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## Host race formation in *Tetranychus urticae*: genetic differentiation, host plant preference, and mate choice in a tomato and a cucumber strain

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### Abstract

The two-spotted spider mite, *Tetranychus urticae* Koch, occurs in two colour forms in greenhouses in the Netherlands: a red form on tomato and a green form on cucumber. The evolutionary status of these strains was analysed by studying genetic differentiation, host plant preference, and mate choice. Males of the tomato strain preferred the female (30 h-old) teleiochrysales from the same strain to those of the cucumber strain, independent of the host plants (tomato, cucumber, bean) on which the teleiochrysales were placed. In contrast, males of the cucumber strain were not selective. In a Y-tube olfactometer, females of the cucumber strain were not responsive to host plant volatiles alone. However, in two-choice disc experiments, where females were exposed to both volatile and contact cues, they settled on cucumber leaves in preference to tomato leaves. Females of the tomato strain preferred the odour of tomato leaves and settled on tomato leaves in preference to cucumber leaves. These experimental results provide the first evidence for (1) host-plant independent mate selection in male spider mites and (2) olfactory discrimination between host plants in female spider mites.

Electrophoretic analysis showed much genetic differentiation at the phosphoglucose isomerase locus. The cucumber strain showed large variation with 5 alleles, whereas the tomato strain was fixed for the most common allele of the cucumber strain.

The results suggest that the two strains represent host races. We hypothesize that the tomato strain has originated from the cucumber strain because (1) tomato represents a more hostile host plant to spider mites (due to toxic compounds and glandular hairs) and (2) the tomato strain is genetically impoverished suggesting that it passed through one or more bottlenecks.

### Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) has been reported from a wide range of host plants and it is an important pest of many agricultural crops (Helle & Sabelis, 1985). By studying colonization success on various marginal host plants, Gould

(1979) and Fry (1989) demonstrated its ability to adapt to new host plants. This suggests either considerable phenotypic plasticity or genetic variability in the source population. Whether this colonization success leads to species-wide polyphagy or the formation of host races (Diehl & Bush, 1984) is unknown. As evidence has accumulated over the past 15 years that host race formation is

theoretically likely to occur (Tauber & Tauber, 1989), we are now much in need of experimental evidence (Feder *et al.*, 1990; Menken *et al.*, 1992). In this paper we will address this question for the particular case of two hybridizable strains of *T. urticae* colonizing greenhouse cucumber and tomato (often referred to as the green and the red form; Dupont, 1979; De Boer, 1985).

There are various reasons why this model system is very suitable for addressing the above-mentioned question. First, in the Netherlands cucumber and tomato are grown either alternately or simultaneously in the same greenhouse complex, making host plant shifts in the spider mite population likely to occur. Second, greenhouses in the Netherlands have been shown to be closed systems, as indicated by studies of pesticide resistance patterns found in individual greenhouses (Overmeer *et al.*, 1975). These patterns appeared to be stable and specific, even for pesticides that were out of use for 5–10 years. A third reason to select this model system is that tomato (cv 'Money-maker') and cucumber (cv 'Turbo') differ largely in suitability as a host for *T. urticae*. This difference is, amongst other things, manifested by the presence of glandular hairs on tomato, leading to high spider mite mortality due to entrapment and intoxication (Carter & Snyder, 1985; Snyder & Carter, 1985; Duffey, 1986; van Haren *et al.*, 1987). Cucumber does not have such hairs and seems to be a host plant on which spider mite populations thrive. Hence, given the differential host plant suitability and the isolation of greenhouse populations, spider mites face severe selection when colonizing the crop planted in a particular greenhouse. The fourth reason relates to spider mite biology, as this phytophagous mite has a generation time on bean and cucumber of only 11 days at 25 °C and a high fecundity, making it amenable for an experimental approach of selection processes.

To test the hypothesis that successful colonization has resulted in host race formation the following characteristics of the two strains have been assessed: (1) host plant preference of adult females (measured in Y-tube olfactometer and two-choice disc experiments), (2) mate choice of

adult males (measured as preferential guarding, when offered a choice between the last moulting stages of the females from each of both host plants), (3) electrophoretic determination of the genetic composition of the two strains.

## Materials and methods

Two strains of *T. urticae* were used: one was obtained from tomato, *Solanum lycopersicum* L. (tomato strain), obtained from the Glasshouse Crops Research and Experiment Station at Naaldwijk and the other from cucumber, *Cucumis sativus* L. (cucumber strain), obtained from the (former) Institute for Horticultural Plant Breeding at Wageningen. Both strains were reared for many years on these respective host plants. Stock cultures were transferred to and maintained on common bean leaves, *Phaseolus vulgaris* L., held on wet cotton balls at 23–24 °C, 65% R.H. and 16:8 LD. This host plant was chosen for practical reasons. To maintain selection for adaptations to tomato as a host plant, mites of the tomato strain were transferred from bean leaves to tomato leaves (cv. 'Money-maker') every two months, where they were maintained for three weeks and then returned to bean leaves. All experiments were carried out at 23–24 °C.

To test whether gene flow between the two strains is possible, interstrain crosses were carried out. This was done to validate the results of Dupont (1979) who found that two other strains of the green and red form of *T. urticae* readily hybridized, as evidenced by the production of viable eggs by F1 females. Using virtually the same experimental procedure we tested not only for production of viable eggs in F2, but we also reared the F2 eggs until adulthood and checked whether both sexes were present. The latter check is informative to rule out the possibility of all-male offspring in the F2, which would be the case if the eggs of F1 females of an arrhenotokous species, such as *T. urticae*, were unfertilized.

To examine whether males prefer females originating from the same strain to those from the other strain, two teleiochrysalis females were

placed next to each other on a leaf disc (12 mm in diameter) and then one male was released on it. During half an hour the mites were observed every 5 min to determine whether males tended females. When males had continued their guarding behaviour for 10 min they were considered to have made a choice. As the attractivity depends on their age (Everson & Addicott, 1982), the teleiochrysales were precisely synchronized (preliminary experiments showed that there was no between-strain difference in duration of the teleiochrysalis stage); 30 h- and 3 h-old teleiochrysalis females from each strain were used. The Y-tube olfactometer was used to examine the response of females to odour coming from tomato (cv 'Money-maker'), cucumber (cv 'Turbo') and clean air (Sabelis & Van de Baan, 1983; Janssen *et al.*, 1990). Compared to the set-up used by these authors one important modification had been made with respect to the odour source containers. These consisted of 48 × 33 × 40 cm PVC boxes that were connected to the arms of the olfactometer. As odour sources 1 to 3 potted seedlings of tomato and cucumber were used. The wind speed was 0.6 m/s in each arm. Adult females were introduced individually on the iron wire. After each trial, the iron wire was cleaned by cotton with 70% ethanol solution to remove silk produced by spider mites and dried for a few minutes. The two odour sources were interchanged with respect to the connections to the Y-tube after each series of

5 replicates; the maximum experimental time per female was 5 min.

To further investigate host plant preference of the mites, females were individually introduced on a thin piece of wood (8–10 mm long) interconnecting two leaf discs (15 mm diameter) that originate from either tomato (cv 'Money-maker'), cucumber (cv 'Turbo') or common bean. The wooden bridge was coated with hydrophobic wax. The disc where the mites had settled and the number of eggs laid were recorded after 24 h.

For electrophoretic analysis, only adult females were used. Live females were individually homogenized in 5 µl distilled water. Each homogenized sample was absorbed on Whatman 3MM paper wicks and applied to 12% (w/v) Connaught starch gels. Electrophoresis and staining procedures followed Menken (1982). The following buffer system was used: Running buffer, 0.223M trizma, 0.086M citric acid, pH 6.3; Gel buffer, 0.008M trizma, 0.003M citric acid, pH 6.7. Preparations were analysed at the phosphoglucose isomerase (E.C. 5.3.1.9) locus, following standard staining procedures.

## Results

*Interstrain crosses.* As shown in Table 1, mature offspring of both sexes were obtained from both interstrain crosses. Mortality in the F1 of the in-

Table 1. Crossing between the tomato and cucumber strain of *T. urticae*

Generation:		F <sub>1</sub>						F <sub>2</sub>			
F <sub>0</sub>		Number of		Mortality (%)	Number of		Mortality (%)				
♀♀	X	♂♂	♀♀		eggs	♀♀		♂♂			
Tomato	Tomato	21	137	55	50	23	24	205	53	130	11
	Cucumber	22	192	16	142	18	13	156	11	10	87
	None	21	199	0	152	24					
Cucumber	Tomato	20	171	29	92	29	19	146	4	23	82
	Cucumber	21	258	89	48	47	22	204	116	32	27
	None	20	156	0	105	33					

Table 2. Response of *T. urticae* males of the tomato and cucumber strain when offered a choice between 30 h-old teleiochrysalis females of the tomato strain versus the cucumber strain. The numbers represent the sum of replicate experiments carried out over a period of 3–5 days

Strain of males	No. choices			Ratio <sup>b</sup>	P <sup>c</sup>
	Tomato strain females	Cucumber strain females	O <sup>a</sup>		
On tomato leaves					
Tomato	29	12	48	0.71	0.015
Cucumber	24	14	57	0.63	0.14
On cucumber leaves					
Tomato	58	22	60	0.73	<10 <sup>-4</sup>
Cucumber	34	35	61	0.49	>0.95
On bean leaves					
Tomato	29	12	44	0.71	0.015
Cucumber	25	26	34	0.49	>0.95

<sup>a</sup> O represents the numbers of males that did not choose either female teleiochrysalis within 30 minutes.

<sup>b</sup> The ratio is calculated as tomato/(tomato + cucumber).

<sup>c</sup> P is the critical value of the binomial test on the numbers choosing either the tomato or the cucumber strain when the probability of either result is 0.5.

terstrain crosses did not differ from the mortality in the F1 of both within-strain crosses. However, mortality in the F2 of the interstrain crosses was much higher (c. 85% vs 25%). Such increased mortality in the F2 is a general phenomenon for interstrain crosses in *T. urticae* (De Boer, 1985). Hence, we conclude that both strains belong to the same species, in line with earlier conclusions of Dupont (1979).

*Mate choice experiments.* Table 2 shows the numbers of males that chose 30h-old teleiochrysalis of either the tomato or cucumber strain when observed on tomato, cucumber and bean leaves. On leaves of each host plant, males of the tomato strain tended to choose teleiochrysalis of the same strain rather than those of the cucumber strain, while males of the cucumber strain showed no significant preference.

Table 3 shows the number of males that chose either 30 h- or 3 h-old teleiochrysalis females originating from the tomato and cucumber strains when observed on bean leaves. Males of the tomato strain preferred 30 h-old teleiochrysalis to 3 h-old ones in all cases. When offered a choice

Table 3. Response of *T. urticae* males of the tomato and cucumber strain on bean leaves when offered a choice between 30 h versus 3 h-old teleiochrysalis females of either strain. The numbers represent the sum of replicate experiments, carried out over a period of 2–4 days

Strain of males	No. choices				O <sup>a</sup>	Ratio <sup>b</sup>	P <sup>c</sup>
	Tomato females		Cucumber females				
	30 h	3 h	30 h	3 h			
Tomato	58	10	– <sup>d</sup>	–	52	0.85	<10 <sup>-6</sup>
Tomato	29	–	–	0	25	1.0	<10 <sup>-6</sup>
Tomato	–	13	23	–	23	0.64	0.13
Cucumber	–	–	45	6	69	0.88	<10 <sup>-6</sup>
Cucumber	29	–	–	5	25	0.85	0.004
Cucumber	–	14	20	–	22	0.59	0.39

<sup>a</sup> O represents the numbers of males that did not choose either female within 30 min.

<sup>b</sup> The ratio is calculated as 30 h/(30 h + 3 h).

<sup>3</sup> P is the critical value of the binomial test on numbers choosing 30 h versus 3 h teleiochrysalis females when the probability of either result is 0.5.

<sup>d</sup> Not included in two-choice test.

Table 4. Response of the tomato and cucumber strains of *T. urticae* females to odour coming from clean tomato versus clean cucumber plants in a Y-tube olfactometer. The numbers represent the sum of five replicate experiments

Strain of females	No. choices			Ratio <sup>b</sup>	P <sup>c</sup>
	Tomato plant	Cucumber plant	O <sup>a</sup>		
Tomato	74	52	31	0.58	0.06
Cucumber	49	56	30	0.47	0.56

<sup>a</sup> O represents the numbers of females that did not reach the end of one of the arms during the experiments.

<sup>b</sup> The ratio is calculated as tomato/(tomato + cucumber).

<sup>c</sup> P is the critical value of the binomial test on numbers choosing tomato plants versus cucumber plants when the probability of either result is 0.5.

between 30 h-old teleiochrysales of the tomato strain versus the 3 h-old teleiochrysales of the cucumber strain no male chose the latter. However, males showed no significant preference when 3 h-old tomato and 30 h-old cucumber teleiochrysales were offered.

In the cucumber strain, again males chose 30 h-old rather than 3 h-old teleiochrysales. The same is true for the choice between 30 h-old teleiochrysales of the tomato strain and 3 h-old ones of the cucumber strain. However, no signif-

icant preference was found between 3 h-old teleiochrysales of the tomato strain and 30 h-old teleiochrysales of the cucumber strain.

The most important conclusion from the experiments with 30 h-old teleiochrysales is that males of the tomato strain preferentially guard (and probably also mate with) teleiochrysales of their own strain, whereas males of the cucumber strain do not show a significant preference.

*Host plant preference.* In Y-tube olfactometer experiments, females of the tomato strain tended to prefer odour coming from tomato plants to odour coming from cucumber plants (note that the results border significance), whereas females of the cucumber strain were not selective (Table 4).

In two-choice disc experiments, females of the tomato strain settled on tomato leaves when offered a choice between tomato and cucumber, whereas females of the cucumber strain showed a significant preference for cucumber (Table 5). To investigate possible effects, such as conditioning and selection, of the host plant used for rearing in the laboratory (bean), an extra series of experiments with both strains was done in which bean was offered as an alternative to either tomato or cucumber. These experiments showed that bean was generally less preferred, except for

Table 5. Colonization of *T. urticae* females of the tomato and cucumber strains on different leaves in two-choice disc experiments. The numbers represent the sum of 2-4 replicate experiments

Strain of females	No. females settled on				Ratio <sup>b</sup>	P <sup>c</sup>
	Tomato disc	Cucumber disc	Bean disc	O <sup>a</sup>		
Tomato	42	10	- <sup>d</sup>	4	0.81	$9 \times 10^{-6}$
Tomato	38	-	15	3	0.72	0.002
Tomato	-	36	16	4	0.69	0.008
Cucumber	28	52	-	4	0.35	0.01
Cucumber	29	-	47	8	0.38	0.05
Cucumber	-	72	53	15	0.58	0.11

<sup>a</sup> O represents numbers of females that drowned or moved to another leaf during the experiments.

<sup>b</sup> The ratio is calculated as the left figure over the sum for the two host plants.

<sup>c</sup> P is the critical value of the binomial test on numbers choosing tomato plants versus cucumber plants when the probability of either result is 0.5.

<sup>d</sup> Not included in two-choice test.

Table 6. Allozyme frequency distribution at the *Pgi* locus in the tomato and cucumber strain of *T. urticae*<sup>a</sup>

<i>Pgi</i> locus	Cucumber strain	Tomato strain
96	0.128	
100	0.436	1.0
102	0.102	
106	0.308	
110	0.026	

<sup>a</sup> Numbers of individuals tested were 39 for the cucumber strain and 60 for the tomato strain.

the cucumber strain which settled on bean in preference to tomato.

*Genetic differentiation.* Genetic interpretation was inferred from the banding patterns, typical for a dimeric enzyme, and the generally good agreement with Hardy-Weinberg proportions.

The cucumber strain contained 5 alleles at the *Pgi* locus, whereas the tomato strain was fixed for the most common allele in the cucumber strain (*Pgi-100*; Table 6). The number of alleles in the cucumber strain represents a conservative estimate. Allele 100 is probably heterogeneous; the bands occurred very close to one another and resolution differed somewhat among gels so that we decided not to split it any further. The individuals from tomato did not show any heterogeneity.

## Discussion

We conclude that the cucumber and tomato strain of *T. urticae* are biologically distinct in that the tomato strain prefers tomato plants over cucumber plants and mates assortatively, whereas the cucumber strain prefers cucumber plants and does not exhibit assortative mating. Two evolutionary scenarios are conceivable. First, the differences between the strains have resulted from initial genetic differences between the colonizing populations, unrelated to the host plant to be colonized. Second, the colonizers originated from one interbreeding population, but especially to-

mato acted as the major selective factor leading to the observed population differentiation. We suggest that a host shift has occurred in the past from cucumber to tomato. This is because, as argued earlier, tomato represents a hostile food plant. Initial colonization of tomato by a strain from a favourable host such as lima bean is generally known to be associated with high juvenile mortality and low fecundity (e.g. Fry, 1989). Thus, the colonizing population is likely to experience a bottleneck, resulting in a reduced number of alleles and in a lower amount of overall heterozygosity (Nei *et al.*, 1975; McCommas & Bryant, 1990). Recurrent bottlenecks in subsequent generations may well increase the effects of drift on the genetic composition of the population. Indeed, at the *Pgi* locus we found the tomato strain to be monomorphic for the most common allele of the highly polymorphic cucumber strain. However, one should be cautious in making inferences from two populations only. Clearly, more work is needed to collect similar data in a wide range of populations.

Our data and the proposed evolutionary scenarios lead to two fundamental questions. First, how is genetic variability on cucumber maintained, so as to allow successful shifts to marginal host plants (cf. Fry, 1989). If greenhouse populations were always confronted with one and the same host plant, then variability can only result from mutation-selection balance (Ohta & Kimura, 1975), given that gene flow is highly restricted and possibly even absent in greenhouses in the Netherlands (Overmeer *et al.*, 1975). If alternation of cucumber and tomato was the rule rather than the exception, then one would not expect genetic differentiation between strains unless adaptations to the two host plants are negatively correlated and alternation does not lead to extinction of either of the two genotypes. Hence future research should take into account the planting schedules for greenhouses from which populations are collected.

The second question relates to the phenomenon of assortative mating in the tomato strain: what is the selective advantage of assortative mating on a marginal host? Under greenhouse

conditions food competition among phytophagous mites can be excluded as a selective factor involved in host plant shifts. Hence, were cucumber and tomato grown simultaneously, then assortative mating on tomato would not have a selective advantage, as may be the case for the cucumber strain. Therefore, for assortative mating to evolve in the tomato strain, tomato should now and then be the only food plant available (as is rather common practice in the Netherlands). Under such a planting schedule assortative mating would be the only way to keep together the genes involved in exploitation of tomato as a host plant (co-adaptation).

Possibly, our findings point to a very interesting case of sympatric formation of host races on ecological islands, such as greenhouses. However, as the origins of our strains are not sufficiently specified with respect to the prevailing planting schedules in the greenhouse, there is a need to search for more appropriate greenhouse conditions. Alternatively, one may think of experiments to study the population differentiation process itself in the lab or a small greenhouse. This combination of experimental possibilities makes it a unique system for studying sympatric formation of host races.

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