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Root length density and water uptake distributions of winter wheat under sub-irrigation

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Abstract

As the critical information to study flow transport in soil–plant systems, root distributions and root-water-uptake (RWU) patterns have been studied extensively. However, most root distribution data in the past were collected under surface irrigation. Less research has been conducted to characterize root distributions under sub-irrigation. The objectives of this study were to (1) test if the generalized function of normalized root length density (NRLD) in the literature was applicable to root distributions of winter wheat under natural sub-irrigation, which provides water from subsurface by capillary rise from the water table, and (2) estimate RWU distributions of winter wheat under natural sub-irrigation. Column experiments were conducted to study the distributions of root length density (RLD) and RWU of winter wheat (*Triticum aestivum* L. cv. Nongda 189) during a growing period of 57 days from planting to tillering stages under surface irrigation and natural sub-irrigation. Data of root distributions and soil water content were collected in the experiments with different treatments of irrigation levels. Results showed that the RLD distributions of winter wheat under both surface irrigation and natural sub-irrigation were of similar patterns. The NRLD distributions under sub-irrigation were adequately characterized by the generalized function. An inverse method was employed to estimate the average RWU rate distributions of winter wheat. In addition, based on the potential RWU coefficient and the NRLD function, a simple approach was developed to predict RWU rates at different depths. The predicted RWU rates had a good agreement with the estimated RWU rate distributions using the inverse method.

Abbreviations: DAP – days after planting; FWC – field water capacity; NRLD – normalized root length density; RLD – root length density; RWU – root-water-uptake.

Introduction

Root distributions and root-water-uptake (RWU) patterns are important information for understanding mass flow in soil–plant systems, and for designing and managing efficient and environmental-friendly irrigation practices. For irrigation scheduling, it is necessary to consider the effect of RWU rate on soil water dynamics (Coelho and Or, 1999). Root growth is critical for crops to use soil water and obtain high yields, especially under water deficit conditions (Asseng et al., 1998; Robertson et al., 1993; Xue et al., 2003). Since the root weight method is often insensitive and does not provide information on the active roots because of bias by large and inactive roots (Box and Ramseur, 1993; Coelho

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and Or, 1999), researchers commonly use the root length density (RLD) to characterize root systems (Asseng et al., 1997; Chassot et al., 2001; Zuo et al., 2004a). Enormous effort has been made to study root distributions and RWU patterns of crops. Most of studies were conducted under surface irrigation (Asseng et al., 1998; Chassot et al., 2001; Robertson et al., 1993; Xue et al., 2003). A few of them were related to sub-surface drip irrigation (Coelho and Or, 1999; Phene et al., 1991).

Because of difficulties to measure distributions of RWU rate directly in the laboratory or in the field, some researchers estimated the RWU rate distributions based on the soil water balance method by considering main factors, such as soil water change, irrigation, and precipitation inputs (Asseng et al., 1998; Xue et al., 2003). Others explored optimization methods to determine parameters of RWU models (Coelho and Or, 1996; Hupet et al., 2002; Musters and Bouten, 1999, 2000; Vrugt et al., 2001a, b). It was assumed that the RWU patterns followed predefined functions, such as linear, Bivariate Gaussian (normal, semi-lognormal and lognormal) or exponential functions. In practice, the RWU changes with the soil environment, root growth, and atmospheric conditions. It is difficult to delineate the RWU with a unique distribution function. Recently, an inverse method was developed to estimate the average RWU rate using two successively measured soil water content profiles as input information (Zuo and Zhang, 2002; Zuo et al., 2004b). The advantage of the inverse procedure is that it does not need to assume any specific distribution for the RWU rate. Hupet et al. (2003) also tested the feasibility of the inverse modeling approach to derive RWU parameters from soil water content data. Nevertheless, the use of inverse techniques has some limitations mainly related to the non-uniqueness and instability of the optimized parameter set.

RLD is often used to characterize the root system. However, it is a difficult and time-consuming undertaking to measure and determine RLD distributions accurately, especially in the field, because the distributions change with different soils, plant species, growing seasons, climate conditions, and others. Based on RLD data in the literature, Zuo et al. (2004a) established a generalized function of normalized root length density (NRLD) distributions of wheat. The generalized function of NRLD is only dependent on the normalized root depth but independent of other factors. All the RLD data used for the development of the generalized function were measured under surface irrigation.

Compared with surface irrigation, natural sub-irrigation provides moisture from sub-surface by seepage from adjacent water sources (e.g. canals or rivers) or capillary rise from the water table (Belcher and D'Itri, 1995; Bengtson, 1993; Brandyk, 1993; Crossley, 2004; Kruse et al., 1990). Natural sub-irrigation has been widely accepted as an inherent characteristic of wetland agriculture in some semi-humid and humid areas. Thus far, the RLD and RWU distributions of crops under sub-irrigation have not been well considered. Therefore, the objectives of this study were to (1) test whether the generalized function of Zuo et al. (2004a) was applicable to NRLD distributions of winter wheat under natural sub-irrigation; (2) estimate RWU distributions of winter wheat under natural sub-irrigation.

Materials and methods

Theoretical background

Description of one-dimensional vertical soil water flow in a soil–plant system under evaporative condition is based on Richards' equation combined with a sink term:

$$C(h)\frac{\partial h}{\partial t} = \frac{\partial}{\partial z}\left[K(h)\left(\frac{\partial h}{\partial z} - 1\right)\right] - S(z,t) \qquad (1)$$

$$h(z,0) = h_0(z) \quad 0 \le z \le L \qquad (2)$$

$$\left[-K(h)\left(\frac{\partial h}{\partial z} - 1\right)\right]_{z=0} = -E(t) \quad t > 0 \qquad (3)$$

$$h(L,t) = h_L(t) \quad t > 0 \qquad (4)$$

Here h is the soil matric potential (cm), $C(h)$ the soil water capacity (cm^{-1}), $K(h)$ the soil hydraulic conductivity (cm day^{-1}), $h_0(z)$ the initial soil matric potential in the profile (cm), $E(t)$ soil surface evaporation rate (cm day^{-1}), L the study domain (cm) and $L \ge L_r$, where L_r is the rooting depth defined as the maximal penetrating depth of roots (cm) at the study period, z vertical coordinate originating from the soil surface and positive downwards (cm), t time (d), $h_L(t)$ the matric potential at the lower boundary (cm), and $S(z,t)$ the RWU rate (cm^3 cm^{-3} day^{-1}), defined by (Feddes et al., 1978; Wu et al., 1999):

$$S(z,t) = S(z_r,t) = \gamma(h) S_{\max}(z_r,t) = \gamma(h) \frac{Tp(t)}{L_r} L_{\mathrm{nrd}}(z_r) \tag{5}$$

where z_r ($=z/L_r$) is the normalized root depth ranging from 0 to 1, $\gamma(h)$ a dimensionless reduction function corresponding to the water stress, $S_{\max}(z_r,t)$ the maximal specific water extraction rate under the optimal soil water condition (cm^3 cm^{-3} day^{-1}), $Tp(t)$ the potential transpiration rate (cm day^{-1}), and L_{nrd} the normalized RLD distribution. With two successively measured profiles of volumetric soil water content, namely $\theta(z,0)$ and $\theta(z,T)$ at $t=0$ and $t=T$, respectively, the average RWU rate $\bar{S}(z,T)$ from 0 to T can be estimated using the inverse method by Zuo and Zhang (2002). The distribution $\bar{S}(z,T)$ is dependent only on soil properties, evaporation rate $E(t)$, and the two measured distributions of soil water content ($\theta(z,0)$ and $\theta(z,T)$).

Assuming that the maximal specific water extraction rate $S_{\max}(z_r,t)$ is proportional to RLD under the optimal soil water condition (Feddes et al., 1978; Prasad, 1988), Wu et al. (1999) deduced NRLD (L_{nrd}) as follows:

$$L_{\mathrm{nrd}}(z_r) = \frac{L_d(z_r,t)}{\int_0^1 L_d(z_r,t)\mathrm{d}z_r} \tag{6}$$

where $L_d(z_r, t)$ is the RLD at z_r and t (cm cm^{-3}). Measured RLD data can be transformed into NRLD distributions using Equation (6) and the procedure of Zuo et al. (2004a). Based on retrieval data of wheat's RLD distributions under surface irrigation, Zuo et al. (2004a) established a generalized function of wheat's NRLD distributions as follows:

$$L_{\mathrm{nrd}}(z_r) = 4.522(1-z_r)^{5.228}\exp(9.644 z_r^{2.426}) \tag{7}$$

Under the optimal soil water condition, the RWU rate reaches the maximal specific water extraction rate $S_{\max}(z,t)$, which is only dependent on root growth and climate condition. Feddes et al. (1978) and Prasad (1988) assumed that $S_{\max}(z, t)$ is proportional to the RLD:

$$S_{\max}(z,t) = c_r L_d(z,t) \tag{8}$$

in which the potential RWU coefficient c_r represents the maximal RWU rate per unit RLD, i.e. the volume of water uptake per unit root length per unit time under the optimal soil water condition (cm^3 cm^{-1} day^{-1}). Integrating Equation (8) from soil surface to the rooting depth L_r gives:

$$c_r = \frac{\int_0^{L_r} S_{\max}(z,t)\mathrm{d}z}{\int_0^{L_r} L_d(z,t)\mathrm{d}z} = \frac{Tp(t)A}{TRL(t)} \tag{9}$$

where A is the area on which the RLD is calculated (cm^2), $TRL(t)$ the total root length in the root zone (cm). Since $Tp(t)$ is often calculated and given as an average value over a period, $TRL(t)$ should also be averaged over the computed duration. With Equation (8), Equation (5) is rewritten as follows:

$$S(z,t) = \gamma(h) S_{\max}(z,t) = \gamma(h) c_r L_d(z,t) \tag{10}$$

Equation [10] provides a simpler method to estimate RWU rate if the coefficient c_r is known in a soil–wheat system. The RLD distribution can be estimated using the generalized NRLD function of wheat with the rooting depth L_r and a measured RLD value near the soil surface (Zuo et al., 2004a). The reduction function $\gamma(h)$ represents the degree of water stress, given as a simple linear formula of soil water content as:

$$\gamma[h(z,t)] = \rho[\theta(z,t)] = \begin{cases} 0 & \theta \le \theta_r \\ \dfrac{\theta(z,t)-\theta_r}{\theta_c-\theta_r} & \theta_c < \theta < \theta_r \\ 1 & \theta \ge \theta_c \end{cases}$$

where $\theta(z,t)$ is the soil water content at z and t, θ_r the residual water content (cm^3 cm^{-3}), θ_c a threshold of soil water content (cm^3 cm^{-3}). When soil water content is equal to or greater than θ_c, there is sufficient water for plant growth, called a "sufficient water supply" condition. Equation [11] represents the portion of available soil water to plants. The field water capacity (FWC) has commonly been used as the upper limit of soil water available to plants (Ahuja and Nielsen, 1990; Charlesworth and Stirzaker, 2003; Jensen et al., 1990). In irrigation practice, the threshold

θ_c is often set to be less than the FWC. Boonyatharokol and Walker (1979) evaluated various relationships for estimating the degree of water stress using field measurement data and found that θ_c should be larger than 50% of the FWC (Jensen et al., 1990). Liu et al. (2004) summarized a great deal of experimental data and concluded that the optimal soil water content for winter wheat at the seedling stage in China was about 70–80% of the FWC. In this study, we chose θ_c as 80% of the FWC.

Experiments

An experiment was conducted to investigate RLD and RWU distributions of winter wheat (*Triticum aestivum* L. cv. Nongda 189) under natural sub-irrigation. The natural sub-irrigation condition was simulated by controlling the water table in the soil column using a Mariotte bottle. The experiment was performed in a greenhouse using columns made of polyvinyl chloride (PVC) pipe with 3 treatments: two for different water supplies under sub-irrigation (A-W1 and A-W2) and one for sufficient water supply under surface irrigation (A-CK). Treatment A-CK was irrigated once every 3 days so as to keep the average water content in the root zone not less than 80% of the FWC. The supplied water amount was decided by the water loss from the column within the period, determined by weighing and readings from the time domain reflectometry (TDR) (MP-917, Canada; precision: ± 0.005 cm^3 cm^{-3}). The water table in treatments A-W1 and A-W2 was controlled using a Mariotte bottle for each column. The air entry position of the Mariotte bottle for each column of treatments A-W1 and A-W2 was adjusted to keep the average water content in the root zone not less than 80% and 60% of FWC, respectively. Based on Equation [11], treatments A-CK and A-W1 were under the sufficient water supply condition and treatment A-W2 was under the water stress condition. The FWC for the experiment was chosen as 0.13 cm^3 cm^{-3}, corresponding to water content at –100 cm of soil matric potential (Dane and Topp, 2002).

The diameter of the columns was 15 cm. The column heights were 80, 180, and 180 cm, respectively, for A-CK, A-W1, and A-W2. For each treatment, 16 columns, each of which was cleaved vertically into two parts, were setup to measure wheat root distributions at different depths and times during the growing period. At the beginning of the experiment, the cleaved columns were stuck together and all the columns were sealed with PVC back covers at the bottom. At the bottom of each column for A-W1 and A-W2, a ceramic plate and about 4.5 cm of glass beads were installed before filling soil. The columns were packed with fine sand soil (with a bulk density of 1.65 g cm^{-3}) up to the heights of 77, 172, and 172 cm for A-CK, A-W1 and A-W2, respectively. In addition, two soil columns for each treatment were setup to observe distributions of soil water content by the TDR at depths of 0–15, 15–30, 30–45, 45–60 cm from the soil surface for A-CK, and 0–15, 15–30, 30–60, 60–90, 90–120 cm for A-W1 and A-W2. Totally 54 columns were utilized in the experiment for the different treatments. The soil water retention and unsaturated hydraulic conductivity functions were described using the closed form of van Genuchten (1980), with the parameters as follows: saturated hydraulic conductivity $K_s = 295.2$ cm day^{-1}, saturated soil water content $\theta_s = 0.476$ cm^3 cm^{-3}, residual water content $\theta_r = 0.033$ cm^3 cm^{-3}, and the fitted coefficients $\alpha = 0.0451$ cm^{-1} and $n = 1.986$.

A preliminary test was carried out to establish the relationship between soil water distribution and the air entry position (AEP) of the Mariotte bottle. Based on results of the test, appropriate AEP values were chosen for treatments A-W1 and A-W2. During the experimental period, the controlled AEP values below the soil surface ranged from 80 to 110 cm for A-W1 and from 90 to 130 cm for A-W2.

Winter wheat was planted in the columns with a seed density of 7 plants per column similar to that in the field (400–600 plants per m^2). Above the soil surface, 3 cm of quartz sand was filled to reduce evaporation. Sufficient nutrients were supplied for all the treatments. The experiment lasted for 57 days (from 20 Nov. 2003 to 15 Jan. 2004) from planting to tillering stages of winter wheat. During the experimental period, the conditions for winter wheat growth in the greenhouse were kept as: a photosynthetic photon flux density of 500 μmol m^{-2} s^{-1} over the plants for 14 h per day (from 8:00 to 22:00), the air temperature within 20–25 °C, and a relative humidity of $40 \pm 5\%$. The root sampling was started on 4 Dec. 2003 (14 days after planting – 14 DAP), and conducted every 6 days and for 8 times during the experimental period. At each sampling time, 2 duplicate columns for each treatment were opened for soil cores. The soil cores were cut into 5 cm soil layers, each of which was sampled to measure water content (to supplement and rectify the measured data by the TDR). The remaining of each soil core was put into a meshwork with grids of 0.05 cm in diameter and washed until almost all of the soil disappeared. Then roots were picked up on the meshwork. The roots collected from each soil layer were scanned with a SNAPSCAN 1236 scanner (AGFA, Germany) and analyzed with the WinRHIZO Pro software package (Regent Instruments Inc., Canada). The data were used to determine the RLD distributions.

Another parallel experiment was arranged to examine the soil surface evaporation rate (i.e., $E(t)$ in Equation [3]). The experiment was also performed with three treatments, viz. A0-CK, A0-W1, and A0-W2, the same as the above experiment but without plant in the columns. The evaporation rate in A0-CK was obtained from the water loss by weighing the soil column daily. For treatments A0-W1 and A0-W2, $E(t)$ was calculated from soil water changes in the columns and the amount of water loss from the Mariotte bottle during each root sampling period (6 days). The potential transpiration rate Tp in the greenhouse was obtained from the difference between the average water loss rate in the treatment A-CK and the average soil surface evaporation rate $E(t)$ in the treatment A0-CK during the same period.

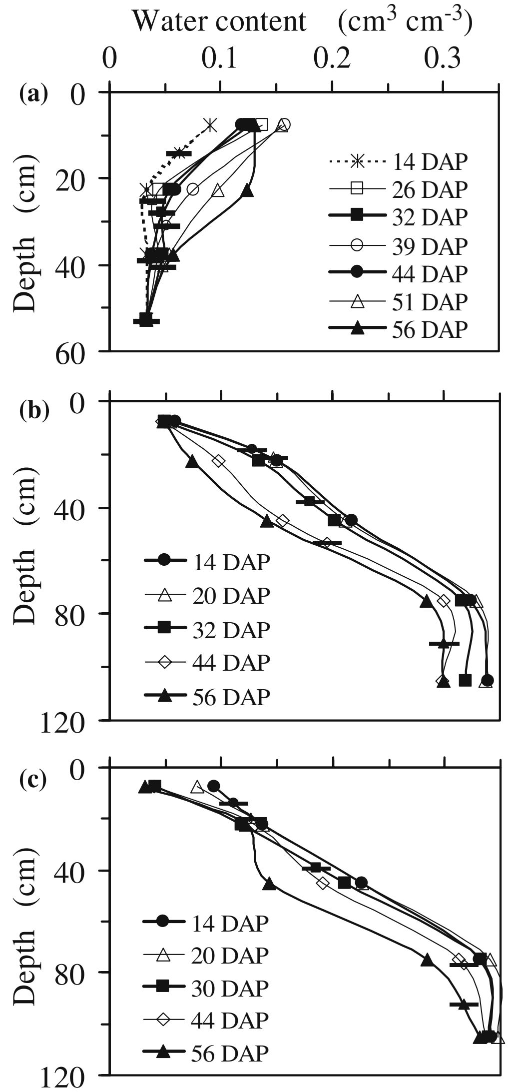

Figure 1. Measured soil water content profiles from 14 DAP (days after planting) to 56 DAP for treatments of (a) A-CK; (b) A-W1; and (c) A-W2. The horizontal bars represent the rooting depths (L_r) of the corresponding time.

Results and discussions

The measured soil water content profiles from 14 DAP to 56 DAP for treatments A-CK, A-W1 and A-W2 are shown in Figure 1a–c, respectively. In Figure 1a, the curves of 14, 32, 44 and 56 DAP were for the water content profiles at 0.5 days before irrigation and the others for those at 0.5 days after irrigation. The different water supply methods resulted in different water content distributions. However, the average water contents in the root zone at different growth stages of winter wheat for treatments A-CK and A-W1 were controlled not less than 80% of FWC to guarantee the sufficient water supply condition (Figure 1a, b). For example, the average water contents in the root zone (the corresponding rooting depths L_r were indicated by horizontal bars in the figures) during 26–32 and 39–44 DAP were about 0.094, 0.105 $cm^3\ cm^{-3}$ for A-CK, and 0.113, 0.122 $cm^3\ cm^{-3}$ for A-W1, respectively, falling in the range of "the optimal soil water content" of winter wheat at the seedling stage (Equation [11]; Liu et al., 2004). Because of the difficulties in controlling the soil water distribution accurately, the average water content in the root zone for

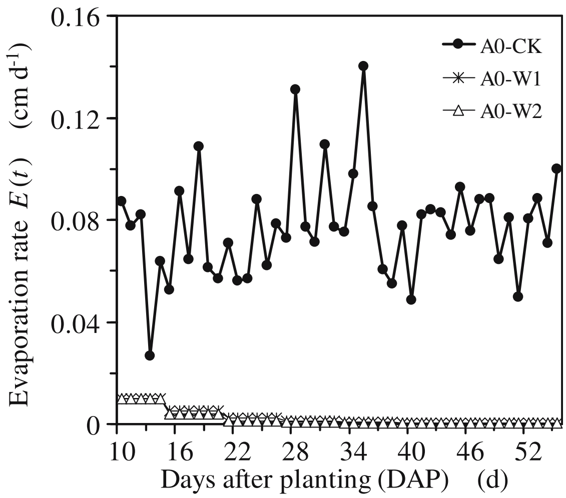

Figure 2. Soil surface evaporation rate $E(t)$ of different treatments during the experimental period.

treatment A-CK during 26–32 DAP was a little lower than the desired requirement of 80% of FWC (0.104 cm^3 cm^{-3}), while the values for treatments A-W1 and A-W2 were slightly higher.

The soil surface evaporation rates measured through the experiment are shown in Figure 2. Although the soil surface was mulched with 3 cm of quartz sand, the surface evaporation rate of treatment A0-CK was significant. The values of $E(t)$ in treatments A0-W1 and A0-W2 under subirrigation were much smaller than that in A0-CK under surface irrigation because the soil water content in the upper soil layer of A0-W1 and A0-W2 was much lower than that of A0-CK (Figure 1).

RLD and NRLD distributions

Measured RLD distributions between 14 and 56 DAP for the three treatments are shown in Figure 3. The values of RLD decreased gradually downwards for all the three treatments. Accompanying with the growth of winter wheat, the rooting depth L_r and RLD in the soil layers increased with time. However, the RLD values displayed considerable discrepancies for the different treatments. For treatment A-CK, most of the roots developed near the soil surface (within 20 cm from the soil surface), few roots beneath 40 cm, and the values of RLD within 20 cm after 26 DAP were several times higher than that of treatment A-W1 (Figure 3a, b). The rooting depth L_r and RLD below 40 cm in A-W1 were much greater than that in A-CK. Compared with A-W1, treatment A-W2 had lower water contents in the upper soil layer and higher RLD values below 40 cm except on 56 DAP (Figures 1b, c and 3b, c). The differences were attributable to the different water content

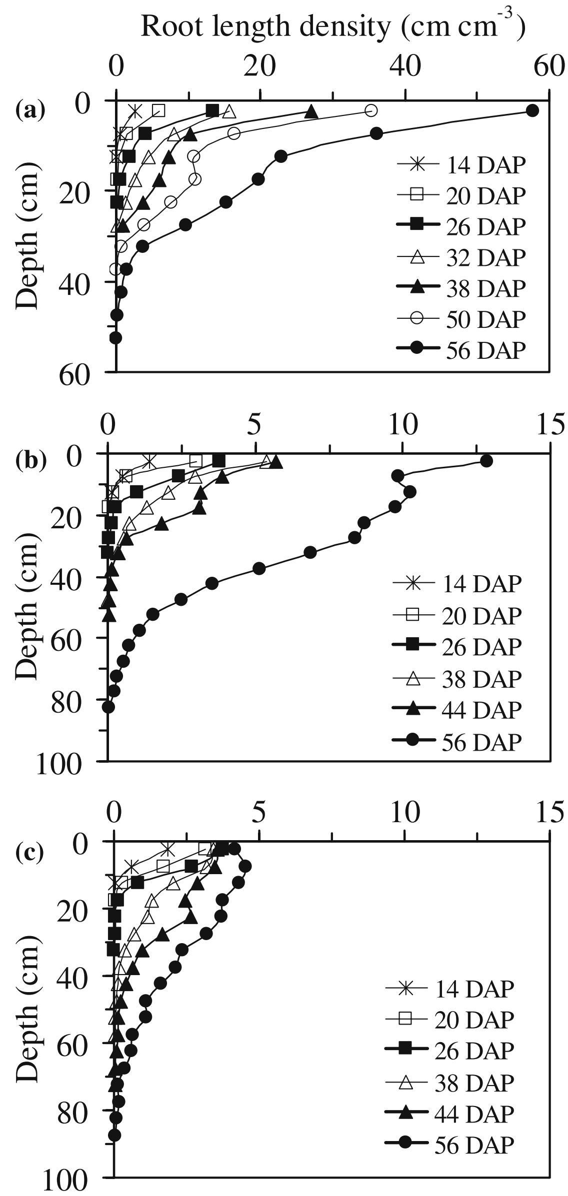

Figure 3. Measured root length density distributions of winter wheat between 14 and 56 DAP for the treatments of (a) A-CK; (b) A-W1; and (c) A-W2.

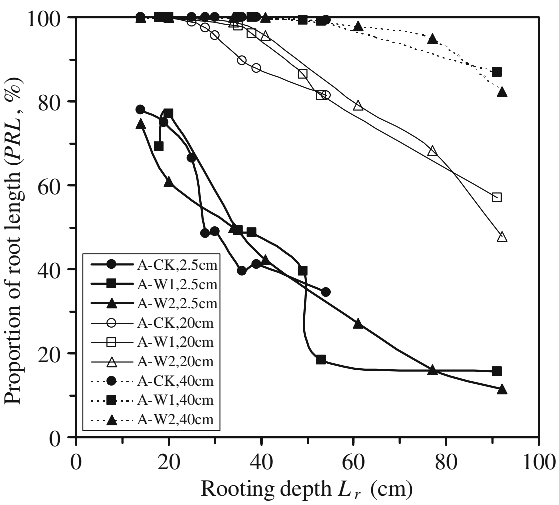

Figure 4. The relationship between the values of L_r and the proportion of root length (PRL) within the depths of 2.5, 20, and 40 cm to total root length in the root zone for different growth periods and different treatments.

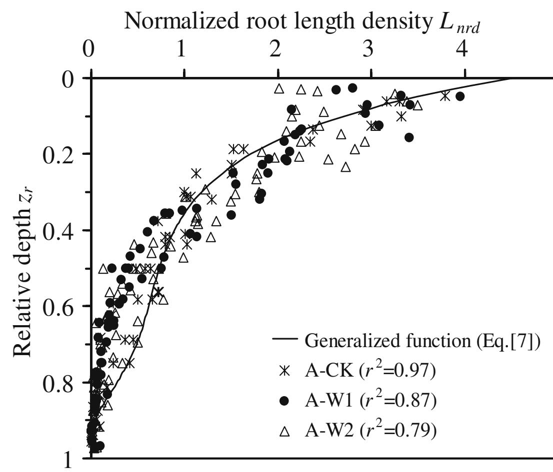

Figure 5. Experimental data (the symbols) of the normalized root length density vs. the relative root depth of winter wheat in treatments of A-CK, A-W1 and AW2, and the generalized function (the solid curve).

distributions. The water content distribution of A-CK was consistent with the RLD distribution, whereas the water content distributions of A-W1 and A-W2 were opposite to the RLD distributions.

On the other hand, the measured RLD distributions showed that the majority of the roots for the three treatments were distributed above 40 cm (Figure 3). Root growth and rooting depth L_r are influenced by many factors such as soil environment (soil texture, structure, water and nutrient, etc.), plant species and growing stages, climates, etc. (Asseng et al., 1997, 1998; Pagès et al., 2000; Xue et al., 2003). However, the experimental results of the wheat's roots mainly concentrating near the soil surface, as reported by many researchers (Asseng et al., 1997, 1998; Xue et al., 2003; Zuo et al., 2004a), gave the insight of root allocation proportions of winter wheat at different depths. The relationship between the proportion of root length (PRL) near the soil surface to the total root length in the root zone and the values of L_r for different growth periods and treatments is shown in Figure 4. As for the same growth period of different treatments, increasing L_r had lower values of RLD and PRL near the soil surface. For all the three treatments, the percentage of root length above 20 and 40 cm was more than 50% and 80%, respectively. The PRL values above different depths (2.5, 20 and 40 cm) decreased with increasing L_r, and the decreasing tendency was very similar for the different treatments. The allocation of winter wheat's roots to different depths appeared only dependent on L_r. The results provided the base to apply the generalized NRLD function (Zuo et al., 2004a) to describe the RLD of wheat under sub-irrigation.

Using the procedure of Zuo et al. (2004a), the measured RLD data were transformed into the NRLD distributions as shown in Figure 5. The generalized function (Equation [7]) was in a good agreement with the measured data under both surface irrigation and sub-irrigation in general, with determination coefficients $r^2 = 0.97$, 0.87, and 0.79 for treatments A-CK, A-W1, and A-W2, respectively. The function characterized the experimental data less accurately at depths between $z_r = 0.6$ and $z_r = 0.8$. The discrepancy was probably resulted from the originally fitting process of the generalized NRLD function. Equation [7] was a statistically fitted function from 89 data sets and 610 data points. Between the relative depths $z_r = 0.6$ and $z_r = 0.8$, scattered data points resulted in relatively poor fitting (Zuo et al., 2004a). Nevertheless, the generalized NRLD function, which was generated from a large population of samples, should provide a rational and representative model. The generalized function developed based on measured RLD data under surface irrigation, is also applicable to describe the RLD distributions of winter wheat under natural sub-irrigation.

The NRLD distribution represents the root allocation proportions of winter wheat at different depths. Since the generalized function was developed and testified (Zuo et al., 2004a) based on measured RLD data collected under different regions and climate conditions in the world, soils (sand, fine dune sand, loamy sand, loam, sandy loam clay, clay, etc.), water and nutrient supplies (N, P, K and other microelements), plant species (*Triticum aestivum* L. (cv. *Factor*, *Molineux*, etc.), *Triticum turgidum* L. conv. *durum*, etc.), growing stages and cropping systems (both in the field and in the laboratory), and under surface irrigation as well as natural sub-irrigation, it indicates that the root allocation proportions of winter wheat at different depths are independent of the various factors and probably determined only by its hereditary features. Nonetheless, this study was performed only in a sandy soil and within a 57-day growing period of winter wheat under simulated natural sub-irrigation in a greenhouse. The soil columns with a 15 cm diameter might limit the root growth to some extent. Further research is needed to verify the generalized NRLD function by collecting data in various conditions, such as in different soils, at various growing periods of winter wheat under sub-irrigation, under other sub-irrigation methods such as sub-surface drip irrigation or underground pipe (ditch) irrigation, and in the field, etc.

Estimations of RWU distributions under sub-irrigation

Using the measured water content profiles (Figure 1b, c), the hydraulic parameters, and the inverse method of Zuo and Zhang (2002), we estimated the average RWU rate distributions during the experimental period in treatments A-W1 and A-W2 (Figure 6). With sufficient water supply, the scope of RWU in treatment A-W1 expanded downwards and the RWU rate increased with the growth of winter wheat except a few cases above 10 cm (Figure 6a), which would result from the adjustment of the air entry position (AEP). The RWU rate in treatment A-W2 showed a similar trend (Figure 6b); however, the values in the up-

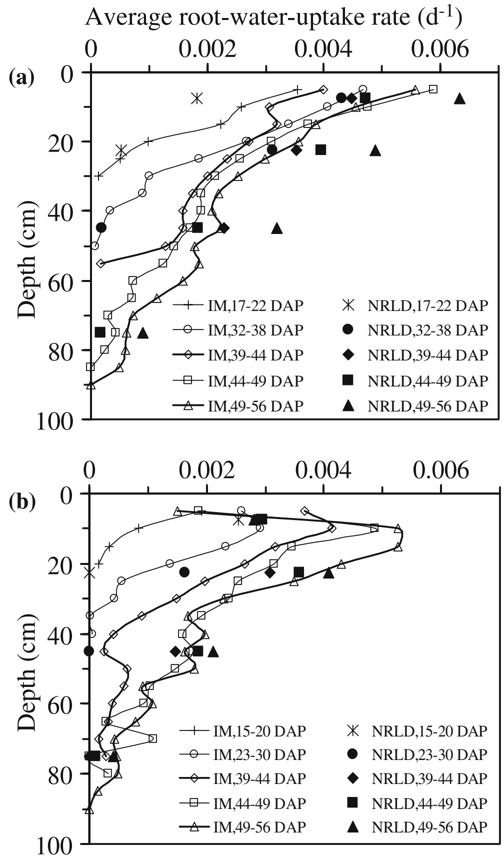

Figure 6. Average RWU rate distributions and RWU rate values of winter wheat estimated using the inverse method (IM, depicted in lines) and the generalized NRLD function (NRLD, depicted in symbols) during the experimental periods for treatments of (a) A-W1 and (b) A-W2.

per soil layer (within the top 20 cm) were smaller and in more irregular patterns than those in treatment A-W1 because of water stress. In Figure 6b, a few abnormal values of RWU rate near the rooting depth on the curve of 44–49 DAP were probably due to the instability feature of the inverse method when the RWU rate approaches zero (Zuo and Zhang, 2002). Because of the measurement errors of soil water content using TDR as high as 0.005 cm^3 cm^{-3}, the errors of estimated RWU rate could reach 0.001 day^{-1}, hence the estimated values of RWU rate near zero would not be reliable.

In the experiment, treatment A-CK was under the optimal soil water condition: with sufficient water supply and the soil water content distributions consistent with the RLD distribution

Table 1. Measured average total root length (*TRL*) in the root zone, measured average potential transpiration rate (*Tp*) and calculated potential root-water-uptake coefficient (c_r) during different periods for treatment A-CK

Period	*TRL* (cm)	*Tp* (cm day^{-1})	c_r (cm^3 cm^{-1} day^{-1})
17–23 DAP*	8307.94	0.174	0.00369
23–29 DAP	15931.28	0.269	0.00298
29–35 DAP	28355.98	0.429	0.00267
35–41 DAP	39569.13	0.589	0.00263
41–47 DAP	53679.02	0.964	0.00317
47–53 DAP	83343.52	1.416	0.00300
Average (± Maximal error)			0.00303 (± 0.00066)

*DAP: days after planting.

Table 2. Root mean squared errors (RMSE) (day^{-1}) of the RWU rate values estimated by the inverse method and the generalized NRLD function of wheat for treatments A-W1 and A-W2 during different growth periods (DAP: days after planting)

Treatment	Estimation period						
	15–20 DAP	17–22 DAP	23–30 DAP	32–38 DAP	39–44 DAP	44–49 DAP	49–56 DAP
A-W1	—*	0.00089	—	0.00049	0.00089	0.00065	0.00114
A-W2	0.00116	—	0.00048	—	0.00103	0.00043	0.00039

*The numbers of the calculated RMSE are corresponding to the estimated RWU rate distribution curves in Figure 6a, b.
Lines '—' indicate the estimation process was not operating in the 'Treatment' and 'Estimation period'.

feature of winter wheat. Therefore, the potential RWU coefficients (c_r) during different experimental periods were calculated using the data of treatment A-CK and Equation [9]. As shown in Table 1, the calculated c_r values ranged from 0.00263 to 0.00369 cm^3 cm^{-1} day^{-1}, with an average of 0.00303 cm^3 cm^{-1} day^{-1}, similar to the upper limit (0.003–0.0031 cm^3 cm^{-1} day^{-1}) reported by Asseng et al. (1998). The values during the six periods were very close to each other within error limits of ± 0.00066 cm^3 cm^{-1} day^{-1}. The result supports the hypothesis that the maximal RWU rate is proportional to RLD under the optimal soil water condition (Feddes et al., 1978; Prasad, 1988).

The RWU rate cannot be measured directly, either in the field or in the laboratory. To check the stability and the accuracy of the inverse method, Zuo and Zhang (2002) introduced a theoretical RWU model to simulate soil water flow with the RWU, and then utilized two simulated soil water content profiles as 'measured' values to estimate the RWU. The results showed that the overall relative errors between the estimated RWU rate distributions by the inverse method and the theoretical values were less than 20%, indicating that the inverse method was reliable for estimation of the RWU rate distribution. Therefore, the average RWU rate distributions from the inverse method were used to evaluate the RWU results estimated by the proposed method (Equation [10]). With the c_r value, we estimated the RWU rate of winter wheat using Equation [10], [11], Equation [7] (the generalized NRLD function), the information of rooting depth L_r, one measured value of RLD at $z = 2.5$ cm, and the observed soil water content profiles. The calculated RWU rates at different depths for treatments A-W1 and A-W2 were compared with the estimated RWU rate distributions by the inverse method in Figure 6a, b, respectively. The corresponding root mean squared errors (RMSE) of the RWU rate values estimated by the inverse method and the generalized NRLD function for different treatments during different growth periods are listed in Table 2. The estimated RWU rate values by the NRLD function compared well with the estimated RWU rate distributions using the inverse method, with RMSE values less than 0.0012 day^{-1} (i.e., resulted in transpiration rate less than 0.12 cm day^{-1} for 100 cm of the rooting depth), which should meet the accuracy requirement of irrigation practice or regional water resources evaluation in most cases. With the potential RWU coefficient c_r and the generalized NRLD function of wheat, estimating the RWU rate distribution in soil–wheat system becomes much easier, requiring only rooting depth, one measured RLD value, and measured soil water content profiles.

So far, many RWU models have been established directly based on the RLD distribution (Coelho and Or, 1996, 1999; Feddes et al., 1978; Hao et al., 2005; Musters and Bouten, 1999, 2000; Prasad, 1988; van Noordwijk and van de Geijn, 1996; Vrugt et al., 2001a, b; Wu et al., 1999). Realistic modeling and prediction of RWU patterns must rely on both the RLD and soil water distributions (Clothier et al., 1990; Coelho and Or, 1999; van Noordwijk and van de Geijn, 1996). The RLD comprises the total length of all collected roots in the soil, including active and inactive roots (Box and Ramseur, 1993; Coelho and Or, 1999; Molz and Remson, 1970; Slatyer, 1960). Only the active roots can effectively extract water from the soil. Root hairs and fine roots are usually considered to be more active for water uptake than larger and thicker roots (Coelho and Or, 1999; Pierret et al., 2005; Slatyer, 1960). At the earlier growth stage (for example, from planting to tillering stages in our case) of winter wheat, the active fine roots are dominating in the root system. Thus, the calculated potential RWU coefficients c_r in this experiment changed in a narrow range and supported the linear hypothesis between the RWU and RLD under the optimal soil water condition (Feddes et al., 1978; Prasad, 1988). Since the coefficient c_r is dependent on the potential transpiration rate and the active root length, it should be cautious when using the coefficient in the circumstances of later growth stages of winter wheat and in the field. The effectiveness of roots and the relationship between the RWU and RLD of winter wheat need further research.

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