https://doi.org/10.17221/93/2017-CJGPB

Genotypic Variation in Pre- and Post-Anthesis Dry Matter Remobilization in Iranian Wheat Cultivars: Associations with Stem Characters and Grain Yield

Mehdi JOUDI[1]* *and Wim VAN DEN ENDE*[2]

[1]*Meshkinshahr College of Agriculture, University of Mohaghegh Ardabili, Ardabil, Iran;*
[2]*Lab of Molecular Plant Biology, Institute of Botany and Microbiology, KU Leuven, Leuven-Heverlee, Belgium*

**Corresponding author: mehdijoudi@gmail.com; joudi@uma.ac.ir*

Abstract

Joudi M., Van den Ende W. (2018): Genotypic variation in pre- and post-anthesis dry matter remobilization in Iranian wheat cultivars: associations with stem characters and grain yield. Czech J. Genet. Plant Breed., 54: 123–134.

The amount of carbohydrate accumulation and remobilization in the wheat stem can be estimated by monitoring changes in stem dry matter. Eighty-one wheat cultivars were examined in the Moghan region of Iran during the 2010–2011 and 2013–2014 growing seasons. Pre- and post-anthesis dry matter remobilization was quantified in the tested cultivars and their associations with stem characteristics and grain yield were investigated. There was substantial variation in stem length, weight, and specific weight among the tested cultivars. The majority of the cultivars did not show pre-anthesis dry matter remobilization in the stem or internodes. In contrast, most of them used stem dry matter that had been stored after anthesis, suggesting that under the given conditions, current photosynthesis along with post-anthesis dry matter remobilization could meet most of the sink demand. Generally, there were no significant associations between stem length and dry matter remobilization ($r = -0.05$ to 0.03; $P \geq 0.05$). Stem weight ($r = 0.42$ to 0.65; $P \leq 0.01$) and specific stem weight ($r = 0.44$ to 0.60; $P \leq 0.01$) measured at 16 days after anthesis correlated positively and significantly with dry weight loss from the stem. Intriguingly, no clear relationships were found between dry matter remobilization and grain yield ($r = -0.13$ to 0.04; $P \geq 0.05$), suggesting that there are no simple relationships between these traits. The association between dry matter remobilization and grain yield may be different depending on the examined cultivars.

Keywords: remobilization; stem specific weight; stem weight; wheat

Wheat (*Triticum aestivum* L.) is the most important source of carbohydrates in many countries where it provides more nourishment for people than any other food source. In some wheat growing regions, such as Iran, winter wheat cultivars are grown under conditions in which moisture and temperature are most often favourable for vegetative growth during autumn and early spring. However, grain filling often occurs when temperatures are increasing and moisture supply is decreasing (terminal droughts). The common end results of such terminal drought stresses are grain shrivelling, reduced test weight and loss in yield (Blum 1998). Carbohydrate accumulation in the stem and their remobilization to the grain in wheat is a mechanism by which the plants could buffer carbon fluctuations during grain filling and partly guarantee the supply of photoassimilates towards grains.

The flow of carbon to the grain from stored stem carbohydrates has been investigated during pre- and post-anthesis studies (Pheloung & Siddique 1991; Bonnett & Incoll 1992; Zhang *et al*. 2013). Dry matter formed prior to anthesis has been estimated to contribute 0–100% of the grain dry matter at maturity (Inoue *et al*. 2004; Užík & Žofajová 2006),

https://doi.org/10.17221/93/2017-CJGPB

while the contribution of dry matter stored after anthesis has been estimated to represent 0–22% of the final grain weight (Pheloung & Siddique 1991; Ma *et al.* 2014).

Although stored stem carbohydrates contribute to grain filling, no clear relationship is found between carbon remobilization and grain yield. Flood *et al.* (1995) studied the relationship between dry matter remobilization in ten wheat cultivars in three locations of Australia and reported that a post-anthesis decrease in stem weight was inversely related to grain yield at one location (Horsham). At Boort and Walpeup there was a negative trend between these two parameters, albeit not significant. In a study in which eight diverse spring wheat genotypes were examined under irrigation and drought stress conditions, Ehdaie and Waines (1996) stated that grain yield and loss in stem dry matter after anthesis showed a negative trend under well-watered field conditions but no relationship under drought. In contrast, Cruz–Agudo *et al.* (2000) working on three spring wheat cultivars declared positive associations between the loss of dry mass from different internodes, yield, grain mass, and mass of grains per ear.

Stem length, weight, and specific weight (weight/length) are three factors affecting carbon storage and its remobilization capacity in the wheat stem. Working with 10 diverse bread and durum wheat cultivars under irrigation and drought stress conditions, Ehdaie *et al.* (2006) reported that dry matter mobilized under well-watered and drought conditions correlated significantly and positively with peduncle, penultimate, and lower internode maximum weight. Stem length did not correlate with stem mobilized dry matter in their study. However, a positive correlation between final plant height and mobilization of stem reserves was reported by Borrell *et al.* (1993). With respect to stem specific weight or stem solidness, Ehdaie and Shakiba (1996) declared that the specific weight of peduncle and penultimate internode at anthesis negatively correlated with water soluble carbohydrate (WSC) levels, both under well-watered and drought conditions. Interestingly, Saint Peirre *et al.* (2010), considering 36 wheat genotypes with different levels of stem solidness, reported that stem solidness correlated positively with WSC per stem and grain yield. All these observations suggest that the relationship between stem characteristics and carbon remobilization needs further exploration.

Growth conditions have pronounced effects on carbohydrate storage in vegetative parts. Under optimal conditions, assimilation and storage of assimilates are high (Blum 1998). Therefore, well-watered and large plants may store more WSC in their stems and contribute more of these carbohydrates to the grain than small plants (Davidson & Chevalier 1992). There is little information on stem dry matter remobilization among a large number of wheat cultivars when both pre- and post-anthesis remobilizations are quantified simultaneously. Given this, we quantified the amount of pre- and post-anthesis remobilization in 81 Iranian wheat cultivars grown under different environmental conditions. The associations between stem reserve remobilization and grain yield were investigated. Possible relationships between stem characteristics and carbohydrate remobilization were also explored.

MATERIAL AND METHODS

Seventy-five Iranian bread wheat cultivars, two foreign bread wheat (Kauz and Montana) and four durum cultivars (Yavarus, Simine, Shovamald, and Stark) released from 1930 to 2006 were considered in the current work (Table 1). They were commonly grown in Iran during this period and covered up to 90% of the total area of cultivation. Experiments were performed at Parsabad, located in the Moghan region in northwestern Iran (39°36'N, 47°57'E and 45 m a.s.l.). Parsabad has a warm Mediterranean climate, with cold winters, humid springs and summers with average annual precipitation of 271 mm.

Trials were conducted over crop seasons 2010–2011 (Year 1) and 2013–2014 (Year 2) under well-watered conditions at the agriculture research farm of Moghan College of Agriculture and Natural Resources, University of Mohaghegh Ardabili. The 81 cultivars were sown (300 seeds/m^2) on Nov 17–19, 2010, as a recommended date for wheat sowing, and on Dec 11, 2013, as a late sowing date, when plants were exposed to higher temperatures during the grain filling period. The experimental design was a simple lattice (9 × 9) with two replications. There were four rows in each plot in a north-south direction; rows were 2 m long with 0.2 m spacing. Fertilizers applied were 200 kg/ha of diammonium phosphate ($(NH_4)_2HPO_4$) and 100 kg/ha of urea ($CO(NH_2)_2$) before planting, and 50 kg/ha of urea top-dressed at jointing. In the 2010–2011 and 2013–2014 seasons, plants were irrigated five and four times from sowing to maturity, respectively. Approximately 55 mm of irrigation water was applied each time.

https://doi.org/10.17221/93/2017-CJGPB

Table 1. Wheat cultivars used in the Parsabad–Moghan experiments during 2010–2011 and 2013–2014 growing seasons

Cultivar No.	Cultivar name	Origin	Year of release in Iran	Cultivar No.	Cultivar name	Origin	Year of release in Iran
1	Arta	Iran	2006	42	Shahi	Iran	1967
2	Azadi	Iran	1979	43	Shole	Iraq	1957
3	Azar 1	Iran	1956	44	Shovamald	CIMMYT	2003
4	Azar2	Iran	1999	45	Shahriar	Iran	2002
5	Atrak	CIMMYT	1995	46	Shirodi	CIMMYT	1997
6	Arvand	Iran	1973	47	Shiraz	Iran	2002
7	Estar	CIMMYT	1995	48	Tabasi	Iran	1951
8	Akbari	Iran	2006	49	Adl	Iran	1962
9	Alborz	CIMMYT	1978	50	Frontana	Brazil	–
10	Alvand	Iran	1995	51	Falat	CIMMYT	1990
11	Alamut	Iran	1995	52	Fongh	China	–
12	Omid	Iran	1956	53	Ghods	Iran	1989
13	Inia	CIMMYT	1968	54	Kaveh	Iran	1980
14	Spring BC Roshan	Iran	1998	55	Gascogne	France	1994
15	Winter BC Roshan	Iran	1998	56	Crossed Alborz	Iran	–
16	Bam	Iran	2006	57	Crossed Shahi	Iran	–
17	Bulani	Iran	-	58	Crossed Falat Hamun	Iran	2002
18	Baiat	Iran	1976	59	Kavir	Iran	1997
19	Bistun	Iran	1980	60	Karaj 1	Iran	1973
20	Pishtaz	Iran	2002	61	Karaj 2	Iran	1973
21	Chamran	CIMMYT	1997	62	Karaj 3	Iran	1976
22	Chanab	Iran	1975	63	Gaspard	France	1994
23	Khazar 1	Iran	1973	64	Gholestan	CIMMYT	1986
24	Khalij	Iran	1960	65	Marun	Iran	1991
25	Darab 2	CIMMYT	1995	66	Marvdasht	Iran	1999
26	Daria	CIMMYT	2006	67	Moghan 1	Iran	1973
27	Dez	CIMMYT	2002	68	Moghan 2	CIMMYT	1974
28	Durum Yavarus	CIMMYT	1996	69	Moghan 3	Iran	2006
29	Rasul	CIMMYT	1992	70	Mahdavi	Iran	1995
30	Roshan	Iran	1958	71	Naz	CIMMYT	1978
31	Zakros	ICARDA	1996	72	Navid	Iran	1968
32	Zarrin	Iran	1995	73	Niknazhad	ICARDA	1995
33	Soisson	France	1994	74	Hamun	Iran	2002
34	Sabalan	Iran	1981	75	Hirmand	Iran	1991
35	Sepahan	Iran	2006	76	Verinak	CIMMYT	–
36	Sorkhtokhm	Iran	1957	77	DN-11	CIMMYT	–
37	Sardari	Iran	1930	78	Stark	CIMMYT	2005
38	Somaye 3	China	-	79	WS-82-9	–	–
39	Siatan	ICARDA	2006	80	Kauz	–	–
40	Simine	Iran	1997	81	Montana	–	
41	Shahpasand	Iran	1942				–

https://doi.org/10.17221/93/2017-CJGPB

In each plot, three main stems from the two middle rows were harvested at random at anthesis, 16 days after anthesis (16 DAA), and at physiological maturity. The main stems were harvested and immediately dried in a forced-air dryer at 70°C for 48 h to minimize respiration and weight losses. Then leaf blade and sheaths were removed from the stem. The length, weight, and specific weight (stem weight/stem length) of each stem were recorded. Total, pre-, and post-anthesis dry matter remobilization amounts were calculated as follows: Total dry matter remobilization = stem weight at 16 DAA – stem weight at maturity; Pre-anthesis dry matter remobilization = stem weight at anthesis – stem weight at maturity; Post-anthesis dry matter remobilization = total dry matter remobilization – pre-anthesis dry matter remobilization (Zhang *et al.* 2013). In the second year (Year 2), oven-dried stems were divided into three segments: the peduncle, penultimate and lower internodes and internode length, weight, specific weight, and dry matter remobilization were measured as described above.

In 2010–2011, grain yield was recorded per square meter. At maturity, 1 m^2 per plot sections was cut at ground level and then grain yield was obtained after threshing. In 2013–2014, there were some non-uniform plots differing from the others in plant density. Therefore the main stem grain yield was measured. To achieve this, ten spikes of main stems were taken at random at maturity; threshed and their averages were obtained as well.

For the traits that were in common between Year 1 and Year 2, analyses of variance (ANOVA) were performed over two years using SAS statistical software (Ver. 9.1.3, 2004). First, data from Year 1 and Year 2 were analysed separately according to a lattice design. Analysed data from Years 1 and 2 were considered as replication 1 and 2, respectively. Replications 1 and 2 were then combined based on a randomized complete block design (RCBD) (Joudi *et al.* 2014). Other data were analyzed separately in each growing season according to a lattice design and adjusted means were considered. Contrast analysis was used to compare wheat cultivars of different origin. The Pearson correlation coefficient was calculated to study the relationships between measured traits. Student's t-test was used to test the significance of the correlation coefficient. Correlation analysis was performed using SPSS statistical software (Ver. 17.0, 1998). Principal component (PC) analysis was conducted using MINITAB (Minitab 16 Statistical Software 2010).

RESULTS

General. Due to late sowing date, and lower temperature that occurred between December and March during the 2013–2014 growing season, establishment of the cultivated plants was delayed until late winter. Table 2 shows that the numbers of days with maximum air temperature exceeding 25 or 30°C during the grain filling period were higher in the second year. Therefore, cultivars in Year 2 were exposed to higher temperature stress during grain filling than those in Year 1.

Combined analysis of variance showed that the main effects for year were significant for the most of the traits that were in common between Years 1 and 2 (Table 3). Similar results were found when the main effects of cultivar were considered. Cultivar × year interaction was also significant for all the traits that were in common across years (Table 3). Significant cultivar × year interaction results from changes in the magnitude of the differences between cultivars in different years or from changes in the relative ranking of cultivars. On the basis of these results, data from Year 1 and 2 are presented separately.

Year 1. Stem length was 69 cm on average at anthesis. Between anthesis and 16 DAA, mean stem length increased 16 cm, reaching 85 cm and then remaining more or less constant until maturity (Table 4). The height of the stems varied considerably among tested cultivars. For example, the highest and the lowest values of stem length at 16 DAA were 119 and 63 cm, respectively (Figure 1a).

Stem weight, averaged among cultivars, was 972 mg at anthesis. From anthesis to 16 DAA, mean stem weight increased significantly to 1604 mg; this trait then decreased to 1183 mg at maturity (Table 4). There

Table 2. Number of days with daily maximum air temperature exceeding 25 or 30°C during grain filling of 81 well-watered wheat cultivars grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 growing seasons (Year 2)

Season	Days number from the earliest anthesis date to the latest maturity date	Days with maximum air temperature	
		> 25°C	> 30°C
Year 1	47	35	9
Year 2	45	43	27

https://doi.org/10.17221/93/2017-CJGPB

Table 3. Mean squares for measured traits (GDD of anthesis (°C); stem length (cm) measured at anthesis, 16 DAA and at physiological maturity; stem weight (mg) recorded at anthesis, 16 DAA and at physiological maturity; SSW measured at anthesis, 16 DAA and at physiological maturity; pre-anthesis, post-anthesis, and total (pre-anthesis + post-anthesis) dry matter remobilization) of 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 and 2013–2014 growing seasons

SOV	df	GDD of anthesis	Stem length			Stem weight			SSW			Dry matter remobilization		
			anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	pre-anthesis	post-anthesis	total (pre + post)
Replication (year)	1	19736648**	455**	8116**	4841**	170**	392**	233*	2.49^{ns}	13.7^{ns}	55**	32.3**	1750**	1310**
Treatment (cultivar)	80	2887**	248**	332**	306**	44**	88**	82**	8.03**	11.5**	6.9*	2.7^{ns}	28.9^{ns}	34.2*
Error (year × cultivar)	80	899**	28.5**	24.3**	35.4**	17**	34**	34**	2.67**	5.1**	4.3**	2.6**	26.9**	22.3**
Averaged error $^{\#}$	128$^{\&}$	91	7.78	5.6	8.8	6	10	12	1.16	1.8	2.1	1.4	10.6	11.0

GDD – growing degree days; DAA – days after anthesis; SSW – stem specific weight; SOV – source of variation; df – degree of freedom; ^{ns}not significant; *significant at $P = 0.05$; **significant at $P = 0.01$; $^{\#}$[(Intra Block Error in Year1+ Intra Block Error in Year2)/2]/Number of Replications; $^{\&}$(df of Intra Block Error in Year1+ df of Intra Block Error in Year2)

Table 4. Basic statistics for stem-related traits of 81 wheat cultivars grown under well-watered conditions at Parsabad–Moghan during the 2010–2011 growing season

	Stem length (cm)			Stem weight (mg)			SSW (mg/cm)			Dry matter remobilization (mg)		
	anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	pre-anthesis	post-anthesis	Total (pre + post)
Minimum	47	63	60	553	1083	736	8.9	13.6	9.7	0	26	3
Maximum	109	119	115	1553	2138	1707	20.2	24.6	21.4	264	939	909
Mean	69	85	83	972	1604	1183	14.3	19.1	14.4	16	408	423
SD	12	14	13	172	253	213	2.2	2.7	1.9	41	182	182
CV	17	16	16	18	16	18	16	14	13	256	44	43

SD – standard deviation; CV – coefficient of variation; DAA – days after anthesis; SSW – stem specific weight

https://doi.org/10.17221/93/2017-CJGPB

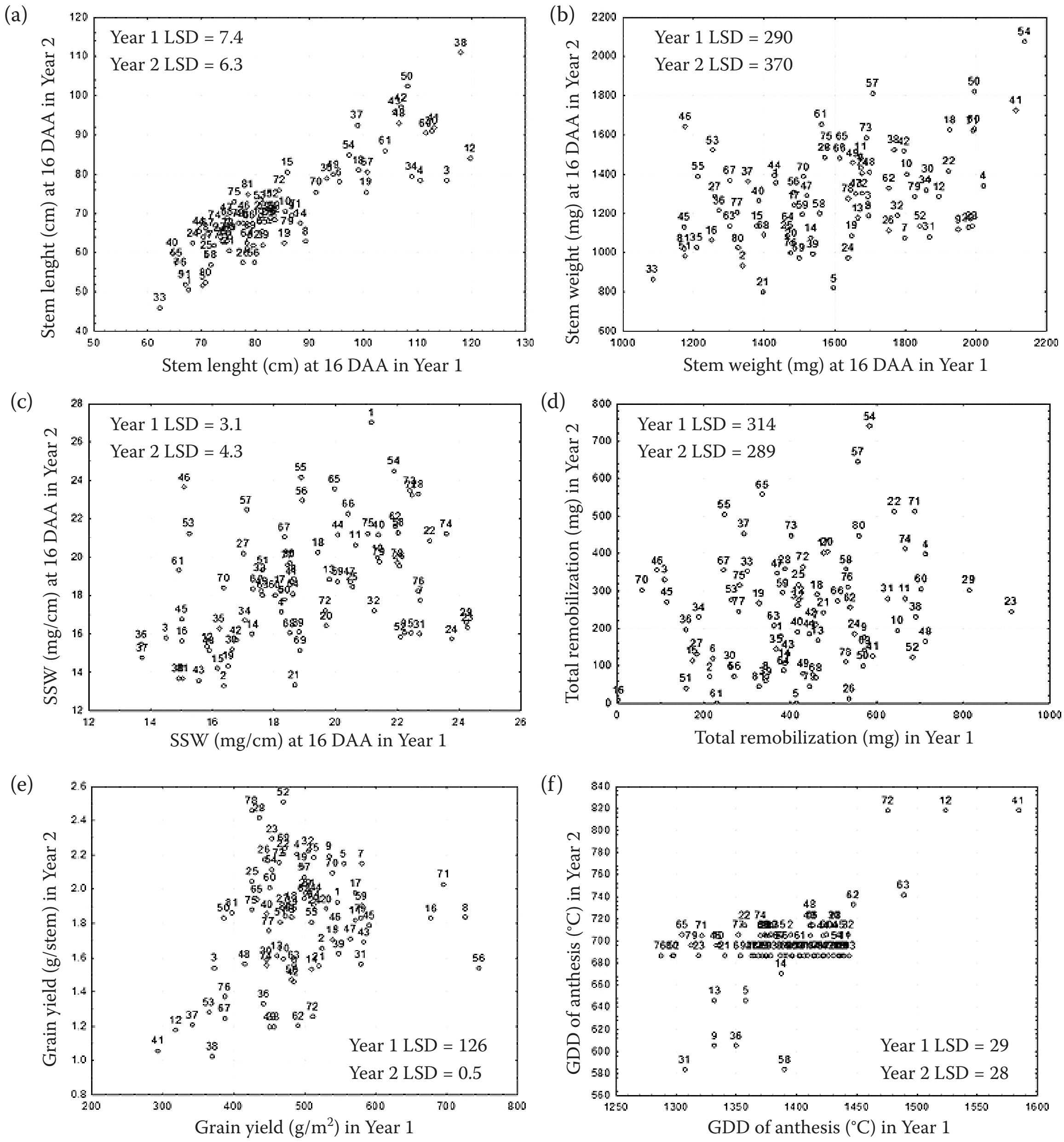

Figure 1. The evaluation of (a) stem length, (b) stem weight, (c) stem specific weight (SSW) recorded at 16 days after anthesis (DAA), (d) stem total dry matter remobilization, (e) grain yield, and (f) growing degree days (GDD) of anthesis in 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 (Year 2) growing seasons; values of least significant differences (LSD) are indicated at 5% probability level; numbers in the figure are cultivars (see Table 1)

Table 5. Contrast analysis for total remobilization of stem (pre-anthesis + post-anthesis remobilization) among Iranian wheat cultivars of different origin grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 (Year 2) growing seasons

Contrast	Year 1		Year 2	
	remobilization (mg)	PR > F	remobilization (mg)	PR > F
Cultivars with Iran origin vs Cultivars with CIMMYT origin	419 vs 452	0.33	263 vs 202	0.03
Cultivars with Iran origin vs Cultivars with ICARDA origin	419 vs 541	0.11	263 vs 262	0.98
Cultivars with CIMMYT origin vs Cultivars with ICARDA origin	452 vs 541	0.26	202 vs 262	0.35

https://doi.org/10.17221/93/2017-CJGPB

was a substantial variation in stem weight among the cultivars. The differences between the highest and the lowest values of stem weight were 1000, 1055, and 971 mg at anthesis, 16 DAA, and maturity, respectively (Table 4 and Figure 1b).

Mean stem specific weight was 14.3 mg/cm at anthesis. This trait increased as a function of time, reaching higher values at 16 DAA and then decreased until maturity (Table 4). Similar to stem length and weight, large variations could be found for stem specific weight among wheat cultivars (Figure 1c).

Most of the cultivars tested during the 2010–2011 growing season did not show pre-anthesis remobilization in their stem. In contrast, all used stem dry matter that had been stored after anthesis (Table 4). Pre- and post-anthesis remobilization means were 16 and 408 mg, respectively. Large genetic variations in total remobilization, pre- plus post-anthesis remobilization were found among wheat cultivars. Total remobilization ranged from 3 to 909 mg (Figure 1d). But, when examined cultivars were classified according to their origin, no significant differences were found between them with respect to total remobilization (Table 5). The proportions of pre- and post-anthesis remobilization in determining the total remobilization were 4% and 96% on average, respectively (Table 4).

Large variations were found among cultivars in grain yield, when grain yield ranged from 293 to 746 g/m^2 (Figure 1e). Crossed Alborz, Akbari, and Naz were the most productive cultivars whereas Shahpasand, Omid, and Sardari performed the worst.

Correlation analysis revealed no significant associations between stem length measured either at anthesis or at 16 DAA and dry matter remobilization (Table 6). Stem weight and stem specific weight recorded at 16 DAA anthesis correlated positively and significantly with dry weight loss from the stem. No clear relationship was found between total remobilization from the stem and observed grain yield (Table 6).

PC analysis based on the nine traits was performed for tested cultivars. Two principal components accounted for 64.5% (34.4% for PC1 and 30.1% for PC2) of the total variance in the data (Table 7). The first principal component had a high positive component loading from stem length and weight and a high negative component loading from SSW and grain yield. Also, the second principal component had a high positive component loading from SSW, stem weight, and stem dry matter remobilization. Therefore, cultivars such as 29 (Rasul), 71 (Naz),

Table 6. Correlation coefficients between measured traits in the main stem of 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 (Year 2) growing seasons

		GDD of anthesis	Stem length at anthesis	Stem length at 16 DAA	Stem weight at anthesis	Stem weight at 16 DAA	SSW at anthesis	SSW at 16 DAA	Total remobilization of stem
Year 1	total remobilization of stem	−0.17^{ns}	0.03^{ns}	0.09^{ns}	0.19^{ns}	0.65**	0.20^{ns}	0.60**	1.00
	grain yield per square meter	−0.21^{ns}	−0.21^{ns}	−0.24*	0.05^{ns}	−0.08^{ns}	0.26*	0.14^{ns}	−0.13^{ns}
Year 2	total remobilization of stem	0.03^{ns}	−0.05^{ns}	0.02^{ns}	−0.03^{ns}	0.42**	−0.01^{ns}	0.44**	1.00
	main stem grain yield	−0.21^{ns}	−0.21^{ns}	−0.24*	0.08^{ns}	−0.04^{ns}	0.30**	0.15^{ns}	0.04^{ns}

GDD – growing degree days; DAA– days after anthesis; SSW – stem specific weight; ^{ns}not significant; *significant at 5% probability level; **significant at 1% probability level

Czech J. Genet. Plant Breed., 54, 2018 (3): 123–134

https://doi.org/10.17221/93/2017-CJGPB

Table 7. Results of principal component analysis for stem-related traits measured at anthesis and 16 DAA and final grain yield in 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 (Year 1) and 2013–2014 (Year 2) growing seasons

	Component	Percent of variance	Cumulative percentage	Stem length at anthesis	Stem length at 16 DAA	Stem weight at anthesis	Stem weight at 16 DAA	SSW at anthesis	SSW at 16 DAA	Total remobilization of stem	GDD of anthesis	Grain yield*
Year 1	PC1	0.344	0.344	0.533	0.546	0.232	0.311	–0.288	–0.260	0.038	0.269	–0.205
	PC2	0.300	0.645	0.048	0.017	0.397	0.461	0.393	0.495	0.457	–0.128	0.055
Year 2	PC1	0.326	0.326	0.550	0.559	0.387	0.390	–0.097	–0.123	0.039	0.175	–0.165
	PC2	0.252	0.578	–0.132	–0.114	0.279	0.402	0.477	0.574	0.338	0.077	0.230

DAA– days after anthesis; SSW: stem specific weight; GDD – growing degree days; *stem grain yield was considered in Year 2

Table 8. Basic statistics for internodes and stem-related traits of 81 wheat cultivars grown under well-watered conditions at Parsabad–Moghan during the 2013–2014 growing season

		Length (cm)			Weight (mg)			Specific weight (mg cm^{-1})			Dry matter remobilization (mg)		
		anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	anthesis	16 DAA	maturity	pre-anthesis	post-anthesis	total (pre + post)
Peduncle	Minimum	20	21	24	138	253	193	5.3	8.4	6.7	0	0	0
	Maximum	51	49	52	470	665	713	16.4	18.0	13.9	70	225	230
	Mean	33	35	35	296	425	378	9.1	12.1	10.7	9	53	62
	SD	6	6	6	67	88	86	1.7	1.9	1.7	17	49	48
	CV	17	18	17	23	21	23	19	16	16	188	92	77
Penultimate	Minimum	12	13	13	160	260	165	8.9	14.7	11.0	0	0	0
	Maximum	32	31	37	443	625	645	28.1	38.7	27.3	93	250	288
	Mean	18	19	19	277	412	333	15.6	22.7	18.0	12	77	88
	SD	3	4	4	58	81	82	3.5	4.6	3.6	21	60	61
	CV	19	19	23	21	20	25	22	20	20	175	78	69
Lower internodes	Minimum	5	9	7	118	225	123	17.0	16.9	14.8	0	0	0
	Maximum	37	36	37	700	863	1318	35.3	39.1	48.9	210	268	298
	Mean	14	17	17	329	449	396	24.0	28.0	23.4	24	69	93
	SD	6	6	6	118	125	159	4.3	5.4	5.3	39	67	69
	CV	41	33	34	36	28	40	18	19	23	162	97	74
Stem	Minimum	45	46	46	510	803	515	10.1	13.3	9.8	0	0	0
	Maximum	109	111	112	1340	2078	2075	23.3	27.0	25.3	258	665	740
	Mean	65	70	71	902	1286	1107	14.0	18.5	15.5	44	199	243
	SD	11	12	13	179	243	267	2.4	3.0	2.8	60	149	152
	CV	18	18	18	20	19	24	31	16	18	136	74	62

SD – standard deviation; CV – coefficient of variation; DAA – days after anthesis

https://doi.org/10.17221/93/2017-CJGPB

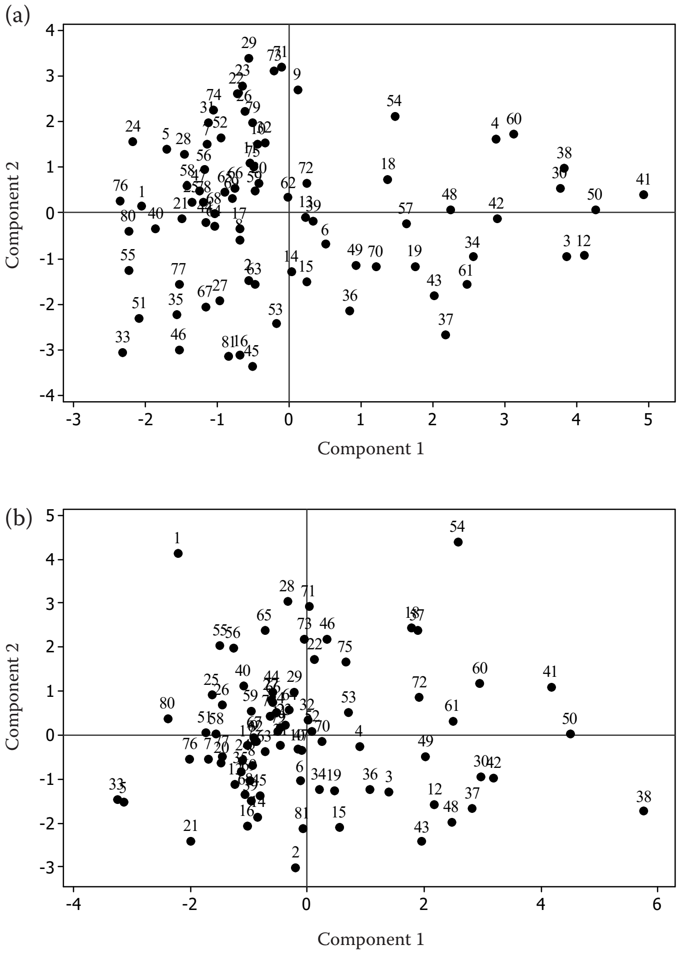

Figure 2. Scatter plots drawn based on the first and second components from principal component analysis using stem-related traits measured at anthesis and 16 days after anthesis (DAA) and final grain yield in 81 wheat cultivars grown at Parsabad–Moghan during 2010–2011 (a) and 2013–2014 (b) growing seasons; numbers in the figures are cultivars (see Table 1)

65 (Marun), and 73 (Niknazhad) with high PC2 and relatively low PC1 could be identified as superior cultivars for dry matter accumulation and recombination in their stem (Figure 2a).

Year 2. Mean stem length was 65 cm at anthesis. It reached 70 cm at 16 DAA, which is 15 cm shorter than the mean stem length observed in Year 1 (Table 8). The proportion of the main stem length partitioned into the length of different segments varied significantly among cultivars. At anthesis, for example, it ranged from 32% to 61% for peduncle, from 22% to 35% for penultimate internode, and from 13% to 42% for lower internodes (data not shown).

The peduncle, penultimate and lower internode weight at anthesis was 296, 277, and 329 mg on average, respectively. Between anthesis and 16 DAA, mean internode weight increased for all main stem segments which were measured (Table 8). The amount of these increases for peduncle, penultimate and lower internodes was 44%, 49%, and 36%, respectively. At 16 DAA, the lower internodes were still the heaviest internodes followed by the peduncle and penultimate internodes (Table 8). After reaching their maximum value, the internode weight decreased until maturity. The percent of internode dry weight loss between 16 DAA and maturity phases was 11%, 19%, and 12% for the peduncle, penultimate and lower internodes, respectively (Table 8). Mean stem weight was lower in Year 2 compared to Year 1 (compare Tables 4 and 8).

The highest values of internode specific weight were observed for the lower internodes, followed by penultimate internode and the peduncle (Table 8). Internode specific weight increased from anthesis to 16 DAA and decreased afterwards. These changes were more evident for the penultimate compared to the other internodes.

The majority of the cultivars examined in Year 2 did not show pre-anthesis remobilization in their internodes. In contrast, most of them showed post-anthesis remobilization (Table 8). Total remobilization mean for the peduncle, penultimate and lower internodes was 62, 88, and 93 mg, respectively. At the main stem level, total remobilization ranged from 0 to 740 mg in the wheat population (Figure 1d).

https://doi.org/10.17221/93/2017-CJGPB

Cultivars originated from Iran showed higher stem remobilization than those originated from CIMMYT whereas no significant difference was found between the former and cultivars of ICARDA origin (Table 5). Total remobilization of the main stem in Year 2 was 243 mg on average, 43% lower than that observed in Year 1 (compare Tables 4 and 8).

The cultivars showed significant differences in stem grain yield where this trait ranged from 1.02 to 2.51 g. Fongh obtained the first rank of this trait followed by two durum wheats Stark and Yavarus. Also, Somaye 3, Shahpasand, and Omid showed the lowest amount of stem grain yield (Figure 1e).

Relationships between the traits studied in correlation analysis showed that there were no clear associations between stem length and dry weight loss from the stem (Table 6). Stem weight and stem specific weight measured at 16 DAA correlated positively and significantly with total dry matter remobilization. Interestingly, there were no clear associations between the loss of dry matter from the stem and main stem grain yield (Table 6).

Results of PC analysis are presented in Table 7. The first component (PC1) explained 32.6% of the total variation and exhibited a high positive correlation with stem length and weight. On the other hand, stem grain yield had a negative effect on PC1. The second component (PC2) explained 25.2% of the total variation and had a high positive correlation with SSW, stem weight, stem dry matter remobilization, and stem grain yield. Thus, cultivars such as 28 (Yavarus), 71 (Naz), 65 (Marun), and 73 (Niknazhad) with high PC2 and relatively low PC1 would be promising candidates in terms of dry matter accumulation, remobilization, and stem grain yield (Figure 2b).

DISCUSSION

As plants are sessile organisms, they are forced to survive in environments with variable environmental stresses such as drought, heat, and cold stresses (Nakashima & Yamaguchi-Shinozaki 2006). Future climate scenarios predict further reductions in winter rainfall and an increase in temperature and atmospheric CO_2 (Ludwig & Asseng 2010), suggesting that during their life cycle in the future, cultivated plants will experience more heat and drought stresses. Temperate crops such as wheat and barley are able to accumulate water-soluble carbohydrates (fructans, glucose, fructose and sucrose, Zhang *et al.* 2015) in their stems when there is an excess of photoassimilates and they reuse these storages in the later growth stages if necessary. This strategy could be considered as an important adaptive trait to future environmental changes and is important in breeding cultivars with improved grain yield.

In our field experiments, wheat plants reached their maximum length between anthesis and 16 DAA, after which there were no further significant changes in plant height. The changes in stem length from anthesis to 16 DAA could be attributed to increases in the upper internode length since the lower parts of the stem remain unchanged in length after anthesis (Scofield *et al.* 2009). From anthesis to 16 days afterwards, internode weights increased, indicative of carbohydrate accumulation in the stem (Joudi *et al.* 2012). The accumulation of reserves in the different internodes started near the end of extension growth. That is to say, the accumulation of reserves in the lower internodes takes place over long periods of time compared to the upper internodes. Accumulation of stem reserves continues until 10–20 DAA when maximal amounts are reached (Schnyder 1993).

Our results revealed substantial genetic variations in internode weight and dry matter accumulation in stems during the early grain growth of wheat. Although differences in phenological events observed between the examined cultivars caused differences in onset and duration of storage reserves, some cultivars with similar developmental phases differed in stem dry matter accumulation (compare Figure 1b and f). Physiological aspects such as photosynthetic rate, sucrose transport, and fructan synthesizing enzymes (Joudi *et al.* 2012 and references therein) and morphological characters such as stem length and stem solidness (Saint Pierre *et al.* 2010) could also result in variations in stem dry weight accumulation.

Stem weight decreased during 16 DAA-maturity phase, indicating the remobilization of stored carbohydrates to the grain. Schnyder (1993) stated that the mobilization of stem WSC generally starts during the period of a nearly constant rate of dry matter accumulation in grains, and coincides with a strong decrease in the net assimilation rate. In the current study, the lower internodes could remobilize more stored dry matter to the grain followed by the penultimate internode and the peduncle. These results are in line with those of Ehdaie *et al.* (2006), stating that growth and development of the lower internodes in wheat occur in early spring when water supply and temperature are favourable for plant growth so that a large portion of assimilates is accumulated in the

https://doi.org/10.17221/93/2017-CJGPB

lower internodes, which in turn could be a major source for dry matter remobilization after anthesis.

The amount of pre-anthesis remobilization in these studies was in the lower range when compared to other studies (Flood *et al*. 1995; Inoue *et al*. 2004; Ma *et al.* 2014). Latiri *et al.* (2013), working on durum wheat with different water and nitrogen supply, reported that three types of remobilization for the same cultivar in the field conditions can occur: (*i*) long-term remobilization (pre-anthesis remobilization) that occurred in rain-fed treatments and also in an irrigated one but with low leaf area index at anthesis; (*ii*) short-term remobilization (post-anthesis remobilization) which was observed only for irrigated treatments and (*iii*) both pre- and post-anthesis remobilizations that took place in rain-fed and irrigated treatments. Užík and Žofajová (2006) worked on winter wheat lines in field experiments and reported that pre-anthesis remobilization was observed only in a year with unfavourable weather conditions, while no pre-anthesis remobilization occurred in a year with favourable weather conditions. All these observations suggest that pre-anthesis remobilization contributes more to grain yield when wheat cultivars produce less biomass from anthesis to maturity than is needed for grain filling. It seems that under our experimental conditions (even with the later sowing date in Year 2), current photosynthesis and post-anthesis remobilization could meet the sink demands.

Stem length measured either at anthesis or at 16 DAA did not generally correlate with total dry matter remobilization. In contrast, stem weight and stem specific weight measured at 16 DAA correlated significantly and positively with stem dry weight loss both during 2010–2011 and 2013–2014 growing seasons. Ehdaie *et al*. (2006) also reported that dry matter mobilized in well-watered and drought conditions correlated positively with internode maximum weight. These results suggest that plant breeders working on stem dry weight remobilization should pay more attention to stem weight and stem specific weight than to stem length.

By using 81 cultivars, we studied the overall association between loss in stem dry weight and grain yield by phenotypic correlation and we found no clear relationships between remobilization from the stem and grain yield. If the loss in stem dry weight is due to remobilization of assimilates to the grain, a positive relationship between grain yield and loss in stem weight after anthesis is expected (Ehdaie & Waines 1996). One possible explanation for the obtained result is that a large population with different agronomical, physiological, and morphological traits was used in the current study. Among plant materials examined, there were some cultivars that had a similar amount of total remobilization but yet differed significantly in their grain yield. Also, there were cultivars with similar yields that showed differences in their total remobilization (data not shown). Depending on the cultivars included in the study and on the environmental conditions (e.g. drought stress severity) in which they are grown, the association between grain yield and dry matter remobilization from the stem may be different (Ehdaie & Waines 1996; Ma *et al*. 2014).

CONCLUSION

A large genetic variation in stem dry matter storage and remobilization observed among Iranian wheat cultivars suggests that these traits could be manipulated in wheat breeding programs. However, improving dry matter accumulation and remobilization from the wheat stem is a challenging task, as there seems to be no simple relationship between these traits and grain yield (see above). Remobilization of dry matter stored before anthesis (pre-anthesis remobilization) was lower in Iranian wheat cultivars than that accumulated after anthesis, suggesting that under the conditions tested, current photosynthesis along with post-anthesis remobilization could meet most of the sink demand. Among stem related traits, stem dry weight and specific weight measured at 16 DAA showed positive associations with dry matter remobilization, suggesting that these traits are valuable tools for incorporation in breeding programs dealing with improved carbohydrate remobilization.

Acknowledgments. Financial supports for these studies were provided by University of Mohaghegh Ardabili. Wim Van den Ende is supported by funding from FWO Vlaanderen.

References

Blum A. (1998): Improving wheat grain filling under stress by stem reserve mobilization. Euphytica, 100: 77–83.

Bonnet G.D., Incoll L.D. (1992): The potential pre-anthesis and post-anthesis contributions of stem internodes to grain yield in crops of winter barley. Annals of Botany, 69: 219–225.

https://doi.org/10.17221/93/2017-CJGPB

Borrell A., Incoll L.D., Dalling M.J. (1993): The influence of the *Rht1* and *Rht2* alleles on the deposition and use of stem reserve in wheat. Annals of Botany, 71: 317–326.

Cruz–Aguado J.A., Rodés R., Pérez I.P., Dorado M. (2000): Morphological characteristic and yield components associated with accumulation and loss of dry mass in the internodes of wheat. Field Crops Research, 66: 129–139.

Davidson D.J., Chevalier P.M. (1992): Storage and remobilization of water-soluble carbohydrates in stem of spring wheat. Crop Science, 32: 186–190.

Ehdaie B., Shakiba M.R. (1996): Relationship of internode–specific weight and water–soluble carbohydrates in wheat. Cereal Research Communications, 24: 61–67.

Ehdaie B., Waines J.G. (1996): Genetic variation for contribution of preanthesis assimilates to grain yield in spring wheat. Journal of Genetic and Breeding, 50: 47–56.

Ehdaie B., Alloush G.A., Madore M.A., Waines J.G. (2006): Genotypic variation for stem reserves and mobilization in wheat: I. postanthesis changes in internode dry matter. Crop Science, 46: 735–746.

Flood R.G., Martin P.J., Gardner W.K. (1995): Dry matter accumulation and partitioning and its relationship to grain yield in wheat. Australian Journal of Experimental Agriculture, 35: 495–502.

Inoue T., Inanaga S., Sugimoto Y., El Siddig K. (2004): Contribution of pre-anthesis assimilates and current photosynthesis to grain yield, and their relationships to drought resistance in wheat cultivars grown under different soil moisture. Photosynthetica, 42: 99–104.

Joudi M., Ahmadi A., Mohamadi V., Abbasi A., Vergauwen R., Mohamadi H., Van den Ende W. (2012): Comparison of fructan dynamics in two wheat cultivars with different capacities of accumulation and remobilization under drought stress. Physiologia Plantarum, 144: 1–12.

Joudi M., Ahmadi A., Mohamadi V., Abbasi A., Mohammadi H. (2014): Genetic changes in agronomical and phenologic traits of Iranian wheat cultivars grown in different environmental conditions. Euphytica, 196: 237–249.

Latiri K., Lhomme J.P., Lawlor D.W. (2013): Grain filling of durum wheat through assimilate remobilization under semi–arid conditions. Experimental Agriculture, 49: 197–211.

Ludwig F., Asseng S. (2010): Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. Agricultural Systems, 103: 127–136.

Ma J., Huang G.B., Yang D.L., Chai Q. (2014): Dry matter remobilization and compensatory effects in various internodes of spring wheat under water stress. Crop Science, 53: 1–9.

Nakashimaa K., Yamaguchi–Shinozak K. (2006): Regulons involved in osmotic stress–responsive and cold stress–responsive gene expression in plants. Physiologia Plantarum, 126: 62–71.

Pheloung P.C., Siddique K.H.M. (1991): Contribution of stem dry matter to grain yield in wheat cultivars. Australian Journal of Plant Physiology, 18: 53–64.

Saint Pierre C., Trethowan R., Reynolds M. (2010): Stem solidness and its relationship to water–soluble carbohydrates: association with wheat yield under water deficit. Functional Plant Biology, 37: 166–174.

Schnyder H. (1993): The role of carbohydrates storage and redistribution in the source–sink relations of wheat and barley during grain filling– a review. New Phytologist, 123: 233–245.

Scofield G.N., Ruuska S.A., Aoki N., Lewis D.C., Tabe L.M., Jenkins C.L.D. (2009): Starch storage in the stems of wheat plants: localization and temporal changes. Annals of Botany, 103: 859–868.

Užík M., Žofajová A. (2006): Translocation and accumulation of dry matter in winter wheat genotypes. Cereal Research Communications, 34: 1013–1020.

Zhang J., Xu Y., Chen W., Dell B., Vergauwen R., Biddulph B., Khan N., Luo H., Appels R., Van den Ende W. (2015): A wheat 1-FEH w3 variant underlies enzyme activity for stem WSC remobilization to grain under drought. New Phytologist, 205: 293–305.

Zhang Y.P., Zhang Y.H., Xue Q.W., Wang Z.M. (2013): Remobilization of water soluble carbohydrates in non–leaf organs and contribution to grain yield in winter wheat under reduced irrigation. International Journal of Plant Production, 7: 97–116.

Received for publication July 4, 2017
Accepted after corrections December 4, 2017
Published online March 21, 2018