INHERITANCE OF REACTION TO *Leveillula taurica* (LEV.) ARN. IN *Capsicum annuum* L.

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ABSTRACT: The use of fungicides to control powdery mildew in sweet pepper has been ineffective and genetic resistance is the best alternative. Resistance sources identified in *Capsicum annuum* L. are rare and unsatisfactory. The purpose of this work was to study the inheritance of *C. annuum* reaction to powdery mildew. Three homozygous powdery mildew resistant parents, HV-12, Chilli and #124 and three susceptible lines, 609, 442 and 428 were used to obtain seven F_1's and respectively their generations F_2: HV-12 x 609, 442 × HV-12, 428 × HV-12, Chilli × 609, #124 × 609, Chilli × HV-12 and #124 × HV-12. The powdery epidemic was natural using inoculum from highly sporulating susceptible pepper host. Powdery mildew host reaction evaluations were carried out during the fruit production using a rating system based on disease severity scales varying from 1 (resistant) to 5 (highly susceptible). The experimental design was completely randomized. The following genetic parameters were estimated: locus numbers, gene action, heritability coefficient, expected selection gain and observed progress in F_3 generation, and possibly allelic relationship among resistance genes of different resistance sources. The HV-12 × 609 cross was the only one that showed absence of dominance. Other genetically analyzed crossings showed dominant and epistatic effects. Resistance was characterized as being due to at least four pairs of genes. The heritability and selection gains estimates were high. The resistance mechanisms of #124, Chilli and HV-12 showed differences in their expression.
Key words: sweet pepper, powdery mildew, genetic resistance, gene action, allelism

HERANÇA DA REAÇÃO À *Leveillula taurica* (LEV.) ARN. EM *Capsicum annuum* L.

RESUMO: O uso de fungicidas no controle do oídio do pimentão tem se mostrado ineficaz, sendo a resistência genética a melhor alternativa. As fontes de resistência identificadas em *Capsicum annuum* L. são raras e não satisfatórias. O objetivo deste trabalho foi estudar a herança da reação de *C. annuum* ao oídio. Três progenitores resistentes e homozigóticos, HV-12, Chilli e #124 e três suscetíveis, 609, 442 e 428 foram usados na obtenção de sete híbridos e respectivas gerações F_2: HV-12 × 609, 442 × HV-12, 428 × HV-12, Chilli × 609, #124 × 609, Chilli × HV-12 e #124 × HV-12. A epidemia de oídio ocorreu de maneira natural a partir de inóculo mantido em plantas de pimentão suscetíveis. As avaliações das reações ao oídio foram feitas na fase de frutificação, através de uma escala de notas de 1 (resistente) a 5 (altamente suscetível). O delineamento experimental utilizado foi inteiramente casualizado. Foram estimados, os números de locos, ação gênica, coeficiente de herdabilidade, ganho de seleção esperado e o progresso observado em F_3 e possíveis relações de alelismo entre os genes que governam a resistência. O cruzamento HV-12 × 609 foi o único em que a reação de resistência mostrou ausência de dominância. Nos demais cruzamentos detectaram-se efeitos dominantes e epistáticos. A herança foi caracterizada sendo governada por no mínimo quatro pares de genes. As herdabilidades e ganhos de seleção estimados foram altos. O mecanismo de resistência dos progenitores resistentes #124, Chilli e HV-12 mostraram diferenças de expressão e natureza genética.
Palavras-chave: pimentão, oídio, resistência genética, ação gênica, alelismo

INTRODUCTION

The powdery mildew, caused by *Leveillula taurica* (Lev.) Arn., is the most important and limiting disease for the sweet peppers crop in greenhouse. The anamorphic of asexual fungus stage found in sweet pepper crop is known as *Oidiopsis taurica* (Braun, 1987).

Besides sweet pepper, powdery mildew infects other plants such as tomato (Correl et al., 1987), eggplant, potato (Palti, 1988), artichoke, cucumber (Molot & Lecoq, 1986), okra, cotton, fava beans (Nour, 1958), leek, garlic and onion (Palti, 1988, Daubeze et al., 1995).

In Brazil, the first report of powdery mildew for sweet pepper was in the Federal District region in 1994 (Boiteux et al., 1994). Sweet pepper and tomato sucessive planting resulted the establishment of the powdery mildew. The symptoms begin with the mature tissue of chlorotic lesions on the down side leaves. Later, they advance and leaf abscission occurs, photosynthetic reduction activity and fruit sun burning (Palti, 1988; Daubeze et al., 1995).

The use of systemic fungicides for control has not been effective. Besides this, its indiscriminate use causes pathogen resistant strains development (Palti, 1988; Bergamin Filho et al., 1995). The best manner of control would be by means of resistant varieties. In *Capsicum annuum* L., partial resistance has not been satisfactory (Shifriss et al., 1992).

Heredity studies of *C. annuum* showed that resistance to powdery mildew is controlled by three pairs of genes (Shifriss et al., 1992) with additive as well as epistatic effects (Daubeze et al., 1995). For Murthy & Deshpande (1997), the resistance was dominant and poligenic and showed allelism differences among the resistant parents.

The inheritance of resistance to powdery mildew has not been studied and all the Brazilian sweet pepper hybrids worldwide are highly susceptible to powdery mildew. The purpose of this paper was to study the sweet reaction inherited of powdery mildew to support further breeding programs.

MATERIAL AND METHODS

Three resistant parents, HV-12, Chilli, #124, and three susceptible ones, 609, 442 and 428, were used to obtain seven hybrids and their respective F_2 generations. The crosses, HV-12 × 609, 442 × HV-12, 428 × HV-12, Chilli × 609, #124 × 609, were meant for the study of the resistance genetic basis. Crosses Chilli × HV-12 and #124 × HV-12 were used to find possible allelism relationships between genes that control the resistance.

In the crosses HV-12 × 609, 442 × HV-12 and 428 × HV-12 F_3 families were obtained starting with the F_2 plants selected for resistance (scores 1 and 2) and desirable fruit quality. The frequency of selected resistant plants F_2 was 24.4% for the cross HV-12 × 609, 33% for 442 × HV-12 and 7.6% for 428 × HV-12.

The experiment was carried out using a high tunnel of plastic in Piracicaba, SP, situated at 22º42’30" S 47º 38’00" W, at an altitude of 546 meters. The epidemic of powdery mildew occurred naturally. The initial inoculation was obtained and maintained by susceptible sweet pepper plants and with a high degree of sporulation. Plants that disseminated the pathogen were intercalated for a ratio one susceptible plant to each fifteen tested acesses.

Seedlings were transplanted into eight-liter pots with a substrate for vegetables from Multiplanta®. The experimental was entirely randomized design with five plants per pot and 25 treatments of which seven were hybrids (F_1), seven F_2 populations, three F_3 populations and six parents and two susceptible checks for a 8,766 plants.

Powdery mildew reaction evaluations were made at fruit development. A scale of scores was used in accordance with the leaf area affected, proposed by Ullasa et al. (1981), of which: 1 – resistant, no symptoms; 2 – moderately resistant, with 10% of the leaf area affected; 3 – moderately susceptible, with 11-20% of the leaf area affected; 4 – susceptible, with 21-50% of the leaf area affected and 5 – highly susceptible with 51% or more of the leaf area affected. Hybrids Margarita and Magali R were used as susceptible checks. The populations evaluation was made when referential check plants achieved maximum score 5.

The following estimates were obtained: (a) the number of segregating loci (based on the frequency in F_2 of the resistant extremes (score 1 or 1 and 2) showed by the resistant parent and by the formula given by Burton, 1951); (b) type of gene action, using the additive-dominant and epistatic model in accordance with Mather & Jinks, (1981), with significance verified by the t test according to Gomes (1990); (c) the broad sense heritability coefficient (h^2); (d) of the gain from selection (Gs) expected in F_3, (e) observed progress in F_3, estimated in accordance with Vencovsky & Barriga (1992), and (f) allelism relationships among the genes that control resistance. The broad sense heritability coefficient was employed for prediction of the selection expected gain in F_3, being adequate in cases of absence of dominance. With any evidence of dominance, the value of Gs is overestimated, serving only as a reference.

RESULTS AND DISCUSSION

Genetic base of heredity

The parent HV-12 showed high resistance (Table 1). According to Shifriss et al. (1992), the resistance expression of the dihaploid variety HV-12 was due to the restriction mechanism the infection, pathogen colonization and leaf retention. Pathogen penetration of Chilli and #124 parentals ocurred, however with colonization restriction as small necrotic lesions, indicating hypersensitivity reaction to the pathogen and consequent defoliation.

The resistance of the variety HV-12 has been long-lasting and consistent. In Brazil it remained resistant for the *L. taurica* isolates in Piracicaba/SP (Blat et al., 2002) and Brasília/DF (Souza & Café-Filho, 2003; Lima, 2002). This material was also resistant in Tunisia, (Bechir, 1993), Israel (Shifriss et al., 1992), France and Italy (Daubeze et al., 1995).

The parents 609, 442 and 428, behaved as susceptible to the pathogen with averages of 4.64, 4.56 and 4.60, respectively. The checks Magali R and Margarita confirmed their high susceptibility showing average scores of 5.00 (Tables 1 and 2).

Table 1 - The number of segregating plants for reaction to *Leveillula taurica* under greenhouse conditions, using severity disease score scale. *Capsicum annuum*. Piracicaba, 2002.

Generations[1]		R[2]	MR[2]	MS[2]	S[2]	AS[2]
		Score 1	Score 2	Score 3	Score 4	Score 5
HV-12	PR	40	0	0	0	0
Chilli	PR	22	23	0	0	0
#124	PR	17	23	0	0	0
609	PS	0	0	1	12	26
442	PS	0	0	7	9	36
428	PS	0	0	0	15	22
Magali R	TS	0	0	0	0	45
Margarita	TS	0	0	0	0	45
HV-12 x 609	F1	0	25	36	6	5
	F2	40	190	204	64	91
	F3	580	259	102	31	6
442 x HV-12	F1	0	21	27	13	4
	F2	25	249	280	40	106
	F3	266	183	103	13	7
428 x HV-12	F1	0	0	16	5	5
	F2	18	172	149	75	219
	F3	93	101	38	14	14
Chilli x 609	F1	0	0	0	1	24
	F2	0	8	52	65	610
# 124 x 609	F1	0	0	3	13	7
	F2	1	99	306	176	511
#124 x HV-12	F1	0	20	31	4	0
	F2	12	366	370	85	95
Chilli x HV-12	F1	0	0	13	20	28
	F2	85	235	200	142	153

[1]PR - resistant parent, PS - susceptible parent, TS - susceptible checks.
[2]R - resistant, MR - moderately resistant, MS - moderately susceptible, S - susceptible, AS - highly susceptible.

Behavior of the hybrids HV-12 × 609, 442 × HV-12 and 428 × HV-12 agreed with that observed by Shifriss et al. (1992), with an intermediate reaction, with averages of 2.87, 3.00 and 3.58, respectively (Table 2). This intermediate reaction might be able to help in the integrated control of the powdery mildew using fungicides or alternative control.

Plant reaction from the crosses Chilli × 609 and #124 × 609, whose parents with different resistance expression from the HV-12, were susceptible with averages of 4.96 and 4.17 in F_1 and 4.74 and 4.00 in F_2, respectively. The parental choice greatly influences results and the breeding program success (Table 2).

The distribution of F_2 individuals for the different scores, in the crosses HV-12 × 609, 442 × HV-12 and 428 × HV-12 fell between the classes 2 and 3 with 66.8%, 75.6% and 50.7%, respectively (Table 1). Few plants had susceptibility degree of the parents 609, 442 and 428 as well few ones were resistant like HV-12. These results agree with those obtained by Daubeze et al. (1995), suggesting a complex genetic control. Crosses Chilli × 609 and #124 × 609, both had the largest proportion of plants showing class 5, with 83.0% and 46.7% respectively (Table 1).

The genetic analysis of the generations showed non-dominance for the cross HV-12 × 609 (Table 2). Crosses 442 × HV-12, 428 × HV-12, Chilli × 609 and #124 × 609 had significant heterosis value in relation to the parents average, indicating dominance expression at least in part of the loci (Table 2). All of the crosses with highly significant dominant gene action displayed epistatic effects, according with the results of Daubeze et al. (1995).

In relation to the averages of the F_1 generations and principally F_2, there was indication of certain degree of dominance for susceptibility, indicating that the resistance alleles are recessive. These results confirm those observed by Shifriss et al. (1992) and Daubeze et al. (1995) (Table 2).

Table 2 - Number of plants (n) and estimatives of averages disease severity scale, respective variances, numbers of segregating loci, heritability (h^2), heterosis (H and H%) and epistasis (C) with significance by the t test and expected selection gain in F_3 (Gs). *C. annuum*. Piracicaba, 2002.

Generation[1]		n	Average	Variance	No. of loci		H[2(3)]	Gs[3]	H[2]	H[2]	C[2]	Averages	
					Frequency	Formula						Expected/ selection	Progressw/ selection
							----- %	-----		%			
HV-12	PR	40	1.00	0.000									
Chilli	PR	45	1.51	0.255									
#124	PR	40	1.57	0.250									
609	PS	39	4.64	0.289									
442	PS	52	4.56	0.526									
428	PS	37	4.60	0.248									
Magali R	TS	45	5.00	0.000									
Margarita	TS	45	5.00	0.000									
HV-12 x 609	F1	72	2.87	0.702					0.05ns	1.8			
	F2	589	2.96	1.320	≥ 2	2	67.9	-26.0			0.12^{ns}		
	F3	978	1.59	0.714								2.89	1.30 (45.0%)
442 x HV-12	F1	65	3.00	0.781					0.22+	7.9			
	F2	700	2.93	1.159	≥ 3	3	54.9	-19.1▲			0.04^{ns}		
	F3	572	1.80	0.806								2.85	1.05 (36.8%)
428 x HV-12	F1	26	3.58	0.654					0.78***	27.8			
	F2	633	3.48	1.658	≥ 3	2	76.5	-34.8▲			0.29*		
	F3	260	2.05	1.205								3.14	1.09 (34.7%)
Chilli x 609	F1	25	4.96	0.040					1.88***	61.2			
	F2	735	4.74	0.401	≥ 4	9	61.1	-35.2▲			0.72***		
#124 x 609	F1	23	4.17	0.423					1.06***	34.1			
	F2	1093	4.00	1.119	≥ 2	2	69.1	-34.8▲			0.36**		
#124 x HV-12	F1	55	2.71	0.358					1.43***	111.7			
	F2	928	2.88	0.933							0.88***		
Chilli x HV-12	F1	61	4.25	0.622					2.99***	238.2			
	F2	815	3.05	1.630							0.30**		

▲Gain of overestimated selection, calculated with h^2 in a broad sense.
[1]PR - resistant parent, PS - susceptible parent, TS - susceptible checks.
[2]In accordance with Mather & Jinks, (1981).
[3]In accordance with Vencovsky & Barriga (1992).
*Significance based on the t test at 5%; **1%; ***0.1%; +between and 5% and 10%; nsnon significant.

To get powdery mildew resistant hybrids both parents have to be both resistant ones. The positive values of heterosis indicated greater character average in the F_1 generation than the parents. In relation to epistasis there was greater disease severity average of the F_2 generation than the expected one.

The number of segregating loci confirmed the results obtained by Shifriss et al. (1992), Daubeze et al. (1995) and Murthy & Deshpande (1997). For the crosses HV-12 × 609 and #124 × 609 at least two genes might be involved in the inheritance, while for the crosses 442 × HV-12 and 428 × HV-12 at least three genes were involved. In the cross Chilli x 609, the results calculated for the frequencies and by the formula of Burton (1951) were different. By the frequencies calculation, at least four genes were detected, while by the formula given by Burton (1951), nine genes might be controlling the resistance to the powdery mildew inheritance. Errors of estimates of the population variance can also be responsile for this discrepancy.

Considering estimated number of genes, it may be concluded that the inheritance of resistance to powdery mildew in *C. annuum* involves several loci (Table 2), which demand a greater selection generations cycles to get homozygosity. This kind of durable poligenic resistance is more difficult to be overcome by pathogenic strains (Van der Plank, 1968).

Heritabilities were high, showing that the powdery mildew reaction in general is not much influenced by environmental conditions. The segregating F_2 population of the cross 428 × HV-12 showed the greatest degree of heritability 76.54% (Table 2).

Selection for resistance

The estimated gains in selection for the F_3 generations were high, showing good prospects for obtaining lines of sweet pepper resistant to powdery mildew. In the F_3 generations of the cross Chilli × 609 and #124 × 609 resistance increase of 35.2% and 34.8%, are expected respectively (Table 2).

Resistance gains seen in the F_3 generations confirm the high heritability coeficient and the selection efficiency done in the F_2 generations. The expected average without selection for the F_3 generation of the cross HV-12 × 609 would be 2.89, but with selection it was 1.59, with a real gain on the average of 1.30 or 45%. In the F_3 population of 442 × HV-12 cross, the expected average without selection would be 2.85. However with selection it was 1.80, a gain in resistance of 1.05 or 36.8%. For the F_3 generation of the cross 428 × HV-12, the average expected without selection would be 3.14, with selection the average value obtained was 2.05, which corresponds 1.09 gain or 34.7% increase (Table 2).

Reaction of hybrids and their F_2 generations among resistant parents

Reaction expressions of the resistant parents HV-12, Chilli and #124 showed distinct genetic systems determining heritability with no allelic differences. The resistance reaction of the HV-12 proved to be reliable one and fulfilled the requirements for a vertical inheritance. On the other hand, resistance expression of hot pepper plants Chilli and #124, with strong restriction and sporulation reduction with small lesion number, indicates horizontal resistance machanism.

Results shown by the F_1 and F_2 generations indicated differences in genetic mechanisms among the resistant parents. In the cross #124 x HV-12, the parents displayed averages of 1.57 (#124) and 1.00 (HV-12), while the F_1 and F_2 generations showed themselves to be more susceptible than the parents, displaying averages of 2.71 and 2.88, respectively. For Chilli x HV-12, the plants of the F_1 and F_2 generations were even more susceptible. The average for the F_1 generation was 4.25 while the Chilli and HV-12 parents were 1.51 and 1.00, respectively. In F_2, there was wide segregation for reactions to powdery mildew with 3.05 average (Table 2).

For both crosses, average contrasts involving the P_1, P_2, F_1 and F_2 generations were significant according to the t test, for heterosis and epistatic effects detections (Table 2). This fact confirms that the parents HV-12 and the hot peppers resistant source to powdery mildew are genetically different with respect to the alleles that control resistance to powdery mildew.

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