Effect of *Maruca vitrata* (Lepidoptera: Crambidae) host plants on life-history parameters of the parasitoid *Apanteles taragamae* (Hymenoptera: Braconidae)

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Abstract

The effect of four host plant species of the herbivore *Maruca vitrata* Fabricius (Lepidoptera: Crambidae) on development time, longevity, fecundity and sex ratio of the parasitoid *Apanteles taragamae* Viereck (Hymenoptera: Braconidae) was investigated under laboratory conditions. The larvae were parasitized when in the second instar. *Maruca vitrata* larvae were fed with flowers of four legumes, i.e. *Vigna unguiculata (*cowpea), *Sesbania rostrata, Lonchocarpus sericeus* and *Pterocarpus santalinoides,* or an artificial diet both before and after parasitization. Experiments were carried out at 25.5 ± 0.3 ℃ and 28.7 ± 0.6 ℃. The parasitoid did not develop in hosts feeding on *L. sericeus, V. unguiculata* at 25 ℃, on *P. santalinoides* at 25 or 29 ℃. *Apanteles taragamae* had the shortest development time on artificial diet at both 25 and 29 °C while the longest development time was on *L. sericeus* at 29 °C. Female wasps took longer to develop compared to males at the two temperatures, regardless of the feeding substrate of their host. The longevity of the wasps at 25 ℃ varied among feeding substrates, but not at 29 ℃. Survival rate of parasitized larvae depends on the feeding substrate. Moreover, of host larvae with *Maruca vitrata* multi-nucleopolyhedrovirus (*Mavi*MNPV) killed larger proportions of wasps at 25 than at 29 ℃, which was likely caused by the difference in parasitoid developmental rate. The proportion of female parasitoids was the lowest on *L. sericeus*. The daily fecundity showed a nonlinear trend regardless of the feeding substrate, indicating that *A. taragamae* is a pro-ovigenic species. The data support the slow growth-high mortality hypothesis.

1 Introduction

Maruca vitrata Fabricius (Lepidoptera: Crambidae) is one of the most ravaging insect pests of cowpea, *Vigna unguiculata* (L.) Walp. (Taylor, 1978; Sharma, 1998). Damage by *M. vitrata* to cowpea is made by its larvae feeding on flower buds, flowers and pods. The crambid develops without diapause and relies on alternate host plants to maintain its population during the cowpea off-season (Taylor, 1978; Bottenberg et al., 1997; Atachi et al., 2002; Arodokoun et al., 2003). Over 50 alternative host plant species have been recorded for *M. vitrata* (Taylor, 1978; Sharma, 1998; Arodokoun et al., 2003). Of these, *Pterocarpus santalinoides*, *Pueraria phaseoloides* and *Centrosema pubescens* play an important role during the long dry season, *Lonchocarpus sericeus* and *L. cyanescens* during the main rainy season and *Tephrosia platycarpa* during the short rainy season (Atachi et al., 2002; Arodokoun et al., 2003). Thus, these host plants constitute a source of *M. vitrata* carry-over. Therefore, an efficient method to control *M. vitrata* should target not only the main cultivated host plant (cowpea) but also the alternative one. With regard to this, biological control should be considered. Several parasitoid species have been recorded to attack *M. vitrata* larvae (Taylor, 1967; Okeyo-Owuor et al., 1991; Tamò et al., 1997; Huang et al., 2003; Arodokoun et al., 2006). Among these, *Apanteles taragamae* Viereck (Hymenoptera, Braconidae) seems to be a promising candidate for classical biological control in Africa (Srinivasan et al., 2009).

Apanteles taragamae is a solitary larval endoparasitoid of the legume pod borer *M. vitrata*. It parasitizes on average 63 % of *M. vitrata* larvae on *Sesbania cannabina* (Retz) (Huang et al., 2003). This parasitoid has been introduced from the World Vegetable Center (AVRDC) in Taiwan to the Benin research station of the International Institute of Tropical Agriculture (IITA) following standard importation procedures for evaluating its potential as a biological control candidate (FAO, 1997).

The development of koinobiont parasitoids such as *A. taragamae* depends on the host quality (Krusse and Raffa, 1999; Dicke, 1999a; Eben et al., 2000; Lill et al., 2002, Uçkan and Ergin, 2002; Harvey, 2005; Gols and Harvey, 2009). These parasitoids develop in hosts that continue to feed and grow (Brodeur and Boivin, 2004). The nutritional quality of a host plant directly affects the biology of herbivorous insects and can influence that of their natural enemies and subsequent trophic levels (Benrey et al.,

1998; Uçkan and Ergin, 2002; Bukovinszky et al., 2008; Gols and Harvey, 2009). The interactions between variation in host plant quality and risk of attack by natural enemies of herbivorous insects have been formalized into the slow-growth, high-mortality hypothesis (Clancy and Price, 1987). Herbivores feeding on plants of low nutritional quality do not necessarily increase damage if their development time is prolonged (slow-growing), because they are longer vulnerable to natural enemy attack (Clancy and Price, 1987; Benrey and Denno, 1997). This hypothesis is yet to be verified for fast-growing herbivorous insects which are reportedly vulnerable to parasitism (Clancy and Price, 1987; Loader and Damman, 1991; Williams, 1999). Moreover, the quality of a host plant can also affect parasitoid development via their herbivorous insect host (Gols and Harvey, 2009). For instance, pigeonpea plants which provide suboptimal nutritional quality (when compared with cowpea and chickpea) to *Callosobruchus maculatus* (Fabricius), led to slower development and higher mortality of *Uscana lariophaga* Steffan, an egg parasitoid of *C. maculatus* (van Huis and de Rooy, 1998).

In this study, we assessed the influence of flowers of four key host plants of *M. vitrata* on the development of *A. taragamae* at different temperatures.

2 Materials and Methods

2.1 Plant materials

Flowers of *S. rostrata, V. unguiculata*, *P. santalinoides,* and *L. sericeus* were used in this study. Flowers of *S. rostrata* and *V. unguiculata* were collected in fields at the International Institute of Tropical Agriculture in Benin, while flowers of the wild host plants *P. santalinoides,* and *L. sericeus* were sampled at Agongue and Sehoue, 70 km East and 90 km North of Cotonou, respectively.

2.2 Insect species

2.2.1 *Maruca vitrata*

Pupae of *M. vitrata* obtained from a stock culture (kept for 50 generations) in the laboratory at the IITA in Benin were placed in open Petri dishes. They were incubated in wooden cages (44 x 45 x 58 cm) with sleeves, having sides of fine mesh and a glass

top, at 27.0 ± 0.6 °C and 60.9 ± 4.6 % relative humidity. Emerging adults were fed using cotton fibres moistened with 10% glucose solution. Four-days-old female moths were transferred in groups of 4 or 5 individuals to transparent cylindrical plastic cups (3 cm diameter x 3.5 cm height) and kept for 24 h to allow for oviposition, which occurred on the inner surface of the cups. Ovipositing females were fed using small pieces of filter paper moistened with 10% glucose solution, which were replaced every 24 h. Cups carrying eggs were kept at the same experimental conditions until the larvae hatched. Larvae were transferred to large cylindrical plastic containers (9 cm diameter x 12 cm height) provided with artificial diet prepared according to Jackai and Raulston (1988), and reared until pupation. Pupae were collected and placed in cages until adult emergence. Eggs used in the experiments were obtained from this mass production.

2.2.2 *Apanteles taragamae*

Cocoons of the parasitoid *A. taragamae* obtained from the stock culture at IITA in Benin were kept in plastic cylindrical cups (4.5 cm diameter x 5 cm height) till adult emergence. A hole (2 cm diameter) punched in the lid of the cups was covered with fine mesh. Adults of *A. taragamae* were fed with honey streaked on the fine mesh of the lid. To allow mated female wasps to parasitize hosts in 24 h, they were offered, two-days-old larvae of *M. vitrata* in a small cylindrical cup (3 cm diameter x 3.5 cm height) containing a piece of the artificial diet. The exposed larvae were reared until cocoon stage. Cocoons were collected and placed in cylindrical cups (4.5 cm diameter x 5 cm height). The mass production of wasps took place in a climate chamber with a temperature of 25.3 ± 0.5 °C (mean ± SD) and a relative humidity of 78.9 ± 5.6 % (mean ± SD).

2.3 Influence of *M. vitrata* host plants on development time, longevity, sex ratio and fecundity of the parasitoid *A. taragamae*

Cups (3 cm diameter x 3.5 cm height) carrying eggs of *M. vitrata* were kept at 25 °C until the larvae hatched. Three flowers of *P. santalinoides, V. unguiculata, S. rostrata, L. sericeus,* or pieces of artificial diet were put in cups containing newly hatched larvae. Flowers of *S. rostrata, L. sericeus* and *P. santalinoides* were carried by a raceme while that of *V. unguiculata* were not. Larvae were submitted to parasitization

by *A. taragamae* when the larvae were two days old. Parasitized larvae were individually transferred to cups (3 cm diameter x 3.5 cm height) and reared at 25.3 ± 0.5 (25) ℃ with 78.9 ± 5.6 % relative humidity and 28.7 ± 0.6 (29) ℃ with 68.1 ± 5.1 % relative humidity using each of the different feeding substrates until they had developed into the cocoon stage. Flowers were daily replaced with new flowers. Cocoons were kept until adult emergence. The numbers of dead larvae, cocoons and emerged adults were recorded. Emerging females were coupled with males of the same age for each feeding substrate to allow mating. Twenty to thirty two-day-old larvae were exposed to each couple of wasps daily until the females died. These larvae were fed on artificial diet. The number of cocoons that developed successfully was recorded for each feeding substrate. In total 200-250 parasitized larvae were reared using each of the feeding substrates at 25 and 29 ℃. Larval mortality was recorded daily. The number of larvae that were killed by *Maruca vitrata* Multi-Nucleopolyhedrovirus (*Mavi*MNPV) was recorded at both temperatures for each feeding substrate. The virus *Mavi*MNPV was reported to infect all larval stages of *M. vitrata* (Lee et al., 2007). Infected larvae were sluggish and pinkish and died within 3 to 4 days following the first contact with the virus. The parasitoid wasp *A. taragamae* was found to acquire and transmit *Mavi*MNPV to healthy *M. vitrata* larvae (Srinivasan et al., 2009).

In parallel, 200 parasitized and non-parasitized larvae were rearing on each feeding diet for 7 days at 25 and 29 ℃. The number of dead larvae was daily recorded.

The life-table parameters of the wasps for each feeding substrate were calculated at 25 and 29 ℃. They are defined according to Birch (1948):

The net reproductive rate (R_0), which is the number of female progeny per female per generation. It is given by the formula:

where:

x is the pivotal age of individuals in days

l_x is the age-specific survival as proportion of individuals still alive at age x

m_x is the age-specific fecundity as female offspring per female.

The intrinsic rate of increase (r_m), given by the formula:

$$1 = \sum l_x m_x e^{-r_m x}$$

where **e** is the base of natural logarithm (ln).

The mean generation time (T), calculated as follows:

$$T = \ln(R_0)/r_m \quad \text{and by approximation} \quad T = (\sum x l_x m_x)/\sum l_x m_x$$

The doubling time T_2 is therefore:

$$T_2 = \ln(2)/r_m$$

The finite rate of increase (λ), expressed as the multiplication per female per unit time:

$$\lambda = e^{r_m}$$

The intrinsic rate of increase, r_m, was calculated using the Jackknife technique (Maia et al., 2000). All these life-table parameters were computed using the SAS program developed by Maia et al. (2000).

3 Statistical analysis

The effects of the different feeding substrates on the development time, longevity and fecundity of *A. taragamae*, were compared using a t-test at 25 °C and the General Linear Model (GLM) procedure of SAS followed by the Turkey-test in the case of significant differences between substrates at 29 °C. The comparison between males and females for the longevity and life cycle was done with a paired t-test. Data on sex ratio were analyzed by using the χ^2 test. Thus, a 2 x 2 or 2 x 4 contingency table based on the chi-square was used to test differences between feeding substrates at 25 °C or 29 °C. Percentage larval survival rate (p) was arcsine $\sqrt{}$ (p/100) transformed prior to the analysis of variance followed by Tukey test in the case of significant differences between feeding substrates. Comparison between survival rate of parasitized and non-parasitized larvae for each feeding substrate was done using a t-test. The t-test was

also used to compare differences between feeding substrates at 25 °C and GLM procedure of SAS followed by Tukey-test in the case of significant differences between substrates at 29 °C for the intrinsic rate of increase, the net reproductive rate, the mean generation time, the doubling time and the finite rate of increase.

4 Results

4.1 Effect of four plant species on life history parameters of *A. taragamae*

The parasitoid *A. taragamae* was unable to develop in *M. vitrata* reared on flowers of *L. sericeus* and *V. unguiculata* at 25 °C, neither on flowers of *P. santalinoides* at 25 and 29 °C (Table 1). The development time of *A. taragamae* from egg to cocoon, from cocoon to adult, and the whole cycle (from egg to adult stage) were significantly influenced by feeding substrates (Table 1).

At 25 °C

Wasps took less time to develop from egg to cocoon and from cocoon to adult when parasitized hosts were reared on artificial diet compared to flowers of *S. rostrata* (t test, t = 3.6 for egg to cocoon, t = 6.1 for cocoon to adult; $P < 0.0001$; Table 1). The life cycle was reduced by 0.8 day for male and female wasps when host larvae were fed with artificial diet compared to flowers of *S. rostrata* (t = 4.3; $P < 0.0001$; Table 1). The male wasps' cycle was 0.7 day shorter than that of females regardless of these feeding substrates. Male wasps lived more than three days longer than females when larvae were fed with flowers of *S. rostrata* (t = 2.4; $P = 0.02$; Table 1), while on artificial diet there was no significant difference. The proportion of female offspring was significantly lower than that of males when the hosts fed on flowers of *S. rostrata*. The sex ratio was not different for wasps developing in hosts feeding on *S. rostrata* compared to artificial diet ($\chi^2 = 0.2$; $P = 0.6$; Table 1).

At 29 °C

The parasitoid successfully developed in *M. vitrata* larvae feeding on three of the four tested flower species. At this temperature, the longest development time (from egg to cocoon, or cocoon to adult, or egg to adult) was observed for wasps in hosts feeding on *L. sericeus* (Table 1). The full development cycle of males was reduced by 0.8 day when compared to that of females when the host was feeding on *S. rostrata,* by 1.1

Table 1: Development time, longevity, and sex ratio of the parasitoid *Apanteles taragamae* when reared in hosts (*M. vitrata*) feeding on flowers of *Sesbania rostrata, Vigna unguiculata, Lonchocarpus sericeus, Pterocarpus santalinoides* or artificial diet at 25 and 29 °C

Parameter	*S. rostrata*	*V. unguiculata*	*L. sericeus*	*P. santalinoides*	Artificial diet
Development time (days):					
- egg-cocoon					
.....- at 25 °C	7.3 ± 0.05(98) a	-	-	-	7.0 ± 0.03(100) b
- at 29 °C	5.1±0.03(80) a	5.4±0.06(74) b	5.8±0.07(68) c	-	5.1 ±0.03(74) a
- cocoon-adult					
.....- at 25 °C	5.2 ± 0.07(79)a	-	-	-	4.8 ± 0.09(74) b
- at 29 °C	5.2 ± 0.06(71)a	5.3 ± 0.05(71) a	5.6±0.18(16) b	-	4.8 ± 0.09(65) c
Development cycle (days):					
- male					
.....- at 25 °C	12.2 ± 0.08(28)aα	-	-	-	11.4 ± 0.1(27)bα
- at 29 °C	10.2±0.09(24)aα	10.2±0.09(12)aα	11.4±0.1(15)b	-	9.6 ± 0.1(25) cα
- female					
.....- at 25 °C	12.9 ± 0.09(28) aβ	-	-	-	12.1 ± 0.2(27)bβ
- at 29 °C	11.0 ± 0.3(24) aβ	11.3 ± 0.3(12)aβ	-	-	10.2 ± 0.2(25)bβ
Longevity (days):					
- male					
.....- at 25 °C	11.9 ± 1.3(28) aα	-	-	-	10.9 ± 1.5(27)bα
- at 29 °C	5.5 ± 0.9(24) aα	5.0 ± 0.6(12) aα	6.3±1.1(15) a	-	5.1 ± 0.8(25) aα
- female					
.....- at 25 °C	8.8 ± 0.9(28) aβ	-	-	-	9.9 ± 0.9(27) aα
- at 29 °C	6.5 ± 0.6(24) aα	4.3 ± 0.7(12) bα	-	-	5.1 ± 0.5(25) abα
Adult emergence rate (%)					
.....- at 25 °C	79.9 ± 2.5 a	-	-	-	73.8 ± 6.6 a
- at 29 °C	88.6 ± 3.9 b	83.3 ± 4.8 b	23.5 ± 2.7 a	-	85.6 ± 3.9b
Sex ratio (% females among progeny)					
.....- at 25 °C	35.4 a*	-	-	-	39.1a
- at 29 °C	34.0 a*	16.9b*	6.3c*	-	38.4 a

Numbers in parentheses represent the number of replications

Means within each row followed by the same Latin letters were not significantly different ($P > 0.05$) with a t-test at 25 °C and ANOVA followed by Tukey test at 29 °C

- : indicates that parameters were not determined because of low number of female wasps (one female obtained from 250 parasitized larvae reared on *L. sericeus* at 29 °C) or unsuccessful development of parasitized larvae (*V. unguiculata* or *L. sericeus* at 25°C; *P.santalinoides* at 25 and 29 °C)

Comparison between male and female: means within each column followed by Greek letters are not significantly different (paired t-test at 5%).

Sex ratio: female percentages followed by the same letter were not significantly different with χ^2 at 5% (based on 2 x 2 (25 °C) or 2 x 4 (29 °C) contingency table) for comparison between feeding substrates

*: indicates that there was significant difference ($P < 0.05$, χ^2) between observed and expected (50%) percentages of the females for the feeding

days on *V. unguiculata,* and 0.6 day on artificial diet ($P < 0.05$; Table 1). In contrast to male ($F = 0.3$; $df = 2, 53$; $P = 0.8$), female wasps that emerged from larvae reared on *S. rostrata* flowers lived longer when compared with females that emerged from larvae reared on cowpea flowers ($F = 6.3$; $df = 2, 34$; $P = 0.005$). The percentage of adult wasps that emerged from cocoons was the lowest on *L. sericeus* (Table 1). The wasp sex ratio was strongly affected by feeding substrates. The proportion of female wasps differed among feeding substrates of *M. vitrata* ($\chi^2 = 11.9$; $P = 0.007$). It was lowest in hosts feeding on *L. sericeus* (6%) followed by *V. unguiculata* (17%) compared to *S. rostrata* and artificial diet (34-38%).

The mean daily fecundity was lower for parasitoids that had been reared in hosts on flowers of *S. rostrata* in comparison to artificial diet at 25 °C (0.74 against 5.85 cocoons/female/day, respectively) ($t = 7.5$; $P < 0.0001$; Figure 1), while no differences were observed between feeding substrates at 29 °C (values ranging from 0.16 to 2.8 cocoons/female/day; $F = 0.89$; df 2, 34; $P = 0.6$; Figure 1). The fecundity of parasitoids reared in hosts on artificial diet at 25 °C was much higher and peaked at 4 days after adult emergence (Figure 1). At 29 °C, the daily fecundity showed a peak at 3, 4, or 5 days after emergence for parasitoids that had developed in hosts on flowers of *S. rostrata,* artificial diet and flowers of *V. unguiculata,* respectively (Figure 1).

The survival rate of parasitized hosts was similar ($t = 0.15$; $P = 0.9$) on *S. rostrata* and artificial diet at 25 °C (Figure 2). Likewise, there were no significant differences for the survival rate of non-parasitized larvae at 25 °C on either of the two feeding substrates ($t = 1.38$; $P = 0.2$) (Figure 2).

Comparison of the survival rate of parasitized larvae reared on *S. rostrata, V. unguiculata, L. sericeus* and artificial diet did not show any significant differences at 29 ° C ($F = 1.23$; $df = 3, 9$; $P = 0.35$) (Figure 2). A similar result was obtained for non-parasitized larvae ($F = 1.59$; $df = 3, 9$; $P = 0.26$). However, at 25 °C, a significant difference was found when we compared the survival rates of parasitized and non-parasitized larvae reared on *S. rostrata* ($t = 10.9$; $P < 0.0001$) and artificial diet ($t = 12.2$; $P < 0.0001$). No differences were observed when we compared the survival rate of parasitized larvae to that of non-parasitized larvae feeding on *S. rostrata* ($t = 1.92$; $P = 0.1$), *V. unguiculata* ($t = 1.58$; $P = 0.58$), *L. sericeus* ($t = 1.19$; $P = 0.28$) and artificial diet ($t = 1.93$; $P = 0.1$) at 29 °C.

A large percentage of dead parasitized larvae showed symptoms of *Maruca vitrata* Multi-Nucleopolyhedrovirus *Mavi*MNPV disease that occurred during the rearing of *A. taragamae* (Figure 3). The percentage of larvae killed by the virus was significantly higher at 25 °C than at 29 °C for all feeding substrates (Figure 3).

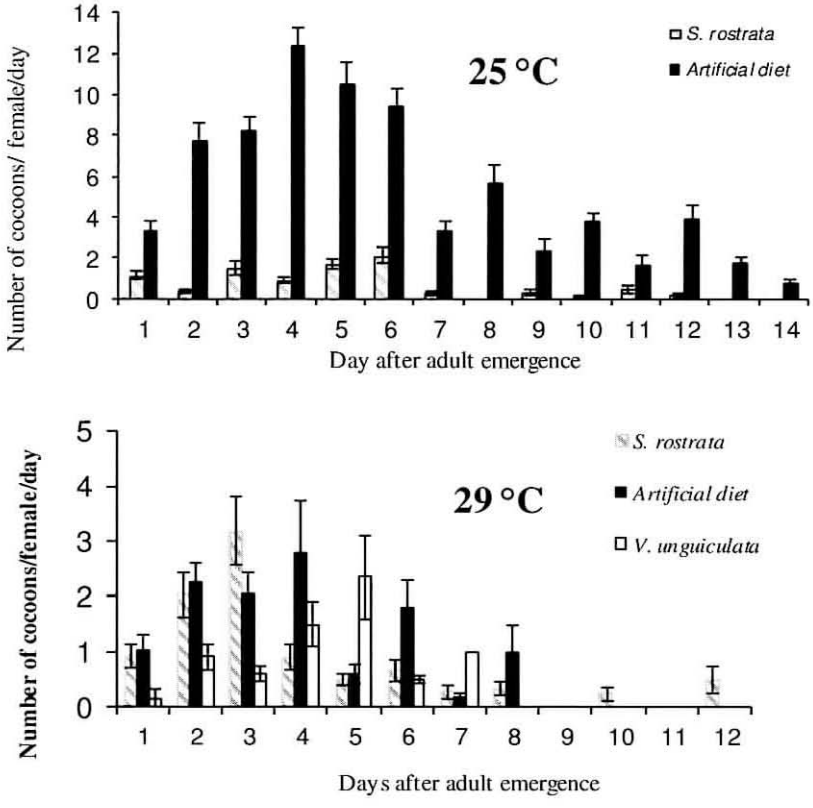

Figure 2: Daily fecundity of the parasitoid *Apanteles taragamae* after developing in its host on *Sesbania rostrata* flowers, or artificial diet at 25 °C and on *S. rostrata* flowers, *Vigna unguiculata* flowers or artificial diet at 29 °C.

Lines in bars represent standard errors of the means

Data on *L. sericeus* were not included in the Figure because of low number of replicates (only one adult female wasp was obtained from 250 parasitized larvae

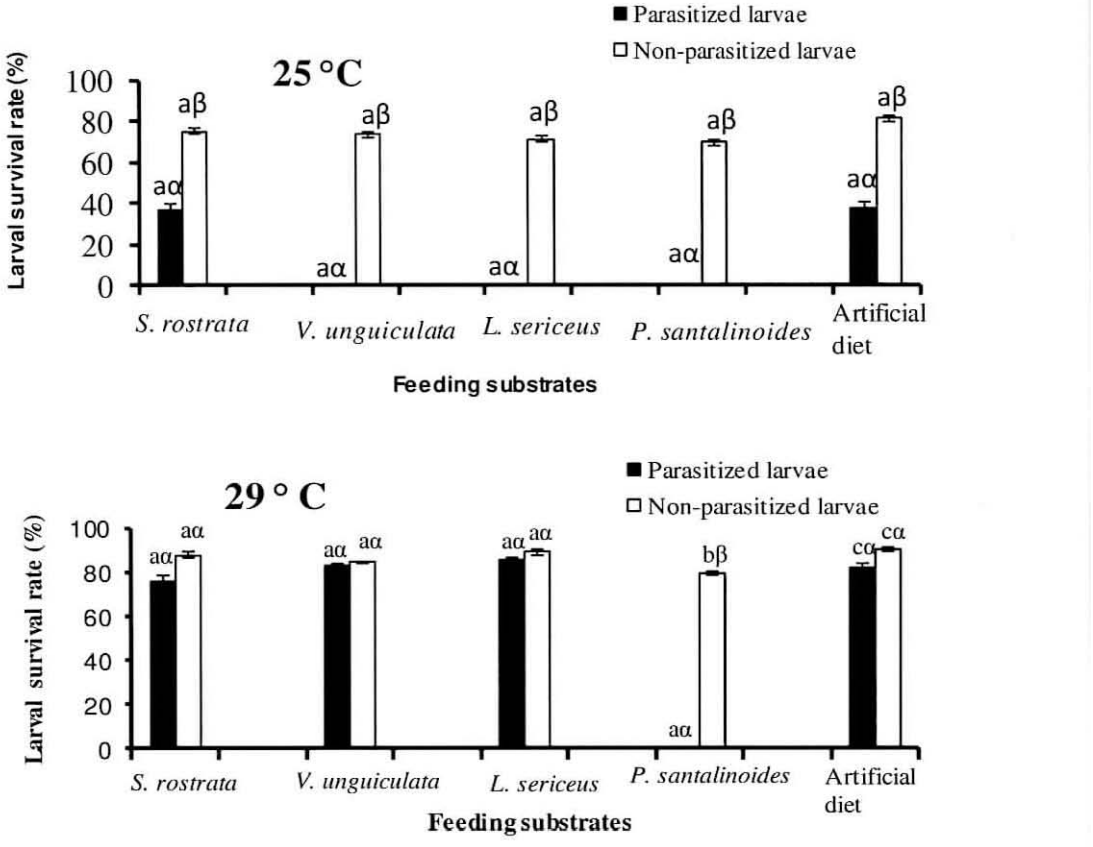

Figure 2: Survival rate of parasitized and non-parasitized *M. vitrata* larvae when reared on *Sesbania rostrata*, *Vigna unguiculata*, *Lonchocarpus sericeus* or *Pterocarpus santalinoides* flowers or artificial diet at 25 and 29 °C

Means were means of four replications; each replication consisted of 50 larvae

Lines in bars represent standard errors of the means

Means followed by the same letter were not significantly different with ANOVA followed by Tukey test or a t-test ($\alpha = 0.05$) at each temperature. Regular letters refer to comparison (ANOVA followed by Tukey test) between feeding substrates for parasitized or non-parasitized larvae at each temperature and Greek letters to comparison (t-test) between parasitized and non-parasitized larvae for each feeding substrate at each temperature.

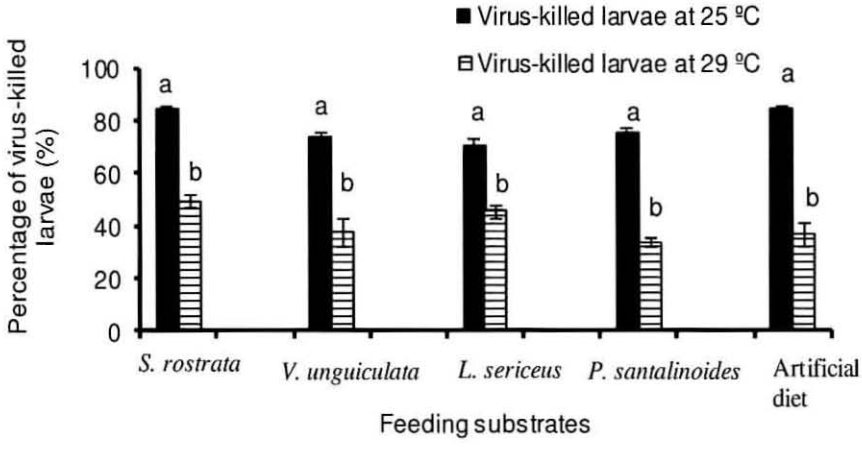

Figure 3: Percentage of dead parasitized larvae reared on flowers of *Sesbania rostrata, Vigna unguiculata, Lonchocarpus sericeus, Pterocarpus santalinoides* or artificial diet showing symptoms of *Maruca vitrata* Multi-Nucleopolyhedrovirus (*Mavi*MNPV) at 25 and 29 ℃.

Means were means of four replications; each replication consisted of 50 larvae

Lines in bars represent standard errors of the means

Regular letters refer to comparison between the two temperatures 25 and 29 ℃ and means followed by the same letter were not significantly different with t-test within each feeding substrate

4.2 Effects of *S. rostrata, V. unguiculata,* and *L. sericeus* flowers on the life table parameters of *A. taragamae*

At 25 ℃, the intrinsic rate of natural increase was 7.5 times higher for parasitoids developing in hosts feeding on artificial diet than those feeding on *S. rostrata* (Table 2). Likewise, the net reproductive rate was about 8 times higher when larvae were fed using artificial diet compared to flowers of *S. rostrata.* In contrast, no significant differences were obtained between the rearing substrates for any of the life table parameters at 29 ° C ($P > 0.05$) (Table 2).

Table 2: Life table parameters of the parasitoid *Apanteles taragamae* when reared in its host (*M. vitrata*) on flowers of *Sesbania rostrata, Vigna unguiculata, Lonchocarpus sericeus, Pterocarpus santalinoides* or artificial diet at 25 and 29 °C

Parameter	*S. rostrata*	*V. unguiculata*	*L. sericeus*	*P. santalinoides*	Artificial diet
Intrinsic rate of increase (r_m) (females/female/day)					
.....- at 25 °C	0.015 ±0.009a	-	-	-	0.145 ± 0.010a
- at 29 °C	0.054 ± 0.024a	0.087 ± 0.085a	-	-	0.112 ± 0.012a
Net reproductive rate (R0) (females/female)					
.....- at 25 °C	0.920 ± 0.187a	-	-	-	7.281 ± 1.018b
- at 29 °C	1.869 ± 0.404a	1.828 ± 1.302a	-	-	3.350 ± 0.390a
Mean generation time (T) (day)					
.....- at 25 °C	12.930 ±	-	-	-	13.515 ± 0.181b
- at 29 °C	0.150b	11.696 ±	-	-	10.370 ± 0.259a
	10.273 ±	0.646a			
	0.063a				
Doubling time (DT) (day)					
.....- at 25 °C	18.775 ±		-	-	4.830 ± 0.390 a
- at 29 °C	2.285b	4.770 ± 0.140a	-	-	6.303 ± 0.639 a
	8.935 ± 0.575a				
Finite rate of increase (λ) (females/female/day)					
.....- at 25 °C	0.994 ± 0.012a	-	-	-	1.157 ± 0.012b
- at 29 °C	1.056 ± 0.02 b	0.992 ± 0.076a	-	-	1.136 ± 0.017b

Means within each row followed by the same letters were not significantly different with a t-test (25 °C) or ANOVA followed by Tukey test (29 °C) with α = 5% for the same plant species

- : indicates that parameters were not determined because of low number of female wasps (one female obtained from 250 parasitized larvae reared on *L. sericeus* at 29 °C) or unsuccessful development of parasitized larvae (case of *V. unguiculata* or *L. sericeus* at 25°C and *P. santalinoides* at 25 and 29 °C)

5 Discussion

After parasitization, the developmental and reproductive success of koinobiont parasitoids is determined by the nutritional value of their hosts that continue to feed, grow and develop (Beckage and Riddiford, 1983). The herbivore's food plants have been reported to influence many parasitoid biological parameters such as development time, sex ratio and survivorship of immature parasitoids (Fox et al., 1990; Harvey and Vet, 1997; Bottrell and Barbosa, 1998; Gols et al., 2008; Gols and Harvey, 2009). In the present study, host plants of *M. vitrata* affected the development time of the parasitoid *A. taragamae*. The longest life cycle at 29 ℃ was obtained when the hosts fed on flowers of *L. sericeus* followed by hosts feeding on flowers of *V. unguiculata*. This finding may be explained by the fact that *L. sericeus* is a leguminous tree with relatively small flowers in comparison to the more succulent flowers of *V. unguiculata* and *S. rostrata*. The small *L. sericeus* flowers may provide a sub-optimal food source to *M. vitrata* larvae, and as a consequence, the wasps take longer to accomplish their life cycle. Although all food substrates were leguminous plants, differences between them can also be explained by the presence of toxic secondary metabolites in the flowers (Barbosa et al., 1986). For instance, given the purplish colour of *L. sericeus* flowers, they could contain anthocyans or polyphenolic compounds which can have a detrimental effect on insect development (van Loon, 1990; Lev-Yadun and Gould, 2008). However, no information on the chemical content of these species is present in the literature.

The life cycle of female parasitoids was longer than that of males, regardless of the feeding substrates at both 25 and 29 ℃. This supports the observation that female parasitoids require more nutritional resources than males to complete their development (Colinet et al., 2005).

In this study, we did not succeed in rearing *A. taragamae* on flowers of *P. santalinoides* which is one of the four key host plants of *M. vitrata*. This finding may be attributed in part to interactions with the Multi-Nucleopolyhedrovirus *Mavi*MNPV that

occurred in the mass rearing of *A. taragamae.* The wasp has been reported to acquire and transmit the virus over several generations (Srinivasan et al., 2009). In our study, this virus affected the development of the wasp by killing infected parasitized larvae. As the viral disease symptoms appear about 3 to 4 days after infection of the *M. vitrata* larvae (Lee et al., 2007), and the wasp needs at least 5 and 7 days to complete its larval development at 29 °C and 25 °C, respectively (Table 1); this suggests that the wasps have better chances to escape the viral disease at 29 °C due to faster development. Furthermore, the wasp would not be able to escape the viral disease if parasitized larvae fed on sub-optimal substrates such as flowers of *P. santalinoides* that did not allow fast larval development.

The detrimental effect of *Mavi*MNPV associated with the relatively low survival rate of parasitized larvae at 25 °C supports the slow-growth, high-mortality hypothesis (Clancy and Price, 1987). Thus, a longer larval development time would increase the risk of attack by *Mavi*MNPV, leading to a higher mortality in parasitized larvae.

Host plant quality can be one of the main factors determining the sex ratio in parasitoids (Jervis et al., 2008). Host size at parasitization may affect sex allocation by female parasitoids at oviposition (Arthur and Wylie, 1959; King, 1987; van Alphen and Visser, 1990; Brodeur and Boivin, 2004; Harvey et al., 2004). Host size before parasitization is dependent upon the feeding rate and nutritional content of herbivore food plants (Harvey et al., 1994). Ovipositing parasitoid females are known to be selective for the sex of the offspring they deposit in their host (Hare and Luck, 1991; Luck et al., 1992; Dicke, 1999a). Thus, male offspring are often oviposited in small hosts whereas female offspring are oviposited in the large ones (Jones, 1982; Dicke, 1999a). Our study revealed a strong effect of *M. vitrata* host plants on the proportion of *A. taragamae* females produced. In plant species where wasp development was slow (for instance *L. sericeus*), the proportion of females was reduced.

The daily fecundity showed a nonlinear pattern indicating a pro-ovigenic characteristic of *A. taragamae.* Indeed, synovigenic females may show a constant daily fecundity for a long period in their lifespan as they mature eggs over time (Jervis et al., 2001). On the other hand, pro-ovigenic insects that have a high egg load at adult emergence exhibit a nonlinear daily fecundity pattern (Ellers et al., 2000).

The high percentage of virus-killed larvae observed for parasitized larvae at 25 °C showed the influence of temperature on viral mortality. This virus-related mortality is

likely to have a differential effect on parasitoid performance in hosts feeding on flower from different plant species.

When the host was fed on artificial diet, the daily fecundity of *A. taragamae* at 25 °C was higher than at 29 °C indicating a negative effect of high temperatures on wasp performance (Dannon et al., 2010a). The optimum temperature for development of *A. taragamae* ranged from 24 to 26 °C (Dannon et al., 2010a). Indeed, insects are not able to regulate their body temperature in response to increasing temperature so that above the upper thermal threshold, enzyme activity or nutrient metabolism are affected and consequently disrupting development and survival (Langridge, 1963).

In summary, *M. vitrata* host plants affected the development time, fecundity and sex ratio of the parasitoid wasp *A. taragamae*. The wasp successfully developed on most of the tested host plants. There are many factors in plants that can affect their suitability to koinobiont parasitoids, including nutrient contents and secondary metabolites. Further research should investigate the biochemical factors in *M. vitrata* host plants that can influence the development and performance of *A. taragamae*.

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Assessing non-target effects and host-feeding of the exotic parasitoid *Apanteles taragamae,* a potential biological control agent of the cowpea pod borer *Maruca vitrata*