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Tomato Breeding for Insect-Pest Resistance

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Abstract

The tomato is susceptible to pest attacks that can lead to damages throughout the crop cycle. Pest control is carried out, mainly, by insecticide and chemical acaricide spraying. However, the use of chemical pest control can cause severe damage to the environment, biological imbalances and deleterious effects on farmers and consumer health, as well as increased production costs. An interesting alternative to minimizing the problems arising from the agrochemical application and maintaining pest populations below the economic damage level is the development of tomato plants displaying resistance to insect and arachnid pests. In this context, the main purpose of this chapter is to provide a review of the techniques applied in this regard, major progresses to date and future prospects for tomato pest-resistance breeding. This chapter is divided into five sections: (1) wild pest-resistant tomato species, (2) allelochemicals that confer pest resistance, (3) techniques used for the introgression of pest resistance genes (4) overview, challenges and prospects for pest-resistant tomato breeding and (5) final considerations.

Keywords: *Lycopersicon* sp., allelochemicals, genetic resistance, insects, mites, wild species

1. Introduction

Tomato breeding, from the characterization of wild accessions to the development and release of new technologies, has contributed considerably to increases in tomato productivity. It is possible that tomatoes cultivation for fresh consumption and processing will become even more competitive in the next years. Therefore, investments are required for the development

of new strains or hybrids, which, allied to productive potential, present pathogen, insect and pest-resistant characteristics and adaptations to adverse climatic cultivation conditions. In addition, measures that improve production techniques, as well as the transportation and commercialization logistics of the final product, are also relevant [1].

Although they display great productive potential, tomato crops are one of the most susceptible to pest attack throughout the crop cycle. Even in protected crops, pest occurrence can cause heavy losses. In general, the main pests that attack this crop in the productive regions worldwide are the biotype B whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aphididae), the aphids *Myzus persicae* and *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae), the thrips *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae), the tomato leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), the leafminer fly *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae), the corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), the tomato fruit bearer moth *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), the caterpillar *H. armigera* and the arachnids *Tetranychus urticae* (Koch) and *evansi* (Baker; Pritchard) (Acari: Tetranychidae) [2–4].

Chemical control by insecticide and acaricide spraying is still the main approach used to control tomato crop pests. However, the use of these products as the sole or main management method can cause severe damage to the environment, such as biological imbalance, deleterious effects on rural and consumer health, as well as increased production costs [5–7].

In order to minimize chemical control problems and maintain pest populations below the level of economic damage, alternative control tactics have been sought for joint use in integrated pest management. Among these, insect and arachnid plant resistance developed by breeding programs is considered ideal, due to relatively low costs, allowing pests to be maintained below the level of economic damage and in balance with their natural enemies. In addition, this technique does not pollute the environment and, above all, does not endanger human health [8–10].

Although cultivated tomato species show great morphological diversity, they present a narrow genetic base due to their domestication having occurred outside South America, which is their center of origin. Therefore, the genetic diversity present in wild tomato species has been explored for the crop breeding. Although these species do not present commercial value due to unfavorable characteristics, such as small and usually pubescent fruits, they display pest-resistant characteristics [11–14].

2. Pest-resistant wild tomato species

In addition to the cerasiform variety, the cultivated tomato *Solanum lycopersicum* L. comprises several wild species, with which it has greater or less interspecific cross-compatibility (Table 1) [11, 15]. These species are native to regions located along the western South America coast, encompassing mainly the Andes in Ecuador, Peru and northern Chile, as well as the Galapagos Islands. Thus, these are species that have developed in a variety of habitats, from

Section	Group	Species	Geographical distribution
<i>Lycopersicon</i>	Lycopersicon	<i>S. lycopersicum</i>	Cultivated worldwide
		<i>S. pimpinellifolium</i>	Coast of Ecuador to Chile
		<i>S. cheesmaniae</i>	Galapagos Islands
		<i>S. galapagense</i>	Galapagos Islands
	Neolycopersicon	<i>S. pennellii</i>	Western Andean slopes from Peru to Chile
	Eriopersicon	<i>S. habrochaites</i>	Mountains of Ecuador and Peru
		<i>S. huaylasense</i>	Callejón de Huaylas, Peru
		<i>S. corneliomulleri</i>	Western Andean slopes of southern Peru
		<i>S. peruvianum</i>	Coast of Peru to the north of Chile
		<i>S. chilense</i>	Chilean coast and southern Peru
	Arcanum	<i>S. Arcanum</i>	Northern Peru, inter-Andean and coastal valleys
		<i>S. chmielewskii</i>	South of Peru
		<i>S. neorickii</i>	Ecuador to Peru, inter-Andean valleys
Lycopersicoides	—	<i>S. lycopersicoides</i>	Southern Peru and northern Chile
		<i>S. sitiens</i>	Southern Peru and northern Chile
Juglandifolia	—	<i>S. juglandifolium</i>	Colombia, Ecuador and Peru andes
		<i>S. ochranthum</i>	Ecuador and Peru andes

Adapted from Peralta et al. [11].

Table 1. Recognized *Solanum* tomato species and their geographical distribution.

sea level in the Pacific Coast to 3300 m of altitude in the Andean mountains of Ecuador, in climates that range from arid to rainy [16].

Genetic diversity between species is expressed through different morphological, physiological and sexual characteristics [17–20]. It is very probable that Andean geography, with its diverse ecological habitats and different climates, contributed significantly to tomato diversity [16].

Wild tomato species are valued for use in breeding programs because they present resistance genes to pests, phytopathogens and abiotic stresses, as well as higher nutritional quality [12–14, 21–27]. During evolution, wild plants underwent selection pressure in order to survive and guarantee their reproduction in their center of origin conditions, developing resistance mechanisms against the most adverse conditions present in their natural environment [20].

The following wild species display resistance to pest insects and arachnids: *S. pennellii*, *S. habrochaites* var. *hirsutum* e var. *glabratum*, *S. galapagense*, *S. peruvianum*, *S. pimpinellifolium*,

S. cheesmaniae and *S. chmielewskii* [12–14, 28–33]. Research has demonstrated the efficiency of these species in the transmission of genes that express certain desirable characteristics, such as the production of glandular trichomes that, in most cases, exude chemical compounds, called allelochemicals [14, 34].

3. Allelochemicals

Allelochemicals are natural chemicals mainly present in higher plants that act as nutritional, antinutritional, herbal, medicinal and pest- and disease-resistance factors. The chemical substances responsible for plant resistance to pest insects and arachnids can be classified into three categories: substances that act on pest behavior (glycosides, alkaloids, terpenes, phenols and essential oils); those that act on pest metabolism, such as secondary metabolites (including some alkaloids and quinones, among others); and antimetabolites, which make essential nutrients unavailable to pests, causing nutritional imbalances [2].

The most important allelochemicals found in wild tomato species are acyl sugars, sesquiterpenes and methyl ketones [28, 35–37]. Acyl sugars (AA), such as acylglycosis and acylsucrose, are found in *S. pennellii* [14, 36, 38, 39] and *S. galapagense* accession [40] leaf trichomes. Sesquiterpenes, mainly zingiberene (ZGB), are found in *S. habrochaites* var. *hirsutum* [35] accessions, while methyl ketone, 2-tridecanone (2-TD), is found in *S. habrochaites* var. *glabratum* accessions [28, 41–43].

3.1. Leaf trichomes

The *Solanum* genus presents seven types of trichomes. Their classification is based on the length of the trichome, the presence or absence of the gland at the apical end and the number of cells that make up the gland, when present. Trichomes are classified into two types, non-glandular trichomes (II, III, V), which are quite similar to each other, differing only in length, and glandular trichomes (I, IV, VI, VII), capitated, with the head, in most cases acting as the allelochemical secretory region [44].

Wild tomato accessions display an abundance of type I, IV and VI trichomes. In contrast, cultivated tomato display mostly type V trichomes, with the rare presence of types I and VI [33]. On the other hand, types I, IV and VI, due to the presence of allelochemicals, are considered to be of major importance in pest resistance (**Figure 1**).

Trichomes, besides acting as chemical barriers, can also act as physical barriers, limiting pest insect and arachnid access to the plant surface, due to trichome density and length [37].

3.2. Acylsugars

Acylsugars (AA) are glucose or sucrose esters containing acyl groups (**Figure 2**) present in type IV glandular trichomes [45]. In *S. pennellii* accession ‘LA 716’, the main AA is 2,3,4-tri-O-acyl-glucose. Its resistance character is presumably due to the fact that it confers a sticky

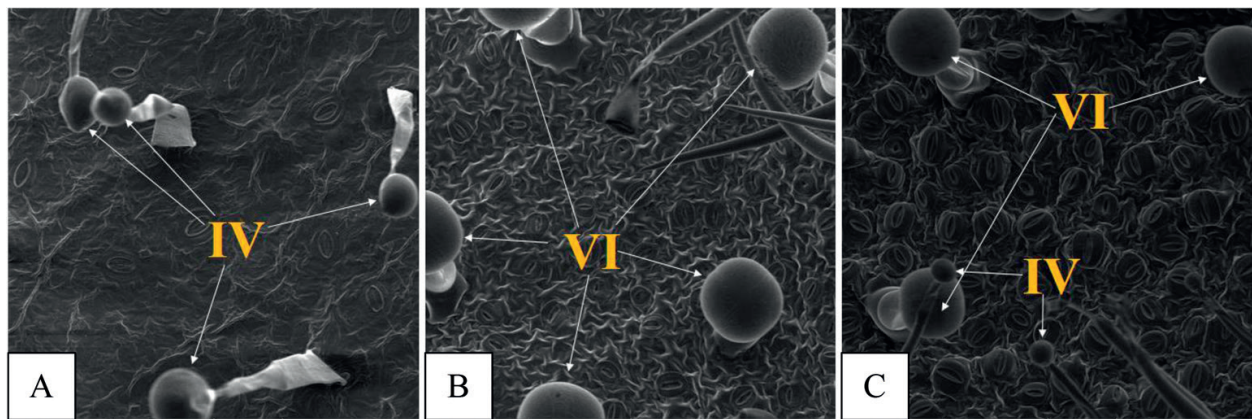


Figure 1. Scanning electron microscopy micrographs of glandular trichomes on the abaxial leaf surfaces of wild tomato species: type IV trichome in *S. pennellii* (A), type VI trichome in *S. habrochaites* var. *glabratum* (B) and type IV and VI trichomes in var. *hirsutum* (C).

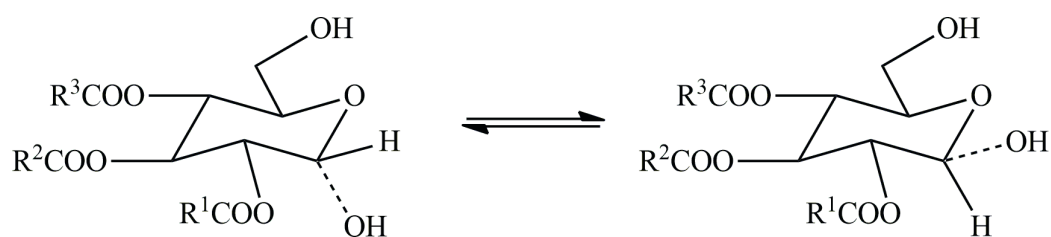


Figure 2. Chemical structure of acylsugars.

appearance to leaf surfaces, which acts as a natural trap, avoiding pest insect oviposition, feeding or even causing deleterious effects on their development [13, 46, 47].

3.3. Zingiberene

Zingiberene (ZGB) is another naturally occurring, biologically active allelochemical that confers pest insect and arachnid resistance to [48]. ZGB is a monocyclic sesquiterpene consisting of three isoprene units, with the molecular formula $C_{15}H_{24}$ (**Figure 3**).

ZGB is present in type IV and VI glandular trichomes, found in the wild species *S. habrochaites* var. *hirsutum* [22]. Accession ‘PI-127826’, rich in ZGB, is resistant to the mite *T. urticae* [49], to the tomato moth [50] and to other pests [32].

3.4. 2-Tridecanone

The allelochemical 2-tridecanone (2-TD) (**Figure 4**) is a sticky liquid that both binds insects to the plant and accumulates in the insect labium, leading to difficulty in feeding [37]. 2-TD is found on the heads of type VI trichomes, mainly in accession ‘PI134417’, referring to var. *glabratum* [51]. This insect-toxic substance is found at higher levels (72-fold) in *glabratum* compared to *S. lycopersicum* [52].

Several studies have observed the association of pest resistance in *S. habrochaites* var. *glabratum* and the presence of the methyl ketone 2-TD [53–55].

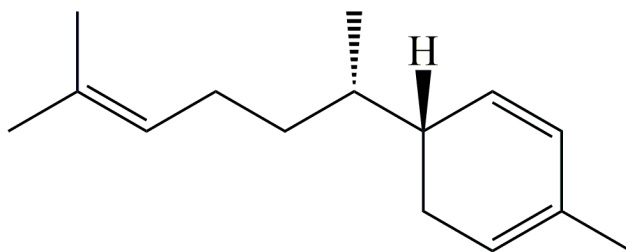


Figure 3. Chemical structure of zingiberene.

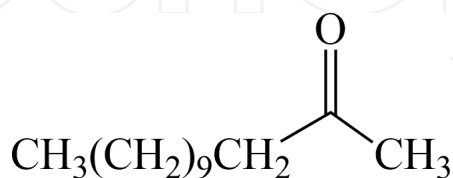


Figure 4. Chemical structure of 2-tridecanone.

4. Techniques used for introgression of pest-resistance genes

To initiate genetic breeding programs aiming at pest insect and arachnid resistance, it is necessary to work with the crop of economic interest and its main pests, in order to select resistance sources, determine the mechanisms/types of resistance involved and structure the program breeding. Regarding the latter, almost all breeding methods can be used, and the choice will depend on the reproduction mode of the plant and the type of gene action that conditions the characters attached to the resistance. Other important aspects should also be considered, such as the need for a large numbers of insects and arachnids for plant infestation/evaluation in replicate experiments, the need for representative pest occurrence conditions, trained personnel to perform the evaluations and method feasibility [56, 57].

Tomato breeding programs aimed at obtaining pest-resistant cultivars have adopted the strategy of incorporating genes responsible for the production of glandular allelochemicals and/or trichomes [58–67]. This strategy has succeeded because the selection for high allelochemical content and, in some cases, glandular trichomes, has led to correlated responses regarding increased resistance to key tomato pests. Breeding programs have commonly performed the hybridization method between pest-resistant wild-type accessions and commercial crops of suitable agronomic value and highly productive traits, followed by backcrossing to the commercial *S. lycopersicum* cultivar (Figure 5). This technique is promising with regard to obtaining lines displaying higher pest insect and arachnid resistance levels [38, 39, 58–60, 64–66].

4.1. Resistance introgression with acylsugars

The first selection of pest-resistant plants in generations descended from interspecific crosses between *S. lycopersicum* and *S. pennellii* accession 'LA-716' (high AA content) took

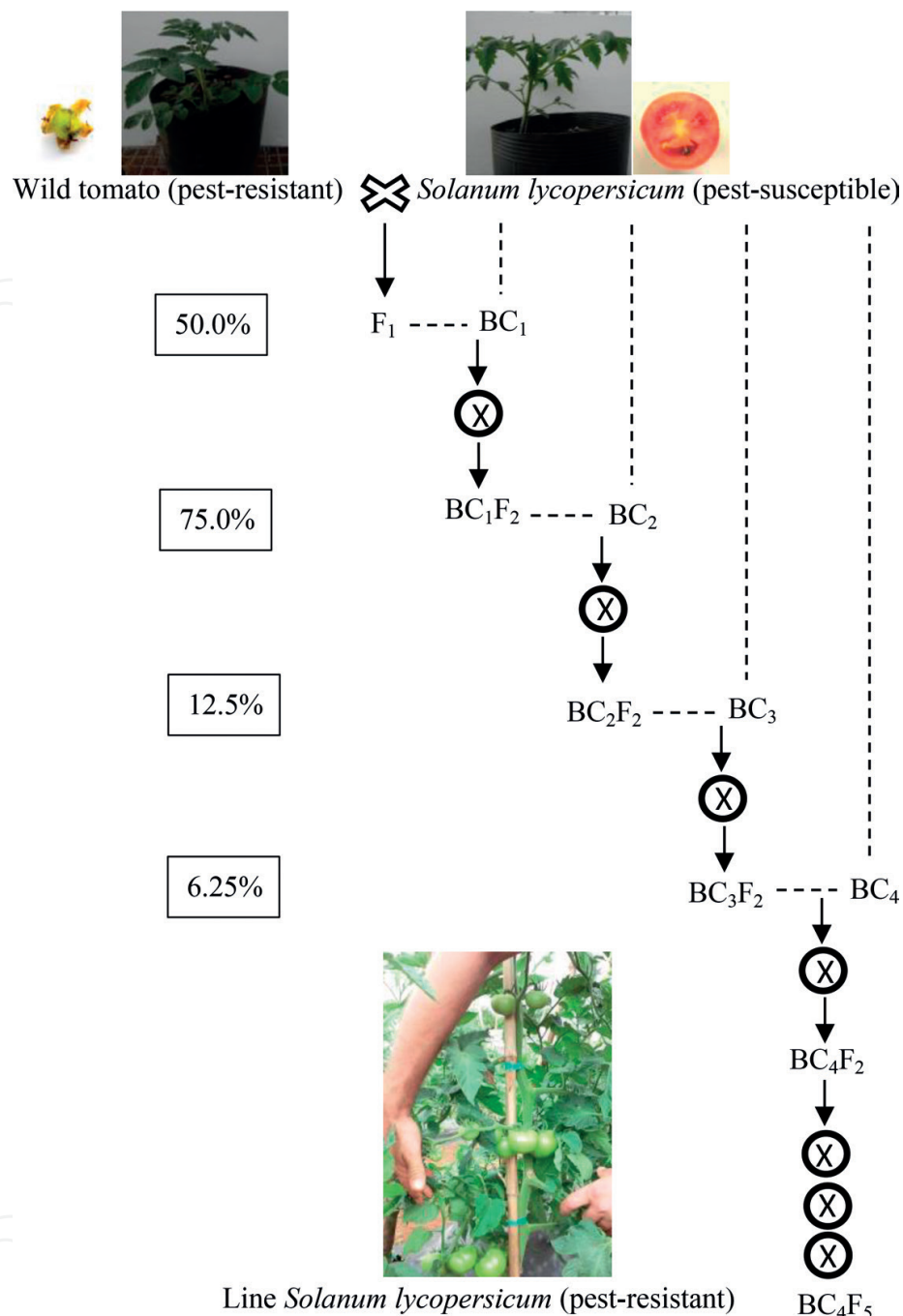


Figure 5. Hybridization (F_1) method between pest-resistant wild-type access and *Solanum lycopersicum*, followed by backcrossing (RC) to the commercial *S. lycopersicum* cultivar until obtaining lines with desirable agronomic characteristics and resistance to pests.

into account morphological and physiological characteristics of plants to identify resistance [13, 68]. These authors also recommend that, for the efficient selection of tomato plants, it is necessary to expose the plants to the pest infestation, allowing for breeding in the quality of the initial evaluation and leading to selection of plants displaying much higher levels of resistance.

When evaluating tomato F_2 genotypes selected for high AA content from interspecific cross-breeding *S. lycopersicum* x accession 'LA-716', high levels of resistance to whitefly were obtained, with a lower oviposition index and 100% of adults trapped in exudates [58]. Thus, resistance evaluations led to the detection of allelochemical efficiency regarding resistance of tomato breeding lines to mites, tomato moths [12], whiteflies [64, 69] and western flower thrips (*Frankliniella occidentalis*) [69]. It was further verified that plants descendants of the crossing between 'LA716' and *S. lycopersicum* are resistant to aphids [13, 61].

Experiments were performed with plants selected for high and low AA content in the F_2 population of the crossing between *S. lycopersicum* 'TOM-584' and accession 'LA-716' and the F_2 population of the first backcrossing for *S. lycopersicum* [59, 60, 69, 70]. These plants were submitted to *T. evansi* mite and whitefly and tomato moth repellency assays, alongside the parent plants, and positive AA effects on mite repellency and the control of other pests were observed. In an experiment with AA-rich tomato genotypes, an even lower oviposition rate of tomato moths and lower damage levels to the plants were observed when compared to genotypes with low allelochemical levels [24].

When studying the inheritance of the AA content character of the 'LA716' accession, an estimate of 1.36 for the number of genes involved is obtained, suggesting a monogenic inheritance [39]. These authors observed a relatively high value for AA content heritability in the broad sense (0.48), indicating that much of the F_2 generation plant variations were genetic in nature. When evaluating AA content inheritance in other studies, the authors observed similar results [24, 71]. Normally, when measured directly, resistance heritability toward insect pests does not present high values, in contrast to what was observed for AA content (which is an indirect selection criterion). These characteristics are due to the difficulty of the environmental control of a direct resistance evaluation system that covers not only the plant and the environment, but also the pest [13].

In the advances made by the breeding programs using the accession 'LA716' as a donor parent, it is verified that AA implies in a variety of interactions between the plant and the pests, including feeding deterrence and changes in pest reproductive potential [13, 68, 69, 70]. As a result of the efforts of breeding programs, tomato lines with high potential to resist pests were developed. The tomato line CU071026, containing high content of AA, was bred from *S. pennellii* accession 'LA716' and contains five introgressions from 'LA716' [64]. In addition, the AA-rich lines TOM-687, TOM-688 and TOM-689 exist [12, 55] and pre-commercial hybrids obtained from an AA-rich tomato inbred line [72].

Studies using *S. galapagense* as an AA source are more recent when compared to *S. pennellii*. As in *S. pennellii*, the presence of AA in *S. galapagense* is closely associated to the presence of type IV glandular trichomes [73]. These authors, when investigating the inheritance of type IV glandular trichome density and its association with whitefly resistance, identified high estimates for heritability, both broadly and in the narrow sense. They suggested that this character displays a relatively simple inheritance and that resistance is associated to a higher density of type IV glandular trichomes. The authors also identified molecular markers for two higher-effect quantitative trait

loci from the *S. galapagense* accession 'LA1401' (one locus located on chromosome 2 and one on chromosome 3), associated to high density of type IV trichomes.

The *S. galapagense* 'PRI9500/PY-8027' accession has been noted as providing higher resistance levels to whitefly by non-preference mechanisms for oviposition and antibiosis [74]. These authors observed a high correlation between higher resistance levels and high density of type IV trichomes, which possibly produce AA and make leaves stickier.

When resistance to the *Helicoverpa armigera* caterpillar (Lepidoptera: Noctuidade) was evaluated in tomatoes obtained from the interspecific cross of *S. lycopersicum* × *S. galapagense*, the F₂ population genotypes, presenting a high density of type IV glandular trichomes, displayed higher resistance levels, both by antibiosis and antixose, than genotypes presenting low glandular trichome density [40].

4.2. Zingiberene resistance introgression

Higher ZGB content is associated with higher resistance levels to mites in populations originating from the cross between *S. lycopersicum* and *S. hirsutum* var. *hirsutum* [22]. Proof of the effectiveness of ZGB regarding whitefly resistance were observed in F₂ generation genotypes of interspecific crosses between *S. lycopersicum* 'TOM-556' and *S. habrochaites* var. *hirsutum* accession 'PI-127826'. Plants containing high ZGB content presented higher resistance levels to pest insects than the commercial tomato *S. lycopersicum* 'TOM-556' (low ZGB content) [75].

A positive genetic correlation between ZGB content and type IV, VI and VII trichome density for an interspecific intersection of *S. lycopersicum* × accession 'PI-127826' was observed [75]. In addition, that study also observed that ZGB content can be explained, in large part, by the action of a single main gene locus, where the var. *hirsutum* allele that conditions high ZGB content is recessive (incompletely) on the *S. lycopersicum* allele. However, the action of another epistatic locus for type IV and VI trichomes was also evidenced.

When investigating ZGB content inheritance in the interspecific intersection between *S. lycopersicum* and *S. habrochaites* var. *hirsutum* accession 'PI-127826', it was observed that leaf ZGB content is controlled by two genes with incomplete dominance in the sense of lower content, presenting greater heritability in the broad sense (81.9%) [26]. When evaluating the synergistic effect between high AA and ZGB leaf content, heterozygous genotypes were used for both characters [6], and the authors observed that the fact that heterozygous double genotypes show the same behavior as the heterozygotes only for ZGB or AA indicates that, although allelochemicals act similarly on the resistance of these genotypes to whitefly, they do not present a synergistic effect in this case. However, in relation to the isolated presence of ZGB or AA, the simultaneous presence of ZGB and AA promoted an increase in the resistance level to tomato moths.

4.3. 2-Tridecanone resistance introgression

The selection of tomato plants containing high 2-TD levels is effective as an indirect screening criterion for pest resistance [41]. However, these authors observed that 2-TD heritability

regarding resistance to pest-arachnids in a segregating generation of the interspecific cross-breeding between *S. lycopersicum* and *S. habrochaites* var. *glabratum* (high 2-TD content) does not fit into a simple additive-dominant model, thus demonstrating a complexity not elucidated in the genetic control of character.

High 2-TD levels present in leaflets provide resistance to *T. urticae* and *ludeni* mite species [43], and it is possible to induce an increase in the level of repellency to *T. urticae* from the backcrossing between *S. lycopersicum* and genotypes containing high 2-TD levels [76]. These authors have identified that mite repellency is related to the presence of higher type VI trichome densities, where 2-TD is concentrated.

When evaluating genotypes presenting different 2-TD leaf concentrations, results indicate that plants containing high 2-TD levels as compared to those with low content are less preferred for feeding and oviposition by the tomato moth [42]. In addition, high 2-TD content is an effective indirect resistance selection criterion when the relationship between 2-TD content in selected genotypes and resistance levels to tomato moth is evaluated [52]. The high 2-TD levels of the BC₂F₄ generation are linked to non-preference oviposition and feeding type resistance mechanisms in tomato moths.

When comparing the degree of resistance to whitefly in tomato lines containing high levels of AA, ZGB and 2-TD, lines containing high 2-TD levels were as effective as those containing high AA and ZGB content [54]. Moreover, when evaluating resistance to aphids (*M. persicae*) in genotypes with different 2-TD, AA and ZGB levels in leaflets [55], the authors observed that TOM-687 and TOM-688 (containing high AA content) and BPX-365G-899-07-04-02 and BPX-367E-238-02 (containing high 2-TD levels) both present antibiosis resistance. The allelochemical 2-TD also displays potential against *T. vaporariorum* [77] and other pest-arachnids.

4.4. *S. peruvianum*, *S. pimpinellifolium*, *S. cheesmaniae* and *S. chmielewskii*

Some *S. pimpinellifolium* [78], *S. cheesmanii*, *S. galapagense* [33], *S. chmielewskii* and *S. chilense* accessions also demonstrate pest resistance [51]. However, the reasons for the resistance of most of these species have not yet been well elucidated.

4.5. Allelochemical quantification techniques

It is necessary to emphasize that genetic tomato breeding programs regarding pests, in general, apply relatively inexpensive colorimetric methodologies to quantify allelochemical content in leaflets and, consequently, identify plants that display the greatest resistance. These techniques allow for acceleration of the selection process and for a large number of plants from a segregating population to be evaluated in a short time. On the contrary, if all the plants of a population were to be exposed to pests to measure resistance, the process would be very laborious.

An efficient methodology proposed by Resende et al. [38], based on a rapid colorimetric method, allows for the nondestructive quantification of AA content in the leaflets of a large number of tomato plants. This reference methodology shows high potential for indirect genotype selection, because it presents low costs and facilitates the non-destructive selection

of individual plants in segregating generations, and is currently being applied by several authors for tomato breeding regarding pests [14, 23, 24, 34, 60]. Moreover, this methodology stands out when compared to new AA content quantification methods in leaflets [79].

Quantification of ZGB content in tomato plants by means of ZGB retention time obtained by gas chromatography and mass spectroscopy has been proposed [80]. However, these techniques do not allow for the evaluation of a high number of plants in a short period of time. Considering this, a rapid, low-cost spectrophotometric methodology was established for ZGB quantification in tomato leaves [81]. This method is now routinely applied in tomato breeding programs regarding pest insects and arachnids [22, 26, 82, 83].

Regarding 2-TD, quantification can be performed through gas chromatography and high performance liquid chromatography [84]. As for ZGB, colorimetric quantification methodologies have been developed that, when compared to chromatographic techniques, allow for the evaluation of a greater number of plants in less time [41, 42, 85]. However, 2-TD quantification through colorimetry in the selection of resistant tomato plants has been shown to be a less efficient technique than those applied in the quantification of AA and ZGB due to the fact that 2-TD content is a more complex genetic inheritance.

Morphological and physiological characteristics can also be used for the selection of tomato plants presenting high allelochemical levels [68]. The main characteristic is the identification and quantification of foliar trichomes based on the quantification of the number of glandular and nonglandular trichomes in leaflets [37]. On the other hand, estimating resistance level regarding pests and associated allelochemicals based on morphological characteristics tends to be more laborious, allowing for the evaluation of a smaller number of plants when compared to colorimetric methodologies.

In general, regardless of the applied technique, it is necessary, at some point, to expose plants identified as containing high allelochemical levels to insect and/or arachnid infestations, in order to efficiently select pest-resistant tomatoes, which allows for confirmation if the selected genotypes actually display good resistance levels.

5. Current overview, challenges and prospects for pest-resistant tomato breeding

In recent years, major transformations in the breeding scenario for several crops have occurred, and this is currently the new reality [85]. In the last 15 years, science and technology investments have taken place that enable training of human resources in the area of plant biotechnology. Classical breeding is still imperative for the development of new cultivars, but new biotechnology techniques using molecular markers can accelerate the selection process. Regarding tomato pest-resistance, many specific molecular markers have not yet been developed. However, this technique may significantly aid in the selection process. Very useful markers have been developed for the identification of plants with high type IV glandular trichome density and high AA content in populations derived from crossings with *S. galapagense* 'LA1401' [73, 86].

Relevant studies have identified quantitative trait loci (QTL) of *S. pennellii* that affect the AA chemistry [64–66, 87–89]. It was observed that some QTL alter the chemotype of AA accumulation in tomato lines descendants of the accession ‘LA 716’ [87]. It is considered that the addition of QTL that alter AA chemotype in tomato line could provide a means of generating AA with stronger resistance [90].

The two main pest tomato breeding programs in the world are under the leaderships of Martha A. Mutschler and Wilson R. Maluf, respectively.

Dr^a. Mutschler is a professor in the Department of Plant Breeding, College of Agriculture and Life Sciences, Cornell University. The Cornell University tomato breeding program conducts important works in relation to the crossed *S. pennellii* accession ‘LA716’ with cultivated tomato to then derive tomato breeding lines with resistance to pests AA-mediated. As a result of these works, the benchmark AA breeding line was developed, CU071026, which produces ~15% of the AA levels of ‘LA716’ but with a different composition [64–66, 69].

Dr. Maluf is a professor at the Department of Agriculture, Federal University of Lavras (UFLA), Brazil and a partner at Hortiagro Sementes SA, a company that maintains a mutual cooperation agreement with UFLA in the breeding and production of vegetable seeds research area. Their work resulted in the obtaining of tomato lines with high foliar levels of AA, ZGB and 2-TD and resistant to pests [6, 12, 55].

The pest insect and arachnid breeding study, coordinated by Dr. Maluf, mainly applies colorimetric methodologies developed or adapted for the quantification of allelochemical content in leaflets and the selection of resistant strains, contributing to pest control and minimizing the intensive use of chemical insecticides in tomato crops. Following Dr. Maluf’s legacy, Dr. Juliano Tadeu Vilela de Resende, a professor at the Department of Agronomy at the Central-West State University (UNICENTRO), Brazil, has also dedicated himself to improving tomato plants regarding pest resistance.

However, other than the research conducted by the Cornell University, UFLA and UNICENTRO research groups, few researchers have developed breeding aimed at obtaining new pest-resistant tomato cultivars. Considering these aspects, it is necessary to stimulate agronomy students to follow the career of the classic tomato pest-breeding, thus avoiding the extinction of committed professionals in this line of research, in a not so distant future.

6. Final considerations

In general, *Solanum lycopersicum* genotypes containing high levels of allelochemicals are promising in the context of advancements aiming at creating lines adequate for both table and processing and displaying pest insect and arachnid resistance. They represent a favorable condition for integrated pest management because they facilitate pest control, reducing the amount of chemicals applied to the crops and, simultaneously, contribute to decreased production costs.

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References

- [1] Geoffrey SK, Hillary NK, Antony KM, Mariam M, Mary MC. Challenges and strategies to improve tomato competitiveness along the tomato value chain in Kenya. *International Journal of Business and Management*. 2014;**9**(9):205-2012. DOI: 10.5539/ijbm.v9n9p205
- [2] Aquino RFBA, Costa RF, Aquino LA, Sá LP. Dinâmica populacional de pragas em tomateiro industrial no norte de Minas Gerais. *Evolução e Conservação da Biodiversidade*. 2011;**2**:47-51
- [3] Pratisoli D, Lima VLS, Pirovani VD, Lima WL. Occurrence of *Helicoverpa armigera* (Lepidoptera: Noctuidae) on tomato in the Espírito Santo state. *Horticultura Brasileira*. 2015;**33**:101-105. DOI: 10.1590/S0102-053620150000100016
- [4] Alvarenga MAR. Tomate: produção em campo, em casa de vegetação e em hidroponia. 2nd ed. UFLA: Lavras; 2013. 457 p
- [5] Baldin ELL, Vendramim JD, Lourenção AL. Resistência de genótipos de tomateiro à mosca-branca *Bemisia tabaci* (Gennadius) biótipo B (Hemiptera: Aleyrodidae). *Neotropical Entomology*. 2005;**34**(3):435-441. DOI: 10.1590/S1519-566X200500030001
- [6] Silva VF, Maluf WR, Cardoso MG, Gonçalves Neto AC, Maciel GM, Nízio DAC, Silva VA. Resistência mediada por aleloquímicos de genótipos de tomateiro à mosca-branca e ao ácaro-rajado. *Pesquisa Agropecuária Brasileira*. 2009;**44**(9):1262-1269
- [7] Wyckhuys KAG, Lu Y, Morales H, Vazquez LL, Legaspi JC, Eliopoulos PA, Hernandez LM. Current status and potential of conservation biological control for agriculture in the developing world. *Biological Control*. 2013;**65**(1):152-167
- [8] Vendramim JD, Nishikawa MAN. Melhoramento para resistência a insetos. In: Nass LL, Valois ACC, Melo IS, Valadares-Inglis MC, editors. Recursos genéticos e melhoramento de plantas. 1st ed. Rondonópolis: Fundação MT; 2001. pp. 737-781

- [9] Gallo D. Entomologia agrícola. 3rd ed. FESALQ: Piracicaba; 2002. 920 p
- [10] Moreira GR, Silva DJH, Carneiro PCS, Picanço MC, Vasconcelos AA, Pinto CMF. Herança de caracteres de resistência por antixenose de *Solanum pennellii* à traça-do-tomateiro em cruzamento com 'Santa Clara'. Horticultura Brasileira. 2013;**31**(4):574-581. DOI: 10.1590/S0102-05362013000400011
- [11] Peralta IE, Spooner DM, Knapp S. Taxonomy of wild tomatoes and their relatives (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, sect. *Lycopersicon*; Solanaceae). Systematic Botany Monographs. 2008;**84**:1-186
- [12] Maluf WR, Silva VF, Cardoso MG, Gomes LAA, Gonçalves Neto AC, Maciel GM, Nízio DAC. Resistance to the South American tomato pinworm *Tuta absoluta* in high acylsugar and/or high zingiberene tomato genotypes. Euphytica. 2010;**176**:113-123. DOI: 10.1007/s10681-010-0234-8
- [13] Goffreda JC, Mutschler MA. Inheritance of potato aphid resistance in hybrids between *Lycopersicon esculentum* and *pennellii*. Theoretical and Applied Genetics. 1989;**78**(2):210-216. DOI: 10.1007/BF00288801
- [14] Dias DM, Resende JTV, Marodin JC, Matos R, Lustosa IF, Resende NCV. Acyl sugars and whitefly (*Bemisia tabaci*) resistance in segregating populations of tomato genotypes. Genetics and Molecular Research. 2016;**16**(1):1-11. DOI: 10.4238/gmr.15027788
- [15] Peralta IE, Knapp S, Spooner DM. Nomenclature for wild and cultivated tomatoes. Tomato Genetics Cooperative Report. 2006;**6**:6-12
- [16] Bergougnoux V. The history of tomato: From domestication to biopharming. Biotechnology Advances. 2014;**32**(1):170-189. DOI: 10.1016/j.biotechadv.2013.11.003
- [17] Peralta IE, Spooner DM. Granule-bound starch synthase (GBSSI) gene phylogeny of wild tomatoes (*Solanum* section *Lycopersicum* [Mill] Wettst. Subsection *Lycopersicum*). American Journal of Botany. 2001;**88**(10):1888-1902
- [18] Peralta IE, Spooner DM. Morphological characterization and relationships of wild tomatoes (*Solanum* L. Section *Lycopersicon*). Monographs in Systematic Botany. 2005;**104**:227-257
- [19] Spooner DM, Peralta IE, Knapp S. Comparison of AFLPs with other markers for phylogenetic inference in wild tomatoes *Solanum* L. section *Lycopersicum* (Mill.) Wettst. Taxon. 2005;**54**(1):43-61
- [20] Zeist AR, Resende JTV, Faria MV, Gabriel A, Silva IFL, Lima Filho RB. Base temperature for node emission and plastochron in tomato species and their hybrids. Pesquisa Agropecuária Brasileira
- [21] Gonçalves-Gervásio RCR, Ciociola AI, Santa-Cecília LVC, Maluf WR. Aspectos biológicos de *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) em dois genótipos de tomateiro contrastantes quanto ao teor de 2-tridecanona nos folíolos. Ciência e Agrotecnologia. 1999;**23**(2):247-251

- [22] Gonçalves LD, Maluf WR, Cardoso MG, Resende JTV, Castro EM, Santos NM, Nascimento IR, Faria MV. Relação entre zingibereno, tricomas foliares e repelência de tomateiros a *Tetranychus evansi*. Pesquisa Agropecuária Brasileira. 2006;**41**(2):267-273. DOI: 10.1590/S0100-204X2006000200011
- [23] Gonçalves LD, Maluf WR, Cardoso MG, Gomes LAA, Nascimento IR. Herança de acilaçúcares em genótipos de tomateiro provenientes de cruzamento interespecífico. Pesquisa Agropecuária Brasileira. 2007;**42**(5):699-705. DOI: 10.1590/S0100-204X200700050001
- [24] Gonçalves Neto AC, Silva VF, Maluf WR, Maciel GM, Nizio DAC, Gomes LAA, Azevedo SM. Resistência à traça-do-tomateiro em plantas com altos teores de acilaçúcares nas folhas. Horticultura Brasileira. 2010;**28**(2):203-208. DOI: 10.1590/S0102-05362010000200011
- [25] Miranda BEC, Boiteux LS, Reis A. Identificação de genótipos do gênero *Solanum* (seção *Lycopersicon*) com resistência a *Stemphylium solani* e *Stemphylium lycopersici*. Horticultura Brasileira. 2010;**28**(2):178-184. DOI: 10.1590/S0102-05362010000200007
- [26] Lima IP, Resende JTV, Oliveira JRF, Faria MV, Resende NCV, Lima Filho RB. Indirect selection of industrial tomato genotypes rich in zingiberene and resistant to *Tuta absoluta* Meyrick. Genetics and Molecular Research. 2015;**14**(4):15081-15089. DOI: 10.4238/2015. November.24.16
- [27] Lucini T, Resende JTV, Oliveira JRF, Scabeni CJ, Zeist AR, Resende NCV. Repellent effects of various cherry tomato accessions on the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae). Genetics and Molecular Research. 2016;**15**(1):1-6. DOI: 10.4238/gmr.15017736
- [28] Williams WG, Kennedy GG, Yamamoto ET, Thacker JD, Bordner J. 2-Tricdecanone—A naturally occurring insecticide from the wild tomato *Lycopersicon hirsutum* f. *glabratum*. Science. 1980;**207**(4433):888-889. DOI: 10.1126/science.207.4433.888
- [29] Snyder JC, Johnson DA, Good DE, Weston PA. Type VI trichome exudates from chemotypes of *L. hirsutum* and *L. hirsutum* f. *glabratum*. Report of the Tomato Genetics Cooperative. 1987;**37**:67-68
- [30] Barona HG, Parra AS, Vallejo FAC. Evaluacion de especies silvestres de *Lycopersicon* spp., como fuente de resistencia a *Scrobipalpus absoluta* (Meyrick) y su intento de transferencia a *Lycopersicon esculentum* Mill. Acta Agronómica. 1989;**39**(1):34-45
- [31] Lourenção AL, Nagai H. Surtos populacionais de *Bemisia tabaci* no estado de São Paulo. Bragantia. 1994;**53**(1):53-59. DOI: 10.1590/S0006-87051994000100006
- [32] Gil MA. Resistencia a insectos en tomate (*Solanum* spp.). Cultivos Tropicales. 2015;**36**(2): 100-110
- [33] Rakha M, Hanson P, Ramasamy S. Identification of resistance to *Bemisia tabaci* Genn. in closely related wild relatives of cultivated tomato based on trichome type analysis and choice and no-choice assays. Genetic Resources and Crop Evolution. 2015;**64**(2):1-14. DOI: 10.1007/s10722-015-0347-y

- [34] Pereira GVN, Maluf WR, Gonçalves LD, Nascimento IR, Gomes LAA, Licursi V. Seleção para alto teor de acil-açúcares em genótipos de tomateiro e sua relação com a resistência ao ácaro-vermelho (*Tetranychus evansi*) e à traça (*Tuta absoluta*). *Ciência e Agrotecnologia*. 2008;**32**(3):996-1004. DOI: 10.1590/S1413-70542008000300045
- [35] Carter CD, Sacalis JN, Gianfagna TJ. Zingiberene and resistance to Colorado potato beetle in *Lycopersicon hirsutum* f. *hirsutum*. *Journal of Agricultural and Food Chemistry*. 1989;**37**(1):206-210. DOI: 10.1021/jf00085a047
- [36] Goffreda JC, Mutschler MA, Avé DA, Tingey WM, Steffens JC. Aphid deterrence by glucose esters in glandular trichome exudate of wild tomato, *Lycopersicon pennellii*. *Journal of Chemical Ecology*. 1989;**15**(7):2135-2147. DOI: 10.1007/BF01207444
- [37] Aragão CA, Dantas BF, Benites FRG. Tricomas foliares em tomateiro com teores contrastantes do aleloquímico 2-Tridecanona. *Scientia Agricola*. 2000;**57**(4):813-816. DOI: 10.1590/S0103-90162000000400035
- [38] Resende JTV, Cardoso MG, Maluf WR, Resende LV, Gonçalves LD. Método colorimétrico para quantificação de acil-açúcares em genótipos de tomateiro. *Ciência e Agrotecnologia*. 2002;**26**(6):69-75
- [39] Resende JTV, Maluf WR, Cardoso MG, Nelson DL, Faria MV. Inheritance of acyl-sugar contents in tomatoes derived from an interspecific cross with the wild tomato *Lycopersicon pennellii* and their effect on spider mite repellence. *Genetics and Molecular Research*. 2002;**1**(2):106-116
- [40] Silva AA, Andrade MC, Carvalho RC, Neiva IP, Santos DC, Maluf WR. Resistência à *Helicoverpa armigera* em genótipos de tomateiro obtidos do cruzamento de *Solanum lycopersicum* com *Solanum galapagense*. *Pesquisa Agropecuária Brasileira*. 2016;**51**(7):801-808. DOI: 10.1590/S0100-204X2016000700002
- [41] Barbosa LV, Maluf WR. Heritability of 2-tridecanone mediated arthropod resistance in an interspecific segregating generation of tomato. *Brazilian Journal of Genetics*. 1996;**19**(3):465-468
- [42] Maluf WR, Barbosa LV, Costa Santa-Cecília LVC. 2-Tridecanone-mediated mechanisms of resistance to the South American tomato pinworm *Scrobipalpus absoluta* (Meyrick, 1917) (Lepidoptera-Gelechiidae) in *Lycopersicon* spp. *Euphytica*. 1997;**93**(2):189-194. DOI: 10.1023/A:1002963623325
- [43] Gonçalves MIF, Maluf WR, Gomes LAA, Barbosa LV. Variation of 2-tridecanone level in tomato plant leaflets and resistance to two mite species (*Tetranychus* sp.). *Euphytica*. 1998;**104**(1):33-38. DOI: 10.1023/A:1018611514287
- [44] Luckwill LC. The Genus *Lycopersicon*: An Historical, Biological, and Taxonomic Survey of the Wild and Cultivated Tomatoes. Aberdeen: Aberdeen University; 1943. 44 p
- [45] Silva VF, Cardoso MG, Moraes JC, Pimentel FA, Gonçalves LD, Neri DKP. Caracterização a avaliação de acil-açúcar sintético no comportamento da mosca-branca (*Bemisia*

- tabaci*) (Gennadius, 1886) biótipo B (Hemiptera: Aleyrodidae) em tomateiro. Ciência e Agrotecnologia. 2008;**32**(5):1408-1412. DOI: 10.1590/S1413-70542008000500008
- [46] Gilardón E, Pocovi M, Hernández C, Olsen A. Papel dos tricomas glandulares da folha do tomateiro na oviposição de *Tuta absoluta*. Pesquisa Agropecuária Brasileira. 2001;**36**(3):585-588. DOI: 10.1590/S0100-204X2001000300025
- [47] Toscano LC, Boiça Júnior AL, Santos JM, Almeida JBSA. Tipos de tricomas em genótipos de *Lycopersicon*. Horticultura Brasileira. 2001;**19**(3):204-206. DOI: 10.1590/S0102-05362001000300009
- [48] Weston PA, Snyder JC. Thumbtack bioassay: A quick method of measuring plant resistance to twospotted spider mites (Acari: Tetranychidae). Journal of Economic Entomology. 1990;**83**(2):501-504. DOI: doi.org/10.1093/jee/83.2.500
- [49] Weston RH, Lindsay JR, Peter DW, Buscall DJ. Factors limiting the intake of feed by sheep. XIV comparisons of voluntary and various transactions in the alimentary tract between lambs and sheep fed roughage diets. Australian Journal of Agricultural Research. 1989;**40**(2):625-642
- [50] Freitas JA, Cardoso MG, Maluf WR, Santos CD, Nelson DL, Costa JT, Souza EC, Spada L. Identificação do sesquiterpeno zingibereno, aleloquímico responsável pela resistência à *Tuta absoluta* (Meyrick, 1917) na cultura do tomateiro. Ciência e Agrotecnologia. 1998;**22**(1):483-489
- [51] Leite GLD. Resistência de tomates a pragas. Unimontes Científica. 2004;**6**(2):129-140
- [52] Labory CRG, Santa-Cecília LVC, Maluf WR, Cardoso MG, Bearzotti E, Souza JC. Seleção indireta para teor de 2-tridecanona em tomateiros segregantes e sua relação com a resistência à traça do tomateiro. Pesquisa Agropecuária Brasileira. 1999;**34**(5):733-740. DOI: 10.1590/S0100-204X1999000500002
- [53] Channarayappa CM, Shivashankar G, Muniyappa V, Frist RH. Resistance of *Lycopersicon* species to *Bemisia tabaci*, a tomato leaf curl virus vector. Canadian Journal of Botany. 1992;**70**(11):2184-2192. DOI: 10.1139/b92-270
- [54] Neiva IP, Andrade Júnior VC, Maluf WR, Oliveira CM, Maciel GM. Papel de aleloquímicos e densidade de tricomas na resistência de tomateiro à mosca-branca. Ciência e Agrotecnologia. 2013;**37**(1):61-67. DOI: 10.1590/S1413-70542013000100007
- [55] Silva AA, Maluf WR, Moraes JC, Alvarenga R, Costa EMR. Resistência a *Myzus persicae* em genótipos de tomateiro com altos teores foliares de aleloquímicos. Bragantia. 2013;**72**(2):173-179. DOI: 10.1590/S0006-87052013005000022
- [56] Painter RH. Insect Resistance in Crop Plants. New York: MacMillan; 1951. 520 p. DOI: 10.1097/00010694-195112000-00015
- [57] Lara FM. Princípios de resistência de plantas a insetos. 2nd ed. Ícone: São Paulo; 1991. 336 p

- [58] Pamplona AMSR. Avaliação de genótipos de tomate *Lycopersicum* ssp. com diferentes concentrações de acilacúcares, quanto a resistência a *Bemisia tabaci* (Gennadius, 1889) (Hemitera: Aleyrodidae) [dissertation]. Lavras: Universidade Federal de Lavras; 2001
- [59] Resende JTV, Maluf WR, Faria MV, Pfann AZ, Nascimento IR. Acylsugars in tomato leaflets confer resistance to the South American tomato pinworm, *Tuta absoluta* Meyr. Scientia Agricola. 2006;**63**(1):20-25. DOI: 10.1590/S0103-90162006000100004
- [60] Resende JTV, Maluf WR, Cardoso MG, Gonçalves LD, Faria MV, Nascimento IR. Resistance of tomato genotypes to the silverleaf whitefly mediated by acylsugars. Horticultura Brasileira. 2009;**27**(3):345-348. DOI: 10.1590/S0102-05362009000300015
- [61] Goffreda JC, Mutschler MA, Tingey WM. Feeding behavior of potato aphid affected by glandular trichomes of wild tomato. Entomologia Experimentalis et Applicata. 1988;**48**(2):101-107. DOI: 10.1111/j.1570-7458.1988.tb01152.x
- [62] Mutschler MA, Doerge RW, Liu SC, Kuai JP, Liedl BE, Shapiro JA. QTL analysis of pest resistance in the wild tomato *Lycopersicon pennellii*: QTLs controlling acylsugar level and composition. Theoretical and Applied Genetics. 1996;**92**(6):709-718. DOI: 10.1007/BF00226093
- [63] Lawson DM, Lunde CF, Mutschler MA. Marker-assisted transfer of acylsugar-mediated pest resistance from the wild tomato, *Lycopersicon pennellii*, to the cultivated tomato, *Lycopersicon esculentum*. Molecular Breeding. 1997;**3**(4):307-317. DOI: 10.1023/A:1009677412902
- [64] Leckie BM, De Jong DM, Mutschler MA. Quantitative trait loci increasing acylsugars in tomato breeding lines and their impacts on silver leaf whiteflies. Molecular Breeding. 2012;**30**(4):1621-1634. DOI: 10.1007/s11032-012-9746-3
- [65] Leckie BM, De Jong DM, Mutschler MA. Quantitative trait loci regulating sugar moiety of acylsugars in tomato. Molecular Breeding. 2013;**31**(4):957-970. DOI: 10.1007/s11032-013-9849-5
- [66] Leckie BM, Halitschke R, DeJong DM, Smeda JR, Kessler A, Mutschler MA. Quantitative trait loci regulating the fatty acid profile of acylsugars in tomato. Molecular Breeding. 2014;**34**(3):201-1213. DOI: 10.1007/s11032-014-0110-7
- [67] Smeda JR, Schilmiller AL, Kessler A, Mutschler MA. Combination of QTL affecting acylsugar chemistry reveals additive and epistatic genetic interactions to increase acylsugar profile diversity. Molecular Breeding. 2017;**37**(8):1-18. DOI: 10.1007/s11032-017-0690-0
- [68] Castelo-Branco M, França FH, Cordeiro CMT, Maluf WR, Resende AM. Seleção em F₂ (*Lycopersicon esculentum* × *L. pennellii*) visando resistência à traça-do-tomateiro. Horticultura Brasileira. 1987;**5**(1):30-32
- [69] Leckie BM, D'Ambrosio DA, Chappell TM, Halitschke R, De Jong DM, Kessler A, Kennedy GG, Mutschler MA. Differential and synergistic functionality of acylsugars in suppressing oviposition by insect herbivores. PLoS One. 2016;**11**(4):1-19. DOI: 10.1371/journal.pone.0153345

- [70] Resende JTV, Maluf WR, Cardoso MG, Faria MV, Gonçalves LD, Nascimento IR, Resende JTV. Resistance of tomato genotypes with high level of acylsugars to *Tetranychus evansi* Baker & Pritchard. *Scientia Agricola*. 2008;**65**(1):31-35. DOI: 10.1590/S0103-90162008000100005
- [71] Baier JE, Resende JTV, Faria MV, Schwarz K, Meert L. Indirect selection of industrial tomato genotypes that are resistant to spider mites (*Tetranychus urticae*). *Genetics and Molecular Research*. 2015;**14**(1):244-252. DOI: 10.4238/2015.January.16.8
- [72] Maciel GM, Maluf WR, Silva VF, Gonçalves Neto AC, Gomes LAA. Híbridos pré-comerciais resistentes a *Tuta absoluta* obtidos de linhagem de tomateiro rica em acilaçúcares. *Horticultura Brasileira*. 2011;**29**(2):151-156. DOI: 10.1590/S0102-05362011000200003
- [73] Andrade MC, Silva AA, Neiva IP, Oliveira IRC, Castro EM, Francis DM, Maluf WR. Inheritance of type IV glandular trichome density and its association with whitefly resistance from *Solanum galapagense* accession LA1401. *Euphytica*. 2017;**213**(53):1-12. DOI: 10.1007/s10681-016-1792-1
- [74] Firdaus S, Heusden AW, Hidayati N, Supena EDJ, Visser RGF, Vosman B. Resistance to *Bemisia tabaci* in tomato wild relatives. *Euphytica*. 2017;**187**(1):31-45. DOI: 10.1007/s10681-012-0704-2
- [75] Freitas JA, Maluf WR, Cardoso MG, Gomes LAA, Bearzotti E. Inheritance of foliar zingiberene contents and their relationship to trichome densities and whitefly resistance in tomatoes. *Euphytica*. 2002;**127**(2):275-287. DOI: 10.1023/A:1020239512598
- [76] Aragão CA, Maluf WR, Dantas BF, Gavilanes ML, Cardoso MG. Tricomas foliares associados à resistência ao ácaro rajado (*Tetranychus urticae* Koch.) em linhagens de tomateiro com alto teor de 2-tridecanona nos folíolos. *Ciência e Agrotecnologia*. 2000;**24**:81-93
- [77] Lin S, Trumble JY, Kumamoto J. Activity of volatile compounds in glandular trichomes of *Lycopersicon* species against two insect herbivores. *Journal of Chemical Ecology*. 1987;**13**(4):837-849. DOI: 10.1007/BF01020164
- [78] Alba JM, Montserra TM, Fernandez-Muñoz R. Resistance to the twospotted spider mite (*Tetranychus urticae*) by acylsucroses of wild tomato (*Solanum pimpinellifolium*) trichomes studied in a recombinant inbred line population. *Experimental & Applied Acarology*. 2009;**47**(1):35-47. DOI: 10.1007/s10493-008-9192-4
- [79] Maciel GM, Silva EC. Proposta metodológica para quantificação de acilaçúcares em folíolos de tomateiro. *Horticultura Brasileira*. 2014;**32**(2):174-177. DOI: 10.1590/S0102-05362014000200009
- [80] Carter CD, Snyder JC. Mite responses in relation to trichomes of *Lycopersicon esculentum* × *Lycopersicon hirsutum* F₂ hybrids. *Euphytica*. 1985;**34**:177-185
- [81] Freitas JA, Maluf WR, Cardoso MG, Benites FRG. Métodos para quantificação do zingibereno em tomateiro, visando à seleção indireta de plantas resistentes aos artrópodes-praga. *Acta Scientiarum Agronomy*. 2000;**22**(4):943-949. DOI: 10.4025/actasciagron.v22i0.2823

- [82] Oliveira CM, Andrade Junior VC, Maluf WR, Neiva IP, Maciel GM. Resistance of tomato strains to the moth *Tuta absoluta* imparted by allelochemicals and trichome density. *Ciência e Agrotecnologia*. 2012;**36**(1):45-52. DOI: 10.1590/S1413-70542012000100006
- [83] Lima IP, Resende JTV, Oliveira JRF, Faria MV, Dias DM, Resende NCV. Selection of tomato genotypes for processing with high zingiberene content, resistant to pests. *Horticultura Brasileira*. 2016;**34**(3):387-391. DOI: 10.1590/S0102-05362016003013
- [84] Nienhuis J, Klocke J, Locy R, Butz A, Balandrin M. Colorimetric assay for 2-tridecanone mediated insect resistance in *Lycopersicon* species. *Hortscience*. 1985;**20**(3):590
- [85] Melo PCT, Melo AMT, Aragão FAS. Melhoramento de Hortaliças no Brasil. In: Nick C, Borém A, editors. *Melhoramento de Hortaliças*. 1st ed. Viçosa: Editora UFV; 2016. pp. 9-60
- [86] Andrade MC. Genetic Control of Glandular Trichome Densities and their Association with Whitefly Resistance from *Solanum galapagense* Accession LA 1401 [Thesis]. Lavras: Universidade Federal de Lavras; 2015
- [87] Schilmiller AL, Shi F, Kim J, Charbonneau A, Holmes D, Jones AD, Last RL. Mass spectrometry screening reveals widespread diversity in trichome specialized metabolites of tomato chromosomal substitution lines. *The Plant Journal*. 2010;**62**(2):391-403. DOI: 10.1111/j.1365-3113X.2010.04154.x
- [88] Schilmiller AL, Charbonneau AL, Last RL. Identification of a BAHD acetyltransferase that produces protective acyl sugars in tomato trichomes. *Proceedings of the National Academy of Sciences*. 2012;**109**(40):16377-16382. DOI: 10.1073/pnas.1207906109
- [89] Schilmiller AL, Moghe GD, Fan P, Ghosh B, Ning J, Jones AD, Last RL. Functionally divergent alleles and duplicated loci encoding an acyltransferase contribute to acylsugar metabolite diversity in *Solanum* trichomes. *The Plant Cell*. 2015;**27**(4):1002-1017. DOI: 10.1105/tpc.15.00087
- [90] Smeda JR, Schilmiller AL, Last RL, Mutschler MA. Introgression of acylsugar chemistry QTL modifies the composition and structure of acylsugars produced by high-accumulating tomato lines. *Molecular Breeding*. 2016;**36**(160):1-21. DOI: 10.1007/s11032-016-0584-6