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The Effects of NaCl Treatment on Water Relations, Growth, and ABA Content in Barley Cultivars Differing in Drought Tolerance

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Abstract Changes in transpiration and stomatal conductance and other characteristics of water relations, growth rate, and ABA content have been followed in short- and long-term experiments in two barley cultivars (cv. Michaelovsky and cv. Prairie) with contrasting drought resistance characteristics. The aim of this work was to reveal the importance of stomatal behavior in salt tolerance and also the involvement of ABA in its control. Salinity stress brought about a reduction in stomatal conductance in both cultivars, but the effect was initially more pronounced in the drought-tolerant cv. Prairie than in the drought-sensitive cv. Michaelovsky. The difference between the two cultivars changed with time, and later on transpiration and stomatal conductance became higher in Prairie than in Michaelovsky. In both the short and the long term, the extent of stomatal closure due to salinity correlated with the level of ABA accumulation in the leaves of the plants. Fast stomatal closure was likely to be responsible for growth resumption after an initial arrest by salt treatment and for the maintenance of extension growth later on, thus enabling its higher rate in Prairie than in Michaelovsky plants. Leaves of Prairie accumulated less toxic chloride ions, which may be the result of a lower transpiration rate observed during the first phase of salt treatment. A subsequent increase in stomatal conductance observed in Prairie is likely to ameliorate their gas exchange and maintain photosynthesis and growth. Thus, differences between the cultivars in the stomatal response to salinity changed with time, which may be why there are discrepancies in the attempts to relate stomatal conductance to salt tolerance observed in literature.

Keywords *Hordeum vulgare* · Salinity · Salt resistance · Barley cultivars · ABA · Transpiration · Stomatal conductivity · Growth

Introduction

Salinity is an important environmental factor that can severely inhibit plant growth and productivity. Improving crops for saline conditions requires an understanding of the mechanisms that enable salt tolerance. In addition to the toxic effects of ions, salinity disturbs the plant's water relations due to decreased availability of water from soil solution as a result of lowered osmotic potential (Munns and others 2006). Stomatal closure observed in salt-treated plants enables amelioration of tissue hydration by limiting water losses (Fricke and others 2004). It may also contribute to limiting the accumulation of toxic ions in plants because their rate of upward passage in the xylem is largely determined by the rate of transpiration (Kerstiens and others 2002).

Involvement of abscisic acid (ABA) in stomatal closure of salt-stressed plants has been frequently discussed (Ruggiero and others 2004; Jiang and Hartung 2007). Although the ability of ABA to close stomata is one well-known effect of this hormone, it was not always possible to relate stomatal closure in salt-stressed plants to changes in the bulk content of ABA in leaves, or to its concentration in xylem sap (Sibole and others 2003). Recently, accumulation of ABA has been observed within 10 min of salinity action on barley plants and related to prompt stomatal

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closure (Fricke and others 2006). This effect was suggested to be important for fast growth resumption and recovery of hydration of the plants. However, it remains unclear if stomatal closure of salt-stressed plants remains beneficial in the long term. Stomatal closure disturbs gas exchange, so there is a need for a trade-off between stomatal closure, which prevents water loss, and stomatal opening, which favors CO_2 uptake for fixation in leaf tissues (Sambatti and Caylor 2007).

The importance of the control of stomatal conductance in enabling salt tolerance may be clearer when comparing plants with different abilities to close stomata under salinity stress. Such a difference may be expected in plants with contrasting drought tolerances. The aim of this research was to follow stomatal responses to salinity in two barley cultivars that differ in drought tolerance. We followed changes in transpiration and stomatal conductance and other characteristics of water relations, growth rate, and ABA content in short- and long-term experiments in the hope of revealing both the importance of stomatal behavior for enabling salt tolerance and the involvement of ABA in its control. Short-term responses to sharp changes in salinity seem of interest due to the often uneven distribution of salts in soil (Jackson and others 1990) and the penetration of rapidly growing roots into salt-enriched soil patches, which inevitably creates sudden problems for water uptake.

Materials and Methods

Experiments were carried out with barley (*Hordeum vulgare* L.) cvs. Prairie (drought-tolerant) and Michaelovsky (drought-sensitive) (Cheshminskaya Research Station, Russia). Plants were grown for 2 days in darkness at 25°C between horizontal glass tubes sealed at the ends, tied together and floated on 0.1-strength Hoagland–Arnon nutrient solution. Then they were grown hydroponically in full Hoagland-Arnon nutrient solution (200 ml per plant changed daily) under 450-μmol photon m^{-2} s^{-1} mercury-arc luminous and sodium-vapor lamps with a 14-h photoperiod at 24°C. When the plants were 8 days old they were exposed to 100 mM NaCl. No NaCl was added to the nutrient solution of the control plants. In preliminary experiments salt concentration was increased by 25 mM per day. Although the main tendencies remained the same as described below, fast effects in the preliminary experiments were less significant, so responses only to immediate exposure to 100 mM NaCl were followed in this work. NaCl concentration was not increased to greater than 100 mM because a further increase in concentration made the growth of both cultivars too slow to reliably compare them under our conditions (great volume of salinized solution per each plant, which was changed daily, and increased availability of toxic salt).

Transpiration was measured as a loss of weight by ten plants drawing water from 50 ml of nutrient solution in a container covered with aluminum foil to minimize surface evaporation. Leaf conductivity to water vapor, interpreted as a measure of stomatal aperture, was measured with a diffusion porometer (Mk3, Delta-T Devices, UK).

An analog inductive electromechanical position sensor was used to monitor extension growth. The output signal from the sensor was tracked continuously and registered with a chart recorder (Fricke and others 2004).

Relative water content (RWC) was determined by floating leaf pieces of known fresh weight (FW) on distilled water for 24 h at 22°C in darkness. The turgid weight (TW) was then determined after blotting and the dry weight was determined after drying for 24 h at 80°C. FW, dry weight (DW), and TW were used to determine relative water content.

Samples for measurement of tissue osmotic potential were obtained after freezing and thawing leaves and expressing sap by squeezing them in a syringe. Osmotic potential was measured with a freezing point depression osmometer (CAMLAB Limited, UK).

The concentration of chloride ions was measured by capillary electrophoresis using an ion analyzer Ionophor (Russia).

For ABA extraction, leaves and roots were homogenized in 80% ethanol and incubated overnight at 4°C. Aqueous residue was diluted with distilled water, acidified with HCl to pH 2.5, and partitioned twice with peroxide-free diethyl ether (ratio of organic to aqueous phases was 1:3). Subsequently, hormones were transferred from the organic phase into 1% sodium hydrocarbonate (pH 7–8, ratio of organic to aqueous phases was 3:1), re-extracted with diethyl ether, methylated with diazomethane, and immunoassayed using antibodies to ABA (Vysotskaya and others 2004). ABA recovery calculated in model experiments was about 80%. Reducing the amount of extractant, based on the calculated distribution of ABA in organic solvents, increased the selectivity of hormone recovery and the reliability of the immunoassay. The high level of reliability of the immunoassay was made possible by the specificity of antibodies and by purification of hormones according to an effective scheme of solvent partitioning (Veselov and others 1992).

Results

Salt treatment led to stomatal closure and resulted in lowered transpiration very soon (in 20 min) after addition of NaCl to the nutrient medium (Fig. 1a). Differences between the cultivars were noticed in short-term experiments. The extent of decline in transpiration was much greater in Prairie than in Michaelovsky plants (Fig. 1a). Stomatal conductance remained lower than in controls throughout the long-term experiments in both cultivars (Fig. 1b). During the first 2 days of salt treatment, stomatal conductance was reduced to a greater extent in Prairie plants, after which it was observed that stomatal conductance was lower in Michaelovsky plants (Fig. 1b).

Measurement of leaf extension by means of an analog inductive electromechanical position sensor showed that salt treatment brought about an immediate cessation of leaf extension followed by negative elongation (shrinkage) (Fig. 2). Growth resumed after about 30 min, with extension returning to within 40–60% of the original value after 40 min. The extent of growth recovery was greater in Prairie than in Michaelovsky plants (t test, $P > 0.99$). Long-term experiments revealed inhibition of growth by salinity manifested in the shorter and less heavy leaves of salt-treated plants (Fig. 3). Similar to short-term

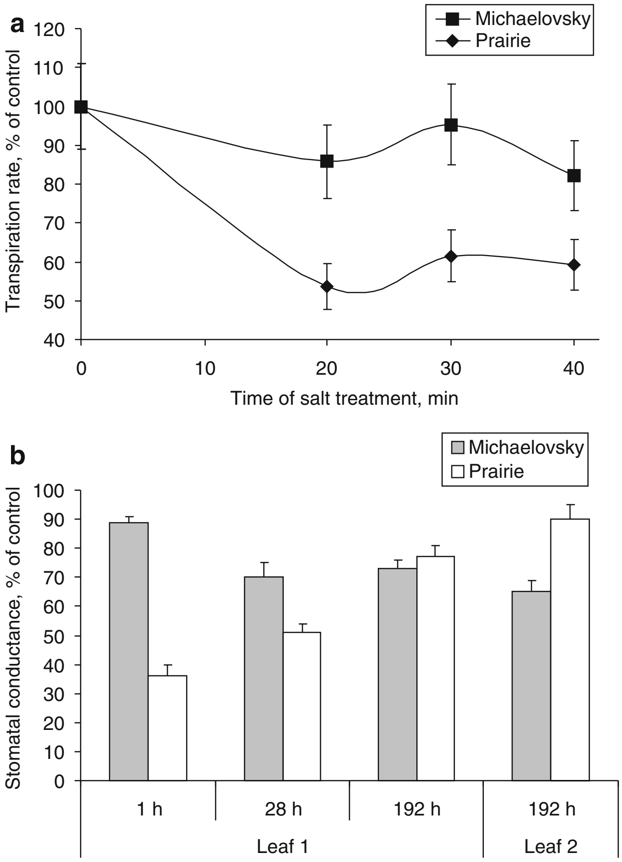

Fig. 1 The effect of salt treatment on transpiration (**a**) and stomatal conductance (**b**) of barley plants of different cultivars (Prairie and Michaelovsky). The transpiration rate of control plants was 68 ± 2 and 81 ± 2 mg $\text{plant}^{-1}\ \text{h}^{-1}$ for Michaelovsky and Prairie, respectively (**a**). Stomatal conductance of the first leaf of control plants after 1 h of salt treatment was 110 ± 10 and 124 ± 14 mmol $\text{m}^{-2}\ \text{s}^{-1}$, and during 2–8 days of salt treatment it was 37 ± 7 and 44 ± 8 mmol $\text{m}^{-2}\ \text{s}^{-1}$ for Michaelovsky and Prairie, respectively. Stomatal conductance of the second leaf of control plants after 8 days of salt treatment was 36 ± 2 and 57 ± 4 mmol $\text{m}^{-2}\ \text{s}^{-1}$ for Michaelovsky and Prairie, respectively

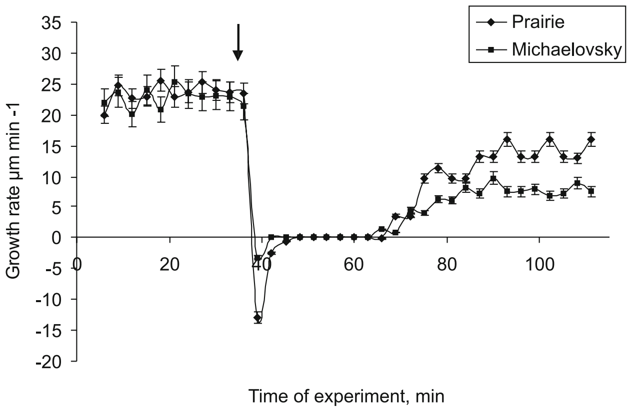

Fig. 2 The effect of adding NaCl into the nutrient solution on the rate of elongation of the first leaf of 7-day-old barley plants of different cultivars (Prairie and Michaelovsky). The time of NaCl addition is indicated by the arrow

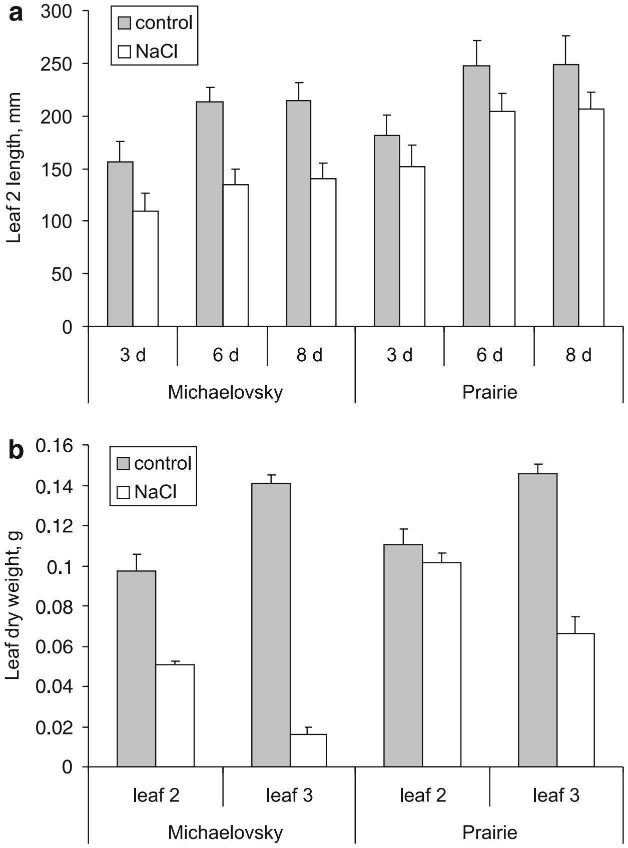

Fig. 3 (**a**) Effect of salt treatment on the length of the second leaf measured on the third (3d), sixth (6d), and eighth (8d) day of salt treatment of different barley cultivars (Prairie and Michaelovsky). (**b**) Effect of salt treatment on dry weight of the second and third leaves after 8 days of salt treatment

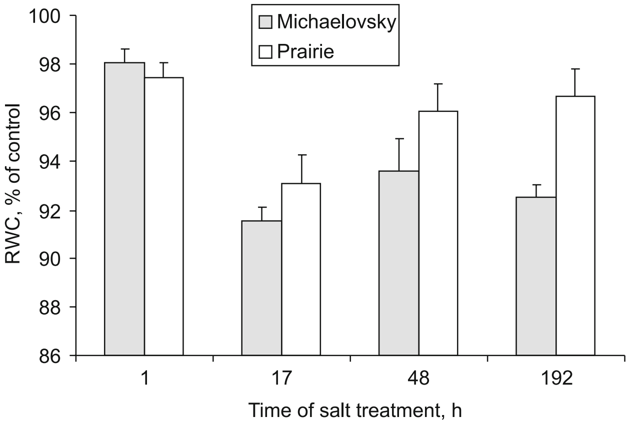

Fig. 4 Effect of salt stress on relative water content (RWC) in the youngest mature leaf of different barley cultivars (Prairie and Michaelovsky). RWC was measured in the first leaf 1, 17, and 48 h after the start of salt treatment; a second leaf was used at 192 h. Relative water content of leaves of control plants was 93 ± 2% and 94 ± 3% for Michaelovsky and Prairie, respectively

experiments, leaf growth was less inhibited in Prairie than in Michaelovsky plants.

RWC started to decrease within 1 h of salt treatment when it was lower in both cultivars than in controls by about 2% (Fig. 4), with the effect persisting until the end of the experiment. Leaf hydration of salt-treated plants was higher in Prairie than in Michaelovsky during the whole week.

Measurement of osmotic potential of leaf sap showed accumulation of osmotically active substances in salt-treated plants (Fig. 5). This tendency may be noticed only 1 h after addition of salt to the nutrient solution. The effect became more pronounced 1 day later and very clear after 8 days, when the osmotic potential of leaf sap was 1.5–2 times higher in salt-treated than in control plants. Long-term-treated plants of Prairie accumulated less solutes than Michaelovsky. The concentration of chloride ions was lower in Prairie than in Michaelovsky leaves (Table 1).

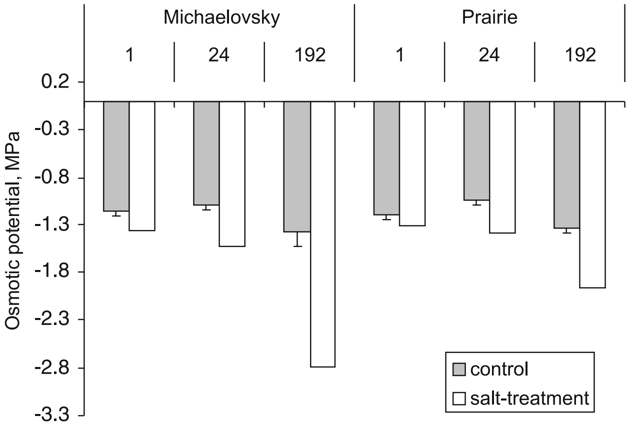

Fig. 5 Osmotic potential of all the leaves of control and salt-treated barley plants of different cultivars (Prairie and Michaelovsky)

Table 1 Concentration of chloride ions (mmol l^{-1}) in shoot and root sap of plants after 8 days of salt treatment

Cultivars	Treatment	Shoot	Root
Michaelovsky	Control	39.4 ± 5.6	8.5 ± 2.8
	NaCl	1078.9 ± 30.4	109.9 ± 19.7
Prairie	Control	47.9 ± 2.8	5.6 ± 2.8
	NaCl	740.8 ± 80	121.1 ± 2.2

ABA accumulated in leaves of salt-treated plants (Fig. 6). The effect was very fast and occurred within 10 min after addition of NaCl to the nutrient medium. During short-term treatment, leaves of Prairie accumulated more ABA than leaves of Michaelovsky. Within 10 min, leaves of salt-treated Michaelovsky and Prairie plants had 2 and 3.5 times more ABA, respectively, than those of controls. Rapid accumulation of ABA was also registered in roots of Prairie but not in roots of Michaelovsky. After 1 day, the difference between the salt-stressed cultivars in their ability to accumulate ABA was even clearer. Then, an almost tenfold increase in ABA content was observed in Prairie plants. With time the pattern of hormonal response changed, as it did in the case of stomatal conductance.

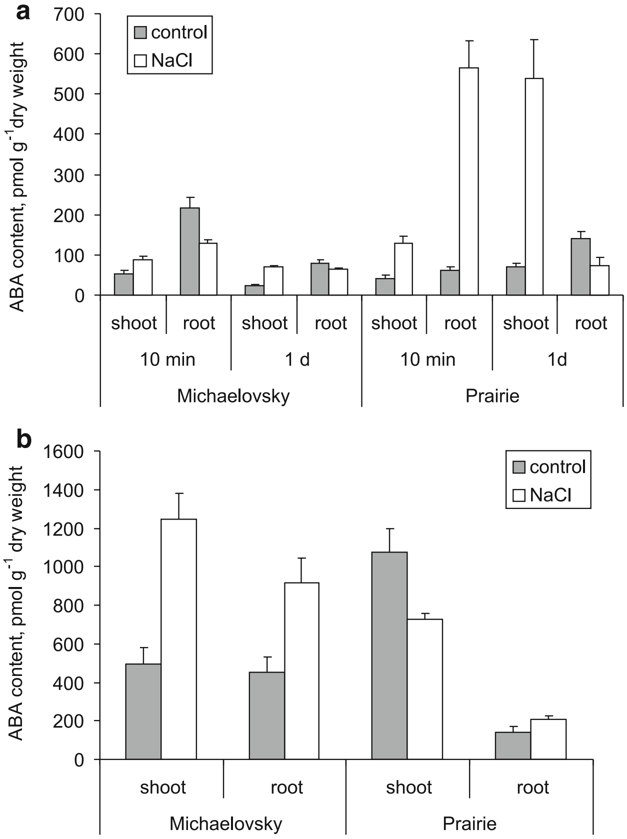

Fig. 6 ABA content in roots and shoots of control and salt-treated barley plants of different cultivars in short-term (**a**) and long-term experiments (**b**). In long-term experiments, ABA content was assayed 8 days after addition of salt to the nutrient medium

Eight days after the start of salt treatment, ABA content remained higher than in controls in Michaelovsky plants but was similar to controls in Prairie plants (Fig. 6).

Discussion

Cell extension results from water uptake and consequently rapid changes in leaf growth rate, measured by an analog inductive electromechanical position sensor, suggested changes in availability of water. Immediate cessation of growth and leaf shrinkage following addition of NaCl to the nutrient medium is an inevitable result of a decline in water uptake from the nutrient solution, whereby the osmotic potential was lowered by addition of NaCl. The resumption of extension growth observed in salt-stressed plants about 30 min after the start of treatment suggests an improvement in water relations, which may be due to a decrease in transpiration (reduced water loss). The pattern of leaf shrinkage and recovery in barley after salt application has already been published (Cramer and Bowman 1991; Munns and others 2000) and has been related to stomatal closure (Fricke and others 2006). However, in experiments by Fricke and others (2006), plants of only one cultivar were used. Comparison of two cultivars allowed us to correlate the greater decline in transpiration observed initially for salt-treated Prairie with their higher rate of leaf elongation. Lower stomatal conductance and higher extension growth rate of Prairie plants persisted 2 days after the start of salt treatment, whereas RWC content was higher in leaves of salt-stressed Prairie plants compared with those of Michaelovsky plants. Therefore, results obtained with different cultivars may serve as additional evidence of the importance of stomatal closure for maintaining leaf hydration and extension leaf growth in salt-stressed plants at the beginning of salinity action.

Stomatal closure may be induced by a decline in leaf hydration (Schultz 2003). RWC content was decreased by salinity and thus stomatal closure may be a consequence of lowered water potential in the salt-stressed plants. However, RWC content was higher in leaves of Prairie plants, whereas their stomatal conductance was decreased by salinity to a greater extent compared to Michaelovsky plants. These results suggest an involvement of chemical signals in the control of stomatal conductance (Davies and others 1994). ABA is well known to stimulate stomatal closure (Mansfild and McAinsch 1995), and the lower stomatal conductance observed in Prairie plants at the beginning of salt treatment may be related to an accumulation of relatively more ABA in the Prairie leaves. Our results are in accordance with those of other studies that showed accumulation of ABA in salt-stressed plants (Moons and others 1995; Mulholland and others 2003; De Costa and others 2007), although there are only a few examples, besides the results reported here, showing such a rapid ABA accumulation in salt-stressed plants (Fricke and others 2004, 2006). Treatment of plants with exogenous ABA increased their salt tolerance (Gómez-Cadenas and others 2003). However, the exact mechanism of its action on plants remains unclear. The relation of ABA accumulation to the growth rate of salt-stressed plants has also been discussed (Cramer and Quarrie 2002). Attempts were made to explain the observed growth responses by a direct effect of ABA on leaf growth of salt-stressed plants in experiments where the effects of stomatal behavior on growth were minimized (Chen and others 2003a; Ruggiero and others 2004). However, revealing the direct effects of ABA, which are not dependent on the effect of ABA on stomatal conductance, demands keeping plants under conditions of saturated humidity, where stomatal function is minimally important. Because in our experiments plants were grown under conditions in which transpiration occurs, we may relate observed accumulation of ABA to its effect on stomata.

It is of interest to discuss possible mechanisms for ABA accumulation in plants. The loss of turgor and reduction in cell size have been shown to increase ABA synthesis (Jia and others 2001). However, there may be another source of ABA accumulation in salt-stressed barley plants. The level of rapid ABA accumulation was highest in the roots of Prairie plants, and it is well known that root-synthesized ABA transported to the shoot influences stomatal closure of plants under soil stresses (Davies and others 2005). Thus, we suggest that part of the ABA accumulated in the leaves of Prairie plants may have originated from the roots.

Thus, at the beginning of the salt-stress reaction, the higher extension growth rate of Prairie plants was due to an improvement of their water relations via ABA-induced stomatal closure. The effect was greater in Prairie than in Michaelovsky. The results obtained at the beginning of the salinity action agree with those of De Costa and others (2007) who suggested that a growth-promoting function, regulated by ABA, is responsible for salt resistance in the first phase of salt stress. The osmotic component of salinity was shown to be more important in the first phase of the growth response, which is in accordance with data obtained at the beginning of our experiments (Munns and others 2006). In some reports, short-term growth experiments measured whole shoot biomass and revealed little difference between genotypes in the response to salinity (Munns and James 2003). However, a recent study of a number of durum wheat genotypes provided evidence for genetic variation in tolerance to osmotic stress (James and others 2008).

Although stomatal closure enables amelioration of water relations, not all of its consequences may be beneficial for plants. Salinity-induced stomatal closure may result in disturbance of gas exchange and inhibition of photosynthesis and growth. The results of gas-exchange studies (James and others 2008) have highlighted the impact of salinity on stomatal conductance and, hence, on limitations in CO_2 assimilation rate. Thus, it seems important to investigate the pattern of stomatal response to salt treatment with time. In our experiments, after 8 days stomatal conductance was higher in plants that managed to accumulate more dry matter under salinity. At the end of our long-term experiments the results agreed with those of James and others (2008) who related higher stomatal conductance in salt-treated plants to a higher CO_2 assimilation rate. Again, a faster growth rate was characteristic of Prairie plants. It is of interest that at the end of our experiments these plants managed to maintain greater leaf RWC despite a higher level of transpiration compared to Michaelovsky plants. This must be due to the ability of these drought-resistant plants to maintain the supply of water to shoots. By this time, and opposite to early responses, stomatal conductance was lower in leaves of Michaelovsky plants and was accompanied by lower RWC. Hence, in the long run, stomatal closure of Mischaelovsky plants may have been caused by the low RWC, either directly or through induction of ABA accumulation. By this time ABA content was at the level of control plants in the case of Prairie, and this may be due to the ability of these plants to maintain higher leaf RWC. Our long-term results are in accordance with the data that show negative correlation of ABA content with leaf hydration and low ABA concentration in leaves of drought-tolerant ecotypes (Peuke and others 2002).

Thus, throughout our experiments the pattern of stomatal response changed in accordance with the change in the level of ABA accumulation: At the beginning, both ABA content and the degree of stomatal closure were greater in Prairie plants; later on, contrary to this, both characteristics were greater in Michaelovsky.

Salt resistance was determined by osmotic adjustment and abscisic acid in newly developed maize hybrids in the first phase of salt stress (De Costa and others 2007). This was due mostly to accumulation of photoassimilates and observed in the first phase of salt stress. Solutes did accumulate to high levels in salt-stressed plants in our experiments. This began soon after the start of salt treatment and by day 8 osmolality under salinity was about 1.5–2 times higher than in control plants. However, at the end of our experiments osmolality increased to a greater extent in more salt-sensitive Michaelovsky plants, likely because of a higher rate of accumulation of toxic ions in these plants. This assumption is supported by the measurement of chloride ion concentration in leaves, which was highest in salt-treated Michaelovsky plants. Although the toxicity of accumulated ions is not manifested while they are sequestered in vacuoles, the effect of toxic ions becomes clear with time, and the higher the rate of their accumulation in shoots, the quicker toxic effects become apparent (Munns and others 2006). Therefore, in the long term, the slower growth of Michaelovsky plants may be due to accumulation of more toxic ions in the leaves and in the vicinity of guard cells, which may induce stomatal closure and inhibition of leaf growth (Robinson and others 1997).

It is important to determine how Prairie plants accumulated less toxic ions. Although they had higher stomatal conductance and transpiration at the end of experiment, their transpiration was lower than in Michaelovsky plants at the beginning of salt treatment. Salt resistance of crop plants depends on their ability to both exclude sodium from the shoot and prevent its accumulation in the cytoplasm of leaf cells (for example, through sequestration in the vacuole), potentially leading to differences in salt tolerance (Tester and Davenport 2003). Although these characteristics cannot be directly related to transpiration rate, inhibition of transpiration diminishes the initial load of passive flow of toxic ions and in this way provides a plant with enough time to switch on other defense mechanisms. Chen and others (2003b) reported that lower transpiration of plants contributes to their greater capacity for salt exclusion. Thus, reduced transpiration limits salt loading of the shoot; this may be useful at least in short-term stress adaptation. This could explain the higher salt tolerance in terms of growth in plants with decreased water flow to the root surface at the beginning of the experiments (Prairie plants being more efficient than Michaelovsky plants).

Data obtained in our experiments show that growth maintenance under salinity depends on both the ability of plants to maintain their water relations and ion homeostasis. At the beginning of salinity action, the ability of plants to close stomata ameliorates their water relations and maintains a higher leaf extension rate. Correlation between the degrees of stomatal closure and levels of ABA accumulation in different cultivars confirms the involvement of this hormone in the control of stomata behavior under salinity treatment. ABA may also contribute to a decline in the flow of toxic ions with the transpiration stream. Although this tendency changes with time, processes that enable rapid responses to salinity give the plant an opportunity to switch on defense mechanisms other than limiting transpiration flow. Over time, reduced stomatal conductance and transpiration may limit nutrient supply, photosynthesis, and growth of the shoot. Literature data on the link between transpiration and salt tolerance are rather contradictory. Results presented herein show that the linkage between transpiration and salt tolerance may change with time, and, while at the beginning of salt action salt tolerance in terms of extension growth and accumulation of toxic ions was enabled by stomatal closure, later on an opposite effect was seen, and a higher rate of dry matter accumulation was linked with the ability of plants to maintain their stomata in an open state. This may in part explain the discrepancy of the literature data.

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