Reproductive Responses of Heat-tolerant Tomatoes to High Temperatures¹

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Abstract. High-temperature responses of heat-tolerant tomato (Lycopersicon esculentum Mill. cvs. Saladette, PI 262934, BL6807, S6916, CIAS161, and VF36) were studied at $38/27^{\circ}$ C day/night temperature. Flower production was reduced in all cultivars except BL6807 which partitioned a greater proportion of total assimilates to the flowers. Only 'Saladette' and VF36 showed a total lack of stigma exsertion, which in effect is functional male sterility. Pollen production was reduced in all cultivars, and there was a lack of pollen dehiscence. Several techniques were used to evaluate gamete viability. There was poor agreement among the 3 methods used to assess pollen viability. 'Saladette' suffered the least reduction for *in vitro* germination but had the greatest loss in seed set when high-temperature pollen was used. Seed set is probably the most reliable method to measure gamete viability is much more difficult to adequately evaluate. According to seed set criteria PI 262934 ovules suffered the least damage due to high temperatures. Whether the male or female gamete was affected more severely depended on genotype. Pollen viability was greatly reduced in PI 262934 but ovule viability was less severely affected. In BL6807 ovule viability was more severely reduced than pollen viability.

High temperatures limit or prevent field production of tomatoes during the summer in many regions of the world and can depress yields in principal production areas because of flower drop. As little as 4 hr exposure to 40° C causes blossom drop in most tomato cultivars (4). Genotypes are available which will set fruit at temperatures well above the normal optimum, but differences in the high temperature response of heat-tolerant genotypes have not been defined. An understanding of such variation will enhance the possibility of breeding for higher levels of heat tolerance.

This work was done to define phenotypic response to high temperature in several heat-tolerant cultivars of diverse origin.

Materials and Methods

Six high-temperature-tolerant tomato cultivars were selected for study:

'Saladette'. A cultivar of determinate compact growth habit with red fruits 4.4-5.7 cm in diameter. It was bred by Paul W. Leeper for production in the lower Rio Grande Valley of Texas.

PI 262934. Cultivar Malintka 101, from the U.S.S.R., obtained from the North Central Regional Plant Introduction Station at Ames, Iowa. Lorenze reported in the Northeastern Regional Plant Introduction Station Report of February 1973 that it has the capacity to set fruits at high temperature. It has a determinate medium-size plant with red fruits 4.2-4.9 cm in diameter.

BL6807. A cold-set selection bred at Beaverlodge, Alberta, Canada. Plants are small, open, and determinate in growth habit. It has a compound inflorescence, and the fruits are 3.4.4.5 cm in diameter. This selection gave the highest fruit set when tested with other lines at a constant temperature of 26.7° C by Charles and Harris (7). Seed of this selection was obtained from R. E. Harris, of Beaverlodge.

S6916. From the same source as the previous selection. According to Charles and Harris (7), S6916 is 'Nagcarlang' from the same source as that of Schaible (25). It is determinate in growth habit, and branches and produces flower clusters profusely. The fruits are pink (because of the colorless skin),

heavily seeded, and about 3.4-4.5 cm in diameter. 'Nagcarlang' was found by Schaible (25) to set fruit abundantly at 26.7° C night temperature.

CIASI61. One of six cultivars sent to C. M. Rick (Vegetable Crops Department, University of California, Davis) by Fidel Lopes L. of the Centro de Investigaceon Agricoles, Sinaloa, Mexico, and described as being the only ones that endure and set fruit under the summer conditions of Sinaloa. Plants of this cultivar are large and indeterminate in growth habit. Fruits are 5.4-7.4 cm in diameter, flattened, pink, and heavily seeded.

VF36. A cultivar bred for processing by G. C. Hanna (Vegetable Crops Department, University of California, Davis). Plants are large, determinate, with good foliage coverage of fruits. According to Rick and Dempsey (22) this cultivar is dependable for setting fruit under temperature extremes, and they consider its low stigma position as one important contributing factor. It has been included in the list of cultivars screened by Santiago (24) under hot humid conditions in the Philippines and by Chaudhary (8) under the hot summer conditions of the North Indian Plains.

High-temperature responses of these cultivars were studied in a "Western Environmental" growth chamber. The high day/night temperature combination selected was 37.8/26.7°C. This was chosen on the basis of previously published research results, particularly those of Schaible (25), and actual summer temperatures in arid subtropical regions.

Temperature in the growth chamber was monitored with 12 thermocouples and a mercury thermometer. The low and high temperatures generally stayed within 0.5 and 1°C, respectively, of the desired temperature. Light intensity at the plant level after five weeks of growth was 720 μ Em² sec¹ of photosynthetically active radiation. Light was synchronized with the day temperature with a 12-hr photoperiod. Relative humidity was 35-45%. Herein, 'high temperature' refers to these growth-chamber conditions. Pollen and ovules developed at high temperature are respectively designated "HTP" and "HTO."

In the greenhouse, night temperature was $20-21^{\circ}$ C and remained fairly constant within this range. The maximum day temperature was $25.6-32.2^{\circ}$, with occasional days exceeding these limits. Relative humidity was 48-62%, and light intensity was $350-500 \ \mu \text{Em}^{-2} \ \text{sec}^{-1}$ with a photoperiod of 13-14 hr. The greenhouse conditions are referred to herein as "normal temperature," and pollen and ovules developed under these conditions are respectively referred to as "NTP" and "NTO".

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Plants were grown in 3.8-liter plastic pots containing sterilized soil composed of sand, peat, and leached soil in equal parts. Plants remained under a normal temperature regime for 23 days from seeding, and thereafter either continued at the same temperature or were transferred to the high temperature. After 30 days from seeding, all plants were watered 3 days a week with half-strength Hoagland's nutrient solution. Distilled water was used on other days.

Each cultivar was represented by 3 plants arranged in a randomized complete-block design in each experiment. Experiment I provided information on vegetative and reproductive responses of the cultivars to high temperatures. Apart from normal care, the only treatment the plants received was daily flower vibration at anthesis using an electric vibrator. Data were obtained on the number of flowers per cluster in the first 4 clusters, percentage of flowers that set fruit, top fresh weight, and number of branches on the main stem and on the branch below the first cluster. Only branches with at least one fully expanded leaf were considered. The experiment was terminated 10 weeks after seeding. Experiment II was used for tests on gamete viability: *in vitro* germination, fruit-setting ability, and seed-setting ability. VF36 was not included in these tests.

Because pollen was meager under the high-temperature regime, the electric vibrator was ineffective in pollen collection. Anthers were removed and brought to a constant-temperature room (25 \pm 1°C). Pollen was scraped from individual anthers with a recurved needle having a flattened end. The pollen-germination medium of Abdalla and Verkerk (1) was used in all tests. It consisted of 5% sucrose in 100 ppm boric acid solution. A drop of medium was placed in each of three 0.8-mm-deep depressions in a microslide. Pollen was tapped gently from the needle over the medium. The slides were placed in a plastic sandwich box of $11 \times 11 \times 3$ cm covered with a wet blotting paper the edges of which were immersed in water. Counts of total pollen grains and grains with pollen tubes were made in 2 nonoverlapping views in each depression under a binocular microscope after 4 hr. Only pollen tubes in excess of 0.07 mm, as indicated by an ocular micrometer, were considered viable. The results are expressed as percentage of germination.

Pollen collected from subsequent flowers as they reached anthesis was used to pollinate flowers developed at normal temperature either immediately or after a short period of deep-freeze storage.

Emasculated flowers were pollinated with normal pollen. Pollen was applied at the beginning of the onset of the night temperature. Fruits were harvested at maturity and weighed individually, and the number of seeds per fruit was determined. Data were obtained also on the number of flowers per cluster in the first 5 clusters and % flowers that set fruit.

Experiment III, conducted in the greenhouse at normal temperature, was similar to Experiment I at the high temperature in that no pruning was done and data were obtained on number of flowers per cluster, number of branches per plant, and top fresh weight. Flowers were used for pollen weight determinations. Open flowers were identified early in the morning and in the afternoon by their position in the cluster and cluster number. Flowers that opened in the morning were used for pollen weight determinations in the early afternoon of the same day, while pollen weight of flowers that opened in the afternoon was determined the next day at 11-12 AM.

Two groups of plants were maintained in the greenhouse, and just before flowering one group was transferred to another greenhouse with similar temperatures but devoid of tomato plants. This set of plants was used to test the fruit and seedsetting capacity of pollen developed at high temperature. Flowers were emasculated 1-2 days before anticipated anthesis. On the day of anthesis most of the petals and sepals were removed to facilitate insertion in the gelatin capsule containing

pollen. It was ascertained that the stigma received adequate pollen. Each cultivar was pollinated with its own high-temperature pollen. Pollination was restricted to the first 5 clusters. As the fruits matured, they were harvested and weighed, and the number of seeds was determined.

The other set of normal-temperature plants was used to provide estimates of the fruit- and seed-setting capacity of ovules and pollen developed at normal temperature. The flowers were vibrated daily. Pollen from the first flower in each plant was used for germination tests by the hanging-drop technique. Fruits were picked at maturity and weighed, and seeds per fruit were counted.

In addition to the growth-chamber data, information was obtained on pollen weight and stigma exsertion from a high-temperature study conducted in the greenhouse in summer. The day/night temperatures in the greenhouse were generally $37-42^{\circ}/27-30^{\circ}C$. Additional details on that study are in the report on the genetic studies (El Ahmadi and Stevens, submitted). Pollen weight was determined for fully opened retlexed flowers. Stigma exsertion refers to the length of that part of the style above the staminal cone.

Results

Flower production. The mean number of flowers per cluster based on the first four clusters varied significantly among cultivars (Table 1). The means under each temperature condition are combined estimates of 2 experiments. At normal temperature, BL6807 and S6916 produced the highest number of flowers per cluster, and CIAS161 the least. At high temperature, flower production was reduced in all cultivars except BL6807. A combined analysis showed a significant cultivar \times experiment interaction. The superiority of S6916 over PI 262934 at normal temperature is lost at high temperature. VF36 showed the most extreme response to high temperature, producing only aborted flowers.

Stigma exsertion. The information on stigma exsertion was obtained in the greenhouse in summer. Flowers of the cultivars S6916, PI 262934, and CIAS161 had their stigmas exserted above the anther cone by more than 1 mm (Table 1). Stigma exsertion was found in very few flowers of BL6807, and in none of Saladette or VF36. At normal temperature stigma position was lowest in VF36.

Pollen production. The majority of flowers developed at high temperature in the greenhouse released no weighable pollen (Fig. 1) when manipulated with the vibrator. The data were not analyzed statistically. The results probably underestimate pollen production at high temperature. They indicate what may be termed dehiscible pollen rather than total quantity produced.

Table 1. Number of flowers per cluster of tomato cultivars grown at normal and high temperatures and stigma exsertion in mm at high temperature.

	No. o (fi	Stigma		
Cultivar	Normal	Femperature High	exsertion (mm) (High temp)	
BL6807	7.6 a ^y	8.8 a	0.3	
S6916	7.5 ab	5.3 b	2.2	
Saladette	6.5 ab	5.6 b	0.0	
PI 262934	6.0 b	5.3 b	1.1	
CIAS161	3.0 c	2.7 c	1.6	
VF36	_	no normal flowers	0.0	

^zLSD from pooled error variance = 0.9.

 $^{\rm y}$ Mean separation within columns by Duncan's multiple-range test, 5% level.

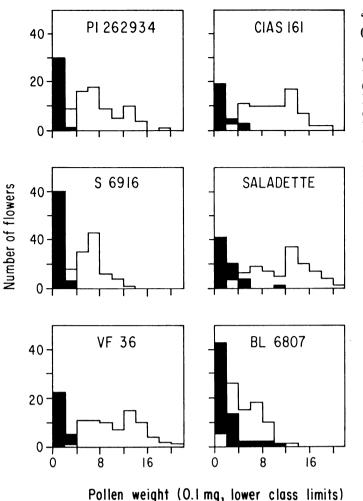


Fig. 1. Frequency histograms for pollen weight per flower. Solid bars = high temperature. Open bars = normal temperature.

At the normal temperature, no flowers were devoid of pollen. Variation among cultivars in pollen production was significant (Table 2). The statistical analysis was based on mean values for each plant.

In vitro pollen germination. The viability of normal-temperature pollen was similar in all cultivars. At high temperature, pollen viability was reduced drastically in all cultivars except

Table 2. Dehiscible pollen weight per flower and percent of *in vitro* pollen germination of tomato cultivars grown at high and normal temperatures.

Cultivar	Mean pollen (mg		Pollen germination ^Z (%) Temperature			
	Temper	ature				
	Normal	High	Normal	High		
Saladette	1.11 a ^y	0.16	50.7	38.7 a		
VF36	1.05 a	0.08		_		
CIAS161	0.99 a	0.11	42.6	14.3 b		
PI 262934	0.75 b	0.03	49.1	12.5 bc		
S6916	0.60 bc	0.03	52.9	6.0 c		
BL6807	0.45 c	0.13	52.2	14.2 bc		

^zLSD from pooled error variance = 10.4

y Mean separation within columns by Duncan's multiple-range test; 5%level. 'Saladette', which showed moderate though significant reduction (Table 2).

Fruit set. An unweighted analysis of variance was performed on data transformed to arcsin values. Inference was based on transformed values, but the data shown are actual percentages (Table 3). Mean separation within each experiment was by Duncan's multiple-range test. Bartlet's test indicated that the error variances were homogeneous, and comparisons were made between means in different experiments using an LSD based on the pooled error variance.

Viability comparisons between pollen developed at high and normal temperatures are based on differences in fruit set when both are applied to normal-temperature flowers. Percent of fruit set was not significantly different among cultivars when both ovules and pollen were developed at normal temperature. Fruit set differed significantly among cultivars when hightemperature pollen was used. BL6807 gave the highest fruit set (Table 3), and CIAS161 the least. In all cultivars except BL6807 the reduction in fruit set was highly significant.

Ovule viability at high temperature is very difficult to estimate since all physiological processes are affected by the heat, and ovule viability may not be the most-limiting factor in all genotypes. Nevertheless, ovule viability was estimated in the same way as pollen viability, by comparing fruit set at normal temperature with that at high temperature when normal pollen is used. The reduction in fruit set was highly significant in all cultivars (Table 3). Saladette and BL6807 had the highest fruit set.

When both ovules and pollen were developed at high temperature, only PI 262934, 'Saladette', and BL6807 set fruit. The improvement in set from using normal-temperature pollen was highly significant for 'Saladette', BL6807, and S6916, but not significant for PI 262934 and CIAS161. The majority of fruits at high temperature developed from the basal flowrs of the cluster in 'Saladette' and PI 262934, but were scattered over the cluster in BL6807 and S6916.

Seed set. A few fruits of 'Saladette' and PI 262934 showed symptoms of blossom-end rot at normal temperature. Seed count and fruit weight included only fruits with little or no symptoms of this disorder.

For statistical analysis of seed set, the fruit was considered the experimental unit, and each cultivar was represented by the total number of fruits from the three plants in each experiment. Individual observations were transformed to square roots before the analysis. Comparisons between means were based on individual *t*-tests. The five cultivars fell into 3 groups with regard to seed content under normal conditions: CIAS161 and S6916 had high seed content, PI 262934 was intermediate, and BL6807 and 'Saladette' had the fewest seeds (Table 4).

High temperature significantly reduced the capacity of pollen to effect fertilization and seed set in all cultivars. The proportion reduction was least in CIAS161 and greatest in 'Saladette'. Similarly, ovule viability was reduced significantly by high temperatures in all cultivars. In BL6807, 75% of the fruits were seedless. CIAS161 set only 2 fruits, although one of those had 104 seeds. For each cultivar, comparisons between seed set with high-temperature pollen and seed set with hightemperature ovules showed the following: S6916 and BL6807 had significantly less seed when ovules developed at high temperature than when pollen developed at high temperature. PI 262934 showed the reverse, and 'Saladette' had similar seed set with high-temperature pollen and high-temperature ovules.

Fruit weight. Statistical analysis was the same as for seed content except that no transformation was made. Significant differences in mean fruit weight among the cultivars were found at normal temperature (Table 4). Fruits resulting from high-temperature pollen were slightly lighter in all cultivars except 'Saladette', although not significantly so. With ovules developed

Table 3. Fruit-setting ability	of ovules and pollen	a (as % flowers se	etting fruit) of tomato	cultivars developed at normal and
high temperatures.			• •	-

				Type of p	ollination ^Z			
	NTO x	NTP	NTO	× HTP	НТО	× NTP	HTO × NTP	
Cultivar	no. of flowers	% set	No. of flowers	% set	no. of flowers	% set	no. of flowers	% set
'Saladette'	106	91.5	89	76.4 b ^y	62	42.7 a	74	2.7 b
S6916	118	91.5	84	71.4 b	81	13.6 b	54	0.0 b
PI 262934	93	90.3	84	67.9 b	93	17.2 b	65	10.8 a
BL6807	113	81.4	90	87.8 a	118	27.3 ab	92	3.3 b
CIAS161	55	76.4	43	39.5 c	46	4.4 c	32	0.0b

 Z NTO = Normal-temperature ovules, NTP = Normal-temperature pollen, HTO = High-temperature ovules, HTP = High-temperature pollen.

^yMean separation within columns by Duncan's multiple-range test, 5% level. LSD from pooled error variance of arcsin data = 8.7.

Table 4. Mean fruit weight and number of seeds per fruit and their correlation coefficients.

				Т	ype of polli	ination				
Cultivar		NTO × NT	Р		NTO × H	TP		HTO × NTP		
	Mean fruit wt (g)	No. of seeds per fruit	Corr. coeff.	Mean fruit wt (g)	No. of seeds per fruit	Corr. coeff.	Mean fruit wt (g)	No. of seeds per fruit	Corr. coeff.	
CIAS161 'Saladette' PI 262934 BL6807 S6916	50.0 a ^Z 35.9 b 27.7 c 25.8 c 22.8 d	121 a ^y 52 c 64 b 50 c 110 a	0.57** 0.48* 0.68** 0.67** 0.76**	46.2 a 37.9 b 24.8 c 22.3 c 19.2 d	49 a 6 c 10 bc 12 b 36 a	0.38ns ^x 0.21ns 0.73** 0.87** 0.90**	32.7 a ^w 34.6 a 20.0 b 9.0 c 5.8 d	45 a ^w 7 b 29 a 0 c 14 ab	0.60** 0.79** -0.26ns 0.67**	

^zMean separation in columns by individual *t*-tests.

yMeans converted from square-root values.

^xCorrelation coefficient not significantly different from zero.

^wMean of 2 fruits only.

*, **Significantly different from zero at the 5% level (*) or 1% level (**).

at high temperature, mean fruit weight was not significantly reduced for 'Saladette', was significantly reduced for PI 262934, and was highly significantly reduced for BL6807 and S6916. Except with CIAS161 the ranking of cultivars with respect to fruit size remained the same under all conditions.

Fruit-weight seed-content correlation. Significant positive correlations between fruit weight and seed number were found at both high and normal temperatures except for BL6807, which at high temperature showed a negative but nonsignificant correlation, i.e., parthenocarpic fruits weighed more than seeded fruits (Table 4).

Discussion

The day/night temperature combination used in this study was higher than previously used. Schaible (25) used the same night temperature (26.7°C), but in conjunction with a lower day temperature of 22.8°. His highest day temperature (30.0°) was used with a low night temperature of 16.7° . Charles and Harris (7) used a constant temperature of 26.7° , and Levy et al., (17) used a day/night temperature of $33/23 \pm 2^{\circ}$. It has generally been believed that high night temperature was the major factor influencing fruit set, but Howlett (12) showed that high day temperature also reduces set.

Flower production. Previous reports on the effects of high temperature on flower production do not agree (1, 7, 17). Aung (3) showed that a decrease in flower production at high

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temperature depends on genotype. A significant cultivar \times temperature interaction was found in the present work; BL6807 was not affected, but the number of flowers per cluster was reduced in all the other cultivars, significantly so in S6916 and 'Saladette'. Flower production in BL6807 seems to have been attained at the expense of vegetative growth; its top weight was reduced by more than 50%. The vegetative growth of VF36 and 'Saladette' was least affected among the cultivars studied, but their flowering response was quite different; VF36 did not produce any normal flowers at high temperature, while 'Saladette' had a reduction in the number of flowers produced.

Pollen production. Levy et al., (17) estimated pollen weight per flower from samples of 10-20 flowers and showed that the heat-tolerant 'Hotset' showed less proportionate reduction in pollen produced than did a heat-sensitive cultivar. The results reported here indicate extreme reduction in pollen production in all cultivars (Table 2). Mean values for pollen weight do not adequately describe pollen production at high temperature, since the majority of flowers did not release any pollen. These experiments do not allow examination of possible correlation between fruit set and pollen production, since handpollination or flower vibration tends to mask differences in pollen production. The extreme reduction of 71-96% in pollen weight, probably due largely to indehiscence, may be a primary factor limiting fruit set at high temperatures under field conditions. Rudich et al. (23) have demonstrated that endothecium

Table 5. Gamete viability	at high	temperature	assessed	by in	vitro	pollen	germination,	fruit set,	and seed	set as perc	cent
of normal viability.											

						Type of	gamete				
	In 1	vitro		Male (pollen)		Female (ovule)				
	germination		Fruit	Fruit set		Seed set		Fruit set		Seed set	
	%		%		%		%		%		
Cultivar	normal	Rank ^z	normal	Rank	normal	Rank	normal	Rank	normal	Rank	
'Saladette'	76	1	84	2	12	5	47	1	13	3.5	
CIAS161	34	2	52	5	40	1	6	5	37	2	
BL6807	27	3	108	1	24	3	34	2	0	5	
PI 262934	25	4	75	4	16	4	19	3	45	1	
S6916	11	5	78	3	33	2	15	4	13	3.5	
		$W^{\mathbf{y}} = 0$.18 n.s.				$r_s^X =$	–0.46 n.s.			

²Ranks assigned according to the degree of viability reduction; a rank of one indicates least reduction in viability.

Y"W" is Kendall's coefficient of concordance applied to ranks. It measures the degree of agreement between methods of assessing pollen viability. Significance test is applied to the sum of squares for ranks.

 x_{r_s} is Spearman's rank correlation coefficient applied to ranks. [For W and r_s see (26).]

formation and the resultant pollen thacea opening did not occur in the heat-sensitive 'Roma', at high temperature. However, 'Saladette' had normal endothecium formation and pollen dehiscence.

Stigma exsertion. As with pollen production, this study eliminated stigma exsertion as a possible barrier to pollination. PI 262934, which exserts its stigma at high temperature, gave the highest fruit set of those tested when both male and female gametes developed at high temperature.

Stigma position, a character with high heritability (17, 22), can be changed by simple breeding techniques. Unless selection of heat-tolerant cultivars is based on the performance of pollinated flowers, valuable germplasm may be overlooked.

Pollen viability. The viability of pollen developed at high temperature was assessed in 3 ways: *in vitro* germination, fruit-setting ability, and capacity to set seed. A summary of the data shows that results with those methods do not agree (Table 5). 'Saladette', which sustained the least reduction in germination, suffered the greatest loss in seed set. On the other hand, S6916, which had the largest reduction in germination, was the second-least affected in seed set. Respective germinations of 11% and 76% of normal by S6916 and 'Saladette' gave corresponding values of 78% and 84% for fruit set. Pollen germination of BL6807 was reduced severely *in vitro*, but fruit set was not affected. Charles and Harris (7) found a similar response with this line. It is possible that, for certain cultivars, fruit set does not depend on pollination.

The unreliability of staining methods and *in vitro* germination in assessing pollen viability was stressed by Calvert (6). Seed set is probably the most reliable method of assessing pollen viability.

Ovule viability. Comparisons of the viability of ovules developed at high temperature and those developed at normal temperature assumed that pollen functioning at high temperature was not a limiting factor. There are 2 reasons why this may be so. First, Smith and Cochran (26) showed that pollen germination slowed considerably at 37.8° C, but was not arrested and continued up to 42 hr, with 6.3% germinated. Iwahori (13) found that fertilization started 18 hours after pollination, and by 24-30 hours the majority of ovules were fertilized. Second, pollen was applied at the onset of the night temperature, which was optimum for pollen germination (1, 27). Pollen thus had 24 hr of optimum temperature interrupted by a 12-hr period of 37.8° , which was expected only to slow pollen tube growth.

Judged by fruit set, ovules were affected by high temperature more drastically than was pollen. Levy et al. (17) found that male gamete viability was affected more seriously than female gametes at high temperature. Seed set indicated that ovule viability was reduced in all cultivars by high temperature and that cultivars differed significantly in this respect. Whether the male or female gamete was affected more severely was found to depend on genotype. The 2 extremes were PI 262934 and BL6807. The effect was more severe on pollen viability in the former, and more severe on ovules in the latter (Table 4). In 'Saladette' and CIAS161, both gametes were affected to the same degree.

Other factors. It has been pointed out frequently that gamete fertility may not be a limiting factor in fruit set at high or normal temperature (8, 9, 16). The data presented here show that fruit set of flowers developed at high temperature was significantly improved by the use of normal pollen and that pollen developed at high temperature had a significantly reduced ability to effect fruit set. Nonetheless, if flower fertility were the only factor involved 'Saladette', PI 262934, and CIAS161 should have given higher fruit set than was actually obtained (Tables 3, 4). Also, BL 6807 gave 27.3% set at high temperature even though fertility as judged by seed set was almost zero. Thus, factors other than gamete viability may limit fruit set at high temperature but were not investigated in this study. Iwahori (15) showed that auxin production was reduced by high temperature. Several workers increased fruit set at high temperature by applying growth chemicals (19, 20, 21). Results of studies on the effects of high temperature on carbohydrate synthesis and translocation are controversial (5, 11, 28, 29). The recent report of the Asian Vegetable Research and Development Center (2) mentioned that a heattolerant cultivar showed a higher net photosynthetic rate at 30-35°C than did a sensitive variety. At lower temperatures, both cultivars were similar. Bar Tsur (4) showed that high temperature reduced photosynthesis more in the heat-sensitive 'Roma' than in the heat-tolerant 'Saladette. He also found that mesophyll resistance was increased by high temperature much more in 'Roma' than in Saladette.'

Perhaps the most significant aspect of these results is that heat-tolerant genotypes do not respond to high temperature in a single general pattern. Several characteristics are needed in a heat-tolerant cultivar, and none of the cultivars studied possessed them all at a satisfactory level, but a genotype with the combined strengths of these cultivars should perform exceptionally well at high temperature.

Literature Cited

- 1. Abdalla, A. A. and K. Verkerk. 1968. Growth, flowering and fruitset of the tomato at high temperature. Neth. J. Agric. Sci. 16:71-76.
- 2. Anonymous. 1974. Asian Vegetable Research and Development Center. Annual Report for 1972-1973:27-32.
- Aung, L. H. 1976. Effects of photoperiod and temperature on vegetative and reproductive responses of *Lycopersicon esculentum* Mill. J. Amer. Soc. Hort. Sci. 101:358-360.
- 4. Bar-Tsur, Avri. 1977. High temperature effects on gas exchange characteristics, flowering and fruit-set in tomatoes. MS Thesis. Hebrew University of Jerusalem, Rehobot, Israel.
- 5. Bohning, R. H., W. A. Kendall, and A. J. Linck. 1953. Effects of temperature and sucrose on growth and translocation in tomato. *Amer. J. Bot.* 40:150-153.
- 6. Calvert, A. 1964. Pollen viability, germination and tube growth in the tomato (*Lycopersicon esculentum* Mill.). A review of the literature. Rep. Glasshouse Crops Res. Inst. 1963, 131-142.
- 7. Charles, W. B. and R. E. Harris. 1972. Tomato fruit set at high and low temperature. Canad. J. Plant Sci. 52:497-506.
- Chaudhary, R. C. 1973. Summer tomatoes in north Indian Plains. I. Problems of fruitlessness and parthenocarpy. *Bhartiya Krishi Anusandhan Patrika* 1:39-44 (In Hindi with English summary).
- 9. Davis, R. M., Jr., P. G. Smith, V. H. Schweers, and R. W. Scheurman. 1964. Independence of floral fertility and fruit set in the tomato. *Proc. Amer. Soc. Hort. Sci.* 86:552-556.
- 10. El Ahmadi, A. B. and M. Allen Stevens. 1978. Genetics of high temperature fruit set in the tomato. J. Amer. Soc. Hort. Sci. Submitted.
- 11. Hewitt, S. P. and O. F. Curtis. 1948. The effect of temperature on the loss of dry matter and carbohydrates from leaves by respiration and translocation. *Amer. J. Bot.* 35:746-755.
- 12. Howlett, F. S. 1962. Introductory Remarks. Proc. Plant. Sci. Symp. Campbell Soup Co., 59-64.
- 13. Iwahori, S. 1965. High temperature injuries in tomato. IV. Development of normal flower buds and morphological abnormalities of flowers treated with high temperature. J. Jap. Soc. Hort. Sci. 34:33-41.
- 14. _____. 1966. High temperature injuries in tomato. V. Fertili-

zation and development of embryo with special reference to the abnormalities caused by high temperature. J. Jap. Soc. Hort. Sci. 35:379-384.

- 15. ______. 1967. Auxin of tomato fruit at different stages of its development with a special reference to high temperature injuries. *Plant & Cell Physiol.* 8:15-22.
- Leopold, A. C. and F. I. Scott. 1952. Physiological factors in tomato fruit set. Amer. J. Bot. 39:310-317.
- 17. Levy, A., H. O. Rabmowitch, and N. Kedar. 1978. Morphological and physiological characters affecting flower drop and fruit set of tomatoes at high temperature. *Euphytica* 27:211-218.
- Lewis, D. 1953. Some factors affecting flower production in the tomato. J. Hort. Sci. 23:207-220.
- 19. Liverman, J. L. and S. P. Johnson. 1957. Control of arrested fruit growth in tomato by gibberellins. *Science* 125:1086.
- Moore, E. L. and W. O. Thomas. 1952. Some effects of shading and parachlorophenoxyacetic acid on fruitfulness of tomatoes. Proc. Amer. Soc. Hort. Sci. 60:289-294.
- Mullison, W. R. and E. Mullison. 1948. Effects of several plant growth regulators on fruit set, yield and blossom end rot of six tomato varieties grown under high temperatures. *Bot. Gaz.* 110: 501-505.
- 22. Rick, C. M. and W. H. Dempsey. 1969. Position of the stigma in relation to fruit setting of the tomato. Bot. Gaz. 130:180-186.
- 23. Rudich, J., E. Zamski, and Yael Regev. 1977. Genotypic variation for sensitivity to high temperatures in the tomato: Pollination and fruit set. *Bot. Gaz.* 138:440-452.
- 24. Santiago, Anthony. 1976. Tomato growing in the humid tropics. World Crops 28:89-91.
- Schaible, L. W. 1962. Fruit setting responses of tomatoes to high temperatures. *Plant Sci. Symp.* Campbell Soup Co., p. 89-98.
- 26. Siegel, S. 1956. Nonparametric statistics. McGraw-Hill, New York.
- 27. Smith, O. and H. L. Cochran. 1935. Effect of temperature on pollen germination and tube growth in the tomato. N.Y. (Cornell) Agr. Expt. Sta. Mem. 175.
- Went, F. W. 1944. Plant growth under controlled conditions. III. Correlation. Amer. J. Bot. 31:597-618.
- 29. White, T. H. 1918. The pollination of greenhouse tomatoes. Md. Agr. Expt. Sta. Bul. 222:92-101.

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Genetics of High-temperature Fruit Set in the Tomato¹

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Abstract. The genetics of high-temperature fruit set was studied with a complete diallel cross using 5 cultivars with excellent high temperature tolerance and a California cultivar lacking stigma exsertion. The cultivars differed genetically for number of flowers per cluster, percent fruit set, number of seeds per fruit and stigma exsertion. At normal and high temperatures recessive genes are associated with greater flower number and heritability for this character was high. Percent fruit set is under the control of a largely additive system with a moderate heritability at high temperature. Nonallelic gene interaction was involved in seed set and dominance components exceeded additive at both temperatures. Heritability for seed set was low at high temperature. Stigma exsertion at high temperature is controlled by partially dominant genes with a high diallel additive component and heritability. The results suggest that a scheme of selection for specific combining ability would be useful to combine the strengths of the high temperature tolerant lines with needed characters from a successful cultivar.

Studies are lacking on the inheritance of fruit set in the tomato (Lycopersicon esculentum Mill.) at high temperature.

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Schaible (13) mentioned results indicating quantitative genetic control of heat tolerance but presented no data.

A study of the reproductive responses of 6 genotypes with superior high temperature fruit-set characteristics showed that they have varying strengths under high temperature conditons (3, 4). BL6807 partitioned more of available photosynthate to flowers and fruits. 'Saladette' had no stigma exsertion. 'Saladette', CIAS161 and BL6807 ha greater pollen dehiscence. CIAS161 and S6916 had the smallest decrease in pollen viability and PI 262934 ovule viability was greater. The combination of

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