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Ambulatory dispersal of the susceptible and propargite-resistant strains of *Tetranychus urticae* and its influence on pesticide resistance dynamics

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ABSTRACT

The distribution of resistant individuals is determined by the amount of movement between populations. The differential rate of dispersal of a susceptible and a pesticide-resistant strain could influence the resistance dynamics under field conditions. The dispersal rate and dispersal efficiency of the susceptible and propargite-resistant strains of *Tetranychus urticae* were measured in separate-release and mixed-release experiments. The diffusion coefficient (D) of both strains did not differ significantly ($P > 0.344$) and an estimate of the asymptotic rate of advance ($2\sqrt{rD}$) (for one generation) was estimated at 0.1047 and 0.0930 cm per degree day for the susceptible and propargite-resistant strains, respectively. The dispersal efficiency of the two strains differed significantly ($P < 0.005$) as more susceptible mites than propargite-resistant mites crossed into specified zones more quickly after 290 and 366 degree days. Significantly ($P < 0.05$) higher number of susceptible adults, immatures and eggs were found in the outer most zone of an arena as compared to that of the propargite-resistant mites. The bioassay of the two strains showed a similar pattern of the spread of the adult females across the specified zones in the mixed-release experiment. The relatively lower dispersive tendency of the propargite-resistant *T. urticae* and the smaller proportion of adult females exhibiting that behaviour increase the chances of developing resistant 'hotspots' in field specially after an acaricide application.

Introduction

Tetranychid mite populations are characterised by cycles of initial colonization by a mated female followed by rapid population growth and localized host exploitation with subsequent dispersal or migration to a new resource (Kennedy and Smitley, 1985). Dispersal and colonization of new hosts are significant elements in the biology of *T. urticae* both contributing to the persistence of the species in natural and artificial ecosystems (Kennedy and Margolies, 1985). Intra-plant dispersal results from a tendency for a portion of the pre-reproductive females to emigrate from the leaf on which they developed, regardless of population density on that leaf (Hussey and Parr, 1963). In a dense aggregation of host plants, crawling (ambulatory dispersal) is also important in inter-plant movement within a host patch or aggregation. Fields of single crops, a characteristic of modern agriculture, act as very large host plant aggregations. Where the canopies of individual plants intertwine, such an arrangement may serve as a single very large plant for a mite population. A large proportion of the spread of mites from the focus of initial colonization may result from mites crawling from plant to plant through intertwined foliage and over the ground (Kennedy and Smitley, 1985).

It is widely recognized that the dynamics of pest populations strongly influence the evolution of insecticide resistance (Georghiou, 1972; Sawicki, 1987, etc.). Gene flow of pesticide resistant traits can provide a new resistance inoculum or can alter the rate of resistance development through immigration of resistant individuals (Croft and Dunley, 1993). The distribution of resistant individuals is determined by the amount of movement between populations on both local and regional spatial scales. Clearly, movement of *T. urticae* could affect acaricide resistance development and maintenance thereafter.

Immigration of susceptible individuals from a surrounding unsprayed habitat into a sprayed crop can slow down resistance development or lead to its reversion, depending on the level of gene flow between populations (Dunley and Croft, 1992). Dispersal within crops can have the same effect if susceptible individuals come from a refuge.

Croft et al. (1989) concluded that the factors influencing regional resistance appeared to be the species pool size of resistant and susceptible populations, the intensity of spraying, the unique host-plant life-cycle, and dispersal attributes of pest. Dunley and Croft (1992) concluded that a measurable influence of dispersal on the evolution of

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pesticide resistance, along with other operational, biological, and genetic factors can help us better predict those strategies which may be most effective in limiting or abating pesticide resistance. Future resistance management programmes will likely require a regional, multi-tactic, multi-crop perspective, with dispersal and gene flow being key input variables for decision making.

The importance of the dispersal of resistant individuals, both on local and regional scales, has been well recognized. Understanding the dispersal behaviour of resistant strains of insects and mites is, therefore, of particular importance. The objectives of the studies reported in this paper was to measure the dispersal rates and the dispersal efficiency (percentage of females crossing a particular distance) of the susceptible and propargite-resistant strains of *T. urticae* released from a particular point. Such a study could predict the within field differential dispersal rates of both strains, and hence, the dispersion of resistant individuals present at a location (important information for the design of sampling plans to document resistance). Moreover, the results of such a study could be used in modelling to predict large scale dispersal of *T. urticae* on both local and regional scales.

Materials and methods

Mite source and experimental layout

A susceptible strain of *T. urticae* was collected from wild hosts from the Lincoln University organic production area. No pesticide of any type had been applied in this area for approximately 20 years. A resistant strain of *T. urticae* was air-freighted from an Auckland (New Zealand) glasshouse where there had been intensive use of miticides. Both strains were reared on French dwarft bean (*Phaseolus vulgaris*, cultivar. 'Tendergreen') in separate controlled temperature (CT) rooms at 21 + 3 °C, 60 + 15% RH and a 16L:8D photoperiod. Bean plants were grown in 15 cm dia plastic pots in a glasshouse and supplied to the colonies when required. The colony of the resistant strain was pressured with propargite (Omite 30WP; Uniroyl Chemicals, Frensono, Calif.; 0.05% ai) twice a month to eliminate any heterozygotes and narrow the response of the strain to the miticide. The LC_{50} of the susceptible and resistant strains were 0.006% ai and 0.403% ai respectively with a resistance ratio of 67 (Shah et al., 2002).

For each replicate in this experiment, 100 bean plants were grown in small plastic pots (10 cm dia, 6 cm high). Pots were arranged inside a box (arena) as a 10 × 10 square with the leaves of the plants touching to form a uniform surface. One-week-old plants were used and maintained at two leaves by trimming new leaves throughout the experiment. The average plant height was 25 cm. The plants were numbered from 1 to 100 and were arranged inside the box that consisted of a 100 × 100 cm wooden frame with 5 cm high wooden sides and 50 cm high upright arms at each corner. Plastic sheets were wrapped around the arms and a thick plastic lining was placed in the bottom of the frame and brought up to cover the 5 cm high sides of the frame. Double sided sticky tape (5 cm wide) was placed just below the inner edges of plastic that surrounds the arena to prevent the escape of mites. The boxes were filled with water to 3 cm depth to prevent the mites crawling to the sides of the arena. The plants were watered regularly.

Separate-release experiment

One hundred adult female mites (3–4 days-old) were released in the centre of each box on plant number 55. Susceptible and propargite-resistant strains of *T. urticae* were released in separate arenas (boxes). The experiment was replicated 4 times.

Around 175 cumulative degree days plants were checked for the presence of adult females. The total number of adult females of *T. urticae* on each plant of an arena was recorded after 212, 250, 290 and 366 degree days (16, 19, 22 and 28 days with an average of 13 degree days per day) after their release. The degree days were calculated by subtracting base temperature from the average daily temperature [base temperature of 10 °C for *T. urticae* (Dover et al., 1979)]. The first three observations aimed at recording the first generation females while the 28 days observation aimed at the second generation adults. At each observation all the plants in each zone were inspected with a hand lens and number of adult females recorded on each plant. After approximately 375 degree days all the leaves were brushed using a leaf brushing machine and the number of adults, immatures and eggs were counted using an 8 × dissecting microscope. The differences in the adult density and total number of adults, immatures and eggs between the two strains were analysed by ANOVA and means separated by $L.S.D._{(\alpha = 0.05)}$ (represented by vertical error bars in all the figures).

The degree of aggregation of the adult *T. urticae* female's populations after 212, 250, 290 and 366 cumulative degree days was measured by Lloyd's index of patchiness (*I*).

$$\textit{Index of patchiness} = I = m^*/\textit{mean}$$

where, mean crowding = m^* = [*mean* + (*variance* / *mean*) − 1] and *I* is Regular ≤ 1 Random ≥ 1 Patchy.

The difference between the two strains was analysed by ANOVA and means separated by $L.S.D._{(\alpha = 0.05)}$.

The distance (cm) dispersed during time *t* (degree days) by adult *T. urticae* females was measured as the distance from the point of release to the stem of the plant with an average female mite density of > 1. Each box was divided into four quadrats and five farthest plants with mite density of > 1 were selected per quadrat and the distance recorded. The average distance in any direction (radius of a circle) was then estimated and the area covered during time *t* was calculated by πR^2. The diffusion coefficient (*D*) was estimated by regressing the square root of the area occupied against time *t* using the Skellam's (1951) relation

$$\sqrt{\pi R^2} = 2t\sqrt{\pi r D}$$

where *R* is the radius, *t* is the time, *r* is the intrinsic rate of increase, *D* is the diffusion coefficient and $2\sqrt{\pi r D}$ is the slope. The diffusion coefficient is therefore:

$$D = \frac{slope^2}{4\pi r}$$

The slopes of the two regression lines (susceptible and propargite-resistant strains) were compared for equality using *F*-test. The dispersal rates (area occupied per generation) were considered significantly different if the slopes for susceptible and propargite-resistant strains were not equal. To measure dispersal efficiency the experimental arena was divided into three zones; the area inside a circle with a radius of 15 cm (zone 1), the area inside a circle with a radius of 30 cm (zone 2) and the area outside a circle with a radius of 30 cm and inside the 100 × 100 cm rectangle (zone 3) (Fig. 1). The dispersal efficiency (Krainacker and Carey, 1990) was measured as the percentage of adult females successfully crossing into zone 2 and zone 3. All calculations were performed in Quattro-Pro (Corel Corp., 1996; version 6.02).

Mixed-release experiment

Under field conditions, both susceptible and resistant strains are present together, therefore, mites of both the strains were released in the same experimental arena to simulate a field situation. The setup of this experiment was the same as described previously except that the mites released in the centre of each arena were half (50) susceptible and half (50) propargite-resistant strain. To compensate for the fitness disadvantage 6–8 extra propargite-resistant adult females were added to each arena since the intrinsic rate of increase (r_m) for the propargite-resistant strain was lower (0.188) compared to 0.214 for the susceptible strain (unpublished data). To estimate number of propargite-resistant and susceptible individuals at prescribed distances, 50 adult females were collected from each zone after 250 and 400 degree days and