Full Length Research Paper

Effect of drought at the post-anthesis stage on remobilization of carbon reserves in two wheat cultivars differing in senescence properties

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Remobilization and transfer of stored food in vegetative tissues to the grains in monocarpic plants require the initiation of whole plant senescence. However, mechanism by which plant senescence promotes remobilization of assimilates that are rather obscure. This study examined the relationship between the senescence induced by water deficits and C remobilization during grain filling. Two wheat cultivars (*Triticum aestivum* L.), Marvdasht and Zagros (sensitive and tolerant to terminal season drought, respectively) grown at a day: night temperature of 22:15°C from anthesis were held as well watered controls (field capacity) or subject to water deficit (50% FC) imposed either from anthesis to 14 days later (WS1) or from 14 days after anthesis to maturity (WS2). Relative water content, photosynthetic activity, chlorophyll content, soluble proteins of flag leaves, level of soluble sugars, in the peduncle (enclosed by the flag leaf sheath) and the penultimate internode and grain yield were assessed. Results showed that, water deficits enhanced the senescence by accelerating loss of leaf chlorophyll and soluble proteins and the loss was more under WS2 than WS1. The net CO_2 assimilation rate (P_N) in flag leaves during water deficit display a strict correlation with the drought sensitivity of the genotypes and showed an early reduction in Marvdasht. Water stress, both at WS1 and WS2, facilitated the reduction in concentration of total soluble sugars in the internodes, promoted the re-allocation of pre-stored C from the peduncle and penultimate to grains. WS2 resulted in more deleterious effect on grain yield than WS1 in both cultivars and led to a smaller kernels and lesser aerial biomass at maturity. The loss was more in Marvdasht than Zagros. The study results suggest that, the senescence and remobilization promoted by water deficits during grain filling are coupled processes in wheat and the mass of soluble sugars in the stems is premier than sugar remobilization efficiency. Varietal differences in the extent of such trait existed. It would be advantageous to select genotypes with greater capacity to do this under water deficit conditions.

Key words: Chlorophyll, flag leaves, grain filling, grain yield, soluble sugar, internodes, photosynthesis, soluble proteins, wheat (*Triticum aestivum* L.).

INTRODUCTION

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. Extensive studies have demonstrated that, post-anthesis water deficits result in early senescence and more mobilization of pre-anthesis stored assimilates to grains in cereals (Kobata et al., 1992; Palta et al., 1994; Yang et al., 2001, 2003). Growth of kernels is reduced depending upon the degree of water stress and on the rate of stress develop-ment, thereby limiting final grain yield (Kobata et al., 1992; Nicholas and Turner, 1992). The reduction was found to be more severe when the stress occurred suddenly rather than gradually (Stone and Nicholas, 1995b) and at early stages of grain filling rather than at later stages (Stone and Nicholas, 1995a). However, varietal differences in the extent of such trait existed.

Wheat genotypes vary in the timing of senescence initiation and also in the subsequent rate of leaf sene-scence. The quest of the causes of differences in leaf

photosynthetic rate among interspecies and/or intra-species of crops may be one of the important strategies of crop engineering (Jiang et al., 2002). So, delaying leaf senescence has become an agronomically desirable trait (Quirino et al., 2000; Subhan and Murthy, 2001). Net flag leaf photosynthesis in wheat contributes about 30 to 50% of the assimilates for grain filling (Sylvester-Bradley et al., 1990) and the initiation of grain filling coincides with the onset of senescence, therefore, photosynthesis of the flag leaf is the most important basis of the formation of grain yield and the onset and rate of senescence are important factors for determining grain yield.

The primary signs of leaf senescence are the breakdown of chlorophyll (Chl) and the decline of photo-synthetic activity (Yang et al., 2001; Gregersen and Holm, 2007). It is generally accepted that, genotypes that are able to sustain photosynthesis in the flag leaf for a longer time tend to yield more.

Under drought, there is a rapid decline in photo-synthesis after anthesis, due to decrease in leaf stomatal conductance and net CO_2 assimilation, limiting the contribution of current assimilates to the grain. Most of the drought-mediated reduction in CO_2 assimilation was attributed to stomatal closure; a part of it was attributed to the direct effect of water stress on the inhibition of CO_2 fixation (Sharkey and Seemann, 1989). The relative magnitude of stomatal and non-stomatal factors in limiting photosynthesis depends on the severity of stress (Kicheva et al., 1994).

Yang et al. (2000, 2001) has shown that, remobilization of stored carbon reserves in wheat is promoted by water stress and that water deficits imposed during grain-filling enhanced plant senescence and accelerated grain-filling. Usually, senescence induced by water deficits shortens grain-filling period and can result in reduction in grain weight (Dingkuhn and Gal, 1996; Zhang et al., 1998). However, a shortened grain-filling period caused by water stress with better use of pre-stored carbon reserves may prove to be beneficial in cases where delayed senescence causes too much carbon left in the straw.
In fact, a high correlation was found between storage of non-structural carbohydrates of wheat stems and yield among several wheat cultivars under drought conditions (Gavuzzi et al., 1997). In wheat, the peduncle and the penultimate internode contained the most storage (Wardlaw and Willenbrink, 1994), with variations in storage and remobilization under different experimental conditions being larger in the penultimate than in the fourth stem internode (Bonnett and Incoll, 1992).

The objective of this study was to determine if early senescence induced by water deficit during the grain filling could enhance carbon remobilization and if such enhancement could improve grain filling in, two wheat cultivars different in drought resistance. An additional objective of the present study was to compare some physiologic traits that are related to water stress, to finding direct correlations between these parameters and grain yield to facilitate the screening and selection of cultivars for drought tolerance.

MATERIALS AND METHODS

Plant materials

The experiment was carried out on the Agricultural Biotechnology Research Institute of Iran (ABRII), in the growing season of 2008 to 2009. Two contrasting cultivars of *T. aestivum* L. Marvdasht (drought sensitive cultivar with high yielding potential under favorable condition) and Zagros (drought tolerant local cultivar) were used. Seeds were sown in porcelain pots (15 cm in height and 16.5 cm in diameter) filled with 2.1 kg of clay-sand-manure 1:1:1(v/v). Cultivation was performed in a greenhouse with 16 h supplemental light (300 µmolm^{-2}s^{-1}of photosynthetically active radiation 22°C) and 8 h darkness (15°C) and at 55 to 60 air humidity. Five uniform plants in each pot were retained after seedling establishment and adequately irrigated with tap water. At three true leaves, pots were placed in a field for forty days for vernalization. The experiment was 2 x 3 (two cultivars and three water regimes) factorial design with six treatment. Each of the treatment had three replications with three sub-samples in a complete randomized block design. The imposition of water stress commenced at heading (stage 59, Zadoks scale; Zadoks et al., 1974) to 14 days later (WS1) and from 14 days after anthesis to physiological maturity (WS2, stage 92, Zadoks scale), to reach 50% FC at both treatments, water was withheld from the plants and the pots weighed daily until the desired stress level was reached (50% FC). Sufficient water was then added to maintain this value on a daily basis. In the control treatment (WW), the soil water status was maintained at FC (soil water potential, ψsoil, at -0.01 to -0.02 MPa) by weighing the pots daily and adding sufficient water to bring the soil moisture to its original value.

Sampling

Plants were harvested at 7, 14, 21, 28 and 35 days after-anthesis (DAA), both the length of peduncle enclosed by the flag leaf sheath and the penultimate internode were subdivided for soluble carbohydrate analyses. Samples selected for soluble carbohydrate analysis were initially frozen in dry ice and stored at -20°C. These samples were later freeze dried to determine dry weight before the sugar extraction. At maturity, ears were harvested to determine the kernel weight, the number of kernels per spike and the thousand-kernel weight. Each measurement was done on plants from three different pots.

Protein content determination

Leaf samples were ground in liquid nitrogen and the powder was dissolved in 1 ml of 50 mM HEPES-NaOH buffer pH 7.6 containing 3 mM DTT. After centrifugation for 10 min at 13000 g, the protein concentration was measured using the method Sedmak and Grossberg (1977), using BSA as standard protein. This allowed all enzymatic activities to be expressed relative to the soluble protein concentration.

Physiological measurements

Relative water content (RWC) was measured in the blades of the flag leaf. Leaf blade segments were weighed (w_i), floated on distilled water at 4°C overnight, weighed again (w_f) and dried at 80°C for 48 h, after which, dry mass was determined (w_d). Relative water content was calculated as: RWC = $(w_i - w_d) (w_f - w_d)^{-1} \times 100$.

The net photosynthetic rate (P_N), stomatal conductance (g_s) were measured with a portable photosynthesis system *LI-6400* (*LI-COR*, Lincoln, USA) on the flag leaves on 7, 14, 21, 28 and 35 DAA. Photosynthetically active radiation (PAR) of 1 800 μmol m^{-2} s^{-1} was provided at each measurement by the *6400-02* light source.

The fully expanded flag leaves on the stated dates were homogenized in ice cold 100% (v/v %) acetone (1.5 ml for 250-mg sample) and extracted for 24 h. Samples were centrifuged at 5,000 g for 15 min at 4°C. The pellet was extracted again with 80% (v/v %) acetone (1.5 ml for 250 mg sample) for 24 h. After centrifugation (5,000 g, 15 min, 4°C), the supernatants were collected. The pigment composition was measured with a double-beam spectro-photometer using the method of Lichtenthaler and Wellburn (1983). This method involves measurement of the light absorbed in the plant extract at 646.8 and 663.2 nm. Six leaves were used for each treatment.

Measurement of water soluble carbohydrate (WSC)

Soluble sugars were determined based on the method of phenolsulfuric acid (Dubois et al., 1956). Individual stem parts were chopped into short lengths and extracted directly into 10 ml of boiling water for 1 h. The supernatant from this extraction was collected and the residue washed with 5 ml of boiling water and finally, rinsed in cold water (Bonnett and Incoll, 1993). All extracts and washings were combined and made up to 5 ml for analysis by high performance liquid chromatography (HPLC). Contents of soluble sugar were expressed as mg Glucose g

The results were analyzed for variance using the SAS statistical analysis package (version 6.12; SAS Institute, Cary, NC, USA). Data from each sampling date were analyzed separately. Means were tested by least significant difference at P 0.05 level (LSD 0.05).

RESULTS

Plant water status and pigment content

Withholding irrigation resulted in reduction in RWC in both drought-sensitive and -tolerant genotypes; the reduction was more pronounced in the drought-sensitive cultivars, Marvdasht. At the end of WS1 (14 DAA), RWC in Marvdasht was lower than Zagros (55 compare to 77%), then increased in both cultivars after re-watering and decreased again thereafter, but with a sharp slop in Marvdasht (Figure 1a). At the onset of inserting WS2, RWC dropped markedly at 21 DAA in both cultivars, however, the loss was more in Marvdasht (20 compare to 50%), then declined gradually and reach to zero at the end of experiment in both cultivars (Figure 1a,b). The RWC of flag leaf in both cultivars maintained higher under WW than WS treatments.

In the WW and WS plants, a relevant differences were observed in the leaves (Chl) throughout the experiment (Figure 2a,b). Loss of chlorophyll (Chl) is an index of progress in leaf senescence. Chl a and b contents decrease steadily in response to water stress in both withholding treatments (WS1 and WS2) and a significant changes were found in the Chl a and b contents at 21 DAA between treatments (Figure 2a to d). The lower Chl contents were measured in stress-watered flag leaves of

the drought-sensitive Marvdasht. The senescence process started earlier in WS2 plants than WS1 in both cultivars (Figure 2a to d).

Photosynthetic performance during grain filling

The P_N of both cultivars under well-watered condition was significantly higher than under water stress and the difference became more pronounced during the late stage of grain growth (Figure 3a, b). The P_N of flag leaf in both cultivars under WW treatment exhibited a more moderate decline with a similar changing pattern in both cultivars, however, Marvdasht had lower values in P_N nearly 5 contrast to 10 μmol m^{-2} s^{-1} CO_2 at the end of experiment. WS1 reduced P_N by 20% in Marvdasht and by 28% in Zagros at 14 DAA compared with those of control, while these values under WS2 were 74 and 31% in Marvdasht and Zagros respectively to control treatment at 21DAA.

Similar to P_N, values of g_s in well-watered treatment were significantly higher than under water stress (Figure 4a,b). Stomatal conductance under both stress regimes was significantly lower than the respective controls at all stages and the differences kept remain with develop-ment. The effect of early stress (WS1) on g_s was evident throughout the experiment; while a rapid reduction in g_s of late stress (WS2) flag leaf corresponded to the time that treatment imposed. Irrespective of treatment, Zagros exhibited higher gs than Marvdasht after anthesis. The difference, however, was less pronounced under water stress.

Protein contents

The amounts of soluble proteins reduced with time in all treatments (Figure 5a, b), although, considerable differences were detected between treatments, as substantial reduction occurred in both cultivars under water stress compared with the control treatment. Irrespective of treatment, Zagros revealed higher soluble proteins content than Marvdasht throughout all stages sampling. Reduction in soluble proteins under WS2 was more remarkable than WS1 from day 14 onwards in Marvdasht, since this difference was not evident until 28 DAA in Zagros (Figure 5b).

Water soluble carbohydrates in the stem

Figure 6 shows the changes with time of WSC content of the peduncle and penultimate internode under all treat-ments. The peak values for total WSC in the peduncle and penultimate internodes, irrespective of treatments were gained at 28 DAA in Zagros, while this event was observed earlier in Marvdasht. The water stress, at either WS1 or WS2 reduced WSC, but the reduction was much
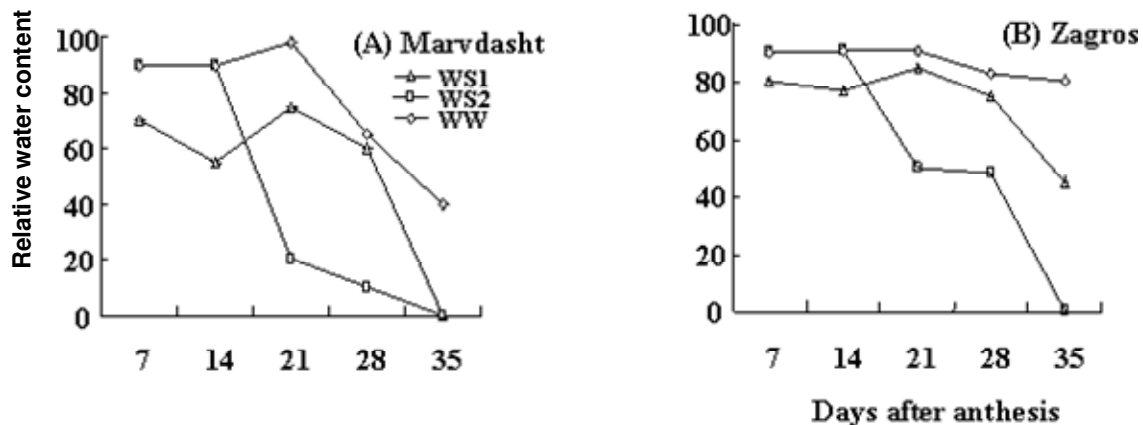
Figure 1. Changes in relative water content (RWC) under different water treatment, well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) flag leaves during grain filling in Marvdasht (A) and Zagros (B) wheat cultivars (*T. aestivum*). Data are means ± SE of three independent samples. SE bars are not shown where they are smaller than symbols.
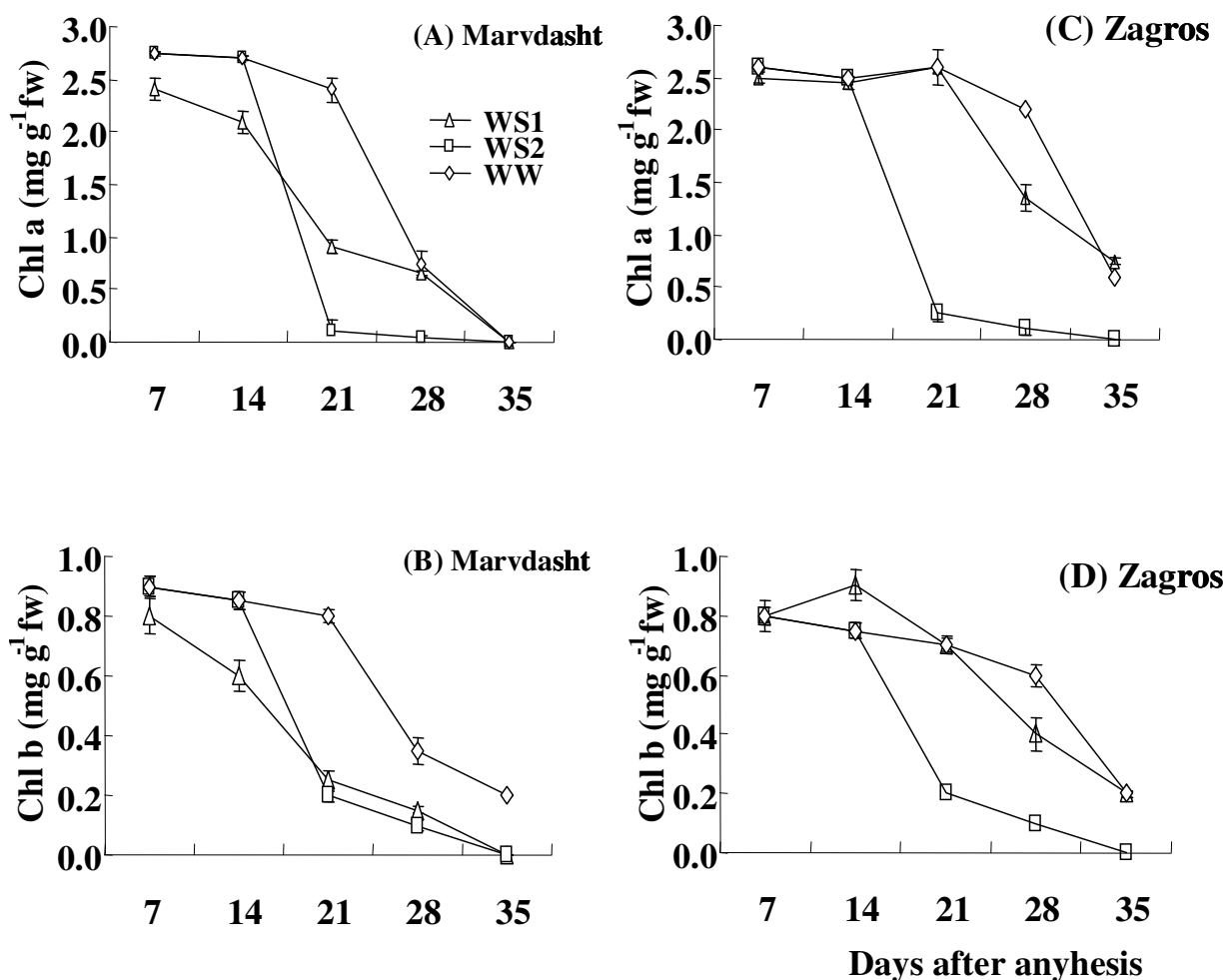

Figure 2. Changes in chlorophyll a and b content in well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) flag leaves during grain filling in Marvdasht (A) and (B) and Zagros (C) and (D) wheat cultivars (*T. aestivum*). Data are means ± SE of three independent samples. SE bars are not shown where they are smaller than symbols.
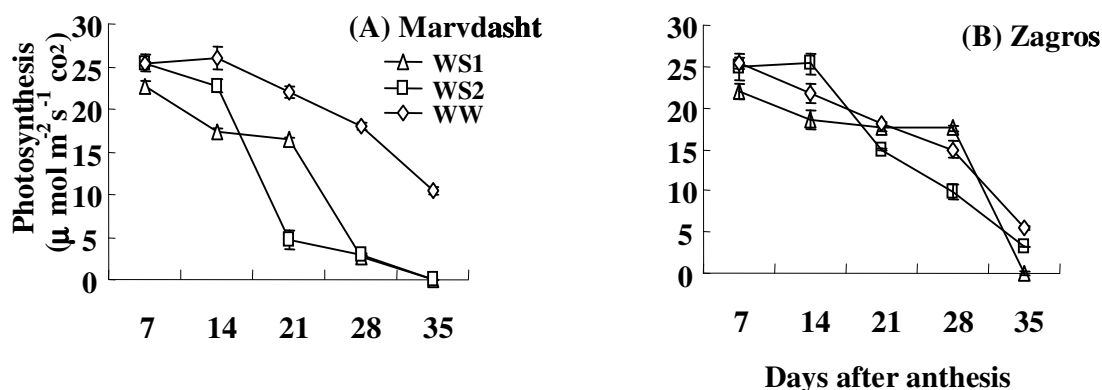
Figure 3. Changes in net photosynthetic rate in well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) flag leaves during grain filling in Marvdasht (A) and Zagros (B) wheat cultivars (*T. aestivum*). Data are means ± SE of three independent samples. SE bars are not shown where they are smaller than symbols.

Figure 4. Changes in stomatal conductance (g_s) in well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) flag leaves during grain filling in Marvdasht (A) and Zagros (B) wheat cultivars (*T. aestivum*). Data are means ± SE of three independent samples. SE bars are not shown where they are smaller than symbols.
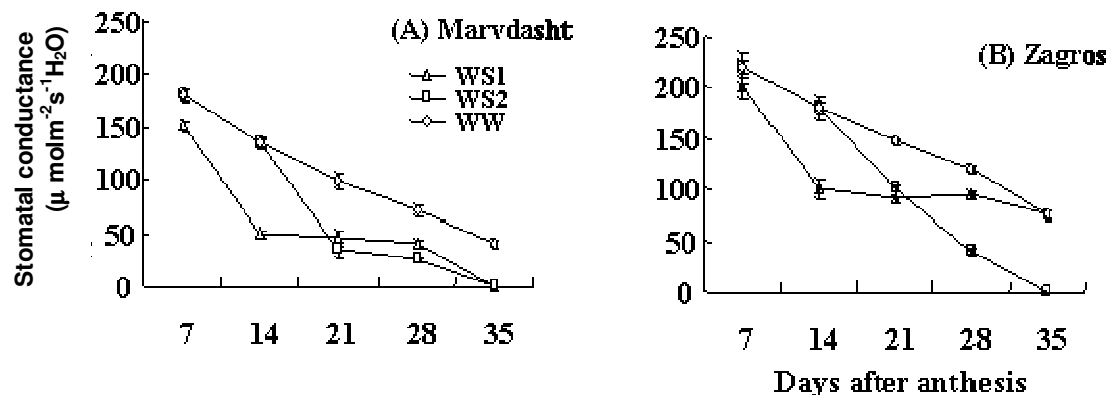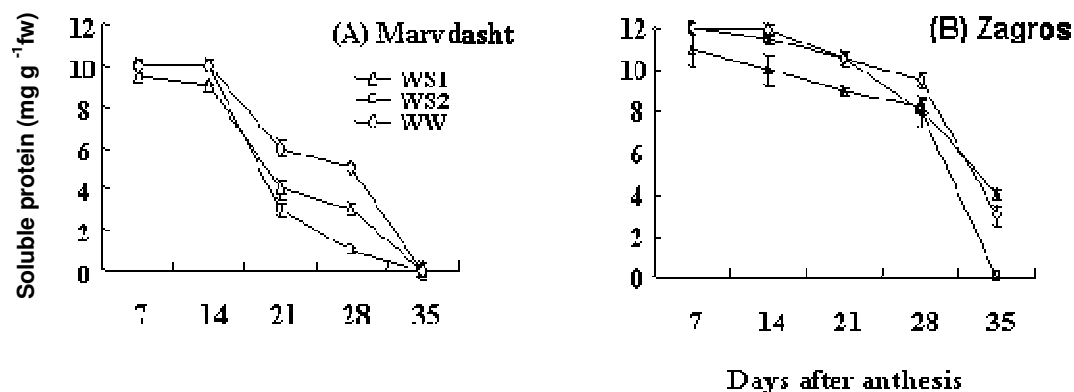

Figure 5. Changes in total soluble proteins in well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) flag leaves during grain filling in Marvdasht (A) and Zagros (B) wheat cultivars (*T. aestivum*). Data are means ± SE of three independent samples. SE bars are not shown where they are smaller than symbols.
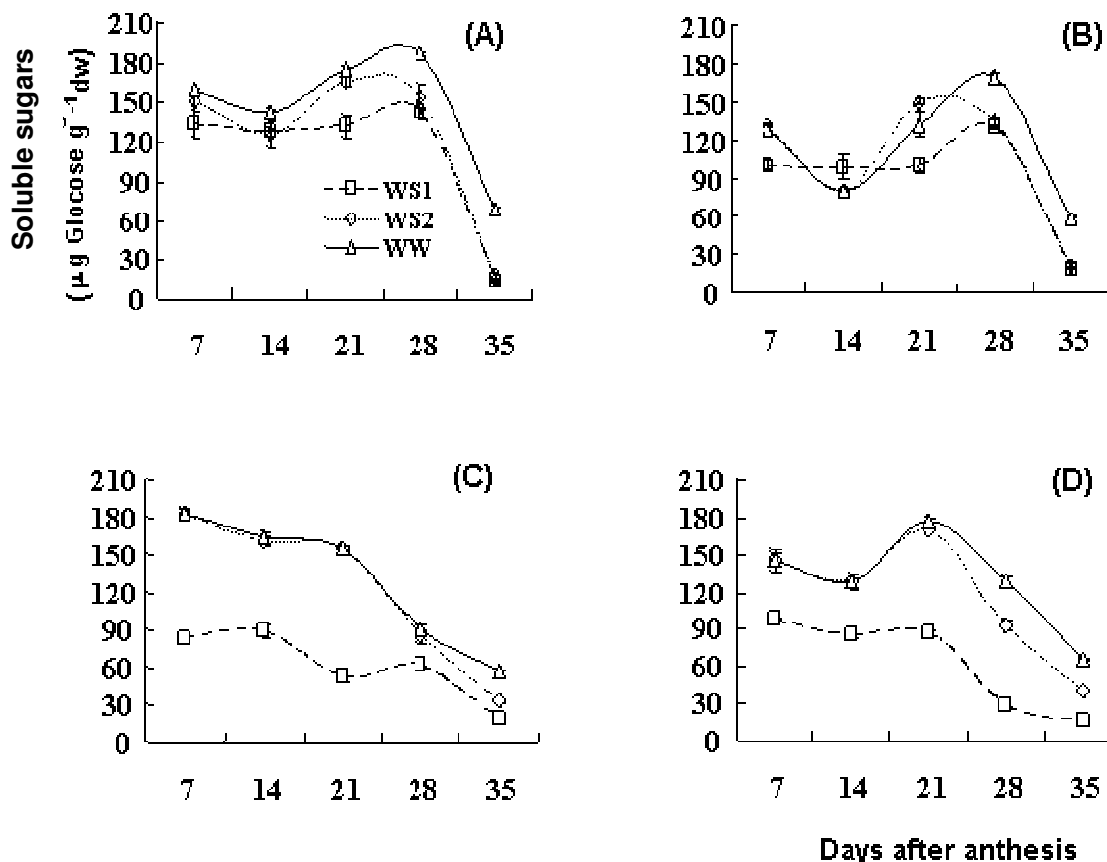
Figure 6. Changes in concentrations of total soluble sugars content of the penultimate (A and C) and peduncle (B and D), in Zagros and Marvdasht wheat cultivars respectively under different water treatment, well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2). Vertical bars represent ± SE of the mean (n=3) where these exceed the size of the symbols.

much more by WS1. The changes in WSC content under WS2 were greater in the penultimate internode than in the peduncle in both cultivars, but the patterns were similar.

The difference between the internodes is to be expected as the peduncle does not accumulate non-structural (storage) carbohydrate until after anthesis when development (elongation) is complete. Up to 21 DAA in each treatment there was little change in total WSC of penultimate in both cultivars (Figure 6 a to c). From 21 to 28 DAA, WSC increased slightly and then substantially decreased under all treatment at the end of the experiment in Zagros, the same pattern of reduction for WSC concentration was observed in Marvdasht, however, a reduced WSC occurred 1 week sooner than Zagros.

Results from the final sample stage showed that, the remobilization efficiency was enhanced by water deficit. Total carbon remobilized was reserve from peduncle and penultimate under WS1 by 70.4 and 81.4 and under WS2 by 105.9 and 150.4 for Marvdasht and 112.1, 128.9 under WS1 and 129.9, 148.4 under WS2 for Zagros, respectively (Table 1).

Similar pattern almost for WSC changing was observed in the peduncle of both cultivars (Figure 6 b to d). From 28 to 35 DAA, there was a fall in WSCs of both internodes, of which a considerable part could be accounted for by the mobilization. The amount of WSC remobilization under water stress was enhanced in both cultivar compare with WW treatment. Table 1 shows the disappearrance of pre C stored in both internodes that was much more in Zagros than Marvdasht and under WS2 than WS1 (Table 1).

Kernel weight and grain yield

Kernel weight was reduced by water deficits when compared with respective well-watered treatment in both cultivars (Table 2). However, reduction in kernel weight stress treatments (Table 2). It is noteworthy that, the grain number per spike was more influenced by WS1 than WS2, but yield gain under WS2 condition, was not enough to fully compensate for the lower kernel weight (Table 2).

Table 1. Maximum and minimum of total soluble sugar content of peduncle and penultimate (at flowering and maturity respectively), remobilization amount and remobilization efficiency in Zagros and Marvdasht genotypes under different water treatment, well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2).

Genotype	Treatment	Maximum concentration of soluble sugar		Minimum concentration of soluble sugar		Remobilization amount		Remobilization efficiency	
		Peduncle	Penultimate	Peduncle	Penultimate	Peduncle	Penultimate	Peduncle	Penultimate
		mg Glucose g^{-1}						Remobilization percent	
Mardasht	WW	227 ± 1.2	145 ± 1.6	56 ± 0.5	64 ± 2.6	171 ± 2.2	80 ± 2.4	75.16	55.46
	WS1	146 ± 3.2	183 ± 2.4	40 ± 2.4	32 ± 1.3	105 ± 4.1	150 ± 3.3	72.33	82.11
	WS2	88 ± 2.2	97 ± 3.1	18 ± 1.1	15 ± 0.9	70 ± 3.5	81 ± 1.9	79.47	84.18
Zagrose	WW	169 ± 2.5	187 ± 3.3	59 ± 0.8	68 ± 2.6	110±4.5	118 ± 4.1	65.1	63.28
	WS1	150 ± 2.7	165 ± 3.9	20 ± 3.7	17 ± 1.4	129±3.2	148 ± 2.8	86.27	89.49
	WS2	129 ± 2.1	141±2.6	17 ± 2.8	12 ± 0.7	112±2.5	128 ± 2.3	86.26	91.2

±, denotes standard error.

Table 2. Effect of different water treatment, well watered (WW), withholding water from anthesis till 14 days later (WS1) and withholding water from 14 days after anthesis till maturity (WS2) on the final number of kernel per spike, kernel weight per spike, the thousand-kernel weight, aerial biomass of plant and harvest index in two wheat cultivars.

Cultivar	Water-deficit treatment	Number of grain per ear	Grain yield per ear (g)	1000 grain dry mass (g)	Aerial biomass (g plant^{-1})	Harvest index (HI)
Marvdasht	WW	50.23 [a]	2.1 [a]	42.02 [a]	3.71 [a]	56 [a]
	WS1	41.97 [c]	0.902 [d]	21.1 [c]	2.17 [d]	41 [d]
	WS2	47.6 [b]	0.7 [e]	16.14 [d]	2.03 [e]	34 [e]
Zagros	WW	32.83 [d]	1.62 [b]	41.1 [a]	3.02 [b]	53 [a]
	WS1	28.43 [e]	1.22 [c]	40.3 [a]	2.42 [c]	50 [b]
	WS2	30.27 [e]	0.99 [d]	31.96 [b]	2.21 [d]	45 [c]
Reductions compared with control (%)						
Marvdasht	WS1	16.4	57	49.8	41.5	26.8
	WS2	5.2	66.7	61.6	45.3	39.3
Zagros	WS1	13.4	24.7	1.9	19.9	5.7
	WS2	7.8	38.9	22.2	26.8	15.1
LSD (0.05)		2.526	0.115	0.102	0.005	2.546

Letters indicate statistical significance at p 0.05 within the same cultivar.

under WS2 was more remarkable than WS1 treatment. In comparison, the reduction in Marvdasht was higher than Zagros under both stress regimes.

The values reductions were 49.8 and 1.9% under WS1 in Marvdasht and Zagros cv, compared with 61.6 and 22.2% under WS2 in the same cultivars, respectively (Table 2). A similar result was obtained for grain yield (Table 2), possibly because only the kernel weight, rather than the spike number or kernel number per spike, was influenced by water deficits during grain filling.

Similar changing also was found for biomass and HI; the result showed that grain production of both cultivars was affected by its biomass accumulation during its vegetative growth period. A positive relationship existed between HI and the amount remobilization during grain filling. WS1 treatment increased mobilization of assimilate stored in vegetative tissue to grains, resulting in greater yield and HI than WS2 (Table 1 to 2).

DISCUSSION

RWC in the leaves of the tolerant (Zagros) and sensitive (Marvdasht) genotypes decreased significantly in response to water deficit, but Marvdasht reached lower RWC values much earlier after water withdrawal, indicating that this cultivar respond to soil drought with a faster decrease in RWC than the tolerant genotype, however, WS2 cause more reduction than WS1 in both cultivars (Figure 1a, b). A rapid development of water stress resulted in a significant reduction in the rate of flag leaf photosynthesis soon after water stress commence-ment causing premature senescence of the flag leaf (Rawson et al., 1983). The significant changes in P_N during drought stress can be explained by earlier senescence, as drought may promote whole-plant senescence in monocarpic plants (Yang and Zhang, 2006). Earlier senescence during water deficit in sensitive and tolerant varieties was indicated by the earlier decline in pigment content (Figure 2 a to d). Marked differences between varieties were observed for soluble proteins under all treatments (Figure 5a, b). As for Chl a and b content and soluble proteins of flag leaves declined during grain filling (Figures 2 and 5), water stress accelerated the decline; however, the loss was more in Marvdasht and the differences achieved a maximum by day 28 from anthesis for each treatment. The study observation also showed that, P_N of the flag leaves declined with age in both cultivars under well-watered treatment, but water stress enhanced such a decline with a more extent under WS2 than WS1, although, Marvdasht showed earlier reduction under both stress treatments than Zagros cv (Figure 3 a, b). Under this condition, g_s were more affected than P_N (Figure 4a, b) and Marvdasht showed lower g_s than Zagros under water stress. A similar result was reported by El Hafid et al. (1998a) that drought susceptible genotypes exhibited lower g_s than tolerant genotypes upon exposure to stress.

The decrease in P_N in water-stressed plants could be explained by the stomatal closure, which reduced CO_2 diffusion and thus c_i. These results consistent with the recent view that an early decrease in photosynthesis under drought is due to increased stomatal resistance (Kicheva et al., 1994; El Hafid et al., 1998b).

Therefore, the photosynthates produced by the flag leaf during grain filling limit the growth of grain. A benefit from such a water deficit is that it can enhance remobilization of carbon reserves from vegetative tissues during grain-filling (Table 1). The contributions become greater when plants are grown under drought stress than under WW treatment.

The fast remobilization under both water stress regime coincide with the fast plant senescence induced by water deficit (Figure 2a to d) and slightly more under most cases (WS1 versus WS2, penultimate versus peduncle and Zagros versus Marvdasht). However, the WSC concentration substantially decreased by WS1 compared with their respective other treatments. The WW treatment left more WSC unused in both internodes cultivars than WS treatments (Figure 6a to d). Compared with Zagros cv., Marvdasht cv. had a lower remobilization under WW treatment, coinciding with its higher P_N during grain-filling (Figure 3a, b), however, Zagros cultivar maintained fairly higher P_N during post-anthesis periods under water stress. Marked differences among varieties in the relative contribution of pre- and post anthesis assimilates to grain yield were also reported by Przulj and Momcilovic (2001).

The continuous growth of grains in the absence of current photosynthate would deplete the reserves and grain growth would cease (Westgate and Boyer, 1985). A reduction in grain yield due to premature demise of sucrose activity (Westgate et al., 1989) and reduction in post anthesis photosynthesis and the amount of remobilizable assimilate (Kobata et al., 1992) has been suggested to be the main account under water stress conditions. In accord with earlier findings (Evers, 1970), the duration of the cell production phase in wheat ranges from 12 to 19 DAA on the conditions and cultivar. Therefore, it seems that the reduced grain weight under water stress conditions observed in the present study compared with their respective WW treatment, was via the effects of stress on cell division processes. Although, the WS2 treatment substantially decreases more kernel weight than WS1 treatment, this reduction was probably due to reduce endosperm cell number that led to reduced sink strength. This, in turn, could confer a critical survival advantage for few versus many seeds in terminal drought environments by reducing sink numbers at a key point in development and thus, secure a sufficient sucrose supply for maturation of a few remaining seeds as observed under WS2 conditions.

In this experiment, obvious differences between treatments with a similar pattern for grain weight in both genotypes were found (Table 2). However, the loss was more in Marvdasht than Zagros under water deficit. A similar result was obtained for grain yield under water

Conclusions

As the sink size was seriously affected by the WS in this experiment, this study speculate that increased carbon remobilization from the stems to grains and accelerate grain-filling rate may be mainly attributed to an enhanced sink activity in Zagros under the WS1.The contribution of pre-anthesis assimilates to grain may be crucial for maintaining yield when adverse climatic conditions reduce photosynthesis and water uptake. Thus, the high contribution of remobilization to grain yield observed in Zagros may be responsible for its known yield stability over early water withdrawal, however, these reserves deposited was not enough to compensate for the lower current assimilation under both water deficit treatments. Conversely, the low contribution of translocates could impair the var. Marvdasht maintain high yield when water stress occur around anthesis, as it was suggested by Frederick and Bauer (1999) for modern high yielding wheat varieties.

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REFERENCES

Bonnett GD, Incoll LD (1992). Effects on the stem of winter barley of manipulating the source and sink during grain filling: Changes in accumulation and loss of mass from internodes. J. Exp. Bot. 44: 75-82.

Bonnett GD, Incoll LD (1993). Effects on the stem of winter barley of manipulating the source and sink during grain filling. II. Changes in the composition of water-soluble carbohydrates of internodes. J. Exp. Bot. 44: 83-91.

Dingkuhn M, Gal PL (1996). Effect of drainage date on yield and dry matter partitioning in irrigated rice. Field Crop Res. 46: 117-126.

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956). Colorimetric method for determination of sugars and related substances. Anal Chem. 38: 350-356.

El Hafid R, Smith DH, Karrou M, Samir K (1998a). Physiological attributes associated with early-season drought resistance in spring durum wheat cultivars. Can. J. of Plant Sci. 78: 227- 237.

El Hafid R, Smith DH, Karrou M, Samir K (1998b). Physiological responses of spring durum wheat cultivars to early-season drought in a Mediterranean environment. Anal of Bot. 81: 363- 370.

Evers AD (1970). Development of endosperm of Wheat. Anal of Bot. 34: 547-555.

Frederick JR, Bauer PJ (1999). Physiological and numerical components of wheat yield. In: Satorre, E.H., Slafer, G.A. (Eds.), Wheat: Ecology and Physiology of Yield Determination. Haworth Press, Inc., New York, USA, pp. 45–65.

Gavuzzi P, Rizz M, Palumbo M, Campanile RG, Ricciardi GL, Borghi B (1997). Evaluation of field and laboratory predictors of drought and heat tolerance in winter cereals. Can. J. Plant Sci. 77: 523–532.

Gregersen PL, Holm PB (2007). Transcriptome analysis of senescence in the flag leaf of wheat. Plant Biotechnol. J. 5:192–206.

Jiang H, Wang XH, Deng QY, Yuan LP, XU DQ (2002). Comparison of some photosynthetic characters between two hybrid rice combinations differing in yield potential. Photosyn. 40: 133-137.

Kicheva MI, Tsonev TD, Popova LD (1994). Stomatal and nonstomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. Photosyn. 30: 107-116.

Kobata T, Palta JA, Turner NC (1992). Rate of development of post-anthesis water deficits and grain filling of spring wheat. Crop Sci. 32:1238–1242.

Lichtenthaler HK, Wellburn AR (1983). Determination of carotenoids and chlorophyll a and b of leaf extracts in different solvents. Biochem. Soc. Trans. 11:591–592.

Nicholas NE, Turner NC (1992). Use of chemical desiccants and senescing agents to select wheat lines maintaining stable grain size during post-anthesis drought. Field Crops Res. 31: 155–171.

Palta JA, Kobata T, Turner NC, Fillery IR (1994). Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. Crop Sci. 34:118–124.

Przulj N, Momcilovic V (2001). Genetic variation for dry matter and nitrogen accumulation and translocation in two-rowed spring barley. I. Dry matter translocation. Eur. J. Agron. 15:241–254.

Quirino BF, Noh YS, Himelblau E, Amasino RM (2000). Molecular aspect of leaf senescence. Trends in Plant Sci. 5: 278-282.

Rawson HM, Hindmarsh JH, Fishe RA, Stockman YM (1983). Changes in leaf photosynthesis with plant ontogeny and relationships with yield per ear in wheat cultivars and 120 progeny. Aust. J. Plant Physiol. 10: 503-514.

Sedmak JJ, Grossberg SE (1977). A rapid, sensitive, and versatile assay for protein using Coomassie brillant blue G250. Anal. Biochem. 79:544–552.

Sharkey SD, Seemann JR (1989). Mild water stress effects on car bon-reduction-cycle intermediates, ribulose bisphosphate carboxylase activity, and spatial homogeneity of photosynthesis in intact leaves. Plant Physiol. 89:1060-1065.

Stone PJ, Nicholas ME (1995a). Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. I. Grain growth. Aust. J. Plant Physiol. 22: 927–934.

Stone PJ, Nicholas ME (1995b). Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance. I. Grain growth. Aust. J. Plant Physiol. 22: 935–944.

Subhan D, Murthy SDS (2001). Senescence retarding effect of metal ions: pigment and protein content and photochemical activities of detached primary leaves of wheat. Photosynthesis, 39: 53-58.

Sylvester-Bradley R, Scott RK, Wright CE (1990). Physiology in the production and improvement of cereals. Home-Grown Cereals Authority Research Review, vol. 18. HGCA, London.

Wardlaw IF, Willenbrink J (1994). Carbohydrate storage and mobilization by the culm of wheat between heading and grain maturity: the relation to sucrose synthase and sucrose-phosphate synthase. Aust. J. Plant Physiol. 21:255–271.

Westgate ME, Boyer JS (1985). Carbohydrate reserves and reproductive development at low leaf water potentials in maize. Crop Sci. 25: 762-769.

Westgate ME, Schussler JR, Reicosk DC, Brenner ML (1989). Effect of water deficits on seed development in soyabean. II. Conversion of seed growth rate. Plant Physiol. 91: 980-985.

Yang J, Zhang J (2006). Grain filling of cereals under soil drying. New Phytol. 169:223–236.

Yang J, Zhang J, Huang Z, Zhu Q, Wang L (2000) Remobilization of carbon reserves is improved by controlled soil-drying during grain filling of wheat. Crop Sci. 40:1645–1655.

Yang J, Zhang J, Wang Z, Zhu Q, Liu L (2001). Water deficit induced senescence and its relationship to the remobilization of pre-stored carbon in wheat during grain filling. Agron. J. 93:196–206.

Yang JC, Zhang JH, Wang ZQ, Liu LJ, Zhu QS (2003). Postanthesis water deficits enhance grain filling in two-line hybrid rice. Crop Sci. 43(6): 2099–2108.

Zadoks JC,Chang TT, Konzak CF (1974). A decimal code for the growth stages of cereals. Weed Res. 14:415–421.

Zhang J, Sui X, Li B, Su B, Li J, Zhou D (1998). An improved water-use efficiency for winter wheat grown under reduced irrigation. Field Crops Res. 59:91–98.