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RESISTANCE OF *SOLANUM* SPECIES TO *PHYTOPHTHORA INFESTANS* EVALUATED IN THE DETACHED-LEAF AND WHOLE-PLANT ASSAYS

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Abstract

The reaction of 82 tomato genotypes belonging to 8 *Solanum* and a *Lycopersicon* species against *Phytophthora infestans* causing late blight was determined using detached-leaf and whole-plant assays. None of the test genotypes was immune or highly resistant. Of the 82 commercial and wild genotypes only TMS-2 (male-sterile and characterized by indeterminate growth) belonging to *Lycopersicon esculentum* was resistant with severity index of 2.4 in the detached-leaf assay on 0-5 scale (where 5 was highly susceptible) and percent disease index (%DI) of 23.3% under the whole-plant assay. Among the remaining genotypes, 41 were susceptible and 40 were highly susceptible under the detached-leaf assay, while 18 were susceptible and 63 were highly susceptible under the whole-plant assay. However, there was a significant difference in %DI for genotypes under the whole-plant assay. The response of whole-plants to inoculation with *P. infestans* in the detached-leaf assay was similar in all cases. The overall screening results indicate that TMS-2 is a good source of resistance and it can be useful for the development of tomato hybrid cultivars resistant to late blight.

Introduction

Tomato (*Lycopersicon esculentum* Mill) is an important vegetable of exceptionally high nutritive value and versatile food use (Afroz *et al*., 2009; Saleem *et al*., 2009; Noureen *et al*., 2010). Late blight, caused by the oomycete pathogen *Phytophthora infestans* (Mont.) de Bary, is an economically important disease of tomato (*L. esculentum*) worldwide including Pakistan (Majid *et al.,* 1992; Yan *et al.,* 2002). The causal pathogen from tomato was first described by Payen in France in 1847 (Payen, 1847**)** and has been found responsible for numerous epidemics since it was first described (Stevenson, 1997). *P. infestans* has a wider host range which includes *L. esculentum, S. tuberosum, S. sarrachoides, S. triflorum, S. dulcamara, S. sisymbriifolium, Nicotiana benthamiana* and plants of the genus *Calibrachoa* (Bectell *et al*., 2006; Dandurand *et al*., 2006; Flier *et al.,* 2003; Lebecka, 2008). *P. infestans* can attack leaves, petioles, stems, fruits and seeds of tomato (Irzhansky & Cohen 2006). Late blight disease may be initiated in nursery and adult plants by air-borne sporangia or by oospores harboring the soil and seed (Rubin & Cohen, 2004; Govers, 2005). Disease symptoms may start as water soaked, pale green irregular leaf lesions, which enlarge, turn brown, shrivel and dry out. Under conditions of moist weather, the underside of the lesions may be covered with a fine white moldy growth composed of sporangiophores and sporangia. On petioles and stems lesions appear at any point as oily, brown areas later turning into black and the whole plant may die. On fruits the disease appears as dark green to brown, greasy, irregular blotches, and fruit become shriveled at later stages. Cool, rainy weather, high relative humidity and heavy dew formation favor the infection, disease progress and sporangia production (Mohan *et al.,* 1996; Stevenson, 1997) which can destroy the unprotected crop within 10 to 14 days (Rubin & Cohen, 2004; Govers, 2005).

In Pakistan late blight was found for the first time by Majid *et al.,* (1992) in Faisalabad. Since its recognition it has been found to be a significant threat for tomato production in the country. Disease-management strategies mainly depend on fungicide applications, which are un-economical and less effective due to increasing resistance of the pathogen against fungicides (Griffith *et al*., 1992). Identification and utilization of genetic resources resistant to *P. infestans* in tomato is the only way to develop late bight-resistant tomato cultivars following appropriate breeding methods. Although vast genetic diversity exists in well adapted cultivars/germplasm in tomato in Pakistan, so far no systematic study on resistance or susceptibility level of existing tomato genetic resources has been conducted. The main objective of the present investigation was to determine the level of resistance in cultivated and wild *Solanaceous* species to identify potential germplasm resistant to late blight disease. Such information would help breeders to develop blight-resistant cultivars.

Materials and Methods

Plant material: Plant material used in the current study comprised of 55 genotypes of *L. esculentum* including 15 commonly grown cultivars (Pakit, Peelo, CC Haus, 88572, Lyp-1, H-24, Picdenato, Tibredo, Titano, T2, UC-134, Roma, Nagina, Money Maker and Riogrande), 2 genotypes of *S. chilense*, 7 of *S. pimpinellifolium*, 1 of *S. cheesmaniae*, 3 of *S. neoricki*, 4 of *S. habrochaites*, 4 of *S. peruvianum*, 3 of *S. chmielewski* and 3 of *S. pennellii* (Table 2). Tomato seeds for each genotype were germinated on moistened filter paper in Petri plates for 5-7 days in darkness at 20°C. Germinated seeds were transplanted into pots and placed in a greenhouse with day/night temperatures of 22/20°C.

Fungal culture and zoospore production: A wild type isolate of *P. infestans* was obtained from naturally infected tomato plants at NIAB, Faisalabad, Pakistan. The culture was obtained by transferring the late blight-infected tissues onto PARP medium (pimaricin + ampicillin + rifampicin + pentachloronitrobenzene agar). For zoospore production and multiplication, older leaves from the middle of the six-week-old plants of the susceptible genotype Nagina were put onto moistened filter paper in 140 mm Petri plates. The adaxial surfaces of these leaves were injured at the centre

using a sterile 10 µl micropipette tip and a 5 µl sporangial suspension, collected from PARP medium was placed on the wound of each leaf for 24 hrs at 18°C in darkness. Then 15 ml of sterilized distilled water was added to the plates and they were further incubated for 2-3 days at 18°C in darkness. The suspension was then filtered through four layers of sterile muslin cloth to remove other fragments. The zoospore suspension was adjusted in sterilized distilled water to a concentration of 5000 zoospores per ml using a haemocytometer.

Detached-leaf assay: Fully expanded leaves were detached from the middle of six-week-old test plants at the petiole in a greenhouse. Leaves were placed adaxial side up on moistened filter paper in glass Petri plates (140 mm dia.). Four leaves per genotype were placed in a Petri plate and each leaf was inoculated with a 20 µl drop of zoospore suspension at the centre on the adaxial surface after injuring with a sterile 10 µl micropipette tip. Each genotype was replicated for three times and inoculated unit was incubated in an incubator at 18°C with a 16 hr photoperiod. Experimental unit was examined 24 hr after inoculation until 7 days post inoculation. The leaf area occupied by blight lesions was estimated using the scale described by Irzhansky & Cohen (2006) after some modifications (Table 1). Individual leaf ratings for each genotype were added and means were calculated to generate the corresponding severity index (SI).

Table 1. Disease scale for rating of tomato late blight.

Disease rating	Symptoms severity for detached-leaf assay	Symptoms severity for whole-plant assay	% Disease index**	Disease response
0	No visible symptoms apparent	No visible symptoms apparent	0	Immune
1	A few minute lesions to about 10% of the total leaf area is blighted	A few minute lesions to about 10% of the total leaf area is blighted and usually confined to the 2 bottom leaves	0.01-10	Highly resistant
2	About 25% of the total leaf area is blighted	Leaves on about 25% of the total plant area are infected	10.01-25	Resistant
3	About 50% of the total leaf area is blighted	Leaves on about 50% of the total plant area are infected	25.01-40	Tolerant
4	About 75% of the total leaf area is infected	Leaves on about 75% of the total plant area are infected	40.01-60	Susceptible
5	Leaves are fully blighted	Leaves on whole plant are blighted and plant is dead	> 60.01	Highly susceptible

Whole-plant assay: Five to six-week-old greenhouse grown plants were sprayed to runoff with a hand sprayer using *P. infestans* zoospore suspension. Inoculated plants were covered with a plastic tunnel to increase humidity and kept at 18-20°C with a 16 hr photoperiod for 7-15 days. There were three replications for each genotype such that each replication had 3 plants. Data regarding the proportion of leaf and plant blighted were visually estimated by using a 0-5 scale to calculate percent disease index (%DI) (Table 1).

Results

Detached-leaf assay: Under the detached-leaf assay none of the test genotypes was found to be disease free. Data presented in Table 2 showed that the tomato genotypes tested varied for their reaction to late blight. Only one genotype, TMS-2, responded as resistant with average SI of 2.4 (Table 2). Among remaining 81 genotypes, 41 were susceptible and 40 were highly susceptible. Among susceptible genotypes some less blighted than others in this group were L06203 (*L. esculentum*); LA0722, LA1261, L03715 & L02707 (*S. pimpinellifolium*); LA2727 (*S. neoricki*), LA1353 & L06145 (*S. habrochaites*), LA0111, L06221 & LA06231 (*S. peruvianum*) and L06057 (*S. chmielewski*) with lowest SI ranges from 3.6 to 3.9. The first symptoms appeared after 48 hrs on all genotypes except TMS-2, in which disease started after 72 hrs. Complete blighting (100%) of leaves occurred in two accessions of *S. chilense* (viz. LA1963 and L06049) after 5 days.

Whole-plant assay: Variable levels of the %DI were found in all the genotypes under the whole-plant assay. None of the test genotypes was disease free. One indeterminate growth type genotype, TMS-2, was rated as resistant to late blight, 18 genotypes were susceptible and 63 were scored as highly susceptible (Table 2). Disease symptoms started on LA1963 and L06049 in the form of small lesions on the bottom leaves 72 hrs after inoculation followed by complete death of the plant within 5 to 7 days of inoculation with 100% DI. The pace of symptom development was slow in the case of TMS-2 which appeared as minor lesions on the lower leaves after 5 days post inoculation and remained localized to a few older leaves on 0-20% with 2-3 infection type range (ITR) till after 15 days of inoculation with 23.3% DI. All the genotypes classified as susceptible and highly susceptible showed blighting on more than 75% portion of the total plant within 6-7 days after inoculation.

Discussion

P. infestans has intensified its genetic variation in recent years that isolates are of high aggressiveness and high virulence. Some isolates are resistant to certain fungicides. To overcome this searching for durable resistance is an important need (Irzhansky & Cohen, 2006). Several commercial tomato cultivars commonly grown in Pakistan are susceptible to late blight and show considerable yield losses under disease-conducive conditions. The present investigations were carried out in Pakistan for the first time to determine the level of resistance of *Solanum* species against late blight and its possible utilization in breeding programs to develop blight-resistant cultivars.

Table 2. Late blight disease rating of the tomato genotypes using the detached-leaf assay in growth chamber and whole-plant assay in a greenhouse.

Solanum species/ genotype/accession	Source of seed	Country of origin	Growth habit	Detached-leaf assay			Whole-plant assay		
				ITR	SI	Disease response	ITR	% DI	Disease response
L. esculentum									
Pakit	AARI, Pakistan	-	ID	4-5	4.66	HS	4-5	75.55	HS
Peelo	AARI, Pakistan	-	D	4-5	4.44	S	4-5	73.33	HS
CC Haus	AARI, Pakistan	-	D	4-5	4.78	HS	4-5	77.78	HS
88572	AARI, Pakistan	-	D	4-5	4.42	S	4-5	84.44	HS
Lyp-1	AARI, Pakistan	-	D	4-5	4.50	HS	4-5	86.67	HS
H-24	AARI, Pakistan	-	D	4-5	4.89	HS	4-5	91.11	HS
Picdenato	AARI, Pakistan	-	D	4-5	4.58	HS	4-5	91.67	HS
Tibrido	AARI, Pakistan	-	D	4-5	4.78	HS	4-5	93.33	HS
Titano	AARI, Pakistan	-	D	4-5	4.89	HS	4-5	86.67	HS
T2	AARI, Pakistan	-	D	4-5	4.11	S	4-5	66.87	HS
UC-134	AARI, Pakistan	-	D	4-5	4.11	S	4-5	71.67	HS
Roma	AARI, Pakistan	-	D	4-5	4.58	HS	4-5	91.67	HS
Nagina	AARI, Pakistan	-	D	4-5	4.92	HS	4-5	96.67	HS
Money Maker	AARI, Pakistan	-	ID	4-5	4.56	HS	4-5	68.89	HS
Riogrande	AARI, Pakistan	-	D	4-5	4.89	HS	4-5	93.33	HS
Rio-J-400	NIAB, Pakistan	-	D	4-5	4.56	HS	4-5	79.70	HS
Rio-Mut-400	NIAB, Pakistan	-	D	4-5	4.68	HS	4-5	81.67	HS
TMS-1	NIAB, Pakistan	-	D	4-5	4.83	HS	4-5	96.67	HS
TMS-2	NIAB, Pakistan	-	ID	2-3	2.40	R	2-3	23.33	R
TMS-3	NIAB, Pakistan	-	ID	4-5	4.11	S	4-5	73.33	HS
LA1226	TGRC, USA	Ecuador	ID	4-5	4.42	S	4-5	88.40	HS
LA1673	TGRC, USA	Peru	D	4-5	4.11	S	4-5	82.20	HS
LA1286	TGRC, USA	Peru	ID	4-5	4.40	S	4-5	88.00	HS
L02875	AVRDC, Taiwan	Hungary	SD	4-5	4.71	HS	4-5	94.29	HS
L06203	AVRDC, Taiwan	Philippines	D	4-5	3.60	S	4-5	72.00	HS
L06170	AVRDC, Taiwan	Taiwan	D	4-5	4.00	S	4-5	71.67	HS
B-21	NIAB, Pakistan	-	ID	4-5	4.71	HS	4-5	82.00	HS
B-22	NIAB, Pakistan	-	D	4-5	4.68	HS	4-5	84.44	HS
B-23	NIAB, Pakistan	-	D	4-5	4.71	HS	4-5	82.20	HS
B-24	NIAB, Pakistan	-	D	4-5	4.71	HS	4-5	82.00	HS
B-25	NIAB, Pakistan	-	D	4-5	4.89	HS	4-5	88.00	HS
B-26	NIAB, Pakistan	-	ID	4-5	4.11	S	4-5	79.70	HS
B-27	NIAB, Pakistan	-	SD	4-5	4.89	HS	4-5	86.33	HS
B-28 (Round fruit)	NIAB, Pakistan	-	D	4-5	4.89	HS	4-5	91.67	HS
B-28 (Conicle fruit)	NIAB, Pakistan	-	D	4-5	4.89	HS	4-5	94.29	HS
B-29	NIAB, Pakistan	-	D	4-5	4.11	S	4-5	73.33	HS
B-30	NIAB, Pakistan	-	D	4-5	4.89	HS	4-5	91.67	HS
B-31	NIAB, Pakistan	-	D	4-5	4.50	HS	4-5	90.00	HS
PAK0010974	NARC, Pakistan	NARC, Pakistan	ID	3-5	4.00	S	3-5	60.00	S
Ch-151	NARC, Pakistan	NARC, Pakistan	D	4-5	4.11	S	4-5	63.20	HS
L04360	NARC, Pakistan	Ecuador	ID	4-5	4.89	HS	4-5	91.67	HS
Walter	NARC, Pakistan	NARC, Pakistan	ID	4-5	4.89	HS	4-5	90.00	HS
PAK140979	NARC, Pakistan	NARC, Pakistan	D	3-5	4.00	S	3-5	60.00	S
PAK10996	NARC, Pakistan	NARC, Pakistan	D	4-5	4.11	S	4-5	73.33	HS
PAK11001	NARC, Pakistan	NARC, Pakistan	ID	4-5	4.58	HS	4-5	91.67	HS
PAK10579	NARC, Pakistan	Korea	D	3-5	4.00	S	3-5	67.70	HS
CHUA F1 TYKING 5	Veitnam	-	ID	4-5	4.58	HS	4-5	81.67	HS
TOMATO F1 No. 5	Veitnam	-	ID	4-5	4.71	HS	4-5	75.55	HS
TOMATO F1 No. 7	Veitnam	-	ID	4-5	4.40	S	4-5	79.70	HS
CH-154	AVRDC Taiwan	-	SD	4-5	4.58	HS	4-5	70.71	HS
CLN-1466P	AVRDC Taiwan	-	D	4-5	4.89	HS	4-5	90.00	HS
CLN-2071C	AVRDC Taiwan	-	ID	3-5	4.00	S	3-5	67.70	HS
CLN-2366A	AVRDC Taiwan	-	D	4-5	4.89	HS	4-5	91.67	HS
PT 4664B	AVRDC Taiwan	-	D	3-5	4.00	S	3-5	72.00	HS
Jury	AARI, Pakistan	-	ID	4-5	4.83	HS	4-5	93.33	HS

Table 2. (Cont'd.).

Solanum species/ genotype/accession	Source of seed	Country of origin	Growth habit	Detached-leaf assay			Whole-plant assay		
				ITR	SI	Disease response	ITR	% DI	Disease response
S. chilense									
LA1963	TGRC, USA	Peru	D	5	5.00	HS	5	100.00	HS
L06049	AVRDC, Taiwan	Peru	D	5	5.00	HS	5	100.00	HS
S. pimpinellifolium									
LA2184	TGRC, USA	Peru	D	4-5	4.40	S	4-5	89.00	HS
LA0722	TGRC, USA	Peru	D	3-5	3.98	S	3-5	58.80	S
LA1261	TGRC, USA	Ecuador	D	3-5	3.98	S	3-5	58.00	S
L03715	AVRDC Taiwan	Peru	SD	3-5	3.75	S	3-5	57.00	S
L02707	AVRDC Taiwan	USA	SD	3-5	3.80	S	3-5	55.00	S
L04166	AVRDC Taiwan	USA	ID	3-5	4.00	S	3-5	53.71	S
L03686	NARC, Pakistan	Ecuador	D	4-5	4.58	HS	4-5	83.33	HS
S. cheesmaniae									
LA0317	TGRC, USA	Ecuador	D	3-5	4.00	S	3-5	61.30	HS
S. neoricki									
LA2727	TGRC, USA	Ecuador	D	3-5	3.57	S	3-5	59.30	S
L06188	AVRDC, Taiwan	Peru	D	4-5	4.80	HS	4-5	81.67	HS
L06238	AVRDC, Taiwan	Peru	D	3-5	4.00	S	3-5	60.00	S
S. habrochaites									
LA1353	TGRC, USA	Peru	SD	3-5	3.58	S	3-5	54.50	S
L06145	AVRDC, Taiwan	Peru	SD	3-5	3.80	S	3-5	51.33	S
L06219	AVRDC, Taiwan	Peru	SD	3-5	4.00	S	3-5	60.00	S
L06223	AVRDC, Taiwan	Peru	SD	3-5	4.00	S	3-5	57.33	S
S. peruvianum									
LA0111	TGRC, USA	Peru	D	3-5	3.80	S	3-5	59.30	S
L06221	AVRDC Taiwan	Peru	D	3-5	3.58	S	3-5	59.30	S
L06127	AVRDC Taiwan	Peru	D	4-5	4.11	S	4-5	61.00	HS
L06231	AVRDC Taiwan	Peru	D	3-5	3.98	S	3-5	60.00	S
S. chmielewski									
LA1306	TGRC, USA	Peru	SD	3-5	4.00	S	3-5	59.30	S
L06057	AVRDC, Taiwan	Peru	D	3-5	3.78	S	3-5	60.00	S
L06208	AVRDC, Taiwan	Peru	D	4-5	4.11	S	4-5	70.71	HS
S. pennellii									
L05763	AVRDC, Taiwan	Mexico	D	4-5	4.57	HS	4-5	72.00	HS
L05776	AVRDC Taiwan	Peru	D	4-5	4.40	S	4-5	70.71	HS
L06240	AVRDC Taiwan	Peru	D	4-5	4.83	HS	4-5	81.67	HS

D= Determinate type; ID= Indeterminate type; SD= Semi-determinate type; SI= Severity index; ITR= Infection type range; % DI= Percent disease index; R= Resistant; S= Susceptible; HS= Highly susceptible; NIAB= Nuclear Institute for Agriculture and Biology; AARI= Ayub Agricultural Research Institute; NARC= National Agricultural Research Council; TGRC= Tomato Genetic Resources Centre; AVRDC= Asian Vegetable Research and Development Centre

All 82 genotypes belonging to 8 *Solanum* and a *Lycopersicon* species screened for resistance to late blight became infected with *P. infestans* using both screening methods. Our results showed that the response of tested genotypes was similar under both methods. All evaluated genotypes with one exception including commercially grown cultivars have been characterized as susceptible to highly susceptible. One indeterminate growth type male-sterile genotype, TMS-2, belonging to *L. esculentum* was found resistant through both screening

methods. This cultivar showed ITR of 2 to 3 whereas other genotypes showed ITR of 4 to 5 with 75 to 100% blighting. This male-sterile genotype can be used as seed parent to develop late blight-resistant hybrids. Our results are in agreement with the previous finding of Vozdova (1975) and Paszkowska & Horodecka (1986), which screened many of *Solanum* spp., against *P. infestans* and found a few resistant to tolerant sources but were unable to find immune or highly resistant sources. However, previously three genes *Ph-1*, *Ph-2* and *Ph-3* were identified as late blight resistant from wild tomato *S. pimpinellifolium* (Irzhansky & Cohen, 2006), but in some areas these genes were unable to provide protection against the local population of the *P. infestans* (Chunwongse *et al.,* 2002; Cohen, 2002; Kim & Mutschler, 2003; Irzhansky & Cohen 2006). This strongly supports our findings for wild tomatoes.

In this study, 12 genotypes from *L. esculentum* (L06210), *S. pimpinellifolium* (LA0722, LA1261, L03715, L02707), *S. neoricki* (LA2727), *S. habrochaites* (LA1353, L06145), *S. peruvianum* (LA0111, L06221, L06231) and *S. chmielewski* (L06057) showed tolerant to susceptible response with the lowest disease severity under the detached-leaf assay, which was supported by the whole-plant assay showing the same ITR followed by less DI percentage. Performance of these genotypes against the high inoculum pressure of *P. infestans* under conducive conditions in the whole-plant assay was also susceptible with considerable DI percentage therefore, these entries were also rejected.

A plant breeding program aiming to develop disease-resistant germplasm or cultivar depends on several factors. The most important factor is the precision of the resistance assessment and successful identification of genetic source(s) of resistance (Pico *et al.*, 1998). Breeding for disease resistance requires efficient, low cost and rapid screening techniques (Foolad *et al.,* 2000). A major difficulty in breeding tomato for late blight resistance has been the screening process. Field screening is a routine procedure and cannot be treated as a reliable procedure since it is seasonal and depend on epidemic conditions. The current results were obtained through detached-leaf and whole-plant assays which showed the highest discrimination between tomato genotypes and were indicated to be efficient and reliable for screening of tomato germplasm for late blight resistance. The comparison of the results between inoculation of detached-leaves and the whole-plant assay showed no major differences. Genotypes showing resistance in the detached-leaf assay also recorded a similar response in the whole-plant assay and vice versa. On the basis of these findings it can be concluded that both methods were deemed practical in terms of screening. However, the detached-leaf assay was found to be most practical because of its simplicity which can reduce both the cost and duration of a screening programme substantially as earlier reported by Goth & Keane (1997), Nelson (2006), Irzhansky & Cohen (2006), Lebecka (2008) and many others.

The results of the present study clearly demonstrate that a good source of resistance to *P. infestans* is available in genotype TMS-2 (*S. lycopersicum*). Genetic analysis of the same study had already been published (Saleem *et al*., 2011). Further studies must be directed on utilization of this valuable male-sterile source as a female parent to develop late blight-resistant hybrid cultivars of tomato.

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