

Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*

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Abstract. Preimaginal development, mortality, aphid consumption rate, and size and weight upon reaching the adult stage of the aphidophagous coccinellids *Hippodamia convergens* Guérin-Ménéville and *Coccinella septempunctata* L. collected from Karditsa, central Greece, were examined at four constant temperatures (14, 17, 20 and 23 °C) and L16:D8. The coccinellids fed on the tobacco aphid, *Myzus persicae nicotianae* Blackman. Egg, larval and pupal mortality was highest at 14 °C reaching 85.0, 73.8 and 29.4% in *H. convergens* and 49.3, 75.4 and 58.8% in *C. septempunctata*, respectively. Total preimaginal development ranged from 57.2 to 70.4 days at 14 °C, and to 16.9 and 22.1 days at 23 °C in *H. convergens* and *C. septempunctata*, respectively. Heavier and larger adults of *H. convergens* were obtained at 17 and 20 °C. In *C. septempunctata* temperature did not affect adult weight while the lowest size was observed at 14 and 17 °C. Day-degrees requirements for preimaginal development in *H. convergens* were 212.9 above a developmental threshold of 11.0 °C. The corresponding values for *C. septempunctata* were 281.5 and 10.7 °C. In *H. convergens* total and daily aphid consumption ranged from 46.8 aphids at 14 °C to 85.0 aphids at 23 °C and from 1.5 aphids at 14 °C to 9.2 aphids at 23 °C, respectively. The corresponding values for *C. septempunctata* were 112.0 and 2.7 at 14 °C and 157.7 and 12.4 at 23 °C. The results show the high potential of both predators as biological control agents against the tobacco aphid. The knowledge obtained could be essential for their appropriate use and for the improvement of mass rearing systems.

Key words: *Coccinella septempunctata*, *Hippodamia convergens*, *Myzus persicae*, tobacco, predation, development, Coleoptera, Coccinellidae

Introduction

Myzus persicae (Sulzer) (Hemiptera: Aphididae) is a polyphagous aphid species that infests over 400 plant species belonging to 40 different

families (Blackman and Eastop, 2002). It is also a notable example of an aphid species in which host-adapted forms have been characterised, e.g. the form adapted to feed on tobacco, *Nicotiana tabacum* L. (Solanaceae) (Blackman, 1987; Margaritopoulos et al., 2000; Blackman et al., 2001). The tobacco-feeding form was given the status of a separate species (Blackman, 1987) but recent molecular studies (Field et al., 1994; Margaritopoulos et al., 1998) showed that this form is best characterized as a subspecies (as *Myzus persicae* ssp. *nicotianae* Blackman) (Margaritopoulos et al., 2003). *Myzus persicae nicotianae* is a worldwide important pest of tobacco causing both direct damage to plants and indirect damage by transmitting important viruses (Kennedy et al., 1962; Mistic and Clark, 1979; Blackman and Eastop, 2002). Reed and Semtner (1992) referred to yield losses of 22–28% due to damages caused by this aphid in Virginia tobacco. Tobacco aphid is also a serious pest of tobacco in Greece, where high populations are usually recorded early or at the end of the tobacco-growing season (Lykouressis and Mentzos, 1995; Tsitsipis et al., unpublished data).

The control of *M. persicae nicotianae* is mostly based on insecticides. However, high levels of insecticide resistance have been observed in many parts of the world (Clements et al., 1999) as well as in Greece (Cox et al., 2001). An effective and more environmentally sound management of the tobacco aphid could consider the utilization of its natural enemies. Aphidophagous coccinellids occur in most cropping systems and their impact on aphid populations is known to be important (Hodek, 1973). Wells and McPherson (1999) found that the coleopteran coccinellid species *Hippodamia convergens* Guérin-Méneville, *Coccinella septempunctata* L. and *Harmonia axyridis* (Pallas) were the most abundant predators in tobacco fields in Georgia, greatly contributing to the regulation of tobacco aphid populations. Furthermore, Norowi and Semtner (1990) concluded that *H. convergens* could suppress aphid populations within 40 days from the establishment of tobacco aphids. In central Greece, surveys in tobacco fields showed that *H. convergens* and *C. septempunctata* were the most commonly found natural enemies of the tobacco aphid (Tsitsipis et al., unpublished data).

Although coccinellids are frequently recorded in several agroecosystems, they show high variability in their potential for population establishment (Elliot and Kieckhefer, 1990) that leads to a reduction of their effectiveness (Kindlmann and Dixon, 1993). Therefore, a better understanding of the factors involved in their field performance could aid towards their most appropriate use in biological control.

Temperature is an important environmental factor that greatly affects the biological characteristics of aphidophagous coccinellids as well

as the dynamics of predator–prey relationships. In general, the effect of temperature on the development of temperate-zone aphidophagous coccinellids, including *C. septempunctata* and *H. convergens*, has been relatively well investigated (Obrycki and Tauber, 1981, 1982; Michels and Behle, 1991a; Miller, 1992). However, it has been reported that in addition to interspecific variation, temperature thresholds and day-degree requirements for development may vary within species. Intraspecific variation may result from genetic differences among individuals and populations (Obrycki and Tauber, 1982) or from environmental factors that affect individuals and populations. In particular, temperature-dependent larval development has been reported to vary with prey species in the coccinellids *Hippodamia sinuata* Mulsant (Michels and Bechle, 1991b) and *Hippodamia parenthesis* (Say) (Orr and Obrycki, 1990). Furthermore, plant species affect the searching efficiency of *H. convergens* (Belcher and Thurston, 1982).

Taking these considerations into account and given that aphidophagous coccinellids–tobacco aphid–tobacco system has not been studied in detail, the current study aims at examining the effect of temperature on: (1) preimaginal development and survival, (2) size and weight upon reaching adult stage and sex ratio, (3) thermal requirements for development and (4) aphid consumption rates of *H. convergens* and *C. septempunctata* feeding on *M. persicae nicotianae* on tobacco.

Materials and methods

Insect rearing

A red clonal culture of *M. persicae nicotianae* was initiated in the laboratory from aphids collected on tobacco in Karditsa, central Greece in 1999. Although both green and red colour forms of the tobacco aphid are found in Greece, the red form predominates in the Karditsa region (Margaritopoulos et al., 2002). The culture was developed on tobacco (cv. B21) potted plants. The plants were kept in cages (40 cm × 45 cm × 50 cm) with a wooden washable flush floor; the two opposite sides and the top were covered with glass and the remaining two sides covered with fine aphid proof muslin to allow aeration. The cages were kept in a controlled environment room at 20 ± 1 °C, 50 ± 5%RH and L16:D8.

Hippodamia convergens and *C. septempunctata* colonies were initiated from approximately 40 adults of each species, collected on

tobacco fields and nearby weeds in Karditsa in 1999. Both predators were reared separately in transparent plastic boxes (8.5 cm × 7 cm × 4 cm) with a 3.5 cm round opening in the top, covered with fine muslin to allow ventilation. In the lower 1/4 of the box a plastic piece was placed to create a separate compartment, in which a piece of moistened moss was placed. In the upper part of the box a tobacco leaf infested with aphids was placed, whose petiole base was inserted into the moss through a hole in the plastic piece. In each box, 2–3 pairs of each predator species were placed and supplied with an overabundance of *M. persicae nicotianae* individuals every 2 days. The tobacco leaves were replaced by fresh ones when it was deemed necessary. The boxes were inspected daily and eggs found were transferred into other boxes to hatch. Newly hatched larvae were introduced individually in transparent plastic cylindrical cages, 4.5 cm in diameter and 2 cm in height, with a hole 2 cm in diameter on their top cover fitted by fine muslin. Larvae were provided with an overabundance of aphids every 1–2 days. The adults emerging in the cages were transferred into the large boxes mentioned above to continue rearing of the next generation (F2). The colonies of both predators were kept at 23 ± 0.5 °C, $50 \pm 5\%$ RH and L16:D8.

In our experiments only predators of F2 generation obtained in the laboratory were used. Although replications through time (=examination of insects from different generations) might lead to more documented results, continuous laboratory rearing of an insect population could lead to genetic changes and to its adaptation to the laboratory conditions. Thus, the results on biological traits, particularly those which undergo natural selection, obtained by experiments replicated in time may not correspond to what happens in nature. Laboratory adaptation can provide spurious evidence for the importance of mutation accumulation in the evolution of aging (Promisov and Tatar, 1998) and can also induce spurious genetic correlations between traits (Service and Rose, 1985). Sgrò and Patridge (2000) suggested that laboratory adaptation is a potential problem that has been ignored in most evolutionary studies and has been also ignored more broadly. Adaptation to captivity has been considered to result in changes in traits that are important in field performance of natural enemies (Mackauer, 1972; van Bergeijk et al., 1989; Geden et al., 1992; Salmanova et al., 1992; Hopper et al., 1993; Jayanth and Bali, 1996; Mohaghegh et al., 1999) and could affect the searching behaviour of predators (Ettifouri and Ferran, 1993; Hénaut et al., 1999). Consequently, in order to avoid such effects we preferred to conduct the experiments soon after the collection of the insects from the field.

Immature development and aphid consumption

Egg hatching and incubation period were studied by placing newly laid eggs (less than 24-h old) of the F2 generation in petri dishes at four different temperatures (14 ± 0.5 , 17 ± 0.5 , 20 ± 0.5 and 23 ± 0.5 °C), $50 \pm 5\%$ RH and L16:D8. Egg hatching was recorded daily and each emerging larva was transferred separately into a Blackman box ($7.7 \text{ cm} \times 4.5 \text{ cm} \times 2 \text{ cm}$), at the base of which there was a piece of water saturated moss (Blackman, 1971). In each box a tobacco leaf was introduced, petiole inserted into the moss. Thirty young apterous adult females of *M. persicae* were placed on the tobacco leaf on a daily basis. The larvae were examined daily for molting. At the same time the aphids found alive were counted and removed, and 30 new young adult apterae were introduced into the box. The tobacco leaf was replaced with a fresh one when necessary. It is worthwhile mentioning, that although the aphids could reproduce during the experimental period (1 day) it was not possible to estimate the offspring number and consequently this presumably small contribution to the diet of the predators. Each egg and the subsequent larva at a specific temperature was considered to be a replication.

The newly emerged adults were weighed in a Precisa 40SM-200A (PAG Oerlikon AG, Switzerland) electronic balance. Before measurements the insects were immobilized by exposure to -20 °C for 2–3 min. In addition, the length and width of the adults were measured under a stereoscope (Nikon SMZ-U). The sex ratio of the emerged adults (F/M + F) was also recorded.

The effect of temperature on the duration of the immature stages was examined using one-way ANOVA, while the effects of temperature and predator species on total preimaginal development were examined using two-way ANOVA. Two-way ANOVA was also used for the effects of temperature and sex on adult size and weight, as well as for the effects of temperature and larval instar on total and daily aphid consumption. Data on total and daily aphid consumption at different temperatures for each predator species were analysed using one-way ANOVA, whereas data on the total and daily aphid consumption during the entire larval development between the two coccinellids were analysed using a two-way ANOVA with temperature and coccinellid species as the two factors. In all cases means were separated by Duncan's test. Survival data of each life stage at all four temperatures were analysed by χ^2 test of independence, and when it was significant, pairwise comparisons were conducted. Data were not transformed prior to analyses. The relationship between rate of development (Y , inverse of developmental period in

days) and temperature of each developmental stage, as well as of total immature development, was investigated by the linear regression model: $Y = a + b * \text{Temperature}$. The lower temperature threshold (D_{th}) for development was determined as the x -intercept of the linear equation ($-a/b$) and the summation of day-degrees (DD) requirements as the inverse of the slope of the above equation. Analyses were conducted using the statistical package SPSS Base 10.0 for Windows.

Results

Preimaginal mortality and development

Egg, larval and pupal mortality of *H. convergens* and *C. septempunctata* are shown in Table 1. Egg mortality was highest at 14 °C in both species reaching 85% and 49% for *H. convergens* and *C. septempunctata*, respectively. However, the differences among temperature treatments were significant only in *H. convergens*. Total larval and pupal mortality of both predators were significantly influenced by temperature, being highest at 14 °C. The first larval instar of both predators suffered much higher mortality than all other instars at 14 °C. Significant differences in mortality between the two predators at each temperature were recorded only in the egg stage at 14 °C, where mortality was significantly higher in *H. convergens* than in *C. septempunctata* ($\chi^2 = 36.7$; $p < 0.001$).

The duration of egg, larval or pupal stages and the total preimaginal development of *H. convergens* and *C. septempunctata* were significantly reduced with temperature increase (Table 2). A two-way ANOVA showed that apart from the effects of temperature ($F = 1309.1$; $df = 3, 130$; $p < 0.001$), the total preimaginal development was significantly different between the two species ($F = 297.1$; $df = 1, 130$; $p < 0.001$) as well as the interaction of temperature and species ($F = 12.6$; $df = 3, 130$; $p < 0.001$).

The sex ratio of *H. convergens* was 42.9, 53.8, 70.0 and 28.6%, and that of *C. septempunctata* 33.3, 47.8, 50.0 and 34.8%, at 14, 17, 20, and 23 °C, respectively. In both species the sex ratio was highest at 20 °C, although the differences among temperatures were not significant ($\chi^2 = 3.69$; $df = 3$; $p < 0.297$ in *H. convergens*, $\chi^2 = 0.957$; $df = 3$; $p < 0.811$ in *C. septempunctata*).

Adult size and weight

Statistical analyses revealed that temperature had a significant effect on adult size in both species, although adult weight upon reaching adult-

Table 1. Percent (%) mortality of *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves at four constant temperatures and L16:D8 (E = number of individuals examined).

Life stage	Temperature (°C)												χ^2 / p		
	14			17			20			23					
	E	%		E	%		E	%		E	%				
	<i>H. convergens</i>														
Eggs	220	85.0a		106	47.2b	45							90	34.4b	38.9/0.01
L1*	65	55.4a		41	39.0a	50							33	27.3a	4.5/0.23
L2	29	27.6a		25	4.0b	23							24	0.0b	10.2/0.02
L3	21	14.3a		24	4.2a	20							24	0.0a	4.2/0.20
L4	18	5.6a		23	0.0a	19							24	0.0a	3.7/0.30
L1-L4	65	73.8a		41	43.9b	50							33	27.3b	10.4/0.01
Pupae	17	29.4a		23	0.0b	19							24	4.2b	12.1/0.01
	<i>C. septempunctata</i>														
Eggs	67	49.3a		68	41.2a	29							35	20.0b	5.6/0.13
L1	69	59.4a		36	44.4ab	56							22	0.0c	13.9/0.03
L2	28	14.3a		20	5.0ab	34							22	0.0b	21.7/0.01
L3	24	8.3a		19	0.0a	28							22	0.0a	5.4/0.14
L4	22	22.7a		19	15.8a	24							22	0.0a	5.5/0.14
L1-L4	69	75.4a		36	55.6a	56							22	0.0b	16.5/0.01
Pupae	17	58.8a		16	18.8b	22							22	0.0b	22.6/0.01

*L1-L4 = larval instars. Percentages in each row followed by a different letter differ significantly by χ^2 -test ($p < 0.05$).

Table 2. Development (in days) of *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves at four constant temperatures and L16:D8.

Life stages	Temperature (°C)											
	14			17			20			23		
	N	Days	F	N	Days	F	N	Days	F	N	Days	F
<i>H. convergens</i>												
Egg	18	8.1 (0.3) a	30	7.2 (0.1) b	30	4.5 (0.2) c	30	3.4 (0.2) d	148.0*			
Larva	12	33.3 (1.7) a	23	20.0 (0.3) b	18	15.7 (0.3) c	23	9.3 (0.2) d	243.5*			
Pupa	12	15.2 (0.6) a	23	9.0 (0.2) b	18	7.2 (0.3) c	23	3.9 (0.1) d	286.7*			
Adult	12	57.2 (1.6) a	23	36.2 (0.4) b	18	27.3 (0.5) c	23	16.9 (0.3) d	660.0*			
<i>C. septempunctata</i>												
Egg	31	9.8 (0.3) a	40	7.4 (0.1) b	30	5.6 (0.2) c	22	3.4 (0.2) d	174.8*			
Larva	7	42.0 (1.9) a	13	24.7 (0.3) b	20	17.5 (0.4) c	22	12.7 (0.1) d	374.3*			
Pupa	7	20.1 (1.1) a	13	13.7 (0.2) b	20	9.7 (0.2) c	22	6.0 (0.1) d	316.4*			
Adult	7	70.4 (2.7) a	13	45.5 (0.5) b	20	32.9 (0.4) c	22	22.2 (0.2) d	660.9*			

Numbers in brackets denote standard error of means. N = number of replications. Means within a row followed by a different letter differ significantly ($p < 0.05$) by Duncan's test. *Denotes significance level $p < 0.001$ in one-way Analysis of variance.

Table 3. Results of ANOVA for the effects of temperature and sex on adult weight, length and width in *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves.

Source of variation	DF	F			p		
		Weight	Length	Width	Weight	Length	Width
<i>H. convergens</i>							
Temperature	3	4.5	12.1	4.3	0.006	0.001	0.006
Sex	1	42.4	40.3	133.7	0.001	0.001	0.001
Temperature * Sex	3	0.3	0.3	1.8	NS*	NS	NS
Error	68						
<i>C. septempunctata</i>							
Temperature	3	0.4	3.6	3.1	NS	0.02	0.03
Sex	1	25.6	34.1	33.6	0.001	0.001	0.001
Temperature * Sex	3	0.9	0.4	1.6	NS	NS	NS
Error	53						

*NS = not significant difference.

hood was significantly affected only in *H. convergens* (Table 3). *H. convergens* attained a significantly higher weight at 17 and 20 °C whereas its length and width were lowest at 14 °C (Table 4). The smallest size of adult *C. septempunctata* was observed at 14 and 17 °C, although the differences were not always significant (Table 4). The sex affects significantly adult weight and size in both species, with the females being heavier and larger than males. Adult weight was significantly correlated with an index of body size (length*width) for both predators ($R = 0.791$; $N = 76$; $p < 0.01$ for *H. convergens* and $R = 0.514$; $N = 61$; $p < 0.01$ for *C. septempunctata*). It appears that most of the female individuals can be distinguished from their conspecific males according to the values of the weight and the index body size, irrespective of temperature (Figure 1). It can also be seen that males and females were overlapped in size and weight in *C. septempunctata* more than in *H. convergens*.

Thermal requirements

The linear regression equations that describe the relationship between temperature and developmental rate as well as temperature threshold and day-degree requirements for each life stage and total immature development of *H. convergens* and *C. septempunctata* are presented in Table 5. The D_{th} was lowest for the egg and highest for pupal

Table 4. Adult characteristics of *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves at four constant temperatures and L16:D8.

Adult characteristics	Temperature (°C)											
	14			17			20			23		
	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean		
<i>H. convergens</i>												
Weight (mg)	12	6.5 (0.5)a	23	7.6 (0.2)b	18	7.7 (0.3)b	23	6.7 (0.2)a				
width (mm)	12	2.7 (0.1)a	23	2.9 (0.1)b	18	2.9 (0.1)b	23	2.8 (0.1)b				
Length (mm)	12	4.0 (0.2)a	23	4.7 (0.1)b	18	4.6 (0.1)b	23	4.5 (0.1)b				
<i>C. septempunctata</i>												
Weight (mg)	7	18.2 (1.1)a	13	18.2 (0.5)a	20	18.2 (0.4)a	22	17.3 (0.3)a				
width (mm)	7	4.1 (0.3)ab	13	4.0 (0.1)ab	20	4.1 (0.1)a	22	4.3 (0.1)b				
Length (mm)	7	6.0 (0.1)ab	13	5.9 (0.1)a	20	6.1 (0.1)ab	22	6.1 (0.1)b				

Numbers in brackets denote standard error of means. N = number of replications. Means within a row followed by a different letter differ significantly ($p < 0.05$) by Duncan's test.

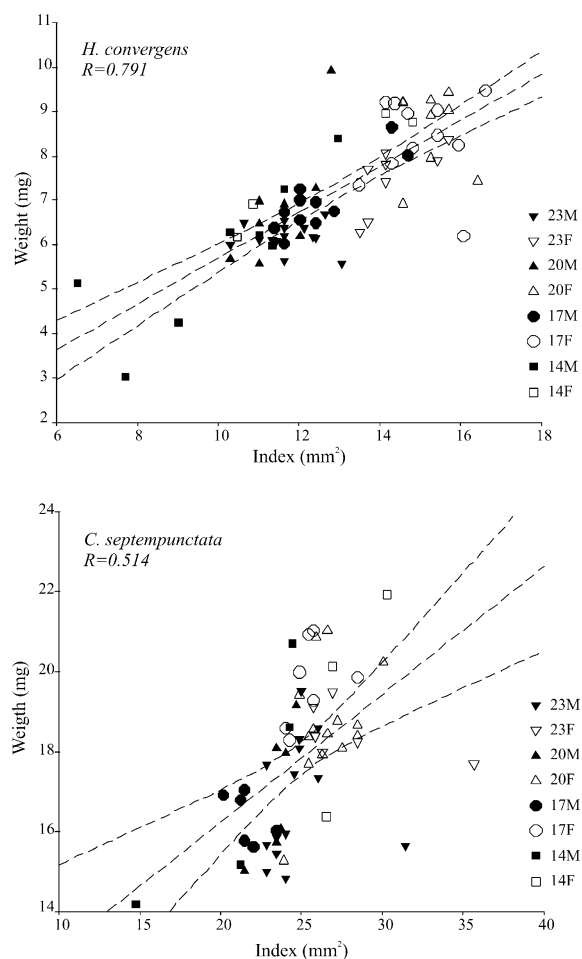


Figure 1. Correlation between weight and a body size index (length \times width) in females and males of *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves at four constant temperatures and L16:D8. 14F, 17F, 20F, 23F: females reared at 14, 17, 20 and 23 °C, respectively. 14M, 17M, 20M, 23M: males reared at 14, 17, 20 and 23 °C, respectively. Dashed lines denote mean prediction responses and confidence intervals.

development, in both predators. Between the two predators, developmental thresholds appeared to be similar but that of larvae was relatively lower for *C. septempunctata* than for *H. convergens*. Egg and pupal development require a similar amount of day-degrees, but larvae require a much greater amount in both predators. Larval, pupal and egg-adult development of *C. septempunctata* required a much greater number of day-degrees than that of *H. convergens*.

Table 5. Developmental threshold (D_{th}) and day-degrees requirements for *Hippodamia convergens* and *Coccinella septempunctata* feeding on *Myzus persicae nicotianae* apterous adults on tobacco leaves.

Life stage	D_{th}	DD	Equation	R^2 (df)	p
<i>H. convergens</i>					
Egg	9.7	43.9	$Y = -0.2218X + 0.02277$	0.61 (1, 106)	<0.05
Larvae	11.2	115.5	$Y = -0.0968X + 0.00866$	0.89 (1, 74)	<0.05
Pupae	11.8	46.2	$Y = -0.2554X + 0.02165$	0.81 (1, 74)	<0.05
Egg-Adult	11.0	212.9	$Y = -0.0516X + 0.00470$	0.91 (1, 74)	<0.05
<i>C. septempunctata</i>					
Egg	10.1	46.4	$Y = -0.2188X + 0.02157$	0.63 (1, 118)	<0.05
Larvae	10.3	162.6	$Y = -0.0636X + 0.00615$	0.94 (1, 59)	<0.05
Pupae	11.5	72.6	$Y = -0.1581X + 0.01376$	0.89 (1, 59)	<0.05
Egg-Adult	10.7	281.5	$Y = -0.0381X + 0.00355$	0.95 (1, 59)	<0.05

Aphid consumption

Regarding the total aphid consumption of *H. convergens* and *C. septempunctata*, the effect of temperature and larval instar as well as their interaction were significant (Tables 6 and 7). Considering separately each larval instar, the total consumption was significantly highest at 23 °C in both species, while among the lower temperatures significant differences were noticed only in the fourth larval instar of *C. septempunctata*. In both predators, the fourth larval instar was the most voracious (Table 7) and the consumption during entire larval development was significantly highest at 23 °C ($F = 47.9$, $df = 3$, 72 , $p < 0.001$ for *H. convergens* and $F = 660.9$, $df = 3$, 58 , $p < 0.001$ for *C. septempunctata*) than at the lower temperatures, among which significant differences were not recorded (Table 7).

The mean daily consumption rate of both species was significantly affected by temperature and larval instar, whereas their interaction was also significant (Tables 6 and 8). Aphid consumption was significantly highest at 23 °C in both predators, whilst it decreased with temperature. In *H. convergens*, the temperature increase had always a significant effect on aphid consumption by the fourth larval instar and this was also recorded in the third instar at temperatures above 17 °C. In *C. septempunctata*, consumption rates of third and fourth instar significantly increased following temperature increase (Table 8). Mean daily consumption rate during entire larval development was significantly increased following temperature increase in *H. convergens* ($F = 335.3$;

Table 6. Results of ANOVA for the effect of temperature and larval instar on total and daily aphid consumption by *Hippodamia convergens* and *Coccinella septempunctata*.

Source of variation	Daily aphid consumption			Total aphid consumption	
	df	F	p	F	p
<i>H. convergens</i>					
Temperature	3	371.2	0.001	55.8	0.001
Larval instar	3	291.7	0.001	428.4	0.001
Temperature * Larval instar	9	30.0	0.001	2.9	0.001
Error	344				
<i>C. septempunctata</i>					
Temperature	3	236.1	0.001	62.1	0.001
Larval instar	3	274.2	0.001	438.4	0.001
Temperature * Larval instar	9	21.8	0.001	27.0	0.001
Error	228				

Table 7. Total consumption of adult *Myzus persicae nicotianae* by larvae of *Hippodamia convergens* and *Coccinella septempunctata* reared at four constant temperatures and L16:D8.

Larval instars	Temperature											
	14 °C			17 °C			20 °C			23 °C		
	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
	<i>H. convergens</i>											
L1	12	2.1 (0.5) aA	23	2.7 (0.3) aA	18	1.8 (0.4) aA	23	7.2 (0.7) bA				
L2	12	4.5 (0.7) aAB	23	4.6 (0.4) aA	18	4.3 (0.8) aA	23	12.0 (1.2) bB				
L3	12	9.0 (1.3) aB	23	8.5 (0.5) aB	18	10.9 (1.1) aB	23	21.0 (1.7) bC				
L4	12	31.0 (2.8) aC	23	30.4 (1.9) aC	18	32.0 (2.1) aC	23	45.0 (1.9) bD				
L1-L4	12	46.8 (3.8) a	23	46.2 (2.3) a	18	49.4 (3.4) a	23	85.0 (2.5) b				
	<i>C. septempunctata</i>											
L1	7	3.4 (0.6) aA	13	3.5(0.4) aA	20	3.5 (0.4) aA	22	7.1 (0.6) bA				
L2	7	7.0 (2.0) aA	13	8.0 (0.7) aB	20	8.3 (1.9) aA	22	15.6 (0.9) bB				
L3	7	16.0 (1.2) aB	13	22.4 (1.2) aC	20	23.8 (2.2) aB	22	34.8 (2.8) bC				
L4	7	85.7 (6.9) aB	13	88.5 (2.7) bD	20	72.1 (4.8) cC	22	100.2 (3.3) dD				
L1-L4	7	112.0 (7.7) a	13	122.0 (2.6) a	20	108.0 (4.7) a	22	157.7 (5.1) b				

Numbers in brackets denote standard error of means. N: number of individuals examined. Means followed by a different small letter within a row and by a different capital letter within a column differ significantly ($p < 0.05$) by Duncan's test.

Table 8. Mean daily consumption of adult *Myzus persicae nicotianae* by larvae of *Hippodamia convergens* and *Coccinella septempunctata* reared at four constant temperatures and L16:D8.

Larval instars	Temperature											
	14 °C			17 °C			20 °C			23 °C		
	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
	<i>H. convergens</i>											
L1	12	0.2 (0.1) aA	23	0.5 (0.1) aA	18	0.4 (0.1) aA	23	3.4 (0.3) bA				
L2	12	0.7 (0.1) aA	23	1.1 (0.1) aB	18	1.5 (0.3) aB	23	5.2 (0.5) bB				
L3	12	1.4 (0.2) aB	23	2.1 (0.1) aC	18	3.7 (0.4) bC	23	11.0 (0.7) cC				
L4	12	2.9 (0.3) aC	23	5.1 (0.3) bD	18	6.8 (0.4) cD	23	16.0 (0.4) dD				
L1-L4	12	1.5 (0.2) a	23	2.3 (0.1) b	18	3.1 (0.2) c	23	9.2 (0.2) d				
	<i>C. septempunctata</i>											
L1	7	0.3 (0.1) aA	13	0.8 (0.1) Aa	20	0.8 (0.1) aA	21	2.3 (0.2) bA				
L2	7	1.0 (0.3) aB	13	1.8 (0.2) aB	20	2.3 (0.3) aB	21	7.7 (0.4) bB				
L3	7	1.8 (0.1) aC	13	4.4 (0.2) bC	20	6.7 (0.7) cC	21	14.2 (0.8) dC				
L4	7	5.6 (0.4) aD	13	8.5 (0.3) bD	20	11.7 (0.5) cD	21	19.6 (0.5) dD				
L1-L4	7	2.7 (0.2) a	13	5.0 (0.1) b	20	6.2 (0.2) c	21	12.4 (0.4) d				

Numbers in brackets denote standard error of means. N = number of individuals examined. Means followed by a different small letter within a row and a different capital letter within a column differ significantly ($p < 0.05$) by Duncan's test.

df = 3, 72; $p < 0.001$) and *C. septempunctata* ($F = 24.4$; df = 3, 58; $p < 0.001$) (Table 8).

Two-way ANOVA revealed that total and daily predation rate during entire larval development was significantly higher in *C. septempunctata* than in *H. convergens* ($F = 512.8$; df = 1, 130; $p < 0.001$ and $F = 169.4$; df = 1, 130; $p < 0.001$, respectively). The interaction temperature X coccinellid species was significant for daily ($F = 4.0$; df = 3, 130; $p < 0.01$) but not for total consumption ($F = 2.2$; df = 3, 130; $p < 0.09$).

Discussion

The tobacco aphid was found to be a suitable prey for the development of both ladybirds *H. convergens* and *C. septempunctata*. Although these predators are polyphagous and several aphid species are suitable for their development (Obrycki and Tauber, 1981; Michels and Behle, 1991a; Miller, 1992, Campbell et al., 1999) *M. persicae nicotianae* has not been previously evaluated as a potential prey for these predators. Therefore, the present results broadened our knowledge on the prey range of both predators.

Preimaginal mortality and development

During development, mortality was highest at the lowest temperature (14 °C) in both predators. The severe mortality of immature stages at temperatures near developmental threshold is a common phenomenon among temperate zone aphidophagous coccinellids (Orr and Obrycki, 1990; Miller, 1992; Rodriguez-Saona and Miller, 1999), whereas lower mortality levels have been reported for the two cold-adapted coccinellid species *Eriopis connexa* Mulsant (Miller and Paustian, 1992) and *Calvia quatuordecimguttata* (L.) (LaMana and Miller, 1995). Egg mortality of *H. convergens* and *C. septempunctata* was similar to those of conspecific Nearctic populations at 16 and 20 °C (Frazer and McGregor, 1992). However, total larval mortality of *H. convergens* fed on *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) ranged from 73.1 to 82.5% at 18 °C (Rodriguez-Saona and Miller, 1995), whereas, Miller (1992) reported egg and larval mortality of 80 and 83% at 17 °C, respectively. The higher mortality rates recorded in these studies than in the current study could be attributed to the different geographical origin of *H. convergens* populations, since the former authors examined Nearctic

populations, and/or to the different prey species used. The same factors may also be responsible for the much higher mortality at lower temperatures during the later stages of development, which Obrycki and Tauber (1982) and Rodrigues-Saona and Miller (1999) reported for their populations of *H. convergens*. By contrast, in both predators examined in the present study, much higher mortality was recorded in the first larval instar than in the older ones or in the pupal stage, particularly at low temperatures. Thus, Greek populations may encounter difficulties in the establishment early in the season due to the high mortality of the first larval instar.

The larger predator *C. septempunctata*, required a significantly longer period to complete development than *H. convergens*. The period of egg, larval and pupal development, when expressed as a proportion of the total preimaginal development in *H. convergens*, ranged between 14–20%, 55–58% and 23–26% whereas in *C. septempunctata* between 14–17%, 53–60% and 27–29%, respectively. The percentages for *H. convergens* are similar to those reported by Miller (1992), ranging from 14–19%, 56–60% and 22–28% at each stage, respectively.

Adult size and weight

The size and weight upon reaching adulthood in *H. convergens* were significantly greater at 17 and 20 °C than in the rest of the temperature treatments. Rodriguez-Saona and Miller (1999) have also reported that adult weight of this species is affected by temperature, and that the heaviest adults were recorded at 22 °C. These results indicate better adaptation of *H. convergens* when temperature fluctuates around 20 °C, which may be important in its field performance or in mass rearing efforts. On the other hand, adult weight of *C. septempunctata* was not affected by temperature. Taking into account that weight is a relative index of fitness, *C. septempunctata* has a competitive advantage since it should perform better at early season conditions. It is worthwhile mentioning here that this statement is possibly valid only when *C. septempunctata* feeds on the tobacco aphid, since aphid prey can affect adult weight in coccinellids (Orr and Obrycki, 1990). This species was the first coccinellid that appeared on tobacco crops in Georgia (Wells and McPherson, 1999) as well as in the region of Karditsa, central Greece (Tsitsipis, unpublished data).

In the present study, females were always larger than males. Such a difference has also been reported in *H. convergens* (Smith, 1966; Rodriguez-Saona and Miller, 1999) as well as in other predatory

coccinellids (Smith, 1966). According to Smith (1966) species in which females are larger than males may adjust their numbers to prey abundance more efficiently, with positive impacts on their field performance. However, this is probably more feasible for *H. convergens* since in *C. septempunctata* a higher portion of the males had values of weight and body size similar to those of females (Figure 1).

Thermal requirements

The developmental threshold of each stage as well as that of preimaginal development was relatively similar between the two species tested, indicating that they could appear on tobacco fields at the same period. However, *H. convergens* required a much smaller number of day-degrees to develop than *C. septempunctata*, apart from the egg stage. Thus, the first mentioned species exhibits a faster development than the latter one. The temperature threshold for egg and pupal development of a *C. septempunctata* population of Palearctic origin were 10.2 and 11.1 °C (Honek and Kocourek, 1988), which are similar to those estimated in the current study. Similar day-degree requirements have been calculated by Obrycki and Tauber (1981) from data of central European populations reported by Hodek (1973) and Jöhnssen (1930), but as with higher developmental threshold (11.9 °C with 216DD and 11.9 °C with 269DD). Therefore, the results of the current and the above studies support Hodek's (1973) suggestion that coccinellid populations of Palearctic origin show similar thermal requirements.

However, our results indicate some differences compared with those reported in studies on populations of Nearctic origin. In *H. convergens* populations from north America thermal requirements for egg development were similar to those estimated in the present study (9.5 °C with 50.2DD and 9.9 °C with 58.8DD, Frazer and McGregor, 1992 and Rodriguez-Saona and Miller, 1999, respectively) but developmental threshold of preimaginal development was relatively higher (12 °C with 230DD and 13.6 °C with 231DD, Obrycki and Tauber, 1982; Rodriguez-Saona and Miller, 1999, respectively). Michels and Behle (1991a) reported in a Nearctic population a lower developmental threshold of preimaginal development (6.7 °C) and higher day-degree requirements (351DD). The thermal requirements for egg (6.8 °C with 50.4DD) and total development (12.1 °C with 196.8DD) of a Nearctic population of *C. septempunctata* (Obrycki and Tauber, 1981) were different from those reported in the present study. Michels and Behle (1991a) in a Nearctic population of *C. septempunctata* found similar day-degree requirements

(275DD) for completion of development to that estimated in the present study, but a higher developmental threshold (11.7 °C). These differences in thermal requirements of populations from different origin within a species indicate the need to undertake relative studies on native coccinellids when trying to evaluate them as biological control agents.

Aphid consumption

Consumption was significantly higher at 23 °C than at the other temperatures, indicating that both species may be more effective in reducing aphid numbers at relatively high temperatures, assuming that other biotic or abiotic factors are favourable. *Coccinella septempunctata* has a greater consumption rate than *H. convergens*, which has been also recorded when both predators fed on *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) (Michels and Behle, 1991a). Consequently, *C. septempunctata* has a higher potential to control dense aphid populations than *H. convergens*. In both predator species the fourth larval instar was always the most voracious. The same trend was also reported for *C. septempunctata* when fed on *S. graminum* (Michels and Behle, 1991a) and for *H. convergens* when fed on *S. graminum* (Michels and Behle, 1991a) and *Therioaphis maculata* (Buck) (Hemiptera: Aphididae) (Campbell and Cone, 1999).

The similar developmental threshold of the species examined in the present study suggests that they could emerge early in the season. However, the seven-spotted lady beetle has a higher potential for establishment because it seems to be more tolerant to early season conditions, since it suffers from lower egg mortality at 14 °C and in addition it attained equivalent mass at different temperatures. Later in the season, *H. convergens* should develop higher numbers since its development requires a lower thermal constant. This is in accordance with the results of Wells and McPherson (1999) showing that during mid season *H. convergens* is the prevailing coccinellid species on tobacco crops. In that period the contribution of *C. septempunctata* in aphid control may further be lowered due to its emigration to other crops (Teddars and Schaefer, 1994; Wells and McPherson, 1999) or due to the reproductive diapause, into which part of its population enters (Katsoyannos et al., 1997). However, *Coccinella septempunctata* should be more effective when populations of the tobacco aphid are high, taking into account its higher consumption rate.

On tobacco apart from coccinellids, the predatory bugs *Macrolophus costalis* Fieber and at a lesser rate *Macrolophus pygmaeus* Rambur (both Hemiptera: Miridae) are also recorded (Dirimanov and Dimitrov, 1975;

Lykouressis et al., 2000). The data gathered in the current study enable us to make an attempt to compare the potential of coccinellid and mirid predators to control the tobacco aphid. *Macrolophus* species should appear earlier in the season, taking into account that the developmental threshold for immature development in *M. pygmaeus* when, fed on *M. persicae* on eggplant, was estimated as 8.7 °C (Perdikis and Lykouressis, 2002). However, later in the season, coccinellids develop faster due to their lower thermal constant for immature development than that of *M. pygmaeus* (439DD) (Perdikis and Lykouressis, 2002).

Coccinellids may face serious difficulties to survive on tobacco plants in periods of aphid scarcity, and probably they migrate to plants with alternative food supply (Wells and McPherson, 1999; Tsitsipis et al., unpublished data). By contrast, *Macrolophus* could remain in position when aphids are scarce because they complete nymphal development feeding exclusively on plant sap of tobacco (Margaritopoulos et al., 2003) and furthermore, they also feed on whiteflies or thrips. However, *M. costalis* and *M. pygmaeus* consume considerably fewer *M. persicae* nymphs during their nymphal development than both coccinellids (Margaritopoulos et al., 2003). Consequently, coccinellids should be more effective when high aphid populations are present, whereas, *Macrolophus* have a higher potential early in the season and in periods when aphid numbers are low. Thus, it may become evident that these two groups of predators may be successfully combined against the tobacco aphid.

In conclusion, data gathered on thermal requirements and prey consumption of *H. convergens* and *C. septempunctata*, show their high potential as biological control agents of *M. persicae nicotianae*. This knowledge could be essential for their most appropriate use but also in efforts to develop efficient mass rearing systems.

However, apart from thermal and dietary requirements, additional work is needed, i.e. studies on fecundity and population increase and on searching efficiency, for a more accurate evaluation of the impact of these predators on tobacco aphid populations.

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