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Inheritance of reaction to *Leveillula taurica* (Lev.) Arn. in *Capsicum baccatum*

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ABSTRACT - Capsicum baccatum *has been considered the best source of resistance against powdery mildew in* Capsicum *spp, while the best resistance sources among hot pepper species are found in* Capsicum baccatum. *The resistance inheritance of this species is unknown and is the focus of this study. Six powdery mildew-resistant parents and three susceptible ones were used to obtain eight F_1 and their respective F_2 generations. The powdery mildew epidemic was induced through infected susceptible plants. Powdery mildew host reaction evaluations were carried out during the fruit setting period using a disease severity grade scale to estimate genetic parameters.* C. baccatum *resistance reaction to powdery mildew was controlled by up to six loci with dominant and epistatic gene action. Heritability estimates were high and ranged from 51.6 to 80.8%. Reactions to powdery mildew in crosses of resistant parents as well as the genetic analyses highlighted genetic similarities with no allelic differences among resistant sources.*

Key words: hot pepper, genetic resistance, powdery mildew, gene action, allelism.

INTRODUCTION

Powdery mildew caused by *Leveillula taurica* is one of the diseases limiting *Capsicum* spp. production. The asexual fungus stage of this pathogen is known as *Oidiopsis taurica* (Braun 1987). Pepper powdery mildew became one the most limiting diseases for greenhouse pepper crop production in dry as well as humid climates. It is a different powdery mildew because its spores are able to store water and germinate under up to 40% of relative humidity (Smith et al. 1999). Powdery mildew in Brazil was first observed by Boiteux et al. (1994) in Brasília-DF in 1994. Continuous cropping and lack of rotation of pepper grown under plastic is responsible for epidemics of this disease.

It is a disease of the adult plant, posing no threat at the juvenile stage, but very severe after fruit maturating stage (Souza and Café Filho 2000). Characteristic symptoms occur on the plant's lower leaves with heavy sporulation. Chlorotic spots occur on the upper leaves with yellowing and defoliation leading to foliar abscission (Palti 1988, Daubeze et al. 1995). Photosynthetic ratio is reduced and fruits become sunscalded. Defoliation can reach up to 75% (Damicone and Sutherland 1999) and a loss of up to 40% (Daubeze et al. 1995).

Systemic fungicides to control powdery mildew are limited because they act specifically on few metabolic processes of the target pathogens, allowing the emergence of fungicide-resistant mutants (Palti 1988, Bergamin Filho et al. 1995). The best way to control powdery mildew would be by genetic resistance. There are earlier reports that the best resistance sources had been identified in *C. baccatum* and *C. chinense* hot pepper (Souza and Café-Filho 2003). Most of the *C. annuum* hot and sweet pepper accessions showed no resistance when compared with *C. baccatum* and *C. chinense* hot peppers (Bidari

1985, Anand et al. 1987, Souza 2000, Blat et al. 2005a). According to Reifschneider et al. (2000), hot pepper varieties of *C. baccatum* and *C. chinense* were not as widespread as *C. annuum*. Resistant genes to the pathogen were possibly maintained in these species during their domestication process.

Inheritance studies of *C. annuum* showed that resistance to powdery mildew is controlled by three genes with additive as well as epistatic effects (Shifriss et al. 1992, Daubeze et al. 1995, Blat et al. 2005b). According to Murthy and Deshpande (1997) however, the resistance was dominant and polygenic and showed allelic differences among the resistant parents.

The reaction of *Capsicum baccatum* hot pepper accessions to powdery mildew has been studied, but not its inheritance. The aim of this work was focused on elucidating the genetics of the reaction to powdery mildew.

MATERIAL AND METHODS

Six resistant parents, Chapéu de Bispo, Ají # 286, BGH 2994, Ají #284, Ají Amarillo # 267 and BGH 0620 and three susceptible ones, Ají # 263, Ají Amarillo #269 and Pimenta ESALQ #154 were used to obtain eight hybrids and their respective F_2 generations (Table 1). The crosses Ají # 263 x Chapéu de Bispo, Ají # 286 x Ají # 263, Ají Amarillo # 269 x Chapéu de Bispo, Pimenta ESALQ #154 x Chapéu de Bispo, Ají # 263 x BGH 2994 were included to study the genetic basis of resistance. Crosses, Ají #284 x Chapéu de Bispo, Ají Amarillo # 267 x Chapéu de Bispo, BGH 0620 x Chapéu de Bispo were used to determine possible allelic relationships between the genes that control the resistance. The Aji # 286 x Aji# 263 hybrid was backcrossed to its resistant parent Aji # 286 for genetic study and also to increase gene resistance frequency for further selection processes to develop hot pepper lines.

The experiment was carried out under a greenhouse at the Plant Science Department of ESALQ/ USP in Piracicaba, SP, Brazil. The epidemic of powdery mildew occurred naturally. The initial inoculation was obtained and maintained by susceptible sweet pepper plants with a high degree of sporulation. A pathogen-disseminating plant was planted in-between every fifteen test-accessions.

Seedlings were transplanted into eight-liter pots filled with Multiplanta® substrate used for chrysanthemum composed of pine bark, vermiculite, peat, macro and micro fertilizers and Humix, plus 5% sand. The experimental design was entirely randomized with five plants per pot and 29 treatments comprising eight hybrids (F_1), eight F_2 generations, nine parents and two susceptible controls, amounting to a total of 5528 plants (Table 2). A larger sample of the F_2 plant population was tested due to a possible polygenic powdery mildew control in *C. baccatum* similar to *Capsicum annuum* L.

Powdery mildew reactions were evaluated from after the fruiting stage, 116 days after sowing. A scale of grades was used to describe the affected leaf area as proposed by Ullasa et al. (1981). This scale ranges from 1 – resistant, no symptoms, 2 – moderate 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, 51% or more of the leaf area affected. The commercial sweet pepper hybrids (*C. annuum* L.) Margarita and Magali R were used as susceptible control and the variety HV-12 and the parent Chapéu de Bispo as resistant control. The reaction was read when the susceptible control plants reached the maximum severity grade of 5.

The following genetic parameters were estimated: (a) number of segregating loci, based on the frequency of the resistant extremes (grade 1 or 1 and 2) in F_2 showed by the resistant parent and also by the expression given by Burton (1951); (b) type of gene action using the additive-dominant and epistatic model as proposed by Mather and Jinks (1981) with significance verified by the t test according to Gomes (1990); (c) the broad-sense heritability coefficient (h^2) and contrasts between generation means measuring heterosis (H) and epistatic effects (C) (Mather and Jinks 1981); (d) gain from selection (Gs) expected in F_3 according to Vencovsky and Barriga (1992). (e) allelic relationships among genes that control resistance. The broad-sense heritability coefficient was employed to predict the expected gain from selection in F_3, being adequate in cases of absence of dominance. When there is any evidence of dominance, the Gs value is overestimated, serving only as reference.

Table 1. Number of segregating plants and degree of resistance to *Leveillula taurica* under greenhouse conditions, according to severity disease grade scale

Generations[1]		R[(2)]	MR[(2)]	MS[(2)]	S[(2)]	HS[(2)]
		grade 1	grade 2	grade 3	grade 4	grade 5
Chapéu de Bispo	RP	24	24	0	0	0
Ají # 286	RP	50	0	0	0	0
BGH 2994	RP	20	0	0	0	0
Ají # 284	RP	8	34	0	0	0
Ají Amarillo # 267	RP	41	5	0	0	0
BGH 0620	RP	17	29	10	0	0
Ají # 263	SP	0	0	0	35	35
Ají Amarillo # 269	SP	0	0	25	15	15
Pimenta ESALQ 154	SP	0	0	23	25	25
HV-12	RC	40	0	0	0	0
Magali R	SC	0	0	0	0	0
Margarita	SC	0	0	0	0	0
Crosses RP x SP						
Ají # 263 x Chapéu de Bispo	F_1	0	30	27	0	0
	F_2	115	154	148	79	79
Ají # 286 x Ají # 263	F_1	16	9	0	0	0
	F_2	333	185	50	6	6
(Ají # 286 x Ají # 263) x Aji # 286	RC	52	4	0	0	0
Ají Amarillo 269 x Chapéu de Bispo	F_1	0	28	17	0	0
	F_2	113	242	180	65	65
Pimenta ESALQ 154 x Chapéu de Bispo	F_1	0	43	14	3	3
	F_2	154	274	149	13	13
Ají # 263 x BGH 2994	F_1	56	4	0	0	0
	F_2	371	164	32	8	8
Crosses RP x RP						
Ají # 284 x Chapéu de Bispo	F_1	10	19	1	0	0
	F_2	197	290	70	3	3
Ají Amarillo # 267 x Chapéu de Bispo	F_1	33	20	0	0	0
	F_2	373	170	43	0	0
BGH 0620 x Chapéu de Bispo	F_1	16	42	1	0	0
	F_2	220	266	95	7	7

[1] RP: resistant parent, SP: susceptible parent, SC: susceptible control, RC: resistant control, RC: backcross
[2] R: resistant, MR: moderately resistant, MS: moderately susceptible, S: susceptible, HS: highly susceptible

RESULTS AND DISCUSSION

Genetic basis of heritability

Resistant parents were 100% with grades ranging from 1 to 2, except BGH 0620 parental that obtained 18% of plants showed grade 3. Aji # 263 was the one the susceptible parent with grade average 4.42 and its plants disease grade ranged from 4 to 5. Two other moderately susceptible parents Aji # 269 and Pimenta ESALQ # 154 had higher plant frequencies with grade 3 to 4 and average 3.37 and 3.52, respectively (Tables 1 and 2).

There was intense defoliation of susceptible parents as well as of their respective F_1 generations. High pathogen pressure was exerted by the susceptible checks on plant lines which induced small necrotic lesions that later coalesced and led to defoliation. These symptoms and reaction were due to the host's hypersensitivity to the pathogen and it was an effective host defense mechanism. The pathogen was able to initial tissue host penetration but was detained by cell collapse and death (Carver et al. 1995, Stadnik and Rivera 2001).

F_1 generations showed highest frequency of plants with grades 1 and 2, considered resistant. Aji #286 x Aji #263 hybrids were the most resistant with an average grade of 1.36 and Aji #263 x BGH 2994 attained an average grade of 1.07. F_2 and F_1 generations showed the highest frequency of plants with grades 1 and 2, ranging from 51.9% for Aji #263 x Chapéu de Bispo; 90.2% for Aji #286 x Aji # 263; 59.2% for Aji Amarillo # 269 x Chapéu de Bispo; 72.6% for Pimenta ESALQ #154 x Chapéu de Bispo and 92.7% for Aji # 263 x BGH 2994 (Tables 1 and 2).

Genetic analyses indicated dominance in most tested crosses. Negative heterosis was highly significant for all crosses except for Aji Amarillo # 269 x Chapéu de Bispo, for which the F_1 mean was lower than that of both parental means (Table 2). This negative heterosis indicated dominance of resistance.

The use of hot pepper hybrids in *C. baccatum* and *C. chinense* is not yet as common as for *C. annuum*. These hot pepper species are grown only in restricted regions of South America. Most of hot pepper exploration in other parts of the world such as India, Korea, Mexico, and USA is based on *C. annuum* hybrids and varieties. It can be said that for *C. baccatum* the hybrid exploration is viable due to its dominant pattern of resistance. There is a good chance of developing a powdery mildew-resistant *C. baccatum* hot pepper hybrid in the short term.

For F_1 with clear dominance effect the corresponding F_2´s showed a negative and highly significant epistasis indicating lower frequency of susceptible plants. A significant epistasis effect was also observed in the backcross of Aji #286 x Aji #263 with the recurrent resistant parent, confirming the corresponding F_2 results (Table 2).

For Ají # 263 x Chapéu de Bispo, Ají # 286 x Ají # 263, Pimenta ESALQ #154 x Chapéu de Bispo and Ají # 263 x BGH 2994, the gene action was additive, dominant and epistatic. Only additive effects were observed for the cross Ají Amarillo # 269 x Chapéu de Bispo (Table 2).

The number of segregating genes varied depending upon the crosses and the estimation procedure. At least two loci were detected for cross Aji #263 x Chapéu de Bispo. For the remaining crosses, the detected number of loci involved in the inheritance of powdery mildew reaction in *C. baccatum* were 3 to 5 for Aji # 263 x BGH 2994 and 4 to 6 for Aji # 286 x Aji # 263 (Table 2).

Heritability values were higher than 50% for all crosses, indicating the potential for further progress towards obtaining resistant hot pepper varieties by selection. The most promising potential for genetic progress was found in cross Ají # 263 x BGH 2994, with a heritability coefficient of 80.8% (Table 2).

The highest expected selection gain in the F_3 generation was found in the segregating population derived from cross Ají # 263 x Chapéu de Bispo, with Gs= -30% (Table 2). A negative gain with a lower scale value indicates a further resistance increase in the next F_3 generation. This indicates a good potential for the development of powdery mildew-resistant hot pepper lines.

Reactions of hybrids and their F_2 generations of resistant x resistant parent crossings

The resistance reactions of all studied parents were similar. The hypersensitivity reaction was similar for the parents Aji #284, Chapéu de Bispo, Aji Amarillo # 267 and BGH0620.

F_1 means were higher than their respective parental due to a positive heterotic effect. Heterosis was however not significant, indicating no dominance for this specific crossing. Similarly, the epistatic effects observed in F_2 generation were not significant (Table 2). This fact showed that the higher disease severity was caused by environmental and not genetic effects.

Similar resistance expression among parents used, the absence of heterosis and non-significant epistasis in their crosses indicated no allelic differences among these resistance sources in *C. baccatum* (Table 2).

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Table 2. Number of plants (n) and mean estimates of disease severity scale; respective variances; numbers of segregating loci; heritability (h2); heterosis (H and H%) and epistasis (C) with significance by the t test; and expected selection gain in F3 (Gs)

Generations[1]		n	Mean	Variance	Nr. loci Frequency	Nr. loci Formula	h^{2} (3) (%)	Gs(3) (%)	H(2)	H(2) (%)	C(2)
Chapéu de Bispo	RP	48	1.50	0.255							
Ají # 286	RP	50	1.00	0.000							
BGH 2994	RP	20	1.00	0.000							
Ají # 284	RP	42	1.81	0.158							
Ají Amarillo # 267	RP	46	1.11	0.099							
BGH 0620	RP	56	1.87	0.475							
Ají # 263	SP	60	4.42	0.247							
Ají Amarillo # 269	SP	40	3.37	0.240							
Pimenta ESALQ 154	SP	48	3.52	0.255							
HV-12	RC	40	1.00	0.000							
Magali R	SC	40	5.00	0.000							
Margarita	SC	40	5.00	0.000							
Ají # 263 x Chapéu de Bispo	F_1	57	2.47	0.254					-0.49***	-16.5	
	F_2	518	2.50	1.256	^{3}2	2	79.9	-30.0[2%]			-0.21*
Ají # 286 x Ají # 263	F_1	25	1.36	0.240					-1.35***	-49.8	
	F_2	574	1.53	0.487	^{3}4	6	62.6	-7.2[2%]			-0.50***
(Ají # 286 x Ají # 263) x Aji # 286	RC	56	1.07	0.067							-0.11*
Ají Amarillo 269 x Chapéu de	F_1	45	2.37	0.240					-0.06	-2.5	
Bispo	F_2	600	2.33	0.815			70.1	-19.3			-0.07
Pimenta ESALQ 154 x Chapéu de	F_1	60	2.33	0.328					-0.18*	-7.2	
Bispo	F_2	590	2.04	0.601			51.6	-10.3[2%]			-0.38***
Ají # 263 x BGH 2994	F_1	60	1.07	0.063					-1.64***	-60.5	
	F_2	577	1.45	0.484	^{3}3	5	80.8	-7.6[2%]			-0.44***
Ají # 284 x Chapéu de Bispo	F_1	30	1.70	0.286					0.05	3.03	
	F_2	560	1.78	0.452							0.10
Ají Amarillo # 267 x Chapéu de	F_1	53	1.38	0.239					0.07	5.38	
Bispo	F_2	586	1.43	0.393							0.09
	F_1	59	1.75	0.227					0.07	4.17	
BGH 0620 x Chapéu de Bispo	F_2	588	1.81	0.549							0.09

[2%] Gain of overestimated selection, calculated with h^2 in the broad sense
[1] RP: resistant parent, SP: susceptible parent, SC: susceptible control, RC: resistant control, RC: backcross
[2] In agreement with Mather and Jinks (1981)
[3] In agreement with Vencovsky and Barriga (1992)
*, ** , *** Significance based on the t test at 5, 1, and 0.1%; + between and 5% and 10%

Herança da reação à *Leveillula taurica* (Lev.) Arn. em *Capsicum baccatum*

RESUMO - Capsicum baccatum *tem sido considerada a melhor fonte de resistência ao oídio do gênero* Capsicum *spp. Apesar disso a herança dessa reação é desconhecida e este é o foco desse estudo. Seis progenitores resistentes e três suscetíveis foram usados na obtenção de oito híbridos e respectivas gerações F_2. A epidemia de oídio ocorreu por meios de plantas susceptíveis infectadas. As avaliações das reações ao oídio foram feitas na fase de frutificação, por meio de uma escala de notas e posteriormente estimados os parâmetros genéticos. A herança em* C. baccatum *é controlada por até seis locos com ação gênica dominante e epistática. As herdabilidades foram altas, variando de 51,6 a 80,8%. As reações apresentadas pelos cruzamentos entre progenitores resistentes e a análise genética mostraram que esses têm o mesmo sistema genético que controla a resistência, não indicando diferenças alélicas.*

Palavras-chave: pimenta, resistência genética, oídio, ação gênica, alelismo.

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