

Water Uptake and Hydraulic Conductivity of Seminal and Adventitious Roots of Five Wheat Cultivars at Early Growth Stage

Y. Emam^{1*}, and E. Bijanzadeh¹

ABSTRACT

To investigate the root anatomy and hydraulic conductivity of wheat cultivars, including Shiraz, Bahar, Pishtaz, Sistan, and Yavaros, a series of controlled environment (growth chamber) experiments were hydroponically conducted at University College of Dublin (UCD), Ireland in 2010. Bahar, Pishtaz and Sistan cultivars were employed as tolerant to drought and Shiraz and Yavaros as sensitive. Twelve plants from each wheat cultivar in three replications were compared in a completely randomized design. Seminal roots had four to five cortical cell layers, and typically one large central metaxylem and 5 ± 1 (in Bahar) to 7 ± 1 (in Yavaros) smaller and circularly arranged peripheral metaxylem vessels. Stellar cells were less lignified in adventitious roots, as compared with seminal roots, and mature xylem vessels of seminal roots of Shiraz and Yavaros cultivars had more lignified walls compared to the other cultivars of the 18 day old plants. Lateral roots of Shiraz cultivar showed the most lignified walls compared to the other cultivars. The highest root hydraulic conductivity in seminal roots was observed in Bahar with the lowest surface area and lignified cell walls. Type of cultivar had also a noticeable effect on flow rate of seminal roots and varied from 2.81 in Shiraz to 3.76×10^{-10} m s⁻¹ in Bahar cultivar. With respect to flow rate and osmotic driving force of seminal and adventitious roots, Bahar and Sistan cultivars had the highest hydraulic conductivity. It was concluded that at the early growth stage of wheat cultivars (3rd leaf stage), root anatomical structures of Bahar and Sistan were more efficient in water uptake and this might be attributed to the less lignified cell wall of the peripheral and central metaxylem zones of the roots in these cultivars.

Keywords: Flow rate, Lateral roots, Osmotic driving force, Peripheral metaxylem.

INTRODUCTION

Wheat (*Triticum aestivum* L.) is the most essential food crop in Iran and many other countries (Emam, 2007). Considering the importance of wheat in Iran, especially in Fars Province, better understanding of the relationship between water uptake and hydraulic conductivity in relation to root anatomy for Iranian wheat cultivars would be a top priority. Cereals appear in all shapes and sizes, yet in physical terms they are variable hydraulic conductors that use a naturally occurring gradient in the energy

content of water (water potential) between root and shoot environment (atmosphere) to drive the water uptake and dissolved mineral nutrients (Knipfer and Fricke, 2010b). Hydraulic resistances, as they occur at the root and shoot level, can limit water flow through the plant, analogous to Ohm's Law (Frensch, 1997).

The water movement in roots is often described as an osmotic pressure in which root membranes play an important role (Knipfer and Fricke, 2010b; Kramer, 1983; Kramer and Boyer, 1995). Also, the physical characteristics of roots are related to their

¹ Department of Agronomy, College of Agriculture, Shiraz University, Shiraz, Islamic Republic of Iran.

* Corresponding author, e-mail: yaemam@shirazu.ac.ir



structure and there is no way to interpret root flow and hydraulic conductivity data without sufficient knowledge of their anatomy (Steudle, 2000; Steudle and Peterson, 1998).

For the movement of water in the soil, plant, and atmosphere, the root hydraulic conductivity is a key parameter contributing to the limitation of water flow rate (Steudle, 2000; Steudle and Jeschke, 1983). In addition to stomata, the water status of the shoot will be largely determined by hydraulic conductivity (Knipfer and Steudle, 2008). Root hydraulic properties could be changed with the magnitude of water flow induced across roots (Passioura and Munns, 1984; Murel *et al.*, 2010). The hydraulic conductivity of a root is a complex parameter because of the complicated structure of the osmotic barrier made up of exodermis, cortex and endodermis (Kramer, 1983; Kramer and Boyer, 1995).

Root anatomy plays a major role in root hydraulic, influencing axial conductance and the distribution of water uptake along the root with a more localized role for aquaporins (Bramely *et al.*, 2009). These membrane integral proteins form water-conducting channels, responsible for the variable hydraulic conductivity of root systems (Javot and Maurel, 2002). Aquaporins can contribute to the control of root water uptake, provided that at least one membrane is crossed between root medium and the xylem, and that water does not move only along the apoplast (Knipfer and Fricke, 2010a).

There are several methods to analyse the hydraulic behaviour of the roots. Among the most commonly used techniques are the root exudation, pressure probe, and vacuum perfusion. These techniques involve different experimental set-ups, can apply different driving forces, and induce different flow rates across the roots (Knipfer and Fricke, 2010b; Knipfer and Steudle, 2008). Data regarding root hydraulic conductivity are required to understand the mechanisms of water uptake by wheat roots (Zhang *et al.*, 2002).

Bijanzadeh and Emam (2011) reported that Bahar, Sistan, and Pishtaz wheat cultivars had resistance to late season drought stress, while Shiraz and Yavaros cultivars were sensitive to drought. They supposed that drought resistance in Bahar, Pishtaz, and Sistan might be related to higher root efficiency in water uptake by seminal and adventitious roots at early growth stages compared to cultivars sensitive to drought such as Shiraz and Yavaros. With respect to different resistances of these cultivars to drought, the root anatomy and water movement of these cultivars at early growth stages need to be known. The main objectives of the present study were the comparison of the root surface area, root fresh weight, seminal and adventitious root dimensions at the third leaf stage of five wheat cultivars, including Shiraz, Bahar, Pishtaz, Sistan, and Yavaros and to determine the hydraulic conductivity of their seminal and adventitious roots.

MATERIALS AND METHODS

Plant Growth in Hoagland Nutrient Solution

Five Iranian wheat cultivars, including Shiraz, Bahar, Pishtaz, Sistan, and Yavaros were grown in a growth chamber, hydroponically at Physiology Lab, Department of Biology and Environmental Science, University College of Dublin (UCD), Ireland in 2010. Bahar, Sistan, and Pishtaz cultivars are tolerant to late season drought and Shiraz and Yavaros are sensitive to drought stress (Bijanzadeh and Emam, 2011). Shiraz, Bahar, and Yavaros are cultivated extensively in Fars Province, while Pishtaz and Sistan are new cultivars in this area. Twelve plants from each wheat cultivar in three replications were compared in a completely randomized design. First, the seeds were bubbled in distilled water for one day and then put in CaSO_4 solution in a 10-liter beaker and were aerated for three days. When seedlings had a root length of

20–30 mm, they were transferred to a hydroponic system, containing a modified half-strength Hoagland nutrient solution [KH_2PO_4 (1.5mM), KNO_3 (2.0 mM), CaCl_2 (1.0 mM), MgSO_4 (1.0 mM), FeNa (18.0 μM), H_3BO_3 (8.1 μM), MnCl_2 (1.5 μM)] (Fricke *et al.*, 1997). Four plants were kept in each 1-liter glass beaker and the nutrient solution was ventilated by a gas exchange pump at a flow rate of 400 mL min^{-1} in growth chamber. Plants grew at a day/night photoperiod of 16/8 hours and temperature of 21/15°C. Relative humidity was 70% and photosynthetic active radiation at the level of the developing leaf 3 was 300–400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Plants were sampled at early growth stages (ZGS13; Zadoks *et al.*, 1974) before the root system became complex and difficult to handle (tangled lateral roots), which made it more likely that damage to roots and electrolyte leakage (hydraulic, solute) would occur (Miller, 1987). In this way, plants were brought out of the Hoagland nutrient solution and root anatomy, root surface area, hydraulic conductivity, growth rate, and water loss of the 14–18 day old plants (ZGS13; Zadoks *et al.*, 1974) were measured as below:

Study of Root Anatomical Structures and Surface Area

Root anatomy was studied on free-hand cross-sections that were made from 5–10 and 40–60 mm root tips (Steudle, 2000). Sections were stained with 0.5% toluidine blue for 1 minute and viewed under bright light for the detection of central and peripheral metaxylem (Knipfer and Fricke, 2010b). For the detection of Casparian bands and lignified cell walls (bright signal), sections were stained for 30 minutes with 0.1% berberine hemisulfate and counterstained for 1–3 minutes with 0.5% toluidine blue (Hachez *et al.*, 2006; Brundrett *et al.*, 1988). Then, sections were observed with a Leica microscope (DM IL; Leica, Wetzlar, Germany) under fluorescence light by a UV/violet filter with an excitation

wavelength of 390–420 nm and captured with a digital camera (Leica, Wetzlar, Germany).

Surface area of the roots was determined after each hydraulic experiment by measuring the length and the radius of the main axis of the roots and the number, length, and diameter of the lateral roots of the 18 day old plants. Surface area was calculated by treating roots as cylinders (according to Knipfer and Fricke, 2010b). Total root area (A_r) was calculated as:

$$A_r = 2\pi r_1 L_1 + 2\pi r_2 L_2 + 2\pi r_3 L_3 + 2\pi r_4 L_4$$

Where, r_1 = Main root radial $\approx 250 \mu\text{m}$; L_1 = Main root length; r_2 = Lateral root (I) radial $\approx 125 \mu\text{m}$; L_2 = Lateral root (I) length; r_3 = Lateral root (II) radial $\approx 62.5 \mu\text{m}$; L_3 = Lateral root (II) length; r_4 = Lateral root (III) radial $\approx 31.25 \mu\text{m}$; L_4 = Lateral root (III) length.

Osmolality Measurements

The osmolality of xylem sap and medium was determined by Picolitre Osmometry (Model P302, UK). Samples were analyzed following collection or were stored beneath a layer of liquid paraffin (to minimize evaporation) in 0.2-ml centrifuge tubes at 4°C for up to 3 days. Osmotic potential (Δp) was calculated as:

$$\Delta p = P_e - P_m$$

Where, P_e = Osmotic potential of the root exudates, P_m = Osmotic potential of the medium.

Measurement of Root Hydraulic Conductivity Using Root Exudation Method

An individual root was attached with the excised root base to a glass capillary (diameter 0.5 mm). The rise of the xylem sap in the capillary was measured at time intervals of 5 minutes over a period of 1 hour. Exudate volume (V_e) was measured after each interval using the capillary diameter and increase in the height of the exudate column, when individual roots were



analysed. Then, V_e was used to determine the hydraulic properties of the roots. V_e and the hydraulic conductivity of the root (L_{pr}) were determined as below:

$$V_e = \pi r^2 h$$

$$L_{pr} = V_e \cdot (1/\Delta t) \cdot (1/\Delta p) \cdot (1/A_r)$$

Where, r = Radial of glass capillary (250 μm); h = Height of the root exudates in glass capillary, t = Time of going up the root exudates in the glass capillary.

Measurement of the Growth Rate and Water Loss

The rate of transpirational water loss of entire plants was determined gravimetrically in the growth chamber. Single wheat plants were placed in a measuring cylinder, which was filled with Hoagland nutrient solution and placed on a balance and water loss was measured daily compared to control (i.e. cylinder with Hoagland nutrient solution without plant) in 14-18 day old seedlings. Also, an inductive electromechanical position sensor (Model PS 44, Germany) was used to monitor extension growth of the third leaf counting from the base. Output signals from the sensor were tracked continuously using a chart recorder that was connected to a computer. Growth rates of the third leaf for the five wheat cultivars were evaluated at different times of the day and averaged to exclude possible temporal effects. Finally, dry matter of the roots and the shoots of the 18 day old seedlings, was measured after being dried in an oven at 75°C till constant mass for 72 hours.

RESULTS AND DISCUSSION

Root Anatomical Structures and Xylem Development

During germination, seminal roots were the first major roots appeared, after radical formation. Adventitious roots appeared when seedlings were 11-13 days old, differing in morphology and anatomy from

seminal roots. The thicker (in diameter) adventitious roots had more cortical cell layers and contained more central metaxylem vessels of larger diameter than the seminal roots (Figure 1). When plants were 14–18 days old (the developmental stage at which they were analysed) there were three to six seminal roots and two to four stem-borne adventitious roots per plant.

Among the wheat cultivars, the length of seminal roots was 83 ± 7 and 87 ± 4 mm when plants were 14 and 18 days old, respectively. In comparison, the length of adventitious roots was 36 ± 7 and 41 ± 4 mm for the 14 and 18 day old plants, respectively.

Mean xylem dimensions and the number of the mature xylem vessels in the seminal and the adventitious roots of the 18 day old wheat plants are shown in Table 1. Seminal roots had a mean diameter of 670 ± 84 μm , between four and five cortical cell layers, and typically one large central metaxylem, and 5 ± 1 (in Bahar) to 7 ± 1 (in Yavaros) smaller and circularly arranged peripheral metaxylem vessels. The peripheral metaxylem vessels were early metaxylem, being fully functional during the early stages of development of a root segment, whereas the central vessel was late metaxylem being the last of the xylem elements to become fully functional (Bramley *et al.*, 2009).

The minimum diameter of the central metaxylem vessels of seminal roots was 30 ± 6 and 32 ± 7 μm at the tip and the base region of the Sistan cultivar, respectively (Table 1). The average diameter of peripheral metaxylem vessels was 16 μm (tip) and 19 μm (base of the seminal root (see Figure 1 and Table 1). Steudle (2000) reported that the diameter of the central metaxylem of the seminal roots varied from 52 to 200 μm at the early growth stages of wheat and barley. Compared with the seminal roots, the adventitious roots were much thicker, having 5-8 cortical cell layers, with 8 peripheral metaxylem in Pishtaz cultivar and 4 in Shiraz. Their central metaxylem vessels were in 40-60 μm from the root tip (Table 1). Zhao *et al.* (2004) reported that in wheat

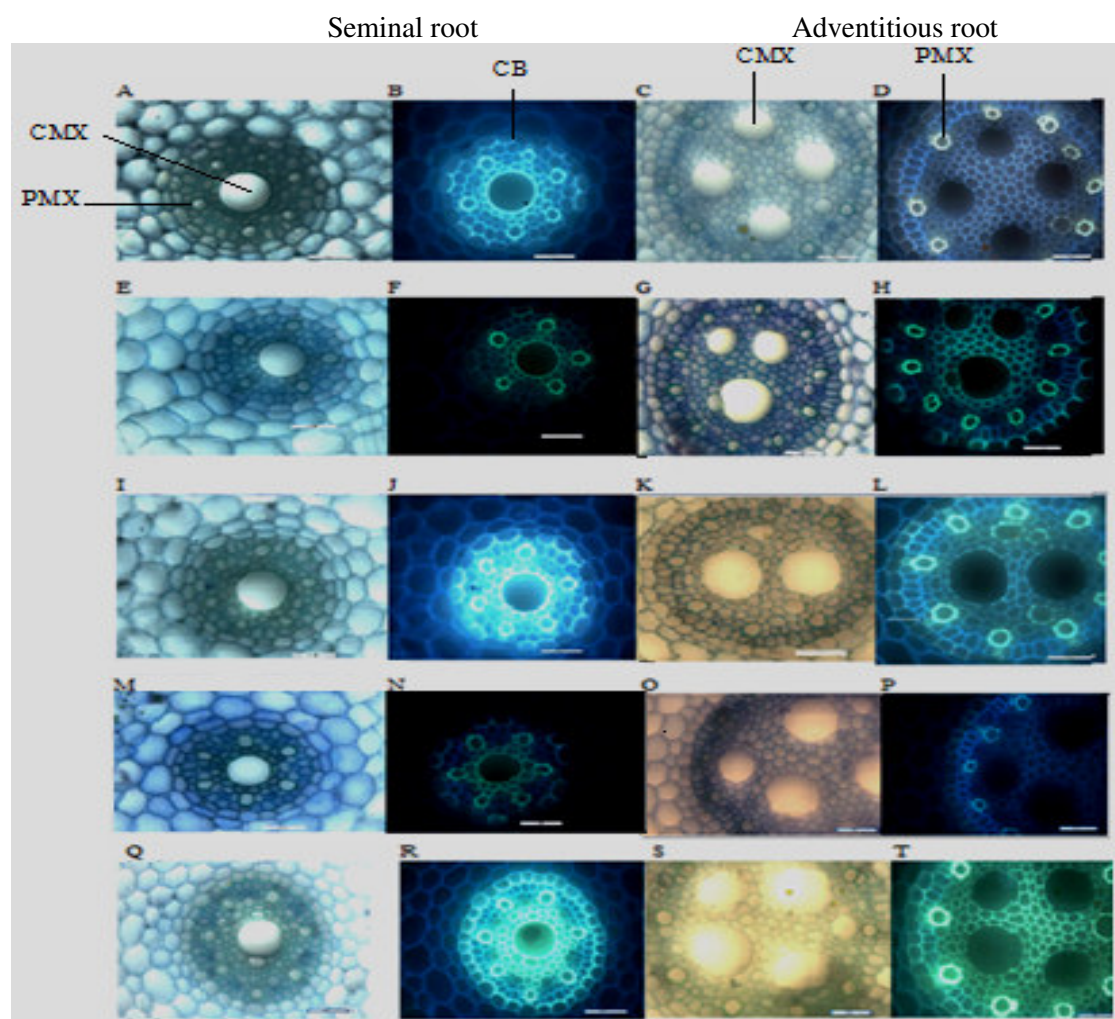


Figure 1. Anatomy and xylem development of seminal and adventitious roots of five wheat cultivars including Shiraz (A-D), Bahar (E-H), Pishtaz (I-L), Sistan (M-P) and Yavaros (Q-T) of the 18 day old plants. Hand cross-sections of seminal roots taken at 40–60 mm from seminal and adventitious roots. Sections in A, C, E, G, I, K, M, O, Q, S were stained with toluidine blue and viewed under bright light; sections in B, D, F, H, J, L, N, P, R, T were stained with berberine hemisulfate and counterstained with toluidine blue and viewed under fluorescence light (390–420 nm) to visualize Casparian bands and xylem development (Brundrett *et al.*, 1988). CMX: central metaxylem; PMX: peripheral metaxylem, CB: Casparian bands. Scale bar is 50 μm in all pictures.

the diameter of the adventitious root was 1.7 to 2.5 fold thicker than the seminal root at the 3 to 6 leaf stage plants.

The mean diameter of the vessels in the adventitious roots was 50 ± 1 and 55 ± 2 μm for the central and 17 ± 2 and 20 ± 1 μm for the peripheral metaxylem at the tip and the base of the root, respectively (Figure 1). In

all cultivars, stellar cells were less lignified in adventitious, as compared with the seminal roots and the mature xylem vessels of the seminal roots of the Shiraz and Yavaros cultivars had the most lignified walls, compared to the other cultivars (bright color, Figures 1-B, F, J, N, R). The amount of lignification area in the xylems of seminal

**Table 1.** Mean xylem dimensions and number of mature xylem vessels of seminal and adventitious roots of wheat cultivars at third leaf stage.

Wheat cultivar	Root type	Root zone	Distance from tip (mm)	Peripheral metaxylem		Central metaxylem	
				Number of vessels	Diameter of vessels (μm)	Number of vessels	Diameter of vessels (μm)
Shiraz	Seminal	Tip	5-10	6 \pm 1 ^a	14 \pm 2	1 \pm 0	33 \pm 11
		Base	40-60	6 \pm 1	18 \pm 6	1 \pm 0	38 \pm 12
	Adventitious	Tip	5-10	8 \pm 2	15 \pm 3	4 \pm 0	50 \pm 8
		Base	40-60	8 \pm 0	17 \pm 5	4 \pm 2	55 \pm 7
Bahar	Seminal	Tip	5-10	5 \pm 1	20 \pm 1	1 \pm 0	36 \pm 10
		Base	40-60	5 \pm 1	22 \pm 2	1 \pm 0	41 \pm 9
	Adventitious	Tip	5-10	9 \pm 1	22 \pm 7	2 \pm 1	48 \pm 2
		Base	40-60	9 \pm 1	23 \pm 5	3 \pm 1	56 \pm 4
Pishtaz	Seminal	Tip	5-10	6 \pm 1	24 \pm 4	1 \pm 0	33 \pm 7
		Base	40-60	6 \pm 1	23 \pm 2	1 \pm 0	36 \pm 9
	Adventitious	Tip	5-10	10 \pm 2	14 \pm 1	2 \pm 1	56 \pm 12
		Base	40-60	10 \pm 1	15 \pm 4	2 \pm 1	60 \pm 10
Sistan	Seminal	Tip	5-10	6 \pm 1	23 \pm 3	1 \pm 0	30 \pm 6
		Base	40-60	6 \pm 1	21 \pm 4	1 \pm 0	32 \pm 7
	Adventitious	Tip	5-10	10 \pm 1	20 \pm 4	3 \pm 1	50 \pm 6
		Base	40-60	10 \pm 1	20 \pm 2	4 \pm 1	56 \pm 10
Yavaros	Seminal	Tip	5-10	6 \pm 1	24 \pm 3	1 \pm 0	31 \pm 4
		Base	40-60	7 \pm 1	20 \pm 2	1 \pm 0	36 \pm 2
	Adventitious	Tip	5-10	10 \pm 2	18 \pm 2	3 \pm 1	49 \pm 2
		Base	40-60	12 \pm 2	19 \pm 1	4 \pm 1	52 \pm 6

^a Values are given as Mean \pm SD of seminal and adventitious roots analyses.

and adventitious roots has an important role in decreasing water uptake and hydraulic conductivity in wheat (Vysotskaya *et al.*, 2004).

In all cultivars, the central metaxylem vessels of the seminal roots were less lignified (Figure 1 and Table 2) compared to the peripheral metaxylems. Indeed, they could be classified as immature, compared to the peripheral metaxylem vessels, which had highly lignified walls (see Figures 1-B, D, F, H, J, L, N, P, R, T; Brundrett *et al.*, 1988; Bramley *et al.*, 2009). Higher lignification thickness of cell wall of central and peripheral metaxylems vessels was observed in Yavaros, Shiraz and Pishtaz

cultivars (Table 2). Casparian bands could be detected more in the seminal, but not in the adventitious roots (Figure 1). Casparian bands appear during the root development prior to the formation of additional wall depositions in the endodermis. Knipfer and Fricke (2010b) showed that in barley, increasing the lignification of cell walls of the peripheral and central metaxylem vessels decreased the hydraulic conductivity and water uptake of Gulf cultivar.

In the adventitious roots, the lowest lignification thickness of cell wall was observed in the peripheral metaxylems of the Sistan wheat cultivar (Table 2 and Figure 1). Knipfer and Fricke (2010a) in a study on

Table 2. The lignified thickness of cell walls in central and peripheral metaxylem vessels of the seminal, adventitious and lateral roots of wheat cultivars.

Wheat cultivar	Seminal roots		Adventitious roots		Lateral roots	
	Peripheral metaxylem	Central metaxylem	Peripheral metaxylem	Central metaxylem	Peripheral metaxylem	Central metaxylem
Shiraz	2.3c	2.0a	0.9a	2.3b	1.2a	1.2a
Bahar	0.9d	0.7b	1.1a	2.0b	0.4d	1.1ab
Pishtaz	2.8b	2.1a	1.3a	2.5a	0.6c	0.9bc
Sistan	0.7d	0.5b	0.6b	1.2c	0.3d	0.6d
Yavaros	3.1a	2.3a	1.2a	2.8a	0.9b	0.8cd
LSD (0.05)	0.25	0.31	0.46	0.33	0.15	0.26

barley suggested that the generally accepted composite model of water transport and the role of the suberin lamellae and the Casparian bands should be revised. Also, Peterson *et al.* (1993) reported that in young maize roots, the formation of a casparian band in the exodermis did not affect hydraulic conductivity.

Interestingly, central and peripheral metaxylems of lateral roots of Shiraz had the most lignified walls in the peripheral and central metaxylems compared to other cultivars, especially Bahar (Table 2 and Figure 2). Lateral roots provide one important means by which plants can increase their absorptive area and their capacity to exploit soil resources (Draye, 2002). Lateral roots are also the major players in the plastic response of the root systems to environmental stimuli, manifested, for example, by increased branching frequencies and/or the length of the laterals in the regions of the localized nutrient supply (Zhang and Forde, 2000).

Root Surface Area, Flow Rate, Osmotic Driving Force, and Hydraulic Conductivity

For the 18 day old plants, Yavaros and Sistan cultivars had the maximum root

surface area of the seminal roots, while the root surface area in Bahar was the least, i.e., $1.12 \times 10^{-3} \text{ m}^2$ (Table 3). The type of the cultivar had a noticeable effect on the seminal root flow rate, which varied from 2.81 in Shiraz to $3.76 \times 10^{-10} \text{ m s}^{-1}$ in Bahar. On the other hand, the maximum osmotic driving force ($P_e - P_m$) was observed in the Yavaros cultivar. Results showed that Bahar with the lowest surface area and lignified cell walls, had the highest seminal root hydraulic conductivity [$6.96 \times 10^{-9} \text{ m s}^{-1} \text{ MPa}^{-1}$], whereas in Yavaros and Shiraz cultivars, these were 3.51 and $3.74 \times 10^{-9} \text{ m s}^{-1} \text{ MPa}^{-1}$, respectively (Table 3 and Figure 1). In contrast to our results, Gallardo *et al.* (1996) showed that in wheat (CV. Kulin) the hydraulic conductivity of the seminal roots ranged from 12.3 to $15.2 \times 10^{-8} \text{ m s}^{-1} \text{ MPa}^{-1}$ at the early growth stages. Also, Zhao *et al.* (2005) reported that from the 3 to 6 leaf stage of wheat (CV. Xiaoyan6), the hydraulic conductivity was 15 to $36 \times 10^{-9} \text{ m s}^{-1} \text{ MPa}^{-1}$ and increased with increasing chromosome ploidy during evolution.

In the adventitious roots, the Shiraz and Yavaros cultivars had higher surface areas, while flow rates of these cultivars were less than those of the Bahar, Sistan, and Pishtaz (Table 3). With respect to the flow rate and the osmotic driving force, the Bahar cultivar had the highest hydraulic conductivity

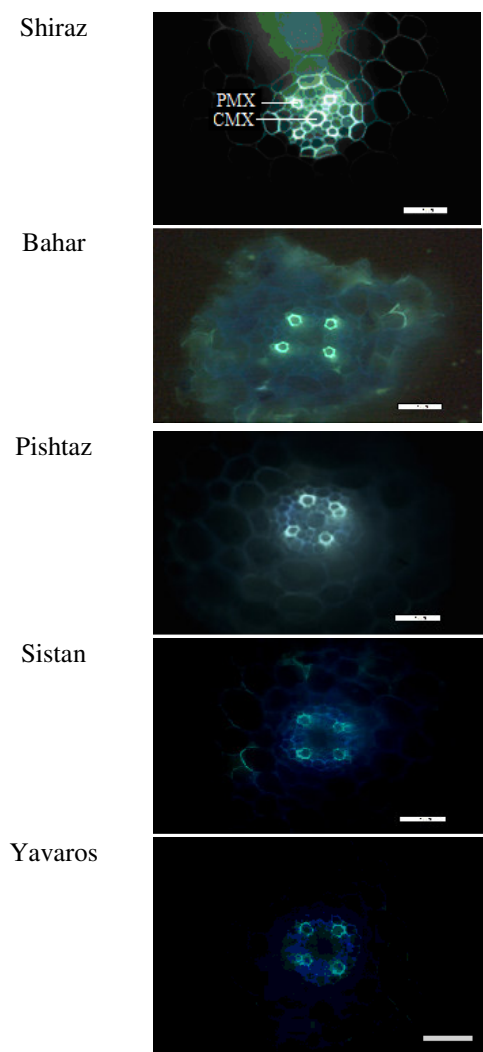


Figure 2. Lateral root anatomy of wheat cultivars at 40-60 cm of root zone of the 18 day old plants. Sections were stained with berberine hemisulfate and counterstained with toluidine blue and viewed under fluorescence light (390–420 nm) to visualize Casparian bands and xylem development (Brundrett *et al.*, 1988). CMX: central metaxylem; PMX: peripheral metaxylem. Scale bar is 50 μm in all pictures.

($2.87 \times 10^{-10} \text{ m s}^{-1} \text{ MPa}^{-1}$). In cereals, changes in the root hydraulic conductivity might be related to difference in surface area, the amount of lignified zone, osmotic driving force and distribution of the seminal and adventitious roots, nutrients concentration and the temperature of the medium (Bramley *et al.*, 2009; Knipfer and Fricke

Table 3. Root surface area, flow rate, osmotic driving force, and hydraulic conductivity of seminal and adventitious roots of hydroponically grown wheat cultivars at third leaf stage.

Wheat cultivar	Seminal roots			Adventitious roots		
	Root surface area $[(\text{m}^2) \times 10^{-3}]$	Flow rate $[(\text{m s}^{-1}) \times 10^{-10}]$	Osmotic driving force (MPa)	Root surface area $[(\text{m}^2) \times 10^{-3}]$	Flow rate $[(\text{m s}^{-1}) \times 10^{-12}]$	Osmotic driving force (MPa)
Shiraz	1.31bc	2.81d	0.075b	0.55b	3.57c	0.022a
Bahar	1.12c	3.76a	0.054d	0.50c	4.31a	0.015a
Pishtaz	1.43b	3.11c	0.067bc	0.54b	3.98ab	0.019a
Sistan	1.92a	3.45b	0.065c	0.53bc	4.12a	0.016a
Yavaros	2.11a	3.01c	0.086a	0.60a	3.62bc	0.021a
LSD (0.05)	0.19	0.23	0.009	0.03	0.37	0.007
						0.85

2010b; Zhao *et al.*, 2004 and 2005). Overall, the hydraulic conductivities of the seminal and the adventitious roots of Bahar and Sistan appeared to be greater than those of the other cultivars (Table 3).

Growth Rate, Water Loss and Root/Shoot Ratio

At 15 days after germination (DAG), the Bahar cultivar had the maximum growth rate of the third leaf compared to the others and this trend continued up to 17 DAG (Figure 3). In contrast, the Shiraz cultivar showed a different trend and its growth rate was decreased from 1.8 mm h^{-1} at 14 DAG, to 1.08 mm h^{-1} at 17 DAG. Wheat cultivars with the higher growth rate and the better establishment at the early growth stage can result in the higher grain yield (Emam, 2007). As plant biomass increased in the growth chamber from 14 to 18 DAG, water loss also increased in all cultivars. However, the increased rate in Shiraz was greater than that of the other cultivars (Figure 4). Also, water loss in the Sistan cultivar was less than those of the others at 18 DAG. Results showed that the Bahar and the Sistan cultivars had the maximum root and shoot fresh weights, respectively. Also, Bahar with a root/shoot ratio of 1.1 ± 0.09 had the highest

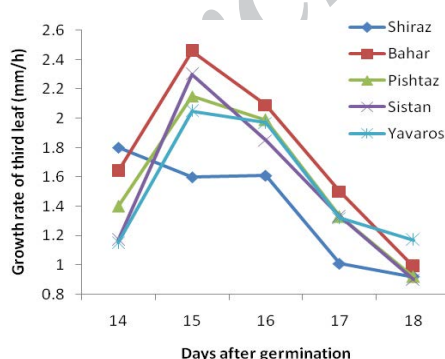


Figure 3. Growth rate (mm h^{-1}) of third leaf of wheat cultivars from 14 to 18 days after germination. Results are Means \pm SD (error bars) of values from 12 plants.

value compared to the other cultivars (Figure 5). Caird *et al.* (2007) reported that root/shoot ratio was an important index in predicting transpiration rate, water uptake,

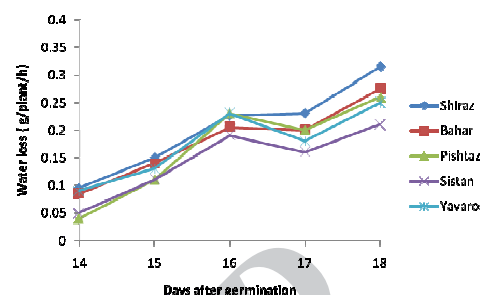
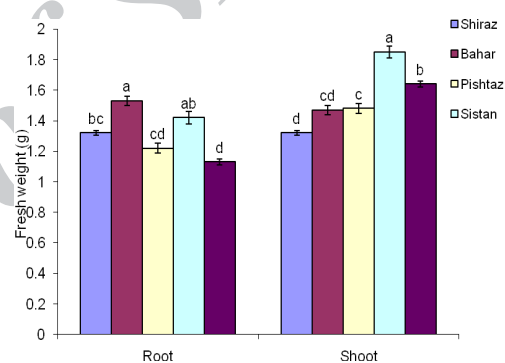
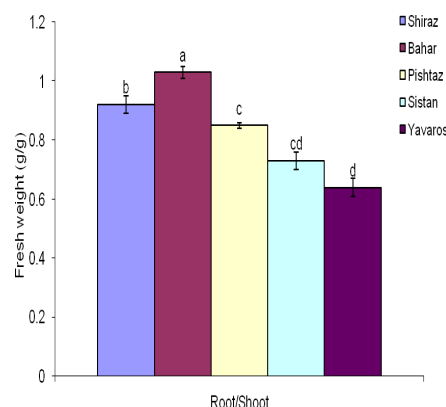


Figure 4. Water loss ($\text{g plant}^{-1} \text{h}^{-1}$) of wheat cultivars from 14 to 18 days after germination. Results are means \pm SD (error bars) of values from 12 plants.



(a)



(b)

Figure 5. Root, shoot (a), and root/shoot (b) fresh weight of wheat cultivars at 18 days after germination. Results are Means \pm SD (error bars) of values from 12 plants.



and the hydraulic conductivity in the C₃ plants. The lowest growth rate (Figure 3) in the Shiraz cultivar might be related to the higher water loss (Figure 4; Steudle, 2000) and more lignified walls in the lateral root (Figure 2; Knipfer and Fricke, 2010a) at the third leaf stage.

It was concluded that the Bahar cultivar (cultivar resistant to drought) with the higher flow rate, hydraulic conductivity, and root/shoot ratio had better performance in water uptake at the early growth stages, compared to the other cultivars, especially with Shiraz cultivar (cultivar sensitive to drought). On the other hand, at the early growth stage of the wheat cultivars (3rd leaf stage), the root structures of the Bahar and the Sistan cultivars appeared to be more efficient for water uptake. This might be attributed to less lignified cell wall, peripheral and central metaxylem zones of the roots compared to the Shiraz and Yavaros cultivars. Further research to compare the root anatomy of drought resistant wheat cultivars may shed more light on this issue.

ACKNOWLEDGEMENTS

The technical assistance of W. Fricke and T. Knipfer in Department of Biology and Environmental Science, UCD College, Dublin, Ireland, is gratefully appreciated. Also, we would like to thank Shiraz University and Ministry of Science, Research and Technology of Iran, for their financial support of this project.

REFERENCES

1. Bijanzadeh, E. and Emam, Y. 2011. Evaluation of Assimilate Remobilization and Yield of Wheat Cultivars under Different Irrigation Regimes in Arid Climate. *Arch. Agron. Soil Sci.* (in press)
2. Bramley, H., Turner, N. C., Turner, D. W. and Tyerman, S. D. 2009. Roles of Morphology, Anatomy, and Aquaporins in Determining Contrasting Hydraulic Behaviour of Roots. *Plant Physiol.*, **150**: 348–364.
3. Brundrett, M. C., Enstone, D. E. and Peterson, C. A. 1988. A Berberine Aniline Blue Staining Procedure for Suberin, Lignin, and Callose in Plant Tissue. *Protoplasma*, **146**: 33–142.
4. Caird, M. A., Richards, J. H. and Donovan L. A. 2007. Night Time Stomatal Conductance and Transpiration in C₃ and C₄ Plants. *Plant Physiol.*, **143**: 4–10.
5. Draye, X. 2002. Consequences of Root Growth Kinetics and Vascular Structure on the Distribution of Lateral Roots. *Plant Cell Environ.*, **25**: 1463–1474.
6. Emam, Y. 2007. *Cereal Production*. 3rd Edition, Shiraz University Press, Shiraz, 190 PP.
7. Frensch, J. 1997. Primary Response of Root and Leaf Elongation to Water Deficits in the Atmosphere and Soil Solution. *J. Exp. Bot.*, **48**: 985–999.
8. Fricke, W. McDonald, A. J. S. and Mattson-Djos, L. 1997. Why Do Leaves and Leaf Cells of N-limited Barley Elongate at Reduced Rates? *Planta*, **202**: 522–530.
9. Gallardo, M., Eastham, J., Gregory P. J. and Turner N. C. 1996. A Comparison of Plant Hydraulic Conductances in Wheat and Lupins. *J. Exp. Bot.*, **47**: 233–239.
10. Hachez, C., Moshelion, M., Zelazny, E., Cavez D. and Chaumont, F. 2006. Localisation and Quantification of Plasma Membrane Aquaporin Expression in Maize Primary Roots: A Clue to Understand Their Role as Cellular Plumbers. *Plant Mol. Biol.*, **62**: 305–323.
11. Javot, H. and Maurel, C. 2002. The Role of Aquaporins in Root Water Uptake. *Ann. Bot.*, **90**: 301–313.
12. Knipfer, T. and Fricke W. 2010a. Root Pressure and a Solute Reflection Coefficient Close to Unity Exclude a Purely Apoplastic Pathway of Radial Water Transport in Barley (*Hordeum vulgare* L.). *New Phytol.*, **187**: 159–170.
13. Knipfer, T. and Fricke W. 2010b. Water Uptake by Seminal and Adventitious Roots in Relation to Whole-plant Water Flow in Barley (*Hordeum vulgare* L.). *J. Exp. Bot.*, **61**: 1–17.
14. Knipfer, T. and Steudle, E. 2008. Root Hydraulic Conductivity Measured by Pressure Clamp is Substantially Affected by

- Internal Unstirred Layers. *J. Exp. Bot.*, **59**: 2071–2084.
15. Kramer, P. J. 1983. *Water Relations of Plants*. Academic Press, New York, 550 PP.
 16. Kramer P. J. and Boyer, M. 1995. *Water Relations of Plants and Soils*. Academic Press, Orlando, 331 PP.
 17. Maurel, C., Simonneau, T. and Sutka, M. 2010. The Significance of Roots as Hydraulic Rheostats. *J. Exp. Bot.*, **61**: 3191–3198.
 18. Miller, D. M. 1987. Errors in the Measurement of Root Pressure and Exudation Volume Flow Rate Caused by Damage during the Transfer of Unsupported Roots between Solutions. *Plant Physiol.*, **85**: 164–166.
 19. Passioura, J. B. and Munns, R. 1984. Hydraulic Resistance of Plants. II. Effects of Rooting Medium, and Time of Day, in Barley and Lupin. *Aust. J. Plant Physiol.*, **11**: 341–350.
 20. Peterson, C. A. Murran, M. and Steudle, E. 1993. Location of Major Barriers to Water and Ion Movement in Young Roots of *Zea mays* L. *Planta*, **190**: 127–136.
 21. Steudle, E. and Peterson, C. A. 1998. How Does Water Get through Roots? *J. Exp. Bot.*, **49**: 775–788.
 22. Steudle, E. 2000. Water Uptake by Plant Roots: An Integration of Views. *Plant Soil*, **226**: 46–56.
 23. Steudle, E. and Jeschke, W. D. 1983. Water Transport in Barley Roots. *Planta*, **158**: 237–248.
 24. Vysotskaya, L. B., Arkhipova, T. N., Timergalina, L. N., Dedov, A. V., Veselov, S. Y. and Kudoyarova, G. R. 2004. Effect of Partial Root Excision on Transpiration, Root Hydraulic Conductance and Leaf Growth in Wheat Seedlings. *Plant Physiol. Bio.*, **42**: 251–255.
 25. Zadoks, J. C., Chang T. T. and Konzak, C. F. 1974. A Decimal Code for the Growth Stages of Cereals. *Weed Res.*, **14**: 415–421.
 26. Zhang, H. M. and Forde B. G. 2000. Regulation of *Arabidopsis* Root Development by Nitrate Availability. *J. Exp. Bot.*, **51**: 51–59.
 27. Zhang, S. Q., Shan, L. and Deng, X. P. 2002. Change of Water Use Efficiency and its Relation with Root System Growth in Wheat Evolution. *Chin. Sci. Bull.*, **47**: 1879–1883.
 28. Zhao, C. X., Deng, X. P., Shan, L., Steudle, E., Zhang, S. and Ye, Q. 2005. Changes in Root Hydraulic Conductivity during Wheat Evolution. *Acta Bot. Sinic.*, **47**: 302–310.
 29. Zhao, C. X., Deng, X. P., Zhang, S. Q., Ye, Q., Steudle, E. and Shan, L. 2004. Advances in the Studies on Water Uptake by Plant Roots. *Acta Bot. Sinic.*, **46**: 505–514.

جذب آب و هدایت هیدرولیک ریشه‌های بذری و نابجای پنج رقم گندم در مراحل اولیه رشد

ی. امام، و ا. بیژن‌زاده

چکیده

به منظور بررسی ساختار ریشه و هدایت هیدرولیک پنج رقم گندم شامل شیراز، بهار، پيشتاز، سيستان و ياواروس یک سری آزمایش در محیط کنترل شده (اتاقک رشد) به صورت هیدروپونیک در دانشگاه UCD، در کشور ایرلند در سال ۲۰۱۰ اجرا شد. ارقام گندم بهار، پيشتاز و سيستان به عنوان مقاوم و ارقام شیراز و ياواروس به عنوان رقم های حساس به تنش خشکی مورد بررسی قرار گرفتند. بیست بوته از هر رقم در قالب طرح کاملاً تصادفی در سه تکرار با یکدیگر مقایسه شدند. ریشه‌های بذری، چهار تا



پنج لایه سلول‌های کورتیکولی و معمولاً یک آوند چوبی مرکزی و 5 ± 1 (در رقم بهار) و 7 ± 1 (در رقم شیراز) آوند چوبی جانبی کوچک تر داشتند که به صورت مدور قرار گرفته بودند. سلول‌های استوانه آوندی در ریشه‌های نابجا در مقایسه با ریشه‌های بذری کمتر چوبی شده بودند و آوندهای چوبی رسیده در ریشه‌های بذری ارقام شیراز و یاواروس میزان سلول‌های چوبی شده بیشتری در مقایسه با سایر ارقام در گیاهان ۱۸ روزه داشتند. ریشه‌های جانبی در رقم شیراز دارای بیشترین دیواره سلولی چوبی شده بودند. بالاترین هدایت هیدرولیک در ریشه‌های رقم بهار مشاهده شد که دارای کمترین سطح ریشه و دیواره سلولی چوبی شده بود. همچنین نوع رقم تاثیر قابل توجهی بر جریان عبور آب در ریشه‌های بذری داشت و از $2/81 \times 10^{-10}$ متر بر ثانیه در رقم شیراز تا $3/76 \times 10^{-10}$ متر بر ثانیه در رقم بهار متغیر بود. با توجه به جریان عبور آب و نیروی ناشی از اسمز ریشه‌های بذری و نابجا، ارقام بهار و سیستان دارای بیشترین هدایت هیدرولیک بودند. می‌توان نتیجه گرفت که در مراحل اولیه رشد ارقام گندم (سه برگی)، ساختارهای آناتومی ریشه ارقام بهار و سیستان دارای کارایی بیشتری در جذب آب بودند و این موضوع ممکن است در ارتباط با کمتر چوبی شدن دیواره سلولی آوندهای جانبی و مرکزی ریشه در این ارقام باشد.