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Morpho-physiological Characterization of Spring Wheat Genotypes under Drought Stress

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Abstract

Water-deficit is a severe abiotic stress and major constraint to wheat productivity with effect on plant growth and development. The objective of this study was to characterize drought tolerant and susceptible spring wheat cultivars on the basis of physiological and yield attributes. The experiment was comprised of two irrigation regimes i.e. irrigated and 65% drought stress and ten wheat cultivars viz. Anmol, Moomal, Sarsabz, Bhittai, Pavon, SKD-1, TD-1, Kiran, Marvi and Mehran. Results indicated significant effect of water stress on stomatal dimension, stomatal conductance, relative leaf water content and grain yield with no effect on stomatal density. The irrigation × cultivars interaction was non-significant for grain yield only. Cultivars like Anmol, Moomal, Bhittai, Sarsabz proved to be drought tolerant with smaller stomatal dimensions, less stomatal conductance and more relative water content under water stress and produced higher grain yield. While decrease in relative water contents and grain yield, and increase in stomatal attributes was observed in drought susceptible cultivars such as Marvi, TD-1 and SKD-1 hence proved to be drought susceptible.

Keywords: Stomatal dimension and density; Relative water content; Yield traits; Drought tolerance; Wheat

Introduction

Drought limits wheat yields by preventing the crop plants from expressing their full genetic potential. Possible improvement of crops for drought tolerance may require a search of physiological attributes and the exploitation of their genetic variation in germplasm (; Farooq *et al.*, 2009; Jatoi *et al*., 2012a). Climatic variability greatly affects the genotypes potential and selection of genotypes with better performance under water stress conditions should increase production of rainfed areas (Rashidi and Seyfi, 2007; Rajaram, 2001). Breeding for improved drought tolerance focuses on breeding cultivars with higher yields under water stress conditions and assumes that such cultivars provide a yield advantage under suboptimal conditions (Turner, 1986; Rajaram, 2001). Ludlow and Muchow (1990) suggested breeding for maximum yield in targeted environments only whereas Rauf *et al*. (2007) suggested developing cultivars for water-limited environments through selection and incorporation of physiological traits by traditional breeding. Nonetheless, most of the breeding programs aim to establish fewer drought-tolerant characters expected to benefit in yield under water-limited conditions.

Changes in agronomic traits are due to variable response of wheat genotypes via morpho-physiological characters. Thus, the development of cultivars for water-limited environments involves incorporation of both physiological and morphological characters that provide drought tolerance. Physiological and anatomical changes in traits such as stomatal density and dimensions, stomatal conductance and relative leaf water content have been considered as important criteria for yield progress because breeders and physiologists regularly select for desirable expression of these traits to maintain both adaptation and optimal yield of crops under water-stress environments (Blum, 1988; Khokar and Teixeira da Silva, 2012). Among the anatomical traits, stomata are specialized epidermal cells that regulate the exchange of water and CO_2 between plant and the atmosphere (Bergmann, 2004). In order to maximise photosynthetic activity while minimizing water loss, pore size of stomata is modulated (Bergmann, 2004). Optimal gas exchange thus requires the regulation of both number and size of stomata and the ability to open and close them (Nadeau and Sack, 2002a, b).

Reduction in stomatal density and dimension could be used in achieving water stress tolerance (Tanzarella *et al*., 1984). The relationship between leaf water use efficiency (WUE) and several physio-biochemical traits was

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determined by Baodi *et al.* (2008) and was revealed that photosynthetic rate, stomatal conductance and transpiration rate were the most important leaf WUE variables under rainfed conditions in wheat. It was also observed that a high leaf WUE in wheat under the rainfed conditions could be obtained by selecting breeding materials with high photosynthesis rate, low transpiration rate and low stomatal conductance.

The control of stomatal aperture with the production of Indole Acetic Acid (IAA) is one of the major methods by which plants regulate water loss. The stomatal density and size of stomata thus play an important role in determining the leaf conductance and transpiration rate (Jones, 1977). It was also reported that lower stomatal conductance in some wheat lines was due to differences in the size of stomata while Adjei and Kirkham (1980) found that the drought tolerant cultivars have higher stomatal resistance than drought sensitive ones for part of the growth cycle in wheat. The effect of stomatal density and dimension may be important processes for plant growth and productivity if the extent of interspecies variations is known. Wheat genotypes MACS 2961 and MACS 2947 with a maximum stomatal density (number per mm^2) on the abaxial (lower) leaf surface of 102 and on the adaxial (upper) leaf surface of 100 had low transpiration rates of 20.1 and 21.4 (mg H_2O cm^{-2} s^{-1}) also gave higher yields (Bilagi *et al*., 2008). Galle *et al*. (2002) observed that water-deficit caused by polyethylene glycol decreased the relative leaf and root growth in cultivars Othalom and Kobomugi under deficit irrigation and stomatal conductance increased significantly in susceptible cultivars by 82.3% (Duan *et al*., 2008). Drought tolerance has been enhanced by incorporating alien genes from wild relatives (Del-Blanco *et al*., 2001; Dreccer *et al*., 2007; Inagaki *et al*., 2007). Relative water content (RWC) has also been reported as an important indicator of water stress in leaves (Merah, 2001) and is closely related to cell volume therefore, it may reflect the balance between water supply to the leaf and transpiration rate (Farquhar *et al*., 1989; Jones *et al*., 1989).

Despite substantial physiological research to understand the response of plants to drought and the underlying genetic variations, few studies report for the development of improved cultivars. The improvement of physiological traits for water-limited environments is unlikely to be universal because some may be important in one region but detrimental in another. Nonetheless, the most useful physiological approaches, as described by Richards (2006) may emphasize include: (i) increased genetic variability in traits for further yield progress, (ii) make more rapid selections of physiological traits that may give a higher heritability than yield, (iii) enable out-of-season selection, i.e. more generations per year, and (iv) use cost effective methods for comparison of potential yield evaluation. Correlations within physiological parameters and with yield traits are also very useful to plant breeders in improving drought tolerance. Any correlation of physiological parameters with yield component traits having high heritability may be useful in serving as indirect selection criteria to improve grain yields in water-deficit environments (Khan *et al*., 2010). Therefore, the main objectives of this study were to evaluate variation in stomatal density and dimensions and relating these anatomical traits with physiological and yield traits for labeling drought tolerant wheat genotypes.

Materials and Methods

Ten spring wheat cultivars such as Anmol, Moomal, Sarsabz, Bhittai, Pavon, SKD-1, TD-1, Kiran, Marvi and Mehran were grown at two irrigation levels (irrigated and 65% drought stress conditions) in 4 litre pots filled with 2.84 kg of compost media. Experiment was laid-out in a randomized complete block with factorial arrangement using three replications during 2009 in the greenhouse at The University of Reading, U.K. The pots of 65% drought stress were maintained at 35% of field capacity and were irrigated with measured quantity of water, while the control irrigated treatment was given water frequently with 7 days interval. No inorganic fertilizer was applied at any stage of crop growth. The temperature during growth period varied from 7 to 44°C and humidity was maintained at 65%.

After the boot stage, the fully expanded flag leaves were selected for stomatal studies. The abaxial (lower) epidermis of the leaves was carefully smeared with nail varnish in the mid-area between the central vein and the leaf edge and the varnish was allowed to set for approximately 20 min. The thin film of nail polish (measuring approximately 10-20 mm) was peeled-off from the leaf surface, mounted on a glass slide, immediately covered with a cover slip, and then lightly pressed with fine point tweezers. The density of stomata (number per mm^2) and their size (μm) for each filmstrip were determined after taking pictures under 10x magnifications with a photomicroscope (Leitz Dialux-20, Camera Sony, DSC-F717, Germany). Stomatal size was defined as the length in micrometers between the junctions of the guard cells at each end of the stoma and is considered the maximum opening potential of the stomatal pore, but not the apertures (Maherali *et al*., 2002). Stomatal density and size reported are averages of nine microscopic field views. Stomatal conductance (mmol m^{-2} s^{-1}) was measured using a Porometer AP4 instrument (Delta Devices, Cambridge, U.K.) between 12:00 noon to 3:00 p.m. The relative leaf water content (RWC) was calculated with the following formula (Schonfeld *et al*., 1988):

$$RWC = \frac{Fresh\ weight - dry\ weight}{Turgid\ weight - dry\ weight} \times 100$$

The grain yield per plant was obtained after harvesting and threshing each plant separately. The analyses of variance were calculated with Genstat (11^{th} edition) by using factorial analysis.

Results

Significant differences were observed due to irrigation regimes and cultivars for stomatal dimensions, stomatal conductance, relative leaf water content and grain yield. Irrigations × cultivars interaction was significant for all the measured traits except grain yield. Water stress had no effect on stomatal density, while cultivars were quite variable for stomatal density under drought stress (Table 1) and cultivars Moomal, Kiran and Bhittai had minimum stomatal density while SKD-1 and TD-1 exhibited more than twice the number of stomatal density (Table 2).

Water stress caused an increase in stomatal dimensions (Table 2; Fig. 2) by 6.09% under drought stress as compared to irrigated control. The range of stomatal dimension in irrigated and drought stress was from 37.2 to 51.3 and 32.2 to 59.7 µm, respectively. Generally, cultivars with less stomatal density under stress correspondingly had smaller stomatal dimensions (Fig. 1). Among the cultivars, Sarsabz, Anmol, and Bhittai had the smaller stomatal dimensions of 23.2, 40.6 and 40.8 µm, respectively and maximum dimensions was recorded by the drought susceptible cultivars TD-1, SKD-1 and Marvi (Table 2).

Both stomatal density and dimensions were correlated with stomatal conductance. In optimum conditions, the stomatal conductance was quite higher (232 mmol m^{-2} s^{-1}) than 121 mmol $m^{-2}s^{-1}$ under drought stress (Table 2). The difference in stomatal conductance among the cultivars was also obvious when more resistance (i.e., lower conductance) was recorded in the drought tolerant cultivars such as Bhittai (77.3 mmol $m^{-2}s^{-1}$), Pavon (79.6 mmol $m^{-2}s^{-1}$), Moomal (89.6 mmol $m^{-2}s^{-1}$) and Anmol (95.5 mmol $m^{-2}s^{-1}$) but had small stomatal dimensions and density. The higher stomatal conductance, however was noted under drought conditions in susceptible cultivars SKD-1 (150 mmol $m^{-2}s^{-1}$) and TD-1 (142 mmol $m^{-2}s^{-1}$). From these results appears high relevancy of these two physiological attributes i.e., stomatal dimension and stomatal conductance have interaction of the plant with drought.

The cultivars expressed differential response to RWC under drought stress and on an average, a considerable reduction of 40.9% in RWC was noticed due to drought stress. The average RWC of cultivars was 48.2 *vs* 81.2% in drought and irrigated conditions, respectively (Table 3). The maximum RWC however was recorded in the cultivars Bhittai, Moomal, and Sarsabz, while minimum RWC was observed in cultivars Marvi, Kiran, SKD-1 and TD-1 under water stress conditions (Table 3).

Grain yield of wheat cultivars decreased substantially (16.2%) under drought and minimum reduction was observed in the cultivars Bhittai, Moomal and Anmol (Table 3). The non-significant interaction of irrigation × cultivar is desirable in the sense that, varietal performance was quite consistent over the irrigation regimes.

The correlation coefficients (r) between physiological and yield traits (Table 4) indicated significant and positive

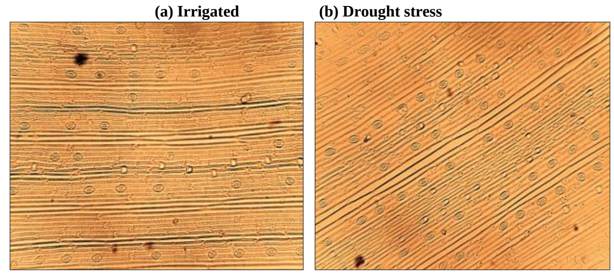

Fig. 1: Stomatal density and dimensions of drought tolerant wheat cv. Sarsabz under irrigated (a) and drought stress (b) conditions

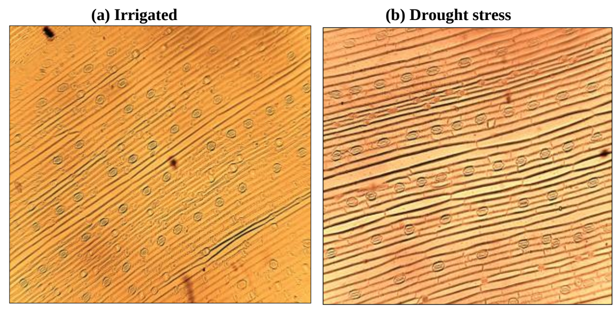

Fig. 2: Stomatal density and dimensions of drought susceptible wheat cv. TD-1 under irrigated (a) and drought stress (b) conditions

associations between stomatal density and stomatal dimension (r = 0.31*), while stomatal dimension expressed significantly negative association with grain yield (r = -0.36**) and RWC (r = -0.33**). These results are very important and indicate that as the stomatal dimension increases, the leaf RWC content decreases, which may be due to more transpiration from large stomatal pores. As RWC decreased due to large stomata, the yield correspondingly decreased in susceptible cultivars under stress conditions. Stomatal conductance exhibited positive association with RWC (r = 0.62**) and grain yield (r = 0.34**) whilst RWC showed positive correlation (r = 0.48**) with grain yield.

Discussion

Significant impact of drought was observed for stomatal dimensions, stomatal conductance, relative leaf water content and grain yield per plant but no effect on stomatal density; however, the cultivars were significantly different for this trait (Table 1). The insignificant effect of water stress on stomatal density may be due to measurement of stomatal density before drought stress was imposed. The significant interaction of irrigation × stomatal density revealed variable response of cultivars to water stress. Rodiyati *et al.* (2005) found that stomatal density does not vary greatly under water-deficit conditions. However, present results are in contradiction to previous reports, where reduction in stomatal density was found

Table 1: Mean squares of physiological and yield attributes of drought tolerant and susceptible spring wheat cultivars under irrigated and drought stress conditions

Source of variation	D.F.	Stomatal density	Stomatal dimensions	Stomatal conductance	Relative leaf water content	Grain yield per plant
Irrigations (Irrig.)	1	9.60	108.27*	217936.00**	16631.45**	3.6359**
Cultivars (Cv.)	9	523.33**	183.08**	4883.00**	101.45*	0.4097**
Irrig. × Cv.	9	735.23**	116.18**	3652.00*	224.35**	0.2416
Error	59	26.36	21.97	1430.00	40.37	0.1182

**, = Significant at $p \le 0.01$ and $p \le 0.05$, respectively

Table 2: Mean values for physiological and yield attributes of drought tolerant and susceptible spring wheat cultivars under irrigated and drought stress conditions

Cultivars	Stomatal density (mm^2)		Stomatal dimension (μm)		Stomatal conductance (mmol $m^{-2}s^{-1}$)	
	Irrigated	65% DS	Irrigated	65% DS	Irrigated	65% DS
Anmol	49.33	35.67	41.47	40.57	190.7	95.5
Bhittai	26.33	34.67	39.43	40.83	271.5	77.3
Kiran	73.33	32.00	47.77	45.57	273.0	133.3
Marvi	33.00	38.00	51.10	57.00	246.0	120.7
Mehran	30.00	40.33	44.43	52.67	266.8	121.3
Moomal	51.33	29.00	40.00	40.53	197.2	89.6
Pavon	32.00	33.00	37.20	46.10	182.8	79.6
Sarsabz	45.00	45.33	47.50	32.23	271.0	107.0
SKD-1	45.67	75.00	51.27	53.00	271.7	149.8
TD-1	29.67	60.67	41.13	59.67	151.5	142.0
Mean	41.56	42.37	44.13	46.82	232.22	111.61
Range	30.0-73.3	32.0-75.0	37.2-51.3	32.2-53.0	151.5-273.0	77.3-149.8
% RD	-	+1.91	-	+6.09	-	-51.94
$LSD_{0.05}$ Irrigations	N.S		2.45		19.77	
$LSD_{0.05}$ Cultivars	6.00		5.48		44.20	
$LSD_{0.05}$ Irrig.× Cv.	8.486		7.75		62.50	

R.D. % = Relative difference in percentage i.e. decrease (-) or increase (+) in 65% drought-stress treatments, Irrig. = Irrigated, Cv. = Cultivars, DS = Drought stress

Table 3: Mean values of relative water content (RWC) and grain yield per plant (g) of drought tolerant and susceptible spring wheat cultivars under irrigated and drought stress conditions

Cultivars	Relative water content		Grain yield per plant (g)	
	Irrigated	65% DS	Irrigated	65% DS
Anmol	79.23	53.18	3.279	2.543
Bhittai	77.53	58.64	3.113	2.934
Kiran	78.57	39	2.811	2.144
Marvi	87.32	34.33	3.017	2.004
Mehran	78.48	40.37	3.257	2.769
Moomal	83.1	58.54	3.207	2.977
Pavan	79.12	56.94	3.143	2.536
Sarsabz	77.81	57.2	3.509	2.496
SKD-1	88.56	43	2.457	2.377
TD-1	85.13	40.67	2.770	2.399
Mean	81.48	48.19	3.030	2.540
Range	77.53-88.56	39.0-85.64	2.457-3.51	2.004-2.98
%RD		-40.86		-16.17
$LSD_{0.05}$ Irrigations	3.321		0.401	
$LSD_{0.05}$ Cultivars	7.43		0.20	
$LSD_{0.05}$ Irrig. × Cv.	10.502		Ns	

R.D. % = Relative difference in percentage i.e. decrease (-) or increase (+) in 65% drought-stress treatments, Irrig. = Irrigated, Cv. = Cultivars, DS = Drought stress

Table 4: Correlation coefficients (r) between physiological and yield traits in spring wheat cultivars

Parameter	Stomatal dimension	Stomatal conductance	Relative water content	Grain yield per plant
Stomatal density	0.31*	0.16	-0.10	-0.14
Stomatal dimension		0.07	-0.33**	-0.36**
Stomatal conductance			0.62**	0.34**
Relative water content				0.48**

**,*, = Significant at $p \le 0.01$ and $p \le 0.05$, respectively under water stress conditions (Quarrie and Jonse, 1977; Moftah and Al-Humaid, 2005). Cultivars were quite variable for stomatal density in drought stress environment and cv. Moomal, Kiran and Bhittai recorded minimum stomatal density suggesting less transpiration rate under drought conditions.

Since plants experience water stress in later stages when sink demand is more active, under such situation, stomatal dimensions become more important to regulate leaf transpiration rate (Praba *et al*., 2009). Here it can be hypothesized that drought tolerant cultivars may have smaller stomatal dimensions than the susceptible ones. The cultivars Sarsabz, Moomal, Anmol and Bhittai recorded less stomatal density and smaller stomatal dimensions, hence may be regarded as drought resistant ones. Mehri *et al*. (2009) evaluated stomatal dimensions in a set of drought tolerant and susceptible wheat cultivars and observed that both stomatal length and area decreased under stress conditions (Spence *et al*., 1986) and such conditions may enhance adaptation to drought stress (Martinez *et al*., 2007). In contradiction to present study findings, Rodiyati *et al*. (2005) found that stomatal aperture did not decrease under water stress conditions. Tanzarella *et al*. (1984) also observed that usually the width and length of the guard cells change very little during stomatal opening whereas an increase in the perimeter of the whole stomatal apparatus occurs.

Stomata density and dimensions were correlated with stomatal conductance and drought stress had significant effect on the stomatal conductance of cultivars tested. The difference in stomatal conductance between cultivars was obvious and more resistance was recorded in the drought tolerant cultivars viz. Bhittai, Moomal and Anmol. From these results, it appears that there is high relevance in at least two attributes i.e., stomatal dimension and stomatal conductance as regards to interaction of the plant with drought. It may be inferred here that cultivars with lower conductance are more drought tolerant. Adjei and Kirkham (1980) found that drought resistant wheat cultivars showed higher stomatal resistance. Jones (1977) reported that although there were large differences in stomatal frequencies, yet the lines had lower conductance at equal leaf water potential due to the changes in stomata size. Similar to present findings, Remy and Walid (2012) observed significant genetic variability among genotypes for transpiration rate and stomatal conductance. Genotypes with less transpiration rate had also less stomatal conductance as found in drought tolerant cultivars.

The RWC had been reported as good indicator of water-stress in leaves (Merah, 2001) and may be used for selection of more reliable drought tolerant wheat genotypes. The cultivars expressed differential response to RWC under drought stress. On an average, a considerable reduction was noticed due to drought stress and in consonance with these results. Ashinie *et al*. (2011) reported that water-deficit conditions inflicted 36.7% decrease in RWC. The maximum RWC however was recorded in drought tolerant cultivars Bhittai, Moomal, and Sarsabz. This indicates that susceptible cultivars such as Marvi, TD-1 and SKD-1 have less water retention potential than tolerant cultivars. Farquhar *et al*. (1989) stated that RWC is closely related with cell volume, hence closely reflects the balance between water supply to the leaf and its transpiration rate. Jones *et al.* (1989) suggested that RWC improves the ability of a plant to recover from stress and consequently produces higher grain yield and also enhances yield stability (Siddique *et al*., 2000).

Although grain yield of cultivars decreased substantially under drought stress and minimum reduction was observed in the cv. Bhittai, Mehran, Moomal, Pavon and Anmol, consequently gave higher yields under drought conditions. The interaction between irrigation × cultivar was non-significant which suggested that tolerant cultivars could reliably be selected and successfully grown in drought environments.

The significant and positive associations between stomatal density and stomatal dimensions were recorded; nonetheless, stomatal dimension expressed negative association with grain yield and RWC. These results are very important indicating that as the stomatal dimension increases, the leaf RWC content decreases, which may result in more transpiration from bigger stomatal size. When the RWC decreased due to larger stomata, the yield correspondingly decreased in susceptible cultivars under stress conditions. Stomatal conductance and RWC exhibited positive correlations with grain yield suggesting that drought tolerant cultivars maintained more water contents under stress conditions and eventually produced higher yields. Similar to these findings, Jatoi *et al.* (2012b) observed significantly positive correlations between RWC and grain yield under water stress conditions.

In conclusion, relative water content and stomatal conductance are reliable traits that determine rate of transpiration from stomata and serve as determinants for drought tolerance in wheat. Using these indicators, cultivars Anmol, Moomal, Bhittai and Sarsabz proved to be drought tolerant, hence can reliably be used in further breeding programs.

References

Adjei, G.B. and M.B. Kirkham, 1980. Evaluation of winter wheat cultivars for drought resistance. *Euphytica*, 29: 255–260

Ashinie, B., T. Kindie and G. Tilahun, 2011. Morphological and physiological attributes associated to drought tolerance of Ethiopian durum wheat genotypes under water deficit condition. *J. Biodiversity Environ. Sci*., 1: 22–36

Baodi, D., L. Mengyu, S. Hongbo, L. Quanqi, S. Lei, D. Feng and Z. Zhengbin, 2008. Investigation on the relationship between leaf water use efficiency and physio-biochemical traits of winter wheat under *rained* condition. *Colloids Surf. B. Biointerfaces*, 62: 280–287

Bergmann, D.C., 2004. Integrating signals in stomatal development. *Curr. Opin. Plant Biol*., 7: 26–32

Bilagi, S.A., D.I. Jirali, M.B. Chetti, S.M. Hiremath and B.N. Patil, 2008. Biophysical, biochemical parameters and their association with yield in dicoccum wheat genotypes. *Karnataka J. Agric. Sci*., 21: 176–180

Blum, A., 1988. *Plant Breeding for Stress Environments*. CRC Press, Boca Raton, Florida, USA

Del-Blanco, I.A., S. Rajaram and W.E. Kronstad, 2001. Agronomic potentials of synthetic hexaploid wheat-derived populations. *Crop Sci*., 41: 670–676

Dreccer, M.F., M.G. Borgognone, F.C. Ogbonnaya, R.M. Trethowan and B. Winter, 2007. CIMMYT-selected derived synthetic bread wheat for rainfed environments: yield evaluation in Mexico. *Field Crops Res*., 100: 218–228

Duan, L., C. Guan, J. Li, A.E. Eneji, Z. Li and Z. Zhai, 2008. Compensative effects of chemical regulation with uniconazole on physiological damages caused by water deficiency during the grain filling stage of wheat. *J. Agron. Crop Sci*., 194: 9–14

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

Farquhar, G.D., S.C. Wong, J.R. Evans and K.T. Hubic, 1989. Photosynthesis and gas exchange. *In*: *Plants under Stress*, pp: 47–69. Jones, H.J., T.J. Flowers and M.B. Jones (eds.). Cambridge University Press, UK

Galle, A., J. Csiszar, I. Tari and L. Erdei, 2002. Changes in water and chlorophyll fluorescence parameters under osmotic stress in wheat cultivars. *Acta Biol. Szeged*., 46: 85–86

Inagaki, M.N., J. Valkoun and M.M. Nachit, 2007. Effect of soil water deficit on grain yield in synthetic bread wheat derivatives. *Cereal Res. Commun*., 35: 1603–1608

Jatoi, W.A., M.J. Baloch, N.U. Khan, M.B. Kumbhar and M.I. Keerio, 2012a. Genetic analysis of physiological and yield traits under drought stress conditions in wheat. *SABRAO J. Breed. Genet*., 44, 9–27

Jatoi, W.A.M. J. Baloch., M.B. Kumbhar and M.I. Keerio, 2012b. Heritability and correlation studies of morpho-physiological traits for drought tolerance in spring wheat. *Pak. J. Agric., Agril. Eng., Vet. Sci*., 28: 100–114

Jones, H.G., 1977. Aspects of water relations of spring wheat (*T. aestivum* L.) in response to induced drought. *J. Agric. Sci*., 88: 267–282

Jones, H.G., T.J. Flowers and M.B. Jones, 1989. '*Plants under Stress*'. Cambridge University Press, Cambridge, UK

Khan, A.S., S.U. Ullah and S. Sadique, 2010. Genetic variability and correlation among seedling traits of wheat (*T. aestivum* L.) under water stress. *Int. J. Agric. Biol*., 12: 247–250

Khokar, M.I. and J.A. Teixeira da Silva, 2012. Evaluation of drought tolerance and yield capacity of barley (*Hordeum vulgare*) genotypes under irrigated and water-stressed conditions. *Pak. J. Agric. Sci*., 49: 307–313

Ludlow, M.M. and R.C. Muchow, 1990. A critical evaluation of traits for improving crop yields in water limited environments. *Adv. Agron*., 43: 107–153

Maherali, H., C.D. Reid, H.W. Polley, H.B. Johnson and R.B. Jackson, 2002. Stomatal acclimation over a sub-ambient to elevated CO_2 gradient in a C3/C4 grassland. *Plant Cell Environ*., 25: 557–566

Martinez, J.P., H. Silva, J.F. Ledent and M. Pinto, 2007. Effect of drought stress on the osmotic adjustment, cell wall elasticity and cell volume of six cultivars of common beans (*Phaseolus vulgaris* L.). *Eur. J. Agron*., 26: 30–38

Mehri, N., R. Fotovat, J. Saba and F. Jabbari, 2009. Variation of stomata dimensions and densities in tolerant and susceptible wheat cultivars under drought stress. *J. Food Agric. Environ*., 7: 167–170

Merah, O., 2001. Potential importance of water status traits for durum wheat improvement under Mediterranean conditions. *J. Agric. Sci*., 137: 139–145

Moftah, A.E. and A.R.I. Al-Humaid, 2005. Effects of anti-transpirants on water relations and photosynthetic rate of cultivated tropical plant (*Polianthes tuberosa* L.). *Pol. J. Ecol*., 53: 165–175

Nadeau, J.A. and F.D. Sack, 2002a. Control of stomatal distribution on the Arabidopsis leaf surface. *Science*, 296: 1697–1700

Nadeau, J.A. and F.D. Sack, 2002b. Stomatal development in Arabidopsis. *In*: *The Arabidopsis Book.* Somerville, C.R. and E.M. Meyerowitz (eds.). American Society Plant Biology, Rockville, Maryland, USA

Praba, M.L., J.E. Cairns, R.C. Babu and H.R. Lafitte, 2009. Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. *J. Agron. Crop Sci*., 195: 30–46

Quarrie, S.A. and H.G. Jonse, 1977. Effects of abscisic acid and water stress on development and morphology of wheat. *J. Exp. Bot*., 28: 192–203

Rajaram, S., 2001. Prospects and promise of wheat breeding in the 21st century. *Euphytica*, 119: 3–15

Rashidi, M. and K. Seyfi, 2007. Effect of water stress on crop yield and yield components of cantaloupe. *Int. J. Agric. Biol.*, 9: 271–273

Rauf, M., M. Munir, M. Hassan, M. Ahmed and M. Afzai, 2007. Performance of wheat genotypes under osmotic stress at germination and early seedling growth stage. *Afr. J. Biotechnol*., 8: 971–975

Remy, S. and S. Walid, 2012. Differential sensitivities of transpiration to evaporative demand and soil water deficit among wheat elite cultivars indicate different strategies for drought tolerance. *Environ. Exp. Bot.*, 84: 1–10

Richards, R.A., 2006. Physiological traits used in the breeding of new cultivars for water-scarce environments. *Agric. Water Manage*., 80: 197–211

Rodiyati, A., E. Arisoesilaningsih, Y. Isagi and N. Nakagoshi, 2005. Responses of *Cyperus brevifolius* (Rottb.) Hassk. And *Cyperus kyllingia* Endl. to varying soil water availability. *Environ. J. Exp. Bot*., 53: 259–269

Schonfeld, M.A., R.C. Johnson, B.F. Carver and D.W. Mornhinweg, 1988. Water relations in winter wheat as drought resistant indicator. *Crop Sci*., 28: 526–531

Siddique, M.R.B., H. Hamid and M.S. Islam, 2000. Drought stress effects on water relations of wheat. *Bot. Bull. Acad. Sci*., 41: 35–39

Spence, R.D., H. Wu, P.J.H. Sharpe and K.G. Clark, 1986. Water stress effects on guard cell anatomy and the mechanical advantage of the epidermal cells. *Plant Cell Environ*., 9: 197–202

Tanzarella, O.A., C.D. Pace and A. Filippetti, 1984. Stomatal frequency and size in *Vicia faba* L. *Crop Sci*., 24: 1070–1076

Turner, N.C., 1986. Crop water deficits: a decade of progress. *Adv. Agron*., 39: 1–51

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