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Genetics of High-temperature Fruit Set in the Tomato[1]

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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. 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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the physiological strengths of these genotypes into a single cultivar should result in extraordinary high temperature of fruit set performance.

Studies of inheritance of stigma position at normal temperature (1, 2, 12) all considered it to be a discrete character. Rick and Dempsey (11) measured the distance between the stigma and the staminal orifice to indicate the degree of stigma exsertion or insertion and found simple genetic control for the character. The only inheritance study of stigma exsertion at high temperature (9) found a broad-sense heritability of 0.43.

The purpose of this study was to define the inheritance of certain reproductive characteristics that are crucial to high temperature fruit set.

Materials and Methods

Six cultivars ('Saladette', BL6807, PI 262934, CIAS161, S6916, and VF36) were used as parents in a complete diallel cross. The physiological basis of their high temperature performance has been described (4). These cultivars were used in the diallel because of their probable use in programs to develop improved cultivars with high temperature performance.

Five replications of the diallel cross progeny were planted in June, 1975. Each replicate consisted of 42 plots representing the 30 hybrids and the parents in duplicate; each plot consisted of 4 plants. Two weeks after seeding, 2 replicates were transplanted to the field and 2 to the greenhouse. Field conditions represented normal temperature, and the greenhouse was kept at high temperature. Plants of the 5th replicate were kept in the high-temperature greenhouse to replace plants that were lost.

Seedlings were transplanted to the field at a spacing of 150 × 120 cm and irrigated immediately. Data were obtained from 2 plants of each progeny in each replicate on: 1) number of flowers and fruits in each of the first 6 clusters; 2) number of seeds per fruit in 5 early fruits per plant.

The greenhouse used for the high-temperature study was fiberglass, transmitting about 50% solar radiation. The groundbed area, about 9 × 30 m, was divided in the center by a walk creating 2 sections used as the 2 replicates of the experiment. Seedlings were planted at 45-cm spacing in rows 60 cm apart.

Temperatures were monitored with 16 thermocouples, 8 in each replicate. An attempt was made to keep the day temperature within 37-42°C. The night temperature, controlled automatically, usually varied between 27 and 30°. At anthesis, flowers on 2 plants of each progeny were self-pollinated with an electric vibrator fitted with a geletin capsule. The following data were obtained: number of flowers and fruits in each of the first 6 clusters (obtained on pollinated plants only), and mean stigma exsertion to the nearest 0.5 mm based on 13-20 flowers per plant.

The data were analyzed with the Jinks-Hayman diallel analysis (5, 6, 7).

Results

Average maternal effects and reciprocal differences, tested by an analysis of variance of diallel tables (5) were found to be nonsignificant at both temperature conditions. There was no indication that the performance of the F_1 depended on the direction of the cross.

Number of flowers per cluster. Variation in number of flowers was highly significant among parents and among F_1s at both temperatures. At normal temperature the F_1s had fewer flowers than the parents but not at high temperature (Table 2). The correlation between mean values for the two environments was highly significant (Table 1).

The W_r, V_r regression was significantly different from zero and not significantly different from one at both temperatures (Fig. 1a and 1b), indicating that a simple additive-dominance model is adequate. $W_r - V_r$ was constant over arrays (Table 4). At normal temperature the position of the arrays along the regression line shows that the parents fell roughly into 3 groups: more dominant than recessive genes (S6916, VF36, PI 262934, and CIAS161); intermediate ('Saladette'); and more recessive than dominant (BL6807) (Fig. 1a). At high temperature the order is about the same except that 'Saladette' moved to a position indicating more dominant genes (Fig. 1b). At both temperatures, recessive genes are associated with higher flower numbers. The correlation is highly significant at normal temperature ($r = 0.92$) and significant at high temperature ($r = 0.89$). It should be noted that BL6807, which has the highest number of flowers per cluster and has mostly recessive genes, is the only parent among those studied which has a branching truss (compound), a character conditioned by a single recessive gene.

The position of the W_r, V_r regression line and the value of $(H_1/D)^{1/2}$ both indicate that dominance is partial at both temperatures (Table 4). Asymmetry of the proportions of positive and negative alleles at loci exhibiting dominance is indicated at both temperatures. Also at both temperatures, dominant genes are more frequent than recessive genes. The relative magnitudes of the genetic components are remarkably similar at both temperatures. Heritability is high and of the same magnitude at both temperatures (Table 5).

Percent fruit set. Analysis was based on $\sqrt{\text{arcsin}}$ values. Differences among parents and among F_1s were highly significant at both temperatures. F_1s averaged significantly higher fruit set than parents under both temperature conditions (Tables 1 & 2). Correlation in fruit set between high and normal temperatures was not significant (Table 1).

The regression of W_r on V_r was significantly different from zero and not significantly different from one at both temperatures (Fig. 2), and $W_r - V_r$ did not vary significantly among arrays (Table 3). Positions of the arrays along the regression line at normal temperature show that the parents fell into 3 groups: more dominant genes, (CIAS161 and VF36); equal proportions of dominants and recessives (S6916 and 'Saladette'); and more recessive genes, (BL6807 and PI 262934) (Fig. 2a). At high temperature the position of certain arrays is changed. Most striking is the reversal of array 6. VF36 became the parent with mostly recessive genes; the others contain mostly dominant genes (Fig. 2b). At normal temperature the correlation between $W_r + V_r$ and Y_r is negative but not significant ($r = -0.50$); at high temperature the correlation is negative and significant ($r = -0.85$), indicating that dominant genes have positive effects, i.e., increased % fruit set.

The position of the W_r, V_r regression lines and the values of $(H_1/D)^{1/2}$ (Table 4) indicate partial dominance for the genes controlling this character at both temperatures. The diallel estimators (Table 4) indicate unequal frequencies of positive and negative alleles under both temperature conditions. The estimator $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ indicates that dominant genes among the parents are less frequent than the recessive genes at normal temperature. That is corroborated by the negative F value (Table 5). At high temperature the situation is reversed. Dominant genes are more frequent (Tables 4 and 5).

The diallel components have much higher values at high temperature, although the relative magnitudes of the additive and dominance components are little changed. Heritability is moderate at high temperature, and high at normal temperature (Table 5).

Number of seeds per fruit. Mean number of seeds per fruit was determined from 20 fruits of each genotype at normal temperature. At high temperature, mean values were determined from widely varying numbers and are thus of unequal precision. Analysis was made on values transformed to logarithms. Differences among parents were highly significant at both temperatures (Table 2). Differences among F_1s were highly significant at normal temperature but not significant at

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Table 1. Number of flowers per cluster, % fruit set and mean number of seeds per fruit of parents, and F_1s at normal and high temperatures and stigma exsertion at high temperature.

Parent or F_1	No. of flowers per cluster		Fruit set (%)		Mean no. of seeds/ fruit		Mean length stigma exsertion (mm) at high temp
	Normal temp	High temp	Normal temp	High temp	Normal temp	High temp	
BL6807 (1)	14.8	11.4	46.0	31.8	48.4	10.6	0.25
Saladette (2)	8.1	8.4	70.2	26.8	101.4	21.0	0.05
CIAS161 (3)	4.0	3.3	81.1	7.6	135.6	34.6	1.65
PI 262934 (4)	7.1	6.6	71.6	40.2	111.1	44.2	1.15
S6916 (5)	6.6	5.4	66.6	28.8	120.0	24.6	2.20
VF36 (6)	4.0	4.0	58.8	2.0	82.4	8.5	0.00
1x2	10.8	8.1	58.2	37.2	84.1	18.3	0.80
1x3	7.7	5.1	81.9	26.4	122.6	49.5	1.80
1x4	8.3	7.1	59.2	31.4	85.0	15.6	1.50
1x5	7.4	7.0	70.8	47.6	129.2	49.9	2.15
1x6	6.8	6.2	62.0	38.5	62.2	40.1	0.05
2x3	5.6	5.2	81.2	25.3	143.9	42.8	2.10
2x4	7.6	7.0	70.4	32.4	119.8	17.2	1.05
2x5	7.2	8.4	78.2	46.5	113.0	52.0	1.70
2x6	6.8	6.2	64.2	31.1	136.3	59.6	0.00
3x4	5.8	4.3	85.5	27.8	158.0	52.2	2.20
3x5	5.4	4.7	85.2	26.0	137.8	64.1	2.35
3x6	5.2	4.3	73.8	21.1	191.6	50.8	1.15
4x5	6.8	7.9	80.3	40.8	131.5	56.6	1.90
4x6	6.1	5.7	57.8	27.3	106.7	42.1	0.25
5x6	5.6	6.2	68.4	29.2	185.0	31.2	1.90
C.V.	9.9	8.0	5.91^z	10.86^z	2.16^y	14.24^y	13.9
LSD	1.4	1.1	7.05	7.34	0.093	0.442	0.36
	r=0.87**		r=–0.03 ns		r=0.56**		

[z] C.V. and LSD obtained from transformed values (arcsin).

[y] Analysis based on log transformation. For comparison, means should be converted to log value.

high temperature. Seed set was significantly greater in the F_1s than in parents at both temperatures (Tables 1 and 2). The correlation in seed set between the 2 environments was highly significant (Table 1).

At normal temperature the regression of W_r on V_r was significantly different from zero and not significantly different from 1.0. The $W_r - V_r$ analysis indicated significant array differences (Table 3). On the other hand the values of $W_r - V_r$ did not vary significantly at high temperature. The regression of W_r on V_r was not significantly different from one (t = 0.93) but it was also not significantly different from zero (t = 2.45). The W_r, V_r graphs were very similar at both temperatures (Fig. 3.) No attempt was made to obtain a better fit. The data will be examined as they are, bearing in mind that an additive-dominance model is probably not adequate for this character.

Table 2. Mean squares for orthogonal comparisons among genotypes.

Character	Temp	Comparison: Among parents	Among F_1s	F_1s vs. parents^z
Flowers per cluster	Normal	31.831**	4.026**	2.704* (–)
	High	17.880**	3.608**	0.625ns (–)
Fruit set (%)	Normal	291.216**	197.301**	316.681** (+)
	High	291.063**	46.601**	511.748** (+)
No. of seeds per fruit (log)	Normal	0.051**	0.035**	0.103**
	High	1.483**	0.089ns	0.996** (+)
Stigma exsertion	High	1.707**	1.286**	2.229** (+)

[z] A plus sign indicates that the mean of all F_1s is higher than the mean of the parents. A minus sign indicates the opposite.

*, **Significant at 5% (*) or 1% (**) level.

VF36 under both conditions appears to be the parent with mostly recessive genes (3). The other parents have more dominant genes except for BL6807, which at normal temperature appears to have more recessive than dominant genes (Fig. 3a). At both temperatures there is a significant association between dominant genes and increased seed set (r = 0.77, high; r = 0.83, normal). The position of the regression line is close to the origin at normal temperature and below the origin at high temperature, indicating overdominance. $(H_1/D)^{1/2}$ indicates overdominance at both temperatures (Table 4). Genes with positive and negative effects are equally frequent at normal temperature but occur with unequal frequencies at high temperature. Dominant and recessive genes are equally frequent at normal temperature but dominant genes are more frequent at high temperature. The dominance components are relatively higher than the additive component at both temperatures (Table 5).

Stigma exsertion at high temperature: Stigma exsertion did not occur at normal temperature. Significant differences were found among parents and among F_1s in the degree of stigma exsertion. Mean stigma exsertion was significantly higher in the F_1s than in the parents (Tables 1, 2). There was no significant correlation between stigma exsertion and the number of fruits produced by the unpollinated plants.

The regression of W_r on V_r was significantly different from zero and not significantly different from one (Fig. 4). $W_r - V_r$ was homogeneous over arrays (Table 3). The parents fell into

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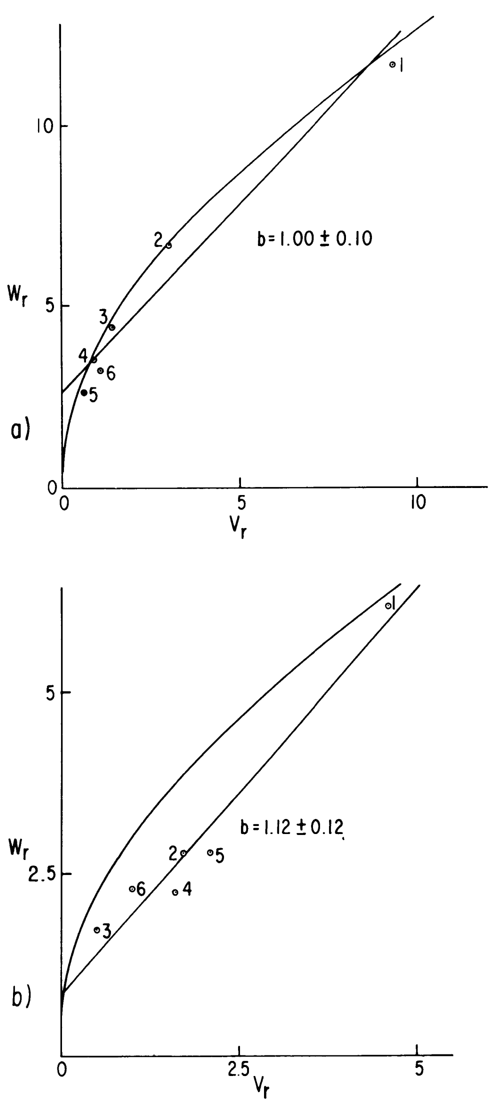

Fig. 1. W_r, V_r regression and limiting parabola for number of flowers per cluster a) at normal temperature, b) at high temperature. Numbers of arrays: 1) BL6007, 2) 'Saladette', 3) CIAS161, 4) PI 262934, 5) S6916, 6) VF36.

Table 3. W_r–V_r mean squares for different characters at normal and high temperatures.

Character	Temp	Source of variation		
		Reps.	Arrays	Error
No. of flowers per cluster	Normal	0.003 ns	0.950 ns	0.674
	High	0.047 ns	0.274 ns	0.306
Fruit set (%)	Normal	4589.871 ns	766.100 ns	985.678
	High	27.298 ns	429.181 ns	359.716
Number of seeds/ fruit (log)	Normal	0.000 ns	0.001**	0.000^z
	High	0.004 ns	0.0046 ns	0.0008
Stigma exsertion	High	0.020*	0.003 ns	0.002

^{z}Small but positive values.

*, **, ^{ns}Significant at 5% (*) or 1% (**) level or nonsignificant (ns).

three groups in array positions along the regression line: mostly recessive genes (BL6807, 'Saladette', and VF36); about equal proportions of dominant and recessive genes (PI 262934); and mostly dominant genes (S6916 and CIAS161). The correlation between parental order of dominance and degree of stigma exsertion was highly significant (r = 0.97). The position of the regression line and the value of $(H_1/D)^{1/2}$ both indicated that stigma exsertion is controlled by partially dominant genes. $H_2/4H_1$ indicated a slight asymmetry in the frequencies of positive and negative alleles (Table 4). The value of $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ and the negative value of F (Tables 4 and 5) show more dominant genes than recessive ones among the parents. The allele additive component "D" was relatively large, and heritability was high (Table 5).

Discussion

Levy (9), using 2 cultivars, found that stigma exsertion showed partial dominance of short styles. The present study found partial dominance for long styles. The parents with exserted stigmas, PI 262934 was genetically different from CIAS161 and S6916 as indicated by array position along the W_r, V_r graph (4). Lewis (10), in a discussion of gene-environment interaction, presented data indicating almost complete dominance for low number of flowers at low temperature 13°C) and absence of dominance at high temperature (25°). The present results indicate partial dominance of low flower number at both temperatures.

Flower production is probably not a limiting factor in fruit yield at high temperature. Although there was a highly significant positive correlation between % fruit set and number of flowers (r = 0.83 for F_1s), valid conclusions about this relationship require the development and use of isogenic lines.

Stigma exsertion is of great importance under high-temperature field conditions. Since the genetic variance for this character is largely additive (Table 5), selection for low stigma position could be effective and rapid.

Seed set is an index of the fertility of both male and female gametes. It was not possible with large populations to examine separate gamete viabilities by the techniques used for the parents in the earlier study (4). The results indicated that nonallelic gene interaction was involved in this character. Although the parents varied significantly in seed content at high temperature, the F_1s did not. Also the F_1s had significantly higher seed content than the parents. The relation of seed content to fruit size was discussed earlier (4). It is unlikely that

Table 4. Values of diallel cross estimators for different characters at normal and high temperatures.

Character	Temp	Estimator		
		$(H_1/D)^{1/2}$	$H_2/4H_1$	$(4DH_1)^{1/2}+F/(4DH_1)^{1/2}-F$
No. of flowers per cluster	Normal	0.52	0.15	4.14
	High	0.67	0.13	2.78
Fruit set (%)	Normal	0.89	0.16	0.89
	High	0.84	0.17	2.59
No. of seeds/ fruit (log)	Normal	1.14	0.23	0.98
	High	1.22	0.16	3.46
Stigma exsertion	High	0.89	0.21	0.65

$(H_1/D)^{1/2}$ = weighted average degree of dominance.
$H_2/4H_1$ = average frequencies of positive and negative alleles at dominant loci.
$(4DH_1)^{1/2}+F/(4DH_1)^{1/2}-F$ = ratio of dominant to recessive alleles.

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Table 5. Diallel variance components and narrow sense heritability for number of flowers per cluster, % fruit set (arcsin) and high temperatures and stigma exsertion at high temperature and number of seeds per fruit (log).

Component	No. of flowers per cluster		Fruit set (%) (√ arcsin)		No. of seeds per fruit (log)		Stigma exsertion at high temp
	Normal temp	High temp	Normal temp	High temp	Normal temp	High temp	
D	15.60 ± 0.71	8.75 ± 0.32	47.87 ± 7.99	137.30 ± 9.53	0.02 ± .003	0.15 ± 0.04	0.83 ± 0.04
H_1	4.21 ± 1.79	3.96 ± 0.80	41.21 ± 0.28	98.05 ± 24.19	0.03 ± .007	0.23 ± 0.11	0.66 ± 0.10
H_2	2.51 ± 1.60	2.11 ± 0.71	25.16 ± 8.12	67.97 ± 21.61	0.03 ± .006	0.15 ± 0.10	0.56 ± 0.09
F	9.90 ± 1.73	5.55 ± 0.77	−14.68 ± 19.52	102.64 ± 23.28	0.0006 ± 0.0067	0.21 ± 0.10	−0.32 ± 0.09
E	0.48 ± 0.27	0.26 ± 0.12	11.43 ± 3.02	12.39 ± 3.60	0.0020 ± 0.0010	0.04 ± 0.02	0.03 ± 0.014
$D-H_1$	11.39 ± 1.58	4.79 ± 0.70	6.66 ± 17.81	39.25 ± 21.24	−0.008 ± 0.006	−0.08 ± 0.09	0.17 ± 0.014
Heritability^z	0.77	0.76	0.69	0.52	0.59	0.30	0.79

^{z}Heritability = $0.5(D + H_1 - H_2 - F)/0.5(D + H_1) - 0.25\ H_2 - 0.5\ F + E$.

direct selection for higher seed set will be pursued as a breeding objective. Unpollinated plants in the greenhouse completely failed to set seed. The relatively good seed set of the pollinated plants shows that gamete viability was not a factor in lack of seed set in the unpollinated plants. Stigma exsertion was probably not a factor, since there were many genotypes that did not exsert stigmas and yet did not set any seed. The most plausible explanation is low pollen production and indehiscence (4).

Genetic analysis of % fruit set showed that the additive genetic variation was larger than the dominance variation (Table 5). The question is which cross or crosses are likely to give the best results. Without information on advanced generations, the question cannot be answered with certainty. Selection of the cross with the highest value has been recommended (8), especially when the genetic variation is largely additive. The highest array values belong to S6916, particularly the F_1s involving this parent with Saladette and BL6807.

The results of the diallel analysis 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 good horticultural type. A cultivar with high yield and good fruit size could be used as the homozygous tester, while a bulk hybrid population of the best high-temperature parents provides the heterozygous population. CIAS161 could be excluded, since it has several undesirable characteristics.

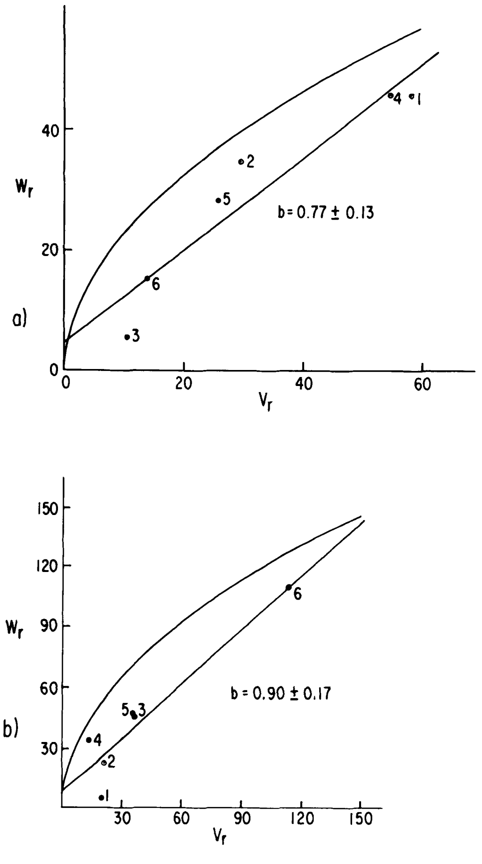

Fig. 2. W_r, V_r regression and limiting parabola for % fruit set at a) normal temperature and b) high temperature. Numbers of arrays: 1) BL6807, 2) 'Saladette', 3) CIAS161, 4) PI 262934, 5) S6916, 6) VF36.

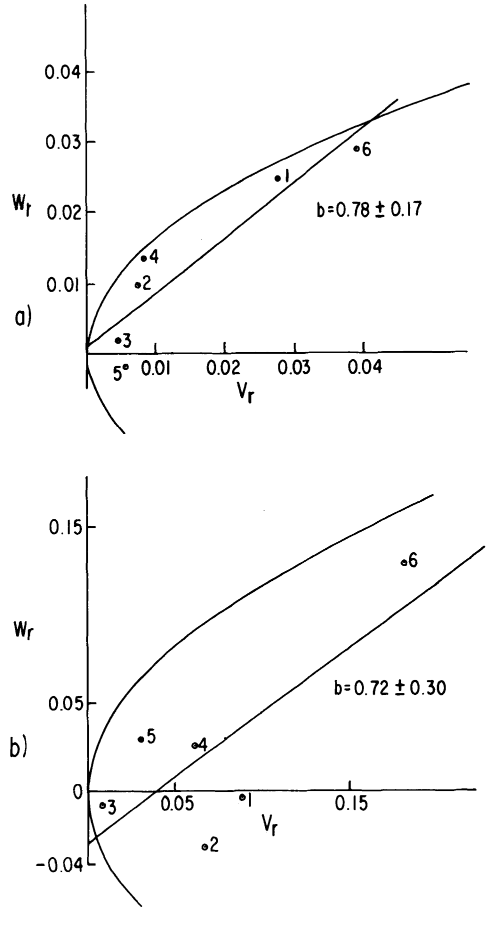

Fig. 3. W_r, V_r regression and limiting parabola for number of seeds per fruit (log) at a) normal temperature and b) high temperature. Numbers of arrays: 1) BL6807, 2) 'Saladette', 3) CIAS161, 4) PI 262934, 5) S6916, 6) VF36.

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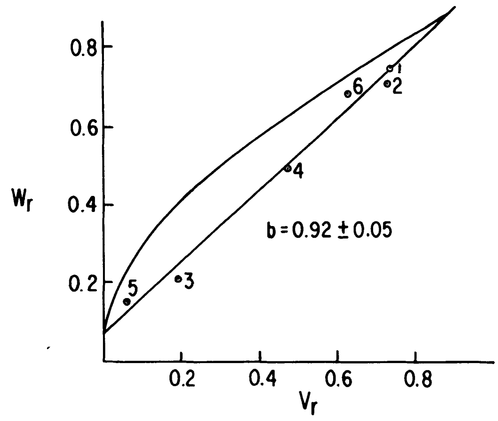

Fig. 4. W_r, V_r regression and limiting parabola for stigma exsertion at high temperature. Numbers of arrays: 1) BL6807, 2) 'Saladette', 3) CIAS161, 4) PI 262934, 5) S6916, 6) VF36.

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Crop Response in a Greenhouse Environmentally Controlled with Air Drawn from a Coal Mine[1]

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Additional index words. carbon dioxide, relative humidity, temperature, *Chrysanthemum morifolium*, chrysanthemum, *Antirrhinum majus*, snapdragon

Abstract. **The environment created by ventilating a greenhouse with mine-air was suitable for the production of high quality spray chrysanthemums (*Chrysanthemum morifolium* Ramat.) and snapdragons (*Antirrhinum majus* L.) from mid-February through November without any additional energy requirement. The environment created in the greenhouse from December to February was extremely humid and favored botrytis development and physiological problems which reduced crop quality.**

A previous study (5) showed that a quonset-greenhouse located in Eastern Kentucky could be heated in winter and cooled in summer with air drawn from an abandoned coal mine. The temperature of the mine-air was 12°C during the winter and rose to 15° during the summer (Table 1). Temperatures inside the greenhouse varied depending upon the temperature difference between the inside and outside and light intensity. On a night when the temperature was –12° outside, the temperature within the greenhouse dropped only to 10°. On cloudy winter days, solar energy warmed the air slightly above the mine-air temperature; on bright winter days, depending upon total solar energy received, the temperature rose at least 6° above that of the mine air. On bright summer days, the mine-air reduced the greenhouse temperature below ambient; when the outside temperature was 36° the temperature within the greenhouse rose only to 28°.

The relative humidity of the mine-air remained at 100% throughout the year. Depending upon solar input or heat loss, the air passing through the greenhouse was either heated or cooled, which caused a change in relative humidity. At night, especially during winter, condensation occurred and the relative humidity remained near 100% (Table 1). On cloudy winter days the relative humidity was also close to 100% and dropped little below this on sunny days. However, on bright summer days when the temperature rose to 29°C, the relative humidity dropped to values as low as 45%.

As the result of oxidation of coal, the CO_2 concentration of the mine-air reached as high as 2500 ppm. Possible toxic gases such as ethylene and methane were not detected (4).

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