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Virulence and vegetative compatibility of Algerian isolates of *Fusarium oxysporum* f. sp. *lentis*

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Summary. Thirty-two isolates of *Fusarium oxysporum* f. sp. *lentis* (*Fol*) were obtained from wilted lentil plants collected from different lentil growing areas in north-western Algeria. Pathogenicity tests were performed on all isolates. The isolates were also assessed for vegetative compatibility using nitrate non-utilising mutants (*nit*). Isolates that formed mutual heterokaryons were placed in the same vegetative compatibility group (VCG). The *Fol* isolates represented a single race but differed in their aggressiveness on susceptible lines. In the vegetative compatibility test, three types of *nit* were obtained (*nit-1, nit-3* and Nit-M) on the basis of the phenotype. *Nit-1* mutants were the most frequent (63%), followed by Nit-M (31%) and *nit-3* (6%). On the basis of their ability to form heterokaryons, all the lentil pathogenic isolates were grouped into a single VCG 0471. This is an indication of the homogeneity of the Algerian *Fol* population.

Key words: Algeria, lentil, VCG.

Introduction

Lentil (*Lens culinaris* Med.) is one of the most important pulses after chickpea; it is a potential crop for dry areas in north-western Algeria (Setti and Bouznad, 1998). Recent surveys in Algeria indicate an increased incidence of a wilt associated with *Fusarium oxysporum* Schlecht. emend. Snyder & Hansen f. sp. *lentis* Vasud. & Srini. (*Fol*). Average losses due to lentil vascular wilt in Algeria are estimated at 10% but can reach 66% (Belabid *et al.*, 2000). The wilt can cause complete failure of the crop, especially when a warm spring is followed by a dry hot summer (Erskine and Bayaa, 1996). No physiological races (*sensu-stricto*) of the pathogen have been reported (Bayaa *et al.*, 1997). The pathogen persists in the soil as chlamydospores that remain viable for several seasons (Erskine and Bayaa, 1996).

Breeding lentil for resistance is considered the most feasible and environmentally sound means to achieve control of lentil vascular wilt (Bayaa *et al.*, 1994). However, this approach has been hampered by the appearance of physiological races (Katan *et al.*, 1994). Race development can be studied by determining the interactions between pathogen isolates and host plant genotypes in a screening test. However, such a procedure is expensive and time-consuming, and results may be equivocal because of variations in growing conditions at a given location, and /or in the planting material used in a given study (Ploetz and Correll, 1988).

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Another way of grouping *Fusarium* isolates is by their ability to form heterokaryons by anastomosis. Isolates that form heterokaryons with each other are vegetatively compatible, and belong to the same vegetative compatibility group (VCG). Because vegetatively incompatible isolates do not form heterokaryons, the potential for genetic interaction between such isolates is limited. Isolates within the same VCG often share common biological, physiological, and pathological characteristics (Ploetz and Correll, 1988).

No sexual stage is yet known for *F. oxysporum*. Consequently, heterokaryosis may play an important role in determining genetic diversity in different populations of this fungus (Puhalla, 1985).

VCG analysis has greatly facilitated studies on the identification and genetic structure of many formae speciales of F. oxysporum. These studies have made it possible to differentiate pathogenic and non-pathogenic isolates of F. o. f. sp. lycopersici (Henni et al., 1998) and of F. o. f. sp. lycopersici (Henni et al., 1998) and of F. o. f. sp. melonis (Gennari and D'Ercole, 1994), to identify physiological races of F. o. f. sp. vasinfectum (Katan and Katan, 1988) and F. o. f. sp. dianthi (Baayen and Kleijn, 1989), to establish the homogeneity between Algerian and Moroccan isolates of F. o. f. sp. albedinis (Tantaoui et al., 1996), and to differentiate formae speciales of F. oxysporum (Puhalla, 1985).

The present study reports on the use of VCGs to determine the genetic groups of a collection of isolates obtained from diseased lentil and the pathogenicity of these isolates since genetic variation could indicate variability (different races) in the local population of Fol.

Materials and methods

Culture media

Difco potato-dextrose agar (PDA) was used to isolate *Fol* from diseased plants. Lentil-dextrose (65 g of boiled lentil seeds + 20 g of dextrose per l) (Erskine *et al.*, 1990) was used to grow inoculum for the pathogenicity tests. Inoculated lentil seedlings were grown on Hoagland liquid medium (Hoagland and Arnon, 1938: in Abbas, 1995).

The media used in the vegetative compatibility study were: minimal medium (MM), with nitrate, chlorate, nitrite and hypoxantine added according to Puhalla (1985) and Correll *et al.*, (1987).

Fungal cultures and preparation of inoculum

Thirty-two isolates of *Fol* were obtained from wilted lentil plants collected from the major lentil growing areas in north-western Algeria (Belabid *et al.*, 2000) (Fig. 1) and one isolate was obtained from Tel Hadya (Syria). The fungus was isolated from the stems of wilted plants as in Bayaa *et al.* (1994). The geographical origin of the isolates is shown in Table 1.

The isolates were identified according to the identification key of *F. oxysporum* (Nelson *et al.*, 1983). The f. sp. *lentis* was defined by inoculation of the isolates on a very susceptible lentil line (ILL 4605). All isolates were single-spored and stored at 5° C in the dark in tubes containing PDA.

Inoculum was prepared by growing the fungus in 50 ml of liquid lentil-dextrose medium and incubating at 20°C for 15 days with agitation. The medium was filtered through eight layers of cheesecloth and microconidia were adjusted to 2.5×10^6 microconidia ml⁻¹ (Bayaa *et al.*, 1994).

Plant material

The *in vitro* pathogenicity test was carried out in the laboratory on five lentil lines differing in their susceptibility to the wilt fungus (ILL 5883, ILL 5588: resistant; ILL 1939, L692-16-1: susceptible; Métropole: moderately susceptible). The lines were obtained from the International Lentil *Fusarium* Wilt Nursery of ICARDA (International Center for Agricultural Research in the Dry Areas, Aleppo, Syria). The local lentil line Métropole was obtained from the ITGC (Institut Technique des Grandes Cultures de Tiaret, Algeria).

Seeds were surface-sterilised using 2% sodium hypochlorite for 3 min, rinsed in sterile water and germinated (10 seeds/pot) for 2 weeks in plastic pots containing 500 g sterilized sand. Pots were then placed in an incubator set at 20°C with a 12h day and irrigated weekly.

Inoculation

Fifteen-day-old seedlings were carefully uprooted and their roots washed under running tap water to remove excess sand. About 0.5 cm of the root tips was cut away with sterilised scissors to facilitate the entry of the pathogen into the roots. The roots were then dipped into 10 ml of inoculum for 10 min (Kannaiyan *et al.*, 1978) and placed in tubes

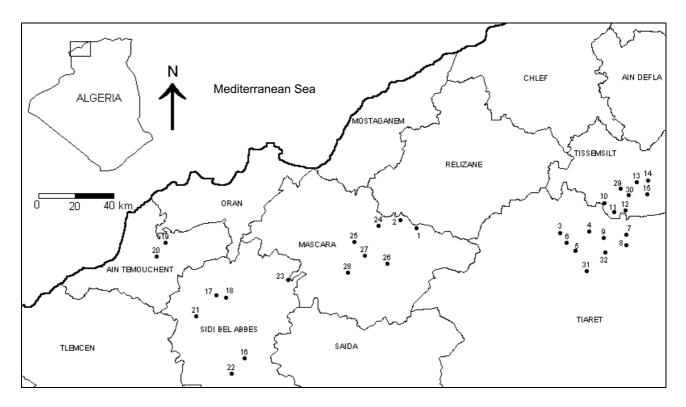


Fig. 1. Sites in Algeria from which isolates of *Fusarium oxysporum* f. sp. *lentis* were obtained. Numbers in the figure refer to numbers of isolates in Table 1.

each containing 70 ml of Hoagland liquid medium. The seedling stems were wrapped with cotton and parafilm to seal the tube. Control seedlings with cut root tips were dipped in sterilised distilled water for 10 min prior to being placed in Hoagland tubes. The tubes were incubated as above. The experiment was a split plot design with 5 replications.

Foliage alteration index

Wilt incidence was recorded from the fifth day after inoculation and continued for three weeks at 2-day intervals. Wilt severity was assessed on individual seedlingds using a 1–9 scale (Bayaa *et al.*, 1995): 1, no symptoms; 3, yellowing of the basal leaves only; 5, yellowing of 50% of the foliage; 7, complete yellowing of the foliage, flaccidity of the top leaves and partial drying; 9, whole plant or part of the plant wilted and/or dry.

After the seedlings were scored for wilt, re-isolation from the stem just above the crown was performed on Petri dishes containing PDA.

ANOVA of the incubation period (number of

days between inoculation and the death of seedlings) was carried out using the STATITCF program (Version 5, copyright 1988).

Determination of VCGs

Production of mutants

The isolates were examined for vegetative compatibility using standard procedures (Puhalla, 1985; Correll *et al.*, 1987). Nitrate non-utilising (*nit*) mutants were generated by growing isolates on minimal agar medium containing potassium chlorate. Plates (9-cm-diameter) of the chlorate media were inoculated at five points with small mycelial plugs and incubated for 7–14 days at 22°C. Chlorate-resistant sectors were screened on Puhalla minimal medium (MM) containing sodium nitrate as the sole nitrogen source. Colonies with thin expanding mycelium were considered to be *nit* mutants.

Phenotype identification

Nit mutants were grown on basal medium amended with different nitrogen sources: sodi-

Isolate	Department	Location of sampling areas	Host cultivars
1	Mascara	Tliouanet 1	Unknown
2	Mascara	Tliouanet 2	Unknown
3	Tiaret	Ain Meriem 1	Métropole
4	Tiaret	Ain Meriem 2	Métropole
5	Tiaret	Ex ITGC	Belkan 755
6	Tiaret	Ex ITGC	Belkan 755
7	Tiaret	Domaine Bouakez 1	Belkan 755
8	Tiaret	Domaine Bouakez 2	Belkan 755
9	Tiaret	Sebbaine 1	Syrie 229
10	Tissemsilt	Amouri 1	Belkan 755
11	Tissemsilt	Amouri 2	Belkan 755
12	Tissemsilt	Amouri 3	Belkan 755
13	Tissemsilt	Ouled Bessam 1	Métropole
14	Tissemsilt	Ouled Bessam 2	Métropole
15	Tissemsilt	Ouled Bessam 3	Métropole
16	Sidi-belabes	Tirmen	Unknown
17	Sidi-belabes	ITGC 1	Flip 88
18	Sidi-belabes	ITGC 2	Flip 88
19	Ain temouchent	Oulhassa	Unknown
20	Ain temouchent	Tedmaya	Unknown
21	Sidi-belabes	Lamtar	ILL 4400
22	Sidi-belabes	Tellagh	ILL 4400
23	Sidi-belabes	Sfizef	Syrie 229
24	Mascara	El-bordj	Syrie 229
25	Mascara	Mamounia	Syrie 229
26	Mascara	Sidi kada	Syrie 229
27	Mascara	F. expérimentale	ILL 1939
28	Mascara	Froha	ILL 4400
29	Tissemsilt	Tasslamt 1	Métropole
30	Tissemsilt	Tasslamt 2	Métropole
31	Tiaret	Domaine Bouhadjar	Métropole
32	Tiaret	Sebbaine 2	Syrie 229
33 (S 31 ^a)	ICARDA, Syria	Tel Hadya	ILL 4605

Table 1. Geographical origin of the *Fusarium oxysporum* f. sp. *lentis* isolates obtained from wilted lentil plant in north-western Algeria.

^a Catalog number in the ICARDA collection.

um nitrate, sodium nitrite and hypoxanthine. Petri dish cultures were incubated under the conditions described and examined after 5 days for mutant identification. On the basis of an ability to grow on the different nitrogen sources, three types of mutants were easily identified. *nit-1* mutants were mutated in a structural locus of nitrate reductase. Those mutants did not grow with nitrate as the only nitrogen source, but they did grow in the presence of nitrite or hypoxantine. *nit-3* mutants were mutated in a locus which was probably involved in the regulation of both nitrate reductase and nitrite reductase. Consequently these mutants did not grow with nitrate or nitrite as the only nitrogen source, but they did grow in the presence of hypoxanthine. Lastly, Nit-M mutants were mutated in one of the loci which were involved in the synthesis of the molybdenum co-factor, which is necessary for both the reduction of nitrate and the hydroxylation of hypoxanthine. Those mutants cannot grow on nitrate or hypoxanthine as the only nitrogen source, but they will grow on nitrite (Correll *et al.*, 1987).

Complementary tests

Vegetative compatibility was determined on the basis of the formation of heterokaryons in the contact area between the two colonies, as shown by the growth of aerial mycelium similar to that of the wild colony. A portion of the Nit-M colony was placed in the middle of the culture dish containing MM, and one portion each of *nit-1* and *nit-3* mycelium from other strains was placed at an equal distance from the Nit-M colony. Complementation between *nit-1* and *nit-3* mutants occurs less frequently than complementation between one of these mutants with a Nit-M mutant (Loffler and Rumine, 1991). Each Nit-M was paired with a *nit-*1 and a *nit-3* from other strains in all possible combinations. All pairings were replicated twice.

The cultures thus prepared were incubated as described above and examined every 5 days for 2 weeks. Complementation was indicated by the formation of a dense aerial wild-type mycelium where two mutants met and formed a heterokaryon. Absence of wild-type growth at the contact zone between two nit mutants of the same parent isolate indicated allelic, overlapping or otherwise non-complementary mutation, or vegetative self-incompatibility. On the other hand, absence of wild-type growth at the contact zone between nit mutants from different parent isolates indicated either noncomplementarity or an inability to form heterokaryons due to a lack of vegetative compatibility. When mutants of different isolates formed a heterokaryon, their parent isolates were assigned to the same VCG (Katan et al., 1994).

Results

Pathogenicity test

Typical symptoms of lentil *Fusarium* wilt were observed when seedlings of L692-16-1 and ILL 1939 (susceptible lines) were inoculated. Foliage alterations of inoculated seedlings included sudden drooping of the leaflets starting from the vegetative points and progressing downward, and finally wilting of the whole plant. All susceptible seedlings (L692-16-1 and ILL 1939) died within three weeks (disease score 9; Table 2). On the other hand, no symptoms were recorded in the resistant lines (ILL 5883 and ILL 5588). The Métropole line was moderately susceptible, with a score between 4.6 and 5.4. The behaviour of *Fol* isolates was homogeneous, with no variation in virulence. It appeared therefore that the isolates studied, including the Syrian one, were homogeneous for the character considered. It was concluded that there is only one race amongst Algerian isolates of *Fol*.

Wilt development in the susceptible L692-16-1 and ILL 1939 lines revealed variations in aggressiveness amongst isolates. Analysis of variance on the incubation period (number of days between inoculation and seedling death) showed significant differences at 5%. This incubation period varied from 7 to 24 days. Based on their aggressiveness, the isolates were divided into 3 groups (Table 3):

- highly aggressive, comprising 16 isolates (50%), which caused drying and death of seedling in 7 to 11 days, with very rapid disease progression. These isolates came mainly from Tissemsilt and Tiaret, where they represented 87 and 55% of isolate, respectively;
- moderately aggressive, represented by 11 isolates (34.3%) which caused seedling mortality in 12–17 days. The isolates in this group came mainly from Mascara and Tiaret. These two departments supplied 72% of all moderately aggressive isolates. Fifty-seven percent and 44% of Mascara and Tiaret isolates respectively were moderately aggressive;
- weakly aggressive, consisting of 5 isolates (15.6%). These isolates caused seedling death in 18–24 days. Disease progression was very slow. The isolates came from Ain Témouchent (100%) and Sidi-Belabes (50%).

VCGs

Mutant chlorate-resistant sectors were obtained from all *Fol* isolates, but there was considerable variation in their recovery rate. The spontaneous chlorate-resistant sectors recovered were unable to utilise nitrate as the sole nitrogen source, and consequently formed thin expansive colonies with no aerial mycelium on MM; these sectors were designated *nit* mutants. No correlation was found between the number of chlorate-resistant sectors and the geographic origin or aggressiveness of isolates.

The phenotypes of the *nit* mutants were determined by their colony morphology on media containing one of three nitrogen sources. *Nit* mutants fell into three phenotypic classes (*nit-1*, *nit-3* and Nit-M). The majority of *nit* mutants recovered were

Isolate	Aggressiveness ^a -			${\rm Wilt\ severity^b}$		
		L692-16-1	ILL 1939	Métropole	ILL 5883	ILL 5588
1	13.8 b	9	9	4.6	1	1
2	$13.2 \mathrm{~b}$	9	9	5	1	1
3	8.4 a	9	9	5.4	1	1
4	$13.2 \mathrm{~b}$	9	9	4.6	1	1
5	8.1 a	9	9	5.4	1	1
6	7 a	9	9	5.4	1	1
7	$13.2 \mathrm{ b}$	9	9	5	1	1
8	8.2 a	9	9	5.4	1	1
9	14 b	9	9	4.6	1	1
10	8.8 a	9	9	5.4	1	1
11	8.6 a	9	9	5	1	1
12	8.3 a	9	9	5.4	1	1
13	8.6 a	9	9	5	1	1
14	14.3 b	9	9	4.6	1	1
15	8.6 a	9	9	5.4	1	1
16	19.4 c	9	9	4.6	1	1
17	21.4 c	9	9	4.6	1	1
18	24 c	9	9	4.6	1	1
19	20.3 c	9	9	4.6	1	1
20	22.6 c	9	9	4.6	1	1
$\frac{1}{21}$	15.8 b	9	9	5	1	1
22	16.6 b	9	9	5.4	1	1
23	10.5 a	9	9	5.4	1	1
$\frac{10}{24}$	10.4 a	9	9	5.4	1	1
25	10.1 a	9	9	5	1	1
26	15.8 b	9	9	5.4	1	1
$\frac{1}{27}$	10.2 a	9	9	5.4	1	1
28	15.8 b	9	9	5	1	1
29	8.8 a	9	9	5	1	1
30	8.8 a	9	9	5.4	1	1
31	8.6 a	9	9	5.4	1	1
32	13.8 b	9	9	5	1	1
33	8.6 a	9	9	5.4	1	1
Control		1	1	1	1	1

Table 2. Aggressiveness and virulence of *Fusarium oxysporum* f. sp. *lentis* isolates inoculated on 5 different lentil lines (L692-16-1; ILL 1939; Métropole; ILL 5883; ILL 5588).

 a Aggressiveness is expressed as length of the incubation period (No. of days between inoculation and the death of seedlings) as the mean of L692-16-1 and ILL 1939.

^b Disease score in the third week according to a 1–9 scale (see Materials and methods). Means followed by the same letter in column are not different statistically (*P*<0.05) according to Newman and Keuls' test.

nit-1 mutants (62.7%), followed by Nit-M (31%) and *nit-3* (6.3%) (Table 4). Nit-M (tester), *nit-1* and *nit-*3 mutants from different isolates were compared in all possible combinations. All the *Fol* isolates formed a single VCG. No incompatibility within isolates was noted. However, there was incompatibility between the Syrian isolate and 27 Algerian isolates. The Syrian isolate was compatible only with isolates 5, 6, 9, 27 and 32, from the Tiaret and Mascara departments.

It was concluded that there is a single VCG and no correlation between the clustering of the isolates and their geographical origin or aggressiveness. The clustering of the *Fol* isolates within a

Deventoriest	Aggressiveness			
Department —	High	Moderate	Weak	Total
Ain Témouchent	$0^{a} (0)^{b}$	0 (0)	2 (100)	2 (6.2)
Sidi-Bel-Abbes	1 (16.6)	2(33.3)	3 (50)	6 (18.7)
Mascara	3(42.8)	4(57.2)	0 (0)	7(21.9)
Tissemsilt	7 (87.5)	1 (12.5)	0 (0)	8 (25)
Tiaret	5(55.5)	4 (44.4)	0 (0)	9 (28.1)
Total	16 (50)	11 (34.3)	5 (15.6)	32

Table 3. Distribution of isolate aggressiveness in relation to geographic origin.

^a No. of strains in each class of aggressiveness.

 $^{\rm b}\,$ In parentheses, percentage of isolates from each department.

Table 4. Number of each *nit*-mutant type selected on characterization media.

Isolate	Nit-M	nit-3	nit-1	Total
1	8ª (28.6) ^b	2 (7.1)	18 (64.3)	28
2	9 (50)	1(5.6)	8 (44.4)	18
3	10(45.5)	0 (0)	12(54.5)	22
4	5(20.8)	3(12.5)	16(66.7)	24
5	3(20)	1(6.7)	11(73.3)	15
6	7(35)	2(10)	11(55)	20
7	8 (34.8)	0 (0)	15(65.2)	23
8	11(35.5)	3 (9.7)	17(54.8)	31
9	12(35.3)	3(8.8)	19(55.9)	34
10	8 (53.3)	2(13.3)	5(33.3)	15
11	6(20.7)	0 (0)	23(79.3)	29
12	9 (33.3)	0 (0)	18(66.7)	27
13	3 (11.1)	0 (0)	24(88.9)	27
14	10(58.8)	2(11.8)	5(29.4)	17
15	10(33.3)	3(10)	17(56.7)	30
16	6 (18.8)	4(12.5)	22(68.8)	32
17	9 (47.4)	3(15.8)	7 (36.8)	19
18	7(33.3)	0 (0)	14(66.7)	21
19	7(22.6)	1(3.2)	23(74.2)	31
20	9 (29)	1(3.2)	21(67.7)	31
21	2(7.1)	2(7.1)	24 (85.7)	28
22	3(11.5)	1(3.8)	22(84.6)	26
23	3 (30)	1(10)	6 (60)	10
24	4(21.1)	2(10.5)	13(68.4)	19
25	8 (29.6)	3(11.1)	16(59.3)	27
26	10(41.7)	4(16.7)	10(41.7)	24
27	10 (40)	1(4)	14(56)	25
28	6 (18.8)	1(3.1)	25(78.1)	32
29	7(33.3)	0 (0)	14(66.7)	21
30	9 (52.9)	0 (0)	8(47.1)	17
31	8 (38.1)	1(4.8)	12(57.1)	21
32	7 (46.7)	2(13.3)	6 (40)	15
33	7 (36.8)	0 (0)	12(63.2)	19
Total	241 (31)	49 (6.3)	488 (62.7)	778

^a In parentheses, percentage of isolates in that group.

single VCG indicates that the genes controlling vegetative compatibility do not differ among isolates.

Discussion

The Algerian population of *Fol* isolated from the stem of wilted lentil formed a single physiological race. There was similarity between most of the Algerian population and the Syrian isolate. Erskine and Bayaa (1996) and Bayaa et al., (1997) reported that there was no evidence of physiological races of Fol in Syria. It is probable that the virulence of the population studied has not evolved, as is the case in the Syrian population. Nevertheless, Fol showed variations in aggressiveness in the populations studied. Similar results on the same formae speciales were previously reported by Abbas (1995) in Syria. The present study showed that 50% of isolates were highly aggressive and 34% moderately aggressive, distributed in almost all the Algerian lentil-producing areas (north-west). This is an important risk to local plant lines, which are moderately susceptible (Métropole) or susceptible (Syria 229). All the aggressive isolates studied came from Tissemsilt (44%) and Tiaret (31%); these two departments are the major lentil-producing areas in Algeria.

It seems also that *Fol* inoculum spreads from one region to another by external contamination of the lentil seeds (Setti and Bouznad, 1998). The exchange of contaminated seeds between farmers probably explains why populations of *Fol* are homogeneous.

Only one VCG was identified among the 32 iso-

lates of Fol, with no correlation being detected between isolate geographical origin and aggressiveness. This is the first VCG study on Fol. According to the numbering system of Puhalla (1985), the code given to F. o. f. sp. lentis is 047-, and the single VCG being described is designated VCG 0471 (Katan and Di Primo, 1999). A single VCG was also observed in other formae speciales of F. oxysporum: tracheiphilum, albedinis, lilii, basilici, matthioli, raphani, tulipae, ciceris, lactucum and melongenae (Katan, 1999). Strains within a VCG are usually more similar genetically than strains distributed across a number of VCGs (Elmer and Stephens, 1989). These findings confirmed the pathogenicity test. Virulence has been and will continue to be a very useful trait for the characterization of diversity among strains of F. oxysporum. Vegetative compatibility, however, is another useful tool for identifying diversity among strains of this fungus. Vegetatively compatible phenotypes are naturally occurring genetic markers that can be used to differentiate strains of Fol.

Isolates from the same geographical area were grouped in one VCG. Similar results have been obtained with *F*. o. f. sp. *albedinis* (Tantaoui *et al.*, 1996) and *F*. o. f. sp. *lycopersici* (Henni *et al.*, 1998). In contrast, a population from one geographical area sometimes exhibits several VCGs: *F*. o. f. sp. *lilii* (Loffler and Rumine, 1991) and *F*. o. f. sp. *melonis* (Gennari and D'Ercole, 1994).

In conclusion, the results showed the presence of a single physiological race, and for this reason, the Algerian population of *Fol* was deemed to be uniform. These results are important for breeding lentils for resistance to wilt.

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