Diallel Analysis of Resistance to Cuticle Cracking in Tomato

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ABSTRACT. Genetic control of cuticle cracking (CC) in tomatoes (*Lycopersicon esculentum* Mill.) was studied using half-diallel analyses and reciprocal hybrid comparisons of five parents and reciprocal F₁ hybrids over 3 years in Bradenton, Fla. Maternal effects were usually not significant, but in general, CC incidence in hybrids with a resistant cultigen as the female parent was lower than if the resistant cultigen was the male parent. General combining ability (GCA) was significant at all harvests, with specific combining ability (SCA) becoming significant under high environmental stress. Narrow-sense and broad-sense heritabilities for CC incidence ranged from 0.45 to 0.69 and 0.62 to 0.89, respectively, increasing directly with environmental stress.

Cuticle cracking (CC) in tomato (*Lycopersicon esculentum*) occurs as hairline cracks in the cuticle that are generally located on the fruit shoulders, but occasionally extend down the sides and even cover the entire fruit surface. CC occurs under field and greenhouse conditions, often leading to significant economic losses to the fresh-market tomato industry (Hayman, 1987). Economic losses will be more severe in growing regions prone to rainy weather when fruit are picked at the vine-ripe stage, since fruit would have more exposure to factors influencing the incidence of CC than if picked at the mature-green stage (Emmons and Scott, 1997, 1998). One of the major constraints to growing extended-shelf-life varieties, which are harvested at the vine-ripe stage, in the eastern United States is the incidence of CC and other types of cracking compared to mature-green-harvested tomatoes. Fruit with low CC severity might be packed and not culled out during grading. Shelf life of affected fruit would be decreased and they could harbor postharvest pathogens, possibly resulting in decay of these and other fruit.

Environmental factors including rainfall 2 weeks before harvest (Emmons and Scott, 1997), high soil conductivity (Hayman, 1987), low night temperature (Hayman, 1987), and high relative humidity (Ehret et al., 1993) have been associated with CC incidence. Anatomical and physiological factors have also been identified that influence CC incidence in tomato. We found (Emmons and Scott, 1997) that fruit exposed to sunlight had greater CC incidence than fruit protected by leaf cover and that fruit from tomatoes grown on the ground had more CC incidence than fruit from staked tomatoes. These results indicate leaf cover is an important factor in CC expression and, thus, varietal resistance. The other important factor in varietal resistance was fruit epicarp (epidermis + cuticle) thickness, where resistant (R) genotypes had thicker epicarps than susceptible (S) genotypes (Emmons and Scott, 1998). Other features such as fruit load, fruit size, pedicel type, and fruit shape had some affect on CC expression, but the results were not conclusive (Ehret et al., 1993; Emmons and Scott, 1998).

Genetic studies of cracking in tomato have been done on radial and concentric cracking, but not CC. Radial and concentric crack-

ing are controlled by different gene systems with genes unique to each type of cracking (Avdeyev, 1979; Cortes et al., 1983; Frazier, 1952; Gill and Nandpuri, 1970; Hudson, 1955; Reynard, 1951; Young, 1958, 1963). Frazier (1936) reported that those two types of cracking may occur at different times of the growing season and under different conditions. CC also occurs independently from either of these other types of cracking, suggesting that it is controlled by another gene system.

The objective of this study was to obtain information on the inheritance of resistance to CC by diallel analyses and reciprocal hybrid comparisons conducted over three seasons. Diallel analysis was considered relevant considering the importance of F₁ hybrids presently used in commercial fresh-market tomato production.

Materials and Methods

Based on the results of previous experiments (Emmons, 1996), five cultigens (cultivars and breeding lines) representing an array of CC sensitivity were chosen for diallel crossing. Cultigens 'Suncoast' ('SC') (Scott et al., 1985) and Fla. 7181 were selected as S parents, whereas Fla. 7497, 'Freshmarket 9' ('FM-9') (Leeper and Cox, 1986), and 'Campbell 28' ('C-28') (Moore, 1971) were chosen as R parents (Emmons, 1996). 'SC' and Fla. 7497 have globe-shaped fruit. Fla. 7181 produces flat-round fruit with jointless pedicels. Fla. 7497 has an arthritic type pedicel, which is swollen above the abscission zone and does not separate from it cleanly. 'FM-9' produces deep-round fruit with a square appearance (Leeper and Cox, 1986) and has jointed pedicels. 'C-28' produces flat-round fruit with jointed pedicels. The five cultigens were reciprocally intercrossed to produce 20 F₁ hybrids.

All experiments were conducted in the field at the Gulf Coast Research and Education Center, Bradenton, Fla. Each cultigen (Table 1) was seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, Ind.) and transplanted into Todd planter flats (3.8-cm³ cell size) (Speedling, Sun City, Fla.) containing a 1 peat : 1 vermiculite mixture. Two weeks before transplanting, 20-cm-high × 81-cm-wide beds of EauGallie fine sand were fumigated with 67% methyl bromide : 33% chloropicrin at 239 kg·ha⁻¹ and covered with black polyethylene mulch. Cultigens were set 8 Mar. 1994 and 1995 and 19 Mar. 1996 in randomized complete-block designs with four replications and eight plants per plot. Plants were spaced 46 cm apart within plots that were 91 cm apart in rows spaced 152 cm apart. Recommended fertilizer and insecticide programs were followed (Hochmuth et al., 1989).

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Table 1. Tomato cultigens grown in 1994, 1995, or 1996 cuticle cracking (CC) experiments.

Cultigen		CC rating	Year ^a		
			1994	1995	1996
Parents					
Campbell 28		Resistant	+	+	+
Freshmarket 9		Resistant	+	+	—
Fla. 7497		Resistant	+	+	+
Suncoast		Susceptible	+	+	+
Fla. 7181		Susceptible	+	+	+
Hybrids					
Campbell 28	x Freshmarket 9		+	+	—
	x Suncoast		+	+	+
	x Fla. 7181		+	—	—
	x Fla. 7497		+	+	
Freshmarket 9	x Campbell 28		+	—	—
	x Suncoast		+	+	—
	x Fla. 7181		+	+	—
	x Fla. 7497		+	+	—
Suncoast	x Campbell 28		+	—	+
	x Freshmarket 9		+	—	—
	x Fla. 7181		+	+	—
	x Fla. 7497		+	—	+
Fla. 7181	x Campbell 28		+	—	—
	x Freshmarket 9		+	—	—
	x Suncoast		+	—	—
	x Fla. 7497		+	—	+
Fla. 7497	x Campbell 28		+	—	—
	x Freshmarket 9		+	—	—
	x Suncoast		+	+	+
	x Fla. 7181		+	+	+

^aCultigen was (+) grown, (—) not grown.

Plants were grown with stake culture and irrigated by seepage from ditches adjacent to the experimental beds.

In 1994, a full diallel of five parents and twenty reciprocal hybrids were planted (Table 1). Five parents and nine hybrids (C-28 x Fla. 7181 missing) were planted in 1995 for a half-diallel. In 1996, four parents (FM-9 omitted) and six reciprocal hybrids from R x S crosses were planted to test reciprocal differences.

In 1994, mature-green and riper fruit were harvested from all plants per plot on 6 June before seasonal rains (harvest 1), 13 June after moderate rain (16.4 cm in three rains) (harvest 2), and 20 June after a significant amount of rainfall (29.7 cm in six rains) (harvest 3). In 1995, mature-green and riper fruit were harvested on an individual plant basis between 30 May and 5 June before seasonal rains (harvest 1) and between 12 and 16 June after a significant amount of rainfall (33.1 cm in six rains) (harvest 2). In 1996, mature-red fruit were harvested on 10 June that had no CC with only one 5.8-cm rain in the 2 weeks before harvest (harvest 1). Mature-green and riper fruit were harvested on 18 June following a 11.5-cm rain in five rains over the 2 weeks before harvest (harvest 2). Data for the 1996 study were used only from harvest 2. The percentage of fruit with CC (incidence) was determined for each cultigen. In previous work (Emmons and Scott, 1997, 1998), CC incidence was found to be a better measure of resistance than CC severity. The incidence data were transformed using the square-root function to make the variances homogeneous (Zar, 1984). Data were analyzed and means were compared by the appropriate procedures of the Statistical Analysis System (SAS Institute, Cary, N.C.). Diallel analyses of Hayman (1954) and Griffing (1956, Model 1) were conducted using a software package provided by Christie et al. (1980).

Results

SPRING 1994 RECIPROCAL HYBRID COMPARISONS AND HALF-DIALLEL. Analysis of variance indicated cultigen, harvest, and harvest x cultigen effects were significant for CC incidence (data not shown). The significant cultigen x harvest effects for CC incidence were due to 'FM-9' and 'FM-9' x Fla. 7497 reciprocal F₁ hybrids, which had no significant differences between harvests, while all other cultigens had significant differences between harvests (data not shown). Due to the harvest x cultigen interaction, further analyses were conducted on a by-harvest basis. At 1994 harvest 1, Fla. 7181 had significantly greater CC incidence than the other parents (Table 2). At 1994 harvest 2, S cultigens 'SC' and Fla. 7181 were not significantly different from each other for CC incidence but were significantly greater than R cultigens 'C-28', 'FM-9', and Fla. 7497, which were not significantly different from each other. At 1994 harvest 3, Fla. 7181 had significantly more CC incidence than all other parental lines and 'SC' showed significantly greater CC than 'C-28'. There were no other significant differences for CC incidence.

Reciprocal differences were insignificant except for the 'C-28' x Fla. 7181 F₁ hybrids at harvest 3, where the hybrid with the R parent as the female had a significantly lower CC incidence than the reciprocal (Table 3). Although overall differences due to maternal effects were not significant, the trend for most of the R x S crosses was in the same direction as for 'C-28' x Fla. 7181, i.e., hybrids with the R parent as female had lower incidence of CC than the reciprocal.

At harvest 1, of the twelve R x S F₁ reciprocal hybrids, two had CC incidences not significantly different from the R parent and

Table 2. Incidence (%) of fruit with cuticle cracking for parents over 3 years.^z

Year	Harvest	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
1994	1	0.1b	1.0b	0.3b	3.1b	21.8a
	2	3.4b	12.4b	9.9b	33.2a	55.7a
	3	15.0c	22.6bc	32.4bc	35.8b	64.9a
1995	1	0.4c	3.8bc	3.2bc	18.7a	7.8ab
	2	7.0c	15.4bc	26.1b	34.9b	55.7a
1996	2	0.2c	---	4.1b	7.3b	15.9a

^zMean separation within rows by Duncan's multiple range test at $p \leq 0.05$.

four had CC incidences significantly lower than the more S parent. Each of those hybrids had Fla. 7181 as the S parent (Table 3). At harvest 2, all twenty hybrids had CC incidences intermediate between both parents, and three were significantly less than the mid-parent (MP) (Table 3). Six of twelve R x S hybrids were not significantly different from the more R parent and five of these had Fla. 7181 as a parent. At harvest 3, six of twenty hybrids had incidences significantly less than the MP (Table 3). Four of twelve R x S reciprocal hybrids, all with Fla. 7181 as a parent, were not significantly different from the R parent. Three of six R x R hybrids, all with Fla. 7497 as a parent, had significantly less CC incidence than both parents; one ('C-28' x Fla. 7497) was not significantly different from the more R parent; and the two 'C-28' x 'FM-9' reciprocal hybrids were identical and intermediate between the parents.

Since overall reciprocal differences were not significant, recip-

rocal F₁ hybrids were pooled and Griffing's (1956) analyses and heritability estimates (Hayman, 1954) were performed on a by-harvest basis. Griffing's Method 2 (half-diallel) Model 1 (chosen parents, limited number) was used for data analysis. General combining ability (GCA) was significant at all harvests, whereas specific combining ability (SCA) was significant at only harvest 3 (Table 4). Narrow-sense and broad-sense heritability ranged from 0.54 to 0.69 and 0.67 to 0.89, respectively, and increased with each harvest (Table 4).

SPRING 1995 HALF-DIALLEL. Analysis of variance indicated harvest and cultigen main and interaction effects were significant for CC incidence (data not shown). CC incidence at harvest 2 was greater than that at harvest 1. Subsequently, all further analyses were conducted on a by-harvest basis. At harvest 1, 'SC' had greater CC incidence than 'C-28', 'FM-9', and Fla. 7497 but not Fla. 7181 (Table 2). Fla. 7181 had higher incidence than 'C-28',

Table 3. Incidence (%) of fruit with cuticle cracking for parents and F₁ hybrids at three harvests in 1994.^z

Female parent	Male parent					Mean ^y
	C-28	FM-9	Fla. 7497	SC	Fla. 7181	
Harvest 1						
C-28	<u>0.1</u>	0.1 ^{ws}	0.5 ^s	1.6 ^s	5.8 ^r	2.0
FM-9	0.2 ^{ws}	<u>1.0</u>	0.2 ^s	8.2 ^s	6.8 ^v	3.8
Fla. 7497	0.4 ^s	1.0 ^s	<u>0.3</u>	4.4 ^s	8.4 ^r	3.6
SC	3.4 ^s	1.7 ^s	6.8 ^u	<u>3.1</u>	11.6 ^v	5.9
Fla. 7181	7.6 ^r	5.6 ^v	4.4 ^v	8.2 ^v	<u>21.8</u>	6.4
Mean ^x	2.9	2.1	3.0	5.6	8.2	
Harvest 2						
C-28	<u>3.4</u>	5.1 ^r	6.8 ^r	9.1 ^v	10.7 ^v	7.9
FM-9	0.1 ^r	<u>12.4</u>	3.6 ^r	17.2 ^s	15.2 ^{ww}	9.0
Fla. 7497	1.7 ^{wr}	5.4 ^r	<u>9.9</u>	17.8 ^s	14.1 ^{ww}	9.8
SC	21.4 ^u	19.7 ^s	20.5 ^s	<u>33.2</u>	38.8 ^s	25.1
Fla. 7181	19.4 ^r	25.1 ^v	19.5 ^v	50.2 ^s	<u>55.7</u>	28.6
Mean	10.6	13.8	12.6	23.6	19.7	
Harvest 3						
C-28	<u>15.0</u>	13.9 ^s	9.8 ^{ww}	28.4 ^s	20.5 ^{wwq}	18.2
FM-9	13.9 ^s	<u>22.6</u>	4.4 ^{wt}	24.4 ^s	32.5 ^v	18.8
Fla. 7497	5.2 ^{wt}	3.1 ^{wt}	<u>32.4</u>	24.6 ^s	34.1 ^v	16.8
SC	24.8 ^s	32.7 ^s	37.3 ^s	<u>35.8</u>	60.1 ^s	38.7
Fla. 7181	43.6 ^u	25.6 ^{ww}	53.3 ^u	42.9 ^v	<u>64.9</u>	41.4
Mean	21.9	18.8	26.2	30.1	36.8	

^zParents are arranged top to bottom and left to right in order from most resistant to most susceptible. Parental means are on their respective diagonals and are underlined.

^yRow mean for hybrids only.

^xColumn mean for hybrids only.

^wSignificantly less than mid-parent ($p \leq 0.05$).

^rNot significantly different from more resistant parent.

^sNot significantly different from more susceptible parent.

^tSignificantly less than both parents ($p \leq 0.05$) (overdominance).

^uNot significantly different from either parent.

^vSignificantly different ($p \leq 0.05$) from both parents.

^qSignificantly less than ($p \leq 0.05$) reciprocal.

Table 4. General combining ability (GCA) and specific combining ability (SCA) (Griffing, 1956; Method 2, Model 1,) and heritability (Hayman, 1954) for incidence of cuticle cracking, Spring 1994 and Spring 1995 half-diallels.

Year	Harvest	Source	df	MS	F
1994	1	GCA	4	0.004	26.345*
		SCA	10	0.0002	1.547
		Error	42	0.0001	
	Narrow-sense (NS) heritability = 0.54				
	Broad-sense (BS) heritability = 0.67				
	2	GCA	4	0.024	32.016*
		SCA	10	0.001	1.270
		Error	42	0.0007	
	NS heritability = 0.63				
	BS heritability = 0.72				
	3	GCA	4	0.023	54.384*
		SCA	10	0.0021	4.981*
		Error	28	0.0004	
	NS heritability = 0.69				
	BS heritability = 0.89				
1995	1	GCA	4	0.003	8.18*
		SCA	10	0.002	4.11*
		Error	28	0.0004	
	NS heritability = 0.45				
	BS heritability = 0.62				
	2	GCA	4	0.024	18.25*
		SCA	10	0.003	2.17*
		Error	42	0.001	
	NS heritability = 0.48				
	BS heritability = 0.68				

*Significant at $p \leq 0.05$.

but it was not significantly different from 'FM-9' and Fla. 7497. There were no significant differences between 'C-28', 'FM-9', and Fla. 7497.

CC incidence in the F_1 hybrids varied at harvest 1 (Table 5). 'FM-9' x 'SC', 'FM-9' x Fla. 7181, and Fla. 7497 x 'SC' hybrids

were not significantly different from their R parent whereas 'C-28' x 'SC' was not significantly different from the S parent. All other hybrids were not significantly different from either parent, with 'C-28' x Fla. 7497 and 'FM-9' x Fla. 7497 significantly lower than the MP.

Table 5. Incidence of cuticle cracking for parents and F_1 hybrids (1995)².

Female parent	Male parent					Mean ^y
	C-28	FM-9	Fla. 7497	SC	Fla. 7181	
Harvest 1						
C-28	<u>0.4</u>	0.6 ^s	0.1 ^{ws}	14.0 ^u	--- ^x	4.9
FM-9		<u>3.8</u>	0.0 ^{ws}	0.3 ^{ww}	3.3 ^y	1.0
Fla. 7497			<u>3.2</u>	7.7 ^y	7.1 ^u	3.7
SC				<u>18.7</u>	7.8 ^s	7.4
Fla. 7181					<u>7.8</u>	6.1
Harvest 2						
C-28	<u>7.0</u>	14.0 ^s	1.7 ^{wt}	23.4 ^u	---	13.0
FM-9		<u>15.4</u>	3.3 ^{wt}	10.3 ^{ww}	21.5 ^y	12.3
Fla. 7497			<u>26.1</u>	15.8 ^t	36.2 ^r	14.2
SC				<u>34.9</u>	40.3 ^s	22.4
Fla. 7181					<u>55.7</u>	32.7

²Parents are arranged top to bottom and left to right in order from most resistant to most susceptible. Parental means are on their respective diagonals and are underlined.

³Mean of offspring with female parent in row as common parent.

^xCross missing due to a seed mix.

^wSignificantly less than mid-parent ($p \leq 0.05$).

^yNot significantly different from more resistant parent.

^uNot significantly different from more susceptible parent.

^tSignificantly less than both parents ($p \leq 0.05$) (overdominance).

^sNot significantly different from either parent.

^rSignificantly different ($p \leq 0.05$) from both parents.

At harvest 2, Fla. 7181 had greater CC incidence than all other cultigens, and 'C-28' had less CC incidence than Fla. 7497 and Suncoast (Table 2). There were no other significant differences. The incidences of CC for two hybrids with 'FM-9' as a parent were similar to the more R parent, one hybrid ('C-28' x 'SC') was similar to the more S parent, while most were skewed toward the more R parent (Table 5). Three hybrids (two R x R and one R x S, all with Fla. 7497 as a parent) were significantly lower than both parents, indicating overdominance.

GCA and SCA were significant and GCA was larger than SCA for both harvests (Table 4). Narrow-sense heritability increased slightly from harvest 1 (0.45) to harvest 2 (0.48) as did the broad-sense heritability (0.62 to 0.68) (Table 4).

SPRING 1996 RECIPROCALLS. Selected parents and reciprocals were grown in Spring 1996 (Table 1) to test further reciprocal differences in CC incidence. 'C-28' had significantly lower incidence of CC than Fla. 7497, 'SC', and Fla. 7181, whereas Fla. 7181 had significantly higher CC incidence than all other parents (Table 2). 'SC' and Fla. 7497 were not significantly different from each other. CC incidence for reciprocals from two of three crosses were significantly different from each other but in opposite directions. CC incidence for Fla. 7497 x Fla. 7181 was significantly less than that of its reciprocal (Table 6). However, CC incidence for 'SC' x 'C-28' was significantly less than that of CC incidence for 'C-28' x 'SC'. Three of six hybrids had incidences of CC significantly less than the MP, two of which had CC incidences not significantly different from the R parent.

Discussion

Consideration of reciprocal differences between hybrids is important to maximize hybrid resistance to CC. In this study it was found that significant reciprocal differences in CC incidence occurred for one ('C-28' x Fla. 7181) out of six R x S crosses only at harvest 3 in 1994 and in two ('C-28' x 'SC' and Fla. 7497 x Fla. 7181) out of three R x S crosses in 1996. In two of the crosses with significant differences ('C-28' x Fla. 7181 and Fla. 7497 x Fla. 7181), the hybrid in which the R cultigen was used as the female parent had lower CC incidence, whereas in the third cross ('C-28' x 'SC') the hybrid in which the R cultigen was used as the male parent had lower CC incidence. In 1994 harvests 2 and 3 there was a nonsignificant tendency for the R parents to produce hybrids with less CC incidence when they were used as the female parent than when used as the male parent (Table 3). Reciprocal differences do not appear to be highly significant for crosses between R and S parents, but using the more R parent as the female could improve

the F₁ hybrid resistance under moderate environmental stress conditions.

Results of Hayman's diallel analyses over 2 years were in partial agreement (data not shown). All genetic effects were controlled by additive or dominant gene action with no epistasis detected. Additive gene effects were of more importance than dominance, though dominance in the direction of lower CC incidence became significant under high environmental stress. The 1994 Hayman analysis also indicated that resistance expressed dominance over susceptibility (data not shown). Thus, most reciprocal hybrids had less CC incidence than their MP at each harvest. Dominance of resistance over susceptibility is in contrast to the genetic control of radial cracking in tomatoes (Reynard, 1951) in which resistance appeared to be recessive to susceptibility.

Significant GCA coupled with moderate heritabilities for our population suggest that progress can be made in breeding for CC resistance. However, predicting the performance of specific F₁ lines would be difficult due to significant SCA effects. For instance, 'FM-9' and 'C-28' had similar resistance to CC, but hybrids with 'FM-9' were more consistently R than those with 'C-28' parentage. Furthermore, Fla. 7181 was generally more S to CC than 'SC', but 18 hybrids with Fla. 7181 were not significantly different from the R parent, whereas only six 'SC' hybrids were similar in CC to the R parent. The data indicate selection for resistance to CC under moderate environmental stress conditions would be most effective. A generation means study was conducted with four of the families from 1994. No realistic genetic estimates could be determined due to high variation in S parents and hybrids. The high variation could not be controlled by cultivation methods tested (Emmons and Scott, 1997) and poses a problem for future genetic studies. The S cultigens frequently produced plants with no CC; therefore, selection for resistance to CC should be based on performance of the population as a whole rather than on the performance of individual plants. Resistance of individual plants in segregating populations should be verified by progeny testing. Our results indicate that plants with high CC incidence would indeed be S and progeny tests would likely confirm this.

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Table 6. Incidence (%) of fruit with cuticle cracking for parents and F₁ hybrids (1996).

Female parent	Male parent ^a			
	C-28	Fla. 7497	SC	Fla. 7181
C-28	<u>0.2</u>	---	7.1 ^x	---
Fla. 7497	---	<u>4.1</u>	5.3 ^w	1.1 ^{xy}
SC	1.3 ^{xy}	4.3 ^w	<u>7.3</u>	---
Fla. 7181	---	5.5 ^{yx}	---	<u>15.9</u>

^aParents are arranged top to bottom and left to right in order from most resistant to most susceptible. Parental means are on their respective diagonals and are underlined.

^xSignificantly less than mid-parent ($p \leq 0.05$).

^wNot significantly different from more resistant parent.

^yNot significantly different from either parent.

^{xy}Significantly less than ($p \leq 0.05$) reciprocal.

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