



HAL
open science

Plant defences for enhanced integrated pest management in tomato

Simona Tortorici, Antonio Biondi, Meritxell Pérez-Hedo, Romain Larbat, Lucia Zappalà

► To cite this version:

Simona Tortorici, Antonio Biondi, Meritxell Pérez-Hedo, Romain Larbat, Lucia Zappalà. Plant defences for enhanced integrated pest management in tomato. *Annals of Applied Biology*, 2022, 180 (3), pp.328-337. <10.1111/aab.12750>. <hal-03959489>

HAL Id: hal-03959489

<https://hal.univ-lorraine.fr/hal-03959489v1>

Submitted on 23 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

1 **Plant defenses for enhanced Integrated Pest Management in tomato**

2 Simona Tortorici¹, Antonio Biondi¹, Meritxell Pérez-Hedo², Romain Larbat³, Lucia Zappalà^{1*}

3

4 ¹ *University of Catania, Department of Agriculture, Food and Environment, via Santa Sofia 100,*
5 *95123, Catania, Italy*

6 ² *Centro de Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones*
7 *Agrarias (IVIA), Carretera Moncada-Náquera km 4,5. 46113 Moncada, Valencia, Spain*

8 ³ *UMR 1121, Laboratoire Agronomie et Environnement (LAE), Université de Lorraine- INRAe,*
9 *Nancy, France*

10 *Corresponding author: lzappala@unict.it

11 Simona Tortorici ORCID ID: 0000-0002-5083-0198

12 Antonio Biondi ORCID ID: 0000-0002-1982-7716

13 Meritxell Pérez-Hedo ORCID ID: 0000-0003-3411-0761

14 Romain Larbat ORCID ID: 0000-0002-9060-5040

15 Lucia Zappalà ORCID ID: 0000-0002-2804-3980

16

17 Running head: Tomato defenses for IPM

18 **Abstract**

19 Plants evolved a series of defense mechanisms to counteract the attack of herbivores. These can
20 impact on food-webs at various trophic levels, in both natural and managed ecosystems, such as
21 crops. The biochemical and ecological bases behind these processes are reviewed here by
22 highlighting the differences in direct and indirect, constitutive and induced defenses. In Integrated
23 Pest Management, several pest control tools are applied in an economically-sound way in order to
24 increase the crop resilience and reduce reliance on synthetic pesticides. Plant resistance is thus a
25 crucial aspect of preventive pest control strategies in several agroecosystems, including tomato. In
26 this context, we review the current literature dealing with the physiology and biochemistry of
27 tomato plants in terms of metabolite pathways and multi-trophic interactions. We also describe
28 recent advances in plant defense related tools obtained by studying the multi-trophic interactions
29 between pests and plants in the tomato system.

30

31 **Key words**

32 HIPV, Induced defense, IPM, invasive species, secondary metabolites

33

34 **Summary**

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

40 **1. Plant defenses within IPM in tomato crops**

41 Integrated Pest Management (IPM) is based on the application of sustainable pest control
42 combining different tools (Ehler 2006). It is a control strategy in which biological, chemical,
43 genetic, physical and agronomic control methods are combined to pursue stable long-term pest
44 control (Larkin 1989). The implementation of an IPM involves three key elements: a) multiple
45 tools used in a compatible way, for example combining pheromone-based methods and the use
46 of natural enemies; b) prevention of high pest densities; c) conservation of biodiversity to
47 increase ecosystem services.

48 In the context of IPM, plant resistance to insect pests plays a key role when designing and
49 implementing sustainable plant protection protocols (Kennedy 2008). Enhancing plant defenses
50 can contribute to IPM combined with rational fertilization, biological control and cultivation
51 methods (Gharekhani & Salek-Ebrahimi 2014; Blazhevski et al. 2018). Influencing and
52 enhancing the plant defensive profile, in which the plant has to pay a cost (i.e., a decreased above
53 ground growth and reduced flowering as consequences of the herbivore attack), can impact
54 insect pests and their natural enemies in commercial tomato crops (Li et al. 2018; de Oliveira et
55 al. 2019). Tomato has been considered a model plant to characterize the defense mechanisms for
56 many other crops. Thus, IPM seems to be a key approach to reach sustainable production in
57 tomato, thereby preserving environmental and human health.

58 Here, we review the current knowledge on plant defenses and their potential impact on tomato
59 pest control packages focusing on the trophic interactions involving tomato and its invasive pests
60 which are causing extensive damage to several tomato production areas worldwide (Biondi et al.
61 2018; Mansour et al. 2018; Rostami et al. 2020).

62 **2. The co-evolution of plant-arthropod interactions**

63 Plant responses to insect herbivory, developed during plant evolution, involve various defense
64 and/or tolerance mechanisms (Ehrlich & Raven 1964). Plants react to herbivores by activating a

66 cascade of resistance mechanisms to defend themselves. These include the modification of the
67 phytohormone profile, thus triggering direct and/or indirect defenses (Thaler et al. 2002; Kant &
68 Baldwin 2007).

69 Plant defenses tend to reduce the fitness of herbivores by reducing their survival and
70 reproduction. Thus, plants and insects may co-evolve, where co-evolution is defined as the
71 process of genetic adaptations in a reciprocal way (Ton et al. 2009; Mithöfer et al. 2012; Dicke
72 & van Loon 2014). When an herbivore successfully evolves to overcome the plant defense
73 mechanisms, it might become a potential threat and it imposes a selective pressure on plants that
74 results in the evolution of herbivore-specific induced defense mechanisms (Bergelson et al.
75 2001; Dodds & Rathjen 2010). Similarly, when a plant adapts to counteract the attack of an
76 herbivore, it has the potential to be a resistant host (Jongsma & Bolter 1997).

77 The suitability of the plants for the herbivores that feed on them and *vice versa*, gene
78 modifications in defense traits and the combinations of the involved plant and insect genotypes
79 are three important aspects in the insect-plant co-evolution (Rasmann & Agrawal 2009; Liu et al.
80 2017). In most cases, co-evolution involves a compromise in which both the host and the
81 herbivore survive and develop sub-optimally due to considerable metabolic costs (Gatehouse
82 2002). Organisms continuously evolve to compete, such as in a game of evolutionary *ping pong*
83 (Arora et al. 2012). In particular, evolution depends on the frequency with which the attack
84 occurs and, above all, in which way insects react (Berenbaum & Zangerl 1998; Kant et al. 2008).

85

86 **3. How plants defend themselves**

87 Identifying and classifying the ecophysiological responses of plants is a key to improve their
88 natural defenses (Ehrlich & Raven 1964). Plant defenses can be classified as constitutive and
89 induced, although often the metabolites implicated are the same or similar (Duffey & Felton
90 1991; Wittstock & Gershenzon 2002). Constitutive defenses include products, structures and
91 compounds of the primary and secondary metabolism that are involved in plant defenses

92 regardless the threat of an herbivores (Hanley et al. 2007; Bar & Shtein 2019). By contrast,
93 induced defenses are activated following an herbivore attack, or other biotic and abiotic stresses,
94 and include products, structures and compounds of the secondary metabolism of the plants
95 subsequently primed (Arimura et al. 2005; Kersch-Becker & Thaler 2019). The response of
96 plants to stresses is a combination of many reactions and mechanisms that indirectly and directly
97 influence their interactions with the ecosystem, even at the multitrophic level and often with
98 long-term consequences (Mithöfer & Boland 2012; Stam et al. 2014).

99 Both constitutive and induced defenses can be direct and indirect. The direct ones influence
100 the performance and development of the herbivore, for example, the accumulation of toxins or
101 the thickening of cell walls (Chen 2008; Yang et al. 2020; Lin et al. 2020). Indirect defenses
102 manipulate (i) the behavior of predators or parasitoids of the herbivore by attracting them to the
103 infested plant; and/or (ii) of neighboring plants by warning them through alarm signals (Coppola
104 et al. 2017). This kind of signaling is mediated by herbivore-induced plant volatiles (HIPVs) that
105 attract the natural enemies toward the infested plant and/or prime pre-infestation defense
106 mechanisms in nearby healthy plants (Fig.1) (Kessler & Baldwin 2002; Pérez-Hedo et al. 2017;
107 Mithöfer et al. 2018). In crop protection, combining all these aspects is crucial for sustainability.
108 However, until quite recently, most mechanistic studies have investigated the relationship
109 between a single pest and a single type of defense-related factor or response. In fact, they have
110 ignored the presence of other defense factors such as those related to complex food webs
111 including concomitant multiple pest attacks (Stout et al. 1999; Stam et al. 2014).

112

113 **3.1. Constitutive defenses**

114 Constitutive defenses exist in plants independently of any herbivore attacks (Goyal et al. 2011).
115 They include structural, mechanical and chemical mechanisms (Dussourd & Denno 1991;
116 Bonaventure et al. 2011). These can be independent from each other or can act synergistically,
117 such as glandular trichomes and their secretory canals, which combine a structural defense and a

118 secretory capacity as mechanical and chemical defense mechanisms (Glas et al. 2012; Wang et
119 al. 2021).

120

121 **3.1.1. Structural and mechanical defenses**

122 Morphological barriers of the plant, e.g., thorns, can prevent feeding by large herbivores while
123 the thickening of the walls, for example, can impair feeding by small herbivores (Wheeler &
124 Krimmel 2015; Mitchell et al. 2016; Jacob et al. 2020). Bitew (2018) found that wild tomato
125 species with high density of glandular and non-glandular trichomes, such as *S. habrochaites* and
126 *S. pennellii*, have an important potential for resisting to *Tuta absoluta* (Meyrick) (Lepidoptera:
127 Gelechiidae). These species and/or these traits could thus be included in future tomato breeding
128 programs, e.g., by identifying the genetic basis involved in the production and density of
129 mechanical barriers. However, this might result in further challenges because trichomes in
130 tomato plants can strongly compromise the establishment of predatory arthropods (including
131 mites and flower bugs) and, thus, the ecological services they provide (Salehi et al. 2016; Paspati
132 et al. 2021).

133

134 **3.1.2. Chemical defenses**

135 Constitutive chemical defenses (e.g., tannins, resins) can be toxic, repellent or antifeedant and
136 can impact on the development of the herbivores by altering the resistance, the fecundity, and the
137 digestive capacities. The toxicity or repellency of these chemical compounds also depend on
138 how the plant stores them. For example, large amounts of toxicants are released by the plant only
139 once the herbivore breaks down specific plant structures by feeding or just moving on the plant,
140 such as resin ducts or glandular trichomes (Dearing et al. 2005; Zhou et al. 2015; Yousaf et al.
141 2018; Giordano et al. 2020). Fractions of tomato trichome extracts can affect predatory mite
142 survival in a concentration-response manner (Paspati et al. 2021).

143 Kennedy (2003) reported that the presence of phenolic compounds, e.g., chlorogenic acid and
144 rutin, in tomato leaves, may inhibit the growth of larvae of two noctuid pests, *Spodoptera exigua*
145 (Hübner) and *Helicoverpa zea* (Boddie). Phenolic compounds are typically synthesized in the
146 green parts of the plants and are considered as constitutive defense chemicals (Harborne 1979).
147 When incorporated into an artificial diet, they inhibit larval development in a dose-dependent
148 manner (Isman & Duffey 1982; Kennedy 2003).

149

150 **3.2. Induced defenses**

151 External factors that interfere with the plant, such as herbivores, can trigger plant defenses (i.e.,
152 signaling cascades) which make the plant synthesizing specific compounds, such as secondary
153 metabolites, and trigger changes in plant physiology. This hampers the fitness, the survival, the
154 development and the fecundity of the feeder (Kant et al. 2004). The success of plant defenses is
155 mediated by a prompt and specific identification of the herbivore. Santamaria et al. (2018)
156 reported how the different feeding mechanisms of herbivores enable the plant to recognize them,
157 through specific plant receptors (PRRs, pattern recognition receptors), damage-associated
158 molecular patterns (DAMPs) and herbivore-associated molecular patterns (HAMPs), and
159 respond accordingly by triggering short-term and long-term defense mechanisms.

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

165 In this context, it was demonstrated that trichome development is correlated with the
166 abundance of jasmonic acid (Boughton et al. 2005; Tian et al. 2012). Paudel et al. (2019) showed
167 that the development of both glandular and non-glandular trichomes in tomato are induced as a
168 result of herbivore damage.

169 Pérez-Hedo et al. (2015a) investigated the implications of different phytohormones involved
170 in tomato plant defenses in response to *N. tenuis* punctures. They evaluated the production of
171 induced defense mechanisms, such as the production of HIPVs playing a key role in tritrophic
172 interactions (Turlings & Erb 2018). These mechanisms are crucial to understanding the evolution
173 of plant-natural enemy relationships (Sabelis et al. 2001; Stahl et al. 2018). Through plant
174 induction, HIPVs can make the plant repellent to herbivores (Engelberth et al. 2004; Frost et al.
175 2008), and/or more attractive to natural enemies of pests (Pérez-Hedo et al. 2015b; Naselli et al.
176 2016; Ayelo et al. 2021). In this context, Conboy et al. (2020) analyzed tomato HIPVs and
177 selected methyl salicylate (MeSA), a plant elicitor that recognizes and triggers intracellular
178 defense signaling in the plant. They evaluated the application of this elicitor in un-infested
179 tomato plants and noted that the *Trialeurodes vaporariorum* (Westwood) (Hemiptera:
180 Aleyrodidae) population was reduced and that there was an 11% increase in the tomato yield.

181 In some cases, insects can modulate HIPV production by the attacked plant (Sarmiento et al.
182 2011). Zhang et al. (2019) demonstrated how *Bemisia tabaci* (Gennadius) (Hemiptera:
183 Aleyrodidae) can manipulate the defense mechanisms of the host plant community by
184 stimulating the attacked plant to emit HIPVs that can prime SA-dependent defenses and suppress
185 JA-dependent defenses in neighboring plants. This would make the neighboring healthy plant
186 more suitable for the imminent attack by *B. tabaci* (Zhang et al., 2019).

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

192

193 **3.2.1. Signal transduction and metabolite pathways in tomato**

194 Plant hormones play a central role for plant signaling networks as response to biotic and abiotic
195 stresses (Robert-Seilianiantz et al. 2007). When an herbivore begins to feed on plant tissues, the
196 damage generates a plant defense response in a generally non-specific way (Frost et al. 2008),
197 and primary and secondary metabolites belonging to disparate chemical classes are produced by
198 plants (Duffey & Stout 1996; Wink 2008). Nevertheless, the signals produced by herbivores can
199 be specific and enable the plant to respond in a much more precise way.

200 The hormone jasmonic acid has a key role in tomato plant resistance to herbivores, mainly
201 chewing ones. This hormone induces the transcription of genes involved in defense metabolism
202 (Turner et al. 2002). It is produced in the signaling octadecanoid pathway and it is synthesized in
203 the chloroplast and peroxisome from linolenic acid, which is released from plant membrane
204 lipids (Chen et al. 2006). Other hormones, such as salicylic acid and ethylene, participate in the
205 signaling pathways involved in the defense mechanisms (Lorenzo et al. 2003; Zarate et al. 2007).

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

215 The next step is the hydrolysis of the pectic component of the cell walls of plants which
216 generates galacturonic acid, a defensive protein of tomato plants, even more precisely oligomeric
217 polymers (oligogalacturonic acid - OGA). The signal which activates expression of the wound-
218 induced polygalacturonase gene appears to be jasmonic acid (Orozco-Cardenas & Ryan 1999),
219 suggesting that this has an earlier effect in the signaling pathway than oligogalacturonic acid. At

220 the end of the signaling pathway of defensive proteins, such as proteinase inhibitors and
221 polyphenol oxidase, hydrogen peroxide is produced and diffused in mesophyll cells through the
222 oxidative burst, near the vascular bundles (Orozco-Cardenas et al. 2001). Once absorbed by
223 insects, hydrogen peroxide negatively affects the permeability of the intestinal wall causing
224 oxidative damage to the insect epithelial cells (Singh & Singh 2021).

225

226 **4. Alterations in the plant defensive profile and their multi-trophic outcomes**

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

230 **4.1 Bottom-up approaches**

231 The bottom-up approaches consist in exploiting the effects of variable availability in the soil of
232 water, of minerals (e.g., potassium and nitrogen), and/or (bio)fertilizers for optimizing the
233 defense mechanisms of the plants (Larbat et al. 2016). Due to bottom-up effects, modified
234 defense volatiles and altered plant metabolism can affect tritrophic interactions (Denno et al.
235 2002; Han et al. 2014; Coqueret et al. 2017; Shehzad et al. 2020). Salinity stress increases the
236 osmotic potential, thus decreasing plant water availability, leaf dietary quality (Romero-Aranda
237 et al. 2001; Manaa et al. 2011; Teklić et al. 2020), and also water availability to the larvae of
238 herbivores. The secondary metabolism of the plant can also be modified by salinity stress, and
239 plants can alter their defense compounds thus affecting the trophic interactions (Ballhorn & Elias
240 2014). In order to resist the salinity stress of plants, insects are able to modify their feeding
241 intensity and to shorten the juvenile development time (Han et al. 2019b).

242 The quantity and quality of the plant watering can enhance the plant defense mechanisms thus
243 affecting the plant resistance to herbivores (Dong et al. 2020; Gutbrodt et al. 2011; Dong et al.
244 2018). Lin et al. (2021) studied how lower water availability increased the levels of two tomato
245 plant defensive proteins, trypsin protease inhibitor and polyphenol oxidase. These resistance

246 factors directly influence the consumption of plant tissues and the performance of *Manduca*
247 *sexta* (Linnaeus) (Lepidoptera: Sphingidae) a specialist caterpillar. Furthermore, in conditions of
248 water deficit, the increase in the concentration of glycoalkaloids in the tomato leaves negatively
249 affects survival, pupal weight and larval development time of *T. absoluta* (Han et al. 2016).

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

255 The quantity and the quality of nitrogen strongly limits herbivore development (Han et al.
256 2020, Kagata & Ohgushi 2012), thus making the concentration of nitrogen important for the
257 survival of insects. The amount of nitrogen and metabolites in plant tissue is affected by nitrogen
258 fertilization. Many primary metabolites, such as carbohydrates, as well as other secondary plant
259 metabolites, such as phenolic acids, flavonoids and glycoalkaloids, are influenced by nitrogen
260 fertilization and can impact insect development (Fritz et al. 2006; Hermans et al. 2006; Larbat et
261 al. 2016; Coqueret et al. 2017). Tomato plants with low nitrogen input produce higher
262 concentrations of defensive secondary metabolites, such as soluble phenolics (i.e., kaempferol-
263 rutinoid, chlorogenic acid and rutin), because their concentration is connected positively with
264 the carbon/nitrogen ratio in tomato tissues (Royer et al. 2013).

265 All these compounds are repellent and/or toxic to various insect pest taxa (Mirnezhad et al.
266 2010). For example, Ramachandran et al. (2020) studied the effects of nitrogen availability on
267 the tolerance to whiteflies in four tomato varieties showing that plants grown at half the optimal
268 quantity of nitrogen had a higher degree of resistance to whiteflies, without a decreasing yield.

269 Tomato plants, in conditions of nitrogen deficit limits, negatively affect the survival, pupal
270 weight and development time of *T. absoluta* (Coqueret et al. 2017). This seems to be due to the
271 low protein content and to the increased number of phenolic compounds and glycoalkaloids in

272 the leaves (Larbat et al. 2016). Overall, in tomato the production of various chemical defense
273 molecules, mainly based on carbon and less on nitrogen, reduces the nutritional value of the
274 leaves for herbivores (Larbat et al. 2012; Royer et al. 2013). In addition, water and nitrogen
275 quantities are positively related, and larvae of *T. absoluta* may thus suffer from a lack of
276 nitrogen-based nutrients in drought-prone plants (Han et al. 2014).

277 Another macro-element that can alter the concentration of defense compounds is potassium
278 (Trejo-Escobar et al. 2019) which has bottom-up effect potentials on the cycle of *B. tabaci* and *T.*
279 *absoluta* in tomato plants. It was showed by Darwish et al. (2021) that treatment with potassium
280 fertilizer as a foliar spray on tomato plants can have a significant impact on decreasing the
281 density of *B. tabaci* nymphs. Sung et al. (2015) studied the low potassium input on the tomato
282 plant and found that there is an accumulation of defense compounds in the plant tissue, such as
283 soluble sugar and putrescine, known to be involved in defense responses of the plant (Liu et al.
284 2020), and a concomitant reduction of the majority of the amino acids.

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

294

295 **4.2 Indirect interactions**

296 Indirect interactions consist of those plant relationships with external factors, such as insects and
297 microorganisms, which can influence plant responses and modify interactions with other

298 members of the system, such as for example natural enemies (Stam et al. 2014). Plant responses
299 lead to morphological or metabolic changes which can subsequently influence indirect
300 interactions with other members of the community (Han et al. 2020). Thus, plant defense profile
301 can be enhanced by a preliminary attack from herbivores (Poelman & Dicke 2018). The initial
302 insect feeding can stimulate the defense pathways of the plant, thereby generating secondary
303 metabolites, including HIPVs, which can interfere with the choice of the host by the pest and the
304 natural enemies. For example, Pérez-Hedo et al. (2015a, b) showed that tomato plants fed by *N.*
305 *tenuis* activate the jasmonic and abscisic (ABA) acid pathways making the plants less attractive
306 to *T. absoluta* and *B. tabaci*, but more attractive toward *Encarsia formosa* Gahan (Hymenoptera:
307 Aphelinidae), one of the most effective whiteflies' parasitoids.

308 Moreover, it was shown how the spider mite feeding on tomato plant causes an emission of
309 HIPVs depending on the induced JA signaling. The methyl salicylate (MeSA) and 4,8,12-
310 trimethyl-1,3(*E*),7(*E*),11-tridecatetraene (TMTT) were emitted after the attack of *Tetranychus*
311 *urticae* Koch (Acarina: Tetranychidae) (Ament et al. 2004; Kant et al. 2008). These volatile
312 compounds have an important role on the indirect defenses to attract natural enemies such as
313 *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae) (De Boer & Dicke 2004).
314 Similarly, Ayelo et al. (2021) found that, among the many HIPV induced by *T. absoluta*, several
315 monoterpenes are useful to attract the zoophytophagous mirid *N. tenuis*, while (E)- β -
316 caryophyllene was found to repel it.

317 Other researches are focused on the evaluation of different tomato types with different
318 production of jasmonic acid and the attraction of natural enemies. The production of jasmonic
319 acid has a key role for the production of defense volatile compounds to attract natural enemies.
320 Indeed, it was analyzed by Thaler et al. (2002) how *P. persimilis* is less attracted to tomato types
321 with jasmonic acid-deficient induced by the feeding of *S. exigua* than tomato types with a good
322 jasmonic acid production.

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

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

338

339 **5. Enhanced plant defenses: an important tool for future tomato IPM programs**

340 Enhanced plant resistance, either constitutive or induced, is and will be a key component of IPM
341 in tomato. Therefore, to promote plant resistance to herbivores, plant resistance inducers could
342 be used, i.e. agents that improve protection against pest attacks by priming plant defense
343 mechanisms. Unlike traditional pesticides, plant resistance inducers do not directly target the
344 insect, but hinder its development indirectly by stimulating the defense responses of the plant.
345 Their implementation in an IPM strategy has been strongly recommended (Siah et al. 2018).

346 Combining plant resistance inducers with pre-infestation would also help to boost protection
347 in plants. Esmaeily et al. (2021) described how resistance in tomato plants was induced by the
348 foliar and root application of resistance inducers, i.e., JA and ABA, in combination with pre-

349 infestation by *N. tenuis*. Such treatment reduced the fitness and the reproduction of *T.*
350 *vaporariourum*, mainly due to an increased activity of plant enzymes and of phenolic content.
351 Moreover, the application of other hormones as resistance inducers, i.e. salicylic acid (SA), β -
352 aminobutyric acid (BABA), methyl jasmonate (MeJA), could amplified plant resistance (Stout et
353 al. 1998; Jafarbeigi et al. 2021). This might suggest that increased plant enzyme activity and
354 phenolic content when combined with pre-infestations and resistance inducers than simple
355 treatment will give better results on plant defense mechanisms. The enhancement of plant
356 resistance to herbivores has also been shown for *T. absoluta*. Several wild tomato accessions
357 have been used extensively to breed several commercial tomato lines with enhanced levels of
358 pest resistance. For example, breeding programs using *S. galapensis*, a wild solanaceous plant,
359 led to commercial tomato varieties resistant and/or tolerant towards herbivores, including *T.*
360 *absoluta* (Snoeren et al. 2017).

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

366 In this context, the use of inducers and of pre-infestation to enhance plant resistance may be a
367 key tool for sustainable pest management programs. Induced plant defenses against insects are
368 indeed an aspect of biochemistry, physiology and genetics of plants deeply studied worldwide
369 and frequently proposed in IPM (Goyal et al. 2011). This means that new technologies to control
370 herbivores are in place and the results obtained are promising (Camargo et al. 2016). Moreover,
371 plastid-mediated RNAi technology could be a powerful tool to develop resistant cultivars against
372 insect pests (Zhang et al. 2015). Indeed, new findings on genes in terms of herbivore resistance
373 are likely to promote additional research in this field.

374

375 **Acknowledgements**

376 Authors are thankful to the funders of this project: the Italian Ministry of Education, University
377 and Research (PRIN Project *Biopesticides for sustainable insect pest control*, BIOPIC); the
378 Italian Ministry of Agricultural, Food and Forestry Policies, ERA-NET action ARIMNET2 2015
379 call (project *Sustainable Tomato Production*, STomP); EU ERASMUS+; the University of
380 Catania (Project *Emergent Pests and Pathogens and Relative Sustainable Strategies*). Authors
381 wish to thank three anonymous referees and the editor for their helpful comments on an earlier
382 version of the manuscript.

383 **References**

- 384 Ament, K., Kant, M. R., Sabelis, M. W., Haring, M. A., & Schuurink, R. C. (2004). Jasmonic
385 acid is a key regulator of spider mite-induced volatile terpenoid and methyl salicylate
386 emission in tomato. *Plant physiology*, 135(4), 2025-2037.
- 387 Appel, H. M., & Cocroft, R. B. (2014). Plants respond to leaf vibrations caused by insect
388 herbivore chewing. *Oecologia*, 175(4), 1257-1266.
- 389 Arimura, G. I., Kost, C., & Boland, W. (2005). Herbivore-induced, indirect plant defences.
390 *Biochimica et Biophysica Acta (BBA)-Molecular and Cell Biology of Lipids*, 1734(2), 91-111.
- 391 Arora, J., Goyal, S., & Ramawat, K. G. (2012). Co-evolution of pathogens, mechanism involved
392 in pathogenesis and biocontrol of plant diseases: an overview. *Plant Defence: Biological*
393 *Control*, 3-22.
- 394 Ayelo, P. M., Yusuf, A. A., Pirk, C. W., Chailleux, A., Mohamed, S. A., & Deletre, E. (2021).
395 Terpenes from Herbivore-Induced Tomato Plant Volatiles Attract *Nesidiocoris tenuis*
396 (Hemiptera: Miridae), a Predator of Major Tomato Pests. *Pest Management Science*.
- 397 Ballhorn, D. J., & Elias, J. D. (2014). Salinity-mediated cyanogenesis in white clover (*Trifolium*
398 *repens*) affects trophic interactions. *Annals of Botany*, 114(2), 357-366.
- 399 Bar, M., & Shtein, I. (2019). Plant trichomes and the biomechanics of defense in various
400 systems, with Solanaceae as a model. *Botany*, 97(12), 651-660.
- 401 Battaglia, D., Bossi, S., Cascone, P., Digilio, M. C., Prieto, J. D., Fanti, P., ... & Trotta, V. (2013).
402 Tomato below ground–above ground interactions: *Trichoderma longibrachiatum* affects the
403 performance of *Macrosiphum euphorbiae* and its natural antagonists. *Molecular plant-microbe*
404 *interactions*, 26(10), 1249-1256.
- 405 Berenbaum, M. R., & Zangerl, A. R. (1998). Chemical phenotype matching between a plant and
406 its insect herbivore. *Proceedings of the National Academy of Sciences*, 95(23), 13743-13748.
- 407 Bergelson, J., Kreitman, M., Stahl, E. A., & Tian, D. (2001). Evolutionary dynamics of plant R-
408 genes. *Science*, 292(5525), 2281-2285.
- 409 Biondi, A., Guedes, R. N. C., Wan, F. H., & Desneux, N. (2018). Ecology, worldwide spread,
410 and management of the invasive South American tomato pinworm, *Tuta absoluta*: past,
411 present, and future. *Annual Review of Entomology*, 63, 239-258.
- 412 Bitew, M. K. (2018). Significant role of wild genotypes of tomato trichomes for *Tuta Absoluta*
413 Resistance. *Journal of Plant Genetics and Breeding*, 2(1), 104.
- 414 Blazhevski, S., Kalaitzaki, A. P., & Tsagkarakis, A. E. (2018). Impact of nitrogen and potassium
415 fertilization regimes on the biology of the tomato leaf miner *Tuta absoluta*. *Entomologia*
416 *Generalis*, 37(2), 157-174.
- 417 Bonaventure, G., VanDoorn, A., & Baldwin, I. T. (2011). Herbivore-associated elicitors: FAC
418 signaling and metabolism. *Trends in Plant Science*, 16(6), 294-299.
- 419 Boughton, A. J., Hoover, K., & Felton, G. W. (2005). Methyl jasmonate application induces
420 increased densities of glandular trichomes on tomato, *Lycopersicon esculentum*. *Journal of*
421 *Chemical Ecology*, 31(9), 2211-2216.
- 422 Camargo, R. A., Barbosa, G. O., Possignolo, I. P., Peres, L. E., Lam, E., Lima, J. E., ... &
423 Marques-Souza, H. (2016). RNA interference as a gene silencing tool to control *Tuta absoluta*
424 in tomato (*Solanum lycopersicum*). *PeerJ*, 4, e2673.

- 425 Chen, H., Jones, A. D., & Howe, G. A. (2006). Constitutive activation of the jasmonate signaling
426 pathway enhances the production of secondary metabolites in tomato. *FEBS letters*, 580(11),
427 2540-2546.
- 428 Chen, M. S. (2008). Inducible direct plant defense against insect herbivores: a review. *Insect*
429 *Science*, 15(2), 101-114.
- 430 Conboy, N. J., McDaniel, T., George, D., Ormerod, A., Edwards, M., Donohoe, P., ... & Tosh, C.
431 R. (2020). Volatile Organic Compounds as Insect Repellents and Plant Elicitors: an Integrated
432 Pest Management (IPM) Strategy for Glasshouse Whitefly (*Trialeurodes vaporariorum*).
433 *Journal of Chemical Ecology*, 46(11), 1090-1104.
- 434 Coppola, M., Cascone, P., Madonna, V., Di Lelio, I., Esposito, F., Avitabile, C., ... & Corrado,
435 G. (2017). Plant-to-plant communication triggered by systemin primes anti-herbivore
436 resistance in tomato. *Scientific Reports*, 7(1), 1-13.
- 437 Coqueret, V., Le Bot, J., Larbat, R., Desneux, N., Robin, C., & Adamowicz, S. (2017). Nitrogen
438 nutrition of tomato plant alters leafminer dietary intake dynamics. *Journal of Insect*
439 *Physiology*, 99, 130-138.
- 440 D'Esposito, D., Manzo, D., Ricciardi, A., Garonna, A. P., De Natale, A., Frusciante, L., ... &
441 Ercolano, M. R. (2021). Tomato transcriptomic response to *Tuta absoluta* infestation. *BMC*
442 *plant biology*, 21(1), 1-14.
- 443 Darwish, A., Attia, M. M., & Khozimy, A. M. (2021). Effect of Some Integrated Pest
444 Management Elements on the Population Density of *Bemisia Tabaci* (Gennadius)(Hemiptera:
445 Aleyrodidae) on Tomato Plants (*Solanum Lycopersicum* L.). *Alexandria Science Exchange*
446 *Journal*, 42(JANUARY-MARCH), 57-68.
- 447 De Boer, J. G., & Dicke, M. (2004). The role of methyl salicylate in prey searching behavior of
448 the predatory mite *Phytoseiulus persimilis*. *Journal of chemical ecology*, 30(2), 255-271.
- 449 de Oliveira, E. F., Pallini, A., & Janssen, A. (2019). Herbivore performance and plant defense
450 after sequential attacks by inducing and suppressing herbivores. *Insect Science*, 26(1), 108-
451 118.
- 452 De Palma, M., Docimo, T., Guida, G., Salzano, M., Albrizio, R., Giorio, P., ... & Tucci, M. (2021).
453 Transcriptome modulation by the beneficial fungus *Trichoderma longibrachiatum* drives water
454 stress response and recovery in tomato. *Environmental and Experimental Botany*, 190, 104588.
- 455 Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites
456 on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual Review of Ecology,*
457 *Evolution and Systematics*, 36.
- 458 Denno, R. F., Gratton, C., Peterson, M. A., Langellotto, G. A., Finke, D. L., & Huberty, A. F.
459 (2002). Bottom-up forces mediate natural-enemy impact in a phytophagous insect
460 community. *Ecology*, 83(5), 1443-1458.
- 461 Dicke, M., & van Loon, J. J. (2014). Chemical ecology of phytohormones: how plants integrate
462 responses to complex and dynamic environments. *Journal of Chemical Ecology*, 40(7), 653-
463 656.
- 464 Dodds, P. N., & Rathjen, J. P. (2010). Plant immunity: towards an integrated view of plant-
465 pathogen interactions. *Nature Reviews Genetics*, 11(8), 539-548.
- 466 Dong, Y. C., Han, P., Niu, C. Y., Zappalà, L., Amiens-Desneux, E., Bearez, P., ... & Desneux, N.
467 (2018). Nitrogen and water inputs to tomato plant do not trigger bottom-up effects on a
468 leafminer parasitoid through host and non-host exposures. *Pest Management Science*, 74(3),
469 516-522.

470 Dong, Y. C., Wang, Z. J., Bu, R. Y., Dai, H. J., Zhou, L. J., Han, P., ... & Desneux, N. (2020).
471 Water and salt stresses do not trigger bottom-up effects on plant-mediated indirect
472 interactions between a leaf chewer and a sap-feeder. *Journal of Pest Science*, 93(4), 1267-
473 1280.

474 Duffey, S. S., & Felton, G. W. (1991). Enzymatic antinutritive defenses of the tomato plant
475 against insects. *Naturally Occurring Pest Bioregulators* 12:166-197.

476 Duffey, S. S., & Stout, M. J. (1996). Antinutritive and toxic components of plant defense against
477 insects. *Archives of Insect Biochemistry and Physiology: Published in Collaboration with the*
478 *Entomological Society of America*, 32(1), 3-37.

479 Duke, S. O., Canel, C., Rimando, A. M., Telle, M. R., Duke, M. V., & Paul, R. N. (2000).
480 Current and potential exploitation of plant glandular trichome productivity. In *Advances in*
481 *Botanical Research Incorporating Advances in Plant Pathology*, ed. DL Hallahan, JC Gray,
482 31:121–51. New York: Academic

483 Dussourd, D. E., & Denno, R. F. (1991). Deactivation of plant defense: correspondence between
484 insect behavior and secretory canal architecture. *Ecology*, 72(4), 1383-1396.

485 Ehler, L. E. (2006). Integrated pest management (IPM): definition, historical development and
486 implementation, and the other IPM. *Pest Management Science*, 62(9), 787-789.

487 Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: a study in coevolution. *Evolution*,
488 586-608.

489 Engelberth, J., Alborn, H. T., Schmelz, E. A., & Tumlinson, J. H. (2004). Airborne signals prime
490 plants against insect herbivore attack. *Proceedings of the National Academy of Sciences*,
491 101(6), 1781-1785.

492 Escobar-Bravo, R., Klinkhamer, P. G., & Leiss, K. A. (2017). Induction of jasmonic acid-
493 associated defenses by thrips alters host suitability for conspecifics and correlates with
494 increased trichome densities in tomato. *Plant and Cell Physiology*, 58(3), 622-634.

495 Esmaeily, S., Samih, M. A., & Izadi, H. (2021). Induced resistance by jasmonic and abscisic
496 acids and *Nesidiocoris tenuis* feeding on *Solanum lycopersicum* against *Trialeurodes*
497 *vaporariorum*. *International Journal of Pest Management*, 67(1), 46-57.

498 Fritz, C., Palacios-Rojas, N., Feil, R., & Stitt, M. (2006). Regulation of secondary metabolism by
499 the carbon–nitrogen status in tobacco: nitrate inhibits large sectors of phenylpropanoid
500 metabolism. *The Plant Journal*, 46(4), 533-548.

501 Frost, C. J., Mescher, M. C., Carlson, J. E., & De Moraes, C. M. (2008). Plant defense priming
502 against herbivores: getting ready for a different battle. *Plant physiology*, 146(3), 818-824.

503 Gatehouse, J. A. (2002). Plant resistance towards insect herbivores: a dynamic interaction. *New*
504 *Phytologist*, 156(2), 145-169.

505 Gharekhani, G. H., & Salek-Ebrahimi, H. (2014). Evaluating the damage of *Tuta absoluta*
506 (Meyrick) (Lepidoptera: Gelechiidae) on some cultivars of tomato under greenhouse
507 condition. *Archives of Phytopathology and Plant Protection*, 47(4), 429-436.

508 Giordano, C., Maleci, L., Agati, G., & Petruccelli, R. (2020). *Ficus carica* L. leaf anatomy:
509 Trichomes and solid inclusions. *Annals of Applied Biology*, 176(1), 47-54.

510 Glas, J. J., Schimmel, B. C., Alba, J. M., Escobar-Bravo, R., Schuurink, R. C., & Kant, M. R.
511 (2012). Plant glandular trichomes as targets for breeding or engineering of resistance to
512 herbivores. *International Journal of Molecular Sciences*, 13(12), 17077-17103.

513 Goyal, S., Lambert, C., Cluzet, S., Merillon, J. M., & Ramawat, K. G. (2012). Secondary
514 metabolites and plant defence. In *Plant Defence: Biological Control* (pp. 109-138). Springer,
515 Dordrecht.

516 Gutbrodt, B., Mody, K., & Dorn, S. (2011). Drought changes plant chemistry and causes
517 contrasting responses in lepidopteran herbivores. *Oikos*, 120(11), 1732-1740.

518 Hamza, R., Pérez-Hedo, M., Urbaneja, A., Rambla, J. L., Granell, A., Gaddour, K., ... & Cañas,
519 L. A. (2018). Expression of two barley proteinase inhibitors in tomato promotes endogenous
520 defensive response and enhances resistance to *Tuta absoluta*. *BMC plant biology*, 18(1), 1-14.

521 Han, P., Becker, C., Le Bot, J., Larbat, R., Lavoit, A. V., & Desneux, N. (2020). Plant nutrient
522 supply alters the magnitude of indirect interactions between insect herbivores: From foliar
523 chemistry to community dynamics. *Journal of Ecology*, 108(4), 1497-1510.

524 Han, P., Desneux, N., Becker, C., Larbat, R., Le Bot, J., Adamowicz, S., ... & Lavoit, A. V.
525 (2019b). Bottom-up effects of irrigation, fertilization and plant resistance on *Tuta absoluta*:
526 implications for Integrated Pest Management. *Journal of Pest Science*, 92(4), 1359-1370.

527 Han, P., Desneux, N., Michel, T., Le Bot, J., Seassau, A., Wajnberg, E., ... & Lavoit, A. V.
528 (2016). Does plant cultivar difference modify the bottom-up effects of resource limitation on
529 plant-insect herbivore interactions?. *Journal of Chemical Ecology*, 42(12), 1293-1303.

530 Han, P., Lavoit, A. V., Le Bot, J., Amiens-Desneux, E., & Desneux, N. (2014). Nitrogen and
531 water availability to tomato plants triggers bottom-up effects on the leafminer *Tuta absoluta*.
532 *Scientific Reports*, 4(1), 1-8.

533 Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. (2007). Plant structural traits
534 and their role in anti-herbivore defence. *Perspectives in Plant Ecology, Evolution and*
535 *Systematics*, 8(4), 157-178.

536 Harborne, J. B. (1979). Variation in and functional significance of phenolic conjugation in
537 plants. In *Biochemistry of Plant Phenolics* (pp. 457-474). Springer, Boston, MA.

538 Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006). How do plants respond to
539 nutrient shortage by biomass allocation?. *Trends in Plant Science*, 11(12), 610-617.

540 Isman, M. B., & Duffey, S.S. (1982). Phenolic compounds in foliage of commercial tomato
541 cultivars as growth inhibitors to the fruitworm, *Heliothis zea*. *Journal of the American Society*
542 *for Horticultural Science* 107: 167-170.

543 Jacob, T. K., Senthil Kumar, C. M., Devasahayam, S., D'Silva, S., Kumar, R. S., Biju, C. N., ...
544 & Ankegowda, S. K. (2020). Plant morphological traits associated with field resistance to
545 cardamom thrips (*Sciothrips cardamomi*) in cardamom (*Elettaria cardamomum*). *Annals of*
546 *Applied Biology*, 177(1), 143-151.

547 Jafarbeigi, F., Samih, M. A., & Alaei, H. (2021). Expression patterns of ASR1, PIN2, and PAL
548 genes in tomato and eggplant after treatment with different inducers. *International Journal of*
549 *Tropical Insect Science*, 1-9.

550 Jongsma, M. A., & Bolter, C. (1997). The adaptation of insects to plant protease inhibitors.
551 *Journal of Insect Physiology*, 43(10), 885-895.

552 Kagata, H., & Ohgushi, T. (2012). Carbon to nitrogen excretion ratio in lepidopteran larvae:
553 relative importance of ecological stoichiometry and metabolic scaling. *Oikos*, 121(11), 1869-
554 1877.

555 Kaloshian, I., & Walling, L. L. (2005). Hemipterans as plant pathogens. *Annual Review of*
556 *Phytopathology*, 43, 491-521.

557 Kant, M. R., & Baldwin, I. T. (2007). The ecogenetics and ecogenomics of plant–herbivore
558 interactions: rapid progress on a slippery road. *Current Opinion in Genetics & Development*,
559 17(6), 519-524.

560 Kant, M. R., Ament, K., Sabelis, M. W., Haring, M. A., & Schuurink, R. C. (2004). Differential
561 timing of spider mite-induced direct and indirect defenses in tomato plants. *Plant Physiology*,
562 135(1), 483-495.

563 Kant, M. R., Sabelis, M. W., Haring, M. A., & Schuurink, R. C. (2008). Intraspecific variation in
564 a generalist herbivore accounts for differential induction and impact of host plant defences.
565 *Proceedings of the Royal Society B: Biological Sciences*, 275(1633), 443-452.

566 Kennedy, G. G. (2003). Tomato, pests, parasitoids, and predators: tritrophic interactions
567 involving the genus *Lycopersicon*. *Annual Review of Entomology*, 48(1), 51-72.

568 Kennedy, G. G. (2008). Integration of insect-resistant genetically modified crops within IPM
569 programs. *Integration of Insect-Resistant Genetically Modified Crops within IPM Programs*,
570 1-26.

571 Kersch-Becker, M. F., & Thaler, J. S. (2019). Constitutive and herbivore-induced plant defences
572 regulate herbivore population processes. *Journal of Animal Ecology*, 88(7), 1079-1088.

573 Kessler, A., & Baldwin, I. T. (2002). Plant responses to insect herbivory: the emerging molecular
574 analysis. *Annual Review of Plant Biology*, 53(1), 299-328.

575 Krischik, V. A., Goth, R. W., & Barbosa, P. (1991). Generalized plant defense: effects on
576 multiple species. *Oecologia*, 85(4), 562-571.

577 Larbat, R., Adamowicz, S., Robin, C., Han, P., Desneux, N., & Le Bot, J. (2016). Interrelated
578 responses of tomato plants and the leaf miner *Tuta absoluta* to nitrogen supply. *Plant Biology*,
579 18(3), 495-504.

580 Larbat, R., Le Bot, J., Bourgaud, F., Robin, C., & Adamowicz, S. (2012). Organ-specific
581 responses of tomato growth and phenolic metabolism to nitrate limitation. *Plant Biology*,
582 14(5), 760-769.

583 Larkin, S. B. C. (1989). Integrated Pest Management. Edited by AJ Burn, TH Coaker and PC
584 Jepson. London: Academic Press (1987), pp. 474. *Experimental Agriculture*, 25(4), 562-562.

585 Li, L., & Howe, G. A. (2001). Alternative splicing of prosystemin pre-mRNA produces two
586 isoforms that are active as signals in the wound response pathway. *Plant Molecular Biology*,
587 46(4), 409-419.

588 Li, X., Garvey, M., Kaplan, I., Li, B., & Carrillo, J. (2018). Domestication of tomato has reduced
589 the attraction of herbivore natural enemies to pest-damaged plants. *Agricultural and Forest
590 Entomology*, 20(3), 390-401.

591 Lin, P. A., Paudel, S., Afzal, A., Shedd, N. L., & Felton, G. W. (2021). Changes in tolerance and
592 resistance of a plant to insect herbivores under variable water availability. *Environmental and
593 Experimental Botany*, 183, 104334.

594 Lin, P. A., Peiffer, M., & Felton, G. W. (2020). Induction of defensive proteins in *Solanaceae* by
595 salivary glucose oxidase of *Helicoverpa zea* caterpillars and consequences for larval
596 performance. *Arthropod-Plant Interactions*, 1-9.

597 Liu, C., Atanasov, K. E., Arafaty, N., Murillo, E., Tiburcio, A. F., Zeier, J., & Alcázar, R.
598 (2020). Putrescine elicits ROS-dependent activation of the salicylic acid pathway in
599 *Arabidopsis thaliana*. *Plant, Cell & Environment*, 43(11), 2755-2768.

600 Liu, X., Bai, J., Huang, L., Zhu, L., Liu, X., Weng, N., ... & Chen, M. S. (2007). Gene
601 expression of different wheat genotypes during attack by virulent and avirulent Hessian fly
602 (*Mayetiola destructor*) larvae. *Journal of Chemical Ecology*, 33(12), 2171-2194.

603 Liu, Z., Zhang, C., Ma, L., Zhou, X., Sun, X., & Ding, J. (2021). Elevated temperature decreases
604 preferences of native herbivores to an invasive plant. *Entomologia Generalis*, 41(2): 137 –
605 146.

606 Lorenzo, O., Piqueras, R., Sánchez-Serrano, J. J., & Solano, R. (2003). ETHYLENE
607 RESPONSE FACTOR1 integrates signals from ethylene and jasmonate pathways in plant
608 defense. *The Plant Cell*, 15(1), 165-178.

609 Manaa, A., Ben Ahmed, H., Valot, B., Bouchet, J. P., Aschi-Smiti, S., Causse, M., & Faurobert,
610 M. (2011). Salt and genotype impact on plant physiology and root proteome variations in
611 tomato. *Journal of Experimental Botany*, 62(8), 2797-2813.

612 Mansour, R., Brévault, T., Chailleux, A., Cherif, A., Grissa-Lebdi, K., Haddi, K., ... & Biondi,
613 A. (2018). Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa.
614 *Entomologia Generalis*, 38(2), 83-112.

615 Megali, L., Glauser, G., & Rasmann, S. (2014). Fertilization with beneficial microorganisms
616 decreases tomato defenses against insect pests. *Agronomy for sustainable development*, 34(3),
617 649-656.

618 Mirnezhad, M., Romero-González, R. R., Leiss, K. A., Choi, Y. H., Verpoorte, R., &
619 Klinkhamer, P. G. (2010). Metabolomic analysis of host plant resistance to thrips in wild and
620 cultivated tomatoes. *Phytochemical Analysis: An International Journal of Plant Chemical and*
621 *Biochemical Techniques*, 21(1), 110-117.

622 Mitchell, C., Brennan, R. M., Graham, J., & Karley, A. J. (2016). Plant defense against
623 herbivorous pests: exploiting resistance and tolerance traits for sustainable crop protection.
624 *Frontiers in Plant science*, 7, 1132.

625 Mithöfer, A., & Boland, W. (2012). Plant defense against herbivores: chemical aspects. *Annual*
626 *Review of Plant Biology*, 63, 431-450.

627 Mithöfer, A., Boland, W., & Maffei, M. E. (2018). Chemical ecology of plant–insect
628 interactions. *Annual Plant Reviews Online*, 261-291.

629 Nalam, V. J., Keeretaweep, J., Sarowar, S., & Shah, J. (2012). Root-derived oxylipins promote
630 green peach aphid performance on *Arabidopsis* foliage. *The Plant Cell*, 24(4), 1643-1653.

631 Naselli, M., Urbaneja, A., Siscaro, G., Jaques, J. A., Zappalà, L., Flors, V., & Pérez-Hedo, M.
632 (2016). Stage-related defense response induction in tomato plants by *Nesidiocoris tenuis*.
633 *International Journal of Molecular Sciences*, 17(8), 1210.

634 Orozco-Cárdenas, M. L., Narváez-Vásquez, J., & Ryan, C. A. (2001). Hydrogen peroxide acts as
635 a second messenger for the induction of defense genes in tomato plants in response to
636 wounding, systemin, and methyl jasmonate. *The Plant Cell*, 13(1), 179-191.

637 Orozco-Cardenas, M., & Ryan, C. A. (1999). Hydrogen peroxide is generated systemically in
638 plant leaves by wounding and systemin via the octadecanoid pathway. *Proceedings of the*
639 *National Academy of Sciences*, 96(11), 6553-6557.

640 Pagadala Damodaram, K. J., Gadad, H. S., Parepally, S. K., Vaddi, S., Ramanna Hunashikatti,
641 L., & Bhat, R. M. (2021). Low moisture stress influences plant volatile emissions affecting
642 herbivore interactions in tomato, *Solanum lycopersicum*. *Ecological Entomology*, doi:
643 10.1111/een.13012.

- 644 Pappas, M. L., Steppuhn, A., Geuss, D., Topalidou, N., Zografou, A., Sabelis, M. W., & Broufas,
645 G. D. (2015). Beyond predation: the zoophytophagous predator *Macrolophus pygmaeus*
646 induces tomato resistance against spider mites. *PLoS One*, 10(5), e0127251.
- 647 Paspati, A., Rambla, J. L., Gresa, M. P. L., Arbona, V., Gómez-Cadenas, A., Granell, A., ... &
648 Urbaneja, A. (2021). Tomato trichomes are deadly hurdles limiting the establishment of
649 *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae). *Biological Control*, 104572.
- 650 Paudel, S., Lin, P. A., Foolad, M. R., Ali, J. G., Rajotte, E. G., & Felton, G. W. (2019). Induced
651 plant defenses against Herbivory in cultivated and wild tomato. *Journal of Chemical Ecology*,
652 45(8), 693-707.
- 653 Pérez-Hedo, M., Alonso-Valiente, M., Vacas, S., Gallego, C., Pons, C., Arbona, V., ... & Urbaneja,
654 A. (2021). Plant exposure to herbivore-induced plant volatiles: a sustainable approach through
655 eliciting plant defenses. *Journal of Pest Science*, 1-15.
- 656 Pérez-Hedo, M., Arias-Sanguino, Á. M., & Urbaneja, A. (2018). Induced tomato plant resistance
657 against *Tetranychus urticae* triggered by the phytophagy of *Nesidiocoris tenuis*. *Frontiers in*
658 *Plant Science*, 9, 1419.
- 659 Pérez-Hedo, M., Bouagga, S., Jaques, J. A., Flors, V., & Urbaneja, A. (2015b). Tomato plant
660 responses to feeding behavior of three zoophytophagous predators (Hemiptera: Miridae).
661 *Biological Control*, 86, 46-51.
- 662 Pérez-Hedo, M., Suay, R., Alonso, M., Ruocco, M., Giorgini, M., Poncet, C., & Urbaneja, A.
663 (2017). Resilience and robustness of IPM in protected horticulture in the face of potential
664 invasive pests. *Crop Protection*, 97, 119-127.
- 665 Pérez-Hedo, M., Urbaneja-Bernat, P., Jaques, J. A., Flors, V., & Urbaneja, A. (2015a). Defensive
666 plant responses induced by *Nesidiocoris tenuis* (Hemiptera: Miridae) on tomato plants.
667 *Journal of Pest Science*, 88(3), 543-554.
- 668 Picanço, M. C., Bacci, L., Crespo, A. L. B., Miranda, M. M. M., & Martins, J. C. (2007). Effect
669 of integrated pest management practices on tomato production and conservation of natural
670 enemies. *Agricultural and Forest Entomology*, 9(4), 327-335.
- 671 Poelman, E. H., & Dicke, M. (2018). Plant-mediated interactions among insects within a
672 community ecological perspective. *Annual Plant Reviews online*, 309-337.
- 673 Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980).
674 Interactions among three trophic levels: influence of plants on interactions between insect
675 herbivores and natural enemies. *Annual Review of Ecology and Systematics*, 11(1), 41-65.
- 676 Ramachandran, S., Renault, S., Markham, J., Verdugo, J., Albornoz, M., & Avila-Sakar, G.
677 (2020). Lower Nitrogen Availability Enhances Resistance to Whiteflies in Tomato. *Plants*,
678 9(9), 1096.
- 679 Rasmann, S., & Agrawal, A. A. (2009). Plant defense against herbivory: progress in identifying
680 synergism, redundancy, and antagonism between resistance traits. *Current opinion in plant*
681 *biology*, 12(4), 473-478.
- 682 Robert-Seilaniantz, A., Navarro, L., Bari, R., & Jones, J. D. (2007). Pathological hormone
683 imbalances. *Current Opinion in Plant Biology*, 10(4), 372-379.
- 684 Romero-Aranda, R., Soria, T., & Cuartero, J. (2001). Tomato plant-water uptake and plant-water
685 relationships under saline growth conditions. *Plant Science*, 160(2), 265-272.
- 686 Rostami, E., Madadi, H., Abbasipour, H., Allahyari, H., & Cuthbertson, A. G. (2020). Pest
687 density influences on tomato pigment contents: the South American tomato pinworm
688 scenario. *Entomologia Generalis*, 41(2).

689 Royer, M., Larbat, R., Le Bot, J., Adamowicz, S., & Robin, C. (2013). Is the C: N ratio a reliable
690 indicator of C allocation to primary and defence-related metabolisms in tomato?
691 *Phytochemistry*, 88, 25-33.

692 Ryan, C. A. (2000). The systemin signaling pathway: differential activation of plant defensive
693 genes. *Biochimica et Biophysica Acta (BBA)-Protein Structure and Molecular Enzymology*,
694 1477(1-2), 112-121.

695 Sabelis, M. W., Janssen, A., & Kant, M. R. (2001). The enemy of my enemy is my ally. *Science*,
696 291(5511), 2104-2105.

697 Salehi, Z., Yarahmadi, F., Rasekh, A., & Sohani, N. Z. (2016). Functional responses of *Orius*
698 *albidipennis* Reuter (Hemiptera, Anthocoridae) to *Tuta absoluta* Meyrick (Lepidoptera,
699 Gelechiidae) on two tomato cultivars with different leaf morphological characteristics.
700 *Entomologia Generalis*, 36(2), 127-136.

701 Santamaria, M. E., Arnaiz, A., Gonzalez-Melendi, P., Martinez, M., & Diaz, I. (2018). Plant
702 perception and short-term responses to phytophagous insects and mites. *International journal*
703 *of molecular sciences*, 19(5), 1356.

704 Sarmiento, R. A., Lemos, F., Bleeker, P. M., Schuurink, R. C., Pallini, A., Oliveira, M. G. A., ...
705 & Janssen, A. (2011). A herbivore that manipulates plant defence. *Ecology letters*, 14(3), 229-
706 236.

707 Shehzad, M., Gulzar, A., Staley, J. T., & Tariq, M. (2020). The effects of drought stress and type
708 of fertiliser on generalist and specialist herbivores and their natural enemies. *Annals of*
709 *Applied Biology*, 178 (2), 377-386.

710 Siah, A., Magnin-Robert, M., Randoux, B., Choma, C., Rivière, C., Halama, P., & Reignault, P.
711 (2018). Natural agents inducing plant resistance against pests and diseases. In *Natural*
712 *Antimicrobial Agents*, Springer, Cham, (pp. 121-159).

713 Singh, I. K., & Singh, A. (Eds.). (2021). Plant-pest Interactions: From Molecular Mechanisms to
714 Chemical Ecology. *Springer*.

715 Snoeren, T. A. L., Sitbon, E., & Levy, D. (2017). U.S. *Patent No.* 9,644,242. Washington, DC:
716 U.S. Patent and Trademark Office.

717 Stahl, E., Hilfiker, O., & Reymond, P. (2018). Plant–arthropod interactions: who is the winner?.
718 *The Plant Journal*, 93(4), 703-728.

719 Stam, J. M., Kroes, A., Li, Y., Gols, R., van Loon, J. J., Poelman, E. H., & Dicke, M. (2014).
720 Plant interactions with multiple insect herbivores: from community to genes. *Annual Review*
721 *of Plant Biology*, 65, 689-713.

722 Stout, M. J., Fidantsef, A. L., Duffey, S. S., & Bostock, R. M. (1999). Signal interactions in
723 pathogen and insect attack: systemic plant-mediated interactions between pathogens and
724 herbivores of the tomato, *Lycopersicon esculentum*. *Physiological and Molecular Plant*
725 *Pathology*, 54(3-4), 115-130.

726 Stout, M. J., Workman, K. V., Bostock, R. M., & Duffey, S. S. (1998). Stimulation and
727 attenuation of induced resistance by elicitors and inhibitors of chemical induction in tomato
728 (*Lycopersicon esculentum*) foliage. *Entomologia Experimentalis et Applicata*, 86(3), 267-279.

729 Sung, J., Lee, S., Lee, Y., Ha, S., Song, B., Kim, T., ... & Krishnan, H. B. (2015). Metabolomic
730 profiling from leaves and roots of tomato (*Solanum lycopersicum* L.) plants grown under
731 nitrogen, phosphorus or potassium-deficient condition. *Plant Science*, 241, 55-64.

732 Teklić, T., Parađiković, N., Špoljarević, M., Zeljković, S., Lončarić, Z., & Lisjak, M. (2020).
733 Linking abiotic stress, plant metabolites, biostimulants and functional food. *Annals of Applied*
734 *Biology*, 178 (2), 169-191.

735 Thaler, J. S., Farag, M. A., Paré, P. W., & Dicke, M. (2002). Jasmonate-deficient plants have
736 reduced direct and indirect defences against herbivores. *Ecology Letters*, 5(6), 764-774.

737 Tian, D., Tooker, J., Peiffer, M., Chung, S. H., & Felton, G. W. (2012). Role of trichomes in
738 defense against herbivores: comparison of herbivore response to woolly and hairless trichome
739 mutants in tomato (*Solanum lycopersicum*). *Planta*, 236(4), 1053-1066.

740 Ton, J., Flors, V., & Mauch-Mani, B. (2009). The multifaceted role of ABA in disease
741 resistance. *Trends in Plant Science*, 14(6), 310-317.

742 Trejo-Escobar, D., Valencia-Flórez, L., Mejía-España, D., & Hurtado, A. (2019, October).
743 Influence of Fertilization on Glycoalkaloid Content in Four Potato Genotypes (*Solanum*
744 *Tuberosum*). In *2019 7th International Engineering, Sciences and Technology Conference*
745 *(IESTEC)* (pp. 36-39). IEEE.

746 Turlings, T. C., & Erb, M. (2018). Tritrophic interactions mediated by herbivore-induced plant
747 volatiles: mechanisms, ecological relevance, and application potential. *Annual Review of*
748 *Entomology*, 63, 433-452.

749 Turner, J. G., Ellis, C., & Devoto, A. (2002). The jasmonate signal pathway. *The Plant Cell*,
750 14(suppl 1), S153-S164.

751 Wang, F., Park, Y. L., & Gutensohn, M. (2021). Glandular trichome-derived mono-and
752 sesquiterpenes of tomato have contrasting roles in the interaction with the potato aphid
753 *Macrosiphum euphorbiae*. *Journal of Chemical Ecology*, 1-11.

754 Wheeler Jr, A. G., & Krimmel, B. A. (2015). Mirid (Hemiptera: Heteroptera) specialists of
755 sticky plants: adaptations, interactions, and ecological implications. *Annual Review of*
756 *Entomology*, 60, 393-414.

757 Wink, M. (2008). Plant secondary metabolism: diversity, function and its evolution. *Natural*
758 *Product Communications*, 3(8), 1934578X0800300801.

759 Wittstock, U., & Gershenzon, J. (2002). Constitutive plant toxins and their role in defense
760 against herbivores and pathogens. *Current Opinion in Plant Biology*, 5(4), 300-307.

761 Yang, F., Zhang, Q., Yao, Q., Chen, G., Tong, H., Zhang, J., ... & Zhang, Y. (2020). Direct and
762 indirect plant defenses induced by (Z)-3-hexenol in tomato against whitefly attack. *Journal of*
763 *Pest Science*, 93, 1243-1254.

764 Yousaf, H. K., Shan, T., Chen, X., Ma, K., Shi, X., Desneux, N., ... & Gao, X. (2018). Impact of
765 the secondary plant metabolite Cucurbitacin B on the demographical traits of the melon aphid,
766 *Aphis gossypii*. *Scientific Reports*, 8(1), 1-10.

767 Zarate, S. I., Kempema, L. A., & Walling, L. L. (2007). Silverleaf whitefly induces salicylic acid
768 defenses and suppresses effectual jasmonic acid defenses. *Plant Physiology*, 143(2), 866-875.

769 Zhang, J., Khan, S. A., Hasse, C., Ruf, S., Heckel, D. G., & Bock, R. (2015). Full crop protection
770 from an insect pest by expression of long double-stranded RNAs in plastids. *Science*,
771 347(6225), 991-994.

772 Zhang, P. J., Wei, J. N., Zhao, C., Zhang, Y. F., Li, C. Y., Liu, S. S., ... & Turlings, T. C. (2019).
773 Airborne host-plant manipulation by whiteflies via an inducible blend of plant volatiles.
774 *Proceedings of the National Academy of Sciences*, 116(15), 7387-7396.

775 Zhou, S., Lou, Y. R., Tzin, V., & Jander, G. (2015). Alteration of plant primary metabolism in
776 response to insect herbivory. *Plant Physiology*, 169(3), 1488-1498.

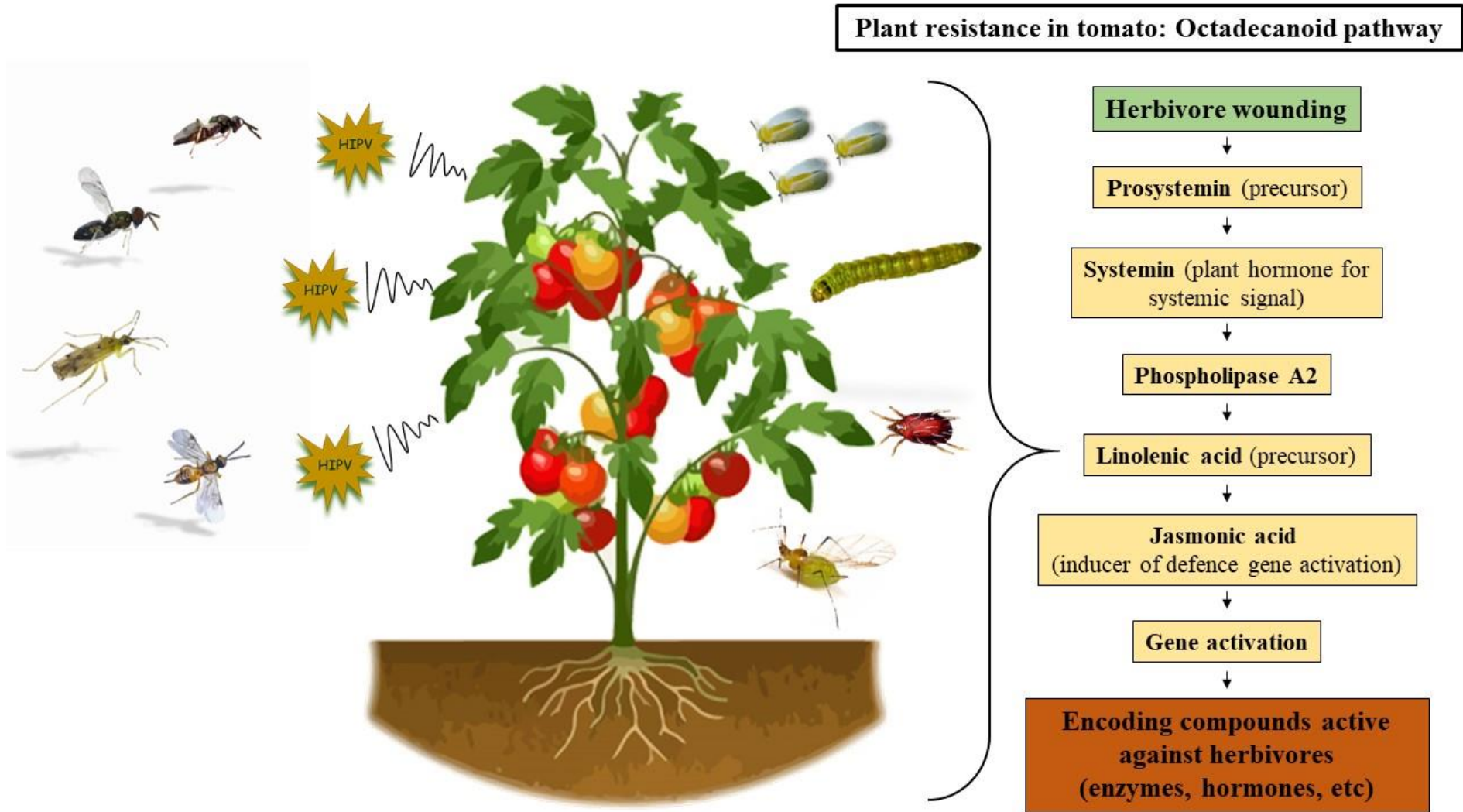
777 **Figure legends**

778

779 **Fig. 1.** Resistance mechanisms of tomato plants induced by its main herbivores involving
780 volatile compounds (Herbivore-Induced Plant Volatiles: HIPVs) and the response of natural
781 enemies as well as the chemical pathway to encoding active compounds against insects
782 (enzymes, hormones, etc)

783 Fig. 1

784



785

786