

Insights on solanaceous resistance against tomato leafminer (*Tuta absoluta*), with emphasis on chemical compounds useful in integrated pest management

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Abstract

For integrated pest management (IPM) and organic farming, breeding resistant varieties is one of the most eco-friendly approaches, that goes along botanicals and other different cultural practices, as the use of companion plants. Among the many pest species that invaded the whole world in the last decades, one of the most frightening is the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), a devastating pest of cultivated tomato worldwide. Tomato is one of the most important agricultural commodities, including the main mean of subsistence in many countries from Africa and middle East. As chemical pesticides failed to control the pest spread and led to many reports of resistant populations, alternative methods for tomato leafminer management must be quickly developed. Many of such alternatives count on a wide range of chemical compounds. The chemical compounds most often responsible for “constitutive resistance”, synthesized by tomato are methyl-ketones (2-tridecanone), sesquiterpenes (zingiberene), and acyl sugars (acylglucose and acylsucrose) while the chemical compounds produced by other plants, used as isolated substances or mixtures, which have antifeedant, growth inhibiting, repellent, and insecticide effects, are azadirachtin, carvacrol, cinnamaldehyde, citronellal, eugenol, linalool, nicotine, pyrethrin, rotenone, thujone, thymol, α -terpineol, 1.8-cineol, etc. Many of them are already commercially available but their efficacy and use differ widely. Therefore, a deeper understanding of the resistance mechanism of solanaceous species related to chemical compounds and substances important for IPM plans developed against *T. absoluta* is required by the breeding programs.

Keywords: constitutive resistance; effective phytochemicals; insect resistance; plant extracts; tomato genotypes

Introduction

Humankind faces today unprecedented challenges, although some may claim that every century of our history had its own crisis. Our generation’ struggle portrays the sustainable development in a globalized world

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on the background of dramatic climate disorders, pandemic crisis, but also critical biodiversity losses, as in insects (Hallmann *et al.*, 2017) and ecosystems risks. Today's agriculture is forced to provide prompt breakthroughs to ensure safe and high-quality food to the world's population, which has grown from less than two billion to nearly 7.7 billion in just less than 100 years (Cohen, 2003; Roser *et al.*, 2020). To ensure the food, each year millions of tons of pesticides are used all around us (FAO and WHO, 2019), and besides their adverse impact on environment and public health (de Oliveira *et al.*, 2014), these synthetic molecules also lead to the development of insecticide-resistance phenomenon (Lietti *et al.*, 2005; Roditakis *et al.*, 2018; Guedes *et al.*, 2019; Silva *et al.*, 2019; Grant *et al.*, 2019). In addition to satisfying market demand, global trade has led to a sudden spread of invasive alien pest species (IAS) (Mack *et al.*, 2000; Hulme, 2009; Biondi *et al.*, 2018; Giorgini *et al.*, 2018), a threat that forced the crop protection industry and farmers to increase or misuse the agricultural inputs above the safe limit. The new (EU) Regulation 2016/2031 on plant health, which entered into force in December 2019, admits the risk of new species being introduced into the Union territory due to globalization of trade and climate change and suggests certain restrictions to reduce the hazards to an acceptable level (EFSA PLH, 2019), but the plant protectionist's experience proved it is not enough. Pests continue to be a threat for human's food security and environment and control measures will always be needed.

Tomato (*Solanum lycopersicum* L.) is one of the most important crops and commodities worldwide, but also one of the most used model systems for genetic studies in plants (Causse *et al.*, 2016). Among Solanaceous species, it has simple diploid genome with 12 chromosome pairs and a genome size of 950 Mb, encoding approximately 35,000 genes that are largely sequestered in contiguous euchromatic regions (Barone *et al.*, 2008). For breeders, many resources were available for genomic research in the last decades, as diverse tomato wild species resources; tomato mutant collections; marker collections; mapped populations; BAC (bacterial artificial chromosome) libraries; TILLING (targeting induced local lesions in genomes) populations; and tomato microarrays, gene silenced tomato lines etc. (Barone *et al.*, 2008), to arrive nowadays having whole genomes sequenced (TGC, 2012; Causse *et al.*, 2016), the SGN (Sol Genomics Network) web portal with genomic and phenotypic data on Solanaceous species (Fernandez-Pozo *et al.*, 2015) or the TGRD (Tomato Genetic Resources Database) (Suresh *et al.*, 2014) and the Breadbase system, the GitHub code hosting platform of SGN (Solegenomics, 2021). Tomato breeding is a success story, as many cultivars are today available for a wide range of traits, including vigour, productivity, resistances to pests and diseases, fruit quality, etc. and the future trend resides in genomics-based breeding (Heuvelink, 2018; Felföldi *et al.*, 2021).

Among the many pest species that invaded the whole world in the last decades, one of the most frightening is the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), a devastating pest of cultivated tomato (Desneux *et al.*, 2010; Desneux *et al.*, 2011; Campos *et al.*, 2017; Biondi *et al.*, 2018). As tomato is one of the most important agricultural commodities, including main means of subsistence in many low and –middle income countries, the control of this threatening pest it's considered a high priority by plant protectionists. Of neotropics origin, the pest always preferred tomatoes, although could be hosted on different Solanaceous crops, as potatoes, sweet pepper, eggplants (Desneux *et al.*, 2010; Bawin *et al.*, 2015; Cherif and Verheggen, 2019) and currently is in transition to polyphagy, as more than 40 plant species, 9 families, including one Monocots, are now reported to be its host (Cherif and Verheggen, 2019; Sylla *et al.*, 2019; Ciceoi and Gutue, 2020). In the 60's, *T. absoluta* became a key pest of South American tomato crops and starting with 2006, puts to a threat the worldwide tomato productions (Santana *et al.*, 2019), mainly in Europe (Desneux *et al.*, 2010; Desneux *et al.*, 2011; Campos *et al.*, 2017), in the Mediterranean region (Moreno *et al.*, 2011; Proffit *et al.*, 2011; Urbaneja *et al.*, 2012), the entire production on the African continent (Brévault *et al.*, 2014; Tonnang *et al.*, 2015; Mansour *et al.*, 2018; Aigbedion-Atalor *et al.*, 2019), in Central America (Verheggen and Fontus, 2019) and in some parts of Asia (Han *et al.*, 2018a, 2018b; Giorgini *et al.*, 2018). *Tuta absoluta* larvae attack tomato plants during all growth stages (de Brito *et al.*, 2015), the young larvae feeding mainly on leaf mesophyll immediately after hatching, but also on plants axillary buds, young shoots, new growths, in developing fruits, mature fruit, significantly reducing the leaf area, causing bud drop, plants cracking, fruit malformation or rot (Moreno *et al.*, 2011). The pest life cycle is a key element in designing the integrated pest

management (IPM) schemes. Although only the larvae are harmful, control measures must be taken in all pest's life stages, according to their specific physiology and feeding habits, for an effective control. In their struggle to save the tomato production, growers applied insecticides as often as 23 treatments per season (Zlof and Suffert, 2012), even more than 2 times a week (Moreno *et al.*, 2011), more than 40 applications per crop cycle (de Brito *et al.*, 2015), and even 60 to 80 insecticide applications per season (Bacci *et al.*, 2019). The intensive use of insecticides on this pest with very high reproductive potential (10–12 generations per year in South America (Bayram *et al.*, 2017), 6 generation in the Mediterranean region (Bayram *et al.*, 2017), 2-5 in Eastern Europe (Karadjova *et al.*, 2013) and ecological selectivity due to its feeding habits (mining only inside the leaves mesophyll) favoured the development of resistance to many different insecticides groups, especially pyrethroids, avermectins, and diamides (de Brito *et al.*, 2015; Guedes *et al.*, 2019; Roditakis *et al.*, 2018; Silva *et al.*, 2019). In fact, in 2021, the Arthropod Pesticides Resistance Database cites 17 active ingredients on which *T. absoluta* has already shown resistance: abamectin, bifenthrin, cartap, chlorantraniliprole, cyfluthrin-beta, cypermethrin-alpha, deltamethrin, diflubenzuron, etofenprox, flubendiamide, indoxacarb, metaflumizone, novaluron, permethrin, spinosad, teflubenzuron, and triflumuron.

For organic farmers the pressure to identify appropriate control measures is even higher. As the insecticide-resistance phenomenon has unknown implications and today's population is more than ever involved in a healthy lifestyle, preferring organic food, there is an urgency to develop safe alternatives of pest control and plant protection (Moreno *et al.*, 2011). As biocontrol alternatives, more than 70 arthropod species, out of which 20% are predators and 80% parasitoids, are mentioned having an activity against *T. absoluta* but only few of them showed a real potential to be included in IPM strategies in the newly invaded areas (Zappalà *et al.*, 2013). Besides cultural control measures, as crop rotation, destruction of infested plant material, destruction of possible weed hosts etc., other environmentally friendly control strategies have been developed, based on the use of the insect's sex pheromones (Florice *et al.*, 2018). Their use has a raising trend on the market, especially for the organic producers, but recent reports on *T. absoluta* deuterotokous parthenogenetic reproduction questions the future use of pheromone management or sterile insect techniques (Caparros Megido *et al.*, 2012).

Therefore, resistant cultivars and plant-derived products depicting pest control potential should be further investigated for a fast introduction in the agricultural production daily routine. All current tomato varieties are attacked by the pest, but some cultivars tend to be less attractive (Proffit *et al.*, 2011; Cherif and Verheggen, 2019) and some new hybrids under testing demonstrate potential to advance in the tomato breeding with resistance to tomato leafminer (Gharekhani and Salek-Ebrahimi, 2014; Ghaderi *et al.*, 2017; Ataide *et al.*, 2017; Sohrabi *et al.*, 2017; Dias *et al.*, 2019). The present paper summarizes the current knowledge regarding the efforts to obtain tomato and other solanaceous resistant lines based on characteristics found in different wild relatives of tomatoes and compiles references regarding other effective phytochemicals that could be alternatively used for *T. absoluta* control.

Solanaceous resistance against *Tuta absoluta*

Although *Tuta absoluta* is devastating cultivated tomato worldwide, this pest has as main hosts also potato (*Solanum tuberosum* L.) and eggplant (*S. melongena* L.) and was documented on 23 different species belonging to *Solanum* genus (Ciceoi and Gutue, 2020). In addition, it was mentioned on 15 other Solanaceous species belonging to ten genera, respectively *Atropa*, *Brugmansia*, *Capsicum*, *Datura*, *Lycium*, *Lycopersicon*, *Nicotiana*, *Physalis* and *Salpichroa* (Cherif and Verheggen, 2019; Ciceoi and Gutue, 2020).

Still, there are some nightshades species resistant to tomato leafminer attack, as *Capsicum annum* L., and *Capsicum chinense* Jacquin var. Cumari do Pará (Silva *et al.*, 2021), and some species inside the *Solanum* genus, as different species of wild tomatoes: *S. habrochaites* S. Knapp & D.M. Spooner (de Oliveira *et al.*, 2020; Silva *et al.*, 2021), *S. cheesmaniae* (Riley) Fosburg (Rakha *et al.*, 2017; Han *et al.*, 2018c). Wild relatives of

tomatoes are today the main source of the identified resistance traits for tomato breeders. According to Han *et al.* (2018c), these resistance traits may be categorised in constitutive resistance, induced resistance, and introduced resistance (Figure 1) and were extensively explained by the authors.

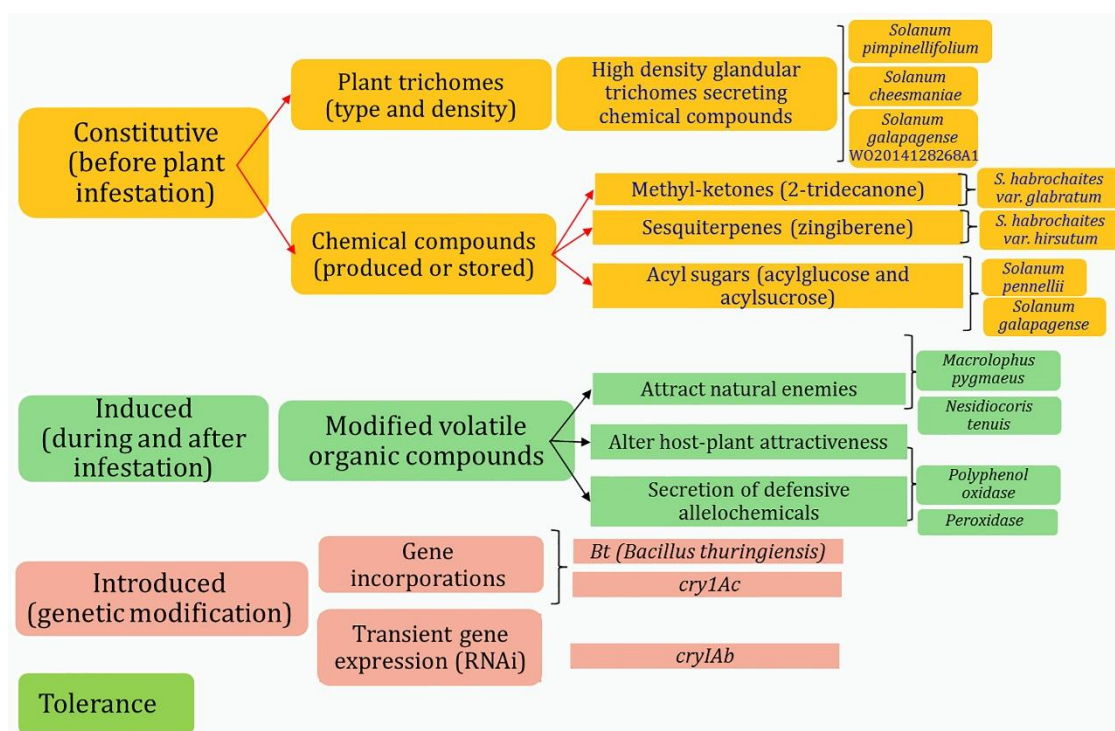


Figure 1. Solanaceous resistance against *T. absoluta* (according to Han *et al.*, 2018c)

Plant constitutive resistance was described by Han *et al.* (2018c), as related to the type and density of plant trichomes and to the chemical compounds produced and stored inside the plant's tissues, or a combination of these two factors. This type of resistance can be passed on to the progeny, for instance descendants of the yellow monkeyflower plants (*Mimulus guttatus* DC.) that have been attacked by insect herbivores have a higher trichome density than plants whose genitors were not attacked (Owens, 2019). Han *et al.*, 2018c, describe the induced resistance as being related to mechanisms that involve the secretion of volatile organic compounds when the plant is attacked, that may either attract tomato leaf miner predators and parasitoids, repel the pest by making the host plant less attractive for oviposition or by accumulation of oxidative enzymes, as polyphenol oxidase and peroxidase at the feeding sites. The introduced resistance is related to permanent or transient genetic modifications of the host species.

Resistance resources related to chemical compounds found in solanaceous species

Inner resistance due to chemical defence response

Traditional cultivated tomato varieties are generally highly susceptible to *T. absoluta* attack, with few being moderately tolerant/resistant (Han *et al.*, 2018c). In contrast, their wild relatives proved to be resistant. Currently, the 13 wild species in the *Solanum* section *Lycopersicon* can be categorised as (i) crossable, with low level of DNA differences - *Solanum pimpinellifolium*, *S. cheesmaniae* and *S. galapagense*, (ii) crossable, with high level of DNA differences *S. chmielewskii*, *S. habrochaites*, *S. neorickii* and *S. pennellii*, and (iii) difficult to cross, with very high level of DNA differences - *S. arcanum*, *S. chilense*, *S. corneliomulleri*, *S. huaylasense* and *S. peruvianum*, but research is making progress, proposing techniques such as embryo rescue (Heuvelink, 2018). Even though interspecific crosses between *S. habrochaites* var. *hirsutum* and *S. lycopersicum*

demonstrated the possibility of transferring the resistance traits to cultivated tomato through breeding (de Oliveira *et al.*, 2020), no commercial line has been released yet based on these parental lines. Studies on wild tomato with low level of DNA differences highlighted resistance traits transfer to *T. absoluta*, are related to high density of glandular trichomes secreting acyl sugars and sesquiterpenes (Rakha *et al.*, 2017). Consequently, Snoeren *et al.* (2017), published the first patent on 'resistant to arthropods' tomato lines, obtained through introgressed DNA sequences from *S. galapagense*. The authors patented 12 single nucleotide polymorphisms (SNPs) from *S. lycopersicum* genome responsible for resistance and/or tolerance to the tomato leafminer, white fly, and spider mite.

Most plant resistance traits to *T. absoluta* related to constitutive resistance due to chemical defence response have been identified in wild tomato relatives, for chemicals included in three main groups, as (i) methyl-ketones (e.g., 2-tridecanone), (ii) sesquiterpenes (zingiberene) and (iii) acylsugars (Han *et al.*, 2018c).

High acylsugar content and/or zingiberene have been related to higher resistance to arthropods. Chemicals-related resistance of wild tomatoes, *S. habrochaites*, has been attributed to volatile compounds such as 2-tridecanone, 2-undecanone, and zingiberene, compounds not found in sensitive cultivars (de Oliveira *et al.*, 2020).

2-Tridecanone

2-Tridecanone (C₁₃H₂₆O) is a chemical compound found so far in 36 plant species, among which *Solanum agrimoniifolium* Rydb. and *S. habrochaites* S. Knapp & D.M. Spooner, two bryophytes, two bacteria and one insect species. It is used as a chemical food additive to modify taste (Q27147536, 2021). Still, this flavour enhancer for humans, is a chemical compound effective in wild tomato plants in preventing *T. absoluta* attack, being present in high levels in trichomes. Its content increases with the increase in trichome density, which is related also with the plant age, as older plants have higher trichome density (Leite *et al.*, 2001).

2-Undecanone

2-Undecanone (C₁₁H₂₂O) is a chemical compound with role in decarboxylase activity, found so far in 53 plant species, among which *Solanum agrimoniifolium* Rydb. and *S. habrochaites* S. Knapp & D.M. Spooner, four bryophytes, two bacteria and two insect species (Q2024187, 2021).

Zingiberene

Zingiberene (C₁₅H₂₄) is a monocyclic sesquiterpene found so far in 45 plant species, among which *Solanum agrimoniifolium* Rydb. and *S. habrochaites* S. Knapp & D.M. Spooner (Q4117486, 2021). It is the most abundant molecule in ginger oil, conferring its specific taste, but it occurs in plant species such as tomato, basil, turmeric, cardamom and sorghum, with the presumed role of defending them against insect pests, by preventing eggs-laying and deterring feeding on the plant. Zingiberene has been shown to confer resistance to insect pests upon tomatoes (ccc). Genotypes with high zingiberene content demonstrated lower appeal for *T. absoluta* egg deposition (de Oliveira *et al.*, 2020). In addition, genotypes exhibiting high contents in both zingiberene and acyl sugars, showed greater resistance than genotypes accumulating only one of these chemicals, indicating a synergistic effect between zingiberene and acyl sugars (Maluf *et al.*, 2010). Zingiberene content has high heritability, (<80%), its production being controlled by two genes with incomplete dominance (de Oliveira *et al.*, 2020).

Acylsugars

Acylsugars are a group of chemical compounds produced in the secretory glandular trichomes of various plants, most often those belonging to the Solanaceae family, including *S. lycopersicum*, *S. pennellii*, *S. habrochaites*, known as biotic stress regulators, usually by deterring herbivorous insect pests (Kim *et al.*, 2012; Ben-Mahmoud *et al.*, 2018;). They are sugar esters, usually of sucrose or glucose, typically including 3–4 fatty acid side chains that vary in orientation, length, and location. Due to their role in physical and/or chemical

plant defence, commercial applications for plant breeding were found appealing (Mandal *et al.*, 2020). For instance, Leckie *et al.* (2016), analysed which acylsugar compositions of the four *S. pennellii* accessions and one acylsugar-producing tomato breeding line was more effective in suppressing oviposition of the whitefly *Bemisia tabaci* Gennadius, tobacco thrips, *Frankliniella fusca* Hinds, and western flower thrips, *Frankliniella occidentalis* Pergande. Their work demonstrated acylsugars ability to alter the distribution of whitefly oviposition and suppress the pest's oviposition, and also that mixtures of components may increase suppression through synergistic interactions, recommending acylsugars use for herbivore oviposition suppression, either through *in planta* production by tomato lines, or as biocides applied by a foliar spray (Leckie *et al.*, 2016).

Kim *et al.* (2012), while assessing acylsugar diversity for 80 accessions of *S. habrochaites*, revealed the presence of at least 34 structurally diverse acylsucroses and two acylglucoses, in distinct phenotypic classes. Analysis of the *Acyltransferase2* gene (*Solyc01g105580*) revealed differences in enzyme activity and gene expression correlated with polymorphism in *S. habrochaites* accessions. Mandal *et al.* (2020), while searching the unknown genes involved in acylsugars synthesis and regulation, based on different levels of this compound found in different accessions of *S. pennellii*, found high-acylsugars-production varieties, and based on gene silencing method confirmed two genes involved in acylsugar biosynthesis.

Weinhold and Baldwin (2011), showed that among the eight types of trichomes found in *Lycopersicon* clade, the type IV trichomes are producing acyl sugars, but in cultivated tomato plants, type IV trichomes are missing at the adult stage, however they are present in juvenile stage, so their presence may be controlled by promoting heterochronic alterations in plant ontogeny (Vendemiatti *et al.*, 2017) and further used in breeding. Maluf *et al.* (2010), demonstrate a synergistic effect between zingiberene and acylsugars, as the team found that genotypes exhibiting high contents of zingiberene and acylsugars showed higher resistance than the genotypes accumulating only one of these chemicals. Still, the fact that no commercial line has been marketed so far based on these characters may be caused by the fact that resistance transfer from these wild species is accompanied by other gene introgression mediating poor horticultural value (Rakha *et al.* 2017).

Currently, the list of genetic resources that were already tested for research on resistant lines based on chemical compounds displays few *S. lycopersicum* varieties and hybrids that are moderately susceptible to *T. absoluta* attack and few more further relatives that holds resistance traits (Table 1).

Grandillo and Cammareri, 2016, provide as a summary QTL (quantitative trait loci) mapping studies for pest resistance-related traits in tomato until 2016, citing 14 studies, none of these referring to tomato leafminer.

Induced resistance due to chemical defence response

The tomato plants can develop inducible resistance mechanisms against *T. absoluta*, mainly mediated through jasmonic acid pathway. These resistance mechanisms involve indirect defence based on volatile organic compound (VOC) emitted by infested plants, that are either attracting the pest natural enemies, in the places where *T. absoluta* was established for long enough to have such enemies, either deterring the pest away, or preventing egg-laying (Han *et al.*, 2018c). A third induced mechanism was highlighted by Coqueret *et al.* (2017), who recently found that a few hours after larval attack, tomato plants accumulated defensive enzymes as polyphenol oxidase and peroxidase close to the feeding site. Therefore, new breeding strategies could explore obtaining tomato lines that are emitting higher amounts of specific VOCs or that are inducing a strong enzymatic defence (Han *et al.*, 2018c).

In the same study the authors have shown an increase in gene expression related to cell wall, sterol and steroid metabolism, leaf development and photosynthesis, when plants were infested with the leafminer. Among these, the transcription factors with up-regulated gene expression are known to control secondary metabolites biosynthesis, trichome formation and jasmonic acid signalling. This indicates an interweaving of plants' mechanisms of defence, as the trichomes not only provide a physical barrier against herbivory attack, but they also produce chemicals that are deterrents to insect oviposition and feeding. (D'Esposito *et al.*, 2021)

Table 1. The list of moderately susceptible and resistant species, varieties, and hybrids to be used in breeding for resistance to *T. absoluta*

Moderately susceptible	Resistant	Reference (DOI)
<i>Solanum americanum</i> Mill.	<i>Capsicum annuum</i> L. (var. All Big)	(Silva et al., 2021)
<i>Solanum aculeatissimum</i> Jacq.	<i>Capsicum chinense</i> Jacquin (var. Cumari do Pará)	(Silva et al., 2021)
<i>Solanum melongena</i> L. (var. Comprida Roxa)	<i>Solanum paniculatum</i> L.	(Silva et al., 2021)
<i>Solanum gilo</i> Raddi (var. Verde Claro)	<i>Solanum habrochaites</i> S.Knapp & D.M.Spooner	(Silva et al., 2021)
	<i>Solanum habrochaites</i> var. <i>hirsutum</i> PI-127826	(de Oliveira et al., 2020)
	<i>Solanum pennellii</i> Correll	(Dias et al., 2019)
	Hybrid RVT A-2010-31-pl#177	(Dias et al., 2019)
	<i>S. peruvianum</i> L. NAV29 and NAV115	(de Falco et al., 2019)
<i>S. lycopersicum</i> L. BR221 (cherry)		(de Falco et al., 2019)
<i>S. lycopersicum</i> L. (var. Early urbana & Super 2270)		(Azadi et al., 2018)
<i>S. lycopersicum</i> L. (var. Cuatomate)		(Kayahan et al., 2018)
<i>S. lycopersicum</i> L. (var) Berlina, Zaman, Golsar, Poolad		(Sohrabi et al., 2017)
	<i>S. galapagense</i> S.C.Darwin & Peralta VI063177	(Rakha et al., 2017)
<i>S. lycopersicum</i> L. HGB-1497 and HGB-674 hybrids		(Ataide et al., 2017)
<i>S. lycopersicum</i> L. (var. Early Urbana Y & Primo Early)		(Ghaderi et al., 2017)
<i>S. lycopersicum</i> L. (var. Grandella)		(Rostami et al., 2016)
<i>S. lycopersicum</i> L. (var. Cluse)		(Gharekhani and Salek-Ebrahimi, 2014)
	BPX-367D-238-02	(de Oliveira et al., 2012)

Resistance resources related to chemical compounds found in non-related to tomato species

Volatile organic compounds of companion plants

Besides natural phytochemicals produced by plants to enhance their own defence mechanisms, plants also release a variety of different VOC, with multiple roles in their interactions with other plants or animals (Proffit et al., 2011). These volatiles are used by herbivore insects during feeding, mating, sheltering, or egg-laying, as these help insects to locate their host plants at different distances. Agronomists included these volatiles properties in the agroecosystem management schemes as a preventive method, both in the field and greenhouses, under the well-known term of *companion plants*. In the same way as in the case of the host plants that display constitutive resistance due to VOC presence, the companion plants can control insect pests either directly, by disrupting host location or deterring their establishment by attracting the pest away, or indirectly, by attracting those natural enemies that control the pest population (Parker et al., 2013). For example, coriander (*Coriandrum sativum* L.) releases volatiles that mask the odours of the tomato, making difficult their recognition by pests (Venzon et al., 2018; Giorgini et al., 2018). Besides attracting pollinators and feeding useful fauna with pollen, companion plants can serve as trap-crops, hosting most pests or they release volatiles, that also attract predators, such as ladybeetles (Venzon et al., 2018).

For tomato, VOCs emitting plants can be grown on the field edge or intercropped with the tomato plants. In Brazil and Costa Rica, but also Spain, tomato association with coriander plants reduced the incidence of *T. absoluta* on tomato plants in greenhouse experiments, and attracts natural parasitoids, such as *Necremnus tutae* (Crisol-Martínez and van der Bloom, 2019). Using dual-choice behavioural assays in flight tunnels, Yarou *et al.*, 2018, demonstrated the oviposition-detering effect of clove basil, *Ocimum gratissimum* L. and basil, *O. basilicum* L. plants against *T. absoluta*, suggesting their use as intercropping plants. Most probably, the ability of adults, mainly females, to locate host plants for feeding and eggs laying was affected by the VOCs. GC-MS analysis of VOCs revealed that *O. gratissimum* had 20 major active compounds while *O. basilicum* had 33 (Yarou *et al.*, 2018).

Recent studies in Spain revealed that using different flowers, as sweet alyssum (*Lobularia maritima* (L.) Desv.), borage (*Borago officinalis* L.), white mustard (*Sinapis alba* L.), yarrow (*Achillea millefolium* L.), buckwheat (*Fagopyrum esculentum* Moench), in field or greenhouse, promotes the attraction and longevity of *Necremnus tutae*, one of the most promising parasitoids used in Spain against tomato leafminer (Crisol-Martínez and van der Bloom, 2018). The impact of chemical non-host resources on tomato - *Necremnus artynes* interactions were explored by Balzan and Wäckers (2013), using sweet alyssum, *Lobularia maritima* L., bishop's flower, *Ammi majus* L., buckwheat, *Fagopyrum esculentum* Moench, redshank, *Polygonum persicaria* L. and coriander, *Coriandrum sativum* L. They concluded that floral resources may enhance the fitness of the parasitoids, but the pest is also able to benefit from the inclusion of supplementary floral nectar.

Understanding these mechanisms and the role played by volatiles that help pests locating their host plant may lead to the development of novel tools for insect management (Proffitt *et al.* 2011).

Volatile organic compounds of plants used as sources for botanicals

Plant extracts have been used for generations to control insect pests on agricultural crops and recent developed plant-derived botanicals are included in integrated pest management schemes (Pavela, 2014; Isman, 2020). Either extracts or pure compounds, they are a promising alternative to conventional pesticides due to their low toxicity to warm-blooded mammals and low adverse effects on the environment due to their high volatility (Moreno *et al.*, 2011). Ancient scripts demonstrate the ability of such compounds to affect plant pests; in India, the use of botanical insecticides was known for 4000 years ago, while China and Egypt protected their stored grains with phytochemicals more than 3200 years ago (de Oliveira *et al.*, 2014). There are thousands of known phytochemicals, and the list is constantly growing with new discoveries. One of the most ambitious phytochemical and ethnobotanical databases mentions 302 phytochemicals derived from 1329 plants with antifeedant activity, 186 phytochemicals derived of 766 plants with insecticide activity and 5 phytochemicals derived from 224 plants with repellent activity (Duke, 2016). Zoubiri and Baaliouamer (2014), cites 214 plant species with pesticide action, while Ikbali and Pavela (2019), cites 76 plant species as sources of essential oils for botanical insecticides against aphids.

There are different types of extracts that proved in different laboratory, greenhouse or field test their effectiveness against *T. absoluta*. Such preparations may be aqueous or alcoholic plant extracts or essential oils extracted by different methods.

The water extracts are the most affordable and easy to be prepared pesticides at small scale, and because the active compounds are water soluble, they are safer for consumers. Usually these are mixtures with unknown compositions and synergic or antagonistic effects may happen. Some experiments proved the water extracts could be very effective, as in one greenhouse experiment, where chinaberry (*Melia azedarach* L.) extracts were highly effective in reducing *T. absoluta* larvae population, including more effective than the chemical control (Ghanim and Abdel Ghani, 2014). Some water extracts showed translaminar, systemic, and contact activity, as in the case of aqueous neem seeds extracts. These extracts lead to 100% mortality both when applied in the soil or on the leaves adaxial surface, indicating that the extracts were absorbed and transferred inside the plant both by roots and leaves (Gonçalves-Gervásio and Vendramim, 2007).

Laboratory assay using alcoholic extract of *Piper amalago* var. *medium* (Jacq.) Yunck., (synonym of *Piper amalago* L.) demonstrate that although of high efficiency, the ethanolic extract induced *T. absoluta* larval mortality before the leaf mesophyll penetration, a fact that might suggest that symptoms of lethargy and low mobility are given by the contact mode of action of neurotoxins from piperaceous derivatives. Such phytochemical candidates may not be useful for *T. absoluta* due to ecological selectivity, as the larvae usually only feeds inside the leaves (de Brito *et al.*, 2015). One isobutylamide, named spilanthol, (E)-N-isobutylundeca-2-en-8,10-diyamide and (R, E)-N-(2-methylbutyl)undeca-2-en-8,10-diyamide were the three most active alkamides compounds isolated from a hexane extract of the aerial parts of *Acmella oleracea* (L.) R.K.Jansen, which lead to 100% mortality on second-instar larvae of *T. absoluta*. All isolated compounds showed insecticidal activity, although spilanthol was the most active, with LD50 = 0.13 $\mu\text{g mg}^{-1}$ (Moreno *et al.*, 2011). In this experiment spilanthol was five times more toxic than a synthetic pyrethroid (permethrin) and almost 321 times more potent than natural extract containing azadirachtin. Essoung *et al.* (2017), in a bioassay using a crude methanol extract of *Caesalpinia welwitschiana* (Oliv.) Brenan leaves found that both the extract and five isolated compounds possess antifeedant and moderate larvicidal activity against second-instar larvae of *T. absoluta* and they identified two new effective compounds, welwitschianalol A and B.

Essential oils (EOs) have low environmental impact due to their high biodegradability, low toxicity to vertebrate animals and multiple modes of action associated to the presence of different active ingredients that hinders the development of resistance in the target pest (Pavela and Benelli, 2016). Many studies demonstrate the efficacy of EOs on pests in the laboratory experiments, but field application must be undertaken for each pest species, due to high volatility, low persistence, poor water solubility, and possible phytotoxicity that EOs have (Giorgini *et al.*, 2018). Nanoencapsulation may help in solving most of these problems (de Oliveira *et al.* 2014). EOs may contain several dozens (20-60) of phytochemicals, usually with two or three main compounds present at high concentrations (20-85%) and many others at trace levels, making difficult the standardization of the products and therefore the authorization process, especially in Europe, where this procedure is over demanding (Pavela and Benelli, 2016). Campolo *et al.*, 2017, found that nano formulated EOs have a higher insecticidal activity than the standard EOs for the ingestion bioassay, but weaker in the ingestion bioassay. In one experiment using *Zataria multiflora* Boiss. EOs, *T. absoluta* adults were more sensitive to fumigated EOs than the egg stage and the second instar larvae, inside the leaf, proving that the life stage is very important when recommending a certain natural treatment.

Umpiérrez *et al.* (2012), tested *Eupatorium buniifolium* Hook. ex Hook. & Arn., and *Artemisia absinthium* L. against *T. absoluta* larvae and characterized their chemical composition and insecticidal activities. *A. absinthium* EO was found to be rich in oxygenated monoterpenes (β -thujone, 56,32%, (Z)-epoxy-ocimene, 14,76%, (Z)-b-ocimene, 4,56%, camphor 3,73%, α -thujone, 1,67%). *E. buniifolium* EO was rich in monoterpene hydrocarbons, as α -pinene, 22% and sesquiterpene hydrocarbons, as (E)- β -guaiene, 10%. Although displaying different composition, both had similar insecticidal activity. Eugenol, isoeugenol and cineol were tested for egg hatchability, oviposition deterrence and repellence against first and fourth *T. absoluta* larval instar, together with clove (*Syzygium aromaticum* (L.) Merr. & L.M.Perry), parsley (*Petroselinum crispum* (Mill.) Fuss) and lavender (*Lavandula angustifolia* Mill.) oils by Moawad *et al.* (2013). Clove oil, eugenol and isoeugenol caused high mortality and the clove oil showed high histological effect on the larvae body wall.

All these findings about effective chemical compounds may open new ways in breeding strategies, although these may seem much further away that using the resistant traits already existing in the tomato close relatives.

Conclusions

The multiple negative impacts of intensive use of synthetic pesticides on environment, humans and other non-target organisms forced researchers and practitioners to develop sustainable methods of prevention and control for the most destructive pests. As *T. absoluta*'s parthenogenetic reproduction might put into shadow some of the currently used control strategies (e.g., pheromone management or sterile insect techniques), spraying remains the most accessible and affordable pest control method for this pest. Phytochemicals might play multiple roles in developing new environmental-friendly methods for this pest control, by their multiple ways of action. Development and validation of IPM programs against tomato leafminer, adapted to each climatic zone, by blending resistant lines, different cultural methods as companion plants and using plant extracts or formulated pure compounds, might be the key for a resilient tomato production for future generations.

Authors' Contributions

Conceptualization: RC; Funding acquisition: AAU, LAB; Project administration AAU, LAB; Writing - original draft RC, MI; Writing - review and editing: AAU, MI, RC, LAB. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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