Heritability Estimates and Gene Effects for Heat-Tolerance Traits in Tomato (*Solanum lycopersicum* L.)

Nai-Ning Chi[1], Kevin M. Crosby[1], and William L. Rooney[2]
[1]Department of Horticultural Sciences, Texas A&M University, College Station, TX 77843
[2]Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843

Introduction

- Tomato is the second most produced and economically important vegetable crop in the U.S. In tropical and subtropical regions, excess radiation and high temperature are often limiting factors in tomato production. In tomato, when day/night temperatures exceed 26°C and 20°C, fruit set is interrupted, which leads to reduction in yield (Lohar and Peat, 1998). Therefore, breeding tomato for heat tolerance has become urgent and crucial.
- The objective of this study is to elucidate the inheritance and the genetic effects controlling the traits related to heat tolerance in tomato by estimating heritability and gene actions and their interactions.

Materials and Methods

- Two populations involving the crosses 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' were used. The female parents (P_1) are heat tolerant breeding lines and the male parents (P_2) are heat susceptible heirloom cultivars. The F_1 hybrids were self-pollinated to produce the F_2 and backcrossed with the parents to produce BC_1P_1 and BC_1P_2 in spring, 2016. Six genetic generations (P_1, P_2, F_1, F_2, $BC_1P_1$and BC_1P_2) were planted in two locations, College Station and Waller, TX. Traits including pollen viability (PV), flower number per cluster (FLC), fruit number per cluster (FRC) and fruit set (FS) were investigated.

- Generation Mean Analysis (GMA):Three parameter model (Mather and Jinks, 1982) was used to estimate the gene actions. Individual scaling test was used to determine the absence or the presence of non-allelic interactions and thus the adequacy of the model, using the following formulas:

$$A = 2\,BC_1P_1 - P_1 - F_1 \qquad V_A = 4V_{BC1P1} + V_{P1} + V_{F1}$$

$$B = 2\,BC_1P_2 - P_2 - F_1 \qquad V_B = 4V_{BC1P2} + V_{P2} + V_{F1}$$

$$C = 4\,F_2 - 2\,F_1 - P_1 - P_2 \qquad V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$$

The standard error (SE) was determined by $SE_{(A)}=(V_A)^{1/2}$, the t values $t_{(A)} = A/SE_{(A)}$,were compared to the tabulated values at 5% and 1% to determine the significance.

The gene actions were estimated with the three-parameter model, using the following formulas:

$$(m) = 0.5\,P_1 + 0.5\,P_2 + 4F_2 - 2\,BC_1P_1 - 2\,BC_1P_2$$

$$(a) = 0.5\,P_1 - 0.5\,P_2$$

$$(d) = 6\,BC_1P_1 + 6\,BC_1P_2 - 8\,F_2 - F_1 - 1.5\,P_1 - 1.5\,P_2$$

$$SE^2_{(m)} = 0.25\,SE^2_{(P1)} + 0.25\,SE^2_{(P2)} + 16\,SE^2_{(F2)} + 4\,SE^2_{(BC1P1)} + 4\,SE^2_{(BC1P2)}$$

$$SE^2_{(a)} = 0.25\,SE^2_{(P1)} + 0.25\,SE^2_{(P2)}$$

$$SE^2_{(d)} = 36\,SE^2_{(BC1P1)} + 36\,SE^2_{(BC1P2)} + 64\,SE^2_{(F2)} + SE^2_{(F1)} + 2.25\,SE^2_{(P1)} + 2.25\,SE^2_{(P2)}$$

The significance was tested with Student's t test with t values calculated as $t_{(m)} = (m)/SE_{(m)}$; $t_{(a)} = (a)/SE_{(a)}$ and $t_{(d)} = (d)/SE_{(d)}$, the values were compared to the tabulated values at 5% and 1% significance levels.

- Board sense heritability (H^2) was calculated as genotypic variance (V_G) / phenotypic variance (V_P). The variance of the F_2 is considered the V_P . The variance of 'TAM Hot-Ty' is the environmental variance (V_E). The H^2 was calculated as $H^2 = (V_P - V_E) / (V_P)$.
- Narrow sense heritability (h^2) was calculated using the variance of F_2 and the backcross generations (Warner, 1952):

$$h^2 = [V_{F2} - (V_{BC1P1} + V_{BC1P2})/2]/V_{F2}$$

$$V(h^2) = 2\,\{ [(V_{BC1P1} + V_{BC1P2})^2/df_{F2}] + (V_{BC1P1}{}^2/df_{BC1P1}) + (V_{BC1P2}{}^2/df_{BC1P2})\} / V_{F2}{}^2$$

Significance was evaluated with the mean and standard error at 5% and 1% significance levels.

Results

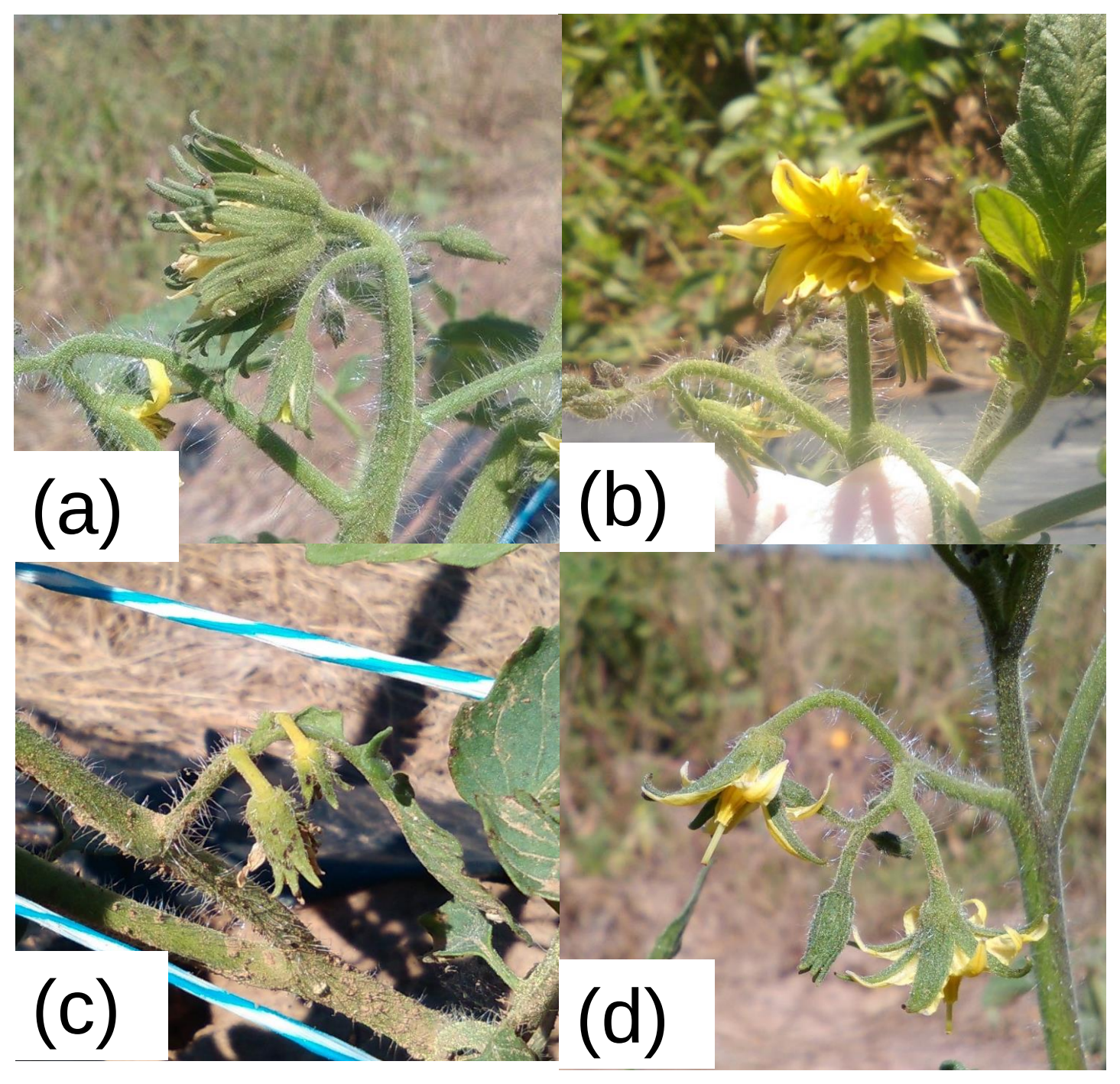

Figure 1. Flower abnormalities occurred in the field at College Station, TX. (a) Abnormal flower; (b) Double ovaries; (c) Flower abscission; and (d) Stigma extrusion.

- At College Station, additive gene action was found significant for all traits in T215VR x 'Manyel' (Table 2). Significant dominance gene action was found higher than additive gene action for pollen viability.

- At Waller, significant dominance gene action was found for fruit number per cluster and fruit set in both crosses, and for flower number per cluster for 'Freshmarket 9' x 'Black Sea Man' (Table 3 and 4).

Table 1 Generation mean analysis of gene effects of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.51 ± 0.24 **	6.22 ± 2.49 ns	4.47 ± 1.88 *	0.58 ± 0.33 ns
(a)	-0.02 ± 0.04 ns	0.41 ± 0.44 ns	0.56 ± 0.33 ns	0.09 ± 0.06 ns
(d)	-0.08 ± 0.69 ns	-7.56 ± 6.99 ns	-6.42 ± 5.27 ns	-0.30 ± 0.93 ns
Scaling test				
A	-0.13 ± 0.17 ns	-1.69 ± 1.76 ns	-1.05 ± 1.37 ns	-0.06 ±0.23 ns
B	0.55 ± 0.16 ns	-1.38 ± 1.65 ns	-0.09 ± 1.25 ns	0.09 ± 0.22 ns
C	-0.31 ± 0.18 ns	-0.69 ± 1.79 ns	1.64 ± 1.35 ns	0.17 ± 0.24 ns

ns, *, ** Nonsignificant or significant at P ≤ 0.05 and P ≤ 0.01, respectively.

Table 2 Generation mean analysis of gene effects of T215VR x 'Manyel' for heat-tolerance traits at College Station.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.12 ± 0.21 ns	1.51 ± 2.14 ns	-0.25 ± 1.60 ns	-0.03 ± 0.28 ns
(a)	0.08 ± 0.04 *	0.69 ± 0.38 *	0.55 ± 0.29 *	0.11 ± 0.05 *
(d)	1.29 ± 0.62 *	4.30 ± 6.28 ns	4.15 ± 4.71 ns	1.12 ± 0.83 ns
Scaling test				
A	0.19 ± 0.17 ns	-0.49 ± 1.71 ns	-0.04 ± 1.29 ns	0.07 ± 0.23 ns
B	0.22 ± 0.15 ns	0.35 ± 1.50 ns	1.02 ± 1.13 ns	0.34 ± 0.20 ns
C	0.01 ± 0.14 ns	-1.89 ± 1.46 ns	-0.47 ± 1.10 ns	0.07 ± 0.19 ns

ns, *, ** Nonsignificant or significant at P ≤ 0.05 and P ≤ 0.01, respectively.

Table 3 Generation mean analysis of gene effects of 'Freshmarket 9' x 'Black Sea Man' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.77 ± 0.14 **	-3.79 ± 2.78 ns	-6.60 ± 1.98 ns	-0.48 ± 0.26 ns
(a)	-0.07 ± 0.03 ns	0.63 ± 0.64 ns	0.54 ± 0.45 ns	0.02 ± 0.06 ns
(d)	-0.43 ± 0.38 ns	21.54 ±7.90 **	22.87 ±5.62 **	2.34 ± 0.75 **
Scaling test				
A	0.02 ± 0.11 ns	-0.54 ± 2.29 ns	0.50 ± 1.63 ns	0.13 ± 0.22 ns
B	-0.14 ± 0.10 ns	0.42 ± 2.11 ns	1.54 ± 1.50 ns	0.19 ± 0.20
C	-0.004±0.14 ns	-10.12±2.85 ns	-7.68 ± 2.03 ns	-0.66 ± 0.27 ns

ns, *, ** Nonsignificant or significant at P ≤ 0.05 and P ≤ 0.01, respectively.

Table 4 Generation mean analysis of gene effects of T215VR x 'Manyel' for heat-tolerance traits at Waller.

	PV (%)	FLC	FRC	FS (%)
Gene effect estimated form three-parameter model				
(m)	0.84 ± 0.12 **	3.74 ± 2.12 *	-0.84 ± 1.72 ns	0.08 ± 0.21 ns
(a)	-0.005±0.03 ns	-0.09 ± 0.57 ns	0.17 ± 0.40 ns	0.05 ± 0.05 ns
(d)	-0.44 ± 0.32 ns	3.85 ± 6.05 ns	8.76 ± 4.61 *	1.11 ± 0.58 *
Scaling test				
A	0.02 ± 0.09 ns	1.33 ± 1.80 ns	1.25 ± 1.28 ns	0.10 ± 0.17 ns
B	-0.15 ± 0.08 ns	-0.85 ± 1.71 ns	-0.00 ± 1.21 ns	0.12 ± 0.16 ns
C	-0.03 ± 0.13 ns	-1.04 ± 2.34 ns	-2.25 ± 1.86 ns	-0.20 ± 0.23 ns

ns, *, ** Nonsignificant or significant at P ≤ 0.05 and P ≤ 0.01, respectively.

- Broad-sense heritability estimates were higher at Waller than at College Station (Table 5). Narrow-sense heritability estimates were found significant for pollen viability and fruit set in T215VR x 'Manyel' at College Station and significant for fruit set in both crosses at Waller. Narrow-sense heritability estimates were low for pollen viability and moderate for fruit set in both crosses at Waller. However, narrow-sense heritability estimate was low in both crosses at College Station.

Table 5. Broad-sense and narrow-sense heritability for heat-tolerance traits of 'Freshmarket 9' x 'Black Sea Man' and T215VR x 'Manyel' at College Station and Waller, TX.

	College Station				Waller			
Cross	'Freshmarket 9' x 'Black Sea Man'		T215VR x 'Manyel'		'Freshmarket 9' x 'Black Sea Man'		T215VR x Manyel'	
	H^2	h^2	H^2	h^2	H^2	h^2	H^2	h^2
PV(%)	0.58	0.39 ± 0.46	0.66	0.11 ± 0.05*	0.91	0.15 ± 1.24	0.94	0.36 ± 0.81
FLC	0.89	0.66 ± 0.63	0.64	0.09 ± 0.52	0.96	0.60 ± 0.44	0.78	0.14 ± 1.23
FRC	0.91	0.62 ± 0.73	0.59	0.11 ± 0.21	0.96	0.15 ± 0.74	0.91	0.45 ± 0.52
FS(%)	0.60	0.28 ± 1.17	0.44	0.25 ± 0.03**	0.93	0.72 ± 0.05**	0.74	0.58 ± 0.14**

***, ** Significant at P ≤ 0.05 and P ≤ 0.01, respectively.**

Conclusions

- Both additive and dominance gene effects are involved in the expression of the heat-tolerance traits, with dominance gene effects being the main contributor.

- The low narrow-sense heritability estimates suggest that single plant selection for heat tolerance in the F_2 will not be effective. Alternative approaches such as recurrent selection should be considered in early generations.

References

- Lohar, D. and Peat, W., 1998. Floral characteristics of heat-tolerant and heat-sensitive tomato (Lycopersicon esculentum Mill.) cultivars at high temperature. *Scientia horticulturae* 73:53-60.

- Mather, K. and I.L. Jinks. 1982. Biometrical Genetics. Third Edition. Champan and Hall, London.

- Warner, J.N. 1952. A method for estimating heritability. *Agron. J.* 44:427–430.