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Communication

Short-Term Leaf Elongation Kinetics of Maize in Response to Salinity Are Independent of the Root

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ABSTRACT

The essentiality of roots to the short-term responses of leaf elongation to salinity was tested by removing the roots of maize (*Zea mays* L.) from the shoots and comparing the initial short-term response of leaf elongation to that with intact plants. Eight-day-old seedlings growing in solution culture were treated with 80 millimolar NaCl and their leaf elongation rate (LER) was monitored with a linear variable differential transformer connected to a computerized data aquisition system. Initially, LER of intact plants was sharply reduced by salinity, then rose rapidly to reach a new steady-state rate about 1.5 hours after salinization. The new steady-state rate of salinized intact plants was about 80% of the control rate. When the roots of nonsalinized plants were excised under the surface of the nutrient solution, excision did not disturb the steady-state LER. When these shoots were salinized, they responded in a manner nearly identical to that of intact plants, indicating that roots are not essential for the modulation of short-term LER of salt-stressed plants.

Salinity reduces the rate of leaf elongation of nonhalophytes. In barley, these reductions are rapid and may be related to a reduction in turgor (12). Several hours after the start of salinity stress, however, leaf elongation is poorly correlated with turgor (11, 12). Munns and Termaat (8) postulate that a "nonhydraulic signal" from the root limits the growth of the shoot when the plant is salt-stressed.

One of the prime candidates for this putative signal is ABA. There is substantial evidence to support this hypothesis (3, 7, 10, 13, 14). In a recent article, Zhang and Davies (14) show that concentrations of ABA in the xylem of maize plants increase with increasing drought; growth and stomatal conductance are inhibited as the ABA concentrations rise, but leaf turgor is unaffected. When concentrations of ABA in the xylem rise by treatments of the root system with ABA, both stomatal conductance and LER[1] are inhibited (14). Thus, it would seem that roots may be the primary sensor for drought stress. Kramer (6) disagrees with the idea that it is a biochemical signal from the root. He argues that direct hydraulic effects are more important during shoot water stress.

In the present paper, we present the results of a simple experiment comparing the effects of salinity on leaf elongation in whole plants and plants whose roots have been excised under water before salinization. We show that the short-term response of plants without roots is essentially identical with the response of whole plants. This indicates that roots are not essential for the modulation of short-term LER of salt-stressed maize plants.

[1] Abbreviations: LER, leaf elongation rate; LVDT, linear variable differential transformer.

MATERIALS AND METHODS

Growth Conditions

Maize (*Zea mays* L. Pioneer hybrid 3906) caryopses were germinated in vermiculite and irrigated daily with a 0.25 concentration Hoagland solution as defined by Bowman and Paul (1). Plants were grown under constant laboratory conditions (25°C, 200 μmol m^{-2} s^{-1} cool-white fluorescent lighting, 24 h d^{-1}) throughout the preculture period. Seven-day-old seedlings were transferred to solution culture (0.25 concentration Hoagland solution) and placed under a metal-halide lamp (350 μmol m^{-2} s^{-1}, 24 h d^{-1}) 1 d before the experiment. Immediately before the start of the growth measurements, the nutrient solutions were siphoned off and replaced with fresh solution. Salt (4 M NaCl) was added to the nutrient solutions to a final concentration of 80 mM.

Leaf Elongation Measurements

Leaf elongation was measured with a LVDT system similar to one previously described (4). Data were collected simultaneously from four LVDTs with a MacAdios II data aquisition system (GW Instruments, Inc., Somerville, MA) interfaced with a MacIntosh II computer. A line was attached from the LVDT system to the tip of the third leaf of an 8-d-old maize plant with an alligator clip. Sponge was glued to the clip teeth to prevent damage to the leaf. LER (μm min^{-1}) was calculated by taking the difference in leaf length (μm) at 2 min intervals and dividing it by 2.

Shoot Excision

Leaf elongation was measured on both intact plants and excised shoots. The root system was excised from the seedling at the mesocotyl with a sharp razor blade. The excision was made under the surface of the nutrient solution to prevent cavitation. Excised roots were carefully removed from the nutrient solution to prevent any possible influence of the roots on the shoots.

RESULTS AND DISCUSSION

Salinity rapidly reduced LER of intact maize plants (Fig. 1). The typical kinetic pattern after exposure to salinity was a sharp reduction of LER immediately after exposure to 80 mM NaCl. LER was completely inhibited for about 30 min, then rose sharply to reach a new steady state (80% of the control) approximately 1.5 h after salinization.

To test the effect of excision on LER, roots of control and salt-stressed plants were excised under the nutrient solution. Steady-state LER was not disturbed by root excision (data not shown). To test whether roots are essential for the short-term kinetic response of LER to salinity, roots were removed 30 min before salinization with 80 mM NaCl. Excised shoots had the same LER as intact plants before salinization and the kinetic pattern in response to salinity was nearly identical (Fig. 2). Again salinity reduced steady-state LER by 20%. Intact and excised shoots treated with isosmotic concentrations of mannitol were similarly affected (data not shown), indicating that the longer term inhibition in excised shoots was not a direct specific effect of NaCl.

These results lead us to conclude that the root system is not essential to the initial responses of LER to salinity. Although signals from the root may influence shoot growth in intact plants, it would appear that the factors limiting LER can also be present in the shoot.

The initial primary signal that leads to a reduction of LER is probably hydraulic. Growth may be inhibited by a reduction of water uptake into the growing zone such as when the xylem water potential suddenly drops (2, 9). This effectively inhibits cell elongation until water uptake is increased by osmotic adjustment or cell wall loosening. It should be noted that the average water potential of the growing zone may not be immediately affected by the sudden drop in xylem water potential (2, 9).

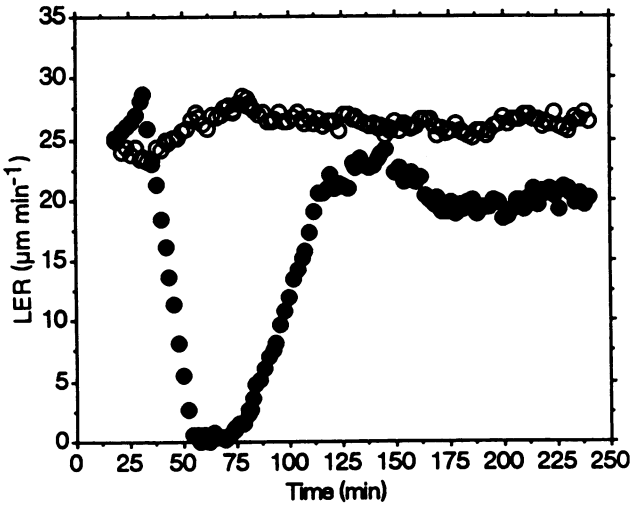

Figure 1. Effect of salinity with time on the LER of the third leaf of intact maize plants. ○, control; ●, 80 mM NaCl was added to the nutrient solution at 30 min. Data represent the mean of five separate experiments. Data from each experiment were smoothed by a moving average to reduce noise. SE for control and 80 mM NaCl were 0.12 and 0.92 μm min^{-1}, respectively.

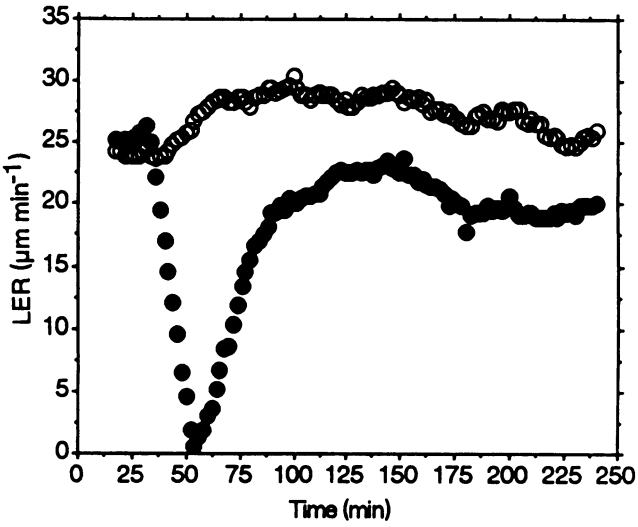

Figure 2. Effect of salinity with time on the LER of the third leaf of excised maize shoots. ○, control; ●, 80 mM NaCl was added to the nutrient solution at 30 min. Data represent the mean of four separate experiments. Data from each experiment were smoothed by a moving average to reduce noise. SE for control and 80 mM NaCl were 0.36 and 0.45 μm min^{-1}, respectively.

When excised shoots are salinized, a sudden drop in the water potential of the xylem would require that the salt solution be transported rapidly from the cut end to the apoplast surrounding the cells of the growing zone. This in turn would cause either a reduction in turgor, water uptake or both. In intact plants, a sudden drop in the water potential of the nutrient solution may cause interruption of water influx or a drop in cell turgor at the root epidermis.

Thiel *et al.* (12) have shown that turgor is rapidly reduced in the growing zone of barley after salinization and rises rapidly as growth resumes. However, the turgor pressure returns to control values, whereas shoot elongation does not. Likewise, steady-state elongation of water-stressed maize leaves is also inhibited, whereas turgor returns to control values (5). The kinetic growth response of maize to salinity in this study was very similar to the responses of water-stressed maize (5) and salt-stressed barley (12), and it is likely that turgor responds similarly as well.

By the time LER reaches a new steady-state, secondary factors may limit LER. These factors may include "nonhydraulic signals" from the root, but clearly in the first few hours root signals are not necessary since steady-state LER was reduced to the same degree in both excised shoots and intact plants after salinization.

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