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MECHANISMS TOLERANCE PLANTS OF CROPS TO HEAT STRESS

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Abstract

Climate change is one of the most important issues globally and one of the most important obstacles facing sustainable development due to the phenomenon of global warming, which has caused a rise in temperatures that poses a serious threat to agricultural production all over the world, so heat stress reduces plant growth and development by affecting the plants main metabolic pathways. Plants have different mechanisms that humans and animals do not have, through which they can adapt and withstand the type and degree of stress including morphological, physiological and molecular mechanisms. At the field level, agricultural management such as soil cover, planting date, water management and variety selection played an important role in reducing the harmful effects of heat stress. External application such as mineral nutrition, growth regulators and natural stimulants have shown beneficial effects for plants growing under high temperatures due to improved growth and plant defense system (antioxidants).

Keywords: Climate change, stress, photosynthesis, reactive oxygen species

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آليات تحمل نباتات المحاصيل للشد الحراري

م. د. سرى جاسم بندر [1]

المستخلص

تعد ظاهرة التغيرات المناخية أحدي القضايا الهامة عالميا واحدى أهم المعوقات التي تواجه التنمية المستدامة وذلك يرجع لسبب ظاهرة الاحتباس الحراري، التي سببت ارتفاعا في درجات الحرارة شكلت تهديدا خطيرا على الانتاج الزراعي في جميع انحاء العالم، اذ يقلل الشد الناتج عن الحرارة من نمو النبات وتطوره نتيجة التأثير على مسارات التمثيل الغذائي الرئيسية للنبات. تمتلك النباتات اليات مختلفة لا يمتلكها الانسان او الحيوان تستطيع من خلالها بأن تتطبع وتتحمل نوع الشد ودرجته ومنها الاليات المورفولوجية والفسيولوجية والجزيئية. وعلى المستوى الحقلي، لعبت الادارة الزراعية كتغطية التربة، موعد الزراعة، ادارة المياه، اختيار الاصناف، دورا مهما في تقليل الاثار الضارة للشد الحراري، واظهرت التطبيقات الخارجية كالتغذية المعدنية، منظمات النمو والمحفزات الطبيعية تأثيرات مفيدة للنباتات التي تنمو تحت درجات حرارة العالية نتيجة لتحسين النمو والنظام الدفاعي للنبات (مضادات الاكسدة).

الكلمات المفتاحية: التغيير المناخي، الشد، التمثيل الكاربوني، انوع الاوكسجين التفاعلية

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Introduction

The reason for the increase in greenhouse gas emissions is global warming, which has resulted in an increase in the temperature of the earth surface, scientists have considered this phenomenon a global catastrophe due to its impact on all sectors of life. Although we do not contribute as much to the emission of greenhouse gases as industrialized countries, however we are one of the countries that have been severely affected by this phenomenon through the agricultural sector due to the world suffering from a scarcity of natural resources, especially water with the expansion of saline lands, this has increased and will increase with the rise in temperature [1]. Heat is one of the most important abiotic environmental and its effects lead to reflection on the growth, functions and productivity of plants, This is because they are organisms that are unable to leave the place where they grow and many temperature-sensitive reactions participate in their growth and development as each type of agricultural crop has an optimal temperature for carrying out its vital processes and deviation from that temperature leads to many physiological and biochemical disorders such as denaturation of proteins and lipids, the death of mitochondria and deterioration of membranes and all of these effects lead to cell starvation, reducing the flow of ions and producing toxic compounds ROS [2] and [3]. As a result, heat stress reduced the global yield of maize 7.4%, wheat 6.0%, soybeans 3.1% and rice 3.2% [4] .The article reviews the different effects of heat stress, the role of morphological, physiological and molecular mechanisms in plants to withstand this stress, in addition to the role agricultural management in increasing tolerance to stress under climate change and increase in temperatures.

EFFECTS OF HEAT STRESS

When plants are exposed to any environmental stress, including heat, their growth is affected to a clear degree as it increases with increasing temperature up to a certain point, then begins to decline with rising temperature. This is a result of the negative impact on many physiological processes in the plant, leading to a shortened life cycle and a decrease in its economic yield. This depends on the intensity of the heat, the duration, the type of crop and its sensitivity to heat [5] and [6].

-Water relations: Heat stress leads to rapid loss of water in the soil (drought) and reduced absorption by plant roots [7], in addition to losing water from plant tissues and leaves due to increased evaporation and then negatively cell metabolism [8] and [9]. Water deficiency also leads to accelerated leaf senescence due to a decrease in the photosynthesis process, which is linked to chlorophyll content, membrane stability, and the production of soluble substances such as glucose, all of these factors affect osmotic adjustment in the plant and water scarcity in the has been linked to increased ROS production [10] and [11].

- Nutrient uptake: As a result of changing the relationship between the source and the sink, reducing the amount of hormones produced in the roots, the concentration of nutrients in the plant decreases [12]. This is due to the negative effect on enzymes involved in nutrient metabolism such as nitrate and ammonium [13]. Heat stress also reduces the absorption of nutrients per unit area due to the decrease in the biomass of the roots and their surface hairs, carbon in the plant (non-structural carbohydrates), and the decrease in its transfer from the shoot to the roots, in addition to the decrease in the production and functions of the absorbed nutrient proteins [12] and [14].

- Photosynthesis: Photosynthesis is one of the most sensitive physiological processes to heat stress, its effect on C3 and C4 [15] and [16]. Many changes occur in chloroplasts, such as damage to carbon metabolism as a result of the closure of the stomata which affects the concentration of carbon dioxide between the cells, thylakoids reactions, grana swelling and loss [17] and [18]. Therefore, the photosystem II (PSII) decrease or stop, which in turn has a negative effect on the pigments of the photosynthesis process including chlorophyll as chlorophyll a and b deteriorate rapidly, this deterioration is associated with increased ROS production [19] and [20]. Heat stress affects the activity of various enzymes such as Rubisco by disrupting the electron transport chain, and enzymes (Invertase, Phosphate Synthase and ADP-glucose pyrophosphorylase), in turn the synthesis of starch and sucrose decrease [21] and [3]. In general, under heat stress it lead to an imbalance as the rate of photosynthesis reduce and photorespiration increase, this is a result of a decrease in the rate of biochemical reactions [22], All these changes varies between genotypes.

- Respiration: Under heat stress, respiration increase to reach its maximum at temperature of 40-50°C, after which respiration in the plant begin to decrease due to damage to its mechanism, as a result mitochondrial activities change [23] and [17]. Increased respiration under heat stress is a result of carbon loss, reduced ATP production and increased ROS generation, in addition to increasing the solubility of oxygen versus carbon dioxide in plant leaves [24] and [25].

- Assimilate partitioning: Heat stress affects the relationship between source and sink, this is a result of the decrease in the process of photosynthesis, its partitioning, and re-distribution of carbon and nitrogen in the plant[26], these negative changes have effects on protein and starch metabolism in leaves, leading to a decrease in yield and quality [15] and [27]. The period of grain filling depends on the metabolic substances formed in the leaves by photosynthesis and on the water soluble carbohydrate solution stored in the stem before anthesis [28], under normal conditions, the grain filling rate depends on the carbohydrates stored in the stem by 30-40%, but under different stresses, including heat and inhibition of the photosynthesis, the percentage increase to 70%. This is the main reason for the variations between genotypes in grain weight under heat stress [29] and [30].

- Reactive oxygen species: Under different stresses, including heat, harmful ROS accumulate in plants including H_2O_2 ,OH-,O_2^- leading to oxidative stress [31]. ROS are mainly generated from the reaction centers of photosystem I and II from plant organelles such as chloroplasts ,mitochondria and ribosomes [32]. These compounds at their natural level in the plant cell have a positive role in regulating cell signals and growth. Under the influence of different stresses their synthesis must be reduced or their toxicity eliminated. Plants have a defense system called antioxidants, among the damages of these compounds is the destruction of cell walls associated with increased production of OH^- in addition to the oxidative damage caused by ROS compounds to plasma membrane lipids as well as to nucleic acids [16], also breakdown the polymeric proteins into soluble forms, which leads to early senescence and programmed cell death [33] and [34].

- Plant growth and development: Heat affect seed germination, which is the first developmental stage in the life of a plant [35]. This is due to the negative impact on the activity of various enzymes responsible for starch breakdown in addition to the impact on the synthesis of abscisic acid (ABA), and on protein synthesis in seed embryos [36]. Under heat stress, cell size decrease leading to a decrease in the growth rate and dry matter productivity of various plants, heat stress causes leaf burn, rolling, tips and drying, leaf senescence and fall [37]. Heat causes phenology a shortened of the plant life cycle, as an increase in temperature (1-2°C) above the optimum level leading to a decrease in final production as a result of the pollen sterility and the number, size and weight of kernels decrease [38] and [29].

Heat tolerance mechanisms

The tolerance mechanism is known as the ability of a growing plant under stress to grow, carry out various functions and produce an economic yield, it is a complex trait resulting from a very large number of genes [37] and [39]. Plants have this mechanisms that humans and animals do not have, but it differs according to genus and type and through it plants can adapt and tolerate the type and degree of stress. Three mechanisms have been identified for plants to tolerate heat stress [14] which are:

- Morphological mechanisms: include avoidance, phenotypic flexibility and phenological changes.
- Physiological mechanisms: include water relations, osmolyte accumulation, cell membrane thermostability, hormonal changes and secondary metabolites.
- Molecular mechanisms: include antioxidants and heat shock proteins.

Morphological mechanisms

-Under heat stress, plants have different morphological mechanisms that enable them to protect themselves such as avoidance which is represented by the ability of plants to carryout metabolic processes in cells and tissues, and adapt in the short term, or phenological and morphological changes are long term [40]. Short term mechanisms include plants having the ability to reduce the absorption of solar radiation through small hairs on the leaf blade, rolling leaf blade parallel to the sun rays which is also increasing the efficiency of the leaves use of water [41]. Intensive transpiration which lowers the leaf temperature thus reducing the harmful effects of heat stress. However, the amount of transpiration in the plant is determined by the size of the stomata and their number in a certain area of the leaf, as most plants have a waxy layer (Cuticular) that covers the leaves and stems of the plant. The thickness of this layer often increases when plants grow in an atmosphere containing low relative humidity, on the opposite plants growing under high humidity have a lower density of stomata than their counterparts growing under low humidity. Plants also have the ability to change the angle of the leaf [42].

-Under heat stress, plants have variations similar to water stress, called phenotypic flexibility, such as the small size of plants due to the small size of the cell [43], The stomata in plant leaves are the main entrance for gas exchange, which constitute 1-2% of the total leaf area and are the active part in the transpiration process, as plants tend to close them to reduce water loss. Plants have multiple leaf modifications such as having small leaves, spines, tendrils or a reduction in leaf area (small size) which helps heat dissipate to the external environment more quickly due to the lower air resistance compared to plants with large leaves, in addition to increasing the xylem vessels in the roots and shoots. Heat stress increases the permeability of membranes and damages mesophyll cells, which become rounded in shape, stroma sheets become swollen, vacuole contents accumulate, mitochondria become empty and there is a change in the structure of thylakoids organization, which greatly affects the process of photosynthesis and respiration in plants [44] and [14].

-Plants also have a set of phenological variations, which are described as variations that occur during the different stages of plant growth and affect the grain yield [45], this depends on the nature of the genotype and the extent of its sensitivity to heat stress. In the vegetative growth stage, heat stress affects the gas exchange stage and the smaller the size of gas exchange the smaller the photosynthesis [15], While during the reproductive stage, heat stress to accelerated anathesis and abortion as a result of the negative effect on the development of pollen grains and then a decrease in seed production in addition to the effect of heat on the period of grain filling, especially wheat crop because of its effect on the quality of flour and bread [46] and [16].

Physiological mechanisms

-Under heat stress, water status is the most important variable as plants tend to maintain stable tissue water status when moisture is available [47]. However, at high temperatures the water statue is severely weakened because water is limited as a result of increased transpiration during the day compared to the night leading to disruption of many physiological processes [48].

-Plants accumulation various compounds with small molecular weights known as Osmolyte such as sugars, proline and alcohols. These compounds increase the survival of plants under different stresses including heat, as they maintain plant functions by adjusting Osmolyte to ensure stable turgor of plant cells, removing the toxicity of ROS and maintaining the effective synthesis of proteins [49] and [50].

-Cell membranes and their functions are sensitive to high temperatures, as they increase the kinetic energy of molecules across membranes, weaken chemical bonds within membrane weaken chemical bonds within membrane molecules, and change the composition of membrane proteins, making the lipid layer of membranes more fluid as a result of protein decomposition or an increase in unsaturated fatty acids, and thus increasing membrane permeability and loss of electrolytes [51]. This depends on the age of the plant or tissue, organ, growth stage, season and plant species, as young leaves are more affected than mature leaves. The relationship between CMT and crop yield under heat stress varies from plant to another, it was found that the relationship was significant between CMT and crop yield in Sorghum while no relationship was found between CMT and yield soybean and wheat [37].

-Under or without environmental stress, plant hormones control all plant activities and functions. It is known as a group of compounds that are produced naturally within the cells and tissues of different plants and in very small concentrations, and differ in their chemical composition and physiological function [52] and [53], while metabolic processes provide the plant with energy and the requirements for growth and development (carbohydrates, amino acids, proteins, etc.). Plant hormones play an important role in controlling the directions and speed of growth of the different parts of the plant to ultimately give the final shape. Under different stresses, including thermal stress plant growth begins to slowdown with a decrease in the rate of synthesis of growth – stimulating hormones such as auxin, gibberellin, cytokinin and an increase in the synthesis of growth – inhibiting hormones such as abscisic acid and ethylene [54].

Factors internal to the plant and external to the soil and climate are linked to the ABA synthesis processes due to the stimulation of ethylene synthesis genes and the enzymes associated with it, ethylene synthesis increases which will lead to a reduction in plant growth. However, due to the action of ABA and its interaction with the action of ethylene, the plant can continue to grow under stress. Therefore, these hormones are called stress hormones as they regulate various physiological processes in the plant as they act as signaling molecules increasing the plants tolerance to heat [14].

- Primary carbon metabolism produces compounds known as secondary metabolites such as Phenolic compound, Carotenoids and Isoprenoids, all of which play important and different roles in plants tolerance to heat stress as protecting the cell structure, lipidic components of thylakoid, PS-II and membranes from ROS damage [55] and [56].

Molecular mechanisms

- Antioxidants play an important and essential role in protecting plants under different stresses, including heat by preventing oxidation and eliminating ROS compounds to achieve the required balance in cell life [57]. Antioxidants are of two types non enzymatic compounds such as Ascorbate, Glutathione, ∝-Tocopherol and Carotenoids or enzymatic compounds such as (SOD), Catalases and other enzymes [29]. However, these enzymes are sensitive to heat because heat increases Malondialdehyde (MDA) in plant leaves which in turn reduces the activity of antioxidant enzymes, Heat tolerant varieties have a stronger defense system compared to sensitive varieties [58] and [14].

-Under heat stress, plants produce specific proteins called heat shock proteins (hsp_s), It has different groups called families depending on the molecular weight and each of them has specific properties and functions [59] and [60]. However, one of its most important functions is to give the plant tolerance to any high temperature that occurs after its synthesis. Also, high temperature causes the aggregation and denaturation of proteins which leads to the death of plant cells, preventing the aggregation of proteins and refolding [61].

Agricultural management

1. Soil covering plays an important in maintaining optimal moisture, as it reduces evaporation, improves water and nitrogen efficiency [17].
2. The optimal planting date is very important for crops under heat stress, as early or late planting affects anthesis, grain filling, maturity period and increase infection with pathogens [62].
3. Water management is important in improving crop production under heat stress, by irrigation scheduling based on critical growth stage, effective irrigation method and application of irrigation based on soil moisture [14].
4. Selecting genotypes that are tolerant to climate changes, including heat stress or planting early-maturing varieties [63].
5. Increasing the mineral nutrition of the crop such as nitrogen, potassium, magnesium, manganese, boron and selenium which play an important role in activating the physiological and molecular processes in the plant. After anthesis it improves the grain protein, cytokinin production, slows down ABA synthesis, stimulates photosynthesis and accumulation of metabolites [64] and [65].
6. Exogenous addition represented by growth stimulants such as plant regulators and alpha-tocopherol (vitamin E)… and others, and their role lies in managing oxidation by regulating ROS, and all these external additions increase the activity of the defense system known as antioxidants. While the endogenous addition of calcium protects chlorophyll from being destroyed by solar radiation, in addition to affecting the function of the stomata and activating the enzymatic antioxidants CAT, SOD, APX and the non-enzymatic

antioxidants tocopherol and ascorbic acid and as a result, the positive effect on tolerance to various stresses including heat [66] and [67].

7. The use of natural stimulants such as amino acids, microorganisms, plant extracts, seaweed and inorganic materials plays a role in regulating various plant processes [68].
8. Treating plants with Oxylipins short-chain reactive represented by the C4-C6 group which show high heat tolerance [69].
9. Stimulating the synthesis of heat shock proteins (HSPs), one of the most important functions of which is to give the plant the ability to tolerance high temperature [70].

Conclusion

Plants are exposed in the environment in which they grow to various types of abiotic stresses that negatively affect their growth, development and productivity, due to climate change heat has become one of the most important environmental stresses that limits agricultural production around the world and a threat to food security. The effects of heat stress on plants are complex in nature and affect all stages of plant growth but the most affected stage is the reproductive stage which is represented by anthesis and grain filling, this is due to the heat causing disturbance in water relations in the leaves, the negative effects on photochemical and biochemical reactions, photosynthetic membranes, changes in the structure of tissues and cell organelles and the production of reactive oxygen species. Plants have three mechanisms that enable them to survive in high temperature environments morphological, physiological and molecular, crops plants use more than one mechanism at a time to withstand high temperatures, management proper of water and nutrient, foliar application of growth and natural stimulants have helped reduce the negative impact of heat stress. However, what molecular genetics offers today in terms of transferring specific genes from crop to another has opened new horizons in breeding new varieties with better tolerance to various stress factors such as high temperature, and this is of great importance in achieving between balancing future population growth and food demand throughout the world.

References

[1] Mahato, A.(2014). Climate Change and its Impact on Agriculture. International Journal of Scientific and Research Publications,4(4):1-6.

[2] Howarth, C. J. (2005). Genetic improvements of Tolerance to High Temperature. Abiotic stresses: Plant resistance through breeding and molecular approaches 1920.

[3] Hasanuzzaman, M., Nahar, K., Alam, M.M., Roychowdhury, R. and Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. International Journal of Molecular Sciences. 14:9643–9684. doi:10. 3390/ijms14059643.

[4] Zhou, R., Yu, X., Ottosen, C.O., Rosenqvist, E., Zhao, L., Wang, Y., Yu, W., Zhao, T. and Wu, Z.(2017). Drought stress had a predominant effect overheat stress on three tomato cultivars subjected to combined stress. BMC plant biology 17: 1-13. doi: 10.1186/s12870-017-0974-x

[5] Xalxo, R., Yadu, B., Chandra, J., Chandrakar, V. and Keshavkant, S. (2020). Alteration in carbohydrate metabolism modulates thermotolerance of plant under heat stress. In S. H. Wani and V. Kumar (eds). Heat Stress Tolerance in Plants: Physiological, Molecular

and Genetic Perspectives, 77-115. doi. org/ 10. 1002/9781119432401.ch5.

[6] Qureshi, H., Abbas , M. H., Jan , T., Mumtaz, K., Mukhtar, H. and Khan, U.(2022). Plant Responses to Heat Stress. Journal Advances of Nutrition Science and Technology, 2(2): 40-53. doi:10.15228/ANST.

[7] Atkinson, N. J. and Urwin, P. E.(2012). The interaction of plant biotic and abiotic stresses: From genes to the field. Journal of Experimental Botany, 63(10): 3523–3544, doi.org/10.1093/jxb/ers100.

[8] Farooq, M., Wahid, A., Kobayashi, N., Fujita, D. and Basra, S.M.A. (2009). Plant drought stress: effects, mechanisms and management. Sustainable Agriculture. 29:185–212. doi:10.1051/agro:2008021.

[9] Karki, P., Subedi, E., Acharya ,G., Bashyal, M., Dawadee, N. and Bhattarai, S.(2021). A review on the effect of heat stress in wheat (*Triticum aestivum* L.). Archives of Agriculture and Environmental Science. 6(3): 381-384. doi.org/10.26832/24566632.2021.0603018.

[10] Ahmad, P., Jaleel, C.A., Salem, M.A., Nabi, G. and Sharma, S. (2010). Roles of enzymatic and nonenzymatic antioxidants in plants during abiotic stress. Critical Reviews in Biotechnol 30:161–175. doi:10.3109/ 07388550903524243.

[11] Hu, S., Ding, Y. and Zhu, C.(2020).Sensitivity and Responses of Chloroplasts to Heat Stress in Plant. Frontiers Plant Science. 11:1-11. doi: 10.3389/fpls.2020.00375.

[12] Huang, D., Wu, W., Abrams, S.R. and Cutler, A.J.(2008). The relationship of drought-related gene expression in Arabidopsis thaliana to hormonal and environmental factors. Journal of Experimental Botany, 59(11):2991–3007.doi.org/10.1093/jxb/ern155

[13] Hungria, M. and Kaschuk, G. (2014). Regulation of N2 fixation and NO3 -/NH4++ assimilation in nodulated and N-fertilized (*Phaseolus vulgaris* L.). exposed to high temperature stress. Environmental and Experimental Botany, 98:32–39.doi.org/10.1016/j.envexpbot.2013.10.010

[14] Hassan, M. U., Chatthaa, M. U., Khana, I., Chatthab, M. B., Barbantic, L., Aamerd, M., Iqbala, M. M., Nawazf, M., Mahmooda, A., Alic, A. and Aslama, M. T.(2020). Heat stress in cultivated plants: nature, impact, mechanisms, and mitigation strategies-a review. Plant Biosystems-an International Journal Dealing with all Aspects of Plant Biology, Pp:1-24. https://doi.org/10.1080/11263504.2020.1727987

[15] Feng, B., Liu, P., Li, G., Dong, S.T., Wang, F.H., Kong, L.A. and Zhang, J.W. (2014). Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. Journal of Agronomy and Crop Science, 200:143–155. doi:10.1111/jac.12045.

[16] Firmansyah, F. and Argosubekti, N.(2020). A review of heat stress signaling in plants. Earth and Environmental Science.pp:1-11. doi:10.1088/1755-1315/484/1/012041.

[17] Akter, N. and Islam, M. R.(2017). Heat stress effects and management in wheat. A review. Agronomy for Sustainable Development, 37: 2-17. doi: 10.1007/s13593-017-0443-9.

[18] Poudel, H., Bhattarai, B., Khanal, B., Pandey, D., Poudel, K., Dhungana, M., Pandey, R. and Dhungana, S.(2021). Effect of Heat Stress in Wheat: A Review. Agriculture and

Environment, 2(5):63-69.doi: AEN-2021-02-05-016

[19] Wang, H., Wang, H., Shaoand, H. and Tang, X.(2016). Recent advances in utilizing transcription factors to improve plant abiotic stress tolerance by transgenic technology. Frontiers in Plant Science, 7:67. doi. org/ 10.3389/fpls.2016.00067

[20] Fahad, S. , Bajwa, A. A., Nazir, U., Anjum, S. A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., Ihsan, M. Z., Alharby, H., Wu, C., Wang, D. and Huang, J.(2017).Crop production under drought and heat stress: Plant responses and management options. Frontiers in Plant Science,8:1-16.doi. org/ 10.3 389/fpls.2017.01147

[21] Vu, J., Gesch, C. V., Pennanen, R. W., Allen, A. H., Boote, L. H. J. and Bowes G. S.(2001). Soybean photosynthesis, Rubisco and carbohydrate enzymes function at supra-optimal temperatures in elevated CO2. Journal of Plant Physiology, 158: 295–307. doi: 10.1078/0176-1617-00290.

[22] Nakamoto, H. and Hiyama, T.(1999). Heat-shock proteins and temperature stress. In: Pessarakli M. (edr.). Handbook of plant and crop stress. New York (NY): Marcel Dekker; p. 399- 416.

[23] Prasad, P. V. and Djanaguiraman, M. (2014). Response of floret fertility and individual grain weight of wheat to high temperature stress: sensitive stages and thresholds for temperature and duration. Functional Plant Biology, 41(12): 1261-1269. doi.org/10.1071/FP14061

[24] Cossani, C.M. and Reynolds, M.P.(2012). Physiological traits for improving heat tolerance in wheat. Plant Physiology, 160(4):1710–1718.doi.org/10.1104/pp.112.207753

[25] Huang, B., Rachmilevitch, S. and Xu, J. (2012). Root carbon and protein metabolism associated with heat tolerance. Journal of Experimental Botany, 63:3455–3465. doi: 10.1093/jxb/ers003.

[26] Taiz, L. and Zeiger, E. (2006). Plant Physiology, 4th Edn. Sunderland, MA: Sinauer Associates Inc. Publishers.

[27] Qaseem, M. F., Qureshi, R., and Shaheen, H. (2019). Effects of pre-anthesis drought, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress. Scientific Reports, 9(1), 1–12, https:// doi. org/ 10. 1038/ s41598 -019-43477-z.

[28] Talukder, A.S.M.H.M., McDonald, G.K. and Gill, G.S.(2013). Effect of short-term heat stress prior to flowering and at early grain set on the utilization of water-soluble carbohydrate by wheat genotypes. Field Crop Research, 47:1–11.doi.org/10.1016/j.fcr.2013.03.013

[29] Farooq, M., Bramley, H., Palta, J. A. and Siddique, K. H.M.(2011). Heat stress in wheat during reproductive and grain-filling phases. Critical Reviews in Plant Sciences, 30:1–17. doi: 10. 1080/ 07352689.2011.615687.

[30] Poudel, P. B. and Poudel, M. R.(2020). Heat Stress Effects and Tolerance in Wheat: A Review. Journal of Biology and Today's World, 9(4):1-6. doi: 10.35248/2322-3308.20.09.217

[31] Garapati, P., Xue, G. P., Munné-Bosch, S. and Balazadeh, S.(2015). Transcription factor ATAF1 in Arabidopsis promotes senescence by direct regulation of key chloroplast maintenance and senescence transcriptional

cascades. Plant Physiology,168: 1122–1139. doi:10.1104/pp.15.00567.

[32] Hemantaranjan, A. , Malik, C.P. and Bhanu, A. N.(2018). Physiology of heat stress and tolerance mechanisms - An Overview. The Journal of Plant Science Research, 33 (1) :55-68.

[33] Young, L.W., Wilen, R.W. and Bonham-Smith, P.C.(2004). High temperature stress of Brassica napus during flowering reduces micro- and megagametophyte fertility, induces fruit abortion, and disrupts seed production. Journal of Experimental Botany, 55(396):485–495. doi: 10. 1093/ jxb/ erh038

[34] Qi, Y., Wang, H., Zou, Y., Liu, C., Liu, Y., Wang, Y. and Zhang, W.(2011). Over-expression of mitochondrial heat shock protein 70 suppresses programmed cell death in rice. FEBS Letters, 585(1):231–239. doi. org/ 10. 1016/ j. febset.2010.11.051

[35] Kaur, H., Sirhindi, G., Bhardwaj, R., Alyemeni, M.N., Siddique, K.H. and Ahmad, P.(2018). 28-homobrassinolide regulates antioxidant enzyme activities and gene expression in response to salt-and temperature-induced oxidative stress in Brassica juncea. Scientific Reports, 8(1): 1-13. doi:10.1038/s41598-018-27032-w

[36] Essamine, J., Ammar, S. and Bouzid, S. (2010). Impact of heat stress on germination and growth in higher plants: physiological, biochemical and molecular repercussion and mechanisms of defense. Journal of Biological Sciences, 10(6): 565–572.

[37] Wahid, A., Gelani, S., Ashraf, M. and Foolad, M. R.(2007). Heat tolerance in 1260 plants: an overview. Environmental and Experimental Botany, 61: 199–223. https:/ /doi. org/ 10. 1016/ j. envexpbot.2007.05.011

[38] Reynolds, M.P., Pierre, C.S., Saad, A.S.I., Vargas, M . and Condon, A.G.(2007). Evaluating potential genetic gains in wheat associated with stress adaptive trait expression in elite genetic resources under drought and heat stress. Crop Science, 47:S-172–189. https://doi.org/10.2135/cropsci2007.10.0022IPBS

[39] Pandey, G. C., Mehta, G., Sharma, P. and Sharma, V.(2019). Terminal heat tolerance in wheat: An overview. Journal of Cereal Research.11(1):1-16. doi. org/10.25174/2249-4065/2019/79252

[40] Srivastava, S., Pathak, A.D., Gupta, P.S., Shrivastava, A.K. and Srivastava, A.K.(2012). Hydrogen peroxide-scavenging enzymes impart tolerance to high temperature induced oxidative stress in sugarcane. Journal of Environmental Biology, 33(3):657–661.

[41] Sarieva, G.E., Kenzhebaeva, S.S. and Lichtenthaler, H.K.(2010). Adaptation potential of photosynthesis in wheat cultivars with a capability of leaf rolling under high temperature conditions. Russian Journal of Plant Physiology, 57(1): 28–36. doi: 10.1134/S1021443710010231

[42] Balla, K., Bencze, S., Bónis, P., Árendás, T. and Veisz, O.(2013). Changes in the photosynthetic efficiency of winter wheat in response to abiotic stress. Central European Journal of Biology.pp:1-12. doi: 10.2478/s11535-014-0288-z.

[43] Rahman, M.M (2004). Response of wheat genotypes to late seeding heat stress. MS Thesis. Department of Crop Botany. Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur, Bangladesh. pp 210.

[44] Peverelli, M. C. and Rogers, W. J.(2013). Heat stress effects on crop performance and tools for tolerance breeding. Rev. FCA UNCUYO, 45(2):349-368.

[45] Salazar-Gutierreza, M.R., Johnsonb, J., Chaves-Cordobaa, B. and Hoogenboom, G.(2013). Relationship of base temperature to development of winter wheat. International Journal of Plant Production 7 (4):741-762.

[46] Wang, X., Hou, L., Lu, Y., Wu, B., Gong, X., Liu, M., Wang, J., Sun, Q., Vierling, E. and Xu, S.(2018).Metabolic adaptation of wheat grain contributes to a stable filling rate under heat stress. Journal of Experimental Botany, 69(22):5531–5545. doi:10.1093/jxb/ery303

[47] Mazorra, L.M., Nunez, M., Echerarria, E., Coll, F. and Sanchez-Blanco, M.J.(2002). Influence of brassinosteriods and antioxidant enzymes activity in tomato under different temperatures. Biologia Plantarum, 45:593–596. https://doi.org/10.1023/A:1022390917656

[48] Tsukaguchi, T., Kawamitsu, Y., Takeda, H., Suzuki, K. and Egawa, Y.(2003). Water status of flower buds and leaves as affected by high temperature in heat tolerant and heat-sensitive cultivars of snap bean (*Phaseolus vulgaris* L.). Plant Production Science, 6: 4–27. https://doi.org/10.1626/pps.6.24

[49] Hare, P.D., Cress, W.A. and Staden, J.V.(1998). Dissecting the roles of osmolyte accumulation during stress. Plant, Cell Environment, 21: 535–553. https://doi.org/10.1046/j.1365-3040.1998.00309.x

[50] Sakamoto, A. and Murata, N.(2002). The role of glycine bataine in the protection of plants from stress: clues from transgenic plants. Plant, Cell Environment, 25: 163–171. https://doi.org/10.1046/j.0016-8025.2001.00790.x

[51] Savchenko, G.E., Klyuchareva, E.A., Abrabchik, L.M. and Serdyuchenko, E.V.(2002). Effect of periodic heat shock on the membrane system of etioplasts. Russian journal of plant physiology. 49: 349–359. https://doi.org/10.1023/A:1015592902659

[52] Gana, A. S.(2010). The role of synthetic growth hormones in crop multiplication and improvement. African Journal of Biotechnology 10(51), pp:10330-10334, doi: 10.5897/AJB10.301

[53] Küpers, J. J., Oskam, L. and Pierik, R. (2020). Photoreceptors regulate plant developmental plasticity through auxin. Plants, 9(8):940. doi: 10.3390/ plants9080940

[54] Larkindale, J. and Huang, B.(2005). Effects of abscisic acid, salicylic acid, ethylene and hydrogen peroxide in thermotolerance and recovery for creeping bentgrass. Plant Growth Regulation, 47:17- 28. https://doi.org/10.1007/s10725-005-1536-z

[55] Sharkey, T.D.(2005). Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, Rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant, cell and environment, 28(3):269–277. https://doi.org/10.1111/j.1365-3040.2005.01324.x

[56] Wahid, A. and Ghazanfar, A.(2006). Possible involvement of some secondary metabolites in salt tolerance of sugarcane. Journal of plant physiology, 163(7): 723–730. https://doi. org/10. 1016/j. jplph. 2005.07.007

[57] Almeselmani, M., Deshmukh, P.S. and Sairam, R.K.(2009). High temperature stress tolerance in wheat genotypes: role of

antioxidant defence enzymes. Acta Agronomica Hungarica, 57(1):1–14. https://doi.org/10.1556/AAgr.57.2009.1.1

[58] Mohammed, A.R. and Tarpley, L.(2010). Effects of high night temperature and spikelet position on yield-related parameters of rice (*Oryza sativa* L.) plants. European Journal of Agronomy. 33(2):117–123. doi. org/ 10. 1016/ j. eja.2009.11.006

[59] Maestri, E., Klueva, N., Perrotta, C., Gulli, M., Nguyen, H.T. and Marmiroli, N.(2002). Molecular genetics of heat tolerance and heat shock proteins in cereals. Plant Molecular Biology, 48(5/6):667–681. https://doi.org/10.1023/A:1014826730024

[60] Feussner, K., Feussner, I., Leopold, I. and Wasternack, C.(1997). Isolation of a cDNA coding for an ubiquitin-conjugating enzyme UBC1 of tomato the first stress-induced UBC of higher plants. FEBS Letters, 409(2): 211–215. https://doi.org/10.1016/S0014-5793(97)00509-7.

[61] Iba, K.(2002). Acclimative response to temperature stress in higher plants: approaches of gene engineering for temperature tolerance. Annual Review of Plant Biology, 53(1):225–245. https:// doi. org/ 10. 1146/ annurev.arplant.53.100201.160729.

[62] Hakim, M., Hossain, A. , Da Silva, J. A. T., Zvolinsky, V. and Khan, M.(2012). Protein and starch content of 20 wheat (*Triticum aestivum* L.) genotypes exposed to high temperature under late sowing conditions. Journal Scientific Research,4: 477- 477. doi: 10.3329/jsr.v4i2.8679

[63] Gouachea, D., Bris, X.L., Bogard, M., Deudon, O., Pagé, C. and Gate, P. (2012). Evaluating agronomic adaptation options to increasing heat stress under climate change during wheat grain filling in France. European Journal of Agronomy, 39:62–70. doi:10.1016/j.eja.2012.01.009

[64] Singh, B., Pathak, K., Verma, A., Verma, V. and Deka, B.(2011). Effects of vermicompost, fertilizer and mulch on plant growth, nodulation and pod yield of French bean (*Phaseolus vulgaris* L.). Vegetable Crops Research Bulletin. 74: 153-165. doi: 10.2478/v10032-011-0013-7

[65] Mengutay, M., Ceylan, Y., Kutman, U. B. and Cakmak, I.(2013). Adequate magnesium nutrition mitigates adverse effects of heat stress on maize and wheat. Plant soil, 368: 57–72. doi: 10.1007/s11104-013-1761-6

[66] Waraich, E., Ahmad, R., Halim A. and Aziz, T.(2012). Alleviation of temperature stress by nutrient management in crop plants: a review. Journal of soil science and plant nutrition,12: 221-244. doi: 10.4067/S0718-95162012000200003

[67] Uprety, D. C. and Reddy, V. (2016). Mitigation technologies to control high temperature stress in crop plants, in Crop Responses to Global Warming. (Berlin: Springer), 117–125. https://doi.org/10.1007/978-981-10-2004-9_5

[68] Van Oosten, M. J., Pepe, O., De Pascale, S., Silletti, S. and Maggio, A.(2017). The role of bio-stimulants and bio effectors as alleviators of abiotic stress in crop plants. Chemical and Biological Technologies in Agriculture, 4: 1-12. doi: 10.1186/s40538-017-0089-5

[69] Yamauchi, Y. (2018). Integrated chemical control of abiotic stress tolerance using biostimulants, in Plant, Abiotic Stress and Responses to Climate Change, 133–143. doi: 10. 5772/ intechopen. 74214.

[70] Ahmad, M., Imtiaz, Nawaz, M., M. S., Mubeen, F. and Imran, A.(2022). What Did We Learn From Current Progress in Heat Stress Tolerance in Plants? Can Microbes Be a Solution? Frontiers in Plant Science, 13:794782. doi: 10.3389/fpls.2022.794782