



## RESEARCH ARTICLE

## OPEN ACCESS

## Reproduction, longevity and life table parameters of *Monosteira unicastata* (Hemiptera: Tingidae) at constant temperatures

Ismael Sánchez-Ramos, Susana Pascual, Cristina E. Fernández, and Manuel González-Núñez

Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, O.A., M.P. (INIA), Plant Protection Dept., Agricultural and Forest Entomology Laboratory. Ctra. de La Coruña Km 7.5, 28040 Madrid, Spain

### Abstract

Information on the effect of temperature on biological parameters of phytophagous insects is one of the tools in IPM programs, as it allows prediction of risk situations in the field. This work reports the effect of temperature on reproductive parameters and longevity of one of the most important current pests of almond orchards in the Mediterranean basin, the poplar lace bug, *Monosteira unicastata* (Mulsant & Rey) (Hemiptera: Tingidae). The temperatures tested were 22, 25, 28, 31, 34 and 37°C, always at 60 ± 10% relative humidity and under a L16:D8 photoperiod. Extreme temperatures had an adverse effect on preoviposition period, total fecundity and daily fecundity while increasing values of oviposition period and adults longevity were registered for decreasing temperatures. Male longevity was higher than female longevity, and mortality pattern differed between sexes for all temperatures but 37°C. The nonlinear Lactin model described accurately the effect of temperature on the intrinsic rate of natural increase of *M. unicastata* populations and predicted the optimum temperature for population increase at 34.1°C, at which the population doubling time is 3.6 days. Produced values of lower and upper thresholds for *M. unicastata* populations were 14.8 and 38.8°C, respectively. This characterizes the poplar lace bug as a very important pest in the Mediterranean basin, with an increasing potential risk in a global warming scenario.

**Additional keywords:** poplar lace bug; reproductive performance; adult survival; intrinsic rate of natural increase; thermal threshold

**Authors' contributions:** ISR, MGN and SP conceived and designed the research. ISR, MGN, SP and CEF performed the experiments. ISR analyzed the data. ISR, MGN and SP wrote the manuscript.

**Citation:** Sánchez-Ramos, I.; Pascual, S.; Fernández, C. E.; González-Núñez, M. (2017). Reproduction, longevity and life table parameters of *Monosteira unicastata* (Hemiptera: Tingidae) at constant temperatures. Spanish Journal of Agricultural Research, Volume 15, Issue 4, e1012. <https://doi.org/10.5424/sjar/2017154-11442>.

**Received:** 23 Mar 2017 **Accepted:** 30 Nov 2017.

**Copyright** © 2017 INIA. This is an open access article distributed under the terms of the Creative Commons Attribution (CC-by) Spain 3.0 License.

**Funding:** Spanish Ministry of Agriculture, Food and Environment (project AEG-08-021-2).

**Competing interests:** The authors have declared that no competing interests exist.

**Correspondence** should be addressed to Ismael Sánchez-Ramos: [ismael@inia.es](mailto:ismael@inia.es)

### Introduction

One of the most important pests of almond trees in the Mediterranean area is the poplar lace bug, *Monosteira unicastata* (Mulsant & Rey) (Maniglia, 1983; Liotta & Maniglia, 1994; García Marí & Ferragut, 2002). This species has been recently detected in the wild also in Canada (Scudder, 2012) where its presence could pose a serious risk for the production areas of almonds in USA, which is by far the largest world producer (USDA, 2017). This insect has been cited attacking other fruit trees such as cherry, peach, plum, pear and forest trees like poplar or willow (Péricart, 1983).

Adults of *M. unicastata* overwinter on the bark of trees, on wild plants or under fallen leaves and in spring they move to young almond leaves where they feed and lay eggs on the underside, thus starting infestations

(Talhok, 1977; Liotta & Maniglia, 1994; García Marí & Ferragut, 2002). Once eggs hatch, nymphs live and feed on the lower side of the leaves, passing through five instars before they reach the adult stage (Talhok, 1977; Péricart, 1983; Sánchez-Ramos *et al.*, 2015). The nymphs are sedentary and gregarious, and if they are disturbed, disperse to regroup later (Bremond, 1938; Vessia, 1961; Neal & Schaefer, 2000). The feeding activity of this insect seriously damages the leaves that weaken, turn yellow and often fall (Talhok, 1977; Liotta & Maniglia, 1994). This defoliation results in smaller fruits, which drop prematurely (Gómez-Menor, 1950; Neal & Schaefer, 2000), and affects negatively to the production of the following year (Liotta & Maniglia, 1994). An additional harmful effect is the accumulation of excrements on the leaves, because this produces a reduction of the gas exchange (Bremond, 1938; Gómez-Menor, 1950).

Very little is known about the reproductive performance and the life table parameters of this lace bug and the scarce information available is based directly on field observations (Bremond, 1938; Vidal, 1939; Vessia, 1961; Maniglia, 1983; Péricart, 1983; Moleas, 1987). Different authors pointed out that overwintering females begin to lay eggs 10-15 days after post-winter emergence (Vessia, 1961; Maniglia, 1983; Moleas, 1987) and they lay 6-15 eggs per day in a single leaf with a total fecundity of 70 eggs (Vidal, 1939; Péricart, 1983). It has been suggested the possibility of parthenogenesis in this insect because some authors found only females after the overwintering recovery (Bremond, 1938; Vidal, 1939). On the contrary, other authors have reported pairs copulating after winter recovery, with males present although in lower proportion with regard to females (Vessia, 1961; Moleas, 1987). According to Vessia (1961), the oviposition can be extended for 20-30 days so the different generations cannot be well differentiated. In accordance with that, it has been indicated that the generations of this insect overlap, so eggs, nymphs and adults coexist simultaneously from June and during the summer (Péricart, 1983). This has been corroborated with field data collected by different authors (Moleas, 1987; Pereira *et al.*, 2008; Marcotegui *et al.*, 2015). The number of generations ranges from 2 to 4, which depends on the geographical area (Péricart, 1983). Thus, in the north of its distribution area only 2 generations occur, whereas in the south, the number of generations can be up to 4. In Spain, there are 3-4 generations with the third generation being the responsible of the greatest injury because at that moment the number of insects is the highest (Gómez-Menor, 1950; García Marí & Ferragut, 2002). The variability in the number of generations can be due to differences in the environmental temperature because insects are poikilothermic organisms so this is one of the main factors affecting their developmental and reproductive rates (Régnière *et al.*, 2012; Régnière & Powell, 2013).

The aim of the present work was to investigate the effect of temperature on reproduction, longevity and life table parameters of *M. unicastata* and to establish the thermal limits for the increase of the populations of this insect. In addition, the possible occurrence of parthenogenesis in this species was checked in the laboratory.

## Material and methods

### Laboratory rearing of *Monosteira unicastata*

A colony of *M. unicastata* was established in the laboratory from wild populations collected in mid spring

from almond trees, *Prunus dulcis* (Mill.) D.A. Webb, placed at the INIA facilities (Madrid). The insects were then transferred to the laboratory and reared on small black poplar plants, *Populus nigra* L., grown from hardwood cuttings, since this possibility is not feasible for almond tree. The cuttings were collected in winter and they were kept refrigerated at 4 °C in 15-20 cm long fragments. When needed, they were planted and grown at 25°C, 70% RH and a L16:D8 photoperiod until the poplars were big enough (about 60 cm height) to be infested. This took approximately one month. Fifty to sixty adults of *M. unicastata* were used to infest four poplar plants. The infested plants were confined in wooden framed cages (60 cm × 50 cm × 45 cm) whose sides were covered with translucent nylon cloth pieces. The frontal nylon cloth piece was removable to manipulate the insects and plants. To maintain the *M. unicastata* population, new poplar plants were grown and periodically infested with adults from the laboratory rearing when the older ones were seriously damaged.

### Plant material

Assays were performed using small rooted cuttings of black poplar. To obtain them, poplar twigs were collected in spring from trees placed in the surroundings of the INIA facilities. Once in the laboratory, the twigs were washed and inspected to discard those with symptoms of infestation, disease or any type of physiological damage. Then, they were divided in small cuttings with a single leaf and a small portion of stem. The cuttings were introduced into nutritive solution (Moutous & Fos, 1973) for a week and those that rooted were selected to be used in the developmental assays, thus assuring that the leaves remained alive during the whole experiment. The rooted cuttings with leaves were introduced into plastic containers (7 cm high × 3.5 cm diameter) with nutritive solution through a small hole (8 mm diameter) made in the lid. The hole was then sealed with plasticine.

### Adult survival and reproduction

The reproduction and longevity of adults were monitored at constant temperatures of 22, 25, 28, 31, 34 and 37°C in environmental chambers (Sanyo MLR-350, Sanyo, Japan). For all temperatures, the other environmental conditions were 60 ± 10% RH and L16:D8 photoperiod. Lace bug subpopulations were acclimated for at least one month at each temperature. No temperatures below 22°C could be tested because of no availability of poplar twigs during the long whole period needed to complete the assays.

Assays were conducted in rearing units consisting of plastic tubes (15 cm high × 5.5 cm diameter) closed at the bottom with the upper lid of a 5.8 diameter Petri dish and covered at the upper part with a piece of translucent nylon cloth fitted with the help of a rubber band, thus allowing ventilation on the rearing cell.

A container with a rooted cutting with a leaf as described above was introduced into each rearing unit together with a <24 h adult pair of *M. unicostata*. To obtain males and females, fifth instar nymphs were taken out of the acclimated subpopulations and put inside rearing units together with a poplar rooted cutting. Fifth instar nymphs were identified according to Bremond (1938), Péricart (1983) and Sánchez-Ramos *et al.* (2015). The following day, the new adults were sexed according to Vessia (1961), paired and transferred singly to new rearing units with new poplar rooted cuttings. Forty to forty five pairs, up to 1-day-old, were established for each temperature. Then, the leaves were inspected daily under a stereomicroscope and all the eggs laid counted. Adult pairs were transferred periodically to new rooted cuttings before the eggs hatched. Checking was performed daily until males and females died. A stock of males was kept from the original fifth instar nymphs to replace any which died before the females. At each temperature, the percentage of fertile mating, the preoviposition, oviposition and postoviposition periods, the eggs laid per female per day (daily fecundity), the total number of eggs per female (fecundity), and the male and female longevity were estimated. Curves of mean daily fecundity per female were determined. The starting number of fertile females was used over the oviposition period of the cohort to obtain these curves. Survivorship curves were obtained by using the daily proportion of surviving males and females.

### Life table parameters

Adult survival and reproduction data at each temperature were used to calculate the life table parameters. The pre-reproductive period and survival and the sex ratio (1:1) were obtained from a previous work (Sánchez-Ramos *et al.*, 2015). The intrinsic rate of natural increase,  $r_m$ , that is, innate capacity of increase in idealized populations under idealized environments, was estimated according to the equation given by Birch (1948):

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

where  $x$  is the age in days,  $l_x$  the age-specific survival rate of females (probability at birth of being alive at age  $x$ ), and  $m_x$  the age-specific oviposition rate (mean number of female offspring produced in a unit of time

by a female aged  $x$ ). The net reproductive rate,  $R_0$ , is given by  $R_0 = \sum l_x m_x$ ; the mean generation time,  $T$ , in days, is given by  $T = \ln R_0 / r_m$ ; the finite rate of natural increase,  $\lambda$ , is given by  $\lambda = e^{r_m}$ ; and the population doubling time,  $PDT$ , is given by  $PDT = \ln 2 / r_m$ . The program  $r_m$  2.0 (Taberner *et al.*, 1993) was used to calculate these parameters. This program provides an estimate of the intrinsic rate of natural increase ( $r_m$ ) variance by means of a bootstrap resampling method. The minimum number of replicates used was 500 as recommended by Meyer *et al.* (1986).

### Evaluation of the occurrence of parthenogenesis

Following the procedures described above, a new laboratory population of *M. unicostata* was established with adults collected in mid spring from almond trees located at the INIA facilities (Madrid). This population was maintained in an insectary at 28-30°C, 70% RH and a L16:D8 photoperiod, and these conditions were used also for the experiments.

When the new laboratory colony had enough number of individuals, fifth instar nymphs were collected and individually transferred to rearing units described above. The development of the nymphs was checked daily and when they reached the adult stage, they were sexed, obtaining in this way virgin females. After 12 days, oviposition was checked and females that had laid eggs were transferred to new rearing units and two males added. Again, oviposition was checked after 12 days, and then the adults were removed. The plants with the eggs from virgin females and those from the same females after mating were inspected for egg hatch. The proportion of samples with hatched eggs from virgin and mated females was established.

### Analytical methods

The effect of temperature on the different reproductive and longevity parameters was analysed by general linear models using temperature as a quantitative factor. The best fitted model of the observed data was used to estimate the preoviposition, oviposition and postoviposition periods, number of eggs per female per day, total number of eggs per female and male and female longevity. The general form of the models is:

$$y = a_0 + a_1 T + a_2 T^2 + a_3 T^3 + \dots + a_n T^n + \varepsilon$$

where  $y$  represents the predicted reproductive or longevity variable,  $T$  is temperature (°C),  $a_i$  are parameters associated with the  $i$ -th term of the predictive variable and  $\varepsilon$  the residual error. The model with the highest significant term of temperature was selected. In addition, a general linear model was performed with

sex as categorical factor and temperature as quantitative factor to test for differences in longevity between males and females. Only significant terms were included in the model. Male and female longevity data were previously transformed by  $\ln(x)$  to meet the assumptions of parametric statistics. The  $\ln(x)$  transformation was the one that best modified the distribution of residuals to satisfy the requirements for parametric tests. Also, chi-squared tests were performed to assess the effect of temperature on the percentage of fertile mating. The level of significance was  $p < 0.05$  in all cases. Analyses were done using Statgraphics® Centurion XVI (StatPoint Technologies, 2009).

A Maxima function (Richter & Söndgerath, 1990) was used to fit the mean daily fecundity per female at each temperature. The equation is

$$f(t) = \alpha t e^{(-\tau t)}$$

where  $f(t)$  represents the mean daily fecundity per female,  $\alpha$  and  $\tau$  are parameters, and  $t$  is time expressed in days after the start of oviposition, so that  $t = 1$  is the first day of oviposition.

Survival of males and females at each temperature were fitted by a Weibull function (Pinder III *et al.*, 1978), whose general form is

$$S(t) = e^{-(t/b)^\beta}$$

where  $S(t)$  represents the probability of surviving to a given age,  $t$  is time,  $b$  is the parameter that describes the scale and  $\beta$  is the parameter that describes the shape of the curve. The shape parameter controls the rate of change of the age-specific mortality rate and, therefore, the general form of the survivorship curve (Pinder III *et al.*, 1978). In addition, the patterns of survival obtained for males and females at each temperature were compared by means of Wilcoxon and logrank tests. The Wilcoxon test tends to be sensitive to differences that are most evident early in time. In comparison, the logrank test tends to be more powerful in detecting differences late in time (Martínez & Naranjo, 2010).

The equation developed by Lactin *et al.* (1995) was used to fit the intrinsic rate of natural increase ( $r_m$ ) data obtained for the different temperatures. This model was selected because it provided the best fit when applied to developmental rate data of *M. unicostata* (Sánchez-Ramos *et al.*, 2015). The expression of this model is

$$r_m(T) = e^{\rho T} - e^{\left[\rho T_{max} - \frac{T_{max} - T}{\Delta}\right]} + \lambda$$

where  $T$  is temperature (°C);  $r_m(T)$  is the intrinsic rate of natural increase at temperature  $T$ ;  $T_{max}$  is the supraoptimal temperature at which  $r_m(T) = \lambda$ ;  $\Delta$  is the range of temperatures between  $T_{max}$  and the temperature at which  $r_m(T)$  is maximum;  $\rho$  describes the acceleration of the function from the low-temperature threshold to

the optimal temperature; parameter  $\lambda$  allows the curve to intersect the abscissa at suboptimal temperatures and, thus, allows estimation of a lower threshold. It is the asymptote to which the function trends at low temperatures.

The Maxima, Weibull and Lactin functions were fitted by iterative non-linear regression based on Levenburg-Marquardt algorithm. Models fitting and parameter estimation were obtained using Tablecurve 2D 5.01 (SYSTAT, 2002).

## Results

### Adult survival and reproduction

The effect of temperature was highly significant for the different reproductive parameters analysed (preoviposition period:  $F_{4,229} = 136.89$ ; oviposition period:  $F_{1,224} = 59.64$ ; postoviposition period:  $F_{2,223} = 16.38$ ; fecundity:  $F_{2,223} = 27.41$ ; daily fecundity:  $F_{3,222} = 71.16$ ; male longevity:  $F_{1,224} = 70.44$ ; female longevity:  $F_{2,223} = 51.39$ ;  $p < 0.0001$  in all cases), except for the percentage of fertile matings, which was not affected by temperature ( $\chi^2_5 = 4.557$ ;  $p = 0.4722$ ), being in all cases greater than 87% (Table 1). As temperature increased, the preoviposition period decreased to reach the lowest value (2.2 days) at 34 °C. Above this temperature, the preoviposition period increased again (3.0 days at 37°C), though this increase was much less pronounced than at low temperatures (8.6 days at 22 °C). In general, the oviposition period increased with decreasing temperatures and fecundity and daily fecundity were adversely affected by extreme temperatures. The highest fecundity ( $\approx 224$  eggs per female) was obtained at 28 °C and the maximum number of eggs per female per day (10 eggs) was recorded at 34 °C, whereas the minimum fecundity ( $\approx 93$  eggs per female) was obtained at 37 °C and the minimum daily fecundity ( $\approx 3$  eggs per female per day) was recorded at 22°C. The postoviposition period followed a similar pattern as the preoviposition period with the lowest value (0.4 days) registered also at 34 °C. Male and female longevity increased as temperature decreased until the highest value was reached at 22 °C (Table 1). In addition, males lived significantly longer than females ( $F_{1,449} = 6.61$ ;  $p < 0.02$ ), and there was no significant interaction between temperature and sex with regard to longevity ( $F_{1,448} = 0.52$ ;  $p = 0.2767$ ). The models describing the temperature response of the reproductive and longevity parameters of *M. unicostata* are shown in Table 2.

The Maxima function fitted well the population mean daily fecundity data for all temperatures, with  $R^2$  values greater than 0.82 (Table 3, Fig. 1). Once



**Table 1.** Reproductive parameters and longevity (mean  $\pm$  SE) of *Monosteira unicostata* at six constant temperatures.

Temperature (°C)	Initial n	Fertile matings (%)	Preoviposition period (days)	Oviposition period (days)	Postoviposition period (days)	Fecundity	Daily fecundity	Male longevity (days)	Female longevity (days)
22	44	97.7	8.6 $\pm$ 0.4 (43)	37.9 $\pm$ 3.8 (42)	5.9 $\pm$ 1.6 (42)	120.0 $\pm$ 12.1 (42)	3.2 $\pm$ 0.2 (42)	72.3 $\pm$ 7.1 (42)	52.5 $\pm$ 4.4 (42)
25	40	92.5	4.4 $\pm$ 0.2 (37)	32.3 $\pm$ 2.1 (36)	2.4 $\pm$ 0.4 (36)	179.6 $\pm$ 15.8 (36)	5.4 $\pm$ 0.3 (36)	57.4 $\pm$ 6.2 (36)	39.2 $\pm$ 2.1 (36)
28	45	95.6	3.1 $\pm$ 0.1 (43)	25.7 $\pm$ 2.0 (40)	1.0 $\pm$ 0.4 (40)	223.6 $\pm$ 20.4 (40)	8.5 $\pm$ 0.3 (40)	40.1 $\pm$ 3.9 (40)	29.5 $\pm$ 2.0 (40)
31	40	87.5	3.0 $\pm$ 0.1 (35)	27.8 $\pm$ 2.7 (33)	0.8 $\pm$ 0.2 (33)	209.0 $\pm$ 19.1 (33)	8.0 $\pm$ 0.4 (33)	46.6 $\pm$ 6.1 (33)	31.5 $\pm$ 2.9 (33)
34	40	95	2.2 $\pm$ 0.1 (38)	20.4 $\pm$ 1.5 (38)	0.4 $\pm$ 0.1 (38)	196.1 $\pm$ 14.5 (38)	10.0 $\pm$ 0.4 (38)	29.1 $\pm$ 2.3 (38)	22.7 $\pm$ 1.5 (38)
37	40	95	3.0 $\pm$ 0.1 (38)	13.8 $\pm$ 1.0 (37)	1.9 $\pm$ 0.7 (37)	93.1 $\pm$ 8.9 (37)	6.3 $\pm$ 0.4 (37)	18.9 $\pm$ 1.4 (37)	18.6 $\pm$ 1.1 (37)

Initial n: initial number of pairs established at each temperature. The sample size used to calculate the reproductive and longevity parameters is indicated within brackets after each value.

**Table 2.** General linear models for the temperature response of reproductive and longevity parameters of *Monosteira unicostata*.

Parameter	n	Model
Preoviposition period	234	$y = 883.1960 (226.8660) - 115.8890 (31.7917)T + 5.7231 (1.6512)T^2 - 0.1255 (0.0377)T^3 + 0.0010 (0.0003)T^4$
Oviposition period	226	$y = 69.7861 (5.6948) - 1.4766 (0.1912)T$
Postoviposition period	226	$y = 59.2760 (12.4749) - 3.7308 (0.8673)T + 0.0590 (0.0147)T^2$
Fecundity	226	$y = -1548.16 (237.9690) + 121.1720 (16.5436)T - 2.0701 (0.2803)T^2$
Daily fecundity	226	$y = 66.4144 (40.7419) - 8.8857 (4.2838)T + 0.3861 (0.1477)T^2 - 0.0051 (0.0017)T^3$
Male longevity	226	$y = 141.6950 (11.7619) - 3.3144 (0.3949)T$
Female longevity	226	$y = 182.9030 (41.2642) - 8.3241 (2.8687)T + 0.1058 (0.0486)T^2$

n is the total sample size used to calculate the reproductive and longevity parameters at all temperatures. The model with the highest significant term of temperature ( $p < 0.05$ ) was selected. All models were highly significant ( $p < 0.0001$ ). Values in parentheses are standard errors of the estimated parameters.

oviposition began, a rapid increase in egg production was observed until the maximum daily egg production was reached. The oviposition peaks predicted by the Maxima function were at 12, 9.5, 8, 8.5, 6.2 and 4.7 days for 22, 25, 28, 31, 34 and 37 °C, respectively. After that, a progressive reduction in daily egg production was observed until oviposition stopped.

The  $R^2$  values obtained by the Weibull distribution for survival were greater than 0.98 for both sexes at all temperatures (Table 4). A differential pattern for males and females was obtained in the range of temperatures between 22 and 34 °C, whereas no difference was obtained at 37 °C (Fig. 2, Table 4). Differences were observed late in time for temperatures ranging between 22 and 34 °C, while only at 34 °C differences were also observed early in time.

### Life table parameters

The highest  $r_m$  value (0.19418) and the shortest mean generation time (20.6 days) and PDT (3.6 days) were obtained at 34 °C (Table 5). Similarly, the Lactin model predicted the optimal temperature for development of *M. unicostata* populations at 34.1 °C, with a  $r_m$  of 0.19104. This model provided a good fit ( $R^2$  of 0.9731) of the  $r_m$  values obtained for the different temperatures, establishing the lower and upper thresholds for population increase at 14.8 and 38.8 °C, respectively (Fig. 3).

### Evaluation of the occurrence of parthenogenesis

Twenty-five of forty-six virgin females (54.3%) were able to laid eggs without mating, but none of

**Table 3.** Parameter estimates for the Maxima function describing the mean daily fecundity per female in *Monosteira unicastata* at six constant temperatures.

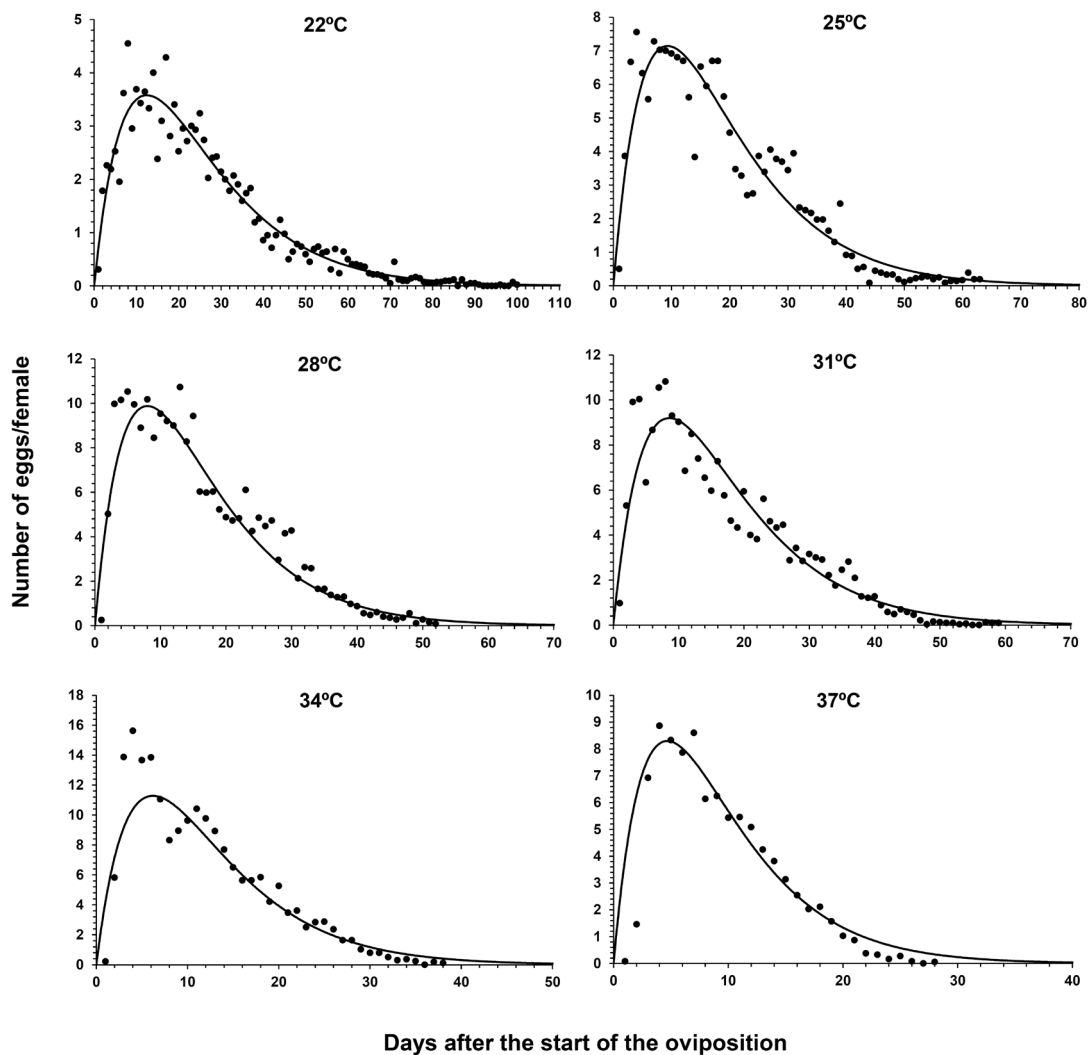
Temperature (°C)	Parameter estimates		$R^2$
	$\alpha \pm SE$	$\tau \pm SE$	
22	$0.7833 \pm 0.0275$	$0.0805 \pm 0.0016$	0.9440
25	$2.0861 \pm 0.1132$	$0.1074 \pm 0.0034$	0.9032
28	$3.3581 \pm 0.1824$	$0.1250 \pm 0.0039$	0.9201
31	$2.9197 \pm 0.1639$	$0.1168 \pm 0.0038$	0.9040
34	$4.9469 \pm 0.4326$	$0.1613 \pm 0.0082$	0.8741
37	$4.8215 \pm 0.5125$	$0.2138 \pm 0.0132$	0.8260

these eggs was able to hatch. Two of these females died before they were mated with the males, so 23 groups of two males and a female were established. Of these, 22 females were able to lay new eggs and in 19 cases (86.4%) these eggs hatched and produced viable nymphs.

## Discussion

The reproductive and life table parameters obtained for *M. unicastata* reveal the good adaptation of this lace bug to the prevailing temperatures in spring and summer in its area of distribution. This had been already shown when the effect of temperature was studied on the developmental rate (Sánchez-Ramos *et al.*, 2015) and had been anticipated before by different authors (Moleas, 1987; Neal & Schaefer, 2000). At temperatures ranging between 25 and 37°C, the populations of this insect are able to double their numbers in less than seven days, what explains the high number of individuals observed at the end of the summer and the damage produced.

The results shown here were obtained at regimes of constant temperatures, so some variability might be expected under the real regimes of fluctuating temperatures registered in the field. However,

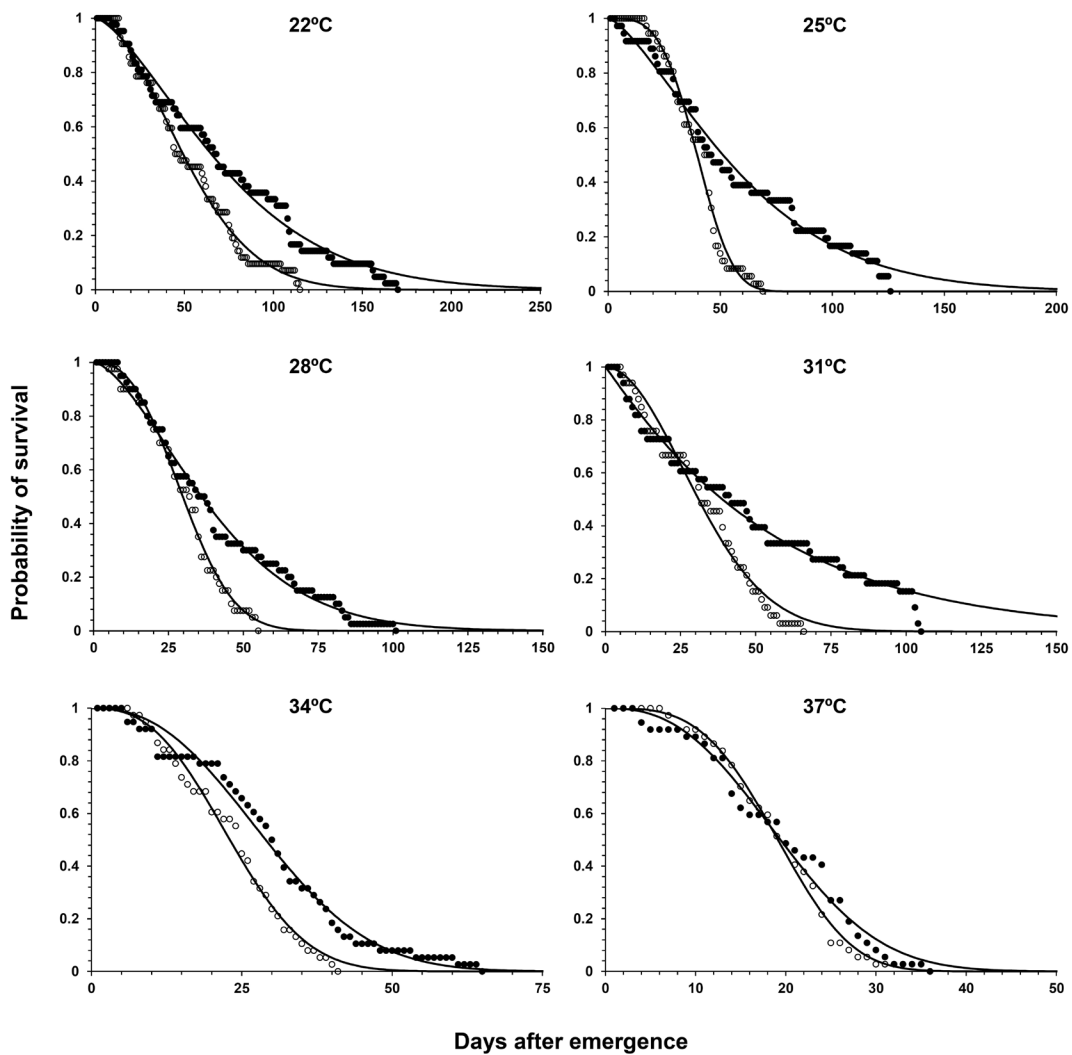


**Figure 1.** Mean daily fecundities (●) of *Monosteira unicastata* and line of best fit by Maxima function (—) at six constant temperatures.

**Table 4.** Parameter estimates for the Weibull function describing the evolution through time of survivorship of *Monosteira unicostata* males and females at six constant temperatures and logrank and Wilcoxon tests obtained at each temperature.

Temperature (°C)	Males			Females			Wilcoxon test		Logrank test	
	b ± SE	β ± SE	R <sup>2</sup>	b ± SE	β ± SE	R <sup>2</sup>	χ <sup>2</sup>	p	χ <sup>2</sup>	p
22	83.4537 ± 0.5360	1.4740 ± 0.0221	0.9879	60.2767 ± 0.3475	1.8211 ± 0.0286	0.9924	3.2011	0.074	7.0404	0.008
25	66.3869 ± 0.4907	1.4108 ± 0.0243	0.9873	43.9396 ± 0.2999	3.5911 ± 0.1178	0.9886	2.4915	0.114	9.0849	0.003
28	45.4575 ± 0.3235	1.5799 ± 0.0268	0.9921	34.3856 ± 0.2278	2.5409 ± 0.0608	0.9928	2.2262	0.136	6.9469	0.008
31	55.1866 ± 0.5125	1.0465 ± 0.0193	0.9850	37.4014 ± 0.4319	1.9489 ± 0.0655	0.9802	1.6811	0.195	7.1108	0.008
34	33.7471 ± 0.2948	2.4083 ± 0.0710	0.9889	26.4662 ± 0.2137	2.6295 ± 0.0792	0.9918	4.6542	0.031	8.1784	0.004
37	22.4207 ± 0.2672	2.5474 ± 0.1096	0.9854	21.3119 ± 0.1341	3.3883 ± 0.0971	0.9958	0.1923	0.661	0.9655	0.326

p values < 0.05 indicate significant differences in the pattern of male and female survival through time.

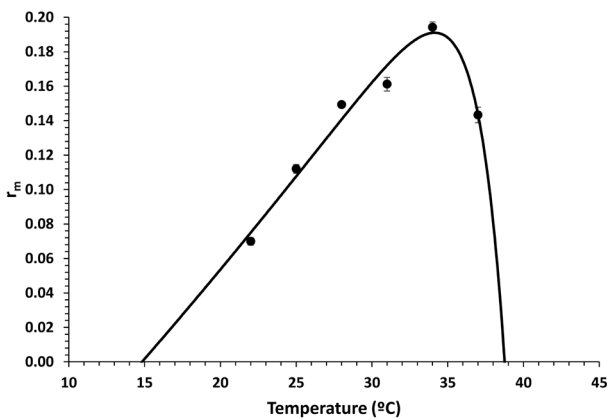


**Figure 2.** Survival probability of males (●) and females (○) of *Monosteira unicostata* and lines of best fit by Weibull function (—) at six constant temperatures.

**Table 5.** Life table parameters for *Monosteira unicastata* at six constant temperatures.

Temperature (°C)	$r_m \pm SE$	(95% CI) <sup>(1)</sup>	$\lambda$	$R_0$	PDT	T
22	0.06994 ± 0.00207	(0.06580 - 0.07408)	1.07244	39.90185	9.9	52.7084
25	0.11203 ± 0.00246	(0.10705 - 0.11701)	1.11854	68.86646	6.2	37.7771
28	0.14933 ± 0.00175	(0.14583 - 0.15282)	1.16105	96.03079	4.6	30.5677
31	0.16120 ± 0.00396	(0.15321 - 0.16920)	1.17492	65.69347	4.3	25.9615
34	0.19418 ± 0.00311	(0.18789 - 0.20047)	1.21431	54.57125	3.6	20.5969
37	0.14333 ± 0.00454	(0.13415 - 0.15251)	1.15411	19.90760	4.8	20.8686

$r_m$ : intrinsic rate of natural increase; <sup>(1)</sup> 95% confidence interval for  $r_m$ ;  $\lambda$ : finite rate of natural increase;  $R_0$ : net reproductive rate; PDT: population doubling time (days); T: mean generation time (days).



**Figure 3.** Lactin model for the intrinsic rate of natural increase ( $r_m$ ) of *Monosteira unicastata* as a function of temperature. (•) Observed  $r_m$  values ± SE; (—) line of best fit by non-linear least squares.  $R^2 = 0.9731$ . Parameters ± SE for non-linear regression curve:  $\rho = 0.0089 \pm 0.0016$ ;  $T_{max} = 41.8742 \pm 3.1297$ ;  $A = 1.8540 \pm 1.3125$ ;  $\lambda = -1.1408 \pm 0.0504$ .

despite this fact, the results are similar, in general, to those reported by other authors coming from field observations. Thus, the preoviposition periods range from a little bit more than 2 days at 34°C to almost 9 days at 22°C. Based on field observations made on almond tree, different authors reported that first eggs were observed around 10-15 days after the emergence of the overwintering adults (Vessia, 1961; Maniglia, 1983; Moleas, 1987). In addition, Maniglia (1983) reported preoviposition periods of 9-11 days for the adults of the first generation and 4-6 for the latter ones. These values agree in general with our findings obtained on black poplar because spring populations are subjected to lower temperatures than summer ones and the daily temperatures registered by Maniglia (1983) through the season ranged between more than 35°C during the day to around 15°C at night. Regarding the oviposition period, Vessia (1961) indicated that it can be as long as 20-30 days according to field observations, what reasonably agree also with the mean values of 14-38 days reported here. However, according to the results by Vidal (1939) in pear tree, *Pyrus communis* L., the

oviposition period that can be deduced from his data about total fecundity and daily fecundity is no more than 12 days, what is shorter than our results and those by Vessia (1961). Moreover, the fecundity reported by Vidal (1939) is also smaller than that obtained in our laboratory assays. Thus, while we have obtained mean values ranging 90-220 eggs per female, Vidal (1939) pointed out that the mean total number of eggs laid by a single female is about 70 eggs. In addition, this author indicated that a female lays 6-15 eggs in a day, whereas we have observed that females were able to lay more than 20 eggs in a day at all temperatures tested, mainly around the days of the oviposition peaks showed in Fig. 1. These differences might be due to the different host species studied. Although pear tree is a common host for this tingid, maybe it is not as suitable as almond tree or black poplar for the reproduction of this species. In addition, since the environmental conditions under which the values reported by Vidal (1939) were obtained are not indicated, sound comparisons cannot be performed with our results. Moreover, it is possible that Vidal (1939) did not consider the whole oviposition period because his values are based in field observations. Curiously, other authors reported that reproduction experiments with females fertilized in captivity were not possible because they died before laying eggs (Vessia, 1961).

Different authors pointed out the possibility of parthenogenesis in *M. unicastata* based on field observations after the winter recovery, in which only females were observed and no copulation with males was registered (Bremond, 1938; Vidal, 1939). Bremond (1938) even isolated fifth instar nymphs and checked that the virgin females obtained from these nymphs were able to lay eggs, similarly to what has been obtained here. However, as Péricart (1983) pointed out, Bremond (1938) did not state if the eggs laid by the virgin females were able to hatch. We have shown here that the eggs laid by females that have not been mated do not hatch and that eggs laid by the same females after copulating with males are viable and hatch. Accordingly, these results suggest that parthenogenesis



does not occur in *M. unicostata*. Similarly, different studies reported that eggs laid by unmated females of other tingids like *Stephanitis pyrioides* (Scott) and *Corythucha cydoniae* (Fitch) failed to hatch (Neal & Douglass, 1988, 1990). This is in accordance with the fact that parthenogenesis is not common in Suborder Heteroptera, since it has been proved only in a few species of families like Mesoveliidae, Miridae and Anthocoridae (Carayon, 1989; Glime, 2015).

For the comparison of the reproductive, longevity and life table parameters among tingids is necessary to consider the differences in suitability of the plants provided as host. For example, the fecundity reported for *C. cydoniae* on *Pyracantha coccinea* M. J. Roemer (Neal & Douglass, 1990) and *Cotoneaster dammeri* C. K. Schneid. (Braman & Pendley, 1993) and for *Corythucha ciliata* (Say) on *Platanus orientalis* L. (Kim *et al.*, 1999) and *Platanus* × *acerifolia* (Aiton) Willd. (Ju *et al.*, 2011) is quite different depending of the host plant species. Similarly, adult longevity of *Stephanitis takeyai* Drake & Maa on *Pieris japonica* (Thunb.) D. Don ex G. Don and *Lyonia elliptica* (C. Wright ex Small) Alain (Tsukada, 1994) and that of *C. cydoniae* on *P. coccinea* (Neal & Douglass, 1990) and *C. dammeri* (Braman & Pendley, 1993) show high variability depending on the host plant. In addition, different lace bugs are adapted to different temperatures and in many cases, reports are provided only for one or a few temperatures, so that is difficult to establish sound comparisons. Taking this into account, it can be concluded that *M. unicostata* reared in black poplar has in general lower fecundities than species such as *S. pyrioides* on *Rhododendron mucronatum* (Blume) G. Don (Neal & Douglass, 1988), *C. cydoniae* on *P. coccinea* (Neal & Douglass, 1990) or *C. ciliata* on *P.* × *acerifolia* (Ju *et al.*, 2011) and similar ones to species such as *Corythucha associata* Osborn & Drake on *Prunus serotina* Ehrh. (Horn *et al.*, 1980), *Gargaphia torresi* Costa on *Gossypium hirsutum* L. (Da Silva, 2004), *Corythucha morrilli* Osborn & Drake on *Helianthus annuus* L. (Rogers, 1977) and *Ambrosia dumosa* (Gray) Payne (Silverman & Goeden, 1979), *Stephanitis pyri* (Fabricius) on *Pyrus malus* L. (Aysal & Kivan, 2008) or *Onchochila simplex* (Herrich-Schaeffer) on *Euphorbia esula* L. (Pecora *et al.*, 1992). For other species like *Corythucha juglandis* (Fitch) on *Juglans nigra* L. (Vogt & McPherson, 1986), *Leptopharsa heveae* Drake & Poor on *Hevea brasiliensis* Müll. Arg. (Cividanes *et al.*, 2004) or *Gargaphia sanchezi* Froeschner on *Phaseolus vulgaris* L. (Van Schoonhoven *et al.*, 1975) lower values of fecundity have been reported. In addition, *M. unicostata* has in general shorter preoviposition periods compared with *C. cydoniae* (Neal & Douglass, 1990; Braman & Pendley, 1993), *C. ciliata* (Kim *et al.*,

1999; Ju *et al.*, 2011), *G. torresi* (Da Silva, 2004), *S. pyri* (Aysal & Kivan, 2008) or *L. heveae* (Cividanes *et al.*, 2004), but they are longer than those reported for *S. pyrioides* (Neal & Douglass, 1988) at similar temperatures. With regard to the oviposition period, this is longer in *C. cydoniae* (Neal & Douglass, 1990) and *S. pyrioides* (Neal & Douglass, 1988) and shorter in *C. ciliata* (Ju *et al.*, 2011). In some cases, shorter oviposition periods are observed at high temperatures and longer at low temperatures, like in *G. torresi* (Da Silva, 2004) and *S. pyri* (Aysal & Kivan, 2008).

Regarding longevity, *S. pyrioides* and *C. cydoniae* live longer than *M. unicostata* (Neal & Douglass, 1988, 1990), although shorter longevity has also been reported for *C. cydoniae* females in a different host plant (Braman & Pendley, 1993). Females of *C. ciliata* (Kim *et al.*, 1999; Ju *et al.*, 2011), *L. heveae* (Cividanes *et al.*, 2004) and *S. pyri* (Aysal & Kivan, 2008) show similar lifespan values than poplar lace bug females, but the longevity of males was shorter than for *M. unicostata*. In the case of *G. torresi*, higher longevity has been reported at low temperatures and shorter at high ones for both males and females (Da Silva, 2004). In addition, *S. takeyai* (Tsukada, 1994) has longer or shorter longevity than *M. unicostata*, depending on the host plant. Moreover, the differences in longevity observed here between males and females have been also reported in *S. pyrioides* (Neal & Douglass, 1988), *C. cydoniae* (Neal & Douglass, 1990) and *G. torresi* (Da Silva, 2004). The higher energy requirements of the females due to egg production could explain these differences in longevity (Da Silva, 2004). However, for other species like *G. sanchezi* (Van Schoonhoven *et al.*, 1975), *C. ciliata* (Ju *et al.*, 2011), *L. heveae* (Cividanes *et al.*, 2004) or *C. morrilli* (Silverman & Goeden, 1979) no differences have been observed and even longer longevity is reported for females of *S. pyri* (Aysal & Kivan, 2008) or *C. morrilli* (Rogers, 1977; Stone & Watterson, 1985) compared to males. In the case of *S. takeyai* (Tsukada, 1994), differences in longevity between males and females depend on the host plant.

Reports on the life table parameters for tingids are scarce. The values obtained here for *M. unicostata* range from 0.070 at 22°C to 0.194 at 34°C, which are approximately similar to those reported for other species. Thus, for *C. ciliata*, the intrinsic rate of natural increase ( $r_m$ ) ranges from 0.048 at 18°C to 0.170 at 28°C (Kim *et al.*, 1999); for *S. pyri*, values from 0.057 at 20°C to 0.129 at 32°C have been cited (Aysal & Kivan, 2008); and in *C. associata*, the capacity for increase ( $r_c$ , an approximate value of  $r_m$  (Laughlin, 1965)) varies from 0.083 after overwintering to 0.141 in the early summer (Horn *et al.*, 1980). In the case of *M. unicostata*, the temperature that provided the

greatest  $r_m$  was 34°C despite the greatest fecundity was recorded at 28°C. This is because this population parameter considers not only the overall egg production but also other parameters like the oviposition rate (daily fecundity) (Table 1) and the speed of development from egg to adult (Sánchez-Ramos *et al.*, 2015) that were the greatest at 34°C. This is similar in *S. pyri*, for which the greatest fecundity was observed at 26°C whereas the greatest  $r_m$  was obtained at 32°C (Aysal & Kivan, 2008). However, in the case of *C. ciliata*, both the maximum fecundity and  $r_m$  were obtained at the same temperature (28°C) (Kim *et al.*, 1999).

The results obtained here contribute to increase the existing knowledge about the effect of temperature on reproduction and population increase of lace bugs and could be used to forecast risk situations when environmental conditions approach to those more suitable for the development of the populations of *M. unicostata*. In addition, this information would be helpful to predict the importance of this pest in a climate change scenario, which would allow this insect to colonize other crops and growing areas different to those already exploited. Data indicate that this pest has a very high potential to invade areas located north of its present distribution area in the Mediterranean basin and south of its recently discovered new distribution area in Canada. On the other hand, increasing temperatures in southern areas does not probably have an effect on populations of *M. unicostata*. Therefore, it is possible that the distribution area of this insect will widen in the near future.

## Acknowledgements

The authors thank H. Sixto [Department of Silviculture and Management of Forest Systems, Forest Research Centre (CIFOR)], INIA, Madrid, for providing the cuttings of poplar.

## References

- Aysal T, Kivan M, 2008. Development and population growth of *Stephanitis pyri* (F.) (Heteroptera: Tingidae) at five temperatures. *J Pest Sci* 81: 135-141. <https://doi.org/10.1007/s10340-008-0198-9>
- Birch LC, 1948. The intrinsic rate of natural increase of an insect population. *J Anim Ecol* 17: 15-26. <https://doi.org/10.2307/1605>
- Braman SK, Pendley AF, 1993. Temperature, photoperiod, and aggregation effects on development, diapause, reproduction, and survival in *Corythucha cydoniae* (Heteroptera: Tingidae). *J Entomol Sci* 28: 417-426. <https://doi.org/10.18474/0749-8004-28.4.417>
- Bremond P, 1938. Le faux-tigre des arbres fruitiers (*Monostira unicostata* Muls.) au Maroc. *Rev Pathol Vég Entomol Agric Fr* 25: 294-307.
- Carayon J, 1989. Parthénogénèse constante prouvée chez deux Hétéroptères: le miride *Campyloneura virgula* et l'anthocoride *Calliodis maculipennis*. *Ann Soc Entomol Fr* 25: 387-391.
- Cividanes FJ, Fonseca FS, Galli JC, 2004. Biología de *Leptopharsa heveae* Drake & Poor (Heteroptera: Tingidae) e a relação de suas exigências térmicas com a flutuação populacional em seringueira. *Neotrop Entomol* 33: 685-691. <https://doi.org/10.1590/S1519-566X2004000600005>
- Da Silva CAD, 2004. Efeitos da temperatura no desenvolvimento, fecundidade e longevidade de *Gargaphia torresi* Lima (Hemiptera, Tingidae). *Rev Bras Entomol* 48 (4): 547-552. <https://doi.org/10.1590/S0085-56262004000400018>
- García Marí F., Ferragut F, 2002. Las plagas agrícolas. MV Phytoma-España SL, Valencia, Spain. 400 pp.
- Glime JM, 2015. Aquatic Insects: Hemimetabola - Hemiptera. In: Bryophyte Ecology, Vol. 2. Bryological Interaction; Glime JM (ed.). Chapter 11-7. Ebook sponsored by Michigan Technol Univ and the Int Assoc of Bryologists.
- Gómez-Menor J, 1950. La chincheta del almendro (*Monostira unicostata* Mulsant). *Bol Patol Veg Entomol Agric* 17: 97-110.
- Horn KF, Wright CG, Farrier MH, 1980. Bionomics of *Corythucha associata* Osborn and Drake. *J Georgia Entomol Soc* 15 (3): 317-327.
- Ju RT, Wang F, Li B, 2011. Effects of temperature on the development and population growth of the sycamore lace bug, *Corythucha ciliata*. *J Insect Sci* 11: 16. <https://doi.org/10.1673/031.011.0116>
- Kim GH, Choi MH, Kim JW, 1999. Effects of temperatures on development and reproduction of the sycamore lace bug, *Corythucha ciliata* (Hemiptera, Tingidae). *Kor J Appl Entomol* 38: 117-121. [In Korean: English abstract].
- Lactin DJ, Holliday NJ, Johnson DL, Craigen R, 1995. Improved rate model of temperature-dependent development by arthropods. *Environ Entomol* 24: 68-75. <https://doi.org/10.1093/ee/24.1.68>
- Laughlin R, 1965. Capacity for increase: A useful population statistic. *J Anim Ecol* 34: 77-91. <https://doi.org/10.2307/2370>
- Liotta G, Maniglia G, 1994. Variations in infestations of the almond tree in Sicily in the last fifty years. *Acta Hort* 373: 277-285. <https://doi.org/10.17660/ActaHortic.1994.373.40>
- Maniglia G, 1983. Osservazioni biologiche sulla *Monostira unicostata* Muls. et Rey (Rhynchota-Tingidae) in Sicilia. *Phytophaga* 1: 27-40.

- Marcotegui A, Sánchez-Ramos I, Pascual S, Fernández CE, Cobos G, Armendáriz I, Cobo A, González-Núñez M, 2015. Kaolin and potassium soap with thyme essential oil to control *Monosteira unicostata* and other phytophagous arthropods of almond trees in organic orchards. *J Pest Sci* 88: 753-765. <https://doi.org/10.1007/s10340-015-0659-x>
- Martínez RLMC, Naranjo JD, 2010. A pretest for choosing between logrank and wilcoxon tests in the two-sample problem. *Metron* 68: 111-125. <https://doi.org/10.1007/BF03263529>
- Meyer JS, Ingersoll CG, McDonall LL, Boyce MS, 1986. Estimating uncertainty in population growth rates: Jackknife vs. Bootstrap techniques. *Ecology* 67: 1156-1166. <https://doi.org/10.2307/1938671>
- Moleas T, 1987. Etologia, ecologia e controllo della *Monosteira unicostata* Muls. et Rey sul mandorlo in Puglia. *Difesa Piante* 10: 469-483.
- Moutous G, Fos A, 1973. Essais de rhizogénèse chez la feuille de Vigne isolée. *Rev Zool Agr Pathol Premier trimestre*: 27-32.
- Neal Jr JW, Douglass LW, 1988. Development, oviposition rate, longevity, and voltinism of *Stephanitis pyrioides* (Heteroptera: Tingidae), an adventive pest of azalea, at three temperatures. *Environ Entomol* 17: 827-831. <https://doi.org/10.1093/ee/17.5.827>
- Neal Jr JW, Douglass LW, 1990. Seasonal dynamics and the effect of temperature in *Corythucha cydoniae* (Heteroptera: Tingidae). *Environ Entomol* 19: 1299-1304. <https://doi.org/10.1093/ee/19.5.1299>
- Neal JW, Schaefer CW, 2000. Lace Bugs (Tingidae). In: *Heteroptera of economic importance*; Schaefer CW, Panizzi AR (eds.). pp: 85-138. CRC Press, Boca Raton, FL, USA. <https://doi.org/10.1201/9781420041859.ch4>
- Pecora P, Rizza A, Stazi M, 1992. Biology and host specificity of *Oncochila simplex* (Hem.: Tingidae), a candidate for the biological control of leafy spurge *Euphorbia esula* L. "complex". *Entomophaga* 37 (1): 79-89. <https://doi.org/10.1007/BF02372976>
- Pereira JA, Pereira S, Armendáriz I, Bento A, 2008. Ciclo biológico e estragos associados a monosteira, *Monosteira unicostata* (Mulsant & Rey, 1852), em amendoeira, no Planalto Mirandês. *Actas do I Congresso Nacional de Produção Integrada e VIII Encontro Nacional de Protecção Integrada*. Moura MLRM (ed.). Escola Superior Agrária de Ponte de Lima, Ponte de Lima (Portugal), Nov 20-21. pp: 225-231.
- Péricart J, 1983. Faune de France. 69. Hémiptères Tingidae Euro-méditerranéens, Fédération Française des Sociétés de Sciences Naturelles, Paris. 618 pp.
- Pinder III JE, Wiener JG, Smith MH, 1978. The Weibull distribution: a new method of summarizing survivorship data. *Ecology* 59: 175-179. <https://doi.org/10.2307/1936645>
- Régnière J, Powell J, Bentz B, Nealis V, 2012. Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. *J Insect Physiol* 58: 634-647. <https://doi.org/10.1016/j.jinsphys.2012.01.010>
- Régnière J, Powell JA, 2013. Animal life cycle models (Poikilotherms). In: *Phenology: An integrative environmental science*; Schwarz MD (ed.). pp: 295-315. Springer.
- Richter O, Söndgerath D, 1990. Parameter estimation in ecology: The link between data and models, VCH Verlagsgesellschaft, Weinheim, Germany. 218 pp.
- Rogers CE, 1977. Laboratory biology of a lace bug on sunflower. *Ann Entomol Soc Am* 70: 144-145. <https://doi.org/10.1093/aesa/70.1.144>
- Sánchez-Ramos I, Pascual S, Fernández CE, Marcotegui A, González-Núñez M, 2015. Effect of temperature on the survival and development of the immature stages of *Monosteira unicostata* (Hemiptera: Tingidae). *Eur J Entomol* 112: 664-675. <https://doi.org/10.14411/eje.2015.087>
- Scudder G, 2012. *Monosteira unicostata* (Mulsant & Rey) (Hemiptera: Tingidae) established in North America, with a key to the genera of Tingidae in Canada. *Entomol Am* 118: 295-297. <https://doi.org/10.1664/12-RA-026.1>
- Silverman J, Goeden RD, 1979. Life history of the lacebug, *Corythucha morrilli* Osborn and Drake, on the ragweed, *Ambrosia dumosa* (Gray) Payne, in Southern California (Hemiptera-Heteroptera: Tingidae). *Pan-Pac Entomol* 55 (4): 305-308.
- StatPoint Technologies, 2009. *Statgraphics® Centurion XVI User Manual*, Statpoint Technologies, Warrenton, VA, USA. 297 pp.
- Stone JD, Watterson GP, 1985. Effects of temperature on the survival and development of the morrill lace bug (Heteroptera: Tingidae) on guayule. *Environ Entomol* 14: 329-331. <https://doi.org/10.1093/ee/14.3.329>
- SYSTAT, 2002. *TableCurve 2D 5.01 for Windows User's Manual*, SYSTAT Software Inc, Richmond, CA, USA.
- Taberner A, Castañera P, Silvestre E, Dopazo J, 1993. Estimation of the intrinsic rate of natural increase and its error by both algebraic and resampling approaches. *Compu Appl Biosci* 9: 535-540. <https://doi.org/10.1093/bioinformatics/9.5.535>
- Talhok AS, 1977. Contribution to the knowledge of almond pests in East Mediterranean countries. VI. The sap-sucking pests. *Z Angew Entomol* 83: 248-257. <https://doi.org/10.1111/j.1439-0418.1977.tb02396.x>
- Tsukada M, 1994. The effect of temperature on the development and longevity of the andromeda lace bug, *Stephanitis takeyai* (Heteroptera: Tingidae) on its two main host plants, *Pieris japonica* and *Lyonia elliptica*. *Appl Entomol Zool* 29: 571-576. <https://doi.org/10.1303/aez.29.571>
- USDA, 2017. *Tree nuts: World markets and trade*. United States Department of Agriculture, Foreign Agricultural Service. 4 pp.

- Van Schoonhoven A, Burbano F, Arenas R, 1975. Notes on the biology of the lace bug *Gargaphia sanchezi* (Hemiptera, Tingidae) a pest of beans (*Phaseolus vulgaris*). Turrialba 25: 237.
- Vessia R, 1961. Studio morfo-biologico della *Monosteira uncostata* Muls. et Rey (Hemiptera - Heteroptera - Tingidae) e difesa del mandorlo. Ann Sper Agrar n.s. suppl. 15: 1-48.
- Vidal JP, 1939. Le faux tigre du poirier (*Monosteira uncostata* Mls. Hem. Heter.). Bull Soc Hist Nat Afr N 30: 329-336.
- Vogt TE, McPherson JE, 1986. Life history and laboratory rearing of *Corythuca juglandis* (Hemiptera: Tingidae) with descriptions of immature stages. Great Lakes Entomol 19: 221-233.