



Research Article

Dissecting the Heat Stress Responses and Effects on Morphology of Tomato Varieties Employing Pre-transplant High Temperature Conditioning

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Abstract | An experiment was conducted to investigate the influence of heat pretreatment conditioning durations (control or no heat pretreatment, 10 hrs, 15 hrs and 20 hrs) on three tomato varieties (Roma, Rio Grande and Yaqui) sown at Horticulture Research Farm, Department of Horticulture, The University of Agriculture Peshawar during 2017 and 2018. Completely Randomized Design (CRD) in growth chamber before transplantation and Randomized Complete Block Design (RCBD) with two factors and three replications after transplanting to the field were used. Tomato seedlings at their 4-leaf stage were subjected to a 35°C temperature stress for 10, 15 and 20 hrs as a pre-transplant hardening method. Both groups HP (heat pretreatment) and NHP (Non-heat pretreatment or Control) were then transplanted to the field. Results revealed that different heat pretreatment durations and varieties significantly affected the growth and yield of tomato. Regarding heat pretreatment durations, number of flower clusters plant⁻¹ (16.06), fruit set percentage (68.33%), number of flowers cluster⁻¹ (8.34), chlorophyll content (50.31 SPAD), leaf relative water content (75.34%), Putrescine concentration (193.95 nmol/g), spermidine concentration (154.59 nmol/g), spermine concentration (36.51 nmol/g), yield (20.14 t ha⁻¹), early flowering (26.99 days) and lowest electrolyte leakage (48.87%) was observed in plants treated with 20 hours heat pretreatment duration as compared to other heat pretreatment durations and control. Concerning tomato varieties, number of flower clusters plant⁻¹ (16.99), fruit set percentage (68.25%), number of flowers cluster⁻¹ (7.91), chlorophyll content (48.06 SPAD), leaf relative water content (80.68%), Putrescine concentration (190.25 nmol/g), spermidine concentration (152.57 nmol/g), yield (21.00 t ha⁻¹) and lowest electrolyte leakage (48.86%) was recorded for Rio Grande as compared to Roma and Yaqui. Also highest spermine concentration (35.72 nmol/g) and early flowering (26.72 days) resulted in Roma as compared to Rio Grande and Yaqui. The interaction effects of heat pretreatment duration and varieties were non-significant for most of the attributes studied except chlorophyll content and number of flower clusters plant⁻¹. It can be concluded that heat pretreatment of 35°C for 20 hours and Rio Grande variety resulted in enhanced growth, biochemical attributes and production of tomato in the agro-climatic conditions of Peshawar.

Received | August 09, 2021; **Accepted** | September 12, 2021; **Published** | October 01, 2021

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Citation | Ullah, G. and G. Ayub. 2021. Dissecting the heat stress responses and effects on morphology of tomato varieties employing pre-transplant high temperature conditioning. *Sarhad Journal of Agriculture*, 37(4): 1384-1402.

DOI | <https://dx.doi.org/10.17582/journal.sja/2021/37.4.1384.1402>

Keywords | Heat conditioning, Tomato, Temperature, Varieties, Yield

Introduction

Abiotic stresses including high or low light intensity, high or low temperature, salinity, metal toxicity and drought or excess moisture highly influence plant growth and productivity (Mittler and Blumwald, 2010; Cramer *et al.*, 2011; Barnabas *et al.*, 2008; Athar and Ashraf, 2009). High temperature is one of the most studied stresses that cause severe damage to the plant photosynthetic process leading to complete inhibition before other symptoms are detected (Berry and Björkman, 1980). Plants can acclimate the changing climatic conditions driven by a rise in temperature which might sometimes result in a deleterious impact on plant physiology (Spicher *et al.*, 2016). The influence on growth and survival directly depends on the duration as well as intensity of the heat stress. Exposure of the plants to a moderately high temperature for a longer duration can be as injurious as an extremely high temperature for a short duration (Georgieva, 1999).

For every specific plant, there exists an optimal temperature, at which the plant productivity is maximal. The most heat sensitive cell function is the chloroplast activity and a high temperature stress results in structural and functional damages. A high temperature stress leads to structural and functional changes in the chloroplast (Sato *et al.*, 2006) and disturbs the hydraulic conductivity of roots and leaves (Morales *et al.*, 2003). Furthermore, a high thermal stress results in reduced enzymatic activity (Ahmad *et al.*, 2010), injuries to the cell membrane and alteration of cell differentiation, elongation and division (Potters *et al.*, 2009; Rasheed, 2009; Smertenko *et al.*, 1997). Eventually, due to decreased photosynthesis, plants have limited resource availability for reproduction in parental and gametophytic tissues leading to starvation (Sumesh *et al.*, 2008; Young *et al.*, 2004).

One of the key components of thermotolerance of a plant is protection against oxidative stress-induced by heat stress (Volkov *et al.*, 2006; Suzuki *et al.*, 2011; Wahid *et al.*, 2007; Adachi *et al.*, 2009). Although there are various hardening methods against temperature stress, high temperature preconditioning considerably decreases the heat induced damage in multiple crops (Colclough *et al.*, 1990; Javanmardi *et al.*, 2014). Studies have proved that tomato plants exhibited good osmotic adjustment as compared to non-conditioned or control plants (Morales *et al.*,

2003). Plants adapt various strategies to tackle elevated temperature stress including short term acclimation and long term morphological and phenological modifications. Many plants adapt an escape mechanism by early maturation of the crop although associated with some yield loss (Adams *et al.*, 2001). The mechanism of response to heat stress is different at different developmental stages and may also vary with respect to tissue type (Queitsch *et al.*, 2000). Thermotolerance acquisition is an autonomous cellular mechanism which results from heat pretreatment of plants to a sublethal high temperature. This strategy protects the plant cells from a subsequent lethal high temperature stress (Vierling, 1991). This experiment aimed to investigate the influence of pre-transplant high temperature conditioning on the performance of tomato varieties in field conditions.

Materials and Methods

The experiment was carried out at Horticulture Research Farm, Department of Horticulture, The University of Agriculture, Peshawar during 2017 and 2018 to see the influence of Pre-transplant high temperature conditioning on the growth and development of tomato varieties under high temperature conditions. The experiment was laid out in a Completely randomized design (CRD) in a growth chamber before transplantation and Randomized Complete Block Design (RCBD) split plot with two factors (different heat pretreatment durations and tomato varieties) and three replications after transplanting in the field.

Seeds of all the three tomato varieties i.e. Roma, Rio Grande and Yaqui were obtained from a local market and were sown in January for raising nursery. Healthy seedlings at their 4- leaves stage were selected for the experiment and transferred to a growth chamber. After heat treatment, seedlings were transplanted to the field during March in the study period. The field was ploughed twice two weeks before the transplantation. Raised beds were prepared with a plant to plant distance of 60 cm and row to row distance of 75cm. The experimental field soil was silty loam in texture having a 7.7 pH. A recommended dose of NPK fertilizer in the form of Urea, Di ammonium phosphate (DAP), and Potassium Sulphate at the rate of 100, 90 and 60 kg ha⁻¹ respectively were applied to the field. Potassium and phosphorus were applied to the soil before seedlings transplantation, while nitrogen fertilizer was given in two split doses. The first dose was given

before transplantation, the second dose was provided after 30 days of seedling transplantation. The soil was well irrigated immediately after transplantation. While, later the irrigation process carried out according to the plant requirement. Manual weeding and hoeing regularly performed to avoid any weeds infestation.

Heat treatment procedure

There were two groups of seedlings; the first group was shifted to a growth chamber for pretreatment at 35 °C for 10, 15 and 20 hrs and then recovered at 25 °C for 2 hrs. The second group served as a control and was transplanted directly to fields without any heat pretreatment.

Parameters studied

Days to flowering

Data were calculated for the total number of days, when the first flower is formed in each randomly selected plant and the means were figured out.

Number of flowers cluster⁻¹

Number of flowers per cluster was calculated for randomly selected plants and mean values were figured out.

Number of flower clusters plant⁻¹

The data regarding number of flower clusters were recorded by counting the total number of flower clusters on each randomly selected plant and figuring out the mean values.

Electrolyte leakage

Total inorganic ions leaked out of the leaf was estimated by the method described by Ben Hamed *et al.* (2007). Twenty leaf discs were taken in a boiling test tube containing 10 mL of DDW, and electrical conductivity was measured (EC_a). The tubes were heated at 45°C and 55 °C for 30 min in a water bath, and similarly electrical conductivity measured (EC_b) each time. Later on, the contents were again boiled at 100 °C for 10 min, and electrical conductivity has been recorded again (EC_c). The electrolyte leakage was calculated using the formula:

$$\text{Electrolyte Leakage (\% age)} = \frac{EC_b - EC_a}{EC_c} \times 100$$

Chlorophyll content (SPAD)

Chlorophyll content was measured with the help of

a chlorophyll meter (Model Number: TYS-A) by recoding the SPAD values of randomly selected leaves for each treatment per replication at the flowering stage.

Leaf relative water content

Fully expanded top most leaves were collected from the upper portion of the main shoot and fresh weight was elaborated. The leaves were immersed in distilled water in a Petri dish for two hrs. The leaves then removed, and the surface water was blotted off to calculate the turgid weight. Samples had been dried in an oven at 70°C to constant weight.

The following formula used to determine the leaf relative water content (Turner, 1981):

$$LRWC (\%) = [(F.W - D.W) / (T.W - D.W)] \times 100 \quad (1)$$

where F.W stands for Fresh weight; D.W for Dry weight and T.W represents Turgid weight.

Polyamines determination (Putrescine, Spermidine and Spermine)(nmol/g)

Freeze-dried tomato leaf material was extracted and dansylated as described by Torrigianiet *al.* (2012). with some modifications. Briefly, 50 mg of finely ground sample was homogenized in 800 µL of 5% ice-cold perchloric acid (PCA) using a hand-held homogenizer. The remaining procedure was exactly as described by Anwar *et al.* (2019). For PAs recovery and calibration curves, authentic PA standards (Sigma-Aldrich, USA) were used as control. PAs were integrated and quantified using Millennium 4.0 from Waters Corporation. PCA-soluble, PCA-soluble hydrolyzed with HCl, and PCA-insoluble after hydrolysis samples were quantified and designated as free, conjugated, and bound forms of each PA, respectively (Anwar *et al.*, 2019).

Yield (t ha⁻¹)

Yield per hectare was determined by weighing tomato fruits of each treatment harvested from each subplot and then converting to tonnes using the formula:

$$\text{Yield (t ha}^{-1}\text{)} = \frac{\text{Yield of sub plot (Kg)} \times 10000 \text{ m}^2}{\text{Area of sub plot (m}^2\text{)} \times 1000}$$

Results and Discussion

Days to flowering

The statistical analysis of the data concerning days

to flowering indicated that heat pretreatment and varieties significantly affected the days to flowering of tomato (Table 1) while the interactions were non-significant. Mean values of the data showed that heat pretreatment of 20 hrs produced early flowering (26.99 days) in tomato, followed by 15 hrs HP (28.44 days), which was at par with that of 10 hrs HP (29.15 days). Late flowering occurred in the tomato plants treated with no HP (31.61 days). Concerning varieties, the highest days to flowering (31.57 days) was taken by Yaqui as compared to Roma plants which took the lowest days to flowering (26.72 days).

The seedling stage has a crucial role in tomato flowering and ultimately fruit production. This stage of plant growth greatly influences flowering to harvest time and its optimization can enhance the quality as well as production yield of tomato crop (Zhan *et al.*, 2003). Flowering and fruit set are two key processes that are sensitive to high temperature and a basis for identifying heat tolerance in tomato (Berry and Uddin, 1988; Hanna and Hernandez, 1982). Thermotolerance is acquired from prior subjecting the plants to a sublethal high temperature pretreatment (Hong and Vierling, 2000). Early flowering with longer heat pretreatment duration might be related to the heat acclimated plants stress avoidance strategy to prevent the issues related to high temperature at the flowering stage (Peet *et al.*, 1997). Heat preconditioning can reduce stress injury by stabilizing the membrane structure, regulating membrane functions, optimize the ion leakage and membrane permeability leading to seedlings tolerance to high temperature stress. Seedlings treated with a longer duration of heat pretreatment flowered earlier as compared to control plants. These results are in conformity with Javanmardi *et al.* (2009) who recorded an early flowering as well as maximum fruit set in heat preconditioned plants as compared to non-acclimated plants.

Number of flowers cluster⁻¹ and number of flower clusters plant⁻¹

Data regarding number of flowers cluster⁻¹ of tomato varieties is presented in Table 1. Statistical analysis of the data revealed that heat pretreatment and varieties significantly affected the number of flowers cluster⁻¹ of tomato plants while there was no significant difference regarding various interactions. The least number of flowers cluster⁻¹ (5.61) were recorded in control tomato plants, while 20 hrs HP treated tomato plants resulted in highest number of flowers cluster⁻¹ (8.34)

which was at par with those of 15 hrs (7.97). As far as varieties are concerned, Rio Grande plants produced highest number of flowers cluster⁻¹ (7.91) followed by Roma (7.48) while the lowest number of flowers per cluster (6.44) resulted in Yaqui plants.

Table 1: Effect of Pre-transplant high temperature conditioning on days to flowering, number of flowers cluster⁻¹ and number of flower clusters plant⁻¹ of tomato varieties.

Heat Treatment (HT) (Hrs)	Days to flowering	Number of flowers cluster ⁻¹	Number of flower clusters plant ⁻¹
0	31.61 a	5.61 c	13.19 c
10	29.15 b	7.19 b	15.31 b
15	28.44 bc	7.97 a	15.72 ab
20	26.99 c	8.34 a	16.06 a
LSD at α 0.05	2.04	0.45	0.44
Varieties (V)			
Roma	26.72 c	7.48 b	15.31 b
Rio Grande	28.85 b	7.91 a	16.99 a
Yaqui	31.57 a	6.44 c	12.92 c
LSD at α 0.05	3.49	0.13	0.61
Interactions (HT x V)	NS	NS	*Fig 3.1

Means followed by similar letter(s) in column do not differ significantly from one another; NS = Non-significant and *, ** = Significant at 5 and 1% level of probability, respectively.

Number of flower clusters per plant of tomato was also significantly affected by heat pretreatment, varieties and interactions (Table 1). The number of flower clusters per plant of tomato were least (13.19), when treated with no HP as compared to the plants treated with 20 hrs HP that resulted in highest number of flower clusters per plant (16.06) followed by 15 hrs HP (15.72) and 10 hrs HP (15.31). Data regarding varieties revealed that the lowest number of flower clusters plant⁻¹ (12.92) was observed in Yaqui plants, while the highest number of flower clusters plant⁻¹ (16.99) was noted in Rio Grande plants. Interactive effects showed that number of flower clusters plant⁻¹ was improved with an increase in HP. However, the increase was maximum at 20 hrs HP in Rio Grande (Figure 1).

Based on the developmental stage, the mean daily temperature for optimum tomato growth and production is around 21 to 25°C (Geisenberg and Stewart, 1986) and a rise in temperature of even a few degrees can adversely affect flowers and fruit set. Plant's reproductive stages especially gametogenesis

and fertilization are most crucial with respect to a rise in temperature. Moreover, meiosis occurs a few days before anthesis, which is a highly temperature sensitive phase of plant growth (Peet *et al.*, 1997). Higher number of flowers in 15 hrs and 20 hrs heat pretreated plants was likely because of the seedlings being hardened by high temperature conditioning before transplantation. A decline in the number of flowers cluster⁻¹ in control plants is similar to the results obtained by Javanmardi *et al.* (2009) who reported a limited reproductive growth in non heat pretreated plants as compared to heat pretreated plants. Furthermore, a longer duration of heat pretreatment of 20 hrs before transplantation enabled the plant to flower early, resulting in an escape from higher temperature stress around the flowering stage and ultimately higher number of flowers cluster⁻¹ (Peet *et al.*, 1997). An abrupt heat treatment (42–45°C) also enables the plants to acclimate high temperature stress during the flowering stage (Larkindale and Vierling, 2008; Suzuki *et al.*, 2008). Qin *et al.* (2008) applied high temperature treatment of 36–38°C to *Arabidopsis thaliana* plants for a short period as a hardening method and then subjected the plants to increased durations of 45°C temperature stress to acquire thermotolerance. Another research investigated the effect of a gradual rise in temperature to achieve acclimation in *Arabidopsis thaliana* seedlings to heat stress of 45°C. A massive build-up of heat shock proteins as well as reactive oxygen species and enzymes was observed during the treatment (Larkindale and Vierling, 2008).

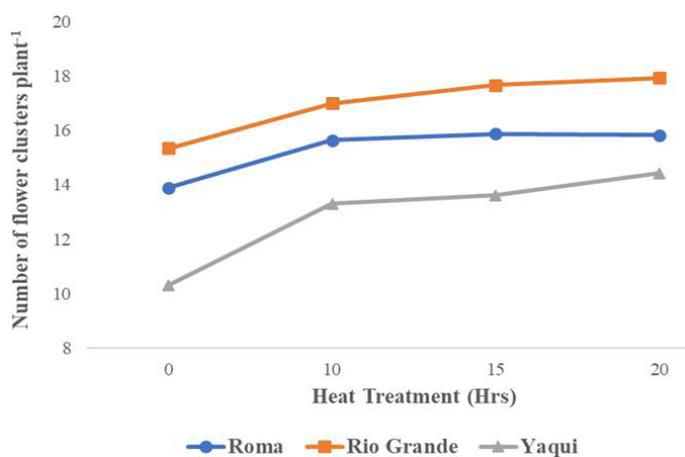


Figure 1: Interactive effect of varieties and heat treatment on number of flower clusters plant⁻¹ of tomato.

Fruit set percentage (%)

Data concerning the fruit set percentage of the tomato crop in response to heat pretreatment and va-

rieties is shown in Table 2. Fruit set percentage was significantly affected by different heat pretreatment levels and varieties while the interaction effect of all the treatments was non-significant. The fruit set percentage increased from (60.70%) in control plants to (68.33%) with 20 hrs HP application, followed by (64.64%) with 15 hrs HP treatment. The highest fruit set percentage (68.25%) was recorded in Rio Grande plants, followed by (64.33%) in Roma, while the lowest fruit set percentage (58.36%) resulted in Yaqui plants.

Plants parts that are most sensitive to high temperature stress are floral and fruiting organs (Wahid *et al.*, 2007). Acquired thermotolerance at the anthesis stage can play a key role in determining the final yield. Higher fruit set percentage in heat pretreated plants for a longer duration might be due to good osmotic adjustment, enabling the plant to maintain leaf pressure potential at an optimum stage during the heat stress conditions leading to normal growth and development. Similar results were also produced by Morales *et al.* (2003) who studied the influence of high temperature conditioning of 30°C and 35°C as preconditioning temperatures and concluded that preconditioned plants had higher pressure potential as well as stomatal conductance as compared to those of non-conditioned plants. Osmolyte production is also known to enhance protein stability and membrane integrity under heat stress conditions (Mirzaei *et al.*, 2012; Sung *et al.*, 2003). Javanmardi *et al.* (2014) investigated the influence of high temperature pretreatment in tomato and observed a higher fruit set and early first flower initiation in heat pretreated plants in comparison with control plants. Heat pretreatment also enables the plant to cope with high temperature stress due to its enhanced membrane integrity, higher levels of proline and carbohydrate content, antioxidant enzyme activities and reduced chlorophyll degradation (Ding *et al.*, 2016).

Significant influence of varieties was noted regarding fruit set percentage. This was in accordance with (Zhou, 2017) who investigated the physiological response of different tomato genotypes to heat stress during seedling as well as anthesis stage and reported a significant influence of cultivars on fruit set of tomato. The heat tolerant genotype continued normal truss formation under high temperature stress indicating normal floral organ growth and development. Also the heat tolerant cultivars maintained a higher level of carbohydrates assimilation and nutrients uptake

Table 2: Effect of Pre-transplant high temperature conditioning on fruit set percentage (%), electrolyte Leakage (%), chlorophyll content (SPAD) and leaf relative water content (%) of tomato varieties.

Heat Treatment (HT) (Hrs)	Fruit set percentage (%)	Electrolyte Leakage (%)	Chlorophyll content (SPAD)	Leaf relative water content (%)
0	60.70 c	57.77 a	41.09 c	62.19 c
10	60.88 c	55.87 b	43.76 b	70.22 b
15	64.68 b	51.43 c	45.59 b	72.51 ab
20	68.33 a	48.87 d	50.31 a	75.34 a
LSD at α 0.05	2.71	1.78	2.13	2.89
Varieties (V)				
Roma	64.33 b	52.36 b	45.28 b	67.05 b
Rio Grande	68.25 a	48.86 c	48.06 a	80.68 a
Yaqui	58.36 c	59.24 a	42.23 c	62.48 c
LSD at α 0.05	2.14	3.06	3.28	3.34
Interactions (HT x V)	NS	NS	*Fig 3.2	NS

Means followed by similar letter(s) in column do not differ significantly from one another; NS = Non-significant and *, ** = Significant at 5 and 1% level of probability, respectively.

(Kumari *et al.*, 2013; Vignjevic *et al.*, 2015) as well as cell wall and vascular invertases activities (Li *et al.*, 2012) under high temperature stress conditions ultimately leading to better fruit set in tomato. These results were also in conformity with (Abdul Baki, 1991), who concluded that tolerant cultivars resulted in more flowers, optimum matured fruits, highest fruit set percentage and highest yield as compared to heat sensitive cultivars both in a greenhouse as well as under field conditions. Severe alterations in photosynthetic rate are induced by heat stress reducing the plant's ability to mitigate the damaging effect of high temperature. Reduced antioxidant capacity and increased dark respiration in heat sensitive cultivar might be the reason for poor performance regarding fruit set in the field (Camejo, 2006).

Electrolyte Leakage (%)

It is clear from Table 2 for electrolyte leakage that there was a significant difference among different heat pretreatment and varieties. The interaction effects for all the treatments remained non-significant. Heat pretreatment of tomato seedlings for a 20 hrs duration resulted in minimum electrolyte leakage (48.87%), followed by (51.43%) with heat pretreatment for 15 hrs duration while maximum electrolyte leakage (57.77%) was recorded in control plants. The mean data regarding varieties showed that minimum electrolyte leakage (48.86%) was noted for Rio Grande plants, while the maximum electrolyte leakage (59.24%) was observed in Yaqui plants.

The temperature as well as duration of heat stress pretreatments, determines the growth and development of the plant under heat stress conditions and the response of the plants vary between growth stages and tissue type. Maintenance of homeostasis and repairing of heat sensitive components provides an insight in the ability of the plant to withstand or acclimate high temperature stress. Higher percentage of electrolyte leakage is an indicator of increased oxidative processes, reduced heat shock proteins production and alterations in membrane permeability resulting in oxidative damage and heat injury to the plant system (Vierling, 1991; Kotak *et al.*, 2007). Reduced membrane integrity as a result of higher electrolyte leakage percentage, lower the ability of the plants to retain solutes as well as water in heat stress conditions (Al-lakhverdiev *et al.*, 2008; Wahid and Shabbir, 2005). To prevent higher electrolyte leakage due to heat stress and to regulate metabolism, plant increases saturated and monounsaturated fatty acids content (Zhang *et al.*, 2005b) which ultimately leads to membrane stability and enhanced heat tolerance (Larkindale and Huang, 2004). Several studies in tomato report that heat treatment induces secondary metabolites accumulation which protects the plant against oxidative damage (Rivero *et al.*, 2001). Heat pretreatment also results in stabilized membrane structure and functions, reduce electrolyte leakage as well as membrane permeability. These results are also in accordance with Javanmardi *et al.* (2014) who reported reduced electrolyte leakage in heat pretreated seedlings as compared to the non-heat pretreated seedlings in pepper

and tomato.

Varieties were also significantly different regarding electrolyte leakage percentage. Reduced electrolyte leakage is a characteristic feature of heat tolerant variety when exposed to high temperature stress along with higher photosynthetic activity and heat avoidance (Nagarajan *et al.*, 2010; Scafaro *et al.*, 2010). Certain genotypes are more tolerant to high temperature and their response to heat stress directly depend on genotypic parameters (Challinor *et al.*, 2007; Prasad *et al.*, 2006). However, (Camejo *et al.*, 2006) also reported an increase in electrolyte leakage in heat sensitive cultivar relating it to alterations in membrane permeability and reduced solute and water retention ability due to high temperature stress. A heat tolerant cultivar Nagcarlang was not influenced by the heat stress and retained its membrane permeability showing the maintenance of its various functioning processes. A higher level of electrolyte leakage is an indicator of reduced functioning of mitochondrial and photosynthetic systems in plant cells (Shanahan *et al.*, 1990; Ristic *et al.*, 1996).

Chlorophyll content (SPAD)

Table 2 shows that heat pretreatment and varieties significantly affected the chlorophyll content of tomato plants. The interactions between heat pretreatment and varieties were also significant. Concerning HP, the highest chlorophyll content (50.31 SPAD) was recorded in plants subjected to 20 hrs heat pretreatment duration, followed by (45.59 SPAD) with 15 hrs heat pretreatment duration, whereas the lowest chlorophyll content (41.09 SPAD) resulted in plants treated with no heat pretreatment duration (Control). Rio Grande plants resulted in the highest chlorophyll content (48.06 SPAD) as compared to those of Yaqui plants that recorded the lowest chlorophyll content (42.23 SPAD). The interaction between heat pretreatment and varieties showed that the chlorophyll content increase with an increase in heat pretreatment duration for all varieties, however heat pretreatment of 20 hrs duration in Rio Grande plants resulted in the highest chlorophyll content (Figure 2).

High temperature stress significantly influences various photosynthetic parameters like chlorophyll a/b levels and chlorophyll/carotenoid ratio and tremendously disturbs the root and leaf water hydraulic conductivity (Wahid, 2007; Morales *et al.*, 2003). Chloroplast is the major source of reactive oxygen species (ROS) in the plant cell. They produce superoxide

radicals and singlet oxygen from the harvested light energy (Salin, 1988). Under various stress conditions like drought, heat and herbicides, photoactivated chlorophyll also excite oxygen to singlet form when the harvested light energy is not used in the electron transport system (Foyer, 2002). Several research studies have confirmed that the association of chlorophyll content with plant heat stress, the results indicates that cultivars having a high greenness level are less prone to high temperature stress (Lopes and Reynolds, 2012; Reynolds *et al.*, 2012; Rossi *et al.*, 2017; Wang *et al.*, 2017). Furthermore, various reports are indicating a devastating influence of high temperature stress on chlorophyll biosynthesis in different plant species (Feierabend, 1977; Tewari and Tripathy, 1998; Takahashi *et al.*, 2008).

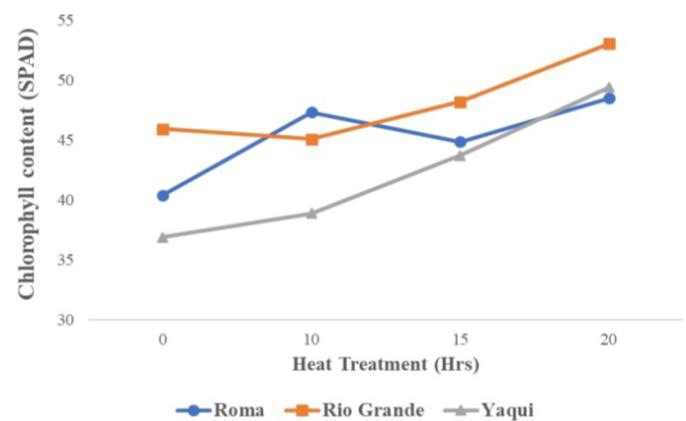


Figure 2: Interactive effect of varieties and heat treatment on chlorophyll content (SPAD) of tomato.

Chlorophyll content also gives an idea of the nutrient absorption as well as photosynthetic assimilation ability of a plant. An increase in chlorophyll content was observed with increasing heat pretreatment duration. The highest chlorophyll content resulted in plants treated with 20 hrs heat pretreatment. Further, Javanmardi *et al.* (2014) investigated the influence of heat preconditioning on chlorophyll content of tomato and pepper leaves and reported that tomato and pepper plants produced a higher chlorophyll content when preconditioned with heat treatment as compared to the non-acclimated plants. An improved chloroplast structure under high temperature stress is also reported to be a result of heat acclimation (Xu *et al.*, 2006). Besides, Morales *et al.* (2003) studied the effect of high temperature preconditioning and thermal shock on tomato cultivar Amalia and reported a significant influence of high temperature pretreatment on chlorophyll content, stomatal conductance as well as net photosynthetic rate. Heat acclimated plants had a

higher degree of thermo-stability, lower chloroplast damage and lipid peroxidation as compared to the non-heat acclimated plants when subjected to a high temperature stress (Xu *et al.*, 2006). The findings are also in conformity with Ibrahim and El-Muqadam (2019) who also obtained similar results and recorded a higher chlorophyll in plants preconditioned with a high temperature hardening treatment. Slower heat treatment results in serious plant injuries including loss of membrane integrity as well as enzymes inactivation in the chloroplast (Howarth, 2005). Similar findings were also obtained by Dutta *et al.* (2009) and Reda and Mandura (2011) who recorded enzymes destruction that regulates chlorophyll synthesis under high temperature stress.

Varieties were also significantly different from one another regarding the chlorophyll content of tomato. Moreover, Wahid and Ghazanfar (2006) observed similar results and concluded that tolerant tomato genotypes produced a higher chlorophyll a:b ratio and a lower chlorophyll: carotenoids ratio when exposed to a higher than optimum temperature stress. These parameters are also used as a tool for indicating thermotolerance and physiological status in tomato plants. In addition, Camejo (2005) investigated the influence of high temperature on photosynthetic activity of two tomato cultivars and recorded an increase in chlorophyll a/b ratio and decrease in chlorophyll/carotenoid ratio in heat stressed Nagcarlang tomato plants. Thermotolerance development in plants also relates to the amount of chloroplast protein synthesis elongation factor under high temperature stress (Moriarty *et al.*, 2002). Heat shock proteins in chloroplast protect the plant from the adverse effects of high temperature stress and play a key role in electron transport (Barua *et al.*, 2003). Accumulation of chlorophyll has also been correlated with thermotolerance in various crop species (Selvaraj *et al.* 2011).

Zhou *et al.* (2015) studied the physiological response of heat stress in different tomato genotypes with different types of heat susceptibility and reported that cultivar 'LA1994' resulting in an altered photosynthetic rate and chlorophyll content as compared to control plants when exposed to a 36/28 °C temperature stress. In support of our findings, Gosavi *et al.* (2014) and Zhou *et al.* (2017) also recorded an increase in total chlorophyll in tolerant genotypes as compared to the susceptible ones.

Leaf relative water content (%)

The leaf relative water content was significantly affected by heat pretreatment and varieties while their interaction was not significant (Table 2). Heat pretreatment of tomato seedlings for a 20 hrs duration resulted in the highest leaf relative water content (75.34%), followed by (72.51%) with heat pretreatment for 15 hrs duration while the lowest leaf relative water content (62.19%) was recorded in control plants. The highest leaf relative water content (80.68%) was recorded in Rio Grande plants, followed by (67.05%) in Roma, while the lowest leaf relative water content (62.48%) resulted in Yaqui plants.

The best way to judge plant water status of cellular water deficit under various stressful conditions is the relative water content (Sekmen *et al.* 2014). A decrease in leaf water content causes leaf desiccation, which initially causes the stomata closure followed by stromal photosynthetic reactions ultimately results in photosynthetic inhibition (Bertolli *et al.* 2012; Zivcak *et al.* 2013). Higher leaf temperature is correlated with an increase in temperature either directly by having some damaging effects in plant tissues or indirectly leads to an increase in plant water deficit. Both leaf relative water content and turgidity can be used as indicators of growth and development under high temperature stress, an increase in temperature triggers evaporative demands and ultimately results in higher transpiration rates as well as reduced water potential (Hall, 2000). High temperature is also considered as the most influential factor that causes a higher plant evaporation demand ultimately contributing towards water deficiency (Karim *et al.* 1997; Simoes-Araujo *et al.*, 2003). Turgidity maintenance is an important factor in optimum plant growth as well as implementing normal cell activities (Farouk, 2011). It is also worth mentioning that decreased leaf relative water content and turgidity loss occur with an increase in transpiration due to high temperature (Cansev, 2012; Turkes, 2003; Yamasaki and Dillenburg, 1999). Studies have confirmed that a decline in relative water content plays a key role in decreased growth in response to osmotic stress in plants (Alexieva *et al.*, 2001). A decrease in leaf relative water content in control plants might be due to not being hardened by heat pretreatment to cope with the heat stress of field conditions after transplanting. Better water retention in heat hardened tomato plants may also be associated with better osmoregulation as well as healthy vegetative growth in the field (Hasthanasombut *et al.*, 2011).

These results are in conformity with other researchers (Khalil and Moursy 1983) who reported promoted growth of various plants due to heat hardening.

Zhou *et al.* (2017) subjected three tomato cultivars to heat and drought stress and recorded a significant decrease in relative water content of all studied cultivars as compared to those of control plants. This also confirms the similar sensitive behavior of all three cultivars to the applied stress. Heat tolerant cultivars have normal growth and development under heat stress conditions because they have improved photosynthesis, water and nutrient use efficiency, membrane stability and assimilate partitioning as compared to heat sensitive cultivars (Camejo *et al.*, 2005; Ahn and Zimmerman, 2006; Momcilovic and Ristic, 2007).

Polyamines (Putrescine, Spermidine and Spermine) (nmol/g)

Data for Putrescine is indicated in Table 3 which elaborates that heat pretreatment and varieties significantly affected Putrescine concentration. The interaction effect of heat pretreatment and varieties didnot show a significant variation in response to Putrescine concentration in tomato plants. The mean data regarding Putrescine concentration revealed that heat pretreatment of tomato plants for 20 hrs duration produced the highest Putrescine concentration (193.95 nmol/g), followed by (185.55 nmol/g), while the lowest Putrescine concentration (173.19nmol/g) was noted in tomato plants applied with no heat pretreatment (Control). Regarding varieties, The Putrescine concentration was highest (190.25 nmol/g) in Rio Grande, followed by (181.68 nmol/g) in Roma while the lowest Putrescine concentration (176.92 nmol/g) was observed in Yaqui plants.

The mean data in Table 3 showed that spermidine was significantly affected by various heat pretreatment durations and varieties. Interactions have no significant effect on the spermidine concentration of tomato plants. Regarding heat pretreatment duration, the highest spermidine concentration (154.59 nmol/g) was recorded in plants subjected to 20 hrs heat pretreatment duration, followed by (152.31 nmol/g) with 15 hrs heat pretreatment duration, whereas the lowest spermidine concentration (138.60 nmol/g) resulted in plants treated with no heat pretreatment duration (Control). The mean data regarding varieties showed that the lowest spermidine concentration (136.58 nmol/g) was noted for Rio Grande plants

while the highest spermidine concentration (152.57 nmol/g) was observed in Yaqui plants.

Table 3: Effect of Pre-transplant high temperature conditioning on spermidine (nmol/g), spermine (nmol/g) and yield (t ha⁻¹) of tomato varieties.

Heat Treatment (HT) (Hrs)	Putrescine (nmol/g)	Spermidine (nmol/g)	Spermine (nmol/g)	Yield (t ha ⁻¹)
0	173.19 c	138.60 b	27.90 c	18.18 c
10	179.10 c	139.33 b	30.36 bc	18.31 c
15	185.55 b	152.31 a	32.04 b	19.21 b
20	193.95 a	154.59 a	36.51 a	20.14 a
LSD at α 0.05	2.75	3.72	3.02	0.47
Varieties (V)				
Roma	181.68 b	149.47 b	35.72 a	18.86 b
Rio Grande	190.25 a	152.57 a	33.21 b	21.00 a
Yaqui	176.92 c	136.58 c	26.18 c	17.03 c
LSD at α 0.05	5.15	3.32	3.91	0.37
Interactions (HT x V)	NS	NS	NS	NS

Means followed by similar letter(s) in column do not differ significantly from one another; NS = Non-significant and *, ** = Significant at 5 and 1% level of probability, respectively.

Data regarding spermine concentration in Table 3 revealed that spermine concentration was significantly influenced by heat pretreatment durations and varieties. The interaction between heat pretreatment durations and varieties was not significant. Heat pretreatment of tomato seedlings for a 20 hrs duration resulted in increased spermine concentration (36.51 nmol/g), followed by (32.04 nmol/g) with heat pretreatment for 15 hrs duration while a decrease in spermine concentration (27.90 nmol/g) was recorded in control plants. The studied tomato varieties were also significantly different from one another regarding spermine concentration. Roma plants resulted in the highest chlorophyll content (35.72 nmol/g), followed by Rio Grande (32.21 nmol/g), as compared to those of Yaqui plants that recorded the lowest chlorophyll content (26.18 nmol/g).

Polyamines, mainly putrescine (Put), spermidine (Spd), and spermine (Spm) are ubiquitous, low molecular weight compounds that are widely distributed in all living organisms (Hussain *et al.*, 2011). For instance, spermidine and spermine synthesis occur in shoot apical meristem in the case of tobacco whereas putrescine is produced in roots (Moschou *et al.*, 2008). In most cases, polyamines in plants tend to work in

adaptive responses to various abiotic stresses and their levels are severely influenced by different stress conditions. Liu *et al.* (2007) has investigated the variations in levels of polyamines by subjecting plants to a range of abiotic stresses like high salinity, high and low temperatures, drought, nutrient deficiency and recorded a significant change in polyamine levels. This change is higher in case of putrescine while spermidine and spermine show a minor increase in case of apple callus when treated with salt (Liu *et al.*, 2006). These results also suggest that changes in polyamine levels are decided by various factors including plant species under investigation, type and condition of stress, stress tolerance capacity of the plant and its physiological status. Increased accumulation of polyamines maintains membrane stability under stress conditions by regulating antioxidant activities and binding strongly with negative charges in proteins and phospholipids (Asthir *et al.*, 2004; Liu *et al.*, 2007; Tiburcio *et al.*, 2014). Polyamines also enhance various growth and developmental processes in plants including stimulation, support and development of flower buds, fruit set, fruit ripening, cell division and response to abiotic stresses (Bouchereau *et al.*, 1999; Groppa and Benavides 2008).

Polyamines promote the photosynthetic activity of chloroplast and prevent lipids peroxidation (Drolet *et al.*, 1986; Floryszak *et al.*, 1992a). Putrescine plays a key role in mitigating harmful effects of stress because of its higher content as compared to spermidine and spermine leading to reduced oxidative damage (Bouchereau *et al.*, 1999). Heat pretreatment hardened tomato plants and produced the optimum amount of polyamines necessary for better growth and development. Similar results were also observed by Goyal and Asthir (2010) who recorded promoted diamine oxidase and polyamine oxidase activities along with an increase in spermidine and spermine content in wheat under high temperature stress conditions. Similar results were also reported in multiple studies regarding an increase in polyamines in different crops and conditions like chickpea and soybean (Nayyar *et al.*, 2005) under drought stress while in Arabidopsis (Sagor *et al.*, 2013), tobacco (Cvikrová *et al.*, 2012), and alfalfa (Königshofer and Lechner 2002) under heat stress conditions. Various research investigations have shown that polyamines role in stress tolerance is mainly by reactive oxygen species ROS homeostasis regulations (Liu *et al.*, 2015). Exogenous application of polyamines as well as over expression of various

polyamine biosynthetic genes enhanced plant ability to tolerate various abiotic stresses (Farooq *et al.*, 2009, Wang *et al.*, 2011a; 2011b; Fu *et al.*, 2014). Various research studies have shown that stress conditions lead to polyamines accumulation but there are some reports of decrease or minimal polyamine alteration when experiments were performed under different conditions (Liu *et al.*, 2006; 2007; 2008).

Considering cultivars, multiple research studies revealed that tolerant cultivars synthesize more spermidine and spermine as compared to sensitive cultivars which tend to produce more putrescine while having the same stress conditions (Krishnamurthy and Bhagwat, 1989; Santa-Cruz *et al.*, 1998; Liu *et al.*, 2004). Overall, heat tolerant cultivars have the ability to accumulate a higher quantity of polyamines as compared to heat sensitive cultivars (Hatmi *et al.*, 2015), Enhanced levels of polyamines confer increased tolerance to different plants in multiple stress conditions (Duan *et al.*, 2008).

Yield ($t\ ha^{-1}$)

The yield of tomato crop was significantly affected by heat pretreatment durations and varieties. However, the interaction between heat pretreatment durations and varieties was not significant (Table 3). Yield increased with an increase in heat pretreatment duration. The highest yield ($20.14\ t\ ha^{-1}$) resulted in tomato plants applied with 20 hrs heat pretreatment duration, followed by ($19.21\ t\ ha^{-1}$) with 15 hrs heat pretreatment duration, whereas the lowest yield ($18.18\ t\ ha^{-1}$) was observed in tomato plants subjected to no heat pretreatment (Control). Regarding various varieties studied during the experiment, the yield was highest ($21.00\ t\ ha^{-1}$) in Rio Grande plants, followed by ($18.86\ t\ ha^{-1}$) in Roma while the lowest yield ($17.03\ t\ ha^{-1}$) was noted in Yaqui plants.

High temperature stress directly as well as indirectly influence the overall yield of tomato. Direct damages of extreme temperature include increased membrane lipid fluidity, proteins denaturation and inhibition as well as enzyme inactivation of mitochondria and chloroplast (Howarth, 2005). A decline in fruit quality and yield of tomato is reported because of poor performance of crop at various developmental stages ranging from vegetative particularly leaves (Camejo *et al.*, 2006; Shanmugam *et al.*, 2013; Sharma *et al.*, 2014) to reproductive growth (Rudich *et al.*, 1977; Abdul-Baki 1991; Firon *et al.*, 2006) under heat stress

conditions. However, the reproductive stage is termed to be most sensitive stage to heat stress in various crops like wheat (Farooq *et al.*, 2011; Shanmugam *et al.*, 2013), tomato (Abdul Baki 1991; Sato *et al.*, 2000) and cotton (Kakani *et al.*, 2005; Snider *et al.*, 2009). High temperature also has a significant damaging effect on at cellular, sub-cellular as well as tissue level of plant structures, ultimately leads to lowered crop yield and development (Wahid *et al.*, 2007). Even at certain extreme high temperature and drought conditions, about 50% crop yield loss has also been reported (Wang *et al.*, 2003). Other researchers recorded significant damage to intermolecular interactions needed for optimum growth and development as a result of high temperature stress (Bita and Gerats, 2013).

Considerable research work has been done to evaluate the influence of heat stress caused by elevated temperatures and its subsequent biochemical, physiological, anatomical, morphological and genetic response in decreasing crop yield (Snider *et al.*, 2010; Camejo *et al.*, 2005; Chen *et al.*, 2012; Vasseur *et al.*, 2011; Min *et al.*, 2014). Heat pretreatment of tomato seedlings enhances yield performance in the field after transplanting. Our results show that an increased duration of heat pretreatment given to tomato seedlings act as a hardening tool to significantly increased yield of tomato crop. The optimum yield of heat pretreated plants was also associated with the ability of hardened plants to maintain high nutrient uptake and carbohydrates assimilation during heat stress (Kumari *et al.*, 2013; Vignjevic *et al.*, 2015). These findings are also in accordance with Yarwood (1961) who reported that leaves exposed to high temperature stress for a specific duration can harden it to bear increased temperature stress than non-treated leaves.

Significant variation yield of tomato crop is also observed regarding different cultivars studied. The influence of heat stress and the response of plants vary between genotypes and stages of development (Wahid *et al.*, 2007). For instance, carbohydrate metabolism and photosynthesis at the leaves stage varies between cultivars and is used as an indicator of heat susceptibility in plants (Camejo *et al.*, 2006; Sharma *et al.*, 2014).

Conclusions and Recommendations

From the results of the experiment, it was concluded that heat pretreatment of 35°C for 20 hrs recorded

the highest reproductive as well as biochemical attributes. Therefore, it is recommended that as a hardening method for tomato transplants to cope with the high temperature stress in field conditions. The Rio Grande variety performed better than other studied varieties, resulting in increased reproductive growth and recommended for cultivation in the agro-climatic conditions of Peshawar, Khyber Pakhtunkhwa-Pakistan. It was also revealed from the results of the experiment that Roma resulted in the earliest flowering and produced the highest spermine content in all treated plants as well as control.

Acknowledgements

I am thankful to HEC, Pakistan for providing me financial assistance under “Indigenous 5000 PhD Fellowship Program” through which I have completed my PhD degree program.

Novelty Statement

For the first time, heat conditioning experiments were conducted on the local tomato cultivars of Peshawar, addressing the issues being faced by the farmers of the tomato growers in the study area.

Author's Contribution

Gulzar Ullah: Principal Author and PhD scholar, designed and conducted research, data collection, analysis and writing of this manuscript.

Gohar Ayub: Major Supervisor, who provided technical guidelines in the whole PhD study and research.

Conflict of interest

The author's declare no conflict of interest

References

- Abdul-Baki, A.A. 1991. Tolerance of tomato cultivars and selected germplasm to heat stress. *J. Am. Soc. Hort. Sci.*, 116 (6):1113 – 1116. <https://doi.org/10.21273/JASHS.116.6.1113>
- Adachi, M., Y. Liu, K. Fujii, S.K. Calderwood, A. Nakai, K. Imai and Y. Shinomura. 2009. Oxidative stress impairs the heat stress response and delays unfolded protein recovery. *PLoS One.*, 4:(11): e7719. <https://doi.org/10.1371/journal.pone.0007719>

- Adams, S.R., K.E. Cockshull and C.R.J. Cave. 2001. Effect of temperature on the growth and development of tomato fruits. *Ann. Bot.*, 88 (05): 869–877. <https://doi.org/10.1006/anbo.2001.1524>
- Ahmad, A., H. Diwan and Y.P. Abrol. 2010. Global climate change, stress and plant productivity. *Abiotic Stress Adaptation in Plants*. 503–521. https://doi.org/10.1007/978-90-481-3112-9_23
- Ahn, Y.J. and J.L. Zimmerman. 2006. Introduction of the carrot HSP17.7 into potato (*Solanum tuberosum* L.) enhances cellular membrane stability and tuberization in vitro. *Plant, Cell Environ.*, 29(1): 95–104. <https://doi.org/10.1111/j.1365-3040.2005.01403.x>
- Alexieva, V., I. Sergiev, S. Mapelli and E. Karanov. 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant, Cell Environ.*, 24(12):1337–44. <https://doi.org/10.1046/j.1365-3040.2001.00778.x>
- Allakhverdiev, S.I., V.D. Kreslavski, V. V. Klimov, D.A. Los, R. Carpentier and P. Mohanty. 2008. Heat stress: An overview of molecular responses in photosynthesis. *Photosynth. Res.*, 98(1–3):541–550. <https://doi.org/10.1007/s11120-008-9331-0>
- Anwar, R., S. Fatima, A.K. Mattoo and A.K. Handa. 2019. Fruit architecture in polyamine-rich tomato germplasm is determined via a medley of cell cycle, cell expansion, and fruit shape genes. *Plants*, 8(10):387. <https://doi.org/10.3390/plants8100387>
- Asthir, B., W. Spoor and C.M. Duffus. 2004. Involvement of polyamines, diamine oxidase and polyamine oxidase in resistance of barley to *Blumeriagraminis* f. sp. *hordei*. *Euphytica*, 136(3): 307–312. <https://doi.org/10.1023/B:EUPH.0000032730.48474.b1>
- Barua, D., C.A. Downs and S.A. Heckathorn. 2003. Variation in chloroplast small heat-shock protein function is a major determinant of variation in thermotolerance of photosynthetic electron transport among ecotypes of *Chenopodium album*. *Funct. Plant Biol.*, 30(10):1071–1079. <https://doi.org/10.1071/FP03106>
- Ben Hamed, K., A. Castagna, E. Salem, A. Ranieri and C. Abdelly. 2007. Sea fennel (*Crithmum maritimum* L.) under salinity conditions: A comparison of leaf and root antioxidant responses. *Plant Growth Regul.*, 53(3):185–194. <https://doi.org/10.1007/s10725-007-9217-8>
- Berry, J. and O. Bjorkman. 1980. Photosynthesis response and adaptation to temperature in higher plants. *Annu. Rev. Plant. Physiol.*, 31(1): 491 – 543. <https://doi.org/10.1146/annurev.pp.31.060180.002423>
- Berry, S. and M. Uddin. 1988. Effect of high temperature on fruit set in tomato cultivars and selected germplasm. *Hort. Sci.*, 23(3): 606–608.
- Bertolli, S.C., G.L. Rapchan and G.M. Souza. 2012. Photosynthetic limitations caused by different rates of water-deficit induction in *Glycine max* and *Vigna unguiculata*. *Photosynthetica*, 50(3):329–36. <https://doi.org/10.1007/s11099-012-0036-4>
- Bitá, C.E. and T. Gerats. 2013. Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. *Front Plant Sci.*, 4: 273. <https://doi.org/10.3389/fpls.2013.00273>
- Bouchereau, A., A. Aziz, F. Larher and J. Martin-Tanguy. 1999. Polyamines and environmental challenges: Recent development. *Plant Sci.*, 140(2): 103–125. [https://doi.org/10.1016/S0168-9452\(98\)00218-0](https://doi.org/10.1016/S0168-9452(98)00218-0)
- Camejo, D., A. Jiménez, J.J. Alarcón, W. Torres, J.M. Gómez and F. Sevilla. 2006. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. *Funct. Plant Biol.*, 33(2):177–87. <https://doi.org/10.1071/FP05067>
- Camejo, D., P. Rodríguez, M.A. Morales, J.M. Dell'Amico, A. Torrecillas and J.J. Alarcón. 2005. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *J. Plant Physiol.*, 162(3):281–9. <https://doi.org/10.1016/j.jplph.2004.07.014>
- Cansev, A. 2012. Physiological effects of high temperature treatments on leaves of olive cv. gemlik. *Plant Arch.*, 12(1):521–5.
- Challinor, A.J., T.R. Wheeler, P.Q. Craufurd, C.A.T. Ferro and D.B. Stephenson. 2007. Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. *Agric. Ecosyst. Environ.*, 119(1–2):190–204. <https://doi.org/10.1016/j.agee.2006.07.009>
- Chen, L., Y. Ren, Y. Zhang, J. Xu, F. Sun, Z. Zhang and Y. Wang. 2012. Genome-wide identification and expression analysis of heat-responsive

- and novel microRNAs in *Populus tomentosa*. *Gene*, 504(2):160-5. <https://doi.org/10.1016/j.gene.2012.05.034>
- Colclough, M., E. Blumwald, and S.J. Colombo. 1990. The induction of heat tolerance in black spruce seedlings. In: Annual Meeting of the American Society of Plant Physiologists. Amer. Soc. Plant Physiol., 93(1):88.
- Cvikrová, M., L. Gemperlová, J. Dobrá, O. Martinová, I.T. Prásl, J. Gubis and R. Vanková. 2012. Effect of heat stress on polyamine metabolism in proline-over-producing tobacco plants. *Plant Sci.*, 182:49-58. <https://doi.org/10.1016/j.plantsci.2011.01.016>
- Drolet, G., E.B. Dumbroff, R.L. Legge and J.E. Thompson. 1986. Radical scavenging properties of polyamines. *Phytochemist*, 25(2):367-71. [https://doi.org/10.1016/S0031-9422\(00\)85482-5](https://doi.org/10.1016/S0031-9422(00)85482-5)
- Duan, J.J., J. Li, S. Guo and Y. Kang. 2008. Exogenous spermidine affects polyamine metabolism in salinity-stressed *Cucumis sativus* roots and enhances short-term salinity tolerance. *J. Plant Physiol.*, 165(15):1620-35. <https://doi.org/10.1016/j.jplph.2007.11.006>
- Dutta, S., S. Mohanty and B.C. Tripathy. 2009. Role of temperature stress on chloroplast biogenesis and protein import in pea. *Plant Physiol.*, 150(2):1050-61. <https://doi.org/10.1104/pp.109.137265>
- El-Moursi, A., K.G. El-Din and S.A. Tarraf. 2012. Physiological response of lupine plant (*Lupinus termis* L.) to heat hardening. *Am. Eurasian J. Agric. Environ. Sci.*, 12(5): 660-663.
- Eltstner, E.F. and W. Osswald. 1994. Mechanisms of oxygen activation during plant stress. *Proc. R. Soc. Edinburgh. Sect. B. Biol. Sci.*, 102: 131-154. <https://doi.org/10.1017/S0269727000014068>
- Farooq, M., A. Wahid and D.J. Lee. 2009. Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. *Acta Physiol. Plant.*, 31(5):937-45. <https://doi.org/10.1007/s11738-009-0307-2>
- Farooq, M., H. Bramley, J.A. Palta and K.H.M. Siddique. 2011. Heat stress in wheat during reproductive and grain-filling phases. *Crit. Rev. Plant Sci.*, 30(6): 491-507. <https://doi.org/10.1080/07352689.2011.615687>
- Farouk, S. 2011. Osmotic adjustment in wheat flag leaf in relation to flag leaf area and grain yield per plant. 2011. *J. Stress Physiol. Biochem.*, 7(2): 117-138.
- Feierabend, J. 1977. Capacity for chlorophyll synthesis in heat-bleached 70S ribosome-deficient rye leaves. *Planta.*, 135(1):83-88. <https://doi.org/10.1007/BF00387980>
- Firon, N., R. Shaked, M.M. Peet, D.M. Pharr, E. Zamski, K. Rosenfeld, L. Althan and E. Pressman. 2006. Pollen grains of heat tolerant tomato cultivars retain higher carbohydrate concentration under heat stress conditions. *Sci. Hort.*, 109(3):212-217. <https://doi.org/10.1016/j.scienta.2006.03.007>
- Floryszak, W.J., E. Grabikowski, J. Kubis and Z. Krzywanski. 1992. The effect of spermidine on lipid peroxidation in wheat leaves during water stress. *Acta Physiol. Plant*, 14(1):3-10.
- Foyer, C.H. 2002. The contribution of photosynthetic oxygen metabolism to oxidative stress in plants. p.33-68. In: Inze, D. and vanMontagu, M. (ed.) *Oxidative stress in plants* Taylor & Francis, London.
- Fu, X.Z., F. Xing, N.Q. Wang, L.Z. Peng, C.P. Chun, L. Cao, L.L. Ling and C.L. Jiang. 2014. Exogenous spermine pretreatment confers tolerance to combined high-temperature and drought stress in vitro in trifoliolate orange seedlings via modulation of antioxidative capacity and expression of stress-related genes. *Biotechnol. Biotechnol. Equip.*, 28(2):192-198. <https://doi.org/10.1080/13102818.2014.909152>
- Geisenberg, C. and K. Stewart. 1986. Field crop management. *Tomato Crop*. 511-557. https://doi.org/10.1007/978-94-009-3137-4_13
- Georgieva, K. 1999. Some mechanisms of damage and acclimation of the photosynthetic apparatus due to high temperature. *Bulg. J. Plant Physiol.*, 25(3-4): 89-99.
- Gosavi, G.U., A.S. Jadhav, A.A. Kale, S.R. Gadakh, B.D. Pawar and V.P. Chimote. 2014. Effect of heat stress on proline, chlorophyll content, heat shock proteins and antioxidant enzyme activity in sorghum (*Sorghum bicolor*) at seedlings stage. *Indian J. Biotechnol.*, 13(3):356-363.
- Goyal, M. and B. Asthir. 2010. Polyamine catabolism influences antioxidative defense mechanism in shoots and roots of five wheat genotypes under high temperature stress. *Plant Growth Regul.*, 60(1):13-25. <https://doi.org/10.1007/s10725-009-9414-8>
- Groppa, M.D. and M.P. Benavides. 2008. Polyam-

- ines and abiotic stress: recent advances. *Amino Acids.*, 34(1):35-45. <https://doi.org/10.1007/s00726-007-0501-8>
- Hall, A.E. 2000. Crop responses to environment. CRC press. <https://doi.org/10.1201/9781420041088>
- Hanna, H.Y. and T.P. Hernandez. 1982. Response of six tomato genotypes under summer and spring weather conditions in Louisiana. *Hort. Sci.*, 17: 758 – 759.
- Hashtanasombut, S., N. Paisarnwipatpong, K. Triwitayakorn, C. Kirdmanee and K. Supaibulwatana. 2011. Expression of OsBADH1 gene in Indica rice (*Oryza sativa* L.) in correlation with salt, plasmolysis, temperature and light stresses. *Plant Omics.*, 4(7):75-81. <https://doi.org/10.1007/s11816-009-0123-6>
- Hatmi, S., C. Gruau, P. Trostel-Aziz, S. Villaume, F. Rabenoelina, F. Baillieul, P. Eullaffroy, C. Clément, A. Ferchichi and A. Aziz. 2015. Drought stress tolerance in grapevine involves activation of polyamine oxidation contributing to improved immune response and low susceptibility to *Botrytis cinerea*. *J. Exp. Bot.*, 66(3):775-787. <https://doi.org/10.1093/jxb/eru436>
- Hong, S.W. and E. Vierling. 2000. Mutants of *Arabidopsis thaliana* defective in the acquisition of tolerance to high temperature stress. *Proc. Natl. Acad. Sci.*, 97(4): 4392-4397. <https://doi.org/10.1073/pnas.97.8.4392>
- Howarth, C.J. 2005. Genetic improvements of tolerance to high temperature. p. 1920. In: Ashraf, M. and Harris, P.J.C., Eds., *Abiotic Stresses: Plant Resistance through Breeding and Molecular Approaches*, Howarth Press Inc. New York.
- Hussain, S.S., M. Ali, M. Ahmad and K.H.M. Siddique. 2011. Polyamines: Natural and engineered abiotic and biotic stress tolerance in plants. *Biotechnol. Adv.*, 29(3): 300-311. <https://doi.org/10.1016/j.biotechadv.2011.01.003>
- Ibrahim, S.K. and L.A. El-Muqadam. 2019. Enhancing thermotolerance of tomato plants (*Lycopersicon esculentum* mill) by heat hardening of seeds. *Bull. Natl. Res. Cent.*, 43(1):110. <https://doi.org/10.1186/s42269-019-0106-x>
- Javanmardi, J. 2009. Scientific and applied basis for vegetable transplant production. Mashad Univ. Press, Mashad, Iran.
- Javanmardi, J., M. Rahemi and M. Nasirzadeh. 2014. responses of tomato and pepper transplants to high-temperature conditioning. *Int. J. Veg. Sci.*, 20(4): 374-391. <https://doi.org/10.1080/19315260.2013.816209>
- Kakani, V.G., K.R. Reddy, S. Koti, T.P. Wallace, P.V.V. Prasad, V.R. Reddy and D. Zhao. 2005. Differences in in vitro pollen germination and pollen tube growth of cotton cultivars in response to high temperature. *Ann. Bot.*, 96(1):59-67. <https://doi.org/10.1093/aob/mci149>
- Karim, M.A., Y. Fracheboud, and P. Stamp. 1997. Heat tolerance of maize with reference of some physiological characteristics. *Ann. Bangladesh Agric.*, 7(2): 27-33.
- Khalil, S. and H.A. Moursy. 1983. Changes in some germination, morphological, physiological and reproductive characters of tomato plants as influenced by heat treatment of seed. *Ann. Agric. Sci. Ain Shams Univ., Cairo.*, 28(3): 1099-1120.
- Königshofer, H. and S. Lechner. 2002. Are polyamines involved in the synthesis of heat-shock proteins in cell suspension cultures of tobacco and alfalfa in response to high-temperature stress? *Plant Physiol. Biochem.*, 40(1):51-9. [https://doi.org/10.1016/S0981-9428\(01\)01347-X](https://doi.org/10.1016/S0981-9428(01)01347-X)
- Kotak, S., J. Larkindale, U. Lee, P. von Koskull-Döring, E. Vierling and K.D. Scharf. 2007. Complexity of the heat stress response in plants. *Curr. Opin. Plant Biol.*, 10(3): 310-316. <https://doi.org/10.1016/j.pbi.2007.04.011>
- Krishnamurthy, R. and K.A. Bhagwat. 1989. Polyamines as modulators of salt tolerance in rice cultivars. *Plant Physiol.*, 91(2): 500-504. <https://doi.org/10.1104/pp.91.2.500>
- Kumari, M., R.N. Pudake, V.P. Singh and A.K. Joshi. 2013. Association of staygreen trait with canopy temperature depression and yield traits under terminal heat stress in wheat (*Triticum aestivum* L.). *Euphytica*, 190(1):87-97. <https://doi.org/10.1007/s10681-012-0780-3>
- Larkindale, J. and E. Vierling. 2008. Core genome responses involved in acclimation to high temperature. *Plant Physiol.*, 146(2):748-61. <https://doi.org/10.1104/pp.107.112060>
- Li, Z., W.M. Palmer, A.P. Martin, R. Wang, F. Rainsford, Y. Jin, J.W. Patrick, Y. Yang and Y.L. Ruan. 2012. High invertase activity in tomato reproductive organs correlates with enhanced sucrose import into, and heat tolerance of, young fruit. *J. Exp. Bot.*, 63(3):1155-66. <https://doi.org/10.1093/jxb/err329>
- Liu, H.P., B.H. Dong, Y.Y. Zhang, Z.P. Liu and

- Y.L. Liu. 2004. Relationship between osmotic stress and the levels of free, conjugated and bound polyamines in leaves of wheat seedlings. *Plant Sci.*, 166(5):1261-7. <https://doi.org/10.1016/j.plantsci.2003.12.039>
- Liu, J.H., H. Inoue and T. Moriguchi. 2008. Salt stress-mediated changes in free polyamine titers and expression of genes responsible for polyamine biosynthesis of apple in vitro shoots. *Environ. Exp. Bot.*, 62(1):28-35. <https://doi.org/10.1016/j.envexpbot.2007.07.002>
- Liu, J.H., H. Kitashiba, J. Wang, Y. Ban and T. Moriguchi. 2007. Polyamines and their ability to provide environmental stress tolerance to plants. *Plant Biotechnol.*, 24(1):117-26. <https://doi.org/10.5511/plantbiotechnology.24.117>
- Liu, J.H., K. Nada, C. Honda, H. Kitashiba, X.P. Wen, X.M. Pang and T. Moriguchi. 2006. Polyamine biosynthesis of apple callus under salt stress: Importance of the arginine decarboxylase pathway in stress response. *J. Exp. Bot.*, 57(11):2589-2599. <https://doi.org/10.1093/jxb/erl018>
- Liu, J.H., W. Wang, H. Wu, X. Gong and T. Moriguchi. 2015. Polyamines function in stress tolerance: From synthesis to regulation. *Front. Plant Sci.*, 6:827. <https://doi.org/10.3389/fpls.2015.00827>
- Lopes, M.S. and M.P. Reynolds. 2012. Stay-green in spring wheat can be determined by spectral reflectance measurements (normalized difference vegetation index) independently from phenology. *J. Exp. Bot.*, 63(10):3789-3798. <https://doi.org/10.1093/jxb/ers071>
- Min, L., Y. Li, Q. Hu, L. Zhu, W. Gao, Y. Wu, Y. Ding, S. Liu, X. Yang and X. Zhang. 2014. Sugar and auxin signaling pathways respond to high-temperature stress during anther development as revealed by transcript profiling analysis in cotton. *Plant Physiol.*, 164(3):1293-1308. <https://doi.org/10.1104/pp.113.232314>
- Mirzaei, M., D. Pascovici, B.J. Atwell and P.A. Haynes. 2012. Differential regulation of aquaporins, small GTPases and V-ATPases proteins in rice leaves subjected to drought stress and recovery. *Proteomics*, 12(6):864-877. <https://doi.org/10.1002/pmic.201100389>
- Momcilovic, I. and Z. Ristic. 2007. Expression of chloroplast protein synthesis elongation factor, EF-Tu, in two lines of maize with contrasting tolerance to heat stress during early stages of plant development. *J. Plant Physiol.*, 164(1):9-9. <https://doi.org/10.1016/j.jplph.2006.01.010>
- Morales, D., P. Rodríguez, J. Dell'Amico, E. Nicolás, A. Torrecillas and M.J. Sánchez-Blanco. 2003. High-temperature preconditioning and thermal shock imposition affects water relations, gas exchange and root hydraulic conductivity in tomato. *Biol. Plant.*, 47(2):203. <https://doi.org/10.1023/B:BIOP.0000022252.70836.fc>
- Moriarty, T., R. West, G. Small, D. Rao and Z. Ristic. 2002. Heterologous expression of maize chloroplast protein synthesis elongation factor (EF-Tu) enhances *Escherichia coli* viability under heat stress. *Plant Sci.*, 163(6):1075-1082. [https://doi.org/10.1016/S0168-9452\(02\)00273-X](https://doi.org/10.1016/S0168-9452(02)00273-X)
- Moschou, P.N., I.D. Delis, K.A. Paschalidis and K.A. Roubelakis-Angelakis. 2008. Transgenic tobacco plants overexpressing polyamine oxidase are not able to cope with oxidative burst generated by abiotic factors. *Physiol. Plant.*, 133(2):140-56. <https://doi.org/10.1111/j.1399-3054.2008.01049.x>
- Nagarajan, S., S.V.K. Jagadish, A.S.H. Prasad, A.K. Thomar, A. Anand, M. Pal and P.K. Agarwal. 2010. Local climate affects growth, yield and grain quality of aromatic and non-aromatic rice in northwestern India. *Agric. Ecosyst. Environ.*, 138(3-4):274-81. <https://doi.org/10.1016/j.agee.2010.05.012>
- Nayyar, H., S. Kaur, Smita, S. Kumar, K.J. Singh and K.K. Dhir. 2005. Involvement of polyamines in the contrasting sensitivity of chickpea (*Cicer arietinum* L.) and soybean (*Glycine max* (L.) Merrill.) to water deficit stress. *Bot. Bull. Acad. Sin.*, 46(4):333-338.
- Peet, M.M., D.H. Willits and R. Gardner. 1997. Response of ovule development and post-pollen production processes in male-sterile tomatoes to chronic, sub-acute high temperature stress. *J. Exp. Bot.*, 48(1):101-11. <https://doi.org/10.1093/jxb/48.1.101>
- Potters, G., T.P. Pasternak, Y. Guisez and M.A.K. Jansen. 2009. Different stresses, similar morphogenic responses: integrating a plethora of pathways. *Plant, Cell Environ.*, 32(2):158-169. <https://doi.org/10.1111/j.1365-3040.2008.01908.x>
- Prasad, P.V.V., K.J. Boote, L.H. Allen, J.E. Sheehy and J.M.G. Thomas. 2006. Species, ecotype and cultivar differences in spikelet fertility and

- harvest index of rice in response to high temperature stress. *F. Crop. Res.*, 95(2-3):398-411. <https://doi.org/10.1016/j.fcr.2005.04.008>
- Qin, D., H. Wu, H. Peng, Y. Yao, Z. Ni, Z. Li, C. Zhou and Q. Sun. 2008. Heat stress-responsive transcriptome analysis in heat susceptible and tolerant wheat (*Triticum aestivum* L.) by using wheat genome array. *BMC Genomics.*, 9(1):432-9. <https://doi.org/10.1186/1471-2164-9-432>
- Qin, Y.S., S.H. Tu, W.Q. Feng and X.F. Sun. 2008. Effects of calcium, magnesium, zinc and boron fertilizers on yield and quality of field tomatoes on Chengdu Plain. *Soil Fertil. Sci. China.*, 3: 57-59.
- Queitsch, C., S.W. Hong, E. Vierling and S. Lindquist. 2000. Heat shock protein 101 plays a crucial role in thermotolerance in *Arabidopsis*. *Plant Cell.*, 12(4):479-92. <https://doi.org/10.2307/3871063>
- Rasheed, R. 2009. Salinity and extreme temperature effects on sprouting buds of sugarcane (*Saccharum officinarum* L.): Some histological and biochemical studies. PhD thesis, Department of Botany, University of Agriculture, Faisalabad, Pakistan.
- Reda, F. and H.M.H. Mandoura. 2011. Response of enzymes activities, photosynthetic pigments, proline to low or high temperature stressed wheat plant (*Triticum aestivum* L.) in the presence or absence of exogenous proline or cysteine. *Int. J. Acad. Res.*, 3(4):108-15.
- Reynolds, M.P., A.J.D. Pask and D.M. Mullan. 2012. Physiological breeding I: interdisciplinary approaches to improve crop adaptation. CIMMYT.
- Ristic, Z., G. Williams, G. Yang, B. Martin and S. Fullerton. 1996. Dehydration, damage to cellular membranes, and heat-shock proteins in maize hybrids from different climates. *J. Plant Physiol.*, 149(3-4):424-32. [https://doi.org/10.1016/S0176-1617\(96\)80144-1](https://doi.org/10.1016/S0176-1617(96)80144-1)
- Rivero, R.M., J.M. Ruiz, P.C. Garcia, L.R. Lopez-Lefebvre, E. Sánchez and L. Romero. 2001. Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. *Plant Sci.*, 160(2): 315-321. [https://doi.org/10.1016/S0168-9452\(00\)00395-2](https://doi.org/10.1016/S0168-9452(00)00395-2)
- Rossi, S., P. Burgess, D. Jespersen and B. Huang. 2017. Heat-induced leaf senescence associated with chlorophyll metabolism in bentgrass lines differing in heat tolerance. *Crop Sci.*, 57(S1): S-169. <https://doi.org/10.2135/cropsci2016.06.0542>
- Rudich, J., E. Zamski and Y. Regev. 1977. Genotypic variation for sensitivity to high temperature in the tomato: pollination and fruit set. *Bot. Gaz.*, 138(4):448-452. <https://doi.org/10.1086/336947>
- Sagor, G.H.M., T. Berberich, Y. Takahashi, M. Niitsu and T. Kusano. 2013. The polyamine spermine protects *Arabidopsis* from heat stress-induced damage by increasing expression of heat shock-related genes. *Transgenic Res.*, 22(3):595-605. <https://doi.org/10.1007/s11248-012-9666-3>
- Salin, M.L. 1988. Toxic oxygen species and protective systems of the chloroplast. *Physiol. Plant.*, 72(3):681-689. <https://doi.org/10.1111/j.1399-3054.1988.tb09182.x>
- Santa-Cruz, A., F. Perez-Alfocea, M. Caro and M. Acosta. 1998. Polyamines as short-term salt tolerance traits in tomato. *Plant Sci.*, 138(1):9-16. [https://doi.org/10.1016/S0168-9452\(98\)00143-5](https://doi.org/10.1016/S0168-9452(98)00143-5)
- Sato, S., M. Kamiyama, T. Iwata, N. Makita, H. Furukawa and H. Ikeda. 2006. Moderate increase of mean daily temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. *Ann. Bot.*, 97(5): 731-738. <https://doi.org/10.1093/aob/mcl037>
- Sato, S., M.M. Peet and J.F. Thomas. 2000. Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic, mild heat stress. *Plant, Cell Environ.*, 23(7):719-726. <https://doi.org/10.1046/j.1365-3040.2000.00589.x>
- Scafaro, A.P., P.A. Haynes and B.J. Atwell. 2010. Physiological and molecular changes in *Oryza meridionalis* Ng., a heat-tolerant species of wild rice. *J. Exp. Bot.*, 61(1):191-202. <https://doi.org/10.1093/jxb/erp294>
- Sekmen, A.H., R. Ozgur, B. Uzilday and I. Turkan. 2014. Reactive oxygen species scavenging capacities of cotton (*Gossypium hirsutum*) cultivars under combined drought and heat induced oxidative stress. *Environ. Exp. Bot.*, 99:141-9. <https://doi.org/10.1016/j.envexpbot.2013.11.010>
- Selvaraj, M. G., G. Burow, J. J. Burke, V. Belam-

- kar, N. Puppala, and M. D. Burow. 2011. Heat stress screening of peanut (*Arachis hypogaea* L.) seedlings for acquired thermotolerance. *Plant Growth Regulat.*, 65(1): 83-91. <https://doi.org/10.1007/s10725-011-9577-y>
- Shanahan, J.F., I.B. Edwards, J.S. Quick and J.R. Fenwick. 1990. Membrane thermostability and heat tolerance of spring wheat. *Crop Sci.*, 30(2):247-51. <https://doi.org/10.2135/cropsci1990.0011183X003000020001x>
- Shanmugam, S., K.H. Kjaer, C.O. Ottosen, E. Rosenqvist, D. Kumari Sharma and B. Wollenweber. 2013. The alleviating effect of elevated CO₂ on heat stress susceptibility of two wheat (*Triticum aestivum* L.) cultivars. *J. Agron. Crop Sci.*, 199(5):340-50. <https://doi.org/10.1111/jac.12023>
- Sharma, D. K., S. B. Andersen, C. O. Ottosen, and E. Rosenqvist, 2014: Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. *Physiol. Plant.*, 153(2): 284-298. <https://doi.org/10.1111/ppl.12245>
- Simões-Araújo, J.L., N.G. Rumjanek and M. Margis-Pinheiro. 2003. Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. *Brazilian J. Plant Physiol.*, 15(1):33-41. <https://doi.org/10.1590/S1677-04202003000100005>
- Smertenko, A., P. Draber, V. Viklický and Z. Opatrný. 1997. Heat stress affects the organization of microtubules and cell division in *Nicotiana tabacum* cells. *Plant, Cell Environ.*, 20(12): 1534-1542. <https://doi.org/10.1046/j.1365-3040.1997.d01-44.x>
- Snider, J.L., D.M. Oosterhuis and E.M. Kawakami. 2010. Genotypic differences in thermotolerance are dependent upon prestress capacity for antioxidant protection of the photosynthetic apparatus in *Gossypium hirsutum*. *Physiol. Plant.*, 138(3): 268-277. <https://doi.org/10.1111/j.1399-3054.2009.01325.x>
- Snider, J.L., D.M. Oosterhuis, B.W. Skulman and E.M. Kawakami. 2009. Heat stress-induced limitations to reproductive success in *Gossypium hirsutum*. *Physiol. Plant.*, 137(2):125-38. <https://doi.org/10.1111/j.1399-3054.2009.01266.x>
- Spicher, L., G. Glauser and F. Kessler. 2016. Lipid antioxidant and galactolipid remodeling under temperature stress in tomato plants. *Front. Plant Sci.*, 7: 167. <https://doi.org/10.3389/fpls.2016.00167>
- Sumesh, K. V., P. Sharma-Natu and M. C. Ghildiyal. 2008. Starch synthase activity and heat shock protein in relation to thermal tolerance of developing wheat grains. *Biol. Plant.*, 52(4): 749-753. <https://doi.org/10.1007/s10535-008-0145-x>
- Sung, D.Y., F. Kaplan, K.J. Lee and C.L. Guy. 2003. Acquired tolerance to temperature extremes. *Trends Plant Sci.*, 8(4):179-87. [https://doi.org/10.1016/S1360-1385\(03\)00047-5](https://doi.org/10.1016/S1360-1385(03)00047-5)
- Suzuki N., S. Koussevitzky, R. Mittler, G. Miller. 2011. ROS and redox signaling in the response of plants to abiotic stress. *Plant Cell Environ.*, 35(2): 259-270. <https://doi.org/10.1111/j.1365-3040.2011.02336.x>
- Suzuki, N., S. Bajad, J. Shuman, V. Shulaev and R. Mittler. 2008. The transcriptional co-activator MBF1c is a key regulator of thermotolerance in *Arabidopsis thaliana*. *J. Biol. Chem.*, 283(14):9269-75. <https://doi.org/10.1074/jbc.M709187200>
- Takahashi, S., S. Whitney, S. Itoh, T. Maruyama and M. Badger. 2008. Heat stress causes inhibition of the de novo synthesis of antenna proteins and photobleaching in cultured *Symbiodinium*. *Proc. Natl. Acad. Sci. USA*, 105(11):4203-4208. <https://doi.org/10.1073/pnas.0708554105>
- Tewari, A.K. and B.C. Tripathy. 1998. Temperature-stress-induced impairment of chlorophyll biosynthetic reactions in cucumber and wheat. *Plant Physiol.*, 117(3):851-8. <https://doi.org/10.1104/pp.117.3.851>
- Tiburcio, A.F., T. Altabella, M. Bitrián and R. Alcázar. 2014. The roles of polyamines during the lifespan of plants: From development to stress. *Planta.*, 240(1):1-8. <https://doi.org/10.1007/s00425-014-2055-9>
- Torrigiani, P., D. Bressanin, K. Beatriz Ruiz, A. Tadiello, L. Trainotti, C. Bonghi, V. Ziosi and G. Costa. 2012. Spermidine application to young developing peach fruits leads to a slowing down of ripening by impairing ripening-related ethylene and auxin metabolism and signaling. *Physiol. Plant.*, 146(1):86-98. <https://doi.org/10.1111/j.1399-3054.2012.01612.x>
- Turkes, M., 2003. Sustainable technological and behavioral options for reducing of greenhouse gas emissions. In Turkish: Sera gazýsalýným larýný nazaltýlmasý için sürdürülebilir teknolo-

- jikvedavranıypsalseçenekler). Fifth Congress of National Environmental Engineering, Ankara, Turkey. 1:267-285.
- Turner, N.C. 1981. Techniques and experimental approaches for the measurement of plant water status. *Plant Soil.*, 58(1-3): 339-66. <https://doi.org/10.1007/BF02180062>
- Vasseur, F., F. Pantin and D. Vile. 2011. Changes in light intensity reveal a major role for carbon balance in *Arabidopsis* responses to high temperature. *Plant Cell Environ.*, 34(9):1563-76. <https://doi.org/10.1111/j.1365-3040.2011.02353.x>
- Vierling, E. 1991. The role of heat shock proteins in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, 42(1): 579-620. <https://doi.org/10.1146/annurev.pp.42.060191.003051>
- Vignjevic, M., X. Wang, J.E. Olesen and B. Woltenweber. 2015. Traits in spring wheat cultivars associated with yield loss caused by a heat stress episode after anthesis. *J. Agron. Crop Sci.*, 201(1):32-48. <https://doi.org/10.1111/jac.12085>
- Volkov, R.A., I.I. Panchuk, P.M. Mullineaux and F. Schöffl. 2006. Heat stress-induced H₂O₂ is required for effective expression of heat shock genes in *Arabidopsis*. *Plant Mol. Biol.*, 61(4): 733-746. <https://doi.org/10.1007/s11103-006-0045-4>
- Wahid A., S. Gelani, M. Ashraf and M.R. Foolad. 2007. Heat tolerance in plants: An overview. *Environ. Exp. Bot.*, 61(3):199-223. <https://doi.org/10.1016/j.envexpbot.2007.05.011>
- Wahid, A. and A. Ghazanfar. 2006. Possible involvement of some secondary metabolites in salt tolerance of sugarcane. *J. Plant Physiol.*, 163(7):723-30. <https://doi.org/10.1016/j.jplph.2005.07.007>
- Wahid, A. and A. Shabbir. 2005. Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. *Plant Growth Regul.*, 46(2):133-41. <https://doi.org/10.1007/s10725-005-8379-5>
- Wang, D. and D.S. Luthe. 2003. Heat sensitivity in a bentgrass variant. Failure to accumulate a chloroplast heat shock protein isoform implicated in heat tolerance. *Plant Physiol.*, 133(1):319-27. <https://doi.org/10.1104/pp.102.018309>
- Wang, J., P.P. Sun, C.L. Chen, Y. Wang, X.Z. Fu and J.H. Liu. 2011. An arginine decarboxylase gene PtADC from *Poncirus trifoliata* confers abiotic stress tolerance and promotes primary root growth in *Arabidopsis*. *J. Exp. Bot.*, 62(8):2899-2914. <https://doi.org/10.1093/jxb/erq463>
- Wang, R., F. Yang, X.Q. Zhang, D. Wu, C. Tan, S. Westcott, S. Broughton, C. Li, W. Zhang and Y. Xu. 2017. Characterization of a thermo-inducible chlorophyll-deficient mutant in barley. *Front. Plant Sci.*, 8: 1936. <https://doi.org/10.3389/fpls.2017.01936>
- Xu, S., J. Li, X. Zhang, H. Wei and L. Cui. 2006. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. *Environ. Exp. Bot.*, 56(3):274-85. <https://doi.org/10.1016/j.envexpbot.2005.03.002>
- Yamasaki, S. and L. Dillenburg. 1999. Measurements of leaf relative water content in *Araucaria angustifolia*. *Rev. Bras. Fisiol. Veg.* 11(2):69-75.
- Yarwood, C.E. 1961. Acquired tolerance of leaves to heat. *Science*, 134(3483): 941-942. <https://doi.org/10.1126/science.134.3483.941>
- Young, L.W., R.W. Wilen and P.C. Bonham-Smith. 2004. High temperature stress of *Brassica napus* during flowering reduces micro- and megagametophyte fertility, induces fruit abortion, and disrupts seed production. *J. Exp. Bot.*, 55(396): 485-495. <https://doi.org/10.1093/jxb/erh038>
- Zhan, J., W. Huang and L. Wang. 2003. Research of weak light stress physiology in plants. *Chinese Bull. Bot.*, 20(01): 43-50.
- Zhang, M., R. Barg, M. Yin, Y. Gueta-Dahan, A. Leikin-Frenkel, Y. Salts, S. Shabtai and G. Ben-Hayyim. 2005. Modulated fatty acid desaturation via overexpression of two distinct ω -3 desaturases differentially alters tolerance to various abiotic stresses in transgenic tobacco cells and plants. *Plant J.*, 44(3):361-71. <https://doi.org/10.1111/j.1365-313X.2005.02536.x>
- Zhou, R., K.H. Kjær, E. Rosenqvist, X. Yu, Z. Wu and C.O. Ottosen. 2017. Physiological response to heat stress during seedling and anthesis stage in tomato genotypes differing in heat tolerance. *J. Agron. Crop Sci.*, 203(1):68-80. <https://doi.org/10.1111/jac.12166>
- Zhou, R., X. Yu, C.O. Ottosen, E. Rosenqvist, L. Zhao, Y. Wang, W. Yu, T. Zhao and Z. Wu. 2017. Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biol.*,

17(1):1-3. <https://doi.org/10.1186/s12870-017-0974-x>

Zhou, R., X. Yu, K.H. Kjær, E. Rosenqvist, C.O. Ottosen and Z. Wu. 2015. Screening and validation of tomato genotypes under heat stress using Fv/Fm to reveal the physiological mechanism of heat tolerance. *Environ. Exp. Bot.*, 118:1-11. <https://doi.org/10.1016/j.envexpbot.2015.05.006>

Zivcak, M., M. Brestic, Z. Balatova, P. Drevenakova, K. Olsovska, H.M. Kalaji, X. Yang and S.I. Allakhverdiev. 2013. Photosynthetic electron transport and specific photoprotective responses in wheat leaves under drought stress. *Photosynth. Res.*, 117(1-3): 529-46. <https://doi.org/10.1007/s11120-013-9885-3>