Gene Action and Heritability of High-temperature Fruit Set in Tomato Line CL5915

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Abstract. High-temperature fruit set (heat tolerance) is a critical trait of tomato (Lycopersicon esculentum Mill.) cultivars targeted for lowland wet season production in the tropics and subtropics. Heat-tolerant Asian Vegetable Research and Development Center (AVRDC) tomato line CL5915-93D4-1-0-3 (CL5915) is a valuable source of heat-tolerance genes for tomato genetic improvement. The gene action of heat tolerance in CL5915 was determined by evaluating the F1, F2, BCP1, and BCP2 of a cross between CL5915 and heat-sensitive line UC204A for fruit set traits in two wet-season trials at AVRDC fields on 5 Aug. 1995 and 10 May 1996. Plants were staked and grown on 1-m × 0.3-m-high raised beds (1.5 m between bed centers) covered with gray plastic mulch overlaid with a layer of rice straw. One row was established per bed and plants spaced 0.4 m apart. Each plot included plants of a single generation and number of rows per plot varied depending upon population size. Entries (generations) were replicated twice and arranged according to a randomized complete-block design. Total N, P2O5, and K2O applied ranged according to a randomized complete-block design. Total N, P0, and K0 applied to the fields were 240, 160, and 240 kg ha−1, respectively. Fields were furrow-irrigated as needed. The number of flowers and fruit set on clusters 2–6 on the main stem was determined on each plant 45 d after transplanting. A fruit was considered set if it enlarged to >0.5 cm diameter. Percentage of fruit set per plant was determined as the total number of fruit divided by the total flower number on clusters 2–6 of the main stem.

Means of the six generations were used to estimate gene action magnitudes for mean fruit number per cluster, number of flowers per cluster, mean percentage of fruit set, and average flower number per cluster by a weighted generation means analysis (Mather and Jinks, 1977) by year. Genetic parameters were estimated by weighted multiple linear regression using the General Linear Model procedure of SAS (SAS Institute, Cary, N.C.) with suppression of the intercept. Data were tested against a three-parameter model, including a midparent value (m), an additive effect (d), and a dominance selection is not effective unless heritability for the particular trait is high (Nyquist, 1991). The objectives of this study were to estimate gene action and the heritability of F1 single plant selection for heat tolerance in CL5915.

Materials and Methods

Generation means. Heat-tolerant, deterninate, fresh-market inbred line CL5915 (P1) was crossed to UC204A (P2), a heat-sensitive processing inbred line, to produce the F1. A small-fruited (35–40 g) inbred line, CL5915 is derived from a complex cross of eight parental lines, including five heat-tolerant lines or cultivars (‘Tamu Chico III’, VC48-1, VC11-1-UG, VC1-1-1-2-1B, and ‘Plum’). UC204A is an inbred line with a fruit size of 70–80 g from California that is commonly grown during the dry season in southern Taiwan for processing. October–February is the most favorable time to produce tomato at AVRDC with mean maximum/minimum air temperatures of 26.3/15.9 °C; during this period the fruit set of CL5915 ranges from 75% to 80% while the fruit set range of UC204A is slightly less (65% to 70%).

The F1 was backcrossed to both parents to produce the BCP, and BCP2, and allowed to self-pollinate to obtain F2 seed. Seed of the parental lines, F1, F2, and backcross generations were sown 6 July 1995 and 11 Apr. 1996 and transplanted, respectively, to AVRDC fields on 5 Aug. 1995 and 10 May 1996. Plants were staked and grown on 1-m × 0.3-m-high raised beds (1.5 m between bed centers) covered with gray plastic mulch overlaid with a layer of rice straw. One row was established per bed and plants spaced 0.4 m apart. Each plot included plants of a single generation and number of rows per plot varied depending upon population size. Entries (generations) were replicated twice and arranged according to a randomized complete-block design. Total N, P0, and K0 applied to the fields were 240, 160, and 240 kg ha−1, respectively. Fields were furrow-irrigated as needed. The number of flowers and fruit set on clusters 2–6 on the main stem was determined on each plant 45 d after transplanting. A fruit was considered set if it enlarged to >0.5 cm diameter. Percentage of fruit set per plant was determined as the total number of fruit divided by the total flower number on clusters 2–6 of the main stem.

Means of the six generations were used to estimate gene action magnitudes for mean fruit number per cluster, number of flowers per cluster, mean percentage of fruit set, and average flower number per cluster by a weighted generation means analysis (Mather and Jinks, 1977) by year. Genetic parameters were estimated by weighted multiple linear regression using the General Linear Model procedure of SAS (SAS Institute, Cary, N.C.) with suppression of the intercept. Data were tested against a three-parameter model, including a midparent value (m), an additive effect (d), and a dominance
effect (h). Models were tested by chi-square for goodness-of-fit and deemed acceptable if the probability of a larger chi-square value was >0.05. If the data did not adequately fit the three component model, then models including one or more epistatic components, additive × additive (i), additive × dominance (j), and dominance × dominance (l), were evaluated for goodness-of-fit. The significance of individual genetic parameter estimates was tested by test and the value was found by dividing each parameter estimate by its respective se.

Parent-offspring regression. F2 plants from CL5915 × UC204A were harvested individually from the 1995 generation means experiment to obtain F2-derived F3 families (F2:3).

F2, trials were sown on 23 Apr. 1996 and 13 Aug. 1997 and transplanted to AVRDC fields on 23 May 1996 and 9 Sept. 1997, respectively. The two parents and the F1 were included in each trial. Trials were arranged in a randomized complete-block design with three replications. Each plot consisted of a 3.5 m-long bed with a single row of seven plants spaced 0.4 m apart. Beds were 1 m wide (1.5 m between bed centers) and 30 cm high. Crop management practices including fertilization rates and mulching were the same as the generation means trials. Fruit set parameters described in the generation means experiments were measured on the five inner plants of each plot.

Heritabilities were estimated by regression of F2:3 family means (averaged over the three replications) on the values of the F2 parents.

Parents and progeny were measured for fruit set traits in different years to reduce inflation of heritability estimates with environmental covariances (Nyquist, 1991). In order to adjust for possible scaling effects of the different environments, regression coefficients were multiplied by the ratio of the phenotypic standard deviation of the parental generation over the phenotypic standard deviation of a sample of the parental generation measured in the offspring environment (Nyquist, 1991). The covariance between F2 and F2:3 family means equals \( \sigma^2_A + \sigma^2_D + \sigma^2_E \), assuming no epistasis involving dominance effects (Hallauer and Miranda, 1981). No adjustment for inbreeding was necessary because the F2 generation is noninbred (Nyquist, 1991).

### Results

#### Generation means.

Mean maximum and minimum air temperatures during fruit set exceeded the temperature range considered optimal for tomato fruit set (Table 1). Fruit set of heat-tolerant parental line CL5915 averaged 26% in 1995, and 30% in 1996 (Table 2). The mean percentage of fruit set and fruit number per cluster of the F1 and BCP exceeded midparent values and were not significantly different from those of CL5915. These data indicate complete dominance for fruit number per cluster and percentage of fruit set toward the heat-tolerant parent. Mean fruit number per cluster of the F1 and BCP were greater than midparent values, significantly greater than UC204A, but significantly less than CL5915. However, percentage of fruit set means of the F1 were not significantly different from CL5915 and, in 1996, percentage of fruit set of the BCP was not significantly different from CL5915. Mean flower number per cluster of the F1 fell slightly above or at the midparent value, indicating little or no dominance for this trait. Since percentage of fruit set is the quotient of mean fruit number per cluster (numerator) over flower number per cluster (denominator), percentage of fruit set means for the F1, F2, and backcross populations were relatively large because the denominator tended to fall at or slightly above midparent values while the numerator values tended to be similar to CL5915.

Table 1. Meteorological data during generation means and heritability experiments, AVRDC, Taiwan, 1995–97.

| Year | Date planting | Mean air temperature (°C) | Relative humidity (%) | Mean daily solar intensity (w·m⁻²) | Total rainfall (mm) |
|------|---------------|---------------------------|----------------------|------------------------------------|-------------------|
| 1995 | 19 June       | 33.0 ± 1.3/25.3 ± 1.4     | 81.0 ± 5.7           | 4336 ± 6992                      | 54                |
| 1996 | 23 May        | 32.0 ± 1.3/23.5 ± 1.5     | 81.7 ± 3.2           | 4530 ± 1600                      | 219               |
| 1997 | 9 Sept.       | 29.7 ± 1.8/21.3 ± 1.9     | 74.6 ± 3.6           | 3689 ± 972                       | 37                |

Table 2. Generation means and gene effects estimates of CL5915 × UC204A evaluated for tomato fruit-set traits under high temperatures, AVRDC, Taiwan, 1995 and 1996.

| n    | Flower/no. cluster | Fruit set (%) | Fruit set (%) |
|------|--------------------|--------------|---------------|
| 1995 | 27/51              | 8.4 ± 0.2a   | 9.3 ± 0.2a    |
| 1996 | 30/40              | 4.4 ± 0.07d  | 5.0 ± 0.12c   |
| F1   | 29/50              | 7.1 ± 0.16b  | 7.3 ± 0.17b   |
| F2   | 122/132            | 6.8 ± 0.12b  | 7.1 ± 0.13b   |
| BCP  | 53/59              | 8.7 ± 0.24a  | 8.7 ± 0.21a   |
| 1995 | 27/51              | 2.5 ± 0.17a  | 2.4 ± 0.13a   |
| 1996 | 30/40              | 0.1 ± 0.03c  | 0.3 ± 0.05c   |
| F1   | 29/50              | 2.3 ± 0.15a  | 2.5 ± 0.11a   |
| F2   | 122/132            | 1.7 ± 0.11b  | 2.1 ± 0.09ab  |
| BCP  | 53/59              | 2.7 ± 0.15a  | 2.7 ± 0.10a   |
| Effect |                           | 1.2 ± 0.12b  | 1.5 ± 0.23b   |
|      | [m]                | 6.5 ± 0.2a** | 7.2 ± 0.11a** |
|      | [d]                | 1.3 ± 0.09a  | 1.4 ± 0.07a** |
|      | [h]                | 1.0 ± 0.18a  | 1.2 ± 0.15**  |
|      | [i]                | 1.5 ± 0.99** | ---           |
|      | [j]                | 5.80**       | 2.78**        |

These results indicate complete dominance for fruit number per cluster and percentage of fruit set toward the heat-tolerant parent. Mean fruit number per cluster of the F1 and BCP were greater than midparent values, significantly greater than UC204A, but significantly less than CL5915. However, percentage of fruit set means of the F1 were not significantly different from CL5915 and, in 1996, percentage of fruit set of the BCP was not significantly different from CL5915. Mean flower number per cluster of the F1 fell slightly above or at the midparent value, indicating little or no dominance for this trait. Since percentage of fruit set is the quotient of mean fruit number per cluster (numerator) over flower number per cluster (denominator), percentage of fruit set means for the F1, F2, and backcross populations were relatively large because the denominator tended to fall at or slightly above midparent values while the numerator values tended to be similar to CL5915.

Generation means analyses indicated a model including simple additive and dominance effects adequately explained the inheritance of mean fruit number per cluster for both years (Table 2), and the magnitude of parameter estimates for additive and dominance effects were similar. Genetic models giving the best fit for mean flower number per cluster and percentage of fruit set were not consistent over years. Simple additive-dominance models were adequate for flower number but not for percentage of fruit set in 1995. However, addition of a nonsignificant additive × dominance component to the model for flower number per cluster was required in 1995 to produce an adequately fitting model. The best-fitting model for percentage of fruit set in 1996 included a nonsignificant negative additive × additive term.

Heritabilities calculated by regression of F2:3 entry means on F2 parents were moderately low or low for fruit set traits in 1996 and 1997 (Table 3). Heritability estimates for percentage of fruit set and fruit number per cluster were similar, indicating that selection for either trait would result in similar rates of gain. Heritabilities were higher in 1996 compared with 1997 and this may be due to environmental differences in the environments.
conditions in 1996 that were similar to those of the parental generation (1995). In 1997, mean air temperatures, relative humidity, and solar intensity were lower than the two previous years because the trial took place during the later part of the wet season; percent fruit set means of CL5915 and UC204A, respectively, were 43.4 and 32.1 and not significantly different from each other.

Discussion

The wet season (summer) in southern Taiwan lasts from about May through September and conditions are very unfavorable for tomato production. During this five-month period, AVRDC weather station data averaged over the last 25 years show a maximum period, AVRDC weather station data average temperature of 23.9 °C and average monthly rainfall of 281 mm. Although these air temperatures are known to adversely affect tomato fruit set, other environmental factors in addition to or in combination with high temperatures probably inhibit tomato fruit set. In particular, high relative humidity with high temperatures may affect fruit set because high humidity would reduce transpiration flow, resulting in greater heating of the plant (Lipton, 1970).

UC204A, the heat-sensitive parental line of this study, produced a relatively healthy vine but set few fruit, the typical response of heat-sensitive cultivars grown in the wet season at the AVRDC. We observed that many UC204A flowers contained undeveloped anther cones and low pollen quantities, or the fruit failed to enlarge. High air temperatures induce problems in the processes of flower formation, gamete formation, pollination, and fertilization, and possibly net plant carbohydrate imbalances in heat-sensitive tomato cultivars (El Ahmadi and Stevens, 1979; Hanna and Hernandez, 1982; Kuo et al. 1979; Peet and Willits, 1993; Stevens and Rudich, 1978). However, carbohydate imbalance is the underlying cause of poor fruit set (Peet and Willits, 1993), then a different breeding strategy will be required.

Results of the generation means experiments support the importance of both additive and dominance genetic effects in conditioning high-temperature fruit set in CL5915. The percentage of fruit set of the F1 equaled that of the heat-tolerant parent CL5915, an indication of complete dominance of the trait for heat tolerance. Partial dominance for heat tolerance or fruit set components has been reported previously (El Ahmadi and Stevens, 1979; Opeia et al., 1988, 1996; Scott et al., 1976; Shelby et al., 1989). However, if carbohydrate imbalance is the underlying cause of poor fruit set (Peet and Willits, 1993), then a different breeding strategy will be required.

The 30% fruit set of CL5915 was superior to the F2 for heat tolerant tomato cultivars during the wet season (Midmore et al., 1997), improvement of the fruit set of heat-tolerant lines would be desirable. Attempts at the AVRDC to increase high-temperature fruit set by incorporating a recessive gene, pat, for parthenocarpy into heat-tolerant lines (AVRDC, 1984) did not succeed. Newer AVRDC lines do not show better fruit set than earlier AVRDC lines such as CL1131 and CL5915. The physiological causes for fruit set reduction in heat-tolerant cultivars (El Ahmadi and Stevens, 1979; Stevens and Rudich, 1978). However, if carbohydrate imbalance is the underlying cause of poor fruit set (Peet and Willits, 1993), then a different breeding strategy will be required.

Heritabilities estimated by regression of F2 entry means on F1 parents can only be considered narrow-sense if dominance variance is negligible. Because dominance genetic variance for fruit set traits in CL5915 is important, heritabilities in this experiment are inflated by α2 and cannot be considered narrow-sense. In addition, parents and offspring were evaluated in different seasons at the same location so heritabilities were also biased by a genotype-by-location component (Nyquist, 1991). Possible scaling effects due to measurement of parents and offspring in different environments were removed by evaluating a second population of the F2 generation with the offspring and multiplying estimates by the correction factor given by Nyquist (1991) and Gibson (1996). The low heritabilities for percentage of fruit set and mean fruit number per cluster under high temperatures imply that single plant selection in the F1 for heat tolerance is not effective. In particular, F2 lines derived from heat-tolerant F1 may not necessarily be heat tolerant. This is probably due in part to reduction in dominance effects associated with increased inbreeding (Hallauer and Miranda, 1983). Some selection in the F1 could be practiced against heat-sensitive plants but most F2 selection should focus on highly tolerant traits. Wessel-Beaver and Scott (1992) estimated a moderately high h2 of 0.60 for high-temperature fruit set based on replicated evaluation of F2 families at two locations. Based on our results and previous studies (Villarreal and Lai, 1979; Wessel-Beaver and Scott, 1992) we would conclude that selection for high-temperature fruit set should be based primarily on replicated family testing in the F3 and later generations.

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