

IMPACT OF FOLIAR APPLIED GLYCINEBETAINE ON GROWTH AND PHYSIOLOGY OF WHEAT (*Triticum aestivum* L.) UNDER DROUGHT CONDITIONS

Muhammad Aown Sammar Raza^{1,*}, Muhammad Farrukh Saleem², Moazzam Jamil¹ and Imran Haider Khan²

¹University College of Agriculture & Environmental Sciences, The Islamia University of Bahawalpur, Pakistan;

²Department of Agronomy, University of Agriculture, Faisalabad, Pakistan

*Corresponding author's e.mail: aown_samar@yahoo.com

Drought is the major abiotic limiting factor for healthy crop growth. Glycinebetaine applied under drought mitigates the adverse effect of drought and improved the plant's tolerance. The present investigation was conducted to find out the response of wheat (*Triticum aestivum* L.) cultivars (Lasani-2008, Auqab-2000) under water deficit conditions to exogenous application of 100 mM glycinebetaine at different growth stages, Zadoks GS 22, GS 60 and GS 73, representing tillering, flower initiation and grain filling stages, respectively. The objective was to find out the best glycinebetaine (GB) application stage for mitigating the negative effect of drought stress on wheat plants. During investigation various growth traits (plant height, spike length, number of spikelets per spike, number of grains per spike, 1000-grain weight and grain yield per plant) and physiological parameters (water potential, osmotic potential and turgor potential) of crop were recorded using standard procedures. Drought stress at all three critical growth stages adversely affected ($P < 0.05$) all the growth, yield and physiological components of wheat plant. The exogenous application of GB at all three critical growth stages improved the drought tolerance of plants and improved the growth, yield and physiological performance of wheat, however, grain filling stage was found more responsive.

Keywords: Wheat, water stress, glycinebetaine, physiological traits, growth and yield

INTRODUCTION

Different abiotic factors affect the growth and yield of the crop plants. Water condition is one of the major abiotic factors that reduce the growth as well as yield of a plant (Souza *et al.*, 2004; Kusvuran, 2012; Saensee *et al.*, 2012). Water deficit occurs in regions of low rainfall, and most wheat is cultivated in such semi arid regions (Deng *et al.*, 2004). A combination of the environmental stresses as heat and drought affects the crop growth simultaneously. Therefore, solely a stress applied in controlled conditions may not correlate well with those in natural conditions (Mittler, 2006). Wheat is one of the most important crops grown in most regions of the world as a staple food (CIMMYT, 1996). Drought stress highly affects the growth and yields of wheat genotypes which results in impaired growth of the plants (Raza *et al.*, 2012a). Under drought, various physiological, biochemical and molecular changes occur in plants to thrive under drought stress (Arora *et al.*, 2002). Various adaptive (resistance) mechanisms in the plants have been developed under water stress conditions to survive under unfavorable conditions. Glycinebetaine (GB), a quaternary ammonium compound, is produced in the plants of many crop species which increases the tolerances of the plant to drought (Raza *et al.*, 2012b), the plants with greater ability of its accumulation under stress are more tolerant (Monyo *et al.*, 1992). Application of this compound

increased the tolerance of the plants under varying level of drought stress by improving or by maintaining the photosynthetic rate of the plants and by protecting chloroplast and thylakoid lamella (Wang *et al.*, 2010). Glycinebetaine spray under drought stress improved the physiological efficiency of plants (Raza *et al.*, 2012b). Plants treated with the spray of 100 mM glycinebetaine had a higher net photosynthetic rate during drought stress than non-GB treated plants.

Results reviewed in this section indicate that under water limited conditions, plant's drought tolerance can be improved by the sufficient supply of GB. However, no work is reported about the timing of GB application. Present study aims at comparative performance of wheat cultivars when given drought stress and sprayed with GB at different critical growth stages.

MATERIALS AND METHODS

Experiment description: The experiment was carried out during 2008-09 in pots (wire house) at Nuclear Institute for Agriculture and Biology (NIAB), Faisalabad, Pakistan (latitude = 31°N, longitude = 73°E, and an altitude of 184.4 meters above the sea level). Physico-chemical analysis of the experimental soil is shown in Table 1.

Table 1. Characteristics of the soil used in experiment.

Characteristics	values
Nitrogen (mg kg ⁻¹ dry soil)	0.33
Phosphorous ((mg kg ⁻¹ dry soil)	4.9
Potassium (mg kg ⁻¹ dry soil)	125
Calcium (mg kg ⁻¹ dry soil)	101
Organic matter (%)	0.83
pH	7.7
Sand (%)	22
Silt (%)	13
Clay (%)	65

Ten seeds were sown per pot, each containing 7 kg dry soil and after 14 days of germination; plants were thinned to four plants per pot. Drought stress was created by withholding irrigation at different growth stages viz. Zadoks GS 22, GS 60 and GS 73, representing tillering, flower initiation and grain filling stages, respectively on two wheat cultivars; Lasani-2008 and Auqab-2000. Glycinebetaine at 100 mM was sprayed with carboxymethyl cellulose (5% solution) as a sticking agent, whereas Tween-20 (0.1% solution) was used as a surfactant for foliar spray. The application/drought induction was scheduled as; T₀ (no drought and no GB spray), T₁ (drought at tillering stage without GB spray), T₂ (drought at tillering stage with GB spray), T₃ (drought at flower initiation stage without GB spray), T₄ (drought at flower initiation stage with GB spray), T₅ (drought at grain filling stage without GB spray) and T₆ (drought at grain filling stage with GB spray). The experiment was laid out in completely randomized design (CRD) with factorial arrangement and replicated thrice.

Agronomic and yield component traits: At maturity the height of the ten plants was measured with a meter rod from base to tip of the spike and average was worked out for each

plant. Length of ten spikes from each treatment was measured with meter rod and average was calculated. Spikes were removed from 10 selected plants in each treatment then number of spikelets was counted and average was worked out. Number of grains per spike was counted manually. Grains from 10 spikes were collected and then calculated as average number of grains per spike. The samples of thousand grains from each treatment were taken at random and weighed in grams. The total number of ears per plant were threshed and weighed in grams and average was worked out to determine the grain yield per plant. Total weight of sun-dried samples was recorded for each treatment. After threshing, grain weight was subtracted from total weight to calculate straw weight.

Physiological attributes: The fully expanded youngest leaf of two plants of each treatment was used to determine the leaf water potential. The measurements were made from 8.00 to 10.00 a.m. with Scholander type Pressure Chamber. The selected leaf, used to determine water potential, was put in a freezer below -20°C for seven days. The frozen leaf material was then thawed and cell sap extracted with the help of a disposable syringe. The sap so extracted was directly used for the determination of osmotic potential using an osmometer (Wescor 5500). The turgor potential (Ψ_p) is the difference between osmotic potential (Ψ_s) and water potential (Ψ_w) values. So it was calculated as (Ψ_p) = (Ψ_w) - (Ψ_s)

RESULTS

Glycinebetaine application under drought at each growth stage of wheat affected the plant height of the both varieties significantly. The statistical results (Table 1) regarding the plant height indicate that both the varieties Lasani-2008 and

Table 1. Effect of glycinebetaine spray on wheat growth and yield under drought condition

Treatments	Plant height (cm)	Spike length (cm)	Spikelets per spike	Grains per spike	1000-grain weight (g)	Grain yield per plant (g)
T ₀	75.67 a	9.55 a	14.00 a	30.00 a	41.92 a	1.24 a
T ₁	68.50 bc	7.83 d	11.49 c	21.00 e	38.14 b	0.70 d
T ₂	72.73 a	8.78 bc	13.03 b	27.00 b	40.90 ab	0.92 bc
T ₃	65.63 c	7.10 e	10.78 d	18.50 f	26.92 d	0.51 e
T ₄	69.29 b	8.31 cd	11.48 c	24.00 c	32.74 c	0.87 c
T ₅	73.03 a	8.82 bc	11.28 cd	22.50 d	24.57 d	0.47 e
T ₆	73.80 a	8.97 ab	13.32 ab	29.00 a	39.25 ab	1.01 b
LSD	3.02	0.61	0.77	1.44	3.18	0.13
Meaningful Orthogonal Contrasts						
Drought vs. no drought	*	*	*	*	*	*
K vs. no K	NS	NS	NS	*	*	*

* = Significant, NS = Non-significant.

Means not sharing the same letters within a column differ significantly at 5% probability.

T₀ = Control (no drought no GB spray), T₁ = Drought at Zadoks GS-22 (tillering) without GB spray, T₂ = Drought at Zadoks GS-22 (tillering) with GB spray, T₃ = Drought at Zadoks GS-60 (flowering) without GB spray, T₄ = Drought at Zadoks GS-60 (flowering) with GB spray, T₅ = Drought at Zadoks GS-73 (grain filling) without GB spray, T₆ = Drought at Zadoks GS-73 (grain filling) with GB spray.

Auqab-2000 showed the same behavior to the GB application. Among drought treatments, maximum plant height (73.80 cm) was achieved by the GB applied under drought at grain filling stage (T_6), while minimum plant height (65.63 cm) was obtained at grain filling stage with no spray of GB under drought. Impact of drought was also significant on plant height. The well watered (control- T_0) plants gained the maximum plant height (75.67 cm). The drought stress reduced the plant height of both the varieties, however this reduction was significant ($P < 0.05$) when stress was created either at vegetative or at flowering stage and was non-significant ($P > 0.05$) when drought was employed at grain filling stage. Variety means showed that drought resistant variety (Lasani-2008) performed better and gave significantly more plant height than drought sensitive variety (Auqab-2000). The varieties and GB interaction was non-significant (Table 1).

Production potential of wheat is determined by its spike length. More the size of the spike more will be the grains number per spike causing high yield and vice versa. Well watered plants gave maximum spike length (9.55 cm). Data (Table 1) indicates that exogenously applied GB improved the spike length in the plants which were kept under drought; more spike length was recorded on the plants applied with GB at grain filling stage (T_6). Deficit water significantly restricted the spike length. The minimum spike length (7.10 cm) was observed when the plants were given drought stress at flowering stage (T_3). Varieties expressed non-significant behavior to spike length. Interactive effect of varieties and treatments was also non-significant (Table 1).

Spikelets number per spike is economically important component of the crop and significantly affected by GB. It improved the number of spikelets per spike under drought stress (Table 1). After the well watered plants (T_0), more number of spikelets per spike was obtained in plants treated by GB under drought at grain filling stage (T_6) than all other treatments except well watered plants (T_0). The lowest number of spikelets was observed in plants which were given water stress at flowering stage and no GB was sprayed. Varieties did show non-significant effect on the parameter under discussion. Varieties vs GB interaction was also non-significant (Table 1).

Glycinebetaine effect was significant on the grains per spike. Its spray under drought improved the number of grains per spike (Table 1). Among drought stressed treatments, the maximum grain number was obtained in plants treated with GB at grain filling stage (T_6) and minimum was observed in plants which were given water stress at flowering stage and no GB was sprayed. Varieties vs GB interaction was non-significant (Table 1). The 1000-grain weight plays a significant role in the final yield of the

wheat. The data (Table 1) showed that drought stress adversely affected the thousand grain weight of wheat. The lowest grain weight was recorded with stress at grain filling stage; however it was at par with the treatment where drought was faced at flowering stage. Glycinebetaine application significantly improved the 1000-grain weight of wheat; although crop gained maximum 1000-grain weight in control treatment (no drought), however it was at par with the treatment where crop faced drought at vegetative or at grain filling stage but GB was applied at these stages while minimum was recorded in case of T_5 (Drought at grain filling stage without GB spray). Both the varieties behaved non-significantly. The interaction was also non-significant (Table 1).

Grain yield is major factor contributing to the economic yield of the crop. Well watered plants (T_0) produced highest grain yield (Table 1). Drought created at any stage (T_1 , T_3 and T_5) significantly reduced grain yield and application of GB at any stage failed to make up this reduction. However, comparison of T_1 vs T_2 , T_3 vs T_4 and T_5 vs T_6 indicated that GB application at any critical crop growth stage significantly increased wheat grain yield. Comparing the efficiency of GB spray at different growth stages (T_2 vs T_4 vs T_6) indicated that maximum grain yield was produced when GB was applied under stress at grain filling stage (T_6). Among all treatments means, minimum grain yield was recorded in T_5 where crop faced drought at grain filling stage and no GB was applied, however it was at par with T_3 (drought at flowering stage and no GB). Varieties showed non-significant behavior; interaction ($T \times V$) was also non-significant (Table 1).

Analyzed data regarding leaf water potential (Figs. 1 & 2) showed that drought stress affected leaf water potential (-MPa) and osmotic potential (-MPa) of both wheat varieties. More negative leaf water potential and osmotic potential was recorded under water deficit conditions than the control at all growth stages (Fig. 1 & 2). Moreover exogenous applications of GB reduced the negative effect of drought on water potential and osmotic potential of plant at each growth stage (Figs. 1 & 2).

Drought stress badly affected leaf turgor potential (MPa) as indicated in (Fig.3). Leaf turgor potential was high under stress (T_0) and was less under drought stress at any growth stage. Exogenous applications of GB at different growth stages (vegetative, flowering and grain filling) ameliorated the negative impact of drought on leaf turgor potential, however more improvement in turgor potential was achieved with its spray at grain filling stage (T_6) and was minimum when crop had not received any GB spray with drought at grain filling growth stage (T_5).

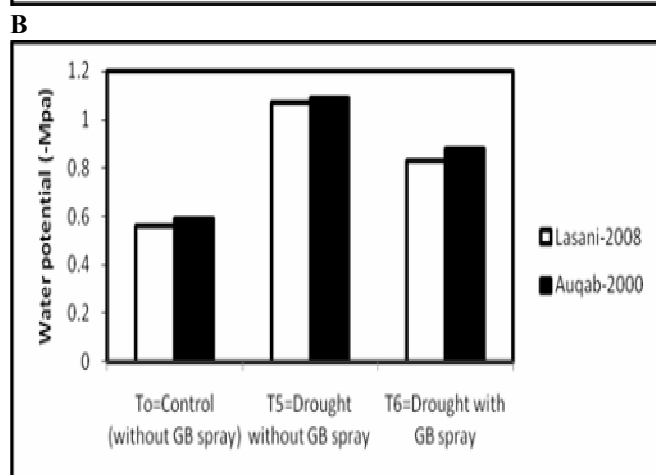
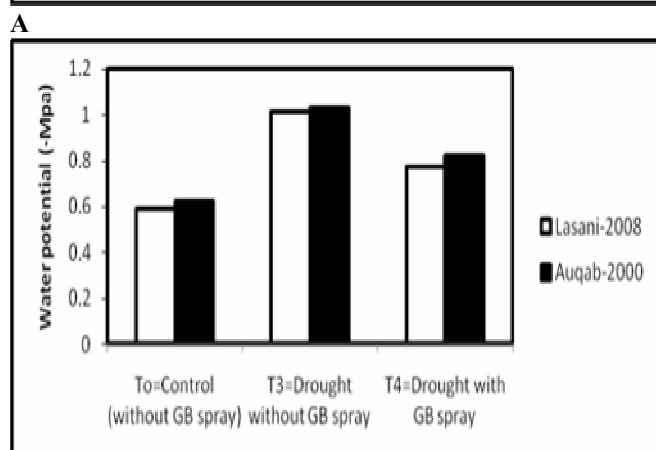
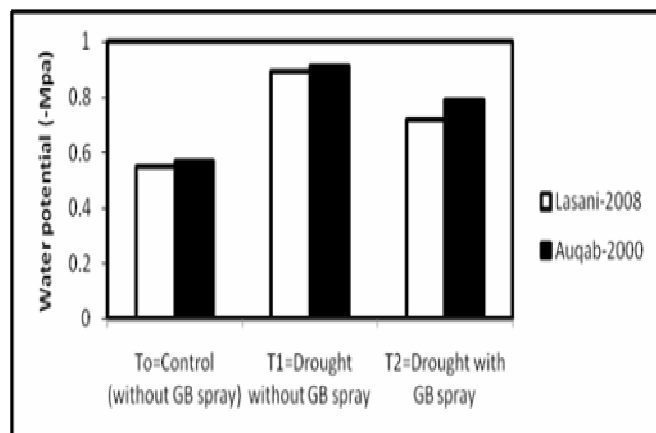


Figure 1. Effect of glycinebetaine (GB) application on water potential (-MPa) of wheat varieties under drought at (A) tillering stage, (B) flowering stage, (C) grain filling stage.

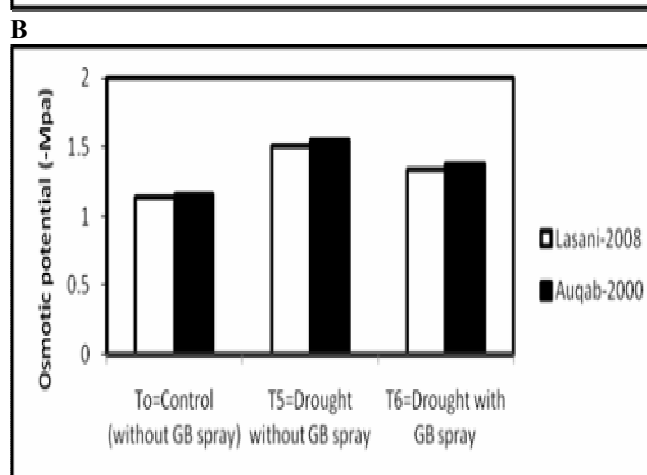
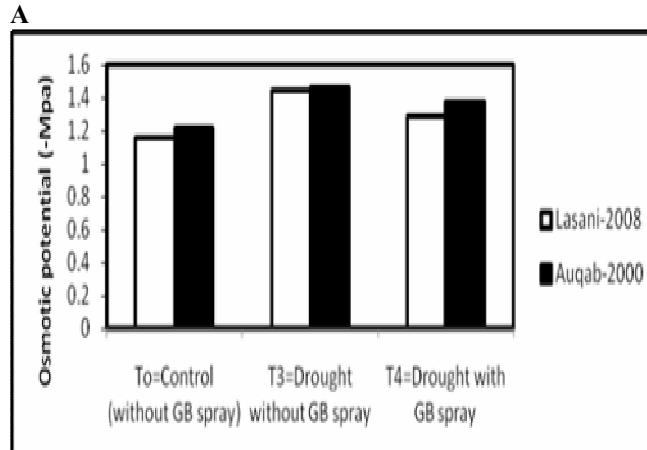
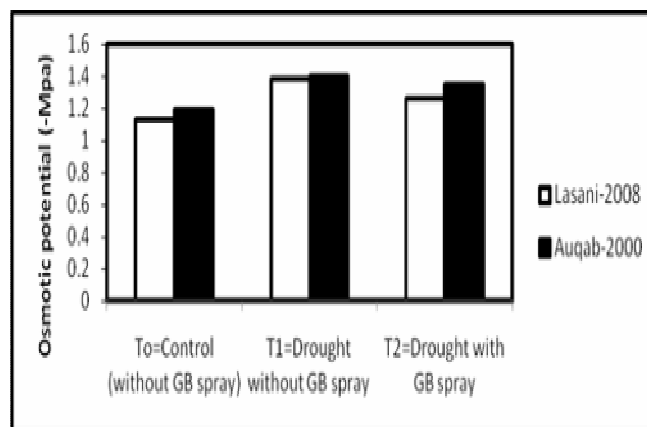


Figure 2. Effect of glycinebetaine (GB) application on osmotic potential (-MPa) of wheat varieties under drought at (A) tillering stage, (B) flowering stage, (C) grain filling stage.

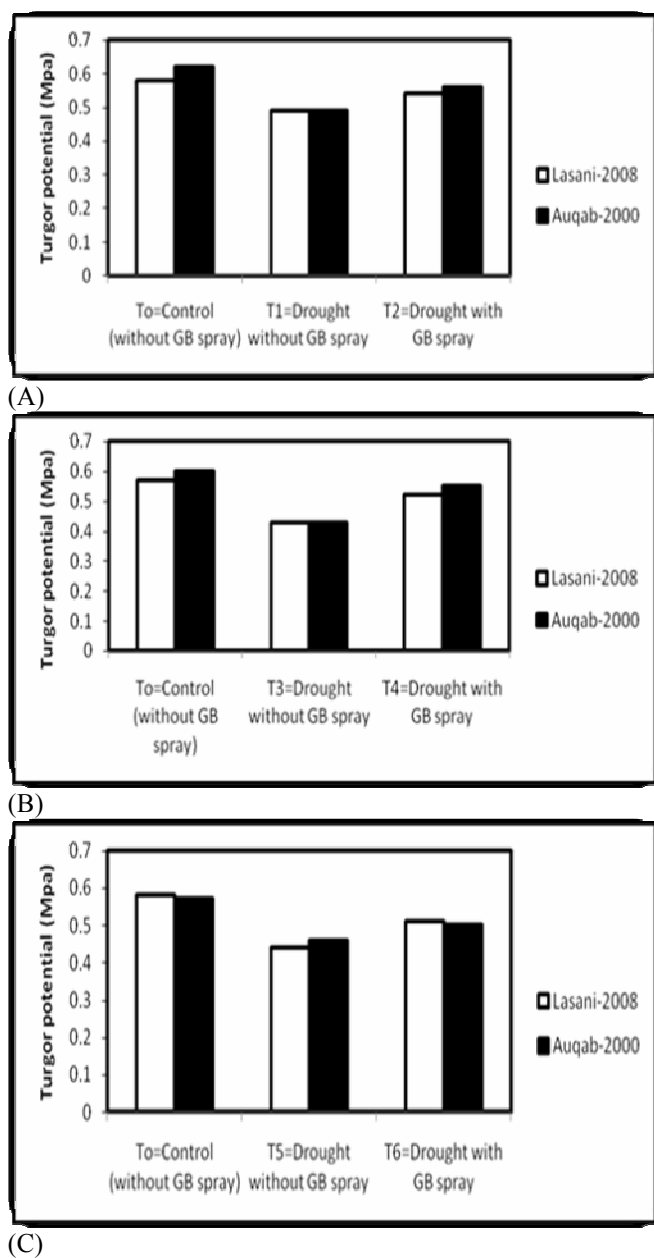


Figure 3. Effect of glycinebetaine (GB) application on turgor potential (MPa) of wheat varieties under drought at (A) tillering stage, (B) flowering stage, (C) grain filling stage.

DISCUSSION

Although varieties in present experiment were selected on the basis of relative drought tolerance by conducting a preliminary screening experiment in laboratory under controlled conditions; however results indicate similar response of both varieties to GB and drought which prove

that none of our varieties can withstand drought condition under natural growing conditions.

Drought stress significantly affected crop growth and development causing decrease in the final yield of wheat which was improved by exogenous application of GB on either growth stage (vegetative, flowering and grain filling). Drought stress, either at vegetative or at flowering stage, reduced the plant height; while the more detrimental effect of water deficit was observed at flowering stage which reduced it by 13.26% than control treatment. During vegetative stage the growth is that of the leaves and tillers mainly, whilst the stem elongates very slowly and it gains its maximum height at the time of onset of floral initiation (Arnon, 1972a). El-Monayeri *et al.* (1984) and Duwayri (1984) observed that drought stress affected the plant height of wheat. The reduction may be due to dehydration of protoplasm, less relative turgidity associated with turgor loss and decreased cell expansion and cell division (Arnon, 1972b). The exogenous spray of glycinebetaine (GB) under water deficit improved the plant height both at vegetative as well as at flowering stage. Because GB proved to increase the tolerance of plant to adverse environmental conditions (Cherian *et al.*, 2006). A marked increase of 5.81% was recorded in plant height of wheat due to GB application under drought at vegetative stage than drought stress imposed without GB spray at same stage in the present study.

Drought stress adversely affected spike length, number of spikelets per spike, number of grains per spike, 1000-grain weight and grain yield of wheat plant. Drought stress at tillering, flowering and grain filling stages reduced wheat crop growth. A marked reduction in ear length, number of spikelets per spike and number of grains per spike (25.65%, 23% and 38.33%, respectively) was recorded by drought stress at flowering stage while more reduction in 1000-grain weight (41.38%) and grain yield (62.09%) was recorded when drought occurred at grain filling stage. Reduced ear length was observed under water deficit by Giunta *et al.* (1993). The reduced ear length at anthesis was due to reduced number of nodes and less node to node distance on the rachis. Maximum decrease in spikelets per spike under drought at flowering stage was reported by Guerra (1995). Reduced spikelets per spike under drought at flowering stage may be due to reduced root growth about the time of spike formation (Hendrix, 1994). Taiz and Zeiger (1991) reported that reduced number of spikelets per ear might be the result of limited photosynthetic activity before spike emergence because spikelets per spike are determined before spike emergence. Reduction in 1000-grain weight and grains per spike due to water stress can be related with decreased photosynthesis. Drought stress reduced photosynthates production and its translocation to reproductive organs (grains) (Asch *et al.*, 2005). Decreased 1000-grain weight under water deficit was reported by Iqbal *et al.* (1999) at

flowering stage and at heading was reported by Khannachopra *et al.* (1994) which might be due to less efficient plant nutrient uptake and limited photosynthetic translation; this hastens maturity and produced shriveled kernels. 1000-grain weight was reduced under drought at flowering (anthesis stage) than at vegetative stage (Sinaki *et al.*, 2007). Drought reduced the leaf area for radiation interception which are photosynthetically active and ultimately resulted in reduced 1000-grain weight, grain yield, number of grains per spike and all yield contributing components (Brisson and Casals, 2005). Final grain yield of wheat depends on its efficient use of water (Sun *et al.*, 2006). Normal water at flowering increased photosynthetic rate and also enhanced duration of grain filling (Zhang *et al.*, 1998), thus improving grain size and ultimately grain yield. Reduced grain yield per plant may be because of disorder in the remobilization of the assimilates from source to mature grain (sink) that resulted in short and shriveled kernels or it may be due to grain weight and grain growth pattern and its position between and within the spikelets that under drought stress showed assimilate limitation (Aggarwal and Sinha, 1984). Drought stress impaired grain yield more, when it occurred at flowering stage (Iqbal *et al.*, 1999). Ravichandran and Mungse (1995) and Ashraf (1998) also observed decreased grain yield per plant under drought stress at flowering stage. The flowering stage proved to be the most sensitive to water deficit and produced the decreased grains per spike (Dornescu, 1983) and less number of flowers to set seed. Drought stress restrained grain yield by decreasing photosynthates due to disturbed ET (evapotranspiration) which contribute in grain yield. Water deficit reduced growth and yield of crops by reducing photosynthesis and chlorophyll contents (Asada, 1999). The difference in ear length in different varieties was due to their genetic makeup (Iqbal *et al.*, 1999). Response of both the varieties (Lasani-2008 and Auqab-2000) under drought was different, Lasani-2008 tolerate much under drought stress than Auqab-2000. Rafiq (2004) concluded the similar results. The extent of tolerance of the wheat crop to water stress may depend on its genetic makeup (Collahu *et al.*, 2002; Collahu *et al.*, 2005). Drought tolerant wheat plants (Nayyar and Walia, 2003) accumulated higher amount of such compounds than the sensitive cultivars.

Water deficit stress either at flowering or grain filling stage lowered the water potential; due to this equal decrease in osmotic potential occurred. This decrease was because of the accumulation of solutes in plant cell (Serraj and Sinclair, 2002). Drought stress at flowering and grain filling stages of wheat considerably reduced leaf turgor pressure. Leaf turgor potential decreased due to reduction in water potential of leaf. Siddique *et al.* (2000) concluded a loss in relative water contents (RWC) of the leaf and leaf water potential, which had significant effect on photosynthesis under water deficit conditions. Similarly Yadave *et al.* (2005) reported the

reduction in total leaf area of the sorghum under drought. Water deficit might be due to reduced turgor adversely affecting leaf expansion, thus the assimilatory surface of the crop is also reduced. The adverse effect of drought stress on plant could be mitigated by conserving water by increase in root penetration, partial closing of stomata and reduction in transpiration (Alfredo and Setter, 2000; Hoad *et al.*, 2001). Different compatible solutes are produced in response to stress conditions (Serraj and Sinclair, 2002). These compatible solutes include glycinebetaine, sugar, polyols, proline and sucrose (Rhodes and Hanson, 1993). These are highly soluble due to their low molecular weight and at high cellular concentration these are non-toxic. Due to these compatible solutes, plants adopt mechanism to resist stress conditions by different ways including stabilization of enzymes, osmotic adjustment and protection of membrane integrity (Bohnert and Jensen, 1996). These solutes also play a role as osmo-protectant by protecting cellular components from dehydration injury. Under drought stress (lower leaf water potential) biosynthesis of glycinebetaine enhanced which finally improved its concentration in leaf (Zhu, 2002; Wahid and Close, 2007). Agboma *et al.* (1997) reported that exogenous application of GB protected the photosynthetic machinery in wheat, maize and sorghum, thereby enhancing the final crop yield. Exogenous application of GB in turnip rape plants improved net photosynthesis and reduced photorespiration under salt and drought stress (Makela *et al.*, 1998). GB spray at flowering stage improved the 1000-grain weight and number of grains per spike through increased photosynthesis by maintaining leaf turgor potential under deficit water. GB improved water deficit tolerance of the plant by maintaining internal water balance (turgor pressure) (Agboma *et al.*, 1997). Serraj and Sinclair (2002) concluded that accumulation of compatible solutes (GB) was increased in plants under drought due to stress resistance mechanism (osmotic adjustment). The GB also increased leaf turgor potential by anchoring enzymes, functional proteins and lipids and maintained thylakoid membrane and electron flow through it (Allakhverdiev *et al.*, 2003). Varietal differences for parameters relevant to leaf water relation were non significant; however, Liu and Li (2005) commented that leaf RWC under water deficits were improved by low transpiration rate due to which the growth and physiological activities of drought resistant genotypes of wheat were ultimately enhanced as compared to drought sensitive.

Conclusion: Drought stress at any critical growth stage of crop negatively affected the physiological performance and reduced the growth and yield of wheat. Foliar application of GB at all critical stages improved the physiological efficiency and all the yield components with grain filling stage being more responsive. On the basis of this experiment

it is recommended that GB is effective if sprayed under drought stress condition.

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REFERENCES

- Agboma, P., M.G.K. Jones, P. Peltonen-Sainio, H. Rita and E. Pehu. 1997. Exogenous glycinebetaine enhances grain yield of maize, sorghum and wheat grown under two watering regimes. *J. Agron. Crop Sci.* 178:29-37.
- Agrawal, P.K. 1986. Seed vigor: Concepts and Measurements. In: J.P. Srivastava and L.T. Simarsk (eds.), *Seed Production Technology* ICARDA, Aleppo, Syria. pp.190-198.
- Alfredo, A.C.A. and T.L. Setter. 2000. Response of cassava to water deficit: Leaf area growth and abscisic acid. *Crop Sci.* 40: 131-137.
- Allakhverdiev, S.I., H. Hayashi, Y. Nishiyama, A.G. Ivanov, J.A. Aliev, V.V. Klimov, N. Murata and R. Carpentier. 2003. Glycinebetaine protects the D1/D2/Cytb559 complex of photosystem II against photo-induced and heat-induced inactivation. *J. Plant Physiol.* 160:41-49.
- Arnon, I. 1972a. Crop production in dry regions. In: N. Polunin (ed.) Vol. 1. Leonard Hill Book, London, pp.203-211.
- Arnon, I. 1972b. Crop production in dry regions. In: N. Polunin N (ed.) Vol. 2. Leonard Hill Book, London, pp.11-19.
- Arora, A., R.K. Sairam and G.C. Srivastava. 2002. Oxidative stress and antioxidative systems in plants. *Curr. Sci.* 82:1227-1238.
- Asch, F., M. Dingkuhn, A. Sow and A. Audebert. 2005. Drought induced changes in rooting patterns and assimilate partitioning between root and shoot in upland rice. *Field Crop Res.* 3:223-236.
- Ashraf, M.Y. 1998. Yield and yield components response of wheat (*Triticum aestivum* L.) genotypes grown under different soil water deficit conditions. *Acta Agronomica Hungarica* 46:45-51.
- Blum, A., B. Sinmena and O. Ziv. 1980. An evaluation of seed and seedling drought tolerance screening tests in wheat. *Euphytica* 29:727-736.
- Bohnert, H.J. and R.G. Jensen. 1996. Strategies for engineering water-stress tolerance in plants. *Trends Biotechnol.* 14: 89-97.
- Brisson, N. and M.L. Casals. 2005. Leaf dynamics and crop water status throughout the growing cycle of durum wheat crops grown in two contrasted water budget conditions. *Agron. Sustain. Dev.* 25:151-158.
- Christen, O., K. Sieling, H. Richterharder and H. Hanus. 1995. Effect of temporary water stress before anthesis on growth, development and grain yield of spring wheat. *Eur. J. Agron.* 321/A: 27-36.
- CIMMYT. 1996. CIMMYT 1995-96 world wheat facts and trends: understanding global trends in the use of wheat diversity and international flows of wheat genetic resources. Mexico, DF.
- Collahu, A. and S.A Harrison. 2005. Heritability of waterlogging in wheat. *Crop Sci.* 45:722-727.
- Collahu, A. and S.A. Harrison. 2002. Losses in wheat due to water logging. *Crop Sci.* 42:444-450.
- Deng, X., L. Shan, S. Inanaga and M. Inoue. 2004. Water-saving approaches for improving wheat production. *J. Sci. Food Agric.* 85(8):1379-1388.
- Dornescu, A. 1983. Effect of yield components in winter wheat variety Fundulea 29. *Agronomie* 27:39-42.
- Duwayri, M. 1984. Comparison of wheat cultivars grown in the field under different levels of moisture. *Cereal Res. Commun.* 12: 27-34.
- El-Monayeri, A., M. Hagazi, N.H. Ezzat, H.M. Salem and M. Tohaun. 1984. Growth and yield of some wheat and some barley varieties grown under different moisture stress levels. *Ann. Agric. Sci.* 20:231-243.
- 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.
- Hendrix, D.L., J.R. Mauney, B.A. Kimball, K. Lewin, J. Nagy and G.R. Hendry. 1994. Influence of elevated CO₂ and mild water stress on nonstructural carbohydrates in field-grown cotton tissues. *Agric. For. Meteorol.* 170:153-162.
- Hoad, S.P., G. Russell, M.E. Lucas and I.J. Bingham. 2001. The management of wheat, barley and oats root systems. *Adv. Agron.* 74:193-246.
- Iqbal, M., K. Ahmad, M. Sadiq and M.Y. Ashraf. 1999. Yield and yield components of durum wheat as influenced by water stress at various growth stages. *Pak. J. Biol. Sci.* 2:11-14.
- Kusvuran, S. 2012. Influence of drought stress on growth, ion accumulation and antioxidative enzymes in okra genotypes. *Int. J. Agric. Biol.* 14: 401-406.
- Khanna-Chopra, R., V.M. Sujata, M. Maheswari, S. Amita and D. Bahukhandi. 1994. K⁺, osmoregulation and drought tolerance- an overview. *Proc. Ind. Natl. Sci. Acad. B.* 61: 51-56.
- Liu, H.S. and F.M. Li. 2005. Root respiration, photosynthesis and grain yield of two spring wheat in response to soil drying. *Plant Growth Regul.* 46:233-240.
- Makela, P., K. Jokinen, M. Kontturi, P. Peltonen-Sainio, E. Pehu and S. Somersalo. 1998. Foliar application of glycinebetaine- a novel product from sugar beet as an

- approach to increase tomato yield. *Indust. Crops Prod.* 7:139-148.
- Mittler, R. 2006. Abiotic stress, the field environment and stress combination. *Trends in Plant Sci.* 11:15-19.
- Monyo, E.S., G. Ejeta and D. Rhodes. 1992. Genotypic variation for glycinebetaine in sorghum and its relationship to agronomic and morphological traits. *Media* 37:283-286.
- Moustafa, M.A., L. Boersma and W.E. Kronstad. 1996. Response of four spring wheat cultivars to drought stress. *Crop Sci.* 36:982-986.
- Nayyar, H. and D.P. Walia. 2003. Water stress induced proline accumulation in contrasting wheat genotypes as affected by calcium and abscisic acid. *Biol. Plant.* 46:275-279.
- Rafiq, M., A. Hussain, A. Ahmad, S.M.A. Basra, A. Wajid, J. Anwar, M. Ibrahim and M.A. Goheer. 2005. Effect of irrigation on agronomic traits of wheat (*Triticum aestivum* L.). *Int. J. Biol. Biotech.* 3:751-759.
- Ravichandran, V. and H.B. Mungse. 1995. Effect of moisture stress on leaf development, dry matter production and grain yield in wheat. *Plant physiology* 9:117-120.
- Raza, M.A.S., M.F. Saleem, I.H. Khan, M. Jamil, M. Ijaz and M.A. Khan. 2012a. Evaluating the drought stress tolerance efficiency of wheat (*Triticum aestivum* L.) cultivars. *Russian J. Agric. Socio-Economic Sci.* 12: 41-46.
- Raza, M.A.S., M.F. Saleem, M.Y. Ashraf, A. Ali and H.N. Asghar. 2012b. Glycinebetaine applied under drought improved the physiological efficiency of wheat (*Triticum aestivum* L.) plant. *Soil Environ.* 31(1):67-71.
- Rhodes, D. and A.D. Hanson. 1993. Quaternary ammonium and tertiary sulfonium compounds in higher plants. *Annu. Rev. Pl. Physiol. Pl. Mol. Biol.* 44: 357-384.
- Saensee, K., T. Machikowa and N. Muangsan. 2012. Comparative performance of sunflower synthetic varieties under drought stress. *Int. J. Agric. Biol.* 14: 929-934.
- Serraj, R. and T.R. Sinclair. 2002. Osmolyte accumulation: can it really help increase crop yield under drought conditions? *Plant Cell Environ.* 25:333-341.
- Shalaby, E.M., H.M.A. El-Rahim, M.G. Mosaad and M.M. Masoud. 1988. Effect of watering regime on morpho-physiological traits and harvest index and its components of wheat. *Assiut J. Agric. Sci.* 19:195-207.
- Siddique, M.R.B., A. Hamid and M.S. Islam. 2000. Drought stress effects on water relations of wheat. *Bot. Bull. Acad. Sin.* 41:35-39.
- Sinaki, J.M., E.M. Heravan, A.H.S. Rad, G. Noormohammadi and G. Zarei. 2007. The effect of water deficit during growth stages of canola. *American-Eurasian J. Agric. Environ. Sci.* 2:417-422.
- Souza, R.P., E.C. Machado, J.A.B. Silva, A.M.M.A. Lagoa and J.A.G. Silveira. 2004. Photosynthetic gas exchange, chlorophyll fluorescence and some associated metabolic changes in cowpea (*Vigna unguiculata*) during water stress and recovery. *Environ. Exp. Bot.* 51:45-56.
- Sun, Y.H., C.M. Liu, X.Y. Zhang, Y.J. Shen and Y.Q. Zhang. 2006. Effects of irrigation on water balance, yield and water use efficiency (WUE) of winter wheat in North China plain. *Agric. Water Manage.* 85: 211-218.
- Taiz, L. and E. Zeiger. 1991. *Plant Physiology*. New York: Benjamin/Cummings.
- Wahid, A. and T.J. Close. 2007. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biol. Plant.* 51:104-109.
- Wang, L.J., L. Fan, W. Loescher, W. Duan, G.J. Liu and J.S. Cheng. 2010. Salicylic acid alleviates decreases in photosynthesis under heat stress and accelerates recovery in grapevine leaves. *BMC Plant Biol.* 10: 34.
- Yadav, S.K., N.J. Lakshmi, M. Maheswari, M. Vanaja and B. Venkateswarlu. 2005. Influence of water deficit at vegetative, anthesis and grain filling stages on water relation and grain yield in sorghum. *Indian J. Plant Physiol.* 10:20-24.
- Zhang, H., T. Oweis, S. Garabet and M. Pala. 1998. Water use efficiency and transpiration efficiency of wheat under rain-fed and irrigation conditions in mediterranean environment. *Plant Soil* 201: 295-305.
- Zhu, J.K. 2002. Salt and drought stress signal transduction in plants. *Ann. Rev. Plants Physiol. Plant Mol. Biol.* 53: 247-273.