

MODELLING MITE DYNAMICS ON APPLE TREES IN EASTERN NORTH AMERICA

J.M. Hardman
Agriculture and Agri-Food Canada, Atlantic
Food and Horticulture Research Centre,
32 Main Street, Kentville,
Nova Scotia B4N 1J5, Canada

W. van der Werf
Wageningen Agricultural University,
Theoretical Production Ecology,
P.O. Box 430,
6700 AK Wageningen, The Netherlands

J.P. Nyrop
Cornell University, Dept. of Entomology,
New York State Agricultural Experiment
Station, Geneva, New York 14456, USA

Keywords: simulation model, apple trees, *Panonychus ulmi*, *Typhlodromus pyri*

Abstract

The model described in this paper simulates seasonal dynamics of *Panonychus ulmi* and the phytoseiid predator *Typhlodromus pyri* on apple trees in Eastern North America. It was originally developed to understand the effect of weather, predation, cannibalism, alternate food for the predator, and uneven mite distribution among leaves on mite dynamics. Overwintering mortality of *T. pyri*, cannibalism, and the uneven distribution of predators and prey among leaves were found to stabilize the predator/prey interaction. The availability of alternate foods for *T. pyri* minimizes the likelihood of predator extinction at the whole-tree level, as is seen in orchards. The model was used to guide tactics of mite management. Early simulations involving optimal times to apply miticides indicated that if there are high densities of *P. ulmi* winter eggs, and mite counts are not done until June, there would be significant damage before the mites are noticed and treatments applied. This insight was relayed to growers who now monitor *P. ulmi* eggs in April and apply treatments if needed to prevent early-season damage. Growers also accepted simulations which suggested that post blossom applications of the miticide Apollo would be more effective than applications made before bloom. Other simulations validated the empirical decision rule that biological control is effective with a *T. pyri*: *P. ulmi* ratio of at least 1:10. The model also indicated the value of introducing *T. pyri* into orchards early in the summer to maximize speed of colonization and biological control. Finally, the model has served to guide research. Discrepancies between simulated and observed densities of mites were usually due to factors not yet included in the model such as aerial dispersal of adult *P. ulmi*, leaf quality, sublethal effects of pesticides on *T. pyri*, feeding competition among predators, and availability of alternate food for *T. pyri*. Considerable research has been done on these factors.

1. Introduction

This model simulates the seasonal dynamics of populations of the European red mite *Panonychus ulmi* Koch and the predatory phytoseiid mite *Typhlodromus pyri* Scheuten on

apple trees in eastern North America, especially Upstate New York, USA and Nova Scotia, Canada. In the 1980's, three different *P. ulmi* models were developed independently by mite researchers: Dan Johnson in British Columbia, Mike Hardman in Nova Scotia and Jan Nyrop in New York. Each wanted to study system behaviour, i.e. to understand the relative importance of factors such as weather, predation, cannibalism, alternative food for the predator, prey dispersal, and mite distribution among leaves on mite dynamics. Starting in 1985 Hardman began blending these models. Two new applications were found for the model: refining tactics of mite management and guidance in setting research priorities.

2. Applications of the model

2.1. Application in guiding management

2.1.1. 1989

Often models point out the obvious, which implies developing a model is a waste of time- we should spend more time thinking. But researchers, and practitioners alike, sometimes miss the obvious and models have therefore been helpful. The obvious arose from simulations with a *P. ulmi*/miticide model which suggested that if there are high counts of *P. ulmi* winter eggs and the mite counts are not done until June, there could be economically significant damage before the mites are noticed and treatments applied (Hardman, 1989). The obvious was told to the provincial entomologist who alerted growers and a pest monitoring company. As a result many growers started applying petroleum oil to prevent early-season damage and *P. ulmi* winter eggs are now monitored in many orchards (Rogers, 1992).

2.1.2. 1990-1991

The model suggested post blossom applications of the miticide Apollo would be more effective in controlling *P. ulmi* and avoiding resurgence than application after bloom. This was for three reasons: 1) leaf surfaces expand less after bloom than before bloom (less growth dilution); 2) more vulnerable life stages are present after bloom; and 3) there is less time for mite populations to recover from treatment. Another insight was the importance in having the predator mite *T. pyri* present in an orchard: even an extremely low density would be sufficient to prevent a population of *P. ulmi* from resurging after treatment. These insights presented at the 1990 annual meeting of Nova Scotia Fruitgrowers Association were widely accepted by growers and extension personnel. As a result, Apollo use in Nova Scotia is nearly always postbloom and growers became more motivated to obtain and conserve *T. pyri*.

2.1.3. 1992

Simulations with the 1992 version of the model indicated that the decision rule for expecting effective biological control with a predator prey ratio of at least 1:10 (Nyrop, 1986) was sound (Van der Werf *et al.*, 1994).

2.1.3. 1993

Observations of Dutch entomologists and output from simulations using the mite model, convinced Hardman of the value of introducing *T. pyri* into orchards early in the summer to maximize speed of colonization and biological control. Observations in 1996 have confirmed model findings: colonization from dormant prunings placed on trees in March-April is at least one year faster than with summer prunings placed on trees in August.

2.2. Application in understanding system dynamics and guiding research (1991-1992)

Cannibalism, the ability of *T. pyri* to survive on alternate foods and the uneven distribution of predators and prey among leaves were seen to be stabilizing factors in interactions between *T. pyri* and *P. ulmi*. Winter survival of *T. pyri* was also considered (Walde *et al.*, 1992). At this point publication of output from the model had two consequences: 1) it spurred researchers to get new data to fill in crucial gaps in knowledge, and 2) it encouraged further development and applications of the model.

The model has been a valuable tool to guide research. It revealed gaps in knowledge which warranted further study including factors that were not known to be so important. Often invalidations, discrepancies between simulated mite densities and those observed in orchards, played an important role in this learning process. Invalidations were usually due to external factors not yet included in the model such as those listed in Table 1. Considerable research has now been done on these factors.

Table 1 - Recent studies that were stimulated by the mite model

Type of data	References
Biological residual life of Apollo on apple leaves	Marshall <i>et al.</i> (1994)
Nitrogen content of apple leaves	Hardman <i>et al.</i> (1998)
More accurate estimation of <i>T. pyri</i> density	Hardman <i>et al.</i> (1997)
<i>T. pyri</i> density and reduced rate of feeding	Wei (1996)
Interactions between predators <i>Z. mali</i> and <i>T. pyri</i>	Magagula (1993), Wei (1996)
Overwintering survival of <i>T. pyri</i>	Moreau (1996), Hardman <i>et al.</i> (1997), Nyrop <i>et al.</i> (1998)
Pollen availability and reduced feeding of <i>T. pyri</i> on <i>P. ulmi</i>	Wei and Walde (1997)
Sublethal effects of pyrethroids on <i>T. pyri</i> predation and oviposition	Moreau and Hardman (unpub. data)
<i>P. ulmi</i> density and residence time of <i>T. pyri</i> on leaves	Lawson and Walde (1993)
Aerial dispersal of <i>P. ulmi</i> and <i>T. pyri</i>	Lawson <i>et al.</i> (1996)
Time series of densities of <i>P. ulmi</i> , <i>T. pyri</i> and other mites	Walde <i>et al.</i> (1997), Moreau and Hardman (unpub. data)
Sampling mites and assessing risk of economic losses	Rogers (1992), Nyrop <i>et al.</i> (1994), van der Werf <i>et al.</i> (1994)

3. Description of the model

3.1. Spatial, temporal and geographic limits of the system

The model is deterministic and is considered applicable to a single tree or to a uniform block of trees. However, the effects of spatial variability on predation are taken into account by simulating events on different classes of leaves using probability models as described below. Simulations may cover dynamics from early March, when trees are still dormant, to leaf fall in October, though shorter intervals (e.g. summer months) may be chosen. Multi-year simulations may be run by using end of season mite densities from one year as input for initial mite densities in the following year after applying an arbitrary value for overwintering survival. This approach was used in Walde *et al.* (1992).

There are definite geographic limits to the model. Firstly, populations of both species of mites in one region of the world differ in temperature responses from populations in other regions. This is true for *P. ulmi* from the cool, moist climate of Nova Scotia in Eastern Canada versus *P. ulmi* from the warm, dry Okanogan Valley of British Columbia in Western Canada. However, New York and Nova Scotian *P. ulmi* seem to have similar temperature responses. With *T. pyri* there are contrasts between populations in Nova Scotia and those in northwestern Europe (Hardman and Rogers, 1991). Secondly a host of site-specific abiotic and biotic factors affect dynamics of *P. ulmi* and *T. pyri* on apple trees. Several of these factors must be measured and included as external functions used as input for the model. Abiotic factors include: rainfall (mm/d), daily maximum and minimum temperatures (°C), and day length (h), which may also be calculated from latitude. Pesticide applications must also be accounted for. Necessary data include dates of application (up to 5), initial concentration of pesticide (ppm), toxicity to each of the life stages of *P. ulmi* and *T. pyri*, and rate of decrease in toxicity due to weathering and decreasing biological availability. Additionally there are parameters for the degree of suppression of predator feeding and oviposition caused by contact with the pesticide. Biotic input data include initial densities and age structures of populations of *P. ulmi* and *T. pyri*; densities of adults and older nymphs of *Zetzellia mali* which feed on eggs of *P. ulmi* and *T. pyri*; immigration of adult female *P. ulmi*; mortality of *P. ulmi* due to insect predators; pollen availability (alternative food for *T. pyri*); and nitrogen content of apple leaves, which affects fecundity of *P. ulmi*.

3.2. Simulating age structure, development, mortality and reproduction

The method to simulate age structure and development, taken from Johnson and Wellington (1984), resembles the boxcar train with no dispersion as described by Goudriaan and van Roermund (1989). Populations of *P. ulmi* and *T. pyri* consist of physiological age classes of individuals, grouped into the life stages eggs, larvae, protonymphs, deutonymphs, young females, ovipositing females and males. The stage-specific rate of development of *P. ulmi* is solely a function of hourly temperature. The rate of development of *T. pyri* is affected by temperature and prey ingestion. Mortality factors for the various life stages of *P. ulmi* include low temperatures, old age, rainfall, crowding, predation by *T. pyri*, *Z. mali* and insect predators, and pesticides. Mortality factors for *T. pyri* include ageing, starvation, cannibalism (adult females and deutonymphs sometimes feed on larvae and protonymphs), predation by *Z. mali* on eggs, and pesticides. Reproductive rates of female *P. ulmi* depend

upon temperature and physiological age of the adults, crowding, leaf injury (which increases with accumulation of mite-days per leaf), and nitrogen content of leaves. Nitrogen content is computed as a function of Julian date. As temperatures decrease and day length shortens in late summer, an increasing proportion of *P. ulmi* nymphs mature into females that lay diapausing eggs which will not hatch until the following spring. Leaf injury, as indicated by an accumulation of *P. ulmi* mite-days, also increases the proportion of females that lay diapausing eggs. For *T. pyri* the age-specific rate of oviposition is a function of temperature, the per capita feeding rate, and any suppression due to direct contact with pesticide or with pesticide residues. Short day length induces reproductive diapause where a decreasing proportion of *T. pyri* lay eggs.

3.3. Effects of alternate sources of food on predation and mite dynamics

Alternate foods for *T. pyri* include pollen, the apple rust mite *Aculus schlechtendali*, the two-spotted spider mite *Tetranychus urticae* Koch and any other edible mites besides *P. ulmi*. If *T. urticae* are present their sampled densities may be interpolated to provide estimates of daily densities which represent another food source for *T. pyri*. The model treats motile life stages of *T. urticae* as having the same food value and catchability for *T. pyri* as equivalent stages of *P. ulmi*. However, *T. urticae* eggs are edible, whereas those of *P. ulmi* are not. The availability of *T. urticae* enhances development, survival and reproductive rates for *T. pyri* and lessens the intensity of predation on *P. ulmi*. Pollen is particularly difficult to include in the functional response equation because its absolute quantity is not known in field studies. Yet, its effect is considered of major importance. A full pollen supply is considered equivalent to providing each nymph and adult *T. pyri* on a leaf with a fully satiating diet of *P. ulmi*. For an adult female this would be equivalent to ingesting 2.5 adult female *P. ulmi* or 10 *P. ulmi* larvae per day at 20°C. In the model, pollen supply declines linearly from a full supply in early summer to a small supply (10% of initial value) by September, as was observed in German vineyards (Eichorn and Hoos, 1990).

3.4. Simulating predation and cannibalism

Predation is calculated for mites on two classes of leaves where class is defined according to occupancy by *T. pyri* and *P. ulmi* (see below). The motivational (hunger) status of predators is not simulated in this model. Single prey functional responses were fitted with the integrated form (Royama, 1971) of the rate equation:

$$dN/dt = b (1 - \exp(-a N / b))$$

where b = maximum predator feeding rate, a = initial slope of the functional response, N is the density of prey, aN is prey supply, and b is predator demand. The supply/demand ratio $R = aN/b$ measures in how far a 'supply' of a prey stage (aN , considering prey density and catchability) meets the 'demand' of the predator (b ; based on predator voracity and handling speed). The parameters a and b are different for each prey-predator combination. When multiple prey are present, the rate at which a prey is eaten is:

$$E_{kj} = b_{kj} * R_{kj} / R_j * (1 - e^{-R_j}) * A_j * P$$

where E_{kj} is the number of prey of life stage k that are eaten per unit time by a predator of life stage j , b_{kj} is predator demand (maximum potential kills of prey of class k per unit time), $(1 - e^{-R_j})$ is fulfilment of predator stage j 's demand by all classes of prey, R_j is the sum of all supply/demand ratios for predator stage j , R_k/R_j is the proportion of demand met for predator stage j that comes from eating prey of class k , A_1 is a proportion that quantifies the effect of pollen feeding on mite feeding and P is a proportion that represents the reduction in feeding due to a pesticide application. The model in its standard form assumes that *P. ulmi* has priority over cannibalism when meeting the demand of *T. pyri*. The equation for cannibalism is:

$$E_{kj} = b_{kj} * R_{kj} / R_j * (1 - e^{-R_j}) * A_1 * A_2$$

where k indicates *T. pyri* larvae or protonymphs and where A_1 and A_2 are correction factors accounting for the fraction of demand met by pollen and *P. ulmi* respectively.

3.5. Spatial considerations and predation

Based on a large data set (Nyrop, 1988), probability distributions describing the allocation of mites among leaves are used to calculate the coincidence of predators and prey on leaves. Six classes of leaves are distinguished (Table 2). Average densities of mites on different classes of leaves are reset every day. Class frequencies are based on negative binomial distributions. The model assumes statistical independence of the distributions of *P. ulmi* and *T. pyri*, so that the proportion of leaves occupied by both species is the product of the proportions occupied by either alone (Nyrop, 1988). For both species, a negative binomial distribution is used with the variance equal to a power function of the mean (Walde *et al.*, 1992).

Table 2 - Classes of leaves as defined by mite occupancy

Leaf class	Number on leaf		Diet composition
	<i>P. ulmi</i>	<i>T. pyri</i>	
1	0	0	-
2	0	=1	Alternate food
3	0	>1	Alternate food, cannibalism
4	≥1	0	-
5	≥1	=1	<i>P. ulmi</i> , alternate food
6	≥1	>1	<i>P. ulmi</i> , alternate food, cannibalism

3.6. Simulating effects of pesticides

The model simulates effects of miticides such as clofentezine and pyrethroid insecticides such as cypermethrin. Selective miticides cause high mortality of *P. ulmi* but not *T. pyri*. Pyrethroid insecticides do not cause mortality among *P. ulmi* or pyrethroid-resistant strains of *T. pyri* but there are sublethal effects: for a period of time, rates of feeding and oviposition of the predator are suppressed. Residues of these pesticides decline

exponentially. Half-lives of residues can be reliably estimated based on determinations of biological activity of residues on field collected leaves sampled at different intervals after an application (e.g. Marshall *et al.*, 1994). Dilution of pesticide residues due to growth and expansion of leaves is also taken into account. Leaf area is a logistic function of physiological time.

4. Availability of the model

In the course of 1998, the model, implemented as an executable FORTRAN computer program, will be made available on the internet at:

<http://res.agr.ca/kentville/personal/hardmanm.htm>.

The program is structured so that the main program largely deals with input/output and makes calls to biologically meaningful modules, the subroutines. A technical report that includes the FORTRAN code and data files is under development and will be published on the internet when finished. This report shows how to use the program and indicates the data sources for the assumptions used in the model.

5. Evaluation of the model

So far, all evaluations of the model have been at the 'whole system level' where simulated densities of mites were compared with densities observed at 7-14 day intervals on apple trees in orchards in Nova Scotia and New York. Observed means per leaf were based on samples of 10-25 leaves per tree from 4-10 trees per treatment. Comparisons were based on the researcher's subjective judgement of agreement or discrepancy between graphs of the two time series. Thus evaluations of the model were both preliminary and partial. Invalidations sometimes occurred, especially where external factors not yet included in the model had a strong effect on mite dynamics. These factors included aerial dispersal of adult *P. ulmi*, leaf quality, sublethal effects of pesticides on *T. pyri* and availability of alternate food for *T. pyri*. One by one effects of these factors were incorporated in the model and, where possible, measurements taken of the external factors. But much data still has to be taken. And even with these additions a problem remains. Due to these degrees of freedom, the model can be made fit as well as one wants to, except when all relevant external functions have been measured in validation experiments, but this is rarely the case. Therefore it remains uncertain whether similarity of model results and observations is due to calibration or to structural correctness of the assumptions, processes and external influences functioning in the simulation. For this reason it is also difficult to delimit situations where the model will or will not be usable. The model may be used to answer many questions but the reliability of the results is unclear.

6. Usefulness of the modelling exercise

The objectives of modelling- to gain a better understanding of mite dynamics, to refine tactics of mite management and to help guide research- were met. The model was particularly useful in raising the consciousness of researchers: first, by pointing out the 'obvious' as in the miticide studies, and second, by highlighting gaps in knowledge which needed further study, including factors that were not known to be so important. Often

discrepancies between simulated mite densities and those observed in orchards played an important role in this learning process. Invalidations led to literature searches, data gathering and refinements to the model, then to new evaluations in an ongoing cycle. Was usage of the model cost effective? The answer is yes. Insights from the model led to changed practices of mite management in Nova Scotia including increased sampling, greater use of dormant (petroleum) oil and refinements in use of Apollo. It is likely that the economic benefits from these practices alone (which are ongoing) may pay for the modelling effort, expensive as it may seem. Would other approaches have been sound alternatives for simulation? Probably not. We don't know of other approaches that complement experimentation so well and allow one to explore the effects of numerous factors on mite dynamics. We believe that simulation and experimentation should proceed in parallel.

Acknowledgments.

We thank Debbie Moreau, Mark Rogers, Erika Bent, Tanya Gerrits, David DeGeus, Jen Cookson, Tiffany Covert, Kim Jansen, Danielle MacNeil, and Kendall Little for help in getting data for developing and testing the model and Maarten Zwankhuizen and Rob Dierckx for their contributions to model development.

References

- Eichorn K. W. and Hoos D., 1990. Investigations on population dynamics of *Typhlodromus pyri* in vineyards of Palatina, Germany (Neustadt, Rhineland Pfalz). Proc. IOBC WPRS Working Group 'Integrated control in viticulture' Sion, Switzerland, 22 Feb.-2 March 1989. Vol. 13: 120-123.
- Goudriaan, J. and van Roermund H.J.W., 1989. Modelling of ageing, development, delays and dispersion. In: Rabbinge R., Ward S.A. and van Laar H.H., Eds., Simulation and systems management in crop protection. Pudoc, Wageningen, pp. 47-80.
- Hardman J. M., 1989. Model simulating the use of miticides to control European red mite (Acarina: Tetranychidae) in Nova Scotia apple orchards. J. Econ. Entomol. 82: 1411-1422.
- Hardman J. M. and Gaul S.O., 1991. Use of Apollo in integrated mite control. 127th Annual Report Nova Scotia Fruit Growers' Association, 1990, pp. 20-25.
- Hardman J.M. and Rogers M.L., 1991. Effects of temperature and prey density on survival, development, and feeding rates of immature *Typhlodromus pyri* (Acari: Phytoseiidae). Environ. Entomol. 20: 1089-1096.
- Hardman J. M., Rogers M.L., Gaul S.O. and Bent E.D., 1997. Insectary rearing and initial testing in Canada of an organophosphate/pyrethroid-resistant strain of the predator mite *Typhlodromus pyri* (Acari: Phytoseiidae) from New Zealand. Environ. Entomol. 26: 1424-1436.
- Johnson D.L. and Wellington W.G., 1984. Simulations of the interactions of predatory *Typhlodromus* mites with the European red mite, *Panonychus ulmi* (Koch). Res. Popul. Ecol. 26: 30-50.
- Lawson A.B. and Walde S.J., 1993. Comparison of the responses of two predacious mites, *Typhlodromus pyri* and *Zetzellia mali* to variation in prey density. Exp. Appl. Acarol. 17: 811-821.

- Lawson D. S., Nyrop J.P. and Dennehy T.J., 1996. Aerial dispersal of European red mites (Acari: Tetranychidae) in commercial apple orchards. *Exp. Appl. Acarol.* 20: 193-202.
- Magagula C.N., 1993. Effects of the predatory mite, *Zetzellia mali* on the activities of a second predatory mite, *Typhlodromus pyri* and assessment of its role in the biological control of *Panonychus ulmi* in a Nova Scotian apple orchard. M.Sc. Thesis, Dalhousie University, Halifax, Canada, 92 pp.
- Marshall D.B., Pree D.J., McGarvey B.D. and Thistlewood H.M.A., 1994. Effects of application date on the persistence of clofentezine residues: implications for management of resistance in the European red mite. *Can. Entomol.* 126: 937-947.
- Moreau, D.L. 1996. Overwintering success of a New Zealand predatory mite *Typhlodromus pyri*: supercooling capacity and response to low temperatures. BSc. Honours Thesis, Acadia University, Wolfville, NS Canada, 41 pp.
- Nyrop J.P., 1988. Spatial dynamics of an acarine predator-prey system: *Typhlodromus pyri* (Acarina: Phytoseiidae) preying on *Panonychus ulmi* (Acarina: Tetranychidae). *Environ. Entomol.* 17: 771-778.
- Nyrop J.P., Binns M.R., van der Werf W. and Kovach J., 1994. Cascading tripartite binomial classification plans to monitor European red mite (Acari: Tetranychidae) through a season: development and evaluation of a new methodology for pest monitoring. *Exp. Appl. Acarol.* 18: 123-153.
- Nyrop J.P., English-Loeb G., and Roda A., 1998. Conservation biological control of spider mites in perennial cropping systems. In Barbosa P., Ed., Perspectives on the conservation of natural enemies of pest species. Academic Press, NY (*in press*).
- Rogers R.E.L., 1992. Development and evaluation of a sampling method and early season treatment thresholds for European red mite, *Panonychus ulmi*, winter eggs on apple trees. In: Plant Industry Project Results 1991, Kentville: Nova Scotia Department of Agriculture and Marketing, pp. 8-14.
- Royama T., 1971. A comparative study of models for predation and parasitism. *Res. Popul. Ecol. Suppl.* 1: 1-91.
- Walde S.J., Nyrop J.P. and Hardman J.M., 1992. Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Exp. Appl. Acarol.* 14: 261-291.
- Walde S.J., Hardman J. M. and Magagula C., 1997. Direct and indirect species interactions influencing within-season dynamics of apple rust mite, *Aculus schlechtendali* (Acari: Eriophyidae). *Exp. Appl. Acarol.* 21: 587-614
- Wei Q., 1996. Some factors influencing the effectiveness of *Typhlodromus pyri* as a biological control agent in Nova Scotia orchards. MSc. thesis, Dalhousie University, Halifax, Nova Scotia, Canada, 87 pp.
- Wei Q., and Walde S.J., 1997. The functional response of *Typhlodromus pyri* to its prey, *Panonychus ulmi*: the effect of pollen. *Exp. Appl. Acarol.* 21: 677-684.
- Werf W. van der, Nyrop J. P. and Hardman J.M., 1994. Sampling predator/prey ratios to predict cumulative pest density in the mite-predatory mite system *Panonychus ulmi*-*Typhlodromus pyri* in apples. In: Sampling to make decisions. *Asp. Appl. Biol.* 37: 41-51.