Journal of Plant Breeding and Crop Science Vol. 3(10), pp. 251-259, 30 September, 2011
Available online http://www.academicjournals.org/JPBCS
ISSN 2006-9758 ©2011 Academic Journals

Full Length Research Paper

Combing the monogenic and polygenic resistant genes to late blight in tomato

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Accepted 13 July, 2011

Late blight is a serious disease affecting tomato production especially in tropical and subtropical regions. Twenty-five crosses were generated from ten diverse parents to combine both the horizontal and vertical late blight resistance genes of late blight. Five inbred lines with polygenic resistance genes derived from interspecific cross *Solanum lycopersicum* × *S. habrochaites* f. *glabratum* were used as testers. The cultivars CN1 and CN2 CELBR as a source for vertical resistance genes *Ph-2* and *Ph-3*. The genotypes were artificially inoculated with mixed isolates of *Phytopthora infestans*. Predominance of GCA effects suggested that additive effects were more important than non-additive effects. The testers lines were highly stable with respect to late blight resistance confirming the presence of polygenic resistance. The analysis of resistance in the inbred lines indicated that the resistance is controlled by recessive genes. The best combinations were NC2 CELBR × 64B and NC1 CELBR × 64B combined the both genetic makeup of resistant genes. The cross CELBR NC2 × 163A was the most suitable for intra-population breeding programs to late blight. The extensive background of resistance genes is promising to maintain its effect through the advanced backcross generations.

Key words: *Solanum lycopersicum* L., *Phytophthora infestans*, combining ability, interspecific cross.

INTRODUCTION

Attempts to breed late blight resistant tomato lines started 64 years ago (Richards et al., 1946) ultimately resulting in the identification of three dominant genes: *Ph*-1 on chromosome 7 (Clayberg et al., 1965), *Ph*-2 on chromosome 10 (Moreau et al., 1998) and *Ph*-3 on chromosome 9 (Chunwongse et al., 1998). Tomato varieties carrying the resistance genes *Ph*-1 or *Ph*-2 provide inadequate control against the local population of the pathogen (Cohen, 2002). Whereas, *Ph*-3 is a strong resistance gene and has been incorporated into many breeding lines of fresh market and processing tomato. However, new *Phytopthora infestans* isolates have been identified which overcome *Ph*-3 resistance (Chunwongse et al., 2002). Race-specific and polygenic resistance have been characterized and exploited in breeding, providing an efficient control of disease severity (Thabuis et al., 2004). The high variability in *P. infestans* populations throughout the world, especially for virulence, has made race-specific resistance genes almost useless in disease control (Andrivon, 1994). With the lack of durability of resistance with single dominant genes that result in hypersensitive resistance (HR), it is probable that new resistance genes that result in HR will not be durable. More emphasis is being given to transfer of quantitative trait resistance to commercial cultivars of tomato.

The original source of the race-specific resistance genes *Ph*-1, *Ph*-2 and *Ph*-3 is the wild *Solanum pimpinellifolium* (Gallegly, 1960; Ignatova et al., 1999). Resistance to late blight has also been observed in wild *Solanum habrochaites* (Lobo and Navarro 1987; Kim and Mutschler, 2000; Abreu, 2005). F_1 progeny resulted from Interspecific crosss between *Solanum lycopersicum* L. cv. Santa Clara × *S. habrochaites* f. *glabratum* accession BGH 6902 exhibited resistance to numerous *P.infestans* isolates under the field conditions of Viçosa, MG state (Abreu, 2005). The choice of parents for use in plant

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breeding programs is one of the most important decisions that a breeder makes (Borém and Miranda, 2005). In tomato, the methodology presented by Griffing (1956), is quite used. This methodology which estimates the general and specific combining abilities of the parents in a diallel cross was developed for four types of diallel tables corresponding to four methods. The most commonly used is Method 2 which includes the n parents and the [n(n-1)/2] crosses in the generation F_1 without reciprocal crosses and the second in use is method 4 which involves only the group of F_1s without parents and reciprocal.

In a hybridization program, selection of parents on the basis of per se performance alone is not a sound procedure since superior lines identified on the basis of per se performance may result in poor recombinants in the segregating generations. Therefore, parents should be chosen on the basis of their combining ability. The general combining ability (GCA) characterizes the average performance of a genotype in a series of hybrids combinations and is mainly associated with additive gene action. The specific combining ability (SCA) is used to characterize the performance of a specific hybrid combination in relation to the average of its parents and is predominantly associated with genetic effects involving dominance. Ramalho et al. (1993) mentioned GCA as a parameter of larger practical importance for breeder since it gives information about the participation of additive gene effects in the variation range of the segregating generations of a cross, allowing to trace the best strategies for the breeding program. The objective of the current study was to develop more durable resistance to late blight in tomato through combine different resources of resistant genes, estimation of general and specific combining ability through half diallel analysis.

MATERIALS AND METHODS

Plant materials

Five inbreed lines of F_9 generation (127F, 64B, 73A, 163A and 133A) indeterminate growth habit were used from previous breeding program of late blight resistance in tomato, Universidade Federal de Vicosa (UFV). These lines resulted from interspecific cross between *S. lycopersicum L.*cv. Santa Clara × *Solanum habrochaites f. glabratum* (Abreu, 2005). These lines possess polygenic resistant genes to late blight were used as pollen source. These lines are indeterminate in growth habit with inferior fruit quality traits.

The following advanced inbred varieties; NC 1 CELBR, NC 2 CELBR and NC 25P were received from Prof. R. Gardner, North Carolina State University. They are homozygous, with determinate growth habit, heavy foliage and large, red-fruited tomato. NC 1 CELBR and NC 2 CELBR incorporate combined early blight resistance (Campbell, 1943 and PI 126445 origin) and have late blight resistance genes (*Ph*-2 and *Ph*-3). It is also resistant to *Verticillium wilt* (Ve gene) and Races 1 and 2 of *Fusarium wilt* (I and I-2 genes). NC 25P is a fresh market plum tomato line with the *Ph*-3 gene for late blight resistance and crimson gene for increased lycopene. It has early blight and *Verticillium wilt* resistance (Ve gene) and resistance to Races 1 and 2 of Fusarium wilt (I and I-2 genes) determinate in habbit with heavy foliage cover. Besides, the following cultivars 'Ikram' (*S. lycopersicum* L.) indeterminate growth habit, round slightly flattened; long life, fruit weight 130 to 150 g, fresh market variety and resistance to Fusarium 1 e 2, Verticilium 1, T.M.V, 'Heinz H7155' (*S. lycopersicum* L.) is processing tomato, oval fruit shape, resistant to *Fusarium* (Race 1), *Verticillium* (Race 1), 'Alambra' F_1 (*S. lycopersicum* L.) indeterminate growth habit, fresh market tomato; fruit weight 200 to 250 g; open field, fresh market variety, resistant to *Fusarium* (Race 1), *Fusarium* (Race 2), *verticillium*, tomato mosaic virus (ToMV) and nematodes were used in addition to 'New York' and 'Caline' which have only the *Ph*-1 resistance gene to late blight as standard varieties susceptible control.

Mating design

Thirty seedlings of each of the 10 selected parents were grown under greenhouse conditions during winter 2008 at Vicosa, MG. Pollens from each inbred line were collected and bulked into plastic plate, 4 cm in diameter with the aid of vibration tool to help pollen-dispersal. The five cultivars were crossed to each of the five lines following the 2 mating design where the parents and F1's were included only. Twenty pollinations for every cross were accomplished during June/July, 2008. It is worth mentioning that the cross NC 25P × inbred lines produced insufficient seeds thus, it has been excluded from the field experiment evaluation.

Field design

Seeds of F_1 were sown in 2nd of March, 2009 in 200-cell trays using commercial peat moss mixture as growing media fertilized once a week with 0.5% solution of N:P:K (15:15:20). Thirty five day-old seedlings were transplanted in the field of Horta de Pesquisa da Universidade Federal de Viçosa (UFV). Viçosa, Minas Gerais state (MG), southeastern Brazil. The applied experiment design was randomized complete block design (RCBD) with 3 replicates, 5 plants per plot with distance 60 cm intra-row and 100 cm inter-row.

Pathogen isolates and preparation of inoculum

To avoid both the specific-race resistance and possible epistatic effect genes of vertical resistance, selection upon the horizontal resistance phenotypes was considered through applied inoculum of mixture isolates of *P. infestans* collected from different regions of several tomato production fields. At early morning, infected leaves of late blight were collected from the commercial fields of tomato and put in polyethylene cases saved in ice tank until reaching the laboratory. The infected leaves were placed in plastic trays to multiply the inoculum. The trays were kept in dark chamber at 18 to 20°C for 24 h. After 24 h, the surface of fresh mycelium on the underside of leaves was very lightly brushed with a toothpick and the toothpick was whisked in chilled, distilled water in a 100-mL beaker to loosen the sporangia. The suspension of each isolate was prepared separately to adjust its concentration. After that equal volume of every suspension was taken and mixed together. The sporangia suspension was kept in the dark at 11 to 12°C for 90 to 100 min to release the zoospores (Nilson, 2006). The concentration was adjusted to 10^3 sporangia ml^{-1}. The inoculation was applied in the 1st of June 2009 after about 2 h of sunset using manual backpack sprayer (20 L volume) applying 20 ml of the sporangia

suspension per plant. The time between the preparation of the suspension and inoculation did not exceed two hours to keep the culture vigorous and maintain infectivity (Abreu, 2005).

Quantify the resistance

All the generations in addition to two standard susceptible varieties were screened against late blight disease under field conditions. The first observation was recorded after 4 days of inoculation and then every 4 days during June 2009. The disease severity was recorded based on the proportion of area or amount of plant tissue that is diseased. To insure optimal conditions for germination of the zoospores, a level of humidity was provided on the leaves to keep a thin film of water using micro sprinklers (full-circle 5 m, 325 ml/mint/micro sprinkler). The spray system was adjusted to turn on 15 min each 3 h over the 24 h, before applying the inoculation. After 4 days from inoculation, the first evaluation of disease severity was started and repeated over time every 4 days for a total of 6 times. During this period of disease development, the average maximum and minimum temperature was 25.2 and 13.7°C, respectively and average relative humidity was 85.7%.

Data collection

Foliar data were converted using the area under the disease progress curve (AUDPC) according to Tooley and Grau (1984), model to account foliar disease, which progressed over time as follow:

$$\text{AUDPC} = \sum_{i=1}^{n} \frac{[R_{i+1} + R_i]}{2} (t_{i+1} - t_i)$$

Where: R = rating (estimated proportion of affected tissue) at the ith observation, t_i = time (days) since the previous rating at the ith observation, n = total number of observations.

To evaluate the disease severity of late blight, the estimators were submitted to training, to use the software 'severity Pro' (Nutter, 1997), a computerized disease assessment training program for foliar diseases. At field, it was evaluated for every leaf on the plant for 9 plants for each F_1 and their parents. It was best to record readings independently (that is, without knowing the value given at the previous reading) at each date, such as having someone else write in the field book or by using a cassette recorder (Henfling, 1987). The selection to the resistance to late blight was done based on the negative values, or in other words, the plants which had minimum values of AUDPC were considered as resistant. In addition to the previous disease variable, it was estimated the percentage of severity at the halfway epidemic (Y_{50}) and at the percentage of severity at the end of epidemic (Y_{max}).

Statistical analysis

Randomized block design experiment was analyzed by standard analyses of variance and tests of significance at P < 0.05 for each trait. The statistical model:

$$Y_{iik} = \mu + G_i + B_i + \varepsilon_{ij} + \delta_{ijk}$$

Yiik= The observe obtained from the *k* individual of i genotype evaluated in j block;
μ = General mean;
G_i = Effect of i genotype considered fixed;
B_j = Effect of j block considered random;
ε_{ij} = Random effect of the variance among plots;
δijk = Random effect of variance within the plants among the plots.

Dunnett's test

Dunnett's test was applied (Dunnet, 1955) at P < 0.05 for comparing each disease variable mean with the control mean. Dennett's test is conducted by computing a t-test between each genotype and the control group using the formula:

$$t_d = \frac{M_i b - M_c}{\sqrt{\frac{2MSE}{n_h}}}$$

Where: M_i is the mean of the ith genotype group, M_c is the mean of the control group, MSE is the mean square error as computed from the analysis of variance and n_h is the harmonic mean of the sample sizes of the experimental group and the control group.

Diallel analysis

The disease variables AUDPC and Y_{max} were used for determination of combining ability and gene effect. The GCA and SCA were determined according to the Griffing (1956), diallel crossing system analyses method 2. Crosses were considered as fixed effects, so the GCA mean square was tested against SCA mean square for estimating the significance of F values. The genotypic value Gij of the single cross hybrid obtained by pollinating maternal parent i by paternal parent j is: Gij = μ + gca*i* + gca*j* + scaij where μ: the overall mean, gca*i*: the general combining ability of parent P*i*, gca*j*: the general combining ability of parent, Pj, scaij : the specific combining ability of parents Pi and Pj. All the statistical analyses, analysis of variance, cluster analysis, comparing between the means and estimation of genetic parameters in the half diallel and segregating populations were applied using GENES software program (Cruz, 2008) and SAS 9.2.

RESULTS AND DISCUSSION

The inheritance analysis of resistance to late blight

After four days of inoculation, the disease symptoms began to show up slightly. In the following days, the heavy rains and low temperature motivated disease development. The female's varieties differed in their resistance expression and susceptibility while the testers were closed in their expression in respect of AUDPC. The inbred line 73A showed highest values comparing with other testers. The offspring resulted from NC 1 CELBR × inbred lines and NC 2 CELBR × inbred lines in these crosses, the lesions were very small and less sporulation as compared with the susceptible varieties 'New York' and 'Caline'. The variable behavior of these crosses may be attributed to the differences in the genetic background and the types of the resistant genes they possess which transmitted from the parents to their progeny. These crosses showed fixed resistant overall the three experimental plots.

Table 1. The mean performance of disease variables Y50, Ymax and AUDPC for the parents, crosses and standard susceptible varieties 'New York' and 'Caline' inoculated with *P.infestans.*

Genotype	Y_{50}	Y_{max}	AUDPC
NC 1 CELBR	0.56	9.73	48.55
NC 2 CELBR	0.00	5.42	25.16
Ikram	23.62^{Ab}	97.89^{ab}	784. 74^{Ab}
Heinz H7155	22.58^{Ab}	90.53^{ab}	683.77
Alambra	24.35^{Ab}	98.56^{ab}	801.90
127F	1.56	22.84	117.91
64B	0.80	25.02	139.96
73A	8.20	23.16	192.50
163A	5.92	24.83	167.32
133A	2.18	23.29	126.22
Ikram × 127F	24.09^{Ab}	92.67^{ab}	677.70^{a}
Ikram × 64B	20.98^{Ab}	91.44^{ab}	694.37
Ikram × 73A	19.89^{Ab}	94.64^{ab}	635.69
Ikram × 163A	13.07^{A}	94.33^{ab}	595.27
Ikram × 133A	13.74^{A}	89.78^{ab}	575.44
NC 1 CELBR × 127F	7.01	24.12	145.29
NC 1 CELBR × 64B	8.88	27.84	125.83
NC 1 CELBR × 73A	10.07	14.26	153.06
NC 1 CELBR × 163A	5.77	18.66	119.30
NC 1 CELBR × 133A	15.90^{A}	20.93	148.64
NC 2 CELBR × 127F	9.79	21.59	85.89
NC 2 CELBR × 64B	4.40	20.03	52.02
NC 2 CELBR × 73A	10.82	19.42	67.09
NC 2 CELBR × 163A	5.93	20.93	59.61
NC 2 CELBR × 133A	8.08	17.70	60.54
Heinz H7155 ×127F	18.00^{A}	84.18^{ab}	665.15
Heinz H7155 × 64B	18.86^{Ab}	77.18^{ab}	644.18
Heinz H7155 × 73A	22.66^{Ab}	86.13^{ab}	756.19 ^{ab}
Heinz H7155 × 163A	20.80^{Ab}	84.44^{ab}	668.20
Heinz H7155 × 133A	22.04^{Ab}	85.84^{ab}	653.41
Alambra × 127F	23.85^{Ab}	96.00^{ab}	739.21^{ab}
Alambra × 64B	23.21^{Ab}	91.00^{ab}	745.89^{ab}
Alambra × 73A	23.76^{Ab}	89.73^{ab}	703.43^{ab}
Alambra × 163A	20.78^{A}	74.44^{b}	603.06
Alambra × 133A	20.21^{A}	86.36^{ab}	715.30^{ab}
New York	26.12^{A}	94.07^{a}	746.17^{a}
Caline	29.03^{b}	92.82^{b}	740.70

*Genotypes that have no significant differences share the same letters by Dunnett's test at 5% of probability.

The female parents showed divergence in respect of resistance to late blight comparing with NC 1 CELBR and NC 2 CELBR. The Alambra cv. showed the highest value of AUDPC (801.90). While NC 1 CELBR and NC 2 CELBR scored the minimum values of AUDPC and had high sufficient vertical analysis probably due to their content of monogenic resistance genes *Ph*-2 and *Ph*-3 (Table 1). Certain genotypes resulted from the crosses NC 1 CELBR and NC 2 CELBR with the inbred lines (127F, 64B, 73A, 163A and 133A) showed well-stability in respect of resistance. That could be interpreted by the fact that their genetic makeup combined both qualitative and polygenic resistant genes for late blight resistance.

The five inbred lines showed similar expression, this may be attributed to the similar genetic factors that responsible for resistance trait with high homozygousity.

The inbred line 73A had the maximum value of AUDPC, 192.50 (Table 1). Three well-defined types of host-pathogen interactions occur for the *P. infestans* in tomato: highly compatible, partially compatible, andincompatible interactions (Gallegly and Marvel, 1955). It was further observed that the moderately resistant commercial hybrids 'Ikram', 'Heinz H7155' and Alambra' exhibited susceptibility and the disease progress rate was higher comparing with the other genotypes. In contrast, some of these varieties; 'Ikram' and Heinz H7155 were recorded to be moderately resistant in another study (Fiorini, 2008). This discrepancy in the type of reaction may be due to change in the virulence genes of the pathogen or environmental factors interactions.

The five crosses resulted from the cross NC 1 CELBR with the five inbred lines showed closed level of resistance to late blight. This may be due to that the testers sharing the same ancestor which they resulted from interspecific cross. The cross NC 1 CELBR × 73A had the maximum value of AUDPC (153.06). While the cross NC 1 CELBR × 163A had the minimum value of AUDPC (119.30). With regard to the cross of NC 2 CELBR with the five inbred lines the results were similar to that obtained from the last cross of NC 1 CELBR. Whoever their crosses showed least values of AUDPC as compared to crosses using NC 1 CELBR parent. This may be attributed to that NC 2 CELBR possesses the resistant gene *Ph*-3 besides the *Ph*-2. The cross NC 2 CELBR ×127F had the maximum value of AUDPC, 85.89 whereas, the cross NC 2 CELBR × 64B had the minimum value of AUDPC, 52.02 (Table 1). The five crosses resulting from crossing Ikram with the five inbred lines showed similar expression level of resistance to late blight. This may be due to the fact that these lines have a high homogenseity-homozygousity as an advanced generation F9. The cross Ikram × 64B had the maximum value of AUDPC (694.37).

The cross Heinz H7155 × 73A had the maximum value of AUDPC (756.17) while the cross Heinz H7155 × 64B had the minimum value of AUDPC. The crosses resulted from Alambra x 5 inbred lines were similar to the previous crossing where the expression of all the crosses had a high values of AUDPC and were considered as susceptible to late blight in current study (Table 1).

Besides, it was observed that the crosses resulting from both the cultivars NC 1 and NC 2 recorded to be more resistance than the crosses resulting from the hybridization between the varieties (Ikram, Heinz H7155 and Alambra) as female parents. The cultivar 'Alambra' was recorded to be a more susceptible genotype through the severity at the end (Y_{max}) and for the area under disease progress curve (AUDPC) scored the values 98.56 and 801.90, respectively (Table 1).

Analysis of inheritance to resistance

Through the results obtained from the genetic analysis of F_2 populations (results not shown) and the mean performance of the parents and their progenies in the half diallel indicating that the resistance in the inbred lines is controlled by recessive genes. This mode of gene action that was observed in the F_1 implied that the homozygote effects were more important than heterozygote effects. This case was demonstrated by Heun (1987), who found that in the commercial cultivars the frequencies of dominant genes are higher than in the inbred lines, with incomplete dominance in both cases. Only a slightly higher mean resistance in generation F_1 was observed as compared to the parents, and no or very little variance was attributable to specific combining ability effects. However, significant differences existed in the average heterosis without their being correlated to the general combining abilities of the common parents. Therefore, it could be conclude that part of the genes conferring quantitative resistance act dominantly and a part act recessively.

Combining ability analysis of late blight resistance

The analysis of variance indicated that both the additive and non-additive genetic effects are included in controlling these traits. The mean squares of GCA (group I only) and SCA were significant for Y_{max} and AUDPC at 1% of probability (Table 2) The high values of mean squares of GCA over the SCA is evidence that the importance of the additive genetic effect rather than the non-additive one. Similar results were found (Nkalubo et al., 2009). A great variability of GCA was observed between different parents indicating the importance of additive genes in controlling the trait under study. The least values of GCA (gi) positive or negative effects indicate that these genotypes do not differ from the general mean of the half diallel population. Whereas, the highest values of gi whether, positive or negative, indicate that the parent is superior or inferior than the others parents in the diallel, with regard to the average performance of the progeny (Cruz and Regazzi, 2001; Sprague and Tatum, 1942). The interpretation of GCA (gi) effects depends on the breeder´s interest. Since the selection to late blight resistance is towards the negative or in other words, the least values of Y_{max} or AUDPC indicate highest level of resistance thus the high negative values of gi are most important to the breeder. The parents NC 1 CELBR and NC 2 CELBR had a significant negative GCA effects (-33.368 and -35.008, respectively) in respect of Y_{max} (Table 3). The inbreed lines 163A and 133A had significant negative ones (-1.103 and –0.577, respectively). With regard to AUDPC, similar implications to Y_{max} (-262,931 and -308.903 for NC 1 and NC 2, respectively and -15.048 and -12.194 for 163A and 133A, respectively). Based on the previous observations, arguably that the additive type of gene action was dominant over non-additive effect because specific

Table 2. Partitioning of genotypes variance (mean squares) in GCA and SCA of the parents and their half diallel crosses for Y_{max} and AUDPC.

S. V.	D. F.	Mean squares†	
		Y_{max}	AUDPC
Genotypes	34	3802.70**	266984.24**
Groups	1	10045.60**	768201.61**
GCA Group I	4	26458.17**	1853654.7**
GCA Group II	4	24.67^{NS}	5535.76^{NS}
SCA I x II	25	532.60**	34900.01**
Error	68	115.06	15047.58
Mean		57.617	423.37
SD		1.846	21.113

^{NS} not significant, significant; * and ** significant and high significant at 1 and 5% of probability, respectively; †Ymax: severity at the end of the epidemic; AUDPC: area under disease progress curve.

combining ability variance is less than those of general combining ability. However, both additive and non-additive genes action were involved in the expression for resistance. Similar findings have also been observed by various authors (Ghanadha et al., 2000; Jagadeesha and Wali, 2006; Singh et al., 2008).

The SCA effects (Sij)

The positive values of specific combining ability effect (Sjj) imply negative unidirectional dominance and the negative sjj values are observed when the deviations due to dominance are positive (Viana, 2000). Moreover, when the SCA effect of a population with itself is null, the population has the same gene frequencies as the average frequencies in the group of the diallel's parents. Furthermore, higher the absolute value of sjj, the greater the differences between the gene frequencies in the population and the average frequencies in the diallel's parents. The crosses NC 1 CELBR × 73A and Alambra × 163A had the two maximum values of Sij (-7.7317 and -3.2562, respectively) for Y_{max}. The best combination was NC 1 CELBR × 73A (Table 4). In contrast, AUDPC in the crosses NC 2 CELBR × 64B and NC 1 CELBR × 64B had the maximum values of Sij (-47.1224 and -19.2846, respectively). The best combination was NC 2 CELBR × 64B since one of its parents (NC 2 CELBR) had the highest combining ability value (-308.903). The best crosses were that involved both NC 2 CELBR and NC 1 CELBR since they are exotic in relation to Brazilian germplasm, a fact that can indicate a favorable contribution of the genetic diversity among the parents for high values of SCA. Crosses between divergent parents with high values of SCA can be explored through breeder by selection for favorable segregated individuals that lead to obtain superior lines (Sharma and Phul, 1994). These crosses have additional advantage that they combine both the vertical resistant genes *Ph-2* and *Ph-2, Ph-3* from the female parents (NC 1 CELBR and NC 2 CELBR, respectively) and the horizontal quantitative resistant genes from the inbred lines resulted from the interspecific cross between *S. lycopersicum* L. cv. Santa Clara × *S. habrochaites* f. *glabratum* accession BGH 6902.

The present evaluation showed that the genotypes NC 1 CELBR and NC 2 CELBR produced the best performing offspring and had the highest combining ability with regard to high level of resistance to late blight in both Y_{max} and AUDPC due to desirable load of resistant genes *Ph*-2 and *Ph*-2 + *Ph*-3, respectively to *P. infestans* with low recorded values of AUDPC. Furthermore, the highest negative values of gi indicate the superiority of these cultivars when compared with the other parents from the two groups.

The cultivars 'Ikram', 'Heinz H7155' and 'Alambra', despite the fact they are well-adapted varieties grown in a large scale in Brazil, but their mean performance relating to the resistance to *P. infestans* was inferior. However, the hybrids are more stable than standard varieties under stress (Janick, 1999). This emphasizes the importance of genetic materials at the inbred-line level in selection programs for resistance to *P. infestans*, such as open-pollinated varieties. In a comparison of modern varieties and long-established landraces, Ceccarelli and Grando (1996) reported that new varieties selected under well-managed conditions were superior to local varieties only under conditions of improved management, but not under extreme low-input conditions.

The genetic variation of *P. infestans* has intensified in recent years mainly due the sexual reproduction of this pathogen via mating of A1 and A2 (Cohen, 2002; Gavino et al., 2000; Rubin and Cohen, 2004). Some recombinant isolates might be more aggressive than their ancestor isolates (Gavino et al., 2000) thus rendering host resistance genes and chemical control (Gisi and Cohen, 1996) inefficient. Searching for durable resistance in tomato against late blight is therefore an important need for the tomato industry. In the present study, the assessment of Ikram, Heniz H7155 and Alambra showed disagreement between the resistance to late blight and

Table 3. Estimation of general combining ability (GCA) effects (gi) of a half diallel mating design involving ten genotypes (Group I and II) for Y_{max} and AUDPC in tomato.

Group	Genotypes	Effects†	
		Y_{max}	AUDPC
I	Ikram	25.896	176.9278
	NC 1 CELBR	-33.368	-262.931
	NC 2 CELBR	-35.008	-308.903
	Heinz H7155	19.250	177.6744
	Alambra	23.230	217.2322
II	127F	1.3173	3.7271
	64B	0.5718	2.966
	73A	-0.2093	20.5493
	163A	-1.1027	-15.0484
	133A	-0.5771	-12.194
	SD (G_i to $G_{i'}$)	1.8464	21.1153

†Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve; SD: standard division of the difference between two estimations.

Table 4. Estimation of specific combining ability (SCA) effects (Sij) of twenty five crosses for Y_{max} and AUDPC disease parameters.

Genotypes	Effect		Genotypes	Effect	
	Y_{max}	AUDPC		Y_{max}	AUDPC
Ikram × 127F	9.8883	91.9654	NC 2 CELBR × 163A	1.4716	109.3965
Ikram × 64B	9.4038	109.3965	NC 2 CELBR × 133A	-2.284	33.1332
Ikram × 73A	13.385	33.1332	Heinz H7155 × 127F	8.0438	78.668
Ikram × 163A	13.9683	28.311	Heinz H7155 × 64B	1.7893	58.459
Ikram × 133A	8.8927	5.6265	Heinz H7155 × 73A	11.5205	152.886
NC 1 CELBR ×127F	0.6016	-0.5857	Heinz H7155 × 163A	10.7238	100.494
NC 1 CELBR × 64B	5.0671	-19.2846	Heinz H7155 × 133A	11.5982	82.849
NC 1 CELBR × 73A	-7.7317	-9.6379	Alambra × 127F	15.8838	113.171
NC 1 CELBR × 163A	-2.4384	-7.8001	Alambra × 64B	11.6294	120.612
NC 1 CELBR × 133A	-0.694	18.6854	Alambra × 73A	11.1405	60.568
NC 2 CELBR × 127F	-0.2884	-14.0135	Alambra × 163A	-3.2562	-4.203
NC 2 CELBR × 64B	-1.1029	-47.1224	Alambra × 133A	8.1382	105.182
NC 2 CELBR × 73A	-0.9317	91.9654			

Y_{max}: severity at the end of the epidemic; AUDPC: area under disease progress curve.

fruit quality. This suggests that the better quality trait varieties will probably be inferior in resistance to late blight. However, the both cultivars CN1 CELBR and CN2CELBR can be used as a good example for explaining the recovery of recombinant inbred in tomato by applying selection in the F_2 generation (Christakis and Fasoulas, 2002) or fixing and transgressing heterosis (Burdick, 1954).

A selection procedure directly at the genotype level would greatly increase the efficiency of breeding efforts (Dekkers and Hospital, 2002) rather than by means of the phenotypic performance only. This is due to environmental influence on the phenotypic measurements, resulting in a biased measure of the true genetic potential of an individual especially in the case of having different biological interaction relationships. Both cultivars NC 1 CELBR and NC 2 CELBR showed good acceptable degree of adaptation under the current experimental conditions of our study with respect to resistance to late blight, *P. infestans* isolates. It is necessary to ensure that the resistance recorded for the crosses resulted from the hybridization between both NC 1 and NC 2 CELBR with the different inbred lines, is quantitative resistance or field resistance (against broad

range of pathogen isolate).

The crosses including NC 1 CELBR and NC 2 CELBR and the inbred lines combined resistant genes from different genetic makeup. However, the NC1 CELBR and NC2 CELBR presented acceptable level in most of fruit quality traits except firmness. The fruits lost their firmness very fast and did not have good storage ability.

Furthermore, the determinate growth habit with heavy foliage and consequently low yield. The progeny result from the crosses between these lines × testers can be explored and the crosses having highest SCA (Sij) effect may be select. This would result in high frequency of favorable alleles in respect of resistance, indeterminate growth habit and at the same time provide an acceptable level of variability in the segregating population that aid in selection to traits of interest. Using backcross method to recover the fruit quality traits is a common approach in this context since the resistant genes have to be selected during each round of backcrossing and furthermore, the possibility to recover the genetic factors responsible of quality especially average fruit weight, pigments, acidity, total soluble solids, flavors and the other quality traits will require many generations of backcrosses.

ACKNOWLEDGEMENTS

The authors are thankful to the Conselho Nacional de Desenvolvimento Científico e Tecnolgico (CNPq), to the Academy of Science for the Developing World (TWAS) for financial support and to Prof. Randy Gardner, North Carolina State University, USA, for supplying part of the genetic material.

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