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Performance of *Myzus persicae* (Hemiptera: Aphididae) clones on different host-plants and their host preference

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Abstract

The performance of eighteen clones of *Myzus persicae* (Sulzer) on pepper and tobacco plants at 20°C and L16:D8 and the choice of young adult apterae between tobacco and pepper leaf-discs were examined. The clones were collected from weeds and peach in two tobacco-growing regions: Katerini, northern Greece and Karditsa, central Greece (only from weeds) and from Lehonia, central eastern Greece where tobacco is not cultivated. All clones did well on both hosts. However, the analysis of data revealed a significant effect of 'region / host plant origin' on aphid performance. The mean values of adult weight, intrinsic rate of increase and fecundity of the clones collected in Lehonia and reared on tobacco were significantly lower than the observed values for clones from Katerini and Karditsa. Aphids from Lehonia had significantly higher mean values for developmental time on tobacco than clones from the other regions whereas the opposite was observed when aphids were reared on pepper. Aphids collected in Lehonia performed better on pepper than those originating from the tobacco-growing regions. A choice test revealed differences among the clones originating from different regions. Fifty three percent and 43% of aphids from weeds and peach from Lehonia, respectively, chose pepper. By comparison 41.5% and 40.0% of aphids from peach and weeds from Katerini, respectively and 49.5% of aphids from Karditsa preferred tobacco. The results are discussed in relation to host specialization in *M. persicae*.

Introduction

Myzus persicae (Sulzer) (Hemiptera: Aphididae) is an extremely polyphagous aphid feeding on host-plant species from over 40 families including several agricultural crops (Blackman & Eastop, 1984). It is considered the major pest of tobacco, *Nicotiana tabacum* L. (Solanaceae) in Greece, causing direct damage to plants and indirect damage by transmitting important non-persistent viruses (Katis *et al.*, 1992).

Myzus persicae shows considerable genetic variation with respect to host-plant adaptation. Weber (1985) examining over 1000 clones originating mainly from potato, *Solanum tuberosum* L. (Solanaceae) and sugarbeet, *Beta vulgaris* L. (Chenopodiaceae) reported a higher performance of clones on hosts from which they originated. Later, Blackman (1987) pointed out that populations of *M. persicae* on tobacco were morphologically distinct from those on other secondary hosts. He concluded that the tobacco form of *M. persicae* consists of a genetically distinct species adapted to tobacco. More recent genetic and morphological studies have provided further evidence that a specific host-adapted form of *M. persicae* occurs on tobacco which is morphologically and genetically distinct from populations on other host-plants (Blackman & Spence, 1992; Margaritopoulos *et al.*, 2000; Blackman *et al.*, 2001), but evidence of identical DNA

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sequence at some loci (Field *et al*., 1994; Clements *et al*., 2000) denotes that some interbreeding has occurred between the two forms and that subspecific status (as *M. persicae* ssp. *nicotianae* Blackman) would be more appropriate (Blackman & Eastop, in press).

It is recognized that morphological, nutritional and biochemical features of host-plants are responsible for the plant range that herbivorous insects can exploit and can act as important selective agents (Thompson, 1988; Bernays & Chapman, 1994). These plant characteristics are major factors involved in host choice and acceptance by aphids (Dixon, 1998 and references therein) and in genotype-specific interactions between aphids and their hosts (Blackman, 1990). In a review of aphid–plant interactions, Blackman (1990) pointed out that more than half of the relevant published studies provided evidence for host-adapted genotypes. Negative trade-offs in host utilization are a potentially important factor for sympatric diversification of insect species. The negative correlation between performance on different host-plants has been demonstrated for the pea aphid *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) (Via, 1991a,b) and the black bean aphid *Aphis fabae* (Scopoli) (Hemiptera: Aphididae) (Mackenzie, 1996; Douglas, 1997). Host specificity in aphids may also be explained by the fact that small differences in the rates of population increase achieved on different plants, amplified by clonal apomictic parthenogenesis, makes the attempt to find the best host advantageous for aphids. Moreover, the correct choice of the host plant is of primary importance for the maximum performance to be achieved. It has also been reported that the relative ground cover and the longevity of plants affect the probability of aphids locating a suitable host (Dixon, 1998).

Our knowledge regarding the relative success of the tobacco aphid *M. persicae* ssp. *nicotianae* and *M. persicae* sensu stricto on different secondary hosts and the nature of aphid host-plant interactions that may be responsible for genetic divergence in *M. persicae* is still limited. The present study aimed to examine the performance of various clones originating from two tobacco and one non-tobacco-growing regions in Greece, cultured on tobacco and pepper, *Capsicum annum* L. (Solanaceae) plants. The preference of the apterous morphs of these clones for the above hosts was also evaluated.

Materials and methods

Aphids and plants

A total of eighteen aphid clones derived from samples collected from peach, *Prunus persica L.* (Rosaceae) and Shepherd's purse, *Capsella bursa-pastoris* L. (Brassicaceae) from three localities in Greece (Katerini, Karditsa, and Lehonia) were used in the study. Katerini, northern Greece and Karditsa, central Greece are the main tobacco growing regions. On the other hand, tobacco is not cultivated in the Lehonia region in central eastern Greece. The aphids from weeds were collected near to tobacco fields in Katerini and Karditsa and pepper fields in Lehonia in early April 2002 and those from peach in mid June of the same year. Clones were established from one parthenogenetic female, all were green except one red from Karditsa, and were reared on excised potato leaves at 17°C and L16:D8. Information regarding the origin of the clones examined is shown in table 1.

Demographic parameters

The performance of *M. persicae* clones over two generations on tobacco (oriental type variety KP14/a) and pepper (variety P-14) plants was examined. Pepper was included in the study because it is a common crop in regions where tobacco is not cultivated. Observations on performance were followed for two generations in order to examine possible acclimation effects. The experiments were performed under constant conditions, 20°C and L16:D8. When tobacco and pepper plants attained the 2–4 true leaf stage, adult apterous virginoparous females from the colony maintained under long days and 17°C were confined on the leaves of the test plants using clip-cages (two cages per plant). After 24 h, females were discarded and one nymph per cage was kept. A total of 30 nymphs per clone per plant species was set up. The condition of the nymphs (dead or alive) was recorded daily until production of the first progeny. Then, nymph production in 12 females per clone per plant species was recorded every two days during the total life span of the adult virginoparae. The first progeny were kept and 12 replicates were set up for the second rearing generation on each plant species. Nymphal mortality, the time from birth to the onset of first reproduction (developmental time) and the total number of progeny produced were recorded. The intrinsic rate of increase was estimated according to the method of Wyatt & White (1977), $r_m = 0.738 * \ln (Md/Td)$, where Td is the developmental time (in days) and Md the number of offspring produced during a period equal to Td from the onset of reproduction.

Adult weight

In another experiment, the weight of apterous females on attaining adulthood was recorded. Adult females from the clonal cultures were caged on tobacco and pepper plants at the 2–4 true leaf stage and were allowed to reproduce for one day. Two of these offspring were kept in each clip cage until reaching adulthood. The aphids were immobilized by exposing them to –18°C for 3–5 min and weighed using a Precisa 40SM-200A (PAG Oerlikon AG, Switzerland) electronic balance. To avoid distortion of measurements,

Table 1. Clones of *Myzus persicae* used in the study.

Clone codes	Plant species	Collection site
LW1–4	*Capsella bursa-pastoris*	Lehonia, central eastern Greece
LP1–4	*Prunus persica*	Lehonia, central eastern Greece
KtW1–3	*Capsella bursa-pastoris*	Katerini, northern Greece
KtP1–4	*Prunus persica*	Katerini, northern Greece
KrW1–3	*Capsella bursa-pastoris*	Karditsa, central Greece

aphids that did not recover were assumed to be dead and were discarded.

Preference tests

Choice experiments were conducted in Petri dishes (9 cm diameter) with young adult apterous females at 20°C and L16:D8. A square opening (1.5 × 1.5 cm) was made in the cover of the Petri dish and covered with fine muslin to allow aeration. Two leaf discs, 3.5 cm in diameter, cut from tobacco and pepper plants at the 2–4 true leaf stage were placed on a moist filter paper (9 cm diameter) near the edge of the Petri dish. Twenty young adult apterous females per clone, derived from the cultures on potato leaves, were placed in each Petri dish. The aphids were confined in an Eppendorf tube that was placed at the edge of the Petri dish opposite the leaf discs. Then, the cap of the tube was opened to free the aphids and the Petri dish was covered. The dishes were rotated through 180°, one and a half hours later. The number of settled aphids was recorded three hours after the beginning of the experiment. This observation period was adopted because preliminary experiments showed that the condition of the leaf discs deteriorated after three hours and the majority of aphids had settled by this time. The choice tests for all clones were performed at the same time and the experiment was replicated ten times.

Statistical analysis

The effect of the factors 'region / host plant origin', 'rearing generation' and 'clone' (random factor) on the demographic parameters of the aphids reared on tobacco and pepper, was examined using nested ANOVA. The effect of the factors 'region/host plant origin' and 'clone' (random factor) on the weight of adults reared on the two hosts was examined using nested ANOVA. Nymphal mortality and host preference were analysed by a χ^2-test.

Results

The results showed that clones of *M. persicae* originating from both tobacco and non-tobacco growing regions were able to utilize tobacco as well as pepper plants. However, nested ANOVA revealed that the factors 'region / host plant origin', 'rearing generation' and 'clone' had a significant effect on the demographic parameters of the aphids reared on tobacco and pepper plants (table 2).

Performance on tobacco

The mean time from birth to the onset of first reproduction after reaching adulthood was significantly higher in aphids from Lehonia (9.7–10.0 days) than those from tobacco-growing regions (8.5–9.0 days). Moreover, the intrinsic rate of increase and fecundity were significantly lower in aphids from Lehonia than those from the other regions. The lowest value of the intrinsic rate of increase was observed in aphids collected from peach in Lehonia (0.229) and the highest in aphids from weeds from Karditsa (0.283). The mean total number of progeny ranged from 28.9 in clones from peach in Lehonia to 45.5 in aphids collected from *C. bursa-pastoris* from Karditsa. The lowest mean longevity was observed in aphids from peach in Lehonia (table 3). The highest mortality was observed in aphids from Lehonia, although the differences were not always significant (table 4).

Performance on pepper

The opposite results were observed on pepper since aphids from Lehonia showed a higher performance than those from the tobacco-growing regions. Developmental time was significantly shorter in aphids from Lehonia (7.8–8.6) than those from Katerini and Karditsa (8.7–9.1). In addition, clones from Lehonia had a significantly higher intrinsic rate of increase (0.260–0.284) than those collected from the other regions (0.246–0.264) (table 3). However,

Table 2. Results (F values) of nested ANOVA for the effects of 'region/host-plant origin', 'clone' and 'rearing generation' on the intrinsic rate of increase (r_m), age at first reproduction (Td), fecundity and longevity of *Myzus persicae* clones reared on tobacco and pepper plants at 20°C and L16:D8.

Source of variation	df	Td	r_m	Fecundity	Longevity
Tobacco					
Intercept	1	92120*	52370*	5138*	16.3*
Region / host-plant origin	4	97.8*	91.6*	42.4*	7.9*
Clone (region/host-plant origin)	13	7.8*	6.7*	4.3*	2.9*
Generation	1	86.9*	52.4*	6.5*	6.4*
Region/host-plant origin × generation	4	112.58*	5.0*	2.0	2.5*
Generation × clone (region/host-plant origin)	13	2.8*	2.8*	3.7*	2.0*
Error	396				
Pepper					
Intercept	1	43000*	79820*	4130*	13710*
Region/host-plant origin	4	26.6*	52.8*	3.8*	1.5
Clone (region/host-plant origin)	13	11.7*	9.1*	8.0*	3.1*
Generation	1	86.7*	41.3*	25.0*	0.3
Region/host-plant origin × generation	4	2.0	4.7*	0.8	0.8
Generation × clone (region/host-plant origin)	13	0.9	3.5*	1.0	1.5
Error	396				

*Denotes significant differences ($P < 0.05$).

fecundity and longevity were about the same in aphids from the former sampling regions (table 3). The lowest nymphal mortality was observed in aphids from Lehonia, although the differences were not always significant (table 4).

Adult weights

The results of nested ANOVA showed a significant effect of region/host-plant origin on the adult weight of aphids reared on tobacco (df = 3, 237, F = 46.1, $P < 0.05$) and pepper plants (df = 3, 237; F = 16.0, $P < 0.05$). Particularly, the mean adult weight of aphids from Lehonia (253.4–239.9 µg) was significantly lower on tobacco than those from Katerini and Karditsa (288.3–313.7 µg). The opposite results were obtained on pepper since the highest adult weight was observed in aphids that were collected from *C. bursa-pastoris* in Lehonia, although differences were not always significant (table 4).

For both hosts, the demographic parameters of the clones examined were improved in the second parthenogenetic rearing generation compared with the first one (table 5). Nested ANOVA revealed that the rearing generation had a significant effect on aphid performance (table 2).

Preference trials

The preference of the 18 *M. persicae* clones between tobacco and pepper leaf-discs is shown in fig. 1. It appeared that in clones from Lehonia, more individuals preferred pepper than tobacco. The opposite was observed in clones that were from tobacco-growing regions. However, in each case a number of aphids chose neither of the two hosts, but were found on the walls of the Petri dishes. The χ^2-test revealed significant differences between the examined regions in host-preference of aphids. The higher proportions of aphids that preferred pepper were observed in the clones that were collected on *C. bursa-pastoris* (53.0%) and peach (42.5%) in the Lehonia region. On the other hand, the percentage of aphids from Lehonia (26.5–29.0%) that chose tobacco was significantly lower than that observed in the clones from Karditsa and Katerini. The proportion of aphids from *C. bursa-pastoris* and peach in Katerini was that chose tobacco 42.5% and 41.5%, respectively. The corresponding percentage of aphids that were collected from *C. bursa-pastoris* in Karditsa was 49.5% (table 6).

Evaluation of the 'optimal host range' hypothesis

Dixon (1998) reported that the optimal host range hypothesis could account for host specificity in aphids. The theory could not be applied to aphids from Lehonia as tobacco is not cultivated in this region, but was tested using data obtained from clones from Katerini since, in this region, aphids were collected from both peach and *C. bursa-pastoris*. The plain around Katerini is approximately 35,200 hectares

Table 3. Mean values (±SE) of demographic parameters for *Myzus persicae* clones (N) collected from different hosts and regions in Greece and reared for two generations on tobacco (T) and pepper (P) plants at 20°C and L16:D8.

Region/host-plant origin	N	Intrinsic rate of increase		Age at first reproduction (days)		Fecundity		Longevity (days)	
		T	P	T	P	T	P	T	P
Lehonia, *Capsella bursa-pastoris*	4	0.244a (0.003)	0.284a (0.003)	9.7a (0.1)	7.8a (0.1)	33.3a (1.3)	36.0a (1.4)	25.9ab (0.5)	26.0ab (0.5)
Lehonia, *Prunus persica*	4	0.229b (0.003)	0.260bc (0.003)	10.0b (0.1)	8.6b (0.1)	28.9b (1.1)	34.2ab (1.5)	25.0a (0.4)	26.6ab (0.5)
Katerini, *Capsella bursa-pastoris*	3	0.283c (0.003)	0.246d (0.004)	8.6c (0.1)	9.1c (0.1)	45.5c (1.6)	32.3b (1.4)	27.1bc (0.5)	26.1ab (0.5)
Katerini, *Prunus persica*	4	0.269d (0.002)	0.253cd (0.003)	9.0d (0.1)	8.9c (0.1)	44.5c (1.2)	32.1b (1.1)	28.1c (0.4)	25.8a (0.4)
Karditsa, *Capsella bursa-pastoris*	3	0.283c (0.003)	0.264b (0.004)	8.5c (0.1)	8.7b (0.1)	45.5c (1.7)	37.7a (1.4)	27.7c (0.6)	27.4b (0.6)

Mean values within a column followed by a different letter differ significantly ($P < 0.05$) by Duncan test.
Twelve individuals were tested from each clone

Table 4. Mean adult weight (±SE) and percentage nymphal mortality of clones (N) of *Myzus persicae* collected from different host-plants and regions in Greece and reared on tobacco (T) and pepper (P) plants at 20°C and L16:D8.

Region/host-plant origin	N	n[1]	Adult weight (µg)		n[2]	Nymphal mortality (%)	
			T	P		T	P
Lehonia, *Capsella bursa-pastoris*	4	20	253a (2.6)	277a (3.5)	60	30.0a	16.3a
Lehonia, *Prunus persica*	4	20	240b (2.9)	259b (3.4)	60	25.8ab	17.5ab
Katerini, *Capsella bursa-pastoris*	3	20	291c (3.6)	242c (3.7)	60	21.1ab	32.8c
Katerini, *Prunus persica*	4	20	288c (4.3)	256b (2.8)	60	18.3b	24.6bc
Karditsa, *Capsella bursa-pastoris*	3	20	314d (7.0)	270a (5.1)	60	17.8b	22.2abc

Mean values and percentages within a column followed by a different letter differ significantly ($P < 0.05$) by Duncan and X^2-test, respectively.
Aphids were reared for one[1] or two[2] generations on the test plants.
n = number of individuals per clone examined.

Table 5. Mean values (±SE) of time from birth to the onset of reproduction (days, Td), intrinsic rate of increase (r_m), fecundity (F), longevity (days, L) and percentage nymphal mortality (M) of *Myzus persicae* clones (N) collected from different host-plants and regions in Greece and reared for two successive generations on (A) pepper and (B) tobacco plants at 20°C and L16:D8.

	Region/host-plant origin	N	First generation					Second generation				
			Td	r_m	F	L	M	Td	r_m	F	L	M
A	Lehonia, SP	4	7.9	0.272	31.7	26.3	17.5	7.8	0.296	40.4	25.7	15.0
	Lehonia, P	4	8.6	0.254	32.5	26.2	21.7	8.5	0.266	35.9	27.0	13.3
	Katerini, SP	3	9.5	0.234	29.6	25.9	37.8	8.7	0.259	35.0	26.3	27.8
	Katerini, P	4	9.2	0.238	30.2	26.5	30.0	8.7	0.269	34.0	25.1	19.2
	Karditsa, SP	3	8.9	0.252	34.9	27.2	24.4	8.4	0.277	40.5	27.6	20.0
B	Lehonia, SP	4	10.4	0.230	33.1	27.1	34.2	9.1	0.258	33.5	24.8	25.8
	Lehonia, P	4	10.3	0.215	25.0	24.6	29.2	9.6	0.242	32.9	25.4	22.5
	Katerini, SP	3	8.7	0.275	44.4	28.1	23.4	8.4	0.291	46.7	26.1	18.9
	Katerini, P	4	9.2	0.265	44.7	29.1	21.7	8.8	0.273	44.3	27.1	15.0
	Karditsa, SP	3	8.6	0.282	43.6	27.6	21.1	8.4	0.285	47.4	27.8	14.5

Twelve individuals were tested from each clone.
SP, *Capsella bursa-pastoris; P, Prunus persica.*

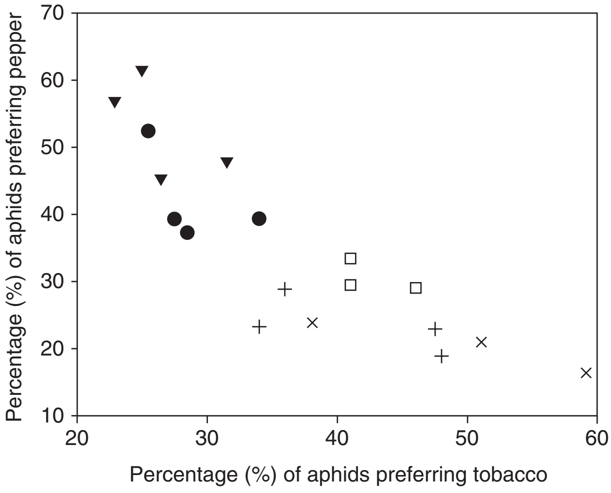

Fig. 1. Host preference of *Myzus persicae* clones used in the study. Clones collected from: ▼, *Capsella bursa-pastoris* in Lehonia (LW1–4); ●, *Prunus persica* in Lehonia (LP1–4); □, *C. bursa-pastoris* in Katerini (KtW1–3); +, *P. persica* in Katerini (KtP1–4); and ×, *C. bursa-pastoris* in Karditsa (KrW1–3).

and the areas devoted to tobacco and pepper are 8226 and 70 hectares, respectively. In Katerini, the longevity of both crops is approximately 130 days (mid May to late September). According to the hypothesis, if an aphid lands on pepper and decides to stay, its benefit will be $R_S = exp(t_p \times r_{mp})$, where t_p is the longevity of the crop and r_{mp} the intrinsic rate of increase of the aphid clone on pepper. Assuming that the aphid has energy for one more flight and decides to fly, then its benefit will be $R_F = C_p \times exp(t_p \times r_{mp}) + C_t \times exp(t_t \times r_{mt})$. C_p and C_t are the probabilities of an aphid locating either pepper or tobacco (= the proportion of ground covered by the plants), t_p and t_t are the longevities of pepper and tobacco and r_{mp} and r_{mt} the intrinsic rates of increase of the aphid clones on pepper and tobacco, respectively. Using the above mentioned data and the intrinsic rates of increase from table 3 the model predicts that the benefit of an aphid leaving pepper in terms of population size at the end of the season will be 2 (calculated for clones from peach) or 27 × higher (calculated for clones from *C. bursa-pastoris*) than that if it decides to stay on pepper. The cost of migration, i.e. the probability of a winged female flying from pepper and not locating tobacco or pepper is $1 - C_p - C_T = 0.764$.

Discussion

The results revealed important interclonal variation in the performance of *M. persicae* on tobacco and pepper plants. The variation was correlated with the origin of aphid clones. In general, aphids collected from the two tobacco-growing regions of Greece (Katerini and Karditsa) performed better on tobacco than those collected from central eastern Greece (Lehonia), where tobacco is not cultivated. The opposite trend was observed on pepper plants, a common crop in the region of Lehonia. It was clear that host plant affected the life parameters of the aphid clones examined. Aphids originating from tobacco-growing regions had a higher performance on tobacco than on pepper plants while the opposite was observed in clones from the Lehonia region.

The differences obtained in this study were not as big as those for *A. fabae* reported by Douglas (1997) who showed that the performance of the aphid on *Tropaeolum majus* L. (Tropaeoloaceae) and *Vicia faba* L. (Fabaceae) was highly negatively correlated. However, the results of the present study revealed significant differences in the performance of clones on tobacco and pepper related to their origin. It is considered that even small differences in the rates of population increase on different plant species amplified by apomictic parthenogenesis make it advantageous for aphids to find the best host. According to Dixon's (1998) optimal host range hypothesis, when an aphid lands on an inferior host its decision to stay or fly and locate a better host, depends on the probability of finding a better host, the time that the two hosts remain suitable for the aphid and the relative rates of increase of the aphid on the hosts. The results obtained here substantiate the hypothesis since the analysis of clones from Katerini showed that it was

Table 6. Host preference of clones (N) of *Myzus persicae* (pooled data) collected from different hosts and regions in Greece.

Region/host-plant origin	N	% aphids preferring	
		Tobacco	Pepper
Lehonia, *Capsella bursa-pastoris*	4	26.5 a	53.0 d
Lehonia, *Prunus persica*	4	29.0 a	42.5 c
Katerini, *Capsella bursa-pastoris*	3	42.5 b	30.5 b
Katerini, *Prunus persica*	4	41.5 b	23.5 ab
Karditsa, *Capsella bursa-pastoris*	3	49.5 b	20.5 a

Percentages in each column followed by a different letter differ significantly ($P < 0.05$) by χ^2-test.

advantageous for alatae to leave pepper and locate tobacco. Although dispersal is hazardous for aphids, the benefits that aphids accrue on a superior host tend to balance possible losses. Approximately one out of every four alatae leaving pepper must find tobacco in order for the clone to gain the maximum benefit. Therefore, the difference in performance between clones originating from tobacco and non-tobacco growing regions could be attributed to the host specialization. Recent morphometric and molecular studies on *M. persicae* clones have revealed genetic and morphological differentiation between aphids from Karditsa and Katerini and those from Lehonia (Margaritopoulos *et al.*, 2000; Blackman *et al.*, 2001; Zitoudi *et al.*, 2001). Margaritopoulos *et al*. (2000) reported that the tobacco-adapted form of *M. persicae* in Greece was not found in regions where tobacco is not cultivated, i.e. Lehonia, although it was found on other herbaceous host plants in tobacco-growing regions. The present findings suggest that the former situation may be explained by the fact that the tobacco aphid is not competitive with *M. persicae* s.s. on crops other than tobacco. It is worthwhile mentioning that other factors may also be involved. Physical barriers such as the mountains surrounding Lehonia region could prevent the invasion of the tobacco aphid.

An effect of rearing generation on aphid performance on both pepper and tobacco plants was observed. The demographic parameters of the clones were improved in the second rearing generation. This suggests an acclimation of the apterous females to the new nutritional environment. The progressive improvement in aphid performance during multiple generations of apomictic parthenogenesis on unfavourable hosts has been also reported for other aphid species such as *Dysaphis anthrisci* (Börner) (Hemiptera: Aphididae), *A. fabae* and *A. pisum* (Shaposhnikov, 1961; Markkula & Roukka, 1970; Mackenzie, 1991). By contrast, Via (1991b) obtained no evidence for changes in the performance of *A. pisum* on alfalfa *Medicago sativa* L. (Fabaceae) and clover *Trifolium pratense* L. (Fabaceae) and Douglas (1997) pointed out that it is difficult to assess whether there are common features to the changes in aphid performance across parthenogenetic generations among aphid species in general. Nevertheless, the increase in performance of the clones in the second generation reported in the present study suggests a reduction in the risk to a winged female of the tobacco aphid, if it decides to stay on pepper.

It is well known that the morphological and chemical characteristics of plant species affect the performance and host preference of phytophagous insects. High densities of secreting and non-secreting glandular trichomes on tobacco leaves result in greater aphid resistance (Greer & Nielsen, 1988; Severson *et al.*, 1992). Glandular hairs of tobacco leaves produce alkaloids (nicotine, nornicotine) that are highly effective against aphids and other insects (Thurston *et al.*, 1966; Thurston, 1970). In addition, studies have shown that diterpenes and sugar esters produced by glandular trichomes are the main chemicals responsible for aphid resistance in tobacco. These compounds affect the selection of plants by alatae and the performance of apterous females (Severson *et al.*, 1985, 1992). Presumably, tobacco-adapted genotypes of *M. persicae* have the ability to counteract the defensive mechanisms of the host-plant and to perform better on this host than the non-tobacco-specialist conspecific clones.

It is worth mentioning that performance experiments, where aphids are caged on the plant without the ability to choose either different hosts or feeding sites on the same hosts may not be always the appropriate way to investigate host specialization. In the present study, the host preference of the aphid clones was examined, although apterous females were used in the trials. The results obtained by choice tests were parallel to those of performance. A higher proportion of aphids from Katerini and Karditsa preferred tobacco to pepper leaf discs. The opposite was observed in aphids from the Lehonia region. The results show that apterae have the potential to recognize the appropriate host. Chemical compounds on the leaf surface or nutritional factors may be responsible for the aphid's decision. It has been reported that host preference of aphids is influenced by experience of the previous host-plant (Lushai *et al*., 1997). However, in the present study, all clones were reared on a common host (potato) different from those used in the performance and choice trials. Presumably, the variation observed in performance and host preference in clones of *M. persicae* is genetically determined.

Aphids from the tobacco-growing regions of Greece showed a relatively good performance on pepper. The good performance of clones derived from tobacco on pepper and other plant species under controlled conditions has been also reported by Semtner *et al*. (1998). It appears that the tobacco-feeding form has the potential to succeed on many host plants. However, the colonization decisions by alate aphids are important factors responsible for the development of populations on particular hosts. Semtner *et al*. (1998) pointed out that although the tobacco form performs well on several plant species under laboratory conditions, it is uncommon on those hosts in the field. The same situation is also observed in the tobacco-growing regions in northern Greece. There, tobacco fields are heavily infested with *M. persicae*, although aphids on other crops (e.g. pepper, cabbage) are rarely found. Regardless of the differences observed in the performance of clones on tobacco and pepper, the results of the present study revealed that apterous females have a tendency to choose the correct host. It seems, therefore, that in host specialization in *M. persicae* both host selection and performance on a certain host are involved.

Blackman (1990) pointed out the need for investigating the behaviour of alate colonizers in order to elucidate aphid host-plant interactions, since the winged female is the morph that makes the choice of an appropriate host. The crucial role of alate colonizers in reproductive isolation of sympatric host-adapted races has been demonstrated in *A. pisum* (Via, 1999; Via *et al*., 2000). The authors suggested that natural selection acting against cross-host alatae leads to premating gene flow barriers since the frequencies of migrants are reduced before sexual reproduction takes place in the autumn. This selection promotes the evolution of improved efficacy of host-plant selection by alate colonizers. Our results, from this view-point, although they contribute to the understanding of host adaptation in *M. persicae*, should be complemented by examination of host selection behaviour in the winged morphs of *M. persicae*, which should give an insight into the presumed reproductive isolation between the tobacco-adapted form and those feeding on other hosts.

The results of the present study revealed that host specialization in *M. persicae* lies in both performance and host-preference. However, further work on comparative studies of feeding behaviour of tobacco and non-tobacco adapted clones and biochemistry of the defence mechanisms of tobacco plants are needed for a more comprehensive understanding of aphid host-plant interactions in *M. persicae*.

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