Heritability of Flower Number and Fruit Set under Heat Stress in Tomato

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Abstract. The growing volatility of the climate, and its potential impact on crop production, has prompted several physiologic and genetic analyses under high-temperature conditions. Tomato is grown in warm temperate, subtropical, and tropical regions of the world, where daytime and nighttime temperatures regularly exceed the optimum temperatures for tomato growth during the summer, exerting stress on tomato production. Recent trends indicate more frequent extreme summer temperatures, which may grow even greater in the future, impacting crop growth. The objective of the current study was to estimate the heritability of flower and fruit set ability of tomato populations under heat stress conditions so that improvement for these traits can be planned. We developed two tomato populations using contrasting parents from the North Carolina State University (NCSU) tomato breeding program and the World Vegetable Center (formerly Asian Vegetable Research and Development Center). The F₂ and F₂-derived F₃ families (F_{2:3} populations) were grown at the Piedmont Research Station (PRS), Salisbury, NC, where summer growing temperatures are warmer than optimum for tomato production. Heritability estimates of the number of flowers per cluster, the number of fruit per cluster, and fruit set (measured as a percentage) were determined in two populations of tomato—NC10137 (NC714 × CLN-2413A) and NC10418 [230 HS-1(99) × NC 1CS]—by regression analysis using the offspring-on-parents method. Broad-sense heritability across the traits was high (47.2%–100%), whereas narrow-sense heritability was very low (1.4%–22.5%). There was a positive correlation between the number of flowers and the number of fruit per cluster ($r = 0.50$, $P < 0.05$), which was in close agreement with previous findings. These findings will be useful in investigating the genetic control of heat stress tolerance in tomato and in facilitating crop improvement in the future.

Tomato (*Solanum lycopersicum* L.) is influenced by some abiotic stresses that have a major impact on fruit quality and yield. Heat stress impacts the crop in several ways, including disruption of pollen development and viability, fertilization, enhancement of premature flower abortion, early fruit drop, and direct damage to fruits, affecting yield and quality. With growing evidence of climate change, increased average temperature, and extreme weather events, there is the potential for significant impacts on agriculture production (Sawicka et al., 2017; Wahid et al., 2007; Wang et al., 2017). Global climate change will impact agriculture production and food security throughout the world (Cheng et al., 2017; Hall, 2001; Meng et al., 2017; Zhou et al., 2017). The evidence of global warming from general circulation models (Intergovernmental Panel on Climate

Change, 2014) has revived the interest in studying yield declines in crops, including tomato at physiologically critical temperatures (Peet et al., 1998; Wahid et al., 2007).

The impact of heat stress is complex; it is influenced by multiple factors, such as intensity, duration, and rate of temperature increase (Cheng et al., 2017; Meng et al., 2017; Zhou et al., 2017). Field-grown tomatoes around the world regularly experience heat stress conditions of 35 °C, whereas 40 to 45 °C temperatures are rare, resulting in annual crop losses resulting from a reduction in photosynthesis capacity and reduced fruit set (Peet et al., 1998; Zhang et al., 2012). In the United States, for instance, many of the leading tomato-growing regions regularly experience heat stress temperatures (Yilmaz and Tolunay, 2012). In California, Florida, and North Carolina, the majority of the major vegetable growing regions are exposed to a yearly average of 90 to 150 d, 150 to 210 d, and 60 to 120 d of ≥ 30 °C, respectively (American Horticultural Society, 1995). Optimum growing temperatures for tomato (*Solanum lycopersicum* L.) are less than 32 °C and 24 °C during the day and night, respectively. Therefore, most of the tomato production regions in these states are at risk of exposing the crop to heat stress temperatures

for part or all of the summer production season. In addition, current U.S. temperature data indicate a trend of an increased frequency of rare high temperatures, especially of elevated nighttime lows (National Oceanic and Atmospheric Administration, 2016). These current trends are reminiscent of the heat waves experienced in the United States during the 1930s, which remain the worst on record (Environmental Protection Agency, 2016). These realities highlight the need for enhanced heat stress-tolerant varieties with desirable horticultural traits.

In tomato, heat stress causes reduced yields because of failure to set fruit and reduced photosynthetic capacity (Peet et al., 1998; Zhang et al., 2011, 2012). High-temperature stress has been reported to affect many physiologic traits, including fresh plant weight, dry weight, and leaf area in tomato (Shaheen et al., 2016; Zhou et al., 2017). Other vegetative effects include reduced photosynthetic efficiency (Bartsur et al., 1985; Criddle et al., 1997), reduced assimilate translocation, reduced mesophyll resistance, and enhanced disorganization of cellular organs (Chen et al., 1982).

The most damaging impact is on fruit yield. The yield reduction is related primarily to reduced fruit set, which may not occur for many reasons, including adverse effects on meiosis of ovules and pollen mother cells, reduced pollen shed resulting from impaired development of the endothecium in the anthers, stigma position (exerted under heat stress), number of pollen grains retained by the stigma, pollen germination, pollen tube growth, ovule viability, fertilization and post-fertilization processes, and growth of the endosperm (Driedonks et al., 2016; Peet et al., 1997; Sato et al., 2002; Zhou et al., 2017). Other indirect yield-reducing effects of heat stress include fruit cracking, malformation of fruits (e.g., catfacing), and a malformed blossom-end scar. In sum, heat stress reduces the fruit number, quality, and marketable yield of tomato.

Heat stress tolerance has been analyzed in different plant species, including *Arabidopsis thaliana* and tomato, investigating the genetic mechanisms of adaptation. Heat shock protein analyses have been reported since the 1970s. In tomato, several studies have tried to identify genes conferring heat stress tolerance so they can be incorporated into breeding materials. Although some interesting and useful information was identified, its introgression into breeding materials has not progressed very well (Bita et al., 2011; Golam et al., 2012; Wahid et al., 2007).

For practical breeding purposes, phenotypic traits associated with heat stress tolerance are measured rather than the direct physiologic mechanisms. There are a few studies from various parts of the world investigating the genetic control of heat stress tolerance in tomato. However, those studies show inconsistent results in terms of genetic control. In genetic analyses, most of the heat stress-related traits were found to exhibit overdominance in inheritance analyses, whereas partial dominance was identified

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for days-to-flowering and the number of trusses per plant (Hazra and Ansary, 2008). Identification of heat tolerance in screening trials of tomatoes has been accomplished by evaluating them for flowering and fruit set traits because these two processes are sensitive to heat stress and are related directly to fruit yield and quality (Abdulkaki and Stommel, 1995; Berry and Uddin, 1988; Beshirelahmadi and Stevens, 1979).

The mechanisms of heat stress tolerance in tomatoes include many growth-related and morphological traits. Pollen viability (germination, tube growth, and fruit set) is negatively affected by heat stress (Zhou et al., 2015) and was found to be the significant factor affecting fruit set in another North Carolina breeding source, over and above heat stress effects on the female reproductive parts (Peet et al., 1998). Heat tolerance in tomato has also been linked to greater leaf pigment, retention of normal stomata (pore size and shape), chloroplasts (shape, lack of starch grain accumulation), and maintenance of the net photosynthesis rate (Zhou et al., 2015).

Increases in heat affect the efficiency of substrate carbon conversion, which drives growth and repair activities. The conversion efficiency in tomato at $\geq 30^{\circ}\text{C}$ is about 25% of the optimum (21°C), which resembles the efficiency levels at the suboptimal temperature of 15°C (Criddle et al., 1997).

In addition, heat stress conditions induce heat shock proteins in heat-tolerant genotypes (Neumann et al., 1987; Nover and Scharf, 1984). These proteins have been suggested to protect plants under heat stress. A tomato chaperone protein, DnaJ, is targeted to the chloroplasts and helps protect the activity of the Rubisco enzyme during heat stress (Wang et al., 2015). Elsewhere, it is reported that only the heat-susceptible lines exhibit the heat stress-induced physiologic perturbations during strong, acute heat stress, which suggests that heat-tolerant lines may also exhibit a greater sort of “buffering” capacity for heat before their systems are disrupted (Camejo et al., 2005, 2006, 2007). Selections from a wide genetic variation have been reported by Shaheen et al. (2016), and molecular characterization would provide further insight into the detailed investigation on the molecular mechanism of heat tolerance in tomato.

Heritability analysis is important to determine the appropriate method of genetic improvement. Heat stress tolerance was found to have low heritability (Hanson et al., 2002). We were interested in assessing the heritability of heat stress tolerance traits—number of flowers, number of fruit per cluster, and fruit set (measured as a percentage)—in two tomato populations derived from crosses between heat-tolerant and heat-sensitive breeding lines when grown under field conditions. Similar traits (number of flowers, number of fruit, and fruit set) have been used for heat stress tolerance studies in tomato (Abdulkaki, 1991; Hanson et al., 2002; Lin et al., 2010). We investigated

heritability in a population derived from the line CLN2413, which was identified to be heat tolerant under extremely high-temperature conditions (Hazra and Ansary, 2008). Another heat tolerant line, 230 HS-1 (99), is the result of the NCSU breeding program and can produce more flowers.

Materials and Methods

Plant materials. One of the F_2 populations (NC10137) was developed by crossing NC714 $\times$ CLN-2413A, whereas the other F_2 population (NC10418) was developed by crossing 230HS-1(99) $\times$ NC 1CS. NC714 is a large-fruited tomato. It was released for its excellent fruit quality and high yield when grown under normal (optimal temperature) environmental conditions (Panthee and Gardner, 2011). However, it is not tolerant to the high-temperature stress conditions regularly encountered in various parts of North Carolina and the southeastern United States. CLN-2413A is a breeding line developed at The World Vegetable Center (formerly Asian Vegetable Research and Development Center), Taiwan. It has been reported to have improved fruit set at high temperatures (Hazra and Ansary, 2008). 230HS-1(99) is an advanced breeding line developed from the North Carolina state tomato breeding program. It is a large-fruited tomato with improved heat tolerance. NC 1CS is a large-fruited tomato breeding line released from NCSU for its high yields and fruit smoothness (Panthee and Gardner, 2011). It is not tolerant to heat stress. Crosses were made in Spring 2010 to produce the F_1 , which were selfed to produce F_2 in Fall 2010.

For field evaluation, seeds were planted in flatbed metal trays in a standard seeding mix (2:2:1, v/v/v) peat moss: pine bark: vermiculite with macro- and micronutrients (Van Wingerden International Inc., Mills River, NC). After 10 d, seedlings were transplanted to 72-cell flats (56×28 cm). Raised plot beds were prepared. Plots were covered with black plastic mulch with drip irrigation according to standard growing practices for North Carolina tomato production. After 4 weeks, plants were transplanted to the field. Six plants of each line were planted with 45 cm of plant-to-plant and 150 cm of row-to-row spacing.

Two F_2 populations of tomato (*Solanum lycopersicum*) consisting of 200 individual plants were grown at PRS, Salisbury, NC, in 2014. F_3 families were developed by selfing the F_2 plants in the field. The F_3 lines were selected from the F_2 populations, consisting of 56 families of the NC10137 population and 60 families of the NC10418 population. These were grown at PRS with two replications consisting of six plants per plot. In both generations (F_2 and F_3 in 2014 and 2015, respectively), ‘Sun Leaper’, ‘Solar Set’, and NC84173 were grown as control genotypes. The PRS soil type was red clay, and natural daylight during this season provided a photoperiod averaging 14 h/10 h day/night, with $\geq 32^{\circ}\text{C}$ day and $\geq 21^{\circ}\text{C}$ night temperatures during the growing seasons (Fig. 1).

Phenotypic data collection. Phenotypic data were collected as described by Hazra and Ansary (2008) and Hanson et al., (2002).

Number of flowers per cluster. The total number of flowers in the second cluster was counted from each plant in the F_2 populations. For the F_3 families, the number of flowers from the third cluster was counted from the middle four plants out of six plants per plot, leaving the first and last plants from each plot uncounted as border plants. Because of the severe heat stress, some plants died, leaving some plots with four or fewer plants. In these cases, up to four plants were assessed regardless of position within the plot. In the F_3 population, flowers were counted in the third cluster because an early season in the first year, herbicide drifts damaged many of the plots, leading to aborted or malformed first and often second clusters. The third clusters across the experiment appeared unaffected and therefore were assessed.

In both years, all the flowers were counted in midseason after most had opened and some had already set fruit. Because some lines often produced many flowers, flower counts were verified later, when fruit set was determined. Unopened flowers were also included in the counts. Flower abortion was common, abscising at the joint, so we included those flowers in our counts based on the remaining peduncle terminal ends. Each cluster in which we counted flowers was marked with flagging tape for assessing fruit set.

Number of fruit per cluster. Fruit was counted shortly before harvest stage on the same cluster where the total flowers were counted. The number of fruit were composed of ripe or green fruit, as well as instances when mature fruit has been knocked off the vine. The green fruit was considered to be any stage of development in which a noticeable swelling of the ovary had occurred.

Fruit set. Fruit set (measured as a percentage) was calculated as follows:

$$\text{Fruit set(\%)} = \frac{\text{Number of fruit}}{\text{Number of flowers}} \times 100.$$

Data analysis. Genotypic differences among all genotypes were determined by PROC GLM with SAS software using genotype as a fixed effect and year as a random effect (SAS Institute Inc, 2012). PROC CORR was used to determine Pearson's correlation coefficients between number of flowers and number of fruit.

Heritability analysis. Broad-sense heritability (H) was estimated using the following variance components from the F_2 population (Falconer and Mackay, 1996; Nyquist, 1991):

$$H^2 = \frac{VG}{VP} = \frac{VA + VD}{VA + VD + VE},$$

where H is broad-sense heritability, VG is genetic variance, VP is phenotypic variance, VA is additive variance, VD is dominance variance, and VE is error variance.

Narrow-sense heritability (h^2) was determined using regression analysis of offspring-on-parent approach using data from the F_2

and F₃ generation, as has been used by Ohlson and Foolad (2015) and as follows (Falconer and Mackay, 1996; Nyquist, 1991):

$$h^2 = \frac{VA}{VA + VD + VE} = \frac{Cov(F_3 \times F_2)}{\sqrt{(VF_3 \times VF_2)}}$$

where h^2 is narrow-sense heritability, VA is additive variance, VD is dominance variance, VE is error variance, VF₂ is variance in the F₂ generation, VF₃ is variance in the F₃ generation, and Cov (F₃ × F₂) is covariance of individuals at the F₂ and F₃ generations.

Results

Number of flowers per cluster. In the F₂ generation, the average number of flowers per cluster was 7.1 in NC10137 (range, 1–15), whereas it was 5.1 (range, 0–9) in NC10418. In the F₃ generation, the average number of flowers per cluster was 5.2 in NC10137 and 4.8 in NC10418 (range, 0–10) (Table 1).

Number of fruit per cluster. In the F₂ generation, the average number of fruit per cluster in the NC10137 population was 4.1 (range, 1–9), whereas it was 3.4 (range, 2–6) in the NC10418 population (Table 1). Similarly, in the F₃ generation, the average number of fruit per cluster was 2.4 (range, 0–6) in the NC10137 population, whereas it was 2.2 (range, 0–5) in the NC10418 population.

Fruit set. Fruit set, which is the indicator of heat stress tolerance, was less in NC10137 compared with NC10418. Average fruit set was 63.2% and 47.7% in the F₂ and F₃ generations in the NC10137 population, respectively (range, 0%–100%). Average fruit set was 70.8% and 49.5% (range, 33.3%–100% and 0%–100%) in the F₂ and F₃ generations, respectively, in the NC10418 population (Table 1).

Frequency distributions for the number of flowers and the number of fruit per cluster from the F₂ and F₃ generation are given in

Figs. 2 and 3. There was a normal distribution in each population as well as in the combined data (Figs. 2 and 3).

Heritability analysis of the F₂ generation. Heritability analyses were performed in two separate F₂ populations, as well as a combined set of data from those F₂ populations. Heritability estimates for the number of flowers ranged from 71.2% in a population (NC10418) derived from 230 HS-1(99) × NC 1CS, whereas it was 86.0% in another population (NC10137) derived from NC714 × CLN-2413A. In the combined population, the heritability estimate for the number of flowers was 85.1% (Table 2). Heritability estimates for the number of fruit per cluster were 47.2% in a population derived from 230 HS-1(99) × NC 1CS and 66.0% in another population derived from NC714 × CLN-2413A. The heritability estimate for the number of fruit from the combined population was 62.8% (Table 2). Heritability estimates for fruit set were almost 100% for individual population data as well as the combined set of data (Table 2).

Heritability analysis of the F₃ generation. Compared with the F₂ generation, heritability estimates for all traits, including the number of clusters, number of flowers, number of fruit, and fruit set, were low in the F₃ generation. The range of narrow-sense heritability estimates for the number of flowers was 2.7% to 10.0%. Similarly, the estimates for the number of fruit ranged from 1.4% to 5.9%, whereas that for fruit set was 4.2% to 7.4% (Table 2). These heritability estimates were calculated by the parent–offspring regression analysis method at the F₃ generation, which gives the narrow-sense heritability.

Correlation analysis. A significant positive correlation was found between the number of flowers and number of fruit ($r = 0.50$, $P < 0.05$) in the F₂ generation. Similar correlations were found between the number of flowers and number of fruit per cluster ($r = 0.26$, $P < 0.05$) in the F₃ generation. Correlation analysis was performed between F₂ and F₃ for the number of flowers and the number of fruit. Fruit set was very low (Fig. 4).

Fig. 1. Monthly average temperature patterns (measured in degrees Celsius) during the study period at the Piedmont Research Station, Salisbury, NC, during 2014 and 2015. Data were collected during July and August when plants started flowering.

Table 1. Descriptive statistics for the number of flowers per cluster, number of fruit per cluster, and fruit set (measured as a percentage) related to heat stress tolerance in F₂ and F₃ populations in 2014 and 2015.

Trait	Generation	Population	Mean	SD	Minimum	Maximum
No. of flowers	F ₂	NC10137	7.1	2.5	1	15
		NC10418	5.1	1.6	2	9
	F ₃	NC10137	5.2	2.0	0	10
		NC10418	4.8	1.8	1	10
No. of fruits	F ₂	NC10137	4.1	1.4	1	9
		NC10418	3.4	0.9	2	6
	F ₃	NC10137	2.4	1.3	0	6
		NC10418	2.2	1.1	0	5
Fruit set (%)	F ₂	NC10137	63.2	23.5	0	100
		NC10418	70.8	21.6	33.3	100
	F ₃	NC10137	47.7	26.8	0	100
		NC10418	49.5	28.9	0	100

Discussion

Our main objective of the current study was to estimate the heritability of heat stress-related traits, including the number of flowers per cluster, number of fruit per cluster, and fruit set to identify the best breeding strategy for our germplasm. We assessed two tomato populations developed from known heat stress-tolerant and heat stress-sensitive lines. The population NC10137_F₂ was developed from NC714 × CLN-2413A, and CLN-2413A was found to be heat tolerant under extreme high-temperature conditions (27.3 to 42.3 °C/13.8 to 22.9 °C day/night) (Hazra and Ansary, 2008). The population NC10418 was developed by crossing 230HS-1(99) × NC 1CS, and previous assessments of 230HS-1 (99) suggested that it carries heat stress tolerance (R. Gardner, personal communication).

Fig. 2. Frequency distribution of an NC10137 F₂ population derived from NC 714×CLN-2413A, and an NC10418 F₂ population of tomato developed from 230 HS-1(99)×NC 1CS in a heat stress evaluation trial at the Piedmont Research Station, NC, in 2014. (A) Number of flowers per cluster. (B) Number of fruit per cluster.

Fig. 3. Frequency distribution of an NC10137 F₃ population derived from NC 714×CLN-2413A, and an NC10418 F₃ population of tomato developed from 230 HS-1(99)×NC 1CS in a heat stress evaluation trial at the Piedmont Research Station, NC, in 2015. (A) Number of flowers per cluster. (B) Number of fruit per cluster.

Table 2. Heritability estimates (measured as a percentage) for the number of flowers per cluster, number of fruit per cluster, and fruit set (measured as a percentage) related to heat set traits in tomato from two separate F₂ populations, as well as combined F₂ and F₃ populations evaluated in Piedmont Research Station, Salisbury, NC, in 2014 and 2015, respectively.

Trait	NC10137		NC10418		Combined	
	Broad sense	Narrow sense	Broad sense	Narrow sense	Broad sense	Narrow sense
No. of flowers	86.0	14.0	71.2	18.9	85.1	10.5
No. of fruit	66.0	8.1	47.2	22.5	62.8	1.4
Fruit set (%)	100.0	20.0	99.8	11.4	99.8	7.3

Broad-sense heritability was determined using the F₂ generation data, and narrow-sense heritability was determined using offspring–parent regression analysis with the F₂ and F₃ data. We found a large differ-

ence between broad-sense and narrow-sense heritability. For example, broad-sense heritability for the number of flowers per cluster was more than 86%, whereas narrow-sense heritability was around 14% in the NC10137

population. Similarly, broad-sense heritability for the number of fruit per cluster was around 66% whereas narrow-sense heritability was around 8% in the NC10137 population (Table 2). Broad-sense heritability includes additive and dominance variance components, whereas narrow-sense heritability relates only to the additive variance (Falconer and Mackay, 1996; Nyquist, 1991). The dominance component might have caused the inflation of the estimates of the broad-sense heritability.

The narrow-sense heritability of the number of flowers and number of fruit per cluster were also low in one of the previous studies, the results of which are in agreement with the

Fig. 4. Determination of correlation coefficients between the F_2 and F_3 generations in a heat stress evaluation trial of tomato. (A) Number of flowers per cluster. (B) Number of fruit per cluster. (C) Fruit set (measured as a percentage).

current findings (Hanson et al., 2002). If there is a high dominance variance component involved in determining heritability, then individual plant selection from the early generation is not useful, because the performance of a single plant may be the result of the dominance component. Selection from a later generation helps to improve efficiency because it has more additive variance components. In the current study, there was a very low correlation between F_2 and F_3 generations for the number of flowers per cluster, number of fruit per cluster, and fruit set (Fig. 4). The low correlation between the F_2 and F_3 generations for these traits and low narrow-sense heritability are in agreement in the current study. In other words, if the narrow-sense heritability were high, correlations between the F_2 and F_3 generations for these traits are expected to be greater.

Narrow-sense heritability for heat stress-related traits was found to be low, and it was concluded that single plant selection is not useful for the improvement of heat stress tolerance in yet another study (Hazra and Ansary, 2008). Instead, those authors suggested that selection based on family means from the F_3 generation and beyond would be the most effective strategy. Because heat stress tolerance appears to be inherited similarly in our populations, we have adopted those recommendations for our future breeding efforts.

An average number of flowers and fruit per cluster in the F_3 generation was less than in the F_2 generation. This might be because the temperatures were warmer in 2015 compared with 2014 during the trial season. Also, the number of flowers and number of fruit per cluster in the F_3 generation should have more additive components and less dominance components. Comparing the two populations, NC10137 had more flowers per cluster as well as fruit per cluster than NC10418.

In some cases, fruit set was as high as 100%, indicating that these lines did not drop any flowers or immature fruit at all. This suggests that those lines had excellent heat stress tolerance ability. Fruit set is one of the most important indicators providing excellent information for plant breeders for the selection of heat stress tolerant materials.

Correlation coefficients between the number of flowers per cluster and the number of fruit per cluster in the F_2 and F_3 generations followed the same trend. Thus, the broad-sense and narrow-sense heritability estimate patterns appear meaningful. Correlation coefficients between the number of flowers and number of fruit per cluster, and the number of fruit per cluster were in agreement with past findings. Although there was a negative correlation between the number of flowers and fruit set in the current study, Lin et al. (2006, 2010) found a nonsignificant positive correlation. Similar correlation trends were also found by Hazra and Ansary (2008).

We also observed inconsistent responses in our heat stress-tolerant and -sensitive controls. The heat stress-tolerant controls ‘Solar Set’ and ‘Sun Leaper’ exhibited moderate fruit set alongside the F_3 families, but were on the lower end of the populations, and the susceptible NC 1CS had even lower fruit set, as expected. Although we were not able to detect significant differences between any of our controls, several F_3 lines had significantly greater fruit set than NC 1CS and several other F_3 lines. Congruent with the current findings, the number of flowers and number of fruit per cluster in heat stress-tolerant and -sensitive genotypes were found to be inconsistent by Abdulbaki (1991).

The heat stress effects were strong in this study as a chronic stress factor. The generally accepted optimum temperature for tomato is 21 °C, whereas 30 to 32 °C is considered to be a damaging level of heat stress. The F_2 generation was subjected to an average temperature of about 24 °C, with 28 d of 32 °C or greater heat (Fig. 1). The F_3 families were subjected to somewhat hotter conditions, with an average temperature of about 27 °C, with 63 d of 32 °C or greater heat (Fig. 1). The appearance of the plots was marginal to very poor, and many clusters did not set fruit at all. At the time of selection, toward the end of the normal harvest stage, the temperatures cooled somewhat each year, and there was apparent recovery growth in the experiments. Plots that generally had exhibited vegetative heat tolerance throughout the growing season naturally recovered better and would have been selected based on overall appearance and

vigor, as well as upper canopy fruiting. Curiously, many of these lines had the low, early fruit set. In contrast, some of the lines with the best fruit set during the warmest heat stress period did not exhibit as vigorous of recovery growth after cooling and had little to no upper canopy fruit set by the end of the season. This feature would cause them to be discarded based on overall appearance at the end of the season. Thus, heat stress tolerance of foliage may not always match sustained fruit set.

Some of the plants had 100% fruit set, which means they did not drop flowers at all, indicating they had a high heat tolerance. In the F_2 generation, the wider the range for any traits, the better the distribution, and the more chances of segregation in a further generation.

It is also possible that the poor vegetative regrowth of the best fruit set lines may be related to having a larger fruit load on a small plant. It will be essential to combine both high fruit set with vigorous canopy recovery. Although these are general observations, it suggests that vegetative and reproductive heat tolerance may be segregating in our material, and that fruit set under high-temperature stress is not necessarily conferred by the same mechanisms that confer foliar tolerance. In the future, it would be interesting to compare early-season (second or third cluster) fruit set with the total harvest to help identify which type of heat stress tolerance is most desirable.

Using a 5 × 5 diallel cross design, Bhattarai et al. (2016) found that additive gene action had the largest effect on morphological traits associated with heat tolerance, whereas yield was conditioned by nonadditive gene action (dominance and overdominance). They also found correlations between yield and yield-attributing traits (early flowering and maturity, more flowers per plant, flower retention, faster fruit set, more fruiting clusters, and more fruit per plant) under heat stress conditions. Yield under heat stress was also found to exhibit high heterosis. We found similar trends in our experiments, in which the heritability of additive heat stress tolerance was low, but was high for nonadditive (dominance) (Table 2). With these findings, we should focus selection for heat stress

tolerance based on the family mean value in later generations.

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