Esterase Activities and Developmental Success of the Citrus Red Mite, *Panonychus citri* (McGREGOR) (Acarina: Tetranychidae), on Several Plants¹

Masahiro OSAKABE

Akitsu Branch, Fruit Tree Research Station, Akitsu, Hiroshima 729-27, Japan

(Received May 9, 1986)

Developmental success from larva to adult and esterase activities of the citrus red mite, *Panonychus citri* (McGREGOR), were investigated in this study. The non-diapausing strain developed well on several citrus varieties, but most of individuals of the diapausing strain did not reach maturity on those plants, except trifoliate orange (GRP1). Japanese pear, peach and trifoliate orange (GRP2) were common host plants for both strains. Mites reared on GRP1 plants had higher esterase activities of E_3 and E_4 electrophoretically separated bands and/or larger activity ratios (E_3/E_4 and E_3/E_5) than those on GRP2 plants. The differences were shown more clearly by the principal component analysis and discriminant function analysis.

INTRODUCTION

In Japan the citrus red mite, *Panonychus citri* (McGREGOR), has both non-diapausing and diapausing strains. The non-diapausing strain has a wider host range than the diapausing strain (UCHIDA, 1982). The non-diapausing strain develops well on the leaves of many citrus varieties although the diapausing strain does not develop successfully on those leaves (SHINKAJI, 1961; MORIMOTO and TAKAFUJI, 1983). When reared on sour orange (*Citrus aurantium* L.) the non-diapausing strain shows higher esterase activity of the E_3 band (separated by agar gel thin layer electrophoresis) than when reared on Japanese pear (*Pyrus serotina* REHDER var. *culta* REHDER) (OSAKABE, 1984).

In this study the developmental success from larva to adult of the 2 strains and the non-specific esterase activities of the non-diapausing strain were examined. Relationships between developmental success and esterase activities were analyzed by several statistical methods.

MATERIALS AND METHODS

This study was carried out from 1983 to 1984.

Mite. Non-diapausing and diapausing strains of the citrus red mite were used. Populations of non-diapausing strain were the Hiratsuka (HSnd) and the Akitsu (AWnd) populations. The HSnd population was collected on citrus grove at Hiratsuka, Kanagawa Prefecture, in 1971 and was reared on seedlings of sour orange in a green

¹ Contribution No. Fruit Tree Res. Stn.: E-100.

house. AWnd mites were collected from satsuma mandarin (*Citrus unshiu* MARC.), sour orange, navel orange (*C. sinensis* OSBECK var. *brasiliensis* TANAKA), Hassaku (*C. hassaku* hort. ex TANAKA), Yuzu (*C. junos* SIEB. ex TANAKA), trifoliolate orange (*Poncirus trifoliata* RAF.), 'Troyer' citrange (trifoliolate orange $\times$ 'Washington' navel), Japanese pear, *Osmanthus fragrans* LOUR. var. *aurantiacus* MAKINO and *O. Fortunei* CARR. at Akitsu in Hiroshima Prefecture from July to October in 1983 and 1984. And AWnd mites were used for electrophoresis immediately. The diapausing strain (TWd) was collected from Japanese pear at Daiei in Tottori Prefecture in 1982 and reared on leaf discs of Japanese pear in a laboratory kept at about 25°C.

Developmental success from larva to adult. All experiments were carried out in the laboratory at about 25°C. Adult females of the HSnd and TWd strains were respectively inoculated on leaf discs (1 $\times$ 1 cm; 3 ♀♀/disc) of sour orange and Japanese pear floating on 0.5% agar gels. On the 2nd day after inoculation the adult females were removed from the discs. Leaf pieces on which eggs had been laid were removed from the gels and dried for 3 days. The dried pieces were placed on test plant leaf discs (2 $\times$ 3 cm) floating on agar gel. Developmental success of HSnd and TWd mites were checked on each test plant leaf 14 days after inoculation with adult females. The plants were 6 kinds of citrus: satsuma mandarin, sour orange, Hassaku, Yuzu, 'Troyer' citrange and trifoliolate orange; and 8 other plants: Japanese pear, peach (*Prunus persica* SIEB. et ZUCC. var. *vulgaris* MAXIM.), apple (*Malus pumila* MILL. var. *domestica* SCHNEIDER), grapevine (*Vitis vinifera* L.), Japanese chestnut (*Castanea crenata* SIEB. et ZUCC.), loquat (*Eriobotrya japonica* LINDLEY), *O. fragrans* and *O. Fortunei*.

Esterase activity. The procedure of thin layer electrophoresis was reported previously (OSAKABE, 1984). Each sample for electrophoresis was prepared from three adult females. The mites were homogenized with 10 μ l of phosphate buffer (ionic strength 0.02 M; pH 8.04) by glass rod. The homogenized sample was absorbed on cellulose acetate membrane (2 $\times$ 15 mm; 2–3 μ l/strip). The supporting media was agar gel (ionic strength 0.02 M; pH 8.04; 20 ml/20 $\times$ 15 cm) containing 2% polyvinylpyrrolidone (K-90). The electrophoresis was performed at constant current of 2 mA/cm width for 60–70 min. After electrical charging, the agar gel plate was sprayed with 1% acetone solution of β -naphthyl acetate. The plate was incubated for 60 min at 37°C and then sprayed with 0.5% solution of Fast Blue B salt to detect the non-specific esterase activities.

Detected isozyme bands (5 $\times$ 15 mm) of esterase were cut off separately from the agar gel plate, and each agar piece was melted in 1 ml phosphate buffer at 85–90°C. Optical densities (O.D.) of each phosphate buffer were measured at 550 nm.

Statistical analysis. Principal component and discriminant function analyses were carried out by computer. The program is "Conversational Multivariate Analysis Packaged Program" of the Computing Centre for Research in Agriculture, Forestry and Fishery.²

RESULTS

Developmental success from larva to adult of non-diapausing and diapausing strains on various plants

Table 1 shows the developmental success of the non-diapausing (HSnd) and the diapausing (TWd) strains on the various host plants. More than 80% of HSnd mites

² It is commented on "OKUNO et al. (1976) *Zoku Tahenryoukaisekihō*. Nikkagiren Publ. Co., Tokyo, 299 pp. (in Japanese)."

Table 1. Developmental success of the non-diapausing (HSnd) and the diapausing (TWd) strains on various plants

Test plant	HSnd		TWd	
	No. of larva	Percent attaining maturity	No. of larva	Percent attaining maturity
Citrus trees				
Satsuma mandarin	41	95.1	409	2.0
Sour orange	34	82.4	215	6.0
Hassaku	—	—	272	1.8
Yuzu	—	—	318	5.3
'Troyer' citrange	—	—	115	0
Trifoliate orange	93	97.9	285	95.4
Japanese pear	56	92.9	227	79.7
Peach	57	91.2	137	74.5
Apple	111	36.0	347	15.3
Grapevine	47	19.1	202	0
Japanese chestnut	53	5.7	276	0
Loquat	53	0	202	0
<i>Osmanthus fragrans</i>	50	2.0	328	0
<i>O. Fortunei</i>	30	0	152	0

Table 2. Distinction of the test plants according to the developmental success of the non-diapausing and the diapausing strains

GRP1:	only the non-diapausing strain developed on ——citrus trees (excluding trifoliate orange)
GRP2:	both strains developed on ——trifoliate orange, Japanese pear and peach
GRP3:	neither strain developed on ——apple, grapevine, Japanese chestnut, loquat, <i>O. fragrans</i> and <i>O. Fortunei</i>

reached maturity on citrus trees, Japanese pear, and peach, only 36.0% and 19.1% of the mites were able to develop on apple and grapevine, respectively. Percentage of the developmental success were less than 10% on Japanese chestnut, loquat, *O. fragrans* and *O. Fortunei*. Over 70% of TWd mites completed development on trifoliate orange, Japanese pear and peach. Conversely, only 15.3% of TWd mites reached maturity on apple, 6.0% on sour orange, 5.3% on Yuzu and 2.0% or less on the other plants.

The test plants were categorized in 3 groups (GRP1, GRP2 and GRP3) according to the developmental success of the non-diapausing and diapausing strains (Table 2).

Esterase activities of non-diapausing strain on various plants

Isozyme patterns of HSnd mites reared on satsuma mandarin, sour orange, Japanese pear and peach, AWnd mites collected from 10 kinds of host plants and TWd mites reared on Japanese pear were detected by electrophoresis. The patterns are shown in Fig. 1. Both populations of the non-diapausing strain had E_3 , E_4 and E_5 bands. In the populations, AWnd showed 2 patterns of esterase zymograms. Namely, mites

Fig. 1. Esterase zymograms of the citrus red mite. I: AWnd mites collected on *Osmanthus fragrans* and *O. Fortunei*, II: AWnd mites on 6 kinds of citrus trees, Japanese pear and peach, III: HSnd mites, IV: TWd mites.

collected on *O. fragrans* and *O. Fortunei* had the E_1 band, but those from 6 kinds of citrus, Japanese pear and peach had the E_2 band. Mites collected from citrus rarely had the E_1 band. On the other hand, the diapausing strain (TWnd) had E_4 , E_5 and E_6 bands but never E_1 – E_3 .

Table 3 shows the esterase activities of electrophoretically separated bands of HSnd mites developed on several plants. Table 4 shows the activity ratios on each plant. The mites on GRP1 plants had clearly higher activities of E_3 and E_4 bands than those on GRP2. For the E_5 band, only the mites grown on satsuma mandarin had significantly higher activity than those grown on GRP2 plants. The activity ratios of E_3/E_4 and E_3/E_5 of the mites on GRP1 plants were greater than those of the mites on GRP2 plants. Differences of the E_4/E_5 ratio between the mites on GRP1 plants and those on GRP2 plants was less clear.

Esterase activities and its ratios of AWnd mites collected on 8 kinds of host plants are shown in Tables 5 and 6, respectively. Mites on GRP1 (except navel orange) exhibited higher activities than on GRP2 in each separated band. The activities of the mites living on satsuma mandarin and Yuzu were significantly different from those of the mites on GRP2. The activity ratios of E_3/E_4 and E_3/E_5 of the mites on GRP1 plants were also larger than those of the mites on GRP2 plants. The mites on satsuma mandarin and sour orange had significantly larger ratios of E_4/E_5 than the mites on GRP2. However, the ratios of the mites on the other 4 plants of GRP1 were not significantly different from those on GRP2.

Table 3. Esterase activities (O. D.) of the non-diapausing strain (HSnd) developed on test plants

Host plant	No. of sample	O. D. ($\times 10^{-3}$) $\pm$ SE ^a		
		E_3	E_4	E_5
GRP1				
Satsuma mandarin	4	318 $\pm$ 26 a	334 $\pm$ 11 a	224 $\pm$ 8 a
Sour orange	4	305 $\pm$ 32 a	269 $\pm$ 15 b	159 $\pm$ 13 b
GRP2				
Japanese pear	4	110 $\pm$ 13 b	198 $\pm$ 16 c	154 $\pm$ 17 b
Peach	4	91 $\pm$ 19 c	153 $\pm$ 27 c	155 $\pm$ 18 b

^a Figures in the same column followed by the same letter are not significantly different at the 5% level by DUNCAN's multiple range test.

Table 4. Activity ratios of esterase bands of the non-diapausing strain (HSnd) developed on test plants

Host plant	Ratio $\pm$ SE ^a		
	E_3/E_4	E_3/E_5	E_4/E_5
GRP1			
Satsuma mandarin	0.95 $\pm$ 0.05 a	1.41 $\pm$ 0.07 a	1.49 $\pm$ 0.05 ab
Sour orange	1.13 $\pm$ 0.08 b	2.00 $\pm$ 0.38 a	1.74 $\pm$ 0.22 a
GRP2			
Japanese pear	0.55 $\pm$ 0.03 c	0.71 $\pm$ 0.04 b	1.31 $\pm$ 0.12 ab
Peach	0.57 $\pm$ 0.04 c	0.60 $\pm$ 0.13 b	1.02 $\pm$ 0.17 b

^a See Table 3.

Table 5. Esterase activities (O. D.) of the non-diapausing strain (AWnd) collected on various plants

Host plant	No. of sample	O.D. ($\times 10^{-3}$) $\pm$ SE ^a			
		E_2	E_3	E_4	E_5
GRP1					
Satsuma mandarin	8	231 $\pm$ 22 a	551 $\pm$ 56 a	584 $\pm$ 41 a	319 $\pm$ 7 a
Yuzu	8	267 $\pm$ 30 a	316 $\pm$ 51 a	406 $\pm$ 47 a	308 $\pm$ 32 a
Hassaku	8	193 $\pm$ 38 ab	213 $\pm$ 42 b	302 $\pm$ 58 b	224 $\pm$ 46 b
Sour orange	8	123 $\pm$ 19 bcd	227 $\pm$ 34 b	292 $\pm$ 38 b	154 $\pm$ 24 bcd
'Troyer' citrange	4	200 $\pm$ 37 abc	173 $\pm$ 36 bc	251 $\pm$ 50 bcd	178 $\pm$ 37 bcd
Navel orange	8	99 $\pm$ 19 d	118 $\pm$ 11 c	158 $\pm$ 15 d	102 $\pm$ 12 d
GRP2					
Trifoliolate orange	12	105 $\pm$ 18 d	126 $\pm$ 14 c	191 $\pm$ 24 bc	173 $\pm$ 13 bc
Japanese pear	8	115 $\pm$ 19 cd	58 $\pm$ 12 c	170 $\pm$ 6 cd	126 $\pm$ 10 cd

^a See Table 3.

Table 6. Activity ratios of esterase bands of the non-diapausing strain (AWnd) collected on various plants

Host plant	Ratio $\pm$ SE ^a		
	E_3/E_4	E_3/E_5	E_4/E_5
GRP1			
Satsuma mandarin	0.94 $\pm$ 0.05 a	1.74 $\pm$ 0.08 a	1.86 $\pm$ 0.05 a
Sour orange	0.78 $\pm$ 0.05 ab	1.55 $\pm$ 0.16 a	1.98 $\pm$ 0.12 a
Navel orange	0.75 $\pm$ 0.04 bc	1.24 $\pm$ 0.14 b	1.65 $\pm$ 0.19 ab
Hassaku	0.70 $\pm$ 0.04 bc	0.98 $\pm$ 0.05 b	1.40 $\pm$ 0.08 b
Yuzu	0.76 $\pm$ 0.05 abc	0.99 $\pm$ 0.06 b	1.31 $\pm$ 0.04 b
'Troyer' citrange	0.68 $\pm$ 0.01 bcd	0.97 $\pm$ 0.03 bc	1.42 $\pm$ 0.04 b
GRP2			
Trifoliolate orange	0.48 $\pm$ 0.01 d	0.71 $\pm$ 0.04 cd	1.47 $\pm$ 0.06 b
Japanese pear	0.35 $\pm$ 0.07 e	0.46 $\pm$ 0.09 d	1.34 $\pm$ 0.09 b

^a See Table 3.

Principal component analysis of esterase activities

The relationship between esterase activities of the mites and the host plants was examined by principal component analysis. E_2 band is not common band among the populations of non-diapausing strain (OSAKABE, 1984). The activity ratio of E_4/E_5 did not show clearly the difference between the mites on GRP1 and GRP2. For the principal component analysis, activities of E_3 – E_5 bands and the activity ratios of E_3/E_4 and E_3/E_5 were used as variables. The analysis was made on a correlation matrix.

Cumulative contribution rate of the 1st (z_1) plus 2nd (z_2) principal components to original data was 96.4% in HSnd mites and 95.5% in AWnd mites. About 96% of original data of each population, therefore, could be explained by z_1 and z_2 . Also, all contribution rate of z_1 plus z_2 to each variable was above 90%. Thus, z_1 and z_2 were used for the next analysis.

Figure 2 shows the factor loadings of HSnd and AWnd mites. Figure 3 shows dispersions of the component scores. According to factor loading, the z_1 axis of HSnd mites indicated activities of E_3 and E_4 , and the ratios of E_3/E_4 and E_3/E_5 . The dispersion showed that z_1 values of the mites on GRP1 plants were larger than the values on GRP2 plants. The individuals on satsuma mandarin and on sour orange were also clearly separated.

In the dispersion of AWnd mites, the coordinate axis was rotated on the basis of factor loadings, then z_1' and z_2' axes were made new coordinate axes. The z_1' axis indicated activities of each esterase band. When each activity ratio was large, z_2' score took the small value. In this case, the principal components of the mites on GRP1 spread on the plane of coordinates. Thus, the difference between GRP1 and GRP2 was not clear in the comparison of dispersions of HSnd mites. But, z_1' values of mites on GRP2 were small and z_2' values were large, while many of the mites on GRP1 plants

Fig. 2. Factor loadings of 1st (z_1) and 2nd (z_2) components of HSnd and AWnd mites in principal component analysis. i: E_3 , ii: E_4 , iii: E_5 , iv: E_3/E_4 , v: E_3/E_5 . Arrows in the figure of AWnd show the direction in which z_1 – z_2 axes were rotated, and z_1' – z_2' are new axes.

Fig. 3. Dispersion of 1st (z_1) and 2nd (z_2) component scores of HSnd and AWnd mites. z_1' – z_2' axes in the figure of AWnd are new axes rotated on the basis of factor loadings (show Fig. 2). GRP1, $\blacktriangle$: mites on satsuma mandarin; $\blacktriangledown$: sour orange; $\bullet$: Yuzu, Hassaku, navel orange and 'Troyer' citrange. GRP2, $\circ$: Japanese pear; $\triangle$: peach; $\triangledown$: trifoliate orange.

had positive z_1' values and/or negative z_2' values. There were wide differences, especially between the mites on satsuma mandarin and those on GRP2 plants.

Discriminant function analysis

For the calculations of discriminant function the same variables as for the principal component analysis were used. Statistical significance between the means of the variables of mites on GRP1 and GRP2 at the 1% level by HOTELLING's T^2 test was seen in both HSnd and AWnd populations. Thus linear discriminant functions of each population were set up between GRP1 and GRP2. Host plants of the mites were judged as either GRP1 or GRP2 by the functions. Formulas of the functions were:

$$\text{HSnd: } z = -40.822 + 130.068x_1 + 80.320x_2 - 154.036x_3 + 63.596x_4 - 24.873x_5$$

$$\text{AWnd: } z = -15.838 - 21.538x_1 - 11.037x_2 + 42.975x_3 + 14.800x_4 + 6.436x_5$$

(x_1 – x_3 : each activity of E_3 – E_5 bands, x_4 and x_5 : activity ratios which were E_3/E_4 and E_3/E_5)

If the values of "z" is positive, the mite is determined to have been on plants of GRP1. If the value is negative, its host plant is judged to be one of GRP2 plants. Probability that misdiscrimination occurred was 0.1% in HSnd mites and 9.3% in AWnd mites.

Figures 4 and 5, respectively, show the differences between the MAHALANOBIS' generalized distances of each sample from GRP1 and those from GRP2. The differences were equal to the values of $-2z$. Host plants of all HSnd mites were determined correctly in the results of judgment. In the discrimination of AWnd mites, though host plants of 4 samples were misjudged and 2 samples were not determined, about 90% of samples were correctly judged as to host plant groups. In this case, the difference between mites on satsuma mandarin and Japanese pear was particularly clear.

The differences of MAHALANOBIS' generalized distances between GRP1 and GRP2 for each sample of HSnd mites were larger than that of AWnd mites as in the principal component analysis.

Fig. 4. Differences of the MAHALANOBIS' generalized distances in HSnd mites. D_1 and D_2 : the distances from the mite groups on GRP1 and GRP2 plants, respectively.

Fig. 5. Differences of the MAHALANOBIS' generalized distances in AWnd mites. D_1 and D_2 : see Fig. 4.

DISCUSSION

The development of citrus red mite was investigated on 14 species of plants including 6 kinds of citrus in this study (Table 1). UCHIDA (1982) tested the development of citrus red mite on 19 species of plants. His results approximated the results of this study. It was thus confirmed that the diapausing strain could not develop on most of the citrus varieties and that the Japanese pear and peach were common hosts to the 2 strains. This study also showed that the diapausing strain developed well on trifoliate orange, a deciduous species. We have been considered that all individuals of the citrus red mite on citrus trees belong to the non-diapausing strain. But the result indicates a possibility that the mites of diapausing strain, as well as the non-diapausing strain, are living on trifoliate orange, which is a kind of citrus trees. The diapausing strain, however, could not develop on 'Troyer' citrange which was a hybrid of trifoliate orange $\times$ 'Washington' navel. The developmental rate of the diapausing strain on 'Washington' navel was not investigated in this study but it was suggested to be very low from the results with other citrus trees. Thus the difference seems to be caused by some genetic factor of the plants, and that may be a secondary plant substance. These interest us in studies of interactions in mites and its host plants.

α - or β -naphthyl acetate are usually used as substrates for detection of the non-specific esterase activities (VAN ASPEREN, 1962; KUWAHARA et al., 1982). The esterases of citrus red mite responsible for the hydrolysis of α - and β -naphthyl acetate show similar zymogram patterns as revealed by agar-gel electrophoresis. Whichever substrates were used, the esterases also showed similar values for the bimolecular rate constants and similar inhibition patterns by a inhibitor (dichlorvos) (OSAKABE, 1985). Thus, only β -naphthyl acetate was used for detection of the esterase activities in this study. The patterns of the esterase bands separated by the electrophoresis were the same as those described by OSAKABE (1984) (Fig. 1). As the mites of non-diapausing strain commonly had E_3 - E_5 bands, the 3 bands were used to discuss how to relate its activity to the host plants.

MULLIN and CROFT (1983) reported on esterase activities of the two-spotted spider mite, *Tetranychus urticae* KOCH, using α -naphthyl acetate as the substrate. They showed differences in the activities among the mites on various host plants. Esterase activities of the citrus red mite were also influenced by the host plants (Tables 3 and 5), and the changes in its ratios were also observed (Tables 4 and 6). In this study, the multivariate analyses were carried out for a synthetic discussion of the differences of esterase activities and activity ratios of the mites. First, the differences were tried to analyze by the principal component analysis. As a result, the alterations which occurred in esterase activities and activity ratios of both HSnd and AWnd mites were shown more clearly by the dispersions of z_1 and z_2 principal components. And the cumulative contributions of the two principal components were very high in both populations. Therefore the method of the statistical analysis was useful to express the relationships between the host plants and the esterase activities of mites including activity ratios. The influences of the kinds of the host plants on HSnd and AWnd mites were similar. Namely, mites on GRP1 plants showed higher activities and/or larger activity ratios in comparison with the mites on GRP2 (Figs. 2 and 3). The results suggested that the mites on those 2 groups of host plants could be discriminated by a statistical method. Next, after confirmation of the statistical significance between the mean variables of mites on

GRP1 and GRP2, host plant groups of the mites were tried to determine with the linear discriminant functions. The host plant groups were distinctly separated by the discriminant functions in both HSnd and AWnd mites (Figs. 4 and 5), and the probability of misdiscrimination were below 10%. These results showed that the influences of the kinds of host plants on esterases of the citrus red mite were expressed more clearly by the multivariate analyses in comparison with when the influences were evaluated with only the activities.

The numbers of eggs laid by the non-diapausing strain on pear and peach (GRP2) were larger than those on citrus trees (GRP1), and the intrinsic rates of natural increase on GRP2 plants were higher than those on GRP1 plants (FURUHASHI and NISHINO, 1979; UCHIDA, 1982; MORIMOTO and TAKAFUJI, 1983). These results (including the developmental success of the 2 strains) suggested that esterases induced by GRP1 plants were concerned with the metabolism of a plant substance. And it was seemed that the existence of the substance might have an adverse effect on the rate of increase in the non-diapausing strain and on the development of the diapausing strain.

MULLIN and CROFT (1983) also showed host-related alterations of epoxide hydrolase and aldrin epoxidase. There are many reports on relationships between detoxifying enzyme activities of insects and their host plants, e.g., the mixed-function oxidases (YU, 1982 a; AHMAD, 1983; YU and ING, 1984; BRATTSTEN et al., 1977), and on several of the detoxifying enzymes (YU, 1982 b, 1983, 1984). BERRY et al. (1980) described the midgut microsomal aldrin epoxidase of the variegated cutworm larvae, *Peridroma saucia* (HÜBNER). The epoxidase was higher in larvae fed peppermint leaves than in larvae fed on artificial diet or other host plants. And the former were more tolerant to some insecticides than the latter. In the citrus red mite, TAKEHISA and TANAKA (1967) and TANAKA et al. (1972) said E_1 and E_2 esterase bands were generally detected in organophosphorus compound-resistant individuals. The results of this study showed that alterations of activities and activity ratios of E_3 - E_5 esterase bands were caused by its host plants. The induction of some other detoxifying enzymes might also be occurring in the citrus red mite, and this might cause alterations in tolerance to some acaricides.

ACKNOWLEDGEMENTS

The author wishes to express their sincere thanks to Dr. K. INOUE, Fruit Tree Research Station, for encouragement, Dr. S. MIYAI, National Institute of Agro-Environmental Sciences, for guidance in the statistical analysis, Mr. S. KOBAYASHI, Akitsu Branch, Fruit Tree Research Station, for critical reading of the manuscript, Dr. C. E. KENNETT, University of California, Berkeley, for revise the manuscript and the members of Akitsu Branch, Fruit Tree Research Station for many suggestions.

REFERENCES

- AHMAD, S. (1983) Mixed-function oxidase activity in a generalist herbivore in relation to its biology, food plants, and feeding history. *Ecology* **64**: 235-243.
- BERRY, R. E., S. J. YU and L. C. TERRIERE (1980) Influence of host plants on insecticide metabolism and management of variegated cutworm. *J. Econ. Entomol.* **73**: 771-774.
- BRATTSTEN, L. B., C. F. WILKINSON and T. EISNER (1977) Herbivore-plant interactions: Mixed-function oxidases and secondary plant substances. *Science* **196**: 1349-1352.
- FURUHASHI, K. and M. NISHINO (1979) Reproductive capacity of citrus red mite, *Panonychus citri*, McG. on three fruit trees. *Bull. Shizuoka Citrus Exp. Sta. Jpn.* **15**: 41-44 (in Japanese with an English summary).

- KUWAHARA, M., T. MIYATA, T. SAITO and M. ETO (1982) Activity and substrate specificity of the esterase associated with organophosphorus insecticide resistance in the Kanzawa spider mite, *Tetranychus kanzawai* KISHIDA (Acarina: Tetranychidae). *Appl. Ent. Zool.* **17**: 82–91.
- MORIMOTO, N. and A. TAKAFUJI (1983) Comparison of diapause attributes and host preference among three populations of the citrus red mite, *Panonychus citri* (McGREGOR) occurring in the southern part of Okayama prefecture, Japan. *Jap. J. appl. Ent. Zool.* **27**: 224–228 (in Japanese with an English summary).
- MULLIN, C. A. and B. A. CROFT (1983) Host-related alterations of detoxification enzymes in *Tetranychus urticae* (Acari: Tetranychidae). *Environ. Entomol.* **12**: 1278–1282.
- OSAKABE, M. (1984) Esterase zymogram of the citrus red mite, *Panonychus citri* (McGREGOR), on citrus and pear. *Jap. J. appl. Ent. Zool.* **28**: 1–4 (in Japanese with an English summary).
- OSAKABE, M. (1985) Properties of non-specific esterases of the citrus red mite, *Panonychus citri* (McGREGOR), which hydrolyze α - and β -naphthyl acetate. *Jpn. J. Appl. Ent. Zool.* **29**: 50–54 (in Japanese with an English summary).
- SHINKAJI, N. (1961) On the diapause of the citrus red mite, *Panonychus citri* (McGREGOR). *Bull. Hort. Stn. Nat. Tokai-Kinki Agric. Exp. Sta.* **6**: 64–76 (in Japanese with an English summary).
- TAKEHISA, T. and M. TANAKA (1967) Kanten hakusou denkieidouhou ni yoru mikanhadani yakuzai teikousei no kenteihou ni tsuite. *Proc. Assoc. Plant Prot. Kyushu* **13**: 126–132 (in Japanese).
- TANAKA, M., K. INOUE and K. KITA (1972) Studies on acaricide resistance of citrus red mite, *Panonychus citri* (McG.). IX Genetical proof on an estimating method of phenkapton-resistance by E_1 esterase band in the citrus red mite. *Bull. Hortic. Res. Sta. Jpn. Ser. D* **7**: 39–44 (in Japanese with an English summary).
- UCHIDA, M. (1982) Ecological studies on the abundance and diapause of spider mites and the damage caused by the spider mites in Japanese pear orchards. *Spec. Bull. Tottori Fruit Tree Exp. Stn.* **2**: 1–63 (in Japanese with an English summary).
- VAN ASPEREN, K. (1962) A study of housefly esterases by means of a sensitive colorimetric method. *J. Insect Physiol.* **8**: 401–416.
- YU, S. J. (1982 a) Induction of microsomal oxidases by host plants in the fall armyworm, *Spodoptera frugiperda* (J. E. SMITH). *Pestic. Biochem. Physiol.* **17**: 59–67.
- YU, S. J. (1982 b) Host plant induction of glutathione S-transferase in the fall armyworm. *Pestic. Biochem. Physiol.* **18**: 101–106.
- YU, S. J. (1983) Induction of detoxifying enzymes by allelochemicals and host plants in the fall armyworm. *Pestic. Biochem. Physiol.* **19**: 330–336.
- YU, S. J. (1984) Interactions of allelochemicals with detoxication enzymes of insecticide-susceptible and resistant fall armyworms. *Pestic. Biochem. Physiol.* **22**: 60–68.
- YU, S. J. and R. T. ING (1984) Microsomal biphenyl hydroxylase of fall armyworm larvae and its induction by allelochemicals and host plants. *Comp. Biochem. Physiol.* **78C**: 145–152.