*Bulletin of Insectology* ***64*** *(1): 135-143, 2011*
ISSN 1721-8861

# The performance of *Macrosiphoniella millefolii* and *Myzus persicae* on *Achillea collina*

**Pablo Morlacchi[1], Annamaria Giorgi[2], Giuseppe Carlo Lozzia[1], Johann Baumgärtner[1]**
[1]*Dipartimento di Protezione dei Sistemi Agroalimentare e Urbano e Valorizzazione delle Biodiversità, Università degli Studi di Milano, Italy*
[2]*Dipartimento di Produzione Vegetale, Università degli Studi di Milano, Italy*

## Abstract

This paper compares the development of the polyphagous aphid *Myzus persicae* Sulzer, considered as a generalist, and the oligophagous aphid *Macrosiphoniella millefolii* (De Geer), considered as a specialist, on yarrow (*Achillea collina* Becker ex Reichenbach). Yarrow is a medicinal plant rich in bioactive secondary metabolites that have possible effects on the development of phytophages, including aphids. Age specific life tables for cohorts developing under different constant temperatures were constructed and analyzed using standard techniques, and complemented with Jackknife estimates of the intrinsic rate of increase and its standard error. The parthenogenetic wingless morphs of the two species differed in the immature developmental time and survival, and in adult fecundity and life span. At high temperatures, the intrinsic rate of increase as the overall metric of performance tended to be higher for the generalist than for the specialist aphid species, while the opposite appears to occur at low and medium temperatures. Further insight into the complex interactions between yarrow and aphids requires that their genetic diversity is taken into account. The study of yarrow-aphid-natural enemy population interactions requires additional information on biomass dynamics, aphid morph differentiation and the performance of biological control agents.

**Key words:** Secondary metabolites, temperature, Jackknife estimate, intrinsic rate of increase.

## Introduction

Yarrow (*Achillea collina* Becker ex Reichenbach) is a medicinal herb belonging to the *Achillea millefolium* L. aggregate, that is adapted to temperate climates and poor soil quality (Cernaj *et al.*, 1991). Yarrow is cultivated in the European Alps and commonly used in traditional medicine for digestive, anti-inflammatory, analgesic and antipyretic activity properties, and to treat skin inflammations and wounds (Willuhn, 2002). Besides their role in pharmacology, secondary metabolites are generally known to influence the phytophagous species (Moran and Thompson, 2001; Chrzanowski and Leszczynski, 2008). Among phytophages infesting yarrow there are the aphids *Macrosiphoniella millefolii* (De Geer) and *Myzus persicae* Sulzer (Rhynchota Aphididae).

The oligophagous *M. millefolii* is a holocyclic species. It is a specialist feeding on *Achillea* spp. and related genera such as *Tanacetum* spp. (Sobhani, 1970; Schmitz, 1998). In alpine environments, *M. millefolii* is an important component of the yarrow-aphid-natural enemy system. In contrast, *M. persicae* is a polyphagous, holocyclic aphid, that attacks more than 30 plant families including many economically important species worldwide, and it is an important vector of virus diseases (van Emden *et al.*, 1969; Hill, 1983). Yarrow was reported as a host plant for *M. persicae* by Manachini and Cinanni (2004). We note, however, that *M. persicae* was absent from yarrow in alpine field.

As a result of evolutionary processes, the specialists are often assumed to be generally better adapted to the host plant and to its chemical constituents than generalists, and hence may exhibit a relatively better performance (Smith and Smith, 2001). In fact, specialist insects may be adapted to plants containing toxic compounds that are handled through enzymatic detoxification, excretion, sequestration and behavioural responses (Rhoades, 1979; Berenbaum and Zangerl, 1998; Lukasik, 2007; Bažok *et al.*, 2009; Hopkins *et al.*, 2009). However, even in well studied systems such as the Brassicaceae system including the *Arabidopsis thaliana* (L.) Heynh. model plant, relatively little is known about how either specialists or generalist use these processes to overcome host plant glucosinolates (Hopkins *et al.*, 2009). In the case of yarrow, neither the performance of specialist and generalist insects nor the underlying processes have been studied in detail.

The purpose of this paper is to assess and compare the performances of the two aphid species on yarrow. Birch (1948) and Messenger (1964) pioneered the use of life tables for assessing the performances of insects. Here, the assessment is done by the construction and analysis of age-specific life tables for wingless, parthenogenetic morphs of the two species feeding on the *A. collina* “SPAK”. This cultivar has been selected for a high content of secondary compounds. The results will provide a basis for planning future work aiming at elucidating the complex interactions between yarrow and arthropod phytophages.

## Materials and methods

### Plant cultivation and aphid rearing

Seeds of *A. collina* of the cultivar ‘SPAK’ used in this study were provided by Valplantons Bio (Saillon, CH). The seeds were sown in trays containing a light soil and allowed to germinate in a greenhouse at 26 ± 1 °C; 65 ± 5% RH; 16:8 L:D).

As needed, 5 weeks old plants were transplanted in pots (12.5 cm diameter, 11 cm height), and after establishment were used as hosts for rearing aphids. A plastic cylinder (Ø 11.5 cm, height 30 cm), was placed on the pot as a cage for the aphids; the top of the cylinder was closed with gauze to prevent the aphids from escaping and to allow air circulation.

Seeds of *Pisum sativum* L., cv. Progress No. 9 dwarf peas, were obtained from the Consorzio Agrario of Parma, and used as host plant for *M. persicae*. Pea seed were sown weekly in large pots (Ø 20 cm) using perlite (Agrilit® 3) as a substrate. One week after germination, the seedlings were infested with aphids.

*M. millefolii* specimens were collected in the fields during the growing season, and maintained in the laboratory on yarrow at 21 °C, 70 ± 5% RH, 16:8 L:D. Colonies of *M. persicae* were made available by the Institute of Entomology of Piacenza. The colonies were maintained on *P. sativum* seedlings inside a climatic chamber, with constant conditions (21 ± 1 °C; 65 ± 5% RH; 16:8 L:D). Periodically, yarrow and pea plants were replaced to guarantee host plant freshness and quality, and to avoid crowding in the colonies.

## Experiments

The 3 week-old yarrow seedlings were individually transplanted in pots (Ø 6.3 cm, height 8 cm) and kept in the greenhouse for another week before the experiments. The transplanted yarrow was covered with a transparent pot of the same size and, to prevent the aphids from escaping, the edges of the two pots were connected with a plastic film. The top of the cage was covered with gauze to permit air circulation.

Cohort experiments began 4 weeks after sowing *A. collina*. Two days before the beginning of the experiments, single adults of each species were put on individual plants, and individuals born within 24 hours were placed individually on caged plants. On average, a cohort consisted of 10 individuals that were placed in one of 5 bioclimatic chambers with constant conditions of 10, 15, 25 and 28 °C (65 ± 5% RH; 16:8 L:D), respectively. For *M. millefolii* only, we conducted an additional experiment at 21 °C and 16:8 L:D. The development of individuals in all cohorts was monitored daily, or every 2 days if conditions prevented more frequent monitoring.

The fecundity of each adult was monitored regularly until the end of the life span. Developmental times of immature individuals, and adult longevity and fecundity rates were interpolated if needed to yield daily values for entering into age-specific life tables calculations.

## Data analysis

### Immature development and survival

Numerous functions relating developmental rates *r(T)* to constant temperatures have been proposed (Kontodimas *et al.*, 2004). In this work, we prefer a function with few parameters and high predictive capabilities, rather than a complex function with possibly better explicative but inferior predictive qualities. Equation 1 in Brière *et al.* (1999) appears to be appropriate for this purpose:

$$r(T) = \alpha\, T(T - T_l)\sqrt{T_u - T} \qquad [1]$$

where $T$ = temperature, α = constant, $T_l$ = lower developmental threshold, and $T_u$ = upper developmental threshold. Barlow (1962) and Mackauer and Way (1976) provided estimates for the lower threshold for *M. persicae*. From their work, we derived the lower threshold $T_l = 4.5$ The survival $s_1$ of immature life stages was represented by a BETA function because of its capacity and flexibility to represent the temperature-dependent survival patterns:

$$s_1(T) = \kappa\,(T - T_l)^{\lambda}(T_u - T)^{\gamma} \qquad [2]$$

where $T$ = temperature, $\kappa$ = scaling parameter, $\lambda$ and $\gamma$ = BETA function parameters, $T_l$ = lower developmental threshold, and $T_u$ = upper developmental threshold. The values of the parameters $T_l$ and $T_u$ were obtained in equation [1].

### Age-specific fecundity and survival of adults

The observed age specific fecundity is represented by a function proposed by Bieri *et al.* (1983):

$$m(a) = \phi_1 \frac{(a - \phi_2)}{\phi_3^{(a-\phi_2)}} \qquad [3]$$

where $a$ = age, in days, and $\phi_1$, $\phi_2$ and $\phi_3$ = parameters. The widely used Gompertz function represents the observed age specific survival $s_2$ (Strehler, 1977):

$$s_2(a) = \omega_1 e^{\left[\omega_2 e^{\omega_3 a}\right]} \qquad [4]$$

where $a$ = age in days, and $\omega_1$, $\omega_2$, $\omega_3$ = parameters.

### Temperature-specific fecundity and life span

The temperature-dependent life span $l$ of adults and the total fecundity $f$ are represented by:

$$l(T) = a_1\, T(T - T_l)(T_u - T)^{b_1} \qquad [5]$$

$$f(T) = a_2 T(T - T_l)(T_u - T)^{b_2} \qquad [6]$$

where $T$ = temperature, $a_1$, $a_2$ ,$b_1$, $b_2$ = constants, $T_l$ = lower developmental threshold, and $T_u$ = upper developmental threshold. The values of the parameters $T_l$ and $T_u$ were obtained in equation [1].

### Intrinsic rate of increase

The intrinsic rate of increase $r_m$ combines developmental time, fecundity and mortality in a statistics that is widely used to represent the performance of a population (Birch, 1948). We used the method of Hulting *et al.* (1990) for computing mean $r_m$ and the standard error. This method is based on the Jackknife method proposed by Meyer (1957). Equation 1 in Brière *et al.* (1999) is used to describe the dependency of $r_m$ on the temperature:

$$r_m(T) = a_3 T(T - T_l)(T_u - T)^{b_3} \qquad [7]$$

where $T$ = temperature and $a_3$, $b_3$ = parameters; the lower and upper temperature thresholds $T_l$ and $T_u$ were obtained in equation [1].

The parameters $a$, $\kappa$, $\lambda$, $\gamma$, $a_1$, $a_2$, $a_3$, $b_1$, $b_2$, $b_3$, $\phi_1$, $\phi_2$, $\phi_3$, $\omega_1$, $\omega_2$, $\omega_3$, estimated via non-linear regression techniques using SPSS software. For *M. millefolii* the upper and the lower developmental threshold were also estimated, while for *M. persicae*, only the value of the upper developmental threshold was included in the pa-

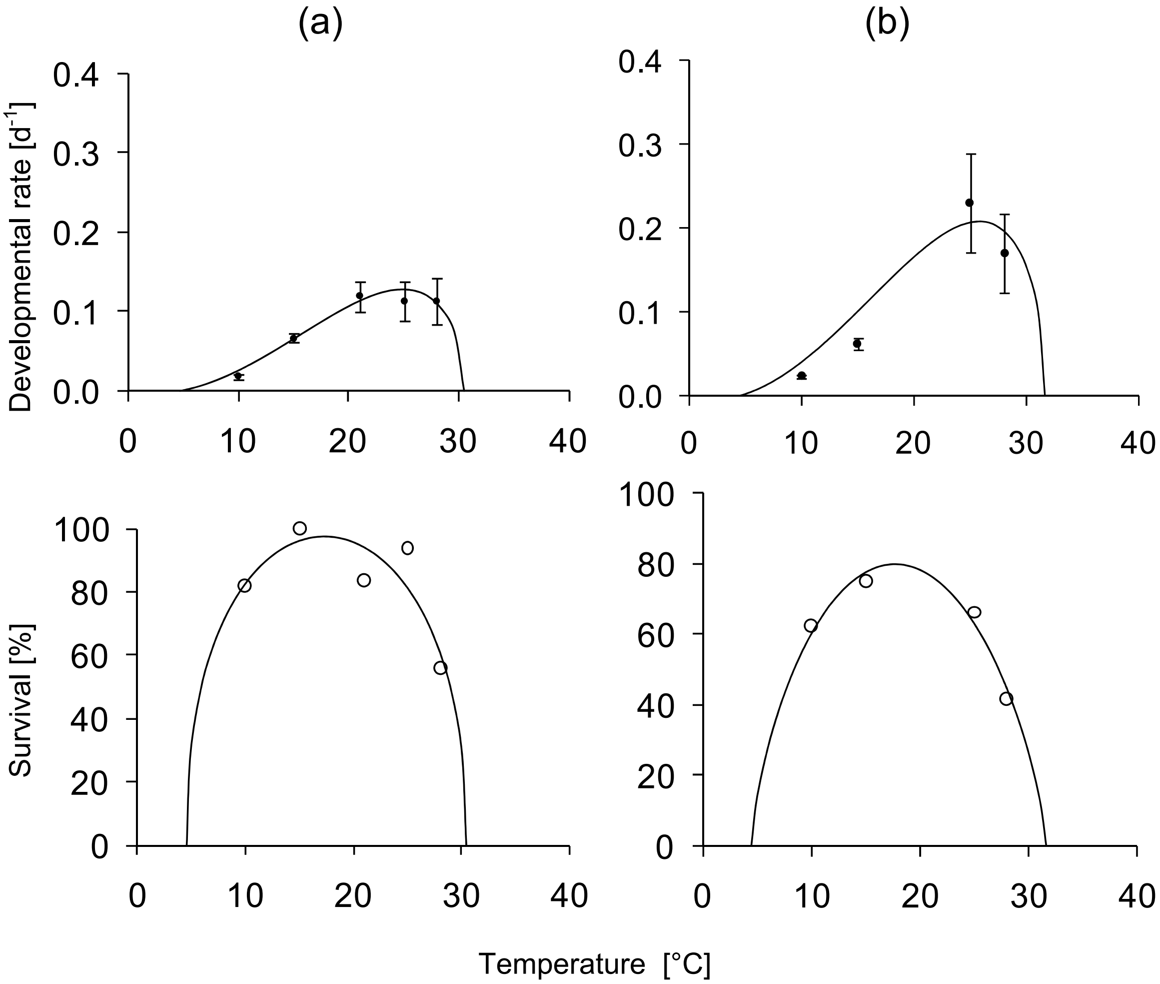

**Figure 1.** Developmental rate and survival of immature *M. millefolii* (a) and *M. persicae* (b) life stages at different temperatures. Black circles are the observed developmental rates (*r*; mean ± SE), the continuous line represents the rate $r(T)$ predicted by equation [1]; empty circles are the observed survival percentages ($s_1$), the continuous line represents the survival $s_1(T)$ calculated by equation [2]. The parameters are given in tables 1 and 2.

rameter estimation procedure. To estimate the parameters for equation [3] and equation [4], we used the observations made for both species at 10, 15, 25 and 28 °C.

## Results

### Immature development and survival

Figure 1 shows that the developmental rates between the lower and upper threshold temperatures are adequately described by equation [1] with the parameter estimates listed in tables 1 and 2. Between 10 and 21 °C, the rate of development of the two species exhibits an approximately linear increase with temperature. In the case of *M. millefolii*, the rate reaches a plateau between 21 and 28 °C and abruptly decreases with increasing temperatures toward the upper temperature threshold. The rates of the generalist *M. persicae* are generally higher than the ones calculated for *M. millefolii.*

Figure 1 also shows that equation [2], with the parameter estimates given in tables 1 and 2, satisfactorily represents the temperature specific survival of the immature life stages between the upper and lower developmental thresholds. The survival of both aphids displays an approximately symmetrical pattern between the lower and the upper threshold. In general, the survival of the specialist *M. millefolii* is higher than that of the generalist *M. persicae*.

### Age-specific fecundity and survival of adults

Temperature has a strong influence on the age-specific fecundity and the life span of the adults. Figure 2 summarizes the results obtained for both species at relatively low temperatures (10, 15 °C) and relatively high temperatures (25, 28 °C), and shows that these life table elements are adequately represented by equations [3] and [4].

At 10 °C, the reproduction of the specialist *M. millefolii* starts after 60 days and continues for a period of 57 days during which the daily maximum production per capita is 8 aphids, while the median life span is 129 days. At 15 °C, reproduction starts after 15 days and aphids produce a maximum of 61 nymphs during a period of about 59 days; the median life span is 31 days. At 25 °C, the adults start reproducing after 8 days and the fecundity decreases to 20 nymphs per aphid in 23 days,

**Table 1.** Life table parameter values with standard errors for the specialist aphid *M. millefolii* on yarrow.

| Developmental rate parameters (equation [1]) | | | Survival function parameters (equation [2]) | | |
|---|---|---|---|---|---|
| $\alpha$ | $T_l$ | $T_u$ | $\kappa$ | $\lambda$ | $\gamma$ |
| 1.08E-04 ± 1.41E-05 | 4.7 ± 1.61 | 30.4 ± 0.48 | 11.26 ± 13.1 | 0.42 ± 0.28 | 0.43 ± 0.4 |

| Age-specific fecundity parameters (equation [3]) | | | | Age-specific survival parameters (equation [4]) | | |
|---|---|---|---|---|---|---|
| T (ºC) | $\phi_1$ | $\phi_2$ | $\phi_3$ | $\omega_1$ | $\omega_2$ | $\omega_3$ |
| 10 | 0.28 ± 0.048 | 1.04 ± 0.004 | 52.15 ± 1.411 | 1.01 ± 0.006 | 2.0E-08 ± 1.69E-08 | 0.13 ± 0.006 |
| 15 | 10.04 ± 1.195 | 1.11 ± 0.008 | 14.27 ± 0.403 | 1.07 ± 0.03 | 0.005 ± 0.002 | 0.10 ± 0.009 |
| 25 | 10.25 ± 0.72 | 1.21 ± 0.01 | 7.27 ± 0.139 | 1.16 ± 0.064 | 0.07 ± 0.024 | 0.09 ± 0.009 |
| 28 | 0.5 ± 0.317 | 1.32 ± 0.138 | 6.61 ± 0.708 | 1.03 ± 0.042 | 0.02 ± 0.008 | 0.22 ± 0.022 |

| Life span parameters (equation [5]) | | Total fecundity parameters (equation [6]) | |
|---|---|---|---|
| $a_1$ | $b_1$ | $a_2$ | $b_2$ |
| 7.10E-07 ± 7.91E-07 | 4.74 ± 0.40 | 3.91E-04 ± 2.43E-04 | 2.31 ± 0.24 |

| Intrinsic rate of increase parameter (equation [7]) | |
|---|---|
| $a_3$ | $b_3$ |
| 9.46E-05 ± 5.36E-05 | 0.82 ± 0.26 |

**Table 2.** Life table parameter estimates with standard errors for the generalist aphid *M. persicae* feeding on yarrow.

| Developmental rate parameters (equation [1]) | | | Survival function parameters (equation [2]) | | |
|---|---|---|---|---|---|
| $\alpha$ | $T_l$ | $T_u$ | $\kappa$ | $\lambda$ | $\gamma$ |
| 1.57E-04 ± 2.88E-05 | 4.5 | 31.6 ± 2.0 | 1.95 ± 2.81 | 0.69 ± 0.33 | 0.72 ± 0.25 |

| Age-specific fecundity parameters (equation [3]) | | | | Age-specific survival parameters (equation [4]) | | |
|---|---|---|---|---|---|---|
| T (ºC) | $\phi_1$ | $\phi_2$ | $\phi_3$ | $\omega_1$ | $\omega_2$ | $\omega_3$ |
| 10 | 0.33 ± 0.039 | 1.04 ± 0.002 | 39.79 ± 1.416 | 1.03 ± 0.012 | 7.24E-05 ± 4.4E-05 | 0.07 ± 0.004 |
| 15 | 1.54 ± 0.424 | 1.09 ± 0.018 | 10.79 ± 3.875 | 1.57 ± 0.207 | 0.12 ± 0.058 | 0.06 ± 0.01 |
| 25 | 11.99 ± 2.572 | 1.23 ± 0.033 | 4.44 ± 0.358 | 1.03 ±0.022 | 0.02 ± 0.006 | 0.19 ± 0.013 |
| 28 | 2.66 ± 1.452 | 1.58 ± 0.234 | 5.11 ± 0.37 | 1.17 ± 0.197 | 0.05 ± 0.064 | 0.17 ± 0.068 |

| Life span parameters (equation [5]) | | Total fecundity parameters (equation [6]) | |
|---|---|---|---|
| $a_1$ | $b_1$ | $a_2$ | $b_2$ |
| 1.91E-12 ± 3.69E-12 | 8.922977 ± 0.636163 | 5.20E-04 ± 4.12E-04 | 2.10 ± 0.30 |

| Intrinsic rate of increase parameter (equation [7]) | |
|---|---|
| $a_3$ | $b_3$ |
| 1.69E-04 ± 1.29E-04 | 0.58 ± 0.35 |

while at 28 °C the aphids are barely able to reproduce, giving birth to only 2 nymphs after 11 days during a very short period of 2 days; the median life span is 17 days.

The generalist *M. persicae* is generally less productive, giving birth to half the number of aphids than the specialist, while the age-specific survival is similar. At 10 ºC, the reproduction starts earlier (day 43rd) and lasts longer (110 days) than in the case of *M. millefolii*; the median life span is 128 days. At 15 ºC, adults start to reproduce after 17 days and continue for 46 days, producing a maximum of 11 aphids during a median life span of 34 days. At 25 ºC, the beginning of reproduction is on day 14 and lasts until day 35; the peak is reached on day 32; the median life span is 17 days. At 28 ºC, reproduction begins on day 5 and continues for a period of 16 days; the maximum production of 4 aphids occurs on day 3 after the adult moult, while the median life span is 18 days.

### Temperature-specific fecundity and life span

Figure 3 depicts the effect of constant temperatures on the fecundity and life span of the two aphids. Accordingly, the adults develop and reproduce in the temperature interval delimited by the lower and upper thresholds of 4.7 and 30.4 ºC for the specialist, and of 4.5 and 31.6 ºC for the generalist aphid, respectively. The high temperatures have similar effects on the two species which can hardly reproduce and survive at 28 °C. Interestingly, at 10 ºC, the females of the specialist produce on average a total of 17.6 nymphs, while the generalist produces 25.7 aphids. However, at 15 ºC the performance is reversed, with *M. millefolii* producing 42.5 aphids and *M. persicae* giving birth to a total of 14.17 aphids.

### Intrinsic rate of increase

Figure 4 shows that the equation [7] with the parameter estimates given tables 1 and 2 satisfactorily represent the dependency of the intrinsic rate of increase on temperatures between the lower and upper thresholds (4.7 and 30.4 ºC for the specialist *M. millefolii*, and of 4.5 and 31.6 ºC for the generalist *M. persicae*, respectively). In both cases, the decrease at high temperatures toward the threshold begins before 28 ºC. At high temperatures, the intrinsic rate of increase as the overall metric of performance tended to be higher for the generalist than for the specialist aphid species, while the predicted performance of the specialist appears to be better at low and medium temperatures.

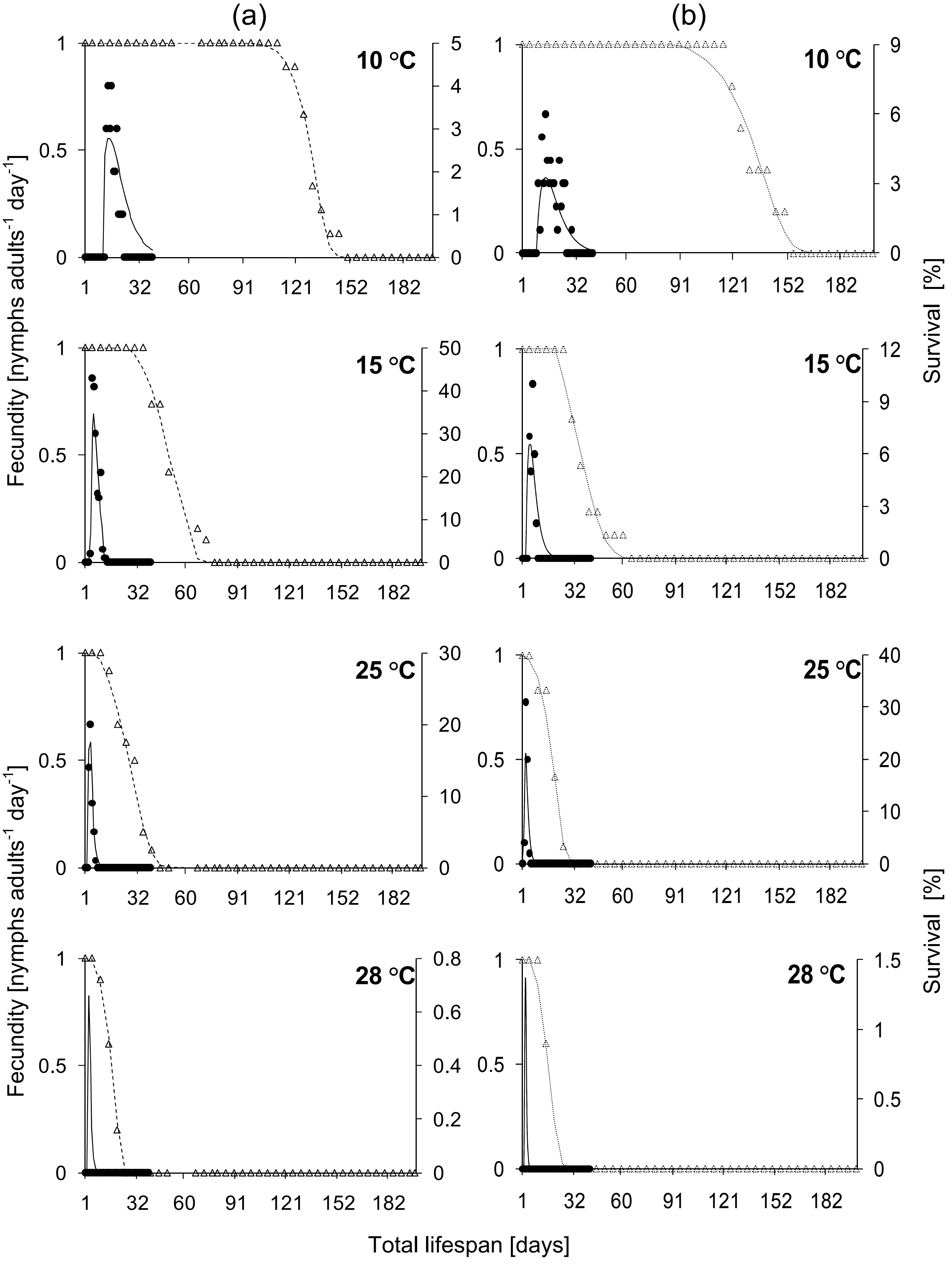

**Figure 2.** Age-specific per capita fecundity and age-specific survival of *M. millefolii* (a) and *M. persicae* (b). On every 5th day, the black circles represent the observed daily nymph production per female, while the continuous line represents the fecundity *m*(*a*) calculated according to equation [3]; on every 5th day, the empty triangles represent the observed proportions of surviving adults ($s_2$), while the dotted line represents the calculated age-specific survival $s_2(a)$ according to equation [4]. The parameters are given in tables 1 and 2.

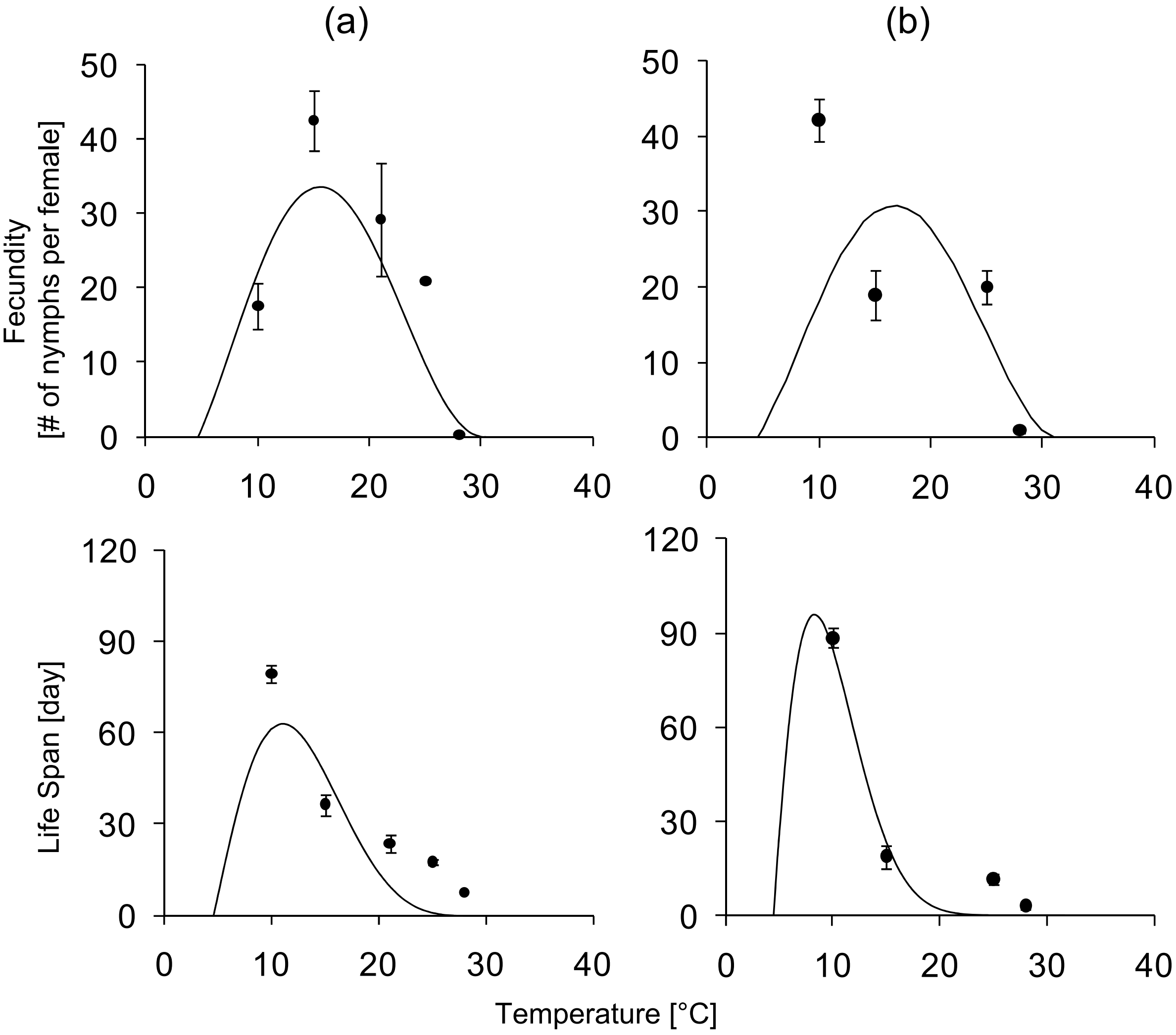

**Figure 3**. The total fecundity per female and the life span of *M. millefolii* (a) and of *M. persicae* (b), in relation to constant temperatures. The dots represent the observed data, i.e. the average total numbers of young produced per female ($M$) and the average life spans ($l$), while the continuous lines represent the predicted fecundity $M(T)$ (equation [6]) and life span $l(T)$ (equation [5]). The parameters are given in tables 1 and 2.

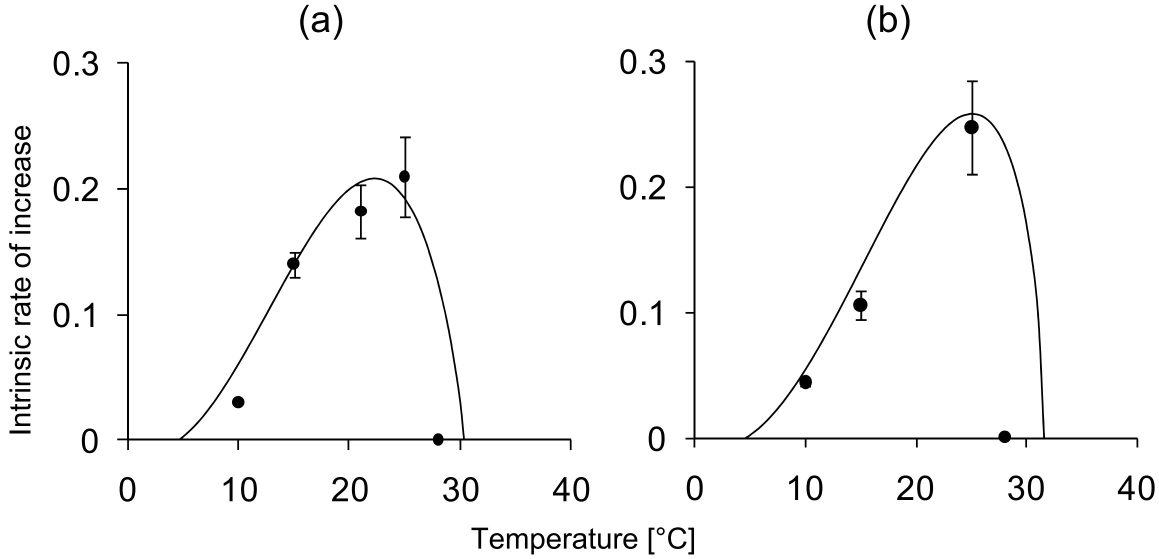

**Figure 4.** The intrinsic rate of increase of *M. millefolii* (a) and *M. persicae* (b), at different constant temperatures. The black circles represent the intrinsic rate of increase with standard errors ($r_m$ ± SE), while the lines represent the calculated intrinsic rates of increase $r_m(T)$ according to equation [7]. The parameters are given in tables 1 and 2.

## Discussion

Our study deals with the effects of a medicinal plant, known for a high content of secondary metabolites, on a generalist and a specialist aphid. Plant effects on phytophages resulting from phytochemical reactions to phytophagous are of great interest in current ecological work (Karban and Baldwin, 1997; Stout *et al*., 1998; Messina *et al*., 2002; Traw and Dawson, 2002). It is generally assumed that the response of the plant negatively affects the performance of phytophages (Karban and Myers, 1989; Trewhella *et al*., 1997). However, experimental work shows inconsistent results (Jermy, 1984; Faeth, 1991; Raupp and Tallamy, 1990; Krischik *et al*., 1991; Agrawal, 1999). In agreement with the general assumption, the performance of *M. persicae*, expressed in developmental time, survival and adult life span as well as in the intrinsic rate of increase, appears to be weaker on yarrow than on other well-studied host plants including *Solanum tuberosum* L., *Nicotiana* spp., *Chrysanthemum* spp., *Piper* spp. and *Cruciferae* species (Wyatt and Brown, 1977; Kuo, 1992; Costello and Altieri, 1994; Otha and Othaishi, 2002; Davis *et al*., 2006; Davis and Radcliffe, 2008; Shahidi-Noghabi *et al*., 2009). However, additional studies are required to ascertain this aspect mainly because of the narrow genetic basis of *M. persicae* described as follows.

In our study, *M. millefolli* was collected in yarrow fields, while *M. persicae* originated from individuals collected on *Prunus* spp. and maintained on *P. sativum*. The narrow genetic basis may be responsible for an underperformance of *M. persicae* on yarrow. Genetically-based differences in the performance of pea aphids (*Acyrthosiphon pisum* Harris) are reported by Via (1991) and Hufbauer (2001). The performance of both aphids under study may be affected by the high content of secondary compounds of the cultivar used. Cabbage (*Brassica oleracea* L.) cultivars, for example, have different glucosinolate profiles that only partly overlap (Poelman *et al*., 2008a). The profiles produced a different ranking order for each of the studied lepidopteran species (Poelman *et al*., 2008b). Hence, to assess the performance of the phytophages in a more comprehensive way than done in this study a wider genetic diversity of both the host plant and the phytophages should be taken into consideration.

If the performance is assessed in terms of immature developmental time and mortality, reproduction and adult life span, *M. millefolii* generally performed better than *M. persicae* across all the temperatures permitting the development. Because of the emphasis given to alpine conditions, lower experimental temperature conditions were given priority over high temperatures. As a result, the estimated upper threshold for *M. persicae* is associated with a high standard error (table 2). The survival of *M. millefolii* nymphs was higher and the life span of adults longer, while the fecundity was similar to the one expressed by *M. persicae* across all the temperatures. However, *M. persicae* had a shorter immature developmental time than *M. millefolii*. Noteworthy are also the responses at 10, 25 and 28 ºC where the age- and temperature-specific fecundities were higher for *M. persicae*. In comparison with *M. persicae*, the performance of *M. millefolii* appears to be better at low and medium and worse at high temperatures. The result confirms that a general assessment of the performance should be done on $r_m$ rather than on single life table parameters, and the entire range of temperatures permitting development should be taken into account, rather than considering favourable temperatures only.

The literature provided inconclusive results regarding comparisons between generalists and specialists. Hopkins *et al*. (2009) expect that a generalist generally performs better than a specialist. Poelman *et al*. (2008b) observed that the performance of the generalist lepidopteran *Mamestra brassicae* (L.) was similar to the specialist lepidopteran *Plutella xylostella* (L.) on Brassicaceae that has a high concentration of host-plant specific secondary chemicals.

The life table statistics obtained in this study could be used for the development of single-species models under unlimited resources (Smith and Smith, 2001). Instead, our work ultimately aims at the study of multitrophic population interactions in the yarrow system. Among the important processes in the dynamics of aphid populations is morph differentiation in response to plant effects and environmental conditions (Holst and Ruggle, 1997; Braendle *et al*., 2006; Frantz *et al*., 2010). Possibly, a generalist responds faster to low food quality by producing winged morphs able to find host plants of better quality. Another important element for consideration in aphid population dynamics is the biomass and energetics of aphids (Gutierrez, 1996). In this study, adults of the specialist *M. millefolii* had a higher fresh weight (5.73 mg ± 0.88, n = 30) than the generalist *M. persicae* (2.75 mg ± 0.076, n = 56). The difference may be due to different immature development times, phloem sap intake and assimilation efficiency. The faster immature development of *M. persicae* may contribute to this difference, while the other aspects relevant for explaining the difference are discussed by Hopkins *et al*. (2009) and Schowalter (2006) who provide general information on the adjustments of feeding behaviour and the increased efficiency in assimilation rates of specialists.

The relationship between numbers and biomass quantity and quality profoundly affects the dynamics of the interactions between parasitoids and hosts, and between predators and prey (Gutierrez *et al*., 1993; Francis *et al*., 2000; Jalali *et al*., 2009; Lundgren *et al*., 2010). Multitrophic population interactions may be influenced by the content of secondary metabolites. In the well studied *Brassica* system for example, the glucosinolate concentrations in a *Brassica nigra* (L.) cultivar, which were 3.5 times higher than concentrations in a *B. oleracea* cultivar, resulted in negative effects on the fourth trophic level, represented by the hyperparasitoid *Lysibia nana* Gravenhorst parasitizing *Cotesia glomerata* L. (Harvey *et al*., 2003).

In conclusion, the parthenogenetic wingless morphs of the specialist and generalist aphid species differed in the immature developmental time and survival, and in adult fecundity and life span. The difference in the intrinsic rates of increase as the overall metric of performance depended on temperature: at high temperatures, the performance tended to be higher for the generalist than for the specialist, while the opposite appeared to occur at low and medium temperatures.

## Acknowledgements

Mr Raselli (www.bioraselli.ch) kindly made available his yarrow fields for aphid collection.

## References

AGRAWAL A. A., 1999.- Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness.- *Ecology*, 80: 1713-1723.

BARLOW C. A., 1962.- The influence of temperature on the growth of experimental populations of *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) (Aphididae).- *Canadian Journal of Zoology*, 40: 145-156.

BAŽOK R., BARČIĆ J. I., EDWARDS C. R., 2009.- Effects of proteinase inhibitors on western corn rootworm life parameters.- *Journal of Applied Entomology,* 129: 185-190.

BERENBAUM M. R., ZANGERL A. R., 1998.- Chemical phenotype matching between a plant and its insect herbivore.- *Proceedings of the National Academy of Sciences of the United States of America,* 95: 13743-13748.

BIERI M., BAUMGÄRTNER J., BIANCHI G., DELUCCHI V., VON ARX R., 1983.- Development and fecundity of pea aphid (*Acyrthosiphon pisum* Harris) as affected by constant temperatures and by pea varieties.- *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 56: 163-171.

BIRCH L. C., 1948.- The intrinsic rate of natural increase of an insect population.- *Journal of Animal Ecology*, 17: 15-26.

BRAENDLE C., DAVIS G. K., BRISSON J. A., STERN D. L., 2006.- Wing dimorphism in aphids.- *Heredity*, 97: 192-199.

BRIÈRE J. F., PRACROS P., LE ROUX A. Y., PIERRE J. S., 1999.- A novel rate model of temperature-dependent development for arthropods.- *Environmental Entomology*, 28: 22-29.

CERNAJ P, GALAMBOSI B., HELEMIKOVA A., 1991.- Effect of spacing and cultivation site on some biological and agricultural properties of *Achillea collina* Becker.- *Herba Hungarica*, 30: 15-26.

CHRZANOWSKI G., LESZCZYNSKI B., 2008.- Induced accumulation of phenolics acids in winter triticale (*Triticosecale* Wittm.) under insect feeding.- *Herba Polonica*, 54: 33-40.

COSTELLO M. J., ALTIERI M. A., 1994.- Abundance, growth rate and parasitism of *Brevicoryne brassicae* and *Myzus persicae* (Homoptera: Aphididae) on broccoli grown in living mulches.- *Agriculture, Ecosystems and Environment*, 52: 187-196.

DAVIS J. A., RADCLIFFE E. B., 2008.- Reproduction and feeding behavior of *Myzus persicae* on four cereals.- *Journal of Economic Entomology*, 101: 9-16.

DAVIS J. A., RADCLIFFE E. B., RAGSDALE D. W., 2006.- Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae).- *Environmental Entomology*, 35: 1461-1468.

FAETH S. H., 1991.- Inducible responses and interactions among oak folivores, pp. 293-324. In: *Phytochemical induction by herbivores* (RAUPP M. J., TALLAMY D.W., Eds).- Wiley, New York, USA.

FRANCIS F., HAUBRUGE E., GASPAR C., 2000.- Influence of host plants on specialist / generalist aphids and on the development of *Adalia bipunctata*.- *European Journal of Entomology*, 97: 481-485.

FRANTZ A., PLANTEGENEST M., SIMON J. C., 2010.- Host races of the pea aphid *Acyrthosiphon pisum* differ in male wing phenotypes.- *Bulletin of Entomological Research*, 100: 59-66.

GUTIERREZ A. P., 1996.- *Applied population ecology: a supply/demand approach*.- Wiley, New York, USA.

GUTIERREZ A. P., NEUENSCHWANDER P., VAN ALPHEN J. J. M., 1993.- Factors affecting biological control of cassava mealybug by exotic parasitoids: a ratio-dependent supply-demand driven model.- *Journal of Applied Ecology*, 30: 706-721.

HARVEY J. A., VAN DAM N. M., GOLS R., 2003.- Interactions over four trophic levels: foodplant quality affects development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid.- *Journal of Animal Ecology*, 72: 520-31.

HILL D. S., 1983.- *Agricultural insect pests of the tropics and their control. 2nd ed*.- Cambridge University Press, New York, USA.

HOLST N., RUGGLE P., 1997.- A physiologically based model of pest-natural enemy interactions.- *Experimental and Applied Acarology*, 21: 325-341.

HOPKINS R. J., VAN DAM N. M., VAN LOON J. J. A., 2009.- Role of glucosinolates in insect - plant relationships and multitrophic interactions.- *Annual Review of Entomology*, 54: 57-83.

HUFBAUER R. A., 2001.- Pea aphid-parasitoid interactions: have parasitoids adapted to differential resistance?- *Ecology*, 82: 717-725.

HULTING F. L., ORR D. B., OBRYCKI J. J., 1990.- A computer program for calculation and statistical comparison of intrinsic rates of increase and associated life parameters.- *Florida Entomologist*, 73: 601-612.

JALALI M. A., TIRRY L., DE CLERCQ P., 2009.- Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae).- *Journal of Applied Entomology*, 133: 615-625.

JERMY T., 1984.- Evolution of insect host relationships.- *American Naturalist*, 124: 609-630.

KARBAN R., BALDWIN I. T., 1997.- *Induced responses to herbivory*.- The University of Chicago Press, Chicago, USA.

KARBAN R., MYERS J. H., 1989.- Induced plant responses to herbivory.- *Annual Review of Ecology and Systematics,* 20: 331-348.

KONTODIMAS D. C., PANAGIOTIS A. E., STATHAS G. J., ECONOMOU L. P., 2004.- Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria.- *Environmental Entomology*, 33: 1-11.

KRISCHIK V. A., GOTH R. W., BARBOSA P., 1991.- Generalized plant defense effects on multiple species.- *Oecologia*, 85: 562-571.

KUO M. H., 1992.- Population parameters of the green peach aphid, *Myzus persicae* (Sulzer) reared on radish and potato at various constant temperatures.- *Plant Protection Bulletin (Taiwan)*, 34: 180-191.

LUKASIK I., 2007.- Changes in activity of superoxide dismutase and catalase within cereal aphids in response to plant o-dihydroxyphenols.- *Journal of Applied Entomology*, 131: 209-214.

LUNDGREN J. G., TOEPFER S., HAYE T., KUHLMANN U., 2010.- Haemolymph defence of an invasive herbivore: its breadth of effectiveness against predators.- *Journal of Applied Entomology*, 134: 439-448.

MACKAUER M., WAY M. J., 1976.- *Myzus persicae* Sulz. an aphid of world importance. In: *Studies in biological control. International biological programme 9* (Delucchi V., Ed.).- Cambridge University Press, Cambridge, UK.

MANACHINI B., CINANNI L., 2004.- First indications on the development of *Myzus persicae* (Sulzer) (Rhynchota Aphididae) on different herbaceous species.- *Bollettino di Zoologia Agraria e di Bachicoltura*, 36: 53-62.

MESSENGER P. S., 1964.- Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system.- *Ecology*, 45: 119-131.

MESSINA F. J., TAYLOR R., KARREN M. E., 2002.- Divergent responses of two cereal aphids to previous infestation of their host plant.- *Entomologia Experimentalis et Applicata*, 103: 43-50.

MEYER D., 1957.- Modified randomization tests for nonparametric hypotheses.- *The Annals of Mathematical Statistics*, 28: 181-187.

MORAN P. J., THOMPSON G. A., 2001.- Molecular response to aphid feeding in *Arabidopsis* in relation to plant defense pathways.- *Plant Physiology*, 125: 1074-1085.

OTHA I., OTHAISHI M., 2002.- Life history parameters of *Myzus persicae* (Sulzer) (Homoptera: Aphididae) reared on Qing-geng-cai at four constant temperatures.- *Japanese Journal of Applied Entomology and Zoology*, 46: 259-261.

POELMAN E. H., BROEKGAARDEN C., VAN LOON J. J. A., DICKE M., 2008a.- Inducing herbivore affects direct defense response against subsequent colonist: contrasting consequences for species abundance in the field.- *Molecular Ecology*, 17: 3352-3365.

POELMAN E. H., GALIART R. J. F. H., RAAIJMAKERS C. E., VAN LOON J. J. A., VAN DAM N. M., 2008b.- Performance of specialist and generalist herbivores feeding on cabbage cultivars is not explained by glucosinolate profile.- *Entomologia Experimentalis et Applicata*, 127: 218-228.

RAUPP M. J., TALLAMY D. W., 1990.- *Phytochemical induction by herbivores*.- Wiley, New York, USA.

RHOADES D. F., 1979.- Evolution of plant chemical defense against herbivores, pp. 3-54. In: *Herbivores: their interactions with secondary plant metabolites*. (ROSENTHAL G. A., JANZEN D. H., Eds).- Academic Press, New York, USA.

SCHOWALTER T. D., 2006.- *Insect ecology. An ecosystem approach*.- Academic Press, London, UK.

SHAHIDI-NOGHABI S., VAN DAMME E. J. M., SMAGGHE G., 2009.- Expression of *Sambucus nigra* agglutinin (SNA-I0) from elderberry bark in transgenic tobacco plants results in enhanced resistance to different insect species.- *Transgenic Research*, 18: 249-259.

SMITH R. L., SMITH T. M., 2001.- *Ecology and field biology. 6th ed*.- Benjamin Cummings, Longman, New York, USA.

SCHMITZ G., 1998.- The phytophagous insect fauna of *Tanacetum vulgare* L. (Asteraceae) in Central Europe.- *Beiträge zur Entomologie*, 48: 219-235.

SOBHANI V. P., 1970.- Biologie, Morphologie und phytopathologische Bedeutung der Macrosiphoniella-Arten und Dactynotus-Art der Schafgarbe (Homoptera: Aphididae).- *Zeitschrift für Angewandte Zoologie*, 57: 145-195; 265-301.

STOUT M. J., WORKMAN K. V., BOSTOCK R. M., DUFFEY S. S., 1998.- Specificity of induced resistance in the tomato, *Lycopersicon esculentum*.- *Oecologia*, 113: 74-81.

STREHLER B. L., 1977.- Time, cells and aging, pp. 103-125. In: *VI Ultimate effects of cellular aging-mortality-a review of theories of mortality* 2nd ed.- Academic, New York, USA.

TRAW M. B., DAWSON T. E., 2002.- Reduced performance of two specialist herbivores (Lepidoptera: Pieridae; Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants.- *Environmental Entomology*, 31: 714-722.

TREWHELLA K. E., LEATHER S. R., DAY K. R., 1997.- Insect induced resistance in Lodgepole pine: effects on two pine feeding insects.- *Journal of Applied Entomology*, 121: 129-136.

VAN EMDEN H. F., EASTOP V. F., HUGHES R. D., WAY M. J., 1969.- The Ecology of *Myzus persicae*.- *Annual Review of Entomology*, 14: 197-270.

VIA S., 1991-. Specialized host plant performance of pea aphid is not altered by experience.- *Ecology*, 4: 1420-1427.

WILLUHN G., 2002.- *Teedrogen und Phytopharmaka* 4th ed.- Wissenschaftliche Verlagsgesellschaft, Stuttgart, Germany.

WYATT I. J., BROWN S. J., 1977.- The influence of light intensity, daylenght and temperature on increase rates of four glasshouse aphids.- *Journal of Applied Ecology*, 14: 391-399.

**Authors' addresses:** Giuseppe Carlo LOZZIA (corresponding author: giuseppe.lozzia@unimi.it), Johann BAUMGÄRTNER, Pablo MORLACCHI, DiPSA, Dipartimento di Protezione dei Sistemi agroalimentare e Urbano, Università degli Studi di Milano, via Celoria 2, 20133 Milano, Italy; Annamaria GIORGI, DiProVe, Dipartimento di Produzione Vegetale, Università degli Studi di Milano, via Celoria 2, 20133 Milano, Italy.

Received October 8, 2010. Accepted April 8, 2011.