Interaction between Greenhouse grown Chrysanthemum and *Frankliniella occidentalis*

A Modelling Approach

Margit Nothnagl
Faculty of Landscape Planning, Horticulture and Agricultural Science
Department of Crop Science
Alnarp

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Abstract

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Growers of floricultural crops are still dependent on chemical insecticides because of low consumer tolerance to damaged produce. More knowledge of natural interactions between insects and their host plants would allow insect pests to be controlled in a more environmentally friendly and effective way.

This thesis analysed the system of biological interaction between the pest *Frankliniella occidentalis* (Western Flower Thrips) and its host plant *Chrysanthemum x morifolium*. Mathematical prediction models were developed to describe the growth and development processes of the plant and the insect population, on the assumption that there is a temperature-dependent interaction between flower growth and development and thrips population growth.

An introductory study developed a method for linking flower growth and development that was used in subsequent studies. The second study aimed to predict growth responses of non-infested chrysanthemum flowers to temperature and irradiation, in order to distinguish between temperature and thrips effects on chrysanthemum flower size. Since *F. occidentalis* feeds on both flowers and leaves, a model constructed in the third study served as a prediction tool for food and habitat distribution for the thrips. By recording the final leaf length, leaf area distribution during the growing period could be re-constructed. The model was later included in the large population growth model as a leaf canopy model.

The effect of three temperature regimes on early population growth of *F.occidentalis* was investigated in detail. The results showed that the observed rapid increase in population size could not be correlated with flower opening. The relative reproduction rate of *F. occidentalis* changed exponentially, probably depending on changes in population density and different reproductive strategies. Therefore, in a final model, population density played an important role during early population growth, whereas a decrease in food supply, in terms of damaged leaf area, controlled population decline at the end of the growth period. At lower temperatures (approx. 20˚C), the population decline could be simulated by simply manipulating food supply, while at higher temperatures (approx. 26˚C), the model underestimated population decline, indicating the need for a stress or migration factor in the system.

Keywords: biological interactions, floriculture, greenhouse production, growth analysis, IPM (Integrated Pest Management), simulation.

Author's address: Margit Nothnagl, Department of Crop Science, Swedish University of Agricultural Sciences, Box 44, SE-230 53 Alnarp, Sweden.

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Appendix

Papers I-V

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I. Larsen, R.U., Birgersson, A., Nothnagl, M. & Karlén, H. 1998. Modelling temperature and flower bud growth in November cactus (*Schlumbergera truncata*, Haw.). *Scientia Horticulturae* 76, 193-203.

II. Nothnagl, M., Kosiba, A. & Larsen, R.U. 2004. Predicting the effect of irradiance and temperature on the flower diameter of greenhouse grown chrysanthemum. *Scientia Horticulturae* 99, 319-329.

III. Larsen, R.U. & Nothnagl, M. 2006. Re-constructing data of leaf area distribution over time in the greenhouse pot chrysanthemum cultivar 'Lompoc'. *Manuscript.*

IV. Nothnagl, M., Kosiba, A., Alsanius, B.W., Anderson, P. & Larsen, R.U. 2006. Analysis of early population growth of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on greenhouse grown chrysanthemum. *Submitted manuscript.*

V. Nothnagl, M., Kosiba, A., Alsanius, B.W., Anderson, P. & Larsen, R.U. 2006. Modelling population dynamics of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on greenhouse grown chrysanthemum. *Submitted manuscript.*

Introduction

Main objective

The main objective of this study was to investigate, analyse and simulate the interaction between *Chrysanthemum x morifolium* and *Frankliniella occidentalis* at different temperatures in a greenhouse environment. The knowledge obtained was intended to serve as a basis for future Integrated Pest Management (IPM) strategies.

General background

Global floricultural industries are dependent on the aesthetic value of their products. Pest infestations can result in enormous economic losses because of consumer intolerance to visible damage or pest presence on commercial plants. The Western Flower Thrips (WFT, *Frankliniella occidentalis* Pergande, Thysanoptera: Thripidae) (Fig. 1A) has become one of the major pests in pot plant production during the past 20 years for three main reasons. First, this pest is hard to detect because of its small size and its thigmotactic behaviour. Consequently, control strategies are often launched too late in the life cycle of the pest, resulting in massive infestations. Second, *F. occidentalis* is able to reproduce at a high rate and even parthenogenetically (Brødsgaard, 1989). Third, this pest has developed resistance to most of the chemical control agents available on the market (Jensen, 2000). Moreover, *F. occidentalis* is an important vector for several severe plant viruses such as the tomato Spotted Wilt Virus (TSWV) or the chrysanthemum stem necrosis virus (CSNV) (Jones, 2005). Biological control with *e.g.* the spider mite *Amblyseius cucumeris* (Shipp & Whitfield, 1991; Jacobson *et al*., 2001; Shipp & Wang, 2003) is effective in vegetable production, where only the fruits are the marketable products and damage to leaves can be tolerated, but is not adequate for floricultural production (de Courcy Williams, 2001). More knowledge about the natural interaction between the thrips and their host plants may help to define future, more effective IPM strategies. This thesis investigated the interaction between *F. occidentalis* and *Chrysanthemum x morifolium*, one of the largest pot plant cultures in global greenhouses (Parrella *et al*., 1999) (Fig. 1B) and one of the host plants of this polyphagous pest. The focus lay not only on the ecological interaction, *e.g.* thrips population dynamics on the plant or plant damage, but also on the effect of abiotic factors such as temperature on this interaction. Growth analysis and mathematical prediction models were used as tools for describing and partly explaining the observed plant and population growth patterns. The study was initiated at the Swedish University of Agricultural Sciences (SLU) with the financial support of the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS).

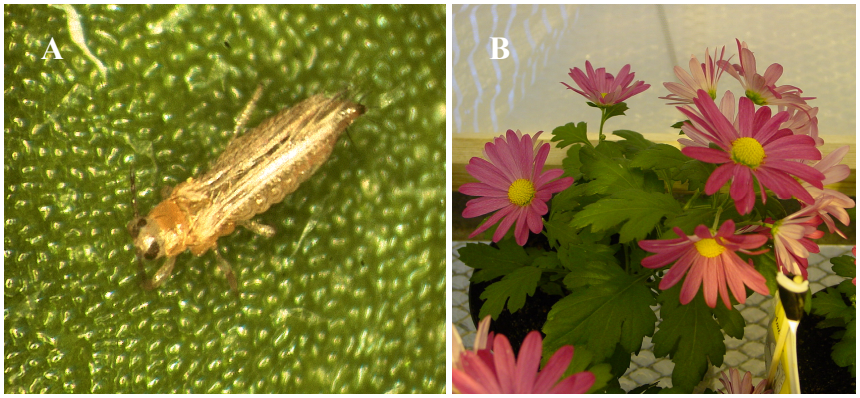

Fig. 1. A) An adult female *Frankliniella occidentalis*. B) *Chrysanthemum x morifolium* 'Lompoc'. Pictures: Margit Nothnagl.

Biological and horticultural background: Plant-insect interactions

Natural plant-insect interactions usually lead to equilibrium (Schoonhoven *et al*., 2005), with advantages and disadvantages but also survival possibilities for both parties. In commercial horticultural production, with its plant monocultures and optimised growing conditions, this equilibrium is not reached and not desired. Although monocultures have the advantage of being easily managed with technological equipment, they exemplify an isolated system without antagonists. Herbivorous insects, which in a natural system are part of the food chain, become pest organisms because they damage the plants directly or indirectly, without being stopped by their natural enemies. Direct damage from an insect pest may for example be caused by feeding or oviposition. Indirect damage might be a decrease in product quality, early plant senescence because of feeding, a reduction of photosynthesis resulting in repressed growth or even the transmission of pathogens from the insect to the plant. However, any damage is a problem for the producer of horticultural products because of the demands of the market. Biological control systems that are based on the theory of natural equilibrium between plants, pests and their antagonists do not deliver satisfactory results in terms of product outcome compared to chemical control systems. More knowledge about the biological background behind plant-insect-antagonist interactions is important to understand and to control insect pests biologically in a more effective way. In the following sections, the ecological interaction between a host plant and a pest and its impact on the horticultural product is discussed from both the insect's side and the plant's side using the model organisms, *F. occidentalis* and *C. x morifolium*.

Plant-insect interactions in horticulture – the insect

One of the major reasons for direct plant damage in horticultural production is the consumption of herbaceous (non-woody) tissue by insect herbivores. For effective control strategies, it is crucial to understand feeding habits and preferences of the pest individuals. In Thysanoptera for example, 90% of all species are herbivorous

(Schoonhoven *et al*., 2005) and in general, the feeding preferences of thrips are controlled by plant age, flower colour, the plant's content of primary and secondary metabolites and whether or not the plant was previously infested (Ananthakrishnan, 1993).

Frankliniella occidentalis is highly polyphagous, with at least 244 plant species as potential hosts (Jensen, 2000). Although *F. occidentalis* prefers feeding on flowers, it can feed on plant foliage and fruits (Mound & Teulon, 1995). It also feeds on prey if available, *e.g.* mite eggs (Trichilo & Leigh, 1988; Agrawal *et al*., 1999) thus acting as a predator in this context. The omnivorous behaviour of *F. occidentalis* is one of the major reasons for its high pest status because it helps the insect to meet its nutritional needs (Agrawal *et al.*, 1999). If, for instance, an infected plant builds up an induced resistance (*e.g.* protease inhibitors that repress oviposition) that would result in a decrease in thrips population size (Annadana *et al*., 2002), *F. occidentalis* changes to feeding on mite eggs than on the low quality plant material (Agrawal *et al*., 1999; Janssen *et al*., 2003). This thrips species also selects different host plants (Janssen *et al*., 2003) or different plant parts, according to their nutritional values. Feeding on nitrogen-rich pollen shortens development time and increases female fecundity (Hulshof *et al*., 2003; Zhi *et al*., 2005; Ugine *et al*., 2006). This positive effect of pollen feeding could be a reason why *F. occidentalis* gathers in flowers and is also known as Western Flower Thrips. Apart from pollen availability, even N-fertilisation of plants and therefore the accumulation of N in their food is advantageous for thrips population growth (Brodbeck *et al*., 2001; Chau *et al*., 2005), since nitrogen in general plays a central role in all metabolic processes as well as in cellular structure and genetic coding of herbivores (Mattson, 1980). More specifically, aromatic amino acids are reported to play an important role in *F. occidentalis* development (Mollema & Cole, 1996). Carbohydrates in plants are also essential nutrients for herbivores, needed to synthesise body tissue and to serve as an energy source (Schoonhoven *et al*., 2005) but have been shown to have less effect on a *F. occidentalis* population than protein levels (Scott Brown *et al*., 2002).

Frankliniella occidentalis, as an herbivorous insect, is morphologically adapted to utilise different food sources. It has asymmetrical, rasping-sucking mouthparts, a primitive form of the piercing-sucking mouthpart type (Pedigo, 1999; Brødsgaard, 1989). A cone-shaped beak is formed from the clypeus, the labrum, parts of the maxillae and the labium. This beak contains the maxillae, the hypopharynx and the left mandible (the right mandible has degenerated) and together these structures form a stylet. The thrips achieve ingestion by scratching host tissue, thrusting the stylet straight through the epidermis and into the next layer of cells (van de Wetering *et al*., 1998, Krenn *et al.*, 2005), taking up liquid food from several cells per penetration (Kindt *et al*., 2003). Pollen feeding occurs by pressing the mouth cone against the grain, piercing the pollen wall with the mandible and sucking up the fluid contents (Kirk, 1984). Males and females differ in their feeding behaviour, with females feeding more frequently and for longer intervals (van de Wetering *et al.*, 1998). Since thrips populations are often female biased and since longer feeding has been proven to be the cause of the typical silvery damage on leaves and florets (Terry & Kelly, 1993), females are assumed

to be responsible for more damage in horticultural products than males. However, the most abundant stages of *F. occidentalis*, the *larvae*, cause most of the damage (Childers, 1997).

Apart from omnivory, another reason for the high pest status of *F. occidentalis* is the often massive infestation, caused by fast development, high reproduction rates and facultative parthenogenesis. During its life cycle, *F. occidentalis* undergoes six different developmental stages: eggs, first and second instar *larvae*, *prepupae*, *pupae* and *imagos*. Most of the kidney-shaped eggs are laid in plant tissue (Childers & Achor, 1995) on the underside of the leaves (Gaum *et al*., 1994) with the help of an ovipositor. The egg-laying sites can be seen as puncture scars on the plant. First instar *larvae* begin feeding upon egg eclosion. Second instar *larvae* move faster, cover great distances and are also active feeders, consuming about three times as much food as the first instar *larvae* (Brødsgaard, 1989). Second instar *larvae* usually move down the plant to pupate in the soil or plant substrate but have also been found to pupate inside floral tubes (Broadbent *et al*., 2003). Prepupal and pupal stages are quiescent non-feeding stages, whereas *imagos* resume feeding (Robb, 1989). Mating occurs two or three days after the last pupal moult and a single male can effectively fertilise a large number of females. If no males are present, females of *F. occidentalis* may reproduce parthenogenetically. Unfertilised eggs always develop into males, whereas most of the eggs laid by fertilised females develop into females (arrhenotoky) (Brødsgaard, 1989). Most thrips complete their life cycle in two to three weeks (Ananthakrishnan, 1993), depending on temperature. Since *F. occidentalis* is a polyphagous species and the *imagos* are winged, it is likely that they move between plants if necessary (Mound & Teulon, 1995), *e.g.* because of overcrowding or senescence of the inflorescences. Females disperse more readily than males (80% females: 60% males) (Rhainds & Shipp, 2003). As in many other herbivores, thrips growth and development is dependent on temperature and host plant conditions.

Plant-insect interactions in horticulture – the plant

What makes a plant a suitable host plant for a herbivorous insect? What are the consequences of an infestation for the host plant? Is the plant able to defend itself? How does the plant-insect interaction affect the plant as a horticultural product, which should be free of damage in order to meet customer demands? In the following section these questions are addressed on the basis of the *Chrysanthemum x morifolium* - *Frankliniella occidentalis* interaction.

The chemical constitution of the plant is the prime factor in its interaction with the insect world (Schoonhoven *et al*., 2005). The insect is first attracted to the plant for example by flower colour (Blumthal *et al*., 2005) or by volatiles (Teulon *et al*., 1999). Since in many natural plant-insect interactions both parts benefit (mutualism), the most common reason for allurement is pollination by the insect. When the insect reaches the host plant, physical and chemical plant surface characteristics are important. After probing and evaluation of the sensory information gathered, the insect either rejects or accepts the plant for feeding and oviposition and plant damage starts soon thereafter.

A plant is not an ideal food source for an insect. Contents of essential nutrients such as nitrogen, in plant tissues are much lower than those required for optimal insect metabolism and growth (Schoonhoven *et al*., 2005) and most carbohydrates are in the form of the indigestible cellulose (Schowalter, 2000). Nevertheless, there must be several advantages with a plant diet, since even omnivorous insects like *F. occidentalis* actively choose to feed on plant material. One advantage might be the high water content in many plant tissues. Although sap-sucking insects like *F. occidentalis* usually have to deal with excess water, they are still terrestrial, need water for their metabolism and are especially vulnerable to desiccation when a new exoskeleton is forming (Schowalter, 2000). Moreover, nutritional values of plant tissues for insects rise with rising water contents (Schoonhoven *et al*., 2005). Young leaves, for example, usually contain more water and are therefore preferable food sources for most herbivores. Nevertheless, *larvae* of polyphagous species (*e.g. F. occidentalis*) generally prefer mature leaves, probably because young leaves usually also contain higher levels of toxic secondary plant substances than older leaves (van Dam *et al*., 1996). For omnivores, the plant also provides florets and pollen as food sources with a higher protein content than leaves. Feeding on plants may also have ecological advantages for the insect. The search costs for feeding on a plant are small compared to prey feeding. The environment in which the feeding occurs is often sheltered against natural enemies or insecticides, so that the insect can maximise its food intake, without being disturbed. Moreover, the distance to egg-laying sites is small and the sites are often well hidden. In the example of the interaction between *C. x morifolium* and *F. occidentalis*, the host plant with its complicated flower structure (*Asteraceae*) offers the thrips many hiding possibilities and protected egg-laying sites, *e.g.* between the ray florets or in the flower base (Childers, 1997).

Insect feeding and oviposition on host plants cause direct damage that often remarkably reduces the quality of the plants as horticultural products. For example, *F. occidentalis* damages *C. x morifolium* by sucking sap from leaf and floret cells. The cells are filled with air, become silvery shining, collapse and the tissues around them turn brown (Lewis, 1973). Small puncture scars from the insects' mouthparts and ovipositors can be observed all over the surface of an infested plant. Near the scars and silvery spots, black dots of insect excrement can usually be found. Feeding on developing tissues (*e.g.* meristems) results in deformation of the plant parts or even distortion of buds and leaves (Fig. 2). Indirect damage by herbivorous insects such as *F. occidentalis* can for instance take the form of a reduction in photosynthesis (Shipp *et al*., 1998), resulting in repressed growth. As shown in a study by van Dijken *et al*. (1994), plant length and leaf area of *C. x morifolium* are reduced by a thrips infestation, by proportional amounts in several different cultivars. Even the number of flower buds and the flower and leaf dry mass of *C. x morifolium* are reduced by a thrips infestation (Davies *et al*., 2005) and inflorescences senesce earlier (Rhainds & Shipp, 2003). Another important type of indirect plant damage caused by *F. occidentalis* is the transmission of pathogens, such as the tomato spotted wilt virus (TSWV) or the chrysanthemum stem necrosis virus (CSNV) (Jones, 2005) by injecting virus-containing saliva into viable cells (van de Wetering, 1999).

Fig. 2. Plant damage caused by feeding and oviposition of *Frankliniella occidentalis*. Pictures: Margit Nothnagl.

The host plants respond to herbivory in several ways. These responses can be divided into avoidance or tolerance strategies and direct or indirect resistance. For example, the plant has several possibilities to avoid surface damage (direct damage). Glandular or non-glandular trichomes have been shown to decrease damage by *Thrips tabaci* in cotton (Arif *et al*., 2004), while epicuticular waxes perform a similar function in early white cabbage (Trdan *et al*., 2004). In contrast, only 24% of the resistance mechanisms against *F. occidentalis* on *Dendranthema grandiflora* (synonymous with *Chrysanthemum x morifolium*) could be explained by morphological characteristics of the plant, whereas 76% could be derived from the plant's chemical composition (de Jager *et al*., 1995). Direct and indirect resistance in plants can be independent of damage or induced by herbivory (Schoonhoven *et al*., 2005). Synthesising secondary metabolites that are toxic to the herbivores or change their fecundity, behaviour or population growth is an example of a direct, induced resistance strategy of the plant. For thrips it is known that phenolics as by-products of tissue repair in response to feeding injury apparently reduce feeding and alter both fecundity and the duration of postembryonic development. However, thrips are able to adapt very quickly by excreting the potentially toxic plant defence substances (Ananthakrishnan, 1993). In contrast to direct resistance responses of the plant, which affect the herbivore itself, indirect resistance responses such as the emission of predator-attracting volatiles affect the surroundings of the herbivore.

Finally, host plant growth and development influence the population dynamics of insect pests and therefore also damage characteristics. Knowledge of host plant growth is important when determining the carrying capacity of the plant, the number of insect individuals that can be supported by the existing resources (Schowalter, 2000). The effect of host plant development on an insect population can be explained by the example of *F. occidentalis* and *C. x morifolium*. Due to their high nutritional quality, florets and pollen have been shown to have a positive effect on thrips fecundity (Trichilo & Leigh, 1988). Because of the host plant's

deterministic growth pattern this high quality food source is first provided towards the end of plant development. Consequently, during the vegetative phase of the host plant the thrips population grows slowly whereas the generative phase provides favourable population growth conditions. Flowers from plants with deterministic growth patterns, such as *C. x morifolium* and many other ornamentals are usually long living compared to the often ephemeral flowers from plants with continuous growth and development (*e.g.* cucumber). In plants with ephemeral flowers the majority of *larvae* are found on leaves (Higgins, 1992) whereas in plants with long living flowers both *imagos* and *larvae* are found in the flowers (Trichilo & Leigh, 1988; van Dijken *et al.*, 1995). This results in high damage in the most important parts of the marketable ornamental plants, the flowers.

The role of horticultural practices in plant-insect interactions

In the previous sections the biological background of plant-insect interactions was presented. Most of this information can be used in horticultural production. Since such production systems are artificial and the focus lies on plant health and appearance, there are several cultural procedures such as climate regulation, irrigation and fertilisation that affect the plant-insect relationship. These are discussed in the following section, again using the example of the model organisms *F. occidentalis* and *C. x morifolium*.

Both the photoperiod and the amount of light (daily radiation integral) are known to have major effects on the growth and flowering of chrysanthemums (Machin & Scopes, 1978). *Chrysanthemum x morifolium* is a short-day plant, which means that flowering is induced by dark periods that last longer than at least 9½ hours per day (Post, 1948). In floricultural production this response is used to regulate flowering time in relation to market demands. By covering the plants with black cloth, the daylength can be shortened during summer and year-round production of flowering *C. x morifolium* becomes possible. The amount of short days needed for flowering varies depending on cultivar. The development of *F. occidentalis* is also affected by daylength (Brødsgaard, 1994). The total developmental time of the thrips decreases with increasing daylength due to shorter developmental times of second instar *larvae* and pupal stages. Moreover, intrinsic rates of increase as well as net reproductive rates increase with longer photoperiods, but the mean number of offspring is not affected by different photoperiods. However, the daily rate of egg laying per female is lower at short daylengths, indicating that *imagos* are less active with long periods of darkness. In short-day plants like *C. x morifolium*, relatively high light intensities are necessary for adequate photosynthesis (1.2 and 1.6 MJ m^{-2} day^{-1}) (Machin & Scopes, 1978). On the other hand, only low light levels are necessary to extend short photoperiods and induce long-day responses. Low light intensities have been shown to delay the change from vegetative to generative growth in *C. x morifolium* (Cockshull & Hughes, 1971; Hughes & Cockshull, 1972) and high light levels (2.5 and 3.75 MJ m^{-2} day^{-1}) lead to significant increases in dry weight (Cockshull & Hughes, 1971). The effect of light intensity and light integral on population growth of *F. occidentalis* is a matter for future research.

Temperature is another important climate factor that can easily be changed in a greenhouse in order to manipulate plant growth and development. In general, temperature affects the rate of photosynthesis, respiration, water and nutrient absorption, translocation and transpiration in plants (Larcher, 1994; Taiz & Zeiger, 1998). For *C. x morifolium*, it has been shown that the optimum temperature for flower growth and development is around 20˚C (Adams *et al*., 1998; Larsen & Persson, 1999). Flower size decreases with increasing temperature (Nothnagl *et al*., 2004) and stem elongation rate increases with higher average day temperatures (Carvalho & Heuvelink, 2001). Temperature also plays an important role for resistance mechanisms (Pedigo, 1999). Moreover, temperature is described as the main factor influencing insect growth and development. Robb (1989) investigated the development rates of every single developmental stage of *F. occidentalis* at different temperatures and found the optimum temperature for development to be around 30˚C. Air humidity is dependent on temperature and plays an important role for the water balance in the plant, which affects transpiration and the uptake of nutrients from the soil and CO_2 from the surrounding air. Increasing relative humidity has also been shown to decrease pupal mortality of thrips (Kakei & Tsuchida, 2000) and greater population growth occurs under a higher relative humidity, regardless of substrate (Zhi *et al*., 2005).

Fertilisation with nitrogen-rich fertilisers usually improves plant quality and therefore increases population growth of *F. occidentalis* (Brodbeck *et al*., 2001; Chau *et al*., 2005). On the other hand, excessively high levels of nitrogen can suppress thrips population growth. Although the reason for such suppression is not known, it is proposed that insects are adapted to 'normal' nitrogen concentrations and that adverse conditions therefore have a negative effect on population growth (Schoonhoven *et al*., 2005). High nitrogen availability could also lead to changes in the secondary metabolism of the plant and a resulting increased production of defence substances (Schoonhoven *et al*., 2005).

IPM (Integrated Pest Management) strategies for WFT – insecticides, natural enemies, resistance in plants

Frankliniella occidentalis is difficult to control because of its omnivorous behaviour and its adaptability (*e.g.* high reproductive rate, parthenogenesis) but also because of its resistance to chemical control agents (Jensen, 2000). Many different studies have been conducted in order to find effective Integrated Pest Management (IPM) control strategies for this pest. IPM combines biological, physical and chemical control agents with the emphasis on environmental friendly pest management (Jacobson, 1997). One of the most important strategies for IPM of *F. occidentalis* is exclusion. In northern Europe the pest is often imported by cuttings and cannot survive outside the greenhouse. Control and quarantine of the new plant material may avoid an infestation. In other countries, where the thrips invade greenhouses through open vents, screening systems incorporating a cooling strategy are important exclusion devices. Exclusion can also be achieved by good sanitation, avoidance of continuous cropping under one roof and disposal of plant residues (Robb & Parrella, 1995). Because of the thigmotactic behaviour of thrips, damage in flower buds usually remains undetected until some time after the injury

(Childers, 1997). In order to discover thrips pests at a sufficiently early stage, monitoring with *e.g.* sticky traps is important during the plant cultivation period. Once *F. occidentalis* is monitored in the greenhouse, insecticides *e.g.* with the active ingredient Spinosad can be applied (Cloyd & Sadof, 2000; Jones *et al*., 2005). However, because of its resistance, small size and secretive habit of hiding in the inner whorls of flowers and buds, chemical control of *F. occidentalis* is still difficult (Heungens *et al*., 1989; de Jager *et al.*, 1993; Annadana *et al*., 2002). Good coverage and penetration into the dense flowers, buds and terminal foliage is essential for chemical control and is enhanced by smaller droplet size (Robb & Parrella, 1995).

One of the biggest problems with chemical control agents apart from environmental effects is their either direct or indirect negative influence on biological control agents (Jones *et al*., 2005). One natural enemy of *F. occidentalis* is the spider mite *Amblyseius cucumeris* (Acarina: Phytoseiidae) (Fig. 3A) (Shipp & Whitfield, 1991; de Courcy Williams, 2001; Jacobson *et al.*, 2001), which may be released into a plant production system as a precautionary measure (Jacobson *et al.*, 2001). The fact that *A. cucumeris* does not feed on thrips developmental stages other than first instar *larvae* (Shipp & Wang, 2003) may be compensated for by adding *Orius* species (Hemiptera: Anthocoridae) (Fig. 3B), which are able to attack a wide range of thrips life stages (Skirvin *et al.,* 2006). Lately, entomopathogenic nematodes (Ebssa *et al.*, 2006) and fungi (*e.g.* Beauveria bassiana) (Ugine *et al.*, 2006) have also been investigated as new biological control agents of *F. occidentalis*. However, biological control is still not considered an option for producers of flowering pot plants (*e.g. C. x morifolium*) because damage cannot be fully avoided.

Fig. 3. Examples of natural enemies of *Frankliniella occidentalis*. A) *Amblyseius cucumeris* B) *Orius laevigatus*. Pictures from www.biobest.be with the kind permission of Biobest N.V., Biological Systems.

Another important research area concerning IPM strategies against *F. occidentalis* apart from natural enemies is host plant resistance. As described above, induced plant responses may affect the behaviour and growth of the attacking herbivorous insect but even naturally occurring proteinase inhibitors in plant tissues may be protective against invading insects (Green & Ryan, 1972). Variations in host plant resistance to *F. occidentalis* have been reported in several

studies (de Jager *et al*., 1993; van Dijken *et al*., 1995; Mollema & Cole, 1996; de Kogel *et al*., 1997) and will probably also be the objective of future research.

Analytical background – Growth analysis and prediction systems

Models are simplifications of reality. They can be used for quantitative descriptions of animal or plant growth, as practical prediction tools for growers or as descriptive and analytical tools for research and teaching purposes (Gary *et al*., 1998). In horticulture, models are often used for yield predictions (Dayan *et al*., 1993; Marcelis *et al*., 1998), predictions of growth and development (Charles-Edwards & Acock, 1977; Charles-Edwards *et al*., 1979; Larsen & Hidén, 1995; Lieth & Pasian, 1991; Nothnagl *et al*., 2004) or predictions of plant morphology (Prusinkiewicz, 1998; Heuvelink *et al*., 2001). In horticultural entomology, most of the modelling studies concern population dynamics (Birch, 1948; Wang & Shipp, 2001), insect development (Wagner *et al*., 1984; Goudriaan & van Roermund, 1989; Hilbert, 1995) or simulations of predator-prey systems (Wyatt, 1983; Bernstein, 1985; van Roermund *et al*., 1997).

In general, models can be divided into deterministic or stochastic models, and empirical or mechanistic models. Deterministic models produce identical results on each simulation occasion with constant parameter values and environmental settings, whereas stochastic models take biological variability into account (Dent & Walton, 1997). Empirical models simply describe processes, whereas mechanistic models are hierarchic and try to explain the mechanisms behind the processes, by transferring information from the lower hierarchic levels to the higher levels. For the modeller it is important to define the scope of the model and the number of state variables that should be predicted. The more complex the model, the higher the probability of non-predictable interactions. Dent and Walton (1997) describe this trade-off between detail and comprehensibility in model building.

Growth models

In the present study, models were built to describe insect population increments and plant growth. Such growth models are often based on growth analysis, a scientific tool that uses mathematical equations to describe biological growth patterns. Since growth is a dynamic phenomenon that occurs over a period of time, differential equations are used to describe it. The integrated form of the equation illustrates the actual growth pattern. The equations used in this study are described by Thornley & Johnson (1990) and summarised in Table 1.

The simplest form of a growth equation is *linear* growth (Fig. 4A). It is an empirical equation, based on experimental observations. The growth pattern follows that of a straight line with a constant slope (k_{lin}). The *exponential* equation (Fig. 4B) is often used to describe plant or population growth in unlimited environments. During exponential growth, the growth machinery of a plant is proportional to dry mass and all individuals in a population reproduce in

proportion to the existing size of the population. The specific (or relative) growth rate, depending on the proportion of dry mass or population size that constitutes growth machinery, is constant. In an ideal situation, the more individuals there are in the population, the more individuals will be added. The graph of this equation increases slowly in the beginning and rises as the population size increases.

Table 1. *Growth equations used in this study in their differentiated and integrated forms.*

Growth equation	***Differentiated form – growth rate***	***Integrated form – growth curve***
Linear	$\frac{dy}{dt} = k_{lin}$	$y = k_{lin}t + d$
Exponential	$\frac{dy}{dt} = k_{\exp} y$	$y = y_0 e^{k_{\exp} t}$
Mono-molecular	$\frac{dy}{dt} = k_{mon}(y_f - y)$	$y = y_f - (y_f - y_0)e^{-k_{mon}t}$
Logistic	$\frac{dy}{dt} = k_{\log} y(1 - \frac{y}{y_f})$	$y = \frac{y_0 y_f}{y_0 + (y_f - y_0)e^{-k_{\log} t}}$
Richards equation	$\frac{dy}{dt} = \frac{k_{rich} y(y_f^n - y^n)}{n y_f^n}$	$y = \frac{y_0 y_f}{[y_0^n + (y_f^n - y_0^n)e^{-k_{rich}t}]^{1/n}}$

The *monomolecular* growth equation (Fig. 4C) can be applied in situations where substrate becomes limiting for growth. If, for example, the nutrients in a peat substrate are all used as the plant grows, the plant growth will decrease and finally stop. The graph of this equation rises rapidly in the beginning and approaches an upper asymptote. The biological hypothesis behind *logistic* growth (Fig. 4D) is that both dry mass or population size and substrate are limiting growth. However, in the beginning of the growing period, where the substrate even in a limited environment is abundant, the absolute growth rate increases until it reaches a peak, at the inflection point (Fig. 4D). After that, the growth rate decreases, mostly because of substrate limitations. This results in an s-shaped growth curve. The logistic growth equation is one of the most commonly applied equations for growth description, probably due to its simplicity. However, this model is not flexible enough to fit all sigmoid growth curves. The *Richards equation* mentioned in Table 1 is another empirical tool to describe an s-shaped growth pattern with a higher generality, since an additional parameter *n* defines the shape of the curve (Richards, 1959).

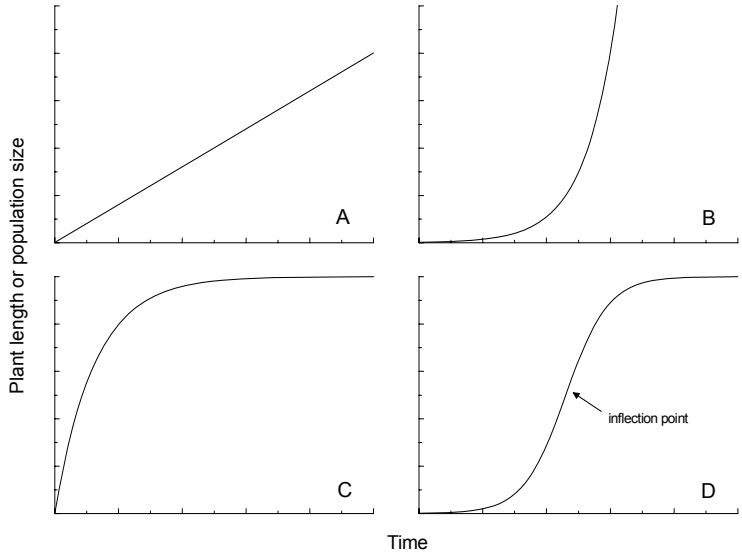

Fig. 4. Graphs of the main growth equations used for growth analysis. A) linear, B) exponential, C) monomolecular and D) logistic.

Development models – Heat sum and the 'unit index' system

Development can be defined as a series of physiological events that describe the maturation of an organism. Although they are results of underlying continuous processes, these events are discrete happenings. The simplest models used for predicting development are the 'heat sum' models. They are based on the assumptions that the rate of development (*R*) is correlated to temperature, and within a limited temperature range, that this relationship is linear (Angus *et al.*, 1980/1981). The mean temperature for each day above a certain threshold value, under which no development occurs, is measured and summed (Thornley & Johnson, 1990). According to this, a certain heat sum (expressed in degree-days) corresponds to a certain developmental stage. However, the development of organisms that are influenced by factors other than temperature (*e.g.* daylength or irradiation level) cannot be adequately predicted by a 'heat sum' model (Major *et al.*, 1975). Moreover, the model is not useful above an upper threshold temperature, when development and temperature are no longer linearly related.

Apart from the 'heat sum' model, a unit index system may be used to describe development. In this index, which starts from 0 (*e.g.* flower initiation) every single stage of development is related to a final stage 1, where development is assumed to be completed (*e.g.* flower anthesis) (Thornley & Johnson, 1990; Hidén & Larsen, 1994). The rate of development (*R*) can then be calculated by the following equation:

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

where d is the number of days needed from the start of development to the final stage of development. One advantage with this system is that events happening on different astronomical dates can be compared in relation to the index scale. Moreover, other factors that influence development except temperature can easily be included in such a system. The multiplicative approach (Major *et al.*, 1975; Angus *et al.*, 1981; Larsen & Persson, 1999; Nothnagl *et al.*, 2004) shown in Eq. 2 describes the daily developmental rate (R) as *e.g.* a function of average daily temperature and irradiation levels.

$$R = f_{(T)} f_{(I)} \quad (2)$$

Linking development to a growth variable that can be measured continuously (*e.g.* flower size in Paper I and II) may help to get a better overview of the biological events occurring during the growth and development period of an organism.

Objectives and hypotheses of Papers I-V

In general, Paper I provided a method that was then used throughout the other studies. Papers II and III were introductory analyses of thrips population dynamics on a living host plant, which were dealt with in Papers IV and V.

In **Paper I** the hypothesis was that flower growth and development are linked and that this relationship is influenced by temperature. The objective was to connect a unit index system for flower development to flower size and to predict the relationship by a dynamic model. This model would make it possible to calculate flower development stages from flower growth variables and *vice versa*. The growth-development relationship developed was then used as a basis for the chrysanthemum growth models in Papers II and III and also for the thrips population growth models (Papers IV and V).

The original hypothesis in **Paper II** was that chrysanthemum flower growth would show a similar exponential pattern to *Schlumbergera truncata* used in Paper I. The objective was to predict flower growth in relation to flower development, depending on temperature. The study in Paper II was also conducted with respect to the hypothesis that chrysanthemum flower size decreases with a thrips infestation because of flower deformation. To distinguish between temperature and feeding effects on flower growth, a prediction tool was first established to simulate the effect of temperature on flower size of *C. x morifolium* without any infestation.

Since *F. occidentalis* also feeds on leaves, the aim of **Paper III** was to build a model to predict leaf area distribution in greenhouse chrysanthemum as a measure of habitat and food source distribution for the thrips. The hypothesis was that the number of leaves and the time of leaf unfolding in relation to shoot development would be pre-determined when the plant was grown under constant short-day

conditions and that leaf development would be terminated with flower initiation. Consequently, the model had to be able to reconstruct leaf area distribution during the growing period by measuring the final leaf area alone.

In **Paper IV** the objective was to analyse early thrips population growth with respect to flower availability (nitrogen-rich food source). The hypothesis was that the thrips reproduction rate would increase when flowers were available. The knowledge gained by the system analysis in Paper IV was then used as a basis for a prediction model (Paper V).

The aim of the study in **Paper V** was to establish a prediction tool, which had to be able to describe thrips population growth at different temperatures on greenhouse chrysanthemum as a basis for future IPM strategies. The hypotheses were that population density plays an important role in the initial phase of thrips population growth, that food supply is important for thrips population growth and that temperature is the climate factor, mostly affecting thrips population growth and development.

Materials and methods

Model descriptions and assumptions

Different growth equations were used in this thesis in order to describe plant and population growth. In the following section, they are listed in their differentiated and in their integrated form. In Paper I flower elongation was simulated using an exponential growth equation:

$$\frac{dL}{dInd} = kL \quad \ldots \text{ for } 0 \geq Ind \leq 1 \tag{3}$$

$$L = L_0 e^{bInd} \quad \ldots \text{ for } 0 \geq Ind \leq 1 \tag{4}$$

where L is the length of the flower bud, Ind is the flower development index, which substitutes for time, k is the relative growth rate, L_0 is the initial length of the flower bud at $t = t_0$ and b substitutes for the relative growth rate.

In the first chrysanthemum model a combination of a linear and a monomolecular model illustrated the growth of the flower bud and the opening procedure of the flower, respectively (Paper II):

Linear: $$\frac{dD}{dInd} = k_{lin} f_{(T_{lin})} f_{(I_{lin})} \quad \ldots \text{ for } Ind_s \leq Ind \leq Ind_{crit} \tag{5}$$

Monomolecular: $$\frac{dD}{dInd} = \frac{dD_{\max}}{dInd} f_{(T_{mon})} f_{(I_{mon})} \quad \ldots \text{ for } Ind > Ind_{crit} \tag{6}$$

and $$\frac{dD_{\max}}{dInd} = k_{mon}(D_{\max_f} - D_{\max}) \quad (7)$$

integrated: $$D_{\max} = D_{\max_f} - (D_{\max_f} - D_{crit})e^{-k_{mon}Ind} \quad (8)$$

where D is the flower diameter, Ind is the development index, Ind_s is the index value when the flower bud becomes visible, Ind_{crit} is the index value, when the linear phase switches over to the monomolecular phase, k_{lin} and k_{mon} are constants, D_{max} is a maximum flower diameter at optimal climate conditions, D_{maxf} denotes a final maximum flower diameter and D_{crit} is the D_{max} value at Ind_{crit}. The climate functions $f_{(T)}$ and $f_{(I)}$ describe the effect of temperature and irradiation on flower growth, respectively.

In the leaf canopy model in Paper III the Richards equation was used to describe the sigmoid shape of the leaf area increment of individual leaves on the different side shoots of a chrysanthemum plant:

$$A = \frac{A_0 A_f}{\sqrt{A_0^n + (A_f^n - A_0^n)e^{-kIndex)}}} \quad \text{… for } Ind > 0 \quad (9)$$

where A is the leaf area, A_f is the final leaf area, A_0 is the initial leaf area, k and n are constants determining the shape of the growth curve, while Ind_l is the index value corresponding to time of leaf appearance (start of growth).

A double exponential model, an exponential growth equation with an exponentially increasing relative growth rate, was used in Paper IV to analyse the early growth of a *F. occidentalis* population on a chrysanthemum plant in an empirical way. In this growth analysis different temperatures provoked different population and plant growth patterns. The following equations were used:

$$\frac{dWFT}{dt} = kWFT \quad (10)$$

$$WFT = WFT_0 e^{kt} \quad \text{where} \quad k = k_0 e^{(qt)} \quad (11)$$

where WFT is the number of individuals of Western flower thrips (*F. occidentalis*), WFT_0 is the number of WFT at the start of the experiment and t denotes time (days). In the exponentially increasing relative reproduction rate k (eggs females^{-1} days^{-1}), k_0 is the initial value at the start of the experiment, and q determines the rate of change (days^{-1}) of k over time (t).

In Paper V, an array model (Lefkovitch, 1965) combined with the leaf area model from Paper III represented a more mechanistic approach to describe thrips population growth on greenhouse chrysanthemums. In the array system, 100 generations of thrips were simulated independently. The model was based partly

on experimental data and partly on published data (Robb, 1989) and is illustrated as a flow chart (Fig. 5). Development of *F. occidentalis* was simulated using a development index, similar to the plant index in Paper I, II and III. The index values, calculated from Robb (1989) on time of development for the different stages at various temperatures, were used as critical values for transferring individuals from one development stage in the model to the next. To allow temperature effects on thrips developmental rate (R_{dev}) to be described, the Logan equation ($f_{(TL)}$, Logan *et al.*, 1976) was multiplied by a maximum developmental rate (R_{max}), chosen from Robb (1989):

$$R_{dev} = R_{\max} f_{(T_L)} \tag{12}$$

Model simulations were started by introducing an initial insect generation to the system. Population growth was regulated by affecting oviposition rate (R_{ov}):

$$R_{ov} = females \times OC_{\max} \times DF \times FF \tag{13}$$

The number of females was multiplied by a maximum oviposition constant (eggs per female, OC_{max}), a density factor (DF) and a feeding factor (FF). In the model, thrips reproduced parthenogenetically if no mating partners were present (Paper IV), resulting in slow population growth. An assumption for this approach was that males and females had no long distance sensing system for attraction (pheromones). A density factor (DF), represented by a linear relationship to adult density (AD), therefore controlled population growth in the beginning of the growing period:

$$DF = k_1 \times AD \tag{14}$$

where k_1 is a constant. This factor influenced oviposition by ranging from 0 (no infestation) to 1 (no effect of adult density). When the factor reached unity, the population had grown large and population density was not a limiting factor for reproduction. Food limitations in terms of a feeding factor (FF), ranging from 0 to 1, regulated population dynamics after the population peak by decreasing oviposition exponentially. The feeding factor was dependent on the thrips density on the available undamaged leaf area (D_{LAud}), simulated by the leaf area model from Paper III and described by the following equation:

$$FF = e^{(-k_3 D_{LAud})} \tag{15}$$

where k_3 is a constant.

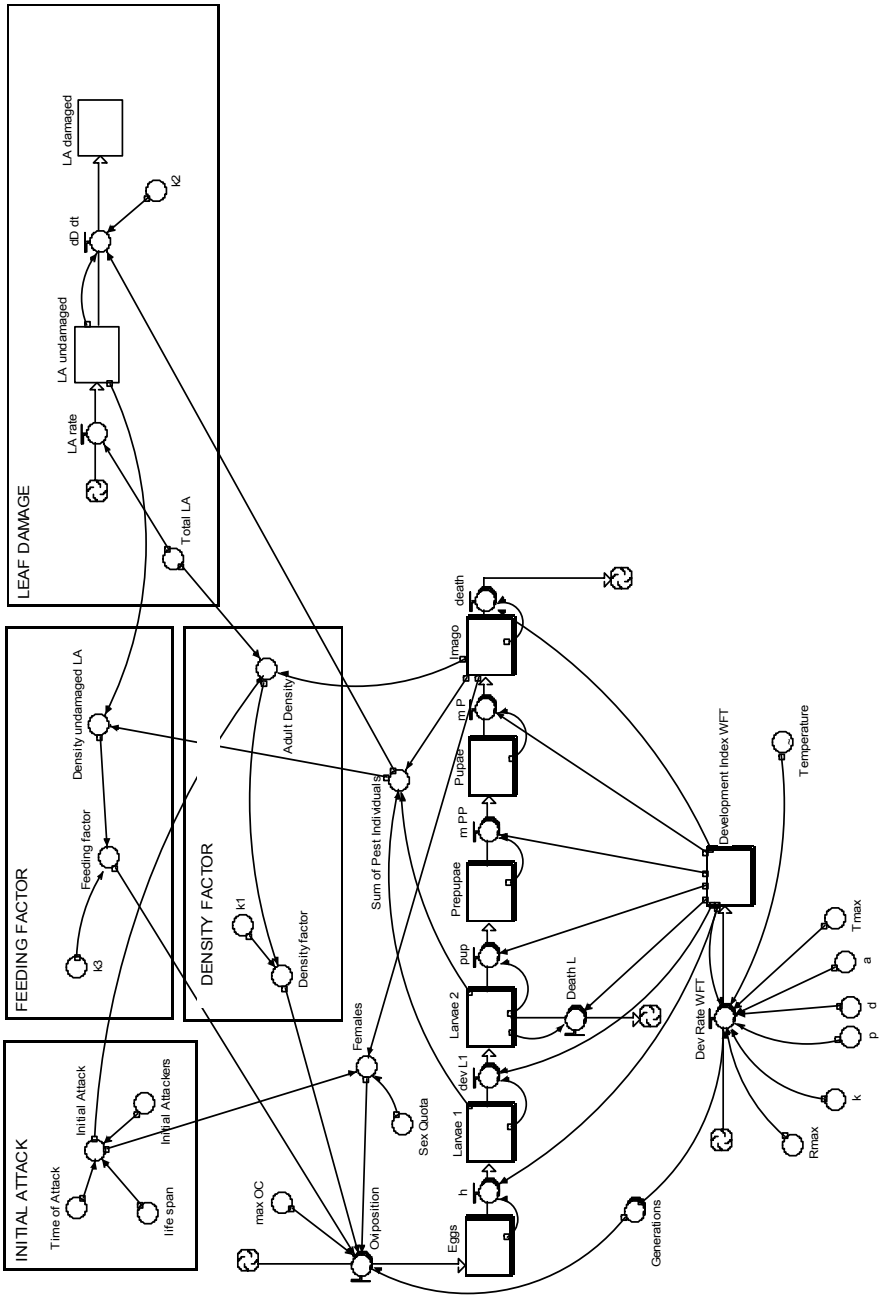

Fig. 5. Flow chart of the population growth model of *F. occidentalis* on greenhouse chrysanthemums. *maxOC* = maxiumum oviposition constant, h = hatching, devL1 = development *larvae*1, pup = pupation, mPP = maturation *prepupae*, mP = maturation *pupae*, LA = leaf area, T_{max} = maximum temperature, R_{max} = maximum developmental rate.

Statistical procedures and model validations

The main statistical procedures for modelling and parameter estimation used during this study were linear and non-linear regression analyses. The applied integration methods with fixed time steps were the Euler (Paper I, II and III) and the 4th-order Runge-Kutta method (Paper V). In Paper I, II and III the PROC NLIN procedure of PC/SAS for Windows, version 8.1 (Statistical Analysis Systems Institute) was used for non-linear regression analyses. The linear regression analyses in Paper II and all regression analyses in Paper IV were carried out in the software programmes ORIGIN 5.0 (Microcal Inc.) and ORIGIN 7.0 (OriginLab Corporation, MA, USA), respectively. Model simulations that were used for parameter estimation, verification of the model data and validation of the model were carried out in POWERSIM 2.02 (Paper II), Microsoft EXCEL (Paper I and III) and STELLA 8.11 (ISSE systems Inc., NH, USA) (Paper IV and V). In Paper III a 2-sample t-test in the statistical programme MINITAB, Release 14 (Minitab Ltd., UK) at a confidence level of 95% was used for comparisons of population size in two different treatments.

The goodness of fit of the models was tested by plotting the predicted data against the observed data and performing a linear regression analysis. The correlation coefficient R^2 obtained indicated the prediction ability of the models. Moreover, the models were tested on data from separate experiments for validation and the goodness of fit was determined as mentioned above.

In Paper III an allometric relationship (Hunt, 1978) between leaf area and leaf length was established by plotting the logarithms of recorded data for both variables against each other in a linear regression analysis.

Experimental setup

All experiments were carried out in the experimental greenhouses of the Swedish University of Agricultural Science in Alnarp, Sweden.

Fig. 6. Cages used for the experiments. Pictures: Margit Nothnagl.

Plant material, cultivation practices and infestation

In Paper I, plants of *S. truncata* 'Eva' were potted in commercial peat compost (Hammenhög K) and grown under long-day conditions (natural light conditions) until they had developed four levels of phylloclades. Then the top layer of the phylloclades was removed and the plants were exposed to short photoperiods (L8:D16) to induce flowering.

In Papers II-V, plant cuttings of *C. x morifolium* 'Lompoc' were obtained from Fides Straathof Export, The Netherlands, and rooted under long-day conditions (L 15-16:D9-8) that were achieved by extending the natural daylength with High Pressure Sodium lamps (Phillips SON-T lamps (400 W, 44 µmol m^{-2} s^{-1}) at 20 ± 2ºC. After two to three weeks, when the roots were well developed, the cuttings were transplanted into a commercial peat (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 in order to promote side shoot formation (Fig. 7) and transferred into greenhouse compartments with different climate installations. In the thrips experiments (Papers IV and V) the plants were kept in cages (50x50x90cm), covered with transparent cloth to prevent the thrips from escaping (Fig. 6). During the remainder of the trials the plants were exposed to short photoperiods (8-10h light per day) to induce flowering. Short photoperiods were achieved by covering the plants with darkening fabric (LS XLS Obscura, Ludvig Svensson AB, Kinna, Sweden). The plants were irrigated once every day and given a liquid fertiliser once every week (Superba Plant 1:100). In the thrips experiments, each plant was infested with two female *F. occidentalis* eight days after the start of the experiment.

Climate recordings and plant measurements

In all experiments, sensors for monitoring photosynthetic photon flux (Skye Instruments Ltd., Llandringdod Wells, UK or Li-Cor Quantum Sensors) were placed between the plants, and thermocouples (type T, copper and constantan) or Pt-100 sensors were used to record air temperature. The climate data were monitored continuously using a datalogger (Intab, Sweden). The length of the flower bud in Paper I was measured by placing a flexible plastic ruler alongside the bud. The diameter of the terminal flower buds and flowers in Paper II was recorded using electronic callipers and the developmental stage of the flower was recorded according to a previously established index (Larsen & Persson, 1999) where zero denotes start of short-day treatment and unity refers to anthesis. The leaf area in Paper III was estimated from the leaf length data, measured with a flexible plastic ruler.

Insect rearing and sampling

The females of *F. occidentalis* used for infestation of *C. x morifolium* were the progeny of females originally reared on green beans and imported from the Netherlands (Koppert B.V., Biological Systems). In the experiment they were reared in cages on *C. x morifolium* 'Lompoc' for six weeks in order to adapt

themselves to the new host plants. Insect sampling occurred by cutting the plants and placing them in turpentine traps (Lewis, 1973) (Fig. 7). The mobile stages of the thrips (*larvae* and *imagos*) moved away from the smell of a cotton ball on the lid moisturised with turpentine and were captured in 70% ethanol. The sampled insects were counted under the microscope.

Fig. 7. Turpentine traps for capture of the movable life stages of *Frankliniella occidentalis* (Picture: Margit Nothnagl) and a schematic model plant of *C. x morifolium* as used in this study. B1-B5 illustrate the base leaves of the cutting and I-V denote the side shoots.

Results and Discussion

The relationship between flower growth and development (Paper I)

The study in Paper I illustrates a method of linking flower development to a growth variable in *Schlumbergera truncata* 'Eva'. A similar approach was used by Fisher *et al.* (1996) on Easter lily. In *S. truncata*, flower growth was characterised by an elongation of the bud and could be described by a modified exponential growth equation. Since the time to anthesis increased with decreasing temperature, the slope of the exponential graph changed with altered temperature conditions. However, the relationship between the rate of flower development and temperature followed a straight line, resulting in a constant slope of the exponential graph at all temperatures, when plotted against a development index scale. With the model from this study it was possible to estimate time to anthesis from bud length recordings at a specified temperature. It was also possible to estimate the temperature needed to target a specified date of sale. This could be useful for research reasons but also in a grower's decision support system.

The same method of linking growth and development was applied to *C. x morifolium* in Paper II and III and for modelling insect populations as shown in Paper V. The discrete stages of development of individuals of *F. occidentalis* were

also described with a relative index scale from zero (egg) to 1 (death). This index was then used as a basis for the array population growth model.

Chrysanthemum growth at different temperatures – flowers and leaves (Papers II and III)

Biology

The final size of chrysanthemum flowers was influenced by temperature and irradiation. The flowers became larger at high irradiation levels and temperatures below the optimum temperature of 20˚C (~15˚C or 4825 mmol m^2 d^{-1}: diameter ~ 70 mm). This is in line with the results of Karlsson *et al*. (1989) but in conflict with the results from Paper I, where final flower size was not affected by temperature. In *C. x morifolium*, low irradiation levels and higher temperatures led to smaller flowers (23.3˚C or 392 mmol m^2 d^{-1}: diameter ~ 55 mm). There was also a tendency for the number of flowers to differ between the temperature treatments. Plants at lower temperatures (20.3˚C) had on average 10 ± 2 flowers, whereas plants at higher temperatures (26.1˚C) had 15 ± 4 flowers. A similar reduction in flower number and flower size has been shown in *Viola* x *wittrockiana* Gams. cvs. (Warner & Erwin, 2006). In the thrips experiments described in Papers IV and V, flowers of thrips-infested plants were smaller compared to uninfested plants, 54.5 ± 7.9 and 67.8 ± 2.4 mm diameter, respectively. This difference in flower diameter was due to deformations of the flowers and was more pronounced at higher temperatures (22.3 ± 16.1 mm diameter versus 52.8 ± 3.7 mm).

Leaf area distribution was investigated in Paper III. On average, the different side shoots (1-5, Fig. 7) formed 8-11 leaves.

Analysis and modelling

In contrast to *S. truncata* in Paper I, where the flowers grew exponentially, flower growth in *C. x morifolium* 'Lompoc' (Paper II) showed a pattern of two visible growth phases. The first phase was linear and the second phase could be illustrated by a monomolecular growth curve. Prior to the linear phase, there was an exponential phase of microscopic growth and development of the bud (Charles-Edwards *et al*., 1979). The reason for the different growth patterns in Papers I and II lay in the shape of the flowers and the process of flower opening. For chrysanthemum, the growth of the receptacle and the bracts surrounding it followed a linear pattern. At flower opening, when the ray florets expanded, the result was a monomolecular growth pattern.

Although the experiments in Paper II were carried out at three different sets of temperature and irradiation conditions in the greenhouse, the critical development index values for the start of the linear phase (Ind_S = 0.24) and for the switch between the linear and the monomolecular phase (Ind_{crit} = 0.89) always lay at the same values. This shows that the pattern of flower growth follows flower development, independent of temperature or irradiation levels. The same index

values could be used for two other chrysanthemum cultivars ('Miramar' and 'Rage'), indicating that this might be a general pattern for chrysanthemums (Fig. 8).

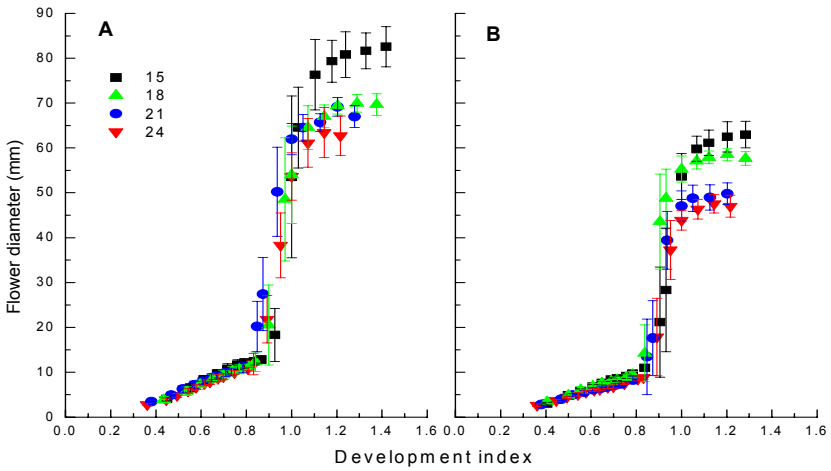

Fig. 8. Flower diameter growth of two other cultivars of *Chrysanthemum x morifolium* at four different temperatures. The critical index value for the switch from the linear to the monomolecular growth phase of the cultivar 'Lompoc' lay at 0.89. A) 'Miramar'. B) 'Rage'. Symbols are mean values of ten observations and error bars are the standard deviations.

The Richards function (Richards, 1959) gave a good fit to the leaf area data (R^2 ~ 0.9) in Paper III. Chrysanthemum leaves appeared according to the primordial production order before flower initiation (Larsen & Hidén, 1995). We postulated that leaf development would terminate with flower initiation, that the primordial leaves would then already differ in size and that these differences would determine the inflection points of the individual leaf growth curves. The time of leaf unfolding for the individual leaves was simulated by assigning different values to the corresponding initial leaf areas ($A_{01} - A_{011}$). The model overestimated the data from the validation trial but this was probably due to the different leaf numbers of the plants and the plants being subjected to minor water stress. In summary, it was possible to re-construct leaf area distribution of *C. x morifolium* only by measuring the final leaf length. This was included as a leaf area model in the thrips population growth model.

Thrips population dynamics at different temperatures on chrysanthemum in closed cages (Papers IV and V)

Biology

To allow different growth patterns of both, the plants and the insect populations to be compared, different temperatures in the three greenhouse compartments were chosen in the thrips experiments (Papers IV and V). However, during early

population growth of the insects almost the same population growth pattern could be observed at all temperatures. The population increased slowly during the first 60 ± 5 days and grew rapidly thereafter. This rapid growth phase was most pronounced at the lowest temperature conditions (20.3°C) and, as shown in Fig. 9, it was exclusively caused by a rapid increase in *larvae* (~ 200 individuals).

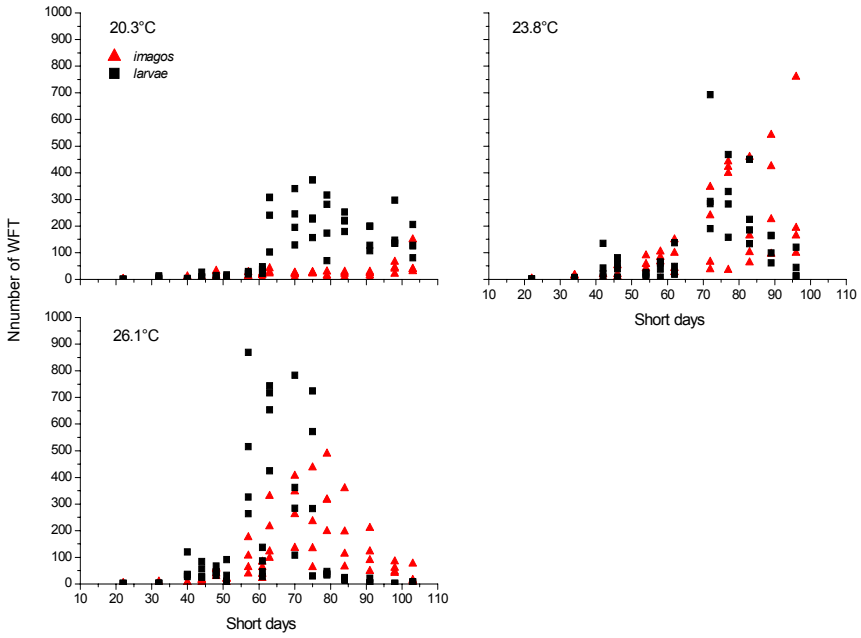

Fig. 9. Dispersal of *imagos* and *larvae* during the three temperature experiments (26.1˚C, 23.8˚C, 20.3˚C). WFT = Western Flower Thrips.

The amount of *imagos* remained at a constant low level (~ 20 individuals) until approximately day 95. Then a slow increase could be observed even in *imago* numbers. At 23.8˚C, the population increase in *larvae* and *imagos* seemed to be in phase. In the highest temperature treatment (26.1˚C), the *larvae* population increased early, but the *imago* population followed soon thereafter (5-10 days after *larvae*). According to Robb (1989), temperature affects thrips developmental time, preoviposition period, number of offspring per female and adult longevity. It was probably a combination of these effects that caused the observed growth patterns. The fact that adult longevity decreases with increasing temperature could be an explanation for the observed fast decline in population size at the highest temperature treatment (26.1˚C). It could also be interpreted as an effect of food limitations and stress because of the lack of migration possibilities (Rhainds & Shipp, 2003).

The dispersal of *imagos* and *larvae* on the plant is also important for reproduction. In Papers IV and V, the probable impact of population density on population growth in its initial phase was described. Low *imago* density per unit

plant area may lead to parthenogenetic reproduction, which results in males (Brødsgaard, 1989). In our experiments, where two isolated females were placed on a plant in a cage, the lack of males in the beginning of the experiment and the resulting parthenogenesis was probably the cause of the slow population growth. The following rapid increase in population size could not be correlated with flower availability and assumed nutritious food supply (Paper III, Fig. 10).

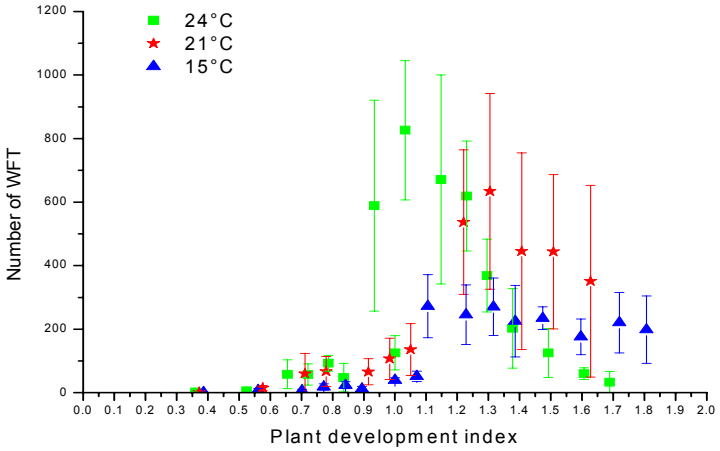

Fig. 10. Thrips population growth in relation to chrysanthemum flower development index. Flower opening occurs from the index values 0.6 to 1.

Therefore, we postulated that the start of sexual reproduction, probably together with continuous parthenogenesis, resulted in the higher numbers of individuals within a short period of time (5-10 days). Hence, the initial infestation strength and especially the sex ratio of the initial generation are important for the later population growth pattern. The high numbers of *larvae* in all temperature treatments reveal the importance of correct timing of IPM strategies against *F. occidentalis*. Since thrips density has been shown to have a significant effect on the level of silvery damage (de Jager *et al.*, 1993), control agents released after the massive reproductive phase described above can only decrease the population but not reduce the damage to plant parts. In Sweden, most *F. occidentalis* are imported into greenhouses as eggs on cuttings. These eggs may be fertilised or unfertilised and therefore develop into males or females. According to our hypothesis, depending on the ratio between males and females and the amount of eggs, sexual or parthenogenetic reproduction will occur and the population will grow faster or slower, respectively. The question remains which reproductive strategy the thrips 'choose' and which factors influence this choice. Knowledge in this area is sparse (Moritz, 1997) but important for the understanding of thrips population dynamics.

The relevance of different food sources for thrips population growth patterns was tested in another experiment (Paper IV). By removing the flowers from half of the experimental plants, the thrips were deprived of a food source that should be favourable according to several studies (Trichilo & Leigh, 1988; Brodbeck *et al.*, 2001; Hulshof *et al.*, 2003). The results showed a trend for the population to be

smaller when no flowers were available. However, no significant statistical differences in population size could be detected in the different treatments, indicating that the importance of flowers as nitrogen contributors and their impact on population dynamics might be overstated. This is in line with the findings of Kiers *et al.* (2000). Confirmation of this suggestion can also be found in the model in Paper V, where flower area was not included as a food source for the thrips and population growth could still be predicted. However, thrips gather in flowers when available rather than staying on the leaf surfaces, as Fig. 11 illustrates. This was also shown by Chau *et al.* (2005).

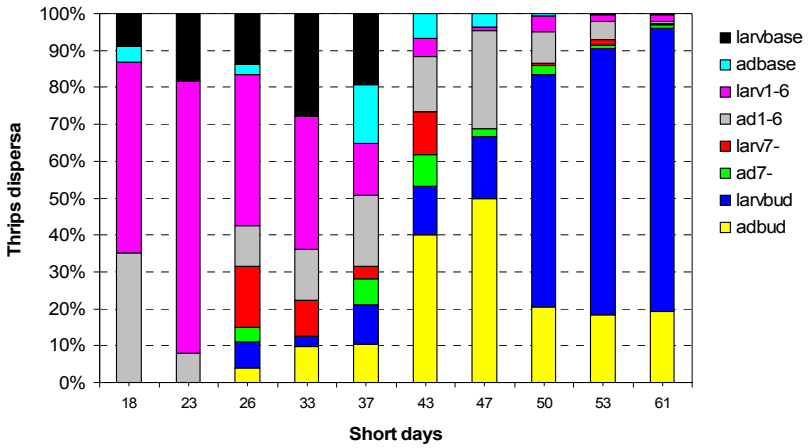

Fig. 11. The dispersal (%) of Western flower thrips on all side shoots of a chrysanthemum plant in the greenhouse at an average daily temperature of 19.7˚C, where *larvbase* = *larvae* on the 5 base leaves below the pinching point, *adbase* = *imagos* on the 5 base leaves below the pinching point, *larv1-6* = *larvae* on the first to the sixth leaf from the pinching point upwards, *ad1-6* = *imagos* on the first to the sixth leaf from the pinching point upwards, *larv7-* = *larvae* on leaves from the seventh leaf upwards and *ad7-* = *imagos* on leaves from the seventh leaf upwards.

The migration to flowers may be due to the higher nutritional quality of pollen and florets compared to leaves (Higgins, 1992; de Jager *et al.*, 1993) but it may also be caused by an attracting signal or a combination of both. An ecological reason for this behaviour could be better mating (Terry, 1997) and hiding possibilities and even a better chance to migrate to other host plants when the old plants get overcrowded and the food becomes limited because of high individual numbers (Rhainds & Shipp, 2003).

Damage evolvement was strongest at the highest temperature and is probably directly related to the amount of pest individuals (van Dijken *et al.*, 1994). Another explanation could be a higher feeding activity at higher temperatures (van de Wetering *et al.*, 1998).

Analysis and modelling

In Paper IV the early population growth of *F. occidentalis* on *C. x morifolium* was analysed in more detail. An exponential growth equation was expected to fit the data, since it is the generally accepted equation to describe population growth (Birch, 1948). It was shown that the rapid increase in population size after day 60 could not be described by a simple exponential equation and it was concluded that the relative reproduction rate of *F. occidentalis* was not constant over time. The first hypothesis was that the relative rate changed in a two step system, probably depending on above mentioned changes in the way of reproduction from parthenogenesis to sexual reproduction or high quality food availability (flower opening). This means that the relative reproduction rate should have been at a low constant level in the beginning of population growth and should have increased to a higher constant level when the change in reproduction or food availability had occurred. However, apart from the negative results from the food availability trial, such a two step model was complicated and unstable since it contained many parameters that could not be fixed. Therefore the hypothesis of an exponentially increasing relative reproduction rate was tested and the results showed that such a model gave a better fit than the original exponential growth equation (Paper IV). However, the question remains if adequate model predictions are possible in a Swedish greenhouse production site, where the initial thrips generation may consist of both males and females and the long parthenogenetic phase with slow population growth probably does not exist.

The model in Paper V fitted the experimental data well with R^2-values varying from 0.975 to 0.514. The last value was probably mostly due to an underestimation of population decay at the end of the high temperature experiment. The results show that the simplifications in the model, like the overall development index for the thrips and the elimination of flowers as food sources, were justifiable. The parameter estimations of the Logan function were based on Robb's data (1989) and other parameter values were also taken from already published literature (*e.g.* sex ratio, life span). The data from Robb (1989), which were achieved in laboratory experiments, seemed to be conferrable to greenhouse conditions. The combination of an array model (the simulation of several traceable generations independently of each other), the Logan equation for the prediction of the temperature effect and a development index demonstrated a possibility to simulate thrips population dynamics without including age structures or delay functions (Goudriaan & van Roermund, 1989). A weakness with the model was the underestimation of the population decay at the high temperature treatment. It seems as if the inhibiting effect on oviposition was not enough at these conditions, where dynamic processes like growth, development and mortality occurred rapidly. A possibility for managing this problem would be to include a function in the model, which additionally removes individuals from the system. This function could depend on population density (stress factor) or migration possibilities but since it was not part of the current study, these suggestions might be the base for future research.

Conclusions

From the current study, more knowledge was gained of temperature effects on the growth and development of pot plants and the population dynamics of *Frankliniella occidentalis* on greenhouse grown chrysanthemum. Mathematical models were used as prediction tools. The most important conclusions from the study are the following:

1. The general relationship between flower growth and development was not influenced by temperature in *Schlumbergera truncata* 'Eva' and *Chrysanthemum x morifolium* 'Lompoc' ('Miramar' and 'Rage'). In *C. x morifolium*, different irradiance levels did not change the general growth – development relationship, either. In *S. truncata* the relationship can be used as a prediction tool in commercial production.

2. Flower size increased with decreasing temperatures and increasing irradiance conditions. The flower growth pattern of *C. x morifolium* can be described as a linear phase (flower bud growth) and a monomolecular phase (flower opening).

3. Leaf area distribution in *C. x morifolium* may be re-constructed for the whole growing period from data of final leaf area.

4. The relative reproduction rate is not constant during population growth of *Frankliniella occidentalis* on greenhouse grown chrysanthemum. The process can be described as an exponential model with an exponentially increasing relative reproduction rate. The rapid increase in population size could not be correlated with flower opening. The impact of flowers as high quality food sources on population growth may therefore be overstated. Switching between reproductive strategies by *F. occidentalis* (parthenogenesis and sexual reproduction) could be possible reasons for the changes in the relative reproduction rate.

5. Temperature is the major influencing climate factor for thrips development and population growth. Population density might also play an important role in the beginning of population growth and was successfully included in the final simulation model. Population declines could be simulated by food limitations in terms of damaged leaf area at lower temperatures. At higher temperatures, other factors might have to be included into the model to be able to predict population declines.

The established models may be used as tools for future IPM strategies by providing information about population dynamics in relation to the plant's growth and development at different temperatures.

Future perspectives

In the thesis research is presented which focuses on both the host plant and the insect. This attempt of analysing the biological system rather than isolated details is an example for a general mechanistic and dynamic approach to the problem. For future research there are several possible continuing directions.

1. *The applied approach for biological control of Frankliniella occidentalis on greenhouse grown chrysanthemum.*
   The established model on population dynamics could be enlarged by introducing biological control agents into the system. There is a need for more effective biological control of pests in floricultural production, and the model can be used for this purpose. The model could *e.g.* predict application dates, the amount of needed control agents, plant damages etc.

2. *The theoretical approach of biological system analysis.*
   The plant-insect interaction should be investigated further. Many new questions arose during the study. One example is the effect of the host plant on the insect, *e.g.* the influence of different plant growth patterns on thrips population dynamics, the plant as a food source, plant defence mechanisms, the importance of plant volatiles on the interaction etc. On the other hand, the insect's behaviour and its reproductive strategies are important topics. What are the prerequisites for parthenogenesis? Which reproductive strategies do the omnivorous thrips 'choose' depending on host plant and external conditions?

3. *The density and the feeding factor (DF and FF).*
   In the population model in Paper V, a density and a feeding factor were introduced. These factors are speculative and future research is needed to validate the hypotheses behind their use.

Biological system analysis can be seen as a way of addressing the complex problem of plant-insect interactions and the current study has shown that it can be applied successfully in a horticultural production system. In this context, the prediction model presented may be a tool for improving production techniques and IPM strategies. However, environmentally friendly pest control in flowering plants will always be difficult if consumer demands for damage- and insect-free plants remain at the current high level. Informing consumers about ecological systems, IPM strategies and the negative effect of chemical control agents on humans and the environment will therefore always be an important task for future researchers in this field.

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