Article

Phenotypic variability of *Phytophthora capsici* isolates in Guanajuato

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Abstract

Phytophthora capsici, is the causal agent of 'pepper wilt', one of the most important diseases of this crop. To establish efficient control strategies, it is necessary to know the diversity of the pathogen, for this, this research was carried out whose objective was to determine the degree of variability of 29 monozoosporic isolates obtained from pepper (*Capsicum annuum* L.) from six municipalities of the state of Guanajuato and two reference strains of A1 and A2. All were characterized by growth form, type of compatibility, growth at 35 °C, sensitivity to mefenoxam, and degree of virulence. The results obtained indicate that the isolates presented 5 forms of growth: stellate (62.5%), turulous (15.62%), stoloniferous (12.5%), filamentous (6.25%) and petaloid (3.12%); its growth at 35 °C was less than 30.7% compared to the control grown at 27 °C, its compatibility type was 65.5% of the A1 type, intermediate sensitivity to mefenoxam was found in 65.5% of the isolates, the rest being sensitive. The most virulent isolate was D3 and the avirulent ones were D8, D11 and D12, all from Dolores Hidalgo. There is no direct relationship between growth form, growth at 35 °C, type of compatibility, resistance to mefenoxam, and degree of virulence.

Keywords: pepper wilt, population diversity, sensitivity to mefenoxam.

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Introduction

Among the phytosanitary problems for the production of the pepper crop in Mexico, the 'pepper wilt' or 'drying plant' is the most important disease in all pepper-producing regions in the country. In the state of Guanajuato, about 90% of the planted area is affected to a greater or lesser degree by this disease. Under favorable conditions it can cause losses of 40 to 100% of the cultivated area. The symptomatology of this disease is associated with a group of organisms being the main *Phytophthora capsici* Leonian, a filamentous, diploid, heterothalic oomycete (Erwin and Ribeiro, 1996).

Various strategies have been developed to control this pathogen, highlighting among them: chemical and cultural control, as well as the development of resistant cultivars. If it is considered that the efficiency and durability of the control measures depend, among other factors, on the genetic variation of the pathogen, it would be important to assess it and know its distribution within and between populations of *P. capsici*, in hosts or particular regions (McDonald and Linde, 2002). The assessment of diversity at present is based mainly on morphological and physiological characteristics. Among the morphological characters, the sexual state of *Phytophthora* stands out, which involves the production of two morphologically differentiated gametangia: the oogonium, A1 female structure and the antheridium, A2 male structure (Martin *et al*., 2012).

Among the most prominent physiological features for the characterization of *Phytophthora* species are: cardinal growth temperatures, abundance of sporulation in liquid media, the appearance of colonies in culture media, and hyphal thickenings. The colonies of *P. capsici* are characterized according to the pattern they present in the culture medium, the branching of the hyphae can have a petaloid, stellate, rosette, irregular, concentric pattern and with sparse, mealy or cottony aerial mycelium and its cardinal growth temperatures are: the minimum temperature 10 °C, the optimum 28 °C and the maximum for growth greater than 35 °C (Erwin and Ribeiro, 1996).

Another of the characteristics used for the study of diversity and that also has practical implications, is resistance to fungicides such as metalaxyl and mefenoxam, fungicides commonly used worldwide for the control of this oomycete, which have been reported resistance in populations around the world (Lamour and Hausbeck, 2003). Resistant isolates have been shown to be equal to or more virulent than susceptible ones, thus making resistance to these compounds an important characteristic for the management of this disease and used as a marker to characterize populations.

Materials and methods

Strains

29 isolates of *P. capsici* identified using the keys of Erwin and Ribeiro (1996) were used, which were obtained from plants with symptoms of 'wilting', in 12 commercial production lots of different varieties and hybrids of poblano, güero, serrano, jalapeño and chilaca peppers, located in the municipalities of: Dolores Hidalgo, San Luis de la Paz, Juventino Rosas, Silao, Salvatierra and Cortazar in Guanajuato.

The reference strains for the PCT17 (A1) and PCC6 (A2) compatibility types used were donated by Dr. Sylvia Patricia Fernandez Pavia from the Plant Pathology Laboratory-UMSNH. Monozoosporic cultures were made from all the isolates including the reference strains according to the protocol of Erwin and Ribeiro (1996). The cultures were maintained in V8C solid medium (160 ml of V8 juice, 3 g $CaCO_3$ and 840 ml of deionized water), transferring them every 6 weeks.

Colony growth pattern

For the description of the growth pattern, 1 cm diameter mycelium discs were seeded from all isolates on V8C agar, incubated at 27 °C for six days in the dark. The shapes of the colonies were determined by comparing them with the patterns described by Erwin and Ribeiro (1996).

Growth at 35 °C

From each isolate, an 8 mm diameter disk with mycelium 3 to 5 days old was seeded in the center of a petri dish with V8C medium. The colony diameter was measured along two perpendicular axes, every 48 h for eight days, and the growth rate was calculated at 27 and 35 °C. Two tests with three repetitions were carried out for each isolation and the average obtained was taken as the result. The growth percentage at 35 °C was calculated considering the growth at 27 °C as 100%.

Compatibility type

The type of mating was determined by co-cultivating each of the monozoosporic isolates of *P. capsici*, with each of the strains of known compatibility type A1 and A2. The confrontations were carried out by placing in Petri dishes with V8C agar, mycelium fragments of the problem isolate and of the strain of known compatibility type, with a separation of three centimeters between them. The boxes were incubated 2.5 weeks at 27 °C in the dark. Oospore formation was examined under a microscope (10X objective). Isolates that produced oospores with strain A1, but not with A2, were determined as A2 mating type and those that produced oospores with A2 were determined as A1.

Sensitivity to mefenoxam

8 mm diameter agar discs from the 31 monozoosporic cultures were transferred to petri dishes with V8C medium with and without mefenoxam. 100 ppm of mefenoxam (Ridomil Gold-EC, Syngenta, Greensboro, NC, 48% ai) was used, added to the medium prior to being emptied into petri dishes (Lamour and Hausbeck, 2000). The plates were incubated in the dark, at 25 ºC for 7 days. The radial growth of the mycelium was evaluated every 24h, measuring the diameter in two directions (perpendicular) obtaining the average.

The relative growth percentage was calculated considering as 100% the average growth of each isolate grown in medium without mefenoxam (Lamour and Hausbeck. 2000; Fernandez-Pavia, *et al*. 2004). Two tests were carried out with three replications per isolate. The monozoosporic isolates were classified according to the scale established by Lamour and Hausbeck (2000). Being sensitive (S) those that had a relative growth less than 30%, intermediate sensitivity (SI) of 31-90% and insensitive (I) greater than 90% growth.

Virulence analysis

Three repetitions were carried out, with each isolate, using three plants/repetition in the stage of three to four true leaves of the Sonora Anaheim variety (Seminis). The inoculation was carried out by placing the seedlings in sterile flasks with 50 ml of water, to each one a solution of 10^4 zoospores ml^{-1} was added, plus an antibiotic (100 mg ml^{-1} ampicillin) to prevent the growth of bacteria.

The inoculated plants were placed in a growth chamber at 25 ºC and the damage was evaluated after 5 days, using the scale described by Parker and Grau (1992): 0: healthy plant; 1: necrosis and obstruction at the base of the stem; 2: necrosis, obstruction at the base of the stem and partial wilt; 3: necrosis, obstruction at the base of the stem, advanced wilt; 4: total death of the plant.

Results and discussion

Colony growth pattern

Five growth patterns were found in the analyzed population, the stellate type being the most frequent (62.5%), followed by filamentous (15.62%), stoloniferous (12.5%), torulous (6.25%) and petaloid (3.12%) (Figure 1). A variation in growth patterns was observed throughout the state, as well as high variability within some municipalities, such as Dolores Hidalgo, where three types of growth were found, and Cortazar, which in three samples has three types of growth.

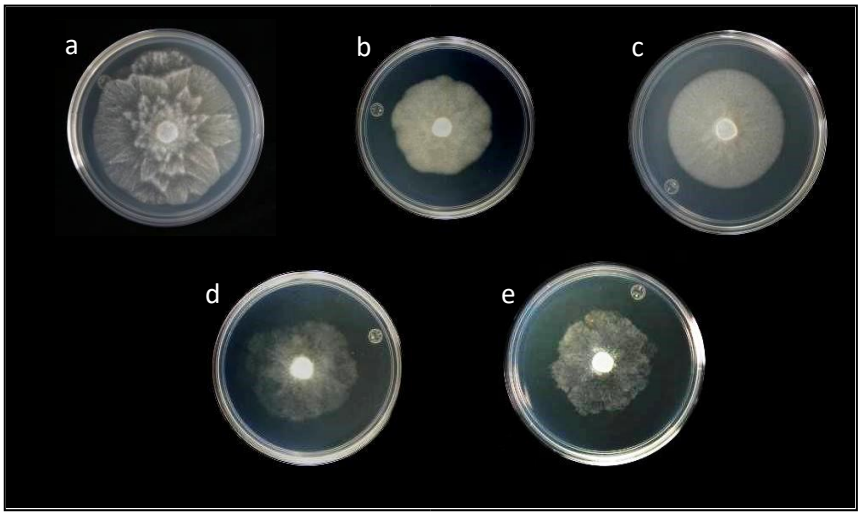

Figure 1. Morphotypes of *P. capsici* colonies from the state of Guanajuato observed in PDA. a) stellate; b) Filamentous; c) stoloniferous; d) torulous; and e) petaloid.

In contrast to Silao and San Luis de la Paz that all their isolates show a type of growth (Table 1). With a smaller sample size, a greater diversity in growth forms was observed in the state of Guanajuato than in the isolates of New Mexico, USA (Fernández-Pavia *et al*., 2004), Illinois, USA. (Islam *et al*., 2005) and Chihuahua, Mexico (Sánchez-Gurrola *et al*., 2019), coinciding with these studies that stellate growth is the most frequent.

Table 1. Morphological and physiological characteristics of 31 monoosporic cultures of *Phytophthora capsici*.

Municipality	Key	Type of pepper	Growth type	Compatibility type	Increase at 35 °C[1] (%)	Mefenoxam sensitivity[2] (100 ppm)	Virulence degree[3]
Dolores Hidalgo	D1	Poblano	Stellate	A1	15.16	SI (68%)a	2
	D2	Poblano	Stoloniferous	A2	8.74	SI (43%)c	2
	D3	Poblano	Stellate	A1	17.48	SI (63%)ab	4
	D4	Poblano	Stellate	A2	14.22	SI (55%)b	1
	D5	Poblano	Stoloniferous	A2	11.91	SI (56%)b	3
	D6	Poblano	Stellate	A2	11.86	SI (39%)c	2
	D7	Poblano	Stellate	A2	11.41	S (27%)cd	2
	D8	Poblano	Stoloniferous	A1	11.25	S (25%)d	0
	D9	Poblano	Torulous	A1	12.49	S (30%)cd	1
	D10	Poblano	Torulous	A1	0	S (18%)de	1
	D11	Poblano	Torulous	A1	7.51	SI (44%)c	0
	D12	Poblano	Torulous	A1	5.95	SI (71%)a	0
Silao	S1	Güero	Stellate	A1	19.62	SI (38%)c	1
	S2	Güero	Stellate	A2	16.62	SI (51%)bc	1
	S3	Güero	Stellate	A1	22.28	SI (48%)bc	1
	S4	Serrano	Stellate	A1	3.21	SI (52%)bc	1
	S5	Jalapeño	Stellate	A2	18.28	S (24%)d	1
	S6	Jalapeño	Stellate	A2	8.71	SI (54%)b	1
	S7	Jalapeño	Stellate	A2	16.34	S (12%)e	1
Salvatierra	SA3	Chilaca	Torulous	A1	6.6	SI (36%)cd	2
San Luis de la Paz	SP1	Poblano	Stellate	A1	18.29	S (16%)de	2
	SP2	Poblano	Stellate	A1	4.23	S (22%)d	2
	SP3	Poblano	Stellate	A2	23.32	S (15%)de	2
Juventino Rosas	J1	Jalapeño	Filamentous	A1	8.3	SI (39%)c	3
	J2	Poblano	Stellate	A1	15.32	S (18%)de	2
	J3	Jalapeño	Filamentous	A1	7.86	SI (47%)bc	2
Cortazar	CT1	Jalapeño	Stoloniferous	A1	28.37	S (28%)cd	1
	CT3	Jalapeño	Petaloid	A1	12.57	SI (40%)c	2
	CT4	Jalapeño	Stellate	A1	30.67	SI (59%)ab	2
Reference strains	PCC	SD	Stoloniferous	A2	23.21	SI (54%)b	1
	PCT	SD	Stoloniferous	A1	11.36	SI (55%)b	1

[1]= growth percentage considering 100% growth at 27 ºC; [2]= sensitivity to mefenoxam; S= sensitive; SI= intermediate sensitivity; I= insensitive; [3]= scale; 0= no symptoms; 1= stem damage; 2= partial wilt and chlorosis; 3= advanced wilt; 4= dead plant.

As in the aforementioned works, in this study, no clear relationship between the type of growth was found with the other characteristics evaluated. Variation in colony morphology has been observed in *P. capsici* for several years and is considered a first indication of the existing diversity (Bowers *et al*., 2007).

Growth at 35 °C. The average growth rate at 27 °C of the monozoosporic cultures was 12.82 mm day^{-1}, this growth was higher than that reported by Tamietti and Valentino (2001), who found for 20 isolates of *P. capsici* an average growth rate of 0.81 mm day^{-1} and the one reported by Fernández-Pavia *et al*. (2004) of 9 mm day^{-1} for New Mexico isolates grown at 30 °C.

The average growth rate of the monozoosporic cultures at 35 °C was 1.7 mm day^{-1}, varying between 0 and 3.87 mm day^{-1} (data not shown); this result is lower than that obtained by Islam *et al*. (2005), who observed that the growth rate at this temperature for isolates from Illinois ranged from 3.1 to 10.1 mm day^{-1} and that reported by Granke *et al*. (2011) who found an average growth of 3.4 mm day^{-1} in 122 isolates of *P. capsici* originating from 12 countries. The growth percentage of the Guanajuato isolates at 35 °C ranged from 0 to 30.7%, all the isolates with the exception of CT4, had a growth lower than 30% (Table 1).

This result is in contrast to that obtained for isolates from New Mexico whose growth varied between 11 and 100% (Fernández-Pavia *et al*., 2004). But it agrees with what was reported by Tlalpal-Bolaños *et al*. (1995) who report that isolates from Mexico grow poorly at this temperature.

This growth suggests that the Guanajuato isolates have less adaptation to high temperatures, this may be due to the thermal conditions in which they have evolved, since according to INEGI (2013), historically the average annual temperature in Guanajuato is 18 °C and the highest average temperature is around 30 °C and occurs in the months of May and June when the growing cycle for fresh pepper is ending in this state.

Compatibility type

All the isolates were heterothallic and the distribution of the types of compatibility in the state was random and in some fields the two types of compatibility were found coexisting, with a predominance of type A1 (65.5%) being observed in the state (Table 1).

Worldwide, the identification of both types of compatibility in *P. capsici* collections has been frequently reported by different researchers, such as Fernández-Pavia *et al*. (2004), who, when characterizing 59 isolates from southern New Mexico, USA, found a random distribution of both types of A1 and A2 compatibility and demonstrated their coexistence in a single field, pointing to A1 as the of higher frequency in a ratio of 2:1 with respect to A2. Tamietti and Valentino (2001), in a collection of 26 isolates originating from northern Italy, found 19 of type A1, 3 of type A2 and 4 heterothallic. Islam *et al*. (2005) report in a collection of 57 isolates carried out in Illinois USA, 31 of type A1 and 26 of type A2. Meitz *et al*. (2010) found 42 of type A1 and 36 of type A2 in a collection of 78 isolates from South Africa.

In Mexico, Castro-Rocha *et al*. (2016) analyzed 81 isolates of *P*. *capsici* from four states, including 14 isolates from Guanajuato. They report the presence of 32 isolates with mating type A1, 43 with type A2, and 6 homothallic in the total population. The presence of both types of compatibility has also been confirmed in pepper-producing areas in the states of Aguascalientes, Chihuahua, Mexico City, Jalisco, Michoacán and Zacatecas (Rodríguez-Moreno *et al*., 2004; Silva-Rojas *et al*., 2009; Castro-Rocha *et al*., 2016).

The presence of the two types of compatibility in Guanajuato was reported by Perez-Moreno *et al*. (2003), who when analyzing 8 isolates obtained in two municipalities of this state, report 4 of type A1 and 4 of type A2, this was confirmed by the work of Castro-Rocha *et al*. (2016) who report having found in Guanajuato 5 isolates of type A1, 6 of type A2 and 3 homothallic.

Coinciding with the results of the present work, both types of mating have been identified within the same plot by several researchers (Gobena *et al*., 2012a; Jiang *et al*., 2015; Barchenger *et al*., 2017). This indicates that the management of the disease will be more difficult, due to the genetic diversity generated by sexual reproduction, which can originate new genotypes resistant to chemical treatments or with greater pathogenic capacity or virulence and isolates capable of breaking the resistance of varieties in less time.

Sensitivity to Mefenoxam

65.5% of the isolates presented intermediate sensitivity to mefenoxam at 100 ppm, the rest being sensitive (Table 1). The growth of the mycelium of the isolates with intermediate sensitivity was malformed, with short hyphae and in some cases turulous.

The insensitivity of *P*. *capsici* isolates to this chemical compound has been reported for several years, it has been pointed out that it is due to the fact that oomycetes, although morphologically similar to true fungi, are genetically and biochemically different (Erwin and Ribeiro, 1996) and are not susceptible to most broad-spectrum fungicides, for this reason, growers tend to rely on a limited number of fungicides.

The most popular worldwide and those that have been abused in their use, are the fungicides of the phenylamide class, specifically metalaxyl and its enantiomer mefenoxam (Ridomil Gold EC) (Lamour and Hausbeck, 2000), of which has established that their mode of action is site-specific and that tolerance to them is conditioned by a single locus that has a greater effect and incomplete dominance, subject to modification by genes with minor effects (Fabritius *et al*., 1997).

Furthermore, it has been reported that insensitivity to mefenoxam also confers insensitivity to metalaxyl in field populations of *P*. *capsici* in bell pepper (Parra and Ristaino, 1998). In Guanajuato, mefenoxam and metalaxyl have been used for more than a decade in the cultivation of pepper, so the appearance of isolates insensitive to these products was to be expected.

Isolates with insensitivity to metalaxyl were reported for the first time in Guanajuato by Pérez-Moreno *et al*. (2003), who report having found nine isolates insensitive to metalaxyl. These results and those found in this work suggest that although isolates insensitive to mefenoxam have not yet been found in the state of Guanajuato, there is a tendency to develop resistance, which could be a problem in the short term.

Since, according to studies carried out by Lamour and Hausbeck (2001), once resistance to mefenoxam or metalaxyl has been established, the use of these should be limited, since the frequency of resistant isolates does not decrease for two years, even eliminating the application of the chemical and using crop rotation.

Virulence analysis

Two of the most virulent isolates D3 and D5 and the three non-virulent isolates D8, D11 and D12 found in Guanajuato, originate from the municipality of Dolores Hidalgo, which reflects a high variability in this characteristic, this could be attributed to the presence of the two types of mating in this municipality, which would suggest the existence of sexual reproduction and therefore the appearance of new pathogenic races, but when analyzing other municipalities, it is found localities such as Silao where the two types of mating were also found, but only one virulence level in their isolates and the other case is that of Juventino Rosas and Cortazar where there is only one type of compatibility and variation in the degree of virulence (Table 1).

The lack of correlation of virulence with other characteristics such as mating type, radial growth at 27 and 35 °C, agrees with the studies reported by Fernández-Pavia *et al*. (2004) and Tamietti and Valentino (2001). The high diversity in virulence present in the municipality of Dolores Hidalgo could be related to the type of host, since although it is the same type of pepper that is planted, all of them are creole varieties and practically each producer has his own variety and produces his seed, which generates a selection process.

This could have caused each creole to develop different defense mechanisms to avoid or limit the damage caused by *Phytophthora*. Thus, pathogens would have to evolve to generate new virulence mechanisms that allow them to elude host defenses. Causing the hosts to evolve to generate new defenses to face the new virulence mechanisms of the pathogens.

These reciprocal selection pressures between the virulence mechanisms of the pathogen and the defense of the plant, would be reflected in the diversity in virulence that is being found. This would have to be tested with other studies since it was not the objective of this work.

The population of *Phytophthora capsici* from Guanajuato is characterized by its high levels of diversity, similar to that reported by several authors for other populations of this pathogen (Lamour and Hausbeck, 2001; Hausbeck and Lamour, 2004; Gevens *et al*., 2008; Meitz *et al*., 2010; Lamour *et al*., 2011; Gobena *et al*., 2012b), so this diversity must be considered when designing strategies for its control.

Conclusions

There is phenotypic variability among the isolates of *P. capsici* from Guanajuato. In Guanajuato the two types of mating are found, with A1 being the predominant one. There are municipalities where the two types of compatibility coexist isolated.

A high proportion of *P. capsici* isolates have developed intermediate resistance to Mefenoxam. There is a high diversity in virulence present in the municipality of Dolores Hidalgo.

No direct relationship is observed between growth form, growth at 35 °C, type of compatibility, resistance to mefenoxam, and degree of virulence.

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