

Life Table and Population Parameters of *Nasonovia ribisnigri* (Homoptera: Aphididae) at Different Constant Temperatures

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ABSTRACT Age-specific life tables of the lettuce aphid, *Nasonovia ribisnigri* (Mosley), feeding on lettuce were determined at different constant temperatures under controlled conditions. Our results showed that the proportion of alates increased with increasing temperatures, remaining below 7% at 16°C and increasing to 40–57% at a temperature above 20°C. The longest developmental time of apterous aphids was obtained at 8°C (31.5 d), and the shortest was at 26°C (6.2 d), whereas the developmental time of alates was always 0.7–1.1 d longer than for apterous. Most aphids needed four instars to reach adult stage, but at 8, 26, and 28°C, many individuals passed through five or six molts. Age-specific survivorship (l_x) was always above 90% at the temperature range of 16–24°C. Mortality rate (q_x) was rather low but constant at 8°C. However, mortality was high at 28°C and occurred mainly in the last nymphal instars and adult stage. Unexpectedly, no nymphs were produced by the adult morphs at 28°C, but effective fecundity was high at 8°C. Fecundity for alates was always lower than for the apterous aphids at the same temperature. The largest intrinsic rate of natural increase (r_m), and the mean relative growth rate (RGR) occurred at 24°C, for both apterous and alate morphs, and the lowest at 8°C. Our results show that lettuce aphid is better adapted to survive and reproduce at low (8°C) than at high (28°C) temperatures, and its best performance occurred at 20–24°C.

KEY WORDS *Nasonovia ribisnigri*, lettuce aphid, survival, fecundity, population parameters

THE LETTUCE APHID, *Nasonovia ribisnigri* (Mosley), is a major pest of lettuce (*Lactuca sativa* L.) crops distributed in temperate regions of Europe, where it originates (Blackman and Eastop 1984, Reinink and Dieleman 1993, Parker et al. 2002, Nebreda et al. 2004). It has recently become a major pest of outdoor and indoor lettuce crops worldwide (Emmett 1992), including western United States (Palumbo 2000) and New Zealand (Stufkens and Teulon 2003). Also, the aphid invaded Tasmania in 2004 and, therefore, has become a serious threat to Australian lettuce production (Teulon 2004).

The life cycle of *N. ribisnigri* is holocyclic heteroecious between its primary *Ribes* sp. and secondary hosts such as Asteraceae (*Cichorium* sp., *Crepis* sp., *Hieracium* sp., *Lactuca* sp., *Lampsana* sp.), Scrofulariaceae (*Euphrasia* sp., *Veronica* sp.), and Solanaceae (*Nicotiana* sp., *Petunia* sp.) species (Blackman and Eastop 1984).

Nasonovia ribisnigri deposit their young near the terminal growing young leaves of lettuce (Palumbo 2000) and colonize the wrapper leaves inside the developing heads (Mackenzie and Vernon 1988), causing leaf distortion and vigor reduction in seedlings. At harvest, they present a significant cosmetic problem

because the presence of living aphids on the leaves reduces the market value or makes lettuce totally unmarketable. Physical postharvest treatments (vacuum and controlled atmosphere with CO₂) could be a valuable strategy to reduce cosmetic damage (Liu 2003).

The living and feeding site preference of the lettuce aphid reduces the efficacy of insecticide treatments, and therefore, an increasing number of applications of broad-spectrum pesticides are needed to control the pest (Chaney and Wunderlich 2000). This practice has resulted in rapid resistance to several insecticides (Rufingier et al. 1997, Barber et al. 1999) and accumulation of unacceptable pesticide residues (Sances et al. 1993). Implementation of integrated pest management (IPM) programs are needed to avoid or reduce these risks in lettuce crop production (Chaney and Wunderlich 2000).

Recent studies have addressed the population development, damage, and control of *N. ribisnigri* on head lettuce (Palumbo 2000, Palumbo and Hannan 2002), phenology to forecast infestation (Collier et al. 1994), and distribution within fields and plants (Mackenzie and Vernon 1988). In the same way, the biology of *N. ribisnigri* on three different lettuce cultivars was studied under laboratory conditions (La Rossa et al. 2000), and their life table parameters were compared (Vasicek et al. 2002).

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Temperature being the main abiotic factor affecting population growth and life statistics of aphids (Messenger 1964, Howe 1967, Andrewartha 1973). Several works have been published on the relationships between temperature on population growth and life table statistics of various aphid species (Michels and Behle 1988, Michels and Behle 1989, Kieckhefer et al. 1989, Kieckhefer and Elliott 1989, Asin and Pons 2001). It is also known that population development of *N. ribisnigri* in the field is well correlated with heat unit accumulation (Palumbo 2000, Liu 2004). However, little information exists on how specific constant temperature affects *N. ribisnigri* life table statistics under controlled conditions.

The aim of this work was to study the effects of different constant temperature on the life table statistics of *N. ribisnigri* feeding on lettuce plants. This information will be used to develop a degree-day based phenological model for effective forecasting of the occurrence of *N. ribisnigri* in the field.

Materials and Methods

Lettuce Plants. Seeds of a romaine type were sown in plastic pots (10 cm diameter) containing a mixture of soil and vermiculite (50:50). Each seedling was transplanted at the cotyledon stage to individual pots (60 replicates). Plants were used to begin the experiments when they reached the one-leaf stage. Three times a week the seedlings were irrigated with nutritive solution 20:20:20 (N:P:K; Nutrichem 60; Miller Chemical and Fertilizer, Hanover, PA). The seedlings were maintained in a growth chamber at a temperature of 26:20°C (day:night) and a photoperiod of 14:10 h (L:D) until the experiments began.

Aphid Colony. *Nasonovia ribisnigri* adults were obtained from a laboratory culture initiated from the progeny of one virginoparous apterous female collected in a lettuce field at Villa del Prado (Madrid, Spain) in 1999 and maintained on lettuce cultivar "Cazorla" inside insect-proof cages in a growth chamber at a temperature of 23:18°C (day:night) and a photoperiod of 16:8 h (L:D).

Experimental Conditions. Aphids of nearly equal age and weight were selected to start the experiments. For this purpose, 10 alate adult aphids from the colony were placed for 24 h in a plastic cage (9 cm diameter and 3 cm high) containing two filter paper disks and one lettuce leaf. The petiole of the leaf was wrapped with absorbent paper and was inserted into an eppendorf tube (1.5 ml) containing water, so that the leaf could maintained turgor as long as possible. After 24 h, adults were removed, and newly born nymphs were collected and reared on lettuce leaves in plastic cages as described above until they reached the adult stage. Lettuce leaves were replaced every 2–3 d during this period. Aphids were removed just after they reached the adult stage and introduced for 12 h in new plastic cages to collect newborn nymphs. These nymphs of the same age were used to begin the experiments. Cohorts of 60 first-instar nymph were individually placed on individual lettuce seedlings and maintained

inside an environmental growth chamber (MLR-350; Sanyo, Gallenkamp PCL, UK). Each study was conducted at a fixed constant temperature (8, 12, 16, 20, 24, 26, and $28 \pm 0.5^\circ\text{C}$). All experiments were conducted at a photoperiod of 14:10 h (L:D) and a relative humidity of $60 \pm 5\%$. The growth chamber was equipped with 15 daylight fluorescent (40 W) lamps that provided $15.3 \mu\text{mol}/\text{m}^2/\text{s}$ of light intensity to the plants located ≈ 20 cm from the light source.

Each nymph was observed daily to record the timing and number of nymphal stadia produced and the mortality at the same time of the day (1000–1200 hours). The presence of exuviae was used to determine molting. When the aphids reached adult stage, the morph, number of progeny per adult, and adult mortality were recorded daily during a time equivalent to the time from birth to onset of reproduction, also called prereproductive period (d) (Wyatt and White 1977). The neonate nymphs were removed daily with a fine-hair brush. Developmental time for each instar and the total developmental time from birth to adulthood for both alate and apterous aphids were calculated for each individual at each temperature.

Calculation of Life-Table Statistics. Mortality, expressed as a mortality rate (qx) was calculated as follows: $qx = dx/nx$, where x = age interval (day), dx = number dying during the age interval x to $x + 1$, and nx = number of survivors at start of age interval x .

Age-specific survival (lx) and age-specific fecundity (mx) (Price 1984) were calculated for each morph and temperature. The product of age-specific survival and age-specific fecundity called reproductive expectation ($lxmx$) was calculated during a time equivalent to the prereproductive period. The sum of reproductive expectation ($\sum lxmx$) calculated as described above was used as a measure of population growth at each of the temperatures used in our study.

Other population parameters such as intrinsic rate of natural increase (r_m) and mean generation time (T_d) were calculated using the Wyatt and White (1977) equation: $r_m = 0.738 (\log_e Md)/d$, where d is the prereproductive period, Md is the number of young produced in a reproductive period equal to d , and 0.738 is a correction factor. Generation time (T_d) was calculated as follows: $T_d = d/0.738$.

For aphids, the mean relative growth rate (\overline{RGR}) is closely and positively correlated with the intrinsic rate of natural increase (r_m) as follows $r_m = 0.86\overline{RGR}$ (Dixon 1987). Therefore, \overline{RGR} can be easily calculated as $\overline{RGR} = (0.86 \log_e Md)/d$.

Statistical Analysis. All the parameters recorded for nymphal and adult stages as well as for apterous and alate morphs at each of the temperatures studied were subjected to a one-factor analysis of variance (ANOVA). Data on the life-table parameters recorded were previously transformed by $\ln(x + 1)$ to reduce heteroscedasticity. Statistical analysis was performed using Superanova v. 1.11 (Abacus Concepts 1989) and Statview 4.01 software (Abacus Concepts 1992) for Macintosh. Mean comparisons of each parameter be-

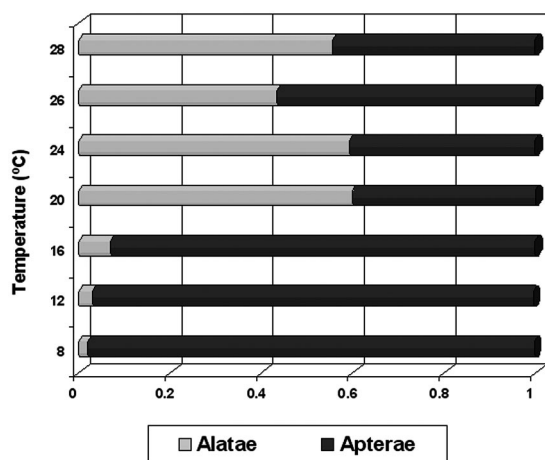


Fig. 1. Proportion of alatae and apterae of *N. ribisnigri* obtained at different temperatures.

the different temperatures were made using least significant difference (LSD) Fisher test ($P = 0.05$) (Fisher 1935).

The relationship between the relative growth rate (RGR) with temperature (T) was calculated and fitted to a curvilinear regression line using SPSS v. 12.05 statistical package (SPSS 2003) and plotted using SigmaPlot v. 7 for Windows (SPSS 2001).

Results

Proportion of Alate Morphs. Temperature had a strong effect on the proportion of alate and apterous individuals in the population of *N. ribisnigri*. The percentage of alates remained rather constant (40–57%) at the range of 20–28°C (Fig. 1). However, at a temperature of $\leq 16^\circ\text{C}$, most of the adult morphs were apterous (93%). Therefore, the data obtained at temperatures of 20–28°C were analyzed separately for apterous and alate morphs. We also observed that the aphids remained pale orange in color at a temperature equal to or above 16°C, but at temperatures below 16°C, aphid color changed to dark brown.

Developmental Time. For apterous aphids, significant differences in developmental time were ob-

served in the range between 8 and 26°C ($F = 933.96$, $df = 6,217$; $P < 0.0001$; Table 1). Developmental time decreased with increasing temperatures at the range of 8 (31.5 d) to 26°C (6.3 d), whereas it started to slightly increase at 28°C (7.0 d). Table 1 also shows that the mean developmental time for the first instar nymph was generally longer than for the rest of the nymphal instars.

The developmental time of alates was significantly ($F = 53.94$; $df = 3,85$; $P < 0.0001$) different among the temperature range of 20–26°C, but alates always required more time than apterous to complete the immature stage (Tables 1 and 2). There were no significant differences in the developmental time of alates between 26 and 28°C (Table 2). Data on the developmental time of alates subjected to a temperature $\leq 16^\circ\text{C}$ were not analyzed because very few individuals developed into alates at such low temperatures (Fig. 1).

All of the aphids completed four nymphal instars before reaching the adult stage at temperatures of 12, 16, 20, and 24°C. However at 8°C, 20% of the total aphid population passed through a fifth nymphal instar that lasted 6.8 d (Table 1), and at 26 and 28°C, the percentage of individuals that completed five nymphal instars was 30 and 32.5%, respectively. At 26 and 28°C, some aphids even went into a sixth nymphal instar, but all died before reaching the adult stage. At 8°C fifth-instar nymphs had no mortality, but 50% of them died after reaching the adult stage.

Survival. Age-specific survivorship curves of *N. ribisnigri* among all the temperatures used in our study are shown in Fig. 2. Survival rates (lx) of the total number of aphids was very high at temperatures between 16 and 24°C, reaching a maximum value at 20°C, at which no mortality was recorded. High temperatures (26–28°C) affected the survivorship of *N. ribisnigri* more than low temperatures (8–12°C).

High temperatures (26–28°C) had a higher impact on the mortality rate (qx) of adults and late nymphal instars than on early nymphal instars (Fig. 3). Consequently, the cohorts reared at 26 and 28°C showed an evident type I curve (Slobodkin 1962). However, low temperatures (8°C) induced a rather low but constant mortality to all nymphal instars and adults,

Table 1. Developmental time of nymphal instars of apterous *N. ribisnigri* at different constant temperatures

Temperature (°C)	n^a	Days in stadia ^b					Total ^c
		First	Second	Third	Fourth	Fifth	
8	45	8.8 ± 0.34a	8.4 ± 0.56a	7.0 ± 0.37a	5.7 ± 0.2a	6.8 ± 0.70	31.5 ± 0.42a
12	56	5.2 ± 0.10b	3.2 ± 0.10b	3.9 ± 0.14b	3.4 ± 0.19b	—	15.8 ± 0.27b
16	54	4.2 ± 0.07c	3.1 ± 0.07b	2.2 ± 0.09c	1.9 ± 0.08c	—	11.5 ± 0.20c
20	24	2.6 ± 0.10d	1.4 ± 0.10c	2.0 ± 0.10c	1.9 ± 0.07c	—	8.0 ± 0.14d
24	24	2.0 ± 0.00d	1.0 ± 0.00c	1.8 ± 0.08c	1.7 ± 0.09c	—	6.5 ± 0.13e
26	17	1.9 ± 0.06d	1.2 ± 0.11c	1.9 ± 0.11c	1.1 ± 0.09d	—	6.3 ± 0.11e
28	4	2.0 ± 0.40d	1.2 ± 0.25c	1.5 ± 0.29c	2.2 ± 0.48e	—	7.0 ± 0.41de

Means ± SE within a column followed by the same letter are not significantly different ($P < 0.05$; LSD Fisher).

^a No. individuals reaching the adult stage.

^b Between 12 and 24°C, all individuals passed through four instars before reaching the adult stage. At 8°C, 12 individuals passed through a fifth instar.

^c Developmental time (days) for the whole nymphal period (from birth of nymphs until adult stage).

Table 2. Developmental time in days of nymphal instars of alate *N. ribisnigri* at different constant temperatures

Temperature (°C)	n ^a	Days in stadia				Total ^b
		First	Second	Third	Fourth	
20	36	2.7 ± 0.07a	1.6 ± 0.10a	2.6 ± 0.08a	2.2 ± 0.07a	9.2 ± 0.10a
24	35	2.0 ± 0.03b	1.4 ± 0.08ab	1.9 ± 0.05b	1.8 ± 0.05b	7.3 ± 0.08b
26	13	2.0 ± 0.00b	1.5 ± 0.14b	1.7 ± 0.13b	2.4 ± 0.38b	7.9 ± 0.31c
28	5	2.0 ± 0.14b	1.6 ± 0.40ab	2.2 ± 0.50b	2.4 ± 0.51b	8.2 ± 0.20c

Means ± SE within a column followed by the same letter are not significantly different (*P* < 0.05; LSD Fisher).

^a No. individuals reaching the adult stage.

^b Developmental time (days) for the whole nymphal period (from birth of nymphs until adult stage).

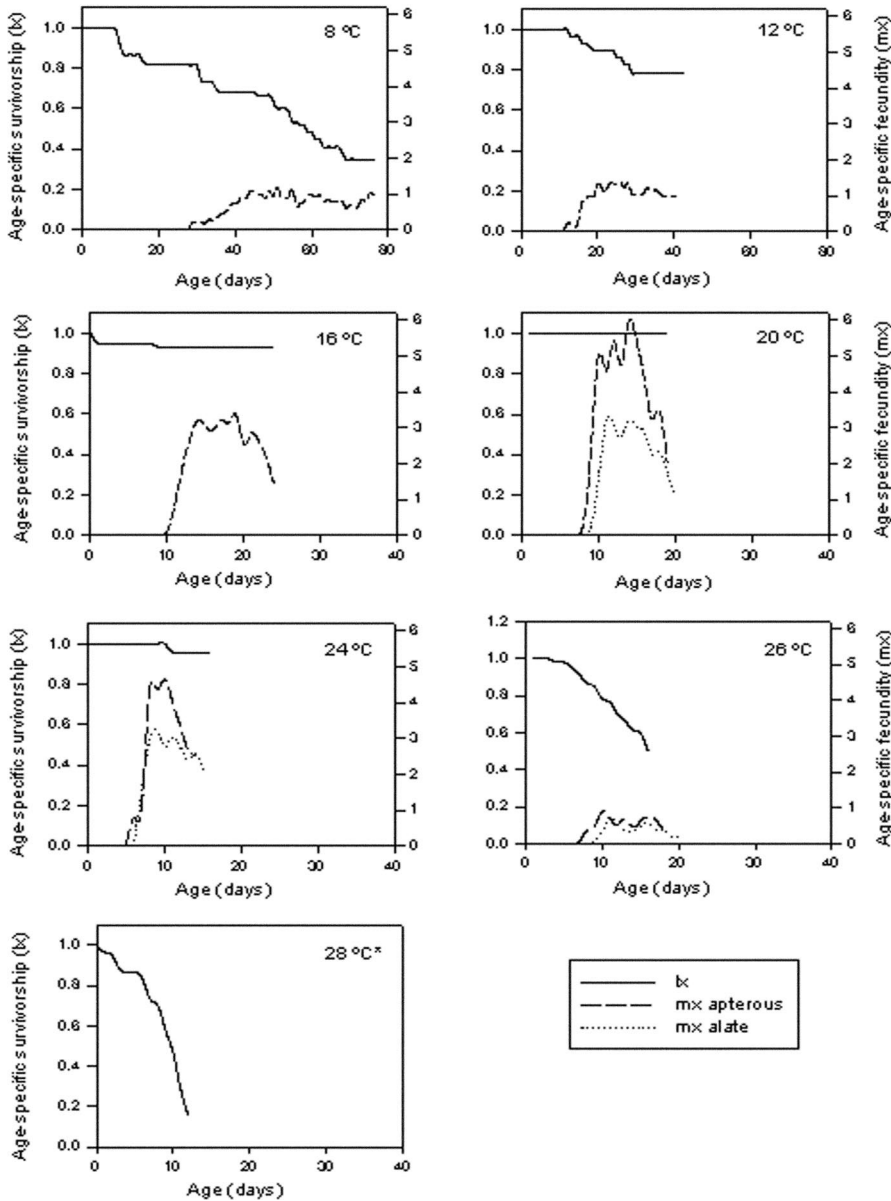


Fig. 2. Age-specific survivorship (*lx*) and age-specific fecundity (*mx*) of *N. ribisnigri* at different constant temperatures. At 28°C, no nymphs were obtained.

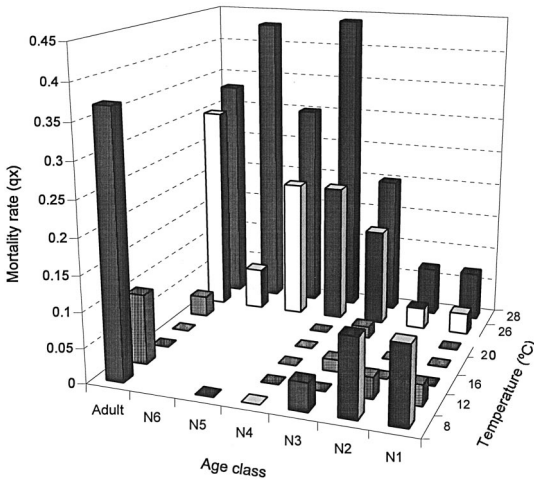


Fig. 3. Mortality rate (qx) of *N. ribisnigri* at different age classes and temperatures.

closely resembling a type II survivorship curve. At a temperature of 12°C, the mortality always remained below 20% (Fig. 2).

Fecundity. All adult aphids were able to reproduce at all temperatures except at 28°C, where no nymphs at all were produced. Reproduction began immediately (<24 h) after the last molt for temperatures in the range of 16–24°C, and therefore, aphid developmental time was similar to the prereproductive period. However, aphids developing at 8, 12, and 26°C had a delay of 2, 2.4, and 3 d, respectively, between their last molt and onset of reproduction.

Figure 2 shows that age-specific fecundity (mx) curves varied substantially among temperatures. At 8°C, the mean number of nymphs/female per day was low (≈ 1 nymph), but remained rather constant during a period of time equivalent to the prereproductive phase (≈ 40 d). The mean daily fecundity (number of nymphs/female) increased with temperature in the range of 12–24°C, but a reduction in fecundity was observed at a temperature of 26°C.

Age-specific fecundity (mx) and fecundity in a period equivalent to the prereproductive time (Md), on average, was higher for apterous than for alate aphids at all of the three temperatures where pair-wise comparisons were possible (Fig. 2; Table 3). Fecundity of apterous aphids was significantly higher at 16 and 20°C compared with the rest ($F = 96.34$; $df = 5,176$; $P < 0.0001$; Table 3). The lowest fecundity was observed at 26°C (3.3 nymphs/female). Fecundity of alates also showed the same general trend: highest fecundity at 20°C and lowest at 26°C (23.6 ± 1.2 and 2.2 ± 0.4 , respectively; $F = 14.53$; $df = 2,72$; $P < 0.0001$).

Population Growth Parameters. The sum of the reproductive expectation of apterous aphids for a time equivalent to the prereproductive period (Σlmx) reached its highest value at 20°C (46.9) and the lowest at 26°C (4.2). The reproductive expectation of alate aphids followed a similar trend (Table 3).

Table 3. Population parameters of apterae and alatae morphs of *N. ribisnigri* at different constant temperatures

Temperature (°C)	n^a	Apterous					Alates				
		$Md \pm SE$	Σlmx	$r_m \pm SE$	$\overline{RGR} \pm SE$	$Td \pm SE$	$Md \pm SE$	Σlmx	$r_m \pm SE$	$\overline{RGR} \pm SE$	$Td \pm SE$
8	22	22.5 ± 2.2a	19.8	0.074 ± 0.02a	0.087 ± 0.002a	47.3 ± 0.6e	—	—	—	—	—
12	48	17.5 ± 0.8b	23.0	0.127 ± 0.02b	0.148 ± 0.002b	24.2 ± 0.4d	—	—	—	—	—
16	53	31.9 ± 0.8c	33.4	0.224 ± 0.04c	0.261 ± 0.005d	15.5 ± 0.2c	—	—	—	—	—
20	24	29.5 ± 1.4c	46.9	0.332 ± 0.06e	0.386 ± 0.007e	11.0 ± 0.2b	27.4	0.255 ± 0.06a	0.297 ± 0.06a	12.5 ± 0.15a	—
24	23	22.1 ± 1.0a	27.2	0.372 ± 0.11f	0.433 ± 0.013f	8.9 ± 0.2a	22.7	0.302 ± 0.06b	0.354 ± 0.08b	9.9 ± 0.1b	—
26	12	3.4 ± 0.5d	4.2	0.173 ± 0.09c	0.206 ± 0.011c	11.6 ± 0.5b	3.3	0.120 ± 0.01c	0.140 ± 0.01c	14.4 ± 0.7c	—

Means ± SE within a column followed by the same letter are not significantly different ($P < 0.05$; LSD Fisher).

^a No. individuals reaching adult stage.

Md , effective fecundity; Σlmx , sum of the product of age-specific survivorship (lx) and age-specific fecundity (mx) during a time equal to a prereproductive period; r_m , intrinsic rate of natural increase; \overline{RGR} , mean relative growth rate; Td , generation time.

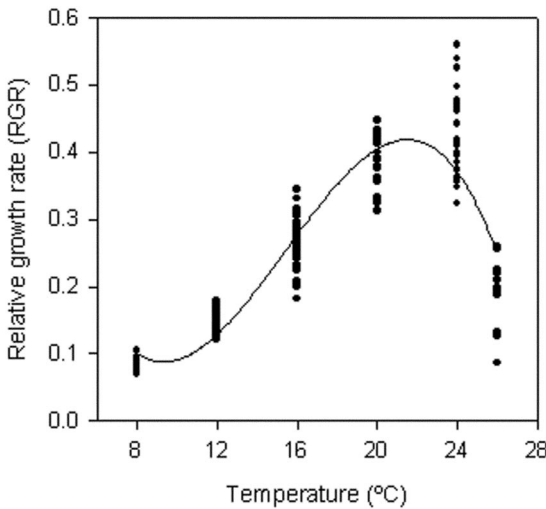


Fig. 4. Relationship between relative growth rate (\overline{RGR} ; dots) and temperature for apterous *N. ribisnigri*. Fitted regression line equation: $y = 0.968 - 0.220T + 0.017T^2 - 0.0004T^3$ ($R^2 = 0.85$).

The intrinsic rate of natural increase (r_m) showed significant differences at the different range of temperatures used in our study both for apterous ($F = 475.64$; $df = 5,175$; $P < 0.0001$) and alates ($F = 69.40$; $df = 2,72$; $P < 0.0001$). The lowest r_m value was observed at 8°C for apterous aphids (0.074) and at 26°C for alate aphids (0.120). The highest r_m value was obtained at 24°C for both apterous and alate aphids (0.372 and 0.302, respectively; Table 3).

Mean relative growth rate (\overline{RGR}) of apterous aphids increased with increasing temperatures from 8 to 24°C (0.087 ± 0.002 and 0.433 ± 0.013 , respectively; $F = 481.43$; $df = 5,176$; $P < 0.0001$). The highest value for \overline{RGR} of alates was recorded also at 24°C (0.354 ± 0.08 ; $F = 69.40$; $df = 2,72$; $P < 0.0001$). The relationship between the \overline{RGR} values of apterous aphids and temperature was curvilinear ($y = 0.968 - 0.220T + 0.017T^2 - 0.0004T^3$; $R^2 = 0.85$), with maximum \overline{RGR} occurring at 24°C (Fig. 4).

There were significant differences in the mean generation time (Td) among temperatures for both apterous ($F = 820.09$; $df = 5,176$; $P < 0.0001$) and alate ($F = 124.193$; $df = 2,75$; $P < 0.0001$) morphs. As opposed to r_m and \overline{RGR} , the mean generation time decreased with increasing temperatures, reaching the lowest value at 24°C for both apterous (8.9 d) and alate aphids (9.9 d; Table 3).

Discussion

Temperature determines the physiological state of poikilothermic organisms, and as a consequence, is the key variable regulating their survival, fecundity, and population growth. Information on how temperature can influence the life cycle of a given insect pest is essential to develop effective integrated pest management (IPM) strategies. The response of aphids to

temperature has been used in the past to develop degree-day based models to forecast aphid outbreaks (Collier et al. 1994, Ro et al. 1998). Dixon (1987) showed that the length of time required for an aphid from birth to adult is variable and dependent on two intrinsic factors, birth weight and whether the morph is winged or unwinged, and two extrinsic factors, food quality and temperature. In our study, food quality was probably affected when aphids developed at a constant temperature of $\geq 26^\circ\text{C}$, because these temperatures are well above the range for optimum development of lettuce (15–20°C) (Flint 1987). Lettuce plants that developed at a constant temperature of $\geq 26^\circ\text{C}$ were unable to form a rosette of leaves, which is the preferred feeding site of *N. ribisnigri*.

Our results reported here show that *N. ribisnigri* was sensitive to changes in temperature, affecting the proportion of alates being produced as well as their developmental time, survival, and fecundity. Low temperatures dramatically reduced the proportion of alates in the population of *N. ribisnigri*. Apterous aphids were the predominant morph at a temperature of $\leq 16^\circ\text{C}$, and the proportion of alates increased to almost 60% at a temperature of 20°C and remained rather constant in the range of 20–28°C. Dixon (1998) found that cereal aphids reared in isolation never give rise to alate forms even if they are reared on plants of poor quality; in consequence, our results suggest that the occurrence of *N. ribisnigri* alates is probably related to an increase of rearing temperature more than with any other factor. Liu (2004) observed that the proportion of *N. ribisnigri* alates under field conditions did not vary significantly with increases in population density. Therefore, an increase in temperature ($T \geq 20^\circ\text{C}$) will have a significant increase in the proportion of *N. ribisnigri* alates being produced in the field, and this will increase seasonal movement and dispersal of the population.

We observed that the developmental time of both alate and apterous morphs of *N. ribisnigri* decreased with increasing temperatures in the range of 8–26°C. The shortest developmental period of *N. ribisnigri* was obtained at 24–26°C (≈ 6 d), a similar period as the one reported for aphids that colonize winter cereals (Dean 1974). Alates of *N. ribisnigri* had a longer developmental time than the apterous morph (0.7–1.1 d longer), which has been observed in other aphid species as well (Liu and Hughes 1987, Kieckhefer et al. 1989, Liu and Yue 2001).

For apterous aphids, low temperatures had a much stronger effect on the duration of the nymphal period than high temperatures. This nonlinear response of *N. ribisnigri* to temperature is clearly observed from 8 to 12°C, because a 4° increase produced a 50% reduction in its developmental time (from 31.5 to 15.8 d), whereas the same 4° increase from 12 to 16°C reduced its developmental time in only 9% (from 15.8 to 11.5 d). Increases in temperature $> 24^\circ\text{C}$ had a very small influence on developmental time of both apterous and alate morphs of *N. ribisnigri*.

Generally, an aphid passes through four nymphal instars in developing from birth to adult (Dixon 1987).

In our study, the number of nymphal instars of *N. ribisnigri* changed with temperature, and a variable number of *N. ribisnigri* individuals developed into a fifth-instar (at 8, 26, and 28°C) or even into a sixth-instar nymph (at 26 and 28°C), in agreement with the results reported by La Rossa et al. (2000). They found that *N. ribisnigri* reared at constant 10°C on three different lettuce cultivars went through five instar nymphs before reaching the adult stage. Similarly, *Diuraphis noxia* (Mordvilko) exhibited a variable number of instars (four to six) during the course of its development at different temperatures (Michels and Behle 1988, Nowierski et al. 1995). Survival of *N. ribisnigri* was more affected by high (26–28°C) than by low temperatures (8°C). The highest survivorship obtained in our study was at 20°C, the same as for *Rhopalosiphum padi* L. and *Macrosiphum avenae* (F.) developing on winter wheat (Dean 1974).

High temperatures were very detrimental to the reproduction of *N. ribisnigri* because no nymphs were produced at 28°C, a result similar to *Sitobion avenae* reared on wheat at a temperature of 30°C (Acreman and Dixon 1989, Asin and Pons 2001). Age-specific fecundity shape curves varied widely with temperature. From 8 to 12°C daily, fecundity was low but remained rather stable during most of the reproductive period, whereas at higher temperatures (16–24°C), fecundity was more concentrated in the first days (2–8 d) of reproduction. Similar reproduction strategies have been observed for *Schyzaphis graminum* (Rondani), *R. padi*, and *D. noxia*, reared on wheat at constant and fluctuating temperatures (Michels and Behle 1989). The temperature associated to the shortest generation time (T_d) and highest potential for population increase (highest r_m value) of *N. ribisnigri* was 24°C for both apterous and alate morphs. However, reproductive expectation was highest at 20°C because no mortality was observed at that given temperature. In a similar way, *A. gossypii* showed the highest r_m value at 25°C on different hosts and rearing conditions (Van Steenis and El-Khawass 1995, Xia et al. 1999), as well as *Myzus persicae* (Sulzer) feeding on Brussels sprouts (*Brassica oleracea* variety 'gemmifera') (El Din 1976).

The best curvilinear fit for the relationship between \overline{RGR} (or r_m) and temperature of *N. ribisnigri* was a third-degree polynomial function of similar shape to the one described for *Therioaphis trifolii* f. *maculata* (Buckton) feeding on different alfalfa cultivars (Ruggle and Gutierrez 1995).

Fecundity and intrinsic rate of population increase of alates was lower than for apterous individuals of *N. ribisnigri*, which means that population growth will increase more rapidly in case that an apterous colonizes a given plant. This reduction in the fecundity of alates has been explained by the fact that winged aphids have smaller gonads (20% reduction in size) than apterous aphids, which seems to be a trade-off between the investment in gonads and lipid reserves needed for flight (Dixon et al. 1993).

This study has shown that *N. ribisnigri* is very sensitive to changes in temperature and that it is very well

adapted to develop and reproduce under low temperature conditions, although the optimum temperature for population increase was in the range of 20–24°C. Our results agree with observations in Arizona on head lettuce crops where *N. ribisnigri* population seemed to increase in early March when the average daily temperature was ≈ 18 –20°C (60–65°F) and had a sharp decline in population abundance in April where daytime highs exceeded 32°C (90°F), concluding that temperature and planting date had a strong influence on the seasonal abundance of the lettuce aphid (Palumbo 2000, Palumbo and Hannan 2002). Because this aphid species is one of the most important pests of lettuce worldwide, and control is always difficult, it is very important to forecast the early occurrence of lettuce aphid in the field. The information reported in our work is essential to develop or improve existing mathematical models as well as to optimize the environmental conditions needed for mass rearing of this aphid as a host for natural enemy production.

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