PHYTOPHTHORA NICOTIANAE PATHOGENIC TO PEPPER IN NORTHWEST SPAIN

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SUMMARY

Seven strains of *Phytophthora nicotianae* were isolated from pepper plants (*Capsicum annuum*) showing collar and root rot in northwest Spain and were identified using standard taxonomic criteria. The pathogenic behaviour of the isolates was studied in *Capsicum annuum* under greenhouse and growth chamber conditions in comparison with that of *Phytophthora capsici*. Differences between isolates of the two species and great variation within the strains of *P. nicotianae* were observed. The genetic compatibility of these strains was studied and the importance of some taxonomic criteria was considered. *P. capsici* isolates were all A1 while those of *P. nicotianae* had the A2 compatibility type. Criteria for distinguishing the two species are discussed.

Key words: *Capsicum annuum,* pepper, root rot, collar rot, *Phytophthora nicotianae.*

INTRODUCTION

Phytophthora capsici Leonian (Pc) has for a long time been considered the only *Phytophthora* species pathogenic to pepper (Leonian, 1922; Tucker, 1931; Satour and Butler, 1968; Messiaen *et al*, 1991). *Phytophthora nicotianae* has been described as a pathogen of several crops including *Capsicum annuum* (Kendrick, 1923; Nolla, 1929; Tasugi and Ikeda, 1939; Borzini, 1956; Rao, 1970; Bartual *et al.*, 1991; Allagui *et al.*, 1995, Allagui and Lepoivre 1996; Erwin and Ribeiro,1996). Waterhouse (1963, 1974) and Waterhouse and Waterson (1964a, 1964b) described the varieties *nicotianae* and *parasitica* of *P. nicotianae*, but these are no longer accepted (Hall, 1993). In Europe records of *P. nicotianae* as a pathogen of pepper are few (Borzini, 1956) whereas *P. capsici* has been considered the main collar and root rot pathogen (Messiaen *et al*, 1991, Bartual *et al*, 1991; Pomar et al, 2001).

Descriptions of the symptoms of *P. nicotianae* on pepper differ among authors: some describe fruit rot (Bhardwaj and Sharma, 1985; Bhardwaj *et al.*, 1985; Ashok-Yadav *et al.*, 1995; Sharma, 1998) and seedling blight (Erwin and Ribeiro, 1996), while others report collar and root rots which later kill the plant (Borzini, 1956; Allagui *et al.*, 1995). Allagui and Lepoivre (1996) describe the symptoms of *P. nicotianae* as dry necrosis of roots and collar, rarely progressing along the stem and never affecting fruits or leaves. The death of the plant occurs late at the stage of full production. *P. capsici*, on the other hand, produces soft, water-soaked, dull green spots that rapidly elongate under favorable conditions to cover more than one-quarter of the plant. Progress of the lesions is usually more rapid along the extremities of the plant than in the centre. Infected tissues become dry, sunken, and parchment-like, turning a straw colour (Allagui and Lepoivre, 1996; Erwin and Ribeiro, 1996).

The aims of the present paper are to describe *P. nicotianae* as a pathogen of pepper in northwestern Spain and evaluate its pathogenic behaviour on *Capsicum annuum* in comparison with that of *P. capsici*.

MATERIALS AND METHODS

Fungal isolates. Nineteen fungal isolates were studied, thirteen of which were obtained from wilted plants of *C. annuum* showing collar and root rots. The diseased plants were collected from farms in northwest Spain during 2001. The other six isolates, used as reference, were supplied by the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands. The characteristics of these isolates are shown in Table 1.

Growth media and methods. Chlamydospore production and morphology of the isolates were studied on V8 medium (Tello *et al*, 1991) and potato dextrose agar (Rapilly, 1968). The isolates were grown in the dark at 25 ºC. Sporangium formation was induced by growing the isolates on 1% potassium nitrate solution under U.V. light for 8 to 12 days. For each isolate, the width and length of 25 sporangia were measured.

The growth rate at 36 ºC was measured every 24 h during 5 days, on 3 replicates per isolate, on V8 medium in the dark. Oospore production and determination of mating types were done using V8 medium.

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Table 1. Fungal isolates from *Capsicum annuum* under study.

Code	Year of isolation	Origin	Fungal species
PA-1	2001	A Coruña – Spain	*P. capsici*
PA-5	2001	A Coruña – Spain	*P. capsici*
PA-4	2001	A Coruña – Spain	*P. capsici*
RO-4	2001	A Coruña – Spain	*P. capsici*
BE-3	2001	A Coruña – Spain	*P. capsici*
BE-4	2001	A Coruña – Spain	*P. capsici*
CBS-254.93 *	1993	South Africa	*P. capsici*
CBS-554.88 *	1988	Mexico	*P. capsici*
CBS-521.77 *	1977	Netherlands	*P. capsici*
CBS-370.72 *	1972	United States	*P. capsici*
Png01	2001	Pontevedra-Spain	*P. nicotianae*
Png02	2001	Pontevedra-Spain	*P. nicotianae*
Png03	2001	Pontevedra-Spain	*P. nicotianae*
Png04	2001	Ourense-Spain	*P. nicotianae*
Png05	2001	Ourense-Spain	*P. nicotianae*
Png06	2001	Ourense-Spain	*P. nicotianae*
Png07	2001	Ourense-Spain	*P. nicotianae*
CBS-410.87 [a]	1987	Germany	*P. nicotianae*
CBS-411.87 [a]	1987	Germany	*P. nicotianae*

[a] *Phytophthora* reference isolates supplied by the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands.

The reference isolates used for determining mating types are specified in Table 1. CBS-521.77 and CBS-410.87 belong to the A1 mating type while CBS-370.72 and CBS-411.87 are A2.

Host preparation. Pepper cv California Wonder was used in inoculation tests, which were conducted under both greenhouse and growth chamber conditions. In the first, the host was grown on plastic trays in a glasshouse at 16 to 22 ºC. The rooting medium was a 1:1 mixture of peat and sand previously sterilised at 120ºC for 45 min. In the growth chamber the trays were kept at 22 -28 ºC with illumination of 30,000 lux for 16 h per day.

Inoculum and plant inoculation. Fungal cultures were grown on V8 juice agar (Erwin and Ribeiro, 1996) at room temperature (24ºC) for 7 days. Each inoculum was prepared by seeding pieces of the cultured isolate into 120 ml of sterile 1% potassium nitrate solution in six petri dishes, and growing this culture under U.V. light at 24ºC for 7 days to stimulate sporangium formation. When abundant sporangia were formed, the growth medium was replaced by sterile distilled water, the petri dishes were cooled to 5ºC for 30 min, then left at 24ºC for 3 h to stimulate discharge of zoospores. The zoospore sospension was filtered using a Whatman paper No 1, vibrated for a period of 1 min and adjusted to the inoculation dose of 20,000 zoospores ml^{-1} using a Burker camera. (Bartual *et al*., 1991). Each plant was inoculated at the 6-leaf stage by dripping 5 ml of the zoospore suspension onto the collar of each plant using a sterile micropipette (Gil Ortega *et al*., 1995).

Experimental design. The two experiments had a completely randomized design with 3 replications per isolate and 20 plants per replication-isolate interaction. Disease severity readings were made at 7, 14, 21 and 28 days post inoculation on each plant of every pot, using the following scale: 0 = no symptoms (0% of disease); 1= small rot lesions on the base of the stem, up to the30 % of diseased plants; 2 = 31-50% of diseased plants; 3 = 51-70% of diseased plants; 4 = 71-90% of diseased plants; 5 = dead plant, 100% diseased (Kim and Hwang, 1992).

Statistical analysis. The ANOVAs of disease severity readings were made after transforming the data of each plant with the following formula: $Y = \text{arc sin} \sqrt{X/100}$, where X is the disease index reading in percentage of each plant. The mean comparisons were made employing Duncan´s multiple range test. The ANOVA and mean comparison of the length/width relation of the sporangia of each isolate were made using the same test. The analyses were made using the software SAS System version 8.2.

RESULTS

Mycelium characteristics. The main mycelium characteristics are given in Table 2. All isolates produced papillate sporangia, indicating that they belong to group I or II (Stamps *et al.*, 1990).

Neither *P. nicotianae* nor *P. capsici* produced sex organs on PDA with daylight. When crosses were made between isolates of different mating types to obtain oogonia and antheridia, all isolates produced anphigynous antheridia. We confirmed the presence of abundant chlamydospores on isolates Png01, Png02, Png03, Png04, Png05, Png06 and Png07. These strains belong to *P. palmivora* MF1 and MF2 or *P. nicotianae*. *P. capsici* produced very few or no chlamydospores.

All isolates grew well at 36ºC, so the strains Png01, Png02, Png03, Png04, Png05, Png06 and Png07 could therefore be classified as *P. nicotianae* (*P. palmivora* does not grow at 36ºC). These differed from the rest in their sporangia, which were all caducous and clearly obturbinate in form. The sporangium length/width ratio, always less than 1.33, and the coralloid form of the hyphae of these strains were typical of *P. nicotianae* (Bartual *et al.*, 1991, Allagui *et al.*, 1996).

The rest of the isolates (PA-1, PA-5, PA-4, RO-4, BE-3 and BE-4) had ellipsoidal non-obturbinate sporangia, with a length/width ratio always higher than 1.7, and a non-coralloid mycelium, all typical characteristics of *P. capsici*. These isolates belonged to the A1 mating type, while the strains Png01, Png02 and Png04 were all A2.

Table 2. Morphological characteristics of the mycelium.

Isolate	chlamydospores	Growth	Sporangia			Mycelium	Antheridium	Species
		at 36 ºC	type	caducous	L/l*			
PA-1	no	yes	ellipsoidal papillate	not	1.99 b	not coralloid	anphigynous	*P. capsici*
PA-4	no	yes	ellipsoidal papillate	not	1.87 bc	not coralloid	anphigynous	*P. capsici*
BE-4	no	yes	ellipsoidal papillate	not	1.85 bc	not coralloid	anphigynous	*P.capsici*
254.93	no	yes	ellipsoidal papillate	not	1.71 c	not coralloid	anphigynous	*P.capsici*
554.88	no	yes	ellipsoidal papillate	not	2.19 a	not coralloid	anphigynous	*P.capsici*
Png01	yes	yes	obturbinate papillate	yes	1.29 d	coralloid	anphigynous	*P. nicotianae*
Png02	yes	yes	obturbinate papillate	yes	1.32 d	coralloid	anphigynous	*P. nicotianae*
Png03	yes	yes	obturbinate papillate	yes	1.18 d	coralloid	anphigynous	*P. nicotianae*
Png04	yes	yes	obturbinate papillate	yes	1.19 d	coralloid	anphigynous	*P. nicotianae*
Png05	yes	yes	obturbinate papillate	yes	1.22 d	coralloid	anphigynous	*P. nicotianae*
Png06	yes	yes	obturbinate papillate	yes	1.18 d	coralloid	anphigynous	*P. nicotianae*
Png07	yes	yes	obturbinate papillate	yes	1.27 d	coralloid	anphigynous	*P. nicotianae*
410.87	yes	yes	obturbinate papillate	yes		coralloid	anphigynous	*P. nicotianae*
411.87	yes	yes	obturbinate papillate	yes		coralloid	anphigynous	*P. nicotianae*

* Figures followed by the same letter do not significantly differ, based on Duncan´s multiple range test at P=0.05.

Table 3. Mating types of the isolates studied.

Isolate	cross with *P. capsici*		cross with *P. nicotianae*		Mating type
	A1	A2	A1	A2	
PA-1	-	+	-	+	A1
PA-5	-	+	*	+	A1
PA-4	-	+			A1
RO-4	-	+	*	+	A1
BE-3	-	+	*	+	A1
BE-4	-	+	*	+	A1
Png01	-	-	+	-	A2
Png02	-	-	+	-	A2
Png03	-	-			
Png04	-	-	+	-	A2
Png05	-	-	+	-	A2
Png06	-	-			
Png07	-	-			

+ = oospore formation within the crossing line of the two isolates.
* = scarce oospore formation outside the crossing line of the two isolates, no oospore formation within this line.
- = no oospore formation
A1, A2 = mating types.

Pathogenicity tests. The pathogenic behaviour of the strains was studied by inoculation on the same pepper variety under different temperature conditions, first in a greenhouse, then repeated in a growth chamber. The aim of these tests was to compare the progress of the infection of *P. capsici* and *P. nicotianae* on the same host.

In the greenhouse pathogenicity test, plants inoculated with isolates Png01, Png05 and Png07 (classified as *P. nicotianae*) showed severe collar and root rot symptoms 15 days post inoculation, while the disease produced by Png02 and Png04 was less severe. These symptoms were very similar to those observed on the farms. The strains PA-1, PA-5, PA-4, RO-4 and BE-4 (classified as *P. capsici*) behaved uniformly, producing collar and root rots four days post inoculation. *P. nicotianae* was in general less pathogenic but more variable in this test than *P. capsici* (Table 4, Fig. 1 and 2).

The main aim of the following test was to confirm the pathogenicity of the *P. nicotianae* isolates under high temperature conditions. Under growth chamber conditions the first symptoms on plants inoculated with *P. nicotianae* were already observed six days post inoculation. On the 8th day plants inoculated with *P. capsici* were almost dead while *P. nicotianae* only produced necrosis on the base of the inoculated plants. The pathogenicity of the *P. nicotianae* strains in this test was slightly more uniform than under greenhouse conditions but the differences with *P. capsici* were clearer (Table 5, **Fig. 3**).

Table 4. Pathogenic behaviour of five isolates each of both *P. nicotianae* and *P. capsici* under greenhouse conditions.

Isolate	Disease index	(%)	Species
Png 01	3.31 (66.21)	ab *	*P. nicotianae*
Png 02	0.48 (9.58)	e *	*P. nicotianae*
Png 04	0.33 (6.50)	e *	*P. nicotianae*
Png 05	1.62 (32.25)	d *	*P. nicotianae*
Png 07	2.75 (54.92)	c *	*P. nicotianae*
RO-4	3.67 (73.45)	a	*P. capsici*
PA-1	3.60 (72.07)	a	*P. capsici*
PA-4	3.23 (64.67)	ab	*P. capsici*
PA-5	3.65 (72.89)	a	*P. capsici*
BE-4	2.98 (59.44)	bc	*P. capsici*
Controls	0.0 (0.0)	f	Non inoculated

Disease index means on the variety California Wonder 28 days post inoculation. Disease index rated from 0 (0% disease) to 5 (100% disease). * Means followed by the same letter do not significantly differ, based on Duncan´s multiple range test at P=0.05.

Coincidence of the symptoms obtained in the pathogenicity tests with those observed on the farms, as well as the reisolation of the pathogen from the inoculated plants – Koch´s postulates – let us confirm that *P. nicotianae* is, as well as *P. capsici*, a pepper pathogen responsible for collar and root rots in the northwest of Spain (Table 6).

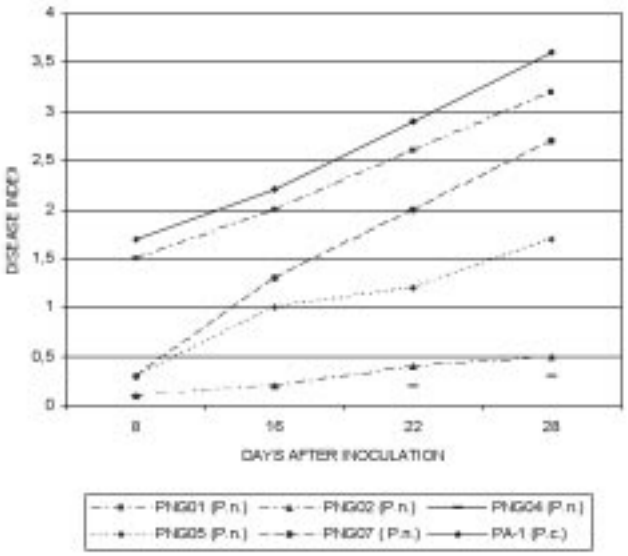

Fig. 1. Progress of infection of *P.capsici* and *P. nicotianae* under greenhouse conditions; mean disease index 8, 16, 22 and 28 days post inoculation.

Table 5. Pathogenic behaviour of five isolates each of both *P. nicotianae* and *P. capsici* under growth chamber conditions.

Isolate	Disease index	(%)	Species
Png 01	4.53 (90.53)	b *	*P. nicotianae*
Png 03	3.71 (73.94)	c *	*P. nicotianae*
Png 04	3.98 (79.55)	c *	*P. nicotianae*
Png 05	3.76 (74.91)	c *	*P. nicotianae*
Png 06	4.88 (97.67)	ab *	*P. nicotianae*
Png 07	4.57 (91.08)	ab *	*P. nicotianae*
PA-1	5.00 (100.00)	a	*P. capsici*
CBS-254.93	4.70 (93.92)	ab	*P. capsici*
Controls	0.0 (0.0)	f	Not inoculated

Disease index means on cv California Wonder 16 days post inoculation. Disease index from 0 (0% disease) to 5 (100% disease). * Figures followed by the same letter do not significantly differ, based on Duncan´s multiple range test at P=0.05.

Table 6. Reisolation of *P. nicotianae* and *P. capsici* from plants exposed to pathogenicity tests under growth chamber conditions.

Isolate	% reisolation [a]	
	P. capsici	*P. nicotianae*
Png 01	0	57
Png 03	0	63
Png 04	0	55
Png 05	0	33
Png 06	0	100
Png 07	0	77
PA-1	100	0
CBS-254.93	100	0
Controls	0	0

[a] Percentage of diseased plants with positive reisolation of the pathogen.

DISCUSSION

Identifications in this paper are based on Stamps *et al.* (1990). Papillate and caducous sporangia, anphigynous antheridia, abundance of chlamydospores and growth rate at 36ºC let us classify isolates Png 01, Png02, Png03, Png04, Png05, Png06 and Png07 as *P. nicotianae*. The dimensions of the sporangia were not an important criterion in classifying the strains, as has been previously noted by Allagui *et al.* (1995) and Tucker (1931); while the isolates classified as *P. nicotianae* always had a length/width ratio lower than 1.4 – typical of *P. nicotianae* for some authors (Waterhouse, 1963) – those of *P. capsici* varied greatly in this character.

Apart from tobacco (*Nicotiana tabacum*), *P. nicotianae* has been traditionally reported as a pathogen of citrus (Kloz *et a.l*, 1958; Tsao, 1969), of tomato (Messiaen *et al.*, 1991) and of carnation (Hine and Aragaki, 1952; Tramier and Andreoli, 1969; Tello, 1990); some authors consider it as a pathogen with a wide host range including pepper (Kendrick, 1923; Nolla, 1929; Tasugui and Ikeda, 1939; Borzini, 1956; Rao, 1970; Allagui *et al.*, 1995; Allagui and Lepoivre, 1996, Erwin and Ribeiro, 1996). In Spain Bartual *et al.* (1991) isolated *P. nicotianae* from pepper plants with collar and root rot, collected in central Spain (Ciudad Real and Toledo). Elsewhere in Europe *P. nicotianae* has only been noted as a pathogen of pepper in Italy (Borzini, 1956), being described as causing collar rot.

Most work on the interaction *P. nicotianae* – *Capsicum annuum* are from North America (Kendrick, 1923; Nolla, 1929), Japan (Tashugui and Ikeda, 1939) or India (Rao, 1970), though Allagui *et al.* (1995) and Allagui and Lepoivre, 1996) not only isolated and confirmed the pathogenicity of the fungus on pepper in Tunisia but also tested different methods of inoculation and evaluated the tolerance to the pathogen of several pepper varieties. These authors noted that zoospore injection to the collar of the plant is the most appropiate inoculation method for pathogenicity tests on *C. annuum.* Previous studies had recomended other methods with variable results: inoculation of mycelial suspension or foliar inoculation of a zoospore suspension (Ponchet *et al.*, 1975).

Variation in the progress of infection within isolates of *P. nicotianae* and in comparison with that of *P. capsici*, was also observed by Allagui and Lepoivre (1996) after inoculating several isolates of the two species on different varieties of *C. annuum*. The morphological uniformity of the former strains of *P. nicotianae* var. *nicotianae* and *P. parasitica* that led Hall (1993) to redefine

Fig. 2. Symptoms of *Phytophthora nicotianae* infection in pepper cv California Wonder: a, b, necrosis on the base of the plants; c, general view of symptoms in the growth chamber 16 days post inoculation.

the species was not accompanied by uniformity in pathogenesis.

It is also important to mention the ability of *P. nicotianae* to infect different hosts. Erwin and Ribeiro (1996) mention 301 different hosts of this pathogen including *Allium cepa*, *Dianthus caryophillus*, *Lycopersicum esculentum* and *C. annuum.* Ponchet (1975) confirmed the pathogenicity of a strain of this species, isolated from carnation plants with collar and root rot, on pepper and tomato. If this ability is also confirmed with the strains from northwest Spain, where crop rotation between tomato and pepper or the rotation from carnation to horticultural crops is frequent, the correct identification of *P. nicotianae* and *P. capsici* will be of special

importance for diagnostic laboratories and for growers, specially if we consider that persistence of the inoculum in the soil is different for the two species: *P. nicotianae* can persist in soil for longer than *P. capsici* because of its chlamydospores, as well as its tendency to homothallism.

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