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Influence of Water Deficit during Different Growth and Developmental Stages on the Contribution of Stored Pre-Anthesis Assimilates to Grain in Selected Durum and Bread Wheat Genotypes

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Abstract: Under water deficit conditions, declining photosynthesis and the subsequent decline in assimilates during the grain filling stage can increase the contribution of pre-anthesis assimilates stored in the stems, to grain filling in order to prevent severe reduction in grain yield. Results of the present study, which tested five durum and bread wheat genotypes under four irrigation regimes in different growth and developmental stages, have shown that apart from the contribution of pre-anthesis assimilates to grain filling, which increased during the one-leaf until grain filling period under water deficit, dry matter translocation and dry matter translocation efficiency decreased at the floral initiation to grain filling stage. The remobilization contribution of pre-anthesis assimilates increased by 20% under water limitation during grain filling compared to optimum irrigation. In addition to this, genotype G2 (durum wheat) and cultivar G3 (bread wheat) exhibited the highest contribution of pre-anthesis assimilates to grain filling, which was associated with longer day to the heading and the plant height under the optimum moisture conditions. Furthermore, the spike dry weight, spike harvest index and spike partitioning coefficient were also higher in the G2 and G3 genotypes.

Key words: Floral initiation, grain filling, pre and post-anthesis, remobilization, water deficit,

INTRODUCTION

Drought stress creates negative effects on crop growth and productivity through several ways, such as by decreasing its photosynthetic capabilities. However, crops have also reacted to water deficit using different complex mechanisms. Hence, improving grain yield under water deficit conditions has been considered as a very sound and important applied method in arid regions of the globe (Blum, 1998; Chaves and Oliverira, 2004; Zhang *et al.,* 2008).

Grain filling which is subjected to many biotic and abiotic stresses in most wheat growing areas, often begins when the temperatures are rising and water resources are declining. As water supply becomes limiting, drought stress causes kernel shriveling and the reduction of 1000-kernel weight, grain yield and yield stability. Thus, drought tolerance, and yield, has been a major objective for plant breeding programs (Blum, 1998; Ehdaie *et al.,* 1988; 1989).

Several researchers have suggested that grain structure and development in wheat depends on carbon provided from three sources, namely, photosynthetic assimilation, remobilization of pre-anthesis assimilates stored mainly in the stem and also the retransformation of assimilates stored temporarily in the stem after anthesis. In addition to this, photosynthetic assimilation as a source of carbon for grain filling depends on the light intensity reaching the leaves of the plant after anthesis. Furthermore, any stress, especially drought, can also decrease photosynthesis after anthesis (Bium, 1998; Kobata *et al.,* 1992; Schnyder, 1993; Ehdaie and Waines, 1996; Yang *et al.,* 2000). Photosynthetic assimilates can be limiting for the grain filling, even under mild drought conditions. Hence, the carbon reserves in the stem can be an important carbon source for grain filling (Yang *et al.,* 2000; Gent, 1994). Both grain dry matter accumulation and the canopy respiration are approximately identical sinks for the photosynthetic assimilates, and together their total demand for assimilates are greater in comparison with canopy photosynthesis during the grain filling stage (Blum, 1998). Therefore, internode reserves including the peduncle, penultimate, and the lower internodes, which are components of the stem in wheat, are eventually necessary for complete grain filling (Ehdaie *et al.,* 2006).

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Yang *et al.* (2000) Gent,(1994) and Plaut *et al.* (2004) reported that under suitable conditions sufficient carbohydrate accumulate in the stem before the grain-filling period. They also suggested that adequate carbohydrate storage may be dependent on plant traits, and can promote high yield potential at the pre-anthesis stages.

It has been reported that canopy photosynthesis rapidly decreases after the anthesis stage under terminal drought conditions Ehdaie *et al*., (2006). Furthermore, flag leaf photosynthesis cannot support both respiration and grain filling . Consequently, the contribution of current photosynthetic assimilates to grain filling decreases and a considerable quantity of the stem reserved carbohydrates are needed and to translocat the grains during grain filling in wheat (Rawson *et al.,* 1983; Austin *et al.,* 1977).

Even under sufficient water, the pre-anthesis assimilate reserves in the stems and sheaths of wheat and rice contribute around 10 – 40% to the final grain weight (Gebbing and Schnyder, 1999). Nevertheless, several researchers (Pata *et al.,* 1994; Asseng and Herwaarden, 2003; Plaut, 2004) as have reported that under water deficit conditions, the remobilization of the stem reserves to the grain will become more critical for grain yield. In addition, the stem reserve mobilization and its rate of development can be affected under the water deficit conditions during grain filling. Other results have shown a small contribution of pre-anthesis assimilates to grain under favorable moisture conditions (Rawson and Evans, 1971; Austin *et al.,* 1984) while contribution of pre-anthesis assimilates to grain can increase under the water deficit (Austin *et al.,* 1977; Aggarwal and Sinha, 1984). Since water limitations does not increase remobilization and environmental conditions decreases photosynthetic assimilation there is a greater demand for the stem reserves during the grain filling (Rawson *et al.,* 1983: Kiniry, 1993).

There were two vital traits stabilizing grain yield under the water stress during the grain-filling period. These are the capacity for photosynthetic assimilate storage in the stems and the efficiency of its remobilization to the grains. It has been reported that wheat grown under water deficit may depend more on water soluble carbohydrates of the stem reserves during the grain filling compared to current assimilates (Rawson *et al.,* 1971). Other studies have shown that the remobilization increases during plant senescence and early grain filling (Yang *et al.,* 2000). Recent studies have also shown the importance of water-soluble carbohydrates in the stems as a physiological trait indicative of the drought tolerance. It also contributes as a main carbon source for the grain yield, under the limited photosynthesis due to drought stress during grain filling (Ehdaie *et al.,* 2006; Diab *et al.,* 2004; Van Herwaarden *et al.,* 2006).

With regard to the association between agronomical aspects and assimilates during grain filling, there is a positive relationship between the harvest index and dry matter mobilization efficiency during grain filling. The mobilization of stored pre-anthesis assimilates to grains increased under moderate water deficit conditions during grain filling. It resulted in higher grain yield and water use efficiency in winter wheat varieties, which were related to the longer maturity duration and higher dry matter mobilization efficiency that finally improved harvest index (Zhang *et al.,* 2008).

Several researchers have reported the different contribution of the remobilization of pre-anthesis assimilates to the grain, among various genotypes of bread and durum wheat and triticale under optimum and water deficit conditions. The remobilization of pre-anthesis assimilates to the grain was reduced under water deficit conditions in Hongwangmai but increased in Haruhikari bread wheat cultivars (Inoue *et al.,* 2004), whilst Roshan and Chamran Iranian bread wheat cultivars produced the highest and lowest remobilization values, respectively (Ghodsi, 2004). In other studies on durum wheat genotypes, the dry matter translocation efficiency changed from 9% in old cultivars to 20% in modern cultivars. Also, the contribution of pre anthesis assimilates to grain yield increased by 31% in modern cultivars (Alvaroa *et al.,* 2008).

This study investigates the contribution of pre-anthesis assimilates stored in the stems, to grain filling in five durum and bread wheat genotypes under four irrigation regimes in different growth and developmental stages.

MATERIALS AND METHODS

Field Experimental Setup:

Two field experiments were carried out during the 2007-2008 growing season at the Khorasan-e- Razavi Agricultural and Natural Resource Research Center, Iran. The field experiments were laid out in Mashhad (36°, 13′ N latitude and 59°, 40′ E, elevation 985 m) and Neishabour (37°, 36 N and 48°, 58 E, elevation 1320 m) Research Stations in a split-plot arrangement based on a complete randomized block design with three replications. Irrigation regimes were considered as the main plots and included four different irrigation levels: D1, optimum water condition; D2, water limitation at the one-leaf to floral initiation stage; D3, water limitation at the floral initiation to anthesis stage with the prevention of precipitation using a mobile rain shelter; D4, water limitation at anthesis to late of grain filling stage and the prevention of precipitation. Sub-plots were assigned to five wheat genotypes, four promising durum lines and one bread wheat cultivar. The soil texture at the experimental fields was clay loam. Soil pH and EC (ds m^{-1}) was 8-8.1 and 1.7-2.2, respectively. Before sowing, the fields were fertilized with 50, 90, and 50kg NPK/ha. Additionally, 70 kg N was top-dressed and split into two applications. The seeds for the experiments were obtained from the elite durum yield trial (EDYT, 2006-2007) in the Seed and Plant Improvement Institute (SPII), Iran. Table 1 presents the genotype pedigree of the seeds used in the study.

To prevent the occurrence of diseases, the experimental seeds were covered with the fungicide Carboxin Thiram. Weeds were chemically controlled during the growing stages**.** In the experimental design, each plot consisted of 12 rows, 3 meters in length spaced 20 cm apart. From this the sub-plot size was calculated as 7.2 m^2 (12 x 3 x 0.2) and the seed density was 450 seed m^{-2} based on 1000-kernel weight. In order to compute the yield and yield component, the following parameters and traits were observed during the course of the study;

Measurement of Traits:

•Remobilization of Pre-anthesis Assimilates:

Twenty main shoots (including leaves and spikes) were randomly selected from each plot and cut at the soil surface at the anthesis and maturity stages. Different parameters describing the dry matter mobilization and remobilization within the plant were calculated according to Ghodsi (2004)], Nazeri (2005), Arduini *et al.* (2006) and Dordas *et al.,*(2008) as follows:

$$DMT = DMS\,a - DMS\,m$$
$$DMTE = [DMT / DMS\,a] \times 100$$
$$CPAA = (DMT / GY) \times 100$$

In these formulas, DMT is dry matter translocation (mg $plant^{-1}$); DMSa is dry matter shoot at anthesis; DMSm is dry matter shoot at maturity (leaf + culm + chaff); DMTE is dry matter translocation efficiency (%); CPAA is contribution of pre-anthesis assimilates to grain (%); and GY is grain yield (mg $plant^{-1}$)

•Spike dry weight (SPDW) and spike harvest index (SHI):

In order to compute SPDW and SHI, twenty plant stems (including leaves and spikes) were randomly selected from each plot at anthesis and the physiological maturity stages. The samples were kept in an incubator for 3 days at 80°C and the shoot and spike dry weight measured separately in the laboratory. The spike harvest index was calculated according to Donaldson (1996) and Robertson and Guinta (1994)] as follows;

$$SHI\ \% = (SPDW / TDMS) \times 100$$

In this formula SPDW is spike dry weight at anthesis and TDMS is total dry matter shoot at physiological maturity.

Data Analysis:

Data from the two locations were statistically analyzed by the MSTAT-C software package. In addition, the homogeneity between locations was assessed using the Bartlett's test to determine if location data could be combined and compared. Finally, comparative analyses of the means were performed by the Duncan's Multiple Range Test ($P < 0.01$).

RESULTS AND DISCUSSION

Remobilization of Pre-anthesis Assimilates:

As shown in Table 2 below, a combined analysis of variance revealed that dry matter translocation (DMT) was significantly affected (at $P<0.05$) under the water deficit conditions. However both the dry matter translocation efficiency (DMTE) and contribution of pre-anthesis assimilates to grain (CPAA) were highly significantly affected ($P<0.01$) by genotype effects and also by the interaction effect of water deficit and genotype (Table 2).

As shown Fig.1, there was no significant difference in DMT between the optimum irrigation treatment and the D2 and D3 water deficit treatments. The highest DMT (832 mg plant^{-1}) was exhibited in the D2 treatment whilst the lowest DMT (482 mg plant^{-1}) was translocated to grain under the D4 treatment conditions (water limitation at anthesis to grain filling stage). The highest DMT observed under moderate water deficit conditions (D2) was in agreement with the results of Zhang *et al.* (2008), but not with studies carried out by Nazeri (2005) and Ghodsi (2004) on triticale and bread wheat cultivars, respectively. On the other hand, the reduction of DMT under the D4 treatment which showed a critical stage for the remobilization of the stem reserves to the grains, was similarly reported in previous studies by Palta *et al.* (1994) Ghodsi (2004) and Plaut *et al.* (2004).

With regard to the different effects of the genotypes on remobilization of dry matter in the durum and bread wheat grains during the grain filling, the results of present study, as shown in Table 3, was in agreement with those reported by Inoue *et al.* (2004) Ghodsi (2004) and Álvaroa *et al.* (2008). The bread wheat cultivar (G3) exhibited the highest DMT of 836 mg plant^{-1} compared to the genotype G1 which showed a DMT of 521mg plant^{-1}, although there was no significant difference between the G3 with G2 and G5 durum wheat genotypes.

The dry matter translocation efficiency (DMTE) and the contribution of pre- anthesis assimilates to grain (CPAA) under optimum irrigation and water deficit conditions manifested different trends in their values (Fig. 2). The DMTE exhibited a similar trend as that shown with dry matter translocation (DMT) (Figs.1 and 2). Surprisingly the application of the different irrigation regimes in the D1 to D4 treatments, increased the contribution of the pre-anthesis assimilates to grains (CPAA). As shown in Fig. 2, the CPAA was 52% under favorable irrigation (D1) and increased to 73.5% under water deficit conditions during the anthesis until late grain filling period. It has been reported that a rapid decrease in canopy photosynthesis after the anthesis, under the terminal drought conditions, caused a reduction in the contribution of current assimilates to grain filling [14].Consequently, a considerable amount of stem reserved carbohydrates are translocated to grains during the grain filling period (Gent, 1994; Rawson and Evans, 1971). The 21% increase in CPAA observed in present study is in agreement with the above reports. However, it has been suggested that water limitation itself does not increase the remobilization, but environmental conditions that decrease current assimilation causes a greater requirement for the stem carbohydrate reserves during the grain filling (Rawson *et al.,* 1983; Kiniry, 1993).

The effects of genotype on the dry matter translocation efficiency (DMTE) and the contribution of pre-anthesis assimilates to grain (CPAA) as shown in Table 3, shows that the G2, G3 and G5 genotypes recorded the higher values. However, the CPAA for the G2 promising durum wheat genotype exhibited highest value amongst all the genotypes studied. Genotypic differences in DMTE and CPAA values has been reported between and within durum and bread wheat cultivars, which is similar with the results of the present study (Inoue *et al.,* 2004; Alvaroa *et al.,* 2008; Ghodsi, 2004).

As shown in Fig. 3, the interaction effect of genotype and water deficit with genotype on the dry matter translocation efficiency (DMTE) showed two remarkable results. The genotype G2 showed the highest DMTE before and after anthesis under the D3 and D4 water treatments, in addition to being the most stable genotype amongst all the genotypes studied under optimum irrigation and the water deficit conditions. The DMTE value changed by about only 5%, from 25% to 30%, in the G2 genotype, whilst it ranged from 14 to 36% in the G5 genotype. On the other hand, the DMTE for the other genotypes, except for genotype G3, decreased significantly under the D4 (water limitation at anthesis to grain filling) treatment.

The interaction effect of genotype and water deficit with genotype (Fig.4) on the contribution of the pre-anthesis assimilates to grain (CPAA), showed that the CPAA increased considerably with the application of water deficit during the D2 (one-leaf to floral initiation), D3 (floral initiation to anthesis) and D4 (anthesis to late grain filling) for all the genotypes studied. However, the CPAA value surprisingly increased in the G2 durum wheat genotype under the D3 and D4 water deficit conditions compared to the other genotypes, similar to the reports of Inoue *et al.* (2004) and Álvaroa *et al.* (2008) on bread and durum wheat cultivars. This suggests that the superior characteristics of the G2 genotype in relation to the remobilization of pre-anthesis assimilates during grain filling makes it a good candidate as a durum wheat drought tolerance genotype in the future. Several researchers have confirmed that the water soluble carbohydrates in stems contribute the main carbon source for grain yield under terminal limited photosynthetic conditions due to drought stress during the grain filling. It has also been introduced as a physiological indicator related to drought tolerance (Ehdaie et al., 2006; Diab *et al.,* 2004; Van Herwaarden *et al.,* 2006).

The important and considerable role of plant source and sink in the remobilization of the pre-anthesis assimilates to grain is well known and documented and thus an investigation on the effective parameters for improving their capacity during different plant growth and developmental stages can help to increase remobilized carbohydrates (Blum, 1998; Kuhbauch and Thome, 1989). It has been demonstrated that under certain and suitable conditions, the stem reserve accumulation can become the main source of adequate carbohydrate storage before the grain filling period, depending on the plant traits improved at the pre-anthesis (Yang *et al.,* 2001; Plaut *et al.,* 2004). Therefore, longer days to heading and plant height in the G2 and G3 genotypes in comparison with the other genotypes studied under the optimum moisture conditions could have an effect on enhancing stem carbohydrate reserves before the heading stage (Table 3). On the other hand, to have a sizeable sink increasing requirement and demand for translocation of assimilates to grain. Spike dry weight, spike harvest index and spike partitioning coefficient which are known as the sink capacity indices (Blum, 1998; Slafer, 1996) exhibited higher values in the G2 and G3 genotypes compared to the other genotypes (Table 3). Consequently, a strong source and sink effect and their balance in these genotypes have improved remobilization parameters and enhanced the contribution of pre-anthesis assimilates to grain during grain filling in the G2 genotype and Chamran bread wheat cultivar (Figs. 2 and Table 3).

Table 1: List of durum and bread wheat genotypes used in study

Genotype no	Pedigree	Genotype
G1	HAI-OU_17/GREEN_38	Durum wheat
G2	RASCON_37/BEJAH_7	Durum wheat
G3	CHAMRAN	Bread wheat
G4	RASCON_39/TILO_1	Durum wheat
G5	GARAVITO_3/RASCON_37//GREEN_8	Durum wheat

Table 2: Combined analysis of variance for dry matter translocation (DMT), dry matter translocation efficiency (DMTE), contribution of pre-anthesis assimilates to grain (CPAA), spike dry weight (SPDW), spike harvest index (SHI) and grain yield (GY) in durum and bread wheat genotypes under different water deficit conditions.

		Mean square (MS)					
Variation sources	df	DMT mg plant^{-1}	DMTE (%)	CPAA (%)	SPDW (gr m^{2})	SHI (%)	GY (t ha^{-1})
Location (L)	1	117187	1.26^{ns}	913^{ns}	2834^{ns}	23.9 ^{ns}	2.6 ^{ns}
Replication (R)	4	12150	8.35	84.7	18.4	1.7	0.3
Water deficit (D)	3	679823*	945**	2420**	21476**	68**	59.8**
L× D	3	32823*	21.7^{ns}	78^{ns}	1.89 ^{ns}	0.3 ^{ns}	0.1 ^{ns}
Error	12	6425	7.45	30.2	26.6	0.8	0.1
Genotype (G)	4	389225*	520**	723.6**	5222**	21**	2.4*
L× G	4	39721^{ns}	27.3^{ns}	36.7^{ns}	2.09 ^{ns}	0.2 ^{ns}	0.2 ^{ns}
D×G	12	38199^{ns}	97.8**	223.3**	200 ^{ns}	5.4**	0.9*
L× D ×G	12	34844**	34.8**	17.5^{ns}	2.52^{ns}	0.2 ^{ns}	0.3 ^{ns}
Error	64	6322	5.8	29.2	6075	0.8	0.2
CV %	-	11.42	9.80	8.52	6.95	12.88	8.02

*Significant difference at $P < 0.05$; ** Highly significant difference at $P < 0.01$; ns: Not significant

Table 3: Dry matter translocation (DMT), dry matter translocation efficiency (DMTE), contribution of pre- anthesis assimilates to grain (CPAA), spike dry weight (SPDW), plant height (PLH), spike harvest index (SHI), spike partitioning coefficient (SPC) , day to heading (DH) and grain yield (GY) in different durum and bread wheat genotypes

Genotype	DMT mg plant^{-1}	DMTE (%)	CPAA (%)	SPDW gr m^{-2}	SHI (%)	SPC (%)	GY t ha^{-1}
G1	521.7^{c}	17.8^{b}	56.4^{b}	112^{c}	6.2^{bc}	7.1^{d}	5.1^{c}
G2	801.7^{a}	28.3^{a}	71.5^{a}	116^{b}	7.6^{a}	8.7^{b}	5.5^{ab}
G3	835.9^{a}	29.2^{a}	64.1^{ab}	132^{a}	8.1^{a}	9.5^{a}	5.6^{a}
G4	635.5^{bc}	22.5^{ab}	61^{b}	110^{d}	6.7^{b}	7.9^{c}	4.8^{c}
G5	685.6^{ab}	25.4^{a}	63.9^{ab}	91^{e}	5.8^{c}	7.1^{d}	5.1^{bc}
LSD	160	6.95	8.1	2.83	0.56	0.68	0.37
Sx	40.7	1.07	1.24	0.65	0.09	0.1	0.09

Column sharing the same letters indicates no significant differences at $P < 0.01$)

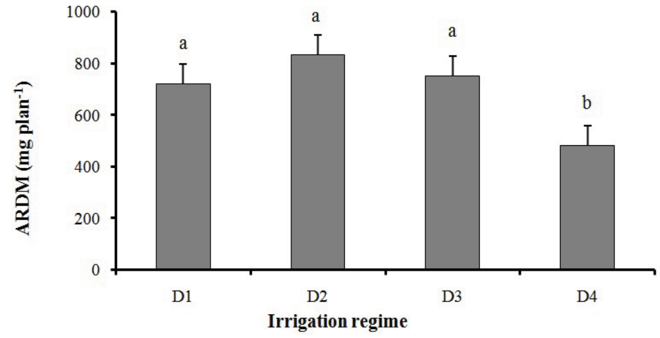

Fig.1: The effect of different irrigation regimes on dry matter translocation

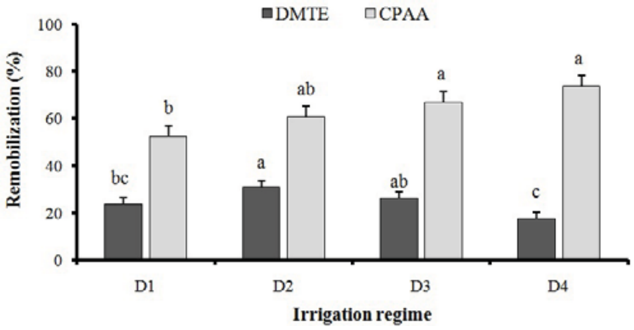

Fig. 2: The effect of different irrigation regimes on dry matter translocation efficiency and contribution of pre-anthesis assimilates to grain

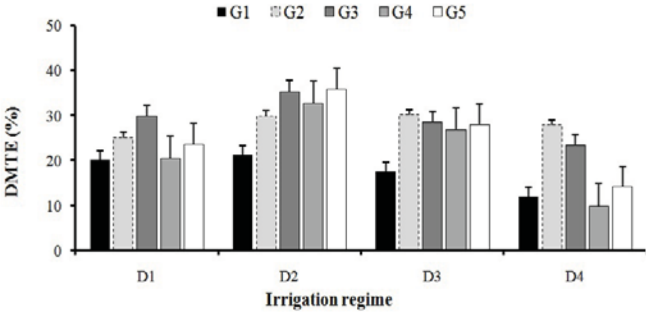

Fig. 3: Interaction effect of water deficit × genotype on dry matter translocation efficiency

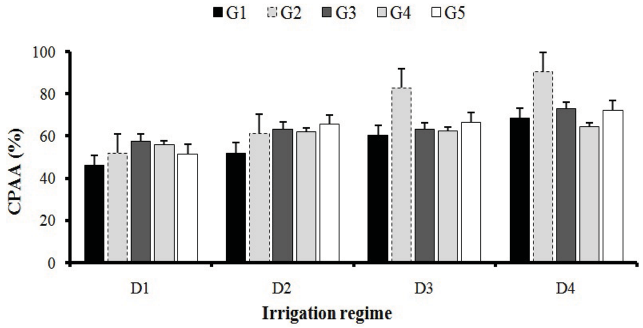

Fig. 4: Interaction effect of water deficit × genotype on the contribution of pre- anthesis assimilates to grain

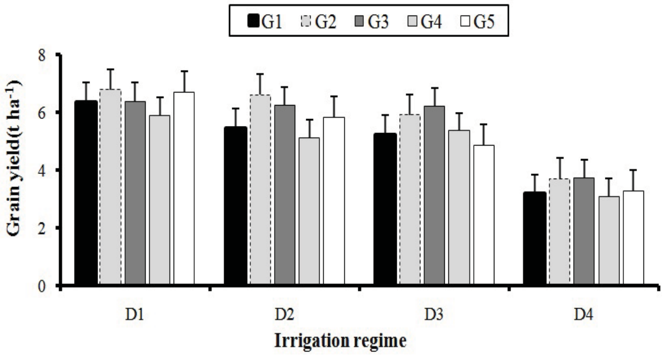

Fig. 5: Interaction effect of water deficit ×genotype on the grain yield

Conclusion:

The limited production of current photosynthetic assimilates during grain filling increases the contribution of the pre-anthesis assimilates stored in the stems, which are translocated to the sink tissues (mainly grain) under the water deficit conditions. It is a physiologically complex process subjected to water stress during grain filling. Our results indicated that although the contribution of pre-anthesis assimilates to the grain increased during the one-leaf until grain filling period under water deficit conditions, both dry matter translocation and dry matter translocation efficiency decreased during the floral initiation and grain filling. The highest assimilate contribution was made under water limitation condition at the anthesis to late grain filling period. While at the same stage, dry matter translocation and dry matter translocation efficiency exhibited the lowest values. Amongst genotypes studied, the G2 promising durum wheat and G3 bread wheat (Chamran) genotypes exhibited the most promising remobilization parameters. Particularly the contribution of pre-anthesis assimilates to grain enhanced in the G2 genotype during the grain filing stage. It appears that longer days to heading and plant height under optimum moisture conditions could have an effect on enhancing stem carbohydrate reserves before the heading stage. On the other hand, the spike dry weight, the spike harvest index and the spike partitioning coefficient, as the plant sink capacity indices, indicated higher values in the G2 and G3 genotypes. Consequently, the strong source and sink and their balance in these genotypes improved remobilization and hence enhanced the contribution of pre-anthesis assimilates to grain during the grain filling period. In addition to this, the lower reduction in grain yield during grain filling under water deficit conditions observed in the G2 and G3 genotypes could be due to dominant remobilization traits in these genotypes.

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REFERENCES

Álvaroa, F., F. Isidrob, D. Villegasa, F.L. García del Mora. and R. Conxita, 2008. Breeding effects on grain filling, biomass partitioning, and remobilization in mediterranean durum wheat. Agron J., 100: 361-370.

Aggarwal, P.K. and S.K. Sinha, 1984. Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought environment. Ann. Bot., 53: 329-340.

Asseng, S. and A.F. van Herwaarden, 2003. Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. Plant and Soil., 256: 217-229.

Austin, R.B., J.A. Edrich, M.A. Ford. and R.D. Blackwell, 1977. The fate of the dry matter, carbohydrates and C lost from the leaves and stems of wheat during grain filling. Ann. Bot., 41: 1309-132.

Arduini, I., A. Masoni, L. Ercoli. and M. Mariotti, 2006. Grain yield, and dry matter and nitrogen accumulation and remobilization in durum wheat as affected by variety and seeding rate. Eur J Agron., 25: 309-318.

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

Chaves, M.M. and M.M. Oliverira, 2004. Mechanisms underlying plant resilience to water deficits: Prospects for water-saving agriculture. J Exp Bot., 55: 2365-2384.

Diab, A.A., B. Teulat-Merah, N. Ozturk, Z.D. Benscher, 2004. Identification of drought-inducible genes and differentially expressed sequence tags in barley. Theor. Appl. Genet., 109: 1417-1425.

Dordas, C.A., A.S. Lithourgidis, T. Matsi. and N. Barbayiannis, 2008. Application of liquid cattle manure and inorganic fertilizers affect dry matter, nitrogen accumulation, and partitioning in maize. Nutr. Cycl. Agroecosyst., 80: 283-296.

Donalson, E., 1996. Crop traits for water stress tolerance .American Jurnal of Alternative Agriculture, 11: 89-94.

Ehdaie, B., J.G. Waines. and A.E. Hall, 1988. Differential responses of landrace and improved spring bread wheat genotypes to stress environments. Crop Sci., 28: 838-842.

Ehdaie, B. and J.G. Waines, 1989. Adaptation of landrace and improved spring wheat genotypes to stress environments. J. Genet. Breed., 43: 151-156.

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

Ehdaie, B., G.A.M. Alloush, A. Madore. and J.G. Waines, 2006. Genotypic variation for stem reserves and mobilization in wheat. Crop Sci., 46: 2093-2103.

Gent, M.P.N., 1994 . Photosynthetic reserves during grain filling in winter wheat. Agron J., 86: 159-167.

Gebbing, T. and H. Schnyder, 1999. Pre-anthesis reserve utilization for protein and carbohydrate synthesis in grains of wheat. Plant Physiol., 121: 871-878.

Ghodsi, M., 2004. Ecophysiological aspects of water deficit on growth & development of wheat cultivars. PhD. Thesis. University of Tehran.Iran.

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

Johnson, R.C., R.E. Witters. and A.J. Ciha, 1981. Daily patterns of apparent photosynthesis and evapotranspiration in a developing winter wheat crop. Agron. J., 73: 414-418.

Kiniry, J.R., 1993. Nonstructural carbohydrate utilization by wheat shaded during grain growth. Agron J., 85: 844-849.

Kobata, T., J.A. Palta. and N.C. Turner, 1992. Rate of development of post anthesis water deficits and grain filling of spring wheat. Crop Sci., 32: 1238-1242.

Kuhbauch, W. and U.Thome, 1989. Nonstructural carbohydrates of wheat stems as influenced by sink-source manipulations. J Plant Physiol., 134: 243-250.

Nazeri, M., 2005. Study on response of triticale genotypes at water limited conditions at different developmental stages. PhD. Thesis. University of Tehran.Iran.

Plaut, Z., B.J. Butow, C.S. Blumenthal, C.S. and C.W. Wrigley, 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Res., 86: 185-198.

Palta, J.A., T. Kobata, N.C. Turner, N.C. and I.R. Fillery, I.R, 1994. Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. Crop Sci., 34: 118-124.

Rawson, H.M. and L.T. Evans, 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust. J. agr. Res., 22: 851-863.

Rawson, H.M., J.H. Hindmarsh, R.A. Fi. and Y.M. Stockman, 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.

Robertson, M.J. and F. Giunta, 1994. Response of spring wheat exposed to pre- anthesis water stress. Aust.J.Agric.Res., 45: 19-35.

Schnyder, H., 1993. The role of carbohydrate storage and redistribution in the source - sink relations of wheat and barley during grain filling. New Phytologist, 123: 233-245.

Slafer, G.A., 1996. Differences in phasic development rate amongst wheat cultivars independent of responses to photoperiod and vernalization. A viewpoint of the intrinsic earliness hypothesis. Journal of Agricultural Science, 126: 403-419.

Van Herwaarden, A., R. Richards. and J. Angus, 2006. Water soluble carbohydrates and yield in wheat. The Australian Society of Agronomy. Proceedings of 13th Agronomy Conference.(http://www.regional.org.au/au/asa/2003/c/6/vanherwaarden .htm).

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

Yang, J.C., J.H. Zhang, Z.Q. Wang. and Q.S. Zhu, 2001. Activities of starch hydrolytic enzymes and sucrose-phosphate synthase in the stems of rice subjected to water stress during grain filling. J Exp Bot., 52: 2169-2179.

Zhang, X., S. Chen, H. Sun, D. Pei. and Y.Wang, 2008. Dry matter, harvest index, grain yield and water use efficiency as affected by water supply in winter wheat. Irrig. Sci., 27: 1-10.