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Root pruning enhances wheat yield, harvest index and water-use efficiency in semiarid area



Research

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ARTICLE INFO

Water soluble carbohydrates

Keywords:

Seeding rate

Root pruning

Nitrogen rate

Soil water

ABSTRACT

Improved management practices are necessary to increase grain yield and water-use efficiency of rainfed winter wheat in semiarid environments. Yield and its components, evapotranspiration, and accumulation and apparent remobilisation of stem water soluble carbohydrates (WSC) were measured to understand the effects of root pruning and its interactions with seeding rate, water and nitrogen supply. Two factorial studies under straw mulching with continuous wheat were established in the Loess Plateau of China. Study 1 was repeated over four seasons and included six treatments from the combination of three root treatments, i.e. root pruning in winter before dormancy (RPw), root pruning at the re-green stage in spring (RPs) and untreated control (CK), and two seeding rates. Study 2 was repeated over three seasons and included twelve treatments from the combination of two root treatments from the combination of three pre-soving soil water levels. Yield ranged from 2571 to 7722 kg ha⁻¹, harvest index from 0.28 to 0.56, and water-use efficiency from 5 to 20 kg ha⁻¹ mm⁻¹. Root pruning improved grain yield, harvest index and water-use efficiency by 6–11% across environmental conditions. Grain yield increased more (i) by pruning roots in spring than in winter, (ii) in high plant density than in low plant density crops, and (iii) in low-yielding conditions. It is concluded that spring root pruning is a viable option to improve wheat yield and water use efficiency under straw mulching in semiarid environment.

1. Introduction

Globally, 69% of the cereal area is rainfed, including 40% of rice, 66% of wheat, 82% of maize and 86% of other coarse grains (Venkateswarlu and Shanker, 2012). In northern and north-western China, dryland agriculture accounts for more than 70% of total farmland, and 25 million hectares are located in the Loess Plateau (Bai et al., 2009). Water shortage and large variation in inter- and intra-annual precipitation are major constraints to agricultural production in this area (Guo et al., 2012; Zhang et al., 2012). Hence, there is the need to improve crop yield and water-use efficiency (WUE, yield per unit evapotranspiration). Root pruning is a potential tool for modulating crop growth, dry matter allocation, water use and yield. Root pruning has been used to control tree size and to improve yield on apples (Ferree and Knee, 1997; Khan et al., 1998), peaches (Richards and Rowe, 1977) and other fruit trees (Wajja-Musukwe et al., 2008; Du et al., 2012). Effects of root pruning on cereal yield vary. For example, Shi et al. (1999) have shown that root pruning in winter increased tiller fertility

and spike number, and raise the contribution of post-anthesis photosynthesis and carbohydrate mobilization to grain, thereby increasing wheat grain yield. Wang et al. (2004) reported that root pruning could increase rice grain yield under upland but not under paddy conditions. Xu et al. (2016) found that vertical root pruning decreased grains per ear, grain weight and grain yield of summer maize. Pot experiments showed that root pruning increased wheat spike weight and yield under drought, but not with a complete water supply (Wang et al., 2007). In the field, root pruning increased winter wheat yield, harvest index and water-use efficiency under conventional practice (Fang et al., 2010a, b; Ma et al., 2010), and to a certain extent under straw mulching (Hu et al., 2015). In addition, a positive interaction between root pruning and fertilizer rate has been reported for wheat grain yield (Li, 2002).

Effect of root pruning on wheat yield has been related to reduction of ineffective tillers, and increased grain number and grain weight (Shi et al., 1999; Li, 2002; Ma et al., 2010; Fang et al., 2010a, b; Hu et al., 2015). Root pruning can shift water use from earlier to later development, enhance leaf photosynthetic rate, promote accumulation of post-

https://doi.org/10.1016/j.fcr.2018.10.013



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Received 14 March 2018; Received in revised form 17 October 2018; Accepted 21 October 2018 0378-4290/ © 2018 Elsevier B.V. All rights reserved.

anthesis dry matter and mobilization to grain which are conducive to improved grain weight (Fang et al., 2010a, b; Ma et al., 2010). The impact of root pruning on accumulation and mobilization of labile assimilates is unclear. Additionally most studies of root pruning have been carried out under conventional practice. Straw mulching alters soil water and thermal conditions, which may in turn influence crop responses to root pruning.

In this study, winter wheat was grown under straw mulching to assess grain yield, and its components, evapotranspiration and WUE in response to (i) the interaction between timing of root pruning and seeding rate; (ii) the interaction between root pruning, pre-sowing soil water level and nitrogen rate. Additionally, we tested responses of the accumulation and remobilization of water soluble carbohydrates (WSC) to root pruning and its role in contributing yield formation.

2. Materials and methods

2.1. Soil and weather

We conducted two studies at Wangdong (35.14 °N, 107.41 °E, 1206 m above sea level), Shaanxi Province in the Loess Plateau. The soil is Heilu (Zhu et al., 1983) with a silt loam texture according to the USDA classification system. Soil organic matter content was 14.4 g kg⁻¹, total nitrogen was 1.0 g kg⁻¹, nitrate nitrogen was 12.9 mg kg⁻¹, ammonium nitrogen was 1.8 mg kg⁻¹, available phosphorus was 18.7 mg kg⁻¹, available potassium was 157 mg kg⁻¹, and bulk density was 1.21 g cm⁻³ at 0–20 cm depth before experiment establishment in 2012.

The average annual precipitation of the site is 578 mm with 55% falling between July and September (1957–2009), and the annual average temperature is 9.3 °C (Wu et al., 2012). The annual mean frost free period is 194 days and pan evaporation is 1552 mm. The water table is below 60 m and thus groundwater is unavailable for plant growth.

During the experimental period (2012–2016), precipitation was measured at weather station located about 1 km away from the experimental field. Total precipitation (Table 1) was below the long-term mean in the first and fourth seasons and higher in the second and third seasons. Drought was severe in the first season as shown by the aridity index of 0.17 during the crop cycle (Hu et al., 2018). Frost occurred in early April in 2013 and 2015 (beginning of jointing), and hail occurred during grain filling in 2015 (May 30, 2015).

2.2. Crops and experimental design

The experiment was conducted with continuous winter wheat, one crop per year. Crops were sown between late September and early October and harvested in late June to early July next year, with intervening 3.5 month fallow (Table 1). Crop phenology was monitored regularly using the Decimal Code (DC) of Zadoks et al. (1974); Table 1

presented dates of sowing, anthesis and harvest. Wheat straw was temporarily removed for sowing and incorporation of fertilizers with a rotary plough, and restored to 0.6 kg stubble m^{-2} with periodic additions of straw to maintain this amount during the experiment. Experiments were hand-sown with winter wheat Changhan 58, a commonly used semi-dwarf, high-tillering variety released in 2004. Weeds and diseases were managed as recommended locally. Briefly, phoxim was applied at seeding to control underground pests; glyphosate was used to control weeds in mid-November and mid-March, and triadimefon for control of wheat stripe rust before anthesis. In the second and third seasons, some tillers died; in the fourth season crops were sprayed with cyhalothrin (Hu et al., 2018) for protection against wireworms (Elateridae) at stem elongation (DC39).

2.2.1. Study 1

This study was conducted during four seasons from June 2012 to July 2016. Pre-sowing fertiliser included 150 kg N ha⁻¹ as urea and $75 \text{ kg P}_2\text{O}_5 \text{ ha}^{-1}$ as triple superphosphate in the first three seasons, and $120 \text{ kg N} \text{ ha}^{-1}$ and $75 \text{ kg P}_2\text{O}_5 \text{ ha}^{-1}$ in the last season. The study included six treatments resulting from the factorial combination of three root pruning treatments, i.e. root pruning in winter before dormancy (DC23) (RPw), root pruning at the re-green stage (DC29) in spring (RPs) and untreated control (CK), and two seeding rates: conventional seeding rate (CS) was 300–400 seeds m^{-2} , and is the recommended rate for conventional practice (Liang and Meng, 2007); high seeding rate (HS) was 375-480 seeds m⁻² and represents 125% of conventional. Roots were cut with a spade at a distance of 3 cm from the wheat rows down to 13 cm depth at one side of every row in the plot (Fig. 1), as in Hu et al. (2015). Treatments were arranged in a randomized block design with four replicates. Plot size was 20 m^2 (4 × 5 m) including 20 rows spaced at 0.25 m.

2.2.2. Study 2

This study was conducted during three seasons from July in 2013 to July in 2016. Table 1 shows sowing, anthesis and harvest dates. Crops were grown under conventional seeding rate (as in exp. 1), and were fertilised with 75 kg P_2O_5 ha⁻¹ as triple superphosphate in all seasons.

The study included twelve treatments resulting from the factorial combination of two root pruning treatments, i.e. root pruning in spring (RPs) as above and untreated control (CK), two nitrogen rates applied as urea, and three pre-sowing soil water levels. The nitrogen rates were 150 and 200 kg N ha⁻¹ in the first two seasons, and 120 and 180 kg N ha⁻¹ in the last season (90% at sowing and 10% applied via foliar spraying at anthesis). The lower nitrogen rate is that recommended locally. Three pre-sowing soil water levels were established 15 d before sowing: unirrigated control (low, W0), and plots irrigated with 67 mm (medium, W1) and 133 mm (high, W2). The irrigation mode was flooding with underground water. Treatments were arranged in a randomized block design with four replicates. Plot size was 15 m² (3 × 5 m) including 20 rows spaced at 25 cm.

Table 1

Wheat sowing date and days from sowing to anthesis and harvest. Average temperature during in-crop season (from wheat sowing to harvest). Precipitation during three periods: fallow (from wheat harvest at the end of June or early July to sowing in the late September or early October), in-crop season, and total (fallow + in-crop season) in studies 1 and 2.

Study	Season	Sowing date	Anthesis (DAS)	Harvest (DAS)	Average temperature (°C)	Precipitation (mm)		
					In-crop season	Fallow	In-crop season	Total
	1	2012/9/21	235	276	7.2	337	160	497
1	2	2013/9/29	233	279	7.3	392	252	644
	3	2014/10/2	227	277	8.1	345	277	622
	4	2015/9/25	231	281	7.1	217	223	440
	1	2013/9/30	233	278	7.3	392	252	644
2	2	2014/10/3	226	276	8.1	345	277	622
	3	2015/9/24	233	282	7.1	217	223	440



Fig. 1. A sketch of root pruning in wheat filed experiments.

2.3. Sampling and measurements

Table 2

Water content in the soil profile, down to 3 m at 0.2 m intervals, was measured gravimetrically at sowing and maturity (DC92) in a pooled sample of two soil cores per replicate.

At maturity, grain yield, aboveground biomass, ear number, grains per ear and grain weight were measured, and harvest index and grains number per unit area were calculated. The estimation of both yield and shoot biomass were based on a sample of 5 m^2 per plot, ear population was based on 0.5 m^2 , and grains per ear were counted on ten ears per plot. Harvest index was calculated as grain yield divided by shoot biomass.

Stem samples (0.2 m^2) , excluding leaf sheath, were taken at anthesis

(DC65) and maturity to determine water soluble carbohydrates by the anthrone method (Yemm and Willis, 1954).

2.4. Calculations and statistical analyses

Crop evapotranspiration (ET) was estimated as precipitation plus change in water storage between sowing and harvest (Zhang et al., 2013, 2014). The experimental area is flat, hence the assumption of negligible runoff. For the precipitation and soil under study, infiltration is mostly limited to the top 2 m; as we measured soil moisture to 3 m, deep percolation was considered negligible. Water-use efficiency was calculated as grain yield divided by ET.

Stem water soluble carbohydrates content, apparent translocation (amount and ratio) were calculated as follows (Edreira et al., 2014):

Stem WSC content (kg ha⁻¹) = stem WSC concentration (%) × stem biomass (kg ha⁻¹) / 100;

Stem WSC translocation amount (kg ha^{-1}) = stem WSC content at anthesis – stem WSC content at maturity;

Stem WSC translocation ratio (%) = (stem WSC translocation amount / stem WSC content at anthesis) \times 100. This calculation overestimates translocation, as respiration is assumed to be negligible, hence the term "apparent".

Repeated measures ANOVA (general linear model) was used to evaluate the effects of treatments on crop traits. When F-values were significant, multiple comparisons of means were performed using the least significant difference method (LSD) at 0.05 probability. Traits were compared in scatter plots of root pruning treatments vs controls, and linear regressions were fitted to quantify departures from y = xrepresenting no difference between treatments; reduced major axis method was used to account for error in both *x* and *y* (Ludbrook, 2012). All statistical analysis was performed through SPSS 18.0 software.

Wheat yield, yield components, evapotranspiration (ET) and water-use efficiency (WUE) in a factorial study combining root pruning treatments (control (CK) and root pruning in winter (RPw) and spring (RPs)), and seeding rates (high (HS) and conventional (CS)). *P* values are from ANOVA testing effect of season (S), seeding rate (SR), winter root pruning (RPw), spring root pruning (RPs) and their interactions.

Season	Seeding rate	Root pruning	Grain yield (kg ha ⁻¹)	Biomass (kg ha ⁻¹)	HI	Grain No. (m ⁻²)	Grain weight (mg)	ET (mm)	WUE (kg ha ^{-1} mm ^{-1})
2012-13	HS	CK	2748 a	7710 a	0.36 b	8213 a	45.6 a	556	4.95
		RPw	3076 a	7087 a	0.43 a	8532 a	44.6 a	/	/
	CS	CK	3393 a	7875 a	0.43 a	9483 a	45.9 a	515	7.27
		RPw	2571 b	6349 b	0.41 b	6652 b	46.0 a	/	/
2013-14	HS	CK	6157 a	16700 a	0.37 a	19854 a	35.7 a	500 a	12.33 a
		RPw	6215 a	16139 a	0.39 a	20042 a	35.8 a	509 a	12.22 a
	CS	CK	6060 a	17145 a	0.35 b	20980 a	34.4 a	500 a	12.14 a
		RPw	6233 a	16226 a	0.38 a	20471 a	35.6 a	522 a	12.09 a
2014-15	HS	CK	3207 b	10539 b	0.30 a	14561 b	40.6 a	433 a	6.93 b
		RPw	4123 a	12688 a	0.32 a	16298 a	39.5 a	/	/
		RPs	4411 a	13962 a	0.32 a	16138 a	40.2 a	409 a	11.71 a
	CS	CK	3023 c	10090 c	0.30 a	13713 c	40.6 a	422 a	7.16 b
		RPw	4028 b	12166 b	0.33 a	15567 b	38.8 a	/	/
		RPs	4633 a	14281 a	0.32 a	16176 a	38.8 a	398 a	12.05 a
2015-16	HS	CK	6467 a	12744 a	0.51 a	15543 a	50.8 a	468 a	13.90 ab
		RPw	5244 b	10661 b	0.49 a	13738 b	49.5 a	388 b	13.66 b
		RPs	6773 a	13204 a	0.51 a	16353 a	51.9 a	451 ab	15.64 a
	CS	CK	6414 a	12769 a	0.50 a	15934 a	50.9 ab	457 a	14.08 a
		RPw	5844 b	11446 b	0.51 a	14007 b	49.3 b	409 b	14.36 a
		RPs	6200 ab	12309 a	0.50 a	15173 ab	51.5 a	444 ab	13.96 a
P value		S	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
		SR	0.737	0.603	0.346	0.752	0.391	0.519	0.208
		RPw	0.782	0.084	0.010	0.416	0.129	0.106	0.950
		RPs	< 0.001	< 0.001	0.185	0.001	0.824	0.032	< 0.001
		$S \times SR$	0.951	0.766	0.166	0.691	0.460	0.729	0.018
		$S \times RPw$	< 0.001	< 0.001	0.198	0.067	0.134	0.031	0.892
		$S \times RPs$	< 0.001	< 0.001	0.364	< 0.001	0.135	0.713	< 0.001
		$SR \times RPw$	0.554	0.707	0.267	0.297	0.743	0.425	0.743
		$SR \times RPs$	0.829	0.907	0.890	0.490	0.381	0.908	0.163
		$S \times SR \times RPw$	0.004	0.530	0.001	0.413	0.703	0.775	0.761
		$S \times SR \times RPs$	0.017	0.038	0.878	0.011	0.660	0.956	0.075

The different letters represent significant difference between root pruning treatments at the same seeding rate each year (P < 0.05).

3. Results

3.1. Grain yield, its components and harvest index

3.1.1. Study 1

Table 2 shows yield, its components and ANOVA. Yield varied from 2571 kg ha⁻¹ for winter pruning at conventional seeding rate in 2012-13 to 6773 kg ha^{-1} for spring pruning at high seeding rate in 2015-16. ANOVA indicated that grain yield was significantly affected by season, spring root pruning, interactions between season and winter or spring pruning, and season × seeding rate × winter or spring pruning interactions. For example, spring pruning markedly increased grain yield compared with controls in the third season but not in the fourth season. and winter pruning increased yield in the third season, but reduced yield in the first and fourth seasons, with no difference in the second season. Spring pruning increased grain yield compared with CK at both seeding rates in low-yielding conditions (2014-15), but the increment was higher at conventional than at high seeding rate. Winter pruning significantly reduced grain yield at conventional but not at high seeding rate in low-yielding conditions, but consistently reduced grain yield in high-yielding conditions. Harvest index varied from 0.30 for CK at high and conventional seeding rate in 2014-15 to 0.51 for spring pruning and CK at high seeding rate, and for winter pruning at conventional seeding rate in 2015-16. Three sources of variation affected harvest index: season, winter pruning, and season × seeding rate × winter pruning interaction. Grain yield was more closely related to biomass (r = 0.76, P < 0.0001) than to harvest index (r = 0.53, P = 0.01), and correlated with grain number (r = 0.75, P < 0.0001) but not with grain weight (P = 0.62).

At high seeding rate, spring pruning showed higher grain yield, biomass and grain number in the third season compared with controls, but had no effect in the fourth season (Table 2). Winter pruning had no effect on grain yield, biomass and yield components in the first two seasons. However, winter pruning increased grain yield, biomass and grain number compared with controls in the third season. In contrast, winter pruning reduced grain yield, biomass and grain number in the last season. Winter and spring pruning showed no effect on HI except for winter pruning in the first season. Both winter and spring pruning had no effect on grain weight compared with controls in all seasons.

At conventional seeding rate, winter and spring root pruning increased grain yield, biomass and grain number compared with CK in the third season, with larger effects for spring pruning. In the last season, spring pruning had no effect on grain yield, biomass or yield components compared with CK. However, winter pruning reduced grain yield, biomass and grain number in the first and last seasons compared with CK, with no difference in the second season. Winter pruning reduced HI in the first season but increased it in the second season compared with CK; both winter pruning and spring pruning did not affect HI in the third and fourth seasons.

3.1.2. Study 2

Yield and its components are shown in Table 3, and Table 4 shows ANOVA. Yield varied from 2984 kg ha⁻¹ for unpruned controls with low N rate and medium pre-sowing soil water in season 2014-15 to 7722 kg ha⁻¹ for root pruning with low N rate and high pre-sowing soil water in season 2015-16. ANOVA indicated season, nitrogen rate and root pruning significantly affected grain yield, with multiple interactions. For example, root pruning produced higher grain yield than CK in the first two seasons but not in the third season. Root pruning increased grain yield compared with CK at both nitrogen rates and the increment was higher at high than at low N rate, but yield under root pruning was similar at both low and high N rates. Season and pre-sowing soil water and root pruning also interacted improving grain yield in low-yielding conditions, and low or medium pre-sowing soil water levels but not in high pre-sowing soil water level. Harvest index varied from 0.28 for CK with high N rate and low pre-sowing soil water level in 2014-15 to 0.56 for root pruning with high N rate and low and medium pre-sowing soil water levels in 2015-16. It was affected by season, root pruning, water supply, and multiple interactions (Table 4). For example, root pruning increased HI in the first two seasons but not in the third season. The interaction between pre-sowing soil water and nitrogen rate affected HI; for example, high N rate reduced HI compared with low N rate with low pre-sowing soil water but with medium and high pre-sowing soil water. Grain yield was more closely related to harvest index (r = 0.86, P < 0.0001) than biomass (r = 0.52, P = 0.001) and correlated more strongly with grain number (r = 0.87, P < 0.0001) than with grain weight (r = 0.53, P = 0.001).

Root pruning increased grain yield, HI, grain number and grain weight in the first two seasons, but had no effect in the last season (Table 3). In the first season, root pruning significantly increased grain yield and grain number compared with CK at high N rate under low and medium pre-sowing soil water levels, and at low N rate under high presowing soil water level. Higher HI was also detected in root pruning than in CK in most cases except at high N rate under low pre-sowing soil water level. In the second season, root pruning increased grain yield and grain number at both nitrogen rates in low and medium pre-sowing soil water levels. Root pruning also increased HI compared with CK in most cases except at low N under high pre-sowing soil water level.

3.1.3. Pooled data

Owing to the complex interactions involved, individual season or study did not show consistent patterns for the effect of root pruning on yield. Plotting yield of crops with pruned roots against untreated controls showed larger yield gain when yield of controls decreased from 7.5 to 2.7 t ha⁻¹ (Fig. 2a). The increase in harvest index with root pruning ranged from 0.04 to negligible when the harvest index of controls increased from 0.28 to 0.55 (Fig. 2b). Across sources of variation, root pruning increased grain yield by 7% and HI by 6% compared with controls.

3.2. Evapotranspiration and water-use efficiency

3.2.1. Study 1

Evapotranspiration was largely unaffected by the experimental sources of variation, except for seasonal conditions, spring root pruning, and season × winter root pruning interaction (Table 2). Changes in yield with treatments therefore drove changes in WUE. Following the responses of yield, spring root pruning increased WUE more than winter pruning. Where spring root pruning increased yield it also improved water-use efficiency; for example WUE increased from 6.9 kg ha⁻¹ mm⁻¹ in controls to 11.7 kg ha⁻¹ mm⁻¹ in spring-pruned crops at high seeding rate in 2014-15 (Table 2). Across sources of variation, spring root pruning reduced evapotranspiration by 4% and increased WUE by 27% relative to controls; winter root pruning reduced evapotranspiration by 5% and showed similar WUE relative to controls.

The effect of root pruning interactions for yield were also reflected in interactions for WUE. For example, spring root pruning improved WUE compared with controls in the third but not in the fourth season, and winter root pruning showed similar WUE relative to controls in the second and fourth seasons. Seeding rate and season presented interactive effects on WUE; for example, in the very dry season 2012-13, high seeding rate showed distinctly lower WUE than conventional seeding rate, but no difference in the other three seasons.

3.2.2. Study 2

Evapotranspiration ranged from 441 mm in 2014-15 to 529 mm in 2013-14 (P < 0.0001). Evapotranspiration increased and water-use efficiency decreased with increasing pre-sowing soil water contents (Table 3). Nitrogen rate did not affect evapotranspiration, hence nitrogen effects on water-use efficiency were mediated by changes in yield as discussed above. Generally, root pruning reduced

Table 3

Yield, yield components, evapotranspiration (ET) and water-use efficiency (WUE) of wheat crops in a factorial study combining three pre-sowing soil water levels: low W0, medium W1 and high W2; two nitrogen rates: low LN and high HN, and two root pruning treatments: root pruning in spring RPs and control CK, during three seasons in study 2.

Season	Pre-sowing soil water level	Nitrogen rate	Root pruning	Grain yield (kg ha ⁻¹)	Biomass (kg ha ⁻¹)	HI	Grain No. (m ⁻²)	Grain weight (mg)	ET (mm)	WUE (kg ha ⁻¹ mm ⁻¹)
2013-14	WO	LN	СК	5977 a	17350 a	0.34 b	20392 a	35.9 a	502 a	11.90 b
			RPs	6282 a	16370 a	0.38 a	22041 a	36.1 a	450 b	13.98 a
		HN	CK	5682 b	15827 b	0.36 a	20105 b	32.4 a	496 a	11.60 b
			RPs	6686 a	18182 a	0.37 a	22111 a	35.2 a	437 a	15.44 a
	W1	LN	СК	6300 a	16506 a	0.38 b	21617 a	35.0 a	547 a	11.61 a
			RPs	6597 a	15972 a	0.41 a	21941 a	38.8 a	542 a	12.60 a
		HN	CK	5939 b	14732 a	0.40 b	19944 b	35.7 a	518 a	11.51 a
			RPs	6497 a	15207 a	0.43 a	21368 a	37.9 a	524 a	12.59 a
	W2	LN	CK	5674 b	15733 a	0.36 b	20312 b	33.9 a	583 a	9.74 b
			RPs	6373 a	15621 a	0.41 a	22989 a	37.5 a	577 a	11.05 a
		HN	CK	6131 a	16002 a	0.38 b	21908 a	36.8 a	589 a	10.43 a
			RPs	6471 a	15673 a	0.41 a	22613 a	37.3 a	585 a	11.07 a
2014-15	W0	LN	CK	4633 b	14066 a	0.33 b	15573 b	39.3 a	377 a	12.38 b
			RPs	5115 a	13218 a	0.39 a	17128 a	42.5 a	343 a	14.90 a
		HN	CK	3035 b	10764 b	0.28 b	13342 b	40.3 a	391 a	7.77 b
			RPs	4266 a	12177 a	0.35 a	14907 a	42.3 a	381 a	11.25 a
	W1	LN	CK	2984 b	10257 a	0.29 b	12851 b	37.2 a	489 a	6.14 b
			RPs	3590 a	10851 a	0.33 a	14505 a	38.6 a	454 a	7.93 a
		HN	CK	3559 b	11661 b	0.31 b	14612 b	40.7 a	454 a	7.87 b
			RPs	4906 a	13975 a	0.35 a	16594 a	41.2 a	440 a	11.27 a
	W2	LN	CK	4503 a	13477 a	0.33 a	15953 a	38.1 a	479 a	9.47 a
			RPs	4203 a	12835 a	0.33 a	14831 a	40.7 a	489 a	8.60 a
		HN	CK	3359 a	11196 a	0.30 b	13941 a	38.4 a	506 a	6.64 a
			RPs	3512 a	11020 a	0.32 a	14268 a	39.4 a	491 a	7.16 a
2015-16	W0	LN	CK	7343 a	13595 a	0.54 a	20244 a	50.2 a	409 a	18.06 b
			RPs	7352 a	13318 a	0.55 a	20260 a	50.5 a	375 a	19.96 a
		HN	CK	6984 a	12636 a	0.55 a	19662 a	49.2 b	415 a	16.82 a
			RPs	6834 a	12161 a	0.56 a	19025 a	50.9 a	429 a	15.95 a
	W1	LN	CK	7059 a	12909 a	0.55 a	19580 a	50.9 a	440 a	16.10 a
			RPs	7157 a	13093 a	0.55 a	19828 a	50.5 a	421 a	17.09 a
		HN	CK	6740 a	12525 a	0.54 a	19002 a	49.7 a	439 a	15.38 b
			RPs	7051 a	12648 a	0.56 a	19216 a	50.9 a	420 a	16.81 a
	W2	LN	CK	7528 a	14521 a	0.52 a	21420 a	50.1 a	511 a	14.73 a
			RPs	7722 a	14273 a	0.54 a	21465 a	52.1 a	492 a	15.71 a
		HN	CK	6967 a	13375 a	0.52 a	19281 a	50.5 a	522 a	13.43 a
			RPs	7360 a	13408 a	0.55 a	20125 a	51.8 a	499 a	14.81 a

Note: different letters represent significant difference between CK and RPs at a given nitrogen rate (P < 0.05).

evapotranspiration (Table 4), which was mainly related to a reduction of 50 mm in non-irrigated, low-fertilised crops in 2013-14 (Table 3). The effects of root pruning and its interactions on WUE were largely mediated by their effects on yield. For example, pre-sowing soil water and root pruning interacted, whereby root pruning significantly improved WUE at low but not at medium and high pre-sowing soil water levels. Overall, root pruning reduced evapotranspiration by 4% and increased WUE by 13% compared with controls.

3.2.3. Pooled data

Plotting water-use efficiency of crops with pruned roots against controls showed spring pruning increased WUE from 1.13 to 1.78 kg ha^{-1} mm⁻¹ and winter pruning changed WUE from 0.43 to -0.75 kg ha^{-1} mm⁻¹ when the water-use efficiency of controls reduced from 18.1 to 4.95 kg ha^{-1} mm⁻¹ (Fig. 2c). Across sources of variation, root pruning increased WUE by 11% compared with controls.

Table 4

P-values from ANOVA testing effect of season (S), pre-sowing soil water level (W), nitrogen rate (N), root pruning treatment (RP) and their interactions on wheat grain yield, shoot biomass, harvest index (HI), yield components, evapotranspiration (ET), and water-use efficiency (WUE, yield per unit ET) in study 2.

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Item	Yield	Biomass	ні	Grain No.	Grain weight	ET	WUE
S	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W	0.089	0.001	0.002	0.078	0.932	< 0.001	< 0.001
Ν	< 0.001	0.001	0.902	0.014	0.720	0.686	< 0.001
RP	< 0.001	0.317	< 0.001	0.001	0.001	0.019	< 0.001
S imes W	< 0.001	< 0.001	< 0.001	0.331	0.014	0.029	< 0.001
$S \times N$	0.008	0.294	< 0.001	0.339	0.322	0.402	< 0.001
$S \times RP$	0.007	0.246	0.001	0.080	0.460	0.965	0.052
$W \times N$	< 0.001	0.004	0.001	0.126	0.395	0.170	< 0.001
$W \times RP$	0.103	0.147	0.251	0.698	0.938	0.515	0.005
$N \times RP$	0.010	0.004	1.000	0.745	0.707	0.604	0.315
$S\times W\times N$	< 0.001	< 0.001	< 0.001	0.003	0.155	0.777	< 0.001
$S \times W \times RP$	0.002	0.081	< 0.001	0.183	0.693	0.355	< 0.001
$S \times N \times RP$	0.123	0.058	0.020	0.802	0.564	0.911	0.029
$W \times N \times RP$	0.423	0.122	0.271	0.884	0.480	0.679	0.699
$S \times W \times N \times RP$	0.363	0.172	0.486	0.527	0.761	0.862	0.024



Fig. 2. Comparison of grain yield (a), harvest index (b) and water-use efficiency (c) of rootpruned and control wheat crops. Closed symbols are root pruning in winter, and open symbols are root pruning in spring. Red symbols indicate the published data in Hu et al. (2015). Data from studies 1 and 2 including seeding rates, pre-sowing soil water levels and nitrogen rates. Solid lines and equations are Model II regression accounting for error in both x and y. Red line is RPs vs CK, blue line is RPw vs CK and black line is RPs, RPw vs CK. Significance of regressions is indicated as *, ** for P < 0.05 and P < 0.01, respectively. Asterisks next to parameters indicate intercept is different from zero and slope different from 1 based on 95% confidence intervals (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).



Tables 5 and 6 present stem WSC traits and corresponding statistics. In both studies, spring root pruning had a highly significant effect on stem WSC content at maturity, and apparent translocation of stem WSC in absolute and relative terms. In both studies, seasonal conditions modulated the effect of root pruning on stem WSC traits, as reflected in significant interactions (Tables 5 and 6). In study 1, the interaction between seeding rate and winter pruning affected stem WSC at maturity and translocation ratio, and seeding rate \times spring pruning interaction only affected stem WSC translocation ratio. In study 2, the interaction between root pruning and initial water content affected all four stem

Table 5

Water soluble carbohydrates (W	WSC) content in wheat ste	m at anthesis and maturity	, and apparent translocation	(amount and ratio)) in studies 1 and 2.
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Study	Season	Treatment		WSC at ar (kg ha ⁻¹)	nthesis		WSC at (kg ha⁻	maturity -1)		WSC trans amount (l	slocation $(1000 \text{ g} \text{ ha}^{-1})$		WSC trar	slocation rati	o (%)
				СК	RPw	RPs	СК	RPw	RPs	СК	RPw	RPs	СК	RPw	RPs
1	2012-13	HS		236 a	171 b	244 a	154 a	92 b	92 b	81 b	79 b	153 a	34 c	46 b	62 a
		CS		282 a	162 b	253 a	112 a	113 a	103 a	170 a	49 b	150 a	58 a	30 b	59 a
	2013-14	HS		893 a	864 a	899 a	265 a	186 b	188 b	628 a	678 a	711 a	70 b	78 a	79 a
		CS		935 a	1026 a	871 a	226 a	234 a	179 b	709 a	792 a	692 a	76 a	77 a	77 a
	2014-15	HS		1348 a	1313 a	1444 a	515 a	441 c	480 b	833 b	872 ab	964 a	62 b	66 a	67 a
		CS		1393 ab	1353 b	1472 a	525 a	455 b	406 c	868 b	898 b	1066 a	62 c	66 b	72 a
	2015-16	HS		1562 ab	1405 b	1706 a	114 b	150 a	107 b	1448 ab	1256 b	1600 a	93 a	89 b	94 a
		CS		1615 b	1592 b	1790 a	126 b	155 a	133 b	1488 b	1437 b	1657 a	92 a	90 Ъ	93 a
2	2013-14	W0	LN	642 a	/	596 a	250 a	/	197 b	392 a	/	399 a	61 a	/	62 a
			HN	621 a	/	683 a	285 a	/	210 b	336 b	/	473 a	52 b	/	69 a
		W1	LN	688 a	/	674 a	235 a	/	185 a	453 a	/	490 a	67 a	/	72 a
			HN	560 b	/	790 a	231 a	/	246 a	329 b	/	544 a	58 b	/	69 a
		W2	LN	689 a	/	721 a	298 a	/	229 b	391 b	/	492 a	57 b	/	68 a
			HN	733 a	/	820 a	254 a	/	270 a	479 a	/	549 a	65 a	/	66 a
	2014-15	W0	LN	1321 a	/	1374 a	623 a	/	417 b	698 b	/	957 a	53 b	/	69 a
			HN	1397 a	/	1298 a	716 a	/	461 b	682 b	/	837 a	49 b	/	64 a
		W1	LN	1297 b	/	1731 a	673 a	/	695 a	624 b	/	1036 a	48 b	/	60 a
			HN	1512 b	/	1665 a	695 a	/	592 b	818 b	/	1073 a	54 b	/	64 a
		W2	LN	1352 a	/	1473 a	567 a	/	631 a	784 a	/	841 a	57 a	/	57 a
			HN	1823 b	/	2053 a	841 a	/	883 a	981 a	/	1170 a	54 a	/	57 a
	2015-16	W0	LN	1234 a	/	1356 a	97 a	/	89 b	1137 a	/	1266 a	92 a	/	93 a
			HN	1260 a	/	1264 a	99 a	/	98 a	1161 a	/	1166 a	92 a	/	92 a
		W1	LN	1606 a	/	1519 a	127 a	/	110 b	1479 a	/	1408 a	92 a	/	93 a
			HN	1219 b	/	1575 a	123 a	/	99 b	1096 b	/	1476 a	90 b	/	94 a
		W2	LN	1496 b	/	1778 a	101 a	/	113 a	1395 b	/	1666 a	93 a	/	94 a
			HN	1439 a	/	1417 a	111 a	/	96 a	1329 a	/	1321 a	92 a	/	93 a

Note: different letters represent significant (P < 0.05) difference between treatments at same seeding rate each year in study 1 and significant difference between treatments at same nitrogen rate and pre-sowing soil water level each year in study 2.

WSC traits. To interpret the complex responses of stem WSC, we aggregated the data from both studies in one-to-one comparisons between crops with pruned roots and controls (Fig. 3a–d). At anthesis, stem WSC content increased under spring pruning, but did not change under winter pruning (Fig. 3a). At maturity, stem WSC content dropped from 27 to 71 kg ha⁻¹ under spring pruning, and from -1 to 133 kg ha⁻¹ under winter pruning when the stem WSC content of controls increased from 97 to 841 kg ha⁻¹ (Fig. 3b). Consequently, stem WSC translocation

Table 6

P-values from ANOVA testing effect of season (S), seeding rate (SR), winter root pruning (RPw), spring root pruning (RPs) in study 1 and season (S), pre-sowing soil water level (W), nitrogen rate (N), root pruning treatment (RP) in study 2, and their interactions on wheat stem water soluble carbohydrates (WSC) content at anthesis and maturity, and apparent translocation (amount and ratio).

Study	Item	WSC content at anthesis	WSC content at maturity	WSC translocation amount	WSC translocation ratio
1	S	< 0.001	< 0.001	< 0.001	< 0.001
	SR	0.010	0.587	0.011	0.361
	RPw	0.041	< 0.001	0.344	0.751
	RPs	0.086	< 0.001	0.006	0.001
	$S \times SR$	0.348	0.002	0.553	0.718
	$S \times RPw$	0.153	< 0.001	0.023	0.010
	$S \times RPs$	0.078	< 0.001	0.148	0.015
	$SR \times RPw$	0.262	< 0.001	0.789	< 0.001
	$SR \times RPs$	0.681	0.519	0.642	0.032
	$S \times SR \times RPw$	0.276	< 0.001	0.195	< 0.001
	$S \times SR \times RPs$	0.850	< 0.001	0.551	0.004
2	S	< 0.001	< 0.001	< 0.001	< 0.001
	W	< 0.001	< 0.001	< 0.001	0.591
	N	0.056	< 0.001	0.743	0.336
	RP	< 0.001	< 0.001	< 0.001	< 0.001
	S imes W	0.007	< 0.001	0.065	0.050
	S imes N	< 0.001	< 0.001	< 0.001	0.800
	$S \times RP$	0.193	< 0.001	0.022	0.002
	$W \times N$	0.001	< 0.001	0.086	0.531
	$W \times RP$	0.001	< 0.001	0.026	0.012
	$N \times RP$	0.726	0.329	0.467	0.331
	$S\times W\times N$	< 0.001	< 0.001	0.002	0.029
	$S \times W \times RP$	0.282	< 0.001	0.480	0.084
	$S \times N \times RP$	0.061	0.001	0.369	0.605
	$W \times N \times RP$	0.040	0.318	0.010	0.214
	$S \times W \times N \times RP$	0.001	0.073	0.001	0.052



Fig. 3. Comparison of water soluble carbohydrates (WSC) in wheat stem between root-pruned and control wheat crops. Open symbols are root pruning in spring, and closed symbols are root pruning in winter. Stem WSC content at anthesis (a) and maturity (b), apparent translocation amount (c) and ratio (d). Solid line and equation are Model II regression accounting for error in both *x* and *y*. Red line is RPs vs CK, blue line is RPw vs CK, and black line is RPs, RPw vs CK. Correlation between wheat grain yield, WSC apparent translocation amount (e) and ratio (f) of wheat crops. Open circles are controls, closed triangles are root pruning in winter, and open triangles are root pruning in spring. Data from studies 1 and 2 including seeding rates, pre-sowing soil water levels and nitrogen rates. Significance of regression equation are indicated as *, ** for P < 0.05 and P < 0.01, respectively. Asterisks next to parameters indicate intercept is different from zero and slope different from 1 based on 95% confidence intervals (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

amount changed from 81 to 179 kg ha⁻¹ under spring pruning, and from 5 to -52 kg ha⁻¹ under winter pruning when the stem WSC translocation amount of controls increased from 81 to 1488 kg ha⁻¹ (Fig. 3c). The stem WSC translocation ratio increased from 1 to 14% under spring pruning, and had little change under winter pruning when the stem WSC translocation ratio of controls was reduced from 93 to 34% (Fig. 3d). Generally, crops with spring root pruning increased stem WSC content at anthesis by 8% and decreased stem WSC content at maturity by 13%, hence the increase in apparent translocation amount (16%) and ratio (9%) compared to controls. Yield correlated with apparent stem WSC translocation (Fig. 3e–f). Across sources of variation, spring root pruning increased stem WSC apparent translocation that could

account for 29% of grain yield increase.

4. Discussion

4.1. Responses of wheat grain yield and harvest index to root pruning under mulching: comparisons with conventional practice, and interactions with seeding rate and nitrogen

Under straw mulching in this study, root pruning improved grain yield and harvest index as previously reported under conventional practice (Yu et al., 1985; Li, 2002; Fang et al., 2010a, b; Ma et al., 2010). This can possible be ascribed to (i) reduction of ineffective tillers

and associated water use (Richards, 1988; Motzo et al., 2004; Duggan et al., 2005a); (ii) putative increase of root biomass and water uptake in deeper soil layers (Fang et al., 2010b); (iii) increase grain number (Tables 2 and 3), and (iv) more translocation of WSC (Fig. 3c, Table 5).

Under straw mulching, crops that were root pruned in spring outyielded crops pruned in winter (Fig.2a, Table 2). In contrast, winter and spring root pruning returned similar yield under conventional practice (Yu et al., 1985; Ma et al., 2008b; Fang et al., 2010a). This discrepancy might be related to soil water and thermal conditions under straw mulching as compared with conventional practice. Under straw mulching, more favourable soil water and thermal conditions before winter freeze could promote shoot and root growth relative to conventional practice. This enhancement in wheat growth might favour regrowth in spring. Further, spring pruning might further limit development of small tillers at low temperature in early spring (Hu et al., 2018) and favour bigger tillers and population structure improving grain yield as observed under conventional practice (Li, 2002; Ma et al., 2008b; Fang et al., 2010a).

Under straw mulching spring root pruning improved grain yield at both recommended and higher seeding rates, but with larger effects at high seeding rate across four seasons (Table 2, Hu et al., 2015). This is in agreement with results under conventional practice (Fang et al., 2010a, b). Similar to trials under conventional practice (Li, 2002), spring root pruning improved grain yield at both nitrogen rates (Table 3). However, in our study high nitrogen rate reduced grain yield compared with recommended nitrogen rate in the control treatments (Tables 3 and 4). This reduction mainly resulted from the extreme season in 2014-15, which was wet and hail happened after anthesis. The high nitrogen rate led to bigger biomass at anthesis (data not shown), but severe lodging after the hail event might have impacted accumulation dry matter after anthesis, as reflected in the lower harvest index (Table 3).

Root pruning improved grain yield with a general reduction in seasonal evapotranspiration, hence the increase in water-use efficiency as found under conventional practice (Ma et al., 2008a, 2010; Fang et al., 2010a). The reduction in seasonal evapotranspiration was mainly related to restricted water use before anthesis (Fang et al., 2010a, b; Ma et al., 2010) since soil water content was similar at sowing and harvest between treatments (Fig. s1 and Fig. s2). Thus, root pruning might have changed the partitioning of crop transpiration before and after anthesis, and this might have contributed to improved yield and harvest index (Passioura, 1977; Sadras and Connor, 1991; Fereres and Soriano, 2007).

4.2. Responses of wheat grain yield to root pruning: interactions with water availability and the role of carbohydrate reserves

The effects of root pruning on yield were (i) larger under lowvielding conditions, (ii) mediated by harvest index, (iii) related to grain number, and to a lesser extent with individual grain weight, and (iv) associated with apparent translocation of labile carbohydrates. More grains per unit area relate to (i) crop growth rate in the critical period from DC31 to 10 days after flowering, and (ii) partitioning to reproduction, whereas (iii) heavier grain relates to potential grain size defined by carpel size, and grain filling (Sadras and Slafer, 2012). Our findings highlight the importance of allocation of crop resources in response to root pruning, and are consistent with the role of reserves for grain yield under stress (Bidinger et al., 1977; Blum, 1998; Yang et al., 2000). Previous studies have shown that root pruning reduced ineffective tillers (Shi et al., 1999; Fang et al., 2010a; Hu et al., 2015), and its imposed stress causes lower photosynthetic activity (Fang et al., 2010b), which might have contributed to increased WSC content at anthesis (van Herwaarden et al., 2003; Dreccer et al., 2009, 2012), and thereby a greater potential translocation of WSC to developing grain (Duggan et al., 2005b). In addition, source-sink ratio modulates translocation of labile carbohydrates (Sadras et al., 1993). In our study, root pruning improved grain number, i.e., increased sink demand, which may have stimulated more translocation of stem WSC to grains. Further study is needed to clarify the mechanism of storage and mobilisation of labile carbohydrates in response to root pruning.

Root pruning can increase wheat yield and WUE under the prevailing conditions of our trials. Machinery to implement this practice at the field scale is presently lacking for wheat (Lü et al., 2009), but has been developed and implemented for more profitable horticultural trees (Richards and Rowe, 1977).

5. Conclusion

Spring root pruning improved wheat grain yield, harvest index and water-use efficiency under various environmental conditions. Its effectiveness was more obvious in low-yielding conditions, especially in combination with high seeding rate or dry summer fallow. Apparent translocation of stem water soluble carbohydrates partially mediated the effect of spring root pruning on grain yield. The implementation of root pruning at farm scale requires new machinery.

Acknowledgements

This study was financially supported by Natural Science Foundation of China (No. 31170411, 31672243) and Special-Funds of Scientific Research Programs of State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau (A314021403-C4). We also thank the Changwu Agro-ecological Experimental Station on the Loess Plateau, Chinese Academy of Sciences, for providing the climate data and other supports during experimental period.

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