






Original Article

Life tables of the ladybird beetles *Harmonia axyridis*, *Cycloneda sanguinea* and *Hippodamia convergens* reared on the greenbug *Schizaphis graminum*

Tabelas de vida das joaninhas *Harmonia axyridis*, *Cycloneda sanguinea* e *Hippodamia convergens* alimentadas com o pulgão-verde *Schizaphis graminum*

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Abstract

The Asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) is a biological control agent that also may adversely impact other coccinellid species. Life table parameters were used to assess the population growth potential and the effects of interspecific competition between the invasive lady beetle *H. axyridis* and the native coccinellids *Hippodamia convergens* and *Cycloneda sanguinea* (Coleoptera: Coccinellidae) under laboratory conditions at 25 °C, using *Schizaphis graminum* (Hemiptera: Aphididae) as prey. The effects of the abiotic factors air temperature and humidity on these coccinellids by conducting a survey in a sorghum crop under average conditions of 18.1 °C and 53.5%, respectively, were also assessed. Fecundity was higher in *C. sanguinea* (1021.0 eggs per female) and *H. axyridis* (1029.2 eggs per female) than in *H. convergens* (484.5 eggs per female). The majority of the life table parameters showed no significant differences. The instantaneous rates of population increase (r_m) of *C. sanguinea*, *H. axyridis*, and *H. convergens* were 0.195, 0.198, and 0.194 d⁻¹, respectively. Based on the life table parameters obtained in this study, all three species of Coccinellidae showed a similar capacity to control a *S. graminum* population.

Keywords: aphids, Asian lady beetle, biological control, Coccinellidae, interspecific competition, native species.

Resumo

A joaninha asiática *Harmonia axyridis* (Coleoptera: Coccinellidae) é um agente de controle biológico que pode afetar negativamente outras espécies de coccinélidos. Parâmetros da tabela de vida foram usados para avaliar o potencial de crescimento populacional e os efeitos da competição interespecífica entre o coccinélido exótico *H. axyridis* e os coccinélidos nativos *Hippodamia convergens* e *Cycloneda sanguinea* (Coleoptera: Coccinellidae) em condições de laboratório a 25 °C, usando *Schizaphis graminum* (Hemiptera: Aphididae) como presa. Também foram avaliados os efeitos dos fatores abióticos temperatura e umidade do ar sobre esses coccinélidos por meio de levantamento em uma cultura de sorgo sob condições médias de 18,1 °C e 53,5%, respectivamente. A fecundidade foi maior em *C. sanguinea* (1021,0 ovos por fêmea) e *H. axyridis* (1029,2 ovos por fêmea) do que em *H. convergens* (484,5 ovos por fêmea). A maioria dos parâmetros da tabela de vida não apresentou diferenças significativas. As taxas intrínsecas de aumento (r_m) de *C. sanguinea*, *H. axyridis* e *H. convergens* foram 0,195, 0,198 e 0,194 d⁻¹, respectivamente. Com base nos parâmetros da tabela de vida obtidos neste estudo, as três espécies de Coccinellidae mostraram uma capacidade semelhante de controlar uma população de *S. graminum*.

Palavras-chave: pulgões, joaninha asiática, controle biológico, Coccinellidae, competição interespecífica, espécies nativas.

1. Introduction

Coccinellidae includes natural predators of agricultural pests such as aphids, coccids, whiteflies, psyllids, and mites (Hodek and Evans, 2012). The lady beetles *Hippodamia convergens* (Guérin-Méneville, 1842), *Harmonia axyridis* (Pallas, 1773), and *Cycloneda sanguinea* (L., 1763)

(Coleoptera: Coccinellidae) are placed in the tribe Coccinellini (Milléo and Meira, 2012; Escalona et al., 2017) and are important biological control agents of aphids, a significant concern in crops worldwide (Blackman and Eastop, 2007; Phoofolo et al., 2007; Rocca et al.,

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Received: April 20, 2022 – Accepted: July 6, 2022



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2017). Intraguild predation is related to predation on a heterospecific competitor (Polis et al., 1989). This process is observed among coccinellids, and the interactions involved can decrease the beetles' potential to inhibit the development of aphid populations (Vance-Chalcraft et al., 2007; Grez et al., 2012). However, the defensive capability and larval dispersal observed in coccinellids can inhibit these ecological interactions (Rocca et al., 2017).

Cycloneda sanguinea and *H. convergens* are native to the Americas (Vargas et al., 2013; Rocca et al., 2017). These coccinellids are widely distributed in South America and are abundant in many Brazilian agroecosystems (Sarmiento et al., 2007; Medeiros et al., 2010). *Cycloneda sanguinea* is one of the main aphidophagous native species in Brazil (Martins et al., 2009). The Asian lady beetle *H. axyridis* is native to central and eastern Asia (Zhang et al., 2016). In Brazil, *H. axyridis* was first recorded in 2002 in the state of Paraná, and is currently found in the south, southeast, and midwest regions (Martins et al., 2009; Koch et al., 2011; Ducatti et al., 2020). Climate matching with its native range is an essential factor that probably makes the southern region of South America suitable for *H. axyridis* (Koch et al., 2006). In addition, besides being a strong intraguild predator, *H. axyridis* has certain characteristics such as large size, polyphagous feeding habit, good dispersal ability, short generation time, high immature survival, and high fecundity that contribute to its invasion success (Santos et al., 2009; Hodek and Evans, 2012; Katsanis et al., 2013; Raak-van den Berg et al., 2018).

Indigenous aphidophagous guilds can successfully control invasive aphid species (Michaud, 2002; Colares et al., 2015). Therefore, a strategy for controlling invasive aphids should promote the use of native species of coccinellids before considering introductions of exotic coccinellids, which may pose environmental risks (Michaud, 2002; Lanzoni et al., 2004; Roy et al., 2011). For example, introductions of *H. axyridis* in several countries negatively impacted agroecosystems because this coccinellid acted as a fruit pest and threatened non-target organisms (Koch et al., 2006; Koch and Galvan, 2008; Roy et al., 2011). Several authors (Michaud, 2002; Katsanis et al., 2013; Brown and Roy, 2018) have reported population declines and predation on native coccinellid species by *H. axyridis* in agroecosystems around the world. *Harmonia axyridis* is also associated with displacement of *H. convergens* and *C. sanguinea* in Brazilian agroecosystems (Martins et al., 2009).

Life tables provide information on insect fecundity and survival patterns and are essential tools to study population ecology (Price, 1984). Life table studies of coccinellids also help to recognize the potential consequences of interspecific competition for the effectiveness of these predators as biological control agents (Dixon et al., 1997; Lanzoni et al., 2004). Because records of *H. axyridis* in Brazil are relatively recent, no study has yet used age-specific life tables to compare this predator's population growth with *H. convergens* and *C. sanguinea* fed on green aphids. In the field, aphids are the primary food source for most species of the tribe Coccinellini (Milléo and Meira, 2012; Escalona et al., 2017). Among aphid species, the greenbug, *Schizaphis graminum* (Rondani, 1856) (Hemiptera: Aphididae), is considered an essential food of *H. convergens*,

H. axyridis, and *C. sanguinea*, that is, as a prey, *S. graminum* ensures completion of larval development, low mortality, and high fecundity, among other characteristics of these coccinellids (Michaud and Qureshi, 2006; Phoofolo et al., 2007; Hodek and Evans, 2012). *Schizaphis graminum* is distributed throughout Europe, Asia, Africa, and North and South America and feeds almost exclusively on members of Poaceae, being one of the most important pests of cereal crops (Blackman and Eastop, 2007; Vakhide and Safavi, 2014). In this study, *H. convergens*, *H. axyridis*, and *C. sanguinea* were reared under laboratory conditions on *S. graminum*, with the objective of constructing and comparing life table parameters of these coccinellid species. The study also assessed the effects of abiotic factors on the populations of these coccinellids in a sorghum crop.

2. Material and Methods

2.1. Coccinellid rearing

The experiment was performed in the Laboratório de Ecologia at the Faculdade de Ciências Agrárias e Veterinárias (FCAV), Universidade Estadual Paulista, Jaboticabal, São Paulo, Brazil. The individuals of the coccinellid species and *S. graminum* used in this study were collected from leaves of grain sorghum, *Sorghum bicolor* (L.) Moench (Poaceae). The host-plant species was located in the farm fields (21°14'52"S, 48°16'04"W) of the FCAV. The aphids were kept in 45-cm sections of stalks of the sorghum cultivar BRS 310 in glass containers filled with 300 mL of water and sealed with polyvinyl chloride (PVC) film. The water and sorghum stalks were replaced weekly. Ten pairs of each coccinellid species were placed in cages consisting of 10 × 10-cm PVC tubes, lined on the inside with sulfite paper and sealed with voile mesh. The adult coccinellids were fed daily with eggs of *Ephesia kuehniella* Zeller, 1879 (Lepidoptera: Pyralidae) and a diet composed of brewer's yeast and honey in a ratio of 2:1, according to Santos et al. (2009). All containers were maintained in a climate-controlled room at 25 ± 1 °C and a 12-h photoperiod. Adult coccinellids were sexed according to the morphological characters of females and males described by Kovár (1996).

2.2. Life table studies

Egg development and survival were determined by taking 100 fresh eggs of each coccinellid species from the laboratory breeding stock and maintaining 3–4 egg batches in Petri dishes (9 cm in diameter). To obtain adult coccinellids for the study, 30 newly hatched larvae of each species were transferred to individual Petri dishes (9 cm in diameter) and were monitored until molting to adult stage. Nymphs and adults of *S. graminum* were offered ad libitum to each coccinellid larva. Ten pairs of each species were formed, and each pair was placed in a 350-mL clear plastic cup and fed daily with *S. graminum*. The eggs were counted and removed until the females died. Eggs, larvae, and adults were assessed daily and maintained in a climate-controlled chamber at a constant temperature of 25 ± 1 °C, 12-h photoperiod, and 70 ± 10% relative humidity.

The parameters for the life tables were obtained according to Price (1984), as follows: specific fecundity (m_x) is the number of descendants produced per female at age x and that resulted in females; survival rate (l_x) is the life expectancy to age x , expressed as a fraction of an initial population of one female; net replacement rate ($R_0 = \sum(m_x \cdot l_x)$) is the number of daughters that replace an average female over a generation; mean generation time ($T = \sum(m_x \cdot l_x \cdot x) / \sum(m_x \cdot l_x)$) is the average of the period during which the progeny are produced; instantaneous rate of population increase ($r_m = \ln R_0 / T$); finite rate of population increase ($\lambda = e^{r_m}$); and population doubling time [$DT = \ln(2) / r_m$]. The parameters of the life tables were analyzed using the Jackknife technique (Meyer et al., 1986). The means were compared through the t-test at 5% probability, using the software package Lifetable SAS (Maia et al., 2000).

2.3. Field study

A survey was conducted to determine the relationship between abiotic factors and the populations of *C. sanguinea*, *H. convergens*, and *H. axyridis* in a field of Bolivian giant sorghum AGRI 002E, *S. bicolor*, cultivated in the experimental area of the Instituto Biológico (21°10'26"S, 47°51'04"W), Ribeirão Preto, northeastern São Paulo. The regional climate is considered in the Köppen system as Aw climate, tropical rainy with dry winter (Rolim et al., 2007).

Sorghum was sown on 15 March 2021 in an area of 4 ha, with 0.90-m row spacing and a density of 12 plants/m². No pesticide was applied during the survey. Adult coccinellids were sampled by visual examination, by randomly selecting ten plants in the crop interior. Sampling was done two or three times a week in June and July 2021, totaling ten sampling dates. Exemplars of *H. convergens*, *H. axyridis*, and *C. sanguinea* were collected from the plants and identified according to Kovár (1996). The relationship between temperature and humidity and the coccinellid abundance was examined by means of the Pearson correlation. The analysis was based on the total number of individual coccinellids found on each sampling date. Regarding abiotic factors, the sum of the rainfall intensity (mm) and the means of the maximum and minimum air temperature (°C) and relative humidity (%), recorded in the seven days before the sampling date were used. Data analysis was conducted with SAS (2002) statistical software.

3. Results

3.1. Survival and fecundity

Females of *C. sanguinea* started to lay eggs 3–4 days after emergence, which occurred on day 13 (Figure 1). The oviposition period was observed throughout the entire adult stage and extended from day 18 to 105, with a peak on day 24 (17.6 eggs). During most of this period, the specific fecundity remained constant, and the total fecundity was 1021.0 eggs per female. The adult survival rate gradually declined beginning approximately on day 33, and adults reached maximum survival at day 92.

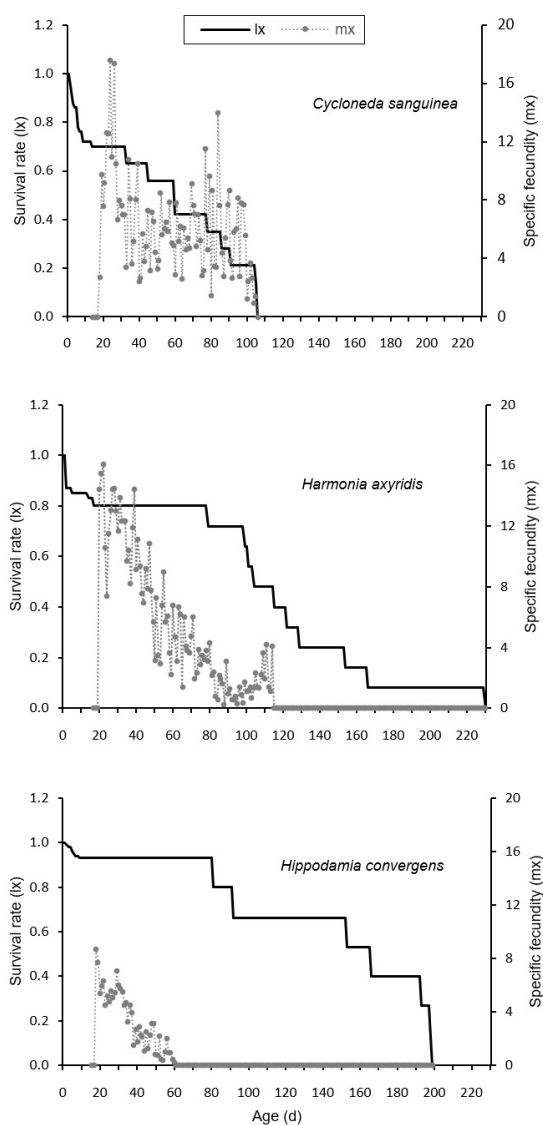


Figure 1. Survival rate (l_x) and specific fecundity (m_x) of three species of Coccinellidae fed on *Schizaphis graminum*.

The oviposition period of *H. axyridis* occurred from day 20 to 114, with a peak on day 22 (16.1 eggs) (Figure 1). Females started laying eggs 3–4 days after emergence (day 17) and maintained until the age of 114 days, reaching a total fecundity of 1029.2 eggs per female. The adult survival rate remained constant until approximately day 78, followed by a gradual decline until day 165, at which point the rate remained stable up to the maximum survival at day 213.

Oviposition of *H. convergens* started 1–2 days after emergence on day 16. The species showed a linear decrease in fecundity from the beginning of the oviposition period to approximately day 60, when the females ceased egg laying, with a total fecundity of 484.5 eggs per female (Figure 1). The oviposition period occurred between the 18th and the 60th day, with a peak of 8.7 eggs per female

at the age of 8 days. Adult survival remained constant up to day 80, decreased until day 92, and then remained constant until day 152. After this period, adult survival decreased linearly and reached a maximum survival of 183 days.

3.2. Life table parameters

The net replacement rate ($R_0 = 401.49$ female offspring) of *H. axyridis* was significantly higher than the $R_0 = 136.31$ female offspring of *H. convergens*; while *C. sanguinea* showed a similar R_0 ($R_0 = 278.24$ female offspring) to both species (Table 1). These values resulted in 1.8 and 2.9 times greater R_0 for *H. axyridis* than *C. sanguinea* and *H. convergens*, respectively. Similar values of mean generation time (T), population doubling time (DT), instantaneous rate of population increase (r_m), and finite rate of population increase (λ) were observed in all three species.

3.3. Field study

The survey carried out revealed greater abundance of *H. axyridis* than *H. convergens* and *C. sanguinea* in the sorghum crop (Table 2). The species of aphid observed infesting sorghum was *Melanaphis sacchari* (Zehntner) (Hemiptera: Aphididae). The correlation analysis indicated a significant positive relationship between the minimum air temperature and the number of individuals of *H. convergens* ($r = 0.71$; $p = 0.02$) and *H. axyridis* ($r = 0.68$; $p = 0.03$); these coccinellids exhibited no significant correlation with the maximum air temperature (Table 2). There was no significant correlation between *C. sanguinea* and the abiotic factors.

4. Discussion

The increase and decrease in the oviposition rate (age-specific fecundity) during the adult periods of *H. axyridis*, *C. sanguinea*, and *H. convergens* followed Omkar and Mishra (2005), who documented the oviposition rate for short- and long-lived female coccinellids. Short-lived coccinellids reproduce uniformly (almost constantly) during their lifetime, as observed for *C. sanguinea* (Figure 1). Milléo et al. (2014) also reported an almost constant oviposition rate for *C. sanguinea* fed on *E. kuehniella* eggs. In contrast, long-lived females show a significant and rapid increase in reproductive activity, followed by progressive lessening, a characteristic shown by *H. axyridis* and *H. convergens*, in this study.

Aphids have features that make them suitable or challenging as prey for coccinellids. Aphid populations often occur in high densities in discrete patches in a crop field and tend to be ephemeral and unpredictable (Kindlmann and Dixon, 1993; Hodek and Evans, 2012). According to the authors, when a prey patch becomes unsuitable for oviposition, a female coccinellid must search for other favorable patches (Kindlmann and Dixon, 1993; Hodek and Evans, 2012). Therefore, aphidophagous predators must have beneficial features that help them to successfully exploit this type of prey. Female coccinellids tend to disperse as a strategy to disperse their eggs widely in the area where they live (Evans, 2003). Although the dynamics of searching behavior of coccinellids is not sufficiently understood (Pervez and Yadav, 2018), the present findings indicated that the almost constant reproductive activity that continues through the entire

Table 1. Estimated laboratory life table parameters for three species of coccinellids fed on *Schizaphis graminum*.

Species	Parameters				
	R_0	T	r_m	λ	DT
<i>C. sanguinea</i>	223.54 ± 33.45ab	27.73 ± 1.92a	0.195 ± 0.01a	1.215 ± 0.02a	3.55 ± 0.27a
<i>H. axyridis</i>	401.49 ± 111.17a	30.18 ± 1.93a	0.198 ± 0.01a	1.219 ± 0.01a	3.48 ± 0.12a
<i>H. convergens</i>	136.31 ± 35.17b	25.26 ± 0.84a	0.194 ± 0.01a	1.214 ± 0.01a	3.56 ± 0.13a

R_0 = net replacement rate (female offspring); T = mean generation time (days); r_m = instantaneous rate of increase (d^{-1}); λ = finite rate of increase (d^{-1}); DT = population doubling time (days). Means followed by the same letter in a column do not differ significantly based on the t-test ($P = 0.05$); ± values are SE.

Table 2. Pearson correlation coefficients (r) for the relationship of coccinellid abundance to temperature and humidity in a sorghum crop.

Abiotic factor	<i>C. sanguinea</i>	<i>H. convergens</i>	<i>H. axyridis</i>
Tmax	- 0.59	0.43	0.36
Tmin	- 0.40	0.71*	0.68*
RHmax	0.35	0.33	0.06
RHmin	0.49	0.57	0.43
Rainfall	Not observed during the survey period		
Total no. individuals	14	17	86
N	10	10	10

*Significant ($P < 0.05$). Tmax, Tmin = maximum and minimum temperature; RHmax, RHmin = maximum and minimum relative humidity; N = number of data pairs.

adult stage of *C. sanguinea* may favor this native coccinellid in distributing eggs throughout its adult life.

In comparison to the fecundity values found for the coccinellids in the current study, Arshad et al. (2020) reported lower values for *H. convergens* fed on the aphids *Aphis gossypii* Glover (251.0 eggs per female) and *Lipaphis erysimi* (Kalt.) (319.7 eggs per female) (Hemiptera: Aphididae). In contrast, higher fecundity was observed for *C. sanguinea* (998.0 eggs per female), *H. axyridis* (4453.5 eggs per female), and *H. convergens* (1189.4 eggs per female) reared on *E. kuehniella* eggs (Milléo et al., 2014) and for *H. axyridis* (1565.7 eggs per female) on pollen and *E. kuehniella* eggs (Zazycki et al., 2015) and *A. gossypii* (1375.79 eggs per female) (Dargazani and Sahragard, 2020). Higher fecundity was also reported for *H. convergens* (729.15 eggs per female) reared on *Aphis craccivora* Koch, 1854 (Hemiptera: Aphididae) (El-Heneidy et al., 2008). The causes of variation in the fecundity of coccinellids are diverse and depend on several factors such as temperature, photoperiod, age of the parents, length of the oviposition period, and quality and quantity of food (Nedvéd and Honěk, 2012; D'Ávila et al., 2016; Lima et al., 2018).

The net replacement rate (R_0) and the population doubling time (DT) of *C. sanguinea*, *H. axyridis*, and *H. convergens* differed from those in earlier studies (Abdel-Salam and Abdel-Baky, 2001; Lanzoni et al., 2004; Milléo et al., 2014; Arshad et al., 2020). Milléo et al. (2014), using a diet consisting of *E. kuehniella* eggs, found higher R_0 values for *H. axyridis* (2226.89 female offspring), *C. sanguinea* (499.0 female offspring), and *H. convergens* (450.15 female offspring) than the values found in this study. The authors reported DTs of 5.73, 4.99, and 4.35 days, respectively, for *C. sanguinea*, *H. axyridis*, and *H. convergens*, which demonstrates that the coccinellids required at least 1.4 times longer than in this study for their populations to double in size. Abdel-Salam and Abdel-Baky (2001) reported R_0 values of 289.11 and 234.96 female offspring and DTs of 4.53 and 5.72 days for *H. axyridis* reared respectively on fresh and frozen eggs of *Sitotroga cerealella* Olivier, 1819 (Lepidoptera: Gelechiidae). Lanzoni et al. (2004) found an R_0 value of 26.27 female offspring for *H. axyridis* reared on the green peach aphid, *Myzus persicae* (Sulzer, 1776) (Hemiptera: Aphididae). Castro-Guedes et al. (2016) reported a similar DT, but a significantly higher R_0 for *H. axyridis* reared on *Brevicoryne brassicae* (L., 1758) ($R_0 = 320.5$ female offspring) and *Cinara atlantica* (Wilson, 1919) ($R_0 = 373.77$ female offspring) (Hemiptera: Aphididae) than on frozen eggs of *E. kuehniella* ($R_0 = 277.43$ female offspring). R_0 values for *H. convergens* differed significantly when the species was reared on *L. erysimi* ($R_0 = 159.85$ female offspring) and *A. gossypii* ($R_0 = 87.85$ female offspring) (Arshad et al., 2020). In addition to fecundity, other biological traits of coccinellids such as survival, longevity, and consequently life table parameters can be affected by the quality and quantity of food (Hodek and Evans, 2012; Nedvéd and Honěk, 2012; Arshad et al., 2020). These potentially influencing factors help to clarify the differences in the values for net replacement rate (R_0) and population doubling time (DT) observed in the above-mentioned studies.

According to Raak-van den Berg et al. (2018), the short generation time (T) characteristically found in *H. axyridis* contributes to its rapid population growth and consequently its invasion success. In the current study, *C. sanguinea* and *H. convergens* showed generation times (T) significantly similar to *H. axyridis*, indicating that the three coccinellids may have comparably short generation times when *S. graminum* is present, improving the effectiveness of these coccinellid species as biological-control agents (Dixon et al., 1997). A low T for *H. convergens* (38.34 d) in comparison to *H. axyridis* (55.49 d) was reported by Milléo et al. (2014).

The instantaneous rate of population increase (r_m) refers to the maximum population growth rate under optimal space, food, and intraspecific influence, and is considered the most useful life table parameter for comparing the growth rates of different populations (Price, 1984). The r_m values found for *C. sanguinea*, *H. convergens*, and *H. axyridis* in this study are higher than those reported in previous studies (Lanzoni et al., 2004; Milléo et al., 2014; Zazycki et al., 2015; Arshad et al., 2020). The high values of r_m shown by these coccinellids here demonstrated that *S. graminum* is a suitable essential prey for them (Hodek and Evans, 2012). Consequently, *C. sanguinea*, *H. axyridis*, and *H. convergens* have good potential for controlling *S. graminum* (Phoofolo et al., 2007). Several species of aphidophagous coccinellids (kept under similar conditions to this study, that is, in the laboratory at 25 °C, but fed on other aphid species than *S. graminum*) showed a lower instantaneous rate of increase (r_m) than those obtained here: *Adalia bipunctata* (L.) ($r_m = 0.081$ d⁻¹; Lanzoni et al., 2004), *Ceratomegilla undecimnotata* Schneider, 1792 ($r_m = 0.142$ d⁻¹), and *Propylea quatuordecimpunctata* (L., 1758) ($r_m = 0.166$ d⁻¹) (Kontodimas et al., 2008), *Hippodamia variegata* (Goeze, 1777) ($r_m = 0.156, 0.181, \text{ and } 0.183$ d⁻¹; Golizadeh and Jafari-Behi, 2012), *Coccinella novemnotata* Herbst, 1793 ($r_m = 0.171$ and 0.184 d⁻¹; Ugine and Losey, 2014), and *Cheilomenes sexmaculata* (F., 1781) ($r_m = 0.166$ d⁻¹; Zhao et al., 2015).

Many factors are thought to contribute to the success of aphidophagous coccinellids in a habitat. Besides climatic conditions (Ameixa et al., 2019), other important factors are microclimate, mainly insolation (Honěk, 1985); type of crop; high plant density; adjacent habitats (Vandereycken et al., 2013); and aphid species (Hodek and Evans, 2012). Among the climatic factors, temperature is the most important because of its strong influence on the development, survival, and distribution of insects (Messenger, 1959; Campbell et al., 1974; Omkar and Pervez, 2016). *Hippodamia convergens* and *H. axyridis* are warm-adapted species (Nedvéd and Honěk, 2012). Also, the thermal requirements of *H. axyridis* are comparable to those of *H. convergens* in warm temperatures (Miller, 1992; LaMana and Miller, 1998), which indicates that both of these coccinellids can potentially survive under similar thermal environmental conditions (Messenger, 1959; Campbell et al., 1974; LaMana and Miller, 1998; Jarošík et al., 2015). The results of the coccinellid survey conducted in northeastern São Paulo support this supposition. The correlation analysis in the study demonstrated that *H. convergens* and *H. axyridis* both increased in abundance when the minimum air

temperature was higher, and that these coccinellids were not affected by the maximum air temperature. This information suggests that *H. convergens* and *H. axyridis* can survive under similar thermal environmental conditions, as previously reported.

Knowledge of the biological traits of coccinellids is necessary to evaluate the potential rate of population increase. These attributes also enable us to estimate the potential for competition among these predators and to estimate the success of an invasive species (Lanzoni et al., 2004; Raak-van den Berg et al., 2018). The present study revealed that *H. convergens*, *H. axyridis*, and *C. sanguinea* have similar life table traits when fed on *S. graminum*. Based on their instantaneous rates of population increase (r_m), all three species of Coccinellidae have the potential to act as biological-control agents of *S. graminum*. *Harmonia axyridis* showed high fecundity and a net replacement rate (R_0) significantly higher than the values recorded for *H. convergens* and similar to those for *C. sanguinea*. These biological traits, together with those previously described, such as large size, and good dispersal ability, among others (Santos et al., 2009; Hodek and Evans, 2012; Katsanis et al., 2013; Raak-van den Berg et al., 2018), may contribute to the invasion success of *H. axyridis*. *Cycloneda sanguinea* is less sensitive to minimum temperature changes than *H. convergens* and *H. axyridis*, and the pattern of its oviposition rate may provide this native coccinellid with a potential advantage in distributing its eggs throughout its adult life.

Acknowledgements

We are grateful to Professor José C. Barbosa for his assistance with statistical analyses. We also thank the Fundação de Amparo à Pesquisa do Estado de São Paulo for financial support (grant 2007/07348-1) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico for providing a scholarship to the second author (grant 301735/2012-3).

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