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Resistance of pepper germplasm to *Phytophthora capsici* isolates collected in northwest Spain

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Abstract

One single pathotype (race 0) was identified among eight tested isolates of *Phytophthora capsici* (Leonian) collected in northwest Spain, after inoculation tests using pepper cultivars of different origin, including the well known reference resistant cultivar Serrano Criollo de Morelos 334. Complete resistance to *P. capsici* was not found after the inoculation of 23 local genotypes of *Capsicum annuum* with three different isolates of this oomycete, collected in northwest Spain. However significant differences in virulence were found for the three *P. capsici* isolates inoculated into the local pepper germplasm, using disease data based on results of genotype-isolate interactions. Virulence test as well as breeding methods for resistance to the pathogen are also discussed.

Additional key words: Blight, *Capsicum annuum,* pathogenic variation, races.

Resumen

Resistencia en germoplasma de pimiento a aislados de *Phytophthora capsici* recopilados en Galicia

Se inocularon ocho aislados de *Phytophthora capsici* Leonian sobre genotipos de *Capsicum annuum* con origen diverso, incluyendo la línea Serrano Criollo de Morelos 334, conocida por su elevada resistencia al patógeno, encontrándose un único patotipo (raza 0) en Galicia. La inoculación de tres aislados de *P. capsici* recopilados en Galicia sobre 23 líneas locales de *Capsicum annuum,* no permitió encontrar ninguna fuente de resistencia completa al patógeno. Sin embargo, el análisis de la varianza del factor gravedad de la enfermedad en el ensayo de inoculación de *P. capsici* sobre germoplasma local de pimiento mostró diferencias significativas en la interacción genotipo-aislado, así como diferencias de virulencia entre los aislados inoculados. Se discute también la metodología de evaluación de la virulencia de este patógeno sobre *C. annuum,* así como los métodos de mejora genética de la resistencia al mismo.

Palabras clave adicionales: *Capsicum annuum,* razas, tristeza, variación patogénica.

Introduction

Phytophthora capsici Leonian is a destructive oomycete pathogen of many cultivated species, including *Capsicum annuum* (Barksdale *et al.,* 1984; Bosland and Lindsey, 1991; Reifschneider *et al.,* 1992; Goldberg, 1995). Although the disease was well known in Spain a long time ago, it was not documented until 1964 (Davila, 1964), and since then has been persistent in this country (Bartual *et al.,* 1991) as well as in chile producing areas throughout the world (Goldberg, 1995).

The use of resistant cultivars, crop rotation, modifications of cultural practices, as well as adequate doses of fungicides or biological control strategies, are the best approaches to control the *Phytophthora* disease (Black and Berke, 1998; Woo *et al.,* 2005). The exclusive use of fungicides has been unsuccessful to control the disease in certain pepper growing regions (Kim *et al.,* 1989; Bosland and Lindsey, 1991; Parra and Ristaino, 1998). Despite extensive breeding efforts, no pepper cultivars with universal resistance to *P. capsici* have been commercially released (Oelke *et al.,* 2003).

C. annuum - *P. capsici* interactions have already been reported (Clerjeau *et al.,* 1976; Pochard and Daubeze, 1980; Pochard *et al.,* 1983; Reifschneider *et*

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al., 1986; Gil Ortega *et al.,* 1987, 1995). The existence of physiological races was first proposed by Polach and Webster (1972) and, due to the interest in this disease, several studies were carried out (Kim and Hwang, 1992; Gil Ortega *et al.,* 1995; Hwang *et al.,* 1996; Black and Berke, 1998; Rende *et al.,* 2002; Oelke *et al.,* 2003). The physiological races within *P. capsici* differ according to the origin of the isolates: Gil Ortega *et al.* (1995) pointed out the existence of two vertical pathotypes in Spain; Black and Berke (1998), studying isolates from Taiwan, classified them into four different pathotypes; and Oelke *et al.* (2003), studying strains from different origins world-wide, identified nine different physiological races.

The interaction between different genotypes of a host and isolates of a pathogen was formerly studied to demonstrate the existence of physiological races of a parasite (Van der Planck, 1968). Vertical resistance implies a differential interaction between host cultivars and pathogen races (Van de Planck, 1968).

Three experiments were carried out with the following aims: (i) pathotype determination of the *P. capsici* isolates collected in northwest Spain according to the methods proposed by Gil Ortega *et al.* (1995); (ii) evaluation of the resistance of the northwestern pepper germplasm to three *P. capsici* isolates collected in this part of the country; (iii) virulence of *P. capsici* isolates collected in northwest Spain.

Material and Methods

Pathogens

Ten isolates of *P. capsici* were used (Table 1). Seven were obtained from diseased pepper plants, collected in northwest Spain, and one, PAT-1, was supplied by the University of A Coruña (Spain). Isolates 370.72 and 521.77 were included as a reference and were provided by the Centraalbureau voor Schimmelcultures (The Netherlands). For pathogen isolation stem and collar fragments were collected from diseased plants. The surface of these fragments was disinfected with 0.6% sodium hypochlorite for 3 min, washed with sterile distilled water for 1 min and plated on PDA (potato dextrose agar) medium (Rapilly, 1968). The fungi and oomycetes were grown at 22°C and microscopic observations were carried out every 24 h. After incubation for 10 days, isolates of *P. capsici* were obtained. The taxonomical criteria used to identify the *Phytophthora* species were those described by Stamps *et al.* (1990).

Table 1. Isolates of *P. capsici* used in the study

Isolate	Origin	Year of isolation
PA-1	A Coruña - Spain	2001
PA-5-3	A Coruña - Spain	2001
PA-5	A Coruña - Spain	2001
PA1/02	A Coruña - Spain	2002
RO-4	Pontevedra - Spain	2001
BE-4	A Coruña - Spain	2001
BE-3	A Coruña - Spain	2001
PAT1	A Coruña - Spain	1999
370.72	United States	1972
521.77	The Netherlands	1977

Host plants

The 26 pepper genotypes included in this study are shown in Table 2. Twenty-three of them corresponded to *C. annuum* germplasm from the CIAM (Centro de Investigaciones Agrarias de Mabegondo, A Coruña). Yolo Wonder and two resistant lines, SCM 334 (Serrano Criollo de Morelos 334) and PI201234, were used to determine the *P. capsici* pathotypes, according to the criteria described by Gil Ortega *et al.* (1995).

Inoculation assays

P. capsici isolates were grown on V8 juice agar medium at room temperature for 7 days (Erwin and Ribeiro, 1996). Each inoculum was prepared by seeding pieces of the isolate into sterile 0.01 M potassium nitrate solution distributed in petri dishes. To stimulate the sporangium formation, the cultures were maintained under light at 24°C for seven days. When abundant sporangia were formed, the sterile solution was replaced by sterile distilled water and the plates were maintained at 5°C for 30 min and then left at laboratory temperature (20 – 24°C) for 3 h to release the zoospores. The zoospore solution was filtered using a Whatman paper no. 2 and adjusted to 2×10^4

Table 2. Origin of the inoculated *C. annuum* genotypes

Genotype	Origin	Type of local cultivar	Type of pepper[1]	Type of genotype
CO5A	A Coruña - Spain	Couto	C4	Improved line
CO5B	A Coruña - Spain	Couto	C4	Landrace
CO5C	A Coruña - Spain	Couto	C4	Landrace
CO10A	A Coruña - Spain	Couto	C4	Improved line
CO10B	A Coruña - Spain	Couto	C4	Landrace
CO10C	A Coruña - Spain	Couto	C4	Landrace
CO12B	A Coruña - Spain	Couto	C4	Improved line
CO12C	A Coruña - Spain	Couto	C4	Landrace
CO18A	A Coruña - Spain	Couto	C4	Landrace
CO18B	A Coruña - Spain	Couto	C4	Improved line
CO18C	A Coruña - Spain	Couto	C4	Landrace
CO2.20	A Coruña - Spain	Couto	C4	Landrace
CO3.25	A Coruña - Spain	Couto	C4	Landrace
CO5.04	A Coruña - Spain	Couto	C4	Landrace
CO5.14	A Coruña - Spain	Couto	C4	Landrace
CO7.20	A Coruña - Spain	Couto	C4	Landrace
CO2.16	A Coruña - Spain	Couto	C4	Landrace
CO3.15	A Coruña - Spain	Couto	C4	Landrace
PA-124	A Coruña - Spain	Padrón	C4	Improved line
PA-129	A Coruña - Spain	Padrón	C4	Improved line
PA-141	A Coruña - Spain	Padrón	C4	Improved line
PA-158	A Coruña - Spain	Padrón	C4	Improved line
PA-172	A Coruña - Spain	Padrón	C4	Improved line
Yolo Wonder	United States	—	A1	Commercial variety
SCM 334	Mexico	—	C1	Landrace
PI 201234	United States	—	C1	Landrace

[1] Pepper type according to Pochard's classification (Pochard, 1966).

zoospores per ml (Bartual *et al.,* 1991). When the plants had six leaves, the collars were inoculated with 5 ml of the solution (Gil Ortega *et al.,* 1995).

The inoculation tests were conducted under greenhouse and growth chamber conditions. Pepper plants were grown in plastic trays in a greenhouse at 20 ± 2°C. Seeds of the different genotypes were sown in a sterilized mixture of peat:sand (1:1 v v^{-1}), on plastic trays of 32 × 30 × 20 cm. For growth chamber assays, the trays were kept about 22°C (without light) to 28°C (during the light period) with a luminic flux of 30000 lux for 16 h.

The pathotype determination experiments had a complete block design with three replicates and 20 plants per replicate, and consisted in the inoculation of cultivars Yolo Wonder, PI 201234 and SCM 334 with ten *P. capsici* isolates, nine collected in Spain and the reference strain 370.72. The assays were carried out inoculating one isolate at a time, in a growth chamber.

Evaluation of the resistance of the northwestern pepper germplasm to *P. capsici* isolates had a complete block design with three replicates per isolate-cultivar interaction and 20 plants per replicate. In this test, 24 pepper lines – 23 local germplasm and the susceptible Yolo Wonder – were inoculated with three *P. capsici* isolates with different origin – BE-4, PA-1, and RO-4 were collected in the northern, central and southern Galicia respectively – under greenhouse conditions.

The virulence test had a split-plot design with the isolate as the whole plot and the cultivars as the subplots randomized within the isolates. Each cultivar-isolate interaction had three replicates with 20 plants per replicate. In this test, five *C. annuum* genotypes of different origin were inoculated

simultaneously in a greenhouse with three *P. capsici* isolates collected in northwest Spain.

Disease severity was read 28 days after inoculation on each plant, using the scales described by Kim and Hwang (1992) (from 0 – symptomless plant, 0% of disease – to 5 – dead plant, 100% of disease).

Statistical analysis

For the disease severity data, the analysis of variance was carried out after the transformation of the data of each plant using the following formula: $Y = \text{arc sin}\sqrt{X/100}$, where X is the disease index rating as a percentage. The pathotype determination tests were analyzed separately for each individual isolate, performing mean comparisons by means of a Duncan's multiple range test. The analysis of variance for the resistance of northwestern pepper germplasm to *P. capsici* isolates was performed considering the cultivar as fixed effect and the isolate and block as random effects. The mean comparisons of cultivar tolerance to each of the isolates of the oomycete were performed by means of the Waller-Duncan's multiple range test at $P < 0.05$. Analysis of variance for disease severity in the virulence test of the *P. capsici* isolates was carried out considering a mixed model with the cultivar as fixed effect and the isolate and block as random effects. The mean pairwise comparisons of cultivar tolerance to each of the isolates of the oomycete were performed by means of the Tukey multiple range test at $P < 0.001$. These analyses were performed using the software SAS System version 8 (SAS, 1999).

Results

P. capsici pathotypes

All of the isolates tested were identified as pathotype 0. The isolates under study infected cv Yolo Wonder but did not produce a clear disease reaction on the SCM334 or PI 201234 cultivars. The disease symptoms produced by all of the isolates differed between cultivars. Those observed in the susceptible Yolo Wonder included collar rots, which progressively ascended along the stems, and complete wilting. The roots of the infected plants were usually necrotic and also had clear rots. However, these disease symptoms were not observed on SCM 334. Only slight root rots were observed on PI201234 when inoculated with the most virulent isolate PA-1. A significant pathogenic variation was observed on Yolo Wonder when inoculated with different isolates, the disease ranged from 1.44 to 5 (Table 3).

Table 3. Results of the identification of pathotypes of *P. capsici* in northwest Spain. Mean disease ratings of *C. annuum* germplasm inoculated with *P. capsici* isolates under greenhouse conditions

Isolate	Yolo	PI 201234	SCM 334	Pathotype
PA-5-3	1.44 a	0.0 b	0.0 b	0
PA-1	4.97 a	0.04 b	0.0 b	0
PA-5	4.24 a	0.001b	0.0 b	0
RO-4	4.51 a	0.0 b	0.0 b	0
PAT-1	2.65 a	0.00 b	0.00 b	0
PA1/02	5.00 a	0.03 b	0.00 b	0
BE-3	5.00 a	0.00 b	0.00 b	0
BE-4	2.7 a	0.00 b	0.00 b	0
370.72	5.00 a	0.0 b	0.0 b	0
Pathotype 1	S (≥ 1.25)	S (> 1.25)	R (< 1.25)	
Pathotype 0	S (≥ 1.25)	R (< 1.25)	R (< 1.25)	

Means followed by the same letter on each row do not significantly differ according to the Duncan's multiple range test at $P < 0.05$. S: Susceptible (more than 25% of disease rating calculated on the basis of the scale); R: Resistant (less than 25% of disease rating).

Resistance of *C. annuum* to *P. capsici*

The symptoms induced by three Spanish isolates of *P. capsici* (PA-1, RO-4 and BE-4) were similar for all pepper cultivars and did not differ from those described in a previous experiment for cv Yolo Wonder. For resistant genotypes SCM 334 and PI 201234, the stem rot was exclusively limited to the base of the collar, and plant wilting did not take place during the experiment; these were the typical symptoms produced by *P. capsici* on peppers in northwest Spain. The symptoms on the susceptible control Yolo Wonder were similar to those described on the local genotypes but stem wilting usually took place at an earlier stage.

Table 4 shows that most of the genotypes were moderately resistant to at least one of the *P. capsici* isolates tested, BE-4, but they were susceptible to the most virulent one, PA-1. The number of genotypes that were significantly more resistant than the control, Yolo Wonder, differed according to the isolate: there were seven genotypes when inoculated with PA-1, eight with RO-4 (being five of them different from those observed after the inoculation with PA-1) and twenty-two with BE-4. This fact, in addition to the differences observed among the genotypes, is caused by a genotype-isolate interaction, confirmed by analysis of variance of the disease ratings (Table 5).

These differences in virulence of the BE-4 isolate compared with the other two, PA-1 and RO-4, were also confirmed by the analysis of variance (Table 5), where the *F*-value of the entry isolate was much higher than the rest of the effects and was also significantly different from zero at $P < 0.001$.

Table 4. Resistance of *C. annuum* germplasm to three isolates of *P. capsici* collected in northwest Spain. Average of the disease rating of three replications of 20 plants per replication, calculated on the basis of 0 (0% disease) - 5 (100% disease) scale, four weeks after inoculation

Pepper line	PA-1	RO-4	BE-4
CO5A	2.42 *	2.53 *	0.09 *
CO5B	4.25	2.52 *	1.42 *
CO5C	3.47 *	3.73	0.91 *
CO10A	3.84	3.45	1.23 *
CO10B	3.82	4.65 *	0.55 *
CO10C	4.20	4.21 *	1.78 *
CO12B	4.32	2.80 *	1.06 *
CO12C	4.32	2.82 *	1.52 *
CO18A	3.62 *	3.45	1.32 *
CO18B	4.47	4.24	1.12 *
CO18C	4.19	4.53 *	0.93 *
CO2.20	4.72	2.41 *	0.97 *
CO3.25	4.78	4.57 *	2.01 *
CO5.04	3.70 *	4.27 *	0.99 *
CO5.14	4.17	4.52 *	1.47 *
CO7.20	3.64	4.05	2.80
CO2.16	4.82	4.88 *	0.93 *
CO3.15	3.30 *	4.85 *	1.30 *
PA124	3.14 *	3.09 *	0.62 *
PA129	3.49 *	1.98 *	0.28 *
PA141	4.39	2.57	1.32 *
PA158	4.55	3.02 *	0.57 *
PA172	4.09	4.05	0.40 *
Yolo Wonder	4.66	3.69	3.05

*: Statistically different from the susceptible control Yolo Wonder according to the Waller-Duncan's multiple range test at $P < 0.05$.

Virulence of pepper genotypes with different origin to *P. capsici* isolates collected in northwest Spain

The disease symptoms recorded in Yolo Wonder, CO 7.20 and PA 158 after the inoculation of isolates PA1/02, RO-4 and PA-1 of the oomycete, previously employed in other tests, were similar to those previously described for susceptible cultivars. The inoculation of these isolates in the resistant genotypes SCM 334 and PI 20234 did not produce any disease symptom of the disease (Table 6). The virulence of these isolates in this experiment was similar to that recorded in the pathotype determination tests (Table 3) with certain pathogenic variation observed in Yolo Wonder probably due to the different conditions of the two experiments (the first was carried out in a greenhouse and the second in a growth chamber).

The three isolates, previously classified as pathotype 0, did not differ in virulence on these pepper genotypes as was confirmed by the analysis of variance (Table 7) for the disease ratings, where the isolate effect was not statistically significantly different from zero. However either the cultivar or the isolate-cultivar effects were significantly different from zero.

Discussion

One vertical pathotype (race 0) of *P. capsici* was identified in Galicia (northwest Spain). The variation of pathogenic response was lower than that previously

Table 5. Analysis of variance (ANOVA) for disease ratings in the interaction of three *P. capsici* isolates with *C. annuum* germplasm collected in northwest Spain

Source of variation	Degree of freedom	Sum of square	Mean square	*F*-value
Total	4243	2071.3		
Isolates	2	634.79	317.4	125.6 ***
Cultivar	23	106.33	4.62	2.09 *
Isolate*Cultivar	46	101.68	2.21	7.61 ***
Block/isolate	6	15.16	2.53	8.70 ***
Error	4166	1209.6	0.2903	

Disease rating data are the arcsin of the square root transformation (arcsin $\sqrt{X}$) of the percentage of disease ratings in the diseased plants, calculated on the basis of the scale. ***, **, *: Effects significantly different from zero at the $P < 0.001$, 0.01, and 0.05 respectively in a mixed model with cultivar as fixed effect and isolate and block as random effects.

Table 6. Mean disease ratings in the interaction of three *P. capsici* isolates collected in northwest Spain with five *C. annuum* genotypes of different origin, calculated on the basis of 0 (0% disease) – 5 (100% disease) scale, four weeks after the inoculation under greenhouse conditions

Cultivar	PA 1/02	RO-4	PA-1
Yolo Wonder	3.77 *	3.40 *	2.70 *
SCM 334	0.00	0.00	0.00
PI 20234	0.00	0.00	0.00
CO7.20	4.13 *	3.44 *	2.90 *
PA158	3.63 *	2.50 *	2.25 *

*: Statistically different from the resistant control SCM 334, for each isolate, according to the Tukey pairwise comparison test at $P < 0.001$ in a mixed model with cultivars considered as fixed effects and isolates and block considered as a random effects.

Table 7. Analysis of variance table for disease ratings in the interaction of three *P. capsici* isolates with five *C. annuum* genotypes of different origin

Source of variation	Degrees of freedom		*F*-value
	Numerator	Denominator	
Isolates	2	6	4.43 NS
Cultivar	4	785	928.61 ***
Isolate*Cultivar	8	785	37.36 ***

Disease rating data are the arcsin of the square root transformation (arcsin $\sqrt{X}$) of the percentage of disease ratings in the diseased plants, calculated on the basis of the scale. ***: Effects significantly different from zero at the $P < 0.001$ in a mixed model with cultivars considered as fixed effects and isolates and block considered as a random effects. NS: not significant at $P < 0.001$ for the same model.

observed for other Spanish isolates (Gil Ortega *et al.,* 1995). Two vertical pathotypes - races 1 and 0 - had been previously confirmed among the Spanish isolates, but their geographical distribution had not been reported (Gil Ortega *et al.,* 1995). These results agree with those of previous studies that suggested an oligogenic resistance response where the individual host genes may interact specifically with pathogen virulence genes (Cristinzio *et al.,* 1992; Gil Ortega *et al.,* 1992; Reifschneider *et al.,* 1992; Black and Berke, 1998; Walker and Bosland, 1999). The differences in pathogenic response for SCM 334 or PI 201234 and the remaining cultivars are a result of typical vertical interactions.

For the local *C. annuum* germoplasm, the results were different. Slight cultivar-isolate interactions were observed - although the isolate-cultivar interaction effect was significantly different from zero, the *F* value was much lower than the remaining effects in the analysis of variance (Table 5) - which may support the idea of a poligenic response as previously reported (Pochard and Daubeze, 1980; Clerjeau *et al.,* 1981; Palloix *et al.,* 1990; Bartual *et al.,* 1991, 1994; Lefebvre and Palloix, 1996). These interactions may be due to a poligenic resistance where individual genes are vertical and operate on a gene-for-gene basis with virulence genes of *P. capsici,* as a result of a gene-for-gene action between polygenes of the host and those of the pathogen, as proposed by Parlevliet and Zadocks (1977) for other pathosystems. This theory -to be confirmed with molecular studies - may not be inconsistent with that of Gil Ortega *et al.* (1995), who proposed the existence of vertical pathotypes on the

P. capsici- C. annuum interactions in Spain, as resistance regulation in *P. capsici* may differ depending on the origin of the resistance source in use and the susceptible parent's genetic background (Bosland, 1998; Walker and Bosland, 1999).

The existence of one single vertical pathotype *sensu* Gil Ortega *et al.* (1995), in this part of the country, differed from situations described elsewhere. Recent findings on isolates of different origin have demonstrated the existence of up to nine isolates identified as different physiological races (Oelke *et al.,* 2003). This may be due to the differential set of cultivars employed in the virulence tests. Considering cultivars as CO10A or PA158, we can find a certain variation in virulence among some *P. capsici* isolates from this Spanish region (BE-4 and PA-1).

The reactions of the 23 *C. annuum* genotypes tested provide valuable information for breeding programs. Most of the pepper lines showed resistance to the less virulent isolates but were susceptible to others. No sources of complete resistance to *P. capsici* were found among the local pepper germplasm. However, the great variation in resistance among the pepper genotypes may lead to the accumulation of resistance alleles intercrossing different genotypes with intermediate resistance to the pathogen. A recurrent selection method seems to be the best one to improve the resistance level of the pepper genotypes in northwestern Spain (Palloix *et al.,* 1990; Bartual *et al.,* 1991). To transfer complete resistance to *P. capsici,* well-known resistance sources such as SCM 334 should be involved in breeding programs including backcrosses with local germplasm.

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References

BARKSDALE T.H., PAPAVIZAS G.S., JOHNSTON S.A., 1984. Resistance to foliar blight and crown rot of pepper caused by *Phytophthora capsici.* Plant Dis 68, 506-509.

BARTUAL R., LACASA A., MARSAL J.I., TELLO J.C., 1994. Epistasis in the resistance of pepper to *Phytophthora* stem blight (*Phytophthora capsici* L.) and its significance in the prediction of double cross performances. Euphytica 72, 149-152.

BARTUAL R., MARSAL J.L., CARBONELL A., TELLO J.C., CAMPOS T., 1991. Genética de la resistencia a *Phytophthora capsici* Leon en pimiento. Bol San Veg Plagas 17, 1-124.

BLACK L.L, BERKE T., 1998. Breeding for *Phytophthora* resistance in pepper. Eucarpia Meeting on Genetics and Breeding of Capsicum & Eggplant, Avignon, France pp. 115-119.

BOSLAND P.W., LINDSEY D.L., 1991. A seedling for *Phytophthora* root rot of pepper, *Capsicum annuum.* Plant Dis 75, 1048-1050.

CLERJEAU M., PITRAT M., NOURISSEAU J.G., 1976. La résistance du piment *(Capsicum annuum)* a *Phytophthora capsici* IV. Etude de l'agressivité de divers isolates, au niveau des feuilles, des tiges et du collet de plantes sensibles et résistantes. Ann Phytopathol 8, 411-423.

CLERJEAU M., LATERROT H., LECOQ H., PITRAT M., 1981. Orientations actuelles de la selection de varieties résistantes aux maladies chez les plantes maraîchéres. Agronomie 1, 41-48.

CRISTINZIO G., ZEMA V., ERRICO A., SACCARDO F., 1992. Introduction of resistance genes to *Phytophthora capsici* into cultivar of *Capsicum annuum* 'Friariello'. Capsicum Newsletter, Special issue, pp. 189-193.

DAVILA M., 1964. La enfermedad de la tristeza del pimiento. Boletín Informativo de Plagas de Campo 18, 10-11.

ERWIN D.C., RIBEIRO O.K., 1996. *Phytophthora* diseases world-wide. APS Press, St. Paul, Minnesota, USA. 592 pp.

GIL ORTEGA R., PALAZÓN ESPAÑOL C., CUARTERO ZUECO J., 1987. Response of pepper to inoculation with *Phytophthora capsici* at different day lengths and temperatures. Capsicum Newsletter 6, 68-69.

GIL ORTEGA R., PALAZÓN ESPAÑOL C., CUARTERO ZUECO J., 1992. Genetic relationships among four pepper genotypes resistant to *Phytophthora capsici.* Plant Breeding 108, 118-125.

GIL ORTEGA R., PALAZÓN ESPAÑOL C., CUARTERO ZUECO J., 1995. Interactions in the pepper-*Phytophthora capsici* system. Plant Breeding 114, 74-79.

GOLDBERG N.P., 1995. Chile pepper diseases. NM State Univ Coop Ext circ. New Mexico.

HWANG B.K., KIM Y.J., KIM C.H., 1996. Differential interactions of *Phytophthora capsici* isolates with pepper genotypes at various plant growth stages. Eur J Plant Pathol 102, 311-316.

KIM Y.J., HWANG B.K., PARK K.W., 1989. Expression of age-related resistance in pepper plants infected with *Phytophthora capsici.* Plant Dis 75, 745-747.

KIM E.S., HWANG B.K., 1992. Virulence to Korean pepper cultivars of isolates of *Phytophthora capsici* from different geographic areas. Plant Dis 76, 486-489.

LEFEBVRE V., PALLOIX A., 1996. Both epistatic and additive effects of QTLs are involved in poligenic induced

resistance to disease: a case study, the interaction pepper - *Phytophthora capsici* Leonian. Theor Appl Genet 93, 503-511.

OELKE L.M., BOSLAND P.W., STEINER R., 2003. Differentiation of race specific resistance to *Phytophthora* root rot and foliar blight in *Capsicum annuum.* J Am Soc Hortic Sci 128, 213-218.

PALLOIX A., DAUBEZE A.M., PHALY T., POCHARD E., 1990. Breeding transgressive lines of pepper for resistance to *Phytophthora capsici* in a recurrent selection system. Euphytica 51, 141-150.

PARLEVLIET J.E., ZADOCKS J.C., 1977. The integrated concept of diseases resistance; a new view including horizontal and vertical resistance in plants. Euphytica 26, 5-21.

PARRA G., RISTAINO J., 1998. Insensitivity to Ridomil Gold (mefenoxam) found among field isolates of *Phytophthora capsici* causing *Phytophthora* blight on bell pepper in North Carolina and New Jersey. Plant Dis 82, 711.

POCHARD E., 1966. Données experimentales sur la selection du piment *Capsicum annuum* L. Ann Amélior Plantes 16, 185-197.

POCHARD E., DAUBEZE A., 1980. Recherche et evaluation des composantes d'une résistance polygenique: la résistance du piment á *Phytophthora capsici.* Ann Amélior Plantes 30, 377-398.

POCHARD E., MOLOT P.M., DOMINGUEZ G., 1983. Étude de deux nouvelles sources de résistance à *Phytophthora capsici* Leon. chez le piment: confirmation de l'existence de tríos composantes distinctes dans la résistance. Agronomie 3, 333-342.

POLACH F.J., WEBSTER R.K., 1972. Identification of strains and inheritance of pathogenicity in *Phytophthora capsici.* Phytopathol 62, 20-26.

RAPILLY F., 1968. Les techniques de mycology en Pathologie Vegétale. Ann Epiphyties 19 (N.º H.S.), 1-102.

REIFSCHNEIDER F.J.B., ADALBERTO C., CAFÉ-FILHO C., REGO A.M., 1986. Factors affecting expression of resistance in pepper *(Capsicum annuum)* to blight caused by *Phytophthora capsici* in screening trials. Plant Pathol 35, 451-456.

REIFSCHNEIDER F.J.B., BOITEUX L.S., DELLA VECCHIA P.T., POULOS J.M., KURODA N., 1992. Inheritance of adult-plant resistance to *Phytophthora capsici* in pepper. Euphytica 62, 45-49.

RENDE Q., JIANCHENG D., JIANGTAO G., ZHIMOU G., QI R.D., DING J.C., GU J.T., GAO Z.M., YUE Y.D., 2002. Preliminary studies on pathogenicity and physiological specialization of *Phytophthora capsici.* Acta Phytophylacica Sinica 29(2), 189-190.

SAS INSTITUTE INC., 1999. SAS/STAT/IML user's guide, Version 8. 4th edn., SAS Institute, Cary, NC.

STAMPS D.J., WATERHOUSE G.M., NEWHOOK F.J., HALL G.S., 1990. Revised tabular key to the species of *Phytophthora.* Mycol Papers 162, 1-28.

TIAN D., BABADOOST M., 2004. Host range of *Phytophthora capsici* from pumpkin and pathogenicity of isolates. Plant Dis 88, 485-489.

VAN DER PLANCK J.E., 1968. Disease resistance in plants. APS Press, London. 206 pp.

WALKER S.J., BOSLAND P.W., 1999. Inheritance of *Phytophthora* root rot and foliar blight resistance in pepper. J Amer Soc Hort Sci 124(1), 14-18.

WOO J., YU J., KIL K., RO P., TAE K., 2005. Changes in pathogenesis-related proteins in pepper plants with regard to biological control of phytophthora blight with *Paenibacillus illinoisensis.* BioControl 50, 165-178.