Integrated Pest Management of *Tuta absoluta*: practical implementations across different regions around the world

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Abstract

The South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), has invaded most Afro-Eurasian countries, and is threatening worldwide tomato production. Various strategies have been developed and implemented to manage this pest species. Here we present a timely review on the up-to-date development and practical implementation of Integrated Pest Management (IPM) programs for tomato crops across different regions infested by *T. absoluta*. While insecticide resistance is a growing concern, biological control via releasing or conserving arthropod natural enemies and sex pheromone-based biotechnical control are the most successful management practices. Agronomic control-related research is an emerging area where the soil fertilization and/or irrigation, as well as breeding of resistant cultivars, have the potential to enhance IPM efficacy. Surveys in the native areas (i.e. South America), early-invaded areas (i.e. first report between 2006-2012) and newly-invaded areas (i.e. first report after 2012) showed that the progams used by growers evolved along with the areas and time since invasion. Growers in the early-invaded areas shifted more rapidly from chemical control to biological control compared to those from the native area. For all areas, the greatest concern is related to control failure risk following chemical insecticide applications and the high cost associated with either biological or biotechnical control methods. The information gathered from the native and/or early-invaded areas may help achieve a more effective management in newly-invaded areas. Lastly, researchers are expected to break the bottlenecks of some key issues that would enable lowering application cost of novel biorational alternative management options.

Keywords

Invasive alien species, chemical control, biological control, pheromone, plant resistance, IPM

Author contributions

ND, PH, AB conceived and designed the work. ND, PH, RM, AB, JA, TB, MRC, AC, RNCG, JK, AVL, MGL, MPH, AU, FJV, LZ provided text based on bibliography review. ND, PH, RM, AB, KA, AA, JA, YB, FC, AC, RDV, FE, DMF, KH, KI, MJH, CCJ, MK, HTL, HM, TM, AM, GM, SAM, RSN, AO, CR, MR, ER, PRS, FHW, MHW, SW, YBZ provided original information on current and past IPM *Tuta absoluta* strategies. ND, PH, RM, AB analyzed and presented the data. All authors revised and approved the manuscript.

Key message

Major advances of fundamental and applied research have been made on the management of *Tuta absoluta*.

Use of pheromones, biological control, and agronomic and cultural control are important components of the IPM programs.

The IPM programs evolved along with the range and time after initial invasion, and show a decline in chemical control and an increase in non-chemical alternatives.

Introduction

Biological invasions are major components of global change, since they are increasingly challenging to modern agriculture due to the growing intensity of trade and human mobility (Simberloff et al. 2013; Paini et al. 2016; McNitt et al. 2019). Among invasive alien species, arthropod pests pose a significant threat to the stability of agricultural and natural ecosystem, and hence the implementation of Integrated Pest Management (IPM) programs is often required to suppress pest levels (Desneux et al. 2010). IPM is a science-based decision-making process that enables sustainable control of insect pests while posing minimum harm to the environment (Kogan et al. 1998). It can be implemented by timely pest sampling/monitoring to estimate pest densities, being combined with judicious pesticide use and various “green” management methods including trapping and use of synthetic pheromones, biological control by conserving and/or releasing arthropod natural enemies, agronomic and cultural control through habitat manipulation, and use of resistant varieties (Kogan 1998; Desneux et al. 2007; Meissle et al. 2011; Ragsdale et al. 2011). To some extent the need of IPM programs for invasive arthropod pests is comparable and even greater than those for endemic ones (Witzgall et al. 2008; Ragsdale et al. 2011; Furlan 2014; Haye et al. 2016; Deligeorgidiset al. 2019; Moreau et al. 2019; Santoiemma et al. 2020; Shah et al. 2020).

The South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), recently reinstated as *Phthorimaea absoluta* Meyrick (Chang and Metz 2021), is a destructive pest on tomato. So far, *T. absoluta* has invaded more than 90 countries outside of South America (EPPO 2021), thus becoming a serious threat to tomato production worldwide and a lesser extent a pest of other economically important solanaceous crops, including potato, eggplant, pepper and tobacco (Desneux et al. 2010, 2011; Campos et al. 2017; Mansour et al. 2018; Han et al. 2019a; Verheggen and Fontus 2019). Various biological and ecological characteristics of this species have contributed to its observed invasiveness and high feeding damage potential to solanaceous crops. These characteristics include the cryptic nature of larvae, high reproduction potential with multiple overlapping generations, strong dispersal capacity as well as moderate or high resistance to commonly-used insecticides (Urbaneja et al. 2013; Biondi et al. 2018; Cherif et al. 2019a; Guedes et al. 2019). The spread of *T. absoluta* to new regions has led to significant yield losses, fruit quality reduction (Rostami et al. 2020), increased pest control costs (Desneux et al. 2011), and heavy reliance on chemical insecticides (Biondi et al. 2018). This combination of *T. absoluta* problem dynamics has further disrupted local tomato IPM programs in these areas (Desneux et al. 2010; Han et al. 2018; Han et al. 2019a; Mansour et al. 2019).

By combining preventative and curative tactics against *T. absoluta*, IPM programs ought to be built by researchers and growers in vast invaded areas. In the past two decades, significant technological advances have been made in the areas of pest detection, pest surveillance, pest feeding damage assessment, and timely selection and application of management options. Despite the development of new pest control technologies, not all countries have the same economic access to a new tool, despite stakeholders having full awareness, interest and recognition of the benefits of a particular control tactic. Sharing knowledges is important, but the steps taken to transfer this knowledge and making it accessible/affordable and compatible with unique local farming practices & market interests is also key. Still, we should note that sharing knowledge on the management techniques being used in each region is the first step for building regional collaborations. This effort could improve IPM programs in different regions and hence cross-border pest management success (Han et al. 2019a). We readily assume that a successful management of the pest in one country/region may largely lower the risk in the other neighboring ones. Therefore, we provide a comprehensive review on current advances in management options and the IPM programs being used in the regions where this pest is distributed. In addition, we collected over 30 questionnaires data from the key researchers who had interviewed with local farmers, technicians and/or policy makers. These data allowed us to compare the components of IPM packages used in the native area (i.e., South America), early-invaded areas (i.e., Mediterranean basin, Europe, Northern and Eastern Africa, Middle East, 2006-2012) and newly-invaded areas (e.g., Sub-Saharan Africa, Central America, Asia; after 2012).

Chemical control

Insecticide use and invasive species

Insecticides are a major component of insect pest control in conventional agricultural systems. Starting in the 1960s, the use of insecticides in farming operations came under heavy scrutiny when their unintended effects in the ecosystem became widely recognized (Cooper and Dobson 2007; Aktar et al. 2009; Köhler and Triebskorn 2013; Guedes et al. 2016). Nevertheless, insecticides are routinely used for their key advantage of generating immediate, cost-effective pest reductions, especially when invasive species are the target pests, but effective pest control alternatives are lacking (e.g. it takes time to develop appropriate control options) (Lockwood et al. 2013; Liebhold et al. 2016; Guedes et al. 2019; McLaughlin and Dearden 2019). The rationale has also been applied to *T. absoluta* since chemical insecticide applications are the main control method to contain *T. absoluta* outbreaks (Guedes and Picanço 2012; Guedes and Siqueira 2012; Campos et al. 2017; Biondi et al. 2018; Mansour et al. 2018; Guedes et al. 2019; Rwomushana et al. 2019). Chemical control remains a dominant management tactic against *T. absoluta*, specifically in open-field tomatoes (Biondi et al. 2018). Young tomato seedlings with little leaf coverage favor *T. absoluta* early colonization, as the pest could attack stem buds with subsequent leaf-mining during canopy development and later fruit infestation. This pattern of attack not only affects three different plant parts throughout its development, but also allows the insect protection against insecticide spraying while hidden in these plant structures (i.e., stem bud, leaf, fruit) (Picanço et al. 1998; Guedes and Picanço 2012). Moth adults are mostly neglected in toxicological studies and are seldom considered a major target for chemical control (Biondi et al. 2015).

Ever-changing patterns of insecticide use

Chemical control of *T. absoluta* has had limited success, yet the reception of this pest in newly invaded areas is often characterized by a sharp rise in insecticide applications attempting to halt the spread of invasive populations and reduce impending yield losses (Guedes and Picanço 2012; Guedes and Siqueira 2012). For example, the 10-12 sprayings required for pest control prior to *T. absoluta* invasion in Brazil more than doubled reaching over 30 applications per tomato cultivation cycle at the onset of this species introduction (Guedes and Siqueira 2012). Such a heavy application harms the natural control by beneficial arthropods which could otherwise be saved when generally less insecticide is applied (Nieves et al. 2015). A similar scenario was reported in Europe and North Africa (Desneux et al. 2011; Mansour et al. 2018), and it is also expected in early-invaded and newly-invaded regions (Campos et al. 2017; Biondi et al. 2018; Han et al. 2019a).

Adjuvants of insecticide formulations, timing of insecticide applications and spraying technologies are important for improving chemical control of *T. absoluta*. For example, early season prophylactic application of insecticides in combination with mineral oil well before vertical tutoring (otherwise known as trellising) of the plant has commenced is known to reduce the severity of *T. absoluta* infestations later in the season (Picanço et al. 1998; Guedes and Picanço 2012). Nonetheless, the control difficulties and the management consequences stemming from intensive insecticide use have led to a succession in insecticides most frequently used against *T. absoluta*, as well-documented in South America, the region of origin and early spread of this species. Organophosphates and pyrethroids were the early groups of insecticides used against the pest in South America, starting in the 1960’s and extending up to the 1990’s (Siqueira et al. 2000a; Lietti et al. 2005). The subsequent decline in organophosphate use in the region was achieved by cartap, abamectin, and intensified pyrethroid use (Siqueira et al. 2000a, b, 2001). The late 1990’s and early 2000’s were met with the use of the oxadiazine indoxacarb and a surge in use of chitin synthesis inhibitors (Silva et al. 2011; Gontijo et al. 2013), followed by the subsequent increase in popularity of the pyrrole chlorfenapyr, the spinosyns (particularly spinosad), and the diamides chlorantraniliprole and flubendiamide by the mid-2000’s (Silva et al. 2011, 2016; Gontijo et al. 2013). These latter 4 compounds remain in active use at present, but spinosad among them is allowed in organic tomato production systems where azadirachtin and toxins of *Bacillus thuringiensis* (Berliner) (*Bt*) (Bacillaceae) serve as alternatives (Silva et al. 2011; Biondi et al. 2018).

The historical insecticide use pattern observed in South America for *T. absoluta* control has been observed in other invaded regions for similar underlying reasons. The use of organophasphate and pyrethroids against *T. absoluta* in Europe took place early on at the onset of its introduction by the late 2006, which was reported in Spain (Desneux et al. 2010). As it further spread to coastal European and North African countires (Campos et al. 2017; Biondi et al. 2018), the chemical control was soon followed by the use of indoxacarb, avermectins, spinosyns and more recently by the reliance on diamide insecticides (Haddi et al. 2012, 2017; Roditakis et al. 2018). Similarly, in West Asia regions the initial chemical control approach for *T. absoluta* began with organophosphates and pyrethroids and subsequently transitioned to other pesticide chemistries, such as diamides, with azadirachtin and *Bt* toxins also playing a role in some contexts as organic cultivation (Kader et al. 2017; Zibaee et al. 2018). The fast evolution of insecticide resistance among *T. absoluta* populations and associated control failures seems to be the key determinant in the observed changes in pattern of insecticide use.

Insecticide resistance, control failure and other concerns

Pest population genetic resistance is a common consequence of unbalanced insecticide use, which largely drives the pest control dynamics observed for *T. absoluta* worldwide (Guedes and Siqueira 2012; Biondi et al. 2018). This was earlier recognized in South America, and then elsewhere (Biondi et al. 2018; Guedes et al. 2019), reaching nearly 60 instances of resistance to 24 insecticides worldwide as recorder in the Arthropod Pesticide Resistance Database (https://www.pesticideresistance.org) and recent compilation (Guedes et al. 2019). Initial detection of insecticide resistance in *T. absoluta* populations from South America involved organophosphate and pyrethroid insecticides (Salazar and Araya 1997; Siqueira et al. 2000b; Salazar and Araya 2001; Lietti et al. 2005), apparently motivating the subsequent use of cartap and abamectin. Latter, low to moderate levels of resistance to abamectin and cartap were also reported in Brazil (Siqueira et al. 2000b; Siqueira et al. 2001; Silva et al. 2016), where pyrethroid resistance receded (Silva et al. 2011). Detection of indoxacarb resistance soon followed in the region, but ranging only from low to moderate levels (Silva et al. 2011; Silva et al. 2016), while subsequent resistance to chitin synthesis inhibitors reached high levels by mid-2000's (Silva et al. 2011). Spinosad and diamide resistance was then detected in South America and seems to be expanding (Reyes et al. 2012; Campos et al. 2014, 2015; Silva et al. 2016).

The rapid development of insecticide resistance observed among *T. absoluta* populations in Europe and North Africa is directly linked to the insecticide resistance history of this pest in South America (Roditakis et al. 2015, 2017a, 2017b, 2018). A crucial point that should not be overlooked is that, the invasive strain of *T. absoluta* from South America (cental Chile) (Guillemaud et al. 2015) that was found in Spain in 2006, was most likely already resistant to pyrethroids. This factor likely catalyzed the ensuing insecticide resistance problems with *T. absoluta* as it spread throughout Eurasia and Africa (Haddi et al. 2012). Thus, not only is the species invasion a matter of concern but also the genetics of the invading population or strain of *T. absoluta* (Guedes and Siqueira 2012; Biondi et al. 2018). Widespread resistance to organophosphates, pyrethroids and other compounds enhances the likelihood of the unwelcome introduction of insecticide resistant populations of *T. absoluta* to new areas. This emphasizes the importance of profiling this genetic process/phenomenon and recognizing its spread to new areas to allow its containment and mitigation.

Two additional considerations are also important regarding the chemical control of *T. absoluta* – the likelihood of insecticide control failure due to insecticide resistance and non-targeted effects of insecticides. Failure of chemical control is not always due to insecticide resistance but to unsuitable application (i.e., application that does not follow the best practices for any given situation, such as total volume use, plant coverage, and use of adjuvant to improve insecticide retention), and faulty recommendations (i.e., not incorporating suitable formulation, proper adjuvant and spraying conditions etc.). However, unlike insecticide resistance, the risk of insecticide control failure is seldom surveyed since it is frequently neglected. Nonetheless, such survey is possible and desirable requiring some adjustments to the well-known bioassay procedures for detection and monitoring of insecticide resistance – the use of realistic bioassay methods reflecting insecticide field exposure and standard endpoints tuned to the efficacy thresholds required for commercial field use of insecticides (Guedes 2017). This assessment on control failure likelihood has received increasing attention with *T. absoluta*, which was initially surveyed in Brazil, but is also taking place elsewhere (Silva et al. 2011; Gontijo et al. 2013; Roditakis et al. 2013; Silva et al. 2015).

The second consideration refers to unintended consequences of insecticides on non-target species (Desneux et al. 2007). Some of the consequences of non-targeted insecticide exposure include (i) stress to non-targeted species including natural enemies and pollinators, among others; (ii) inadvertent selection for insecticide resistance on non-targeted species (again including natural enemies and other pest species); (iii) shifts in species pest dominance and status, and (iv) community stress (Barbosa et al. 2015; Guedes et al. 2016, 2017). These consequences were little studied in the context of *T. absoluta* control with insecticides, but both the putative whitefly species and the tomato borer *Neoleucinodes elegantalis* (Gueneé) (Lepidoptera: Crambidae) may co-occur with *T. absoluta* and influence the host plant response to *T. absoluta*, besides of potentially determining the pattern of insecticide use in the field. This is so because high whitefly infestation for instance may minimize incidence of *T. absoluta* and thus become the primary target of insecticide use (Biondi et al. 2018; Guedes et al., 2019). Regardless, the subject is well-worthy of attention.

Essential oil – based botanical insecticides

As for other pest insects (Benelli et al. 2019; Pavela et al. 2020), the most developed botanical insecticides for *T. absoluta* so far are formulated with essential oils produced from botanical extracts (Soares et al. 2019). Several works have examined the lethal and/or sublethal (e.g. behavior) effects of essential oils derived from citrus peel (Campolo et al. 2017), cardamom (Chegini and Abbasipour 2017) and ajwain (Piri et al. 2020), which all demonstrated significant efficiency in repelling and/or controlling the pest. Growers are recommended to use those essential oil products alone and/or combined with other biorational options, such as arthropod predators and microbial pesticides (Mansour and Biondi 2020). However, several limitations, such as optimized and authorized formulations, for the practical inclusion of essential oils into IPM programs are still occurring (Pavela and Benelli 2016). Moreover, the compatibility of essential oils with biocontrol agents should be evaluated case by case (Biondi et al. 2012; Soares et al. 2019; Campolo et al. 2020). These reasons, together with cost, efficacy, and reliability, may limit the use of this control option by growers so far.

Trapping and use of pheromones

Sex pheromones are chemical cues released by an organism to attract conspecifics of the opposite sex for mating. In moths, males typically fly upwind toward attractant cues released by females (Cardé and Minks 1995). Due to their vital role in mediating insect mating behavior, the use of sex pheromones has been one of the focal points of pest control research, especially for moths of economic importance. The earliest, most widespread and successful application of sex pheromones is their use in detection and pest population monitoring. They were later used to control insect populations, through mass trapping and mating disruption (Witzgall et al. 2010). Like most lepidopteran species, the sex pheromone of *T. absoluta* consists of a blend of volatile molecules, evoking long-range male attraction as well as elicitation of a courtship behavior (Linn et al. 1987). Typically, female *T. absoluta* initiate the male calling behavior in the early morning with the release a two-component sex pheromone consisting of a major component, (3E, 8Z, 11Z)-tetradecatrien-1-yl acetate (TDTA), found in 90% of calling females sex glands, and a minor component, (3E, 8Z)-tetradecadien-l-yl acetate (TDDA), accounting for the remaining 10% (Attygalle et al. 1996; Griepink et al. 1996; Svatoš et al. 1996). Their synthesis has been improved, leading to higher yields and stereoselectivity (Puigmartí et al. 2015). These molecules are used in field monitoring efforts, mass trapping and mating disruption for *T. absoluta* (Caparros Megido et al. 2013).

Monitoring

The *T. absoluta* sex pheromone was used to increase the sensitivity of existing monitoring traps (both Delta traps and bucket traps), allowing earlier detection of small populations and rapid implementation of adequate management strategies (Benvenga et al. 2007). In an early field experiment, pheromone traps baited with 100 μg of TDTA were shown to catch on average 1200 males per trap per night, while less than a hundred of individuals were caught in the control (Ferrara et al. 2001). Under greenhouse conditions, catches were shown to increase linearly with pheromone release rates, until reaching a maximum number of captured individuals achieved with traps releasing 150μg of TDTA per day (Vacas et al. 2013). The pheromone release rate is affected by a variety of factors, including the pheromone packaging and the dispenser itself. The baseline release rates should be adjusted as needed for maximum pest control performance under different environmental conditions. For example, higher pheromone release doses are typically needed in open field habitats exposed to desert climates (e.g., 3 mg) than under greenhouse conditions where the pheromone is not readily wind dissipated (e.g., 500 µg) (Hassan and Al-Zaidi 2010). These pheromone quantities can be slightly lower by the addition of 5-10% of TDDA (Lobos et al. 2013). However, whether addition of TDDA increases trap efficiency and/or fedility remains to be assessed. Because commercially produced pheromones (either containing both components or only the main pheromone component) attract non-target moths, survey programs should include a dissection-based identification of the trapped moth before initiating a management strategy (Roda et al. 2015).

A wide diversity of trap designs has been tested in field in the last decade, with dark-colored Delta traps being the most recommended design (Uchôa-Fernandes et al. 1994; Roda et al. 2015; Abd El-Ghany et al. 2016). These traps are typically made from paper or plastic into a triangular prism shape, left open at both ends, with placement of a sticky panel insert at the interior trap base and a pheromone lure suspended above the insert, but under the trap roof, for protection from the elements. Alternatively, water-filled bowls in combination with the pheromone lure can also be used for populations monitoring. Trap positioning with respect to vegetation (height, densities) influences the monitoring results (Ferrara et al. 2001), with traps located just above the plant height to be the most efficient. Definitive trap density guidelines have not been established and can vary by region and information source consulted (e.g., published literature, trap manufacturer). However, an initial reliable monitoring program can be achieved with 1 to 4 traps/ha (Mansour et al. 2019). Based on the number of males caught per pheromone trap, the risk of infestation can be evaluated, and should be considered low for less than 3 individuals/week, moderate if between 4 and 30 individuals/week, and high for more than 30 individuals/week (Monserrat Delgado 2008).

Mass trapping

In general, mass trapping methods for reduction of *T. absoluta* population levels combine the use of lures, to attract one or both sexes, with large insect retention traps (Witzgall et al. 2010). Trap designs can include those described previously, i.e., Delta or water-filled bowl traps, or other modified versions (Lobos et al. 2013). Similar traps are sometimes used for monitoring and mass trapping, but water traps are usually preferred to Delta traps, which quickly saturate in case of large pest population. When the killing agent is a chemical (e.g. cypermethrin), this strategy is called lure and kill (Howse et al. 1998).

In addition to the lure that consists of a semiochemical blend, the mass trapping setup can include a light source to increase moth attraction (Hassan and Al-Zaidi 2010; Cocco et al. 2012; Castresana and Puhl 2017). Because the mate-finding communication system of *T. absoluta* is guided by a female-produced sex pheromone, only males are caught in these traps, leading to a decrease in mating events and a reduction in crop damage (Jones 1998; Witzgall et al. 2010). However, the particular mating behavior and reproduction characteristics of *T. absoluta* represent challenges that counter the efficacy of mass trapping efforts. *Tuta absoluta* males are polygynic and mate on average 6.5 times (Silva 2008), and a large proportion of males must be trapped before a population can be controlled (Jones 1998; Witzgall et al. 2010). For the females, Caparros Megido et al. (2012) demonstrated that they are able to lay viable eggs without mating with males (i.e., parthenogenesis) even though the rate is relatively low. The female also shows polyandry that greatly increases its reproductive outputs, and the benefits for the female are greater when she copulates with several different virgin males than to the same male (Lee et al. 2014). Interestingly, *T. absoluta* has recently been found to show polygyny (Wang et al. 2021), which may further undermine the effectiveness of mass trapping.

While pheromone-based monitoring involves only a limited number of traps per hectare, mass trapping requires placing a higher number of traps in various strategic positions in the crop field to remove a high proportion of male insects from the pest population. For example, in Tunisia, the recommended density of Delta traps or water traps were 32 or 36 traps. ha^{-1} for open-field mass trapping, and 2 Delta- or water traps for a 500 m^2 greenhouse (Mansour et al. 2019). The doses of sex pheromone to be loaded on the diffuser are usually claimed to be similar to those used for monitoring efforts, even if some authors suggest adapting the pheromone dose to the level of infestation (Chermiti and Abbes 2012). Lobos et al. (2013) noticed that higher numbers of

T. absoluta were captured near upwind borders of tomato fields suggesting that treatments should be concentrated near upwind parts of fields. Mass trapping is rarely sufficient to control a *T. absoluta* population, and should be used in conjunction with other control measures to reach an acceptable level of damage (Cherif et al. 2018).

Mating disruption

The mating disruption strategy aims to interfere with the mate-searching efficacy of males by saturating the environment during key periods with a synthetic female pheromone. Reductions in successful mating events lead to lower pest levels and minimal crop damage (Cocco et al. 2013; Caparros Megido et al. 2013). The release of large amount of sex pheromone is necessary to achieve significant results, with 500 to 1000 pheromone dispensers per hectare being deployed (Vacas et al. 2011; Cocco et al. 2013). But even by using 50 g. ha^{-1} of sex pheromone, several factors can make this strategy inefficient to reduce the damage, including the pest population density, the migration of mated females to the treated area, and the ability of female *T. absoluta* to reproduce parthenogenetically (Michereff Filho et al. 2000; Caparros Megido et al. 2012). This is why studies on the application of the mating disruption strategy against *T. absoluta* in open fields and protected tomato crops showed mixed results (Michereff Filho et al. 2000; Vacas et al. 2011; Cocco et al. 2013). In addition, the size of the areas treated could also affect the efficacy of mating disruption, and it is assumed to perform better in large farms than small plantings. Even if the efficiency of this method is improved, its viability might be limited by its total cost to farmers, which must include pheromone production and dispenser application.

Biological control with microorganisms

A great number of entomopathogens are lethal to *T. absoluta* including bacteria, fungi and nematodes. Microbial biopesticides are usually not as harmful to environment as chemical insecticides, and tend to be safer for humans and other vertebrates, and are compatible with other groups of beneficial organisms such as arthropod natural enemies (González-Cabrera et al. 2011; Mollá et al. 2011; Mansour and Biondi 2020).

Bacteria

Different subspecies of *B. thuringiensis* (*Bt*) including *Bt* kurstaki and *Bt* aizawai are used widely to manage the lepidopteran pests on most vegetable crops. These groups are dominated microbial biopesticides as they are selective, safe, and also affordable (Lacey 2016). The bacteria of this category produce cry toxins which cause a specific mode of action. In the case of their efficiency, sometimes they are comparable with chemicals in terms of the effect and other traits. Cry toxins as a group of δ-endotoxins proteins produced by *Bt* during the sporulation phase are effective on a variety of insect orders (Schnepf 1998). The bacteria could also produce and secrete the vegetative insecticidal proteins (Vip) during the vegetative growth stage. Sellami et al. (2014) evaluated the toxicity of *Bt* Vip3Aa16 protein against *T. absoluta*. This toxin has higher potency than the δ-endotoxins of *Bt* subsp. *kurstaki* Strain HD1. The commercial formulations based on *Bt* have been developed as a key component of the IPM strategy against *T. absoluta*. Earlier studies documenting the effects of *Bt*-based insecticides on *T. absoluta* were conducted in South America (Giustolin et al. 2001; Theoduloz et al. 2003), and additional complementary studies has been done in invaded areas. In Spain, *Bt*-based insecticides against *T. absoluta* have been assessed in laboratory, greenhouse and open-field conditions. They showed that *Bt*-based insecticides are highly efficient in controlling *T. absoluta,* with the first instar larvae being the most susceptible compared to the second and third instar larvae (González-Cabrera et al. 2011). The suitable selection of *Bt* concentrations (e.g. 90.4 MIU l^{-1}) together with desired subspecies of *Bt* including subsp. *kurstaki* or subsp. *aizawai* are able to reduce the pest density by more than 95%. Spraying the same concentration of the product each week could achieve satisfactory management efficacy with lower cost (Urbaneja et al. 2012). Furthermore, Mollá et al. (2011) demonstrated that when *Bt* was used immediately after the initial detection of *T. absoluta* on plants, it did not interfere with the pest control efficacy of the commercial predator *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae) when released because *T. absoluta* eggs were available. Consequently, the combined use of *Bt*-based insecticides with the release or conservation of this predator forms a multi-stage integrated management for *T. absoluta*. In North Spain, another predator *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) is often used in combination with *Bt*-based insecticides that are highly effective in controlling the first instar larvae of *T. absoluta* (Urbaneja et al. 2012).

Entomopathogenic fungi

The entomopathogenic fungus, *Beauveria bassiana* (Bals.) Vuill. (Ascomycota: Hypocreales) is a common microbial agent that causes mortality in a wide range of pest insects. This fungus exhibits epiphytic and endophytic activity against *T. absoluta* (Allegrucci et al. 2011; Klieber and Reineke 2016). The survey on the efficacy of a commercial mycoinsecticide based on *B. bassiana* against all instars of *T. absoluta* showed that the corrected mortality reached 30% to 50% (Klieber and Reineke 2016). The establishment of the fungus with endophytic behavior could overcome the shortcomings during conventional usage of fungal-based pesticides including poor persistence of the spores in the environment or high susceptibility to environmental stressors like UV radiation or rainfalls (Vega 2018). In this case, one concern related to endophytic inoculation of the fungi is the corresponding metabolites which might enter the food web. This concern should be considered during the registration process of the products and requires in-depth studies (Vega 2018). Nevertheless, entomopathogenic fungi like *B. bassiana* have various beneficial roles that have implications for managing *T. absoluta* infestations. This fungus has been shown to improve plant health by increasing uptake of water and plant nutrients, promoting root biomass and development via mycorrhiza-like and endophytic interactions because they induce systemic plant defense and antagonistic effects on phytopathogens (Dara 2019; Tall and Meyling 2018). Moreover, a liquid formulation based on strains of the fungus *Metarhizium anisopliae* (Ascomycota: Hypocreales) together with irrigation could cause high mortality to *T. absoluta* pupae (Contreras et al. 2014). Nevertheless, nematode use against *T. absoluta* will boil down to cost, efficacy, and reliability.

Viruses

Several granulovirus isolates from *Phthorimaea operculella* (Zeller) (Lepidoptera: Gellechiidae) (i.e., PhopGV) have been collected worldwide and evaluated in terms of insecticidal activity, which indicated differences depending on their geographical origin (Carpio et al. 2012; Vickers et al. 1991). Mascarin et al. (2010) demonstrated that a Brazilian PhopGV was able to infect *T. absoluta*, resulting in delayed larval growth and decreased pupation. Gómez Valderrama et al. (2017) reported the morphological characterization and classification of two Colombian granuloviruses: VG013, isolated from *T. absoluta,* and VG003, isolated from *Tecia solanivora* Povolný(Lepidoptera: Gelechiidae). This study showed that both viruses could kill *T. absoluta* larvae.

Entomopathogenic nematodes

Entomopathogenic nematodes (EPNs) are also able to infect four instars of *T. absoluta* inside or outside leaf galleries in both laboratory and greenhouse experiments (Batalla-Carrera et al. 2010; Turkoz and Kaskavalci 2016; Van Damme et al. 2016; Mutegi et al. 2017; Kamali et al. 2018). These studies indicated that both *Heterorhabditis bacteriophora* (Poinar) (Nematoda: Heterorhabditidae) and *Steinernema carpocapsae* (Weiser) (Rhabditida: Steinernematidae) have ideal potency to be used in foliar and soil applications for *T. absoluta* management programs on greenhouse-grown tomatoes. Moreover, they are able to control other greenhouse pests including the greenhouse whitefly, *Trialeurodes vaporariorum* (West.) (Hemiptera: Aleyrodidae) and the western flower thrip, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Ebssa et al. 2004, Rezaei et al. 2015; but see Buitenhuis and Shipp 2005 for a low nematode infection in *F. occidentalis*). Nematode efficacy and their compatibility with other biological control agents or other agrochemicals promote their use within the IPM strategy.

Biological control with arthropods

A variety of arthropod natural enemies have been explored to control *T. absoluta*. Overall, predators and parasitoids have received equal efforts for research and practical use. Much advances have been made on the use of native biocontrol agents, whereas the classical biological control by importing the natural enemies from native range of *T. absoluta* has been rare. Such an inbalance could at least be attributed to (i) the “first-strike advantage” of large research efforts on native natural enemies (e.g., the mirid predators and trichogrammatid parasitoids in Europe); (ii) the complicated procedure required by the legal framework of Convention on Biological Diversity for conducting classical biological control.

Predators

At least 60 species of generalist arthropod predators, belonging to 26 families have been detected preying upon *T. absoluta*. Of them, more than 50 species have been recorded in South America whereas ten, mainly hemipterans, have been reported in newly invaded European countries (Ferracini et al. 2019). Some of these species play an important role in the natural regulation of *T. absoluta* populations in its area of origin (Miranda et al. 1998; Picanço et al. 2011; Bacci et al. 2018). However, in the early-invaded areas the importance of IPM programs based on the use of predators for *T. absoluta* control quickly became evident (Arnó et al. 2009). Current field results indicate that the intentional use of commercially available predators for biological control of *T. absoluta* has only been successful in early-invaded areas of southern Europe (Mollá et al. 2011; Calvo et al. 2012a; Oztemiz et al. 2012; Urbaneja et al. 2012; Arnó et al. 2018a; Biondi et al. 2018). It is still too early to determine if similar predator-based biological control practices are having a significant impact in other areas recently invaded by *T. absoluta* (Shaltiel-Harpaz et al. 2016; Varshney and Ballal 2017; Ismoilov et al. 2020; Mansour and Biondi 2020). Nevertheless, the two commercially available predatory mirid bugs, *N. tenuis* and *M. pygmaeus*, have emerged as key biological control agents for *T. absoluta* in Europe (Pérez-Hedo et al. 2021a). The success obtained with the use of mirids in European tomatoes has prompted other geographical regions, mainly in the American continent, to explore for native mirids (Pérez-Hedo et al. 2021b; Roda et al. 2020). The effectiveness of mirid predators, such *N. tenuis* and *M. pygmaeus*, lies among others mainly in two biological traits: i) mirids are able to consume large amounts of *T. absoluta* eggs (Arnó et al. 2009; Urbaneja et al. 2009; Sylla et al 2016), and ii) thanks to their zoophytophagy behavior they can remain in the crop during periods of prey scarcity (Thomine et al. 2020; Pérez-Hedo et al. 2021a). On this last point, field data collected during the last 10 years conclusively shows that early predator establishment is crucial for control of *T. absoluta*. Effective control of *T. absoluta* is very difficult if mirids are released when *T. absoluta* is already established on the crop (Urbaneja et al. 2012). To achieve this premise, mirids can either be conserved or released following two types of augmentative strategies: predator inoculation after transplanting and pre-planting releases in the nurseries. Due to the diverse climatic conditions in which the tomato is produced and the zoophytophagy of these biocontrol agents, the use of mirid bugs for *T. absoluta* control may require insecticide treatments under certain circumstances to either complement the action of the predators or prevent crop damage due to their feeding. In this case, the selection of the insecticide has to be done carefully to fulfil the desired goal (Arnó and Gabarra 2011; González-Cabrera et al. 2011; Mollá et al. 2011; Zappalà et al. 2012; Urbaneja et al. 2013).

Predatory mirid bug inoculation after transplanting

A common practice for biological control of greenhouse tomato pests in Europe, particularly for whiteflies, is the inoculative release of *N. tenuis* and *M. pygmaeus* at a rate of 1-2 individual(s)/m^2, occurring 3-4 weeks after transplantation (Gabarra et al. 2006; Calvo et al. 2009). This strategy can also be effective for managing *T. absoluta* during short crop cycles when transplantating begins at the end of winter and the crop season can last until summer (Mollá et al. 2009). In these crops, mirids are released when *T. absoluta* pressure is low; hence it is possible that mirids may establish their populations before the populations of *T. absoluta* increase. During this crop cycle, temperatures increase with time which favors both the predators and the pest. If *T. absoluta* increases faster than the predator populations, the predator-prey balance could be prey-biased. As a consequence, treatments as selective as possible on mirid bugs will be needed (e.g. *Bt*-based insecticide). This scenario is more frequent when the control relies on *M. pygmaeus* because it is less voracious than *N. tenuis* (Mollá et al. 2009; Pérez-Hedo et al. 2015). A different situation occurs when *N. tenuis* is released and the predator could build up high populations at the time the crop is still growing. In this case, even if a successful control of the pest is achieved, the predator may damage the crop due to its phytophagy (Castañé et al. 2011; Pérez-Hedo and Urbaneja 2016). Therefore, insecticide sprays to reduce *N. tenuis* populations have to be recommended, although the complete elimination of the predator is not advisable.

Predatory mirid bug inoculation before transplanting

In the nursery, adult predators are released at a dose of 0.5-1 individuals per seedling-plant and initially fed with eggs of *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) (but see Messelink et al. 2014: food sprays with *Artemia* cysts (bine shrimp eggs) will be less costly than *E. kuehniella*). The eggs laid by mirids hatch very soon after transplanting, allowing a very early and homogeneous predator establishment on the crop. This strategy began at the end of the 90s to facilitate the establishment of *M. pygmaeus* for *B. tabaci* control (Lenfant et al. 2000), and has become popular in recent years with the use of *N. tenuis* to control *T. absoluta* (Calvo et al. 2012a, b). It has proved to be highly successful in long-cycle tomato crops that start under medium-high pest levels in late summer, as for example in tomato greenhouses in Almeria (southeast of Spain). In these cycles and using this strategy, *N. tenuis* establishes rapidly which guarantees good control of *B. tabaci* and *T. absoluta* until the arrival of winter when both, *N. tenuis* and pest levels decrease as temperatures. In spring when temperatures rise, *N.tenuis* populations start to build-up again shortly before the end of the crop, when risk of yield damage is much lower. It is not common that *N. tenuis* populations reach harmful levels during the winter. However, in certain years with very mild winters insecticide sprays are needed to contain predator populations. If the populations of *N. tenuis* do not recover properly, the predator-prey equilibrium can be broken especially in spring where the populations of *T. absoluta* can grow faster than those of *N. tenuis* and insecticides may be also needed to slow the built-up of the pest. In that case, complementary management strategies such as egg parasitoid releases (Chailleux et al. 2013a; Gabarra et al. 2014), use of pheromones for mass trapping and/or sexual disruption (Caparros Megido et al. 2013) and conservation of indigenous native parasitoids (Zappalà et al. 2013; Gabarra et al. 2014), may be needed for *T. absoluta* control.

Predatory mirid bug conservation

Conservation of predatory mirids has been a key practice for tomato IPM programs for years in the Mediterranean region (Albajes and Alomar 1999; Bompard et al. 2013; Arnó et al. 2018a). After *T. absoluta* invasion, these programs have been shown useful for controlling this pest (Arnó et al. 2009; Jaworski et al. 2015) and, in some areas, the conservation of mirids is considered very important for a successful pest management. The role of the natural habitats and landscape elements around crops in the colonization of tomato crops by mirid bugs has been widely documented (Alomar et al. 2002; Castañé et al. 2004; Gabarra et al. 2004; Aviron et al. 2016; Ardanuy et al. 2018; Agustí et al. 2020). In this context, the use of ecological infrastructures such as flower margins with selected plants, mainly *Calendula officinallis* L. (Asteraceae)*,* aims to nourish *M. pygmaeus* near tomato crops. This strategy is successfully used in Northeast Spain and Southeast France to increase the number and earliness of predators colonizing the crop and improve pest control (Lambion 2011, 2014; Balzan 2017; Ardanuy et al. 2018). However, the implementation of the conservation biological control strategy has promoted not only *M.*

pygameus but also *N. tenuis*, with the latter being risky for summer crops as explained above. Cultivation of *Sesamum indicum* (L.) (Pedaliaceae) as companion plant has been proposed as a method to reduce the damage caused by *N. tenuis* in the tomato crop (Biondi et al. 2016; Naselli et al. 2016). The provision of sugar dispensers on tomato plants could also limit plant damage by diminishing mirid phytophagy (Urbaneja-Bernat et al. 2018). In addition, promoting particular indirect interactions among various pests in a single crop could enhance biocontrol services provided by generalist predators (van Veen et al. 2006; Desneux & O'Neil 2008; Desneux et al. 2019). Recent works demonstrated that such indirect interactions could occur between *T. absoluta* and other pests inhabiting tomato crops when mirid predators are released (e.g. *M. pygmaeus*, Bompard et al. 2013; Jaworski et al. 2015; Han et al. 2020), and that these interactions may be used as levers for optimizing IPM programs (Chailleux et al. 2014a).

Parasitoids

Close to 100 species of hymenopteran parasitoids belonging to Chalcidoidea, Chrysidoidea, Ichneumonoidea, have been recorded in association with *T. absoluta* throughout the world, primarily in South America, but only a few promising species have been considered for the development of biological control strategies, including conservation, augmentative, and classical biological control options (Desneux et al. 2010; Biondi et al. 2013; 2018; Gabarra et al. 2014; Biondi et al. 2018; Salas Gervassio et al. 2019a). When comparing the South American parasitoid complex of *T. absoluta* in its native and invaded ranges of distribution, a strong pattern of adaptation to the new host can be observed, with 53 species forming new associations in a bit more than 12 years from the invasion start (Salas Gervassio et al. 2019a). It is noteworthy that only three parasitoid species, namely *Neochrysocharis formosa* (Westwood), *Trichogramma dendrolimi* (Matsumura) and *Trichogramma exiguum* (Girault), were recorded in association with *T. absoluta* in both native and recently invaded areas (Ferracini et al. 2019).

Egg parasitoids

To date, all egg parasitoids used for controlling *T. absoluta* belong to the Trichogrammatidae family. Members of this group attack the eggs of several insects within more than eight orders.

They have been used extensively in biocontrol programs for the large-scale management of lepidopteran pests (Huang et al. 2020; Qu et al. 2020; Cherif et al. 2021; Zang et al. 2021). In South America, at least eight trichogrammatid species are commercially available for biological control of *T. absoluta*, but their field use is still limited. The biology, ecology, and taxonomy of the Neotropical species *Trichogramma pretiosum* (Riley) has been well studied and a commercial strain is available in Brazil, Chile, Colombia, Ecuador, and Peru. The use of *T. pretiosum*, alone or in combination with *Bt* formulations, has proven successful for control of *T. absoluta* in Brazil (Parra and Zucchi 2004; Medeiros et al. 2009). Indeed, integration with chemical control is only possible by using reduced-risk pesticides (González 2003). Use of *Trichogramma nerudai* (Pintureau & Gerding) and *Trichogrammatoidea bactrae* (Nagaraja) was also evaluated. Field releases of *T. nerudai* in greenhouse tomatoes were carried out in Corrientes province, Argentina, and proved to be effective in reducing *T. absoluta* population densities (Tezze and Botto 2004; Virgala and Botto 2010). Currently, this species is commercialized in Chile. The species *T. bactrae* is mass-reared and released in Chile and Peru to control *T. absoluta*. Other congeners such as *T. galloi* (Zucchi) in Brazil; and *T. pintoi* (Voegele) *T. exiguum* (Girault), *T. fuentesi* (Torre), and *T. cacoeciae* (Marchal) in Peru are available from commercial insectaries in South America.. The species *T. bactrae* and *T. cacoeciae* are under study in early-invaded regions by *T. absoluta*, such as Northern Africa.

Among egg parasitoids of *T. absoluta* used in Europe, high parasitism rates (>90%) were reached under greenhouse conditions following releases of *Trichogramma achaeae* (Nagaraja and Nagarkatti), both alone and in combination with the mirid predator *N. tenuis* (Cabello et al. 2009, 2015; Oliveira et al. 2017). Similarly, a slightly higher *T. absoluta* control level was achieved by combining the release of *T. achaeae* with the mirid *M. pygmaeus* (Chailleux et al. 2013b). Thus, the parasitoid *T. achaeae* has been commercialized as *T. absoluta* biocontrol agent in Europe and Northern Africa. By running a laboratory screening of 29 European strains of *Trichogramma* parasitoids against *T. absoluta* (Chailleux et al. 2012), one strain of *Telenomus euproctidis* (Girault) appeared promising compared to *T. achaeae*, because *T. euproctidis* shows a higher parasitism rate, higher fertility, higher proportion of females and higher capacity of entering in diapause under cold storage conditions in biocontrol company facilities. However, it did not perform efficiently under greenhouse conditions (Chailleux et al. 2012). The combination of several variables, such as the rearing system (plant and host egg) and temperatures (during development and use) could strongly influence the efficiency of these biological control agents, in terms of longevity and fertility (Cascone et al. 2015).

In Africa, augmentative biological control of *T. absoluta* using native Trichogramma egg parasitoids has only been implemented in a couple of North African countries, i.e., Tunisia and Egypt (Mansour and Biondi 2020). Release of *T. cacoeciae* and *Trichogramma bourarachae* (Pintureau & Babault) significantly reduced *T. absoluta* densities and plant damage either in protected or open field tomatoes in Tunisia (Zouba and Mahjoubi 2010; Zouba et al. 2013; Cherif et al. 2019b). Moreover, several strategies have proven to be useful in Egypt: (i) releases of either the indigenous *T. euproctidis* or the cosmopolitan *T. achaeae* (50 or 75 parasitoids/m^2) (ii) *Bt* var. *kurstaki* application combined with releases of *Trichogramma evanescens* (Westwood) (70-75 adults/m^2) and mass trapping, (iii) releases of *T. achaeae* combined with releases of the predator *Macrolophus caliginosus* (Wagner) (Hemiptera: Miridae), and application of *Bt*, (iv) releases of *T. bactrae* in combination with mass trapping, or (v) releases of *T. evanescens* at seedling stage, significantly reduced insect densities and crop damages in northern Egyptian open field and greenhouse tomato crops (Khidr et al. 2013 ; El-Arnaouty et al. 2014 ; Kortam et al. 2014 ; Goda et al. 2015; Rizk 2016). As far as we know, the practical use of parasitoids for managing *T. absoluta* in Sub-Saharan Africa has not been documented.

In Asia, use of trichogrammatid parasitoids for control of *T. absoluta* has only been attempted in Turkey, Iran and Saudi Arabia (Mansour and Biondi 2020). Combined releases of the parasitoid *T. evanescens* and the predatory mirid *N. tenuis* were proven to significantly reduce fruit infestation in greenhouse tomatoes in the western Mediterranean region of Turkey (Keçeci and Öztop 2017). Similarly, releases of *Trichogramma embryophagum* (Hartig) parasitoids (20 adults per plant) along with *Bt* application or release of *Trichogramma brassicae* (Bezdenko), combined with spinosad spraying, significantly decreased *T. absoluta* densities and leaf mines in Iranian greenhouse tomato crops (Alsaedi et al. 2017; Jamshidnia et al. 2018).

Larval parasitoids

In the case of larval parasitoids only *Dolichogenidea (=Apanteles) gelechiidivoris* (Marsh), *Pseudapanteles dignus* (Muesebeck) (Hymenoptera: Braconidae), *Dineulophus phthorimaeae* (de Santis) and *Necremnus tutae* (Ribes and Bernardo) (Hymenoptera: Eulophidae) have been considered as part of IPM programs in South America and Europe (Salas Gervassio et al. 2019a, 2019b). Currently, the utility of these parasitoids is restricted to conservation biological control programs. One species, *D. gelechiidivoris* sourced from Peru, is being studied to develop a classical biological control program for *T. absoluta* in Africa (Aigbedion-Atalor et al. 2020).

In Chile, the importance of natural parasitism was recognized by Larrain (1987) who recommended avoiding early insecticide sprays to enhance the activity of *D. phthorimaeae* and *D. gelechiidivoris*. In the 80’s, in Colombia, Agudelo and Kaimowitz (1997) reported levels of larval parasitism up to 70% and the implementation of an IPM technology based on the conservation of *Apanteles* spp., releases of the *Trichogramma* spp. and treatments with *Bt*. The level of adoption and pest control success of this program is uncertain; however, its use decreased with time and ended up being minimal. More recently, Morales et al. (2014) evaluated the effectiveness of the parasitoid *D. gelechiidivoris* alone or together with sex pheromone traps, and obtained better results with the combination of both strategies. Despite all these efforts, Herrera Rocha et al. (2018) reported chemical control being widely used in Colombia and indicates that biological control will only be possible if combined with selective pesticides.

In Argentina, spontaneously occurring larval parasitism in commercial fields is caused mainly by *P. dignus* (Sánchez et al. 2009, Salas Gervassio et al. 2016), although it is found coexisting with with another parasitoid *D. phthorimaeae* on a same leaf (Luna et al. 2010). Several studies revealed important levels of parasitism up to 75% in non-sprayed fields and up to 26% in crops with frequent insecticide applications (Sánchez et al. 2009, Luna et al. 2010, Nieves et al. 2015). This undoubtedly contributes to the natural biological control of the pest. Preliminary releases of

P. dignus done in experimental tomato crops were not very successful (Folcia 2013). Further experimental work done on *P. dignus* by Salas Gervassio (2017) in tomato greenhouses, including evaluation of release rates on crop yield and fruit damage, is providing promising results for pest control.

In Europe and the Mediterranean Basin, the situation does not differ much. Out of all the indigenous parasitoids that use *T. absoluta* as host (Zappalà et al. 2013, Gabarra et al. 2014), only a few are considered as potential biocontrol agents. *Necremnus tutae* (Ribes & Bernardo), first identified as *N.* nr. *artynes* (Walker) (Chailleux et al. 2014b; Gebiola et al. 2015), is the only species that was mass reared in bio-factories, although currently it is not commercially available. Since biological control of the pest in this region is massively relying on the use of predatory mirid bugs from the very beginning (Urbaneja et al. 2012), the combined use of both predator and parasitoid agents were examined (Calvo et al. 2016). This latter study showed that releases of the parasitoid were not necessary to control *T. absoluta* after pre-planting application of the predatory bug *N. tenuis*. However, the role of parasitoids in conservation biological control is recognized in Tunisia (Abbes et al., 2014) and in Spain (Arnó et al. 2018b). In fact, an IPM program based on the conservation of *N. tutae* together with releases of *N. tenuis* and *T. achaeae* and the use of mating disruption is currently being recommended in Southeast Spain (Crisol and van der Blom 2018).

Agronomic and cultural control

Agronomic practices *via* manipulation of fertilization and irrigation have the potential for achieving *T. absoluta* control through bottom-up effects (Han et al. 2019b). For instance, lower nitrogen (N) input resulted in lower performance of *T. absoluta* in tomato plants via bottom-up forces (Han et al. 2014; 2016), but did not disrupt the efficiency of biocontrol agents (Han et al. 2015a, 2015b; Dong et al. 2018). These findings were encouraging for reaching the goal of IPM; however, they were obtained from manipulative microcosm and/or mesocosm experiments, which may not translate into population effects at larger-scales, e.g., greenhouses. If we carry out inundation release of biocontrol agents (e.g. *M. pygmaeus* and/or *N. tutae*) for controlling *T. absoluta* under greenhouse conditions, it is important to monitor the population growth of *T. absoluta* when the crops are treated with varying levels of nitrogen fertilizers. Reduced N fertilizer may impede tomato growth, but it may also help reduce the damage by *T. absoluta,* which could jointly affect tomato yield and quality. Moreover, applying less N fertilizer to crops has the potential to secure and even boost crop yields when applied in an appropriate way, while posing limited environmental damage (Chen et al. 2014). There is a trade-off in this issue, and it is important to figure out how much N fertilizer could result in a multi-beneficial situation, i.e., lower fertilizer input, enhanced pest control, and increased yields. This agronomic practice could be applied both for greenhouse and open-field tomatoes.

Adoption of resistant cultivars is another option that could be implemented in IPM programs against *T. absoluta*. A novel tomato cultivar has the potential to confer resistance to *T. absoluta* (Snoeren et al. 2017), but its performance in greenhouses and/or fields has not been assessed. In addition, insecticidal hybrid SN19 gene- and Cry1Ac gene-mediated resistance have been successfully developed in potato and tomato, respectively (Ahmed et al. 2017; Selale et al. 2017). So far, however, no tomato cultivar has been commercially available for targeting *T. absoluta*. The rapid development and robust risk assessment of those resistant cultivars are necessary before they could be adopted by growers in large areas. Notably, breeding of novel insect-resistant cultivars expressing long dsRNA that target pest essential genes in plastids (Zhang et al. 2015; 2017), being highly species-specific and thus environmental-safe, could be a promising component of the IPM package against *T. absoluta*.

For both greenhouse and open-field tomatoes, routine surveillance and removel of infested leaves from young seedlings in the early season reduce the initial population size of the moth, which could considerably lower the risk of population eruption during the season. Though labor-intensive, these practices are the most straightforward, thus lowering the follow-up of management inputs. For greenhouse tomatoes, several options could minimize the crop infestation by *T. absoluta*. First, physical barriers such as compartment exclusion by fine mesh and the design of double doors in the entry into greenhouses could be helpful to reduce infestation risk (Desneux et al. 2010; Biondi et al. 2018). Second, removal of alternative host plants inside/around the greenhouses could help suppress *T. absoluta* population. However, this practice requires growers to identify the wild plant species that may act as potential seasonal bridge hosts (Arnó et al. 2019). Efforts are thus needed to update the list of alternative host plant species and train growers to target these plants for removel in each region (e.g. Ciceoi and Gutue 2020). Third, crop rotation shifting from tomato to other non-solanaceous crops (e.g. leafy vegetables) could break the life cycle of *T. absoluta*, thus limitng the population build-up. Last but not the least, exposing the greenhouse fields to ambient temperature in winter, notably in certain regions with a cold winter, can kill a large proportion of remaining pest individuals that attempted to overwinter in the shelter (Li et al. 2020).

Developed IPM programs

A standardized questionnaire form was designed and disseminated to the researchers from nearly 30 countries who work on *T. absoluta* management (see Supplementary Materials). The form includes choice questions where scores are requested, and open questions where detailed answers are requested. The contacted researchers responded to a questionnaire by gathering knowledge on the importance/diffusion of each IPM strategy (i.e., warning and early diagnosis, cultural, biotechnical, biological and chemical control) for managing *T. absoluta*, in three main tomato-producing areas during three main periods: (i) before 2006 (only for the native area), i.e., before the first record of the pest outside its area of origin; (ii) 2006 – 2012 (for native and early invaded areas), i.e., the Mediterranean region and Central Europe invasion period; (iii) after 2012 (for the three areas: native, early invaded, and newly invaded areas), i.e., the sub-Saharan Africa, Asia and Central America invasion period. Further practical information on the current needs of the tomato industry for a suitable control of *T. absoluta* was gathered as well. For contacted researchers, information has been provided after interviewing local farmers, technicians, policy makers and by reading outreach and scientific documents in each concerned country. Four questionnaires for three countries in the native area (Brazil, Argentina and Colombia), 13 questionnaires for the early invaded area (12 countries) and 17 questionnaires for the newly invaded area (14 countries) have been obtained. For each questionnaire, an overall score of 100% was divided among the five *T. absoluta* control approaches according to their importance in a given area during a given period. The average values of these percentages are presented in Figure 1. One limitation of our study is that the questionnaire survey does not allow us to obtain estimated costs associated with each control tools in different areas.

***Tuta absoluta* IPM temporal and geographical evolution**

Tuta absoluta is currently considered a major concern in almost all tomato-producing areas around the world (Supplementary Materials: Tables S1, S2 and S3). Applying synthetic chemical pesticides has been the most adopted IPM management tool by farmers to cope with *T. absoluta* infestations in tomatoes, regardless of the area or the period (Figure 1). This management approach has mainly involved several in-season sprays of broad-spectrum active substances belonging to various insecticide chemical sub-groups including indoxacarb (oxadiazines), chlorantraniliprole (diamides), emamectin benzoate and abamectin (avermectins), deltamethrin (pyrethroids), and spinosad (spinosyns) (Tables S1, S2 and S3). However, it is worth mentioning that there has been a remarkable reduction of chemical pesticide input for managing *T. absoluta* in all concerned tomato-producing areas worldwide, and especially, this has been the case in the early invaded area as compared to the native area (Figure 1). Furthermore, the reduction in chemical insecticide use in the native area (South America) started to become more evident after the year 2006, with no significant reduction in insecticide use until recently. This fact provides evidence that chemical insecticides are a necessity for South American farmers for controlling *T. absoluta*, and apparently, they do not rely on pesticide-free, more expensive alternative biorational control options.

Although not commonly used in native and newly invaded areas, the biological control with arthropod natural enemies through releases of *Trichogramma* spp. egg parasitoids and/or the predatory mirid bugs *N. tenuis* or *M. pygmaeus* or by applying the microbial pesticide *Bt* has been of great interest in early-invaded area, i.e., Europe and Middle East and North Africa region since the year 2012 (Figure 1, Tables S1, S2 and S3). Importantly, as shown by Figure 1, the main goal of using biological control in early invaded countries has been to reduce the overuse, and in some cases, the misuse of hazardous chemical pesticides that have proved to generate detrimental side effects on non-target arthropods, human health and the environment, in addition to the resistance to pesticides in *T. absoluta* populations. In this context, major concerns have been rising in all geographical areas about the occurrence of resistance in *T. absoluta* to both spinosad and chlorantraniliprole insecticides. As a result, management options such as trapping and use of pheromones, cultural tactics (removal of infested leaves and fruits, using resistant tomato varieties, insect proof nets, soil solarization, destruction of alternative host weeds) and warning and early diagnosis (pheromone-based monitoring) are equally applied as important components within IPM packages in all different areas and the three time-intervals (Figure 1). This indicates that these options, being less effective if applied alone, could be considered as permanent, complementary tools to other more effective options such as chemical control and/or biological control. In a future attempt to ensuring a more sustainable and effective pest management action, regardless of the invasion area, a promising research avenue would be to evaluate, in collaboration with farmers and their advisors, the effectiveness of various tool combinations, e.g. biopesticide application + release of parasitoids and/or predators, pheromone mass trapping or mating disruption + biopesticide application, etc. Notably, in new invasion areas, parasitoids and predators would have to be discovered, evaluated, and imported, which would bring in national or regional governmental efforts.

The temporal and geographical evolution of IPM programs is in line with the concept of prioritizing those pest control tactics that take into account their relative environmental impact, as stated in Kogan and Bajwa (1999). These authors also emphasized that adoption of IPM is conceived at three levels of integration, starting with systems based on a single tactical approach such as using economic thresholds for better timing of pesticide applications, but later replacing that control measure with non-chemical tactics such as biological controls, cultural control etc. It is encouraging to note that such a trend has already been shown in the native range and the early-invaded range (Figure 1). Thus, following this approach, it is expected that in the near future – and in light of important progresses made on *T. absoluta* management- the use of chemical control can be drastically reduced, mostly in developing countries and that new phytosanitary alternatives must be promoted.

Current challenges for farmers

Based on the questionnaires performed in collaboration with South American farmers and plant protection professionnals, the current challenges for farmers in *T. absoluta* native range countries (Brazil, Argentina and Colombia) are mainly linked to the high economic cost associated with over-use of chemical insecticides, and to the adoption of alternative non-chemical, eco-friendly management options (Table S1).

In early-invaded countries in Europe, farmers currently have major concerns about the high cost associated with multiple sprays of pesticides, the absence or lack of knowledge on the occurrence and biology of *T. absoluta*, the high cost associated with alternative non-chemical techniques, the development of resistance to spinosad and chlorantraniliprole, the adverse effect of the omnivorous predatory bug *N. tenuis* whenever acting as a crop pest, the detrimental side effects of synthetic pesticides on predators such as *N. tenuis* and *M. pygmaeus* in greenhouses, and finding suitable techniques for minimizing or eliminating pesticide residues, as required by the European and international market (Table S2). Regarding early-invaded countries in the Middle Eastern/North African region, current challenges for farmers are not very different from those stated earlier, linked to European countries (Table S2). Indeed, in Tunisia, Morocco, Saudi Arabia and Turkey, the main current challenges for managing *T. absoluta* mainly include the high cost associated with multiple sprays of pesticides, the observed control failure by the active ingredients used due to development of pest’s resistance, the high cost associated with alternative non-chemical control options, and the problematic adverse side effects of insecticides on predatory mirid bugs.

In newly-invaded countries located either in sub-Saharan Africa, Asia or Central America, the absence or lack of knowledge on the occurrence and biology of the pest, the high cost associated with multiple insecticide sprays, the high cost associated with alternative non-chemical techniques, the control failure after several chemical insecticide applications, the negative side effects of insecticides on various ecosystem components as well as on farmers and consumers, and the lack of awareness on the correct use of insecticides represent the most common current challenges for farmers (Table S3).

Therefore, we conclude that the current challenges for farmers for effectively managing this pest are continent-independent within the same range, but could be considered as continent or country-dependant among the three different areas (native, early invaded, and newly invaded) that are characterized by different agro-ecosystems that could influence the pest's occurrence and bio-ecology. This is reported despite the existence of some similarities in farmers' general perceptions and trends in the three different areas. From this perspective, it should be pointed out that another potential challenge, i.e., the global impact of climate change on both the pest's bio-ecology and the already implemented management approaches, could come into focus in the near future in all concerned areas.

Farmers' expectations from researchers

Farmers in native range countries have expressed similar expectations from researchers, which are mainly linked to development of novel sustainable alternatives to chemical insecticides despite the promising control performance by insecticides in South America. This is mainly due to the frequent occurrence of resistant populations to several active ingredients used there, especially when considering that *T. absoluta* has been present in tomato-producing areas for a long time (Table S1).

As shown in Table S2, expectations from researchers are not quite different between European and North African/Middle Eastern farmers belonging to early-invaded countries. In the latter, the most common expectations from the questionnaires are to find sustainable solutions to both the pest's resistance to some chemical pesticides and phytophagy of the predator *N. tenuis* that frequently causes plant damage, and to further promote biological control as a primary alternative to chemical control. This can be performed either through identification and assessment of effective natural enemies or via development, registration and commercialization of novel effective microbial insecticides and Insect Growth Regulators (IGRs). Besides, testing and recommending effective and economically profitable biorational pest management combinations by researchers is considered a future task of utmost importance for farmers in early-invaded countries.

In contrast to native and early-invaded areas, as management strategies for *T. absoluta* are still in progress in African, Asian and Central American newly-invaded countries, finding a solution to the pest's resistance to pesticides is not currently considered a research expectation from farmers (Table S3). In these geographical areas where the pest is still spreading in most tomato-producing regions, providing recommendations on the most effective, but selective, chemical insecticides to control *T. absoluta*, developing cheaper biorational chemical-free alternatives such as the use of microbial pesticides and breeding resistant tomato cultivars constitute the most common research expectation from farmers.

Hence, apparently, farmers' expectations from researchers is area and time period-dependant because in some (native and early invaded) areas, researchers already tested and recommended to implement the most suitable pest management approaches, but this has not been yet achieved in the newly-invaded area where further time would be necessary to better evaluate the pest status and spread, its bio-ecology as well as overall agro-ecological and economic impacts following the invasion by *T. absoluta*.

Conclusions

We offer a timely review on the up-to-date development and practical implementation of IPM programs targeting *T. absoluta*. While chemical control could be suggested for limited use, owing to its multifaceted side effects as well as rapid development of insecticide resistance by the pest, many advances were made on the fundamental and applied research related to either biological or biotechnical control. Specifically, the combined use of different management options has been largely tested under greenhouse conditions, which have achieved satisfactory IPM goals (Biondi et al. 2018). Agronomic control-related research is an emerging and fertile area where modulation of soil fertilization and/or irrigation, as well as the breeding of resistant cultivars are very likely to enhance the efficacy of IPM (Han et al. 2019b). In practice, the IPM programs evolved along with the range and time of invasion. The lessons and knowledge gathered from the native range and/or early-invaded areas will be useful for the relevant stakeholders in newly-invaded areas. The biggest challenges for worldwide tomato growers, while they may somehow differ across continents, are the control failures by chemical pesticides and the high cost associated with biological and biotechnical control techniques (until further research to lower costs). Accordingly, researchers are expected to break the bottlenecks of some key issues that could enable lowering application costs, e.g., how to improve the biological control via increasing the mass-rearing capacity of key biocontrol agents and biocontrol efficacy in the field. Another challenging issue is the low extension/transfer ratio of the research findings from the research institutions to the actual stakeholders and farmers, which hints to the important roles of national agricultural administrations and local government in increasing the dissemination of effective control tactics against the pest.

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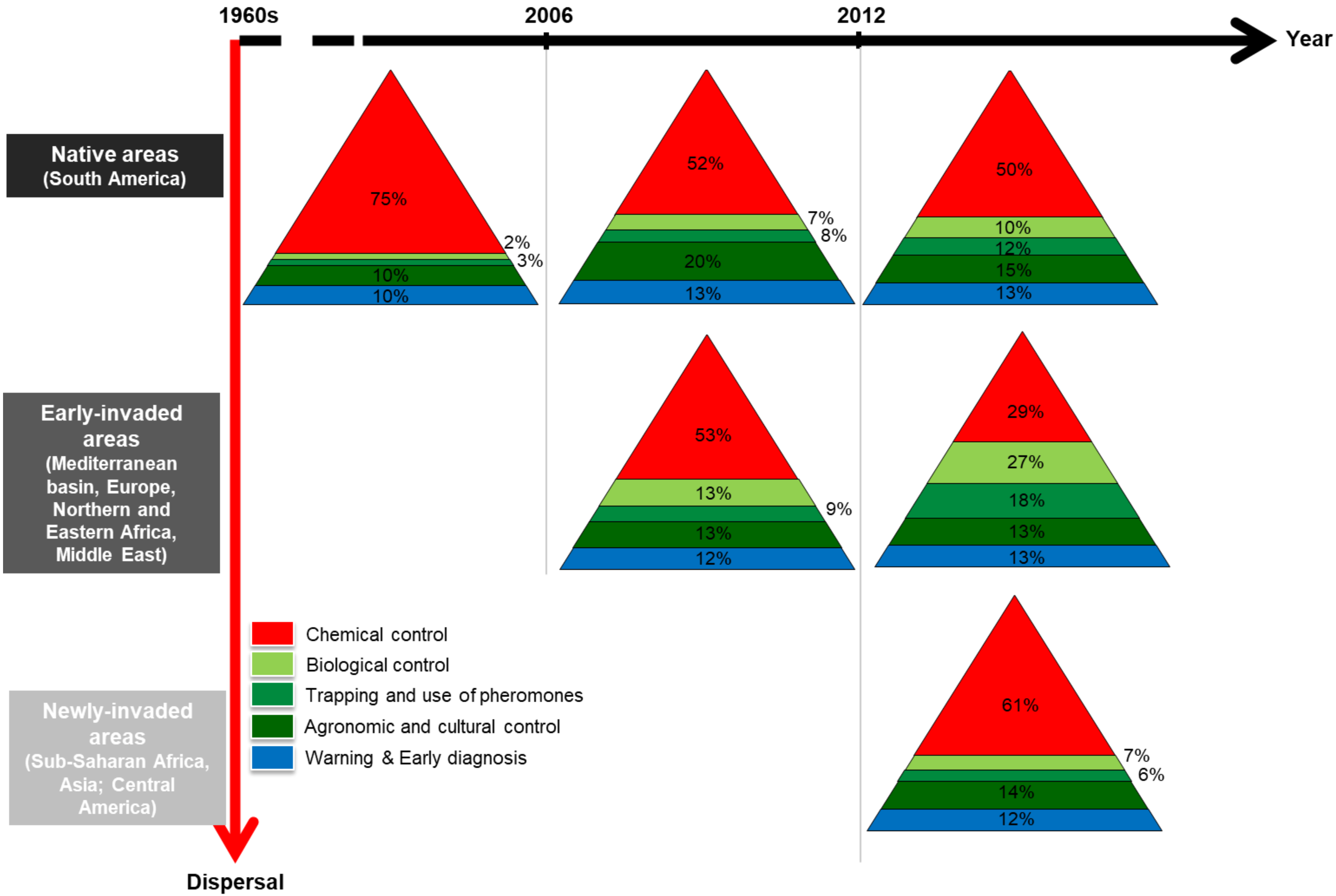
Ethical approval

This article does not contain any studies with human participants or animals (other than insects) performed by any of the authors.

Conflict of Interest

The authors declare no conflict of interests.

Figure 1. Diagrams on the proportion among control strategies employed within Integrated Pest management packages against *Tuta absoluta* in the native (<2006), early invaded (2006-2012) and recently (>2012) invaded ranges, during three time-intervals.


1960s
2006
2012
Year
Native areas
(South America)
75%
2%
3%
10%
10%
52%
7%
8%
20%
13%
50%
10%
12%
15%
13%
Early-invaded areas
(Mediterranean basin, Europe, Northern and Eastern Africa, Middle East)
53%
13%
9%
13%
12%
29%
27%
18%
13%
13%
Newly-invaded areas
(Sub-Saharan Africa, Asia; Central America)
61%
7%
6%
14%
12%
Chemical control
Biological control
Trapping and use of pheromones
Agronomic and cultural control
Warning & Early diagnosis
Dispersal