Sublethal effects of fenpyroximate and pyridaben on two predatory mite species, Neoseiulus womersleyi *and* Phytoseiulus persimilis *(Acari, Phytoseiidae)*

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Sublethal effects of fenpyroximate and pyridaben on two predatory mite species, *Neoseiulus womersleyi* and *Phytoseiulus persimilis* (Acari, Phytoseiidae)

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Abstract Laboratory bioassays were conducted to evaluate the sublethal effects of fenpyroximate and pyridaben on life-table parameters of two predatory mites species, *Neoseiulus* (= *Amblyseius) womersleyi* and *Phytoseiulus persimilis*. In these assays, young adult females were treated with three sublethal concentrations of each acaricide. The life-table parameters were calculated at each acaricide concentration, and compared using bootstrap procedures. For each acaricide, the LC_{50} estimates for both species were similar, yet the two species exhibited completely different susceptibility when the population growth rate was used as the endpoint. Exposure to both acaricides reduced the net reproduction rate (R_o) in a concentration-dependent manner and their EC_{50}s were equivalent to less than LC_7. Two different scales of population-level endpoints were estimated to compare the total effect between the species and treatments: the first endpoint values were based on the net reproductive rate (fecundity λ) and the second endpoint values incorporated the mean egg hatchability into the net reproductive rate (vitality λ). The fecundity λ decreased in a concentration-dependent manner for both acaricide treatments, but the vitality λ decreased abruptly after treatment of *N. womersleyi* with pyridaben. The change

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in the patterns of λ revealed that the acaricide effects at the population level strongly depended on the life-history characteristics of the predatory mite species and the chemical mode of action. When the total effects of the two acaricides on *N. womersleyi* and *P. persimilis* were considered, fenpyroximate was found to be the most compatible acaricide for the augmentative release of *N. womersleyi* after treatment.

Keywords *Tetranychus urticae* · Phytoseiid predators · Life table · Population growth rate · Fecundity · Fertility

Introduction

Several predatory mite species have been used to control *Tetranychus urticae* Koch populations in various crop systems (Oatman et al. 1977a, b; Helle and Sabelis 1985; Malais and Ravensberg 1992; Greco et al. 1999, 2005; Jung et al. 2004; Rhodes et al. 2006). *Neoseiulus* (= *Amblyseius*) *womersleyi* (Schicha) is a native and dominant predatory mite species in apple orchards in Korea (Jung et al. 2003). This species has been successfully used in some tea plantations for the biological control of *T. urticae* (Kim et al. 1997). *Phytoseiulus persimilis* Athias-Henroit, which has been successfully used as a biological control agent of *T. urticae* in greenhouse crops (Helle and Sabelis 1985), has been imported and used to treat greenhouse crops such as roses, cucumbers, and strawberries in Korea (Kim and Yoo 2002).

Several studies have indicated that the predatory mites alone may not be able to maintain *T. urticae* populations below the economic injury level, although their efficacy for biological control of *T. urticae* on various crops has been proven (Helle and Sabelis 1985; Greco et al. 1999, 2005; Jung et al. 2004). Because control of *T. urticae* is often partially successful through the use of predatory mites, especially when the mite density is high, the use of acaricides is needed to achieve reductions in *T. urticae* that are economically relevant (Malezieux et al. 1992). Thus, success in implementing biological control of *T. urticae* is partially dependent on the compatibility of natural enemies with current pesticides used in targeted agricultural systems. To harmoniously combine biological and chemical control methods, evaluation of the effects of acaricides on the predatory mites is needed because pesticides can often disrupt the trophic relationships that these beneficial species have, which can result in direct mortality or adverse sublethal effects.

Understanding the effects of sublethal concentrations on mortality, fecundity, egg consumption and fertility of phytoseiids is important to their successful integration into augmentation programs (Sáenz-de-Cabezón Irigaray et al. 2007). Many studies have examined the side effects of various insecticides and acaricides on these predatory mite species (Zhang and Sanderson 1995; Spollen and Isman 1996; Kim et al. 1999; Kim and Yoo 2002). Most studies have examined the acute toxicity of the acaricides on the predatory mites and the LC_{50} is the common endpoint used to estimate acaricide toxicity. Along with the acute toxicity assessment (LC_{50}), sublethal effects such as the reproduction of survivors and survivors of progeny after chronic exposure to acaricides should be considered to obtain a more realistic prediction of the effects of an acaricide. Several authors have suggested that the best method to evaluate and combine the lethal and sublethal effects of pesticides is by life table analysis (Gentile et al. 1982; Stark et al. 1997; Kim et al. 2004). The life table measurements integrate age-specific survivorship and fecundity into a single parameter of population response such as the finite rate of population growth (λ) or intrinsic rate of increase (r_m) (Van Leeuwen et al. 1985), and they

provide a measure of population growth, which may be integrated into a mathematical model. Accordingly, by using 'population growth rate', it is possible to more accurately measure the toxicity of pesticides on beneficial organisms (Kim et al. 2004). However, few researchers have adopted these approaches to evaluate the effects of pesticides on predatory mites at higher levels of organization than the individual (Stark et al. 1997).

Fenpyroximate and pyridaben, which belong to the family of mitochondrial electron transport inhibitors (METIs), were first introduced to Korea in the early 1990s for the control of *T. urticae* (Cho et al. 1995) and are still widely used in various crop and pest systems in Korea (Park et al. 2005; Kwon et al. 2008). These METI-acaricides inhibit complex I (NADH: ubiquinone oxidoreductase) of the mitochondrial respiratory pathway, most likely by binding to a subunit of the associated electron transport particles (Hollingworth and Ahammadsahib 1995; Van Pottelberge et al. 2009). Good efficacy against all developmental stages of *T. urticae* has been reported (Hirata et al. 1995; Stumpf and Nauen 2001), but resistance to these acaricides has already been reported in Korea (Cho et al. 1995; Suh et al. 2006).

In this study, the sublethal effects of fenpyroximate and pyridaben on *N. womersleyi* and *P. persimilis* were measured to predict their overall effects at the population level. Knowledge of the population-level effects of fenpyroximate and pyridaben are needed for the successful implementation of integrated pest management. In this study, three endpoints were used and compared to better understand the effects of the acaricides: acute concentration mortality estimates (48 h-LC_{50}s), net reproductive rate (R_o) and population growth (λ). The R_o and λ were determined by constructing an age specific life table. Also, median effective concentrations (EC_{50}s) of the R_o and λ for each acaricide and mite species were estimated, and compared with the predicted probit mortalities.

Materials and methods

Chemicals tested

Formulated fenpyroximate (5 suspension concentrate; Dongbu Hannong Chemicals, Seoul, Korea) and pyridaben (20 wettable powder; Hankook Samgong Chemicals, Seoul, Korea) were tested. These two acaricides were chosen because they have very different activity against the fecundity and egg hatchability of *T. urticae* (Kim et al. 2004).

Serial dilutions were prepared in deionized water. All dilutions of each acaricide were prepared fresh each day. All the bioassays performed in this study were conducted under the following conditions: 25 ± 2°C, 60–80% RH and a photoperiod of 16:8 (L:D) h.

Maintenance of test organisms

Tetranychus urticae was maintained in the laboratory at 23–28°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h after they were collected from a commercial rose greenhouse at Buyeo, Chungnam Province, Korea in 1993. *T. urticae* adult females collected from the rose greenhouse were transferred to kidney bean plants (*Phaseolus vulgaris* L.), containing 3–6 fully developed leaves in an acryl cage (30 × 30 × 60 cm), and maintained at 25 ± 0.5°C, with 60 ± 10% RH and a photoperiod of 16:8 (L:D) h.

Colonies of two predatory mite species, *N. womersleyi* and *P. persimilis*, were obtained from the Seoul National University, Seoul, Korea and the National Institute of Agricultural Science and Technology, Suwon, Korea, respectively. The *N. womersleyi* were originally

obtained from commercial apple orchards in Korea and *P. persimilis* were provided by the Koppert Biological Systems (Koppert BV, Berkel en Rodenrijs, The Netherlands).

Neoseiulus womersleyi were maintained on detached kidney bean leaves infested with various stages of *T. urticae*. The detached kidney bean leaves were maintained in a relatively fresh state by placing the stems into a plastic plate with holes, and the plate was placed in a stainless steel tray filled with water. Kidney bean leaves were replaced when the leaves became deteriorated (Lee and Ahn 2000). *P. persimilis* were reared at all stages of *T. urticae* on bean leaves cut from plants infested with spider mites. These leaves were placed on moistened cotton in Petri dishes (15 cm in diameter), and the dishes were held in a transparent plastic box that was maintained at 60% RH. The plastic boxes were placed in an incubator controlled at 25 ± 2°C. *P. persimilis* were transferred to new leave infested with *T. urticae* every 1–2 days.

To obtain a cohort of either adult female predatory mite species, 20 adult females and 10 males of each predator species were inoculated on the detached kidney bean leaf infested with various stages of *T. urticae*, and allowed to lay eggs. The adults were then removed after 24 h. The leaf containing the eggs of predator mites was placed upside down on a water-saturated cotton pad (21 × 9 × 2 cm) in a plastic container (25 × 11 × 4 cm) and the container was incubated under the following conditions: 25 ± 2°C, 60–80% RH and a photoperiod of 16:8 (L:D) h. Several sets were prepared to ensure a large number of predator eggs. *T. urticae* eggs were supplied as food after the predator eggs were hatched. Adult cohorts (<2 days old) produced from this procedure were used throughout this study.

Acute toxicity to adult predator mites species

Acute toxicity of fenpyroximate and pyridaben to adult female *N. womersleyi* and *P. persimilis* was determined using a residual contact bioassay described by Spollen and Isman (1996), rather than through direct contact toxicity. Because acaricides are used to reduce the pest population before release of biological control agents in biological control programs (Malezieux et al. 1992), the direct contact toxicity is not an accurate approach to measure toxicity and thus was not used in this study.

Leaf disks (5.8 cm in diameter) were cut from bean plant leaves, and placed in Petri dishes (9.8 cm diameter), which contained a water-saturated cotton pad. Twenty *T. urticae* females were placed on the leaf disk, and allowed to lay eggs for 24 h producing at least 100 *T. urticae* eggs per leaf disk. The leaf disks were then sprayed with aqueous product using a Potter spray tower (Burkard Scientific, Uxbridge, Middlesex, UK), calibrated to deliver 1.6 mg/cm^2 after a 5 s settling time. Six logarithmically spaced concentrations were tested for each predator mite species. Controls were treated with distilled water. Five leaf disks were prepared for each concentration. After 1 h of drying at room temperature, ten young adult females (<2 days old) of each predator species were placed on each leaf disk. The Petri dishes were placed inside humidity boxes in an incubator. Mortality was assessed 48 h after treatment. Adult female mites were considered dead if their appendages did not move when touched with a camel's-hair brush. The whole experiment was repeated three times at different dates. Control mortality did not exceed 5% in all the tests.

Sublethal effects on adult survivals, reproductions and egg hatchability

Sublethal concentrations were chosen from the 48-h acute concentration–response relationship (Table 1) generated for adult females of *N. womersleyi* and *P. persimilis*. The sublethal concentrations used in this study were listed in Table 2. The sublethal

Table 1 Median lethal concentration (LC_{50}) estimated for *Neoseiulus womersleyi* and *Phytoseiulus persimilis* exposed to fenpyroximate and pyridaben for 48 h at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Species	Fenpyroximate (ml/l)					Pyridaben (mg/kg)				
	n	Slope (±SE)	LC_{50} (95% FL)	*df*	χ^2	n	Slope (±SE)	LC_{50} (95% FL)	*df*	χ^2
N. womersleyi	450	3.09 ± 0.92	67.6 (30.9–102.2)	5	5.99	450	3.12 ± 0.90	178.7 (108.8–80.1)	5	6.23
P. persimilis	320	6.58 ± 0.08	27.8 (21.1–2.4)	5	7.02	320	3.17 ± 0.75	98.1 (71.8–27.2)	5	6.38

Table 2 List of sublethal concentrations[a] of fenpyroximate and pyridaben used for life table analysis and egg consumption tests with *Neoseiulus womersleyi* and *Phytoseiulus persimilis*

Concen	Fenpyroximate (ml/l)		Pyridaben (mg/kg)	
	N. womersleyi	*P. persimilis*	*N. womersleyi*	*P. persimilis*
LC_1	–	12.3	–	18.1
LC_5	–	15.6	–	29.7
LC_{10}	–	17.7	–	38.7
LC_{10}	25.9	17.7	69.4	38.7
LC_{30}	46.6	23.1	121.4	67.0
LC_{50}	67.6	27.8	178.7	98.1

[a] Concentration of LC_{10}, LC_{30} and LC_{50} of fenpyroximate and pyridaben for *P. persimilis* is used for egg consumption test, and the other concentrations are for life table analysis for both species

concentrations selected for *N. womersleyi* were LC_{10}, LC_{30} and LC_{50} for both acaricides (see Table 2 for actual concentrations). However, the sublethal concentrations selected for *P. persimilis* were LC_1, LC_5 and LC_{10} for both acaricides because concentrations higher than these values resulted in a dramatic decrease in egg production, which prevented us from evaluating sublethal effects.

A leaf disk (13.8 cm in diameter) with eggs of *T. urticae* was placed in a Petri dish supported by a cotton pad filled with distilled water. Prior to introducing the predatory mites, the leaf disc containing an ample amount of *T. urticae* eggs (>100 eggs) was sprayed with predetermined sublethal concentrations of fenpyroximate or pyridaben as described above. After spraying, the leaf disks were transferred to new Petri dishes containing water-saturated cotton and air dried for 1 h. Five young female adult cohorts (<2 days old) were transferred to the leaf using a camel's-hair brush and the Petri dish was placed under the following conditions: 25 ± 2°C, 60 ± 10% RH, and a photoperiod of 16:8 (L:D) h.

Mite populations on each treated leaf disk were examined daily for up to 6 days by recording the number of eggs, immatures, and adults. The 6-day time frame for observation was chosen because it provided enough time to reproduce (egg laying and hatching) and not enough time to develop into adults. The treated leaf disks were observed continuously for 6 days without removing newly laid eggs, because monitoring reproduction by following all individual eggs was too labor-intensive. Therefore, the cumulative numbers of eggs and immatures were recorded at each day of observation. The mean number of eggs per female per day (ET_x) was calculated using the following equation (Kim et al. 2004):

$$ET_x = \left[\frac{(E_x - E_{x-1}) + (I_x - I_{x-1})}{N_{x-1}}\right], \quad (1)$$

where E, I and N were the number of eggs, immatures and adult survivors, respectively at day x or $x - 1$. An ET_x value of equal or below 0 at day x indicates that no eggs were produced during day $x - 1$ and x. Survivorship of initial adult female populations was estimated daily for 6 days. This experiment was replicated nine times per treatment.

Sublethal effect on egg consumption

Twenty adult females *T. urticae* were allowed to lay eggs on the leaf disk (5.3 cm in diameter) for 24 h, and the leaf disk was treated with fenpyroximate or pyridaben. *T. urticae* females were removed and eggs counted under a dissecting microscope. The number of eggs per disk was fixed to 100 by removing the remaining eggs. The sublethal treatment concentrations used for these experiments were 48-h LC_{10}, LC_{30} and LC_{50} of each acaricide for both predatory mite species (Table 2). Concentrations exceeding these values resulted in no or very few egg consumption.

Young adult females of each species were collected from the maintenance stock and placed on the clean bean leaves. After 24 h, females with high activity (sustained walking) were selected for this experiment. Two young adult females of each predator species were added to the treated leaf disk. The numbers of *T. urticae* eggs consumed were counted 3 days after treatment under a dissecting microscope.

Effects of sublethal exposure of acaricides on population growth

An age-classified model was derived from the age-specific survivorship (l_x) and fecundity (m_x) schedules, which were generated for each species in each acaricide treatment. These life tables were used to construct age-classified projection matrices (Leslie matrices) using a daily projection interval for up to 6 days. The survival probabilities (P_i) and fertilities (F_i) in the matrix were calculated using the following birth-flow formula (Levin et al. 1996),

$$P_i = \frac{l(i+1) + l(i)}{l(i) + l(i-1)} \quad \text{and} \quad F_i = \frac{(l(0)l(1))^{1/2}}{2}(m_i + P_i m_{i+1}), \quad (2)$$

where $l(i)$ was the survivorship from emergence to age i and m_i was the average number of female offspring per female in age class i. The female proportion among the offspring (sex ratio of offspring) was set to 0.71 for *N. womersleyi* (Toyoshima and Amano 1998) and 0.80 for *P. persimilis* (Laing 1968).

The population growth rate was calculated as the dominant eigenvalue λ of each matrix (Caswell 1996). The λ value provides information regarding the status of the population, where $\lambda > 1$ indicates an increasing population, $\lambda < 1$ indicates a declining population, and $\lambda = 1$ indicates no change in population with time. The net reproductive rate (R_o) was also calculated from each treatment using the age-classified matrix (Caswell 2001). R_o was the number of female offspring produced by the average female in a cohort over her lifetime (King 1966).

Fenpyroximate and pyridaben have very different ovicidal effects on *T. urticae* (Kim et al. 2004). To incorporate the infertility rate of eggs into the demographic analysis,

another projection matrix including mean egg hatch rates (h_x) was constructed (Kim et al. 2004). This projection matrix incorporated the mortality-corrected production of female offspring ($\sum l_x m_x h_x$) at three sublethal concentrations of each acaricides. An average hatch rate for each treatment was estimated by dividing the total numbers of eggs produced by the total number of immatures produced. Estimates of the λ values without incorporating the hatch rate into the life table matrix was represented as "fecundity λ" and incorporation of the hatch rate was represented as "vitality λ". Relative reduction (RR) of the vitality λ to the fecundity λ in a percentile scale was estimated using the following equation (Kim et al. 2004),

$$\mathrm{RR} = \left(1 - \left(\frac{\text{vitality}\lambda}{\text{fecundity }\lambda}\right)\right)100. \tag{3}$$

Since the acaricide treatment concentrations were different between species and experiments, the effects on reproduction, egg consumption and population growth rate were compared using median effective concentrations (EC_{50}s). The EC_{50}s were estimated by fitting the data to the following model (Haanstra et al. 1985):

$$y = \frac{c}{(1 + \exp(b(\phi - a)))}, \tag{4}$$

where y was the reproduction, egg hatching rate or λ, ϕ was the natural logarithm of the test concentrations, a was the logarithm of the EC_{50}, b was the slope parameter and c was the reproduction or λ in the controls. The maximum likelihood method was used to find the best-fitting a and b. Substitutions were made for the EC_{50}s into the probit equations to determine the corresponding predicted probit mortalities at those concentrations (Stark et al. 1997).

General statistical analysis

Concentration-mortality regressions were estimated by probit analysis (POLO-PC) (LeOra Software 1987). Differences in toxicity between predatory mite species were considered significant when the 95% fiducial limits did not overlap.

Differences in the mean egg hatch rate and egg consumption at sublethal concentrations were tested using analysis of variance (ANOVA) followed by the Tukey's honest significant difference (HSD) test to generate mean separations (SAS Institute 1996). The hatch rate data were transformed using square-root transformation prior to performing ANOVA. To test for significant differences in the λs among treatments, 95% confidence intervals were estimated using the bootstrap procedure described by Levin et al. (1996). Non-overlap of the 95% confidence limits was the criterion used to assess significance of differences in both treated and untreated females.

Results

Concentration-mortality estimates

A comparison of the LC_{50} values indicated that both mite species were equally susceptible to fenpyroximate or pyridaben, but the LC_{50}s of *P. persimilis* to fenpyroximate and pyridaben were 2.4- and 1.8-times lower than those of *N. womersleyi* (Table 1).

Sublethal effects on adult survivals and fecundities

The effects of sublethal concentrations of fenpyroximate and pyridaben on the daily survivorship and fecundity of *N. womersleyi* and *P. persimilis* adults are shown in Figs. 1 and 2, respectively. The survivorships of the adults declined in a concentration-dependent manner for both acaricides. Direct comparison between the two mite species was not performed because the scale of the sublethal concentrations tested were different. When changes in the survivorship curves were compared between acaricides within an exposure regime, the response of the two mite species to the acaricides was different. The slope of the curves for *N. womersleyi* decreased more rapidly as the sublethal concentration increased when treated with fenpyroximate. The opposite trend was observed for *P. persimilis*, where the survivorship curves greatly decreased when *P. persimilis* was treated with pyridaben.

Daily fecundity decreased in the same concentration-dependent manner as the survivorship, resulting in a decline of the R_o (Table 3). The fecundity patterns of populations exposed to sublethal concentrations were similar to those of the control populations, but exposure to the acaricides reduced the fecundity, where the reduction was great when *P. persimilis* was treated with fenpyroximate and when *N. womersleyi* was treated with pyridaben.

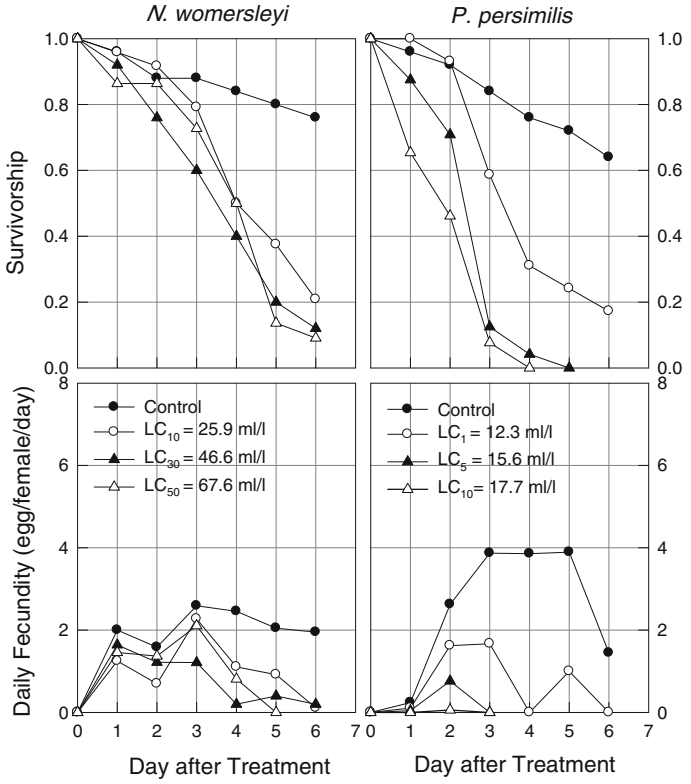

Fig. 1 Age specific survivorship and age specific daily fecundity of *Neoseiulus womersleyi* and *Phytoseiulus persimilis* when exposed to three sublethal concentrations of fenpyroximate at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

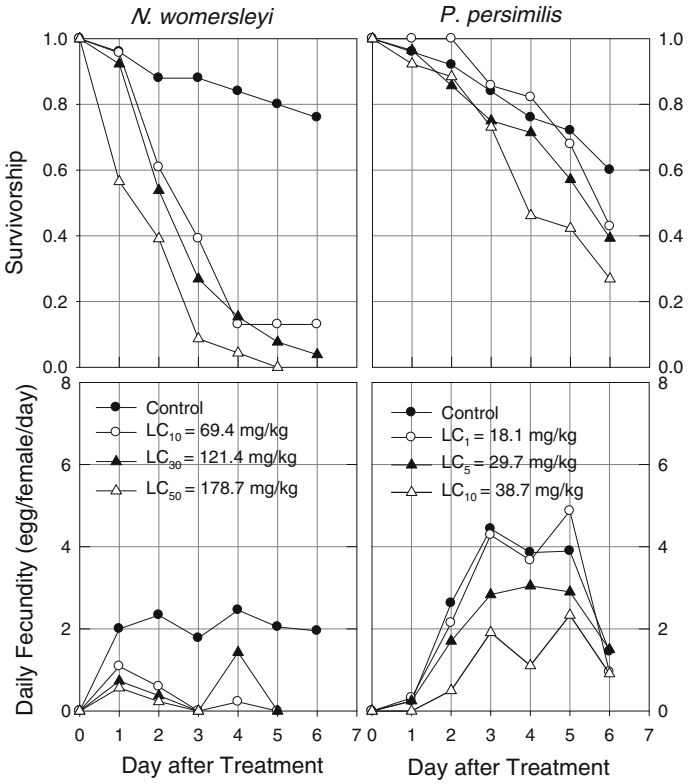

Fig. 2 Age specific survivorship and age specific daily fecundity of *Neoseiulus womersleyi* and *Phytoseiulus persimilis* when exposed to three sublethal concentrations of pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Sublethal effects on reproductions and egg hatching

When the R_o values of the untreated controls were compared between species, the values for *N. womersleyi* were lower than those for *P. persimilis*, ranging from 7.61 to 7.65 for *N. womersleyi* and from 10.04 to 10.37 for *P. persimilis* (Table 3). The R_o values decreased as the concentration of fenpyroximate and pyridaben increased for both mite species, but the sensitivity to reproduction for the acaricides was different between the two species. At the same sublethal concentrations, a higher reduction was observed when the *N. womersleyi* was exposed to pyridaben; however, the opposite trend was observed for *P. persimilis*.

For *N. womersleyi*, the effective concentration that reduced R_o (EC_{50}) by 50% was 14.6 ml/l for fenpyroximate and 12.4 mg/kg for pyridaben. The solved probit values for the EC_{50} concentrations using the LC_xs were significantly different between the two acaricides; the mortality for fenpyroximate and pyridaben was estimated to be 3.0 and <1%, respectively. A similar result was observed on *P. persimilis*, but the corresponding probit mortality was higher for pyridaben treatment than for fenpyroximate treatment. This result suggested that the sublethal concentrations of both acaricides affected the reproduction of predatory mites.

Table 3 Net reproductive rates (R_o) and their median effective concentration (EC_{50}[a]) with the corresponding predicted acute probit mortality (%) for *Neoseiulus womersleyi* and *Phytoseiulus persimilis* when exposed to three sublethal concentrations of fenpyroximate and pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Species	Concen.[b]	Fenpyroximate		Pyridaben	
		R_o	EC_{50} (ml/l)	R_o	EC_{50} (mg/kg)
N. womersleyi	Control	7.65	14.6 ± 2.0 (3)[c]	7.61	12.4 ± 2.6 (<1)
	LC_{10}	3.23		1.01	
	LC_{30}	3.10		0.77	
	LC_{50}	2.37		0.29	
P. persimilis	Control	10.04	10.9 ± 1.0 (<1)	10.37	32.8 ± 1.0 (7)
	LC_1	2.54		10.29	
	LC_5	0.46		6.60	
	LC_{10}	0.02		2.86	

[a] EC_{50} value was estimated using Eq. 4

[b] See Table 2 for corresponding concentration in an active ingredient of each LC_x value estimated for fenpyroximate and pyridaben

[c] Values in parenthesis indicated that percent mortality assessed by probit analysis corresponding to the concentration value as lethal concentration levels (LC_x)

Table 4 Mean egg hatching rate (± SEM) of *Neoseiulus womersleyi* and *Phytoseiulus persimilis* when exposed to three sublethal concentrations of fenpyroximate and pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Concen.[a]	*N. womersleyi*		Concen.[a]	*P. persimilis*	
	Fenpyroximate	Pyridaben		Fenpyroximate	Pyridaben
Control	0.97 ± 0.05aA	0.97 ± 0.05aA	Control	0.98 ± 0.02aA	0.98 ± 0.02aA
LC_{10}	0.90 ± 0.09aA	0.48 ± 0.15bB	LC_1	0.93 ± 0.04aA	0.93 ± 0.05aA
LC_{30}	0.90 ± 0.07aA	0.43 ± 0.14bB	LC_5	0.96 ± 0.07aA	0.89 ± 0.14aA
LC_{50}	0.71 ± 0.18bA	0.24 ± 0.25cB	LC_{10}	0.92 ± 0.10aA	0.83 ± 0.21aA

Means within columns followed by the same lowercase letter or means within rows followed by the same uppercase letter are not significantly different at $\alpha = 0.05$ by Tukey's HSD test after a significant ANOVA

[a] See Table 2 for corresponding concentration in an active ingredient of each LC_x value estimated for fenpyroximate and pyridaben

The viabilities of eggs, determined by the egg hatching rate, in the controls were not significantly different between species (*t* test, $P < 0.05$) and at least 97% of the eggs were successfully hatched (Table 4). No sublethal effects on egg viability of *P. persimilis* were detected within the exposure regime, but very significant effects were observed for *N. womersleyi* (fenpyroximate: $F = 3.52$, $df = 3$, 152, $P < 0.05$; pyridaben: $F = 8.48$, $df = 3$, 152, $P < 0.001$). When *N. womersleyi* was treated with fenpyroximate, the egg viability gradually decreased as the sublethal concentration increased and reached 71% at the highest treatment concentration (LC_{50}). In contrast, when *N. womersleyi* were treated with pyridaben, the viability drastically decreased and was 24% at the same concentration.

Sublethal effects on egg consumption

The number of consumed eggs per female predatory mite for both *N. womersleyi* and *P. persimilis* decreased significantly as the acaricide concentration increased for both treatments (fenpyroximate—*N. womersleyi*: $F = 3.25$, $df = 3, 165$, $P < 0.05$; pyridaben—*N. womersleyi*: $F = 8.56$, $df = 3, 165$, $P < 0.001$, fenpyroximate-*P. persimilis*: $F = 4.21$, $df = 2, 125$, $P < 0.001$; pyridaben-*P. persimilis*: $F = 7.54$, $df = 2, 125$, $P < 0.001$) (Table 5). Because no or very few eggs were consumed at the LC_{50} for *P. persimilis*, these data were excluded from further data analysis. Both mite species consumed significantly more eggs in the fenpyroximate treatment than in the pyridaben treatment when compared at the same sublethal concentration (t test, $P < 0.05$).

The EC_{50} for egg consumption was 59.74 and 18.36 for *N. womersleyi* and *P. persimilis* in fenpyroximate treatments, respectively, and the corresponding probit mortality was 44 and 12% (Table 5). However, in the pyridaben treatment, a probit mortality of <1% reduced the egg consumption by 50%. This result demonstrated that the sublethal concentrations of pyridaben affected the egg consumption of predatory mite species more severely than did equal sublethal concentrations of fenpyroximate.

Comparisons of the finite rate of increase (λ) based on fecundity and vitality schemes

The two population growth rates (fecundity λ and vitality λ) for *N. womersleyi* and *P. persimilis* were compared between the two different acaricide treatments (Tables 6, 7). For the untreated controls, the estimated two population growth rates were very similar, as demonstrated by the overlapping 95% confidence intervals; however, the values were uniformly higher for *N. womersleyi* than for *P. persimilis*.

Both population growth rates decreased as the acaricide concentrations increased, but the effects were significantly different between *N. womersleyi* and *P. persimilis*. For *N. womersleyi*, the negative effect of pyridaben on the population growth was greater than that of pyridaben at the same sublethal concentration (Table 6). However, the opposite trend was observed for *P. persimilis* and the negative effect was great when fenpyroximate was used (Table 7). When *N. womersleyi* populations were exposed to pyridaben, the fecundity λ and vitality λ was <1 even at the lowest sublethal concentration (LC_{10}), indicating that the population was in decline. In contrast, both population growth rates were >1 at all tested fenpyroximate concentrations, which indicated that exposed populations were able to sustain relatively high rates of growth. However, the opposite was true for *P. persimilis*. When *P. persimilis* were treated with pyridaben, all the population growth rates were >1, but the growth rates were <1 when they were treated with fenpyroximate after LC_1 treatment.

The vitality λ was always smaller than the fecundity λ because the vitality λ included the egg viability (egg hatchability into the life table matrix) (Tables 6, 7). The difference between the vitality and fecundity λ values resulted from the different effects of the acaricides on the egg viabilities. The relative reduction (RR) of the vitality λ to the fecundity λ was small in fenpyroximate treatment for *N. womersleyi*, while the RR was high for pyridaben treatment, which increased in a concentration-dependent manner. The RR was 61.54 when treated at the LC_{50} of pyridaben, indicating that 61.54% of the reduction in population growth was due to egg viability. The RR of *P. persimilis* remained relatively constant within the exposure regime and the highest RR (5.22) was observed for pyridaben at LC_{10} (Table 7). Therefore, it can be concluded that the population growth of *N. womersleyi* was more severely affected by pyridaben than by fenpyroximate treatment

Table 5 Mean number of egg consumption (± SEM) and their median effective concentration (EC_{50}) with the corresponding predicted acute probit mortality (%) of *Neoseiulus womersleyi* and *Phytoseiulus persimilis* when exposed to three sublethal concentrations of fenpyroximate and pyridaben for 3 days at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Concen.[a]	*N. womersleyi*				*P. persimilis*			
	Fenpyroximate	EC_{50} (ml/l)	Pyridaben	EC_{50} (mg/kg)	Fenpyroximate	EC_{50} (ml/l)	Pyridaben	EC_{50} (mg/kg)
Control	54.7 ± 6.4aA	59.7 ± 1.1 (44)[b]	58.1 ± 10.6aA	7.2 ± 1.4 (<1)	54.7 ± 6.4aA	18.4 ± 0.4 (12)	58.1 ± 10.6aA	1.5 ± 0.1 (<1)
LC_{10}	48.4 ± 2.7bA		12.5 ± 4.8bB		31.3 ± 5.6bA		12.1 ± 7.6bB	
LC_{30}	31.8 ± 3.4cA		10.1 ± 3.5bB		10.0 ± 2.5cA		10.1 ± 5.9bA	
LC_{50}	25.2 ± 3.1cA		7.9 ± 2.7bB		–[c]		–	

Means within columns followed by the same lowercase letter or means within rows followed by the same uppercase letter are not significantly different at $\alpha = 0.05$ by Tukey's HSD test after a significant ANOVA

[a] See Table 2 for corresponding concentration in an active ingredient of each LC_x value estimated for fenpyroximate and pyridaben

[b] Values in parenthesis indicated that percent mortality assessed by probit analysis corresponding to the concentration value as lethal concentration levels (LCx)

[c] Very few egg consumptions were observed at this concentration

Table 6 Comparison of two population growth rates (fecundity λ and vitality λ)[a] with bootstrap-estimated 95% confidence limits for *Neoseiulus womersleyi* exposed to three sublethal concentrations of fenpyroximate and pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Concen.[b]	Fenpyroximate			Pyridaben		
	Fecundity λ	Vitality λ	RR[c]	Fecundity λ	Vitality λ	RR[c]
Control	2.29 ± 0.11 a	2.24 ± 0.17 a	2.18	2.35 ± 0.19 a	2.30 ± 0.15 a	2.13
LC_{10}	1.76 ± 0.10 b	1.66 ± 0.22 b	5.68	0.99 ± 0.21 b	0.60 ± 0.21 b	39.39
LC_{30}	1.68 ± 0.12 b	1.55 ± 0.18 b	7.74	0.88 ± 0.09 b	0.61 ± 0.14 b	30.68
LC_{50}	1.67 ± 0.26 b	1.42 ± 0.13 b	14.97	0.39 ± 0.12 c	0.15 ± 0.09 c	61.54

Means within columns in each chemical followed by the same letter are not significantly different based on non-overlapping the 95% confidence limits

[a] Estimates of λ values without and with hatch rate are represented as fecundity λ and vitality λ, respectively

[b] See Table 2 for corresponding concentration in an active ingredient of each LC value estimated for fenpyroximate and pyridaben

[c] Relative reduction $= \left(1 - \left(\frac{\text{Vitality}\lambda}{\text{Fecundity}\lambda}\right)\right)100$

Table 7 Comparison of two population growth rates (fecundity λ and vitality λ)[a] with bootstrap-estimated 95% confidence limits of *Phytoseiulus persimilis* when exposed to three sublethal concentrations of fenpyroximate and pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Concen.[b]	Fenpyroximate			Pyridaben		
	Fecundity λ	Vitality λ	RR[c]	Fecundity λ	Vitality λ	RR[c]
Control	2.09 ± 0.12 a	2.08 ± 0.17 a	0.48	2.12 ± 0.28 a	2.11 ± 0.21 a	0.47
LC_1	1.44 ± 0.09 b	1.43 ± 0.20 b	0.69	2.11 ± 0.11 a	2.05 ± 0.14 a	2.84
LC_5	0.67 ± 0.12 c	0.66 ± 0.18 c	1.49	1.81 ± 0.08 b	1.73 ± 0.12 b	4.42
LC_{10}	0.15 ± 0.09 d	0.15 ± 0.14 d	0.00	1.34 ± 0.19 c	1.27 ± 0.19 c	5.22

Means within columns in each chemical followed by the same letter are not significantly different based on non-overlapping the 95% confidence limits

[a] Estimates of λ values without and with hatch rate are represented as fecundity λ and vitality λ, respectively

[b] See Table 2 for corresponding concentration in an active ingredient of each LC value estimated for fenpyroximate and pyridaben

[c] Relative reduction $= \left(1 - \left(\frac{\text{Vitality}\lambda}{\text{Fecundity}\lambda}\right)\right)100$

because of the combined reduction in reproduction and egg viability. In contrast, *P. persimilis* was more strongly affected by fenpyroximate treatment primarily because of the reduction in reproduction.

The population-level EC_{50} values, which is defined as the exposure concentration that reduced λ by 50%, and the predicted probit mortality for *N. womersleyi* and *P. persimilis* were estimated based on the two population growth rate scales: the fecundity λ and vitality λ (Table 8). A large discrepancy between the EC_{50} and LC_{50} values was observed in this study. When *N. womersleyi* were treated with fenpyroximate, the EC_{50} values were 104.5 ml/l for fecundity λ and 82.5 ml/l for vitality λ. These concentrations were equivalent to the predicted probit mortality of 72 and 61%, respectively. In particular, the pyridaben concentration that caused a 2–3% adult *P. persimilis* mortality could reduce the fecundity λ and the vitality λ by 50%. The predicted probit mortality at EC_{50} using

Table 8 Median effective concentration (EC_{50}[a]) on two population growth rate estimates (fecundity λ and vitality λ) and the corresponding predicted acute probit mortality (%) for *Neoseiulus womersleyi* and *Phytoseiulus persimilis* exposed to three sublethal concentrations of fenpyroximate and pyridaben at 25 ± 2°C, 60–80% RH, and a photoperiod of 16:8 (L:D) h

Acaricide	*N. womersleyi*		*P. persimilis*	
	Fecundity λ	Vitality λ	Fecundity λ	Vitality λ
Fenpyroximate (ml/l)	104.5 (72)[b]	82.5 (61)	13.9 (4)	13.9 (2)
Pyridaben (mg/kg)	84.1 (15)	54.9 (5)	43.5 (13)	42.9 (12)

[a] EC_{50} value was estimated using Eq. 4

[b] Values in parenthesis indicated that percent mortality assessed by probit analysis corresponding to the concentration value as lethal concentration levels (LC_x)

the vitality λ values for each acaricide indicated that development of *N. womersleyi* and *P. persimilis* populations could be severely limited by low lethal concentrations except for the combination of fenpyroximate and *N. womersleyi*.

Discussion

Availability of approved acaricides to control *T. urticae* is diminishing in Korea, because of a widespread resistance of *T. urticae* to the available acaricides in the fields (Kim and Yoo 2002; Lee et al. 2003; Kwon et al. 2010). Therefore, maintaining the effectiveness of the available acaricides is essential to the management of *T. urticae*. Several field populations of *T. urticae* have already developed high levels of fenpyroximate and pyridaben resistance in spite of their short-term use in Korea (Cho et al. 1995; Suh et al. 2006), and thus a treatment schedule for these chemicals should be carefully managed to maintain their efficacy by reducing the risk of developing rapid resistance. The resistance management guidelines given for the METI-acaricides by the Insecticide Resistance Action Committee (IRAC) should be strictly followed: only a single application of one METI-compound per season is recommended due to the high risk for increasing widespread METI resistance in *T. urticae* (Stumpf and Nauen 2001). Because of this, a combination of METI-acaricides and biological control agents is a crucial component to mitigating pesticide resistance as well as developing effective IPM programs.

Demographic analyses provide the most complete picture of the population-level consequences of individual responses to pesticides because this analysis allows one to combine lethal and sublethal effects into a meaningful measurement (Stark et al. 1997; Sáenz-de-Cabezón Irigaray et al. 2007; Stavrinides and Mills 2009; Hamedi et al. 2010). Mean longevity and individual fecundity are commonly used endpoints to assess sublethal effects. The assessment of sublethal effects based on these endpoints, and the extrapolation of this information to higher systems (e.g., populations and communities), may result in fallacious conclusions in terms of the predicted exposure response (Walthall and Stark 1997). In this study, the ovicidal effect was shown to play an important role in population development in two predatory mite species, especially when *N. womersleyi* were treated with pyridaben. Therefore, the effects of treatment on egg hatch rates should be incorporated into the life table analysis for a full assessment of the impact of pesticides on biological control.

In this study, there was an apparent discrepancy between reproduction and population growth rates. The EC_{50}s for the R_os were very low, but the values for the population growth rates were relatively high. In the case of the fenpyroximate—*N. womersleyi* combination, the EC_{50} for R_o was 14.6 ml/l, which was equivalent to a 3% probit mortality, but the EC_{50} for the vitality λ values was 104.50 ml/l, which was equivalent to a 61% probit mortality. The different effects of the acaricides on the survivorship and fecundity of each mite species are the most likely reason for these results. Therefore, knowing the specific parameter that causes the reduction in reproduction or population growth rate may be important for introducing predatory mite species in IPM.

According to our results, when the total effects of fenpyroximate and pyridaben treatment on *N. womersleyi* and *P. persimilis* were considered, fenpyroximate was found to be the most compatible acaricide for the augmentative release of *N. womersleyi* after treatment. The vitality λ-EC_{50} for *N. womersleyi* was 82.51 ml/l, which was higher than the field recommended concentration (25 ml/l) of this acaricide (Table 8). Kim et al. (2004) reported that the vitality λ-EC_{50} for *T. urticae* was lower than the field recommended concentration, 10.18 ml/l. Also, fenpyroximate did not significantly affect the activity of *N. womersleyi*, as measured by the *T. urticae* egg consumption rate, compared to pyridaben treatment (Table 5). These findings demonstrate that fenpyroximate can be used in combination with *N. womersleyi* since this acaricide only minimally effected egg consumption. Amano et al. (2004) showed that these acaricides were moderately harmful to *N. womersleyi*. The pyridaben—*N. womersleyi* combination would not be effective for use in IPM programs for controlling *T. urticae* because of its strong ovicidal effects on *N. womersleyi* and negative impact on egg consumption (Tables 4, 5). In addition, augmentative release of *P. persimilis* would not be compatible with fenpyroximate nor pyridaben treatments. If *P. persimilis* is the only option for use in biological control programs, a low concentration of pyridaben may be used in combination with this mite species. According to the acute mortality study (Table 1), no *P. persimilis* adults can survive at a treatment concentration of 250 mg/kg, which is the field recommended concentration of pyridaben. Kim et al. (2004) reported that pyridaben could greatly reduce the population growth rate of *T. urticae* due to its negative effects on reproduction and strong ovicidal effect at very low concentration, and the vitality λ-EC_{50} was determined to be 2.0 mg/kg. Release of *P. persimilis* can further decrease the *T. urticae* population following treatment at low concentrations ranging between 2.0 and 10.0 mg/kg. This low-concentration strategy with biological control agents within an IPM system can help to reduce selective pressure and the development of resistance (Roush 1989; Dent 2000).

In this study, specific sublethal effects of these chemicals, which are crucial to the continued use of *N. womersleyi* and *P. persimilis* by Korea's vegetable and fruit producers, were identified. The results suggest that fenpyroximate could be used for selective METI in a IPM program with biological control agent, *N. womersleyi*, because fenpyroximate did not alter the population growth rate at the field recommended concentration. However, care should be taken in translating these laboratory tests results into predictions of field performance (Hoy and Cave 1985; Zhang and Sanderson 1995). Kogan (1986) emphasized the need to base pest management decision in the field on sound principles of population ecology. The same must be said for laboratory bioassays conducted to predict pesticide efficacy for populations in the field based on the results of laboratory bioassays. Villanueva-Jiménez and Hoy (1998) also reported that field trials provide more information on pesticide-pest-natural enemy interactions. In conclusion, the total effects of fenpyroximate and pyridaben reported in this study should facilitate the integration of biological and chemical controls for *T. urticae* into fruit and vegetable crop systems in Korea.

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