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Grain yield, dry matter accumulation and remobilization, and root respiration in winter wheat as affected by seeding rate and root pruning

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ABSTRACT

Field experiments conducted in 2007/08 and 2008/09 at the Changwu Agricultural Research Station on the Loess Plateau of China comprised three seeding rates (SR1: 225 seeds m^{-2}, SR2: 280 seeds m^{-2}, and SR3: 340 seeds m^{-2}) and two root pruning treatments (W: root pruning in the over-wintering period and S: root pruning at the spring-growth stage), with the un-pruned wheat plants as controls. In the severe drought toward the end of the growing season of 2008, grain yield decreased as the seeding rate increased, but under the more favorable conditions in 2009 the reverse was true. Averaged over the seeding rates, grain yield was significantly increased in both W and S in both years; grain yield and yield components were higher in W; and S recorded the highest water use efficiency. The interaction between seeding rate and root pruning was not statistically significant. Leaf area index (LAI) and tiller density were higher as seeding rates increased whereas in W and S, increased LAI and decreased tillers significantly, but had no effect on fertile tillers. The rate of leaf photosynthesis was lower and root respiration was significantly higher at higher seeding rates, whereas in root pruning treatments, significantly higher leaf photosynthetic rate and lower root respiration were observed. Soil water contents were lower as seeding rate increased. A significant decrease in water use before stem elongation was observed in W, while S consumed less soil water than W and the control over the whole growing season. Post-heading accumulation of dry matter and its remobilization from vegetative parts to the grain was significantly greater at higher seeding rates. Post-heading accumulations of dry matter and grain yield were also significantly greater in W and S than the un-pruned plants, although pruning reduced both dry matter remobilization and its contribution to grain yield. The possibility of reducing the proliferation of roots to increase yields at higher seeding rates and conserving the soil water at different growing stages in water-limited environments is discussed.

1. Introduction

As a major world crop, winter wheat has shown increased yields following advances in breeding and crop management. Seeding rate is known to influence grain yield, and research has clearly demonstrated higher seeding rate in wheat as one of the means of obtaining higher grain yield (Blue et al., 1990; Tompkins et al., 1991a,b; Pan et al., 1994; Sunderman, 1999; Bavec et al., 2002; Arduini et al., 2006; Hiltbrunner et al., 2007), but only up to an optimum seeding rate (Holt and Timmons, 1968; De Bruin and Pedersen, 2008). Seeding rates above the optimum result in lower grain yields because of higher competition between plants (Hiltbrunner et al., 2007). For example, Carr et al. (2003) and Wood et al. (2003) found that grain yield in wheat was higher with 250 than with 450 seeds m^{-2}. The optimal seeding rate is different for different climatic conditions, especially rainfall distribution, during the growing season (Blue et al., 1990; Tompkins et al., 1991a,b; Anderson et al., 2004; Del Cima et al., 2004; Arduini et al., 2006). Usually, seeding rates that lead to higher than optimal planting density lead to higher yields unless water is limited (Blue et al., 1990; Tompkins et al., 1991a,b; Lloveras et al., 2004). In grain crops, both current assimilation transferred directly to kernels and remobilization of assimilates stored in vegetative plant parts contribute to grain yield (Gebbing et al., 1999; Arduini et al., 2006) and may buffer the yield against unfavorable climatic conditions during grain filling (Tahir and Nakata, 2005). Tompkins et al. (1991a,b) and Arduini

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et al. (2006) showed that higher than optimal seeding rates led to greater accumulation of dry matter before anthesis, but whether these stored assimilates contribute to greater grain yield remains uncertain.

In the study region, winter wheat and spring maize, sown in September and April respectively, are the main crops on which farmers depend. Given the semi-arid climate of the study area in the Loess Plateau, where average annual precipitation ranges from 300 to 600 mm with over 60% of the annual rainfall occurring in July to September (Kang et al., 2003), water stress usually occurs at the grain-filling stage of winter wheat and frequently results in greater allocation of dry matter to roots allowing greater uptake of water (Davies and Zhang, 1991; Leport et al., 1998; Huang and Gao, 2000; Bryla et al., 2001). However, other reports show that smaller root systems use less water and are less competitive than bigger root systems (Zhang et al., 1999; Zhang and Zhang, 2000) and that breeding, by inadvertently selecting for smaller root systems (Siddique et al., 1990; Li and Chen, 2002; Li et al., 2003; Fan et al., 2008), appears to have lowered the competitive ability and raised the water-use efficiency (WUE) of wheat.

Wang et al. (2007) and Ma et al. (2008) showed that root pruning in winter wheat decreased water consumption during the vegetative stage and improved WUE by lowering competitive ability but had no marked effect on grain yield. This work was only conducted at one plant density and raises the question whether in a semi-arid environment root pruning to reduce the rooting density and water use in the vegetative stage will increase or maintain yields at higher planting densities.

Few studies have examined the effect of root pruning in wheat at different seeding rates in the field. The present study sought to investigate, under field conditions, the effect of different seeding rates and root pruning before and after the over-wintering stage on grain yield and its components in winter wheat. The accumulation of dry matter was recorded at heading and at maturity to assess the contribution of pre- and post-anthesis assimilates to grain yield at different seeding rates and with or without root pruning. The aim of the experiment was to determine whether root pruning increased or maintained yields of winter wheat at higher than optimal planting densities when grown in a semi-arid environment.

2. Materials and methods

2.1. Site description

Field experiments were conducted over two growing seasons – October 2007 to June 2008 and October 2008 to June 2009 – at the Chinese Academy of Sciences' Changwu Agricultural Research Station, which lies in a typical area of the semi-arid Loess Plateau in China's Shaanxi province (107°40′30″E, 35°14′30″N, 1200 m above the sea level). The mean annual temperature is 9.1 °C, the cumulative temperature above 10 °C is 3029 °C, and the average annual frost-free period is 171 d. The long-term (1957–2001) average annual precipitation is 584 mm, 68% of which occurs between June and September. The soil is mostly Heilu (Calcic Kastanozems, FAO) with a bulk density of 1.36 g cm^{-3}, a field capacity of 26% (determined gravimetrically), and a permanent wilting coefficient of 10%. Precipitation and maximum and minimum temperatures were measured manually, at the research station, 10 m from the site.

Rainfall and temperature during the two seasons are shown in Fig. 1. In both years, temperatures during the growing season were similar and close to the long-term mean, whereas rainfall was below the long-term mean (Fig. 1), with 204 mm in 2007/08 and 184 mm in 2008/09. In 2008, precipitation from March to May (42 mm) was only 37% of the long-term mean (120 mm), indicating a severe drought toward the end of the growing season. Although these 3 months were twice as wet (97 mm) in 2009 as in 2008, precipitation was still 19% less than the long-term mean.

2.2. Experimental design

The cultivar of winter wheat (*Triticum aestivum* L.) used in the experiment was 'Changwu 135', which is widely used by farmers in the region. Each plot measured 3 m × 3 m. Following a basal dose of nitrogen (120 kg ha^{-1}), phosphorus (60 kg ha^{-1}), and potassium (48 kg ha^{-1}), wheat was sown 5 cm deep in rows spaced 20 cm apart on 20 September in both years. The seeding rates were: SR1 (225 seeds m^{-2} the optimal seeding rate for the region); SR2, 280 seeds m^{-2}; and SR3, 340 seeds m^{-2}. Two root pruning treatments were: W (roots pruned on 15 November just at the beginning of over-wintering period) and S (root pruned on 15 March at the beginning of the spring-growth stage); un-pruned plants (CK) served as the control. Pruning involved trimming the secondary lateral roots back to about 3 cm from the plant up to a depth of 13 cm along the vertical axis with a sharp knife, the blade of which was 25 cm long and marked off in millimetres (e.g. as described by Ma et al., 2008). Each treatment was replicated three times in a randomized complete block design.

2.3. Methods

2.3.1. Plant sampling

To determine the extent of redistribution of assimilates during grain filling, plants were harvested at the heading stage (Zadoks et al., 1974, stage 59) and at physiological maturity (Zadoks stage 92). Plants from 1 m^2 area of each plot were cut manually at the ground level and separated into culms, spikes, and green and dead leaves at heading and into culms, leaves, chaff, and grain at maturity (only in 2009). Samples of all plant parts were dried to constant weight in a forced-draft oven at 75 °C. At both harvests, the total number of culms and spikes was recorded and the percentage of head-bearing culms calculated. At heading, 20 representative plants were sampled to measure the leaf area using a CI-203 area meter (CID Inc, Camas, Washington, USA). The following observations were recorded at maturity: grain yield, thousand-kernel-weight, the number of spikes, and grain yield per spike, and harvest index (HI) was calculated.

Post-heading dry matter (DM) was calculated as the difference between dry matter of aerial plant parts at physiological maturity and at heading. Dry matter remobilization during grain filling (DMR) was calculated, following the method of Cox et al. (1986) and Papakosta and Gagianas (1991), as:

$$\begin{aligned}\mathrm{DMR} &= (\text{DM of the aerial plant parts at heading}) \\ &\quad - (\text{DM of leaves} + \text{culms} + \text{chaff at maturity}).\end{aligned}$$

The contribution of pre-heading DM to grain (CDMRG) was calculated as:

$$\mathrm{CDMRG} = \frac{\mathrm{DMR}}{\text{DM of grain at maturity}} \times 100$$

2.3.2. Water use efficiency

A CPN 503 (InstroTek Inc., Raleigh, North Carolina, USA) neutron moisture meter was used to measure soil moisture content every 20 cm up to a depth of 200 cm. The moisture content of the upper 20 cm layer was measured gravimetrically. The neutron probe was calibrated against the soil moisture content in wet and dry profiles determined gravimetrically at the experimental site. Readings were taken after 64 s.

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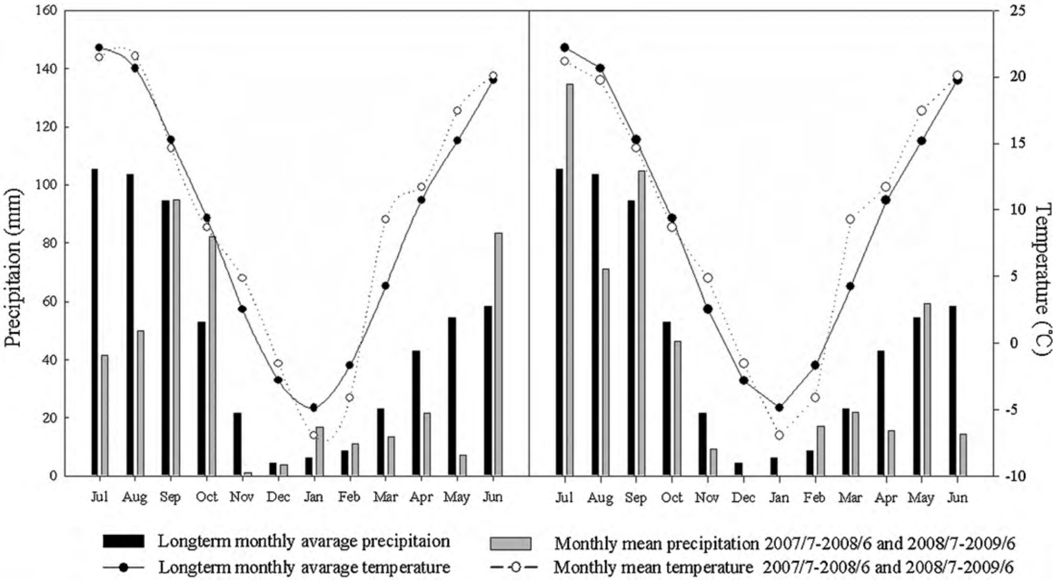

Fig. 1. Precipitation and temperature in 2007/08 (left) and 2008/09 (right) and the long-term means at the experimental site.

Runoff was prevented from the experimental plots and water loss due to deep drainage was assumed to be negligible. Actual crop evapo-transpiration (ET, mm) and water consumption between two soil moisture content measurements or over the whole growing season were estimated from by the equation:

$$ET_c = P + \Delta W$$

where ET_c is actual crop evapo-transpiration, ΔW is the change in soil water stored in the upper 200 cm of the soil between sowing and maturity, and P is the rainfall recorded at the site.

Water use efficiency for grain yield (WUE_{gr}) was calculated based on the following equation:

$$WUE_{gr}(\mathrm{g\ m^{-2}\ mm^{-1}}) = \frac{Y}{ET_c}$$

where Y is the grain yield per unit area.

2.3.3. *Rates of photosynthesis and root respiration*

Rates of photosynthesis and root respiration were measured at anthesis in 2008 and 2009. The instantaneous photosynthetic rate of the flag leaf was measured using a LI-6400 (LI-COR, Inc., Lincoln, Nebraska, USA) portable gas exchange system from 09:00 h to 11:00 h in 7–12 flag leaves in each plot. Root respiration was measured 1 day after measuring leaf photosynthesis. Shoots were cut at soil level before measuring root respiration and the total CO_2 efflux from the soil. Each plot was sampled at two points, and each sample comprised two measurements, one centered over the cut stems and the other taken at the mid-point between the rows, to represent total soil respiration. Respiration from bare soil was measured in three bare plots nearby. Root respiration was estimated by subtracting the bare-soil respiration from the total soil respiration. The soil CO_2 efflux was measured with a closed-chamber system (SRC-1 with EGM-4, PP-Systems, Hitchin, Herts, UK). The chamber was flushed with air prior to placing it on the soil and then inserted into the soil to a depth of 3 cm. Measurements commenced after approximately 5 s.

2.4. *Statistical analysis*

The data obtained were analyzed by standard two-way ANOVA using SPSS 11.0. Comparisons within the factors were performed by a multiple range test using the method of LSD at $P = 0.05$. Mean values are reported along with their standard errors.

3. Results

3.1. *Grain yield and its components*

Averaged over the root pruning treatments, in 2008 grain yield decreased linearly with increasing seeding rate by 8% and 15% in SR2 and SR3, respectively. However in 2009, the pattern was reversed with grain yield increasing by 7% and 16% in SR2 and SR3, respectively (Fig. 2). The number of grains per unit area significant decreased by increased seeding rate in 2008, whereas the reverse result was observed in 2009. Increasing the seeding rate increased spike density, but decreased other yield components except the number of grains per unit area, and had no effect in thousand-kernel-weight (TKW) in 2009 (Table 1). Harvest index was highest at the lowest seeding rate in both years and the difference was significant.

Averaged over the three seeding rates, grain yield of W was similar in that of S in 2008, but W was significantly greater than S in 2009. Pruning significantly increased grain yield compared to unpruned plants: 7.0% and 13.6% in 2008 and 2009 respectively in the case of W (winter pruning) and 7.6% and 10.9% in the case of S (spring pruning), averaged over the three seeding rates (Fig. 2). The increase came from all the yield components except grains per spike in 2008 and spike density in 2009 (Table 1). The highest values of harvest index and WUE were observed in S and were higher ($P < 0.05$) than those in the control (CK).

Correlation analysis, after combining the data for the 2 years, showed that grain yield was strongly correlated with grains m^{-2} ($r^2 = 0.97$, $P < 0.01$), spike number ($r^2 = 0.95$, $P < 0.01$) and with grain yield per spike ($r^2 = 0.88$, $P < 0.01$).

3.2. *Leaf area index and population structure*

In 2008 seeding rate had no significant effect on LAI. However in 2009, higher seeding rates led to higher LAI at heading, the values of which were lower ($P < 0.05$) in SR1 and SR2 than in SR3 (Table 2). The total number of tillers (fertile tillers: those with a head and infertile tillers: those without a head) per unit area increased linearly with seeding rate whereas the number of tillers per plant decreased (Table 2).

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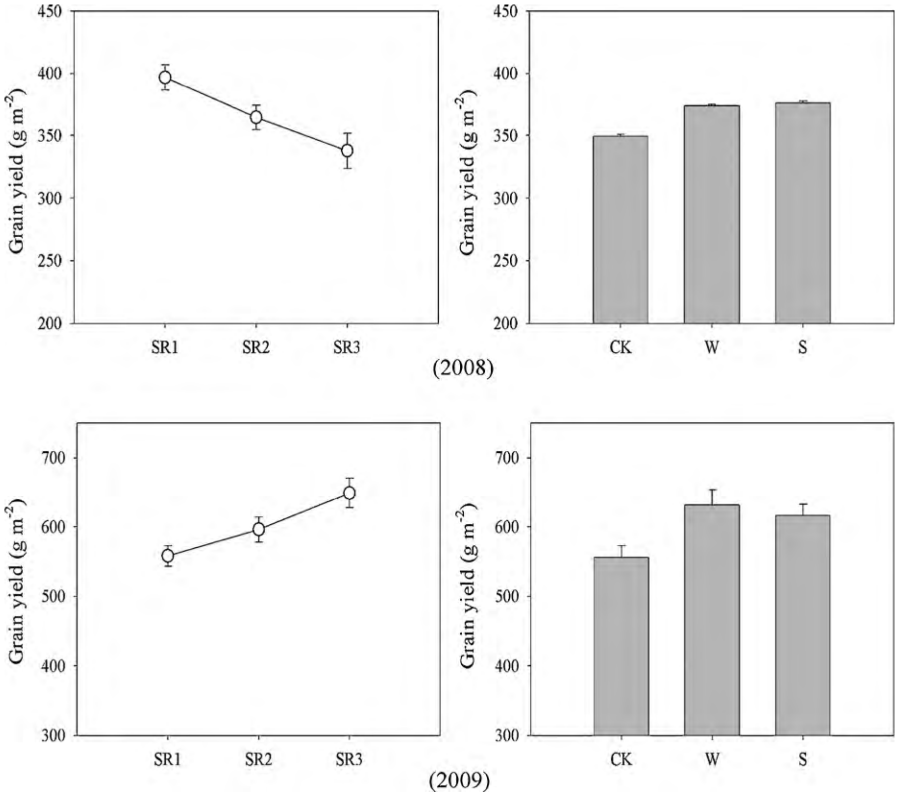

Fig. 2. Grain yield of winter wheat as affected by seeding rate (left) and root pruning (right). Bars represent ± S.E. ($n = 3$). SR1: 225 seeds m^{-2}, SR2: 280 seeds m^{-2}, SR3: 340 seeds m^{-2}, CK: un-pruned plant; W: roots pruned in the over-wintering period; S: roots pruned at spring-growth stage.

Averaged over the seeding rates, root pruning increased the values of LAI in both seasons (Table 2) and decreased tiller density and the number of tillers per plant ($P < 0.05$), but the two pruning treatments did not differ significantly from each other (Table 2). Root pruning decreased the total number of tillers (Table 2) but had little effect on the number of fertile tillers (spikes), indicating that root pruning had decreased the proportion of infertile tillers (Table 1), a decrease that, together with increased LAI, may have led to improved canopy structure.

3.3. *Rates of photosynthesis and root respiration*

At anthesis, higher seeding rates decreased the rate of flag leaf photosynthesis (Pn) and increased the rate of root respiration (Rr) but with significant differences between SR1 and SR3 in both years, leading to a significant decrease in the ratio of leaf photosynthesis to root respiration (Pn:Rr), a measure of root efficiency (Liu and Li, 2003) (Table 3).

In contrast, leaf photosynthetic rate increased and root respiration rate decreased in the root pruning treatments, leading to a

Table 1
Effects of seeding rate and root pruning on spike density, proportion of fertile tillers, grains per spike, grain yield per spike, thousand-kernel-weight, harvest index, and water use efficiency in two growing seasons of winter wheat.

Treatment	Spike density (No. m^{-2})	Spikes per tiller (%)	No. of grains (grains m^{-2})	Grain yield (grams per spike)	TKW (g)	HI	WUE (g m^{-2} mm^{-1})
2008							
Seeding rate (seeds m^{-2})							
225 (SR1)	405.8b	48.47a	8485.3a	0.75a	36.44a	0.30a	3.36a
280 (SR2)	403.6b	43.77b	7975.1b	0.74a	35.56a	0.25c	2.20b
340 (SR3)	423.9a	43.22b	7308.0c	0.61b	33.66b	0.27b	1.46c
Root pruning							
CK (control)	391.2b	40.18b	7452.4c	0.66b	34.21b	0.26b	2.27b
W (pruned in winter)	431.1a	47.92a	8561.6a	0.73a	35.99a	0.28ab	2.23b
S (pruned in spring)	411.1ab	47.39a	7815.0b	0.70ab	35.46ab	0.29a	2.51a
2009							
Seeding rate (seeds m^{-2})							
225 (SR1)	668.8c	65.78ab	13911.0c	1.00a	47.90a	0.41a	1.81b
280 (SR2)	757.6b	62.44b	14828.5b	0.98a	47.40a	0.37b	1.90b
340 (SR3)	874.0a	67.12a	17025.5a	0.92b	47.83a	0.34c	2.14a
Root pruning							
CK	771.2a	61.67b	15007.6c	0.90b	46.16b	0.35b	1.70b
W	767.7a	67.17a	15914.4a	1.01a	48.73a	0.37ab	2.06a
S	761.4a	66.88a	15585.9b	0.98a	48.25a	0.38a	2.09a

Within the two sets of treatments, seeding rate and root pruning, numbers followed by the same letter are not significantly different at $P < 0.05$. TKW, thousand-kernel-weight; HI, harvest index; WUE, water use efficiency.

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Table 2
Effects of seeding rate and root pruning on leaf area index, tiller density, and tillers per plant at heading in two growing seasons in winter wheat.

Treatment	LAI ($m^2\ m^{-2}$)	Tiller density (No. m^{-2})	No. of tillers per plant
2008			
Seeding rate (seeds m^{-2})			
225 (SR1)	3.80a	837.3c	3.72a
280 (SR2)	3.73a	922.2b	3.29b
340 (SR3)	3.95a	980.8a	2.89c
Root pruning			
CK (control)	3.27b	973.5a	3.56a
W (pruned in winter)	4.07a	899.7b	3.23b
S (pruned in spring)	3.90a	867.4b	3.11b
2009			
Seeding rate (seeds m^{-2})			
225 (SR1)	3.45b	1016.7c	4.52a
280 (SR2)	3.57b	1213.3b	4.33a
340 (SR3)	4.21a	1302.1a	3.83b
Root pruning			
CK	3.09b	1250.6a	4.46a
W	4.24a	1143.0b	4.11b
S	4.16a	1138.5b	4.11b

Within the two sets of treatments, seeding rate and root pruning, numbers followed by the same letter are not significantly different at $P < 0.05$. LAI, leaf area index; CK, un-pruned plants; W, roots pruned in the over-wintering period; S, roots pruned at the spring-growth stage.

higher Pn:Rr ratio, although the two root pruning treatments did not differ (Table 3). Root respiration measured at anthesis indicated that the substrate requirement and bioenergetics of root respiration did not differ appreciably between W and S.

3.4. Soil water content

At sowing, there were no significant differences in soil water storage among three seeding rate treatments (Fig. 3, left). At the stem elongation and maturity stage, soil water contents were always highest in SR1 in both years ($P < 0.05$). In 2008, the value of soil water content was significantly higher in SR2 than SR3, but not significant in 2009 (Fig. 3, left). Roots in the upper layers faced water shortage in both years at maturity, especially in 2008.

Root pruning in winter (W) primarily led to a significant decrease in water use prior to stem elongation stage in both seasons, but there were no differences between S and the control (Fig. 3, right). At maturity, soil water storage of W was lower or not different to that of the control ($P > 0.05$), while the greatest values were observed in S and were higher than CK and W ($P < 0.05$) in deep soil layers (100–200 cm) in 2008 and all soil layers in 2009 (Fig. 3, right). These findings clearly demonstrate that the root-pruning delayed the use of soil water at different growing stages. Wheat roots pruned in winter saved more water before the stem elongation stage, while roots pruned in spring used less soil water than winter pruned roots and the un-pruned controls.

Table 3
Effects of seeding rate and root pruning on the rate of photosynthesis in the flag leaf (Pn, per unit leaf area), the rate of respiration of roots (Rr, per unit land area), and the Pn:Rr ratio at anthesis in two growing seasons in winter wheat.

Treatment	Pn ($mg\ CO_2\ m^{-2}\ s^{-1}$)	Rr ($mg\ CO_2\ m^{-2}\ s^{-1}$)	Pn:Rr ratio
Mean values in 2008			
Seeding rate (seeds m^{-2})			
225 (SR1)	0.59a	0.21b	2.81a
280 (SR2)	0.56b	0.25a	2.24b
340 (SR3)	0.54b	0.25a	2.16b
Root pruning treatments			
CK (control)	0.53b	0.24a	2.21b
W (pruned in winter)	0.58a	0.23b	2.52a
S (pruned in spring)	0.58a	0.23b	2.52a
Mean values in 2009			
Seeding rate (seeds m^{-2})			
225 (SR1)	1.01a	0.18b	5.61a
280 (SR2)	0.98b	0.18b	5.44a
340 (SR3)	0.98b	0.19a	5.16b
Root pruning treatments			
CK	0.96b	0.20a	4.80b
W	1.01a	0.18b	5.61a
S	0.99a	0.18b	5.50a

Within the two sets of treatments, seeding rate and root pruning, numbers followed by the same letter are not significantly different at $P < 0.05$.

Table 4
Effects of seeding rate and root pruning on dry weight of culms, leaves, spikes, and aerial parts of winter wheat at heading and at physiological maturity in 2009.

Treatment	Dry weight ($g\ m^{-2}$)			
	Leaves	Culms	Spikes	Aerial part
Mean values at heading				
Seeding rate (seeds m^{-2})				
225 (SR1)	322.7c	525.6b	137.3c	985.5c
280 (SR2)	390.6b	598.5b	159.9b	1149.1b
340 (SR3)	427.8a	713.9a	181.3a	1341.0a
Root pruning				
CK (control)	365.0b	653.4a	169.0a	1188.4a
W (pruned in winter)	395.6a	610.4a	155.6b	1161.5a
S (pruned in spring)	480.6b	591.3b	153.9b	1125.8b
Mean values at maturity				
Seeding rate (seeds m^{-2})				
225 (SR1)	201.8c	353.7c	824.2c	1379.7c
280 (SR2)	233.4b	401.8b	977.0b	1612.2b
340 (SR3)	278.2a	458.9a	1189.6a	1926.7a
Root pruning				
CK	231.9b	424.5a	927.5b	1583.8b
W	252.3a	400.6a	1034.5a	1687.5a
S	229.2b	389.3b	1028.8a	1647.3a

Within the two sets of treatments, seeding rate and root pruning, numbers followed by the same letter are not significantly different at $P < 0.05$.

3.5. Accumulation and remobilization of dry matter

At heading as well as at maturity, the dry weight of the total above-ground plant parts increased with increasing seeding rate, with significant differences between SR1 and SR3 (Table 4). Post-heading dry matter accumulation and post-heading retranslocation increased significantly with seeding rate (Fig. 4). Post-heading dry matter accumulation and the percentage contribution of remobilized dry matter to grain yield did not differ significantly between the two lower seeding rates (Fig. 4).

In W and S, post-heading dry matter accumulation between heading and maturity was 33% greater, and remobilization of dry matter lower by approximately 30 g m^{-2}, than in CK (Fig. 4). Both the pruning treatments resulted in lower contributions of remobilized dry matter (CDMRG) to grain yield than that observed in CK ($P < 0.1$), but the difference was small (30.5% CDMRG in CK, 33.5% CDMRG in W and S) (Fig. 4). Post-heading dry matter accumulation was markedly greater in pruned plants than in un-pruned plants, but resulted in consistently lower remobilization to the grain.

One unexpected finding was the interaction between root pruning and seeding rate did not found statistically significant for any of the measured traits.

4. Discussion

A seeding rate of 225 seeds m^{-2} is considered optimal for wheat in the semi-arid region of the Loess Plateau where the study was conducted. This was clearly the case in 2008 with the growing season marked by a prolonged dry spell during grain filling. In 2009, however, when the grain filling occurred during more favorable weather, although total precipitation remained below average, higher seeding rates increased the yield. This higher yield indicates

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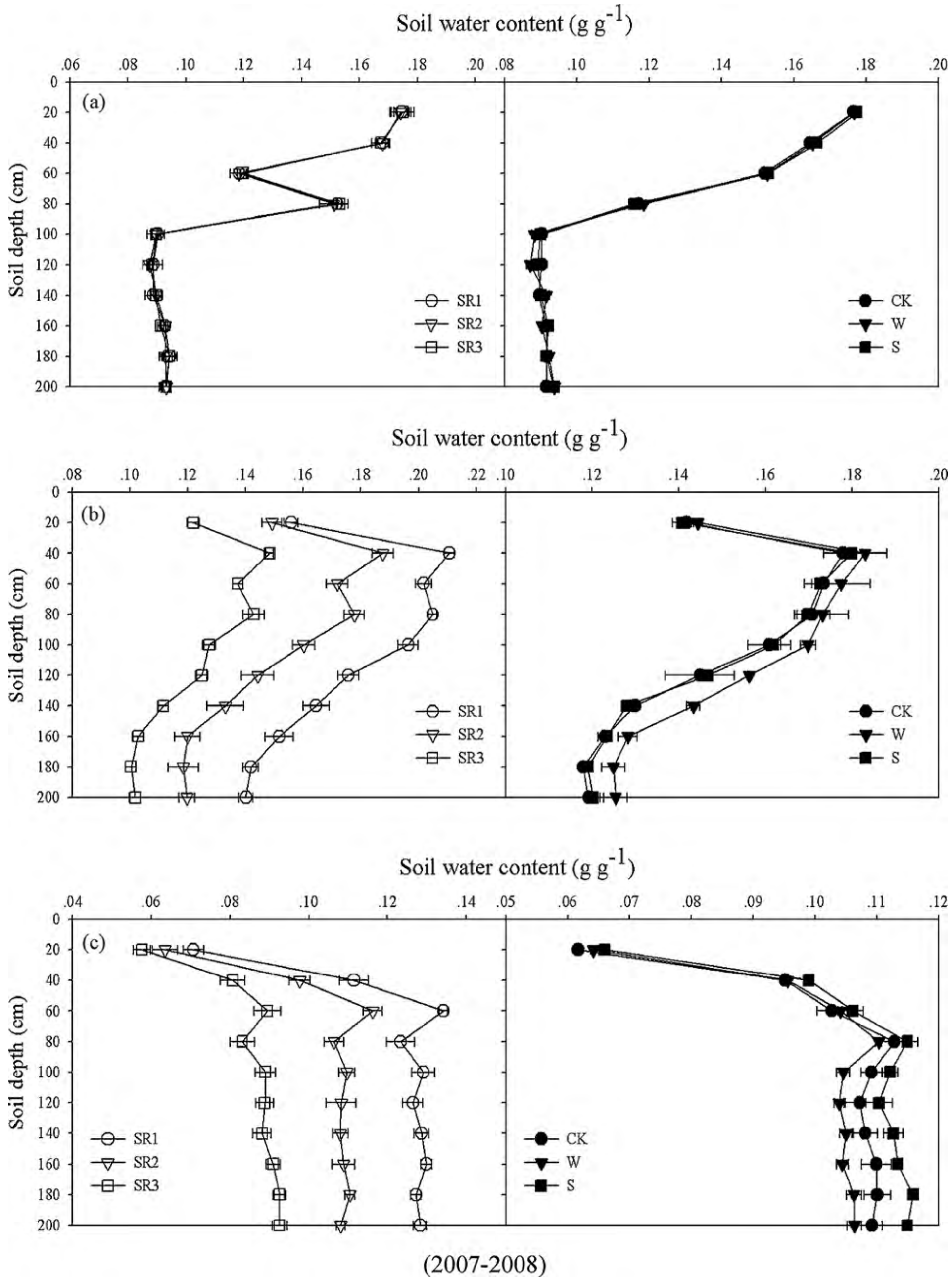

Fig. 3. Soil water content as affected by seeding rate (left) and root pruning (right). (a) Before sowing in 2007/08. (b) Stem elongation in 2007/08. (c) Maturity in 2007/08. (d) Before sowing in 2008/09. (e) Stem elongation in 2008/09. (f) Maturity in 2008/09. Horizontal bars represent ± S.E. ($n = 3$). SR1: 225 seeds m^{-2}, SR2: 280 seeds m^{-2}, SR3: 340 seeds m^{-2}, CK: un-pruned plant; W: roots pruned in the over-wintering period; S: roots pruned at the spring-growth stage.

that the optimal rate in average or above-average seasons is probably above 225 seeds m^{-2}. Similar results have been reported by several authors (Blue et al., 1990; Tompkins et al., 1991a,b; Hanson et al., 2008). In the drought year, the decrease in yield as a result of the higher seeding rate could be the result of greater competition for soil water (more soil water used before stem elongation by higher seeding rate) which in turn decreased dry matter production and thus yield (Kamel et al., 1983; Hiltbrunner et al., 2007). In both dry and wet years, total tiller density increased with the increase in seeding rate, but in 2008 the proportion of infertile tillers was lower than that in the wetter 2009, resulting in significantly higher spike density and LAI in 2009 at the highest seeding rate than that at the lowest seeding rate. The higher tiller density would have resulted in earlier canopy closure. Wall and Kanemasu (1990) reported that crop density was positively correlated with net productivity; they also found that early canopy closure at higher crop densities increased light interception efficiency and, as a result, crop productivity. Some researchers (Puckridge and Donald, 1967; Singer et al., 2007), however, reported the opposite results: they found that higher plant densities increased crop dry matter production up to a point, beyond which the absorption of radiation by the canopy, and thus crop productivity, were lowered.

Correlation analysis of grain yield and its components showed that the higher grain yield was primarily due to the greater number of grains per unit area, directly related to the higher number of spikes per unit area, and secondly due to the higher grain yield per spike, a similar result to Arduini et al. (2006). While spike number increased with the increase in seeding rate, grain yield per spike decreased. Tompkins et al. (1991a,b) and Hiltbrunner et al. (2007) reported that greater seeding rate increased grain yield because the

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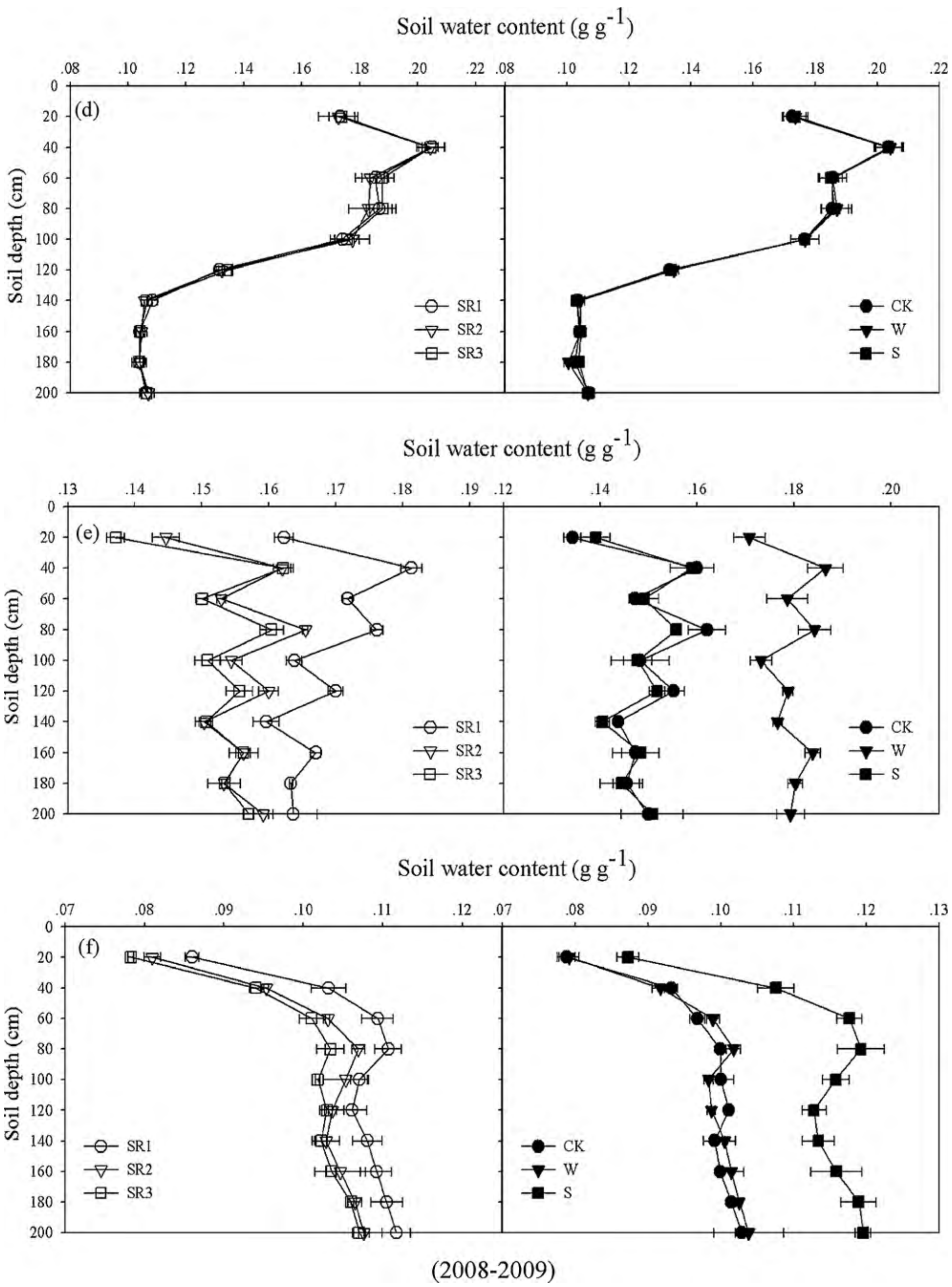

Fig. 3. (*Continued*).

increase in the number of spikes per unit area offset the decrease in the number of kernels per spike. Many studies have found a positive correlation between seeding rate and both grain yield and mean kernel weight (Blue et al., 1990; Geleta et al., 2002; Wood et al., 2003; Arduini et al., 2006), but our study suggests that this correlation depends on availability of moisture. In 2008, when rainfall during the growing season was well below average, kernel weight decreased significantly with increasing seeding density; in 2009, which was not as dry as 2008, seeding rate had no effect on kernel weight, an observation consistent with that made by Carr et al. (2003).

Similar to this study some other studies have shown that higher planting densities result in denser canopy and greater water consumption (Boogaard et al., 1996; Zhang et al., 2006; El-Hendawy et al., 2008), which, in turn, leads to water shortage in the upper soil layers (Zhang et al., 2006). In the present experiment, because of the late-season drought (low rainfall between March and May) roots in the upper layers faced water shortage and higher plant densities with greater root biomass production (Douglas et al., 2004), may have aggravated the effect of water stress, especially in the top soil layers. It is now well known that even if only part of the root zone is dry, levels of abscisic acid (ABA) in the xylem sap and in leaves increase (Stoll et al., 2000). Higher seeding rates consumed more soil water before the stem elongation stage, which led to less water available for use at anthesis. This lead to decreased stomatal conductance as well as decreased photosynthesis (also noted by Ramachandra Reddy et al., 2004). This association may explain why the rate of photosynthesis was lower and the rate of root respiration higher at higher plant densities. Besides, soil drying is often accompanied by nutrient deficiency (Crabtree et al., 1998), and although plants are known to compensate for the deficiency by increasing the quantity of root exudates (Davidson et al., 2000) that increase

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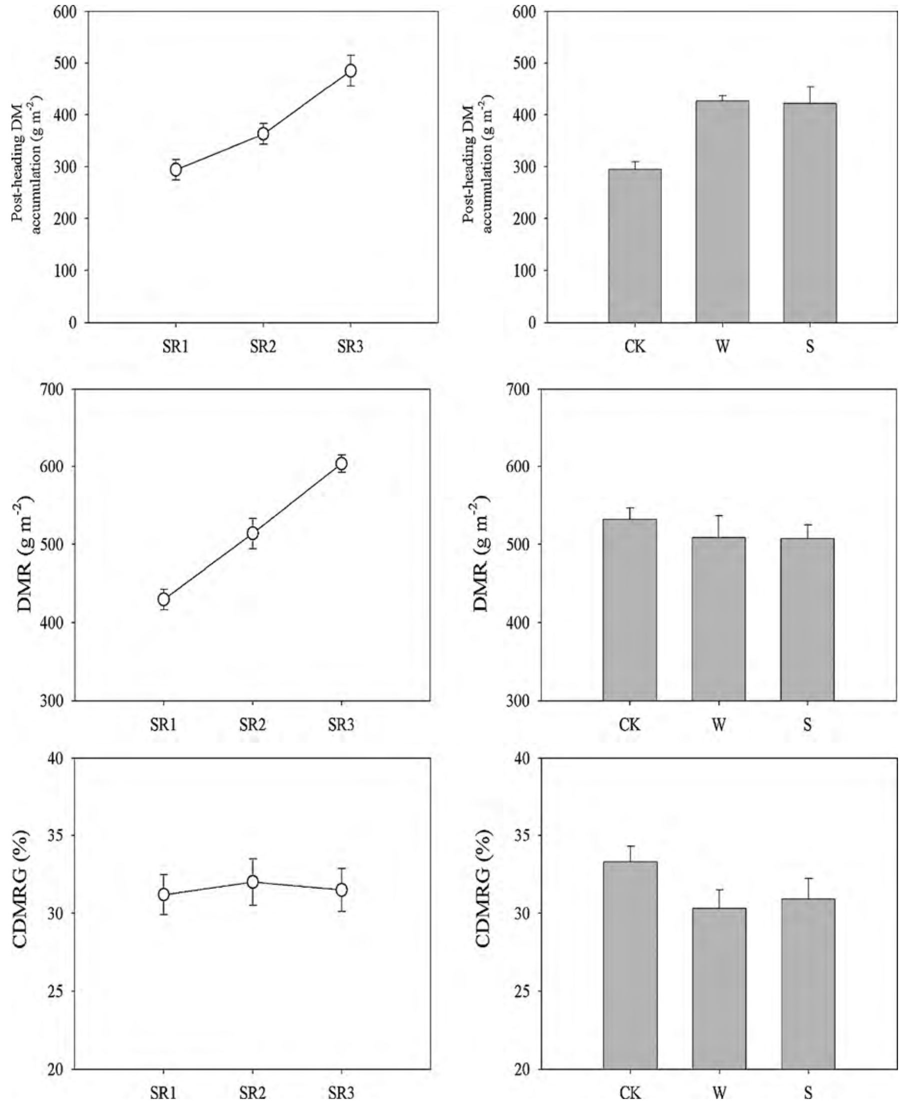

Fig. 4. Post-heading dry matter (DM) accumulation, dry matter remobilization (DMR), and the percentage contribution of dry matter remobilization to grain yield (CDMRG) in winter wheat as affected by seeding rate (left) and root pruning (right). Bars represent ± S.E. ($n = 3$). SR1: 225 seeds m^{-2}, SR2: 280 seeds m^{-2}, SR3: 340 seeds m^{-2}, CK: un-pruned plant; W: roots pruned in the over-wintering period; S: roots pruned at the spring-growth stage.

in turn, increases both energy consumption and the rate of root respiration.

Increasing the seeding rate also resulted in increased post-heading accumulation of dry matter and its remobilization from aerial parts to grain yield. Arduini et al. (2006) explained that higher seeding rates increased photosynthetic area, and therefore light interception by the canopy, an explanation supported by the present experiment. In addition, the dry weight of aerial parts at heading increases with the increase in seeding rate, and that increase is a potential source of remobilization (Tompkins et al., 1991a,b; Przulj and Momcilovic, 2001; Arduini et al., 2006), an observation that may also explain why remobilization was higher at the higher seeding rates.

Averaged over the seeding rates, the root pruning treatments led to marked differences in the values of most of the recorded characters. Both treatments increased all the yield components, with significant increases in grain yield when roots were pruned in winter (W), compared to that in un-pruned plants. This increased yield occurred despite the lower tiller density that almost certainly arose because the root pruning prevented the development of tillers associated with nodal roots that were removed during pruning (Klepper et al., 1984). However, root pruning increased the proportion of fertile tillers and spike density in 2008. The increased grain yield per spike, primarily from increased kernel weight, together with more grains per unit area, resulted in higher yields from wheat the roots of which had been pruned in winter. Ma et al. (2008, 2009) reported that root pruning reduced water consumption at the vegetative stage, making more soil water available to the plants after anthesis; In our study, root pruning in winter used less water before stem elongation stage, while root pruning in spring saved more water at the vegetative phase, therefore root pruning may have subjected the plants to less water stress during grain filling and improved post-heading accumulation of dry matter. In addition, the measured rates of photosynthesis and root respiration point to better water availability. The plants the roots of which had been pruned had significantly ($P < 0.05$) higher photosynthetic rates and lower root respiration rates at anthesis than those in which the roots were not pruned. A recent study showed that root pruning reduced root biomass in the upper soil layer (Ma et al., 2008), and as root respiration is a major consumer of photosynthetic carbon, the pruning conserved energy and increased the quantity of photosynthetic carbon available for growth.

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Root pruning also significantly increased LAI, lowered the number of tillers per plant and reduced tiller density, resulting in a plant population and canopy structure that was closer to the optimum. The number of tillers per plant is a function of competition for nitrogen or light (Masle, 1985; Paynter and Hills, 2009). Pruning the roots during the vegetative stage led to fewer tillers (Belford, 1981; Ma et al., 2008, 2009) and reduced uptake of soil water, and fewer tillers during the tiller elongation period meant less competition among tillers of the same plant (Ma et al., 2008). Berry et al. (2003) concluded from an experiment on winter wheat that infertile tillers negatively affect yield in most situations by competing for resources with fertile tillers, the effects being more severe in times of drought. Pruning the roots of winter wheat in winter meant not only that fewer nodal roots were damaged at that early stage but also offered a longer time for recovery for roots that were damaged. The result was higher tiller density and dry matter accumulation in the above-ground parts. In other words, treatment W had a smaller influence than treatment S did on the accumulation of above-ground biomass.

Wardlaw (1990) and Masoni et al. (2007) reported in cereals that the rate of photosynthesis after flowering was positively correlated with the quantity of carbon assimilates. Given that root respiration consumes a high proportion of photosynthates, any decrease in carbon consumption by the root system would potentially improve yields if the carbon is re-allocated to grains (Weiner, 1990). This logic may explain the greater accumulation of dry matter post-heading observed in the pruning treatments. Furthermore, water stress during grain filling shortens the grain-filling period but increases the remobilization of dry matter to grains (Gallagher et al., 1976; Kobata et al., 1992; Ercoli et al., 2008; Estrada-Campuzano et al., 2008).

The results indicate that root pruning reduced tiller density, increased photosynthesis at flowering and resulted in increased grain yield, and that these benefits arose from conservation of water in the vegetative phase for use during grain filling. These benefits were observed in both a season with a very low rainfall during grain filling and one with near average spring rainfall during grain filling, with the benefit being proportionally higher in the dry year. In this semi-arid region, we expected root pruning would provide greater benefit by conserving water and maintaining yields at high density than at low density, particularly in the dry year. However, statistically the interaction was not significant and our hypothesis that root pruning would be more beneficial at higher planting densities as a result of reduced water use in the vegetative phase thereby increasing or maintaining yields has not been proven.

5. Conclusions

The present study has shown that the yield response to seeding rate depends on rainfall, particularly the rainfall in spring that coincides with the grain-filling period. The conservative strategy adopted by farmers in the region is typical of subsistence farmers who are interested in maintaining yield stability in variable rainfall environments rather than maximizing yields in high rainfall years (Abbo et al., 2010). Root pruning in winter increased the accumulation of dry matter post-heading and resulted in higher grain yield, whereas root pruning in spring consumed less soil water, resulting in the highest WUE. Root pruning reduced the total number of tillers but not the number of spikes, conservation of water in the vegetative phase and greater availability of water at the grain-filling stage. Considering the possible economic benefits, this analysis suggests that higher seeding densities for winter wheat in average-rainfall years, particularly if combined with root pruning during the overwintering period, can ensure greater availability of water at the time of grain filling.

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