

Influence of heat stress on growth and physiological activities of potato (*Solanum tuberosum* L.)

Influencia del estrés por temperatura en las actividades de crecimiento y fisiológicas de papa (*Solanum tuberosum* L.)

Naz N¹, F Durrani¹, Z Shah², NA Khan¹, I Ullah¹

Abstract. The progress and development of crops like potato are harmfully affected by increased heat stress throughout the world. Stress caused by increased heat adversely affects germination and seedling growth which result in a reduced crop development and yield. The present research was carried out to know the influence of heat stress on growth indices and physiological processes of potato (*Solanum tuberosum* L.). The heat stresses C- Control (25 °C); T1-45 °C, and T2-40 °C were applied in separate growth chambers to the plants, after 25 days from their germination. Increased heat stress considerably decreased the chlorophyll *a* and *b* pigments of potato plants. Increased heat stress reduced the growth of potato and resulted in a major reduction of the leaf relative water content, leaf fresh weight and leaf dry weight of potato. Proline and soluble sugar concentrations were evidently enhanced in potato plants when they were associated with increased heat stress.

Keywords: *Solanum tuberosum*; Proline; Relative water content; Soluble sugar.

Resumen. El progreso y desarrollo de las cosechas como la papa son afectadas negativamente por un incremento del estrés por temperatura en todo el mundo. El estrés causado por un incremento de la temperatura afecta negativamente la germinación y el crecimiento de las plántulas lo cual resulta en un menor desarrollo y rendimiento de los cultivos. La presente investigación se condujo para conocer la influencia del estrés por temperatura en los índices de crecimiento y procesos fisiológicos de la papa (*Solanum tuberosum* L.). Los estreses por temperatura: T1- 45 °C y T2-40 °C se aplicaron a las plantas en cámaras de crecimiento separadas, después de 25 días desde la germinación. El tratamiento control se estableció en 25 °C. Un mayor estrés por temperatura disminuyó considerablemente los pigmentos clorofila *a* y clorofila *b* en las plantas de papa. Un mayor estrés por temperatura redujo el crecimiento de las plantas de papa y resultó en una gran reducción del contenido de agua relativo foliar, y de los pesos fresco y seco de las plantas de papa. Las concentraciones de prolina y azúcares solubles evidentemente aumentaron en las plantas de papa cuando ellas estuvieron expuestas a un mayor estrés por temperatura.

Palabras clave: *Solanum tuberosum*; Prolina; Contenido de agua relativo; Azúcares solubles.

¹ Department of Botany University of Science and Technology Bannu KP, Pakistan.

² Department of Biotechnology University of Science and Technology Bannu KP, Pakistan.

Address correspondence to: Noor Ahmad Khan, e-mail: shahnoor1asad1@gmail.com

Received 19.XII.2017. Accepted 5.VII.2018

INTRODUCTION

Potato (*Solanum tuberosum* L.) is a member of the Solanaceae family, and is widely grown in Pakistan. The land of Pakistan is mostly very fertile and suitable for potato growth. However, the temperature of that area exceeds the limits required for its growth. Mostly, potato crops grow under 16-30 °C although they might grow up to 35 °C. It is considered an important vegetable crop in Pakistan. The baskets of vegetables of Pakistan are incomplete without potato. It means it is among one of the major food crops after rice and wheat. It is widely used as a vegetable for its high nutritional value in Pakistan. There is a high quantity of protein and edible energy in potato, and due to this quality potato is mostly used as a food source in Pakistan. Therefore, potato is a good source to contribute to the nutritional security of the nation (Ahmed et al., 2012).

When plants are treated with heat stress, alterations occur at a molecular level which cause changes in appearance of genes and accretion of transcripts. Therefore, the plants produce stress-related proteins to tolerate the stressful situations such as heat shock proteins (Iba, 2002). Nowadays, it is concluded that sugarcane leaves have three dehydrins with low molecular weight, which are produced in large quantity against heat stress (Wahid & Close, 2007). Turf grass adapted to heat produce fewer amount of reactive oxygen species (ROS) due to the rapid formation of ascorbic acid and glutathione as compare to non-adapted cool season turf grass (Xu et al., 2006). Stress produced by heat breaks up the chemical bonds of the cell membrane and denatures proteins of the membrane (Savchenko et al., 2002). Even when plants are exposed to low or moderate heat stress, the sink and source activities are reduced resulting in low growth rate and reduced crop yield (Taiz & Zeiger, 2006). Shoot dry weight, relative water content and total uptake rate in maize are significantly decreased; however, the leaf area of sugarcane is affected in a small amount under high heat stress (Wahid, 2007). Cell membrane becomes more permeable and mesophyll cells are severely destructed under heat stress in *Vitis vinifera* (grapes) (Zhang et al., 2005). Changes in different characteristics of photosynthesis under heat stress are the clear indicators of heat tolerance because they have a correlation with growth. A decrease in photosynthesis causes limited plant growth under heat stress. Photochemical reactions in the thylakoid membranes, and carbon metabolism in the stroma, are primarily injured under high heat stress (Wise et al., 2004). In grapes plants, the chloroplasts of mesophyll cells become rounded, stromal lamella becomes swollen, and the vacuole forms a mass, while the mitochondria becomes empty by disrupting its cristae. Such alterations cause reductions in photosynthesis and respiration (Zhang et al., 2005).

High temperature stress badly affects internal anatomy at tissue and cellular level as well as at sub-cellular level. All such changes under heat stress cause reduced plant growth and productivity. Glycinebetaine (GB) is produced under dif-

ferent stresses such as Salinity or heat stress, which acts as a good solute in plants under such stressful situations (Sakamoto & Murata, 2002). Under stress situations the capability of GB production varies from species to species (Ashraf & Foolad, 2007). For instance, GB is produced in large quantity in maize (Quan et al., 2004) and sugarcane due to heat stress (Wahid & Close, 2007). In other kinds of plants such as mustard (*Brassica* spp.), rice (*Oryza sativa*), tobacco (*Nicotiana tabacum*) and *Arabidopsis* (*Arabidopsis thaliana*) GB is also produced. Another important protein is proline accumulated in high amounts in plants under normal ecological stresses (Kaviraj Kishore et al., 2005). Proline and GB production buffer the redox potential of cells on ecological stresses such as heat (Wahid & Close, 2007). Under heat stress, an increase of soluble sugar content occurs in sugarcane plants, which involves a greater insinuation for heat tolerance (Wahid & Close, 2007). Heat stress situations negatively affect the plant water status when there is scarcity of water (Machado & Paulsen, 2001). Reduction of water availability is due to an increased temperature stress (Simoes-Araujo et al., 2003). Secondary metabolites are formed as a result of primary carbon metabolism (Wahid & Ghazanfar, 2006). Similarly, severe heat stress situations enhance the formation of phenolic compounds. Phenylalanine ammonia-lyase (PAL) is said to be an important and main enzyme of the phenylpropanoids pathway. In response to heat stress, there is an increased activity of PAL as a cell reaction to such stress. Heat stress enhances the production of phenolics and inhibits their oxidation, which activate the adaptation processes to heat stress such as in watermelon *Citrullus vulgaris* (Rivero et al., 2001). Time of flowering up to seed set is increased by heat stress (Wheeler et al., 2000). High night temperature adversely affected the photosynthesis in rice plants resulting in a 10% reduction of yield because of a 1 °C rise in temperature (Peng et al., 2004). In case of corn, 29 °C temperature increased the yield; 30 °C temperature increased the yield in soybean, and 32 °C temperature increased the yield in cotton (Smith et al., 2008).

As a result of human activities, there has been an increase in the CO₂ levels, and a global air temperature increase. Because of this, the physiological and morphological functions of plants have been adversely affected. The world temperature is increasing due to increase in CO₂ levels and other gasses in the atmosphere due to human activities, which have adversely affected the plants and other organism's normal life (Houghton et al., 2001). In the absence of heat stress situations, the net photosynthetic rate and biomass have been shown to increase in C₄ species (Ghannoum et al., 2000). The most adverse effect of heat stress on plants is the destruction of the photosynthetic activity of the plant, in which the (PSII) of the light reaction (Heckathorn et al., 2002) and the RUBISCO activase enzymes of the dark reaction are mostly impaired (Crafts-Brandner & Salvucci 2002). However, at an optimum temperature increase, an elevated CO₂ level has a good effect

on plants. At heat stress, an elevated CO₂ level can also have a positive (Taub et al., 2000), negative (Taub et al., 2000) or good effect on C₃ species, and an adverse effect on C₄ species for photosynthesis and growth (Wang et al., 2008).

Aims and objectives. The main objectives of the project were: (1) to investigate the effect of heat stress on growth and physiology of potato, and (2) to determine the mechanism of heat stress tolerance of potato by analyzing soluble sugar content and proline.

MATERIALS AND METHODS

Plant material. Similar size seeds (Tubers) of *Solanum tuberosum* L. were obtained from the Agricultural Research Centre, Sarai Naurang District Lakki Marwat KPK, Pakistan. Seeds (Potato tubers) were sown in plastic pots (8 × 12 cm) filled with a combination of clay soil and sand (100:100) under growth chamber conditions in the Department of Botany, University of Science and Technology, Bannu.

Plant growth conditions and heat stress. After 24 days of germination all pots of potato plants were kept in the growth chamber at three different temperatures: Control 25 °C; T₁–45 °C, and T₂–40 °C. After 24 hours all plants were harvested and analyzed for the following parameters.

Morphological parameters. Analysis of plant growth was performed by observing the fresh weight (FW) and dry weight (DW) of leaf tissues using a digital balance. The DW was taken by treating the plant materials with heat at 50 °C for 48 h in a hot air oven.

Physiological parameters.

Relative water content (%). The following formula was used to determine the leaf relative water content (%; RWC) according to the method of Gao (2000):

$$\text{RWC} = \frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}} \times 100$$

where FW: Fresh weight, TW: Turgid weight and DW: Dry weight.

Photosynthetic pigments. Chlorophyll concentration was calculated according to the Arnon technique (1949). Extraction of chlorophyll was performed using 80% acetone; the absorbance of the chlorophyll extract was measured at 663 and 645 nm. Leaf tissue (0.1 g) was dissolved in 80% acetone using a mortar and pestle. The centrifugation was made at 1200 x g. for 10 min to get a homogenate of plant tissues. Again the 80% acetone was used to re-homogenize the pellet. The process was repeated until the formation of a colourless pellet. The absorbance of the supernatant, at 663 and 645 nm, was measured by a UV-visible spectrophotometer.

Proline concentration. The method of Bates et al. (1973) was applied to measure the proline concentration. Fresh leaf samples of 0.5 g were placed in a mortar containing 10 mL of 3% sulfosalicylic acid. Leaf samples were grinded with a pestle and filtered through filter paper into test tubes. Two mL of the filtrate were taken to another test tube, and then 2 mL of glacial acetic acid and ninhydrin reagent were added, respectively. Then a water bath was used to boil the samples at 100 °C for one hour. After heating, the samples were allowed to cool down on ice, and then 4 mL of toluene were added and shaken to produce two layers. The upper layer was then collected, and its absorbance was measured at 520 nm wavelength using a spectrophotometer.

Soluble sugar concentration. Soluble sugars were determined based on the method of Dubois (1956). For this purpose, fresh leaf samples of 0.5 g were taken into a test tube containing 10 mL of 80% ethanol. Leaf samples were heated in a water bath for 1 hour at 80 °C. Half a mL of this leaf extract was taken into a test tube having distilled water (0.5 mL) and 1 mL of phenol (18%). Samples were then incubated at room temperature for one hour. Finally, 2.5 mL sulphuric acid were added to the samples, shaken and measured the optical density at 490 nm using a spectrophotometer.

Statistical analysis. One-way ANOVA was used for statistical analysis, and the least significant difference (LSD) test (Steel & Torrie 1984) was used to compare treatment means. The software used to conduct the statistical analyses was Statistics (version 8.1 USA).

RESULTS

In our investigations, the leaf fresh and dry weights of potato were significantly reduced after exposure to both temperatures (T₁ and T₂) of heat stress over the control. The increase of heat stress reduced the fresh and dry weights of potato as compared to the control (Table 1). Similarly, the relative water content of potato showed an evident decrease, when it was exposed to an increased heat stress as compared to the control (Table 1). It was also clear from the results of Figure 1 that proline was accumulated in higher amounts in those potato plants that were exposed gradually to an increased heat stress over the control. It showed that an increased heat stress exhibited a higher amount of proline in potato plants. Figure 2 showed that the production of soluble sugars in potato plants was markedly increased as heat stress (T₁ and T₂) also increased over the control. Figure 3 showed that the photosynthetic pigment chlorophyll *a* exhibited a very clear reduction when potatoes were exposed to a higher heat stress gradually (T₁ and T₂) over the control. Figure 4 also showed that the chlorophyll *b* concentration of potato was significantly reduced when it was exposed to high heat stresses as compared to the control.

Table 1. Influence of heat stress on leaf relative water content, leaf fresh weight and leaf dry weight of potato. Treatments: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Tabla 1. Influencia del estrés por temperatura en el contenido relativo de agua y los pesos fresco y seco foliares. Tratamientos: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Treatments	RWC (%)	Leaf fresh weight (g)	Leaf dry weight (g)
C: 25 °C	35.543 ± 0.341 a	0.37 ± 0.082 a	0.12 ± 0.024 a
T1 45 °C	15.521 ± 0.031 c	0.23 ± 0.023 c	0.06 ± 0.007 c
T2 40 °C	23.113 ± 0.039 b	0.27 ± 0.029 b	0.09 ± 0.009 b

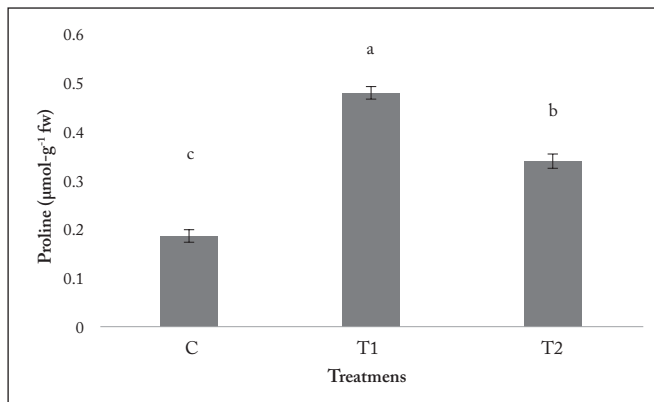


Fig. 1. Influence of heat stress on accumulation of proline in potato. Different letters represent statistical differences among treatments. Treatments: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Fig. 1. Influencia del estrés por temperatura en la acumulación de prolina en papa. Letras diferentes representan diferencias estadísticas entre tratamientos. Tratamientos: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

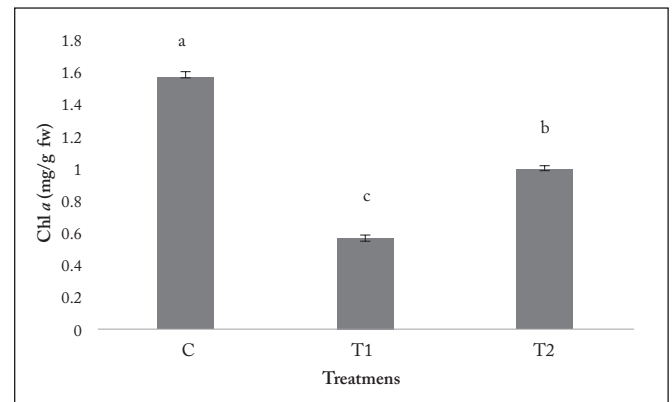


Fig. 3. Influence of heat stress on chlorophyll a concentration in potato. Different letters represent statistical differences among treatments. Treatments: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Fig. 3. Influencia del estrés por calor en la concentración de clorofila a en papa. Letras diferentes representan diferencias estadísticas entre tratamientos. Tratamientos: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

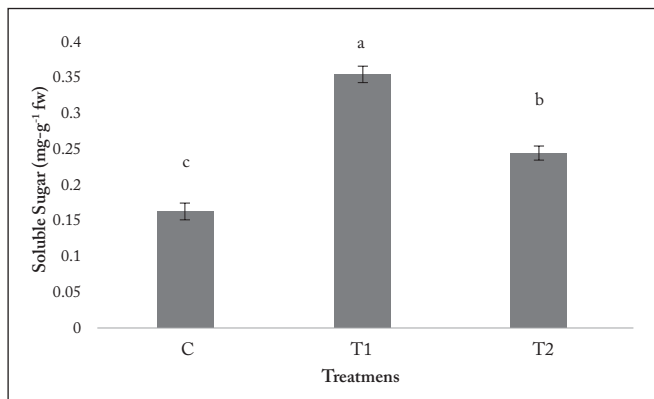


Fig. 2. Influence of heat stress on soluble sugar concentration in potato. Different letters represent statistical differences among treatments. Treatments: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Fig. 2. Efecto del estrés por temperatura en la concentración de azúcares solubles en papa. Letras diferentes representan diferencias estadísticas entre tratamientos. Tratamientos: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

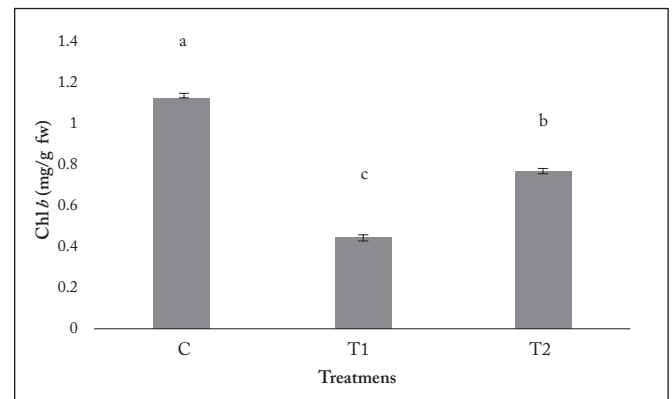


Fig. 4. Influence of heat stress on chlorophyll b concentration in potato. Different letters represent statistical differences among treatments. Treatments: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

Fig. 4. Influencia del estrés por temperatura en la concentración de clorofila b en papa. Letras diferentes representan diferencias estadísticas entre tratamientos. Tratamientos: C= Control (25 °C); T₁= 45 °C; T₂= 40 °C.

DISCUSSION

In our study, leaf fresh and dry weights of potato were evidently decreased by the high temperature stress (Table 1); potato plants were very sensitive to a very high temperature stress. These results agree with previous findings of Watkinson et al. (2006), who reported that high temperature stress reduced the fresh and dry weights of plants. During our experiment, the relative water content of potato was also significantly reduced by increased heat stress over the control (Table 1). These results also support the findings presented by Mane et al. (2008). These authors reported that relative water content in plants was expressively reduced by severe drought and heat stresses; therefore, drought and heat stresses are said to have a key role in water deficit of plants. Figure 1 showed that proline accumulation was directly proportional to increases in heat. Accumulation of proline has significantly increased with increases in heat stress conditions. These results are in agreement to previous work presented by Teixeira and Pereira (2006), who showed that proline accumulation enhanced in response to drought stress conditions in potato plants. High heat stress (45 °C) resulted in 0.5% proline accumulation in potato leaves as compared to the control (0.2%). The lowest heat stress (40 °C) also resulted in the accumulation of proline by up to 0.3% in potato leaves over the control (0.2%). During our experiment, the accumulation of proline at higher temperatures increased to avoid damage of plants by ROS. These results are similar to previous findings of Timlin et al. (2006). These researchers reported that high amounts of proline were produced in wheat plants when they were exposed to a high temperature stress. Results in Figure 2 represent that leaf soluble sugar concentrations of potato significantly increased at higher heat stress in comparison to controls. Saltmarsh et al. (2006) also indicated that soluble sugar contents increased in *Cladium mariscus* when it was exposed to drought stress. Izanloo et al. (2008) also reported accumulation of sugar content under drought stress, which is responsible for osmotic functions, turgidity and stabilizing of cell membranes. In our findings sugar concentration of potato leaves was improved up to 0.36% at the higher temperature (45 °C) stress, and 0.25% at the lower temperature (40 °C) stress over the control (0.16%) in leaves of potato. These results are also in favor of earlier works of Nosrati et al. (2014). These authors reported that sugar content is enhanced by water stress in canola cultivars. Results presented in Figure 3 and 4 showed that photosynthetic pigments chlorophyll *a* and *b* were significantly reduced by increasing temperature stress as compared to the control. Similar findings were reported by Camejo et al. (2005). These authors indicated that photosynthetic pigments of tomato were adversely affected by exposure to higher temperature stress. Chlorophyll *a* concentration decreased down to 0.6% and 1% at 45 °C and 40 °C, respectively, as compared to the control (1.6%). Chlorophyll *b* concentration was reduced up to 0.4% and 0.7% at 45 °C and 40 °C, respectively, as compared to the control at 25 °C

(1.6%). This decline might be due to the damage of chloroplast structure. Our results are in agreement with earlier works by Kumar et al. (2012). These authors reported that high temperature stress resulted in reduced chlorophyll *a* and *b* contents of rice, when they were treated with high temperature stress. In our experiments, high temperature stress resulted in a decreased concentration of chlorophyll *a* and *b* on potato. These results obviously show that chlorophyll damage is directly linked with the sensitivity of potato plants to a high temperature stress with respect to their chlorophyll contents. These results are similar to previous findings of Jagtap et al. (1998), who reported that chlorophyll content declined in *Sorghum bicolor*. L. when it was exposed to a high temperature stresses.

ACKNOWLEDGMENTS

The main basis, chemicals used in experiments and lab facilities for this research work were arranged by Doctor Neelofar Naz and co-workers especially Noor Ahmad Khan. The Laboratory of Plant Sciences, Department of Botany, University of Science and Technology Bannu and Department of Biotechnology University of Science and Technology Bannu provided the facilities for this research work. We acknowledge the Father of Neelofar Naz, Mr, Umer Daraz Khan, and also Mr. Maqsood Khan, partner of Doctor Neelofar Naz, for their support in this project.

REFERENCES

- Ahmad, M., M. Rafiq & A. Ali (2012). An analysis of technical efficiency of potato farmers in Pakistani Punjab. *The Bangladesh Journal of Agricultural Economics* 22: 79-86.
- Arnon, D.I. (1949). Copper enzyme in isolated chloroplasts polyphenol oxidase in *Beta vulgaris*. *Journal of Plant Physiology* 24: 1-5.
- Ashraf, M. & M.R. Foolad (2007). Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany* 59: 206-216.
- Bates, L., R.P. Waldren & I.D. Teare (1973). Rapid determination of free proline for water-stress studies. *Plant and Soil* 39: 205-207.
- Camejo, D., P. Rodríguez, M.A. Morales, J.M. Dell'Amico, A. Torrecillas & J.J. Alarcon (2005). High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *Journal of Plant Physiology* 162: 281-289.
- Crafts-Brandner, S.J. & M.E. Salvucci (2002). Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. *Plant Physiology* 129: 1773-1780.
- Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers & F. Smith (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28: 350-356. doi:10.1021/ac60111a017.
- GAO, F. (2000). Experimental technology in plant physiology. World Books Publishing Company, China.
- Ghannoum, O., S. von Caemmerer, L.H. Ziska & J.P. Conroy (2000). The growth response of C4 plants to rising atmospheric CO₂ partial pressure: a reassessment. *Plant Cell & Environment* 23: 931-942.

- Heckathorn, S.A., S.L. Ryan, J.A. Baylis, D.F. Wang, E.W. Hamilton, L. Cundiff & J.T. Houghton (2001). *Climate Change 2001: The Scientific Basis*, Cambridge Univ. Press, New York.
- Iba, K. (2002). Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. *Annual Review of Plant Biology* 53: 225-245.
- Izanloo, A., A.G. Condon, P. Langridge, M. Tester & T. Schnurbusch (2008). Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. *Journal of Experimental Botany* 59: 3327-3346.
- Jagtap, V., S. Bhargava, P. Streb & J. Feierabend (1998). Comparative effect of water, heat and light stress on photosynthetic reaction in *Sorghum bicolor* L. Moench. *Journal of Experimental Botany* 49: 1715-1721.
- Kavi Kishore, P.B., S. Sangam, R.N. Amrutha, P.S. Laxmi, K.R. Naidu, K.R.S.S. Rao, S. Rao, K.J. Reddy, P. Theriappan & N. Sreenivasulu (2005). Regulation of proline biosynthesis, degradation, uptake and transport in higher plants: its implications in plant growth and abiotic stress tolerance. *Current Science* 88: 424-438.
- Machado, S. & G.M. Paulsen (2001). Combined effects of drought and high temperature on water relations of wheat and sorghum. *Plant Soil* 233: 179-187.
- Mane, S.P., C.V. Robinet, A. Ulanov, R. Schafleitner, L. Tincopa & A. Gaudin (2008). Molecular and physiological adaptation to prolonged drought stress in the leaves of two Andean potato genotypes. *Functional Plant Biology* 35: 669-688. doi: 10.1071/FP07293.
- Nosrati, S., M.G. Zanjan & D.E. Asli (2014). Fluctuations of proline concentration and soluble sugars content affected drought stress in canola (*Brassica napus* L.) seedlings. *Journal of Applied Science and Agriculture* 9: 497-502.
- Peng, S., J. Huang, J.E. Sheehy, R.C. Laza, R.M. Visperas, X. Zhong, G.S. Centeno, G.S. Khush & K.G. Cassman (2004). Rice yield decline with higher night temperature from global warming. In: E.D. Redona, A.P. Castro & G.P. Llanto (eds.), pp. 46-56. *Rice Integrated Crop Management: Towards a RiceCheck system in the Philippines*, Nueva Ecija, Philippines, PhilRice.
- Quan, R., M. Shang, H. Zhang, Y. Zhao & J. Zhang (2004). Engineering of enhanced glycine betaine synthesis improves drought tolerance in maize. *Plant Biotechnology Journal* 2: 477-486.
- Ranjee, R., L. Kumar, G. Suneha, K. Sushil, L. Sharma, S. Khushboo, L. Kritika, A. Gadpayle, L. Narender Kumar, K. Gyanendra, L. Manorama Singh & D. Raj (2012). Protection against heat stress in wheat involves change in cell membrane stability, antioxidant enzymes, osmolyte, H₂O₂ and transcript of heat shock protein. *International Journal of Plant Physiology and Biochemistry* 4: 83-91.
- Rivero, R.M., J.M. Ruiz, P.C. García, L.R. López-Lefebvre, E. Sánchez & L. Romero (2001). Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. *Plant Science* 160: 315-321.
- Sakamoto, A. & N. Murata (2002). The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. *Plant Cell Environment* 25: 163-171.
- Saltmarsh, A. & S. Rambal (2006). Contrasted effects of water stress on leaf functions and growth of two emergent cooccurring plant species, *Cladium mariscus* and *Phragmites australis*. *Aquatic Botany* 84: 191-198.
- Savchenko, G.E., E.A. Klyuchareva, L.M. Abrabchik & E.V. Serdyuchenko (2002). Effect of periodic heat shock on the membrane system of etioplasts. *Russian Journal Plant Physiology* 49: 349-359.
- Smith, S., N. Golborne, L. Gohar, J. Lowe & J. Davey (2008). Building a low-carbon economy – the UK's contribution to tackling climate change: Chapter 1 Technical Appendix: Projecting global emissions, concentrations and temperatures. The Stationary Office, Norwich, UK.
- Steel, R.G.D. & J.H. Torrie (1984). *Principles and procedures of statistics* (2nd Ed.). M.C Graw Hill Book Co; Singapore. pp. 172-177.
- Taiz, L. & E. Zeiger (2006). *Plant Physiology*. Sinauer Associates Inc. Publishers, Massachusetts.
- Taub, D.R., J.R. Seemann & J.S. Coleman (2000). Growth in elevated CO₂ protects photosynthesis against high-temperature damage. *Plant, Cell & Environment* 23: 649-656.
- Teixeira, J. & S. Pereira (2006). High salinity and drought act on an organ-dependent manner on potato glutamine synthetase expression and accumulation. *Journal of Experimental Botany* 60: 121-126.
- Timlin, D., S.M.L. Rahman, J. Baker, V.R. Reddy, D. Fleisher & B. Quebedeaux (2006). Whole plant photosynthesis, development, and carbon partitioning in potato as a function of temperature. *Agronomy Journal* 98: 1195-1203.
- Vara Prasad, P.V., P.Q. Craufurd, R.J. Summerfield & T.R. Wheeler (2000). Effect of short episodes of heat stress on flower production and fruit set of groundnuts (*Arachis hypogaea* L.). *Journal of Experimental Botany* 51: 777-784.
- Wahid, A. (2007). Physiological implications of metabolites biosynthesis in net assimilation and heat stress tolerance of sugarcane sprouts. *Journal of Plant Research* 120: 219-228.
- Wahid, A. & T.J. Close (2007). Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biologia Plantarum* 51: 104-109.
- Wahid, A. & A. Ghazanfar (2006). Possible involvement of some secondary metabolites in salt tolerance of sugarcane. *Journal of Plant Physiology* 163: 723-730.
- Wang, D., S.A. Heckathorn, D. Barua, I.P. Josh, E.W. Hamilton & J.J. Lacroix (2008). Effects of elevated CO₂ on the tolerance of photosynthesis to acute heat stress in C₃, C₄, and CAM species. *American Journal of Botany* 95: 165-176.
- Watkinson, J.I., L. Hendricks, A.A. Sioson, C. Vasquez-Robinet, V. Stromberg, L.S. Heath, M. Schuler, H.J. Bohnert, M. Bonierbale & R. Grene (2006). Accessions of *Solanum tuberosum* ssp. *andigena* show differences in photosynthetic recovery after drought stress as reflected in gene expression profiles. *Plant Science* 171: 745-758.
- Wise, R.R., A.J. Olson, S.M. Schrader & T.D. Sharkey (2004). Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant Cell & Environment* 27: 717-724.
- Xu, S., J. Li, X. Zhang, H. Wei & L. Cui (2006). Effects of heat acclimation pre-treatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turf grass species under heat stress. *Environmental and Experimental Journal of Botany* 56: 274-285.
- Zhang, J.H., W.D. Huang, Y.P. Liu & Q.H. Pan (2005). Effects of temperature acclimation pre-treatment on the ultrastructure of mesophyll cells in young grape plants (*Vitis vinifera* L. cv. Jingxiu) under cross-temperature stresses. *Journal Integrative Plant Biology* 47: 959-970.