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## Original Article

### Impact of low temperature and host plant on *Tuta absoluta*

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**Running head:** *Tuta absoluta at low temperature on host plants*

*Key words:* *Solanum nigrum*, black nightshade, *Solanum lycopersicum*, tomato, Solanaceae, tomato pinworm, invasive pest, life table parameters, oviposition preference, low-temperature exposure, alternative host, oligophagous insect

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## Abstract

Alternative host plants are among the key factors influencing the spread of invasive pests because they are utilized as a food source and provide shelter in unfavorable conditions. The South American tomato pinworm (SATP), *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), has a high behavioral and physiological plasticity enabling it to rapidly spread in several countries. Among the multiple strategies used by SATP in the invasion process is the use of alternative host plants including black nightshade (BNS), *Solanum nigrum* L. (Solanaceae), a perennial plant widely distributed across all habitats worldwide. Besides the life table and behavioral parameters of SATP on tomato, its survival and reproduction in low temperatures on alternative host plants should be assessed to evaluate the likely spread in temperate regions with harsh winters. In our study, comparing solanaceous species through generations, the primary difference was in the mean generation time with SATP reared on BNS, whereby it had a longer development time than larvae and pupae reared on tomato plants. Adults preferred tomato plants even if they had been reared as larvae on BNS. Exposure periods of 7, 14, and 21 days to 4 °C indicated that more than 50% of SATP pupae reared on BNS plants survived more than 14 days. The survival of SATP reared on tomato plants exceeded 21 days and after exposure to 4 °C, females reared on both plants remained fertile. The life table and behavioral parameters recorded demonstrated a significant potential of BNS to support the development of SATP, also at low temperature. Therefore, even with effective border surveillance and phytosanitation processes in place, invasion through an alternative host is possible and difficult to detect.

## Abbreviated abstract

*Tuta absoluta* (Lepidoptera: Gelechiidae) is an oligophagous pest primarily of tomato plants. However, it can develop on black nightshade, *Solanum nigrum* (Solanaceae), an alternative host plant that occurs spontaneously in all continents. Age-stage life table analysis of *T. absoluta* revealed oviposition preference behavior of females. Additionally, the survival of pupae at low temperature (4 °C) indicated this pest feeds on both host plants and black nightshade has a high potential for *T. absoluta* development and reproduction.

## Graphic for Table of Contents

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## Introduction

Invasive pests have a destructive impact on native biodiversity, increase the economic cost of food production, and directly influence human health (Pimentel et al., 2000). One of the factors influencing the success of invasive pests is closely related to their potential hosts (Worner et al., 2013) and often commercial crops that are distributed worldwide. However, alternative host plants are neglected due to low or no commercial value even though they are ecologically invaluable for local biodiversity, beneficial organisms, and ecosystem services (Wratten et al., 2012; Parolin et al., 2014; Gurr et al., 2018; Hatt et al., 2019; Wang et al., 2020). In alternative host plants, multiple studies are aimed at understanding the biological and behavioral parameters of invasive pests. However, the survival and reproduction of invasive pests in response to abiotic factors outside their host range should be explored to increase knowledge of the mode and likelihood of invasion (Gutierrez et al., 2008).

The South American tomato pinworm, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (SATP), is a major pest of tomatoes worldwide (Desneux et al., 2010, 2011; Biondi et al., 2018). This is due to its rapid spread resulting in increased tomato production costs and threats to ecological ecosystems in newly invaded areas (e.g., Asplen et al., 2015; Roques et al., 2016). There are considerable concerns regarding the rapid geographic expansion of SATP in the tomato-growing regions due to their biological traits that hinder effective control (McNitt et al., 2019; Campos et al., 2021; Ponti et al., 2021). In addition to previously documented infected areas (Campos et al., 2017; Sankarganesh et al., 2017; Sylla et al., 2017; Han et al., 2018, 2019; Mansour et al., 2018; Sylla et al., 2019; Tabuloc et al., 2019; Verheggen & Fontus, 2019), SATP was recently reported in western China (Li et al., 2021), threatening local production and the export of fresh tomatoes to countries without SATP infestation (Xian et al., 2017; Han et al., 2018).

Although SATP is an oligophagous insect, most studies have been conducted on tomato plants (Gharekhani & Salek-Ebrahimi, 2014; Rostami et al., 2017, 2020; Bacci et al., 2019). However, research has demonstrated the suitability of SATP to black nightshade (BNS), *Solanum nigrum* L. (Solanaceae) (Proffit et al., 2011; Bawin et al., 2015; Abbes et al., 2016; Arnó et al., 2019; Idriss et al., 2020). Black nightshade plants can serve as a food source and shelter for SATP in seasonally unfavorable periods, remaining in the area for long periods. These plants are also considered a spontaneous growth non-crop plant, having widespread distribution on all continents (Edmonds & Chweya, 1997). Given their broad geographical distribution and suitability for

SATP, it becomes increasingly difficult to effectively control SATP and concerns regarding its infestation and subsequent control intensify.

Life table parameters of insects play a significant role in ecology and integrated pest management (Price et al., 2011) and have become popular in entomological research since the introduction of demography for studies of insect populations in the early 1960s (Morris, 1959; Varley & Gradwell, 1970; Carey, 2001). These studies are useful for characterizing population dynamics and understanding the impact of abiotic and biotic factors on biological parameters (Carey, 2001; Pereyra & Sánchez, 2006; Gharekhani & Salek-Ebrahimi, 2014; Rostami et al., 2017; Bacci et al., 2019). Traditional life tables neglect the role of males and their differentiation by stage (Leslie, 1945; Birch, 1948). However, age-stage two-sex life tables have been enhanced to incorporate the contribution of both genders and variable development rates among individuals (Zhang et al., 2019; Chi et al., 2020). In addition, life tables can be used to detect small variation among species of host plants and even among species in the same family, such as BNS and tomato plants (Bawin et al., 2016).

The oviposition behavior of invasive pests on suitable host plants could also be used to determine the processes and success of biological invasions (Sylla et al., 2019). Some theories and hypotheses explain host plant choice in insects but the most common theory is the preference-performance hypothesis (Jaenike, 1978; Mayhew, 1997; Desneux et al., 2009; Monticelli et al., 2019). This hypothesis states that adult females will choose the most favorable host plant on which to oviposit because of the limited ability of immature stages to move between plants. This concept therefore assesses the performance of immature stages in terms of biological parameters (Mayhew, 1997). This contrasts with the controversial Hopkins' host selection principle stating that regardless of host number in a species, female adults will always prefer to oviposit on the host species on which they developed as larvae and the first adult experience after the pupal stage (Hopkins, 1916; Jaenike, 1978; Prager et al., 2014). Previous studies have emphasized that SATP prefers to feed on tomato plants and typically neglects other solanaceous species (Proffit et al., 2011; Caparros Megido et al., 2014; Ataide et al., 2017).

The success of an invasion goes beyond biological and behavioral parameters of invasive pests on suitable host plant. Besides the suitability of host plants for SATP, limiting temperatures for development should also be investigated to further understand the likelihood of geographic spread of this pest. Previous surveys have shown potential survival of SATP at temperatures below the threshold for development and facultative diapause induction on tomato plants (Van

Damme et al., 2015; Kahrer et al., 2019; Campos et al., 2021). However, no information is documented concerning survival below the temperature threshold of SATP development and its reproduction after exposure periods at low temperatures on BNS plants. As tomato and BNS plants are acceptable sources of food and shelter for SATP, the goals of this study were to assess (1) life table parameters on both solanaceous species, (2) oviposition preference on the host plants, and (3) pupal survival and adult reproduction after exposure periods of 7, 14, and 21 days to 4 °C.

## **Materials and methods**

### **Plant production**

Black nightshade seeds were collected in July 2017 near the French National Research Institute for Agriculture, Food and the Environment (INRAE), Sophia-Antipolis, France. Pesticide-free BNS and tomato (cv. Marmande) plants were grown from seeds germinated in a climate chamber at  $24 \pm 2$  °C,  $65 \pm 5\%$  r.h., and L16:D8 photoperiod and used as hosts for SATP. After germination, BNS and tomato seedlings were planted in 320-ml plastic pots in a commercial organically fertilized soil (Tonusol, Nice, France) and transferred to a greenhouse at  $20 \pm 2$  °C and  $65 \pm 5\%$  r.h. The mean daytime global irradiance inside the greenhouse was maintained at  $449.5 \text{ W m}^{-2}$  using shading as required. Plants were fertilized with a nutrient mineral solution developed by INRAE ( $\text{NO}_3 = 1 \text{ mol m}^{-3}$ ,  $\text{H}_2\text{PO}_4 = 0.21 \text{ mol m}^{-3}$ ,  $\text{SO}_4 = 0.055 \text{ mol m}^{-3}$ ,  $\text{K} = 0.641 \text{ mol m}^{-3}$ ,  $\text{Ca} = 0.215 \text{ mol m}^{-3}$ ,  $\text{Mg} = 0.114 \text{ mol m}^{-3}$ , adjusted to pH  $6.0 \pm 0.2$  using 0.2 M aqueous solution of  $\text{H}_2\text{SO}_4$ ) (Han et al., 2014).

### **Insect colonies**

Two SATP colonies, one on tomato plants and the other on BNS, were established in the rearing room ( $3.0 \times 1.5 \times 2.5 \text{ m}$ ) using cages ( $55 \times 75 \times 80 \text{ cm}$ ), covered with a fine nylon mesh under controlled conditions ( $24 \pm 2$  °C,  $65 \pm 5\%$  r.h., and L16:D8 photoperiod) (Biondi et al., 2012). The initial SATP colony was established from ca. 190 individuals collected in tomato plants in July 2009 at the INRAE Campus, Alénia, France. The first SATP colony was reared on tomato plants for larval feeding, a shelter for pupae stages and a substrate for oviposition. A water-honey solution (50:50 vol/vol) was provided ad libitum for adults on a small cotton ball. The same methodology was used for the SATP colony reared on BNS. Establishment of the SATP colony on BNS occurred from 50 SATP pairs collected from the SATP colony reared on tomato plants.

Subsequently, these pairs were placed in cages with only BNS for oviposition. After the eggs hatched, larvae began to feed on BNS. Thus, this SATP colony received only BNS for larval feeding, a shelter for pupae, and substrate for female oviposition. As with the above methodology, a water-honey solution was provided ad libitum for adults. To maintain the two SATP colonies, BNS and tomato plants collected from the greenhouse were used, as described in the plant production subsection, and were separately placed inside cages with SATP adults serving as substrate for oviposition and food for first and second instars. Every 7 days thereafter, plants with SATP eggs were moved to a second cage and new plants were provided. Insects were maintained in three cages: (1) oviposition, first and second instars, (2) third and fourth instars and pupae, and (3) adults. The experiment started when the SATP colony reared on BNS plants was in the second generation and the SATP colony reared on tomato plants were in the ca. 90th generation. The colonies remained separated until the end of the experiments.

### **Life table experiments**

The life table parameters of the SATP on BNS and tomato plants were separately assessed during two consecutive generations (F1 and F2). BNS and tomato plants collected from the greenhouse were separately housed in four incubators (Aqualytic Liebherr model TC445 S; Tintometer, Dortmund, Germany) under controlled conditions at  $24 \pm 1$  °C,  $65 \pm 5$  % r.h., and L16:D8 photoperiod. The total replications used in the experiment were 12 for BNS and 12 for tomato plants, and plants were used ca. 45 days after sowing (DAS). One plant leaf covered with a transparent cylindrical plastic box (10 cm diameter, 5 cm high) was considered a sample unit. Each plant received three transparent boxes representing 36 replicates for both BNS and tomato plants in completely randomized blocks design. The boxes were supported on the ground using a wooden stick to prevent leaves from breaking. Subsequently, three SATP neonates (<24 h old) were carefully placed with a fine paintbrush on a leaf inside of each transparent box. The box was sealed with a fine nylon mesh at the top to prevent larvae escaping and allow for ventilation. Larval stages of SATP were assessed daily until the pupal stage at which point the pupae were weighed. After adult emergence, 30 SATP pairs were transferred into a small plastic cage for mating (Biondi et al., 2012). These cages were maintained in the laboratory under controlled conditions at  $24 \pm 2$  °C,  $65 \pm 5$  % r.h., and L16:D8 photoperiod in a randomized design. The small plastic cages were composed of two plastic cups to assess daily female oviposition. The upper cup was 15 cm high with a volume of 700 ml and a 1-cm-diameter hole in the bottom to allow the

insertion of a leaf (BNS or tomato) allowing access to water in the second cup (11 cm high, 350 ml). A fine nylon mesh was affixed to the top of the first plastic cup with a rubber band to allow ventilation and, as needed, was removed to assess the BNS and tomato leaves. After the assessment of oviposition, a new leaf was placed inside the small plastic cage as described above.

### **Behavioral assay**

Female oviposition-preference of SATP on BNS and tomato plants was tested in cages (55 × 75 × 80 cm) under laboratory-controlled conditions (24 ± 2 °C, 65 ± 5 % r.h., and L16:D8 photoperiod). Black nightshade and tomato plants from the greenhouse (45 DAS), as described above, were used. Two BNS and tomato plants were placed diagonally in each corner of the cage with a total of 26 replicates in a completely randomized design. At each replicate of the oviposition-preference test, BNS and tomato plant positions were changed randomly to reduce any effect of position. Four SATP pairs (emergence <24 h ago) from the SATP colony reared on BNS plants were released inside the cage with both solanaceous species. The same methodology was performed with SATP adults from the colony reared on tomato. Thus, four SATP pairs (<24 h old) from the SATP colony reared on tomato were released inside the cage with solanaceous species to the oviposition-preference test. A water-honey solution (50:50 vol/vol) was provided ad libitum in a small cotton ball. The SATP pairs remained within a cage for 24 h. After this period, the SATP eggs were counted separately on each part (adaxial and abaxial leaf sides, petioles, and stems) of the BNS and tomato plants under a stereoscope microscope (10× magnification).

### **Exposure to 4 °C**

Larvae of SATP from colonies reared separately on BNS and tomato plants were allowed to develop to the pupal stage in the rearing room under controlled conditions (24 ± 2 °C, 65 ± 5 % r.h., and L16:D8 photoperiod). Ten SATP pupae (<24 h old), collected in SATP colonies reared separately on BNS and tomato plants, were placed separately inside a Petri dish (9 cm diameter, 1.5 cm high). Five Petri dishes, each containing 10 pupae from the SATP colony reared on BNS (total of 50 pupae) and tomato plants (50 pupae), were housed at 24 ± 1 °C, 65 ± 5 % r.h., and L16:D8 photoperiod, in a completely randomized design. The sensor (TFH 620; Ebro Electronic, Ingolstadt, Germany) was used to monitor temperature inside the incubator. A temperature of 4 °C inside the incubator was achieved over 3 days, reducing the temperature gradually from 24 to 4 ±

1 °C and maintaining the conditions of  $65 \pm 5$  % r.h., and L16:D8 h photoperiod. The pupae were exposed to this temperature for 7, 14, and 21 days. After each exposure period, the temperature was gradually increased over 3 days from 4 to  $24 \pm 1$  °C, maintaining the conditions of  $65 \pm 5$  % r.h., and L16:D8 photoperiod. Pupae were then placed under laboratory conditions at  $24 \pm 1$  °C,  $65 \pm 5$  % r.h., and L16:D8 photoperiod until adult emergence. The adults emerging were counted and adults with deformed wings were excluded from the analysis. After adult emergence, 20 SATP pairs were placed in a small plastic cage system, as described above, for mating. The small plastic cages were maintained in the laboratory at  $24 \pm 2$  °C,  $65 \pm 5$  % r.h., and L16:D8 photoperiod. The SATP eggs laid on BNS and tomato plants were counted in the first 3 days because peak SATP female oviposition occurs during the first 3 days after mating (Pereyra & Sánchez, 2006).

### Statistical analysis

*Life table analysis.* The life-history data for SATP were analyzed using the age-stage, two-sex life table method (Chi et al., 2020). The net reproductive rate ( $R_0$ ), the mean duration of one generation ( $\tau$ ), intrinsic rate of increase ( $r$ ), and finite rate of increase ( $\lambda$ ) were calculated using the TWSEX-MSChart procedure (Chi, 2019). The variances and standard errors of the life table parameters were estimated using 100 000 bootstrap samples (Efron & Tibshirani, 1986) and compared across BNS and tomato treatments. The age-stage survival rate ( $s_{xj}$ ), i.e., the probability that the insects survive to age  $x$  and in stage  $j$ , is calculated as

$$s_{xj} = \frac{n_{xj}}{n_{01}} ,$$

where  $n_{xj}$  is the number of insects alive at age  $x$  and stage  $j$  and  $n_{01}$  is the number of larvae used at the beginning of the life table study. The age-specific survival rate  $l_x$ , the proportion surviving to age  $x$ , is calculated as

$$l_x = \sum_{j=1}^m s_{xj} ,$$

where  $m$  is the number of life stages. The age-stage specific fecundity  $f_{xj}$  is the number of offspring produced by an individual at age  $x$  and stage  $j$ . Adult SATP females produce offspring at the seventh life stage,  $f_{x7}$ , and the remaining  $f_{xj}$  are all zero;  $f_{x7}$  is calculated as

$$f_{x7} = \frac{E_x}{n_{x7}} ,$$

where  $E_x$  is the total number of eggs produced by all females ( $n_{x7}$ ) at age  $x$ . The age-specific fecundity ( $m_x$ ), i.e., the age-specific fecundity of individuals at age  $x$ , is calculated as

$$m_x = \left( \sum_{j=1}^m S_{xj} f_{xj} \right) / \left( \sum_{j=1}^m S_{xj} \right).$$

The age-specific net maternity ( $l_x m_x$ ) is the total number of offspring produced at age  $x$ , taking into account the survival rate ( $l_x$ ). The mean generation time ( $T$ ) was estimated as  $T = \ln R_0 / r$ . The intrinsic rate of increase ( $r$ ) was estimated by the equation  $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$  (Goodman, 1982).

*Behavioral assay.* The normality and homoscedasticity assumptions of the number of SATP eggs oviposited on separate parts of the plant (adaxial and abaxial sides of the leaves, stem, and petiole) were verified by the Kolmogorov–Smirnov test. Female oviposition-preference on adaxial and abaxial leaf sides, stem and petiole of BNS and tomato plants were then compared using a paired t-test.

*Exposure to 4 °C.* After each exposure period of 7, 14, and 21 days to 4 °C, the survival of SATP pupae was analyzed by linear regression. The regression model selected was supported by the adjusted  $R^2$  and the regression model with the highest adjusted  $R^2$  was used as it had greater explanatory power for the data. Female oviposition was adjusted in a nonlinear polynomial regression of the third order for both solanaceous species. The regression model selected for oviposition data was supported by the adjusted  $R^2$ . All statistical analyses were performed using SAS University Edition and figures were obtained using SigmaPlot v.14.

## Results

### Transgenerational life table experiment

The net reproductive rates ( $R_0$ ) of SATP on BNS and tomato plants were similar between generations within and between solanaceous species (Table 1). On tomato, the intrinsic rate of increase ( $0.099 \text{ day}^{-1}$ ) and finite rate of increase ( $1.14 \text{ day}^{-1}$ ) were both lower in generation F1 than in F2 ( $0.135$  and  $1.10 \text{ day}^{-1}$ , respectively; Table 1). Furthermore, the mean generation time was lower in generation F2 than F1 (28.54 vs. 30.62 days; Table 1).

In SATP reared on BNS plants, the gross reproductive rate (118.2 vs. 61.3 offspring per individual) and fecundity (151.6 vs. 107.7 eggs per female) were higher in generation F1 compared to F2, whereas in generation F2 compared to F1 the mean generation time (31.61 vs.

28.4 days) and longevity (32.19 vs. 25.1 days) were higher (Table 1).

Mean generation time in generation F1 from SATP reared on tomato plants was higher than when reared on BNS (30.6 vs. 28.4 days). In generation F2, SATP reared on tomato plants had a lower mean generation time than when reared on BNS (28.6 vs. 31.6 days; Table 1).

Overall, the duration of egg and adult stages of SATP did not differ between generations within solanaceous species, nor between solanaceous species within generations (Table 2). The mean development time of SATP reared on BNS plants was higher in generation F1 than in generation F2 to the first (3.6 vs. 2.9 days), second (3.4 vs. 2.5 days), and third (3.6 vs. 2.4 days) instars. The mean development time of fourth instars was lower in generation F1 than in F2 (3.4 vs. 3.9 days). Duration of the pupal stages was similar in generations F1 and F2 (Table 2). When SATP was reared on tomato plants, the mean duration of the first instar (1.8 vs. 3.3 days) and the pupal stage (8.3 vs. 9.8 days) was shorter in generation F1 than in F2, whereas the fourth instar lasted longer in generation F1 than in F2 (4.6 vs. 3.1 days); duration of the second and third instars did not differ between generations (Table 2).

Significant differences in mean development time were found between host plants; in generation F2 stage duration was longer for SATP reared on BNS plants than for SATP reared on tomato plants, whereas in F1 stage duration was shorter for SATP reared on BNS plants than for SATP reared on tomato plants (the only exception were the first instars, which lasted significantly shorter on tomato in the F1 generation) (Table 2). The age-stage specific survival rates ( $s_{xj}$ ) of SATP on BNS and tomato plants in generations F1 and F2 are illustrated in Figure 1.

Pupal weights in generation F1 of SATP females reared on BNS (5.0 mg) and tomato plants (4.7 mg) were higher than pupal weight of the males reared on BNS (3.6 mg) and tomato plants (3.9 mg) (Figure 2A). In generation F2, only the pupal weight of females (5.4 mg) was higher than that of males reared on BNS (3.8 mg) (Figure 2B). Between generations of SATP reared on BNS plants, male pupae from F1 and F2 weighed less than F2 female pupae (Figure 2C). The same pattern was found between generations for SATP reared on tomato plants (Figure 2D).

### **Behavioral assay**

Adult SATP reared on BNS deposited more eggs on the abaxial and adaxial sides of tomato leaves than on the abaxial and adaxial parts of BNS (Figure 3A). Adult moths reared on tomato laid more eggs on the adaxial side of tomato leaves than on the adaxial side of BNS leaves; on the abaxial

leaf sides the egg numbers did not differ between plant species (Figure 3B). Only a few eggs were laid on the petiole or the stem, and these numbers did not differ between plant species (Figure 3).

### **Exposure to 4 °C**

The survival of SATP on BNS and tomato plants after exposure for 7, 14, or 21 days to 4 °C were analyzed by linear regression (Figure 4). Survival on BNS declined more rapidly than on tomato. After 21 days at 4 °C, almost no moths survived on BNS, whereas survival on tomato plants was >70% (Figure 4).

SATP females reared on BNS surviving at 4 °C for 14 days remained fertile – they still laid eggs (Figure 5). Likewise, after exposure for 21 days to 4 °C, females reared on tomato plants had remained fertile (Figure 5).

### **Discussion**

Most studies examining demographic parameters of SATP have not found differences between BNS and tomato plants (Abbes et al., 2016; Arnó et al., 2019) and even when natural enemies were added to the system, no differences in SATP development rates were observed (Ingegno et al., 2017). However, our study investigated life table parameters of SATP reared separately on BNS and tomato plants through two generations. Interestingly, we revealed that the potential of SATP development on BNS plants was reduced through generations. The average offspring number produced per individual during their lifetime, i.e., the gross reproductive rate, was reduced together with fertility and increased longevity of the SATP. Even with the reduction shown in SATP life table parameters on BNS plants, this was not different from the tomato plants except for mean generation time. An in-depth examination of mean generation time revealed differences in larvae and pupal stages between the two host plants. A shorter generation time could be a physiological strategy acquired in the natural selection process over time, mainly by larvae feeding on tomato plants to reduce SATP exposure time to natural mortality factors (Bacci et al., 2019) such as natural enemies and abiotic factors (Biondi et al., 2018).

There are exceptional cases where herbivorous insects experience a faster development on plants of unsuitable food quality (Han et al., 2016). More typical is the rapid development of herbivorous insects in relation to high (suitable) food quality for larvae (Awmack & Leather, 2002; Greenberg et al., 2002; Pereyra & Sánchez, 2006; Knolhoff & Heckel, 2014). This suggests

differences in the available nutritional quality and/or production of plant metabolites that can impair the development and reproduction of SATP (Bawin et al., 2015, 2016). We revealed that pupal weight for SATP reared on BNS and tomato plants was similar, although females were heavier than males. Therefore, BNS plants have a high potential for supporting the development and reproduction of SATP to a similar level as its primary host.

Invasive herbivores exhibit behavioral and physiological phenotypic plasticity to overcome intra- and interspecific differences in plant quality, thereby exploring and adapting to new host plant species (Agrawal, 2001; Ghalambor et al., 2007; Knolhoff & Heckel, 2014; Bawin et al., 2015). The challenges are particularly significant for female insects because preference for high-quality hosts is critical when larvae have low mobility (Thompson, 1988; Craig & Itami, 2008). South American tomato pinworm larvae are confined to the host plant on which eggs were laid due to the limited mobility of first and second instars (Galdino et al., 2015). In our study, SATP females had a preference to oviposit on tomato plants regardless of whether the adult was previously reared on BNS or tomato plant and preferably laid eggs on adaxial leaf parts of the tomato plants. Considering the preference-performance hypothesis, oviposition preference may also be related to the place and number of eggs laid on a specific part of the host plant.

The selection of high-quality hosts is linked with oviposition behavior of females producing clusters of eggs (Mangel, 1987; Hopper, 1999; Galdino et al., 2015). An incorrect decision by females could have fatal consequences, whereas the laying of single eggs will be more akin to a risk-spreading strategy. Although SATP females preferentially oviposited on tomato adaxial leaf parts, a risk-spreading strategy should be considered as it is an invasive species with high phenotypic plasticity. Our results are in agreement with a meta-analysis examining oviposition preference in lepidopteran females that showed most offspring were more likely to survive on plant types preferred by ovipositing females (Gripenberg et al., 2010). The biological and behavioral parameter results of SATP therefore contribute to the preference-performance hypothesis. Alternatively, the most common explanation is the 'mother knows best' principle (Valladares & Lawton, 1991; Mayhew, 1997; García-Robledo & Horvitz, 2012; Pan et al., 2019) and these results refute Hopkins' host selection principle (Hopkins, 1916).

During adverse weather conditions (for instance during winter), abiotic factors are unfavorable and tomato plants become scarce forcing SATP to adopt diverse strategies to survive (Nyamukondiwa et al., 2013; Van Damme et al., 2015; Machekano et al., 2018; Cherif et al., 2019; Kahrer et al., 2019; Tarusikirwa et al., 2020; Campos et al., 2021). These strategies have

been extensively studied, including facultative diapause and survival of pupae in temperatures below critical thresholds for SATP development (Van Damme et al., 2015; Kahrer et al., 2019; Campos et al., 2021). Prior studies have not provided information on the survival of SATP at 4 °C for various exposure periods on alternative host plants. BNS is a global weed that has adapted to a broad range of environmental conditions (Edmonds & Chweya, 1997) and several studies have indicated the high potential of BNS for SATP development and reproduction. Our results revealed that BNS plants are a source of food and shelter, and importantly >50% of SATP pupae survived 14 days below the temperature threshold for development ( $\theta_L = 7.39$  °C; Campos et al., 2021). Not only did long exposure periods allow for female survival but those individuals were capable of successful oviposition. Besides facultative diapause of SATP fed on tomato plants (Campos et al., 2021), these pests rapidly spread through trade in vegetables (McNitt et al., 2019).

The survival and reproduction after exposure at low temperature may explain their rapid spread in many countries, including most recently in regions of China (Li et al., 2021). Even with effective surveillance mechanisms and phytosanitary expertise to intercept infested vegetables, ever-growing tourism and increasing intra-continental trade enhance the likelihood of rapid range expansion through alternative hosts. The study of invasive pests in spontaneous alternative plants (by using tools such as life table and behavioral parameters) is therefore critical, including their tolerance for exposure to extreme temperatures. Such research should be prioritized to enable a better understanding of the mode of spread of pests and their invasion into new areas. Knowledge of movement pathways of SATP on host plants is fundamental in reducing the likelihood of their introduction into new environments and provides insights into forecasting trends and identifying the most suitable management options.

## **Conclusions**

The net reproductive rates were similar between generations of SATP within tomato and BNS, and between the plant species within generations. Through two generations, there was a difference in the life table parameters of SATP reared on BNS in the mean generation time, gross reproductive rate, fecundity and longevity, and SATP reared on tomato plants differed in intrinsic rate of increase, finite rate of increase, and mean generation time. In the comparison between plant species, only mean generation time differed in the two generations. A closer investigation through life table analysis on the age-stage of SATP indicated that larval and pupal stages reared on BNS had longer mean development times than those reared on tomato plants. Furthermore, as expected,

females were heavier than males regardless of the plant species or generation. Both SATP females reared separately on BNS or tomato plants had an oviposition preference for the adaxial side of tomato leaves. At 4 °C, >50% of SATP pupae reared on BNS plants survived >14 days whereas the pupal stage reared on tomato plants survived >21 days. Following exposure at 4 °C, females reared on BNS and tomato plants remained fertile.

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### **References**

- Abbes K, Harbi A, Elimem M, Hafsi A & Chermiti B (2016) Bioassay of three solanaceous weeds as alternative hosts for the invasive tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae) and insights on their carryover potential. *African Entomology* 24: 334-342.
- Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294: 321.
- Arnó J, Gabarra R, Molina P, Godfrey KE & Zalom FG (2019) *Tuta absoluta* (Lepidoptera: Gelechiidae) success on common solanaceous species from California tomato production areas. *Environmental Entomology* 48: 1394-1400.
- Asplen MK, Anfora G, Biondi A, Choi D-S, Chu D et al. (2015) Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities. *Journal of Pest Science* 88: 469-494.

- Ataide LMS, Arce CCM, Curtinhas JN, da Silva DJH, DeSouza O & Lima E (2017) Flight behavior and oviposition of *Tuta absoluta* on susceptible and resistant genotypes of *Solanum lycopersicum*. *Arthropod-Plant Interactions* 11: 567-575.
- Awmack CS & Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47: 817-844.
- Bacci L, da Silva ÉM, Martins JC, Soares MA, Campos MR & Picanço MC (2019) Seasonal variation in natural mortality factors of *Tuta absoluta* (Lepidoptera: Gelechiidae) in open-field tomato cultivation. *Journal of Applied Entomology* 143: 21-33.
- Bawin T, Dujeu D, De Backer L, Fauconnier M-L, Lognay G et al. (2015) Could alternative solanaceous hosts act as refuges for the tomato leafminer, *Tuta absoluta*? *Arthropod-Plant Interactions* 9: 425-435.
- Bawin T, Dujeu D, De Backer L, Francis F & Verheggen FJ (2016) Ability of *Tuta absoluta* (Lepidoptera: Gelechiidae) to develop on alternative host plant species. *Canadian Entomologist* 148: 434-442.
- Biondi A, Desneux N, Amiens-Desneux E, Siscaro G & Zappalà L (2012) Biology and developmental strategies of the palaearctic parasitoid *Bracon nigricans* (Hymenoptera: Braconidae) on the neotropical moth *Tuta absoluta* (Lepidoptera: Gelechiidae). *Journal of Economic Entomology* 106: 1638-1647.
- Biondi A, Guedes RNC, Wan F-H & Desneux N (2018) Ecology, worldwide spread, and management of the invasive South American tomato pinworm, *Tuta absoluta*: past, present, and future. *Annual Review of Entomology* 63: 239-258.
- Birch LC (1948) The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* 17: 15-26.
- Campos MR, Béarez P, Amiens-Desneux E, Ponti L, Gutierrez AP et al. (2021) Thermal biology of *Tuta absoluta*: demographic parameters and facultative diapause. *Journal of Pest Science* 94: 829–842.
- Campos MR, Biondi A, Adiga A, Guedes RNC & Desneux N (2017) From the Western Palaearctic region to beyond: *Tuta absoluta* 10 years after invading Europe. *Journal of Pest Science* 90: 787-796.
- Caparros Megido R, De Backer L, Ettaïb R, Brostaux Y, Fauconnier ML et al. (2014) Role of larval host plant experience and solanaceous plant volatile emissions in *Tuta absoluta* (Lepidoptera: Gelechiidae) host finding behavior. *Arthropod-Plant Interactions* 8: 293-304.

- Carey JR (2001) Insect biodemography. *Annual Review of Entomology* 46: 79-110.
- Cherif A, Attia-Barhoumi S, Mansour R, Zappalà L & Grissa-Lebdi K (2019) Elucidating key biological parameters of *Tuta absoluta* on different host plants and under various temperature and relative humidity regimes. *Entomologia Generalis* 39: 1-7.
- Chi H (2019) TWSEX-MSChart: A Computer Program for the Age Stage, Twosex Life Table Analysis. <http://140.120.197.173/ecology/Download/Twosex-MSChart.zip>. Give date when accessed
- Chi H, You M, Atlıhan R, Smith CL, Kavousi A et al. (2020) Age-stage, two-sex life table: an introduction to theory, data analysis, and application. *Entomologia Generalis* 40: 102-123.
- Craig JT & Itami JK (2008) Evolution of preference and performance relationships. Specialization, Speciation, and Radiation. *The Evolutionary Biology of Herbivorous Insects* (ed. by KJ Tilmon), pp. 22-28. University of California Press, Berkeley, CA, USA.
- Desneux N, Barta RJ, Hoelmer KA, Hopper KR & Heimpel GE (2009) Multifaceted determinants of host specificity in an aphid parasitoid. *Oecologia* 160: 387-398.
- Desneux N, Luna MG, Guillemaud T & Urbaneja A (2011) The invasive South American tomato pinworm, *Tuta absoluta*, continues to spread in Afro-Eurasia and beyond: the new threat to tomato world production. *Journal of Pest Science* 84: 403-408.
- Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G, Arpaia S et al. (2010) Biological invasion of European tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control. *Journal of Pest Science* 83: 197-215.
- Edmonds JM & Chweya JA (1997) Black Nightshades, *Solanum nigrum* L. and Related Species. IPGRI, Rome, Italy.
- Efron B & Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science* 1: 54-75.
- Galdino TVdS, Picanço MC, Ferreira DO, Silva GAR, de Souza TC & Silva GA (2015) Is the performance of a specialist herbivore affected by female choices and the adaptability of the offspring? *PLOS One* 10: e0143389.
- García-Robledo C & Horvitz CC (2012) Parent-offspring conflicts, 'optimal bad motherhood' and the 'mother knows best' principles in insect herbivores colonizing novel host plants. *Ecology and Evolution* 2: 1446-1457.
- Ghalambor CK, McKay JK, Carroll SP & Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments.

Functional Ecology 21: 394-407.

- Gharekhani GH & Salek-Ebrahimi H (2014) Life table parameters of *Tuta absoluta* (Lepidoptera: Gelechiidae) on different varieties of tomato. *Journal of Economic Entomology* 107: 1765-1770.
- Goodman D (1982) Optimal life histories, optimal notation, and the value of reproductive value. *American Naturalist* 119: 803-823.
- Greenberg SM, Sappington TW, Sétamou M & Liu TX (2002) Beet armyworm (Lepidoptera: Noctuidae) host plant preferences for oviposition. *Environmental Entomology* 31: 142-148. .
- Gripenberg S, Mayhew PJ, Parnell M & Roslin T (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecology Letters* 13: 383-393.
- Gurr GM, Reynolds OL, Johnson AC, Desneux N, Zalucki MP et al. (2018) Landscape ecology and expanding range of biocontrol agent taxa enhance prospects for diamondback moth management. A review. *Agronomy for Sustainable Development* 38: 23.
- Gutierrez AP, Ponti L, d'Oultremont T & Ellis CK (2008) Climate change effects on poikilotherm tritrophic interactions. *Climatic Change* 87: 167-192.
- Han P, Bayram Y, Shaltiel-Harpaz L, Sohrabi F, Saji A et al. (2019) *Tuta absoluta* continues to disperse in Asia: damage, ongoing management and future challenges. *Journal of Pest Science* 92: 1317-1327.
- Han P, Lavoit AV, Le Bot J, Amiens-Desneux E & Desneux N (2014) Nitrogen and water availability to tomato plants triggers bottom-up effects on the leafminer *Tuta absoluta*. *Scientific Reports* 4: 4455.
- Han P, Wang, ZJ, Lavoit AV, Michel T, Seassau A et al. (2016) Increased water salinity applied to tomato plants accelerates the development of the leaf miner *Tuta absoluta* through bottom-up effects. *Scientific Reports* 6: 32403.
- Han P, Zhang Y-N, Lu Z-Z, Wang S, Ma D-Y et al. (2018) Are we ready for the invasion of *Tuta absoluta*? Unanswered key questions for elaborating an integrated pest management package in Xinjiang, China. *Entomologia Generalis* 38: 113-125.
- Hatt S, Xu QX, Francis F & Osawa N (2019) Aromatic plants of East Asia to enhance natural enemies towards biological control of insect pests. *Entomologia Generalis* 38: 275-315.
- Hopkins AD (1916) Economic investigations of the scolytid bark and timber beetles of North America, US Department of Agriculture Program of Work 1917, p. 353.

Hopper KR (1999) Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology* 44: 535-560.

Idriss GEA, du Plessis H, Khamis FM, Ekesi S, Tanga CM & Mohamed SA (2020) Host range and effects of plant species on preference and fitness of *Tuta absoluta* (Lepidoptera: Gelechiidae). *Journal of Economic Entomology* 113: 1279-1289.

Ingegno BL, Candian V & Tavella L (2017) Behavioural study on host plants shared by the predator *Dicyphus errans* and the prey *Tuta absoluta*. *Acta Horticulturae* 1164: 377-382.

Jaenike J (1978) On optimal oviposition behavior in phytophagous insects. *Theoretical Population Biology* 14: 350-356.

Kahrer A, Moyses A, Hochfellner L, Tiefenbrunner W, Egartner A et al. (2019) Modelling time-varying low-temperature-induced mortality rates for pupae of *Tuta absoluta* (Gelechiidae, Lepidoptera). *Journal of Applied Entomology* 143: 1143-1153.

Knolhoff LM & Heckel DG (2014) Behavioral assays for studies of host plant choice and adaptation in herbivorous insects. *Annual Review of Entomology* 59: 263-278.

Leslie PH (1945) On the use of matrices in certain population mathematics. *Biometrika* 33: 183-212.

Li X-W, Li D, Zhang Z-J, Huang J, Zhang J-M et al. (2021) Supercooling capacity and cold tolerance of the South American tomato pinworm, *Tuta absoluta*, a newly invaded pest in China. *Journal of Pest Science* 94: 845–858.

Machekano H, Mutamiswa R & Nyamukondiwa C (2018) Evidence of rapid spread and establishment of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in semi-arid Botswana. *Agriculture and Food Security* 7: 48.

Mangel M (1987) Opposition site selection and clutch size in insects. *Journal of Mathematical Biology* 25: 1-22.

Mansour R, Brévault T, Chailleux A, Cherif A, Grissa-Lebdi K et al. (2018) Occurrence, biology, natural enemies and management of *Tuta absoluta* in Africa. *Entomologia Generalis* 38: 83-112.

Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos* 79: 417-428.

McNitt J, Chungbaek YY, Mortveit H, Marathe M, Campos MR (2019) Assessing the multi-pathway threat from an invasive agricultural pest: *Tuta absoluta* in Asia. *Proceedings of the Royal Society B* 286: 1-9.

- Monticelli LS, Nguyen LTH, Amiens-Desneux E, Luo C, Lavoit A-V et al. (2019) The preference–performance relationship as a means of classifying parasitoids according to their specialization degree. *Evolutionary Applications* 12: 1626-1640.
- Morris RF (1959) Single-factor analysis in population dynamics. *Ecology* 40: 580-588.
- Nyamukondiwa C, Weldon CW, Chown SL, le Roux PC & Terblanche JS (2013) Thermal biology, population fluctuations and implications of temperature extremes for the management of two globally significant insect pests. *Journal of Insect Physiology* 59: 1199-1211.
- Pan H, Tena A, Xiu C, Liu B, Lu Y & Desneux N (2019) Floral feeding increases diet breadth in a polyphagous mirid. *Journal of Pest Science* 92: 1089-1100.
- Parolin P, Bresch C, Poncet C & Desneux N (2012) Functional characteristics of secondary plants for increased pest management. *International Journal of Pest Management* 58: 369–377.
- Pereyra PC & Sánchez NE (2006) Effect of two solanaceous plants on developmental and population parameters of the tomato leaf miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Neotropical Entomology* 35: 671-676.
- Pimentel D, Lach L, Zuniga R & Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50: 53-65.
- Ponti L, Gutierrez AP, Campos MR, Desneux N, Biondi A & Neteler M (2021) Biological invasion risk assessment of *Tuta absoluta*: mechanistic versus correlative methods. *Biological Invasions*. Accepted 07-27-2021.
- Prager SM, Esquivel I & Trumble JT (2014) Factors influencing host plant choice and larval performance in *Bactericera cockerelli*. *PLOS One* 9: e94047.
- Price PW, Denno RF, Eubanks MD, Finke DL & Kaplan I (2011) *Insect Ecology: Behavior, Populations and Communities*. Cambridge University Press, Cambridge, UK.
- Proffitt M, Birgersson G, Bengtsson M, Reis R, Witzgall P & Lima E (2011) Attraction and oviposition of *Tuta absoluta* females in response to tomato leaf volatiles. *Journal of Chemical Ecology* 37: 565-574.
- Roques A, Auger-Rozenberg M-A, Blackburn TM, Garnas J, Pyšek P et al. (2016) Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biological Invasions* 18: 907-920.
- Rostami E, Madadi H, Abbasipour H, Allahyari H & Cuthbertson AG (2020) Pest density influences on tomato pigment contents: the South American tomato pinworm scenario.

Entomologia Generalis 40: 195-205.

- Rostami E, Madadi H, Abbasipour H, Allahyari H & Cuthbertson AGS (2017) Life table parameters of the tomato leaf miner *Tuta absoluta* (Lepidoptera: Gelechiidae) on different tomato cultivars. *Journal of Applied Entomology* 141: 88-96.
- Sankarganesh E, Firake DM, Sharma B, Verma VK & Behere GT (2017) Invasion of the South American tomato pinworm, *Tuta absoluta*, in northeastern India: a new challenge and biosecurity concerns. *Entomologia Generalis* 36: 335-345.
- Sylla S, Brévault T, Bal AB, Chailleux A, Diatte M et al. (2017) Rapid spread of the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), an invasive pest in Sub-Saharan Africa. *Entomologia Generalis* 36: 269-283.
- Sylla S, Brévault T, Monticelli LS, Diarra K & Desneux N (2019) Geographic variation of host preference by the invasive tomato leaf miner *Tuta absoluta*: implications for host range expansion. *Journal of Pest Science* 92: 1387-1396.
- Tabuloc CA, Lewald KM, Conner WR, Lee Y, Lee EK et al. (2019) Sequencing of *Tuta absoluta* genome to develop SNP genotyping assays for species identification. *Journal of Pest Science* 92: 1397-1407.
- Tarusikirwa VL, Mutamiswa R, English S, Chidawanyika F & Nyamukondiwa C (2020) Thermal plasticity in the invasive south American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Journal of Thermal Biology* 90: 102598.
- Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata* 47: 3-14.
- Valladares G & Lawton JH (1991) Host-plant selection in the holly leaf-miner: does mother know best? *Journal of Animal Ecology* 60: 227-240.
- Van Damme V, Berkvens N, Moerkens R, Berckmoes E, Wittemans L et al. (2015) Overwintering potential of the invasive leafminer *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) as a pest in greenhouse tomato production in Western Europe. *Journal of Pest Science* 88: 533-541.
- Varley GC & Gradwell GR (1970) Recent advances in insect population dynamics. *Annual Review of Entomology* 15: 1-24.
- Verheggen F & Fontus RB (2019) First record of *Tuta absoluta* in Haiti. *Entomologia Generalis* 38: 349-353.

Wang Y, Yao F, Soares MA, Basiri SE, Amiens-Desneux E et al. (2020) Effects of four non-crop plants on life history traits of the lady beetle *Harmonia axyridis*. *Entomologia Generalis* 40: 243-252.

Worner SP, Gevrey M, Eschen R, Kenis M, Paini D et al. (2013) Prioritizing the risk of plant pests by clustering methods; self-organising maps, k-means and hierarchical clustering. *NeoBiota* 18: 83-102.

Wratten SD, Gillespie M, Decourtye A, Mader E & Desneux N (2012) Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems and Environment* 159: 112-122.

Xian X, Han P, Wang S, Zhang G & Liu W (2017) The potential invasion risk and preventive measures against the tomato leafminer *Tuta absoluta* in China. *Entomologia Generalis* 36: 319-333.

Zhang Y, Guo L, Atlihan R, Chi H & Chu D (2019) Demographic analysis of progeny fitness and timing of resurgence of *Laodelphax striatellus* after insecticides exposure. *Entomologia Generalis* 39: 221-230.

### Figure captions

**Figure 1** Survival rate ( $s_{x_i}$ ) of *Tuta absoluta* at each stage – egg, larvae (instars 1-4), pupae and adults (female and male) – on black nightshade and tomato in generations F1 and F2.

**Figure 2** Mean (+ SD) pupal weight (mg) of female and male *Tuta absoluta* larvae reared on black nightshade (BNS) and/or tomato for generations F1 and F2. Larvae were reared on the two plants separately in the (A) F1 and (B) F2, or for both generations on either (C) black nightshade or (D) tomato. Means within a panel capped with different letters are significantly different (Tukey's test:  $P < 0.05$ ).

**Figure 3** Mean (+ SD) number of eggs laid by *Tuta absoluta* on parts – leaves (adaxial and abaxial), petiole, and stem – of black nightshade (BNS) and tomato. Moth adults had either been reared on (A) BNS or (B) tomato plants. Asterisks indicate significant preference for tomato (paired t-test:  $P < 0.05$ ).

**Figure 4** Survival (%) of *Tuta absoluta* pupae on black nightshade and tomato after exposure for 7, 14, and 21 days to 4 °C.

**Figure 5** Oviposition (no. eggs/3 days) of *Tuta absoluta* females on black nightshade and tomato after exposure for 7, 14, and 21 days to 4 °C.

**Table 1** Mean ( $\pm$  SE) life table parameters of *Tuta absoluta* on *Solanum nigrum* and *S. lycopersicum* in generations F1 and F2

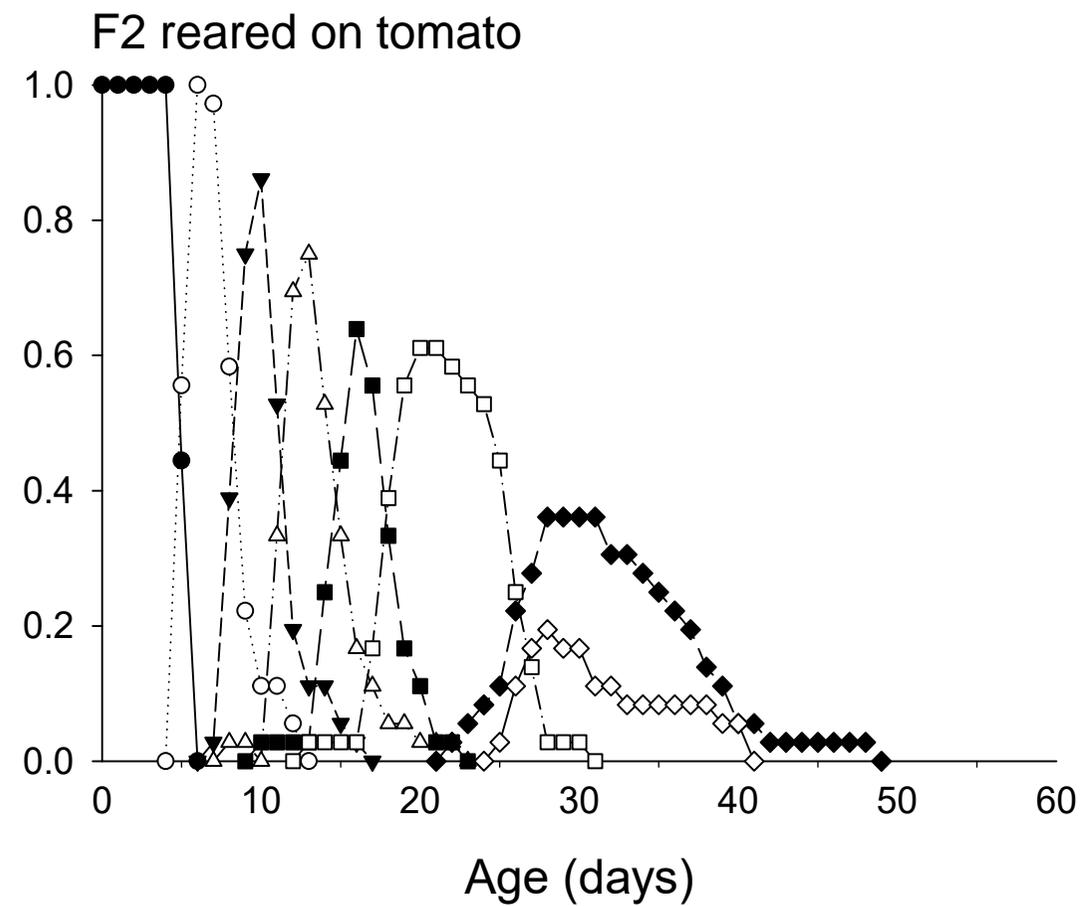
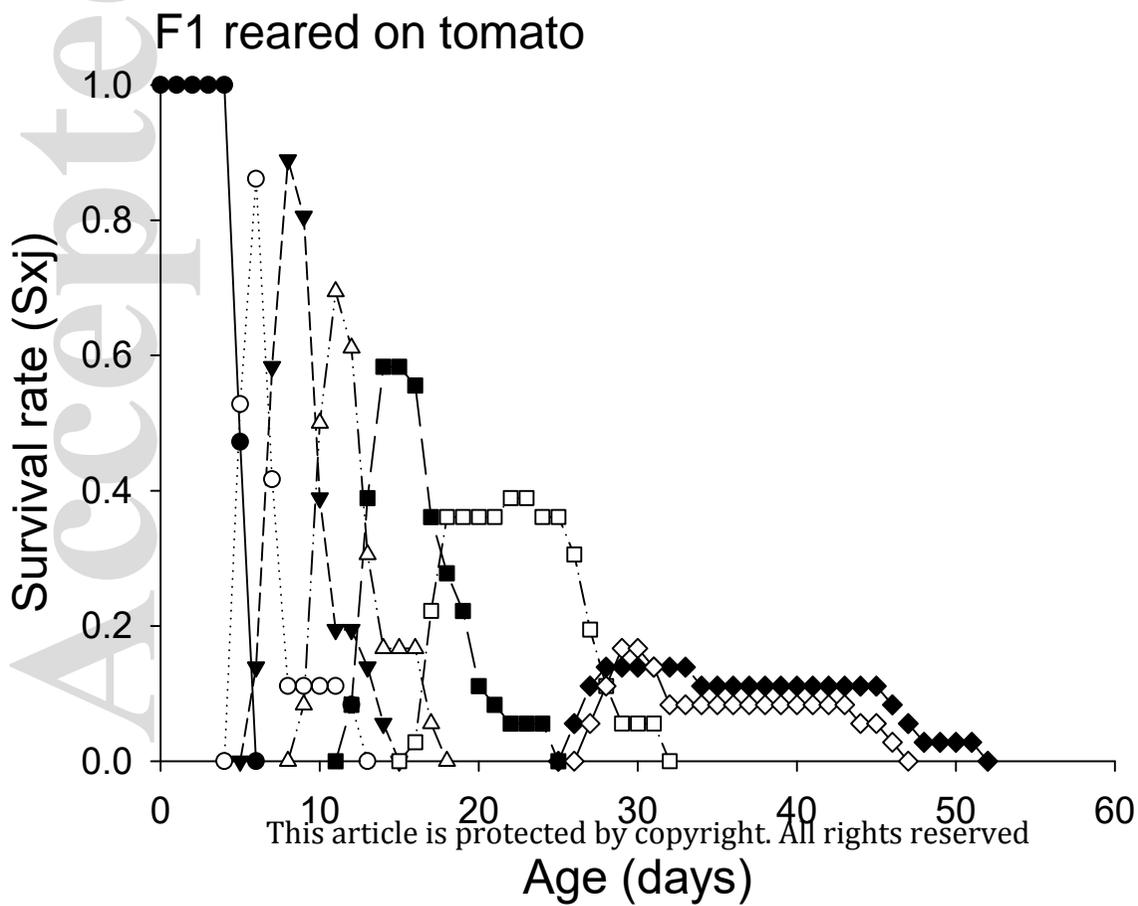
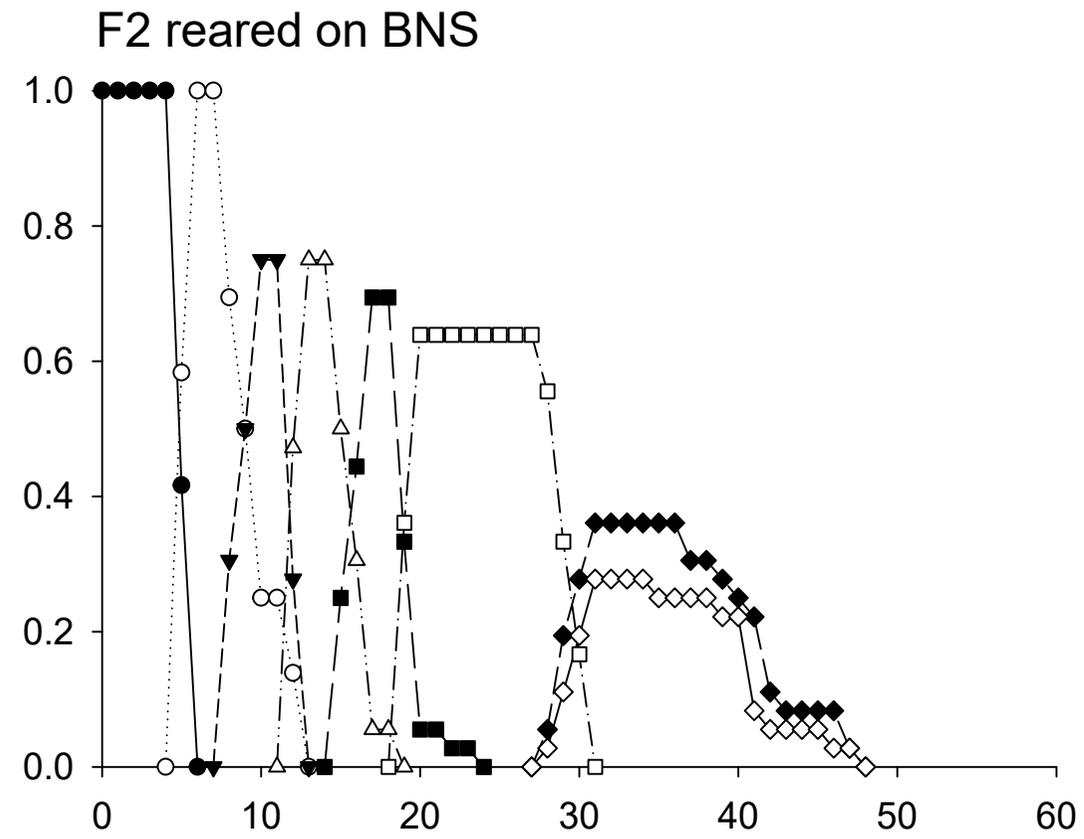
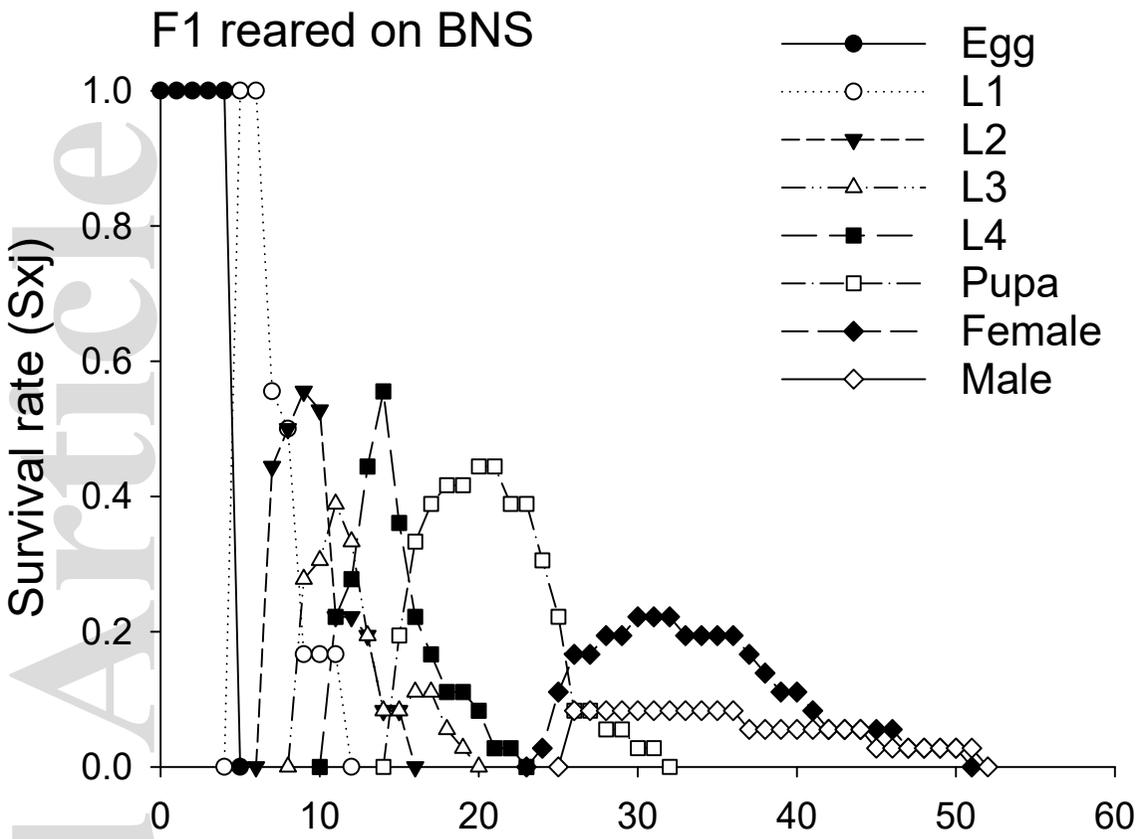
Parameters	Generation	<i>Solanum nigrum</i>	<i>Solanum lycopersicum</i>
Net reproductive rate, $R_0$ (offspring/individual)	F1	37.889 $\pm$ 11.279	20.472 $\pm$ 8.841
	F2	38.889 $\pm$ 9.718	47.167 $\pm$ 11.265
Intrinsic rate of increase, $r$ (day <sup>-1</sup> )	F1	0.128 $\pm$ 0.012	0.0986 $\pm$ 0.017b
	F2	0.116 $\pm$ 0.009	0.1350 $\pm$ 0.010a
Finite rate of increase, $\lambda$ (day <sup>-1</sup> )	F1	1.136 $\pm$ 0.014	1.1036 $\pm$ 0.018a
	F2	1.123 $\pm$ 0.010	1.1445 $\pm$ 0.011b
Mean generation time, $T$ (days)	F1	28.399 $\pm$ 0.882aB	30.6230 $\pm$ 0.430aA
	F2	31.606 $\pm$ 0.317bA	28.5430 $\pm$ 0.745bB
Gross reproductive rate, GRR (offspring/individual)	F1	118.150 $\pm$ 22.781a	70.520 $\pm$ 23.372
	F2	61.310 $\pm$ 13.356b	89.960 $\pm$ 16.457
Fecundity, $F$ (eggs/female)	F1	151.560 $\pm$ 11.466a	147.400 $\pm$ 22.109a
	F2	107.690 $\pm$ 12.943b	121.290 $\pm$ 14.491a
Longevity (days)	F1	25.110 $\pm$ 2.066a	25.690 $\pm$ 2.043
	F2	32.190 $\pm$ 2.222b	28.970 $\pm$ 1.671

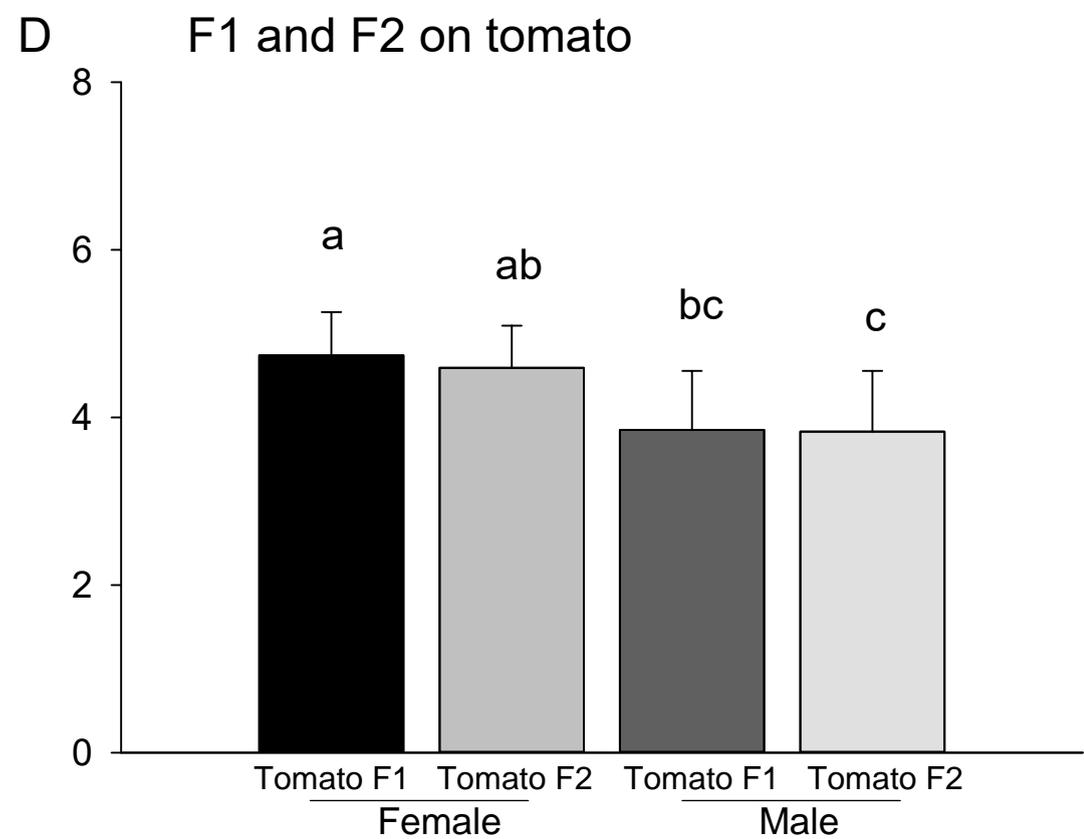
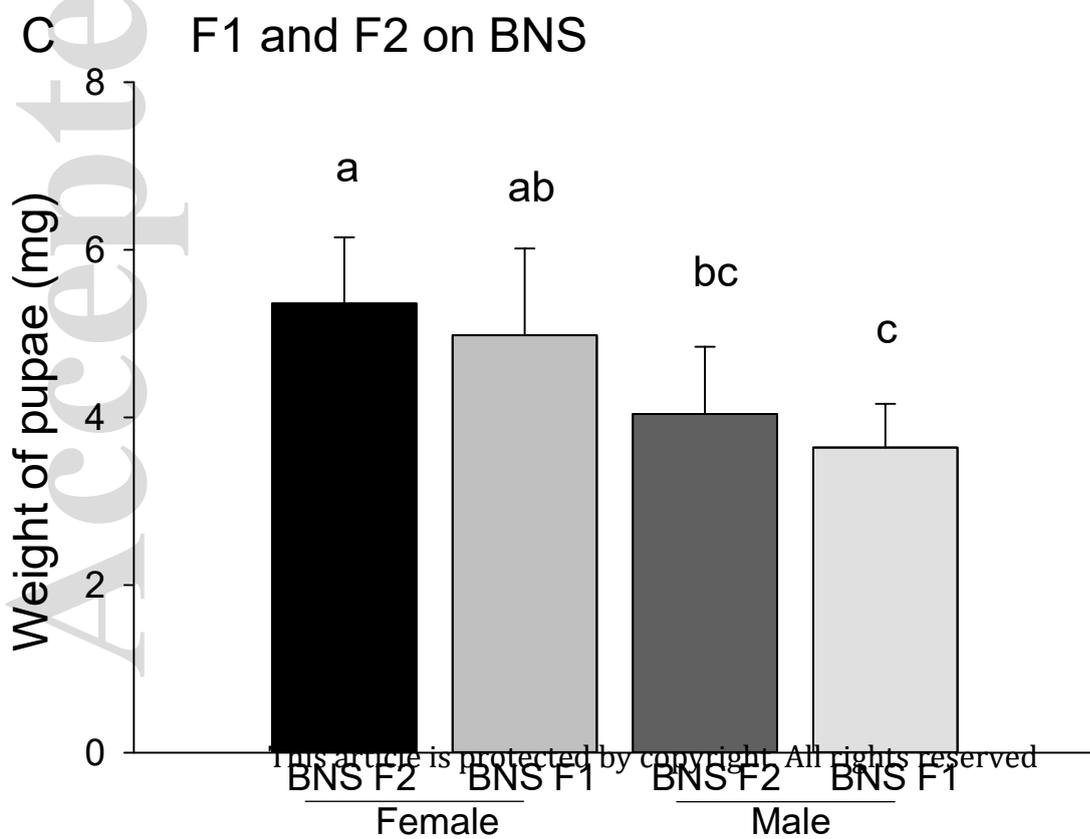
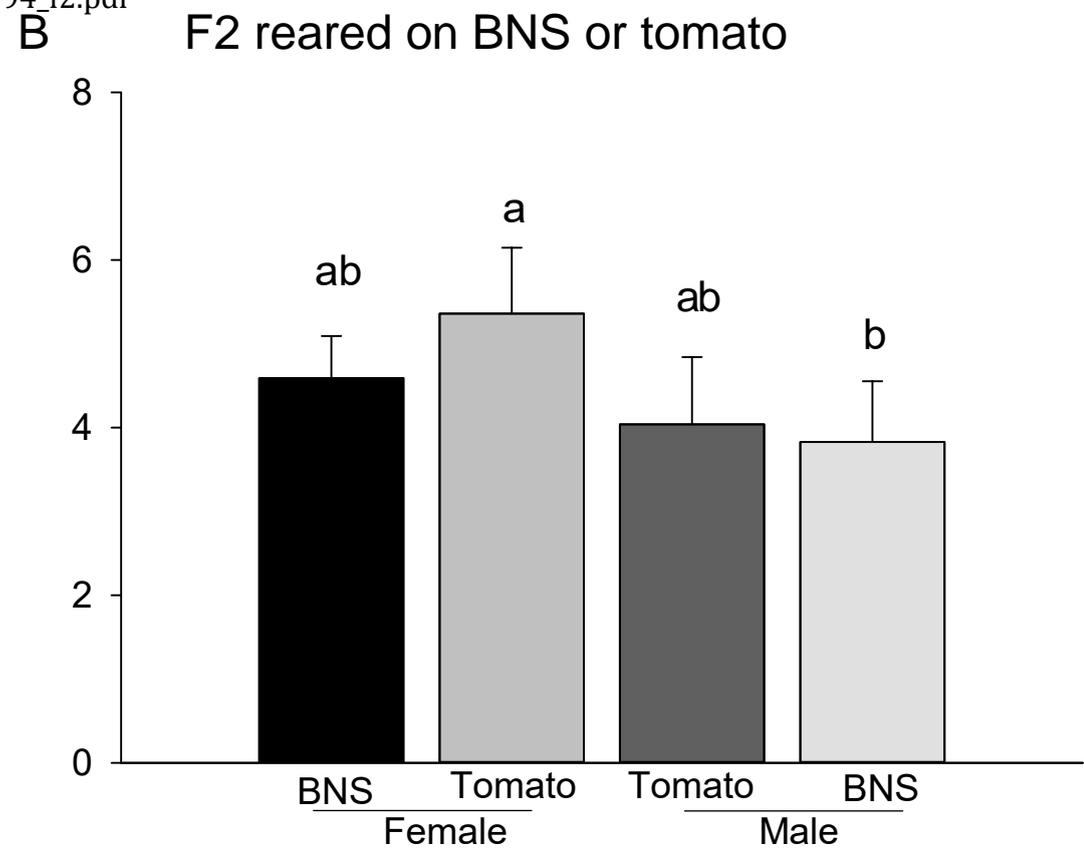
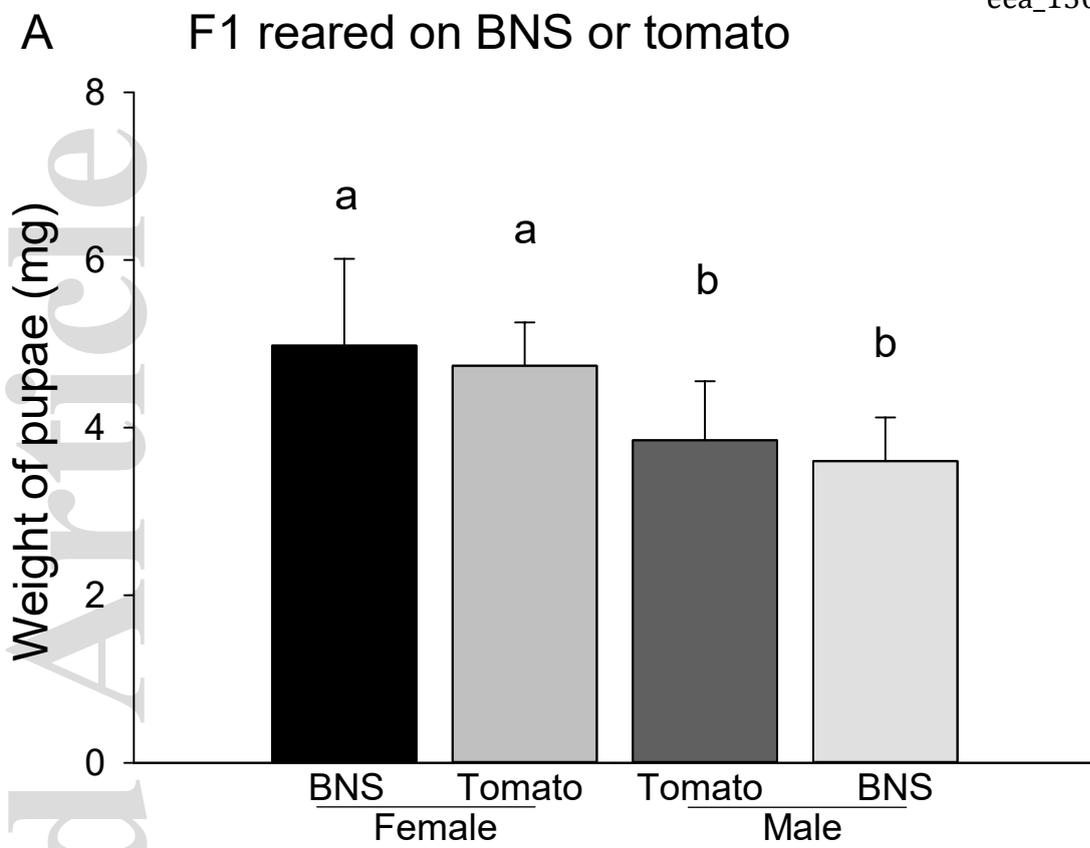
Means within a row followed by different uppercase letters, and within a column followed by different lowercase letters, are significantly different (paired bootstrap test based on the confidence interval of differences of 100,000 replicates:  $P < 0.05$ ).

**Table 2** Mean ( $\pm$  SE) development time (days) in each *Tuta absoluta* stage on *Solanum nigrum* and *S. lycopersicum* in generations F1 and F2

<i>Tuta absoluta</i> stages	Generation	<i>Solanum nigrum</i>	<i>Solanum lycopersicum</i>
Eggs	F1	5.44 $\pm$ 0.08	5.47 $\pm$ 0.08
	F2	5.41 $\pm$ 0.08	5.44 $\pm$ 0.08
First instar (L1)	F1	2.87 $\pm$ 0.18aA	1.75 $\pm$ 0.08aB
	F2	3.55 $\pm$ 0.10b	3.30 $\pm$ 0.15b
Second instar (L2)	F1	2.50 $\pm$ 0.30aA	3.22 $\pm$ 0.15B
	F2	3.44 $\pm$ 0.10bA	2.96 $\pm$ 0.10B
Third instar (L3)	F1	2.38 $\pm$ 0.11aA	3.09 $\pm$ 0.06B
	F2	3.60 $\pm$ 0.10b	3.30 $\pm$ 0.12
Fourth instar (L4)	F1	3.88 $\pm$ 0.17aA	4.62 $\pm$ 0.34aB
	F2	3.43 $\pm$ 0.10bA	3.09 $\pm$ 0.06bB
Pupae	F1	9.91 $\pm$ 0.35	9.81 $\pm$ 0.41a
	F2	10.21 $\pm$ 0.26A	8.28 $\pm$ 0.38bB
Adults	F1	14.58 $\pm$ 1.58	14.27 $\pm$ 2.23
	F2	12.17 $\pm$ 0.73	10.28 $\pm$ 1.02

Means within a row followed by different uppercase letters, and within a column followed by different lowercase letters, are significantly different (paired bootstrap test based on the confidence interval of differences of 100 000 replicates:  $P < 0.05$ ).



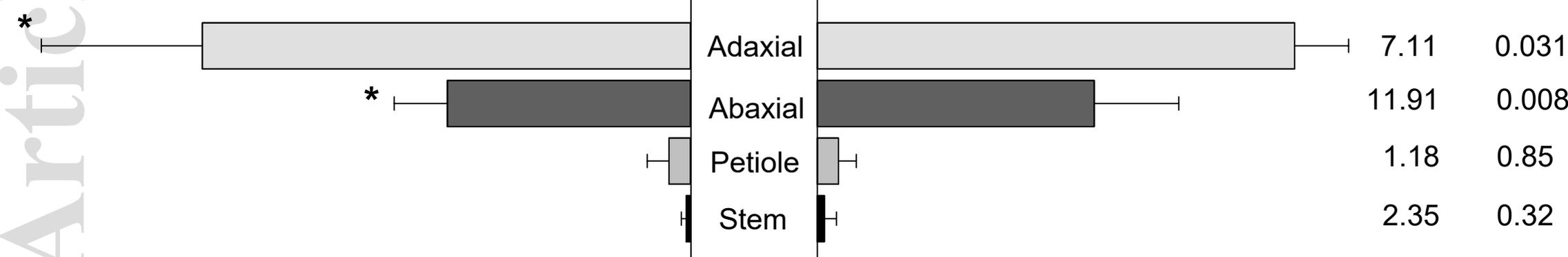


**A** Adults reared on BNS

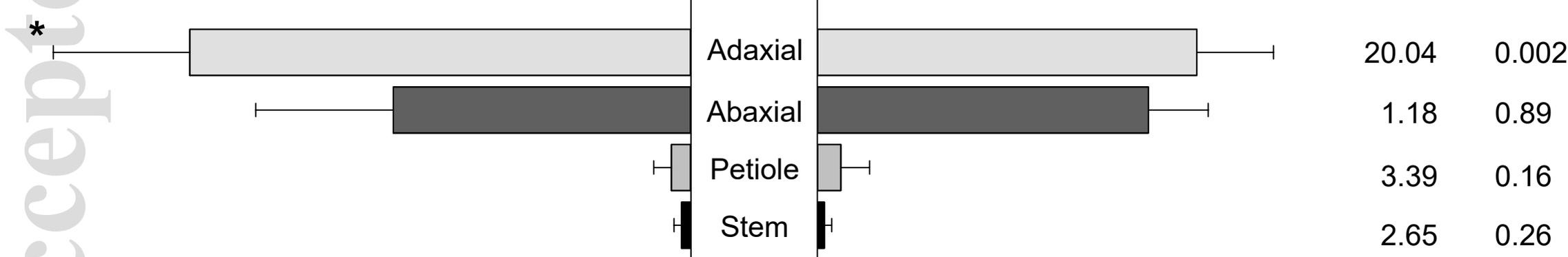
Tomato

BNS

t P



**B** Adults reared on tomato



120 100 80 60 40 20 0 0 20 40 60 80

No. eggs deposited

Accepted Article

