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**Bottom-up effects of irrigation, fertilization and plant resistant traits  
on *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae): implications  
for integrated pest management**

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1 **Abstract:** Soil abiotic factors and plant traits are able to trigger bottom-up effects  
2 along the tri-trophic interaction plant—herbivore—natural enemy. The consequences  
3 could be useful for controlling the insect herbivores. The South American tomato  
4 pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), a devastating invasive  
5 pest on tomato and other Solanaceae plants, is currently threatening the tomato  
6 production worldwide. Recent knowledge on bottom-up effects on this pest has been  
7 gained, with fertilization, irrigation, plant traits, as well as their interactions being the  
8 major sources of these effects. Evidence is now emerging on how they impact on the  
9 performances of the moth from the perspective of tri-trophic interactions. In this  
10 review, we summarize the essential experiments studying the bottom-up effects on *T.*  
11 *absoluta* and discuss the implications of those findings for the integrated pest  
12 management programs. Future promising research directions are then proposed.

13

14 **Key words:** plant chemical defense; plant adaptation/tolerance; tri-trophic  
15 interactions; breeding; plastid genome transformation; agro-ecosystems

16

17 **Key message:**

- 18  $\Sigma$  The devastating invasive pest, *Tuta absoluta* (Meyrick) (Lepidoptera:  
19 Gelechiidae), is likely to be controlled by diverse bottom-up effects via  
20 manipulation of soil abiotic factors and plant traits.
- 21  $\Sigma$  Resource input manipulations, such as fertilization and irrigation, have great  
22 potential to be included in the Integrated Pest Management (IPM) package, but  
23 more studies are needed to test **such** effects at larger scales.
- 24  $\Sigma$  Enhanced plant resistance, being either intrinsic, induced or genetically-modified,  
25 are useful components of IPM.

26

27

28 **Author contribution:**

29 PH, ND and AVL conceived the manuscript. All authors wrote the manuscript. All  
30 authors read and approved the manuscript.

31

32 **Introduction**

33

34 Plants are the primary producers in most terrestrial ecosystems, where they embody  
35 the basis of the food webs, insects being a dominant group among plant consumers.  
36 Thus, plant-insect interactions have long been the central subject for understanding  
37 insect and plant community structure and dynamics (Bruce 2015). Herbivorous insects  
38 rely on the consumption of plant materials to obtain water and nutrients for their  
39 survival and development, but in the meantime they have to cope with plant chemical  
40 and physical defenses (Schoonhoven et al. 2005). Furthermore, changing abiotic  
41 conditions alter the plant nutritional and defensive profiles, which may trigger cascade  
42 effects on organisms from higher trophic levels, including herbivorous insects and  
43 their natural enemies: the so-called “bottom-up” effects (Hunter and Price 1992;  
44 Denno et al. 2002). Over the last decade, recent knowledge has been gained on this  
45 subject, indicating a potentially high application value of such effects for managing  
46 insect pests in agro-ecosystems (Chen et al. 2010; Han et al. 2014; Becker et al. 2015;  
47 Han et al. 2015; Zhong et al. 2017). Invasive alien insect pests are often armed with  
48 competitive biological traits such as a high growth rate and reproduction potential that  
49 makes them especially difficult to manage (Hufbauer and Torchin 2007). We believe  
50 that bottom-up effects are an essential and effective component of successful  
51 Integrated Pest Management (IPM) programs against invasive pests.  
52 The South American tomato pinworm, *Tuta absoluta* (Meyrick, 1917) (Lepidoptera:  
53 Gelechiidae), originated from South America, is a devastating pest on tomato and

54 other Solanaceous plants (Desneux et al. 2010). Since its first detection outside its  
55 native areas, in Spain in 2006, *T. absoluta* has rapidly spread across Europe, Africa,  
56 middle-East and Central Asia in the following years, considerably threatening the  
57 tomato industry worldwide (Desneux et al. 2011; Campos et al. 2017; Xian et al.  
58 2017). Many attempts have been made to combat this pest. Chemical control was the  
59 first option. It proved efficient, but high resistance to various insecticide classes in this  
60 moth was recently emerged (Campos et al. 2014, 2015; Silva et al. 2016; Roidakis et  
61 al. 2017; 2018). The methods preventing pest mating, including male annihilation  
62 and/or mating disruption by using synthetic pheromones, have been shown effective  
63 (Vacas et al. 2011; Cocco et al. 2013), but the emerging evidence of deuterotokous  
64 parthenogenesis in *T. absoluta* might compromise their efficacy (Caparros Megido et  
65 al. 2012). Biological control has been implemented widely using indigenous natural  
66 enemies (Zappala et al. 2013) and is currently the most promising component of the  
67 IPM package. However, the efficacy of natural enemies in suppressing *T. absoluta*  
68 populations may be altered by environmental abiotic factors through bottom-up  
69 effects triggered by agronomic practices such as irrigation and fertilization. Moreover,  
70 plant constitutive and/or induced resistance traits against *T. absoluta* are another  
71 source of bottom-up effects, which may interact with irrigation and fertilization and  
72 jointly affect the performance of *T. absoluta*, counterpart natural enemies and their  
73 interactions.

74 In recent years, there has been a growing body of literatures reporting on how bottom-  
75 up effects take place and how the association of diverse fields - plant ecophysiology -

76 chemical ecology and behavioral ecology- may help to understand the underlying  
77 mechanisms (Chen et al. 2010; Han et al. 2014, 2015, 2016; Becker et al. 2015;  
78 Larbat et al. 2016; Coqueret et al. 2017; Dong et al. 2017). The knowledge gained  
79 from those studies is a good starting point and should encourage future research  
80 efforts. Therefore, we provide a timely review on the empirical studies addressing  
81 bottom-up effects of fertilization, irrigation and plant resistant traits on *T. absoluta*.  
82 The implications of bottom-up effects for the integrated pest management and future  
83 research directions are discussed.

84

## 85 **Bottom-up effects of fertilization and irrigation**

86

### 87 *Irrigation*

88

89 Water, in terms of quantity as well as quality, is an important abiotic factor able to  
90 influence the interactions between plants and herbivorous insects. In the global  
91 change context, water consumption by agricultural systems has to be optimized.  
92 Especially dry regions like the Mediterranean Basin face the challenge of reducing the  
93 quantity of water used for food production while, at the same time, maintaining  
94 economically sustainable yields. Salinity is another major environmental issue and a  
95 substantial constraint to plant growth (Debouba et al 2006). Sodium chloride (NaCl) is  
96 one of the most common components in soil or irrigation water, causing salinity stress  
97 in plants (Mahajan & Tuteja 2005). Unlike in natural ecosystems such as salt marshes  
98 where many species have evolved to tolerate high salinity (Parida & Das 2005), crops

99 and particularly tomatoes are not very tolerant to salinity (Greenway & Munns  
100 1980). They embody the important greenhouse crops in many semi-arid regions where  
101 salinity in soil and groundwater constitutes a major issue in crop production (Cuartero  
102 & Fernandez-Munoz, 1999). It has been shown that the quantity and the quality of  
103 water inputs are able to impact the second trophic level, including the herbivorous *T.*  
104 *absoluta*, through plant-mediated effects as well as the third trophic level, including *T.*  
105 *absoluta* natural enemies (Han *et al* 2014, 2015b, 2016a).

106

107 Leaf miners develop very intimate relationships with their host plants since the larvae  
108 penetrate and feed within the tissues and are therefore considered highly relevant to  
109 test plant-mediated bottom-up effect of water inputs (Inbar 2001). Recent studies have  
110 demonstrated that water input variations can significantly affect *T. absoluta* biological  
111 traits (Han *et al* 2014, 2016a): water limitation reduced the survival as well as the  
112 pupal weight and slowed down the larval development (Han *et al* 2014, 2016a) (See  
113 Figure 1). This supports the “plant vigor hypothesis” (Price 1991), since *T. absoluta*  
114 survived better and developed faster on tomato plants with a better growth status (Han  
115 *et al* 2014). Yet, the net effect of water-limitation on the host plant and thus the  
116 herbivore strongly depends on the frequency and severity of water limitation (Huberty  
117 & Denno, 2004).

118 Which physiological changes in the host plants could explain the effects on  
119 *T. absoluta* biological traits? Varying water availability may change plant nutritional  
120 quality and chemical defenses both of which can affect the performance of insect

121 herbivores (Gutbrodt et al 2011, Tariq et al 2012) (Fig 1). (i) Plant water content is  
122 generally a useful index of its nutritional value for many lepidopterous larvae  
123 (Schoonhoven 2005). Han *et al* (2014) suggested that *T. absoluta* larvae's difficulties  
124 to obtain enough water explain their decelerated development. Water not only acts as  
125 an indispensable prerequisite for herbivore metabolism, facilitating efficient nutrient  
126 utilization (Scriber, 1977), its limitation furthermore decreases the nitrogen  
127 availability for herbivores by decreasing plant nitrogen and protein contents  
128 (Ximénez-Embún et al., 2016). Accordingly, there are reports showing that water-  
129 limited and/or wilted foliage is more difficult to digest (Slansky & Scriber 1985,  
130 Gutbrodt 2011) than turgid foliage. (ii) Water limitation can alter the regular level of  
131 plant chemical defense, leading to either enhanced or reduced resistance to herbivores  
132 (Inbar 2001, Gutbrodt 2011). Han *et al* (2016a) observed that the concentration of leaf  
133 glycoalkaloids increased in tomato plants subjected to water limitation, accompanied  
134 by negative indirect effects on *T. absoluta* survival and development. So far, however,  
135 the toxicity of these compounds is not known for *T. absoluta*.

136

137 Salinity can also trigger bottom-up effects on *T. absoluta* (Han *et al* 2016b): adding  
138 salt to the plant's nutrient solution shortened the pest development time but did not  
139 reduce the pupal mass although insects have the faculty to pupate with a lower body  
140 mass under adverse conditions like reduced host plant quality. At least three different  
141 mechanisms could explain that salinity has deleterious effects on herbivorous insects:  
142 (i) Increasing salt concentration in the irrigation water raises the osmotic potential

143 and, thus, decreases plant water availability (Soria & Cuartero 1997, Romero-Aranda  
144 & Cuartero 2001). Similar to drought, salinity stress can thus affect *T. absoluta*  
145 development by reducing larva water availability ; (ii) salinity stress can also lead to  
146 excessive accumulation of Na<sup>+</sup> and Cl<sup>-</sup> ions in leaves (Manaa et al 2011), which  
147 lowers leaf dietary quality for *T. absoluta* larvae ; (iii) furthermore, elevated soil  
148 salinity may induce changes in plant secondary metabolism, *i.e.* plant chemical  
149 defense (Ballhorn & Elias, 2014). Although Han *et al* (2016b) did not observe any  
150 correlations between the concentration of leaf glycoalkaloids and the development of  
151 *T. absoluta*, other defense compounds in tomato leaves may increase in response to  
152 high salinity: phenolic compounds, for instance, have been observed to accumulate in  
153 tomato fruits (Flores *et al* 2015) and might respond similarly in leaves. The possible  
154 negative effects of these three mechanisms on insect development may, to some  
155 degree, be counterbalanced by higher concentrations of amino acids due to higher  
156 proteolytic activities in salt-stressed tomato leaves (Debouba et al 2016). This may  
157 explain why *T. absoluta* managed to reach a normal pupal mass after a reduced larval  
158 development time on NaCl stressed plants (Han *et al* 2016b). It is assumed that larvae  
159 have the potential to adapt their feeding strategy, spending less time for larval  
160 development to cope with salinity stress.

161

162 *Fertilization*

163

164 Fertilization is required to preserve soil fertility of cultivated fields and to maintain

165 crop productivity. Nitrogen is one of the key macro-elements that impacts plant  
166 quality, both in terms of nutritional value and defensive profile and thus triggers  
167 bottom-up effects on herbivore insect performances. Many studies have shown that *T.*  
168 *absoluta* larvae feeding on tomato plants grown with low nitrogen inputs, had reduced  
169 survival rates and delayed development (Han et al. 2014; Han et al. 2016; Larbat et al.  
170 2016; Coqueret et al. 2017; Dong et al. 2017; Blazhevski et al. 2018). This has been  
171 ascribed to the low protein content (higher foliar C/N ratio as well) and enhanced  
172 accumulation of constitutive phenolics and glyco-alkaloids in the leaves (Han et al.  
173 2016; Larbat et al. 2016). Such alterations in plant chemical profile are consistent with  
174 previous studies (Inbar et al. 2001; Le Bot et al. 2009; Royer et al. 2013). All these  
175 findings support the *nitrogen limitation* hypothesis (White 1993) (See figure 1)  
176 especially in the case of Lepidopteran insects.

177 Potassium is another macro nutrient able to mediate bottom-up effects on *T. absoluta*.  
178 Sung *et al* (2015) found that the metabolite profile of K-deficient tomato leaves was  
179 characterized by an increased concentration of soluble sugars and a general decrease  
180 in most amino acids, except for arginine, glutamine, proline and citrulline. Whether or  
181 not K-limitation affects tomato defense compounds is not well studied: to our  
182 knowledge, there is only one publication so far, investigating the effect on fruit  
183 composition (Flores *et al* 2015). The authors found that a low K-level caused variable  
184 but strong cultivar-dependent effects, increasing chlorogenic acid concentration while  
185 decreasing or unaffected that of rutin and other phenolic compounds in one of two  
186 studied cultivars. In the model plant *Arabidopsis thaliana* potassium-limitation led to

187 the accumulation of plant defense compounds like glucosinolates and an overall  
188 increased defense against leaf chewers by interfering with the jasmonic acid-mediated  
189 signaling pathway (Amtmann *et al* 2008). The consequently possible bottom-up  
190 effects on *T. absoluta* have received very little attention so far. Leite *et al* (2004)  
191 found no effect of tomato leaf K content on *T. absoluta* preference or performance,  
192 measured as oviposition events and number of mines. Similarly, Blazhevski *et al*  
193 (2018) detected almost no effect of reduced tomato leaf K on *T. absoluta* life history  
194 traits. The only significant effects were that reduced K retarded larval development  
195 and slightly decreased the intrinsic rate of population development. Yet, the  
196 mechanisms are unclear.

197

#### 198 **Bottom-up effects of plant resistant traits**

199

200 *Tuta absoluta* has reached the economic pest status and is now considered as a key  
201 pest on tomato crops (Desneux *et al* 2011; Campos *et al* 2017). This status explains  
202 why the main research on plant resistant traits against *T. absoluta* has focused on  
203 tomato. However, we must keep in mind that the plant host range of *T. absoluta* is  
204 broader as it is able to develop on many Solanaceous species, tomato, potato and  
205 European black nightshade (*Solanum nigrum*) being the most suitable (Abbes *et al*  
206 2016, Desneux *et al* 2010, Biondi *et al* 2018). It can also oviposit and develop on  
207 several plants belonging to the Amaranthaceae, Convolvulaceae, Fabaceae and  
208 Malvaceae families (Bawin *et al* 2016). Studying this broader plant host range might

209 bring innovations in the search of resistant plants against *T. absoluta*.

210 Cultivated tomatoes (*S. lycopersicum*) are generally highly susceptible to *T. absoluta*,  
211 and recent tomato population screenings identified only moderately resistant cultivars  
212 (Gharekhani and Salek-Ebrahimi, 2014; Rostami et al., 2017; Sohrabi et al., 2016,  
213 2017). Most plant resistant traits to *T. absoluta* have been identified in wild tomato  
214 relatives. Resistant traits may be multiple, integrating resistance by antixenosis and  
215 antibiosis (Gharekhani and Salek-Ebrahimi, 2014). They are categorized as either  
216 constitutive resistance (naturally present in the plant before infestation), induced  
217 resistance by the presence of *T. absoluta* on the plant or introduced resistance via  
218 genetic modification.

219

220 *Constitutive resistance traits* - In wild tomato species, plant resistant traits to *T.*  
221 *absoluta* are mainly related to the type and density of leaf trichomes (Fernandes et al.  
222 2012; Sohrabi et al. 2016, 2017) and the compounds produced and stored inside. Both  
223 provide a constitutive protection against the leafminer since contact with the leaf is a  
224 key component for inducing *T. absoluta* oviposition (Proffit et al 2011). Three main  
225 chemical classes have been identified, methyl-ketones (notably 2-tridecanone; Maluf  
226 et al., 1997), sesquiterpenes (notably zingiberene; Azevedo et al., 2003, Bleeker et al  
227 2012) and acyl sugars (Resende et al., 2006). The former two are abundant in *S.*  
228 *habrochaites* (previously referred as *L. hirsutum*) whereas the latter is present in *S.*  
229 *pennellii*. The resistance assessment of descendants from interspecific crossing  
230 between *S. lycopersicum* and *S. habrochaites* on the one hand and *S. lycopersicum* and

231 *S. pennellii* on the other hand, led to the conclusion that each chemical class mediates  
232 *T. absoluta* resistance through both antixenosis and antibiosis: the compounds  
233 mentioned above impair egg laying and larval feeding, leading to antixenosis or larval  
234 toxicity, leading to antibiosis (Bleeker et al 2012; de Azevedo et al 2003; Resende et  
235 al 2006). In addition, genotypes exhibiting high contents in both zingiberene and acyl  
236 sugars, showed greater resistance than genotypes accumulating only one of these  
237 chemical, indicating a synergistic effect between zingiberene and acyl sugars (Maluf  
238 et al., 2010). Despite the demonstration of higher resistance of these interspecific  
239 hybrids, no commercial line has been released, yet. This is probably due to both the  
240 distance separating *S. lycopersicum* from those two wild tomato species and the fact  
241 that resistance transfer from these species is accompanied by other gene introgression  
242 mediating poor horticultural value (Rakha Mohamed et al., 2017).

243 [Studies on wild tomato close to \*S. lycopersicum\*, i.e. \*S. galapagense\*, \*S. cheesmaniae\* and \*S.\*](#)  
244 [pimpinellifolium](#) highlighted also resistant traits to *T. absoluta* (Rakha Mohamed et al., 2017).

245 [These species as well have a high density of glandular trichomes secreting acyl sugars and](#)  
246 [sesquiterpenes and it may be expected that their resistance to \*T. absoluta\* is linked to these traits.](#)

247 [Due to a shorter distance between these species and the domesticated tomato, the objective of](#)  
248 [breeders to obtain \*S. lycopersicum\* lines resistant to \*T. absoluta\* may be easier to achieve. Indeed,](#)  
249 [a first patent for commercial tomato lines resistant to arthropods including the leaf](#)  
250 [miner has already been published \(Snoeren et al. 2014, US Patent US 20140283191](#)  
251 [A1 US2017/0240910 A1\). These lines have been obtained through introgressed DNA](#)  
252 [sequences from \*S. galapagense\*. The patent encompasses 12 single nucleotide](#)

253 polymorphisms (SNP) displayed on several chromosomes of the *S. lycopersicum*  
254 genome that confer resistance and or tolerance to *T. absoluta*, white fly (*Bemisia*  
255 *tabaci*) and spider mite (*Tetranychus urticae*). This indicates that the commercial  
256 development of *T. absoluta* resistant tomato cultivars is underway.

257

258 *Induced resistant traits* - Upon infestation by *T. absoluta*, tomato plants are able to  
259 develop inducible resistance mechanisms that are mainly produced through the  
260 jasmonic acid pathway. These resistance mechanisms involve indirect defense *via*  
261 modified volatile organic compound (VOC) blends emitted by infested plants  
262 (Strapasson et al., 2014; Backer et al., 2015; Silva et al., 2017). Some of these VOCs  
263 are known to attract *T. absoluta* natural enemies belonging to the Miridae family, like  
264 *Macrolophus pygmaeus* (De Backer et al 2015), *M. basicornis*, *Engytatus varians* and  
265 *Campyloneuropsis infumatus* (Naselli et al 2017; Backer et al., 2017; Silva et al.,  
266 2018). Modification of the VOC blend might also alter host-plant attractiveness as  
267 plant volatiles are involved in *T. absoluta* orientation toward its host plants (Proffit et  
268 al 2011). In addition, plant resistance induction could promote the direct expression of  
269 defensive allelochemicals. Indeed, Coqueret et al. (2017, supplementary data)  
270 highlighted recently that a few hours after the onset of larval feeding, tomato plants  
271 induce the accumulation of defensive enzymes (polyphenol oxidase, PPO; Peroxidase,  
272 POD) at the feeding site and in distant organs. Such inducible defense provides good  
273 opportunities for new breeding strategies to obtain tomato lines (i) emitting higher  
274 amounts of selected VOCs able to increase plant attractiveness to pest natural enemies

275 or (ii) inducing a strong enzymatic defense.

276

277 *Introduced plant resistance* - Another aspect of resistance can be gained by genetic  
278 modifications. For instance, expression of insecticidal proteins like *Bt* (*Bacillus*  
279 *thuringiensis*) can be incorporated into the tomato genome (Bergougnoux 2014;  
280 Selale et al. 2017). In the latter study, introduction of the *cry1Ac* gene to the tomato  
281 genome was achieved and a single copy of the gene in the hemizygous condition was  
282 sufficient to confer tolerance to *T. absoluta*. Development of transgenic *Bt* tomato  
283 lines may have great potential for area-wide adoption in both greenhouses and open  
284 fields. Such technology may promote pest management in agro-ecosystems, as  
285 documented in the case of *Bt* cotton (Lu et al. 2012).

286 RNA interference (RNAi) technology may also play an important role in tomato  
287 genetic transformation aimed at resistance to *T. absoluta*. RNAi is a mechanism for  
288 post-transcriptional gene silencing conserved in most eukaryotes and has proven to be  
289 a powerful tool for gene function studies. RNAi can also be applied for pest control: if  
290 the sequences of double-stranded RNA (dsRNA), the trigger of RNAi, target essential  
291 genes of insects, it provokes the endogenous RNAi machinery of pest, thus result in  
292 the silencing of these genes which leads to impaired growth and even death of pest.  
293 Over the past decade, RNAi-mediated pest control has emerged as an important  
294 alternative alongside *Bt*-based strategies (Zhang et al. 2017). Although transgenic  
295 plants expressing dsRNA targeted against insect genes can impair pest growth and  
296 development, efficient control of insects and complete protection of plants were only

297 recently achieved by plastid-mediated RNAi technology (Zhang et al. 2015). Because  
298 plastids of plant cells do not have an RNAi pathway and because the number of copies  
299 of plastid genome is extremely high, 1,000 - 2,000 copies of the plastid genome in a  
300 typical leaf mesophyll cell (Bock 2014), long dsRNAs in transplastomic (plastid  
301 genome transformed) potato plants can be stably accumulated, reaching up to 0.4% of  
302 total cellular RNA, being at least two orders of magnitude higher than that of nuclear-  
303 transformed plants.

304 Whether or not *T. absoluta* can be controlled by this approach remains to be  
305 investigated. Recently, the transcriptome data showed that most of the core genes of  
306 RNAi pathway such as Dicer-like and Argonaute and putative orthologous Sid-1  
307 genes are present in *T. absoluta*, suggesting the feasibility of RNAi for controlling this  
308 pest (Camargo et al. 2015). The application of RNAi has recently been shown as a  
309 promising approach for controlling *T. absoluta*: by targeting against *Vacuolar ATPase-*  
310 *A* and *Arginine Kinase* genes of *T. absoluta*, feeding tomato leaflet uptaking *in vitro*  
311 synthetic dsRNA or transgenic plants expressing dsRNA to 1st instar larvae led to  
312 significant knock-down of targeted genes and reduced growth of *T. absoluta*.

313 However, full plant protection and high larval mortality of *T. absoluta* have not been  
314 achieved probably due to a low expression of dsRNA in transgenic plants (Camargo et  
315 al. 2016). As a plastid transformation protocol for tomato plants has been well  
316 established (Ruf et al. 2001), it would be workable to express long dsRNA in plastids  
317 targeting *T. absoluta* to enhance the resistant levels of tomato plants.

318

319 **Implications for IPM**

320

321 Manipulating irrigation and fertilization inputs seems to offer promising agronomic  
322 leverage for IPM packages against *T. absoluta* that are based on bottom-up effects  
323 (Han et al. 2014; 2016). In these studies, however, the impacts on fruit yield and  
324 quality have not been considered, which refrains us from drawing the definite  
325 conclusion that low nitrogen and water input are valuable to improve the management  
326 of *T. absoluta*. We propose, therefore, that future research efforts should attempt to  
327 trade off a part of crop yield for a gain in pest management. There are great potentials  
328 for reducing fertilizers and water inputs in greenhouse productions (Le Bot et al.  
329 1998; Le Bot and Adamowicz, 2005) suggesting that we may be on the way to  
330 develop a win-win situation, strengthening pest management while gaining important  
331 ecological and economic benefits.

332

333 Modern crop cultivars often display a diversity of tolerance to sub-optimal abiotic  
334 environments (Ballhorn et al. 2011). For instance, some crop cultivars have been  
335 deliberately selected to withstand various environmental stresses, such as nitrogen  
336 deficiency (Feng et al. 2010) or drought (Cattivelli et al. 2008). One of our recent  
337 studies show, surprisingly, that the negative bottom-up effects of limited nitrogen and  
338 water inputs can cascade up to *T. absoluta* even though the tomato cultivars exhibited  
339 various adaptive or tolerance traits to those resource limitations (Han et al. 2016). In  
340 other words, the use of resistant cultivars may “kill two birds with one stone”, *i.e.* by

341 preserving the negative bottom-up effects of limited resources on the herbivorous  
342 insects while allowing the cultivars to cope with sub-optimal conditions. This finding  
343 would not only apply to low-input farming systems, but also benefit pest control on  
344 cultivars grown in arid areas or semi-barren lands around the world, *e.g.*, drought-  
345 prone environments (Farooq et al. 2009).

346

347 Bottom-up effects of irrigation, fertilization and/or plant resistance traits may cascade  
348 up onto the organisms from higher trophic levels (*e.g.* arthropod natural enemies),  
349 thus favoring or compromising the pest control efficacy (*e.g.* “nitrogen” reviewed by  
350 Chen et al. 2010). In general, abiotic factors and plant resistance traits can trigger  
351 bottom-up effects on natural enemies either (a) directly via impacts on natural  
352 enemies foraging behavior or (b) indirectly via trophic cascade through their  
353 prey/host. A small number of studies investigated bottom-up effects reaching the third  
354 trophic level (Han et al 2015a, b; Dong et al 2017, Becker et al in prep). So far,  
355 however, the fourth trophic level has not been investigated (*e.g.* intraguild predation  
356 among natural enemies or hyperparasitism). Omnivorous predators, mainly  
357 Heteroptera species, *e.g.* *M. pygmaeus* and *Nesidicoris tenuis* are the most commonly  
358 used predators in biological control programs against *T. absoluta* (Zappala et al 2013;  
359 Biondi et al 2018). Similarly, the larval-parasitoid *Necremnus tutae* (Hymenoptera:  
360 Eulophidae) can be used in biocontrol strategies against *T. absoluta* (Calvo et al 2016,  
361 Naselli et al 2017). Both are often applied in greenhouses where resources availability  
362 can be easily manipulated.

363

364 *Bottom-up effects on predators* – Omnivorous predators acquire nutrients and energy  
365 from both host plants and insect prey (Janssen et al 2003). Their efficacy as biocontrol  
366 agents may vary with biotic and abiotic variables (Symondson et al 2002). Yet, little is  
367 known about possible plant-mediated bottom-up effects that can be triggered by  
368 manipulated resource availability and their impact on predators. Han *et al* (2015a)  
369 demonstrated the importance of water supply: highly irrigated plants attracted more  
370 *M. pygmaeus* adults than those receiving low water input. In another study, the same  
371 authors showed that water limitation decreased the feeding activity of *M. pygmaeus*,  
372 on prey as well as on host plants, reducing the predator's longevity by nearly 30%  
373 (Han *et al* 2015b). The positive correlation between the two feeding activities  
374 indicates a physiological link (*Facilitation hypothesis*, Gillepsie & McGregor 2000)  
375 (See Figure 1): omnivorous predators must feed on plant tissue to obtain the water  
376 required for key biological processes, for instance producing saliva needed for extra-  
377 oral digestion of prey (Cohen 1998, Sinia et al 2004). Han *et al* (2015b) assumed that  
378 water deficit in the plant tissue restricted *M. pygmaeus* ability to digest preyed eggs,  
379 which in turn decreased predator longevity. However, it is also possible that the  
380 simultaneous decrease in plant and prey feeding arose from elevated concentrations of  
381 defense compounds in plant tissues (Inbar et al 2001, Kaplan and Thaler 2011).  
382 According to the “*mother knows best*” hypothesis (Kohandani et al. 2017), mated  
383 females should avoid oviposition on water-stressed plants. However, another  
384 omnivorous predator species preferred to lay eggs on water-stressed plants but on

385 which nymphs failed to perform better (Seagraves et al. 2011). Regarding plant  
386 resistance, tomato cultivars with higher trichome densities were shown to reduce the  
387 predation rate of Hemipteran predatory bugs on *T. absoluta*, at odds with biological  
388 control (Salehi et al. 2016; Bottega et al. 2017).

389

390 *Bottom-up effects on parasitoids* - Plant water and nitrogen availability could trigger  
391 bottom-up effects on parasitic wasps and thereby alter the top-down control forces  
392 provided by parasitoids. The only two studies conducted on this topic, however, did  
393 not find strong effects of plant water or nitrogen supply on *N. tutae* (Becker *et al* in  
394 prep, Dong *et al* 2017), suggesting that this biocontrol agent would not suffer negative  
395 ecological consequences. Yet, in both studies, the number of parasitoid offspring  
396 showed a tendency to be sensitive to plant water limitation depending on plant  
397 nitrogen status, which should be taken into account when designing IPM packages  
398 comprising this biocontrol agent. Additionally, the slower development of *T. absoluta*  
399 on water-limited leaves (Han *et al* 2014) might result in higher parasitism rates  
400 because larvae remain for a longer time in the developmental stages preferred by the  
401 parasitoids, *i.e.* the second instar regarding *N. tutae* (Dong *et al* 2017). Large-scale  
402 long-term experiments should be interesting to investigate if the *slow-growth-high-*  
403 *mortality* hypothesis (Benrey & Denno 1997) applies in this scenario. In another  
404 experiment, humic fertilizer and vermicompost applied to the soil enhanced  
405 population growth parameters of a *Trichogramma* parasitoid species on eggs of *T.*  
406 *absoluta* (Mohamadi et al. 2017). This is puzzling as it is unlikely that the quality of

407 *T. absoluta* eggs be affected by tomato fertilization, and we may suggest that such  
408 experiment should be repeated while checking fertilization effects on tomato VOC  
409 emission and their effects on parasitoids.

410

411 Both parasitoids and predators use herbivory-induced plant volatiles (HIPV) to locate  
412 their host/prey – this interaction has become famous as the plants’ “cry for help”  
413 (Dicke *et al* 1989, Turlings *et al* 1990, Dicke and Baldwin 2010). Abiotic factors have  
414 the potential to change the quality and quantity of these HIPV blends (See Becker *et*  
415 *al* 2015 for a review). As a result, the “chemical communication” between plants and  
416 natural enemies might be disturbed if such changes render the “chemical messages”  
417 incomprehensible to the natural enemies. Alternatively, these changes might be of no  
418 consequence or even improve the communication, *e.g.* by adding information on the  
419 plant’s status. Yet, the consequences for biological control services remain heavily  
420 understudied. HIPV blends associated to feeding *T. absoluta* larvae contain higher  
421 proportions of  $\delta$ -selinene when emitted from water-limited compared to well-  
422 watered tomato leaves and higher proportions of the monoterpene  $\beta$ -myrcene when  
423 emitted from tomato leaves containing elevated compared to low leaf N (Becker *et al*  
424 *in prep*). These are very small changes and it is rather unlikely that it would affect  
425 communication with parasitoids or predators. Still, a negative impact on attraction and  
426 arrest cannot be excluded without behavioral assays on commercially important  
427 biocontrol agents. The manipulation of HIPV blends in order to optimize host/prey  
428 detection by natural enemies harbors a great potential to be exploited in future IPM

429 packages.

430

### 431 **Conclusions and future directions**

432

433 The evidence of bottom-up effects of fertilization, irrigation and plant resistant traits  
434 on *T. absoluta* has been shown. In practice, bottom-up effects might become an  
435 effective component of the IPM program against this pest. In order to verify this  
436 prognosis, knowledge about the ecological consequences of bottom-up effects on *T.*  
437 *absoluta* has to be expanded. Further studies considering tritrophic interactions are  
438 needed to draw convincing conclusions. Future investigations on the bottom-up  
439 effects would benefit from the following strategies.

#### 440 a) *Assessing the bottom-up effects on T. absoluta at larger-scale*

441 Most findings about plant-mediated bottom-up effects on *T. absoluta* have been  
442 obtained at an individual level using microcosms. Only a few studies focused on *T.*  
443 *absoluta* populations in greenhouses or in the open field (*e.g.* plant cultivar resistance:  
444 Sohrabi et al. 2016) whereas monitoring of population dynamics has been done on  
445 other insect pests such as whiteflies and beet armyworm (Bentz et al. 1995; Bi et al.  
446 2003; Chen et al. 2008). Experiments conducted on other insects clearly show that  
447 bottom-up effects studied on individuals do not consistently translate into population  
448 effects, suggesting that it is crucial to separate the effects acting on individuals from  
449 those acting on populations (Zaugg et al. 2013). Therefore, more research efforts are  
450 required on *T. absoluta* under greenhouse and/or field conditions in order to get

451 convincing conclusions (Han et al. in prep.). One should note that assessing the  
452 bottom-up effects of fertilization, irrigation and plant resistance in large-scale  
453 conditions is straightforward, but costly and labor consuming.

454

455 b) *Disentangling the role of plant phenotypic variations from the observed bottom-up*  
456 *effects*

457 Two aspects of plant phenotypic plasticity, *i.e.*, plant resistance to *T. absoluta* and  
458 plant tolerance and/or adaptation to abiotic stress, should be taken into account when  
459 designing experiments. Tomato cultivars adapted to resource limitation maintain their  
460 ability to mediate the effects of resource limitation on the pest (Han et al. 2016 a or  
461 b???) and this gives good grounds for studying further this interaction. Future  
462 experiments should thus be designed to include a wide range of tomato cultivars  
463 showing either adaption or resistance traits to allow for a concrete assessment on the  
464 role of those factors in bottom-up effects. This calls, therefore, for renewed  
465 collaborative interdisciplinary research bridging entomology, plant physiology and  
466 crop breeding.

467

468 c) *Identifying how the bottom-up effects influence the interspecific interactions*

469 Surprisingly little is known about how the invasive species *T. absoluta* interacts with  
470 endemic pest species that share the same micro-habitat and/or arthropod natural  
471 enemies. It remains unknown for instance, how *T. absoluta* initial presence affects the  
472 oviposition preference of the subsequent attacker *Helicoverpa armigera* on tomato

473 and its subsequent larval performance. Do the effects vary across contrasting levels of  
474 water/nitrogen inputs (*i.e.* bottom-up effects)? Answering these questions is required  
475 to predict the spatio-temporal pattern of field damages, where multiple pests coexist.  
476 Various chemical mechanisms are involved in species interactions, including  
477 herbivory-induced VOCs (Becker et al. 2015; De Backer et al. 2015; Silva et al. 2017)  
478 and/or plant defensive secondary compounds (Tan et al. 2012). Moreover, it is  
479 important to consider their common enemies among the arthropod community in  
480 order to clarify how bottom-up effects influence the indirect interactions among insect  
481 herbivores (Poelman and Dicke 2014; Stam et al. 2014).

482

483 d) *Breeding novel cultivars*

484 With the emergence of chemical insecticide and *Bt* resistances among insects, it  
485 becomes very urgent to develop new and alternative approaches for efficient pest  
486 control. Over the past decade, RNAi-mediated pest control has emerged as an  
487 important alternative alongside the *Bt*-based strategy (Zhang et al. 2017). Expression  
488 of long double-stranded RNAs against pest essential genes in plastids can reach a very  
489 high level and thus offer full crop protection that is both highly specific to target pests  
490 and environmentally-safe (Zhang et al. 2015). It would be an interesting challenge to  
491 investigate whether or not *T. absoluta* can be controlled by this promising approach.

492

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494

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497

498

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501

502

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504

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768 **Figure 1:** Bottom-up effects of the plant nutrient solution on *Tuta absoluta* and its  
769 natural enemies, the larval parasitoid *Necremnus tutae* and the omnivorous predator  
770 *Macrolophus pygmaeus*. Reduced supply of nitrogen (N), potassium (K), or water as  
771 well as increased salinity (NaCl) in the nutrient solution can affect plant nutritional  
772 quality and plant defense. These changes can in turn have an impact on higher trophic  
773 levels and affect the performance of *T. absoluta* as well as *M. pygmaeus* and *N. tutae*.  
774 Solid line arrows indicate direct interactions. Broken line arrows indicate indirect  
775 ones. Dotted line arrows indicate open questions. C: carbon, VOC: volatile organic  
776 compounds.

777 \*While only nitrogen- and only water-limitation did not affect *N. tutae*, they exhibit  
778 the strong tendency to do in interaction and should be considered carefully.

779 \*\*The increasing defense response and defense compound content has not yet been  
780 demonstrated for tomato leaves.

781 This figure is based on the following publications: Amtmann et al 2008, Becker et al  
782 in prep, Blazhevski et al 2018, Debouba et al 2016, Dong et al 2017, Flores et al 2015,  
783 Han et al 2014, 2015a, 2015b, 2016a, 2016b, Larbat et al 2016, Manaa et al 2011,  
784 Slansky & Scriber 1985, Sung et al 2015.

