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Stay Green Character at Grain Filling Ensures Resistance against Terminal Drought in Wheat

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Abstract

Water shortage is the main constraint limiting crop productivity across the globe especially when it occurs at reproductive and grain filling stages. This study was conducted to monitor the mechanisms of drought resistance, during reproductive stages (booting, heading anthesis and post-anthesis stages) by monitoring the stay green character, water use efficiency, grain filling rate, grain filling duration, grain yield and harvest index. Seeds of wheat cultivars C-591, Chakwal-50, Dharabi-2011, BARS-2009, Uqab-2000, Sehr-2006, Shafaq-2006, Faisalabad-2008, Lasani-2008 and Mairaj-2008 were sown in 10 kg soil filled pots on November 25, 2011. The drought stress was applied at the respective reproductive stage, which continued till maturity. Controlled plants were well-watered throughout the crop ontogeny. Pots were maintained at 70% water holding capacity (WHC; well watered) till booting stage and then managed drought stress was induced as per treatment maintaining 35% WHC (drought stress). Drought stress at all the stages significantly influenced the crop performance in all the tested cultivars. Severity of drought was more when it was imposed at booting and heading stages while was less devastating when imposed at anthesis and grain filling stages. Cultivars Chakwal-50 and Mairaj-2008 showed more stay gray character and took longer duration for grain filling, which resulted in the maintenance of higher grain weight and grain number per spike, grain yield and water use efficiency under stress conditions. In drought sensitive cultivars (BARS-2009, Uqab-2000), the drought increased the grain filling rate, while grain filling duration was substantially decreased. To conclude, stay green character, grain filling rate and duration under drought stress may be used as selection criteria for developing and/or screening wheat cultivars for drought resistance at reproductive stages.

Keywords: Bread wheat; Grain filling; Leaf senescence; Drought stress

Introduction

Globally, crop production is being affected due to drought (Pan *et al.,* 2002; Araus, 2004; Shahbaz *et al.,* 2009) and rapid changes in recent climatic conditions have further worsened the situation (Pan *et al.*, 2002). About 40 to 60% of the world agricultural land is affected by drought (Shahryari and Mollasadeghi, 2011a), and frequency of extreme drought spells will increase in coming future (Rennenberg *et al.*, 2006). Drought severely limits the growth, performance, and productivity of wheat (Chaves and Oliveira, 2004; Shahryari and Mollasadeghi, 2011b), depending upon the plant developmental stage (Vijendra Das, 2000; Lopez *et al.,* 2003).

Drought stress is more detrimental when it occurs at reproductive and grain filling stages. For example, drought stress at reproductive stages in wheat affects pollination (Ashraf, 1998), reduces grain filling rate and duration resulting in reduced grain weight and grain yield (Royo *et al.,* 1999; Gupta *et al.*, 2001; Kamali *et al*., 2009). Moreover, drought stress induces male sterility in wheat and reduces grain set by ~40 to 50% (Saini and Aspinall, 1981). It also influences the endosperm cell number by decreasing the sink capacity to mount up dry matter resulting in lower grain yield (Nicolas *et al.*, 1985; Ober *et al.*, 1991). In another study, drought significantly decreased the spike length, grain weight, grain yield and harvest index of wheat (Bayoumi *et al.*, 2008). Moreover, drought stress reduces the grain solute and water potentials (Westgate and Boyer, 1986), which is pivotal to metabolic events occurring during grain filling (Adams and Rinne, 1980). Drought stress at reproductive stage lowers the allocation of dry matter to grains thus decreasing the grain filling rate (Madani *et al.*, 2010; Khakwani *et al.,* 2012).

To adopt to drought stress conditions, plant species have evolved various mechanisms. Different plant species maintain stay-green character during senescence (Thomas and Smart, 1993; Spano *et al.,* 2003; Hörtensteiner, 2009), due to which photosynthesis in stay green mutants continues for longer time resulting in higher yields than the non-stay-green mutants (Thomas and Howarth, 2000; Zheng *et al.*, 2009). Stay green genotypes maintained normal

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photosynthesis during drought due to delayed expression of senescence related genes (Lim *et al.*, 2007). Moreover, genotypes that maintained better grain filling during drought stress were better able to cope with the stress conditions (Khakwani *et al.*, 2011). Similarly, in a water-limiting environment, grain yield is dependent upon the amount of water used by the crop referred to as water use efficiency and harvest index (Passioura, 1977). Improvement in any of these factors in a water-limited environment may result in increased yield in stressful conditions.

Although screening for drought resistance in wheat has been carried out by many scientists, little work is available about the screening of wheat cultivars for drought resistance at reproductive stage on the basis of their stay green character and grain filling. So, this study was aimed at to screen different wheat cultivars for drought resistance on the basis of their stay green character.

Materials and Methods

The experiment was conducted in soil-filled pots placed in the glass house of University of Agriculture, Faisalabad (latitude 31°N, longitude 73°E and altitude 184.4 masl), Pakistan, during 2011-2012. Seed of wheat variety Mairaj-2008 were obtained from Regional Research Institute, Bahawalpur and seeds of wheat cultivars C-591, Uqab-2000, BARS-2009, Dharabi-2011 and Chakwal-50 were obtained from Barani Agricultural Institute Chakwal, while seeds of wheat cultivars like Sehr-2006, Shafaq-2006, Fsd-2008 and Lasani-2008 were obtained from Wheat Research Institute, AARI, Faisalabad, Pakistan. Individual pot was weighted and the pots were filled with 10 kg soil. Experimental soil was sandy loam in soil texture and determined for pH (8.1) EC (0.33 dS m^{-1}), organic Matter (0.95%), total nitrogen (0.060%) available phosphorous (4.9 ppm) and exchangeable potassium (167 ppm).

Experiment was laid down in Completely Randomized Design in factorial arrangement with three replications. Crop was sown in soil-filled pots on 25 November, 2011. Initially, 10 seeds were sown in each pot, which were thinned to six plants per pot after complete emergence. Fertilizers were applied at 0.5-0.45-0.38 N-P-K g/pot using urea (46% N), diammonium phosphate (DAP) (18%N, 46% P_2O_5) and sulfate of potash (50% K_2O) as sources of fertilizer. Whole of the phosphorous, potassium and nitrogen was applied as basal dose.

Pots were maintained at 70% WHC (well watered) till booting stage. Then drought stress was applied at booting stage, heading stage, anthesis stage and post-anthesis stage by maintaining moisture at 35% WHC at each reproductive stage until maturity. The pots maintained at 70% WHC were taken as control. Weather data during the experimental period are given in Table 1.

Height of all plants from each pot was taken at maturity and averaged. Five spikes were selected at random from each pot, their length was measured and averaged. Chlorophyll content was measured with the help of chlorophyll meter (CCM-200 plus). The meter was clamped over leafy tissue to get an indexed chlorophyll content reading in less than 2 sec. Three spikes were randomly taken from each pot after the start of anthesis with 7 days interval to record grain filling rate. The grains from all the three spikes were extracted and oven dried. Then the grain filling rate was (GFR) calculated from the following formula:

$$GFR= (W_2 – W_1) / (t_2 – t_1)$$

W_1= Total dry weight of spikes at the first harvest
W_2= Total dry weight of spikes at the second harvest
t_1 = Date of observation of first dry matter
t_2 = Date of observation of second dry matter.

Number of days from heading to physiological maturity was taken as grain filling duration. Grains from the each of the five spikes were threshed manually and counted. A sub-sample of 100 grains was taken from each pot, weighed and 100-grains weight was calculated. The crop was harvested, tied into bundles and sundried for a week. Total wheat biomass of sun-dried samples was recorded for each treatment by using an electric balance. The crop was threshed manually and grain weight for each treatment was recorded by an electric balance in grams. Harvest index was calculated as the ratio of grain yield to total (above ground) biological yield.

Water use efficiency (WUE) was calculated as the ratio between grain yield harvested and water used (Viets, 1962). Transpiration efficiency was calculated as the ratio between biological yield harvested and water used.

Data collected on all parameters was analyzed statistically by using MSTAT-C software on computer (Crop and Soil Sciences Department of Michigan University). Least significance difference (LSD) test at 5% probability level was applied to compare the treatments means (Steel *et al.*, 1996).

Results

Analysis of variance indicated that drought stress at different reproductive stages affected the plant height, spike length, chlorophyll content index, grain filling rate, grain filling duration, spike length, grains per spike, grain weight, grain yield, biological yield, harvest index, water use efficiency and transpiration efficiency of all tested wheat cultivars (Table 2). Similarly all wheat cultivars differed significantly for all the recorded parameters (Table 2). However, the interaction of different wheat cultivars and wheat reproductive stages was non-significant for all studied parameters (Table 2). A maximum plant height was observed in Sehr-2006 followed by C-591, while it was the minimum in Fsd-2008 followed by Lasani-2011 (Table 3). A maximum spike length was observed in Sehr-2006 followed by Mairaj-2008, while it was the minimum in C-591 (Table 3). Chlorophyll content index was highest in C-591 followed by Mairaj-2008 and Chakwal-50, while it

Table 1: Weather data during the wheat season 2011-2012

Months	Maximum temperature (°C)	Minimum temperature (°C)	Relative humidity (%)	Rainfall (mm)	Sunshine hours
November	27.6	13.3	61.2	0.00	8.5
December	20.9	4.2	59.1	0.00	6.9
January	17.3	3.2	69.6	3.80	7.2
February	18.4	4.6	62.1	8.00	7.3
March	25.9	11.7	58.2	1.50	8.3
April	32.7	18.0	59.1	10.50	9.2

Source: Agricultural Meteorology Cell, Department of Crop Physiology, University of Agriculture, Faisalabad, Pakistan

Table 2: Analysis of variance for the effect of terminal drought on agronomic, yield-related and physiological traits of different wheat cultivars

SoV	DF	Mean sum of squares											
		PH (cm)	SL (cm)	CCI	GFR (g day^{-1})	GFD (days)	GPS	100-GW (g)	BY (g/pot)	GY (g/pot)	HI (%)	WUE (kg m^{-3})	TE (g kg^{-1})
Varieties (V)	9	243.25 **	3.60 **	49.68 **	0.0049 **	4.90 **	135.82 **	0.33 **	79.80 **	42.81 **	400.84 **	0.014 **	0.027 *
Drought (D)	4	523.05 **	6.84 **	142.30 **	0.0206 **	76.11 **	836.86 **	8.18 *	291.06 **	105.63 **	405.46 **	0.015 **	0.035 **
V × D	36	17.44	0.87	1.17	0.0015	1.90	18.79	0.12	15.83	5.38	38.44	0.002	0.007
Error	100	21.40	0.61	12.28	0.0004	1.40	31.07	0.15	19.58	3.74	18.56	0.001	0.008
Total	149											s	

SOV = Source of variation; DF = Degree of freedom; ** = Significant at p 0.01; * = Significant at p 0.05; PH= Plant height; SL= Spike length; CCI = Chlorophyll content index; GFR= Grain filling rate; GFD= Grain filling duration; GPS= Grains per spike; 100-GW= 100-Grain weight; BY= Biological yield; GY= Grain yield; HI= Harvest index; WUE= Water use efficiency; TE= Transpiration efficiency

Table 3: Effect of terminal drought on agronomic, yield-related and physiological traits of different wheat cultivars

Treatments	PH (cm)	SL (cm)	CCI	GFR (g day^{-1})	GFD (days)	GPS	100-GW (g)	BY (g/pot)	GY (g/pot)	HI (%)	WUE (kg m^{-3})	TE (g kg^{-1})
Wheat cultivars												
Mairaj-2008	80.15 de	10.55 ab	27.51 ab	0.11 bc	30.11 ab	34.2 a	3.35 a	29.26 d	8.57 ab	28.42 a	0.17 b	0.60 e
C-591	85.87 ab	8.37 f	28.79 a	0.08 e	29.51 abc	25.6 d	3.07 bc	32.05 bcd	4.76 e	14.95 d	0.09 f	0.66 cde
Chakwal-50	82.58 bcd	9.58 de	27.38 ab	0.11 bc	30.18 a	34.1 a	3.30 ab	33.78 abc	9.97 a	28.75 a	0.19 a	0.69 a-d
Dharabi-2011	82.27 cd	10.01 bcd	23.57 de	0.11 c	29.51 abc	32.5 ab	3.09 abc	33.50 abc	5.88 de	17.66 cd	0.12 ef	0.69 a-d
Sehr-2006	86.43 a	10.74 a	26.11 bc	0.08 e	29.71 abc	26.3 cd	3.17 ab	32.40 bcd	8.12 bc	25.18 b	0.16 bc	0.67 bcd
BARS-2009	78.52 ef	9.26 e	23.06 e	0.14 a	29.18 c	29.4 bcd	2.82 c	31.15 cd	5.10 e	16.34 cd	0.10 f	0.64 de
Uqab-2000	84.93 abc	10.22 abc	25.89bcd	0.12 ab	28.18 d	30.3 abc	3.04 bc	36.09 a	5.44 e	15.33 d	0.11 f	0.74 a
Fsd-2008	75.32 f	9.57 de	25.27 b-e	0.09 de	29.26 bc	29.6 bc	3.08 abc	35.70 a	6.88 cd	19.30 c	0.14 cde	0.73 ab
Lasani-2008	76.18 f	9.70 cde	26.99 abc	0.10 cd	29.85 abc	27.3 cd	3.20 ab	34.67 ab	7.88 bc	22.44 b	0.16 bcd	0.71 abc
Shafaq-2006	77.75 ef	9.87 cd	24.67 cde	0.11 bc	29.31 bc	29.8 bc	3.15 ab	36.34 a	6.92 cd	18.75 c	0.14 de	0.75 a
LSD value	3.35	0.57	2.54	0.01	0.86	4.04	0.28	3.21	1.40	3.12	0.02	0.07
Stage of drought stress												
Control	82.09 a	10.23 a	29.15 a	0.13 a	31.00 a	34.2 a	3.73 a	3.73 a	9.68 a	25.95 a	0.15 a	0.68 abc
Booting stage	73.63 b	9.29 c	23.48 d	0.06 d	26.80 c	21.8 c	2.37 e	2.37 e	4.67 d	15.83 c	0.10 c	0.65 bc
Heading stage	83.50 a	9.66 bc	24.44 cd	0.11 c	29.51 b	27.2 b	2.89 d	2.89 d	5.92 c	19.67 b	0.13 b	0.67 c
Anthesis stage	83.52 a	9.84 ab	26.00 bc	0.12 b	30.10 b	33.2 a	3.22 c	3.22 c	6.93 b	20.42 b	0.15 a	0.71 ab
Grain filling stage	82.27 a	9.92 ab	26.55 b	0.12 b	30.00 b	33.1 a	3.44 b	3.44 b	7.57 b	21.69 b	0.16 a	0.72 a
LSD Value	2.37	0.40	1.80	0.01	0.61	2.86	0.20	2.27	0.99	2.21	0.02	0.05

Means sharing the same case letter for main effects do not differ significantly at $p < 0.05$; PH= Plant height; SL= Spike length; CCI = Chlorophyll content index; GFR= Grain filling rate; GFD= Grain filling duration; GPS= Grains per spike; 100-GW= 100-Grain weight; BY= Biological yield; GY= Grain yield; HI= Harvest index; WUE= Water use efficiency; TE= Transpiration efficiency

as the lowest in BARS-2009 (Table 3). Grain filling rate was the greatest in BARS-2009 followed by Uqab-2000, while the lowest in C-591 and Sehr-2006 (Table 3). Grain filling duration was the maximum in Chakwal-50 followed by Mairaj-2008, while it was the minimum in Uqab-2000 (Table 3). Maximum grains per spike were found in Mairaj-2008 followed by Chakwal-50, while a minimujm one in C-591 (Table 3). Highest 100 grain weight was obtained from the seeds of Mairaj-2008 followed by Chakwal-50, Sehr-2006, Lasani-2008 and Shafaq-2006 but a lowest in BARS-2009 (Table 3). Biological yield and transpiration efficiency was higher in Shafaq-2006 followed by Faisalabad-2008 (Table 3). Maximum grain yield, harvest index and water use efficiency were obtained in Chakwal-50 followed by Mairaj-2008 while they were the minimum in BARS-2009 and Uqab-2000 (Table 3).

Discussion

Drought stress at all reproductive stages reduced grain filling rate and duration, grain weight, grain yield and water use efficiency than control (well watered). Severity of drought stress was more when it was applied at booting stage followed by heading, anthesis and grain filling stages.

More reduction in yield related traits in term of grain weight, grains per spike and grain yield was recorded at early reproductive stages (booting and heading), which seems to be due to prolonged exposure to drought stress at these stages than anthesis and grain filling stage. Moreover, more yield reduction at early reproductive stages may be attributed to hampered pollination and seed set (Ashraf, 1998; Farooq *et al.*, 2009), which seemingly reduced the number of ear heads and number of grains per spike (Dencic *et al.*, 2000; Mary *et al.*, 2001). Zhang and Oweis (1999) reported that wheat crop is most sensitive to drought stress from stem elongation to heading stage. We experienced reduction in grain filling rate and duration in all cultivars due to drought stress than control. In earlier studies, it has been reported that drought stress applied at reproductive stage reduces grain filling rate, grain weight and grain yield (Giunta *et al.*, 1993; Royo *et al.*, 1999; Gupta *et al.*, 2001). Recently, Khakwani *et al.* (2012) reported reduction in yield related traits of wheat when drought stress was applied at booting or anthesis stage. In another study, significant reduction in yield related traits was observed when drought was imposed at reproductive phases (Bayoumi *et al.*, 2008). Decrease in 1000-grain weight due to drought stress in present study was due to shriveling of the grains.

From the above findings (Table 3), Chakwal-50 followed by Mairaj-2008 emerged as drought resistance cultivars. This highest grain yield in Chakwal-50 and Mairaj-2008 may be due to higher chlorophyll content index, more grain weight per spike, more grain weight and enhanced water use efficiency in both these cultivars than other wheat cultivars. Chlorophyll content index is a stay green character of plant (Thomas and Howarth, 2000). Drought stress causes leaf senescence which results in degradation of chlorophyll and disorganization of the photosynthetic apparatus (Matile *et al.*, 1996, 1999) resulting in lower crop yields. However, plant species maintaining stay green character are able to photosynthesize for longer times by a delay in senescence (Spano *et al.*, 2003; Hörtensteiner, 2009). Grain filling rate and grain filling duration was not affected due to drought stress in Chakwal-50 and Mairaj-2008 and these cultivars took maximum duration for grain filling. Better grain filling in these cultivars under drought stress may be attributed to the better availability of photoassimilates from source to sink as a result of leaf photosynthesis for relatively longer time period under drought stress (Khakwani *et al.*, 2011).

Reduction in grain yield in drought sensitive (Uqab-2000 and BARS-2009) wheat cultivars may be due to negative influence of drought stress on endosperm cell number, which affected the sink capacity to accumulate dry matter (Nicolas *et al.*, 1985; Ober *et al.*, 1991). In drought sensitive cultivars, grain filling rate was increased and grain filling duration was decreased due to drought stress (Uqab-2000 and BARS-2009). Drought stress at reproductive stages causes senescence and grain filling duration is reduces; however grain filling rate is increased (Gebbing and Schnyder, 1999; Plaut *et al.*, 2004; Yang and Zhang, 2006). Poor grain filling in drought sensitive cultivars may be due to reduced grain water potential (Westgate and Boyer, 1986) which influences the metabolic events during grain filling (Adams and Rinne, 1980; Saab and Obendorf, 1989). In a study, Zhang *et al.* (1998) concluded that grain filling rate was increased when drought stress was imposed.

The highest harvest index in Chakwal-50 and Mairaj-2008 may be due to improved resistance to drought due to provision of assimilates to the young spike (Austin, 1994). In a water-limiting environment grain yield is dependent on water use efficiency and harvest index (Passioura, 1977). Improvement in any one of the above factors in a water-limited environment should result in increased yield in stressful conditions. The cultivar C-591 possesses excellent stay green character (personnel observation). During rabi season of 2011-2012, cultivar C-591 was cultivated at farmer field and no rainfall was received after leaf boot stage but stay green character was more obvious in C-591 till at harvest than other wheat cultivars planted in rainfed area (Personnel observation). Although chlorophyll contents were highest in C-591 in recent study but grain yield, water use efficiency was lower in C-591 which may be due to minimum spike length, less grains per spike. C-591 is a tall stature variety and less grain yield in this cultivar may be due to translocation of more assimilates to the vegetative part than the reproductive growth. Stay green character of C-591 must be considered in the future studies for developing new wheat cultivars to cope with the climate change.

In conclusion, severity of drought stress was higher at booting and heading stage. As a whole, drought stress at booting, heading, anthesis and post anthesis stages caused a yield reduction of 29.1-75.7%, 24.3-43.8%, 10.2-40.5%, 7.4-35%, respectively than control (well watered), which was due to hampered assimilate partitioning to grain. Better grain filling and stay green character resulted in increased grain weight, grain per spike and grain yield of the tolerant cultivars. The use of drought tolerant cltivars (Chakwal-50 and Mairaj-2008) for the incorporation of stay green character in the future wheat materials is recommended.

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References

Adams, C.A. and R.W. Rinne, 1980. Moisture content as a controlling factor in seed development and germination. *Int. Rev. Cytol.*, 68: 1–8

Araus, J.L., 2004. The problem of sustainable water use in the Mediterranean and research requirements for agriculture. *Ann. Appl. Biol.*, 144: 259–272

Ashraf, M.Y., 1998. Yield and yield components response of wheat (*Triticum aestivum* L.) genotypes tinder different soil water deficit conditions. *Acta Agron. Hung.*, 46: 45–51

Austin, R.B., 1994. Plant breeding opportunities. *In: Physiology and Determination of Crop Yield*, pp: 567–586. Boote, K.J. (ed.). CSSA, The American Society of Agronomy, Madison, Wisconsin, USA

Bayoumi, T.Y., M.H. Eid and E.M. Metwali, 2008. Application of physiological and biochemical indices as a screening technique for drought tolerance in wheat genotypes. *Afr. J. Biotechnol.*, 7: 2341–2352

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

Dencic, S., R .Kastori, B. Kobiljskia and B. Duggan, 2000. Evaluation of grain yield and its components in wheat cultivars and landraces under near optimal and drought conditions. *Euphytica*, 113: 43–52

Farooq, M., A. Wahid., N. Kobayashi., D. Fujita and S.M.A. Basra, 2009. Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.*, 29: 185–212

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

Giunta, F., R. Motzo and M. Deidda, 1993. Effect of drought on yield and yield components of durum wheat and triticale in a Mediterranean environment. *Field Crops Res.*, 33: 399–409

Gupta, N.K., S. Gupta and A. Kumar, 2001. Effect of water stress on physiological attributes and their relationship with growth and yield of wheat cultivars at different stages. *J. Agron. Crop Sci.*, 186: 55–62

Hörtensteiner, S., 2009. Stay-green regulates chlorophyll and chlorophyll-binding protein degradation during senescence. *Trends Plant Sci.*, 14: 155–162

Kamali, M.R.J., H. Asadi and T.N. Mirak, 2009. *Irrigated and Dry Land Wheat Research Strategic Program*, p: 245. Agricultural Research, Education and Extension Organization (In Persian), Iran

Khakwani, A.A., M.D. Dennett and M. Munir, 2011. Early growth response of six wheat varieties under artificial osmotic stress condition. *Pak. J. Agric. Sci.*, 48: 121–126

Khakwani, A.A., M.D. Dennett, M. Munir and M. Abid, 2012. Growth and yield response of wheat varieties to water stress at booting and anthesis stages of development. *Pak. J. Bot.*, 44: 879–886

Lim, P.O., H.J. Kim and H.G. Nam, 2007. Leaf senescence. *Annu. Rev. Plant Biol.*, 58: 115–136

Lopez, C.G., G.M. Banowetz, C.J. Peterson and W.E. Kronstad, 2003. Dehydrin expression and drought tolerance in seven wheat cultivars. *Crop Sci.*, 43: 577–582

Madani A., A.H.S. Rad, A. Pazoki, G. Nourmohammadi and R. Zarghami, 2010. Grain filling and dry matter partitioning responses to source: sink modifications under post-anthesis water and nitrogen deficiencies in winter wheat (*Triticum aestivum* L.). *Acta Sci. Agron.*, 32: 145–151

Mary, J.G., J.C. Stark, K.O. Brien and E. Souza, 2001. Relative sensitivity of spring wheat grain yield and quality parameters to moisture deficit. *Crop Sci.*, 41: 327–335

Matile, P., S. Hörtensteiner and H. Thomas, 1999. Chlorophyll degradation. *Ann. Rev. Plant Physiol. Plant Mol. Biol.*, 50: 67–95

Matile, P., S. Hörtensteiner, H. Thomas and B. Kraütler, 1996. Chlorophyll breakdown in senescent leaves. *Plant Physiol.*, 112: 1403–1409

Nicolas, M.E. R.M. Gleadow and M.J. Dalling, 1985. Effect of post anthesis drought on cell-division and starch accumulation in developing wheat grains. *Ann. Bot.*, 55: 433–444

Ober, E.S., T.L. Setter, J.T. Madison, J.F. Thompson and P.S. Shapiro, 1991. Influence of water deficit on maize endosperm development. Enzyme activities and RNA transcripts of starch and zein synthesis, abscisic acid, and cell division. *Plant Physiol.*, 97: 154–164

Pan, X.Y., Y.F. Wang, G.X. Wang, Q.D. Cao and J. Wang, 2002. Relationship between growth redundancy and size inequality in spring wheat populations mulched with clear plastic film. *Acta Phytoecol. Sin.*, 26: 177–184

Passioura, J.B., 1977. Grain yield harvest index and water use of wheat. *J. Aust. Inst. Agric.*, 43: 117–120

Plaut, Z., B.J. Butow, C.S. Blumenthal and 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 Crop Res.*, 86: 185–198

Rennenberg, H., F. Loreto, A. Polle, F. Brilli, S. Fares, R.S. Beniwal, and A. Gessler, 2006. Physiological response of forest trees to heat and drought. *Plant Biol.*, 8: 556–571

Royo, C., J. Voltas and I. Romagosa, 1999. Response of four spring wheat cultivars to drought stress. *Crop Sci.*, 36: 982–986

Saab, I.N. and R.L. Obendorf, 1989. Soybean seed water relations during in situ and in vitro growth and maturation. *Plant Physiol.*, 89: 610–616

Saini, H.S. and D. Aspinall, 1981. Effect of water deficit on sporogenesis in wheat (*Triticum aestivum* L.). *Ann. Bot.*, 48: 623–633

Shahbaz, K., A.H. Munir and J.X. Mu, 2009. Water management and crop production for food security in China: a review. *Agric. Water Manage.*, 96: 349–360

Shahryari, R. and V. Mollasadeghi, 2011a. Correlation study of some traits affecting yield and yield components of wheat genotypes in terms of normal irrigation and end drought stress. *Adv. Environ. Biol.*, 5: 523–532

Shahryari, R. and V. Mollasadeghi, 2011b. Introduction of two principle components for screening of wheat genotypes under end seasonal drought. *Adv. Environ. Biol.*, 5: 519–522

Spano, G., N.D. Fonzo, C. Perrotta, C. Platani, G. Ronga, D.W. Lawlor, J.A. Napier and P.R. Shewry, 2003. Physiological characterization of `stay green' mutants in durum wheat. *J. Exp. Bot.*, 54: 1415–1420

Steel, R.G.D., J.H. Torrie and D.A. Dickey, 1996. *Principles and Procedures of Statistics: a Biometric Approach*, 3rd edition. McGraw Hill Book Co. Inc., New York, USA

Thomas, H. and C.J. Howarth, 2000. Five ways to stay green. *J. Exp. Bot.*, 51: 329–337

Thomas, H. and C.M. Smart. 1993. Crops that stay green. *Ann. Appl. Biol.*, 123: 193–201

Viets, F.G., 1962. Fertilizers and the efficient use of water. *Adv. Agron.*, 14: 223–264

Vijendra Das, L.D., 2000. *Problems Facing Plant Breeding.* CBS Publishers and Distributors, New Delhi, India

Westgate, M.E. and J.S. Boyer, 1986. Reproduction at low silk and pollen water potentials in maize. *Crop Sci.*, 26: 951–956

Yang, J. and J. Zhang, 2006, Grain filling of cereals under soil drying. *New Phytol.*, 169: 223–236

Zhang, J., X. Sui, B. Li, B. Su, J. Li and D. Zhou, 1998. An improved water-use efficiency for winter wheat grown under reduced irrigation. *Field Crops Res.*, 59: 91–98

Zhang, H.P. and T. Oweis, 1999, Water-yield relations and optimal irrigation scheduling of wheat in the Mediterranean region. *Agric. Water Manual*, 38: 195–211

Zheng, H.J., A.Z. Wu, C.C. Zheng, Y.F. Wang, R. Cai, X.F. Shen, R.R. Xu, P. Liu, L.J. Kong and S.T. Dong, 2009. QTL mapping of maize (*Zea mays*) stay-green traits and their relationship to yield. *Plant Breed.*, 128: 54–62

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