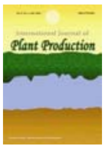

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Remobilization of water soluble carbohydrates in non-leaf organs and contribution to grain yield in winter wheat under reduced irrigation

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Abstract

The remobilization of water soluble carbohydrates (WSC) has an important role for grain yield. This study investigated the accumulation and remobilization of WSC in non-leaf organs (chaff, upper stem, and lower stem) and their contribution to grain yield, under different irrigation levels (rainfed, reduced irrigation, and full irrigation) and seeding rate treatments (450, 600 and 750 plants m^{-2}) using two winter wheat cultivars, Shijiazhuang 8 (SJZ-8) and Lumai 21 (LM-21), in two field experiments. Results showed that decreasing irrigation and increasing seeding rates increased WSC accumulation and remobilization, remobilization efficiency, and contribution to grain yield in non-leaf organs. When the organs are ranked from highest to lowest in terms of the WSC accumulation amount, remobilization amount, remobilization efficiency, and contribution to grain yield, they are: the lower stem, the upper stem, and then the chaff. And between cultivars, these amounts were higher in SJZ-8 than in LM-21. The total contribution, pre-anthesis contribution, and post-anthesis contribution of WSC remobilization from all non-leaf organs to grain yield ranged from 11.7 to 21.5%, 4.8 to 9.4%, and 6.9 to 12.1%, respectively. This increase in WSC accumulation, remobilization, and contribution to grain yield in non-leaf organs is an important reason high grain yields can be maintained in water-saving and optimal high density management systems.

Keywords: Winter wheat; Non-leaf organs; Water soluble carbohydrate; Grain yield.

Introduction

Accumulation, translocation and distribution of carbohydrates (C) in wheat have an important impact on harvest index (HI) and grain yield. In general, grain filling in wheat depends on C from two resources: current assimilation, and remobilization of reserves stored in the stem and other parts, either pre-anthesis or post-anthesis (Pheloung and Siddique, 1991). These mobile reserves are called nonstructural carbohydrates (NSC) or water soluble carbohydrates (WSC). The main component of WSC stored in wheat non-leaf organs (stem and chaff) is fructan. Other WSC components include sucrose, glucose, fructose, and various oligosaccharides (Winzeler et al., 1990; Pollock and Cairns, 1991). Stored WSC may act as a buffer to maintain a steady rate of grain filling, especially when current photosynthesis is seriously impaired due to drought or other stresses. Many studies have shown that water stress during grain filling promotes plant senescence and increases remobilization of pre-anthesis stored C reserves to grain (Austin et al., 1980; Kobata et al., 1992; Zhang et al., 1998; Gebbing and Schnyder, 1999; Xue et al., 2006). Studies have also shown that increasing seeding rates leads to greater pre-anthesis dry matter accumulation (Tompkins et al., 1991a; Tompkins et al., 1991b; Arduini et al., 2006).

Under non-stress conditions, accumulated WSC may represent more than 40% of the stem dry weight (McCaig and Clarke, 1982; Blacklow et al., 1984), but these stored reserves may contribute only 5 to 20% to the final grain yield (Davidson and Chevalier, 1992; Borrell et al., 1993; Shakiba et al., 1996). However, when photosynthetic activity is depressed by drought or heat after anthesis, grain filling becomes more dependent on remobilized stem reserves, which may then represent 22 to 80% of the dry matter that accumulates in the grain (Bidinger et al., 1977; Bell and Incoll, 1990; Davidson and Chevalier, 1992; Blum et al., 1994; Xue et al., 2006). There are two factors involved in the extent of contribution of stored reserves to grain yield in wheat (Ehdaie and Waines, 1996). The first factor is the ability to store assimilates in the stem, and the second factor is the efficiency with which the stored reserves are remobilized and translocated to the grain. Thus, promoting the accumulation and remobilization of stored reserves in the stem is an important way to fully use carbohydrates and increase HI and grain yield (Davidson and Chevalier, 1992).

In the northern China Plain, water is a limiting factor for grain yield of winter wheat because drought always occurs during the growing season. Additional water must be supplied to achieve high yields for winter wheat.

However, extensive irrigation in traditional farming systems has led to serious environment problems (Lan and Zhou, 1995). In order to effectively use the water stored in the soil and to enhance water use efficiency (WUE), researchers at China Agricultural University have developed a water-saving farming system at the Wuqiao Experimental Station, Hebei, China (Li and Zhou, 2000). In this system, we found that high yields can be achieved under reduced irrigation (e.g., two irrigations instead of four) and higher seeding rates (> 600 plant m^{-2}). Decreased irrigation developed an optimal canopy structure, increased the contribution of non-leaf organs (peduncle, sheath, and ear) photosynthesis to grain yield, enhanced root growth in deeper soil layers, and increased WUE (Zhang et al., 2011). However, we did not explore how the reduced irrigation and high seeding rate affected remobilization of WSC in non-leaf organs. We hypothesized that remobilization of WSC in the non-leaf organs stem and chaff may also be increased and contribute to maintaining high yields under reduced irrigation and high seeding rates.

Stem internodes include the peduncle, penultimate internodes and the lower internodes. The peduncle and penultimate internodes account for about 45% of the maximum mass of the stem, and the lower stem internodes account for 55% (Borrel et al., 1993). There are differences among internodes in the amount of WSC that are accumulated and remobilized (Wardlaw and Willenbrink, 1994; Shakiba et al., 1996). Under well-watered field conditions, the possible contribution of stem reserves from both peduncle and penultimate internodes to final grain yields was 10.2% and 8.4% for a tall and a semidwarf near-isogenic wheat line, respectively (Borrel et al., 1993). However, little is known for the contribution of WSC in different internodes to grain yield under water stress and high seeding rate conditions. The objectives of this winter wheat study were: 1) to investigate the changes of WSC in chaff (rachis and glumes without grain), upper stem (peduncle and penultimate internodes) and lower stem, from anthesis to maturity; 2) to investigate the contribution of WSC from these non-leaf organs to grain yield under different irrigation and seeding rate treatments.

Materials and Methods

Experimental field and meteorological conditions

These winter wheat experiments were conducted at the Wuqiao Experiment Station of China Agricultural University at Cangzhou, Hebei province, China, in the 2002-2003 growing season. Soil was clay-loam with an average bulk density of 1.5 g cm^{-3} in the upper 100 cm layer. The underground water level was 6-9 m. Maximum water storage in the upper 2 m soil layer was 640 mm, and available water storage was 420 mm. Soil moisture at maximum field capacity was 0.22 g g^{-1}, while the wilting point was 0.076 g g^{-1}. Total rainfall in the wheat growth period during 2002-2003 was 112.1 mm.

Plant materials and experimental design

Two winter wheat cultivars, Shijiazhuang 8 (SJZ-8) and Lumai 21 (LM-21), were used for two experiments and sown on October 13, 2002. The first experiment had three irrigation treatments, which included I_0 (no water applied during spring, "rainfed"), I_2 (1500 m^3 ha^{-1}, 50% applied at stem elongation and 50% at anthesis, "reduced irrigation") and I_4 (3000 m^3 ha^{-1}, 25% of which was applied at jointing, booting, anthesis and grain filling, respectively, "full irrigation"). The seeding rate for this experiment was 600 plants m^{-2}. The second experiment had three seeding rates including SR_1 (450 plants m^{-2}), SR_2 (600 plants m^{-2}) and SR_3 (750 plants m^{-2}), under reduced irrigation condition (1500 m^3 ha^{-1}, 50% applied at stem elongation and 50% at anthesis). For both experiments, the experimental design was a randomized complete block design with three replications and plot size of 50 m^2. All plots in the two experiments received 225 kg N ha^{-1} (as urea), 300 kg P ha^{-1} (as ammonium monoacid phosphate), 150 kg K ha^{-1} (as potassium sulfate), 15 kg Zn ha^{-1} (as zinc sulfate) and 30 m^3 ha^{-1} chicken manure, before sowing. No fertilizer was applied during the growing season.

Data collection

In each plot, plants from two 50 cm rows (avoiding border rows) were harvested at 5-day intervals from anthesis to maturity. Samples were separated into leaf, upper stem (peduncle, penultimate internodes and leaf sheath), lower stem (the rest of the stem including leaf sheaths), chaff (rachis and glumes without grain) and grain. The samples were dried at 80 ^oC to constant weight and weighed. After dry weight was determined, the samples were milled and stored for WSC analysis. The grain yield at maturity is reported on a 13.0% moisture basis, while the HI is the ratio of dry mass of grain (0% moisture) to biomass aboveground at maturity.

WSC concentration was measured according to the method of Shakiba et al. (1996) with some modification. First, dry powder of 400 mg was extracted with 5 ml of distilled water at 60 ^oC for 30 min. The extract was then removed using Pasteur pipettes and the residue was re-extracted two times following the same procedure. The three extracts were combined and dried in a vacuum centrifuge and stored at 4 ^oC. The extract was resuspended in 1 ml of distilled water and deionized on 1 ml Amberlite Monobed resin columns. Carbohydrates were eluted with 9 ml distilled water, dried in a vacuum centrifuge and resuspended in 60 μl distilled water. Individual carbohydrates (sucrose, glucose, fructose and fructan) were separated by HPLC on a Aminex HPX-87C carbohydrate analysis column (BIO-RAD), maintained at 85 ^oC, using HPLC grade water as the mobile phase with a flow rate of 0.6 ml min^{-1} and quantified by refractive index monitoring. The WSC concentration in this study was the sum of sucrose, glucose, fructose and fructan concentrations. The WSC amount was obtained by multiplying WSC concentration by dry mass per m^2. The WSC remobilization amount, remobilization efficiency, and contribution to grain yield, were calculated using the formulas below:

Total WSC remobilization amount (TRA) = Maximum WSC amount-WSC amount at maturity; Pre-anthesis WSC remobilization amount (PreRA)= WSC amount at anthesis-WSC amount at maturity; Post-anthesis WSC remobilization amount (PostRA) = Total WSC remobilization amount-Pre-anthesis WSC remobilization amount; Total WSC remobilization efficiency (TRE) = Total WSC remobilization amount×100/Maximum WSC amount; Pre-anthesis WSC remobilization efficiency (PreRE) = Pre-anthesis WSC remobilization amount × 100 / WSC amount at anthesis; Total WSC contribution to grain yield (TRC) = Total WSC remobilization amount × 100 / Grain yield; Pre-anthesis WSC contribution to grain yield (PreRC) = Pre-anthesis WSC remobilization amount × 100 / Grain yield; Post-anthesis WSC contribution to grain yield (PostRC) = Post-anthesis WSC remobilization amount × 100/Grain yield.

Statistical treatment

The data were analyzed using SAS (1997). The analysis of variance was conducted using the general linear model and means were tested by least significant difference at $P<0.05$ level.

Results

Remobilization of WSC in non-leaf organs and contribution to grain yield under different irrigation treatments

There was a significant difference in final biomass, grain yield, and HI, among the three irrigation treatments for each of the two cultivars (Table 1). In general, the biomass and grain yield increased as irrigation increased, however, there was no significant difference in grain yield between I_2 and I_4 irrigation levels, and decreasing irrigation significantly increased HI.

Table 1. The aboveground biomass, grain yield and HI at maturity in different irrigation treatments.

Cultivar	Treatment	Biomass (g m^{-2})	Grain yield (g m^{-2})	HI
SJZ-8	I_0	1378.4^c	749.3^b	0.47^a
	I_2	1524.4^b	786.4^a	0.45^b
	I_4	1594.3^a	778.7^a	0.42^c
	Mean	1499.0	771.5	0.45
LM-21	I_0	1175.2^b	644.5^b	0.48^a
	I_2	1333.3^a	693.4^a	0.45^b
	I_4	1394.5^a	707.8^a	0.44^b
	Mean	1301.1	681.9	0.46
Cultivar (C)		***	***	**
Irrigation (I)		***	***	***
C×I		ns	*	*

Values with different letters indicate significant differences between irrigation treatments for each cultivar at P<0.05; ns: not significant; $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

The WSC accumulation in non-leaf organs of SJZ-8 and LM-21 increased gradually after anthesis, reached the maximum between 6 days after anthesis (6 DAA) and 12 DAA and then decreased (Figure 1). At anthesis, the WSC amount of the upper stem in I_0 was significantly higher than in I_2 and I_4 treatments, while there was no significant difference in WSC amount in the lower stem and chaff among treatments. This showed that reducing irrigation can promote pre-anthesis WSC accumulation in the upper stem. The maximum WSC amount for the I_0 treatment in the lower stem and chaff in SJZ-8 occurred at 6 DAA, while the maximum WSC for other treatments occurred at 12 DAA, showing that, for SJZ-8, reduced irrigation caused WSC in the chaff and lower stem to reach their maximums earlier. Among the different organs, WSC decreased from the lower stem, to the upper stem, to the chaff. Comparing the two cultivars, SJZ-8 had more WSC than LM-21.

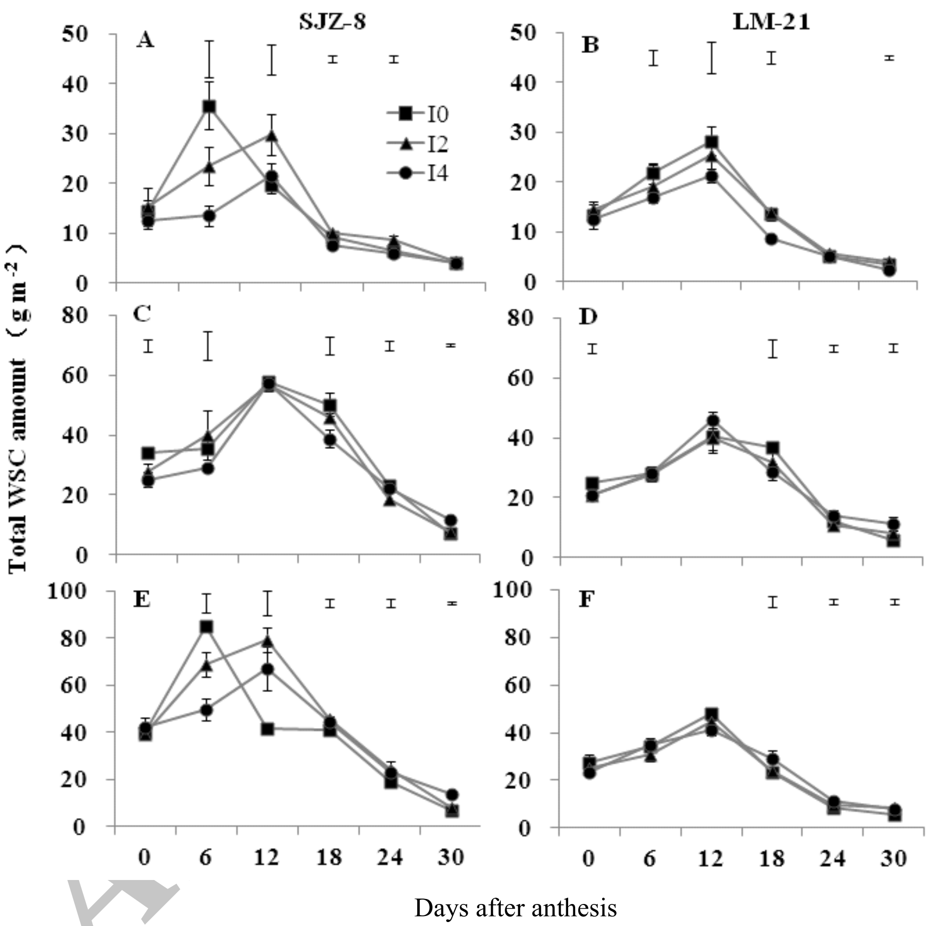

Figure 1. Dynamics of total WSC accumulation amount in chaff (A, B), upper stem (C, D), and lower stem (E, F), in SJZ-8 and LM-21, in different irrigation treatments (the vertical bars are LSD at P=0.05).

The WSC in non-leaf organs mostly began to decrease at 12 DAA (Figure 1), showing that WSC began to transfer to grain at this time. Except for TRA in the lower stem and total non-leaf organs, there was no significant cultivar by irrigation interaction for TRA, PreRA and PostRA, in non-leaf organs (Table 2). For the chaff, there was no significant difference in TRA, PreRA and PostRA, between the two cultivars (Table 2); however, SJZ-8 had significantly more WSC remobilization than LM-21 in the upper stem, lower stem and total non-leaf organs (Table 3). When the organs are ranked from highest to lowest in terms of WSC remobilization amount, they are: the lower stem, the upper stem, and then the chaff (Table 3). Except for TRA in the upper stem, PreRA in chaff and PostRA in total non-leaf organs, irrigation treatments had a significant effect on WSC remobilization amount in the different organs (Table 2). PostRA in the upper stem increased as irrigation level increased; however, TRA and PreRA in the upper stem and TRA, PreRA and PostRA in the chaff, lower stem, and total non-leaf organs, all increased as the irrigation level decreased (Table 3). The proportion of PreRA in TRA ranged from 32.9 to 53.9% in the chaff, 27.5 to 56.1% in the upper stem, 42.0 to 53.3% in the lower stem and 40.6 to 50.0% in total non-leaf organs. The proportion of PreRA in TRA increased with decreasing irrigation in the upper stem and total non-leaf organs.

Table 2. Analysis of variance for water soluble carbohydrate (WSC) remobilization amount (RA), remobilization efficiency (RE) and contribution to grain yield (RC), in chaff, upper stem, lower stem and total non-leaf organs, in different irrigation treatments.

Organ	Variable	WSC remobilization amount			WSC remobilization efficiency		WSC contribution to grain yield		
		TRA	PreRA	PostRA	TRE	PreRE	TRC	PreRC	PostRC
Chaff	Cultivar (C)	ns	ns	ns	ns	ns	ns	ns	ns
	Irrigation (I)	***	ns	**	ns	ns	***	ns	**
	C×I	ns	ns	ns	*	ns	ns	ns	ns
Upper Stem	Cultivar (C)	***	***	***	**	**	***	***	*
	Irrigation (I)	ns	***	**	***	***	*	***	**
	C×I	ns	ns	ns	ns	ns	ns	ns	ns
Lower Stem	Cultivar (C)	***	***	***	**	**	***	***	***
	Irrigation (I)	***	**	*	***	***	***	***	**
	C×I	*	ns	ns	**	*	ns	ns	ns
Total	Cultivar (C)	***	***	***	**	**	***	***	**
	Irrigation (I)	***	***	ns	***	***	***	***	*
	C×I	*	ns	ns	*	ns	ns	ns	ns

T: total; Pre: pre-anthesis; Post: post-anthesis; ns: not significant; *P<0.05; **P<0.01; ***P<0.001.

Table 3. The water soluble carbohydrate (WSC) remobilization amount (RA), remobilization efficiency (RE) and contribution to grain yield (RC), in chaff, upper stem, lower stem and total non-leaf organs, in different irrigation treatments.

Cultivar	Organ	Treatment	Remobilization amount ($g\ m^{-2}$)			Remobilization efficiency (%)		Contribution to grain yield (%)		
			TRA	PreRA	PostRA	TRE	PreRE	TRC	PreRC	PostRC
SJZ-8	Chaff	I_0	31.6^{a}	10.4^{a}	21.2^{a}	88.6^{a}	71.9^{a}	4.2^{a}	1.4^{a}	2.8^{a}
		I_2	25.4^{ab}	10.9^{a}	14.5^{ab}	85.1^{a}	71.3^{a}	3.2^{ab}	1.4^{a}	1.8^{ab}
		I_4	17.7^{b}	8.5^{a}	9.2^{b}	81.2^{a}	67.9^{a}	2.3^{b}	1.1^{a}	1.2^{b}
		Mean	24.9	9.9	15.0	85.0	70.4	3.2	1.3	2.0
	Upper stem	I_0	51.0^{a}	27.1^{a}	23.9^{b}	87.9^{a}	79.5^{a}	6.8^{a}	3.6^{a}	3.2^{b}
		I_2	49.4^{a}	19.9^{b}	29.5^{a}	86.5^{b}	71.8^{b}	6.3^{b}	2.5^{b}	3.8^{ab}
		I_4	45.5^{b}	13.2^{c}	32.3^{a}	79.3^{c}	52.4^{c}	5.8^{c}	1.7^{c}	4.1^{a}
		Mean	48.6	20.1	28.6	84.6	67.9	6.3	2.6	3.7
	Lower stem	I_0	78.8^{a}	33.1^{a}	45.6^{a}	92.2^{a}	83.2^{a}	10.5^{a}	4.4^{a}	6.1^{a}
		I_2	71.7^{a}	31.4^{a}	40.3^{ab}	90.3^{a}	80.2^{b}	9.1^{a}	4.0^{ab}	5.1^{ab}
		I_4	53.3^{b}	28.4^{a}	24.9^{b}	78.9^{b}	67.2^{c}	6.8^{b}	3.6^{b}	3.2^{b}
		Mean	67.9	31.0	36.9	87.1	76.9	8.8	4.0	4.8
	Total	I_0	161.4^{a}	70.6^{a}	90.8^{a}	90.1^{a}	79.9^{a}	21.5^{a}	9.4^{a}	12.1^{a}
		I_2	146.5^{a}	62.2^{b}	84.3^{a}	88.1^{a}	75.7^{b}	18.6^{b}	7.9^{b}	10.7^{ab}
		I_4	116.5^{b}	50.1^{c}	66.4^{b}	79.5^{b}	62.7^{c}	15.0^{c}	6.4^{c}	8.5^{b}
		Mean	141.5	61.0	80.5	85.9	72.8	18.4	7.9	10.5
LM-21	Chaff	I_0	24.7^{a}	9.8^{a}	14.9^{a}	87.2^{ab}	71.9^{a}	3.8^{a}	1.5^{a}	2.3^{a}
		I_2	21.5^{a}	10.6^{a}	10.9^{a}	84.3^{b}	72.7^{a}	3.1^{ab}	1.5^{a}	1.6^{ab}
		I_4	19.1^{a}	10.3^{a}	8.8^{a}	89.3^{a}	81.8^{a}	2.7^{b}	1.4^{a}	1.2^{b}
		Mean	21.8	10.2	11.5	86.9	75.5	3.2	1.5	1.7
	Upper stem	I_0	34.4^{a}	19.3^{a}	15.2^{a}	85.1^{a}	76.5^{a}	5.3^{a}	3.0^{a}	2.4^{a}
		I_2	32.1^{a}	12.6^{b}	19.6^{a}	79.4^{ab}	60.7^{b}	4.6^{a}	1.8^{b}	2.8^{a}
		I_4	34.6^{a}	9.5^{b}	25.1^{a}	75.1^{b}	45.3^{c}	4.9^{a}	1.3^{c}	3.5^{a}
		Mean	33.7	13.8	20.0	79.9	60.8	5.0	2.0	2.9
	Lower stem	I_0	42.3^{a}	21.7^{a}	20.6^{a}	88.3^{a}	79.4^{a}	6.6^{a}	3.4^{a}	3.2^{a}
		I_2	36.0^{ab}	16.9^{ab}	19.1^{a}	81.1^{b}	66.7^{b}	5.2^{b}	2.4^{b}	2.8^{a}
		I_4	32.9^{b}	15.4^{b}	17.5^{a}	80.3^{b}	65.4^{b}	4.7^{b}	2.2^{b}	2.5^{a}
		Mean	37.1	18.0	19.1	83.2	70.5	5.5	2.7	2.8
	Total	I_0	101.4^{a}	50.7^{a}	50.7^{a}	87.0^{a}	77.0^{a}	15.7^{a}	7.9^{a}	7.9^{a}
		I_2	89.6^{a}	40.0^{b}	49.6^{a}	81.2^{b}	66.1^{b}	12.9^{b}	5.8^{b}	7.2^{a}
		I_4	86.6^{a}	35.2^{b}	51.4^{a}	79.9^{b}	61.6^{b}	12.2^{b}	5.0^{b}	7.3^{a}
		Mean	92.5	42.0	50.6	82.7	68.2	13.6	6.2	7.4

Values with different letters indicate significant differences between irrigation treatments for each cultivar and each organ at $P<0.05$; T: total; Pre: pre-anthesis; Post: post-anthesis.

There was no significant difference in TRE and PreRE in the chaff between the two cultivars or among irrigation treatments; however, there were significant differences in TRE and PreRE in the upper stem, lower stem, and total non-leaf organs (Table 2). TRE ranged from 81.2 to 89.3%

for the chaff, 75.1 to 87.9% for the upper stem, 78.9 to 92.2% for the lower stem and 79.5 to 90.1% for total non-leaf organs (Table 3). PreRE ranged from 67.9 to 81.8% for the chaff, 45.3 to 79.5% for the upper stem, 65.4 to 83.2% for the lower stem, and 61.6 to 79.9% for total non-leaf organs (Table 3). TRE and PreRE in the upper stem, lower stem, and total non-leaf organs significantly increased as irrigation level decreased. In particular, for the upper stem, the PreRE increased by 37.0% and 33.9% in the I_2 treatment compared to the I_4 treatment for both SJZ 8 and LM-21 (Table 3).

There was no significant cultivar by irrigation interaction in WSC contribution to grain yield (Table 2). For all cultivars and irrigation levels, the TRC ranged from 2.3 to 4.2% for the chaff, 4.6 to 6.8% for the upper stem, 4.7 to 10.5% for the lower stem, and 12.2 to 21.5% for total non-leaf organs (Table 3). For the chaff, the two cultivars had no differences in TRC, PreRC and PostRC; however, irrigation significantly affected TRC and PostRC (Table 2). For the upper stem, lower stem, and total non-leaf organs, both cultivar and irrigation affected TRC, PreRC and PostRC (Table 2). Comparing the two cultivars, TRC, PreRC and PostRC in SJZ-8 were higher than in LM-21, for example, the PreRC in total non-leaf organs for SJZ-8 ranged from 6.4 to 9.4%, while that of LM-21 ranged from 5.0 to 7.9%. The TRC and PreRC of all non-leaf organs increased as irrigation level decreased (Table 3). The proportion of PreRC in TRC ranged from 32.9 to 53.8% in the chaff, 27.4 to 55.9% in the upper stem, 42.1 to 53.2% in the lower stem and 40.6 to 50.0% in total non-leaf organs. The proportion of PreRC in the upper stem and total non-leaf organs increased as irrigation level decreased. The proportion of PostRC in TRC ranged from 46.2 to 67.1% in the chaff, 44.1 to 72.6% in the upper stem, 46.8 to 57.9% in the lower stem and 50.0 to 59.4% in total non-leaf organs. As irrigation level decreased, the proportion of PostRC increased in chaff and lower stem.

Remobilization of WSC in non-leaf organs and contribution to grain yield under different seeding rates

Seeding rate had a significant effect on biomass, grain yield and HI, in both cultivars (Table 4). The low seeding rate (SR_1, 450 plants m^{-2}) resulted in a lower yield than the two higher seeding rates (SR_2, 600 plants m^{-2}; SR_3, 750 plants m^{-2}); however, there was no significant difference in yield between SR_2 and SR_3 for SJZ-8, indicating that for this cultivar, the seeding rate of 600 plants m^{-2} is optimum for high yield. HI was higher at the higher seeding rate (SR_3) for both cultivars, which may be related to WSC remobilization of non-leaf organs. The WSC accumulation in non-leaf organs of SJZ-8 and LM-21, in all three seeding rates, increased gradually after anthesis, reached the maximum from 6 DAA to 18 DAA, and then decreased thereafter (Figure 2). At anthesis, WSC amount in the lower stem and chaff of SJZ-8, but only in the chaff of LM-21, was higher at higher seeding rates (SR_2 and SR_3) than at the lowest seeding rate (SR_1). It seems then that the WSC accumulation in non-leaf organs of SJZ-8 is more sensitive to seeding rate than it is in LM-21 and increasing seeding rate can promote WSC accumulation in the lower stem and chaff. The maximum WSC amount of non-leaf organs was greater at high seeding rates (SR_2 and SR_3) than in the low seeding rate, and mostly occurred earlier. As with the different irrigation treatments, when the organs are ranked from highest to lowest in terms of WSC remobilization amount, they are: the lower stem, the upper stem and then the chaff. And comparing the two cultivars, the WSC amount in SJZ-8 was higher than that in LM-21.

Table 4. The aboveground biomass, grain yield and HI at maturity in different seeding rate treatments.

Cultivar	Treatment	Biomass (g m^{-2})	Grain yield (g m^{-2})	HI
SJZ-8	SR_1	1454.3[a]	757.2[b]	0.45[b]
	SR_2	1524.4[a]	786.4[ab]	0.45[b]
	SR_3	1503.8[a]	797.3[a]	0.46[a]
	Mean	1494.2	780.3	0.45
LM-21	SR_1	1273.6[b]	672.1[b]	0.46[b]
	SR_2	1333.3[ab]	693.4[b]	0.45[c]
	SR_3	1356.2[a]	735.2[a]	0.47[a]
	Mean	1321.0	700.2	0.46
Cultivar (C)		***	***	***
Seeding rate (SR)		***	***	***
C×SR		ns	ns	*

Values with different letters indicate significant differences between seeding rate treatments at $P<0.05$; ns: not significant; [*]$P<0.05$; [***]$P<0.001$.

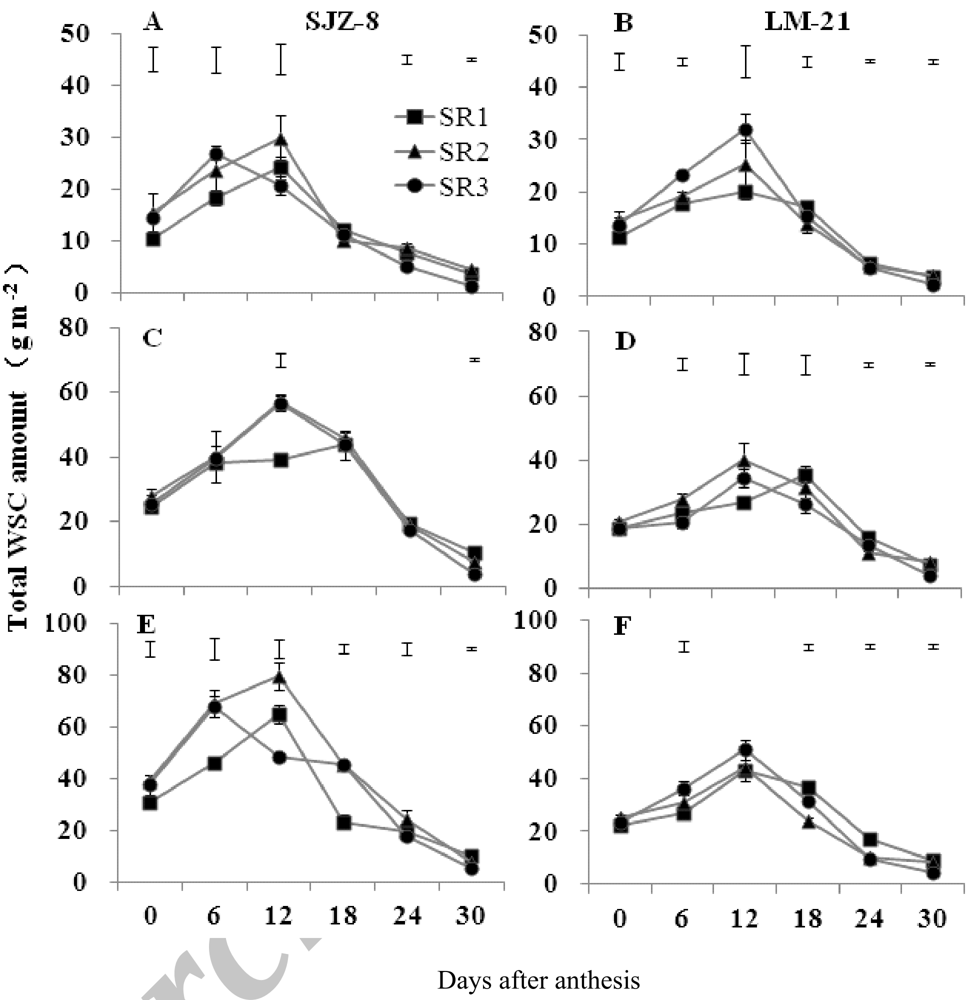

Figure 2. Dynamics of total WSC accumulation amount in chaff (A, B), upper stem (C, D), and lower stem (E, F), in SJZ-8 and LM-21, in different seeding rate treatments (the vertical bars are LSD at P=0.05).

The changes in WSC remobilization amount between cultivars and among organs in different seeding rate treatments were similar to those in irrigation treatments (Table 5). Generally, seeding rate significantly affected the TRA and PreRA in the chaff, upper stem, lower stem, and total non-leaf organs, as well as the PostRA in the upper stem (Table 5). The TRA and PreRA increased as seeding rate increased from SR_1

to SR_3, however, there was no significant difference between SR_2 and SR_3 in most cases (Table 6). The effect of seeding rate on PostRA varied with cultivars. For SJZ-8, higher seeding rates (SR_2 and SR_3) resulted in higher PostRA in the upper stem, but seeding rate did not affect PostRA in the lower stem and chaff. For LM-21, SR_3 had higher PostRA than SR_2 and SR_1 in the lower stem and chaff. There was a significant cultivar by seeding rate interaction for TRA in all the non-leaf organs, PreRA in the lower stem and total non-leaf organs, and PostRA in the upper and lower stem. However, increasing seeding rate mainly increased the remobilization of pre-anthesis WSC in non-leaf organs. The proportion of PreRA in TRA ranged from 32.8 to 51.6% for the chaff, 39.3 to 48.9% for the upper stem, 38.0 to 51.6% for the lower stem and 38.5 to 47.7% for total non-leaf organs. In general, the proportion of PreRA increased as seeding rate increased; however, there was no further increase for LM-21 above SR_2.

Table 5. Analysis of variance for water soluble carbohydrate (WSC) remobilization amount (RA), remobilization efficiency (RE) and contribution to grain yield (RC), in chaff, upper stem, lower stem, and total non-leaf organs, in different seeding rate treatments.

Organ	Variable	WSC remobilization amount			WSC remobilization efficiency		WSC contribution to grain yield		
		TRA	PreRA	PostRA	TRE	PreRE	TRC	PreRC	PostRC
Chaff	Cultivar (C)	ns	ns	ns	**	ns	ns	ns	ns
	Seeding rate (SR)	***	***	ns	***	***	***	**	ns
	C×SR	*	ns	ns	ns	ns	*	ns	*
Upper stem	Cultivar (C)	***	***	***	*	*	***	**	**
	Seeding rate (SR)	***	***	**	***	***	***	**	*
	C×SR	**	ns	*	**	*	**	ns	*
Lower stem	Cultivar (C)	***	***	***	***	***	***	***	***
	Seeding rate (SR)	**	***	ns	***	***	*	***	ns
	C×SR	**	*	*	***	ns	**	ns	**
Total	Cultivar (C)	***	***	***	***	***	***	***	**
	Seeding rate (SR)	***	***	ns	***	***	**	***	ns
	C×SR	*	*	ns	*	*	ns	ns	ns

T: total; Pre: pre-anthesis; Post: post-anthesis; ns: not significant; $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$.

Table 6. The water soluble carbohydrate (WSC) remobilization amount (RA), remobilization efficiency (RE) and contribution to grain yield (RC), in chaff, upper stem, lower stem and total non-leaf organs, in different seeding rate treatments.

Cultivar	Organ	Treatment	Remobilization amount ($g\ m^{-2}$)			Remobilization efficiency (%)		Contribution to grain yield (%)		
			TRA	PreRA	PostRA	TRE	PreRE	TRC	PreRC	PostRC
SJZ-8	Chaff	SR_1	20.4^{a}	6.7^{b}	13.6^{a}	84.7^{b}	64.5^{b}	2.7^{a}	0.9^{b}	1.8^{a}
		SR_2	25.4^{a}	10.9^{ab}	14.5^{a}	85.2^{b}	70.1^{b}	3.2^{a}	1.4^{ab}	1.8^{a}
		SR_3	25.6^{a}	13.2^{a}	12.4^{a}	95.2^{a}	91.2^{a}	3.2^{a}	1.7^{a}	1.6^{a}
		Mean	23.8	10.3	13.5	88.4	75.3	3.0	1.3	1.7
	Upper stem	SR_1	33.1^{b}	14.1^{b}	19.0^{b}	75.7^{c}	57.0^{c}	4.4^{b}	1.9^{b}	2.5^{b}
		SR_2	49.4^{a}	19.9^{a}	29.5^{a}	86.5^{b}	72.0^{b}	6.3^{a}	2.5^{a}	3.8^{a}
		SR_3	52.9^{a}	21.8^{a}	31.2^{a}	93.6^{a}	85.7^{a}	6.6^{a}	2.7^{a}	3.9^{a}
		Mean	45.1	18.6	26.6	85.3	71.6	5.8	2.4	3.4
	Lower stem	SR_1	55.0^{b}	20.9^{b}	34.1^{a}	84.6^{b}	67.6^{c}	7.3^{b}	2.8^{b}	4.5^{a}
		SR_2	71.7^{a}	31.4^{a}	40.3^{a}	90.3^{a}	80.2^{b}	9.1^{a}	4.0^{a}	5.1^{a}
		SR_3	62.2^{b}	32.1^{a}	30.1^{a}	92.1^{a}	85.7^{a}	7.8^{b}	4.0^{a}	3.8^{a}
		Mean	63.0	28.1	34.8	89.0	77.8	8.1	3.6	4.5
	Total	SR_1	108.4^{b}	41.7^{b}	66.7^{a}	81.7^{c}	63.2^{c}	14.3^{b}	5.5^{b}	8.8^{a}
		SR_2	146.5^{a}	62.2^{a}	84.3^{a}	88.1^{b}	75.7^{b}	18.6^{a}	7.9^{a}	10.7^{a}
		SR_3	140.8^{a}	67.1^{a}	73.7^{a}	93.2^{a}	86.7^{a}	17.7^{a}	8.4^{a}	9.2^{a}
		Mean	131.9	57.0	74.9	87.7	75.2	16.9	7.3	9.6
LM-21	Chaff	SR_1	16.1^{b}	7.5^{b}	8.6^{b}	80.8^{c}	66.1^{b}	2.4^{b}	1.1^{a}	1.3^{b}
		SR_2	21.5^{b}	10.6^{ab}	10.9^{b}	84.3^{b}	72.7^{b}	3.1^{b}	1.5^{a}	1.6^{b}
		SR_3	29.8^{a}	11.3^{a}	18.4^{a}	92.7^{a}	82.6^{a}	4.0^{a}	1.5^{a}	2.5^{a}
		Mean	22.5	9.8	12.6	85.9	73.8	3.2	1.4	1.8
	Upper stem	SR_1	28.2^{a}	11.5^{b}	16.7^{a}	79.2^{b}	60.6^{b}	4.2^{a}	1.7^{a}	2.5^{a}
		SR_2	32.1^{a}	12.6^{ab}	19.6^{a}	79.5^{b}	60.8^{b}	4.6^{a}	1.8^{a}	2.8^{a}
		SR_3	30.5^{a}	14.9^{a}	15.6^{a}	88.5^{a}	79.0^{a}	4.1^{a}	2.0^{a}	2.1^{a}
		Mean	30.3	13.0	17.3	82.4	66.8	4.3	1.8	2.5
	Lower stem	SR_1	34.5^{b}	13.5^{b}	21.0^{b}	79.8^{b}	60.7^{b}	5.1^{b}	2.0^{a}	3.1^{ab}
		SR_2	36.0^{b}	16.9^{ab}	19.1^{b}	81.0^{b}	66.7^{b}	5.2^{b}	2.4^{a}	2.8^{b}
		SR_3	46.4^{a}	18.6^{a}	27.7^{a}	91.0^{a}	80.3^{a}	6.3^{a}	2.5^{a}	3.8^{a}
		Mean	39.0	16.3	22.6	83.9	69.2	5.5	2.3	3.2
	Total	SR_1	78.8^{b}	32.4^{b}	46.4^{a}	79.8^{b}	61.9^{b}	11.7^{a}	4.8^{b}	6.9^{a}
		SR_2	89.6^{ab}	40.0^{ab}	49.6^{a}	81.3^{b}	66.1^{b}	12.9^{a}	5.8^{ab}	7.2^{a}
		SR_3	106.6^{a}	44.8^{a}	61.7^{a}	90.7^{a}	80.3^{a}	14.5^{a}	6.1^{a}	8.4^{a}
		Mean	91.7	39.1	52.6	83.9	69.4	13.0	5.6	7.5

Values with different letters indicate significant differences between seeding rate treatments for each cultivar and each organ at $P<0.05$; T: total; Pre: pre-anthesis; Post: post-anthesis.

There was no significant difference in chaff PreRE between the two cultivars; however, SJZ-8 had significantly higher PreRE in the upper stem, lower stem and total non-leaf organs, and significantly higher TRE in all the non-leaf organs, than did LM-21 (Tables 5 and 6). The TRE ranged from

80.8 to 95.2% for the chaff, 75.7 to 93.6% for the upper stem, 79.8 to 92.1% for the lower stem and 79.8 to 93.2% for total non-leaf organs (Table 6). The PreRE ranged from 64.5 to 91.2% for the chaff, 57.0 to 85.7% for the upper stem, 60.7 to 85.7% for the lower stem and 61.9 to 86.7% for total non-leaf organs (Table 6). TRE and PreRE in non-leaf organs significantly increased as seeding rate increased (Table 6).

There was no significant difference in TRC, PreRC and PostRC in the chaff between the two cultivars; however, seeding rate affected TRC and PreRC in the chaff. For the upper stem, lower stem, and total non-leaf organs, both cultivar and seeding rate affected TRC, PreRC and PostRC (Table 5). The TRC ranged from 2.4 to 4.0% for the chaff, 4.1 to 6.6% for the upper stem, 5.1 to 9.1% for the lower stem, and 11.7 to 18.6% for total non-leaf organs (Table 6). The contributions of WSC from the upper stem, lower stem and total non-leaf organs were higher in SJZ-8 than in LM-21 (Table 6). The PreRC in total non-leaf organs for SJZ-8 and LM-21 were 5.5 to 8.4% and 4.8 to 6.1%, respectively. In general, the TRC and PreRC increased as seeding rate increased (Table 6). The proportion of PreRC in TRC ranged from 33.1 to 51.6% for the chaff, 39.1 to 48.8% for the upper stem, 37.9 to 51.6% for the lower stem and 38.5 to 47.7% for total non-leaf organs. The pre-anthesis WSC contributed more to grain yield in higher seeding rates (SR_2 and SR_3) than in the lower seeding rate (SR_1). The proportion of PostRC in TRC ranged from 48.4 to 66.9% for the chaff, 51.2 to 60.9% for the upper stem, 48.4 to 62.1% for the lower stem, and 52.3 to 61.5% for total non-leaf organs. In general, the proportion of PostRC decreased as seeding rate increased.

Discussion

Studies have shown that non-leaf organs (e.g., ear, stem and sheath) have double roles in wheat grain filling: first, they have actual or potential photosynthetic capability (Araus et al., 1993) with some advantages over leaves during drought or heat stress conditions (Wang et al., 2001; Tambussi et al., 2007); second, their stored reserves contribute to grain filling by remobilization during plant sensence (Ehdaie et al., 2006; Ehdaie et al., 2008). We previously reported that the photosynthetic contribution of the non-leaf organs the ear, peduncle and sheath, accounted for 73-81% of the total contribution of organs above the flag leaf node to wheat grain weight, and the contribution increased under reduced irrigation and higher seeding rates (Zhang et al., 2011). In this study, we investigated the remobilization of stored reserves in non-leaf organs and contribution to grain yield under different irrigation and seeding rate treatments. The results showed that the remobilization amount, remobilization efficiency of total WSC and contribution to grain yield, in non-leaf organs, increased as irrigation decreased or seeding rate increased. Because of these increases in the contribution of photosynthesis and remobilization from non-leaf organs, a high yield was maintained at the reduced irrigation level I_2 and the higher seeding rate SR_2.

Comparing the two cultivars in this study, SJZ-8 generally had more WSC accumulation, remobilizilation and contribution to grain yield than LM-21. Another study using post-anthesis desciccation to simulate drought also showed genotypic difference in the ability to remobilize dry matter to maintain grain growth (Hossain et al., 1990). Our results demonstrated that adoption of higher seeding rates and selecting proper cultivars are important for improving WSC accumulation and remobilization under reduced irrigation management systems in winter wheat in the environment of the North China Plain.

In this study, reducing irrigation increased the accumulation of pre-anthesis WSC in the upper stem, while increasing seeding rate promoted the accumulation of WSC in the lower stem and chaff, and both irrigation and seeding rate increased the remobilization of WSC in stem and chaff. The contribution of total WSC in the chaff, upper stem, and lower stem to grain yield ranged from 2.3 to 4.2%, 4.1 to 6.8% and 4.7 to 10.5%, respectively, and the contributions increased as irrigation decreased or seeding rate increased. Borrel et al. (1993) showed that under well-watered field conditions, the contribution of the upper stem (peduncle and penultimate internode) to final grain yields was 8.4 to 10.2%. The reason the data in this study was lower than that of Borrel et al. (1993) may be due to the difference in cultivar and irrigation treatments.

The contributions to grain yield from total WSC and pre-anthesis WSC remobilization, in total non-leaf organs, ranged from 11.7 to 21.5 and 4.8 to 9.4%, respectively. As irrigation decreased and seeding rate increased, these contributions increased. The contribution of pre-anthesis WSC to yield in this study was in the lower range of that reported in several other studies in either winter wheat or spring wheat. In their studies, the contribution of pre-anthesis WSC to grain yield in wheat ranged from 5 to 90%, depending on environment, nitrogen supply, crop growth, and seasonal evapotranspiration

(Asseng and van Herwaarden, 2003; Foulkes et al., 2002; Yang et al., 2000; Xue et al., 2006). In general, pre-anthesis WSC contributed more to yield in semiarid environments (36-88%, Xue et al., 2006) than in humid environments (11-53%, Foulkes et al., 2002; Yang et al., 2000). The contribution of pre-anthesis WSC to yield was also related to yield level, and the contribution was generally much less with high yields than low yields (Asseng and Van Herwaarden, 2003). They showed that the contribution of pre-anthesis WSC to yield was generally less than 20% when yield was > 600 g m^{-2}, so the lower contribution of pre-anthesis WSC to yield in this study may be related to the higher yield level (about 700 g m^{-2}).

Also in this study, a higher seeding rate resulted in greater accumulation, remobilization of WSC in non-leaf organs and greater contribution to grain yield. Many studies have demonstrated that a higher seeding rate is an important management strategy for obtaining higher grain yield in wheat (Tompkins et al., 1991a; Tompkins et al., 1991b; Sunderman, 1999; Arduini et al., 2006; Hiltbrunner et al., 2007). Wheat yield generally increases as seeding rate increases up to an optimum seeding rate (De Bruin and Pedersen, 2008). Higher seeding rates increase photosynthetic area and light interception by the canopy and result in higher dry matter accumulation at anthesis (Arduini et al., 2006). Among the three yield components (spikes per unit area, kernels per spike and kernel weight), higher seeding rate mainly increased spikes per unit area (Tompkins et al., 1991a; Tompkins et al., 1991b; Hiltbrunner et al., 2007). In turn, the increased number of spikes (stems) in higher seeding rates increases the potential source of remobilization (Tompkins et al., 1991a; Tompkins et al., 1991b; Arduini et al., 2006; Xue et al., 2006). In this study, we increased the seeding rate at reduced irrigation and late sowing (one week later than the normal sowing date) and obtained higher yield. Under full irrigation, plants grew fast and were prone to lodging, so a higher seeding rate was not beneficial to increasing grain yield.

In conclusion, there was a significant difference in total WSC accumulation amount, remobilization amount, remobilization efficiency and contribution to grain yield among non-leaf organs, with the greatest amounts coming from the lower stem, next the upper stem and then the chaff. And it was demonstrated that these qualities increased as irrigation decreased or as seeding rate increased, such that high yields were maintained in a water-saving and optimal high density cultivation combination system in winter wheat.

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