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Genetic Analysis of Acaricide Resistance in Citrus Red Mite, Panonychus citri (McG.)

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Abstract
Genetic mechanisms of increase, persistence, decrease and decline of major acaricide resistance in citrus red mite, Panonychus citri (McG.), were studied. Dicofol resistance in P. citri was mainly due to a single, incompletely recessive major gene. The result of the experiments on fitness indicated that the reproduction rate of the resistant strain was lower than that of the susceptible one, in particular under a high temperature condition (30°C) or under a special feeding condition such as seriously damaged leaves of host trees. This was caused by a lower rate of egg production in the resistant mites. The dicofol susceptibility in a mite population originally composed of a 1 : 1 mixture of resistant and susceptible strains from the same origin was examined in 17 generations at 25°C. After 13 generations, susceptibility of the mixed population increased remarkably. The result indicates that the resistant mites (RR) have lower fitness values than the susceptible mites (SS, RS) under either favorable (25°C) or unfavorable conditions for reproduction of the spider mites in an acaricide-free environment. Amitraz resistance was due to a single, incompletely dominant major gene. The values of fitness of benzomate and amitraz resistant mites were almost equal to those of susceptible mites in an acaricide-free environment.

Discipline: Insect pest
Additional key words: amitraz, benzomate, dicofol, fitness, reversion

Introduction

Some parameters influencing selection process in the development of insecticide resistance have been identified among the genetic, biological and operational factors[8,9]. It is very necessary to analyze genetic mechanisms of increase, persistence and decrease of insecticide resistance of spider mites in establishing effective measures for control. Among others, fitness is one of the most important factors that shows the degree of advantage in natural selection. If a homozygote and a heterozygote of resistance gene have both lower values of fitness than a homozygote of susceptible one in an acaricide-free environment, the acaricide resistance of the population is expected to decline gradually.

Genetic studies on major acaricide resistance in citrus red mite, *Panonychus citri* (McG.), were undertaken in a framework of population genetics. The present paper reviews the results of those studies with emphasis placed on the genetic basis and the fitness of dicofol, benzomate and amitraz resistance.

Genetic analysis of dicofol resistance

Dicofol had been used in Japan since 1957 to control *P. citri*. The development of resistance of *P. citri* to dicofol took place in several apple groves in 1965 and also in several citrus groves during the period 1966 to 1968. The pattern of increase or decrease in resistance level of *P. citri* to dicofol was different from that to the other acaricides. It was often observed under field conditions that dicofol resistance of *P. citri* increased gradually through the selections with dicofol, while it decreased rather rapidly when the selection was relaxed. To analyze a genetic mechanism of this pattern, a study on the changes of susceptibility of mite populations to dicofol and the genetic basis of resistance was

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undertaken. It also included comparisons of the fitness, i.e., the reproduction rate, viability and oviposition rate, between dicofol resistant (R) and susceptible (S) strains from the same origin. Based on the data of the change in dicofol susceptibility of a mixed population of those two strains, a relative value of fitness of the resistant mites was estimated by a simulation method.

Some crosses were made between a dicofol resistant strain selected from a Yoshii population in Fukuoka Prefecture and a susceptible strain of an Ogi population collected from Saga Prefecture. The results obtained from the cross experiment are shown in Fig. 1. Susceptibilities of the F_1 and the B_1 adult females are compared with each other by using log concentration-probit mortality lines and curve. No significant differences in susceptibilities are found between the reciprocal crosses. However, the susceptibilities of the hybrid adult females are fairly higher than the average level of both resistant and susceptible parental strains. Thus, it is suggested that the dicofol resistance be manifested as a recessive character. The results of a series of backcrossings indicate that the log concentration-probit mortality curve obtained fits well the expected one, based on a hypothesis that one major gene is responsible for the resistance to dicofol[14].

In order to evaluate the fitness, reproduction rates at 25°C and 30°C in the dicofol resistant and susceptible strains of citrus red mite from the same origin were investigated. The reproduction rate of the resistant strain was lower than that of the susceptible one, in particular under a higher temperature condition (30°C) or under a special feeding condition such as seriously damaged leaves of host trees. This was caused mainly by a lower rate of egg production in the resistant mites.

It is generally observed in actual field populations, that individuals with different genotypes are concomitantly involved especially after introduction of acaricides. Taking such concomitance into account, a 1 : 1 mixed population of the resistant and susceptible mites was reared under an acaricide-free condition in the laboratory to analyze relationships between

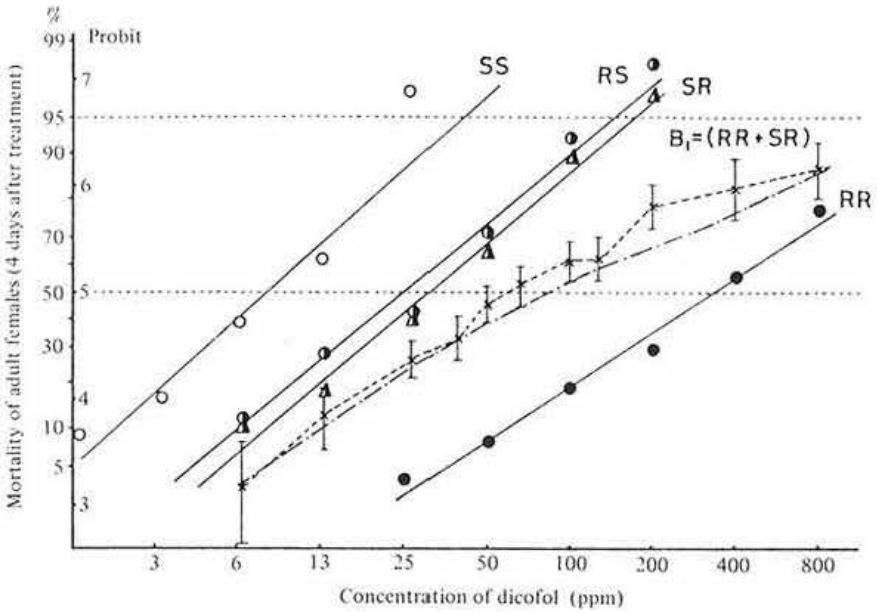

Fig. 1. Dicofol susceptibilities of adult females in resistant strain (RR), susceptible strain (SS), the hybrids (RS, SR) and backcross progeny (B_1) of *P. citri* (1972)
—·—: Theoretical probit mortality line of the backcross progeny drawn on the basis of a hypothesis that dicofol resistance is due to a single major gene.
Total number of adult females tested: SS; 550, RS; 738, SR; 774, B_1(RR+SR); 1,447, RR; 652.
Each vertical line gives 98% confidence interval.

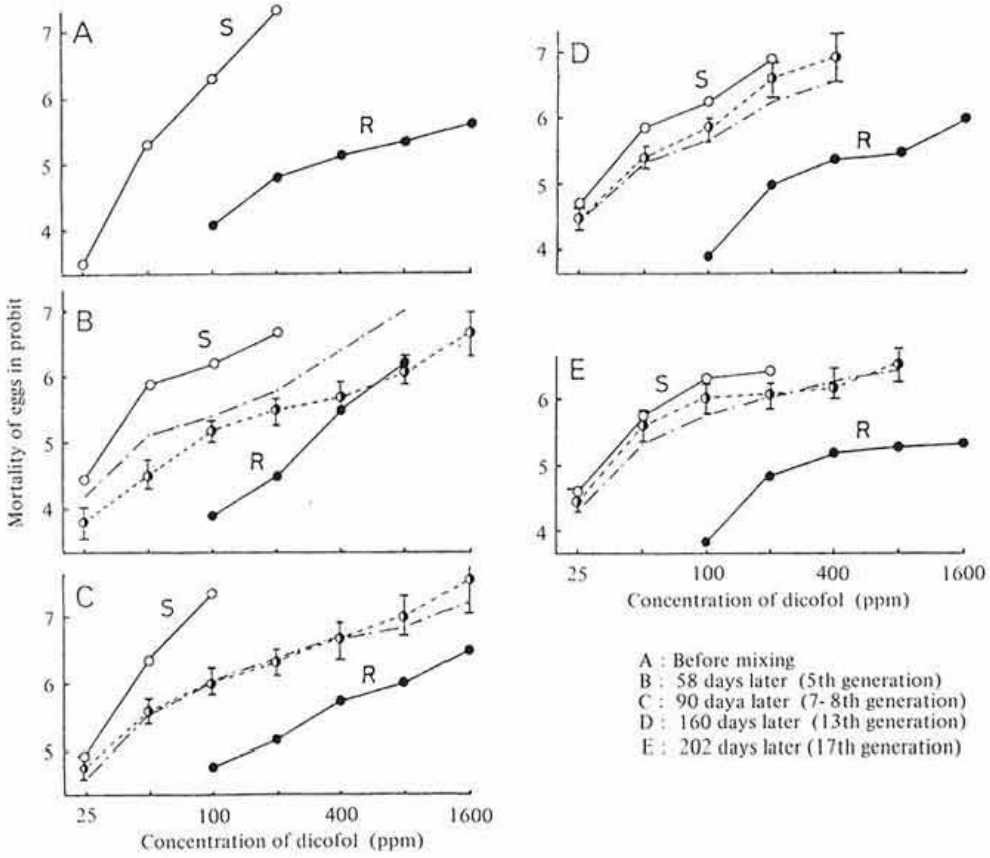

Fig. 2. Changes of dicofol susceptibilities of eggs in resistant strain (R), susceptible strain (S) and a mixed population (R+S) of two strains of *P. citri* (25°C)
---------- : Actual experimental dicofol susceptibility of a mixed population.
—·— : Theoretical dicofol susceptibility of a mixed population is drawn on the basis of a simulation where relative value of fitness of resistant mites is 0.75.
Each vertical line gives 98% confidence interval.

dicofol resistance level and value of fitness in *P. citri* under competitions among the individuals with various genotypes.

In order to estimate the proportions of resistant and susceptible mites within the population, the dicofol susceptibility of eggs was tested at various intervals. Results of such tests are shown in Fig. 2. Dicofol susceptibility of the mixed population increased gradually from generation to generation. Thus, it is evident that the resistant mites have lower value of fitness than the susceptible mites under an acaricide-free environment. Based on the experimental data on the dicofol susceptibility of the mixed population, the relative value of fitness of the resistant mites was estimated by a computer simulation. The experimental value agreed well with the calculated one, and the relative value of fitness of the resistant mites was 0.75.

When the dicofol resistance has developed in a mite population, a reversion to susceptibility could be obtained by relaxing the selection. The periods required for the change to susceptibility vary, depending on the frequencies of the resistance gene in the course of time as well as on the environmental conditions after relaxation of the selection. It is shown that the reversion would require 30–58 generations[15]. In the citrus groves in Japan where dicofol resistance has actually developed, it is necessary to pause the use of dicofol for 2–4 years in order to induce the reversion to susceptibility.

Genetic analysis of benzomate resistance

Resistance of *P. citri* to benzomate which had been used in Japan since 1971, increased rapidly in several citrus growing areas in 1974, since that acaricide was distributed widely to other areas. The fitness of benzomate resistant *P. citri* was examined.

A benzomate resistant population was collected from a citrus grove in Yamakawa, Fukuoka Prefecture, 1975. The mite population collected was subjected to selections 7 times regarding its resistance and susceptibility to benzomate. The selected populations were used as resistant and susceptible strains.

The fitness, i.e., viabilities, oviposition rates and reproduction rates, in benzomate resistant (RR, RS) and susceptible (SS) strains was compared under various temperature conditions. Under the following two conditions, one was a constant temperature of 25°C and the other was daily fluctuated temperatures of 18–35°C, there were no significant differences in the longevity of the adult females, the number of egg/female/day and the intrinsic rate of natural increase (r_m) between those strains.

Two mixed populations originally composed of resistant and susceptible strains at the ratios of 1 : 1 and 1 : 4, were reared without any selection for benzomate susceptibility for 26 generations under daily fluctuated temperatures of 18–35°C. They were tested 7 times on their susceptibility to benzomate. The results of the tests showed that the susceptibility to benzomate of the two mixed populations was almost unchanged for 26 generations.

From these results, it could be concluded that the fitness of the resistant mites (RR, RS) is almost equal to that of the susceptible one (SS) under either favorable (25°C) or higher temperature conditions in an acaricide-free environment[16]. It is expected, therefore, that the resistance to benzomate may develop easily by selections since it is due to a complete dominant major gene[24], and the benzomate resistance of the population, once developed, may not decline for a long period of time.

Genetic analysis of amitraz resistance

Susceptibility of *P. citri* to amitraz which had been used in Japan since 1975, has gradually declined in several citrus growing areas since 1978. Investigations were made with special emphasis placed on the degree of development of resistance to amitraz in a mite population acquired through continuous selections with amitraz and its genetic basis.

There were large differences in amitraz susceptibiliy between the selected population (R) and the unselected population (S) sampled from a citrus grove which has never been treated earlier with amitraz. A maximum value of the ratio of R to S, or 158–fold, was recorded in terms of the LC_{50} value. An amitraz resistant strain selected from an Ehime population and a susceptible strain from a Hiratsuka population were crossed and backcrossed. The results of these tests showed that amitraz resistance of the eggs in *P. citri* was mainly due to a single, incompletely dominant major gene.

The fitness, consisting of viabilities, age-specific fecundities and reproduction rates, in the amitraz resistant (RR, RS) and susceptible (SS) strains of the Ehime population was compared under various environmental conditions. There were no significant differences among the strains, except for the results obtained under the constant temperature of 25°C.

Two mixed populations originally composed of resistant (RR) and susceptible (SS) strains with the ratios of 1 : 1 and 1 : 9, were reared without any selection for amitraz susceptibility for 32 generations under daily fluctuated temperatures ranging between 20°C and 30°C. They were tested 5 times on their susceptibility to amitraz. The results of these tests showed that the susceptibility to amitraz of the two mixed populations remained unchanged for 32 generations.

From these results, it is concluded that the values of fitness of the resistant mite populations (RR, RS) are almost equal to those of the susceptible population (SS) in an acaricide-free environment[17]. It is expected that the amitraz resistance of the population, once developed, may not decline for a long period of time, just as the benzomate resistance.

General discusson

Genetic analyses of acaricide resistance to various compounds have been undertaken in *Tetranychus urticae, T. Kanzawai, T. pacificus, Panonychus ulmi* and *P. citri*. It is found that the resistance is generally due to monogenic and dominant or semi-dominant characters (Table 1). In addition, a single

Table 1. Genetic types and fitness in insecticide resistance of tetranychid mites

Compound	Species of mites[a)]	Genetic type	Fitness[b,c)]
Amitraz	*P. citri*	Monog./semidom.[17)]	RR = RS = SS[17)]
Benzomate	*P. citri*	Monog./dominant[24)]	RR = RS = SS[16)]
Binapacryl	*P. ulmi*	Monog./semidom.[3)]	–
Chlordimeform	*T. kanzawai*	Monog./semidom.[22)]	–
Cyhexatin	*T. urticae*	Polyg./semirec.[4)]	RR < SS[7)]
	T. kanzawai	Polyg./semirec.[18)]	(RR = SS)[18)]
	P. ulmi	Polyg./semirec.[29)]	(RR = RS = SS)[29)]
	T. pacificus	Monog./semirec.[11)]	(RR = RS = SS)[11)]
Demeton	*T. urticae*	Monog./recessive[35)]	RR < SS[5,30)]
	T. urticae	Monog./dominant[27)]	–
	T. urticae	Monog./semidom.[10)]	–
Demeton-S-methyl	*P. ulmi*	Monog./semidom.[2)]	–
Dicofol	*T. urticae*	Monog./recessive[28,34)]	(RR < SS)[19)]
			RR < SS[21)]
	T. kanzawai	Monog./semirec.[22,25)]	RR = SS[25)]
	P. ulmi	Monog./semirec.[29)]	RR = SS[29)]
	P. citri	Monog./semirec.[14)]	RR < RS = SS[15)]
Dimethoate	*P. ulmi*	Monog./semidom.[2)]	–
Estox	*T. kanzawai*	Monog./dominant[25)]	–
Hexythiazox	*P. citri*	Monog./semirec.[20,33)]	–
Malathion	*T. urticae*	Monog./dominant[31)]	(RR < SS)[23)]
Parathion	*T. urticae*	Monog./dominant[10)]	RR < SS[30)]
	T. urticae	Monog./recessive[35)]	–
	P. ulmi	Monog./dominant[2)]	–
	T. pacificus	Monog./dominant[1)]	–
Phenkapton	*P. citri*	Monog./semidom.[13)]	(RR = SS)[32)]
Phentoate	*T. kanzawai*	Monog./semidom.[22)]	–
Propargite	*T. pacificus*	Monog./semirec.[12)]	(RR = RS = SS)[12)]
Tetradifon	*T. urticae*	Monog./dominant[26)]	–
	T. urticae	Monog./semidom.[27)]	–
	P. ulmi	Monog./dominant[3)]	–
Vamidothion	*P. ulmi*	Monog./semidom.[2)]	–

a): *P.*; *Panonychus*, *T.*; *Tetranychus*.
b): RR; Resistant strain, SS; Susceptible strain, RS; Heterozygous individual.
c): ( ); Mite strains from different origins.

major gene and also some modifying genes, which augment the effect of the major gene, might be involved in the resistant characters to some of these compounds. But dicofol, hexythiazox and propargite resistance is due to monogenic and semi-recessive or recessive characters. Cyhexatin resistance is mainly due to a polygenic, semi-recessive character.

Studies on the fitness in insecticide resistance of the spider mites are rather limited as shown in Table 1. As far as cyhexatin, demeton, dicofol and parathion resistance of *T. urticae* and dicofol resistance of *P. citri* are concerned, the resistant mites have lower fitness than the susceptible ones under an insecticide-free environment.

The fitness of resistant individuals also affects the stability in acaricide resistance of populations of spider mites. In recent years, the reversion of resistance in cyhexatin resistant *T. urticae* has been observed under a field condition[6,7)].

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