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Tomato trichomes: trade-off between plant defenses against pests and benefits for biological control agents

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Original research

ABSTRACT


Trichomes are a first line of defense of plants against herbivorous arthropods, but they can also act as a barrier against natural enemies hampering biological control programmes. Despite the abundance of trichome types on tomato plants, many herbivorous arthropods can still evade these defenses. Over the past decades, numerous studies have evaluated the impact of tomato trichomes on phytophagous arthropods, yet few have examined their effects on biological control agents. Moreover, studies on the complex tri-trophic interactions among tomato plants, arthropod pests, and natural enemies remain limited, highlighting the need for further research to deepen our understanding of these relationships. Understanding the effects of tomato trichomes on both pests and biological control agents could enhance pest management strategies, informing tomato breeding and biological control programs. To support ongoing research and practical applications, this paper reviews the effects of tomato trichomes on the development of pests, including that of phytophagous mites and their natural enemies, with a particular focus on predatory mites. Current challenges and future directions are discussed.

Keywords *Solanum*; mite; insect; plant resistance; tri-trophic interactions; biocontrol; parasitoid; predator

Introduction

Trichomes are modified plant epidermal cells, forming a hairlike protuberance (Glas *et al.* 2012; Chang *et al.* 2019). The shape, length and density of trichomes can vary among species, genotypes and plant organs (Glas *et al.* 2012; Rakha *et al.* 2017b). Found in approximately 30% of vascular plant species, trichomes serve as a first line of defense against herbivorous arthropods. However, they can also hinder natural enemies by affecting feeding, oviposition, host and prey accessibility and foraging behaviour of predators and parasitoids, potentially reducing the efficiency of biological control (Duffey *et al.* 1986; Cortesero *et al.* 2000; Kennedy 2003; Glas *et al.* 2012; Kaur and Kariyat 2020). This review focuses on the cultivated tomato (*Solanum lycopersicum* L, formerly *Lycopersicon esculentum* Miller) and on its wild relatives (*Solanum* spp.) due to (i) the economic significance of tomatoes crop, with global production reaching 189 million tons in 2021 (FAOSTAT 2022); (ii) decades of research on the defensive role of trichomes against herbivorous arthropods in solanaceous plants and (iii) the possibility for trichomes to impede the survival and effectiveness of natural enemies, potentially compromising biological control efforts.

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In Solanaceae, trichomes are classified into two categories based on their shape and function: glandular trichomes (GT) and non-glandular trichomes (NGT). GTs have glandular cells at their tips that can release secondary metabolites including essential oils, toxic substances and sticky compounds, which can impact the viability and dispersal of arthropods on their plant (Southwood 1986; Cortesero *et al.* 2000; Kennedy 2003; Glas *et al.* 2012). NGTs do not release any secondary metabolite but may act as a physical barrier preventing arthropods from feeding and moving (Kariyat *et al.* 2018, 2019).

Many herbivorous arthropods are able to 'bypass' these defenses on tomato plants becoming significant pests (Wakil *et al.* 2017). To mitigate the impact of pesticides on human health and the environment, it is essential to identify alternative solutions. While biological control is recognized as a promising strategy, its implementation in tomato crops remains particularly challenging due to the negative effects of trichomes on natural enemies, including parasitoids and predators (Kennedy *et al.* 2003). Numerous studies have examined the impact of tomato trichomes on phytophagous arthropods; however, few have explored their effects on biological control agents. Additionally, research on the complex tri-trophic interactions among tomato plants, arthropod pests and their natural enemies is limited, highlighting the need for further investigation into these interactions. A deeper understanding of the impact of tomato trichomes on both pests and biological control agents is required to enhance sustainable pest management strategies, including the development of new tomato varieties and the optimization of biological control programs. To support these advancements, this paper presents a review of the effects of tomato trichomes on the development of pests, including phytophagous mites, and their natural enemies, with a particular focus on predatory mites. Additionally, current and future challenges are also discussed.

Overview of tomato pests and associated natural enemies influenced by tomato trichomes

The key tomato pests most extensively studied in relation to trichome types and densities are the whiteflies - *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood) (Maliepaard *et al.* 1995; Freitas *et al.* 2002), the tobacco hornworm *Manduca sexta* (L.) (Farrar and Kennedy 1987; Kariyat *et al.* 2017), the fruit worm *Helicoverpa zea* (Boddie) (Farrar and Kennedy 1987), the tomato leafminer *Tuta absoluta* Meyrick (Resende *et al.* 2006), several aphid species such as *Macrosiphum euphorbiae* (Thomas) and *Aphis gossypii* Glover (Musetti and Neal 1997; Verheggen *et al.* 2009) and phytophagous mites (Rakha *et al.* 2017a), especially the two-spotted spider mite (*Tetranychus urticae* Koch), the tomato spider mite (*Tetranychus evansi* Baker & Pritchard) (Acari, Tetranychidae) and the tomato russet mite [*Aculops lycopersici* (Tryon)] (Acari, Eriophyidae). The two-spotted spider mite is one of the most significant pests globally due to its ability to feed on a diverse range of host plants (Van Leeuwen *et al.* 2010). The tomato spider mite became an important tomato pest, notably in Africa since the end of the 20th century (Navajas *et al.* 2013). The tomato russet mite is a minute pest that feeds on various Solanaceae species causing plant death. Its small size allows it to hide beneath trichomes, making it difficult to control and reducing the effectiveness of both pesticide sprays and natural enemies (Vervaeke *et al.* 2021).

Several natural enemies are reported to be affected by tomato trichomes: *Trichogramma* spp. (Kayshyap *et al.* 1991), Tachinidae flies (Farrar *et al.* 1992), Coccinellidae (Heinz and Zalom 1996), lacewings (Simmons and Gurr 2004; Gassman and Hare 2005), predatory bugs (Barbour *et al.* 1993; Economou *et al.* 2006; Bottega *et al.* 2017), Syrphidae (Verheggen *et al.* 2009) and predatory mites especially those of the family Phytoseiidae (e.g. Cédola and Sanchez 2003; Seelmann *et al.* 2007; Paspati *et al.* 2021).

Tomato trichomes and plant resistance to arthropod herbivory

In cultivated tomato and its closest wild relatives [i.e. *Solanum cheesmaniae* (L. Riley) Fosberg, *S. chilense* (Dunal) Reiche, *S. galapagense* Darwin & Peralta, *S. habrochaites* Knapp & Spooner, *S. peruvianum* L., *S. pimpinellifolium* L.], trichomes have multicellular structures and have been classified into different functional types based on the number of cells, shape and presence of glandular cells at the tip (Luckwill 1943; Simmons and Gurr 2005). In 1943, Luckwill was the first to describe seven types of trichomes in *Lycopersicum* spp. (now *Solanum* spp.). As this classification was incomplete (i.e. *S. pennellii* Correll was missing) (Simmons and Gurr 2005), Channarayappa *et al.* (1992) and Glas *et al.* (2012) proposed a revision defining eight types of trichomes (Table I, Figure 1) with basically two main categories: (i) **GTs** corresponding to types I, IV, VI and VII, having ‘heads’ with one or more glandular cells releasing exudates and (ii) **NGTs** corresponding to types II, III, V and VIII, with no glandular cells at the tip (Simmons and Gurr 2005). In cultivated tomato and its wild relatives, types and densities of trichomes vary among plant organs (Glas *et al.* 2012), species and cultivars (Rakha *et al.* 2017b), and even in relation to plant age or biotic factors (temperature, photoperiod) (Simmons and Gurr 2005).

Trichomes can have physical and chemical effects on herbivorous arthropods. Both GTs and NGTs can physically hinder the dispersal of phytophagous arthropods, while GTs release compounds that are either repellent or toxic to arthropods (see Table 2).

Physical effects

NGTs can restrict herbivore movement, however their effects have been insufficiently studied and the role of NGTs in plant resistance to arthropods requires further investigation (Bar and Shtein 2019; Karabourniotis *et al.* 2020). Kariyat *et al.* (2019) showed that the *M. sexta* mean mass was lower and development time longer when feeding on leaves of *Solanum elaeagnifolium* Cavanilles, having higher NGT densities compared to control treatment. Kariyat *et al.* (2017) observed that the NGTs of *Solanum carolinense* L. affect pre- and post-ingestion of *M. sexta*, by damaging the gut of caterpillars. Regarding mites, Oliveira *et al.* (2018) did not observe any negative effect of high densities of NGTs on several life parameters of *T. urticae*; while the preferred tomato variety was *S. lycopersicum* L. cv. Redenção which had the highest density of NGTs.

In contrast, GTs are the most extensively studied trichomes in terms of physical role in arthropod defense. On tomato, the GT types IV and VI are the most associated with pest resistance (Simmons and Gurr, 2005). Vosman *et al.* (2018) showed that all varieties resistant to several insects [*T. vaporariorum*, *Myzus persicae* (Sulzer), *Frankliniella occidentalis* (Pergande), *Spodoptera exigua* (Hubner)] possess GT types I and IV on their leaves, suggesting

Table 1 Brief description of trichome types in tomato and its wild relatives (according to Luckwill 1943, Simmons and Gurr 2005, Ben-Israel *et al.* 2009 and Glas *et al.* 2012).

Type	Glandular trichomes (GT) / Not glandular trichomes (NGT)	Length	Short description
I	GT	6-10 cells / 2-3 mm long.	Long with small and round glandular cells at the top, with a multicellular basis.
II	NGT	5-8 cells / 0.2-1.0 mm long	Similar to type I but shorter and non-glandular, with a multicellular basis.
III	NGT	4-8 cells / 0.4-1.0 mm long	Similar to type II with an unicellular and flat basis.
IV	GT	0.2-0.4 mm long	Similar to type I but shorter. Glandular trichome with an unicellular and flat basis and one glandular cell at the top.
V	NGT	0.2-0.4 mm long	Similar to type IV but non-glandular. Three cells.
VI	GT	0.1 mm long	Thick and short with four secretory cells at the tip. There are different shapes of the glandular cells: spheric, lobe, intermediate.
VII	GT	0.05 mm long	Very short with 4-8 cells at the top.
VIII	NGT	Length not documented (see Glas <i>et al.</i> 2012)	Trichome with one basal and thick cell with a leaning cell at the tip.

Table 2 Effect of tomato trichomes on herbivorous arthropods. Pest and life history parameters affected, type of effect and of trichomes involved, and plant organs and molecules studied. References are presented in chronological order of publication. NA: data not available or not specified; GT: Glandular Trichomes; NGT: Non Glandular Trichomes.

References	Year	Pest	Life parameters affected	Mechanical / Antibiose or Antixenose	Trichomes studied	Organs	Molecules	Type of correlation
Williams et al. (1980)	1980	<i>Manduca sexta</i> , <i>Heliothis zea</i> , <i>Aphis gossypii</i>	Mortality	NA	NA	Leaves	2-tridecanone	Negative
Farrar and Kennedy (1987)	1987	<i>M. sexta</i> , <i>H. zea</i>	Larval mortality	NA	NA	artificial diet	2-undecanone	Negative
Lin et al. (1987)	1987	<i>Keiferia lycopersicella</i> , <i>Spodoptera exigua</i>	Mortality	NA	Type VI	Leaves	2-tridecanone, 2-undecanone	Negative
Van Haren et al. (1987)	1987	<i>Tetranychus urticae</i>	Mortality (entrapment)	NA	Density of GTs (type VI)	Stem	NA	Negative
Goffreda et al. (1988)	1988	<i>Macrosiphum euphorbiae</i>	Mortality (entrapment and toxicity)	NA	Density type IV	Leaves	NA	Negative
Good and Snyder (1988)	1988	<i>T. urticae</i>		NA	Density type VI		NA	No effect
Carter et al. (1989)	1989	<i>Leptinotarsa decemlineata</i>	Mortality	NA	Density type VI	Leaves	Zingiberene	Negative
Channarayappa et al. (1992)	1992	<i>Bemisia tabaci</i>	Fecundity (numbers of eggs and nymphs), Adult mortality	non-preference	Density of type VIc	Leaves	NA	Negative
Heinz and Zalom (1995)	1995	<i>B. tabaci</i>	Oviposition	NA	Density trichomes		NA	Positive
Maliepaard et al. (1995)	1995	<i>Trialeurodes vaporariorum</i>	Mortality, oviposition	NA	Density type VI	Leaves	NA	Negative
Chatzivalsileiadis and Sabelis (1997)	1997	<i>T. urticae</i>	Mortality, egg viability	NA	NA	Toxicity bioassays (immersion)	2-tridecanone and 2-undecanone	Negative
Musetti and Neal (1997)	1997	<i>M. euphorbiae</i>	Mortality	NA	NA	Plant extract	2-tridecanone and 2-undecanone	Negative
Chatzivalsileiadis and Sabelis (1998)	1998	<i>T. urticae</i>	Mortality	NA	NA	Leaves	2-TD and 2-undecanone	Negative
Snyder et al. (1998)	1998	<i>B. tabaci</i>	Oviposition, Attractancy	NA	Density type IV	Leaves	NA	Negative
Chatzivalsileiadis et al. (1999)	1999	<i>T. urticae</i>	Mortality	NA	Type VI	Leaves and stem	2-tridecanone	Negative
Leite et al. (1999)	1999	<i>Aculops lycopersici</i>	Attack rate	NA	Density type VI	Leaves	2-tridecanone	Negative
Aragão et al. (2000)	2000	<i>T. urticae</i>	Distance travelled (spread)	NA	Density type VI	Leaves	2-tridecanone	Negative
Maluf et al. (2001)	2001	<i>Tetranychus evansi</i>	Mite repellence	NA	Density type IV	Leaves	Zingiberene	Negative
Freitas et al. (2002)	2002	<i>B. tabaci</i>	Number of adult, number of nymphae	NA	Densities types IV, VI and VII	Whole plant, leaves	Zingiberene	Negative
Muigai et al. (2002)	2002	<i>B. tabaci</i>	Oviposition, mortality	NA	NA	Leaves	2-undecanone	Negative
Resende and Maluf (2002)	2002	<i>T. urticae</i>	Repellency	NA	NA	Leaves	acyl-sugars	Negative
Azevedo et al. (2003)	2003	<i>Tuta absoluta</i>	Feeding and ovipositing (Leaflet lesion, percent leaflets attacked, overall plant damage)	NA	NA	Whole plant	Zingiberene	Negative
Cédola and Sanchez (2003)	2003	<i>T. urticae</i>	Fecundity	Antibiosis	Density GTs	Leaves	NA	Negative
Gonçalves et al. (2006)	2006	<i>T. evansi</i>	Repellency (distance walked by mite)	NA	Density type VI	Leaves	Zingiberene	Negative
Resende et al. (2006)	2006	<i>T. absoluta</i>	Plant damages, leaflet lesion, percentage of attack leaflet	NA	NA	Whole plant	acyl-sugars	Negative
Maluf et al. (2007)	2007	<i>T. urticae</i>	Mite repellence (distances walked by mites)	NA	Density type VI	Leaves	Zingiberene	Negative
Sacidi et al. (2007)	2007	<i>T. urticae</i>	Oviposition, mortality, leaf damage score	NA	Density of type IV	Leaves	acyl-sugars	Negative
Alba et al. (2009)	2009	<i>T. urticae</i>	Mortality, oviposition	Antibiosis	Density type IV	Leaves	acyl-sugars	Negative
Resende et al. (2009)	2009	<i>B. tabaci</i>	Oviposition and nymph development	Antibiosis	NA	Leaves	acyl-sugars	Negative
Maluf et al. (2010)	2010	<i>T. absoluta</i>	Oviposition	NA	NA	Leaves	Zingiberene	Negative
Onyambus et al. (2011)	2011	<i>T. evansi</i>	Adult survival	NA	Density type I	Leaves	NA	Negative
Blecker et al. (2012)	2012	<i>B. tabaci</i> , <i>T. urticae</i> , <i>T. evansi</i> , <i>M. sexta</i> , <i>L. decemlineata</i>	Fecundity, survival	Antibiosis	Density type VI	Leaves	Zingiberene, 7-epizingiberene	Negative
Leckie et al. (2012)	2012	<i>B. tabaci</i>	Development	NA	Density type IV	Whole plant	acyl-sugars	Negative
Dias et al. (2013)	2013	<i>T. absoluta</i>	Non preference for oviposition and suppression of larval development	Antixenose and antibiosis	NA	Leaves	acyl-sugars	Negative
Lucatti et al. (2013)	2013	<i>B. tabaci</i>	Adult and pre-adult survival, oviposition rate	NA	Density type I and IV	Leaves	acyl-sugars	Negative
Antonious and Snyder (2015)	2015	<i>T. urticae</i>	Repellency, fecundity (number of eggs)	NA	NA	Tomato leaf extracts sprayed on bean leaves	2-tridecanone, 2-undecanone, 2-dodecanone, 2-pentadecanone	Negative
Baier et al. (2015)	2015	<i>T. urticae</i>	Distance travelled (spread)	NA	NA	Leaves	acyl-sugars	Negative
Keskin and Kumral (2015)	2015	<i>T. urticae</i>	Survival, damages rate	NA	Density of type VI	Leaves	NA	Negative
Lima et al. (2015)	2015	<i>T. absoluta</i>	Fecundity (number of eggs), plant damages, lesions types, percentage of attacked leaflets	NA	NA	Whole plant, leaves	Zingiberene	Negative
Lucini et al. (2015)	2015	<i>T. urticae</i>	Fecundity (Free choice test), number of mite (Free choice test), fecundity and oviposition (no-choice test) duration of stages, viability of nymph stage	Antixenose and antibiosis	Density type IV	Leaves	acyl-sugars	Negative
Dias et al. (2016)	2016	<i>B. tabaci</i>	Non preference for oviposition and suppression of larval development	Antixenose and antibiosis	NA	Leaves	acyl-sugars	Negative
Leckie et al. (2016)	2016	<i>B. tabaci</i> , <i>Frankliniella fusca</i> , <i>Frankliniella occidentalis</i>	Oviposition	NA	NA		acyl-sugars	Negative
Andrade et al. (2017)	2017	<i>B. tabaci</i>	Fecundity	NA	Density type IV	Leaves		Negative
Kariyat et al. (2017)	2017	<i>M. sexta</i>	damaging the gut of caterpillars	Mechanical	NGTs	artificial diet, leaves	NA	Negative
Racka et al. (2017a)	2017	<i>T. urticae</i>	Fecundity (number of eggs)	Antixenose and antibiosis	Density of type IV	Leaves	acyl-sugars	Negative
Racka et al. (2017b)	2017	<i>B. tabaci</i>	Fecundity (numbers of adults, eggs, nymphs), Adult mortality	NA	Density of type IV	Leaves	NA	Negative
Oliveira et al. (2018)	2018	<i>T. urticae</i>	Egg incubation period, mortality of nymphs, fecundity	Antibiosis	Densities type IV and VI. NGT	Leaves	Zingiberene	Negative for GT. No effect for NGT.
Vosman et al. (2018)	2018	<i>T. vaporariorum</i> , <i>Myzus persicae</i> , <i>F. occidentalis</i> , <i>S. exigua</i>	Survival (adults, larvae), oviposition, larval weight	NA	Presence of type I and IV	Leaves	NA	Negative
Kariyat et al. (2019)	2019	<i>M. sexta</i>	larval growth, mean caterpillar mass, development time	Mechanical	NGTs	artificial diet	NA	Negative
Dawood and Snyder (2020)	2020	<i>T. urticae</i>	Repellency	NA	NA	filter paper	Alcohol and Epoxy Alcohol of Zingiberene	Negative
Kortbeek et al. (2021)	2021	<i>B. tabaci</i>	Survival	NA	Density type I and IV	Leaves	acyl-sugars	Negative
Vervae et al. (2021)	2021	<i>A. lycopersici</i>	Survival	NA	NA	NA	NA	Positive

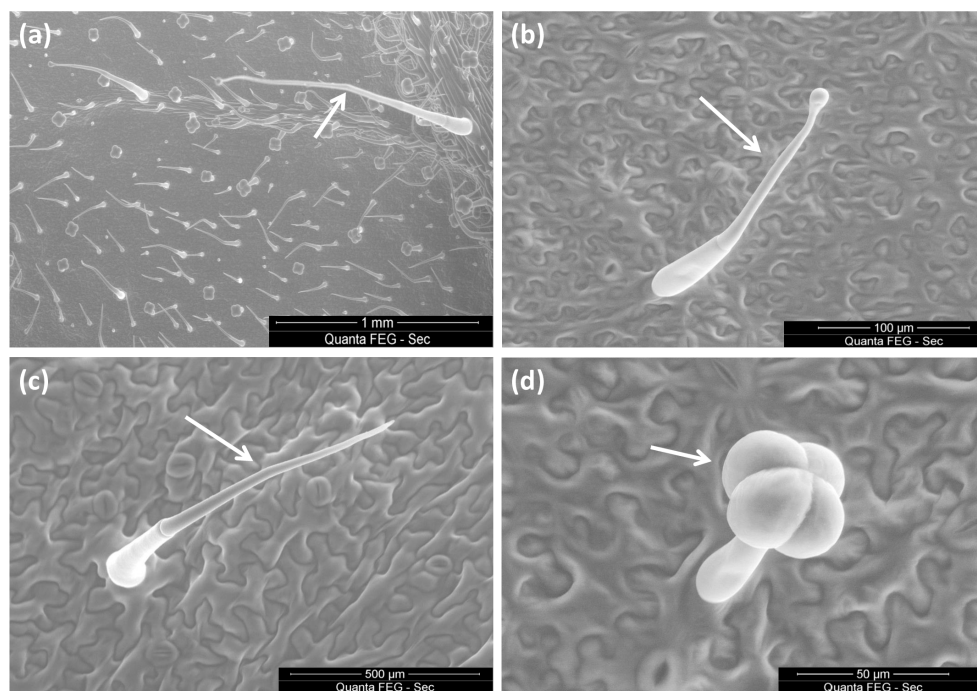


Figure 1 Main tomato trichome types affecting arthropods. Scanning electron micrographs showing general aspect. (a) – Type I on a leaf of *S. lycopersicum* cv. Clomimbo (x 100); (b) – Type IV on a leaf of *S. cheesmaniae* (x 800); (c) – Type V on the stem of *S. peruvianum* (x 200); and (d) – Type VI on a leaf of *S. cheesmaniae* (x 600).

that they are essential for plant resistance (in agreement with Firdaus *et al.* 2013; Lucatti *et al.* 2013). Arthropods die by being trapped by sticky exudates of GTs, such as acyl-sugars (Duffey 1986; Cédola and Sánchez 2003; Glas *et al.* 2012). GTs of cultivated tomatoes and wild relatives also act as a physical barrier, which interfere with *B. tabaci* feeding, oviposition and survival (Channarayappa *et al.* 1992; Rakha *et al.* 2017b).

Similarly for mites, Van Haren *et al.* (1987) studied the ability of *T. urticae* to walk on tomato stems with high density of GTs type VI (*S. lycopersicum* cv. ‘Turbo’) and showed that 55% of *T. urticae* were entrapped after a 2 hour period. When screening tomato genotypes for resistance to *T. urticae*, Keskin and Kumral (2015) showed that the tomato variety with the lowest mite damage had the highest density of type V NGTs and type VI GTs. Tabary *et al.* (2024) showed that types I and IV GTs on the petiole had the highest impact on the settlement and dispersal of *T. urticae*, when studying eight tomato and wild *Solanum* genotypes. In contrast with observations made of *Tetranychus* spp., trichomes do not act as a physical barrier to the movement and development of *A. lycopersici*. Because of its small size, with a length of less than 200 μm and a width of 50 μm , and a worm-like body, it can move between the trichomes, thereby protecting it from predation (Sabelis and Bruin 1996; Vervaeet *et al.* 2021).

Chemical effects

A significant body of research has focused on the chemical effects of GTs, particularly regarding the detrimental impact of compounds secreted from their tips. These compounds are associated with three plant resistance mechanisms: antixenosis, antibiosis and tolerance. Antixenosis (or ‘non-preference’) corresponds to a repellent effect of the resistant plant compared to a susceptible one (Rakha *et al.* 2017b; Santamaria *et al.* 2020). Antibiosis affects life history parameters of arthropods (survival, development, fecundity, etc.) after plant feeding, resulting in lower fitness, survival rate, oviposition and development (Rakha *et al.* 2017b; Santamaria *et*

al. 2020). Tolerance refers to the plant's ability to sustain high densities of arthropods without experiencing damaging effects (Santamaria *et al.* 2020).

GTs produce a large range of (i) non-volatile compounds such as acyl-sugars (Kroumova and Waner 2003) and protease inhibitors (Glas *et al.* 2012); and (ii) low volatile exudates such as phenylpropanoids (Gang *et al.* 2001), terpenoids (Gershenson and Dudareva 2007), phenolics (Karabourniotis *et al.* 2020), methyl ketones (Fridman *et al.* 2005), and flavonoids (Treutter 2006). In tomatoes, each type of trichome produces different compounds depending on species, cultivar; plant age and type of organs (Glas *et al.* 2012; Rakha *et al.* 2017b). The most studied compounds are acyl sugars, methyl ketones and sesquiterpenes (terpenoids).

Acyl-sugars

Acyl-sugars are non-volatile secondary metabolites that contribute to physical (stickiness) and chemical plant defenses (Schillmiller *et al.* 2008; Glas *et al.* 2012; Rakha *et al.* 2017a). Different mixtures of acyl-sugars produced by tomato and their wild relatives can have detrimental effects on arthropods (McDowell *et al.* 2011; Lucatti *et al.* 2013). Positive correlations between acyl-sugars concentration and type IV trichomes on leaves have been observed by Alba *et al.* (2009) and Lucini *et al.* (2015). However, the same type of trichome may produce different type of exudate depending on plant species and cultivars (Rakha *et al.* 2017b). No relationship was found between GT type VI and acyl-sugars secretion in both cultivated and wild tomatoes (Fan *et al.* 2019). Several studies have demonstrated a relationship between type I and IV GTs, acyl-sugars and resistance to insect pests. According to Simmons and Gurr (2005), acyl-sugars have antixenosis effects on phytophagous insects. Dias *et al.* (2013) observed that high acyl-sugars concentrations (secreted by F2 generation obtained from crosses between *S. lycopersicum* cv. 'Redenção' x *S. pennellii* 'LA716') was associated to resistance to *T. absoluta* with a non-preference for oviposition (antixenosis) and the suppression of larval development (antibiosis). Similar observations were noted for *B. tabaci*, with a positive correlation between acyl-sugars secretions and non-preference for oviposition and suppression of larval development (Dias *et al.* 2016). Resende *et al.* (2009), studied the resistance of genotypes [crosses between *S. lycopersicum* cv 'TOM 584' and *S. pennellii* (LA716)] to *B. tabaci*, and found that the lowest number of nymphs was observed on genotypes with high acyl sugar content. Lucatti *et al.* (2013), found that resistance to *B. tabaci* of *S. galapagense* accessions was correlated with high concentrations of acyl-sugars and densities of GT types I and IV. Kortbeek *et al.* (2021) showed that the density of GT types I and IV on leaves of a large number of cultivated tomato and wild species was a strong predictor for resistance to *B. tabaci* due to the production of acyl-sugars. Snyder *et al.* (1998) observed a lower oviposition and a reduced attractiveness of *B. tabaci* on *S. habrochaites* accessions with high densities of GTs type IV and also suggested that this might be due to acyl-sugars secretions. However, *B. tabaci* population growth was higher on tomato cultivars with pubescent leaves compared to hairless ones, attributed to higher oviposition rate of females (Heinz and Zalom 1995). This may be explained by the preference of *B. tabaci* to lay eggs at the base of leaf trichomes (Berlinger *et al.* 1986).

Acyl-sugars also have a negative impact on mites, particularly *T. urticae*, which has been the focus of extensive study. Saeidi *et al.* (2007) showed that density of GT type IV and resistance to mites increased with plant age. Alba *et al.* (2009), performing crosses between cultivated tomato and the wild species *S. pimpinellifolium* (TO-937), showed that a high density of GT type IV and high acyl-sugars content, both increase mortality of spider mites (antibiosis effect characterized by high mortality and reduced oviposition). Similar results were obtained by Rakha *et al.* (2017a), showing a positive correlation between resistance to *T. urticae*, density of GT type IV and acyl-sugars contents in *S. galapagense*, *S. pimpinellifolium* and *S. cheesmaniae*. In contrast, no clear link between GT type VI and resistance to *T. urticae* was observed, consisting with results of Good and Snyder (1988). Lucini *et al.* (2015) worked on different genotypes, including crosses between the cultivated tomato (cv. Redenção) with

low acyl-sugars content and the wild genotype *S. pennellii* with high acyl-sugars content (LA-716). They showed that *T. urticae* preferred tomato genotypes with low acyl-sugars content, suggesting a non-preference resistance (antixenosis).

Methyl ketones

Methyl ketones are secondary metabolites mainly produced by GTs type VI. The 2-tridecanone (2-TD) and 2-undecanone have been associated with pest resistance in tomato (Williams *et al.* 1980; Farrar and Kennedy 1987; Lin *et al.* 1987; Chatzivasileiadis *et al.* 1999; Maluf *et al.* 2007; Ben-Israel *et al.* 2009). A positive correlation was observed between densities of GTs types IV and VI and the secretion of 2-TD (Aragão *et al.* 2000; Simmons and Gurr 2005; Ben-Israel *et al.* 2009). Among the three forms of glandular cells in GTs type VI, the spherical cells have been linked to a higher production of methyl ketones (Ben-Israel *et al.* 2009). Several studies showed that these two sticky compounds have negative effects on bollworms *H. zea*, tobacco hornworms *M. sexta*, potato aphids *M. euphorbiae*, cotton aphids *A. gossypii*, *B. tabaci* and *T. vaporariorum* (Williams *et al.* 1980; Maliepaard *et al.* 1995; Musetti and Neal 1997). By contrast, other studies have found no effect of the 2-undecanone on *M. sexta* (Farrar and Kennedy 1987 in Simmons and Gurr 2005). These apparently inconsistent observations might be due to different levels of methyl-ketones produced in type VI trichomes between and among *Solanum* spp. (Simmons and Gurr 2005) or different plant organs (concentrations of 2-TD being higher in stems trichomes) (Chatzivasileiadis *et al.* 1999).

Methyl ketones are also known to have deleterious effects on phytophagous mites. Chatzivasileiadis and Sabelis (1997, 1998) showed that 2-TD and 2-undecanone are highly toxic to *T. urticae*, and suggested a bioaccumulation of 2-TD. Chatzivasileiadis *et al.* (1999) showed that *T. urticae* reared on tomato accumulate 2-TD when foraging on the stems. On *S. habrochaites* var. *hirsutum*, they demonstrated that just one or two contacts of mites with GTs type VI cause 50% mortality (antibiosis). Four methyl ketones of *S. habrochaites* accession LA 407 (2-tridecanone, 2-undecanone, 2-dodecanone, 2-pentadecanone) revealed the presence of repellent and anti-fecundity effects on *T. urticae* (antibiosis and antixenosis) (Antonious and Snyder 2015). 2-TD and 2-undecanone produced by GTs are also toxic to *A. lycopersici* (Leite *et al.* 1999).

Sesquiterpenes

Sesquiterpenes are terpenoids considered to be the most diverse class of plant metabolites, with more than 50,000 known molecules (Vranová *et al.* 2012). Their roles are diverse, being primary metabolites involved in photosynthesis and respiration and secondary metabolites involved in plant-pathogen interactions playing a major role in plant defenses (Dudareva *et al.* 2006). Zingiberene (ZGB) is the most studied sesquiterpene for its role in pest resistance. Produced mostly by GTs types IV and VI in tomatoes, it has often been associated to high levels of arthropod resistance (Maluf *et al.* 2001; Kennedy 2003; Maluf *et al.* 2007; Schilmiller *et al.* 2009; Oliveira *et al.* 2018). Some studies, such as Carter *et al.* 2002 did not find a correlation between secretions of sesquiterpenes and GTs type IV, while others including Maluf *et al.* 2001, reported the opposite.

ZGB was particularly associated to resistance to *B. tabaci* and *T. absoluta* (Freitas *et al.* 2002; Azevedo *et al.* 2003) and Freitas *et al.* (2002) showed a reduced number of *B. tabaci* on plants with high ZGB concentrations. Bleeker *et al.* (2012) also observed a negative correlation between concentration of ZGB and fecundity of *B. tabaci* (antibiosis). Studies also showed negative effects of ZGB on feeding and oviposition of *T. absoluta* (Azevedo *et al.* 2003; Lima *et al.* 2015). Azevedo *et al.* (2003) studying the resistance to *T. absoluta* of five genotypes (F2 generation from crosses between *S. lycopersicum* cv. 'TOM-556' and *S. habrochaites* var. *hirsutum* accession 'PI127826'), observed lower leaflet lesion (feeding deterrence), percentage of leaflets attacked (oviposition) and overall plant damage on genotypes with higher ZGB content. Studying resistance to *T. absoluta* of F2 genotypes obtained after crossing *S.*

lycopersicum cultivar 'Redenção' x *Solanum habrochaites* var. *hirsutum* ('PI-127826'), Lima *et al.* (2015) observed that genotypes having high ZGB concentration in leaves presented lower oviposition compared to susceptible genotypes. Maluf *et al.* (2010) also observed higher resistance of *T. absoluta* in genotypes with high acyl-sugars and high ZGB content. Other sesquiterpenes are also toxic to arthropods such as for instance 7-epizingiberene which, associated to ZGB, decreased the fecundity of *B. tabaci* (antibiosis) (Bleeker *et al.* 2012).

Sesquiterpenes also negatively affect development and survival of spider mites and Maluf *et al.* (2001) found a positive correlation between GTs type IV, ZGB concentration and repellence to *T. evansi* (antixenosis). Oliveira *et al.* (2018) showed that genotypes with high ZGB concentration had high densities of GTs type IV and VI and were less preferred by *T. urticae*, suggesting an antibiosis effect. These results are consistent with findings from several other studies (e.g. Gonçalves *et al.* 2006) on *T. evansi*. In addition, Dawood and Snyder (2020) working on compounds (alcohol and epoxy alcohol of zingiberene) secreted by trichomes of wild tomatoes showed that the alcohols of ZGB were significantly more repellent to *T. urticae* than ZGB.

Utilizing trichome-associated chemical compounds in tomato breeding programs

Selection of genotypes with both high concentration of toxic compounds and high density of GTs types IV and VI may be significant for tomato breeding programs. Regarding the chemical compounds mentioned above, Zeist *et al.* (2019) noted that resistance exists in wild tomato species as highlighted in this review, but the mechanisms underlying this resistance remain to be better elucidated.

Tomato breeding programs for pest resistance have focused on the main chemical compounds secreted by tomato trichomes mentioned above (acyl-sugars, methyl ketones and sesquiterpenes). Most of these programs were based on crosses between tomato and closely related wild species - *S. pimpinellifolium*, *S. pennellii*, *S. galapagense* and *S. habrochaites*.

To create cultivars with high acyl-sugars contents, crosses were conducted between *S. lycopersicum* and *S. pennellii* (accession 'LA-716') possessing high acyl-sugars contents (Zeist *et al.* 2019). After several backcrosses, the descendants were resistant to *B. tabaci*, *T. absoluta*, *M. euphorbiae*, *F. occidentalis* and *T. urticae* (Goffreda *et al.* 1988; Goffreda and Mutschler 1989; Maluf *et al.* 2010; Leckie *et al.* 2012, 2016; Baier *et al.* 2015; Lucini *et al.* 2015), resulting in the production of several tomato lines (Cornell tomato breeding program, USA e.g. CU071026 with five introgressions from LA-716). Crosses were also performed between cultivated tomato and *S. galapagense*, resulting in tomato resistant to *B. tabaci* (Firdaus *et al.* 2013). Alongside these studies, scientists have focused on understanding the genetic basis of acyl-sugars secretion. Resende and Maluf (2002) suggested that secretion of acyl-sugars in LA-716 is attributable to monogenic resistance. In 2013, the Quantitative Trait Locus (QTL) Wf-1 was identified as being associated to the presence of GTs type IV and acyl-sugars production (Firdaus *et al.* 2013). Schillmiller *et al.* (2012) highlighted the role of the gene Solyc01g105580 (SIAT2), expressed in the single tip cells of GTs type IV, that encodes an acetyl-CoA-dependent acyltransferase enzyme. In vitro, RNAi suppression of this gene in *S. lycopersicum* cv. M82 resulted in a lower acyl-sugar acetylation. Finally, Andrade *et al.* (2017) worked on the genetic basis of high density of GTs type IV and identified two major-effect QTLs on *S. galapagense* accession LA-1401. Further information on acyl-sugar biosynthesis genes and acyl-sugar pathways could enhance future breeding programs aimed to integrate resistance to arthropod pests.

Methyl ketones have also been regarded as promising candidates for developing new varieties resistant to many phytophagous arthropods. High levels of 2-TD compounds are already considered an effective screening criterion in breeding programs devoted to develop resistant cultivars, especially derived from crosses between *S. lycopersicum* and *S. habrochaites* var. *glabratum* (Barbosa and Maluf 1996). However, the genetic basis of high 2-TD secretions

seems to be complex and requires further investigation (Zeist *et al.* 2019). Indeed, Barbosa and Maluf (1996) demonstrated that, in crosses between *S. lycopersicum* x *S. habrochaites* var. *glabratum*, heritability does not fit into a simple additive-dominant model.

Crosses between *S. lycopersicum* and *S. habrochaites* var. *hirsutum* (accession PI-127826) were conducted to develop plants resistant to *B. tabaci*, *T. absoluta* and *T. evansi* (Freitas *et al.* 2002; Gonçalves *et al.* 2006; Lima *et al.* 2015). Furthermore, it was observed that ZGB appears to be controlled by two genes with incomplete dominance (Lima *et al.* 2015).

Impact of trichomes on biological control agents of tomato pests

Efficiency of natural enemies is influenced by tri-trophic interactions involving the prey and the host plant (Kennedy *et al.* 2003). Tomato trichomes will affect the behaviour and biology of natural enemies, both predators and parasitoids, directly (by influencing foraging activities, dispersal, development) and indirectly (through bioaccumulation resulting from feeding on preys containing toxic compounds) (Table 3).

Effects of trichomes on parasitoids

Tomato trichomes appear to reduce parasitoid movements and to affect their life-traits through physical and toxic effects, resulting in lower parasitism success, however studies on this topic are scarce. The walking speed of *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) was reduced on tomato cultivars with high densities of GTs type VI on leaves, and high levels of 2-tridecanone (Kayshyap *et al.* 1991). A higher mortality of *Archytas marmoratus* (Townsend) (Diptera, Tachinidae) was observed on leaves of *S. habrochaites* with high densities of GTs type VI, associated with a toxic effect of 2-TD (Farrar *et al.* 1992).

Table 3 Effect of tomato trichomes on natural enemies. Target pest and life history parameters affected, type of trichomes involved, plant organs and molecules studied. References are presented in chronological order of publication. NA: data not available or not specified; GT: Glandular Trichomes.

References	Year	Predator or parasitoid	Pest	Life parameters affected	Trichomes studied	Organs	Molecules	Type of correlation
Shah <i>et al.</i> (1982)	1982	<i>Adalia bipunctata</i>	NA	Fell of the plant, foraging efficiency	Density of trichomes	Leaves	NA	Negative
Van Haren <i>et al.</i> (1987)	1987	<i>Phytoseiulus persimilis</i>	<i>Tetranychus urticae</i>	Mortality (entrapment)	Density GTs	Stem	NA	Negative
Kauffman and Kennedy (1989)	1989	<i>Trichogramma</i> spp.	<i>Heliopsis</i> spp.	rate of parasitism	Density of type VI	Whole plant	NA	Negative
Kashyap <i>et al.</i> (1991)	1991	<i>Trichogramma pretiosum</i>	NA	walking speed, mortality (entrapment), escape	Density type VI	Leaves	methyl ketones	Negative
Kashyap <i>et al.</i> (1991)	1991	<i>Telenomus sphingis</i>	NA	escape, landing rates	Density type VI	Leaves	methyl ketones	Negative
Farrar <i>et al.</i> (1992)	1992	<i>Archytas marmoratus</i> , <i>Eucelatoria bryani</i>	<i>H. zea</i>	Mortality (toxic, entrapment), dessication of the host	Density of type VI	Leaves	methyl ketones	Negative
Barbour <i>et al.</i> (1993)	1993	<i>Coleomegilla maculata</i>	<i>Manduca sexta</i>	Egg consumption, mortality	Density type VI	Leaves	2-TD, 2-undecanone	Negative
Barbour <i>et al.</i> (1993)	1993	<i>Geocoris punctipes</i>	<i>M. sexta</i>	Egg consumption, mortality	Density type VI	Leaves	2-TD, 2-undecanone	Negative
Farrar and Kennedy (1993)	1993	<i>A. marmoratus</i>	<i>Heliopsis zea</i>	rate of parasitism	Artificial diet	Artificial diet	methyl ketones	Negative
Nihoul (1994)	1994	<i>P. persimilis</i>	NA	Rate of entrapment	Number and size of trichomes; amount of exudates	Stem	NA	Negative
Heinz and Zalom (1996)	1996	<i>Delphastus pusillus</i>	<i>Bemisia tabaci</i>	fecundity, walking speed	Density of trichomes	Leaves	NA	Negative
Coll <i>et al.</i> (1997)	1997	<i>Orius insidiosus</i>	NA	Foraging ability	Density of trichomes	Leaves	NA	Negative
De Clercq <i>et al.</i> (2000)	2000	<i>Podisus nigripinus</i>	<i>Spodoptera exigua</i>	Predation ability, searching efficiency	Density GTs	Whole plant, leaves	NA	Negative
Cédola <i>et al.</i> (2001)	2001	<i>Neoseiulus californicus</i>	<i>T. urticae</i>	Egg consumption, adult consumption	Density GTs	Leaves	NA	Negative
Cédola and Sanchez (2003)	2003	<i>N. californicus</i>	<i>T. urticae</i>	No life traits impacted	Density of trichomes	Leaves	NA	Negative
Simmons and Gurr (2004)	2004	<i>Mallada signata</i>	<i>Mysis persicae</i>	Predation rate, cannibalism, mortality (entrapment)	Density type IV	Leaves	NA	Negative
Economou <i>et al.</i> (2006)	2006	<i>Macrolophus pygmaeus</i>	<i>M. persicae</i>	time allocation activity	Density type VI	Leaves	NA	Negative
Economou <i>et al.</i> (2006)	2006	<i>Orius niger</i>	<i>M. persicae</i>	time allocation activity	Density type VI	Leaves	NA	Negative
Mulatu <i>et al.</i> (2006)	2006	<i>Diadegma pulchripes</i>	<i>Phthorimaea operculella</i>	rate of parasitism	Density of trichomes	Leaves	NA	Negative
Voigt <i>et al.</i> (2007)	2007	<i>Dicyphus errans</i>	NA	Attachment ability, traction forces	length, diameter, density of trichomes	Leaves	NA	Positive
Verheggen <i>et al.</i> (2009)	2009	<i>Episyrphus balteatus</i>	NA	Movement and predatory rate	Density of trichomes	Stem	NA	Negative
Sato <i>et al.</i> (2011)	2011	<i>Phytoseiulus macropilis</i>	<i>T. urticae</i>	locomotion, prey consumption, oviposition	Densities of trichomes	Leaves, stem	NA	Negative
Buitenhuis <i>et al.</i> (2014)	2014	<i>Amblyseius swirskii</i>	NA	Walking speed, predation rate, oviposition rate	Density of trichomes	Leaves	NA	Negative
Bottega <i>et al.</i> (2017)	2017	<i>P. nigripinus</i>	<i>T. absoluta</i>	survival, adult longevity, larval prey consumption, foraging behavior	Density type I and IV	Leaves	NA	Negative
Bueno <i>et al.</i> (2018)	2018	<i>Campyloneurospis infumatus</i> , <i>Engytatus varians</i> , and <i>Macrolophus basicornis</i>	<i>T. absoluta</i>	Predation rates, foraging efficiency, locomotion, feeding activities	Density of trichomes	Leaves, stem	NA	Neutral
Voigt <i>et al.</i> (2019)	2019	<i>Dicyphus errans</i>	<i>Aphis gossypii</i> , <i>Aulacorthum circumflexum</i> , <i>Aulacorthum solani</i> , <i>Macrosiphum euphorbiae</i> , <i>M. persicae</i> ; <i>Echinothrips americanus</i> , <i>Planococcus citri</i> , <i>Trialeurodes vaporariorum</i>	Attachment force, body weight, consumption rate	length, diameter, density of trichomes	Whole plant	NA	Positive
Paspati <i>et al.</i> (2021)	2021	<i>A. swirskii</i>	NA	Adult survival, dispersal	GTs	Leaves, stem	Acyl sugars	Negative
Savi <i>et al.</i> (2021)	2021	<i>Phytoseiulus longipes</i>	<i>Tetranychus evansi</i>	Intrinsic rate, predation potential	Density GTs	Leaves	NA	Negative

On tomato plants with a high secretion of methyl-ketones, rates of parasitism of *H. zea* by *A. marmoratus* were lower compared to tomato plants without methyl-ketones (Farrar and Kennedy 1993). Mulatu *et al.* (2006) studied the impact of trichomes on the development and parasitism rate of *Diadegma pulchripes* (Kokujev) (Hymenoptera, Ichneumonidae), a parasitoid of the potato tuber moth *Phthorimaea operculella* (Zeller) (Lepidoptera, Gelichiidae). These authors showed that the moth was not affected by the plant trichome density, but *D. pulchripes* failed to parasitize larvae on tomato leaves. Similar observations were made for *Trichogramma* spp., which exhibited lower parasitism rates of *Heliothis* spp. on tomato varieties with high density of GTs type VI (Kauffman and Kennedy 1989).

Effects of trichomes on predators

Physical effects

Studies generally emphasise that trichomes negatively impact the foraging behaviour and predator movements, of both insects and mites. Shah (1982) found that larvae of *Adalia bipunctata* L. (Coleoptera, Coccinellidae) had difficulty staying on the plant and fell off after an average of 20 minutes and also observed a lower foraging efficiency, with a higher percentage of unsuccessful attempts to capture prey. Likewise, the predator *Delphastus catalinae* (Horn) (Coleoptera, Coccinellidae) (previously named *D. pusillus*) exhibited a lower walking speed on tomato leaves with a high trichome density, compared to tomato leaves with low trichome density (Heinz and Zalom 1996). Coll *et al.* (1997) showed that *Orius insidiosus* (Say) (Heteroptera, Anthocoridae) had a greater foraging ability on leaves on bean and corn, which had a low total number of trichomes, compared to tomato plants, with high trichomes density. A high GTs type IV density can also increase the number of predators entrapped by trichomes on tomato leaves, as cited by Simmons and Gurr (2004) for *Mallada signatus* (Schneider) (Neuroptera, Chrysopidae). Nymphs of the two predatory bugs *Macrolophus pygmaeus* (Rambur) (Hemiptera, Miridae) and *Orius niger* (Wolff) (Heteroptera, Anthocoridae) also presented a reduced mobility on leaves of tomato varieties with high density of GTS type VI (Economou *et al.* 2006). Movement and predation rates of the predatory larvae of *Episyrphus balteatus* (De Geer) (Diptera, Syrphidae) were also lower on tomatoes with high density of trichomes on the stem compared to other plant species with lower trichome densities like bean and potato (Verheggen *et al.* 2009).

Unlike most predators, some Miridae predators have shown good adaptation to plants with high trichome densities. Walking behaviour and *T. absoluta* predation rates of *Campyloneuropis infumatus* (Carvalho), *Engytatus varians* (Distant), and *Macrolophus basicornis* (Stal) was evaluated on two tomato lines with different densities of glandular trichomes - TOM 587 and TOM 687, the latter with exhibiting 179% greater glandular trichome density than the former (Bueno *et al.* 2019); and it was also observed that the three mirid species easily climbed the sticky stems of both tomato lines and eggs of *T. absoluta* were found on leaflets located on plant apex. Predation rates, grooming, probing, and feeding activities as well as the time spent until prey encounter were not influenced by trichomes density for none of the three mirids. The mirid is *Dicyphus errans* (Wolff) is known for being a trichome-well adapted species. Studies showed that this slim-body, long-slender leg and curved-claws omnivorous predator is not hindered in its movements on plants with high densities of trichomes, including the tomato cv. Grit. Voigt *et al.* (2007) demonstrated a positive relationship between the diameter and length of plant trichomes and attachment forces of this predator walking on the plant surface. Subsequently, Voigt (2019) showed that fecundity, hatching rate, juvenile development and consumption rate are positively correlated with the safety factor (attachment force/body weight).

Regarding the mechanical effects of trichomes on predatory mites, studies have primarily concentrated on Phytoseiidae. Tomato trichomes can hamper phytoseiids dispersal and thus prey consumption (Cédola and Sanchez 2003; Paspatis *et al.* 2021). Conversely, plant trichomes may also provide benefits for these predatory mites: the hair-like structures may serve as a refuge from hyper-predators or abiotic constraints aiding in food detection (pollen and prey)

(Seelmann *et al.* 2007). Entrapment of predatory mites on GTs (physical effect), was observed on several cultivated varieties and wild species of tomato. In 1987, Van Haren *et al.* showed that approximately 60% of *Phytoseiulus persimilis* Athias-Henriot (Acari, Phytoseiidae) were trapped on stem trichomes after a 2-hours observation period. On varieties without trichomes on stems, all predatory mites reached the next leaf in a short period in 2 to 15 minutes. Type VI trichomes on stems are the most important barrier for predatory mite dispersion (Luckwill 1943). Buitenhuis *et al.* (2014) observed that *Amblyseius swirskii* Athias-Henriot walked at a lower speed on tomato plants (*S. lycopersicum* var. Big Dena) with high density of trichomes compared to the other host plants tested (*Gerbera jamesonii* Bolus ex. Hooker var. Festival, *Chrysanthemum x grandiflorum* Ramat var. Chesapeake, *Rosa kordesii* Wulff var. William Baffin).

Lower predation and oviposition rates were also noted. Cédola *et al.* (2001) found that tomato trichomes limited the efficiency of the predatory mite *Neoseiulus californicus* (McGregor) to control *T. urticae* compared to other host plants and other phytoseiids such as *P. persimilis* on bean leaves (Everson 1979) or *Neoseiulus cucumeris* (Oudemans) to control *F. occidentalis* on cucumber and sweet pepper leaves (Shipp and Whitfield 1991). In their study on the efficacy of *Phytoseiulus macropilis* (Banks) and *Phytoseiulus longipes* Evans in controlling *T. urticae* on tomato plants, Sato *et al.* (2011) found that the density of trichomes on the plant surface negatively affected the performance of both predators. However, the webbing produced by *T. urticae* provided a way for the predators to circumvent the detrimental effect of trichomes. Webbing could thus have physical effects by reducing contact between the predator and trichomes and providing a suitable oviposition site (Roda *et al.* 2001). However, when plants are covered with webbing, spider mite infestation is typically so high that predatory mites may not be effective enough to control the pest.

In addition to the phenotypic traits of tomato lines, such as type and density of glandular trichomes, biotic factors (temperature and relative humidity) can influence the phenology of trichomes and, consequently, their impact on predatory mites. High mortality rates of *P. persimilis* on tomato plants are observed in the spring and summer due to the entrapment by trichome exudate. Glasshouse experiments revealed that the rate of immobilization was positively correlated with rising temperatures (Nihoul 1994). This factor should therefore be considered when managing pest control in greenhouses.

Toxic effects on predators

Trichomes also negatively impact on fecundity and growth of several predators. Barbour *et al.* (1993) worked on the impact of trichomes on two predators of *H. zea*, *Coleomegilla maculata* (De Geer) (Coleoptera, Coccinellidae) and *Geocoris punctipes* (Say) (Hemiptera, Lygaeidae), and observed greater mortality of both predators in presence of GTs type VI on leaves due to methyl ketones. On tomato plants with a high density of trichomes, *D. catalinae* had a lower fecundity compared to those with a smaller number of trichomes (Heinz and Zalom 1996). Likewise, Bottega *et al.* (2017) observed that the survival, adult longevity, number of consumed prey and foraging behaviour of the stink bug *Podisus nigrispinus* (Dallas) (Heteroptera, Pentatomidae) were negatively affected by GTs types I and IV on leaves of tomato genotypes resistant to *T. absoluta*, limiting the potential success of biological control.

Trichomes also negatively impact on the survival and the life history traits of predatory mites, particularly due to the toxicity of the compounds secreted by GTs. In 2003, Cédola and Sánchez observed that tomato cultivars with a high density of trichomes negatively affected the survival of *N. californicus*. Paspati *et al.* (2021) observed that *A. swirskii* individuals preferred to remain on sweet pepper rather than on tomato. The same authors noted that acyl sugars accumulate on the mite's cuticle, joints and mouth parts hypothesizing that these sugars likely penetrate through the cuticle. The accumulation of toxic exudates in mites that come in contact with GTs merits further investigation, as it may help explain the unsuitability of many predators on tomato plants (see details below in 'Importance of tri-trophic interactions on biological control agents').

Several studies demonstrated lower efficiency of predators on tomatoes with a high density of trichomes; however, the reasons for this reduced efficiency are not addressed in the publications. Barbour *et al.* (1993) showed that *C. maculata* exhibited reduced consumption of *H. zea* eggs in laboratory bioassays on the wild tomato *Solanum hirsutum f. glabratum* (accessions PI 134417) secreting methyl ketones in the apical area of GTs. Lower attack rates of *T. absoluta* by *P. nigrispinus* on tomato plants have also been observed compared to eggplant and, sweet pepper (De Clercq *et al.* 2000). According to the authors, these results may be attributed to the presence of GTs on tomato although this has not been tested. Simmons and Gurr (2004) observed a lower number of aphids predated by *M. signata* on tomato plants with high density of trichomes.

Importance of tri-trophic interactions for biological control agents

Predation efficiency can be influenced by the impact of herbivorous arthropods on the plant physiology. For instance, Van Houten *et al.* (2013) observed that in presence of *A. lycopersici*, GTs undergo discoloration after which they dry out and fall off. This damage allows *Amblydromalus limonicus* (Garman and McGregor) to successfully establish in the area where the trichomes had fallen off. However, the biological control was not effective, as pest populations remained very high and russet mites had dispersed, colonizing the entire plant.

Another important aspect is the indirect prey-mediated effects of tomato on predators and parasitoids. Savi *et al.* (2021) hypothesized that the lower predation rates and biological performance of *P. longipes* feeding on *T. evansi* in tomato cultivars with high GT densities could be due to the consumption by the predator of a prey that has accumulated a high concentration of toxic compounds such as methyl ketones. In 2007, Koller *et al.* observed that *N. californicus* had a longer developmental time and lower oviposition rate when feeding on *T. evansi* strains reared on tomato compared to a bean-reared strain. These results align with findings from other studies. Moraes and McMurtry (1987) observed that *P. persimilis* gained more weight when fed with *T. urticae* reared on bean compared to *T. urticae* reared on *Solanum douglasii* (nightshade). They hypothesized that an unknown factor, possibly in the hemolymph or tissues of the prey, might explain these results. Escudero and Ferragut (2005) observed a lower efficiency of *P. persimilis* and *N. californicus* when feeding on *T. evansi* reared on potato. They hypothesized that this may partially be due to toxic compounds consumed by *T. evansi*. Ferrero *et al.* (2014b) showed that two populations of *P. longipes* collected from solanaceous plants infested with *T. evansi* were able to develop when feeding on *T. evansi* on tomato, whereas this was not possible for a *P. longipes* strain found on non-solanaceous plants feeding on *T. urticae*. One hypothesis was that both direct and indirect effects of tomato might influence the feeding behaviour of *P. longipes* on tomato. Further studies are needed to investigate bioaccumulation of toxic compounds across different food chain levels to better understand their impact on the biology of natural enemies and, consequently, on biological control.

What would happen to herbivorous and predators if trichomes were removed from tomato plants? The effect of tomato mutant lines presenting distorted trichomes on aerial tissues (which disrupt the accumulation of sesquiterpene and polyphenolic compounds; see Kang *et al.* 2010b) on the performance of predatory mites – *P. persimilis* and *A. limonicus* – in controlling mite pests (*T. urticae* and *A. lycopersici*) has been evaluated. Legarrea *et al.* (2022) showed that predatory mites perform better and can reduce phytophagous mite densities more quickly on ‘hairless’ tomato mutants than on cultivated tomatoes (cv. Ailsa Craig).

Perspectives on using predatory mites for the biocontrol of tomato pests

While the biological control of tomato pests presents a promising strategy, it remains challenging, particularly due to the detrimental effects of trichomes on natural enemies. For predatory mites, all the most commonly used species for the control of phytophagous mites and thrips – the phytoseiid mites *P. persimilis*, *P. macropilis*, *N. californicus* and *A. swirskii* – have showed to be negatively affected by tomato trichomes (Van Haren *et al.* 1987; Cédola and Sánchez

2003; Sato *et al.* 2011; Paspati *et al.* 2021). This has prompted efforts to identify alternative predatory mite species that might be better adapted to tomato. One of the strategies could be prospection for adapted species or wild populations on tomato, other solanaceous, or even other phenotypically similar host plants.

In the review by Tixier *et al.* (2020 a) on Phytoseiidae biodiversity on Solanaceae worldwide, 215 species of Phytoseiidae were reported on 99 species of Solanaceae, and authors indicate that the adaptation of Phytoseiidae to Solanaceae seems to be a recent occurrence, except in the Neotropical region. This may explain why many European phytoseiid species are not adapted to tomato. The Neotropical region has the highest number of reports and species of phytoseiid mites, likely because it is also the area of the origin of Solanaceae (Olmstead 2013). The currently cultivated tomato crops have originated in the central area of South America (Blanca *et al.* 2012, 2015; Razifard *et al.* 2020), making this region particularly promising for the study of biological control agents. Many surveys have been carried out in Brazil, especially to search for natural enemies of *T. evansi* on tomatoes (Rosa *et al.* 2005; Furtado *et al.* 2006, 2014; Fiaboe *et al.* 2007; Silva *et al.* 2008). Among the species found, *P. longipes* performed well when fed on *T. evansi* and *T. urticae* on tomato plants. Biological parameters of this predator were widely studied (see Furtado *et al.* 2007; Ferrero *et al.* 2007, 2014a; Savi *et al.* 2021) and promising results were obtained on its capacity to control *T. evansi* on different tomato genotypes (Savi *et al.* 2021), and some field studies confirmed its efficacy (Ferrero *et al.* 2014b). The ecological risk of releasing this predator on a large scale outside its natural range, particularly in areas where *T. evansi* is a pest in Africa, should be carefully assessed.

Surveys of predatory mites in South America have also focused on identification of predators of the tomato russet mite *A. lycopersici* and on the Tarsonemidae mite *Polyphagotarsonemus latus* (Banks) (Silva *et al.* 2016; Duarte *et al.* 2021). Based in the distribution, abundance, number of host plants, and the association with the target pest, the Phytoseiidae species considered as potential biological control agents were, *Typhlodromalus aripo* De Leon, *Euseius sibelius* (De Leon), *Phytoseius guianensis* De Leon, *Euseius citrifolius* Denmark and Muma, and *Neoseiulus idaeus* Denmark and Muma. It is worth note that species of the genera *Phytoseius* and *Typhlodromalus*, are classified as subtype IIIA, according to McMurtry *et al.* (2013); i.e. generalist predators that live on pubescent leaves. These phytoseiid mites possess morphological features, such as a small and laterally compressed idiosoma, which facilitate movements between leaf trichomes. This adaptation allows the mites to colonize microhabitats that larger species do not occupy, thereby avoiding potential competition while benefiting from the presence of prey that also prefers the same microhabitats, e.g. *A. lycopersici* (McMurtry *et al.* 2013). The efficacy of some of these predatory mites on tomato and other Solanaceae host plants remains to be fully evaluated.

In addition to the predatory mites identified as potential biological control agents from prospection surveys in the area of origin of tomato, species associated with trichome-rich plants in Europe have also been considered. From surveys conducted in Southern France, the Phytoseiidae *Typhlodromus (Anthoseius) recki* Wainstein shows promising characteristics (Tixier *et al.* 2020 b; Tabary *et al.* 2024). Evaluation of the effect of tomato trichome types on the development, survival and dispersal of *T. (A.) recki* on six tomato cultivars and two wild *Solanum* genotypes showed that this predator was not affected by plant characteristics when testing a favourable predator/prey (*T. urticae*) ratio (1:1) (Tabary *et al.* 2024). *Typhlodromus (A.) recki* is also the most reported species on Solanaceae in Europe. This generalist predator efficiently feeds on *A. lycopersici*, *T. urticae* and *T. evansi*, demonstrating promising dispersal abilities on plants with trichomes including *in vitro* tomato stems (Tixier *et al.* 2020b).

Another predatory mite family, besides the Phytoseiidae, the Iolinidae family, has been considered for biological control in tomato. Although previously understudied, species in this family are now considered promising, particularly for the control of *A. lycopersici*. Two species, *Pronematus ubiquitus* (McGregor) and *Homeopronematus anconai* (Baker), have been reported to feed and reproduce on *A. lycopersici* (Kawai and Hacque 2004; Pijnakker *et al.* 2022). In laboratory conditions, *P. ubiquitus* with an adult size of 200-300 µm, showed to be

small enough to walk across trichomes and prey on *A. lycopersici*. This mite shows a predation efficacy up to 78% in field conditions (Vervaeke *et al.* 2021). Pijnakker *et al.* (2022) showed that when *P. ubiquitous* was released on tomato plants 14 weeks before the introduction of *A. lycopersici* (the period during which mites were giving supplementary feeding with pollen), the predator successfully prevented pest damages on plants. These authors also showed that *P. ubiquitous* was able to reduce powdery mildew [*Pseudoidium neolycopersici* (L. Kiss) L. Kiss] and stated that these Iolinidae mites can offer dual protection for tomato plants by controlling both a pest and a pathogen. Regarding spider mites, the suppression of *T. urticae* associated with *P. ubiquitous* releases was suggested by Van de Velde (2021) but this would need to be clarified further. Likewise, greenhouse trials demonstrated that *P. ubiquitous* and *H. anconai* are able to reduce damages of *A. lycopersici*, especially preventing outbreaks in short-term trials (Pijnakker *et al.* 2020, 2022). It is worth noting that this mite is already mass-produced and commercialized in Europe.

General considerations

Methodologies, achievements and next steps

As discussed in this review, numerous studies have been conducted to understand how trichomes may impact arthropod survival in tomato. With respect to the specific role of each type of trichome, the knowledge of the effect of NGT on arthropods in comparison to GT is rather limited and indicate that very high densities of NGT restricts the dispersal of arthropods. It should be noted that many of the studies focus primarily on herbivorous arthropods, with significantly less emphasis on natural enemies.

When studying the impact of trichomes on natural enemies, lower efficiency is associated with high densities of GTs; however, the underlying mechanisms (chemical, physical) are not well understood. In general, studies focusing on the impact of trichomes on parasitoids are limited. The few studies available describe various deleterious effects. Predatory arthropods, including insects and phytoseiid mites have both a lower survival and development rates in presence of high densities of GTs. Few studies are available on direct and indirect (bioaccumulation) toxicity of the molecules secreted by trichomes. Detailed information on the relationships between predators and phenotypic traits of plants could assist breeders in incorporating traits are favourable to natural enemies into the selection processes for tomato lines.

Most studies have been conducted in the laboratory settings, often performed on detached leaves or leaf disks. However, trichome densities can vary significantly among different plant organs, even of the same plant cultivar. Therefore, a preliminary step would involve conducting further studies on the entire plant, followed by field studies.

The studies included in this review vary in their methodologies, making it challenging to compare trichome densities across publications. Additionally, there is significant variability across plant species, cultivars, organs, and plant age.

Perspectives of tomato pest control

Tomato trichomes have physical and chemical deleterious effects on arthropods, both on pests and on biological control agents. GTs tend to have more detrimental effects on arthropods than NGTs. This explains why most studies have concentrated on them. Small GTs of Solanaceae, as types IV and VI, are more likely to act both as physical and chemical defenses. Toxic effects of trichomes affecting several life history parameters, such as survival, fecundity, and duration of life-stages by different resistance mechanisms (antixenosis, antibiosis and tolerance) have been found for several pests and natural enemies. A more detailed understanding of these interactions is still necessary to support the development of effective pest management strategies. The quest for more sustainable approaches to control pests that circumvent tomato trichome defense mechanisms remains a challenge for researchers. Efforts have focused particularly on

enhancing plant genetic resistance and identifying of biological control agents that perform well on tomato.

Secretion of acyl-sugars, methyl ketones and sesquiterpenes have been considered as promising traits to be selected for pest resistance in tomato breeding programs, while focusing mostly on crosses between tomato and closely related wild species – *S. pimpinellifolium*, *S. pennellii*, *S. galapagense*, *S. habrochaites*. Toxic compounds can exert antixenotic and antibiotic effects in both phytophagous insects and mite populations; therefore, tomato breeding programs can produce genotypes with resistance to a wide range of arthropod pests. For breeders, such aspects may offer a significant advantage. However, a better understanding of genetic basis of such resistance is still necessary to ensure its sustainability, whether it is monogenic or polygenic. Furthermore, distribution and density of trichomes vary among plant organs that can also be affected by biotic and abiotic parameters, which adds complexity to the development of genetic resistance.

There is widespread consensus on the critical need for biological control solutions for tomato pests; however, most species in the diverse group of natural enemies, both parasitoids (i.e. Trichogrammatidae, Tachinidae, Ichneumonidae,) and predators (Coccinellidae, Antho-coridae, Chrysopidae, Syrphidae, Pentatomidae, Phytoseiidae), are not well adapted to tomato trichomes. Concerning predatory mites, efforts have mainly focused on the prospection for tomato/Solanaceae adapted species in South America, the region of origin for tomato, as well as on trichome rich plants in Europe. Field surveys have identified promising candidates, and the efficiency of some of these candidates has begun to be evaluated. Besides, reduced-size iolinid predatory mites can keep *A. lycopersici* populations below damage threshold and are already available commercially in Europe. Therefore, while further research is necessary, it can be stated that the prospects for using predatory mites as biological control agents on tomatoes are encouraging. It is important to emphasize that, similar to any other cropping system, biological control must be integrated with other pest management strategies.

How to integrate plant resistance and biological control to manage tomato pests

Different pest management strategies must be combined to achieve satisfactory efficacy. However, the known conflict exists between bottom-up (e.g. plant defenses) and top-down (e.g. biological control) strategies (Riddick and Simmons 2014; Peterson *et al.* 2016), as constitutive plant defense traits can affect top-down control negatively.

In the context of the tomato pest control, the trade-off between plant resistance and biological control should be addressed. This balance could be achieved by breeding tomato lines with a moderate arthropod resistance level that does not render them entirely unsuitable for biological control agents, thereby allowing for the survival and development of most trichome-adapted species of natural enemies. Most research to date has concentrated on either one strategy or the other; however, success in the field will depend on an integrated approach. It is evident that breeding programs should incorporate the evaluation of biological control agents, and their efficacy should be assessed on cultivars with contrasting phenotypes. In addition, tri-trophic interactions, which have implications for biological control programs, and considered in the development of pest control strategies, as they can strongly influence the efficiency of natural enemies.

It would be wise to exercise caution when considering the suggestions from breeders to explore the option of removing resistance traits from tomato lines (see Legarrea *et al.* 2022). These suggestions have been based on experimental studies that demonstrated higher performance of mutants in which plant defenses were removed or minimized, thereby allowing them to more effectively suppress mite pest populations. It is important to note that only one group of pests and natural enemies was evaluated in these studies. Before implementing breeding programs aimed at removing tomato defenses, it is crucial to assess the effect on all major groups of pests and natural enemies, as well as on plant physiology and performance.

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