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Review

Comprehensive Understanding of Selecting Traits for Heat Tolerance during Vegetative and Reproductive Growth Stages in Tomato

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Abstract: Climate change is an important emerging issue worldwide; the surface temperature of the earth is anticipated to increase by 0.3 °C in every decade. This elevated temperature causes an adverse impact of heat stress (HS) on vegetable crops; this has been considered as a crucial limiting factor for global food security as well as crop production. In tomato plants, HS also causes changes in physiological, morphological, biochemical, and molecular responses during all vegetative and reproductive growth stages, resulting in poor fruit quality and low yield. Thus, to select genotypes and develop tomato cultivars with heat tolerance, feasible and reliable screening strategies are required that can be adopted in breeding programs in both open-field and greenhouse conditions. In this review, we discuss previous and recent studies describing attempts to screen heat-tolerant tomato genotypes under HS that have adopted different HS regimes and threshold temperatures, and the association of heat tolerance with physiological and biochemical traits during vegetative and reproductive growth stages. In addition, we examined the wide variety of parameters to evaluate the tomato's tolerance to HS, including vegetative growth, such as leaf growth parameters, plant height and stem, as well as reproductive growth in terms of flower number, fruit set and yield, and pollen and ovule development, thereby proposing strategies for the development of heat-tolerant tomato cultivars in response to high temperature.

Keywords: climate change; heat tolerance; heat stress regimes; tomato breeding program; vegetative and reproductive growth stages; heat tolerance traits

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1. Introduction

Industrialization and urbanization have continuously accelerated climate change, as seen in the increase in air temperature to date [1,2]. The global average temperature is predicted to increase by approximately 0.3 °C in every decade, thereby rising by 1–4 °C from the year 2081 to 2100 compared to the temperature recorded from 1986 to 2005, according to the Intergovernmental Panel on Climatic Change (IPCC) [3,4]. An elevated temperature of approximately 3–4 °C may result in a drastic reduction in crop yields by a maximum of 35% in Asia, Africa, and the Middle East [5].

High temperature (HT) is closely associated with heat stress (HS), which is one of the major abiotic stresses, including temperature, drought, salinity, and flooding [5]. HS is a detrimental abiotic factor that influences global crop productivity by compromising crop growth during the vegetative and reproductive growth stages [5–7]. In general, HS is considered to be an elevation of temperature over a threshold level for a substantial amount of time, leading to irreversible impairments in crop growth and development [8].

A transiently elevated temperature of 10–15 °C above the optimum temperature for plant growth and development is termed as "heat" or "thermal" shock [8,9]. HS is a complex process with many factors, including the intensity and total duration of HT and the speed of the temperature increase [9,10]. For example, the frequency and period of HT can affect the occurrence and intensity of HS in a certain climatic zone during the day or night. In definition, HS tolerance is termed as the survival capability of a plant to grow, develop, and/or produce economic yields in response to HT [8,10].

Tomato (*Solanum lycopersicum*) plants, which belong to the *Solanaceae* family, are grown in a wide variety of climate conditions and areas from tropical to temperate regions. The tomato was introduced to Europe in the 16th century and then spread to the Mediterranean [11]. It is the second most important vegetable crop worldwide after the potato [12]. The cultivation area has reached almost 5,000,000 hectares and worldwide tomato yields amount to 181,000,000 metric tons (FAO, http://www.fao.org/faostat/ (accessed on 7 February 2022)). Tomatoes are consumed fresh and are also a major ingredient in a wide array of cuisines, as well as for sauces and juices [13]. In particular, the tomato fruit is a rich source of vitamins A and C and antioxidants, including lycopene, β-carotene, phenolics, and minerals but is low in calories [14–16], contributing to the maintenance of human health.

Climate change is likely to significantly reduce crop yield in the future [17–19], and a daily temperature that is a few degrees above the average can significantly affect vegetative and reproductive parameters, such as seedling growth, plant height (PH), leaf length and width, pollen grain viability, and the fertility of the female parts [20–22]. Its optimal average day and night temperatures range from 21 to 30 °C and from 18 to 21 °C, respectively [23]. Tomato production is frequently threatened by HS in diverse cultivated regions [24,25]. HT and drought stress are likely to have a negative impact on the growth, development, and yield of tomato plants in fields, leading to reduced production in its main producing regions from the year 2050 to 2100 [22].

The effect of HS on tomato plants has chiefly been evaluated during the reproductive stage owing to the importance of its fruits, as well as its sensitivity at the reproductive stage [26–28]. When the day temperature is above optimum, this induces developmental disorders in the flower organs (stamen and ovule) and in fruit development (fruit set, weight and quality, and seed number) [26–31]. In addition, a study has shown that the treatment of transient HS (>45 °C, 20 min) results in programmed cell death (PCD) in tomato fruits via DNA fragmentation and cytochrome c release, and induces caspase-like enzyme activity [32]. Vegetative growth parameters are likewise influenced under HS in many crops [8]. Non-photochemical quenching (NPQ), chlorophyll content, photosynthetic rate, transpiration rate, stomatal conductance, and CO_2 assimilation are negatively affected by HS, resulting in a reduced growth rate [19,26,33,34].

The evaluated traits and factors in HS conditions are significantly varied among genotypes and growth stages in tomato plants, suggesting that the correlations among these traits and factors can vary during the vegetative and reproductive growth stages [35,36]. It is important to find the association in terms of HT tolerance between germination or seedling stages and flowering stages in tomato plants [37–39] for enhancing the speed of tomato breeding by the early selection of heat-tolerant genotypes as an indirect selection. However, substantial knowledge gaps exist in our understanding of the correlation between vegetative and reproductive growth-related traits or factors under HS.

The development of heat-tolerant tomato cultivars is crucial for adapting to elevated temperatures at present and in the future [5,20], but some bottlenecks and difficulties exist in identifying and applying the traits associated with heat tolerance in breeding programs. There has been a different understanding of the definition of plant responses to HT and a lack of in-depth understanding of the genetic basis and architecture regarding the heat tolerance mechanism during the vegetative and reproductive growth stages [1,20,40]. These problems have led to a deficiency of common screening methods and protocols on evaluating heat-tolerant traits, as well as in screening and selecting heat-tolerant genotypes to date. Consequently, the identification of heat-tolerant genotypes seems not to be reproducible and reliable to some degree [41]. In this review, we provide an overview of the knowledge of the response of tomato plants to HT, which includes diverse HS regimes, as well as trait associations and key factors related to heat tolerance during the vegetative and reproductive growth stages. Lastly, we examine some promising traits associated with heat tolerance in tomato plants, with a discussion of recent correlation studies using a large number of genotypes.

2. Types of Heat Stress Regimes in Tomato Plants

The concept of HS is projected to assess temperature intensity and duration and the speed of increments in temperatures [8]. The application of proper HS treatment is a key point when screening heat-tolerant plants. Yeh et al. [42] and Mesihovic et al. [41] reported four major HS regimes for screening the heat-tolerant germplasm in *Arabidopsis* and crop species, suggesting that directly applied HS (DAHS) should be applied for basal thermo-tolerance, pre-induced HS for acquired thermo-tolerance (ATT), gradient HS for ATT, and mild chronic HS (MCHS) for mild heat thermo-tolerance (MHTT) for ATT in greenhouse and open-field conditions [41]. Two HS regimes, DAHS and MCHS, are mainly utilized in screening for and studying the heat tolerance of tomato plants in response to HT at physiological and molecular levels. In general, DAHS is applied for a short period of screening (from an hour to a day) with a high temperature of ≥45 °C during the vegetative and/or reproductive stages [41,43]. MCHS is used for a longer period of screening with mild high temperatures of 30–36 °C, ranging from several days to the entirety of the plant growth and developmental cycle [41,44]. The MCHS regime has been more widely applied than the DAHS regime to tomato plants for screening heat tolerance in terms of the reproductive parameters, including pollen germination and viability with flower and fruit characteristics in both greenhouses and open fields [20]. This is because the MCHS regime more closely resembles natural field conditions and/or it is difficult to maintain the DAHS regime in field conditions. Tomato plants exhibit different physiological responses to DAHS and MCHS [29]. The effects of HS on tomato cultivars vary significantly, depending on growth stages and experimental environment conditions including the temperature range, light intensity and quality, relative humidity and others; sometimes, different definitions of the same traits have caused variation in HS effects [41]. Therefore, it is indispensable to establish common screening methods and protocols to identify heat-tolerant tomato genotypes by considering the aforementioned climate conditions in a certain target area and/or expanded geological location.

3. Optimum Temperature Range and Heat Stress Threshold in Tomato Plants

Some studies have shown that a night temperature of 13 °C maintains a good fruit set, [45] while night temperatures ranging from 15–20 °C influence the increment of marketable yields of tomatoes [46]. However, the daily average temperature (DAT) is more crucial than the day or night temperature or the difference between day and night temperatures during the reproductive processes in tomato plants [20]. For example, the increments or differentials of day and night temperature did not show constant patterns of flower number and fruit weight, but a DAT of 29 °C considerably diminished the fruit number and weight, and the seed number per fruit in comparison with those in a DAT of 25 °C. Moreover, when the average night temperature was 19.2 °C, which is just below the upper critical point (20 °C), and the DAT was 26.8 °C led to a significant decrease in the fruit set of the tomato plants [30,45]. It has been demonstrated that a DAT of 25–30 °C is markedly optimal for the net assimilation rate [47]. DATs of 21–24 °C [48], 22–25 °C [49], and 22–26 °C [24] are optimal for fruit set and yield. An average temperature of approximately 21.3 °C, with an average day and night temperature of 27.3 and 15.1 °C [30], and 26.3 and 15.6 °C [50], are also beneficial for the fruit set and yield of tomato plants, respectively.

The threshold temperature of crops is defined as a value of DAT where a decline in crop growth begins and can be termed as the lower/base and upper threshold temperatures of plant development [4]. This has been determined via the environmental regulation of laboratory and field conditions. Lower and upper threshold temperatures in plant development represent points below and above those at which plant growth and development ceases, respectively [8]. The lower threshold temperatures vary depending on plant species, such as spinach (2 °C), pea (4.4 °C), pumpkin (13 °C), and tomato (15 °C) [51]. However, 0 °C is often considered to be a predicted lower threshold temperature for cool-season plants [52]. Notably, the upper threshold temperatures are critical for tropical and subtropical crops, which are important limiting factors for determining crop yields. The upper threshold temperatures also vary among plant species, such as wheat (26 °C), tomato (30 °C), corn (38 °C) and cotton (45 °C), and even among genotypes within the same species [8]. The determination of an exact upper threshold temperature is also difficult since the physiological responses of plants to different environmental stimuli, as well as to habitats, vary greatly [4,8]. For example, when the ambient temperature was over 35 °C as an upper threshold temperature, the seed germination rate, vegetative growth, flowering time, and fruit set and ripening were significantly inhibited in tomato plants [8]. On the other hand, an upper threshold temperature of only 30 °C can damage tomato plants at the period of seedling emergence [4,26], suggesting that the evaluation of threshold temperatures for tomato plants must be performed in each growing stage to apply these threshold temperatures for screening heat-tolerant genotypes.

4. The Response of Vegetative and Reproductive Growth to Heat Stress in Tomato Plants

4.1. Leaf Growth, Plant Height, and Stem Diameter

Many studies have been conducted to determine heat tolerance in tomato plants using diverse vegetative growth parameters, including leaf growth, PH, and stem diameter (SD) under HS. Leaf-growth parameters, such as the fresh and dry leaf weight and leaf area, have been assessed under different HS regimes. Abdelmageed et al. [53] reported that these parameters in three heat-tolerant tomato cultivars were less and smaller at 37/27 °C (day/night) and pre-heat shock than in 26/20 °C (day/night) with no pre-heat shock. In the other study, however, leaf number and area in three tomato cultivars were not significantly different between the control conditions (CK) of 26/20 °C (day/night) and heat stress conditions of 32/26 °C (day/night) [54]. Moreover, Zheng et al. [55] have investigated the leaf area of tomato plants under two HS conditions of 38/18 °C and 41/18 °C (day/night) and three relative humidity conditions (50%, 70%, and 90%). The leaf area was significantly reduced in two HT regimes with 50% relative humidity (RH), in comparison with a CK of 28/18 °C (day/night) in 50% RH, but it was similar and/or larger in two different HT regimes combined with higher RHs, suggesting an alteration of the HS response by RH. In our recently published study with 38 tomato accessions [56], the leaf length and width were not significantly affected under HT greenhouse conditions with CK and MCHS (19.7/35 °C and 20.2/38.8 °C of the average daily minimum/maximum temperatures, respectively).

The contrasting responses to HS among studies were also observed in PH and SD. In the HS regime of 36/28 °C (day/night) and a CK of 26/18 °C (day/night), there were no apparent differences in PH and SD between a tolerant and a susceptible genotype [39]. Zheng et al. [55] also assessed PH and SD in the aforementioned HS and CK conditions; the difference in PH under HS was remarkable, whereas that in SD was not significant when compared to CK. In our previous study, the PH and SD in most of the 38 tomato accessions increased regardless of fruit types [56]. Bhattarai et al. [57] have recently reported that the PH and SD among 18 cultivars were dramatically decreased in a constant HS regime maintaining 36/28 °C (day/night) in growth chambers, in comparison with those in greenhouses set to 26/20 °C (day/night). These contrasting results indicate that vegetative growth parameters cannot be general indicators for heat tolerance and may not be appropriate for indirect selection in tomato breeding programs for heat tolerance.

4.2. Pollen Development

In tomato plants, HS causes negative effects not only on pollen development and viability but also on ovule development, embryogenesis, and viability [20,58]. The fact that HT affects the fruit set or number more than flower number implies that HT has a greater effect on the process of fertilization. Indeed, reduced fertility is a common problem associated with HT during meiosis and fertilization periods in tomato plants [59]. When pollinated with pollens matured in HT, female plants grown in optimal temperature conditions did not produce fruits, whereas female plants grown in HT that were pollinated with pollens matured in optimal temperature conditions could bear fruits [28].

Favorable temperatures for pollen germination and pollen tube length are between 15 and 22 °C in vitro [60] and 25 °C in vivo [61]. Temperatures above 30 and 35 °C reduce the pollen germination rate and pollen tube growth [61,62]. Since the pollen development stage is very sensitive to HS and is critical for determining fruit set and yield in HS [9,41,63], most of the studies of HT tolerance in tomato plants have been focused on the pollens. HT significantly reduces pollen viability [8,28,37,64,65], germination [56,61] and number [37]. Frank et al. [66] reported that pollen viability is significantly diminished in flowers of three to seven days before the anthesis stage under DAHS (43–45 °C, 2 h), whereas the pollen germination rate and the number of pollen grains were not significantly reduced. The pollen's germinability was influenced by a higher DAHS (50 °C, 2 h) in flowers of 2, 7, and 9 days before anthesis in the tomato cultivar "MicroTom" [21]. In addition, the long period of MCHS (32/26 °C, day/night) for young tomato plants or 1–2 weeks before anthesis had a negative effect on pollen development [29]. Pressman et al. [67] showed that the total number of pollen grains, pollen germinability, and viability are noticeably decreased in MCHS (32/26 °C, day/night) in comparison with CK (28/22 °C, day/night). The number of pollen grains and the percentage of viable pollen grains are also lower in MCHS (32/26 °C, day/night) than those in CK (28/22 °C, day/night) [29].

Remarkably, the response of pollen traits is genotype-dependent. In our previous study, the pollen germination of 23 tomato accessions and the pollen tube length of 28 tomato accessions were significantly reduced under MCHS conditions among a total of 38 accessions [56]. Other studies also reported genotype-dependent HT tolerance in pollen germination [68] and viability [37]. Positive correlations were observed between fruit set and pollen viability [37] or pollen germination and tube length [56,68], although the correlation of the latter two was not significant. HT treatment applied to pollen donor plants before and during pollen release caused significant reductions in seed number and fruit set in comparison with HT treatment that was applied to the developing ovule after pollination [28]. These results suggest that the effects of HT are most significant during pollen maturation, rather than during pollen germination and tube growth or fertilization [69].

4.3. Ovule Development

HS also causes the abnormal development of female reproductive organs [20] or reduced female fertility [37] in tomato plants, although the female gametophyte is generally considered to have more heat tolerance than its male counterpart. It is noticeable that HS influences ovule development under open-field and greenhouse conditions, leading to the malfunction of both male and female reproductive organs at the same time [21,69]. Ovule development is significantly affected by MCHS. The fruit set, number and weight, and seediness were significantly reduced when DAT during the pollination inclined from 25–26 °C to 28–29 °C, even though pollens for pollination were collected under optimal temperatures of 26/22 °C (day/night) [20]. Similarly, Xu et al. [37] reported a reduction in female fertility and seediness in fruit under MCHS (32/26 °C, day/night) when hand-pollinating using pollens from both MCHS and optimal temperature samples (25/19 °C, day/night). In addition, the interactions of pollen and pistil are essential for pollen tube growth from the stigma to the ovules; therefore, a pistil exposed to HS would be dedicated to the considerable regulation of pollen performance in vivo [42,70–72]. These studies suggest the importance of the synergistic effect of male and female organs to achieve the resulting level of fertility under HS [73]. However, it is not likely that the evaluation of female fertility by screening a large number of germplasms is to be recommended, due to the labor-intensive evaluation process, including hand-pollination and counting seeds in fruits [63].

4.4. Flower and Fruit Development

Flowering and fruit set may be the most critical index in the evaluation of heat-tolerant tomato cultivars under HS [74]. Notably, a failure in normal pollen development and female fertility results in a drastic reduction in flower number, fruit weight, fruit set, and seediness under MCHS, in comparison with CK conditions [20,24,68]. For example, HS influenced floral abortion, which led to 80% of flower abscission and a resulting decrease in fruit set [9,75]. In addition, tomato plants exposed to MCHS (DAT of 34 °C/19 °C, day/night) caused 34% of flower abscission and decreased the fruit set by 71% [76]. Heat-tolerant genotypes have been successfully selected according to high fruit set and yield under HT in open fields and greenhouses or growth chambers (36/28 °C, day/night) [19,57], implying that these traits can be utilized for selecting heat-tolerant genotypes in tomato plants.

5. Physiological and Biochemical Responses of HS Tolerance in Tomato

HS directly influences the alteration of photosynthetic parameters, including the net photosynthetic rate (*Pn*), CO_2 assimilation, transpiration rate (*Tr*), stomata conductance (*Ci*), Photosystem II (PSII, *Fv/Fm*), and chlorophyll contents [33,77], which are closely related to delayed plant growth and development. The ability to adjust the accumulation of primary and secondary metabolites and proteins is also important for plants to display heat tolerance [5,78]; heat-tolerant tomato genotypes with a high fruit set and pollen viability might have this ability. In the plants, primary metabolites such as soluble sugars, glycine betaine, and proline accumulate in response to HS [8]. The production of these osmolytes under HS may increase the protein stability and membrane bilayer structure [79].

5.1. Photosynthesis

Photosynthetic apparatus under HS causes the severe malfunction of chloroplasts, which are dedicated to the generation of ATP and metabolites in plants [4,80]. Thus, good performance of the photosynthetic apparatus under HS would be seen in the capability of the plant to overcome stress conditions in response to HS [81]. In particular, since HS prohibits successful chlorophyll biosynthesis, chlorophyll content (chl*a* and chl*b*) could be utilized as a reliable evaluation index for identifying heat-tolerant plants [26]. In tomato plants, the chlorophyll *a*/*b* ratio decreased and the chlorophyll/carotenoid ratio increased in a heat-tolerant tomato cultivar under DAHS (45 °C, 2 h) compared to CK (25/20 °C, day/night), whereas *Pn*, the CO_2 assimilation rate, and PSII (*Fv/Fm*) were reduced in heat-susceptible cultivars [26]. In addition, PSII was sensitively stimulated by HS and *Fv/Fm*; the ratio representing the maximum quantum efficiency of PSII is often utilized to measure the normal or better performance of chloroplasts under HS [82].

5.2. Soluble Sugars

Soluble sugars are necessary for pollen viability and germination. An imbalance in the sugar metabolism caused by HS is associated with the failure of tomato plant fruit set [29]. When developing tomato anthers are continuously exposed to HT, the carbohydrate metabolism is altered, resulting in the reduction of the number of pollen grains per flower and pollen viability [67]. Heat-tolerant tomato genotypes have a higher carbohydrate concentration in pollen grains than susceptible ones under HS [21]. In addition, heat-tolerant tomato genotypes accumulate more soluble sugars in their leaves under HS than susceptible ones at the flowering and anthesis stages [39], possibly due to their better performance in maintaining carbohydrate synthesis under HS.

5.3. Proline

The development and fertility of pollens depend on local proline biosynthesis in mature pollen grains, as well as during the later microspore development stages [83]. Proline also functions as a molecular chaperone, regulating the protein structure and protecting cell damage in stress conditions [84,85]. In tomato plants, the disruption of proline transport to the anther may be a possible cause of the reduction in pollen viability [29]. Proline accumulation in pollens is affected more significantly in heat-susceptible tomato cultivars than in heat-tolerant ones [38]. The proline content in leaves can be a useful measure of stress in tomato plants [86]. Changes in proline content under HT, as well as the endogenous level of proline content, differ according to genotypes [87]. Seedlings of a heat-tolerant cultivar accumulate significantly less proline in leaves than those of a susceptible one in HT [36]. The proline content of a tolerant cultivar did not show significant change but that of a susceptible one showed a continuous increase during the HT treatment period [36].

To understand the relationship between proline content and HT tolerance in tomatoes and to test the possibility of using proline content in heat tolerance screening, we grew 43 tomato genotypes in greenhouses where the temperature set-point for ventilation was 28 °C and 40 °C for CK and MCHS, respectively. The proline content, pollen germination, pollen tube length, and fruit set and yield of 43 genotypes were investigated; correlation analyses were conducted according to Sherzod et al. [56]. In CK, the proline content in leaves was significantly correlated with pollen germination ($r = 0.377$ *) and fruit set ($r = 0.415$ **) (Table 1) but no significant correlation was observed between proline content and other traits in MCHS (Table 2). The significant correlation between pollen germination and fruit set in CK but not in MCHS may be due to differences in genotype-dependent proline accumulation in leaves [36], resulting in disrupted proline transport in HT [29]. The results indicate that the use of proline content in leaves for heat tolerance screening is still premature and further study is necessary.

Table 1. Correlation between biochemical and reproductive traits at control temperatures (28 °C).

	Proline Content	Pollen Germination	Pollen Tube Length	Fruit Yield	Fruit Set
Proline content	1				
Pollen germination	0.337 *	1			
Pollen tube length	0.139	0.488 **	1		
Fruit yield	0.009	−0.152	−0.113	1	
Fruit set	0.415 **	0.025	−0.207	0.127	1

* and ** indicate significant difference at $p < 0.05$ and $p < 0.01$ levels, respectively.

Table 2. Correlation between biochemical and reproductive traits at high temperatures (40 °C).

	Proline Content	Pollen Germination	Pollen Tube Length	Fruit Yield	Fruit Set
Proline content	1				
Pollen germination	0.288	1			
Pollen tube length	0.078	0.610 **	1		
Fruit yield	−0.175	0.075	−0.120	1	
Fruit set	−0.003	−0.037	−0.043	0.354 *	1

* and ** indicate significant difference at $p < 0.05$ and $p < 0.01$ levels, respectively.

5.4. Glycine Betaine

Glycine betaine is a compatible osmolyte and plays an important role in osmoregulation in plants. It is synthesized in both chloroplasts and cytoplasm, but only glycine betaine in chloroplasts is positively related to stress tolerance [88]. This implies that high glycine betaine content may not necessarily account for enhanced stress tolerance. In tomato plants, however, glycine betaine significantly increased in heat-stressed tomato plants, in comparison with non-stressed plants [89]. The exogenous application of glycine betaine to heat-stressed tomato plants enhanced seed germination, the expression of heat-shock genes, and the accumulation of heat-shock protein 70 [90] and fruit yield in open fields [91].

5.5. Secondary Metabolites

Secondary metabolites also play a critical role in pollen growth and germination, osmotic regulation, the scavenging of reactive oxygen species (ROS), and membrane fluidity, as well as the signaling pathways contributing to pollen viability and fruit set [92]. HT increased the accumulation of soluble phenolics and the activity of phenylalanine by ammonia-lyase, the principal enzyme in the biosynthesis of phenolic compounds, as an acclimated mechanism against HS [93]. A significant increase in total flavonoids including kaempferol was observed in tomato plants under HS conditions during the pollen development stage [94]. In addition, the accumulation of polyamines, such as spermidine and spermine, is required for pollen germination in tomato plants [62,95], while polyamine accumulation in transgenic tomato plants enhances HT tolerance [96]. However, no effect of HT on the level of polyamine was observed in a recent study of tomato plants [94].

5.6. Superoxide Dismutase

HS affects the overproduction of ROS, destroying essential cellular components and structural elements [97]. Superoxide dismutase (SOD) helps break down harmful oxygen molecules and is considered a defense enzyme against oxidative stress [98]. In tomato plants, DAHS (>40 °C) for three hours in both ambient and root zone temperatures caused a decrease in total specific SOD activity in two tomato genotypes, one of which has heat tolerance, but no significant difference in SOD activity was observed between the two cultivars [26]. In our recent study, however, HS with 38/30 °C (day/night) for three days resulted in a significant increase in SOD activity in two cultivars, and a significant difference between the two cultivars in terms of SOD activity was also observed [87]. The contrasting results may be due to the small number of genotypes used and the different environmental conditions. Further studies are needed, with a large number of genotypes in the same environment, to clarify the role of SOD activity in the heat tolerance of tomato plants.

6. Traits Related to Direct and Indirect Selection for Heat-Tolerant Genotypes in Tomato Plants

As discussed earlier, many physiological and biochemical traits are related to heat tolerance in tomato plants. However, most of the previous studies were based on a few genotypes and the results were genotype-dependent; therefore, these traits cannot be general predictors in screening or selecting heat-tolerant genotypes in the tomato. There have been a limited number of correlation studies between fruit set and/or yield as well as other traits in HS that use a large number of tomato genotypes having various degrees of heat tolerance. A correlation study is particularly important for indirect selection to identify heat-tolerant genotypes. In this section, we examine promising target traits for direct and indirect selection for heat-tolerant genotypes, based on correlation studies with a large number of genotypes. To our knowledge, no such correlation study was conducted in tomato plants among fruit traits and soluble sugars, glycine betaine, secondary metabolites, and SOD activity. The proline content did not show any significant correlation with traits related to heat tolerance in HS (Table 2). Therefore, this will not be discussed here.

6.1. Traits for Direct Selection for Heat Tolerance

Reproductive rather than vegetative growth is more vulnerable to HS in many crops including the tomato [69]. Vegetative traits were also not significantly correlated with fruit yield and fruit set in HT among 38 [56] and 13 tomato genotypes [37], respectively, despite fruit set and yield being considered as the main targeted traits for heat-tolerance screening in tomato plants. Therefore, most studies on heat tolerance in tomato plants have been focused on reproductive growth. HS significantly decreased the fruit set and the number of fruits per truss [31,37,56,99–101], which were significantly correlated with reduced fruit yield [56]. However, the effect of HS on flower number per truss is somewhat controversial; there were reports of a reduction [37,102,103], no change [20,28,29,104], and even an increase [56] in flower number under HS. The obvious decrease in fruit set or number but not in flower number under HT among tomato genotypes indicates that floral development may not be the key physiological trait that confers heat tolerance on tomato plants.

Fruit set and yield have been the main traits used for screening heat tolerance among tomato genotypes [63], although fruit drops after fruit set have also increased under HT [37,102]. Various tomato genotypes have been screened, based on fruit set and yield [24,63,68]. However, the fruit set is calculated from the ratio of the number of fruits divided by that of flowers and can be significantly affected by a reduction [37,102,103] or increase in the number of flowers [56]. Therefore, the fruit set in HS is inevitably affected by the changes in the number of flowers in HS, which can also affect the correlation between fruit set and other traits, resulting in a lower correlation with fruit yield than fruit number [56]. Therefore, breeders working with tomato genotypes who have increased the flower number per truss under HS should consider fruit number per truss instead of fruit set for the trait to achieve direct selection for heat tolerance.

Different fruit traits must be considered, depending on cultivars with different fruit sizes, in the screening of heat-tolerant genotypes since some traits associated with heat tolerance differ according to tomato fruit size [56]. For example, both the fruit number per truss and fruit set were significantly and positively correlated with fruit yield in cherry tomato genotypes (>50 g) but only the fruit number per truss was significantly correlated with fruit yield in large fruit types (<100 g) [56]. This is because an increase or decrease in flower number per truss does not significantly affect the fruit set in cherry tomato genotypes, which have much more flowers per truss than large fruit genotypes; however, the increase or decrease by one or two flowers in large fruit genotypes significantly affects the fruit set. In addition, in cherry tomato types, heat-tolerant genotypes can be pre-selected, simply by looking at the previous fruit yield data collected in optimum temperature conditions, because a significantly positive correlation was observed between fruit yields in CK and MCHS conditions that was not observed among large fruit genotypes [56].

6.2. Traits for Indirect Selection for Heat Tolerance

Vegetative growth parameters should be avoided regarding heat tolerance since recent studies with a large number of tomato accessions showed that these parameters were not significantly correlated with fruit set [37] and fruit yield [56] in HT, which are key indicators for heat tolerance. Besides this, there was no association between seedling and reproductive growth stages in HT [56]. Therefore, the selection of heat-tolerant tomato genotypes based on seedling performance and vegetative growth parameters in HT should be conducted very carefully, although selection in the early growth stages can facilitate the breeding process.

Pollen traits may be promising candidates for indirect selection when screening tomato accessions in HS. In particular, pollen viability and germination may be promising candidates for indirect selection for heat tolerance since many of the studies discussed above reported an association between pollen traits and fruit set or yield. However, careful consideration must be taken when applying pollen traits for the selection of heat-tolerant lines in breeding programs since the results of these studies were largely based on a few genotypes and showed genotype-dependent responses. Studies using a large number of genotypes showed somewhat contrasting results. Pollen germination was not significantly correlated with fruit set [68] and fruit yield [56], when using 11 and 38 genotypes, respectively, and both fruit set and yield when using 43 genotypes (Table 2) in HS. In another study with 13 tomato genotypes, significantly positive correlations were observed between pollen viability and fruit set and fruit number in tomato plants [37]. In addition, no significant correlation was observed between pollen tube length and fruit set or number [56,68]. These contrasting results might be due to different HS regimes and environmental conditions (pollens receiving heat stress in a Petri dish [68], and plants in pots [37] and in soil in greenhouses [56]). The procedures for pollen tests were also different, such as pollen viability [37] and germination [56,68]. A standardized procedure to screen for pollen tolerance to HS must be developed and applied in future studies and breeding programs.

Membrane thermostability may be a good candidate for indirect selection for heat tolerance and should generally be measured by ion or electrolyte leakage. In tomato plants, the level of ion leakage differed by tomato genotypes and significantly decreased under HS [37]. Heat-tolerant genotypes showed less electrolyte leakage than susceptible ones in tomato plants [26,36]. In a study using 13 tomato cultivars, fairly good correlations between ion leakage and fruit set ($r = -0.444$) or pollen viability ($r = -0.294$) were observed, although they were not significant [37]. In an experiment using a larger population (43 cultivars), a significantly negative correlation ($r = -0.9$) between electrolyte leakage and fruit yield was observed [57]. These correlation studies suggest the potential of ion or electrolyte leakage for heat tolerance screening in tomatoes.

The index of *Fv/Fm* has been utilized when screening large numbers of tomato genotypes in HS from seedlings to mature plant stages [82]. Specifically, *Fv/Fm* of 28 genotypes was measured under DAHS and MCHS conditions, following three different HS regimes, under conditions from a climate chamber to an open field. Tolerant genotypes that were selected by higher *Fv/Fm* in HS displayed a lower level of leaf heat injury, as well as a higher fruit yield [82]. Moreover, in a correlation experiment using four heat-tolerant and four susceptible cultivars, *Fv/Fm* was significantly correlated with plant dry weight under four days of HS ($r = 0.974$) in a climate chamber, which was significantly correlated with fruit dry weight ($r = 1.00$) and fruit set ($r = 0.984$) in field conditions [82]. The study may suggest that the parameters associated with photosynthetic apparatus can be applied to the rapid detection of heat-tolerant tomato plants during the early vegetative growth stage. However, correlation analyses were not performed with the same plant types or under the same environmental conditions; therefore, *Fv/Fm* is still far from sufficient as a predictor of HT tolerance. Further study is essential with a larger number of genotypes and trait investigations in the same plant type and environment.

7. Conclusions and Future Perspectives

According to a recent IPCC report, it is certainly a matter of major concern that climate change will be detrimental to food security. In particular, HS, an elevated temperature above a threshold level, can negatively influence plant behaviors during the entire growth and development cycle in both greenhouse and open-field conditions, thereby leading to the diminishing of the fruit set, quality, and yield of tomatoes. It is, therefore, essential to develop tomato cultivars that are tolerant of HS. Since the different organs and growth stages of tomato plants exhibit different sensitivities in response to HS, different HS regimes should be properly applied from seedlings to reproductive growth stages. In this review, we have discussed recent attempts in screening and breeding for heat tolerance in tomato plants under different HS regimes. In addition, we discussed the diverse selecting traits shown during the vegetative and reproductive growth stages and provided an association between the traits and the key biochemical factors, which can be effectively utilized to screen and/or select a large number of tomato genotypes under HS conditions. Finally, we proposed effective direct and indirect selection strategies to develop heat-tolerant tomato cultivars presenting promising candidate traits that are significantly correlated with fruit set and yield under HS.

Further studies are required with a large number of tomato genotypes to identify the key traits for indirect selection since there is still a lack of correlation studies for HS tolerance using a large population. In addition, further study is necessary to establish the effect of HS on the marketable yield of tomato plants. Seedling selection to accelerate the breeding process will apparently not be applied in the near future for the selection of heat-tolerant tomato genotypes due to the contrasting results of an association between the seedling and reproductive stages. To increase the efficiency of developing heat-tolerant tomato cultivars, it is also necessary to develop a marker-assisted selection system. Since the traits related to heat tolerance show quantitative inheritance, the development of molecular markers can be conducted with bi-parental quantitative trait loci mapping and genome-wide association studies, with plenty of sequence information being obtained from whole-genome sequencing, re-sequencing, and genotyping-by-sequencing. Emerging genome-editing techniques, including the CRISPR/Cas 9 system, can be adopted in the future to introduce or neutralize beneficial or deleterious genes, respectively, in elite tomato lines.

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