



The role of black nightshade in population development of tomato russet mite (*Aculops lycopersici*)

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Abstract

The tomato russet mite (TRM), *Aculops lycopersici* (Tyron), is a significant pest of tomato (*Solanum lycopersicum* L.), with the ability to infest various solanaceous plants and some species outside this family. This study investigated the role of black nightshade (*Solanum nigrum* L.), a globally widespread weed, as an alternative host for TRM and its implications for pest dynamics. The development time, survival rate, and reproductive parameters of TRM were compared between tomato and black nightshade. While TRM developed more rapidly and exhibited higher survival rates on tomato, black nightshade supported higher fecundity and a greater proportion of female offspring. These findings suggest that black nightshade can act as a viable host of TRM. Further experiments evaluated the adaptability of TRM populations to switch between tomato and black nightshade. No significant fitness costs were observed when populations were transferred between these hosts, indicating high adaptability. Additionally, we assessed the colonization potential of TRM on hosts in three different plant families, including pepper (*Capsicum annuum* L.), field bindweed (*Convolvulus arvensis* L.), petunia (*Petunia hybrida* L.), tobacco (*Nicotiana tabacum* L.), and white goosefoot (*Chenopodium album* L.). Among these, only black nightshade and field bindweed supported population growth rates comparable to tomato, while white goosefoot supported TRM for short periods. The results highlight the significance of black nightshade as a reservoir host for TRM, potentially serving as a “green bridge” that facilitates pest survival during the absence of tomato crops in the field. These findings highlight the need for TRM management strategies to include effective weed control to disrupt the pest’s lifecycle and reduce its economic impact on tomato cultivation, especially in regions with mild winters. In addition, tomato germplasm with effective resistance to TRM appears to be generally lacking.

Keywords Tomato pest · Solanaceae · Population growth rate · Life table parameters · Eriophyoidea · Integrated pest management

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Key message

- Black nightshade supports TRM survival, acting as a “green bridge” between tomato crops.
- TRM adapts seamlessly between tomato and black nightshade without fitness costs.
- Non-solanaceous weeds may serve as refuges for TRM without sustaining population development.
- Weed control can disrupt the TRM lifecycle and reduce pest pressure, particularly in warm climates.

Introduction

Eriophyoid mites (Acariformes: Eriophyoidea) are among the smallest arthropods inhabiting aboveground parts of plants. Most superfamily members are considered specialized phytophages specific to one or a few closely related host plant species (Skoracka et al. 2010). Only a few eriophyoid species are recognized as generalists, e.g. *Abacarus hystrix* (Nalepa), *Aceria tosichella* Keifer, *Trisetacus relocatus* Bagnjuk et Shevchenko, able to develop on multiple plant species belonging to different families. However, recent studies utilizing integrative approaches show that these eriophyoid species are better characterized as unresolved complexes of cryptic species, comprising multiple genetically distinct taxa ranging from broad generalists to highly specific on a single host species (Skoracka et al. 2010, 2012, 2013; Lewandowski et al. 2014; Cvrković et al. 2016; Laska et al. 2018). Unlike these species, the tomato russet mite (TRM) *Aculops lycopersici* (Tyron), appears to be a distinct, monophyletic, oligophagous species with little to no genetic variation between European and South American populations (Duarte et al. 2023). To date, it has been recorded from multiple Solanaceae and some non-solanaceous hosts (Rice and Strong 1962; Perring 1996; Duarte et al. 2023).

The TRM is an important pest of tomato (*Solanum lycopersicum* L.) with a global distribution (Moerkens et al. 2018; Vervaeke et al. 2021), feeding on upper and lower epidermal cells of stems and leaves (Royalty and Perring 1988; Pfaff et al. 2020). High TRM population densities lead to yellowish-brown stems, leaves drying, and fruits rusting (Royalty and Perring 1988; Haque and Kawai 2002). Such damage can lead to over 65% crop loss (Duarte et al. 2023). However, the severity of damage depends not only on mite density but also on the susceptibility of the plants and cultivars to these mites; different species/varieties of *Solanum* host plants display different symptomatology or damage severity upon infestation (Kitamura and Kawai 2006).

The spread and proliferation of TRM have likely been facilitated by the global distribution of *S. lycopersicon*, which is typically highly susceptible to this mite. According to Duarte et al. (2023), the most plausible explanation for the spread of TRM across continents is the adoption of tomato as an alternate host in areas where the putative original wild host species and domesticated tomato co-occurred. This host adaptation may have taken place before the intercontinental expansion of tomato as a cultivated crop in the sixteenth century. Under greenhouse conditions, TRM populations can increase rapidly on tomato plants, with significant growth observed just six weeks after infestation (Haque and Kawai 2002). Rice and Strong

(1962) demonstrated that black nightshade can be a more suitable host than tomato, and that TRM is also capable of developing on field bindweed (*Convolvulus arvensis* L.), a common non-solanaceous weed. Although TRM can persist and overwinter under field conditions, this is limited to warmer regions of the world, typically at lower latitudes. In cooler climates (e.g. temperate zones), environmental conditions are not conducive to outdoor survival, and the mite overwinters only in protected environments such as greenhouses (Perring and Farrar 1986).

The ability to exploit a range of host plants increases the likelihood that TRM can locate alternative hosts when the quality of the crop host declines or during seasonal crop transitions, allowing populations to persist between cropping cycles. This adaptive strategy mirrors the host-use flexibility observed in other eriophyid mites. Laska et al. (2021) demonstrated that *A. tosichella* is capable of surviving and reproducing on alternative, suboptimal hosts when its preferred host is absent; this study also showed that populations could be maintained for multiple generations on sink hosts, enabling rapid recolonization of cultivated crops when they reappear in the agroecosystem. This finding supports the hypothesis that TRM populations may similarly persist and increase on non-crop vegetation, posing a significant economic threat to subsequent crop hosts—a dynamic documented for many herbivorous pests (Norris and Kogan 2000, 2005; Kumar et al. 2021). Understanding the role of wild hosts may improve IPM approaches (Miller et al. 2013). In this context, it is essential to understand the relationship between pest species and target crops, as well as other plants that may represent alternative food sources (Norris and Kogan 2000, 2005; Kumar et al. 2021; Laska et al. 2021).

Black nightshade (*Solanum nigrum* L.) was selected as an alternative host to tomato in this study of the role of weeds in managing TRM. This common weed has been reported in over 37 crops worldwide, including tomato plantations, reducing tomato yields by up to 80% through competition for resources (Defelice 2003). It can also support many pests and pathogens that attack crops (Kumral and Çobanoğlu 2015), including TRM (Perring 1996). The primary objective of this study was to compare the life history parameters of TRM fed on tomato and black nightshade. Of particular importance, we investigated the adaptation costs when TRM populations were transferred between hosts and we assessed the ability of TRM populations reared on tomato to adapt to black nightshade.

Materials and methods

Stock colony of TRM

A stock colony of *A. lycopersici* came from the Department of Applied Entomology, WULS-SGGW, in Warsaw, Poland,

where these mites have been reared for 14 years. Young, potted tomato (*S. lycopersicum* ‘Tomimaru Muchoo’ variety) plants were kept in a rearing chamber SANYO (MLR-350H) under controlled conditions (25 ± 1 °C temperature, $70 \pm 5\%$ RH, 16 h photoperiod). Two new plants were added to the rearing chamber every two weeks, replacing the two plants that were most damaged by TRM.

Before starting experiments, about 300 mites/plant of TRM were transferred to black nightshade and the tomato plant variety ‘Mei Shuai,’ which was selected for further research based on preliminary experiments (see ‘Susceptibility of tomato varieties to TRM’ below). These plants of both species were kept separately, in mesh cages (30 µm mesh size), for three weeks (about three generations) under the same conditions.

Plant material

Seeds of tomato (*S. lycopersicum*, cv. ‘Mei Shuai’) and black nightshade (*S. nigrum* collected from a field near Warsaw) were sown to ensure plant availability for all experimental procedures. The plants were grown in gardening soil in plastic pots, 12 cm diameter, in a rearing chamber (Sanyo MLR-350H) at 25 ± 1 °C temperature, $70 \pm 5\%$ RH, and 16 h photoperiod. For experiments conducted in Munger cells, leaves were cut from plants approximately one month after germination. Younger plants with three fully developed leaves were used to study the population growth rate of TRM reared on different tomato varieties and on a few alternative host plants; the tomato varieties used were pink tomato—Mei Shuai (Seminis), Malduo, Manekro (Syngenta), and Tomimaru Muchoo (De Ruiter), chocolate-coloured tomato—Bucanero (Yuksel Tohum), red large tomato—Securitas RZ, Pareso RZ, and Kivu RZ (Rijk Zwaan), and red cherry tomato—Cheramy and Eyre RZ (Rijk Zwaan). In addition to black nightshade, alternative host species included bell pepper (*Capsicum annuum* L. ‘Clavesol’ (Rijk Zwaan)), field bindweed (*Convolvulus arvensis* L.), tobacco (*Nicotiana tabacum* L. ‘Xanti’), petunia (*Petunia hybrida* L. ‘Starlet’ (Selecta One)), and white goosefoot (*Chenopodium album* L.), which were planted in the same way as the tomatoes and black nightshade.

Susceptibility of tomato varieties to TRM

Ten young plants from each tomato variety, each with three true leaves, were each infested with 10 adults of TRM. The plants were then placed in cages of fine mesh stretched over a metal frame measuring $30 \times 12.5 \times 12.5$ cm and put into a rearing chamber maintaining constant conditions (25 ± 1 °C, $70 \pm 5\%$ RH, photoperiod 16 h). Twice a week, the plants were watered. Fourteen days after the establishment of the experiment, the plants were cut down, and the eggs and live

mobile stages of TRM were counted. The results of these bioassays were used to select a single tomato variety for further testing.

Development and life history parameters on different hosts

Separate stock colonies of TRM were established on detached leaves of tomato (cv. ‘Mei Shuai’) and black nightshade to study the developmental time of eggs and immature stages, survival rate, and sex ratio. All leaves were placed lower side upwards in Munger cells, as described by Druciarek et al. (2014). One fertilized female of TRM was placed on each leaf for 24 h to lay eggs. Females were then removed, leaving only one egg on each leaf. Leaf surfaces were monitored every 24 h, and the developmental stage of each mite was recorded (50 replicates/plant species).

To assess mite reproduction parameters (viz. fecundity, oviposition period, female longevity), quiescent nymphs originating from each stock colony were individually transferred to 50 Munger cells for each plant species under study. After moulting from nymph to female adult, a male reared separately from unfertilized eggs was added to each cell. The cells were monitored daily by recording and removing the eggs each female laid until she died. To maintain leaves in good condition, the tissue paper in Munger cells was watered daily. All experiments were conducted in a SANYO MLR-350H rearing chamber under the aforementioned conditions. Life tables were constructed from the observed age-specific survival rate (l_x) and specific fecundity rate (m_x) [net reproductive rate (R_0), mean generation time (T), doubling time (T_D), intrinsic rate of population increase (r_m), and finite rate of population increase (λ)] (Birch 1948; Southwood 1978).

Host acceptance by TRM

Two experiments were performed to study the host acceptance of TRM. In the first, the mites from the stock colonies adapted to tomato (*S. lycopersicon*, cv. ‘Mei Shuai’) and black nightshade (*S. nigrum*) plants were studied. Ten randomly selected adult mites from a population adapted to tomato were transferred to each of ten plants of the same tomato variety, as well as to each of ten plants of black nightshade. Conversely, the same number of TRM specimens adapted to black nightshade were transferred to ten plants of the same species, as well as ten plants of tomato. All the plants were placed in fine mesh cages ($30 \times 12.5 \times 12.5$ cm) and kept in rearing chambers under constant conditions (25 ± 1 °C, $70 \pm 5\%$ RH, 16 h photoperiod). After 14 days, the plants were cut down, and all developmental stages of TRM, including eggs, were counted.

The second host-acceptance experiment evaluated the possibility of colonization of new host plants. The

experiment was conducted in the same way as described above but the source population of TRM was adapted to *S. lycopersicon*, cv. ‘Mei Shuai’ and mites were transferred to six known host plants of TRM: tomato, black nightshade, bell pepper, field bindweed, tobacco, petunia; and one non-host species, white goosefoot. The data acquired were used to calculate the per capita population growth rate (r). If $r < 0$, the population size decreased; if $r > 0$, the population size increased, whereas $r = 0$ corresponded to no change in the population size (Skoracka et al. 2022).

Statistical analyses

The software programme STATISTICA version 13.0 (TIBCO Software Inc., Palo Alto, California, USA) was used to analyse the experimental results. The Shapiro–Wilk test was applied to assess the sample distribution’s normality. When the data did not demonstrate a normal distribution, the Mann–Whitney non-parametric t-test was selected to evaluate differences between the two plants; otherwise, a Student’s t-test was used. When the assumptions required for ANOVA were not met, such as when the data did not follow a normal distribution, the Kruskal–Wallis test was used as a non-parametric alternative to determine if there were statistically significant differences between more than two groups. Dunn’s test was used for pairwise comparisons after a Kruskal–Wallis test. Throughout these analyses, statistical significance was acknowledged when the p-value derived from the tests fell below 0.05. To assess the variation in population parameters, the bootstrap technique was applied according to Klimov and O’Connor (2013). This process created 1000 bootstrap samples, from which the means and standard deviations (SD) of R_0 , T , T_0 , r_m , and λ for each bootstrap sample were calculated. Afterwards, ANOVA was applied to the data, followed by Tukey’s test ($\alpha = 0.05$).

For the sex ratio comparison, the confidence intervals (CI) for proportion and Z score for two population proportions were used. The Kaplan–Meier procedure was used to calculate CI for the estimated survival function at various times (Kryś and Gront 2021; Sachs et al. 2022). The median numbers of days of survival were compared between *S. lycopersicum* and *S. nigrum* using Mood’s median test (Divine et al. 2018).

Results

Influence of tomato varieties on TRM development

The population growth rate of TRM populations varied significantly, depending on the tomato variety ($p < 0.001$). Differences were observed when the mites fed on tomatoes from the pink tomato group, specifically the varieties ‘Malduo’,

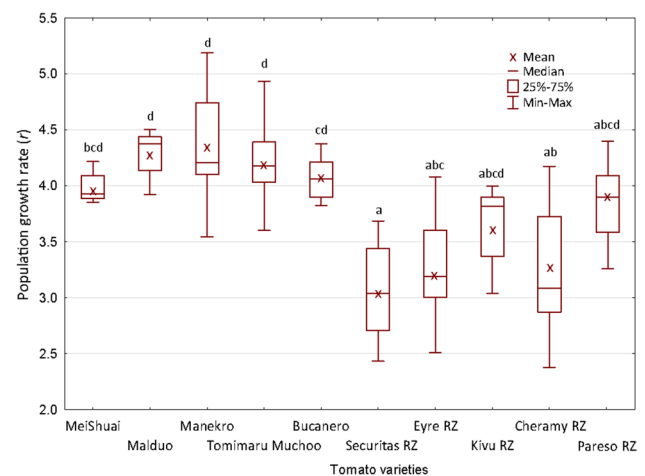


Fig. 1 Population growth rate of *Aculops lycopersici* on ten tomato cultivars

‘Manekro’, ‘Tomimaru Muchoo’, and the red tomato variety ‘Securitas’. The population of TRM mites that developed on the chocolate-coloured tomato variety ‘Bucanero’ exhibited a growth rate similar to populations on most of the other studied varieties, except ‘Securitas’ and ‘Cheramy’. Notably, the TRM population that developed on the variety ‘Mei Shuai’, from the pink tomato group, differed only from the population that developed on ‘Securitas’ (Fig. 1). Given the high rate of TRM population development associated with the ‘Mei Shuai’, as well as the homogeneity and low variance of the data compared to other varieties, this variety was chosen for the experiments comparing TRM life history parameters on tomato vs. black nightshade.

Developmental and reproductive parameters

The developmental time of immature individuals (from egg to adult) was notably shorter on tomato than on black nightshade (Table 1). The difference was particularly notable in the accelerated development of female immatures on tomato compared to black nightshade. Conversely, no difference was observed among male immatures on the two hosts. Overall, larvae exhibited significantly shorter developmental periods on tomato than on black nightshade. However, the duration of development of the remaining instars was similar on both host plants (Table 1).

The survival rate from egg to adult was significantly lower on black nightshade compared to tomato. No larval mortality was observed on tomato, whereas 19% of larvae perished on black nightshade ($p = 0.002$; Table 2).

Female cohorts of TRM reared on both host plants exhibited no differences in terms of longevity, pre- and post-oviposition periods, or daily fecundity. However, a significant distinction was observed regarding total fecundity, with

females feeding on black nightshade laying more eggs than those on tomato (see Table 3). The population reared on black nightshade yielded a higher female count than that on tomato. The calculated sex ratio, representing the proportion of females to the total number of adult specimens, was 10%, greater on *S. nigrum* than on *S. lycopersicum* ($p=0.01$; Table 3).

Altogether, life table parameters computed from the presented data indicate that tomato is a slightly superior host plant compared to nightshade. Despite the significantly higher net reproductive rate observed on black nightshade than on tomato, both the intrinsic and finite rates of population increase were significantly higher on tomato than on black nightshade. These differences matched the reduced mean generation time of TRM feeding on tomato, while the population doubling time was shorter on tomato compared to black nightshade (Table 4).

Survival curves of TRM on tomato and black nightshade are shown in Fig. 2. The survival rates showed the same trend on both host plants and were not significantly divergent ($p=0.0513$). The median number of days after which TRM females died was 12 and 14 for *S. lycopersicum* and *S. nigrum*, respectively; this difference was not statistically significant (Mood's median test $p=0.064$).

Table 1 Comparison of the developmental length (day length mean $\pm$ SD) of juvenile stages of *Aculops lycopersici* on *Solanum lycopersicum* 'Mei Shuai' and *Solanum nigrum*

Stage	<i>n</i>	<i>Solanum lycopersicum</i>	<i>n</i>	<i>Solanum nigrum</i>	<i>p</i> -value
Egg	47	2.3 $\pm$ 0.6	47	2.6 $\pm$ 0.9	0.07
Larvae	47	1.4 $\pm$ 0.5	38	2.0 $\pm$ 0.9	0.01
Nymph	43	1.7 $\pm$ 0.5	32	1.6 $\pm$ 0.8	0.30
Egg-Adult	43	5.5 $\pm$ 0.7	32	6.2 $\pm$ 1.3	0.02
Egg-Adult (female)	32	5.3 $\pm$ 0.7	28	6.1 $\pm$ 1.4	0.04
Egg-Adult (male)	11	5.9 $\pm$ 0.8	4	6.0 $\pm$ 1.4	0.95

Table 2 The survival rate of juveniles (mean rate $\pm$ SD) of *Aculops lycopersici* on *Solanum lycopersicum* 'Mei Shuai' and *Solanum nigrum*

Stage	<i>n</i>	<i>Solanum lycopersicum</i>	<i>n</i>	<i>Solanum nigrum</i>	<i>p</i> -value
Egg	47	0.94 $\pm$ 0.03	47	0.94 $\pm$ 0.03	1.000
Larvae	47	1.00 $\pm$ 0.00	38	0.81 $\pm$ 0.06	0.002
Nymph	43	0.91 $\pm$ 0.04	32	0.84 $\pm$ 0.05	0.298
Egg-Adult	43	0.86 $\pm$ 0.05	32	0.64 $\pm$ 0.07	0.011

Table 3 Oviposition duration (days $\pm$ SD), length of life, total fecundity (eggs/female $\pm$ SD), daily fecundity (eggs/female/day $\pm$ SE), and sex ratio (females/all adults) of *Aculops lycopersici* females on *Solanum lycopersicum* 'Mei Shuai' and *Solanum nigrum*

Parameters	<i>Solanum lycopersicum</i>	<i>Solanum nigrum</i>	<i>p</i> -value
Preoviposition	0.9 $\pm$ 0.6	1.0 $\pm$ 0.4	0.27
Oviposition	10.1 $\pm$ 3.8	11.2 $\pm$ 4.1	0.31
Postoviposition	1.0 $\pm$ 1.7	1.5 $\pm$ 1.6	0.10
Longevity of female	12.0 $\pm$ 3.4	13.7 $\pm$ 3.9	0.07
Total fecundity	28.2 $\pm$ 12.8	36.6 $\pm$ 16.4	0.03
Daily fecundity	2.8 $\pm$ 0.8	3.3 $\pm$ 1.1	0.10
<i>n</i>	35	38	
sex ratio	0.7 $\pm$ 0.1	0.8 $\pm$ 0.1	0.01

Females of TRM began laying eggs the day after moulting to adult form and achieved the peak of their fertility on the fourth day, on both host species. However, on that day, females laid more eggs on black nightshade than tomato. After this day, the number of eggs decreased until the 19th and 21 st days following eclosion from eggs on tomato and black nightshade plants, respectively (Fig. 3).

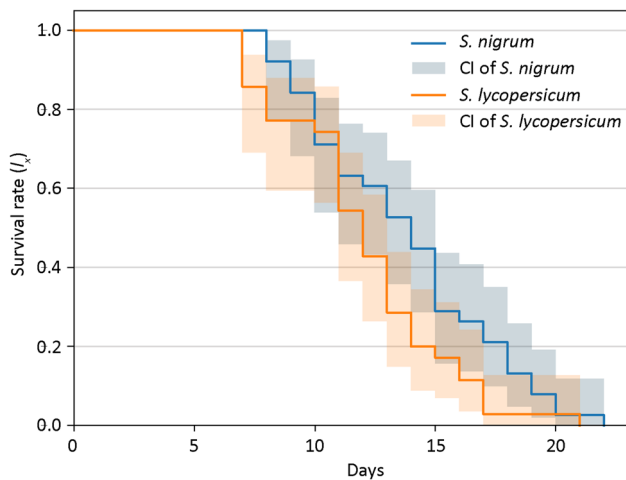
Host acceptance by TRM

The population of TRM adapted to tomato was able to survive on all studied plants although their fitness differed significantly depending on the host ($p<0.001$). On plants belonging to the family Solanaceae (tomato, black nightshade, field bindweed, bell paper, tobacco, petunia), the value of population growth rate was higher than zero, indicating an increase in population size. There were no significant differences in the fitness of the population of TRM adapted to tomato when developed on black nightshade compared to the original host. Among solanaceous plants, the least suitable hosts were tobacco and pepper (Fig. 4). The r value was below zero only in the population tested on white goosefoot (*Ch. album*), which belongs to a different family, Amaranthaceae. The number of specimens at the end of the white goosefoot experiment ranged from 1 to 11.

The fitness of TRM populations adapted to tomato or black nightshade differed significantly ($p=0.02$) in reciprocal transfer experiments. The population adapted to tomato transferred to a second tomato plant showed a significantly higher population growth rate than the population adapted to black nightshade moved to a second black nightshade plant. However, the population adapted to black nightshade had better fitness when transferred to tomato than to black

Table 4 Life table parameters of *Aculops lycopersici* on two host plant species (day $\pm$ SD)

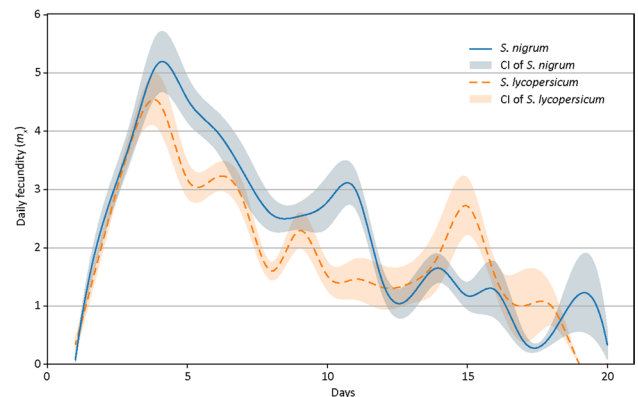
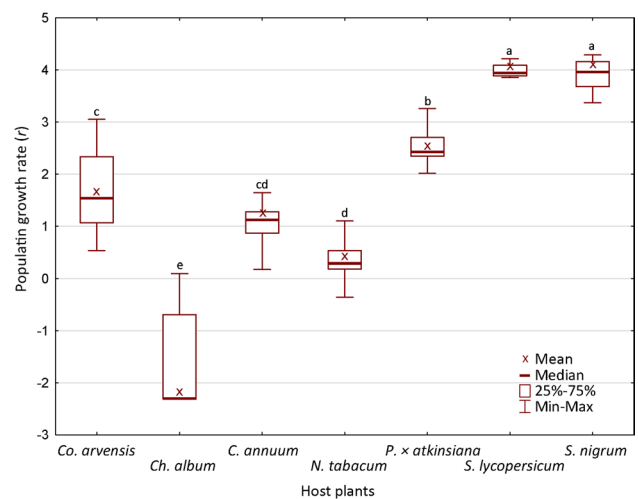
Parameters	<i>Solanum lycopersicum</i>	<i>Solanum nigrum</i>	p-value
Net reproductive rate (R_0)	16.51 $\pm$ 1.22	19.04 $\pm$ 1.40	< 0.001
Mean generation time (T)	11.12 $\pm$ 0.27	12.39 $\pm$ 0.23	< 0.001
Intrinsic rate of population increase (r_m)	0.25 $\pm$ 0.01	0.24 $\pm$ 0.01	< 0.001
Finite rate of population increase (λ)	1.29 $\pm$ 0.01	1.27 $\pm$ 0.01	< 0.001
Population doubling time (TD)	2.75 $\pm$ 0.05	2.92 $\pm$ 0.06	< 0.001
n	35	38	

**Fig. 2** Survival rate of females of *Aculops lycopersici* on *Solanum lycopersicum* and *Solanum nigrum*

nightshade, while the population adapted to tomato exhibited similar fitness on both host plants (Fig. 5).

Discussion

Weeds growing outside of crop fields can serve as alternative hosts for pests like TRM, supporting overwintering populations and complicating area-wide integrated pest management strategies (Norris and Kogan 2005; Defelice 2003; Thomas et al. 2004; Werle et al. 2014). One such weed is *Solanum nodiflorum* Jacq., part of the *S. nigrum* complex (Jacoby and Labuschagne 2006), which has been identified as a particularly suitable host of TRM (Rice and Strong 1962). These authors reported that TRM females laid more eggs on black nightshade than on tomato, indicating that it may be a preferred host. Abou-Awad (1979) also showed that females reared on *S. nigrum* leaves at 25 °C reached adulthood within five days, lived for 22 days, and laid an average of 16 eggs. In our study, development on black nightshade was slightly slower—females reached adulthood after six days and lived eight days less—but total fecundity was more than twice as high as observed by Abou-Awad (1979).

**Fig. 3** Daily fecundity of females of *Aculops lycopersici* on *Solanum lycopersicum* and *Solanum nigrum***Fig. 4** Fitness of *Aculops lycopersici* population adapted to tomato, measured as population growth rate (r) on different host plants. A box plot for the r parameter represents a box between the first and third quartiles and a line along the second quartile to indicate the median, whiskers depict the minimums and maximums beyond the first and third quartiles, and an “x” represents the average. Letters indicate homogenous groups according to the Tukey test at $\alpha = 0.05$

The longer developmental time and lower survival rate of TRM immatures indicate that black nightshade is a less suitable host than tomato at early life stages. In contrast, no significant differences were observed in the longevity

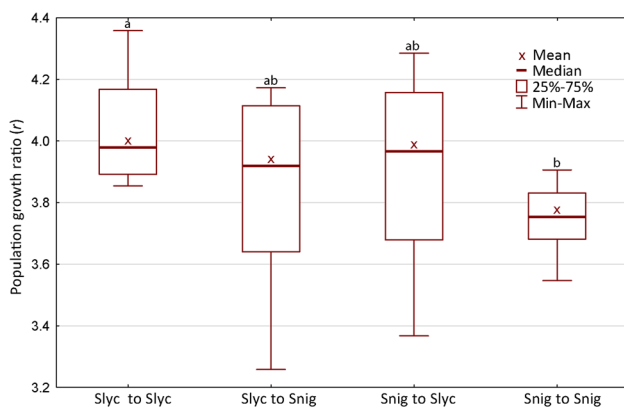


Fig. 5 Fitness of *Aculops lycopersici* populations adapted to *Solanum lycopersicum* (Slyc) or *Solanum nigrum* (Snig), measured as the population growth rate (r) when transferred to tomato or black nightshade. A box plot for the r parameter represents a box between the first and third quartiles and a line along the second quartile to indicate the median, whiskers depict the minimums and maximums beyond the first and third quartiles, and an “x” represents the average. Letters indicate homogeneous groups according to the Dunn’s procedure at $\alpha=0.05$

or reproductive parameters of females reared on the two hosts. Notably, females feeding on black nightshade exhibited higher fecundity, which likely contributed to a greater net reproductive rate in that population, albeit accompanied by a longer mean generation time. Meanwhile, intrinsic and finite rates of natural increase were higher on tomato, although both populations required less than three days to double in size. The life history parameters observed in our study were lower than those reported by Haque and Kawai (2003), who recorded an intrinsic rate of natural increase of 0.29 for TRM on tomato cv. ‘House Momotaro’. However, other studies—such as those by Metwally et al. (2020) and Al-Azzazy and Alhewairini (2018)—reported similar or lower values, likely due to differences in experimental temperature or tomato cultivar. In the experiments presented here, most tomato varieties exhibited only limited protection from TRM development, with significantly reduced population growth recorded only for the ‘Securitas’ cultivar. These findings suggest that tomato cultivar can influence TRM performance, particularly in terms of fecundity and female longevity, although immature development time remained largely consistent. Taken together, these results highlight the need for future studies to include both highly resistant and highly susceptible tomato cultivars when assessing host suitability for TRM. Including wild tomato progenitors, alongside black nightshade and other potential hosts, may also help identify the original ancestral host of TRM.

Prior studies have revealed the ability of TRM to develop on different species of host plants. Rice and Strong (1962) tested 30 solanaceous plant species, plus *Co. arvensis* (field bindweed, family Convolvulaceae) for TRM acceptance and

the relative susceptibility of these species to mite feeding. In 11 cases, TRM feeding caused severe damage or killed the plants, while mite development rates varied on the other plant species. Field bindweed was among the more susceptible plants in that study, with high populations of TRM. While Rice and Strong (1962) observed no TRM development on *Nicotiana* species, our study detected limited development on *N. tabacum*, suggesting the possibility of marginal population growth. Similarly low TRM fitness was recorded on bell pepper, aligning with earlier reports that classified it as a suboptimal host compared to field bindweed. These findings confirm general trends but also highlight variability among cultivars, underlining the importance of choosing the same cultivars across studies when possible, as well as selecting highly- and less-susceptible cultivars when comparing across putative host species. Such recommendations should apply to most arthropod-plant studies where variation in host resistance or tolerance to the arthropod is known. TRM population in this study declined only on white goosefoot (*Ch. album*), a weed from the Amaranthaceae family, taxonomically more distant from Solanaceae than field bindweed. Although population growth was not observed, a few individuals survived after 14 days, possibly due to short-term feeding. Similar off-host survival has been reported for other eriophyoids, and occasional reproduction on secondary, unrelated hosts has been observed in *A. tosi-chella* (Skoracka et al. 2013), suggesting that TRM may also temporarily persist on some otherwise unsuitable species under favourable conditions.

The results of our studies indicate that among the studied plants, tomato, and black nightshade were the best hosts for TRM. On the remaining hosts, including confamilial species, the reproduction rate of TRM was attenuated. Host preferences for some plant species above others have been commonly observed for polyphagous species (Skoracka et al. 2010). In our study, TRM populations adapted to the ‘Mei Shuai’ variety of tomato showed higher fitness on this host than populations adapted to black nightshade, indicating a slight advantage in performance on the cultivated host. Similar patterns of host range expansion without fitness loss compared to the original host have been observed in *Tetranychus urticae* Koch (Salehipourshirazi et al. 2021), another polyphagous mite species, suggesting that such flexibility may be a general trait among some plant-feeding mites. However, the results of transfer experiments presented here showed no differences in the fitness of adapted populations when they were moved between two suitable host species. This may suggest that a population of TRM can migrate between tomato and black nightshade, which commonly accompanies this crop as a weed, while bearing no cost of adaptation to either host. As such, black nightshade, which is commonly present between seasons of field tomato cultivation, could serve this pest not only as a food source but also as an

overwintering refuge. A similar role of alternative hosts has been documented for *A. tosichella*, with populations able to persist on smooth brome (*Bromus inermis* Leyss.) between wheat crops (Laska et al. 2021).

Tomato cultivars with dense trichomes may support higher TRM densities, as these structures offer shelter from predators and facilitate mite movement (van Houten et al. 2013), reducing the effectiveness of a biological control component of an integrated pest management (IPM) strategy meant to reduce pesticide application (Aysan and Kumral 2018). Thus, lack of trichome density may be an important consideration when choosing a tomato cultivar in regions at risk of TRM infestations. In addition, with regard to a host-plant resistance component of an IPM strategy (e.g. Rector et al. 1998; 2002), our results show that among the ten tomato varieties selected for this study, none reduced TRM population development to an acceptably low rate on their own.

Alternative hosts such as weeds can sustain pest populations between crop cycles and increase pest pressure in subsequent seasons (Kumar et al. 2021). The results presented here indicate that within an IPM system, weed management may contribute to effective control of TRM, as many common weeds can serve as alternative host plants and possibly green bridges for this pest. Among such hosts, black nightshade has been identified as the most suitable alternative host for TRM, on a par with tomato. This suggests that black nightshade may play a crucial role as an overwintering refuge, facilitating the pest's survival and subsequent re-infestation of tomato crops. Additionally, field bindweed might also create favourable conditions for TRM development, and white goosefoot might support the survival of TRM populations for a limited time, despite the taxonomic distance between these species and the genus *Solanum*, which contains the most preferred hosts of TRM. However, we cannot exclude that with favourable conditions during overwintering, some specimens might survive on these hosts until spring. Diverse weed flora may therefore significantly influence TRM dynamics in tomato fields. By controlling black nightshade and other host weeds during the off-season, farmers can minimize TRM reservoirs and reduce the pest's impact during the growing season. Furthermore, the relatively small effect of different tomato varieties on TRM populations suggests that in addition to prioritizing weed management, especially weed species closely related to the crop, non-chemical control measures, such as identifying and developing tomato germplasm with effective resistance to TRM, should be a research priority to contribute to sustainable TRM management and mitigate the development and spread of this pest among tomato crops.

Author contributions

AS and ML conceived and designed research with the support of SS, BR, and EWG. AS and ML conducted experiments. AS, ML and EWG processed and analyzed data. AS, ML, BR, SS interpreted results. AS and ML wrote the manuscript with assistance of SS, BR, and EWG. All authors read and approved the manuscript.

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Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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