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Altered flower retention and developmental patterns in nine tomato cultivars under elevated temperature

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Abstract

Moderately elevated temperature effects on flower development were examined in nine tomato cultivars (*Lycopersicon esculentum* Mill.). Plants were grown under high (HT, 32/28 °C day/night temperatures) and control (CT, 26/22 °C) temperature conditions. Fate of flowers developed was categorized as seeded fruit, parthenocarpic fruit, undeveloped flowers, or aborted flowers. Although HT decreased seeded fruit set in all nine cultivars, the degree of sensitivity and the pattern of reaction to the elevated temperature differed among cultivars. FLA7156 was the most tolerant cultivar, although under HT seeded fruit set was less than half that at CT (22.5% compared to 46.8%). The remaining cultivars had very few or no seeded fruit set at all at HT. The percentage of parthenocarpic fruit increased at HT compared to CT in all cultivars. Aborted flowers also increased in FLA7156, NC8288, NCHS1 and NC46E, but did not change in 'Piedmont', NC279HS, and NC403HS, or decreased in 'Fresh Market 9' and TH318. Reduction of flower abortion and increase of parthenocarpic fruit set can be advantageous traits for breeding of high temperature tolerant tomato cultivars.

Keywords: *Lycopersicon esculentum* Mill.; Parthenocarpy; Undeveloped flowers; Flower abortion; High temperature stress

1. Introduction

Tomato plants are widely grown in sub-tropical regions where they often experience high temperatures during fruit set. It has been reported that heat stress can occur at temperatures just a few degrees above optimal (mean daily temperatures of 27 and 29 °C) (Peet et al., 1997,

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1998). Such moderately elevated temperature stress may not disrupt biochemical reactions fundamental for normal cell functioning since the temperatures are still in the range that a tomato plant would grow normally. Also, the majority of protein synthesis would not be affected under moderately elevated temperature stress below 35 °C (Alberts et al., 1994). However, microsporogenesis would be significantly disturbed, and consequently fruit set would decrease (Sato et al., 2000). Specifically, pollen germination and release seem to be the most sensitive physiological processes to such a stress (Peet et al., 1998; Sato et al., 2000, 2002). Although reduced fruit set is a common response to elevated temperatures, an increase in parthenocarpic fruit set, rather than an increase in flower abortion, has been reported in a heat-sensitive tomato cultivar (Sato et al., 2001). Formation of parthenocarpic fruit is a useful trait in some vegetable crops, including processing tomatoes, because seeds need not be removed. We evaluated the incidence of seeded fruit, parthenocarpic fruit, undeveloped flowers, and aborted flowers of nine tomato cultivars under chronic, moderately elevated temperatures to determine how common the parthenocarpic response was in cultivars rated as either tolerant or susceptible to high temperature from field trials.

2. Materials and methods

2.1. Plant materials

Nine inbred lines of determinate (D) and indeterminate (ID) tomato (*Lycopersicon esculentum* Mill.) differing in temperature sensitivity were selected from North Carolina (NC8288: D, NC297HS: ID, NCHS1: D, NC403HS: D, NC46E: D, ‘Piedmont’: ID; Gardner, 1985, 1990, 1992, 1993), Florida (FLA7156: ID, Scott et al., 1986), Texas (‘Fresh Market 9’: ID, Leeper and Cox, 1986), and Louisiana (TH318: D, Hanna et al., 1992). Seeds were sown in a gravel:peat-lite mixture (1:1 in volume) and placed in a germination room equipped with mist irrigation benches. Day/night temperatures were maintained at 26/22 °C. Seedlings were transplanted to 6 cm diameter peat pots (Jiffy Strips, Jiffy Products, Shippagan, Canada) filled with gravel:peat-lite mixture (2:1 in volume) at 7 days after seeding (DAS) and maintained in a Phytotron greenhouse at 26/22 °C. Seedlings were transplanted to 20 cm diameter pots filled with a gravel:vermiculite mixture (2:1 in volume) at 25 DAS. Four chambers were prepared, two chambers were set at 26/22 °C day/night temperatures as controls (CT) and the other two chambers were set at 32/26 °C day/night temperatures for high temperature (HT) treatment. Humidity was not controlled, however, it was not significantly different between chambers (see Section 3). Six plants of each cultivar were assigned to CT (three for each chamber) and eight to HT (four for each chamber), the plants were then moved into the appropriate chambers. Plants were randomized within chambers once a week. The mixed T-12, cool-white fluorescent and 100 W incandescent lamps provided 500 μmol photon m^{-2} s^{-1} at pot surface level from 7 a.m. to 7 p.m. in each chamber. Phytotron standard nutrient solution was provided twice daily (Thomas and Downs, 1991). At 48 DAS, we observed anthesis in the first flower and started to pollinate flowers daily with a commercial electric pollinator, a standard procedure in controlled environment tomato production. We continued pollination at least every other day until 73 DAS.

2.2. Harvest, flower inventory, and data analysis

All plants were harvested at 83 DAS and pollinated flowers were categorized as having produced seeded fruit, parthenocarpic (seedless) fruit, undeveloped flowers, or aborted flowers. Fruits containing visible seeds in medial cross-section were recorded as seeded, while those without seed were recorded as parthenocarpic. Fruits and flowers still attached to the peduncle at harvest but not large enough for visual examination of seed content were recorded as undeveloped flowers. Aborting flowers, yellowing or partial separation in the abscission layer, and peduncles without fruits or flowers were recorded as aborted flowers. Seeded fruit, parthenocarpic fruit, undeveloped flowers, and aborted flowers are shown as percentages as well as actual numbers because the number of flowers can vary with cultivar and temperature (Peet et al., 1997; Sato et al., 2001). Percentage in each category was calculated by dividing the number of flowers in that particular category by the total number of pollinated flowers. Percentages calculated for each plant were averaged for each cultivar to show mean percentage.

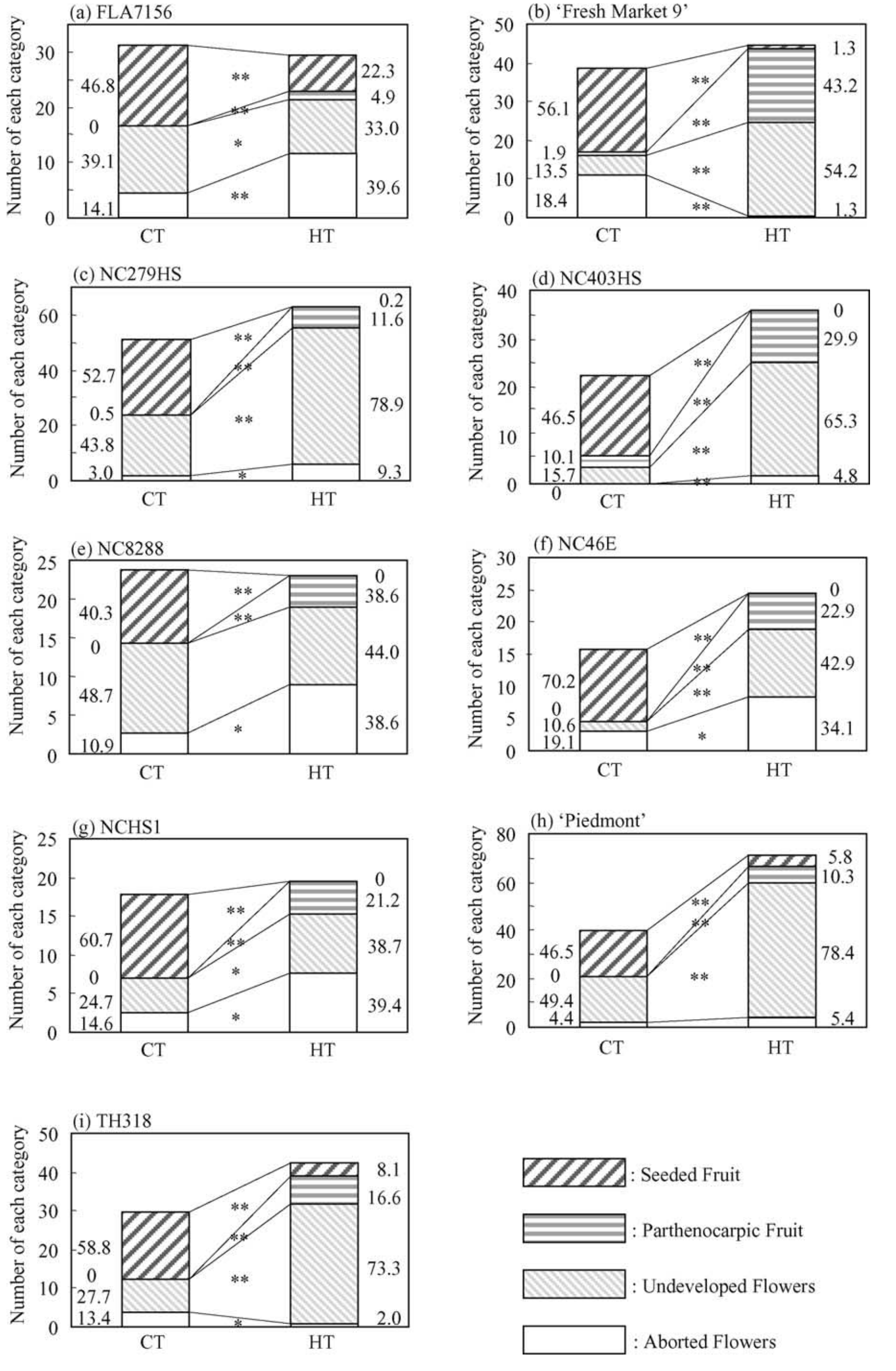
The actual number were analyzed using STATISTICA statistical software (StatSoft Inc., Tulsa, OK) for one-way analysis of variance (ANOVA) and *t*-test. For all analyses, individual seeded fruit, parthenocarpic fruit, and aborted flower data were grouped over individual fruit trusses into an average for the plant.

3. Results and discussion

Actual temperature measurement of chambers indicated $(32 \pm 1.2)/(26 \pm 1.1)\,^{\circ}\mathrm{C}$ in the HC, $(26 \pm 1.1)/(22 \pm 0.9)\,^{\circ}\mathrm{C}$ in the CT chamber. Humidity was $(90 \pm 2)/(95 \pm 1)$ and $(88 \pm 2)/(95 \pm 1)$ (relative humidity, day/night) in the CT and HT chambers, respectively.

No significant effect of chambers in same temperature treatment was observed on the number of flowers, seeded fruit, parthenocarpic fruit, undeveloped flowers or aborted flowers by ANOVA (data not shown). Thus, data of two chambers in the same temperature treatment were combined. In five cultivars, HT significantly increased the number of flowers per plant: NC279HS ($P < 0.05$), NC403HS ($P < 0.01$), NC46E ($P < 0.05$), 'Piedmont' ($P < 0.01$), and TH318 ($P < 0.05$). However, no significant differences in flower number was found between the CT and HT in the remaining four cultivars: FLA7156, 'Fresh Market 9', NC8288, and NCHS1.

HT decreased the percentage of seeded fruit significantly in all nine cultivars, and for the most part, also significantly increased the proportion of parthenocarpic fruit, undeveloped flowers, and aborted flowers. The pattern of allocation to the different categories of flower fate differed greatly between cultivars, however, both under CT and HT. FLA7156 (Fig. 1a) was the most high temperature tolerant cultivar tested, setting 6.6 seeded fruit (22.3%) in HT compared to 14.6 seeded fruit per plant (46.8% of all flowers produced) in CT. 'Piedmont' (Fig. 1h) and TH318 (Fig. 1i) were able to set a few fruit at moderately elevated temperatures: 5.1 and 8.1% seeded fruit in HT, respectively. 'Fresh Market 9' (Fig. 1b) and NC403HS (Fig. 1g) produced less than 2% seeded fruit and NC8288 (Fig. 1e), NC279HS (Fig. 1c), NCHS1 (Fig. 1d) and NC46E (Fig. 1f), produced no seeded fruit at HT.


(a) FLA7156
46.8
0
39.1
14.1
22.3
4.9
33.0
39.6
(b) 'Fresh Market 9'
56.1
1.9
13.5
18.4
1.3
43.2
54.2
1.3
(c) NC279HS
52.7
0.5
43.8
3.0
0.2
11.6
78.9
9.3
(d) NC403HS
46.5
10.1
15.7
0
0
29.9
65.3
4.8
(e) NC8288
40.3
0
48.7
10.9
0
38.6
44.0
38.6
(f) NC46E
70.2
0
10.6
19.1
0
22.9
42.9
34.1
(g) NCHS1
60.7
0
24.7
14.6
0
21.2
38.7
39.4
(h) 'Piedmont'
46.5
0
49.4
4.4
5.8
10.3
78.4
5.4
(i) TH318
58.8
0
27.7
13.4
8.1
16.6
73.3
2.0
Number of each category
CT
HT
: Seeded Fruit
: Parthenocarpic Fruit
: Undeveloped Flowers
: Aborted Flowers

In addition to reducing seeded fruit set, HT increased parthenocarpic fruit set significantly in all cultivars, but the percentage varied between cultivars. 'Fresh Market 9' had the highest percentage of parthenocarpic fruit (43.2%) under high temperature, and FLA7156, the lowest (4.9%). Under control conditions, the highest percentage of parthenocarpic fruit was 10.1% in NC403HS, with the other cultivars having 1.9% or less parthenocarpic fruit.

The proportion of undeveloped flowers also increased significantly in all cultivars with moderately elevated temperatures, except for FLA7156 where it declined from 39 to 33% and for NC8288, where the change was not significant. Under HT, the proportion of undeveloped flowers ranged from 33% in FLA7156 to 78.4% in 'Piedmont'. Under control conditions, the proportion of undeveloped flowers ranged from 10.6% in NC46E to 48.7% in NC8288. For seven of the nine cultivars, under high temperature, more flowers remained on the vine without developing than any other category (seeded or parthenocarpic fruit or aborted).

The proportion of aborted flowers also increased significantly in most cultivars, but in TH318 and 'Fresh Market 9', it declined and in 'Piedmont' the increase was not significant. Under elevated temperatures, the highest proportion of aborted flowers occurred in NCHS1 (39.4%) and the lowest in 'Fresh Market 9' (1.3%). Under CT, the highest percentage was found in 'Fresh Market 9' (18.4%), and the lowest in 'Piedmont' (4.4%). Interestingly, for all the cultivars except FLA7156 and NCHS1, the predominate response to high temperature stress was not to abort flowers, but rather to retain them as undeveloped flowers. Although high temperature stress generally increases flower abortion in tomatoes, a reduction of aborted flowers under moderately elevated temperature was observed in NC8288 in a previous study (Sato et al., 2001), in which, a slow transition of undeveloped flowers into parthenocarpic fruit was also observed in this cultivar. Parthenocarpic cultivars have been reported as high temperature tolerant (George et al., 1984; Rotino et al., 1997).

Thus, increased flower abortion at high temperature, often used for screening, did not occur in three of the six cultivars, and the increase in flower abortion was actually highest in the cultivar with the most heat tolerance in terms of seeded fruit set (FL7156). Thus, in selecting plants for high temperature tolerance, flower retention should not be the only characteristic evaluated. Seeded fruit set would be a better indication of heat tolerance, at least until parthenocarpic cultivars are developed with acceptable fruit quality. Further classification of flower fates under high temperature stress, will give useful information for breeding programs, as cultivars differ significantly in their response patterns.

Generally when flowers abort at elevated temperatures, it is interpreted as an indication that the plant is under carbohydrate stress, and source–sink relations are disturbed (Bertin, 1995; Seginer et al., 1994). For example, Wien and Turner (1994) reported that bud abortion in pepper plants increased while fruit set decreased under low irradiance and was associated with low sugar content in the buds. In the case of moderately elevated temperatures, however, reductions in photosynthesis did not appear to account for cultivar differences in

Fig. 1. Moderately elevated temperature effects on the formation of seeded fruit, parthenocarpic fruit, undeveloped flowers and aborted flowers of nine tomato (*L. esculentum* Mill.) cultivars under control (CT, 26/22 °C day/night temperatures) and high (HT, 32/26 °C) temperatures. Number on the side of the bar represents the percentage of each category. * and ** represent significant difference between temperature treatments at $P < 0.05$ and $P < 0.01$ levels, respectively.

heat tolerance (Sato et al., 2000, 2001), with all cultivars (FL7156, NC8288, 'Piedmont', 'Fresh Market 9' and TH318) having similar photosynthetic rates at elevated temperatures. The primary factor affecting seeded fruit set under moderately elevated temperature stress in NC8288 was considered to be a disruption of male reproductive development (Peet et al., 1998; Sato et al., 2002). Thus differences between cultivars in rates of abscission under elevated temperatures may be genetic, rather than resulting from lowered carbohydrate availability. Ueda et al. (1996) suggested that the increased abscission was due to changes in sugar metabolism and increased cellulase activity in the abscission zone.

Some cultivars may be able to retain undeveloped flowers on the plant without fertilization, at least under some conditions. In this case, flowers may eventually develop into parthenocarpic fruit. Thus in selecting tomato cultivars for elevated temperatures, flower fates: seed fruit, parthenocarpic fruit; undeveloped flowers, aborted flowers; should be differentiated and selection conducted in accordance with the goals of the breeding program.

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