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Root pressure probe can be used to measure the hydraulic properties of whole root systems of corn (*Zea mays* L.)

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ABSTRACT. Root pressure probes have been widely employed to measure the hydraulic properties of roots from various plants in the past two decades. However, they have not been used on the whole root systems of any gramineous seedling. Taking corn seedling as material, the feasibility of a root pressure probe determining hydraulic parameters of whole root systems was investigated in this study. Hydraulic conductivities of single root and root system grown hydroponically as well as soil-cultured corn seedlings were determined by root pressure probe, the values were 12.01×10^{-8} m s^{-1} MPa^{-1}, 10.88×10^{-8} m s^{-1} MPa^{-1} and 8.56×10^{-8} m s^{-1} MPa^{-1}, respectively. The figures for the hydraulic conductivity of root systems grown under hydroponic culture and determined by pressure chamber (22.89×10^{-8} m s^{-1} MPa^{-1}) were of the same order of magnitude. It was concluded that root pressure probes can be used to measure the hydraulic conductivity of corn seedling root system by connecting them to the mesocotyl rather than the stem.

Keywords: Corn; Root hydraulic conductivity; Root pressure probe.

INTRODUCTION

A root pressure probe is one widely used technique for determining the water relations of plant roots. Hydraulic parameters of single root segments (root tips) or root systems can be measured in this way (Steudle et al., 1987; Steudle and Meshcheryakov, 1996). This technique relies on the fact that excised root will exude xylem sap due to the active accumulation of solutes in the xylem. If exudation is stopped by attaching a "root manometer," pressure will develop in the system and can be measured continuously (Steudle, 1993). Since a root pressure probe was used to determine hydraulic conductivity of barley individual roots for the first time (Steudle and Jeschke, 1983), it has been extensively used to investigate the water relations of roots from various plants such as corn (Steudle et al., 1987; Zhu and Steudle, 1995), rice (Miyamoto et al., 2001), barley (Steudle and Jeschke, 1983), onion (Melchior and Steudle, 1993), cucumber (Lee et al., 2005) and some woody plants (Steudle and Heydt, 1997). Of these, corn was the most popular material used to explore the plant water relations under different environmental conditions (Frensch and Steudle, 1989; Peterson et al., 1993; Peterson and Steudle, 1993; Steudle et al., 1993; Liu et al., 2007). However, most of these data were obtained from single root segments. Although some researchers applied a root pressure probe to the whole root system of tree seedlings or cucumber seedlings belonging to the dicotyledon (Rüdinger et al., 1994; Steudle and Meshcheryakov, 1996; Steudle and Heydt, 1997; Lee et al., 2005), they have not been applied to gramineous root systems. Certainly, other techniques—such as pressure chambers, evaporation flux, and hydrostatic pressure-induced reverse flow—could all be used to determine the hydraulic conductance or conductivity of root systems (Tyree, 2003), but a root pressure probe has the advantage of being able to determine all the important parameters for water and solute transport. Moreover, due to the different properties of various measuring methods, the hydraulic conductivity values reported in the literature have varied greatly, even for for the same species (Yang and Granz, 1996; Mu et al., 2006).

The root water uptake composite model was obtained from a combination of hydraulic paramenters obtained at the root cell level and from single root segments, which showed that water enters roots through three parallel pathways (the apoplastic, symplastic, and transmenbrane

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pathways). Different pathways dominate under different enviornments (Steudle and Peterson, 1998; Steudle, 2000). However, to further our understanding of the hydraulic architecture of roots, it is important to investigate root hydraulics at different levels, in root cells, root zones and segments, fine roots, coarse roots, and root systems (Steudle and Meshcheryakov, 1996).

From the standpoint of methodology, the application of a root pressure probe to the corn root system raises three questions:

Is it possible to measure the hydraulic conductivity of the whole root system with a root pressure probe in corn?

On which part of the corn seedling is it proper to affix the root pressure probe?

Can a root pressure probe be applied to corn plants without digging the root system out of the soil?

This work aims to estimate the feasibility of applying a root pressure probe to the whole root system of corn. The experimental results were confirmed from the evidence based on anatomical information and the data from a pressure chamber, as well as from values obtained from single roots to which root pressure probes had been applied.

MATERIALS AND METHODS

Plant materials and growth conditions

Hydro-culture. Corn caryopses were sterilized by 1% NaClO. Seeds were then germinated in Petri dishes with two layers of filter paper and watered with nutrient solution (1.5 mM KH_2PO_4, 2.0 mM KNO_3, 1.0 mM $CaCl_2$, 1.0 mM $MgSO_4$, 18 μM FeNaEDTA, 8.1 μM H_3BO_3, 1.5 μM $MnCl_2$ at a pH of 5.8) for 5 d at 25°C in the dark. Etiolated seedlings were then transferred to aerated hydroponic culture vessels with 1/2 strength Hoagland nutrient solution and kept in a growing cabinet (KG-206SHL-D, Japan) at 27/20°C (day/night) under a photoperiod of 14/10 h (day/night), a relative humidity of 60-70 %, and a maximum photon flux density (PFD) of 1200 μmol m^{-2} s^{-1}. The measurement could be extended after the plant leaves had turned green.

Soil culture. The same sterilized seeds as mentioned in the hydo-culture section were germinated for 48 h, then sown in pots that contained a 3:1:1 (v/v) mixture of peat, vermiculite, and perlite. These pots were watered every day and kept under the same conditions applied to the hydroponic seedlings mentioned above.

Root hydraulic conductivity (Lp_r) measurements

Pressure chamber measurements. This measurement comprised two parts: one was performed on stems and the other on mesocotyls. The former was measured with a pressure chamber after the shoot was cut off at distances of 3-4 cm from the base of the stem; the latter was done after cutting off the shoot at the top end of the elongated mesocotyl. The detailed root pressurization processes were performed as described by Liu et al. (2001) with some modifications. The root system (mainly the primary root) was inserted into a pressure chamber container filled with distilled water. The cut stump of the stem was put carefully through the soft plastic washer of the metal lid. The seal was tightened using a low-viscosity dental paste. An appropriate pressure (P_0, 0.12 MPa), which was the highest pressure under which sap flow could be exuded without damage to the plant tissue, was first determined. From here, pressure was lowered step by step from P_0 with an interval of 0.02 MPa. Under each pressure step, the exuded sap (V, m^3) was collected for 60 s (t) with at least three replications after the flow rate was stabilized. The weight of the exuded sap was determined using an analytical balance with an accuracy of 0.1 mg. Because distilled water was supplied for measuring root, the density of exuded sap was assumed as 1 $g \cdot cm^{-3}$. After experiments, root surface area (A_r, m^2) was measured. The flow rate Jv ($m^3 \cdot m^{-2} \cdot s^{-1}$) was calculated by $Jv = V / (A_r \times t)$.

After the experiments on the stem were finished, the stump of the stem was cut off at the top of mesocotyl. Then the mesocotyl stump was put carefully through the soft plastic washer of the metal lid, and the same process of pressurization on the root system was conducted.

At last, root hydraulic conductivity, Lp_r ($m \cdot s^{-1} \cdot MPa^{-1}$) was determined from the slope of the regression line by plotting Jv against the series of hydrostatic pressure applied, i.e., $Lp_r = J_v / \Delta P$.

Root pressure probe measurements. *Measurements of root system*—The root systems of corn plants were excised close to the top of their mesocotyls and tightly fixed to a root pressure probe using cylindrical silicon seals. The inner diameters of the seals were adapted to the diameters of the mesocotyls and adjusted by a screw. The seals were water-tight but did not interrupt water flow in the xylem. The probe was filled with silicon oil and water so that a meniscus formed in the measuring capillary that was used as a point of reference. Root pressure (P_r in MPa) was measured with a pressure transducer, and the data from the transducer were digitized and directly fed into a computer for calculation of root hydraulic data. Stable pressure usually will develop within 3-5 h. Hydrostatic relaxations were performed by pushing water into the cut end of the mesocotyls with the aid of the metal rod, or by withdrawing water out of the cut end of mesocotyl with the aid of the metal rod. Transient responses in root pressure followed, which allowed Lp_r to be calculated from the measuring system constant or from the half-times of pressure relaxations (Steudle et al., 1987; Rüdinger et al., 2000).

Great care was taken to remove all air bubbles from the measuring system. Air bubbles would have dampened changes in root pressure and reduced system sensitivity. The measuring system requires constant elasticity, but this requirement (elastic modulus, β) is not met when air bubbles are present. Some of the volume displacement of the rod goes to compress the bubbles, and their pressure is inversely proportional to the volume (according to the ideal gas law) (Tyree, 2003). After each measurement, the proper function of the seals was confirmed by cutting off the mesocotyls. When the root xylem remained open, root pressure dropped to zero, and half-times decreased dramatically (hydraulic conductance increased) after the cut. Otherwise, the experiment was discarded. Hydraulic conductivity (Lp_r) could be obtained from the following equations:

$$Lp_r = \frac{\ln 2}{A_r \cdot \beta \cdot T_{r1/2}} \quad (1)$$

A_r= root surface area; β=elastic coefficient of measuring system; $T_{r1/2}$=half time of water exchange across root.

$$\beta = \frac{\Delta P_r}{\Delta V_s} \quad (2)$$

Measurements of individual root—Individual root segments without root hair were excised from root system and then mounted on a root pressure probe. The process of hydrostatic relaxations and the calculation of Lp_r was same as described for root system measurement above.

Anatomical structure

Freehand cross-sections were generated for different parts of the corn seedling—root, mesocotyl and stem—to clarify their anatomical structure. Sections were stained with TBO (Toluidine Blue O), examined with a light microscope, and photographed by digital camera.

Measurement of root area

After the root pressure probe measurement, the root surface area was measured using Root Image Analysis Software CID-400 (CID, Inc. Vancouver, WA). Root systems were stained with Methyl Blue for 12 h, and then root sections were imaged using a a digital scanner. Each single root was taken as a cylinder, and the surface area was calculated from its diameter and length, subtracting the apical part where the xylem elements were immature (apical 20 mm of roots; Peterson et al., 1993).

RESULTS

Characteristics of anatomy structure in mesocotyl, primary root, and stem

To pass from the soil solution into vascular tissue, water has to flow radially across a series of concentric cell layers. These layers include the epidermis, exodermis, several layers of cortex, endodermis, xylem parenchyma cells, and finally the vessel (Steudle and Peterson, 1998). The mesocotyl of corn seedlings has a root-like anatomy with a central stele surrounded by a cylindrical cortex and epidermis (Desrosies, 1996). In corn seedlings, the vessels of corn root are arranged in a circle in the stele (Figure 1B). Vascular bundles which consist of xylem and phloem are dispersed in the cross-section of the stem (Figure 1C). Several vessels of mesocotyl cluster together randomly, and then half of these clusters form a half circle with the other part of the vessels also dispersed in the central part of the mesocotyl cross section (Figure 1A). Compared with the stem, the structure of mesocotyl is more similar to root. A big air space among the leaves means that connecting the stem to the root pressure probe is inappropriate (Figure 1C), because this probe cannot function properly with air bubbles in the measuring system.

Root pressure probe experiments

Steady root pressure was established 3-5 h after corn root systems were connected to the root pressure probe. Root pressure values varied between 0.05 and 0.17 MPa. The half-times and elastic modulus were calculated from pressure relaxation curves that resulted from water flow induced by moving the metal rod (see Material and Methods; Figure 2). Then Lp_r was calculated according to Equation (1) and (2). Data in Table 1 showed that the half-times of pressure relaxation in individual roots were much longer than the halftimes of root systems. Half-time values were 6.1 s for individual roots and 1.04 s and 1.41 s for root systems grown in hydroponic culture and soil culture, respectively (Table 1). However, the root surface areas were also different: the Lp_r values in corn root segments, root systems grown in hydroponic culture and root systems grown in soil were 12.01×10^{-8} m s^{-1} MPa^{-1}, 10.88×10^{-8} m

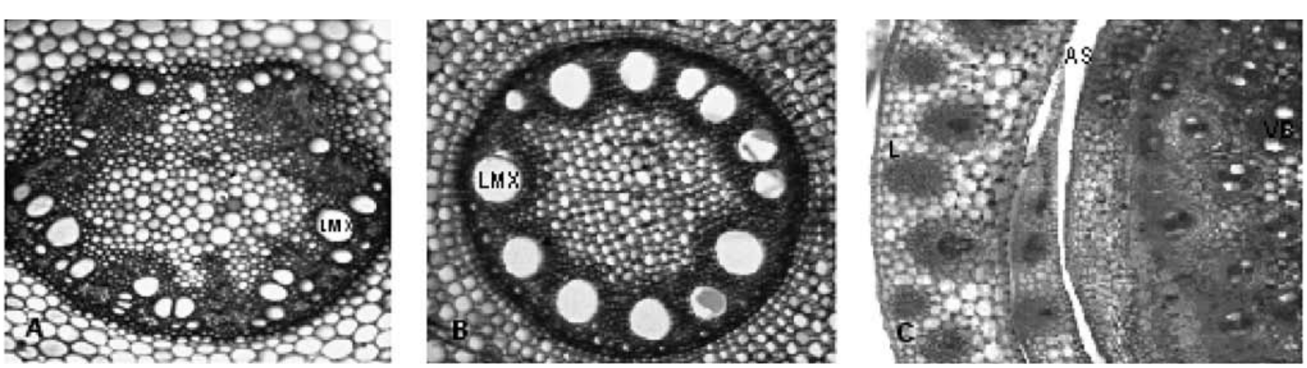

Figure 1. Light microscopic pictures for freehand cross-sections of TBO-stained corn mesocotyl (A), root (B) and stem (C). Abbreviations: AS, air space; VB, Vascular bundle; LMX, late metaxylem; L, leaf.

s^{-1} MPa^{-1} and 8.56×10^{-8} m s^{-1} MPa^{-1}, respectively, and these were of the same order of magnitude (Table 1).

Steady-state hydraulic experiments by pressure chamber

At different pressure steps, the water flow rate per unit surface area of root system (Jv_r) was plotted with pressure (Figure 3). For the same plant at a certain pressure step, the volume of water flow measured at the mesocotyl was slightly higher than that of the stem. However, the hydraulic conductivities, which were the slopes of the plotted lines, from different measurements at the stem and mesocotyl were similar, that is, 2.289×10^{-7} m s^{-1} MPa^{-1} and 2.292×10^{-7} m s^{-1} MPa^{-1}, respectively. These values indicated that there was no effect of dependence between hydraulic conductivity and the measurement location.

DISCUSSION

The results of this study show that a root pressure probe can be used to measure the hydraulic properties of the corn root system by mounting mesocotyls of corn seedlings on it. In herbaceous plants, the steady state values of root pressure have been found to range between 0.05 and 0.5 MPa (Kramer, 1983). The values of root pressure reported here for corn root systems were within this range. To the best of the authors' knowledge, this is the first detailed description of a root pressure probe application to a corn root system. Steudle and his co-workers (1987) have suggested that the halftimes of intact root systems could be much shorter than those of individual roots. The results in this study, which were 1.04 s for root system and 6.1 s for individual roots, respectively, were in line with this suggestion.

Several techniques for determining the hydraulics of whole root systems were described in the literature, including evaporation flow (Tsuda and Tyree, 2000), pressure chamber (Gallardo et al., 2002; Mu et al., 2005, 2006), HPFM (Tsuda and Tyree, 2000; Smith and Roberts, 2003), and tension-induced flow (Huang and Nobel, 1994; Vercambre et al., 2002). However, evaporation flow is limited by the accuracy of field measurements

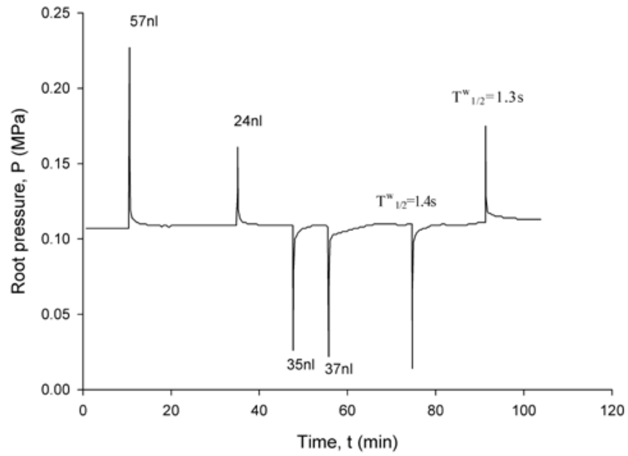

Figure 2. Time course of pressure during a typical experiment with root pressure probe on corn root system sitting in soil. (A) Measurements of the elasticity of measuring system for determining Lp_r of root system; (B) Examples of hydrostatic pressure relaxations of whole root system.

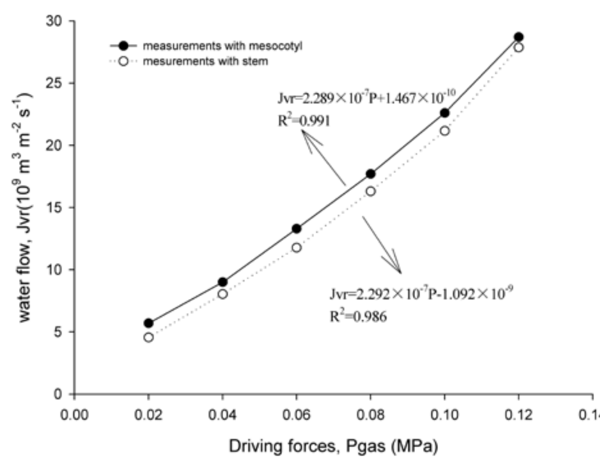

Figure 3. Steady-state water flow per unit surface area root system (Jv) as a function of applied driving force for stem part experiment (open circles with dotted line) and mesocotyl part experiment (closed circles with solid line). Hydraulic conductivities were calculated from the slop of the graphs shown in the figure.

Table 1. Methodological comparison between several root pressure probe measurements and pressure chamber experiments.

Measurements	$T_{w1/2}$ (s)	Ar×10^4 (m^2)	Lp_r×10^8 (m s^{-1} MPa^{-1})
A	6.1±1.61	3.768±0.625	12.01±1.28
B	1.04±0.22	24.388±7.836	10.88±1.63
C	1.41±0.27	31.794±10.762	8.56±1.19
D	-	34.33±8.709	22.89±3.37

Measurement A: root pressure probe measurements for individual roots; measurement B: root pressure probe measurements for root system grown in hydroponic culture; measurement C: root pressure probe measurements for root systems sitting in soil; measurement D: pressure chamber measurements for root system grown in hydroponic culture.

$T_{w1/2}$: Half-time of pressure relaxation during root pressure probe experiment; A_r: Root surface area for all experiments; Lp_r: Root hydraulic conductivity.

Note: Half-time values are mean ± SE of four experiments, other values are mean ± SD of four experiments.

of water potential in the stem, in the root, in the soil-root interface, and in the soil; pressure induced flow through root systems was shown to be an inappropriate method for characterizing absolute hydraulic properties because the externally applied pressure can induce flow through pathways external to the system (Koide, 1985). Root pressure probes work under natural conditions with root pressure building up gradually, an advantage over other techniques. Moreover, compared with HPFM, root pressure probes minimized the effects of unstirred layers in pressure relaxation mode during measurements (Knipfer et al., 2007).

Lan and Lou (2001) found that nodes of the mesocotyl have higher resistance for solute translocation than internode tissue. The results from pressure chamber experiments in this study indicated that the mesocotyl nodes might also have slightly higher resistance to axial water flow. However, this difference had no effect on the measurements of root hydraulic conductivity. It indicated that the results of hydraulic conductivity from the root pressure probe, with which mesocotyls were connected, were reliable in this study.

Data in Table 2, which listed Lp_r values of herbaceous plants, varied for different species at different ages under different techniques. The data obtained in this study was in the range of those prior results. From a physiological and morphological point of view, plants from different species or from one species at different ages have different root morphology and anatomical structure. Therefore, based on the theory of relationship between structure and function, these root systems would have different water uptake ability. With regard to the present study, Lp_r values for root systems grown in soil are 15% lower than those of plants grown hydroponically. This could be possibly explained by the anatomical differences between root systems grown in different substrates. Because a root system of soil culture may have a better developed exodermis and endodermis with more hydrophobic substance, resistance to water flow entering the xylem from the rhizosphere is higher. Resistance at the soil-root surface is evidently higher than at the root-water surface, which could be another reason for the lower Lp_r in soil-culture root systems. Secondly, we found the Lp_r value of root segments to be slightly different from that of root systems, even when both were from plants grown in hydroponic culture (Table 1). As mentioned in Materials and Methods, hydraulic conductivity is an average value for whole root system surface area, demonstrating water permeability per unit area of root surface. Because of the requirements of the root pressure probe technique, only new root segments without root hair can be selected for individual root measurements (Steudle et al., 1987). These root segments are mostly composted of root tips—the most active area for water and solute absorption (Pan, 2002). However, the whole root system might include some root area which is low permeable or non-permeable for water (extremely resistant to water flow) such as highly suberized root segments, but the overall (geometric) surface area of root

Table 2. Comparison of root hydraulic conductivity values derived from the literature.

Herbaceous plants	Culture regime	Age	Technique	Root types	$Lp_r \times 10^8$ ($m\ s^{-1}\ MPa^{-1}$)	References
Winter wheat	Soil culture	25d	Potometer	Individual roots	5.0-85	Huang and Dong (2000)
Barley	Hydro-culture	6-13d	Root pressure probe	Excised individual roots	0.4-1.3	Steudle and Jeschke (1983)
Corn	Soil culture	35d	Potometer	Individual roots	39.2	Li et al. (2002)
Corn	Hydro-culture	5-13d	Root pressure probe, hydrostatic force	Excised individual roots	9.4-11.5	Steudle et al. (1989)
Corn	Soil culture	60d	Pressure chamber	Excised root system	19.919	Liu et al. (2001)
Corn	Hydro-culture	15d	Pressure chamber	Excised root system	19.25	Mu et al. (2005)
Rice	Hydro-culture	31-40d	Pressure chamber	Excised root system	3.2-9.4	Miyamoto et al. (2001)
Rice	Aeroponics	31-40d	Pressure chamber	Excised root system	3.2-11.6	Miyamoto et al. (2001)
Rice	Hydro-culture	31-40d	Root pressure probe, hydrostatic force	Excised individual roots	2.5-7.5	Miyamoto et al. (2001)
Rice	Aeroponics	31-40d	Root pressure probe, hydrostatic force	Excised individual roots	1.2-4.4	Miyamoto et al. (2001)
Tomato	Soil culture	60d	Potometer	Individual roots	38.2	Zwieniecki and Boersma (1997)
Alfalfa	Hydro-culture	8-9 leaf stage	Pressure chamber	Excised root system	83-110	Li et al. (2007)
Onion	Hydro-culture	6-22d	Root pressure probe, hydrostatic force	Excised individual roots	14	Melchior and Steudle (1993)

systems were used to calculate Lp_r values. That is to say, if the "effective surface area" is only a fraction of the geometric surface area, and water uptake would only take place in the younger parts of fine roots, this would increase the absolute value of Lp_r when referring to a smaller area (Steudle and Meshcheryakov, 1996). Hence, a higher Lp_r value of root segments was found in this study compared with that of root system.

It should be noted that the Lp_r values from pressure chamber experiments were almost double the values obtained by root pressure probe measurements. Liu et al. (2001) have shown that the application of a descending pressure process yields more precise results than ascending pressure. For the descending pressure process, we took the highest pressure for the first step and then lowered it step by step, which insured that the interspace between root cells was filled with water at the first pressure step and the apoplastic pathway could contribute more to water transport across root. In contrast, a root pressure probe measures roots working under natural conditions without applied environmental pneumatic gas. Therefore, pressure chamber experiments yielded higher values of Lp_r than root pressure probe experiments.

Root pressure probe works better with small root systems than large ones (Tyree, 2003). For the measurements here, a mesocotyl of at least 2 cm is necessary to mount a plant root system on a root pressure probe. Zheng and Fan (1998) investigated the growth characteristics of corn, rice, and wheat mesocotyls. Corn had an extendable mesocotyl; the growth of rice mesocotyl depended on the variety used, environmental conditions and plant regulators; wheat mesocotyl could not extend during seedling development. Measurements of the wheat root system might be impossible by the technique presented here. Nevertheless, this method could not be used on corn seedlings beyond the three-four leaf stage because the adventitious root will emerge on the mesocotyl and on the nodes between shoot and mesocotyl with the development of seedlings. The presence of mesocotyl adventitious root would bring more air to the measuring system. Despite these limitations, measurements of the hydraulic properties of root systems were performed successfully here, and further comprehensive investigation could be carried out by the combination of a root pressure probe and cell pressure probe to study the water relations of corn roots at the levels of single root and whole root systems as well as at those of the single cell. Therefore, it was concluded that the root pressure probe can be used to measure the Lp_r of the corn seedling root system. The mesocotyl of the corn seedling is the most appropriate part to connect to the probe during the experiments. At the same time, the root system was not required to be excavated from the cultivated substrate when corn seedlings were grown in pots. A root pressure probe can be applied to the whole root systems of corn seedlings and even to other gramineous seedlings grown under different conditions.

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根壓力探針在玉米整株根系導水率測定中的應用

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近二十年來，壓力探針技術被廣泛地應用於植物根系吸水特性的研究，但由於技術上的原因，一直沒有實現對禾本科植物幼苗整株根系水力學特性的測定。本研究在室內溶液培養及土壤培養條件下，採用根壓力探針技術對玉米整株根系導水率進行了方法上的探討。玉米幼苗莖部在其完全發育之前是由數片幼葉包裹而成，其間充滿空氣，不適宜與根壓力探針連接進行測定，而中胚軸由於具有與根相似的解剖特徵，從而可以將根壓力探針連接於玉米中胚軸上進行玉米幼苗整株根系導水參數的測定。採用根壓力探針技術對溶液培養的玉米單根、整株根系以及土壤培養條件下的整株根系的導水率進行了測定，其導水率值分別為 12.01×10^{-8} m s^{-1} MPa^{-1} 、10.88×10^{-8} m s^{-1} MPa^{-1} 和 8.56×10^{-8} m s^{-1} MPa^{-1} ，與壓力室技術所測得的水培玉米整株根系導水率（22.89×10^{-8} m s^{-1} MPa^{-1}）進行比較，其值在同一數量級上。因此，根壓力探針技術可以用於一定苗齡的玉米幼苗整株水分關係的研究。

關鍵詞： 玉米 ； 根導水率 ； 根壓力探針。