

Review

INSECT RESISTANCE IN TOMATO (*Solanum* spp.).

Reseña bibliográfica Resistencia a insectos en tomate (*Solanum* spp.)

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ABSTRACT. Most tomato cultivars are susceptible to a wide range of arthropod pests, which can cause significant losses, including complete destruction of the crop. The use of chemicals has had a negative impact on the environment, which has led the scientific community to assess the genetic resistance as a key element in the Integrated Pest Management (IPM) as a more durable and safe. Few results of genetic resistance to insects in the wild species of the genus *Solanum* and in particular, its introgression into cultivated tomato. This paper compiles the main findings regarding genetic resistances possessing wild species, which have been associated, in most cases, to the presence of glandular trichomes and the type of substance they store: type trichomes IV and VI present in *S. habrochaites* S. Knapp & DM Spooner and type IV glandular trichomes present in *S. pennellii* Correll and *S. pimpinellifolium* L. Besides the physical effect that could exercise the trichomes on insect behavior, the resistances are based primarily on the effect of antibiotic and antixenótic reserve compounds in trichomes. The three main groups of allelochemicals associated with these resistances are methylketones, sesquiterpenes and acilazúcares. In this paper we report the main sources of resistance to insect pests have been found in wild *Solanum* species. It also discusses the limitations and perspectives of introgression of insect resistance in tomato.

RESUMEN. La mayoría de los cultivares de tomate son susceptibles a una variedad amplia de plagas de artrópodos, las que ocasionan pérdidas cuantiosas, incluida la devastación del cultivo. La comunidad científica valora la resistencia genética como un elemento clave en el Manejo Integrado de Plagas (MIP), como una vía más duradera e inocua con el ambiente. Son escasos los resultados obtenidos en el estudio de la resistencia genética a insectos en las especies silvestres del género *Solanum* y, en particular, su introgresión al tomate cultivado. En este trabajo se muestran los principales resultados en cuanto a las resistencias genéticas que poseen las especies silvestres, asociadas, en su mayoría, a la presencia de tricomas glandulares y al tipo de sustancia que estos almacenan: tricomas glandulares tipo IV y VI, presentes en *S. habrochaites* S. Knapp & D.M. Spooner y tricomas glandulares tipo IV presentes en *S. pennellii* Correll y *S. pimpinellifolium* L. Además del efecto físico que pudieran ejercer los tricomas sobre la conducta de los insectos, las resistencias se basan, fundamentalmente, en el efecto antibiótico y antixenótic que provocan los compuestos almacenados en estos. Los tres grupos principales de aleloquímicos asociados a estas resistencias son las metilcetonas, los sesquiterpenos y los acilazúcares. En este trabajo, además de informar las principales fuentes de resistencia a plagas de insectos que se han encontrado en las especies silvestres de *Solanum*, se discuten las limitaciones y perspectivas de la introgresión de la resistencia a insectos en el tomate.

Key words: trichomes, antibiosis, antixenosis, pests, breeding

Palabras clave: tricomas, antibiosis, antixenosis, plagas, mejora genética

INTRODUCTION

Cultivated tomato (*Solanum lycopersicum* L.) is one of the most important vegetables from

human consumption either to eat fresh or processed industrially. It is the second vegetable crop (after potatoes) of higher consumption and more popular as a garden crop in the world (1).

Despite the great amount of cultivars has been generated and marketed in this species, it is most susceptible to a wide variety

of arthropod pests that provoke considerable losses, including the complete destruction of crops. (2)

The arthropod community associated to pests in tomato is broad. It includes numerous species of aphids, white flies, thrips, lepidoptera, coleoptera, diptera and some mite species (3, 4).

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It requires, often, the use of chemical products with a negative impact in the environment (5), resistant population appearance of insect, new pests and biological imbalances that affect men and natural enemies of insect-pest (6).

Nowadays it has encouraged the creation of alternative control method, biological, with less chemical damage to the environment because it uses pathogen or insect predators and insecticides plants, nevertheless as examples of effective control by this way, in occasions it is not satisfactory. Another strategy to control pests would be the use of resistant cultivars for its durability and safety. It has been limited due to most cultivars do not have a high level of resistance to allow a significant reduction in chemical, providing few commercial cultivars with specific insect resistance (3).

In modern agriculture, Host Plant Resistance (HPR from English) is incorporated into the Integrated Pest Management (IMP from English) as an integral program in order to regulate arthropod pests. In addition of ecological benefits that entails, the use of resistant cultivars to arthropods is good for producers because the cost to control pest is implicit in the seed cost (11). To have progress in obtaining resistant cultivars to arthropods and integrate them in IMP programs, should be an interdisciplinary collaboration that good exploit of chances offered by the genomic of arthropods with these purposes and progress in research the molecular basis of resistance to arthropods (12).

In tomato crop despite the wide genetic variability present and exploitable in wild species of *Solanum* (7), there are few resistant cultivars to arthropods. *Wild species related*, *S. habrochaites* S. Knapp & D.M. Spooner, *S. peruvianum* L. and *S. pennellii* Correll have mainly been reported as resistant pattern to lots of arthropod pests.

Also some resistance to insects have been found in species as *S. lycopersicum* L., *S. pimpinellifolium* L., *S. cheesmaniae* (L. Riley) Fosberg, *S. chmielewskii* (C.M. Rick, Kesicki, Hobbes y M. Holle) D.M. Spooner, G.J. Anderson & R.K. Cansen and *S. chilense* (Dunal) Reiche (9). However, the introgression of these resistances in tomato cultivars has been limited by difficulties in maintaining uniform levels required for selection of the resistance (10) and other difficulties involved in complex traits introgressed from wild species to the cultivated tomato.

In this paper, some fundamental elements of insect resistance in plants and the particular case of the resistance in some of the wild species of tomato (*Solanum* spp.) and the limitations and perspectives offered to improve tomato occur, alternatively pest control.

RESISTANCE TO INSECTS IN PLANTS

Most of the time, plants face various environment factors, among them are: temperature fluctuations, light intensity and its quality, water availability, a wide range of pests, pathogens and phytophagous animals (13). Phytophagous affect vegetable tissue integrity to obtain nutrients contained in foliage, seeds, pollen, nectar, roots and stems that they need for living and reproducing(14). Due to this plants should protect themselves from multiple "consumers" that come from different types of herbivorous (mammals, snails, and insects) and even typical parasites (insects, mites, fungi, and bacteria) or phytopathogens.

Continuously, plants face various environmental factors, among which are included: temperature fluctuations, light intensity and quality, water availability, a wide range of viruses, pathogens and phytophagous

animals (13). Herbivores affect the integrity of plant tissues to obtain nutrients in the foliage, seeds, pollen, nectar, roots or stems, they need to live and breed (14). Broadly, the plant must be protected from the many consumers who come in search of food, several types of herbivores (mammals, snails and insects), to typical parasites (insects, mites, fungi and bacteria) or phytopathogens.

To protect from the wide range of consumers, plants, likewise, have developed a great amount of mechanisms. In this section those main concepts related to the genetic resistance of the host plant pest, some generic and applicable to herbivores or arthropods will refer; others refer, in particular, to insects.

A response of plants to herbivores is complex. Genes that are activated against attack by herbivores are strongly correlated with the feed mode of herbivores and the degree of damage to the tissue at the feed way (15). Plants, during their evolution, have developed mechanisms of "defense" essentially responsible allelochemicals or biophysical factors incompatible interactions between an arthropod and a resistant plant (12).

These "defenses" of plants can be direct or indirect. Direct ones are those in which only the plant and its "aggressor" take place in antagonistic interactions (16) include those plant structures (the tissue hardness, pubescent, glandular and non-glandular trichomes) that serve as obstacles to arthropod. Also, those allelochemicals contained in plant tissues exhibiting antifeedant, toxic, or repellent effects arthropods that attack such as cyanogenic glycosides, digestive enzyme inhibitors, lectins, glucosinolates, and terpenoids, alkaloids (17, 18).

In indirect ones, however, other organism, foreign predators, parasitoids, releasing to plant its "aggressors" (19) involved; They consist of volatile organic compounds that are released by plants, once they have been damaged by the arthropod pest and these compounds can attract natural predators and parasitoids of phytophagous or repel oviposition of this on the ground (20).

Direct strategies "defense" of plants are divided artificially in: constitutive and induced, depending on whether the defense mechanisms of the plant were present or not before this contact occurs with the herbivore. Both types of defense can coexist to prevent colonization and hinder feeding, growth, development and fertility / fertility of herbivores (13, 21). This kind of direct "defense" is the most interest from the genetic improvement point of view of the host plant, above all, the effective combination of constitutive and induced mechanisms that reinforce the response of the plant against the pest.

However, the development of defense mechanisms has a "cost" to the plant, which could be reflected in a decrease in its vegetative and reproductive development. In this sense, the plant must balance the responses induced and constitutive "defense" without sacrificing its viability, longevity and reproduction (15). An example of this is usually observed at times when the "attacked" plant by a plague shortens its life cycle and reproduce, albeit precariously.

For many years, research on the defensive response of plants to phytopathogens presence was very poor and many aspects were not understood (22); however, in recent years

have intensified investigations related to understanding types and mechanisms of plant defense, especially against herbivorous arthropods, as in modern agriculture, the resistance of the host plant is an integral component in control of arthropod pests in programs integrated pest management (IPM) (23).

It is necessary, given the focus of genetic improvement of this article, defining what is meant by arthropods resistant plant. To do this, we have taken CM Smith criteria, set out in its recent review about the molecular basis of resistance to arthropod host plant resistance (HPR, English host plant resistance) is the sum of the genetically inherited qualities having a plant of a cultivar or species, resulting in that, this is less damaged by the arthropod pest which susceptible plant that lacks these qualities (12). As can be seen, this author considers the damage caused by the pest on the ground, compared with the susceptible host plant, not referring to effects on the arthropod.

For the breeder to assess accurately, the damage caused by the plague in the host, it should establish a controlled and standardized way, which is difficult and expensive, in the case of insect pests. In early stages, especially, may not be limited only to plant response in the field, under free choice of insect; because many other factors, outside the "defense" of the plant, could be influencing this behavior. The lack of standardized assessment of the resistance sources and subsequently, to selection stages, has in our opinion, the main cause of limited results have been achieved in improving resistance to pest methods in plants.

It has made more progress in the study of allelochemicals associated with resistance on the plant. The importance of these allelochemicals in the "defense" of plants has been explained by some authors by antixenotics or antibiotic effects that these have on herbivores (24).

Antibiosis and antixenosis concepts are clearly defined. Antibiosis: adverse effects caused by a resistant plant on survival, development, or fertility of an arthropod. Antixenosis: no preference reacting of arthropod for a resistant plant when allelochemicals or biophysical factors affect negatively the behavior of arthropod, causing the late acceptance or rejection of the plant as host (12).

The antixenosis, including resilience as an example of this mechanism is given by a set of features, color, odor, taste of the plant, which cultivar is less preferred for the herbivore to the process of oviposition and food. Mechanisms may be physical (presence of trichomes, waxy surfaces, tissue hardness) or chemicals as repellent (terpenes, oils) or dissuasive (alkaloids, flavonoids, lectinas, phenols, tannins)^A.

The occurrence expression of this mechanism in a plant is its inability to serve as host of a herbivorous insect, forcing these to change host plant to feed and make oviposition. This mechanism reduces the rate of initial accumulation, and subsequent, of the insect population (25).

^A Pérez Rosero, M. Mejoramiento genético en *Solanum lycopersicum* para la resistencia al pasador del fruto *Neoleucinodes elegantalis* Gene (Lepidoptera: Crambidae). [Tesis de Maestría]. Universidad Nacional de Colombia. Facultad de Ciencias Agropecuarias. Palmira, Colombia. 2010, 113 pp.

Meanwhile, the antibiosis affect the survival, development or arthropod fertility, attempting to use resistant plant as host, causing mortality or decreasing the growth rate of this (12). This resistance type acts as a natural insecticide produced by the plant to protect the insect may be due to the presence of chemical factors such as proteins, toxins (alkaloids, ketones, organic acids), inhibitors (alpha amylase, trypsin, proteases) or physical factors (hypersensitive growth, trichomes, silica deposits). These can cause a lethal effect on nymphs, preventing their development; excessive prolonging life or preventing reproduction of this in the resistant cultivar (26, 27).

Another term that handles, frequently, between farmers and breeders is plant tolerance to insects. Tolerance is a polygenic trait that allows the plant to withstand or recover from the damage that causes the arthropod, without the survival and growth of arthropods that attack (12) is affected. This feature of the plant is important for agriculture and there are cultivars tolerant of different species that are commercially exploited, for lack of cultivars with resistance genes. However, little is known about tolerance, since it is difficult to measure and is confused usually with quantitative resistance forms (28).

While it is true that plant breeders and entomologists, using conventional methods of plant breeding, resistant cultivars have developed to some arthropods in the last 50 to 60 years; for many of these cultivars, resistance genes have not been named and the bases of the resistance mechanisms are unknown, although they are used in cropping systems worldwide, to reduce the damage caused by insects and mites. By contrast, only a few genes have been identified and incorporated into cultivars using classical genetic approaches (29, 30, 31).

At present, there are numerous opportunities to use advances in molecular techniques to identify more efficiently, controlling and manipulating resistance genes to arthropods in cultivars. However, it will have to achieve effective interdisciplinary collaborations for the successful integration of these cultivars in the programs of integrated pest management tactics of biological, chemical and cultural control (12).

RESISTANCE TO INSECTS IN TOMATO

The tomato crop is no exception, with regard to the overall situation of cultivated plants. At present, commercial tomato cultivars have not enough high levels of pest resistance to reduce, significantly, the pesticide application. Therefore, the addition of resistant cultivars integrated pest management, in order to reduce the cost and environmental impact of the application of chemicals during cultivation, is a goal to achieve, for most of pests.

In general, resistance mechanisms that have been studied in tomato, usually are identified in two groups: 1) those that are associated with the leaf trichomes presence (glandular and non-glandular) and substances secreted and 2) those associated with lamella leaf, fruit or growth habit of the plant (32).

The resistance in tomatoes has been associated mostly to the first group, specifically the presence of glandular trichomes; no specific mechanism is present constitutively in the plant and which is related to the substance type they store. Trichomes, considered differentiated epidermal cells are uni or multi cell structures that cover surfaces of leaves and stems of plants and which differ in their morphology and function.

The trichomes classification by their morphology is based on criteria for typological and morphological differentiation and it was performed for tomato in 1943 by Luckwill, who identified seven types of trichomes distributed in different *Solanum* species (I-VII). Later, after reviewing this classification, an additional type proposed, trichome type VIII (See table) (32). However, the classification for functionality is related that are glandular trichomes (those possessing differentiated cells that store different substances or compounds) or non-glandular.

The non-glandular trichomes (II, III, V and VIII) are highly similar, differing only in length, according to some authors; however, the glandular trichomes (I, IV, VI and VII) containing and capable of releasing allelochemicals which have been associated with resistance insects (33).

Glandular trichomes in plants have been associated with the production of volatile and nonvolatile secondary metabolites, including acylsugars, terpenoids, phenylpropanoid and flavonoid (34, 35). There are reports about the diversity of allelochemicals present in the glandular trichomes of wild tomato species and that they are associated with resistance to pests: methylketones, sesquiterpenes and acylsugars (2), are the three most famous, perhaps being the most studied groups.

It has been shown that trichomes present in wild tomato species (Table) confer resistance to many taxa that may constitute pests, although researches on tomato have been focused on Hemiptera and Lepidoptera, as main pests. Arthropod resistance is associated frequently with high densities of glandular trichomes type IV and VI and allelochemicals that contain essentially the tridecanones (methylketones), sesquiterpenes (terpenoids) and acylsugars.

Distribution of trichomes different types in tomato^B

Genre <i>Solanum</i> , section <i>Lycopersicon</i>	I	II	III	IV	V	VI	VII	VIII
<i>S. habrochaites</i>	+	+	+			+	+	
<i>S. lycopersicum</i>	+	+		+	+	+	+	+
<i>S. pennellii</i>				+		+		
<i>S. cheesmaniae</i> , <i>S. galapagense</i>					+			
<i>S. pimpinellifolium</i>			+	+	+	+		
<i>S. peruvianum</i> , <i>S. arcanum</i> , <i>S. corneliomuelleri</i> , <i>S. huaylasense</i>		+	+ ^a		+	+	+	
<i>S. chilense</i>					+	+		+
<i>S. chmielewskii</i>					+	+		
<i>S. neorickii</i>					+	+		

a Described in variety *F. glandulosum* by Luckwill, 1943, actual *S. corneliomuelleri*

b Described in line TO-937 (36)

^B Alba J. M. Herencia de los mecanismos de resistencia a araña roja en tomate. [Tesis de Doctorado]. Departamento de Biología Vegetal. Facultad de Ciencias. Universidad de Málaga. 2006. 242 pp.

Among wild species most studied for its resistance to arthropods is *S. habrochaites*. In this species, which grow abundantly, trichomes type IV and VI described resistance to over 16 species of pests. Only an entry, PI 134417 (*S. habrochaites* var. *Glabratum*), carries 12 of these 16 resistance to pests that have been reported (32). Other accessions, LA 407, PI 134418 and PI 126449, of this species and type, have proved resistant to pests; also, accessions of *S. habrochaites* var. *hirsutum*, LA 1624 and LA 1362 have been studied for their resistance.

Among the most important pest which this species has shown resistance are *Tuta absoluta* Meyrick (37, 38, 39, 40), *Neoleucinodes elegantalis* Guenée, *Tetranychus* (41, 42, 43, 44), *Bemisia tabaci* (Genn.) (45), *Helicoverpa zea* (Boddie), *Trialeurodes vaporariorum* (Westw) (46), *Keiferia lycopersicella* (Wals.), *Spodoptera exigua* (Hübner) (47), among others.

Several authors discuss the possible association of insect resistance in *S. habrochaites* (quoted as *glabratum* type) in the presence of methylketones (tridecanones). Tridecanones generally have an effect both toxicity

and repellency. Two secondary metabolites have isolated, 2-tridecanone and 2-undecanone (44, 48, 49, 50, 51, 52) present in the glandular trichomes type VI in *S. habrochaites* var. *glabratum* and proved their effect mainly 2-tridecanone, against pests of *T. urticae* (43, 53, 54), whiteflies (56), *T. vaporariorum* (45, 57) and absolute T. (55), among others.

Genetic control of 2-tridecanone is complex. Some authors report that the legacy of high levels of this compound is controlled by at least three recessive genes (58, 59) and also have reported values of broad-sense heritability of $0,61 \pm 0,18$ at suggesting that selection for the same could be effective as indirect selection criteria for resistance to arthropod (60). Also, they have been identified between 3 and 5 QTLs involved in the synthesis of 2-tridecanone in cross *S. lycopersicum* and *S. habrochaites* (49, 61).

Another group of compounds that confer insect resistance to tomato is the sesquiterpenes, Family terpenoids and found in trichomes *S. habrochaites*. The zingiberene (a type of sesquiterpene) is produced by the glandular trichomes type VI present in *S. habrochaites* var. *hirsutum*.

It has been associated high concentrations of the resistance zingiberene insects, *T. evansi* (62), *T. urticae*, (44, 63); *B. tabaci* (64) and *T. absoluta*. (65), among others. Also sesquiterpenes were detected in trichomes type IV of the species *S. habrochaites* var. *hirsutum* (43).

Some reports reveal the complexity of their heritage. The segregation observed in F2 generation (*S. lycopersicum* x *S. habrochaites*) for the trichome density indicated that this follows a genetic additive-dominance controlled by the action of a recessive major gene, influenced by some minor genes (64), also, some advances have been reported about the presence of synthesizing genes for different sesquiterpenes and have been cloned NILs nearly isogenic lines (66).

An aspect to define prior to an improvement program is the allelochemical/ trichome type is more suitable for indirect selection of plant resistance to the pest. Thus, studies with *Bemisia argentifolii* (67) it was shown that high levels of 2-tridecanone induced low levels of repellency and toxicity of 2-undecanone, high levels of repellency and fumigant activity

while the zingiberene caused high toxicity and repellency.

Once, chosen to incorporate character, it must know its type of heredity or genes involved, as this will determine the strategy to improve the technique to use and how to select. In fact, they do not yet have sufficient data to support the hereditary basis of the presence of trichomes / allelochemicals responsible for resistance in *S. habrochaites*. This has greatly hampered, along with other factors such as the character complexity and management of insect populations, this species has been merely exploited as a source of resistance to pests, despite being the most studied with this purpose.

Meanwhile, in this species *S. pennellii*, resistance to nine arthropod pests has been explained by the trichome presence of type IV, primarily on the LA 716 inlet, which is resistant to eight of these pests (32). This inlet has shown high levels of resistance to numerous pests, complex whitefly *B. tabaci/B argentifolii*, *Macrosiphum euphorbiae* (Thomas), *Myzus persicae* (Sulzer), *Tetranychus* spp. and lepidoptera pests (68, 69, 70), including *T. absoluta* (71, 72).

In the case of *S. pennellii*, pest resistance has been attributed to high levels acylsugars (5), a third allelochemicals family related to pest resistance in tomato. These compounds have been found in glandular trichomes type IV exudates and they are responsible for the resistance to *S. pennellii* at the LA 716 inlet (73), demonstrating an adverse effect on several herbivorous arthropods (74, 75).

Lines have been achieved of *S. lycopersicum* (TOM-687, TOM-688, TOM-689) with high acylsugars content, demonstrating that these compounds have mediated the resistance effectiveness to a broad spectrum of pests, *T. urticae*, *B. argentifolii* and *T. absoluta*. The mode single inheritance acylsugar content, informed by Resende et

al, in 2002 and confirmed later by Gonçalves et al., in 2007, it favored the production of these lines; introgress in cultivated tomato, high acylsugar contents present in LA 716 (5).

On the other hand, at least 5 QTLs were involved in the inheritance of the acylsugar content on this inlet (76); while moderate heritability values ($h_2 = 0,476$) were reported (77). Anyway, more accurate to describe in greater detail the heritage of this character and locate gene regions involved all studies are required. However, aforementioned results confirm that progress can be made in obtaining improved lines, with better conditions to face plagues through indirect selection for high levels of allelochemical, even though it can not have markers to conduct a assisted selection for pest resistance.

Recently it reported the presence of high densities of type IV trichomes and the high acylsugar content present in *S. pimpinellifolium* in the TO-937 input (78), related to resistance pests. It has studied the resistance inheritance to *T. urticae* and the presence of type IV trichomes present in TO-937, which tomato line ABL 14-8 was obtained, resistant *T. urticae* and *T. evansi*. The resistance was controlled by a single locus, the greatest effect, and dominant; but modulated by unknown loci of minor effects. By contrast, the trichome presence was governed by two dominant not linked loci.

The inheritance mode relatively simple of acylsugars presence in trichomes type IV TO-937 indicated that introgression of the resistance into commercial cultivars could be made, successfully, from a wild species close to the cultivated tomato (36, 79). This was demonstrated by obtaining the ABL 14-8 line through conventional breeding with resistance levels also to whitefly

(*B. tabaci*) (80) and *T. absoluta* (81).

It is very little known about the resistance in *S. peruvianum* (82). Among few reports is, resistance to *Tetranychus ludeni* Zacher and *Aculops lycopersici* (Massee) (83) and *T. evansi*. (84); similarly, other species that had associated with pest resistance (*S. lycopersicum*, *S. cheesmaniae*, *S. chmielewskii* and *S. chilense*) (9).

Most recent work reports looking important pest resistance, whiteflies, being transmissive of virus; and *Tuta*, to emerge as a devastating plague, used as sources of resistance *S. habrochaites* species, *S. pennellii* and *S. pimpinellifolium*.

Some authors have suggested that future research aimed at tomato resistance to whiteflies, could be heading genotypes having glandular trichomes type IV, as they are abundant in *S. pennellii*, *S. habrochaites*, *S. habrochaites* f. *glabratum* (33) and *S. pimpinellifolium* (80) and decrease problems related to the transmission of viruses by *B. tabaci* biotype B.

It has paid much attention to pest resistance related to acylsugar production, exuded by the trichomes type IV *S. pennellii*, identifying five quantitative trait loci (QTLs, English Quantitative traits loci) and two epistatic interactions controlling this character. To facilitate the work of improving future work for fine mapping of QTLs that determine the high content of acylsugars (85) are raised. Also, the group of Dr. WR Maluf, from the Federal University of Lavras, Brazil; have successfully achieved to introgress high levels of acylsugars in tomato lines (TOM-687, TOM-688, TOM-689) and demonstrated the broad spectrum of resistance conferred by this allelochemical against three major pest in tomatoes; *T. urticae*, *B. argentifolii* and *T. absoluta* (5).

Introgression of resistance to tomato pests associated

with the trichome density and allelochemicals content is being made by various working groups; however, to obtain lines with allelochemical high levels and high density of trichomes is necessary to deepen the genetic control knowledge of these characters to facilitate the improvement process.

Another aspect that should be taken into account is the long-term viability of tomato resistance associated with the presence of trichomes to control pests in the crop, because it is not yet sufficiently documented. There is a possibility that arthropods to develop resistance to toxins contained in the trichomes, especially the resistance for antibiosis, which is usually controlled by major genes, this could be transitory arise insect populations that are affected by genes plant resistance. Another potential drawback is that, in some cases, the resistance level by antibiosis in a cultivar may be incompatible with some biological control agents, which is not convenient if it is consider that resistant cultivars would be an integral part of a program integrated pest control.

By contrast, "defenses" based on glandular trichomes could be more durable if multiple toxins found in the exudates of glandular trichomes of some wild *Solanum* species are combine and also it is favorable that chemical and physical mechanisms are combine (eg entrapment). The combination with the antixenotic effect of glandular trichomes exudates could also increase the durability of this mechanism to repel pests without damaging significantly insect populations.

These factors make finding the host plant resistance is attractive in this way, despite the lack of information available in some areas. Also, negative effects of pesticides and the growing number of insects which are becoming resistant to synthetic pesticides,

justify continued research in these resistance mechanisms.

An aspect to consider in improving resistance pest is the practical difficulty in the resistance introgression from wild species to the cultivated tomato mainly for those from *S. habrochaites* and *S. pennellii*. That's an advantage of resistance being reported by the presence of type IV trichomes, containing acylsugars in *S. pimpinellifolium*, very close to *S. lycopersicum*.

In short, improving resistance to pests in tomato has had lots of difficulties; however, results of new technology application to the study of mechanisms and heritage provide elements that increase introgression effectiveness; as identifying of markers associated with resistance to enable assisting the selection during production of tomato cultivars resistant to insect pests.

BIBLIOGRAPHY

1. Foolad, M. R. y Panthee, D. R. Marker-Assisted Selection in Tomato Breeding. *Critical Reviews Plant Sciences*, 2012, vol.31,pp.93-123. ISSN:0735-2689.
2. Labate, J. A.; Grandillo, S.; Fulton,T.; Muños, S.; Caicedo, A. L.; Peralta, I.; Ji, Y.; Chetelat, R. T.; Scott,J. W. y Gonzalo, M. J. / et al./ Tomato. En: *Genome Mapping and Molecular Breeding in Plants*. Editor: Chittaranjan Kole, Ed. Springer-Verlag BerlinHeidelberg. 2007, vol. 5, vegetables, cap. 1, pp. 1-95. ISBN: 13 978-3-540-34535-0.
3. Foolad, M. R. Genome mapping and molecular breeding of tomato. *International Journal of Plant Genomics*, 2007, vol. 52. ISSN: 16875389.
4. Lindhout, P. Genetics and Plant Breeding. En: *TOMATOES*, Editor: Heuvelink Ep., Ed. CAB International. 2005, cap. 2, pp. 21-52.
5. Maluf, W. R.; Maciel, G. M.; Augusto Gomes, L. A.; Cardoso,M.G; Gonçalves, L. D.; Da Silva, E. C. y Knapp, M. Broad-Spectrum Arthropod Resistance in Hybrids between High- and Low-Acylsugar Tomato Lines. *Crop Sci.*, 2010, vol. 50, pp. 439-450. ISSN: 0011-183X.
6. Brunherotto, R. y Vendramim, J. D. Bioatividade de extratos aquosos de *Melia azedarach* L. sobre o desenvolvimento de *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) em Tomateiro. *Neotropical Entomology*, 2001, vol. 30, pp. 455-459. ISSN: 1519-566X.
7. Bai, Y. y Lindhout, P. Domestication and Breeding of Tomatoes: What have We Gained and What Can We Gain in the Future?. *Annals of Botany*, 2007, vol. 100, pp. 1085-1094. ISSN: 0305-7364.
8. Kennedy, G. G. Resistance in tomato and other *Lycopersicon* species to insect and mite pests. En: *Genetic improvement of Solanaceous crops*. Eds. Razdan, M. K.; Mattoo, A. K., Ed. Science Publ, Enfield, NH, USA. 2007, vol. 2, pp. 488-519.
9. Farrar,R.R.J.y Kennedy,G.G. Insect and mite resistance in tomato. En: *Genetic Improvement of tomato. Monographs on Theoretical and Applied Genetics*. Editor: Kalloo, G. Ed. Springer-Verlag, Berlin Heidelberg. 1991, vol. 14, pp. 122-141.
10. Stevens, M. A. y Rick, C. M. Genetics and breeding. En: *The tomato crop: a scientific basis for improvement*. Eds.: Atherton, J. G.; Rudich, J. Ed. Chapman and Hall, London. 1986, pp. 35-109. ISBN: 978-94-010-7910-5.
11. Smith, C. M. Plant Resistance to Arthropods: Molecular and Conventional Approaches. Ed.: Dordrecht, The Netherlands, Springer. 2005, 423 pp.
12. Smith, C. M y Clement, S. L. Molecular Bases of Plant Resistance to Arthropods. *Annual Review of Entomology*, 2012, vol. 57, pp. 309-328. ISSN: 0066-4170.

13. Walling, L. L. y Kaloshian, I. Hemipterans as plant pathogens. *Annual Review of Phytopathology*, 2005, vol. 43, pp. 491-521. ISSN: 0066-4286.
14. Walling, L. L. Avoiding Effective Defenses: Strategies Employed by Phloem-Feeding Insects. *Plant Physiology*, 2008, vol. 146, pp. 859-866. ISSN: 0032-0889.
15. Walling, L. L. The Myriad Plant Responses to Herbivores. *Published Journal of Plant Growth Regulation*, 2000, vol. 19, pp. 195-216. ISSN: 0167-6903.
16. Howe, G. A. y Jander, G. Plant immunity to insect herbivores. *Annual Review of Plant Biology*, 2008, vol. 59, pp. 41-66. ISSN: 1543-5008.
17. Sadasivam, S. y Thayumanavan, B. Molecular Host Plant Resistance to Pests. New York: Marcel Dekker, 2003. 479 pp.
18. Smith, C. M. Biochemical plant defenses against herbivores: from poisons to spices. En: All Flesh is Grass, Plant-Animal Interrelationships Series: Cellular Origins, Life in Extreme Habitats and Astrobiology. Eds.: Dubinsky Z. y Seckbach, J. Ed. Berlin: Springer. 2010. 485 pp.
19. Sabelis, M. W.; Janssen, A. y Kant, M. R. The enemy of my enemy is my ally. *Science*, 2001, vol. 291, pp. 2104-2105. ISSN: 0036-8075.
20. Kessler, A. y Baldwin, I. T. Plant responses to insect herbivory: the emerging molecular analysis. *Annual Review of Plant Biology*, 2002, vol. 53, pp. 299-328. ISSN: 1543-5008.
21. Alba, J. M.; Joris, J.; Bernardus, G.; Schimmel, C. J. y Kant, M. R. Avoidance and suppression of plant defenses by herbivores and pathogens. *Journal of Plant Interactions*, 2011, vol. 6, pp. 221-227. ISSN: 1742-9145.
22. Ojito-Ramos, K. y Portal, O. Introducción al sistema inmune en plantas. *Biotecnología Vegetal*, 2010, vol. 10, pp. 3-19. ISSN: 2074-8647.
23. Stout, M. J. Types and mechanisms of rapidly induced plant resistance to herbivorous arthropods. En: Induced Resistance for Plant Defence, Editores: Walters, D.; Newton, A. y Lyon, G. Ed.: Oxford: Blackwell. 2007. 271 pp.
24. Cubero. Introducción a la mejora genética vegetal. 2^a Ed. Mundiprensa. Madrid. 2003.
25. Sharma, H. C. Biotechnological Approaches for Pest Management and Ecological Sustainability. Ed. BocaRaton, FL: CRC Press. 2009. 526 pp.
26. Cardona, C. Resistencia varietal a insectos. En: Entomología económica y manejo de plagas. Ed. Universidad Nacional de Colombia, Palmira. 2008. 99 pp.
27. Estrada, J. Pastos y forrajes para el trópico colombiano. Editor: Escobar Velásquez, L. F. Ed. Universidad de Caldas. 2002. 506 pp. ISBN: 958-8041-76-7.
28. Ribeiro do Vale, F. X.; Parlevliet, J. E.; Zambolim, L. Concepts in plant disease resistance. *Fitopatol. Bras.*, 2001, vol. 26, pp. 577-589. ISSN: 1678-4677.
29. Berzonsky, W. A.; Ding, H.; Haley, S. D.; Harris, M. O. y Lamb, R. J. /et al./ Breeding wheat for resistance to insects. *Plant Breeding Reviews*. 2010, vol. 22, DOI: 10.1002/9780470650202.ch5.
30. Birch, A.; Jones, A. T.; Fenton, B.; Malloch, G. y Geoghegan, I.; /et al./ Resistance-breaking raspberry aphid biotypes: constraints to sustainable control through plant breeding. *Acta Hortic.*, 2002, vol. 585, pp. 315-317. ISSN: 0567-7572.
31. Bus, V. G. M.; Chagné, D.; Bassett, H. C. M.; Bowatte, D. y Calenge, F. /et al./ Genome mapping of three major resistance genes to woolly apple aphid (*Eriosoma lanigerum* Hausm.). *Tree Genetics and Genomes*, 2008, vol. 4, pp. 233-236. ISSN: 1614-2942.
32. Díez, M. J. y Nuez, F. *Tomato*. En: Handbook of plant Breeding. Eds.: Prohens, J. y Nuez, F. Ed. Valencia, Springer, 2008. pp. 249-323. ISBN: 978-0-387-74108-6.
33. Oriani, M. A. D. y Vendramim, J. D. Influence of Trichomes on Attractiveness and Ovipositional Preference of *Bemisia tabaci* (Genn.) B Biotype (Hemiptera: Aleyrodidae) on Tomato Genotypes. *Neotropical Entomology*, 2010, vol. 39, pp. 1002-1007. ISSN: 1519-566X.
34. Wagner, G. J.; Wang, E. y Shepherd, R. W. New approaches for studying and exploiting an old protuberance, the plant trichome. *Annals of Botany, London*, 2004, vol. 93, pp. 3-11. ISSN: 0305-7364.
35. Kant, M. R.; Ament, K.; Sabelis, M. W.; Harin, M. A. y Schuurink, R. C. Differential timing of spider mite-induced direct and indirect defenses in tomato plants. *Plant Physiology*, 2004, vol. 135, pp. 483-495. ISSN: 0032-0889.
36. Fernández-Muñoz, R.; Salinas, M.; Álvarez, M. y Cuartero, J. Inheritance of resistance to two-spotted spider mite and glandular leaf trichomes in wild tomato *Lycopersicon pimpinellifolium* (Jusl.) Mill. *Journal of the American Society for Horticultural Science*, 2003, vol. 128, pp. 188-195. ISSN: 0003-1062.
37. Gilardón, E.; Gorustovich, M.; Petrinich, C.; Olsen, A.; Hernández, C.; Collavino, G. y Gray, L. Evaluación del nivel de resistencia de plantas de tomate a la polilla del tomate (*Tuta absoluta* Meyrick) mediante un bioensayo simple. *Revista de la Facultad de Agronomía, La Plata*, 1998, vol. 103, pp. 173-176. ISSN: 1669-9513.
38. Gilardón, E.; Pocovi, M.; Hernández, C. y Olsen, A. Papel dos tricomas glandulares da folha do tomateiro na oviposição de *Tuta absoluta*. *Pesquisa Agropecuária Brasileira, Brasília*, 2001, vol. 36, pp. 585-588. ISSN: 1678-3921.
39. Oliveira, C. M. D.; De Andrade, V. C. Jr.; Maluf, W. R.; Neiva, I. P. y Maciel, G. M. Resistance of tomato strains to the moth *Tuta absoluta* imparted by allelochemicals and trichome density. *Ciênc. agrotec., Lavras*, 2012, vol. 36, pp. 45-52. ISSN: 1413-7054.

40. Gilardón, E.; Gorustovich, M.; Collavino, G.; Hernández, C.; Pocoví, M.; Bonomo, M. L. C. y Olsen, A. Resistencia de líneas de tomate a la polilla del tomate (*Tuta absoluta* Meyr.) en laboratorio y a campo. *Invest. Agr. Prod. Prot. Veg.*, 2002, vol. 17, pp. 35-42. ISSN: 0211-4682.
41. Carter, C. D. y Snyder, J. C. Mite response in relation to trichomes of *Lycopersicon esculentum* x *L. hirsutum* F2 hybrids. *Euphytica*, 1985, vol. 34, pp. 177-185. ISSN: 1573-5060.
42. Carter, C. D. y Snyder, J. C. Mite responses and trichome characters in a full-sib F2 family of *Lycopersicon esculentum* x *L. hirsutum*. *Journal of the American Society for Horticultural Science*, 1986, vol. 111, pp. 130-133. ISSN: 0003-1062.
43. Weston, P. A.; Johnson, D. A.; Burton, H. T. y Snyder J. C. Trichome secretion composition, trichome densities and spider mite resistance of ten accessions of *Lycopersicon hirsutum*. *Journal of the American Society for Horticultural Science*. 1989, vol. 114, pp. 492-498. ISSN: 0003-1062.
44. Maluf, W. R.; Campos, G. A. y Cardoso, M. G. Relationship between trichoma types and spider mites (*Tetranychus evansi*) repellence in tomatoes with respect to zingiberene contents. *Euphytica*. 2001, vol. 121, pp. 73-80. ISSN: 1573-5060.
45. Rakha, M. T.; Scott, J. W.; Hutton, S. F. y Smith, H. Identification of trichomes, loci and chemical compounds derived from *Solanum habrochaites* accession LA1777 that are associated with resistance to the sweetpotato whitefly, *Bemisia tabaci* in tomato, *S. lycopersicum*. En: 43 Tomato Breeders Roundtable Abstracts, Ithaca, NY., 2011, October, pp. 9-11.
46. Dimock, M. y Kennedy, G. The role of glandular trichomes in the resistance of *L. hirsutum* f. *glabratum* to *Heliotis zea*. *Entomologia Experimentalis et Applicata*, Dordrecht, 1983, vol. 44, pp. 263-268. ISSN: 0013-8703.
47. Lin, S.; Trumble, J. y Kumamoto, J. Activity of volatile compounds in glandular trichomes of *Lycopersicon* species against two insect herbivores. *Journal of Chemical Ecology*, New York, 1987. vol. 13, pp. 837-849. ISSN: 15731561.
48. Kennedy, G.; Farrar, R. y Kashyap, R. 1991. 2-Tridecanone-glandular trichome-mediated insect resistance in tomato. Ed. American Chemical Society, Washington, DC. pp. 150-165.
49. Zamir, D.; Ben-David, T.; Rudich, J. y Juvik, J. Frequency distributions and linkage relationships of 2-tridecanone in interspecific segregating generations of tomato. *Euphytica*, 1984, vol. 33, pp. 481-488. ISSN: 0014-2336.
50. Magalhaes, S. T. V. D.; Jham, G. N.; Picanco, M. C. y Magalhaes, G. Mortality of second-instar larvae of *Tuta absoluta* produced by the hexane extract of *Lycopersicon hirsutum* f. *glabratum* (PI 134417) leaves. *Agricultural and Forest Entomology*. 2001, vol. 3, pp. 297-303. ISSN: 1461-9555.
51. Aragão, C. A.; Maluf, W. R.; Dantas, B. F.; Gavilanes, M. L. y Cardoso, M. G. et al. Tricosas foliares associados à resistência ao ácaro-rajado (*Tetranychus urticae* Koch.) em linhagens de tomateiro com alto teor de 2-tridecanona nos foliolos. *Ciéncia e Agrotecnologia*, 2000, vol. 24, pp. 81-93. ISSN: 1413-7054.
52. Williams, W. G.; Kennedy, G. G.; Yamamoto, R. T.; Thacker, J. D. y Bordner, J. 2-tridecanone, naturally occurring insecticide from the wild tomato *Lycopersicon hirsutum* f. *glabratum*. *Science*, 1980, vol. 207, pp. 888-889. ISSN: 0036-8075.
53. Chatzivasileiadis, E. A. y Sabelis, M. W. Toxicity of methyl ketones from tomato trichomes to *Tetranychus urticae* Koch. *Experimental & Applied Acarology*, 1997, vol. 21, pp. 473-484. ISSN: 1572-9702.
54. Chatzivasileiadis, E. A.; Boon, J. J. y Sabelis, M. W. Accumulation and turnover of 2-tridecanone in *Tetranychus urticae* and its consequences for resistance of wild and cultivated tomatoes. *Experimental and Applied Acarology*, 1999, vol. 23, pp. 1011-1021. ISSN: 1572-9702.
55. Laboratory, C. R. G.; Santa-Cecília, L. V.; Maluf, W. R.; Cardoso, M. D.; Bearzotti, E. y Souza, J. C. Seleção indireta para teor de 2-tridecanona em tomateiros segregantes e sua relação com a resistência a traça-do-tomateiro. *Pesquisa Agropecuária Brasileira*, 1999, vol. 34, pp. 733-740. ISSN: 1678-3921.
56. Channarayappa, S. G.; Muniyappa, V. y Frist, R. H. Resistance of *Lycopersicon* species to *Bemisia tabaci*, a tomato leaf curl virus vector. *Canadian Journal of Botany*, 1992, vol. 70, pp. 2184-2192. ISSN: 0008-4026.
57. Maliepaard, C.; Bas, N.; vanHeusden, S.; Kos, J.; Pet, G.; Verkerk, R.; Vrielink, R.; Zabel, P. y Lindhout, P. Mapping of qtls for glandular trichome densities and *Trialeurodes vaporariorum* (greenhouse whitefly) resistance in an F₂ from *Lycopersicon esculentum* x *Lycopersicon hirsutum* f. *glabratum*. *Heredity*, 1995, vol. 75, pp. 425-433. ISSN: 0018-067X.
58. Fery, R. L. y Kennedy, G. G. Inheritance of a factor in *Lycopersicon hirsutum* f. *glabratum* conditioning resistance to the tobacco hornworm. *HortScience*, 1983, vol. 18, 169 pp. ISSN: 0018-5345.
59. Fery, R. L.; Kennedy, G. G. y Sorenson, C. E. Genetic analysis of 2-tridecanone concentration and resistance to the tobacco hornworm (*Manduca sexta*) and the Colorado potato beetle (*Leptinotarsa decemlineata*) in *Lycopersicon* species. *HortScience*, 1984, vol. 19, pp. 562. ISSN: 0018-5345.

60. Barbosa, L. V. y Maluf, W. R. Heritability of 2-tridecanone-mediated arthropod resistance in an interspecific segregating generation of tomato. *Revista Brasileira de Genética*, 1996, vol. 19, pp. 465-468. ISSN: 0100-8455.
61. Nienhuis, J.; Helentjaris, T.; Slocum, M.; Roggero, B. y Schaefer, A. Restriction-Fragment-Length-Polymorphism analysis of loci associated with insect resistance in tomato. *Crop Science*, 1987, vol. 27, pp. 797-803. ISSN: 0011-183X.
62. Gonçalves, L. D.; Maluf, W. R.; Cardoso, M. G.; Resende, J. T. V.; Castro, E. M.; Santos, N. M.; Nascimento, I. R. y Faria, M. V. Relação entre zingibereno, tricomas foliares e repelência de tomateiros a *Tetranychus evansi*. *Pesquisa Agropecuária Brasileira*, 2006, vol. 41, pp. 267-273. ISSN: 1678-3921.
63. Weston, P. A. y Snyder, J. C. Trichome exudates of *Lycopersicon hirsutum* and their relevance to mite resistance. *Hortscience*, 1988, vol. 23, pp. 767. ISSN: 0018-5345.
64. Freitas, J. A.; Maluf, W. R.; Cardoso, M. D.; Gomes, L. A. A. y Bearzotti, E. Inheritance of foliar zingiberene contents and their relationship to trichome densities and whitefly resistance in tomatoes. *Euphytica*, 2002, vol. 127, pp. 275-287. ISSN: 0014-2336.
65. Azevedo, S. M. D.; Faria, M. V.; Maluf, W. R.; de Oliveira, A. C. B. y de Freitas, J. A. Zingiberene-mediated resistance to the South American tomato pinworm derived from *Lycopersicon hirsutum* var. *hirsutum*. *Euphytica*, 2003, vol. 134, pp. 347-351. ISSN: 0014-2336.
66. Van der Hoeven, R.; Monforte, A. J.; Breeden, D.; Tanksley, S. D. y Steffens, J. C. Genetic control and evolution of sesquiterpene biosynthesis in *Lycopersicon esculentum* and *L. hirsutum*. *Plant Cell*, 2000, vol. 12, pp. 2283-2294. ISSN: 1040-4651.
67. Muigai, S. G.; Schuster, D. J.; Bassett, M. J.; Scott, J. W. y McAuslane, H. J. Mechanisms of resistance in *Lycopersicon* germplasm to the whitefly *Bemisia argentifolii*. *Phytoparasitica*, 2002, vol. 30, pp. 347-360. ISSN: 0334-2123.
68. Gentile, A. G.; Webb, R. y Stoner, A. K. Resistance in *Lycopersicon* and *Solanum* to greenhouse white flies. *Journal of Economic Entomology*, 1968, vol. 61, pp. 1355-1357. ISSN: 0022-0493.
69. Gentile, A. G.; Webb, R. y Stoner, A. K. *Lycopersicon* and *Solanum* resistant to the carmine and the two-spotted spider mite. *J. Econ. Entomol.*, 1969, vol. 62, no. 70, pp. 834-836. ISSN: 0022-0493.
70. Juvik, J. A.; Berlinger, M. J.; Ben-David, T. y Rudich, J. Resistance among accessions of genera *Lycopersicon* and *Solanum* to four of the main insect pests of tomato in Israel. *Phytoparasitica*, 1982, vol. 10, pp. 145-156. ISSN: 0334-2123.
71. França, F. H.; Maluf, W. R.; Ferreira-Rossi, P. E.; Miranda, J. E. C.; Coelho, M. C. F.; Castelo-Branco, M. y Resende, A. M. Breeding for resistance to *Scrobipalpula absoluta* (Meyrick) among *Lycopersicon* accessions in Brazil. En: Management practices for tomato and pepper production in the tropics. Editor: Green, S. K. Ed. AVRDC, Taiwan. 1989, pp. 113-122.
72. Resende, J. T. V.; Maluf, W. R.; Faria, M. V.; Pfanni, A. Z. y Nascimento, I. R. Acylsugars in tomato leaflets confer resistance to the South American tomato pinworm, *Tuta absoluta* Meyr. *Sci. Agríc.*, 2006, vol. 63, pp. 20-25. ISSN: 0103-9016.
73. Goffreda, J. C.; Mutschler, M. A.; Ave, D. A.; Tingey, W. M. y Steffens J. C. Aphid deterrence by glucose esters in glandular trichome exudate of wild tomato *Lycopersicon pennellii*. *Journal of Chemical Ecology*, 1989, vol. 15, pp. 2135-2147. ISSN: 0098-0331.
74. Goffreda, J. C.; Mutschler, M. A. y Tingey, W. M. Feeding behavior of potato aphid affected by glandular trichomes of wild tomato. *Entomologia Experimentalis et Applicata*, 1988, vol. 48, pp. 101-107. ISSN: 1570-7458.
75. Nombela, G.; Beitia, F. y Muñiz, M. Variation in tomato host response to *Bemisia tabaci* (Hemiptera : Aleyrodidae) in relation to acyl sugar content and presence of the nematode and potato aphid resistance gene *Mi*. *Bulletin of Entomological Research*, 2000, vol. 90, pp. 161-167. ISSN: 0007-4853.
76. Blauth, S. L.; Churchill, G. A. y Mutschler, M. A. Identification of quantitative trait loci associated with acylsugar accumulation using intraspecific populations of the wild tomato, *Lycopersicon pennellii*. *Theor. Appl. Genet.*, 1998, vol. 96, pp. 458-467. ISSN: 1432-2242.
77. Resende, J. T. V.; Maluf, W. R.; Cardoso, M. G.; Nelson, D. L. y Faria, M. V. Inheritance of acylsugar contents in tomatoes derived from interspecific crosses with wild tomato *Lycopersicon pennellii* and their effect on spider mite repellence. *Genetics and Molecular Research*, 2002, vol. 1, pp. 106-116. ISSN: 1676-5680.
78. Fernández-Muñoz, R.; Domínguez, E. y Cuartero, J. A novel source of resistance to the two-spotted spider mite in *Lycopersicon pimpinellifolium* (Jusl.) Mill.: its genetics as affected by interplot interference. *Euphytica*, 2000, vol. 111, pp. 169-173. ISSN: 0014-2336.
79. Alba, J. M.; Montserrat, M. y Fernández-Muñoz, R. Resistance to the two spotted spider mite (*Tetranychus urticae*) by acylsucroses of wild tomato *Solanum pimpinellifolium* trichomes studied in a recombinant inbred line population. *Experimental and Applied Acarology*, 2009, vol. 47, pp. 35-47. ISSN: 1572-9702.

80. Rodríguez-López, M. J.; Garzo, E.; Bonani, J. P.; Fereres, A. y Fernández-Muñoz, R.; et al. Whitefly resistance traits derived from the wild tomato *Solanum pimpinellifolium* affect the preference and feeding behavior of *Bemisia tabaci* and reduce the spread of tomato yellow leaf curl virus. *Phytopathology*, 2011, vol. 101, pp. 1191-1201. ISSN: 0031-949X.
81. Escobar, R.; Rodríguez-López, M. J.; Alba, J. M.; Fernández-Muñoz, R.; Baccarin, P.; Castelo-Branco, M.; Boiteux, L. S. y Fonseca, M. E. N. Resistencia a *Tuta absoluta* en una entrada de la especie silvestre de tomate *Solanum pimpinellifolium*. En: Encuentro Internacional sobre *Tuta absoluta*. La Polilla del Tomate, un Grave Problema en Expansión, Valencia (España). Ed. PHYTOMA, España, 2010, no. 217, pp. 126-127.
82. Murungi, L. K.; Knapp, M.; Masinde, P. W.; Onyambu, G.; Gitonga, L. y Agong, S. G. Host-plant acceptance, fecundity and longevity of *Tetranychus evansi* (Acari: Tetranychidae) on selected tomato accessions. *African Journal of Horticultural Science*, 2009, vol. 2, pp. 79-91. ISSN: 1998-9326.
83. Picanço, M.; Leite, G. L. D.; da Mota, W. F. y Cangemi, R. C. Resistência de introduções de *Lycopersicon peruvianum* a *Tetranychus ludeni* (Koch) (Acari: Tetranychidae) e *Aculops lycopersici* (Massee) (Acari: Eriophyidae). *Agrociencia*, 1997, vol. 13, pp. 73-76. ISSN: 1405-3195.
84. Silva, C. A. D.; da Lourançao, A. L. y de Moraes, G. J. Resistencia de tomateiro ao acaro vermelho *Tetranychus evansi* Baker and Pritchard (Acari: Tetranychidae). *Anais da Sociedade Entomológica do Brasil*, 1992, vol. 21, pp. 147-156. ISSN: 0301-8059.
85. Leckie, B. M.; Jong, D. M. D. y Mutschler, M. A. Quantitative trait loci increasing acylsugars in tomato breeding lines and their impacts on silverleaf whiteflies. *Mol Breeding*, 2012, vol. 30, pp. 1621-1634. ISSN: 1380-3743.

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