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Plant defences for enhanced integrated pest management in tomato

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Abstract

Plants developed a series of defence mechanisms to counteract the attack of herbivores. These can impact on food-webs at various trophic levels, in both natural and managed ecosystems, such as crops. The biochemical and ecological bases behind these processes are reviewed here by highlighting the differences in direct and indirect, constitutive and induced defences. In integrated pest management (IPM), several pest control tools are applied in an economically sound way in order to increase the crop resilience and reduce reliance on synthetic pesticides. Plant resistance is thus a crucial aspect of preventive pest control strategies in several agroecosystems, including tomato. In this context, we review the current literature dealing with the physiology and biochemistry of tomato plants in terms of metabolite pathways and multitrophic interactions. We also describe recent advances in plant defence-based control tools obtained by studying the multitrophic interactions between pests and plants in the tomato system.

KEYWORDS

HIPV, induced defence, invasive species, IPM, secondary metabolites

SUMMARY 1

Plants defend themselves from herbivore attacks through a complex array of defence mechanisms that can be either constitutive or induced, direct or indirect. This review reports some recent advances on all these aspects, including an overview of the biochemical bases behind these mechanisms focusing on recent studies on induced defences in tomato plants after the attack by key pests.

PLANT DEFENCES WITHIN IPM IN 2 TOMATO CROPS

Integrated pest management (IPM) is based on the application of sustainable pest control combining different tools (Ehler, 2006; Gugliuzzo et al., 2021; Santoiemma, Tonina, Marini, Duso, & Mori, 2020). It is a control strategy in which biological, chemical, genetic, physical and agronomic control methods are combined to pursue stable long-term pest control (Desneux et al., 2022; Larkin, 1989; Tait et al., 2021). The implementation of an IPM involves three key elements: (a) multiple tools used in a compatible way, for example, combining pheromonebased methods and the use of natural enemies, (b) prevention of high pest densities, and (c) conservation of biodiversity to increase ecosystem services.

In the context of IPM, plant resistance to insect pests plays a key role when designing and implementing sustainable plant protection protocols (Kennedy, 2008). Enhancing plant defences can contribute to IPM combined with rational fertilisation, biological control and cultivation methods (Blazhevski, Kalaitzaki, & Tsagkarakis, 2018; Gharekhani & Salek-Ebrahimi, 2014). Influencing and enhancing the plant defensive profile, in which the plant has to pay a cost (i.e., a decreased above-ground growth and reduced flowering as consequences of the herbivore attack), can impact insect pests and their natural enemies in commercial tomato crops (de Oliveira, Pallini, &

Janssen, 2019; Li, Garvey, Kaplan, Li, & Carrillo, 2018). Tomato has been considered a model plant to characterise the defence mechanisms for many other crops. Thus, IPM seems to be a key approach to reach sustainable production in tomato, thereby preserving environmental and human health.

Here, we review the current knowledge on plant defences and their potential impact on tomato pest control packages focusing on the trophic interactions involving tomato and its invasive pests which are causing extensive damage to several tomato production areas worldwide (Biondi, Guedes, Wan, & Desneux, 2018; Han et al., 2019; Mansour et al., 2018; Rostami, Madadi, Abbasipour, Allahyari, & Cuthbertson, 2020).

3 | THE COEVOLUTION OF PLANT-ARTHROPOD INTERACTIONS

Plant responses to insect herbivory, developed during plant evolution, involve various defence and/or tolerance mechanisms (Ehrlich & Raven, 1964). Plants react to herbivores by activating a cascade of resistance mechanisms to defend themselves. These include the modification of the phytohormone profile, thus triggering direct and/or indirect defences (Kant & Baldwin, 2007; Thaler, Farag, Paré, & Dicke, 2002).

Plant defences tend to reduce the fitness of herbivores by reducing their survival and reproduction. Thus, plants and insects may coevolve, where coevolution is defined as the process of genetic adaptations in a reciprocal way (Dicke & van Loon, 2014; Mithöfer & Boland, 2012; Ton, Flors, & Mauch-Mani, 2009). When an herbivore successfully evolves to overcome the plant defence mechanisms, it might become a potential threat and it imposes a selective pressure on plants that results in the evolution of herbivore-specific induced defence mechanisms (Bergelson, Kreitman, Stahl, & Tian, 2001; Dodds & Rathjen, 2010). Similarly, when a plant adapts to counteract the attack of an herbivore, it has the potential to be a resistant host (Jongsma & Bolter, 1997).

The suitability of the plants for the herbivores that feed on them, the insect herbivore species in interaction with the plant and the gene modifications in plant and insect defence traits are three important aspects in the insect-plant coevolution (Liu et al., 2007; Rasmann & Agrawal, 2009). In most cases, coevolution involves a compromise in which both the host and the herbivore survive and develop suboptimally because of considerable metabolic costs (Gatehouse, 2002). Organisms continuously evolve to compete, such as in a game of evolutionary *ping pong* (Arora, Goyal, & Ramawat, 2012). In particular, evolution depends on the frequency with which the attack occurs and, above all, on the behavioural and genetic responses of the insect (Berenbaum & Zangerl, 1998; Kant, Sabelis, Haring, & Schuurink, 2008).

4 | HOW PLANTS DEFEND THEMSELVES

Identifying and classifying the ecophysiological responses of plants is a key to improve their natural defences (Ehrlich & Raven, 1964). Plant defences can be classified as constitutive and induced, although often the metabolites implicated are the same or similar (Duffey & Felton, 1991; Wittstock & Gershenzon, 2002). Constitutive defences include products, structures and compounds of the primary and secondary metabolism that are involved in plant defences regardless of the threat of an herbivore (Bar & Shtein, 2019; Hanley, Lamont, Fairbanks, & Rafferty, 2007). By contrast, induced defences are activated following an herbivore attack, or other biotic and abiotic stresses, and include products, structures and compounds of the secondary metabolism of the plants subsequently primed (Arimura, Kost, & Boland, 2005; Kersch-Becker & Thaler, 2019). The response of plants to stresses is a combination of many reactions and mechanisms that indirectly and directly influence their interactions with the ecosystem, even at the multitrophic level and often with long-term consequences (Mithöfer & Boland, 2012; Stam et al., 2014).

Both constitutive and induced defences can be direct and indirect. The direct ones influence the performance and development of the herbivore, for example, the accumulation of toxins or the thickening of cell walls (Chen, 2008; Lin, Peiffer, & Felton, 2020; Yang et al., 2020). Indirect defences manipulate (a) the behaviour of predators or parasitoids of the herbivore by attracting them to the infested plant; and/or (b) of neighbouring plants by warning them through alarm signals (Coppola et al., 2017). This kind of signalling is mediated by herbivore-induced plant volatiles (HIPVs) that attract the natural enemies toward the infested plant and/or prime preinfestation defence mechanisms in nearby healthy plants (Figure 1) (Kessler & Baldwin, 2002; Pérez-Hedo et al., 2017). In crop protection, combining all these aspects is crucial for sustainability. However, until guite recently, most mechanistic studies have investigated the relationship between a single pest and a single type of defence-related factor or response. In fact, they have ignored the presence of other defence factors such as those related to complex food webs including concomitant multiple pest attacks (Stam et al., 2014; Stout, Fidantsef, Duffey, & Bostock, 1999).

4.1 | Constitutive defences

Constitutive defences exist in plants independently of any herbivore attacks (Goyal, Lambert, Cluzet, Mérillon, & Ramawat, 2012). They include structural, mechanical and chemical mechanisms (Bonaventure, VanDoorn, & Baldwin, 2011; Dussourd & Denno, 1991). These can be independent from each other or can act synergistically, such as glandular trichomes and their secretory canals, which combine a structural defence and a secretory capacity as mechanical and chemical defence mechanisms (Glas et al., 2012; Wang, Park, & Gutensohn, 2021).

4.1.1 | Structural and mechanical defences

Morphological barriers of the plant, for example, thorns, can prevent feeding by large herbivores while the thickening of the walls, for example, can impair feeding by small herbivores (Jacob et al., 2020;



FIGURE 1 Resistance mechanisms of tomato plants induced by its main herbivores involving volatile compounds (herbivore-induced plant volatiles [HIPVs]) and the response of natural enemies as well as the chemical pathway to encoding active compounds against insects (enzymes, hormones, etc.)

Mitchell, Brennan, Graham, & Karley, 2016; Wheeler Jr & Krimmel, 2015). Bitew (2018) found that wild tomato species with high density of glandular and nonglandular trichomes, such as *Solanum habrochaites* and *Solanum pennellii*, have an important potential for resisting *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). These species and/or these traits could thus be included in future tomato breeding programmes, for example, by identifying the genetic basis involved in the production and density of mechanical barriers. However, this might result in further challenges because trichomes in tomato plants can strongly compromise the establishment of predatory arthropods (including mites and flower bugs) and, thus, the ecological services they provide (Paspati et al., 2021; Salehi, Yarahmadi, Rasekh, & Sohani, 2016).

4.1.2 | Chemical defences

Constitutive chemical defences (e.g. tannins, resins) can be toxic, repellent or antifeedant and can impact on the development of the herbivores by altering the resistance, the fecundity and the digestive capacities. The toxicity or repellency of these chemical compounds also depends on how the plant stores them. For example, large amounts of toxicants are released by the plant only once the herbivore breaks down specific plant structures by feeding or just moving on the plant, such as resin ducts or glandular trichomes (Dearing, Foley, & McLean, 2005; Giordano, Maleci, Agati, & Petruccelli, 2020; Yousaf et al., 2018; Zhou, Lou, Tzin, & Jander, 2015). Fractions of tomato trichome extracts can affect predatory mite survival in a concentration-response manner (Paspati et al., 2021).

Kennedy (2003) reported that the presence of phenolic compounds, for example, chlorogenic acid and rutin, in tomato leaves, may inhibit the growth of larvae of two noctuid pests, *Spodoptera exigua* (Hübner) and *Helicoverpa zea* (Boddie). Phenolic compounds are typically synthesized in the green parts of the plants and are considered as constitutive defence chemicals (Harborne, 1979). When incorporated into an artificial diet, they inhibit larval development in a dosedependent manner (Isman & Duffey, 1982; Kennedy, 2003).

4.2 | Induced defences

External factors that interfere with the plant, such as herbivores, can trigger plant defences (i.e., signalling cascades) which make the plant synthesise specific compounds, such as secondary metabolites, and trigger changes in plant physiology. This hampers the fitness, the survival, the development and the fecundity of the feeder (Kant, Ament, Sabelis, Haring, & Schuurink, 2004). The success of plant defences is mediated by a prompt and specific identification of the herbivore. Santamaria, Arnaiz, Gonzalez-Melendi, Martinez, and Diaz (2018) reported how the different feeding mechanisms of herbivores enable the plant to recognise them, through specific plant receptors (pattern recognition receptors), damage-associated molecular patterns and herbivore-associated molecular patterns and respond accordingly by triggering short-term and long-term defence mechanisms.

Herbivore attack may affect metabolomic content in plant tissues. As described by Pappas et al. (2015) and Pérez-Hedo, Arias-Sanguino, and Urbaneja (2018) in tomato plants as response to the attack of Macrolophus pygmaeus (Rambur) and Nesidiocoris tenuis (Reuter) (Hemiptera: Miridae), induced defences are primed both locally and systemically. This involves different signalling pathways related to systemin, jasmonic acid (JA or jasmonate) and salicylic acid (SA).

In this context, it was demonstrated that trichome development is correlated with the abundance of JA (Boughton, Hoover, & Felton, 2005; Tian, Tooker, Peiffer, Chung, & Felton, 2012). Paudel et al. (2019) showed that the development of both glandular and nonglandular trichomes in tomato is induced as a result of herbivore damage.

Pérez-Hedo, Urbaneja-Bernat, Jaques, Flors, and Urbaneja (2015) investigated the implications of different phytohormones involved in tomato plant defences in response to N. tenuis punctures. They evaluated the production of induced defence mechanisms, such as the production of HIPVs playing a key role in tritrophic interactions (Turlings & Erb. 2018). These mechanisms are crucial to understanding the evolution of plant-natural enemy relationships (Sabelis, Janssen, & Kant, 2001; Stahl, Hilfiker, & Reymond, 2018). Through plant induction. HIPVs can make the plant repellent to herbivores (Engelberth. Alborn, Schmelz, & Tumlinson, 2004; Frost, Mescher, Carlson, & De Moraes, 2008) and/or more attractive to natural enemies of pests (Ayelo et al., 2021; Naselli et al., 2016; Pérez-Hedo, Bouagga, Jaques, Flors, & Urbaneja, 2015). In this context, Conboy et al. (2020) analysed tomato HIPVs and selected methyl salicylate (MeSA), a plant elicitor that recognises and triggers intracellular defence signalling in the plant. They evaluated the application of this elicitor in un-infested tomato plants and noted that the Trialeurodes vaporariorum (Westwood) (Hemiptera: Alevrodidae) population was reduced and that there was an 11% increase in the tomato yield.

In some cases, insects can modulate HIPV production by the attacked plant (Sarmento et al., 2011). Zhang et al. (2019) demonstrated how *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) can manipulate the defence mechanisms of the host plant community by stimulating the attacked plant to emit HIPVs that can prime SA-dependent defences and suppress JA-dependent defences in neighbouring plants. This would make the neighbouring healthy plant more suitable for the imminent attack by *B. tabaci*.

Moreover, herbivore attack may affect the polyphenol oxidase (PPO) and protease inhibitors (PIs) in plant tissues, resulting in hampered larval growth (D'Esposito et al., 2021). The larval growth of insects that feed on damaged leaves decreases and this demonstrates that tomato plants show a greater degree of resistance after herbivore attack (Escobar-Bravo, Klinkhamer, & Leiss, 2017; Hamza et al., 2018).

4.2.1 | Signal transduction and metabolite pathways in tomato

Plant hormones play a central role for plant signalling networks as response to biotic and abiotic stresses (Robert-Seilaniantz, Navarro, Bari, & Jones, 2007). When an herbivore begins to feed on plant tissues, the damage generates a plant defence response in a generally nonspecific way (Frost et al., 2008), and primary and secondary metabolites belonging to disparate chemical classes are produced by

plants (Duffey & Stout, 1996; Wink, 2008). Nevertheless, the signals produced by herbivores can be specific and enable the plant to respond in a much more precise way.

The hormone JA has a key role in tomato plant resistance to herbivores, mainly chewing ones. This hormone induces the transcription of genes involved in defence metabolism (Turner, Ellis, & Devoto, 2002). It is produced in the signalling octadecanoid pathway and it is synthesised in the chloroplast and peroxisome from linolenic acid, which is released from plant membrane lipids (Chen, Jones, & Howe, 2006). Other hormones, such as SA and ethylene, participate in the signalling pathways involved in the defence mechanisms (Lorenzo, Piqueras, Sánchez-Serrano, & Solano, 2003; Zarate, Kempema, & Walling, 2007).

In tomato plants, the preliminary step in the signalling and defensive response pathway is the segmentation of the precursor prosystemin, a leaf constitutive polypeptide (Figure 1). Specific enzymes contained in the saliva of herbivores can activate the catalysis of the peptides in the cell membrane leading to the transformation of prosystemin into the peptide systemin, a plant hormone (Li & Howe, 2001; Ryan, 2000). Thanks to systemin, which is translocated in the plant phloem, defensive signalling can become systemic throughout the plant. The defensive signal transduction activates phospholipase A2, which in turn releases linolenic acid from membrane lipids. Linolenic acid acts as a precursor for the synthesis of the octadecanoid pathway of JA.

In the next step, the pectinic component of the cell walls of plants is split into oligomeric polymers (oligogalacturonic acid – OGA) which are defensive proteins of tomato plants. The signal which activates expression of the wound-induced polygalacturonase gene appears to be JA (Orozco-Cardenas & Ryan, 1999), suggesting that this has an earlier effect in the signalling pathway than in OGA. At the end of the signalling pathway of defensive proteins, such as proteinase inhibitors and PPO, hydrogen peroxide is produced and diffused in mesophyll cells through the oxidative burst, near the vascular bundles (Orozco-Cárdenas, Narváez-Vásquez, & Ryan, 2001). Once absorbed by insects, hydrogen peroxide negatively affects the permeability of the intestinal wall causing oxidative damage to the insect epithelial cells (Singh & Singh, 2021).

5 | ALTERATIONS IN THE PLANT DEFENSIVE PROFILE AND THEIR MULTITROPHIC OUTCOMES

External biotic and abiotic factors, such as for example irrigation and fertilisation inputs, or the preliminary priming by other insects, or by HIPVs from infested plants, could enhance plant resistance mechanisms, thereby offering a significant boost in sustainable tomato IPM.

5.1 | Bottom-up approaches

The bottom-up approaches consist in exploiting the effects of variable availability in the soil of water, minerals (e.g. potassium and nitrogen) ³³² WILEY_ Annals of Applied Biology aab

and/or (bio)fertilisers for optimising the defence mechanisms of the plants (Larbat et al., 2016). Because of bottom-up effects, modified defence volatiles and altered plant metabolism can affect tritrophic interactions (Coqueret et al., 2017; Denno et al., 2002; Han, Lavoir, Le Bot, Amiens-Desneux, & Desneux, 2014; Shehzad, Gulzar, Staley, & Tarig, 2020). Salinity stress increases the osmotic potential, thus decreasing plant water availability, leaf dietary quality (Manaa et al., 2011; Romero-Aranda, Soria, & Cuartero, 2001; Teklić et al., 2020) and also water availability to the larvae of herbivores. The secondary metabolism of the plant can also be modified by salinity stress, and plants can alter their defence compounds thus affecting the trophic interactions (Ballhorn & Elias, 2014). In order to resist the salinity stress of plants, insects are able to modify their feeding intensity and to shorten the juvenile development time (Han et al., 2019).

The quantity and quality of the plant watering can enhance the plant defence mechanisms thus affecting the plant resistance to herbivores (Dong et al., 2018; Dong et al., 2020; Gutbrodt, Mody, & Dorn. 2011). Lin. Paudel. Afzal. Shedd. and Felton (2021) studied how lower water availability increased the levels of two tomato plant defensive proteins, trypsin PI and PPO. It was shown how these resistance factors directly influence the consumption of plant tissues and the performance of Manduca sexta (Linnaeus) (Lepidoptera: Sphingidae) a specialist caterpillar (Lin et al., 2021). Furthermore, in conditions of water deficit, the increase in the concentration of glycoalkaloids in the tomato leaves negatively affects survival, pupal weight and larval development time of T. absoluta (Han et al., 2016).

Volatile organic compounds (VOCs) are affected by water limitation in tomato plants, and this influenced the plants' level of attraction for T. absoluta and B. tabaci adults preferring moderately stressed and nonstressed plants, respectively (Pagadala Damodaram et al., 2021). VOCs can also be altered by temperature as demonstrated by the invasive weed Alternanthera philoxeroides, although this did not influence its attraction for two herbivores (Liu et al., 2021).

The quantity and the quality of nitrogen strongly limit herbivore development (Han et al., 2020; Kagata & Ohgushi, 2012), thus making the concentration of nitrogen important for the survival of insects. The amount of nitrogen and metabolites in plant tissue is affected by nitrogen fertilisation. Many primary metabolites, such as carbohydrates, as well as other secondary plant metabolites, such as phenolic acids, flavonoids and glycoalkaloids, are influenced by nitrogen fertilisation and can impact insect development (Coqueret et al., 2017; Fritz, Palacios-Rojas, Feil, & Stitt, 2006; Hermans, Hammond, White, & Verbruggen, 2006; Larbat et al., 2016). Tomato plants with low nitrogen input produce higher concentrations of defensive secondary metabolites, such as soluble phenolics (i.e. kaempferol-rutinoside, chlorogenic acid and rutin), because their concentration is connected positively with the carbon/nitrogen ratio in tomato tissues (Royer, Larbat, Le Bot, Adamowicz, & Robin, 2013).

All these compounds are repellent and/or toxic to various insect pest taxa (Mirnezhad et al., 2010). For example, Ramachandran et al. (2020) studied the effects of nitrogen availability on the tolerance to whiteflies in four tomato varieties showing that plants grown at half the optimal quantity of nitrogen had a higher degree of resistance to whiteflies, without a decreasing yield.

Tomato plants, in conditions of nitrogen deficit limits, negatively affect the survival, pupal weight and development time of T. absoluta (Coqueret et al., 2017). This seems to be because of the low protein content and the increased number of phenolic compounds and glycoalkaloids in the leaves (Larbat et al., 2016). Overall, in tomato the production of various chemical defence molecules, mainly based on carbon and less on nitrogen, reduces the nutritional value of the leaves for herbivores (Larbat, Le Bot, Bourgaud, Robin, & Adamowicz, 2012; Royer et al., 2013). In addition, water and nitrogen quantities are positively related, and larvae of T. absoluta may thus suffer from a lack of nitrogen-based nutrients in drought-prone plants (Han et al., 2014).

Another macro-element that can alter the concentration of defence compounds is potassium (Trejo-Escobar, Valencia-Flórez, Mejía-España, & Hurtado, 2019) which has bottom-up effect potentials on the cycle of B. tabaci and T. absoluta in tomato plants. It was showed by Darwish. Attia. and Khozimy (2021) that treatment with potassium fertiliser as a foliar spray on tomato plants can have a significant impact on decreasing the density of *B. tabaci* nymphs. Sung et al. (2015) studied the low potassium input on the tomato plant and found that there is an accumulation of defence compounds in the plant tissue, such as soluble sugar and putrescine, known to be involved in defence responses of the plant (Liu et al., 2020), and a concomitant reduction of the majority of the amino acids.

Biological fertilisers have received considerable attention in the last years for their potential employment in sustainable crop protection. Beneficial microorganisms can enhance plant performance and plant defences under different conditions, such as herbivore attack. For example, Trichoderma longibrachiatum modulates the expression of classes of transcription factors and of genes involved in plant photosynthesis and antioxidant defences (De Palma et al., 2021). Megali, Glauser, and Rasmann (2014) showed how the mix of beneficial microorganisms, brought to the soil, affects the yield of tomato plants and enhances the defences of the plant from the attack of Spodoptera littoralis (Boisduval) (Lepidoptera: Noctuidae). This could have been attributed to the increased presence of glycoalkaloids, such as tomatine, which influence the development of the insect.

5.2 Indirect interactions

Indirect interactions consist of those plant relationships with external factors, such as insects and microorganisms, which can influence plant responses and modify interactions with other members of the system, such as for example natural enemies (Stam et al., 2014). Plant responses lead to morphological or metabolic changes which can subsequently influence indirect interactions with other members of the community (Han et al., 2020). Thus, plant defence profile can be enhanced by a preliminary attack from herbivores (Poelman & Dicke, 2018). The initial insect feeding can stimulate the defence pathways of the plant, thereby generating secondary metabolites, including HIPVs, which can interfere with the choice of the host by the pest and the natural enemies. For

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example, Pérez-Hedo, Bouagga, et al. (2015) and Pérez-Hedo, Urbaneja-Bernat, et al. (2015) showed that tomato plants fed by *N. tenuis* activate the jasmonic and abscisic acid (ABA) pathways making the plants less attractive to *T. absoluta* and *B. tabaci*, but more attractive toward *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae), one of the most effective whiteflies' parasitoids.

Moreover, it was shown how the spider mite feeding on tomato plant causes an emission of HIPVs depending on the induced JA signalling. The MeSA and 4,8,12-trimethyl-I,3(*E*),7(*E*), I 1-tridecatetraene were emitted after the attack of *Tetranychus urticae* Koch (Acarina: Tetranychidae) (Ament, Kant, Sabelis, Haring, & Schuurink, 2004; Kant et al., 2008). These volatile compounds have an important role in the indirect defences to attract natural enemies such as *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) (De Boer & Dicke, 2004). Similarly, Ayelo et al. (2021) found that, among the many HIPV induced by *T. absoluta*, several monoterpenes are useful to attract the zoophytophagous mirid *N. tenuis*, while (E)- β -caryophyllene was found to repel it.

Other researches are focused on the evaluation of different tomato types with different production of JA and the attraction of natural enemies. The production of JA has a key role in the production of defence volatile compounds to attract natural enemies. Indeed, it was analysed by Thaler et al. (2002) how *P. persimilis* is less attracted to tomato types with JA-deficient induced by the feeding of *S. exigua* than tomato types with a good JA production.

Pérez-Hedo et al. (2021) studied how specific HIPVs, isolated from tomato plants attacked by *N. tenuis*, for example, (Z)-3-hexenyl propanoate, can indirectly prime the defences of healthy plants. In a tomato greenhouse, they tested how the selected HIPVs, constantly released by polymeric dispensers, can prime commercial tomato plant defences for more than 2 months and thus reduce the attack of key pests. Indeed, these HIPVs elicited the production of secondary metabolites, the expression of JA and SA signalling marker genes and a large number of protein inhibitors. In addition, the levels of *T. absoluta* and *T. urticae* infestation were significantly lower in the treatment with the (Z)-3-hexenyl propanoate.

Moreover, microorganisms can also be useful for recruiting pest natural enemies indirectly. Battaglia et al. (2013) studied how the use of the plant growth promoting fungus *T. longibrachiatum* can affect the tomatoherbivore-parasitoid/predator multitrophic system. The soil inoculation with *T. longibrachiatum* boosted the development and reproduction of *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) but also of the generalist predator *M. pygmaeus*. Moreover, *T. longibrachiatum*-infected plants have been shown to be more attractive toward the aphid parasitoid Aphidius ervi Haliday (Hymenoptera: Braconidae) and *M. pygmaeus*.

6 | ENHANCED PLANT DEFENCES: AN IMPORTANT TOOL FOR FUTURE TOMATO IPM PROGRAMMES

Enhanced plant resistance, either constitutive or induced, is and will be a key component of IPM in tomato. Therefore, to promote plant resistance to herbivores, plant resistance inducers could be used much more intensely, for example, the exploitation of agents that improve protection against pest attacks by priming plant defence mechanisms could be pursued. Unlike traditional pesticides, plant resistance inducers do not directly target the insect, but hinder its development indirectly by stimulating the defence responses of the plant. Their implementation in an IPM strategy has been strongly recommended (Siah et al., 2018).

Combining plant resistance inducers with preinfestation would also help to boost protection in plants. Esmaeily, Samih, and Izadi (2021) described how resistance in tomato plants was induced by the foliar and root application of resistance inducers, that is, JA and ABA, in combination with preinfestation by N. tenuis. Such treatment reduced the fitness and the reproduction of T. vaporariourum, mainly because of an increased activity of plant enzymes and of phenolic content. Moreover, the application of other hormones as resistance inducers, that is, SA, β -aminobutyric acid, methyl jasmonate, could amplify plant resistance (Jafarbeigi, Samih, & Alaei, 2021; Stout, Workman, Bostock, & Duffey, 1998). This might suggest that increased plant enzyme activity and phenolic content when combined with preinfestations and resistance inducers, instead of distinct and separated treatments with only inducers or only preinfestation, will give better results on plant defence mechanisms. The enhancement of plant resistance to herbivores has also been shown for T. absoluta. Several wild tomato accessions have been used extensively to breed several commercial tomato lines with enhanced levels of pest resistance. For example, breeding programmes using S. galapensis, a wild solanaceous plant, led to commercial tomato varieties resistant and/or tolerant toward herbivores, including T. absoluta (Snoeren, Sitbon, & Levv. 2017).

Despite intensive work on these aspects and the worldwide relevance of the tomato industry, very few current tomato cultivars are tolerant to *T. absoluta*. It has been hypothesised that a low level of genetic variability has been introduced while domesticating tomato, and the consequent loss of genes controlling the production of plant defence allelochemicals, may have caused the tomato lack of tolerance to *T. absoluta* (Snoeren et al., 2017).

In this context, the use of inducers and preinfestation to enhance plant resistance may be a key tool for sustainable pest management programmes. Induced plant defences against insects are indeed an aspect of biochemistry, physiology and genetics of plants deeply studied worldwide and frequently proposed in IPM (Goyal et al., 2012). This means that new technologies to control herbivores are in place and the results obtained are promising (Camargo et al., 2016). Moreover, plastid-mediated RNAi technology could be a powerful tool to develop resistant cultivars against insect pests (Zhang et al., 2015). Indeed, new findings on genes in terms of herbivore resistance are likely to promote additional research in this field.

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