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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)- 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

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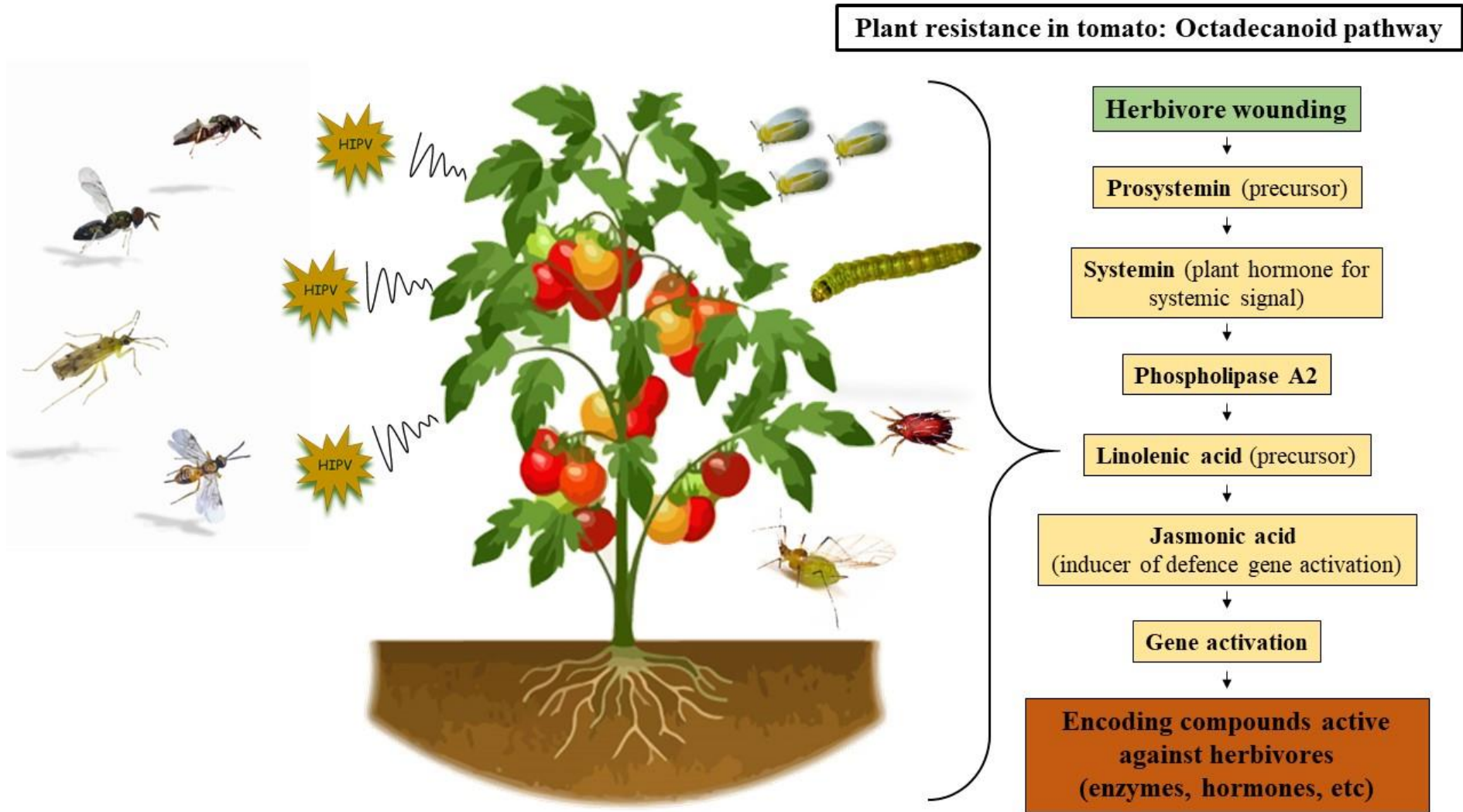
777 **Figure legends**

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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