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REGULAR ARTICLE

Wheat root growth responses to horizontal stratification of fertiliser in a water-limited environment

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Abstract
Background and aims We were interested to determine the effects of horizontal stratification of nutrient-rich zones within different layers of the soil profile in water-limited environments on root growth and crop yield. This is practically relevant to large areas of China, many of which have been over-fertilized.
Methods We used soil-filled rhizotrons 1.4 m deep to grow wheat. Three different nutrient-rich horizontal stratifications were used at depths of 0–40, 60–100 and 0–140 cm. The soil was packed to a density of 1.5 g cm^{-3}, at a matric potential of −10 kPa. The wheat was grown until it was at terminal drought. Low soil hydraulic conductance preserved the horizontal nutrient stratification.
Results Plants grown in rhizotrons with a surface layer (0–40 cm) of nutrients had the greatest root growth, water uptake and yield. When nutrients were uniformly distributed throughout the rhizotron (0–140 cm), root growth was restricted to the surface layer. Measurements of soil moisture indicate this was because the roots became impeded.
Conclusions Nutrient enrichment of the surface layer was the most effective at promoting deep roots, higher water uptake and yield under water-limited conditions. Heterogeneous nutrient distribution can modify root growth and water uptake.

Keywords Root proliferation · Water-limited · Horizontal nutrient stratification · Wheat

Introduction

Water is essential for crop production because plants need water for growth and tissue expansion (Morison et al. 2008; Wilkinson and Davies 2010). However, China's water availability per capita is only one quarter of the world average (Wang et al. 2008b; Du et al. 2010). The outlook for water shortage is especially dire on the North China Plain, one of the main grain production areas in China (Kendy et al. 2003; Deng et al. 2006; Wang et al. 2008a; Hu et al. 2010b; Fan et al. 2012). The region comprises 33.8 % of the national arable land of China, but has only 3.85 % of the national water resources (Fan et al. 2012). The relationship between grain yield and water-use has been described by the Passioura equation ((Passioura 1977), *Grain yield = Transpiration × Transpiration efficiency × Harvest index*). Increases in any of these three components will

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translate into greater yield. Thus, there is a need to develop new genotypes and/or improve management of cropping systems to maximise water-use efficiency and/or water uptake. Of particular importance is how nutrient distribution within the soil profile affects root growth and hence water uptake.

On the North China Plain there is an intensive farming system which has over-used nutrients (about 550 kg N ha^{-1} yr^{-1} applied to two crops per year) for decades, based on the traditionally assumed notion of 'high input, high output' (Zhang et al. 2012; Shen et al. 2013). Excessive fertilizer (especially N) application and poor management has contributed to high soil nitrate-N accumulation and losses of N to the environment (Ju et al. 2006; Qiu et al. 2012). Soil NO_3^--N enriched in the top 90 or 100 cm of the soil was above 200 kg N ha^{-1} under conventional N practice in intensive wheat-maize systems (Liu et al. 2003; Cui et al. 2008). When soil nitrate levels are high, root biomass and root to shoot ratio decrease, more roots are found in the topsoil layer and root growth, especially of lateral roots, is depressed (Durieux et al. 1994; Wang et al. 2003; Mi et al. 2010).

A larger proportion of root biomass located in deep soil layers can maintain greater transpiration rates (Lopes and Reynolds 2010). Modelling work has concluded that root system architecture, with a larger investment in fine roots deep in the soil, will increase crop yields by accessing extra soil water resources from the whole soil profile (King et al. 2003; Lynch and Brown 2012). The promotion of water captured from subsoil by dryland wheat (*Tritcum aestivum* L.) can make a big contribution to yield (Kirkegaard et al. 2007; Richards 2008; Lilley and Kirkegaard 2011). Increasing root system access to water deep in the soil profile may be a promising way to increase water capture under water-limiting conditions (Mi et al. 2010; Dodd et al. 2011; Jin et al. 2013; Trachsel et al. 2013; White et al. 2013). However, whether the site of nutrient application can regulate root growth, thereby altering crop water-use, is an important issue that may increase crop productivity under water-limited conditions (Hodge 2010; Jin et al. 2013; Shen et al. 2013), but this issue has been relatively unexplored. Soil nutrient heterogeneity must be considered when designing soil management strategies aimed at improved overall resource use efficiency, particularly water-use efficiency (Farley and Fitter 1999; Fransen et al. 1999; Hodge 2004; Tittonell et al. 2005; Hodge 2006; De Kroon 2007). However, the evidence on the role of spatial heterogeneity of soil nutrients on plant growth has been acquired mainly from studies of nutrient patches (Hodge 2004; Hutchings and John 2004; Wang et al. 2013). These "nutrient pocket" studies are not so relevant to understanding the intensive farming system in China where pronounced vertical nutrient gradients have developed due to surface nutrient applications and flood irrigation (Zhu and Chen 2002; Ju et al. 2004; Hu et al. 2005; Fang et al. 2006; Fan et al. 2012). Fang et al. (2006) found that under a lower level of soil moisture content (70±15 % of field capacity), high N application rate (300 kg N ha^{-1}, surface broadcast) significantly increased NO_3^--N content in the topsoil and soil profile below 40 cm.

Although Drew and co-workers (Drew 1975; Drew and Saker 1975; 1978) have shown that roots proliferate in nutrient-rich stratified layers, these were well-watered (continuously irrigated with nutrient solution). However, primary root length is regulated by water availability rather than nitrate supply (Forde and Zhang 1998; Walch-Liu and Forde 2008; Chapman et al. 2011). Even in sand culture systems the elongation of primary roots increases with decreasing water availability irrespective of root surface nitrate availability (Chapman et al. 2011). That root physiology responds to water potential is well reported (Sharp et al. 1988; Verslues et al. 1998; Whalley et al. 1998; Van Der Weele et al. 2000; Roycewicz and Malamy 2012). In this work, we explored the effects of horizontal stratification of nutrient-rich zones on root growth and water capture when the soil profile is allowed to dry, and hence water-limited. Three possible scenarios of relevance to large areas of China's intensive agriculture (Fan et al. 2012; Zhang et al. 2012; Shen et al. 2013) were simulated (1) uniformly nutrient-rich profile, (2) nutrient-rich surface layer and (3) a nutrient depleted surface layer with nutrient-rich layer at depth. We tested the hypothesis that a heterogeneous nutrient distribution with depth will increase root growth and hence water uptake in comparison with a uniform (homogeneous) soil profile.

Materials and methods

Plant material

Seeds of a *Rht-B1a* NIL (near isogenic line) in a Mercia background were germinated between two sheets of wet filter paper (Whatman No. 1, 150 mm diameter) in Petri dishes which were wrapped in black nylon fabric to exclude light.

Soil

We used a loamy sand soil (Butt Close, see also Whalley et al. 2008) obtained from Rothamsted experimental farm at Woburn, Bedfordshire, UK. It had 87.5 % sand, 5.5 % silt and 7.2 % clay and organic carbon content of 1.0 % (by weight). The water release characteristic of the soil was measured with standard laboratory methods (Gregory et al. 2010).

Experimental treatments and approach

To investigate the effects of root response to nutrient distribution, plants were grown in rhizotrons: 145 (high) × 38 .8 (wide) × 8 (deep) cm (Fig. 1). One wall of the rhizotron was glass and during the experiment they were inclined at approximately 15 °, which allowed the roots to follow the glass face. We used three types of nutrient placement: (1) Uniform (0–140 cm, nutrient-rich at all soil depths), (2) surface soil of 0 to 40 cm and (3) deep layers of 60 to 100 cm. The experiment was carried out in a controlled environment (CE) room with day/night temperatures of 22 and 18 °C, respectively, and a 14 h day length. The relative humidity was 70 % during the day and 80 % at night. Lighting was by fluorescent tubes, with supplementary tungsten lighting, and the photosynthetic photon flux density was 450 μmolm^{-2} s^{-1} at plant height.

The soil was packed to a bulk density of 1.5 g cm^{-3}. In nutrient poor areas, deionised water was added to the loamy sand soil and mixed evenly to raise the moisture content to the required level (170 g kg^{-1}, gravimetric soil moisture content) to give a matric potential of −10 kPa. In the nutrient-rich areas, Hoagland‘s standard solution (($Ca(NO_3)_2.4H_2O$ 2.00 mM, KCl 4.00 mM, $CaCl_2.2H_2O$ 4.00 mM, $MgSO_4.7H_2O$ 2.00 mM, $[CH_2N(CH_2COO)_2]_2$ FeNa 0.05 mM, $Na_2SiO_3.5H_2O$ 0.06 mM, KH_2PO_4 1.00 mM, H_3BO_3 50 μM, $MnCl_2.4H_2O$ 15 μM, $ZnSO_4.7H_2O$ 0.8 μM, $CuSO_4.5H_2O$ 0.3 μM; $NaMoO_4.2H_2O$ 0.1 μM) was used to mix with soil to the equivalent soil moisture (170 g kg^{-1}, gravimetric soil moisture content). The concentration of nitrogen and phosphorus (mg kg^{-1} soil) in the background (un-amended) and amended soil (with nutrients added) is shown in Table 1. The N level of uniform treatment was equivalent to 200 kg N ha^{-1} in the field.

A single pre-germinated seed (two-day old) was placed at the midpoint in the top of the rhizotron against the glass face at a depth of 1 cm. Once planted, the seed received no further watering, simulating a terminal drought and avoiding any redistribution of nutrients. Twice each week root elongation against the glass face (Fig. 1) was traced onto transparent films. The rhizotron was separated into 14 (20 × 20 cm) areas to observe root growth. The length of traced roots on the transparency film was determined with the use of a scanner running WinRhizo software (Regent Instruments Inc., Quebec, QC, Canada). At harvest, shoot dry weight, total nitrogen and carbon content were measured with a Leco combustion analyser.

A soil moisture profile probe (Model PR1, Delta-T Devices, Burwell, UK), incorporated in approximately a third of the width of each rhizotron, monitored soil moisture content daily at multiple depths in the soil profile: 10, 20, 30, 40, 60 and 100 cm (Whalley et al. 2004). The volume of soil sampled the profile probe is heavily weighted to the surface of the probe and the region outside the rhizotron had a negligible effect on the instrument. At harvest, gravimetric soil moisture content (θ_g) of each 10 cm layer was measured. Plant water-use was calculated by the following equation,

$$Water\ use\ (mm) = \sum_{t=1}^{n} \left(\theta_g \rho Di\right) \tag{1}$$

θ_g (g g^{-1}) is the gravimetric soil moisture content, ρ is the dry bulk density and n is the number of soil layers of thickness D (rhizotron was separated to 15 layers). Soil nitrate and ammonium were measured using the Skalar SANPLUS.

Statistics

The experiment was performed twice with 2 replicates of each treatment. This degree of replication is consistent with other rhizotron studies (e.g. Fender et al. 2013). The data were analysed as a fully randomized experiment. The data were analysed with Genstat® V16 (VSN International Ltd). To analyse root growth data periods of growth were grouped into set of 5 days and 4 groups were chosen for separate analysis (10 to 15, 35 to 40, 55 to 60 and 60 to 65 days). The residual diagnostic plots indicated that a transformation was needed to stabilize the variance. The transformation used was the

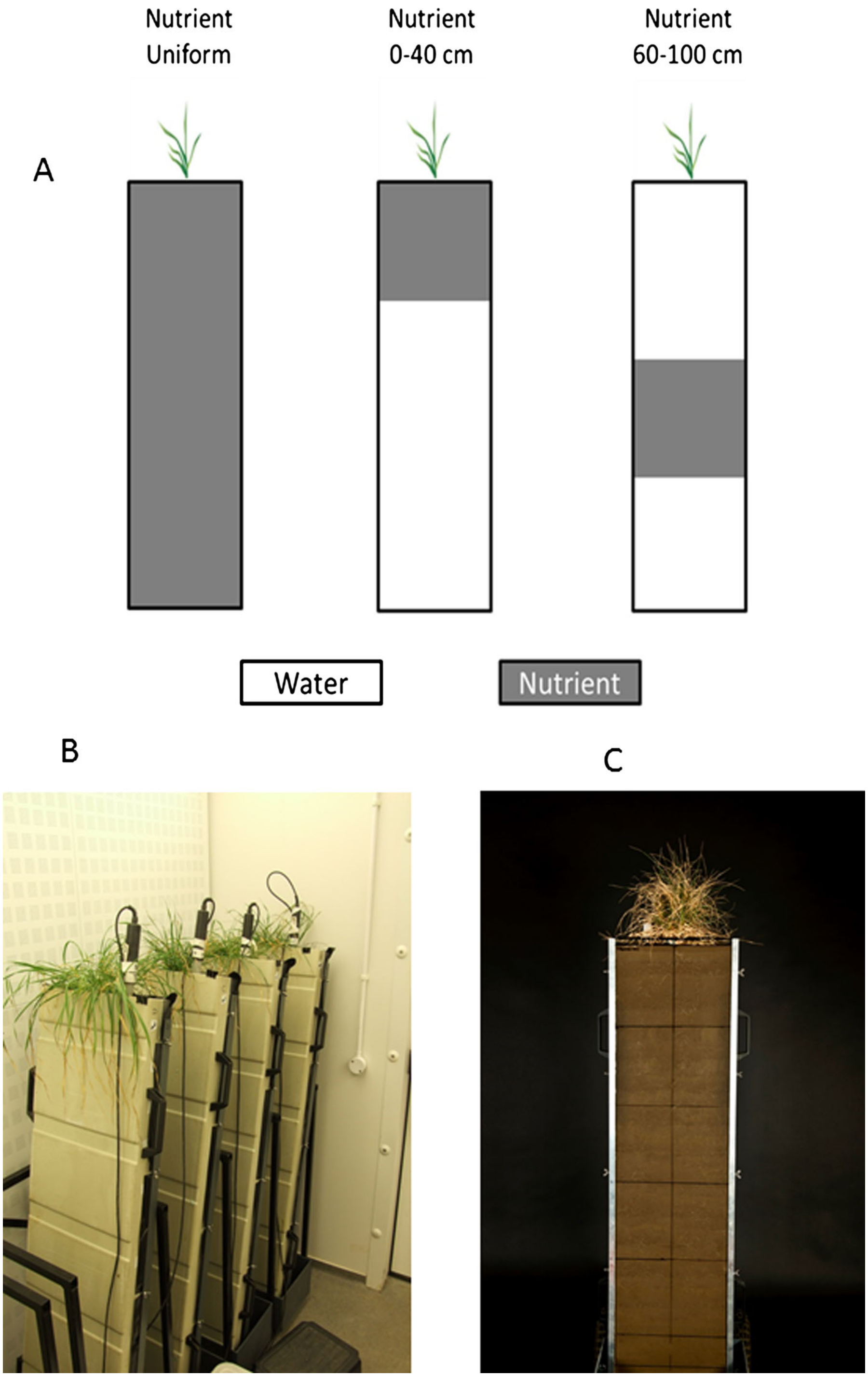

Fig. 1 The schematic representation (**a**) of the experiment, three nutrient scenarios were placed as (1) nutrient-rich profile (Uniform, 0–140 cm), (2) nutrient-rich surface layer (0–40 cm) and (3) a nutrient depleted surface layer with nutrient-rich layer at depth (60–100 cm). In nutrient poor areas, deionised water (Water) was added to instead of Hoagland's nutrient solution (Nutrient). The soil-filled rhizotrons were mounded in a rack at an incline of 15 ° at CE room (**b**). Soil moisture was monitored with dielectric probes. Root growth could be recorded by observing roots elongating against a glass face (**c**)

Table 1 The concentration of total nitrogen and phosphorus (mg kg^{-1} soil) in the background (sample soil) and amended soil (soil to which nutrient was added). Nutrient placement was uniform (homogenous nutrient concentration throughout the soil profile), nutrient in the surface layer from 0 to 40 cm or nutrient in the deep layer from 60 to 100 cm

	Background soil	Amended soil
NH_4-N + NO_3^--N	25.9	68.1
PO_4^--P	91.8	107.9

square root of the original values. In order to capture the shapes of the response of transformed root length density with depth, spline modelling in REML was used. For our data root length density data we used estimates of the least significant difference (LSD) to allow comparison between any two means for a given time period. Other data were analysed by ANOVA or curve fitting.

Results

Soils

The water release characteristic of the soil used is shown in Fig. 2. The soil was mixed with water (or nutrient solution) at 170 g kg^{-1} (gravimetric moisture content), which corresponds to a matric potential of −10 kPa. The negligible flow of water to depth during the early part to the experiment was confirmed by observation of stable water content readings from the PR1 Profile probe at all depths (data not shown). We also note that in the uniform nutrient treatment the water content at the bottom of the rhizotron at the end of the experiment was still nearly 170 g kg^{-1} indicating that no drainage occurred.

We estimated matric potential (Whalley et al. 2013) using the water release curve (Fig. 2) from measurements of water content. Estimates of matric potential between 35 and 40 days are shown in Fig. 3. It should be noted that these estimates are somewhat imprecise, due to the non-linear nature of the water release curve at low water contents (see Fig. 2). The water release curve is sensitive to soil density and although both the rhizotrons and cores used to determine the water release characteristics were packed to the same density, they may not be identical. Nevertheless, the data in Fig. 3 shows that in the treatment with uniform nutrient content, the surface layer was dryer and hence stronger (Whalley et al. 2007) than the other treatments, which is consistent with the greater root length density in the surface layers in that treatment at day 40 (see following section).

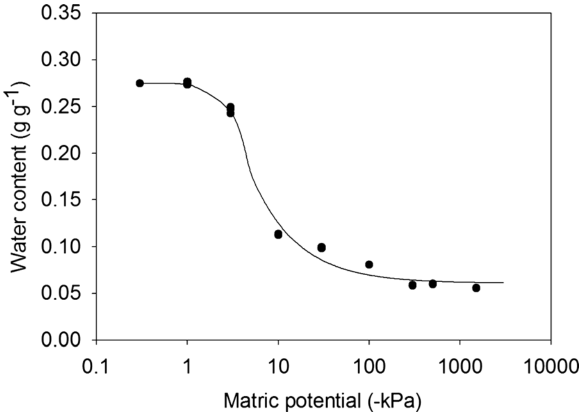

Fig. 2 Water release characteristics measured on re-packed samples of soil from Butt Close. The curve shown is fitted to the Van Genuchten soil water characteristic model (Vangenuchten 1980), $\theta=(\theta_s-\theta_r)\ [1+(ah)^n]^{-m}+\theta_r$ where θ is the water content (g g^{-1}) and θ_s and θ_r are saturated and residual water contents (g g^{-1}) respectively, h (–kPa) is matric potential. a, n and m are empirical coefficients. The values of a, n and m are 0.3980, 30.2920 and 0.0286 respectively

At terminal drought, wheat plants growing in the treatment with a nutrient-rich surface layer (0–40 cm) had dried the soil the most (Fig. 4a). This was consistent with the greater root length density (see following section) in this treatment compared to the other two treatments. At the end of the experiment the soil at depth was relatively well watered (Fig. 4) in all treatments.

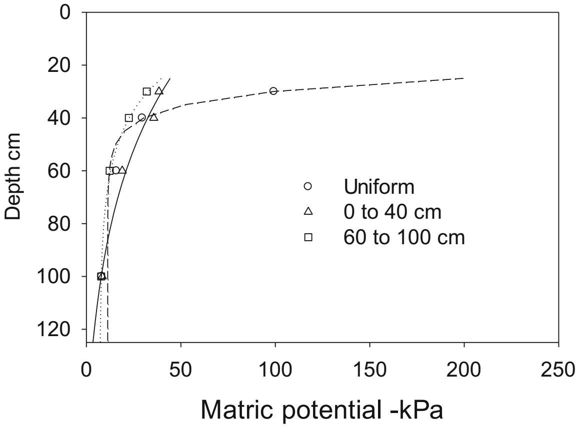

Fig. 3 Matric potential at day 40 was calculated from the water release curve (Vangenuchten 1980) (Fig. 2). Matric potential data were fitted to the function $\psi=A+B\ \exp(Rd)$ where A, B and R are fitted parameters and d is depth. Grouped regression revealed that these relations were significantly different from each other at $P=0.028$

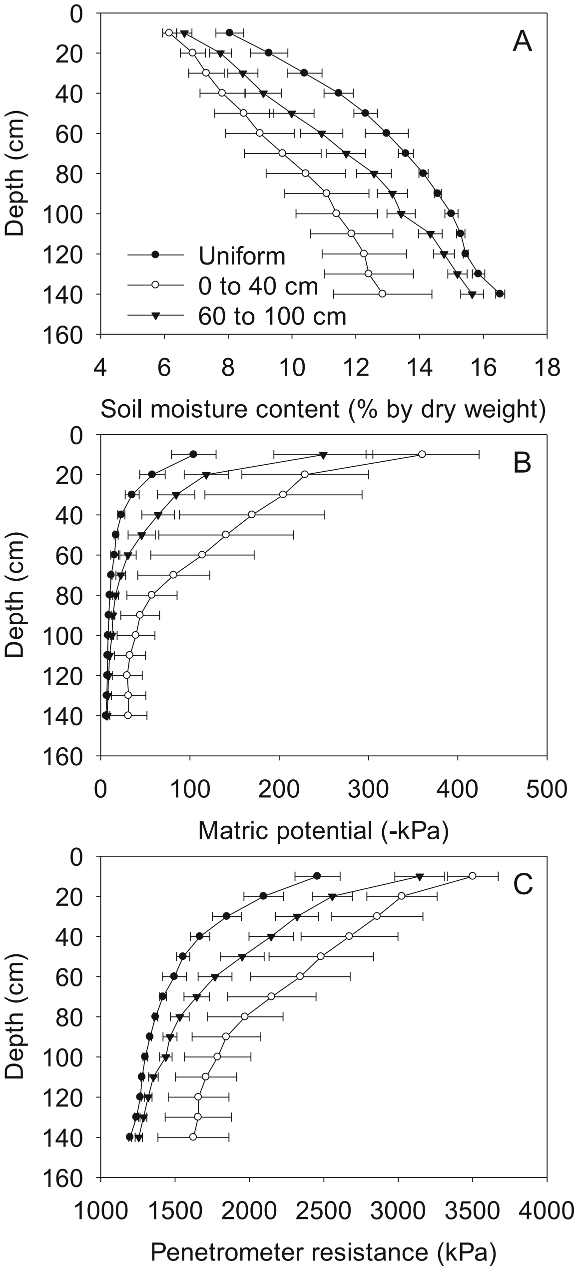

Fig. 4 Final profiles of the soil moisture content, matric potential and penetrometer resistance at terminal drought (Days 65). Water content was determined from oven drying of soil cores. Matric potential was calculated from the water release curve (Vangenuchten 1980) (Fig. 2). The penetrometer resistance was calculated by the equation of $\log_{10} Q = 0.35\ (\pm 0.009) \log_{10} \sigma_W + 0.93\ (\pm 0.0572)\ \rho + 1.2623\ (\pm 0.0832)$ (Whalley et al. 2007), where Q (kPa) is the penetrometer resistance, σ_W (kPa) is effective stress and ρ (g cm^{-3}) is the bulk density (1.5 g cm^{-3} of rhizotron soil in the experiment here). The standard error of the mean is indicated

Rhizotrons and plant growth

Different horizontal stratification of nutrient placement had a great effect on root distribution with depth (Fig. 5). At days 35 to 40 the root length density in the top 40 cm was simply related to the nutrient placement. However, in deeper layers root length density was not related to soil nutrient concentration. Following terminal drought at the end of the experiment (Days 60 to 65), deeper roots (below 1 m) were most abundant in the rhizotrons which only had a surface (0–40 cm) layer of nutrient-rich soil. Uniform nutrient placement resulted in the fewest deep roots.

Photographs of the roots at the end of the experiment revealed many observations reported in field-grown plants (Fig. 6). Gaps that developed between the root and the soil were most likely due to root shrinkage (Fig. 6a), since the loamy sand soil has very small shrinkage. Root hairs (Fig. 6b) grew between the root and soil. Roots that grew against the glass face of the rhizotron were often clumped (Fig. 6c) and not distributed uniformly.

Although ANOVA showed that the shoot dry matter was similar for the different treatments (P=0.069, 2 df), shoot growth was closely correlated to water-use irrespective of the nutrient placement (Fig. 7). The effect of nutrient distribution was to alter the spatial distribution of roots (Fig. 5) and thereby influence the access to soil water. A uniform nutrient distribution throughout the rhizotron was the least effective approach for maximizing water uptake (Fig. 4). The N concentration in the shoots was not greatly affected by the distribution of N in the soil and there was no evidence that the shoot growth was limited by low N uptake (Table 2) or soil nutrient availability at the end for the experiment (Table 3).

Discussion

The most striking result is that soil profiles which are uniformly rich in nutrients were the least effective in promoting deep rooting and water uptake from depth (Fig. 7). While nutrient-rich conditions triggered root proliferation, as seen in the treatment with a nutrient-rich surface layer (Fig. 5), it was surprising that higher root growth was not seen at all layers in the treatment uniformly rich in nutrients. A possible explanation is that the greater root growth, as observed initially in the surface layers of this treatment, resulted in more intense soil

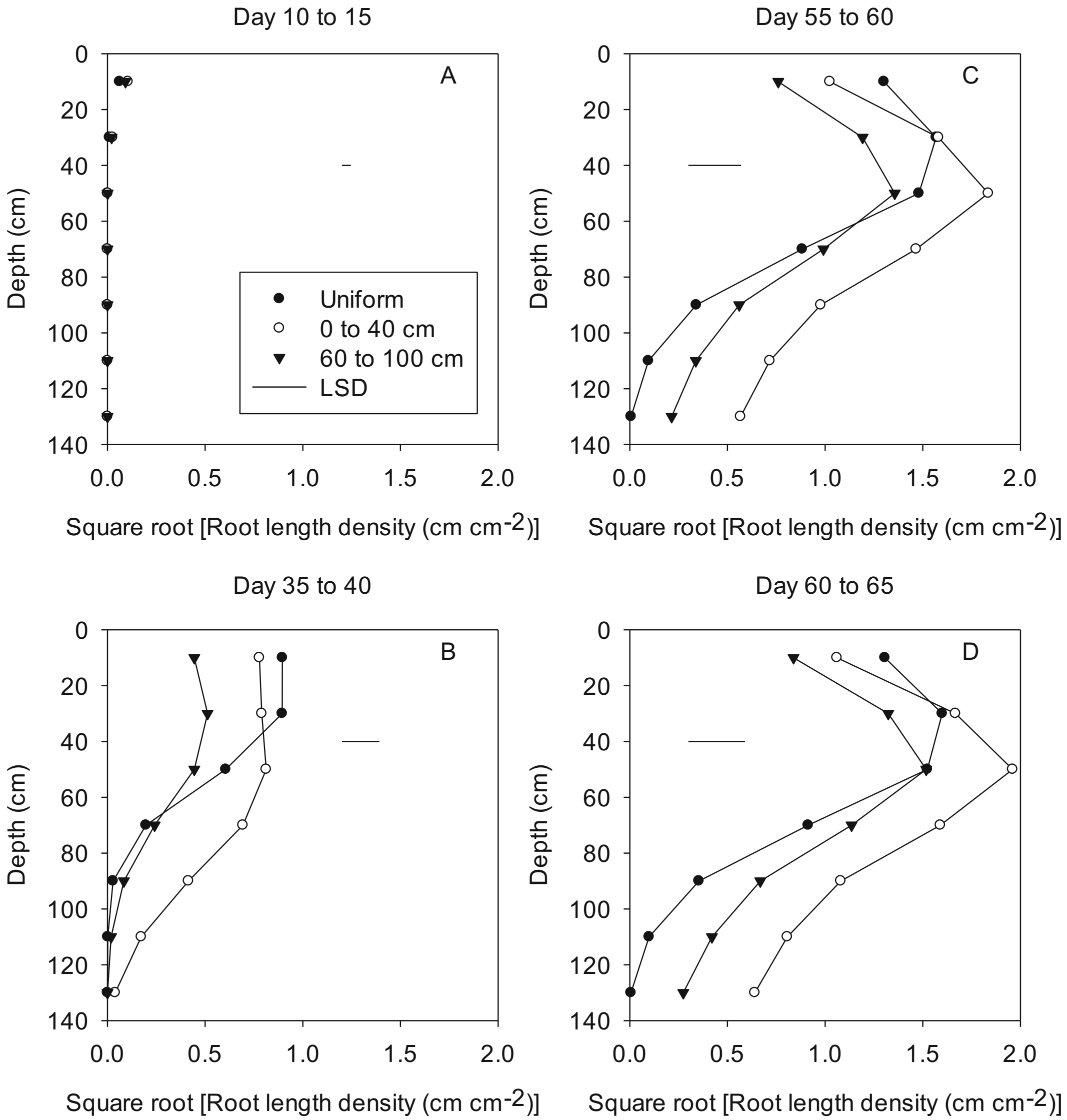

Fig. 5 Root profiles with depth at different growth stages. Values are mean of four replicates of the period of 5 days. The horizontal bars in each graph indicate the size of the least significant differences (LSD) to allow comparison of any two means from any depth combination (df 116). All statistical comparisons are made on the *square root scale*, chosen to stabilize the variance

drying and increased soil mechanical impedance (Fig. 3), such that the root elongation may have been inhibited by strong soil (Bengough et al. 2011; Jin et al. 2013).

Previously published work, which has been mainly restricted to the surface 10 cm shows that roots proliferate in nutrient-rich patches (Day et al. 2003; De Kroon and Mommer 2006; Kume et al. 2006; Jing et al. 2010; Croft et al. 2012), our data showed root growth at greater depths was not enhanced with a nutrient band placed between 60 and 100 cm (Fig. 5). Root growth and/or proliferation decreased with depth in the soil profile. A water-limited environment can suppress the branching in favour of deeper rooting (Chapman et al. 2011).

We allowed the soil to dry (Fig. 4) whereas in most other studies of heterogeneous nutrient distribution, soil water was maintained by hydroponics or specific culture (Robinson 1994; Trapeznikov et al. 2003). Drew (1975) grew barley (*Hordeum vulgare* cv. Proctor) in sand where horizontal stratification of nutrients was maintained by recirculating nutrient solution through a sand culture. Li et al. (2010) also grew white lupin (*L. albus* L. cv. Kiev) and He et al. (2003) grew rice (*Oryza sativa* L.)

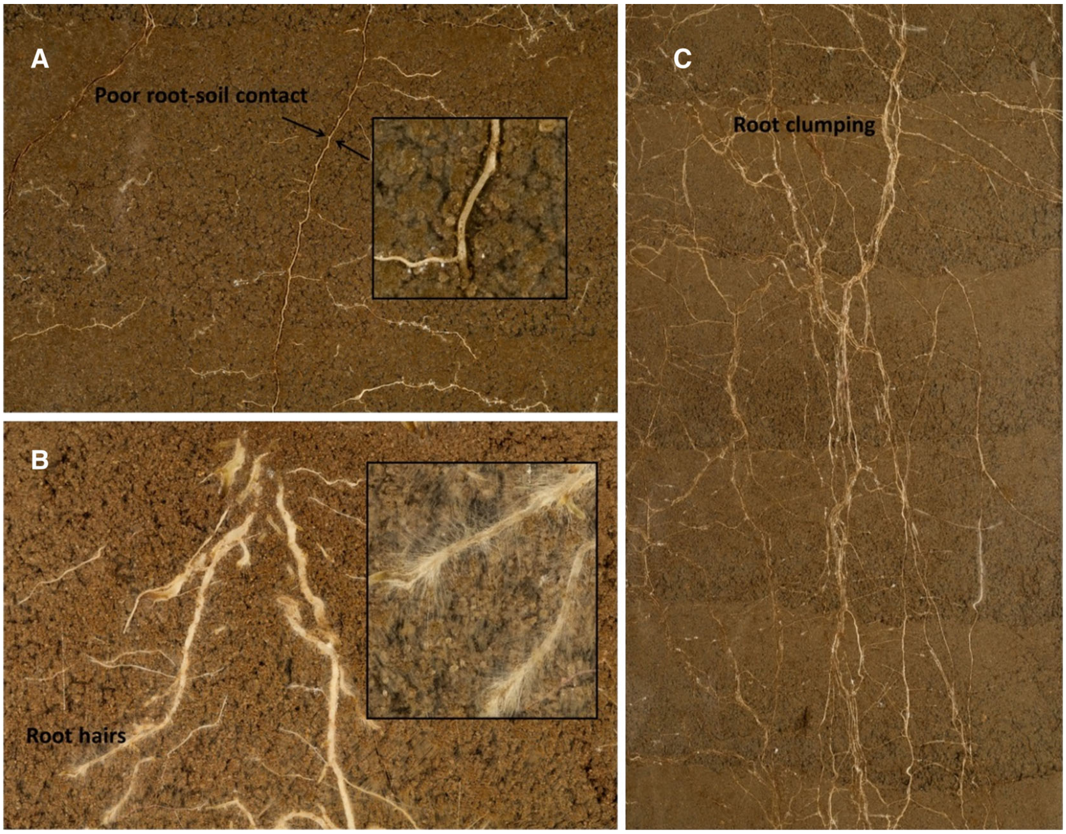

Fig. 6 Photographs of the roots at the end of the experiment. (**a**) Gaps between the root and the soil, (**b**) Root hairs grew between the root and soil, and (**c**) Roots were clumping against the rhizotron glass face

irrigated by capillary action through holes at the bottom of each pot during the period of the experiments. In our approach, horizontal nutrient stratification initially imposed in the rhizotrons were maintained by low soil conductivity to water; there was minimal water flow due to gravity, which was confirmed from measurements of the soil moisture meters by noting that the water content at a bottom of the rhizotron did not increase during the experiment.

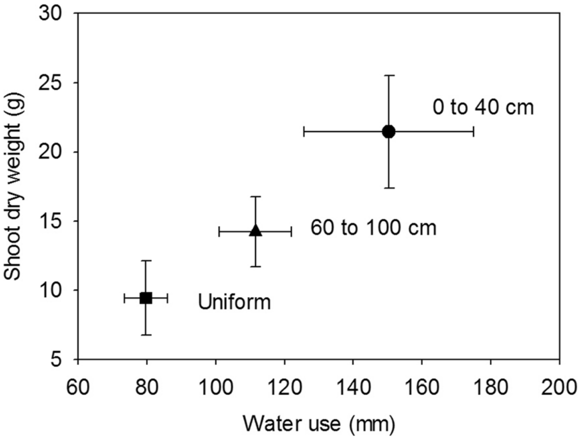

Fig. 7 The relationship between shoot dry biomass and water-use at the end of the experiment for different treatments. The standard errors are indicated

Even under terminal drought, water was available in the rhizotron at relatively high matric potentials (> −50 kPa) at depths greater than 80 cm (Fig. 4) and available for root uptake (Herkelrath et al. 1977; Dodd et al. 2010). At depth, root length density declined and roots were clumped in soil pores and channels with poor root-

Table 2 Nitrogen and carbon content of plant shoots. Values are mean ± SE of four replicates, different lower case letters denote significant difference (P<0.05) among treatments

	Total N and C of shoot samples		
	Uniform	0–40 cm	60–100 cm
N g kg^{-1}	34±2a	35±1a	36±2a
C g kg^{-1}	416±3a	422±3a	412±4a

Table 3 Soil available nitrogen (mg kg^{-1}) measured from different depths at the end of the experiment. Values are mean±SE of four replicates, different lower case letters denote significant difference ($P<0.05$) among treatments

	Treatments		
Soil depth (cm)	Uniform	0–40 cm	60–100 cm
20	22.0±2.5a	12.6±2.0b	11.0±1.3b
50	38.9±2.9a	18.4±3.7b	22.7±4.0b
80	45.9±3.6a	25.4±5.6b	36.9±5.4ab

soil contact (Fig. 6). Root clumping may have been encouraged by roots growing along the rhizotron glass face (Fig. 6c) rather than clumping within pre-existing pores as is the case in the field (White and Kirkegaard 2010). However, even in our rhizotron this is likely to result in less effective water uptake compared with a more uniform spatial distribution of roots. Apart from poor spatial distribution of roots, gaps between the soil and roots (Fig. 6a) may also have contributed to poor water uptake. In our experiment this was almost certainly due to root shrinkage, because the loamy sand soil we used had minimal ability to shrink.

The North China Plain has a typical monsoonal climate with 70–80 % of annual rainfall concentrated in the period from June to September (Hu et al. 2010a). Traditional farmer practice is to surface-apply N fertilizer before the heavy rainfall or flood irrigation (Fang et al. 2006). Thus, heavy rainfall and irrigation during the summer months in the North China Plain may cause great nitrate leaching in soil profile (Wang et al. 2010). Soil nitrate-N content in the top 90 cm of the soil profile should be maintained within the range of 154–159 kg N ha^{-1} for high yield wheat production (Cui et al. 2013) and to reduce the N losses to the environment (Cui et al. 2006). This tends to result in deep nutrient-rich soil layers. In our experiment a uniformly nutrient-rich soil profile (with greater total nutrient load) did not increase shoot growth ($P=0.069$) or plant nitrogen uptake (Table 2) relative to other treatments. These results are compatible with observations that traditional (excessive) N usage by Chinese farmers (Huimin, Shandong province, on average 369 kg N ha^{-1} to winter wheat ($n=370$)), does not significantly enhance grain yield (Cui et al. 2006, 2010; Peng et al. 2012; Zhang et al. 2012), however, there have been reported decreases in crop yield (Shen et al. 2013). These are likely to be due to the effect of nutrient placement on root growth (Fig. 5) and hence access to water (Fig. 7). Our study suggests that in regions which are likely to be water-limited (Li et al. 2005; Deng et al. 2006; Wang et al. 2008b; Fan et al. 2012), high rates of fertiliser application which over time result in deep nutrient-rich profiles, are likely to provide the least effective environment for water uptake by roots (Mi et al. 2010; Zhang et al. 2012).

Conclusions

In a laboratory simulation of a water-limited soil profile, using 1.4 m deep rhizotrons, root growth was greatly affected by the vertical distribution of nutrients. A treatment with a nutrient-rich surface layer with nutrient poor subsoil was the most effective at promoting deep rooting and water uptake. In a treatment with a deep nutrient-rich soil, to a depth of 1.4 m, deep rooting was restricted as was water uptake. Shoot biomass was simply related to water-use irrespective of the spatial distribution of nutrients. We found that at the end of the experiment when the plants were at terminal drought, there was water at depth which was not accessed by the roots. Our experiments were performed in water-limiting conditions with layered regions of nutrient-rich soil; our results differed from those reported for the conjunctive application of nutrient and water in localized patches, which tend to show that roots are more responsive to nutrient-rich patches in soil.

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