TRENDS IN AGRICULTURE SCIENCE

Popular Article

Vol.3 Issue 02 February 2024, Page: 1435-1442

Amelioration of High Temperature Stress in Crop Plants Employing Thermo-tolerant Microbes

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https://doi.org/10.5281/zenodo.10702496

Summary

Incidences of high temperature stress impacting crop productivity across the world. Extreme events such as global warming, heat waves, prolonged water deficit condition are likely to further increase in the coming future due to climate change. A wide range of adaptation and mitigation strategies required to cope with high temperature stress. Efficient resource management practices and development of better crop breeds can help to overcome the heat stress tolerance to some extent. However, resource management and crop improvement strategies being long drawn and cost intensive, there is a need to develop simple and low-cost biological methods for the management of thermal stress. In respect to thermo-tolerant mechanism, Microorganisms could play a significant role for sustainable crop production. Some microbial symbionts are involved to mediate plant stress response through enhancing thermal-tolerance. Several meta–analysis studies in response to thermal stress tolerance found to be higher biomass and photosynthesis under heat stress conditions. Some studies revealed that significantly decreased accumulation of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) indicated a lower oxidation level in the colonized plants, which was also correlated with the higher activity of catalase, peroxidase, and glutathione reductase enzymes due to microbial colonization under heat stress.

Introduction

Constant rise of the ambient temperature due to continuous climate change is one of the worldwide issues and has devastating impact on the sustainable crop production (IPCC, 2019). Thermal stress causes adverse impact on the growth, development and physiological mechanism on the plants (Hassan et al., 2021). Thermal–stress is the serious threat responsible for crop loss across the world. Various measures have been standardized and can be taken to reduce the effect of thermal–stress. Plants develop varying levels of adaptation, avoidance, acclimatization, and tolerance mechanisms to cope with thermal–stress through morphological, physiological, biochemical, and molecular strategies. The atmospheric temperature higher than normal range leads to cascade of cellular function and release heat shock proteins (HSPs) that help to minimize the loss of plants at cellular level. The role of microbes on plant stress in response to thermal–stress has been given attention in last few years (Zhao, et al., 2021). In Several studies, it has

Published: 25 Feb. 2024
ISSN: 2583-7850

found that some plant species associated with microbial symbionts may insfluence responses of the host plant to thermal–stress. Microbes associated with plant thermal–stress tolerance are ubiquitous and pay attention in plant ecology and physiology (Dastogeer, et al., 2020). Moreover, microbes produce the wide range of compounds to impact the responses of plants at the molecular level, triggering the biosynthesis of pigments, secondary metabolites, hormones, antioxidants, and alkaloids (Naamala and Smith, 2021).

Thermo-tolerant Microbes

Thermo–tolerant microbes are biological agents associated with heat–tolerance mechanism. Several microbes have been identified to cause thermo–tolerance. Thermo–tolerance is the complex mechanism achieved by production of proline and glycine betaine. Proline and glycine betaine are the two compounds which contributes to thermoregulation Exopolysaccharides are one of the biological substances released by bacterium under heat stress condition containing 97% water, which improve the moisture content in the soil (Ali, et al., 2020). Endophytes are Plant Growth-Promoting Rhizobacteria is the two identified thermo–tolerant microbes actively involved in the thermo–regulation under high–temperature stressed condition (Shekhawat, et al., 2022).

Endophytes are microbes used as biostimulants to produce compounds involved in the development of tolerance against heat stress. Most of the endophytes symbiotically are associated with plant cell mad mediates heat stress mitigation. The modes of action of the endophytes for promoting growth under heat – stress have been reported by many researchers (Mukhtar, et al., 2022). Park et al., (2017) reported the effects of endophytic microbe *SA187* on Arabidopsis thaliana and wheat plants and he found that *Enterobacter*sp.*SA187* induced thermo–tolerance in plants by promoting thermo–priming.

Plant Growth-Promoting Rhizobacteria (PGPR) is another bacterium which promotes plant growth under heat stress through colonizing roots of plants. Plant Growth-Promoting Rhizobacteria promotes plant growth directly or indirectly. They promote plant growth directly by regulation nitrogen fixation, phosphate solubilisation and by accelerating the synthesis of plant growth regulators like Indole–3 acetic acid, gibberellic acid and cytokinin under heat stressed condition. Indirectly, they also promote plant growth under heat stress by producing proline, sugars, organic acids, and glycine betaine (Basu, et al., 2021).

Role of Thermo–tolerant microbes under thermal–stress

Thermo–tolerant microbes induced physiological changes such as photosynthesis, respiration, stomatal closure under heat–stress condition. They also mitigate heat–stress through nitrogen fixation, production of enzyme ACC-deaminase and phytohormones.

Thermal–stress breaks photosynthetic pigments and inhibits the proper growth and development of plants. Studies revealed that heat–stress condition inhibited RuBP production involved in the electron transport chains. Enzymes involved in the metabolic processes in photosystem are also inactivated when plant subjected to thermal–stress is the major cause of the lowering of photosynthesis (Qu, et al., 2021). Some oxygenic microbe's (cyanobacteria) having light-harvesting have been identified and played crucial role under heat–stress during convert light energy into chemical energy through photosynthesis. Respiratory mechanism of the plants is also influenced under high temperature. Plant and beneficial microbe interaction minimized stress level and promote plant growth by maintaining nitrogen, hydrogen, sulphur, and oxygen levels in a biogeochemical cycle (Scafaro, et al., 2021).Stomatal conductance is one of the important physiological mechanisms of the green plants enhanced under high temperature by accelerating water loss through transpiration. Plant–microbial interaction enhances the production of abscisic acid (ABA), which causes stomatal closure to protect plants from water loss (Bharath, et al., 2021).

The process of conversion of gaseous N_2 is into biological forms of NH_3 and NH_4 used as macronutrient by green plants are also affected by thermal–stress. Prolonged heat–stress accelerates nitrogen accumulation in the meristematic cells of the plant plays important role in energy metabolism, protein synthesis, and photosynthesis (Radecker, et al., 2022). Several microbes have been identified to mitigate heat stress by enhancing nitrogen fixation. Furthermore, symbiont relationship of plants with nitrogen fixating microbes improve the soil nitrogen concentration, rhizobacterial population levels, soil nitrogenase activities and nitrogen uptake by plants (Moynihan, et al., 2022).

ACC-deaminase is 1-Aminocyclopropane-1-carboxylate enzyme produce by some microbes accelerate plant growth by sequestering and splitting plant-produced ACC, producing alfa-ketobutyrate and ammonia. Plant–microbial interaction promotes production of ACC-deaminase, which moderated ethylene metabolism and resulted in better heat tolerance (Singh, et al., 2022). Diverse groups of microbes enhance thermal–stress in various crop species are given in the table.

Table: Microbial thermal response on various plant species

Host Crops	***Symbiont Microbes***	***Response under thermal–stress***	***References***
Wheat	*Bacillus amyloliquefaciens* (Bacteria)	*B. amyloliquefaciens* (UCMB5113) improved heat stress tolerance by reducing ROS and transcript level.	Abd El-Daim et al., (2014)
	Bacillus amyloliquefaciens (Bacteria)	Enhanced heat tolerance by modifications in wheat leaf transcript.	Abd El-Daim, et al., (2018)

	B. velezensis (Bacteria)	*B. velezensis* (5113) regulate metabolic pathways of amino acids, proteins to develop heat tolerance.	Abd El-Daim, et al., (2019)
	P. putida (Bacteria)	*P. putida* (AKMP7) increased vegetative growth, dry biomass, chlorophyll, sugars, proline, starch, amino acids under heat stress.	Ali, et al., (2011)
	Arbuscularmycorrhizal(Fungi)	AMF increased grain number in wheat plants, alters nutrient allocation and tiller number composition in the plants under heat-stress.	Cabral, et al., (2016)
Durum wheat	Endophytic Ascomycetousmitosporic fungi	Improved the hydrothermal time (HTT) and energy of germination (EG) value to enhanced resistance in heat stress.	Hubbard, et al., (2012)
		Improve photosystem II in wheat plants during vegetative growth.	Hubbard, et al., (2014)
Sorghum	*Pseudomonas sp.* (Bacteria)	*Pseudomonas* sp. strain AKM-P6 enhanced tolerance of sorghum seedlings.	Ali, et al., (2009)
	B. cereus, Providenciarettgeri, M. odoratimimus (Bacteria)	Increased plant growth, antioxidant, enzyme activities and decreased proline, contents in plants under heat stress and enhanced heat tolerance.	Bruno, et al., (2020)
Cucumber	Theromophilic endophytic fungus	Increased thermal–tolerance stress by maximizing quantum efficiency of photosystem II, photosynthesis rate, and water use efficiency.	Ali, et al., (2018)
Cullen plicata	*Thermomyceslanuginosus* (Endophytic fungus)	Enhanced heat stress tolerance by changing secondary metabolite accumulations and antioxidant activities.	Ali, et al., (2019)
Tomato	*S. deserticola and S. constrictum*	Reduced oxidative stress by decreasing lipid peroxidation, H_2O_2 levels and enhancing antioxidant enzyme activities.	Duc, et al., (2018)
	Paraburkholderiaphytofirmans (Bacteria)	Improved tomato growth by enhancing chlorophyll content, accumulations of sugars, amino acids, proline, and malate.	Issa, et al., (2018)
	B. cereus (Bacteria)	Protect tomato seedlings against heat stress by balancing ABA, SA, APX, GSH, SOD, Fe, P, and K.	Khan, et al., (2020a)
Perennial ryegrass	*Epichlofestucae* (Endophytic fungus)	The endophyte strain AR37 synthesized alkaloids at high temperature and increase tolerance level	Hennessy, et al., (2016)
	A. flavus (Endophytic fungus)	Regulate concentration of ABA, proline, phenols, flavonoids, catalase and ascorbic acid oxidase against heat stress.	Ismail, et al., (2019)
	A. niger (Endophytic fungus)	*A. niger protected*plants from thermal stress by increasing biomass and chlorophyll content, AAO, CAT, GR, SOD, POD, proline and phenolics.	Ismail, et al., (2020a)
	A. violaceofuscus (Endophytic fungus)	Increased the total chlorophyll content, ROS, ABA, and proline.	Ismail, et al., (2020b)

	Rhizopus oryzae (Endophytic fungus)	*R. oryzae*, isolated from *A. capillus-veneris* improve heat tolerance by inducing phenolics, flavonoids, SA, IAA, AAO, CAT, proline, sugar, lipids.	Ismail, et al., (2020c)
Pipper	*Penicillium resedanum* (Endophytic fungus)	*P. resedanum* (LK6) increased the shoot length, shoot fresh and dry wrights of *C. annuum* L. under heat stress.	Khan, et al., (2013)
	P. resedanum (Endophytic fungus)	*P. resedanum* (LK6) improved plant height and dry weight under heat stress	Khan, et al. (2015)
Crocus sati vus	*Exophiala sp. (LHL08)* (Endophytic fungus)	Modulate heat stress by influencing physio-biochemical traits under thermal–stress.	Khan, et al., (2012b)
	Paecilomycesformosus (LHL10) (Endophytic fungus)	*P. formosus* (LHL10) improved growth chlorophyll contents under stress conditions.	Khan, et al. (2012a)
Soybean	*B. cereus* (Bacteria)	Mitigate heat–stress by synthesizing GA, IAA, ABA, and SA.	Khan, et al. (2012b)
Ryegrass	*A.aculeatus* (Endophytic fungus)	Improved heat tolerance by enhancing photosynthetic apparatus in heat stress	Li, et al. (2021)
Maize	*Glomus sp.*	Alter PSII h under high temperature and protect plants.	MathurandJajoo (2020)
Tomato	*B. cereus* (Bacteria)	Promoted shoot, root length, leaf surface area, fresh and dry under heat stress	Mukhtar, et al. (2020)
Rice	*Chaetomium sp.* (Fungus)	Increased roots and shoot growth under heat stress.	Sangamesh, et al. (2018)
Wheat	*B. safensis and Ochrobactrumpseudogrignonense* (Bacteria)	PGPR enhanced thermo-tolerance by reduction of ROS production, cellular damage, enhanced chlorophyll content, and accumulation of osmolytes.	Sarkar, et al. (2018)
Arabidopsis thaliana	*Enterobacter sp.* (E. bacterium)	SA187 enhanced the expression of heat-responsive genes.	Shekhawat, et al. (2020)
Rice	*P. formosus* (Endophytic fungus)	*P. formosus* LWL1formed hormones and secondary metabolites in Dongjin Japanese rice.	Waqas, et al. (2015)
Maize	*G. etunicatum (AM fungus)*	Maize plants inoculated by AM fungus performing better in terms of stomatal conductance and transpiration.	Zhu, et al. (2011)

References

Abd El-Daim I. A., Bejai S., Fridborg I., Meijer J. (2018). Identifying potential molecular factors involved in *Bacillus amyloliquefaciens* 5113 mediated abiotic stress tolerance in wheat. *Plant Biol.* 20 271–279. 10.1111/plb.12680

Abd El-Daim I. A., Bejai S., Meijer J. (2014). Improved heat stress tolerance of wheat seedlings by bacterial seed treatment. *Plant Soil* 379 337–350. 10.1007/s11104-014-2063-3

Abd El-Daim I. A., Bejai S., Meijer J. (2019). *Bacillus velezensis* 5113 induced metabolic and molecular reprogramming during abiotic stress tolerance in wheat. *Sci. Rep.* 9 1–18. 10.1038/s41598-019-52567-x

Ali A. H., Abdelrahman M., Radwan U., El-Zayat S., El-Sayed M. A. (2018). Effect of Thermomyces fungal endophyte isolated from extreme hot desert-adapted plant on heat stress tolerance of cucumber. *Appl. Soil Ecol.* 124 155–162. 10.1016/j.apsoil.2017.11.004

Ali A. H., Radwan U., El-Zayat S., El-Sayed M. A. (2019). The role of the endophytic fungus, *Thermomyceslanuginosus*, on mitigation of heat stress to its host desert plant *Cullen plicata*. *Biol. Futura* 70 1–7. 10.1556/019.70.2019.01

Ali S. Z., Sandhya V., Grover M., Kishore N., Rao L. V., Venkateswarlu B. (2009). *Pseudomonas* sp. strain AKM-P6 enhances tolerance of sorghum seedlings to elevated temperatures. *Biol. Fertil. Soils* 46 45–55. 10.1007/s00374-009-0404-9

Ali S. Z., Sandhya V., Grover M., Linga V. R., Bandi V. (2011). Effect of inoculation with a thermotolerant plant growth promoting *Pseudomonas putida* strain AKMP7 on growth of wheat (*Triticum* spp.) under heat stress. *J. Plant Interact.* 6 239–246. 10.1080/17429145.2010.545147

Anli, M.; Baslam, M.; Tahiri, A.; Raklami, A.; Symanczik, S.; Boutasknit, A.; Ait-El-Mokhtar, M.; Ben-Laouane, R.; Toubali, S.; Rahou, Y.A. Biofertilizers as strategies to improve photosynthetic apparatus, growth, and drought stress tolerance in the date palm. Front. Plant Sci. **2020**, 11, 516818.

Basu, A.; Prasad, P.; Das, S.N.; Kalam, S.; Sayyed, R.; Reddy, M.; El Enshasy, H. Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: Recent developments, constraints, and prospects. Sustainability **2021**, 13, 1140.

Bharath, P.; Gahir, S.; Raghavendra, A.S. Abscisic acid-induced stomatal closure: An important component of plant defense against abiotic and biotic stress. Front. Plant Sci. **2021**, 12, 324.

Bruno L. B., Karthik C., Ma Y., Kadirvelu K., Freitas H., Rajkumar M. (2020). Amelioration of chromium and heat stresses in Sorghum bicolor by Cr6+ reducing-thermotolerant plant growth promoting bacteria. *Chemosphere* 244:125521. 10.1016/j.chemosphere.2019.125521

Cabral C., Ravnskov S., Tringovska I., Wollenweber B. (2016). Arbuscularmycorrhizal fungi modify nutrient allocation and composition in wheat (*Triticumaestivum* L.) subjected to heat-stress. *Plant Soil* 408 385–399. 10.1007/s11104-016-2942-x

Dastogeer, K. M., Tumpa F. H., Sultana A., Akter M. A., Chakraborty A. (2020). Plant microbiome–an account of the factors that shape community composition and diversity. *Curr. Plant Biol.* 23:100161. 10.1016/j.cpb.2020.100161

Duc N. H., Csintalan Z., Posta K. (2018). Arbuscularmycorrhizal fungi mitigate negative effects of combined drought and heat stress on tomato plants. *Plant Physiol. Biochem.* 132 297–307. 10.1016/j.plaphy.2018.09.011

Hassan M. U., Chattha M. U., Khan I., Chattha M. B., Barbanti L., Aamer M., et al. (2021). Heat stress in cultivated plants: nature, impact, mechanisms, and mitigation strategies—A review. *Plant Biosyst. Int. J. Deal. Aspects Plant Biol.* 155 211–234. 10.1080/11263504.2020.1727987

Hennessy L. M., Popay A. J., Finch S. C., Clearwater M. J., Cave V. M. (2016). Temperature and plant genotype alter alkaloid concentrations in ryegrass infected with an Epichloëendophyte and this affects an insect herbivore. *Front. Plant Sci.* 7:1097. 10.3389/fpls.2016.01097

Hubbard M., Germida J. J., Vujanovic V. (2014). Fungal endophytes enhance wheat heat and drought tolerance in terms of grain yield and second-generation seed viability. *J. Appl. Microbiol.* 116 109–122. 10.1111/jam.12311

Hubbard M., Germida J., Vujanovic V. (2012). Fungal endophytes improve wheat seed germination under heat and drought stress. *Bot. Botanique* 90 137–149. 10.1139/B11-091

IPCC, (2019). *An IPCC Special Report on the Impacts of Global Warming of 1.5° C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways.* Geneva: IPCC.

Ismail I., Hamayun M., Hussain A., Afzal Khan S., Iqbal A., Lee I.-J. (2019). *Aspergillusflavus* promoted the growth of soybean and sunflower seedlings at elevated temperature. *BioMed Res. Int.* 2019:1295457. 10.1155/2019/1295457

Ismail I., Hamayun M., Hussain A., Iqbal A., Khan S. A., Lee I. J. (2018). Endophytic fungus aspergillus japonicus mediates host plant growth under normal and heat stress conditions. *Biomed Res. Int.* 2018:7696831. 10.1155/2018/7696831

Ismail I., Hamayun M., Hussain A., Iqbal A., Khan S. A., Lee I.-J. (2020a). *Aspergillusniger* boosted heat stress tolerance in sunflower and soybean via regulating their metabolic and antioxidant system. *J. Plant Interact.* 15 223–232

Ismail I., Hussain A., Mehmood A., Qadir M., Husna H., Iqbal A., et al. (2020c). Thermal stress alleviating potential of endophytic fungus rhizopus oryzae inoculated to sunflower (*Helianthus annuus* L.) and Soybean (*Glycine max* L.). *Pak. J. Bot.* 52 1857–1865. 10.30848/Pjb2020-5(10)

Issa A., Esmaeel Q., Sanchez L., Courteaux B., Guise J.-F., Gibon Y., et al. (2018). Impacts of *Paraburkholderiaphytofirmans* strain PsJN on tomato (*Lycopersicon esculentum* L.) under high temperature. *Front. Plant Sci.* 9:1397. 10.3389/fpls.2018.01397

Khan A. L., Hamayun M., Radhakrishnan R., Waqas M., Kang S.-M., Kim Y.-H., et al. (2012a). Mutualistic association of *Paecilomycesformosus* LHL10 offers thermotolerance to *Cucumis sativus*. *Antonie van Leeuwenhoek* 101 267–279. 10.1007/s10482-011-9630-x

Khan A. L., Hamayun M., Waqas M., Kang S. M., Kim Y. H., Kim D. H., et al. (2012b). Exophiala sp.LHL08 association gives heat stress tolerance by avoiding oxidative damage to cucumber plants. *Biol. Fertil. Soils* 48 519–529. 10.1007/s00374-011-0649-y

Khan A. L., Kang S. M., Dhakal K. H., Hussain J., Adnan M., Kim J. G., et al. (2013). Flavonoids and amino acid regulation in Capsicum annuum L. by endophytic fungi under different heat stress regimes. *Sci. Hortic.* 155 1–7. 10.1016/j.scienta.2013.02.028

Khan A. L., Waqas M., Lee I.-J. (2015). Resilience of *Penicillium resedanum* LK6 and exogenous gibberellin in improving *Capsicum annuum* growth under abiotic stresses. *J. Plant Res.* 128 259–268. 10.1007/s10265-014-0688-1

Khan M. A., Asaf S., Khan A. L., Jan R., Kang S. M., Kim K. M., et al. (2020b). Thermotolerance effect of plant growth-promoting *Bacillus cereus* SA1 on soybean during heat stress. *BMC Microbiol.* 20:175. 10.1186/s12866-020-01822-7

Khan M. A., Asaf S., Khan A. L., Jan R., Kang S.-M., Kim K.-M., et al. (2020a). Extending thermotolerance to tomato seedlings by inoculation with SA1 isolate of *Bacillus cereus* and comparison with exogenous humic acid application. *PLoS One* 15:e0232228. 10.1371/journal.pone.0232228

Li X., Zhao C., Zhang T., Wang G., Amombo E., Xie Y., et al. (2021). Exogenous *Aspergillusaculeatus* enhances drought and heat tolerance of perennial ryegrass. *Front. Microbiol.* 12:593722. 10.3389/fmicb.2021.593722

Mathur S., Jajoo A. (2020). Arbuscularmycorrhizal fungi protects maize plants from high temperature stress by regulating photosystem II heterogeneity. *Ind. Crops Product.* 143:111934. 10.1016/j.indcrop.2019.111934

Moynihan, M.A.; Goodkin, N.F.; Morgan, K.M.; Kho, P.Y.; Lopes dos Santos, A.; Lauro, F.M.; Baker, D.M.; Martin, P. Coralassociated nitrogen fixation rates and diazotrophic diversity on a nutrient-replete equatorial reef. ISME J. **2022**, 16, 233–246.

Mukhtar T., Rehman S. U., Smith D., Sultan T., Seleiman M. F., Alsadon A. A., et al. (2020). Mitigation of heat stress in *Solanum lycopersicum* L. by ACC-deaminase and exopolysaccharide producing *Bacillus cereus*: effects on biochemical profiling. *Sustainability* 12:2159. 10.3390/su12062159

Mukhtar, T.; Ali, F.; Rafique, M.; Ali, J.; Afridi, M.S.; Smith, D.; Mehmood, S.; Souleimanov, A.; Jellani, G.; Sultan, T. Biochemical Characterization and Potential of Bacillus safensis

Strain SCAL1 to Mitigate Heat Stress in Solanum lycopersicum L. J. Plant Growth Regul. **2022**, 1–16.

Naamala J., Smith D. L. (2021). Microbial derived compounds, a step toward enhancing microbial inoculants technology for sustainable agriculture. *Front. Microbiol.* 12:634807. 10.3389/fmicb.2021.634807

Park, Y.-G.; Mun, B.-G.; Kang, S.-M.; Hussain, A.; Shahzad, R.; Seo, C.-W.; Kim, A.-Y.; Lee, S.-U.; Oh, K.Y.; Lee, D.Y. Bacillus aryabhattai SRB02 tolerates oxidative and nitrosative stress and promotes the growth of soybean by modulating the production of phytohormones. PLoS ONE **2017**, 12, e0173203.

Qu, Y.; Sakoda, K.; Fukayama, H.; Kondo, E.; Suzuki, Y.; Makino, A.; Terashima, I.; Yamori,W. Overexpression of both Rubisco and Rubiscoactivase rescues rice photosynthesis and biomass under heat stress. Plant Cell Environ. **2021**, 44, 2308–2320.

Radecker, N.; Pogoreutz, C.; Gegner, H.M.; Cárdenas, A.; Perna, G.; Geißler, L.; Roth, F.; Bougoure, J.; Guagliardo, P.; Struck, U. Heat stress reduces the contribution of diazotrophs to coral holobiont nitrogen cycling. ISME J. **2022**, 16, 1110–1118.

Sangamesh M., Jambagi S., Vasanthakumari M., Shetty N. J., Kolte H., Ravikanth G., et al. (2018). Thermotolerance of fungal endophytes isolated from plants adapted to the Thar Desert, India. *Symbiosis* 75 135–147. 10.1007/s13199-017-0527-y

Sarkar J., Chakraborty B., Chakraborty U. (2018). Plant growth promoting rhizobacteria protect wheat plants against temperature stress through antioxidant signalling and reducing chloroplast and membrane injury. *J. Plant Growth Regul.* 37 1396–1412. 10.1007/s00344-018-9789-8

Scafaro, A.P.; Fan, Y.; Posch, B.C.; Garcia, A.; Coast, O.; Atkin, O.K. Responses of leaf respiration to heatwaves. Plant Cell Environ. **2021**, 44, 2090–2101.

Shekhawat K., Sheikh A., Mariappan K., Jalal R., Hirt H. (2020). *Enterobacter* sp. SA187 mediates plant thermotolerance by chromatin modification of heat stress genes. *bioRxiv* [Preprint]. 10.1101/2020.01.16.908756

Shekhawat, K.; Almeida-Trapp, M.; García-Ramírez, G.X.; Hirt, H. Beat the heat: Plant-and microbe-mediated strategies for crop thermotolerance. Trends Plant Sci. **2022**.

Singh, R.P.; Ma, Y.; Shadan, A. Perspective of ACC-deaminase producing bacteria in stress agriculture. J. Biotechnol. **2022**, 352, 36–46.

Smail I., Hamayun M., Hussain A., Khan S. A., Iqbal A., Lee I. J. (2020b). An endophytic fungus *Aspergillusviolaceofuscus* can be used as heat stress adaptive tool for *Glycine max* L. and *Helianthus annuus* L. *J. Appl. Bot. Food Qual.* 93 112–125. 10.5073/Jabfq.2020.093.014

Waqas M., Khan A. L., Shahzad R., Ullah I., Khan A. R., Lee I. J. (2015). Mutualistic fungal endophytes produce phytohormones and organic acids that promote japonica rice plant growth under prolonged heat stress. *J. Zhejiang Univ. Sci. B* 16 1011–1018. 10.1631/jzus.B1500081

Zhao J., Lu Z., Wang L., Jin B. (2021). Plant responses to heat stress: physiology, transcription, noncoding RNAs, and epigenetics. *Int. J. Mol. Sci.* 22:117. 10.3390/ijms22010117

Zhu X. C., Song F. B., Liu S. Q., Liu T. D. (2011). Effects of arbuscularmycorrhizal fungus on photosynthesis and water status of maize under high temperature stress. *Plant Soil* 346 189–199. 10.1007/s11104-011-0809-8