

## PHYSIOLOGICAL CHARACTERISATION OF A POPULATION OF *PHYTOPHTHORA CAPSICILEON*. FROM NORTHERN ITALY

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### SUMMARY

Among 26 isolates of *Phytophthora capsici* from pepper and zucchini plants collected mainly in Piedmont (northern Italy) 19 belonged to A1, 3 to A2 mating type and 4 were homothallic. All the isolates grew between 10 and 38°C showing significant differences in mycelial growth and optimal growth temperature in the range of 25-32°C. 65.4% of the isolates were sensitive to metalaxyl and the others moderately sensitive; nevertheless 50% of them had MIC values  $\geq 500 \mu\text{g ml}^{-1}$ . All the isolates were highly sensitive to dimethomorph, showing mean  $EC_{50}$ ,  $EC_{90}$  and MIC values of 0.48, 0.90, and  $1.02 \mu\text{g ml}^{-1}$ . A differential set of 9 plant species (pepper, tomato, eggplant, *Solanum nigrum*, melon, squash, pea, French bean and Lima bean) allowed the isolates to be grouped in 13 pathogenicity classes depending on their ability to infect different plant species; all were pathogenic on pepper, 79% on tomato, 58% on *S. nigrum*, 38% on eggplant; 95% were pathogenic on squash and 20% on melon; 33% caused a root rot on pea and 8% on French bean, but none on Lima bean. Moreover, the isolates belonging to the same pathogenicity group differed in virulence on two differential sets of pepper.

*Key words:* mating type, temperature, fungicides, wild plants, vegetables.

### INTRODUCTION

*Phytophthora capsici* Leon. is the causal agent of pepper blight, foot and root rot, a serious world-wide disease. First described on pepper (Leonian, 1922) it was then associated with blight and soft-rot of other vegetables such as melon, cucumber, watermelon, pumpkin (Kreutzer, 1937; Tompkins and Tucker, 1937, 1941; Wiant and Tucker, 1940), eggplant, tomato (Bodine,

1935; Kreutzer *et al.*, 1940) and other crops (Mchau and Coffey, 1995). In Italy *P. capsici* is also the causal agent of fruit rots on squash (*Cucurbita moscata* Duchesne ex Poiret) (Noviello *et al.*, 1977), blight of young leaves, flowers and fruits on zucchini (*Cucurbita pepo* L.) (G. Tamietti, unpublished).

The control of this fungus, based on agronomic, genetic and chemical measures (Garibaldi *et al.*, 1975; Clerjeau and Beyriès, 1977; Della Pietà *et al.*, 1980; Tamietti and Ritucci, 1986; Kim and Hwang, 1992; Hwang and Kim, 1995) is difficult and frequently ineffective. The failure of the control measures may be due to combinations of high density and virulence of the inoculum (Bowers and Mitchell, 1991), the ability of the fungus to rapidly increase its population in the presence of rainfall or irrigation (Ristaino *et al.*, 1992), and to select strains resistant to fungicides (Romano and Garibaldi, 1984; Parra and Ristaino, 1998; Pennisi *et al.*, 1998) or able to overcome the genetic resistance introduced to the commercial lines. Yet, a low effectiveness of metalaxyl and of some improved lines of pepper have been observed in fields where no selective pressure had been previously applied (G. Tamietti, unpublished). Since a better knowledge of the pathogen population may help to set-up more efficient control strategies, we tried to draw a physiological characterisation of the local population of *P. capsici* based on mating type, cardinal temperatures, fungicide behaviour, host range, and virulence on partially resistant pepper lines.

### MATERIALS AND METHODS

**Fungus isolates and inoculum preparation.** *P. capsici* was isolated mainly from diseased pepper and zucchini plants grown in the chief horticultural areas of Piedmont (northern Italy). Two isolates, P2 and P3, were kindly supplied by the Department of Plant Pathology of Naples University. More information about the isolates is given in Table 1.

*P. capsici* was sub-cultured on agarised vegetable broth (V8), pH 7.00, and stored at 10°C. Mycelial inoculum was produced by growing the fungus in Petri

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**Table 1.** Isolates of *P. capsici* studied.

Isolate	Host	Area of origin, year	Isolate	Host	Area of origin, year
P1	pepper	Fossano (CN), 1997	P14	pepper	Savigliano (CN), 1991
P2	pepper	Naples (Dpt Plant Path.)	P16	pepper	Cerasea (CN), 1991
P3	pepper	Naples (Dpt Plant Path.)	P17	pepper	Racconigi (CN), 1997
P4	pepper	Salerno (SA), 1995	P18	pepper	Frassineto Po (AL), 1991
P5	pepper	Asti (AT), 1990	P19	pepper	Cuneo (CN), 1990
P6	pepper	Santhià (VC), 1997	P20	pepper	Albenga (SV), 1996
P7	pepper	Carignano (TO), 1997	P21	pepper	Asti (AT), 1991
P8	pepper	Carmagnola (TO), 1997	P22	pepper	Asti (AT), 1996
P9	tomato	Nichelino (TO), 1996	P23	pepper	Albenga (SV), 1996
P10	pepper	Fossano (CN), 1991	P24	zucchini	Tronzano (VC), 1992
P11	pepper	Rocca de'Baldi (CN), 1991	P25	zucchini	Santhià (VC), 1993
P12	pepper	Frassineto Po (TO), 1991	P26	zucchini	Santhià (VC), 1993
P13	pepper	Casale Popolo (AL), 1991	P27	zucchini	Carrù (CN), 1996

dishes on V8 at  $25 \pm 1^\circ\text{C}$ . Zoospores were obtained by incubating 1 cm<sup>2</sup> mycelium plugs, from 7-10 day old cultures in Petri dish on diluted (20%) V8 agar, at  $25 \pm 1^\circ\text{C}$  under fluorescent light in 20 ml of soil extract. Soil extract was prepared by suspending 200 g of horticultural soil in 1000 ml of tap water and kept overnight at  $20^\circ\text{C}$ . The water phase was clarified by filtration on paper and successive centrifugation, and adjusted to pH 7.00; it was then sterilised at  $120^\circ\text{C}$ , 20 min. After 4 days the cultures were checked for the production of sporangia and cooled at  $10^\circ\text{C}$  for 10-15 min to promote the liberation of zoospores. The resulting suspensions were vigorously shaken for 5 min to obtain the incystment of all the zoospores. Cyst concentration was determined with a haemocytometer and adjusted to 25,000 cysts ml<sup>-1</sup>.

**Laboratory tests.** To identify the mating type, culture disks (5 mm in diameter) of each isolate from a 7-day old culture on V8-agar were paired with known A1 and A2 mating type isolates. The dual cultures were incubated at  $25 \pm 1^\circ\text{C}$  for 7 days in the dark and checked for oospore production.

To determine the growth cardinal temperatures, culture disks were placed at the centre of Petri plates on V8-agar (3 per temperature) and the cultures incubated in a range of temperatures between  $5-40 \pm 0.3^\circ\text{C}$ . After 5 days 2 orthogonal diameters of each colony were measured and corrected for the size of the initial agar disk (5 mm).

To assess the fungicide behaviour, 20% diluted V8-agar was amended with 0 (as control), 0.1, 1, 10, 100,

150 and 500 µg ml<sup>-1</sup> metalaxyl or 0.1, 0.5, and 1 µg ml<sup>-1</sup> dimethomorph and distributed in Petri plates. Test solutions were made by adding 1 ml 1000-fold concentrated stock solutions in methanol to 1 litre of molten, cooled (*ca*  $50^\circ\text{C}$ ) agar medium before plating (8 ml per plate). Control medium contained 0.1% methanol with no fungicides. Disks of mycelium on agar (5 mm in diameter) were obtained from actively expanding colonies of each isolate, and were placed upside down on the medium. Three plates were prepared for each isolate and fungicide concentration. Plates were incubated at  $25^\circ\text{C}$  for 5 days; after this time the diameter of the control colonies was more than 50 mm. Colony diameters (2 orthogonal diameter: 2) were measured and corrected for the size of the initial agar plug. EC<sub>50</sub>, EC<sub>90</sub> and MIC (concentration for 50, 90 and 100% effect) were calculated. The mycelium growth inhibition due to 5 µg ml<sup>-1</sup> metalaxyl was also calculated. According to the values of such parameters the isolates were assigned to decreasing classes of sensitivity, 5 for metalaxyl and 4 for dimethomorph.

All laboratory tests were independently replicated 3 times.

**Pathogenicity tests.** Ten seedlings of pepper 'Quadrato d'Asti' (QAT) (*Capsicum annuum* L.), tomato 'Bonny Best' (*Lycopersicon esculentum* Mill.), eggplant 'Bellezza nera' (*Solanum melongena* L.), *Solanum nigrum*, zucchini 'Genovese' (*Cucurbita pepo* L.), melon 'Retato degli ortolani' (*Cucumis melo* L.), pea 'Alderman' (*Pisum sativum* L.), French bean 'Sciabola rossa' (*Phaseolus vulgaris* L.), Lima bean (*Phaseolus lunatus* L.), were

inoculated as soil drench with cystospore suspensions (25,000 ml<sup>-1</sup>, 1 ml per plant) of each isolate. The inoculated plants were grown in a growth chamber under 14 h photoperiod at 25°C during the day and 23°C during the night. Every 4 days the number of the infected plants was recorded for a period of 20 days. This assay was carried out in duplicate.

'QAT' (very sensitive) and 5 selected lines obtained by crossing 'QAT' with 'PI 201234' (Tamietti and Matta, 1984) were separately inoculated with 13 *P. capsici* isolates as cystospore soil drench as previously described. The number of diseased plants was recorded weekly from day 4<sup>th</sup> to 40<sup>th</sup> after the inoculation. The trial was carried out on 20 plants (one plant per pot) and repeated a second time with similar results.

In another experiment 'QAT' and some selected breeding lines, genetically stabilised through androgenesis and differing in susceptibility to *P. capsici* (Nervo *et al.*, 1995), were inoculated by placing a pathogen culture disk on V8-agar on a transversal section made on the stem next to the first branching and protecting the inoculum with an aluminium cap. The inoculated plants were placed in a growth chamber at 25°C and 14 h photoperiod. The stem length colonised by the pathogen was recorded 3, 7 and 10 days after the inoculation. The data were statistically analysed and the means compared with Tukey's test. The experiment was performed on 7 pepper lines and 16 isolates of *P. capsici* (24 plants per isolate).

## RESULTS

Nineteen out of 26 isolates of *P. capsici* (73%) were shown to belong to the A1 mating type, 3 to the A2 mating type and 4 were self compatible.

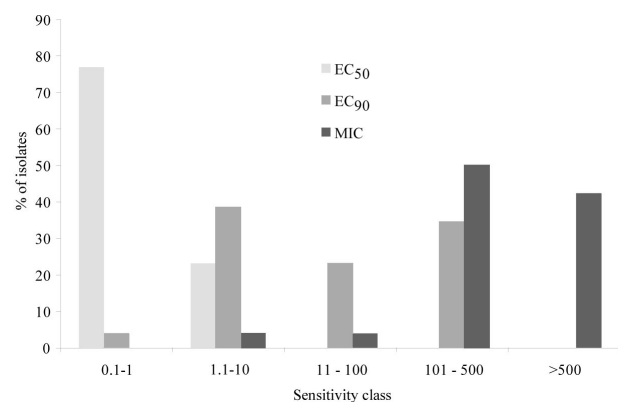
None of the tested isolates developed at 5 and 40°C, and only 50% of them developed at 7°C. All the isolates grew at 10 and 38°C. 10% of the isolates showed an optimal growth temperature of 25°C, 50% of 28°C, 40% between 30 and 32°C. The radial growth of each isolate at its optimal temperature showed striking differences among isolates, ranging between 0.49-1.06 mm per day (Table 2).

*P. capsici* isolates exhibited stronger differences in sensitivity to metalaxyl than to dimethomorph.

The EC<sub>50</sub> of metalaxyl ranged between 0.1-1 µg ml<sup>-1</sup> on 77% and between 1-10 µg ml<sup>-1</sup> on 23% of the isolates. The EC<sub>90</sub> values were comprised between 1.1-10, 11-100 or 101-500 µg ml<sup>-1</sup> on 38%, 20% and 35% respectively; only 1 isolate out of 26 had EC<sub>90</sub> less than 1 µg ml<sup>-1</sup>. The MIC values were less than 100 µg ml<sup>-1</sup> in the cases of 8% of the isolates, ranged between

**Table 2.** Growth rate (mm per day) at the optimal growth temperature of 20 *P. capsici* isolates on V8-agar.

<i>P. capsici</i> isolate	Growth rate (mm per day)	Tukey's test P = 0.01	Opt. T growth
P20	0.49	H	28
P19	0.58	H	28-30
P16	0.62	GH	30
P3	0.65	GH	25
P23	0.72	FGH	28
P24	0.74	EFGH	28
P18	0.76	DEFGH	28-32
P26	0.79	DEFG	30-32
P 10	0.81	CDEF	28
P13	0.83	CDEF	28-30
P21	0.83	CDEF	28
P27	0.83	CDEF	28
P22	0.85	CDEF	30-32
P11	0.88	CDEF	25-28
P 12	0.90	BCDE	28
P2	0.93	ABCD	32
P25	0.98	ABCD	28-32
P4	1.00	ABC	30
P5	1.00	AB	28
P9	1.06	A	28

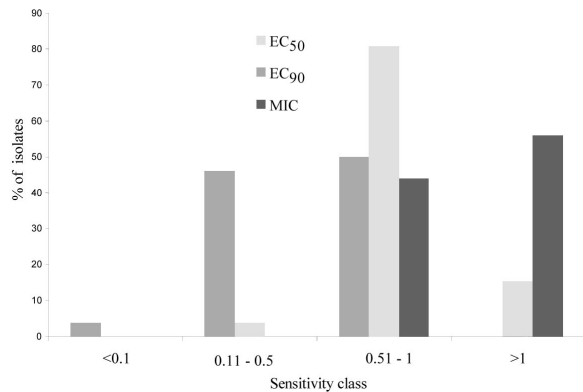


**Fig. 1.** EC<sub>50</sub>, EC<sub>90</sub>, and MIC for 23 isolates of *P. capsici* in response to metalaxyl.

101-500 µg ml<sup>-1</sup> on 50% of the isolates or were higher than 500 µg ml<sup>-1</sup> (Fig. 1).

The EC<sub>50</sub> of dimethomorph were less than 0.1 µg ml<sup>-1</sup>, between 0.11-0.5 or 0.51-1 µg ml<sup>-1</sup> on 4%, 46%, and 50% of the isolates. The EC<sub>90</sub> were between 0.51-1 µg ml<sup>-1</sup> except on 5 isolates. The MIC values of dimethomorph ranged between 0.6-1 µg ml<sup>-1</sup> or were higher than 1 µg ml<sup>-1</sup> on 44% and 56% of the isolates respectively (Fig. 2).

The isolates showed strong differences in pathogenicity on a set of different vegetable plants: all were pathogenic on pepper, 79% on tomato, 58% on *S. nigrum*, 37% on eggplant; 95% were pathogenic on zucchini and 20% on melon; 33% caused a root rot on



**Fig. 2.** EC<sub>50</sub>, EC<sub>90</sub>, and MIC for 23 isolates of *P. capsici* in response to dimethomorph.

pea and 8% on French bean, but none on Lima bean. The isolates showed to belong to 13 pathogenicity classes: 1 isolate only was specialised on pepper and 2 on pepper and zucchini; all the other isolates had 3 or more hosts and differed in their ability to cause disease in at least one species of plant (Table 3).

*P. capsici* isolates showed also differences in virulence on the susceptible pepper ‘QAT’ and on breeding lines coming from ‘QAT’ x ‘PI 201234’ selected for re-

sistance. All the tested isolates were virulent on ‘QAT’; however a few of them, namely P19, P11, P13, P10, P12, P21 were markedly more virulent on ‘QAT’ than the others. Isolates P19, P11, P13, P20, P3, P2 were also virulent, although to a different extent, on all the 5 pepper lines bred for resistance to *P. capsici*. P6 was slightly virulent on 4 resistant lines only. Isolates P10, P12, P21 were moderately virulent on 3 different sets of lines (B, C, D.1; A, B, C; A, C, D.2 respectively) and P16 on line B only; P5 and P18 were only virulent on the susceptible variety ‘QAT’ (Table 4).

Ten days after inoculation the length of the stem lesions on ‘QAT’ ranged from 90 to 147 mm depending on the isolate. Among the tested isolates P4, P24, P17 and P7 were the more and P2, P18, P5, P23 and P26 the less virulent on ‘QAT’, but their virulence rank was changing on the other pepper lines. All the lines selected for resistance and genetically stabilised through androgenesis appeared to resist to the progression of the different isolates more than ‘QAT’. Some pepper lines, such as B004DH44, C47DH9, F208DH2, appeared on the average to perform better than the other lines, although not constantly with all the isolates (Table 5).

**Table 3.** Pathogenicity of *P. capsici* isolates on 9 plant species 20 days after the inoculation with 25,000 cystospores per plant suspended in water.

Isolate	Pepper	Eggplant	Tomato	<i>S. nigrum</i>	Melon	Zucchini	Pea	F. bean	L. bean
P2	*1	0	0	0	0	0	0	0	0
P3	1	0	0	0	0	1	0	0	0
P5	1	0	0	0	0	1	0	0	0
P25	1	0	0	1	0	1	1	0	0
P20	1	0	0	1	1	1	1	0	0
P12	1	0	1	1	1	1	1	1	0
P17	1	0	1	1	1	1	0	1	0
P1	1	0	1	1	1	1	0	0	0
P8	1	0	1	1	1	1	0	0	0
P18	1	0	1	0	0	1	0	0	0
P10	1	0	1	0	0	1	0	0	0
P9	1	0	1	0	0	1	0	0	0
P16	1	0	1	1	0	1	0	0	0
P26	1	0	1	1	0	1	0	0	0
P19	1	0	1	1	0	1	0	0	0
P21	1	1	1	1	0	1	0	0	0
P24	1	1	1	1	0	1	0	0	0
P11	1	1	1	1	0	1	0	0	0
P27	1	1	1	1	0	1	1	0	0
P7	1	1	1	1	0	1	1	0	0
P4	1	1	1	0	0	1	1	0	0
P22	1	1	1	0	0	1	1	0	0
P23	1	1	1	0	0	1	1	0	0
P6	1	1	1	0	0	1	0	0	0

\* 1 = positive response; 0 = negative response.

**Table 4.** Virulence of 13 *P. capsici* isolates on 6 lines of pepper (from 'QAT' x 'PI201234') with different susceptibility to root and crown rot, expressed as disease incidence 40 days after the root inoculation with a cystospore suspension.

<i>P. capsici</i> isolates	Pepper lines					
	A	B	C	D.1	D.2	QAT
P19	50	100	54	78	75	100
P11	75	70	54	33	50	100
P13	75	70	46	78	75	100
P20	25	70	46	75	25	75
P3	25	50	23	75	63	75
P2	8	38	8	25	25	50
P6	8	10	8	0	13	88
P12	25	30	8	0	0	100
P10	0	13	23	38	0	100
P21	8	0	8	0	13	100
P16	0	10	0	0	0	38
P5	0	0	0	0	0	75
P18	0	0	0	0	0	25

**DISCUSSION**

The results confirm that *P. capsici* is a highly variable organism showing populations with a great level of diversity in temperature requirement and sensitivity to diphenylamides and dimethomorph fungicides, in pathogenicity to different crops and wild plants and in parasitic specialisation on new lines of pepper.

Waterhouse (1963) reported 11°C as minimal growth temperature for *P. capsici*. In this study, 50% of the isolates developed at 7°C, whereas, in accordance with Ho (1981) and Waterhouse (1963), all isolates grew at temperatures higher than 35°C. They also showed strong differences, between 25 and 32°C, in the optimal temperature growth and in the growth rate, as observed in previous works (Mchau and Coffey, 1995). No relation seems to exist among the optimal and the minimal and maximal growth temperatures.

**Table 5.** Virulence of some *P. capsici* isolates on a differential set of pepper, inoculated by placing a V8-disk culture on a transversal section made on the stem next to the first branching, expressed as length of the lesions (mm) 10 days after the inoculation.

Isolate	Pepper lines						
	B004 DH 44	B004 DH 16	B079 DH 3	F 208 DH 2	C47 DH 9	C47 DH 7	QAT
P7	35.2 A*	91.7 AB	77.0 ABC	57.7 A	47.6 A	68.1 BC	135.7 AB
P19	31.5 AB	69.2 BC	52.4 CD	32.6 CD	38.7 B	72.6 B	107.6 DE
P4	28.6 BC	113.5 A	97.6 A	33.3 CD	36.7 B	112.9 A	146.7 A
P23	27.0 BC	67.9 BC	30.9 DE	28.1 CDE	29.3 BCD	32.6 DE	100.4 EF
P24	25.9 BCD	93.9 AB	82.0 ABC	46.2 AB	36.9 B	61.0 BCD	145.6 A
P1	22.5 CD	52.9 CD	68.3 BC	24.4 CDE	29.4 BCD	29.0 E	126.7 BC
P27	22.1 CD	68.5 BC	64.9 BC	31.2 CD	30.8 BC	63.1 BCDE	109.5 DE
P9	21.6 CD	38.7 CDE	32.0 DE	23.7 CDE	21.1 DE	54.9 BCDE	107.6 DE
P21	22.4 CD	51.5 CD	85.7 AB	35.6 BC	30.4 BCD	41.1 CDE	112.1 DE
P12	21.8 CD	13.7 E	60.1 BC	24.9 CDE	7.2 F	40.3 CDE	127.0 BC
P26	19.5 D	18.2 DE	64.6 BC	16.6 E	6.6 F	38.9 CDE	102.0 EF
P25	18.9 D	52.0 CD	72.1 ABC	22.1 DE	22.5 CDE	29.4 E	120.2 CD
P17	21.5 CD	39.6 CDE	69.1 BC	26.9 CDE	19.5 E	32.5 DE	139.1 AB
P5	18.7 D	38.2 CDE	22.8 E	28.8 CDE	25.7 CDE	61.9 BCD	100.2 EF
P18	4.4 E	20.2 DE	10.7 E	21.1 DE	7.2 F	47.7 CDE	90.9 F
P2	2.3 E	36.0 CDE	14.7 E	33.4 CD	30.0 BCD	76.0 B	90.1 F

\* Means of a same column with a same letter are not significantly different ( $P = 00.1$ ) following the Tukey's test.

Large differences among the isolates of *P. capsici* were observed in the sensitivity to metalaxyl.

According to the criteria proposed by Parra and Ristaino (1998), 65.4% of our isolates can be considered sensitive to metalaxyl because they were inhibited by more than 60% at 5 µg ml<sup>-1</sup>, and the others intermediate, as they were inhibited by less than 60% at 5 µg ml<sup>-1</sup> and more than 60% at 100 µg ml<sup>-1</sup>. Since the intermediate isolates were obtained from plants collected in fields not treated with metalaxyl, it is likely that isolates with moderate sensitivity to this fungicide do pre-exist to the treatments in the pathogen population. This situation is similar to that previously shown in Piedmont (Tamiotti and Ritucci, 1986). Likely the substantial stability of the *P. capsici* populations is due to a reduced usage of metalaxyl on pepper and zucchini in this region. All our isolates were less sensitive to metalaxyl than strains tested by Romano and Garibaldi (1984) in Italy and Coffey and Bower (1984) in Central-America ( $EC_{50} \leq 0.1$  µg ml<sup>-1</sup>), and, with few exceptions, more sensitive than strains isolated in southern Italy (Pennisi *et al.*, 1998). These differences may reflect the level of metalaxyl usage in different times and horticultural areas.

The responses to dimethomorph, that was highly effective against all the tested isolates, appeared to be less diversified among isolates than to metalaxyl.

In contrast to the South of Italy (Pennisi *et al.*, 1998), the vast majority of the isolates collected in Piedmont both on pepper and zucchini proved to belong to the A1 mating-type, whereas only a few isolates belonged to the A2 mating-type or were homothallic. Even if the number of the A2 mating-type isolates is too small to enable a correct evaluation, the data give a rough indication that no correlation exists between mating-type and sensitivity to the tested fungicides.

The report of *P. capsici* on different hosts (Mchau and Coffey, 1995) is in itself a marker of the variability present in the pathogen population. The existence of marked pathological specialisation in *P. capsici* has been confirmed by the results of the experimental inoculations carried out on 9 plant species that allowed 13 pathogenicity groups to be distinguished. Moreover, within the same pathogenicity group the isolates differed in virulence on pepper lines. Some examples are given by the behaviour of the isolates P3 and P5 or P18 and P9 that belong to the same pathogenicity group, but showed different virulence on the pepper lines A, B, C, D<sub>1</sub> and D<sub>2</sub> of 'QAT' x 'PI 201234' or on the second differential set of pepper. The behaviour was similar in other isolates like P16 and P19, P21 and P11, P19 and P26.

Polach and Webster (1972) concluded that the pathogenicity is controlled by a separate gene or gene sys-

tem on each host species, and by two gene loci on 'Yolo Wonder' pepper, but they were unable to make hypothesis about the inheritance of the pathogenicity on Smith's 493-2 pepper (PI 201234). The inheritance of the pathogenicity of *P. capsici* was not a specific aim of this research, but the data obtained indicate that the pathogenicity on pepper is polygenic. Actually the tested isolates caused, on each pepper line, stem lesions with length increasing in a continuous way; and the percentages of diseased plants belonging to the same line varied in the same way also when the pathogen was inoculated by soil drench.

Although the temperature plays an important role in the development of the disease incidence and severity (Cristinzio and Noviello, 1980; Reifschneider *et al.*, 1986), the virulence of our isolates was neither related to the *in vitro* radial growth nor to the optimal growth temperature.

The pathological variability of *P. capsici* is a serious handicap for the breeding of resistant varieties (Clerjeau *et al.*, 1976; Palloix *et al.*, 1988). Actually we ourselves had to deal with such a difficulty several times in our attempts to improve the genetic resistance of pepper to *P. capsici*. Moreover, the broad host spectrum of the pathogen can be a serious constraint to certain control methods, such as crop rotations, in the field to control the disease.

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