

Tomato genotype resistance to whitefly mediated by allelochemicals and *Mi* gene

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ABSTRACT

Allelochemicals and *Mi*, nematode-resistant gene, are found in wild tomato species and can provide resistance to insect pests. The aim of this study was to check the resistance of tomato (*Solanum lycopersicum* L.) genotypes with different foliar allelochemical contents (acylsugar and/or zingiberene) associated with and not associated with the *Mi* gene against the whitefly (*Bemisia tabaci* biotype B). Fifteen tomato genotypes were tested for resistance against whitefly (Santa Clara, TOM-695, TOM-556, TOM-584, TOM-684, TOM-687, TOM-688, TOM-759, TOM-760, ZGB-703, ZGB-704, TOM-778, TOM-779, TOM-780, and PI-127826). Genotypes with high acylsugar (AS) (TOM-687 and TOM-688) as well as those with high zingiberene (ZGB) contents (ZGB-703 and ZGB-704) had lower oviposition and a lower number of nymphs when compared with genotypes with low AS and ZGB contents and without the *Mi* gene (Santa Clara, TOM-695, TOM-556, and TOM-584). The genotypes carrying the *Mi* gene, associated with low allelochemical contents, were less preferred for whitefly oviposition compared with susceptible genotypes with low AS and ZGB contents and without the *Mi* gene. When both the AS and ZGB allelochemicals were present in the same genotypes (TOM-778, TOM-779, and TOM-780), they showed a synergistic effect; the number of whitefly eggs and nymphs decreased in genotypes with high AS and ZGB compared with genotypes that had only one of these allelochemicals. However, the number of whitefly eggs and nymphs of genotypes with high AS and ZGB contents, individually or combined, was less than for genotypes carrying the *Mi* gene. These results indicate that allelochemicals are more effective than the *Mi* gene to provide resistance to whitefly.

Key words: *Bemisia tabaci*, plant breeding, secondary substances, *Solanum lycopersicum*.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is widely cultivated in the tropical and subtropical regions of the world. Brazil is the eighth largest tomato producer worldwide, and the occurrence of phytosanitary problems is a limiting factor for its production (Toloy et al., 2018). Among the most frequent pests, the whitefly (*Bemisia tabaci* biotype B and *B. argentifolii* Bellows & Perring [Hemiptera: Aleyrodidae]) is considered as an important insect pest; it causes direct damage due to loss of the photosynthetically active area, and leads to yield losses (Desneux et al., 2011). It also causes indirect damage because it is a *Geminivirus* virus vector, which is responsible for irreversible physiological disorders (Inoue-Nagata et al., 2016).

Pesticides are mostly used for pest control in tomato. Insecticides are systematically applied by spraying, generally two or three applications a week in the warmer seasons. Several problems can occur such as residue accumulation in fruits, worker poisoning, environmental pollution, and increased production costs (Silva et al., 2009; 2013).

The development of pest- and arthropod-resistant genotypes through crop breeding programs is a viable alternative to solve problems arising from the indiscriminate use of agrochemicals. Programs developed in Brazil have pursued the introgression strategy of insect-resistant alleles, which are present in wild tomato species and elite inbred lines (Silva et al., 2013; Andrade et al., 2017; Vosmam et al., 2018). Pest resistance in these wild species is mediated by allelochemicals, which are generally associated with glandular foliar trichomes (Resende et al., 2006; Maluf et al., 2007; Andrade et al., 2018; Silva et al., 2018).

Tomato genotypes with high allelochemical levels were obtained from controlled interspecific hybridization between cultivated tomato and wild species. For example, *S. pennellii* Correll produce the acylsugar (AS) allelochemical (Resende et al., 2006) and *S. habrochaites* S. Knapp & D.M. Spooner var. *hirsutum* produces zingiberene (ZGB), a sesquiterpene hydrocarbon (Maluf et al., 2001; Freitas et al., 2002). These allelochemicals provide resistance to whitefly (*B. tabaci* biotype B) (Hemiptera: Aleyrodidae) (Resende et al., 2009; Silva et al., 2009; Maluf et al., 2010; Neiva et al., 2013, Andrade et al., 2017), South American tomato pinworm (*Tuta absoluta*) (Lepidoptera: Gelechiidae) (Goncalves Neto et al., 2010; Oliveira et al., 2012), mites (*Tetranychus urticae* and *T. evansi*) (Acari: Tetranychidae) (Maluf et al., 2007), leafminer (*Liriomyza trifolii*) (Silva et al., 2018), and aphid (*Myzus persicae*) (Silva et al., 2013).

The *Mi* gene produces resistance to nematodes *Meloidogyne* spp. in tomato (Smith, 1994). Furthermore, the effectiveness of this gene to provide resistance to other pests has also been reported. Kaloshian et al. (1995) and Rossi et al. (1998) reported tomato resistance to aphid *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) associated with the presence of the *Mi* gene. Nombela et al. (2003) and Rodríguez-Álvarez et al. (2017) found that the *Mi-1.2* gene, or another gene linked to it, gives resistance to *B. tabaci* in tomato genotypes (*S. lycopersicum*). Resistance to *B. tabaci* in tomato mediated by the *Mi* gene, or another gene linked to it, was also observed, and the influence of AS content was tested. However, there are no reports comparing resistance levels against whitefly in tomatoes bearing ZGB associated with AS and the *Mi* gene.

The aim of this study was to quantify the resistance to whitefly (*B. tabaci* biotype B) of tomato genotypes with different foliar allelochemical contents (AS and/or ZGB) associated or not associated with the *Mi* gene.

MATERIALS AND METHODS

The experiment was carried out in a greenhouse at the Horticultural Experimental Station-HortiAgroSementes Ltda., Palmital Farm in the municipality of Ijaci (21°14'16" S; 45°08'00" W; 918 m a.s.l.), Minas Gerais, Brazil and in the Horticulture Sector of the Universidade Federal de Lavras (UFLA) in the municipality of Lavras (21°14'43" S; 45°59'59" W; 918 m a.s.l.), Minas Gerais, Brazil.

Fifteen tomato genotypes belonging to the tomato breeding program of the UFLA, which exhibited different AS, ZGB, and *Mi* gene levels were evaluated (Table 1). The Santa Clara, TOM-695, TOM-556, and TOM-584 inbred lines were used as susceptible controls, whereas the *S. habrochaites* var. *hirsutum* PI-127826 accession was used as the resistant control.

All 15 tomato genotypes were previously selected. Genotypes with high AS and ZGB foliar contents were selected based on their concentration in the leaflets by the colorimetric method proposed by Freitas et al. (2002) and Resende et al. (2006). Genotypes bearing the *Mi* allele were selected in nematode resistance assays.

Seeds of all genotypes were sown in polystyrene trays with 128 cells and containing commercial substrate (Tropstrato HA Hortaliças, Vida Verde, Mogi Mirim, São Paulo, Brazil). Afterward, plants were transplanted 40 d after sowing in plastic pots (500 mL) containing a mixture of soil, commercial substrate, sand, lime, and NPK.

For *B. tabaci* biotype B infestation, whitefly rearing was established in the Horticulture Sector of the UFLA in a 12 m² greenhouse; the chapel type protective structure (4 m × 3 m) consisted of 100 µ thick clear plastic cover and anti-aphid netting on the sides. Adult insects were collected in 'Santa Clara' tomato plants and then transferred to a screened greenhouse. Approximately 50 'Santa Clara' plants (which showed low ZGB and AS contents and susceptibility to whitefly) were used for oviposition and feeding the insects. These plants were also used as an infestation source and kept in the greenhouse during the experiment.

All 15 genotypes were transported 24 d after transplanting to another greenhouse with anti-aphid netting previously infested with *B. tabaci* biotype B; this greenhouse was also located in the Horticulture Sector of the UFLA. The experiment was established in the greenhouse with a completely randomized design (CRD), one plant per pot, and six replicates for each of the 15 treatments.

Table 1. Description of evaluated tomato genotypes, mean number of eggs and nymphs on 2 cm² leaf area measured at 6 and 20 d, respectively, after *Bemisia tabaci* biotype B infestation in the upper third of tomato plants.

Genotypes ^(a)	Foliar content			Reference	Mean number of eggs 2 cm ² leaflet	Mean number of nymphs 2 cm ² leaflet
	Acylsugar	Zingiberene	<i>Mi-1</i> gene			
T1 Santa Clara	Low	Low	No	Silva et al. (2008)	63.12h	94.25i
T2 TOM-695	Low	Low	No	Nizio et al. (2008)	51.21g	81.62h
T3 TOM-556	Low	Low	No	Resende et al. (2006)	52.21g	79.71h
T4 TOM-584	Low	Low	No	Resende et al. (2006)	50.96g	80.83h
T5 TOM-684	Low	Low	Yes	Resende et al. (2006)	43.33f	69.58g
T6 TOM-687	High	Low	No	Personal communication	31.08e	55.67f
T7 TOM-688	High	Low	No	Pereira et al. (2008)	28.42d	55.75f
T8 TOM-759	High	Low	Yes	Pereira et al. (2008)	23.50c	50.50c
T9 TOM-760	High	Low	Yes	Personal communication	24.42c	52.38d
T10 ZGB-703	Low	High	No	Maluf et al. (2001)	25.63c	53.50e
T11 ZGB-704	Low	High	No	Maluf et al. (2001)	23.33c	54.42e
T12 TOM-778	High	High	No	Personal communication	22.25b	44.00b
T13 TOM-780	High	High	No	Personal communication	20.50b	44.25b
T14 TOM-779	High	High	No	Personal communication	21.37b	43.67b
T15 P1-127826	Low	Very High	No	Toscano et al. (2001)	1.00a	1.04a

^(a)Lines homozygous for the described characteristics.

Means followed by the same letter in the columns belong to the same group according to the Scott-Knott test ($p \leq 0.05$).

Six days after infestation, oviposition was evaluated by counting the number of eggs in a 2 cm² leaf area on four leaflets of the upper third of each plant with a binocular loupe with 20X to 80X magnification (Oksn 9585, Atibaia, São Paulo, Brazil). Twenty days after the infestation of sampled leaflets, previously marked with white tape, these were evaluated for the number of last instar nymphs with a binocular loupe. Mean temperature and RH between the infestation period and nymph count ranged from 11.2 to 20.3 °C and 52% to 100%, respectively.

After verifying the normality and homogeneity of variance by the Shapiro-Wilk and Bartlett tests, respectively, data concerning the number of *B. tabaci* eggs and nymphs were transformed into $(x + 0.5)^{1/2}$ before performing ANOVA. Means were grouped by the Scott Knott test ($p \leq 0.05$) and contrasts selected from genotype clusters with different allelochemical contents and bearing the *Mi* gene, and were calculated with the Sisvar statistical software (Ferreira, 2011).

RESULTS AND DISCUSSION

According to the F-test, significant differences were observed between tomato genotypes that were tested for all evaluated traits (Table 1). Inbred lines with high AS or ZGB contents (T5 to T15) or only carrying the *Mi* gene (T5) showed less preference for both oviposition and reduced number of nymphs compared with the Santa Clara, TOM-695, TOM-556, and TOM-584 genotypes used as susceptible controls.

The Santa Clara, TOM-695, TOM-556, and TOM-584 genotypes were allocated in clusters with the highest oviposition and number of nymphs indicated by the Scott-Knott test (Table 1). These four genotypes are the most susceptible; they have in common the absence of the *Mi-1* gene and lower contents of both allelochemicals. In contrast, inbred lines with high AS and/or ZGB contents (T6 to T15) as well as the inbred line with low allelochemical contents, but carrying the *Mi-1* gene (T5), were less preferred for oviposition and reproduction when compared with the most susceptible controls (T1 to T4).

On the other hand, ‘TOM-687’ and ‘TOM-688’ that produced high AS contents, were allocated in clusters with significantly lower means than those of the T1 to T4 inbred lines (Tables 1 and 2, Contrast C1). These results prove the effectiveness of high foliar AS concentrations to produce resistance to whitefly, as previously described (Resende et al., 2009; Oliveira et al., 2012; Neiva et al., 2013). For ‘TOM-687’ and ‘TOM-688’, oviposition was reduced by 50.76% and 54.97% compared with ‘Santa Clara’, while the number of nymphs was reduced by 40.93% and 40.85%, respectively.

Inbred lines with high ZGB, low AS content, and without the *Mi* gene (ZGB-703 and ZGB-704) also showed a significant level of antixenosis for oviposition and fewer whitefly nymphs when compared with the susceptible controls (Santa Clara, TOM-695, TOM-556, and TOM-584) (Tables 1 and 2, Contrast C2). The adverse effect of genotypes with high ZGB

Table 2. Contrasts of interest estimates used to compare resistance to whitefly between genotypes and/or clusters of genotypes with different contents of acylsugar (AS) and zingiberene (ZGB) and resistance to nematodes.

Id.	Contrast of interest	Description	Number of eggs estimate	Number of nymphs estimate
C1	$[(T1+T2+T3+T4)/4 - (T6+T7)/2]$	Genotypes with low AS and ZGB and without <i>Mi</i> gene vs. genotypes with high AS, low ZGB, and without gene <i>Mi</i>	24.63**	28.40**
C2	$[(T1+T2+T3+T4)/4 - (T10+T11)/2]$	Genotypes with low AS and ZGB and without <i>Mi</i> gene vs. genotypes with high ZGB and low AS	29.89**	30.15**
C3	$[(T1+T2+T3+T4)/4 - (T12+T13+T14)/3]$	Genotypes with low AS and ZGB and without <i>Mi</i> gene vs. genotypes with high AS and ZGB	33.00**	40.13**
C4	$[(T1+T2+T3+T4)/4 - (T5)]$	Genotypes with low AS and ZGB and without <i>Mi</i> gene vs. genotypes with low AS and ZGB with <i>Mi</i> gene	11.04**	14.52**
C5	$[(T1+T2+T3+T4)/4 - (T8+T9)/2]$	Genotypes with low AS and ZGB and without <i>Mi</i> gene vs. genotypes with high AS and low ZGB and with <i>Mi</i> gene	23.96**	26.62**
C6	$[(T5) - (T6+T7)/2]$	Genotypes with low AS and ZGB and with <i>Mi</i> gene vs. genotypes with high AS, low ZGB, and without <i>Mi</i> gene	13.58**	13.88**
C7	$[(T5) - (T10+T11)/2]$	Genotypes with low AS and ZGB and with <i>Mi</i> gene vs. genotypes with low AS, high ZGB, and without <i>Mi</i> gene	18.85**	15.62**
C8	$[(T5) - (T12+T13+T14)/3]$	Genotypes with low AS and ZGB and with <i>Mi</i> gene vs. genotypes with high AS, high ZGB, and without <i>Mi</i> gene	21.96**	25.61**
C9	$[(T5) - (T8+T9)/2]$	Genotype with low AS and ZGB and with <i>Mi</i> gene vs. genotypes with high AS, low ZGB and with <i>Mi</i> gene	19.38**	18.14**
C10	$[(T6+T7)/2 - (T10+T11)/2]$	Genotypes with high AS, low ZGB, without <i>Mi</i> gene vs. genotypes with low AS, high ZGB and without <i>Mi</i> gene	5.27**	1.75 ^{ns}
C11	$[(T6+T7)/2 - (T12+T13+T14)/3]$	Genotypes with high AS, low ZGB, without <i>Mi</i> gene vs. genotypes with high AS, high ZGB and without <i>Mi</i> gene	8.38**	11.74**
C12	$[(T6+T7)/2 - (T8+T9)/2]$	Genotypes with high AS, low ZGB, without <i>Mi</i> gene vs. genotypes with high AS, low ZGB and with <i>Mi</i> gene	5.79**	4.27**
C13	$[(T10+T11)/2 - (T12+T13+T14)/3]$	Genotypes with low AS, high ZGB, without <i>Mi</i> gene vs. genotypes with high AS, high ZGB and without <i>Mi</i> gene	3.11**	9.98**
C14	$[(T10+T11)/2 - (T8+T9)/2]$	Genotypes with low AS, high ZGB, without <i>Mi</i> gene vs. genotypes with high AS, low ZGB and with <i>Mi</i> gene	0.52 ^{ns}	2.52**

** , ^{ns} Significant and nonsignificant at the 0.01 probability level, respectively, according to the F-test.

contents in the biological development of whitefly (*B. tabaci* biotype B) has been previously reported (Silva et al., 2009; Oliveira et al., 2012; Neiva et al., 2013). The presence of ZGB, although discrete, was significantly more effective than AS in reducing oviposition and number of nymphs (Contrast C10). For ‘ZGB-703’ and ‘ZGB-704’, oviposition was reduced by 59.39% and 63.04% as related to ‘Santa Clara’, while the number of nymphs was reduced by 43.24% and 42.26%, respectively. Effects on whitefly survival provided by AS and ZGB, simultaneously present in the TOM-778, TOM-779, and TOM-780 inbred lines, were efficient to induce less preference to oviposition and fewer nymphs when compared with inbred lines with low content of these allelochemicals (Contrast C3); they were also more efficient than genotypes containing only one type of allelochemical such as high AS content (Contrast C11) or high ZGB content (Contrast C13).

The genotype carrying only the *Mi* gene (TOM-684) exhibited moderate resistance when compared with the susceptible controls (Table 2, Contrast C4). Genotypes with high AS contents and with the *Mi* gene (TOM-759 and TOM-760) had higher resistance to oviposition and fewer whitefly nymphs than the susceptible lines (Table 2, Contrast C5). There was a reduction of 46.42%, 44.42%, and 26.18% in the number of nymphs per leaflet in lines carrying the *Mi* gene: TOM-759 (AS + *Mi* gene), TOM-760 (AS + *Mi* gene), and TOM-684 (*Mi* gene), respectively. However, this resistance was lower than values reported by Nombela et al. (2003), who observed a reduction of 50% in the mean number of nymphs when compared with plants that did not carry the *Mi* resistance allele. Such differences may be justified by the relative magnitude influenced by temperature.

Inbred lines with high AS (TOM-687 and TOM-688), high ZGB content (ZGB-703 and ZGB-704), and high contents of both allelochemicals (TOM-778, TOM-779, and TOM-780) showed higher resistance to oviposition and lower number of whitefly nymphs compared with the genotype TOM-684, which carries the *Mi* gene (Table 2, Contrasts C6, C7, and C8). Therefore, the resistance level provided by *Mi* is lower than AS and ZGB separately or by AS and ZGB associated in the same genotype. Inbred lines with a high AS content and carrying the *Mi* gene (TOM-759 and TOM-760) were more

resistant to oviposition and exhibited fewer nymphs than the line with only the *Mi* gene (TOM-684) (Tables 1 and 2, Contrast C9). On the other hand, 'TOM-759' and 'TOM-760' (high AS + *Mi*) were also more resistant to oviposition and exhibited fewer nymphs than 'TOM-687' and 'TOM-688', which only have high AS content (Table 2, Contrast C12).

Thus, the combined effect in oviposition due to the high AS content plus the presence of the *Mi* gene (high AS + *Mi*) is similar to the effect provided by high ZGB content. The effect of high AS + *Mi* as related to the number of nymphs is higher than the effect by ZGB (Table 2, Contrast 14).

The results obtained in the present study were similar to those reported by Nombela et al. (2003) and confirmed that the *Mi-1* gene is involved in the partial resistance to *B. tabaci* biotype B in *S. lycopersicum*. Some studies also reported that *Mi* gene is efficient in controlling *M. euphorbiae* (Kaloshian et al., 1997; 2000; Goggin et al., 2001) and nematodes (*Meloidogyne* spp.) in tomato (Goggin et al., 2001; Mantelin et al., 2011; Atamian et al., 2012).

None of the genotypes were as resistant to whitefly as the wild accession PI-127826 (Table 1), indicating that the ZGB-703 and ZGB-704 inbred lines, both derived from 'PI-127826', do not have all the genes responsible for resistance to whitefly. Therefore, these inbred lines had a resistance level similar to lines with high ZGB content, indicating that they have the same resistance mechanism.

In the present study, genotypes with high AS and ZGB contents had adverse effects on the biological development of *B. tabaci* biotype B. Similar results were found by Silva et al. (2009) and Neiva et al. (2013) for *B. tabaci* biotype B and for other pests such as *Tuta absoluta* and *Myzus persicae* (Oliveira et al., 2012; Silva et al., 2013).

Resistance levels to *B. tabaci* biotype B oviposition mediated by AS and ZGB in the same genotypes (TOM-778, TOM-779, and TOM-780) were significantly higher than in genotypes with only one allelochemical in their structure (Table 2, Contrasts C10, C11, and C13). Silva et al. (2009) found different results with respect to *B. tabaci* biotype B in which the double heterozygote genotypes had the same behavior as heterozygotes for ZGB or AS, and there was no synergistic effect of the simultaneous presence of ZGB and AS.

These results indicate that high AS and ZGB contents and the presence of the *Mi* gene are associated with higher resistance to whitefly in tomato. However, resistance levels provided by the presence of the *Mi* gene are lower than by high AS and/or ZGB contents. High ZGB content gives a similar resistance level for nymph survival in a high AS content, but it is slightly more effective than the latter in reducing oviposition.

Genotypes with high simultaneous AS + *Mi* were more resistant to whitefly than genotypes with only high AS or only the *Mi* gene. Genotypes with high AS + ZGB content exhibited a higher resistance level than genotypes with high AS or high ZGB content. It would seem that genotypes with the simultaneous presence of high AS and ZGB contents and with the *Mi* gene (high AS + high ZGB + *Mi*) could provide even higher resistance levels. To test this hypothesis, it is necessary to obtain a genotype that has the three traits, which is not available at the present time.

CONCLUSIONS

High foliar contents of allelochemicals such as acylsugar (AS) and zingiberene (ZGB) associated with the presence of the *Mi* gene in tomato plants may lead to higher resistance to whitefly. The resistance to whitefly mediated by the *Mi* gene is lower when compared with resistance levels mediated by AS and ZGB or simultaneously mediated by AS and ZGB. The combined effect of high AS content associated with the presence of the *Mi* gene is greater when compared with the effect of only high ZGB content on the resistance to whitefly.

REFERENCES

- Andrade, M.C., Silva, A.A., Carvalho, R.C., Andrade, S.J., Oliveira, A.M.S., Francis, D.M., et al. 2018. Quantitative trait loci associated with trichomes in the *Solanum galapagense* accession LA1401. Genetic Resources and Crop Evolution 1-15. <https://doi.org/10.1007/s10722-018-0644-3>.
- Andrade, M.C., Silva, A.A., Neiva, I.P., Oliveira, I.R., De Castro, E.M., et al. 2017. Inheritance of type IV glandular trichome density and its association with whitefly resistance from *Solanum galapagense* accession LA1401. Euphytica 213:1-12. <https://doi.org/10.1007/s10681-016-1792-1>.
- Atamian, H.S., Eulgem, T., and Kaloshian, I. 2012. SIWRKY70 is required for *Mi-1*-mediated resistance to aphids and nematodes in tomato. Planta 235:299-309. doi:10.1007/s00425-011-1509-6.

- Desneux, N., Luna, M.G., Guillemaud, T., and Urbaneja, A. 2011. The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. *Journal of Pest Science* 84:403-408. doi:10.1007/s10340-011-0398-6.
- Ferreira, D. 2011. Sisvar: a computer statistical analysis system. *Ciência e Agrotecnologia* 35:1039-1042. <http://dx.doi.org/10.1590/S1413-70542011000600001>.
- Freitas, J.A., Maluf, W.R., Cardoso, M.D., Gomes, L.A.A., and Bearzotti, E. 2002. Inheritance of foliar zingiberene contents and their relationship to trichome densities and whitefly resistance in tomatoes. *Euphytica* 127:275-287. <https://doi.org/10.1023/A:1020239512598>.
- Goggin, F.L., Williamson, V.M., and Ullman, D.E. 2001. Variability in the response of *Macrosiphum euphorbiae* and *Myzus persicae* (Hemiptera: Aphididae) to the tomato resistance gene *Mi*. *Environmental Entomology* 30:101-106. <https://doi.org/10.1603/0046-225X-30.1.101>.
- Goncalves Neto, A.C., Silva, V.F., Maluf, W.R., Maciel, G.M., Nízio, D.A.C., Gomes L.A.A., et al. 2010. Resistência à traça-do-tomateiro em plantas com altos teores de acilaçúcares nas folhas. *Horticultura Brasileira* 28:203-208. <http://dx.doi.org/10.1590/S0102-05362010000200011>.
- Inoue-Nagata, A.K., Lima, M.F., and Gilbertson, R.L. 2016. A review of geminivirus (begomovirus) diseases in vegetables and other crops in Brazil: Current status and approaches for management. *Horticultura Brasileira* 34:8-18. <http://dx.doi.org/10.1590/S0102-053620160000100002>.
- Kaloshian, I., Kinsey, M.G., Ullman, D.E., and Williamson, V.M. 1997. The impact of *Meu1*-mediated resistance in tomato on longevity, fecundity and behavior of the potato aphid, *Macrosiphum euphorbiae*. *Entomologia Experimentalis et Applicata* 83:181-187. <https://doi.org/10.1046/j.1570-7458.1997.00170.x>.
- Kaloshian, I., Kinsey, M.G., Williamson, M.V., and Ullman, E.D. 2000. *Mi*-mediated resistance against the potato aphid *Macrosiphum euphorbiae* (Hemiptera: Aphididae) limits sieve element ingestion. *Environmental Entomology* 29:609-695. <https://doi.org/10.1603/0046-225X-29.4.690>.
- Kaloshian, I., Lange, W.H., and Williamson, V.M. 1995. An aphid-resistance locus is tightly linked to the nematode-resistance gene, *Mi*, in tomato. *Proceedings of the National Academy of Sciences of the United States of America* 92:622-625. <https://doi.org/10.1073/pnas.92.2.622>.
- Maluf, W.R., Campos, G.A., and Cardoso, M.G. 2001. Relationships between trichome types and spider mite (*Tetranychus evansi*) repellence in tomatoes with respect to foliar zingiberene contents. *Euphytica* 121:73-80. doi:10.1023/A:1012067505361.
- Maluf, W.R., Inoue, I.F., Ferreira, R.P.D., Gomes, L.A.A., Castro, E.M., and Cardoso, M.G. 2007. Higher glandular trichome density in tomato leaflets and repellence to spider mites. *Pesquisa Agropecuária Brasileira* 49:1227-1235. <http://dx.doi.org/10.1590/S0100-204X2007000900003>.
- Maluf, W.R., Silva, V.F., Cardoso, M.G., Gonçalves Neto, A.C., Maciel, G.M., and Nízio, D.A.C. 2010. Resistance to the South American tomato pinworm *Tuta absoluta* in high acylsugar and/or high zingiberene tomato genotypes. *Euphytica* 176:113-123. <https://doi.org/10.1007/s10681-010-0234-8>.
- Mantelin, S., Peng, H.C., Li, B., Atamian, H.S., Takken, W.L.F., and Kaloshian, I. 2011. The receptor-like kinase *SISERK1* is required for *Mi-1*-mediated resistance to potato aphids in tomato. *Plant Journal* 67:459-471. doi:10.1111/j.1365-313X.2011.04609.x.
- Neiva, I.P., Andrade Júnior, V.C., Maluf, W.R., Oliveira, C.M., and Maciel, G.M. 2013. Role of allelochemicals and trichome density in the resistance of tomato to whitefly. *Ciência e Agrotecnologia* 37:1. <http://dx.doi.org/10.1590/S1413-70542013000100007>.
- Nízio, D.A.C., Maluf, W.R., Figueira, A.R., Nogueira, D.W., Silva, V.F., e Gonçalves Neto, A.C. 2008. Caracterização de genótipos de tomateiro resistentes a begomovírus por marcador molecular codominante ligado ao gene *Ty-1*. *Pesquisa Agropecuária Brasileira* 43:699-1705. <http://dx.doi.org/10.1590/S0100-204X2008001200009>.
- Nombela, G., Williamson, V.M., and Muñiz, M. 2003. The root-knot nematode resistance gene *Mi-1.2* of tomato is responsible for resistance against the whitefly *Bemisia tabaci*. *Molecular Plant-Microbe Interactions* 16:645-649. doi:10.1094/MPMI.2003.16.7.645.
- Oliveira, C.M., Andrade Júnior, V.C., Maluf, W.R., Neiva, I.P., and Maciel, G.M. 2012. Resistance of tomato strains to the moth *Tuta absoluta* imparted by allelochemicals and trichome density. *Ciência e Agrotecnologia* 36:45-52. <http://dx.doi.org/10.1590/S1413-70542012000100006>.
- Pereira, G.V.N., Maluf, W.R., Santos, C.D., Gonçalves, L.D., Nascimento, I.R., Gomes, L.A.A., et al. 2008. Seleção para alto teor de acilaçúcares em genótipos de tomateiro e sua relação com a resistência ao ácaro vermelho (*Tetranychus evansi*) e a traça (*Tuta absoluta*). *Ciência e Agrotecnologia* 32:996-1004. <http://dx.doi.org/10.1590/S1413-70542008000300045>.
- Resende, J.T.V., Maluf, W.R., Cardoso, M.G., Gonçalves, L.D., Faria, M.V., and Nascimento, I.R. 2009. Resistance of tomato genotypes to the silverleaf whitefly mediated by acylsugars. *Horticultura Brasileira* 27:345-348. <http://dx.doi.org/10.1590/S0102-05362009000300015>.
- Resende, J.T.V., Maluf, W.R., Faria, M.V., Pfann, A.Z., and Nascimento, I.R. 2006. Acylsugars in tomato leaflets confer resistance to the South American tomato pinworm, *Tuta absoluta* Meyr. *Scientia Agricola* 63:20-25. <http://dx.doi.org/10.1590/S0103-90162006000100004>.

- Rodríguez-Álvarez, C., Muñiz, M., and Nombela, G. 2017. Effect of plant development (age and size) on the *Mi-1*-mediated resistance of tomato to whitefly *Bemisia tabaci*. *Bulletin of Entomological Research* 107:768-776. doi:10.1017/S0007485317000281.
- Rossi, M., Goggin, F.L., Milligan, S.B., Kaloshian, I., Ullman, D.E., and Williamson, V.M. 1998. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. *Proceedings of the National Academy of Sciences of the United States of America* 95:9750-9754. <https://doi.org/10.1073/pnas.95.17.9750>.
- Silva, A.A., Andrade, M.C., Maluf, W.R., Moraes, J.C., and Rezende, J.F. 2018. Resistance of tomato plant genotypes with high foliar allelochemical contents to the leafminer *Liriomyza trifolii*. *Arquivos do Instituto Biológico* 84:1-6. <http://dx.doi.org/10.1590/1808-1657000892015>.
- Silva, V.F., Cardoso, M.G., Moraes, J.C., Pimentel, F.A., Gonçalves, L.D., e Neri, D.K.P. 2008. Caracterização e avaliação de acilaçúcar sintético no comportamento da mosca-branca *Bemisia tabaci* (Gennadius, 1886) biótipo B (Hemiptera: Aleyrodidae) em tomateiro. *Ciência e Agrotecnologia* 32:1408-1412. <http://dx.doi.org/10.1590/S1413-70542008000500008>.
- Silva, V.F., Maluf, W.R., Cardoso, M.G., Gonçalves Neto, A.C., Maciel, G.M., Nízio, D.A.C., et al. 2009. Resistência mediada por aleloquímicos de genótipos de tomateiro à mosca-branca e ao ácaro-rajado. *Pesquisa Agropecuária Brasileira* 44:1262-1269. <http://dx.doi.org/10.1590/S0100-204X2009001000008>.
- Silva, A.A., Maluf, W.R., Moraes, J.C., Alvarenga, R., e Costa, E.M.R. 2013. Resistência a *Myzus persicae* em genótipos de tomateiro com altos teores foliares de aleloquímicos. *Bragantia* 72:173-179. <http://dx.doi.org/10.1590/S0006-87052013005000022>.
- Smith, P.G. 1994. Embryo culture of a tomato species hybrid. *Proceedings of the American Society of Horticultural Science* 44:413-416. doi:dx.doi.org/10.1590/S0102-05362002000400019.
- Toloy, R.J., Mituti, T., Freitas, D.M.S., Maluta, N.K.P., Silva, T.N.Z., Lopes, J.R.S., et al. 2018. Features of the relationship between *Tomato severe rugose begomovirus* and *Bemisa tabaci* MEAM1 reveal that the virus is acquired during a probe lasting only one minute. *European Journal of Plant Pathology* 151:541-547. doi:10.1007/s10658-017-1388-1.
- Toscano, L.C., Boiça Júnior, A.L., Santos, J.M., e Almeida, J.B.S.A. 2001. Tipos de tricomas em genótipos de *Lycopersicon*. *Horticultura Brasileira* 19:204-206. <http://dx.doi.org/10.1590/S0102-05362001000300009>.
- Vosman, B., van't Westende, W.P.C., Henken, B., van Eekelen, H.D.L.M., Vos, R.C.H., and Voorrips, R.E. 2018. Broad spectrum insect resistance and metabolites in close relatives of the cultivated tomato. *Euphytica* 214:46. <https://doi.org/10.1007/s10681-018-2124-4>.