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REPRODUCTIVE COMPATIBILITY BETWEEN POPULATIONS OF THE CITRUS RED MITE, *PANONYCHUS CITRI* (MCGREGOR) (ACARINA: TETRANYCHIDAE)[1]

Akio TAKAFUJI and Hiroaki FUJIMOTO

Entomological Laboratory, College of Agriculture,
Kyoto University, Kyoto 606, Japan

INTRODUCTION

It is well known that there is some degree of infertility barriers between different populations of the arrhenotokous spider mites of the family Tetranychidae (eg. DILLON, 1958; BOUDREAUX, 1963; HELLE and PIETERSE, 1965; OVERMEER and VAN ZON, 1976; DE BOER, 1980, 1981, 1982; DE BOER and VEERMAN, 1983). Such reporoductive incompatibility has been most commonly observed between populations of the two-spotted spider mite, *Tetranychus urticae* KOCH, for example, between populations occurring in adjacent glasshouses (eg. HELLE and PIETERSE, 1965) and also between natural populations that are far apart (eg. DE BOER, 1981). The majority of the incompatibility observed in the spider mites of the genus *Tetranychus* is only partial, expressed as either of the two ways: an increased proportion of infertile F_1-females and an increased inviability of F_2-eggs.

The citrus red mite, *Panonychus citri* (MCGREGOR) studied in the present paper is a serious pest both on deciduous fruit trees such as pear or peach and on citrus, in Japan. It is known that there are at least two types of the citrus red mite: one is a diapausing type that overwinters as diapausing eggs on twigs of deciduous trees and is distributed in the higher altitudal areas, and the other is a non-diapausing type occurring on both citrus and deciduous trees in the lower altitudal zones (SHINKAJI, 1961a, 1979). The former can develop and reproduce on pear but not on citrus, but the latter can do so on both of them (SHINKAJI, 1961b; UCHIDA, 1982; MORIMOTO and TAKAFUJI, 1983). There are some other differences between the two types, such as the difference in the egg size (SHINKAJI, 1961a; UCHIDA, 1982) and that in the esterase activity (OSAKABE, 1984).

In the intermediate altitudal areas in Japan, pear and citrus trees are in some cases grown adjacently. In such areas, TAKAFUJI and MORIMOTO (1983) have shown that the two types of *P. citri* occur in the same pear orchards, though it is not certain whether the non-diapausing type is maintaining its population on pear throughout winter.

The present study was undertaken to examine the reproductive compatibility between the diapausing type from pear, the non-diapausing type from pear and that from citrus, as well as the intra- and inter-populational compatibility of each type of the citrus red mite.

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MATERIALS and METHODS

Populations

Table 1 lists the populations of *P. citri* used in the present study. There were five populations for the diapausing pear type (**DP**), one for the non-diapausing pear type (**NP**) and three for the citrus type (**C**). The diapausing populations were collected as overwintered eggs from twigs of pear trees in early spring before hatching, the non-diapausing population on pear as adult females from leaves of pear trees in September when the population began to increase its number, and the citrus populations were sampled as adult females from citrus leaves. In the laboratory controlled at 25°C: 60–70% RH: 16L-8D, the mites were reared on detached pear and citrus leaves for the pear and citrus type, respectively. The leaves were pressed on water-soaked cotton placed on 1 cm thick foam plastic in water-filled petri dishes (9 cm in diameter and 1.4 cm in depth). The leaves were taken from trees grown in flower pots under outdoor conditions.

Prior to the experiments, the diapause incidence of each of the populations was tested. At 20°C, the eggs oviposited by individual females of each population were exposed to various daylengths until they reached adulthood, and the females thus reared were allowed to lay eggs. These eggs were tested for hatchability at 25°C whether or not they were in diapause. For the daylengths of shorter than 12 h, all the eggs produced by the females of the DP populations were in diapause (FUJIMOTO and TAKAFUJI, unpublished).

Copulation

Duration of copulation was scored in crosses between the pear and citrus type as well as in crosses between mates of the same types to study the mating success between the different types. Mating behaviour of the two-spotted spider mite has been well studied (eg. CONE et al., 1971: PENMAN and CONE, 1974): males are attarcted to a quiescent female deutonymph (the last stage before adulthood) by the sex pheromone and webs that the female produces; then they remain motionless beside or on top of the

Table 1. Populations of *P. citri* used in the present study, showing their collection records.

Host plant	Type	Population	Location		Date of collection	Stage of mites collected
Pear	Diapausing (DP)	A_p	Amagi, Fukuoka	33°17″N	Apr. 8, 84	Eggs on twigs
		K_p	Kaho, Fukuoka	33°21″	Apr. 8, 84	Eggs on twigs
		S_p	Sairyuji, Okayama	34°41″	Feb. 6, 84	Eggs on twigs
		M_p	Momoezuki, Okayama	34°41″	Feb. 6, 84	Eggs on twigs
		T_p	Daiei, Tottori	35°29″	Mar. 14, 84	Eggs on twigs
	Non-diapausing (NP)	O_p	Takatsuki, Osaka	34°51″	Sep. 10, 84	Adults on leaves
Citrus	Non-diapausing (C)	U_c	Ushimado, Okayama	34°37″	Feb. 21, 83	Adults on leaves
		S_c	Sairyuji, Okayama	34°41″	Feb. 21, 83	Adults on leaves
		E_c	Shimada, Shizuoka	34°49″	Mar. 22, 84	Adults on leaves

female. As soon as the female has completed the last moult, the male goes beneath the female body, seizes the body by the forelegs and inseminates. This mating pattern is the same as in the citrus red mite.

In the present copulation study, quiescent female deutonymphs of each type were separated from the colony and as soon as they completed the last moult, they were individually transferred to detached pear leaves of 2 sq. cm placed on water-soaked cotton in petri dishes as described above, and 1 min later a fresh adult male was added to each leaf. The duration of copulation scored in this study was the length of time from the onset of seizing of a female by a male to its abandonment. Observations were made under a binocular microscope with a continuous illumination at temperature ranging from 23° to 26°C. The majority of males copulated within 10 min after introduction, but if they did not proceed to copulation behaviour within 2 h, which was seen in only 1 or 2 at most out of 15 to 25 pairs of each combination, observations were stopped. Observations were made of the following crosses: Mp × Mp, Sc × Sc, Uc × Uc; Sc × Uc, Mp × Sc and their reciprocals.

Egg hatchability and survival of immatures in progeny from crosses between different populations

Crossing experiments included intra- and inter-populational crosses within each of the DP, NP and C types and crosses among the different three types, with a reciprocal cross in each pair.

Twelve to 18 female quiescent deutonymphs of each population were separated from the colony and were introduced onto a detatched pear leaf of approximately 25 cm^2, together with 10 to 12 adult males to allow mass crosses between them for 48 h. This ratio of males to females was large enough for the males to copulate with all the females, as preliminary experiments showed that a single adult male was capable of mating with at least 15 females during that period. After 48 h, males were removed, and the females were allowed to lay eggs for 3 to 4 days and then they were removed. Hatchability of the eggs thus collectively produced was scored 10 days after females were removed when all viable eggs must have been hatched.

The survival of immatures was scored from about 50 individuals randomly sampled from the eggs produced as above: in each cross five newly-hatched larvae were transferred onto each of 10 detached pear leaves of about 1.5 sq. cm placed on water-soaked cotton in petri dishes described above (5 leaves were spaced in each petri dish). As it is known that both pear and citrus types can develop well and reproduce on pear, pear leaves were provided as food in this experiment. Survival of immatures was checked daily until they reached the adult stage or died, and sex ratio was determined based from the individuals that successfully reached adulthood. The leaves were not renewed during the experiment. Individuals which were accidentally drowned were excluded from the data. All experiments were carried out at 25°C: 60–70% RH: 16L.

Results

Copulation

In all the combinations tested, more than 90% of males attempted to copulate within 10 min after introduction and many copulated within a few minutes. Duration of copulation between mates of the pear type (M_p) was rather constant. This was also the case in the intra- and inter-populational copulation in the citrus type (S_c and U_c). In addition, the durations of copulation for the pear and citrus types were similar to each other, the average being 12 to 13 min (Table 2 and Fig. 1). This duration of copulation of *P. citri* was far longer than that of *T. urticae* which was only 2 to 3 min (Dieleman and Overmeer, 1972) or that of *T. kanzawai* which was also about 2 to 3 min on the average (Ozawa and Takafuji, unpublished).

The duration of copulation between the pear and citrus type differed greatly between the reciprocal crosses. The duration of copulation between citrus male (S_c ♂) and pear female (M_p ♀) was significantly longer than that between mates of each type (Table 2 and Fig. 1) and there were very few interruptions of insemination, showing that there was no barrier for successful copulation. On the contrary, copulation in the reciprocal cross, i.e., that between pear male (M_p ♂) and citrus female (S_c ♀), was sometimes broken off prematurely and the duration varied greatly between pairs (Table 2). Some interrupted copulation and left the partner only 1 to 3 min after insemination (Fig. 1), suggesting the existence of some barrier for successful copulation. Such partial behavioural isolation was described in the copulation of different strains of *T. urticae* (Dieleman and Overmeer, 1972) and between closely related species of spider mites such as between *T. urticae* and *T. cinnabarinus* (Smith et al., 1969) or between *T. urticae* and *T. kanzawai* (Ozawa and Takafuji, unpublished).

The results obtained here show that copulation does occur between pear and citrus type, and they also suggest, though indirectly, that males of diapausing pear type may have a preference for a partner of its own type, but not citrus males.

Table 2. Duration of copulation in crosses between the same and different populations of *P. citri*.

Cross*	No. of Pairs	Duration of Copulation (min)**	Coefficient of Variation (%)
M_p♀ × M_p ♂	17	12.3±1.9	15.1
M_p♀ × S_c ♂	22	17.3±3.0	17.2
S_c♀ × M_p ♂	23	6.8±3.6	53.4
S_c♀ × S_c ♂	15	13.0±2.5	19.5
U_c♀ × U_c ♂	19	12.3±3.3	26.8
S_c♀ × U_c ♂	25	12.7±2.1	16.2
U_c♀ × S_c ♂	25	12.4±1.8	14.8

* M_p; diapausing pear type: S_c and U_c; citrus type

** Mean±S.D.

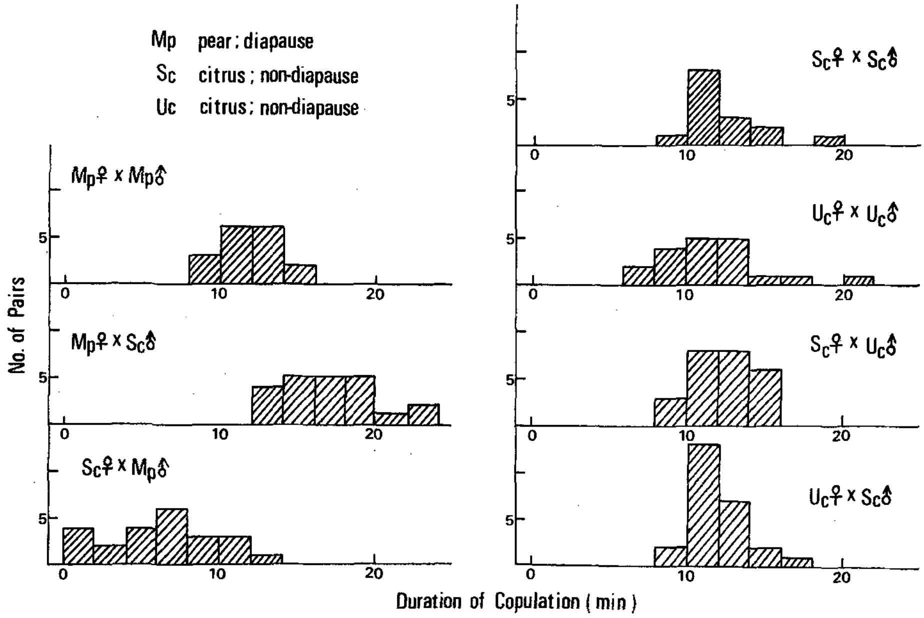

Fig. 1. Duration of copulation between mates of the same and different types of *P. citri*, showing the frequency distribution from each cross.

Egg hatchability, survival of immatures and sex ratio of F_1 progeny

Crossing between the same types. Tables 3 and 4 list the results of crosses between mates of DP and those between mates of C respectively. Hatchability of eggs from intra-populational crosses of each type was more than 95%. The survival rate throughout the immature stage tended to be slightly lower (but not significantly; $p>0.02$*) for DP, as compared to that for C, showing that the former type tended to be slightly less vigorous or slightly less tolerant of deterioration of pear leaves (Fig. 2). The sex ratio (♀/(♂+♀)) differed considerably among populations, ranging from 0.51 to 0.80.

Inter-populational crosses between the three populations of C showed that there was no appreciable incompatibility between them, as there was no significant ($p>0.10$*) reduction either in egg hatchability or survival rate compared to that observed in the intra-populational crosses (Fig. 2). INOUE (1972) also showed that there was no reduction in egg hatchability in F_1 from crosses between populations of citrus type, though a significant reduction was observed in the hatchability of F_2 eggs from crosses between a few of the populations. However, for DP the survival rate from the inter-populational crosses was significantly ($p<0.01$*) lower than that from the intra-populational crosses, showing that there was a partial incompatibility between some of the DP populations. There were reciprocal differences (but not significant) in survival rate and sex ratio for inter-populational crosses of DP (Fig. 2), and there was a tendency for the survival rate to vary directly with the proportion of females, implying that fertilized individuals, i.e. female immatures, might have been subjected to a higher mortality.

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* MANN-WHITNEY's *U* test (two tailed).

Table 3. Egg hatchability, survival rate of immatures and sex ratio in the F1 progeny from crosses between populations of the diapausing pear type (DP).

DP♀×DP♂	Hatchability (%)	Survival rate (%) in immature stage	Survival rate (%) from egg to adult	Sex ratio (♀/(♀+♂))
intra-populational cross				
$A_p \times A_p$	98.4(352)	85.7(49)	84.3	0.64
$K_p \times K_p$	98.9(177)	77.1(48)	76.3	0.73
$S_p \times S_p$	96.6(147)	74.0(50)	71.5	0.51
$M_p \times M_p$	95.0(50)	86.7(58)	82.4	0.67
$T_p \times T_p$	95.7(117)	88.0(50)	84.2	0.80
inter-populational cross				
$A_p \times S_p$	98.6(147)	63.3(49)	62.4	0.58
$S_p \times A_p$	76.4(77)	66.0(50)	63.4	0.71
$A_p \times T_p$	95.7(116)	66.0(50)	63.2	0.58
$T_p \times A_p$	95.5(202)	42.6(47)	40.7	0.45
$A_p \times K_p$	98.1(103)	73.5(49)	72.1	0.72
$K_p \times A_p$	98.1(54)	55.3(47)	54.2	0.69
$K_p \times M_p$	98.2(226)	46.9(50)	46.9	0.57
$M_p \times K_p$	93.5(107)	38.8(50)	36.3	0.53
$K_p \times T_p$	96.6(59)	64.0(50)	61.8	0.59
$T_p \times K_p$	95.3(193)	70.0(50)	66.7	0.74
$M_p \times T_p$	90.9(77)	76.0(50)	69.1	0.81
$T_p \times M_p$	98.7(152)	66.7(48)	65.8	0.56

Numerals in parentheses are the number of individuals tested.

Table 4. Egg hatchability, survival rate of immatures and sex ratio in the F1 progeny from crosses between populations of the citrus type (C).

C♀×C♂	Hatchability (%)	Survival rate (%) in immature stage	Survival rate (%) from egg to adult	Sex ratio (♀/(♀+♂))
intra-populational cross				
$U_c \times U_c$	95.2(252)	94.8(156)	90.2	0.67
$S_c \times S_c$	94.5(271)	90.7(43)	85.7	0.71
$E_c \times E_c$	97.8(92)	86.0(50)	84.1	0.65
inter-populational corss				
$U_c \times S_c$	94.3(407)	94.0(50)	88.6	0.73
$S_c \times U_c$	95.7(606)	84.0(50)	80.4	0.78
$U_c \times E_c$	98.9(93)	98.0(50)	96.9	0.69
$E_c \times U_c$	99.1(107)	83.7(49)	82.9	0.83
$S_c \times E_c$	99.3(283)	86.0(50)	85.3	0.61
$E_c \times S_c$	99.1(205)	86.0(50)	85.2	0.70

Numerals in parentheses are the number of individuals tested.

Crosses between DP and C. No adult females were produced at all from crosses between DP and C of either direction (Tables 5 and 6) and this was consistent in all the crosses between different populations, clearly indicating that there was a complete reproductive incompatibility between these two types. Interestingly, there was a highly significant ($p<0.001$*) reciprocal difference in the egg hatchability and also a significant ($p<0.01$*) difference in the survival rate (Fig. 2). The egg hatchability of the F_1 from DP♀×C♂ was much lower than that from C♀×DP♂ and this was also consistent in all the crosses tested. The survival rate also was lower for the F_1 from DP♀×C♂

Table 5. Egg hatchability, survival rate of immatures and sex ratio in the F_1 progeny from crosses between populations of the diapausing pear type (DP ♀) and those of the citrus type (C ♂).

DP ♀ × C ♂	Hatchability (%)	Survival rate (%) in immature stage	Survival rate (%) from egg to adult	Sex ratio (♀/(♀+♂))
$A_p \times S_c$	65.7(178)	77.6(49)	51.0	0
$A_p \times U_c$	72.7(308)	95.8(48)	69.6	0
$K_p \times S_c$	82.7(231)	80.0(50)	66.2	0
$K_p \times U_c$	79.2(236)	70.0(50)	55.4	0
$K_p \times E_c$	68.0(366)	76.0(50)	51.7	0
$S_p \times S_c$	75.2(101)	56.0(50)	42.1	0
$M_p \times S_c$	77.2(342)	48.9(47)	37.8	0
$M_p \times U_c$	71.1(249)	64.0(50)	45.5	0
$T_p \times U_c$	80.0(115)	80.0(50)	64.0	0
$T_p \times E_c$	64.3(157)	78.0(50)	50.2	0

Numerals in parentheses are the number of individuals tested.

Table 6. Egg hatchability, survival rate of immatures and sex ratio in the F_1 progeny from crosses between populations of the citrus type (C ♀) and those of the diapausing pear type (DP ♂).

C ♀ × DP ♂	Hatchability (%)	Survival rate (%) in immature stage	Survival rate (%) from egg to adult	Sex ratio (♀/(♀+♂))
$U_c \times A_p$	95.5(221)	94.0(50)	89.8	0
$U_c \times K_p$	99.1(432)	98.0(50)	97.1	0
$U_c \times M_p$	97.2(109)	85.1(47)	82.7	0
$U_c \times T_p$	97.9(141)	85.4(48)	83.6	0
$S_c \times A_p$	97.4(153)	96.0(50)	93.5	0
$S_c \times K_p$	99.3(303)	100.0(50)	99.3	0
$S_c \times S_p$	99.0(201)	78.0(50)	77.2	0
$S_c \times M_p$	99.0(192)	90.0(50)	89.1	0
$E_c \times K_p$	98.4(184)	84.0(47)	82.7	0
$E_c \times T_p$	97.7(130)	80.0(45)	78.2	0

Numerals in parentheses are the number of individuals tested.

than from C ♀ × DP ♂, although it differed considerably among crosses, ranging from 49 to 96%.

Crosses between NP and DP, and between NP and C. No adult females were obtained at all from crosses between NP and DP (Table 7). The result of this cross was quite similar to that in crosses between DP and C: the egg hatchability of F_1 from crosses between DP ♀ and NP ♂ was much lower than that from its reciprocal cross (Fig. 2).

Apparently, no incompatibility was observed between NP and C; there was no reduction either in egg hatchability or survival rate, and the sex ratio showed normal values (Table 7 and Fig. 2).

Discussion

The present study shows that there is an extremely severe reproductive isolation between the diapausing and non-diapausing type of *P. citri*. This reproductive incompatibility found in this species is far more intense than that observed between different populations of *T. urticae* and is severer even than the incompatibility between *T. urticae* and its sibling species, *T. cinnabarinus*. The reproductive incompatibility for *T. urticae*

Table 7. Egg hatchability, survival rate of immatures and sex ratio in the F_1 progeny from crosses between a population of non-diapausing pear type (NP), populations of the diapausing pear type (DP) and those of the citrus type (C), with the result for an intra-populational cross of the NP population.

Cross	Hatchability (%)	Survival rate (%) in immature stage	Survival rate (%) from egg to adult	Sex ratio (♀/(♀+♂))
NP ♀ × NP ♂				
$O_p \times O_p$	99.2(383)	96.0(50)	95.2	0.81
NP ♀ × DP ♂				
$O_p \times A_p$	94.3(194)	94.0(50)	88.6	0
$O_p \times T_p$	98.4(187)	91.8(50)	90.3	0
DP ♀ × NP ♂				
$A_p \times O_p$	54.5(176)	96.0(50)	52.3	0
$T_p \times O_p$	77.0(278)	68.0(50)	52.4	0
NP ♀ × C ♂				
$O_p \times S_c$	97.9(238)	96.0(50)	94.0	0.75
$O_p \times E_c$	98.1(258)	94.1(51)	92.3	0.77
C ♀ × NP ♀				
$S_c \times O_p$	97.5(163)	96.1(51)	93.7	0.78
$E_c \times O_p$	98.5(199)	90.2(51)	88.8	0.87

Numerals in parentheses are the number of individuals tested.

is most commonly expressed as a partial hybrid sterility (eg. HELLE and PIETERSE, 1965; OVERMEER and VAN ZON, 1976; DE BOER, 1980, 1981, 1982), although there is a case in which a very severe hybrid inviability, i.e., mortality in a pre-reproductive stage of the hybrid females, was found (DE BOER and VEERMAN, 1983). There is also a report that crossing between *T. urticae* and *T. cinnabarinus* did produce fertile F_2 females, revealing that there is a gene exchange between the two species (DUPONT, 1979), though this is obviously rare.

It seems that fertilization of eggs does not occur between males of the diapausing pear type (DP ♂) and females of the citrus type (C ♀) of *P. citri*, indicating that there is a fertilization block, i.e., there is either a mechanical or gametic isolation between them. However, the unstable copulation between DP ♂ and C ♀ suggests that some slight behavioural isolation also may be responsible for the fertilization block.

On the other hand, there is no barrier for successful copulation in the reciprocal cross, i.e., between C ♂ and DP ♀ and it is unlikely that mating itself affected the fertilization block. Although no F_1 adult females were produced also from this cross, the increased egg and immature mortality imply that some eggs may have been fertilized but they did not hatch and/or immatures that hatched from the eggs failed to reach adulthood. Fertilization may have enhanced the egg mortality and thus a severe hybrid inviability may be involved in this cross.

The present study reveals that the non-diapausing pear type (NP) is compatible with the citrus type (C), whereas it is completely incompatible with the diapausing pear type (DP). It is known that the NP is quite similar to the C in several aspects: both can

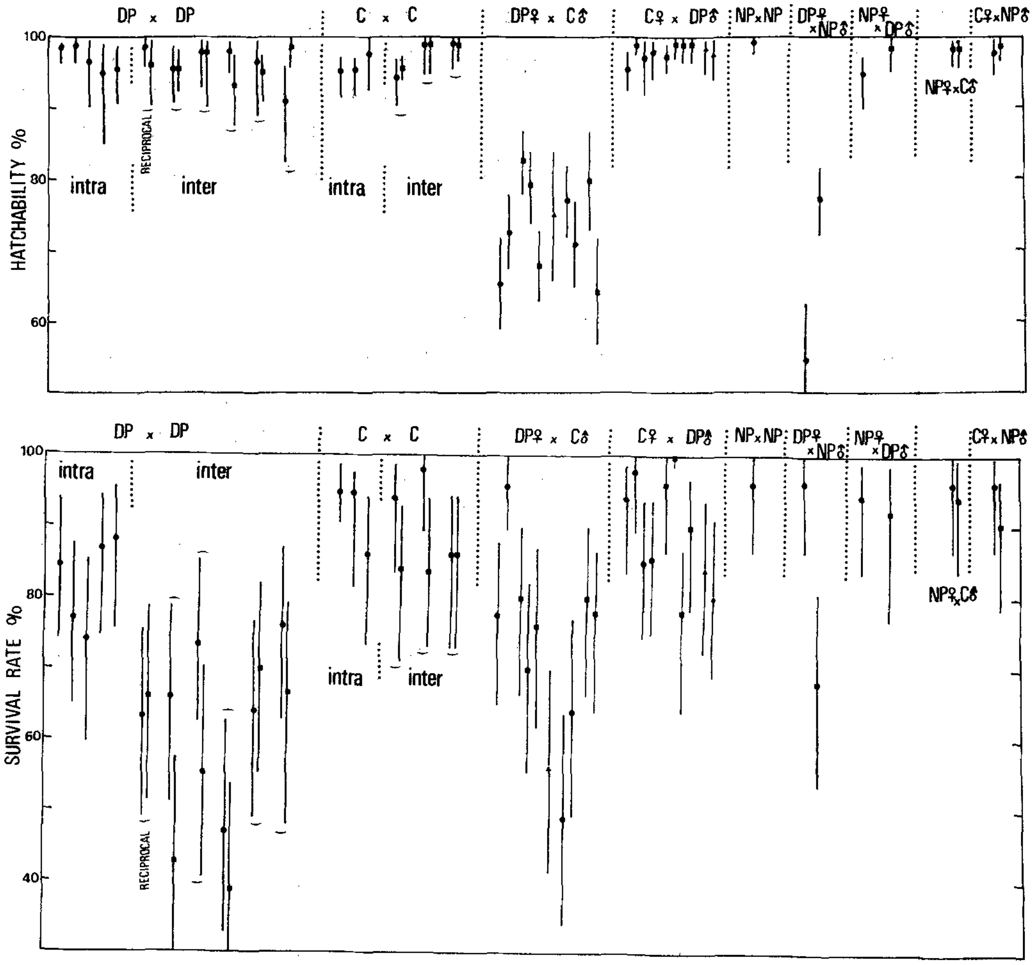

Fig. 2. Summary of the results of the crossing experiments shown in Tables 3 to 7. Upper and lower graphs show the egg hatchability and the survival rate of immature stages, respectively. Vertical lines indicate the 95% confidence interval.

develop and reproduce on citrus (Morimoto and Takafuji, 1983) and the fecundity and egg size are similar to each other (Morimoto and Takafuji, 1983; Shinkaji, 1961a; Takafuji and Fujimoto, unpublished). In addition, populations of the NP do not occur on pear from spring to summer but suddenly increases in number in early autumn in the central or western part of Japan (Takafuji and Morimoto, 1983; Takafuji and Fujimoto, unpublished), suggesting that they may be comprised of the immigrants from other evergreen hosts such as citrus. It remains unclear whether or not the non-diapausing type on pear may be a different one from that occurring on citrus.

Summary

Reproductive compatibility was studied among populations of different types of the citrus red mite, *Panonychus citri* (McGregor), i.e., the diapausing type from pear (DP),

the non-diapausing type from citrus (C) and that from pear (NP).

Copulation was also observed between mates of different types (DP and C). Only in crosses between C ♀ and DP ♂, was copulation occasionally broken off prematurely; duration of copulation varied considerably between pairs and the average duration was much shorter than that between DP ♀ and C ♂ and than that in crosses between mates of the same types.

No F_1 adult females were produced at all from crosses between DP and C, showing that there was a complete reproductive isolation between the two types. There was a significant reciprocal difference in the egg hatchability and survival rate of immatures in the F_1 progeny; mortality in the eggs and that in the immature stage were significantly higher in crosses between DP ♀ and C ♂, as compared to those in the reciprocal cross. This suggested that fertilization may have occurred in the former cross, whereas it seemed that eggs were not fertilized in crosses between the C ♀ and DP ♂.

The NP was compatible with the C, whereas it was completely incompatible with the DP. Thus, there was a complete reproductive incompatibility between the diapausing and non-diapausing type of *P. citri*.

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ミカンハダニの個体群間の reproductive compatibility

高藤晃雄・藤本博明

ミカンハダニ *Panonychus citri* (McGregor) のナシ寄生・休眠タイプ (DP)，カンキツ寄生・非休眠タイプ (C) およびナシ寄生・非休眠タイプ (NP) の間の reproductive compatibility を交配実験によって調べた．

交尾は異なったタイプ間でもみられたが，DP ♂ と C ♀ 間では交尾が中断されるケースがあり，交尾時間にはバラツキが大きく，他の組み合せ（同じタイプ間および C ♂×DP ♀）にくらべて平均交尾時間がはるかに短かった。

DP と C の交配からの F_1 には，どの地域個体群をとっても♀成虫が全く得られず，これらの間には明らかに完全な生殖的隔離がみられた．たゞ F_1 の卵のふ化率および幼若虫生存率には正逆交雑で有意な差がみられ，DP ♀×C ♂ ではふ化率がかなり低くなり，また幼若虫の死亡率も若干高くなった．このことから，この交配からの F_1 卵の一部は受精はしたが，受精卵がふ化しなかったり，ふ化しても生育過程で死亡したことが考えられた．これに対し，C ♀×DP ♂ からの卵は受精しておらず，受精前の隔離があるように思われた．

一方，NP と C は完全に compatible であるのに対し，NP と DP には完全な隔離があった．

このように，ミカンハダニの休眠タイプと非休眠タイプ間には地域を問わず，完全な生殖的隔離がみられた．