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## Vegetative Compatibility Groups among *Fusarium solani* Isolates Causing Potato Dry Rot

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**Abstract:** Thirty-eight isolates of *Fusarium solani* from potato tubers originated from Ardabil, Tehran and Hamadan Provinces of Iran, were grouped in 15 Vegetative Compatible Groups (VCGs) using nitrate non-utilising (*nit*) mutants. Within the 15 VCGs, seven groups contained one member and the other eight groups had at least two members each. To discover any possible relationship between the Iranian VCGs determined in this research and those from New Zealand, these mutants were paired with *nit* mutants of 22 isolates from five plant species in New Zealand. Therefore, out of 60 studied isolates 24 VCGs were identified. The results revealed high genetic divergence among isolates studied. There was no correlation between VCGs and virulence; however, there was some correlation between VCGs and geographical origin of isolates.

**Key words:** VCGs, *nit* mutants, *Fusarium solani*, stored potatoes, Iran

### INTRODUCTION

*Fusarium* dry rot is a post-harvest disease of potato (*Solanum tuberosum* L.) and is of world wide significance (Hooker, 1991). Several *Fusarium* species cause potato dry rot. The predominant causal agents are *F. solani* (Mart.) Sacc. (teleomorph: *Nectria haematococca* Berk. and Broome), *F. oxysporum* Schltdl. and *F. sambucinum* Fuckel. (Hooker, 1991; Theron and Holz, 1991; Sharifi *et al.*, 2004; Nasr-Esfehami and Mortazavi, 2004). *Fusarium solani* is a soil-borne plant pathogen causing diseases on 16 different vegetable crops including peas, beans and cucurbits (Hawthorne and Rees-George, 1996). Twenty-five years ago, Puhalla developed a method by which isolates within different formae speciales of *F. oxysporum* could be classified in Vegetative Compatibility Groups (VCGs) (Swift *et al.*, 2002). Puhalla (1985) identified and classified isolates of *F. oxysporum* through genetic concepts instead of morphological criteria (growth rate, temperature tests, host range, etc.). A vegetative compatible group consists of isolates that are vegetatively compatible with other isolates (Glass and Kuldau, 1992). While sexual compatibility is usually controlled by one or several loci with two or several alleles, vegetative compatibility is mediated by multiple loci called vegetative incompatibility loci, *vic* or *het* loci (Leslie, 1993; Perkins *et al.*, 1982; Puhalla and Spieth, 1985). Determination of VCGs is a criterion to study genetic similarities and the number of VCGs for a species indicates the occurrence or the absence of sexual

reproduction between populations of that species (Kistler *et al.*, 1998). Isolates in a VCG often share pathological and physiological attributes as well as geographic origins. Consequently, vegetative compatibility has been used to study the origins of and relatedness among plant pathogenic fusaria (Swift *et al.*, 2002). Population genetic studies on 63 isolates of *F. moniliforme* (*F. verticillioides*) using VCGs as a marker accommodated the isolates into 43 VCGs and such a great degree of variation indicates the occurrence of sexual cycle in this species (Kistler *et al.*, 1998). With asexually reproducing fungi, vegetative compatible isolates are genetically more similar than incompatible ones. Isolates belonging to the same VCG are similar in their colony morphology, antibiotic production, virulence and isozyme patterns (Elmer, 1991). Compared with the more precise molecular techniques, studies with VCGs have broad application in analysing fungal populations (Douhan and Johnson, 2001). The objective of this study was to determine the regional diversity among Iran isolates of *F. solani* based on VCGs and to identify the most effective chlorate media for generation of *nit* mutants of *F. solani* for VCG complementation pairings.

### MATERIALS AND METHODS

**Fungal strains:** Thirty-eight strains were isolated from 110 potato stores with dry rot symptom in the fall of 2001 in Ardabil, Tehran and Hamadan Provinces

of Iran. Twenty-two other isolates were provided from Horticultural and Food Research Institute of New Zealand. Information on hosts and geographical

origins is given in Table 1. Conidia taken from 5-7 day old cultures on Potato Dextrose Agar (PDA) were streaked on Water Agar to obtain single spore cultures for each

Table 1: Details of Iranian and New Zealand strains of *F. solani* identified as members of multi-strain Vegetative Compatibility Groups (VCGs)

Strains	Host	Geographical origin	Pathogenicity tests results		VCG
			Tuber rot mean <sup>a</sup>	Homologous groups <sup>b</sup>	
ICMP2059	<i>Cucumis sativa</i>	NZ. Whangarei	1.67	HIJK	01
ICMP5249	<i>C. sativa</i>	NZ. Whangarei	2.83	FG	01
BTH865	<i>C. melonis</i>	NZ. Whitford	0.50	MNOP	02
BTH872	<i>C. melonis</i>	NZ. Whitford	0.33	NOP	02
BTH430	<i>Cucurbita maxima</i>	NZ. Pukekohe	0.00	P	03
BTH431	<i>C. maxima</i>	NZ. Pukekohe	0.00	P	03
BTH929	<i>C. maxima</i>	NZ. Pukekohe	0.17	OP	04
BTH930	<i>C. maxima</i>	NZ. Pukekohe	0.00	P	04
BTH931	<i>C. maxima</i>	NZ. Pukekohe	1.17	JKLM	04
ICMP7047	<i>Pisum sativum</i>	NZ. Hawkes Bay	1.33	IJKL	05
SAM67	<i>P. sativum</i>	NZ. Hawkes Bay	0.00	P	05
SAM616	<i>P. sativum</i>	NZ. Hawkes Bay	1.00	KLMN	05
SAM822	<i>P. sativum</i>	NZ. Hawkes Bay	0.00	P	05
SAM7277	<i>P. sativum</i>	NZ. Hawkes Bay	0.00	P	05
SAM434	<i>P. sativum</i>	NZ. Lincoln	3.00	BFG	06
SAM440	<i>P. sativum</i>	NZ. Lincoln	4.00	BC	06
SAM515	<i>P. sativum</i>	NZ. Hawkes Bay	0.00	P	07
SAM1021	<i>P. sativum</i>	NZ. Canterbury	1.00	KLMN	07
ICMP8587	<i>P. sativum</i>	NZ. Auckland	3.67	BCDE	08
SAM512	<i>P. sativum</i>	NZ. Hawkes Bay	0.50	MNOP	08
ICMP1998	<i>Lycopersicon esculentum</i>	NZ. Titirangi	2.33	GH	09
ICMP3730	<i>L. esculentum</i>	NZ. Titirangi	0.83	LMNO	09
F156	<i>Solanum tuberosum</i>	I. Hamadan-Kabudarahang	3.00	EFG	10
F159	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.33	IJKL	10
F159a	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.67	HIJK	10
F217	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.17	JKLM	10
F208	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	3.33	CDEF	10
F209	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	1.33	IJKL	10
F210	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	0.33	NOP	10
F211	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	2.00	HI	10
F51	<i>S. tuberosum</i>	I. Hamadan-Bahar	1.17	JKLM	11
F51a	<i>S. tuberosum</i>	I. Hamadan-Bahar	1.67	HIJK	11
F51s	<i>S. tuberosum</i>	I. Hamadan-Bahar	2.00	HI	11
F213	<i>S. tuberosum</i>	I. Hamadan-Bahar	3.00	EFG	11
F130	<i>S. tuberosum</i>	I. Ardabil-Ardabil	4.17	B	11
F130a	<i>S. tuberosum</i>	I. Ardabil-Ardabil	3.67	BCDE	11
F134	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	5.00	A	12
F135	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	4.17	B	12
F94	<i>S. tuberosum</i>	I. Tehran-Firozkuh	0.50	MNOP	12
F204	<i>S. tuberosum</i>	I. Tehran-Absard	0.00	P	13
F204s	<i>S. tuberosum</i>	I. Tehran-Absard	0.00	P	13
F218	<i>S. tuberosum</i>	I. Tehran-Absard	3.17	DEF	13
F17	<i>S. tuberosum</i>	I. Hamadan-Hamadan	3.17	DEF	14
F17b	<i>S. tuberosum</i>	I. Hamadan-Hamadan	2.83	FG	14
F36	<i>S. tuberosum</i>	I. Ardabil-Nir	1.17	JKLM	15
F36s	<i>S. tuberosum</i>	I. Ardabil-Nir	1.33	IJKL	15
F62	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	0.17	OP	16
F62s	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	0.00	P	16
F157	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	3.00	EFG	17
F219	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	3.83	BCD	17
F24	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.67	HIJK	18
F168	<i>S. tuberosum</i>	I. Ardabil-Ardabil	2.00	HI	19
F132	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.67	HIJK	20
F131	<i>S. tuberosum</i>	I. Ardabil-Ardabil	4.17	B	21
F162	<i>S. tuberosum</i>	I. Ardabil-Ardabil	1.83	HIJ	22
F60	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	1.50	IJKL	23
F155	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	3.17	DEF	24
F61	<i>S. tuberosum</i>	I. Hamadan-Kabudarahang	1.83	HIJ	?
F184	<i>S. tuberosum</i>	I. Ardabil-Ardabil	0.33	NOP	?
F207	<i>S. tuberosum</i>	I. Tehran-Firuzkuh	5.00	A	?

<sup>a</sup> = Average dry rot index value obtained from three replicates with 4 tubers 3 week post-inoculation. 0 = no dry rot; 5 = 100% dry rot. <sup>b</sup> = Homologous groups obtained by Duncan's multiple range analysis (p<0.05). There is no significant statistical difference between the isolates with similar letters. ? = The isolates it was not possible to generate a *nitM* mutant

isolate. The single-spore cultures were preserved on Synthetic Nutrient-poor Agar (SNA, Nirenberg, 1976) and stored at 4°C.

**Pathogenicity tests:** Using a sharp steel rod (2 mm diameter) two holes, 8 mm deep, were formed in tubers, one at the apical and one at the stem end. Each isolate was inoculated on 4 tubers at the two holes on each tuber (Theron and Holz, 1989). Inoculum was prepared by transferring conidia to Carnation-Leaf Agar (CLA, Nelson *et al.*, 1983) and incubating at 25°C for two weeks. Conidia were washed using sterile distilled water, counted in a haemocytometer and the suspension diluted to  $1 \times 10^4$  conidia/mL. The tubers were placed in new paper bags and incubated for two weeks in a controlled environment chamber at 10°C and 90% relative humidity. Experiments were carried out at three replicates. Tubers were cut diagonally through the inoculation points and the degree of rot estimated on a 0 to 5 scale used by Theron and Holz (1989). A completely randomized design analysis was conducted for disease severity parameter using SAS (1982). A Duncan's multiple range test was used to separate means.

#### **Media**

**Basal medium (BM):** This medium was used to prepare other media needed to determine VCGs (Correll *et al.*, 1987).

**Minimal medium (MM):** The medium was made by adding 2 g of NaNO<sub>3</sub> to 1 L of BM. This medium was sterilized and used to identify *nit* mutants and to determine VCGs through complementation tests (Correll *et al.*, 1987).

**PDC medium:** Thirty-nine grams of PDA (potato dextrose agar), 5 g agar, 15-30 g KClO<sub>3</sub> were dissolved in distilled water and mixed.

The final volume of the suspension was adjusted to 1 L by adding distilled water. The medium was used to create mutations in the isolates. First KClO<sub>3</sub> was used at the rate of 15 g L<sup>-1</sup> (1.5%) and if the actively growing sectors were not produced, the amount of KClO<sub>3</sub> was gradually increased to 30 g L<sup>-1</sup> (3%) (Correll *et al.*, 1987; Hawthorne *et al.*, 1992).

**Chlorate minimal medium 1 (MMC<sub>1</sub>):** The medium composed of L-asparagine (1.6 g), NaNO<sub>3</sub> (2 g), KClO<sub>3</sub> (30-56 g) and BM to the final volume of 1 L (by adding distilled H<sub>2</sub>O) was prepared and sterilized as above. The medium was also used to create mutants from isolates. The isolates that did not produce sectors on PDC with 3% KClO<sub>3</sub>, were transferred to MMC<sub>1</sub> with 4.5%,

then 5% KClO<sub>3</sub> and finally 5.6% for those that did not form sectors (Hawthorne *et al.*, 1992; Hawthorne and Rees-George, 1996).

**Chlorate minimal medium 2 (MMC<sub>2</sub>):** The medium was made of L-threonine (2.3 g), NaNO<sub>3</sub> (2 g), KClO<sub>3</sub> (45 g), adjusted to the final volume of 1 L by addition of BM. The medium was applied to create mutants and resulted in higher number of *nitM* mutants.

**Chlorate minimal medium 3 (MMC<sub>3</sub>):** This medium was made of urea (1 g), NaNO<sub>3</sub> (2 g), KClO<sub>3</sub> (45 g) adjusted to the final volume of 1 L by adding BM.

**Generation of *nit* mutants:** Nit mutants were generated following the method used by Correll *et al.*, (1987). A mycelial block (approximately 2 mm<sup>3</sup>) cut from PDA was transferred to the centre of Petri dishes containing PDC, MMC<sub>1</sub>, MMC<sub>2</sub> and MMC<sub>3</sub> in triplicates. The inoculated Petri dishes were incubated in the dark at 25°C for 21 days and inspected regularly. Fast-growing sectors were transferred onto Minimal Media (MM) (Hawthorne and Rees-George, 1996; Klittich and Leslie, 1988).

**Recognition of *nit* mutants:** To identify *nit* mutants, small mycelial blocks from each fungal cultures were taken from the margin of fast-growing sectors, transferred into the plates with Minimal Medium (MM) and incubated at 25°C for 4-5 days. Cultures producing characteristically thin and expansive growth with no aerial mycelium were considered *nit* mutants and were transferred to SNA slants and stored at 4°C.

**Phenotypic classification of *nit* mutants:** To identify the *nit* mutants, generated mutants were transferred as slices of 2×1×1 mm from SNA onto the following 5 media each containing a different nitrogen source (Correll *et al.*, 1987): Nitrate culture medium (that was prepared by adding 2 g NaNO<sub>3</sub> into 1 L of BM), ammonium culture medium (1 g ammonium tartrate into 1 L of BM), nitrite culture medium (0.5 g sodium nitrite into 1 L of BM), Uric acid culture medium (0.2 g uric acid into 1 L of BM) and hypoxanthine culture medium (0.2 g hypoxanthine compound into 1 L of BM). The plates were incubated at 25°C for 4 days. Then the mutants were phenotypically classified based on their mode of growth (wild-type or mutant and compared with the criteria presented in Table 2).

**Complementation tests:** All *nit* mutants were subjected to complementation tests. Three mutants that originated

Table 2: Identification of *nit* mutants of *Fusarium solani* by growing on different nitrogen sources

Mutations	Mutant designation	Grows on nitrogen sources				
		Nitrate	Nitrite	Ammonium	Hypoxanthine	Uric acid
None	Wild-type	+	+	+	+	+
Nitrate reductase structural locus	<i>nit1</i>	-	+	+	+	+
Nitrite reductase structural locus	?	-	-	+	+	+
Pathway-specific regulatory locus	<i>nit3</i>	-	-	+	+	+
Molybdenum cofactor loci	<i>nitM</i>	-	+	+	-	+
Major nitrogen regulatory locus	?	-	-	+	-	+

+: Typical wild-type growth, -: Thin growth with no aerial mycelium, ?: Mutants were not recovered

from an individual isolate (*nit<sub>1</sub>*, *nit<sub>3</sub>* and *nitM*) were plated on Minimal Media (MM), so that a 2 mm<sup>2</sup> block of *nitM* for each isolate was placed in the center of a plate containing Minimal Medium (MM) and several blocks of *nit<sub>1</sub>* and *nit<sub>3</sub>* cultures from the same isolate were placed at the distance of ca. 1-2 cm from *nitM* block in the center. The plates were incubated at 25°C for 7-14 days. The growth of aerial mycelium in confrontation between two colonies was an indicator of vegetative self-compatibility and such phenotypes were selected for the next step of studies and determination of VCGs. Absence of the aerial mycelium was taken as a sign for vegetative incompatibility and such colonies were discarded to avoid error and confusion.

**Determination of VCGs:** Different combinations of mutant forms were plated next to each other (by a distance of 1-2 cm) on MM. Development of a stable heterokaryon and appearance of wild type in the frontal area of two auxotrophic colonies was taken as a sign for compatibility of two contacting colonies.

**RESULTS**

All the isolates shown in Table 1 were tested for pathogenicity on potato cv. Ajax. First symptoms appeared at the second week after inoculation. The significant differences were found between the disease severities of *F. solani* isolates (p<0.01). Ten out of 60 isolates were non-pathogenic (Table 1). Thirty-eight *F. solani* isolates collected from Iran were grown on chlorate media (PDC, MMC1, MMC2 and MMC3). Total number of sectors was 331, out of which 263 *nit* mutants were not able to grow normally on the Minimal Medium (MM) containing sodium nitrate and 68 remaining sectors that were able to grow normally, were not considered as *nit* mutants and therefore were discarded (Table 3). Such mutants are called 'potassium chlorate resistant isolates' and these are known as chlorate resistant utilizing nitrate (Crm) (Bowden and Leslie, 1992). Five different nitrogen sources were used (added to BM) in order to identify phenotypic classes. The frequencies of *nitM*, *nit<sub>1</sub>* and *nit<sub>3</sub>* phenotypes were 13.9, 43.5 and 22.1%, respectively (Table 3).

Table 3: Frequency of phenotypic classes of *nit* mutants from 38 Iranian isolates of *Fusarium solani* on chlorate-containing media

Phenotypic classes <sup>a</sup>	No. of <i>nit</i> mutants	Percentage of <i>nit</i> mutants
<i>nit1</i>	144	43.5
<i>nit3</i>	73	22.1
<i>nitM</i>	46	13.9
Wild type	68	20.5
Total	331	

<sup>a</sup>: According to Correl *et al.* (1987)

Fifteen VCGs were determined for Iranian isolates (Table 1). For F61, F184 and F207 isolates it was not possible to generate a *nitM* mutant and therefore they did not undergo the complementation tests. Because their *nit<sub>1</sub>* and *nit<sub>3</sub>* mutants were incompatible with *nitM* mutants of other isolates, it was not possible to assign them to their relevant VCGs or to place them in independent VCGs. Therefore, their VCG status is indicated by a question mark (Table 1). Out of 15 VCGs determined for the 38 *F. solani* isolates, seven groups contained a single member and eight groups contained at least two members each. To find out the possible correlation among the VCGs identified from stored potatoes of Ardabil, Hamadan and Tehran Provinces with the VCGs of 22 isolates of *F. solani* isolated from five different host plants in New Zealand, a pairing test was carried out. The 22 New Zealand isolates were classified into nine VCGs. No compatibility was found between Iranian isolates and those from New Zealand. In total 60 isolates of *F. solani* were tested during this investigation and they were assigned to 24 VCGs. *Fusarium solani* isolates obtained from Ardabil were group 10 with 3 members, groups 11 and 15, each with 2 members and groups 18, 19, 20, 21 and 22 each with only 1 member (Table 1). Isolates from Tehran Province were placed in four groups: 10 (with 4 isolates), 12 (with 1 isolate), 13 (with 3 isolates) and 17 (with 2 isolates). To be mentioned that the corresponding VCG of an isolate out of 11 from this province was not determined (Table 1). Of 14 isolates from Hamadan Province one isolate was placed in group 10 and four isolates were classified in group 11. VCGs 12, 14 and 16 contained two members each and VCGs 23 and 24 had only one member each. Of 14 isolates from this province, one isolate were placed in an unknown group due to the absence of their *nitM* mutants (Table 1).

## DISCUSSION

For many fungi, particularly those that are plant-pathogenic, vegetative compatibility is a useful method for determination of genetic diversity within a species (Correll *et al.*, 1987; Ploetz and Shepard, 1989). In general, strains within a VCG tend to be more genetically similar than strains in different VCGs (Leslie, 1993). The results from the present investigation indicate that there is a great degree of genetic variation among isolates from different geographical origins. There was no correlation between virulence of the isolates and the VCGs. However, there was some correlation between VCGs and geographical origin of the isolates, but even isolates from the same geographic origin (in Iran) were found to be genetically diverse. Therefore, it can be predicted that there are other highly diverse populations of *F. solani* in other parts of Iran if it is investigated. Hawthorne and Rees-George (1996) have accommodated 22 isolates of *F. solani* in nine different VCGs and demonstrated high genetic variability with *F. solani*.

The high genetic diversity observed in *F. solani* populations from Iran and New Zealand might be due to the occurrence of the sexual state of the fungus and the genetic recombination that occurs as the result of sexual reproduction. Another possibility is that there are several species to be described within the *F. solani* species complex. This is already discovered that *F. solani* species complex comprises several morphologically distinct species and the taxonomy of *F. solani* needs to be revised (H. Nirenberg, BBA, Berlin, Germany, pers. comm.). Mating populations could be used as a way to reduce the complexity of the range of *F. solani*. Morphology of colonies and conidia were so diverse among the isolates studied here, but they were all within the range of *F. solani* *senso lato*. In order to correlate the great extent of variation revealed from VCGs with morphology, a comprehensive taxonomic revision is required, integrating morphological and molecular approaches, pathogenicity and VCGs.

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