






Combining ability of tomato inbred lines to bacterial wilt resistance

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ABSTRACT: Tomato is one of the most important crops worldwide. Bacterial wilt (BW), caused by *Ralstonia spp.*, is a major disease for tomato production around the world, especially in tropical and subtropical regions. Currently in Brazil, only commercial hybrids are available as resistant rootstocks for use in infested areas, and we lack information regarding resistance to aggressive strains. Thus, the aims of this work were to estimate combining abilities of five tomato inbred lines and hybrids and to identify resistant genotypes for using as rootstocks resistant to *Ralstonia solanacearum* biovar 2, phylotype II, one of the most aggressive strains in Brazil. Combining abilities for BW resistance were assessed through full diallel crossings among five tomato inbred lines without reciprocals. The experiment was carried out in a greenhouse, in a complete randomized blocks design, using 15 genotypes (hybrids and parents). Additive genetic effects showed to be the most important for controlling bacterial wilt. The inbred line Hawaii 7996 exhibited the highest general combining ability among the five parents assessed. The hybrid Hawaii 7996 × Rodade was the best crossing in terms of resistance and specific combining ability, which was greater than those of all other hybrids. Although Hawaii 7996 remains as a major source for BW resistance, further researches are needed to better understand the resistance dynamics, seeking to develop hybrids with transgressive segregations and more stable resistance against aggressive strains and thrive under environmental conditions highly favorable to bacterial wilt infection.

Key words: *Solanum lycopersicum* L., *Ralstonia spp.*, diallel analysis.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetables in the world, with crops covering more than 54,000 hectares in Brazil (FAO 2019). Considering the tropical conditions of Brazil, several diseases may limit the crop production⁴, including bacterial wilt (BW), caused by the *Ralstonia solanacearum* complex, which is one of the most destructive pathogen, not only on tomato, but also on solanaceous species (Mansfield et al. 2012)⁵. This is a cosmopolitan soil-borne pathogen that affects roots and vascular system (xylem) of hosts, as found in hundreds of plant species from more than 50 botanical families (Hayward 1991, Lopes and Quezado-Duval 2005).

The *Ralstonia* complex stands out as one of the most worrisome bacterial pathogens worldwide, especially due to its aggressiveness and wide range of hosts (Mansfield et al. 2012). The reaction of tomato genotypes to the disease due to the presence of distinct variants of the pathogen is well known and should be considered in breeding programs focused on resistance to bacterial wilt (Lopes et al. 1994, Lopes and Boiteux 2004, Wicker et al. 2007).

⁴ Amorim, L.; Rezende, J.A.M. and Bergamin Filho, A. (2011). Manual de Fitopatologia. v 1. Princípios e Conceitos. São Paulo: Editora Agronômica Ceres.

⁵ Lopes, C.A. (2015). Bacterial Wilt – a threatening disease of tomato cultivated under warm temperatures. Brasília, DF: Embrapa Hortaliças. Comunicado Técnico, 109.

In Brazil, a survey on the *Ralstonia* complex indicated that tomatoes are affected by two species, *R. solanacearum*, which presents wide distribution and higher genetic diversity, and *R. pseudosolanacearum*, which is more prevalent in warmer environments, more frequently found in the northern and northeastern regions of the country (Santiago et al. 2017).

The expansion of tomato plantations throughout Brazil, combined with the intense crop succession with solanaceous and other hosts in the same area, especially under protected cultivation, contributed to aggravate the problem due to increases in bacterial population in the soil (Lopes et al. 2015).

As many other soil-borne pathogens, BW control is challenging, and the infestation of an area hampers the cultivation on it, since the pathogen survives in the soil for a long time as a saprophyte or associated to weeds and cultivated host species (Genin 2010). In addition, single control methods is almost always insufficient, and integrated management with preventive control techniques is recommended (Lopes 2015). Currently, one of the most efficient strategies to enable its growing in infested areas has been the use of resistant species, due to its low cost and easy adoption, especially after the prohibition of phytosanitary products used for soil fumigation⁶.

Resistance is complex, race-specific and exhibits unstable behavior (Lebeau et al. 2013, Lopes et al. 2015). Morpho-anatomical approaches show that it may be linked to root structure and architecture, as well as accumulation of gum in vascular tissues, forming physical barriers to the flow of bacterial cells (Grimault et al. 1994, Nakaho et al. 2000). In this sense, grafting has been implemented as one of the most efficient strategies to allow growing in infested areas, by providing increased vigor and protection against biotic and abiotic stresses (Singh et al. 2017), among which BW stands out (Grimault et al. 1994, McAvoy et al. 2012, Rivard et al. 2012, Lopes and Mendonça 2014).

Many studies have been carried out to understand the genetic control of BW resistance in several crops, including tomato, through diallel arrangement (González and Summers 1995, Singh and Asati 2011), and identifications of genomic regions controlling resistance (Thoquet et al. 1996, Kim et al. 2018). Besides being simple, diallel arrangement enables to estimate general (GCA) and specific (SCA) combining abilities, which are good indicators of genetic control underlying resistance traits. GCA refers to additive genetic interactions plus additive \times additive epistasis, while SCA refers to non-additive genetic effects (Griffing 1956a).

The main objectives of this work were to assess the BW resistance index of five tomato inbred lines using a strain of race 1, biovar 2, phylotype II of *R. solanacearum*, identified by its unusually high aggressiveness in a previous study (Lopes et al. 2015), in order to: estimate combining abilities (general and specific) of tomato inbred lines presenting different BW resistance levels through diallel arrangement; and select the best inbred line or biparental combination for a breeding program focused in the bacterial wilt resistance in tomato.

MATERIAL AND METHODS

Plant material and hybridization

Five tomato inbred lines from the germplasm bank of the Genetics Department of the Escola Superior de Agricultura “Luiz de Queiroz” of Universidade de São Paulo (ESALQ/USP), Piracicaba, SP, Brazil, were crossed to provide 10 hybrid combinations, following a full diallel arrangement without reciprocals. These inbred lines consisted of four inbred lines reported as resistant to BW [Hawaii 7996–University of Hawaii (Wang et al. 2013), Rotam-4–ARC-VOPI–South Africa (Bosch et al. 1990), Rodade–Horticultural Research Institute–South Africa (Bosch et al., 1985), and Vietnamese–no information available], and one inbred line susceptible to BW (TPN-191–ESALQ/USP, Brazil). Parental inbred lines were grown and crossed in a greenhouse in the winter of 2016. Seeds of the hybrids and parents (self-pollination) were collected from full-ripe fruits, washed, and stored under 10°C and 20% relative humidity.

⁶Lopes, C. A. and Mendonça, J. L. (2014). Enxertia em tomateiro para o controle da murcha-bacteriana. Brasília: Embrapa Hortaliças. Circular técnica 13.

Inoculum preparation and inoculation

The inoculation was carried out using the strain CNPH-488 (*R. solanacearum*, race 1, biovar 2, phylotype II) from the bacterial working collection of the Brazilian Agricultural Research Corporation (Embrapa Hortaliças). The culture was plated in Kelman medium (Kelman 1954) and remained there for 48 h at 28°C in a bio-oxygen demand (BOD) chamber. Typical colonies of the pathogen were subcultured in Kelman liquid medium and kept growing in a shaker for 24 h at 28°C and 80 rpm. Then, the bacterial suspension was diluted in sterile water and adjusted to an optical density ($OD_{600nm} = 0.3$) equivalent to 10^8 colony-forming unit (CFU)·mL⁻¹ (Wang et al. 1998, Wang et al. 2000), using a spectrophotometer.

The inoculated seedlings presented two fully expanded leaves; they were grown in polystyrene trays (31 mL·hole⁻¹) with coconut fiber substrate (nutrients were provided according to protocols for the plant, not shown). The roots of the seedling were wounded with a scalpel to promote pathogen penetration, and 5 mL of the bacterial suspension was poured on each plant. Trays with the inoculated seedlings were immediately placed in a chamber for 48 h (85% relative humidity with daytime and night-time temperatures of 30-32°C and 25-27°C, respectively). The seedlings were then transplanted to 10-L pots containing a commercial substrate (Basaplant®), in the summer of 2017.

Greenhouse trial

The experiment was carried out in a randomized complete block design, with four replications. Each replication was composed of six pots containing four plants per pot, totalizing 24 plants per plot. Nutrients were provided to plants according to Miranda et al. (2011). The pots were spaced 0.30 m within the plot and 1.20 m between plots and blocks.

Disease evaluation and data analysis

Plants were evaluated until 21 days after inoculation, using the Winsted and Kelman (1952) protocol. The disease incidence score was evaluated daily by a single trained person, from the fifth day after inoculation onwards, considering the means of visual assessments of each plot. A descriptive scale was used to quantify the disease symptoms, with scores ranging from 1 (absence of symptoms) to 5 (dead plant) (Nielsen and Haynes Jr. 1959). Wilt intensity (I) percentage was calculated as Eq. 1:

$$I = \left[\sum \frac{n_i \times v_i}{V \times N} \right] \times 100 \quad (1)$$

in which: n_i : the number of plants with the respective index; v_i : the scale index (1 to 5); V : the highest observed index; N : the number of plants assessed.

In the present research, bacterial resistance level (R) percentage was presented as $R = 100 - I$, to clarify the data analysis and discussion. Analysis of variance (ANOVA) of bacterial R were performed following the Eq. 2:

$$y_{ij} = \mu + b_j + g_i + \varepsilon_{ij} \quad (2)$$

in which: y_{ij} : the average value of the genotypes (parents and hybrids); μ : the general mean; b_j : the block effect; g_i : the genotype effect; ε_{ij} : the experimental error.

Mean comparisons for bacterial R were carried out using the Tukey's test at $p < 0.05$.

SCA and GCA were estimated using the method 2, model 1 (fixed) of Griffing (1956b), according to the Eq. 3:

$$y_{ij} = \mu + g_i + g_j + s_{ij} + \varepsilon_{ij} \quad (3)$$

in which: y_{ij} : the average value of the hybrid ($i \neq j$) or progenitor ($i = j$); μ : the general mean; g_i and g_j : the effects of the GCA related to the parents i and j , respectively; s_{ij} : the effect of the SCA of the parents i and j ($s_{ij} = s_{ji}$); ε_{ij} : the experimental error.

The experimental data were analyzed using the R program (R Core Team, 2021).

RESULTS AND DISCUSSION

The results showed a better performance for the inbred line Hawaii 7996, which presented a R of 73.3 (Table 1). The other inbred lines were severely affected, with almost 100% of dead plants ($R \sim 0$), confirming the aggressiveness of the *R. solanacearum*, biovar 2, phylotype II (CNP4-488). The R of the hybrids ranged from 0 to 44.17%; the hybrid Rodade × Hawaii 7996 had the best performance (Table 1). No other hybrids showed satisfactory resistance.

Table 1. Comparison of means of resistance level to bacterial wilt (*Ralstonia solanacearum* strain, biovar 2, phylotype II) of five tomato inbred lines and their 10 hybrid combinations*.

Parents	Resistance level (%)
Rotam-4	3.06 c
Rodade	3.78 c
Vietnamese	0.28 c
Hawaii 7996	73.34 a
TPN191	0.00 c
Hybrids	
Rotam-4 × Rodade	0.00 c
Rotam-4 × Vietnamese	2.50 c
Rotam-4 × Hawaii 7996	9.17 c
Rotam-4 × TPN191	0.00 c
Rodade × Vietnamese	10.00 c
Rodade × Hawaii 7996	44.17 b
Rodade × TPN191	5.00 c
Vietnamese × Hawaii 7996	16.39 c
Vietnamese × TPN191	0.42 c
Hawaii 7996 × TPN191	14.17 c

*Means followed by the same letter do not differ from each other by the Tukey's test at $p < 0.05$.

Higher resistance levels were expected for some hybrids, since the inbred lines Hawaii 7996, Rotam-4, and Rodade are reported as resistant genotypes used in tomato breeding programs to increase resistance to bacterial wilt (Bosch et al. 1985, González and Summers 1995, Wang et al. 2000, Cardoso et al. 2006). However, only Hawaii 7996, among these inbred lines, showed satisfactory results regarding resistance to this strain. Contrastingly, the inbred line Vietnamese, which was also reported as resistant in previous studies, showed high susceptibility, similarly to the control, the susceptible inbred line TPN-191, indicating that the inbred line Vietnamese might have a strain-specific resistance, mainly to South Asian strains. In fact, strains or isolate-specific resistance has been observed in the literature (Lopes et al. 2015).

Significant additive (GCA) and non-additive (SCA) genetic effects ($p < 0.05$) were found for BW resistance (Table 2), indicating that GCA and SCA might be underlying the resistance control. Nevertheless, the mean square ratio of $GCA/SCA = 1.55$ shows that the BW resistance of this set of inbred lines is mostly controlled by additive genetic effects and additive × additive and epistatic interactions, as shown by other studies found in the literature (González and Summers 1995, Hanson et al. 1998).

Table 2. Mean square estimates of general and specific combining abilities (GCA and SCA), and residual effect for the resistance level to *Ralstonia solanacearum*, biovar 2, phylotype II (%), evaluated through full diallel among five tomato inbred lines.

Source of variation	Degrees of freedom	Mean squares
Genotypes	14	1,247.72*
GCA	4	1,165.25*
SCA	10	116.16*
Residual	28	29.55
Coefficient of variation (%)	-	44.73

*Significant by the F test at $p < 0.01$.

In the present study, only the inbred line Hawaii 7996 showed positive and significant estimates for GCA (Table 3). There are evidences that Hawaii 7996 has favorable alleles for BW resistance, such as those reported by Wang et al. (2013). A diallel analysis of Hawaii 7996-related genotypes showed that Hawaii 7997 was the only inbred line with positive GCA effects over locations and generations, reinforcing the importance of those sources for BW resistance (Hanson et al. 1998). The hybrid Hawaii 7996 × Rodade exhibited higher resistance level (R = 44.17%) than the other hybrids. Additionally, the hybrid Hawaii 7996 × Rodade presented the highest SCA values (Table 3), which can be explained by the additive and non-additive genetic effects on this inbred line combination.

Table 3. General combining ability effect (\hat{g}_i) and specific combining ability effect estimates (\hat{s}_{ij}) for the resistance level (%) to *Ralstonia solanacearum*, biovar 2, phylotype II, evaluated through full diallel among five tomato inbred lines.

Parents	\hat{g}_i
Rotam-4	-9.20
Rodade	0.44
Vietnamese	-6.23
Hawaii 7996	19.30
TPN-191	-8.23
Standard deviation (σ_{g_i})	11.84
Hybrids	\hat{s}_{ij}
Rotam-4 × Rodade	0.88
Rotam-4 × Vietnamese	6.15
Rotam-4 × Hawaii 7996	-22.52
Rotam-4 × TPN 191	7.62
Rodade × Vietnamese	-4.37
Rodade × Hawaii 7996	17.63
Rodade × TPN 191	-3.34
Vietnamese × Hawaii 7996	-10.38
Vietnamese × TPN 191	-1.35
Hawaii 7996 × TPN 191	-2.03
Standard deviation ($\sigma_{s_{ij}}$)	10.78

Hybrids involving TPN-191 (susceptible inbred line) presented, in general, negative SCA values (Table 3), since this inbred line was the most susceptible among all the genotypes tested. The identification of the F₁ hybrids that achieve better performance than the parents is desirable for plant breeding programs focused on the development of hybrids. However, in the case of BW, it was not possible. Four out of the five inbred lines (Rotam-4, Rodade, Hawaii 7996, and Vietnamese) were previously characterized as resistant to BW; thus, the mean resistance level of the hybrids (from crosses among genotypes) would be higher. However, it is necessary to consider the aggressiveness of the *R. solanacearum*, biovar 2, phylotype II (CNP4-488), which was used for inoculation, as seen in previous studies (Lopes et al. 2015).

Two unmistakable outcomes can be brought up based on these results. The first is that only the inbred line Hawaii 7996 has significant resistance level for *R. solanacearum*, biovar 2, phylotype II (CNP4-488), which is a threat, considering its advance in tomato growing regions. The second is that, although the hybrid Hawaii 7996 × Rodade has not reached the averages of the genitor Hawaii 7996, the high SCA estimates for this combination indicate a potential to move forward with selections to develop inbred lines with higher resistance levels. The main advantage in the latter case would be the complementation of other resistance traits, since the inbred line Hawaii 7996 has small and soft fruits and it is resistant only to BW. For example, Rodade is also resistant to fusarium wilt (FW), a

soil-borne disease, providing the possibility of selecting plants resistant to BW and FW, besides improving fruit size by including the parent Rodade, which has larger fruits (data not presented). This result, together with those found on the literature, shows the importance of accounting for GCA when focusing on the improvement of resistance to BW. Breeding schemes that explore additive effects increase the chances to obtain better inbred lines, such as those with intrapopulation recurrent selection.

This study also confirmed the strong aggressiveness of the CNPH-488 strain of *R. solanacearum*, which is a cause of a worrisome scenario concerning the lack of resistance sources available for breeding genotypes resistant to biovar 2, phylotype II. Moreover, considering that the percentage of dead plants was very high in the present experiment, it was not possible to estimate whether there is some sort of increment of resistance to BW under naturally infested soils.

CONCLUSION

Based on the results, the following conclusions are presented:

- Only the inbred line Hawaii 7996 showed a satisfactory level of resistance to *R. solanacearum*, biovar 2, phylotype II (CNPH-488), under the conditions of this study;
- The inbred line Hawaii 7996 showed the highest overall combining ability for BW resistance, proving to be a promising genotype for use in genetic breeding programs focused on improving resistance to BW;
- The crossing Hawaii 7996 × Rodade was the only combination that presented positive and relevant values of GCA for resistance to bacterial wilt;
- Additive genetic effects should be considered as a breeding strategy for BW resistance for tomato crops.

AUTHORS' CONTRIBUTION

Conceptualization: Piotto, F. A., Lopes, G. L. and Lopes, C. A.; **Methodology:** Piotto, F. A., Lopes, G. L. and Lopes, C. A.; **Investigation:** Lopes, G. L., Nomura, J. V. N. and Nandi, G. N.; **Writing – Original Draft:** Piotto, F. A., Lopes, G. L., Nomura, J. V. N. and Nandi, G. N.; **Writing – Review and Editing:** Piotto, F. A. and Lopes, C. A.; **Funding Acquisition:** Piotto, F. A. and Lopes, G. L.; **Supervision:** Piotto, F. A.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

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