

Evaluation of the accumulation of assimilates and remobilization in wheat (*Triticum aestivum* L.) genotypes under limited irrigation conditions

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ABSTRACT: The accumulation of assimilate remobilization in wheat genotypes was investigated under limited irrigation at research farm of Seed and Plant Improvement Institute, Karaj, Iran. The experiment was a split-plot with Irrigation treatment (optimum condition, water limited condition from stem elongation stage, heading stage and milky stage of grain) as the main plots and genotypes as subplots. The results showed that dry matter at flowering and maturity, the translocated dry matter, remobilization efficiency, and contribution of pre-anthesis assimilate to grain filling, spike harvest index and spike partitioning coefficient were affected by the irrigation regimes. Genotypes studied had no effect of traits. Results indicated that dry matter at flowering and maturity, spike harvest index and contribution of pre-anthesis assimilates to grain filling were also influenced by irrigation* genotype effects. A higher yield potential was found to be in genotype c-85d-9. This investigation highlighted that despite negative effects of drought stress on physiological traits, there are wheat genotypes with good performance drought conditions.

Keywords: wheat, drought stress, genotype, remobilization.

INTRODUCTION

In the natural environments, plants often grow under various stresses and their growth, metabolism and yield is severely affected. Biotic agents (insects, bacteria, fungi and viruses) and abiotic factors (light, temperature, water availability, food and soil structure) can affect the growth of higher plants. Drought stress is an abiotic factor limiting agricultural production (Reddy et al., 2004), and water shortage is a major factor limiting crop growth and production (Lawlor, 2002; Flexas et al., 2004). The amount of available water was found to be a factor limiting crop production (Ho et al., 2004). Plant growth and development is dependent on the sun's energy used to produce carbohydrates during photosynthesis in leaves. A part of carbohydrates produced is used for the development of the tissues and additional carbohydrates are transferred from the production site to consumption or storage location. Accordingly, the plant organs can be divided into two categories: sources and sinks.

Pre-anthesis assimilation of stem reserves is considered as a factor inhibiting against drought stress and mitigate the effect of stress on yield. In most cases, drought stress increases the transfer of stem reserves if the plants are subjected to water stress (Yang and Zhang, 2005). Generally, water stress reduces the current photosynthesis and increases contribution of remobilization during the grain filling. Thus, varieties with higher efficiency in remobilization of assimilates is found to be more tolerant to drought stress and show lower yield losses (Yang et al., 2000; Niu et al., 1998; Blum, 1998; Ehdaie and Waines., 1996). In a three-year study, Gent (1994) found that under adequate moisture conditions at grain filling, canopy respiration and dry matter accumulation in the grains were the main directions for use of photo-assimilates produced by leaves and their contribution of assimilates was found to be higher than that of current assimilates. As a result under these conditions, the stored assimilates in the stem are used to meet the need of these directions. Water stress at the grain-filling period induces early senescence, decreases photosynthesis, and shortens the grain-filling period; nonetheless, it

increases the remobilization of nonstructural carbohydrate from the vegetative tissues to the grain (Yang and Zhang, 2005). Yang and Zhang (2005) reported that water stress during the grain-filling period shortened the grain-filling period from 41 to 31 d, however, it enhanced the grain-filling rate and remobilization of pre-stored carbohydrate to the grains. It seems that controlled soil drying at the later grain-filling stage may induce plant senescence, and thus increase re-translocation of the pre-stored carbon reserve in the stem and sheath (Yang and Zhang, 2005). Yang *et al.* (2000) studied water stress occurring after pollination on two wheat cultivars and found that under controlled drought conditions, somehow during the night the plant can absorb enough water and its photosynthesis is not so much affected by the availability of water, water stress induces whole-plant senescence and enhances remobilization of carbon from vegetative tissues to grains, and accelerates the grain-filling rate. According to Yang and Zhang, (2005), in lodging-resistant cultivars/hybrids that often maintain their green tissue, the final grain weight was higher when the grain filling depends on both the current photosynthesis and the remobilization of storage compounds. Ahmadi and Baker (2000) found that the degree of drought caused severe wilt (non-refundable) in wheat after flowering remarkably decreased the remobilization of assimilates to sink. They also reported that the processes transporting the material to grains and convert it into starch were somewhat resistant to short-term drought. In such circumstances, photosynthesis is strongly influenced by the type of drought stress, leading to the dominance of resource limitations. Results of Yang *et al.* (2000) studies on the response of wheat cultivars to drought stress occurring at pollination showed that the reduced photosynthesis induced by drought stress decreased grain weight, however, it increased the remobilization of assimilates, highlighting insufficient remobilization to sustain grain weight compared to non-stress conditions. The occurrence of water stress after flowering can affect the biochemical allocation of assimilates between different sources of plant. Contribution of stem reserves in grain filling was reported to be 20-30% in previous studies under non-stress conditions (Gebbing and Schnyder, 1999; Ravindar *et al.*, 1982; Wardlaw and Willenbrink, 2000).

Ehdaie *et al.* (2006) determined assimilates remobilization of diverse wheat cultivars grown under well-watered and droughted field conditions and found two types of characteristics involving in the amount of stored carbohydrate sources contribute to the formation of grain yield of wheat as follows; 1) the ability to store assimilates in stems and 2) remobilization efficiency of materials stored in various parts of the stems to grains. Potential for accumulation of carbohydrates in the stem parts of wheat and also their remobilization depends on the length and density of carbohydrates. The amount of reserves increases with increasing the length and density of different parts of stem (Blum *et al.*, 1994).

Then, it can be concluded that even under optimal moisture, the current photosynthesis cannot fill the grains alone and partly related to the transfer of stored assimilates (Flexas *et al.*, 2004; Yang *et al.*, 2000), but the importance of this process is when plants are subjected to water stress which prevents the further reduction in grain yield. The aim of this study was to investigate the importance of remobilization and cognitive the traits related to remobilization process under water stress.

MATERIALS AND METHODS

To assess the accumulation and remobilization of assimilates in wheat genotypes under limited irrigation, a field trial was conducted during 2011-2012 at Research Field of Seed and Plant Improvement Institute, Karaj, Iran (35°59' N, 50°75' E, and 1312.5 m above sea level) with the average annual precipitation of 251.2 mm. Soil samples were taken randomly from depths of 0 - 30 and 30 - 60 cm to determine physical and chemical properties. Soil type was clay loam with organic matter of 0.44, pH of 7.8, EC of 1.7 dS m⁻¹, P and K values of 3.3 and 175 ppm, respectively. The experiment was laid out in split plot based on a complete randomized block design with three replications. Treatments were different regimes of irrigation (full irrigation, water stress from stemming by the end of growing season, water stress from spiking by the end of growing season, water stress from milky stage by the end of growing season) as main plots and wheat genotypes (c-85d-8, c-85d-9, c-85d-13, er-88-5, er-88-6, er-88-12 and Pishgam) as subplots.

To determine the amount of dry matter transferred by remobilization, 20 plants (including all the leaves and spikes) were randomly harvested at anther emergence and maturity stages from the inner rows of plots to preclude any edge effects. Samples were oven-dried at 80 °C for 72 hours and then stem, spike without grain, finally internodes and grain weight per spike (only at maturity stage) and total dry matter were weighed.

The amount of dry matter translocated (DMT) and contribution of pre-anthesis assimilate to grain filling (CPAAG) were calculated using the following equations (Papakosta and Gagianas, 1991);

$$\text{DMT} = \text{DMA} - (\text{DMM} - \text{GW})$$

$$*100\text{CPAAG} \% = (\text{DMT}/\text{GW})$$

Where, DMT is The amount of dry matter translocated, DMA is dry matter at anther emergence, DMM is dry matter at physiological maturity, GW is grain weight and CPAAG donates to contribution of pre- anthesis assimilate to grain filling.

Remobilization efficiency (RE), spike harvest index (SHI) and spike partitioning coefficient (SPC) were estimated according to the following relations (Donaldson, 1999);

$$RE \% = \frac{DMT}{DMA} \times 100$$

$$SHI \% = \frac{SDWA}{DMM} \times 100$$

$$SPC \% = \frac{SDWA}{DMA} \times 100$$

where SDWA is spike dry weight at the stage of anther emergence

All data were subjected to ANOVA using the GLM procedure of SAS (SAS Institute, 2002). Treatment means were separated using Duncan test at $P < 0.05$.

RESULTS AND DISCUSSION

Results indicated that DMA, DMM, DMT and RE % at 1% level, CPAAG %, SHI % and SPC % at the 5% level were affected by water stress (Table 1). All traits evaluated showed the best performance when water stress occurred at stemming but SHI (Table 2). The poorest performance for all traits evaluated except CPAAG and SHI was also observed when water stress occurred at spiking (Table 2).

Gent (1994) found that canopy respiration and grain dry matter accumulation were approximately equal sinks for photosynthate and, together, caused the canopy photosynthesis doesn't enough in grain filling. Observations showed that grain dry matter accumulation at flowering was found to be high under optimum moisture, temperature (Flexas et al., 2004) and nutrition (Yang and Zhang, 2005) which percentage of this matter is expected to store in grains. The rate of remobilization was detected to be within the range of 8%-95% in different cereals (Gebbing and Schnyder, 1999; Reddy et al., 2004), which is agreement with the finding of present study.

A higher ratio of dry matter allocation to the spike was observed under water stress compared to optimum conditions (Table 2). The percentage of CPAAG increased when water stress happened from stemming by spiking but this increase was not significant (Table 1). An increase in the ratio of dry matter allocation to the spike was attributed to higher reduction in total dry matter at flowering because spike dry matter reduction under this condition was insignificant compared to optimum conditions (Table 2). The proper moisture conditions after the stress period, especially during the grain filling period led to that plant can largely compensate the effects of mild water stress occurring at the beginning of the growing season. No significant difference was therefore found between stress and optimum conditions of moisture in term of the ratio of dry matter transferred (DMT), the percentage of remobilization and remobilization efficiency due to the proper condition after water stress (Table 2). A lower remobilization percentage of assimilates was observed when water stress occurred at milky stage (Table 2).

The maximum (1.86 g) and minimum (1.61 g) dry matter at flowering stage was related to when water stress happen at stemming and spiking, respectively (Table 2).

Unsuitable conditions occurred during the grain filling at spiking which was along with shortened grain-filling period resulted in the decrease in current photosynthesis and increase in respiration due to water stress. Also, the increase in the capacity of sinks because of the formation of spike structure in the proper conditions before flowering led to an increase in remobilization percentage of assimilates for grain filling.

Analysis of variance showed that the traits studied were influenced by different genotypes of wheat (Table 1). Genotype er-88-5 was detected to be high in DMA, DMM and DMT and genotype c-85d-9 was found to be high in CPAAG, RE, SHI and SPC as well (Table 2). Genetic diversity in remobilization percentage of assimilates among wheat cultivars (Blum, 1998; Ehdaie et al., 2006; Ehdaie and Waines, 1996) and triticale (Yang and Zhang, 2005) has been reported.

DMA, SHI, CPAAG at the level of 5% and DMM at the level of 1% was also affected by the water stress* genotype effects (Table 1). Genotype er-88-5 showed the best performance in DMA, DMM and DMT when irrigation limitation happen at stemming (Table 3). Results also showed that genotype c-85d-9 had a higher efficiency in CPAAG, RE, SHI and SPC under full irrigation conditions (Table 3).

A lower DMA, DMM and SPC were found in Genotype er-88-12 under water stress at spiking. Also, the lowest DMT was found in genotype pishgam under water stress at milky stage. On the other hand, genotype c-85d-13 showed a lower performance in CPAAG, RE, SHI when water stress induced at milky stage (Table 3).

The present study highlighted that genotype c-85d-9 had the best performance in term of the studied traits (Table 3). Genetic diversity in remobilization percentage of assimilates among wheat cultivars (Blum, 1998; Ehdaie et al., 2006; Ehdaie and Waines, 1996) and triticale (Yang and Zhang, 2005) has been reported which is in agreement with the finding of present study. Overall, results of this investigation indicated that the remobilization of

assimilates is a process which prevents a higher grain yield loss when plants are subjected to water stress. This process occurred when plant are exposure to water stress at the end of growing season which is typical under Mediterranean climate. So, optimum irrigation conditions before flowering and during the formation of the young spike will cause the formation of a sink strong and in these circumstances, if the plant is exposed to water stress at the end of the growing season, remobilizationof storedassimilatesindifferent organs of plant increases because of the sink demand and plays a greater share in grain filling. Therefore, management strategies shouldbe taken to avoid exposing the plant to water stress before the flowering stage and consequently with the formation of a sink strong at the end of the season (which is common), remobilization of assimilates plays a greater role in improving the yield. Future studies should be designed using the photosynthetic inhibitors in order to examine the role of current photosynthesis and remobilization in grain filling and eventually grain yield under irrigation limited conditions.

Table 1. Analysis of variance of moisture regimes for contribution of pre-anthesis assimilate to grain filling (CPAAG %), remobilization efficiency (RE %), spike harvest index (SHI %), spike partitioning coefficient (SPC %), dry matter at anther emergence (DMA), dry matter at physiological maturity (DMM) and dry matter translocated (DMT)

SOV	df	Mean of square							
rep	2	CPAAG	RE	SHI	SPC	DMA	DMM	DMT	
Water stress	3	1.008	30.67	22.52	18.07	0.15	0.32	99.83	
E1	6	10.17*	68.75**	22.70*	29.03*	0.20**	0.97**	388.78**	
genotype	6	9.023	188.11	62.03	20.11	0.014	0.747	587.79	
Genotype* Water stress	18	12.45*	9.24ns	13.75*	7.28ns	0.081*	0.415**	28.16ns	
E2	12	7.321	21.56	11.86	27.003	0.069	0.201	25.03	
E total	47	10.41	40.34	19.53	16.53	0.07	0.39	126.37	
CV %		3.69	22.01	22.37	18.29	12.03	16.48	23.65	

NS, * and **non-significant and significant at 1% and 5%, respectively.

Table 2. Mean comparison of moisture regimes and genotypes for contribution of pre-anthesis assimilate to grain filling (CPAAG %), remobilization efficiency (RE %), spike harvest index (SHI %), spike partitioning coefficient (SPC %), dry matter at anther emergence (DMA), dry matter at physiological maturity (DMM) and dry matter translocated (DMT)

Treatment		CPAAG (%)	RE (%)	SHI (%)	SPC	DMA (g)	DMM (g)	DMT (g)
Water stress	FI	96.38a	13.59a	17.90a	23.34ab	1.77a	2.60a	24.07a
	SFS	96.49a	13.71a	15.81b	25.40a	1.81a	2.63a	24.72a
	SS	96.47a	10.06b	17.96a	22.63b	1.61b	2.18b	16.12b
	SMS	95.06b	11.18b	16.65ab	23.60ab	1.64b	2.35ab	11.05c
	c-85d-8	96.33a	12.72a	17.83a	24.70a	1.68a	2.45a	21.00a
Genotype	c-85d-9	97.02a	13.23a	18.09a	25.58a	1.69a	2.39a	22.22a
	c-85d-13	93.94a	11.06a	15.78a	22.86a	1.66a	2.50a	18.64a
	er-88-5	96.50a	13.19a	16.69a	23.45a	1.81a	2.62a	23.71a
	er-88-6	96.89a	12.15a	17.00a	23.30a	1.71a	2.39a	20.67a
	er-88-12	96.76a	10.59a	17.36a	22.68a	1.73a	2.31a	18.70
	pishgam	96.24	12.00a	16.83a	23.63a	1.66a	2.41a	20.22a

Values followed by the same letter within a row are not significantly different at the 5% level of probability according to Duncan's test (FI= full irrigation, SFS= stress at stemming, SS= stress at spiking, SMS= stress at milky stage)

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Table 3. Mean comparison of interaction between moisture regimes and genotypes for contribution of pre-anthesis assimilate to grain filling (CPAAG %), remobilization efficiency (RE %), spike harvest index (SHI %), spike partitioning coefficient (SPC %), dry matter at anther emergence (DMA), dry matter at physiological maturity (DMM) and dry matter translocated (DMT)

Treatment	CPAAG (%)	RE (%)	SHI (%)	SPC (%)	DMA (g)	DMM (g)	DMT (g)
FI* c-85d-8	95.28a	10.35ab	19.45ab	27.76a	1.93ac	2.75ae	19.84ac
FI* c-85d-9	98.58a	16.87a	22.98a	28.49a	1.68bd	2.09ef	25.06ac
FI* c-85d-13	97.16a	13.11ab	18.68ab	24.82a	1.53cd	2.24cf	19.96ac
FI* er-88-5	96.84a	15.12ab	16.89ab	25.18a	1.62bd	2.44bf	26.88ac
FI* er-88-6	96.45a	13.31ab	16.33ab	25.00a	1.76bd	2.69af	23.64ac
FI* er-88-12	96.98a	11.21ab	17.86ab	22.96a	1.99ab	2.66af	23.60ac
FI*pishgam	93.34a	15.17ab	13.15b	23.57a	1.91ac	3.36a	29.48ab
SFS* c-85d-8	95.86a	15.19ab	16.42ab	25.79a	1.72bd	2.70ae	26.29ac
SFS* c-85d-9	96.17a	14.48ab	16.11ab	24.04a	1.94ac	2.94ac	27.39ac
SFS* c-85d-13	95.89a	13.25ab	13.79b	20.20a	1.71bd	2.49bf	23.39ac
SFS* er-88-5	97.05a	14.74ab	14.92b	21.58a	2.16a	3.13ab	31.86a
SFS* er-88-6	96.93a	14.00ab	15.80ab	21.53a	1.85ad	2.68af	25.40ac
SFS* er-88-12	95.58a	9.72ab	16.54ab	23.72a	1.69bd	2.43bf	16.33bc
SFS*pishgam	97.82a	14.60ab	17.09ab	21.57a	1.58bd	2.02ef	22.40ac
SS* c-85d-8	97.91a	12.51ab	18.22ab	24.11a	1.55cd	2.10ef	18.65ac
SS* c-85d-9	96.74a	10.84ab	16.73ab	22.42a	1.60bd	2.19cf	17.38bc
SS* c-85d-13	95.33a	9.20ab	16.88ab	23.75a	1.63bd	2.35bf	15.28bc
SS* er-88-5	96.96a	10.01ab	20.44ab	24.35a	1.69bd	2.17cf	16.82bc
SS* er-88-6	96.00a	8.58b	18.74ab	25.21a	1.74bd	2.34cf	15.00bc
SS* er-88-12	97.33a	10.48ab	16.35ab	20.82a	1.46d	1.95ef	15.31bc
SS*pishgam	95.09a	8.81b	18.33ab	24.54a	1.58cd	2.13df	14.38c
SMS* c-85d-8	96.26a	12.83ab	17.23ab	24.67a	1.54cd	2.25cf	19.22ac
SMS* c-85d-9	96.60a	12.49ab	16.52ab	23.83a	1.56cd	2.33cf	19.06ac
SMS* c-85d-13	87.33b	8.69b	13.75b	22.66a	1.76bd	2.93ad	15.93bc
SMS* er-88-5	95.14a	11.15ab	14.49b	22.67a	1.75bd	2.74ae	19.28ac
SMS* er-88-6	98.19a	12.72ab	17.14ab	21.47a	1.47d	1.89f	18.62ac
SMS* er-88-12	97.18a	10.92ab	18.68ab	23.25a	1.77bd	2.21cf	19.56ac
SMS*pishgam	94.71a	9.42ab	18.76ab	24.86a	1.59bd	2.12ef	14.64c

Values followed by the same letter within a row are not significantly different at the 5% level of probability according to Duncan's test (FI= full irrigation, SFS= stress at stemming, SS= stress at spiking, SMS= stress at milky stage)