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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

Key message:

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

Author contribution:

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

Introduction

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

The South American tomato pinworm, *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae), originated from South America, is a devastating pest on tomato and

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

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

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

Bottom-up effects of fertilization and irrigation

Irrigation

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

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

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

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

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

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

(i) Increasing salt concentration in the irrigation water raises the osmotic potential

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

Fertilization

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

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

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

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

Bottom-up effects of plant resistant traits

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

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

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

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

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

or (ii) inducing a strong enzymatic defense.

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

RNA interference (RNAi) technology may also play an important role in tomato genetic transformation aimed at resistance to *T. absoluta*. RNAi is a mechanism for post-transcriptional gene silencing conserved in most eukaryotes and has proven to be a powerful tool for gene function studies. RNAi can also be applied for pest control: if the sequences of double-stranded RNA (dsRNA), the trigger of RNAi, target essential genes of insects, it provokes the endogenous RNAi machinery of pest, thus result in the silencing of these genes which leads to impaired growth and even death of pest.

Over the past decade, RNAi-mediated pest control has emerged as an important alternative alongside *Bt*-based strategies (Zhang et al. 2017). Although transgenic plants expressing dsRNA targeted against insect genes can impair pest growth and development, efficient control of insects and complete protection of plants were only

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

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

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

Implications for IPM

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

Modern crop cultivars often display a diversity of tolerance to sub-optimal abiotic environments (Ballhorn et al. 2011). For instance, some crop cultivars have been deliberately selected to withstand various environmental stresses, such as nitrogen deficiency (Feng et al. 2010) or drought (Cattivelli et al. 2008). One of our recent studies show, surprisingly, that the negative bottom-up effects of limited nitrogen and water inputs can cascade up to *T. absoluta* even though the tomato cultivars exhibited various adaptive or tolerance traits to those resource limitations (Han et al. 2016). In 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

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

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

packages.

Conclusions and future directions

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

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

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

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

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

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

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

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

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

d) *Breeding novel cultivars*

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

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494

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497

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501

502

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504

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

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

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

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

