

Reproductive isolation between *Tetranychus lintearius* and two related mites, *T. urticae* and *T. turkestanii* (Acarina: Tetranychidae)

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ABSTRACT

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Gorse, *Ulex europaeus* L. (Leguminosae), is a serious weed in New Zealand and some other temperate parts of the world. *Tetranychus lintearius* Dufour (Tetranychidae) has been released in New Zealand as a biological control agent for the weed. Before it could be introduced from Europe, it was necessary to show that *T. lintearius* is reproductively isolated from closely related pest mites.

Crosses and reciprocal crosses were made between *T. lintearius* and four populations of *T. urticae* Koch, and between *T. lintearius* and one population of *T. turkestanii* (Ugarov and Nikolski). In a second experiment, males of a second population of *T. lintearius* were crossed with females of five *T. urticae* populations. The sex-ratio of F₁ progeny in both experiments suggested that *T. lintearius* was reproductively isolated from the other species, and could therefore be used as a biological control agent for gorse.

INTRODUCTION

Gorse, *Ulex europaeus* L. (Leguminosae:Genisteae), is a serious weed of pastoral land and forest areas in New Zealand and several other temperate countries (MacCarter and Gaynor, 1980). The potential of *Tetranychus lintearius* Dufour (Acarina:Tetranychidae) as an agent for the biological control of this weed has been evaluated by DSIR Plant Protection, and the species has been released in New Zealand (Hill et al., 1989).

Determining the taxonomy of the mite genus *Tetranychus* L. has always been difficult, because the species within the genus are morphologically very similar. Pritchard and Baker (1955) proposed that the name *T. telarius* L. should be used for a group of closely related species including *T. lintearius*, but observed that the resulting complex probably contained a number of species and subspecies. This has since proven to be the case. Zwölfer (1963)

identified '*T. telarius*' as one of the most damaging phytophagous species attacking gorse in Europe, and recommended further research to determine whether it was a race which fed exclusively on this plant. Shortly after this, Van Eynhoven (1967) re-established the gorse-feeding *T. lintearius* as a distinct species and described the characteristics that distinguished it from other species of the '*T. telarius*' complex. The most important of these were the pattern of integumentary folds on the dorsum of *T. lintearius* females and the total lack of lobing on those folds in both summer and winter. Stone (1986) questioned the stability of these two characters, but confirmed Van Eynhoven's view that *T. lintearius* is a valid species on the basis of the shape of the aedeagus and empodium II of males.

Reproductive isolation in tetranychid mites has been studied extensively. Males, which are haploid, develop from unfertilised eggs, while females develop from fertilised eggs and are diploid. The presence of females in the progeny of two parent mites therefore proves successful fertilisation. Failure to produce female offspring when cross-mated (e.g. Jordaan, 1977), or poor performance of apparent hybrids (Helle and van de Bund, 1962; Boudreaux, 1963; El-Enany et al., 1983) has been used extensively to demonstrate reproductive isolation between related species (e.g. Jordaan, 1977). Reproductive incompatibility between parents can also lead to high egg mortality (De Boer and Veerman, 1983).

Many *Tetranychus* species are serious agricultural and horticultural pests in most parts of the world (Jeppson et al., 1975). Some of these pests, for example *T. cinnabarinus* Boisduval and *T. urticae* Koch, appear morphologically different but have been synonymised because they can hybridise more or less freely (Dupont, 1979). On the other hand, Boudreaux (1963) and others have shown that different degrees of incompatibility can be found even between morphologically indistinguishable strains of *T. urticae*.

Partly because of uncertainty about reproductive isolation between species, tetranychid mites have never intentionally been imported into any country for the biological control of weeds. Hill and Stone (1986) pointed out that many tetranychid species would make good biological control agents, but that care was needed to ensure that they would not interbreed with pest mites, or damage any plants other than the target weed. This extensive study of the degree of reproductive isolation of *T. lintearius* from two related tetranychids was therefore carried out to demonstrate whether or not it was a suitable biological control agent for gorse. The study examines the amount of reproductive isolation between *T. lintearius* and strains of two closely related tetranychid species, *T. urticae* and *T. turkestanii* (Ugarov and Nikolski). *Tetranychus urticae* was chosen because it is the most important mite pest of horticultural crops in New Zealand. It is one of only nine *Tetranychus* species present there (Manson, 1987). *Tetranychus turkestanii* was chosen because its aedeagus is

more like that of *T. lintearius* than any other species (W. Helle, personal communication, 1984). This suggests that the two species are closely related.

MATERIALS AND METHODS

Origin of test mites

For the first series of experiments carried out in 1984, *T. lintearius* were collected from gorse at Porthtowan, Cornwall, Great Britain, and were reared on detached gorse shoots as described below. *Tetranychus urticae* colonies were obtained from an experimental culture at Glasshouse Crops Research Institute, West Sussex, Great Britain (strain GC), a glasshouse at Silwood Park, Ascot, Berkshire, Great Britain (SP), a glasshouse at Ashurst Lodge, Silwood Park (AL), and from a glasshouse in Auckland, New Zealand (AK). The colony of *T. turkestanii* was supplied by Prof. W. Helle, The University of Amsterdam, The Netherlands. *Tetranychus urticae* and *T. turkestanii* colonies were maintained on leaf cultures as described below.

A second series of crosses between *T. urticae* females and *T. lintearius* males was carried out in 1987. *Tetranychus lintearius* were collected from gorse at Chobham Common, Berkshire, Great Britain. The *T. urticae* strains were obtained from a glasshouse at Silwood Park (strain 1), a culture at the Glasshouse Crops Research Institute (strain 2), a glasshouse at the Grassland Research Institute, Berkshire (strain 3), a culture at Wye College, Kent, Great Britain (strain 4), and a glasshouse at Ashurst Lodge (strain 5).

Crosses between T. lintearius females and T. urticae males

Spines were stripped from the basal 4 cm of an 8-cm gorse stem. The stem was placed in a 4-cm-tall vial of water through a small hole in a plastazote[®] stopper. A band of Fluon[®] was painted around the neck of the vial to stop mites walking up onto the stem. Such gorse stems survived for approximately 20 days, which was long enough to complete a full generation of *T. lintearius*. Five female late deutonymphs of *T. lintearius* were added to each stem. Two days later stems were divided into three groups. Five virgin male *T. urticae* were added to one-third of the stems. There were two controls for each cross. Five virgin male *T. lintearius* were added to one-third of the stems, while female *T. lintearius* were left unmated on the remaining stems. Crosses and their controls were labelled and stored together, but not touching, in a 10-l perspex box to minimise air movement. Experiments were carried out at 23°C. After two days, all males were removed from stems to avoid excessive harassment of ovipositing females. On the sixth day, females were counted and removed from the stem, and eggs were counted. The oviposition rate was recorded as the number of eggs laid per surviving female per day. Eighteen days

later, the progeny were sexed and counted and percentage survival to maturity was calculated. Results were compared between crosses and appropriate controls.

Crosses between T. urticae females and T. lintearius males — series 1

Dwarf-bean plants (*Phaseolus vulgaris* L.) were grown in pots in an open glasshouse. Three small detached bean leaves were placed on a wad of wet cotton wool in 10-cm-diameter plastic dishes with perforated bases. These stood in a tray of water. Five or ten female *T. urticae* teliochrysalids that were about to emerge were placed on each leaf. One cross and two controls were set up in each dish one day later. Five or ten virgin male *T. lintearius* were added to one leaf. Five or ten virgin *T. urticae* males were added to a second leaf as controls, and females on the third leaf were left unmated. These unmated controls were included to detect the presence of migrating *T. urticae* males within the experiment. Females amongst the progeny in this control would indicate contamination of the experiment. Experiments were carried out at 23°C. After one day all males were removed. After a further two days, females were counted and removed from all leaves. The eggs were counted and the oviposition rate was calculated as the number of eggs laid per surviving female. After eight more days, surviving progeny were sexed and counted. Percentage survivorship from egg to maturity was calculated.

Several mass-crosses were also carried out using the four strains of *T. urticae*. Approximately 50 female *T. urticae* teliochrysalids were placed on a leaf with 25 male *T. lintearius*. After three days, adult mites were removed and the number of eggs laid was estimated. After nine days, the experiment was examined very closely for the presence of females. There were no controls for these crosses. Female offspring from all crosses were isolated as teliochrysalids and crossed back to the paternal species using the same method. In two cases, adults emerged before this could be done. These were inbred with sibling males and crossed back to *T. lintearius* males in the next generation.

Crosses between T. urticae females and T. lintearius males — series 2

The methods employed were similar to those used in the first series of crosses, but greater effort was made to minimise the possible contamination of experiments by vagrant mites. The cross was set up by placing 20 female teliochrysalids on the excised leaf. The next day, 20 virgin male *T. lintearius* were added to the leaf. These were removed one day later. Two days after that, the surviving females were counted and removed and the eggs were counted. When adults appeared they were sexed and counted. The control crosses were carried out in separate dishes in precisely the same way, except that *T. urticae* males were added instead of *T. lintearius* males. An additional

series of controls was also carried out to try to detect whether the test dishes could become contaminated by unwanted *T. urticae* males or females despite precautions taken against contamination. These controls were carried out in exactly the same way as the crosses, except that males were not added.

A number of precautions were taken to prevent contamination of the experiments. Tests and controls were set up in separate dishes, each of which stood in a tray of water. There were two water barriers present, including the wet cotton wool. Each dish was covered with a lid ventilated with a very fine mesh. Bean leaves were microscopically examined for the presence of mites and their eggs before being used in the tests.

Crosses between T. turkestanii females and T. lintearius males

The method developed for series-1 crosses between *T. urticae* females and *T. lintearius* males was used. One mass-cross was also carried out.

A Student's *t*-test was used to compare oviposition rates in one experiment. Data were normally distributed.

RESULTS

Crosses between T. lintearius females and T. urticae males

Mites mated freely, and behaviour appeared normal. Fifty-nine attempted crosses were carried out using 313 *T. lintearius* females, yielding 2818 eggs (Table 1). Only males developed from these eggs, which indicated that there was no fertilisation between the species. Controls containing male and female *T. lintearius* yielded both male and female offspring in a ratio of 4.5:1. No females were ever produced in the unmated controls, which showed that there were no male *T. lintearius* migrating between treatments. These results demonstrate a high degree of reproductive isolation between the parental species.

TABLE 1

Results of crosses between *T. lintearius* females and three strains of *T. urticae* males

	<i>T. urticae</i> strain			Total
	Auckland	Silwood Park	GCRI	
Number of replicates	23	17	19	59
Number of parent females	147	79	87	313
Number of eggs laid	1026	772	1020	2818
Number of males produced	670	685	737	2092
Number of females produced	0	0	0	0
Replicates with females	0	0	0	0

There was no significant difference between the oviposition rate of females mated by *T. urticae* males and by *T. lintearius* males ($t=1.36$, $P=0.18$). Unmated females laid significantly fewer eggs than those mated by *T. urticae* males ($t=2.24$, $P=0.03$). This suggests that the act of mating stimulated egg production in females, irrespective of paternal species (De Boer, 1979). There was no significant difference in the viability of eggs in any of the three treatments. This suggests that the isolation mechanism is probably lack of effective fertilisation, rather than any lethality of hybrid embryos.

Cross between T. urticae females and T. lintearius males — Series 1

Mites mated freely and showed apparently normal reproductive behaviour. The 72 crosses carried out involved 444 females, and yielded approximately 7500 eggs. Of the adults produced, 99.7%, or 5577, were males. Two of the four *T. urticae* strains produced only male progeny, but 19 female mites were produced from four of the 72 replicates (Table 2).

There was no significant difference between the oviposition rates of females mated by either *T. urticae* or *T. lintearius*, or in the viability of eggs produced by crosses and unmated controls. This suggests that the lack of females amongst the progeny was because fertilisation did not occur, rather than because of selective mortality of fertilised embryos.

Mass-crosses were not counted accurately, but F_1 progeny were examined closely to identify females. One replicate yielded three females and approxi-

TABLE 2

Results of crosses between *T. urticae* females of four different strains and males of *T. lintearius* (Series 1)

	<i>T. urticae</i> strain				
	Auckland	Silwood Park	GCRI	Ashurst Lodge	Total
Number of replicates	46	11	10	5	72
Number of parent females	201	110	83	ca. 50	ca. 444
Number of eggs laid	3740	1864	1573	ca. 300	ca. 7477
Number of males produced	2717	1420	1213	246	5596
Number of females produced	15	0	4	0	19
Replicates with females	2	0	2	0	4
Mass crosses					
Number of replicates	1	2	2	—	5
Number of parent females	—	—	—	—	—
Number of eggs laid	—	—	—	—	—
Number of males produced	ca. 300	ca. 650	ca. 597	—	ca. 1544
Number of females produced	0	0	3	—	3
Replicates with females	0	0	1	—	1

mately 200 males. The remaining five crosses yielded approximately 1300 males but no females (Table 2).

Females appeared amongst the progeny in a total of five replicates, which at first suggests that the two species crossed successfully. However, it is more likely to have been the result of experimental contamination. Such contamination was shown in three of the 49 replicates of crosses involving the Auckland strain, which were rejected because *T. urticae* males were discovered on the leaves during the experiment. These mites presumably migrated from intraspecific controls within the same container. Similar, four replicates of unmated controls yielded female progeny. This could only occur if the controls were contaminated with wild mite eggs on the substrate bean leaves, or if male mites migrated onto the leaf and mated with parent females.

There were five separate cases where females were found amongst the progeny of crosses. In one case, two female and 57 male teliochrysalids were produced. Both females died before emergence. In the second case, 13 female teliochrysalids were formed along with ten males. This is close to the sex-ratio expected from intraspecific mating (Table 3), and is much higher than that normally achieved in the progeny of incompatible parents. Six of the females

TABLE 3

Results of crosses between *T. urticae* females and *T. lintearius* males (Series 2)

	<i>T. urticae</i> strain					
	1	2	3	4	5	Total
Cross						
Number of replicates	5	6	8	6	6	31
Number of parent females	100	120	160	120	120	620
Number of eggs laid	389	1028	679	331	702	3129
Number of males produced	175	494	376	156	364	1565
Number of females produced	0	0	35	0	0	35
Replicates with females	0	0	1	0	0	1
Unmated controls						
Number of replicates	3	3	5	3	3	17
Number of parent females	60	60	100	60	60	340
Number of eggs laid	610	344	599	97	104	1754
Number of males produced	231	86	254	72	47	690
Number of females produced	0	38	22	0	0	60
Replicates with females	0	1	1	0	0	2
Mated controls						
Number of replicates	5	5	5	5	5	25
Number of parent females	100	100	100	100	100	500
Number of eggs laid	627	552	308	276	502	2265
Number of males produced	89	130	84	55	116	474
Number of females produced	214	227	128	86	162	817
Replicates with females	5	5	5	5	5	25

emerged. Four were mated to *T. lintearius* males, and laid 66 eggs over three days but produced no female offspring. Two were mated to *T. urticae* males, laid 25 eggs over three days and produced offspring in the ratio of 2.1:1 ♀:♂.

In the third case, two female teliochrysalids amongst 24 males emerged earlier than expected and mated with sibling males. This early emergence strongly suggests that they were not the progeny of the cross but hatched from wild mite eggs on the substrate bean leaves. Selfed mites laid eggs freely. When female teliochrysalids of the F_2 were mated back to *T. lintearius* males, there were no females amongst their progeny.

In the fourth case, two female teliochrysalids were produced along with 43 males. They were mated with four *T. lintearius* males but laid a total of only four eggs before dying. The eggs hatched but did not reach maturity.

Lastly, three females were found amongst the progeny of one mass cross (Table 2). As in case 3, they emerged earlier than expected and mated with sibling males. Also, as in case 3, these females may have hatched from wild mite eggs on the substrate bean leaf. They laid many eggs. Twelve teliochrysalids of the next generation were crossed back to *T. lintearius* males, but there were no females amongst their progeny. All of the females produced during the experiment were therefore crossed back to *T. lintearius* males in the F_1 or F_2 generation. No female progeny resulted.

Crosses between T. urticae females and T. lintearius males — Series 2

The results of this series of crosses are shown in Table 3. All 25 control crosses using *T. urticae* males produced both males and females, showing that successful mating and fertilization occurred under the condition of the test. Fifteen of the 17 unmated controls produced males only. The two dishes in which females were produced had been contaminated despite the precautions taken. Thirty-one crosses between *T. urticae* females and *T. lintearius* males were carried out using 620 *T. urticae* females. A total of 3129 eggs were laid. Thirty of these experimental crosses produced males only, despite many observations of mating in these dishes. There was only one exception (Table 3). In this case, contamination is assumed since one of the unmated controls set up simultaneously with this test also produced females. This replicate can therefore be rejected. The results show quite clearly that *T. lintearius* males are unlikely to be able to successfully fertilize *T. urticae* females.

Crosses and reciprocal crosses between T. lintearius and T. turkestanii

Eleven crosses were carried out between 76 *T. lintearius* females and *T. turkestanii* males. A total of 386 eggs were laid, and these yielded 276 male mites. No females were produced (Table 4). Ten reciprocal crosses involving

TABLE 4

Results of crosses and reciprocal crosses between *T. lintearius* and *T. turkestan*

	Type of cross		
	<i>T. lintearius</i> ♀ × <i>T. turkestan</i> ♂	<i>T. turkestan</i> ♀ × <i>T. lintearius</i> ♂	<i>T. turkestan</i> ♀ × <i>T. lintearius</i> ♂ (mass)
Number of replicates	11	10	1
Number of parent females	76	79	—
Number of eggs laid	386	1167	—
Number of males produced	276	1037	ca. 500
Number of females produced	0	0	0
Replicates with females	0	0	0

79 *T. lintearius* females yielded only 1037 males amongst their progeny. No females were produced. This was also true of the mass-cross (Table 4).

These results demonstrate that *T. lintearius* and *T. turkestan* are reproductively isolated.

DISCUSSION

A species introduced for the biological control of a weed must be genetically stable and reproductively isolated from related species already resident. This is to avoid increasing the vigour of resident species, and to minimise the chances of significant behavioural changes in introduced species. Caution is especially important in the case of tetranychid mites, some species of which appear to be genetically unstable (Overmeer and van Zon, 1976).

Well-established techniques were used in these experiments to determine reproductive isolation between the tested mite species. These rely on the inability of cross-mated parents to produce viable female offspring, either because females are absent from the F_1 , or because F_1 females perform poorly. It is not unusual for a small proportion of the F_1 progeny of crosses to be female, but such hybrids are either inviable (Boudreaux, 1963), sterile (Ghobrial et al., 1969; El-Enany et al., 1983), or produce very few viable offspring (Dillon, 1958; Helle and van de Bund, 1962). In such cases, the parents also are assumed to be genetically isolated (Helle and van de Bund, 1962).

The total lack of female progeny from a long series of crosses between males of *T. urticae* or *T. turkestan* and *T. lintearius* females is very strong evidence that *T. lintearius* is a distinct species, and is reproductively isolated from *T. urticae* and *T. turkestan*. Unfortunately, the results from a few crosses between the nine strains of *T. urticae* females and *T. lintearius* males are less clear.

In two of the replicates, the non-viable females may indeed have been hybrids, as described by Boudreaux (1963) and others. The females that appeared in four other replicates were almost certainly the results of intraspecific mating and contamination of the experiment. Such contamination was clearly shown in unmated controls. Apparent hybrids could not cross successfully back to *T. lintearius* males, which confirms this interpretation. Other evidence of reproductive isolation includes lack of females amongst progeny of the reciprocal cross, and the complete isolation between *T. turkestanii* and *T. lintearius*.

In an independent study of reproductive incompatibility, H. Bolland (W. Helle and H. Bolland, personal communication, 1984) also has shown that *T. lintearius* is a separate entity from closely related tetranychids.

Tetranychus lintearius is behaviourally different from other tetranychids. It forms discrete, long-lived colonies which live within a tent-like web and move around the host plant en masse. This behaviour is rare among tetranychid species (D. MacFarlane, personal communication, 1984). The mite has never been recorded from any host plant other than gorse. Stone (1986) has shown that its growth rate, fecundity and life-span are very different from those of related pest species. De Boer (1985) has pointed out that hybridisation opportunities between species are severely limited by spatial separation on different host plants and by differences in webbing. The host specificity of *T. lintearius* (Hill and O'Donnell, 1991) and the unusual webbing it produces both assist in separating this species from other *Tetranychus* spp. The biology of *T. lintearius*, coupled with its inability to hybridise with other tetranychid species, therefore suggests that it is a discrete species and so can be considered as a possible biological control agent against gorse.

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