

# Hydraulic conductivity of whole root system is better than hydraulic conductivity of single root in correlation with the leaf water status of maize

Zixin MU<sup>1,3</sup>, Suiqi ZHANG<sup>2,3,\*</sup>, Linsheng ZHANG<sup>1</sup>, Aihua LIANG<sup>1</sup>, and Zongsuo LIANG<sup>1,2</sup>

<sup>1</sup> Life Science College of Northwest A&F University, Yangling Shaanxi 712100, P. R. China

<sup>2</sup> Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling Shaanxi 712100, P. R. China

<sup>3</sup> State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Yangling Shaanxi 712100, P. R. China

(Received June 20, 2005; Accepted November 23, 2005)

**ABSTRACT.** Under hydroponic culture conditions, we studied the relationship between two different types of root hydraulic conductivity of maize (*Zea mays* L.) and its leaf water status. The results have proved the inaccuracy of the single root hydraulic conductivity ( $Lp_{sr}$ ) to describe the ability of water uptake by maize roots, which can be better described by the whole root systems hydraulic conductivity ( $Lp_{wr}$ ). Moreover,  $Lp_{wr}$  can be measured easier. Although the whole roots surface area (WRA), which integrated all the root characters, such as root dry weight, volume and length, represent the interaction between root and soil (or water in soil solutions) better, there is no significant relationship between WRA and  $Lp_{wr}$  and leaf water potential because part of the roots has no activity for water uptake. However, active root surface area (ARA) truly reflects the level of root metabolic activity and root function efficiency, i.e., the ratio of the active roots to the whole roots. Hence, ARA has a significant linear correlation with  $Lp_{wr}$ . Because of the high plasticity of plant root systems architecture and metabolism under changed water and nutrition conditions, the relationship between single root  $Lp_{sr}$  and whole root  $Lp_{wr}$  and between WRA and ARA are not positively linear correlated. Results demonstrate that the whole root  $Lp_{wr}$  described by ARA can reflect more accurately both the water uptake by plant roots and the leaf water status than the single root  $Lp_{sr}$ .

**Keywords:** Active root surface area (ARA); Maize; Single root hydraulic conductivity ( $Lp_{sr}$ ); Water channels (aquaporins); Whole root surface area (WRA); Whole root systems hydraulic conductivity ( $Lp_{wr}$ ).

## INTRODUCTION

Root hydraulic conductivity ( $Lp_r$ ), is one of the major parameters reflecting root water uptake ability. It has a close correlation with plant water relations under both normal and stressed conditions. The study of root water uptake has been made progress recently from the anatomical structure of the root to molecular level, i.e., water channel (aquaporin) activity (Steudle, 2000a, b; 2001). Moreover, many measurements are developed including transpiration method, pressure chamber, potometers, root pressure probe and cell pressure probe (Zwieniecki and Boersma, 1997; Barrowclough et al., 2000; Steudle, 2000a). However, due to the high plasticity of plant root systems both in architecture and metabolism (Gunse et al., 1997; Liang et al., 1997; Joslin et al., 2000; Linkohr et al.,

2002; Lopez-Bucio et al., 2003), and the different properties among various measuring methods, the root  $Lp_r$  were highly variable even for the same plant species. These results in a meaningless comparison between different data, and even results in confusion. For example,  $Lp_r$  was usually used to describe plant root water uptake abilities, but most of these results are obtained from root pressure probe or cell pressure probe measurements, which mean most of them are data of single root hydraulic conductivity ( $Lp_{sr}$ ) or root cell hydraulic conductivity ( $Lp_{cr}$ ). Because of the variety of single root development phase in root systems, and even the tissue-specific hydraulic conductivity along a single root could be different (Barrowclough et al., 2000; North and Nobel, 1998, 2000), many questions remain to be answered. Two of the key questions are (1) whether  $Lp_{sr}$  or  $Lp_{cr}$  should be used to describe the capability of whole root system water uptake and water transport, and (2) what is the contribution of whole roots surface area (WRA) to the root water uptake? In this paper, we present results to illustrate the relationship of two types of root hydraulic

\*Corresponding author: E-mail: sqzhang@ms.iswc.ac.cn;  
Tel: +86-29-87010897 (O); Fax: +86-29-87092387.

conductivity and of two types of root surface area, respectively, in hope to study their contributions to plant water relations.

## MATERIALS AND METHODS

### Plant materials and growth conditions

Seeds of maize (*Zea mays* L. HD4) were sterilized for 20 min in 0.2%  $\text{HgCl}_2$  solution. After washing several times with distilled water, seeds were transferred to a culture medium mixed with vermiculite and quartz sand (v/v; 2/3) for 3 d. Temperature was kept at 25°C during the germination. When roots were 5–6 cm long, seedlings were transferred to plastic barrels (depth: 20 cm and diameter: 18 cm; contained 2 seedlings each). Barrels were covered by double layer black plastic cloth to keep the roots in dark. Barrels were placed in a climate chamber (KG-206SHI-D, made in Japan). Growing conditions were light intensity: 250–300  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ ; day/night rhythm: 14/10 h; temperature 27/20°C; Relative humidity: 60–70%. Everyday air pump was used to ventilate the solution 3–4 times, each time 1 h. The growing solution was replaced every 2 d. At first, the barrels were filled with distilled water, and then replaced by half-strength Hoagland nutrient solution after seedlings have adapted for 1 d. There were three nutrition treatments: control (half-strength Hoagland nutrient solution); low N (N concentration was 1/3 of the control, using 1.7 mol/l  $\text{CaCl}_2$  and 1.7 mol/l  $\text{K}_2\text{SO}_4$  to complement the concentration of  $\text{Ca}^{2+}$  and  $\text{K}^+$ ); low P (P concentration was 1/3 of the control, using 0.85 mol/l  $\text{K}_2\text{SO}_4$  to complement  $\text{K}^+$ ). In addition, there were two water conditions: control (no water stress) and water stress simulated by adding PEG-6000 to the growth medium (water potential: -0.2 MPa). 15 d old seedlings (including germination) were used in the experiments. Each treatment has six repetitions.

### Root hydraulic conductivity ( $L_{p_r}$ ) measurements

Root hydraulic conductivity was measured using the pressure chamber method as described by Javot et al. (2003) with some modifications. Root system or single root (primary root) detached from maize seedlings were inserted into the container of a pressure chamber filled with growing solution. The cut stump was put carefully through the soft plastic washer of the metal lid. The seal was tightened using a low-viscosity dental paste. A balance pressure ( $P_0$ ), which was the ex-pressure when the sap exuded initially, was determined at first. Pressure was increased from  $P_0$  (MPa) to  $P_0 + 0.5$  (MPa) at an interval of 0.1 MPa. Under each pressure, when the flow rate was stabilized (about 5 min), the exuded sap ( $V$ ,  $\text{m}^3$ ) was collected for 5 min. The collections were repeated at least three times at a 1 min interval. The weight of the exuded sap was determined using an analytical balance with an accuracy of 0.01 mg. After experiments, root surface area ( $S$ ,  $\text{m}^2$ ) was measured. The flow rate  $J_v$  ( $\text{m}\cdot\text{S}^{-1}$ ) was calculated by  $J_v = V / (S \times t)$ . Root hydraulic conductivity,  $L_{p_r}$

( $\text{m}\cdot\text{S}^{-1}\cdot\text{MPa}^{-1}$ ) was determined from the slope of the regression line by plotting  $J_v$  against hydrostatic pressure ( $P_0 - (P_0 + 0.5)$  MPa), i.e.,  $L_{p_r} = J_v / \Delta P$ .

### Root surface area measurements

The whole roots surface area (WRA) was measured using Root Image Analysis Software CID-400 (CID, Inc. Vancouver, WA). Samples were washed and dyed by 0.5% methylene blue for 10 h. Then the image of the roots was scanned by a numerical scanner to analyze the WRA.

The determination of active root surface area (ARA) was described by Zou (1995). Methylene blue solution was used at a concentration of 0.2 mM. The volume of methylene blue solution used was about 10 times of the root samples volume, and was divided into three beakers marked by No. 1, 2, 3, respectively. The sample roots, washed with distilled water and the residual water on its surface removed with filter paper, were soaked into the three beakers one after the other for 1.5 min in each beaker. Then 0.5 ml solution was taken out from each beaker, diluted by 20 times with distilled water, and the OD values were measured in 660 nm wavelengths. The residual amount of methylene blue in three beakers were obtained according to standard curve, and calculated the amount of methylene blue absorbed by root samples in each beaker.

$$\text{ARA (m}^2\text{)} = A_3 \times 1.1 \text{ m}^2$$

(ARA is active root surface area;  $A_3$  is the amount of methylene blue absorbed by root samples in No. 3 beaker; 1.1  $\text{m}^2$  is the area of methylene blue when it is presented in a single molecular layer).

### Leaf water potential ( $\psi_w$ ) document

Leaf  $\psi_w$  was measured using pressure chamber under excised conditions as described by Turner (1988). Completely expanded leaves were sampled from the upper part of the maize seedlings.

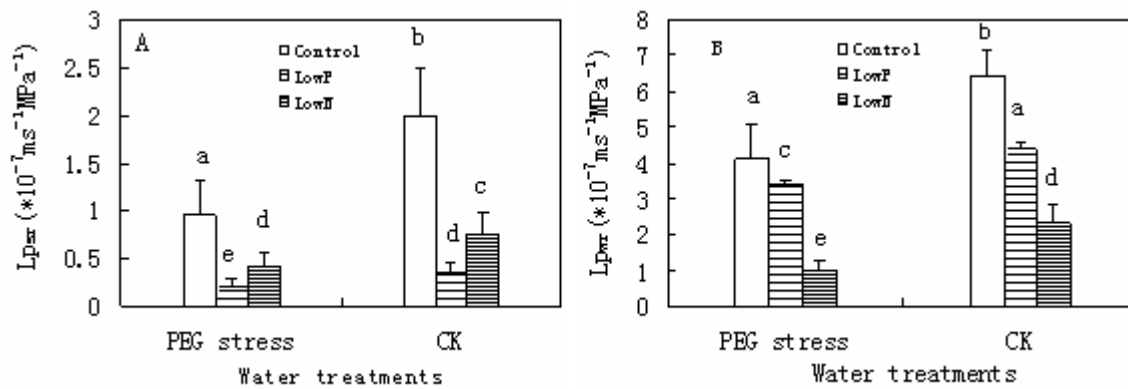
### Statistics

All data were analyzed by Microsoft Excel and SPSS software.

## RESULTS

### There is different changing trends for both $L_{p_{wr}}$ and $L_{p_{sr}}$ under different water and nutrition conditions

It can be seen that regardless of water conditions, both N- and P-deficiency caused a decrease in  $L_{p_r}$  of maize, not only in single root but also in whole root system (Figure 1A, B). The difference is, compared with N-deficiency treatments, the P-deficiency treatments had a higher  $L_{p_{wr}}$  but a lower  $L_{p_{sr}}$ . Except of N-deficiency treatment, water has lower effect on whole root system than on single root, because water stress made the  $L_{p_{wr}}$  of Control and P-deficiency treatments declined 36.2% and 22.7%, respectively,



**Figure 1.** The single root hydraulic conductivity ( $Lp_{sr}$ ) (A) and whole root systems hydraulic conductivity ( $Lp_{wr}$ ) (B) under six treatments. The seedling was 15d old, and treated 10d before measurement.  $Lp_i$  was determined at the same time each day, and maintained the environmental temperature held constant. Each bar is the means  $\pm$  SE (for  $Lp_{sr}$ ,  $n=30$ ; for  $Lp_{wr}$ ,  $n=10$ ). Different letters are used to indicate means that differ significantly ( $p < 0.05$ ).

and made the  $Lp_{sr}$  of them declined 52.5% and 42.8%, respectively. This meant that for the same plant, its  $Lp_{wr}$  and  $Lp_{sr}$  response differently to both the same and different environmental stress.

### There are different changing trends for both WRA and ARA under different water and nutrition conditions

Table 1 indicated that regardless of water conditions, the ratio of ARA/WRA varied between N- and P- deficiency. Compared with N-deficiency treatments, the P-deficiency treatments had a higher ARA but a lower WRA, and therefore had a high ratio of ARA/WRA. Drought also decreased both ARA and WRA, but the decreasing degree are different among the three nutrient conditions. For ARA, the decreasing degree for Control and N-deficiency treatments are greater than for P-deficiency treatment (They are 48.3%, 48.8% and 42.8% respectively), however, for WRA, the decreasing degree for Control and N-deficiency treatments are lower than P-deficiency treatment (They are 28.7%, 27.8% and 34.4% respectively), hence

the ratio of ARA/WRA for (Low P + PEG) treatment is nearly equal (Control + PEG) treatment and significantly greater than (Low N + PEG) treatment. In summary, it is clear that, N-deficiency had effect on the absolute values of ARA while P-deficiency affected the relative values, the two nutrients function differently in root area served as water uptake. This also indicated that ARA and WRA have different response to environmental stress.

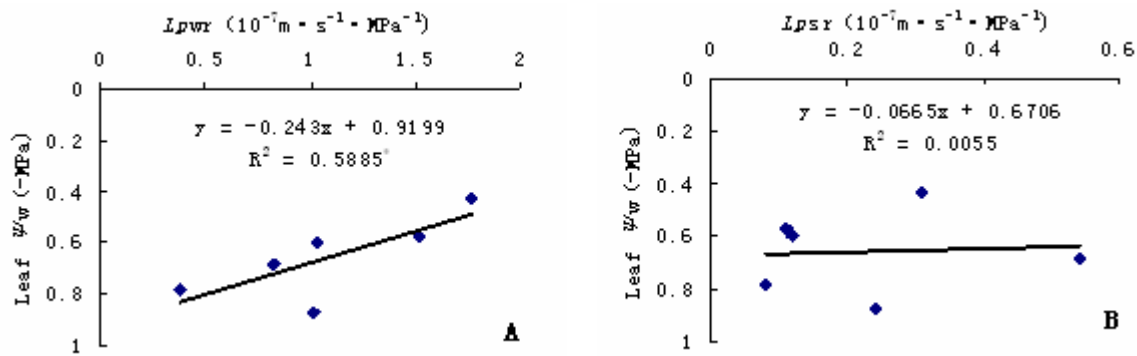
### Relationships between the Two Types of $Lp_i$ and leaf water potential ( $\Psi_w$ )

The root system contains various single roots. Due to different growing conditions and the spatial distributions along root axis, the  $Lp_{sr}$  differed significantly (Doussan et al., 1998; North and Nobel, 1998, 2000; Jackson et al., 2000). Although we selected the same position as well as the same age of the seedlings, we found that there was non-relevant or low relevant between single root  $Lp_{sr}$  and its leaf water potential (Figure 2B). However, as Figure 2A showed, there is a significant positive relation between  $Lp_{wr}$  and leaf water potential.

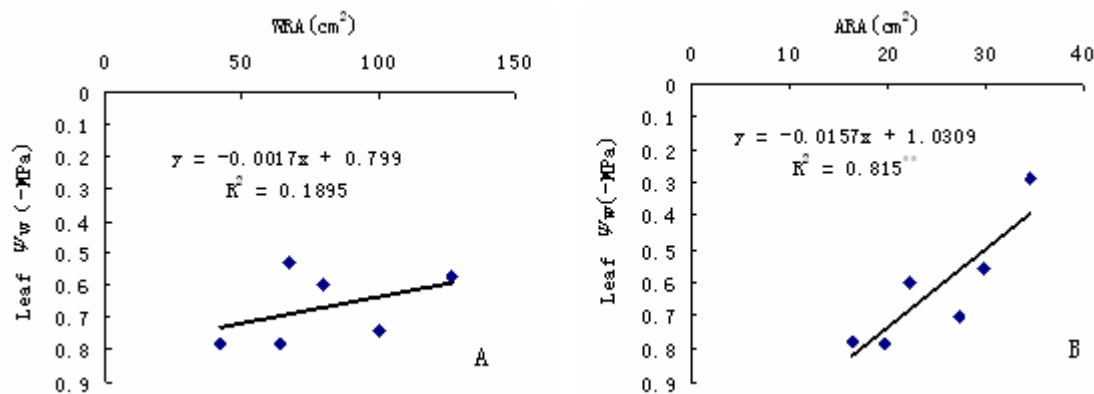
**Table 1.** Root surface area of maize under two water and three nutrient conditions.

	Treatments					
	Control	Control + PEG	Low N	Low N + PEG	Low P	Low P + PEG
ARA ( $\text{cm}^2$ )	110.61 $\pm$ 10.45 <sup>a</sup>	57.24 $\pm$ 3.54 <sup>b</sup>	50.43 $\pm$ 2.75 <sup>bc</sup>	25.82 $\pm$ 4.28 <sup>d</sup>	61.41 $\pm$ 2.36 <sup>b</sup>	35.15 $\pm$ 1.78 <sup>c</sup>
WRA ( $\text{cm}^2$ )	127.00 $\pm$ 8.21 <sup>a</sup>	90.50 $\pm$ 5.32 <sup>c</sup>	101.51 $\pm$ 12 <sup>b</sup>	73.51 $\pm$ 3.85 <sup>cd</sup>	87.45 $\pm$ 1.65 <sup>c</sup>	57.39 $\pm$ 3.21 <sup>d</sup>
ARA/WRA (%)	87 $\pm$ 8 <sup>a</sup>	63 $\pm$ 4 <sup>bc</sup>	49 $\pm$ 7 <sup>c</sup>	35 $\pm$ 4 <sup>d</sup>	70 $\pm$ 2 <sup>b</sup>	61 $\pm$ 2 <sup>bc</sup>

Data (means  $\pm$  SE) were compiled from individual measurements ( $n=20$ ), and the experimental conditions are correspondence with  $Lp_i$  measurements. a:  $n=15$ ; b:  $n=10$ . WRA: whole root surface area; ARA: active root surface area. Superscripted letters indicate statistically different groups at ( $p < 0.05$ ).



**Figure 2.** Relation between two root hydraulic conductivity (A: whole root systems hydraulic conductivity,  $L_{pwr}$ ; B: single root hydraulic conductivity,  $L_{psr}$ ) and leaf water potential ( $\Psi_w$ ). \*Means significant at 0.05 level.



**Figure 3.** Relation between both root surface area (A: whole root surface area, WRA; B: active root surface area, ARA) and leaf water potential ( $\Psi_w$ ). \*\*Means significant at 0.01 level.

### Relationships between the two types of root surface area and leaf water potential ( $\Psi_w$ )

There was almost non-relevant between WRA and leaf water potential by making regression analysis, while a significant positive relevant between ARA and leaf water potential had been found (Figure 3A, B). This indicated that leaf water status is mainly correlated with root metabolism activity (or ARA), but not with root bio-mass (or WRA).

### Relationships between two types of root surface area and whole root $L_{pwr}$

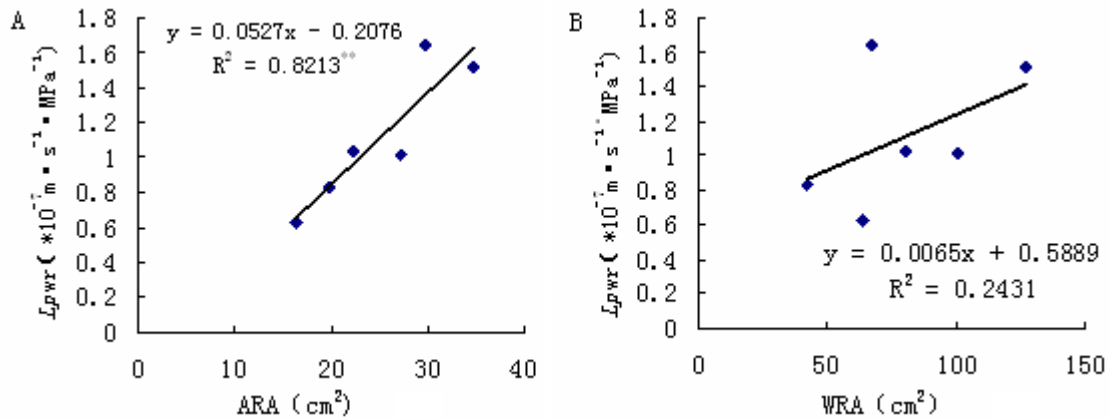
It is well known that under normal conditions of both water and nutrition, root surface area increased, the root volume conducting water is increased too. This in turn, increased the ability of root water uptake (Jackson et al., 2000). However, with the changes of growing conditions, especially in the case of water or nutrition deficient conditions, the WRA is not always identical with the ARA (Table 1). This may due to varieties of root systems in architecture and metabolism activity zones. For roots, the main part to absorb water is the ARA. Figure 4 showed a positive linear relationship between ARA and whole root  $L_{pwr}$ , but it is non-relevant between WRA and whole root  $L_{pwr}$ .

## DISCUSSIONS

### The whole root $L_{pwr}$ is not equal single root $L_{psr}$ , and correlates with the leaf water potential better

In previous study, we have explored the difference between  $L_{psr}$  and  $L_{pwr}$  among maize varieties under single nutrition stress, and explained the phenomenon in term of the plasticity of root architecture and of water channel activity (Mu et al., 2003). In the present paper, from water and nutrient double stresses, we found that phosphate stress had stronger effect on  $L_{psr}$ , but less effect on  $L_{pwr}$  than nitrate stress (Figure 1A, B).

Single root  $L_{psr}$  and whole root  $L_{pwr}$  reflect root water uptake from two different levels. The whole root  $L_{pwr}$  can better reflect the indirect effect of both developmental and environmental factors on the root water uptake and represents an integrated effect among different single root (Lopez-Bucio et al., 2003). In contrast, the single root  $L_{psr}$  relatively reflects the effects of extra- and intro-factors on the water transport resistance through single root cylinder. It has been shown in the literatures that, depending on transpiration requirements, roots are able to switch between apoplastic pathway and cell-to-cell pathway (the



**Figure 4.** Relation between two type root area (A: active root surface area, ARA; B: whole root surface area, WRA) and whole root hydraulic conductivity ( $L_{pwr}$ ). \*\* Means significant at 0.01 level.

composite transport model; Steudle, 2000a, b; 2001). It has been shown too that the activity and abundance of water channel proteins (or aquaporins) in the root plasma membrane play a significant role in the cell-to-cell pathway for maize (Maurel and Chrispeels, 2001; Chaumont et al., 2001; Aroca et al., 2005). Interestingly plant aquaporins were regulated (gated) by phosphorylation, pH, pCa, osmotic pressure and salinity, heavy metals, temperature, nutrient deprivation, or anoxia and oxidative stresses (Luu and Maurel, 2005). This means the characteristics of aquaporins represent a highly plasticity like plant root architecture, which together result in a highly variable root hydraulic conductivity under different external environments. In a certain condition, such as a limited water or nutrition deprivation, the decreased ability of single root water uptake might be compensated for by the increase of whole absorbing area of the root systems—an increase of whole root systems water uptake ability (Jackson et al., 2000; Javot and Maurel, 2002; Mu et al., 2003). At the same time, in the circumstance of a relative high single  $L_{p_{sr}}$  (such as water or nutrition localized addition), the whole root  $L_{p_{wr}}$  may be not the highest due to the decrease of whole root system area. Thus the relationship between the single root  $L_{p_{sr}}$  and the whole root  $L_{p_{wr}}$  are not linear (Mu et al., 2003), and the latter can better reflect leaf water status (Figure 2).

### The root active surface area ARA represents better hydraulic conductance and leaf water potential than WRA

The multitude of fine roots is the most active part of the system in acquiring water and nutrients, with its own multitude of root tips, sites of intense chemical activity that strongly modify the soil around them, and mobilize reluctant ions (McCully, 1995, 1999). Since different water or nutrients application bring out variable of the fine roots, for example, in *Arabidopsis*, N- or P-nutrients deprivation had a contrasting effect on its lateral roots and root hairs, i.e., the former kept a constant lateral root density while the latter increased it, and both of them accelerated lateral

root elongation (Linkohr et al., 2002). Besides, it has been shown that phosphate stress significantly increased root hair density and length (Bates and Lynch, 1996; Ma et al., 2001). Under water stress conditions, especially in the fields, the drought is preceding gradually from the upper soil layers to the deeper soil layers. Often, the deeper roots are active roots as compared with the upper ones. However, when water was re-supplied, the situation reversed because more fine roots could be produced from the upper roots (Liang et al., 1997; Jackson et al., 2000). Evidence suggests that compared with N-deficiency, P-deficiency greatly increased active roots area, as found (Table 1).

In addition to environmental conditions, root activity can also be regulated by the developmental status of the roots (Schiefelbein and Benfey, 1991; Lynch, 1995; Blum and Sullivan, 1997; Graham and Nobel, 1999). In conclusion, plant root systems are plasticity in both architecture and metabolism activity resulting in the difference between WRA and ARA. The former contributes to root biomass, whereas the latter, which is the major functional section of whole root systems and usually distributes in the root hair region, contributes to root functional efficiency (such as water uptake ability) (Figure 3B, Figure 4A).

### The axial resistance in xylem does not be ignored under stress conditions

Xylem vessels, composed of dead cells, well known for their low resistance in water transport, were usually ignored. However, under stress conditions, especially under water deficient, cavitations occurred in xylem could significantly increase the axial resistance (decrease the hydraulic conductivity) (Zwieniecki et al., 2001; Stiller et al., 2003). Except for refilled after rewater, Zwieniecki et al. (2001) found that increasing concentrations of ions flowing through the xylem of plants produced rapid, substantial, and reversible decrease in hydraulic resistance, and this ion-dependent mechanism allow plants to compensate for decrease in hydraulic conductivity induced by cavitations. It is very likely that this is also the mechanism of improving plant drought-resistance by nutrition addition.



It is clear that root cell  $Lp_{cr}$  cannot reflect root axial resistance, while single root  $Lp_{sr}$  can. However, because single roots in different layers along root systems axis have different radius and length of xylem conduits, their axial resistance differed greatly (Jackson et al., 2000). Thus, whether from radial hydraulic conductivity or from axial hydraulic conductivity, can  $Lp_{sr}$  only reflect the hydraulic properties of one layer or of one site where the single root located (Figure 2B). On the other hand, the axial resistance in stem xylem also affects water transport under stress conditions, and in turn affects plant water relations. For the  $Lp_{wr}$  measured in the present study, we retained a segment of stem, so the data also partially reflect the capacity of water transport in the stem. We conclude that whole root  $Lp_{wr}$  not only reflects plant root water uptake ability, but also represents root water transport capacity, due to it integrates both radial and axial resistances of the root system (Figure 2A).

**Acknowledgements.** We are grateful for the support of the Key Innovation Project of the Chinese Academy of Science (KZCX3-SW-444), the Chinese National Natural Science Foundation (30571127), the Innovation Project of the Institute of Soil and Water Conservation, the Chinese Academy of Sciences, the Ministry of Water Resources (SW05101), and the Youth Science Foundation of Northwest A&F University.

## LITERATURE CITED

- Aroca, R., G. Amodeo, S. Fernández-Illescas, E.M. Herman, F. Chaumont, and M. J. Chrispeels. 2005. The role of aquaporins and membrane damage in chilling and hydrogen peroxide induced changes in the hydraulic conductance of maize roots. *Plant Physiol.* **137**: 341-353.
- Barrowclough, D.E., C.A. Peterson, and E. Steudle. 2000. Radial hydraulic conductivity along developing onion roots. *J. Exp. Bot.* **51**: 547-557.
- Bates, T.R. and J.P. Lynch. 1996. Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. *Plant Cell Environ.* **19**: 529-538.
- Blum, A. and C.Y. Sullivan. 1997. The effect of plant size on wheat response to agents of drought stress. I. Root drying. *Aust J. Plant Physiol.* **24**: 35-41.
- Chaumont, F., F. Barrieu, E. Wojcik, M.J. Chrispeels, and R. Jung. 2001. Aquaporins constitute a large and highly divergent protein family in maize. *Plant Physiol.* **125**: 1206-1215.
- Doussan, C., G. Vercambre, and L. Pages. 1998. Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption distribution of axial and radial conductances in maize. *Ann. Bot.* **81**: 225-232.
- Graham, E.A. and P.S. Nobel. 1999. Root water uptake, leaf water storage and gas exchange of a desert succulent: implications for root system redundancy. *Ann. Bot.* **84**: 213-223.
- Gunse, B., C. Poschenrieder, and J. Barcelo. 1997. Water transport properties of roots and root cortical cells in proton- and Al-stressed maize varieties. *Plant Physiol.* **113**: 595-602.
- Jackson, R.B., J.S. Sperry, and T.E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci.* **5**: 482-488.
- Javot, H., V. Lauvergeat, V. Santoni, F. Martin-Laurent, J. Guclu, J. Vinh, J. Heyes, K.I. Frank, A.R. Schaffner, D. Bouchez, and C. Maurel. 2003. Role of a single aquaporin isoform in root water uptake. *Plant Cell.* **15**: 509-522.
- Javot, H. and C. Maurel. 2002. The role of aquaporins in root water uptake. *Ann. Bot. (Lond.)* **90**: 301-313.
- Joslin, J.D., M.H. Wolfe, and P.J. Hanson. 2000. Effects of altered water regimes on forest root systems. *New Phytol.* **147**: 117-129.
- Liang, B.M., R.E. Sharp, and T.I. Baskin. 1997. Regulation of growth anisotropy in well-watered and water-stressed maize roots (I. Spatial distribution of longitudinal, radial, and tangential expansion rates). *Plant Physiol.* **115**: 101-111.
- Linkohr, B.I., L.C. Williamson, A.H. Fitter, and O. Leyser. 2002. Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*. *Plant J.* **29**: 751-760.
- Lopez-Bucio, J., A. Cruz-Ramírez, and L. Herrera-Estrella. 2003. The role of nutrient availability in regulating root architecture. *Curr. Opin. Plant Bio.* **6**: 280-287.
- Luu, D.T. and C. Maurel. 2005. Aquaporins in a challenging environment: molecular gears for adjusting plant water status. *Plant Cell Environ.* **28**: 85-96.
- Lynch, J. 1995. Root architecture and plant productivity. *Plant Physiol.* **109**: 7-13.
- Ma, Z., D.G. Bielenberg, K.M. Brown, and J.P. Lynch. 2001. Regulation of root hair density by phosphorus availability in *Arabidopsis thaliana*. *Plant Cell Environ.* **24**: 459-467.
- Maurel, C. and M.J. Chrispeels. 2001. Aquaporins, a molecular entry into plant water relations. *Plant Physiol.* **125**: 135-138.
- McCully, M.E. 1995. How do real roots work? *Plant Physiol.* **109**: 1-6.
- McCully, M.E. 1999. Roots in soil: unearthing the complexities of roots and their rhizospheres. *Annu. Rev. Plant Physiol. Mol. Biol.* **50**: 695-718.
- Mu, Z. X., S. Zhang, X. Yang, and Z. Liang. 2003. Effect of nitrogen and phosphorus-deficiency on maize root hydraulic conductivity. *J. Plant Physiol. Mol. Biol.* **29**: 45-51. (in Chinese)
- North, G.B. and P.S. Nobel. 2000. Heterogeneity in water availability alters cellular development and hydraulic conductivity along roots of a desert succulent. *Ann. Bot.* **85**: 247-255.
- North, G.B. and P.S. Nobel. 1998. Water uptake and structural plasticity along roots of a desert succulent during prolonged drought. *Plant Cell Environ.* **21**: 705-713.
- Schiefelbein, J.W. and P.N. Benfey. 1991. The development of plant roots: new approaches to underground problems. *Plant*

- Cell. **3**: 1147-1154.
- Steudle, E. 2000a. Water uptake by plant roots: an integration of views. *Plant Soil*. **226**: 45-56.
- Steudle, E. 2000b. Water uptake by roots: effects of water deficit. *J. Exp. Bot.* **51**(Special Issue): 1531-1542.
- Steudle, E. 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **52**: 847-875.
- Stiller, V., H. Renee Lafitte, and J.S. Sperry. 2003. Hydraulic properties of rice and the response of gas exchange to water stress. *Plant Physiol.* **132**: 1698-1706.
- Turner, N.C. 1988. Measurement of plant water status by pressure chamber-technique. *Irrig. Sci.* **9**: 289-308.
- Zou, Q. 1995. Guide to Physiological and Biochemical Experiments. Agricultural Press, Beijing China, pp. 30-31. (in Chinese)
- Zwieniecki, M.A. and L. Boersma. 1997. A technique to measure root tip hydraulic conductivity and root water potential simultaneously. *J. Exp. Bot.* **48**: 333-336.
- Zwieniecki, M.A., P.J. Melcher, and N. Michele Holbrook. 2001. Hydrogel control of xylem hydraulic resistance in plants. *Science* **291**(9): 1059-1062.

## 整株根系水導較單根水導更能反映玉米葉片的水分狀況

慕自新<sup>1,3</sup> 張歲岐<sup>2,3</sup> 張林生<sup>1</sup> 梁愛華<sup>1</sup> 梁宗鎖<sup>1,2</sup>

<sup>1</sup> 西北農林科技大學生命學院

<sup>2</sup> 中國科學院、水利部水土保持研究所

<sup>3</sup> 黃土高原土壤侵蝕與旱地農業國家重點實驗室

在室內溶液培養條件下，研究了玉米（*Zea mays* L.）在整株根系和單根兩個水準上的水力學導度與植株水分狀況間的關係。結果表明用單根水導表示根系吸水能力具有不準確性，而在其他外界條件一定時，整株根系水導即可直接反映根系吸水能力。另外從測試方法上看，整株根系水導的測定更容易，也更準確。在根系水導的度量方法上，根系總表面積雖然綜合了根系重量、體積、長度各方面的特性，準確地反映了根系與土壤及土壤溶液中水分的接觸情況，但由於無效根的存在，它與整株根系水導、植物整體水分狀況間的相關性不顯著；而活躍吸收面積由於真實地反映了根系的代謝活力大小及根系的功能效率，即實際充當吸水功能的根系的大小，因此與整株根系水導、植物整體水分狀況間具有顯著的相關性。由於不同水肥處理下根系發育的高度可塑性和水肥供應在空間位置上的非均一性，致使單根水導與整株根系水導，根系表面積與活躍吸收面積間均成非線性關係，甚至無相關性。因此只有用活躍吸收面積表示的整株根系水導才能準確反映植物整體根系的輸水狀況和植物整體水分關係。

**關鍵詞：**玉米；單根水導；整株根系水導；水通道蛋白；活躍吸收面積；根系總面積。