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

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3

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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)- $\beta$ -  
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),  $\beta$ -  
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



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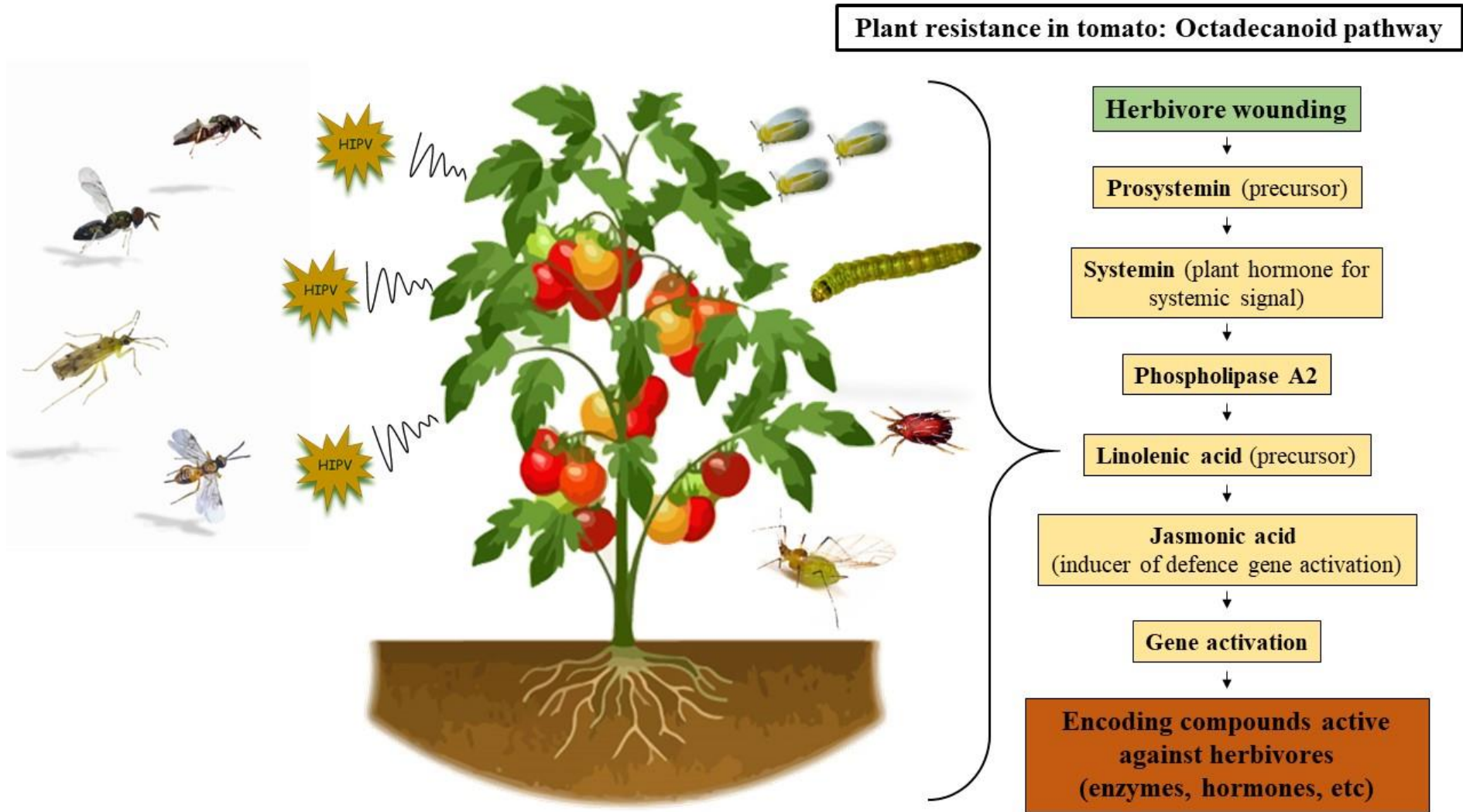
777 **Figure legends**

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

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