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Article

Acylsugars in tomato varieties confer resistance to the whitefly and reduce the spread of fumagine

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ABSTRACT: Whiteflies (*Bemisia tabaci*) are a serious threat to tomato (*Solanum lycopersicum*) yield and production since all varieties are highly susceptible to this insect. The wild tomato *Solanum pennellii* shows resistance towards whiteflies infestation due the high contents of acylsugars presents in its leaflets, which is not observed in *S. lycopersicum*. Thus, plants from the F_2BC_2 population derived from the cross between the cultivar *S. lycopersicum* 'Redenção' and *S. pennellii* (accession LA-716) were selected for acylsugars levels and evaluated for resistance to whitefly and fumagine, a saprophyte fungus from genus *Capnodium* (sooty mold) that grows on leaves using whiteflies excretion. Biological behavior of *B. tabaci* was significantly influenced by the levels of acylsugars on the leaflets of the different genotypes. *Solanum pennellii* and the genotypes with higher acylsugars contents exhibited the lowest whitefly oviposition preference, number of nymphs, exuviae and adult survival. Also, the percentage of leaf coverage with fumagine was significantly reduced on leaves of the *S. pennellii* and the genotypes with higher acylsugars. Thus, it confirms that the use of *S. pennellii* LA-716 enabled the introgression of genes to increase the degrees of resistance in the F_2BC_2 genotypes. Finally, the results presented suggest that the genotypes RVTA-2010-31-177pl#39, RVTA-2010-31-319pl#214 and RVTA-2010-83-347pl#257 can be used as potential sources of genes for resistance to *B. tabaci* in tomato breeding programs.

KEY WORDS: *Solanum lycopersicum*, *Solanum pennellii*, *Bemisia tabaci*, *Capnodium*.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is among the most important vegetable crops worldwide and constitutes a highly nutritious food for millions of people. As for any other crop plant, tomato yield and quality are adversely affected by serious pests, including whiteflies (*Bemisia tabaci*). This insect brings direct damage to plants by feeding with sap secretion, which contains vital nutrients, triggering uneven fruit ripening. During this process, they can also serve as a vector of many virus diseases (Islam et al. 2018). Infestation of whitefly populations on tomato also promote the growth of saprophytic fungi fumagine (*Capnodium* sp.) due the sugary excretions left on leaves (honeydew). Fumagine colonization leads to growth of darkly pigmented hyphae on adaxial leaf surface, decreasing sunlight penetration and, as a consequence, the plant photosynthetic capacity. This disease may seriously harm tomato fruit yield and quality (Cameron et al. 2013).

In general, the commercial varieties are susceptible to whiteflies and the control of this pest is predominantly based on insecticides application, which is costly and environmentally hazardous. In addition, the excessive and constant use of these products compromises their performance along time, as more pests become resistant to them. The availability of alternative practices, such as resistant varieties use, are essential to provide integrated pest control (Gilbertson et al. 2011).

Also, resistant tomato genotypes that limit whitefly access and feeding might reduce the occurrence of fumagine and the process of plant virus transmission.

The restricted genetic variability in *S. lycopersicum* species is a limiting factor to the development of new tomato varieties. The selection during domestication and tomato breeding promoted the erosion of important genes and reduction of genetic diversity. The genetic variability present in wild tomato is 90% higher than in domesticated cultivars (Tanksley and McCouch 1997). As a consequence, many traits, including pest resistance, are not present on *S. lycopersicum* specie. In contrast, there is extensive knowledge about arthropods pest resistance on wild tomato species, which may serve as donor of genes in breeding programs (Gonçalves Neto et al. 2010; Oriani et al. 2011). In particular, *Solanum pennellii* has high breeding potential for whitefly resistance, since this specie have shown lower whitefly adult survival, lower nymph viability and lower oviposition rate (Firdaus et al. 2012).

The resistance mechanisms identified on tomato wild relatives are based on the presence of allelochemicals that are exuded by glandular trichomes (Gonçalves Neto et al. 2010; Lucini et al. 2015). The species *S. pennellii* have type IV glandular trichomes, which are also found on other wild species, such as *Solanum galapagense* and *Solanum pimpinellifolium*, but not on *S. lycopersicum* (Firdaus et al. 2012). The acylsugar is an important compound present on these glandular trichomes and may play a major role on pest resistance, possibly by the toxic effect on arthropods (Resende et al. 2006). A study involving *S. pennellii* showed that it was possible to reduce the whitefly oviposition rate on susceptible tomato treated with purified acylsugars extracts from *S. pennellii* (LA-716) (Leckie et al. 2016). Likewise, introgression of these traits—glandular trichomes containing acylsugars—in tomato cultivated plants had reduced whitefly infestation as well as other important pests (Pereira et al. 2008; Su et al. 2018). Interspecific hybridization between cultivated and wild species may increase genetic variability required for development of new varieties. However, in most cases this is not a simple task as an intensive backcrossing and efficient selection procedure is needed. In the specific case of resistance to pests, high acylsugars content in the leaflets, may constitute an efficient indirect criterion of selection (Resende et al. 2006). Thus, plants from the F_2BC_2 population derived from the cross between the cultivar *S. lycopersicum* 'Redenção' and *S. pennellii* (accession LA-716) were selected for acylsugars levels and evaluated for resistance to whitefly and fumagine.

METHODS

Tomato genotypes and growing seedlings

The tomato genotypes selected by Dias et al. (2016) from a F_2BC_1 population for high levels of acylsugars (RVTA-2010-31-177, RVTA-2010-83-347, RVTA-2010-31-319 and RVTA-2010-31-310) were used as parents and pollen sources for crosses with *S. lycopersicum* 'Redenção', obtaining the F_1BC_2 generation which, after self-fertilization, originated the F_2BC_2 population. The selection of contrasting genotypes for acylsugars content occurred in 600 seedlings of the F_2BC_2 population.

The levels of acylsugars were quantified in young and expanded leaflets according to the methodology proposed by Resende et al. (2002). To determine acylsugars levels, six leaf discs of each plant were removed with a 1 cm diameter punch and placed in test tubes. Subsequently, the acylsugars were extracted with the addition of 2 mL of dichloromethane and vortexed for 30 s. The extract obtained after saponification reactions and acid sucrose hydrolysis was subjected to the colorimetric test for reducing sugars, as proposed by Somogyi (1952). The samples were analyzed in a UV visible spectrophotometer model Cary 60 UV-Vis (Agilent Technologies, USA) and the absorbance was measured at a wavelength of 540 nm. The acylsugars concentrations in the leaflets were directly proportional to the absorbance values, which was used for the selection of genotypes. Values above 0.210 nm were considered for high-acylsugars content and values below 0.110 nm for low-acylsugars content. Following this standard, 50 tomato seedlings of cultivar Redenção (*S. lycopersicum* with low-acylsugars) and 50 seedlings of the wild genotype LA-716 (*S. pennellii* with high-acylsugars) were used as a standard of high and low allelochemical content. The F_2BC_2 genotypes were selected indirectly for laboratory resistance based on absorbance values.

The genotypes were cloned from axillary shoots, rooted and transplanted into polyethylene pots (5 dm^3) containing a mixture of commercial substrate and soil (1:1). In each pot was added 18 g of nitrogen, phosphorus and potassium in the 4–14–8 formulation. The acidity correction was performed according the crop demand, with the application of 2.6 g of calcium carbonate per pot. The plants were not submitted to phytosanitary control to avoid interference on the results.

Whitefly resistance test in F_2BC_2 tomato genotypes

The whiteflies *B. tabaci* were collected from commercial greenhouse tomato production in Faxinal city, state of Paraná, Brazil. For the rearing of *B. tabaci*, individuals were kept and multiplied on common bean (*Phaseolus vulgaris*) cultivar Uirapuru. The seedlings were grown in pots and packed in cages made with voile fabric (100 × 100 cm) in a greenhouse at 25 ± 3 °C with daily irrigation. From five to eight days after emergence, the adults were used for bioassays.

The bioassay was conducted in a greenhouse (temperature 27 ± 4 °C, humidity 75 ± 3% and photophase of 12 h) with a completely randomized design with 14 treatments, in four replications where each plant was considered a plot. The treatments were eight F_2BC_2 tomato genotypes selected for high acylsugars content, four F_2BC_2 genotypes selected for low acylsugars content, and the parents *S. pennellii* accession LA-716 and commercial cultivar Redenção (*S. lycopersicum*), used as controls for resistance and susceptibility, respectively. On the pre-flowering stage, the selected genotypes and the parents were infested with whitefly adults.

For infestation, an average of five whitefly adults of the same age were released on tomato leaflets, this is defined as beginning of economic damage (Hussain et al. 2019). The number of eggs, nymphs and exuviae were counted at seven, 14, 21, and 28 days after infestation. For this, three previously marked leaflet (thirds) were removed from the plants and taken to the Plant Physiology/Horticulture laboratory, where the number of eggs on the leaflet abaxial surface were counted on a 2 cm^2 area with a stereomicroscope. The number of eggs, nymphs and exuviae for each genotype was recorded as the average of the three leaflets. The number of adults was estimated in three leaflets with similar leaf area from upper, medium, and lower thirds. The values obtained were weighted to obtain the averages of each genotype.

Level of colonization by fumagine

The colonization of the fungus fumagine on plants leaf area was assessed 28 days after infestation with the whitefly. Upper, middle and lower leaves from four plants of each treatment were sampled and the adaxial surface analyzed using program QUANT v.1.0.1. in 300 dpi resolution. The percentage of leaf coverage with fumagine was calculated from each treatment.

Data analysis

In the bioassays with *B. tabaci*, the attractiveness index was estimated as in Eq. 1:

$$\mathrm{AI} = \frac{2G}{(G + S)} \tag{1}$$

where AI = attractiveness index, G = number of insects attracted to the evaluated genotype and S = number of insects attracted to the susceptible standard (*S. lycopersicum* 'Redenção'). The AI values varied between zero and two, where AI = 1 indicates a similar attraction between the evaluated genotypes (repellent test plant) and the standard (attractive test plant); AI < 1 corresponds to less attraction (greater repellency) to the genotype; and AI > 1 indicates a greater attraction to the evaluated genotype in relation to the standard. This index was adapted from Lin et al. (1990) and Baldin et al. (2005).

The index of preference for oviposition was determined using Eq. 2:

$$\mathrm{IPO} = \left[\frac{(T - P)}{(T + P)}\right] \times 100 \tag{2}$$

where T = number of eggs in the treatment and P = number of eggs in the standard genotype, cultivar Redenção. The index ranges from +100 (very stimulating) to –100 (total deterrence), with a value of zero indicating neutrality. The classification of the genotypes was made by comparing the average of treatment eggs with the average of the cultivar Redenção.

Lilliefors and Bartlett tests were used to test the normality and homogeneity of the data, respectively. When the data were not normal, they were previously transformed into $(x + 0.5)^{1/2}$ and sine arc of $(x + 0.5)^{1/2}$ to normalize them. Analysis of variance was, then, conducted, and the means were compared by Scott–Knott test. In the bioassay, orthogonal contrasts were estimated between groups of genotypes with contrasting levels of acylsugars, to characterize differences in levels of resistance to pests according to the levels of acylsugars. Associations among the variables evaluated were estimated using Pearson correlations through network correlation approach. Principal component analysis (PCA) was also performed. All statistical analyses were performed using the R software through the 'agricolae', 'FactoMiner', 'ggplot2', and 'qgraph' packages.

RESULTS AND DISCUSSION

Plants synthesize several specialized metabolites that act in resistance to herbivory. Normally, the enzymes that produce these specialized metabolites arise from proteins derived from duplicated and specialized genes (Fan et al. 2019; Liu et al. 2019). Among these metabolites, acylsugars notably found in *S. pennellii*, have been reported to be responsible for direct and indirect protection against herbivores (Luu et al. 2017). Its low toxicity generates interest for plant breeding, in particular to tomato.

In this study, contrasting genotypes were selected for acylsugars levels in a population derived from the cross between the genotypes 'Redenção' (*S. lycopersicum*) and LA-716 (*S. pennellii*). The genotypes RVTA-2010-31-177pl#28 (=RVTApl#28), RVTA-2010-31-177pl#39 (=RVTApl#39), RVTA-2010-83-347pl#61 (=RVTApl#61), RVTA-2010-31-177pl#113 (=RVTApl#113), RVTA-2010-31-177pl#177 (=RVTApl#177), RVTA-2010-31-177pl#180 (=RVTApl#180), RVTA-2010-31-319pl#214 (=RVTApl#214), RVTA-2010-83-347pl#257 (=RVTApl#257) and RVTA-2010-83-347pl#359 (=RVTApl#359) exhibited the highest levels of acylsugars. The genotypes RVTA-2010-83-347pl#77 (=RVTApl#77), RVTA-2010-31-310pl#205 (=RVTApl#205) and RVTA-2010-83-347pl#301 (=RVTApl#301) presented the lowest levels of acylsugars (Table 1).

Table 1. Acylsugar content, number of eggs, number of nymphs, number of adults, number of exuviae, and damage of fumagine (Fum) in tomato F_2BC_2 genotypes with different levels of acylsugar subjected to whitefly infestation.

Genotype[a]	Acylsugar content (540 nm)[b]	Number of eggs (2 cm^2)	Number of nymphs (2 cm^2)	Number of exuviae (2 cm^2)	Number of adults (leaf-let)	Damage of fumagine (%)
S. pennellii H	0.483a	0.00e	0.00f	0.00e	0.31f	16.72d
RVTApl#28 H	0.361b	10.00e	44.87d	4.00d	6.38c	14.40d
RVTApl#39 H	0.456a	3.13e	27.38e	3.75d	4.81d	4.58e
RVTApl#61 H	0.293d	11.50d	66.38c	10.25c	6.70b	32.55c
RVTApl#113 H	0.312c	9.94d	48.00d	1.50e	6.63b	26.29c
RVTApl#177 H	0.225d	12.56d	11.75f	0.25e	5.63c	2.96e
RVTApl#180 H	0.348c	11.63d	58.38c	5.75d	2.69e	40.61b
RVTApl#214 H	0.421a	9.56d	43.00d	0.50e	2.94e	24.68c
RVTApl#257 H	0.311c	13.75d	63.13c	4.00d	5.95b	28.09c
RVTApl#359 H	0.211d	11.06d	74.38b	2.75d	5.50b	29.49c
RVTApl#77 L	0.109e	17.75c	99.75a	23.50b	7.19b	42.10b
RVTApl#205 L	0.064f	22.38b	76.25b	10.50c	7.63b	40.14b
RVTApl#301 L	0.101e	18.79c	89.50a	36.75a	17.81a	51.21b
Redenção L	0.110e	25.69a	102.38a	10.75c	8.06b	70.29a
Coefficient of variation (%)		22.38	16.82	22.72	14.96	23.49
Contrast		–8.34**	–48.24**	–17.10**	–4.40**	28.90**

[a] Means followed by the same letter do not differ by Scott–Knott test at significance level of 5%.

**Significant contrast at 1% level of significance between groups of genotypes classified as containing high (H) and low (L) acyl sugars.

Biological behavior of *B. tabaci* was significantly influenced by the levels of acylsugars on the leaflets of the different F_2RC_2 genotypes, cultivar Redenção and the wild species *S. pennellii* LA-716, for which oviposition, number of nymphs, exuviae and adult survival were monitored. Detailed results on these analyzes are shown in Table 1, where in Scott–Knott test revealed the arrangement of distinct groups for each variable. The average number of deposited eggs on tomato genotypes leaves ranged from 0.00 (*S. pennellii*) to 25.69 per 2 cm^{-2} ('Redenção'). Based on this attribute, the genotypes were classified into five groups. *Solanum pennellii* and the genotype RVTApl#39 exhibited the lowest whitefly oviposition preference. The number of eggs was also significantly reduced in the remaining genotypes when compared to cultivar Redenção and genotype RVTApl#205, which have low levels of acylsugars (Table 1).

Nymphs survival also differed among the genotypes, ranging from 0.00 (*S. pennellii)* to 102.38 nymphs per 2 cm^{-2} ('Redenção'). According to these variables, the genotypes were arranged in six distinct groups. The group with the lowest nymphs population was composed by *S. pennellii* and the genotype RVTApl#177. The genotypes RVTApl#77 and RVTApl#301 as well as the cultivar Redenção harbored the highest nymphs population. It is worth noting that, with the exception of genotype RVTApl#359, all genotypes containing high acylsugars levels showed significantly reduced number of nymphs when compared to cultivar Redenção and genotypes with low acylsugars levels (Table1). In addition to the direct effect of the high acylsugars content in the wild species *S. pennellii* and in some genotypes, the reduction in nymph abundance may be a reflection of the lower oviposition in these genotypes. Similar results were also described by Gouveia et al. (2018) and Dias et al. (2016).

Exuvia is the arthropod exoskeleton after ecdysis and can represent an important factor on determining the plant resistance as it demonstrates the number of nymphs that can effectively reach adult stage. In this study, the number of exuviae ranged from 0.0 (*S. pennellii*) to 36.75 exuviae per 2 cm^{-2} (RVTApl#301) and the genotypes were arranged in five distinct groups. Similar to previous results, the group with the lowest number of exuviae was composed by *S. pennellii* and the genotypes RVTApl#177, RVTApl#113 and RVTApl#214, all genotypes described as high acylsugars levels (Table 1).

The number of adults ranged from 0.31 (*S. pennellii*) to 17.81 per leaflet (RVTA-2010pl #301). Only the wild access *S. pennellii* was part of the group with lowest number of adults, although the presence of whitefly was significantly reduced on some genotypes with high levels of acylsugars (RVTApl#180, RVTApl#214 and RVTApl#39) compared with the remaining genotypes and the cultivar Redenção (Table 1). In view of all the whitefly resistance characteristics evaluated, the number of live adults is perhaps the most important, as, at this stage, the insect causes all types of possible damage, direct and indirect, with emphasis on food, the transmission of viruses and the excretion of sugary substances, responsible for the development of fumagine (Su et al. 2018). The percentage of leaf coverage with fumagine varied among the genotypes, ranging from 4.58 to 70.29%. *Solanum pennellii* and the genotypes RVTApl#39 and RVTApl#177 exhibited the lowest leaf coverage with fumagine. Also, the presence of fumagine was significantly reduced on leaves of the remaining genotypes compared with the genotypes RVTApl#77, RVTApl#205, RVTApl#301 and the cultivar Redenção (Table 1).

The C1 contrast analysis demonstrated inverse and significant relationship ($p < 0.01$) between genotypes with high and low acylsugar levels for all analyzed variables, demonstrating efficiency of the chemical factors present on the genotypes on the deterrence of the whitefly. The C2 contrast analysis also demonstrated the inverse and significant relationship between the genotypes with high and low acylsugar levels for the presence of fumagine (Table 1).

According to the values of the attractiveness index estimated after 24 h of infestation, all genotypes with high acylsugar content were classified as repellent to *B. tabaci* when compared to the susceptible standard genotype *S. lycopersicum* 'Redenção' (Fig. 1). Besides, the preference index for oviposition, calculated in the bioassay, classified all materials with high levels of acylsugars as not preferred to oviposition by *B. tabaci*, when compared to susceptible *S. lycopersicum* 'Redenção' and the allelochemical low genotype (Fig. 1). S*olanum pennellii* showed the lowest attractiveness to whitefly, followed by the genotypes RVTApl#180 and RVTApl#214, both selected for high levels of acylsugars. The others high-content genotypes showed medium to low attractiveness, while the low-content allelochemical genotypes, including the standard cultivar Redenção, showed high attractiveness to *B. tabaci*, biotype B (Fig. 1).

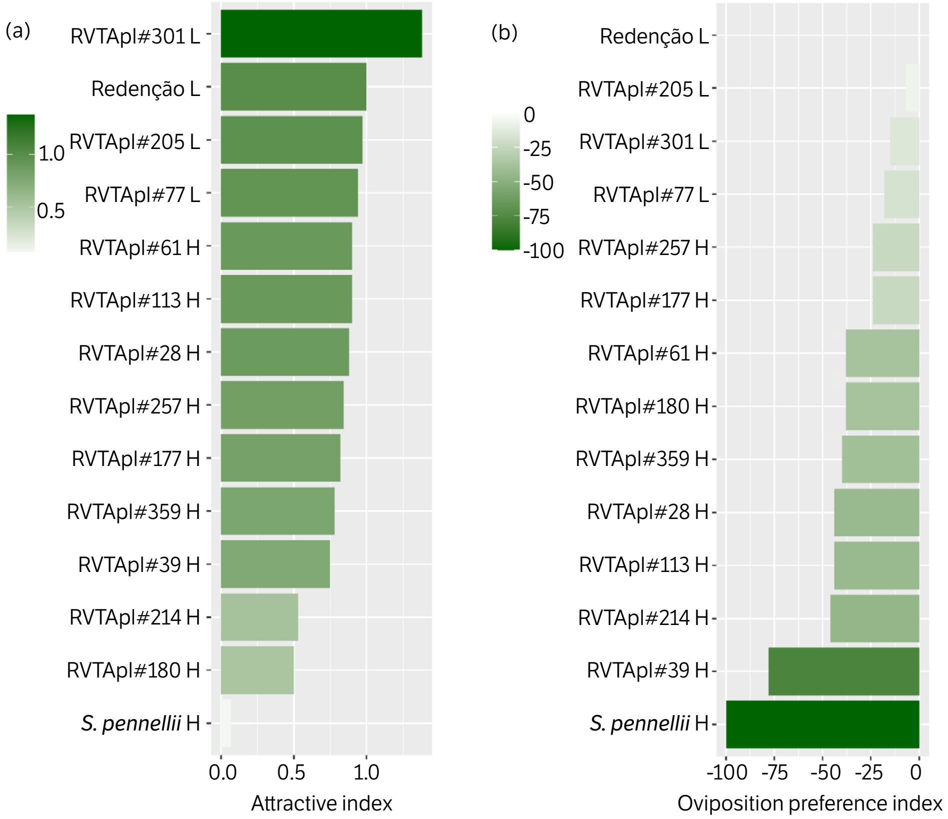

Figure 1. Attractiveness index - IA (a) and preference index for oviposition - IPO (b) in tomato genotypes with contrasting levels of acylsugars by whitefly.

The results of Pearson correlation analysis revealed that there was significant and negative correlation between acylsugars content and the number of eggs (−0.78), number of nymphs (−0.77), number of exuviae (−0.65) and number of adults (−0.64) on the evaluated genotypes. The correlation also revealed that there was a significant negative correlation between acylsugar content and percentage of leaf coverage with fumagine (−0.64) (Fig. 2).

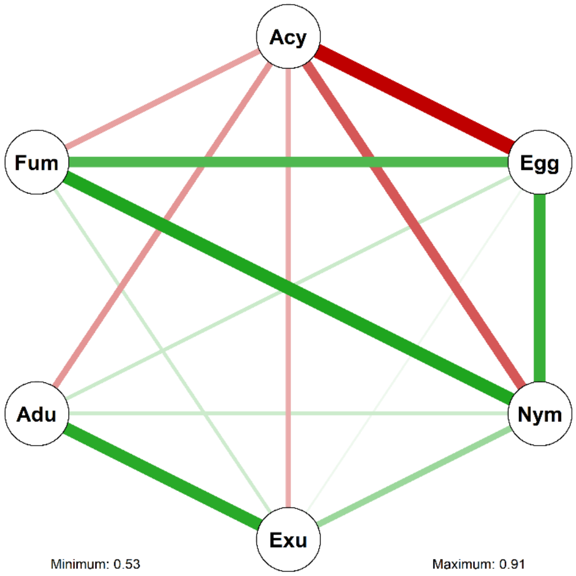

Figure 2. Network correlation of the variables acylsugar content (Acy), number of eggs (Egg), number of nymphs (Nym), number of adults (Adu), number of exuviae (Exu), and damage of fumagine (Fum).

The PCA, which explains 90.87% of the data variability through the first two principal components (PC1 and PC2), shows that the highest levels of acylsugars contributed to separate the genotypes into four groups. Group one contains the genotypes RVTApl#61, RVTApl#77 and RVTApl#301. In the group two are the genotypes *S. pennellii*, RVTApl#28, RVTApl#39 and RVTApl#113, all selected for high levels of acylsugars. Group three is formed by the genotypes RVTApl#214, RVTApl#177 and RVTApl#180, also with high levels of allelochemical. Group four contains the low acylsugars genotypes, 'Redenção', RVTApl#205, RVTApl#359 and RVTApl#257. The left quadrant of the graph display genotypes with high acylsugars levels, with opposite vectors for the quadrants, which refers to the lowest whitefly number of eggs, nymphs, exuviae and adults. Genotypes arranged in the right hemisphere had a large abundance of eggs, nymphs, exuviae and adults (Fig. 3).

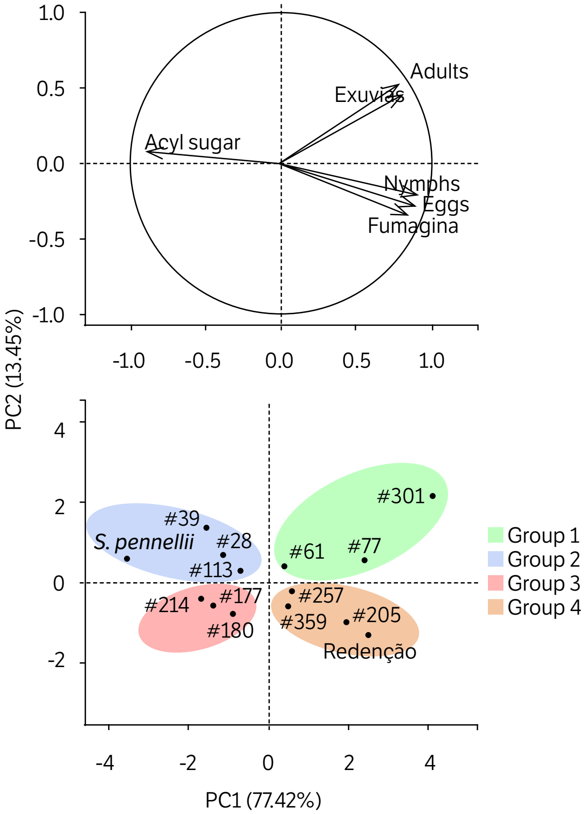

Figure 3. Principal component analysis of 14 tomato genotypes evaluated for the variables acylsugar content (Acy), number of eggs (Egg), number of nymphs (Nym), number of adults (Adu), number of exuviae (Exu) and damage of fumagine (Fum).

Acylsugars are largely known for conferring deleterious effects on insects life cycle. Possibly, the high levels of this allelochemical in the wild species *S. pennellii* and genotypes selected for high levels interfered in the biological behavior of *B. tabaci*. In the bioassays, it was possible to observe that the adults of *B. tabaci* rejected the genotypes with high acylsugars content. For this arthropod, the number of eggs deposited on leaflets of *S. lycopersicum* 'Redenção' (the susceptible standard treatment) and the genotypes with low acylsugar content was higher compared to *S. pennellii* (the resistant standard treatment) and the genotypes with high acylsugar content.

Various researches emphasize the effect of acylsugars on the control of pest arthropods (Ben-Mahmoud et al. 2018), including the whitefly (Dias et al. 2016). The deterrence imposed by the pest occurs through mechanisms of the type antixenosis and antibiosis (Lucini et al. 2015), in which genotypes with high levels of this substance decrease the preference for feeding and oviposition, as it was observed in the present research. Results presented by Rodríguez-López et al. (2011) in experiments with a breeding line derived from the wild tomato *S. pimpinellifolium* in a *S. lycopersicum* background show that acylsucrose is an antixenotic factor that deters the landing and settling of *B. tabaci*. Moreover, these structures delay stylet penetration, resulting in a reduced ability to reach the phloem. In another similar study, it was shown that acylsucrose-producing tomato plants, also derived from the wild tomato *S. pimpinellifolium*, modifies the innate behavior of *B. tabaci* for settling and feeding on the abaxial surface, forcing them to feed on the adaxial side of tomato leaves. This altered behavior is likely due to the presence of deterrent acylsugars secreted by the type IV glandular trichomes, which are mainly located on the abaxial surface and almost absent on the adaxial leaf surface, demonstrating that whiteflies can avoid the presence of glandular trichome exudates (Rodríguez-López et al. 2012). These results are consistent with previous findings that report lower whitefly oviposition in tomato genotypes with high levels of acylsugars in segregating population (Dias et al. 2016; Lucini et al. 2015).

The phenotypic expression for high levels of acylsugars in advanced populations from the cross between *S. pennellii* and *S. lycopersicum* has been reported in research involving backcrosses (Maluf et al. 2010; Smeda et al. 2018). The inheritance of acylsugars contents is mediated by a maximum of two genes, not discarding minor genes with an additive effect (Baier et al. 2015) and epistatic effects when in interaction with the pest (Smeda et al. 2018). Thus, segregations for allelochemical content are commonly observed in advanced populations (Oliveira et al. 2020). Genotyped strains with high levels of acylated sugar were crossed with *S. pennellii* in a survey conducted by Leckie et al. (2012). These authors found that the segregating population obtained showed variations in the levels of acylated sugars in the offspring, as found in the present study.

In general, all solanaceous have higher or lower acylsugars as a secondary metabolite and with different chemical structure (Liu et al. 2019). However, the shape of this acylsugars may have an influence on the pest behavior, being more or less effective. Among the most important types, present in wild tomato *S. pennellii*, *S. galapagense* and *S. pimpinelifollium*, are acylglucose and acylsucrose. Thus, it is inferred that not only the content of the allele chemical acts in the control of the pest but also the type. According to Fan et al. (2019) when attacked by a pest, a similar type of inversion is synthesized, transforming acylsucrose into acylglucose, which has the greatest effect on herbivory. This fact explains the occurrence of genotypes that present high levels of acylsugars and low levels of resistance to a pest, as observed for the genotype RVTApl#359, in the present research.

Acylsugars are synthesized from sucrose and acyl-CoA, commonly available through biosynthetic pathways. It is known that environment interaction, for example, allows the synthesis of acylsugars acylhydrolases (ASHs), which remove the acyl chains from specific positions, modifying its structure, creating alternative substrates (Schilmiller et al. 2016). Understanding the mechanisms by which the acyl-CoA substrates originate the acylsugars can lead to interesting strategies to manipulate their synthesis and also weave strategies to improve tolerance to pests, and explain how phenotype expression occurs in segregating populations (Leckie et al. 2016).

CONCLUSION

The results of this study show that acylsugar content in tomato affects the preference and feeding behavior of *B. tabaci* and reduce the spread of fumagine. Thus, it confirms that the use of *S. pennellii* LA-716 enabled the introgression of genes to increase the degrees of resistance in the F_2BC_2 genotypes. Finally, the results presented suggest that the genotypes RVTA-2010-31-177pl#39, RVTA-2010-31-319pl#214 and RVTA-2010-83-347pl#257 can be used as potential sources of genes for resistance to *B. tabaci* in tomato breeding programs. The results obtained show that the genetic improvement of this species, mediated by allelochemicals present in wild species, is an excellent alternative for obtaining cultivars with better adaptation to sustainable production systems.

AUTHORS' CONTRIBUTION

Conceptualization: Resende, J. T. V.; **Methodology:** Dias, D. M. and Resende, J. T. V.; **Investigation:** Dias, D. M., Resende, N. C. V., Zanin, D. S. and Lima Filho, R. B.; **Writing – Original Draft:** Erpen-Dalla Corte, L. and Zeffa, D. M.; **Writing – Review and Editing:** Resende, J. T. V.; **Funding Acquisition:** Resende, J. T. V.; **Resources:** Resende, J. T. V.; **Supervision:** Resende, J. T. V.

DATA AVAILABILITY STATEMENT

The data will be available upon request.

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