increases in plant tissues. In this phase, plants with different abilities

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to exclude or sequester toxic ions will display different levels of salt tolerance. For plants to be salt-tolerant, the toxic Na^+ and Cl^- ions must be excluded from sensitive tissues, particularly leaf mesophyll cells because these are the primary source of photoassimilates and, ultimately, yield (Wang *et al*., 2002; Munns, 2002). It is generally accepted that increased K^+/Na^+ selectivity during uptake and reduced Na^+ translocation from the root to the shoot contribute to the overall salt tolerance in many crop species (Tester and Davenport, 2003; Munns, 2005). The xylem is the major route for the transport of ions, including sodium, into the shoot. Regulation of xylem solute content will therefore be an important component of the regulation of shoot solute composition and salt tolerance (De Boer and Volkov, 2003; Watson *et al*., 2001).

Cocksfoot, *Dactylis glomerata*, is an important perennial, sod-forming pasture grass. It can now be found widely distributed around the world in different habitats. Some forms of this species are cultivated, while other wild forms are used for livestock feeding in moderate and semi-arid lands. It is sown for soil protection or grazing as a mixture with other perennial grasses and legumes (Trejo-Calzada and O'Connell, 2005). So far, few studies have been done on the salt tolerance of *D. glomerata*. Decrease in dry matter production of *Festuca rubra* was shown to be lower compared to *Holcus lanatus*, *Lolium perenne* and *D. glomerata* under salinity (Ashraf *et al*., 1986). Also, growth characteristics, water relations and proline accumulation of NaCl-selected and non-selected leaf-derived embryogenic calli of *D. glomerata* L. have been studied under NaCl stress. Growth in the selected line was greater than that of the non-selected line at all levels of NaCl between 50 and 300 mM (Dutta Gupta *et al*., 1995). Therefore, as is the case in many other species, one would expect considerable variation in salt tolerance within *D. glomerata*, reflecting differences in the habitat of populations (Neumann, 1997; Chartzoulakis *et al*., 2002; Essa, 2002). Two varieties of this species were used in the present study, namely the Hispanica variety, native to Iran where it thrives under arid and semiarid climates and Frontier, a commercial variety that is utilized for land reclamation in temperate climates.

In the present study, the salt tolerance of the Hispanica and Frontier varieties of *D. glomerata* were compared after different duration of salt exposure, to confirm that salinity stress shifts from an osmotic stress to a toxicity stress and to examine if drought tolerance confers salinity tolerance in the shorter or longer term. We hypothesized that the drought tolerant variety would be more salt tolerant in the short term and that salt tolerance in the longer term would be mainly related with the ability to exclude Na and Cl from the leaf tissue. In this regard, growth, photosynthesis, transpiration, water potential and concentration of ions in tissues and xylem sap were compared in these varieties.

MATERIALS AND METHODS

Plant material and growth condition: Seeds of *Dactylis glomerata* L. var. Frontier, obtained from the Crop Development Center Okayama, Japan and of *Dactylis glomerata* L. var. Hispanica (Roth) Koch (botanic variety) collected from north east Iran were germinated in an incubator at 20±1°C. Seedlings with equal sizes were transplanted in 20 boxes filled with about 10 L of Hoagland nutrient solution in a greenhouse (Okayama University, Japan). The culture solution was stored in four containers, each for one treatment (80 L capacity). Culture solution circulated between pots and main boxes and was aerated continuously. Treatments including 0, 50, 100 and 150 mM NaCl were started three weeks after transplanting. Salinity treatments increased stepwise to avoid osmotic shock. The pH of the nutrient solution (6.3±0.2) was adjusted daily and the nutrient solution was changed weekly. The average daily maximum and minimum temperatures in the greenhouse during the growing period were 32 and 17°C, respectively. The relative humidity varied between 45 and 79%. Four randomly chosen plants from each variety and treatment were harvested every other week and used for subsequent physiological analyses.

Gas exchange measurements: CO_2 assimilation (net photosynthesis) and transpiration were measured using a portable gas exchange system (ADC Infrared Gas Analyzer type LCA4 with PLC4 chamber, Hertfordshire, England) every other week. Measurements were taken under growth conditions from 10 am to 3 pm, at a CO_2 concentration of approximately 360 μmol mol^{-1} and relative humidity of 45-55%. The photon flux densities were within the range of 800-1200 μmol m^{-2} sec^{-1}. Each leaf was measured for 7 min and the parameters were recorded every 30 sec. Data obtained when readings were stable, usually the last 4 min, were used.

Mineral analysis: Shoots and roots were separated and then divided into two parts. One was dried, powdered and analyzed for total nitrogen and carbon concentration using automatic analyzer (C-N Corder, Yanaco, TNC-600, Japan). The other was frozen in -20°C. About 0.8 g of frozen material was grounded in liquid nitrogen, extracted with distilled water, mixed with a homogenizer, boiled for 15 min in a water bath and the supernatant separated by centrifugation. Extractions were performed three times and the resulting supernatants were pooled. The supernatants were analyzed for Na^+, Mg^{2+}, NH_4^+, K^+, Ca^{2+}, Cl^-, NO_3^- and SO_4^{2-} by ion chromatography (HIC-6A Shimadzu co. Japan) (Abdolzadeh *et al*., 1998).

Xylem sap collection and water potential measurement: Xylem sap was collected from the decapitated roots (Abdolzadeh *et al*., 1998). The decapitated roots were sealed in a pressure chamber and pressurized gradually until the first drop of sap appeared (balancing pressure) and the pressure raised for another 0.05-0.1 MPa. The exuded sap was collected with a syringe, immediately frozen and analyzed for concentration of ions.

Water potential was determined using the pressure chamber technique described by Turner (1981).

Statistical analysis: The experiment was carried out in a completely randomized design. All data were subjected to analysis of variance and LSD test using SAS statistical software.

RESULTS

Growth: High salinity (150 mM NaCl treatment) induced senescence and drying of old leaves in both varieties. Dry weight of the Hispanica variety was much lower than that of the Frontier variety in the non-saline control (Table 1). After three weeks of salt treatments, the only dry weight of high salt-treated (100 and 150 mM NaCl) Hispanica plants was significantly lower than that of control plants, whereas dry weight of Frontier plants was decreased markedly at all levels of NaCl. Total dry weight of Hispanica and Frontier varieties in the 150 mM NaCl treatment was about 31 and 65% less than the controls, respectively. After five weeks of salt treatments, shoot dry weight of the Frontier variety showed stepwise decreases with salt concentration. Between week 3 and 5, the impact of salinity, based on comparison of dry weight of salt-treated and control plants, became greater in Hispanica, but smaller in Frontier. The tiller number per plant decreased with increasing salinity, but to a lesser extent than shoot dry weight (Table 1).

The photosynthetic rate decreased in plants due to level and duration of the salinity treatment. In week 1, the photosynthetic rate decreased more sharply with increasing salinity in Frontier than in Hispanica (Fig. 1). In contrast, after 3 and 5 weeks exposure to salinity, Frontier variety indicated lower decrease in photosynthetic rate. The decrease of photosynthetic rate at first, third and fifth week was almost similar in Frontier variety. In contrast in Hispanica variety, effect of salinity on photosynthetic rate became more severe by time.

Water status: The transpiration rate was significantly lower in Frontier than Hispanica in the non-salt treated control plants and decreased markedly in both varieties due to salt treatments and exposure time (Fig. 1). Salinity induced a greater decline in transpiration rate of Hispanica than Frontier.

Water potential in the control condition (Ψ) was significantly higher in Frontier (Fig. 2). In week 1, the decrease of Ψ due to salinity was more severe in Frontier than Hispanica. However, after 3 and 5 weeks exposure to NaCl, Ψ decreased more sharply in Hispanica. Relative water content did not change significantly in the Hispanica variety but decreased markedly in the shoots of Frontier after five weeks of treatments (Table 1).

Concentration of minerals in plants: The concentrations of Na^+ and Cl^- were low in control plants but increased in both varieties under salinity (Table 2). The Na^+ and Cl^- concentrations in roots were lower in Hispanica than Frontier under salinity. In contrast, the concentration of Na^+ and Cl^- was higher in shoots of the Hispanica variety.

Table 1: Effects of salinity on dry weight of shoot and root, total dry weight expressed as a percentage of the control and tiller number of the Frontier and Hispanica varieties of *D. glomerata* during five weeks of treatment

Varieties	NaCl treatments	Dry weight of shoot (g) Week 3	Dry weight of shoot (g) Week 5	Dry weight of root (g) Week 3	Dry weight of root (g) Week 5	Total dry weight (%) Week 3	Total dry weight (%) Week 5	Relative water content week 5 (%) Shoot	Relative water content week 5 (%) Root	Tiller No. week 5
Frontier	0 mM	14.10±2.25a	20.62±1.69a	2.67±0.32a	4.79±0.42a	100.00	100.00	89.25±1.93a	90.25±2.57a	32.25±3.72a
	50 mM	6.07±1.37b	11.30±2.25b	1.34±0.33b	3.21±0.87b	41.17	57.10	84.50±1.68ab	90.00±0.65a	24.67±2.96ab
	100 mM	5.14±0.06b	7.42±1.00bc	1.39±0.27b	3.07±0.32b	38.98	41.29	78.75±1.22b	90.00±0.50a	16.50±1.19bc
	150 mM	4.85±1.11b	3.96±0.60c	1.09±0.12b	3.27±0.56b	35.37	28.44	78.00±1.08b	89.75±2.17a	14.00±2.04c
Hispanica	0 mM	2.70±0.39a	8.79±0.34a	0.78±0.09a	1.73±0.36a	100.00	100.00	76.35±2.63a	88.51±0.75a	19.25±4.07a
	50 mM	2.80±0.60a	2.89±0.50b	0.94±0.04a	0.87±0.21b	107.26	34.74	76.01±1.50a	88.56±0.58a	14.00±1.52ab
	100 mM	1.70±0.32b	2.34±0.39b	0.71±0.04a	0.90±0.08b	69.33	30.77	76.11±1.03a	89.54±0.91a	14.00±2.16ab
	150 mM	1.71±0.19b	2.30±0.39b	0.72±0.19a	0.76±0.08b	69.78	29.02	74.24±1.00a	87.29±0.85a	10.25±1.10b

Means±SE (n = 5) with different letter are significantly different at $p<0.05$ by LSD test within variety

Table 2: Effects of NaCl treatments on concentration of K^+, Na^+, Cl^-, Mg^{2+}, Ca^{2+} (mg g^{-1} dry weight) and K^+/Na^+ ratio in shoots and roots of the Frontier and the Hispanica varieties of *D. glomerata* after five weeks

		Na^+		Cl^-		K^+		Mg^{2+}		Ca^{2+}		K^+/Na^+	
Varieties	NaCl treatments	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
Frontier	0 mM	3.56±0.92a	1.57±0.79a	22.670±4.89a	6.13±0.91a	59.79±7.89a	15.25±1.56a	1.82±0.34a	0.74±0.07a	1.35±0.26a	0.43±0.07a	16.79a	9.73a
	50 mM	11.74±1.78b	8.13±0.64b	44.860±3.19b	18.11±1.99b	45.78±5.74ab	10.52±1.86b	1.44±0.41a	0.52±0.07a	0.87±0.23ab	0.40±0.03a	3.90b	1.29b
	100 mM	17.37±1.33c	8.46±0.90c	69.720±5.58c	22.07±1.57c	34.62±2.54b	9.22±1.39b	1.12±0.12b	0.43±0.16a	0.69±0.06ab	0.37±0.07a	1.99c	1.09b
	150 mM	24.11±1.78d	14.10±2.96d	70.830±6.72c	29.05±8.29c	33.68±2.95b	5.49±1.99c	1.17±0.21b	0.55±0.04a	0.71±0.12b	0.62±0.11a	1.40c	0.39c
Hispanica	0 mM	2.06±0.73a	1.31±0.88a	8.650±1.14a	5.11±2.18a	25.39±4.11a	10.53±3.26a	1.22±0.17a	0.29±0.10a	0.89±0.13a	0.10±0.07a	12.32a	8.01a
	50 mM	19.92±3.04b	2.36±0.46b	37.563±5.83b	9.02±0.74b	23.93±2.32a	4.42±0.94ab	1.31±0.15a	0.21±0.05a	0.76±0.09a	0.13±0.03a	1.20b	1.87b
	100 mM	24.60±2.91c	6.06±1.77c	80.840±11.53c	17.16±2.02c	26.14±4.29a	2.80±0.51bc	126.00±0.29a	0.23±0.05a	0.82±0.20a	0.11±0.06a	1.06b	0.46c
	150 mM	29.44±3.96c	8.38±1.14c	83.510±9.92c	14.63±1.86c	20.70±6.20a	1.80±0.54c	0.95±0.28a	0.19±0.07a	0.50±0.17a	0.20±0.10a	0.70c	0.21d

Means±SE (n=4) with different letter are significantly different at $p<0.05$ by LSD test within variety

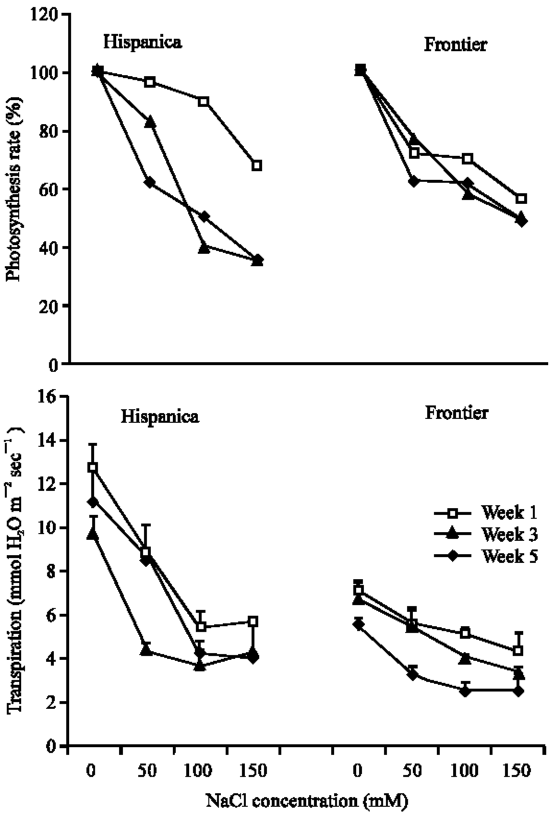

Fig. 1: Changes in photosynthetic and transpiration rate of the Hispanica and Frontier varieties of *D. glomerata* after one, three and five weeks of NaCl treatments. Values are means±SE in four plants

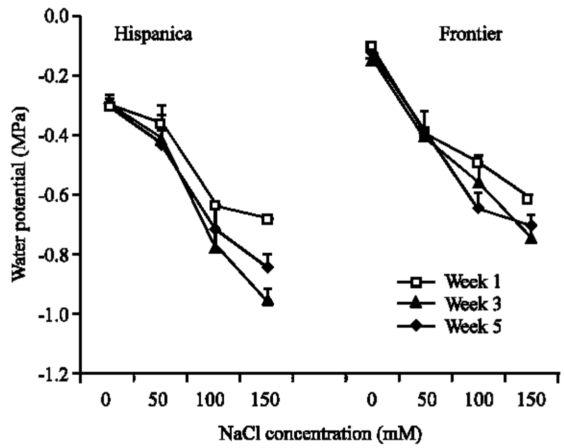

Fig. 2: Changes in water potential of the Hispanica and Frontier varieties of *D. glomerata* after one, three and five weeks of NaCl treatments. Values are means±SE in four plants

The chloride concentration in roots and shoots was always greater than the corresponding sodium concentration at all salinity levels.

The K^+ concentration was markedly higher in Frontier than Hispanica in the control condition (Table 2). A significant decrease was observed in the concentration of K^+ in both shoots and roots of Frontier and roots of Hispanica under salt stress, however, K^+ concentration did not change significantly in the shoots of Hispanica.

The concentration of Mg^{2+} and Ca^{2+} in both shoots and roots was markedly higher in Frontier than in Hispanica (Table 3). Mg^{2+} and Ca^{2+} concentrations decreased markedly in shoots of Frontier under salinity; however, their concentrations did not change significantly neither in roots of Frontier nor in the shoots and roots of Hispanica.

Concentration of minerals in xylem sap: The concentration of both Na^+ and Cl^- in the xylem sap increased with increasing salinity levels in both varieties (Fig. 3). In week 1, the increase of Na^+ and Cl^- in xylem sap due to salinity was higher in Frontier than Hispanica. However, in Frontier variety, only a slight increase was observed in Na^+ and Cl^- concentration from week 1 to 5. On the other hand, in Hispanica, the Na^+ and Cl^- concentrations in xylem sap of the 100 and 150 mM NaCl treatments increased markedly by the fifth week.

The concentration of K^+ in xylem sap was significantly higher in Frontier than Hispanica under control condition (Fig. 4). Potassium concentration in the

Table 3: Effects of NaCl treatments on concentration of NH_4^+-N, NO_3^--N, organic-N and total-N (mg g^{-1} dry weight) in shoots and roots of the Frontier and the Hispanica varieties of *Dactylis glomerata* after five weeks

		NH_4^+-N		NO_3^- -N		Total -N		Organic-N	
Varieties	NaCl treatments	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots
Frontier	0 mM	0.91±0.04	0.90±0.22	18.37±3.97a	8.97±1.86a	35.64±1.61a	19.01±1.12a	16.36±2.73b	9.13±1.39b
	50 mM	0	0	14.24±4.52a	6.87±1.03a	32.99±2.39a	20.04±1.70a	18.75±3.68b	13.17±1.21a
	100 mM	0	0	4.79±0.77b	4.09±0.95b	30.96±1.56a	19.32±1.49a	26.17±1.67a	15.24±1.11a
	150 mM	0	0	6.20±1.42b	3.47±0.55b	31.75±1.64a	19.25±1.56a	25.55±1.11a	15.78±1.49a
Hispanica	0 mM	0.66±0.26	0.61±0.12	7.52±0.23a	5.98±2.22a	39.02±2.56a	18.22±0.81a	30.84±1.42a	11.63±2.27b
	50 mM	0	0.94±0.23	6.55±2.17ab	1.74±0.30b	37.27±4.30a	16.55±1.16a	30.72±3.83a	13.87±1.09b
	100 mM	0	0	2.65±0.92b	1.99±0.58b	33.01±2.18a	18.06±0.51a	30.36±2.22a	16.07±1.14a
	150 mM	0	0	1.47±0.36b	0.96±0.4b	35.41±1.22a	13.83±0.68b	33.95±1.27a	12.87±0.29b

Means±SE (n = 4) with different letter are significantly different at $p<0.05$ by LSD test within variety. Organic-N = (Total-N) - [(NH_4^+-N) + (NO_3^--N)

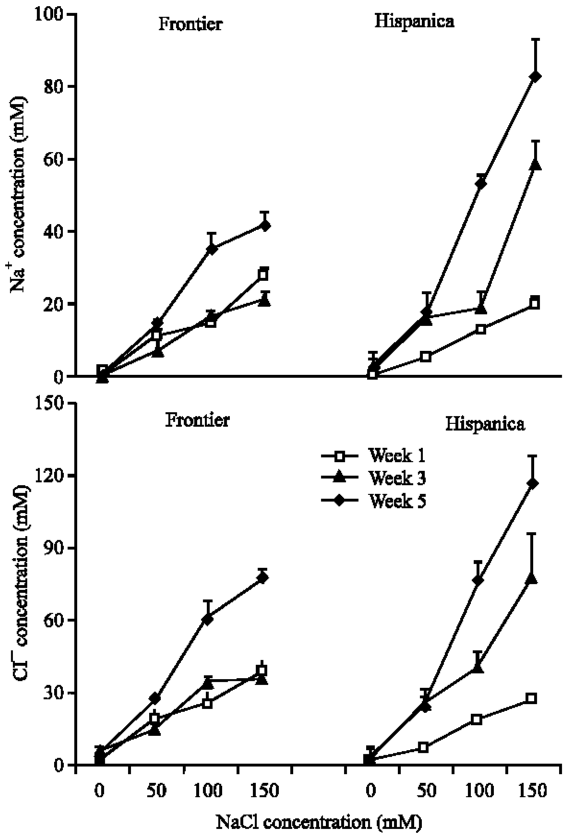

Fig. 3: Changes in concentration of Na^+ and Cl^- in xylem sap of the Frontier and Hispanica varieties of *D. glomerata* after five weeks of NaCl treatments. Values are means±SE in four plants

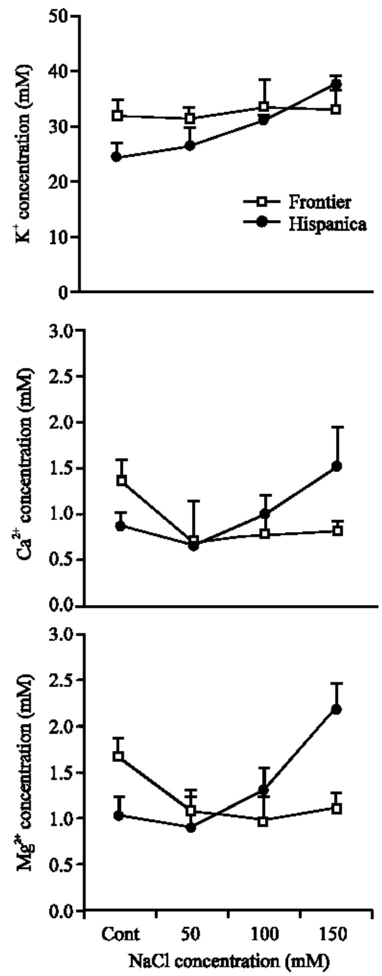

Fig. 4: Changes in concentration of K^+, Mg^{2+} and Ca^{2+} in xylem sap of the Frontier and Hispanica varieties of *D. glomerata* after five weeks of NaCl treatments. Values are means±SE in four plants

xylem sap increased markedly in Hispanica under salinity but did not change significantly in Frontier.

In xylem sap, the concentration of Mg^{2+} and Ca^{2+} were higher in Frontier than Hispanica under control conditions, however, their concentrations increased in Hispanica and decreased in Frontier (Fig. 4). Consequently, concentrations of both Mg^{2+} and Ca^{2+} in xylem sap were higher in Hispanica than Frontier under 150 mM NaCl salinity.

Concentration of nitrogen forms in plants: The total-N concentration did not change significantly in roots or shoots of either Hispanica or Frontier under salinity except for the roots of Hispanica at 150 mM NaCl treatment (Table 3). The NO_3^--N concentration was markedly higher in both shoots and roots of Frontier than Hispanica in control condition. Concentration of NO_3^--N declined in both varieties under salinity. Decrease of NO_3^--N concentration was more severe in Hispanica than Frontier. The organic-N concentration was markedly higher in Hispanica than Frontier under control conditions and in salt treatments. Organic-N concentration did not change markedly in Hispanica but increased in both roots and shoots of Frontier under salinity. The NH_4^+-N concentration was negligible and decreased in both varieties under salinity.

DISCUSSION

The major objective of the present study was to evaluate if the two aspects of salinity, namely water deficiency and ion toxicity, are manifested differently in contrasting ecotypes of *D. glomerata*. In the first three weeks, growth of the Frontier variety was more affected by salinity than growth of the drought tolerant Hispanica variety; however, by week 5, this trend had reversed.

When plants are exposed to salinity, they immediately experience osmotic stress due to a low water potential of the substrate. In contrast, ion toxicity does not manifest itself until ions have accumulated to toxic levels in the tissue (Munns, 1993; Munns, 2005). In present study, the smaller impact of salinity on the Hispanica variety up to week 3 is probably related to its drought tolerance, being a variety adapted to (semi-)arid conditions. In response to salinity, Hispanica, compared to Frontier, displayed a greater decrease in transpiration and a smaller reduction in relative water content while reductions of water potential were similar. This may indicate a more adaptive response of Hispanica to osmotic stress, partly by reduced water use and partly by osmotic adjustment. The higher organic-N concentration in Hispanica than in Frontier is probably related to the higher accumulation of N-containing osmo-protectants, as has been reported for other grass species (Tester and Davenport, 2003; Sairam and Tyagi, 2004; Munns, 2005). Similarly, Huang and Redmann (1995) have reported better water status in the wild barley (drought adapted) than the cultivated ones under salinity. Although Hispanica had a smaller effect of salinity up to week 3, Frontier always had higher water potentials and relative water contents. It may indicate adaptation of this variety to moderate climate condition.

The uptake of electrolytes, mostly Na^+ and Cl^-, upon long term exposure to salinity, can have the desirable effect of reducing water potential and thus allowing water uptake from saline substrate, but may also cause damage to plant metabolism. The timescale over which Na^+ and Cl^- specific damage is manifested depends on the rate of accumulation of these ions in leaves and the effectiveness of Na^+ and Cl^- compartmentation within leaf tissues and cells (Munns, 1993; Tester and Davenport, 2003). Our data show that the exclusion of Na^+ and Cl^- from sensitive tissues of leaves was more effective in Frontier than in Hispanica that may indicates the lower Na^+ and Cl^- transportation to shoots via xylem stream in the Frontier variety under salinity. Apparently, Frontier showed more potential to exclude toxic ions from the sensitive tissues. The K^+ concentration in both shoots and roots was significantly higher in Frontier than in Hispanica, however, K^+ concentration in Frontier decreased due to salinity in both shoots and roots. In spite of a significant decrease in transpiration, K^+ concentration in xylem sap of Frontier did not change significantly and consequently K^+ transportation to the shoot via xylem decreased. In contrast, in Hispanica, K^+ concentration increased in the xylem sap as the transpiration flow decreased. Our point measurements do not allow the calculation of a salt budget, but shoot tissue analysis showed that Hispanica was able to maintain similar concentrations under salinity as in controls. An inverse relationship between xylem flow rate and xylem sap ion content has previously been reported by Raveh and Levy (2005) and Munns *et al.* (2006). In Hispanica, maintenance of shoot K^+ concentrations seems to have happened at the expense of root K^+ concentrations. The lower K^+ uptake and higher transition of K^+ via xylem led to a drastic decrease of K^+ concentration in roots. Despite no change of K^+ concentration in the shoot, K^+/Na^+ ratios decreased more in Hispanica than in Frontier under salinity (Table 2). In the 100 mM NaCl treatment, K^+/Na^+ ratios were less than one in both shoots and roots of the Hispanica variety but only in the roots of the Frontier variety. This ratio has been considered a critical factor in salt tolerance in several species (Wang *et al.*, 2002). In soybean, olive and rice this ratio is related to salt tolerance of different varieties. (Chartzoulakis *et al.*, 2002; Essa, 2002; Walia *et al.*, 2005). It is generally accepted that increased K^+/Na^+ selectivity and reduced Na^+ translocation from the root to the shoot contribute to the overall salt tolerance in glycophytes (Tester and Davenport, 2003; Rivelli *et al.*, 2002). After long term exposure to salinity (five weeks), higher concentrations of Na^+ and Cl^- and lower K^+/Na^+ ratio in Hispanica resulted in a more severe decrease in growth in comparison to Frontier.

The results of the present study indicate that the responses of two varieties of *Dactylis glomerata* to salinity change with the duration of their exposure to salinity. In the short-term, water status and growth of the drought adapted Hispanica variety were least affected by salinity. In the longer term, the Frontier variety showed higher salt tolerance through better exclusion of toxic ions from shoots resulting in higher shoot K^+/Na^+ ratios.

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