Europ.J.Hort.Sci., **72** (6). S. 248–254, 2007, ISSN 1611-4426. © Verlag Eugen Ulmer KG, Stuttgart

Analysis of Early Population Growth of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) on Greenhouse Grown Chrysanthemum

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Summary

Several investigations show that flowers are a preferable food source for the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). A study was initiated to see how population growth of a *F. occidentalis* population on greenhouse grown chrysanthemum was affected by flower growth and development. The hypothesis was that the relative reproduction rate of thrips was not constant over time but increased when flowers were available. Plants of the chrysanthemum pot plant cultivar 'Lompoc' were infested with female western flower thrips and grown at three different temperatures. The results showed that thrips growth and development was stimulated by an increased temperature, and that the increase was not correlated with the effect of temperature on chrysanthemum flower development. Since there was no significant difference between thrips grown on plants with or without flowers, the original hypothesis could not be supported. The results indicated further that the relative reproduction rate increased over time. A growth equation with an exponentially increasing relative reproduction rate fitted the data better (R^2-values from 0.529 to 0.826) than a traditional exponential equation (R^2-values from 0.434 to 0.728). It was proposed that intrinsic factors within the population, such as population density, the probability of finding a mating partner, and the switching from parthenogenesis to sexual reproduction, were the cause for the increasing relative reproduction rate during early population growth.

Key words. *Chrysanthemum* x *morifolium* – western flower thrips – *Frankliniella occidentalis* – flower development – growth analysis – population dynamics – plant-insect interaction

Introduction

The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) has been a major pest in the global flower industry for the last 20 years (Reimherr 1989; Brødsgaard 1989; Robb 1989). The high pest status is partly due to the often massive infestation and the potential of the insect to generate resistance towards most agents available for chemical control (Jensen 2000). Although biological control is an option, it has not been successful in floriculture (De Courcy Williams 2001; Sengonca et al. 2004) due to the "zero tolerance" in the industry towards damages on flowers and leaves caused by the pest. To administer beneficial predators efficiently, and to avoid plant damages, more detailed knowledge about thrips population dynamics and their interaction with the host plant is needed. Chrysanthemum (*Chrysanthemum* x *morifolium*) is an important crop known for its sensitivity towards thrips infestation (Broadbent et al. 1990; De Jager et al. 1997; De Kogel et al. 1998; Den Belder et al. 1999). In the current study we focussed on the relationship between early population growth of *F. occidentalis* and flower growth and development of pot chrysanthemum (*C.* x *morifolium* 'Lompoc') in a greenhouse environment.

Early insect population growth in an unlimited environment was previously described as an exponential increase with a constant growth rate (Birch 1948). Food supply is a factor in a population's environment, which may become limiting. In the case of *F. occidentalis* many studies showed that alternations in food availability and quality due to flower growth and development affected adult female fecundity and therewith population growth (Trichilo and Leigh 1988; De Jager et al. 1993; Brodbeck et al. 2001; Hulshof et al. 2003; Ugine et al. 2006). *C.* x *morifolium* with its deterministic growth pattern provides more favourable food only towards the end of the plant's growing period. Therefore we hypothesized that the reproduction rate of *F. occidentalis* on *C.* x *morifolium* is not constant over time but rises with the availability of flowers. This could be a possible explanation for the often observed dramatic increase in population size, which results in a massive infestation. The question arises if the thrips reproduction rate is constantly low in the beginning, when only leaves are available and then switches over to another constant but higher reproduction rate towards the end of the plant growth period, when flower buds open. Another possibility would be that the reproduction rate is directly dependent on flower growth and development and therefore changes continuously over time.

The objective of the following study was to identify if and how the thrips' reproduction rate changes over time and to see how this is correlated to the development of the host plant. The aim was also to see if it is possible to mathematically describe the process for future use in a prediction system.

Materials and Methods

Temperature influences both thrips development and population growth (LUBLINKHOF and FOSTER 1977; ROBB 1989) and chrysanthemum growth and development (CATHEY 1954; LARSEN and PERSSON 1999) but in different ways. Consequently, the pest and host plants were investigated at different greenhouse temperature regimes to compare various growth patterns. Population growth data and flower growth data were then compared and analysed.

Experimental setup

Experiments were carried out in three greenhouse compartments with the mean temperatures of 20.3±2, 23.8±2 and 26.1±2 °C, respectively. *C.* x *morifolium* 'Lompoc' cuttings (Fides Straathof Export, The Netherlands) were rooted for three weeks at long day conditions (L15:D9) and then transplanted into 11 cm pots filled with peat based growing medium (Hasselfors K). Nine pots each were placed into a cage (50 x 50 x 90 cm) covered with transparent cloth. In total, there were eight cages in 20.3 and 26.1 °C (72 plants) and twelve cages in 23.8 °C (108 plants). On the first day of the experiment the plants were pinched above the fifth leaf and short day treatment was started (L8:D16). Eight days after the start of the experiment each plant was infested with two female *F. occidentalis*. The females were the prodigies of females originally imported from the Netherlands (Koppert B.V., Biological Systems) and reared on *C.* x *morifolium* 'Lompoc' for six weeks. At 23.8 °C flower buds were removed in half of the cages (54 plants), as soon as they became visible, in order to examine favourable food availability effects on the thrips population.

During the whole experimental period (three months) samples of four plants each per temperature and food availability treatment were collected 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 adults, 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 remained 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. 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).

Statistical procedure

In the study the following exponential functions were used for analysing the data:

$$WFT = WFT_0 e^{kt} \qquad (1)$$

Here WFT denotes the number of individuals of *F. occidentalis*, k is the relative reproduction rate (eggs females^{-1} days^{-1}), t denotes time (days), and WFT_0 is the number of thrips at the start of the experiment. Throughout the analysis, WFT_0 was set to two individuals according to the experimental setup.

It was proposed that the early growth of the flower bud, in terms of biomass, is exponential (CHARLES-EDWARDS et al. 1979). If the relative reproduction rate (RRR) of the thrips (k) is directly related to the growth of the flower bud, then it should change exponentially over time giving the following equation:

$$k = k_0 e^{(qt)} \qquad (2)$$

Here k_0 is the initial value of k at the start of the experiment, and q determines the rate of change (days^{-1}) of k over time (t). A positive q value will result in a more powerful increase in the number of insects towards the end of the studied growth period, compared to a traditional exponential growth curve.

When studying the experimental data, the concept of traditional exponential growth was first tested by fitting Eq. (1) to the data. After this, the concept of an exponentially increasing relative reproduction rate was tested by fitting the joint function of Eq. (1) and Eq. (2), to the same data as before. The goodness of the fit between the first and second fit was then compared. This was done for data from all three temperature treatments and for the treatment where the flowers had been removed from the plants.

Exponential fits and regression analyses were done in the graphical programme ORIGIN 7.0 (OriginLab Corporation, MA, USA). Comparisons of the two food availability trials were done by using a 2-sample t-test in the statistical programme Minitab, Release 14 (Minitab Ltd., UK) at a confidence level of 95 %.

Results

Temperature and food availability treatments

Population growth of the pest on the host plant showed the same general pattern throughout all temperatures. During the first 60±5 days of short-day treatment the thrips population grew slowly and reached no more than 50 insects at lower temperatures (20.3 °C) and 100 insects at higher temperatures (23.8, 26.1 °C) (Fig. 1). After this first growth period, there was a brief and strong increase in thrips population. This second growth phase lasted longer in the high temperature trials than at the lower temperature (Table 1). It was followed by a decrease in population that was slight at lower temperatures but more pronounced at higher temperatures.

Table 1. Estimated start from time of pest application and estimated duration of growth phase two at different temperatures. The values were estimated from the experimental data.

Temperature (°C)	Start of growth phase 2 (days)	flower index	Duration (days)
20.3	61	1.09	2
23.8	62	0.95	10
26.1	51	0.79	12

Although the mean value of the maximum thrips population was smaller on plants where flower buds were removed than on plants with flowers (Fig. 2), there was no significant difference between the two treatments ($p>0.05$).

Growth analysis

Although fitting of Eq. (1) to the data from 23.8 °C was acceptable (R^2=0.728), there was a trend of the function to overestimate the data from day 45 to day 60 (Fig. 3). This trend became more pronounced when the function was fitted to the data from 20.3 and 26.1 °C, resulting in R^2-values of 0.434 and 0.508, respectively.

By replacing the constant relative reproduction rate in Eq. (1) with an exponentially increasing reproduction rate (Eq. (2)) the exponential model fitted the data with R^2-values of 0.529 at 26.1 °C and 0.826 at 20.3 °C which was considerably better than for the previous function (Fig. 3). The estimated parameter values for Eq. (1) and (2) are summarized in Table 2.

Fitting Eq. (2) to the population growth data on the plants, where flower buds were removed, resulted in k_0 values that resembled those of the 26.1 °C temperature treatment (Table 2). R^2-values were slightly higher (0.754) than by fitting Eq. (1) to the data (R^2=0.739) (Fig. 4).

When plotted against the temperature the initial value of the relative reproduction rate (k_0) increased with increasing temperature whereas the changing rate of the relative reproduction rate (q) decreased with increasing temperature (Fig. 5).

When population growth was compared to chrysanthemum flower diameter growth, the results indicated that the plants and the insects were reasonably well coordinated at 26.1 °C (R^2=0.686). At the lower temperatures the thrips population peaked first after the flower was fully open (Fig. 1).

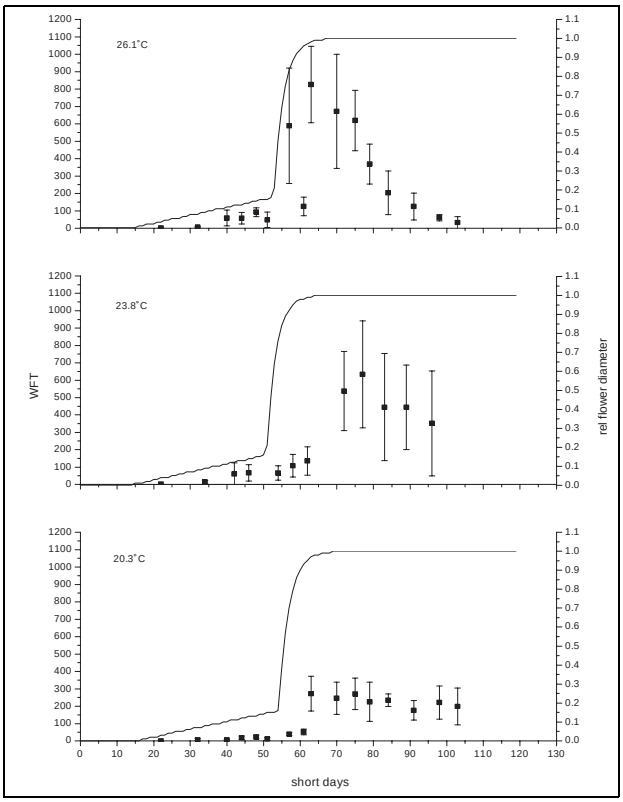


Fig. 1. Population growth of *Frankliniella occidentalis* on greenhouse grown pot chrysanthemum at three temperatures (squares and standard deviations, n = 4) compared to a simulated relative flower growth. The relative flower growth is described as a process going from zero to unity, where unity corresponds to a fully opened flower bud (WFT is an abbreviation for western flower thrips).

Discussion

The results confirm our preliminary suggestion that the relative rate of reproduction during early population growth of *F. occidentalis* on a plant with a deterministic growth pattern like *C.* x *morifolium* is not constant. On the other hand, the hypothesis that the availability of pollen after flower opening is responsible for the increase in relative reproduction rate could not be supported. Although there was a good correlation between thrips population growth and flower growth at 26.1 °C, the results of the trials where flowers were removed, showed the same increase in reproduction rate as in the treatments where flowers were available as food sources. The fact that the thrips population growth and flower development were not fully synchronised at all temperatures in the study might also indicate that the change in relative reproduction rate is dependent of endogenous changes within the population rather than the presence of growth stimuli from the host plant.

Although there was no significant difference in population size when thrips were grown on plants with or without flowers, there was a trend towards larger mean population on plants with flowers. This would be in line with the findings of Trichilo and Leigh (1988) and Hulshof et al. (2003), showing that the availability of pollen plays an important role for female fecundity. However, Zhi et al. (2005) did not find a significant difference in population size with or without pollen over short time periods (14 days) but they suggest that such differences might have been observed if populations persisted for a longer time. Similarly, in our experiments, the populations had access to pollen only towards the end of the plants' growing periods and in limited amounts. Depending on the size of the populations and the consumption activities of the insects, the pollen supply will probably be depleted relatively soon. From the results one could sug-

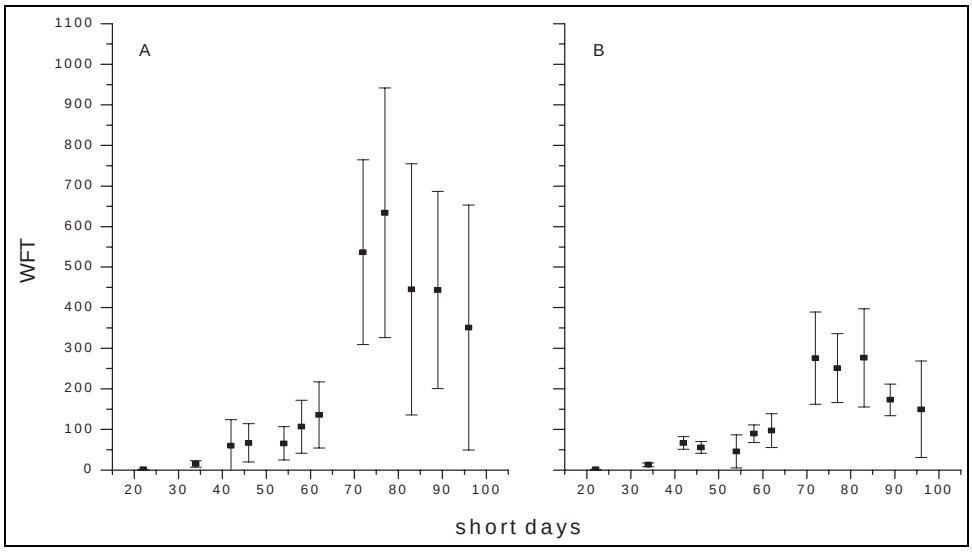


Fig. 2. *Frankliniella occidentalis* population growth on *Chrysanthemum* x *morifolium* with and without flowers at 23.8 °C. A: Flowering chrysanthemum plants. B: Flower buds removed when visible.

Table 2. Estimated parameters and asymptotic standard errors for the exponential equations (1) and (2) with a constant and an exponentially growing relative reproduction rate (RRR), respectively.

RRR	Temperature treatment (°C)	Parameters		
		k	k_0	q
Constant	26.1	0.090±0.002		
	23.8 with flowers	0.076±0.001		
	23.8 without flowers	0.067±0.001		
	20.3	0.068±0.002		
Exponential increase	26.1		0.0510±0.0270	0.009±0.009
	23.8 with flowers		0.0390±0.0120	0.010±0.004
	23.8 without flowers		0.0510±0.0110	0.004±0.003
	20.3		0.0003±0.0003	0.088±0.014

gest that the time period of pollen availability was too short in the high temperature treatments with large populations to see the effect on female fecundity. In the low temperature treatment, on the other hand, the slow decrease of the relatively small population could among others be a result of the effect of the high quality food on female fecundity. We probably also would have found a significant difference in population size in trials at this temperature with and without flowers. This should be studied in a forthcoming experiment.

The results indicate further that the relative reproduction rate can be simulated as an exponential increase during the whole growing period. This was originally chosen with reference to the exponential growth of the flower bud (Charles-Edwards et al. 1979) and our expectation that it would influence the growth pattern of western flower thrips. Since our results indicate that the flower bud is probably not the reason for the increase in relative reproduction rate, it is more likely that the increase is caused by mainly intrinsic factors within the population. The following scenario might explain the process. The first eggs of the two initial females are probably a result of sexual reproduction and will therefore develop into both females and males. Apart from the initial females, the early population will consist of immature individuals. Consequently, in the next step the initial females will most likely lay eggs parthenogenetically, for the population to survive. During the early phase of infestation, the isolated females of *F. occidentalis* are known to reproduce through parthenogenesis (Brødsgaard 1989). Eggs from unfertilized females will only develop into males. This will explain the slow population growth pattern during the first 60 days of our experiment. Because of their long life span the females will eventually switch from parthenogenesis to sexual reproduction by mating with their sons (Mound and Teulon 1995). As the larvae become mature, adults mating will increase and sexual reproduction will become predominant. Most of the offspring from fertilized females will be female (Brødsgaard 1989), resulting in a rapid increase in population growth. This will lead to an increased population density, resulting in an increased probability of mating. Consequently, the relative reproduction rate will increase. The population density will probably only at very low densities have an effect on the mating rate. Eventually, the population density will be high, various generations will overlap and the relative reproduction rate will become stable. The brief and strong increase in population during growth phase two in our experiments will represent this situation. When the carrying capacity of the host plants eventually is passed,

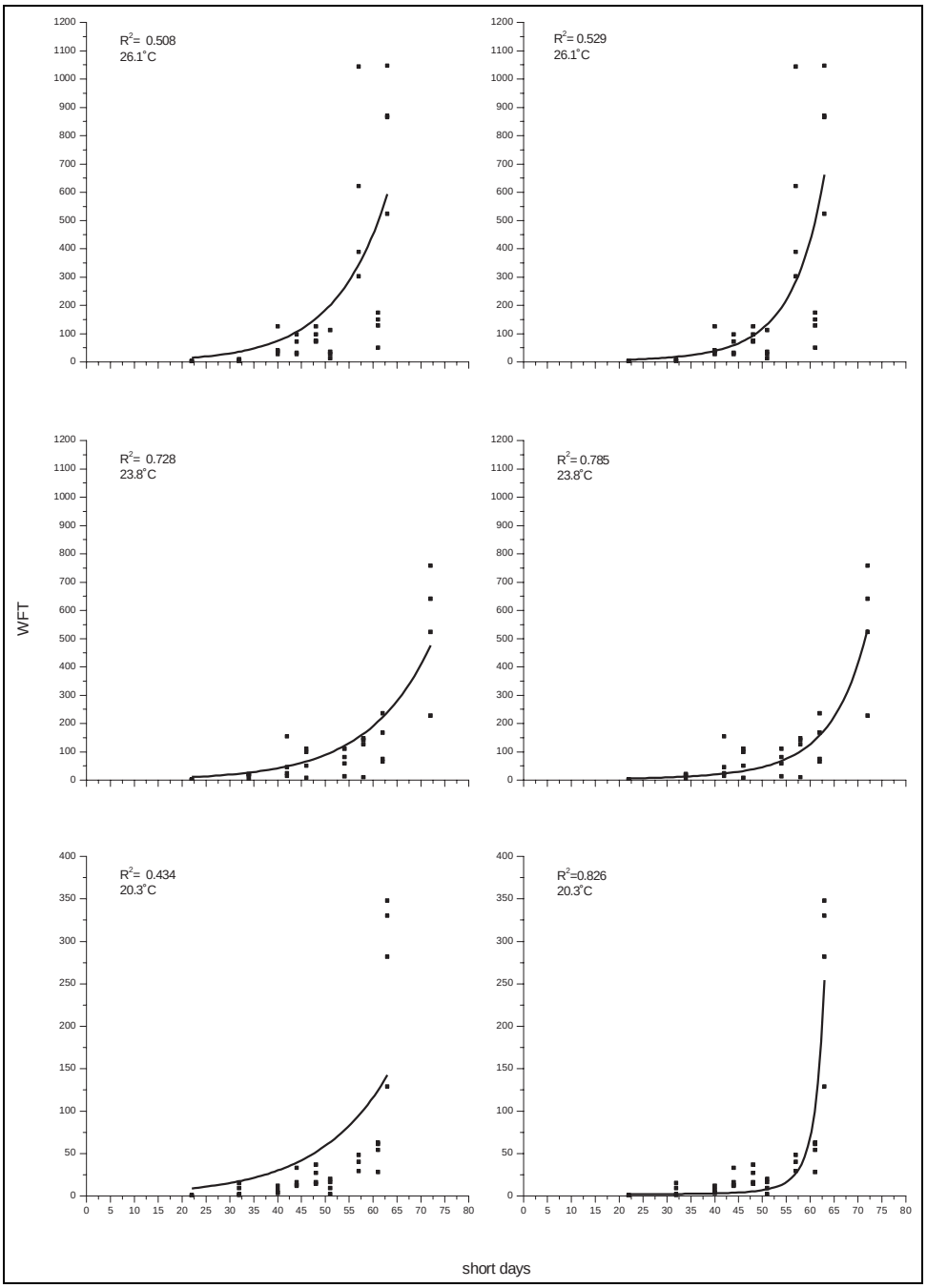


Fig. 3. Results of the fitting of exponential growth equations to the early growth data of a *Frankliniella occidentalis* population on *Chrysanthemum* x *morifolium* at three different temperatures. Left column: constant relative reproduction rate. Right column: exponentially increasing relative reproduction rate. Scales on the Y-axes vary between the rows.

the rate of reproduction will decrease. Depending on various extrinsic and intrinsic factors (e.g. competition for food, host plant supply, control, mortality) the population will decline. The hypotheses in the scenario mentioned above are in line with the speculations of REYNOLDS and FRECKLETON (2005), who mention strong density dependence early in the population growth that decreases when the carrying capacity is approached.

The scenario above might also explain the recorded temperature responses. At temperatures below the optimum temperature for western flower thrips (27–30 °C) the development from egg to adult will take longer time (15–40 days compared to ten days at optimum temperature) (ROBB 1989). Since the insects also will move slower at lower temperatures, this will reduce the probability of meeting a mating partner at low population densities. As a result, it will take a longer time for the population to reach growth phase two at lower temperatures, compared to higher temperatures.

If our conclusion concerning the density and the probability of finding a mating partner is correct, then one would expect a similar population growth pattern in commercial greenhouse cultivation as in our experiments. The only difference will be that the host plant supply is probably higher and that the thrips have the possibility of migrating to new host plants. The initial generation of thrips will probably first spread out between the plants, the density will be low and with it the

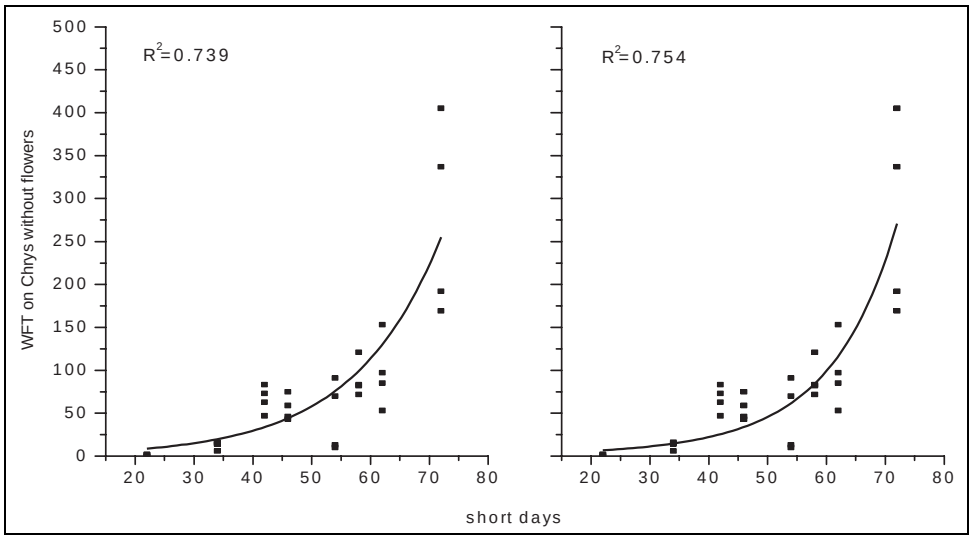


Fig. 4. Fit of an exponential growth equation with a constant (left column) and an exponentially increasing (right column) relative reproduction rate to the early growth data of a *Frankliniella occidentalis* population on greenhouse grown chrysanthemum without flowers at 23.8 °C.

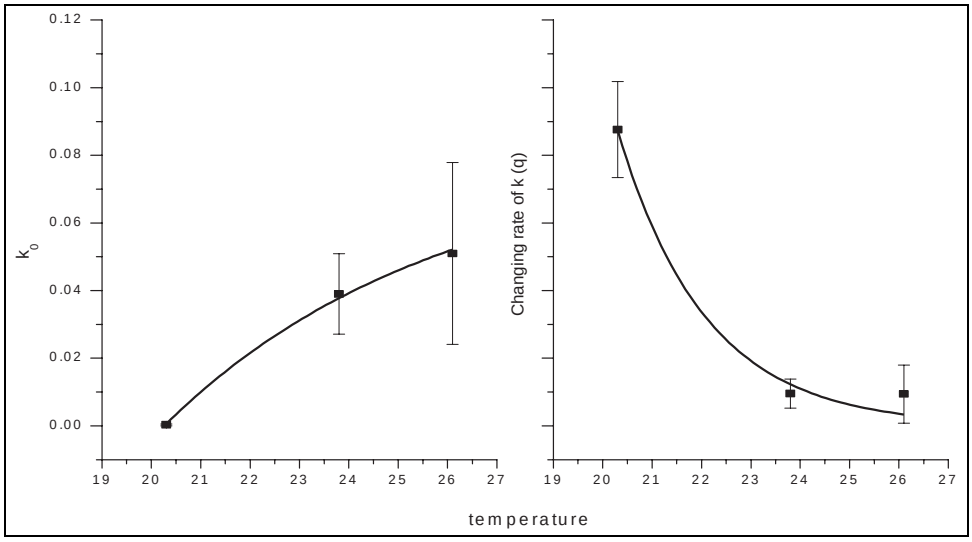


Fig. 5. The initial value of the relative reproduction rate (k_0) and the changing rate (q) in relation to temperature.

relative reproduction rate. The rate will increase with increasing density and sexual reproduction and if host plant availability is not a limiting factor then one would expect a long period of exponential population growth. However, in small production systems or in short term crops with a deterministic growth pattern like in *C.* x *morifolium* host plant availability can become a limiting factor. Insect migration to other host plants will then be crucial for population survival and growth. Since thrips females disperse more readily from host plants, e.g. because of overcrowding or senescence of the inflorescences than males (80 % females : 60 % males) (RHAINDS and SHIPP 2003), situations can arise, even in commercial chrysanthemum production, where the females alone reach a new host plant and where a scenario, similar to the one described above, takes place. In long term crops with a continuous flower or fruit production, like cucumber, it is more likely that the population growth pattern follows that of a traditional exponential growth as it is shown in the study of JAROŠÍK et al. (1997). However, in the initial phase of an infestation, when the density and the probability of meeting a mating partner are low even in long term crops, a simple exponential model underestimates the population growth pattern whereas a model with an exponentially increasing relative reproduction rate gives a better fit (Fig. 6). This suggests that the results from this study can probably even be applied to other host plants of *F. occidentalis*, and that the exponentially increasing relative reproduction rate may have a wide practical application for predictions of early population growth of this pest.

Acknowledgements

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

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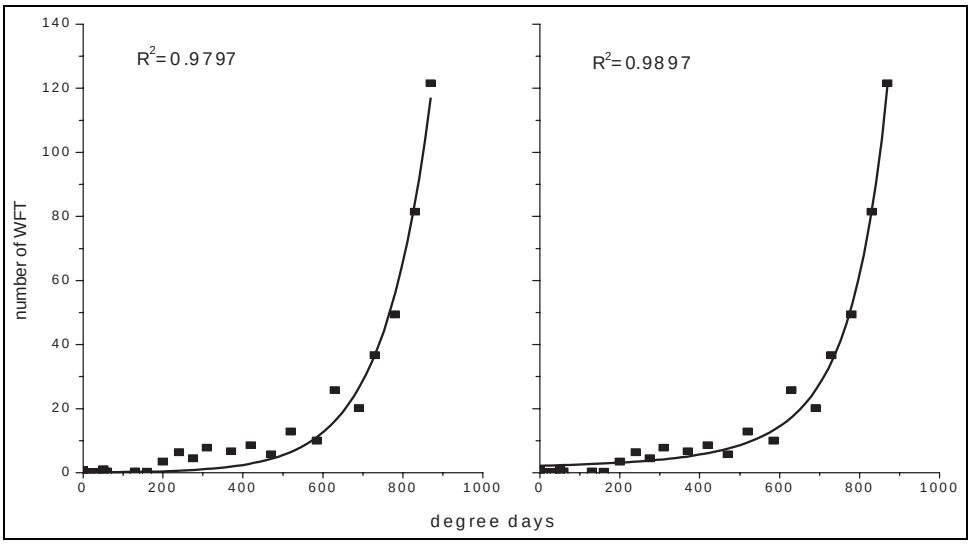


Fig. 6. Fit of an exponential growth equation with a constant (left column) and an exponentially increasing (right column) relative reproduction rate to growth data of a *Frankliniella occidentalis* population on greenhouse grown cucumber (thrips leaf^{-1}). Calculated from previously published data (Jarošík 1997).

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Received June 8, 2006 / Accepted March 15, 2007

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