Effects of temperature, photoperiod and humidity on the life history of *Gargaphia decoris*

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Abstract The sap-sucking lace bug *Gargaphia decoris* Drake (Hemiptera: Tingidae) is a biological control agent released in New Zealand to control the invasive small tree or shrub *Solanum mauritianum* Scopoli (Solanaceae). The aim of this study was to investigate the effect of temperature, photoperiod and humidity on selected *G. decoris* life history traits. The selected traits were measured at six different temperatures (10, 15, 20, 25, 27.5 and 30 °C), three photoperiods (L:D 6:16, 14:10 and 16:8) and two relative humidity (RH) levels (50 and 70 ± 10%). Eggs and nymphs did not survive in the 10 °C and 30 °C treatments. The net reproductive rate (R_0) resulted in population growth at all temperatures, but was highest at 25 °C. Egg hatch rate was highest at L:D 8:16, and nymphal and adult survival was better at L:D 16:8. Egg hatch was higher at 50 ± 10% RH and adult survival and population growth were higher at 70 ± 10% RH. These results will help to predict the persistence of established *G. decoris* populations and the potential for establishment at new release sites.

Keywords Tingidae · *Solanum mauritianum* · Environment · Life table · Biological control

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Introduction

Biological control of weeds using insects, when successful, is one of the most cost-effective practices for the management of invasive species (Culliney 2005). However, the efficacy of biocontrol agents can be compromised by a variety of environmental factors, which may act together to reduce insect fitness (e.g. development, survival, fecundity, fertility and longevity). Temperature, photoperiod and humidity, for example, have each been shown to influence the establishment and success of biocontrol agents (Byrne et al. 2002; Cowie et al. 2016b; Bean et al. 2007). Therefore, knowledge on how environmental factors affect a biocontrol agent is a key to predicting success.

The sap-sucking lace bug *Gargaphia decoris*, native to parts of Argentina and southern Brazil, has a high potential to suppress the population of the

invasive tree *Solanum mauritianum* Scopoli (Drake and Ruhoff 1965; Olckers and Borea 2009). This is because besides its host specificity, it bears a number of fitness traits that an effective biocontrol agent usually has (Olckers 2000). For example, *G. decoris* females are highly fecund. They can oviposit numerous eggs (up to 900 eggs), and are capable of having consecutive egg batches during their lifetime (Hayes 1996; Olckers 2000). This allows an overlap of generations on the same plant, thus increasing the chances of inflicting significant feeding damage to the host plant (Cowie et al. 2016a). This bug is a long-lived insect (up to 145 days) with short development times (30 days at 22 ± 3 °C), suggesting that it is highly capable of substantial population growth (Olckers 2000). South Africa was the first country to release *G. decoris* as a biocontrol agent, and after early reports of success, New Zealand introduced and released the insect in 2009 (EPA 2009; Olckers and Borea 2009; Witt 2007). Despite the reported establishment of populations and extensive damage on *S. mauritianum*, populations densities have strongly fluctuated with sporadic outbreaks (Klein 2011; Olckers and Borea 2009), and with a preference for semi-shaded areas in both South Africa (Patrick and Olckers 2011) and New Zealand (Fowler 2014). Initially, low temperatures were suggested to be the cause for the low densities of *G. decoris* found in the field (Hope and Olckers 2011), but later it was dismissed that low temperatures would affect *G. decoris* establishment by performing thermal assessments, and rather suggested that other causes might be involved (e.g. predation). However, thermal assessment studies were based on establishment observations in the field (Barker and Byrne 2005; as cited in Olckers 2011) and it is unknown at what extent environmental conditions influence *G. decoris* fitness. Here we apply the first systematic study into the effect of environmental conditions on fitness to explore whether environmental conditions are a likely predictor of success.

In the present study, we aimed to test how environmental conditions influenced *G. decoris* fitness and thus performance, and provide knowledge for prediction of its persistence and establishment in the field. We carried out a series of experiments to examine dynamics of various traits of *G. decoris* in response to different temperatures, photoperiods and humidity conditions.

Materials and methods

Insect and plant material

The *G. decoris* colony used in this study was derived from a glasshouse colony at Manaaki Whenua Landcare Research Ltd, Auckland, New Zealand (NZ). The colony had been maintained since then in a climate-controlled room at Massey University, Palmerston North, New Zealand. The insects were fed on *S. mauritianum* plants (15 cm from the top of the pot) with at least three fully matures leaves, grown in 0.75 l pots at 25 °C with a photoperiod of L:D 14:10 hours and $50 \pm 10\%$ RH during the duration of the experiment (2013–2017). To maintain a constant source of plant material, *S. mauritianum* seeds were sown and reared in a glasshouse at Massey University Plant Growth Unit, Palmerston North, New Zealand. Plants were maintained in a climate-controlled glasshouse at daily average minimum and maximum temperatures of 17.1 °C and 24.1 °C, respectively. Plants that reached a height of approximately 15 cm from the top of the pot were used for the experiments.

Temperature

Gargaphia decoris development from egg to adult was evaluated at six different temperatures: 10, 15, 20, 25, 27.5 and 30 ± 1 °C, with a photoperiod of L:D 14:10 and $50 \pm 10\%$ RH in environmental chambers (Sanyo MLR-350T; Japan) and climate-controlled rooms. Egg batches from different sets of *G. decoris* parents were collected from the colony by cutting off the part of the leaves where the egg batches were located. The leaf pieces with egg batches were then placed in plastic Petri dishes (8.5 cm diameter) lined with moist paper towel and incubated in climate-controlled rooms at one of the test temperatures. Each egg batch (approx. 30 eggs) was considered a sampling unit, with a total of ten egg batches per temperature. The eggs were checked daily (09:00–11:00) and the number of nymphs emerging each day was recorded until no nymphs emerged for more than two consecutive days.

To evaluate nymphal development, ten newly emerged nymphs from each of the ten egg batches were collected using a fine brush. Each group of ten nymphs were placed on a separate potted *S. mauritianum* plant (0.75 l pots). Thus we had ten *S.*

mauritianum plants with ten nymphs each. The plants had at least two fully matured leaves and allocated to one of the tested temperatures for nymphal development. To prevent the lace bugs from wandering into the soil, each pot was fitted with a plastic lid which fitted perfectly along the edges of the pot. The plastic lid had a hole in the center which surrounded the plant stem, isolating the stem and leaves of the plant from the soil. To contain the insects, each potted plant was fully covered with an inverted plastic container. Fine metal mesh was placed at the top of container to allow ventilation. Nymphs on potted plants were observed daily and the duration and survival of each nymphal stage (instar) was recorded. Each nymphal stage was differentiated according to descriptions by Olckers (2000). Observations continued until the last surviving nymph emerged as an adult.

For each group of ten nymphs, the number of adult females (identified as F_1), the life cycle duration (number of days it took to develop from egg to adult), and nymphal instar survival (percentage of surviving nymphs at each nymphal stage) were recorded at each temperature tested. For each temperature this experiment was replicated three times.

To compare adult reproduction and lifespan across temperatures, three lace bug pairs (F_1 adults) were randomly selected from the adults that emerged from the prior experiment. To ensure that pairs were not siblings, adults were sourced from different egg batches. For each temperature there were 30 pairs tested. This procedure was replicated three times. Each F_1 female was allowed to copulate and lay eggs during their lifetime and several reproductive parameters were recorded: (1) the number of females that oviposited successfully (i.e. produced egg batches that hatched), (2) the length of the pre-oviposition period (i.e. number of days counted from the day the female was placed with the adult male until the presence of an egg batch), (3) total number of eggs laid per female, (4) number of egg batches laid per female, (5) number of eggs per batch, (6) number of eggs in the first batch, and (7) proportion of eggs that hatched from the first batch.

Plants with F_1 adults were monitored daily to record the adult's lifespan and to check for egg batches. In a congeneric species *G. solani*, female investment in maternal care is associated with a significant reduction in fecundity (Tallamy and Denno 1982). Therefore, to avoid maternal care affecting the fecundity in *G.*

decoris, only the first egg batch oviposited was selected for further analysis. Once an egg batch was observed, it was collected and placed in plastic Petri dish for incubation under similar environmental conditions as the parents. When F_2 nymphs emerged, they were counted, placed on a new potted *S. mauritianum* plant, and followed until they reached adulthood. The F_2 adults were sexed and their survival (percentage of F_2 nymphs that moulted to adults) was recorded. During the experiment, plants were replaced with the new ones when at least 75% of the leaves were damaged.

Photoperiod and humidity

To evaluate the effect of photoperiod on *G. decoris* life history, the development from egg to adult was monitored at three different photoperiods L:D 8:16, 14:10 and 16:8 and at a constant temperature of 20 °C and $50 \pm 10\%$ RH. In a separate experiment, the effect of humidity was evaluated at $50 \pm 10\%$ and $70 \pm 10\%$ RH at 20 °C and L:D 16:8 photoperiod. The procedure and recorded variables were as described for the temperature experiment. There were three replicates for each photoperiod and humidity experiment.

Life table calculations

To examine the effect of temperature, photoperiod and humidity on *G. decoris* population growth, we calculated life table parameters using data collected from the above experiments. The intrinsic rate of natural increase (r_m, females per females per day) was estimated by solving the Lotka–Euler equation, $\sum e^{-r_m x} l_x m_x = 1$ as described by Wilson (2000). Other life table parameters: net reproductive rate [$R_0 = \sum l_x m_x$ mean generation time [$T = \log_e(R_0)/r_m$, days], doubling time [$DT = \log_e(2)/r_m$, days] and finite rate of increase [$\lambda = e_r$] were calculated for each female that laid eggs and their SE was computed using the jackknife method (Caswell 1989).

Statistical analysis

Gargaphia decoris development time, nymphal survival, fecundity, fertility and life table parameters were compared across different temperatures, photoperiods and humidity levels using Analysis of

Variance (ANOVA) followed by Tukey's HSD test for comparison of means at $p < 0.05$. These data were tested for normality using the Shapiro–Wilks test. If data violated the assumptions of normality after log-transformations were performed, data were analyzed using the non-parametric Kruskal–Wallis test and the Dunn's multiple comparison test. Linear and quadratic regression for developmental rate (1/d), using temperature as a predictor variable (15 °C to 27.5 °C) were conducted. Following the assumption that development rate is proportional to temperature, the thermal constant for development (K) required for development was calculated as the reciprocal of the slope (1/slope) of a regression line fitted to the developmental data. All data was analyzed using R (R Development Core Team 2014). The estimation of the distribution of survival times was obtained by calculating the survival distribution function. The LIFETEST procedure (SAS 9.3) was used to compare survival curves using the non-parametric Wilcoxon test as reported in SAS Institute Inc. (2009).

Results

Effect of temperature on *G. decoris* development and population growth

Eggs kept at 10 °C failed to hatch, and nymphs that emerged at 30 °C died after one day. For the remaining treatments where egg and nymphal development did occur (i.e. 15–27.5 °C), the mean (± SE) developmental duration of *G. decoris* eggs, nymphs and total life cycle duration were all significantly affected by temperature treatment (slowest development at 15 °C and fastest at 25 °C) (Table 1). The influence of temperature on development rate was adequately described by linear and quadratic regression models (Table 2). The egg hatch, total nymphal development and life cycle better fit a quadratic regression (Fig. 1). However, the development rate of each developmental stage better fit a linear regression model (Table 2). Due to the gap in tested temperatures between 27.5 °C and 30 °C in this experiment, non-linear models such as Brière or Logan model (Logan et al. 1976; Briere et al. 1999) could not be used.

Effect of temperature on *G. decoris* survival

The lowest and highest total survival (from egg to adult) were observed at 15 and 25 °C ($27.6 \pm 4.1\%$ and $39.8 \pm 4.3\%$, respectively) although these differences were not statistically significant (data not shown). There were significant effects of gender and temperature on *G. decoris* longevity. On average, females lived 29–33% longer than males. This was significant at all temperatures but at 20 °C (Wilcoxon test: $\chi_1^2 = 9.48$, $p < 0.01$ for 15 °C; $\chi_1^2 = 2.08$, $p = 0.149$ for 20 °C; $\chi_1^2 = 17.83$, $p < 0.01$ for 25 °C; $\chi_1^2 = 7.51$, $p < 0.01$ for 27.5 °C) (Fig. 2). Adult survival was higher at lower temperatures (Wilcoxon test: $\chi_3^2 = 18.50$, $p < 0.01$ for females; $\chi_3^2 = 13.70$, $p < 0.01$ for males) (Fig. 2).

Effect of temperature on *G. decoris* fecundity and life table parameters

Temperature significantly affected some of the reproductive parameters of *G. decoris*. The total number of eggs was on average 94% higher at 20 °C and 25 °C compared to 15 °C (Table 3). A similar trend was observed for the number of eggs laid per female and eggs per batch. The pre-oviposition period increased as the temperature decreased ($F_{3,8} = 5.16$, $p < 0.05$). The number of eggs in the first batch was significantly higher at 20 °C. However, significant differences were found only between 15 °C and the rest of the temperatures tested. The number of egg batches laid per female ($F_{3,8} = 2.07$, $p = 0.18$), the number of females that oviposited successfully ($F_{3,8} = 2.42$, $p = 0.14$) and the percentage of eggs that hatched ($F_{3,8} = 0.78$, $p = 0.53$) were not significantly affected by temperature (Table 3).

Most of the life table parameters for *G. decoris* were affected by temperature. Net reproductive rate (R_0) was highest at 25 °C and lowest at 15 °C, and was positive at all temperatures, denoting increasing populations. The intrinsic rate of natural increase (r_m) and finite rate of increase (λ) were highest at 20–25 °C and significantly decreased at 15 °C. Doubling time (DT) and mean generation time (T) were lowest at 25 °C and highest at 15 °C (Table 4).

Table 1 Mean development time (from egg to adulthood) in days (± SE) of *Gargaphia decoris* at four constant temperatures, with a constant photoperiod of L:D 14:10 and RH of 50 ± 10%

Temp. (°C)	Eggs	Nymphal stages					Nymphal period	Life cycle
		1°	2°	3°	4°	5°		
15	20.56 ± 0.39 a	7.50 ± 0.54 a	8.50 ± 0.54 a	9.21 ± 0.34 a	10.39 ± 0.29 a	15.39 ± 0.33 a	51.77 ± 0.82 a	71.73 ± 1.00 a
20	11.32 ± 0.79 b	4.84 ± 0.21 b	4.32 ± 0.20 b	4.75 ± 0.21 b	6.12 ± 0.20 b	9.28 ± 0.32 a	29.76 ± 0.54 b	41.32 ± 0.61 b
25	7.70 ± 0.25 c	3.78 ± 0.20 b	2.78 ± 0.20 b	3.5 ± 0.20 b	3.4 ± 0.20 c	5.78 ± 0.15 b	18.51 ± 0.53 c	29.97 ± 0.56 c
27.5	6.47 ± 0.27 c	3.10 ± 0.14 b	2.89 ± 0.10 b	3.27 ± 0.15 b	3.42 ± 0.12 c	5.40 ± 0.14 b	20.24 ± 0.79 c	24.29 ± 0.39 c
K	0.90 ± 1.11	2.33 ± 0.43	1.96 ± 0.51	1.92 ± 0.52	1.64 ± 0.61	1.02 ± 0.98	0.36 ± 2.72	0.26 ± 4.00

Means followed by the same letter within a column are not significantly different (Tukey's HSD test, α = 0.05). The K represents the thermal constant for development, calculated as 1/slope of a linear regression fitted to the development data (see Fig. 1 and Table 2)

Table 2 Linear and quadratic regressions for development rate (x, day^{-1}) of *Gargaphia decoris* developmental stages at four constant temperatures: 15 °C, 20 °C, 25 °C, and 27.5 °C

Developmental stage	Regression model	Statistics
Egg hatch	$73.74 - 4.89x + 0.09x^2$	$R^2 = 0.98$, $F_{2,9} = 250.70$, $p < 0.01$
	$35.75 - 1.11x$	$R^2 = 0.91$, $F_{1,10} = 107.30$, $p < 0.01$
First instar	$13.95 - 0.43x$	$R^2 = 0.66$, $F_{1,10} = 22.80$, $p < 0.01$
Second instar	$15.64 - 0.51x$	$R^2 = 0.76$, $F_{1,10} = 36.06$, $p < 0.01$
Third instar	$16.28 - 0.52x$	$R^2 = 0.81$, $F_{1,10} = 48.54$, $p < 0.01$
Fourth instar	$18.85 - 0.61x$	$R^2 = 0.88$, $F_{1,10} = 78.01$, $p < 0.01$
Fifth instar	$30.60 - 0.98x$	$R^2 = 0.82$, $F_{1,10} = 51.90$, $p < 0.01$
Total nymph cycle	$185 - 12.25x + 0.22x^2$	$R^2 = 0.98$, $F_{2,9} = 288.30$, $p < 0.01$
	$89.52 - 2.75x$	$R^2 = 0.91$, $F_{1,10} = 108.10$, $p < 0.01$
Life cycle	$242.07 - 15.48x + 0.27x^2$	$R^2 = 0.98$, $F_{2,9} = 232.80$, $p < 0.01$
	$125.91 - 3.92x$	$R^2 = 0.92$, $F_{1,10} = 132.30$, $p < 0.01$

The type of regression model (linear vs. quadratic) was selected based on best fit

Effect of photoperiod on *G. decoris* life history traits

Photoperiod significantly affected only the mean percentage of egg hatch ($F_{2,6} = 8.43$, $p < 0.05$) and total nymphal survival (nymph to adult emergence) ($F_{2,6} = 5.47$, $p < 0.05$). The highest percentage of egg hatch and total survival were observed at L:D 16:8 photoperiod. Egg hatch and survival at L:D 14:10 were both lowest, but not significantly different to the L:D 8:16 treatment (Fig. 3).

Adult longevity was significantly affected by photoperiod. Females ($\chi_2^2 = 12.05$, $p < 0.01$) and males ($\chi_2^2 = 7.66$, $p < 0.01$) lived longer at L:D 16:8 photoperiod (♀75.79 ± 0.54 days, ♂76.26 ± 3.82 days), compared to the L:D 14:10 photoperiod (♀67.33 ± 17.31 days, ♂50.83 ± 13.89 days). No significant differences were observed in the longevity of females between L:D 8:16 and 16:8 photoperiods ($p = 0.43$) or in the longevity of males between L:D 8:16 and 14:10 photoperiods ($p = 0.19$) (data not shown).

Photoperiod significantly affected all measured *G. decoris* population growth parameters. The R_o was positive in all tested photoperiods, indicating population growth, with a faster rate at L:D 16:8 photoperiod ($r_m = 0.52 ± 0.001$) and lower rate at L:D 14:10 photoperiod ($r_m = 0.15 ± 0.001$). The time to produce one generation and to double it were shorter at L:D 16:8 photoperiod (T = 9.60 ± 0.02, DT = 1.33 ± 0.003 d) and longer at L:D 14:10 photoperiod (T = 25.20 ± 0.05, DT = 4.52 ± 0.03 d) (data not shown).

Effect of relative humidity on *G. decoris* life history traits

Relative humidity only affected the mean percentage of egg hatch ($F_{2,6} = 8.21$, $p < 0.05$). The percentage of egg hatch was significantly higher at 50 ± 10% RH (88.10 ± 0.34) than at 70 ± 10% RH (75.03 ± 4.57). Adult longevity was significantly affected by humidity. Adults lived longer at 70% RH ($\chi_1^2 = 10.74$, $p < 0.01$), but females lived longer than males at both RH ($\chi_1^2 = 3.96$, $p < 0.05$). Relative humidity affected all measured *G. decoris* population growth parameters. The R_0 indicates that population growth took place at both 50 and 70% RH. The R_0 was higher at 70% RH, the r_m was higher at 50% RH. Therefore T and DT were both shorter at 50% RH (data not shown).

Discussion

We show that all tested environmental conditions (temperature, photoperiod and humidity) are likely to affect persistence and establishment of *G. decoris*. Immature stages are unlikely to develop at temperatures below 10 °C or above 30 °C. Although *G. decoris* was able to develop at 15 °C, nymphal development was very slow. This indicates that, for *G. decoris* to achieve a population increase necessary to inflict considerable damage to the host plant, temperatures should be higher than 15 °C. Currently, *G. decoris* is established in the North Island of New Zealand, specifically in the low-lying coastal areas of the Bay of Plenty, Auckland and Northland regions (Landcare Research, unpublished data), where mean
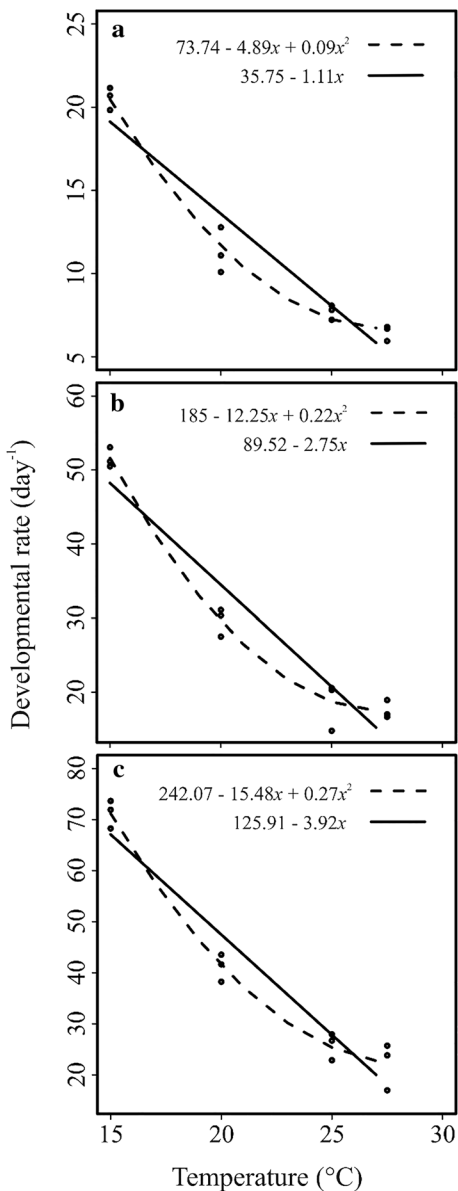
Fig. 1 Development rates (day^{-1}) for *Gargaphia decoris* developmental stages at four different constant temperatures: 15 °C, 20 °C, 25 °C, and 27 °C, as predicted by quadratic and linear regression models in **a** egg hatch, **b** total nymphal cycle, and **c** total life cycle. Open circles (n = 12) represent the experimental data (mean developmental rates), lines represent the fitted quadratic (dashed) and linear (solid) regressions

annual temperatures range from 14 °C to 16 °C and summer temperatures easily achieve ≥ 20 °C but very seldom reach 30 °C (Chappell 2013a, b, c). The establishment of *G. decoris* in these areas has likely benefited from the more stable coastal climate, with

less extreme fluctuations in temperature compared to inland regions which typically experience both hotter and colder temperatures that sometimes drop below 0 °C (Chappell 2013a, b, c).

Temperature is known to be the most restrictive environmental factor for insects (Bale et al. 2002). However, temperature effects on insects are intertwined with other environmental factors such as photoperiod and humidity (Simelane 2007), and such interactions between environmental factors may restrict the persistence and establishment of biocontrol agents (Byrne et al. 2002; Bean et al. 2007; Cowie et al. 2016b). For example, life table parameters reported in this study suggest that population growth of *G. decoris* is likely to be restricted to summer months at the Bay of Plenty, Auckland and Northland sites. The optimal month for population growth is likely to be December when there is a long photophase (≈ 15 h), RH of at least 70% and higher temperatures. After December, the photophase length is reduced to approximately 13 to 14 h (January–March) (LINZ, Land Information New Zealand 2018). We observed that a photoperiod of L:D 14:10, while enabling population growth, was less optimal than a photoperiod of L:D 16:8, despite sustained otherwise optimal temperatures and RH. The reduced egg hatch and survival of *G. decoris* at a 14 h photophase suggests that there are critical photoperiods that can trigger a change in the performance of this biocontrol agent. However, L:D 14:10 photoperiod conditions did not induce reproductive diapause, as has been reported for other insects when subjected to critical photoperiods (Beck 1980). We show that a short photophase (8 h) resulted in better performance and fitness of *G. decoris* than 14 h. A short photophase is known to induce diapause in some insects (Saunders 1987) and such impact often is in conjunction with lower temperatures (Taylor et al. 1995; Saunders 2014). Thus, in the present study we do not have evidence that photoperiod induces diapause in *G. decoris,* but it is possible that diapause may occur under conditions of short photophase and low temperature (< 20 °C).

Our data help to interpret a previous finding in South Africa and New Zealand that *G. decoris* shows a preference for shade conditions under field situations (Patrick and Olckers 2011; Fowler 2014). We show that *G. decoris* thrives under the tested environmental conditions present at those field study sites. Therefore, the reason for *G. decoris* seeking shade is likely to be

Fig. 2 Survival probability of *Gargaphia decoris* females and males across four constant temperatures: 15 °C, 20 °C, 25 °C, and 27.5 °C. Solid lines represent the survival probability of females and dashed lines represent the survival probability of males
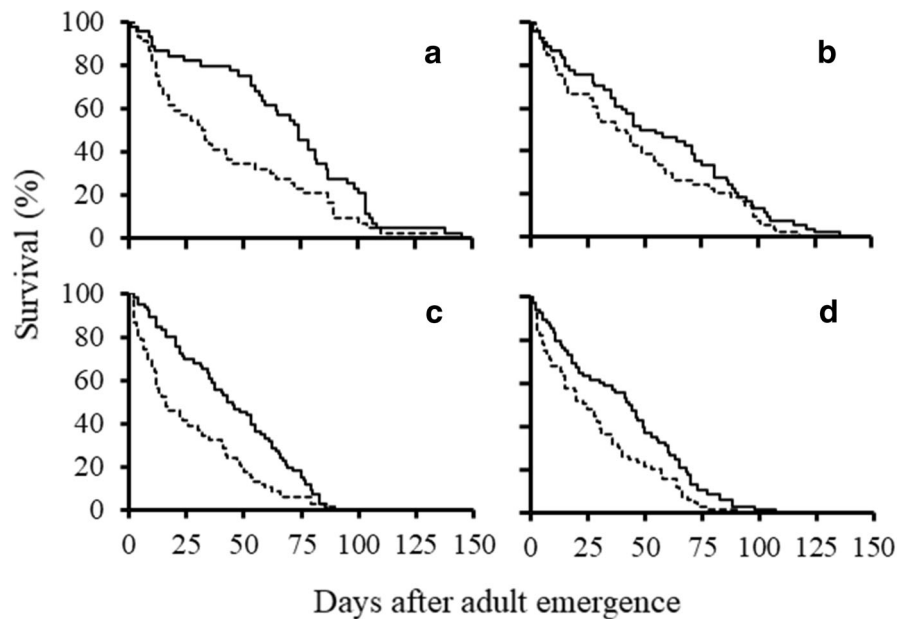
Table 3 Effect of four constant temperatures on fecundity parameters (± SE) of *Gargaphia decoris* females, at a constant photoperiod of L:D 14:10 and RH 50 ± 10%

Factor	Temperature (°C)				Statistic $F_{3,8}$
	15	20	25	27.5	
Total no. eggs	37 ± 25.11 b	560 ± 239.40 a	703.33 ± 283.18 a	249.67 ± 101.83 ab	4.65*
No. eggs laid per female	15.25 ± 3.99 b	60.16 ± 11.11 a	62.09 ± 13.05 a	29.72 ± 8.28 ab	5.64*
No. egg batches	2 ± 1.00	13.67 ± 5.04	16 ± 6.08	9 ± 3.21	2.07 ns
No. egg per batch	15.25 ± 3.99 b	37.88 ± 4.27 a	40 ± 2.55 a	25.2 ± 5.74 ab	7.29*
Pre-oviposition period (days)	55 ± 3.61 a	40.63 ± 12.30 ac	24.81 ± 1.86 bc	23.97 ± 0.88 bc	5.16*
Females that oviposited successfully (%)	15.06 ± 5.10 b	47.55 ± 16.19	41.54 ± 14.84	27.52 ± 1.81	1.66 ns
No. eggs in first batch	16 ± 4.62 b	43.05 ± 5.64 ac	39.23 ± 6.27 bc	26.43 ± 5.69	4.41*
% Egg hatched (first batch)	36.69 ± 5.49	60.76 ± 15.66	55.97 ± 10.27	63.91 ± 6.32	0.80 ns

Means followed by the same letter within a row are not significantly different (Tukey's HSD test, α = 0.05)

ns not significant

*p < 0.05

some other untested environmental factors. For example, Cowie et al. (2016a) suggested that the preference for shade plants could be a result of observed damage to the photosynthetic machinery of the host plant under high light intensities, which ultimately could decrease plant host quality. Alternatively, biotic factors like predation could drive this preference, as proposed by Cowie et al. (2018).

In conclusion, the results of this study demonstrate that all environmental parameters tested have an effect on *G. decoris* fitness, and that environmental conditions are likely to be a major limiting factor for the establishment and persistence of this biocontrol agent. Therefore, there will be geographical constraints on where the biocontrol agent is likely to be useful, and these findings may also help explain the current

Table 4 Life table parameters (mean ± SE) of *Gargaphia decoris* at four constant temperatures, a constant photoperiod of L:D 14:10 and a RH of 50 ± 10%; n is the number of females used to calculate parameters

Parameters	Temperature (°C)				Statistics x_3^2
	15 (n = 2)	20 (n = 24)	25 (n = 33)	27.5 (n = 19)	
Net reproductive rate (R_o), female offspring per female	3.50 ± 0.50	48.50 ± 1.57 b	54.30 ± 0.28 a	24.91 ± 1.10 c	58.31***
Intrinsic rate of natural increase (r_m), 1/time	0.04 ± 0.01	0.15 ± 0.00 b	0.20 ± 0.00 a	0.14 ± 0.00 c	64.51***
Finite rate of increase (λ), dimensionless	1.04 ± 0.01	1.17 ± 0.00 b	1.22 ± 0.00 a	1.15 ± 0.00 c	64.51***
Mean generation time (T), days	34.07 ± 0.82	25.20 ± 0.07 a	20.23 ± 0.07 b	22.90 ± 0.17 c	67.74***
Doubling time (DT), days	19.32 ± 2.69	4.52 ± 0.03 b	3.51 ± 0.02 c	4.97 ± 0.07 a	64.51***

Means with the same letter within a row are not significantly different (Dunn's test, α = 0.05). Data for 15 °C were excluded from statistical analysis due to small sample size—only two females successfully produced offspring at 15 °C, suggesting unsuitability of this temperature for population growth even though data present positive increase values

*** $p < 0.001$
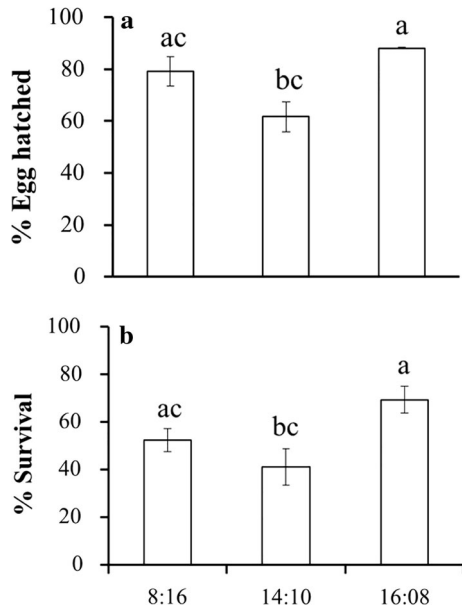
Fig. 3 Mean (± SE) percentage of egg hatched (**a**) and percentage total survival (nymphs to adult) (**b**) of *Gargaphia decoris* grown at three different photoperiods (L:D), with constant 20 °C temperature and 50 ± 10% RH. Means with the same letter are not significantly different (Tukey HSD test, α = 0.05)

establishment patterns in places like New Zealand. We present the life history of this insect at a level of detail not previously available, across a range of environmental conditions. Such information could be integrated into ecoclimatic models for helping to predict establishment, persistence, and seasonal population fluctuations at potential release sites. In addition, future climate scenarios could be explored to see how the real or potential insect distribution might change. It is suggested that a detailed life history, as presented here for *G. decoris,* should be performed as part of standard assessments of insect suitability, prior to introductions of biological control agents.

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