Host Plant Preference and Genetic Compatibility of the Kanzawa Spider Mite, *Tetranychus kanzawai* KISHIDA (Acari: Tetranychidae)

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The developmental success and the oviposition of the Kanzawa spider mite, *Tetranychus kanzawai* KISHIDA, on 44 species of plants were studied for four populations collected from tea, pear, hydrangea and kudzu vine. Of the plants tested, 14 were common hosts of the four populations. The tea plant was utilized only by the tea population, and the hydrangea plants only by the pear and hydrangea populations. These three populations could utilize the kerria plant, while the kudzu population could not. In intrapopulation crosses, all populations produced both female and male progeny. Interpopulation crosses among the three (tea, pear and hydrangea) populations were successful. However, female mites of the kudzu population were reproductively incompatible with males from all of the other populations. Thus, it was concluded that *T. kanzawai* consists of the tea-associated, the hydrangea-associated (pear and hydrangea), and the kerria-avoiding (kudzu) populations. In addition, the kudzu population was determined to differ in reproductive traits from the other populations.

Key words: *Tetranychus kanzawai*, host race, host-associated population, reproductive incompatibility, gene flow

INTRODUCTION

The Kanzawa spider mite, *Tetranychus kanzawai* KISHIDA, has been found on a wide range of host plants and is known as one of the most injurious mite species to various agricultural crops (JEPPSON et al., 1975; EHARA and SHINKAJI, 1996). There have been many studies on the ecology and control of this species: e.g., on seasonal fluctuations on tea (OSAKABE, 1967; HAMAMURA, 1986), pear (UCHIDA, 1982), grapevine (INOUE et al., 1986) and eggplant (OHTANI et al., 1991); on biological control (HAMAMURA, 1986; HO, 1990); and on insecticide resistance (KUWAHARA, 1982; MIZUTANI et al., 1988). Because of the paucity of information on the host plants of *T. kanzawai*, it was initially thought that each population should be able to injure not only its own host but also those infested by other populations. However, YAMADA and TSUTSUMI (1990) reported that a hydrangea population could not develop on tea leaves. This suggests that *T. kanzawai* may consist of host races and/or host-associated sibling species.

The host races are defined as conspecific populations that differ genetically in their host affiliations. This is a well-known phenomenon in phytophagous insects and mites (DIEHL and BUSH, 1984; FUTUYMA and PETERSON, 1985; AKIMOTO, 1990; ABE, 1991; GOTOH et al., 1993). Whether putative host-associated populations are really host races depends on the extent of gene flow occurring between them, because in some cases putative host races have

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Table 1. Collections of *Tetranychus kanzawai* used in this study

Population	Locality	Geographic coordinates	Date
Tea (<i>Camellia sinensis</i>)	Kanaya, Shizuoka	34°48'N–138°23'E	May 19, 1993
Japanese pear (<i>Pyrus pyrifolia</i>)	Yachiyo, Chiba	35°55'N–140°04'E	Mar. 16, 1993
Hydrangea (<i>Hydrangea macrophylla</i> var. <i>macrophylla</i>)	Tsukuba, Ibaraki	36°13'N–140°04'E	Mar. 29, 1993
Kudzu vine (<i>Pueraria lobata</i>)	Ami, Ibaraki	36°00'N–140°11'E	Jun. 5, 1993

been found to be completely isolated sibling species with no gene flow (GUTTMAN et al., 1981; FUTUYMA, 1983; MENKEN and ULENBERG, 1987; PASHLEY, 1988). Therefore, cross experiments are essential to affirm the existence of host races in mite species.

In the present study, the host ranges of four *T. kanzawai* populations collected from tea, pear, hydrangea and kudzu vine were examined to clarify whether host-associated populations existed in the polyphagous species. Crossing experiments were then conducted to elucidate whether gene flow occurred between the putative host-associated populations.

MATERIALS AND METHODS

Mites. Table 1 summarizes the four populations used in this study. Laboratory stocks of these populations were maintained on leaf discs (ca. 25 cm²) of the original host plants placed on a water-saturated polyurethane mat in a Petri dish (9 cm diam.). In winter, when Japanese pear, hydrangea and kudzu vine leaves are not available because of complete defoliation, the mites collected from these hosts were reared on the common bean leaves (*Phaseolus vulgaris* L.). All experiments were carried out at 25°C, 60–70% R.H. and LD 16:8.

Developmental success and oviposition on various plants. The host ranges of the four populations were determined by both the survival rate of immatures and the fecundity of females that matured on test plants (KITASHIMA and GOTOH, 1995). Forty-four different plants listed in Table 2 were used for examination. About 10 newly hatched larvae from each population were randomly selected from the stock cultures and placed on each of 6 leaf discs of the test plants. All leaf discs were checked daily to record the number of survivors and their developmental stages until they reached adulthood. Females in the teleiochrysalis stage on the test plants were individually transferred onto new leaf discs (ca. 4 cm²) and kept with an adult male for mating. After initiating oviposition, each female was allowed to lay eggs for 5 days on leaf discs, and then the number of eggs deposited was recorded.

Various criteria have been in use to determine host plants in spider mites (UCHIDA, 1982; ASHIHARA, 1987; GOTOH and NOGUCHI, 1990; OSAKABE, 1993; KITASHIMA and GOTOH, 1995), which accounts for the difficulty in comparing host ranges among conspecific populations or among populations of closely related species. It is desirable to unify the criterion. In the present study, we used a simple criterion whereby a plant is determined as a host plant when the developmental rate is $\geq 70\%$ and when the total number of eggs laid during the first 5 days of the oviposition period is ≥ 15 .

Crossing. To examine reproductive compatibility, crosses among the four populations

were made over two generations. Crossing experiments were carried out on the common bean leaves. Females in the teleiochrysalis stage were obtained from each stock culture, and each female was transferred onto a small leaf disc (ca. 4 cm²) together with a male adult from the same or different population. Males were removed 2 days after the females matured. After the start of oviposition, each female was allowed to lay eggs for 5 days and was then removed. Eggs on leaf discs were checked every day to determine the hatchability, survival rate and sex ratio. Female progeny (F₁) were also mated with a male obtained from each of the parent cultures. The same procedure was followed for the next generation. Arcsin-transformed values were used for analyzing the sex ratios.

RESULTS

Developmental success and oviposition on various plants

Table 2 shows the developmental success and the total number of eggs laid by a female on 44 test plants in the four populations of *T. kanzawai*. Developmental success and oviposition values satisfying the criteria are denoted in Table 2 by asterisks and daggers, respectively. Fourteen species in five families were found to be host plants for all four populations. These were *Hydrangea paniculata*, *Fragaria* × *ananassa*, *Prunus mume*, *P. persica*, *P. × yedoensis*, *Pyrus pyrifolia*, *Rosa wichuraiana*, *Phaseolus vulgaris*, *Pueraria lobata*, *Robinia pseudo-acasia*, *Trifolium pratense*, *Ficus carica*, *Morus bombycis* and *Clerodendron trichotomum* (Table 2). No other plants served as a host for the kudzu population.

Theaceous plants were considered non-suitable host trees for the mites, and only the tea plant was a suitable host for the mites collected from tea plants (Table 2). About 30% of the pear population larvae reached maturity and oviposited on tea plants, but the developmental rate was not increased in the next generation (down to 27.0%).

The pear and hydrangea populations could develop and oviposit successfully on *Hydrangea macrophylla* var. *macrophylla*, *H. macrophylla* f. *normalis* and *H. macrophylla* var. *thunbergii*, whereas the tea and kudzu populations could not (Table 2).

Kerria japonica was a host plant for the tea, pear and hydrangea populations, but the kudzu population could not survive more than 5 days on this plant (Table 2). *Malus domestica* and *Callicarpa japonica* were observed as host plants for the tea and hydrangea populations, respectively (Table 2).

In summary, 21 out of 44 plant species tested appeared to be host plants of at least one of the four populations of *T. kanzawai*. The host ranges were different among the four populations; the hydrangea populations had the widest range of host plants (19 species), followed by the pear population (18 species), the tea population (17 species) and the kudzu population (14 species).

Crosses between the four populations

Table 3 shows the results of crosses among the four populations of *T. kanzawai*. In the intrapopulation crosses, hatchability of eggs was greater than 94.9% on average, with a range from 82.7 to 100%, and the percentage of females was more than 78%, ranging from 71.8 to 89.7%. The survival rates in the juvenile stages were similar among these crosses.

In the reciprocal crosses between the tea, pear and hydrangea populations, the hatchability, survival rate of immatures and sex ratio did not significantly differ from those in the intrapopulation crosses (TUKEY-HSD test, $p > 0.05$; Table 3).

The cross between the tea population females and the kudzu population males pro-

Table 2. Developmental success of four *T. kanzuwai* populations from larva to adult and the number of eggs laid during the first 5 days of the oviposition period on various plants

Test plant ^a	% Maturity in the population ^b				Total no. of eggs/♀ in the population			
	Tea	Pear	Hydrangea	Kudzu	Tea	Pear	Hydrangea	Kudzu
Theaceae								
<i>Camellia hiemalis</i>	0	0	0	0	— ^c	—	—	—
<i>C. japonica</i>	0	0	0	0	—	—	—	—
<i>C. japonica</i> var. <i>rosacea</i>	0	0	0	0	—	—	—	—
<i>C. sasanqua</i>	0	0	0	0	—	—	—	—
<i>C. sinensis</i> ⁺	96.7*	29.1	0	0	20.7† (18) ^d	13.5 (10)	—	—
<i>Cleyera japonica</i>	0	0	0	0	—	—	—	—
<i>Eurya japonica</i>	0	0	0	0	—	—	—	—
<i>Stewartia monadelphica</i>	0	0	0	0	—	—	—	—
<i>S. pseudo-camellia</i>	0	0	0	0	—	—	—	—
<i>Ternstroemia gymnanthera</i>	0	0	0	0	—	—	—	—
Saxifragaceae								
<i>Deutzia crenata</i>	80.0*	78.3*	75.0*	78.3*	9.3 (16)	8.7 (17)	9.4 (15)	8.6 (16)
<i>Hydrangea hirta</i>	93.3*	93.3*	98.3*	91.7*	5.7 (11)	6.3 (14)	4.7 (12)	3.8 (17)
<i>H. macrophylla</i> var. <i>macrophylla</i>	0	80.0*	98.3*	0	—	20.8† (18)	22.4† (16)	—
<i>H. macrophylla</i> var. <i>acuminata</i>	0	67.4	90.0*	0	—	15.4† (13)	14.2 (16)	—
<i>H. macrophylla</i> f. <i>normalis</i>	14.0	85.0*	81.7*	13.8	—	29.4† (17)	20.7† (15)	—
<i>H. macrophylla</i> var. <i>thunbergii</i>	0	96.7*	98.3*	0	—	23.5† (17)	28.1† (16)	—
<i>H. paniculata</i>	80.0*	85.0*	95.0*	85.0*	20.5† (14)	22.9† (17)	23.2† (17)	22.6† (16)
<i>Saxifraga stolonifera</i>	0	0	0	0	—	—	—	—
Rosaceae								
<i>Amelanchier canadensis</i>	75.0*	80.0*	95.2*	91.7*	7.8 (16)	11.6 (18)	9.8 (12)	10.6 (18)
<i>Crataegus laevigata</i>	51.7	61.7	55.0	71.7*	6.7 (12)	5.0 (11)	5.4 (15)	6.6 (14)
<i>Eriobotrya japonica</i>	0	0	0	0	—	—	—	—
<i>Fragaria</i> × <i>ananassa</i> ⁺	93.1*	81.7*	91.7*	84.8*	20.0† (16)	27.9† (17)	23.9† (15)	26.7† (15)
<i>Kerria japonica</i>	88.3*	91.7*	88.3*	0	30.3† (16)	30.6† (16)	30.7† (17)	—
<i>Malus domestica</i> ⁺	78.3*	91.7*	87.7*	88.3*	15.9† (15)	14.2 (13)	14.9 (17)	14.3 (16)
<i>Photinia glabra</i>	0	0	0	0	—	—	—	—
<i>Prunus mume</i>	90.0*	95.0*	91.7*	90.0*	24.9† (17)	29.9† (17)	28.9† (17)	27.7† (17)
<i>P. persica</i>	96.6*	81.5*	93.2*	100*	21.5† (16)	23.8† (18)	25.4† (16)	22.2† (16)

<i>P. × yedoensis</i>	91.7*	90.0*	96.7*	95.0*	19.5† (17)	16.7† (16)	18.7† (17)	18.1† (18)
<i>Pyrus pyrifolia</i> var. <i>culta</i> ^a	80.0*	88.3*	88.0*	86.7*	37.0† (12)	37.4† (14)	31.5† (17)	30.9† (16)
<i>Rhaphiolepis umbellata</i>	0	0	0	0	—	—	—	—
<i>Rosa hirtula</i>	0	0	0	0	—	—	—	—
<i>R. wichuraiana</i>	96.7*	96.7*	95.0*	96.7*	26.0† (14)	26.4† (14)	24.7† (14)	25.1† (14)
<i>Sorbus commixta</i>	61.7	56.0	56.7	58.0	11.3 (15)	9.1 (17)	8.3 (14)	11.6 (18)
<i>Stephanandra incisa</i>	45.0	50.0	56.7	66.7	3.9 (13)	4.9 (18)	4.2 (17)	8.9 (18)
Leguminosae								
<i>Phaseolus vulgaris</i> ^a	91.7*	87.5*	88.3*	91.7*	39.5† (12)	46.6† (12)	46.4† (12)	47.3† (13)
<i>Pueraria lobata</i>	95.0*	91.7*	91.7*	98.5*	40.8† (15)	38.5† (17)	43.9† (16)	48.5† (18)
<i>Robinia pseudo-acacia</i>	78.3*	77.8*	85.3*	91.7*	33.5† (13)	36.3† (16)	38.4† (14)	39.5† (13)
<i>Trifolium pratense</i>	93.3*	91.7*	91.7*	91.4*	20.0† (12)	24.3† (15)	23.8† (17)	20.0† (14)
<i>Wisteria floribunda</i>	76.7*	77.8*	76.7*	86.7*	1.7 (7)	2.4 (7)	2.3 (7)	3.2 (9)
Moraceae								
<i>Broussonetia kazinoki</i>	85.0*	81.7*	86.7*	85.0*	11.7 (18)	10.9 (17)	11.4 (18)	11.1 (14)
<i>Ficus carica</i>	90.0*	91.7*	98.3*	96.7*	38.9† (18)	39.4† (17)	36.4† (16)	44.2† (15)
<i>Morus bombycis</i> ^a	95.0*	98.3*	98.2*	98.3*	41.0† (23)	44.5† (28)	37.1† (24)	43.9† (34)
Verbenaceae								
<i>Callicarpa japonica</i>	91.4*	95.0*	93.3*	88.3*	12.7 (18)	14.2 (18)	16.0† (18)	13.7 (18)
<i>Clerodendron trichotomum</i>	85.1*	95.0*	81.4*	93.3*	30.9† (17)	29.7† (17)	32.2† (18)	29.0† (16)

^a The nomenclature of the plants is primarily according to KUROKAWA (1988). Plus indicates nomenclature according to ONO et al. (1989).

^b Average of 6 replicates. Each replicate consisted of 9 to 12 individuals (58 to 63 larvae in total). Asterisks indicate values above 70.0%.

^c —: Not tested.

^d Numbers in parentheses indicate the number of females tested, and daggers the values above 15.0 eggs.

Table 3. Number of eggs laid during the first 5 days of the oviposition period, hatchability, survival rate of immatures and sex ratio in the F₁ progeny from crosses among four populations of *T. kanzawai*

Cross			<i>n</i> ^a	No. of eggs/♀ ^b	Hatchability (%) ^b	Survival rate (%) in immature stage ^b	Sex ratio (%) (♀/(♀ + ♂)) ^b
Female	×	Male					
Tea		Tea	23	41.0 ± 1.19	94.9 ± 1.29	96.1 ± 0.77	80.8 ± 1.03
Pear		Pear	28	44.5 ± 1.14	99.5 ± 0.30	98.2 ± 0.47	84.8 ± 0.58
Hydrangea		Hydrangea	20	38.8 ± 0.79	98.3 ± 0.54	98.6 ± 0.39	78.3 ± 0.55
Kudzu		Kudzu	34	43.9 ± 1.22	99.2 ± 0.36	97.8 ± 0.65	82.7 ± 0.46
Tea		Pear	22	40.6 ± 0.90	99.7 ± 0.19	99.2 ± 0.25	80.4 ± 0.67
Tea		Hydrangea	23	32.8 ± 1.18	98.6 ± 0.64	95.2 ± 1.06	80.7 ± 1.34
Tea		Kudzu	21	37.3 ± 0.99	98.8 ± 0.50	99.1 ± 0.28	72.6 ± 1.32
Pear		Tea	24	28.6 ± 1.01	99.6 ± 0.37	95.9 ± 0.70	79.0 ± 1.02
Pear		Hydrangea	33	35.2 ± 1.34	99.1 ± 0.46	96.5 ± 0.60	79.7 ± 0.82
Pear		Kudzu	24	42.1 ± 0.93	99.1 ± 0.33	99.7 ± 0.16	20.6 ± 5.66
Hydrangea		Tea	34	39.8 ± 1.01	99.3 ± 0.32	98.3 ± 0.38	80.9 ± 0.72
Hydrangea		Pear	30	37.0 ± 1.12	99.5 ± 0.23	96.8 ± 0.71	80.5 ± 0.77
Hydrangea		Kudzu	23	33.6 ± 1.45	97.6 ± 0.76	99.1 ± 0.36	18.3 ± 4.20
Kudzu		Tea	19	36.6 ± 0.80	99.1 ± 0.51	99.4 ± 0.41	0
Kudzu		Pear	32	40.1 ± 0.78	99.1 ± 0.31	97.8 ± 0.74	0
Kudzu		Hydrangea	31	49.1 ± 1.11	99.3 ± 0.29	97.5 ± 0.74	0

^a Number of females tested.^b Mean ± S.E.

duced normal progeny with a female-biased sex ratio (Table 3). However, crosses between either the pear or hydrangea females and the kudzu males resulted in male-biased sex ratios (TUKEY test, $p < 0.05$). In crosses between the kudzu females and the tea, pear or hydrangea males, no female adults were produced, although the hatchability and survival rates of juveniles were similar ($p > 0.05$) to those in the intrapopulation crosses.

When F₁ females obtained from crosses among the tea, pear and hydrangea populations were mated with males from each of their parent populations, no significant difference in sex ratio was observed as compared with those in the intrapopulation crosses (TUKEY test, $p > 0.05$; Table 4). On the other hand, a drastic reduction in hatchability was observed when F₁ females that originated from crosses between kudzu males and tea, pear or hydrangea females, were mated with males from either of the F₁ parent populations. There was no change in the sex ratio of F₂ obtained from crosses between F₁ females and males from the paternal (kudzu) population (TUKEY test, $p > 0.05$), except for the (hydrangea ♀ × kudzu ♂) × kudzu ♂ cross ($p < 0.05$). On the other hand, only male adults were produced in crosses between F₁ females and males from the maternal (tea, pear and hydrangea) populations. These results clearly indicate that there was a genetic incompatibility between the kudzu population and the tea, pear or hydrangea populations, which was particularly notable in unidirectional crosses.

DISCUSSION

The present study shows that the four populations of *T. kanzawai* tested have different ranges of host specificity, but 14 plants (from five families) of 44 tested plants are common hosts of the four populations. Of these, *Hydrangea paniculata*, *Prunus mume*, *Rosa wichuraiana*,

Table 4. Number of eggs laid during the first 5 days of the oviposition period, hatchability, survival rate of immatures and sex ratio in the F₂ progeny from crosses among four populations of *T. kanzawai*

Cross			<i>n</i> ^a	Total no. of eggs/♀ ^b	Hatchability (%) ^b	Survival rate (%) in immature stage ^b	Sex ratio (%) (♀/(♀ + ♂)) ^b
Female	×	Male					
(Tea × Pear) ^c		Tea	23	35.6 ± 0.89	99.2 ± 0.32	99.5 ± 0.24	71.8 ± 1.31
(Tea × Pear)		Pear	24	41.0 ± 0.98	99.4 ± 0.27	99.7 ± 0.19	71.9 ± 1.37
(Tea × Hydrangea)		Tea	23	37.2 ± 0.79	99.0 ± 0.38	99.8 ± 0.16	76.6 ± 0.98
(Tea × Hydrangea)		Hydrangea	23	39.4 ± 0.64	99.5 ± 0.22	99.2 ± 0.33	71.7 ± 1.12
(Pear × Tea)		Pear	29	44.8 ± 1.45	99.1 ± 0.47	90.8 ± 1.05	79.4 ± 1.12
(Pear × Tea)		Tea	21	42.6 ± 0.84	99.2 ± 0.34	99.4 ± 0.27	72.2 ± 1.10
(Pear × Hydrangea)		Pear	28	52.4 ± 1.40	99.1 ± 0.34	91.8 ± 0.88	80.6 ± 1.27
(Pear × Hydrangea)		Hydrangea	22	41.2 ± 0.79	99.2 ± 0.32	99.4 ± 0.29	68.7 ± 0.75
(Hydrangea × Tea)		Hydrangea	21	34.9 ± 1.00	99.0 ± 0.44	99.4 ± 0.26	75.8 ± 1.05
(Hydrangea × Tea)		Tea	23	42.0 ± 0.77	99.2 ± 0.38	99.3 ± 0.24	69.3 ± 0.90
(Hydrangea × Pear)		Hydrangea	27	49.2 ± 1.18	98.8 ± 0.40	91.2 ± 0.88	79.5 ± 0.87
(Hydrangea × Pear)		Pear	23	39.5 ± 1.02	98.8 ± 0.51	99.4 ± 0.30	69.2 ± 1.11
(Tea × Kudzu)		Kudzu	20	33.4 ± 1.02	48.0 ± 3.17	98.1 ± 0.69	65.9 ± 2.24
(Tea × Kudzu)		Tea	22	38.9 ± 0.79	35.8 ± 3.66	99.0 ± 0.46	0
(Pear × Kudzu)		Kudzu	20	36.8 ± 2.19	65.9 ± 3.53	88.5 ± 1.88	69.9 ± 2.92
(Pear × Kudzu)		Pear	18	33.7 ± 1.49	50.7 ± 4.37	91.8 ± 1.93	0
(Hydrangea × Kudzu)		Kudzu	22	31.6 ± 1.75	46.8 ± 2.96	94.7 ± 1.23	50.4 ± 4.84
(Hydrangea × Kudzu)		Hydrangea	21	27.1 ± 1.47	40.4 ± 3.88	92.3 ± 2.01	0

^a Number of females tested.^b Mean ± S.E.^c Female parent × male parent.

Ficus carica and *Callicarpa japonica* have not previously been recorded as host plants. It was also determined that *T. kanzawai* consisted of the tea-associated, the hydrangea-associated (pear and hydrangea), and the kerria-avoiding (kudzu) populations. As gene flow between the tea- and the hydrangea-associated populations was observed, these populations can be considered as host races, i.e., the tea race for the tea population, and the hydrangea race for both the pear and hydrangea populations.

The present results indicate that the tea, pear and hydrangea populations are reproductively compatible with one another, while the kudzu population is unidirectionally incompatible with other populations. Reproductive incompatibility between conspecific populations originating from different plants or localities has been found in the two-spotted spider mite, *Tetranychus urticae* KOCH (DE BOER, 1982 a, b; GOTOH et al., 1993; GOTOH and TOKIOKA, 1996), and *T. quercivorus* EHARA et GOTOH (GOTOH et al., 1995). The incompatibility observed in *T. urticae* and *T. quercivorus* mainly occurred by nucleus-cytoplasm interactions, resulting in a much lower hatchability and a male-biased sex ratio (FRY, 1989; GOTOH et al., 1995). This feature is explained by the high mortality of fertilized eggs destined to become females. In contrast, the incompatibility in *T. kanzawai* occurred by the high hatchability of eggs without female progeny, which is due to failure in unidirectional fertilization. Thus, the cause of cross incompatibility in *T. kanzawai* differs from that in *T. urticae* and *T. quercivorus*. Crossing experiments after the third generation are required to determine how incompatibility is brought about through filial generations.

The present study shows that the kudzu population is genetically different from those

of the other three populations in host range and cross incompatibility. It will be necessary to determine how and to what extent genetic differences exist among *T. kanzawai* populations on various host plants.

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