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Changes in genotypic composition of *Myzus persicae* (Hemiptera: Aphididae) on tobacco during the past two decades in Japan

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Abstract

Ninety-nine and 476 clones of *Myzus persicae* (Sulzer) were sampled on tobacco at Kyoto (Shimogamo) (1996–2000) and at 23 other localities (1998–1999) in Japan, respectively. The clones were classified into colour-esterase forms, distinguished by combinations of body colour and electrophoretically detectable esterases, to verify the changes in genotypic composition during the past two decades. Fifteen and 31 colour-esterase forms were found at Kyoto (Shimogamo) and at 23 other localities, respectively. Fourteen (representing *c*. 95% of the total clones sampled) and 24 (*c*. 44%) colour-esterase forms, respectively, were different from those found on tobacco during 1978–1985. The frequency of the green form and the very highly insecticide-resistant form increased. More than half of the colour-esterase forms found in the present survey were newly detected. The factors associated with these changes are discussed.

Introduction

Myzus persicae (Sulzer) (Hemiptera: Aphididae) is an aphid pest of great economic importance damaging various crops throughout the world (van Emden *et al*., 1969). A form of this species feeding on tobacco, *Nicotiana tabacum* L. (Solanaceae), has been reported to be different in morphology and allele frequency from that on other host plants (Blackman, 1987; Blackman & Spence, 1992; Margaritopoulos *et al*., 1998, 2000; Terradot *et al*., 1999). Takada & Tamura (1987) reported that the tobacco-feeding form in Japan was comprised of clones of particular genotypes, which were mostly dark red in body colour and not very highly resistant to organophosphorus (OP) insecticides. It has been suggested that the tobacco-feeding form shares some characters enabling it to colonize tobacco, where a sticky exudate is secreted on the plant surface and a toxic alkaloid, nicotine, exists in the leaf tissues (Takada & Tamura, 1987; Takada, 1988b).

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The Japanese clones of the tobacco-feeding form sampled during 1978–1985 were mostly intermediate or androcyclic, two of the four life-cycle categories of *M. persicae* defined by Blackman (1971), indicating that a large part of the populations on tobacco continued to reproduce parthenogenetically under short-day conditions (Takada & Tamura, 1987). The genotypic composition on tobacco at the same locality did not change drastically with the year (Takada, 1986; Takada & Tamura, 1987). These findings suggested that the particular genotypes on tobacco mostly overwintered parthenogenetically on alternative hosts, such as weeds (Takada & Tamura, 1987). When the aphid populations on tobacco were examined at Kyoto (Shimogamo) in 1996, they differed considerably in genotypic composition from those sampled at the same site during 1979–1981(Takada & Tamura, 1987). Clones of green colour and those very highly resistant to OP insecticides were found at a higher frequency. Such changes in genotypic composition on tobacco might have occurred in a wide range of localities in Japan.

The objective of this study was to re-examine the genotypic composition of *M. persicae* on tobacco in Japan and compare the results with those obtained previously by

Takada & Tamura (1987), to assess the changes during the past two decades.

Materials and methods

Sampling

Thirty, 43, 60, 60 and 60 plants of tobacco, *N. tabacum* 'MC-1', were cultivated in 1996, 1997, 1998, 1999 and 2000, respectively, at the Shimogamo Branch of the University Farms of Kyoto Prefectural University, Shimogamo, Kyoto, without application of any insecticide. In June of each year, a few adult wingless parthenogenetic females of *M. persicae* were sampled from every one to three plants along the row in the experimental plot.

In 1998–1999, aphids were also sampled from tobacco fields at 23 other localities in Japan (fig. 1, table 1), 14 of which were in common with those sampled by Takada & Tamura (1987). Aphid samples were collected from plants at least 5 m apart from each other in 1–9 fields at each locality.

Clonal culture

Ninety-nine and 467 clonal cultures were established from a single adult wingless parthenogenetic female of *M. persicae* from each tobacco plant at Kyoto (Shimogamo) and 23 other localities in Japan, respectively. All the clones were maintained on seedlings of broad bean, *Vicia faba* L. var. *minor* (Fabaceae), in culture vials (20 mm in diameter, 150 mm high) in long-day conditions, 15L:9D, at 15 or 18°C. Prior to electrophoresis, sub-cultures of the clones were reared for three or more successive generations on excised leaves of radish, *Raphanus sativus* L. 'Tokinashi' (Brassicaceae), in glass tube cages (35 mm in diameter, 150 mm high) in 15L:9D at 20°C. This technique was adapted because certain esterases of *M. persicae* were detected more clearly when aphids were reared on radish than on other plant species (Shigehara & Takada, unpublished data).

Electrophoresis

Esterases of the clones established were determined by vertical slab polyacrylamide gel electrophoresis, using 1-naphthyl acetate as substrate. The procedures were as described by Takada (1979), except for the higher concentration of total acrylamide (8%) in the gels used in this study. Certain clones with known esterase pattern were used as standards in every gel.

Classification of the clones into colour-esterase forms

In the Japanese populations of *M. persicae*, a total of 17 esterase bands (bands A-L, M', M, N, N', O in order of R_f value) have been detected by electrophoresis (Takada, 1979; Shigehara & Takada, unpublished data). Different electromorphs among clones have been found at six of the loci detected, three at esterase-1 locus (AB, BC, CD), two at esterase-2 locus (+, –), two at esterase-3 locus (+, –), eight at esterase-4 locus (= RAE, resistance associated esterase: –, ±, +1, +2, +3, +4, +5, +6, differing in intensity), four at esterase-5 locus (—, IK, IJKL, JL), and three at esterase-6 locus (M'MN, MN, MNN') (Takada, 1979, 1986; Shigehara & Takada, unpublished data). Shigehara & Takada (unpublished data) found that a total of 864 different esterase patterns are theoretically possible, if an interdependent assortment between esterase-3 and esterase-5 loci is taken into account. In addition, if the 864 different esterase patterns are multiplied by three variants of body colour (yellow, green, red) of this aphid, a total of 2592 colour-esterase forms are distinguishable. So far 76 (F-1 to F-22 and F-24 to F-77: Takada, 1986) and 26 other colour-esterase forms (Shigehara & Takada, unpublished

Table 1. Collection records of clones of *Myzus persicae* from tobacco in Japan.

Locality[1]	Abbreviation	Tobacco type (cultivar)	Date of collection	No. of fields	No. of clones
Morioka, Iwate	MRO	Various	1 Sep 1999	2	16
Oohasama, Iwate	OOH	Burley (Michinoku-1)	1 Sep 1999	9	55
Obanazawa, Yamagata	OBN	Burley (Michinoku-1)	25 Aug 1999	2	29
Higashine, Yamagata	HGS	Burley (Michinoku-1)	25 Aug 1999	1	6
Ooe, Yamagata	OOE	Burley (Michinoku-1)	24 Aug 1999	2	15
Asahi, Yamagata	ASH	Burley (Michinoku-1)	24 Aug 1999	1	3
Iide, Yamagata	IID	Burley (Michinoku-1)	24 Aug 1999	2	16
Funahiki, Fukushima	FKS	Local breed (Matsukawa)	10 Jul 1999	1	1
Mashiko, Tochigi	MSK	Flue-cured (Tsukuba-1)	14 Jul 1999	1	18
Oyama, Tochigi	OYM	Various	14 Jul 1999	2	33
Hotaka, Nagano	HTK	Burley (Michinoku-1)	12 Jul 1998	3	27
Hamamatsu, Shizuoka	SHM	Local breed (Shiroenshu)	1 Aug 1999	3	22
Toyohashi, Aichi	TYH	Flue-cured (Coker 319)	9 Jul 1999	3	33
Youkaichi, Shiga	YKI	Flue-cured (MC-1)	21 Jun 1999	1	16
Tango, Kyoto	TNG	Flue-cured (MC-1)	7 Aug 1998	2	20
Amino, Kyoto	AMN	Flue-cured (MC-1)	7 Aug 1998	1	8
Yasaka, Kyoto	YSK	Flue-cured (MC-1)	30 Jul 1998	1	4
Kurashiki, Okayama	KRS	Flue-cured (Virginia 115)	28 Jun 1999	2	23
Bisei, Okayama	BSI	Flue-cured (MC-1)	28 Jun 1999	1	6
Kasaoka, Okayama	KSO	Flue-cured (Virginia 115)	28 Jun 1999	2	24
Chiran, Kagoshima	KGS	Flue-cured (Coker 319)	14-15 Jun 1999	6	33
Itoman, Okinawa	ITM	Flue-cured (Okinawa-2)	5 Apr 1999	4	33
Ishigaki, Okinawa	ISG	Flue-cured (Okinawa-2)	5 Apr 1999	2	26

[1]Municipality, Prefecture.

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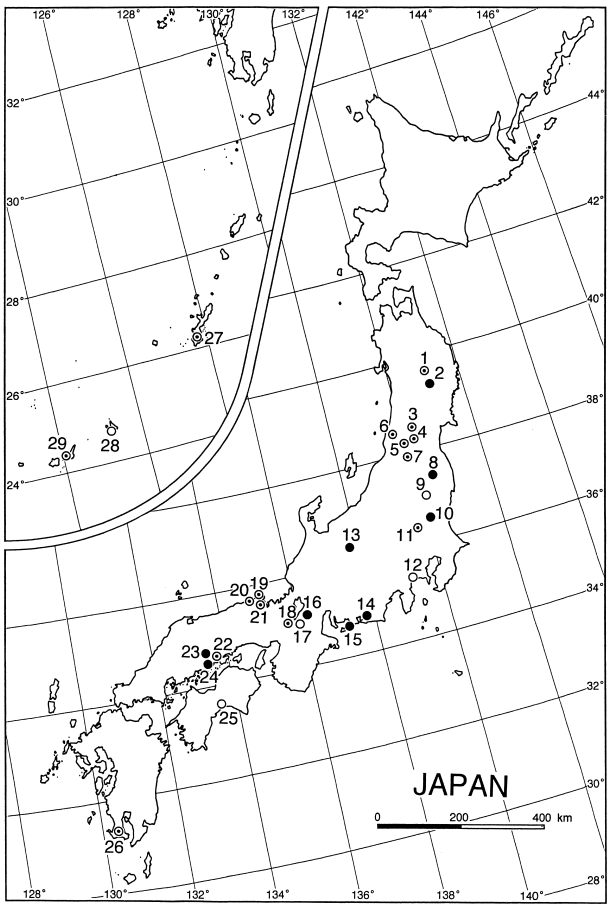

Fig. 1. Localities where the clones of *Myzus persicae* were collected from tobacco. ○, in the previous survey during 1978–1985 (Takada & Tamura, 1987); ●, in the present survey during 1996–2000; ⊙, in both surveys. 1, Morioka; 2, Oohasama; 3, Obanazawa; 4, Higashine; 5, Ooe; 6, Asahi; 7, Iide; 8, Funahiki; 9, Kuroiso; 10, Mashiko; 11, Oyama; 12, Hadano; 13, Hotaka; 14, Hamamatsu; 15, Toyohashi; 16, Youkaichi; 17, Moriyama; 18, Kyoto (Shimogamo); 19, Tango; 20, Amino; 21, Yasaka; 22, Kurashiki; 23, Bisei; 24, Kasaoka; 25, Nangoku; 26, Chiran; 27, Itoman; 28, Miyako; 29, Ishigaki.

data) have been found among *c*. 2000 clones of *M. persicae* collected in Japan.

In the present study, the colour-esterase forms of the clones established were determined according to the nomenclature of Takada (1986). Newly detected colour-esterase forms were assigned with a letter indicating the body colour (Y, yellow; G, green; R, red) and a triple number indicating the electromorphs at four polymorphic esterase loci: esterase-1 locus (1, AB; 2, BC; 3, CD), esterase-2/-3 loci (0, –/–; 1, +/–; 2, +/+; 3, –/+) and RAE locus (0, – and ±; 1, +1; 2, +2; 3, +3; 4, +4; 5, +5; 6, +6), respectively. The electromorphs at the two other polymorphic esterase loci, esterase-5 and esterase-6, were not included in this notation because most clones examined showed the same electromorphs, (IK) and (MN), respectively.

Results

Survey at Kyoto (Shimogamo)

Five green and ten red colour-esterase forms were found among 99 clones of *M. persicae* sampled on tobacco at Kyoto (Shimogamo) during 1996–2000 (table 2). Two green and five red colour-esterase forms were newly detected. The red form predominated over the green form in all years (representing 80.0–92.3%, mean 85.9% of the clones examined) (table 2, fig. 2b). Three red colour-esterase forms, R106, R116, R206, were found every year, and six other colour-esterase forms were found in two or three successive years (table 2).

There was one colour-esterase form with RAE activity (+1), three with RAE (+2), one with RAE (+3), five with RAE (+4) and five with RAE (+6), but no colour-esterase forms with RAE (–) or RAE (±) were found (fig. 3b). The five colour-esterase forms with RAE (+6) were all newly detected. All three red colour-esterase forms that were found frequently every year had RAE (+6), and the proportion of clones with RAE (+6) reached 53.5% of the total clones examined (fig. 3b).

Survey at 23 other localities in Japan

Eleven green and 20 red colour-esterase forms were found among 467 clones sampled on tobacco during 1998–1999 (table 3), with 13 colour-esterase forms in common with those found at Kyoto (Shimogamo) (table 2). Six green and ten red colour-esterase forms were newly detected. The red form (60.6–100% of the clones examined) predominated over the green form at all localities surveyed. The green form was found at ten localities which were

Table 2. Colour-esterase form of *Myzus persicae* clones collected from tobacco at Kyoto (Shimogamo).

Date of collection	No. of clones												
	Green form			Red form								Other colour-esterase forms	Total
	F-12	F-42	F-53	F-18	F-24	F-63	F-70	R131	R106	R116	R206		
4 Jun 1996	1			2		5			1	2	1		12
13 Jun 1997	3		1	1	6				3	6	4		24
23 Jun 1998	1		1		1			2	5	5	11		26
10 Jun 1999		1					3		2	5	2	G306: 1,G316: 1	15
13 Jun 2000	3	1			1		5	6	1	2	1	R313: 1, F-20:1	22

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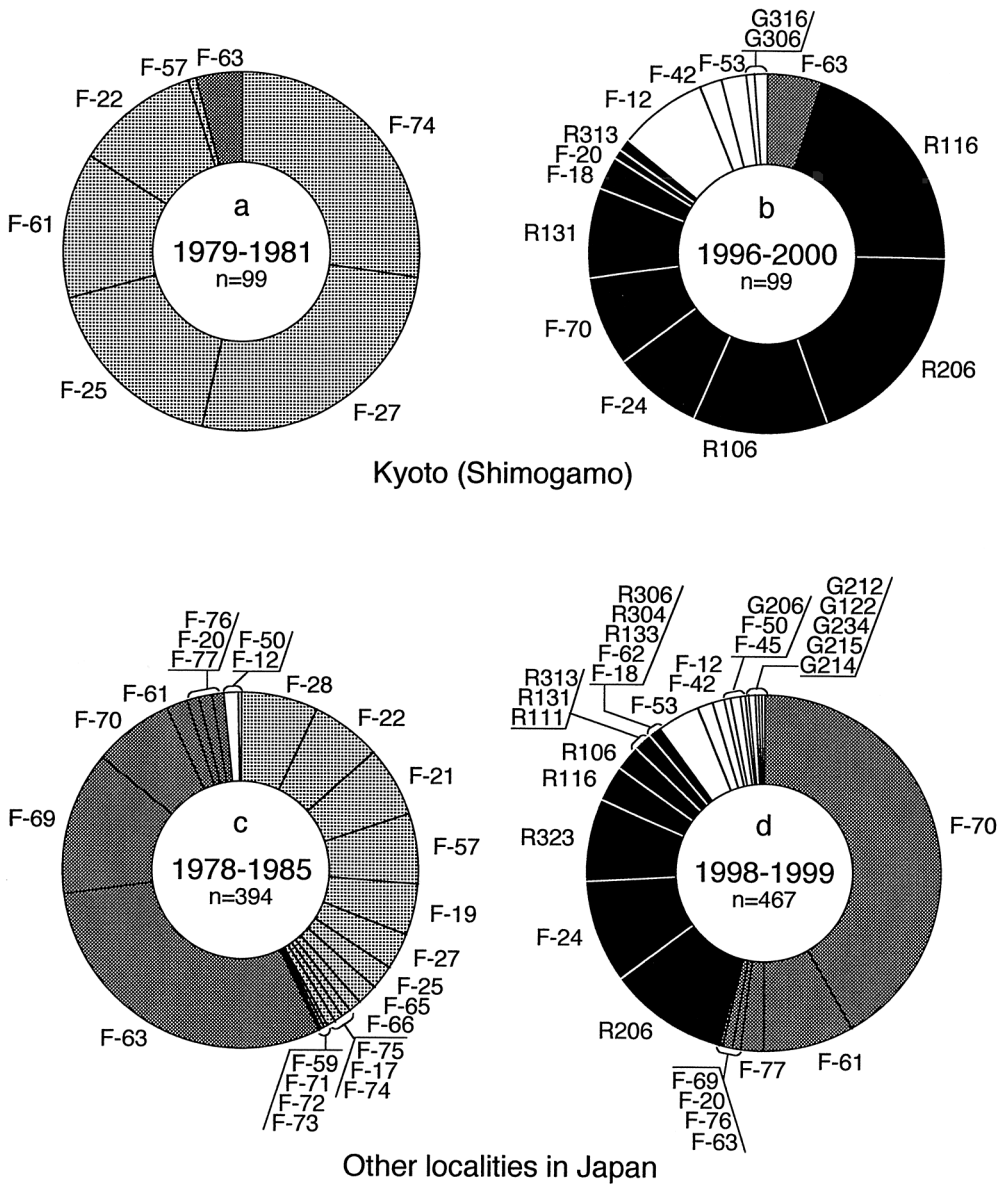

Fig. 2. Changes in proportion of colour-esterase forms in the samples of *Myzus persicae* collected from tobacco at Kyoto (Shimogamo) (a and b) and other localities in Japan (c and d). ▦, red form found only in the previous survey; ▩, red form found in both surveys; ■, red form found only in the present survey; □, green form. The data of 1978–1985 (a and c) are taken from Takada & Tamura (1987).

geographically distant, representing 10.1% of the total clones examined (table 3, fig. 2d). Eleven red colour-esterase forms were found at two or more localities, and five colour-esterase forms were found over a wide range of localities notably: F-24, from Youkaichi to Ishigaki; F-61, from Morioka to Youkaichi; F-70, from Morioka to Itoman; R206, from Morioka to Ishigaki; R323, from Chiran to Ishigaki (table 3). F-70 was predominant in north-eastern localities, and accounted for 41.5% of the total clones examined (fig. 2d).

There were two colour-esterase forms with RAE activity (+1), six with RAE (+2), three with RAE (+3), 14 with RAE (+4), one with RAE (+5) and five with RAE (+6), but no colour-esterase forms with RAE (–) or RAE (±) were found (fig. 3d). The five colour-esterase forms with RAE (+6) were all newly detected. F-70 had RAE (+4), and the proportion of clones with RAE (+5) and RAE (+6) was 17.1% (fig. 3d).

Discussion

Changes in genotypic composition

Clones belonging to the same colour-esterase form are not necessarily genetically homogeneous. However, most clones of the same colour-esterase form of *M. persicae* found on tobacco in the present survey seemed to be closely related, because they were found in successive years (table

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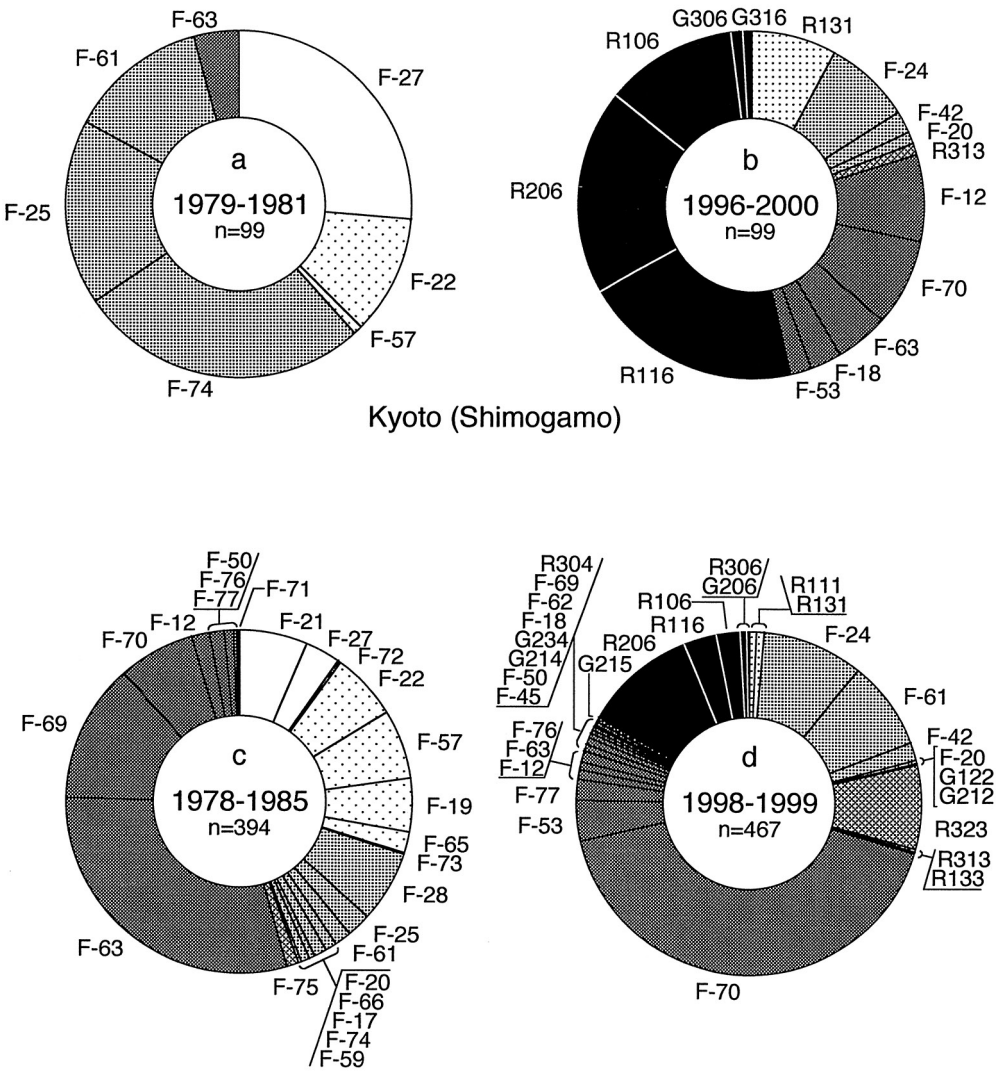

Fig. 3. Proportions of colour-esterase forms with different RAE activity levels in the samples of *Myzus persicae* collected from tobacco at Kyoto (Shimogamo) (a and b) and other localities in Japan (c and d). □, RAE activity (−); ⊡, (±); ⊡, (+1); ▦, (+2); ▩, (+3); ▩, (+4); ■, (+5); ■, (+6). The data of 1978–1985 (a and c) are taken from Takada & Tamura (1987).

2) and at geographically close localities (table 3). In addition, 15 clones belonging to 13 different colour-esterase forms found in the present survey, showed mostly intermediate or androcyclic responses to a short photoperiod (Shigehara & Takada, unpublished data), suggesting that they mostly overwintered parthenogenetically.

In a previous survey, Takada & Tamura (1987) found seven colour-esterase forms among 99 clones sampled on tobacco at Kyoto (Shimogamo) during 1979–1981, and 25 colour-esterase forms among 394 clones sampled on tobacco at 20 other localities in Japan during 1978–1985. The present survey showed that the genotypic composition of *M. persicae* on tobacco in Japan has changed substantially during the last 20 years. At Kyoto (Shimogamo), only one red colour-esterase form, F-63, was found in both the previous and present surveys, which comprised 4.0% and 5.0% of the clones sampled, respectively. The remaining 95.0% of the total clones sampled at Kyoto (Shimogamo) in the present survey consisted of two red (F-70, 20) and one green (F-12) colour-esterase form (17.2%), which were found on tobacco at localities other than Kyoto (Shimogamo) in the previous survey, two red (F-24, 18) and two green (F-42, 53) colour-esterase forms (15.2%), which were formerly found on plants other than tobacco (Takada, 1986), and seven newly detected colour-esterase forms (62.6%). At other localities in Japan, seven red (F-70, 61, 77, 63, 76, 20, 69) and two green (F-12, 50)

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colour-esterase forms were found in both the previous and present surveys, which comprised 57.1% and 55.9% of the total clones sampled, respectively. The remaining 44.1% of the total clones sampled at localities other than Kyoto (Shimogamo) in the present survey consisted of three red (F-24, 18, 62) and three green (F-53, 42, 45) colour-esterase forms (15.8%), which were formerly found on plants other than tobacco (Takada, 1986), and 16 newly detected colour-esterase forms (28.3%).

Features of the changes

Change in proportion of colour form

Colour-esterase forms with green colour increased in number from zero to five (14.1% of the total clones) at Kyoto (Shimogamo) (fig. 2a,b), and from two to 11 (1.8% and 10.1% of the total clones, respectively) at the other localities in Japan (fig. 2c, d).

In eastern Asia, including Japan, the tobacco-feeding form of *M. persicae* was mostly red in body colour, although all three colour forms occurred on other host plants (Takada, 1988a). Recently, however, the green form was reported to be found commonly on tobacco in Korea (Chae *et al.*, 1998) and China (Yang *et al.*, 1998) as well. Outside eastern Asia, on the other hand, the tobacco-feeding form of *M. persicae* had been entirely green in body colour until the mid-1980s (Blackman, 1987; Takada, 1988a). The red form has rapidly increased and predominated on tobacco in southeastern USA since 1985 (Harlow *et al.*, 1991) and recently in parts of Greece, Spain, France and Germany (Margaritopoulos *et al.*, 1998, 2000, 2002; Kephalogianni *et al.*, 2002). Thus, the proportion of the colour forms in eastern Asia has been changing differently from that in other parts of the world.

The red form in southeastern USA had selective advantages due to a higher reproductive potential (Lampert & Dennis, 1987), and this could partly explain the rapid increase in number relative to the green form already present (Blackman, 1987). The green form in the present results comprised a minority at any locality, and did not increase in frequency at Kyoto (Shimogamo) over the five year survey period, unlike the red form in southeastern USA which showed a considerable increase. The cause of the increase in frequency of the green form during the past two decades in Japan remains to be determined.

Development of organophosphorus-insecticide resistance

Colour-esterase forms with RAE activity (+5) and RAE (+6) increased in number from zero to five (53.5% of the total clones) at Kyoto (Shimogamo), and from one to six (0.25% and 17.1% of the total clones, respectively) at other localities in Japan. On the other hand, colour-esterase forms with RAE (–) and RAE (±), which were formerly three in number at Kyoto (Shimogamo) and eight at other localities in Japan (38.4% and 29.9% of the total clones, respectively), disappeared totally.

In southeastern USA, the red form that has predominated on tobacco since 1985 showed a higher esterase activity and resistance to OP insecticides (Harlow *et al.*, 1991). In the UK,

Table 3. Colour-esterase form of *Myzus persicae* clones collected from tobacco at 23 localities in Japan.

Locality[1]	No. of clones																	
	Green form					Red form											Other colour-esterase forms	Total
	F-12	F-42	F-45	F-50	F-53	F-24	F-61	F-63	F-70	F-76	F-77	R131	R106	R116	R206	R323		
MRO	1						3		3						8		G212: 1	16
OOH							8		40	2			1		4			55
OBN	1						13	1	13						1			29
HGS							1		4						1			6
OOE							5		10									15
ASH									3									3
IID							6		8	2								16
FKS									1									1
MSK						1			17									18
OYM							3	3	11				8	1	2		G215: 2, F-20: 1, G234: 1, G122: 1	33
HTK				1					22				1		2		F-18: 1	27
SHM									18			2			2			22
TYH	1	2							22		2	1		2	2		G234: 1	33
YKI	1					1	1							8	3		F-62: 1, R306: 1	16
TNG						7			8		2				3			20
AMN						1			1		3						R111: 3	8
YSK						1			3									4
KRS		5			1	1			4					4	7		R133: 1	23
BSI						2			3						1			6
KSO						8			2						8	6		24
KGS			1		12	5					2					11	R313:2	33
ITM	1				5	14			1						3	3	G214:2,G206:3, R304: 1	33
ISG			2	2		3									2	16	F-69: 1	26

[1]Abbreviations as listed in table 1.

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the frequency of a very highly OP-resistant form, R_3, which corresponds to forms with RAE (+5) and RAE (+6) in this study, occured in less than 3% in samples collected in the field up to 1995 (Foster *et al*., 1998). This was attributed to the fact that aphids with higher resistance to OP insecticides suffered greater winter mortality (Foster *et al*., 1996) and showed a lower tendency to move from senescing leaves (Foster *et al*., 1997), mainly due to the pleiotropic effects of the knockdown resistant (*kdr*) mechanism on nerve function and aphid response to external stimuli (Foster *et al*., 1999), which was in strong linkage disequilibrium with the resistance to OP insecticides in UK populations (Field *et al*., 1997). Foster *et al*. (1998), however, reported that the frequency of R_3 exceeded 50% in most of the 44 samples collected in 1996, taking account of atypical events in that year, including climatic conditions, which promoted an increased use of insecticides, especially pyrethroids, to which the *kdr* mechanism confers target-site resistance (Field *et al*., 1997).

It was also reported on Japanese populations that although colour-esterase forms with RAE (+5) and RAE (+6) were detected in aphids from many localities, their proportions were less than 15% in any sample (Takada, 1986). If these very highly resistant forms in Japan also have a reduced response to external stimuli and show lower winter viability, the increase in frequency of these forms revealed in this study may have been associated with recent conditions of warming climate, which could reduce the adverse effects on their parthenogenetic overwintering, because all of the clones of these forms examined were non-holocyclic (Shigehara & Takada, unpublished data).

On the other hand, two of the five predominant colour-esterase forms found at many localities in the present survey (table 3), F-24 and F-61, had a moderate RAE activity (+2). This indicates that some factors other than resistance to OP insecticides also contributed to the fitness.

It might be possible that colour-esterase forms with RAE (+5) and RAE (+6) found in the present survey were 'revertant' (Sawicki *et al*., 1980). If so, these forms may have had reduced expression of the RAE genes in the previous survey, but produced offspring with higher RAE activity under more recent insecticidal selective pressure. In this case, a single clone might be classified into two different colour-esterase forms according to the RAE activity level. The authors have reared at least one clone each of 20 colour-esterase forms found in the present survey, including those with RAE (+5) and RAE (+6), for about three years without any insecticidal pressure, and none has yet changed in RAE activity. It seems that revertant aphids are still uncommon in Japan.

Origin of newly detected colour-esterase forms

Eighteen (ten red and eight green) colour-esterase forms were newly detected on tobacco in the present survey (tables 2 and 3).

On the assumption that the tobacco-feeding form of *M. persicae* outside eastern and central Asia was continuously parthenogenetic, Blackman (1987) suggested that the red form in southeastern USA might be a fresh introduction or a mutant of the green form already present on tobacco there. The latter view was based on the morphological similarity to the green form and on the possession of a chromosomal translocation associated with resistance to OP insecticides, which some of the green form possessed. Recently, however, significant proportions of clones of *M. persicae* on tobacco in Greece have been reported to be involved in sexual reproduction, in association with the abundance of the primary host, peach, *Prunus persica* (L.) Batsch (Rosaceae) (Margaritopoulos *et al*., 2002).

In Japan, peach trees were common throughout the range of localities surveyed in this study. The clones of the tobacco-feeding form sampled during 1978–1985 and in the present survey were mostly intermediate or androcyclic (Takada & Tamura, 1987; Shigehara & Takada, unpublished data). Clones of these life-cycle forms produce a few sexuals, which are capable of producing hybrid clones (Blackman, 1971). Thus the new colour-esterase forms detected in the present survey were presumably generated by recombination and survived subsequent selections in the parthenogenetic phase.

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