

Effect of High Temperature on the Growth and Reproduction of Corn Aphids (Homoptera: Aphididae) and Implications for Their Population Dynamics on the Northeastern Iberian Peninsula

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ABSTRACT The development, reproduction and longevity of corn aphids *Rhopalosiphum padi* (L.), *Sitobion avenae* (Fabricius) and *Metopolophium dirhodum* (Walker) were studied at 18, 22, 25, 27.5 and 30°C. Only nymphs of *R. padi* survived at 30°C, but the adult reproductive capacity was very low. *Rhopalosiphum padi* performed better than *M. dirhodum* at all temperatures tested, and better than *S. avenae* over the range of 22–27.5°C. The better performance of *R. padi* was due to a lower nymphal mortality, lower developmental and prereproductive times and a higher intrinsic rate of increase (r_m). *Sitobion avenae* had a higher r_m than *M. dirhodum* at all temperatures. The most suitable temperature for population development was $\approx 28.5^\circ\text{C}$ for *R. padi*, 26.5°C for *S. avenae* and 24.5°C for *M. dirhodum*, suggesting the ability of aphid populations to adapt to high temperatures in the Iberian peninsula. The role of temperature as a key factor in determining aphid population dynamics in the northeastern Iberian peninsula is discussed.

KEY WORDS corn aphids, aphids, corn, temperatures, development, fecundity

THE NORTHEASTERN IBERIAN peninsula has a characteristically Mediterranean climate with a mean maximum temperature of 30°C from June to August and a minimal relative humidity of $\approx 35\text{--}40\%$, and a rainfall slightly above 100 mm). Corn is the main summer arable crop, covering almost 50,000 ha in irrigated lands. The acreage is increasing as more land is under irrigation.

Aphids are common pests of corn in the region (Piqué et al. 1998). Although their economic importance varies with time and space. The major damage, however, is in the first half of the crop season, when they cause direct feeding damage and transmit maize dwarf mosaic virus (Asin and Pons 1999) and barley yellow dwarf luteoviruses (Comas et al. 1993).

Rhopalosiphum padi (L.), *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Walker) are the most abundant aphid species attacking corn in the northeastern Iberian Peninsula (Pons et al. 1994; Asin 2000). The population dynamics of the three aphid species on corn have been studied in the region and showed three distinct periods: (1) aphid settlement and early build-up (from early May to mid-June), (2) aphid scarcity (from early June to mid-August) and (3) late build-up (from mid-August to mid-September) (Pons et al. 1989; Asin 2000). A similar pattern has also been recorded in other countries of the Mediterranean Basin (Moreau 1981, Chansigaud and Vaillant 1987).

The factors affecting the population dynamics have not been sufficiently studied, but some causes have been suggested (Pons et al. 1989): temperature affect-

ing development, reproduction and survival, the regulatory role of natural enemies, and the effect of the host plant on aphid performance. The effect of temperature on aphid performance on winter cereals has been studied by several authors (Dean 1974, Lykouressis 1985, Kieckhefer et al. 1989, Elliot and Kieckhefer 1989, Zhou and Carter 1992, Sengonca et al. 1994). However, no data about aphids feeding on corn are known except those of Kuroli (1984) for *R. padi*. Temperature is the main abiotic factor affecting aphid bionomics (Campbell et al. 1974, Harrington et al. 1995), but geographically separated populations may have differential developmental and population growth rates as affected by temperatures (Kieckhefer et al. 1989; Harrington et al. 1995).

This article reports the effect of temperature on development, reproduction and survival of the corn aphids, *R. padi*, *S. avenae* and *M. dirhodum*, to better understand their population dynamics on corn in Northeastern of the Iberian peninsula, a region with a Mediterranean climate.

Materials and Methods

The aphids used in the experiment were obtained from cultures maintained at the UdL-IRTA (Universitat de Lleida- Institut de Recerca i Tecnologia Agroalimentaria) glasshouse on durum wheat ('Mexa'). Cultures of *R. padi*, *S. avenae* and *M. dirhodum* were established from aphids caught on winter cereals in several places of the irrigated area of Lleida (northeastern Iberian peninsula).

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A low-content DIMBOA (Castañera, personal communication) corn cultivar ('Prisma G-4730', Syngenta Seeds) was used in the experiment. Corn was grown in the glasshouse in clay pots (16 cm in diameter and 15 cm high) until the plants had six complete expanded leaves. Only the central part of the fourth leaf was used in the experiment.

The experiment was conducted in climatic chambers with Gro-lux lights (2000 lx) and with a temperature control of $\pm 1^\circ\text{C}$, $\approx 35\%$ RH, and a photoperiod of 16:8 (L:D) h. The experiment consisted in exposing cohorts of *R. padi*, *S. avenae*, and *M. dirhodum* to a range of constant temperatures according to the temperature regime of the region during the corn crop cycle. Average mean temperatures (from 1990 to 2000) are around 18°C in May, 21°C in June, 24.5°C in July and August, 19.5°C in September, and 14.5°C in October. However, the maximum temperature from the second half of June to August usually exceeds 30°C and there are several hours above this temperature every day. The following temperatures were used: 18, 22, 25, 27.5, and 30°C . In the case of *M. dirhodum* the test at 30°C was not done because at 27.5°C nymphal mortality was 100%.

To confine the aphids, transparent cylindrical plastic cages (53 mm in diameter, 32 mm high) were used. Previous to their use, the cages were immersed in a solution of 0.5% sodium hypochlorite for a day, rinsed with tap water and dried at room temperature. To compare the temperature and relative humidity of the chamber with those inside the cage, temperature and relative humidity loggers (StowAway, Onset Computer, Pocasset, MA) were connected to some cages.

One alate fourth instar (F_0 generation) was caged individually, containing a piece of corn leaf (about 40 mm long) from plants reared in the glasshouse placed on a disc of filter paper wet with distilled water. The resulting alate (F_0) was left in the cage until it had produced 5–10 offspring (F_1 generation) or for a maximum of 3 d, whichever came first. Every day the cage was replaced with a clean one containing a wet disc of filter paper. The piece of leaf was exchanged for a fresh one every 2 d and the aphids were moved to the piece of fresh leaf using a fine camel's-hair brush, to avoid damaging the aphids' mouthparts. However, while the nymphs were in the first instar, the piece of fresh leaf was added into the cage and the old one was not removed, allowing the aphids to change to the new leaf when they wished. The maximum time that a piece of leaf was left within the cage was 4 d. The nymphs were allowed to develop to adults within the cages, and their developmental stage was recorded daily to allow the developmental time (T_d) to be estimated. Nymphal mortality was recorded.

When the F_1 aphids were adults, some of them were caged individually and fed with pieces of corn leaf as before. These aphids were used to determine the following: (1) the day on which their first offspring (F_2 generation) was born; (2) the prereproductive time or number of days from the birth of F_1 to their onset of reproduction (T_{pr}); (3) the effective fecundity (Fe) or number of nymphs produced during a period equiv-

alent to the prereproductive time; (4) the effective reproductive rate (Fe/T_{pr}) for that period; (5) the total fecundity (Ft); (6) the reproductive life (L_r); (7) the total reproductive rate (Ft/L_r); (8) the intrinsic rate of increase (r_m) using Wyatt and White's (1977) equation [$r_m = 0.738 (\log_e Fe)/T_{pr}$]; and (9) the lifetime (L_t).

The aphids in cages were monitored at 24-h intervals. Cast skins and nymphs that died or were born were removed each day from the cages when the aphids were monitored.

Analysis of variance (ANOVA) (PROC GLM, SAS Institute 1989) was used to compare, within each aphid species, the effect of temperature on the variables studied. Means were separated using Student-Newman-Kuels test. Data of percent mortality were normalized using the transformation $y = \arcsin (x/100)^{1/2}$ before the ANOVA was performed.

Kieckhefer et al. (1989) found that the developmental rate of the instars of *S. avenae* fitted very well to Taylor's nonlinear model (1981). We also used this model to fit the relationship between temperature and values of developmental and prereproductive rates and some of the parameters describing reproductive capacity (rates of effective fecundity and total fecundity and intrinsic rate of increase) obtained in the experiment for *R. padi*, *S. avenae* and *M. dirhodum*. Taylor's (1981) model uses the following equations:

$$R(t) = R_{max} \cdot \exp \left\{ -1/2 \cdot [(t - t_u)/c_1]^2 \right\} \quad t < t_u \\ = R_{max} \cdot \exp \left\{ -1/2 \cdot [(t - t_u)/c_2]^2 \right\} \quad t > t_u,$$

where $R(t)$ is the rate of the variable studied, t_u is the temperature at which the maximum rate occurs, R_{max} is the rate at temperature t_u , c_1 , and c_2 are shape parameters describing the spread of the curve, and t is constant temperature. The parameters of the model (R_{max} , t_u , c_1 , and c_2) were estimated using a nonlinear regression procedure (PROC NLIN, SAS Institute 1989).

Results

The temperature inside the cages was very similar to that of the chamber ($\pm 0.1^\circ\text{C}$) but the relative humidity was higher ($\approx 85\%$). The results of nymphal mortality, development and reproductive capacity and longevity of *R. padi*, *S. avenae*, and *M. dirhodum* are shown in Tables 1, 2, and 3, respectively.

Nymphal Mortality. The highest values of nymphal mortality were at 30°C for *R. padi* and *S. avenae*, but whereas at this temperature all nymphs of *S. avenae* died, mortality of *R. padi* was only 45%. Mortality of nymphs of *M. dirhodum* increased with temperature and all the nymphs died at 27.5°C .

Development. The time required for complete development (T_d) decreased for *R. padi* and *S. avenae* when the temperature increased from 18 to 27.5°C the shortest time being observed at the latter. At 30°C *S. avenae* and *M. dirhodum* failed to complete development. The shortest developmental time of *M. dirhodum* was at 25°C .

Table 1. Mortality (%) of overall immature stages of <i>R. padi</i> , <i>S. avenae</i> and <i>M. dirhodum</i> at five constant temperatures						
Temp, °C	<i>n</i>	<i>R. padi</i>	<i>n</i>	<i>S. avenae</i>	<i>n</i>	<i>M. dirhodum</i>
18	80	25.5 ± 3.82bc	72	9.1 ± 2.02d	50	34.1 ± 4.56c
22	75	34.8 ± 3.51b	66	44.0 ± 4.32b	56	43.9 ± 5.13b
25	65	31.7 ± 3.82b	65	31.9 ± 3.93c	62	50.4 ± 5.23b
27.5	78	18.3 ± 2.92c	55	33.5 ± 4.80c	70	100.0a
30	77	45.2 ± 4.07a	85	100.0a		
<i>F</i> ^a		7.80		110.10		61.45
<i>P</i>		0.0001		0.0001		0.0001

Values are means ± standard errors. Values within an column, followed by the same letter are not significantly different according to the Student-Newman-Keuls test. Before analysis of variance values were transformed to $y = \arcsin (x/100)^{1/2}$. *n* = number of replications.
^a Degrees of freedom for *R. padi* = 4, *S. avenae* = 4 and *M. dirhodum* = 3.

Within the range of temperatures tested, the pattern followed by the prereproductive time (*Tpr*) was the same as that of *Td* for *R. padi* and *M. dirhodum*. The shortest *Tpr* of *R. padi* was again at 27.5°C, but at 30°C the time to the onset of reproduction was nearly double. For *M. dirhodum*, the shortest *Tpr* was achieved at 25°C the highest temperature at which nymphs survived to adulthood. The *Tpr* of *S. avenae* was shorter at 25°C than at 27.5°C.

Values of the developmental rate and prereproductive rate of the three species fitted adequately to Taylor's (1981) model (Fig. 1A and B), with values of *R*² all >0.96.

Developmental and prereproductive rates of *R. padi* and *S. avenae* were higher than those of *M. dirhodum* at any temperature within the range tested (Fig. 1A and B). Both rates for *R. padi* were lower than for *S. avenae* below 18°C but higher at greater temperatures (Fig. 1A and B).

Reproductive Capacity and Life Span. *R. padi* had the highest effective fecundity (*Fe*) at 25°C, but the highest effective reproductive rate (*Fe/Tpr*), total fecundity (*Ft*), total reproductive rate (*Ft/Lr*) and intrinsic rate of increase (*r_m*) were at 27.5°C. At 30°C, the reproductive capacity of this species was very low.

The highest *Fe* and *Ft* of *S. avenae* was at 18°C, but reproductive rates (*Fe/Tpr*, and *Ft/Lr*) were higher at 25°C, as was *r_m*. The reproductive performance (*Fe*, *Ft*, *Fe/Tpr*, *Ft/Lr*, *Lr*, *r_m*) of *S. avenae* at 27.5°C was much lower than at the other temperatures. The reproductive capacity (*Fe*, *Ft*, *r_m*) of *M. dirhodum* achieved the highest values at 22°C.

Rates of effective reproduction and total reproduction and intrinsic rate of increase for *R. padi*, *S. avenae* and *M. dirhodum* fit very well to Taylor's (1981) model (Fig. 1C–E) with all values of *R*² = 0.99.

Reproductive rates and intrinsic rate of increase of *R. padi* and *S. avenae* were higher than those of *M. dirhodum* within the range of temperatures tested (Fig. 1C–E). At 18°C, the rates of *S. avenae* were slightly higher than those of *R. padi*, but whereas the rates of *S. avenae* remained quite stable, the rates of *R. padi* increased with temperature up to ≈28°C (Fig. 1C–E).

The reproductive life and life span of the three aphid species decreased when the temperature increased. There was an abrupt decrease in reproductive life at 30°C for *R. padi*, at 27.5°C for *S. avenae* and at 25°C for *M. dirhodum*. Reproductive life and lifetime of *R. padi* were shorter than those of the other

Table 2. Development of <i>R. padi</i> , <i>S. avenae</i> and <i>M. dirhodum</i> at five constant temperatures						
Temp, °C	<i>n</i>	<i>R. padi</i>	<i>n</i>	<i>S. avenae</i>	<i>n</i>	<i>M. dirhodum</i>
Developmental time (<i>Td</i>) ^a						
18	71	8.8 ± 0.18a	72	9.0 ± 0.10a	46	10.8 ± 0.24a
22	70	6.2 ± 0.10b	53	8.0 ± 0.13b	40	8.7 ± 0.15b
25	62	5.4 ± 0.07c	59	7.3 ± 0.12c	40	7.5 ± 0.15c
27.5	76	4.6 ± 0.05d	44	6.6 ± 0.12d		
30	41	6.2 ± 0.10b				
<i>F</i> ^b		213.27		82.69		77.18
<i>P</i>		0.0001		0.0001		0.0001
Prereproductive time (<i>Tpr</i>) ^a						
18	71	9.3 ± 0.23a	72	9.5 ± 0.09a	46	11.5 ± 0.30a
22	70	6.5 ± 0.10c	53	8.4 ± 0.13c	40	9.4 ± 0.18b
25	62	5.8 ± 0.09d	59	8.2 ± 0.13c	40	8.5 ± 0.21c
27.5	76	4.9 ± 0.05e	44	8.8 ± 0.23b		
30	41	8.1 ± 0.09b				
<i>F</i> ^b		177.17		20.97		41.62
<i>P</i>		0.0001		0.0001		0.0001

Values are means ± standard errors. For each aphid species and variable, values within a column followed by the same letter are not significantly different according to the Student-Newman-Keuls test. *n* = number of replications.
^a Days.
^b Degrees of freedom for *R. padi* = 4, *S. avenae* = 3 and *M. dirhodum* = 2.

Table 3. Reproduction and longevity of *R. padi*, *S. avenae* and *M. dirhodum* at five constant temperatures

Temp, °C	<i>n</i>	<i>R. padi</i>	<i>n</i>	<i>S. avenae</i>	<i>n</i>	<i>M. dirhodum</i>
Effective fecundity (<i>Fe</i>) ^a						
18	148	25.3 ± 0.99b	205	29.3 ± 0.55a	137	19.5 ± 0.69a
22	139	25.8 ± 1.00b	134	26.0 ± 0.60b	102	20.9 ± 0.75a
25	142	32.7 ± 0.85a	174	25.2 ± 0.50b	68	13.0 ± 1.02b
27.5	171	31.7 ± 0.80a	91	6.2 ± 0.38c		
30	81	1.6 ± 0.21c				
<i>F</i> ^b		138.02		256.63		22.09
<i>P</i>		0.0001		0.0001		0.0001
Total fecundity (<i>Ft</i>) ^a						
18	148	39.5 ± 2.06ab	205	45.9 ± 1.42a	137	24.4 ± 1.12a
22	139	35.2 ± 1.79b	134	41.3 ± 1.63b	102	26.0 ± 1.28a
25	142	42.4 ± 1.64a	174	39.2 ± 1.19b	68	14.3 ± 1.24b
27.5	171	45.0 ± 1.47a	91	6.2 ± 0.38c		
30	81	1.6 ± 0.21c				
<i>F</i> ^b		73.13		120.79		20.28
<i>P</i>		0.0001		0.0001		0.0001
Reproductive life (<i>Lr</i>) ^c						
18	148	13.1 ± 0.53a	205	16.3 ± 0.49a	137	13.3 ± 0.39a
22	139	7.9 ± 0.06b	134	13.6 ± 0.86b	102	11.1 ± 0.42b
25	142	7.6 ± 0.27b	174	13.2 ± 0.33b	68	6.1 ± 0.46c
27.5	171	6.9 ± 0.18b	91	3.9 ± 0.20c		
30	81	1.1 ± 0.12c				
<i>F</i> ^b		130.27		72.22		63.66
<i>P</i>		0.0001		0.0001		0.0001
Intrinsic rate of increase (<i>r_m</i>)						
18	148	0.26 ± 0.007d	205	0.26 ± 0.002b	137	0.20 ± 0.004b
22	139	0.37 ± 0.008c	134	0.29 ± 0.003a	102	0.24 ± 0.005a
25	142	0.45 ± 0.007b	174	0.30 ± 0.004a	68	0.21 ± 0.011b
27.5	171	0.52 ± 0.006a	91	0.15 ± 0.007c		
30	81	0.05 ± 0.007e				
<i>F</i> ^b		589.17		227.81		15.43
<i>P</i>		0.0001		0.0001		0.0001
Lifetime (<i>Lt</i>) ^c						
18	148	26.1 ± 0.58a	205	27.9 ± 0.64a	137	29.2 ± 0.48a
22	139	15.4 ± 0.40b	134	22.6 ± 0.86b	102	23.4 ± 0.44b
25	142	14.4 ± 0.40b	174	22.2 ± 0.33b	68	16.6 ± 0.55c
27.5	81	12.7 ± 0.22c	91	15.1 ± 0.25c		
30	81	12.3 ± 0.24c				
<i>F</i> ^b		201.47		61.90		150.70
<i>P</i>		0.0001		0.0001		0.0001

Values are means ± standard errors. *n* = number of replications. For each aphid species and variable, values within a column followed by the same letter are not significantly different according to the Student-Newman-Keuls test.

^a Nymphs/female.

^b Degrees of freedom for *R. padi* = 4, *S. avenae* = 3 and *M. dirhodum* = 2.

^c Days.

two species. However, considering the time spent in reproduction in relation to the lifetime (*Lr/Lt*), *S. avenae* showed the highest proportions and *M. dirhodum* the lowest for the range 18–25°C. At 27.5°C the time spent by *R. padi* in reproduction was two times that of *S. avenae*. Similar results appear when we consider the time spent in reproduction during the adult life span (*Lr/Lt-Td*). *R. padi* spent between 76 and 85% of its adult life in reproduction in the range 18–27.5°C, whereas *S.avenae* spent longer (86–93%) but in a shorter range of temperatures (18–25°C), and ≈45% when the temperature was 27.5°C. *M. dirhodum* was the species that spent the least part of its adult life in reproduction (67–72%) in the range 18–25°C.

Discussion

Nymphal Mortality. Although a considerable amount of literature is available on the effect of low temperatures on aphid mortality, there is very little information on the effects of high temperatures (see Harrington et al. 1995 as an example). It has been stated that 30°C is a lethal temperature for nymphs of *S. avenae*, *M. dirhodum* and *R. padi* for aphids collected in Britain (Dean 1974). The results obtained in our experiment agree only partially with this conclusion. Whereas the mortality of *S. avenae* nymphs reached 100% at 30°C and *M. dirhodum* reached 100% at 27.5°C, 55% of nymphs of *R. padi* were able to survive at 30°C.

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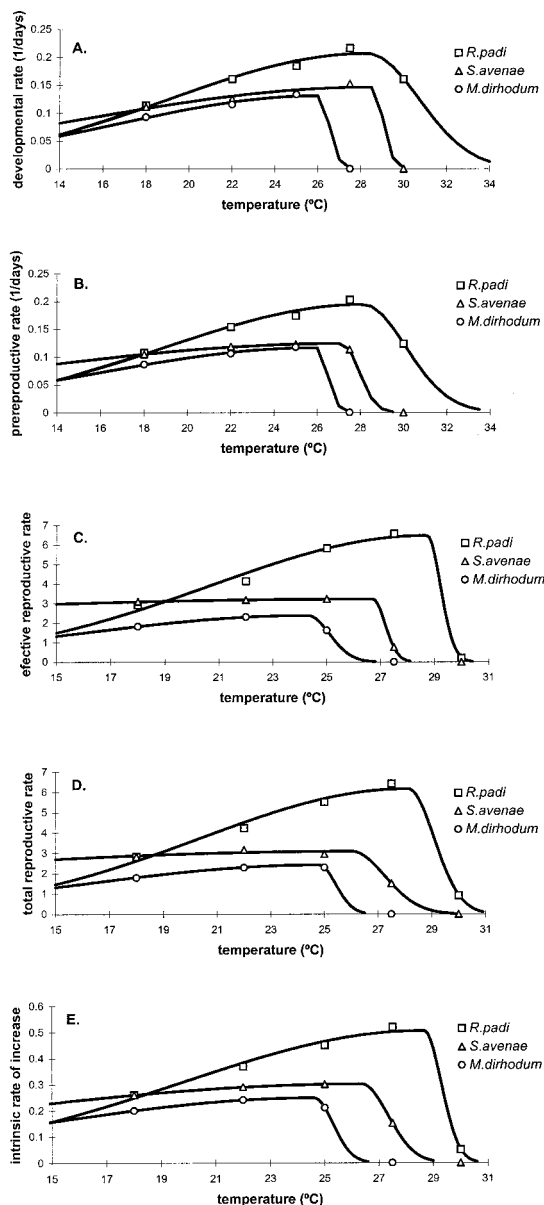


Fig. 1. Taylor's (1981) model fitted to (A) the developmental rate, (B) the prereproductive rate, (C) the effective reproductive rate, (D) the total reproductive rate, and (E) the intrinsic rate of increase of *R. padi*, *S. avenae* and *M. dirhodum*.

Nymphal mortality rates recorded by Dean (1974) for *M. dirhodum*, *R. padi* and *S. avenae*, and those recorded by Zhou and Carter (1992) for *M. dirhodum*, were lower than those of our experiment. This could be explained by the methodology used: though the nymphs were carefully managed, some of them could have been killed when we changed leaf pieces in the cage.

The fact that the percentages of *M. dirhodum* nymphs that died increased with temperature, and all

nymphs died at 27.5°C, suggest that nymphs of this species are not as well adapted to high temperatures as those of the other two species. Nymphs of *R. padi* were the most high-temperature resistant. The tolerance of *R. padi* to high temperatures has been reported in South Australia (De Barro 1992) where the temperature mortality threshold at the base of a pasture sward was 32°C and temperature $\geq 39^\circ\text{C}$ causes mortality to exceed 90%.

Development. The faster development of *R. padi* than *S. avenae* and *M. dirhodum* suggests that the first species is better adapted to the high temperatures tested. The time required for *R. padi* to reach complete development (T_d) and the period to onset of reproduction (T_{pr}) decreased as the temperature increased up to 27.5°C. However, the time required increased between 27.5 and 30°C, indicating that both upper developmental thresholds were $<30^\circ\text{C}$. Taylor's model for development and prereproductive rates gave a temperature of $\approx 28^\circ\text{C}$ at which maximum rate occurs (Fig. 1 A and B). Using barley as host-plant, Elliot and Kieckhefer (1989) found that the maximum rate of development and prereproductive rate of *R. padi* from the northern plains of the United States was $\approx 26^\circ\text{C}$. Dean (1974), also working with barley but with English clones, reported 25°C as the temperature at which developmental time was the shortest. These differences could be attributed to the different host plants tested, whose nutritional quality has a great influence on the development of aphids (Dixon 1987). However, Kuroli (1984) found that the lowest developmental time of a Hungarian population of *R. padi* on corn was at 21°C within the range 17–25°C, but longer (9.1 d) than the minimum recorded by Dean (1974), Elliot and Kieckhefer (1989) and ourselves in our experiment, which was ≈ 4.5 d. Therefore, host-plant does not seem to be the main reason for the differences found.

The developmental time of *S. avenae* decreased as the temperature increased up to 27.5°C. There was no development to adult at 30°C. Thus, maximum rate of development will be closer to 27.5°C than 30°C. Calculations from Taylor's model gave a value of 28.0°C (Fig. 1A). However, the time required to reach onset of reproduction decreased within the range 18 to 25°C but increased at 27.5°C, indicating that the maximum rate was below that temperature. The value calculated from Taylor's model was 27.0°C (Fig. 1B). Kieckhefer et al. (1989) reported 24.6°C as the temperature at which the maximum rate of development was achieved. Dean (1974) recorded that the fastest development to adult was at 25°C and to onset of reproduction at 22.5°C, and Lykouressis (1985), using a British clone different than Dean's one, recorded 25°C for the fastest development to adult and to onset of reproduction. Our values of the upper development threshold were higher than those reported by these authors.

The maximum rate of development to adult and to onset of reproduction of *M. dirhodum* from Taylor's model was at 25.5°C (Fig. 1A and B). This temperature is higher than the 20°C reported by Dean (1974) as the

temperature at which the development of *M. dirhodum* was fastest but similar (25°C) to that reported by Zhou and Carter (1992) for another English aphid culture feeding on wheat seedlings.

Reproductive Capacity and Life Span. The reproductive capacity of *R. padi* increased up to 27.5°C but was extremely low at 30°C, indicating that the optimum temperature was between the two values. The maximum rates of reproduction and the intrinsic rate of increase from Taylor's model were above 28.0°C (Fig. 1 C–E). Dean (1974) reported a total fecundity of this species of 41 nymphs per female at 25°C, which is quite similar to the 42.2 recorded in our experiment. However, he found higher values of fecundity at lower temperatures (15 and 20°C), though the reproductive period was not longer at 20°C. In our experiment, length of reproductive life decreased when the temperature increased, and therefore, the reproductive rates increased with the increase of temperature.

Fecundity of *S. avenae* decreased slightly with the increase in temperature, but the rates remained nearly constant (Fig. 1 C and D). Fecundity was much lower at 27.5°C than at 25°C, and the maximum rates from Taylor's model were ≈26°C (Fig. 1 C and D). Dean (1974) recorded the highest fecundity and reproductive rate of *S. avenae* on barley at 20°C and fecundity and reproductive rate were higher than in our experiment.

Metopolophium dirhodum shows lower fecundity at 25°C than at 22°C, and the same occurs with reproductive rates. Values of the upper threshold of reproductive rates from Taylor's model were ≈24.5°C (Fig. 1 C and D). Dean (1974) found the highest fecundity of *M. dirhodum* feeding on barley at 20°C and fecundity at 25°C was only four nymphs per female. However, Zhou and Carter (1992) found that the total fecundity was not significantly affected by temperature.

Dean (1974) recorded *S. avenae* as the species with the longest reproductive life and life-span, followed by *M. dirhodum* and *R. padi*. Sengonca et al. (1994), for aphids collected in Germany, also reported a longer reproductive life for *S. avenae* than *R. padi*. Although these authors used barley as the host-plant and the range of temperatures tested was lower than in our experiment, our results up to 25°C agree with theirs. However, *R. padi* spent more time in reproduction than *M. dirhodum* and more time than *S. avenae* at temperatures over 25°C. These results suggest that populations of *R. padi* will be renewed more quickly.

Aphid Performance. *R. padi* had higher rate of development, prereproductive rate and effective reproductive and total reproductive rates than *M. dirhodum* in the whole range of temperatures tested, and higher than *S. avenae* from 22 to 27.5°C. *S. avenae* and *M. dirhodum* (Fig. 1) show lower slopes in rates curves, indicating that these two species do not respond as well as *R. padi* to high temperatures. The greater response of *R. padi* to temperature allows it to produce greater populations than the other two species at high temperatures. This disagrees with the results of Honek (1985) in the Czech Republic who

pointed out that *R. padi* are negatively influenced by extreme high temperatures.

The most suitable temperature for growth and reproduction was ≈28.5°C for *R. padi*, ≈26.5°C for *S. avenae* and ≈24.5°C for *M. dirhodum*. This pattern agrees with that reported by Dean (1974) on barley. However, in all cases the temperatures at which performance was better were higher than those reported by the studies of Dean (1974), Kuroli (1984), Lykouressis (1985), Elliot and Kieckhefer (1989) and Kieckhefer et al. (1989). The reasons for these differences in aphid performance are unclear, but a geographic separation of the populations tested could be one. Kieckhefer et al. (1989) and Harrington et al. (1995) pointed out that temperature may influence populations of different geographic origin differently. Although responses to high temperatures of aphid populations from different geographic origins on corn have not been tested, *R. padi* clones from Lleida showed a different reproductive capacity and intrinsic rate of increase to English clones when they were fed on winter wheat (Pons and Tatchell 1995). Therefore, aphids from the Lleida basin, with a Mediterranean climate, could be more adapted to high temperatures than aphid populations from northern latitudes with colder climate. The tolerance of high temperatures of South Australia *R. padi* populations (De Barro 1992) would support this assumption.

Temperature and Aphid Population Dynamics in the Lleida Basin. Although the experiment was conducted at constant temperatures, and some differences may occur in comparison with natural fluctuating temperatures, especially around thresholds (Harrington et al. 1995), the results obtained in our experiment could go a long way toward explaining the phases of the corn aphid population dynamics in the Lleida basin.

Metopolophium dirhodum is the early species colonizing corn, followed by *S. avenae* and *R. padi*. During the first period of aphid settlement (May–June), *M. dirhodum* is the predominant species (Asín and Pons 1998), but at the beginning of July this species disappears from the corn fields and is only occasionally found on corn plants for the rest of the season. From May to mid-June, daily average air temperatures at crop level rarely exceed 25°C, allowing *M. dirhodum* to survive, develop and reproduce. Temperatures increase greatly at the end of June and in July, with many days on which temperatures above 30°C last for several hours. Moreover, by the end of June, the plant canopy does not yet completely cover the soil surface and the temperature 40 cm above soil level is higher than the air temperature. Under these conditions, only *R. padi* can survive to some extent. *S. avenae* can survive and remain on corn plants in years with lower temperatures in July, as occurred in 1993 (Asín 2000) and 2000 (Pons unpublished data). Only years with abnormally low July temperatures allow *M. dirhodum* populations to remain during the summer months, as occurred in 2000 (Pons unpublished data). In the second half of August the temperature is milder and the relative humidity in corn fields higher than before.

However, populations of *S. avenae* and *M. dirhodum* that have not been able to survive through the summer do not reappear. At the end of the corn-growing season *R. padi* is the main aphid species. Therefore, temperature plays an important role in determining the population dynamics of *R. padi*, *S. avenae* and *M. dirhodum* on corn in the Lleida Basin. De Barro (1992) pointed out that lethal high temperatures play a dominant role in determining aphid numbers over the summer in South Australia.

Secondary substances, especially 2,4-dihydroxy-7-methoxy-1,4-benzoaxin-3-one (DIMBOA), are regarded as a common corn defense against aphids (Long et al. 1977; Beck et al. 1983). However, Bing et al. (1990) did not find an effect of DIMBOA on *R. maidis*. The concentration of DIMBOA in corn leaves is high a few days after germination, but decreases rapidly and is low 20 d after germination, when corn is at the fourth leaf stage (Morse et al. 1991; Cambier et al. 2000). In the northeastern Iberian Peninsula the aphid population peaks in the first period of its population dynamics (early build up) are recorded at 4–7 leaf stages (Pons et al. 1989; Asín 2000; Pons and Albajes 2001). Thus, DIMBOA cannot be considered as the main reason that populations decrease after the peak.

In conclusion, our results show that temperature is a key factor in the development of aphid populations in corn fields of Northeastern Iberian peninsula. It plays an important role in the decrease of populations at the end of June and in the relative abundance of aphid species throughout the season.

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