Temperature-dependent development of three parasitoids of the leafminer fly *Liriomyza huidobrensis*

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Abstract

Leafminers flies (Diptera: Agromyzidae) are important pests in Peruvian highlands and coastal vegetable cropping systems, where more than 60 hymenoptera parasitoids constitute a natural source of biological control. The parasitoid *Chrysocharis flacilla* (Eulophidae) has the highest abundance in the southern part of the Peruvian coast while *Phaedrotoma scabriventris* (Braconidae) is the major parasitoid in the highlands. *Halticoptera arduine* (Pteromalidae) occurs in both agroecologies at high numbers. Temperature-dependent development of the three parasitoids was assessed to understand the comparative advantage of each species as biocontrol agent in different agro-climates. Biological development parameters were studied at five constant temperatures (10, 15, 20, 25, 30°C) in their main host *Liriomyza huidobrensis.* At 10ºC no development occurred in all three species. Above 15ºC, development time decreased with increasing temperature in all parasitoid species. *H. arduine* was the less tolerant to high temperature (30°C). Fertility of *P. scabriventris* decreased with increasing temperatures. In contrast, the fertility of *C. flacilla* increased with increasing temperature, but no progenies were observed at 10ºC. *H. arduine* did not follow a clear trend with respect to temperature. The temperature strongly influenced the proportion of males and females in the progenies off all species. The analyses of developmental time, fertility and progeny sex ratios suggest that *P. scabriventris, H. arduine* and *C. flacilla* have their optimum temperature between 15 to 20ºC, at 20ºC, and between 25 to 30ºC, respectively. The results clearly demonstrate the adaptation of the three species to different agro-climates and indicate their potential as biocontrol agents under specific temperature conditions.

Keywords: Biological control, integrated pest management, Halticoptera arduine, Phaedrotoma scabriventris, Chrysocharis flacilla.

Introduction

The pea leafminer *Liromyza huidobrensis* Blanchard (Diptera: Agromyzidae) is a highly polyphagous leafminer capable of inflicting severe damage to field and horticultural crops. Originating in the New World, it has been globally distributed with the worldwide trade of vegetables and ornamentals (Shepard *et al.*, 1998; Rauf *et al.*, 2000). The leafminer fly has developed resistance to insecticides and biological control using parasitoids is suggested as an important management option (Johnson *et al.,* 1980; Parrella *et al.,* 1984).

Liriomyza species are known to have many natural enemies, particularly in the regions of origin in the New World (Murphy and LaSalle, 1999; Waterhouse and Norris, 1987). Noyes (2004) listed over 300 species of agromyzid parasitoids, and over 80 species that are known to attack various *Liriomyza* species. Mujica and Kroschel (2008) observed in the central coast of Peru a rich complex of 63 species of parasitoids, with the endoparasitoids *Halticoptera arduine* (Walter) (Pteromalidae) (48.2%) and *Chrysocharis flacilla* Walker (Eulophidae) (19.5%) as the most important species. On the other hand, in the central highlands of Peru at altitudes of about 3300 m, *Phaedrotoma scabriventri*s Nixon (Braconidae) has been described as an important parasitoid reaching a mean parasitism rate of 32.6% of *L. huidobrensis* in faba bean (*Vicia faba* L.) (unpublished data). All three parasitoids are also reported as primary parasitoids of agromyzid leafminers in a wide range of leafminer fly host plants in the Neotropics. Further, they are adapted to different agroecological zones between 0 to 4000 m asl and are important parasitoids of *L. huidobrensis* in natural, urban and agricultural systems (Hansson 1987, De Santis 1983, Neder de Roman and Arce de Hamity 1986, Salvo et al. 2005, Mujica and Kroschel 2007).

The high abundance of the three parasitoids *H. arduine*, *C. flacilla* and *P. scabriventri*s in different agroecologies of Peru as well as their wide host plant and leafminer fly adaptation indicate their high potential to be used as biocontrol agents in classical biocontrol programs of *L. huidobrensis* in other parts of the world (Mujica and Kroschel 2008). To better understand their optimum temperature requirements and their potential use in different agro-climates the objectives of this comparative study was to investigate the temperature-dependent development and reproduction potential of the three species in a wide range of temperatures.

Materials and methods

Insect origin and rearing conditions.- Laboratory cultures of the parasitoids *H. arduine* and *C. flacilla* were established from individuals reared from *L. huidobrensis* infested potato (*Solanum tuberosum* L.) leaves collected in the Cañete valley, Lima at an altitude of 50 m. *Phaedrotoma scabriventris* was obtained from *L huidobrensis* infested faba beans (*Vicia faba* L.) in Huancayo, Junin, at 3300 m. Rearing of the parasitoids was carried out using the host *L. huidobrensis* and faba bean as the host plant, respectively. For culture maintenance and experimental studies, late second to early third instar larvae of *L. huidobrensis* and 30-day old faba bean plants were used. Leafminer fly and parasitoid cultures were maintained at a temperature of 20ºC at a photoregime of 12:12 (L:D).

Influence of temperature on immature development.- Six *L. huidobrensis*-infested faba bean plants were placed in a wooden rearing cage (45 x 30 x 25 cm) and exposed to 50 mated parasitoid females for 12 hours at 20ºC. Afterwards, leaves were cut at the petiole base and placed in 1-liter plastic containers, which were transferred to incubators of five constant temperatures (10, 15, 20, 25 and 30ºC). Leaves were preserved until leafminer larvae emerged and pupated. Leafminer pupae were monitored daily until the emergence of adults. For *H. arduine* supplementary experiments were carried out at 18ºC.

Influence of temperature on progeny development (fertility).- For these experiments 1-liter transparent plastic cylinders (15 cm high, 7 cm wide) were used, which had a 5 cm diameter hole closed with nylon gauze on top for ventilation. Four faba bean leaves containing about 40-50 *L. huidobrensis* late second to early third-instar larvae were placed in one 50 ml glass vial filled with water and covered with the plastic cylinders. A set of 20 pairs of newly emerged male and female parasitoids of each species were transferred individually into the plastic cylinders, which were stored in incubators at temperatures of 10, 15, 20, 25 and 30ºC. The parasitoids had access to a honey solution, which was dropped onto the nylon gauze. After 24 hours, leaves were replaced by new *L. huidobrensis* infested leaves, which procedure was repeated daily until the female parasitoids had died. Removed leaves were stored in Petri dishes (9 cm diameter) at 20ºC until leafminer fly pupation. Then, pupae were removed from leaves and after hatching number and sex of parasitoid species recorded. Female parasitoids that died before day 1 or did not produce any offspring were excluded from the analysis.

Statistical analysis.- Data from immature and progeny development were analyzed with one-way analysis of variance, and means were separated with Kruskal-Wallis test at $P \leq 0.05$ or $P \leq 0.02$. Linear regression analysis was applied to determine temperature-dependent development rate (D), where D=1/d, with d being the time in days for parasitoids to complete development until the adult stage. Also, linear regression analysis calculated the lower threshold temperature for development (T_{min}).

Results

Influence of temperature on immature development.- At 10ºC no development occurred in all three parasitoids. Above 15ºC, the development time decreased with increasing temperature in all parasitoid species (Table 1). *H. arduine* successfully completed development in the temperature range of 15 to 25ºC. This species was least tolerant to high temperatures and no development occurred at 30ºC. Across all temperatures tested, development at 25ºC was significantly faster ($P \leq 0.001$). For *P. scabriventris,* developmental time ranged between 12 days at 30ºC to 31.9 days at 15ºC ($P \leq 0.001$). The total developmental time for *C. flacilla* ranged between 22.3 days at 30ºC to 29.73 days at 15ºC. A mean decrease of 18.1, 6.5 and 2.5 days in the developmental time for each 5ºC increase in temperature was calculated for *H. arduine P. scabriventris* and *C. flacilla,* respectively. The theoretical development threshold (T_{min}) was lowest for *P. scabriventris* (6.18ºC) and highest for *C. flacilla* (9.63ºC) (Table 2).

Table 1. Total development time (in days, from egg to adult) of *Halticoptera arduine*, *Phaedrotoma scabriventris* and *Chrysocharis flacilla* in larvae of *Liriomyza huidobrensis* at different constant temperatures

Temperature (ºC)	*H. arduine*		*P. scabriventris*		*C. flacilla*	
	n	Mean[a] ± SE	n	Mean ± SE	n	Mean ± SE
10		All died[b]		All died	7	All died
15	10	55.90 a ± 0.48	50	31.92 a ± 0.27	26	29.73 a ± 1.36
18	32	31.66 b ± 0.38		-----[c]		-----
20	30	30.30 b ± 0.31	50	21.60 b ± 0.21	31	27.68 a ± 0.65
25	37	19.81 c ± 0.13	50	16.46 c ± 0.23	50	25.18 b ± 0.47
30		All died	50	12.04 d ± 0.19	50	22.34 c ± 0.43

[a] Means in the same column followed by same letter are not significantly different at P • 0.05
[b] All died prior to adult emergence
[c] No data available

Table 2. Estimated parameters of the linear model fitted to median development rate (1/day) for immature life-stages of *Halticoptera arduine*, *Phaedrotoma scabriventris* and *Chrysocharis flacilla*

Parasitoid species	Regression equation	R^2	T_{min} (ºC)
H. arduine	Y = 0.0031x - 0.028	0.9742	9.03
P. scabriventris	Y = 0.0034x - 0.021	0.9884	6.18
C. flacilla	Y = 0.0074x - 0.071	0.7102	9.63

Influence of temperature on progeny and sex ratio.- The fertility of the three parasitoid species was significantly affected by temperature (Table 3). The parasitoid *H. arduine* showed a high variability in the progeny development with regard to temperature. Lowest development was observed at 10° and 30° C with 40.3 and 31.8 progenies per female, respectively. In contrast, most progenies developed at 15° and 30° C, with 60.4 and 75.6 progenies per female.

P. scabriventris developed lowest numbers of progenies at 10°C (36.2 progenies female) and highest at 15°C (151.2 progenies per female); at temperatures above 15° C the progeny development decreased gradually, but did not differ significantly at 20°C (122.9±4 progenies per female). At 25° C and 30°C, 85.2 and 81.4 progeny/female were produced, respectively. Compared to *P. scabriventris, C. flacilla* had a lower rate of progenies at all temperatures. At 10ºC, no progenies developed, but with increasing temperature from 15° to 30°C progeny production increased significantly from 13.2 to 47.5 progenies per female.

Generally in all three species, the progeny production per female and day increased with increasing temperature. The optimal temperature for progeny production, defined as the temperature at which the fertility rate is highest, was 30ºC for *P. scabriventris* and *C. flacilla* with 6.0 and 3.2 progenies per female respectively and 25ºC for *H. arduine* with 1.9 progenies. In the case of age-specific fertility, most offspring were produced during the first eight days at 20, 25 and 30ºC for all three parasitoid species. The highest peak of progeny development was reached at 30ºC for *P. scabriventris* (12.4 progenies at day 3), at 25ºC for *H. arduine* (6.5 progenies at day 2), and at 20ºC for *C. flacilla* (13.8 progenies at day 1). As the temperature decreased the number of days to reach the peak of progeny development increased for *P. scabriventris* and *H. arduine*. However, this trend was not observed in *C. flacilla,* in which species the progeny emergency peak occurred at all temperatures between the first and second day.

Table 3. Fertility, progeny rate, peak of progeny production and sex ratio of *Halticoptera arduine*, *Phaedrotoma scabriventris* and *Chrysocharis flacilla* at five constant temperatures

Species /Temperatures	n	Fertility (progenies/female)	Progeny rate (progenies/female/day)	Peak of progeny production		Sex ratio (Female: Male)
				Progeny	Day	
H. arduine						
10	10	40.3 b ± 9.5	0.4	2.7	39	0.18:1
15	10	60.4 a ± 12.7	0.7	3.9	19	0.05:1
20	10	39.4 b ± 8.0	0.9	4.3	8	0.95:1
25	10	75.6 a ± 13.4	1.9	6.5	7	0.08:1
30	10	31.8 c + 5.9	1.6	4.7	7	0.21:1
P. scabriventris						
10	30	36.2 c ± 5.5	0.4	1.6	20	0.66:1
15	30	151.2 a± 14.6	3.4	9.1	10	0.76:1
20	30	122.9 a ± 3.4	4.6	7.9	6	1:1
25	30	85.2 b ± 4.4	4.3	8.1	5	1.18:1
30	30	81.4 b ± 7.3	6.0	12.4	3	1.31:1
C. flacilla						
10	32	------[b]	------	-----	-----	-----
15	33	13.18 b ± 1.5	0.3	2.0	1	434:1
20	31	36.51 a ± 3.1	1.2	13.8	1	188.7:1
25	35	43.34 a ± 4.6	2.3	6.8	1	59.7:1
30	31	47.52 a ± 8.5	3.2	10.0	2	7.7:1

[a] Means in the same column followed by same letter are not significantly different at P• 0.05
[b] No offspring developed

In all three parasitoids, the sex ratio was highly affected by temperature, but most in *C. flacilla and H. arduine* (Table 3, Fig. 1). For *P. scabriventris,* female progeny increased with increasing temperature with a female:male sex ration of 0.66:1 at 10ºC and 1.31:1 at 30ºC, respectively. A balanced sex ratio of 1:1 was registered at 20ºC. In all temperatures, *C. flacilla* has a much higher proportion of females; interestingly, at low temperatures at 15ºC a female:male proportion of 434:1 was recorded. In *H. arduine*, male progenies dominated in all temperatures. Only at 20ºC, an almost balanced female:male sex ratio of 0.96:1 was observed.

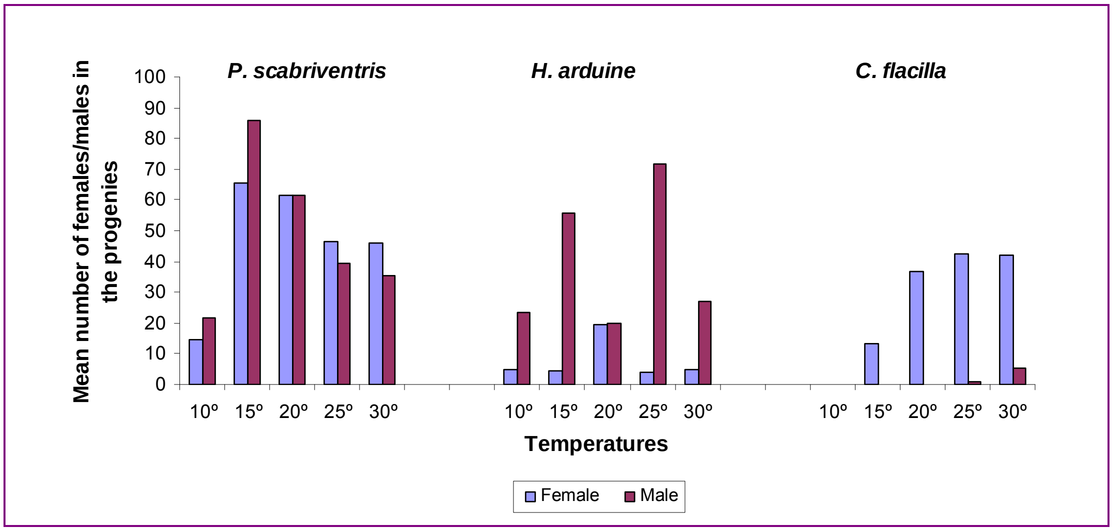

Figure1. Mean number of males and females in the progenies of the parasitoids *Phaedrotoma scabriventris, Halticoptera arduine* and *Chrysocharis flacilla* developed at different constant temperatures

Discussion

An overall good understanding of the temperature requirements of natural enemies is important for classical biocontrol programs in order to select the best potential candidates for the target regions under consideration. *Halticoptera arduine*, *Phaedrotoma scabriventris* and *Chrysocharis flacilla* are important leafminer fly parasitoids and are predominating in different agroecologies of Peru and South America.

Our temperature studies were carried out between 10 to 30ºC, and not surprisingly the developmental time of all three parasitoid species decreased with increasing temperature. This is a common phenomenon in insects and not only in parasitoids that immature development time is directly dependent on temperature, with much shorter durations at higher temperatures (Jervis *et al*., 2005). Similar trends have been observed in other leafminer fly parasitoids like *Chrysocharis pentheus* (Walker) (Hondo *et al.* 2006), *C. pubicornis* (Zeltersted) (Baeza *et al.* 2007), *C. parski* (Crawford) (Christie and Parrella, 1987), *Diglyphus isaea* (Walker) (Bazzocchi *et al.* 2003) and *Ganaspidium utilis* Beardsley (Lopez *et al*., 2005).

A theoretical minimum threshold of development of 6.18ºC could be established for *P. scabriventris,* which is among the parasitoids investigated in the study the most tolerant species to low temperature. This is also reflected in its native distribution and higher abundance and efficacy at higher altitudes in the Andes compared to *H. arduine* and *C. flacilla*. In contrast, our studies showed that the development time of *C. flacilla* is less dependent on temperature.

A short development time relative to its host is considered a desirable attribute for the selection of parasitoids (Jervis *et al*., 2005). For its immature development *L. huidobrensis* needs 43.6, 22.5 and 16.1 days at 15ºC, 20ºC and 25ºC on beans (*Phaseolus vulgaris* L.); and at 30ºC no adults develop from pupae (Lanzoni *et al.* 2002). Thus, our study could illustrate that *P. scabriventris* needs much shorter periods of development especially at low temperatures (15ºC: 31.9 days; 20ºC: 21.6 days) to complete its development compared to the leafminer fly.

Fertility varied between the species and *P. scabriventris* and *H. arduine* produced progenies in the temperature range from 10 to 30ºC; in contrast *C. flacilla* developed no progenies at 10ºC. For *P. scabriventris* and *H. arduine,* the optimum temperature for oviposition is between 15 and 20°C, and for *C. flacilla* between 20 to 30ºC. This difference among species is a common pattern in the relationship between temperature and the fertility of parasitoids (van Lenteran *et al.,* 1987), and is consistent with the general assumption that insects cannot mature their eggs or are unable to oviposit outside their tolerable temperature range (Greenfield and Karandinos, 1976).

From our results we can derive that the maximum tolerable temperature for *C. flacilla* is even above the temperatures tested in our study.

For *H. arduine* and *P. scabriventris* we found a female:male sex ratio of 1:1 at 20°C. The proportion of females of *H. arduine* was significantly lower at temperatures below and above the optimum temperature of 20°C. Similar responses to temperature were observed for *Opius* dissitus Muesebeck (Bordat *et al.,* 1995). Instead, Lopez *et al.* (2004) found that *Halticoptera circulus* (Walker) produced higher male progenies at 26ºC. The parasitoid *P. scabriventris* produced more females at temperatures higher than 25ºC. According to Denlinger and Yocum (1998) this behavior is a response to extreme temperature conditions; the stress for females is higher and mating may fail which would lead to a smaller female population in the next generation. The majority of parasitoids of the order Hymenoptera have a facultative parthenogenesis of an arrenotokia type (De Bach, 1985) as it is the case in *H. arduine* and *P. scabriventris*. Progenies composed of male recombinants allow for a better phenotypic adaptation to changing environmental conditions (Moreno, 1982). In *C. flacilla,* the female proportion was about 330% to 60% higher at temperature of 15 to 25ºC. Thus, one female of *C. flacilla* can produce more female progenies than the other two parasitoids at similar temperatures. In this respect, Abe and Tahara (2003) pointed out that parasitoids of an thelytokus type have advantages over the arrhenotokia type in mass rearing, because they do not "waste" expensive hosts for the production of males.

Duale (2005) considered that survival, growth and population development of parasitoids depend not only on the oviposition rate or fecundity, but to a greater extent on the appropriate environment, which mostly limits and affects the geographical distribution of parasitoids. Viable parasitoids of *H. arduine, P. scabriventris* and *C. flacilla* did not further develop in leafminer fly larvae at 10ºC, and in the case of *H. arduine* also not at 30ºC. Taking into account the strong temperature-dependent sex ratio in our parasitoids studied, the optimal temperatures for development of *P. scabriventris, H. arduine* and *C. flacilla* are between 15-20ºC, 20ºC and 25ºC.

Conclusion

The present study identified the optimal temperature range for the development and fertility of the leafminer fly parasitoids *H. arduine, P. scabriventris* and *C. flacilla*. The analysis of complementary life-table parameters such as net reproductive rate, intrinsic rate of increase, mean generation time, etc. will follow and allow to model the potential population growth and development in different agro-climates.

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