New sources of partial resistance to bacterial spot race T2 in processing tomatoes

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ABSTRACT

Bacterial leaf spot of tomato is caused by four Xanthomonas species, among which Xanthomonas vesicatoria race T2 predominates in Uruguay. Difficulties in integrated disease management and the rapid spread of the pathogen led to investigations of genetic resistance. This study aimed to identify resistance sources to bacterial leaf spot race T2 in tomato for processing. Twelve genotypes were evaluated under field conditions in 2010 and 2011. Plants were spray-inoculated with a suspension of bacteria (10⁸ cfu/mL) 15 days after transplantation. Incubation period, disease severity on leaves, and the percentage of fruits with symptoms at harvest were determined. The incubation period did not differ among the genotypes. The genotype ‘Hawaii 7981’ had the lowest leaf severity on the leaves, followed by ‘Loica’. The lines (derived from the cultivar ‘Loica’) LB97, LB99, LB60, and LB76, and the cultivar ‘Ohio 8245’ showed intermediate levels of severity on leaves, whereas ‘H9997’, ‘Cuyano’, LB85, and ‘NUN6011’ presented higher severities. The differences in disease severity of the leaves were similar over the years, while incidence of symptoms in fruit was more variable. Next to ‘Hawaii 7981’, the cultivars ‘Loica’ and ‘Ohio 8245’ were identified as new sources of partial resistance to bacterial spot race T2.

Keywords: Xanthomonas vesicatoria, Solanum lycopersicum, quantitative resistance, durable resistance, tomato breeding.

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Bacterial spot is one of the main diseases affecting open field tomato (Solanum lycopersicum) and pepper (Capsicum annuum) crops. The disease is present worldwide and is a major problem in tropical and subtropical regions (Jones et al., 1991; EPPO/CABI, 2006). Bacterial spot attacks leaves, stems, and fruits causing economic losses due to defoliation and the development of brown scabby lesions on fruits (Jones et al., 1991).

Pohronezny & Volin (1983) estimated a range of total marketable yield losses from 17% to 52% due to late and early bacterial spot infections, respectively. Jones et al. (2004) demonstrated that four distinct Xanthomonas species (X. vesicatoria, X. euvesicatoria, X. perforans, and X. gardneri) composed of five races (e.g. T1, T2, T3, T4, and T5) cause bacterial diseases on tomato. In Uruguay, race T2 (X. vesicatoria) is the most widespread according to field survey data, and X. gardneri is also present (Montelongo, 2012). Cultural and chemical applied measures are often ineffective to control bacterial spot (Yang & Francis, 2006; Stall et al., 2009). Therefore, genetic resistance acquires great interest in integrated disease management to reduce yield losses (Stall et al., 2009). Many hypersensitive resistance genes have been identified (Jones & Scott, 1986; Astua-Monge et al., 2000; Scott
et al., 2001). However, the genetic diversity of the causal agent, and its great capacity to mutate and overcome genetic barriers are challenges for breeders in the development of cultivars with durable resistance (Quezado-Duval & Camargo, 2004). An alternative strategy could be the utilization of partial resistance sources, where usually several no race-specific genes with small effect are involved (Scott et al., 2006; Stall et al., 2009). Partial resistance to Xanthomonas sp. in tomato is based on several components, such as the latency period, the rate of infection leading to differences in the number of spots and severity on foliage, and bacterial population growth rate (Silva-Lobo et al., 2005; Berrueta et al., 2014).

Considering the problem caused by this pathogen in Uruguay, during 2005, the National Institute for Agronomical Research (INIA Uruguay) began a tomato breeding project with the aim of obtaining cultivars with adaptation to local environmental conditions and resistance to diseases, including the bacterial spot disease. The objective of this research was to identify sources of resistance to bacterial spot race T2 in processing tomato germplasm in field screenings.

**MATERIAL AND METHODS**

**Experimental design and inoculation**

Experiments were conducted at the INIA Wilson Ferreira Aldunate Experimental Station (34°40′S; 56°20′W), located in Rincon del Colorado, department of Canelones, Uruguay, during 2010 and 2011. The soils were classified as Phaeozems with a silty-clay texture. During the seasons 2010 and 2011, respectively, the mean temperatures were 22.5 and 17.5°C, the total precipitation 403 and 201 L/m², and the average relative humidity 87 and 71%.

Twelve tomato genotypes were included in field screening during each season. These genotypes were commercial cultivars, hybrids, and breeding lines (Table 1). Among these, ‘Hawaii 7981’ and ‘Florida 216’ contain the Xv3 gene that confers resistance to bacterial spot race T3 (Scott et al., 1996; Stall et al., 2009). The advanced lines LB60, LB76, LB85, LB97, and LB99 (seventh generation selection) were developed by the INIA's tomato breeding project. In 2011, ‘Florida 216’ was replaced by the new breeding line LB99, which contains several valuable traits, whilst ‘Florida 216’ has the same resistance gene than ‘Hawaii 7981’ (Scott et al., 1996) with lower results. All genotypes were sown in planter flats with a commercial horticultural substrate and seedlings grown under greenhouse. After 40 days, the seedlings were transplanted into the field. The transplanting dates were January 2nd 2010 and January 10th 2011.

A X. vesicatoria race T2 strain was selected based on virulence from the bacterial spot strains collection at INIA Uruguay, and used for inoculations. This strain was isolated in 2007 from a fruit spot sample collected in Colonia, Uruguay. Species determination was made using multiplex PCR, with specific primers developed by Koenraadt et al. (2009) and confirmed by phylogeny of the hrpB region (Montelongo, 2012).

Plants of each genotype were arranged in a randomized complete-block design with four replications. Each replication consisted of 15 plants, set in three rows spaced 1.6 m apart with 0.25 m between plants. Plant density was 75000 plants/ha. The inoculum was prepared by growing the X. vesicatoria race T2 strain for 48 h at 28±2°C on nutrient agar (Oxoid Ltd., UK). Bacterial cells were initially suspended in 8 g NaCl in 1000 mL distilled water and the concentration was adjusted to 10⁶ cfu/mL using a spectrophotometer (600 nm) and verified by plate counting. Plants were spray-inoculated 15 days after transplantation. Before inoculation, field plots were irrigated by sprinklers to promote opening of plant stomata and to increase the incidence of infection. Fertilization consisted of 200 kg/ha nitrogen (N), 150 kg/ha potassium (K₂O), and 150 kg/ha phosphorus (P₂O₅).

**Evaluation of resistance to bacterial spot**

Incubation period, leaf severity, and fruit incidence were measured in the evaluation of tomato resistance to bacterial spot. The incubation period was measured as the time (days) between inoculation and the appearance of symptoms in 50% of the plants in each plot was determined by daily evaluations. Disease severity was evaluated 20 days after inoculation. The fourth leaf from the top of each plant was scored using the diagrammatic scale developed by Mello et al. (1997), where 1 = 1%; 2 = 5%; 3 = 15%; 4 = 25%, and 5 = 50% of the leaf surface affected. Bacterial spot incidence on fruits was evaluated 90 days after transplantation. One-hundred tomato fruits were harvested from each plot, and the percentage of fruit with symptoms was determined.

**Statistical analysis**

Data of incubation period was subjected to analysis of variance and means were separated with Tukey’s test (p<0.05) (SAS, v. 9.1.3.).

Disease severity and incidence on fruits (proportion of infected fruits) are not normal distributed variables, therefore an analysis of variance is not the proper way to analyze them. Disease severity is an ordinal categorical variable that can be considered with a multinomial distribution for the 'number of plants in each severity level', as an extension of the Poisson binomial distribution for counting variables (Spyrides-Cunha et al., 2000; Galván et al., 2008). Similarly, a binomial distribution was assumed for the number of infected fruits among the total number of evaluated fruits to estimate the proportion of infected fruits. These two variables were analysed using Generalized Linear Models (GLIMMIX) in SAS, in which the threshold values and means were estimated (McCullagh & Nelder, 1989). Genotype profiles were compared by simple contrasts, and the mean severity level for each treatment was calculated as the sum of plants rated at a particular value multiplied by its probability. Genotype effects were tested using an F-test calculated from the quotient of two Chi-square deviances and the residual deviance from the model. Means were separated using Tukey-Kramer test (p<0.05).
Cluster analysis using Ward’s method (average linkage) was performed to group the genotypes on the basis of disease severity and percentage of infected fruits. Cluster analysis allows integrating different variables to classify the genotypes according to resistance level. Pseudo F and pseudo t² indicators were used as cutoff criterion for determining the number of groups.

Correlations between incubation period, disease severity, and percentage of infected fruits were estimated using Spearman’s correlation index (p=0.01).

RESULTS AND DISCUSSION

In the season 2010, differences between genotypes in leaf disease severity profile and percentage of fruits with symptoms were highly significant (p<0.0001 and p<0.002, respectively), whereas in the season 2011 significant differences between tomato genotypes were observed for leaf disease severity (p=0.0008; N= 240) and also in disease incidence on fruits (p<0.0001; N= 48).

The incubation period for all tomato genotypes lasted between 4.5 and 6 days. However, in both years, no significant differences among the genotypes were detected (Table 2). A longer incubation period may indicate greater resistance to tissue colonization by the pathogen. Therefore, fewer pathogenic cycles may occur within the season, resulting in fewer symptoms and reduced epidemics (Silva-Lobo et al., 2005). The host genotype, pathogen race, and environmental conditions can affect the duration of the incubation period (Yang & Francis, 2006). In this study, incubation period durations among field-grown tomato genotypes were not significantly different, as found also under controlled conditions (Berrueta et al., 2014). Therefore, this variable was not useful in distinguishing the genetic materials by bacterial spot resistance. However, Lugon-Lima et al. (2005), Silva-Lobo et al. (2005), and Mendez de Souza et al. (2008) successfully used the incubation or latency period to distinguish between resistant and susceptible genotypes grown under field and greenhouse conditions. According to Silva-Lobo et al. (2005), resistant genotypes had a latency period of 8 to 9 days, while susceptible genotypes had a latency period of 6 days. Controlled conditions are recommended to enhance the assessments of the incubation period (Silva-Lobo et al., 2005).

The high mean incidence of bacterial spot on fruits (37% in 2010 and 22% in 2011) demonstrates the importance of the disease in Uruguay, and confirms the severe yield losses this disease can cause. Scott et al. (1989) observed a maximum fruit incidence of 11% in field evaluations, which was much lower than the 58% observed in 2010 and 38% in 2011 in our experiments for the most susceptible genotypes.

In 2010, ‘Hawaii 7981’, ‘Loica’, LB97, LB60, LB76, and ‘Florida 216’ showed the lowest infection on fruits, and significantly differed from the cultivar ‘Cuyano’, which had the highest percentage of fruits with symptoms of bacterial spot (Table 2). ‘Ohio 8245’, ‘Tospodoro’, LB85, and ‘NUN 6011’ were not distinguished from the other genotypes. In 2011, the disease incidence on the fruits of the lines LB99, LB60, and ‘Tospodoro’ was significantly lower than that observed in ‘Hawaii 7981’, ‘Ohio 8245’, LB97, and ‘H9997’, which presented the highest disease incidence on fruits.

The disease incidence on fruits highlights the differences between crop seasons, which may be due to different environmental conditions during the sensitive period of the fruits. This period extends from initial fruit set to 40 days later, and susceptibility to infection is highest from day 5 to 19 following anthesis (Scott & Jones, 1989). Fruit infection by bacterial spot is favoured by frequent rainfall and high temperatures (Yang & Francis, 2006; Marcuzzo, 2009). However, fruit resistance may be inconsistent

| Genotype  | Type               | Origin/provider                  |
|-----------|--------------------|----------------------------------|
| Cuyano    | Commercial hybrid  | Syngenta Seeds                   |
| Florida 216 | Breeding line    | Univ. Florida, USA               |
| H9997     | Commercial hybrid | Heinz Seeds                      |
| Hawaii 7981 | Breeding line    | University of Florida, USA       |
| Loica     | Cultivar          | Roma x Platense (Gallardo & Calvar, 1992) |
| LB60      | Breeding line     | Loica x Heinz 9497 (González et al., 2010) |
| LB76      | Breeding line     | Loica x Hazera 3523 (González et al., 2010) |
| LB85      | Breeding line     | Loica x Heinz 6803 (González et al., 2010) |
| LB97      | Breeding line     | Loica x Granadero (González et al., 2010) |
| LB99      | Breeding line     | Loica x Granadero (González et al., 2010) |
| NUN 6011  | Commercial hybrid | Nuhhems B.V.                     |
| Ohio 8245 | Cultivar          | Ohio State University, USA       |
| Tospodoro | Cultivar          | Embrapa                          |
New sources of partial resistance to bacterial spot race T2 in processing tomatoes

between years, even when inoculated under controlled conditions (Scott et al., 1989). Environmental variability makes difficult the selection for resistance based on fruit incidence. This difficulty was confirmed in these experiments, because in 2010 (season with a higher occurrence of rainfall, relative humidity, and average temperatures) all genotypes had a high incidence of bacterial spot on fruits. Meanwhile, in 2011, some genotypes could be considered as moderately resistant to infection on fruits.

The severity assessments on foliage allowed for differentiation of genotypes according to their level of resistance to bacterial spot race T2. Such assessment has effective application for assessing tomato germplasm, and the diagrammatic scale allowed for the quick identification of the leaf area affected by the disease. The ranking of genotypes and the probability of each tomato genotype being allocated into a particular severity level are shown in Figure 1, whereas means in Table 1 are only indicative of the overall data distribution, and were calculated as the summation of each severity value multiplied by the probability of fitting this value. In 2010, from the comparisons by contrasts of the severity profiles, ‘Hawaii 7981’ had a 0.65 probability of having low disease severity (i.e. 5% of the leaf area affected) and its profile was significantly different from all the other genotypes (p<0.05). The cultivar ‘Loica’ followed ‘Hawaii 7981’ with a 0.88 probability of having 10% leaf disease severity, and its profile was significantly different from all other genotypes. Line LB97 and cultivar ‘Ohio 8245’ presented a high probability (0.98) of having very low leaf disease severity (i.e. between 1 and 5% of the leaf affected). This genotype profile was not significantly different from ‘Loica’, which had a 0.94 probability of having leaf severity between 1 and 5%. Thereafter, ‘Ohio 8245’, LB60, LB76, and LB97 which had probabilities greater than 0.70 of having leaf severity between 1 and 5%, did not significantly differ from ‘Loica’, but significantly differed from ‘H9997’, the most diseased genotype. Finally, ‘Tospodoro’, ‘NUN 6011’, and ‘H9997’ were ranked last, each having leaf disease severities between 15 and 25% of the leaf area affected (Figure 1).

Cluster analysis based on leaf disease severity and fruit incidence in 2010 suggested three groups of genotypes.

### Table 2. Mean bacterial spot disease severity, incubation period, and fruits with bacterial spot symptoms (%) in tomato genotypes during 2010 and 2011. Disease severity data were collected 20 days post-inoculation (média da severidade da doença mancha-bacteriana aos 20 dias após da inoculação, período de incubação e frutos com mancha-bacteriana (% ) em genótipos de tomateiro durante as estações de 2010 e 2011). Uruguay, INIA Las Brujas, 2010-2011.

| Genotype     | Disease severity | Incubation period (days)* | Fruits with symptoms (%)* | Disease severity | Incubation period (days)* | Fruits with symptoms (%)* |
|--------------|------------------|---------------------------|---------------------------|------------------|---------------------------|---------------------------|
| Hawaii7981   | 2.4              | 7.0<sup>NS</sup>          | 35 a                      | 1.7              | 6.0<sup>NS</sup>          | 32 cd                     |
| Loica        | 3.1              | 7.5                       | 31 a                      | 1.9              | 6.0                       | 14 abc                    |
| LB97         | 3.9              | 6.0                       | 30 a                      | 2.2              | 5.5                       | 32 cd                     |
| LB99         | -                | -                         | -                         | 2.3              | 6.0                       | 8 a                       |
| Ohio 8245    | 4.0              | 7.0                       | 40 ab                     | 2.1              | 6.0                       | 38 d                      |
| Tospodoro    | 4.3              | 6.0                       | 36 ab                     | 2.6              | 6.0                       | 12 ab                     |
| LB60         | 4.3              | 5.5                       | 30 a                      | 2.1              | 6.0                       | 9 ab                      |
| LB76         | 4.5              | 5.5                       | 32 a                      | 2.1              | 5.5                       | 13 abc                    |
| LB85         | 4.7              | 5.0                       | 42 ab                     | 2.3              | 5.0                       | 19 abc                    |
| Florida 216  | 4.7              | 6.5                       | 31 a                      | -                | -                         | -                         |
| NUN 6011     | 4.8              | 6.0                       | 40 ab                     | 2.6              | 5.0                       | 20 abcd                   |
| Cuyano       | 5.0              | 6.5                       | 58 b                      | 2.4              | 5.5                       | 27 bcd                    |
| H9997        | 5.2              | 5.5                       | 45 ab                     | 3.0              | 4.5                       | 36 d                      |

Disease severity: Weighted mean disease severity on a scale (severidade da doença: média ponderada da severidade da doença na escala): 1= 1%; 2= 5%; 3= 10%; 4= 15%; 5= 25%; 6= 50%; *Means within columns followed by a common letter are not significantly different (Tukey’s test at p<0.05) {médias dentro das colunas seguidas da mesma letra não são significativamente distintas pelo teste de Tukey, p<0.05}; <sup>NS</sup>Differences between means of all genotypes are not statistically significant (diferenças entre médias não são estatisticamente significativas); LB 99 was not evaluated in 2010, and Florida 216 was not evaluated in 2011 (LB99 não foi avaliada na estação de 2010 e Florida 216 não foi avaliada na estação de 2011).
Cluster analysis based on data from 2011 suggests that tomato genotypes fold in four groups by disease severity and fruit incidence (R square 0.86) (Figure 2B). ‘Loica’ and ‘Hawaii 7981’ comprised the most resistant group (mean leaf severity: 1.7 to 1.9; fruits with symptoms: 31 to 58%) (Table 2). The second group, with intermediate resistance, included the lines LB76, LB90, and ‘Ohio 8245’ (mean leaf severity: 2.1 to 2.3; fruits with symptoms: 8 to 38%). The third group of moderately susceptible genotypes was composed of ‘Cuyano’, ‘NUN 6011’, and ‘Tospodoro’ (mean leaf severity: 2.3 to 2.6; fruits with symptoms: 12 to 27%). The last group was composed of ‘H9997’, which was the most susceptible to bacterial spot genotype (mean leaf severity: 3.0; fruits with symptoms: 32%) (Table 2).

The genotype ‘Hawaii 7981’ showed low levels of leaf tissue affected, and was one of the most resistant genotypes to bacterial spot race T2. In previous experiments, this cultivar also showed high levels of resistance under growing chamber conditions (Berrueta et al., 2014). In contrast, Scott et al. (1997) found that T2 strains caused a susceptible reaction in ‘Hawaii 7981’. Scott et al. (2001) mentioned that minor genes are involved in the field resistance of ‘Hawaii 7981’ to race T3, which hinders the transfer of resistance to commercial cultivars. These minor genes could be involved in the resistance to race T2 observed in the present study.

The cultivar ‘Loica’ showed high levels of field resistance in the foliage and the fruits. This result is consistent with experiments conducted under growing chamber conditions, where the number of spots in the terminal leaflet, and the growth of bacterial population into the leaf were significantly lower for ‘Loica’ (Berrueta et al., 2014). For these reasons, ‘Loica’ can be considered as a new source of partial resistance to bacterial spot race T2. This cultivar was developed from a cross between the tomato cultivars ‘Roma’ and ‘Platense’ at INTA (Instituto Nacional de Tecnología Agropecuaria) Argentina in 1973 (Gallardo & Calvar, 1992). Besides its partial resistance to T2, ‘Loica’ stands out for its high level of field resistance to Tomato Spotted Wilt Virus derived from the cultivar ‘Platense’ (Gallardo & Calvar, 1992). In Uruguay, ‘Loica’ has many years of multiplication and evidenced adaptation to the local agro-ecological conditions (González et al., 2010).

The lines LB97, LB76, LB60, and LB 99 showed intermediate levels of resistance to bacterial spot. These lines were developed from crosses using ‘Loica’ as one of the parents (González et al., 2010). Therefore, our results demonstrate that the resistance of ‘Loica’ can be partially transferable to its progeny. ‘Ohio 8245’ showed an intermediate level of resistance to race T2, which is coincident with Silva-Lobo et al. (2005). This line is also resistant to other tomato diseases, such as Fusarium wilt (Race 1) and Verticillium wilt, and has a high level of resistance to Colletotrichum spp. (Berry et al., 1991).

‘Florida 216’ did not show field resistance to race T2. This line holds the Xv3 gene, and was developed by backcrossing plants with the resistance...
New sources of partial resistance to bacterial spot race T2 in processing tomatoes

Hortic. bras., v. 34, n. 3, jul. - set. 2016

The most susceptible genotypes in both years were ‘Cuyano’, ‘H9997’, and ‘NUN 6011’. The latter two hybrids occupy the major area of the processing tomato in Uruguay, and their high susceptibility to bacterial spot is commonly observed in commercial fields (Berrueta et al., 2012).

Disease severity was negatively correlated with incubation period, and the Spearman correlation coefficient was -0.51 (p= 0.0002) in 2010, and -0.47 (p= 0.0006) in 2011. This indicates a significant and negative moderate correlation between these variables. Hence, the longer plants take to manifest symptoms, the lower the severity on the foliage. This indicates a relationship between these variables, despite no significant differences in the incubation periods between genotypes. In 2010, the correlation between fruit incidence and leaf severity was significant (r= 0.45), while in 2011 there was no correlation between these factors. These results are consistent with those of Silva et al. (1998), who also obtained low correlation coefficients (r= 0.40). Scott & Jones (1989) proposed that resistance in leaves and fruits are governed by separate systems of genetic control. In 2010, we observed a low, but significant correlation between fruit incidence and leaf severity. One possible explanation could be that less severity on leaves indicates a lower inoculum density in plants, resulting in reduced fruit infection (Silva et al., 1998).

The correlation between disease severity and fruit incidence was significant in 2010 (r= 0.45; p= 0.0013), but not significant in 2011.

In summary, this research identified quantitative differences between tomato genotypes in response to bacterial spot race T2 in field screening. New sources of partial resistance to bacterial spot race T2 were identified, as the cultivar ‘Loica’, whose resistance was transferred to breeding lines. The genetic basis of resistance present in this genotype remains to be studied. ‘Hawaii 7981’ showed high partial resistance, in contrast with previous studies. Furthermore, cultivar ‘Ohio 8245’ was confirmed as a source of partial resistance to this race. The field assessment of disease severity in leaves and incidence on fruit at harvest allowed for genotype differentiation by their level of resistance to bacterial spot. The disease severity in the leaves was highly consistent between years despite climatic variation between growing seasons.

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