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

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Received 8 August 2005

Accepted 1 October 2005

ABSTRACT - Capsicum baccatum has been considered the best source of resistance against powdery mildew in Capsicum spp. 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 F₁ and their respective F₂ 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 score 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 indicated 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 most limiting diseases for *Capsicum* spp. production. The asexual fungus stage of this pathogen is known as *Oidiopsis taurica* (Braun 1980). Pepper powdery mildew became one of 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 an adult plant disease with no threat at the juvenile stage, but very severe after fruit maturing stage (Souza and Cafè Filho 2003). 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% (Damiconi 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...
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 et al. 1985, Anand et al. 1987, 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), 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, Aji # 286, BGH 2994, Aji #284, Aji Amarillo #267 and BGH 0620 and three susceptible ones, Aji # 263, Aji Amarillo #269 and Pimenta ESALQ #154 were used to obtain eight hybrids and their respective F2 generations (Table 1). The crosses Aji # 263 x Chapéu de Bispo, Aji # 286 x Aji # 263, Aji Amarillo # 269 x Chapéu de Bispo, Pimenta ESALQ #154 x Chapéu de Bispo, Aji # 263 x BGH 2994 were included to study the genetic basis of resistance. Crosses, Aji #284 x Chapéu de Bispo, Aji 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 pots and set 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 being eight hybrids (F1), eight F2 generations, nine parents and two susceptible controls, amounting to a total of 5528 plants (Table 2). A larger sample of the F2 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 after the fruiting stage, 116 days after sowing. A scale of scores 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 (score 1 or 1 and 2) in F2 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 (h2) and contrasts between generation means measuring heterosis (H) and epistatic effects (C) (Mather and Jinks 1981); (d) gain from selection (Gs) expected in F3 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 F3, 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 score scale

<table>
<thead>
<tr>
<th>Generations</th>
<th>R(2) Score 1</th>
<th>MR(2) Score 2</th>
<th>MS(2) Score 3</th>
<th>S(2) Score 4</th>
<th>HS(2) Score 5</th>
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<td>24</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
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<tr>
<td>Aji # 263</td>
<td>SP 0</td>
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<td>0</td>
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<td>25</td>
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<tr>
<td>Aji Amarillo # 269</td>
<td>SP 0</td>
<td>0</td>
<td>25</td>
<td>15</td>
<td>0</td>
</tr>
<tr>
<td>Pimenta ESALQ 154</td>
<td>SP 0</td>
<td>0</td>
<td>23</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>HV-12</td>
<td>BC 40</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Magali R</td>
<td>SC 0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>Margarita</td>
<td>SC 0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
</tr>
</tbody>
</table>

Covers RP x SP

| Aji # 263 x Chapéu de Bispo | F₁ 0 | 30 | 27 | 0 | 0 |
| F₂ 115 | 154 | 148 | 79 | 22 |
| Aji # 286 x Aji # 263 | F₁ 16 | 9 | 0 | 0 | 0 |
| F₂ 333 | 185 | 50 | 6 | 0 |
| (Aji # 286 x Aji # 263) x Aji # 286 | BC 52 | 4 | 0 | 0 | 0 |
| Aji Amarillo 269 x Chapéu de Bispo | F₁ 0 | 28 | 17 | 0 | 0 |
| F₂ 113 | 242 | 180 | 65 | 0 |
| Pimenta ESALQ 154 x Chapéu de Bispo | F₁ 0 | 43 | 14 | 3 | 0 |
| F₂ 154 | 274 | 149 | 13 | 0 |
| Aji # 263 x BGH 2994 | F₁ 56 | 4 | 0 | 0 | 0 |
| F₂ 371 | 164 | 32 | 8 | 2 |

Covers RP x RP

| Aji # 284 x Chapéu de Bispo | F₁ 10 | 19 | 1 | 0 | 0 |
| F₂ 197 | 290 | 70 | 3 | 0 |
| Aji Amarillo # 267 x Chapéu de Bispo | F₁ 33 | 20 | 0 | 0 | 0 |
| F₂ 373 | 170 | 43 | 0 | 0 |
| BGH 0620 x Chapéu de Bispo | F₁ 16 | 42 | 1 | 0 | 0 |
| F₂ 220 | 266 | 95 | 7 | 0 |

1 RP: resistant parent, SP: susceptible parent, SC: susceptible check, RC: resistant check, BC: 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 scores ranging from 1 to 2, except BGH 0620 parental that obtained 18% of plants showing score 3. Aji # 263 was the susceptible parent with score average 4.42 and its plants disease score ranged from 4 to 5. Two other moderately susceptible parents Aji # 269 and Pimenta ESALQ # 154 had higher plant frequencies with score 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 F1 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 hypersensitivity by 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).

F1 generations showed highest frequency of plants with scores 1 and 2, considered resistant. Aji #286 x Aji #263 hybrids were the most resistant with an average score of 1.36 and Aji #263 x BGH 2994 attained an average score of 1.07. F2 and F1 generations showed the higher frequency of plants with scores 1 and 2, ranging for F2 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 F1 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 F1 with clear dominance effect the corresponding F2’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 F2 results (Table 2).

For Aji # 263 x Chapéu de Bispo, Aji # 286 x Aji # 263, Pimenta ESALQ #154 x Chapéu de Bispo and Aji # 263 x BGH 2994, the gene action was additive, dominant and epistatic. Only additive effects were observed for the cross Aji 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 Aji # 263 x BGH 2994, with a heritability coefficient of 80.8% (Table 2).

The highest expected selection gain in the F3 generation was found for the segregating population derived from cross Aji # 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 F3 generation. This indicates a good potential for the development of powdery mildew-resistant hot pepper lines.

Reactions of hybrids and their F2 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.

F1 means were higher than their respective parents due to a positive heterotic effect. Heterosis was however not significant, indicating no dominance for this specific crossing. Similarly, the epistatic effects observed in F2 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).

ACKNOWLEDGEMENTS

The first author was supported by a scholarship of FAPESP/Brazil.
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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)

<table>
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<tr>
<th>Generations¹</th>
<th>n</th>
<th>Mean</th>
<th>Variance</th>
<th>Nr. loci</th>
<th>h²(%)</th>
<th>Gs(%)</th>
<th>H(%)</th>
<th>H%(%)</th>
<th>C(%)</th>
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<td>Chapéu de Bispo</td>
<td>RP</td>
<td>48</td>
<td>1.50</td>
<td>0.255</td>
<td>-0.49***</td>
<td>-16.5</td>
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<td>Aji # 286</td>
<td>RP</td>
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<td>0.000</td>
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Crosses RP x SP

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<td>45</td>
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Crosses RP x RP

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<tr>
<td>Aji Amarillo # 267 x Chapéu de Bispo</td>
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<td>586</td>
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<td>BGH 0620 x Chapéu de Bispo</td>
<td>F₂</td>
<td>588</td>
<td>1.81</td>
<td>0.549</td>
<td>0.09</td>
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¹RP: resistant parent, SP: susceptible parent, SC: susceptible check, RC: resistant check, BC: backcross
²In agreement with Mather and Jinks (1981)
³In agreement with Vencovsky and Barriga (1992)
* *, ** , *** Significance based on the t test at 5, 1, and 0.1%; + between and 5% and 10%

Gain of overestimated selection, calculated with h² in the broad sense
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 F2. 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* foi 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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