Agronomy Research **13**(5), 1202–1214, 2015

Remobilization assay of dry matter from different shoot organs under drought stress in wheat (*Triticum aestivum* L.)

M. Golabadi[1,*], P. Golkar[2] and B. Bahari[1]

[1]Department of Agronomy and Plant Breeding, Collage of Agriculture, Isfahan (Khorasgan) Branch, Islamic Azad University, P.O. Box: 81595-158 Isfahan, Iran
[2]Institute of Biotechnology and Bioengineering, Isfahan University of Technology, P.O. Box: 84156-2781 Isfahan, Iran
[*]Correspondence: m.golabadi@khuisf.ac.ir

Abstract. Remobilization of dry matter during the grain filling period in wheat is capable of helping the plant recover its grain yield under drought stress. In this study, the genotypic variation of different traits related to dry matter remobilization were measured in seven genotypes of wheat under the three different environment conditions of well-watered, drought stress at heading stage with application of extra nitrogen fertilizer (30%), and drought stress in Isfahan, Iran. Analysis of variance showed that the genotypes were different not only in their dry matter remobilization from the spike, the stem, the peduncle, and the leaf sheath but also in their current photosynthesis. Different environmental conditions were found to affect dry matter remobilization from the leaves and sheath, current photosynthesis, grain yield, and the relative contributions by the stem and the spike to grain yield. The highest values of spike and stem contribution to grain yield were obtained under drought stress while current photosynthesis was found to be the sole supplier for grain filling in normal conditions. Application of extra nitrogen fertilizer under drought stress was found to reduce the loss of grain yield in some genotypes as a result of enhanced vegetative growth, reserve accumulation, and dry matter remobilization to the grain.

Key words: nitrogen, photosynthesis, stem, spike, water deficit.

INTRODUCTION

Receiving only an average annual precipitation of 240 mm, Iran is located in a semi-arid region (Kardavani, 1988), where drought stress is the most serious environmental factor affecting crop yield (Bradford 1994; Blum, 2011). Loss of yield is the main concern of plant breeders in such regions and they, hence, seek to maintain yield under drought stress conditions (Golabadi et al., 2006). Water deficit, particularly during the post-anthesis and seed filling stages, is one of the main limiting factors of wheat production in most parts of the Middle Asia and the Middle East including Iran (Kardavani, 1988). Although drought stress may occur in both early- and late-seasons, the highest drought-induced yield loss is caused by that during the post-anthesis stage (Blum, 2011). Current photosynthesis, as an important carbon source for grain filling, depends on the absorption of effective light by the green parts of plants such as the stem, spikes, and awns (Borras et al., 2004) after the pollination stage (Austin, 1989). Depending on environmental conditions, portions of these materials may be redistributed to developing grains during post-pollination stages. The redistribution of the substances stored in transient sources to the sink organs is called remobilization (Gardner et al., 2003). Under drought stress, the photosynthesis loss is compensated for by the remobilization of material reserves to the grain (Yang & Zhang, 2006). Drought stress leads to reduced grain weight, grain yield, and photosynthetic rate as a result of reduced availability of assimilates for export to the sink organs (Kim et al., 2000; Blum, 2011). The amount of dry matter accumulation in the source organs varies from 58 to 48 percent in favorable and unfavorable conditions, respectively, while it also depends on the cultivar and environmental conditions (Ebadi et al., 2007). Studies have shown that reserve remobilization could contribute to 5–20% of the final grain yield under non-stress conditions, while it might rise to 40–60% under stressful growing conditions (Blum, 1998). On the whole, about 10% to 30% of the stem carbohydrates which are extant before and after anthesis are sent to the grain-bearing organ; this remobilization can be more than 70% in some grain crops (Wang et al., 1995; Setter et al., 1998).

Cereals, including wheat and barley, are of primary importance for the food security in the 21st century (Distelfeld et al., 2014). Globally, wheat is one of the most important crops providing over 20% of the calories consumed by the world's population and a similar proportion of protein by about 2.5 billion people (Braun et al., 2010). Different physiological processes are involved in grain development and wheat crop yield under water stress conditions (Austin, 1989). Grain filling period in most regions of wheat cultivation is diminished by high temperature and low moisture (Schnyder, 1993). Drought stress decreases grain yield of wheat due to reduced sink strength and source capacity (Yang et al., 2001). Grain filling rate in wheat depends on the current photo-assimilate supply and the capacity of remobilizing carbohydrate reserves from the vegetative organs to the grains under drought stress (Wang et al., 1995). Ehdaie and Waines (1996) found that about 50% of the grain yield in some of the wheat genotypes was dependent on pre-anthesis reservoirs under drought stress and detected genetic differences in the photo assimilate contents of the vegetative organs and their remobilization to the grain for yield recovery in wheat.

Wheat genotypes that are able to recover from post-anthesis stresses require improved understanding of source–sink relationship and physiological process that determine the magnitude of multiple stresses on grain growth (Spiertz et al., 2006).

This study was conducted to evaluate: 1) the role of stem, spike, peduncle, and internode organs as material reserves on dry matter remobilization to grain in different wheat genotypes under 'normal', 'drought', and ' drought + extra nitrogen fertilizer' treatments; 2) the genotype diversity with regard to remobilization from different organs.

MATERIALS AND METHODS

Field experiment

This experiment was carried out at Research farm of Department of Agriculture, Islamic Azad University in Khurasgan region of Isfahan (1,517 m above sea level with 51°36′ longitude and 32°63 latitude) at central geographical region of Iran during November 2014 to June 2015. This region had arid and hot climates. The means of annual precipitation and daily temperature were 120 (mm) and 16°C, respectively.

The soil was loam-silt (30% clay, 53% silt and 17% sand) with 1.1% organic matter,0.11% N, 45 mg kg^{-1} phosphorous, 415 mg kg^{-1} potassium, EC 3.9 dSm^{-1} and pH 7.8. This study was conducted as a split plot based in a completely randomized block design with three replications. Three various regimes of drought stress and different genotypes of wheat were considered as main and sub plots, respectively. The genotypes including: Kavir, Ghods, Pishtaz, Rowshan, Sepahan, Line No. 9 and Line No. 11. Different irrigation treatments were normal irrigation (no stress), stop irrigation at 50% of heading stage (Zadoks 55) and stop irrigation at 50% of heading stage (Zadoks 55) plus application of 30% of extra nitrogen (N) fertilizer. Based on soil analysis, required fertilizers were used as follows: 50 kg ha^{-1} phosphorus as triple super phosphate ($Ca(H_2PO_4)_2 \cdot H_2O$), 50 kg ha^{-1} potassium as potassium chloride [KCl] and 250 kg ha^{-1} nitrogen as urea. Phosphorus, potassium and half of nitrogen fertilizers were added before sowing and the rest of nitrogen divided to two equal sections including at tillering and before heading stages. Each experimental sub- plots consisted of five rows with length of 5 m and inter rows distance of 25 cm. The sowing was done in mid -November. The sowing rate was 400 seeds per square meter. The three meter distance was considered between main plots to avoid water exchange. The final harvest was done at a square meter and using its was as obtained grain yield. The plots were treated periodically, pre- and post-emergence, with herbicides, to promote weed- development.

Measurement of studied traits

Remobilization traits were measured ten days after anthesis on 30 randomly selected stems from each plot at the stages of anthesis and physiological maturity. At anthesis stage, selected plants transported to the laboratory. In the lab, spike, peduncle, other internodes and the leaves and sheath were separated from stems and then placed inside a paper bag. These samples were dried for 72 hours at 70–72°C, after drying, the leaf sheath was separated from the stems and then each part was weighed. The same procedure was repeated at maturity stage (Zadoks 92). Then using the relations 1, 2, 3 and 4 the attributes associated with remobilization from vegetative organs to grain was calculated.

Dry matter remobilization (mg per plant) were calculated by difference of total dry matter (TDM) at different parts of plant (stem, spike, peduncle, other internodes, leaves and sheath) at anthesis by total dry matter at maturity in the same organ (Papakosta & Gagianas, 1991; Ehdaie & Waines, 1996), according to following formulae:

Dry matter remobilization (DMR) = ($TDM_{anthesis} - TDM_{maturity}$) × 100.

Current photosynthesis (CP) = Grain yield $_{30\ spike}$ – $DMR_{30\ spike}$ (Rawson and Evans, 1971).

Relative portion of spike reserves on grain yield (RPSP) %= DRM_{spike} / grain yield.

Relative portion of stem reserves on grain yield (RPST) %= DRM_{stem} / grain yield.

Analysis of variance carried out by SAS (9.1) and MSTATC soft wares. The mean comparisons were done by using least significant difference (LSD) test at 5% of probability.

RESULTS

Water deficit stress treatments were found to have significant effects on current photosynthesis (CP), proportion ratio of spike on stem (PRST), proportion ratio of stem on spike (PRSP), grain yield and remobilization of dry matter from the leaves and sheath (RDLS) (Table 1). Different genotypes of wheat showed significant differences in CP, grain yield and remobilization from different organs except for the internodes (Table 1). The effect of genotype × environment interaction was significant for the contribution of remobilization from spike, peduncle, leaves and sheath to grain yield, current photosynthesis and proportion ratio of spike on grain yield (Table 1). The highest (28.8) and the lowest (3.6) coefficients of variation (CV) % among the evaluated genotypes belonged to remobilization of dry matter from stem (RDST) and remobilization of dry matter from peduncle (RDP), respectively (Table 1).

Table 1. The analysis of variance for current photosynthesis, proportion ratio of spike and stem on grain yield and remobilization from different organs to grain in wheat under drought stress

S.O.V	df	CP$^{¥}$	PRSP	PRST	GY	RDI	RDLS	RDP	RDST	RDSP
Rep.	2	24.7*	0.08	0.04	0.04	0.06	0.02	0.01	0.07	0.02
Environ.	2	964.5**	0.44*	0.26*	0.95**	0.06	0.2**	0.06	0.08	0.01
$E_a^{¥}$	4	12.1	0.08	0.09	0.05	0.1	0.1	0.1	0.1	0.07
Genotype	6	18.5*	0.09	0.08	0.17*	0.03	0.1**	0.02*	0.05*	0.05*
G× E	12	18.6*	0.21*	0.06	0.1	0.04	0.1**	0. 1**	0.04	0.1**
E_b	36	6.9	0.08	0.07	0.07	0.05	0.03	0.07	0.04	0.04
CV%		15.5	23.1	28.7	19.5	8.4	6.7	3.6	8.1	7.6
R^2		0.91	0.61	0.49	0.62	0.55	0.78	0.58	0.54	0.65

¥: E_a: Rep.×Environ; Eb: Residuals; C.V: Coefficient of variation; R^2: Coefficient of determination; CP: Current photosynthesis; PRSP: Proportion ratio of spike on grain yield; PRST: Proportion ratio of stem on grain yield; RDSP: Remobilization of dry matter from spike; RDST: Remobilization of dry matter from stem; GY: Grain yield; RDP: Remobilization of dry matter from peduncle; RDI: Remobilization of dry matter from other internodes; RDLS: Remobilization of dry matter from leaves and sheath.

Current photosynthesis, proportion of stem and spike on grain yield and remobilization of dry matter in different environments

Current photosynthesis and the relative contributions of stem and spike to grain yield revealed significant differences among the different test environments (Table 2). The mean value of current photosynthesis was higher in the normal treatment, but the contribution stem remobilization to grain yield was greater in the treatments of drought/N fertilizer and drought than normal (Table 2). The contribution stem remobilization to grain yield was greater in drought and drought/ N fertilizer than normal condition (Table 2). No significant differences were observed among the means for remobilization from different organs under different water deficits, except for that from the leaves and sheath (Table 2). The highest (0.39) and the least (0.17) of remobilization of dry matter from leaves and sheath (RDLS) were denoted to normal and drought/N fertilizer treatments, respectively (Table 2).

Table 2. Effect of water deficit treatments on current photosynthesis, proportion ratio of spike and stem on grain yield and remobilization (mg plant^{-1}) of dry matter from several shoot organs

	CP$^{¥}$	PRSP	PRST	GY	RDSP	RDST	RDP	RDI	RDLS
Environment									
Normal	9.9^{a}	16.8^{b}	23.5^{b}	638.1^{a}	0.21^{a}	0.3^{a}	0.07^{a}	0.23^{a}	0.39^{a}
Drought/ N Fertilizer	3.1^{b}	26.3^{a}	35.2^{a}	185.9^{b}	0.22^{a}	0.28^{a}	0.06^{a}	0.22^{a}	0.17^{b}
Drought	3.3^{b}	24.9^{ab}	31.1^{a}	162.5^{b}	0.18^{a}	0.23^{a}	0.05^{a}	0.17^{a}	0.21^{b}

Means followed by the same letter was not significantly different at 0.05 level using LSD test.
*, **: significant at P<0.05 and P<0.01, respectively; ns: not significant.
¥: CP: current photosynthesis; PRST: proportion ratio of stem on grain yield; PRSP: proportion ratio of spike on grain yield; GY: Grain yield; RDSP: Remobilization of dry matter from spike; RDST: Remobilization of dry matter from stem; RDP: Remobilization of dry matter from peduncle; RDI: Remobilization of dry matter from other internodes; RDLS: Remobilization of dry matter from leaves and sheath.

Table 3. The mean comparison of current photosynthesis, proportion ratio of spike and stem on grain yield and remobilization (mg plant^{-1}) of dry matter from several shoot organs in different genotypes of wheat

Genotype	CP$^{¥}$	PRSP	PRST	GY (gm^{-2})	RDSP	RDST	RDP	RDI	RDLS
Kavir	6.9^{a}	13.2^{a}	24.3^{a}	329.2^{abc}	0.15^{b}	0.25^{b}	0.04^{b}	0.21^{a}	0.17^{b}
Ghods	4.8^{ab}	28.1^{a}	31.1^{a}	293^{bc}	0.25^{b}	0.27^{b}	0.05^{b}	0.21^{a}	0.23^{ab}
Pishtaz	3.2^{b}	26.3^{a}	41.1^{a}	386.9^{a}	0.2^{b}	0.32^{a}	0.06^{b}	0.26^{a}	0.32^{a}
Rowshan	3.4^{b}	23.5^{a}	29.9^{a}	231.9^{c}	0.17^{b}	0.22^{b}	0.07^{b}	0.15^{a}	0.29^{a}
Sepahan	7.7^{a}	23.6^{a}	23.9^{a}	372.7^{a}	0.26^{a}	0.28^{b}	0.05^{b}	0.23^{a}	0.29^{a}
Line - 9	6.6^{a}	18.7^{a}	25.6^{a}	382.2^{a}	0.18^{b}	0.23^{b}	0.03^{bc}	0.19^{a}	0.18^{b}
Line - 11	5.3^{ab}	25.2^{a}	33.3^{a}	298.9^{abc}	0.22^{b}	0.31^{a}	0.11^{a}	0.21^{a}	0.31^{a}

Means followed by the same letter was not significantly different at 0.05 level using LSD test.
*, **: significant at P<0.05 and P<0.01, respectively; ns: not significant.
¥: CP: current photosynthesis; PRST: proportion ratio of stem on grain yield, PRSP: proportion ratio of spike on grain yield, GY: Grain yield; RDSP: Remobilization of dry matter from spike, RDST: Remobilization of dry matter from stem, RDP: Remobilization of dry matter from peduncle, RDI: Remobilization of dry matter from other internodes, RDLS: Remobilization of dry matter from leaves and sheath.

Current photosynthesis, proportion of stem and spike on grain yield and remobilization of dry matter in different genotypes

Mean comparisons of dry matter remobilization from different organs of the shoot to the grain along with CP, PRSP and PRST and grain yield values in different genotypes are presented in Table 3. Among the studied genotypes, the highest current photosynthesis was obtained with Sepahan (7.7) whereas Pishtaz recorded the lowest (3.2) (Table 3). The highest grain yield (386.9 gm^{-2}) was observed at Pishtaz that showed significant difference with Rowshan and Ghods genotypes (Table 3). The highest remobilization of dry matter from spike (RDSP) and peduncle (RDP) were observed at Sepahan (0.26) and Line-11 (0.11), respectively (Table 3). Clearly, the Pishtaz genotype showed superiority among the genotypes evaluated with respect to its remobilization of dry matter from stem (0.32), but showed no significant difference with Line-11 (Table 3). The remobilization of dry matter from other internodes (RDI) showed no significant difference among evaluated genotypes (Table 3). Also, the highest remobilization of dry matter from leaves and sheath was denoted to Pishtaz genotype (0.32), and it was significant with the genotypes of Kavir and Line-9 (Table 3).

Genotype × environment interaction of studied traits

The genotype × environment interaction revealed that the value of dry matter remobilization from the peduncle had different reactions to stress treatments in different genotypes (Fig. 1). The RDP in drought/ N fertilizer was significantly more than drought in Line-11 (Fig. 1), *vise vera* the RDP was more in normal than drought treatments in Rowshan genotype (Fig. 1). Dry matter remobilization from the peduncle recorded its highest value with line –11 (0.16) under the drought/N fertilizer application treatment as compared to other treatments (Fig. 1). It was concluded that these genotypes were capable of exploiting their peduncle reserves in a drought-stressed environment, especially when extra N fertilizer was applied.

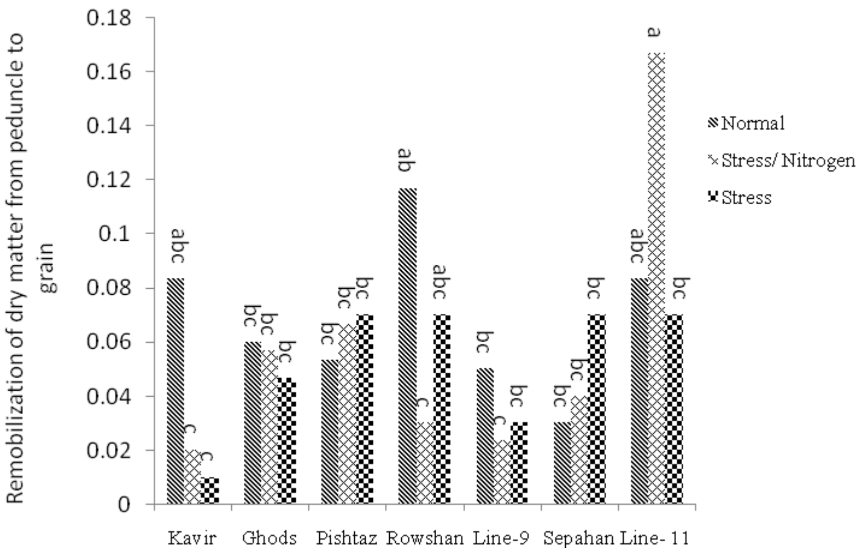

Figure 1. Genotype × environment interaction for remobilization from peduncle to grain.

The effects of genotype × environment interaction on dry matter remobilization from the spike to the grain are presented in Fig. 2. Clearly, the highest rate of RDSP was observed in Sepahan (0.51) under the drought/N fertilizer treatment that was significantly different with other genotypes, except for Line-11 (Fig. 2).

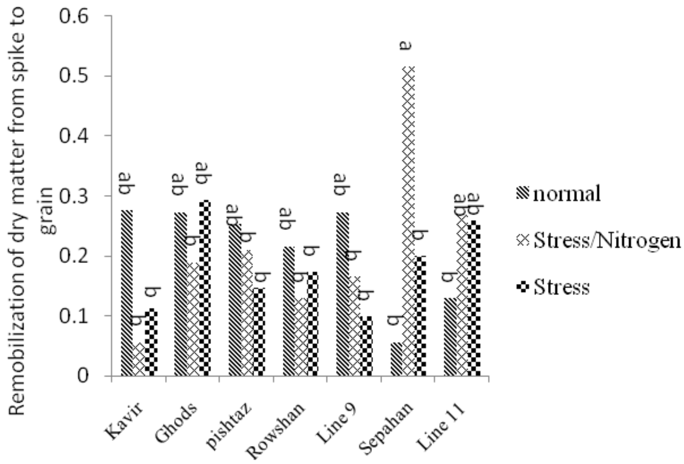

Figure 2. Genotype × environments interaction for remobilization from spike to grain.

The effects of genotype × environment interaction on dry matter remobilization from leaves and sheath are presented in Fig. 3. The genotypes of Ghods, Kavir, Rowshan, Line-9 and Line-11 showed higher rates of remobilization from leaves and sheath in normal condition, rather than drought/N fertilizer treatment (Fig. 3).

Remobilization from leaves and sheath in the Pishtaz and Sepahan genotypes under the drought/N fertilizer treatment were higher than those under drought stress (Fig. 3), which explains the benefits of using extra nitrogen in these genotypes under drought stress conditions. The Rowshan genotype, however, recorded the highest rate (0.41) for RDLS and RDST under drought stress treatment, that showed significant different from Kavir and Line-9 genotypes (Fig. 3). Also, this genotype had more RDLS at drought stress rather than drought/ N fertilizer.

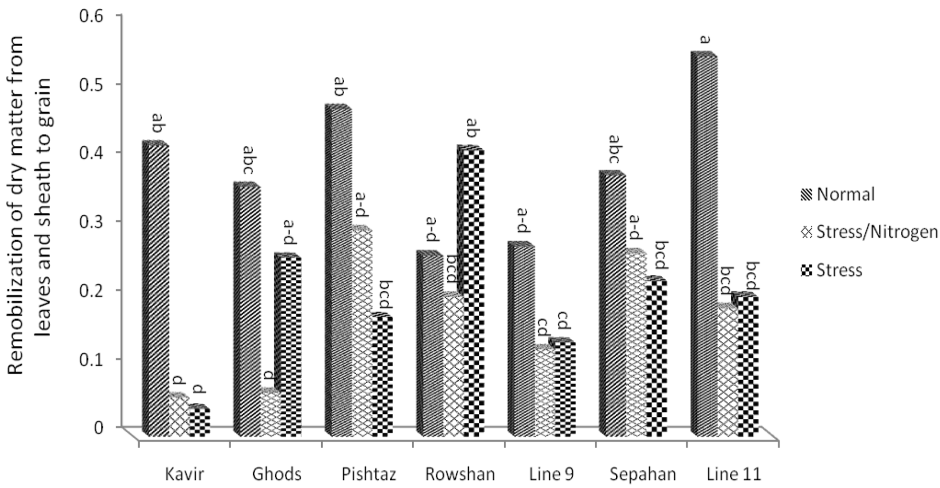

Figure 3. Genotype × environments interaction for remobilization from leaves and sheath to grain.

The genotype× environment interaction showed different relative ration of spike on grain yield for genotypes under normal condition, but they showed no significant difference under drought stress (Fig. 4). According to Fig. 4, the spike had the highest contribution to grain yield at the genotypes of Sepahan, Line 11 and Ghods under the stress/extra N fertilizer treatment (Fig. 4) rather than normal treatment.

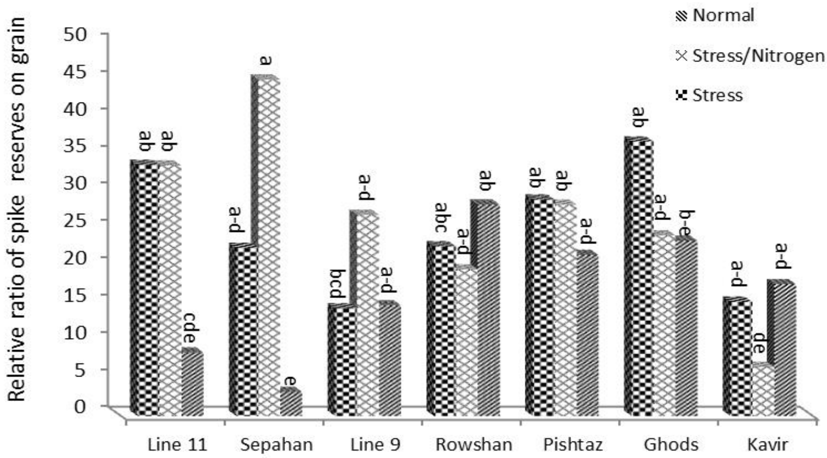

Figure 4. Genotype × environments interaction for relative ratio of spike on grain yield.

DISCUSSION

Before the anthesis stage, the amount of photosynthetic assimilates exceeds the plant's demand; therefore, the extra photo-assimilates accumulate in the shoot to be eventually stored in such secondary sources as stem, peduncle, and leaf sheath (Ebadi et al., 2007). Environmental stresses such as drought, especially during grain filling, lead to declining photosynthesis when the importance of secondary sources in grain filling becomes more pronounced. The highest dry matter remobilization values from the stem, the peduncle, the internodes, and the leaf sheath observed under normal irrigation implied the greater vegetative growth of various plant organs including the leaf sheath in the non-stress environment, which naturally explained the decreasing effect of water deficit on the dry matter translocation to sink (grain) organs (Blum, 2011). The relative contributions of dry matter remobilization from the spike and the stem to final grain yield depending on the genotype and environmental conditions (Blum, 1998; Ebadi et al., 2007). Similar to our findings, Ehdaei et al. (2006) reported higher values of the peduncle's mobile reserves under normal conditions than under stress conditions. Contrary to the present results, however, increased values of remobilization by the next internode (11%) and for other internodes (5%) have been reported under drought-stressed conditions (Yang et al., 2001; Ehdaei et al., 2006). The superiority of the Sepahan genotype for dry matter remobilization from the spike under drought/N fertilizer conditions explains the good adaptability of this genotype to drought stress as a result of consuming the spike assimilate reserves for grain filling. The Kavir, Ghods, and Rowshan cultivars were not capable of using the extra nitrogen present to increase ear reserves and to redistribute them to the grain. These genotypes showed higher remobilization rates under drought stress conditions than in the drought/ N fertilizer treatment. The higher rate of remobilization from the spike observed in the drought/N fertilizer treatment compared to the non-stress treatment is in good agreement with the findings of Ehdaei et al. (2006). The contribution of spike to grain yield was found to be significantly influenced by the drought stress conditions; Ahmadi et al. (2004) reported different results in their study. It may be concluded that the quantity of spike assimilate reserve and its remobilization efficiency are related to the sensitivity or the tolerance of genotypes to drought stresses, a finding that is different from those reported previously (Ahmadi et al., 2004).

The highest yields by the genotypes under normal conditions may be attributed to the longer grain filling period and the enhanced grain filling ratio under no-stress conditions (Ebadi et al., 2007). Several studies have indicated that grain yield in wheat primarily originates as a result of translocation from the vegetative parts after anthesis (Haberle et al., 2008). Fathi (1997) found that increased nitrogen fertilizer had no considerable effect on yield increase under drought stress, which is confirmed by our results in this study. It had been previously reported that extra nitrogen would give rise to only a slight influence on the reaction by the plant under drought stress and that nitrogen consumption efficiency would increase if sufficient water was present (Palta et al., 1994). However, average ranges of yield components have also been reported in the Pishtaz genotype (Golabadi & Golkar, 2013). This finding indicates that the stress tolerating mechanism had been really active in this cultivar so that yield reduction was prevented and grain yield increased under drought stress. The highest value of grain yield observed in Pishtaz genotype also confirms the influence of the assimilate reserves on preventing yield reduction under drought stress. Similar to our results, Pheloung and Siddique (1991) found that, compared to the potentially lower yielding cultivars, the high yielding ones with lower reserve storage suffered greater reductions in grain yield under drought stress during the grain filling period. It is noteworthy that the superior grain yield of Kavir to that of Rowshan could be compromised by its better reaction to some yield components such as spike number per plant and some of its physiological traits (Golabadi & Golkar, 2013). Blum (1998) also maintained that it would be possible to recover grain yield under stress by remobilization from the stem to the seed. No significant differences were observed in dry matter remobilization from the stem in the different drought treatments. Palta et al. (1994), however, reported that stem reserve remobilization is affected by water stress during grain filling and that the intensity of water stress may affect shoot reserve remobilization. During the grain filling period, stem weight begins to decrease, which indicates the consumption of the stored materials in the following growth stages (Rawson & Evans, 1971; Evans & Wardlow, 1996). The higher contribution of the stem to grain yield observed in the drought stress treatment as compared to the normal conditions is in agreement with the findings of previous studies (Sabry et al., 1995; Niu et al., 1998). Stem reserve is an important source of carbon for grain filling (Blum, 2011). Lopez-Castaneda and Richards (1994) reported an obvious relationship between grain yield and weight reduction of stem after anthesis in wheat, barley, triticale, and oat. Ehdaie et al. (2006) reported that wheat growth depends more on its stem reserves for grain filling than on current photosynthesis. Considering the fact that endosperm cells start to be filled two weeks after anthesis, the extra photo-assimilates must then accumulate in the stem (Schnyder, 1993). In other words, cultivars with a higher stem dry matter content exhibit a higher potential for storing photo-assimilates under favorite conditions in the early growth stage (before the onset of the dry season). This may be an advantage when the stored materials are transferred to the grain at a higher efficiency. The reaction of Rowshan genotype, with its relative semi-dwarf trait, was similar to that observed by Borrell et al. (1993) who reported that wheat dwarfness genes (Rht_1 and Rht_2) reduced the reserves in the stem (35%) and in the internodes (39%), which amount to a reduction of 21% in stem height. Ehdaei et al. (2006), in contrast, reported that there was no relationship between remobilization from the stem and stem height. The genotypes of Pishtaz, Sepahan, and Line-11 exhibited greater heights in the drought/N fertilizer treatment than in the drought stress condition (data not shown), indicating the complementary effect of nitrogen application on plant height. The significant differences observed among the genotypes in their rates of dry matter remobilization from the peduncle imply their physiological and morphological differences in terms of dry matter accumulation and remobilization of these assimilates to the grain (Ebadi et al., 2007). In the source–sink relationship for dry matter allocation, it is mainly the closest source that plays the more important role (Ebadi et al., 2007). Peduncle serves as a carbon source close to the grain; its dry matter could, therefore, be easily translocated to the grain when an environmental stress arises. Previous studies reported that the peduncle before the internode and the leaf sheath are the major places for dry matter accumulation and redistribution to the grain (Daniels & Alcock, 1982). The reducing current photosynthesis during grain filling observed in the water deficit treatments in this study has also been reported previously (Schnyder, 1993; Palta at al., 1994; Ahmadi et al., 2004). Under these conditions, the enhanced stem reserves and their remobilization serve as an important supporting process that can largely compensate for the reducing grain yield (Budakli et al., 2007). Ehdaie et al. (2006) noted that wheat crops grown in dry land areas would depend more on their stem reserves for grain filling than on current photosynthesis and the efficiency of dry matter transfer depends on the stem dry weight at anthesis and that higher dry matter contents give rise to great material transfers. Rowshan exhibited a similar mechanism for grain filling; however, it failed to achieve a high grain yield under drought stress conditions because this genotype does not have the genetic potential for high yield in all environments.

CONCLUSIONS

The results of the present study suggest that grain yield in wheat cultivars under water deficit conditions and photosynthetic inhibition of sources at the beginning of the grain filling period are controlled more by the source than by the sink limitation. Stem and spike were found to play important roles in supplying assimilate reserves for the grain filling process under stress conditions. This is while in normal conditions it is solely the current photosynthesis that supplies the materials required for grain filling without any need to the vegetative growth reserves. It seems that tolerant cultivars have a relatively higher capability for storing photo-assimilates while they are also more efficient in transferring their reserves under stress conditions.

In our study, leaf sheath dried quickly under drought stress and showed no considerable increase in remobilization. Other organs such as stem, spike, peduncle, and other internodes, however, exhibited increased rates of remobilization in the drought/N fertilizer treatment compared to the drought-stressed conditions. This indicates the higher photosynthetic assimilate reserves in these organs due to their higher vegetative growths as a result of the greater amounts of nitrogen present. Also, the increased remobilization by the peduncle in the drought/N fertilizer treatment compared to the drought stress one implies the supplementary effects of nitrogen as a result of enhanced peduncle assimilate reserves and their fast remobilization to the grain under stress conditions. The highest value of remobilization from the leaf sheath in the Rowshan genotype under drought stress might have been due to the plant's strife to remain green under drought stress and also to the genetic properties of this genotype which produced small amounts of reserves in the leaf sheath for complete use under stress conditions. This genotype can, therefore, be exploited in future breeding programs aimed at identifying the mechanisms involved in remobilization improvement. At this study, Among the different assimilate sources, the spike and the stem were found to have more important contributions to grain filling, a potential that can be exploited in the production of wheat cultivars with higher grain yields. Based on our findings, the evaluated genotypes showed significant difference for remobilization of dry matter from spike, stem, peduncle, leaves and sheath. The Pishtaz genotype in this study was found to have the highest grain yield but the lowest current photosynthesis, which confirms the idea that more efficient and greater use was made of the available reserves for grain filling in the absence of high current photosynthesis. So, the Pishtaz genotype may be recommended as the candid genotype for cultivation in drought regions because of its higher spike contribution to grain yield; its efficient material remobilization from the stem, the internodes, and the leaf sheath; and finally its grain yield.

REFERENCES

Ahmadi, A., Si-o-Semardeh, A. & Zali, A.A. 2004. A comparison between the capacity of photoassimilate storage and remobilization, and their contribution to yield in four wheat cultivars under different moisture regimes. *Iran J. Agric. Sci*. **35**(4), 921–931.

Austin, R.B. 1989. Maximizing crop production in water-limited environments. In: Baker FWG (Ed). Drought Resistance in Cereals. CAB International, pp. 13–25.

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

Blum, A. 2011. Plant breeding for water- limited environments. Springer. 255 pp. (In English)

Borras, L., Slafer, G.A. & Otegui, M.E. 2004. Seed dry weight response to source-sink manipulation in wheat, maize and soybean: a quantitative reappraisal. *Field Crops Res*. **86**, 131–146.

Borrell, A.K., Incoll, L.D. & Dalling, M.J. 1993. The influence of the *rht1* and *rht2* alleles on the deposition and use of stem reserves in wheat. *Ann. Bot.* **71**, 317–326.

Bradford, K.J. 1994. Water stress and the water relations of seed development: A critical review. *Crop. Sci*. **34**, 1–11.

Braun, H.J., Atlin, G. & Payne, T. 2010. Multi-location testing as a unit to identify plant response to global climate change. In: Reynolds MP, ed. Climate change and crop production. Surrey, UK: CABI Climate Change Series, 115–138.

Budakli, E., Celik, N., Turk M., Bayram, G. & Tas, B. 2007. Effects of post anthesis drought stress on the stem reserve mobilization supporting grain filling of two rowed barley cultivars at different levels of nitrogen. *J. Biol. Sci*. **7**, 949–953.

Daniels, R.W. & Alcock, M.B. 1982. A reappraisal of stem reserve contribution to grain yield in spring barley (*Hordeum vulgare* L.). *J. Agric. Sci*. **98**, 347–355.

Distelfeld, A, Avni, R. & Fischer, A.M. 2014. Senescence, nutrient remobilization, and yield in wheat and barley. *J. Exp. Bot*. **65**(14), 3783–3798.

Ebadi, A., Sajed, K. & Asgari, R. 2007. Effects of water deficit on dry matter remobilization and grain filling trend in three spring barley genotypes. *J. Food Agric. Environ.* **5**(2), 359–362.

Ehdaie, B. & Waines, J.G. 1996. Genetic variation for contribution of pre anthesis assimilates to grain yield in spring wheat. *J. Genet. Breed*. **50**, 47–56.

Ehdaie, B., Alloush, G.A., Madore, M.A. & Waines, G. 2006. Genotypic variation for stem reserves and mobilization in wheat: I. Postanthesis changes in internode dry matter. *Crop Sci.* **46**, 735–746.

Evans, L.T. & Wardlow, I.F. 1996. Photoassimilate distribution in plants and crops source-sink relationship. In: wheat. Eds. E. Zanneki, A.A. Sehalten. NewYork. PP: 501–518.

Fathi, G., McDonald, G.K. & Lance, R.C.M. 1997. Effects of post anthesis water stress on the yield and grain protein concentration of barley grown at two levels of nitrogen. *Aust. J. Agric. Res*. **48**, 67–80.

Gardner, F.P., Pearce, B. & Mitchell, R.L. 2003. Physiology of Crop Plants. Jodhpur Scientific, 328 p.

Golabadi, M., Arzani, A. & Maibody, S.A.M. 2006. Assessment of drought tolerance in segregating populations in durum wheat. *Afr. J. Agric. Res*. **1**(5), 162–171.

Golabadi, M. & Golkar, P. 2013. Compensation of grain yield reduction under drought stress by extra N fertilizer in bread wheat. *Int. J. Agric. Res. Rev*. **3**(3), 629–634.

Haberle, J., Svoboda, P. & Raimanová, I. 2008. The effect of post-anthesis water supply on grain nitrogen concentration and grain nitrogen yield of winter wheat. *Plant Soil Environ.* **54**, 304–312.

Kardavani, P. 1988. The Arid Lands. Tehran University Press, 376 p. (In Persian).

Kim, J.Y., Mahé, A., Brangeon, J. & Prioul, J.L. 2000. A maize vacuolar invertase, IVR2, is induced by water stress. Organ/tissue specificity and diurnal modulation of expression. *Plant Physiol*. **124**, 71–84.

Lopez-Castaneda, C. & Richards R. A. 1994. Variation in temperate cereals in rainfed environments I. Grain yield, biomass and agronomic characteristics. *Field Crops Res*. **37**, 51–62.

Niu, J.Y., Gan, Y.T., Zhang, J.W. & Yang, Q.F. 1998. Post-anthesis dry matter accumulation and redistribution in spring wheat mulched with plastic film. *Crop Sci.* **38**,1562–1568.

Palta, J.A., Turner, C. & Filery, I.R. 1994. Remobilization of carbon and N in wheat as influenced by post-anthesis water deficits. *Crop Sci.* **34**,118–124.

Papakosta, D.K. & Gagianas, A.A. 1991. Nitrogen and dry matter accumulation, remobilization and losses for Mediterranean wheat during grain filling. *Agron. J.,* **83**, 864–870.

Pheloung, P.C. & Siddiqe, H.M. 1991. Contribution of Stem Dry Matter to Grain Yields in Wheat Cultivars. *Aust. J. Plant Physiol*. **18**, 53–64.

Rawson, H.M. & Evans, L.T. 1971. The contribution of stem reserves to grain development in a range of cultivars of different height. *Aust. J. Agric. Res.* **22**, 851–863.

Sabry, S.R.S., Smith, L.T & Smith, G.M. 1995. Osmoregulation in spring wheat under drought and salinity stress. *J. Genet. Breed*. **49**, 55–60.

SAS Institute. 2003. SAS/STAT User's Guide, Version 9**.** 1. SAS Institute, Cary. NC.

Schnyder, H. 1993. The role of carbohydrate storage and redistribution in the source-sink relation of wheat and barley during grain filling-a review. *New phytol.* **123**, 233–245.

Setter, T.L., Anderson W.K., Asseng, S., & Barclay, S. 1998. Review of the impact of high shoot carbohydrate concentration on maintenance of high yields in cereals exposed to environmental stress during grain filling. CAB Abstract. **51**, 23.

Spiertz, J.H.J., Hamer, R.J., Xu, H.Y., Primomartin, C., Don, C. & Van De Putten, P. E. L. 2006. Heat stress in wheat; effects on grain weight and quality within genotypes. *J. Eur. Agron*. **25**(1), 89–95.

Wang, Z.M., Wang, S.A. & Su, B.A. 1995. Accumulation and remobilization of stem reserves in wheat. CAB Abstract. **25**, 10.

Yang, J. & Zhang, J. 2006. Grain filling of cereals under soil drying. *New Phytologist* **169**, 223–236.

Yang, J., Zhang, J., Wang, Z., Zhu, Q. & Liu, L. 2001. Water deficit-induced senescence and its relationship to remobilization of pre-stored carbon in wheat during grain filling. *Agron. J.* **3**, 196–206.

Zadoks, J.C., Chang, T.T. & Konzak, C.F. 1974. A Decimal Code for the Growth Stages of Cereals, *Weed Res.* **14**, 415–421.