Europ.J.Hort.Sci., **73** (1). S. 12–19, 2008, ISSN 1611-4426. © Verlag Eugen Ulmer KG, Stuttgart

Modelling Population Dynamics of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on Greenhouse Grown Chrysanthemum

M. Nothnagl, A. Kosiba, B. W. Alsanius, P. Anderson and R.U. Larsen
(Division of Horticulture, Swedish University of Agricultural Sciences, Alnarp, Sweden)

Summary

Knowledge about pest-host plant relationships is important for effective pest control in greenhouse crop production. Mathematical models may help to qualify and quantify these relationships and may therefore be used as prediction tools in decision support systems. In the current study, population dynamics of the polyphagous pest *Frankliniella occidentalis* (Western Flower Thrips) were investigated on greenhouse grown chrysanthemum and a dynamic prediction model was established. Previously published data were used to simulate thrips development. Thrips population growth was mainly dependent on temperature, population density and food availability. The damaged leaf area, caused by the pest infestation, was simulated separately. Greenhouse experiments were conducted at three different temperatures to be able to compare different plant and population growth patterns. Thrips samples were taken during the whole cultivation period and *Larvae* and adult thrips were summarized as pest individuals in the population. The model fitted the data well during the early population growth phase but underestimated population decay, due to the lack of migrations possibilities (cage experiments), at high temperatures.

Key words. *Chrysanthemum* x *morifolium* – *Frankliniella occidentalis* – greenhouse crop production – growth analysis – modelling – pest control – simulations – Western Flower Thrips.

Introduction

Modern floricultural industry is based on protected cultivation of monocultures, making it possible to implement rational production strategies with predictable timing schedules. Together with the introduction of high technology in greenhouses, the use of monocultures offers the potential for biological process control, where computers via crop models, image analysis and biosensors, in the future may directly control the entire production process. The disadvantage with the system is its sensitivity to pests and diseases. As a result, automatic decision support systems of the future must be able to incorporate the knowledge of pest population dynamics in order to predict different scenarios depending on a chosen action. Such predictions may also be the base for decisions about effective pest management strategies. The linkage of prediction models concerning pests to crop production models is therefore an important issue in horticultural science.

Crop production models in horticulture are often used to simulate yield, crop management (Gary 1998) or the visual produce quality (Prusinkiewicz 1998; Heuvelink et al. 2001). Modelling crop management in flowering plants with a deterministic growth pattern often means to predict the time to flowering in relation to surrounding climate conditions (Charles-Edwards et al. 1979; Larsen et al. 1998; Larsen and Persson 1999). Most of the modelling studies in horticultural entomology, on the other hand, are dealing with e.g. population dynamics of a species (Birch 1948; Wang and Shipp 2001), insect development (Goudriaan and Van Roermund 1989; Hilbert 1995) or simulations of predator-prey systems (Skirvin et al. 2002). However, only a few studies have focussed on modelling pest-host plant relationships (Van Roermund et al. 1997; Wang and Shipp 2001).

Frankliniella occidentalis (Western Flower Thrips) is one of the most serious crop pests in global greenhouse production (Reimherr 1989). They feed on leaves and flowers of their host plants and cause silvery damage, deformations (Den Belder et al. 1999) and early senescence of e.g. flowers (Rhainds and Shipp 2003). *F. occidentalis* are also vectors for the Tomato Spotted Wilt Virus (Van De Wetering 1999). Chemical control is difficult because of the thrips' thigmotactic behaviour, their small size and their ability to become resistant to insecticides (Jensen 2000). Control with natural enemies may function well in vegetable production (Jacobson et al. 2001; Shipp and Wang 2003; Ebssa et al. 2006) but is not sufficient in floricultural production, where no damages are tolerated by the consumers (De Courcy Williams 2001). In order to gain more knowledge about the pest's natural life conditions several studies have been focussed on the development of *F. occidentalis* and the establishment of life tables (Robb 1989; Gaum et al. 1994; Van Rijn et al. 1995). Others described the importance of temperature (Lublinkhof

and FOSTER 1977; ROBB 1989; SHIPP and GILLESPIE 1993; ISHIDA et al. 2003) or high quality (nitrogen rich) food availability (TRICHILO and LEIGH 1988; BRODBECK et al. 2001; CHAU et al. 2005) on thrips population growth.

The objective of the current study was to investigate population dynamics of *F. occidentalis* on the ornamental host plant *Chrysanthemum* x *morifolium* and to build a simple but still partly mechanistic model, which can predict this interaction. The simulations should then be the base for future IPM (Integrated Pest Management) strategies, like e.g. timing of biological control agent release. The model is based on the following hypotheses:

1) Population density plays an important role in the initial phase of thrips population growth (NOTHNAGL et al. 2007).
2) Food supply will be important for thrips population growth.
3) Temperature is the climate factor, which mostly affects thrips population growth and development.

Materials and Methods

In the study a dynamic model was first developed describing the life cycle of *Frankliniella occidentalis* on a living plant of *Chrysanthemum* x *morifolium*. The objective of the model was to predict the thrips population size during the plant's life span. The model simulates the development and number of individuals from each generation of the insect. A model for leaf area growth in chrysanthemum (Larsen and Nothnagl unpublished) was connected to the thrips model, to estimate the insect population density in relation to the plant leaf area. Data for estimation of model parameters were either taken from previous publications (ROBB 1989) or collected from greenhouse experiments. Model simulations were then verified in relation to these data. Finally, a validation of the model predictions was done with data from yet another experiment.

Model theory

General structure. For the model construction and simulations the software package STELLA 8.1.4 (ISEE Systems, NH, USA) was used. In the model we chose to follow the development of 100 daily generations in the thrips population separately. This was done by using vectors (single dimension arrays) with 100 positions each, where every single daily generation was assigned to a specific position in the vector. A vector was assigned to each stage of thrips development as illustrated in the STELLA flow chart (Fig. 1). Each cohort of thrips enters the system at the *Oviposition* stage and leaves after the *Imago* stage (death).

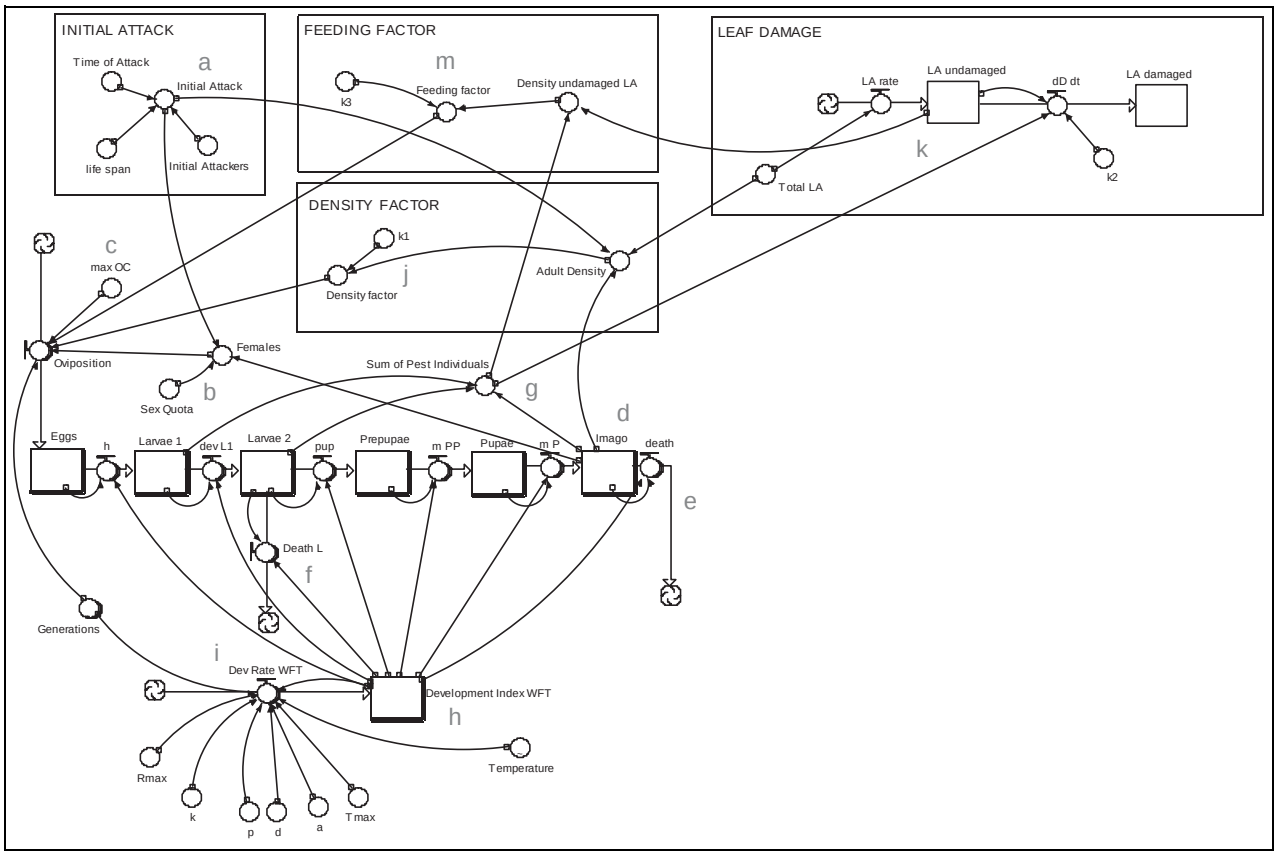


Fig. 1. A flow chart in STELLA 8.1 of the population growth model for *Frankliniella occidentalis* on *Chrysanthemum* x *morifolium*. Circles illustrate constants or calculated values whereas rectangular boxes contain simulated values. Multiplied boxes illustrate single dimension arrays with 100 positions. Circles with a tap on top illustrate flow rates and clouds denote variables not included in the simulation system.

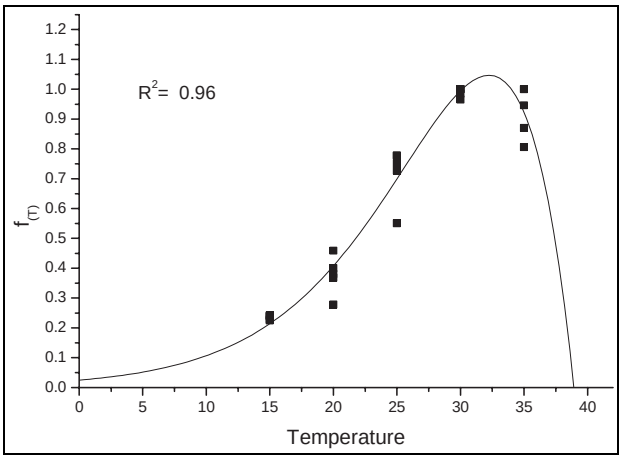


Fig. 2. The Logan function that describes the correlation between the development temperature function (f_T) of *Frankliniella occidentalis* and temperature. The shown data are taken from a previous publication (ROBB 1989).

The size of each generation is dependent of the number of females and an oviposition constant. The rate of reproduction is controlled by population density and the amount of available food (un-grazed leaf area). Therefore, a sub-model of host plant leaf area was linked to the model. Furthermore, temperature was chosen as the most important factor influencing the rate of thrips development and the duration of each generation at a specific stage of development. The effect of temperature on development rate is modelled using the Logan equation (Fig. 2).

Thrips reproduction and development. A simulation is started with an initial infestation by fertile adult individuals, where the number of initially attacking individuals, their life span and the time of infestation can be specified (Fig. 1a). A sex ratio of 0.65:0.35 (females:males) (WANG and SHIPP 2001) determines the amount of females in this initial and all the future generations (Fig. 1b). Oviposition is regulated by a maximum oviposition constant (Fig. 1c), which denotes the maximum daily amount of eggs per female, a density factor and a feeding factor. These factors are described later. The individuals that will hatch from the eggs will pass four more discrete stages of development (*Larvae* 1 and 2, *Prepupae*, *Pupae*) before the stage of adulthood, *Imago* is reached (BRØDSGAARD 1989) (Fig. 1d). The total average life span for the imagos has been estimated to approximately 40 days (ROBB 1989). They are then removed from the system by natural death (Fig. 1e). Immature mortality occurs mainly during the larval period (VAN RIJN et al. 1995). Consequently 7 % of the immatures (VAN RIJN et al. 1995) are removed from the system after the second larval stage (Fig. 1f). Only *Larvae* and *Imagos* are harmful to the plant. All individuals from these two developmental stages are therefore summed up during the simulations for the purpose of estimating population size and potential damage on the plant (Fig. 1g).

Population development rate. To simulate the transfer between the different developmental stages a development index has been established (Fig. 1h). This index ranges from 0 (egg stage) to 1 (death of *Imago* of the individual generation). Index values corresponding to each stage of development were estimated from previously published data for the life length of the individuals in every single stage (ROBB 1989). Based on the index the thrips development rate (Fig. 1i) was estimated by the following equation

$$R = \frac{1}{d} \qquad (1)$$

where *d* is the number of days needed from egg to imago. Since the development of *F. occidentalis* is mainly temperature dependent (BRØDSGAARD 1989) the impact of this climate factor on the development rate can be described as

$$R = R_{max} \times f_{(T)} \qquad (2)$$

where $f_{(T)}$ is a temperature dependant function. This approach was chosen since it offers the possibility of including more climate functions if needed. Here the temperature function will vary from zero to unity depending on the temperature conditions. The relationship can be described by the double exponential equation by LOGAN (1976) (Fig. 2):

$$f_{(T)} = a\left[(1 + ke^{-pT})^{-1} - e^{-b}\right] \text{ where } b = \frac{T_{max} - T}{d} \qquad (3)$$

The parameters k, a, p and d are constants, the variable T denotes the average daily temperature and T_{max} is a maximum temperature. The Logan function was previously used for the description of different life history traits (VAN RIJN et al. 1995).

Population reproduction rate, population density and leaf area. It is assumed that population growth of *F. occidentalis* is, apart from natural mortality, regulated by the rate of oviposition. In the model this is simulated by the following relationship:

$$R_{ov} = \text{females} \times OC_{max} \times FF \times DF \quad \text{if time} > \text{time of attack} \qquad (4)$$

where R_{ov} is the rate of oviposition, the number of females is calculated from the adults multiplied with the sex ratio mentioned above and the OC_{max} denotes the maximum oviposition constant. The FF (feeding factor) and the DF (density factor) are both factors, which vary between 0 and 1 and limit oviposition, when they are less than 1. The density factor (DF) (Fig. 1j) was included since it is believed that adult density on the plant and with it the probability of sexual reproduction has a major influence on initial population growth (NOTHNAGL et al. 2007). In the model the DF is therefore represented by a linear relationship to adult density

$$DF = k_1 \times AD \qquad (5)$$

where k_1 is a constant and AD is the adult density, which is calculated as the number of *Imagos* divided by the total leaf area of the chrysanthemum plant. The leaf area was simulated with a previously developed model describing the growth of the host plant canopy (Larsen and Nothnagl unpublished). From the total leaf area

the thrips damaged area was calculated by the following equation:

$$LA_d = k_2 \times SPI \times LA_{ud} \qquad (6)$$

where LA_d is the damaged leaf area, k_2 is a constant, SPI denotes the sum of pest individuals, that is the sum of *Larvae* 1 and 2 and adults and LA_{ud} refers to the undamaged leaf area. The undamaged leaf area (LA_{ud}) (Fig. 1k) is needed for the calculation of the feeding factor (FF) (Fig. 1m), which illustrates the effect of food supply on the population and is dependant on the total population density compared to the undamaged leaf area:

$$FE = e^{(-k_3 D_{LA_{ud}})} \qquad (7)$$

FF is the feeding factor; k_3 is a constant and $D_{LA_{ud}}$ is the population density on the undamaged leaf area. $D_{LA_{ud}}$ is simulated by the model by dividing the sum of pest individuals (Larvae and *Imagos*) with the calculated undamaged leaf area.

Experimental set-up

Experiments for collecting data for model parameter estimations (k_1, k_2, k_3, OC_{max}) were carried out in three greenhouse compartments with the mean average temperatures of 20.3±2.0, 23.8±2.0 and 26.1±2.0 °C, respectively. Cuttings of *Chrysanthemum* x *morifolium* 'Lompoc'(Fides Straathof Export) were rooted at long day conditions (L15:D9) and when the roots were well developed (after three weeks) the cuttings were transplanted in a commercial peat compost (Hasselfors K) in 11 cm pots, with one cutting per pot. At the start of the experiments the plants were pinched above the fifth leaf and short day treatment was started (L8:D14). Females of *F. occidentalis*, the prodigies of females originally imported from the Netherlands (Koppert B.V., Biological Systems), were reared on *C.* x *morifolium* 'Lompoc' for six weeks and each plant in the experiment was infested with two females, 8 days after transplantation. To prevent the thrips from escaping, nine plants each were placed into quadratic cages (50x50x90 cm) which were covered with transparent cloth. In total, there were eight infested cages in 20.3 and 26.1 °C (72 plants) and twelve cages in 23.8 °C (108 plants). Two extra cages were placed in the 20.3 and 26.1 °C compartments, used as control cages without any thrips infestation.

During the experimental period of three months, four plants each were sampled from the cages, by cutting the entire plant at the base. The amount of *F. occidentalis* on leaves and flowers together was determined by transferring the sampled plants from the cages into turpentine traps (Lewis 1973). The mobile developmental stages of the thrips, *Larvae* and *Imagos*, fled from the smell of a cotton ball moisturized with turpentine and were captured in ethanol. The sampled insects were counted under the microscope. The samples were taken after a schedule, so that the amount of plant resources for the thrips populations in the cages was equal for all cages during the entire experimental period.

The flower development was registered throughout the whole experiment, using the unit index described by Larsen and Persson (1999). This involves the start of short day treatment being denoted as zero, while the appearance of the first anthers (anthesis) is denoted as unit. The flower diameter was measured with an electric calliper throughout the experiments. Sensors for monitoring photosynthetic photon flux (Skye Instruments Ltd., Llandringdod Wells, UK) were placed between the plants and thermocouples (type T, copper and constantan) were used to record air temperature. The climate data were monitored continuously using a datalogger (Intab, Sweden).

Parameter estimations and simulations

The temperature dependency of *F. occidentalis* development was described by the Logan equation and based on Robb's data (1989). The highest temperature dependant developmental rate was selected from these data for each individual developmental stage. The rates at the remaining temperatures were then related to the highest rate and the values for all stages together were plotted against temperature. The five parameters for the Logan function mentioned above were then estimated by using a non-linear regression analysis (Levenberg-Marquardt) in the graphical software package ORIGIN 7.5 (OriginLab Corporation, MA, USA). The parameter T_{max} was fixed to 40 °C in order to meet convergence criteria during the iterations. Values for the maximum oviposition constant, the constants needed for the calculation of DF and FF (k_1 and k_3) and for the calculation of the damaged leaf area (k_2) were estimated by simulations. A second order polynomial model was fitted to the values for the k_1 parameter at different temperatures T,

$$y = A + B_1 T + B_2 T^2 \qquad (8)$$

whereas an exponential decay function was chosen to fit the values for the k_3 parameter at different temperatures *T*

$$y = A_1 e^{(-T/c)} + y_0 \qquad (9)$$

Model simulations were done using the fourth order Runge-katta integration method with a time step of one day. The results from the simulations were compared to real observations using a linear regression analysis (ORIGIN 7.5, OriginLab Corporation, MA, USA).

Validation

Data from an earlier experiment were used for model validation. The validation trial was carried out at a temperature of 19.7±2.0 °C in the greenhouse with the same experimental setup as described above. The collected population growth data were compared to model simulations, based on the specific climate data, monitored throughout the validation experiment.

Results

The used chrysanthemum cultivar reached anthesis between 57 (20.3 °C) and 61 (26.1 °C) days after start of short day treatment. Plants at the lowest temperature were hardly thrips damaged whereas damage was more pronounced at high temperatures.

During the first 52±5 days after the infestation, the thrips population grew slowly at all temperatures. Then

Table 1. Estimated development index values for *Frankliniella occidentalis*. Calculated from Robb 1989.

Index Eggs – *Larvae* 1	0.092
Index *Larvae* 1 – *Larvae* 2	0.141
Index *Larvae* 2 – *Prepupae*	0.255
Index *Prepupae* – *Pupae*	0.287
Index *Pupae* – *Imago*	0.361
Index *Imago* – Death	1.000

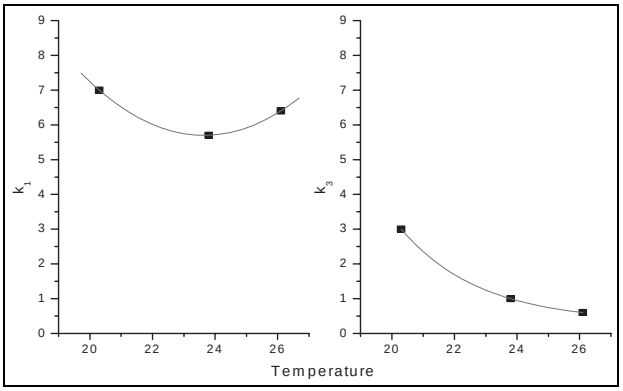


Fig. 3. The relationship between the estimated parameters and temperature of the density factor (k_1) and the feeding factor (k_3) in the population growth model of *F. occidentalis* on chrysanthemum.

there was a brief but strong increase in population size after which the population started to decline again. The strong increase seemed to be more extreme at the highest and the lowest temperature but more moderate at the intermediate temperature (23.8 °C). However, missing data in the 23.8 °C dataset during the rapid increase phase makes it difficult to fully interpret the growth pattern. At the highest temperature (26.1 °C) the population declined most rapidly, followed by the population at the 23.8 °C treatment, whereas the population at the lowest temperature (20.3 °C) declined more slowly. The maximum size of the populations at the different temperature treatments is summarized in Table 4.

The model fitted the data relatively well with R^2-values from 0.514 to 0.975 (Fig. 4). However, there was a tendency of underestimating the rapid population growth at 60 days in 20.3 °C. A slight underestimation during the beginning of population growth could be observed at 23.8 °C. Although the model fitted the growth phase of the population at 26.1 °C well, it was not able to predict the rapid decay in population size after day 80. In the validation trial the model fitted the data well with an R^2-value of 0.987 but shows a trend of underestimating population growth (Fig. 5).

Fitting the Logan function to the laboratory data for thrips development published by Robb (1989) worked well resulting in an R^2-value of 0.96 from the non-linear regression. The five estimated parameters for this function are shown in Table 2. The values for the developmental index for *F. occidentalis*, which also were calculated from Robb's data (1989), are described in Table 1. Constant model parameter estimations are summarized

Table 2. Parameter estimations for model simulations of population growth of *Frankliniella occidentalis* (WFT).

Parameter	Unit	Estimate	ASS
R_{max}	d^{-1}	0.10386	–
k		105.93	±39.66
α		2.65	±1.72
p		0.151	±0.031
d		4.18	±0.84
T_{max}	°C	40	–
OC_{max}	eggs female^{-1} day^{-1}	8	–
k_2	number of WFT^{-1}	0.000063	–
time of attack	days	8	–
initial attackers	females	2	–
life span	days	20	–
A		70.83	–
B_1		−5.51	–
B_2		0.12	–
A_1		8099.71	–
c		2.53	–
y_0		0.33	–

Table 3. Parameter estimations for fitting the model to the validation data. k_1 and k_3 are estimated graphically from Fig. 3.

Parameter	Estimate
OC_{max}	8
k_1	7.7
k_2	0.000063
k_3	4.5

Table 4. Maximum number of pest individuals in the populations at the experimental temperatures.

Mean temperature °C	Mean maximum number of individuals	Standard deviation
20.3	272	± 100
23.8	826	± 219
26.1	634	± 308

in Table 2. Since the parameters from Eq. (5) and (7) (k_1 and k_3) vary with temperature, the relationships between temperature and these parameters are plotted in Fig. 3. The estimated parameters for the fitted equations to these relationships (Eq. (8) and (9)) are also summarized in Table 2. Varying validation parameters were obtained graphically from Fig. 3 and together with the constants they are summarized in Table 3.

Discussion

In general, the model predictions were satisfying, indicating that the assumptions that the model simplifications

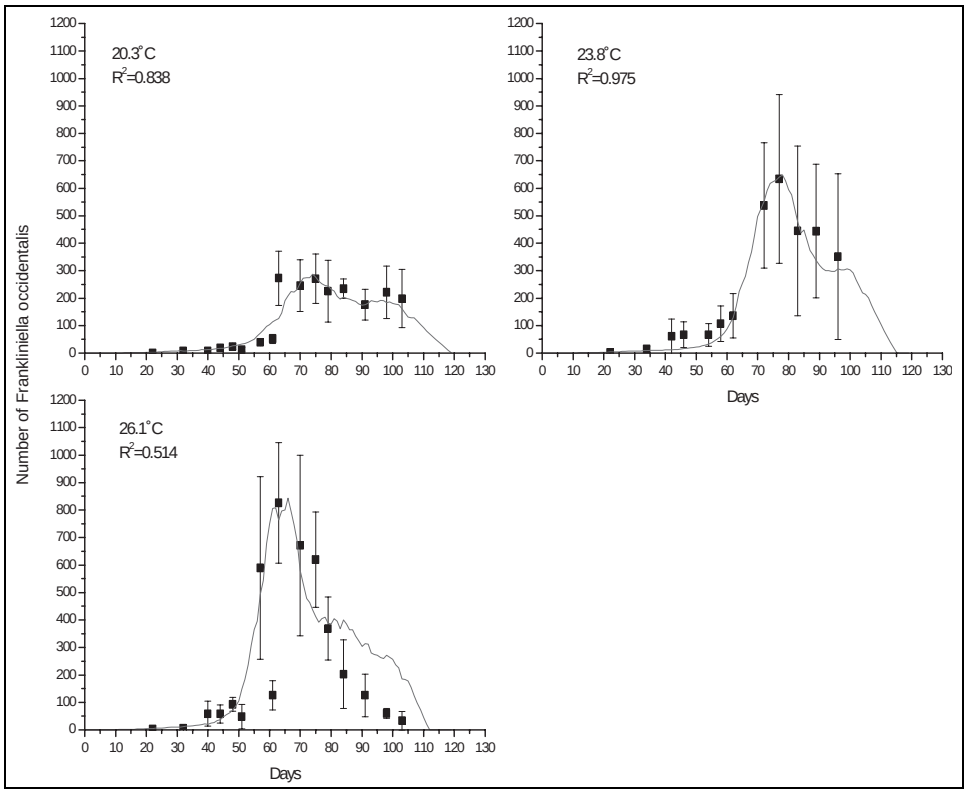


Fig. 4. Model fit of a population growth model for *Frankliniella occidentalis* on *Chrysanthemum* x *morifolium* at three different temperatures. Squares are actual observations and the line illustrates the model.

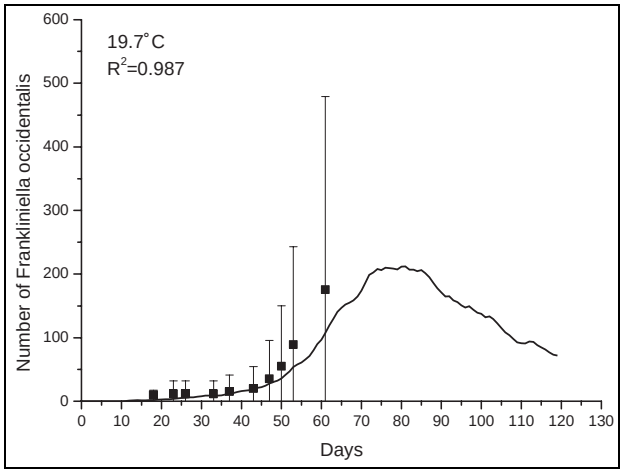


Fig. 5. Results from the validation trial for the population growth model of *Frankliniella occidentalis* on greenhouse grown chrysanthemum. Squares are actual observations and the line illustrates the model.

were based on were reasonable. In other words, it is possible to build an efficient simulation model for a complex plant-insect interaction system with only the most important background information incorporated and therefore with only a few parameters. The simplicity of the model allows it that other models easily can be attached to it, as done with the leaf area model of Larsen and Nothnagl (unpublished) but dictates also the deficiencies of the model.

The current model is for example only dependent of the factors temperature, population density and food availability. Although temperature is the most important factor that influences thrips population growth and development (Lublinkhof and Foster 1977; Robb 1989; Shipp and Gillespie 1993) other climate factors, like humidity or photoperiod have also been shown to have an effect (Shipp and Gillespie 1993; Brødsgaard 1994; Kakei and Tsuchida 2000; Ishida et al. 2003). Drastic variations in any of these factors might cause major discrepancies between observed and simulated population growth. However, if needed, the structure of the model makes it possible to include the factors in the future.

The effect of population density on population growth is simulated by the density factor. A previous growth analysis of a thrips population led to the assumption that adult thrips density plays an important role for the way of reproduction (parthenogenesis or sexual reproduction) (Nothnagl et al. 2007) during the early phase of population growth. The low density at the start of the experiments (two females, lacking male partners) should therefore be the direct cause for the low growth rate of the early thrips population. Reynolds and Freckleton (2005) also describe a general density dependency during early insect population growth, but they assume that low density will give a high growth rate that eventually weakens as the population approaches its carrying capacity. The proposed high initial growth rate is in direct contrast to our findings and the differences might be due to a unique behaviour of *F. occidentalis*, host plant characteristics or to the experimental setup.

In closed systems as in our cage experiments, food availability will eventually become a limiting factor for population growth. Therefore the model contains a feeding factor, which suppresses oviposition according to the decrease in undamaged (eatable) leaf area. *F. occidentalis* can feed on both leaves and flowers (Mound and Teulon 1995), but they prefer flowers. Flowers with their pollen were also shown to have a positive effect on female thrips

fecundity and population growth, (TRICHILO and LEIGH 1988; DE JAGER et al. 1993; UGINE et al. 2005; ZHI et al. 2005). However, flower area was not included in the feeding factor since it was assumed that when food became a limitation for a population, the flowers already were totally damaged so that the thrips instead were forced to feed on the remaining undamaged leaves.

The fact that the model was not able to simulate the fast decay in population at the highest temperature (26.1 °C) could be due to overcrowding. Thus, competition between the individuals for food or habitat and the stress level were probably high. The natural reaction would then have been to flee from the situation and search for another host plant (TRAVIS et al. 1999; RHAINDS and SHIPP 2003), but since the experiments were carried out in cages, the insects had no migration possibility. Together with the food limitations mentioned above, that led to the observed fast decay in population size. In a greenhouse situation the insect migration would have been possible and the decay would probably not have been that strong.

In summary, the current model may be used as a prediction tool for a *F. occidentalis* population on greenhouse grown chrysanthemum, especially in countries where this pest survives outdoors and the host plants are infested by invading flying females. Since plants in commercial Swedish greenhouses are most often infected by eggs on imported cuttings, the population growth curve may look different in the beginning of an infestation. However, when the adult thrips start to migrate from the first host plant because of overcrowding, it is likely that a situation with isolated females and therefore a population growth pattern like in this study will appear.

Model predictions of population growth of *F. occidentalis* may also be used in decision support systems for effective IPM strategies. They may e.g. help to find out the right timing for an application of chemical or biological control agents to avoid a massive infestation. Another practical application lies in the simulation of the amount of leaf damage on the plant caused by the pest. However, more research is needed to be able to simulate the amount of control agents that gives the most satisfying control results and the least damages and their interaction with the pest and the host plant.

This study shows once again the complexity of ecological interaction systems (SCHOONHOVEN et al. 2005). Modelling such systems is a difficult task where the researchers continuously have to take decisions about limitations in the study. From the current approach it became clear that it is important to find out which factors are superior to others in their effect on the system. If these factors then are taken into consideration, relatively simple models can give satisfying predictions.

Acknowledgments

This research was funded by a grant from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS).

References

BIRCH, L.C. 1948: The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. **17**, 15–26.

BRODBECK, B.V., J. STAVISKY, J.E. FUNDERBURK, P.C. ANDERSEN and S.M. OLSON 2001: Flower nitrogen status and populations of *Franklinella occidentalis* feeding on *Lycopersicon esculentum*. Entomol. Exp. Appl. **99**, 165–172.

BRØDSGAARD, H.F. 1989: *Frankliniella occidentalis* (Thysanoptera: Thripidae) – a new pest in Danish greenhouses. A review. Tidsskrift for planteavl: Danish J. Plant and Soil Sci. **93**, 83–91.

BRØDSGAARD, H.F. 1994: Effect of photoperiod on the bionomics of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). J. Appl. Ent. **117**, 498–507.

CHARLES-EDWARDS, D.A., K.E. COCKSHULL, J.S. HORRIDGE and J.H.M. THORNLEY 1979: A model of flowering in Chrysanthemum. Ann. Bot, London **44**, 557–566.

CHAU, A., K.M. HEINZ and DAVIES JR. F.T. 2005: Influences of fertilization on population abundance, distribution and control of *Frankliniella occidentalis* on chrysanthemum. Entomol. Exp. Appl.**117**, 27–39.

DE COURCY WILLIAMS, M.E. 2001: Biological control of thrips on ornamental crops: Interaction between the predatory mite *Neoseiulus cucumeris* (Acari: Phytoseiidae) and Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on cyclamen. Biocontrol Sci.Techn. **11**, 41–55.

DE JAGER, C.M., R.P.T. BUTÔT, T.J. DE JONG, P.G.L. KLINKHAMER and E. VAN DER MEIJDEN 1993: Population growth and survival of western flower thrips *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on different chrysanthemum cultivars. Two methods for measuring resistance. J. Appl. Entomol. **115**, 519–525.

DEN BELDER, E., R.I. VALCHEVA and J.A. GULDEMOND 1999: Increased damage by western flower thrips *Frankliniella occidentalis* in chrysanthemum intercropped with subterranean clover. Entomol. Exp. Appl. **91**, 275–285.

EBSSA, L., C. BORGEMEISTER and H.M. POEHLING 2006: Simultaneous application of entomopathogenic nematodes and predatory mites to control western flower thrips *Frankliniella occidentalis*. Biol. Control **39**, 66–74.

GARY, C., J.W. JONES and M. TCHAMITCHIAN 1998: Crop modelling in horticulture: state of art. Sci. Hort., Amsterdam **7**, 3–20.

GAUM, W.G., J.H. GILIOMEE and K.L. PRINGLE 1994: Life history and life tables of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on English cucumbers. B. Entomol. Res. **84**, 219–224.

GOUDRIAAN, J. and H.J.W. VAN ROERMUND 1989: Modelling of ageing, development, delays and dispersion. In: Simulation and systems management in crop protection. Pudoc, Wageningen.

HEUVELINK, E., J.H. LEE and S.M.P. CARVALHO 2001: Modelling visual product quality in cut chrysanthemum. Acta Hort. **566**, 77–84.

HILBERT, D.W. 1995: Growth-based approach to modelling the developmental rate of arthropods. Environ. Ecol. **24**, 771–778.

ISHIDA, H., T. MURAI, S. SONODA, H. YOSHIDA, Y. IZUMI and H. TSUMUKI 2003: Effects of temperature and photoperiod on development and oviposition of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Appl. Entomol. Zool. **38**, 65–68.

JACOBSON, R.J., P. CROFT and J. FENLON 2001: Suppressing establishment of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) in cucumber crops by prophylactic release of *Amblyseius cucumeris* Oudemans (Acarina: Phytoseiidae). Biocontrol Sci. Techn. **11**, 27–34.

JENSEN, S.E. 2000: Insecticide resistance in the western flower thrips, *Frankliniella occidentalis*. Int. Pest Man. Rev. **5**, 131–146.

KAKEI, Y. and K. TSUCHIDA 2000: Influences of relative humidity on mortality during the pupal stage of *Thrips palmi* (Thysanoptera: Thripidae). Appl. Entomol. Zool. **35**, 63–67.

LARSEN, R.U., A. BIRGERSSON, M. NOTHNAGL and H. KARLÉN 1998: Modelling temperature and flower bud growth in November cactus (*Schlumbergera truncata* Haw.). Sci. Hort., Amsterdam **76**, 193–203.

LARSEN, R.U. and L. PERSSON 1999: Modelling flower development in greenhouse chrysanthemum cultivars in relation to temperature and response group. Sci. Hort., Amsterdam **80**, 73–89.

LEWIS, T. 1973: Thrips, their biology, ecology and economic importance. Academic Press, London, New York.

LOGAN, J.A., D.J. WOLLKIND, S.C. HOYT and L.K. TANIGOSHI 1976: An analytic model for description of temperature dependant rate phenomena in arthropods. Environ. Entomol. **5**, 1133–1140.

Lublinkhof, J. and D.E. Foster 1977: Development and reproductive capacity of *Frankliniella occidentalis* (Thysanoptera: Thripidae) reared at three temperatures. J. Kansas Entomol. Soc. **50**, 313–316.
Mound, L.A. and D.A.J. Teulon 1995: Thysanoptera as phytophagous opportunists. In: Parker, B.L., Skinner, M. and Lewis, T. (eds.): Thrips biology and management. Plenum Press New York and London, 3–19.
Nothnagl, M., A. Kosiba, B.W. Alsanius, P. Anderson and R.U. Larsen 2007: Analysis of early population growth of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on greenhouse grown chrysanthemum. Europ. J. Hort. Sci. **72**, 248–254.
Prusinkiewicz, P. 1998: Modelling of spatial structure and development of plants: A review. Sci. Hort., Amsterdam **74**, 113–149.
Reimherr, P. 1989: Der Kalifornische Thrips, heute ein Hauptschädling im Zierpflanzenbau. Taspo Mag. **16**, 25–28, 35–36.
Reynolds, J.D. and R.P. Freckleton 2005: Population dynamics: Growing to extremes. Science **309**, 567–568.
Rhainds, M. and L. Shipp 2003: Dispersal of adult Western Flower Thrips (Thysanoptera: Thripidae) on Chrysanthemum plants: Impact of feeding-induced senescence of inflorescences. Environ. Entomol. **32**, 1056–1065.
Robb, K.L. 1989: Analysis of *Frankliniella occidentalis* (Pergande) as a pest of floricultural crops in California greenhouses. PhD-dissertation. University of California, Riverside.
Schoonhoven, L.M., J.J.A. Van Loon and M. Dicke 2005: Insect-Plant Biology. Oxford University Press, UK.
Shipp, J.L. and T.J. Gillespie 1993: Influence of temperature and water vapor pressure deficit on survival of *Frankliniella occidentalis* (Thysanoptera:Thripidae). Environ. Entomol. **22**, 726–732.
Shipp, J.L. and K. Wang 2003: Evaluation of *Amblyseius cucumeris* (Acari: Phytoseiidae) and *Orius insidiosus* (Hemiptera: Anthocoridae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse tomatoes. Biol. Control **28**, 271–281.
Skirvin, D.J., M.E. De Courcy Williams, J.S. Fenlon and K.D. Sunderland 2002: Modelling the effects of plant species on biocontrol effectiveness in ornamental nursery crops. J. Appl. Ecol. **39**, 469–480.
Travis, J.M.J., D.J. Murrell and C. Dytham 1999: The evolution of density-dependent dispersal. Proc. Royal Soc. London **266**, 1837–1842.
Trichilo, P.J. and T.F. Leigh 1988: Influence of resource quality on the reproductive fitness of flower thrips (Thysanoptera: Thripidae). Ann. Entomol. Soc. Am. **81**, 64–70.
Ugine, T.A., S.P. Wraight and J.P. Sanderson 2006: Influences of impatiens pollen and exposure to *Beauveria bassiana* on bionomics of western flower thrips *Frankliniella occidentalis*. Biol. Control **37**, 186–195.
Van De Wetering, F. 1999: Effects of thrips feeding on tospovirus transmission in chrysanthemum. PhD-dissertation. Agricultural University Wageningen, The Netherlands.
Van Rijn, P.C.J., C. Mollema and G.M. Steenhuis-Broers 1995: Comparative life history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber. B. Entomol. Res. **85**, 285–297.
Van Roermund, H.J.W., J.C. Van Lenteren and R. Rabbinge 1997: Biological control of greenhouse whitefly with the parasitoid *Encarsia formosa* on tomato: An individual -based simulation approach. Biol. Control **9**, 25–47.
Wang, K. and J.L. Shipp 2001: Simulation model for population dynamics of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse cucumber. Environ. Entomol. **30**, 1073–1081.
Zhi, J., G.K. Fitch, D.C. Margolies and J.R. Nechols 2005: Apple pollen as a supplemental food for the western flower thrips, *Frankliniella occidentalis*: Response of individuals and populations. Entomol. Exp. Appl. **117**, 185–192.

Received July 25, 2006 / Accepted May 18, 2007

Addresses of authors: M. Nothnagl, A. Kosiba, B. W. Alsanius (corresponding author), P. Anderson, R.U. Larsen, Division of Horticulture, Swedish University of Agricultural Sciences, P.O. Box 44, S - 253 30 Alnarp, Sweden, e-mail: Beatrix.Alsanius@ltj.slu.se.