

Response of leaf elongation and nutrient status in growing leaves of wheat to salinity

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Abstract

Elongation of grass leaves is spatially distributed in the growth zone. The reduced leaf growth under saline conditions should be much more closely associated with metabolic/nutritional changes within the most actively growing tissues than in the whole or non-growth tissues. Our objective was to quantify spatial distributions of nutrients and their net deposition rates in the growth and non-growth zones of wheat leaves under saline conditions. Plants were grown in soils with or without 120 mM NaCl in growth chambers. Leaf elongation was spatially decreased by salinity. However, the concentrations of nutrients in leaves under saline conditions increased, decreased or did not change depending on the location in the leaves and on the nutrients. The growth zone is a strong sink for nutrients. Although salinity altered the patterns of spatial distribution of nutrients in the growing leaves of wheat and increased Cl^- and Na^+ concentrations in the growing leaves, limitation of leaf growth may not be due to ionic toxicity, deficiency or utilization of carbohydrates in the growing tissues.

Introduction

Leaf development of wheat largely determines the rate of plant growth (Williams 1975). Our early study (Hu 1996) showed that the elongation rate, final length and width of wheat leaves on the mainstem were reduced by 20–30% at 120 mM NaCl. However, the mechanisms of salt effect on leaf growth are still poorly understood. Since leaf elongation of grasses is restricted to a small region near the leaf base (Kemp 1980), reduced leaf growth under saline conditions should be much more closely associated with metabolic/nutritional changes within the most actively growing tissues than the whole or non-growing tissues. The continuity equation is a statement of the law of mass conservation. This equation can be used to calculate the local net deposition rate of nutrients in growing leaves of grasses, and thus to investigate sink and source relationships (Silk 1984). The objective of this study was to quantitatively evaluate the spatial distribution of leaf elongation, inorganic and organic nutrients and their deposition in the growth zone of wheat leaf 4 of the main stem during its linear growth phase in soil treated with 0 or 120 mM NaCl.

Materials and methods

Six seeds of spring wheat (*Triticum aestivum* L. cv. Lona) per pot were sown in 1.5 l pots containing an illitic-chloritic silt loam. The soil was initially watered to 0.25 g $\text{H}_2\text{O g}^{-1}$ dry soil (soil matric potential: $\Psi_m = 0.03$ MPa) with one strength modified Hoagland solution. 120 mM NaCl was obtained by adding NaCl to the nutrient solution. The experiment was conducted in a growth chamber with a 16 h photoperiod (light intensity: $550 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (PPFD); air temperature: 20°C day/night; relative humidity: 55–65%).

Spatial distribution of relative elemental growth rate

(R_e) of leaf 4 was measured by pinning the 15 holes with a fine needle at 3 mm intervals started from the leaf base. Each treatment had 16 replications.

For analyses of spatial distribution of inorganic ion and sucrose concentrations, the sampling started at 3 h (0900 h) and 13 h (1900 h) into the 16 h photoperiod 3 days after emergence of leaf 4. The elongation zone was carefully freed from surrounding leaf sheaths and then cut with a razor blade from the stem at the leaf base. The excised leaf blade was cut, beginning at the leaf base, into six segments 5 mm long followed by three 10 mm and three 20 mm long. Each treatment was replicated twice. About 120 leaf segments from the same position were combined into a sample for analysis of inorganic ion concentrations and segments from 20–30 blades for the analysis of sugar concentration.

Concentrations of ions (Na^+ , K^+ , Ca^{2+} and P) were determined with an Inductively Coupled Plasma Emission Spectrometer (ICP model Liberty 200, Varian Australia Pty. Ltd., Mulgrave, Victoria, Australia). Chloride and NO_3^- were determined with a chloride-selective electrode (Chloride analyzer 926, Corning Ltd., Halstead, Essex, England) and NO_3^- with an HPLC detector (LC 75, Perkin-Elmer Co., Norwalk, CT, USA). Sucrose was measured according to enzymatic methods from a kit from Boehringer Mannheim with a Kontron spectrophotometer (UVIKON 810, Tegimenta AG, Rotkreuz, Switzerland).

Local net deposition rates (D , $\text{mmol kg}^{-1} \text{FW h}^{-1}$ or $\text{g FW}^{-1} \text{h}^{-1}$) of nutrients were calculated by the one-dimensional version of the continuity equation as described by Silk (1984):

$$D = (\partial P / \partial t) + V_d (\partial P / \partial x) + (R_e P),$$

where P is nutrient concentration (e.g., $\text{mmol kg}^{-1} \text{FW}$), t is time (h), and x is distance (mm) above the base of the leaf

blade. V_d is the displacement velocity of a segment (mm h^{-1}) (which was derived from R_e) (Hu 1996; Hu and Schmidhalter, 1998).

Results and discussion

Relative elemental growth rate was spatially decreased by salinity (Fig. 1). However, the concentrations of nutrients on a fresh weight basis under saline conditions increased, decreased or did not change depending on the location in the leaves and nutrients (Fig. 2). For example, salinity did not change the K^+ and P concentrations, but increased Ca^{2+} and sucrose concentrations and decreased NO_3^- concentrations (Figs 2, 3A). Data of the net deposition rates (NDR) (Figs 3B, 4) showed that the growth zone is a strong sink for nutrients. The greater difference in the NDR of Ca^{2+} , NO_3^- , Na^+ , Cl^- and sucrose

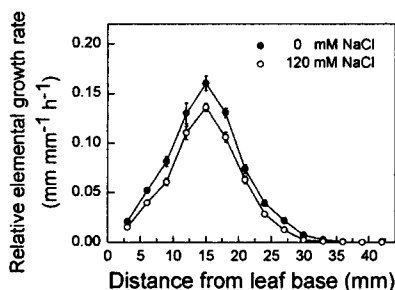


Figure 1. Spatial distribution of relative elemental growth rate of leaf 4 in the growth zone of the mainstem of wheat grown in soil with 0 and 120 mM NaCl during the linear phase of leaf elongation. Error bars represent standard errors.

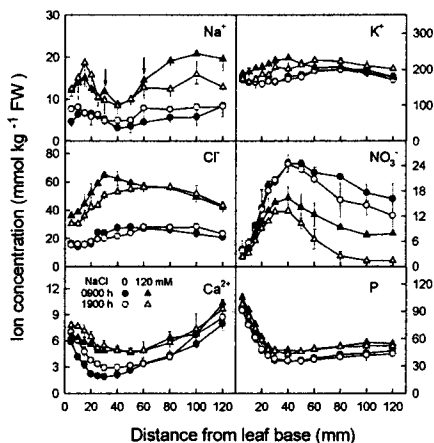


Figure 2. Spatial distributions of Na^+ , K^+ , Ca^{2+} , P, Cl^- and NO_3^- concentrations in the growing leaf 4 on the mainstem of wheat grown in soil with 0 and 120 mM NaCl at two harvest times. Arrows indicate the end of growth zone and of the leaf sheath.

decreased by salinity (Hu 1996), the increased concentrations of Ca^{2+} and sucrose under saline conditions were mainly due to the lowered water deposition, i.e. the reduction in cell expansion was greater than the increase in their net deposition. Higher accumulation of Na^+ and Cl^- may be due to their higher deposition rate. Decreased deposition of NO_3^- may result from the higher uptake of Cl^- . Although Cl^- and Na^+ concentrations in growing and non-growing tissues were increased by salinity, their concentrations were much lower than suggested toxic levels, indicating the reduced leaf growth is not associated with the toxicity of Cl^- and Na^+ .

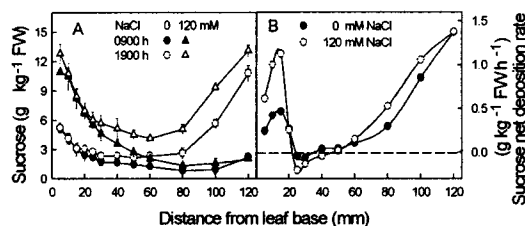


Figure 3. Spatial distributions of sucrose concentration at two harvest times and of local net deposition rate of sucrose in the growing leaf 4 of wheat grown in the soil with 0 and 120 NaCl.

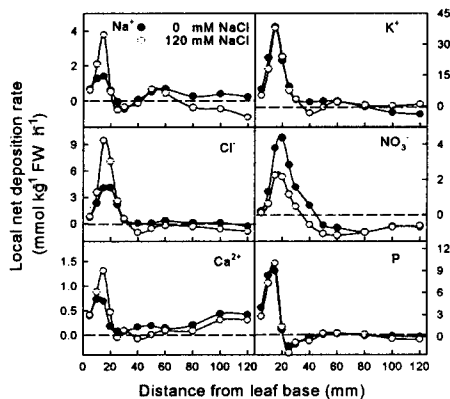


Figure 4. Spatial distributions of local net deposition rates of Na^+ , K^+ , Ca^{2+} , P, Cl^- and NO_3^- in the growing leaf 4 of wheat grown in the soil with 0 and 120 mM NaCl.

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between two treatments occurred at the mid of the growth zone (Figs 3, 4). Since net deposition of water was