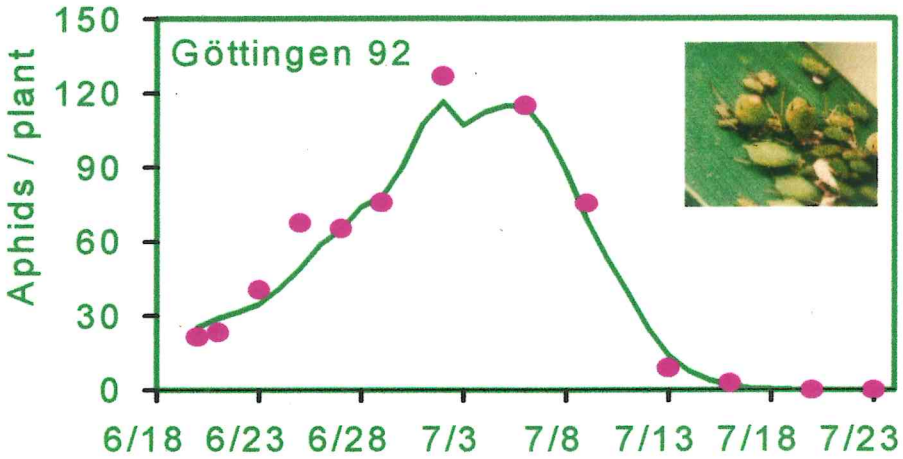
Modelling and simulation of the population dynamics of *Metopolophium dirhodum* (Walker) (Homoptera: Aphididae) in northern Germany



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Zusammenfasssung

Ein Simulationsmodell zur Beschreibung der Populationsdynamik von *Metopolophium dirhodum* (Walker) (Homoptera: Aphididae) im Winterweizen in Norddeutschland

Ma, Chunsen

Ein detailliertes Simulationsmodell zur Beschreibung der Populationsdynamik der Bleichen Getreideblattlaus, *Metopolophium dirhodum*, in Winterweizenfeldern in Norddeutschland wurde entwickelt. Das Modell, das in Visual Basic programmiert wurde, benutzt zur Initialisierung und Steuerung fünf Eingangsvariable: Die initiale Dichte aller Entwicklungsstadien der Blattlaus, die gemessene tägliche Durchschnitt- und Maimaltemperatur sowie das beobachtete oder interpolierte tägliche Wachtumsstadium des Weizens und die Dichte der Syrphiden als Schlüsselantagonisten.

Das Simulationsmodell beruht auf einem System von Kernmodellen (compartment models) für die Larvenstadien L_{1-3} (zusammengefaßt), L_4 und für die adulte Aphiden. Es enthält drei zentrale Submodelle für die Entwicklung, die Reproduktion und das Überleben. Die Kernmodelle wurden als sogenannte "boxcar-Modelle" konstruiert, um der Problematik der dynamischen Entwicklung der Alterstadien während der Populationsentwicklung gerecht zu werden und eine schrittweise Modellierung zu erreichen. Dem Submodell „Entwicklung" liegt eine Normalverteilung zugrunde. Der Einfluß der Temperatur, der die Aphiden während der Entwicklung ausgesetzt sind, wurde im "boxcar model" besonders berücksichtigt und diente als Basis zur Modellierung der Fekundität. Weibull-Modelle dienten zur Beschreibung der täglichen kumulativen Fekundität und der Mortalität der adulten Aphiden während des Alterungsprozesses der Adulten. Zusätzlich wurde ein Prädationsmodell, beruhend auf dem Einfluß der jeweiligen Syrphidendichte in Beziehung zur Aphidendichte und der Temperatur, in das Blattlausmodell integriert.

Als wesentlicher, bisher in der Literatur nicht berücksichtigter Einfluß und Schlüsselparameter für ein Gesamtmodell der Populationsdynamik von *M. dirhodum* erwies sich der Einfluß hoher Temperaturen auf Überlebensrate, Reproduktion und Lebensdauer der Aphiden. Die notwendigen Daten für ein entsprechendes Submodell wurden experimentell durch Exposition von L_2, L_3 und L_4 Larven sowie Adulten bei 27, 29, 31 und 33°C für 1, 2, 4 und 6 Tage (8 h/Tag) gewonnen. Die Empfindlichkeit der Aphiden gegenüber hohen Temperaturen stieg mit dem Entwicklungsstadium deutlich an. Die Überlebensrate und die Fekundität nahmen mit Zunahme der Expositionsdauer und der Temperatur ab.

Lineare Regressionen simulierter mit beobachteten Populationsdichten von neun Weizenfeldern in verschiedenen Gebieten Niedersachsens in unterschiedlichen Jahren zeigten, daß das Modell die Populationsdichte und die Altersstruktur der Population generell sehr genau abbildete. Sichere und robuste Simulationen sind sowohl bei hohen (Göttingen, Grossenwieden und Hiddestorf 1992) als auch mittleren (Göttingen und Hiddestorf 1991, Ruthe 1994) Dichten möglich. Eine recht gute Validität zeigt sich auch bei niedrigen Dichten (Göttingen 1993). Das Modell ist bei extrem niedrigen Aphidendichten (Ruthe 1995 und 1996) weniger genau. Simulationsexperimente und Sensitivitätsanalysen zeigten, daß auf den meisten Feldern die initiale Aphidendichten (*IPD*) zum Ende der Weizenblüte (EC 69) und die täglichen Maximaltemperaturen (*MaxT*) vor der mittleren Milchreife einen größeren Einfluß auf die Populationsdynamik hatten als das Wachstumsstadium der Pflanzen (*GS*), die tägliche Durchschnittstemperatur (*TX*) und Antagonistendichte (*NE*). Hohe *IPD*, milde *MaxT* und geringe *NE* waren die Hauptgründe für Massenvermehrungen, wohingegen bei niedrigen *IPD*, hohen *MaxT* und *NE* nur geringe Aphidendichten erreicht wurden. Im Vergleich zu anderen Modellen für *M. dirhodum* oder für die Große Getreideblattlaus, *Sitobion avenae,* besitzt dieses Modell eine hohe Genauigkeit, einen breiten Gültigkeitsbereich (regional) und benötigt nur relativ einfach zu erhebende Eingangsdaten.

Schlüselworte: Simulation, Modellierung, *Metopolophium dirhodum*, hohe Temperaturen

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1 Introduction

1.1 General importance of cereal aphids

In 1998, the world-wide total production figures for wheat, barley and oat were 589.3, 138.6 and 25.6 million tons respectively. The total production of these three crops represents about 36.4% of the total production of cereals, which is the largest agricultural production in the world (FAO 1999). Cereal aphids are one of the most important pests in the world (Kröber & Carl 1991), e.g. in Asia (Liu et al. 1986, Luo et al. 1988, Chen et al. 1994, Li et al.1994), North America (Johnston & Bishop 1987, Feng et al. 1992, Voss et al. 1997, Boeve & Weiss 1998) and Australia (De Barro 1992). The first serious outbreaks of cereal aphids in Europe were recorded in 1968, particularly in the UK, France and Germany (Vickerman & Wratten 1979). Subsequently, cereal aphids became one of the best-studied (Dixon 1987) and the most important pests of cereals in Europe during the past 25 years (Vickerman & Wratten 1979, Rabbinge et al. 1981, Poehling 1988, Basedow et al. 1994, Wetzel 1995, Niehoff 1996, Niehoff & Staeblein 1998).

In Europe, *Sitobion avenae* F., feeding mainly on the ears, and *Metopolophium dirhodum* (Walker) (both Homoptera: Aphididae), a leaf feeder, are the predominant aphid species in winter wheat (Vickerman & Wratten 1979, Carter et al. 1980, Tenhumberg 1993, Niehoff & Staeblein 1998). *Rhopalosiphum padi* L. (Homoptera: Aphididae) is less common in central Europe but is the primary pest of wheat in Scandinavia (Leather et al. 1989, Kurppa 1989, Hansen 1991).

M. dirhodum is a cosmopolitan pest of cereals (Farrell & Stufkens 1988). In many years, this aphid is the most abundant among the three cereal aphid species in Germany (Gräpel 1982, Ohnesorge 1988, Niehoff 1996) and central European countries (Honek 1991a). The major outbreaks in England in 1979 (Dewar et al. 1984, Cannon 1986), in Scotland in 1982 (Dewar et al. 1980), in Spain in 1986 (Pons et al. 1989) and in Germany in 1992 (Niehoff, 1996) with extremely high infestation levels demonstrated the pest potential of this aphid. In Germany, an average peak density of 150 aphids/tiller was recorded in 1992 in some fields.

1.2 Damage caused by M. dirhodum

During the early period of the past 25 years, research focussed on *S. avenae*, since its feeding habit suggested much more importance concerning yield losses compared to *M. dirhodum*. However, more detailed studies on damage potentials of both species indicated that *M. dirhodum* can be also an important factor to reduce the yields, if this species occurs in high densities at sensitive periods of cereal development (George 1974, Wratten 1975, 1978, Rabbinge et al. 1981, Holt et al. 1984, Oakley et al. 1993, Basedow et al. 1994, Wetzel 1995, Niehoff 1996, Niehoff & Staeblein 1998). The same numbers or aphid units of *M. dirhodum* settling on the flag leaf during flowering and milky ripe stage caused, on average, half of the yield losses compared to *S. avenae* feeding on ears (Wratten 1975, Vereijken 1979, Niehoff & Staeblein 1998).

M. dirhodum can affect the yield of cereals in three different ways. First, aphids directly feed on plants, thereby reducing the flow of carbohydrates and nitrogen to the developing grain. Second, *M. dirhodum* excretes honeydew on the surface of the plants, leading to a reduction of photosynthesis and possible induction of sooty mould and premature leaf senescence (Rabbinge et al. 1981, Rabbinge et al. 1983, Rossing & van de Wiel 1991, Xi et al. 1985). The infestations of *M. dirhodum* on the flag leaf markedly accelerate the senescence of top five leaves (Wratten 1975, Wratten & Redhead 1976). Third, *M. dirhodum* is one of the vectors of barley yellow dwarf virus (BYDV) (Waterhouse & Helms 1985), although it has minor importance in the virus transmission in Germany (Fiebig & Poehling 1998). In addition, during probing, apterous adults of *M. dirhodum* cause damage to the mesophyll cells (Brzezina et al. 1986).

Yield losses in wheat caused by *M. dirhodum* can range from less than 1% to more than 30% (George 1974, Lowe 1974, Wratten 1975, Watt & Wratten 1984, Basedow et al. 1994, Niehoff 1996, Lemke 1999). In the UK, Zhou and Carter (1989) reported about 12% yield loss in 1979, moreover, 15 % yield losses were measured by Watt and Wratten (1984) under an early infestation of *M. dirhodum* in wheat. Holt et al. (1984) determined 27 – 30 % yield reductions of wheat when infested with about 500 aphid unit days between mid-flowering and late milky-ripe stage. In addition,

experiments with artificial infestations performed by Niehoff and Staeblein (1998) in Germany showed that 12% yield loss can be caused by a constant density of 20 *M. dirhodum* per flag leaf from mid flowering to soft dough ripe, or even 17% yield reductions by 40 aphids/tiller in wheat. All these results indicate that *M. dirhodum* is economically an important pest of cereals.

1.3 Control threshold of cereal aphids

About a decade ago, the increasing abundance of cereal aphids especially in regions with intensive winter wheat production resulted in almost regular insecticide treatments of large areas, such as in northern Germany (Poehling, 1988) and in the UK (Wratten & Mann 1988, Wratten et al. 1990, Mann et al. 1991), to prevent severe yield losses. As large areas are treated by insecticides at the same time, the diversity and population densities of natural enemies are reduced (Powell et al. 1985). The incidence of predatory insects (Carabidae, Syrphidae and Coccinellidae) in Germany was lower in fields that had been treated repeatedly with insecticides than in untreated ones (Basedow 1990). Not only insecticides, but also herbicides, exert a negative effect on the abundance and diversity of the arthropod fauna in wheat growing areas (Basedow 1995). Many insecticides, such as pyrethroid, lambda-cyhalothrin, sumicidin and fenvalerate, proved to be toxic for spiders and can suppress the activity of spiders, especially of *Erigone atra* males for several weeks (Dinter & Poehling 1992a and b).

To reduce the unnecessary insecticide application, a decision-making system based on the infestation-yield relationship is necessary. Several action thresholds were developed in Germany and they were summarised by Wetzel (1995). One of the pronounced thresholds was developed by Basedow et al. (1994) based on 44 experiments in Germany, i.e. four aphids per ear and/or flag-leaf at the end of flowering. This threshold was taken as the official action threshold for spraying insecticides in Germany (Niehoff & Staeblein 1998). The threshold is very simple and easy to use, however, it does not consider the population changes of aphids after the end of flowering. In some cases, such as in the field investigated by Niehoff (1996) at Göttingen in 1991, 3.7 aphids / flag-leaf and 1.2 aphids/ear were detected in the non-sprayed plot at end of flowering. Although this density was above the

action threshold, the aphid population did not continue developing to a high density but collapsed immediately at the beginning of water ripe. The weight of thousand grains was not significantly reduced compared to the insecticide treated plots, which indicated that the spraying was not necessary. Moreover, the same number of aphids can cause different levels of yield loss when they occur at different growth stages of the plant (Holt et al. 1984). Thus, economic thresholds should change according to plant growth stages. To improve IPM with better flexible thresholds, accurate estimations of the dynamics of aphid infestation are necessary.

1.4 Simulation models as useful tools for cereal aphid control and research

Simulation models are powerful tools to predict the population densities of aphids. Frequent field sampling and counting of aphids and their natural enemies are a direct and accurate method to estimate pest population densities. However, it is a tedious work, and requires special knowledge. Thus, it is a difficult, time-consuming, inconvenient and expensive way for farmers and/or extension agents to monitor the population dynamics of aphids and their natural enemies. Therefore, a cheaper but accurate and convenient method for population dynamic prediction is needed. Simulation strategies, based on computer aided models, have been shown to possess these characteristics and are powerful tools for the population prediction (e.g., Huffaker 1980, Carter et al. 1982, Zhou & Carter 1989, Freier et al. 1996).

A simulation model is also a useful tool to analyse the population dynamics (Carter et al. 1982, Rossberg et al. 1986, Holz & Wetzel 1989, Wetzel 1995, Freier et al. 1996a). Since the population dynamics of cereal aphids are determined by many complicated processes, and each process is affected by sets of factors that may interact with each other, it is very difficult and expensive to handle many different factors in field experiments for understanding the population dynamics. With the model, however, a set of simulation experiments can be done to detect the effect of each component on the population dynamics of the aphids. The sensitivity analysis and the analysis of the importance of each biotic and abiotic factor can be carried out with the model to explain the mechanisms of the population dynamics of the aphids.

Simulation models can help to reduce the sampling frequency. In some field trials, such as aphid resistance tests and chemical control tests, the monitoring of aphid density is required. The sampling is usually carried out once a week. Because of the high productivity and short generation time of aphids, the population can increase very fast under favourable conditions. Weekly sampling is often insufficient to detect the detailed population changes in a week, especially around the population peak since the peak density may occur between two times of sampling. It is hard to increase the sampling frequency, because it implies the sampling work would be doubled (twice a week). However, with the aid of the simulation model this gap could be filled. In other words, the simulation model can be used to reduce sampling frequency in field investigations for various purposes.

1.5 Summary of the modelling works for cereal aphids

Simulation models for *S. avenae* have been developed to predict the population densities of the pest in the UK (Carter & Rabbinge 1980, Carter et al. 1982) and in the Netherlands (Rabbinge et al. 1979). The first German simulation model of *S. avenae*, PESTSIM-MAC, was developed by Freier (1983). This model was subsequently incorporated in the Winter Wheat Agroecosystem (AGROSIM-W) model of Bellmann et al. (1986) by Rossberg et al. (1986). Recently, Freier et al. (1996) improved their PESTSIM-MAC and renamed the newest version as GTLAUS 3.7 that includes the interaction between wheat, *S. avenae* and its predators. In addition, Friesland (1994) developed and implemented the simulation model of *S. avenae*, "LAUS", in the software package "AMBER". For simulating virus disease transmission in winter wheat and winter barley, a simulation model called "BONN-LAUS" was developed in Germany (Kleinhenz et al. 1996).

All these models listed above are developed for *S. avenae*. The models developed in England by Carter et al. (1982), and in Germany by Freier (1983), Rossberg et al. (1986) and Freier et al. (1996a) are the most famous simulation models for *S. avenae* in Europe. The methodology developed in these models is very useful for other modellers. The difficulties in applying these two pronounced models include 1) complicated inputs (more than ten input variables), especially the inputs related to

natural enemies and immigrations and 2) the insufficient accuracy of the model output.

So far, very few efforts have been devoted for developing simulation models for *M. dirhodum*. The only existing *M. dirhodum* model is the one created by Zhou et al. (1989) for the UK. This model followed the similar structure of the model built by Carter et al. (1982) but did not include natural enemies. Consequently, it could only accurately predict aphid dynamics in one of the four compared fields. So far, no further attempts have been made to simulate the population dynamics of *M. dirhodum*. However, the question could be raised if the simulation models developed for *S. avenae* can be adapted to *M. dirhodum*?

1.6 Adaptation of the simulation models of S. avenae to M. dirhodum

Carter et al. (1982) tried to adapt their *S. avenae* model to *M. dirhodum*. Field data show that *M. dirhodum* and *S. avenae* coexist on wheat plants, but their relative ratio varies between years and fields (Ankersmit & Carter 1981, Dedryver 1989, Niehoff 1996). This implies that some important ecological differences between the two species must exist. A simulation model for *S. avenae* cannot necessarily be used to predict the population dynamics of *M. dirhodum*. The initial population density, the host plant, weather conditions and natural enemies are four kinds of ecological factors that might affect the population dynamics of the two species in possibly different ways.

Sitobion avenae, an partly anholocyclic aphid species, overwinters on various Gramineae, including winter wheat seedlings, whereas holocyclic *M. dirhodum* clones overwinter on roses (Ankersmit & Carter 1981, Hand & Hand 1986, Hand 1989). Anholocyclic colonies of *M. dirhodum* have been reported in England (Dean 1974b, 1978) and in western but not in northern Germany (Weber 1985). The different overwintering strategies of the two species may result in different immigration patterns. Consequently, the method to determine the initial population density for *S. avenae* may be not suitable for *M. dirhodum* in simulation models.

As mentioned above, the feeding site preferences of the two species are different. *S. avenae* feeds on the flag leaf until ear emergence and subsequently moves to the

ears (Wratten & Redhead 1976). By contrast, *M. dirhodum* predominantly attacks leaves, in particular flag leaves (Wratten & Redhead 1976, Vickerman & Wratten 1979, Kröber & Carl 1991). Consequently, the two aphid species may have different reactions to the physiological changes of host plants, caused by different factors such as drought and powdery mildew infections (Pesel & Poehling 1988) and nitrogen fertilisation (Honek 1991b, Zhou & Carter 1991, Duffield et al. 1997). Therefore, the model to describe the effects of the host plant on *S. avenae* may not be accurate for *M. dirhodum*.

Precipitation, humidity and wind influence the population dynamics of cereal aphids (Rautapää 1979, Basedow 1987, Cannon 1986). However, it is not known whether these conditions affect the two aphid species differently. Temperature has a strong effect on various life table parameters of cereal aphids (Dean 1974a, Zhou & Carter 1992). Comparing duration of development, mortality, lifetime fecundity and intrinsic rate of increase of the two species (Dean 1974a), *M. dirhodum* performs as good as or even better than *S. avenae* when the temperatures are less than 20°C. However, when the constant temperature increases to 25°C, the intrinsic rate of increase of *M. dirhodum* (0.4) is much lower than that of *S. avenae* (2.0). In contrast to *S. avenae,* no individuals of *M. dirhodum* can survive to adults at 27.5°C. Therefore, *M. dirhodum* may be more sensitive to unfavourable high temperatures than *S. avenae*. A hypothesis can be formulated that high temperatures > 27°C are one of the important liming factors for the population development of *M. dirhodum* in northern Germany. Thus, the model to calculate the effect of temperature for *S. avenae* may not be accurately adapted for *M. dirhodum*.

For aphid predators, a prey preference for either *S. avenae* or *M. dirhodum* has not been studied. The most important aphid predators in wheat fields in northern Germany, the syrphids, mainly *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae) (Poehling 1988, Tenhumberg 1993, Tenhumberg & Poehling 1994) are oligophagous species (Hodek & Honek 1996). Thus, a possible prey preference of predators is not likely to be a major reason for varying population densities of the two aphid species. However, the choice of an appropriate habitat concerning microclimate is important for syrphid larvae. Optimum relative humidity for syrphid larvae ranges between 70-90%. Syrphid larvae prefer to predate in humid and cool

habitats (Honek 1983). In dry and warm summers, the microclimate around the leaves, the feeding site of *M. dirhodum*, is more humid and cooler than the ear where *S. avenae* feeds. Therefore, *E. balteatus* females may prefer to oviposit on leaves, increasing the chances that *M. dirhodum* instead of *S. avenae* becomes the more important prey for the larvae. Consequently, the predation model for *S. avenae* may not fit for *M. dirhodum*.

Cereal aphid densities vary between regions (Poehling et al. 1991, Ohnesorge & Schier 1989). The cropping system, the landscape architecture (e.g. availability of other host plants, flower sources and over-wintering plants), community of natural enemies, the crop structure and soil fertility etc. may be rather specific for a particular region and have distinct impact on the population dynamics of cereal aphids. Northern Germany is one of the major cereal production areas in the country. More regional forecasts would improve the threshold model in this area. Therefore, locality/region has to be considered in any modelling attempt. However, a simulation system based on particular local or regional conditions has to be developed and validated with field data from this locality and/or region.

Based on the economic importance of *M. dirhodum*, the present status of aphid control and the difference between *S. avenae* and *M. dirhodum* that are discussed in above six chapters, it is necessary to develop a new simulation model for *M. dirhodum* with relative simple inputs and high simulation accuracy.

1.7 General objectives of the study

The objectives of this study include two aspects. The main objective is to develop a computer simulation system that can provide detailed information on the population dynamics of *M. dirhodum*. The information would facilitate the actual aphid warning system, i.e. the fixed simple action threshold (Basedow et al. 1994, Wetzel 1995). Ultimately this model should be made available to farmers in northern Germany.

In addition, the simulation program will be used as a tool for studying the aphid population dynamics in such systems. Simulation experiments elucidate which factors govern the population dynamics of *M. dirhodum*, and help to quantify their relative importance. Sensitivity analyses will identify the input factor for which the data should be collected in a high accuracy.

2 Simulation model and simulation program

2.1 General structure of the simulation model

The population dynamics of *M. dirhodum* in fields are complicated processes. System analysis can be a helpful tool to investigate complex systems. Therefore, the simulation model of the aphids is constructed following a system analysis approach. The field populations of *M. dirhodum* are considered as an ecological system. The various development stages of *M. dirhodum* are treated as system elements. The population densities of the aphids are described by state variables and the changing rates of various biological processes (development, survival etc.) are considered as rate variables. The rate variables transfer effects of environment factors to state variables in the population system. Various biotic and abiotic factors that affect the aphids are defined as environment factors.

Compartment models are built based on the life cycle of the aphid (Figure 2-1). Alate adults immigrate into the winter wheat field and commence to establish colonies by producing new larvae (1st instar). The 1st instar develops into 2nd, 3rd, 4th instar and finally moults to adults. Adults again produce new larvae. The first three instars experience the same biological processes (only development and survival) and have similar developmental and survival rate. In many field studies, e.g. Niehoff (1996) and Lemke (1999) in northern Germany and Carter et al. (1982) in the UK, the numbers of apterous and alate adults, apterous and alate 4th instar larvae (L4), and the pooled numbers of 1st, 2nd and 3rd instar larvae (L13) were counted separately. Therefore, in the simulation model, the mixture of 1st, 2nd and 3rd instar larvae is described with a single compartment, i.e. L13. Dixon (1998) summarised three types of alate inducing periods during aphid development, i.e. 1) prenatal, 2) pre- and postnatal, and 3) postnatal morph determination. However, the morph of all those aphid species was induced not later than the first instar. In the simulation model, the morph of the aphid is decided at birth (Carter et al. 1982). Therefore, the apterous and alate for all stages are separately described with compartment model. Thus, six compartments are constructed (Fig. 2-1). The details of the compartment model will be described in a separated chapter.

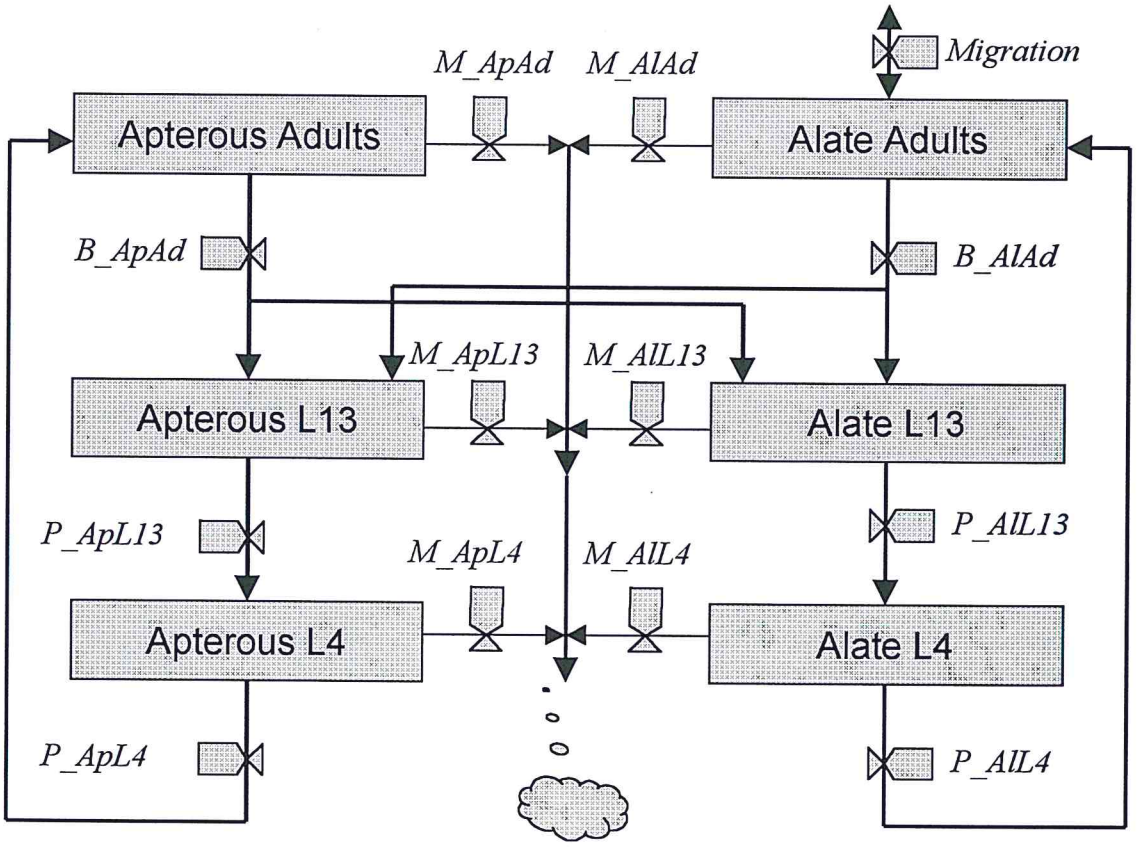


Fig. 2-1 Structure of the simulation model of *M. dirhodum*. Names of variables are compound of letters that represent different meanings: "***B_***" = reproduction rate; "***P_***" = developmental transition rate; "***M_***" = mortality; "***Ap***" = apterous morph; "***Al***" = alate morph; "***L13***" = 1st to 3rd instar larvae; "***L4***" = 4th instar larvae; "***Ad***" = adults.

The population density of *M. dirhodum* in each compartment depends on five fundamental biological processes: development, reproduction, survival, morph determination and migration (immigration and emigration). The changes of those five processes are represented with rate variables. The number of aphids in all compartments depends on survival rates. Besides survival rate (*Survival*), the number of L13 also depends on the reproduction rate of the adults (*Reproduction*), the transition rate from L13 to L4 (*P_ApL13* for apterous and *P_AlL13* for alate) and the proportion of alate aphids (*PAlate*). The number of L4 is also related to *P_ApL13* or *P_AlL13* and the transition rate from L4 to adult (*P_ApL4* and *P_AlL4*). Logically adults have no development transition rate since it is the last stage in the life cycle. The number of alate adults is defined by *P_ApL4* or *P_AlL4* and the emigration rate,

i.e. 1 - settlement rate. The general relationship between the densities of each stage and the fundamental biological processes can be expressed as follows:

$AptL13 = f(Survival, Reproduction, P\_ApL13, PAlate)$

$AlaL13 = f(Survival, Reproduction, P\_AlL13, PAlate)$

$AptL4 = f(Survival, P\_ApL13, P\_ApL4)$

$AlaL4 = f(Survival, P\_AlL13, P\_AlL4)$

$AptAd = f(Survival, P\_ApL4)$

$AptAd = f(Survival, P\_AlL4, PSettle)$

The five fundamental biological processes are affected by various environmental factors. All those biotic and abiotic environmental factors are divided into the following four categories: weather, host plant, natural enemies and other factors, for instance, other pests and farming practice. Each category includes a set of factors. The effects of these factors on the five fundamental biological processes are briefly expressed in Table 2-1.

Some environmental factors play more important roles than others do in the five fundamental biological processes. The daily average and maximum temperatures, the plant growth stage, and the population density of syrphids were selected as important ecological factors affecting the population dynamics of *M. dirhodum* under field conditions. Moreover, the population density of aphids is also considered, since it is an important factor for the morph determination of *M. dirhodum* and for the predation rate of syrphids. The quantitative effects of constant temperature on the development, survival and reproduction of the aphids have been investigated by Dean (1974a), Zhou and Carter (1992), and Hu and Gui (1985). The respective mathematical models were used to express the effect of daily average temperature on those biological processes. While the effect of plant growth stages on *M. dirhodum* has not been studied in detail, a rough model was built from the limited data (Watt 1979, Vereijken 1979, Howard & Dixon 1992, Zhou & Carter 1992). Some factors, such as high temperature for several hours per day, may be very important for the population dynamics of *M. dirhodum* (Honek 1985, Chen et al. 1994) but no

detailed data could be found. Thus, additional laboratory experiments on the effect of high temperatures on life table parameters of *M. dirhodum* were carried out to gather the necessary data for the model development. The data sets used for building the sub-models will be explained in detail in the specific sub-models for each biological process.

Table 2-1 Effects of ecological factors on fundamental biological processes of the population dynamics of *M. dirhodum*.

	General	Migration	Development	Fecundity	Mortality	Morph
WEATHER						
Temperature	Y*	Y	YM	YM	YM	
Maximum	Y	Y	Y	YM	YM	
Minimum	Y	Y	Y	Y	Y	
Rainfall	Y	Y			Y	
Humidity	Y				Y	
Wind	Y	Y			Y	
HOST PLANT						
Growth stage	Y	YM	YM	YM	YM	YM
Variety	Y		Y	Y	Y	
Density	Y				Y	
Plant vigour	Y					
NATURAL ENEMIES						
Predators	Y				Y	
Ladybirds	Y				Y	
Syrphids	Y				YM	
Chrysopids	Y				Y	
Polyphagous	Y				Y	
Parasitoids	Y				Y	
Entomophthora	Y				Y	
OTHER ORGANISMS and FARMING PRACTICE						
Sitobion avenae	Y					Y
Rhopalosiphium padi	Y					Y
BYDV	Y					
Rust	Y					
Nematodes	Y					
Irrigation	Y					
Herbicides	Y					
Fungicides	Y					

Y*, variables in lines have effects on variables in columns; M represents the factor was incorporated in the simulation model)

The population density of *M. dirhodum* at a given time can be calculated based on the initial population density and the daily changing rate of the five fundamental

biological processes. A simple way to obtain the initial population density is to count the number of aphids in field samples. For plant growth stages older than the end of flowering (GS 69), the number of immigrating and emigrating alate adults was assumed to be dynamically balanced (immigration = emigration). In this study, aphid density at GS 69 was used as the initial population density.

Based on weather data, data on the plant growth stages and densities of natural enemies, the development transition rate, the survival and reproduction rate, the proportion of alate and the settlement rate of alate adults can be calculated with the respective sub-models. Furthermore, the daily population density of *M. dirhodum* can be computed with compartment models by using input data, i.e. the initial population density and the rates obtained from the specific sub-models.

The simulation model was incorporated into a simulation program. The program was written in the programming language Visual Basic (Microsoft Corporation 1993a, b and c). The program was designed to manage the input database, to carry out simulations with the model and to visualise the simulation results. The program was constructed in structured modules and procedures. Each procedure has a special function in the simulation program. Systat 6.0.1 (SPSS Inc. 1996) was the main program used in parameter estimations for sub-models, in model validation and sensitivity analyses. Marquardt's method in Systat 6.0.1 was used to estimate the parameters for non-linear models. All the sub-models were assembled in the simulation program.

2.2 Structure of the simulation program

The simulation program was structured in three basic components: input, model, and output. A general controller was designed to manage the three components for implementing various tasks. The general structure of the program is shown in Fig. 2-2.

2.2.1 Input module

The input part supplies the initial population density and environmental conditions of the aphids to the simulation model. The most important inputs on the population dynamics of aphids are divided into two sub-categories, i.e. weather data and user's specified data. A set of convenient forms (or windows) was designed as user's

interface in the input module. These interface forms provide the different controls for the user who can select a specific location and the beginning and ending dates of the simulation. As weather conditions at different locations and different years were stored in the database, the name of the location and the beginning and ending dates are used to locate the weather data set required for starting a simulation.

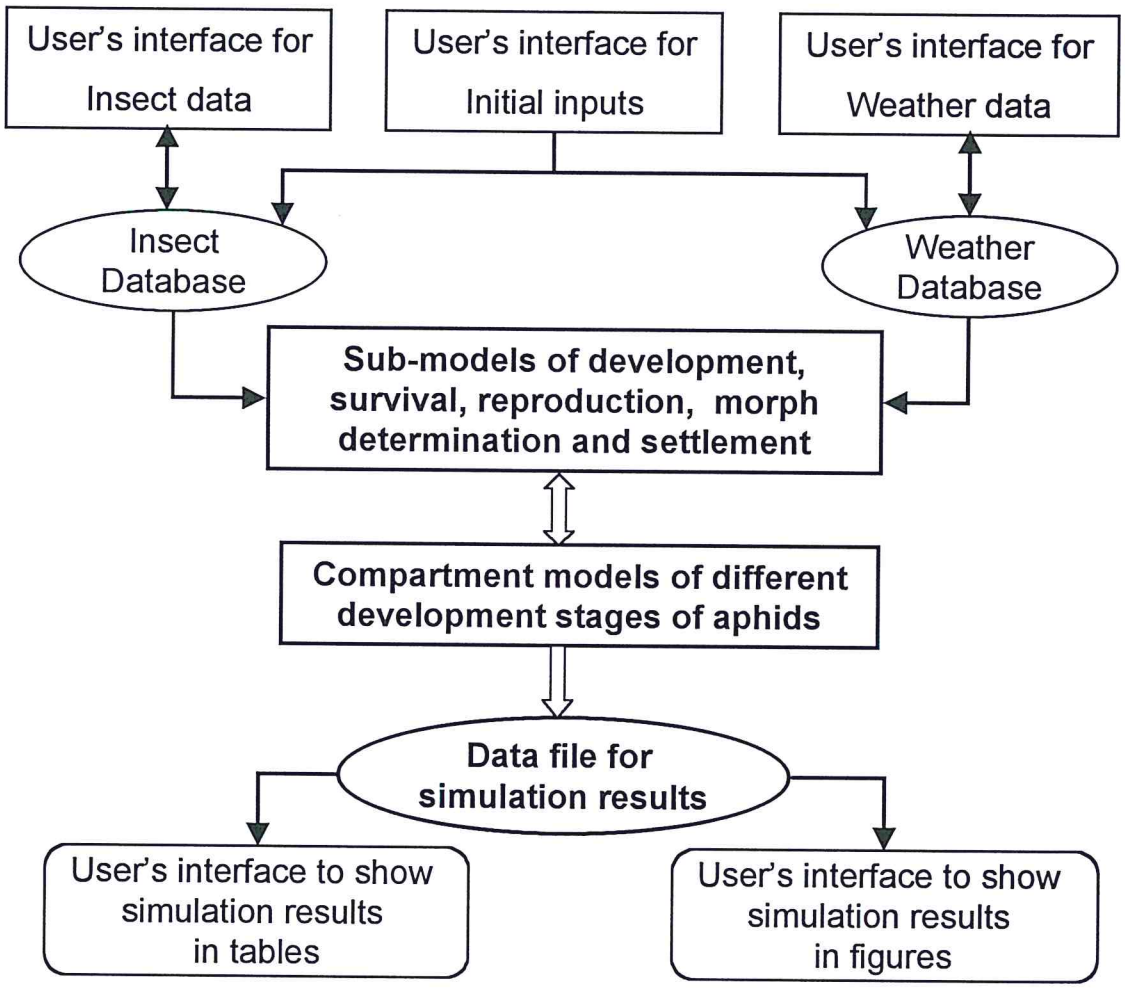


Fig. 2-2 Structure of the simulation program of the population dynamics of *M. dirhodum*

A database, **Weather.mdb** was created in 'Access' to handle the weather data. With help of the program, any other database format (e.g., dBase, Foxbase etc) can be easily attached to **Weather.mdb**. Here, **Weather.mdb** consists of weather data from four locations in northern Germany (Göttingen, Hiddestorf, Grossenwieden and Ruthe) from 1991-1996. The data are arranged in form of tables, with one table comprising all entries for one year at one location, thus having 365 records. Each

record includes the Julian day, date, the daily average air temperature, the daily maximum and minimum air temperature, and the daily precipitation and other weather data for wind and sunshine.

A database for *M. dirhodum*, **Aphids.mdb**, was created to handle the data on aphids and their natural enemies. Records in the database included the Julian day, date, plant growth stage (GS), densities of 1st to 3rd instar larvae, apterous and alate 4th instar larvae, apterous and alate adults and densities of syrphid larvae. **Aphids.mdb** supplies data on initial population density of the aphids, syrphids and plant growth stages for aphid density simulations, and aphid data for visual (i.e. tables or graphs) comparisons between observed and simulated population dynamics of *M. dirhodum*. The format and the structure of **Aphids.mdb** were similar to **Weather.mdb** in the program.

2.2.2 Output module

The output module presents simulation results in form of tables or graphs. Commands were designed on the form of output table for selecting the layout of population densities, or other results, such as development transition rates, mortality, fecundity, or plant growth stage.

The output module is designed to visualise simulation results in various types of graphs and different items of simulation results from the model. Four menu groups were created to execute all graphic functions. The "Compartments" Menu included six options: 1st to 3rd instar larva (L13), apterous and alate 4th instar larva (L4) and adult. The "Results" menu consists of population density, development rate, mortality, fecundity and the plant growth stage. In the "Graph" menu, different graphic types, colours, legends, titles, fonts, layouts and labels can be selected. The "Operation" menu includes items to activate the table or the general controller form, and to terminate the program.

2.2.3 Simulation module

The simulation model is the most important part in the simulation system. In order to build the program logically, to debug easily and to improve it gradually, the program is designed in a structured approach. The simulation model consists mainly of two modules, i.e. the module of compartment models and the module of biological

process sub-models. The compartment module includes six procedures that describe the corresponding six compartments. The module of biological processes contains five procedures for the five sub-models, i.e. sub-models of development rate, survival rate, reproduction rate, proportion of alate and settlement rate of alate adults. Procedures that were commonly used by other procedures, such as the procedure of linear interpolation and normal distribution, were arranged separately in an independent part. A general procedure named "simulator" was designed to call different procedures according to the sequence defined by the model structure.

The details of the simulation model were described in chapter 2.1 and will be further described in each specific sub-model.

2.2.4 General controller of the simulation program

The whole simulation program was controlled by a user's interface, called **general controller** (Fig. 2-3). Seven command buttons were designed to carry out seven different functions of the simulation program. The **initial inputs**, **insect database**, and **weather database** commands are designed to activate one or more of the corresponding interface forms that supply convenient controls for observing and editing the data. The **simulation running** command starts the simulation. The **tables** or **graphs** commands activate the presentation of the simulation results as tables or graphs, respectively.

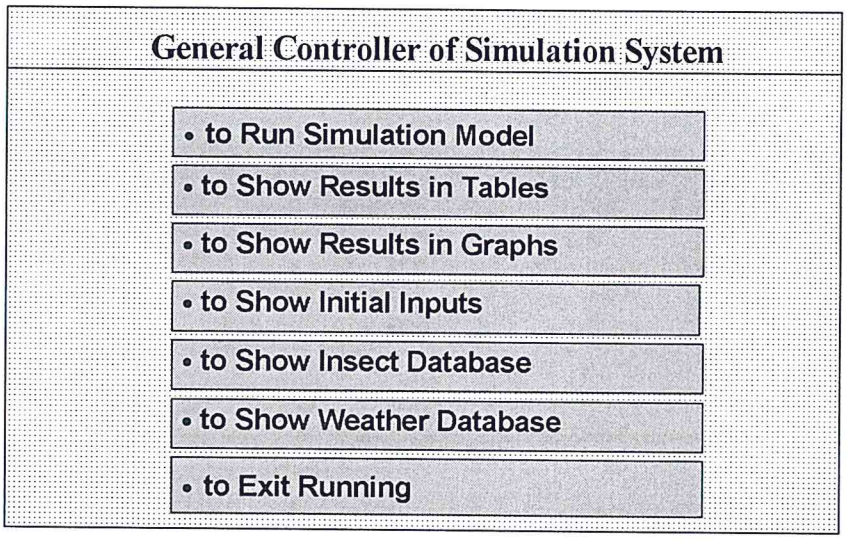


Fig. 2-3 General Controller of the simulation program for population dynamics of *M. dirhodum*.

3 Effects of high temperature on survival and reproduction of *M. dirhodum*

Temperature is one of the key-factors influencing the development, survival and reproduction of aphids. The development time, survival rate and fecundity of *M. dirhodum* at different constant temperatures have been tested under laboratory conditions. Larvae of *M. dirhodum* cannot finish their development when temperatures exceed 30°C and adults do not produce offspring at temperatures higher than 27°C (Dean 1974a, Zhou & Carter 1992). The most suitable temperature range for *M. dirhodum* is between 15 – 22°C. However, in the field temperatures fluctuate, particularly between day and night. Weather data from the German Weather Service for Göttingen and Hanover show, that during May-August in 1991-1996 the daily average temperatures were lower than 25°C. However, daily average temperatures around 20 – 24°C were often accompanied with maximum temperatures exceeding 27°C. Using only the effects of daily average temperatures on life table parameters of *M. dirhodum* ignores the possible detrimental impact of maximum temperatures on the aphids.

So far, little is known on the effects of high temperatures (27 - 33°C) and varying exposure times on the development time, survival, and fecundity of *M. dirhodum*. Therefore, laboratory experiments were conducted to precisely assess the effects of high temperatures and exposure time on different development stages of *M. dirhodum*.

3.1 Materials and methods

Stock culture of *M. dirhodum*: Aphids were reared on one-week old spring wheat seedlings, cv "Remus". Pots with seedlings were placed in a cage (90 cm × 60 cm × 60 cm) which was constructed with four sides covered by fine nylon net and with a transparent plastic glass on top. Standard rearing conditions were constant temperature, 20°C, and photo period 16 L: 8 D. Every two weeks wheat seedlings were renewed.

Host plants: Wheat seeds were sown in 12 cm diameter pots, with approximately 15 seedlings/ pot. Pots were kept in the greenhouse until the first two to three leaves

were fully expanded, and then either moved to the stock culture cage or to growth cabinets for subsequent experimentation. A commercial nematode product (*Steinernema feltiae*) was used for biological control of mushroom flies (Diptera: Sciaridae).

Test insects: According to Zhou and Carter (1992), development time for 1st, 2nd and 3rd instar larvae of *M. dirhodum* at 20°C is about two days, whereas 4th instar larvae require about 61 hours. Synchronised development stages of *M. dirhodum* were obtained as follows: Depending on the developmental stage to be tested, approximately 8.5, 6, 4 and 2 days before the start of the experiments, adults from the stock culture were moved into clip cages (4 cm diameter × 2.5 cm height), using a fine camel brush. Three aphids were kept per clip cage, and the cages were fixed with two bamboo sticks to one leaf of the plant. Ca. 12 hours later, the adults were removed and the newly born first instar larvae were transferred to a clean clip cage, and remained on the plant until the beginning of the respective experiments.

Experimental protocol: Five aphids of a defined developmental stage were transferred into a clean clip cage. Each treatment included six clip cages per plant. One hour later, plants with clip cages were placed in growth cabinets under varying temperatures. At different times, plants were moved between the growth cabinets and the standard rearing room, the latter set at constant 20°C. After high temperature treatments, plants remained for 24 hours in the standard rearing room. Thereafter, the numbers of surviving and dead individuals, as well as offspring were counted under the microscope. This procedure was repeated on the following day and subsequently every five days until all adults of the initially introduced aphids had died. The temperatures in the growth cabinets were recorded with miniature data loggers (Gemini Dataloggers Ltd., UK). The temperature variation for a given temperature was approximately ±1°C. Experimental treatments of different *M. dirhodum* development stages, temperatures and exposure times are summarised in Table 3-1.

Table 3-1 Treatment combinations in the experiment for effects of high temperature, development stages of the aphids and exposure time on *M. dirhodum*.

Temperature (°C)	Exposures (days×hours/day)	Adult	4th instar	3rd instar	2nd instar
33	1×8	Y	Y	Y	Y
33	2×8	Y	Y	Y	Y
31	1×8	Y	Y	Y	Y
31	2×8	Y	Y	Y	Y
31	4×8	Y	Y	Y	Y
31	6×8	Y	Y	Y	Y
29	1×8	Y	Y	Y	Y
29	2×8	Y	Y	Y	Y
29	4×8	Y	Y	Y	Y
29	6×8	Y	Y	Y	Y
27	1×8	Y	Y	Y	Y
27	2×8	Y	Y	Y	Y
27	4×8	-	Y	-	-
27	6×8	-	Y	-	-

Y, data were collected for the treatment; -, the data were not collected for the treatment

Statistical analysis: The effects of high temperatures, developmental stage of *M. dirhodum* and exposure time and all interactions, i.e. three first order and one second order interactions on fecundity, longevity and survival rate of the aphids were separately analysed using the general linear model procedure (GLM) of SAS (SAS institute Inc.1996). The significance of the interactions could be judged from the results of the above analysis. The analysis should follow different ways for significant and non-significant interactions.

If the interactions were not significant, the effect of each level of each factor on fecundity, longevity and survival rate was compared using multiple comparisons based on adjusted least-square means (LSMEANS) and Tukey-Kramer method. For example, if the interactions did not significantly influence the fecundity, then the fecundity data at different aphid stages and exposure times were pooled for each level of temperature. The LSMEANS of the fecundity at different temperatures were compared. The multiple comparisons for the aphid stages and exposure times followed the same procedure as for temperatures. The analysis methods for longevity and survival rates followed the same procedure as for the fecundity.

In case of the significant interactions, for example, if the survival rates were significantly affected by the interaction of temperature and the developmental stage, one of the temperature levels, e.g. 29°C was fixed, the survival rates at different exposure times were pooled and the multiple comparisons (LSMEANS) were implemented to compare the differences between each development stages at 29°C. Similar multiple comparisons were done for each factor related to significant interactions.

3.2 Results

3.2.1 Fecundity

Table 3-2 Mean lifetime fecundity per adult as influenced by temperature, exposure time, and development stage of *M. dirhodum*.

Temp (°C)	Exposures days×hour/day	Adult		4th instar		3rd instar		2nd instar	
		$\overline{X}$ [a]	SEM	$\overline{X}$	SEM	$\overline{X}$	SEM	$\overline{X}$	SEM
33	1×8	14.00	13.67	21.02	11.81	42.42	6.35	38.79	6.16
33	2×8	8.50	5.89	20.88	7.37	41.33	5.01	39.40	7.48
31	1×8	46.46	2.17	37.02	4.81	41.38	2.80	46.61	5.75
31	2×8	33.21	7.99	22.94	9.86	42.19	2.46	46.56	7.61
31	4×8	28.88	0.83	17.63	6.86	38.54	5.34	37.60	2.89
31	6×8	2.25	2.25	5.00	3.00	24.08	10.61	29.96	9.17
29	1×8	50.78	0.11	40.97	4.97	51.10	7.50	51.98	5.83
29	2×8	42.87	2.80	40.39	2.94	46.20	5.20	55.18	1.72
29	4×8	31.50	3.50	38.38	1.88	45.92	4.92	51.23	4.18
29	6×8	30.75	4.75	35.08	1.58	41.00	5.50	43.79	1.21
27	1×8	55.16	2.49	48.53	7.62	55.28	2.53	52.18	2.83
27	2×8	45.75	2.75	42.22	0.87	52.15	6.45	54.88	1.93
27	4×8	-	-	43.88	0.72	-	-	-	-
27	6×8	-	-	41.33	0.67	-	-	-	-

[a], $\overline{X}$ and SEM are the means and standard errors of the means, respectively; -, data are not collected.

Table 3-2 shows the lifetime fecundity of *M. dirhodum* after different stages of *M. dirhodum* were treated with various high temperatures for eight hours per day for one to six days. The highest mean lifetime fecundity (55.28 nymphs / adult) occurred when the 3rd instar larvae were exposed at 27°C for eight hours and the lowest (2.25 nymphs / adult) could be measured when the adults were treated at 31°C for eight hours per day for six days. The high temperature, exposure time and developmental stage had a significant influence on the lifetime fecundity of aphids (Table 3-3).

Because all interactions between the three factors had not significant effects on the lifetime fecundity (Table 3-3), main effects of the three factors at different levels were compared separately.

Table 3-3 Analysis of variance on effects of high temperatures, exposure times and aphid stages on the lifetime fecundity of *M. dirhodum*.

Source	SS	MS	*F*	*df*	*P*
Temp	9049.05	3016.35	20.08	3	0.0001
Expose	6223.08	2074.36	13.81	3	0.0001
Temp×Expose	972.54	138.93	0.93	7	0.4908
Stage	7639.16	2546.39	16.96	3	0.0001
Temp×Stage	2189.04	243.23	1.62	9	0.1204
Expose×Stage	1083.47	120.39	0.80	9	0.6157
Temp×Expose×Stage	528.23	35.22	0.23	15	0.9986
Error	14417.72	150.19		96	
Total	42102.28			145	

SS, represents sum of squares; MS, represents mean sum of squares.

3.2.1.1 The effects of high temperatures on lifetime fecundity

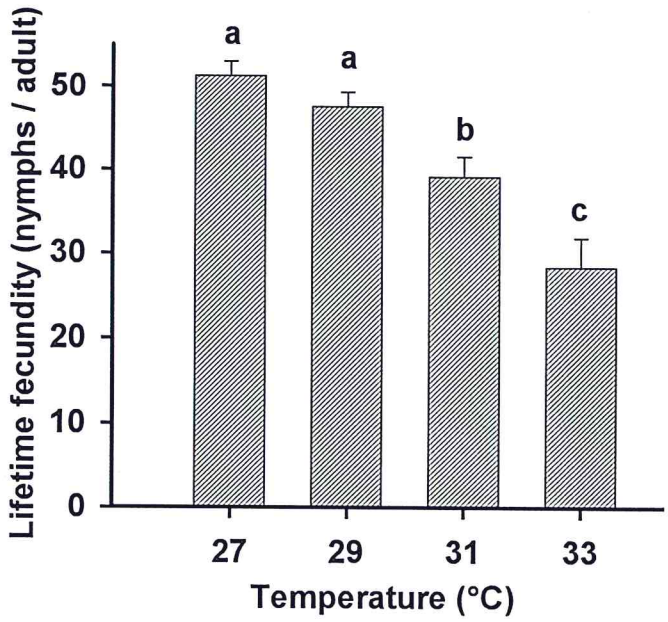


Fig. 3-1 Means and standard errors of the lifetime fecundity of *M. dirhodum* after they were exposed to different high temperatures for eight hours per day for one and two days. Different letters above each bar indicate significant difference between temperatures at P=0.05 based on Least Square Means.

Increasing the temperature lead to a decrease in lifetime fecundity of *M. dirhodum* (Fig. 3-1). The significantly lowest total number of offspring per adult aphid was recorded after previous exposure to 33°C. Irrespective of the effects of exposure times and aphid stage, on average, aphids exposed for one and two days to 27, 29,

31, and 33 °C produced 51, 47, 39 and 28 nymphs per adult, respectively. High temperature over 29°C significantly reduced the fecundity of *M. dirhodum*.

3.2.1.2 The effects of development stages on lifetime fecundity

The multiple comparison revealed that the effect of exposed stages on the lifetime fecundity could be grouped, i.e. group 1 with 2nd and 3rd instar larvae and group 2 with 4th instar larvae and adults (Fig. 3-2). The matured aphids were more sensitive to unfavourable high temperatures than the young ones. High temperature during the ovary development of aphids had a significantly negative effect on the lifetime fecundity of *M. dirhodum*.

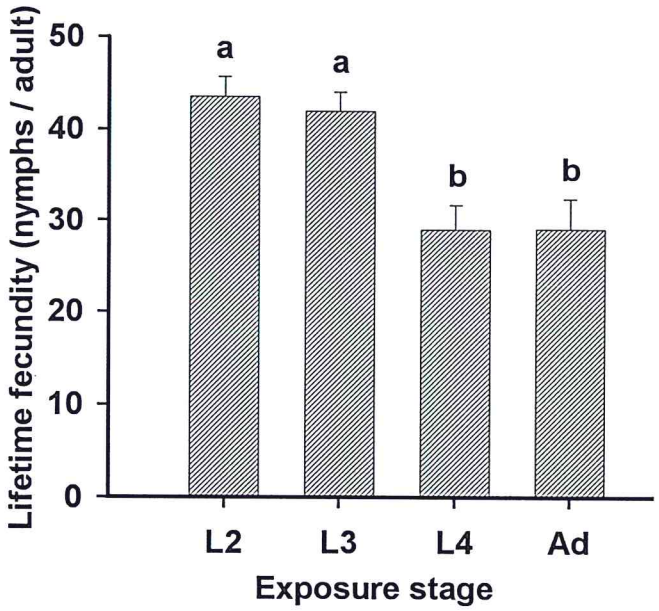


Fig. 3-2 Means and standard errors of the lifetime fecundity of *M. dirhodum* after different stages of the aphids, 2nd, 3rd and 4th instar larvae and adult were exposed to high temperatures. Different letters above each bar indicate significant differences between aphid stages at P=0.05 based on Least Square Means.

3.2.1.3 The effects of exposure times on lifetime fecundity

The total number of offspring produced during the whole lifetime of the aphids were inversely related to exposure time (Fig. 3-3). The lowest number occurred after the maximum tested exposure time. The means of lifetime fecundity of *M. dirhodum* when different stages of aphid were exposed to 29° to 31°C for one, two, four and six days were about 45, 39, 34 and 23 nymphs per adult, respectively.

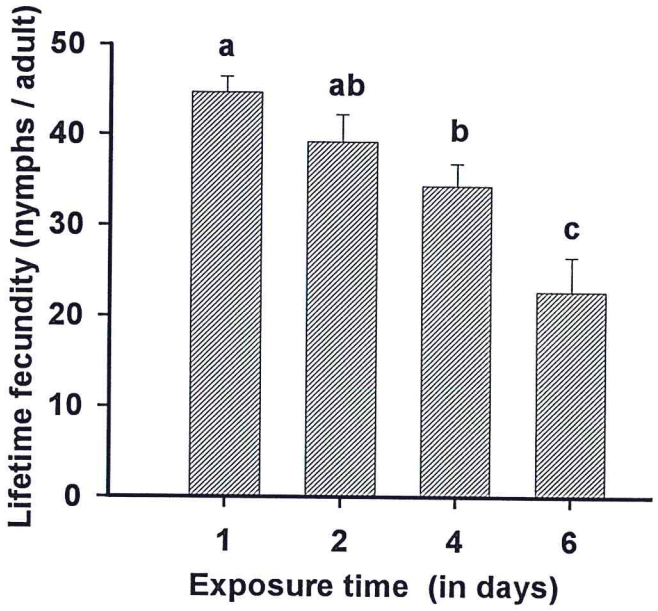


Fig. 3-3 Means and standard errors of the lifetime fecundity of *M. dirhodum* after high temperature treatments (29 and 31°C) for eight hours per day for different days. Different letters above each bar indicate significant differences between exposure times at P=0.05 based on Least Square Means.

3.2.2 Longevity

Table 3-4 The effects of the temperature, exposure time, and development stage on the mean longevity of *M. dirhodum* (in days).

Temp (°C)	Exposures days×hour/day	Adult $\overline{X}$ [a]	Adult SEM	4th instar $\overline{X}$	4th instar SEM	3rd instar $\overline{X}$	3rd instar SEM	2nd instar $\overline{X}$	2nd instar SEM
33	1×8	13.00	10.79	14.81	5.78	30.10	3.67	23.54	2.18
33	2×8	12.00	9.52	12.05	5.49	24.85	3.36	29.47	6.96
31	1×8	36.77	1.03	15.26	1.89	27.23	5.02	34.28	5.32
31	2×8	26.35	5.72	10.76	2.51	22.69	3.14	35.11	6.56
31	4×8	24.38	8.19	20.00	6.85	29.35	7.25	33.19	2.07
31	6×8	2.50	2.50	7.50	5.30	20.58	7.43	32.69	3.23
29	1×8	29.87	3.47	25.83	5.67	33.50	5.00	36.00	3.50
29	2×8	27.17	1.17	25.75	1.75	25.10	3.40	38.83	6.33
29	4×8	32.50	0.00	28.96	4.79	30.00	4.50	31.65	2.85
29	6×8	30.00	5.00	25.21	1.04	28.00	2.50	29.69	5.81
27	1×8	33.75	1.25	26.70	4.80	38.50	3.00	33.75	2.25
27	2×8	36.88	0.63	25.68	2.43	30.95	0.45	31.30	2.50
27	4×8	-	-	34.75	4.75	-	-	-	-
27	6×8	-	-	29.38	3.13	-	-	-	-

[a], $\overline{X}$ and SEM are the means and standard errors of the means, respectively; -, data are not collected.

Table 3-4 summarises the effects of temperature, exposure time, and developmental stage on the longevity of *M. dirhodum*. All three factors significantly influenced the longevity of *M. dirhodum*, but the interactions between the three factors were not

significant (Table 3-5). The shortest longevity (2.5 days) occurred after adults were exposed six days to 31°C with 8 hours/day.

Table 3-5 Analysis of variance of the effects of high temperatures, exposure times and aphid stages on the longevity of *M. dirhodum*.

Source	SS	MS	*F*	*df*	*P*
Temp	2801.18	933.73	9.28	3	0.0001
Expose	1171.42	390.47	3.88	3	0.0115
Temp×Expose	350.55	50.08	0.50	7	0.8341
Stage	3958.04	1319.35	13.11	3	0.0001
Temp×Stage	1337.52	148.61	1.48	9	0.1674
Expose×Stage	1074.00	119.33	1.19	9	0.3127
Temp×Expose×Stage	865.82	57.72	0.57	15	0.8884
Error	9658.90	100.61		96	
Total	21217.42			145	

SS, represents sum of squares; MS, represents mean sum of squares.

3.2.2.1 The effects of high temperatures on longevity

The longevity of *M. dirhodum* decreased as temperature increased and the highest temperatures tested lead to a significantly shorter longevity (Fig 3-4). On average aphids exposed for one and two days to 27, 29, 31, and 33 °C survived for 32, 30, 26 and 20 days, respectively.

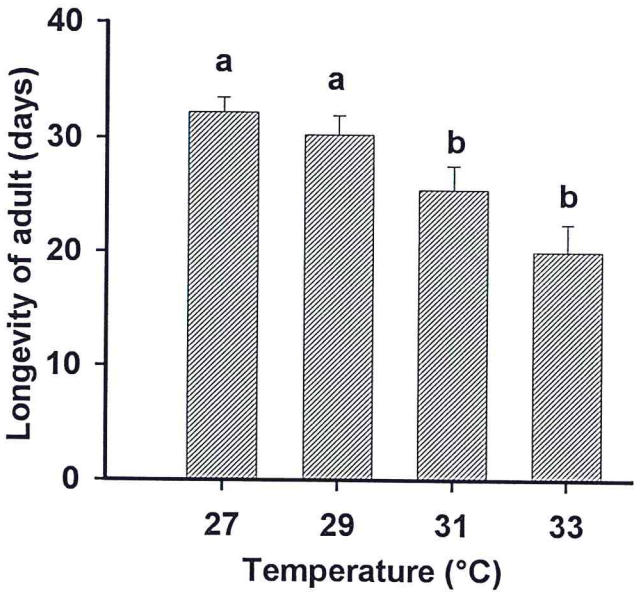


Fig. 3-4 Means and standard errors of the longevity of *M. dirhodum* after different high temperature treatments for eight hours per day for one and two days. Different letters above each bar indicate significant differences between temperatures at P=0.05 based on Least Square Means.

3.2.2.2 The effects of development stage on longevity

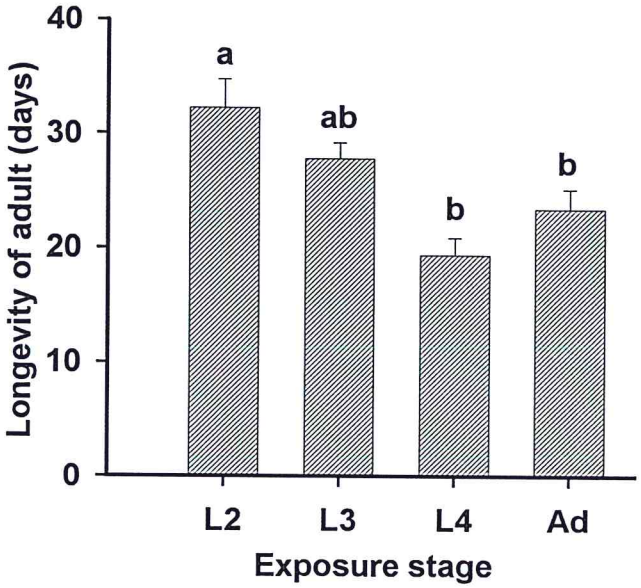


Fig. 3-5 Means and standard errors of the longevity of *M. dirhodum* after different stage of aphids, 2nd, 3rd and 4th instar larvae and adult, were exposed to high temperatures. Different letters above each bar indicate significant differences between aphid stages at P=0.05 based on Least Square Means.

3.2.2.3 The effects of different exposure times on longevity

Compared to the different high temperatures, exposure time had a less pronounced effect on the longevity of *M. dirhodum* (Fig. 3-6). Longevity was yet significantly lowest after the maximum tested exposure time.

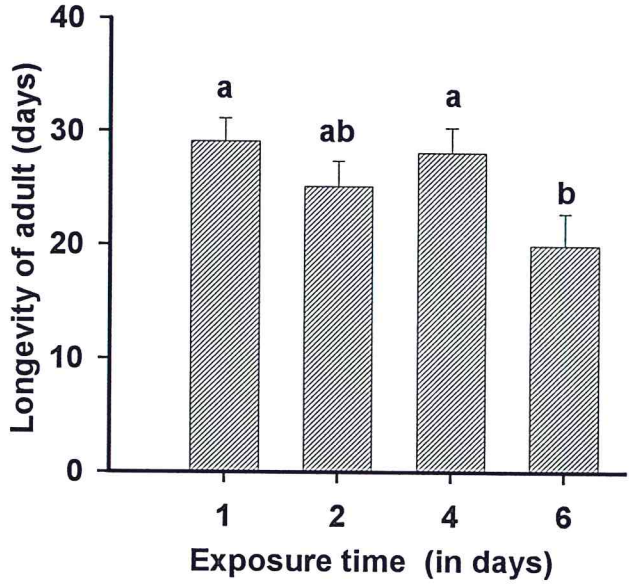


Fig. 3-6 Means and standard errors of the longevity of *M. dirhodum* after high temperature treatments (29 and 31°C) for eight hours per day for different days. The different letters above each bar indicate significant differences between exposure times are significant at P=0.05 based on Least Square Means.

3.2.3 Survival rate

Table 3-6 Mean survival rates of *M. dirhodum* after exposing different development stages *M. dirhodum* to high temperatures for varying exposure times.

Temp (°C)	Exposures days×hour/day	Adult		4th instar		3rd instar		2nd instar	
		$\overline{X}$ [a]	SEM	$\overline{X}$	SEM	$\overline{X}$	SEM	$\overline{X}$	SEM
33	1×8	0.10	0.06	0.60	0.14	0.90	0.06	0.60	0.00
33	2×8	0.10	0.06	0.45	0.21	0.65	0.15	0.45	0.13
31	1×8	0.75	0.05	0.85	0.10	1.00	0.00	0.67	0.06
31	2×8	0.75	0.05	0.75	0.13	0.80	0.00	0.40	0.10
31	4×8	0.20	0.08	0.25	0.10	0.70	0.06	0.60	0.14
31	6×8	0.05	0.05	0.15	0.10	0.30	0.13	0.50	0.13
29	1×8	0.80	0.20	1.00	0.00	1.00	0.00	1.00	0.00
29	2×8	0.80	0.20	0.90	0.10	1.00	0.00	0.80	0.20
29	4×8	0.40	0.00	0.70	0.10	1.00	0.00	1.00	0.00
29	6×8	0.30	0.10	0.70	0.10	0.70	0.10	0.90	0.10
27	1×8	0.90	0.10	1.00	0.00	1.00	0.00	0.90	0.10
27	2×8	0.80	0.00	0.90	0.10	1.00	0.00	1.00	0.00
27	4×8	-	-	0.90	0.10	-	-	-	-
27	6×8	-	-	0.80	0.00	-	-	-	-

[a], $\overline{X}$ and SEM are the means and standard error of the means, respectively; -, data are not collected.

Table 3-7 Analysis of variance of the effects of high temperatures, exposure times and aphid stages on the survival rates of *M. dirhodum*.

Source	SS	MS	*F*	*df*	*P*
Temp	3.88	1.30	38.28	3	0.0001
Expose	3.20	1.07	31.57	3	0.0001
Temp×Expose	0.49	0.07	2.06	7	0.0551
Stage	2.45	0.82	24.12	3	0.0001
Temp×Stage	0.75	0.08	2.46	9	0.0144
Expose×Stage	1.38	0.15	4.53	9	0.0001
Temp×Expose×Stage	0.20	0.01	0.39	15	0.9797
Error	3.25	0.03		96	
Total	15.59			145	

SS, represents sum of squares; MS, represents mean sum of squares.

Survival rates of the aphids varied after different developmental stages of *M. dirhodum* were exposed to different high temperatures for different exposure days. The lowest survival rate was 5% after adults were exposed at 31°C for 6 days 8 hours per day (Table 3-6). Analysis of variance revealed that survival rates, in contract to lifetime fecundity and longevity, were significantly affected not only by the

tree factors but also by the interactions between aphid stage and other two factors (Table 3-7).

3.2.3.1 The effects of temperatures and aphid stages on survival rates

Table 3-8 Multiple comparisons for the survival rates of *M. dirhodum* at different high temperatures and aphid stages.

Temp	27°C (LSM)	29°C (LSM)	31°C (LSM)	33°C (LSM)
L2	0.950±0.04 a	0.925±0.05 a	0.541±0.05 a	0.525±0.08 a
L3	1.000±0.04 a	0.925±0.05 a	0.700±0.05 b	0.775±0.08 a
L4	0.950±0.04 a	0.825±0.05 a	0.500±0.05 a	0.525±0.08 a
Adult	0.850±0.04 a	0.575±0.05 b	0.437±0.05 a	0.100±0.08 b

LSM, represents the adjusted least square means; the LSM of the survival rates followed by different letters with in columns are different at P=0.05. the LSM for 27°C and 33°C are obtained from exposures for one and two days, eight hours per day.

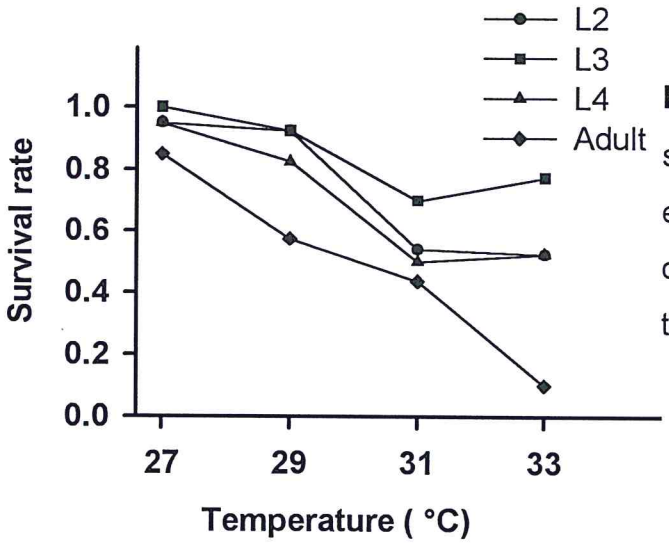


Fig. 3-7 The least square means of survival rates of *M. dirhodum* after exposing different development stages of the aphids to different high temperatures.

The effects of various high temperature regimes and aphid stages on the average survival rates of *M. dirhodum* are shown in Fig. 3-7 and Table 3-8. In general, survival rates of the aphids decreased as the temperature increased. Compared to larva stage the adult stage had lower survival rates, which indicates that adults are more sensitive to high temperature. Exposing adults at 33°C resulted in the lowest survival rate in the experiment. After the high temperature treatment, more L3 survived than other stages at all temperatures although this effect became significant only when the temperature reached 31°C. The survival rates of L2 and L4

were similar at all temperatures. The multiple comparison revealed all stages had similar survival rates at 27°C but not at other tested temperatures.

3.2.3.2 The effects of exposure times and aphid stages on survival rates

Fig. 3-8 shows that the mean survival rate of *M. dirhodum* is generally decreased, as the exposure time increased but not for L2. The old aphids had significantly lower survival rates than the young ones. The survival rate of L3 was highest, followed by the second and fourth larval instars, whereas adults suffered highest mortality. Exposing different stages of the aphids at high temperatures for two days with eight hours per day could not lead to significant difference in survival rates (Table 3-9).

Table 3-9 Multiple comparisons for the survival rates of *M. dirhodum* under different conditions of aphid stages and exposure times

Temp	1*8 (LSM)	2*8 (LSM)	4*8 (LSM)	6*8 (LSM)
L2	0.792±0.04 a	0.663±0.07 a	0.800±0.08 a	0.700±0.09 a
L3	0.975±0.04 b	0.863±0.07 a	0.850±0.08 a	0.500±0.09 b
L4	0.862±0.04 ab	0.750±0.07 a	0.475±0.08 b	0.425±0.09 b
Adult	0.638±0.04 c	0.613±0.07 a	0.300±0.08 b	0.175±0.09 b

LSM, represents the adjusted least square means; the LSM of the survival rates followed by different letters within columns are different at P=0.05. The LSM for exposure time 4 and 6 days (8 hours per day) are from 31 and 29°C.

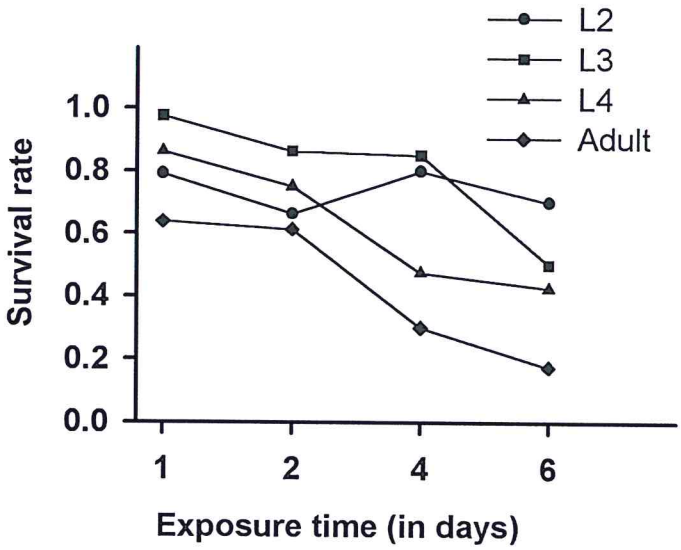


Fig. 3-8 The Least square means of the survival rates of *M. dirhodum* after exposing different development stages of the aphids for different exposure times.

3.3 Discussion

Extreme high temperature is reported to be a limiting factor for the population development of *M. dirhodum*. With a correlation analysis of the field data, Honek (1985) found that the peak density of *M. dirhodum* was negatively related to the number of days at which daily maximum temperatures exceeded 27°C. Based on a analysis of aphid density data and weather conditions, Chen et al. (1994) suggested that the low density of *M. dirhodum* in Beijing, China, was due to high temperatures. This study first time experimentally proved that for *M. dirhodum*, high temperatures from 27 to 33°C caused significantly lower fecundity, shorter longevity and lower survival rate (Table 3-3, 3-5, 3-7).

A constant temperature of 27.5°C reduced the fecundity of cereal aphids to zero, and at constant 30°C, a zero survival rate for adults was recorded (Dean 1974a and Zhou & Carter 1992). Moreover, Botto et al. (1980) reported that the offspring died in the stage L3 at constant 27°C. However, the results from this study indicate that not only the actual degree of temperature but also the exposure time exert a strong influence on the aphids. We measured the lifetime fecundity of the aphids is still high (41-55 nymphs /adult) under 27°C if the exposure time is shorter than 6 days with 8 hours/day. Moreover, the temperature 31°C cannot cause zero survival rates if exposure time is less than four day with 8 hours per day (Table 3-2, Table 3-6).

Constant temperatures between 20 and 25°C had no negative effect on *M. dirhodum*; on the contrary, the intrinsic rate of increase raised as the constant temperatures increased up to 25°C (Zhou & Carter 1992). However, according to our experiment design, 25°C daily constant temperature is equivalent to 35°C for 8 hours and 20°C for 16 hours per day. This temperature is high enough to kill most *M. dirhodum*, because our experiment results show that the lifetime fecundity and survival rate were dramatically reduced to 9-14 nymphs/adult and 10% by exposing adult to 33°C for 8 hours (Table 3-2, Table 3-6).

The data collected by constant temperature experiments do not differentiate the effect of exposure time on aphids, directly applying these results to simulation model may mislead the population predictions. However, our experiment demonstrated the

detailed survival and reproduction rates at different temperatures for different times. The results can be incorporated in the simulation model for *M. dirhodum*.

Heating had significant stronger negative effects on the matured stages (L4 and adults) than on young larvae (L2 and L3) (Fig.3-2, 3-5, 3-7, 3-8). Lykouressis (1985) found that the 1st and 2nd instar of *S. avenae* can withstand higher temperature than the 3rd and 4th instars, as their development rate is much less affected from 25°C upwards. Kaakeh and Dutcher (1993) concluded that 3rd and 4th instar nymphs and adults of the pecan aphids *Monelliopsis pecanis* and *Melanocallis caryaefoliae* (Both Homoptera: Aphididae) withstand a wide range of temperatures better than 1st and 2nd instar nymphs under a constant high temperature regime (30, 34, 37 and 40°C) for 1-5 hours. The results from our experiments and the two papers commonly indicate that the 3rd instar is most tolerant to high temperature. Since 1st and 2nd instar larvae have smaller body size and lower mobility than older instars and adults, they could not avoid fast heating by moving. They may not withstand the sudden heating by the extremely high temperatures. However, if the temperature is intermediate high (25-33°C), and not only the survival but also the reproduction are used to evaluate the effect of high temperature on aphids, young instars can withstand the damage of high temperature better than the matured stages.

Since tested aphids stay at the same temperature during their whole life, the difference between development stages in tolerance to high temperature can not be detected by constant temperature experiments. However, by our experiment the relationship between the heat tolerance and development stage of the aphids is demonstrated. This finding can be considered in the simulation model.

The reproduction of adults is not only affected by the present temperature, but also by the temperature previously experienced during larval development. The lifetime fecundity after exposing L2 and L3 to 31°C for six days with eight hours per day was reduced to less than 30 nymphs / adult (Table 3-2). This is supported by the fact found in *Aphis pomi* De Geer (Carroll & Hoyt 1986) and *Myzus persicae* (El-Din 1976) (Both Homoptera: Aphididae), that the fecundity is reduced by high temperatures experienced by the parental generation. This finding is important for the simulation,

because the results from constant temperature experiment do not include this information.

As described in the introduction of this chapter, the temperature difference between day and night in fields was often over 15°C. The daily average temperature hardly ever reached 25°C, but the maximum temperature quite often exceeded 27°C during the major occurrence season of the aphids. Therefore, it is difficult to accurately determine the effects of temperature on the survival and reproduction of *M. dirhodum* using the data from constant temperature experiments. Using daily/hourly average temperature based on the results from constant temperature experiments would over/under-estimate the impact of temperatures on the aphids. To correct the bias caused by using daily average temperatures, the effects of high temperatures on longevity, survival rate and reproductive rate should be incorporated in the simulation model.

4 Sub-model of development

4.1 Sub-model of development time and its standard error

Temperature is the most important factor to determine the development of aphids (Dean 1974a, Zhou & Carter 1992). The duration of development and its standard error for each larva stage at different constant temperatures, ***DurationT*** and ***StdErrorT***, are used as the primary data in the calculation of development time. Different developmental speeds were found in apterous and alate aphids (Cannon 1984). The effects of aphid morph are incorporated in the model with a correction coefficient (D_MP). The duration of development and its standard error can be calculated with equation 4.1.

$$\begin{aligned} Duration &= DurationT \cdot D\_MP \\ StdError &= StdErrorT \cdot D\_MP \end{aligned} \qquad (4.1)$$

The duration ($Duration$) and its standard error ($StdError$) can be used to calculate the mean physiological age ($AgeL$) of aphids and the standard error of the age ($ErrL$). $AgeL$ and $ErrL$ are used to calculate the development transition rate later in this chapter. All these variables can be estimated with the following procedures.

4.1.1 Effects of temperatures on the developmental speed

The development of the aphids at different temperature levels performs in different ways. Under a moderate temperature, the developmental speed of an insect ($V(T) = 1/DurationT$) increases as the temperature rises. When temperature is out of the moderate (too low or too high), the insect development slowdowns or even stops. Wang et al. (1982) developed a model to describe this phenomenon. The model consisted of three elements. The main element was a logistic function representing the development of an insect in accordance with the common rule of biochemical reactions under moderate temperature. Two other elements expressed the adjustment of the insect to low and high temperatures. The weather data from 1991 to 1996 in Göttingen and Hanover indicate that the average temperatures during growing seasons in northern Germany were over 5°C, thus the effect of low temperature on development is ignored in this model, but the effect of high temperature is considered. The upper threshold temperature for the development of

larvae of *M. dirhodum* is assumed to be 32°C because the aphids mortality reach 90% at 33°C. Wang's model is adopted to describe the duration of development (*DurationT*) at a given temperature (*TX*) (equation 4.2).

$$DurationT = \frac{1}{K \cdot \left(1 - e^{-\frac{32-TX}{\delta}}\right)} \cdot \left(1 + e^{-r(TX-T_0)}\right) \qquad (4.2)$$

K is potential saturated development speed at high temperature. r is exponential increase rate of development speed as the temperature increases. T_0 is the favourable temperature for development. δ is a parameter to express the tolerance of the larvae to high temperature.

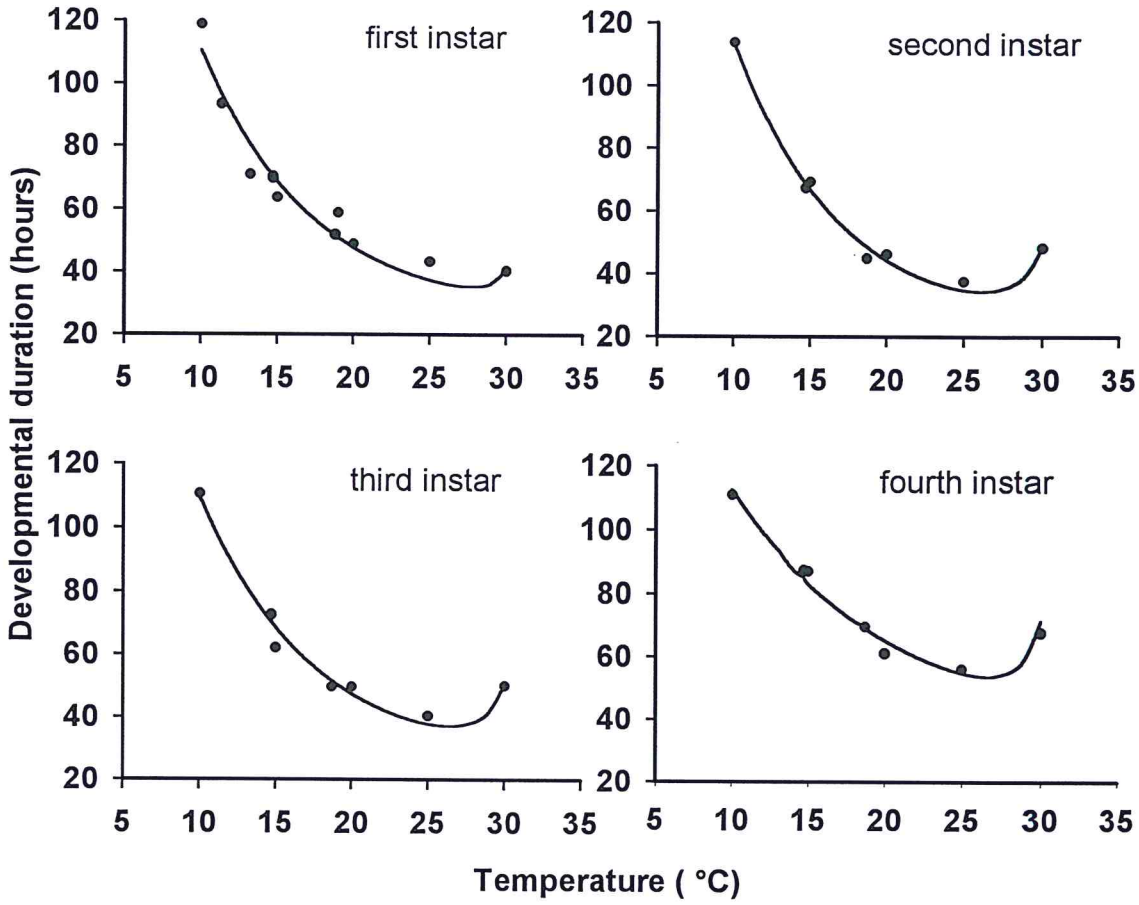


Fig. 4-1 Duration of development of *M. dirhodum* larvae at different temperatures. Dots represent the average duration of development measured by Cannon (1984), Hu and Gui (1985) and Zhou and Carter (1992). Lines represent the predicted duration of *M. dirhodum* from equation 4.2.

The average developmental duration of *M. dirhodum* at different temperatures measured by Cannon (1984), Hu and Gui (1985) and Zhou and Carter (1992) is used to estimate parameters of the model. The parameters are listed in Table 4-1. The relationship between temperature and developmental duration is accurately described with the model (Fig. 4-1). The corrected R^2 was very high (Table 4-1).

Table 4-1. Parameters of the development model (equation 4.2) between the duration of development and temperatures for different instars of *M. dirhodum*.

Stage	n	r	T_0	K	δ	R^2	P
1st Instar	11	.13668	18.5	.03797	1.3	0.9469	<0.01
2nd Instar	8	.14232	20.0	.04543	2.4	0.9913	<0.01
3rd Instar	8	.13143	19.5	.04087	2.2	0.9803	<0.01
4th Instar	7	.09117	19.0	.02907	1.7	0.9819	<0.01

4.1.2 Effects of temperature on standard error of developmental duration

The effect of temperature on the standard error of developmental duration *StdErrorT* is assumed to be in accordance with the developmental duration. *StdErrorT* at a given temperature (TX) can be determined by equation 4.3 that has a similar structure with equation 4.2.

$$StdErrorT = \frac{1}{a \cdot \left(1 - e^{-\frac{b-TX}{c}}\right)} \cdot \left(1 + e^{-d(TX-f)}\right) \qquad (4.3)$$

a, b, c, d and f are regression parameters in equation 4.3. The data from Dean (1974a) and Zhou and Carter (1992) are used to estimate these parameters (Table 4-2). The standard errors of the duration of development at different temperatures are accurately described with equation 4-3 (Fig. 4-2). The model has high corrected R^2 (Table 4-2).

Table 4-2 Parameters of the model (equation 4.3) between the standard error of the duration of development and temperatures for different instars of *M. dirhodum*.

Stage	n	a	b	c	d	f	R^2	F
1st Instar	13	1.1786	13.15	1.16	0.7871	31.88	0.992	297.5**
2nd Instar	13	1.1046	12.91	1.00	0.7659	30.99	0.976	153.4**
3rd Instar	13	0.9944	12.90	0.57	0.7267	30.63	0.982	154.9**
4th Instar	12	0.7351	11.57	3.21	1.1333	32.09	0.943	48.2**

**, indicate that the model is significant at the level of P<0.01.

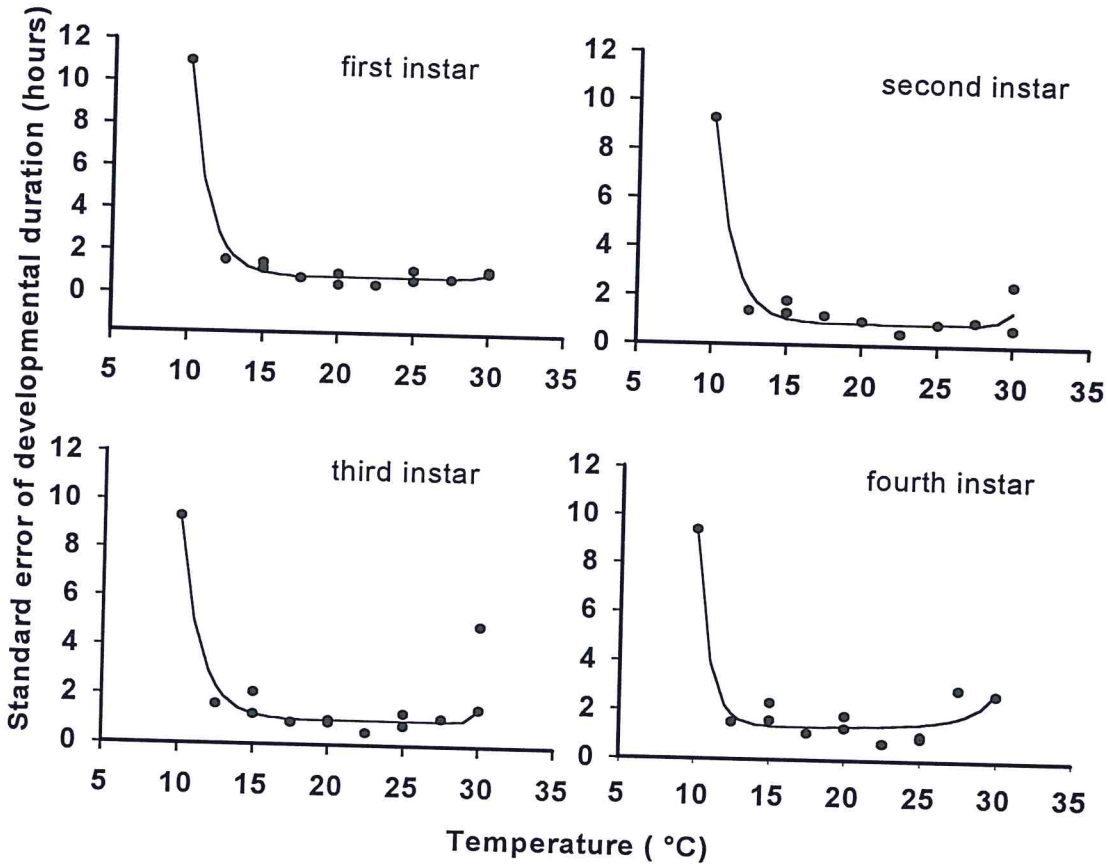


Fig. 4-2 Standard errors of the duration of development of *M. dirhodum* larvae at different temperatures. Dots represent the standard error of duration determined by Dean (1974a) and Zhou and Carter (1992). Lines represent predictions from the equation 4.3.

4.1.3 Effects of apterous and alate morph

The data from Cannon (1984) showed that duration of development of alate larvae was about 1.2 times longer than that of apterous larvae at 14.7°C. Since the parameters in equation 4.2 and 4.3 were estimated for apterous larvae, the value of the correction coefficient (D_MP) for apterous and alate 4th instar larvae is set to 1.0 and 1.2 respectively.

4.2 Sub-model of longevity of adults

The longevity of adults is influenced by temperature, plant growth stage, and the aphid morph (Watt 1979, Zhou & Carter 1992). The experiment in the present study (see chapter 3.2.2) indicate that high temperatures above 27°C reduce the longevity of the adults. The longevity at different constant temperatures ($LongevityT$) is used as

the basic data in the longevity calculation. Effects of other factors are incorporated as correction coefficients.

$$Longevity = LongevityT \cdot L\_HT \cdot L\_GS \cdot L\_MP \cdot L\_TT \quad (4.4)$$

L_HT, L_GS, L_MP, L_TT are correction coefficients that represent effects of high maximum temperature, plant growth stage, the aphid morph and the temperature types respectively. The values of these variables are derived as follows.

4.2.1 Effects of average temperature

As adults could not normally survive and reproduce at constant high temperature (higher than 25°C), the longevity of adults at constant higher temperatures is not available from the literature. The data for modelling an accurate relationship between temperature and longevity of adults are not sufficient. Based on the data from Zhou and Carter (1992), the longevity (in days) of adults at a given daily mean temperature between 10°C and 25°C ($LongevityT$) can be calculated with a rough polynomial model (equation 4.5).

$$LongevityT = 57.23 - 4.496TX + 0.108TX^2 \quad (4.5)$$

4.2.2 Effect of maximum temperature

The experimental results in this study show that exposing *M. dirhodum* to high temperatures above 27°C for 8 hours per day has a significant negative effect on the longevity of adults. For sake of the convenience in programming, the effects of high temperature, exposure time and exposed stage of the aphids on longevity (L_HT) were incorporated in a single polynomial model (equation 4.7). Since the high temperatures during the 2nd and 3rd instar had no significant effects on the adult longevity, only the longevity data for the 4th instar and adults in Table 3-5 in chapter 3.2.2 were used to build the model. Before parameters are estimated, mean longevity data in Table 3-4 are transformed with equation 4.6.

$$L\_HT = \overline{X} / \overline{X}_{\max}$$
$$MT = T - 26 \qquad (4.6)$$
$$Age = \frac{1}{Expo} \cdot \sum_{k=1}^{Expo} (Age_k - 8)$$

$\overline{X}$ is the mean longevity and $\overline{X}_{\max}$ is the maximum mean longevity (=36.88 days). T is the temperature. $Expo$ is the number of exposure days at high temperature with 8 hours per day (Table 3-4). Age_k in the model is the age of aphids (in days) when they are treated with high temperatures. It represents the effect of exposed developmental stages of *M. dirhodum* on the longevity. 27°C is assumed the threshold of high temperature over which the aphids would suffer from the high temperature. In order to avoid MT from to be zero when temperature is 27°C, MT is set to T-27+1, i.e. $MT = T$-26. The constant 8 represents the duration of development of the aphid larva at standard rearing conditions (20°C).

Finally, the effect of high temperature on the longevity of the aphids can be expressed as equation 4.7.

$$L\_HT = 1.0 + .096144Age - .015629MT \cdot Expo - .00833MT^2 - .00458159MT \cdot Expo \cdot Age \qquad (4.7)$$

The model significantly describes the effects of high temperatures on longevity of *M. dirhodum* (F = 187.8 > $F_{0.01}$ = 4.31; df = 4, 22). The mean corrected R^2 is 0.80. All parameters are significant at $P < 0.05$ level.

The model is developed by using the experiment data under the controlled conditions in the laboratory. The independent variables should be prepared using equation 4.8 to fit the field conditions before applying the model in the simulation. The daily maximum temperatures are assumed equivalent to the high temperatures in the experiment. If the maximum temperature is lower than 27°C, the effect of high temperatures on longevity is ignored. The daily maximum temperature ($MaxT_k$) experienced by adults since the first day they developed to 4th instar is checked. $Expo$ is the number of days with maximum temperature over 27°C during the period. MT is the average transformed high temperature that aphids experienced since the

first day of 4th instar larvae developed. *Age* in the model is the average age (in days) at which aphids are exposed to high temperatures. Since the effect of high temperature on survival is displayed normally two days later, a two days delay is assumed. Thus, *Expo*, *MT* and *Age* can be calculated with equation 4. 8.

$$Expo = \sum_{k=1}^{i-2} Expo_k \qquad (If\ MaxT_k \geq 27°C,\ Expo_k = 1,\quad If\ MaxT_k < 27°C,\ Expo_k = 0)$$

$$MT = \frac{1}{Expo} \cdot \sum_{k=1}^{i-2} (MaxT_k - 26) \quad (If\ MaxT_k < 27°C, MaxT_k = 26) \qquad (4.8)$$

$$Age = \frac{1}{Expo} \cdot \sum_{k=1}^{i-2} (Age_k - 8) \qquad (If\ MaxT_k < 27°C,\ Age_k = 8)$$

where, $MaxT_k$ is maximum temperature at day k. i is the age of aphids in days.

With the independent variables in equation 4.8, the correction coefficient of high temperature on the longevity can be calculated with equation 4.7. If maximum temperatures never surpass 27°C, i.e. *Expo* = 0, the calculations of equation 4.8 is not carried out and L_HT is directly set to 1.0.

4.2.3 Effect of plant growth stage

Zhou and Carter (1992) showed that mean longevity of the adult aphids feeding on plant stage from middle inflorescence emerging (*GS* 55) to middle milky ripe was 2.3 times longer than those feeding during middle milky ripe (*GS* 73) to early dough ripe (*GS* 83). Watt (1979) found that survival rate in the first seven days of the adult stage was high (0.89) before the middle of the milky ripe stage (<*GS* 73). The survival rate decreased to 0.54 during the milky ripe stage (*GS* 73-85). The adults did not survive after *GS* 85. The effect of plant growth stages on the adult longevity can be expressed with a logistic model:

$$L\_GS = \frac{1}{1 + \left(\frac{GS}{L_{50}}\right)^a} \qquad (4.9)$$

where L_GS is the correction coefficient used in calculating the adult longevity influenced by the plant growth stage (*GS*), L_{50} is the *GS* at which the longevity of adult is shortened to 50%, a is the gradient to determine the decreasing speed of

L_GS as GS increases. The data related to the effects of plant growth stage on the longevity of adults are not sufficient to accurately estimate the parameters of the model. Nevertheless, according to the data of Watt (1979) and Zhou and Carter (1992), L_{50} and a were determined as GS 79.5 and 130, respectively.

4.2.4 Effects of aphid morph

The longevity of apterous adults is supposed to be longer than that of alate adults. Since reliable data could not be found in publications, Zhou et al. (1989) assumed that longevity of alate adults was half of the longevity of apterous adults. This is adopted for this study by setting L_MP = 1.0 for apterous adults and 0.5 for alate adults.

4.2.5 Effects of fluctuating temperatures

The results from Zhou and Carter (1992) showed that adults survived longer in fluctuating temperatures than in constant temperatures, even if the average values of the two temperatures were similar. The longevity of adults at fluctuating temperature regimes (average at 18.7°C) was 23.8 days. Using equation 4.5, the longevity of adults at a constant temperature of 18.7°C is estimated from the longevity at 15°C and 20°C as 10.92 days. Therefore, L_TT is set to be 1 under constant temperature conditions, but L_TT under fluctuating temperature conditions should be 23.8 /10.92 = 2.179.

4.3 Daily age increment and the physiological age of aphids

In the simulation model, the rate variables related to the development of the larvae and the ageing of the adults are frequently used. The daily age increment of the larvae (DpL_j) at day j can be calculated from the duration of development ($Duration_j$) (equation 4.10) under the conditions of day j. The daily age increment of the adult (DpA_j) can be expressed as the reciprocal of the longevity.

$$DpL_j = 1/Duration_j$$
$$DpA_j = 1/Longevity_j \qquad (4.10)$$

The physiological age of the larvae ($AgeL_i$) and the adults ($AgeA_i$) at day i can be estimated by accumulating the daily age increments since the first day of a larval stage or the first day of adults (equation 4.11).

$$AgeL_i = \sum_{j=1}^{i}(DpL_j)$$
$$AgeA_i = \sum_{j=1}^{i}(DpA_j) \qquad (4.11)$$

4.4 Developmental transition model (normal distribution model)

The aphid individuals born at different hours on the same day cannot uniformly finish their development. In addition, small differences in development speed exist among different individuals, even if they are reared under the same conditions. Since the duration of development of each instar lasts only 2-2.5 days at 20°C (Zhou & Carter 1992), this non-uniformity should be incorporated in the development model in calculating the development of an aphid cohort born on the same day. The developmental transition from one stage to the next stage of the aphids is assumed to follow a normal distribution (Fig. 4-3).

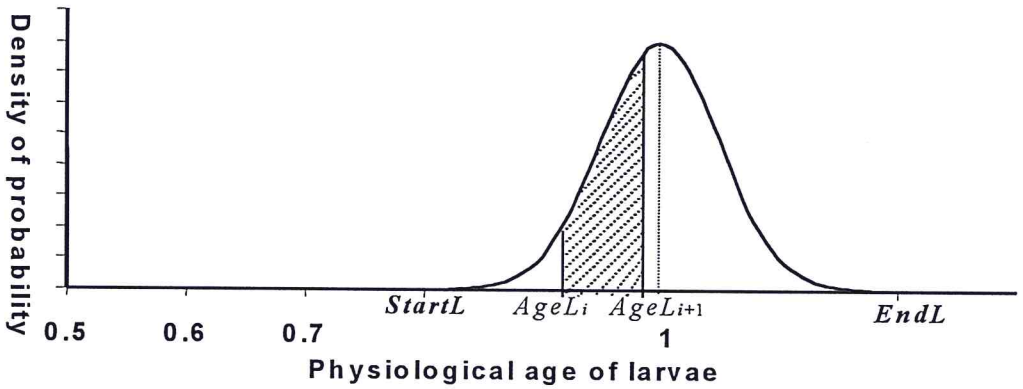


Fig. 4-3 Normal distribution model for developmental transition of larvae. ***StartL, EndL*** = age when larvae start and finish the developmental transition from young stage to the next older stage, respectively. $AgeL_i$, $AgeL_{i+1}$ = the age at day i and day i+1 respectively.

For the standard normal distribution (mean=0, standard error=1), when the independent variable changes from -3.9 to +3.9, the accumulated probability is

0.49995+0.49995=0.9999 (Pan 1986). In the development transition distribution, the average physiological age of the larva cohort should be 1 and the standard error can be represented by ($ErrL_{i+1}$). When the age ($AgeL_i$) increases from 1-3.9 $ErrL_{i+1}$ to 1+3.9 $ErrL_{i+1}$, 99.99% of the individuals in the cohort finish their development and transit into the next development stage. Therefore, the age of aphids of a cohort at which the transition starts or ends can be expressed as follows:

$$\begin{aligned} StartL &= 1-3.9ErrL_{i+1} \\ EndL &= 1+3.9ErrL_{i+1} \end{aligned} \qquad (4.12)$$

Fig. 4-3 shows a way to calculate the daily development transition rate (PL) of the cohort when the age of the larvae increase from $AgeL_i$ at day i to $AgeL_{i+1}$ at day i+1. Apparently, PL can be expressed as the area between the start point ($StartL$) to $AgeL_i$ being subtracted from the area between $StartL$ to $AgeL_{i+1}$ under the curve (Equation 4.13).

$$PL = P\_Normal(AgeL_{i+1}) - P\_Normal(AgeL_i) \qquad (4.13)$$

The cumulative probability ($P\_Normal(Y)$) for the standard normal distribution can be calculated with the standard normal distribution model:

$$P\_Normal(Y) = \int_{-\infty}^{Y} \frac{1}{\sqrt{2\pi}} \cdot e^{-\frac{1}{2}t^2} dt \qquad (4.14a)$$

where Y is the physiological age of an instar of aphids. Integral equation 4.14a can be transformed to equation 4.14b.

$$\begin{aligned} P\_Normal(Y) &= 1-\Phi(Y) && \text{for } Y \le 0 \\ P\_Normal(Y) &= \Phi(Y) && \text{for } Y > 0 \end{aligned} \qquad (4.14b)$$

$\Phi(Y)$ in equation 4.14b can be calculated with the following expression (Gao 1995):

$$\Phi(Y) = \frac{1}{2} + \left(\frac{1}{\sqrt{2\pi}} \cdot e^{-\frac{1}{2}Y^2}\right) \cdot \left(Y + \frac{Y^3}{3} + \frac{Y^5}{3\times 5} + \cdots + \frac{Y^{2i+1}}{(2i+1)!!} + \cdots + \frac{Y^{25}}{25\times 23\times 21\times \cdots \times 7\times 5\times 3\times 1}\right) \qquad (4.14c)$$

In order to calculate the probability area of the normal distribution for development of aphids, the normal distribution with average age=1, standard error = $ErrL_{i+1}$ has to be transformed into the standard normal distribution. $AgeL_i$ and $AgeL_{i+1}$ can be transformed into $Y1$ and $Y2$ with equation 4.15 to fit the cumulative probability model for the standard normal distribution (equation 4.14).

If $AgeL_{i+1} < StartL$, then

$$Y1 = StartL$$
$$Y2 = StartL \qquad \text{(4. 15a)}$$

If $StartL < AgeL_{i+1} < EndL$, then:

$$Y1 = StartL \qquad \text{for } AgeL_i \leq StartL$$
$$Y1 = (AgeL_i - 1)/ErrL_i \qquad \text{for } AgeL_i > StartL \qquad \text{(4. 15b)}$$
$$Y2 = (AgeL_{i+1} - 1)/ErrL_{i+1}$$

If $AgeL_{i+1} \geq EndL$, then:

$$Y1 = (AgeL_i - 1)/ErrL_i \qquad \text{for } AgeL_i < EndL$$
$$Y1 = EndL \qquad \text{for } AgeL_i \geq EndL$$
$$Y2 = EndL \qquad \text{(4.15c)}$$

To calculate the development transition rate of the aphids in a specific cohort, the physiological age of the aphids ($AgeL_i$) and the standard error ($ErrL_i$) have to be determined first. The details how to calculate $AgeL_i$ and $ErrL_i$ of each cohort will be described in the compartment model in chapter 7.

5 Sub-model of reproduction

5. 1 Lifetime fecundity of adults

Similar to the aphid development, the reproduction of aphids is also influenced by different ecological factors (Table 2-1). The total lifetime fecundity per adult at different temperatures (*BirT*) is used as the basic fecundity in the calculation of total lifetime fecundity. Effects of other factors can be represented by correction coefficients. The total lifetime fecundity at different conditions (*BirTot*) is described with equation 5.1.

$$BirTot = BirT \cdot F\_HT \cdot F\_GS \cdot F\_MP \qquad (5.1)$$

F_HT, *F_GS* and *F_MP* are the correction coefficients that express effects of maximum temperature, plant growth stage and the aphid's morph on the total lifetime fecundity respectively.

5.1.1 Effects of average temperature

The total lifetime fecundity at different constant temperatures varied (Dean 1974a; Zhou & Carter 1992; Hu & Gui 1985). The total number of new larvae produced by one apterous adult of *M. dirhodum* (*BirT*) at different temperatures (TA_i) can be calculated with a polynomial equation (equation 5.2). The parameters in the model were estimated using the data from Dean (1974a) and Zhou and Carter (1992).

$$BirT = -484.74 + 185.77TA_i - 25.5356TA_i^2 + 1.67736TA_i^3 - 0.0516874TA_i^4 + 0.000595883TA_i^5 \qquad (5.2)$$

If temperature (TA_i) is lower than 6.5°C or higher than 28.6°C, *BirT* is set to zero. The model can accurately describe the fecundity of aphids at different temperatures (Fig. 5-1). The corrected R^2 is 0.9953. The F test indicates that the model significantly describes the relationship (F = 592.17 > $F_{0.01}$ = 99.33, df = 6, 2).

Under field conditions, aphids born at different days most probably experience different temperatures. In order to make the simulation more realistic, the weighted mean temperature (TA_i) that aphids experienced since they were born up to now, is considered to be equivalent to the aphid rearing temperature that was used to build equation 5.2.

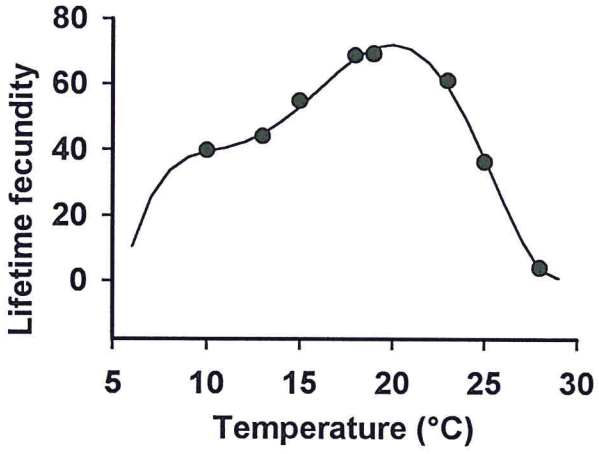


Fig. 5-1 Total lifetime fecundity per adult at different temperatures.

Dots represent total lifetime fecundity of *M. dirhodum* from Zhou and Carter (1992) and Dean (1974a). The line represents the predicted total lifetime fecundity from equation 5.2.

5.1.2 Effect of daily maximum temperature

Significant effects of high temperature on the total lifetime fecundity of *M. dirhodum* have been detected in this study. For conveniently incorporating effects of high temperature, exposure time and exposed aphid stage on the total lifetime fecundity in the simulation routine, a polynomial model (equation 5.4) are established. Before estimating the parameters of equation 5.4, the data in Table 3-2 in chapter 3.2.1 are transformed with equation 5.3.

$$\begin{aligned} H\_HT &= \overline{X} \Big/ \overline{X}_{\max} \\ MT &= T - 26 \\ Age &= \frac{1}{Expo} \cdot \sum_{k=1}^{Expo} (Age_k - 8) \end{aligned} \qquad (5.3)$$

$\overline{X}$ is the mean total lifetime fecundity and $\overline{X}_{\max}$ is the maximum mean total lifetime fecundity (= 55.28 offspring per adult) in Table 3-6. T, $Expo$ and Age_k have the same meanings as in equation 4.11 in chapter 4.3.2. The effect of high temperature on the total lifetime fecundity can then be expressed as follows:

$$\begin{aligned} F\_HT = {} & 1.0 + 0.077501\ Age - .011186\ MT \cdot Age - .01936\ MT \cdot Expo \\ & - .0128624\ Age \cdot Expo - 0.0099156\ MT^2 + .0068358\ Age^2 \end{aligned} \qquad (5.4)$$

The model accurately describes the effects of high temperature on the total lifetime fecundity (F = 443.0 > $F_{0.01}$ = 3.24; df = 6, 44). The mean corrected R^2 is 0.843. All parameters are significant at $P < 0.05$ level.

Equation 5.4 can be used to calculate the correction coefficients of maximum temperature (F_HT) (see equation 5.1). To apply the model in field conditions, independent variables of equation 5.4 are calculated with the same method used in the model that describes the effects of high temperature on longevity (equation 4.8 in chapter 4.3.2).

5.1.3 Effects of plant growth stage

Aphids that fed on different growth stages of host plants had different total lifetime fecundity (Vereijken 1979, Watt 1979, and Zhou & Carter 1992). Vereijken (1979) demonstrated that the mean multiplication of aphids in bio-mass in 14 days during the period between flowering and milky ripe (15.6 mg/mg between GS 65-73) was higher than during milky ripe (9.3 mg/mg between GS 73-79). Zhou and Carter (1992) concluded that adults that fed on plants from middle inflorescence to middle milky ripe (GS 55-75) produce more larvae (46) than those (32) fed during middle milky ripe to early dough ripe (GS 75-83) at the constant temperature 19±1°C.

A logistic model can be used to describe the correction coefficient of plant growth stage on total lifetime fecundity (F_GS) under the influence of the plant growth stage (GS):

$$F\_GS = \frac{1}{1+\left(\frac{GS}{F_{50}}\right)^{a}} \qquad (5.5)$$

F_{50} is the average GS at which the total lifetime fecundity of adult decreased to 50%. a is the gradient to determine the decreasing speed of F_GS. However, the published data are not sufficient to accurately estimate these two parameters. Based on the limited data from the publications cited above, values of F_{50} and a were determined approximately as GS 77.5 (late milky ripe) and 130, respectively.

5.1.4 Effects of morph

According to Wratten (1977), apterous adults consistently produce more offspring than alate adults. On average, each apterous adult produced 51.03 larvae and each alate adult deposited 40.05 larvae on barley at 20°C. Since the total lifetime fecundity in model 5.2 is for apterous adults, the correction coefficient (F_MP) for the

apterous adult is set to 1.0. The F_MP for the alate adult should be 40.05/51.03 = 0.7848.

5.2 Model for distribution of total lifetime fecundity over adult life span

5.2.1 Establishment of the model

The number of larvae produced by an adult at a given day can be derived from its lifetime fecundity and the proportion of the lifetime fecundity allocated to the day. The model for computing the proportion of total lifetime fecundity distributed in each simulation step (*BirthAgeP*) can be built according to the reproduction curve of *M. dirhodum* from Dean (1974a), Hu and Gui (1985), and Zhou and Carter (1992). The lifetime fecundity (*BirTot*) and the longevity of the adults include effects of temperature and other ecological factors (equation 5.1 and equation 4.4). *BirthAgeP* is only considered as a function of the adult age. However, the daily fecundity and the reproduction duration vary greatly with those factors. In order to remove the effect of these factors from the reproduction distribution model, the data from Dean (1974a), Hu and Gui (1985), and Zhou and Carter (1992) should be transformed with a normalisation method.

The daily newly born larvae ($Fecundity_j$) from the three publications mentioned above are transformed to the cumulative fecundity per aphid up to day i (equation 5.6).

$$Sum_i = \sum_{j=1}^{i} Fecundity_j \qquad i = 1, 2, \ldots \ldots N \tag{5.6}$$

N = the last day of reproductive duration.

Proportion of the cumulative fecundity up to day i ($SumF_i$) in the lifetime fecundity is calculated as follows:

$$SumF_i = Sum_i / Sum_N \qquad i = 1, 2, \ldots \ldots N \tag{5.7}$$

The physiological age of adults can be expressed as the cumulative reciprocal of the longevity.

$$AgeA_i = \sum_{j=1}^{i} \frac{1}{Longevity_j} \qquad i = 1, 2, \ldots \ldots N \tag{5.8}$$

Then, the physiological age of the adults is transformed to normalised physiological age (NPA_i) with equation 5.9.

$$NPA_i = AgeA_i / B_{50} \tag{5.9}$$

B_{50} is the physiological age of adults at which the number of larvae born arrives at 50% of lifetime fecundity.

The data transformed with equation 5.7 and 5.9 are shown in Fig. 5-2. The figure demonstrates that the relationship between the cumulative proportion of new larvae ($SumF_i$) and the normalised physiological age (NPA_i) can be described with a Weibull function (equation 5.10).

$$SumF_i = 1 - e^{-\left(\frac{NPA_i - \gamma}{\eta}\right)^{\beta}} \tag{5.10}$$

where, γ, η, and β are regression parameters that are estimated as γ = - 0.4006, η = 1.6342 and β = 2.2450 using the data in Fig. 5-2.

The model accurately describes the distribution of fecundity over the normalised physiological age of adults (F = 23529 > $F_{0.01}$ = 4.0; df = 3, 113). The mean corrected R^2 is as high as 0.9901.

With the proportion of cumulative fecundity from equation 5.10, the proportion of the lifetime fecundity allocated in each simulation step ($BirthAgeP$) during the age period between NPA_i and NPA_{i+1} can be calculated as follows (Fig. 5-2).

$$BirthAgeP = SumF_{i+1} - SumF_i \tag{5.11}$$

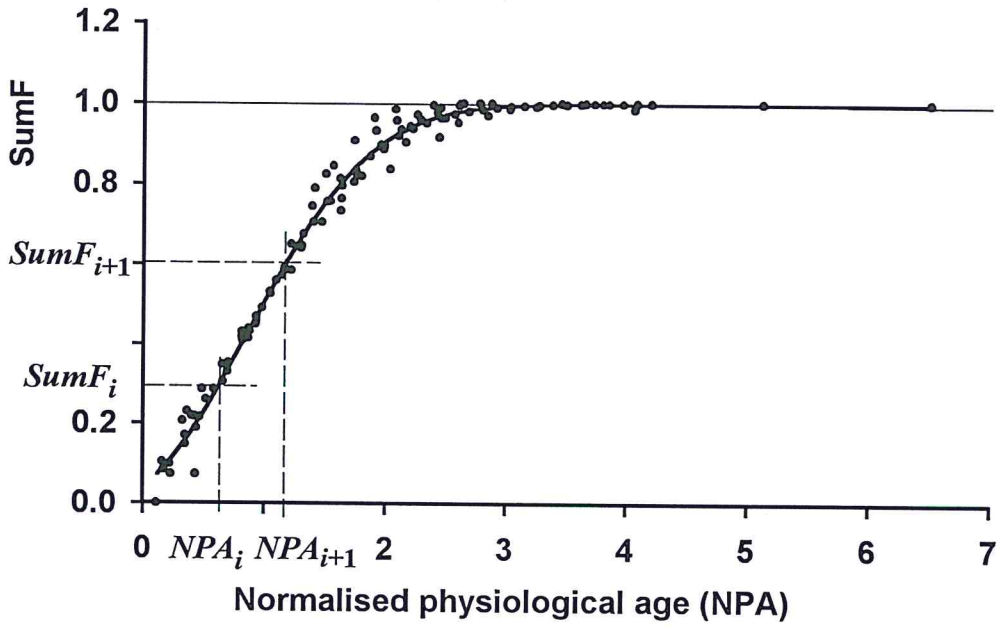


Fig. 5-2 Proportion of cumulative fecundity on normalised physiological age scale in the lifetime fecundity of *M. dirhodum*. Data points are calculated from Zhou and Carter (1992), Dean (1974a) and Hu and Gui (1985), the line represents model 5.10.

5.2.2 Application of the reproduction model in the simulation model

Before equation 5.10 and equation 5.11 can be used in the simulation model, the normalised physiological age (NPA_i) of the adults has to be calculated to fit the field conditions (equation 5.9). The physiological age of adults in a cohort ($AgeA_i$) can be obtained by equation 4.11. However, B_{50}, the physiological age at which 50% of reproduction is finished, was not a constant at different temperatures. It decreases as the temperature increases. B_{50} can be calculated from the daily average temperature with a linear regression model (equation 5.12). The data from in Zhou and Carter (1992) are used in the regression.

$$B50 = 0.859 - 0.022TX \qquad R^2 = 0.961 \tag{5.12}$$

6 Sub-model of survival

In order to handle the calculation conveniently, the survival rate is divided into two categories according to the action mode of ecological factors. The first ($SL1$ for larvae or $SA1$ for adults) is the basic survival rate at the normal conditions (temperature 10°C to 20°C in the growing season). The second ($SL2$ for larvae or $SA2$ for adults) is the occasional survival rate caused by unfavourable factors that appear occasionally such as extreme high daily maximum temperatures. The number of aphids killed by predators ($SyrphidP$) is not included in both survival rates but is calculated separately with a predation model. The survival rates of larvae (SL) and adults (SA) can be expressed as the products of the basic survival rates and the occasional survival rate (equation 6.1).

$$\begin{aligned} SL &= SL1 \cdot SL2 \\ SA &= SA1 \cdot SA2 \end{aligned} \qquad (6.1)$$

Since only the effect of high temperature is incorporated in the occasional survival rate in this study, $SL2$ and $SA2$ are equal to the survival rate at high daily maximum temperatures (Sur_HT). The detailed calculation of $SL1$, $SA1$ and Sur_HT will be described later in this chapter.

6.1 Basic survival rate of larvae

Since the larvae develop from one instar to the next instar (or stage), the mortality of the larvae usually is assessed by dividing the total number of dead larvae during the whole duration of the stage by the total number of larvae at the beginning of the stage. However, the daily survival rate ($SL1$) is more useful for simulating the daily population density of the aphids. Equation 6.2 is derived to transform the mortality of a larval stage into the daily survival rate.

$$\begin{aligned} MpL &= MBasic \cdot DpL \\ SL1 &= 1 - MpL / (1 + MpL - MorL_i) \end{aligned} \qquad (6.2)$$

In the model, $MorL_i$ is the cumulative mortality from the first day of the stage to day i. For a specific cohort, $MorL_i$ can be calculated by the compartment model. MpL is the allocation proportion of the basic mortality ($MBasic$) of a stage to one day. It is assumed that the distribution of total mortality over physiological age is

homogeneous. DpL is the daily age increment of aphids and can be calculated from the reciprocal of duration of development (equation 4.10).

$MBasic$ is the basic mortality that is only affected by average temperature and plant growth stage. Similar to the reproduction model, the survival rate of larvae at different temperatures (SLT) can be used as basic data in the calculation of $MBasic$ (equation 6.3). The effect of the plant growth stage (GS) is considered as a correction coefficient (SL_GS).

$$MBasic = 1 - (SLT \cdot SL\_GS) \tag{6.3}$$

According to Dean (1974a), the mortality of the larvae was around 10%, when larvae developed at 10°C to 20°C. When the temperature was higher than 25°C, the mortality reached nearly 20%. All individuals died at 30°C. 10% is adopted as the mortality of the aphids between 10°C and 25°C in this model (thus SLT = 100%-10%) In case of the daily average temperature over 25°C and below 30°C, SLT is determined by linear interpolation. Since 70% of the total duration of development of the larvae is allocated to the 1st to 3rd instar (L13) and 30% to the 4th instar (L4) (Zhou & Carter 1992), the total mortality during the larval stage is allocated to the first three instars and the 4th instar 70% and 30%, respectively.

The results from Watt (1979) show that the survival rate of *M. dirhodum* is high (0.87) until the middle of milky-ripe stage (<GS 73), but decreases (0.23) during the milky-ripe stage (GS 73-GS 85). All aphids are dead after soft dough ripe (>GS 85). Since the effect of plant growth stage on the survival rate is a continues process, a logistic model can be used to calculate the larval survival rate under the influences of the host growth stage:

$$SL\_GS = \frac{1}{1 + \left(\frac{GS}{SL_{50}}\right)^{a}} \tag{6.4}$$

SL_{50} is the GS at which the survival rate of larvae is reduced to 50%. a is the gradient to determine the decreasing speed of SL_GS as GS increases. The available data are not sufficient to accurately estimate the parameters of the model. According to the

limited data from Watt (1979), SL_{50} and a were determined as 77.5 and 130, respectively.

6.2 Basic mortality of adults caused by ageing

Ageing of the adults, which is dominated by temperature and influenced by the plant growth stage and aphid morph, is similar to the development of the larvae. The mortality caused by ageing ($AgeingMorP$) can be treated as the basic mortality of adults. Thus, the basic survival rate of adult ($SA1$) in equation 6.1 can be expressed as follows:

$$SA1 = 1 - AgeingMorP \tag{6.5}$$

The ageing of adults can be quantified by the physiological age of the adults that is derived from longevity. As the effects of basic factors such as average temperature and plant growth stage etc. on the mortality have been incorporated in the calculation of longevity, the mortality of adult can be expressed as a function of the physiological age. The survival data from the life table (Hu & Gui 1985) and survival curves (Zhou & Carter 1992, Dean 1974a) of *M. dirhodum* are used for the development of the model. A similar method, like modelling the reproduction distribution over the adult lifetime (chapter 5.2.1) is used to build the adult mortality model.

The cumulative mortality of adults up to day i, $SumM_i$ can be calculated based on the daily mortality ($Mortality_j$) from the three publications cited above:

$$SumM_i = \sum_{j=1}^{i} Mortality_j \qquad i = 1, 2, \ldots \ldots N \tag{6.6}$$

in which N is adult age in days at which all adults died.

The physiological age of adults ($AgeA_i$) can be calculated by accumulating the reciprocal of the longevity (equation 4.10) and then normalised by following equation:

$$NPA_i = AgeA_i / M50 \tag{6.7}$$

where $M50$ is the physiological age at which 50% adults died already.

From equation 6.6 and 6.7, the scattered dots in Fig. 6-1 are calculated. The relationship between the cumulative mortality of adults and the normalised physiological age can be described with a Weibull function:

$$SumM_i = 1 - e^{-\left(\frac{NPA_i - \gamma}{\eta}\right)^{\beta}} \qquad (6.8)$$

in which γ, η and β are regression parameters that are estimated as γ = -0.9748, η = 2.057 and β = 6.7266 using the data (scattered dots) in Fig. 6-1. Equation 6.8 accurately described the mortality of adults caused by ageing over the normalised physiological age (corrected R^2 = 0.9394; F=1955.7>$F_{0.01}$=3.9; df =3, 160).

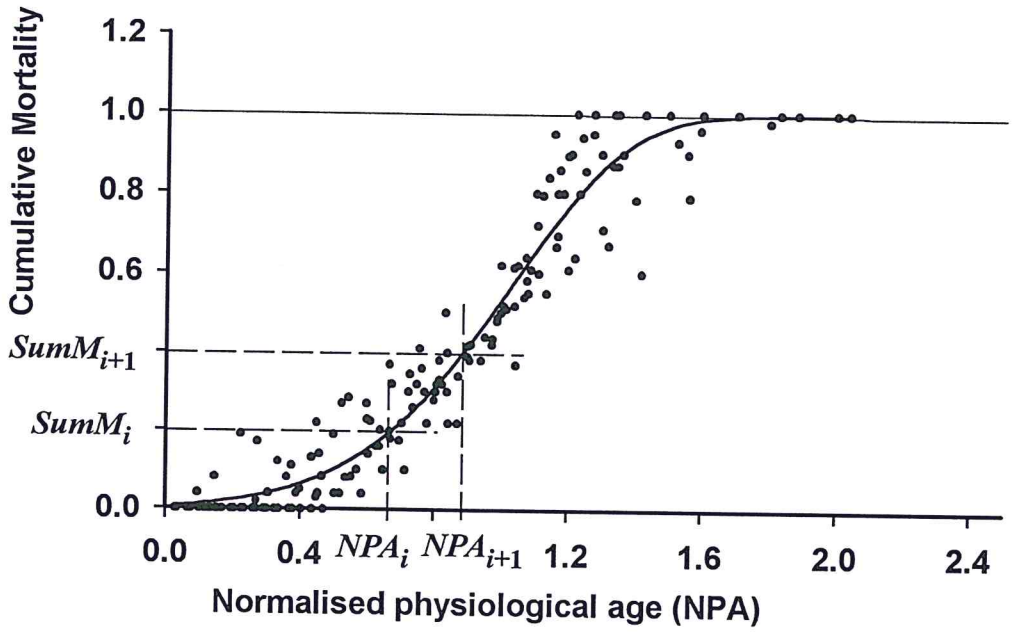


Fig. 6-1. Cumulative mortality of adults in relation to the normalised physiological age. Dots represent cumulative mortality of adults calculated from the experimental data of Dean (1974a), Hu and Gui (1985) and Zhou and Carter (1992). The line in the graph of the cumulative mortality is calculated from equation 6.8.

Fig. 6-1 demonstrates that the mortality of adult $AgeingMorP$ between NPA_i and NPA_{i+1} can be expressed as the difference between the cumulative mortality up to NPA_i and that up to NPA_{i+1} (equation 6.9).

$$AgeingMorP = SumM_{i+1} - SumM_i \qquad (6.9)$$

Prior to applying equation 6.8 and equation 6.9 in the simulation model, the normalised physiological ages of the adults (NPA_i) have to be calculated. The method described in chapter 5.2.2 is adopted here to calculate NPA_i.

6.3 Mortality caused by high temperature

The survival rates of the different stages of the aphids are significantly influenced by high temperature and exposure time (Chapter 3.2.3), and thus it can be determined by integrating the effects of the two factors. Prior to build the model, the tested high temperatures (T) and the exposure times ($Expose$) in Table 3-6 were transformed into two independent variables, MT (represent the current high temperature) and HT (the effective accumulation of high temperatures experienced by the aphids), by following equations:

$$\begin{aligned} MT &= T - 26 \\ HT &= MT \cdot Expose \end{aligned} \qquad (6.10)$$

In equation 6.10, 27°C is assumed the threshold temperature at or over which the survival of the aphids is negatively influenced. To avoid the effective high temperature MT being zero, 27-1 = 26°C is used in the data transformation.

The survival rates fluctuate between zero and one. Two logistic models can be used to describe the survival rate influenced by MT and HT separately. To integrate the effects of MT and HT, the survival rates are expressed as combined logistic model:

$$Sur\_HT = \frac{a_0}{1+\left(\frac{MT}{MT_0}\right)^b} \cdot \frac{a_0}{1+\left(\frac{HT}{HT_0}\right)^c} \qquad (6.11)$$

in which a_0 is the maximum survival rate. MT_0 and HT_0 represent the critical point of MT and HT at which the survival rate is reduced to 50%. b and c are the gradients that determine the decreasing speed of the survival rate as MT and HT increases. Parameters in the model of the different developmental stages were estimated using the transformed data from Table 3-6. Equation 6.11 was highly significant for all development stages (Table 6-1). The model accurately predicted the survival rates of different stages of the aphids at different high temperatures (Fig. 6-2).

Table 6-1 Parameters and the statistical evaluation of the survival model (equation 6.11)

Stage	n	a_0	MT_0	b	HT_0	c	F	R^2 [a]
Ad [b]	12	0.911	6.90	118.019	14.17	3.306	206.2 **	0.965
L4	14	0.967	8.10	4.461	19.36	3.095	175.4 **	0.906
L23	12	1.006	9.04	2.276	30.20	3.317	155.8**	0.844

[a], corrected R^2; [b], Ad = adults, L4 = 4th instar, and L23 = average of L2 and L3; models are significant at $P< 0.01$.

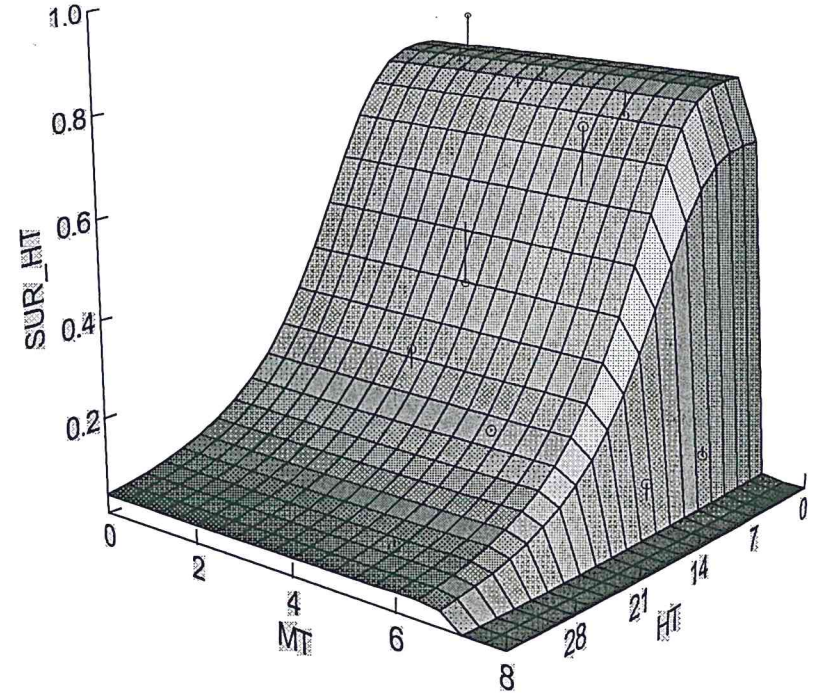
Before equation 6.11 can be applied in the calculation of survival rates in field conditions, values of MT_i and HT_i have to be determined as follows:

$$MT_i = MaxT_{i-2} - 26 \qquad \text{for } MaxT_{i-2} \geq 27°C$$

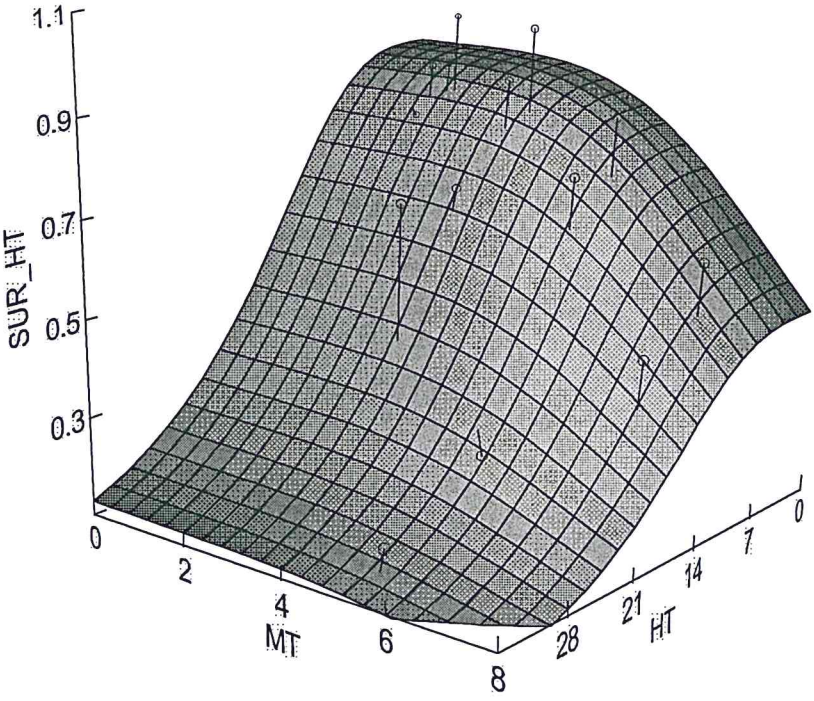
$$MT_i = 0 \qquad \text{for } MaxT_{i-2} < 27°C \qquad (6.12)$$

$$HT_i = \sum_{k=1}^{i-2} MT_k$$

$MaxT_k$ represents the maximum temperature on day k; i is the age of an aphid stage in days up to the current simulation day; MT_i is the transformed high temperature two days ago (since the effect of high temperature on survival is displayed two days later); and HT_i is the transformed accumulative high temperature experienced by the aphids.



Adults



L4

Fig. 6-2 The relationship between the survival rates of adults (top) and 4th larval instar (bottom) of *M. dirhodum* and transformed high temperatures (*MT*) and accumulative high temperatures (*HT*). The surfaces are graphs of equation 6.11. Small circles with line represent the observed data and the residues between observations and predictions.

6.4 Predation of syrphids on aphids

Since syrphids are the most important natural enemies of *M. dirhodum* in north Germany (Poehling 1988, Poehling & Borgemeister 1989, Tenhumberg 1993, Tenhumberg & Poehling 1994), the effect of syrphids is incorporated in the simulation model. The number of aphids killed by syrphids in a cohort of aphids (*SyrphidP*) can be expressed as a function of the number of syrphid larvae (*NumSyr*), daily aphid consumption per syrphid larva (*ComsumR*) and the proportion of aphids in the cohort (Num_i) to the total number of aphids (*TotNum*) on the plant (equation 6.13).

$$SyrphidP = \frac{Num_i}{TotNum} \cdot NumSyr \cdot ConsumR \cdot W \qquad (6.13)$$

W is the average aphid number per mg bio-mass of the mixed development stages and W = 5.62 is measured by Tenhumberg (1993). The number of aphids in the boxcar and the total density of aphids have been calculated from the compartment models. The number of syrphid larvae is treated as an input of the simulation model. The daily predation per syrphid larva is affected by several factors. The daily aphid consumption per syrphid larva at different constant temperatures (*ConsumRT*) is used as the basic predation rate in the calculation of *ConsumR*. The effects of aphid density (*AphidN*) and differences between field and laboratory tests (*F_Field*) are incorporated as correction coefficients. *ConsumR* is expressed as equation 6.14.

$$ConsumR = ConsumRT \cdot AphidN \cdot F\_Field \qquad (6.14)$$

6.4.1 Effect of temperature

Tenhumberg (1993) tested the aphid consumption of *Episyrphus balteatus* at different constant temperatures. The data in table 76 from Tenhumberg (1993) are used to establish a rough model of aphid consumption. The total prey consumption per larva (*ConsumRT*) at different temperatures (*TX*) can be calculated by a polynomial equation:

$$ConsumRT = -26.986 + 5.168TX - 0.148TX^2 \qquad (6.15)$$

No data are available to estimate the effects of the temperatures that are lower than 14°C or higher than 22°C on the aphid consumption. If the daily average

temperature is out of the tested temperature range, it is assumed that *ConsumRT* changed according to the model extrapolation (Fig. 6-3).

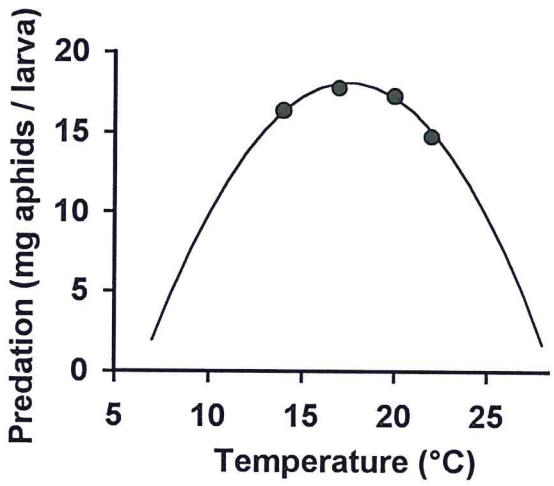


Fig. 6-3 Daily consumption of prey in bio-mass of aphids per syrphid larva at different temperatures. The dots represent the observed predation from Tenhumberg (1993) and the line is the predicted daily predation from model 6.15.

6.4.2 Effect of aphid density

Tenhumberg (1993) developed a model to describe aphid consumption (V) of *Episyrphus balteatus* at different potential prey densities (the number of aphids per syrphids):

$$V = \frac{k \cdot (TotNum / NumSyr)^2}{(TotNum / NumSyr)^2 + D^2} \qquad (6.16)$$

in which k and D are estimated as 396 and 246, respectively.

ConsumR in equation 6.14 was obtained under a sufficient aphid supply. The correction coefficient actually is the relative proportion between the voracity of syrphids under insufficient aphid supply to that under sufficient aphid supply. The voracity of syrphids under sufficient aphid supply in the field cage was 396 (Tenhumberg 1993). Therefore, the correction coefficient, *AphidN* can be derived from equation 6.17. When the potential aphid density is greater than 650, *AphidN* was assumed 1.0. When total number of aphids per tiller is very low, the syrphid larvae cannot find enough aphids from one plant, and they might move to other plants to search aphids. Detailed data on the predation of syrphids at a very low

aphid density per plant are not available. The voracity of syrphid larvae is assumed very low, if the total number of aphids per plant is less than 3.

$$AphidN = 0.001 \quad \text{for } TotNum < 3$$

$$AphidN = 1 \quad \text{for } TotNum/NumSyr > 650 \qquad (6.17)$$

$$AphidN = \frac{k \cdot (TotNum / NumSyr)^2}{(TotNum / NumSyr)^2 + D^2} \quad \text{for } TotNum \geq 3,\ TotNum / NumSyr \leq 650$$

6.4.3 Differences of aphid consumption between field and laboratory

Tenhumberg (1993) estimated the maximum aphid consumption in the field cage as 396, whereas in laboratory it was about 1032 aphids per *Episyrphus balteatus* larva. *M. dirhodum* is not the only aphid species in the field, and the proportion of *M. dirhodum* in total number of the three species of cereal aphids varies from field to field. In most cases, however, about 70% of the aphids belong to *M. dirhodum* (Niehoff 1996). Therefore, F_Field is supposed to be:

$F\_Field = 0.7 \times 396/1032 = 0.2686$

7 Compartment model and running the simulation model

Compartment models were built as the framework for simulating the population dynamics of *M. dirhodum*. The compartment models transfer calculation results from the sub-models for development, reproduction, survival, morph determination and alate adults settlement as model inputs, implement the simulation calculation and finally produce the simulation results. The structure and dynamic expression of these compartment models will be presented in this chapter.

Aphids at different developmental stages undergo different biological processes (Fig. 2-1). Survival and reproduction curves from Dean (1974a) and Zhou and Carter (1992) indicate that aphids of the same development stage (adult) but of different ages have different reproduction and mortality rates. A population usually consists of individuals of different ages. In order to obtain realistic simulations, the effect of the aphid age on the rate of reproduction and mortality has to be incorporated in a simulation model for aphids. The principle of the boxcar model, developed by de Wit and Goudriaan (1978) and first applied in aphid simulation by Carter et al. (1982), is used to construct the compartment models that enable a separate computing of the population changes of aphids of different age classes.

In this type of model, to consider the dynamic changes of age classes of aphids by stepwise computing, each compartment contains certain number of boxcars. Newly born aphids are always placed in the first boxcar, and individuals of the same age remain together and are members of the same boxcar. It is assumed that individuals born on the same day have the same age. It is further assumed that the individuals of the same age and under the same ecological conditions have the same reproduction and survival rate. The individuals in one boxcar are moved to the next during a simulation step (in this study defined as one day). When aphids in a particular boxcar have finished the development of the stage, they are transferred to the first boxcar of the next compartment. The transition of aphids between boxcars and compartments is driven by reproduction, growth and development of the aphids.

The total number of boxcars needed per compartment depends on the simulation interval and the maximum duration of the developmental stage. The maximum duration of development of any larval instar of *M. dirhodum* is about five days at 10°C, and the maximum average longevity of adults is about 21 days at 10°C (Zhou &

Carter 1992). Weather data from Göttingen and Hanover in 1991 to 1996 indicate that average temperatures during the growing seasons are higher than 10°C in northern Germany. However, the duration of development and longevity of *M. dirhodum* under fluctuating temperatures may be longer than that under constant temperatures (see chapter 4.2.5) in growth chambers (Zhou & Carter 1992). Therefore, 20 and 40 boxcars were set up for larvae and adults, respectively.

The status of a boxcar is described with state variables. The changes of the state variables for each boxcar in each simulation step can be calculated from rate variables of various biological processes. The method to calculate the values of state variables will be described in this chapter.

7.1 Compartment model of larvae

7.1.1 Variables used in the compartment model of larvae

The status of a boxcar is defined by four state variables. The changes in development and survival during each simulation step can be represented with four rate variables. In addition, two auxiliary variables are used to transform the mortality in the whole stage into the daily survival rate. The biological meanings of variables are explained in Table 7-1.

Table 7-1 Fundamental state and rate variables of a boxcar in larvae compartment

State variables	
$NumL_i$	Number of larvae in a boxcar
$AgeL_i$	Physiological age of larvae in a boxcar
$ErrL_i$	Standard error of the larva's physiological age in a boxcar
TL_i	Weighted mean of temperatures experienced by the larvae
Rate variables	
DpL	Age increment during one simulation step
$SigL$	Updated standard error of age during one simulation step
PL	Transition rate from a stage into next stage during one simulation step
SL	Survival rate during one simulation step
Auxiliary variables	
$MorL_i$	Cumulative mortality of the larvae in a boxcar
MpL	Proportion of the mortality in a stage allocated to one simulation step

In order to simplify the expressions of the models, i is used to represent the serial number of the simulation step, i = 1, 2, ... 20.

7.1.2 Updating calculations for state variables in a boxcar

When new nymphs are produced, the four state variables can be calculated on the bases of their values at previous simulation step:

$$\begin{aligned} NumL_{i+1} &= NumL_i \cdot (1-PL) \cdot SL - SyrphidP \\ AgeL_{i+1} &= AgeL_i + DpL \\ ErrL_{i+1} &= (ErrL_i \cdot AgeL_i + SigL \cdot DpL)/(AgeL_i + DpL) \\ TL_{i+1} &= (TL_i \cdot AgeL_i + TX \cdot DpL)/(AgeL_i + DpL) \end{aligned} \qquad (7.1)$$

The number of larvae on day i+1 ($NumL_{i+1}$) is obtained by subtracting the number of larvae killed by natural enemies ($SyrphidP$) from the product of the number of larvae on day i ($NumL_i$), survival rate (SL) and remaining rate (1-PL). The age of the aphid larvae on day i+1 ($AgeL_{i+1}$) is derived by adding age increment from day i to i+1 (DpL) to the age at day i ($AgeL_i$). The standard error of the age up to day i+1 ($ErrL_{i+1}$) is the weighted mean of the standard error. It is updated by computing the weighted mean of the standard error up to day i ($ErrL_i$) and the standard error at day i+1 ($SigL$). The average temperature experienced by the aphid larvae up to day i+1 (TL_{i+1}) is updated by computing the weighted mean of the daily average temperature up to day i (TL_i) and the temperature at day i+1 (TX).

The number of aphids in each boxcar ($NumL_i$) is the most important state for the compartment. The age ($AgeL_i$) and its standard error ($ErrL_i$) are used to calculate the probability of age specific transition from one compartment to the next (equation 4.15). The weighted average temperature (TL_i) is used to calculate the mean temperature experienced by adults (TA_i) in the compartment model of adults. These rate variables are the communicators between the compartment model and the different sub-models e.g. on development and survival.

In publications (Dean 1974a, Zhou & Carter 1992), the aphid mortality is usually calculated by dividing the number of dead aphids during the whole development stage by the number of aphids at the beginning of the stage. In simulation model, however, mortality is calculated by dividing the number of dead aphids in a simulation interval (one day in this study) by the number of aphids at the beginning of the

simulation step. The cumulative mortality ($MorL_{i+1}$) and the mortality during a simulation step (MpL) are mortality values based on the aphid number at the beginning of the stage. Both $MorL_{i+1}$ and MpL are used to calculate the survival rate in each simulation step (equation 6.2). For each boxcar, $MorL_{i+1}$ is expressed as the accumulation of MpL :

$$MorL_{i+1} = MorL_i + MpL \tag{7.2}$$

Another important output of a boxcar is the number of nymphs ($NewD_{i+1}$) transferred from the current boxcar to the first boxcar of the next compartment. It can be expressed as the product of the transition rate (PL) and the aphid number in the boxcar ($NumL_{i+1}$):

$$NewD_{i+1} = NumL_{i+1} \cdot PL \tag{7.3}$$

Since the models in equation 7.1 are dynamic models, initial values of the five state variables are needed to start the simulation. The initial values can be set as follows:

$NumL_1 = NewAptL + NewAlaL$ (for compartment of 1st to 3rd instar)

$NumL_1 = NewDev$ (for compartment of 4th instar)

$$\begin{aligned} AgeL_1 &= DpL \\ ErrL_1 &= SigL \\ TL_1 &= TX \end{aligned} \tag{7.4}$$

The number of first instar larvae in the first boxcar is equal to the number of newly born larvae by apterous and alate adults ($NewAptL$ and $NewAlaL$). The total number of newly developed larvae ($NewDev$) from last previous developmental stage is calculated from the compartment model of the previous stage. TX is the average temperature on the first simulation day. It can be read from the weather database.

The rate variables used in equation 7.1 to 7.4 can be computed from the sub-models for various biological processes. The age increment and its standard error can be calculated from duration of development ($Duration$) and its standard error ($StdError$) using $DpL = 1/Duration$ and $SigL = StdError / Duration$. $Duration$ and $StdError$ are obtained from sub-models of development (equation 4.1). The developmental transition rate (PL) is calculated from the transition sub-model in chapter 4.4

(equation 4.13). The survival rate (*SL*) and the mortality rate (*MpL*) can be computed using the sub-model of survival (equation 6.1 and 6.2). The aphid number predated by syrphids (*SyrphidP*) is obtained from a predation model (equation 6.13). The total number of newly born larvae (*NewAptL* and *NewAlaL*) can be calculated from the compartment model of adults.

7.1.3 Outputs of the compartment model of larvae

When calculations in boxcars are finished, three useful outputs can be obtained by summing up items of each boxcar in the same compartment. The most important output for the simulation is the total number of aphids in the compartment (*TotalL*). Total number of newly developed aphids from one stage to the next stage (*NewDev*) is used as the initial population density of the next compartment. The weighted mean temperature that aphids experienced (*NewLT*) can be used as the initial mean temperature for the next compartment. The calculation formulas of these output variables are expressed as equation 7.5.

$$
\begin{aligned}
TotalL &= \sum_{i=1}^{20} NumL_i \\
NewDev &= \sum_{i=1}^{20} NewD_i \\
NewLT &= \frac{1}{NewDev} \cdot \sum_{i=1}^{20} (NewD_i \cdot TL_i)
\end{aligned}
\qquad (7.5)
$$

7. 2 Compartment models of adults

7.2.1 Variables used in the compartment model of adults

In contrast to the larval stage, all individuals in the adult stage do not develop forward into a new stage. Adults produce the new larvae of 1st instar. Alate adults can emigrate. The reproduction, ageing and morph determination are the essential biological processes for adults. Consequently, the compartment model for adults is slightly different from the model for larvae.

Three state variables are defined to describe the status of a boxcar of adult compartments. "*i*" is the serial number of the boxcar in adult compartment (*i* = 1, 2, ...40). Two rate variables are used to calculate the state variables for each boxcar of

adults in each simulation step. The biological meaning of the variables is shown in Table 7-2.

Table 7-2 Fundamental state and rate variables of a boxcar in the adult compartment

State variables	
$NumA_i$	Number of adults in a boxcar
$AgeA_i$	Physiological age of adults in a boxcar
TA_i	Weighted mean temperature that adults experienced
Rate variables	
DpA	Age increment of adults during one simulation step
SA	Survival rate of adults during one simulation step

7.2.2 Updating calculations for state variables

In the adult compartment, state variables of a boxcar can be calculated on the bases of the values of the previous simulation step (equation 7.6).

$$\begin{aligned} NumA_{i+1.} &= NumA_i \cdot SA - SyrphidP \\ AgeA_{i+1} &= AgeA_i + DpA \\ TA_{i+1} &= (TA_i \cdot (a + b \cdot AgeA_i) + b \cdot TX \cdot DpA)/(a + b \cdot AgeA_{i+1}) \end{aligned} \qquad (7.6)$$

The number of the adult aphids on day i+1 ($NumA_{i+1}$) is calculated by subtracting the number of adults killed by natural enemies ($SyrphidP$) from the product of the number of the adults on day i ($NumA_i$) and the survival rate (SA). The age of the adults on day i+1 ($AgeA_{i+1}$) is obtained by summing up the age at day i ($AgeA_i$) and the age increment from day i to i+1 (DpA). The average temperature that the adults experienced since they were born up to day i+1 (TA_{i+1}) is updated by calculating the weighted mean of daily average temperature up to day i (TA_i) and the temperature at day i+1 (TX). The duration of larva stage is about 40.4% (a = 0.404) and the longevity of adults is about 59.6% (b = 0.596) of the whole surviving duration of *M. dirhodum* (calculated from Zhou & Carter 1992). TA_i is applied to compute the life fecundity in the fecundity sub-model (equation 5.2).

Similar to the compartment models of larvae, the models described in equation 7.6 are dynamic. To run the models, initial values of the three state variables are required. The number of aphids in the first boxcar of the adult compartment is the

number of newly developed adults (*NewDev*) from the compartment of 4th instar larvae. The initial value of TA_1 is set as the weighted average temperature that the aphids experienced in their larval stage since they were born (*NewLT*) and can be expressed as follows:

$$\begin{aligned} NumA_1 &= NewDev \\ AgeA_1 &= DpA \\ TA_1 &= NewLT \end{aligned} \tag{7.7}$$

The number of new larvae born by the adults in a boxcar during each simulation step ($NewBL_i$) can be computed by equation 7.8.

$$NewBL_i = NumA_i \cdot BirTot \cdot BirthAgeP \tag{7.8}$$

In the model, $NumA_i$ is the number of adults in a boxcar, *BirTot* is the updated potential of lifetime fecundity, and *BirthAgeP* is the proportion of *BirTot* allocated in each simulation step.

The variables used in equation 7.6 to 7.8 can be obtained from various sub-models. The weighted average temperature experienced by adults (*NewLT*) is calculated by equation 7.5. The age increment (*DpA*) is calculated from the model for ageing of adults (equation 4.10). The total lifetime fecundity (*BirTot*) and its daily distribution (*BirthAgeP*) are obtained from two separate sub-models (equation 5.1 and 5.11). The survival rate (*SA*) and the predation rate (*SyrphidP*) can be estimated from sub-models of survival (equation 6.1) and predation (equation 6.13), respectively.

7.2.3 Outputs of the compartment model of adults

Based on the values of state variables in each boxcar, three outputs of the adult compartment can be obtained by summing up the values of the state variables of each boxcar (equation 7.9).

$$\begin{aligned} TotalA &= \sum_{i=1}^{40} (NumA_i \cdot PSettle) \\ NewAptL &= \sum_{i=1}^{40} (NewBL_i \cdot (1 - PAlate)) \\ NewAlaL &= \sum_{i=1}^{40} (NewBL_i \cdot PAlate) \end{aligned} \tag{7.9}$$

Zero emigration of apterous adults is assumed in the model. The total number of adults in a compartment (*TotalA*) is the main output of the compartment. Two total numbers of newly born 1st instar larvae that are supposed to develop into apterous and alate adults respectively (*NewBAptL* and *NewBAlaL*) are determined and put in the first boxcar in the first compartment of larva.

In equation 7.9, the proportion of alate aphids (*PAlate*) can be calculated from a sub-model on morph determination that was originally developed by Carter et al. (1982) for *S. avenae* and was applied by Zhou et al. (1989) for *M. dirhodum* (equation 7.10). The value of *PAlate* is between 0 and 1. If *PAlate* is greater than 1, it is set to 1. If *PAlate* is less than 0, it is set to 0. *GS* is the plant growth stage in the decimal code (Zadoks et al. 1974).

$$PAlate = -27.189 + 2.603(TotalL + TotalA) + 0.847GS \qquad (7.10)$$

The emigration of alate adults is influenced by the plant growth stage (Howard & Dixon 1992). A logistic model can be used to describe the relationship between the probability of alate adults that settle on the original field (*PSettle*) and the plant growth stage:

$$PSettle = \frac{1}{1+\left(\frac{GS}{PS_{50}}\right)^{a}} \qquad (7.11)$$

in which, PS_{50} is the *GS* at which the settlement probability of alate adults decreases to 50%. a is the parameter to determine the decreasing speed of *PSettle*. Up to now, the available data are not sufficient to accurately estimate the parameters in the model. Based on the limited data from Howard and Dixon (1992), PS_{50} and a were determined as 73.3 and 45, respectively.

7.3 Running the simulation model

Compartment models presented in early part of this chapter and sub-models on development, reproduction and survival described in the previous three chapters, were assembled together in the simulation program according to the model structure (Fig. 2-1) and the program structure (Fig. 2-2) that were described in chapter 2. The simulation program has been thoroughly verified, i.e. it has been tested to see that

the computer program in fact operates on input data in the intended way (Loomis et al. 1979), by program debugging and detailed examinations of the program.

After the model verification, the program can be used to simulate the population dynamics of *M. dirhodum* under the field conditions. Validation is the process of comparing the model's predictions with reality. The field observed data from nine fields (Table 7-3) are used to validate the model.

Table 7-3 Source of field observation data of *M. dirhodum* used in the model validation

Observation Locations	Observation Year	Source
Göttingen	1991,1992, 1993	Niehoff (personal communication)
Hiddestorf	1991, 1992	Niehoff (personal communication)
Grossenwieden	1992	Niehoff (personal communication)
Ruthe, Hannover	1994, 1995, 1996	Lemke (personal communication)

These data included the seasonal population densities of the 1st to 3rd instar larvae, the 4th instar larvae, and the adults of *M. dirhodum*, the later two separated in apterous and alate. Since the observation interval was about 3 to 7 days, the daily values of the plant growth stage (*GS*) and syrphid density (*NE*) were estimated by linear interpolation. The weather data for Göttingen and Hanover from 1991 to 1993 were obtained from the German Weather Service. The weather data for Ruthe from 1994 to 1996 were got from the Weather Station in Ruthe.

To validate the model, the daily aphid population densities in each of the nine fields have to be simulated with the program. Before running the simulation model, the initial information must be put in. The population densities of apterous and alate adults, 4th instar larvae and 1st to 3rd instar larvae around *GS* 69 are used as the initial population densities, put in the first boxcar of each compartment. The data about the physiological age of the initial population are not available. It is assumed that the average physiological age of the initial population is "0.1". The days on which the simulation will start and end and the location of simulation are put in, according to the data sets in Table 7-3. The simulation program transfers the model inputs, i.e. daily average temperature (*TX*) and daily maximum temperature (*MaxT*) from the weather database and the plant growth stage (*GS*) and the number of syrphids (*NumSyr*) from insect database, to the simulation model. Simulations are run for the nine fields and

the simulated population densities are printed out in tables. The simulated results can be compared with the data observed in the fields.

8 Results of simulations

To validate the simulation model, a simple linear regression was used for analysing the relationship between the field observation and the model prediction. The model is $Y = a + bX$ where Y and X represent simulated and observed population densities respectively. Intercept a and slope b describe the constant and proportional differences between simulated and the observed densities. If a is not significantly different from zero, simulation accuracy and precision can be indicated by the slope b and the adjusted square of the correlation coefficient R^2. Here the simulation precision is defined as the similarity between the simulated and the observed curve shape of population dynamics. The accuracy refers to the similarity between the simulated and observed densities. The closer the values of b and R^2 to 1.0, the more accurate and precise the simulation is. The hypothesis test (assumed a = 0 and b = 1) is used to identify whether the differences between simulated and observed population densities are significant or not.

8.1 Overall comparison between simulated and observed aphid densities

The daily total number of aphids per tiller (*Sum*) was obtained by summing up the daily number of 1st to 3rd instar (L13), 4th instar larvae (L4) and adults (*Ad*). Nine data sets for the nine fields were merged into one data set that included two columns of data, i.e. simulated and observed daily total number of aphids (*SimSum* and *ObsSum* respectively). The relationship between *SimSum* and *ObsSum* of all nine fields is described by following equation:

$$SimSum = 0.356 + 1.059 ObsSum \qquad n = 77, \qquad R^2 = 0.927,\ P < 0.001 \qquad (8.1)$$

The high adjusted R^2 (0.927) indicates that simulations are rather precise. The hypothesis test illustrates that the intercept is not significantly different from zero (P = 0.773>0.05). The slope (1.059) is not significantly different from 1.0 (P = 0.089>0.05). The range of fluctuation for simulated aphid densities around the observed densities is about ±7% in the confidence interval of 95%. The regression and the hypothesis test revealed that simulations are generally rather accurate (Fig. 8-1A).

Since the damage caused by one 4th instar larva (L4) or adult is threefold by one 1st to 3rd instar larva (L13) according to the definition of aphid unit (Niehoff & Staeblein 1998), it is necessary not only to simulate the total number of aphids but also the numbers of aphids in different stages. To know the general validity of the model in simulating the stage structure of aphids, i.e. the relative proportion of L13, L4 and adults in the population, the simulated (*SimStage*) and observed (*ObsStage*) densities of every stage for all fields were pooled together. A linear regression was carried out to analyse the relationship between *SimStage* and *ObsStage* (equation 8.2).

$$SimStage = 0.274 + 1.041 ObsStage \quad n = 231, R^2 = 0.916, P < 0.001 \qquad (8.2)$$

The hypothesis test revealed that the intercept was not significantly different from zero (P = 0.405>0.05) and the slope was just not significantly different from one (P = 0.052>0.05). The fluctuation range of simulated density around the observed density was about ± 4.1% in the confidence of 95%. The model accurately simulated the stage structure of the aphid populations (Fig. 8-1B).

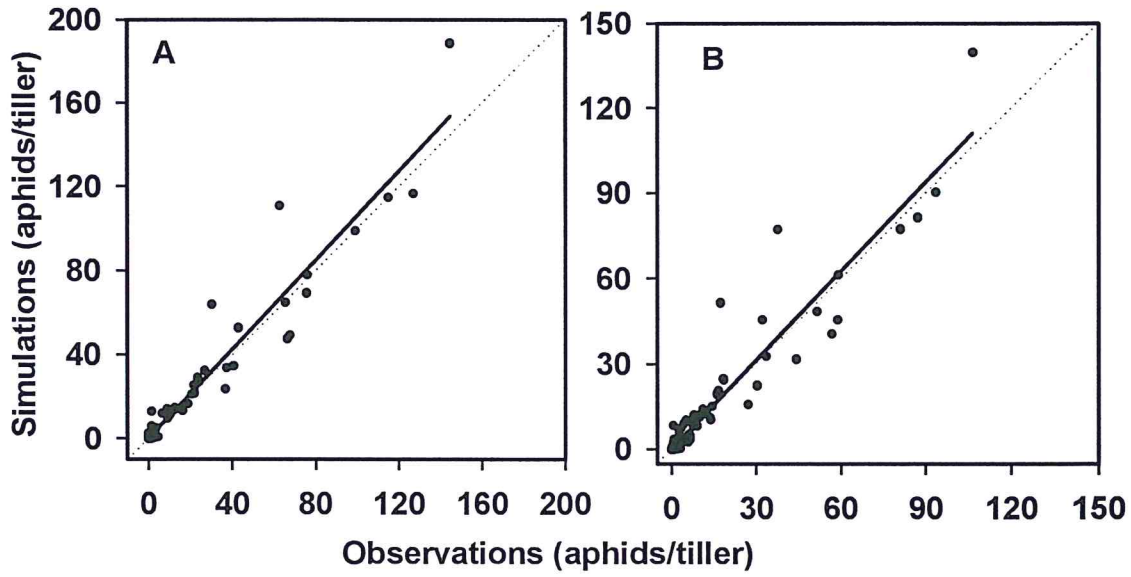


Fig. 8-1 Comparison between the simulated and the observed (**A**) daily total number of aphids per tiller and (**B**) the number of every stage of aphids for all nine fields together. Dots represent the simulated number of aphids per tiller vs. the observed one. Linear regression lines in chart **A** and **B** are based on equation 8.1 and 8.2 respectively.

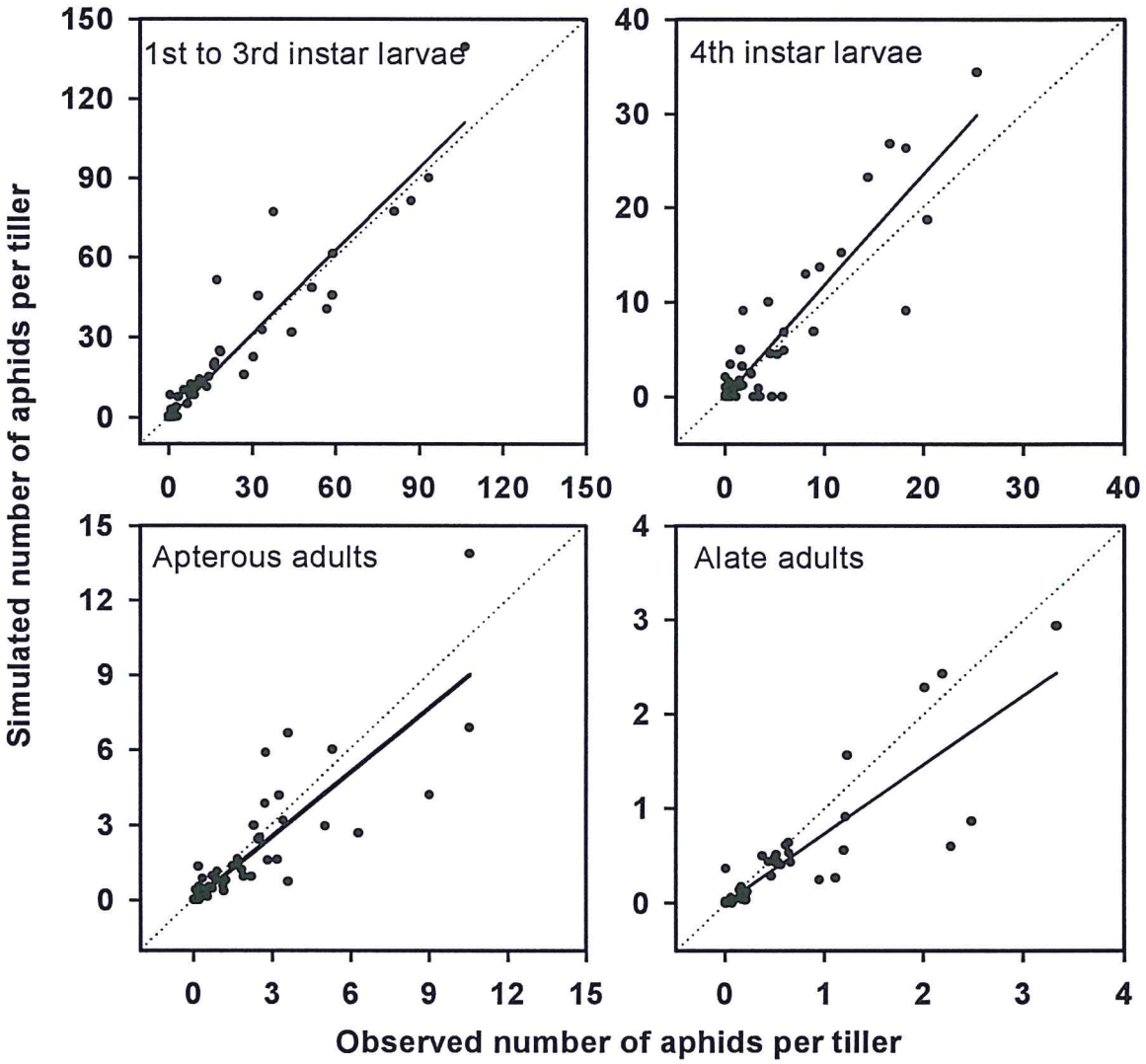


Fig. 8-2 Comparison between simulated and observed population densities of 1st to 3rd instar larvae, 4th instar larvae, apterous adults and alate adults for all nine fields. Dots represent the simulated number of each aphid stage per tiller vs. the observed one. Lines are based on linear regressions in Table 8-1.

To analyse the validity of the model in simulating the number of each developmental stage of the aphids, the predicted and the observed data were compared. The numbers of L13, L4, apterous adults and alate adults were pooled over the nine fields (separately for each stage). Relationships between simulations (Y) and observations (X) of each stage were again described by the linear regression model $Y = a + bX$. However, all intercepts a were not significantly different from zero. Forcing the regression line through the origin, the linear lines were expressed as $Y = bX$. The regression results are shown in Table 8-1. As the slope for L13 was not

significantly different from 1.0, the simulation model accurately predicted the densities of L13 (Fig. 8-2). However, the slope for the 4th instar larvae was significantly greater than 1.0. Slopes for apterous and alate adults were significantly lower than 1.0. Thus the model generally overestimated the density of 4th instar larvae and underestimated the densities of adults (Fig. 8-2).

Table 8-1 Linear regression between the simulated and the observed population densities of aphid stages (L13, L4, Apterae and Alatae) for all nine fields and hypothesis test of "slope = 1.0"

Stage	Linear regression (n = 77)				Hypothesis test (b=1)	
	R^2	F	$P<$	b±95% confidence	F	P
L13	0.926	946.6	0.001	1.047±0.068	1.9	0.172
L4	0.870	510.4	0.001	1.183±0.104	12.2	0.001
Apt	0.801	306.8	0.001	0.854±0.097	9.0	0.004
Ala	0.733	338.6	0.001	0.733±0.079	44.9	<0.001

8.2 Comparison of simulated and observed densities in each field

8.2.1 High population densities

In 1992, *M. dirhodum* reached high peak densities at Göttingen (127 aphids/tiller) Hiddestorf (66 aphids/tiller) and Grossenwieden (144 aphids/tiller). Fig. 8-3, 8-4 and 8-5 show that the model provided accurate simulations of the population development during the phases of building up, but the accuracy of the predictions at population breakdown was reduced at the later two locations.

Göttingen 1992

For the field sampled at Göttingen in 1992, the model accurately simulated the population increase during late June, the peak at the beginning of July and the collapse after July 6 (Fig. 8-3). The simulated and observed total number of aphids in each stage of *M. dirhodum* were very closely related (Table 8-2). The simulated population dynamics of L13 was very similar to the observed (R^2 = 0.986, b = 0.923) (Fig. 8-3). The simulated number of L4 was slightly higher than the observed (P = 0.04<0.05), especially after the peak at the beginning of July. The model precisely predicted the shape of the dynamics of the adults, but significantly underestimated the number of adults since the slope was significantly lower than 1.0 (P <0.001).

Table 8-2 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Göttingen 1992**.

Stage	Linear regression (n = 13)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.991	1281.9	0.001	0.946±0.058	4.2	0.063
L13	0.986	857.1	0.001	0.923±0.068	5.9	0.032
L4	0.893	99.7	0.001	1.291±0.281	5.1	0.044
Ad	0.933	167.7	0.001	0.618±0.104	64.1	<0.001

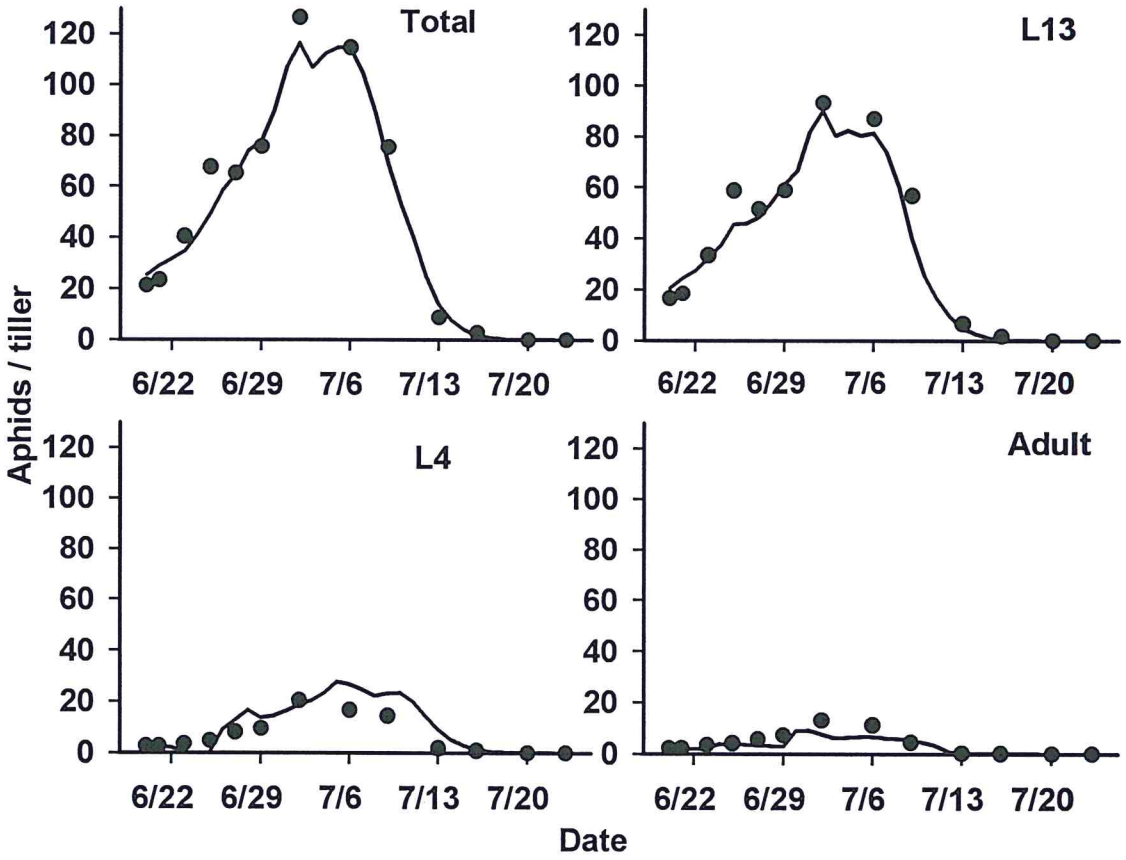


Fig. 8-3 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Göttingen 1992**

Grossenwieden 1992

The high adjusted R^2 in Table 8-3 for the field sampled at Grossenwieden in 1992 indicates that the simulated number of all stages of *M. dirhodum* per tiller and the numbers of L13, L4 or adults per tiller were highly correlated with those observed. With the model, the total population increase before the peak at the end of June was accurately predicted, but the population densities at the peak and after the peak were overestimated about 27% (Fig. 8-4). The simulated densities of L13 and L4 followed the same pattern as the total population densities. The slope (b = 1.119) of the regression line for adults was significantly higher but not far away from 1.0, indicating that the simulated adult number was close to the observed (Fig. 8-4).

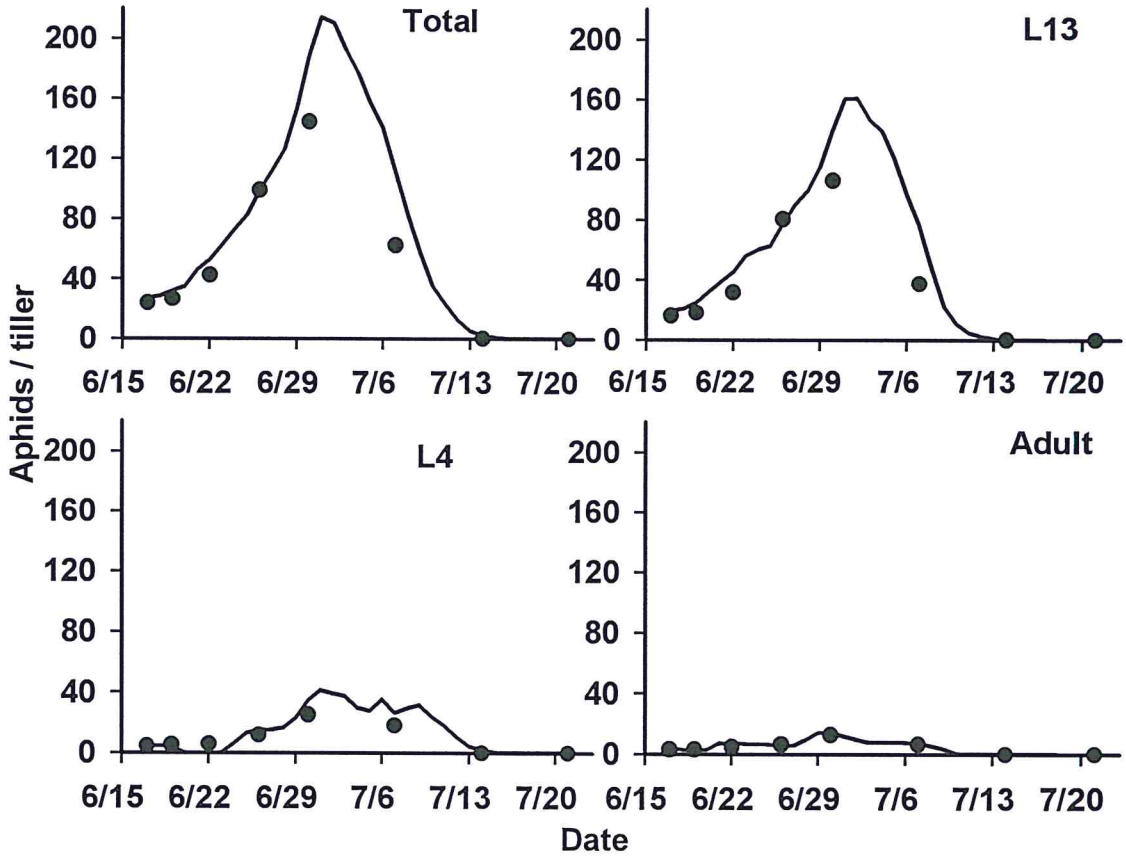


Fig. 8-4 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Grossenwieden 1992**.

Table 8-3 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Grossenwieden 1992**.

Stage	Linear regression (n = 8)				Hypothesis test	
	R^2	F	$P<$	b±95% confidence	F	P
Sum	0.972	239.8	0.001	1.265±0.193	10.5	0.014
L13	0.955	148.3	0.001	1.255±0.243	6.1	0.042
L4	0.964	188.2	0.001	1.320±0.228	11.1	0.013
Ad	0.987	548.5	0.001	1.119±0.113	6.2	0.042

Hiddestorf 1992

The situation at Hiddestorf in 1992 was similar to Grossenwieden in 1992. The simulation model rather accurately predicted the total population densities of *M. dirhodum* before the peak, but overestimated the densities during the population collapse (Fig. 8-5). The regression analysis indicated that the similarity of the shape of the simulated and observed dynamics of the total population densities was not that high (R^2 = 0.820). However, there was no significant difference between the slope of the regression equation and 1.0, which indicates that observation and simulation were not significantly different (P = 0.421>0.05). Although the simulation precision for L13 was not very high (R^2 = 0.71), the simulated number of L13 was not significantly different from the observed (P = 0.872>0.05) (Fig. 8-5). The model just significantly underestimated the number of L4 (P = 0.049 < 0.05). The simulated and the observed population dynamics of the adults were rather similar (R^2 = 0.88). The simulated number of adults was not significantly different from the observed, because the slope of regression was not significantly different from 1.0.

Table 8-4 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Hiddestorf 1992**.

Stage	Linear regression (n = 7)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.820	27.4	0.002	0.947±0.443	0.087	0.778
L13	0.707	14.5	0.009	0.958±0.617	0.028	0.872
L4	0.719	15.3	0.008	0.614±0.384	6.078	0.049
Ad	0.880	44.2	0.001	1.254±0.462	1.808	0.227

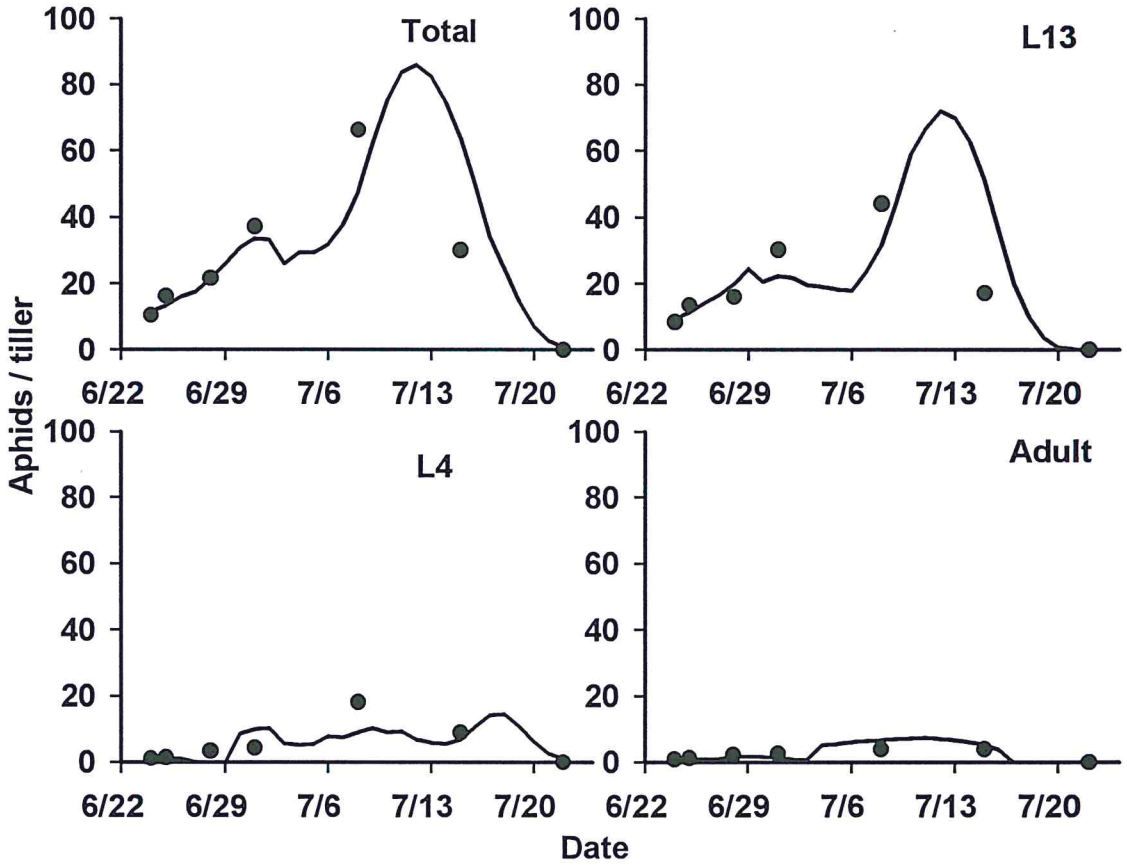


Fig. 8-5 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Hiddestorf 1992**.

Although the correlation coefficients between predictions and observations for the field sampled at Hiddestorf in 1992 were not as high as in the other two outbreak fields, the general accuracy of the simulation was acceptable for both total densities and for each stage of *M. dirhodum*.

The validation analyses for the three fields in 1992 indicate that the simulation model can be used to simulate the population dynamics of *M. dirhodum* in situations with high aphid densities.

8.2.2 Medium population densities

The patterns of population dynamics of *M. dirhodum* in the fields sampled at Göttingen in 1991 (Fig. 8-6) and at Ruthe in 1994 (Fig. 8-8) were similar. The peak densities in both fields were between 10 to 15 aphids per tiller. The peak density in the field sampled at Hiddestorf in 1991 was about 37 aphids/tiller, which was higher

than in the other two fields (Fig. 8-7). These three fields represented fields with a medium population size.

Göttingen 1991

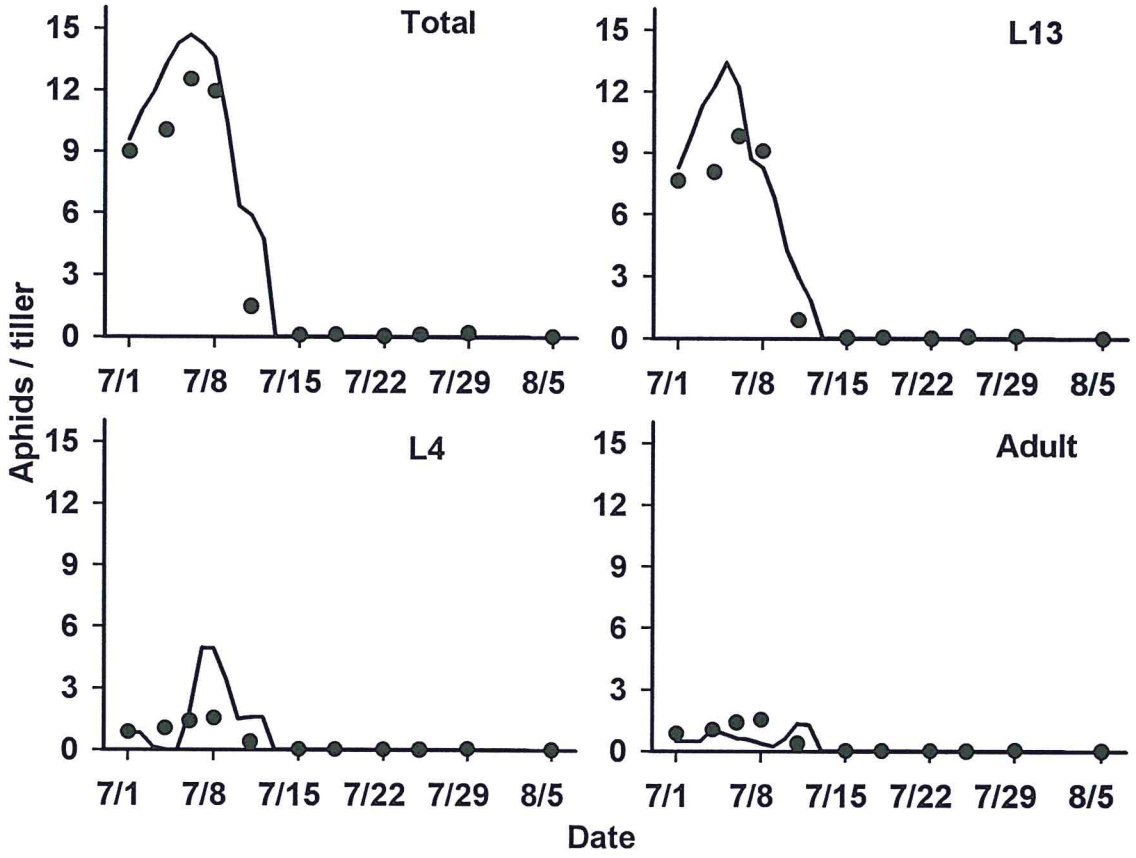


Fig. 8-6 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Göttingen 1991**.

For the field sampled at Göttingen in 1991, the model provided an accurate simulation of *M. dirhodum* population development, i.e. short increase during the first week of July, abrupt collapse in three days from July 8 to 10, and the extreme low level persistent from middle July to early August (Fig. 8-6). As already indicated, the simulated total densities of *M. dirhodum* are highly correlated with those observed (Table 8-5). The tendency of the simulated population dynamics was in accordance with that observed. The hypothesis test showed that the slope was significantly greater than 1.0. The simulation model overestimated the total number of *M. dirhodum* per tiller about 19%. For L13, the shape of the simulated dynamic curve

was similar to that observed (R^2 = 0.960), but the simulated number was higher than the observed. Although the precision of the simulation was not that high for L4 and the adults, the simulated densities of both stages were not significantly different from the observed one.

Table 8-5 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Göttingen 1991**.

Stage	Linear regression (n = 7)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.970	327.7	<0.001	1.189±0.146	8.3	0.016
L13	0.960	237.0	<0.001	1.188±0.172	6.0	0.035
L4	0.665	19.9	0.001	1.801±0.900	3.9	0.076
Ad	0.472	9.0	0.014	0.626±0.466	3.2	0.105

Hiddestorf 1991

The aphid population increase during early July and the population collapse after July 9 in the field sampled at Hiddestorf in 1991 were accurately predicted by the simulation model. The peak time was correctly simulated, but not the peak density (Fig. 8-7). The accuracy of the simulation was slightly reduced by the underestimation of the peak density, but it was still acceptable (Table 8-6). The slope of the linear regression equation (b = 0.804) was not significantly different from 1.0 (P = 0.121>0.05). In general, simulated and observed total numbers of *M. dirhodum* per plant were not significantly different. Although shapes of the simulated dynamics of L13 and L4 were slightly different from those observed, the model rather reasonably predicted the numbers of L13 and L4, since the slopes of the regression equations for L13 and L4 were not significantly different from 1.0. The number of adults was significantly underestimated by the model.

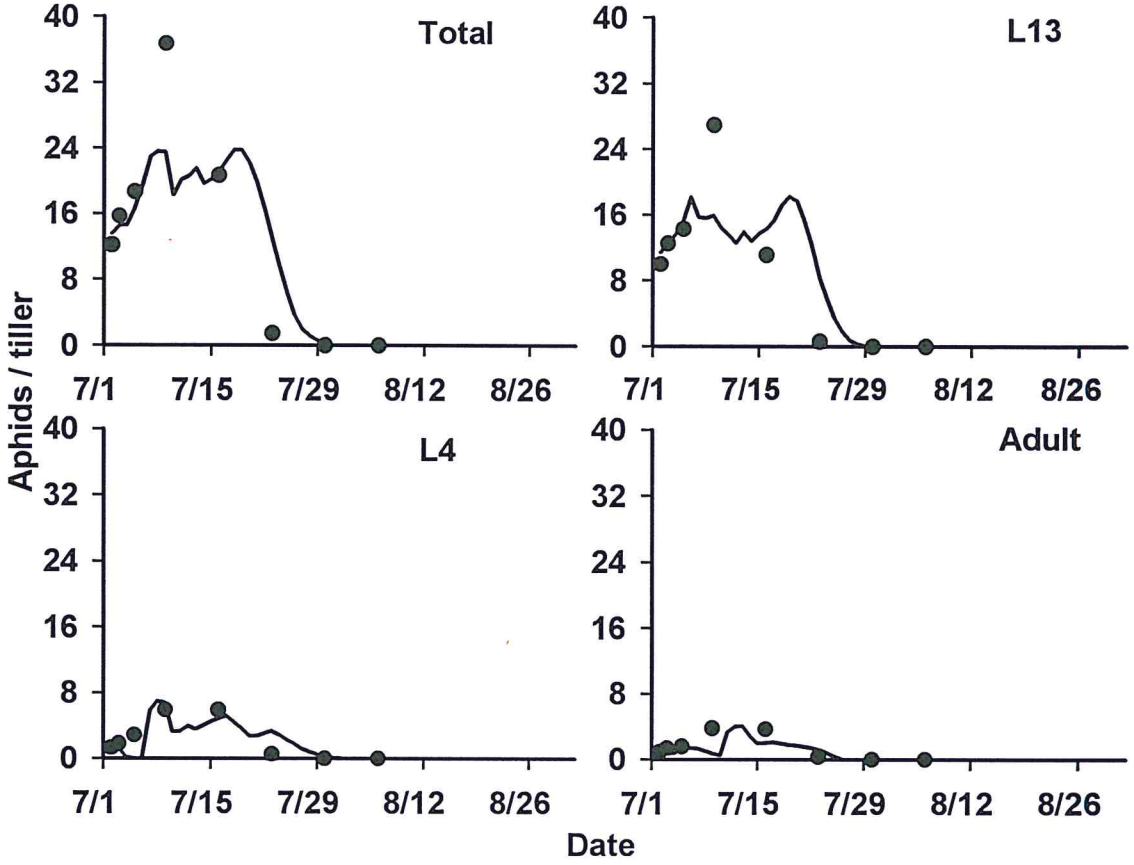


Fig. 8-7. Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Hiddestorf 1991**.

Table 8-6 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Hiddestorf 1991**.

Stage	Linear regression (n = 8)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.882	52.3	<0.001	0.804±0.263	3.1	0.121
L13	0.852	40.3	<0.001	0.826±0.308	1.8	0.222
L4	0.791	26.5	0.001	0.901±0.414	0.3	0.588
Ad	0.701	16.4	0.005	0.450±0.263	24.6	0.002

Ruthe 1994

For the field sampled at Ruthe in 1994, the model accurately predicted the population development, i.e. the abrupt increase during late June, the collapse during early July and the maintenance at extremely low densities for more than two weeks in middle and late July (Fig. 8-8). The slope was not significantly different

from 1.0 (P = 0.129>0.05). The model was able to accurately simulate the shape and densities of the aphid population. The model correctly simulated the dynamic tendency of L13, but significantly overestimated the peak density of L13. As the simulated and observed number of L4 was not related, the simulation model could not successfully simulate the number of L4. The precision of the simulation of adults was low (R^2 = 0.806) due to the underestimation of numbers of adults at the peak. The hypothesis test indicated that the slope is not significantly different from 1.0. Thus, the simulated numbers of adults were not significantly different from the observed (Table 8-7).

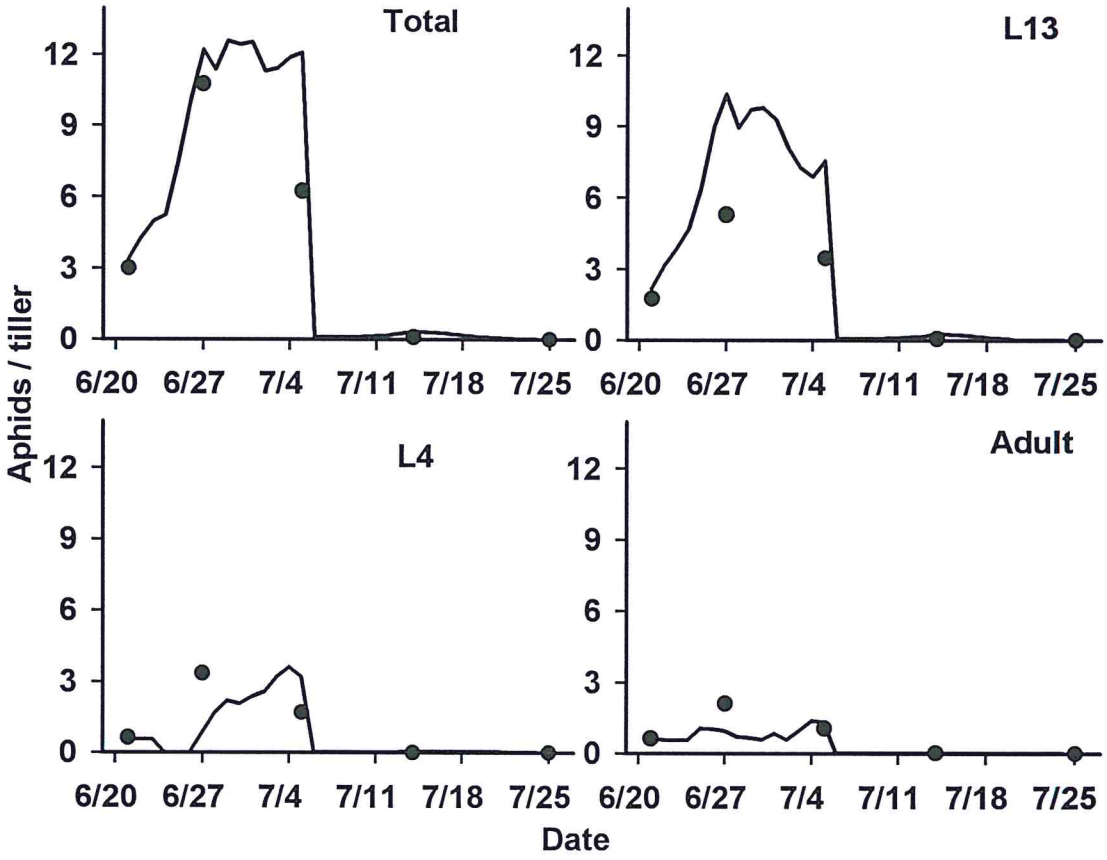


Fig. 8-8 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Ruthe 1994**.

Based on the analysis for the three fields described above, it can be concluded that the model is valid for simulating the population dynamics at a medium level of density such as at Göttingen 1991, Ruthe 1994 and Hiddestorf 1991.

Table 8-7 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Ruthe 1994**.

Stage	Linear regression (n = 8)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.938	60.5	0.001	1.325±0.473	3.6	0.129
L13	0.988	321.1	<0.001	1.966±0.305	77.5	0.001
L4	0.466	3.5	0.135	0.606±0.901	1.5	0.291
Ad	0.806	16.6	0.015	0.638±0.434	5.3	0.082

8.2.3 Low population densities

Göttingen 1993

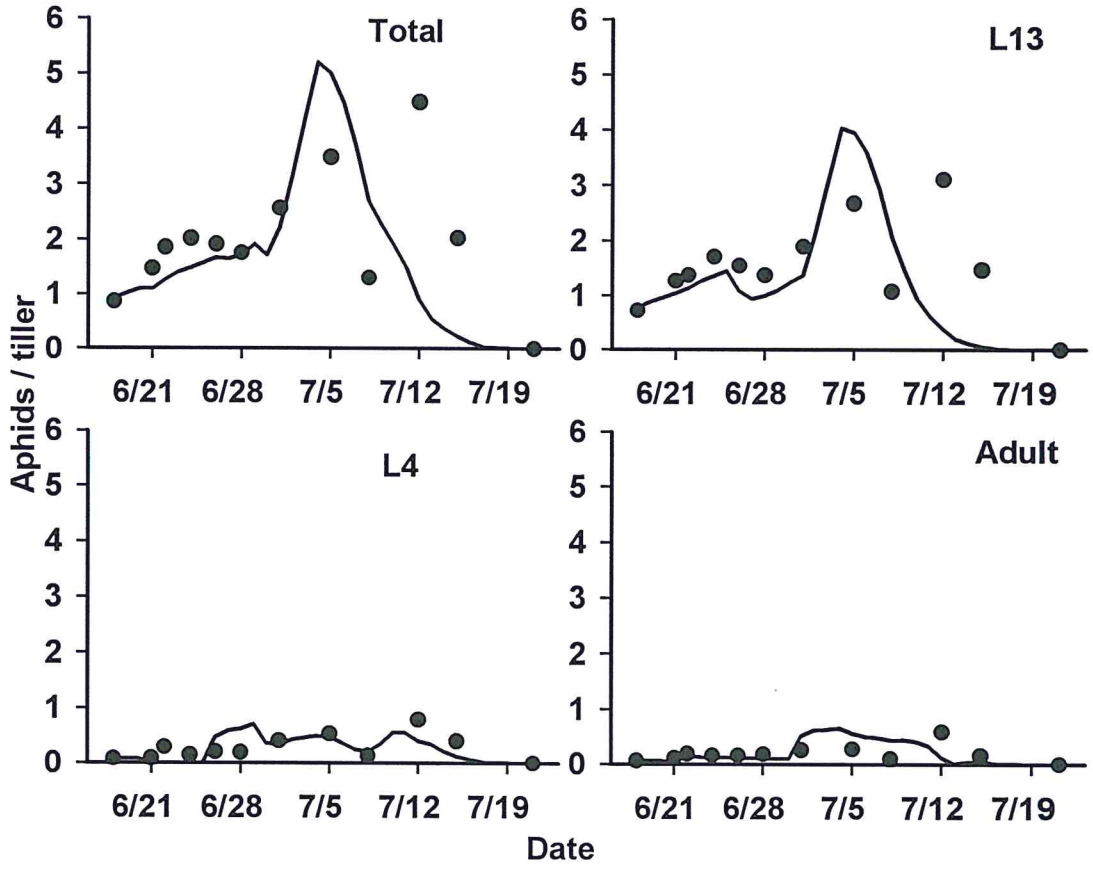


Fig. 8-9 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Göttingen 1993**.

Among the nine fields that were used to validate the model, the field sampled at Göttingen in 1993 was the only field in which the aphid population remained at a low level with the peak density of less than five aphids per tiller.

The model accurately predicted the aphid number before July 8 (Fig. 8-9). As the model did not successfully predict the second peak in middle July, in which the plants had been already very senescent (*GS* 81), the precision of the simulations of the total densities and of the numbers in each stage was rather low (Table 8-8). Even so, the linear regressions between the simulated and observed densities were significant. The hypothesis test showed that all slopes of the regression equations were not significantly different from 1.0. Although the simulation model was not able to predict the second peak in the late growth stages of winter wheat, the model still was acceptable for the low level of population development at Göttingen in 1993. Furthermore, as the damage caused by aphids is not that serious after *GS* 81, the second peak was not important from an economic point of view.

Table 8-8 Parameters of the linear regression line $Y = bX$ between the simulated (Y) and the observed (X) population densities of *M. dirhodum* and hypothesis test of "slope b = 1", **Göttingen 1993**.

Stage	Linear regression (n = 8)				Hypothesis test	
	R^2	F	P	b±95% confidence	F	P
Sum	0.664	21.7	0.001	0.732±0.346	2.913	0.116
L13	0.643	19.8	0.001	0.730±0.361	2.712	0.128
L4	0.595	16.2	0.002	0.698±0.382	3.020	0.110
Ad	0.456	9.3	0.011	0.764±0.553	0.877	0.369

8.2.4 Very low population densities

In 1995 and 1996 the population densities of *M. dirhodum* were extremely low in the fields sampled in Ruthe. Although such low densities were of no economic importance, the simulations were still carried out. In 1995, almost all observed densities were zero except the densities on June 27 and July 24 with 0.167 and 0.1 aphids per tiller respectively. In 1996, the observed peak density was less than 1.2 aphids per tiller.

Ruthe 1995

The model could not describe zero densities at Ruthe in 1995. However, the absolute number of *M. dirhodum* predicted was less than 0.18 aphids per tiller during the whole simulation period (Fig. 8-10).

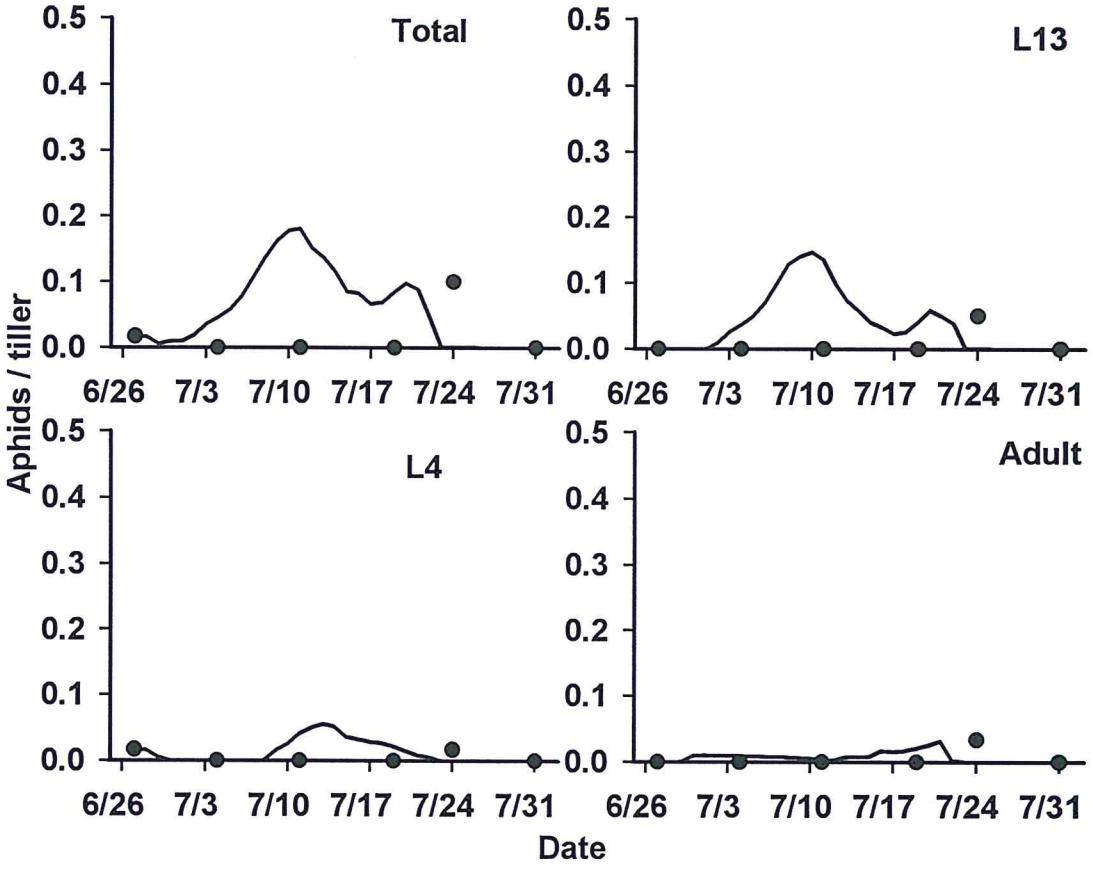


Fig. 8-10 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Ruthe 1995**.

Ruthe 1996

For the field sampled at Ruthe in 1996, the model was not able to predict the peak of *M. dirhodum* at the end of July and beginning of August. The simulated densities were lower than 0.12 aphids per tiller (Fig. 8-11).

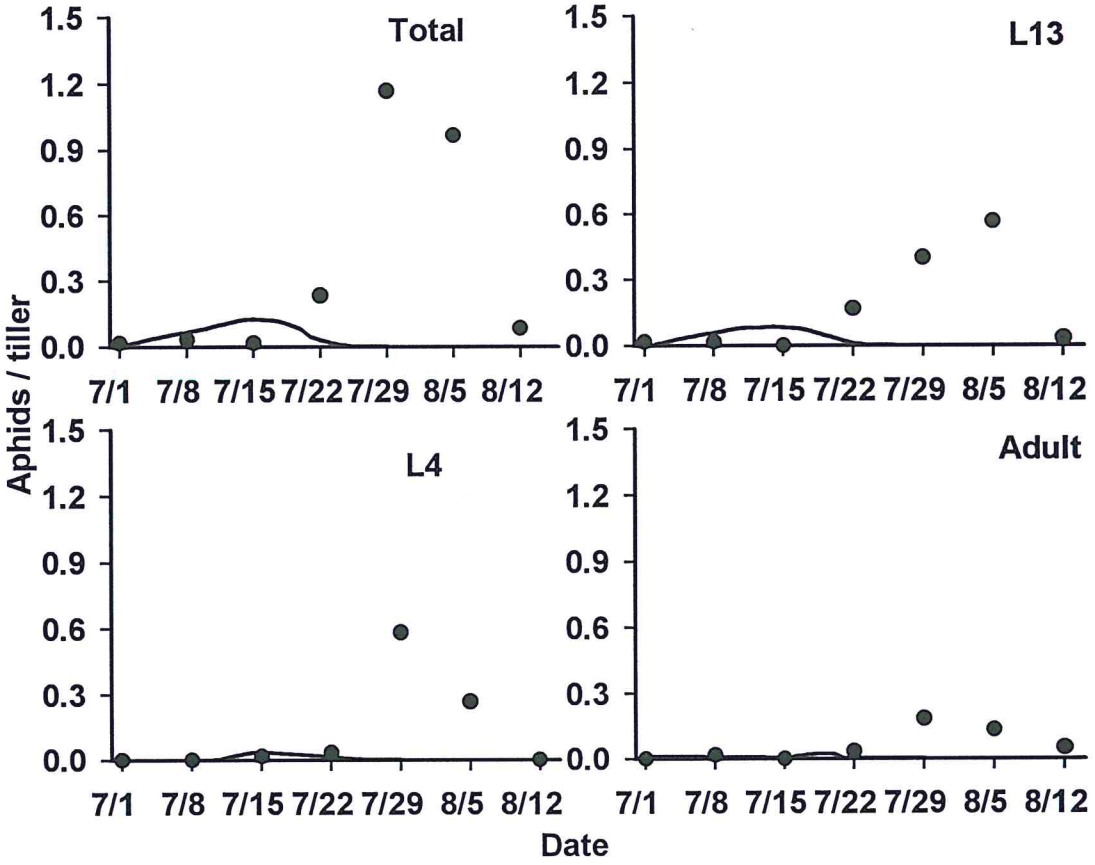


Fig. 8-11 Observed (dots) and simulated (lines) numbers of all stages (Total), young larvae (L13), old larvae (L4) and adults (apterae and alatae) of *M. dirhodum* per wheat tiller, **Ruthe 1996**.

Although the simulated population densities in both years at Ruthe were not acceptable from a statistical point of view, the predictions of the model were not unreasonably different from the extreme low level of the observations. Furthermore, as the recognisable densities appeared on very old plants (*GS* > 83), aphids could hardly cause any damage to those plants. Thus from an economic point of view, the model was practically acceptable in predicting extreme low levels of population densities of *M. dirhodum*.

8.3 The mechanism of population dynamics of M. dirhodum

The population dynamics of *M. dirhodum* varied greatly in the nine different fields. What were the main reasons for the specific population pattern in a given field? The initial population densities (*IPD*), daily average temperature (*TX*), daily maximum temperature (*MaxT*), daily scored or interpolated plant growth stage (*GS*) and the number of syrphid larvae (*NE*) were selected as the most important factors to determine the population dynamics of the aphids in the present study. The model validation indicated that using those five factors led to sets of highly accurate simulations for the nine fields. Therefore, the specific pattern of the population dynamics in a given field can be explained by the relationship between the inputs (the five factors) and outputs (the population dynamics) of the model. Simulation experiments can be used to analyse the relationship.

8.3.1 Methods for analysing favourability and importance of factors

To analyse the importance of each factor on the population dynamics of the aphids in a specific field, one of the nine fields was selected as a standard field and the inputs and outputs of the standard field were compared with those of other fields. Since the aphid population at Göttingen in 1992 had an outbreak that was very well simulated, it was selected as a standard field. Two kinds of simulation experiments were implemented in this study.

The first kind of experiment was used to explain the favourability (this word from Berg et al. 1995) of input conditions to the aphid population development. Favourability is an indicator to describe how favourable a factor is for the aphid population development. Values of the five input variables in the standard field were defined as the standard inputs. The simulated daily population densities in the standard field are considered as the standard outputs. The favourability of each factor in the standard field was assumed to be 1.0.

The mechanism of the population development is analysed by the simulation under a special condition, i.e. one of the five standard inputs is replaced by the corresponding inputs of a specific field (Table 8-9).

Table 8-9 Input combinations in the favourability analysis for the field at Göttingen in 1991.

Factors	*IPD*	*GS*	*TX*	*MaxT*	*NE*
F_{IPD}**	*Go*91*	*st*	*st*	*st*	*st*
F_{GS}	*st**	*Go*91	*st*	*st*	*st*
F_{TX}	*st*	*st*	*Go*91	*st*	*st*
F_{MaxT}	*st*	*st*	*st*	*Go*91	*st*
F_{NE}	*st*	*st*	*st*	*st*	*Go*91

*, *Go*91 represents the original value of a factor in the field sampled at Göttingen in 1991, *st* is the standard value of a factor from the standard field at Göttingen in 1992.

**, F_{IPD}, F_{GS}, F_{TX}, F_{MaxT} and F_{NE} are the input conditions for the simulation experiments to analyse the role of *IPD*, *GS*, *TX*, *MaxT* and *NE* in population dynamics of the aphids, respectively.

The accumulated population density during the simulation period was used to represent the population size. The relative favourability (*Favourability*(F_i) of factor i (F_i) to the population development of *M. dirhodum* was expressed with equation 8.3.

$$Favourability(F_i) = \frac{\sum_{j=b}^{e}(TotalL_{F_i}(j) + TotalA_{F_i}(j))}{\sum_{j=b}^{e}(TotalL_{st}(j) + TotalA_{st}(j))} \qquad (8.3)$$

where b and e are the days at which the simulation started and ended, respectively. *TotalL* and *TotalA* are the total number of larvae and adults, respectively. j is the simulation day. *st* represents the standard input conditions and F_i represents the specific conditions in which factor i of the five standard inputs is replaced by the corresponding input of a specific field.

The second kind of simulation experiment was used to explain why the specific pattern of the aphid population dynamics appeared in each given field. In other words, how big was the contribution of each factor to the specific population pattern. Values of the five input variables of the standard field (at Göttingen in 1992) were used as the standard condition for the simulation. The importance of each factor was analysed with the simulation under a set of specific conditions: one of the five original inputs of a given field was replaced by the corresponding standard inputs of the standard field. For example, to analyse the importance of *IPD* for the population pattern of the field at Göttingen in 1991, *IPD* at Göttingen in 1991 was replaced by *IPD* of the standard field. The other factors were kept at the original values of the

field at Göttingen in 1991 (Table 8-10). The simulation experiments to analyse the importance of other factors followed the same procedure explained for *IPD*. The method described for the field at Göttingen in 1991 was also used in the analyses of the other fields.

Table 8-10 Input combinations in the importance analysis of each factor for the field at Göttingen in 1991.

Factors	*IPD*	*GS*	*TX*	*MaxT*	*NE*
F_{IPD}**	*St*	*Go*91	*Go*91	*Go*91	*Go*91
F_{GS}	*Go*91*	*st*	*Go*91	*Go*91	*Go*91
F_{TX}	*Go*91	*Go*91	*st*	*Go*91	*Go*91
F_{MaxT}	*Go*91	*Go*91	*Go*91	*st*	*Go*91
F_{NE}	*Go*91	*Go*91	*Go*91	*Go*91	*st*

*, **, see the footnotes of Table 8-9

Linear regression analyses of the relationships between the simulated daily population densities with original inputs (*SumOrigin*) and alternative inputs (*SumAlternate*) for each field were carried out. In the model $SumAlternate = b \cdot SumOrigin$, the regression coefficient b was used as an indicator to represent the similarity between the population sizes of *SumOrigin* and *SumAlternate*. The adjusted R^2 is an indicator that refers to the similarity of curve shapes of the population dynamics that were simulated using the original and the alternative inputs. If replacing the original value of a factor in a specific field by the corresponding value of the standard field resulted in a strong deviation of R^2 and slope b from 1.0, the factor would be considered as an important factor in determining the population pattern in this specific field.

8.3.2 Favourability of ecological factors

The relative favourability of each factor for the simulated population development of *M. dirhodum* in the nine fields is illustrated in Fig. 8-12. The relative favourability of *IPD* was in a good agreement with the population size in each field (Fig. 8-12A and 8-12F). The highest relative favourability of *IPD* appeared in the field with maximum population size, at Grossenwieden in 1992. The relative favourability of *IPD* took a medium values and the population reached intermediate densities in Hiddestorf in 1991 and 1992. The initial population densities were very low in the field at Göttingen in 1993 and at Ruthe in 1995 and 1996, and the aphid populations in

these three fields also remained at very low levels. A high initial population density around *GS* 69 was a strong indication for a population outbreak.

For the favourability of *TX*, only the values for the fields at Göttingen in 1993 and at Ruthe in 1996 were lower compared to the situation in Grossenwieden 1992. (Fig. 8-12B). The low average temperatures in these two cases inhibited the population development. The average temperatures in other fields were more favourable than in Grossenwieden in 1992. In most of the nine fields, high average temperatures were not necessarily preconditions for a population outbreak.

The *GS* in most fields was as favourable as or even more favourable than in the standard field at Göttingen in 1992 (Fig. 8-12C). Since the simulation started at *GS* 65 for the field at Göttingen in 1991 and at *GS* 61 for the field at Ruthe in 1994, the relative favourability of *GS* in those two cases was high. A very slow development of wheat occurred during mid July at Ruthe in 1995, resulting in a high relative favourability of *GS* in this field. However, the aphid populations in those three cases did not reach a high level. Even the lowest favourability of *GS* at Ruthe in 1996 (0.97) was not far away from the outbreak case at Göttingen in 1992 (1.0). Therefore, *GS* alone was not a critical factor leading to a population outbreak.

MaxT plays a negative role in the population development. A low favourability of *MaxT* means a strong negative influence on the population development. Low favourability of *MaxT* occurred at Göttingen in 1991 and at Ruthe in 1994. *MaxT* at Göttingen in 1991 during *GS* 65-77 were between 26°C and 32.4°C for 11 days. High favourability of *MaxT* appeared in two fields with low population densities at Göttingen in 1993 and at Ruthe in 1996, and in two outbreak fields at Grossenwieden and Hiddestorf in 1992. *MaxT* at Göttingen in 1993 and at Ruthe in 1996 was lower than 25°C from the end of flowering (*GS* 69) to late milky ripe (*GS* 77). The situations in 1992 at the two locations were similar. *MaxT* from *GS* 69 to early milky ripe (*GS* 73) were below 27°C. No extreme high temperature seriously limited the population building up. Daily average temperatures changed in accordance with daily maximum temperatures. However, they had contrasting effects

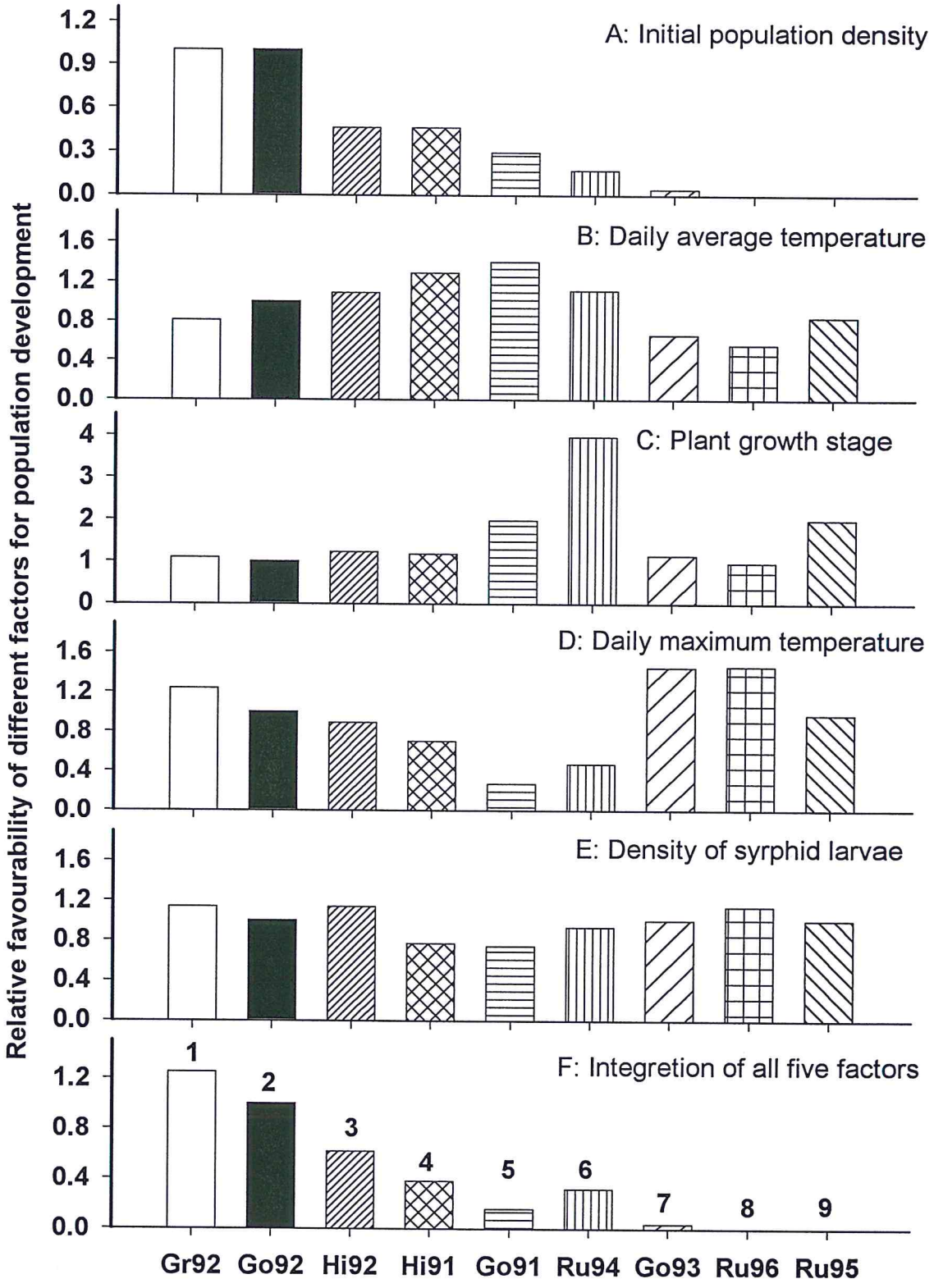


Fig. 8-12 The relative favourability of different factors to the population development of *M. dirhodum*. The numbers above the bars in the last figure (F) represent the density ranks of the field observations. The favourability of each factor at Göttingen in 1992 was assumed to be 1.0.

on the population development of *M. dirhodum*. The co-ordinated effects of the average temperature and the maximum temperature will be presented in the sensitivity analysis.

Syrphids did not occur in the two outbreak fields at Hiddestorf and Grossenwieden in 1992. The zero densities of syrphids were very suitable for the population development of aphids (Fig. 8-12E). A low *NE* level in the outbreak field at Göttingen in 1992 was also a favourable condition for the aphid population development. In fields with very low aphid populations, *NE* was not an important factor to suppress the population development such as in the fields sampled at Ruthe in 1995 and 1996. High *NE* levels in the fields with a medium aphid population level, such as at Göttingen and Hiddestorf in 1991 and at Ruthe in 1994, were not very suitable for the population development. The analysis indicated that syrphid larvae could reduce the population size by 21%-40% if other factors in these three fields remained at the constant levels of the standard field. A light occurrence of natural enemies was another important reason for the population outbreak.

As the aphid population develops under the integrated influences of the five factors, the effects of favourable factors can be counteracted by other unfavourable factors. The integrated favourability (*Integrated_F*) is defined as the product of the favourability of each factor (*Favourability*(F_i)):

$$Integated\_F = \prod_{i=1}^{5} Favourability(F_i) \qquad (8.4)$$

The rank of the integrated favourability of each field was generally in accordance with the rank of population size of each field (Fig. 8-12F). The analysis revealed that if the favourability of each factor was not very low, the population had a high chance for an outbreak. If the high initial population densities coincided with a mild maximum temperature and low density of natural enemies, such as at Grossenwieden, Göttingen and Hiddestorf in 1992, the population will break out.

8.3.3 Importance of ecological factors

The population development was characterised by the shape of the population dynamic curve and the population size. The shape and the size in each field

depended on the initial population densities and the biotic and abiotic conditions of the environment. To get a clear explanation of the observed population dynamics in each field, the effects of each factor on the size and the shape of the population curve were analysed separately by a linear regression of the simulated daily population densities calculated with the original input conditions (*SumOrigin*) and the alternative input conditions (*SumAlternate*). The method was described in chapter 8.3.1.

8.3.3.1 Fields with high population densities

Hiddestorf 1992

In 1992, the population dynamics of the aphids at Hiddestorf and in the standard field were not very similar (R^2 = 0.756). The aphid population size in Hiddestorf was about 40% lower compared to the standard field.

When the *IPD* of the field sampled at Hiddestorf in 1992 was replaced by the *IPD* of the standard field, the maximum population size was 44% higher than that of the original simulation (Fig. 8-13A1). *TX* was not an important factor resulting in a difference of the population development between the field at Hiddestorf in 1992 and the standard field (R^2 = 0.995, b = 1.008). The replacement of *GS* led to a 28% reduction of the population size (Fig. 8-13A3). The *GS* at Hiddestorf in 1992 was more favourable than that of the standard field. The alternative *MaxT* did not significantly change the population size (b = 1.026, P = 0.472). Eliminating the effect of *MaxT* resulted in a big increase of the population size (b = 2.101) (Fig. 8-13A4). Similar to the standard field, the negative effect of *MaxT* on the population development of *M. dirhodum* in this field was very strong. The density of syrphid larvae in the field sampled at Hiddestorf was zero. Adding the effect of *NE* of the standard field to the field at Hiddestorf reduced the population size by about 23% (Fig. 8-13A5).

The low *IPD* was the only reason for the lower population size of the field at Hiddestorf in 1992 compared to that of the standard field. The environment at Hiddestorf in 1992 was as favourable as or even more favourable than that of the standard field. The favourable *GS*, mild *MaxT*, and lacking *NE* gave important contributions to the population outbreak at Hiddestorf in 1992.

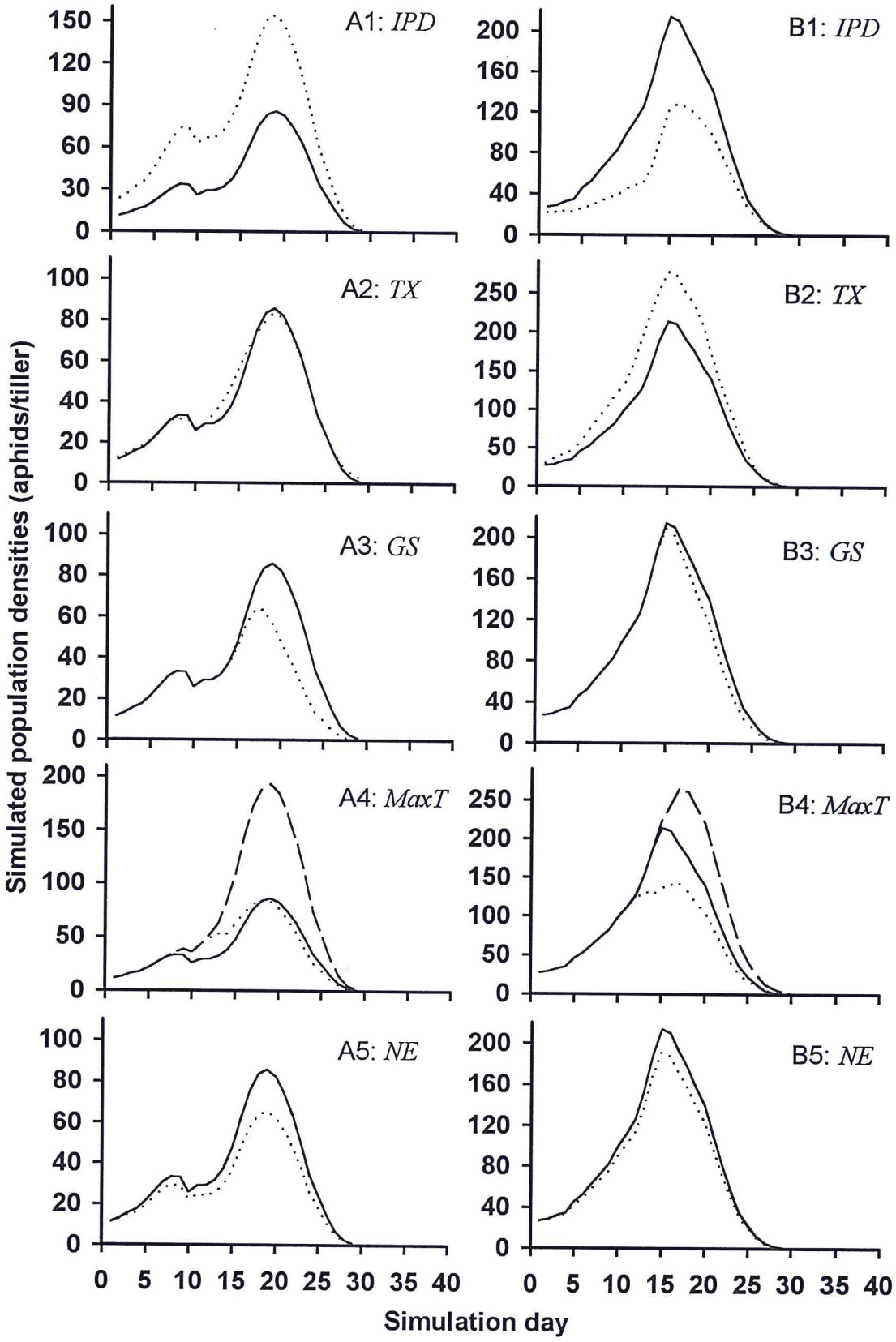


Fig. 8-13 Simulated population dynamics under different conditions: original (solid line), alternative (dotted line) and without effects of high temperatures or natural enemies (dash line). **A: Hiddestorf 1992** and **B: Grossenwieden 1992**.

Grossenwieden 1992

The population size in the field at Grossenwieden in 1992 was the largest among the nine fields. The simulated population size in the standard field was about 38% smaller than that in the field at Grossenwieden in 1992. The replacement of all five factors had little influence on the shape of population curve (all $R^2 > 0.93$), but had significant effects on the population size.

The replacement of *IPD* resulted in a 41% reduction of the total population size (Fig. 8-13B1). The higher *IPD* was the main reason for the higher aphid abundance in this field. The *TX* at Grossenwieden in 1992 was lower than that in the standard field. The replacement of *TX* resulted in a 25% increase of the population size (Fig. 8-13B2). The substitution of *GS* led only to a small reduction of the population size (b = 0.939). The population size simulated by using the alternative *MaxT* was about 27% lower than by using the original *MaxT* (Fig. 8-13B4). It indicated that the negative effect of *MaxT* at Grossenwieden in 1992 was significantly less than that in the standard field. Removing the effect of *MaxT* led to a 23% increase of the population size. *NE* was zero at Grossenwieden in 1992. The high population density at Grossenwieden in 1992 can be partly explained by the lack of syrphids.

High *IPD*, together with low *MaxT* and zero *NE* at Grossenwieden 1992 were the main reasons for the outbreak with the largest population size among all nine fields.

8.3.3.2 Fields with a medium population densities

Göttingen 1991

The regression analysis revealed that the population dynamics in the field at Göttingen in 1991 was totally different from that of the standard field (R^2 = 0.212). Replacing *IPD*, *TX*, *GS* and *NE* by the values in the standard field did not result in great changes of the curve shape (for all, R^2>0.93), but led to certain changes of the population size (Fig. 8-14A).

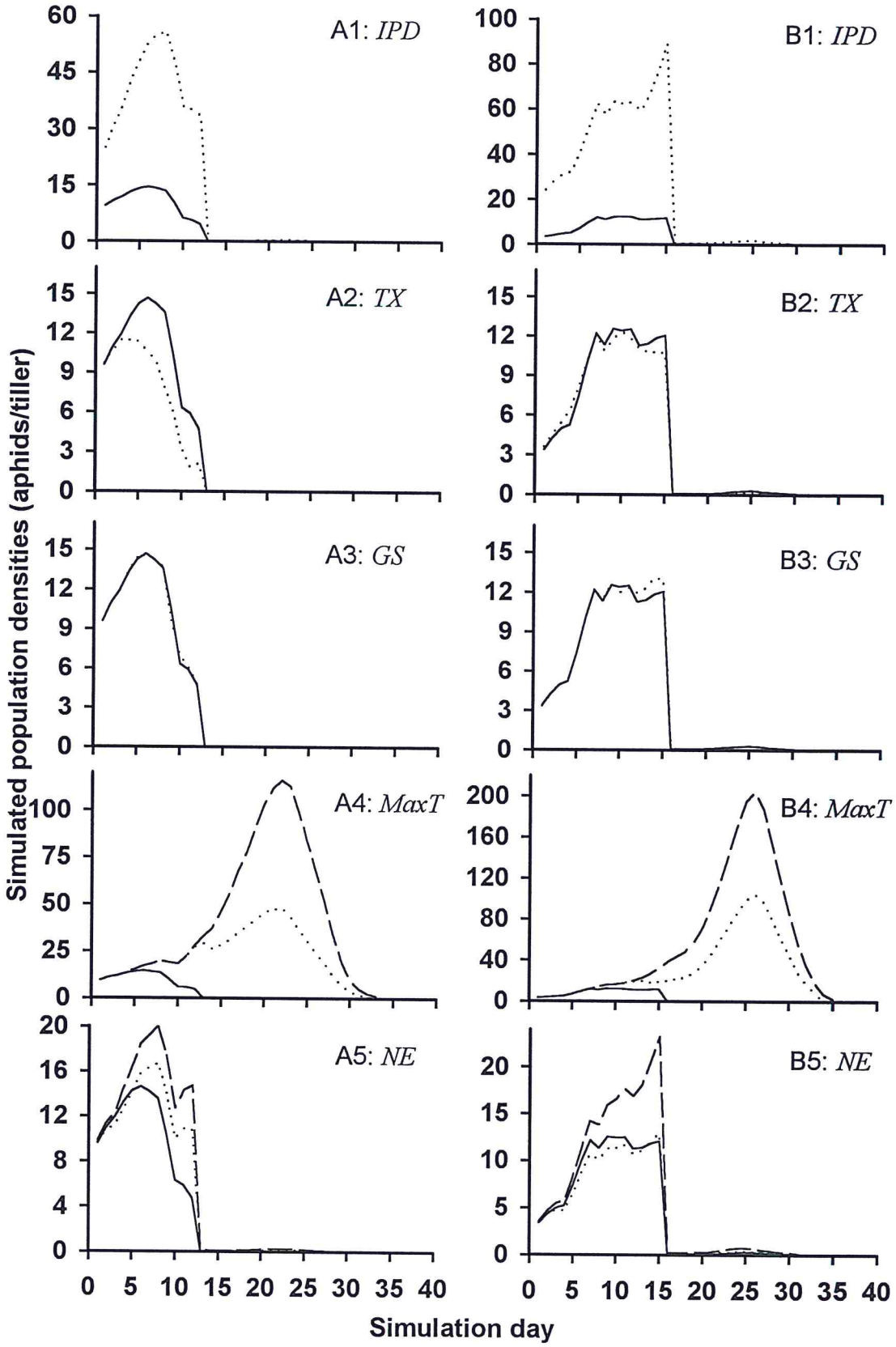


Fig. 8-14 Simulated population dynamics under different conditions: original (solid line), alternative (dotted line) and without effects of high temperatures or natural enemies (dash line). **A: Göttingen 1991** and **B: Ruthe 1994**.

A large increase of the population size (b = 3.683) caused by the replacement of *IPD* indicated that the low *IPD* was responsible for the medium population level in this field (Fig. 8-14A1). The alternative *TX* of the standard field resulted in a smaller population (b = 0.757). The high *TX* was an important factor to stimulate the population increase in the early season (Fig.8-13A2). The changes of *GS* had no effects on the population dynamics (b = 0.999). The replacement of *MaxT* resulted in great changes both in shape and size of the population dynamics. Removing *MaxT* from the model caused a non-significant regression relationship (P>0.32) (Fig. 8-14A4). High *MaxT* was the most important factor to keep the population at a medium level. The population size increased over 12% by the replacement of *NE* of the standard field. *NE* had a stronger control effect on *M. dirhodum* at Göttingen in 1991 than in the standard field. Removing the effect of *NE* led to a 30% increase of the population size. Syrphid larvae played an important role in regulation of the population development.

The strong negative effect of high *MaxT* was the main factor in forming the shape of the population curve at Göttingen in 1991. High *MaxT* combined with low *IPD* and strong syrphid predation contributed most to the population pattern in the field at Göttingen in 1991.

Ruthe 1994

The importance of each factor on population dynamics at Ruthe in 1994 was very similar to the situation of the field at Göttingen in 1991 (Fig. 8-14A and B). Alternating *IPD*, *TX*, *GS* and *NE* by the corresponding values of the standard field did not cause big changes to the shape of population curve (all R^2>0.97), but resulted in changes of the population size.

Low *IPD* (b = 5.578) was one of the important reasons that prevented the population from outbreak. *TX* (b = 0.966) and *GS* (b = 1.022) were minor important factors influencing the population dynamics. The high *MaxT* was the main factor responsible for the population dynamics in this field, since the replacement (R^2 = 0.05) and the elimination (R^2 = 0.02) of *MaxT* resulted in big deviations of R^2 from 1.0. Strong predation (*NE*) gave a certain contribution to the size of the population (Fig. 8-14B5).

Hiddestorf 1991

The difference in the shape of the population curves between the field at Hiddestorf in 1991 and the standard field were not that big (R^2 = 0.903), but the population size in the field at Hiddestorf in 1991 was only about one-fourth of the standard field. All alternative conditions did not strongly modify the shape (all adjusted R^2 > 0.92). However, the size greatly increased by using the replaced values of *IPD*, *MaxT* and *NE* as model inputs.

The replacement of *IPD* resulted in a 2.3 times bigger population size of aphids compared to those simulated using the original conditions (Fig. 8-15A1). Medium *IPD* was one of the important reasons for the medium population size in this field. *TX* (b = 1.05) and *GS* (b = 0.91) were not the main factors to determine the population dynamics in this field. Fig. 8-15A4 shows that the replacement of *MaxT* resulted in a larger population size (b = 1.84). By removing the effect of *MaxT*, not only the population size greatly increased (b = 2.77), but also the curve shape (R^2 = 0.798) changed. The high *MaxT* greatly restricted the population development. *NE* in Hiddestorf in 1991 played a very important role in the population control. Reducing *NE* to the level of the standard field led to a 34% increase of the population size. When the effect of *NE* was removed, the shape of the population dynamic curve changed (R^2 = 0.89) and the population size increased by more than 80% (Fig. 8-15A5). This indicated that syrphid larvae belonged to the most important factors to control the aphids from outbreak in the field in Hiddestorf in 1991.

The low *IPD* combined with high *MaxT* and high density of syrphids determined the population size on a medium level in the field at Hiddestorf in 1991.

8.3.3.3 Fields with a low population densities

Göttingen 1993

The simulated population size in the field at Göttingen in 1993 was as small as 3.2% of those in the standard field. The shape of the population curve was only slightly modified by the replacement of each factor (all adjusted R^2 > 0.96).

When the extreme low *IPD* in the field at Göttingen in 1993 was replaced by the *IPD* of the standard field, the population size dramatically increased to an outbreak level

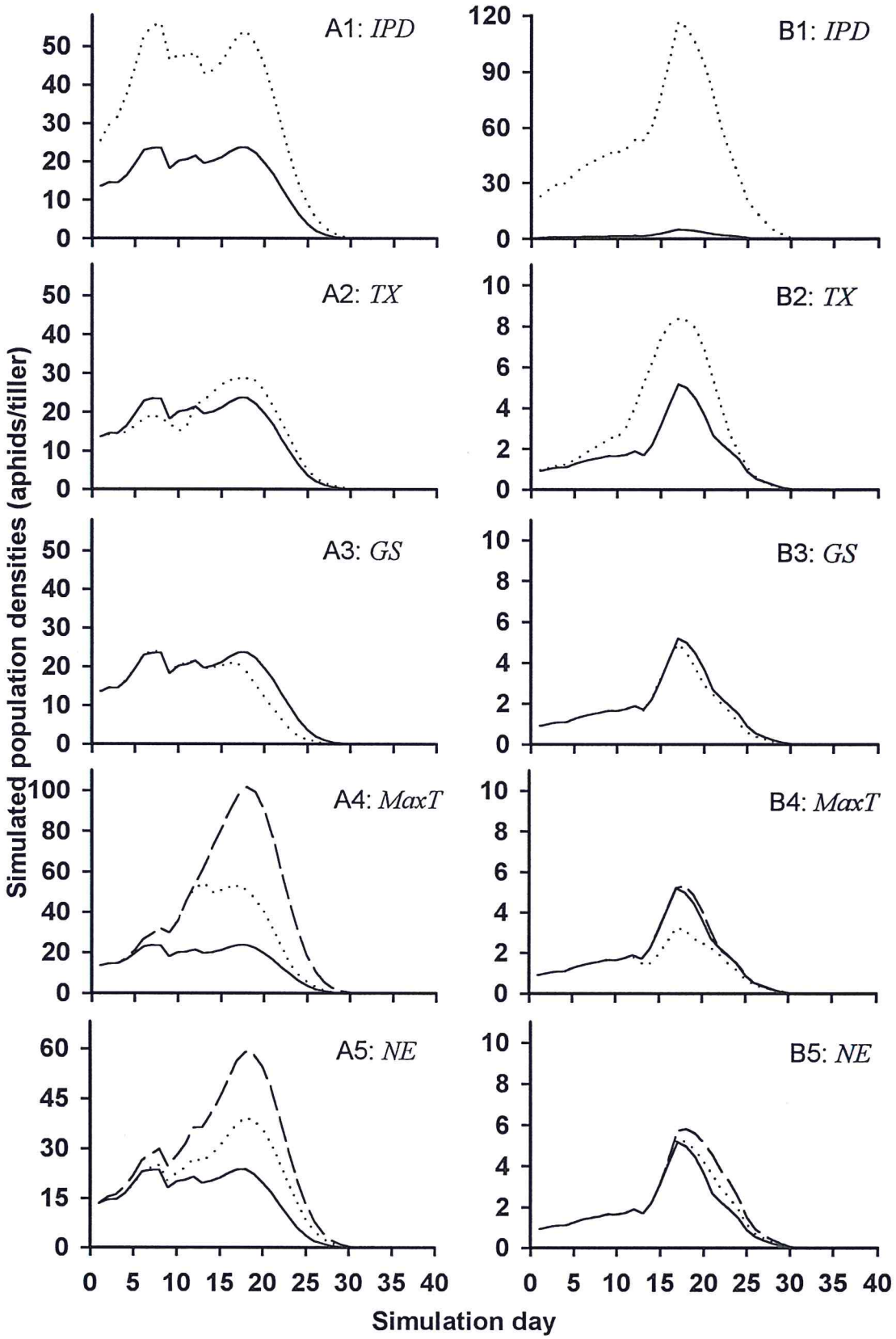


Fig. 8-15 Simulated population dynamics under different conditions: original (solid line), alternative (dotted line) and without effects of high temperatures or natural enemies (dash line). **A: Hiddestorf 1991** and **B: Göttingen 1993**.

(Fig. 8-15B1). Increasing *TX* to the level of the standard field resulted in an 80% increase of the population size (Fig. 8-15B2). These low *TX* restricted the population development. *GS* was not an important factor for the population dynamics (b = 0.91). *MaxT* was so low (hardly over 27°C) that the population size did not change much by removing the effect of *MaxT* (b = 1.037). Replacing *NE* by the syrphid number of the standard field did not result in a large change of the population size (b = 1.069). Effect of *NE* on aphid population control at Göttingen in 1993 was similar to that in the standard field. However, eliminating the effect of syrphids resulted in a 20% increase of the aphid population size. Predation of syrphids played again certain role in the population control of *M. dirhodum* at Göttingen in 1993.

In spite of the lower negative effects of *MaxT* and the slightly more favourable *GS* in the field at Göttingen in 1993 than in the standard field, the extreme low *IPD* combined with the low *TX* and the effective predation of syrphids prevented the aphid population from reaching a high level in this field.

8.3.3.4 Fields with an extremely low population densities

The population size of *M. dirhodum* at Ruthe in 1995 and 1996 were extremely low.

Ruthe 1995

The substitution of *IPD* resulted in the simulated population size as large as in the outbreak case, i.e. in the standard field (Fig. 8-16A1). The extremely low *IPD* led to almost zero abundance of the population. The replacement of *TX* and *GS* resulted in minor decreases of the population size (Fig. 8-16A2 and A3). The *MaxT* at Ruthe in 1995 was higher than that of the standard field. Alternative *MaxT* caused big changes in both the shape and the size. Extremely high maximum temperatures at Ruthe in 1995 played an important role in the aphid population control (Fig. 8-16A4). Replacing and removing *NE* increased the simulated population size significantly (Fig. 8-16A5). Syrphid larvae gave a remarkable contribution to the extremely low population density at Ruthe in 1995.

The analysis indicated that *TX* and *GS* were slightly more favourable at Ruthe in 1995 than in the standard field, but the extreme low *IPD*, the unsuitable *MaxT* and the strong predation of syrphids led to an extremely small population size.

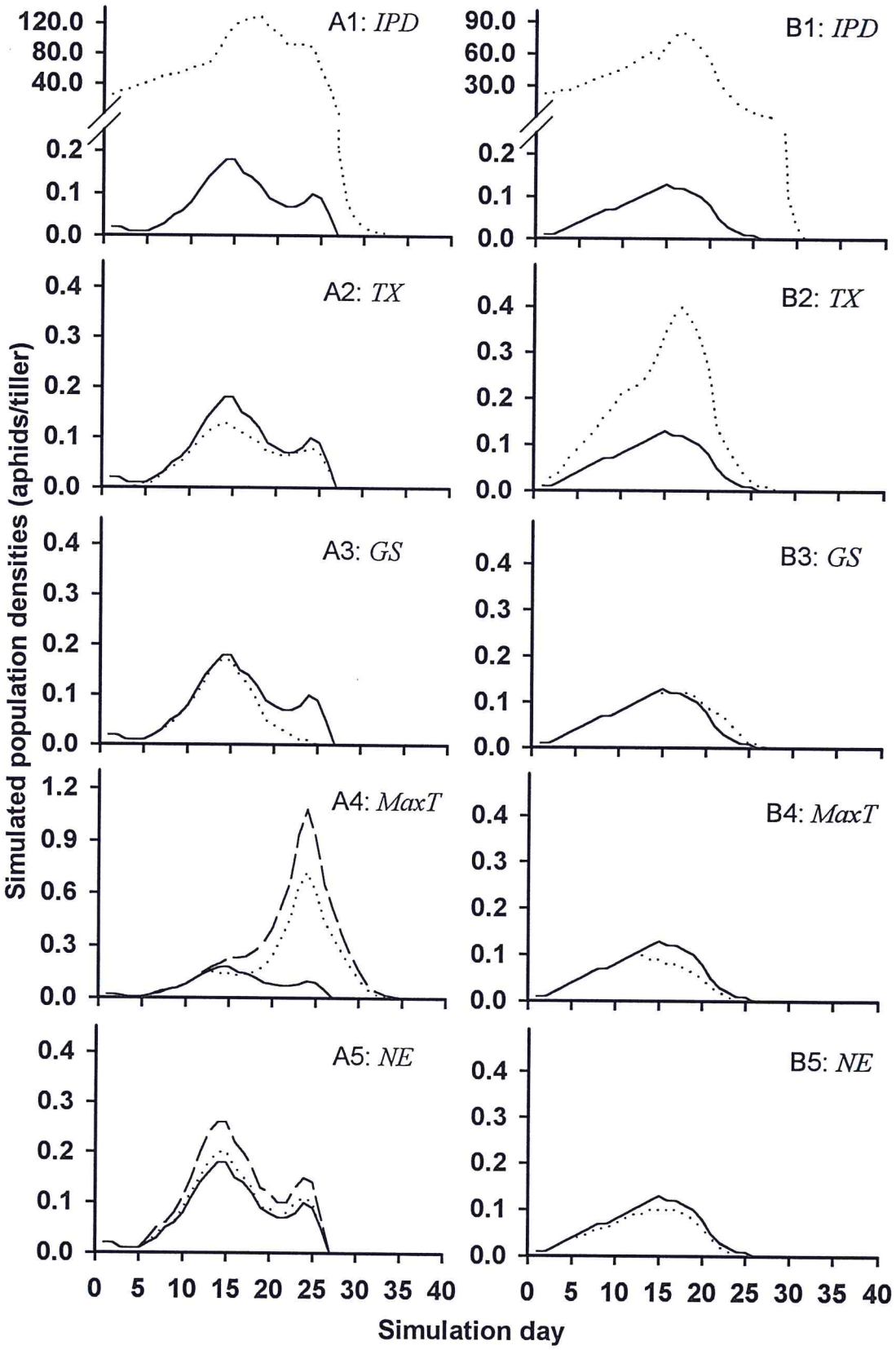


Fig. 8-16 Simulated population dynamics under different conditions: original (solid line), alternative (dotted line) and without effects of high temperatures or natural enemies (dash line). **A: Ruthe 1995** and **B: Ruthe 1996**.

Ruthe 1996

The very low *IPD* was the first dominant factor responsible for a very low population level in the field at Ruthe 1996 (Fig. 8-16B1). The low *TX* was responsible for the low aphid density (Fig. 8-16B2). The slightly unfavourable *GS* reduced the population size a bit. *MaxT* was so low that removing *MaxT* did not influence the population density. *NE* was not important because the aphid densities are extremely low at Ruthe in 1996.

Extremely low *IPD* integrated with low *TX* was the main reason for the extremely low population development at Ruthe in 1996.

8.4 Sensitivity analysis

Sensitivity analysis can be used to identify the input factors for which the data should be collected in a high accuracy to obtain reliable simulation results. Small positive and negative changes are made artificially to individual components of the simulation model, and the responses of the model are determined. If a small change in a component leads to a large change in model output, then this component is sensitive and must be known very accurately. Usually, two kinds of components that may affect the population dynamics are concerned in the sensitivity analysis. The first group of components is the fundamental biological processes such as development, reproduction, survival, morph determination and settlement of alate adults in fields. The second is the input variables such as the initial population density (*IPD*), daily average temperature (*TX*), daily maximum temperature (*MaxT*), plant growth stage (*GS*) and number of syrphid larvae (*NE*).

The sub-models of development, reproduction, survival, alate determination and alate settlement are the basic elements of the simulation model. As the importance of these components in simulating the population dynamics of aphids is already well known, the sensitivity analyses of these components are not very necessary. Therefore, the sensitivity analysis present here is only focused on the initial population and the other four input factors.

8.4.1 Methods of the sensitivity analysis

The simulated population density for the field sampled at Göttingen in 1992 was very close to the observed data. All five input factors were important for the population development in this field. Therefore, the field at Göttingen in 1992 was chosen as an example for the sensitivity analysis. Certain changes to one of the six components, *IPD* (±5% and ±10%), stage structure of *IPD* (proportion of L13, L4 and adult ±5% and ±10%), *TX* (±1°C and ±2°C), *GS* (±1 and ±2), *MaxT* (±1°C and ±2°C) and *NE* (±50% and ±100%) were made separately. Other inputs were kept at the original values. The simulation program was run under the changes of input factors and the daily population densities were calculated. General effects of *MaxT* and *NE* were analysed separately by removing the effect of *MaxT* and *NE*, i.e. setting the *MaxT* lower than 27°C and *NE* to zero.

Simple linear regression analysis was carried out to test the effect of the changes of each factor on the population dynamics of *M. dirhodum*. The simple linear model $Y = b \cdot X$ was used in the regression analysis. Y and X represent the simulated daily total population densities under the changed and under the original input conditions, respectively. The adjusted R^2 and slope b were used to describe the similarity of the population curve shape and the population size under the original and small changed input conditions. Values of R^2 and b close to 1.0 indicate that the model does not sensitively response to the small changes of the factor.

8.4.2 Sensitivity to initial population density

The changes of *IPD* by ±5% or ±10% did not alter the shape of the population dynamics but resulted in a nearly 1:1 proportional response in the population size (Table 8-11). Initial populations with different densities developed in a proportional way under the same conditions. The distance between different curves gradually enlarged as the population density increased, reached a maximum at the peak and finally decreased as the population collapsed (Fig. 8-17A).

In the model application, an overestimation of *IPD* would lead to a nearly 1:1 overestimation of the population size. A slightly inaccurate *IPD* would not change the time course of the aphid population development. However, an accurate data collection of *IPD* is important for a reliable simulation of the population density.

Table 8-11 Linear regression $Y = bX$ between simulated population densities using the original (X) **initial population density (*IPD*)** and those changed (Y) *IPD* on the base of the original *IPD* at Göttingen in 1992.

IPD	Linear regression (n = 34)			
	R^2 [a]	F	$P<$	b [b]
-10%	1.00	4659990	0.001	0.891
-5%	1.00	17467700	0.001	0.946
+5%	1.00	355719	0.001	1.039
+10%	1.00	337230	0.001	1.093

[a], R^2 is adjusted R^2 for the linear regression. It indicates the similarity between shapes of simulated population dynamics using the original and the artificially changed *IPD*.

[b], b is the slope of the linear regression model. It indicates the similarity between the simulated population densities with the original and the changed *IPD*.

8.4.3 Sensitivity to stage structure of initial population

Two sensitivity analyses were separately carried out to evaluate the sensitivity to the two stage structures, i.e. 1) the proportion of L13 and L4, and 2) the proportion of L4 and adult. The effects of the changes for the two stage structures are shown in Table 8-12 and Table 8-13, respectively.

Changing the proportion of L13 to L4 did not change the shape of the population curve (all adjusted R^2 > 0.99) in all cases but greatly changed the simulated population size (Table 8-12). The 5% and 10% changes of the relative proportion of L13 and L4 modified the population densities of the aphids by around 11% and 21%, respectively, given by the changes of the slope b. The populations with different stage structures developed in a similar way during the early phase of the population increase. The distance between the population dynamic curves gradually increased as the population increased. The biggest distance appeared during the peak. As the population declined, the distance diminished (Fig. 8-17B).

Table 8-12 # Linear regression $Y = bX$ between simulated population densities using the original (X) **proportion of L13 and L4** in the initial population density (IPD) and the changed (Y) proportions of the two stages on the base of the original age structure at Göttingen in 1992

Proportion of L13 : L4	Linear regression (n = 34)			
	R^2	F	$P<$	b
L13 + 10% IPD and L4 -10% IPD	0.991	3783.5	0.001	0.792
L13 + 5% IPD and L4 - 5% IPD	0.998	15923.3	0.001	0.886
L13 – 5% IPD and L4 + 5% IPD	0.999	24836.6	0.001	1.114
L13 – 10% IPD and L4 +10% IPD	0.996	7520.0	0.001	1.228

#, symbols are explained in the footnotes of Table 8-11.

The changes of the proportion of L4 to adults led to apparent differences of the population development during the phase of population increase. However, the differences became smaller during the population peak and collapse (Fig. 8-17C, Table 8-13). Since the proportion of L4 in the whole population was not high, the changes of the proportion of L4 to adult did not affect the population size as strongly as the changes of the proportion of L13 to L4 did.

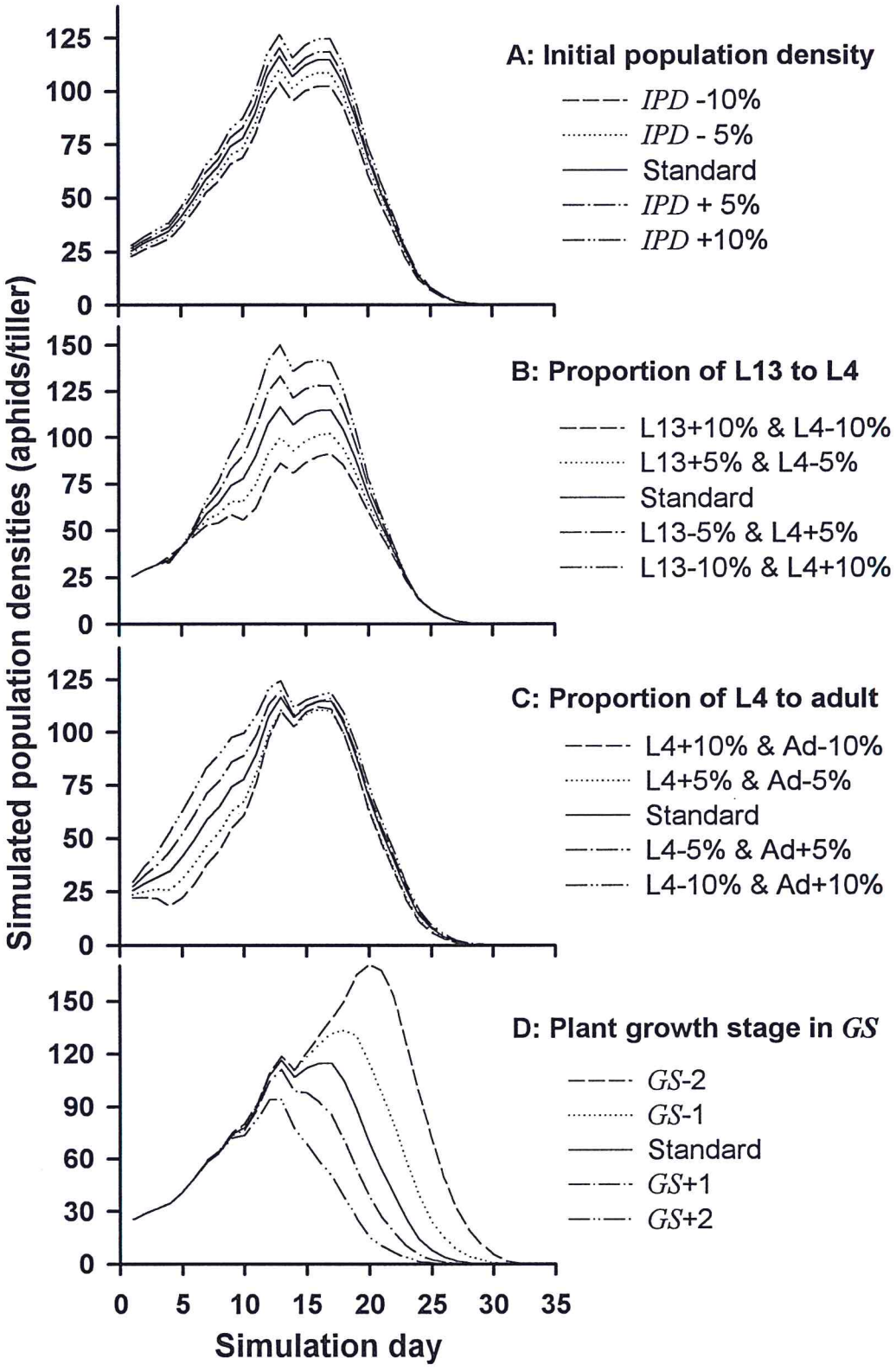


Fig. 8-17 Simulated population dynamics using the original and artificially changed conditions for the initial population densities (*IPD*), the stage structure of the initial population and the plant growth stages (*GS*), based on the original conditions at Göttingen in 1992.

Table 8-13 # Linear regression $Y = bX$ between simulated population densities using the original (X) **proportion of L4 and adult** in the initial population density (IPD) and the changed (Y) proportions of the two stages on the base of the original age structure at Göttingen in 1992.

Proportion L4:Ad	Linear regression (n = 34)			
	R^2	F	$P<$	b
L4 + 10% IPD and Ad -10% IPD	0.985	2159.6	0.001	0.893
L4 + 5% IPD and Ad - 5% IPD	0.996	9014.1	0.001	0.921
L4 – 5% IPD and Ad + 5% IPD	0.996	7803.1	0.001	1.055
L4 – 10% IPD and Ad +10% IPD	0.987	2467.6	0.001	1.124

#, symbols are explained in the footnotes of Table 8-11.

Increasing the proportions of the aphid stages in IPD, that were closer to the reproduction period, i.e. L4 and adult, had a significant positive effect on the population development of *M. dirhodum*. Overestimating the proportion of L4 or adult in IPD could lead to a significant overestimation of the population size. A slightly inaccurate stage structure of IPD would not change the shape of the population dynamic curve of *M. dirhodum*. Nevertheless, a careful differentiation between the three stages, i.e. L13, L4 and adults, is necessary for an accurate simulation of the population density.

8.4.4 Sensitivity to plant growth stage

Compared to the sensitivity analysis for IPD, the model responded to the small changes of GS in a different way. Changes of GS by ±1 or ±2 apparently changed the shape of the population curves. However, reducing GS modified the shape of the population curve a little bit more than increasing GS. Small changes of GS caused big unsymmetrical changes of the simulated population dynamics. The minor increases of GS led to bigger changes of the population density than the same amount of decreases of GS (Fig. 8-17D and Table 8-14).

Under different GS conditions, aphid populations with the same IPD developed at similar rate during the phase of population increase. The aphid population on older plants (by increasing GS) started to collapse and disappear earlier than on younger plants (by decreasing GS). Large differences appeared during the later part of the population development (Fig. 8-17D).

Table 8-14 # Linear regression $Y = bX$ between simulated population densities using the original (X) **plant growth stage (*GS*)** and the changed (Y) *GS* on the base of the original *GS* at Göttingen in 1992.

GS	Linear regression (n = 34)			
	R^2	F	$P<$	b
-2	0.801	132.7	0.001	1.290
-1	0.959	767.0	0.001	1.143
+1	0.969	1020.1	0.001	0.846
+2	0.866	212.8	0.001	0.655

#, symbols are explained in the footnotes of Table 8-11.

Slightly inaccurate records of *GS* not only resulted in a significant error in determining the shape of the population development of *M. dirhodum* but also caused great changes of the population size. Overestimation of *GS* could lead to an earlier estimation of the population peak and an underestimation of the population level.

8.4.5 Sensitivity to daily average temperature

Systematic changes of *TX* by ±1°C or ±2°C only slightly modified the shape of the population curve (all adjusted $R^2 > 0.98$) but greatly changed the simulated population densities. The sensitivity of the model to *TX* depended on the original level of *TX*. The model was more sensitive to minor changes of *TX* that were close to the original *TX* at Göttingen in 1992 than those far away from it (Table 8-15, Fig. 8-18A). The aphid populations developing under the same *IPD* but different *TX* conditions performed a similar increase at the beginning of the simulation. The distance among different curves of the population dynamics gradually became wider as the population increased, but were gradually reduced as the population decreased (Fig. 8-18A).

Fixing the daily maximum temperature as the original in Göttingen 1992, the increase of *TX* played a positive role in the population development of *M. dirhodum*. A slight inaccurate record of *TX* would not result in a big change of the shape of the population development of *M. dirhodum*. Since a change of *TX* by 1°C altered the population size by 15%, the accurate record of *TX* was very important for a reliable simulation of the population density. The overestimation of *TX* would result in a significant overestimation of the population size.

Table 8-15 # Linear regression $Y = bX$ between simulated population densities under the original (X) **average temperature (*TX*)** and the changed (Y) *TX* on the base of the original *TX* at Göttingen in 1992.

TX	Linear regression (n = 34)			
	R^2	F	$P<$	b
-2°C	0.984	2008.0	0.001	0.724
-1°C	0.995	7205.2	0.001	0.853
+1°C	0.998	13978.4	0.001	1.150
+2°C	0.998	19374.6	0.001	1.239

#, symbols are explained in the footnotes of Table 8-11.

8.4.6 Sensitivity to daily maximum temperature

The changes of *MaxT* by ±1°C or -2°C only slightly modified the shape of the population curve (R^2 > 0.97). However, an increase of +2°C resulted in a totally different pattern of the population dynamics of *M. dirhodum*. The small change of *MaxT* caused a big unsymmetrical change of the simulated population dynamics (Fig. 8-18B and Table 8-16). The model response both in shape and in population size was more sensitive to a *MaxT* increase than to a decrease. Removing the effect of *MaxT* led to a population increase by 45%.

Table 8-16 # Linear regression $Y = bX$ between simulated population densities under the original (X) **daily maximum temperature (*MaxT*)** and the changed (Y) *MaxT* on the base of the original *MaxT* at Göttingen in 1992.

MaxT	Linear regression (n = 34)			
	R^2	F	$P<$	b
<27°C*	0.933	459.2	0.001	1.455
-2°C	0.981	1665.8	0.001	1.226
-1°C	0.989	3086.3	0.001	1.165
+1°C	0.975	1289.1	0.001	0.652
+2°C	0.331	16.3	0.001	0.246

#, symbols are explained in the footnotes of Table 8-11.

*, *MaxT* was set to a value below 27°C to remove the effect of *MaxT* on the population development (27°C was assumed as the threshold for negative effects of high temperature on *M. dirhodum*, according to the experiment results in chapter 3).

Fig. 8-18B demonstrates that high *MaxT* drastically restrained the population development. The systematically adding 2°C to the original *MaxT* led to an abrupt early collapse of the aphid population. However, the populations under lower *MaxT* (-1° and -2°C on the base of *MaxT* at Göttingen in 1992) continued their development and reached higher population peaks.

Since the size and even the shape of the population development were greatly changed by increasing *MaxT* in the warm weather conditions like at Göttingen in 1992, the accurate record of *MaxT* is extremely important for a reliable simulation of the population dynamics. When *MaxT* is between 26°C and 33°C, any severe error in recording *MaxT* would dramatically change the population dynamics.

8.4.7 Sensitivity to co-ordinated changes of *TX* and *MaxT*

The daily average temperature (*TX*) and daily maximum temperature (*MaxT*) play an opposite role in the simulation model for *M. dirhodum*. High *TX* is usually accompanied by high *MaxT* under field conditions. The positive effect of *TX* on the population development can then be reduced by the negative effect of high *MaxT*. The relationship between *TX* and *MaxT* can be described by a simple linear model (equation 8.5). The slope 1.29 was estimated using the weather data at Göttingen and Hanover from 1991 to 1996 during the simulation periods for all nine fields.

$$MaxT = 1.29\,TX \qquad (8.5)$$

The regression model accurately described the relationship between *TX* and *MaxT* (adjusted R^2 = 0.996; n = 288; F = 79502.7; P<0.0001). The regression revealed that *MaxT* was usually about 1.3 times of *TX*. In other words, if *TX* increased by 1°C, *MaxT* would increase by 1.3°C. Using this relationship, the sensitivity of the model to the co-ordinated changes of *TX* and *MaxT* was analysed.

The co-ordinated reduction of *TX* and *MaxT* changed the shape of the population dynamics only slightly (all adjusted R^2 > 0.99). Co-ordinately reducing *TX* by 2°C and *MaxT* by 2.6°C (= 1.3×2°C) only led to a 9% reduction of the population size. The reduction of *TX* by 1°C and *MaxT* by 1.3°C did not change the population size, since the slope, 0.998, was not significantly different from 1.0 (P = 0.862>0.05). The increase of *TX* by 1°C and *MaxT* by 1.3°C changed the shape a little bit, but reduced the population size by 33%. The increase of *TX* by 2°C and *MaxT* by 2.6°C led to big changes of the population development by an early abrupt population collapse (Fig. 8-18C, Table 8-17).

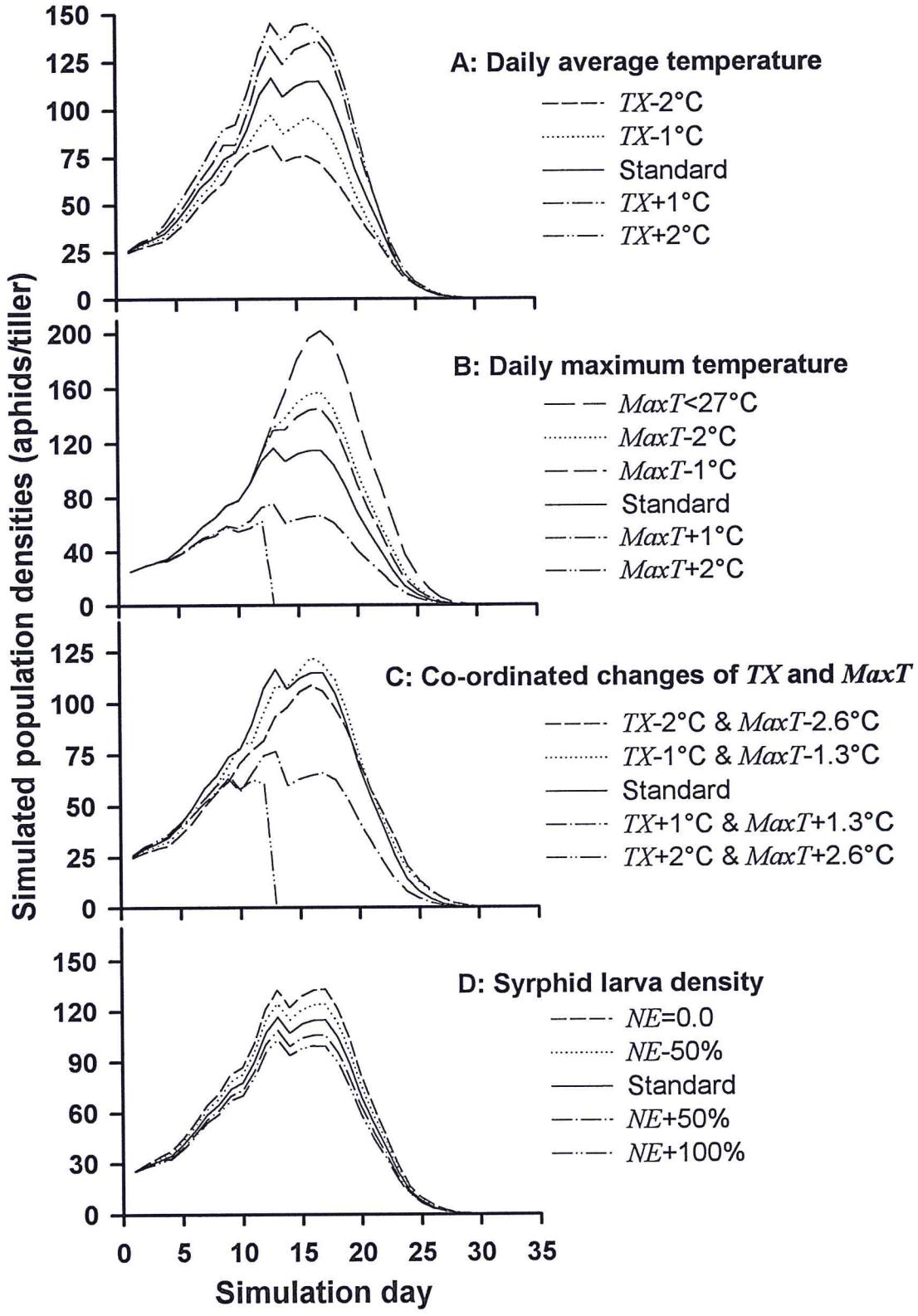


Fig. 8-18 Simulated population dynamics using the original and artificially changed conditions for the daily average temperatures (*TX*), daily maximum temperatures (*MaxT*), the co-ordinated changes of *TX* and *MaxT*, and syrphid larva densities, based on the original conditions at Göttingen in 1992.

The sensitivity of the model to temperature changes depends on the original temperature level. For the temperature level at Göttingen in 1992, the sensitivity of the model to the co-ordinated changes of *TX* and *MaxT* was lower than that of *MaxT* alone. All co-ordinated changes of *TX* and *MaxT* resulted in a certain reduction of the population densities, which indicate that the combination of *TX* and *MaxT* at Göttingen in 1992 was near the most favourable temperature condition for the population development of *M. dirhodum*. The correct measurement of *TX* and *MaxT* is indispensable to accurate simulations of the population dynamics of *M. dirhodum*.

Table 8-17 # Linear regression $Y = bX$ between simulated population densities under the original (X) *TX* and *MaxT* and **co- ordinately changed (*Y*) *TX* and *MaxT*** on base of the data at Göttingen in 1992.

TX and *MaxT*	Linear regression (n = 34)			
	R^2	F	$P<$	b
TX-2°C and *MaxT*-2.6°C	0.991	3476.4	0.001	0.905
TX-1°C and *MaxT*-1.3°C	0.995	6392.0	0.001	0.998
TX+1°C and *MaxT*+1.3°C	0.968	983.5	0.001	0.662
TX+2°C and *MaxT*+2.6°C	0.325	15.9	0.001	0.263

#, symbols are explained in the footnotes of Table 8-11.

8.4.8 Sensitivity to syrphid larva density

At Göttingen in 1992, the syrphid density (*NE*) was very low (only 0.04 larvae per tiller at the syrphid population peak), but the aphid density was very high (127 aphids per tiller at the peak). Therefore, the proportion of syrphid density to aphid density was very low. In order to make the sensitivity detectable, the changes of *NE* by ±50% and ±100% were adopted in the sensitivity analysis for *NE*.

The changes of syrphid larva density (*NE*) by ±50% and ±100% had almost no influence on the shape of the population curve (adjusted $R^2 \geq 0.999$) and caused only small and symmetrical changes of the simulated population densities. By removing the effect of *NE* (*NE* = 0), the population densities would be about 14% higher than the original simulation (Fig. 8-18D, Table 8-18).

Fig. 8-18D shows that the population development curves at different conditions of *NE* were close to each other at the beginning of the population increase and at the end of the population decrease. The distances between curves were relatively wider during the population peak.

The increase of *NE* had a small but significantly negative linear effect on the population development of *M. dirhodum*. A slightly inaccurate *NE* would not change the shape of the population development of *M. dirhodum*. The underestimation of *NE* would lead to an overestimation of the population size. The sensitivity analysis revealed that the slightly inaccurate estimation of syrphid numbers might not lead to a big error in the estimation of the population densities of *M. dirhodum*, especially in outbreak fields. However, when the population size of *M. dirhodum* occurred at a medium level, such as in the field at Hiddestorf in 1991, changes of *NE* could significantly modify the population size. In most cases, the aphid population level is unknown, therefore, an accurate sampling of *NE* is still necessary.

Table 8-18 # Linear regression $Y = bX$ between simulated population densities using the original (X) **syrphid larva density (*NE*)** and the changed (Y) *NE* on the base of the original *NE* at Göttingen in 1992.

NE	Linear regression (n = 34)			
	R^2	F	$P<$	b
-100%	0.999	59312	0.001	1.141
-50%	1.000	209133	0.001	1.070
+50%	1.000	157365	0.001	0.929
+100%	0.999	38446	0.001	0.880

#, symbols are explained in the footnotes of Table 8-11.

9 Application and extension of the model

9.1 Model application for yield loss estimation

Since *M. dirhodum* occurs together with *S. avenae* and *R. padi* in wheat fields, yield loss caused by *M. dirhodum* should be combined with the yield loss caused by the other two species in practical application. However, only the population densities of *M. dirhodum* were simulated in this study. The yield loss caused by *S. avenae* can be calculated by the simulation models developed by Carter et al. (1982) or Freier et al. (1996a). In this chapter, the yield loss caused by *M. dirhodum* is discussed.

The yield loss can be calculated by multiplying aphid densities by the yield loss per aphid per day. To calculate the yield loss caused by cereal aphids, aphid units (AU) are usually used. One AU is equal to three 1st to 3rd instar larvae (L13) or one 4th instar larva (L4) or one adult (Niehoff & Staeblein 1998). The number of aphid units at day i (AU_i) in a field can be calculated from the simulated population densities of L13, L4 and adults at day i. Zhou et al. (1989) summarised the daily yield loss (YLR) per aphid unit at different crop growth stages (Table 9-1) based on the results for *M. dirhodum* (Holt et al. 1984) and *S. avenae* (Lee et al. 1981). However, the only publication related to YLR at different GS (Holt et al. 1984) did not supply the data on the yield loss per aphid per day at detailed GS. Thus, the data in Table 9-1 were adopted in the yield loss calculation here.

Table 9-1 *Yield loss as a proportion of the potential yield per aphid unit day of *M. dirhodum*

Plant growth stage	Proportional yield loss / aphid unit /day
$GS < 40$	0.0
$40 \leq GS < 55$	1.556×10^{-4}
$55 \leq GS < 60$	3.765×10^{-4}
$60 \leq GS < 70$	4.870×10^{-4}
$70 \leq GS < 77$	3.830×10^{-4}
$77 \leq GS < 83$	1.920×10^{-4}
$83 \geq GS$	0.0

*: after Zhou et al. 1989

The yield loss (YL_n) for the period between the starting of simulation and end of the season can be calculated as follows:

$$YL_n = \sum_{i=1}^{n} YLR_i \cdot AU_i \qquad (9.1)$$

where i =1, 2, ... n, n is serial number of the simulation day. The yield loss per aphid unit at day i (YLR_i) can be found in Table 9-1 by checking the plant growth stage at day i. To calculate the yield loss caused by *M. dirhodum* during the whole growing season, the yield loss for the period before the starting of simulation (YL_0) has also to be included. As sampling or estimating the population density for the period before the starting of the simulation is a tedious and expensive work, a relationship between the yield loss before *GS* 69 and the population density at *GS* 69, i.e. the initial population density (IPD), would be very useful to solve the problem.

Niehoff (personal communication) and Lemke (personal communication) had investigated the population densities of *M. dirhodum* in nine fields. They sprayed insecticides at *GS* 69 to control the aphids and estimated yields in the nine fields (Niehoff 1996, Lemke 1999). Therefore, it is possible to use those data to establish a relationship between the population density at *GS* 69 and relative yield losses before *GS* 69. The population density at *GS* 69 is transformed into a number of aphid units (IPD_{au}). A logistic model can be used to describe the relationship between YL_0 and IPD_{au}:

$$YL_0 = \frac{a}{1+\left(\frac{IPD_{au}}{b}\right)^{-c}} \qquad (n = 9;\ P<0.001) \qquad (9.2)$$

where a = 0.0407; b = 6.1051; c = 2.2861. The model accurately (corrected R^2 = 0.996) described the relationship between the number of aphid units at *GS* 69 and the relative yield loss caused by the aphids before *GS* 69 (Fig. 9-1).

The cumulative yield loss after *GS* 69 at day n ($Yield\_Loss_n$) is the sum of YL_0 and YL_n:

$$Yield\_Loss_n = a \times (YL_0 + YL_n) \qquad (9.3)$$

According to the dry mass loss caused by *S. avenae* and *M. dirhodum* measured by Niehoff and Staeblein (1998), the calculated yield loss per aphid unit per day caused by *M. dirhodum* is about 70% (a = 0.7 in equation 9.3) of that caused by *S. avenae*. The simulated yield loss due to *M. dirhodum* in different fields can be demonstrated in Fig. 9-2.

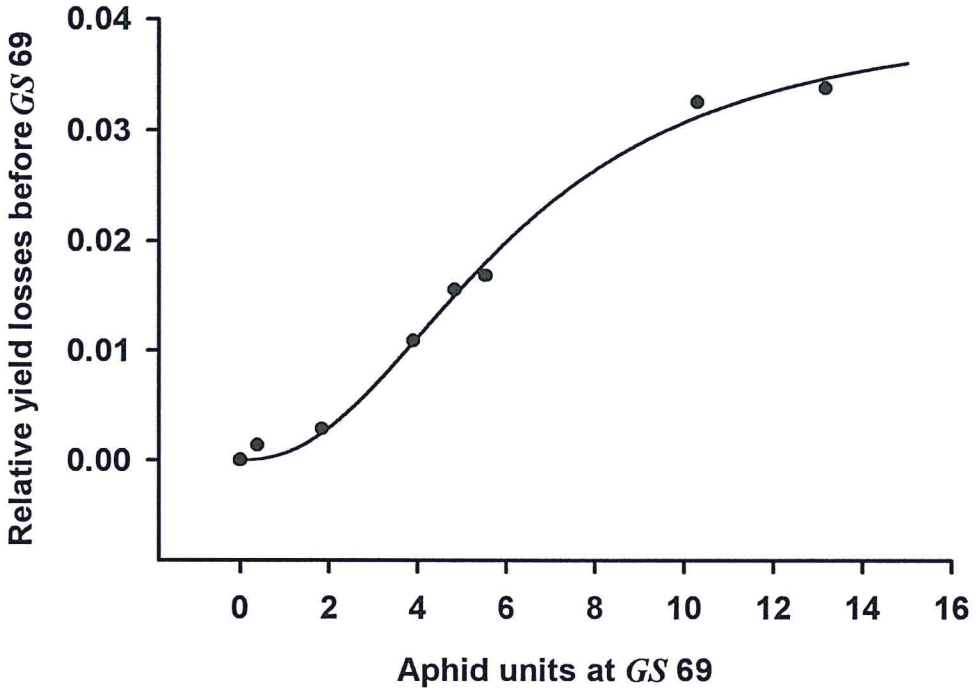


Fig. 9-1 Relationship between relative yield losses caused by the aphids before end of flowering (*GS* 69) and the number of aphid units of *M. dirhodum* at *GS* 69. The line is calculated from equation 9.2, dots are observed data from Niehoff (1996) and Lemke (1999).

Since yield losses assessed in the field (Niehoff 1996, Lemke 1999) were caused by three aphid species together, it is not easy to separate the yield loss caused only by *M. dirhodum*. Therefore, predictions in Fig. 9-2 are not compared with the observations. However, the total yield loss caused by cereal aphids can be calculated by combining this model with the simulation model for *S. avenae*. The economic loss (DM/ha) caused by aphid infestation can be calculated with the price of wheat grain (DM/ton) multiplied by the yield loss (ton/ ha). When the economic loss (DM/ha) caused by cereal aphids reaches the control cost (DM/ha), insecticide

application becomes meaningful in monetary terms. The aphid population level at this critical point is called "economic injury level" (Pu et al. 1990).

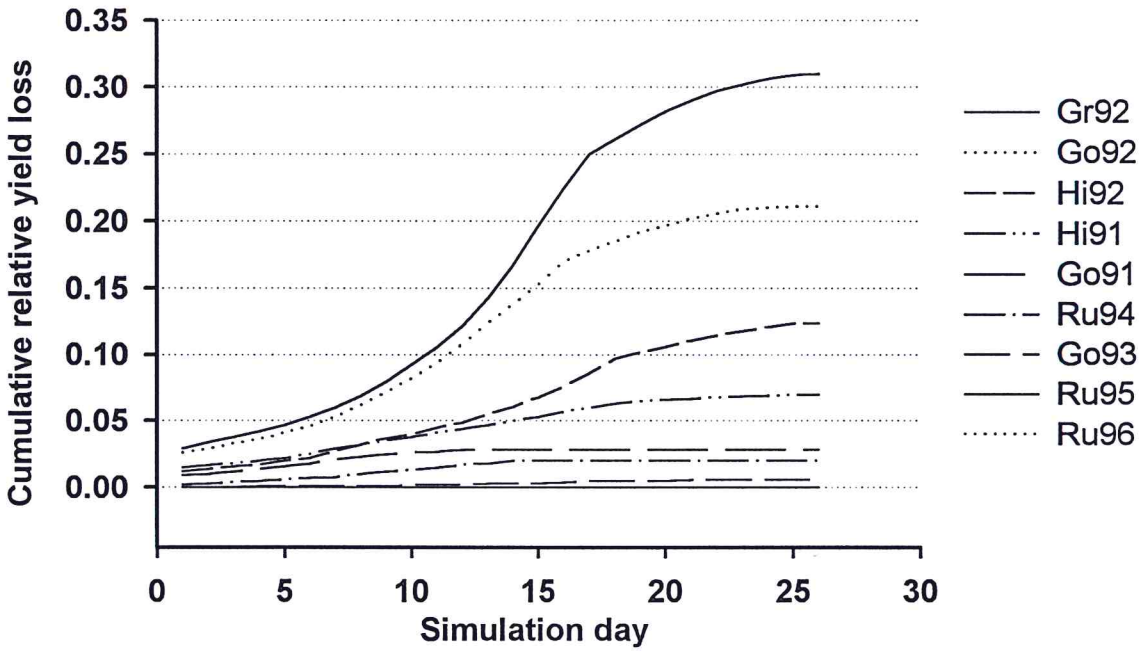


Fig. 9-2 Simulated cumulative proportional yield loss caused by *M. dirhodum* in nine different fields. Gr92.....Ru96 represent the name of location and observation year, such as Gr92 = Großenwieden 1992, Go92 = Göttingen 1992, Hi92 = Hiddestorf 1992, Ru94 = Ruthe 1994.

The yield loss estimation in Fig. 9-2 was partly dependent on the yield loss rate per aphid unit per day (YLR_i) which is influenced by the plant growth stage and the aphid density. The accuracy of YLR_i might be reduced by those non-detailed data. Further detailed experiments on the relationship between GS and YLR_i are necessary to improve the accuracy.

The aphid density may play an important role in determining yield loss per aphid unit per day (YLR_i). According to Niehoff and Staeblein (1998), when the aphids had infested the wheat between GS 65 and 83 with a constant density of about 10, 20 and 40 aphids per flag leaf, YLR_i were calculated as 0.000167, 0.000315 and 0.000317, respectively. This implies that a light infection (less than 10 aphids / flag leaf) results in a relatively small YLR_i, when the infection is higher than 20 aphids / flag leaf, YLR_i is doubled, but remains constant for higher densities. Basedow et al.

(1994) suggested that the action threshold for applying insecticide in Germany is three to five aphids (mixture of *M. dirhodum* and *S. avenae*) per ear and flag leaf at the end of flowering (*GS* 69). However, a low density does not result in a significant yield loss (Niehoff & Staeblein 1998). Thus, the yield loss caused by *M. dirhodum* could be lower in the fields with low population densities (Göttingen 1991, 1993, and Ruthe 1994, 1995, 1996). As detailed data about the relationship between aphid density and yield loss are not available, this relationship was not taken into the calculation in Fig. 9-2. Further data collections are needed to fill this gap.

Since the damage caused by *S. avenae* and by *M. dirhodum* is different (Niehoff & Staeblein 1998), the economic injury level should consider the proportion of *M. dirhodum* in the aphid population. In addition, the economic injury level considers only the cost-benefit relationship in one growing season. However, the ecological benefit could bring economic profit on the long run for farmers. All points discussed above indicate that the economic injury level should be higher than 3 to 5 aphids per plant for fields in which *M. dirhodum* is the dominant species.

9.2 Model for determining the plant growth stage

Host plants supply aphids with the essential habitat and nutrition. The micro ecological environment of aphids changes as host plants grow and develop from one stage to another. The sensitivity analysis revealed that the simulation model was very sensitive to changes of the plant growth stage. In order to diminish the simulation error caused by inaccurate *GS*, the field scored *GS* in intervals between three days and one week were used as one of the five inputs in this study. The daily *GS* between any two scored *GS* was calculated by linear interpolation. Usually, to get *GS* by direct scoring in the field is more accurate than an indirect estimation, e.g. predicting with a model. However, the direct scoring does not only need extra expenses, but also special knowledge to rank the plant growth stage. When weekly scoring of *GS* is not possible, obtaining *GS* from a model may be an alternative option.

A simple polynomial model of *GS* was developed by Carter et al. (1982) and then used by Zhou et al. (1989). Since the cumulative temperature was directly used in their model, any error of the cumulative temperature in the early growth stages of

wheat can result in a systematic error for the whole season. In order to diminish the systematic error and to improve the accuracy of the model, the daily average temperatures are transformed into a special cumulative temperature ($SumT_i$) using equation 9.4.

$$SumT_i = \sum_{j=b}^{i}(TX_j) - \sum_{j=b}^{d69}(TX_j) \qquad (9.4)$$

in the model, j is the Julian day of a year, j = 1, 2, ... 365; b is the Julian day at which the initial GS is scored as GS_b ; i is Julian day of a year when $GS \geq GS_b$ and $d69$ is Julian day of a year at which GS = 69; TX is the daily average temperature. Field data used in this study indicated that the aphid population mainly developed during the plant growth stage (GS) around 69 (between 60-80) and the simulation usually started at GS 69. This growth stage is selected as the middle point of GS during the main season for the data transformation. TX_j, b and $d69$ can be checked directly from the daily average temperatures from the German Weather Service and GS scored twice a week by Niehoff (1996) at Göttingen and Hiddestorf from 1991 to 1993.

Thus, a new plant growth stage model can be expressed as follows:

$$GS = 69 + 0.0557SumT_i - 0.0000415SumT_i^2 \qquad n = 80,\ P < 0.001 \qquad (9.5)$$

After the data transformation using equation 9.4, the cumulative temperature at GS 69 is the same for all of the field observations ($SumT_{d69} = 0$). The model can reasonably describe the plant growth stage by the cumulative temperature (corrected R^2 = 0.9244) (Fig. 9-3).

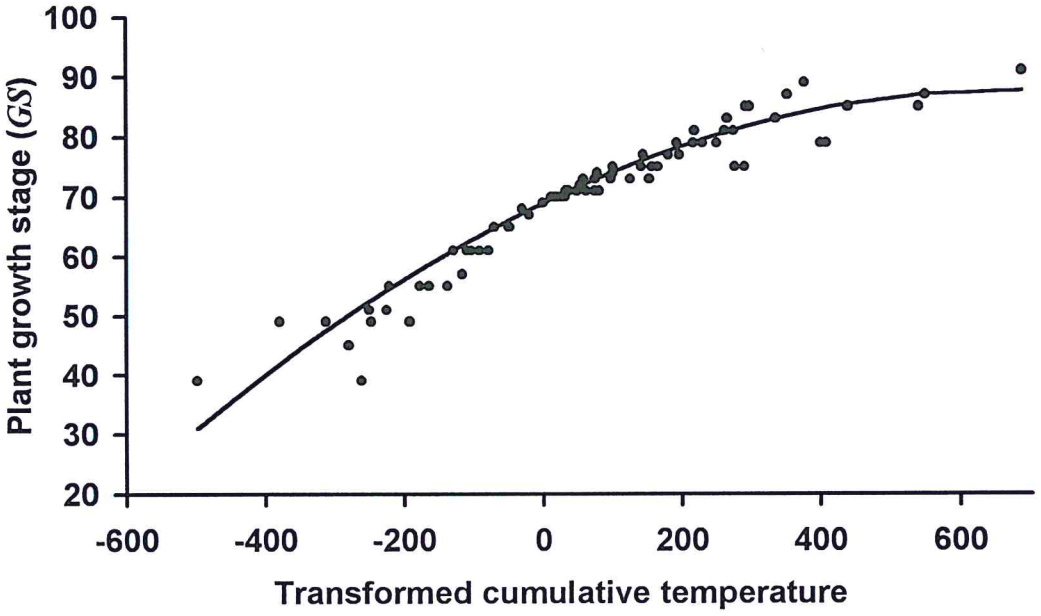


Fig. 9-3 The relation between transformed accumulated temperature and the plant growth stage in decimal codes (GS) according to Zadocks et al. (1974). Dots represent observed GS and lines are simulated GS with equation 9.5.

To apply equation 9.5 to calculate the plant growth stage (GS_i) at a given Julian day i, only one field scoring at a certain day and the daily average temperature from that day onwards during the growing season are needed. If the plant growth stage is scored as GS_b at day b, equation 9.5 should be valid with the unknown $SumT_b$:

$$GS_b = 69 + 0.0557 SumT_b - 0.0000415 SumT_b^{\,2} \qquad (9.6)$$

Two solutions can be obtained by solving this quadric equation. The smaller of the two solutions is the value of $SumT_b$. Thus, $SumT_i$ can be obtained from:

$$SumT_i = \sum_{j=b+1}^{i} TX_j + SumT_b \qquad (9.7)$$

in which TX_j , the daily average temperatures, can be read from the weather database. Thus, the plant growth stage (GS_i) at a given day i can be calculated with equation 9.5 using the value of $SumT_i$ derived from equation 9.7.

9.3 Model for the syrphid population dynamics

Syrphids are the most important aphid specific predators of cereal aphids in northern Germany (Poehling 1988, Poehling & Borgemeister 1989, Tenhumberg & Poehling 1994). The dominant species of syrphids in cereal fields is *Episyrphus balteatus* (Niehoff 1996). The analysis for the importance of each factor in this study revealed that syrphid larvae played an important role in the population dynamics of *M. dirhodum* in many cases. Therefore, syrphids were selected as the only predator in the simulation model.

In the prey consumption model, the number of syrphid larvae is an input variable of the model. It is a very difficult for users, especially for farmers, to do the field sampling to measure the predator density once or twice a week. The sensitivity analysis indicated that the population dynamics of *M. dirhodum* is not very sensitive to minor changes of syrphid number. Thus, the estimation of the population density of syrphids does not need a very high accuracy. Therefore, to build a simulation model to estimate the population dynamics of syrphids becomes one of the attractive solutions although difficult to achieve. An ideal simulation model for syrphid population dynamics should only use weather data, aphid data and simple initial population density of syrphids as inputs. Since the larva is the only stage that can predate aphids, the main output of the model should be the number of syrphid larvae.

The model can consist of four compartments: adult, egg, larva and pupa. The number of boxcars that is needed in each compartment can be determined according to the duration of each stage. The boxcar model can be built in a similar way like the aphid model. The compartment model can be used as a framework for the population simulation. The program modules for compartments of the aphids can also be consulted for programming the compartment model of syrphids. Therefore, the important points to build a simulation model for syrphids are to establish sub-models of development, reproduction and survival of syrphids. Because of the importance of *Episyrphus balteatus*, this species is taken as an example for modelling syrphid dynamics.

9.3.1 Sub-model of syrphid development

The duration of development of syrphids highly depends on temperature. Data from Tenhumberg (1992), Hart et al. (1997), Bhat and Ahmad (1988), Zeki and Kilincer (1990), and Roy and Basu (1977) were used to build a sub-model to calculate the length of development (in hours) of *Episyrphus balteatus* for eggs (*Dur_Egg*), larvae (*Dur_Larva*), pupae (*Dur_Pupa*) and whole immature stages (*Dur_Total*) at different temperatures (*TX*). A set of simple polynomial models was used to calculate the duration at a given daily average temperature (equation 9.8).

$$
\begin{aligned}
Dur\_Egg &= 24.17 - 1.97T + 0.0448T^2 \quad R^2 = 0.826 \quad n = 13 \quad P<0.01 \\
Dur\_Larva &= 105.74 - 9.36T + 0.219T^2 \quad R^2 = 0.935 \quad n = 16 \quad P<0.01 \\
Dur\_Pupa &= 102.83 - 9.12T + 0.2148T^2 \quad R^2 = 0.963 \quad n = 16 \quad P<0.01 \\
Dur\_Total &= 246.94 - 21.91T + 0.517T^2 \quad R^2 = 0.986 \quad n = 12 \quad P<0.01
\end{aligned}
\qquad (9.8)
$$

Geusen-Pfister (1987) found that the maximum longevity of adults for both sexes was 80 days, the average longevity 39.4 days, which was used as the longevity in the simulation model for syrphids.

The duration of development of the larval stage of *Episyrphus balteatus* is extended when the number of preys is low (Poehling & Borgemeister 1989). In addition, some other factors may determine longevity such as the availability of certain species of flowering plants, temperature, egg load etc. However, no relevant research results are available to be used to build an accurate model. Detailed experiments are necessary for establishing reliable sub-models of development and longevity of syrphids.

9.3.2 Sub-model of syrphid reproduction

Data on the egg production of syrphid females are very variable when experiments of different authors were compared. Bhat & Ahmad 1988 found that *E. balteatus* produced 70-80 eggs per female at 25°C and 60-65% RH, but no eggs were laid in the absence of aphids. However, Geusen-Pfister (1987) measured the mean fecundity per female as 780 eggs in a greenhouse under 15-35°C and 39-95% RH.

The mean sex ratio of female to male is 0.93. These data were used as total fecundity in the simulation model.

The total fecundity of a syrphid may not be a constant but a variable influenced by the size of the adults, aphid abundance, temperature, and food supply, e.g. the abundance and quality of flowering plants. Data on these aspects are not sufficient to be used in modelling the fecundity of *E. balteatus* so far. Further experiments are required.

If the total fecundity of a syrphid is known, the allocation of it to each age is required in the reproduction model. The oviposition counts of syrphids in intervals of two days (Geusen-Pfister 1987) are used to build a model to allocate the total fecundity at a given age. The age of adults in days is transformed into physiological age (*Age*) by dividing the adult age in days by the average longevity of the adults. The cumulative number of eggs oviposited over the whole lifetime can be transformed into cumulative oviposition rates by dividing the cumulative ovipositions of every two days by the total oviposition. The proportion of the lifetime fecundity distributed over the physiological age of adults (*EggLaying_P*) can be described by a Chapman model (SPSS Inc. 1997):

$$EggLaying\_P = a(1-e^{-b\cdot Age})^c \qquad n = 43 \quad R^2 = 0.99 \quad P < 0.001 \qquad (9.9)$$

where a, b and c are regression parameters estimated as a = 1.05, b = 1.87 and c = 4.28. The model can accurately describe the proportion of total fecundity allocated to a given physiological age of the adults (corrected R^2 = 0.99).

However, the behaviour of syrphids is different from that of aphids because syrphid adults have a high mobility to select the fields where they can find a suitable habitat and prey. The number of eggs laid within the wheat field does not only depend on the reproduction rate of adults, but also on the abundance of aphids. Tenhumberg (1993) described the relationship between aphid density and syrphid egg density with a simple linear regression model:

$$EggSyrphid = -0.005 + 0.0067 \cdot TotalAphid \qquad R = 0.81 \quad n = 18 \qquad (9.10)$$

EggSyrphid and *TotalAphid* are the number of syrphid eggs per tiller and the number of aphids per tiller, respectively. This model can be adopted in the present study.

The final egg density of syrphids can be described with a function that includes three factors: number of female adults in a field trap, density of aphids and daily deposition per female. The flowering plant resources may give a certain contribution to the egg density, but are not considered here in a quantitative manner.

9.3.3 Sub-model of syrphid survival

According to Geusen-Pfister (1987), the mortality of egg, larva and pupa of *Episyrphus balteatus* are about 46.2%, 22.4% and 7.7% in the greenhouse, respectively. 50% males and females die within 27 and 38 days after emergence, respectively. The maximum longevity of adult is about 80 days. These data can be used as the primary data in the calculation of survival rate. The effect of other factors can be incorporated as correction coefficients.

Similar to the development process of the larva and pupa stage, ageing of adult is dominated by temperature. Because the physiological age can represent the effect of the temperature on the ageing of adults, the mortality can be expressed as a function of the physiological age. A method, similar to modelling the mortality of the aphid adults caused by ageing (chapter 6.2), can be used to calculate the mortality of syrphid adults at a given normalised physiological age. The relationship between the cumulative mortality of adults (*CumuMort*) and the normalised physiological age (*Age*) can be described with a simple linear regression model:

$$CumuMort = 0.1167 + 0.419 Age \qquad R^2 = 0.974 \quad n = 43 \qquad (9.11)$$

The model accurately described the relationship between the mortality of syrphid adults and the physiological age of adults.

High temperature, relative humidity, rainfall, aphid species and abundance, parasitoids of syrphids and the intra-guild interaction among different species of natural enemies may also influence the mortality of syrphid larvae. However, the

quantitative information is not sufficient for modelling. Experiments are necessary to clarify those aspects.

Although the information that can be used in modelling syrphid dynamics is not enough, a preliminary model was built. Some of the parameters could be assumed according to expert's experience. The model can be improved as the knowledge on the relationships between biological processes of syrphids and various factors gradually increases. Another way is simply to build a black box model (regression model) with the field data. However, the application of the black box model may be limited to the area where the field data are collected since the system is not clearly understood.

10 Discussion

10.1 Comparison between the simulation model and previous models

10.1.1 Model Inputs

The previously published simulation models for cereal aphids require many input data to calculate the population dynamics. The input data needed in the simulation model for *S. avenae* built by Carter et al. (1982) in England include: daily maximum and minimum temperatures; the accumulated day degrees above 6°C; initial plant developmental stage; the number of tiller/m² at flowering or after; the start and finish days for both aphid immigration and presence of coccinellids, entomopathogenic fungi and hymenopteran parasitoids; daily suction trap catches of the aphids and the concentration factor; daily number of each instar of coccinellids; and hourly mortality caused by these parasites. In the only published simulation model for *M. dirhodum* in England (Zhou et al. 1989), input data are not clearly mentioned, however, according to the model description, the inputs may include most of the data used by Carter et al. (1982) except the natural enemies. The original simulation model for *S. avenae* population dynamics in Eastern Germany (PESTSIM-MAC) uses ten driving variables, i.e. mean daily temperature, precipitation, phloem sap supply to aphids, plant growth stage, number of ears/m², degree of aphid parasitism of apterous and alate 3rd to 4th instar larvae and adults, fungal infestation of aphids and predator abundance (Rossberg et al. 1986). Freier et al. (1996a) improved PESTSIM-MAC and renamed the newest version as GTLAUS 3.7. The model inputs are not listed, but temperatures every two hours, the initial population densities of each stage of both aphids and coccinellids at the end of flowering (*GS* 69) are emphasised (Triltsch et al. 1998), and the daily densities of other predators, parasitoids and entomopathogenic fungi are required (Freier et al. 1996a).

Compared to the above simulation models, the model described here uses much fewer input variables to simulate the population dynamics of *M. dirhodum* in winter wheat in northern Germany, i.e. initial population density of each development stage of aphids, daily average temperatures, daily maximum temperatures, weekly plant growth stages and weekly densities of syrphid larvae. Two of the five inputs i.e. the daily average temperature and the daily maximum temperature were commonly used

in the other models. Data on maximum, minimum and average temperature can relative easily be obtained from local or regional weather service agencies, or recorded in the field, using electronic thermometers. The remaining three inputs, i.e. the initial population density of the aphids, the plant growth stage and the density of natural enemies were obtained in different ways in the models mentioned above. Thus, they are compared in next chapters.

10.1.1.1 Initial aphid population

All models on aphid population development require information on the initial population density to start the simulation. Carter et al. (1982) and Zhou et al. (1989) used the daily suction trap catches of the aphids, enabling simulations earlier than *GS* 69. However, the construction and maintenance of suction traps only for monitoring cereal aphid immigration are very expensive. To correlate suction trap caches and densities of alate adults in fields, sampling of aphids in suction traps and in the fields during several years is needed. Yet, the populations on the crop and in the suction trap only occasionally showed temporal similarities (Dean 1978). Even if a reliable correlation exists, counting, separating and identifying cereal aphids from suction trap samples on a daily or weekly basis are tedious, expensive, and time consuming and require specialised knowledge, since the taxonomy of alatae is not very simple. In PESTSIM-MAC, an immigration model is used to describe the number of immigrated aphids in response to the accumulated temperatures above 7°C (Rossberg et al. 1986). However, in GTLAUS 3.7 (Freier et al. 1996a, Triltsch et al. 1998) and our model, the densities of each stage at *GS* 69 are used as the initial population.

Compared to suction-trap catches, direct sampling in the field at *GS* 69 is a comparatively easy and cheap way to estimate the initial population densities. Moreover, many farmers or extension service agencies are used to sample at *GS* 69 which is the officially recommended time to estimate whether the aphid density in their fields reached the action threshold for spraying in Germany (Basedow et al. 1994).

10.1.1.2 Plant growth stage

The plant growth stage has been used as an important variable in all simulation models for cereal aphids. A simple polynomial model to calculate the plant growth stage in decimal codes (Zadoks et al 1974) dependent on accumulated temperature was developed by Carter et al. (1982) in their simulation model for *S. avenae* and subsequently implemented by Zhou et al. (1989) in their *M. dirhodum* model. This polynomial model is simple and easy to use, but may be not accurate for varieties that have different development patterns, and even for different soil and water conditions (Carter et al. 1982). A physiological model for winter wheat, called TRISIM, developed by Matthäus et al. (1986), was used in PESTSIM-MAC (Rossberg et al. 1986). This physiological model can calculate the plant growth stage and phloem sap availability of the plants for the aphids. However, TRISIM is very complicated in its use, and it is difficult to estimate the model parameters. In GTLAUS, a wheat ontogenesis model developed by Wernecke and Clause (1992) was used (Freier et al. 1996a).

Since our model is very sensitive to minor changes of *GS*, an accurate estimation of *GS* is very important. Thus field scored *GS* data, collected in an interval from three days to one week, were used as one of the five inputs. The daily *GS* values were calculated by linear interpolation between two observed *GS* data points. This technique improved the accuracy of the simulation but increased the monitoring work. However, if the weekly scoring of *GS* is not possible for some model users, the polynomial model described in chapter 9.2 (equation 9.5) can also be used to determine the *GS* data needed for the simulation.

10.1.1.3 Natural enemies

Natural enemies play an important role in the control of aphid populations, although the importance of each natural enemy species varies in different regions. Zhou et al. (1989) did not include natural enemies in their simulation model for *M. dirhodum*. Carter et al. (1982) considered coccinellids, parasitoids and fungi in their model for *S. avenae* in England. In eastern Germany, Rossberg et al. (1986) ranked the degree of parasitism of apterous and alate L3 + L4, and adults separately and treated them as four inputs in PESTSIM-MAC. These authors also included fungal infestation of

aphids, and the number of aphid predators in their simulation. The natural enemy complex of aphids is very diverse. Some species are of a particular importance in a certain region, but not in others. For instance, in northern Germany the most important natural enemies of aphids are syrphids (Tenhumberg 1993, Niehoff 1996), whereas coccinellids are of greater importance in Norfolk, in the UK, (Carter et al. 1980) and in eastern Germany (Freier et al. 1996b). However, it is very complicated for modellers to handle all natural enemies in a simulation model and extremely difficult for model users to get the reliable input data of so many natural enemy species. Thus, in our model, only the effect of syrphids on the survival of the aphids is considered.

In all previously published simulation models of cereal aphids, natural enemy densities obtained by direct sampling in the field were used as inputs. However, weekly sampling of syrphid larva density is very time consuming. Freier et al. (1996a) used a simulation model to estimate the population density of coccinellids in GTLAUS 3.7. A simulation model for syrphids could therefore be an alternative method to assess the population densities of the hoverflies in the field. The syrphid simulation model described in chapter 9.3 is a first attempt to describe syrphid population dynamics with a model. The model is not yet well established because some elements of the syrphid biology and ecology, e. g. the effect of flowering plants on the longevity, reproduction of adults, are still poorly understood. However, as the knowledge on syrphids increases, the model can be improved gradually.

10.1.2 Model structure

10.1.2.1 Structure of the compartment model

In simulation models, compartment models are commonly used to describe the population dynamics of the different development stages of aphids. Carter et al. (1982) designed in total ten compartments to describe the populations of apterous and alate 1st, 2nd, 3rd, 4th instar larvae and adults. Rossberg et al. (1986) placed the 1st and 2nd instars, and the 3rd and 4th instars together in two compartments, whereas the alate 4th instar, immigrants, apterous and alate adults were treated as four individual compartments in PESTSIM-MAC. Freier et al. (1996) kept the same structure in GTLAUS 3.7. During the modelling processes, we observed that the number of

compartments was of minor importance for the simulation results. The first three instars have the same biological processes, i.e. survival, growth and development, and their development speed and survival rate are very similar (Dean 1974a, Zhou & Carter 1992). Usually, the 1st to 3rd instar larvae are not separately recorded during field sampling (Niehoff 1996, Lemke 1999). In order to facilitate the use of field data as the initial population density of each development stage of the aphids, the first three instars were considered as one compartment. Thus, six compartments were constructed in our model. They are apterous and alate 1st to 3rd instar, 4th instar larvae and adults.

10.1.2.2 Sub-model of reproduction

Carter et al. (1982) and Zhou et al. (1989) used the means of the fecundity at four different temperatures (i.e., 10, 15, 20 and 25°C) as the constant lifetime fecundity, which is homogeneously allocated to each hour-degree (H°). Rossberg et al. (1986) used a second order polynomial model to describe the effect of temperature on the fecundity of the aphids in PESTSIM-MAC. All authors mentioned above considered only the immediate effect of temperature on the reproduction, meaning that the reproduction rate at a time unit is only affected by the current temperature, but is independent from the temperature previously experienced by the aphids.

Little is known on the mechanism how temperature affects the reproduction of cereal aphids. Aphids start developing their ovaries prior to the adult stage. The environmental conditions during the development of ovaries may thus influence the subsequent reproduction. For instance, starvation in early development stages of *M. dirhodum* significantly reduces the lifetime fecundity (Grüber & Dixon 1988). Thermal history is very important for interpreting the fecundity of another aphid, *Myzus persicae* (Homoptera: Aphididae) (El-Din 1976). Moreover, the history of high temperatures in the parent generation can severely reduce the progeny birth weight and the reproductive rate in the F1 in *Aphis pomi* (Homoptera: Aphididae) (Carroll & Hoyt 1986). Our experimental results also indicate that the lifetime fecundity is related to the high temperature received by the aphids.

In this study, the temperature received by the aphids since they were born was tracked via the boxcar routine. The weighted average temperature previously

experienced by the aphids was calculated and used in a polynomial model to compute the lifetime fecundity. Consequently, the simulation accuracy is improved.

Zhou et al. (1989) and Rossberg et al. (1986) did not clearly describe the effect of high maximum temperature on the reproduction of *M. dirhodum* in their simulation models. Carter et al. (1982) defined the reproductive rate to be zero if hourly temperatures exceeded 30°C. Moreover, the reproductive rate was reduced linearly to zero between 20 and 30°C in their model. However, in our model, based on the experimental results, the effects of daily maximum temperature on fecundity were described with a model which includes three independent variables: temperature, exposure time, and the age of aphid (equation 5.4). Since high temperatures strongly slow down the population development in the cases with high daily maximum temperature, e.g. at Göttingen in 1991 and at Ruthe in 1994, the simulation accuracy for these fields was greatly improved by adding the effects of this factor.

Carter et al. (1982) and Zhou et al. (1989) did not incorporate the effect of adult age on the fecundity in their simulation models, as they assumed that adults only survive for a short period. However, an adult produces different numbers of larvae at different ages (Dean 1974a, Hu & Gui 1985, Zhou & Carter 1992). Results from our experiments indicate that adults of *M. dirhodum* can survive as long as one month at 20°C. Rossberg et al. (1986) used three conditional straight lines (together with the x-axis they form a trapezium) to describe the effect of adult age on fecundity. However, the daily reproduction does not change abruptly as age increased. In our simulation model, a Weibull function model was successfully developed to describe the accumulated reproduction vs. adult age. The daily reproduction is obtained by subtracting the accumulated reproduction at previous day from that at present day. The results show that the Weibull model can accurately simulate the daily allocation of total fecundity during the entire life span of adults (Fig. 5-2).

In addition to temperature, the plant growth stage is considered as an important factor for reproduction in all published simulation models for cereal aphids. Carter et al. (1982) and Zhou et al. (1989) used four conditional constants to describe the effect of plant growth stage on the reproduction. However, it is unlikely that plant growth stages affect reproduction in conditional constants. Rossberg et al. (1986)

used two conditional lines in their reproduction model, whereas we developed a rough logistic model, representing the gradual effect of plant growth stage.

By developing a calculation method for the weighted average temperature and applying this concept in a simulation model, at the first time the effect of temperature on the lifetime fecundity was successfully modelled. Weibull functions have been used to describe insect development (Wagner et al. 1984), and mortality (Bartlett & Murray 1986, Tingle & Copland 1989, Prasad 1990), but not to simulate the reproduction rate. Thus, the modelling method described in chapter 5.2 is of potential use for modelling the reproduction of other insects than aphids.

10.1.2.3 Sub-model of survival rate

The mean survival rates at different constant temperatures (not including 30°C) were used as fundamental survival rates of the aphid larvae in the present study, as well as in the models of Carter et al. (1982) and Zhou et al. (1989). In addition, Rossberg et al. (1986) considered rainfall as a mortality factor in their model. The effects of plant growth stages were commonly considered in the calculation of survival rates in all mentioned models. Conditional constant survival rates (Carter et al. 1982 and Zhou et al. 1989), a linear equation (Rossberg et al. 1986) and a preliminary logistic model (in the present study) were used to express the effect of the plant stage on aphid survival.

In the models of Carter et al. (1982), it was assumed that adults die as soon as they reach the average longevity. The survival curves from Dean (1974a), Hu and Gui (1985) and Zhou and Carter (1992) indicate that the adult longevity is not uniform. Thus, in the present model, a Weibull function model was developed to describe the distribution of the accumulated mortality at different ages, and the results show that the daily mortality caused by ageing can be accurately calculated with this function.

The effect of high maximum temperature on the survival rate of *M. dirhodum* was not considered in all other models of cereal aphids mentioned above, however, in this study, it turn out to be an important reason for the survival rate reduction and was expressed with a set of combined logistic models. Due to the incorporation of the effect of high maximum temperature, the simulation accuracy could be improved considerably.

10.1.2.4 Sub-model of development

In all simulation models for cereal aphids, temperature was considered the only factor to determine the development rate. Carter et al. (1982) used a simple linear regression model to describe the development rate for all stages of *S. avenae* at different temperatures. In contrast, Rossberg et al. (1986) used a sigmoidal development model. Zhou et al. (1989) developed two conditional linear regression models to calculate the development rate of *M. dirhodum* at the temperature regimes above and below 20°C. In this study, the development rate of *M. dirhodum* at normal and high temperature regimes was derived from a non-linear model developed by Wang et al. (1982). In addition, a model to calculate the standard error of the duration of development was established and used in the development transition model.

The effect of temperature on the longevity of the adult aphids was expressed in accumulated temperatures, using hour-degree (H°), by Carter et al. (1982) and Zhou et al. (1989), while Rossberg et al. (1986) described it with a third order polynomial model. A second order polynomial model was used in the longevity model of the present study. The effect of plant growth stage on longevity was expressed with conditional constants (Carter et al. 1982, Zhou et al. 1989), a straight line (Rossberg et al. 1986) and a preliminary logistic model (present study). Results from Zhou and Carter (1992) indicate that adults of *M. dirhodum* can survive about two times longer under fluctuating compared to constant temperatures. Therefore, the influence of the type of temperature, i.e., constant or fluctuating, on longevity was considered in our model. The effect of high maximum temperature on the longevity of *M. dirhodum* was not included in the previous aphid models (Carter et al. 1982, Zhou et al. 1989 and Rossberg et al. 1986), but considered in our study.

10.1.2.5 Simulation interval and developmental transition model

The effects of constant temperatures on the development, reproduction and survival are normally used in all simulation models of cereal aphids mentioned above. Three simulation intervals and corresponding average temperature of the three intervals are used in these simulation models, i.e. one hour (Carter et al. 1982, Zhou et al.

1989), two hours (Triltsch et al. 1998) and one day (Rossberg et al. 1986, Freier et al. 1996a and our model).

Constant 27.5°C leads to zero fecundity and constant 30°C results in zero survival (Dean 1974a and Zhou & Carter 1992). The weather data for Göttingen and Hanover (Lemke 1999, German Weather Service) indicated that hourly or double-hourly temperatures during growing seasons often surpass 27°C, or even reach 32°C. Since all models mentioned above use the population density at previous step to calculate that at the current step, zero survival caused by 30°C at particular step can result in zero densities at following steps. However, in reality, treating aphids until 30°C for one or two hours cannot cause zero survival. Our experimental results (Table 3-2 and 3-6 in chapter 3) indicate that survival and reproduction of *M. dirhodum* at temperatures above 27°C are highly dependent on the exposure time. Even 31°C for less than 8 hours did not result in zero reproduction and survival. To avoid the problem caused by such an "artificial" zero survival, Carter et al. (1982) and Zhou et al. (1989) used an average survival rate of the larvae at 10, 15, 20 and 25°C but excluded 30°C as a constant survival rate. However, they ignored the fact that the survival rate is reduced by 30°C constant temperature. In GTLAUS 3.7, the method to handle this problem is not mentioned (Triltsch et al. 1998).

In PESTSIM-MAC (Rossberg et al. 1986), GTLAUS (Freier et al. 1996) and our model, daily average temperatures were used to calculate the development, reproduction and survival. The daily average temperature is normally below 27°C, and the problem caused by hourly temperature does not appear in this situation. Since the development rates appear to be similar under both constant temperatures in the laboratory and fluctuating temperatures in the field (Cannon 1984), the difference of development at daily average temperature and hourly temperature may not be important for the simulation results. However, the intrinsic rate of increase raises as the constant temperatures increase up to 25°C (Zhou & Carter 1992), but the equivalent fluctuating temperatures greatly reduce the fecundity (Table 3-2) and survival rates (Table 3-6). The importance of the effect of short but high temperature on the aphids was ignored in PESTSIM-MAC (Rossberg et al. 1986).

Both daily and hourly simulations have their own problems and advantages in the applications of the results from constant temperature experiments. The daily simulation only needs the daily weather data that may be obtained easier and less expensive. Moreover, it can largely reduce the running time of the simulation. However, it may reduce the development uniformity of individuals. In the simulation models in England, the effective temperature of a particular instar was accumulated in hour-degrees (H°) and compared with the constant development time in H°. If the H° of the instar is greater than this constant limit, the aphids in that age class develop into the next instar (Carter et al. 1982). Since the simulation interval is only one hour, it can ensure individuals in the same boxcar having the same age. However, the daily simulation may cause that the aphids in the same boxcar require different times to finish their development. Thus, a normal distribution model was developed to describe the developmental transition rate of the aphids from one stage to another by using the age of aphids and the standard error of the age in this study. To correct the overestimation of survival and reproduction caused by our long simulation interval, the effects of short but high temperature were incorporated in our model in which the survival rates, longevity and reproduction are reduced as high daily maximum temperature ($MaxT > 27°C$) and the number of days with $MaxT > 27°C$ and the age of the aphids increased (Fig. 6-2 and equation 4.7 and 5.4).

The method used in modelling the aphid population dynamics in this study somehow successfully solved the problems caused by long simulation step and supplies a general example for simulating the ontogenesis of insects using daily average temperatures.

10.1.3 Model outputs

10.1.3.1General accuracy of the simulation models for cereal aphids

Compared with the only published simulation model for *M. dirhodum* (Zhou et al. 1989), our model has a high accuracy and a wide reliability. The model was validated with data from nine different fields, collected in six years at four different locations. The linear regression analysis revealed an excellent match between simulated and observed population densities (adjusted R^2 = 0.927. slope=1.059). 95% of the simulated densities fluctuated around the observed densities within a 7% deviation.

Zhou et al. (1989) only used data from three years to validate their model. Moreover, these authors did not do regression analyses between the predictions and observations, but their figures indicate that the predicted population densities were largely overestimated in two of the three years. In addition, compared with simulation models for *S. avenae* (Carter et al. 1982), our model also possesses a higher accuracy. Carter et al. (1982) validated their model using data from 1976 to 1980 collected in nine fields in England. Only in two out of nine cases, the population densities of *S. avenae* were accurately estimated. In the publications of PESTSIM-MAC and GTLAUS, detailed comparisons between simulated and observed data are not presented, only some cases with high accuracy, such as at Bezirk Halle in 1982 and 1984 (Holz & Wetzel 1989, Wetzel 1995) are shown.

The predictions from all models mentioned above are more accurate for the aphid densities during population building up than for those during population collapse, which consequently results in the low accuracy in their simulation. The most common failure is overestimation. In the seven inaccurate prediction cases in Carter et al. (1982), only aphid density in one case was underestimated, but in six cases largely overestimated. The model by Zhou et al. (1989) also largely overestimated aphid densities during the collapse phase of the populations. Therefore, some important control factors must be incorporated in the simulation models to stop the simulated density increase at a correct time (at peak) and furthermore to reduce the simulated values. Natural enemies are usually used as an important control factor. Zhou et al. (1989) did not consider the natural enemies, which may be one of the reasons for the overestimation. Carter et al. (1982) included the impact of parasitoids, fungi and coccinellids on *S. avenae* in their model, however, the simulated population densities during the crash of the aphid population did not correspond with the field data. Rossberg et al. (1986), Holz and Wetzel (1989) and Freier et al. (1996a) could demonstrate that aphid population densities would be several times bigger without the impact of natural enemies. These authors concluded that beneficials are the major factors causing the population collapse. However, the simulation results show that the including of natural enemies is not sufficient to suppress the population increase. This may be related to the unreliable field data collection of the natural enemies, but also implies that other important factors may exist, but have not been

(properly) incorporated in their model. In the earlier stage of the model development, we also found the population density during the later period of the simulation was too high compared to the observed population in some cases. In time sequences, the density of natural enemies cannot be responsible for aphid population collapse. Based on the analysis of the field and weather data, we found the maximum temperature might be an important factor to suppress the population development and cause the early collapse. Therefore, an experiment was carried out to detect the effect of short but high temperature on the survival and reproduction of the aphids. The experimental results were incorporated in our simulation model and dramatically improved the simulation accuracy for some cases, e.g. Göttingen 1991 and Ruthe 1994. High temperature was also considered in GTLAUS 3.7, but was only considered as an important factor for the interactions between *S. avenae* and coccinellids based on their experiment results on the effect of increasing temperature on the wheat-aphids-predator system (Freier et al. 1996a). The aphid population was reduced through the high temperature promoting the predation of coccinellids and accelerating the senesces of wheat (Freier et al. 1996b, Triltsch et al. 1998). They did not measure the direct effect of the high temperature on aphids alone, thus may have neglected the negative impact of high temperature on the aphids, which is important for an accurate simulation in cases where coccinellids are unimportant.

10.1.3.2 Simulation accuracy for the individual fields

Although simulations of the population dynamics of *M. dirhodum* in all nine fields were generally quite accurate, simulation accuracy in some cases still needs to be improved. The model significantly overestimated the population size of L4 and underestimated the population size of adults. Since the total aphid population densities were accurately simulated, the overestimation of L4 may be due to an underestimation of the adults. As the distinguishing between L4 and adults in large-scale population samplings is rather difficult, simple identification errors may partly explain the lack of accuracy in some of the estimations.

The model failed to predict the extreme low densities in the early part of the season and the small peaks after late July in Ruthe 1995 and 1996. The effect of syrphids on the survival rate was calculated mainly according to the total number of *M. dirhodum*.

The effect of aphid species other than *M. dirhodum* on the predation rate of syrphids could not be perfectly included in the model, leading to an underestimation of the predation rate of the syrphids because the predation rate were reduced by very low aphid density in our predation model. As densities of aphids were very low before late July, the sample size was probably too small for an accurate estimate of the aphid and syrphid number. The underestimation of *M. dirhodum* densities at the end of the season in Ruthe 1995 and 1996, and in Göttingen 1993 was apparently due to overestimating the effect of plant growth stage on the population development of the aphids. The model did not accurately predict peak aphid densities in Hiddestorf 1991. It is difficult to explain this with the field data, but may be related to the sampling accuracy, because the density at the peak is the only point, which is not accurately described by the model. It might have been caused by an overestimation of the high maximum temperature in the field. Other reasons, such as a local shower, might also reduce the maximum temperature, which is lower than the data from the weather station in Hanover. The model overestimated *M. dirhodum* densities during the population crashes in Grossenwieden 1992 and Hiddestorf 1992. Mainly because the other predators rather than syrphids were not included in the simulation model. The details will be discussed later in next chapter.

10.2 Factors not perfectly taken into consideration

10.2.1 Natural enemies

The simulation model presented here considered only one of the most important group of aphidophagous predators, i.e., syrphids. The effects of other aphid predators and parasitoids were neglected. However, as described in the last chapter, this may result in an inaccurate simulation. The average proportion of larvae of syrphid, coccinellid and chrysopid in 1992 for three sites (Göttingen, Grossenwieden and Hiddestorf) is 58%, 23% and 19%, respectively (Niehoff 1996). However, the proportion of syrphid in the later two sites was much lower, so that the coccinellids and chrysopids are important stenophagous species in these two cases. However, the predation by coccinellids and chrysopids and the impact of parasitoids were not included in the model. Thus, the underestimation of the impact of natural enemies other than syrphids might have been the main reason for the overestimation of *M.*

dirhodum densities during the population crashes in Grossenwieden 1992 and Hiddestorf 1992.

Coccinellids and chrysopids are proved also to be important natural enemies of aphids in eastern Germany (Freier et al. 1996b, Freier et al. 1997, Rappaport & Freier 1998, Triltsch & Freier 1998). Since the abundance of coccinellids always increase during the later part of the season, a close correlation between coccinellid predation and the population breakdown of cereal aphid is often observed (Poehling & Borgemeister 1989). Thus, the overestimated *M. dirhodum* population densities in the simulation during the population breakdown might have been due to neglecting the impact of aphid natural enemies other than syrphids. Consequently, the simulation accuracy of this model might be reduced in situations where non-syrphid natural enemies of aphids predominate.

The model could be significantly improved if the impact of ladybird beetles and aphid parasitoids would be incorporated.

In most studies on the relationship between predators and aphids only the relative proportion of aphids and predators were considered. For instance, Tenhumberg (1993) carried out experiments either in small containers in the laboratory or in field cages. However, under the field conditions, even if the relative proportion of predator and prey remains on the same level, the absolute densities of predators and prey per plant may vary to a large extend. Predatory efficacy may be reduced in the field at low absolute densities, because the predators have to spend extra time and energy to search for preys. Thus, the daily prey consumption of a predator not only depends on the predator : prey ratio but also on the absolute aphid and predator densities per plant or square meter. Hence, further research is needed for improve predation models at low population densities of both predators and preys.

The predation efficacy of coccinellids for *S. avenae* is enhanced at high temperatures unfavourable for the aphids (Freier & Triltsch 1996, Freier et al. 1996 and Triltsch 1997). However, the effects of high temperatures on the predation efficacy of syrphids is still not very clear and could therefore not be incorporated in this simulation model. Consequently, further experimental studies on the effects of high

temperatures on development, survival, reproduction and predation efficacy of syrphids are needed.

10.2.2 Rainfall

Varying effects of rain on the population development of cereal aphids have been reported. Heavy rainfall can dramatically reduce aphid populations (Ba-Angood & Stewart 1980). According to Lourenco and Oliveira (1983), in Portugal rainfall rather than natural enemies or temperature is the main factor regulating the population density of cereal aphids, mainly *R. padi*. Basedow (1987) observed, that heavy rainfall significantly reduced the density of *S. avenae* at the milky ripe stage but not at water ripe, but had no significant effect on *R. padi*. Cannon (1986) considered rainfall by itself not an important mortality factor, but apparently dislodgement of aphids by gusts of wind appeared to be important. Korchagin (1979) even concluded that higher total precipitation in May and June could cause abnormal increase of cereal aphids (mainly *Diuraphis noxia*, Homoptera: Aphididae) in Kazakhstan.

Heavy rainfall (115-173 mm) per day can wash off aphids from their host plant (Kushnerik 1981). Zuniga (1985) evaluated the direct effect of rainfall on aphid colonies in wheat. Simulated strong rainfall at a rate of 30 mm/h for 30 minutes resulted in a drop off of most aphids (*R. padi* and *S. avenae*) from the wheat seedlings. However, under natural rainfall conditions (i.e., 7.4 mm/ 24 h), on average 45.6% of *R. padi*, *S. avenae*, *M. dirhodum* and *Schizaphis graminum* (Homoptera: Aphididae) left the plants. Likewise, Knaust and Poehling (1996) observed, that rain has a positive effect on aphid spread. Disturbances of leaves caused by strong gusts of wind or large rain droplets are of considerable importance for the initiation of aphid dispersal (Mann et al. 1995). Rainfall may mechanically kill aphids. However, so far the data related with the further fate of aphids after they fell down are insufficient to build an accurate model. In this study, we found that the aphids were washed off from wheat seedlings by irrigation in the stock culture cage. Most of them climbed up to plants again later. Initially the effect of rainfall on the survival rate of cereal aphids according to the data from Mann et al. (1995) was incorporated in this model, but since it did not significantly improve the simulation accuracy, it was subsequently removed from the model.

The number of cereal aphids infected by Entomophthorales increased during and after heavy rainfall (Dean & Wilding 1971 and 1973). However, the precipitation was more associated with the fungal infection of *S. avenae*, which inhabits upper portions of the host crop, but had little effect on that of *M. dirhodum*, which inhabits more humid microenvironments (Feng et al. 1991). However, negative effects of rainfall on the aphid population development may be as well compensated by some indirect positive effects of rainfall. Rainfall enhanced dispersal can be helpful for aphids to find new host plants, particularly at times of high population densities. Rainfall may reduce unfavourable high temperatures for the aphids. Moreover, rainfall normally has a positive effect on plants, thus improving the host plant quality for the aphids.

By consequence, it is at present rather difficult to incorporate the various different effects of rainfall on the population development of cereal aphids in general and on *M. dirhodum* in particular into simulation models. Thus, more data from controlled experiments are needed to improve the simulation accuracy.

10.2.3 Downwards moving and dislodging

M. dirhodum may find favourable conditions for feeding and staying by moving between different parts of the plant, and between plants. Feeding sites of *M. dirhodum* differ during the growing season (Cannon 1986). In field studies in northern Germany, Niehoff (1996) demonstrated that the proportion of *M. dirhodum* on the flag leaf varies over years. In a year with high maximum temperatures during the period of aphid infestation, the proportion of aphids on the flag leaves was low (30%). However, in years with comparatively lower maximum temperatures, the proportion of aphids on flag leaves increased to 54-60%. In a field experiment in France, *M. dirhodum* usually stayed on lower leaves (Dedryver 1978), possibly caused by the high temperatures on the upper part of the plants. Therefore, *M. dirhodum* might be able to avoid unfavourable temperatures by moving to lower parts of the plants.

M. dirhodum may also avoid unfavourable conditions by dislodging from the original host plant. High temperatures may be one of the factors that can cause *M. dirhodum* dislodging. Results from a laboratory experiment, conducted within the framework of the here presented study, show that when aphids were introduced into a growth

chamber with high temperatures, most adults and older instar larvae dropped from the plants to the soil, apparently searching for cool gaps on the surface. When the aphids were later returned to normal temperature conditions (i.e. 20°C), they immediately climbed on the plants. Since moist soil was heated up slower than air, aphids can possibly reduce the detrimental effects of high temperatures by moving to the soil surface. Thus in the field, aphids may spend periods of high temperatures preferably in the lower strata of the host plants and/or on the moist soil surface under the shadow, though the latter increases the risk of predation, e.g. by carabids and staphylinids (Janssens & De Clercq 1990, Winder 1990). Parasitoids (Ruth et al. 1975) and predators (Brodsky & Barlow 1986, Losey & Denno 1998) were found to be important factor for aphid dislodging. For example, considerable numbers of *Schizaphis graminum* (Hom: Aphididae) left plants on which the parasitoid *Lysiphlebus testaceipes* (Hym. : Braconidae) was present and fell to the ground on which they were killed by high soil temperatures (when air temperature was 29°C, the soil temperatures range from 45 to 54°C). The pea aphid, *Acyrthosiphon pisum*, drops off the host plant when confronted by coccinellids and syrphids (Brodsky & Barlow 1985, Losey & Denno 1998), and it less likely drop when the environment was hot and dry than when it was more benign (Dill et al. 1990). Thus, the drop behaviour of aphids may be related to soil moisture. Since the mobility of young aphid larvae is very low (Knaust & Poehling 1996), this behaviour is important only for the old instar larvae and adults.

In this study the effects of high temperature on *M. dirhodum* were tested in clip cages, which implies that the aphids had no chance to escape the detrimental effects of high temperatures. In the field, herbicides and fungicides may also cause dislodging of aphids. However, possible dislodging of *M. dirhodum* was not considered in this model, and may thus be one of the reasons for the lack of simulation accuracy in certain cases, because the aphid dislodging may lead to sampling errors for aphid densities.

Since aphid densities on ears and flag leaves are used to determine the economic threshold of cereal aphids in Germany (Basedow et al. 1994, Niehoff & Staeblein 1998), the downward movement and dislodging and the subsequent re-climbing of

M. dirhodum may be important factors for a reliable estimation of the aphid populations. Therefore, more research should be devoted to detailed studies on the dislodging and re-climbing behaviour of *M. dirhodum*, particularly with regard to high temperatures and rainfall pattern.

10.2.4 Morph determination

The morph determination model used in this study was originally developed for *S. avenae* (Carter et al. 1982). The model is based on the plant growth stage and the aphid density. Apterous aphids produced significantly more alatae when reared on mature plants (milky ripe stage) than on young plants (Howard & Dixon 1992). Crowding was found to be an important factor inducing apterous and, to a less extent, alate parents of *M. dirhodum* to produce alate progeny (ElKhider 1979). Therefore, the alate production of the aphid can be expressed as a function of plant growth stage and total population density. *M. dirhodum* on laboratory grown plants produces much less alatae than in the field (Howard & Dixon 1992). This indicates that the plant growth stage and the population density may not be the only factors governing the alatae production. Therefore, the morph determination model for *S. avenae* of Carter et al. (1982) may not be accurate enough for *M. dirhodum*. On the other side, the accurate differentiation between alate and apterous 4th instar larvae in large-scale samplings may not be very easy. That inaccurately observed data were used to compare with the predicted results may also be one of sources for the differences between the observations and simulations.

10.2.5 Temperature difference between field and weather station

In the present simulation, the weather data at Hanover (1991-1992) from the German Weather Service were used to simulate the aphid densities at Grossenwieden in 1991 that is about 60 km south west of Hanover, and at Hiddestorf in 1991-1992 that is about 25 km south of Hanover, since the weather data at those villages are not available. It is possible that weather conditions in the sampling fields are different from the weather station, especially the short rainfall and hourly temperature influenced by the short rainfall. The daily average temperatures recorded in the fields at Göttingen 1991 to 1993 (Niehoff 1996) differ from those collected by the weather station. Since the model is very sensitive to even small changes in temperature, the

observed differences between the predictions and the observations might be due to differences between data from the weather stations and the actual meteorological conditions in the respective fields.

10.2.6 Host plant

Host plants supply aphids with the essential nutrition. The population development of the aphids depends on the plant growth stage (Vereijken 1979, Watt 1979). In this study, high *GS* values were considered one of the most important factors for the crash of aphid populations at the end of the season. Old host plants do not support high aphid densities. However, since aphids can survive on the green leaf area even at late *GS* stages, Howard and Dixon (1992) believed that *GS* values have no effect on aphid population development. For low aphid densities, this may be true. For example, in Göttingen 1993 and Ruthe 1996, aphids could survive on the plants as late as *GS* 85. Since this apparently inverse density dependent effect of high *GS* values on *M. dirhodum* populations was not properly considered in this model, low densities at late *GS* stages, such as in Göttingen 1993, and Ruthe 1995 and 1996, were not successfully simulated.

The plant growth stage was the only host plant quality related index used in this study. Daily average temperature was the only independent variable in the plant growth stage model. However, the plant growth stage may also be affected by other factors than temperature, such as soil water, fertiliser and variety. In fact, the effect of host plants on aphid population development can be mainly explained by the nutritional quality of the hosts. Any factor that could directly or indirectly change the nutrition status of the host plant could influence the population development of the aphids.

The nutritional quality of host plants for aphids doesn't only depend on the quantity but also on the quality of phloem sap (Rossberg et al. 1986). The composition and concentration of amino acids in the phloem sap change with different host species, plant growth stages (Weibull 1987) and plant parts (Kuo-Sell 1989). These differences may cause *M. dirhodum* and *S. avenae* to feed on different parts of the plant (Kuo-Sell 1989).

Crop management practices, drought and infections by diseases may indirectly influence the aphid population development through changes in the quality of the host plants. The nutritional status of plants significantly affects *M. dirhodum*. The fecundity of aphids reared on nutritionally stressed plants was significantly lower (Grüber & Dixon 1988). High nitrogen application levels can substantially increase population densities in *M. dirhodum*, but only to a much lesser extend in *S. avenae* (Weibull 1987, Zhou & Carter 1991, Duffield et al. 1997, Honek 1991b). High nitrogen doses enhance dry mass allocation to upper parts of the plants and increase the relative size of the leaves, and *M. dirhodum* may thus profit from higher leaf quality (Honek 1991b). Drought stressed winter wheat is more favourable for *M. dirhodum*, but not for *S. avenae* (Pesel & Poehling 1988). However, according to Pons and Tatchell (1995) drought stress reduces the subsequent reproductive capacity of *S. avenae* and *R. padi*. Feeding on leaves infested by powdery mildew increased the fecundity of *M. dirhodum* (Pesel & Poehling 1988). BYDV infestations can significantly promote the population development of cereal aphids (Ajayi & Dewar 1982, Fereres et al. 1989). However, Fiebig and Poehling (1998) found BYDV plays a negative role in population development of aphids but can stimulate alate production. Infestation by root gall nematodes (*Meloidogyne* spp.) changed the free amino acids and sugars in the phloem sap of oat, increased the content of sucrose, and led to a decrease in the total concentration of amino acids and amides (Sell & Kuo-Sell 1989). After a nematode infestation, the mortality of *M. dirhodum* was enhanced and the fecundity and bio-mass production of the aphids was reduced (Sell & Kuo-Sell 1990). Farming intensity affects population densities of *M. dirhodum* but not of *S. avenae*. Decreasing the farming intensity was clearly related to lower infestation levels of wheat plants with *M. dirhodum* (Hasken & Poehling 1995).

Such factors were not included in the simulation model presented here. However, incorporating host plant quality related factors other than plant growth stages might significantly improve the accuracy of the model.

10.3 Model applications

10.3.1 Key factor analysis

The population dynamics of cereal aphids are very complicated. The biotic and abiotic ecological factors and interactions among them (Table 2-1) result in a specific pattern of the population development in each field. To understand the effect of the most important factors on the aphid population density by experiments is very difficult. For example, five possibly important factors are selected in our study. A perfect experiment testing these five factors, each factor with four levels, is practically not possible to implement. Single or double factor experiments are usually carried out ignoring the possible interactions between tested factors and those not included in the experiment. It is also difficult to reliably explain the population dynamics of cereal aphids by statistically analysing the field data, because the statistical models normally are suitable to analyse the relationship between population densities at one point (e.g. at the peak for a number of fields) and the possibly responsible ecological factors. Usually, the detailed changes of the population dynamics cannot be clearly explained by the analysis.

However, a simulation model, which has been successfully validated, can be effectively used to analyse the mechanisms of the population dynamics by doing simulation experiments. Usually, the sensitivity analysis is applied to investigate the key factor for the population dynamics of cereal aphids (Carter 1982, Rossberg 1986, Freier et al. 1996, Thriltsch et al. 1998). The same procedure was followed in the earlier sensitivity analysis in our studies. However, we found that this method is not suitable to identify the key factor for population dynamic changes, because the sensitivity of the model to a factor is always related to the original value. For example, the model does not sensitively react to the daily maximum temperature changes of ± 1°C or ± 2°C in Göttingen 1993 because of the very low maximum temperature ($MaxT$). However, this does not indicate that $MaxT$ is not an important factor for regulating the population dynamics. $MaxT$ is proved to be a critical factor for the population development after the end of flowering (GS 69) in most cases in our study. On the other side, the model is always sensitive to the plant growth stage (GS), which actually is a very stable factor in most cases and is usually not

responsible for the specific population pattern in a field. To get a clear image why the population density in a field is so different from another, a direct way is to replace the original ecological conditions of this field by the corresponding conditions in the compared field. Based on this principle, a standard field was selected and compared with other fields by sets of simulation experiments under replaced ecological conditions of the standard field. Thus the relative favourability of each factor for the population development in each field was successfully evaluated. The aphid population density is accurately explained by the integrated favourability of all ecological factors. The importance of each factor in regulating the population pattern of a given field was also analysed. The key factor for the population pattern of different fields was clearly shown in Fig. 8-13, 14, 15 and 16. The method, to calculate the favourability and the importance of ecological factors with a simulation model, was the first time used in the key factor analysis of cereal aphid population development. It supplied a new way for analysing the mechanisms of population dynamics.

Based on the analysis of the favourability and the importance of ecological factors, many interesting results are obtained. Relatively high *IPD* at *GS* 69, e. g. 10 aphids per tiller at Hiddestorf in 1992, is a precondition for a population outbreak. The daily average temperature (*TX*) and the nutrition supplied by host plants (*GS*) are the essential driving variables for the population development. Low *TX* during the early part of the season or early-matured host plants would slightly restrict the population development of *M. dirhodum*. Unfavourably high temperatures (*MaxT*) and the impact of natural enemies (*NE*) have a significantly negative influence on the aphid population development. Early population crashes are mainly caused by these two factors.

According to the analyses of the simulation results, outbreak conditions of *M. dirhodum* in northern Germany can be summarised as follows: 1) High initial population density at *GS* 69 (e.g. at Göttingen, Grossenwieden and Hiddestorf in 1992); 2) Moderate daily average temperatures (about 17-20°C) between *GS* 69 and *GS* 75; and 3) Low population densities of aphid predators between *GS* 69 and *GS* 75.

If one of the following three scenarios occurs, no outbreaks of *M. dirhodum* will be expected: 1) The initial population density of *M. dirhodum* at *GS* 69 is low (e.g. at Ruthe in 1995 and 1996, and at Göttingen in 1993); consequently aphids will not have sufficient time to build up high population levels before the wheat becomes mature; 2) The daily average temperature is higher than 25°C between *GS* 69 and *GS* 75; 3) High population densities of aphid predators between *GS* 69 and *GS* 75 (e.g. at Göttingen in 1993).

10.3.2 Decision-making for spraying

To reduce the cost and to overcome the problem caused by application of insecticides, e.g. reducing the diversity and diminishing the population densities of natural enemies (Powell et al. 1985, Basedow 1990, Basedow 1995, Dinter & Poehling 1992a and b), unnecessary insecticide application should be avoided. Several action thresholds were developed in Germany (Wetzel 1995). One of these thresholds is officially recommended for spraying insecticides, i.e. four aphids per ear and/or flag-leaf at the end of flowering (Basedow et al. 1994). This threshold is very simple and can be used easily.

However, since the aphid density usually is still low before *GS* 69, the damage is not very big (Niehoff 1996, Lemke 1999). The aphids at and after *GS* 69 can cause the major yield loss (Lee et al. 1981, Watt & Wratten 1984, Oakley et al. 1993). Niehoff & Staeblein (1998) found that constant aphid densities of 10 *M. dirhodum* per flag-leaf or five *S. avenae* per ear do not cause significant reduction of the thousand seed weight during *GS* 65 to *GS* 83. This indicates that four aphids per ear and flag-leaf cannot result in a significant yield loss, if the aphid density does not increase after *GS* 69. In other words, the population development after *GS* 69 rather than the population density at *GS* 69 causes the yield loss. Therefore, determining the aphid population density after *GS* 69 becomes the most important issue for the decision making.

Our favourability analysis shows that in most of the nine fields, the aphid population size after *GS* 69 is related to the initial population densities (*IPD*), i.e. the aphid densities at *GS* 69 (Fig. 8-12A and 8-12F). Further simulation experiments analysing

the contribution of each factor to the changes in the population dynamics show that *IPD* is a very important factor to determine the population development level after *GS* 69 (e.g. Fig. 8-15A1 and 8-15B1). The sensitivity analysis also demonstrates that population development after *GS* 69 is nearly 1:1 proportionally related to the changes of *IPD*. These analyses demonstrate that *IPD* is a strong indicator for the population development after *GS* 69. Therefore, the use of *IPD* to judge whether the aphid density is above the action threshold may fit many cases, e.g. most of the fields in the 44 experiments from Basedow et al. (1994). However, in this action threshold, the population development after *GS* 69 is not considered.

The results from our analysis of the favourability and the importance of ecological factors also illustrate that *IPD* is not the only important factor in determining the population densities after *GS* 69. The daily maximum temperature (*MaxT*) also played a very important role in seven of the nine cases, e.g. in Göttingen 1991 ((Fig. 8-14A4), Ruthe 1994 (Fig. 8-14B4) and Hiddestorf 1991 (Fig. 8-15A4). Our simulation experiments indicate that if a relatively high aphid density at *GS* 69 and very high temperature simultaneously appeared after *GS* 69, the aphid population cannot reach a high level. Ignoring the detrimental effect of high temperature may result in an unnecessary spraying. For example, in the fields at Göttingen in 1991 and at Ruthe in 1994, the aphid numbers were above the action threshold at *GS* 69, but high temperature resulted in an early population collapse (Fig. 8-6, Fig. 8-8). Thus, the weight of thousand grains or the yield was not significantly reduced compared to the insecticide treated plots (Niehoff 1996, Lemke 1999). In addition, *NE* is also important if the population density is high (e.g. Fig. 8-14A5 and 8-14B5, Fig 15A5). Several action thresholds for spraying, developed in eastern Germany (Holtz & Wetzel 1989, Holtz et al 1994, Rappaport & Freier 1998), do not only depend on the number of aphids but also the density (or abundance rank) of natural enemies.

Compared to the decision-making system based only on the population density at *GS* 69, our simulation model supplies an option, which is more accurate but uncomplicated. The aphid population density at *GS* 69 is only used as the initial population density in our model. The population densities after *GS* 69 are accurately predicted by considering the effects of daily average and maximum temperatures

before and after *GS* 69, since the reproduction of the aphids is not only influenced by the actual temperature but also by the thermal history of the aphids during the past. The sampled aphid density at *GS* 69 and the simulated daily aphid density after *GS* 69 can be used to calculate the aphid unit days. Combining these aphid unit days with the yield loss rate per aphid unit per day (Zhou et al. 1989), the daily updated accumulative yield loss can be calculated (Fig. 9-2). According to the cost-benefit consideration, a permitted maximum yield loss can be determined. When the accumulative yield loss is above the permitted maximum yield loss, a spraying is suggested.

Since the daily maximum temperatures have stronger influences on the population development after *GS* 69 than natural enemies in most of the studied fields, our model can be used in the decision making by the simulating the population densities after *GS* 69 under the condition of excluding the effect of natural enemies but including the detrimental effect of high daily maximum temperature. Collecting data of natural enemies and incorporating them in the decision-making are always difficult and unlikely to be implemented. Sensitivity analyses show that syrphids in total are important but not very sensitive factors for the population development of aphids. Thus, the preliminary syrphid model built in this study can be used to simulate the syrphid density based on the initial number of syrphids at *GS* 69. Although the syrphid model is not perfect at present, it can be improved as the understanding on syrphid ecology increases. Thus, the population density after *GS* 69 can be determined in a reliable level. Promisingly, farmers can sit in front of their computers to calculate the profit they may get from the aphid control.

11 Summary

The rose grain aphid, *Metopolophium dirhodum* is one of the most important pests of cereals in Europe. Although in general the population dynamics of aphids are complicated processes, it is possible to predict the population density and to analyse the mechanisms of population dynamics of aphids by means of simulation models. However, the numerous models developed for *Sitobion avenae* cannot be transferred for modelling the dynamics of *M. dirhodum*, because of the difference in overwintering strategy, feeding position, and reactions to environmental conditions of the two aphids. Therefore a new detailed simulation model was developed to describe the population dynamics of *M. dirhodum* in winter wheat fields in Northern Germany.

The simulation model has been constructed following the system analysis approach. It includes compartment models for L_{1-3} (summed) and L_4 larval instars as well as for adults. These compartment models are constructed with 'boxcars' and are used as the framework to simulate the changes in the population dynamics based on the life cycle of the aphid. The status of a boxcar is described by state variables, for instance the number of aphids, the mortality, the age and its standard error, and the average temperature that the aphids experienced. The number of aphids of the same age group (in the same boxcar) at a present day is calculated based on the number of aphids at the previous day and the daily updated development, reproduction, surviving, morph determination and migration. The following five model input variables affect these processes: initial population density of each aphid stage, measured daily average and maximum temperature, observed or interpolated daily wheat growth stage and density of syrphids as the key natural enemies.

The effect of high temperatures, a factor neglected in previous models, proved to be of paramount importance for the population development of *M. dirhodum*. The relevant data were gained in a set of laboratory experiments on the survival rate, longevity and fecundity of *M. dirhodum* after exposing L_2, L_3 and L_4 instars as well as adults for 8h/day to 27, 29, 31 and 33°C, respectively. Results indicate that mature stages of *M. dirhodum* are more sensitive to extreme temperatures than the young larval instars. With increasing exposure time to high temperatures the survival rate and life fecundity are reduced. There is an apparent tendency that the survival rate,

longevity and life fecundity decreases as temperature increases. This information was used to build three sub-models, describing the effects of high daily maximum temperatures on survival, reproduction and longevity of *M. dirhodum*.

The simulation model includes sub-models on development, reproduction and survival. Effects of temperature and aphid morph on the development duration and its standard error are incorporated in the normal distribution model describing the developmental transition rate. Daily reproduction is calculated using the updated lifetime fecundity and the fecundity allocation over the total lifetime. Daily average and maximum temperature, plant growth stage and the aphid's morph influence the lifetime fecundity. The temperature experienced by the aphids since they were born is tracked via the compartment model and used in the calculation of the lifetime fecundity. Weibull models are constructed to describe the daily accumulative fecundity and mortality of aphids during the adult age. A predation model for syrphids was established and related to aphid density under the influence of various temperature regimes.

For the validation of the simulation model, simulated and observed population densities from nine fields, collected in different years at some areas in Lower Saxony, were correlated. The simulations of the population density and the age (stage) structure of the aphid population were not significantly different from the observations. The model is valid and robust to simulate high (Göttingen, Grossenwieden and Hiddestorf 1992) and medium densities (Göttingen and Hiddestorf 1991, Ruthe 1994). It is reasonably valid for low densities as well (Göttingen 1993). Although the model did not successfully predict the extreme low population densities (Ruthe 1995 and 1996), it was practically acceptable from an economical pint of view.

Simulation experiments indicate that in most fields initial aphid density (*IPD*) at the end of flowering and the daily maximum temperatures (*MaxT*) prior to mid milky-ripe stage are more important for the population dynamics than the plant growth stages (*GS*), the daily average temperature (*TX*) and the effects of syrphids (*NE*). However, *NE* is an important factor in the fields with medium population level. The conditions favouring a population outbreak of *M. dirhodum* in northern Germany (e.g. at

Göttingen, Hiddestorf and Grossenwieden in 1992) can be characterised in three points: 1) *IPD* at the end of flowering is high (e.g. >10 aphids/tiller); 2) *TX* is mild (e.g. 17-20°C) and 3) predator densities are not very high (<0.05 syrphid larvae/tiller) from end of flowering to medium milky-ripe. On the other hand, no outbreak will occur if one of the following three conditions is fulfilled: low *IPD* (<1 aphids / tiller) at the end of flowering (e.g. Göttingen 1993, Ruthe 1995 and 1996), high *TX* (> 25°C) (e.g. Göttingen 1991, Ruthe 1994) and high density of predators (>0.2 syrphids / tiller) from end of flowering to medium milky-ripe.

The sensitivity analysis showed that the model is very sensitive to small changes of *GS*, *MaxT*, *IPD* and *TX*. Slightly inaccurate records of *GS* and *MaxT* result in a significant error in simulating the shape of the population curve as well as the level of aphid density. Slightly inaccurate estimates of *IPD*, its stage structure and *TX* lead to minor changes in the shape of the population dynamics, but result in inaccurate prediction of the population density. Slightly inaccurate inputs of syrphid number do not cause big errors in the estimation of population densities of the aphids, especially when the ratio of syrphids to aphids is very small.

In comparison to already existing simulation models for *M. dirhodum* (Zhou et al. 1989) or for *S. avenae* (Carter et al 1982, Rossberg et al. 1986, Freier et al 1996a) the model has a high level of accuracy and requires relative simple input data. It can be applied not only to predict the population dynamics, but also to estimate the yield loss caused by *M. dirhodum*, which can be used in decision making for spraying. In the future, the simulation model can be extended by including the simulation of the population dynamics of the syrphids, based on the sub-models already presented.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides Statt, daß ich die vorliegende Arbeit selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe sowie daß diese Arbeit noch keiner anderen Prüfungskommission als Diplomarbeit oder ähnliche Prüfungsarbeit vorgelegt worden ist.

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