Pollen Viability and Fruit Set of Tomato Genotypes under Optimum- and High-temperature Regimes

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Abstract. Heat-tolerant and -sensitive *Lycopersicon esculentum* Mill. and *L. pimpinellifolium* (Jusl.) Mill. genotypes were grown in the greenhouse under optimum- (27/23C, day/night) and high-temperature (35/23C) stress regimes. Heat tolerance levels in the genotypes were established by determining percent fruit set at high and optimum temperatures. Under optimum temperature, fruit set ranged from 41% to 84% and from 45% to 91% in the heat-sensitive and heat-tolerant genotypes, respectively. Under high temperature, no fruit set in the most heat-sensitive genotypes. Fruit set in the heat-tolerant genotypes ranged from 45% to 65%. In vitro germination and tube growth of pollen taken from genotypes grown under optimum temperature conditions were determined before and after subjecting the pollen to 45C for 1, 2, and 4 hours. The response of pollen to heat treatments was genotype dependent and not a general predictor of fruit set under high-temperature stress.

Heat stress adversely affects the vegetative and reproductive growth processes of tomato plants and ultimately reduces yield and fruit quality (Abdul-Baki, 1991; Dane et al., 1991; Wessel-Beaver and Scott, 1992; Yakir et al., 1984). Development of tomato cultivars with improved fruit set under high temperatures would be valuable for tomato crop production in regions where the temperature during part of the growing season reaches $\geq 35^{\circ}\text{C}$ or higher (Johnson and Hall, 1953; Stevens and Rudich, 1987). Under field conditions in hot, tropical, or arid regions, high temperatures ($\geq 35^{\circ}\text{C}$) can prevail for days and may extend into a portion of the dark period of the 24-h light–dark cycle (Abdalla and Verkerk, 1968). Efforts to introduce heat tolerance to the heat-sensitive commercial cultivars have prompted interest in developing criteria for evaluating germplasm from domesticated and wild tomato species for heat tolerance (Opeña et al., 1979; Villareal et al., 1978; Weaver and Timm, 1989). The most commonly used criterion for tomato heat tolerance is the ability of plants to set fruit following exposure to high temperature. The effort and cost incurred in field evaluation of germplasm for heat tolerance is high. Identifying techniques that could be used to screen many plants quickly and economically for high-temperature tolerance would be valuable in identifying heat-tolerant germplasm.

Several factors may contribute to reduced tomato fruit set under high temperatures and can be considered as potential selection criteria. These factors include reduced flower production, ovule and pollen viability, and pollen dehiscence (ElAhmadi and Stevens, 1979). Additionally, stigma and stylar exertion in response to high temperatures (ElAhmadi and Stevens, 1979) and reduced photosynthetic and assimilate translocation rates (Bar-Tzur et al., 1985; Dinar and Rudich, 1985) may adversely affect fruit setting ability. Although all heat-tolerant genotypes do not respond similarly to high temperatures, lack of viable pollen is widely believed to be a major cause of poor fruit set at high temperatures. Weaver and Timm (1989) reported a positive correlation between heat tolerance and pollen viability maintenance after briefly exposing flowering plants in the greenhouse to high temperatures. Also, Dane et al. (1991) noted reduced pollen fertility after prolonged periods of high temperature in the field.

Our study was undertaken 1) to determine heat tolerance of some cultivated and wild tomato genotypes when grown in the greenhouse and 2) to assess in vitro germination and tube growth of pollen subjected to heat stress before germination as a reliable screening tool for whole-plant heat tolerance.

Materials and Methods

Eleven tomato genotypes, consisting of the cultivated tomato (*L. esculentum*) and a related wild species (*L. pimpinellifolium*), were selected for testing based on differences in fruit set when subjected to heat stress (Abdul-Baki, 1991; Villareal et al., 1978). The five *L. esculentum* genotypes were commercially available cultivars ('Duke', 'Floradade', and 'Long Keeper') and lines AVRDC-CL-1131-

0-0-43-8-1 and AVRDC-CLN-475BC₁F₂-265-4-19 obtained from the Asian Vegetable Research and Development Center, Taipei, Taiwan. The *L. pimpinellifolium* accessions tested were plant introductions (PI) 270450, 270441, 365914, 205009, 365916, and 365917 obtained from the U.S. Dept. of Agriculture, Plant Introduction Station, Geneva, N.Y. Seeds were planted in 72-cell flats (cell size, 4 × 4 × 6 cm) filled with a 1 peat : 1 horticultural grade vermiculite (w/w) mixture (Jiffy Mix Plus; Jiffy Products, Batavia, Ill.) and were grown in the greenhouse under a 27/23 ± 2C day/night cycle. At the two true-leaf stage, five plants of each genotype were transferred to a greenhouse and maintained under a heat-stress regime of 35/23 ± 2C (day/night). A second set of five plants each was maintained in another greenhouse under optimum temperatures of 27/23 ± 2C (day/night). These two sets of plants received identical management practices (fertilizing, watering, staking, and daily mechanical flower pollination) for growing tomatoes commercially in the greenhouse. Percent fruit set was determined by scoring flower counts on all inflorescences present and fruit produced until at least six inflorescences had set fruit. A fruit was considered set when its diameter reached ≥ 0.5 cm (Abdul-Baki, 1991; Shelby et al., 1978; Weaver and Timm, 1989).

Plants grown under our optimum temperature conditions served as a pollen source in the in vitro tests for determining the effect of heat exposure on pollen germination and pollen tube growth. In vitro germination and pollen tube growth from each genotype were determined as described by Abdul-Baki (1992), using pollen samples collected two to three times a week from the first five to six inflorescences. The pollen was removed from the flowers by mechanical vibration and mixed; eight 0.3-mg subsamples were placed in moisture-tight, 35-mm petri dishes and were sub-

Table 1. Flowering and fruit set of tomato genotypes under normal and heat-stress growing conditions in the greenhouse.

Genotype	Fruit set (%) ^z		Reduction in fruit set under heat stress (%)
	Temp		
	Optimum	High	
AVRDC- CL-1131 ^y	71 bc	65 a	8
PI 270450	91 a	53 ab	42
Floradade	45 e	46 b	0
AVRDC- CLN-475 ^y	65 dc	45 b	31
PI 270441	82 ab	27 c	67
Duke	54 de	13 cd	76
PI 365914	84 ab	6 d	93
PI 205009	83 ab	0 d	100
PI 365916	60 cd	0 d	100
PI 365917	82 ab	0 d	100
Long Keeper	41 e	0 d	100

¹Letters denote mean separations within each column by Duncan's multiple range test at $P \leq 0.05$.

²AVRDC-CL-1131 = AVRDC-CL-1131-0-0-43-8-1; AVRDC-CLN-475 = AVRDC-CLN-475BC₁F₂-265-4-19.

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jected to heat-stress treatment for 1, 2, and 4 h at 45°C. An initial sample was not heat-treated and served as a control. Subsequent to heat treatment, pollen germination and tube growth were determined after 2 h incubation at 27°C and were scored for normal germination, abnormal germination, and no germination (Abdul-Baki, 1992). Average pollen tube growth was determined on 20 pollen grains chosen at random from various locations of the pollen sample.

Results and Discussion

The percent fruit set by the cultivated and wild genotypes grown at optimum temperature conditions was generally high, irrespective of genotype heat tolerance (Table 1). Heat-stress conditions reduced the percent fruit set in all genotypes tested except 'Floradade'. AVRDC-CL, PI 270450, 'Floradade', and AVRDC-CLN were classified as heat tolerant based on their fruit-setting ability under high temperatures. Reduction of fruit set under heat stress in these heat-tolerant genotypes ranged from 0% in 'Floradade' to 42% in PI 270450. PI 270441 and 'Duke' displayed intermediate, but relatively low, percent fruit set when subjected to heat stress. In contrast with heat-tolerant genotypes, PIs 365914, 205009, 365916, 365917, and 'Long Keeper' displayed marked sensitivity to high temperature. The percent reduction in fruit set of these heat-sensitive genotypes ranged from 93% to 100%.

Prior studies also have noted a decline in percent fruit set of heat-sensitive genotypes under high-temperature stress (Dane et al., 1991; Rudich et al., 1977; Weaver and Timm, 1989; Wessel-Beaver and Scott, 1992). In a field evaluation of tomato germplasm for heat tolerance, Villareal et al. (1978) reported high levels of heat tolerance in all of the *L. pimpinellifolium* accessions examined in our study. In contrast with those results, we determined that PIs 365914, 205009, 365916, and 365917 displayed marked sensitivity to high temperatures. These differences likely may reflect the effects of sustained heat stress imposed by our greenhouse conditions and the temperature variability inherent in screening

for heat tolerance under field conditions in the Villareal et al. study.

Pollen collected from heat-tolerant and heat-sensitive tomato genotypes under nonheat-stressed conditions exhibited a wide range of germination and tube growth. For example, percent normal germination of pollen before the heat treatment was highest (20.1%) in PI 270450 and lowest (0.4%) in AVRDC-CL, both heat-tolerant genotypes (Table 2). Consistent with observed percent pollen germination, percent fruit set in PI 270450 was higher than that noted in AVRDC-CL at optimum temperature (Table 1). However, under heat-stress conditions, both genotypes exhibited similar percent fruit set. These results suggest that germination of nonheat-stressed pollen is not related to heat tolerance, as ascertained by percent fruit set, because high and low percent pollen germination was found in heat-sensitive and heat-tolerant genotypes. Similarly, pollen tube growth under nonheat-stressed conditions seems to be unrelated to high-temperature tolerance (Table 2).

To facilitate selection of high-temperature-tolerant genotypes, a selection scheme was developed using pollen grains collected from plants grown under normal conditions, and subjecting this pollen, which had not received prior high-temperature stress, to 1, 2, and 4 h of high temperature (45°C). The effects of high temperature and exposure duration on pollen germination and pollen tube growth were evaluated (Table 2). Treatment of pollen for 1 h at 45°C caused significant reductions in percent germination and pollen tube growth of 'Duke' and PIs 270441, 365914, and 205009. The 1-h exposure also caused a significant decrease in pollen tube length of 'Duke', PI 205009, and 'Long Keeper'. Reduction in percent pollen germination and subsequent tube growth generally became more severe, compared to the control, as the high-temperature exposure was extended to 2 and 4 h. AVRDC-CL, PI 270450, 'Floradade', and AVRDC-CLN were of particular interest. No significant reductions in pollen germination were evident after 1 or 2 h of high temperature exposure. After 4 h of heat treatment, genotypes AVRDC-CL and PI 270450 maintained similar percent

pollen germination and pollen tube growth to those noted under optimum conditions. Notably, no significant reductions in pollen germination were evident in the heat-sensitive genotypes PI 365916, PI 365917, and 'Long Keeper' after ≥ 1 h of heat treatment. PIs 365916 and 365917, classified as heat sensitive to fruit set, maintained normal pollen germination, and PI 365916 maintained normal pollen tube growth after ≤ 4 h of heat treatment. Responses in pollen tube growth to heat treatments were generally consistent with the effect of heat treatments on pollen germination (Table 2). The germination of pollen that received no heat treatment was significantly correlated ($r = 0.401$) with percent fruit set (Table 3); correlations between percent fruit set and germination and pollen tube growth in response to 1, 2, or 4 h of high-temperature pollen exposure were not significant.

Lack of significant correlation between percent fruit set at high temperature and pollen germination or tube growth following heat treatment suggests that different mechanisms contribute to heat tolerance in these genotypes. Various mechanisms that condition heat tolerance have been noted by Stevens and Rudich (1978) and include pollen production and viability as well as pollen dehiscence, ovule viability, and stigma and stylar exsertion. Shelby et al. (1978) reported a slight but significant decline in pollen viability from plants subjected to high temperature. They concluded that insufficient pollination was likely a major cause of reduced fruit set at high temperature and that reduced pollen and embryo viability were minor factors.

Differences in heat tolerance of tomato genotypes were determined based on percent fruit set of genotypes grown under high-temperature stress conditions. The results demonstrate maintenance of pollen germination after high-temperature exposure in heat-tolerant and some heat-sensitive genotypes and illustrate that pollen viability in response to a brief high-temperature exposure is a quick but not definitive means for determining heat tolerance in tomato. The results also demonstrate that using pollen viability as a selection criterion for high-temperature tolerance is

Table 2. Effect of heat treatment on percent normal pollen germination and pollen tube growth.

Genotype	Duration of heat treatment (h)							
	0		1		2		4	
	Germination (%)	Tube length (μ m)	Germination (change) ^z	Tube length (change) ^z	Germination (change) ^z	Tube length (change) ^z	Germination (change) ^z	Tube length (change) ^z
AVRDC-CL-1131 ^y	0.4	10.4	1.1	15.2	-0.2	-10.4	-0.2	-10.4
PI 270450	20.1	99.5	-6.3	8.9	-12.9	-9.3	-9.3	-3.7
Floradade	1.8	63.7	-1.0	-47.2	-0.8	-33.7	-1.5*	-58.0*
AVRDC-CLN-475 ^y	2.7	91.9	-0.7	-30.2	-1.9	-54.0*	-2.3*	-72.3*
PI 270441	6.0	82.7	-3.6*	-24.0	-5.4*	-60.1*	-5.0*	-49.0*
Duke	4.2	85.6	-3.2*	-58.9*	-2.8*	-41.5*	-3.7*	-54.7*
PI 365914	5.3	140.7	-2.9*	-33.4	-4.5*	-81.7*	-4.9*	-108.4*
PI 205009	8.4	117.8	-5.4*	-35.0*	-7.2*	-46.9*	-6.5*	-47.4*
PI 365916	10.3	142.4	-4.7	-10.8	-7.3*	-52.3	-6.6	-37.5
PI 365917	13.1	150.9	-2.3	-33.1	-7.1	-65.9	-7.7	-105.4*
Long Keeper	1.9	62.2	0.5	-26.1*	-1.0	-41.1*	-1.6*	-45.7*

^zAbsolute change relative to 0-h heat treatment for percent germination and tube length in micrometers.

^yAVRDC-CL-1131 = AVRDC-CL-1131-0-0-43-8-1; AVRDC-CLN-475 = AVRDC-CLN-475BC₁F₂-265-4-19.

*Significantly different from the 0-h control within the same row by Dunnett's *t* test at $P \leq 0.05$.

Table 3. Correlations between percent fruit set and germination and growth of tomato pollen tubes in response to heat treatment.

Pollen heat treatment (h)	<i>r</i> values	
	Normal germination (%)	Pollen tube length (μm)
0	0.401**	0.226
1	0.111	-0.261
2	0.083	-0.220
4	0.260	-0.106

**Significant at $P = 0.01$.

genotype specific and that factors independent of pollen viability may influence sensitivity to heat.

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