

Plant-Insect Interactions

Host plant selection is linked to performance in *Phthorimaea absoluta* (Lepidoptera: Gelechiidae)

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Subject Editor: Xoaquin Moreira

Received on 3 March 2024; revised on 17 April 2024; accepted on 7 May 2024

The evolution of oviposition preference in insects is considered a key evolutionary strategy in the context of host–plant interaction. It is hypothesized that insects maximize the survival and fitness of the subsequent generations by preferring specific host plant(s), known as the “preference–performance hypothesis.” In this study, we tested whether adult host preference reflects the immature performance in an oligophagous insect, *Phthorimaea absoluta* Meyrick, a rapidly emerging invasive pest in Asia, Africa, and Europe. Based on a preliminary survey of the potential host plants of *P. absoluta*, we selected 6 Solanaceae species, namely, tomato, potato, eggplant, black nightshade, sweet pepper, and tobacco, for the oviposition preference studies. The results indicated that the tomato was the most preferred host in no-, dual- and multiple-choice assays, followed by potato, eggplant, and black nightshade. Subsequently, the insect life-table parameters were found to be superior on tomato compared to other hosts. The order of oviposition preference on the host plants was strongly correlated with the life-table parameters of *P. absoluta*. Thus, we provide clear evidence for the preference–performance hypothesis in the host selection behavior of *P. absoluta*. We also emphasize the necessity of conducting oviposition behavior research at various geographic locations to develop tailor-made integrated pest management programs.

Key words: invasive insect, Solanaceae, preference–performance hypothesis, Gelechiidae, two-sex life table analysis

Introduction

Host–plant preference in phytophagous insects results from adaptive interactions between the insect and the plant (Jermy 1984, Mayhew 1997, Agosta 2006). Therefore, host plants significantly affect the life-history traits of insects feeding them, ultimately affecting their survival and fitness (Jermy 1984, Mayhew 1997, Sauvion et al. 2005, Agosta 2006, Negi et al. 2018). Insects generally prefer host(s) that provide high reproductive output (Futuyma and Moreno 1988, Ning et al. 2017). Mono- and oligophagous insects are adapted to a single or narrow range of host plants, whereas polyphagous insects can survive and reproduce on a wider range of hosts (Bernays and Graham 1988, Hardy and Otto 2014). Furthermore, polyphagous insects may accept less suitable plant species only without a preferred host, as their survival and reproduction would be assured if they did not have a superior fitness advantage (Awmack and Leather 2002, Leather and Awmack 2002).

The female’s oviposition preference plays a crucial role in the host selection process (Renwick 1989), as the mother’s choice can significantly influence the survival and fitness of her offspring. The “preference–performance” (P–P) Hypothesis (Jaenike 1978), also known as the “mother knows best” hypothesis (García-Robledo and Horvitz 2012, Rigsby et al. 2014) emphasizes that the adult will select the host that maximizes larval performance in terms of development (Valladares and Lawton 1991, Wehling and Thompson 1997, Singer 2008). Thus, the P–P relationship is expected to stabilize when larval performance is superior on the host plants preferred by adult females for oviposition; however, studies have also reported a negative or weak P–P relationship (Gripenberg et al. 2010, Friberg et al. 2015). For example, in a recently emerged invasive insect pest, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), larval performance was independent of the maternal oviposition choice (Sotelo-Cardona et al. 2021). In general, polyphagous insects with a broader

diet are expected to have a weaker relationship between P–P than oligophagous insects with a narrow diet (Gripenberg et al. 2007, Roslin and Salminen 2009). Thus, the strength of the P–P relationship varies across different ecological contexts and insect life-history strategies (Gripenberg et al. 2007).

The South American tomato moth, *Phthorimaea absoluta* Meyrick (Lepidoptera: Gelechiidae), formerly known as *Tuta absoluta*, is a serious invasive pest native to South America that threatens tomato production in most countries in Africa, America, Asia, and Europe (Tropea Garzia et al. 2012, Guimapi et al. 2020). However, it occasionally attains pest status in potato crops (Megido et al. 2013). Apart from tomato and potato, *P. absoluta* has also been reported on more than 50 host plants that are commercially cultivated and its wild relatives (Bawin et al. 2016, Biondi et al. 2017, Guimapi et al. 2020). Furthermore, *P. absoluta* showed variation in developmental duration and life-table parameters when feeding on different host plants, compared to the primary host, tomato, under both laboratory and field conditions (Chailleux et al. 2013, Sridhar et al. 2015, Idriss et al. 2020). Additionally, *P. absoluta* has shown a shorter developmental rate (Pereyra and Sánchez 2006, Negi et al. 2018), higher survival rate (Negi et al. 2018), fecundity (Bawin et al. 2016), pupal weight (Pereyra and Sánchez 2006, Megido et al. 2013, Bawin et al. 2016, Negi et al. 2018), and longer oviposition days (Abbes et al. 2016, Negi et al. 2018) when feeding on the primary host (tomato) compared to other species. The variation in nutrient availability among the host plants is expected to influence the feeding and developmental duration (Pereyra and Sánchez 2006, Negi et al. 2018), resulting in considerable variation in the reproductive potential of the insect (García-Robledo and Horvitz 2012).

Under natural conditions, *P. absoluta* has been observed ovipositing on other plant species only when the primary host (tomato) was unavailable (Tonnang et al. 2015, Bawin et al. 2016). Also, *P. absoluta* showed more preference for a few hosts that were genetically closely related to tomato (Bawin et al. 2015). This could be because genetically related plants would produce similar secondary metabolite profiles that could be analogous to chemicals emitted by tomato (Bawin et al. 2015). However, studies of the insect's host plant preference have not been consistent across space (Bawin et al. 2016, Sylla et al. 2019). For instance, *P. absoluta* populations from France preferred eggplant over potato, while *P. absoluta* populations from Senegal showed an equal preference for both eggplant and potato. This geographical difference in oviposition behavior may be due to the proportional availability of hosts under field conditions. Studies have also demonstrated the changes in insect oviposition preference when presented with multiple host plant combinations (Sylla et al. 2019). In Sudan, *P. absoluta* preferred black nightshade and French bean to potato, while in Ethiopia, *P. absoluta* laid more eggs on potato than on sweet pepper and other crops (Abbes et al. 2016). Such variations in the oviposition preference depended on the composition and abundance of host plants in a given area and the adaptive advantages they conferred (Sylla et al. 2019). Moreover, a broad spectrum of host preference behavior could have context-specific implications, highlighting the need for regional studies to address these challenges.

Regarding economic relevance, in India, *P. absoluta* caused yield losses of up to 100 percent (Sridhar et al. 2015) if pest control measures were not initiated in time. Such reports have increased recently despite the availability of pest management technologies. It is crucial to investigate insect behavior relevant to the specific agroecosystems under consideration to develop a knowledge base for designing more effective pest management approaches.

With this background, the study was conducted to explore (i) the oviposition preference of the *P. absoluta* population under different host combinations and (ii) whether the performance of the *P. absoluta* population is related to oviposition preference. Furthermore, we discuss the implications of our study regarding the insect's potential to spread under the prevailing agroecological conditions.

Materials and Methods

Laboratory Rearing of *P. absoluta*

The insect sample was initially identified based on the larval and adult morphological traits and collected from tomato crop cultivated under greenhouse conditions in the premises of I B Seeds Pvt Ltd., Bengaluru, India (12° 54' 17.9244" N, 77° 30' 32.8032" E) during 2018. The test population was propagated in the laboratory according to a protocol developed by Galdino et al. (2011). The adults used for all the experiments were collected from this laboratory-reared population. All laboratory experiments were conducted at the Department of Entomology, University of Agricultural Sciences, Bengaluru, India, during 2018–2019.

Oviposition Preference of *P. absoluta* on Different Host Plant Species

Oviposition preference of the adults was assessed through no-choice, dual-choice, and multiple-choice assays. A preliminary "no-choice" behavioral assay using 6-wk-old plants of 8 different host species grown commercially in South India (tomato—*Solanum lycopersicum* L.; potato—*Solanum tuberosum* L.; eggplant—*Solanum melongena* L.; sweet pepper—*Capsicum annum* L.; tobacco—*Nicotiana tabacum* L.) and the wild relatives (tropical soda apple—*Solanum viarum* L.; black nightshade—*Solanum nigrum* L.; Indian nightshade—*Solanum indicum* L.). All plants were grown under controlled conditions [30 ± 5 °C, 70 ± 5% RH, and 13:11 h photoperiod regime (L:D)], and plant material was collected and used in accordance with relevant guidelines. Subsequently, plant species receiving more than 5 eggs per plant (an estimated lower limit value of eggs in the population), namely, tomato, potato, eggplant, sweet pepper, tobacco, and black nightshade were considered for further oviposition preference studies (Supplementary Fig. S1). In all oviposition choice experiments, 1-day-old mated adults were released at a rate of 2 pairs (2 males and 2 females) per plant and allowed to lay eggs for 3 days. On the 4th day, the adults were removed from the cage, and the number of eggs laid on different parts of the plant was recorded. A cotton swab dipped in 10% sugar solution was provided as a food source for the adults during assays. All the assays were conducted under controlled conditions [26 ± 2 °C, 70 ± 5% RH, and 13:11 h photoperiod regime (L:D)]. The performance of immatures reared on different host species, and their effect on developmental and fitness parameters were studied through life-table analysis.

No-choice assay.

Based on the preliminary screening assay results, 6 host species, namely, tomato, potato, eggplant, black nightshade, sweet pepper, and tobacco were considered for the no-choice assay. The no-choice assays were conducted in meshed cages (1.14 m × 1.14 m × 1.14 m) in a poly house [26 ± 2 °C, 70 ± 5% RH and 13:11 h photoperiod regime (L:D)]. Two 6-wk-old plants of each host species were separately placed in different cages, and this setup was replicated 8 times. One-day-old mated adults were released at a rate of 2 pairs (2 males and 2 females) per plant, and the number of eggs on each plant was recorded after 3 days. The effect of host plants on oviposition was

analyzed using a generalized linear model (GLM), with the number of eggs per plant as the response variable and the host plant as the predictor. Means were compared using Tukey's HSD post hoc test in IBM SPSS statistical software (Version 20).

Dual-choice assay.

About 6-wk-old plants from the different host species viz., tomato, potato, eggplant, and black nightshade were considered for dual-choice assays. Tobacco and sweet pepper were excluded as they received significantly low numbers of eggs in the previous no-choice assay. To rule out the possibility of natal host plant influence on the oviposition preference behavior of the insect (Prager et al. 2014), adults were reared separately on each host plant species for 3 consecutive generations before the experiment. These populations of *P. absoluta* developed on different hosts were assessed for oviposition behavior. All dual-choice assays were conducted by providing 4 plants of each of 2 host species, one of which is common (tomato) in all assays. This methodology was adapted from Srinivasan et al. (2013) and conducted under controlled conditions [26 ± 2 °C, $70 \pm 5\%$ RH and 13:11 h photoperiod regime (L:D)]. Each host plant was placed equidistantly in a circle to form a semicircle with a radius of 1-m in the mesh cages ($3 \text{ m} \times 3 \text{ m} \times 3 \text{ m}$), and this experiment was replicated 8 times. One-day-old mated adults were released at a rate of 2 pairs (2 males and 2 females) per plant, and the number of eggs on each plant was recorded after 3 days. The mean and standard deviation of the number of eggs on each plant species were calculated, and pair comparison with Student's "t" test was used to analyze the difference in the eggs laid on tomato versus other hosts using IBM SPSS statistical software (Version 20).

Multiple-choice assay.

Oviposition preference of *P. absoluta* in the presence of several hosts was tested in a multiple-choice assay using the methodology developed by Srinivasan et al. (2013). Two 6-wk-old plants of each of the selected host plant species were randomly arranged circularly with a 1 m radius from the center in the cages ($3 \text{ m} \times 3 \text{ m} \times 3 \text{ m}$) under poly house conditions [26 ± 2 °C, $70 \pm 5\%$ RH and 13:11 h (L:D)]. One-day-old mated adults were released at the rate of 2 pairs (2 males and 2 females) per plant, and the number of eggs on each plant was recorded after 3 days. This experiment was replicated 8 times. The oviposition preference of the host plants was analyzed using a GLM where the number of eggs per plant was considered the response variable, and host plants were the predictors. Further, means were compared using Tukey's HSD post hoc test in IBM SPSS statistical software (Version 20).

Two-Sex Life-Table Analysis

Following the individual rearing technique, *P. absoluta* populations were reared on 60-day-old host plants from different host species. Initially, the insect population was reared under laboratory conditions [26 ± 2 °C, $70 \pm 5\%$ RH and 13:11 h (L:D)] on tomato, potato, eggplant, and black nightshade before setting up the experiment. About 25 eggs laid by one-day-old females on each host species were collected from rearing cages. Each egg was reared in a Petri plate (100 mm diameter) and provided with its respective host plant leaf that was cushioned on a wet cotton towel. Petri plates were monitored daily to record the duration and survival rate of different developmental stages, viz., egg, larvae, and pupae of the insect. The old leaves were replaced with new leaves ad libitum. The pupae were later identified as male or female based on the position of 2 small tubercles present on the 8th (female) or a longitudinal suture on the 9th (male) abdominal segment (Genç 2016). Upon emergence, the virgin male and female moths were paired. Each pair was released into separate cages ($1.14 \text{ m} \times 1.14 \text{ m} \times 1.14 \text{ m}$) and provided with 30-day-old host plants. The number of eggs laid by each pair was recorded every day. Adults were monitored under laboratory conditions [26 ± 2 °C, $70 \pm 50\%$ RH, and 13:11 h (L:D)] until they completed their life span. Further, each individual's abdomen was dissected to reconfirm the sex of the individual (Fig. 1).

Life-table data was analyzed using the "TWOSEX_MSChart" program (Chi 2021) developed based on the theory of age-stage, 2-sex life table (Chi and Liu 1985, Chi 1988, Negi et al. 2018). The developmental period, reproductive parameters (fecundity and total oviposition days), and population parameters viz., age stage survival rate (S_{xj} , where age = x , and stage = j), age-specific survival rate (l_x : the probability that a newly laid egg survives to age x), age-specific fecundity (mx), mean generation time (T : the period that a population requires to increase to R_0 -fold of its size as the time approaches infinity), intrinsic rate of increase (r : the rate at which a population increases when resources are infinite), finite rate of increase (λ : the rate at which a population increases when resources are finite), net reproductive rate (R_0 : number of females that replace the mother) (Chi and Liu 1985, Chi et al. 2020) were calculated using the below-mentioned formulae:

(l_x : the probability that a newly laid egg survives to age x) (Eq. 1)

$$l_x = \sum_{j=1}^{\delta} S_{xj} \quad (1)$$

where δ is the last stage of the study cohort.

The age-specific fecundity of the population, mx (Eq. 2) was calculated as:

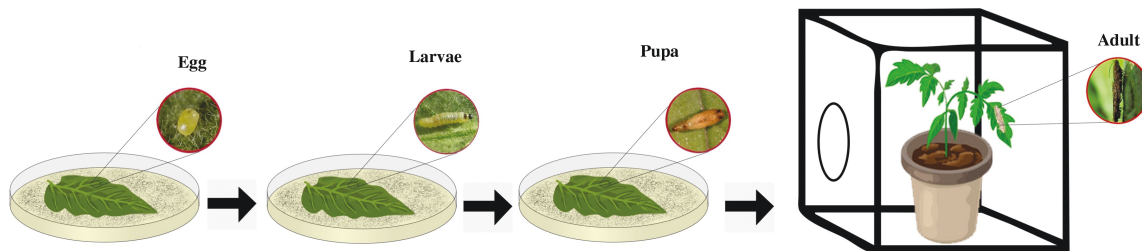


Fig. 1. The protocol adopted for life-table analysis using the individual-rearing method. Eggs collected from a one-day-old adult pair were incubated on a single host plant leaf kept on a wet cotton towel in a Petri plate (100 mm diameter) and monitored daily. Thus, there were 25 such leaf-egg sets for each host plant studied. At the pupal stage, males and females were segregated and paired; pupal pairs were transferred to the cage where a 30-day-old host plant was placed for mating and egg-laying.

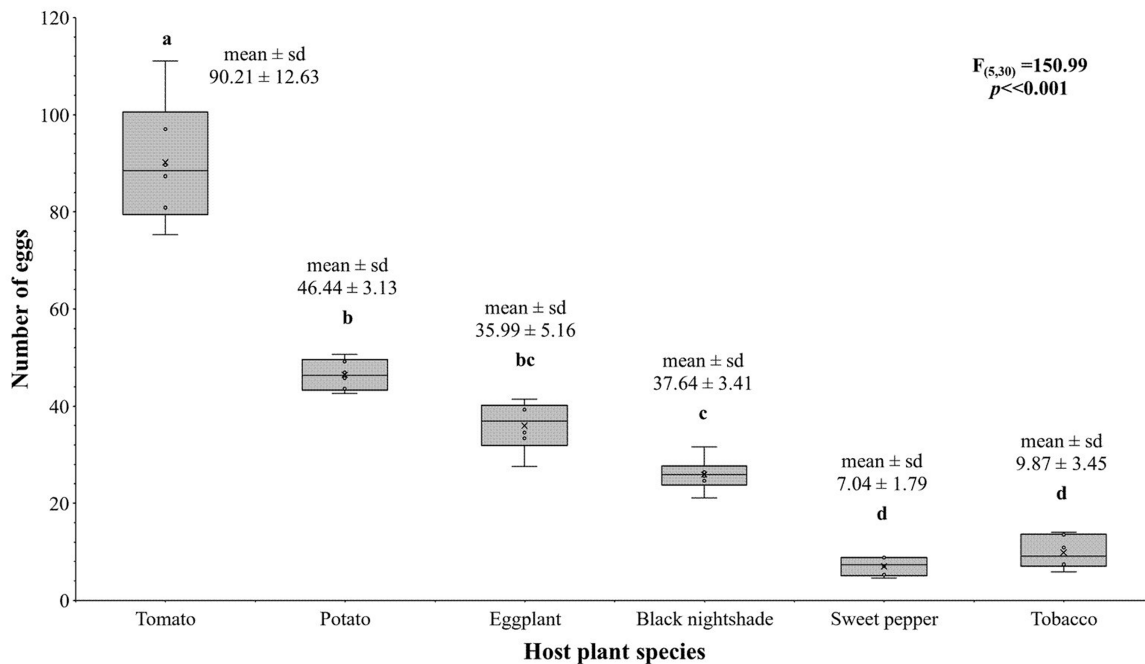


Fig. 2. The number of eggs (mean \pm SD) laid by *P. absoluta* on different host plant species in no-choice assay. The box represents first, median, and third quartile values, respectively, from top to bottom lines, whereas the whiskers on both sides represent ranges between minimum and maximum values. Different letters indicate significant differences in average egg load among host species.

$$m_x = \frac{\sum_{j=1}^{\delta} S_{xj} f_{xj}}{\sum_{j=1}^{\delta} S_{xj}} \quad (2)$$

The net reproductive rate, R_0 (Eq. 3), which represents the mean number of offspring that an individual can produce during its lifetime, was calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

The intrinsic rate of increase, r (Eq. 4), was estimated using the iterative bisection method from the Euler–Lotka formula

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (4)$$

The finite rate of increase, λ (Eq. 5), and the mean generation time, T , were then calculated as follows:

$$\lambda = e^r \quad (5)$$

$$T = \frac{\ln R_0}{r} \quad (6)$$

The mean and standard error of the life-table parameters were estimated by using the bootstrap procedure (Chi and Liu 1985, Efron and Tibshirani 1994, Huang and Chi 2012a, b, 2013) with bootstrap number $n = 100,000$ to ensure precise estimates. The paired bootstrap test was conducted to compare life-table parameters in “TWOSEX_MSChart” program.

Correlation Between the Preference and Life-Table Parameters

The proportional eggs laid on each host plant species in the choice and no-choice experiments were averaged and used as a proxy for each host’s “oviposition preference.” To test the P–P hypothesis in *P. absoluta*, Pearson’s correlation was performed between the oviposition preference and estimated life-table parameters of the insects

reared on different host plants. The analysis was run using IBM SPSS statistical software (version 20).

Results

Oviposition Preference

No-choice assay.

When insects were not given any choice of host plants (i.e., no-choice assay), the number of eggs deposited on the tomato was significantly higher than other host plants. Further, the potato plants received 45% less eggs, while eggplant and black nightshade were deposited with much lesser eggs (60% and 58%, respectively) compared to the tomato ($F_{5,30} = 150.99$; $P < 0.001$). The number of eggs deposited on tobacco and sweet pepper plants was nonsignificantly different between them and very low compared to tomatoes. Therefore, these 2 host plant treatments were removed from the other subsequent assays (Fig. 2).

Dual-choice assay.

When insects were given 2 host plant choices (i.e., dual-choice assays), tomato plants were preferred over other host plant species, irrespective of the hosts on which the insects were reared, and a significantly higher number of eggs were deposited on tomato compared to other host plants (Table 1). In dual-choice experiments, the number of eggs laid on tomato plants alone varied significantly according to the host plants on which insects were reared ($F_{3,7} = 158.40$; $P < 0.001$). Furthermore, when the adults reared on tomato were introduced in the dual-choice assays, the number of eggs laid on tomato varied in the presence of different host plant species. More specifically, when black nightshade and eggplants were given as a choice together with tomato, more than 90% of eggs were laid on tomato, whereas when potato was given as a choice, 72.23% of eggs were laid on tomato. A similar proportion of eggs laid on tomato was observed when *P. absoluta* was reared on different host plants (Table 1).

Table 1. The number of eggs laid by *P. absoluta* on host plants in dual-choice assays after rearing on different species. The Student's *t*-test compares the mean number of eggs laid on the tomato plants and the corresponding alternate host plants

Rearred host	Choice plants	Tomato		Alternate host		<i>t</i> -Test value	<i>P</i> value	Preference for tomato (%)
		No. of eggs (mean ± SD)	No. of eggs (mean ± SD)	No. of eggs (mean ± SD)	No. of eggs (mean ± SD)			
Tomato	Tomato–potato	90.79 ± 76.92	35.23 ± 26.43	36.39	<0.001	72.23		
Tomato	Tomato–eggplant	119.83 ± 38.54	22.95 ± 16.45	30.64	<0.001	90.01		
Tomato	Tomato–black nightshade	143.87 ± 112	15 ± 10.17	37.28	<0.001	91.06		
Potato	Tomato–potato	41 ± 20.60	17.04 ± 10.56	24.56	<0.001	70.69		
Eggplant	Tomato–eggplant	23.45 ± 9.12	3.83 ± 3.97	26.03	<0.001	86.67		
Black nightshade	Tomato–black nightshade	15.04 ± 9.1	0.91 ± 0.6	21.66	<0.001	94.59		

Multiple-choice assay.

When all 4 host species were given together as choice plants, the tomato received significantly more eggs than other host plant species ($F_{3,7} = 556.10; P < 0.001$). On average, the number of eggs laid on tomato was 4 times higher than on potato, 8 times higher than eggplant, and 20 times higher than black nightshade (Fig. 3).

Performance of *P. absoluta* on Host Species

Developmental duration of *P. absoluta*.

The developmental duration of the life stages of the insect varied when reared on different host plants. The egg duration ranged between 3 and 5 days, and there was no significant difference among the insects reared on different host plant species (Table 2). However, the larval durations were on an average lowest on potato and tomato, whereas it extended to 1.2- and 1.5-folds when the insect fed on eggplant and black nightshade when compared to tomato. Similarly, the pupal duration was longest on eggplant (1.35-fold more) compared to tomato, with the lowest duration recorded. There was only a marginal difference in the pupal duration of insects reared on potato and Indian black nightshade. Consequently, preadult (egg to pupae) duration was 1.2-fold longer in the individuals reared on eggplant and black nightshade compared to tomato and potato (Table 2). The adult life span of insects reared on tomato and potato increased on average by 25% and 20%, respectively, compared to those reared on eggplant and black nightshade. The highest number of female adult moths survived on tomato, followed by potato, with a 9% decrease in female adult survivability. However, there was a 30% decrease in adult female survival on eggplant and nightshade compared to tomato. Among the adults, female moths lived longer (40%) than male moths, regardless of the host plant species (Table 2). It is to be noted that plants on which the larvae took longer to grow and had longer pupal periods, while the adults lived for a shorter period. Consequently, total life cycle duration did not significantly vary among the insects reared on different host species (Table 2).

Reproductive parameters.

The total oviposition days of the adult females significantly varied across different host plants. Oviposition duration of females on the eggplant and black nightshade were shorter by 33% and 11% compared to tomato and potato, respectively. Commensurate with the duration, female fecundity was 2-fold higher in tomato and 1.3-fold higher in potato than eggplant and black nightshade, respectively (Table 2).

Survival rate.

The number of individuals surviving to the subsequent stage (survival rate) was compared among the populations reared on the different host plant species across all the developmental stages. The survival rates of individuals in the egg stage were similar to all host species. The egg hatching commenced on all the hosts from the third or 4th day. The larvae developed on tomato showed the highest survival rate compared to those on other host species (Figs. 4 and 5). Contrarily, on other host species, larval survival rates significantly decreased, especially between 3 and 7 days after hatching. Subsequently, larvae started to attain the pupal stage on the 7th day after eclosion on all the hosts except the black nightshade, while on the black nightshade, pupal stage commencement was delayed by 5 days. Subsequently, adult emergence was initiated on the 18th day in the population reared on tomatoes and showed the highest survival rate. Considering all the stages of *P. absoluta*, the highest survival rate was observed in tomatoes, followed by potatoes, when compared to eggplant (Fig. 4).

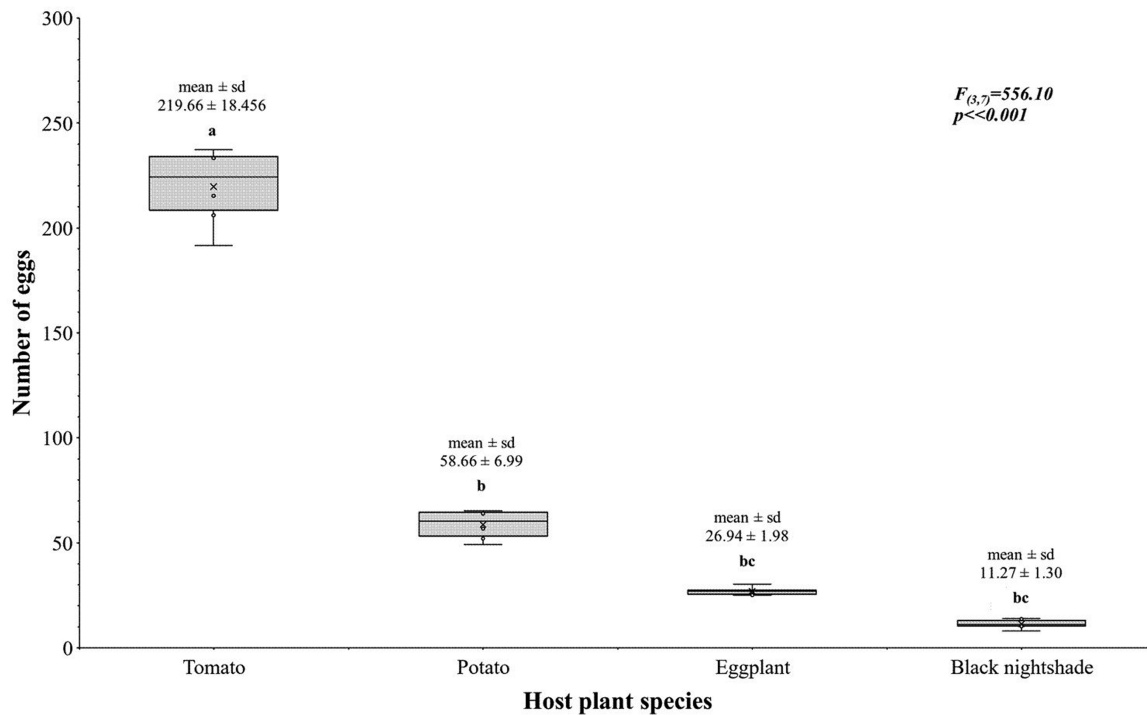


Fig. 3. The number of eggs (mean \pm SD) laid by *P. absoluta* on different host plant species in multiple-choice oviposition assay. The box represents first, median, and third quartile values, respectively, from top to bottom, whereas the whiskers on both sides represent the ranges between minimum and maximum values. Different letters indicate significant differences in average egg load among host species.

Life-table parameters.

The intrinsic rate of increase (r) and finite rate of increase (λ) of the individuals were higher on the tomato compared to the other host plant species evaluated (Table 3). This implies that the *P. absoluta* population could grow faster on tomato than other hosts. However, potato and eggplant could be the next best option for population growth, rather than the black nightshade, which had the lowest values of growth parameters.

This was also corroborated by the fact that the mean generation time (T -days) of the insect was significantly shorter by 20% in tomato compared to other host plant species (Table 3). Likewise, the net reproductive rate was significantly higher on *P. absoluta* grown on tomato and potato compared to eggplant and black nightshade, indicating that almost twice as many daughters replace their mother on tomato compared with insects reared on potato, and differences were more evident when compared to eggplant and black nightshade, where the difference was almost 3-fold.

Correlation Between Preference and Performance

There was a significant strong correlation between the oviposition preference and all the life-table parameters, i.e., intrinsic rate of increase (r) ($r = 0.932$, $df = 2$, $P = 0.034$), finite rate of increase (λ) ($r = 0.956$, $df = 2$, $P = 0.022$), net reproductive rate (R_0) ($r = 0.989$, $df = 2$, $P = 0.006$) and fecundity ($r = 0.985$, $df = 2$, $P = 0.007$), except mean generation time (T) ($r = -0.850$, $df = 2$, $P = 0.075$) (Fig. 6).

Discussion

The oviposition preference of *P. absoluta* has been extensively studied worldwide (Bawin et al. 2015, 2016, Abbes et al. 2016, Sylla et al. 2019, Idriss et al. 2020). The observed variation in adult preference behavior has been linked to inherent differences among populations that have likely evolved due to the availability and abundance of

nearby hosts (Sylla et al. 2019). However, the adaptive significance of oviposition preference in *P. absoluta* has been little sparsely tested in the past (Wang et al. 2020). In this study, we assessed the consequence of the adult preference pattern for subsequent generations and discussed the relevance of the observed “preference-performance” pattern in detail.

There were 3 major outcomes from the present study: (i) *P. absoluta* preferred tomato plants for oviposition despite the availability of other alternative host plants; (ii) the oviposition preference of *P. absoluta* was independent of its natal host species; and (iii) the performance of the insect population in terms of developmental, duration and life-table parameters was overall superior on tomato compared to other host species. Furthermore, the most preferred host for oviposition was also the one that maximized larval survival and subsequent reproductive potential.

The process of finding a suitable host by the adult insect involves the perception of multiple signals produced by the host plant (Renwick and Chew 1994, Carlsson et al. 1999, Tholl et al. 2006, Teles Pontes et al. 2010). In general, it is known that plants belonging to the same family emit a number of common and species-specific volatiles by which insects can differentiate between closely related species (Proffitt et al. 2011, Megido et al. 2014). In addition, tomato plants already infested by the pest are less preferred by *P. absoluta* than those free of the pest (Anastasaki et al. 2018). Thus, the insect’s preference or nonpreference for the hosts can be attributed to the presence/absence of specific chemicals produced by the plants (Proffitt et al. 2011). For example, adults of *P. absoluta* were attracted to the plants (tomato—*S. lycopersicum*) that produced higher concentrations of terpenes (Megido et al. 2014). They rejected nonhost plants (watermelon—*Citrullus lanatus* L.) that produced “green organic volatiles” (Proffitt et al. 2011). In the present study, the role of volatiles in oviposition preference behavior was not investigated. However, in the choice experiments, the chemicals

Table 2. Life-table parameters of life-history parameter viz., developmental time, adult longevity, total life cycle, oviposition days, adult preoviposition period (APOP), total preoviposition period (TPOP), fecundity and oviposition days of *P. absoluta* reared on 4 host species. Standard errors were estimated using 100,000 bootstrap resampling. Data followed by the same lower-case letter within a row were not significantly different based on a paired bootstrap test at a 5% significance level

Parameters	Insect stage	Host plant species			
		Tomato	Potato	Eggplant	Black nightshade
Developmental time (days)	Eggs	3.84 ± 0.55 ^a	4.04 ± 0.45 ^a	3.65 ± 0.65 ^a	4.09 ± 1 ^a
	Larvae	9 ± 0.66 ^c	9.05 ± 0.86 ^c	11 ± 1.17 ^b	13.87 ± 1.19 ^a
	Pupae	7.96 ± 0.56 ^b	8.15 ± 0.67 ^{ab}	10.33 ± 0.9 ^a	8.08 ± 0.64 ^{ab}
	Preadults	21 ± 1.41 ^b	21.3 ± 1.63 ^b	25 ± 1.73 ^a	26 ± 1.47 ^a
	Adults	13.78 ± 3.38 ^a	13.05 ± 2.52 ^a	10.53 ± 2.07 ^b	11.31 ± 1.75 ^b
Adult longevity	Female	16.64 ± 1.63 ^a	15.44 ± 0.53 ^b	12.43 ± 1.27 ^c	12.67 ± 1.37 ^c
	Male	11.17 ± 2.21 ^a	11.09 ± 1.58 ^a	8.88 ± 0.64 ^b	10.14 ± 1.07 ^b
Total life cycle		34.61 ± 3.51 ^b	34.35 ± 3.6 ^b	35.53 ± 2.97 ^{ab}	37.31 ± 2.81 ^a
	APOP	1.00 ± 0 ^a	1.22 ± 0.44 ^a	1.00 ± 0 ^a	1.00 ± 0 ^a
TPOP		22.00 ± 1.41 ^b	23.44 ± 1.42 ^b	26.86 ± 1.35 ^a	27.67 ± 1.21 ^a
	Fecundity	145.98 ± 9.89 ^a	96.58 ± 8.27 ^b	72.83 ± 6.26 ^c	69.84 ± 5.96 ^c
Oviposition days		11.55 ± 1.81 ^a	10.11 ± 1.45 ^b	8.86 ± 1.07 ^c	8.67 ± 1.03 ^c

produced by the 2 host species could likely interfere with each other as the choice plants were not physically isolated. However, despite such possible chemical interference, the pest showed a clear preference for tomato over other crops, suggesting 2 possibilities: (i) the insect may use a specific combination of volatile chemicals and other cues and/or (ii) the volatile chemicals may be strong enough to create a gradient within the small microenvironment so that the pest is still able to discriminate between host plants.

By selecting a suitable host for oviposition, the mother ensures the survival of its progeny by providing optimal sources of nutrition to the young insects (Hwang et al. 2008). When nutrient supply (from plants) and demand (of the developing insect) mismatch, insects tend to adopt different compensatory responses such as altering the consumption or improving metabolic efficiency, ultimately shaping the life-history traits such as extension of developmental duration (Simpson and Simpson 1990, Lavoie and Oberhauser 2004) and/or reduced fecundity (Schade and Vamosi 2012). The other secondary metabolites and the defensive chemicals would influence larval performance and nutrition. Consequently, the oviposition preference behavior has evolved to maximize larval survival (Anderson et al. 2013); on the other hand, adults are adapted to select the plants on which they have developed as larvae. Evidently, the oviposition preference behavior of several lepidopteran insects such as *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) (Moreau et al. 2008), and *Spodoptera littoralis* (Anderson et al. 2013) reported being influenced by larval experience on which they were reared. However, larval experience-mediated oviposition preference has been challenged with contrasting information. For instance, in *Helicoverpa armigera* L. (Lepidoptera: Noctuidae), oviposition preference was induced by larval experience only when reared on tobacco (*N. tabacum* L.) and hot pepper (*C. annum* L.). However, feeding on cotton could not induce the same effect on adult females for oviposition preference (Hu et al. 2018). Similarly, in another study on *P. absoluta*, the female adult preference towards tomato plants over 3 potato cultivars was observed only when the larval stages were reared on tomato plants. In contrast, the insect population reared on any of the potato cultivars failed to show preference towards tomato or any of the potato cultivars (Megido et al. 2014). Similarly, in this study, the oviposition preference towards tomato was not affected by larval host experience (natal host). This was evident in dual-choice assays, indicating the possibility of other factors involved in host preference behavior in *P. absoluta*. Such preference towards specific traits might also help identify more suitable individuals than less suitable ones within a host species (Petrén et al. 2021). For instance, when resistant and susceptible tomato genotypes were presented to *P. absoluta* females, susceptible genotypes were preferred over resistant genotypes (Ataide et al. 2017) due to the presence of higher quantity of aminobutyric acid and lower quantities of acyl sugar and other organic acids (Simpson and Simpson 1990).

Further, in the present study, the proportional distribution of egg load on the tomato varied with the presence of different host species. For instance, in the presence of black nightshade, the insect laid more eggs on tomatoes than potatoes, which were kept as a choice crop. This oviposition preference remained similar irrespective of the host plants upon which larvae were reared. However, when the insects were reared on a host species other than tomato, the total fecundity of females reduced, and consequently, the number of eggs laid on either of the choice hosts was less compared to females that were reared on tomato. This result was also supported by a life-table analysis conducted during this study.

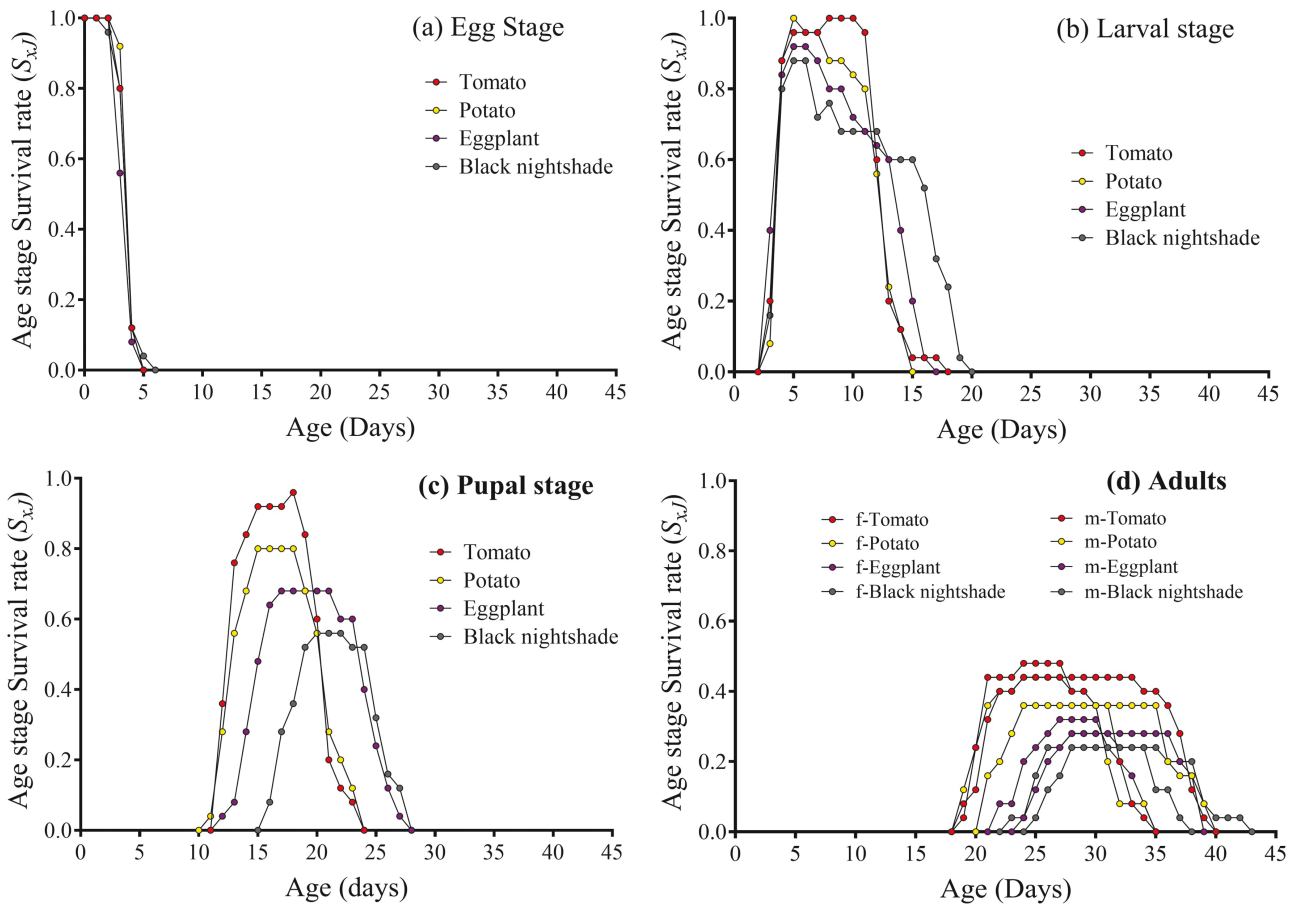


Fig. 4. The stage-specific survival rate of *P. absoluta* during A) egg, B) larval, C) pupal, and D) adult stages reared on different host species. The line colors indicate the host species on which the insects were reared. The letters "m" and "f" indicate the male and female individuals, respectively, in graph D).

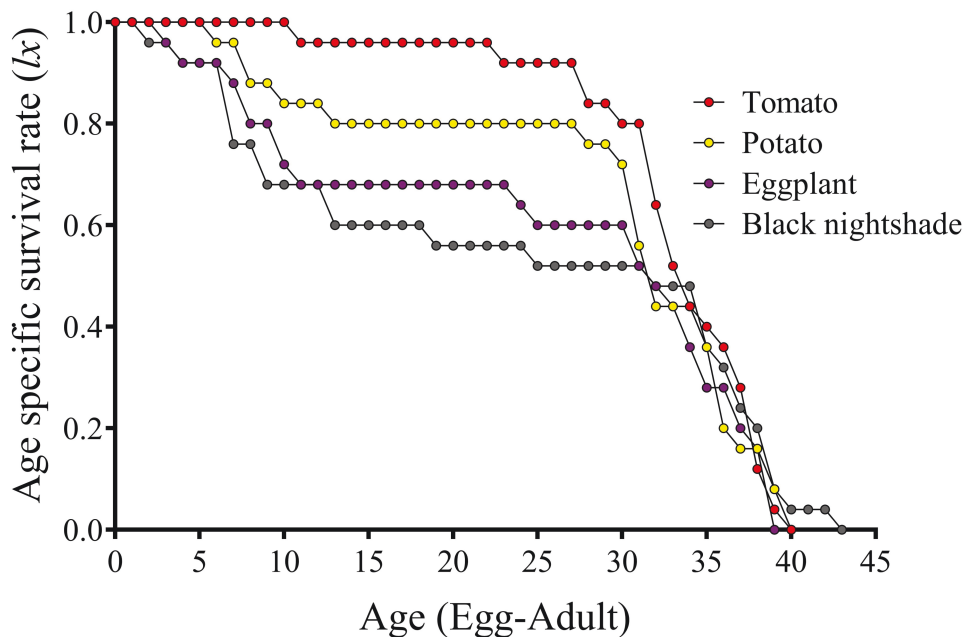


Fig. 5. Survival rate (l_x) of *P. absoluta* throughout its different developmental stages, viz., egg, larvae, pupae, and adult on different host species.

The oviposition preference hierarchy of *P. absoluta* observed during this study follows this order: tomato > potato > eggplant > black nightshade. Furthermore, the performance of the immature stages and

the subsequent generation followed a similar trend as in the preference for oviposition, and this was reflected in the correlation between oviposition preference and the life-table parameters of the insects reared

Table 3. Life-table parameters viz., intrinsic rate of increase (r), finite rate of increase (λ), mean generation time (T), net reproductive rate (R_0), and fecundity of *P. absoluta* reared on selected host species. Standard errors were estimated using 100,000 bootstrap resampling. Data followed by the same lower-case letter within a row were not significantly different based on a paired bootstrap test at a 5% significance level

Parameters	Tomato (mean \pm SE)	Potato (mean \pm SE)	Eggplant (mean \pm SE)	Black nightshade (mean \pm SE)
r (individuals/individual/day)	0.16 \pm 0.009 ^a	0.13 \pm 0.011 ^{bc}	0.09 \pm 0.012 ^{bc}	0.09 \pm 0.01 ^c
λ (finite rate of increase)	1.17 \pm 0.011 ^a	1.13 \pm 0.012 ^{bc}	1.10 \pm 0.013 ^{bc}	1.09 \pm 0.01 ^c
T (days)	26.67 \pm 0.41 ^a	28.03 \pm 0.42 ^{ab}	31.14 \pm 0.58 ^b	32.16 \pm 0.55 ^b
R_0 (no. of female individuals/female)	64.31 \pm 15.09 ^a	34.90 \pm 9.71 ^{ab}	20.74 \pm 6.84 ^b	19.42 \pm 6.99 ^b
Fecundity (no. of eggs/female)	145.98 \pm 9.89 ^a	96.58 \pm 8.27 ^b	72.83 \pm 6.26 ^c	69.84 \pm 5.96 ^c

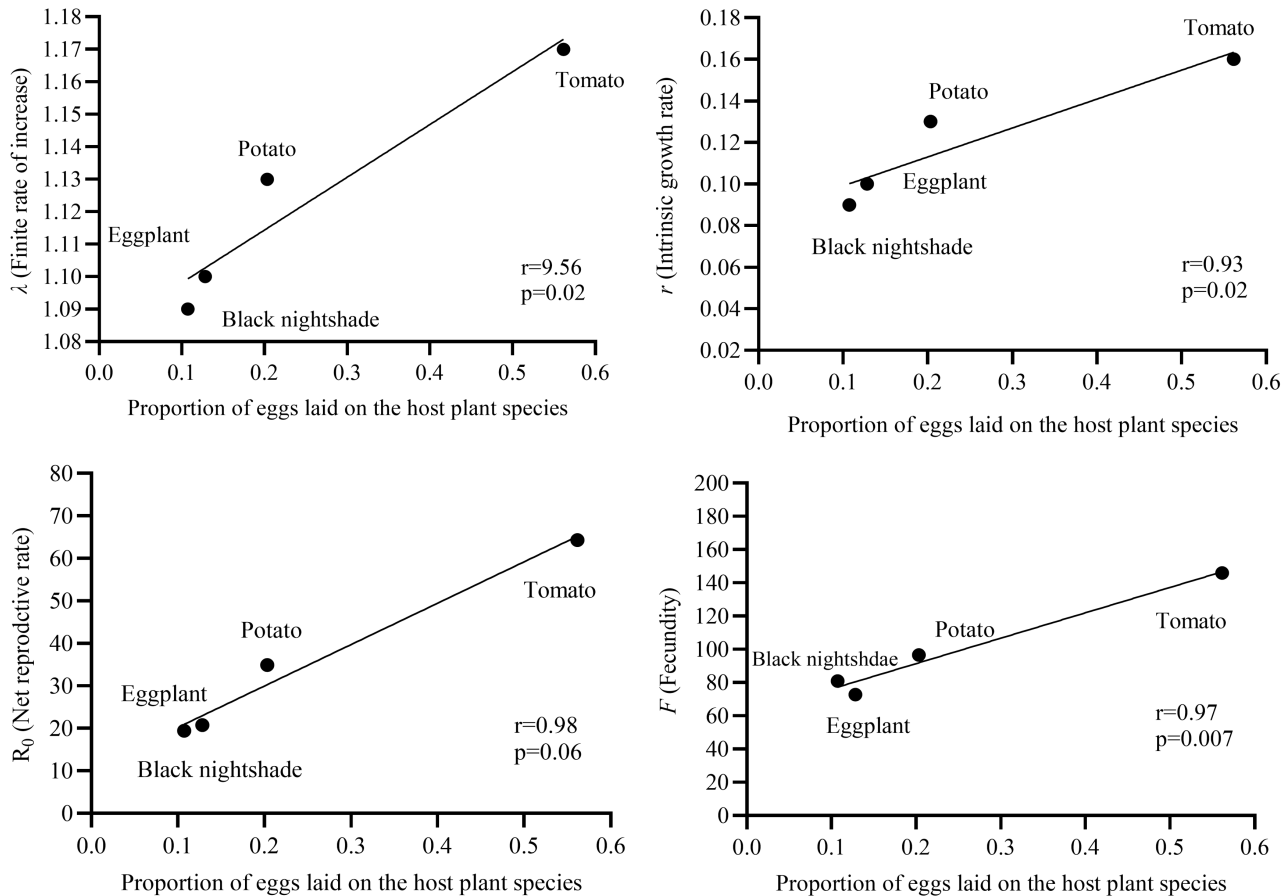


Fig. 6. Correlation between the proportion of eggs laid by *P. absoluta* on different host plant species and different life-table parameters: A) finite rate of increase (λ), B) intrinsic growth rate (r), C) net reproductive rate (R_0), and D) fecundity.

on different host plants. Similar patterns were observed in other insects when different performance indicators, such as pupal weight or size, were studied. For instance, the adults of the potato tuber moth, *P. operculella* preferred to lay eggs on the *S. tuberosum* and *N. tabacum* leaves compared to other Solanaceous species, such as *S. melongena* and *S. lycopersicum*. Subsequently, larvae performed well on *S. tuberosum* and *N. tabacum* by gaining more pupal weight and a higher survival rate compared to less preferred host plants (Wang et al. 2020). In general, the effect of host plants on performance parameters such as developmental duration, rate of survival, body weight, and reproductive rate has been reported earlier in *P. absoluta* (Pereyra and Sánchez 2006, Sridhar et al. 2015, Abbes et al. 2016, Negi et al. 2018, Idriss et al. 2020) and they are consistent with the present study. The

host plant was said to be more suitable when insects showed shorter developmental duration, higher survival, and higher reproductive rates (Pereyra and Sánchez 2006, Abbes et al. 2016, Kanle et al. 2019). The larval survival rate and female fertility were higher on tomato (Abbes et al. 2016, Silva et al. 2021) and potato (Silva et al. 2021) than on the American black nightshade (*Solanum americanum* Mill.), green pepper (*C. annuum* L.) and the pepper (*Capsicum chinensis* Jacquin) (Silva et al. 2021). Further, population growth parameters such as intrinsic rate of increase (r), finite rate of increase (λ), and net reproductive rate (R_0) were higher in tomato compared to other Solanaceous hosts (Kanle et al. 2019). Such changes in life-history traits, in turn, influence the individuals interacting with competitors, predators, and resources (Kondoh and Williams 2001).

The invasiveness of *P. absoluta* is attributed to its wide host range, adaptability to biotic and abiotic conditions, and high fecundity (Tonnang et al. 2015, Biondi et al. 2017). Earlier studies showed variations in all these parameters across geographical locations, indicating the importance of region-specific studies of the insect. Our findings on host preference behavior and its consequence on the population parameters provide insights to develop suitable integrated pest management tools (Silva et al. 2021) in south Indian farming conditions. We conducted a preliminary survey (Supplementary Fig. S1) to explore potential host plants for *P. absoluta* available in and around the tomato crop in southern parts of Karnataka, India. Unlike the previous reports, wild relatives such as *S. viaram* and *S. indicum* (Smith et al. 2018) could not elicit the expected oviposition response in adults under no-choice experiments in a controlled environment in laboratory conditions. Thus, these plants might not act as alternate hosts when the tomato is unavailable in the field. On the other hand, in our study, black nightshade attracted adults to oviposition and host the *P. absoluta* population. Also, the plants that grow naturally in these farming areas are often not weeded out by the farmers as their leaves and fruits are edible (Jain et al. 2011). Such practices could increase pest persistence as it can harbor pest populations when the tomato is not grown at a lower rate. Continuous availability of the primary and secondary host species could lead to pest population growth in a very short span of time. Less competitive natural enemies could also accentuate it, as *P. absoluta* is an invasive pest in India. Thus, carefully selecting crop intercropping strategies and practicing clean cultivation appear to be simple and effective strategies to reduce pest establishment.

Acknowledgments

The authors want to thank Dr. Peter M. Hanson, Global Plant Breeding Lead Scientist, World Vegetable Center and Dr. Purushottam, I and B Seed Ltd. for providing generous support for conducting the experiments by channelizing the funding; Prof. Dr. Hsin Chi, National Chung Hsing University, Taiwan for providing guidance on using life-table analysis, Dr. K.N. Ganeshaiah, and Dr. N.S. Prasanna for providing useful comments on the earlier version of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding

This research was funded by the Federal Ministry for Economic Cooperation and Development (GIZ Project number 16.7860.6-001.00), Germany, and core donors to the World Vegetable Center: Taiwan, UK Foreign, Commonwealth & Development Office (FCDO), United States Agency for International Development (USAID), Australian Centre for International Agricultural Research (ACIAR), Germany, Thailand, Philippines, Korea, and Japan.

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administration [equal], Resources [equal], Supervision [equal], Writing—review & editing [equal]).

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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