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Propensity of the Tomato Leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), to Develop on Four Potato Plant Varieties

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Abstract The tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), is now considered to be one of the most damaging invasive pests of tomatoes in the world. Tomato is regarded as the main host of *T. absoluta*, but the pest can also feed, develop and reproduce on other cultivated Solanaceae, such as potato (*Solanum tuberosum* L). In the present study, we examined the ability of *T. absoluta* to develop on four commonly cultivated varieties of potato, under laboratory conditions. The survival rate of *T. absoluta* did not differ between the five tested host plants (tomato: *Solanum lycopersicum* cv. Moneymaker; and potato: *Solanum tuberosum* cv. Spunta, Charlotte, Nicola, and Bintje), but its development time (egg to pupation) was significantly affected. Compared to tomato, development times were longer on Bintje and shorter on Nicola, Charlotte, and Spunta. These results show the high capacity of *T. absoluta* to develop on potato crops.

Resumen El minador de la hoja en tomate, *Tuta absoluta* (Lepidoptera: Gelechiidae), está considerado actualmente como una de las plagas invasivas de mayor daño en tomates en el mundo. Se considera al tomate como el hospedante principal de *T. absoluta*, pero la plaga también se puede alimentar, desarrollar y reproducir en otras Solanáceas cultivadas, como la papa (*Solanum tuberosum* L.). En el presente estudio examinamos la habilidad de *T. absoluta* para desarrollarse en cuatro variedades de papa cultivadas comunmente, bajo condiciones de laboratorio. El nivel de sobrevivencia de *T. absoluta* no difirió entre los cinco hospedantes probados (tomate: *Solanum lycopersicum* cv. Moneymaker; y papa: *Solanum tuberosum* cv. Spunta, Charlotte, Nicola, y Bintje), pero su tiempo de desarrollo (de huevo hasta pupa) se afectó significativamente. En comparación con el tomate, los tiempos de desarrollo fueron más largos en Bintje y más cortos en Nicola, Charlotte, y Spunta. Estos resultados muestran la alta capacidad de *T. absoluta* para desarrollarse en cultivos de papa.

Keywords Host plant · *Solanum lycopersicum* · *Solanum tuberosum* · South American tomato moth · Fitness

Introduction

The tomato leafminer, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), is considered to be a key pest of the tomato (*Solanum lycopersicum* L.; Solanaceae), under both field and greenhouse cultivation, in South America, Europe and Mediterranean countries (Miranda et al. 1998; EPPO/OEPP 2005; Pereyra et al. 2006; Urbaneja et al. 2009; Desneux et al. 2010; Desneux et al. 2011). This pest has spread rapidly since its introduction to Europe in 2006, and within just a few years its world status has completely changed, from a South American tomato pest into a major threat to world tomato production (Desneux et al. 2011). The moth is now present on the EPPO A2 list of pests recommended for regulation as quarantine pests (EPPO/OEPP 2011). Despite *Tuta absoluta* is considered as a major tomato pest, the applicable rules are unclear. The only recommendations

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are that plants for planting and tomato fruits originating from countries where *T. absoluta* occurs, should be free of the pest (EPPO/OEPP 2005).

Tuta absoluta is considered an oligophagous insect that damages solanaceous plants, especially tomatoes (Siqueira et al. 2000). It can also feed, develop and reproduce on other cultivated Solanaceae, such as eggplant (*Solanum melongena* L.), potato (*S. tuberosum* L.), sweet pepino (*S. muricatum* L.), and tobacco (*Nicotiana tabacum* L.) (Galarza 1984; Garcia et al. 1987; Colomo et al. 2002; Pereyra et al. 2006; Desneux et al. 2010). In the wild, *S. nigrum* L., *S. elaeagnifolium* L., *S. bonariense* L., *S. sisymbriifolium* Lam., *Nicotiana glauca* Graham, *Lycopersicum puberulum* Phil., *Datura ferox* L., and *D. stramonium* L. are also cited as potential host plants (Garcia et al. 1987; Pereyra et al. 2006). In Europe, *T. absoluta* has been reported in a Sicilian greenhouse on Cape gooseberry (*Physalis peruviana* L.) and has also been found elsewhere in Italy on *Lycium* sp., on bean (*Phaseolus vulgaris* L.; Magnoliopsida: Fabaceae) and *Malva* sp. (Magnoliopsida: Malvaceae) (Tropea Garzia 2009; Desneux et al. 2010).

Among host plants of *T. absoluta*, potato is the fifth most important commodities, with more than 300 million tons produced in 2010 (FAO 2010). Tomato production is half that of potato, with 150 million tons produced in 2010 (FAO 2010). Potato crops are an open-field production concentrated in Europe and Asia, with more than 80 % of world production on these two continents (FAO 2010). This pest could probably spread to nearby potato crops, which could potentially result in significant yield loss by feeding on aerials parts of the plants, as has been reported in Peru and, more recently, in Portugal and in Turkey (Campos 1976; Desneux et al. 2011; Morrison et al. 2011; Unlu 2012). In the present study, we examined the ability of *T. absoluta* to develop on four commonly cultivated varieties of potato, under laboratory conditions.

Materials and Methods

Plant and Insect Cultures

Tomato (*Solanum lycopersicum* cv. Moneymaker) and potato (*Solanum tuberosum* cv. Spunta, Charlotte, Nicola, and Bintje) plants were cultivated in a greenhouse (25±5 °C) in plastic pots (20 cm diameter × 20 cm height) filled with loam (VP113BIO; Peltracom, Belgium) and grown with a 16 L :8D photoperiod.

In July 2011, 200 third instar larvae of the tomato leafminer, *Tuta absoluta*, were collected from a commercial tomato plantation located in Saint-Andiol (France), and were subsequently kept under laboratory conditions at 24± 1 °C, 60–70 % RH, and with a 16 L:8D photoperiod. Five separate *T. absoluta* colonies were each reared on tomato, Spunta, Charlotte, Nicola, or Bintje within net cages (each 46.5×46.5×46.5 cm). Caterpillars were provided with fresh plants three times a week until pupation. Five generations were raised on each type of host plant before starting any experiment, to eliminate the effect of food reserves in the eggs and on the emerging larvae (Hasan et al. 2011) and also to keep an important ratio of females and males in the colonies to avoid parthenogenetic reproduction of the females and consequently, a decrease of their fitness (Caparros Megido et al. 2012).

Evaluation of *Tuta absoluta* Fitness on Tomato and Potato Host Plants

One hundred *Tuta absoluta* eggs were taken from each leafminer population. Each egg was individually placed in a petri dish (5 cm diameter) lined with moistened filter paper and containing an excised leaf from one of the host plants. Each Petri dish was considered to be a replicate (thus $n=100$ for each host plant). After the larvae hatched, their food (one corresponding host-plant leaf) was changed every day and water was added to humidify the filter paper until pupation. Individuals were sexed according to the methods of Coelho and França (1987) and male and female pupae were grouped in couples. Each pupae couple was placed in an individual Petri dish containing a moistened filter paper and a single corresponding host-plant leaf until adult emergence. Following adult emergence, males and females were left together in the Petri dishes for their entire lives. After visual observation of the first mating, the number of eggs laid on a single plant leaf was evaluated daily until the female died. These observations were possible because first mating usually occurs after adult emergence. Water was supplied to each Petri dish (more precisely, to the filter paper), every 2 days, in order to optimize adult survival. During the development of the insects, egg-laying date, hatching date, pupation date, adult emergence date, and sex were recorded for each individual. Pupal weight was not recorded, since the ratio between fecundity and pupal weight is often masked by other factors and should thus be treated with caution when attempting to understand oviposition (Leather 1988).

Experiments were carried out under laboratory conditions (24±1 °C, 65±5 % RH, and 16 L:8D photoperiod) and were monitored using an automatic datalogger (HOBO RH/TEMP 8 K; Onset Computer Corporation, Bourne, Massachusetts, USA).

Statistical Analyses

One-way ANOVAs were applied to compare the mean development times of each life stage of *Tuta absoluta* on the various host plants. When assumptions of the one-way ANOVA (normality of populations and homoscedasticity) were not met, Kruskall-Wallis tests were applied, followed by Mann–Whitney comparisons of specific samples pairs. Chi-square tests of independence were applied to compare survival percentages at each life stage and sex ratios on each variety studied. All tests were performed using Minitab® v.16 software (http://www.minitab.com/fr-FR/default.aspx).

Results

Development and Survivorship

Mean development times (± SE) of *T. absoluta* eggs were statistically different according to the host plants on which the adults completed their life cycle (Table 1). Embryonic development was shortest on Charlotte (4.80±2.27 days) and longest on Bintje (7.02±1.27 days). Egg viability on Spunta (80.2 %) was significantly greater than on Charlotte and Nicola (64.0 % and 66.0 %, respectively; Table 1).

Larval development time also differed according to host plant. *Tuta absoluta* larvae fed on Nicola, Spunta and Charlotte developed faster (11.39±2.63 days, 11.34±0.2 days and 10.80±2.32 days, respectively) than those fed on any other host plant, while larvae reared on tomato and Bintje had the longest development times (13.72±2.24 and 14.02±3.67 days, respectively; Table 1). No differences in larvae survival percentages were observed between the five host plants. However, chi-squared association tests performed on sample pairs indicated a significant difference between Spunta (which exhibited the lowest survival rate) and Nicola and Charlotte (which demonstrated the highest survival rates).

Pupae obtained from larvae fed on Bintje developed more slowly (10.23±1.92 days) than those obtained from larvae fed on all other host plants (Table 1). Pupal development time was faster on Spunta and Nicola (7.83±1.34 days and 7.20±1.52 days, respectively; Table 1). Despite these divergences in pupal development time, there were no significant differences in pupal survival rates, which ranged from 76.3 % on Spunta to 93.7 % on Nicola.

Significant differences in development time from egg to pupation were observed between the different host plants. Insects fed on Charlotte developed faster (24.12±4.64 days) than those reared on any other host plant (Table 1). There were no significant differences in survival rates from egg to pupation, which ranged from 44.0 % on Nicola to 53.0 % on Bintje.

Sex Ratios, Longevity and Reproduction

The sex ratio (male/female) of *T. absoluta* did not differ significantly among the five host plants. However, adult longevity was significantly different between different host plants (Table 1). Adults lived longest on Bintje (14.19±7.35 days) and shortest on Spunta (8.22±2.00 days; Table 1). *Tuta absoluta* fecundity (eggs/females) was not significantly different (although it was almost significant) between the five host plants (Table 1). Nonetheless, Mann–Whitney comparison tests performed on sample pairs demonstrated a significant difference between Charlotte, which had the lowest fecundity rate (25.47±8.08 eggs/female; Table 1), and tomato, which had one of the highest fecundity rates (50.62±5.01 eggs/female, Table 1).

Discussion

Tuta absoluta is known to develop on various cultivated and non-cultivated Solanaceous species (Vargas 1970; Campos 1976; Garcia et al. 1987; Colomo et al. 2006; Desneux et al. 2010). Although tomato is considered as the primary host of

Table 1 Biological traits of *Tuta absoluta* on different host plants

	Host plants						
	Tomato	Potato					
Biological traits	Moneymaker	Bintje	Nicola	Charlotte	Spunta	Statistical analyses	*P*
Embryonic development (day)	5.81±0.17a	7.02±0.17b	6.73±0.16b	4.80±0.32d	5.59±0.27c	$H_4=49.43$	<0.001
Egg viability (%)	75.00ab	77.00 ac	66.00 ac	64.00c	80.17a	$\chi 2=10.53$	0.032
Larval development (day)	13.72±0.32a	14.02±0.5a	11.39±0.4b	10.80±0.33b	11.34±0.2b	$H_4=58.59$	<0.001
Pupal development (day)	8.51±0.24a	10.23±0.26b	7.20±0.23c	8.52±0.32a	7.83±0.17ac	$F_{4,248}=20.87$	<0.001
Adult longevity (day)	12.47±0.90ab	14.19±1.01a	10.45±0.84b	12.42±1.04ab	8.22±0.26c	$H_4=26.99$	<0.001
Egg to pupation development (day)	28.04±0.34a	31.26±0.65b	25.32±0.47c	24.12±0.66c	24.76±0.24c	$H_4=87.60$	<0.001
Fecundity rate (eggs per female)	50.62±5.01a	41.36±8.19ab	55.80±17.1ab	25.47±8.08b	39.65±7.73ab	$H_4=8.99$	0.061

T. absoluta, it has also been demonstrated that the moth is able to develop on potato (Campos 1976; Notz 1992; Pereyra et al. 2006; Desneux et al. 2010). In this study, we tested the ability of *T. absoluta* to develop on four varieties of potato (cv. Bintje, Charlotte, Nicola, and Spunta) compared to tomato (cv. Moneymaker) under identical laboratory conditions.

The studies of holometabolous insects such as lepidopterans are often limited to observing only the larval stage, which is the host-feeding stage. A frequent assumption for this case in the context of life history theory is that adaptation at the larval stage (i.e., high survival rate and shorter development time) is the primary determinant for overall adaptation of the species (Krainacker et al. 1987). Indeed, in herbivorous insects, high survival rates and shorter development times are considered to be indicators of better food quality (Awmack et al. 2002; Greenberg et al. 2002; Pereyra et al. 2006). Development time is considered as the period between the hatching of larva from eggs and its metamorphosis to the adult stage and the survival rate is the rate of survival of all stages during the development time (Mousseau et al. 1991). In this study, survival rates of *T. absoluta* did not differ between the five tested host plants, but development times (egg to pupation) were significantly affected. Compared to tomato, development times were longer on Bintje and shorter on Nicola, Charlotte and Spunta. Since shorter insect development times indicate greater suitability of a host plant (Awmack et al. 2002; Greenberg et al. 2002), Charlotte, Spunta, and Nicola were found to be better host plants for *T. absoluta* than tomato and Bintje. Pereyra et al. (2006) demonstrated that developmental times were shorter on tomato than on potato (cv. Spunta) and thus concluded that tomato was a more suitable host for *T. absoluta*. However, the opposite was observed in our study, in which developmental times were shorter on Spunta than on tomato. The differences between the two experiments could be explained by the tomato variety used as controls: cv. Moneymaker in our study and cv. Platense in the Pereyra et al. (2006) study. Anyway, in the two experiments, results show the high capacity of *T. absoluta* to develop equally on potato and tomato with high intraspecific variation in host suitability.

In most of the holometabolous herbivores, the particular host plant a larva will eat is decided by the mother's oviposition preference. Consequently, oviposition site is a critical factor for the development of the larvae (Mitchell 1981). High fecundity rates (number of eggs per female) in herbivorous insects, and particularly Lepidoptera, are also considered to be an indicator of a high-quality host plant (Awmack et al. 2002). From an evolutionary perspective, the basic premise for host plant choice is a simple one: females will maximize their fitness by laying their eggs on plant types on which their offspring will perform the best (Gripenberg et al. 2010). Although there are convincing examples of cases where female host plant (or part thereof) choice does not match offspring performance, the general rule is clearly a positive association (Thompson 1988; Valladares et al. 1991; Almohamad et al. 2007; Gripenberg et al. 2010). Normally, in the case of poor-quality plants, a female insect may effectively improve its oviposition behavior by reducing the number of eggs laid on each plant (Awmack et al. 2002). However, oviposition strategies may be governed by a variety other than nutritive value of the host such as the presence of predators and parasites or the size and the quality of the host (Mitchell 1981).

In this study, the only significant difference in the fecundity of *T. absoluta* was between Charlotte and tomato. Fecundity is strongly influenced by adult longevity (Leather 1988), and since Charlotte was characterized by one of the highest adult longevities observed in this study, it would be reasonable to expect a high fecundity rate. Nevertheless, the results showed that females identified Charlotte as a low-quality plant, despite the fact that three of the most important biological parameters (development time, larval survival rate, and adult longevity) seemed to be beneficial to the development of their offspring. It is important to notice that survival of eggs (a biological parameter also highly consistent with the adult fecundity) from adults that were reared on Charlotte was lower (75 % of egg viability) compared with egg survival from adults reared on tomato (64 % of egg viability). This could be a positive argument for the female choice on Charlotte while the percentage of egg viability, in this study, is higher for the tested host plants than the previously reported egg viability on tomato (55 % of egg viability) (Miranda et al. 1998). Finally, this unexpected correlation may be a consequence of various factors, such as temporal variations in host plant quality or conflicting demands on adults other than oviposition (Agosta 2006). Another hypothesis could suggest a repulsive action on the part of Charlotte leaves against *T. absoluta* oviposition. Females are known to detect small variations in volatile signatures in different tomato cultivars and to adapt their oviposition accordingly (Proffit et al. 2011). An investigation of volatiles emitted by the tested host plants, followed by behavioral assays, may provide insights into the differences in fecundity observed in the present study.

Despite the small differences observed between the tested varieties, it was concluded that potato and tomato have similar suitability for *T. absoluta* development, on the basis of four of the most important biological traits: development time, larval survival rate, adult longevity, and fecundity. Pereyra et al. (2006) also observed the satisfactory development of *T. absoluta* on potato plants and suggested that, under favorable field conditions (including climate, geography and phenological coincidence), populations of *T.*

absoluta could become a real problem to potato crops. *Tuta absoluta* has been reported to consume potato crops in several South American countries, including Colombia, Peru, Chile, and Argentina (Campos 1976; Garcia et al. 1987; Colomo et al. 2002; Pereyra et al. 2006). However, there have been few recent observations of potato crop infestations in Europe or countries of the North African Mediterranean Basin. That being said, this apparent absence of attacks on potato crops by *T. absoluta* in these areas could be attributed to a lack of published data, confusion with *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae), or because tomato greenhouses and potato fields are too distant from each other (Badaoui et al. 2010; CAPS 2010).

Host plant species in the wild could provide reservoirs or refuges for the pest. Actually, some wild hosts are cited to be potential host for the development of *T.* absoluta but nothing is known on the pest fitness on these wild solanaceous plants (Garcia et al. 1987; Pereyra et al. 2006). The restricted presence of wild host plants and also a reduced insect capacity to develop on these plants may limit the spread of the pest. There is a real need to study the exact repartition of these wild host plants and the fitness of the pest on these same plants. Moreover, other wild solanaceous plants could be tested, such as *Hyoscamnus niger* and *Nicandra physalodes*, which could probably be suitable hosts for *T. absoluta* in Europe and in North America. Temperature is also known to have a direct influence on insect activity and development rates (Pradhan 1946). Barrientos *et al*. (1998) demonstrated that *T. absoluta* developed faster with increasing temperature: 76.3 days at 14 °C, 39.8 days at 19.7 °C, and 23.8 days at 27.1 °C. In countries with temperate climates, *T. absoluta* is likely to occur in tomato greenhouses where it may establish permanent populations if hosts are available throughout the year (Desneux et al. 2010; Desneux et al. 2011). Lower open-field temperatures during the winter may explain the absence of *T. absoluta* in most potato production regions of northern Europe (Desneux et al. 2010).

Predicted future climate warming should facilitate faster development times, greater winter survival rates and more generations per year (Bale et al. 2002). As a consequence, it is expected that *T. absoluta*, together with other multivoltine species, will expand its geographic range to higher latitudes and altitudes, as already observed in a number of common butterfly species (Bale et al. 2002). However, in Mediterranean countries characterized by warm temperate climates, only two occurrence of *T. absoluta* infestation on potato has been reported, from Portugal and more recently from Turkey (Morrison et al. 2011; Unlu 2012). This implies that additional parameters, such as the total area of potato crops in a region, the proximity of tomato and potato crops, or the presence of intermediary wild host plants, may influence the spread of the pest.

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