Gene Introgression from Crop Wild Relatives into Cultivated Tomato for Heat Stress Tolerance

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Abstract: Tomato (*Solanum lycopersicum L.*) is a crucial vegetable crop worldwide, facing significant challenges due to climate change-induced heat stress. Elevated temperatures negatively impact tomato productivity by disrupting various physiological and reproductive processes. To mitigate these challenges, there is increasing interest in harnessing genetic resources from crop wild relatives (CWRs) through introgression breeding. This review explores recent advancements in understanding heat stress tolerance mechanisms in tomatoes and the prospects of introgressing heat tolerance genes from CWRs into cultivated tomato varieties. The complex responses of tomato plants to heat stress, focusing on reproductive traits, pollen viability, and physiological and biochemical adaptations are discussed. Additionally, highlight the genetic basis of heat tolerance and the role of various genes, QTLs, and enzymes in mediating heat stress responses. Furthermore, review emerging biotechnological approaches, including transcriptomics, proteomics, genome-wide association studies (GWAS), metabolomics, and advanced imaging techniques, for enhancing heat stress tolerance in tomatoes. Finally, we address the challenges and opportunities in introgression breeding and emphasize the importance of utilizing CWRs as valuable genetic resources for developing heat-tolerant tomato varieties

1 INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is a vital fruit vegetable crop worldwide, self-pollinating and diploid with 2n = 24 chromosomes and a genome size of about 950 Mb (Barone et al., 2008). It boasts a genetic linkage map and wide germplasm resources (http://tgrc.ucdavis.edu) and ranks as the world's second-largest major vegetable commodity. Climate change, a global threat highlighted by the IPCC (Leisner et al., 2020, Shahzad et al., 2021), significantly impacts tomato production, leading to abnormal price fluctuations. Climate change is expected to reduce total agricultural crop yields by 4.5 to 9% from 2010 to 2039 (Mahapatra, 2014), affecting plants with abiotic stresses like drought, heat, cold, salt, and heavy metals (Buono & Regni, 2023). Despite the cultivation of approximately 7500 tomato cultivars, most are susceptible to stress (Singh et al., 2020). Breeders are increasingly pressured to enhance stress tolerance using various breeding tools, with crop wild relatives (CWRs) presenting an untapped genetic diversity reservoir, especially for stress tolerance traits (Dempewolf et al., 2017). Introgression breeding plays a crucial role in broadening the genetic base and improving stress tolerance in tomatoes to meet current and future challenges in crop production.

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2 IMPACT OF HEAT STRESS

Tomato growers struggle with heat-sensitive cultivars, exacerbating vulnerability to rising temperatures. High temperatures hinder tomato growth and yield by disrupting various biological processes, resulting in decreased productivity (Gonzalo et al., 2020). A 2-4°C temperature rise disrupts gamete development and flower maturation, reducing seed yield (Solankey et al., 2018). Tomato heat tolerance, a complex trait, links to flower structure and metabolic processes, impacting proline, polyamine, and carbohydrate levels (Alsamir et al., 2017a; Sato et al., 2006; Song et al., 2002). Yeh et al. (2012) identified four primary thermo-tolerance categories in tomatoes: short-term acquired thermotolerance, long-term acquired thermotolerance, basal thermotolerance, and thermotolerance to moderately high temperatures. Heat stress response in tomatoes is genotype and developmentally dependent, altering gene expression in post-anthesis fruit (Gonzalo et al., 2021).

2.1 Pollen Viability

Heat stress affects pollen viability in anthers, crucial for fruit setting (Alsamir et al., 2017a). High temperatures emphasize the importance of pollen viability for fruit setting, showing a consistent positive correlation in studies (Zhou et al., 2015). Tomato studies show heat stress lowers pollen viability and quantity, highlighting genotype selection for heat tolerance (Xu et al., 2017a; Driedonks et al., 2018a). Metabolites like proline, glutathione, phytohormones, flavonoids, polyamines, and carbohydrates impact pollen survival in heat stress, showcasing intricate biochemical regulation (Paupière et al., 2014). Advancements in high-throughput phenotyping, like image analysis and impedance flow cytometry, automate pollen number and viability analysis, aiding in efficient heat stress assessment (Dreccer et al., 2019). Open-access image-based tools, such as Pollen Counter, enhance accessibility and accuracy in pollen counting and viability assessment (Tello et al., 2018).

2.2 Physiological and Biochemical Trait

Physiological and biochemical responses to high temperature stress are vital indicators of plant stress tolerance, impacting health and productivity (Zhou et al., 2019). Maintaining optimal carbohydrate levels, chlorophyll content, and photosynthetic efficiency is crucial for pollen quality and plant performance during heat stress (Firon et al., 2006). Segregating generations reveal complex genetic basis for traits like chlorophyll content and PSII's quantum efficiency (Fv/Fm) (Wen et al., 2019). Metabolite profiling aids thermotolerant resource identification, enhances breeding efficiency (Raja et al., 2019; Driedonks, 2018; Mazzeo et al., 2018). Soluble sugars affect anther & pollen development. Thermotolerant types have more fructose & glucose (Raja et al., 2019; Driedonks, 2018; Mazzeo et al., 2018). Compounds like proline, glycine betaine, flavonoids, jasmonic acid, and indole-3-acetic acid affect fruit set, pollen fertility, and stress tolerance in plants through osmotic adjustment (Hungria and Kaschuk, 2014; Giri, 2013). Heat stress reduces photosynthesis, stomatal conductance, and membrane stability in tomatoes, correlating with decreased inflorescence, pollen viability, and fruit setting (Hungria and Kaschuk, 2014; Giri, 2013). Plants adapt to heat stress through biochemical and physiological changes, aiding crop heat tolerance enhancement via breeding and management. Mechanisms like carbohydrate regulation, chlorophyll maintenance, and osmotic adjustment offer pathways for improvement. Metabolite profiling and genetic studies aid in identifying thermotolerant genetic resources and targeted breeding strategies.

3 CROP WILD RELATIVES (CWRs) RESERVOIR FOR CROP IMPROVEMENT

Crop wild relatives (CWRs) are vital genetic resources for crop improvement, offering ancestral diversity for domesticated crops (Choudhary *et al.,* 2017). Wild tomato relatives provide useful traits for breeding (Olivieri *et al.,* 2020; Dempewolf *et al.,* 2017). Wild tomato species vital for heat tolerance due to important genes (Zhang *et al.,* 2017). An introgression population of *Solanum neorickii* is recognized as a potent complement to the extensively examined *Solanum pennellii* (Brog *et al.,* 2019). Recent studies have assessed the genetic variability in a panel of cultivated and wild tomatoes with varying levels of heat tolerance using genomic and phenotypic analysis (Ayenan *et al.,* 2021). Long-term mild heat stress studies on wild tomato species, like *S. pimpinellifolium*, highlight their adaptive potential for heat stress, aiding local adaptation (Driedonks *et al.,* 2018).

Table 1: Enzyme involved in heat stress tolerance.

Enzyme	Function	Reference
Heat Shock Proteins (HSPs)	Chaperone proteins aid protein folding during heat stress	Wang *et al.* (2004)
Superoxide Dismutase (SOD)	Antioxidant enzymes combat superoxide radicals in heat stress	Mittler *et al.* (2012)
Catalase (CAT)	Antioxidant enzyme breaks down hydrogen peroxide into water and oxygen	Hasanuzzaman *et al.* (2019)
Glutathione Peroxidase (GPX)	Antioxidant enzyme catalyzing the reduction of hydrogen peroxide and organic hydroperoxides	Foyer and Noctor (2011)
Heat Shock Factor (HSF)	Transcription factor controls heat shock protein expression during heat stress	Kotak *et al.* (2007)
Ascorbate Peroxidase (APX)	Antioxidant enzyme uses ascorbate to neutralize hydrogen peroxide	Sharma *et al.* (2012)

3.1 Introgression

Introgression, a genetic phenomenon characterized by the transfer of genetic material between species through repeated backcrossing, offers a pathway for enhancing heat tolerance in tomatoes. Introgression from *Solanum pimpinellifolium* enhances heat tolerance in tomatoes by expanding genetic diversity, enabling breeding of thermo-tolerant varieties (Ayenan *et al.,* 2021). Additionally, investigation finds heat-tolerant tomato E42's genome linked to wild *S. pimpinellifolium*, revealing 35 key adaptation genes (Graci *et al.,* 2023). Heat-tolerant genotypes enhance fruit quality via backcross hybridization (Ibrahim, 2016). Tolessa *et al.* (2013) studied tomato introgression lines from *S. esculentum and L. chmielewskii*, examining pollen viability and fruit set under moderate heat. Kubond *et al.* (2023) found positive effects of S. habrochaites alleles on tomato traits via trait-genomic region associations, suggesting potential for improving fruit quality in cultivated tomatoes. However, Poudyal *et al.* (2017) demonstrated that using *Solanum habrochaites* rootstock boosts tomato yield in cold/drought. Vitale *et al.* (2023) found that *Solanum pennellii* IL12-4-SL outperformed M82 in heat tolerance, showing more flowers, better pollen, and sustained photosynthesis under stress.

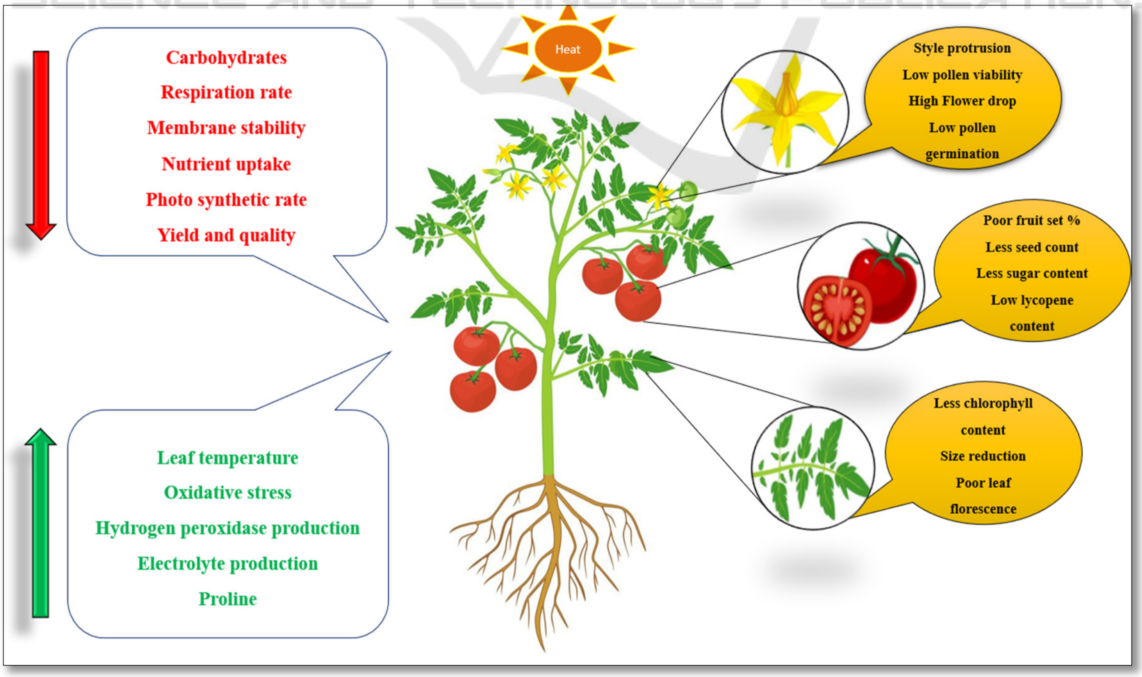

Figure 1: Impact on heat stress tolerance.

Table 2: CWRs for heat stress tolerance

Wild relatives	Reference
S. pennellii	Gonzalo *et al.*, 2021
S. pimpinellifolium	Gonzalo *et al.*, 2021
S. cheesmanii	Golam, F *et al.*, 2012
S. chmielewskii	Nahar, K. *et al.*, 2011
S. peruvianum	Driedonks *et al.*, 2018

3.2 Challenges in Introgression

Despite the sterility of progenies, linkage drag, and self-incompatibility in wild tomatoes, various techniques have been developed to broaden the genetic base of cultivated tomatoes (96). These techniques include embryo rescue, advanced backcross QTL analysis, chromosome segment substitution lines (CSSL), backcross inbred lines (BIL), and introgression lines (ILs), targeting linkage drag (Tanksley *et al.,* 1996; Ali *et al.,* 2010; Bessho-Uehara *et al.,* 2017). For instance, studies have demonstrated the potential for creating hybrid *S. lycopersicum* × *S. sisymbriifolium* and *S. lycopersicum* × *S. peruviyanum* plants through embryo rescue techniques, showcasing the effectiveness of these methods in overcoming breeding barriers and expanding genetic diversity in tomato breeding programs (Piosik *et al.,* 2019).

3.3 Genes and QTLs for Heat Stress Tolerance

Tomato heat tolerance traits influenced by additive, dominant, and epistatic gene effects, varying with germplasm (Dane *et al.,* 1991). Research finds genes & QTLs linked to heat tolerance in tomatoes, aiding breeding. Traits like inflorescence count, pollen viability, and others show additive & dominance QTL effects, with additive effect more significant (Xu *et al.,* 2017b; Driedonks *et al.,* 2018). Although QTL linked to tomato performance under heat stress were found by several studies, their applicability for breeding was limited due to the lack of mapping onto chromosomes. Conversely, QTL linked to traits related to heat tolerance were discovered by Xu *et al.,* (2017b); Driedonks, (2018); Wen *et al.,* (2019). Assessment of high-temperature stress on tomato yield, identification of stable genotypes, and analysis of QTL and transcriptome changes related to heat response were conducted (Bineau *et al.,* 2021). Conventional QTL mapping, QTL-seq, and RNA-seq were used to pinpoint heat-tolerance QTLs and stress-responsive genes, expediting breeding for heat-tolerant varieties (Wen *et al.,* 2019). Study found genetic basis of heat tolerance in tomato reproductive traits, identifying QTLs, including one for pollen viability (Xu *et al.,* 2017). Genome-wide association studies on tomato genotypes in control and high temps pinpointed heat tolerance genes, emphasizing markers for inflorescence and fruit traits (Alsamir *et al.,* 2019). Research identifies genes & QTLs for heat tolerance traits in tomatoes using QTL mapping, QTL-seq, RNA-seq & GWAS, aiding breeding of resilient varieties.

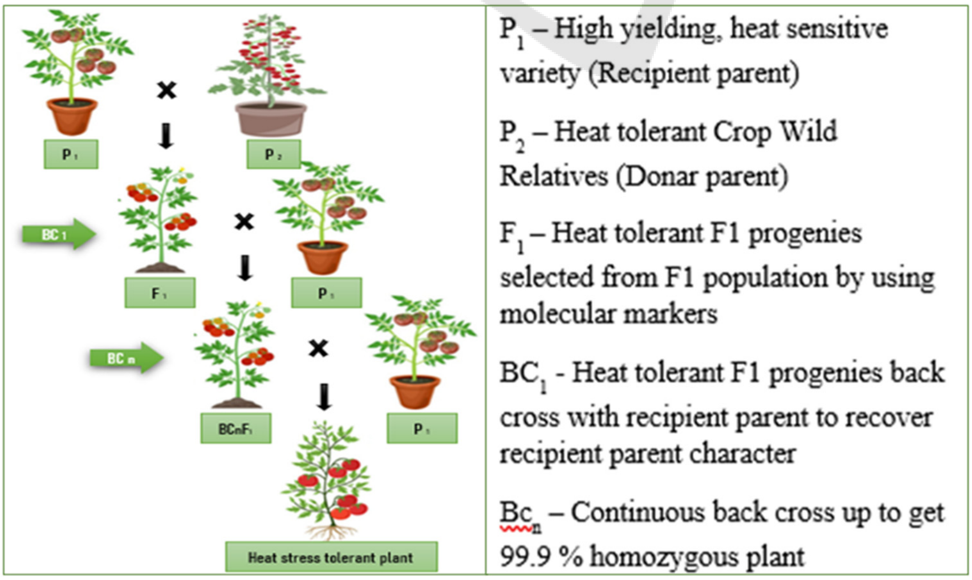

Figure 2: Backcross Breeding

Table 3: Gene/Locus involved in Heat stress tolerance.

Gene/Locus Symbol	Function	Related Trait / Phenotypes	References
SOD	Antioxidant enzyme	Antioxidant defense	Zhou *et al.,* 2019
APX	Antioxidant enzyme	Antioxidant defense	Zhou *et al.,* 2019
SENU3	Senescence-associated cysteine proteinase	Leaf senescence	Drake *et al.,* 1996; Xiao *et al.,* 2014
HsfA1 a, b, c, d	Transcriptional activators to HS	Transcription regulatory network	EI - Shershaby *et al., 2019*
HsfB1	Later gene in transcription regulatory network	Transcription regulatory network	EI - Shershaby *et al., 2019*
TTS, TGL11	Pistil-specific expression	Flower morphology	Müller et al., 2016
TAP3, TM6, PI	Class B activity	Flower morphology	Müller et al 2016
CLV	Signal peptide, shoot, and floral meristem regulation	Shoot and floral meristem	Fletcher, 2018; Quinet et al., 2019
WUS	Homeodomain transcription factor, shoot and floral meristem regulation	Shoot and floral meristem	Fletcher, 2018; Quinet *et al.,* 2019

3.4 Emerging Techniques

Recent advancements in transcriptomics and proteomics have enabled researchers to identify key genes and proteins involved in tomato's response to heat stress. For example, Tian *et al.* (2021) analysed heat-stressed tomato plants' gene expression, revealing heat tolerance-related gene changes. GWAS identified genetic loci linked to heat stress tolerance in tomatoes, aiding in pinpointing candidate genes for validation. For instance, Ruggieri *et al.* (2018) GWAS links heat tolerance genes in tomatoes. Metabolomic studies reveal metabolic changes and potential biomarkers under heat stress.

4 CONCLUSION

The Research on heat stress tolerance in tomatoes should focus on genetic basis and mechanisms, utilizing biotechnological tools like gene editing and GWAS. Improving introgression breeding methods from crop wild relatives is vital. Collaboration among researchers, breeders, and farmers is key for validating and deploying heat-tolerant varieties. Addressing socio-economic factors is crucial for global impact on food security and sustainability. Tomato breeding for heat stress promises resilience amid climate change.

REFERENCES

Ali, M. L., Sanchez, P. L., Yu, S. B., Lorieux, M., & Eizenga, G. C. (2010). Chromosome segment substitution lines: a powerful tool for the introgression of valuable genes from Oryza wild species into cultivated rice (O. sativa). *Rice*, *3*(4), 218-234.

Alsamir, M., Ahmad, N. M., Keitel, C., Mahmood, T., & Trethowan, R. (2017b). Identification of high-temperature tolerant and agronomically viable tomato (S. lycopersicum) genotypes from a diverse germplasm collection. *Adv. Crop Sci. Tech*, *5*(110), 10-4172.

Alsamir, M., Ahmad, N. M., Mahmood, T., & Trethowan, R. (2017a). Morpho-physiological traits linked to high temperature stress tolerance in tomato (S. lycopersicum L.). *American Journal of Plant Sciences*, *8*(11), 2681.

Alsamir, M., Ahmad, N., Arief, V., Mahmood, T., & Trethowan, R. (2019). Phenotypic diversity and marker-trait association studies under heat stress in tomato (Solanum lycopersicum L.). *Australian Journal of Crop Science*, *13*(4), 578-587.

Ayenan, M. A. T., Danquah, A., Hanson, P., Asante, I. K., & Danquah, E. Y. (2021). Identification of new sources of heat tolerance in cultivated and wild tomatoes. *Euphytica*, *217*, 1-16.

Ayenan, M. A. T., Danquah, A., Hanson, P., Asante, I. K., & Danquah, E. Y. (2021). Identification of new sources of heat tolerance in cultivated and wild tomatoes. *Euphytica*, *217*, 1-16.

Bessho-Uehara, K., Furuta, T., Masuda, K., Yamada, S., Angeles-Shim, R. B., Ashikari, M., & Takashi, T. (2017). Construction of rice chromosome segment substitution lines harboring Oryza barthii genome and evaluation of yield-related traits. *Breeding science*, *67*(4), 408-415.

Bineau, E., Diouf, I., Carretero, Y., Duboscq, R., Bitton, F., Djari, A., ... & Causse, M. (2021). Genetic diversity of tomato response to heat stress at the QTL and transcriptome levels. *The Plant Journal*, *107*(4), 1213-1227.

Brog, Y. M., Osorio, S., Yichie, Y., Alseekh, S., Bensal, E., Kochevenko, A., ... & Fernie, A. R. (2019). A Solanum neorickii introgression population providing a powerful complement to the extensively characterized Solanum pennellii population. *The Plant Journal*, *97*(2), 391-403.

Choudhary, M., Singh, V., Muthusamy, V., & Wani, S. H. (2017). Harnessing crop wild relatives for crop improvement.

Climate.gov. (2022). Climate Change 2022: Impacts, Adaptation and Vulnerability. Available at: https://www.ipcc.ch/2022/02/28/pr-wgii-ar6/

Dane, F., Hunter, A. G., & Chambliss, O. L. (1991). Fruit set, pollen fertility, and combining ability of selected tomato genotypes under high-temperature field conditions. *Journal of the American Society for Horticultural Science*, *116*(5), 906-910.

De Candolle, A. L. P. P. (1886). Origin of cultivated plants (reprint 1964).

Del Buono, D., Regni, L., & Proietti, P. (2023). Abiotic stresses, biostimulants and plant activity. *Agriculture*, *13*(1), 191.

Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop science*, *57*(3), 1070-1082.

Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop science*, *57*(3), 1070-1082.

Drake, R., John, I., Farrell, A., Cooper, W., Schuch, W., & Grierson, D. (1996). Isolation and analysis of cDNAs encoding tomato cysteine proteases expressed during leaf senescence. *Plant molecular biology*, *30*, 755-767.

Dreccer, M. F., Molero, G., Rivera-Amado, C., John-Bejai, C., & Wilson, Z. (2019). Yielding to the image: How phenotyping reproductive growth can assist crop improvement and production. *Plant science*, *282*, 73-82.

Driedonks, N. J. (2018). *From flower to fruit in the heat-Reproductive thermotolerance in tomato and its wild relatives* (Doctoral dissertation, [Sl]:[Sn]).

Driedonks, N., Wolters-Arts, M., Huber, H., de Boer, G. J., Vriezen, W., Mariani, C., & Rieu, I. (2018). Exploring the natural variation for reproductive thermotolerance in wild tomato species. *Euphytica*, *214*, 1-12.

El-Shershaby, A., Ullrich, S., Simm, S., Scharf, K.-D., Schleiff, E., and Fragkostefanakis, S. (2019). Functional diversification of tomato HsfA1 factors is based on DNA binding domain properties. *Gene* 714:143985.

Fletcher, J. C. (2018). The CLV-WUS stem cell signaling pathway: a roadmap to crop yield optimization. *Plants*, *7*(4), 87.

Foyer, C. H., & Noctor, G. (2011). Ascorbate and glutathione: the heart of the redox hub. *Plant physiology*, *155*(1), 2-18.

Giri, A. (2013). *Effect of acute heat stress on nutrient uptake by plant roots*. The University of Toledo.

Golam, F., Prodhan, Z. H., Nezhadahmadi, A., & Rahman, M. (2012). Heat tolerance in tomato. *Life Sci. J*, *9*(4), 1936-1950.

Gonzalo, M. J., Nájera, I., Baixauli, C., Gil, D., Montoro, T., Soriano, V., ... & Monforte, A. J. (2021). Identification of tomato accessions as source of new genes for improving heat tolerance: From controlled experiments to field. *BMC Plant Biology*, *21*(1), 1-28.

Graci, S., Ruggieri, V., Francesca, S., Rigano, M. M., & Barone, A. (2023). Genomic insights into the origin of a thermotolerant tomato line and identification of candidate genes for heat stress. *Genes*, *14*(3), 535.

Hasanuzzaman, M., Bhuyan, M. B., Zulfiqar, F., Raza, A., Mohsin, S. M., Mahmud, J. A., ... & Fotopoulos, V. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*, *9*(8), 681.

Hungria, M., & 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.

Ibrahim, E. (2016). Tomato breeding for heat stress conditions. *European Journal of Academic Essays*, *3*(2), 87-93.

Kotak, S., Larkindale, J., Lee, U., von Koskull-Döring, P., Vierling, E., & Scharf, K. D. (2007). Complexity of the heat stress response in plants. *Current opinion in plant biology*, *10*(3), 310-316.

Kubond, B. A., & St. Clair, D. A. (2023). Bin mapping of water stress tolerance-related, fruit quality, and horticultural traits in tomato introgression lines derived from wild Solanum habrochaites. *Crop Science*, *63*(2), 568-584.

Leisner, C. P. (2020). Climate change impacts on food security-focus on perennial cropping systems and nutritional value. *Plant Science*, *293*, 110412.

Mahapatra, S. (2014). Impact of climate change on Indian agriculture. *Climate Change Effect on Crop Productivity*, 213.

Mazzeo, M. F., Cacace, G., Iovieno, P., Massarelli, I., Grillo, S., & Siciliano, R. A. (2018). Response mechanisms induced by exposure to high temperature in anthers from thermo-tolerant and thermo-sensitive tomato plants: a proteomic perspective. *PloS one*, *13*(7), e0201027.

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G. A. D., Tognetti, V. B., Vandepoele, K., ... & Van Breusegem, F. (2011). ROS signaling: the new wave?. *Trends in plant science*, *16*(6), 300-309.

Müller, F., Xu, J., Kristensen, L., Wolters-Arts, M., de Groot, P.F., Jansma, S.Y., et al. (2016). High-temperature-induced defects in tomato (*Solanum lycopersicum*) anther and pollen development are associated with reduced expression of B-class floral patterning genes. *PLoS ONE* 11:e0167614.

Nahar, K., & Ullah, S. M. (2011). Effect of water stress on moisture content distribution in soil and morphological characters of two tomato (Lycopersicon esculentum Mill) Cultivars. *Journal of Scientific Research*, *3*(3).

Olivieri, F., Calafiore, R., Francesca, S., Schettini, C., Chiaiese, P., Rigano, M. M., & Barone, A. (2020). High-throughput genotyping of resilient tomato landraces to detect candidate genes involved in the response to high temperatures. *Genes*, *11*(6), 626.

Paupière, M. J., Van Heusden, A. W., & Bovy, A. G. (2014). The metabolic basis of pollen thermo-tolerance: perspectives for

Piosik, Ł., Ruta-Piosik, M., Zenkteler, M., & Zenkteler, E. (2019). Development of interspecific hybrids between Solanum lycopersicum L. and S. sisymbriifolium Lam. via embryo calli. *Euphytica*, *215*, 1-20.

Poudyal, D., Akash, M., Khatri, L., Shrestha, D. S., & Uptmoor, R. (2017). Solanum habrochaites introgression line grafted as rootstock in cultivated tomato maintains growth and improves yield under cold and drought stresses. *Journal of Crop Improvement*, *31*(4), 589-607.

Quinet, M., Angosto, T., Yuste-Lisbona, F. J., Blanchard-Gros, R., Bigot, S., Martinez, J. P., & Lutts, S. (2019). Tomato fruit development and metabolism. *Frontiers in plant science*, *10*, 1554.

Raja, M. M., Vijayalakshmi, G., Naik, M. L., Basha, P. O., Sergeant, K., Hausman, J. F., & Khan, P. S. S. V. (2019). Pollen development and function under heat stress: from effects to responses. *Acta Physiologiae Plantarum*, *41*,

Ruggieri, V., Francese, G., Sacco, A., D'Alessandro, A., Rigano, M. M., Parisi, M., ... & Barone, A. (2014). An association mapping approach to identify favourable alleles for tomato fruit quality breeding. *BMC plant biology*, *14*(1), 1-15.

Sato, S., Kamiyama, M., Iwata, T., Makita, N., Furukawa, H., & Ikeda, H. (2006). Moderate increase of mean daily temperature adversely affects fruit set of Lycopersicon esculentum by disrupting specific physiological processes in male reproductive development. *Annals of botany*, *97*(5), 731-738.

Shahzad, A., Ullah, S., Dar, A. A., Sardar, M. F., Mehmood, T., Tufail, M. A., ... & Haris, M. (2021). Nexus on climate change: Agriculture and possible solution to cope future climate change stresses. *Environmental Science and Pollution Research*, *28*, 14211-14232.

Sharma, P., Jha, A. B., Dubey, R. S., & Pessarakli, M. (2012). Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. Journal of Botany, 2012.

Singh, A., Shamim, M., Singh, A., & Singh, R. P. (2020). Genes, QTLs and linked molecular markers conferring the resistance for various biotic stresses in tomato cultivar.

Solankey, S. S., Akhtar, S., Neha, P., Kumari, M., & Kherwa, R. (2018). Screening and identification of heat tolerant tomato genotypes for Bihar. *Journal of Pharmacognosy and Phytochemistry*, *7*(4S), 97-100.

Song, J., Nada, K., & Tachibana, S. (2002). Suppression of S-adenosylmethionine decarboxylase activity is a major cause for high-temperature inhibition of pollen germination and tube growth in tomato (Lycopersicon esculentum Mill.). *Plant and cell physiology*, *43*(6), 619-627.

Tanksley, S. D., & Nelson, J. C. (1996). Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theoretical and Applied Genetics*, *92*, 191-203.

Tello, J., Montemayor, M. I., Forneck, A., & Ibáñez, J. (2018). A new image-based tool for the high throughput phenotyping of pollen viability: evaluation of inter-and intra-cultivar diversity in grapevine. *Plant methods*, *14*(1), 1-17.

Tian, Y., Wang, H., Zhang, Z., Zhao, X., Wang, Y., & Zhang, L. (2021). An RNA-seq analysis reveals differential transcriptional responses to different light qualities in leaf color of Camellia sinensis cv. Huangjinya. *Journal of Plant Growth Regulation*, 1-16.

Vitale, L., Francesca, S., Arena, C., D'Agostino, N., Principio, L., Vitale, E., ... & Rigano, M. M. (2023). Multitraits evaluation of a Solanum pennellii introgression tomato line challenged by combined abiotic stress. *Plant Biology*.

Wang, W., Vinocur, B., Shoseyov, O., & Altman, A. (2004). Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends in plant science*, *9*(5), 244-252.

Wen, J., Jiang, F., Weng, Y., Sun, M., Shi, X., Zhou, Y., ... & Wu, Z. (2019). Identification of heat-tolerance QTLs and high-temperature stress-responsive genes through conventional QTL mapping, QTL-seq and RNA-seq in tomato. *BMC plant biology*, *19*, 1-17.

Xiao, H.-J., Yin, Y.-X., Chai, W.-G., and Gong, Z.-H. (2014). Silencing of the *CaCP* gene delays salt-and osmotic-induced leaf senescence in *Capsicum annuum* L. *Int. J. Mol. Sci.* 15, 8316–8334.

Xu, J., Wolters-Arts, M., Mariani, C., Huber, H., & Rieu, I. (2017a). Heat stress affects vegetative and reproductive performance and trait correlations in tomato (Solanum lycopersicum). *Euphytica*, *213*, 1-12.

Yeh, C. H., Kaplinsky, N. J., Hu, C., & Charng, Y. Y. (2012). Some like it hot, some like it warm: phenotyping to explore thermotolerance diversity. *Plant Science*, *195*, 10-23.

Zhang, H., Mittal, N., Leamy, L. J., Barazani, O., & Song, B. H. (2017). Back into the wild—Apply untapped genetic diversity of wild relatives for crop improvement. *Evolutionary Applications*, *10*(1), 5-24.

Zhou, R., Kong, L., Wu, Z., Rosenqvist, E., Wang, Y., Zhao, L., ... & Ottosen, C. O. (2019). Physiological response of tomatoes at drought, heat and their combination followed by recovery. *Physiologia Plantarum*, *165*(2), 144-154.

Zhou, R., Kong, L., Yu, X., Ottosen, C. O., Zhao, T., Jiang, F., & Wu, Z. (2019). Oxidative damage and antioxidant mechanism in tomatoes responding to drought and heat stress. *Acta Physiologiae Plantarum*, *41*, 1-11.