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Improving Wheat Grain Yield under Water Stress by Stem Hydrocarbon Reserve Utilization

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Abstract: Current assimilation and remobilization of dry matter during grain filling in wheat subjected to different levels of water deficit during phenological growth stage. The experiment was conducted as split plot. Time of water stress and levels considered as main and sub plots, respectively. water stress treatments exposed at jointing, anthesis and seed filling stage and levels of water stress include, Full Irrigation (FI), Low Water Stress (LWS), Moderate Water Stress (MWS) and High Water Stress (HWS). Grain yield and dry matter accumulation and remobilization were negatively affected by water stress. The lowest grain yield was obtained from HWS and when water stress occurred at anthesis. Dry matter accumulation at LWS was 4.87%, at MWS was 14.86% and at HWS was 26.55% lower than FI, respectively. Spike density and the number of kernel per spike were affected similarly and decreased with water deficit increased. The decrease in the number of spikes per unit area due to LWS, MWS and HWS was 13, 23 and 30% compared to FI, respectively. As the water stress was imposed at jointing stage, the lowest number of spikes per unit area and when imposed at anthesis, the lowest number of kernel per spike was obtained. With increase in water stress intensity, the contribution of mobilized DM (DMRC) to grain yield increased. The highest DMRC value obtained from HWS with 25.37%.

Key words: Accumulation, growing stage, post-anthesis, remobilization

INTRODUCTION

Water stress commonly occurs during the growing season and the intensity of stress depends on the duration and frequency of water-deficit. In Iran, wheat is typically planted in autumn or early winter and harvested in early summer. Thus, it is generally assumed that the crop is grown when rainfall and temperature are favorable until anthesis. In these environments drought conditions during grain filling often involves also heat stress, which reduces the duration of grain filling. The common end-result of these stresses is reduced grain weight and loss in yield, depending upon the degree of water stress and the rate of stress development (Nicholas and Turner, 1992; Stone and Nicholas, 1995). Drought stress suppresses leaf expansion, tillering and midday photosynthesis and reduces photosynthetic rates and leaf area due to early senescence (Kramer and Boyer, 1995). All of these factors are responsible for a reduction in dry matter accumulation and grain yield under drought.

Current assimilation as a source of carbon for grain filling depends on the light intercepting viable green surfaces of the plant after anthesis. This source is normally diminishing due to natural senescence and the effect of various stresses (Wang *et al*., 2001). At the same time the demand by the growing kernel is increasing, in addition to the demand posed by maintenance respiration of the live plant biomass. Canopy respiration and grain dry matter accumulation were approximately equal sinks for photosynthate and together, were greater than canopy photosynthesis in grain filling (Gent, 1994). During grain filling, grains accumulate carbohydrates from different sources: current assimilates produced by photosynthesis in leaves and stems, assimilates redistributed from reserve pools stored in vegetative pares and their subsequent transport to the ear (Ercoli *et al*., 2008) and assimilates produced by the ear (Plaut *et al*., 2004). The production of new photosynthetic products may become limited under water stress, due to decrease in leaf stomatal conductance and net CO_2 assimilation (Blum *et al*., 1988).

The remobilization of assimilates is, an active process that involves translocation of stored reserves from stems and sheats to grain (Zhang *et al*., 1998). While root storage is important in some legumes and other species, there is no evidence that root or leaves are as important as stems for reserve storage in the small grains. Small grains stems store carbohydrates in the form of glucose, fructose, sucrose and starch, but the main reserve is fructan (Wardlaw and Willenbrink, 1994). In cereals, grains are the most important sink for carbon and nitrogen after anthesis. Available carbons assimilate for grain

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production is determined by carbon assimilation during the grain-filling period plus assimilate reserves stored in the straw. The productivity of cereals depends not only on the accumulation of dry matter, but also on its effective partitioning to plant parts of economic importance and this is a key to yield stability particularly under drought stress (Kumar *et al.*, 2006). Remobilization of reserves to grain is critical for grain yield if the plants are subjected to water stress during grain filling (Ehdaei *et al.*, 2006; Gallagher *et al.*, 1976; Palta *et al.*, 1994). It is known that among cereals and particularly in wheat, pre-anthesis assimilates help in yield stability during terminal drought stress (Blum *et al.*, 1994).

The objectives of this study were to quantify the production and redistribution of dry matter to the grain filling and how this varied among water stress treatments at different phenological stages.

MATERIALS AND METHODS

Site description and experimental design: Field experiment was carried out at research farm of Shahrood University of Technology in 2006. The area is located at latitude of 36°25'N and longitude of 54°57' E at an elevation of 1345 m. The annual mean precipitation, temperature and relative humidity are 156.6 mm, 14.4°C and 48%, respectively. The soil was clay loam characterized by a pH, 7.8; EC, 3.9 dS m^{-1} and organic carbon, 0.75% (Table 1). In this experiment wheat variety, Omid , that currently used in local production was grown. The experiment was conducted as split plot based on randomized complete block design with four replication. Time of water stress and intensity considered as main and sub plots, respectively. water stress treatments exposed at jointing , anthesis and seed filling stage and intensity of water stress include, Full irrigation (FI, control), Low water stress (LWS, irrigation at 75% FC), Moderate water stress (MWS, irrigation at 50% FC) and High water stress (HWS, irrigation at 25% FC). Before experiment soil samples from farm were collected and in laboratory soil moisture characteristics curve were determined using pressure plate apparatus and plants were re-irrigated when appropriate water potential obtained with daily sampling. Each plot measured 2.5 by 4 m and contained 10 furrows 4 m in length. All sampling conducted within a central 2 by 3 m.

Table 1: Soil chemical properties of the top soil layer (0-30 cm)

Texture	OC (%)	pH	EC (d S m^{-1})	N (%)	P (%)
loamy clay	0.75	7.78	3.9	0.04	6.4
Texture	K (%)	Fe (mg kg^{-1})	Mn (mg kg^{-1})	Zn (mg kg^{-1})	Cu (mg kg^{-1})
loamy clay	230	2.72	6.44	0.54	0.78

Biomass and yield determination: At anthesis and maturity plants were cut at ground level and separated into leaves, culms and spikes. All the plant parts were oven dried at 65°C to reach constant weight for dry weight determination. To determine remobilization during grain filling, plants were harvested at anthesis (stage 60 of the scale of Zadoks *et al.*, 1974) and at physiological maturity (stage 90).The following parameters, related to dry matter accumulation and remobilization within the wheat plant, were calculated following Arduini *et al.* (2006) and Masoni *et al.* (2007), as:

Post-anthesis dry matter accumulation as difference between dry matter of the whole plant at anthesis and at physiological maturity.

Dry matter remobilization (DMR) = DM of the whole plant at anthesis-DM of roots, leaves and culms at maturity.

$$\text{DMR efficiency} = \frac{\text{DMR}}{\text{DM of the whole plant at anthesis}} \times 100$$

$$\text{Contribution of DMR assimilates to grain} = \frac{\text{DMR}}{\text{Gain yield at maturity}} \times 100$$

Statistical analysis: Data were statistically treated by ANOVA, Least Significant Difference (LSD) test at probability level 0.05 was used to separate the means when the ANOVA F-test indicated a significant effect of the treatments.

RESULTS

Shoot dry weight and grain yield: Analysis of variance showed significant difference between water stress regimes on shoot dry weight and grain yield. Increasing stress intensity, caused shoot dry weight and grain yield similarly reduced (Table 2). Average over plant growth stage, the highest value of shoot dry weight obtained from full irrigation followed by LWS, MWS and HWS treatments. Also the greatest grain yield was obtained from irrigation at FI with 426.3 g m^{-2} and decreased with the increase of water stress (380.2, 331.8 and 285.7 g m^{-2} for LWS, MWS and HWS, respectively). Results of this

Table 2: Total dry weight and grain weight of wheat plants at different phenological stage as affected by water stress

Treatment	Shoot DW (g m^{-2})	Grain yield (g m^{-2})	Spike (n m^{-2})	Kernel per spike (n)	Harvest index (%)
FI	1027.50*a	426.30a	473.30a	33.92a	41.90a
LWS	930.10b	380.20b	414.30b	29.33b	41.02b
MWS	849.37c	331.80c	364.60c	27.08c	38.77c
HWS	773.60d	285.70d	331.43d	24.50d	37.22d
Jointing	951.07a	351.30b	377.13b	31.06a	36.81b
Anthesis	894.25b	312.60c	394.25ab	26.00c	34.51c
Grain fill	840.15c	404.10a	416.20a	29.06b	47.87a

*Values followed by the same letter(s) in each column are not significantly difference at $p \leq 0.05$

study showed water stress treatments at different phenological stage significantly affected shoot dry weight and grain yield. Water stress at jointing stage had the lowest effects on shoot dry weight. Whereas the lowest grain yield was 312.6 g m^{-2} and obtained when water stress occurred at anthesis. Spike density and the number of kernel per spike were affected similarly by water stress treatments and strongly decreased with water deficit increased. As a consequence, the decrease in the number of spikes per unit area due to LWS, MWS and HWS was 13, 23 and 30% compared to FI, respectively. The increase of water stress intensity progressively reduced the number of kernel per spike (Table 2). As the water stress was imposed at jointing stage, the lowest number of spikes per unit area was obtained. Also when water stress imposed at anthesis, the lowest number of kernel per spike was obtained (26 kernels per spike). Harvest index was decreased with the increase of water stress. As a consequence the reduction of harvest index due to LWS, MWS and HWS as compared with full irrigation was 2, 7.5 and 9.2%, respectively. Average over water stress treatments, the lowest harvest index was obtained from water stress exposed at anthesis (Table 2).

In this study the highest shoot dry weight and number of kernel per spike were obtained with FI at jointing stage and also the greatest grain yield and number of spike per meter square were obtained , with FI at grain filling. The highest amounts of HI obtained at grain filling with FI and LWS stress levels (Table 3).

From anthesis to maturity a decrease in dry matter was observed in leaves, culms and roots, whereas, owing to spikes growth, whole plant dry weight at maturity was increased. Average over the water stress treatments, the amount of post-anthesis dry matter accumulation differed among phenological stages (Fig. 1). Accumulation was 16.2% lower when water stress occurred at anthesis than jointing and 38.2% lower when water stress occurred at grain filling than jointing and also 22% lower at grain filling than anthesis (Fig. 1). Dry matter accumulation was affected negatively by water stress treatments. Dry matter accumulation at LWS was 4.87%, at MWS was 14.86% and at HWS was 26.55% lower than FI, respectively (Fig. 1a, b). The effects of water stress treatments at phenological stage was striking on the remobilization of plant photoassimilates (Fig. 2a, b). Water stress imposed at jointing stage had a 39% and 174% lower dry matter remobilization compared to plants subjected to water stress at anthesis and grain filling stage, respectively. Also dry matter remobilization at anthesis had a 97% lower dry matter remobilization than at grain filling stage.

Results of this research showed, remobilization efficiency was also 27.5% higher at anthesis and 116.5% at grain filling compared to jointing stage. Also DMER was about 70% higher at grain fill than anthesis. Results showed the Remobilization efficiency was nearly constant among water stress treatments and the mean value of this parameter was 17.7%. The mean contribution of mobilized DM to grain yield was about 23% and differed among phenological stages (14, 21.82 and 33.10% at jointing, anthesis and grain filling, respectively) (Fig. 2). With increase in water stress intensity, the contribution of mobilized DM to grain yield increased. The highest DMRC value obtained from HWS with 25.37% (Fig. 2).

Table 3: Water stress and application time interaction effects on Total dry weight and grain weight of wheat plants

Phonological stage	Water stress	Shoot DW ($g\ m^{-2}$)	Grain yield ($g\ m^{-2}$)	Spike ($n\ m^{-2}$)	Kernel per spike (n)	Harvest index (%)
Jointing	FI	1128.0a*	437.1c	429.0bc	37.50a	38.72d
	LWS	945.5c	354.3e	391.5cd	31.00c	37.53e
	MWS	899.3de	325.5fg	368.0de	29.00cd	36.27f
	HWS	831.5f	288.2h	320.8f	26.75de	34.72g
Anthesis	FI	1033.0b	373.5d	466.5b	30.00c	36.14f
	LWS	940.5c	331.0f	433.0bc	27.25d	35.19g
	MWS	837.0e	295.3h	351.5def	24.75e	33.86h
	HWS	766.5g	250.7i	326.0ef	22.00f	32.86i
Grain fill	FI	921.5cd	468.4a	524.5a	34.25b	50.85a
	LWS	904.3dc	455.3b	418.5c	29.75c	50.36a
	MWS	811.8f	374.7d	374.3d	27.50d	46.18b
	HWS	723.0h	318.0g	347.5def	24.75e	44.08c

*Values followed by the same letter in each column are not significantly difference at p = 0.05

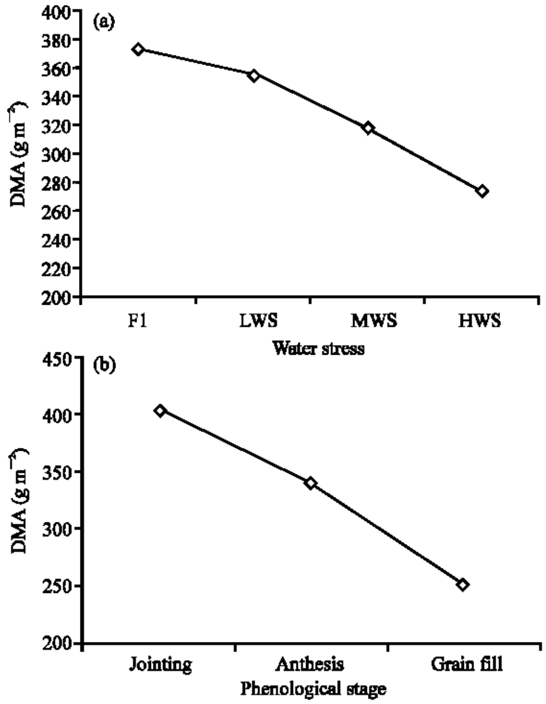

Fig. 1: Post-anthesis dry matter accumulation (DMA) of wheat as affected by (a) water stress at different growth (b) phenological stage

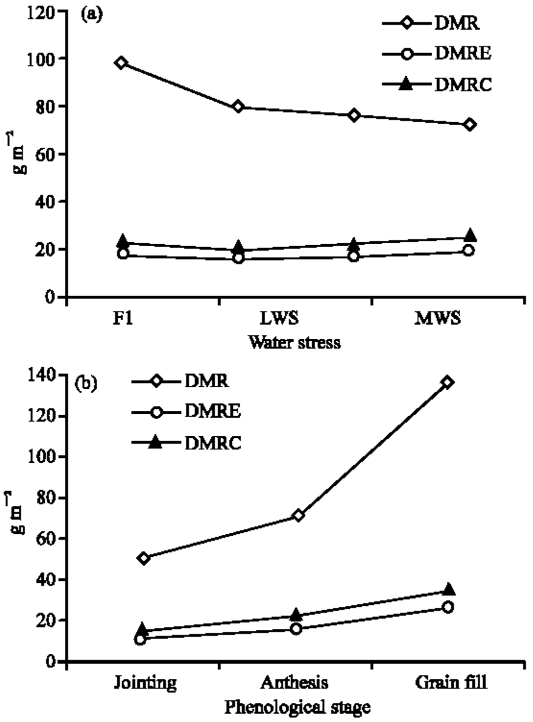

Fig. 2: Post-anthesis dry matter remobilization into grain (DMR), remobilization efficiency (DMRE) at (b) different phonological stage as affected by (a) water stress and contribution of remobilization to grain yield (DMRC)

DISCUSSION

In present research, FI had higher grain yield compared to stressed plants ,as water stress reduced plant dry weight and plant storage capacity. The former decreased the photosynthetic capacity and the assimilates available for remobilization, the latter decreased the number of kernels per spike. In this research water stress during anthesis greatly reduced grain yield. The yield reduction resulted from a little decrease of the number of spike m^{-2} and a great decrease of kernels per spike .These results suggest that water stress affects more the fertilization of flowers. Guttieri *et al.* (2001) and Zhang *et al.* (1998) found that drought reduced grain yield due to a reduction in kernel growth rate, whereas Altenbach *et al.* (2003) demonstrated that kernel size and thus yield reduction, was due to the shortening of the duration of grain filling. The fact that water stress effects on growth and yield are species and variety dependent is well known. Moreover, sensitivity to drought varies by development stage. Zhang and Oweis (1999) reported that the sensitive growth stages of wheat to soil water deficits were from stem elongation to booting, followed by anthesis and milking. Stone and Nicholas (1995) found that the reduction to be more severe when the water stress occurred at early stages of grain filling rather than at later stages.

In this study, most of the dry matter in the wheat plant was accumulated before anthesis and significant mobilization of dry matter from vegetative plants parts to grain occurred during grain filling. The relation between dry matter accumulation during wheat growth and water stress was negative. The decrease due to water stress was higher in grain filling. The four water regimes showed a different behavior, as they ranked in the different order for post-anthesis dry matter accumulation and grain yield. The highest value was obtained from FI treatments. The higher grain yield of FI was associated with a higher number of kernels per spike, which confirms that genetic yield gains in wheat are primarily due to an increase in the number of kernels per unit area. Water stress caused a decrease in dry matter transport from vegetative organs to kernels. We interpret this as a result of assimilate retention within the shoot for osmotic adjustment of water-stressed plants. Plants, which are exposed to water stress or salinity, have a tendency to perform osmotic adjustment by increasing solute content in order to avoid dehydration and wilting. Whilst ions mostly contribute to this adjustment in the case of salinity, sugars and amino acids are significant contributing factors under water stress. Competition may thus exist between two potential sinks, namely the developing kernels and a stress adjusting process in the leaves requiring assimilates. (Plaut *et al.*, 2004). In drought stressed plants; also the higher temperature hardly caused a further decrease in dry matter transport rate.

Non-structural carbohydrates are stored within the stem, sheath and leaves. In fact, high correlation observed between storage of non-structural carbohydrates of wheat stems and yield of wheat cultivars under drought conditions (Kuhbauch and Thome, 1989). Present results showed small differences between DMR when water stress occurred at jointing and anthesis (i.e., 17.2 g m^{-1}) that resulted in a low size of the sink, i.e., the spikes and consequently, the small assimilate demand for total grain growth is greatly met by current assimilation during grain filling and low remobilization is needed. Whereas With the increase of plant biomass, the amount of dry matter remobilized increased 65.9 g plant^{-1} between anthesis and grain filling. The interaction between ear size and the demand for stem storage seems to depend on the environment (Bonnett and Incoll, 1993), either that before or during grain filling.

In this study post-anthesis dry matter accumulation and remobilization in wheat plants were decreased by water stress. When severe water stress occurred, accumulation and remobilization of dry matter was greatly reduced. The difference of remobilized dry matter between FI and LWS, MWS and HWS was about 18.39, 21.05 and 25.7 g m^{-1}. Kuhbauch and Thome (1989) showed stem reserve mobilization or the percentage of stem reserves in total grain mass is affected by water deficit during grain filling. Palta ***et al.*** (1994) found that post anthesis assimilation was reduced by 57% in drought conditions. In bread wheat, Yang *et al.* (2000) have found that an enhancement of remobilization of pre stored carbon to grain partially compensate the reduced current assimilation due to water stress. Others have shown that both post anthesis photosynthesis and remobilized assimilates are negatively affected (Ehdaei *et al*., 2006; Plaut *et al*., 2004). The demand by the grain yield sink is a primary factor in determining stem reserve mobilization. When sink size was reduced by water stress, more reserves were stored in the stem, As compared with intact ears (Kuhbauch and Thome, 1989).

Among cereals and particularly in wheat, pre-anthesis assimilates help in yield stability during terminal drought stress (Blum *et al*., 1994). Leaves and culms accounted for about 80% of remobilized dry matter in grain, the remaining 20% was given by roots and chaff. The contribution of stored carbohydrates may, thus, become the predominant source of transported materials (Bidinger *et al*., 1977; Blum *et al*., 1994).

Results of this study showed despite of treatment application, the overall contribution of hydrocarbon reserve on grain yield was 23% which agree with finding that in wheat, pre-anthesis assimilate reserves from stem and sheaths contribute 25-33% of the final grain weight (Gallagher *et al*., 1976). It is interesting that the relative contribution of vegetative organs to grain dry weight and Post- anthesis remobilization efficiency of dry matter under water deficit was higher than in unstressed plants. Results of present study showed, the contribution of dry matter remobilization to grain yield was increased by water stress from 23% at FI to 25.37% at HWS. This response was consistent with the results of Ercoli *et al.* (2008), found that the contribution of dry matter remobilization to grain yield was increased by water stress from 45% at FI to 51% at HWS. Van Herwaarden *et al.* (1998) showed that under dry conditions in the field, the apparent contribution of stored assimilates could be 75-100% of grain yield, as compared with 37-39% under high rainfall conditions. Gallagher *et al.* (1976) estimated that pre-anthesis reserves contributed up to 74% to grain yield of wheat when crops suffered from severe post-anthesis drought. It is therefore to be expected that estimates of the relative contributions of stem reserves to grain yield would vary among the different reports, according to the experimental conditions and cultivars used. In each environment the relative contribution of remobilization to grain yield depends mainly on source/sink interactions during grain filling. Environmental conditions that decrease current assimilation during grain filling cause a greater demand for stem reserves for grain filling. The present study emphasizes that the contribution of vegetative organs was a very significant source for kernel filling in both stressed and non-stressed plants. In water-stressed plants, however, dry matter stored in vegetative organs are a much more limited source. This explicates the reduced daily rates of dry matter transport from vegetative organs to kernels under water deficit.

In conclusion, the results from this study demonstrate that in wheat post-anthesis water stress greatly reduced grain yield at all water stress treatments. Plants grown at high water stress, however had lower dry matter and lower grain yield at all phenological stages.

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