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Original article (Orijinal araştırma)

Pleiotropic effects of propargite on life-table parameters of susceptible and resistant strains and reciprocal *F1* hybrids of *Tetranychus urticae* Koch, 1836 and their implications for population growth[1]

Tetranychus urticae Koch 1836'nin hassas ve dirençli ırklarının ve karşılıklı *F1* çapraz melezlerinin yaşam tablosu parametreleri üzerine propargite'in pleiotropik etkileri ve bunların popülasyon gelişimi üzerine çıkarımlar

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Abstract

Demographic toxicological studies or life-table response experiments have been proposed as a more reliable approach for predicting pesticide impact in the field. Life-table parameters of the susceptible, propargite-resistant and reciprocal *F1* hybrids of *Tetranychus urticae* Koch, 1836 (Prostigmata: Tetranychidae) were studied in the presence and absence of propargite residues at LC_{50} and LC_{99} of susceptible strain at Lincoln University, New Zealand. The life history data of all individuals were analyzed using the age-stage, two-sex life table. Treatment with LC_{50} of the susceptible strain did not affect the duration of developmental time of any strain. LC_{99} of the susceptible strain, however, prolonged the developmental time of the propargite-resistant strain by approximately 2 d. The intrinsic rate of increase (r_m), R_o and total progeny production of the propargite-resistant strain and $S♂ \times R♀$ hybrid treated with LC_{50} of the susceptible strain were higher compared to that of the susceptible strain and $R♂ \times S♀$ hybrid. Population projections were used to study the effects of relatively small differences in the life-table parameters of strains/hybrids of *T. urticae*. For the untreated control groups, the susceptible strain gave the highest population projection after 10 generations. In groups treated with LC_{50} of the susceptible strain, the projected population size showed that the number of adult females of the propargite-resistant strain superseded that of the susceptible strain. The hybrid $S♂ \times R♀$ increased most from treatment with the LC_{50} of the susceptible strain. The differential success of different strains could, therefore, change resistance frequency throughout a growing season at a location.

Keywords: Intrinsic rate of increase, life-table parameters, population projection, propargite, resistance, *Tetranychus urticae*

Öz

Demografik toksikolojik çalışmalar ya da yaşam tablosu tepki denemeleri, tarlada insektisit etkisini öngörmek için daha güvenilir bir yaklaşım olarak önerilmektedir. *Tetranychus urticae* Koch, 1836 (Prostigmata: Tetranychidae)'nin hassas, propargite karşı dirençli ve karşılıklı *F1* çapraz melezlerinin yaşam tablosu parametreleri, Lincoln Üniversitesi (Yeni Zelanda)'nde hassas ırkın LC_{50} ve LC_{99}'unda propargite kalıntılarının varlığında ve yokluğunda çalışılmıştır. Tüm bireylerin yaşam tablosu verileri, yaş-evre, iki cinsiyetli yaşam tablosu kullanılarak analiz edilmiştir. Duyarlı ırkın LC_{50} değerleri, herhangi bir ırkta gelişim zamanını etkilememiştir. Bununla birlikte, hassas ırkın LC_{99}'u, propargite dirençli ırkın gelişim süresini yaklaşık iki gün uzatmıştır. Duyarlı ırkın LC_{50} değerleri, propargite dirençli ırkın ve $S♂ \times R♀$ hibridinin kalıtsal üreme yeteneği (r_m), R_o ve toplam döl verimi, hassas ırk ve $R♂ \times S♂$ hibritine kıyasla daha yüksek bulunmuştur. Popülasyon tahminleri, *T. urticae*'nin ırkları / melezlerinin yaşam tablosu parametrelerindeki nispeten küçük farklılıkların etkilerini incelemek için kullanılmıştır. Uygulama yapılmayan kontrol grupları için hassas ırk 10 dölden sonra en yüksek popülasyon tahminini vermiştir. Duyarlı ırkın LC_{50} değeri uygulanan gruplarda, tahmin edilen popülasyon büyüklüğü, propargite dirençli ırkın ergin dişi sayısının, hassas ırkın yerine geçtiğini göstermiştir. Hibrid $S♂ \times R♀$, hassas ırkın LC_{50}'si ile uygulamadan en fazla artmıştır. Bu yüzden, farklı ırkların kademeli başarısı, bir bölgede yetiştirme sezonu boyunca direnç sıklığını değiştirebilir.

Anahtar sözcükler: Kalıtsal üreme yeteneği, yaşam tablosu parametreleri, popülasyon tahmini, propargite, direnç, *Tetranychus urticae*

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Introduction

Insecticide resistance is an example of evolutionary change where the insecticide acts as a powerful selective sieve (Crow, 1957). The rate of change in allele frequency in a population under the influence of selection pressure is a function of the initial allele frequency, dominance, population structure and the relative fitness of the various genotypes (Roush & McKenzie, 1987). However, resistant genotypes must be at some fitness disadvantage in the absence of the pesticide, otherwise resistance alleles would be very common prior to selection (Crow, 1957). Studies carried out on diverse groups of arthropods have reported some deleterious effects of resistance on their life history characteristics. For example, Schulten (1968) reported reduced fertility, fecundity and development rates for an organophosphorus-resistant strain of *Tetranychus urticae* Koch, 1836 (Prostigmata: Tetranychidae). Kono (1987) also reported lower survival rate, egg production and intrinsic rate of increase (r_m) for the dicofol-resistant strain of *T. urticae*. Kasamatsu & Ogawa (1992) studied the reproductivity of fenpropathrin-resistant and susceptible strains of *T. urticae* at 20, 25 and 30ºC and the lower r_m values for the resistant strain at each temperature suggested a lower fitness value of that strain.

Other insect pests have also been found to have fitness related costs associated with insecticide resistance. Reduced relative fitness of resistant genotypes in insecticide-free environments is characteristic of many insect species (Sayyed et al., 2008). Udeaan & Judge (1990) reported significantly longer larval period in the phosphine-resistant strain of *Trogoderma granarium* Everts, 1898; and Trisyono & Whalon (1997) also found slower larval development, reduced fecundity and shorter oviposition periods in a *Bacillus thuringiensis* Berliner, 1915 resistant strain of Colorado potato beetle, *Leptinotarsa decemlineata* Say, 1824.

Demographic toxicological studies or life-table response experiments have been proposed as a more reliable approach than the lethal dose estimates for predicting pesticide impact in the field since they show effects of pesticides on survivors, thus providing a measure of impact on the population growth rate (Robertson & Worner, 1990; Robertson & Preisler, 1992; Stark & Banks, 2003). Differences in the biological parameters affecting the net replacement rate (R_o) and the intrinsic rate of population increase (r_m) are of particular interest to insecticide resistance management (Haubruge & Arnaud, 2001). Although life-table bioassays impose some limitations, Stark & Banks (2003) stated that the population growth rate approach should be adopted more widely, if we are to improve our knowledge about toxicant impacts on arthropods.

Kheradmand et al. (2007) also emphasized the importance of the life-table parameters for analyzing and understanding the impact of an external factor on the growth, survival rate, reproduction and increase rate of an arthropod population. These parameters influence population growth rates of an insect in the current and next generations (Frel et al., 2003). The susceptibility of an individual to insecticides may vary greatly with sex and developmental stage, therefore, stage differentiation and the male population should be taken into consideration (Chi & Liu, 1985; Chi, 1988).

Roush & Daly (1990) suggested that in any study of the fitness of resistant arthropods the susceptible-resistant hybrid (heterogeneous) strain should be included because of the high frequency of heterogeneous individuals occurring in populations during the early development of resistance. In addition, a study of the life-table parameters of pesticide susceptible and resistant strains and susceptible-resistant reciprocal *F1* hybrids ($R^{♂} \times S^{♀}$ and $S^{♂} \times R^{♀}$) in the presence and absence of the pesticide residues is required. All such strains are continuously exposed to pesticides in the field; therefore, comparisons of the different life-table parameters in the presence and absence of pesticide residues may better explain the dynamics of resistance and would assist the development of more appropriate sampling plans and resistance management programs.

The objectives of the studies reported in this paper were, 1) to determine the effects of propargite on life-table parameters of the susceptible and propargite-resistant strains and susceptible-resistant reciprocal *F1* hybrids of *T. urticae* in the presence and absence of propargite residues, and, 2) to explore the impact of any differences in these parameters on the frequency of propargite-resistant individuals in the population.

Material and Methods

Mite source

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 about 20 years. A resistant strain of *T. urticae* was air freighted from a glasshouse in Auckland, New Zealand where there had been intensive use of miticides including propargite. Both strains were reared on French dwarf bean (*Phaseolus vulgaris* cv. Tendergreen) in separate controlled temperature rooms at 21±3ºC, 60±15% RH and a 16:8 h L:D photoperiod at Lincoln University New Zealand. Bean plants were grown in 15 cm diameter plastic pots in a glasshouse and supplied to the colonies when required. The colony of the resistant strain was sprayed with 0.05% propargite (Omite 30WP; Uniroyal Chemicals, Frensno, CA, USA) twice a month to eliminate any heterozygotes and narrow the response of the strain to the miticide. At LC_{95}, the resistance ratio (RR_{95}) for propargite-resistant, $R^{\male} \times S^{\female}$ and $S^{\male} \times R^{\female}$ were 1200, 28 and 78 times, respectively (Shah et al., 2002).

Backcrossing of susceptible and propargite-resistant strains of *Tetranychus urticae*

To obtain the reciprocal *F1* hybrids, thirty newly emerged adult females of both susceptible and propargite-resistant strains of *T. urticae* were transferred separately to single whole bean leaves. Each leaf was placed in a Petri dish on moist cotton wool with the lower surface facing upward. One adult male from the opposite strain was released on to each leaf. After 24 h of oviposition the mites were removed from the leaves and the eggs counted. The emerging *F1* hybrid, and the susceptible and propargite-resistant adult females were used in the following life-table parameter study.

Life-table parameter study of the susceptible and propargite-resistant strains, and reciprocal *F1* hybrids of *Tetranychus urticae*

Construction of the fertility life-table and determination of developmental time

Fifteen adult females from the susceptible and propargite-resistant strains and the $R^{\male} \times S^{\female}$ and $S^{\male} \times R^{\female}$ *F1* hybrids were transferred to bean leaves within a 10 mm diameter circle of Tracktrap® (used to prevent the escape of mites). As nothing was known about the genetic status of propargite-resistant individuals the symbols (*R* and *S*) are used for convenience. After 24 h of oviposition all adult mites were removed and the eggs were sprayed under a Potter tower at 69 kpa with propargite 30WP using either the LC_{50} (0.006% ai) or LC_{99} (0.032% ai) of the susceptible strain (Shah et al., 2002). Control groups were treated with water only.

Each Petri dish with a cohort size of four to six eggs per dish was considered one replicate giving a total of about 70 mites per strain or hybrid. The Petri dishes were maintained under a 16:8 h L:D photoperiod at 22.4±1.5ºC with 50±5% RH. Leaves were changed every second day after the eggs had hatched. The life-table data for all individuals for each developmental stage including the chrysalis stage were recorded at 12 h intervals until all had died.

Fertility life-tables were constructed for the susceptible and propargite-resistant strains and *F1* hybrids. The following life-table parameters were calculated using the methods of Carey (1993): adult longevity; mean total progeny production per female; pre- and post-ovipositional periods; birth rate (*b*); death rate; age structure; number of eggs/female/d and percentage of mites reaching adulthood and sex ratio (expressed as the percentage females).

Calculation of age-stage, two-sex life table

The life history raw data of all individuals (males, females and those dying before the adult stage) were analyzed according to the age-stage, two-sex life-table theory (Chi & Liu, 1985; Chi, 1988). The age-stage-specific survival rate (s_{xj}) (with x = age in days and j = stage); the age-stage-specific fecundity (f_{xj}); the age-specific survival rate (l_x); the age-specific fecundity (m_x); and the population growth parameters [the intrinsic rate of increase (r); the finite rate of increase ($\lambda = e^r$); the gross reproductive rate (GRR); the net reproductive rate (R_0) and the mean generation time (T)] were calculated accordingly. The age-specific survival rate includes both male and female, and is calculated according to Chi and Liu (1985) as:

$$lx = \sum_{j=1}^{k} s_{xj} \quad (1)$$

and

$$mx = \frac{\sum_{j=1}^{k} s_{xi} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \quad (2)$$

where, k is the number of stages.

The intrinsic rate of increase is estimated by using:

$$\sum_{x=0}^{\omega} e^{-r(x+1)}\, lxmx = 1 \quad (3)$$

with age indexed from 0 to ω (maximum age).

The GRR is calculated as GRR = Σm_x.

Data analysis and population parameters (r, λ, GRR, R_0 and T) for group-reared life table based on matrices N and F_{total} were calculated by using the TWOSEX-MSChart program (Chi, 2018).

The means and standard errors of the population parameters were estimated by using the Bootstrap procedure (Meyer et al., 1986; Huang & Chi, 2013). In the bootstrap procedure, a sample of n individuals from the cohort with replacement was taken randomly and the $r_{i\text{-}boot}$ for this bootstrap sample was calculated as:

$$\sum_{x=0}^{\omega} e^{-r_{i\,boot}(x+1)}\, lxmx = 1 \quad (4)$$

where the i-boot represents the i^{th} bootstrap, and l_x and m_x are calculated from the n individuals selected randomly with replacement. Generally, the data on the same individual are repeatedly selected. This procedure was repeated m times (m = 10,000) and computed the mean of these m bootstraps as:

$$r_B = \frac{\sum_{i=1}^{m} r_{i-boot}}{m} \quad (5)$$

The variance ($VARr_B$) and standard error (SEr_B) of these m bootstraps were calculated as:

$$VARr_B = \frac{\sum_{i=1}^{m} (r_{i-boot} - r_B)^2}{m-1} \quad (6)$$

$$SEr_B = \sqrt{VARr_B} \quad (7)$$

The same methods are used for the corresponding estimates of the finite rate of increase (λ), GRR, R_0 and mean generation time (T).

ANOVA was applied to the life-table data obtained from life history and multiple comparisons were made using $LSD_{(\alpha=0.05)}$ to determine significant differences between stage durations using Quattro Pro (Corel Corp., 1996; version 6.02). The two-sex life-table bootstrap-values of the TSSM were also compared using $LSD_{(\alpha=0.05)}$.

To establish the possible long term (for at least one season with average of 10 generations) influence of comparatively small differences in the parameter values, population numbers were projected over 10 generations (each generation was assumed to receive the same dose of propargite) using the equation:

$$N_t = (\lambda)^t N_0 \qquad (8)$$

where, t is the mean generation time, λ is the finite rate of increase and N_0 is the initial population (100 females). The relative increase or decrease per generation in the number of treated females in relation to the control mites was calculated by dividing the number of females present in the treated generation by that of untreated generation. All calculations were performed using Quattro Pro.

Results

Life-table parameters of the susceptible and propargite-resistant strains of *Tetranychus urticae*

The various life-table parameters of susceptible and propargite-resistant strains and the reciprocal *F1* hybrids of *T. urticae* are given in Tables 1 and 2. The duration of each life stage including the chrysalis stages and the developmental time from egg to adult did not differ significantly among the untreated strains and hybrids (Table 1). The effect of treating eggs of strains and hybrids with the LC_{50} of susceptible strain on the developmental time from egg to adult was also nonsignificant. However, the developmental time of the propargite-resistant strain increased by about 2 d when the eggs were treated with the LC_{99} of susceptible strain. The development time of the propargite-resistant strain with this treatment was significantly greater ($P > 0.001$) than that of both strains and hybrids either untreated or treated with the LC_{50} of the susceptible strain, requiring more time to complete their development from egg to adult. All the newly emerged larvae of susceptible and both hybrid strains died as a result of treatment with the LC_{99} of susceptible strain. Developmental times for males were slightly but not significantly shorter than that for females for all strains and hybrids.

As a consequence of the higher mortality, the calculated parameters, the intrinsic rate of increase (r_m), R_o and total progeny production (Table 1), of the susceptible strain and the $R^{♂} \times S^{♀}$ hybrid treated with LC_{50} of the susceptible strain were lower compared with the control parameters. These parameters also decreased for the propargite-resistant strain treated with LC_{99} of the susceptible strain. In contrast, due to an increased birth rate and slightly decreased mortality, r_m, R_o and total progeny production of the propargite-resistant strain and $S^{♂} \times R^{♀}$ hybrids treated with LC_{50} of the susceptible strain, increased. Changes (either increase or decrease) in these parameters also resulted in a corresponding inverse change in doubling time.

The percentage of females (sex ratio) in both the strains and hybrids increased with treatment by propargite, possibly indicating that males of both the strains and hybrids were more susceptible to propargite than females. However, percentage of propargite-resistant strain females treated with LC_{50} of susceptible strain decreased slightly. The life expectancy of the susceptible strain, propargite-resistant strain and the reciprocal *F1* hybrids treated with LC_{50} of susceptible strain and the propargite-resistant strain treated with LC_{99} of susceptible strain were lower than the control. The largest difference was 5.64 d for the susceptible strain.

Table 1. Duration (d, mean±SE) of developmental stages of susceptible and propargite-resistant strains and reciprocal *F1* hybrids of *Tetranychus urticae* at 22.4°C

Treatment	Egg stage	Larval stage	Proto-chrysalis	Proto-nymph	Deuto-chrysalis	Deuto-nymph	Teliochrysalis		Total duration[a]		Pre-oviposition	Post-oviposition	Adult longevity		Total life span	
							♀	♂	♀	♂			♀	♂	♀	♂
Susceptible strain (LC_{50})	5.27a (0.07)	0.93a (0.09)	0.89b (0.06)	0.96a (0.03)	0.58a (0.05)	0.69a (0.06)	1.71b (0.06)	1.12a (0.08)	11.02a (0.08)	10.37a (0.15)	1.10a (0.08)	1.60a (0.40)	8.54b (1.13)	7.52b (0.98)	19.56b (1.24)	17.89b (1.21)
Control	5.20a (0.12)	1.00a (0.08)	0.70ab (0.12)	0.90a (0.10)	0.70a (0.12)	0.70a (0.10)	1.50b (0.08)	1.00 (0.29)	10.70a (0.09)	10.25a (0.14)	1.20a (0.18)	1.10a (0.40)	8.90b (1.17)	7.32b (0.88)	19.6b (1.33)	17.57b (1.22)
Resistant strain (LC_{50})	5.33a (0.06)	0.83a (0.09)	0.87b (0.06)	0.73a (0.07)	0.87a (0.08)	0.83a (0.05)	1.44b (0.11)	1.34a (0.15)	10.97a (0.12)	10.78a (0.25)	1.40b (0.14)	2.00b (0.35)	9.17b (0.92)	8.14b (1.08)	20.14b (1.40)	18.92b (1.10)
Control	5.50a (0.08)	0.90a (0.10)	0.60a (0.10)	1.00b (0.08)	0.70a (0.12)	1.20b (0.12)	1.20a (0.12)	1.00 (0.08)	11.10a (0.10)	10.83a (0.17)	1.30b (0.20)	2.50b (0.94)	9.30b (0.94)	7.92b (1.12)	20.4b (1.11)	18.75b (1.13)
$R♂ \times S♀$ (LC_{50})	5.17a (0.06)	0.97a (0.06)	0.93b (0.07)	0.77a (0.07)	0.78a (0.06)	0.83a (0.06)	1.57b (0.12)	1.15a (0.15)	11.05a (0.16)	10.60a (0.26)	1.40b (0.21)	1.20a (0.34)	6.00a (0.76)	4.63a (0.93)	17.05ab (1.33)	15.23ab (0.85)
Control	5.20a (0.12)	1.10a (0.10)	0.70ab (0.12)	1.10b (0.10)	0.60a (0.10)	0.90a (0.06)	1.79b (0.13)	1.20 (0.15)	11.29a (0.16)	10.80a (0.12)	1.80c (0.18)	1.60a (1.12)	9.00b (0.84)	8.21b (1.31)	20.29b (1.14)	19.01b (1.06)
$S♂ \times R♀$ (LC_{50})	5.25a (0.09)	1.04a (0.06)	0.89b (0.08)	0.86a (0.06)	0.77a (0.09)	0.96a (0.07)	1.71b (0.09)	1.25a (0.16)	11.46a (0.15)	10.97a (0.23)	1.30b (0.18)	2.30b (0.28)	8.77b (0.74)	7.15b (1.22)	20.23b (1.33)	18.12b (1.03)
Control	5.20a (0.12)	1.00a (0.08)	0.80b (0.12)	0.90a (0.10)	0.70a (0.12)	0.75a (0.11)	1.30a (0.20)	1.25 (0.25)	10.65a (0.31)	10.50a (0.50)	2.20c (0.49)	1.40a (0.49)	5.30a (0.85)	4.22a (0.79)	15.95a (1.01)	14.72a (0.76)
Resistant strain (LC_{90})	5.13a (0.06)	0.97a (0.06)	1.23c (0.11)	0.83a (0.18)	1.04b (0.03)	2.09c (0.1)	2.02c (0.14)	1.75b (0.15)	13.04b (0.21)	12.63b (0.24)	2.10c (0.36)	2.00b (0.49)	8.23b (0.77)	7.78b (1.24)	21.27b (1.42)	20.41b (1.13)
Control	5.50a (0.08)	0.90a (0.10)	0.60a (0.10)	1.00a (0.08)	0.70a (0.12)	1.20b (0.12)	1.20a (0.12)	1.00a (0.08)	11.10a (0.10)	10.83a (0.17)	1.30b (0.20)	2.50b (0.94)	9.30b (0.87)	7.92b (1.12)	20.4b (1.11)	18.75b (1.03)

[a] From egg to adult. Within columns data followed by the same letter are not statistically different ($LSD_{(\alpha=0.05)}$)

Table 2. Life-table parameters (mean±SE) of susceptible and propargite-resistant strains and reciprocal *F1* hybrids of *Tetranychus urticae* at 22.4°C

Treatment	Birth rate (*b*)	Death rate (*d*)	*b*/*d*	Age structure (%)			GRR offspring	Eggs/ female /d	R_o offspring	r_m/d	Total progeny	Generation time	λ/d	Percent females	Life expectancy	% reaching adulthood
				Egg	Immature	Adult										
Susceptible strain (LC_{50})	0.209a (0.04)	0.033a (0.004)	6.29a (2.3)	76.94c (4.31)	17.48a (3.56)	5.58b (1.2)	105.05h (5.56)	5.08c (1.31)	27.97e (1.04)	0.177bc (0.014)	40.30b (8.84)	18.82ab (1.25)	1.193ab (0.042)	70.45ab (5.63)	14.36a (1.22)	66.67b (3.28)
Control	0.203a (0.04)	0.012a (0.004)	16.4d (2.4)	77.47c (4.96)	16.34a (3.96)	6.19b (1.65)	85.96g (5.32)	5.6bc (1.21)	35.08g (2.31)	0.214e (0.013)	49.80b (18.02)	16.63a (1.05)	1.243bc (0.042)	66.32ab (4.21)	20.00b (1.68)	85.71c (6.98)
Resistant strain (LC_{50})	0.199a (0.03)	0.015a (0.004)	13.58c (3.1)	75.86c (5.21)	17.42a 2.58)	6.72b (1.98)	66.49e (6.21)	5.24c (1.41)	32.60f (1.26)	0.194de (0.009)	48.00b (9.58)	17.92ab (1.22)	1.213c (0.042)	62.26ab (3.35)	16.98a (1.39)	80.30bc (6.35)
Control	0.194a (0.03)	0.016a (0.004)	12.46c (3.3)	76.46c (5.43)	16.89a (3.21)	6.64b (1.76)	75.25f (6.52)	4.75bc (1.02)	30.19f (1.99)	0.188d (0.012)	36.80b (16.94)	18.12ab (1.04)	1.204bc (0.042)	65.38ab (6.33)	20.00b (1.59)	78.57bc (5.68)
$R^{♂} \times S^{♀}$ (LC_{50})	0.163a (0.03)	0.019a (0.004)	8.55b (1.21)	69.77a (3.95)	20.74b (2.54)	10.09d (1.24)	53.98d (6.31)	4.12b (0.95)	13.86b (0.92)	0.153ab (0.015)	24.70ab (6.69)	17.23ab (1.31)	1.163a (0.042)	65.38ab (5.67)	16.75a (1.33)	79.10bc (4.39)
Control	0.178a (0.03)	0.013a (0.004)	13.44c (3.12)	73.61b (4.21)	19.23ab (3.36)	7.16b (1.22)	65.86e (5.41)	4.44bc (1.12)	21.50cd (1.03)	0.174bc (0.021)	40.00b (15.52)	17.65ab (1.15)	1.194ab (0.042)	51.32a (3.69)	21.85b (1.27)	67.47b (5.36)
$S^{♂} \times R^{♀}$ (LC_{50})	0.184a (0.04)	0.023a (0.003)	7.87ab (1.98)	73.78b (5.64)	17.75a (3.85)	8.47c (1.23)	48.74c (6.12)	4.35bc (0.86)	18.38c (0.84)	0.161b (0.012)	38.10b (6.38)	18.14ab (1.53)	1.187a (0.042)	64.86ab (4.06)	16.90a (1.15)	71.15b (3.45)
Control	0.135a (0.04)	0.014a (0.003)	9.5b (2.64)	63.6a (4.58)	24.73c (3.34)	11.66d (1.98)	22.72a (4.12)	2.79a (0.75)	7.09a (0.86)	0.148a (0.023)	18.50a (7.50)	15.23a (0.96)	1.144a (0.042)	46.03a (5.03)	19.71b (1.09)	70.80b (4.66)
Resistant strain (LC_{90})	0.175a (0.04)	0.028a (0.003)	6.31a (1.54)	75.49c (6.7)	20.2b (3.58)	4.31a (1.21)	35.46b (3.56)	3.03a (0.56)	17.13c (1.31)	0.148a (0.022)	24.90ab (5.58)	19.25b (1.22)	1.161a (0.042)	90.32b (6.68)	15.30a (1.62)	44.93a (3.36)
Control	0.194a (0.04)	0.016a (0.003)	12.46c (3.1)	76.46c (6.87)	16.89a (3.46)	6.64b (1.33)	75.25f (5.62)	4.75bc (1.03)	30.18f (1.99)	0.188d (0.012)	36.80b (16.94)	18.12ab (1.04)	1.204bc (0.042)	65.38ab (6.33)	20.00b (1.59)	78.57bc (5.68)

Within columns data followed by the same letter are not statistically different ($LSD_{(\alpha=0.05)}$)

Age-stage, two-sex life table

Age-stage-specific survival rate and stage mortality

The age-stage-specific survival rates (s_{xj}) of TSSM show the probability that a newborn will survive to age *x* and develop to stage *j,* the survivorship and stage differentiation and the variable developmental rate (Figure 1). If untreated, there is 0.6, 0.4, 0.4 and 0.6 probability that a newborn egg of the susceptible strain, propargite-resistant strain, $R♂ \times S♀$ hybrid and $S♀ \times R♂$ hybrid of *T. urticae*, respectively, survived to the female adult stage. The probability remains the same if treated with LC_{50} of susceptible strain. There is 0.2, 0.4, 0.4 and 0.2 probability that a newborn egg of the susceptible strain, propargite-resistant strain, $R♂ \times S♀$ hybrid and $S♀ \times R♂$ hybrid of *T. urticae*, respectively, survived to the male adult stage. The probability decreased if treated with LC_{50} of susceptible strain. The lowest survival rate of a newborn egg to male adult stage is related to TSSM receiving LC_{90} of susceptible strain.

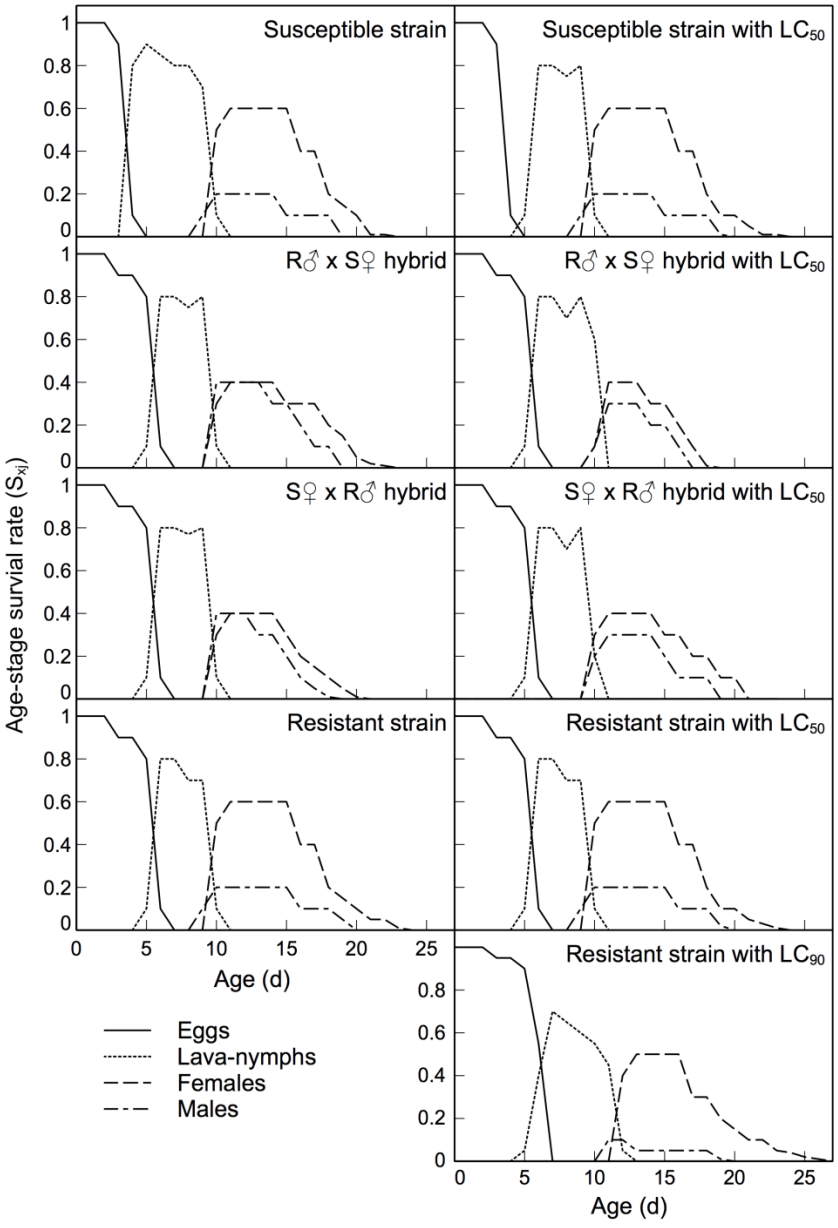

Figure 1. Age-stage-specific survival rate (S_{xj}) of susceptible and resistant strains and *F1* hybrids of *Tetranychus urticae*.

Age-specific survivorship, age and age-stage-specific fecundity

The age-specific survivorship (l_x), mean number of offspring produced by TSSM individuals of the age *x* and stage *j* per d with the age-stage-specific fecundity (f_{xj}) and age-specific fecundity (m_x) of TSSM of strains and hybrids are shown in Figure 2. The start of oviposition of the first female occurred at the age of 10.70, 11.10, 11.29 and 10.65 for the strains and hybrids. Treatment of the resistant strain with LC_{90} of susceptible strain did delay the start of oviposition by 2 d (13.03 d). The highest daily fecundity [peak of *f* (*i*, female)], when untreated, of TSSM for the strains and hybrids was 2.5, 3.0, 3.0 and 2.0 eggs, at the age of 18, 19, 19 and 16, respectively. If treated with LC_{50} of susceptible strain there was a decrease in daily fecundity except the resistant strain. The highest daily fecundity for the resistant strain three times lower when treated with LC_{90} of susceptible strain.

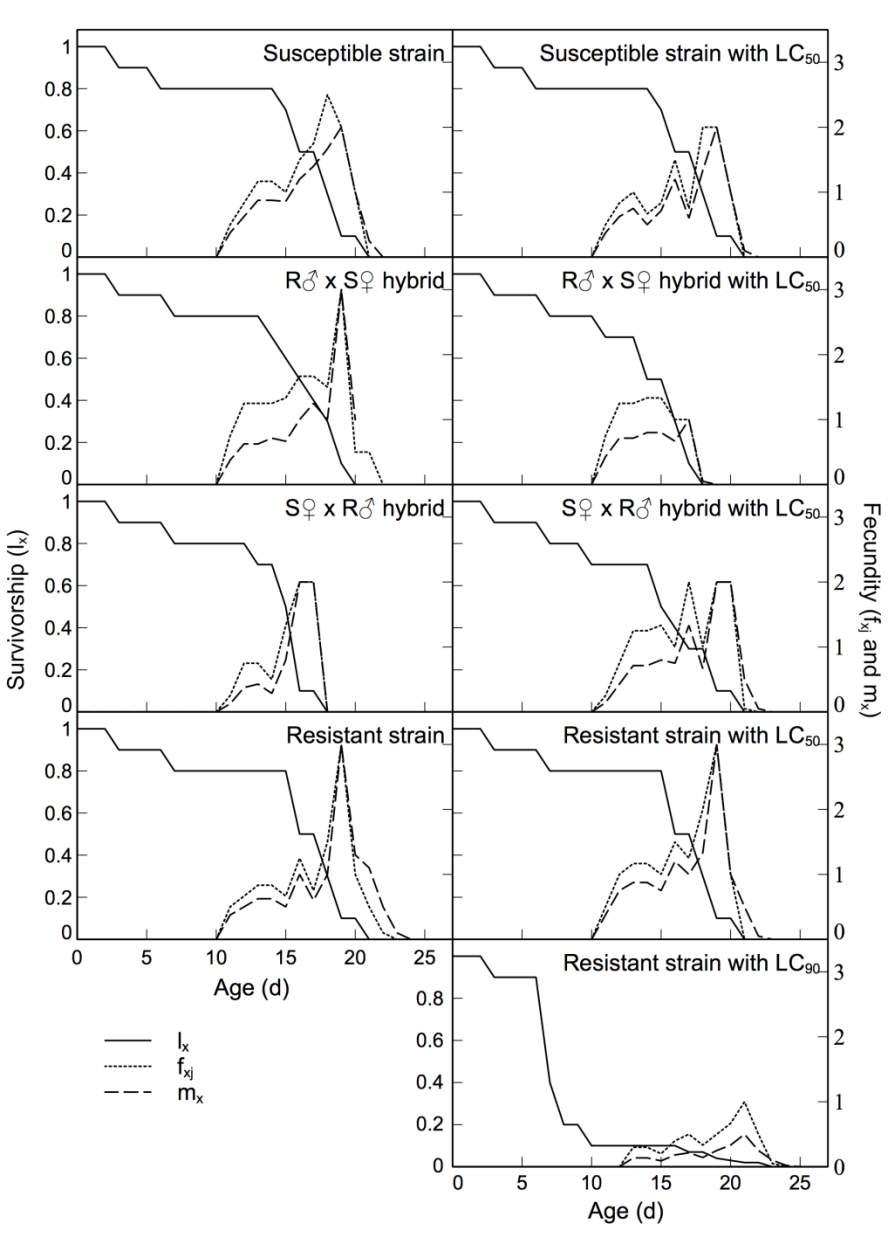

Figure 2. Age-specific survivorship (l_x), age-stage fecundity of female (f_{xj}) (offspring), and age-specific fecundity (m_x) of susceptible and resistant strains and *F1* hybrids of *Tetranychus urticae*, using the age-stage, two-sex life table.

Population projections of the susceptible and propargite-resistant strains and reciprocal *F1* hybrids of *Tetranychus urticae*

Population projections of the number of adult females of *T. urticae* are shown in Figure 3 and the increase or decrease (relative to the control group) in the number of adult females of the susceptible and propargite-resistant strains and *F1* hybrids over 10 generations (using Equation 8) are shown in Figure 4. For the untreated control groups (Figure 3), the susceptible strain gave the highest population projection followed by the propargite-resistant strain, the $R^{\male} \times S^{\female}$ and $S^{\male} \times R^{\female}$ hybrids, respectively. In groups treated with LC_{50} of the susceptible strain (Figure 3), the projected population size after 10 generations showed that the propargite-resistant strain superseded the susceptible strain followed by the $S^{\male} \times R^{\female}$ hybrid, the propargite-resistant strain treated with LC_{99} of susceptible strain and the $R^{\male} \times S^{\female}$ hybrid. Figure 4 clearly shows that the hybrid $S^{\male} \times R^{\female}$ increased most (from treatment with the LC_{50} of the susceptible strain), followed by the propargite-resistant strain, as their numbers increased at each generation (in relation to that of the respective control). The number of adult females decreased with each generation in the susceptible strain and the $R^{\male} \times S^{\female}$ hybrids, as a result of treatment with LC_{50} of the susceptible strain, compared with their untreated group.

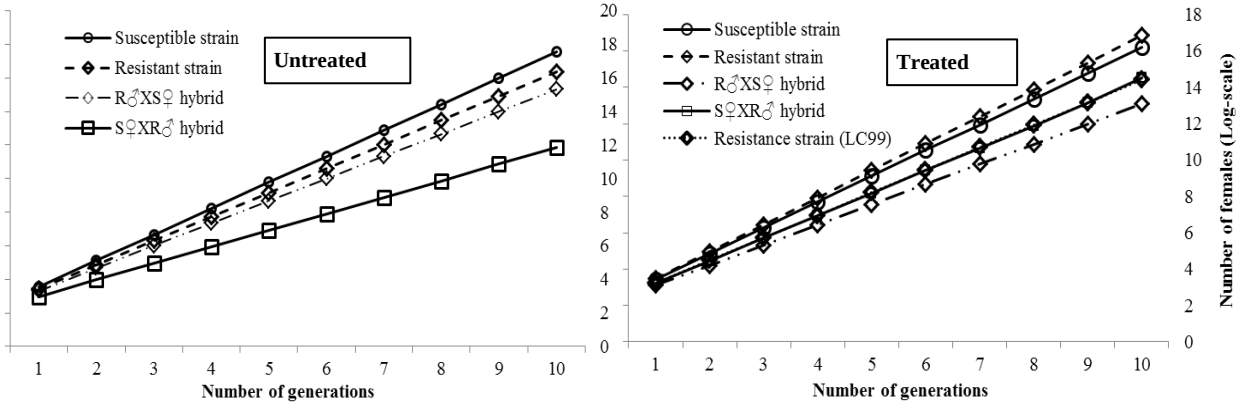

Figure 3. Projected number of untreated and treated *Tetranychus urticae* females of the susceptible and propargite-resistant strains and reciprocal *F1* hybrids after 10 generations.

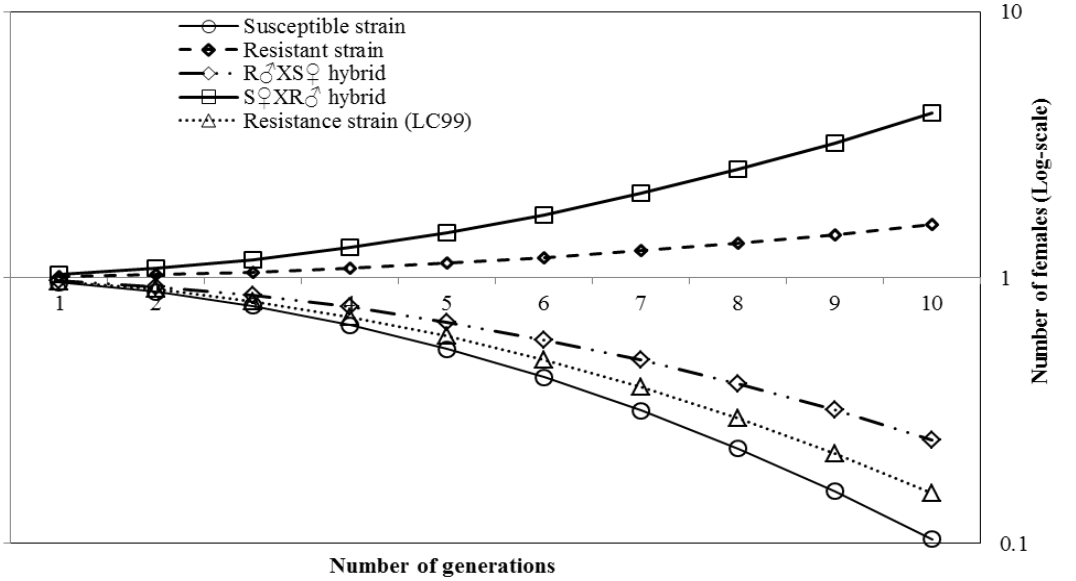

Figure 4. Rate of increase/decrease of number of *Tetranychus urticae* females of the susceptible, propargite-resistant strains and reciprocal *F1* hybrids at each generation treated with LC_{50} of the susceptible strain.

Discussion

Andres (1957) reported a mean developmental time (from egg to adult) of 10.5 and 7.0 d at 24 and 35ºC, respectively, for *T. urticae.* Whereas, Laing (1969) recorded a mean developmental time of 16.9 d for females of *T. urticae* reared on strawberry at an average temperature of 20.3ºC. Carey & Bradley (1982) recorded mean developmental time of 10.5 and 6.2 d at 23.8ºC and 29.4ºC, respectively, for the same species reared on cotton seedlings. Given these data, and assuming a linear developmental rate versus temperature relationship, developmental times of around 11 d would be expected at 22.4ºC as used in this study. Developmental times close to 11 d were recorded for all the strains and hybrids in the control groups and those treated with the LC_{50} of the susceptible strain, and no significant differences were found between these. Several authors have reported no significant difference in the developmental times of the susceptible and resistant strains of different insects, for example, Kasamatsu & Ogawa (1992), Saito et al. (1992) and Omer et al. (1992). Sabelis (1985) suggested that tetranychid mites have been intensively selected for reduced developmental times, and possibly have reached their physiological limit. This may explain why no significant differences were detected in the developmental time among the different strains and hybrids of the control groups.

While the treatment of eggs of both the strains and hybrids with the LC_{50} of the susceptible strain did not significantly affect the developmental time from egg to adult, the treatment of eggs of the propargite-resistant strain with LC_{99} of the susceptible strain did increase the developmental time by about 2 d. No physiological reason for this is evident. All the other strains/hybrids died as a result of this treatment. The higher concentrations (e.g., LC_{99} of susceptible strain) intended to kill spider mites would kill not only the susceptible strain but the heterozygous hybrids as well while the propargite-resistant strain would survive with prolonged developmental time showing pleiotropic effects. This longer developmental time, combined with several other factors shown in Table 2 could possibly decrease the rate of resistance development at any location.

Reported intrinsic rates of increase (r_m) for *T. urticae* differ widely from study to study. Watson (1964) determined r_m to be between 0.202 and 0.256 depending on the age of the host plant. Shih et al. (1976) determined r_m to be 0.336 at 27ºC. Whereas, Laing (1969) reported an r_m of 0.143 at 20.3ºC on cotton seedlings, although Carey & Bradley (1982) reported r_m to be 0.219 at 23.8ºC reared on the same host. Herron & Rophail (1993) reported an r_m values of 0.285 and 0.292 at 28.4ºC and finite rates of increase (λ) of 1.33 and 1.34 for susceptible and clofentezine-hexythiazox-resistant strains of *T. urticae* reared on *P. vulgaris*, respectively. Other researchers have reported the *r*-values of spider mites from 0.212 to 0.480 per d (Razmjou et al., 2008; Sedaratian et al., 2011). In this study the values of r_m was found to be 0.214 and 0.188 per d for untreated susceptible and propargite-resistant strain of *T. urticae.* The finite rates of increase (λ) for the susceptible and propargite-resistant strains of *T. urticae* was 1.243 and 1.204, respectively. The values of both r_m and λ were smaller than those given by Herron & Rophail (1993), which was probably are due to the lower developmental temperature of 22.4ºC.

To estimate the variability of life-table parameters, jackknife and bootstrap techniques are usually used. However, Huang & Chi (2013) reported that the jackknife technique may overestimate the variability. They found that the bootstrap method generated normally distributed estimates and smaller variances. In this study bootstrap technique was used to estimate variability of life-table parameters in two-sex life-table program.

The R_0 value describes the physiological capability of an individual relative to its reproductive capacity. The R_o values of TSSM decreased significantly for the susceptible strain and $R^{\male} \times S^{\female}$ hybrid treated with LC_{50} of susceptible strain, however its value increased for the $S^{\female} \times R^{\male}$ hybrid (from 7.09 to 18.38). The R_o value for TSSM was reported as 11.25 on bean, 29.13 on cowpea and 53.84 on soybean (Razmjou et al., 2009).

The value of r_m for the susceptible strain and the $R^{\male} \times S^{\female}$ hybrid treated with LC_{50} of susceptible strain and the propargite-resistant strain treated with LC_{99} of susceptible strain decreased compared with that of the untreated controls, whereas, that of the propargite-resistant strain and $S^{\male} \times R^{\female}$ treated with LC_{50} of the susceptible strain increased. Wrensch (1985) suggests that such differences, although small, are sufficient for differential success within a species. Roush & McKenzie (1987) were also of the opinion that although the difference in fitness may be small, it is important to determine whether such selective disadvantages are sufficiently large to be useful in practical situations. Figure 4 clearly shows that small (possibly statistically nonsignificant) differences as found in this study have biological significance. If each generation of *T. urticae* receives sublethal concentrations of propargite (e.g., LC_{50} of the susceptible strain), the number of females of the propargite-resistant strain and the hybrid $S^{\male} \times R^{\female}$ would continue to increase with each generation while those of the susceptible strain and $R^{\male} \times S^{\female}$ hybrids would decline increasing the resistance frequency each generation. Also, Smirnova (1987) found that the progeny of resistant females and sensitive males ($S^{\male} \times R^{\female}$) of carbaryl-resistant tick, *Hyalomma plumbeum* (Panzer, 1795), were resistant and resistance increased from generation to generation. Inadequate spray coverage of propargite, possibly producing sublethal effects, could also increase resistance frequency. If each generation of *T. urticae* is treated with higher concentrations intended to kill most of the mites (e.g., LC_{99} of susceptible strain or higher) then all the susceptible and hybrid mites will most likely die. However, the numbers of the propargite-resistant strain would still increase, but at slower rate compared with the untreated resistant strain. Under field conditions, areas poorly sprayed (inadequate coverage) and/or inadequate dosage can be common (Hoy et al., 1998). As a result, in crops where propargite-resistant mites occur, this would increase the chances of an increase in resistance frequency after each application of propargite compared with a field properly sprayed with the right dose where resistance build up would be relatively slow.

The changing frequency/percentage of adult females of the susceptible and propargite-resistant strains and hybrids, based on their differential success (difference in the values of r_m), and propargite application at each generation will continue to change the resistance frequency throughout a growing season at a particular location. For example, Dennehy & Granett (1984) reported an increase in the proportion of locations with detectable levels of dicofol-resistant spider mites late in the cotton growing season. Any decrease in resistance frequency at a location throughout a growing season may be the result of the resistance management strategy in place but any increase in resistance frequency, with continuous selection pressure, could possibly be the result of the differential success of different strains within a species. Application of any selective force, together with a lower number of adults exhibiting dispersal behavior (Shah & Worner, 2018) would then help create areas of intense infestation. Similarly, as Wang et al. (2010) stated, an appropriate resistance management strategy could promote reversion of the resistant populations back to susceptibility.

This study demonstrated that the duration of different life stages changes according to the propargite dosage applied to the field. In case of inadequate dosage (e.g., 0.006% ai) there is higher probability that the propargite-resistant strain and $S^{\male} \times R^{\female}$ hybrid will produce more progeny and increase in population will occur at a higher rate. Depending upon the prevalent resistance frequency, an adequate dosage (e.g., 0.032% ai) may kill the susceptible individuals and hybrids present in the field but the propargite-resistant individuals may still continue to reproduce (although at a slower rate). These finding could be incorporated into any new or existing integrated resistant management program.

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