Impact of relative humidity and water availability on the life history of the predatory mite Amblyseius swirskii

San, Phyu Phyu
Laboratory of Insect Natural Enemies, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

Tuda, Midori
Laboratory of Insect Natural Enemies, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

Takagi, Masami
Laboratory of Insect Natural Enemies, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

https://hdl.handle.net/2324/7179457

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Impact of relative humidity and water availability on the life history of the predatory mite *Amblyseius swirskii*

Phyu Phyu San[a,c]*·Midori Tuda[a,b]*·Masami Takagi[a,b]

[a]Laboratory of Insect Natural Enemies, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Fukuoka, Japan

[b]Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka, Japan

[c]Department of Entomology and Zoology, Yezin Agricultural University, Naypyitaw, Myanmar

*Corresponding authors: Phyu Phyu San and Midori Tuda

Email Address: phyuphyusan@yau.edu.mm (P.P. San), tuda@grt.kyushu-u.ac.jp (M. Tuda)

Abstract   The predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae) is currently used as an efficient biological control agent of thrips, whiteflies and spider mites, which are economically damaging pests of ornamental plants and vegetable crops grown in greenhouses and fields worldwide. Currently, the effects of relative humidity (RH) and water availability on the optimal growth of *A. swirskii* are unknown. Here, we test the combined effects of different levels of RH (33%, 53%, 73% and 92%) and water availability on the development and reproduction of male and female *A. swirskii* feeding on the dried fruit mite, *Carpoglyphus lactis* (Linnaeus). While eggs failed to hatch at 33% RH, the survival rates of the immature stages at $\geq$ 53% RH increased solely in response to water availability and not due to changes in RH. Regarding growth and development, low RH extended the egg–adult duration and pre-oviposition period. We also found that the negative effects of low RH on fecundity were partially or completely eliminated when drinking water was available. For the life table parameters, the highest values of net reproductive rate (R_0) and intrinsic rate of natural increase (r) were achieved at the highest RH and when drinking water was available. Overall, water availability mitigated the negative effect of low RH on female reproduction, and female development was more sensitive to water availability than male development.

Lastly, a comparison of similar research on *A. swirskii* suggested that water availability and RH are more influential on *r* than food source or temperature.

Introduction

The predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae) is used worldwide as an effective biological control agent of whiteflies, thrips and spider mites on greenhouse crops such as sweet pepper, cucumber and ornamental plants (El-Laithy and Fouly 1992; Momen and El-Saway 1993; Messelink et al. 2008; Kim et al. 2009; Calvo et al. 2011). Commercially available since 2005, *A. swirskii* originates from the eastern Mediterranean region and is recognized as a generalist predator that feeds on a variety of insects and mites as well as on pollen and plant exudates (McMurtry and Croft 1997). Stored product mites are used as an alternative source of prey in the mass rearing of *A. swirskii* (Bolckmans and van Houten 2006). Following release, it is important that *A. swirskii* successfully colonize the introduced area in order to control the target pest. Understanding the effects of climate on predatory mites helps to predict their suitability in a release area, and this is particularly important for non-native species. In a given environment, the investigation of life history parameters is critical in evaluating the potential population growth of a species (Birch 1948). Temperature is typically a major driver of population growth in poikilothermic animals (Frazier et al. 2006), and relative humidity (RH) can constrain population growth at optimal temperatures, especially if the animal expends energy balancing hydration at the expense of reproduction (Colloff 2009). Therefore, the subsistence of predatory mites is influenced by the surrounding environment, temperature and RH, all of which are crucial for survival (Helle and Sabelis 1985; Ghazy et al. 2016). Since the initial discovery of *A. swirskii*, however, most studies have focused on aspects of its development and potential effects in biological control under a limited range of temperatures and RHs, apart from a single study of temperature-dependent life history parameters (Lee and Gillespie 2011).

To preserve physiological integrity, predatory mites need to maintain an adequate level of body water (two-thirds of body mass, Yoder 1998) within tolerable limits (Wharton 1985; Hadley 1994). However, water conservation is a major challenge due to their small size (0.2–0.5 mm in length); predatory mites lose water during respiration, by diffusion across the surface of the body and through the secretion of digestive fluids and

reproductive products as well as during oviposition and excretion (Arlian and Veselica 1979). Therefore, the successful release and colonization of predatory mites may be influenced by the RH of the target area (Fatnassi et al. 2015; Shimoda et al. 2019). Species and strains of predatory mites that originate from different geographical regions exhibit varying responses to RH. The effects of RH on the biology of other phytoseiid predatory mites have been noted [egg hatching success of *Euseius finlandicus* (Oudemans), *Typhlodromus pyri* Scheuten and *Kampimodromus aberrans* (Oudemans) (Schausberger 1998; Ferrero et al. 2010); development and longevity of *A. alstoniae* Gupta (Kumari and Sadana 1991); development and mortality of *T. aripo* De Leon (Mutisya et al. 2010); development and life table of *A. largoensis* (Muma) (Gómez-Moya et al. 2018)]. In *A. swirskii*, however, the effects of RH on life history have received little attention.

Predatory mites are not only affected by RH, but by the availability of drinking water as well (Dinh et al. 1988). Water is of major importance to all living things, including those with applications to biological control (Tuda et al. 2006; Tuda 2011). For predatory mites, the availability of free water increases the survival of the immature stages of *Amblydromalus limonicus* (Garman & McGregor) (Liu and Zhang 2017) and the overall survival of *Iphiseius degenerans* (Berlese), *Neoseiulus cucumeris* (Oudemans), *N. californicus* (McGregor) and *Phytoseiulus persimilis* Athias-Henriot (Williams et al. 2004). Furthermore, transpiration rates (water loss) differ between male and female mites (Arlian 1975; Lavadinho 1975). However, the sex-specific effects of RH and water availability on *A. swirskii* are currently unknown. In the present study, we investigate the life history of male and female *A. swirskii* under different levels of RH and water availability in laboratory conditions.

Materials and methods

Predatory mite culture

The predatory mite *A. swirskii* (Israeli strain) and its prey, the dried fruit mite *Carpoglyphus lactis* (Linnaeus), were obtained from Arysta LifeScience Cooperation (Tokyo, Japan). The predators were enclosed in a ventilated plastic container (9 cm diameter × 4 cm height) provisioned with dried fruit mites. The dried fruit mites were supplied with a diet of baker's yeast, following San et al. (2020). The predatory mite cultures were inspected once a week, and fresh diet was added as needed to maintain a healthy stock of dried fruit mites. If fungi developed on the culture over time, both mite species were transferred to a new container with fresh food. The lids of the containers were coated with Parafilm to prevent the mites from escaping. All colonies were kept in an incubator at 25 °C, 70%

RH and a 16 h light: 8 h dark photoperiod. We chose this temperature because, while *A. swirskii* can develop and reproduce between 15–36 °C, its net reproduction is highest at 25 °C (Lee and Gillespie 2011).

Experimental conditions

The experiment was conducted at 33%, 53%, 73% and 92% RH in a climate-controlled chamber held at 25 °C with a 16:8 light:dark photoperiod. To maintain a constant RH, sealed plastic containers ($32 \times 23 \times 10$ cm) were filled with an appropriate saturated salt solution (300 ml); $MgCl_2.6H_2O$, $Mg(NO_3)_2.6H_2O$, $NaAc.3H_2O$ and $Na_2C_4H_4O_6$ were used for the 33%, 53%, 73% and 92% RH treatments, respectively (Winston and Bates 1960). A plastic stage ($31 \times 21 \times 3$ cm) was placed above the surface of the salt solution to be used as a platform for the petri dishes that housed the experimental mites. RH was recorded whenever data were collected (twice per day during the immature stages and once per day during the adult stage) with a calibrated hygrometer (Crecer, Sanmu, Japan) that was kept in the container.

Development, reproduction and life table

For the experiment, gravid adult females from the stock cultures were kept in petri dishes to lay eggs at 25 °C and 70% RH. Newly laid eggs (< 12 h old) were transferred singly using a fine camel-hair brush into the plastic petri dishes (9 cm diameter, one egg per petri dish) used in the experiment. Each petri dish contained a piece of filter paper (3.8×6.0 cm) covered by two pieces of black polyvinyl chloride tape (1.9×7.0 cm each), forming a 'plate' on which the mites were located. The two strips of black tape were oriented side-by-side so that there was a very narrow gap between the two pieces; in treatments where drinking water was available to the mites, this small gap prevented the water from evaporating (Fig. 1). For the treatments with drinking water, about 40 µl of water was added every day to one side of filter paper, and the mites had free access to this water from the larval stage until death. A small piece of plastic (referred to as a 'shelter') was provided as a resting and oviposition site. To prevent the mites from escaping the plate, the periphery of the plate was coated with axle grease (Gillespie et al. 2000). These petri dishes were subsequently maintained inside relative humidity-controlled containers (25 petri dishes per container) prepared for four different levels of RH (33%, 53%, 73% and 92% RH). Seventy-five individual eggs—25 eggs with drinking water (W) and 50 eggs without water (NW, 'no water')— were tested for each RH. Greater numbers of eggs were prepared for the NW treatments because higher mortality was expected.

The duration of each developmental stage (egg, larva, protonymph and deutonymph) was recorded every 12 h until the adult stage was reached. After adult emergence, observations were taken every 24 h until the mite died. During each observation we monitored developmental duration, survival, fecundity and adult longevity. All predatory mites were offered about 15 dried fruit mites as a food source at each observation period. The presence of exuviae on the plate was used to determine whether each mite successfully molted to the next developmental stage. Each newly emerged adult female was individually paired with a male on a new plate in a petri dish. Since more females emerged than males, additional male mites were prepared separately (in the same RH as the females) to supplement the number of emerging males. Preoviposition duration, oviposition duration and daily oviposition rate were recorded for each adult female. The eggs laid by each female were maintained under the same RH as the parents to test the effects of RH on the sex ratio of the offspring. Adult mites were sexed based on their body size and morphology; females are larger than males and possess a large, swollen abdomen.

The survival and reproduction data collected during the experiment were combined to construct age-specific (cohort) life tables for *A. swirskii*. The intrinsic rate of natural increase (r), net reproductive rate ($R_0 = \Sigma\ l_x m_x$, the number of female offspring produced per female), mean generation time (the period between the birth of the parent and that of the offspring), finite rate of increase ($\lambda = e^r$, the population multiplication factor for a unit of time) and gross reproduction rate (GRR = $\sum m_x$, the average number of female offspring produced by a group of females) were calculated according to Chi and Liu (1985) and Chi (1988) using the computer program TWOSEX-MS Chart (Chi 2020). Standard errors of life table parameters were obtained using bootstrap technique, and multiple comparisons were done by the paired bootstrap test, with 100,000 samplings.

Statistical analysis

The effects of RH, water availability and sex, and their interactions on the developmental durations of the immature stages, adult longevity, preoviposition and oviposition periods were analyzed using a parametric survival analysis with the best fit distribution (Weibull, log-normal, exponential, Frechet or log-logistic). If a three-way interaction was not significant, we excluded it from the model and repeated the analysis with the reduced model. The effects of RH and water availability and their interaction on fecundity were analyzed using generalized linear models with a Poisson distribution and a log link function; the effects of these same variables on stage-wise survival rates and on

the sex ratio of the offspring were analyzed using logistic regression with a logit link function. If overdispersion of the data was significant, it was incorporated in the model. Significant factors were then subjected to post-hoc multiple comparison tests with a Holm-Bonferroni sequential correction (Holm 1979). After confirming the normality of the data distribution, oviposition rate was analyzed using a general linear model followed by a Tukey-type post-hoc test. For values of r collected from the literature and this study, a generalized linear model was used to test the relative effects of RH, water availability, temperature and food source with a normal distribution and a log link function as well as the interaction between RH and temperature. A post-hoc multiple comparison test with a Holm-Bonferroni sequential correction was performed to compare r among the different food sources (mites, whiteflies, pollen, prey mixed with pollen and artificial diets). Significance levels for all tests were set at $P = 0.05$. All statistical tests were carried out using JMP (ver. 13.2.1).

Results

Development and adult longevity

Eggs did not hatch at the lowest RH (33%), thus this treatment was excluded from subsequent analyses. The development period of *A. swirskii* was influenced by RH, water availability and sex (Supplementary table S1). Egg duration was significantly longer at 53% RH than at 92% RH (Weibull distribution, Supplementary table S2).

The larval development period was affected by water availability and by the interaction between RH and sex (log-normal distribution, Supplementary table S1). The larval duration was longer when water was available than when water was not available (Supplementary table S2). For the RH × sex interaction, female larvae developed faster at 92% RH than at 73% RH, whereas the development period of male larvae was unaffected by RH (Supplementary table S2). The duration of the protonymph stage was affected by water availability and the interaction between RH and water availability (Supplementary table S1). The protonymph stage was longer when water was unavailable compared to when water was available (log-logistic distribution, Supplementary table S2). For the interaction between RH and water availability, no significant pairwise differences in protonymph duration were detected by multiple comparison tests. The duration of the deutonymph stage was affected by water availability, sex and the interaction between RH and water availability (log-logistic distribution, Supplementary table S1). The deutonymph stage was shortened at 53% RH when water was available and was longer for females than for males (Supplementary table S2). The deutonymph duration was shorter at 53% and 73% RH with water and at 92% RH with no water than at 53% RH with no water (Supplementary table S2).

The overall development time from egg to adult was affected by RH as well as the interactions between RH and water availability, water availability and sex, and RH and sex (Frechet distribution, Supplementary table S1). Egg to adult duration was significantly shorter at 92% RH than at 53% and 73% RH. For the RH × sex interaction, the egg–adult period was shorter at 92% RH than at 53% and 73% RH for females, and shorter at 92% RH than at 53% RH for males (Table 1). For the water availability × sex interaction, the egg–adult duration of females provided with water was shorter than when water was unavailable, whereas male development was not affected by water availability (Table 1). For the RH × water availability interaction, the egg–adult duration at 92% RH regardless of water availability was shorter than at 53% and 73% RH with no water (Table 1).

The adult longevity of *A. swirskii* was affected by sex and the interaction between RH and water availability (log-normal distribution, Supplementary table S1). Females lived significantly longer than males (Table 1). Multiple comparison tests on the interaction between RH and water availability did not detect any significant pairwise differences.

Reproductive parameters

All reproductive parameters of female *A. swirskii* were affected by RH and water availability (Table 2), with the exception of oviposition period (Weibull distribution, Supplementary table S1). At 53% and 73% RH, females had a longer preoviposition period when water was unavailable compared to when water was available; however, water availability did not affect the preoviposition period at 92% RH (Frechet distribution, Fig. 2a). At 53% and 73% RH, mites provided with water had a higher fecundity, which increased with increasing RH (Fig. 2b). At 92% RH, fecundity was unaffected by water availability but was as high as at 73% RH when water was available (Fig. 2b). Overall, oviposition rate increased with increasing RH (Fig. 2c) and with access to drinking water (Fig. 2d).

Age-specific survival and fecundity, and stage-wise survival

Except for at 33% RH, all eggs hatched regardless of RH. Overall survivorship was affected by water availability, and survival rates were higher with water for the larval, protonymph and immature (i.e., egg–adult) stages [0.95 ± 0.01, 0.94 ± 0.02 and 0.80 ± 0.02 with water, and 0.80 ± 0.03, 0.76 ± 0.01 and 0.47 ± 0.05 (mean ± SE) without water for each stage; Table 2]. Patterns in the age-specific survival (l_x) and age-specific fecundities (m_x) of *A. swirskii* varied depending on water availability, but were generally similar at 53%, 73% and 92% RH (Fig. 3). When *A. swirskii* did not have access to drinking water, the survival curves sharply decreased during the younger

life stages, which meant that mortality was higher for the immature stages than it was for adults. When water was available, the survival curves indicated moderate mortality rates throughout life. For age-specific fecundity, newly hatched females without access to water started laying eggs after 7 to 9 days, while those that were provided with water began laying eggs after 6 to 7 days. Peak oviposition occurred during the early oviposition period, after which time egg production gradually decreased across all treatments, with the exception of several peak oviposition periods that occurred at 73% RH when water was available. The highest peak oviposition was observed at 92% RH when water was available (2.34 eggs, 13 days after egg hatching), and the second highest peak was at 92% RH when water was unavailable (1.53 eggs, 12 days after egg hatching).

Life table parameters and sex ratio

R_0, r and λ were higher when water was available and increased with increasing RH especially when water was unavailable (Table 3). The mean generation time was shorter with increasing RH and access to free water. All life table parameters for the predatory mites were better when water was available. The sex ratio of the offspring was affected by RH (Table 2) and was higher at 92% RH (female ratio, 0.831 ± 0.021, mean $\pm$ SE) than at 73% RH (0.683 ± 0.034), but both were not significantly different from the sex ratio at 53% RH (0.712 ± 0.046). Water availability did not affect the sex ratio (Table 2).

RH, water availability and intrinsic rate of increase (r)

Our analysis of r for *A. swirskii* (Table 4) indicated that RH (range 33–92%, $\chi^2_1 = 11.96$, $P = 0.0005$) and water availability ($\chi^2_1 = 7.60$, $P = 0.0058$) may be more influential to r than food source ($\chi^2_4 = 13.16$, $P = 0.0105$) or temperature (range 13–36°C, $\chi^2_1 = 5.27$, $P = 0.0216$) after excluding the non-significant RH $\times$ temperature interaction ($\chi^2_1 = 0.01$, $P = 0.931$). The intrinsic rate of increase r was significantly higher when *A. swirskii* preyed on whiteflies than when feeding on pollen. Intermediate values of r were observed when *A. swirskii* was provided with mites, a mixed diet (pollen and prey) or an artificial diet, but these values of r were not significantly different from those on whiteflies or pollen.

Discussion

The immature developmental stages of *A. swirskii* can be completed at as low as 53% RH, potentially due to a reduction in water loss through the integument or during respiration (Hadley 1994), and reproduction can occur

successfully from 53–92% RH at 25 °C. The tolerance for RH and survival ability of phytoseiid mites are dependent upon their original climate (Dinh et al. 1988). Species of predatory mites that predominately inhabit pantropical regions, which have long rainy seasons, are likely able to complete their development at or above 80% RH (Gómez-Moya et al. 2018). However, *A. swirskii* inhabits relatively dry geographic areas in the Mediterranean, and phytoseiid mites from dry areas are more resistant to low RH than species from humid areas (McMurtry et al. 1976; McMurtry 1980). Adaptations to dry conditions may include morphological traits, physiological processes, and behavioral traits (Swift and Blaustein 1980; Perring and Lackey 1989; Gaede 1992).

Development and adult longevity

The development times of the different immature stages of *A. swirskii* varied based on RH, water availability and sex. Morphological variation is linked to differences in biochemical, metabolic, and physiological processes (Freriksen et al. 1994). A number of studies have found that the developmental duration of some predatory mites is shortened by high RH (Rivard 1961; Ustchekow and Begljarow 1968; Stenseth 1979; Walzer et al. 2007), with few exceptions (Mutisya et al. 2010). In *A. swirskii*, higher developmental rates were achieved for females by providing drinking water. Invertebrate development is influenced by the surrounding RH via many physiological processes in addition to water loss from body surfaces (Buxton 1932) and the availability of drinking water (Mellanby 1958).

Reproductive parameters

Except for at 33% RH, fecundity was optimal at all RH levels if drinking water was available and at 92% RH regardless of water availability (Fig. 2b). Thus, the availability of drinking water is remarkably important for the predator's reproduction, particularly under low RH conditions. But under high water vapor saturation (92% RH), the predatory mites did not require drinking water to lay more eggs. Some arthropods possess an active sorption mechanism by which an adequate amount of water is extracted from the subsaturated atmosphere to compensate for water loss (Nobel-Nesbitt 1969; Wharton and Devine 1968; Arlian 1975).

The oviposition rate considerably increased with higher levels of RH and water availability. Analysis of the reproductive parameters suggests that, while 73% RH might allow for a steady population increase over a relatively long period of time, 92% RH promotes a rapid population surge within a short period of time. The predatory mite *A. swirskii* prefers to lay eggs at high RH and shows a strong hygropreference for reproduction. Because of the

short preoviposition period and high fecundity of *A. swirskii*, population increases will be higher under moist conditions.

Age-specific survival, fecundity and stage-wise survival

The availability of drinking water is important for the survival of immature predatory mites irrespective of RH (Fig. 3). There is some evidence that water availability increases survival in other species of predatory mites (Blommers et al. 1977; Sabelis 1981; Dinh et al. 1988). The age-specific survival curves represent a type-III survivorship pattern, following the classification method of Demetrius (1978).

Eggs are most vulnerable to low RH levels (Sabelis 1981) because this stage is unable to compensate for water loss by feeding on prey or drinking water (Dinh et al. 1988; Bakker et al. 1993; Walzer et al. 2007). Even though the eggs of *A. swirskii* failed to hatch at 33% RH, 100% hatched at 53% RH, which is higher compared to other phytoseiid mites; for example, *I. degenerans*, *N. cucumeris*, *N. californicus* and *P. persimilis* all have poor hatchability at 50–60% RH (Williams et al. 2004).

Sex differences

Female *A. swirskii* larvae developed faster at the highest level of RH (92% RH), whereas the development of male larvae was not affected by RH. Male deutonymphs developed faster than females. While the availability of water decreased the egg–adult development time for females, the male egg–adult period was unaffected by water availability. Overall, females lived longer than males likely due to their larger body size and that they are regulated by different physiological activities and norms (Wigglesworth 1942; Fischer and Fiedler 2000).

Life table parameters and sex ratio

Of the RH regimes at 25 °C, the fastest population increase (the maximum values of R_0 and r) of *A. swirskii* occurred at 92% RH when drinking water was present. High RH and water availability clearly affected the developmental duration, survival and fecundity of *A. swirskii*, which in turn had a positive effect on fitness. The sex ratio of the offspring of a single female tends to be inconsistent (Boudreaux 1963) and varies based on the abundance of consumed prey and by the number of progeny (Abou-Awad and Reda 1992; Toyoshima and Amano 1998), but is not influenced by disturbances during mating or the age of mating females (Saber and Momen 2000). A highly female-biased sex ratio under high RH will enhance the growth rate of a population (Southwood et al. 1974).

RH, water availability and intrinsic rate of increase (*r*)

Our review and analysis of *r* estimated that the effects of water availability and RH are relatively more important than food source and temperature on the intrinsic rate of increase for *A. swirskii*. Regarding food sources, our analysis indicated that when *A. swirskii* feeds solely on the spider mite *Tetranychus urticae* (El-Laithy and Fouly 1992; Riahi et al. 2017), *T. urticae* together with pollen (Riahi et al. 2017) or on an artificial diet (Nguyen et al. 2013), the *r* values are similar to those when feeding on dried fruit mites (this study) at similar RHs, but when *A. swirskii* feeds on the whitefly *Bemisia tabaci* (Nomikou et al. 2001), *r* increases with no statistical significance. Higher RH and water availability should improve *r* whenever any of these food sources are utilized. However, if high RH affects the availability of the food source, then this prediction may not apply (San et al. 2020). Overall, whiteflies may be the best source of food for *A. swirskii*, but fruit mites are just as effective as other species of mites, artificial diets and mixed diets of mites and pollen.

Temperature, however, might affect life history traits of predatory mites at unfavorable RHs; for example, while 84% of *P. persimilis* eggs hatch at 40% RH and 21 °C, only 8% of eggs hatch at 27 °C (Stenseth 1979). In general, the development of female *A. swirskii* is more sensitive to water availability than the development of males. The highest intrinsic rate of increase was achieved when water was available at the highest RH, and the availability of drinking water mitigated the negative effects of low RH on female reproduction. Based on this study, *A. swirskii* should be capable of colonizing habitats that have a moist microclimate and available drinking water. Currently, *A. swirskii* is often recommended for controlling thrips and whiteflies in greenhouses or field crops, particularly at temperatures above 30 °C. In comparison with *N. cucumeris*, *A. swirskii* provides better control of thrips during the summer, especially in temperate regions, whereas both have a similar efficacy during the winter (Buitenhuis et al. 2015). The optimal temperature range of both predators is between 20–32 °C (Cloutier et al. 1995; Lee and Gillespie 2011); however, the recommended production temperature in greenhouses usually falls between 17–25 °C (Shipp et al. 1996). Additionally, the feeding rate of *A. swirskii* is higher under short day lengths (or even complete darkness) than it is under long day lengths (Yousef et al. 1982), which explains the occurrence of *A. swirskii* on the lower surfaces of leaves during the day.

The potential application of phytoseiid mites depends on providing a suitable environment for the agent (Ghazy et al. 2016). By understanding the effects of water availability and RH on *A. swirskii* population growth, this knowledge can be used to outline effective rearing conditions. Under greenhouse conditions, diurnal cycles in

temperatures, RH and light intensity can influence pests and biocontrol agents directly or indirectly, with the indirect effects mediated by induced changes in the host plants. Moreover, because of their diminutive size, even small changes in the microenvironmental conditions at the leaf's surface can affect the biology of plant-dwelling mites. For example, RH levels around the leaf layer (within 0.5–5.0 mm) are slightly higher than ambient due to leaf transpiration (Shipp et al. 2009). Finally, to predict the suitability of this mite for augmentative release in a particular field or greenhouse (Shimoda et al. 2019), future experiments should investigate the effects of changes in temperature, RH and photoperiod throughout the entire growing season of the host plants.

Acknowledgements

Contributions

Phyu Phyu San: conceptualization, methodology, investigation, formal analysis, writing - original draft preparation. Midori Tuda: conceptualization, methodology, formal analysis, writing - reviewing and editing, supervision. Masami Takagi: conceptualization, supervision.

Conflict of interest

The authors declare that there are no conflicts of interest associated with this publication.

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Table 1 Egg–adult developmental duration and adult longevity (mean ± SE) (days) of *Amblyseius swirskii* at different relative humidities (RHs) and water availabilities.

RH %	Water availability	Egg– Adult		Longevity	
		Female [1] [3]	Male [1] [3] [2] [5]	Female [4]	Male [4]
53			7.40 ± 0.21 A		
73			7.18 ± 0.23 A		
92			5.95 ± 0.11 B		
53		7.40 ± 0.27 α	7.39 ± 0.34 α		
73		7.43 ± 0.26 α	6.62 ± 0.45 αβ	31.75 ± 1.53 α	11.83 ± 0.74 β
92		5.89 ± 0.10 β	6.12 ± 0.31 β		
	NW	7.12 ± 0.22 a	6.64 ± 0.30 ab		
	W	6.45 ± 0.16 b	6.82 ± 0.35 ab		
53	NW		7.68 ± 0.33 a		
53	W		7.13 ± 0.25 abc		
73	NW		7.61 ± 0.30 ab		
73	W		6.70 ± 0.34 bcd		
92	NW		5.98 ± 0.17 cd		
92	W		5.91 ± 0.12 d		

NW: no water, W: with water, Significance at $P = 0.05$.

[1] Same letters indicate no significant differences in multiple comparisons for the interaction between sexes and water availability for egg–adult stage.

[2] Same letters indicate no significant differences in multiple comparisons for the interaction between RH and water availability for egg–adult stage.

[3] Same Greek letters indicate no significant differences in multiple comparisons for the interaction between RH and sexes for egg–adult stage.

[4] Same Greek letters indicate no significant differences between females and males for adult longevity.

[5] Same uppercase letters indicate no significant differences between RHs for egg–adult stage.

Table 2 Generalized linear model analysis of survival rates, fecundity and offspring sex ratio and general linear model analysis of oviposition rate of *Amblyseius swirskii* at different levels of relative humidity (RH) and water availability

Sources	Larval survival rate			Protonymph survival rate			Deutonymph survival rate			Egg–adult survival rate			Fecundity			Oviposition rate			Female offspring ratio		
	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	F	P	df	χ^2	P
RH	2	0.44	0.803	2	0.55	0.762	2	5.66	0.059	2	2.04	0.360	2	12.76	0.002	2, 81	43.81	<.0001	2	9.01	0.011
Water availability	1	9.63	0.002	1	12.42	0.0004	1	0.94	0.332	1	24.20	<.0001	1	18.04	<.0001	1, 81	66.08	<.0001	1	0.12	0.734
RH × water availability	2	0.85	0.655	2	0.48	0.788	2	3.32	0.190	2	0.06	0.969	2	7.68	0.022	2, 81	1.70	0.188	2	0.40	0.819

Table 3 Life table parameters (bootstrap mean ± SE) of *Amblyseius swirskii* at different levels of relative humidity (RH) with no water (NW) and with water (W)

Parameters	33% RH	53% RH		73% RH		92% RH	
		NW	W	NW	W	NW	W
Number of females	0	12	13	18	11	18	15
Net reproductive rate (R_0)	0.00	2.54 ± 0.71 d	11.52 ± 2.62 ab	5.78 ± 1.25 c	11.32 ± 3.10 abc	8.26 ± 1.88 bc	14.48 ± 2.44 a
Intrinsic rate of increase (r)	0.000	0.045 ± 0.015 d	0.150 ± 0.017 b	0.097 ± 0.013 c	0.159 ± 0.023 b	0.153 ± 0.018 b	0.236 ± 0.019 a
Finite rate of increase (λ)	0.00	1.05 ± 0.02 d	1.16 ± 0.02 b	1.10 ± 0.01 c	1.17 ± 0.03 b	1.17 ± 0.02 b	1.27 ± 0.02 a
Mean generation time (T), (d)	NA	20.92 ± 2.01 a	16.30 ± 0.79 bc	18.05 ± 1.02 ab	15.30 ± 0.70 cd	13.79 ± 0.91 d	11.34 ± 0.40 e
Gross reproduction rate (GRR)	0.00	9.89 ± 1.27 b	17.84 ± 2.80 a	15.97 ± 2.18 a	17.37 ± 3.79 ab	20.91 ± 3.55 a	18.88 ± 2.33 a

The means followed by same letters in the same row are not significantly different according to the paired bootstrap test based on the confidence interval of differences at the 5 % level.

 NA: not available.

Table 4 Comparison of *r* values of *Amblyseius swirskii* when fed different types of food and reared under different temperature, relative humidity (RH) and water availability conditions

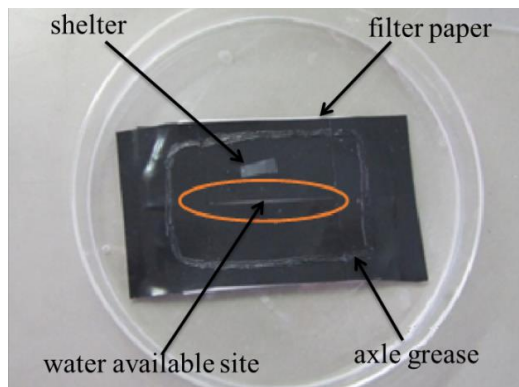| Food sources	*r*	Temperature	RH	Water availability	References
Two-spotted spider mite, *T. urticae*	0.167	26 °C	70%	Yes	El-Laithy and Fouly (1992)
Whitefly, *B. tabaci*	0.208 and 0.213 for different strains	25 °C	60%	Yes	Nomikou et al. (2001)
Tomato russet mite, *Aculops lycopersici*	0.235	28 °C	75%	Yes	Momen and Abdel-Khalek (2008)
A. lycopersici	0.201	25 °C	70%	Yes	Park et al. (2011)
Cattail pollen, *Typha latifolia*	0.185	25 °C	70%	Yes	
T. latifolia	0	13 °C	60%	Yes	Lee and Gillespie (2011)
	−0.002	15 °C	60%	Yes	
	0.016	18 °C	60%	Yes	
	0.076	20 °C	60%	Yes	
	0.135	25 °C	60%	Yes	
	0.145	30 °C	60%	Yes	
	0.160	32 °C	60%	Yes	
	0.134	34 °C	60%	Yes	
	0.067	36 °C	60%	Yes	
Dried fruit mite, *C. lactis*	0.175	23 °C	65%	Yes	Nguyen et al. (2013)
Cattail pollen	0.158	23 °C	65%	Yes	
Artificial diet 1	0.104	23 °C	65%	Yes	
Artificial diet 2	0.181	23 °C	65%	Yes	
Panonychus citri	0.165	25 °C	80%	Yes	Ji et al. (2013)
Suidasia medanensis	0.222	25 °C	70%	Yes	Midthassel et al. (2013)
T. urticae	0.134	25 °C	65%	Yes	Riahi et al. (2017)
Almond pollen	0.180	25 °C	65%	Yes	
Bee pollen	−0.101	25 °C	65%	Yes	
Date pollen	0.080	25 °C	65%	Yes	
Almond pollen + *T. urticae*	0.175	25 °C	65%	Yes	
Bee pollen + *T. urticae*	0.129	25 °C	65%	Yes	
Date pollen + *T. urticae*	0.142	25 °C	65%	Yes	
Cenopalpus irani	0.140	25 °C	60%	Yes	Bazgir et al. (2018)
Eotetranychus frosti	0.179	25 °C	60%	Yes	
C. lactis	0.000	25 °C	33%	No/yes	This study (Table 3)
	0.045	25 °C	53%	No	
	0.097	25 °C	73%	No	
	0.153	25 °C	92%	No	
	0.150	25 °C	53%	Yes	
	0.159	25 °C	73%	Yes	
	0.236	25 °C	92%	Yes	

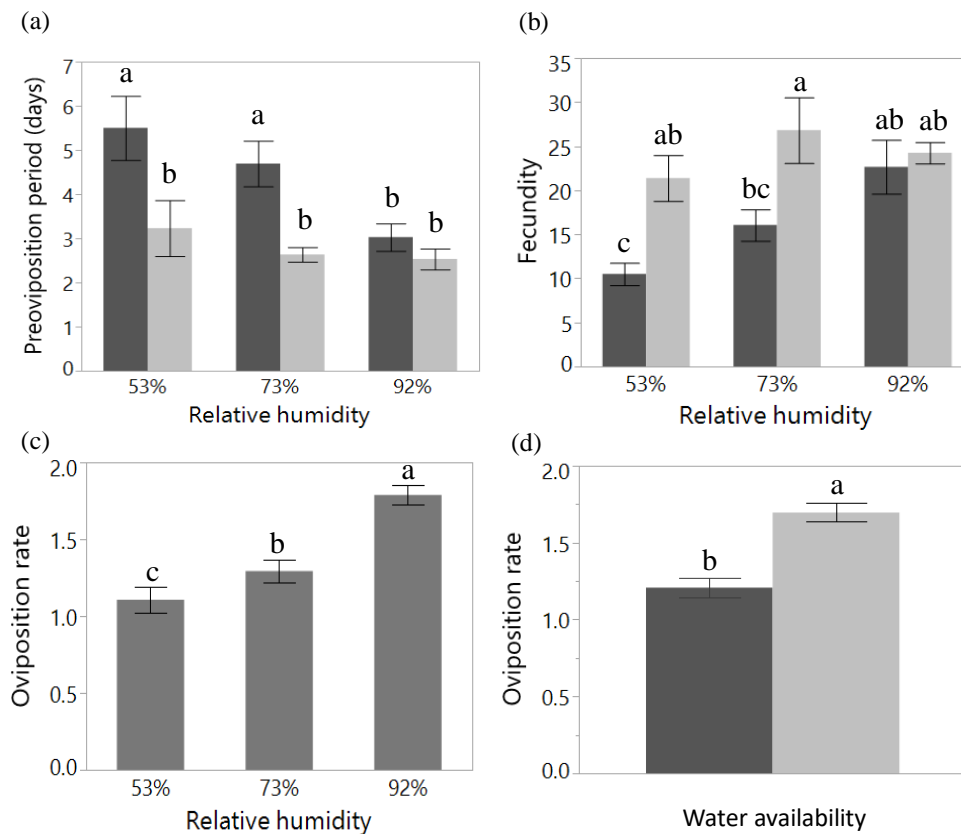**Fig. 1** A plate inside a petri dish for rearing *Amblyseius swirskii.*

Fig. 2 Reproduction parameters of *Amblyseius swirskii* in response to relative humidity (RH) and water availability.

(a) Preoviposition period, (b) fecundity and (c, d) oviposition rate per day. Black, no water; light gray, with water.

Mean ± SE. Same letters indicate no significant differences at *P* = 0.05. For significant interaction effects, all

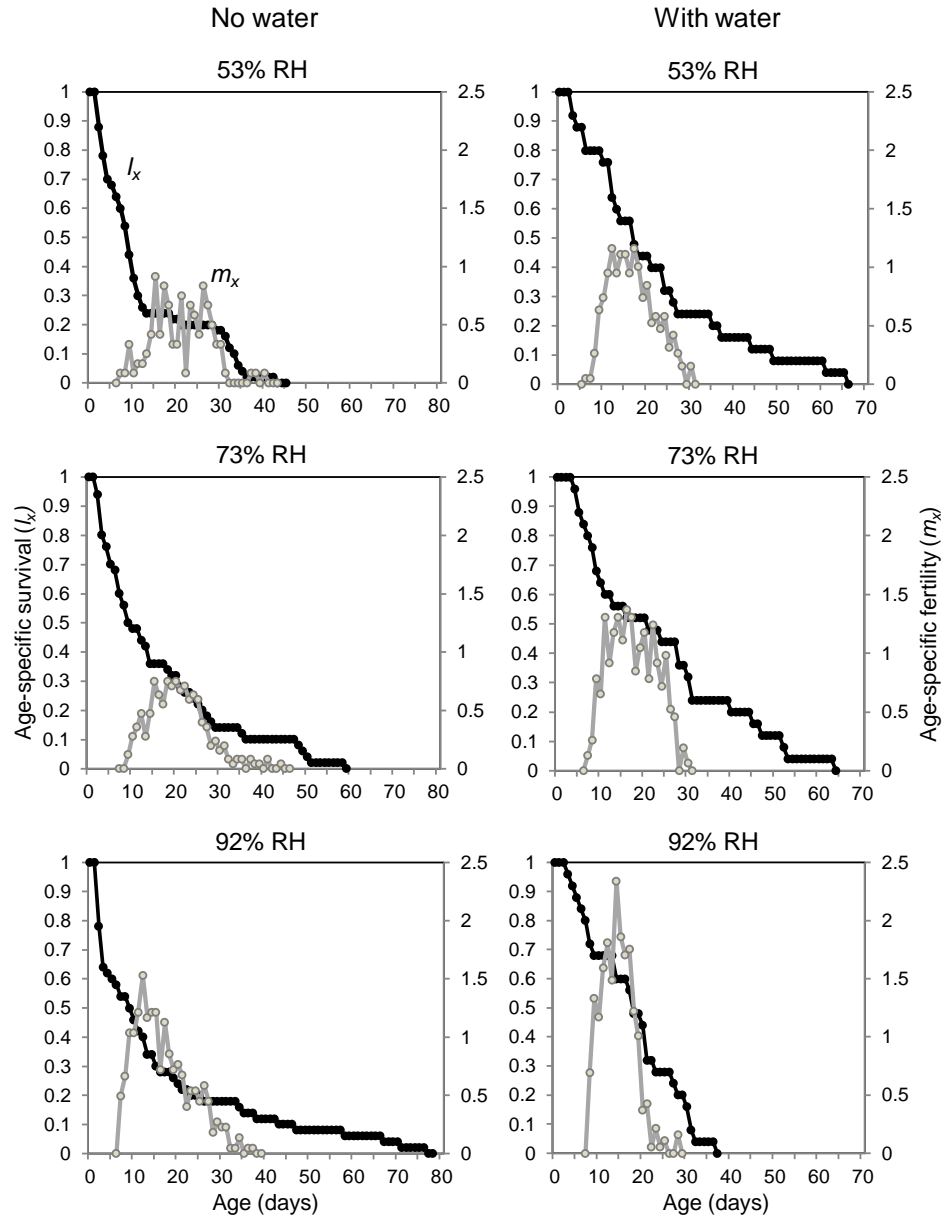pairwise combinations of two factors are compared and shown. Only significant results are presented.

Fig. 3 Age-specific survival (l_x) and age-specific fertility (m_x) of *Amblyseius swirskii* at different levels of relative humidity (RH) and water availability. Black, l_x; gray, m_x.