Plant Knowledge Journal
ISSN: 2200-5390
EISSN: 2200-5404
2(3):99-107 (2013)

Southern Cross Publishing Group
Australia

Effect of post-anthesis water deficiency on storage capacity and contribution of stem reserves to the growing grains of wheat cultivars

Majid Abdoli[1*], Mohsen Saeidi[2], Saeid Jalali-Honarmand[2], Sirus Mansourifar[2] and Mohammad-Eghbal Ghobadi[2]

[1]Department of Agronomy and Plant Breeding, Faculty of Agriculture, Maragheh University, Maragheh, Iran
[2]Department of Agronomy and Plant Breeding, Campus of Agriculture and Natural Recourse, Razi University, Kermanshah, Iran

***Corresponding author: majid.abdoli64@yahoo.com**

Abstract

The experiment described here was carried out to determine the effects of post-anthesis water deficiency stress on dry matter and carbohydrate accumulation and their remobilization from different parts of stem to the growing grain in different wheat cultivars. To this end, an experiment was laid out as a split-plot arranged in a randomized completed block design with three replications during the years 2010-2011. The results showed that post-anthesis water deficit significantly decreased grain yield, TGW and grain number per spike and biomass in evaluated cultivars. The results showed that in all evaluated cultivars maximum weight of peduncle, penultimate and lower internodes, on average, were reached at 14 and 7 days after anthesis and at anthesis, respectively. Post-anthesis water deficiency stress had no significant effect on internodes length and stem weight, but, significantly increased dry matter remobilization and remobilization efficiency of lower internodes by 16.8% and 17%, respectively. Lower internodes had the highest storage capacity of dry matter and remobilization efficiency. Our analyses suggest that, with respect to high amount of dry matter accumulation in lower internodes, increasing of remobilization efficiency of lower internodes can significantly raises grain yield of wheat cultivars especially in arid and semi-arid regions.

Keywords: wheat, water deficiency stress, grain yield, internode, remobilization.
Abbreviations: TGW_Thousand grain weight.

Introduction

Water deficit is the most important limiting factor for crop production (Chaves et al., 2003) and increasingly severe problem in many regions of the world (Passioura, 2007). Among the stresses such as water deficit, salinity, cold and heat, drought is the most important factor in reducing grain yield up to 50 percent (Mittler, 2006; Shao et al., 2008). A common effect of water deficit stress on crop plants is the reduction of fresh and dry biomass production (Farooq et al., 2009; Abdoli and Saeidi, 2012). Plant productivity under water deficit stress is strongly related to the processes of dry matter partitioning and temporal biomass distribution (Kage et al., 2004). The sensitivity of crop plants such as wheat (*Triticum aestivum* L.) to soil drought is particularly acute during the grain-filling period because the reproductive phase is extremely sensitive to plant water status (Anjum et al., 2003; Shao et al., 2008). Carbon requirements for grain growth in wheat are mainly prepared from current assimilation by photosynthesis and remobilization of reserves from the stems (Yang et al., 2000). One of the best approaches to achieve an acceptable wheat grain yield under drought conditions that current assimilation by photosynthesis decreased is using the potential of carbohydrate remobilization to the growing grains. When the photosynthesis was decreased after anthesis, assimilates produced prior the flowering get the more importance. Because the next stages of the plant growth has been provided by the translocation of stem reserves to the growing grain (Blum, 1998). Due to extensive changes in environmental conditions and application of different wheat cultivars, the amount of stem reserves that contributing in formation of grain yield, differed from 5% to 100% in different studies (Blum, 1998; Ehdaie et al., 2006 a, b). Yang et al. (2000) and Plaut et al. (2004) reported that under suitable conditions, acceptable amount of carbohydrates accumulate in the stem before anthesis. They also suggested that carbohydrate storage at the pre-anthesis stages may be dependent on plant traits after anthesis can support grain yield. Some drought tolerant cultivars which have the high potential for storage of photosynthetic assimilates in stem, also have high efficiency in translocation of these assimilate to the growing grains in stress condition (Gavuzzi et al., 1997). Stress condition that caused by water deficit, lead to early maturing of plant. In such circumstances stem carbohydrate remobilization significantly decreases (Kobata et al., 1992; Yang et al., 2001). With respect to the role of carbohydrate remobilization in grain yield stability under water deficit, these traits were used for the selection of resistant cultivars in conditions with terminal water deficit. This study was carried out to determine the amount of

Table 1. Minimum and maximum of temperature and relative humidity also total precipitation during growing season.

Month	Average of temperature (°C)		Monthly total of precipitation (mm)	Average of relative humidity (%)	
	Minimum	Maximum		Minimum	Maximum
Oct.	10.6	30.3	1	13.2	46.4
Nov.	4.5	21.9	31	22.8	66.8
Dec.	-1.5	16.8	24	26.5	62.4
Jan.	-2.2	9.6	50	47.1	91.0
Feb.	-2.7	8.0	65	52.1	94.2
Mar.	0.6	15.4	21	28.1	82.0
Apr.	4.5	20.1	47	24.6	78.8
May.	9.5	23.6	128	33.6	87.4
Jun.	12.8	33.8	0	11.3	51.1
Jul.	17.1	38.5	0	6.6	32.1
Aug.	18.1	39.5	0	6.0	27.7
Sep.	13.8	34.6	0	7.8	32.0

Source: Meteorological Office, Iran.

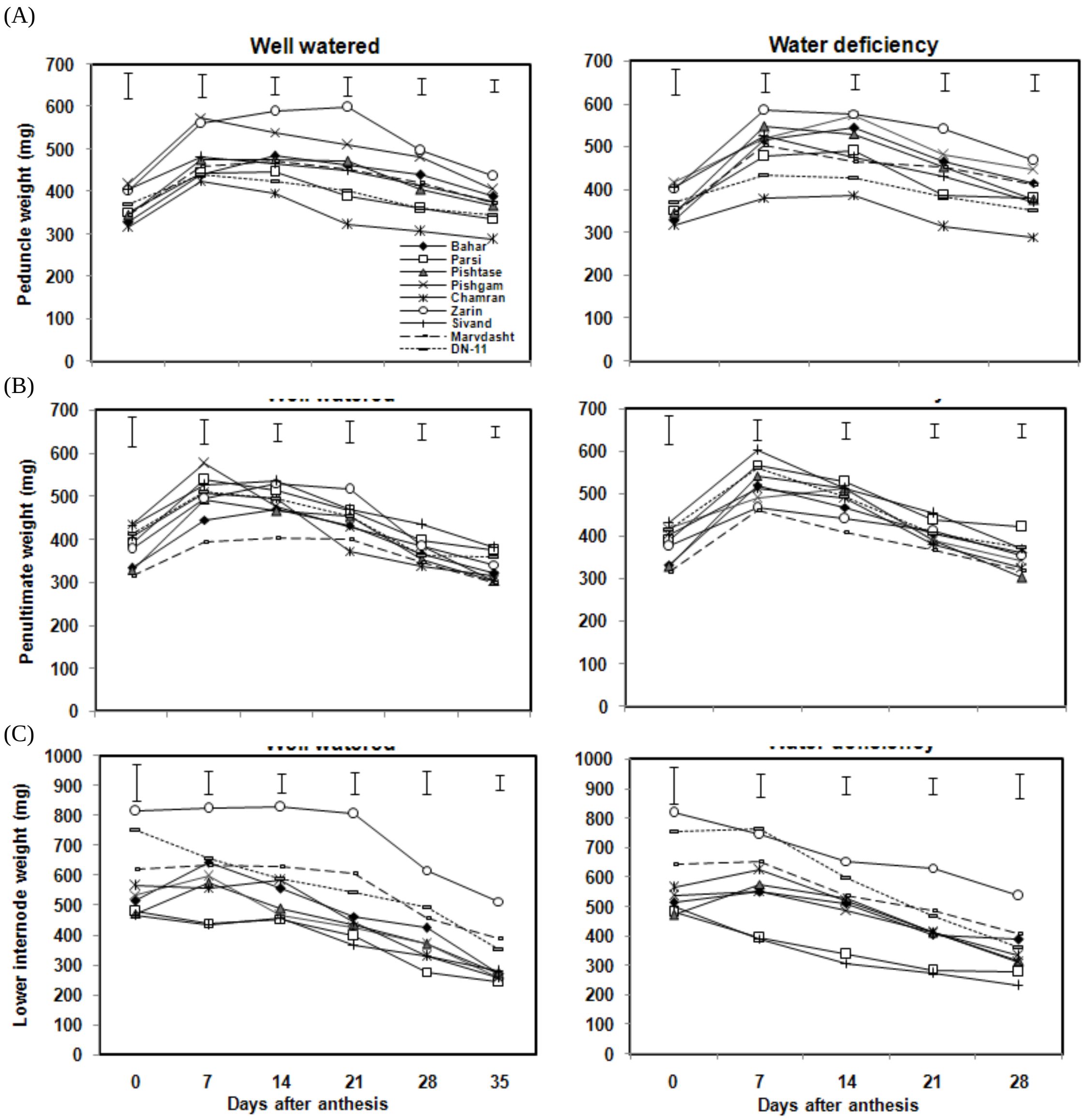

Fig 1. Dry weight changes of peduncle internode (A), penultimate internode (B) and lower internodes (C) during grain filling in seven bread wheat cultivars. Bars represent means ± standard error.

remobilization and Translocation of stem reserves in some cultivars of bread wheat under terminal drought stress.

Results and Discussion

Grain yield and 1000 grain weight

Post anthesis water deficiency stress caused 34 and 26 percent reduction in grain yield and grain weight in average respectively, but had no significant effect on no of grains/spike and no of spikes/m^2. The averages of grain yield and grain weight of different cultivars in controlled condition were 701 g/m^2 and 42.4 g respectively, while under water deficiency stress these values significantly reduced to 463 g/m^2 and 31.2 g. The findings from Shah and Paulsen (2003), when they imposed water deficit at different stages of grain growth separately, showed that significant reduction in grain yield production in these conditions may be result of reducing the production of photo-assimilates (source limitation) for grain filling, reducing the sink power to absorb of photo-assimilates and reducing the grain filling duration. They also reported that probably, the early processes of grain growth (cell division and formation of sink size) are less affected by water deficiency. Therefore, TGW and grain yield reduction under post anthesis water deficiency may be more reflects the lack of photo-assimilates supply for grain filling. These findings also are in agreement with Shah and Paulsen (2003), Yang and Zang (2006) and Ehdaie et al. (2006 a, b). Under control treatment, Chamran (561 g/m^2) cultivar had the lowest and Sivand and DN-11 cultivars (783 and 750 g/m^2 respectively) had the highest grain yield (Table 2). Under Post anthesis water deficiency, the lowest and highest significant reductions in grain yield were seen in Chamran (20%) and Zarin (38%) cultivars respectively. Minimum grain yield production under post anthesis water deficiency was related to the Marvdasht cultivar (410 g/m^2). So, planting of Marvdasht cultivar in such area where there is potential for occurrence of post anthesis water deficit may be associated with high risk. In post anthesis water deficiency, the highest reduction in TGW was seen in Parsi and Marvdasht cultivars and lowest reduction was seen in DN-11 and Chamran cultivars (Table 2).

Number of spike per m^{2}and number of grain per spike

Between control and post anthesis water deficiency conditions, in terms of number of spikes/m^2 and number of grain per spike were no significant differences (Table 2). This result is probably because the potential of these components are formed before spick initiation, so post anthesis water deficiency stress has no significant influence on them (Anjum et al., 2003; Saeidi et al., 2010). It can be seen from the data in Table 2. That significant differences were found among cultivars in terms of grains/spike and number of spike per m^2. In term of the number grains/spike, Zarin and Marvdasht cultivars had the highest (56.8 and 55.8 grains/spike, respectively) and Chamran cultivar (34 grains/spike) had the lowest values. In term of the spikes/m^2 under control condition, Sivand and DN-11 cultivars had the highest (523 and 512 spikes/m^2) and Marvdasht had the lowest values (351 spikes/m^2). Under post anthesis water deficiency stress Sivand (450 spikes/m^2) and Pishgam cultivars had the highest (450 spikes/m^2) and lowest (351 spikes/m^2) values.

Harvest index

The harvest index can be expressed as ability of plants to allocate photosynthetic material to produce economic yield. In terms of this trait under well-watered and post-anthesis water deficiency stress, there was significant variation between cultivars. Post anthesis water stress significantly decreased harvest index in most cultivars (Table 2). In control condition, Pishgam and Chamran cultivars had the highest (64.1%) and the lowest (55.3%) harvest index and in post anthesis water deficiency stress Pishgam and Zarin cultivars had the highest (56.4%) and the lowest (45.8%) harvest index. Significant reduction in harvest index under post anthesis water deficiency stress showed that dehydration stress as shown in Table 2. In 2002, Richards et al. demonstrated that for this reason that harvest index is indicators of the genetic potential of plant to produce economic yield, high harvest index under control treatment can be accompanied with high grain yield under water stress. The findings of the current study are consistent with those of Reynolds et al. (1999, 2009) who found wheat cultivars that have high biological yield and harvest index, most likely have high grain yield under stress and control conditions. A point to note in this connection was that Chamran cultivar under post anthesis water deficiency with lowest reduction in harvest index had also the lowest reduction in grain yield production and Sivand, Zarin and Marvdasht cultivars with highest reduction in harvest index had also the higher reduction in grain yield production. In post anthesis water deficiency, a positive correlation was found between grain weight and harvest index. It means that increasing of grain weight is accompanied with increasing harvest index.

Fertile spikelets and infertile spikelets in each spike

In terms of fertile spikelets in each spike, Marvdasht and Zarin cultivars had the highest (18.1 and 18.2, respectively) and Chamran and Pishtaz cultivars had the lowest (14.8 and 14.9, respectively) values. Zarin and Pishgam cultivar had the lowest (1.5 and 1.6, respectively) and Chamran cultivar the highest (3.88) values of infertile spikelets in each spike (Table 2). The competition between spike and stem for absorb of leaf produced photo-assimilates initiates from beginning of terminal spikelet production, at anthesis and when the upper stem internodes are in growth and development stage in their structure reaches its maximum. Wheat cultivars that have the greater spick should have more power to maintain floret, increase number of grain, grain yield and harvest index (Reynolds et al., 1999).

Internode weight

Post anthesis water deficiency stress had no significant effect on internodes weight (Table 3). Significant variation was found among cultivars for peduncle, penultimate, and the lower internodes weight. Peduncle's weight was varied from 422 mg (in Chamran) to 581 and 604 (in Pishgam and Zarin, respectively). Penultimate's weight varied from 443 mg (in Marvdasht to 572 mg (in Sivand). The lower internodes which had 2 up to 4 internodes in averages had greater weight than the other upper internodes. These results are in agreement with those reported by Ehdaie et al. (2006 a, b). Weight of the lower internodes ranged from 497 mg in Parsi to 799 and 837 mg for DN-11 and Zarin cultivars respectively (Table 3).

Table 2. The effect of post anthesis water deficiency stress on grain yield and its components of improved wheat cultivars.

Cultivars	Grain yield (g/m^2)		Decrease (%)	Biomass (g/m^2)		Harvest index (%)		Number of grain per spike	
	Control	Water deficit		Control	Water deficit	Control	Water deficit	Control	Water deficit
Bahar	724±26	475±37	-34.4	1203±70	933±62	60.2±1.3	50.9±2.4	45.2±1.5	51.2±3.4
Parsi	692±38	437±77	-36.8	1230±81	880±78	56.3±0.6	49.7±4.3	37.2±0.8	40.5±2.8
Pishtaz	705±40	497±54	-29.5	1197±64	933±75	58.9±2.0	53.2±2.0	38.3±2.5	38.1±0.8
Pishgam	718±31	446±63	-37.9	1120±29	790±107	64.1±1.1	56.4±2.2	52.0±3.3	52.6±4.0
Chamran	562±45	447±35	-20.4	1017±70	800±86	55.3±1.2	55.9±2.5	32.6±1.1	35.4±2.2
Zarin	724±37	448±50	-38.2	1253±74	977±69	57.8±0.6	45.8±2.8	57.5±1.1	56.3±4.1
Sivand	783±84	497±71	-36.6	1237±82	980±78	63.3±2.5	50.7±3.5	38.8±0.3	39.6±0.8
Marvdasht	656±20	411±26	-37.4	1063±33	870±51	61.7±0.2	47.2±1.7	56.5±1.1	55.2±5.2
DN-11	750±63	515±76	-31.3	1287±104	937±114	58.3±0.3	55.0±2.7	44.9±4.0	45.0±1.6
Mean	702	464	-33.9	1179	900	59.5	51.6	44.8	46.0
LSD (%5)	154			164		8.4		8.8	
CV (%)	13.0			11.0		12.1		9.51	

Cultivars	1000 Grain weight (g)		Decrease (%)	Number of spike per m^2		Fertile spikelet		Infertile spikelet	
	Control	Water deficit		Control	Water deficit	Control	Water deficit	Control	Water deficit
Bahar	42.1±0.6	31.9±2.7	-24.4	516±19	425±23	17.0±0.4	18.1±1.2	2.27±0.15	1.77±0.03
Parsi	45.4±1.5	29.8±0.4	-34.3	503±28	423±29	15.3±0.1	15.5±0.7	3.17±0.26	2.30±0.25
Pishtaz	46.6±1.4	32.3±2.3	-30.8	503±17	428±44	15.0±0.5	14.6±0.0	2.97±0.23	2.40±0.21
Pishgam	43.2±0.8	32.4±1.8	-24.9	445±34	351±20	16.8±0.1	17.7±1.0	1.80±0.06	1.33±0.45
Chamran	43.2±0.5	36.2±1.8	-16.0	438±27	436±15	14.5±0.6	15.5±0.3	4.03±0.27	3.73±0.44
Zarin	39.2±0.2	27.7±0.8	-29.4	467±38	400±45	18.0±0.6	18.2±0.7	1.77±0.22	1.40±0.35
Sivand	45.5±0.7	32.7±2.9	-28.3	523±10	451±19	15.4±0.1	15.2±0.3	2.80±0.20	2.43±0.34
Marvdasht	36.7±1.3	24.5±0.5	-33.4	405±32	428±31	17.8±0.1	18.6±0.5	1.00±0.15	1.00±0.15
DN-11	39.9±0.5	33.7±0.7	-15.6	512±33	409±46	16.4±1.1	16.5±0.0	2.27±0.30	2.10±0.26
Mean	42.4	31.2	-26.4	479	417	16.2	16.6	2.45	2.05
LSD (%5)	6.1			106		1.5		0.94	
CV (%)	5.40			9.24		6.28		18.4	

The difference among treatments is significant at the 5% level according to LSD test. The values are the Mean ± SE of three replication.

Stem weight of Zarin cultivar was the highest (1943 mg) followed by DN-11 (1784 mg). In contrast, Parsi (1531 mg) had the lowest stem weight (Table 3). Post anthesis water deficit, on average, had no significant effect on the main stem weight.

Genotype × date of harvest interaction

Different trends for post anthesis changes in peduncle weight were observed among different cultivars (Fig 1a). Apart from Zarin cultivar, other cultivars had the greatest peduncle weight at 7 days after anthesis. Zarin had different trend of changes in peduncle weight from other bread wheat cultivars. Maximum weight of peduncle in Zarin cultivar was seen at 21 days after anthesis. Then, remobilization of soluble sugars from peduncle of this cultivar was started later than the other cultivars. Maximum peduncle weight was seen in Zarin and Pishgam cultivar. In control treatment, remobilization of soluble sugars from peduncle was started at 7 to 14 days post anthesis in all cultivar but in Zarin cultivar started 21 to 21 days post anthesis (Fig 1a). Post anthesis water stress put remobilization forward in Zarin cultivar (14 days). Pishgam cultivar had the lowest value of dry weight especially under post anthesis water deficit. As shown in Fig 1b, maximum penultimate weight in most cultivars was seen at 7 days post anthesis, except for Zarin and Bahar which obtained their maximum weight at 14 days post anthesis. DN-11 cultivar in control and post anthesis water deficiency had the lowest penultimate weight. Maximum weight of the lower internodes, on average, was seen at anthesis. Whereas, those of peduncle and penultimate internode were reached 14 to 21 days after anthesis (Fig 1a, 1b and 1c). After obtaining their maximum weight, weight of these internodes were progressively decreased over the time until maturity. The lower internodes, taken together as a stem segment, in Zarin, Sivand, Parsi and DN-11 cultivars were reached their maximum weight at anthesis and in Pishgam, Bahar and Chamran cultivars at 7 days post anthesis (Fig 1c). Under control treatment, this segment in Zarin cultivar had the highest weights, whereas those in Parsi cultivar had the lowest weights. Post anthesis water deficiency significantly decreased dry weight of lower internodes especially in DN-11, Sivand and Parsi cultivars.

Internode length

In order to determinate the effect of post anthesis water deficiency on plants length and genetic variation between cultivars in terms of this traits, average length of all cultivars in both conditions were compared. Post anthesis water deficiency had no significant effect on internodes and total length. There were tremendous variations for internodes length among the cultivars. Zarin had the longest stem (88.3

Table 3. Maximum and minimum weight (mg) of main stem's internodes in different improved wheat cultivars under post anthesis water deficiency.

Treatments	Maximum weight at post anthesis (mg)				Minimum weight at post anthesis (mg)			
	Peduncle	Penultimate internode	Lower internodes†	Stem‡	Peduncle	Penultimate internode	Lower internodes†	Stem‡
Water regimes								
Control	502 a	519 a	660 a	1682 a	377 a	338 a	320 b	1035 a
Water deficit	517 a	531 a	641 a	1689 a	390 a	353 a	358 a	1101 a
Decrease (%)	3.0	2.4	-3.0	0.4	3.3	4.4	11.8	6.3
Cultivars								
Bahar	525 b	502 c	612 cd	1639 cd	403 bc	341 cde	330 bcd	1074 bc
Parsi	475 cd	559 ab	497 d	1531 d	372 cd	404 a	297 cde	1073 bc
Pishtaz	526 b	530 bc	584 cd	1640 cd	379 cd	308 f	293 cde	979 cd
Pishgam	581 a	546 ab	583 cd	1710 bc	425 b	322 ef	283 ed	1029 bcd
Chamran	422 e	529 bc	660 bc	1611 cd	288 e	326 def	315 cde	929 d
Zarin	604 a	504 c	837 a	1943 a	464 a	356 bcd	525 a	1345 a
Sivand	511 b	572 a	537 cd	1619 cd	374 cd	376 ab	256 e	1006 bcd
Marvdasht	502 bc	443 d	747 ab	1692 bc	392 bc	309 ef	398 b	1099 b
DN-11	443 de	542 abc	799 a	1784 b	354 d	367 bc	358 bc	1079 bc

†Internodes below the penultimate. ‡Stem: whole internodes. In each section, means followed by the same letter within columns are not significantly different ($P< 0.05$) according to LSD test.

Table 4. Length (cm) and specific weight (mg cm^{-1}) of main stem's internodes in different improved wheat cultivars under post anthesis water deficiency.

Treatment	Length (cm)				Specific weight (mg/cm)			
	Peduncle	Penultimate internode	Lower internodes†	Stem‡	Peduncle	Penultimate internode	Lower internodes†	Stem‡
Water regimes								
Control	32.2 a	22.4 a	22.1 a	76.7 a	15.6 a	23.3 a	30.4 a	22.0 a
Water deficit	32.1 a	21.8 a	21.0 a	74.9 b	16.1 a	24.5 a	30.9 a	22.6 a
Decrease (%)	-0.3	-2.7	-5.0	-2.3	3.2	5.2	1.6	2.7
Cultivars								
Bahar	33.4 c	20.3 cd	21.5 de	75.2 c	15.7 bc	24.8 bc	28.8 bc	21.9 bc
Parsi	29.9 d	25.7 a	17.8 f	73.5 c	15.9 bc	21.8 e	27.9 c	20.9 c
Pishtaz	34.8 b	21.1 c	20.0 e	75.8 bc	15.2 cd	25.3 b	29.4 bc	21.7 bc
Pishgam	33.0 c	19.4 e	16.1 g	68.5 d	17.7 a	28.1 a	36.3 a	25.0 a
Chamran	28.6 e	23.2 b	22.7 cd	74.5 c	14.9 cd	22.9 cde	29.3 bc	21.7 bc
Zarin	38.2 a	20.6 cd	29.5 a	88.3 a	15.8 bc	24.5 bcd	28.7 bc	22.1 bc
Sivand	30.4 d	25.2 a	17.9 f	73.4 c	16.8 ab	22.8 de	30.2 abc	22.1 bc
Marvdasht	30.4 d	20.2 d	24.4 b	75.0 c	16.6 ab	22.0 e	30.8 abc	22.6 bc
DN-11	31.1 d	23.3 b	23.8 bc	78.1 b	14.3 d	23.4 cde	34.3 ab	22.9 b

†Internodes below penultimate. ‡Stem: length of all internodes. In each section, means followed by the same letter within columns are not significantly different ($P< 0.05$) according to LSD test.

cm) and Pishgam lower stem length (68.5 cm) (Table 4). Zarin had the largest peduncle (38.2 cm) and lower internodes (29.5 cm) and Parsi (25.7 cm) the largest penultimate length. In contrast, Pishgam had the shortest penultimate (19.4 cm) and lower internodes (16.1 cm) length and Parsi the shortest Peduncle length (28.6 cm). Such differences between mentioned traits in different wheat cultivars also reported by Reynolds et al. (1999), Moragues et al. (2006) and Sabet et al. (2009). The lower internodes, on average, reached their maximum length before and at anthesis, except for the penultimate internode in Zarin (data not shown). These results are in agreement with those reported for wheat (Borrell et al., 1993, 1998) and for barley (Bonnett and Incoll, 1992). The time for the peduncle to reach its maximum length varied more among the cultivars. The peduncle was, on average, longer than the penultimate internode in all the cultivars that were examined. The lower internodes consisted of three separate internodes, whereas in Pishgam cultivar they consisted of two and in Zarin cultivar they consisted of four individual internodes. Post anthesis water deficiency stress, on average, reduced the main stem length by 2.3%. The reduction in stem length was reflected more on peduncle length than on penultimate internode length and the lower internodes length (Table 4) as shown before by Borrell et al. (1993) and Ehdaie et al. (2006 a). Contribution of each component of the stem (peduncle, penultimate and lower internodes) in forming of stem length was different. In tall cultivars such as Zarin and Pishtaz, the peduncle made up 43 to 46% of stem length, whereas in Pishgam (the shortest) and Zarin (the tallest) cultivars, it made up 48% and 43% of stem length respectively. The penultimate internode in Pishgam and Zarin cultivars made up only 28% and 23% and the lower internodes made up 23% and 33% of the main stem length respectively. The present findings seem to be consistent with Ehdaie et al. (2006 a) which found these result in other wheat cultivars. The penultimate and the lower internodes, on average, obtained their maximum length at anthesis, whereas the peduncle reached its maximum length 7 days post anthesis (data not shown).

Table 5. Remobilization dry matter (mg) and remobilization efficiency (%) of main stem internodes in different improved wheat cultivars under post anthesis water deficiency

Treatments	Remobilized dry matter (mg)				Remobilization efficiency (%)			
	Peduncle	Penultimate internode	Lower internodes†	Stem‡	Peduncle	Penultimate internode	Lower internodes†	Stem‡
Water regimes								
Control	125 a	181 a	340 a	646 a	24.7 a	34.6 a	51.3 a	38.2 a
Water deficit	128 a	178 a	283 b	588 a	24.6 a	33.1 a	42.6 b	34.5 a
Decrease (%)	1.9	-1.5	-16.8	-9.0	-0.4	-4.3	-17.0	-9.7
Cultivars								
Bahar	123 abcd	161 cd	282 bc	565 ab	23.4 bc	31.9 bc	45.4 ab	34.5 abc
Parsi	103 cd	155 cd	200 c	458 b	21.6 bc	27.7 c	38.8 ab	30.0 c
Pishtaz	147 ab	222 a	291 bc	660 a	27.8 ab	41.4 a	48.5 ab	39.9 a
Pishgam	156 a	225 a	301 abc	681 a	26.8 abc	40.6 a	51.5 ab	39.6 a
Chamran	134 abc	203 ab	345 abc	682 a	31.4 a	38.3 ab	52.3 ab	42.3 a
Zarin	140 abc	148 d	311 abc	599 ab	22.8 bc	28.9 c	37.0 b	30.6 bc
Sivand	137 abc	195 abc	280 bc	612 ab	26.6 abc	33.8 bc	50.5 ab	37.6 abc
Marvdasht	110 bcd	134 d	349 ab	593 ab	21.4 ac	29.9 c	44.8 ab	34.1 abc
DN-11	89 d	176 bcd	441 a	705 a	20.0 c	32.2 bc	53.6 a	38.9 ab

†Internodes below penultimate. ‡Stem: length of all internodes. In each section, means followed by the same letter within columns are not significantly different (P< 0.05) according to LSD test.

Table 6. Mean comparisons of remobilized dry mater (mg) and remobilization efficiency (%) of main stem internodes in different improved wheat cultivars under post anthesis water deficiency

Cultivars	Remobilized dry matter (mg)								Remobilization efficiency (%)							
	Peduncle		Penultimate internode		Lower internodes†		Stem‡		Peduncle		Penultimate internode		Lower internodes†		Stem‡	
	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit	Control	Water deficit
Bahar	117±18	128±27	166±5	156±47	370±48	194±8	653±50	478±79	23.1±3.5	23.6±4.9	34.1±1.4	29.7±8.4	57.4±2.8	33.5±2.9	39.9±2.4	29.1±4.7
Parsi	93±11	113±13	168±27	142±4	258±18	143±86	519±22	398±77	20.4±1.9	22.8±2.0	30.2±3.7	25.1±1.6	50.5±4.1	27.2±13.9	34.1±0.7	25.8±4.8
Pishtaz	116±5	178±16	191±32	253±24	318±64	265±92	625±98	696±130	23.3±1.4	32.3±2.9	37.4±4.4	45.5±3.5	53.1±7.4	43.8±13.9	38.9±4.9	40.9±6.8
Pishgam	171±22	141±41	274±27	175±16	341±17	260±10	786±55	576±49	29.7±3.1	24.0±7.1	47.4±1.7	33.8±2.2	57.1±0.3	45.9±2.8	44.9±1.7	34.4±2.7
Chamran	147±35	121±12	207±13	199±17	353±34	336±20	707±64	657±24	33.1±5.2	29.6±2.6	38.8±1.4	37.8±1.0	54.3±3.4	50.3±3.1	43.6±2.6	41.0±0.7
Zarin	144±32	135±30	177±22	118±28	339±18	283±86	660±36	537±141	23.3±3.6	22.3±4.6	33.0±2.6	24.6±5.2	39.8±2.5	34.2±9.8	33.1±0.8	28.0±6.8
Sivand	122±11	152±24	160±22	231±20	278±58	282±95	561±63	664±94	24.5±2.2	28.7±3.5	29.4±3.3	38.1±1.2	48.9±3.9	52.1±8.3	34.9±3.1	40.2±4.1
Marvdasht	124±39	96±24	126±19	142±30	366±89	332±121	616±142	569±169	24.3±6.9	18.5±4.0	29.4±3.4	30.3±5.0	47.4±5.7	42.3±11.6	35.9±5.5	32.2±7.8
DN-11	93±22	84±11	162±15	189±22	433±120	448±107	689±154	721±133	20.7±4.8	19.4±2.9	31.0±2.8	33.4±2.8	53.2±8.2	53.9±7.5	38.5±6.4	39.4±5.0
Mean	125	128	181	178	340	283	646	588	24.7	24.6	34.5	33.1	51.3	42.6	38.2	34.5
LSD (%5)	99		56		87		235		17.1		6.9		9.7		10.4	
CV (%)	27.7		19.7		40.5		25.7		24.7		16.5		28.0		20.7	

†Internodes below penultimate. ‡Stem: length of all internodes. The difference among treatments is significant at the 5% level according to LSD test. The values are the Mean ± SE of three replication.

Internode specific weight

Significant differences for internodes specific weight were observed among the evaluated cultivars. Maximum specific weight of peduncle was seen in Pishgam (17.7 mg/cm) followed by Sivand (16.8 mg/cm) and Marvdasht (16.6 mg/cm). In contrast, the peduncle of DN-11cultivar (14.3 mg/cm) had the minimum specific weight (Table 4). Pishgam had the highest penultimate internode specific weight (28.1 mg/cm), followed by Pishtaz (25.3 mg/cm). In contrast, Marvdasht (22 mg/cm) and Parsi (21.8 mg/cm) had the lowest penultimate specific weight. The range of specific weight for the lower internodes was from 36.3 mg/cm for Pishgam to 27.9 mg/cm for Parsi (Table 4). Pishgam had the highest stem specific weight (25 mg/cm). In contrast, Parsi (20.9 mg/cm) had the lowest stem specific weight (Table 4).
Post anthesis water deficiency stress had not significant effect on specific weight of stem's parts. No significant reduction in specific weight of different stem's parts despite reduction of photosynthesis rate especially under post anthesis water stress and remobilization may be because of reduction in stem length (2.3%) rather than in stem weight (0.4%). These result also reported by Ehdaie et al. (2006 a).

Dry matter remobilization and efficiency

Mobilized dry matter had not significant difference between control and post anthesis water deficiency. Different cultivar had different amount of dry mater remobilization. Pishgam and DN-11 cultivars had the highest (156 mg) and the lowest (89 mg) value of remobilization respectively. Mobilization efficiency that was estimated as the ratio of mobilized dry matter to maximum weight, showed similar trends (Table 5). In all cultivars mobilized dry matter of peduncle internode decreased under post anthesis water deficit stress treatment, except Pishtaz, Sivand and DN-11cultivars (Table 6). There were significant differences between cultivars in terms of dry mater remobilization from penultimate internode. Pishtaz, Sivand and DN-11 cultivars had greater dry mater remobilization than the other cultivars. The highest remobilization efficiency from penultimate was seen in Pishgam (40.6%) and Pishtaz (41.4%) cultivars respectively. The amount and efficiency of dry mater remobilization of penultimate internode under control and post anthesis water deficiency stress was higher than peduncle. Under control and post anthesis water deficiency stress, the amount of dry mater storage, remobilization and remobilization efficiency of lower internodes was higher than peduncle and penultimate internodes. The findings of the current study are consistent with those of Ehdaie et al. (2006 a) who discussed that the lower internodes should have appropriate length to reach their potential for carbohydrates accumulation before anthesis and a major source for carbohydrates mobilization after anthesis. Post anthesis water deficiency stress, on average, significantly increased the amount of mobilized dry matter by 16.8% and mobilization efficiency by 17%. However, cultivars had significant differences in the case of dry matter mobilized and the efficiency of carbohydrates remobilization from the lower internodes (Table 4). DN-11 cultivar had the highest (441 mg) and Parsi cultivar had the lowest (200 mg) remobilized dry mater and in the case of remobilization efficiency, DN-11 (53.6%) and Zarin cultivars (37.0%) had the lowest and the highest values respectively (Table 5). Post anthesis water deficiency stress decreased remobilized dry mater and remobilization efficiency of lower internodes in all cultivars except of DN-11 cultivar. Finally post anthesis water deficiency stress increased these traits in stem of Pishtaz, Sivand and DN-11 cultivars and decreased them in other cultivars (Table 6). The evidence from this study suggests that peduncle with higher length between different parts of stem had the lowest remobilization dry matter and remobilization efficiency and then the lowest role in grain yield production. The lower internodes had the highest dry mater remobilization and remobilization efficiency compared to another segment of stem and then may be had the highest role in yield production. Zarin cultivar with highest stem length had the lowest dry mater remobilization and remobilization efficiency than the cultivars with shorter stem length. This cultivar also had the maximum reduction of grain yield under post anthesis water deficit stress. Pishgam cultivar with the shortest stem length had the highest dry mater remobilization and remobilization efficiency. Despite the mentioned facts, grain yield reduction of this cultivar under post anthesis water deficiency stress was high. The lowest grain yield reduction under post anthesis water stress comparison to control treatment was seen in Chamran cultivar with short stem length.

Materials and methods

Plant material and treatments

The present study was conducted during 2010-2011 in the field research of the department of agronomy and plant breading, campus of agricultural and natural resource, Razi university in Kermanshah state in the west of Iran (47º, 9′/E; 34º, 21′/ N), 1319 meter elevated from sea level. The research was performed in the field where the previous crop was a corn. The soil was a clay loam (36.1% clay, 30.7% silt) and the experiment was laid out in a split-plot arranged in the base of randomized complete block design with three replications. Evaluated treatments were included, moisture regimes and different improved bread wheat cultivars (*Triticum aestivum* L.). Two levels of moisture regimes (includes: Irrigation in all stages of plant growth normally and post-anthesis water deficiency with withholding of irrigation after anthesis) as the main-plot and different improved cultivars (includes: Bahar, Parsi, Pishtaz, Pishgam, Chamran, Zarin, Sivand, Marvdasht and DN-11) as sub-plot were considered. These cultivars were chosen because of their contrasting grain yield productivity and the highest area under cultivation in the west of Iran. Also, occurred almost every year of post-anthesis water deficit in cultivated area in these regions, was the most reason for selection of these treatments. Date of anthesis was determined from middle rows in each plot when 50% of the spikes had extruded anthers (Ehdaie et al., 2006 a). Each plot included 54 rows 20 cm apart, 4 meter long, 4 and 3 meter distances were taken between test plots and replicates, respectively. Seeds were sown at a density of 400 seeds m^{-2} on 12th October. Based on soil analysis, nitrogenous fertilizer as urea ($CO(NH_2)_2$) was applied prior to planting, as topdressing at tillering stage and at flowering stage, 80 kg ha^{-1} in each stage.

Internode length, specific weight and remobilization content

In each plot, 30 to 40 main tillers from the two middle rows next to the guard rows were tagged as spikes emerged from the flag leaf sheaths. Three main tillers were harvested at random at anthesis and at seven days intervals after anthesis until maturity. The main tillers were harvested from the soil surface. After each harvest, leaf blades were removed and main tillers were immediately dried in a forced-air drier at 70 ^{o}C for 48 h. Then, each main tiller was divided into spike and stem; then leaf sheaths were removed from the stem. Each stem was divided into three segments, namely peduncle (first internode below the spike including the distal node), penultimate internode (the internode below the peduncle including the distal node), and the lower internodes. The length and weight of each segment was measured, and then its specific weight (linear density) was calculated as the ratio of its weight to its length. The relative importance of internode length and weight in determination of specific weight was examined by comparing their standard partial regression coefficients (Draper and Smith, 1981). The magnitude of mobilized reserves in each internode segment was determined based on post-anthesis changes in internode dry weight (Ehdaie et al., 2006 a, b). Remobilization efficiency of dry matter in each internode segment was estimated by the proportion (%) of mobilized dry matter relative to post-anthesis maximum weight of that segment (Ehdaie et al., 2006 a). An approximate standard deviation for mobilization efficiency was determined by assuming the numerator and denominator are independent. In this case, the estimates will be conservative since the numerator (amount of mobilized dry matter) and the denominator (post-anthesis maximum weight) are positively correlated.

Grain yield and its components

Grain yield and Biomass for each cultivar were measured by harvesting 1 m^2 of the central part of each plot at crop maturity. Harvest index was measured by dividing grain yield to biomass production. In order to measuring grain yield components such as: no of grains per spick, fertile and infertile spikelet number, grain weight, 10 plants randomly selected and measurements were performed.

Statistical analysis

Statistical analyses were performed using EXCEL and SAS software. Mean comparisons were also performed using LSD at % 5 level (Steel et al., 1997). Weather data was obtained from Regional Meteorological Centre located near the experimental site (Table 1).

Conclusions

These findings further support the idea that increasing of carbohydrates remobilization from different part of stem does not necessarily increase grain yield production or grain yield stability under variable environments. Higher values of carbohydrates remobilization from different parts of stem that were coincident with lower grain yield in this research showed that may be more respiratory losses of remobilized carbohydrates or more movement of remobilized carbohydrates to the alternative sinks such as young developing tillers and roots in such cultivars may be the main reasons for these results. So, we should be followed wheat cultivars with remobilization of the greater amount of carbohydrates from different part of stems to the growing grains. These cultivars have advantages for the various environmental conditions.

Acknowledgements

The authors would like to thank their colleagues in Agricultural and Natural Resource, university of Razi, Kermanshah, Iran.

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