Eur. J. Entomol. **103**: 337–346, 2006
ISSN 1210-5759

Effect of temperature and photoperiod on the life cycle in lineages of *Myzus persicae nicotianae* and *Myzus persicae* s. str. (Hemiptera: Aphididae)

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Key words. *Myzus persicae*, *Myzus persicae nicotianae*, males, mating females, sexual morphs

Abstract. Male production was examined in 70 *Myzus persicae* s.str and *M. persicae nicotianae* clonal lineages at 17°C and 10L : 14D. Sixty nine were characterised by a partial loss of sexuality (androcyclic producing few males, and intermediates producing some males and mating females), and one was found to be permanently parthenogenetic. High within and between lineage variation was detected. Most (81%) of the clonal lineages produced few males (0–5 males per parent) and only 6% had male production (10–16 males per parent) comparable to that (12–23 males per parent) of seven lineages with a sexual phase (holocyclic) which were examined under the same conditions. The length of prenatal exposure to 10L : 14D increased the production of males. Continuous rearing under 10L : 14D at 12°C adversely affected male production in another intermediate clonal lineage. Temperature was found to affect the production of sexuals and to modify the short day photoperiodic response. The production of males and mating females was higher at 12°C than at 17°C in most of the 20 aforementioned clonal lineages with a partial loss of sexuality. Six lineages were permanently parthenogenetic at 17°C, but two of them produced a few males and the other four a few males and mating females at 12°C. Seven lineages which produced a few males at 17°C, also produced some mating females at 12°C. Lastly, photoperiod similarly affected the production of sexuals in two of the aforementioned clonal lineages, one with a sexual phase and one intermediate, although the regimes for the peak of sexuals were different. In both lineages, however, males appeared in a 0.5–1 h shorter scotophase than mating females.

INTRODUCTION

It is considered that Aphidoidea evolved in the Carboniferous period, approximately 280 million years ago (Dixon, 1998) and since then they have followed several evolutionary pathways. One evolutionary trajectory is cyclical parthenogenesis, the alternation between an annual sexual and several asexual generations, which first appeared in the lower Permian (Heie, 1967; Dixon, 1998). This reproductive strategy combines the advantages of sexuality (i.e. creation of new genotypes, elimination of deleterious mutations) and parthenogenesis which involves the telescoping of generations, providing high rates of population increase. A widespread phenomenon in Aphidoidea, however, is the partial or total loss of sexuality. It is often observed within species, e.g. in certain populations of a species or in genotypes of a given population. The number of species thought to be totally parthenogenetic is rather small (Blackman & Eastop, 2000). This intraspecific variation in reproductive strategy has been studied in several species of the family Aphididae, e.g. *Aphis gossypii* Glover (Takada, 1988), *Sitobion avenae* Fabricius (Dedryver et al., 2001), *Rhopalosiphum padi* (L.) (Simon et al., 1991) and *Myzus persicae* (Sulzer) (Blackman, 1971; Margaritopoulos et al., 2002). Four life cycle categories have been described. There are genotypes (holocyclic) with a sexual phase which produce both males and mating females (in Aphididae, as opposed to Adelgidae and Phylloxeridae, all parthenogenetic females are viviparous and mating females are oviparous), while others (anholocyclic) are permanently parthenogenetic. There are also genotypes with a partial loss of sexuality, which produce mainly parthenogenetic females along with a few males (androcyclic) or with some males and mating females (intermediates). The genotypes with a sexual phase and those with a partial loss of sexuality are not reproductively isolated one from each other; they experience at least some gene flow (Blackman, 1972, Dedryver et al., 1998; Simon et al., 1996, 1999; Delmotte et al., 2001).

The sexual phase is triggered by environmental changes, with photoperiod and temperature being the most crucial factors (Hille Ris Lambers, 1960; Lees, 1966; Kawada, 1987). Photoperiod provides the timing mechanism for sexual morph production. According to Blackman (1974), when genotypes with a sexual phase occur, their photoperiodic response is tuned to local conditions. Temperature often interacts with photoperiod modifying its effect. At temperatures above 25°C, the production of sexuals is inhibited in most aphid species (see Kawada, 1987 and references therein). Temperature is also responsible for the regional pattern of life cycle variation observed in aphids (Blackman, 1974; Rispe et al., 1998; Rispe & Pierre, 1998; Dedryver et al., 2001).

The effect of photoperiod in the production of sexual morphs by genotypes with a sexual phase has been well studied in many aphid species, e.g. *M. persicae* (Matsuka

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& Mittler, 1979; Mittler & Wilhoit, 1990), *Aphis fabae* Scopoli (Hemiptera: Aphididae) (Tsitsipis & Mittler, 1977a, b) and *Megoura viciae* Buckton (Hemiptera: Aphididae) (Lees, 1959), and critical day lengths for their production have been established. The influence of temperature has also been studied extensively in various species, e.g. *Aphis rubicola* (Oestlund) (Brodel & Schaefers, 1980) and *A. fabae* (Tsitsipis & Mittler, 1977a, b). These authors found that temperature differentially affected the production of males and that of mating females. Generally, more males appeared at relatively higher temperatures, while the opposite was observed for mating females. The influence of both photoperiod and temperature in the production of sexuals is mediated by the endocrine system of the aphids through the reduced production of juvenile hormone by the *corpora allata* (Tsitsipis & Mittler, 1977a, b; Mittler et al., 1979; Lees & Hardie, 1981).

Although much attention has been devoted to the abiotic (e.g. temperature, photoperiod) factors affecting the production of sexuals by genotypes with a sexual phase, only a few studies have examined genotypes with a partial loss of sexuality. Blackman (1972) found that temperature (20 vs. 10°C) affected, although differentially, the production of males and winged females by clonal lineages of *M. persicae*, depending on the type of short photoperiodic response (androcyclic and intermediates). Another study is that of Simon et al. (1991) in which various clonal lineages (with either partial loss of sexuality or permanently parthenogenetic) of *R. padi* were examined. An interesting finding was that temperature (15 vs. 10°C) modified the type of short photoperiodic response seen in most of the lineages. By contrast, Blackman (1972) reported stability of the type of short photoperiodic response shown by the clonal lineages of *M. persicae* he examined, regardless of rearing temperature.

There is evidence, therefore, that the photoperiodic response of genotypes with a partial loss of sexuality is variable. It should also be taken into account that high intraclonal variation has been reported in the production of sexuals by these genotypes (Blackman, 1971, 1972; Simon et al., 1991). Many questions, however, are still open. For instance, is intraclonal variation in the production of sexuals by genotypes with a partial loss of sexuality a widespread phenomenon within the *M. persicae* complex? Does the type of short photoperiodic response change with temperature in other aphids apart from *R. padi*? Does photoperiod influence the production of sexuals by genotypes with a partial loss of sexuality in the same manner as in those with a sexual phase?

These questions are investigated in the present study by examining (a) the intraclonal variation in male production by *M. persicae* s. str. and *Myzus persicae nicotianae* with a partial loss of sexuality, (b) the production of sexuals by such lineages reared at two constant temperatures and one short photoperiod, and (c) the sexual morph production by one clonal lineage with sexual phase and another with partial loss of sexuality under various photoperiods at one constant temperature.

MATERIAL AND METHODS

Aphids

In the present study 77 clonal lineages of *M. persicae* s.str. and *M. persicae nicotianae*, collected from various hosts and regions in Greece, were examined (Table 1). The life cycle category of these clonal lineages (holocyclic: with a sexual phase; androcyclic and intermediate: with partial loss of sexuality, the former produce a few males while the latter a few males and mating females; anholocyclic: permanently parthenogenetic) was characterised in a previous study of the life cycle variation of *M. persicae* s. l. in Greece (Margaritopoulos et al., 2002). Most of the clonal lineages were also examined with the multivariate morphometric analysis (Margaritopoulos et al., 2000; J.T. Margaritopoulos, unpubl.) and were assigned as *M. persicae* s. str. or *M. persicae nicotianae*. The lineages were parthenogenetically reared on excised leaves of potato *Solanum tuberosum* L., var. Spunta (Solanaceae) in Blackman boxes (Blackman, 1971), under long day conditions (LD, 16L : 8D) at 17°C until the beginning of the experiments. The assignment of the clonal lineages to a particular experiment was mainly a matter of logistics and also of availability (when a clone was set up).

Production of males by clonal lineages with a partial loss of sexuality

The production of males by 17 (C01–C09, C79, C80, C87–C90, C92, C93) clonal lineages of *M. persicae* s.str. and 32 (C10–C20, C47–C52, C55–C63, C65, C66, C70–C73) of *M. persicae nicotianae* with a partial loss of sexuality was examined under short day conditions (SD, 10L : 14D) at 17°C. All were androcyclic except for one intermediate clonal lineage (C08). Young adult wingless parthenogenetic females from each clonal lineage were transferred from the clonal cultures under LD to SD on excised potato leaves in Blackman boxes. The day after the adults were removed and batches (1–3 aphids each) of their offspring (G1 generation) were reared in separate boxes. Thus, G1 aphids were exposed to SD for 0–1 days prenatally. After they reached adulthood the batches of G1 wingless parthenogenetic females were transferred every four days to new cages until they died. Each batch of G1 aphids constituted one replicate. A total of five to 15 aphids were examined per clonal lineage in three to six replicates. In lineage C06, both G1 aphids that were exposed to SD 0–1 and 7–8 days prenatally were caged individually. In 20 clonal lineages, all of the progeny of the G1 aphids were identified to morph and counted (i.e., winged and wingless parthenogenetic females and males). In the other 29 lineages only the number of males was recorded for logistical reasons. Seven (C41–46, C95) clonal lineages with a sexual phase from the two taxa were examined under the same conditions for the purpose of comparison. The G1 wingless females were reared individually.

To confirm that the aforementioned lineages did not have the ability to produce even a few mating females, about 10% of the winged females produced by the G1 aphids of the clonal lineages examined were caged in batches of 2–3 individuals and their progeny were identified to morph. These were wingless parthenogenetic females and a few males in some cases. In the intermediate lineage C08, however, some mating females were also produced.

In order to investigate the effect of continuous rearing under SD on the different production of morphs, all of the progeny produced by one intermediate *M. persicae nicotianae* clonal

lineage (C94) were examined in successive generations under SD and 12°C. This lineage had not been tested previously at 17°C. Ten to 11 wingless females from G1, G2 and G3 and 9–11 winged females from the G2, G3 and G4 generations reared under SD were caged individually and transferred to new boxes every four days until they died. The number and morph of all progeny produced by these females was recorded.

Effect of temperature on sexual morph production in clonal lineages with a partial loss of sexuality

Twenty *M. persicae nicotianae* clonal lineages (C21–C40) with a partial (C21–30, C32–C40) or total loss of sexuality (C31) were examined under SD at two temperatures (17 and 12°C). At each temperature six to 14 G1 wingless females of each lineage were caged in batches of 1–3 individuals and transferred to new boxes every four days during their entire life. All progeny produced were identified to morph and counted (winged and wingless parthenogenetic females and males; G2 generation). In addition, 10–50 G2 winged females from each clonal lineage were reared (2–5 individuals per box) under the same conditions as their mothers and the morph of their progeny (winged and wingless parthenogenetic females, males and mating females; G3 generation) was recorded. Each batch of wingless or winged females reared in the same box was considered as a replicate. For reasons of comparison, one *M. persicae nicotianae* clonal lineage (C46) with a sexual phase, which was used in the first experiment, was also tested at 12°C under SD.

Effect of photoperiod on the production of sexuals by clonal lineages with sexual phase and partial loss of sexuality

In this experiment the production of different progeny morphs in two *M. persicae* s.str. clonal lineages was investigated at six and five photoperiods, respectively at 17°C (see Fig. 1). The lineages were the same as those used in the first experiment and one had a sexual phase (C95) and the other was intermediate (C08). Eight to 14 G1 wingless females were transferred from LD to the respective photoperiod 0–1 days prenatally. The aphids were caged individually and every two days they were transferred to new boxes until they died. All progeny of the G1 aphid were identified to morph and counted (males, wingless or winged parthenogenetic females). The winged females were reared individually and assigned to three categories according to the morph of their progeny: (i) mainly mating females, (ii) mainly parthenogenetic and few mating females, (iii) exclusively parthenogenetic females.

Statistical analyses

The effect of temperature on the production of the different morphs of progeny by clonal lineages with partial loss of sexuality was examined using ANOVA with the explanatory factors of "clonal lineage" and "temperature". One-way ANOVA was used in comparisons of means when one factor was involved. Data were transformed by the equation $\sqrt{x+1}$ before analysis. Basic statistics and ANOVA were performed using the SPSS ver.10 (SPSS Inc., 1999) statistical package.

RESULTS

Production of males by clonal lineages with partial loss of sexuality

Tables 2 and 3 show the males produced at 17°C by 49 clonal lineages of the two taxa with partial loss of sexuality (androcyclic and intermediates). Data for 20 additional clonal lineages are provided in Table 5. One of these lineages was found permanently parthenogenetic (C31, Table 5). Thus, the total number of lineages which

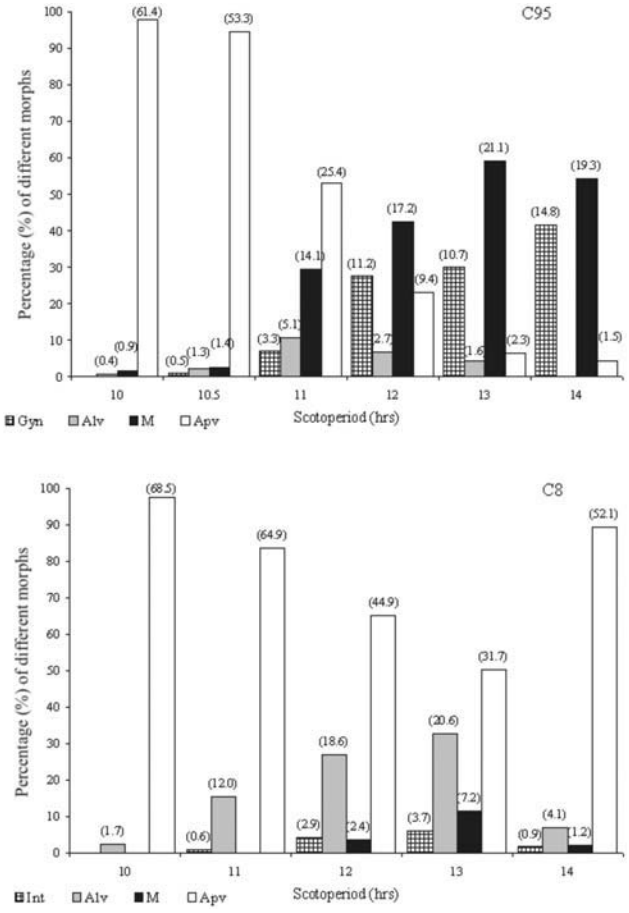

Fig. 1. Percentage of different progeny morphs produced by wingless parthenogenetic females of two *Myzus persicae* s. str. clonal lineages (C95: holocyclic, lineage with a sexual phase, C8: intermediate, lineage with a partial loss of sexuality, see also Table 2 for definition of terms) in the second generation in various scotophases at 17°C. Numbers in brackets denote the average number of each morph produced. Eight to 14 wingless females were examined per lineage in each scotophase. Gyn = winged parthenogenetic females producing mating females, Int = winged parthenogenetic females producing mainly permanently parthenogenetic females and few mating females, Alv = winged parthenogenetic females producing exclusively parthenogenetic females, M = males, Apv = wingless parthenogenetic females.

produced males at 17°C was 68, 17 of *M. persicae* s. str. and 51 of *M. persicae nicotianae*. High between lineages variation was observed in male production in both taxa. In some lineages only one male was produced from ten wingless females of the first generation under SD, while others produced an average of 10–16 males. In general, these 68 clonal lineages showed a much lower male production than the seven lineages with a sexual phase that were also reared at 17°C. The percentage of males produced ranged in androcyclic and intermediate lineages from 0.8 to 16.3% and from 0.0 to 4.5%, respectively. The corresponding percentage in the clonal lineages with a sexual phase ranged from 23.3 to 57.5%. These lineages produced 12–23 males per female (Tables 2, 3). By contrast, 41% of the clonal lineages with partial loss of sexu-

TABLE 1. Clonal lineages of *Myzus persicae* s. str. (*Mp*) and *Myzus persicae nicotianae* (*Mpn*) examined in the present study.

Clonal lineages	Host	Colour	Region*	Collection date	Taxa
C42	peach	green	Volos, CEG	May-95	*Mp*
C41, C43, C92, C95	peach	green	Volos, CEG	May-96	*Mp*
C01-06, C09, C89, C90, C93	peach	green	Volos, CEG	May-97	*Mp*
C07, C87, C88	pepper	green	Heraklio, Crete	Jul-96	*Mp*
C08	pepper	green	Volos, CEG	Jun-96	*Mp*
C79, C80	pepper	green	Volos, CEG	Jun-97	*Mp*
C20	tobacco	green	Agrinio, SCG	Sep-95	*Mpn*
C15-16	tobacco	red	Agrinio, SCG	Jul-96	*Mpn*
C13, C44, C45	tobacco	green	Alexandria, NG	Jun-96	*Mpn*
C14	tobacco	red	Alexandria, NG	Jul-96	*Mpn*
C19	tobacco	red	Amphiklia, SCG	Jul-96	*Mpn*
C60, C62, C65	tobacco	red	Amphiklia, SCG	Jun-97	*Mpn*
C61, C63	tobacco	green	Amphiklia, SCG	Jun-97	*Mpn*
C31-C40	tobacco	red	Amphiklia, SCG	Jul-98	*Mpn*
C10-12, C73	tobacco	green	Anavra, CG	May-96	*Mpn*
C70-72	tobacco	red	Anavra, CG	Jun-96	*Mpn*
C47-52	tobacco	red	Fillipiada, WG	Jun-97	*Mpn*
C46	tobacco	green	Meliki, NG	Jun-99	*Mpn*
C56-59	tobacco	red	Mitropoli, CG	Jun-97	*Mpn*
C66	tobacco	red	Nea Efessos, NG	Aug-97	*Mpn*
C21-24, C26-29, C94	tobacco	red	Nea Efessos, NG	Jul-98	*Mpn*
C25, C30	tobacco	green	Nea Efessos, NG	Jul-98	*Mpn*
C17, C18	tobacco	red	Tsaritsani, CG	Jul-96	*Mpn*
C55	tobacco	red	Tsaritsani, CG	Jul-97	*Mpn*

*NG = northern Greece, CG = central Greece, CEG = central eastern Greece, SCG = southern central Greece. The life cycle category of the lineages was characterised in a previous study of the life cycle variation of *M. persicae* s. l. in Greece (Margaritopoulos et al., 2002).

ality produced less than one male per female, 40% one to five males per female, and only 6% showed a level of male production (10–16 males per female) comparable to that of lineages with a sexual phase (Tables 2, 3 and 5).

An important intraclonal variation in male production of the clonal lineages with partial loss of sexuality was also observed. Although, in almost all lineages, it was not possible to identify the percentage of male producing females since one to three G1 wingless females were reared within the same box, the standard errors of the mean male production suggested high variance. In addition, no males were recorded in 185 out of 312 replications performed for all clonal lineages with partial loss of sexuality examined at 17°C. In two of the lineages (C08: intermediate and C06: androcyclic, see Table 2) examined at 17°C and in another (C94: intermediate, see Table 4) examined at 12°C, in which the G1 wingless females were reared individually in separate boxes, the percentage of male producing females was 14, 50 and 80%, respectively. In lineage C06, the percentage of the G1 male producing females was higher when they were transferred to SD 7–8 days rather than 0–1 days prenatally (67 vs. 50%). Mean male production also increased (8 vs. 4 males), although the difference was not significant ($F_{1, 24} = 2.2$, $P < 0.14$, Table 2).

Table 4 shows the different progeny morphs produced by wingless and winged females of an intermediate clonal lineage (C94) in three successive generations under SD at 12°C. Regarding the progeny of wingless females, the highest mean number of males and winged females appeared in the G2 generation, while that of wingless females in the G3 generation. In the G1 generation the highest percentage of male producing females ($X_2^2 = 8.3$, $P < 0.02$) was also recorded. Concerning the progeny of winged females, the significantly highest mean number of mating females was recorded in the G4 generation, while similar numbers of both morphs were observed in the G3 and G5. Wingless females were by far the most frequent morph produced by the winged females in all three generations, although their number in G5 was twice as high as that observed in G3 and G4.

Effect of temperature on sexual morph production in androcyclic and intermediate genotypes

Tables 5 and 6 show the progeny of the G1 wingless and G2 winged females of 20 *M. persicae nicotianae* clonal lineages with partial loss of sexuality under SD at 12 and 17°C. The G1 wingless females produced mainly wingless and to a lesser extent winged females as well as a number of males. ANOVA revealed a significant effect of temperature on the production of males and winged

TABLE 2. Mean number (± S.E.) of different morphs of progeny produced by wingless parthenogenetic females of *Myzus persicae* s. str. clonal lineages in the second generation at 17°C and 10L : 14D.

Clonal lineages	Life cycle category	n/N	Males	Winged females	Wingless females	Total
C41	H	10/10	22.6 ± 2.3	16.0 ± 1.8	0.7 ± 0.6	39.3 ± 2.8
C43	H	8/8	20.3 ± 1.1	41.8 ± 2.9	0.0	62.1 ± 3.1
C95	H	11/11	19.3 ± 1.6	14.8 ± 2.5	1.5 ± 1.1	35.6 ± 4.0
C42	H	14/14	16.8 ± 1.8	43.6 ± 3.4	1.6 ± 0.8	61.9 ± 3.6
C80	AND	12/4	15.5 ± 0.5	NR	NR	NR
C03	AND	5/3	7.7 ± 4.1	24.0 ± 13.6	28.2 ± 16.4	59.8 ± 11.2
C07	AND	9/3	6.8 ± 1.2	17.2 ± 4.4	23.5 ± 4.8	47.5 ± 5.3
C04	AND	9/3	4.5 ± 3.8	13.3 ± 7.4	28.6 ± 5.3	46.4 ± 5.7
C06	AND	14/14	3.9 ± 1.3	15.7 ± 2.1	20.9 ± 5.3	40.5 ± 5.0
C06*	AND	12/12	8.0 ± 2.1	22.3 ± 4.8	10.1 ± 3.6	40.4 ± 4.8
C92	AND	10/4	3.0 ± 0.5	NR	NR	NR
C93	AND	12/4	2.6 ± 0.5	NR	NR	NR
C01	AND	12/4	1.4 ± 0.8	2.9 ± 1.3	70.8 ± 7.0	75.1 ± 5.2
C87	AND	14/5	1.4 ± 0.3	NR	NR	NR
C79	AND	10/4	1.3 ± 0.3	NR	NR	NR
C90	AND	15/5	1.3 ± 0.3	NR	NR	NR
C05	AND	8/3	1.2 ± 0.9	10.2 ± 1.1	29.6 ± 6.6	41.0 ± 7.1
C08	IN	14/14	1.2 ± 1.1	5.0 ± 2.2	52.1 ± 4.5	58.3 ± 4.0
C02	AND	7/3	1.0 ± 1.0	10.7 ± 2.3	40.9 ± 15.1	52.6 ± 13.8
C09	AND	8/3	0.7 ± 0.7	11.1 ± 5.9	74.6 ± 2.7	86.4 ± 6.0
C89	AND	15/6	0.6 ± 0.2	NR	NR	NR
C88	AND	12/4	0.5 ± 0.2	NR	NR	NR

*Wingless females exposed to SD for 7–8 days prenatal, the others for 0–1 day. N = no. replicates, n = no. wingless females examined over all replications, NR = no records. H = holocyclic genotypes, i.e. with a sexual phase. AND and IN = androcyclic and intermediate genotypes, respectively, i.e. with partial loss of sexuality, they produced mainly permanently parthenogenetic females with few males (androcyclic) or both few males and mating females (intermediate).

females by the G1 wingless females ($F_{1, 226}$ = 18.0, P < 0.001 and $F_{1, 226}$ = 19.4, P < 0.001, respectively) with a non-significant "clonal lineage X temperature" interaction in each case ($F_{19, 226}$ = 0.6, P < 0.88 and $F_{19, 226}$ = 1.6, P < 0.053, respectively). In 17 clonal lineages (C21, C23, C25–27, C28–30, C32–40) the G1 wingless females showed higher male production at 12°C than at 17°C. Similarly, 14 (C22, C23, C26–30, C32–38) lineages produced more winged females at 12°C than at 17°C (Table 5).

The production of males in the clonal lineage with a sexual phase (C46), which was also examined at 17 and 12°C for comparison purposes, was significantly reduced at 12°C ($F_{1, 17}$ = 5.5, P < 0.03). This was associated with lower reproduction compared to that observed at 17°C (Table 3).

In general, the G2 winged females produced mainly parthenogenetic females, and few males and mating females. The effect of temperature on the production of males ($F_{1, 218}$ = 16.0, P < 0.001) and mating females ($F_{1, 218}$ = 23.6, P < 0.001) by the G2 winged females was found to be significant. The "clonal lineage X temperature" interaction was significant only for the production of mating females ($F_{13, 218}$ = 2.5, P < 0.003). In 12 (C21, C23, C25, C26, C28, C29, C32–36, C40) out of 14 clonal lineages, which produced winged females in the G2 under SD at both temperatures, the mean number of males produced by these females was higher at 12°C than at 17°C. Similarly, in nine (C21, C23–25, C29, C32–34, C36) out of these 14 lineages the production of mating females was higher at 12°C than at 17°C. Furthermore, in four clonal lineages that did not produce winged females at 17°C, the winged females produced at 12°C gave birth to both males and mating females.

In both temperatures high intraclonal variation was observed in the production of males and mating females by the G1 wingless and G2 winged females, respectively. Sexual morphs were recorded, however, in fewer replicates (each replicate consisted of batches with 1–3 wingless or 1–5 winged females caged together) at 17°C than at 12°C (15% vs. 39%, X_1^2 = 8.4, P < 0.004, and 14 vs. 53%, X_1^2 = 40.0, P < 0.001 for G1 wingless and G2 winged females, respectively).

Temperature also modified the short day photoperiodic response in 13 out of 20 clonal lineages examined. Four lineages (intermediates) that produced few males and mating females and another two (androcyclic) that produced some males at 12°C showed a permanently parthenogenetic response at 17°C. In addition, seven intermediates at 12°C were characterised as androcyclic at 17°C.

Effect of photoperiod on the production of sexuals by clonal lineages with sexual phase and partial loss of sexuality

The first males in the genotype with a sexual phase appeared at the shortest scotophase (10 h dark per day)

TABLE 3. Mean number (± S.E.) of different progeny morphs produced by wingless parthenogenetic females of *Myzus persicae nicotianae* clonal lineages, with a sexual phase ([a]holocyclic) or partial loss of sexuality ([b]androcyclic, see Table 2 for definition of terms) in the second generation at 17°C (*12°C) and 10L : 14D. N = no. replicates, n = no. of wingless females examined over all replicates, NR = no records.

Clonal lineages	n/N	Males	Winged females	Wingless females	Total	Clonal lineages	n/N	Males	Winged females	Wingless females	Total
[a]**C44**	6/6	22.2±1.4	22.8±0.7	0.2±0.2	45.2±2.1	[b]C50	10/4	3.2±0.5	NR	NR	NR
[a]**C45**	11/11	22.8±2.7	22.9±2.2	0.5±0.5	46.3±3.6	[b]C47	9/3	2.8±0.7	NR	NR	NR
[a]**C46**	9/9	11.8±1.7	37.2±4.6	1.6±1.0	50.6±4.8	[b]C70	12/4	2.3±0.3	NR	NR	NR
[a]**C46***	10/10	6.8±1.4	20.3±3.9	3.5±1.2	30.6.±4.9	[b]C20	8/3	2.0±1.0	2.8±1.7	26.9±3.2	31.7±3.9
[b]C73	3.0	13.4±0.5	NR	NR	NR	[b]C71	9/3	1.7±0.6	NR	NR	NR
[b]C17	5/3	13.0±6.3	9.8±5.7	58.0±13.4	80.8±16.0	[b]C56	9/3	1.7±0.6	NR	NR	NR
[b]C18	5/3	10.3±2.9	5.5±3.3	39.7±14.0	55.5±17.5	[b]C49	9/3	1.3±0.5	NR	NR	NR
[b]C62	4.0	7.6±0.8	NR	NR	NR	[b]C15	6/3	1.3±1.3	7.7±3.8	68.1±5.0	77.1±5.3
[b]C48	9/3	7.1±1.0	NR	NR	NR	[b]C59	9/3	1.2±0.4	NR	NR	NR
[b]C51	12/4	6.8±0.6	NR	NR	NR	[b]C10	8/3	1.0±1.0	2.4±0.8	31.5±4.3	34.9±3.7
[b]C16	9/3	6.8±3.3	4.0±2.0	45.1±18.6	55.9±17.0	[b]C72	14/6	0.8±0.2	NR	NR	NR
[b]C66	10/4	6.6±0.4	NR	NR	NR	[b]C14	7/3	0.7±0.7	3.2±1.2	37.5±4.8	41.3±5.4
[b]C60	9/3	5.8±0.8	NR	NR	NR	[b]C19	8/3	0.5±0.5	2.7±1.2	36.4±5.8	39.6±4.4
[b]C13	9/3	5.2±1.1	6.1±2.8	17.4±6.3	28.7±4.9	[b]C61	12/4	0.4±0.2	NR	NR	NR
[b]C52	11/4	4.7±0.3	NR	NR	NR	[b]C55	8/3	0.2±0.1	NR	NR	NR
[b]C57	15/5	4.3±0.6	NR	NR	NR	[b]C58	10/4	0.1±0.1	NR	NR	NR
[b]C11	14/7	3.9±1.3	6.4±1.5	34.8±6.2	45.0±4.7	[b]C63	12/4	0.1±0.1	NR	NR	NR
[b]C12	10/3	3.3±5.2	5.2±2.3	33.2±17.4	41.7±5.9	[b]C65	12/4	0.1±0.1	NR	NR	NR

and the first winged females (gynoparae) that produce mating females at the scotophase of 10.5 h. Mostly parthenogenetic morphs (64–99%) were produced at scotophases of 10–11 h. However, the percentage decreased as the scotophase increased, while the opposite was observed for males and gynoparae. The highest percentage of males and gynoparae was recorded at scotophases of 13 and 14 h, respectively. In the lineage with partial loss of sexuality (intermediate) the first intermediate winged females (i.e. females that produce mainly parthenogenetic and some mating females) appeared at the scotophase of 11 h and the first males at a one hour shorter scotophase. Parthenogenetic morphs appeared in high percentages (83–100%) at all scotophases, but they were produced less frequently as scotophase increased until the regime of 13 h. Contrary to expectations, their percentage was higher in the regime of 14 h dark per day than in 1–2 h shorter regimes. The highest percentage of males and intermediate winged females appeared at the scotophase of 13 h.

DISCUSSION

The results of the present study showed that most (81%) of the clonal lineages with partial loss of sexuality (androcyclic producing mainly parthenogenetic females and few males, or intermediates producing few males and mating females) of the two taxa of *M. persicae* produced much fewer males (1–5 males per female) than genotypes with a sexual phase (holocyclic) (12–23 males per female). Furthermore, the mean production of mating females by winged females of intermediate genotypes (0.3–4.6) was lower than that reported for *M. persicae* lineages with a sexual phase in previous studies (5.8–16.8: Blackman, 1971, 1972, and 4.7–14.3: Margaritopoulos, 2001). This trend has also been observed in other host-alternating species (*R. padi*: Simon et al., 1991) as well as in smaller samples of *M. persicae* lineages from the UK (Blackman, 1971) and Germany (Waldhauer, 1957). It seems, therefore, that the low production of sexuals by genotypes with a partial loss of sexuality is a constant characteristic in *M. persicae* over a wide geographical area. By contrast, in the non host-alternating species *S. avenae* (Dedryver et al., 1998), higher male production was reported in androcyclic than in genotypes with a sexual phase. The low production of sexuals by genotypes with a partial loss of sexuality in host-alternating aphid species suggests a low contribution to the sexual phase. Considering also the type of inheritance of the life cycle categories (Blackman, 1972), it is expected that these genotypes are found at low frequencies on peach trees where sexual reproduction takes place. This has been demonstrated in *M. persicae* populations from peach trees in mainland Greece (Margaritopoulos et al., 2002). Nevertheless, the contribution of genotypes with a partial loss of sexuality to the sexual phase of a species is also influenced by environmental factors (e.g. winter temperature, relative abundance of primary and secondary hosts) that determine their relative abundance. In non host-alternating aphids the situation may be different since intermediate genotypes, for example, have been frequently recorded (Moran, 1993; Dedryver et al., 1998).

The results showed also that the production of sexuals by genotypes with a partial loss of sexuality is characterised by considerable between and within clonal lineage variation. Variation in male production, but not to such an

TABLE 4. Mean number (± S.E.) of different progeny morphs produced by wingless and winged parthenogenetic females of a clonal lineage (C94) of *Myzus persicae nicotianae* with partial loss of sexuality (intermediate, see Table 2 for definition of term) in successive generations at 12°C and 10L : 14D.

	G2	G3	G4	F2, 28
	Progeny of wingless females			
Winged female	12.3 ± 3.3a	0.3 ± 0.15b	2.4 ± 1.3b	17.9
Wingless females	26.4 ± 9.4a	55.4 ± 5.4b	36.3 ± 4.2b	19.0
Males	11.2 ± 2.9a	0.6 ± 0.64b	0.3 ± 0.2b	19.0
N[1]	10	11	10	
No. wingless females producing males	8	2	1	
	G3	G4	G5	F2, 27
	Progeny of winged females			
Winged females	5.7 ± 1.5a	1.3 ± 0.9a	6.1 ± 2.8a	2.6
Wingless females	22.9 ± 3.8a	19.9 ± 6.3a	44.0 ± 5.8b	5.2
Males	2.1 ± 0.8a	0.3 ± 0.3a	1.9 ± 0.8a	1.8
Mating females	0.2 ± 0.18a	4.6 ± 2.2b	0.2 ± 0.2a	5.2
N[2]	11	9	10	
No. winged females producing males	5	1	6	
No. winged females producing mating females	1	4	1	

N = number of wingless[1] and winged[2] females examined.

extent, has been also observed between *M. persicae* genotypes with a sexual phase from central and northern Greece (Margaritopoulos & Tsitsipis, 2002). The intraclonal variation is a characteristic property of genotypes with partial loss of sexuality not only in *M. persicae* (Blackman, 1971, 1972), but also in other species (e.g. *R. padi*, Simon et al., 1991). There is no valid evidence, however, of any genetic basis for the intraclonal variation observed. Recent molecular studies have clearly shown that aphid parthenogenesis is overwhelmingly apomictic. No recombination occurs during the development of parthenogenetic egg or it is so rare as to be of no consequence (Sunnucks et al., 1996; Wilson et al., 1999, 2003; Hales et al., 2002). Whether epistatic mechanisms, as this involved in the expression of the esterase gene E4 (Field & Blackman, 2003), are responsible for the intraclonal variation in sex determination needs to be investigated. One possible explanation is that proposed by Blackman (1972), who considered that such intraclonal variation was a consequence of an unstable intermediate condition of the mechanism involved in sex determination.

Regardless of the complexity of the short photoperiodic response of genotypes with a partial loss of sexuality, it seems that the mechanism of sex determination, although possibly unstable, is triggered by the same abiotic factors (e.g. temperature, length of photoperiodic regime and duration of exposure to short day) as that of genotypes with a sexual phase.

The photoperiodic mechanism operated rather similarly in two sympatric clonal lineages, one with a sexual phase (holocyclic) and another with partial loss of sexuality (intermediate). In both lineages males appeared at scotophases 0.5–1 h shorter than females. This is a general trend which has been observed in genotypes with a sexual phase of various aphid species, e.g. *Schizaphis graminum* (Rondani) (Mittler & Gorder, 1991) and *Acyrthosiphon pisum* (Harris) (MacKay, 1989), and also *M. persicae* (Mittler & Wilhoit, 1990). Also, in both lineages the proportion of males and that of winged females which produce mating females increased at a scotophase of 12 h and longer. These similarities could be explained by the fact that both lineages are sympatric and presumably adapted to the same environmental factors. Blackman (1974) stated that the photoperiodic responses of aphids must be in tune with extant environmental conditions. Contrary to that observed in the genotype with a sexual phase, the clonal lineage with a partial loss of sexuality produced fewer sexuals at the longest scotophase than in regimes 1–2 h shorter. This may be explained by the fact that the scotoperiod of 14 h dark per day occurs too late in the autumn, when synchronisation with peach can not be achieved. Thus, it could be advantageous for the intermediate lineages to increase the production of females which are able to overwinter parthenogenetically. The possible operating mechanism, however, is as yet unknown. The only opportunity for genotypes with a sexual phase to enhance the possibility of overwintering is to increase the production of mating females instead of males.

A similar reaction of the sex determination mechanism of the genotypes with sexual phase and those with partial loss of sexuality has been also observed in relation to another factor. We found that in one lineage with a partial loss of sexuality, the longer the length of prenatal exposure to short day the higher the mean number of males produced and the percentage of male producing females. This response has also been observed in *M. persicae* genotypes with a sexual phase (Searle & Mittler, 1981; Margaritopoulos & Tsitsipis, 2002) and this was attributed to the longer period of male producing conditions (i.e. decreased titre of juvenile hormone) that the females and their developing oogonia/embryos were exposed to.

Another point is the influence of temperature. The clonal lineages with a partial loss of sexuality produced

TABLE 5. Mean numbers (± S.E.) of different progeny morphs produced by wingless parthenogenetic females of *Myzus persicae nicotianae* clonal lineages, with partial loss of sexuality (AND = androcyclic, IN = intermediate, see Table 2 for definition of terms) or permanently parthenogenetic (AN), in the second generation at 17°C (A) and 12°C (B) and 10L : 14D.

Lineages			n/N	Males	Winged females	Wingless females	Total	Lineages			n/N	Males	Winged females	Wingless females	Total
C21	A	AND	9/4	0.1±0.1	22.5±8.6	34.1±9.0	56.8±5.9	C31	A	AN	7/7	0.0	0.0	53.6±6.2	53.6±6.2
	B	IN	11/6	1.8±1.3	11.3±3.2	52.3±8.9	65.3±9.5		B	AN	13/9	0.0	0.0	41.5±4.3	41.5±4.3
C22	A	AN	10/7	0.0	0.0	46.8±8.7	46.8±8.7	C32	A	AND	12/7	0.4±0.4	2.9±1.8	46.3±7.1	49.6±6.3
	B	IN	13/7	0.0	3.3±1.3	46.9±6.9	50.1±7.1		B	IN	13/9	1.8±0.8	11.7±2.7	40.6±4.0	54.1±5.1
C23	A	AND	11/7	0.4±0.3	3.7±1.8	45.1±5.4	49.2±4.1	C33	A	IN	9/5	0.0±0.0	1.4±0.8	36.2±8.0	37.6±7.6
	B	IN	12/6	3.9±3.8	6.8±2.6	43.2±10.9	53.8±7.4		B	IN	11/7	0.8±0.5	4.1±1.9	42.6±5.4	47.5±4.7
C24	A	AND	11/6	0.0	6.3±3.8	55.5±6.9	61.8±6.8	C34	A	AND	9/7	0.1±0.1	1.4±1.2	47.7±5.2	49.2±4.3
	B	IN	11/5	0.0	1.9±1.5	42.5±6.6	44.4±7.4		B	IN	12/8	2.3±2.1	4.9±2.5	40.9±4.0	48.1±3.3
C25	A	IN	11/7	0.4±0.3	18.4±11.9	39.9±4.6	58.7±9.3	C35	A	IN	9/6	0.3±0.3	1.3±0.8	43.3±5.3	44.9±4.6
	B	IN	9/7	2.1±1.7	14.3±5.0	39.9±6.8	56.4±6.7		B	IN	10/5	1.8±1.4	7.8±3.4	42.3±2.4	51.9±3.9
C26	A	AND	10/5	3.1±1.1	4.7±1.2	21.0±3.2	28.8±3.0	C36	A	AN	10/9	0.0	0.1±0.1	57.3±4.4	57.4±4.4
	B	AND	11/4	5.3±1.4	10.3±2.2	28.5±8.7	44.0±7.3		B	IN	11/8	1.4±1.2	6.6±3.3	41.0±7.1	49.1±3.9
C27	A	AN	12/7	0.0	0.0	54.4±7.2	54.4±7.2	C37	A	AN	9/6	0.0	0.0	50.5±5.1	50.5±5.1
	B	IN	14/10	2.3±2.1	3.1±1.4	36.1±7.1	41.4±5.7		B	IN	13/7	0.1±0.1	0.9±0.6	53.1±4.5	54.1±4.7
C28	A	IN	11/8	0.1±0.1	5.8±3.1	43.4±5.9	49.3±6.3	C38	A	IN	10/8	2.0±0.9	10.3±4.1	32.3±3.9	44.5±3.9
	B	IN	13/5	4.2±2.2	23.1±8.6	25.9±8.0	53.2±2.2		B	IN	13/8	2.2±0.6	11.8±1.3	18.0±4.4	32.0±4.8
C29	A	AND	10/4	0.0	2.6±1.4	53.5±10.7	56.1±9.9	C39	A	AN	8/5	0.0	0.0	44.0±7.4	44.0±7.4
	B	IN	10/7	1.9±1.5	7.2±2.8	33.1±8.8	42.1±5.9		B	AND	10/7	0.3±0.3	0.0	54.3±5.4	54.6±5.3
C30	A	AND	6/5	0.2±0.2	0.0	37.8±7.1	38.0±7.2	C40	A	AN	10/6	0.0	2.1±1.2	55.8±4.5	57.9±4.3
	B	IN	13/9	0.3±0.1	9.9±1.3	34.2±5.2	44.5±5.0		B	AND	10/6	1.2±0.8	1.2±0.9	43.3±2.0	45.6±2.3

N = no. replicates, n = no. wingless females examined over all replicates. Life category characterisation based on progeny of both G1 winged and G2 winged females (see also Table 6).

more males or mating females at 12°C than at 17°C. Also, the sexuals producing females appeared more frequently at 12°C. Temperature affects the production of males via the endocrine system of aphids, particularly juvenile hormone production, and often interacts with photoperiod. In other aphid species more males were produced at relatively higher temperatures by genotypes with a sexual phase, while the opposite was observed for mating females (*A. rubicola*: Brodel & Schaefers, 1980; *A. fabae*: Tsitsipis & Mittler, 1977a, b). Blackman (1972) also stated that male production in a *M. persicae* lineage with a sexual phase was greatly reduced at 10°C compared to 20°C and this was associated with low reproduction at 10°C. It was also found that the proportion of winged females of an intermediate lineage was higher at 10°C while the number of males decreased. The production of mating females was not affected. The androcyclic clones, however, tended to produce more males at 10°C. In our study the clonal lineage with a sexual phase showed a similar response with the conspecific lineage examined by Blackman (1972) or with the same genotypes of the aforementioned species. However, most of the genotypes with a partial loss of sexuality examined here produced more males or mating females at 12°C than at 17°C. The response of genotypes with a sexual phase to different temperatures seems constant within an aphid species and even between different species. The pattern is rather complicated, however, in genotypes with a partial loss of sexuality and differences exist between allopatric conspecific lineages. The most striking finding in the present study, however, is the change of life cycle category in most of the non-holocyclic genotypes examined when reared at 12°C. This is not in accordance with the results of Blackman (1971, 1972) who found a stability of the type of short photoperiodic response shown by *M. persicae* clonal lineages according to temperature. Nevertheless, Simon et al. (1991) observed that temperature modified the response of clonal lineages of *R. padi*, i.e. lineages that were permanently parthenogenetic or produced some males at 15°C, produced a few males or some males and mating females at 10°C, respectively. Therefore, this phenomenon may be widespread among aphid species, although intraspecific differences can also exist. Data from additional species are needed to validate this hypothesis.

These findings suggest that there is an uncertainty on the characterization of the life cycle category of a clonal lineage without a sexual phase or with partial loss of sexuality, given the high intraclonal variation and the effect of temperature. Moran (1993) stated that intermediate genotypes seem more frequent in non host-alternating aphid species. Dedryver et al. (2001) for example found that 43.3% of the *S. avenae* lineages examined were intermediates. By contrast, Blackman (1971) and Margaritopoulos et al. (2002) reported low percentages of such lineages (5.9 and 3.6% respectively)

TABLE 6. Mean numbers (± S.E.) of different progeny morphs produced by winged parthenogenetic females of *Myzus persicae nicotianae* clonal lineages in the third generation at 17 °C (A) and 12 °C (B) and 10L : 14D.

Lineages		n/N	Total	Winged females	Wingless females	Males	Mating females	Lineages		n/N	Total	Winged females	Wingless females	Males	Mating females
C21	A	20/7	19.9±1.9	0.4±0.3	19.5±1.8	0.0	0.0	C31	A	**					
	B	21/5	28.6±8.4	3.8±1.4	24.1±7.5	0.4±0.3	0.4±0.3		B	**					
C22	A	**						C32	A	28/10	30.1±5.1	0.7±0.6	29.4±4.9	0.0	0.0
	B	28/10	22.9±3.8	1.4±0.7	20.3±3.3	0.4±0.4	0.8±0.5		B	50/20	22.7±2.6	2.1±0.5	17.1±2.4	1.7±1.1	1.7±0.4
C23	A	23/6	38.5±6.1	3.2±2.0	33.5±5.1	1.8±1.3	0.0	C33	A	27/11	15.3±3.2	0.0±0.0	15.1±3.2	0.0	0.1±0.1
	B	18/5	21.0±5.0	2.5±1.3	14.6±4.7	1.7±0.7	2.2±1.7		B	22/10	18.1±2.7	3.1±1.3	13.1±2.7	0.1±0.1	1.7±0.9
C24	A	21/6	36.3±4.4	0.9±0.5	34.5±4.0	0.9±0.9	0.0	C34	A	21/9	33.9±6.2	0.5±0.4	33.4±5.9	0.0	0.0
	B	11/7	9.1±2.0	0.0±0.0	7.0±2.8	0.0	2.1±1.1		B	46/17	29.7±6.2	1.5±0.6	23.8±5.9	1.5±0.8	2.9±0.7
C25	A	298	23.6±5.5	1.4±0.7	21.3±4.9	0.6±0.3	0.3±0.2	C35	A	10/4	6.1±6.1	0.2±0.2	4.8±0.3	0.0	1.1±0.7
	B	18/9	36.7±5.7	6.2±2.4	25.5±4.7	2.3±0.7	2.7±1.9		B	23/8	20.2±6.0	3.8±2.1	14.9±4.0	0.9±0.4	0.6±0.3
C26	A	14/5	19.1±4.7	0.2±0.2	18.6±4.6	0.3±0.3	0.0	C36	A	17/8	26.5±4.1	0.1±0.1	26.4±4.2	0.0	0.0
	B	22/5	25.6±4.5	0.5±0.3	24.5±4.1	0.6±0.5	0.0		B	20/8	28.6±3.6	4.7±1.7	19.6±2.7	1.5±0.5	2.8±1.0
C27	A	**						C37	A	**					
	B	20/5	32.1±6.9	2.9±0.6	22.4±6.3	5.3±1.7	1.5±1.1		B	15/9	29.9±5.4	2.0±1.2	27.1±4.3	0.7±0.5	0.8±0.6
C28	A	27/11	19.2±3.6	0.2±0.2	18.5±3.6	0.0	0.5±0.3	C38	A	34/14	20.9±4.3	0.9±0.5	18.0±4.4	0.0	1.8±0.9
	B	22/5	26.2±5.0	2.1±0.9	22.6±4.2	1.0±0.5	0.5±0.5		B	27/15	14.9±2.1	0.4±0.3	13.6±2.2	0.0	0.8±0.5
C29	A	19/6	41.3±3.4	3.1±1.5	37.7±3.3	0.4±0.3	0.0	C39	A	**					
	B	23/6	24.8±3.1	1.6±0.9	18.1±2.0	2.2±0.8	3.0±1.1		B	**					
C30	A	**						C40	A	17/7	31.0±5.0	0.6±0.4	30.4±4.7	0.0	0.0
	B	34/12	13.8±2.4	1.2±0.4	9.6±0.2	0.2±0.2	2.8±1.1		B	29/14	25.7±3.3	0.2±0.1	25.1±3.2	0.4±0.2	0.0

*N = no. replicates, n = no. winged females examined. **No winged females were produced by G1 wingless females.

in the host-alternating *M. persicae*. The authors reared the aphids at 20 and 17°C, respectively and did not test all the winged females produced in the second generation under SD. In the present study the percentages of intermediates at 17 and 12°C were 20 and 75%, respectively. Simon et al. (1991) reported 0 and 4% at 15 and 10°C, respectively. Tatchell & Parker (1990) found also a very low percentage (0.4%) in *R. padi* but they stated that this may be an underestimate due to the rearing protocol of the winged females. Thus, the percentage of intermediate genotypes that occurred in nature may be underestimated at least for some host-alternating species due to high intraclonal variation or to rearing temperature.

Genotypes with a partial loss of sexuality seem to exhibit high phenotypic plasticity and the differing short type photoperiodic response depending on temperature (i.e. increasing production of sexuals as temperature drops) is presumably advantageous for their survival. This is probably related to the different temperatures that aphids experience in autumn. Late in this season, when aphids are exposed to lower temperatures, it is presumably advantageous to increase even slightly the production of males and mating females as the time limits for suitable peach trees shortens. Later, the best strategy is to minimize the production of sexuals since peach will not be available, and as temperature further decreases sexual morphs may not be able to survive. Thus, the reduction of sexuals and the increase of parthenogenetic morphs in successive generations under short day conditions which was observed in one intermediate clonal lineage examined here may be an adaptive trait. Further investigation, however, is needed (e.g. examination of additional lineages) for more general conclusions to be drawn. Finally, the sex determination mechanism in genotypes with partial loss of sexuality seems rather unstable since high intraclonal variation has been observed in many aphid species. The elucidation of this issue could probably give answers whether this variation is adaptive or not.

ACKNOWLEDGEMENTS. This study was supported by the Commission of the European Communities, Tobacco Information, and Research Fund, project 96/T/18 "Management of insect pests and viruses of tobacco using ecologically compatible technologies". It does not necessarily reflect the views of the Commission and in no way anticipates its future policy in this area.

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Received May 17, 2005; revised and accepted September 15, 2005