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Effect of Drought Stress during Grain Filling on Yield and Its Components, Gas Exchange Variables, and Some Physiological Traits of Wheat Cultivars

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ABSTRACT

Terminal drought stress during grain filling period has recently become more common in the semiarid Mediterranean regions, where wheat (*Triticum aestivum* L.) is grown as an important winter cereal crop. The objective of this experiment was to study the effect of terminal drought stress on grain yield, gas exchange variables, and some physiological traits of nine bread wheat cultivars. An experiment was carried out in a split-plot arrangement using randomized complete blocks design with three replications during the 2010-2011 season at the research farm of Razi University, Iran. Based on the results obtained, post anthesis water deficit significantly decreased grain yield, biomass, 1,000 grain weight, and harvest index of wheat cultivars. Under terminal drought stress and control treatments, there were significant differences between cultivars in terms of all traits studied. Also, terminal drought stress decreased leaf net photosynthesis rate (P_n), stomatal conductance (g_s), transpiration rate, Chlorophyll a, b, and a/b, and increased leaf temperature and sub-stomatal CO_2 concentration. Cultivars differed in their response to water stress. In general, tolerant cultivars showed a higher P_n and g_s and leaf water content under both moisture conditions compared with susceptible ones. A greater reduction in g_s and transpiration rate and smaller reduction in P_n under stress condition led to a remarkably higher photosynthetic water use efficiency of the tolerant cultivars. Finally, it can be concluded that planting wheat variety DN-11 in areas with post-anthesis water stress was recommendable for maximizing grain yield.

Keywords: Photosynthesis, Relative water content, Stress susceptibility index, Water use efficiency.

INTRODUCTION

In the Mediterranean climate, wheat grain filling period is subjected to several physical and biotic stresses. Grain growth in wheat depends on current assimilation and remobilization of pre-anthesis assimilates stored in the stem (Kobata *et al*., 1992). Post anthesis water stress reduces carbon assimilation and, hence, the availability of current assimilates for grain filling (Johnson and Moss, 1976). Drought stress generally prevails during grain filling in wheat due to shortage of irrigation, low winter rainfall, and high evaporation demand. Under this terminal drought condition, leaf senescence is accelerated and photosynthetic activity declines.

Wheat genotypes vary both in the timing of senescence initiation and the subsequent rate of leaf senescence. Delaying leaf senescence has become an agronomically desirable trait (Subhan and Murthy, 2001). Flag leaf photosynthesis in wheat contributes about 30% to 50% of the assimilates for grain filling (Sylvester-Bradley *et al*., 1990) and initiation of grain filling coincides with the onset of senescence, therefore, photosynthesis of the flag leaf is an important

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component of the formation of grain yield, and the onset and rate of senescence are important factors for determining grain yield. The primary signs of leaf senescence are the breakdown of chlorophyll and the decline of photosynthetic activity (Gregersen and Holm, 2007). It is generally accepted that genotypes that are able to sustain photosynthesis in the flag leaf for a longer time tend to yield more (Guoth *et al.* 2009). Under drought, there is a rapid decline in photosynthesis after anthesis; due to a decrease in leaf stomatal conductance and net CO_2 assimilation, limiting the contribution of the current assimilates to the grain. Most of the drought-mediated reduction in CO_2 assimilation was attributed to stomatal closure. Another part of it was attributed to the direct effect of water stress on the inhibition of CO_2 fixation (Sharkey and Seemann, 1989). The relative magnitude of stomatal and non-stomatal factors in limiting photosynthesis depends on the severity of stress (Kicheva *et al*., 1994).

Understanding the biochemical and physiological basis of water stress tolerance in plants is vital to select and breed plants for improving crop water stress tolerance (Chaves *et al*., 2003). Historically, research on biochemical changes that occur during leaf senescence focused on loss of photosynthetic pigments, degradation of protein, and re-absorption of mineral nutrients (Lindroth *et al*. 2002). In the present study, we analyzed gas exchange variables and some physiological traits involved in the response of contrasting wheat genotypes to drought stress. Such study will provide valuable information that can be used as the genetic basis of improvement of wheat to enhance yield under stress conditions.

MATERIALS AND METHODS

Experimental Site and Method

The present study was conducted during 2010-2011 at the research farm of Razi University, Kermanshah, located in the west of Iran (47º 9′ E, 34º 21′ N, 1319 m asl). The previous crop was corn. Soil texture was a clay loam (36.1% clay, 30.7% silt) and the experiment was laid out in split-plots arranged in a randomized completed block design with three replications. The study treatments included the improved bread wheat cultivars (*Triticum aestivum* L.) Bahar, Parsi, Pishtaz, Pishgam, Chamran, Zarin, Sivand, Marvdasht, and DN-11. These cultivars were chosen because of their contrasting grain yield productivity and existence of the highest area under cultivation in the west of Iran. Two moisture regimes were applied: irrigation in all stages of plant growth (WW) and post-anthesis water stress, in which irrigation was withheld after anthesis till maturity (WD). The high probability of occurrence of post-anthesis water stress in these regions was the main reason for selecting this treatment. The date of anthesis was recorded for each plot when 50% of the spikes of the main shoots had either visibly exerted anthers or when the anthers that had dehisced were observed through the palea (Ehdaie *et al*., 2006; Estrada-Compuzano *et al*., 2008). Each plot included 54 rows 20 cm apart, 4-m long, 4 and 3 meters distances were taken between test plots and replicates, respectively. Seeds were sown at a density of 400 seeds m^{-2} on 12th October. Based on soil analysis results, 80 kg N ha^{-1} were applied as urea three times: prior to planting, as topdressing at tillering, and at flowering stages. Some weather data during the crop season are presented in Table 1.

Grain Yield and Its Components

Grain yield, biomass, and number of spikes per m^2 for each cultivar were measured by harvesting 2 m^2 of the central part of each plot at crop maturity. Harvest index was measured by dividing grain yield to biomass production. The number of grains per spike and 1,000-grain weight were measured on 10 randomly selected main shoots.

Table 1. The monthly air minimum, maximum and mean temperature, relative humidity, and precipitation at the site of experiment during 2010-2011.

Month	Temperature (C°)			Precipitation	RH (%)		
	Min	Max	Mean	(mm)	Min	Max	Mean
October	10.6	30.3	20.4	1	13.2	46.4	29.8
November	4.5	21.9	13.2	31	22.8	66.8	44.8
December	-1.5	16.8	7.7	24	26.5	62.4	44.5
January	-2.2	9.6	3.7	50	47.1	91.0	69.1
February	-2.7	8.0	2.7	65	52.1	94.2	73.2
March	0.6	15.4	8	21	28.1	82.0	55
April	4.5	20.1	12.3	47	24.6	78.8	51.7
May	9.5	23.6	16.5	128	33.6	87.4	60.5
June	12.8	33.8	23.3	0	11.3	51.1	31.2
July	17.1	38.5	27.8	0	6.6	32.1	19.4
August	18.1	39.5	28.8	0	6	27.7	16.9
September	13.8	34.6	24.2	0	7.8	32.0	19.9

Stress Susceptibility Index

Stress susceptibility index (SSI) was used to differentiate the resistant and susceptible cultivars (Fischer and Maurer, 1987) and was defined as:

SSI= [1-(Ys/Yp)]/SI

Where, *Ys* and *Yp* are grain yield of each cultivar under control and water deficiency, respectively, while SI is Stress index= 1-($\overline{Ys}$)/($\overline{Yp}$), where, $\overline{Yp}$ and $\overline{Ys}$ are the mean grain yield of all cultivars under the control and water deficiency, respectively.

Gas Exchange Parameters

The net photosynthesis rate (P_n), stomatal conductance (g_s), transpiration rate per leaf area (E), leaf temperature (T_l) and intercellular CO_2 concentration (C_i) were measured using a portable photosynthesis system LI-6400 (LI-COR, Lincoln, USA) on the flag leaves on midday (09:00-12:00) at 14 day after anthesis. Photosynthetically-active radiation (PAR) of 1,200-1,600 µmol (photon) m^{-2} s^{-1} was provided at each measurement by the ambient CO_2 concentration of 380-400 ppm and full sunlight. Photosynthetic water use efficiency (PWUE) was calculated by dividing P_n to g_s (Ahmadi and Siosemardeh, 2005). Mesophyll conductance (g_m) was calculated by dividing P_n to C_i (Fischer *et al*., 1998).

Relative Water Content (RWC)

Leaf relative water content (RWC) was estimated according to Henson *et al*. (1981) and Castillo (1996) for each drought period. Samples of flag leaves (0.5 g) were saturated in 100 mL distilled water for 24 hours at 4°C in the dark and their turgid weights were recorded. Then, they were oven-dried at 70°C for 48 hours and their dry weights were recorded. *RWC* was calculated as follows: *RWC (%)= [(FW–DW)/(TW–DW)]×100*, where *FW, DW* and *TW* are fresh weight, dry weight, and turgid weight, respectively.

Chlorophyll Content

The fully expanded flag leaves on the stated dates were homogenized in ice cold 80% acetone (1.5 mL for 250 mg sample) and extracted for 24 hours. Samples were centrifuged at 6,000×g for 15 minutes at 4°C, then, the supernatants were collected. The pigment composition was measured using a double-beam spectrophotometer according to the method described by

Lichtenthaler and Wellburn (1983). This method involves measurement of the light absorbed in the plant extract at 645 and 663 nm (Arnon, 1949).

Chl a (mg g^{-1} fw)= [(12.7×A_{663})-(2.6×A_{645})]×mL Acctone mg^{-1}

Chl b (mg g^{-1} fw)= [(22.9×A_{645})-(4.68×A_{663})]×mL Acctone mg^{-1}

Chl a/b (mg g^{-1} fw)= Chl a/Chl b

Statistical Analysis

Data were subjected to analysis of variance (ANOVA), and means were compared using Duncan's range test at *P*= 0.05. All calculations were performed using the SAS software, version 9.1. The means±SE were used to compare the data.

RESULTS AND DISCUSSION

Grain Yield and Its Components

The results obtained from mean comparison analysis of grain yield and its components are shown in Table 2. Post anthesis water stress caused 34 and 27% reduction in grain yield and 1,000 grain weight in average, respectively. It had no

Table 2. Mean comparisons of grain yield and its components and some morphological traits of wheat cultivars under post anthesis water stress.

Cultivars	Grain yield ($g\ m^{-2}$)		R[c] (%)	Biomass ($g\ m^{-2}$)		Harvest index (%)	
	WW[a]	WD[b]		WW	WD	WW	WD
Bahar	724±26[e]	475±37	-34.4	1604±93	1244±82	45.2±1.0	38.2±1.8
Parsi	692±38	437±77	-36.8	1640±108	1173±104	42.3±0.5	36.7±3.2
Pishtaz	705±40	497±54	-29.5	1596±86	1244±100	44.2±1.5	39.7±1.5
Pishgam	718±31	446±63	-37.9	1493±38	1053±143	48.0±0.8	42.3±1.7
Chamran	562±45	447±35	-20.4	1356±93	1067±115	41.4±0.9	42.3±1.8
Zarin	724±37	448±50	-38.2	1671±99	1302±92	43.4±0.5	34.2±2.1
Sivand	783±84	497±71	-36.6	1650±109	1307±104	47.2±1.9	37.7±2.7
Marvdasht	656±20	411±26	-37.4	1418±44	1160±68	46.3±0.2	35.4±1.3
DN-11	750±63	515±76	-31.3	1716±139	1249±152	43.7±0.2	41.0±2.0
Mean	702±43	464±54		1571±90	1200±107	44.6±0.8	38.6±2.0
Decrease(%)		-33.9			-23.6		-13.5

Cultivars	1000 grain weight (g)		R (%)	Number of grain per spike		Number of spike per m^2		SSI[d]
	WW	WD		WW	WD	WW	WD	
Bahar	42.1±0.6	31.9±2.7	-24.4	45.2±1.5	51.2±3.4	516±19	425±23	1.014
Parsi	45.4±1.5	29.8±0.4	-34.3	37.2±0.8	40.5±2.8	503±28	423±29	1.086
Pishtaz	46.6±1.4	32.3±2.3	-30.8	38.3±2.5	38.1±0.8	503±17	428±44	0.871
Pishgam	43.2±0.8	32.4±1.8	-24.9	52.0±3.3	52.6±4.0	445±34	351±20	1.116
Chamran	43.2±0.5	36.2±1.8	-16.0	32.6±1.1	35.4±2.2	438±27	436±15	0.602
Zarin	39.2±0.2	27.7±0.8	-29.4	57.5±1.1	56.3±4.1	467±38	400±45	1.125
Sivand	45.5±0.7	32.7±2.9	-28.3	38.8±0.3	39.6±0.8	523±10	451±19	1.078
Marvdasht	36.7±1.3	24.5±0.5	-33.4	56.5±1.1	55.2±5.2	405±32	428±31	1.102
DN-11	39.9±0.5	33.7±0.7	-15.6	44.9±4.0	45.0±1.6	512±33	409±46	0.923
Mean	42.4±0.8	31.2±1.5		44.8±1.8	46.0±2.8	479±26	417±30	0.99 1
Decrease(%)		-26.4			2.7		-13.0	

[a] Well Water; [b] Water Deficiency; [c] Percentage decrease down control when water deficiency was applied at post anthesis (%), [d] Stress Susceptibility Index.[e] The data are shown as Means±SE (n= 3).

significant effect on the number of grains per spike and number of spikes per m^2. Averages grain yield and 1,000 grain weight of different cultivars in the controlled condition were 702±43 g m^{-2} and 42.4±0.8 g, respectively. Under water stress, these values significantly decreased to 464±54 g m^{-2} and 31.2±1.5 g. Saeidi *et al*. (2010) showed that significant reduction in grain yield due to post-anthesis water stress may result from a reduction of the production of photo-assimilates (source limitation), the sink power to absorb photo-assimilates, and the grain filling duration. They also reported that, probably, the early processes of grain growth (cell division and formation of sink size) were less affected by water stress. Therefore, grain weight and grain yield reduction under post anthesis water deficiency may reflect more the lack of photo-assimilates supply for grain filling. These findings are in agreement with Ehdaie *et al*. (2006) and Ahmadi *et al*. (2009).

In the control treatment, Chamran (562±45 g m^{-2}) had the lowest grain yield and Sivand and DN-11 (783±84 and 750±63 g m^{-2}, respectively) had the highest (Table 2). Under post anthesis water stress, the lowest and highest reductions in grain yield were noted in Chamran (20%) and Zarin (38%), respectively. Marvdasht had the lowest grain yield production under post-anthesis water stress (411±26 g m^{-2}). Sowing Marvdasht in areas with high coccurrence of post-anthesis water stress may consequently be associated with high risk of crop failure.Under post anthesis water stress, the highest reduction in grain weight was noted seen in Parsi and Marvdasht and the lowest reduction in DN-11 and Chamran (Table 2).

The numbers of spikes per m^2 and grains per spike did not differ between full irrigation and post-anthesis water stress conditions (Table 2). This is probably because the potential of these components was formed before spike initiation, so post-anthesis water stress had no significant influence on them (Araus *et al*., 2002). Such significant differences were found among cultivars in terms of number of grains per spike and number of spikes per m^2. Zarin and Marvdasht had the highest (56.8 and 55.8 grains $spike^{-1}$, respectively) while Chamran (34 grains $spike^{-1}$) had the lowest values. Under well-watered conditions, Sivand and DN-11 had the highest number of spikes per m^2 (523±10 and 512±33 spikes m^{-2}) while Marvdasht had the lowest values (405±32 spikes m^{-2}). Under post-anthesis water stress, Sivand and Pishgam had the highest (450±19 spikes m^{-2}) and lowest (351±20 spikes m^{-2}) values, respectively.

Under both well-watered and post-anthesis water stress conditions, a negative correlation was found between 1,000 grain weight and number of grains per spike (Table 3), indicating that available assimilates were allocated to produce either many small seeds or few larger seeds depending on resource availability (Gambín and Borrás, 2009). This result is consistent with those of Moral *et al*. (2002) who also found a negative correlation between these two traits, related to a compensation effect of yield components on each other.

Harvest index can be expressed as the ability of plants to allocate photosynthetic assimilates to prouduce economic yield. A significant variation was noted for this trait among cultivars, under both well-watered and post-anthesis water stress conditions. Post anthesis water stress significantly decreased harvest index in most cultivars (Table 2). Under well-watered conditions, Pishgam and Chamran cultivars had the highest (48.0±0.8%) and lowest (41.4±0.9%) harvest index, respectively (Table 2). Under post-anthesis water stress Pishgam and Zarin had the highest (42.3±1.7%) and the lowest (34.2±2.1%) harvest index. Significant reduction in harvest index occured under post-anthesis water stress (Table 2) due to a higher reduction in grain yield than in biomass production (Shafazadeh *et al*., 2004). Richards *et al*. (2002) also reported that high harvest index under control treatment can be accompanied with high grain yield under water stress. Reynolds *et al*. (2009) found that wheat cultivars with high biological yield and harvest index, most

Table 3. Correlation coefficients between grain yield, gas exchange variables and physiological traits in wheat cultivars under well watered and post-anthesis water deficit conditions.

Parameters	Conditions	GY [a]	B [b]	HI [c]	1000 GW [d]	NGS [e]	NSP [f]	T_l [g]	C_i [h]	E [i]	g_s [j]	P_n [k]	g_m [l]	PWUE [m]	RWC [n]	Chl a [o]	Chl b [o]	Chl a/b [o]
GY	WW	1																
	WD	1																
B	WW	0.84**	1															
	WD	0.55	1															
HI	WW	0.54	-0.01	1														
	WD	0.36	-0.58	1														
1000GW	WW	0.12	0.16	-0.06	1													
	WD	0.60	-0.21	0.83**	1													
NGS	WW	0.25	0.05	0.45	-0.77*	1												
	WD	-0.42	0.07	-0.46	-0.69*	1												
NSP	WW	0.67*	0.82**	-0.06	0.56	-0.45	1											
	WD	0.20	0.41	-0.29	0.06	-0.55	1											
T_l	WW	-0.63*	-0.68	-0.13	0.47	-0.56	-0.36	1										
	WD	-0.04	-0.38	0.42	0.36	-0.27	-0.32	1										
C_i	WW	-0.09	0.00	-0.18	0.15	-0.34	0.23	0.26	1									
	WD	0.18	0.26	-0.12	-0.07	-0.33	0.30	0.33	1									
E	WW	0.12	-0.14	0.50	-0.54	0.74*	-0.53	-0.13	-0.36	1								
	WD	-0.59	-0.15	-0.36	-0.51	0.76*	-0.41	0.09	-0.12	1								
g_s	WW	0.22	0.04	0.40	-0.62	0.85**	-0.40	-0.52	-0.63*	0.85**	1							
	WD	-0.50	0.01	-0.47	-0.55	0.79*	-0.26	-0.32	-0.26	0.91**	1							
P_n	WW	0.25	-0.04	0.52	-0.06	0.14	-0.05	-0.10	-0.64*	0.52	0.53	1						
	WD	0.44	0.07	0.37	0.36	-0.26	-0.21	0.64	0.73*	-0.03	-0.26	1						
g_m	WW	0.18	-0.11	0.50	-0.01	0.21	-0.17	-0.06	-0.80*	0.55	0.61	0.95**	1					
	WD	0.19	-0.43	0.70*	0.61	-0.13	-0.66*	0.73*	-0.04	0.10	-0.15	0.60	1					
PWUE	WW	0.08	-0.17	0.36	0.56	-0.49	0.16	0.45	-0.29	0.01	-0.16	0.71*	0.67*	1				
	WD	0.52*	0.00	0.51	0.54	-0.64*	0.09	0.62	0.75*	-0.43	-0.64*	0.88**	0.46	1				
RWC	WW	0.15	0.06	0.15	-0.50	0.19	0.03	-0.50	-0.04	-0.16	0.06	0.14	0.00	-0.13	1			
	WD	0.46	0.02	0.38	0.19	0.04	-0.49	-0.22	-0.07	-0.36	-0.24	0.23	0.29	0.18	1			
Chl a	WW	0.23	0.16	0.14	-0.20	0.01	0.31	-0.49	-0.22	-0.03	0.21	0.52	0.34	0.24	0.48	1		
	WD	-0.10	0.03	-0.05	-0.04	0.36	-0.12	0.08	0.29	0.60	0.59	0.37	0.16	0.09	-0.19	1		
Chl b	WW	0.30	0.25	0.15	-0.04	-0.16	0.44	-0.42	-0.21	-0.10	0.10	0.60	0.40	0.41	0.48	0.96**	1	
	WD	0.08	0.18	-0.07	0.00	0.16	-0.03	0.08	0.56	0.39	0.39	0.57	0.16	0.32	-0.01	0.92**	1	
Chl a/b	WW	0.04	-0.08	0.17	-0.42	0.29	-0.03	-0.44	-0.27	0.13	0.36	0.35	0.25	0.00	0.35	0.87**	0.72*	1
	WD	-0.22	-0.16	0.05	0.00	0.50	-0.26	0.08	-0.06	0.70*	0.67*	0.14	0.22	-0.15	-0.27	0.92**	0.68*	1

[a] Grain Yield (g m^{-2}), [b] Biomass (g m^{-2}), [c] Harvest Index (%), [d] 1,000 Grain Weight (g), [e] Number of Grain per Spike, [f] Number of Spike Per m^2, [g] Leaf temperature (C°), [h] Intercellular CO_2 concentration (μmol (CO_2) m^{-2}), [i] Transpiration rate (mmol(H_2O) m^{-2} s^{-1}), [j] Stomatal conductance (mol (H_2O) m^{-2} s^{-1}), [k] Net photosynthetic rate (μmol (CO_2) m^{-2} s^{-1}), [l] Mesophyllzw conductance (mmol(CO_2) m^{-2} s^{-1}), [m] Photosynthetic Water Use Efficiency (μmol (CO_2) mol^{-1} (H_2O)), [n] Relative Water Content (%), [o] chlorophyll a, b, a/b (mg g^{-1} fw).

likely have high grain yield under stress and control conditions. Interestingly, in our study, Chamran had the lowest reduction in harvest index under post-anthesis water stress and also the lowest reduction in grain yield while Sivand, Zarin, and Marvdasht had the highest reduction in harvest index and also the highest reduction in grain yield production. Under post-anthesis water stress, a positive correlation was found between grain weight and harvest index, in good agreement with Koocheki *et al*.(2006).

Evaluation of cultivars by using stress susceptibility index (SSI) allowed selecting susceptible and tolerant cultivars regardless of their yield potential (Siosemardeh *et al*., 2006; Talebi *et al*., 2009). Based on the results, Chamran, Pishtaz, and DN-11 had the lowest *SSI* and can consequently be considered as tolerant to post-anthesis water stress (Table 2).

Photosynthesis and Gas Exchange

The effects of post-anthesis water deficiency stress and cultivar were highly significant for all the measured traits (Figure 1). The interaction between these factors was also significant for all traits, except C_i (Figure 1-C). A dramatic decline was observed with water stress in leaf *RWC* and water potential (Siddique, *et al*., 2000; Basu *et al*., 2004). A reduction in the P_n, g_s and transpiration rate occurred during post-anthesis water stress [(Figure 2, (A, B, and C)]. These findings also are in agreement with Abdoli and Saeidi (2013) and Roohi *et al*. (2013).

Water stress caused a 43% reduction in P_n across cultivars. Similar result has been reported by other investigators (Siddique *et al*., 2000; Stiller *et al*., 2005; Ghaderi *et al*., 2011). This appears to be an important physiological mechanism by which drought can affect growth and productivity of crops such as wheat (Lawlor, 1995; Saeidi *et al*., 2010). The stability of photosynthetic components could be attributed to maintenance of positive leaf turgor under stress as a result of osmotic adjustment (Basu *et al*., 2004). Under well-watered conditions, Pishgam and DN-11 had the highest P_n (25.6±9.3 and 24.5±7.9 μmol (CO_2) m^{-2} s^{-1}, respectively) and Zarin and Parsi the lowest (13.1±4.1 and 13.2±5.2 μmol (CO_2) m^{-2} s^{-1}, respectively). Under post anthesis water stress, Pishtaz and Marvdasht had the highest (17.8±8.5 μmol (CO_2) m^{-2} s^{-1}) and lowest (5.7±3.6 μmol (CO_2) m^{-2} s^{-1}) P_n values, respectively (Figure 1-A). At more severe drought stress, photosynthesis continues to decrease, while the ratio of intercellular/ambient CO_2 concentration increases significantly to values similar to those obtained in well watered plants (Rekika *et al*., 1998). Thus, the decrease in photosynthesis could result from non-stomatal factors affecting photosynthetic capacity, e.g. reduced activity of some Calvin cycle enzymes, inhibition of photosynthetic electron transport, and impaired photophosphorylation capacity (Sharkey and Seemann, 1989; Kicheva *et al*., 1994). Significant positive correlations were found between P_n and both g_m (r= 0.95**) and PWUE (r= 0.88**) (Table 3).

Transpiration rate, net photosynthetic rate, stomatal conductance, and mesophyl conductance decreased but leaf temperature and sub-stomatal CO_2 concentration increased in all nine cultivars when they were exposed to post anthesis water deficiency stress (Figure 1), as one of the first responses of plants to drought is stomatal closure, restricting gas exchange between the atmosphere and the inside of the leaf. Under the controlled conditions, Sivand had the lowest stomatal conductance (0.298 mol m^{-2} s^{-1}) and Pishgam the highest (0.493 mol m^{-2} s^{-1}) (Figure 1-B). Under post anthesis water deficiency, the lowest and highest reductions in g_s were noted in Bahar (61%), Pishgam (77.4%), and DN-11 (78.4%). Minimum g_s under post anthesis water stress was observed in Sivand and Pishtaz (0.083 and 0.088 mol m^{-2} s^{-1}, respectively).

In general, drought tolerant cultivars maintain higher P_n, g_s, and transpiration rate

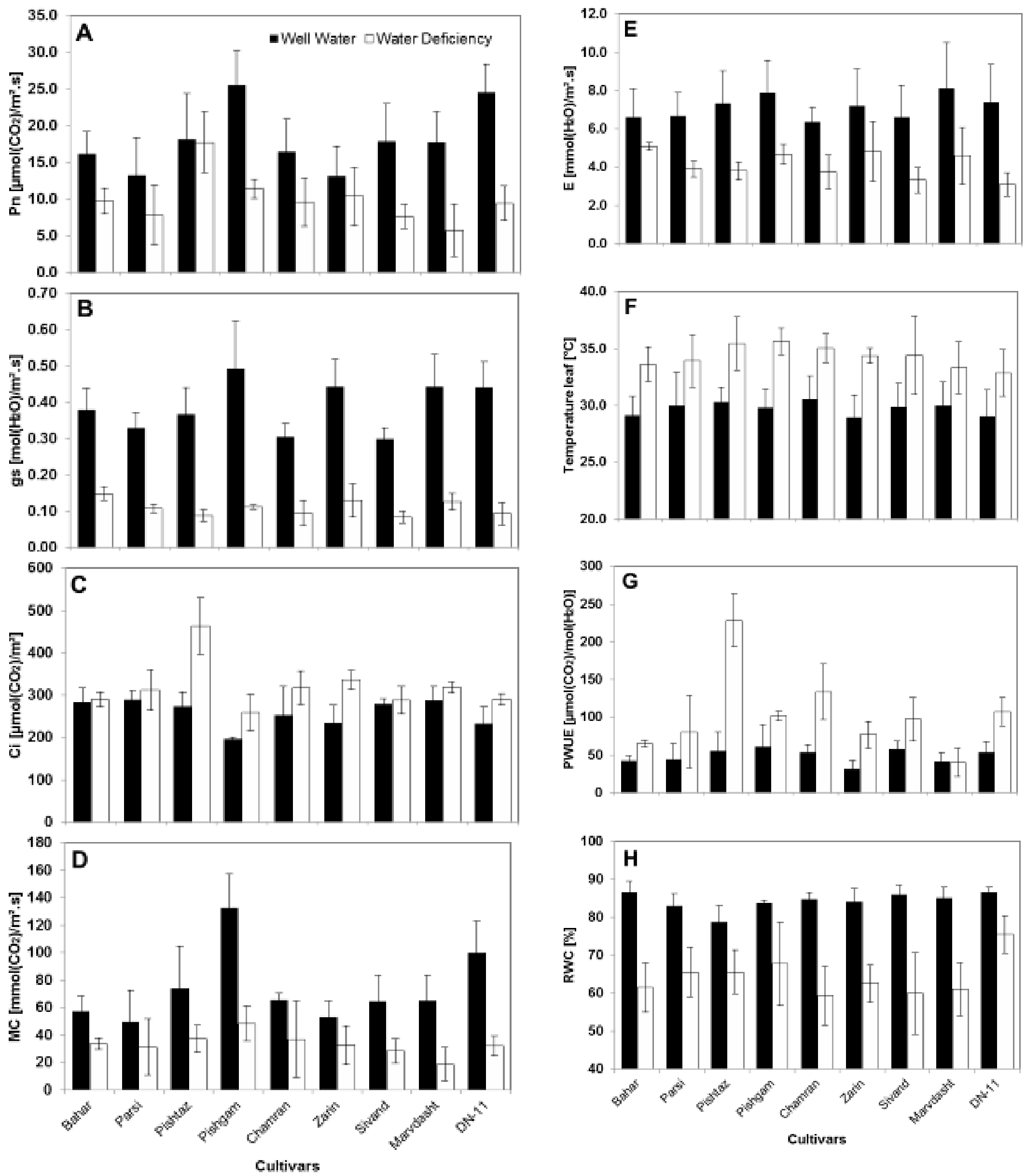

Figure 1. Influence of post anthesis water stress on: (A) P_n: Net photosynthetic rate; (B) g_s: Stomatal conductance, (C) C_i: Intercellular CO_2 concentration; (D) *MC*: Mesophyll Conductance or g_m, (E) *E*: Transpiration rate; (F) T_l: Leaf temperature; (G) *PWUE*: Photosynthetic Water Use Efficiency, and (H) Relative water content, wheat cultivars *RWC* of flag leaf 14 days after anthesis. Vertical bars represent ±SE.

than the susceptible ones under stress conditions (Figure 1). Thus, an ability to maintain high water potential or relative water content under stress conditions could be an adaptive feature. Decline in leaf P_n under water stress was accompanied by decline in leaf *RWC* (Figure 1-H).

Siddique *et al*. (2000) reported that the higher leaf water potential and relative water content of wheat cultivars were associated with a higher photosynthetic rate. Leaf

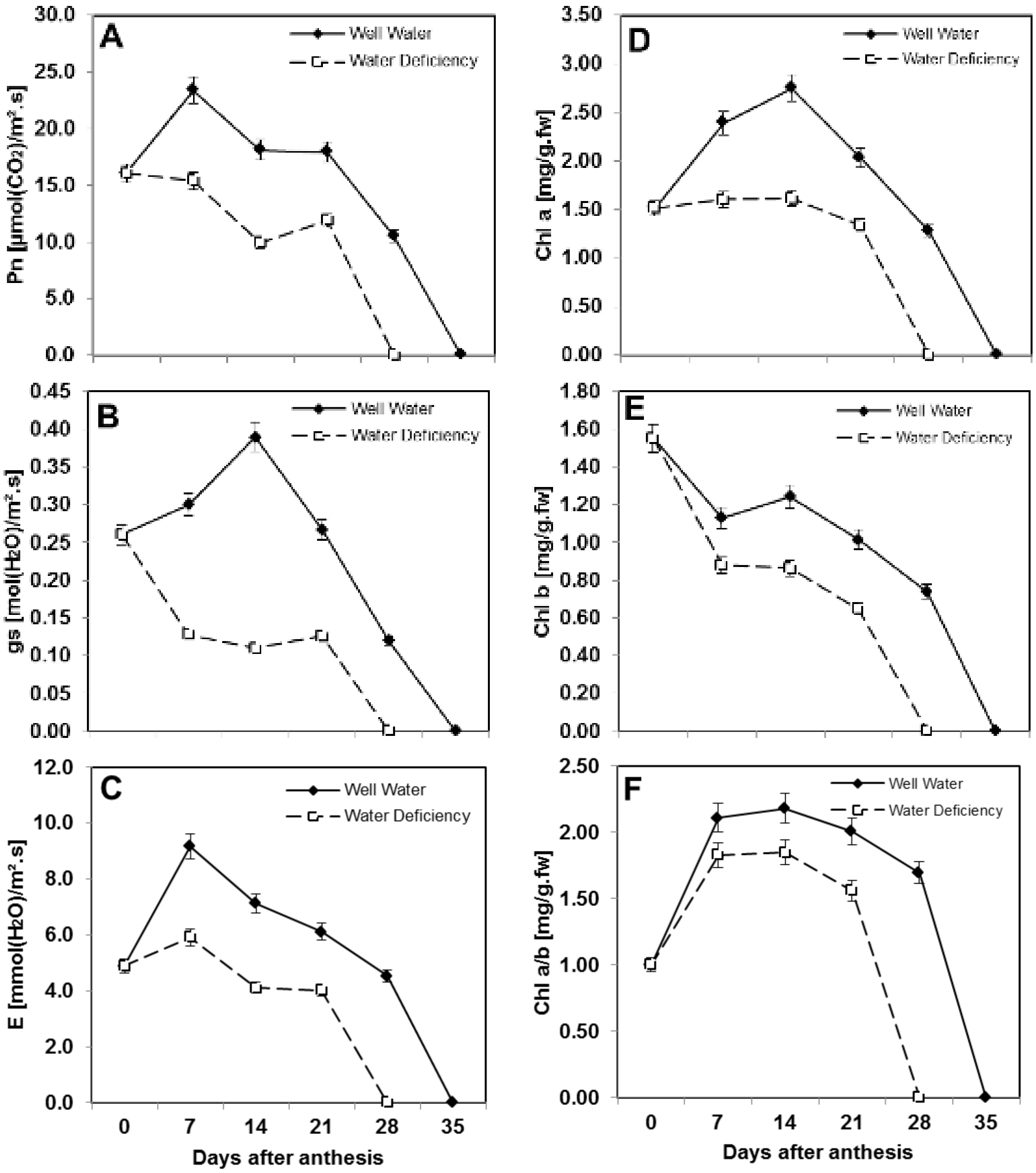

Figure 2. Changes in gas exchange [e.g. (A) P_n: Net photosynthetic rate; (B) $g_{s:}$ Stomatal conductance, (C) E: Transpiration rate] and Chlorophyll (e.g. (D) Chl a; (E) Chl b, (F) Chl a/b] flag leaves in well watered and water stress treatments from anthesis to maturity during grain filling. Vertical bars represent ±SE.

dehydration can lead to turgor loss of guard cells causing passive stomatal closure, which in turn would reduce g_s and, consequently, supply of CO_2 to the fixation site. A remarkable decline in g_s (72%) and P_n (43%) due to water stress implied the importance of stomatal limitation to P_n under water stress in the examined cultivars (Figure 1). Although reduction in g_s under water stress limits P_n, it reduces transpiration water loss, which can be beneficial for plant under limited moisture supply. Compared to the susceptible ones, tolerant cultivars manifested a greater reduction in g_s and transpiration rate, but a smaller reduction in P_n under stress condition [(Figure 1, (A and B)].

The interesting consequence of such responses was the remarkable increase in photosynthetic water use efficiency (PWUE) of the tolerant and decrease in *PWUE* of the susceptible cultivars under post anthesis water stress (Figure 1-G).

Condon *et al*. (2002) explained that the ratio of CO_2 assimilation rate to transpiration rate at the stomata may be one criteria for selecting cultivars with greater yield per unit rainfall in dry land area. It has been hypothesized that any improvement in components of water use efficiency (WUE) would be expected to partially reduce the adverse effects of water stress (Stiller *et al*., 2005). Despite decline in gs, water stress significantly increased Ci (around 24%) [(Figure 1, (B and C)], implying an inability of photosynthesis machinery to utilize internal CO_2 (Luo, 1991; Pasban Eslam, 2011). A higher water-stress-induced increase in C_i was observed in the susceptible cultivars compared to th etolerant ones (Figure 1-C). This indicated a greater sensitivity of photosynthesis apparatus of the susceptible cultivars to water stress. Mesophyll conductance (g_m), proposed by Fischer *et al*. (1998) is another indicator of non-stomatal factors involved in CO_2 assimilation. Water stress reduced the g_m of leaves up to 52%, the reduction being greater in susceptible cultivars than the tolerant ones (Figure 1-D). This ability to maintain high carbon gain appears to confer stress tolerance in crops (Ratnayaka and Kincaid, 2005). Greater decline in g_s and smaller decline in g_m were observed in the tolerant cultivars compared to the susceptible ones. Therefore, it can be concluded that under water stress P_n of tolerant cultivars is primarily limited by stomatal rather than non-stomatal factors (Basu *et al*., 2004).

This kind of limitation could be an advantage to conserve water under limited water supply. In absolute terms, however, transpiration rate and g_s were generally higher in the tolerant than the susceptible cultivars. Stomatal closure under water stress and high irradiance rate may cause photo-oxidative damage to chloroplast, increased leaf temperature (Halder and Burrage, 2003) and reduce uptake of water and nutrient by root as a result of reduced transpiration rate (Verona and Calcagno, 1991). In full irrigation treatment and water-withholding at anthesis conditions, a positive correlation was found between g_s and both transpiration rate (r= 0.85** and 0.91**) and the number of grains per spike (r= 0.85** and 0.79**) (Table 3).

Chlorophyll Content and Relative Water Content

Under well-watered conditions, the highest Chl a, b, and a/b values were obtained in Bahar and DN-11. Under post anthesis water stress, the highest and lowest significant reductions in Chl a were noted in DN-11 (61%) and Parsi (10.9%). The highest and lowest reductions in Chl b were observed in DN-11 (46.8%) and Zarin (4.4%), respectively. However, interactions between cultivars and drought treatment were significant. A reduction in the chlorophyll a and b content occurred during post anthesis water stress (Table 4 and Figure 2). Drought stress induced decrease in pigment contents was previously reported in several plant species, including durum wheat (Loggini *et al*., 1999) and bread wheat (Nyachiro *et al*., 2001; Saeidi *et al*., 2010). The decreased level of chlorophyll content is caused by photo-inhibition and photo-destruction of pigments and pigment-protein complexes and destabilization of photosynthetic membrane both induced by drought. It has been hypothesized that genotypes which keep their stomata open under stress condition while maintaining adequate leaf *RWC* can be considered as suitable for dry region (Blum *et al*., 1981). In the present study, the tolerant cultivars had higher values of transpiration rate and *RWC* indicating their greater ability to

Table 4. Influence of post anthesis water stress on Chlorophyll (Chl) a, b, and a/b of flag leaf (14 days after anthesis) of wheat cultivars.

Cultivars	Chl a (mg g^{-1} fw)		R[c] (%)	Chl b (mg g^{-1} fw)		R (%)	Chl a/b (mg g^{-1} fw)		R (%)
	WW[a]	WD[b]		WW	WD		WW	WD	
Bahar	3.90±0.01[d]	1.92±0.20	-50.7	1.55±0.04	0.94±0.05	-39.3	2.51±0.07	2.03±0.11	-19.3
Parsi	1.48±0.04	1.32±0.07	-11.0	0.91±0.04	0.80±0.02	-12.6	1.63±0.12	1.66±0.13	1.6
Pishtaz	2.65±0.26	1.73±0.30	-34.9	1.21±0.05	0.94±0.09	-21.9	2.19±0.12	1.81±0.13	-17.4
Pishgam	2.73±0.12	1.53±0.20	-43.9	1.24±0.05	0.81±0.08	-35.0	2.20±0.08	1.88±0.07	-14.3
Chamran	2.79±0.11	1.76±0.19	-36.9	1.24±0.06	0.90±0.06	-27.8	2.24±0.04	1.95±0.09	-13.2
Zarin	2.29±0.28	1.90±0.19	-17.2	1.02±0.11	0.96±0.05	-6.1	2.23±0.07	1.97±0.11	-11.7
Sivand	2.62±0.15	1.25±0.09	-52.5	1.27±0.03	0.73±0.03	-42.1	2.07±0.07	1.69±0.06	-18.0
Marvdasht	2.33±0.31	1.60±0.37	-31.6	1.06±0.08	0.83±0.10	-21.2	2.19±0.14	1.86±0.23	-15.1
DN-11	3.96±0.08	1.53±0.13	-61.2	1.67±0.01	0.85±0.03	-48.9	2.37±0.07	1.79±0.09	-24.4
Mean	2.75±0.15	1.62±0.19		1.24±0.05	0.86±0.06		2.18±0.09	1.85±0.11	
Decrease (%)		41.4			30.5			15.2	

[a] Well Water; [b] Water deficiency, [c] Percentage decrease down control when water deficiency was applied at post anthesis (%). [d] The data are shown as Means±SE (n= 3).

uptake water from the soil compared to the susceptible ones.

CONCLUSIONS

Grain yield and 1,000-grain-weight reduction under post anthesis water stress reflect a reduction of photo-assimilates supply for grain filling. Photosynthetic rate is reduced by stomatal, non-stomatal, and leaf water status parameters. Stomatal and non-stomatal inhibition of P_n under stress condition may vary in the susceptible and tolerant cultivars. High leaf P_n, *RWC*, and g_m appear to be involved in drought tolerance. A smaller stress-induced reduction in P_n and a greater stress-induced reduction in g_s leading to increased *PWUE* could be an adaptive response in tolerant cultivars. However, in terms of absolute values, higher transpiration rate and g_s are associated with better performance of tolerant cultivars under stress conditions.

Abbreviations

P_n: Net photosynthesis rate, g_s: Stomatal conductance, *E*: Transpiration rate, T_l: Leaf temperature, C_i: Sub-stomatal CO_2 concentration, Chl: Chlorophyll, DW: Dry Weight, *FW*: Fresh Weight, g_m: Mesophyll conductance, *PWUE*: Photosynthetic Water Use Efficiency, *RWC*: Relative Water Content, *SI*: Stress Index, *SSI*: Stress Susceptibility Index, *TW*: Turgid Weight, *WUE*: Water Use Efficiency.

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ارزیابی تاثیر تنش خشکی طی پرشدن دانه بر عملکرد دانه و اجزای آن، متغیرهای تبادلات گازی و برخی از خصوصیات فیزیولوژیکی ارقام گندم نان

م. سعیدی ، و م. عبدلی

چکیده

تنش خشکی انتهای فصل طی پرشدن دانه گندم در مناطق مدیترانه ای رایج است و گندم یکی از مهمترین غلات زمستانه می باشد. این آزمایش به منظور بررسی تنش خشکی انتهای فصل بر عملکرد دانه، تبادلات گازی و برخی از خصوصیات فیزیولوژیکی نه رقم گندم نان انجام شد. آزمایش به صورت اسپلیت پلات در قالب طرح بلوک کامل تصادفی در سه تکرار طی سال زراعی ۲۰۱۱-۲۰۱۰ در مزرعه تحقیقاتی دانشگاه رازی ایران به اجرا در آمد. نتایج نشان داد که تنش کم آبی پس از گرده افشانی اثر معنی داری بر کاهش عملکرد دانه، بیوماس، وزن هزار دانه و شاخص برداشت در ارقام گندم داشت. در شرایط تنش خشکی انتهای فصل و کنترل رطوبتی، اختلاف معنی داری بین ارقام گندم از نظر صفات مورد مطالعه مشاهده شد. همچنین تنش خشکی انتهای فصل سبب کاهش میزان سرعت فتوسنتز، هدایت روزنه ای، میزان تعرق، کلروفیل a ، b و a/b و افزایش دمای سطح برگ و میزان غلظت دی اکسید کربن زیر روزنه شد. ارقام گندم پاسخ متفاوتی به تنش رطوبتی نشان دادند. به طور معمول، ارقام مقاوم از سرعت فتوسنتز، هدایت روزنه ای و محتوای رطوبت برگ بیشتری در هر دو شرایط رطوبتی برخوردار بودند. کاهش میزان هدایت روزنه ای و میزان تعرق سبب کاهش اندکی در میزان سرعت فتوسنتز در شرایط تنش شد که این امر سبب افزایش کارایی مصرف آب فتوسنتزی در ارقام مقاوم به تنش خشکی آخر فصل گردید.