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Abstract
The South American tomato pinworm, Tuta absoluta (Meyrick), is native to the eastern Neotropics. After invading Spain in 2006, it spread rapidly throughout Afro-Eurasia and has become a major threat to world tomato production. Integrated pest management (IPM) strategies have been developed, but widespread insecticide use has caused selection for insecticide resistances as well as undesirable effects on key beneficial arthropods. Augmentation and conservation biological control relying on omnivorous mirid predators has proved successful for management of T. absoluta, where implementation is dependent on abiotic, biotic (e.g., alternative prey), and
anthropogenic factors (e.g., pesticides). Research has been carried out on larval parasitoids, showing potential for further development of sustainable control. The development of resistant tomato varieties is ongoing, but they are not commercially available yet. Knowledge gaps remain to be filled to optimize IPM packages on tomato crops and to help prevent further spread worldwide.

INTRODUCTION

Invasive species represent a major threat to natural and managed systems (6, 40, 74, 106). Biological invasions have occurred for millennia, but increasing globalization in recent decades has led to a drastic increase in the diversity and magnitude of invasions of new areas by alien species (76); this is particularly true for invasive exotic invertebrates (115). Such invasive species can reduce yields, increase control costs, and result in increased reliance on pesticides in agroecosystems (100, 111, 145), which, in turn, may disrupt preexisting integrated pest management (IPM) programs (106, 111). In addition, the establishment of invasive exotic species has the potential to cause cascading ecological impacts that may extend into natural systems as well (75).

The South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), has been a key pest of tomato in South America since the 1950s, causing drastic tomato yield losses owing to its leaf-mining activity and through fruit infestation in solanaceous vegetables (54). The status of *T. absoluta* completely changed following its invasion in Europe in 2006 and the steady spread across the Afro-Eurasian supercontinent as it shifted from a pest restricted to South America toward a major threat to global tomato production (29, 54). Tomato is one of the most widely cultivated commodities, with 5 million hectares (ha) planted worldwide and 170 million tons produced yearly (58).

We review the invasion history of *T. absoluta* in the Afro-Eurasian supercontinent. In addition, as major tomato-producing regions of the world—notably China, Mexico, and the United States, which account for 25% of the world’s tomato area cropped and 42% of the world’s tomatoes produced (58)—are at high risk of being invaded by *T. absoluta*, we provide a thorough overview of current knowledge on the ecology and management status of this pest, as well as identify potential future issues and research needs.

TAXONOMY, BIOLOGY, HOST RANGE, AND DAMAGE

The species was described from samples collected in Huancayo (Peru) and named *Phthorimaea absoluta* by Meyrick in 1917 but was subsequently classified in different genera (including *Gnorimoschema*, *Scrobipalpula*, and *Scrobipalpuloides*) until it was redescribed as *Tuta absoluta* in 1994 (109). Since then, it has been commonly named the South American tomato pinworm. It belongs to the Gelechiidae, a taxa encompassing >4,000 species and that includes key pests—notably Neotropical ones belonging to the Gnorimoschemini and developing on solanaceous plants—such as *Tecia solanivora* and *Phthorimaea operculella* (47) on potato and *Keiferia lycopersicella* on tomato (146). The two latter species are morphologically similar to *T. absoluta*, and accurate identification requires scrutiny of the shape of the valve and vinculum in male genitalia (108) or using barcoding methods, such as barcoding on cytochrome oxidase I (COI) genes (153).

Solanaceous species are the main host plants of *T. absoluta*, with tomato, potato, and European black nightshade (*Solanum nigrum*) the most suitable (4, 54). However, it can oviposit and develop on several plants belonging to the Amaranthaceae, Convolvulaceae, Fabaceae, and Malvaceae (11). Females use plant volatiles for orientation toward host plants, and leaf contact is a key component
for inducing oviposition (110); the latter is currently the major pitfall for developing effective plantless rearing methods (7). Eggs are yellow and laid individually by females in upper plant parts on young leaves, stems, or sepals (42). The larva feeds by mining the leaf mesophyll, thus producing a thin leaf mine. At high densities, larvae penetrate axillary buds of young stems and/or tomato fruits by mining below sepals (54). Mature larvae usually drop to the soil where they produce a thin, silky cocoon to transform into prepupae and pupae. Adults are crepuscular, and both genders are sexually active by the first day of emergence; both sexes are polygamous and show almost no refractory period. Mate communication relies on female sexual pheromones, and mating lasts from a few minutes up to six hours (86); females can produce ≤260 eggs during a lifetime (137). Interestingly, virgin females from French and Tunisian strains can exhibit deuterotoky parthenogenesis (3, 30), supposedly owing to Wolbachia infection (127); such phenomena have never been described in the native range. The pest affects tomatoes produced for both fresh and processed markets, with larvae causing up to 100% losses when no management methods are efficiently implemented (53). The feeding habits of *T. absoluta* make its presence difficult to detect in the early infestation period, resulting in severe damage on young plants. In addition, feeding activity on fruits directly affects the visual appeal of harvested products and increases costs for fruit postharvest selection before marketing (51).

The optimal temperature for *T. absoluta* development is 30°C (*r_m* = 0.12), and life cycle duration varies from 26 to 75 days, with upper and lower developmental thresholds estimated at 34.6° and 14°C, respectively (92). Although no development or reproduction occurs at low temperature (48), *T. absoluta* shows cold tolerance, with 50% larval, pupal, and adult survival at 0°C (for 11.1, 13.3, and 17.9 days, respectively). There is no evidence of reproductive diapause induced by short days (143). These biological characteristics enable *T. absoluta* to undergo up to 10 generations per year and to survive during cold seasons in protected and open-field crops (i.e., in northern and temperate regions, respectively). However, the pest has been reported to be susceptible to bottom-up effects, notably when tomato plants are subjected to nitrogen and water limitations; in such conditions, its juvenile survival rate decreases and the developmental time increases (71, 73, 84) owing to changes in larval food intake dynamics (46).

**DISTRIBUTION AND QUARANTINE OF *TUTA ABSOLUTA***

**Origin and Recent Spread in the Palaearctic Region**

*Tuta absoluta* was initially described as native to Central America, but recent hypotheses suggest it originated in Peruvian central highlands, spreading to Latin America countries during the 1960s (29, 53). Being well established as a key tomato pest in South America for more than 50 years, *T. absoluta* was then detected in Spain in 2006 (138) and then rapidly spread across the Mediterranean coastal tomato-producing areas (53, 54) (Figure 1). Since then, the pest has spread at an average speed of 800 km per year both eastward and southward. The introduction stemmed from a single initial Chilean population (69) imported into Spain in the early 2000s (58). The species quickly reached economic pest status on tomato in invaded areas, occurring despite plant protection agency efforts (29, 53). The lack of coordinated actions among European countries, both invaded and not yet invaded, has underlined the lack of dedicated structures enabling plant protection agencies to prevent and/or slow down the dispersal of an important invasive pest such as *T. absoluta*.

In the Afro-Eurasian supercontinent, the Asian edge of *T. absoluta* distribution by mid-2017 became western India (120), and unconfirmed reports from Pakistan and Tajikistan noted its presence there as well (29). Pest distribution in eastern Russia has not been documented, and *T. absoluta* might be only sparsely distributed owing to the cold climate and/or absence of suitable
hosts in such high northern latitudes. The African continent has been almost totally invaded in eight years since detection in Morocco in 2008, and invasion was reaching South Africa as of 2016 (129, 132, 136). However, *T. absoluta* has not been officially reported in many central and southwestern African countries (29). Nonetheless, the United States Department of Agriculture–Animal and Plant Health Inspection Service (USDA–APHIS) (140) considers it present in most of these countries, owing to a combination of factors, including (a) the geographic proximity to invaded countries, (b) the lack of geographic barriers, and (c) the likelihood of establishment (e.g., predictions through CLIMEX models) (136). The current distribution of *T. absoluta* in Asia matches the predicted spread timeline suggested by Desneux et al. (53), with the exception of China, which has not yet been invaded (Figure 1) but is at high risk owing to the presence of

![Figure 1](image-url)

**Figure 1**
Current *Tuta absoluta* worldwide invasion history (as of May 2017) and main tomato-planting area at risk of invasion in China and the United States. (a) Invasion timetable and (b) tomato-planting area in the United States (left) and mainland China (right)—the two remaining main tomato-producing countries not yet invaded. The information on pest distribution is based on a compilation of reports from plant protection services and extension specialists, as well as from scientific articles. Data on the planting area for the United States and mainland China are from the United States Department of Agriculture Economics, Statistics and Market Information System (141) and Xian et al. (149), respectively.
the pest in neighboring countries and the vast areas of tomato cultivated, totaling 1 million ha and representing 20% of the world’s tomato-planted surface area (58). The risk of a pan-global distribution with additional invasion is quite high, with recent movement northward from South America to Central America, the rapid spread across Asian and African countries, and human-assisted spread through trading routes, so that countries such as New Zealand, the United States, and Australia may ultimately be invaded. Its occurrence in dry and hot regions in Africa suggests that *T. absoluta* is strongly heat tolerant and can survive as long as host plants are available. By contrast, cold winters, lack of soil moisture, and/or drought stress may be key factors that lower the risk of permanent establishment in northern Europe, most of Russia, and Canada (136).

In *T. absoluta*’s native range, its spread among South American countries has historically been attributed to the fruit trade (22); this hypothesis is now supported by the interceptions of *T. absoluta* at packaging sites of imported fruits in the Netherlands, United Kingdom, Lithuania, and Russia (53). Moreover, tomato greenhouses and plant nurseries may help *T. absoluta* build up populations and survive unfavorable climatic conditions (143). These sites are hot spots, perhaps acting as bridgeheads for further invasion. Evidence of dispersal across geographic barriers (e.g., invasion of isolated islands, such as Cape Verde) and spread across desert areas of Africa and the Middle East underline the importance of human-assisted transport. Data from sampling with pheromone traps and spatial assessments suggest high *T. absoluta* dispersal capacity (63, 121). However, we still lack data on its flight ability (e.g., its use of flight mills and how wind currents contribute to long-range movements). The recent invasion history in Afro-Eurasian and Middle Eastern countries implies that areas with large monocultures of tomato and/or that provide alternative hosts favor *T. absoluta* expansion.

**Quarantine, Monitoring, and Eradication Potential in Noninvaded Regions**

Before invading Spain, *T. absoluta* was included on the list of quarantine pests of the European Plant Protection Organization but was not listed in the Plant Health Directive (2000/29/EC) of the European Commission. Thus, imported tomato materials were not subjected to plant health inspection before entry into Europe, and the omission likely helped initial introduction. In 2009, after entering Europe, the USDA-APHIS issued a federal import quarantine order for materials potentially carrying *T. absoluta*, including on fresh tomatoes and alternative host plants (140). In addition, the USDA quickly released a guidance document providing identification, survey, and control protocols, as well as a list of summarized entry pathways into the United States (139). The North American Plant Protection Organization also established a surveillance protocol for early detection and quarantining in North America (97). Surveys targeting *T. absoluta* have been carried out in the key tomato-producing states of California and Florida. Similar actions have so far been successfully taken by Canada (34) and Australia (148). In addition, an invasion in Mexico would make further spread northward inevitable because 95% of tomatoes imported into the United States are from Mexico (58). Such invasion would threaten US tomato production (58) and potentially raise production costs. Such costs increased by more than 450 € per hectare per cropping season in the first years of European invasion (53).

In 2014, mainland China, the world’s largest producer of tomatoes, established a surveillance plan targeting *T. absoluta* through the Department of Biological Invasions (DBI) of the Chinese Academy of Agricultural Sciences in areas at risk. Monitoring takes place in tomatoes in greenhouses and open fields located in neighboring countries where the pest is present. Monitoring sites include India and Pakistan, as well as near international airports because tomato fruits are often intercepted there. The DBI continuously monitors high-risk areas such as Beijing, Tianjin, Hebei, and Xinjiang using traps based on sex pheromone lures (see Supplemental Figure 1), as well as
by random sampling and by checking cultivated and wild host plants (Supplemental Figure 2). In the case of detection, eradication methods include the destruction (burning) of infested plants, concurrent real-time monitoring using pheromone traps, strict phytosanitary practices, and area-wide joint prevention practices, as well as other control methods, such as biological control (145). In addition, the National Agro-tech Extension and Service Center (NATESC) will monitor the pest to prevent further spread, relying on a network made up of the 41,000 NATESC agricultural stations nationwide (149).

**INTEGRATED MANAGEMENT OF TUTA ABSOLUTA**

**Monitoring, Mass Trapping, and Mating Disruption**

Monitoring of *T. absoluta* populations in tomato crops is usually performed by trapping males and/or by sampling eggs and larvae infesting plants. Male density tends to be negatively correlated with tomato production, but economic thresholds based on male captures are not reliable because trapping is affected by various factors, such as population density and trap and pheromone types (31). The joint use of egg counts and adult trap counts does not seem to be a highly reliable strategy for estimating *T. absoluta* damage (12). Moreover, egg counting is costly in terms of labor, as eggs are small and laid randomly, requiring multiple leaves to be sampled. A more efficient binomial nondestructive sampling plan that allows decision making by checking for the presence of mines only on the middle third of the tomato plant reportedly keeps fruit damage below 1% (43).

The synthetic female sex pheromone is used for early detection and mass trapping of *T. absoluta*. The use of 48 homemade traps (translucent plastic cylinders, 9 × 11 cm, with a 4.5- × 6.5-cm opening) per hectare containing pheromones enabled a greater reduction in leaf infestation compared to conventional insecticides in Argentinean tomato protected crops (88). Pheromone dispensers can be used in association with light sources and water traps to mass trap both adult genders simultaneously (31). Mass trapping could also rely on sticky traps, although the possibility of side effects through non-target captures needs assessment. Mating disruption has been developed for tomato greenhouses where the use of 30–60 g of pheromone per hectare can be sufficiently effective in high-containment glasshouses to control the moth populations and reduce the percentage of damaged fruits but not in open plastic greenhouses, the latter being typical in Mediterranean areas (41, 142). Beyond the studies about the ability of *T. absoluta* to undergo parthenogenesis (30) or multiple mating (86), this finding stresses that effective mating disruption relies primarily on being able to prevent fecund females from immigrating into greenhouses. Finally, similar concerns may apply to the development of the sterile insect technique targeting *T. absoluta*; such a method has proved promising at an overflooding ratio of 15:1 (23).

**Tomato Resistance and Breeding Programs**

Breeding host plants resistant to *T. absoluta* remains an intensively pursued management tactic, particularly since the 1990s (66); the cultivated tomato is highly vulnerable to *T. absoluta*. Although genetic sources of resistance to *T. absoluta* were detected among germplasm bank accessions of *S. lycopersicum* (61, 128), the most promising genetic sources of resistance are from wild tomato (56, 87, 90, 102). Constitutive tomato resistance to *T. absoluta* has been the focus of attention in breeding programs relying on resistance related to leaf allelochemicals or trichome density (49, 66). Glandular trichomes, particularly those containing 2-tridecanone, zingiberene and/or acyl sugars, exhibit high deterrent activity on *T. absoluta* (19, 49, 90, 128). These compounds impair egg laying and larva feeding, leading to antixenosis, and larval toxicity, leading to antibiosis
(19, 49, 144). The initial focus on 2-tridecanone has shifted to increasing leaf zingiberene and acyl sugar content (19, 49, 85, 90). Breeding lines with high acyl sugars have been obtained, and commercial cultivars are expected to be released (55, 85).

Induced resistance mechanisms in tomato are being considered. As a chewing insect, *T. absoluta* triggers the jasmonic acid (JA) pathway, potentially enhancing plant defenses against various pests as a result of cross-effects between distinct plant defense pathways (96, 150). This induction may be involved in (a) constitutively expressed defensive allelochemicals toxic to pests, (b) the release of volatile organic compounds (VOCs) that attract natural enemies, and (c) preventing the release of volatiles necessary for host-plant finding by *T. absoluta* (19, 50, 131).

Manipulating tomato resistance to *T. absoluta* is a promising management tactic but has pitfalls. Focusing solely on constitutive resistance may prevent identifying key mechanisms of importance for overall pest management in tomato. Defensive response pathways are cross-linked, and spatiotemporal patterns of resistance may affect various pest and beneficial species developing on a shared plant (95, 130). Whiteflies trigger negative plant-mediated indirect interactions on *T. absoluta*, whereas the latter foster powdery mildew colony growth in a systemic way (96) (Figure 2), presumably linked to cross-talk between jasmonate and salicylate pathways (134). Overall, manipulating resistance to *T. absoluta* may affect micro- and macroorganism communities on tomato, leading to unanticipated cascading consequences on yield.

### Biological Control

Many species (>160 taxa) have been reported as natural enemies of *T. absoluta* in South America (54) and Afro-Eurasia (152) (exhaustive lists in Supplemental Tables 1 and 2). Most are polyphagous, and no true specialized species have been reported impairing the development of classical biological control against *T. absoluta* (54). By contrast, conservation and augmentative biological control programs have been developed, with increasing interest following the invasion of Europe.

Hemipteran predators, notably anthocorids, geocorids, mirids, nabids, and pentatomids, have been identified as effective predators against *T. absoluta* in both native and invaded areas. In Europe, sustainable control was achieved using omnivorous mirids soon after the pests’ arrival, notably through their use in augmentative, inoculative releases in fields and/or in plant nursery situations (24, 54, 152) and/or through their use in conservation strategies (e.g., using banker plants) (Figure 2) (8, 17, 77). Among mirids, *Nesidiocoris tenuis*, *Macrolophus pygmaeus*, and *Dicyphus* spp. feed on *T. absoluta* eggs and young larvae, slowing down and/or suppressing pest population establishment and growth in tomato crops (80, 94). However, they differ in key ecological characteristics: *N. tenuis* populations can increase when relying only on the *T. absoluta*–tomato system (93), whereas such a system is not fully suitable for *M. pygmaeus* (79, 133), which requires alternative prey-like whiteflies to support population growth (80) (Figure 2). *Dicyphus* spp. is an intermediate case, as it develops well using *T. absoluta* eggs as a sole prey but shows weak population growth on tomato when prey is lacking (1, 78). These mirids have contrasting phytophagous habits on tomato; high population density of *N. tenuis* turns it into a pest when prey is scarce, inflicting necrotic rings on plants and fruits (17, 119). The two other mirids do not cause plant damage, or do so to a lesser extent (32). Interestingly, the polyphagous habits of these mirids can promote indirect interactions among the pests on tomato—for example, *M. pygmaeus*–mediated apparent competition occurs between whiteflies and *T. absoluta* (80), and the alien pest (*T. absoluta*) has led to increased biocontrol of the native whiteflies pests in Europe (20). Various other generalist predators may also provide valuable biocontrol services against *T. absoluta* (e.g., vespids in Brazil) (104), but they have not been effectively used in IPM strategies. Finally, spiders, predatory mites, thrips, lacewings, earwigs, ground beetles, ladybugs, and ants have been reported feeding...
occasionally on *T. absoluta*, but no biocontrol activity has been quantified thoroughly (54, 152) (Supplemental Tables 1 and 2).

Multiple parasitoids have been identified parasitizing *T. absoluta* in South America and in newly invaded regions. Egg parasitoids, notably species of *Trichogramma*, are found in association with *Tuta absoluta*. Other parasitoid species include *Nesidiocoris tenuis*, *Macrolophus pygmaeus*, *Oidium neolycopersici* (powdery mildew), *Dittrichia viscosa*, *Stenomesius japonicus*, *Bracon nigricans*, and *Trialeurodes vaporariorum* (greenhouse whitefly). Photos from M. Bardin (*Oidium neolycopersici* (powdery mildew)), J. Cardina (*Verbascum thapsus*), A. Chailleux (*Macrolophus pygmaeus*, *S. Japonicus*), G. Mittelhauser (*Fagopyrum esculentum*), and P. Santorrromán (*Dicyphus* sp.).

**Figure 2**

Biotic interactions and linkages between *Tuta absoluta* and other components of the tomato agro-ecosystem and neighboring systems. Lines with circles show negative effects in the direction of the circles, and lines with arrows show positive effects in the direction of the arrows. Solid lines show direct interactions, and dashed lines show indirect interactions (mediated by another component of the system; *green* and *red* indicate plant- and natural enemy–mediated indirect interactions, respectively). Thickness of lines and size of circles/arrowheads are proportional to the known or estimated strength of the interactions. Signs and magnitudes of arrows are derived from studies cited and discussed in the review. Other larval parasitoid species are *Stenomesius japonicus* and *Bracon nigricans*. Photos from M. Bardin (*Oidium neolycopersici* (powdery mildew)), J. Cardina (*Verbascum thapsus*), A. Chailleux (*Macrolophus pygmaeus*, *S. Japonicus*, *Trialeurodes vaporariorum* (greenhouse whitefly), and *Trichogramma* sp.), G. Mittelhauser (*Fagopyrum esculentum*), and P. Santorrromán (*Dicyphus* sp.).
*T. absoluta*, but natural parasitism appears low, possibly owing to the poor egg quality for *Trichogramma* offspring development (36, 37). Mass rearing associated with inundative releases of several species, notably *T. pretiosum*, *T. acbeae*, and *T. euproctidis*, proved technically viable as biocontrol agents (up to 90% parasitism) in tomato greenhouses in Brazil, Spain, and Egypt, respectively (57, 101, 152). Still, multiple releases are needed owing to the low suitability of the *T. absoluta*–tomato system for *Trichogramma*, which prevents their establishment in the field (35, 36, 37, 57), thus compromising their economic usefulness against *T. absoluta*. Larval parasitoids (mainly ectoparasitoids) have been documented with most dominant ones belonging to Eulophidae and Braconidae. They often exhibit reproductive and nonreproductive host killing activities, thus maximizing effects on *T. absoluta* (14, 59). The main species studied as potential biological control agents are *Pseudapanteles dignus* and *Dineulophus phthorimaeae*, with up to 40% parasitism in South America (54), and *Bracon nigricans* (14), *Stenomesius japonicus* (38, 39), and *Necremnus tutae* (59) in Europe. The latter has been identified as a new species widely distributed in Mediterranean basin countries following invasion by *T. absoluta* (60). To date, the cosmopolitan eulophid *Neocrysocharis formosa* is the only parasitoid recorded on the pest in both the native and the invaded regions. Parasitoid species attacking pupae of this pest have been only occasionally reported (Supplemental Tables 1 and 2).

Microbial control has been evaluated and relies mostly on commercial strains of *Bacillus thuringiensis* (Bt) var. *kurstaki* and *aizawai* that kill larvae when ingested (64). Other *Bacillus* spp. as well as the fungi *Beauveria bassiana* and *Metarhizium anisopliae* have been studied (21, 45) but have not resulted in commercial products specifically designed for *T. absoluta*. The nematodes (*Steinernema* and *Heterorhabditis* spp.) also reduce plant infestation of *T. absoluta* by 87–95% under laboratory and greenhouse conditions (10), though there has been no reported use in commercial greenhouses or in the field.

Biological control programs against *T. absoluta* should rely on the combined use of complementary biocontrol agents such as parasitoids, microbials (e.g., Bt), and/or mirid predators to maximize biocontrol services (35, 94). However, intraguild predation (IGP) (98, 116) among natural enemies could be detrimental to biocontrol services; thus, combined releases should be carefully assessed before implementation. Increased biological control could be achieved by using such combinations when IGP predation is minor or does not hinder the coexistence and effectiveness of natural enemies during the cropping season (38, 39, 98). For instance, the parasitoid *S. japonicus* and the omnivorous *M. pygmaeus* were found to exhibit complementary functional traits leading to the best control when combined, despite effective kleptoparasitism from the predator (Figure 2) (38, 39).

### Historical Overview of Insecticide Use in Native Range

Insecticide use is the primary tool to manage invasive arthropod pests at the onset of their introduction (106, 111). This occurs with *T. absoluta*, mainly owing to the immediate threat to tomato production coupled with the lack of management alternatives in the invaded areas (29, 53). In South America, *T. absoluta* is notoriously difficult to control because of early colonization of fields; the attack of and injury to multiple plant parts, including the stem apex, leaves, and fruits; and the protection provided by the plant canopy (66). Thus, the chemical control of *T. absoluta* is a rather complex issue, and the level of control achieved is often disappointing. Establishment of large *T. absoluta* populations in tomato fields before plants reach the reproductive stage can compromise insecticide efficacy. Formulation adjuvants and spraying technologies play a major role in circumventing some of these problems, but effective insecticide use against *T. absoluta* remains challenging (66, 105). Altogether, these difficulties, together with the management consequences stemming from intensive insecticide use, have led to successive changes in the compounds used against *T. absoluta*. The early use of organophosphates and pyrethroids during the 1960s was...
replaced by cartap and abamectin, then by the oxadiazine indoxacarb, and later by chitin synthesis inhibitors (66, 67, 126). By the 2000s, the insecticide portfolio included the pyrrole chlorfenapyr, spinosyns, and the diamides chlorantraniliprole and flubendiamide that are in current use (63, 66, 121). Organic tomato production systems are another challenging scenario, with insecticide use limited to a few compounds, such as azadirachtin, spinosyns, and Bt (15, 16, 121, 135). Insecticide use, and overuse, against arthropod pests leads to potential short- and long-term consequences, which may have unpredictable effects on pest management effectiveness and yields (52, 68, 65).

Insecticide Resistance, Control Failure Likelihood, and Side Effects on Biocontrol Agents

Early complaints regarding efficacy of insecticides used against T. absoluta in Chile led to concerns about insecticide resistance (66, 67, 118). Initially, low levels of pyrethroid resistance, followed by further detection of resistance to abamectin, cartap, and the organophosphate methamidophos, were observed in South America (118, 125, 126). Invasion in Europe sparked interest in insecticide resistance among T. absoluta populations (67). Widespread pyrethroid resistance was detected in Europe (112), and moderate resistance to indoxacarb and to the spinosyn spinosad was detected in Europe and South America (27, 63, 67, 121). It prompted diversification of insecticide use on tomato (66, 67) and a notable increase in use of chitin synthesis inhibitors, leading to high levels of resistance to most of these compounds (63, 121). This compounded the problems related to resistance of older insecticides already in use (28, 81, 121, 122). Meanwhile, pyrethroid resistance apparently receded in some areas, as did resistance to abamectin, perhaps resulting from the decreasing use of these compounds (63, 121). Nevertheless, diamide resistance is rising in Brazil and Europe (28, 114). Curiously, reports on chlorfenapyr resistance in T. absoluta populations are still sparse (122).

Studies with insecticide synergists and in vitro activity of detoxification enzymes are suggestive of enhanced detoxification activity by esterases and cytochrome P450-dependent monooxygenases as the main underlying mechanisms of abamectin and spinosad resistance (27, 70, 125). The latter seems also important for cartap and chlorantraniliprole resistance (28, 126). Nonetheless, altered target site sensitivity to chlorantraniliprole and spinosad have been recently reported (28, 113, 124). Altered target site sensitivity is a major pyrethroid resistance mechanism in the tomato pinworm with three kdr/superkdr-type mutations (M918T, T929I, and L1014F) (70, 123). There is a high frequency and congruence of these mutations in South America and Europe.

Insecticide resistance may lead to control failure, justifying the attention paid to this phenomenon (65); however, estimating the likelihood of such failure requires suitable methods. This has been particularly well documented in the case of T. absoluta because of multiple control failures when spraying insecticides (63, 65, 121, 123). The next step would be the use of geographical information systems and spatial analyses in surveys of insecticide resistance in populations of T. absoluta to map the phenomenon and areas of high risk of control failure by insecticides. Such effort will allow the recognition of the regions of concern for further intervention and will also allow forecasting areas at risk of insecticide control failure (65).

Insecticides are detrimental to beneficial arthropods either through direct acute toxicity and/or sublethal effects (52, 89), and the arrival of T. absoluta in the Afro-Eurasian region led to increased usage of insecticides (53) and disruption of IPM programs on tomato. Conventional synthetic pesticides may induce lethal and/or sublethal effects in natural enemies of T. absoluta. Exposure to thiacloprid residues led to reduced feeding activity (e.g., attack rates) of M. pygmaeus (91). Fertility and biocontrol activity of B. nigricans is reduced by exposure to chlorantraniliprole residues only when temperatures are high (35°C) (2). Laboratory studies report few or no effects of
chlorantraniliprole on survival and reproduction of generalist predators (15, 26, 103), but this chemical may compromise the capacity of anthocorid nymphs to reach adulthood (62). By contrast, indoxacarb reduced survival of Heteropteran predators but not fertility (5, 15, 147), and this has been linked to reduced walking activity during contact with residues, thus minimizing predator exposure to this insecticide (103).

Pesticides currently registered for organic farming (including biopesticides) may also threaten the effectiveness of *T. absoluta* natural enemies. Recommended field rates of spinosad cause high mortality in predatory wasps in Brazil, with strong effects lasting more than a month in the absence of rainfall (9). Spinosad also showed high levels of toxicity to the parasitoid *B. nigricans* (2, 18) and multiple other hymenopteran parasitoids (16), including some attacking other tomato pests (e.g., *Eretmocerus warrae*, a parasitoid of *Bemisia tabaci*) (83). By contrast, predator survivorship is usually not affected by spinosad. However, exposure to residues drastically reduce fecundity of mirids and flower bugs (5, 15), and repellent effects as well as reduced mobility have been reported in stinkbugs and earwigs, respectively (26, 51). The avermectin biopesticides (mainly emamectin benzoate and abamectin) do not induce lethal toxicity in the parasitoids *T. pretiosum* and *B. nigricans*; however, they do reduce longevity, fertility, and biocontrol activity (18, 44). Similarly, lower negative effects have been reported for azadirachtin, a compound commonly used in tomato crops (5, 15, 18, 33).

**FUTURE OUTLOOK**

Current simulations and estimates all indicate the potential worldwide spread of *T. absoluta* to all key tomato-growing regions (29, 53, 136). Ongoing reassessments of *T. absoluta* thermal requirements beyond mostly survival and development traits to other demographic parameters in physiologically based demographic models (107) suggest that *T. absoluta* thermal requirements (14–35°C) fit those of optimal tomato cultivation (82, 92). Global warming may favor further establishment in areas not specifically suitable in the past, increasing the importance of this tomato pest.

Regional differences in cropping practices, cultivars, IPM strategies, and climatic conditions will be important, but information will still be needed regarding invading strains and their control-relevant traits such as degree of prepackaged insecticide resistance, potential genetic variability in thermal and/or drought tolerance, and/or possible maternally transmitted endosymbionts (e.g., *Wolbachia*).

The commercial development of *T. absoluta*–resistant tomato cultivars is in progress despite potential deleterious cross-linked traits and/or spatiotemporal patterns of resistance that might affect other pests and/or natural enemies (50, 96). Overall, two main approaches for breeding resistant plants have been considered: *T. absoluta*–resistant transgenic plants and plants with induced resistance. The former involves the production of transgenic tomato plants expressing insecticidal proteins like *Bt* that can be incorporated into the tomato genome. These transgenic tomatoes exhibit resistance to lepidopteran pests (13, 117), and although *T. absoluta* was not the initial target, the strategy is regaining momentum despite controversies that will occur regarding potential wide-scale use (89). RNAi technology may also play an important role in the tomato genetic transformation aimed at resistance to *T. absoluta*, if increased performance against lepidopteran pest species is finally achieved (151). The induction of plant resistance, more particularly through the JA pathway, is a key target for induced plant defenses, as it could promote constitutively expressed defensive allelochemicals, such as proteinase inhibitors and trichomes, as well as modify attractiveness of VOCs. It may enable crop manipulation by either enhancing release of VOCs attractive to natural enemies or by preventing release of VOCs used by *T. absoluta* for host-plant detection (50, 99, 131). Reduced availability of nitrogen and/or water increase tomato (pseudo-) resistance against *T. absoluta* (71, 73, 84), although they may cause cascades affecting omnivorous mirids (72).
Insecticide use remains the key strategy for managing *T. absoluta*. However, continuous selection of insecticide-resistant populations limits the sustainable and commercial life of most insecticides (67). Ironically, in areas where *T. absoluta* is absent, there has been a continuous decline in insecticide use on tomato during the past decade (e.g., in New Zealand) (25), regarding applied amounts and toxicity of products used. Therefore, the successful development and implementation of cost-effective biocontrol methods will remain crucial for future sustainable control as well as for making IPM strategies more robust to potential hazards. Whereas development of management methods in recently invaded areas has benefited to some extent from knowledge learned from the native range, other key aspects remain scarcely documented, particularly at the environmental and economic scales. Perhaps more significant, yet difficult to quantify, are the health and societal costs of such pests. Historically, major invasions, such as this, have caused subsistence farmers to abandon the cultivation of the affected crops, leading to lasting economic insecurity (106).

### SUMMARY POINTS

1. *Tuta absoluta* is a pest of solanaceous plants native to the eastern Neotropics. It was first discovered in Spain in 2006 and has subsequently spread throughout the Palaearctic and African regions. In 10 years, this pest increased from infesting 3% to 60% of the worldwide tomato-cultivated area. It currently represents the main long-term threat for the countries producing the most and third-most tomatoes (China and the United States, respectively).

2. Control strategies have historically relied on the widespread use of insecticides that have resulted in selection for insecticide resistance in many *T. absoluta* populations as well as in side effects on most of the non-target arthropods present in the tomato agro-ecosystems. Such increased insecticide use has disturbed preexisting integrated pest management (IPM) programs in invaded areas, such as Europe.

3. Biocontrol of *T. absoluta* has been developed, and it relies largely on the augmentation and conservation of omnivorous mirid predators, conservation of parasitoid complexes, and use of microbial organisms such as *Bacillus thuringiensis*.

4. *Tuta absoluta* is involved in multiple direct and indirect (plant- and natural enemy-mediated) interactions with other insects and wild and cultivated plants, as well as endemic natural enemies.

5. Multiple sublethal effects, sometimes counterintuitive ones, on natural enemies have been reported for modern slower-acting insecticides and/or biopesticides. This highlights the need to revise the labeling of these products to indicate their compatibility with organic farming requirements and sustainable IPM programs.

### DISCLOSURE STATEMENT

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