Front. For. China (2006) 3: 298–304
DOI 10.1007/s11461-006-0020-x

RESEARCH ARTICLE

SUN Hailong, WU Chu, XU Wenjing, WANG Zhengquan

Variations of root hydraulic conductance of *Fraxinus mandshurica* seedlings in different concentrations of NH_4NO_3 solution

Abstract Absorbing water from soil by roots in vascular plants is an important physiological function and plays an essential role on their water balance. The root hydraulic conductance (L_P) determined by radical water transport inside the root is a major influence on the shoot water status, plant growth, and development. However, a few studies have focused on the effect of different substances on L_P of roots, and the role of radical water transport was poorly understood. Based on the pressure–flux approach, this study used the roots of *Fraxinus mandshurica* seedlings with different treatments, i.e., distilled water, NH_4NO_3 solution, and $HgCl_2$ to determine the effect of various substances on L_P of roots. The objectives are: 1) to evaluate the difference in L_P occurred between distilled water and NH_4NO_3 solution with various concentrations; and 2) to examine the changes of L_P under distilled water and NH_4NO_3 solution with various concentrations after $HgCl_2$ treatment. The results showed that L_P of roots were 18.85×10^{-8} m/(s·MPa) in distilled water, $31.25–34.15\times10^{-8}$ m/(s·MPa) in four NH_4NO_3 solutions (2, 4, 8 and 16 mmol/L), 14.69×10^{-8} m/(s·MPa) in distilled water after $HgCl_2$-treated, and $9.63–13.57\times10^{-8}$ m/(s·MPa) in four NH_4NO_3 solutions after $HgCl_2$-treated, respectively. Aquaporins play an important role in regulating water uptake and transport in roots. NH_4^+ and NO_3^- could stimulate activity of aquaporins, and L_P of roots in NH_4NO_3 solution was distinctly 77% higher than in distilled water. Nevertheless, Hg^{2+} can inhibit activity of aquaporins, and and L_P of roots decreased 22% in distilled water and 68% in NH_4NO_3 solution after treatment by $HgCl_2$ respectively. These evidences suggested that both Hg^{2+}-sensitive aquaporins and ion channels existing in the protoplasm and vacuole membranes could regulate root water uptake, transport, and integral plant water balance.

Keywords root system, root hydraulic conductance, aquaporins, *Fraxinus mandshurica*

Translated from *Acta Phytoecologica Sinica*, 2005, 29(5): 706–712
[译自: 植物生态学报, 2005, 29(5): 706–712]

SUN Hailong, WU Chu, XU Wenjing, WANG Zhengquan (✉)
College of Forestry, Northeast Forestry University,
Harbin 150040, China
E-mail: wzqsilv@mail.nefu.edu.cn

WU Chu
Horticulture Department, Yangtze University,
Jingzhou 434025, China

1 Introduction

Fine root system of plants plays crucial roles in the fluxes of energy and matter in terrestrial ecosystem. Despite the most important organ in vascular plants, it is still unclear how water is transported from the soil to the roots (Liang and Chen, 1996). Recent studies have revealed that root system was a primary factor that limited water uptake in wet soil (Steudle, 1994; Sperry et al., 1998; Steudle and Peterson, 1998), and could contribute up to approximately 50% of the overall hydraulic resistance of the plant (Martre et al., 2001a). Thus, the root hydraulic conductance (L_P) based on the root surface area, which was determined by radical water transport inside the lateral root (Frensch, 1997), has a major influence on the shoot water status, plant growth and development (Frensch, 1997; Kang et al., 1999). Study on L_P is an important objective in understanding the mechanism of water transport in root system.

Casparian band and Suberin lamellae in endodermis and exodermis of roots can block water movement through the root apoplastic pathway (Steudle, 2000) and affect radical water transport significantly (North and Nobel, 1996). Thus, water movement through cell-to-cell pathway becomes more important. In cell-to-cell pathway, unfortunately, cell membrane is another barrier for water movement; however, aquaporins in tonoplast and plasma membrane can greatly improve the radical water transport (Weig et al., 1997; Agre et al., 1998; Kaldenhoff et al., 1998; Schäffner, 1998). Ye and Verkman (1989) first found that mercuric chloride ($HgCl_2$) has a function, which can limit activity of most aquaporins, then $HgCl_2$ has been extensively used to evaluate

the contribution of aquaporins to overall root water transport (Eckert et al., 1999; Javot and Maurel, 2001), and as well as to test variation of L_P. Previous studies focused on L_P had used nutrient solution as the substance in experiments, for instance, *Populus tremuloides* (Wan and Zwiazek, 1999), *Lycopersicon esculentum* (Maggio and Joly, 1995), and *Capsicum anmuum* (Carvajal et al., 1999). Nevertheless, a few studies used distilled water as the substance solution, such as *Opuntia acanthocarpa* (Martre et al., 2001b) and *Zea mays* (Mu et al., 2003). However, these studies ignored the effect of different substances on aquaprins' activity and the rate of water uptake in the same experimental plant because L_P varied with different substance solutions. For example, Na^+ and long-term nutrient stress decreased L_P of roots, NH_4^+ and NO_3^- are major ions that can be absorbed by plants as nitrogen source, but they can not be absorbed until they are dissolved in water. However, the functions of NH_4^+ and NO_3^- that increased or decreased L_P was poorly understood. The objectives of the present investigation on seedling roots of *Fraxinus mandshurica* are: 1) to evaluate the difference in L_P occurred between distilled water and NH_4NO_3 solution with various concentrations; and 2) to examine the changes of L_P under distilled water and NH_4NO_3 solution with various concentrations after $HgCl_2$ treatment. Then the relation between nutrient ions and water uptake, and the inhibition of $HgCl_2$ for aquaporins in the different substances will be revealed from this experiment.

2 Materials and methods

2.1 Plant materials and culture

F. mandshurica seeds pretreated by low temperature treatment were sterilized, and then sowed on a bench in the greenhouse of Northeast Forestry University in April 2002. Culture medium was a 1:1 mixture of washed quartz sand and soil. Temperature of the greenhouse was approximately 25°C maximum in a day and 18°C minimum at night, and average photosynthetic photon flux was approximately 500–800 μmol photons/(m^2·s) during the growing period. The seedlings were watered once a day to maintain soil moisture. While seedlings had grown about 40 days (the average height of seedlings was 20 cm), both seedlings roots and culture medium were excavated carefully from a bench and immersed immediately in the distilled water, and then were rinsed by jets of water. Integrity roots with white color were chosen for this experiment.

2.2 Root L_P

Root hydraulic conductance at the level of whole root system was measured by pressure–flux approach as used by Martre et al. (2001b). The shoot was rapidly cut under distilled water with a razor blade, and the cut stem was immediately inserted into a 20 mm long Tygon tubing, the junction between the tubing and the stele was enwound with string and coated with acrylic copolymer. The tubing by inserting the tubing through a silicone gasket in a brass compression fitting was affixed to a glass capillary (i.d. 0.5 mm) that was half filled with distilled water. If the cuts of roots presented, they were sealed by acrylic copolymer. The root system was then suspended in the beaker of pressure chamber, which was filled with 200 mL of different solutions.

Water flow through the root system was induced by applying a pressure difference. The flow rate (Q_v, m^3/s) was determined by monitoring the movement time (second) of the meniscus at a distance in the capillary. Pressure was first increased to 0.25 MPa. After the flow rate was stabilized, usually within 20 min, and the time of water flow was recorded (six replications were done to check for artifacts). The pressure was successively increased to 0.35, 0.5, and 0.75 MPa, and the time of water flow was recorded at each pressure. Q_V and the volumetric flux density (flow rate per unit root surface area; J_V, m/s) were calculated, and then L_P was calculated as the slope of the relationship between J_V and the applied pressure difference.

The root surface area was calculated from root length and mean diameter (Maggio and Joly, 1995). Roots were taken out from the pressure chamber. Root system immersed in the solution was cut. All lateral roots were cut and put in humid filter paper instantly (to prevent roots from shrinking), and length, stem diameter (D_1) and tip diameter (D_2) of root were determined respectively. Area of each root was calculated by using the equation ($S = \pi L(D_1+D_2)/2$), and then the summation of area of all roots was determined.

2.3 The effects of $HgCl_2$ on L_P

After L_P of six seedling roots was measured in distilled water, these roots were then transferred into 50 μmol/L of $HgCl_2$ solution in another beaker. The roots were immersed in 50 μmol/L $HgCl_2$ solution for 15 min at a pressure of 0.35 MPa, and then the pressure was decreased, and the roots from the 50 μmol/L $HgCl_2$ solution were transferred into distilled water again. After L_P was measured in this distilled water, the roots were slightly rinsed in distilled water and treated in 10 mmol/L β-mercaptoethanol in a new beaker for 15 min at a pressure of 0.35 MPa to measure L_P again.

2.4 L_P in NH_4NO_3 solution of different concentrations

Twelve seedlings were chosen for this experiment. First, the integrity roots of three seedlings were treated for 15 min in the 2 mmol/L NH_4NO_3 solution at a pressure of 0.35 MPa, and L_P of roots was determined under this solution. Then the roots were transferred into 50 μmol/L $HgCl_2$ solution for 15 min at a pressure of 0.35 MPa. After this treatment, the roots were transported into 2 mmol/L NH_4NO_3 solution to

measure L_P. The remaining nine seedlings were separated into three groups, and L_P of roots in these three groups was measured in the NH_4NO_3 solution with three concentrations (4, 8, and 16 mmol/L), and transferred into other beakers for treatment by $HgCl_2$ (50 μmol/L), and repeatedly treated in the same but new NH_4NO_3 solution with three concentrations (4, 8, and 16 mmol/L) again, finally to measure new values of L_P.

3 Results

3.1 Effects of $HgCl_2$ on L_P of roots

At the same condition, by contrast with roots in distilled water, J_V and L_P of roots that were treated by 50 μmol/L $HgCl_2$ solution and by 10 mmol/L β-mercaptoethanol solution changed greatly (Fig. 1). L_P of roots was the highest in distilled water (18.85×10^{-8} m/(s·MPa), Fig. 1a); after treatment by $HgCl_2$, L_P of roots decreased 22% (from 18.85×10^{-8} to 14.69×10^{-8} m/(s·MPa), Fig. 1b). This result showed that $HgCl_2$ inhibited the activity of aquaporins. After the roots were treated by 10 mmol/L β-mercaptoethanol solution again, L_P of roots slightly increased by 6% (from 14.69×10^{-8} to 15.768×10^{-8} m/(s·MPa), Fig. 1c). Both treatments suggested that $HgCl_2$ had obviously inhibited aquaporins, while β-mercaptoethanol had a slight reversal reaction to aquaporins in root tissue. Although reverse by β-mercaptoethanol treatment was only a small portion, L_P decreased or increased during treatments indicated that aquaporins played an important role in control water uptake in *F. mandshurica* seedling roots.

3.2 Difference of L_P in the NH_4NO_3 solution with different concentrations

In the NH_4NO_3 solution with various concentrations (2, 4, 8, and 16 mmol/L), L_P of roots had some differences (Fig. 2). L_P increased ($33.81–34.11\times10^{-8}$ m/(s·MPa)) progressively with increasing concentration (2–16 mmol/L) of NH_4NO_3 and the maximum of L_P was at 8 mmol/L NH_4NO_3 solution (34.149×10^{-8} m/(s·MPa), Fig. 2c). Comparing both L_P in distilled water and NH_4NO_3 solution, the average of L_P in NH_4NO_3 solution (33.33×10^{-8} m/(s·MPa)) was 77% higher than that in distilled water (18.85×10^{-8} m/(s·MPa)). These results suggest that NH_4^+ and NO_3^- can enhance activity of aquaporins, and higher concentration of nitrogen can improve water uptake and transport in roots.

After $HgCl_2$ treatment, L_P still increased which was associated with NH_4NO_3 concentrations in solution (Fig. 3). But the maximum of L_P was at 4 mmol/L NH_4NO_3 solution (13.57×10^{-8} m/(s·MPa), Fig. 3b). In contrast to L_P (33.33×10^{-8} m/(s·MPa), Fig. 2) of roots in NH_4NO_3 solution untreated by $HgCl_2$, the average of L_P (10.78×10^{-8} m/(s·MPa), Fig. 3) of roots treated by $HgCl_2$ significantly reduced by

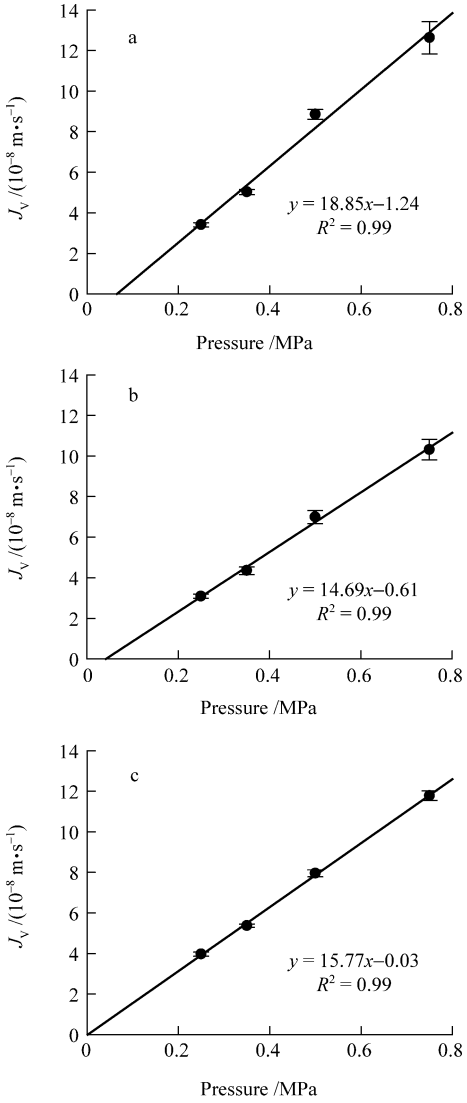

Fig. 1 L_P of *F. mandshurica* seedling roots under different treatments. a: distilled water; b: 50 μmol/L $HgCl_2$ treatment; c: 50 μmol/L $HgCl_2$ and then 10 mmol/L β−mercaptoethanol treatment.

68% ($p<0.001$). On the other hand, L_P in distilled water treatment was 43% higher than the average in NH_4NO_3 solution after $HgCl_2$ treatment, but L_P in $HgCl_2$ treatment (14.69×10^{-8} m/(s·MPa), Fig. 1b) increased by 27%. Nonetheless, the inhibition of $HgCl_2$ on aquaporins had significant difference in distilled water and in NH_4NO_3 solution, and could be enhanced by NH_4NO_3 solution from this experiment.

4 Discussions

4.1 effects of NH_4^+ and NO_3^- on L_P of roots

L_P of plant roots can be affected by many environment factors. Earlier studies have suggested that if plant transpiration, soil water potential, and air temperature did not change,

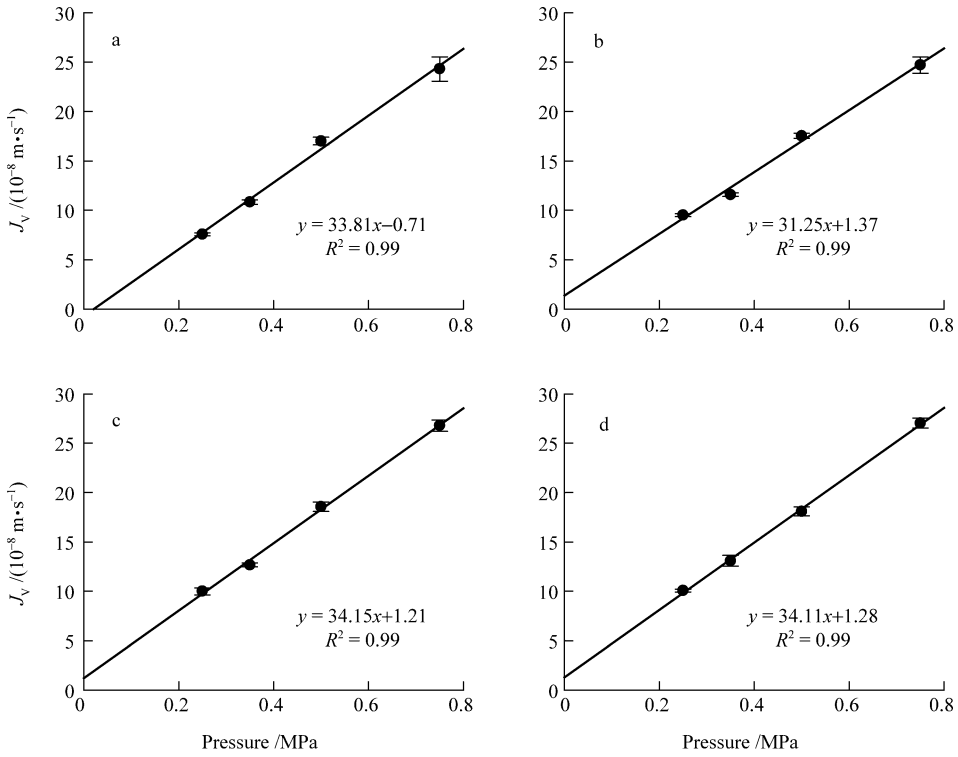

Fig. 2 L_P of seedling roots under NH_4NO_3 solution with different concentrations. a: 2 mmol/L; b: 4 mmol/L; c: 8 mmol/L; d: 16 mmol/L.

L_P of roots should be influenced mostly by plant nutrient status (Clarkson et al., 2000; Steudel, 2000). For example, stress of nitrogen and phosphorus could decrease L_P of roots at the level of individual root and whole roots system. In contrast to *Z. mays* seedlings with sufficient nutrients, L_P of roots associated with nitrogen deficiency stress decreased by 80% (Hoarau et al., 1996), by 47% (Mu et al., 2003), and by 63% (Li et al., 2002), respectively, L_P of roots as well as reduced about 28% in phosphorus deficiency stress (Mu et al., 2003). Nevertheless, these results were derived from the evidences of long-term nutrient stress, and little information about the effects of ions on L_P in short time had been supplied. Our study found that L_P of *F. mandshurica* roots under NH_4NO_3 solution of four concentrations (2, 4, 8, and 16 mmol/L) increased by 77% averagely in contrast with distilled water, suggesting that higher differences of L_P not only depended on long-term nutrient status, but also depended on nutrient ions concentration in the solution simultaneity. However, both the previous reports (Hoarau et al., 1996; Li et al., 2002; Mu et al., 2003) and our result had different mechanisms on L_P. The major difference was that varieties of L_P of roots responded to different nutrient status in the same substance solution. From plant physiological perspective, phosphorus stress can affect activity or quantity of aquaporins in plasma membrane per unit area by post-transcriptional modification of phosphorylation and dephosphorylation (Radin and Matthews, 1989; Hoarau et al., 1996), while nitrogen stress might only influence the quantity of aquaporins in plasma membrane per unit area (Radin and Matthews, 1989; Hoarau et al., 1996). In our experiments (i.e., the same nutrient concentration condition), however, the differences of L_P of roots were derived from various substances, such as distilled water or NH_4NO_3 solution, which might probably be relative to stimulation to activity of aquaporins by ions or exiting ion channels in plasma membrane (Isabel et al., 2002). In addition, Wang et al. (2001) observed that the majority of aquaporins genes could be up-regulated by nitrate in *Lycopersicon esculentum* roots, the expression of genes associated with nitrate uptake, and assimilation decreased after root tissues were treated for 48 h in the nitrate solution, and water uptake by roots would be consistent with stimulation in response to an increase of symplasmic solute concentrations due to the nitrate uptake.

4.2 Effect of $HgCl_2$ on L_P under different substances

Currently, $HgCl_2$ is an effective compound that is used to test the relation between aquaporins and water uptake/or transport in plant root system (Eckert et al., 1999; Javot and Maurel, 2001). The mechanism is that reagents between mercurial ions and Cys residue of aquaporins block water channel and limited water transport in root system (Murata et al., 2000). But the mercurial ions also could react with other proteins that Cys residue exposed in root tissues. Therefore, $HgCl_2$ is an unspecific compound, and the inhibition of this compound resulted in toxicity and un-reversed reaction in metabolism, such as the experiment by Zhang

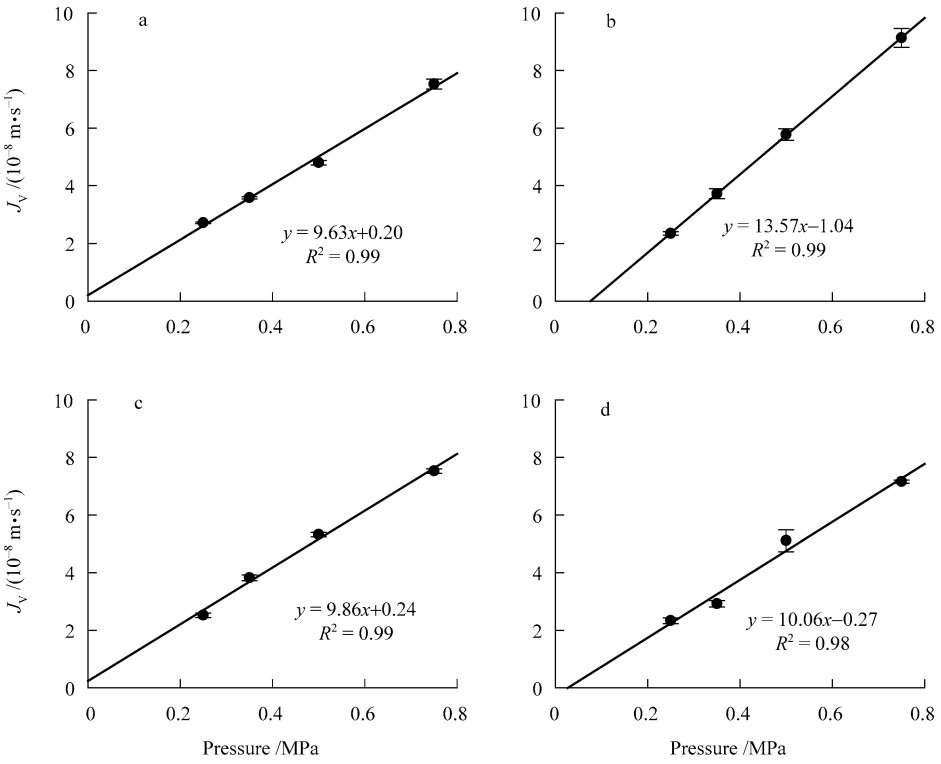

Fig. 3 L_P of seedling roots under NH_4NO_3 solution with different concentrations after $HgCl_2$ treatment. a: 2 mmol/L; b: 4 mmol/L; c: 8 mmol/L; d: 16 mmol/L.

and Tyerman (1999) in *Triticum aestivum* roots. On the other hand, reducing agents, i.e., dithiothreitol or β-mercaptoethanol, could counteract inhibition of mercurial ions. Previous studies have reported that dithiothreitol or β-mercaptoethanol (2–50 mmol/L) could reverse the reduction of L_P in roots by mercurial ions either totally in *P. tremuloides* (Wan and Zwiazek, 1999), *O. acanthocarpa* (Martre et al., 2001b), *T. aestivum* (Carvajal et al., 1996), *C. anmuum* (Barrowclough et al., 2000) or partially in *T. aestivum* (Zhang and Tyerman, 1999), *Brassica napus, Petunia hybrida* Hook. (Morillon and Lassalles, 1999). The dithiothreitol or β-mercaptoethanol might be an effective indicator to detect the inhibition by mercurial ions in examining the process of water uptake and transport in root system.

Plant nutrition could regulate the inhibition of mercurial ions, and L_P of roots hardly decreased in nutrient deficiency, such as the study of *T. aestivum* by Carvajal et al. (1996), which probably was involved with nutrient deficiency decreasing activity and density of aquaporins on plasma membrane (Zhang and Tyerman, 1999; Mu et al., 2003). Our result showed that L_P of *F. mandshurica* roots decreased by 68% averagely in NH_4NO_3 solution of different concentration after treatment by $HgCl_2$, which was similar to other reports whose experimental substances were nutrient solutions after treatment by $HgCl_2$ (Table 1). For instance, the range of L_P decreased from 47-80% in *P. tremuloides* (Wan and Zwiazek, 1999), *L. esculentum* (Maggio and Joly, 1995), *C. anmuum* (Carvajal et al., 1999), *Cucumis melo* (Carvajal et al., 2000), and *Beta vulgaris* (Amodeo et al., 1999). On the other hand, L_P of *F. mandshurica* roots only reduced by 22% in distilled water after treatment by $HgCl_2$ (Table 1), which was much lower than that in *O. acanthocarpa* (32%) (Martre et al., 2001b) and *Z. mays* (53%) (Mu et al., 2003) roots. This difference might be derived from various conducting tissues in woody plants and crops roots.

More recent experiments found that β-mercaptoethanol could reverse the reduction of L_P by mercurial ions entirely in some plants, such as *P. tremuloides* (Wan and Zwiazek, 1999), *O. acanthocarpa* (Martre et al., 2001b), and *C. anmuum* (Barrowclough et al., 2000), but L_P in *T. aestivum* and *Beta vulgaris* roots only reversed partly (Zhang and Tyerman, 1999; Morillon and Lassalles, 1999), which might result from short time treatment and/or low concentration of reducing agents. This was because the concentration of β-mercaptoethanol (5 mmol/L) used in experiments was lower in the studies of *T. aestivum* (Zhang and Tyerman, 1999) and *B. vulgaris* (Morillon and Lassalles, 1999). If higher concentration or long-time treatment by β-mercaptoethanol, the compound of β-mercaptoethanol would absorb more mercurial ions and enhance counteraction of reducing agents. In addition, L_P of *F. mandshurica* roots treated by $HgCl_2$ recovered only by 6% after 10 mmol/L β-mercaptoethanol solution treatment again in our experiment, and 16% of L_P was not reversed. Perhaps the concentration (10 mmol/L) of β-mercaptoethanol solution was lower for *F. mandshurica* roots. In contrast with other experiments (Wan and Zwiazek, 1999), concentration of

$HgCl_2$ (50 μmol/L) in this study was also lower, the toxicity of mercurial ions to root metabolism should be ignored in detecting relationship between aquaporins and water transport in root system.

Table 1 Reductive percent of L_P in different species under distilled water and nutrition solutions after treatment by $HgCl_2$

Plant species	Substance solution	Reduction of L_P	References
Populus tremuloides	One and a half strength Hoagland solution	47%	Wan and Zwiazek, 1999
Lycopersicon esculentum	Half-strength hoagland solution	57%	Maggio and Joly, 1995
Capsicum anmuum	Complete modified Hoagland's nutrient solution	66%	Carvajal et al., 1999
Cucumis melo	Half-strength modified Hoagland's nutrient solution	80%	Carvajal et al., 2000
Beta vulgaris	Root sap solution	80%	Amodeo et al., 1999
Fraxinus mandshurica	NH_4NO_3 solution	68%	This study
Zea mays	Distilled water	53%	Mu et al., 2003
Opuntia acantho-carpa	Distilled water	32%	Martre et al.，2001b
Fraxinus mandshurica	Distilled water	22%	This study

In conclusion, L_P of roots in different substance solutions varied obviously despite the effects of inhibition of mercurial ions or reverse of β-mercaptoethanol on it. Our experiment of *F. mandshurica* seedling revealed that NH_4^+ and NO_3^- could stimulate activity of aquaporins, and L_P of roots in NH_4NO_3 solution was distinctly (77%) higher than in distilled water. Nevertheless, L_P of roots in NH_4NO_3 solution after treatment by $HgCl_2$ decreased remarkably (68%), suggesting that there might be Hg^{2+}-sensitive aquaporins or ion channels (Isabel et al., 2002) in the protoplasm and vacuole membranes of the roots. However, these require to be tested by experiments in the future.

Acknowledgements The authors thank Drs Fan Zhiqiang, Sun Zhihu, and Bai Shangbin who gave them help and provided comments in this experiment, and also thank Zhendong Li for his help in culturing seedlings. This work was supported by the National Natural Science Foundation of China (Grant No. 30130160).

References

Agre P., Bonhivers M., Borgnia M. J., The aquaporins, blueprints for cellular plumbing systems, J. Biol. Chem., 1998, 273: 14,659–14,662

Amodeo G., Dorr R., Vallejo A., Sutka M., Parisi M., Radial and axial water transport in the sugar beet storage root, J. Exp. Bot., 1999, 50: 509–516

Barrowclough D. E., Peterson C. A., Steudle E., Radial hydraulic conductivity along developing onion roots, J. Exp. Bot., 2000, 51: 547–557

Carvajal M., Cerda A., Martinez V., Does calcium ameliorate the negative effect of NaCl on melon root water transport by regulating aquaporin activity? New Phytol., 2000, 145: 439–447

Carvajal M., Cooke D. T., Clarkson D. T., Responses of wheat plants to nutrient deprivation may involve the regulation of water-channel function, Planta, 1996, 199: 372–381

Carvajal M., Martinez V., Alcaraz C. F., Physiological function of water channels as affected by salinity in roots of paprika pepper, Physiol. Plantarum, 1999, 105: 95–101

Clarkson D. T., Carvajal M., Henzler T., Waterhouse R. N., Smyth A. J., Cook D. T., Steudle E., Root Hydraulic conductance: diurnal aquaporin expression and the effects of nutrient stress, J. Exp. Bot., 2000, 51: 61–70

Eckert M., Biela A., Siefritz F., Kaldenhoff R., New aspects of plant aquaporin regulation and specificity, J. Exp. Bot., 1999, 50: 1,541–1,545

Frensch J., Primary responses of root and leaf elongation to water deficits in the atmosphere and soil solution, J. Exp. Bot., 1997, 48: 985–999

Hoarau J., Barthes L., Bousser A., Deléens A., Prioul J. L., Effect of nitrate on water transfer across roots of nitrogen pre-starved maize seedlings, Planta, 1996, 200: 405–415

Isabel B., Anthony R. S., Matthias J. A., Alberto M., Plant aquaporins, Physiol. Plantarum, 2002, 115: 175–182

Javot H., Maurel C., The role of aquaporins in root water uptake, Ann. Bot., 2001, 90: 301–313

Kaldenhoff R., Grote K., Zhu J. J., Zimmermann U., Significance of plasmalemma aquaporins for water transport in *Arabidopsis thaliana*, Plant J., 1998, 14: 121–128

Kang S. Z., Zhang J. H., Liang J. S., Combined effects of soil water content and temperature on plant root :hydraulic conductivity, Acta Phytoecol. Sin., 1999, 23(3): 211–219 [康绍忠，张建华，梁建生，土壤水分与温度共同作用对植物根系水分传导的效应，植物生态学报，1999, 23(3): 211–219]

Li Y. Y., Cao C. L., Shao M. A., Effects of nitrogen stress on root radial and axial hydraulic congductivity of corn, Plant Nutr. Fert. Sci., 2002, 8(2): 192–196 (in Chinese)

Liang Y. L., Chen P. Y., Adjustment of physiological characters of root systems of wheat by soil moisture, nitrogen and phosphorus, Acta Phytoecol. Sin., 1996, 20(3): 255–262 [梁银丽，陈培元，土壤水分和氮磷营养对小麦根系生理特性的调节作用，植物生态学报，1996, 20(3): 255–262]

Maggio A., Joly R. J., Effects of mercuric chloride on the hydraulic conductivity of tomato root systems (Evidence for a channel-mediated water pathway), Plant Physiol., 1995, 109: 331–335

Martre P., Cochard H., Durand J. L., Hydraulic architecture and water flow in growing grass tillers (*Festuca arundinacea* Schreb.), Plant Cell Environ., 2001a, 24: 65–76

Martre P., North G. B., Nobel P. S., Hydraulic conductance and mercury-sensitive water transport for roots of *Opuntia acanthocarpa* in relation to soil drying and rewetting, Plant Physiol., 2001b, 126: 352–362

Morillon R., Lassalles J. P., Osmotic water permeability of isolated vacuoles, Planta, 1999, 210: 80–84

Mu Z. X., Zhang S. Q., Yang X. Q., Liang Z. S., Effect of nitrogen and phosphorus deficiency on maize root hydraulic conductivity, J. Plant Physiol. Mol. Biol., 2003, 29 (1): 45–51 [慕自新，张岁岐，杨晓青，梁宗锁，植物生理与分子生物学学报，2003, 29 (1): 45–51]

Murata K., Mitsuoka K., Hirai T., Walz T., Agre P., Heymann J. B., Engel A., Fijiyoshi Y., Structural determinants of water permeation through aquaporin-1, Nature, 2000, 407: 599–605

North G. B., Nobel P. S., Radial hydraulic conductivity of individual root tissues of *Opuntia ficus-indica* (L.) Miller as soil moisture varies, Ann. Bot., 1996, 77: 133–142

Radin J. W., Matthews M. A., Water transport properties of cortical cells in roots of nitrogen and phosphorus deficient cotton seedlings,

Plant Physiol., 1989, 89: 264–268
Schäffner A. R. Aquaporin function, structure, and expression: are there more surprises to surface in water relations? Planta, 1998, 204: 131–139
Sperry J. S., Adler F. R., Campbell G. S., Comstock J. P., Limitation of plant water use by rhizosphere and xylemconductance: results from a model, Plant Cell Environ., 1998, 21: 347–359
Steudle E., Peterson C. A., How does water get through roots? J. Exp. Bot., 1998, 49: 775–788
Steudle E., The regulation of plant water at the cell, tissue, and organ level: role of active processes and of compartmentation. In: Schultze E. D. (ed), Flux Control in Biological Systems. From Enzymes to Populations and Ecosystems, San Diego, CA: Academic Press, Inc., 1994, 237–299
Steudle E., Water uptake by roots: effects of water deficit, J. Exp. Bot., 2000, 51: 1,531–1,542
Wan X. C., Zwiazek J. J., Mercuric chloride effects on root water transport in aspen seedlings, Plant Physiol., 1999, 121: 939–946
Wang Y. H., David F. G., Leon V. K., Nitrate-induced genes in tomato roots. array analysis reveals novel genes that may play a role in nitrogen nutrition, Plant Physiol., 2001, 127: 345–359
Weig A., Deswarte C., Chrispeels M. J., The major intrinsic protein family of *Arabidopsis* has 23 members that form three distinct groups with functional aquaporins in each group, Plant Physiol., 1997, 114: 1,347–1,357
Ye R., Verkman A.-S. Simultaneous optical measurement of osmotic and diffusional water permeability in cells and lipo-somes. Biochem., 1989, 28: 824–829
Zhang W. H., Tyerman S. D., Effect of low O_2 concentration and azide on hydraulic conductivity and osmotic volume of the cortical cells of wheat roots, Aust. J. Plant Physiol., 1999, 18: 603–613