GENETIC CONTROL OF LATE BLIGHT, YIELD AND SOME YIELD RELATED TRAITS IN TOMATO (LYCOPERSICON ESCULENTUM MILL.)

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Abstract

Genetic control of late blight (LB) and some economic traits was assessed to identify genotypes suitable for the development of late blight resistant hybrids in tomato. 10 F₁ hybrids were derived from crossing of 2 male sterile lines viz., TMS1 and TMS2 with 5 elite lines viz., Nagina, Riogrande, Roma, 88572 and Picdenato according to line x tester technique. Disease resistance was measured using detached leaf and whole plant assay techniques. Data were also recorded for days to maturity, number of fruit per plant, single fruit weight and yield per plant. The analysis of variance showed significant differences among crosses, lines, testers and line x tester interaction for almost all parameters. Estimate of genetic components indicated preponderance of additive type of gene action for detached leaf assay, whole plant assay, number of fruit per plant and yield per plant whereas non-additive type of gene action for days to maturity and single fruit weight. Among parents, TMS2, Nagina, Roma and Picdenato showed significant favorable general combing ability (GCA) effects for disease rating traits while TMS1 and Riogrande indicated desirable GCA effects for yield and some yield related traits. Among hybrids, TMS2 x Roma and TMS1 x Riogrande had significant specific combing ability (SCA) effects for detached and whole plant assays. However, hybrid TMS2 x Roma appeared as good combination of LB resistance as it had both parents with desirable GCA effects. All hybrids showed average type of SCA effects for yield and yield components. Genetic control of LB revealed that a multiple crossing program involving genotypes with high GCA effects would be rewarding to identify LB resistant genotypes in early generations.

Introduction

Tomato (*Lycopersicon esculentum* Mill., 2n=2x=24) belongs to the family *Solanaceae* and is an important commercially grown vegetable all over the world. The average fruit yield of tomato from 2001-2009 in Pakistan indicates stagnant trend of 9.6–10.5 tonnes per hectare (t ha-¹) (Anon., 2009), whereas tomato production in modern agricultural areas ranges from 24–51 t ha-¹ (Anon., 2008). Due to the higher yield potential (60-80%) of hybrid cultivars than that of open pollinated varieties (Tiwari & Choudhury, 1986), the demand for hybrid seed cultivation in the country is increasing steadily amounting to US\$ 5.1 million business during June, 2009 (Anon., 2009).

At present more than 200 tomato diseases are known worldwide (Jones et al., 1997; Akhtar et al., 2008; 2010). Early and late blight diseases causing an incidence of 49-91% in conducive conditions (Azam & Shah, 2003) and lack of high yielding genotypes suitable to develop Late blight (LB) resistant cultivars/hybrids are some of the major constraints of tomato productivity in Pakistan. Cool, humid, rainy conditions favor LB infection. The LB pathogen oomycete attacks leaves, stems, fruits and seeds of tomato (Robin & Choen, 2004) and farmers rely mainly on frequent applications of fungicides for its control. However, resistance of the pathogen to fungicides often hampers the disease control. Genetic control of the resistance are conferred by single dominant, vertical genes that fit well with the hybrid breeding which is common in today's world (Scott & Gardener, 2007). In tomato, a few race-specific quantitative LB-resistance genes have been identified; Ph-1, a single dominant allele effective against race T0 of pathogen mapped on chromosome 7; Ph-2, a partially dominant allele highly effective against T0 but partially to race T1 mapped on chromosome 10 and Ph-3, a single dominant allele mapped on chromosome 9 effective against isolate Pi-16 from Taiwan that overcomes Ph-1 and Ph-2 (Irzhansky & Choen, 2006).

More recently, a new resistant gene (*Ph-5*) mapped on chromosome 1 has been identified which confers strong resistance to several pathogen isolates including those overcoming the previous resistance (Foolad *et al.*, 2008). Transfer of resistance into elite lines and or hybrids is the principal way to develop LB resistance in tomato. Using traditional and contemporary protocols of breeding, breeders have already developed LB resistant cultivars (Laterrot, 1994; Kim & Mutschuler, 2003; Foolad *et al.*, 2006) and hybrids (Guaqiang *et al.*, 2002).

Although vast genetic diversity exists in tomato genetic resources in Pakistan however, no inclusive study is available on genetic control of LB against prevalent strain of *Phytophthora infestans* in the country. On the other hand commercially available cultivars of tomato are susceptible to LB. The objective of this study was therefore, to assess the genetic control of LB and isolate high yielding tomato lines based on mode of gene action controlling the inheritance of LB. Such information will help develop blight resistant tomato cultivars/hybrids in Pakistan.

Materials and Methods

The entire experimental material of the present study comprised of determinate growth type tomato. Two male sterile lines designated as TMS1 and TMS2 were crossed with five elite genotypes viz., Nagina, Riogrande, Roma, 88572 and Picdenato following line x tester technique during 2008 (Kempthorne, 1957). The male sterile lines were used as female line whereas other genotypes were used as pollen parent or tester. Nursery seedlings of 10 F₁ hybrids were raised on well prepared seedbeds in field with day/night temperature 22/20 degree celsius (°C) in 2009. Seedlings were divided into two parts; one part for detached leaf assay and the other part for whole plant assay, yield and yield components. Hybrids were evaluated according to modified line x tester technique (Arunachalam, 1974) where crosses (hybrids) were randomized in replications without parents. This modified technique utilizes the error degree of freedom (d.f) of crosses in contrast to use combined error degree of freedom (crosses + parents) for genetic analysis. The estimates of genetic components and combining ability thus calculated are more precise and reliable (Arunachalam, 1974; Nadaranjan & Gunasekaran, 2005).

Fungal culture and zoospore production: A wild type isolate of *Phytophthora infestans* was obtained from naturally infected tomato plants at NIAB, Faisalabad, Pakistan. Culture was obtained by transferring the late blight infected tissues onto PARP medium. For zoospore production and multiplication, older leaves from the middle of six week old plants of susceptible genotype Nagina were placed on moistened filter paper in 140 millimeter (mm) Petri dishes. Adaxial surface of these leaves were injured at centre using a sterile 10 micro liter (μ l) micropipette tip. A 5 μ l sporangial suspension, collected from PARP medium (pimaricin + ampicillin + rifampicin + pentachloronitrobenzene agar) was then placed on the wound of each leaf for 24 hr at 18°C in darkness. Afterwards, 15 ml of sterilized distilled water

Disease scale for rating of tomato late blight

was added to the plates and 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. Zoospore suspension was adjusted in sterilized distilled water to a concentration of 5000 zoospore per milliliter (ml⁻¹) with haemocytometer (Akhtar *et al.*, 2011).

Detached leaf assay: Fully expended leaves of hybrids growing in nursery beds were detached from middle of the test plants at petiole from the six week old plants. Leaves were placed adaxial side up on moistened filter paper in glass Petri dishes (140 mm diameter). Four leaves per genotype were placed in a Petri dish and each leaf was inoculated with a 20µl drop of zoospore suspension at the centre on the adaxial surface after injuring with a sterile 10µl micropipette tip. Each genotype was replicated for three times and inoculated unit was incubated at 18°C for 16 hour (hr) photoperiod (Akhtar et al., 2011). Experimental unit was examined 24 hr after inoculation till 7 days post inoculation. The leaf area occupied by blight lesions was estimated following the scale described by Irzhansky & Cohen (2006) after some modifications as given under:

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

Evaluation of hybrids for whole plant assay, yield and yield components: Four week old nursery seedlings of hybrids were transplanted in the plastic tunnel following randomized complete block design (RCBD) with three replications keeping bed to bed and plant to plant distance 1.5 meter (m) and 0.5 m, respectively. Each genotype had six plants in each replication. After six weeks, plants were sprayed to run-off with hand sprayer using Phytophthora infestans zoospore suspension. Inoculated plants were kept at 18-20°C with 16 hr photoperiod for 7-15 days. Data recorded on blighted proportion of whole plant was visually estimated by using 0-5 scale to calculate disease index percentage as described earlier for detached leaf assay. Conventional agronomic practices were followed to keep the crop in good condition. At fruit ripening, data were also recorded on days to maturity, number of fruit per plant, single fruit weight (g) and fruit yield per plant (kg).

Statistical analysis: Statistical analysis of additive genetic variation (σ^2 A), dominance genetic variation (σ^2 D), variance of GCA (σ^2 GCA), variance of SCA (σ^2 SCA) for LB, yield and its related traits were performed as described by Arunachalam (1974). Broad sense heritability h²(b.s) was calculated and categorized as low (<0.3), moderate (0.3-0.6) and high (>0.6) Genetic

advance (G.A) was calculated in term of percentage of mean as low (<10%), moderate (10-20%) and high (>20%) as described by Johnson *et al.*, (1955). For detached leaf assay, whole plant assay and days to maturity, significant negative combining ability (GCA and SCA) effects were taken as high to isolate genotypes with high level of resistance/tolerance and early maturity, nonsignificant as average and significant positive as low. However, for number of fruit per plant, single fruit weight and yield per plant, significant positive GCA and SCA effects were taken as high to identify genotypes with high yield and yield components, non-significant as average and significant negative as low.

Mean square values of different traits derived through analysis of variance (Table 1) revealed highly significant differences among crosses and testers for detached leaf assay, whole plant assay, days to maturity, number of fruits per plant, single fruit weight and yield per plant. Lines were highly significant for all the traits except days to maturity and single fruit weight. Line x tester interaction was highly significant for detached leaf assay and whole plant assay, significant for days to maturity, single fruit weight and yield per plant while nonsignificant for number of fruit per plant.

Source	d.f	Detached leaf assay	Whole plant assay	Days to maturity (days)	Number of fruit per plant	Single fruit weight (g)	Yield per plant (kg)
Replications	2	0.02	3.70	8.60	28.37	24.73	0.17
Crosses	9	17.79**	12151.77**	299.06**	8691.86**	454.01**	9.43**
Lines	1	14.42**	9264.66**	13.84	6041.82**	0.01	5.34**
Testers	4	2.34**	1924.12**	190.59**	1684.68**	333.36**	2.66**
Lines ×Testers	4	1.03**	962.99**	94.62*	965.36	120.64*	1.43*
Error	18	0.30	36.71	126.41	1582.21	172.55	2.12

Table 1. Mean squares for analysis of variance in tomato genotypes.

*, ** = Significant at 0.05 and 0.01 levels of probability, respectively

Results

Estimates of genetic components and contribution of lines, testers and line x tester interaction for all the traits are presented in Table 2. The value of σ^2 GCA was higher than that of σ^2 SCA for detached leaf assay, whole plant assay, number of fruits per plant and yield per plant. However, its magnitude was lower as compared to that of σ^2 SCA for days to maturity and single fruit weight. The combining ability ratio (σ^2 GCA/ σ^2 SCA) was more than 1 for all the traits except days to maturity and single fruit weight while degree of dominance $(\sigma^2 D / \sigma^2 A)^{1/2}$ was less than 1 for all the traits except days to maturity and single fruit weight. High broad sense heritability and genetic advance was observed for detached leaf assay, whole plant assay, number of fruits per plant and yield per plant. Moderate heritability and low genetic advance was recorded for days to maturity while moderate heritability and moderate genetic advance was registered for single fruit weight. In total variance, male sterile lines contributed more than tester and line x tester interaction for detached leaf assay, whole plant assay, number of fruits per plant and yield per plant where as testers contributed more for days to maturity and single fruit weight.

The estimates of GCA effects revealed wide differences among lines and testers (Table 3). The line TMS2 was considerably better than TMS1 since it possessed highly significant negative GCA effects for detached leaf assay and whole plant assay. However, for days to maturity, it had negative but average GCA effect. TMS1 expressed significant positive desirable GCA effects for number of fruits per plant and yield per plant. Among testers, three genotypes viz., Nagina, Roma and Picdenato possessed significant negative GCA effects for detached leaf assay and whole plant assay. In contrast to Nagina and Roam, Picdenato had also significantly negative GCA effects for days to maturity. For yield and its components, Riogrande had favorable high GCA effects for single fruit weight and yield per plant whereas Picdenato had high GCA effects for number of fruit per plant.

Table 2.	Estimates of	genetic con	aponents in	tomato	genotypes.
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Source	Detached leaf assay	Whole plant assay	Days to maturity (days)	Number of fruit per plant	Single fruit weight (g)	Yield per plant (kg)
σ^2_{GCA}	0.69	441.15	0.68	284.78	1.10	0.25
σ^2_{SCA}	0.08	79.57	5.54	51.15	6.86	0.08
$\sigma^2_{GCA}/\sigma^2_{SCA}$	8.61	5.54	0.12	5.57	0.16	3.17
$\sigma_{\rm A}^2$	1.38	882.30	1.35	569.55	2.19	0.50
σ^2_{D}	0.08	79.57	5.54	51.15	6.86	0.08
$(\sigma^2_D / \sigma^2_A)^{1/2}$	0.06	0.09	4.10	0.09	3.13	0.16
$\sigma^2 g \sigma^2 p \sigma^2 p \sigma^2 e$	0.65	449.39	8.74	292.62	13.62	0.31
$\sigma^2 p$	0.67	451.43	15.76	380.52	23.21	0.43
$\sigma^2 \hat{e}$	0.02	2.04	7.02	87.90	9.59	0.12
h ² (b.s) ± SE.	0.98 ± 0.07	0.99 ± 0.82	0.55 ± 1.53	0.77 ± 5.41	0.59 ± 1.79	0.72 ± 0.20
Genetic advance in %age of means (at 5%)	46.28	73.69	2.62	48.81	12.30	37.20
Contribution of lines (%)	81.04	76.24	4.63	69.58	0.06	56.65
Contribution of tester (%)	13.18	15.83	63.73	19.38	73.42	28.23
Contribution of line x tester (%)	5.78	7.93	31.64	11.14	26.52	15.12

Table 3.	General	combining	ability	effects of	parents for	different	parameters in tomato

Parents	Detached	Whole	Days to maturity	Number of fruit	Single fruit	Yield per
	leaf assay	plant assay	(days)	per plant	weight (g)	plant (kg)
Lines						
TMS1	0.69**	17.57**	0.68	14.20**	-0.02	0.42**
TMS2	-0.69**	-17.57**	-0.68	-14.20**	0.02	-0.42**
S.E for gca of lines	0.03	0.37	0.68	2.42	0.80	0.09
Testers						
Nagina	-0.29**	-8.96**	-0.68	0.98	1.88	0.08
Riogrande	-0.20**	8.14	-0.95	0.98	4.69**	0.48**
Roma	-0.24**	-5.99**	0.51	-12.69**	0.96	-0.33*
88572	0.45**	10.99**	4.40**	-0.13	-3.16	-0.30*
Picdeneto	-0.12*	-4.18**	-3.28**	10.86*	-4.38**	0.09
S.E for gca of testers	0.05	0.58	1.08	3.83	1.26	0.14

*, ** = Significant at 0.05 and 0.01 levels of probability, respectively

The estimates of SCA effects are given in Table 4. Among hybrids, TMS1 x Riogrande and TMS2 x Roma displayed significant negative SCA effects for detached leaf and whole plant assays. Hybrids viz. TMS1 x 88572 and TMS2 x Nagina had negative and non-significant SCA effects for detached leaf assay but highly significant and negative SCA effects for whole plant assay. The hybrid TMS1 x Picdenato had negative but nonsignificant SCA effects for detached leaf assay and whole plant assay. Most of the hybrids exhibited average SCA effects for yield and yield components.

Hybrids	Detached	Whole	Days to maturity	Number of fruit	Single fruit	Yield per
Trybrius	leaf assay	plant assay	(days)	per plant	weight (g)	plant (kg)
TMS1 x Nagina	0.14	4.26**	-1.62	-0.28	1.94	-0.08
TMS1 x Riogrande	-0.28**	-4.31**	0.99	2.11	-1.32	0.06
TMS1 x Roma	0.26**	8.23**	1.00	-10.21	-2.59	-0.35
TMS1 x 88572	-0.03	-7.46**	-2.54	7.10	-0.74	0.32
TMS1 x Picdeneto	-0.09	-0.72	2.17	1.28	2.71	0.05
TMS2 x Nagina	-0.14	-4.26**	1.62	0.28	-1.94	0.08
TMS2 x Riogrande	0.28**	4.31**	-0.99	-2.11	1.32	-0.06
TMS2 x Roma	-0.26**	-8.23**	-1.00	10.21	2.59	0.35
TMS2 x 88572	0.03	7.46**	2.54	-7.10	0.74	-0.32
TMS2 x Picdeneto	0.09	0.72	-2.17	-1.28	-2.71	-0.05
S.E for hybrids	0.07	0.82	1.53	5.41	1.79	0.20

 Table 4. Specific combining ability effects of parents for different parameters in tomato.

*, ** = Significant at 0.05 and 0.01 levels of probability, respectively

Discussion

In the current investigation, the sample of crosses was sufficient to generate information on genetic control of late blight. After the emergence of seedlings from the soil, the LB may be instigated by air borne sporangia or by oospore of Phytophthora infestans anchoraging the soil or seed. Information about the genetic mechanism controlling LB in tomato is therefore, essential to start a breeding program judiciously. Significant differences among crosses, lines, testers and line x tester indicated the presence of enough genetic variability to be maneuvered for the improvement of blight resistance, yield and yield traits. Comparative analysis of magnitudes of σ^2 GCA, σ^2 SCA, σ^2 GCA/ σ^2 SCA and $(\sigma^2 D/\sigma^2 A)^{1/2}$ of detached leaf assay and whole plant assay indicated major influence of additive gene action over LB resistance. Role of additive gene effects was also prominent for number of fruits per plant and yield per plant. Additive gene effects are associated with homozygosity and fixable in early generations (Mather, 1949). High estimates of broad sense heritability and genetic advance for detached leaf assay, whole plant assay, number of fruit per plant and yield per plant can be accounted mainly due to additive gene effects since value of $\sigma^2 A$ was higher than $\sigma^2 D$ for these traits. Therefore, selection of high yielding and LB resistant genotypes based on detached leaf assay, whole plant assay, number of fruits per plant and yield per plant in early generations is advocated. Manipulation of additive gene action for the development of varieties/lines had already been reported in autogamous crops like tomato (Saleem et al., 2009a) and rice (Saleem et al., 2005). Estimates of σ^2 GCA, σ^2 SCA, σ^2 GCA/ σ^2 SCA and $(\sigma^2 D/\sigma^2 A)^{1/2}$ for days to maturity and single fruit weight disclosed major control of non-additive gene effects. Nonadditive gene effect refers to SCA and is considered as deviation from the additive gene action resulting from intra-allelic interaction like incomplete dominance, complete dominance or over dominance and inter-allelic interaction such that additive x additive, additive x dominance and dominance x dominance (Singh &

Narayanan, 2004). As a result of current study, tomato genotypes with early maturity and higher fruit weight can be developed through heterosis breeding due to higher magnitude of dominance (σ^2 D) component of variations controlling the expression of these traits as suggested by Singh & Narayanan (2004).

Male sterile line TMS2 and testers viz., Nagina, Roma and Picdenato disclosed high values of GCA for detached leaf and whole plant assays therefore; they were rated good general combiner for LB resistance. Likewise male sterile line TMS1 and tester Riogrande were scored good general combiner for yield due to high values of GCA effects. A multiple crossing program involving good combiner parents can be used to develop superior genotypes with LB resistance and high yield (Singh & Narayanan, 2004). Higher contribution of male sterile lines to the total variance for detached leaf assay, whole plant assay, number of fruit per plant and yield per plant indicated more importance of female parents over male parents.

The scrutiny of different crosses with SCA effects and GCA effects showed that SCA effects are not conditional to the GCA effects of the parents. Hybrid TMS2 x Roma emerged from high x high GCA combination of TMS2 and Roma while TMS1 x Riogrande came out from low x high GCA combination of TMS1 and Riogrande for detached leaf assay and whole plant assay, respectively. Hybrid TMS2 x Roma had an extra edge on account of having high x high GCA combinations of the parents. The rest of 8 hybrids had either low x average, high x average, low x high or high x low GCA combinations of female and male parents for detached leaf assay and whole plant assay. Similarly for yield and yield components, all crosses involved parents either high x average, average x low, average x high, high x low, high x high, low x average, low x low and or low x high GCA effects of parents. Assessing the combining ability effects for yield and yield components, Saleem et al., (2009b) in tomato and Hariprasanna et al., (2006) in rice, observed similar distribution of SCA effects in relation to GCA effects of the parental genotypes. Number

of hybrids although displayed desirable SCA effects for days to maturity, number of fruit per plant, single fruit weight and yield per plant but their SCA *per se performance* was not found significant which might be attributed to maternal and pleiotropic gene effects of male sterile lines.

Current investigation on tomato concludes additive type of genetic control for LB resistance, number of fruits per plant and yield per plant whereas non-additive type of genetic control for days to maturity and single fruit weight. Although there is enough affirmation to develop LB resistant lines of tomato in succeeding filial generations however, hybrid breeding programme for high yield coupled with LB resistance appeared rather difficult. It is therefore recommended that another study engaging large number of tester genotypes must be conducted to widen the genetic base of resulting hybrids for high productivity and LB resistance.

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