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SPECIALITE : **BIOLOGIE DES POPULATIONS ET ECOLOGIE**

EFFICACITE DE *HARMONIA AXYRIDIS* (COLEOPTERA: COCCINELLIDAE) COMME AGENT DE LUTTE BIOLOGIQUE CONTRE *MYZUS PERSICAE* (HOMOPTERA : APHIDIDAE)

par

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Avertissement

Ce document est composé de deux parties :

- le texte original en langue anglaise ;

- une version française résumée, dépouillée des tableaux et figures mais se référant aux illustrations de la version originale.

Cette version française permet une prise de connaissance rapide de la conception de l'étude et de ses résultats. La discussion en étant abrégée, c'est à la version anglaise que le lecteur devra se référer pour une meilleure interprétation de la pensée de l'auteur.

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Résumé. Le puceron vert du pêcher, *Myzus persicae* Sulzer, est à l'origine de pertes croissantes dans les vergers commerciaux de pêchers du sud de la France. Des recherches sont entreprises à l'INRA sur la possibilité de contrôle biologique des populations de *M. persicae* à l'aide d'une coccinelle prédatrice introduite, *Harmonia axyridis* Pallas. Nous analysons ici l'efficacité de *H. axyridis* comme agent de lutte biologique contre *M. persicae* , par la modélisation de l'interaction proie-prédateur en fonction de la température. Les données de base pour la caractérisation de ces interactions et l'élaboration d'un modèle de simulation sont établies en laboratoire à la station de Zoologie de l'INRA d'Avignon. Le taux intrinsèque d'accroissement des populations de *M. persicae* atteint son maximum à 24°C, alors que les températures procurant la consommation de proies maximale par la coccinelle se situent aux environs de 25-27.5°C. Le taux de développement des larves de *H. axyridis* approche une valeur maximale lorsque la densité de proies augmente, et présente une réponse à la température typique des organismes poikilothermes. Le taux moyen de survie journalier âge -spécifique de *H. axyridis* s'accroît avec la densité de proies selon une courbe sigmoïde, et répond également à la température. La simulation atteste que l'efficacité des jeunes larves (L1-L3) de *H. axyridis* dans l'élimination de *M. persicae* augmente avec la température. Cette réponse ne se retrouve pas chez les larves de 4ème stade. Les larves âgées sont toujours plus efficaces que les jeunes larves à basses températures, et cet ordre s'inverse à l'autre extrémité de la gamme de températures efficaces (10-30°C), avec une série de transitions lorsque la température augmente. La simulation et les résultats d'expérimentations en conditions semi contrôlées n'établissent pas clairement les conditions de la maîtrise des populations de *M. persicae* par lâchers inondatifs de *H. axyridis* en vergers. L'efficacité du prédateur est moindre en conditions de basses températures, où la proie connaît au contraire un très fort taux d'accroissement de population. Des résultats satisfaisants sont obtenus sur arbres encagés où le lâcher d'un nombre approprié de larves de 3ème stade (50 par arbre) permet l'extinction de populations initiales de 20 pucerons par rameau. La simulation réalisée à partir des températures relevées au cours de l'expérimentation génère des résultats qualitativement conformes à l'observation.

ABSTRACT. Green peach aphid, *Myzus persicae* Sulzer, an important pest in the commercial peach orchards in the Rhone Valley of southern France, has been causing increasing economic losses. Current control methods, are either ineffective or have drawbacks including increased pesticide resistance, destroying natural control mechanisms, contaminating of environment and fruits. To solve these problems, possibility of biological control using an introduced cocccinellid predator, *Harmonia axyridis* Pallas is investigated by researchers in INRA. As an integrated part of this effort, I investigated the effectiveness of *H. axyridis* as a biocontrol agent against *M. persicae*, with the modeling and analysis of the temperature-dependent predator-prey interactions.

Background studies necessary for estimating parameters for describing the temperature-dependent predator-prey interactions and for building a simulation model were conducted by the author in the Zoology Station, INRA, Avignon. The intrinsic rate of population increase of *M. persicae* reaches its maximum value around 24^{o}C, while the optimal temperature for attaining the maximum prey consumption with a fixed prey density is about 25-27.5^{o}C. The developmental rate of larval *H. axyridis* approaches the maximum value as the prey density increases and the developmental rate of *H. axyridis* responds to temperature following a typical poikilothermal pattern. The average age-specific daily survival rate of *H. axyridis* increases with prey density following a sigmoid curve, and is also affected by temperature. Results from simulation analyses are presented suggesting that a major factor limiting the effectiveness of *H. axyridis* lies in the fact that this predator is not very effective under low temperatures when the prey, green peach aphids can attain a fairly high rate of population increase. Simulation also suggested that the effectiveness of young larvae (L1-L3) of *H. axyridis* in eliminating green peach aphids augments as temperature increases, but this pattern does not hold for the 4th instar. From another perspective, older instar larvae are always more effective than the younger ones at low temperatures, but this pattern switches to the reverse order at the other end of the effective temperature range (10-30°C), with a series of transitions in this pattern as temperatures increases within the range of the two extremes. Satisfactory results were obtained in suppressing the population of *M. persicae* using *H. axyridis* by releasing an acceptable number of 3rd instar larvae (50 larvae/tree) at an aphids density of average 20 aphids/shoot on caged trees. Simulation run with temperature data recorded during the experiment generates results qualitatively consistent with the observation.

PREFACE

The potential use of *Harmonia axyridis* Pallas as a biological control agent for innundative release is examined for green peach aphids *Myzus persicae*, an insect pest in commercial peach orchards in southern France, using a simulation model. Chapter 1 describes *M. persicae* as a pest in peach orchards and the history of study on *H. axyridis* in France, and introduces the objectives and approaches of this study with respect to the evaluation of *H. axyridis* as a biological control agent and the modeling of the predator-prey interactions between *H. axyridis* and *M. persicae*.

In Chapter 2, models of the developmental rate and intrinsic rate of population increase of *M. persicae* as functions of temperature are developed upon data of age-specific life tables built for laboratory populations. Some other parameters of the life system of *M. persicae* are also presented in the chapter.

The temperature-dependent functional responses of all the active immature stages of *H. axyridis* to *M. persicae* are discussed in Chapter 3. The number of green peach aphids consumed by *H. axyridis* are modeled as function of both temperature and density of aphids exposed to the predator.

Chapter 4 deals with the developmental rate and survival rate of different larval stages of *H. axyridis* in relation to temperature and prey density. These relationships are described by models. The integration of the two aspects, developmental and survival rate, will account for the temperature- and density-dependence of the rate of change in the number of individual in the cohort of a given larvae stage.

Models described in the above chapter are incorporated in Chapter 5 into a computer simulation model. Simulation results are discussed concerning the effectiveness of *H. axyridis* as a predator of green peach aphids in relation to temperature, predator age, and prey density.

Chapter 6 presents the results of a release trial in the orchard using the experimental exclusion technique. The observation is compared with simulation that is conducted using temperature data recorded during the release trial.

SOMMAIRE

VERSION ORIGINALE

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Chapter 1.

Definition of the system and the approach

1. THE SYSTEM

1.1 The Green peach aphid

Green peach aphid (*Myzus persicae* (Sulzer)) is a world-widely distributed species. It is outstanding in distribution and in host plant range (Van Emden, et al. 1969, Mackauer and way 1976). As a pest, green peach aphid not only causes direct damage but is also able to transmit over 100 virus diseases of plants on about 50 different families including many important crops (Kennedy et al. 1962, Van Emden, et al. 1969, Swenson 1968, Mackauer and way 1976). Perhaps because of its wide distribution and economic importance on several crops, *M persicae* has been extensively and intensively studied and was selected in 1967 as the key aphid species for an international collaborative research project under the IBP/UM (Use and Management of Natural Resources) program (Mackauer and way 1976). It has been an object in the study of physiology, biochemistry, nutrition (Dadd and Krieger 1968, Miles 1968, Parry and Ford 1969), genetics (Ford 1964, Cognetti 1967, Blackman 1972) insecticide resistance (Sudderuddins 1973, Attia and Hamilton 1978, Sawicki et al. 1980, Weber 1985a, b, Devonshire 1989, Sauphanor et al. 1995) and plant-aphid interactions (Van Emden et al. 1969). As an economically important pest, the biology, ecology and control *of M. persicae* have been world-widely studied on potato and sugar beet, its secondary hosts. However, only a few researches (Tamacki 1973, Leclant 1986, 1988) were carried out on the aphid's primary host plant, peach trees, probably because this species was previously not, or was not perceived as, an important pest in peach orchards. In fact, it was generally perceived, and it may still be perceived by some, that peach trees can tolerate a fairly high population of *M. persicae* without measurable economic damage (Mackauer and Way 1976).

In southern France, green peach aphid has been drawing attentions for serious problems it is causing in peach orchards. It attacks the peach flowers and buds in the early spring, which may greatly reduce the production and quality of peach fruits (Leclant 1978). The high population potentials of this pest allows frequent heavy infestations on peach trees which may seriously weaken the vitality of peach trees and affect the fruit production for the following years (Leclant 1970). Moreover, two important factors has made green peach aphid become remarkable as a pest in peach orchard: 1) this aphid was once believed to be the major vector of Sharka, a vital virus disease of peach trees in Europe, which has destroyed some commercial orchards and has presented a major threat to the peach production (more recent researchs on epidemics of Sharka suggests that *M. persicae* has a much less crucial role in the transmission of the viral disease than what had been believed (Sauphanor 1997, personal communication)); and 2) it has manifested an increased resistance to the major groups of insecticides which has resulted in failures of pesticide treatments in peach orchards (Craveti and Cervato 1993).

Few other approaches than chemical methods have been successful in maintaining the population density of green peach aphids at an acceptable low density, which was considered necessary for controlling the epidemics of the virus disease. The intensive use of chemical methods to reduce the economic losses due to this pest and to prevent the spread of virus diseases by controlling the aphid vector has resulted in the development of resistance of this species to major types of pesticides, which has often led to more frequent and more intensive use of pesticides (Weber 1985a, b, Sudderuddins 1973, Attia and Hamilton 1978, Sawicki et al. 1980, Devonshire 1989). The reliance on chemical methods in controlling green peach aphids has been in conflict with integrated control programs aiming at other orchard pests, and may eventually cause intolerable consequences to the environment of the peach growing areas.

Thus, to free the peach production from the direct damage and threat of aphid-mediated virus diseases, and to reduce the environmental risk from pesticide application, there is an urgent need for new and environmentally sound control approaches, including utilization of variety resistance of peach trees and biological control using natural enemies. Research efforts have been made toward these directions in INRA-Research Station of

Zoology at Avignon for years (Sauphanor et al. 1993). This research has been conducted within this context.

1.2 *Harmonia axyridis*

Harmonia axyridis is a predatory coccinellid originated in the East Asia. This species has a wide range of adaptation to various habitats and can prey on a wide range of aphid species (Shanderl 1986). For these reasons, it has been extensively studied and utilized in Japan, China, South Korea and Russia for biological control through conservation and enhancement of natural populations, as well as human augmentation of the natural population (Niijima et al. 1986). A great quantity of researches have been done concerning the biology (Gotoh 1982, Takahashi 1986, Obata 1988, Coderre et al. 1995), ecology (Shanderl et al. 1985, Obata 1986, McClure 1986, 1987), behaviors (Obata 1986, Obata and Hidaka 1987, Osawa 1994), physiology and biochemistry (Ogawa and Ariyoshi 1981), population biology (Hu 1979, Bogdanov and Gagal'chii 1986, Kholin 1991, Osawa and Nishida 1992, Ueno 1994), nutrition and artificial mass rearing (Niijima and Takahashi 1980, Choi 1983, Choi and Kim 1984, Matsuka and Niijima 1985, Shanderl et al. 1986, Wang 1986), as well as the techniques for field application of this coccinellid species (Niijima et al. 1986, Wang 1986). In the United States, this species has been introduced for controlling a variety of pests, mainly including aphids and scales (McClure 1986, 1987, Bryan 1993, De Quattro 1995). Native populations have also been discovered in several locations in the North America (Chapin and Brou 1991, Dreistat et al. 1995, Coderre et al. 1995). A very successful example of using this ladybug as an exotic species for classic biological control has been its being introduced into the USA for controlling the pecan aphids. It has been so successful that in several pecan growing states, the pecan aphid is no longer considered as a substantial pests (Bryan 1993, LaRock and Ellington 1996). But in many locations in the United States this coccinellid has becoming a nuisance to the residents, because they enter the houses in swarm for oversummering or overwintering (Segelken 1994, Robinson 1996).

H. axyridis was introduced to France in the early 1980's by INRA-Laboratory of

Population Biology at Antibes as a potential biological control agent. The fundamental aspects of the biology, ecology and behavior have been studied in details (Shanderl et al. 1985, Shanderl 1986, Ferran et al. 1985). Techniques for mass rearing with eggs of *Ephestia kuehniella* Zeller have been developed and commercial production was made possible (Shanderl et al. 1985, Shanderl 1986). Laboratory and field explorations of the possibility to use this species to control various pests, mostly aphids and scales, have been conducted on a number of crops (Ferran 1996, personal communication). Efforts have been made in trying to use this ladybug for inundative releases, and encouraging success has been gained in biological control against *Macrosiphum rosae* (L.) on rose bushes (Ferran 1996, personal communication). However, there has been so far no other records or evidence showing any substantial success in using this ladybug in controlling insect pests in France. More detailed studies on the evaluation of the effectiveness of this coccinellid as a potential biological control agent against different pests should be conducted before valid conclusion could be made concerning the potential usefulness of this species as a biological control agent in France. In this study, we concentrate on the evaluation of the effectiveness of *H. axyridis* as a biological control agent against green peach aphid.

Two distinct categories for augmenting the use of biological control agent have been recognized (DeBach and Hagen 1964): inoculative and inundative releases. The former refers to releasing relatively small number of beneficial insects as colonizing populations, with the purpose of providing relatively long-term pest regulation through in-field reproduction of the released species. Inundative releases, on the other hand, release large numbers to cause an immediate and direct mortality in the pest population (Stinner 1977). Due to the fact that green peach aphid colonizes peach trees as a primary host only for a rather short period in spring, and moves later on to a vast range of secondary hosts, the coccinellid is unlikely to establish close phenological and habitat with the aphid. Thus, inundative release is a natural choice for utilizing *H. axyridis* as a biological control agent against green peach aphid, that is, the coccinellid is used as an intervention agent for immediate suppression of the aphid population and need to be applied whenever the aphid population exceeded the tolerance threshold.

2. THE APPROACH

2.1 The approach to the evaluation of the effectiveness of the predator

For biological control using inundative releases of biological control agent, the beneficial species is usually not intended to be introduced as a long-term regulatory agent, but rather as a temporary suppressing force of the pest population (Hoyt and Caltagirone 1971, Debach 1974, Stinner 1977). Thus the long-term dynamics of the predator and the prey is of little concern in the evaluation of the effectiveness of the entomophaga. The evaluation of the effectiveness of a biocontrol agent for inundative release can be implemented using several different approaches or their combinations (Huffacker and Kennett 1969, Luck et al. 1988). In the first case, direct field release trials can be conducted and gross cause-effect indication rather than proof is usually yielded based on observations and sampling data (Barlow and Dixon 1980, Luck et al. 1988). Alternatively, life tables can be built for populations of the pest and the released biological control agent under natural or semi-controlled condition to assess the impacts of the natural enemy on the demography and the population trends of the pest, intensive inspections of marked aphid colonies or caged plants or plant parts, both with or without predators, are usually conducted for this methods. Strong proof of the impacts of the predator on the pest population may be obtained (Dixon 1959, Varley and Gradwell 1971, Frazer et al. 1981, Bellows, Jr. T.S. et al. 1992). As a third alternative, laboratory or strictly controlled field populations can be manipulated by using experimental exclusion techniques to determine the quantitative relationships between the major component variables or processes of the system; the system is usually well defined, and simple measurable component processes or relations that contribute to the major behaviors of the system are identified from complex interactions; measured relationships between component variables are synthesized with a model (Varley and Gradwell 1971, Ruesink 1976, Rabbinge and Sabelis 1980). The first approach is technically simple, but economically expensive and ecologically risky if the trial is to be conducted in a meaningfully large spatial scale and to include an inclusive range of release options (Pimentel et at. 1980); the results of the evaluation of the

effectiveness with this approach are directly related to the real situation in practice, but on the other hand, they give little explanation for the consequence (success or failure) of the releases. For the second approach, convincing evidence can be obtained concerning impacts of introducing predators on prey population in a particular experimental setting, but the results are usually dependent on the particular situation and can in no sense be considered to apply to more general situations, since actual experiments are usually hindered by technical difficulties and limited in time and space. The third approach can result in the accumulation of a large amount of detailed information concerning quantitative relationships between various component variables, which is very useful for answering specific questions such as "Is temperature a critical factor that determines the effectiveness of the predator?". The data gathered with this approach can usually be considered as being more general than with the other two approaches, since the experiments for measuring those relationships are usually designed to be conducted, in the first place, under certain "ideal conditions" --- conditions that apply to most, if not all, situations. Some system-specific and situation-specific factors, which were usually left out at the beginning, can be incorporated subsequently according to the need. This approach costs less research effort and resource, and can often provide insights into the mechanisms behind the phenomenal consequences, which is usually very valuable for subsequent researches such as the development of strategies for using the natural enemy in biological control, and even adds to the more general biological control theory (Ruesink 1976, Rabbinge and Sabelis 1980, Susan 1991). However, one inherent weakness of this approach, which results right from its being general, is its being less realistic than the other two approaches, since a lot of details that are regarded as being less relevant to the questions to be answered are dropped out of the model. The model prediction should be considered rather as hypotheses to be tested than as facts to be accepted. The use of any single approach will face some limitations and constraints. In fact, each of the three approaches is better suitable to address certain types of questions, to fit to certain purpose or to be used in certain situation or certain phase of a research project than the others. They should be regarded more as reciprocal approaches rather than competing ones, for example, the modeling approach can usually be used to generate hypotheses that can be

tested using the other two approaches; the field release trials can usually be used to test the predictions made by the model and/or the life table and arrive at the final judgment of the effectiveness of a natural enemy in the real situation. Information from the life table or the model can usually serve to eliminate a large number of options that should otherwise be considered, and raise better defined and more specific questions to be answered, or form more explicit statement to be proved by the field release trials.

The integration of the three approaches has been accepted by the research group in INRA-Research Station of Zoology at Avignon. This thesis deals only with the part of study using the modeling approach. In this study, our major concern is whether *H. axyridis* has the potentials to be used as a effective biological control agent for innundative release against the green peach aphid, in terms of the potential predatory pressure it may pose on the aphid population versus the potentials of aphid population growth, with both sides being dynamically modified by each other and by temperature. The potentials of population growth of the aphid is represented by the intrinsic rate of population increase which is a function of temperature and is subject to a multiplier representing the effect of intra-specific competition. The potential predatory pressure of the ladybeetle is regarded as an integral index of the attack rate, survival and developmental rates of the ladybug. These elements are to be incorporated into a model which can be used to pose and answer questions such as whether this coccinellid can be an effective predator of green peach aphid at all, or within which temperature range the coccinellid possesses the potentials to be a effective predator of green peach aphids.

2.2 The approach to the population modeling

A model is an intellectual construction or artificial analog of a physical system. The purpose for building a model of a system is always to obtain a representation of only the most important features of the system, so that we can study and use the model, instead of the physical system itself, which is more easy to understand and to handle than the real system for certain purposes (Conway and Murdie 1972, Curry and Feldman 1987). It is in

this sense that a perfect copy of the physical system is not only impossible but also unnecessary, and thus, considerable simplifications are always needed, because an exact analog of the system will be as hard to understand, and behave as slowly as the physical system.

Different approaches to modeling population dynamics (no matter a single species or a multi-species system) can be distinguished (Conway 1973, May 1974, Guiterrez 1981, Gets and Guitierez 1982, Dixon 1989, Arino et al.1991, Berryman 1991, Renshaw 1991). Firstly, one can distinguish between analytical models and simulation models. Analytical models usually involve only a limited number of variables and parameters and the relationships between variables are mathematically explicit so that the model be kept simple enough to be analytically tractable. On the other hand, simulation models can incorporate a large number of variables and parameters and the relationships between variables do not need to be mathematically explicit but can be implicitly embedded in the algorithm of computer programs (De Wit and Goudriaan 1978). In fact, there are hardly any models of a particular physical system that can be perfectly put into either of the categories; in most cases, simulation models use some analytical models as frameworks; and analytical models need to incorporate some simulation techniques when being used to tackle specific problems with a specific system. Therefore, it is of little meaning or use to simply label one's model as an "analytical" or "simulation" model, as far as you want to model a specific system. It is perhaps more useful to distinguish a model based on how it is constructed; a model could be obtained by fitting population time series data to simple theoretical models which were built upon fundamental biological and ecological principles; or otherwise, the model could be constructed using parameters measured directly from experiments or observations or derived from calibration or adjustment against the behavior of the system (Berryman 1992). For the former approach, an adequate length of time series data need to be collected and compiled, and the model and system itself need to be pretty simple so as to allow feasible statistical analyses. This method requires that the population time series be stationary or at least be able to be transformed into an stationary time series, so it is most suitable to be used for studying long term macroscopic population changes with one year as the time step. It is of limited use in studying microscopic

population changes, or population with strong seasonality or subject to frequent violent perturbations, such as in many agricultural pest populations. This approach is obviously not suitable for this study. For the latter approach, the system is usually structured reflecting certain biological details, and is thus possible to be reduced into some basic mechanistic sub-units of lower organization-levels which usually have a shorter time scale, so that the parameters in this kind of models are biologically explicit and can be measured directly or be estimated from other quantities. This kind of models are comparatively cheaper to build, and flexible in model complexity, but they often fail to describe and explain the overall long-term behaviors of a real system because of the involvement of different organization levels and different time or/and space scales. Thus, it is more suitable to be used to study specific microscopic behaviors of a system, rather than giving predictions of long-term macroscopic dynamic behaviors of a system. This study will accept this approach.

Another distinction can be made between models which describe population growth as a continuous process and those that describe change of populations with discrete generations or age classes (May 1974). The former includes models with the independent variable (time) being continuous, for which we have differential equations. The latter includes models with the independent variable (t) being discrete, for which we have difference equations. Because the life system of green peach aphid is characterized by high degree of generation overlaps, individuals are born and die at any moment, continuous-time model will be more appropriate and convenient in modeling the population changes.

Distinction can also be made between deterministic models and stochastic models. For deterministic models the population density (N) changes uniquely and continuously by an infinitesimal amount dN in an infinitesimal time dt. For stochastic models the population density is perceived to be a random variable with respect to every $t \in T$ (T is a specific real set). The classic stochastic population models are based on discrete-state processes (Bartlett 1960, Pielou 1977, May 1974) where we have probability distribution function, $f(n, t)$, which defines the probability to find the population to have n individuals at time t, thus the average population and the variance can be calculated at each time point t (Bartlett 1960, May 1974). Obviously, this type of stochastic models gives a more realistic

description of the population process, since in the deterministic model, each member of the population gives birth or dies to some fraction of an individual in each small interval of time, whereas in the stochastic model only whole animals are born and die with specified probabilities. While being more realistic, stochastic population models involve harder calculation and requires more information than their deterministic analogues. And more importantly, for very large populations, this distinction becomes unimportant, as May (1974) argued, the generalized central limit theorems of McNeil and Schach (1971) guarantees that for large value of N (or K, the carrying capacity, in case of logistic population growth) the mean of the population is identical to the deterministic population, and the statistical root-mean-square relative population fluctuation about the mean becomes trivial. This kind of stochasticity rooted in the fact that the population variables are fundamentally discrete ones is termed as "demographic stochasticity" (Bartlett 1960). Stochasticity also arise from the randomness of environmental elements of a population, for which a random variable of specified probability distribution is often added to the rate of population change (Conway 1972, May 1972).

Another way to classify models is based on the model complexity, in the 70's and early 80's, the so called general-purpose large-scale system models was strongly advocated, they were characterized by involving a huge number of variables and parameters, and a wide range of interactions, being built for serving general purposes (Logan 1993). It turned out that those huge general-purpose large-scale model were even harder to understand and operate than the real system and were thus of little use. Recently, there has been such a tendency that people are turning back to those small specific-purpose models which are characterized by incorporating only a minimum number of variables and parameters and serve certain well-defined specific purposes (Logan 1993). This study will accept the modeling approach with a very specific purpose --- evaluating the effectiveness of *H. axyridis* as a predator of *M. persicae*, so the model will keep only the most relevant elements.

In this study, three major components will be incorporated in the model: the temperature-dependent population increase rate of *M. persicae*, the temperature-dependent functional response of *H. axyridis* to *M. persicae*, and the temperature-

dependent rates of development and survival of the larval stage of the predator. These elements are to be coupled in a dynamic simulation model (Fig. 1-1).

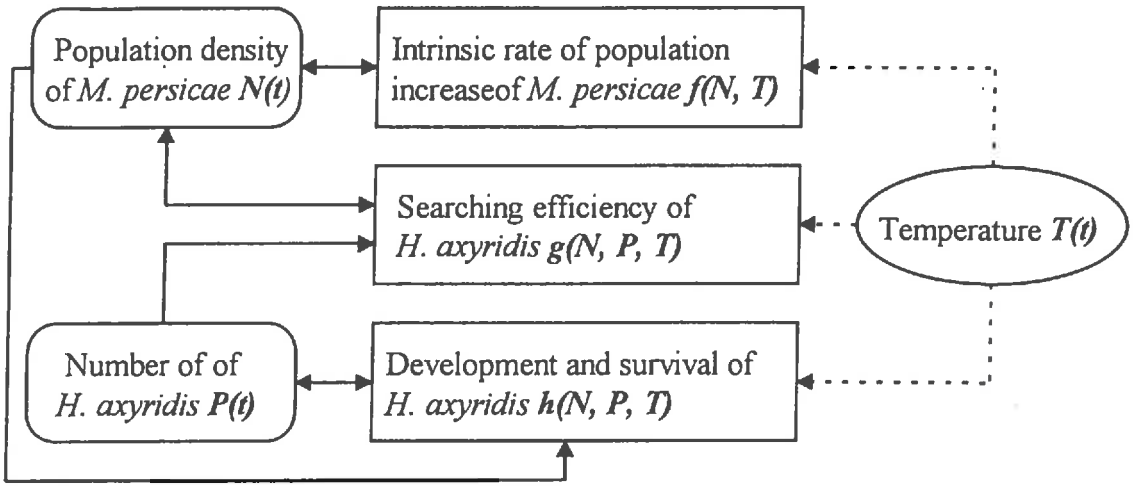

Fig. 1-1 Diagram of a conceptual model for the temperature-mediated predator-prey interactions between *Harmonia axyridis* and *Myzus persicae*.

3. OBJECTIVES

There are two major reasons for using the modeling approach to evaluate the effectiveness of *H axyridis* as a biological control agent against *M. persicae*. Firstly, a model can serve to identify key factors that determine the effectiveness of the predator, increase our understanding of the consequence, which is critical in determining under what conditions the inundative releases would have the greatest or least chance of providing feasible control against the target pest. The model can also be used to direct field release trials and provide supplementary information on the field evaluations. Secondly, the model can provide a framework for more detailed system-specific or field-level tactic models in the following phase of researches for developing field application tactics and decision making concerning the optimum timing and numbers of the predator to release. The optimization of these two variables can greatly reduce costs as well as increase efficiency, particularly against highly vagile and fecund prey species like *M. persicae*. Even in case

that the predator turns out not to be a effective predator of *M. persicae*, the model can still be used in predicting the right kind of natural enemies that should be considered as potential biological control agents.

The objective of this study is to use the modeling approach to evaluate the potential effectiveness of *H. axyridis* as a biological control agent against *M. persicae* within the limit of the population potentials of the prey, the searching efficiency of the predator and the sustainability of the predator in relation to the prey abundance, and the temperature-dependence of these processes, to enhance the understanding of the consequences of field release trials, to identify areas where more information is needed and provide guidelines for further field evaluations and application.

Chapter 2.

Effects of Temperature on the Demography and Intrinsic Rate of population Increase of *Myzus persicae* (Sulzer) (Homoptera: Aphididae)

Introduction

In the context of developing more effective and rational approaches and strategies for controlling green peach aphid (*Myzus persicae*) in peach orchards, including evaluating the effectiveness of biological control agents and developing strategies for field application, which is the major concern of this study, information on the potentials of population increase of the aphid is critical. A classic approach to the study of insect population increase often include the intrinsic rate of population increase (r_m) of the insect and the most important factors modifying this parameter. The intrinsic rate of population increase is a concept firstly developed by Lotka (1925). By definition it is the maximum rate of population increase attained under optimal environmental conditions representing the genetic and physiological characteristics of a species, which subjects to modifications of environmental conditions (Barlow 1962, Dean 1974, Deloach 1974). The intrinsic rate of population increase has a number of component variables: the developmental rate of immature stages, the fecundity and age-specific reproductive profile and the survival rate of the immature and adult stages (Birch 1948, Barlow 1962, Dixon 1987). These component variables can be measured by building life tables of the aphid under specific conditions. The modification of the intrinsic rate of population increase may result from: food quality, temperature, competition, and polymorphism, etc. (Frazer 1987). In this study, we will not take into account the food quality of green peach aphid, which may result greatly from the seasonal variation in the physiological status of the host plants, as during most of the season from March, when the aphid eggs begin to hatch in the peach orchards, to May, when the aphids begin to move out of the peach orchards, the green peach aphid colonizes mainly the growing new shoots (Davis and Landis 1951, Leclant

1972, 1976, Tamaki 1973,). We may assume that the variation in the food quality for green peach aphids during the rising phase of the aphid population is bounded within a certain favorable range. The effects of morph determinations will not be included in this study either, as our purpose is to investigate the aphid population of the parthenogenetic generations in peach orchards in Spring. The effects of intra-specific competition can be included by incorporating the value of carrying capacity in the model. For our purpose of this study --- evaluating the effectiveness of natural enemies, the temperature-dependent intrinsic rate of population increase is of major interest, because temperature has a regular annual seasonal trends and considerable random variation in the fields, and has been identified as an major factor causing the most detectable and predictable changes in the insect population increase rate (Messenger 1964, DeLoach 1974, Goldman and Carpenter 1974, Eyring and Urry 1975, Logan et al. 1976, Sharpe and DeMichele 1977, Tamaki 1982), and seaching efficiency (Goldman and Carpenter 1974, Tamaki and Long 1978, Mack et al. 1981) and persistence of predators (Mack and Smilowitz 1982).

There have been researches published on the intrinsic rate of population increase of parthenogenetic generations of green peach aphid on secondary hosts such as potato (Barlow 1962), tobacco (Harrison 1969) and cabbage (Deloach 1974), but we have found no published work on the intrinsic rate of population increase on peach trees.

The objective of this work is to measure the intrinsic rate of population increase of green peach aphid as modified by temperature under laboratory conditions, which can serve as a parameter for models to be used in evaluating the effects of extrinsic modifiers of the population dynamics of green peach aphid such as predators and variety resistance of host plants.

Material and Methods

Plants. Peach seedlings in the stage of 15-20 leaves, which were obtained from the germination of peach cones of the variety 305, were used as the host plants of green peach aphid. These seedlings were cultured in 5x8.2 cm cylindrical plastic jars using a complete

nutritive solution with the following composition in mol m^{-3}: $MgSO_4.7H_2O$ 1; KCl 0.2; K_2SO_4 1.5; KH_2SO_4 0.5; Fe EDDHA (ethylenediamine-di(o-hydroxyphenylacetic acid)) 0.1; H_3BO_3 0.001; $MnCl_2.4H_2O$ 0.003; $CuSO_4$ $0.7x10^{-4}$; $ZnSO_4$ $0.15x10^{-3}$; $MoNH_4$ $0.15x10^{-3}$. The peach seedlings were watered with distilled water every three days, and the nutritive solution was supplemented every week. A sheet of paper in black color was put at the bottom of the peach seedlings, covering the plastic jars, with the stalk passing through a hole, so that the white-colored exuvia of the aphids could fall on this sheet of black paper and be easily found.

Aphids. Laboratory colonies of parthenogenetic viviparous green peach aphids used in this experiment were originated from the fundatrix collected from the experimental orchard of INRA at Montfavet in March, 1992. These aphid colonies were maintained on peach seedlings cultured with nutritive solution in a climatized chamber with temperature being maintained at $21.0\pm0.5°C$, relative humidity at approximately 60% and the photoperiod being the same with the natural photoperiod. For the experiments, adult aphids were put on each of the peach seedlings for producing viviparous nymphs, 4 hours later, these adults and excessive nymphs were removed from the seedlings, with only one nymph being left on each seedling.

Observation. The peach seedlings carrying a aphid nymph which had been delivered for no longer than 4 hours were placed inside incubators in which temperature was kept at 12.5, 16, 18, 20, 24, 26, 27.5 or 30°C respectively. In each incubator were placed a rectangular plate filled with water and pieces of plastic sponge soaked in the water to raise the relative humidity. However, we failed to maintain the same level of relative humidity for all the incubators which had different temperatures. An average relative humidity was kept approximately at 56% for the incubator of 13°C, 54% for 16°C, 55% for 20°C, 42% for 24°C, 46% for 27,5°C, and 44% for 30°C. The photoperiod was maintained at 14:10 in all the incubators using two 8 w fluorescent tubes. The air circulation of the incubators was made by an installed ventilator. Twenty replicates were used for each temperature treatment. The aphids were checked everyday, and the time of molting, dying of the nymphs and the number of new-born nymphs reproduced each day by the adults were recorded. The young nymphs were removed each day after the observation.

Analysis of data. The demographic data obtained for each temperature from above observations were used to build age-specific life tables. The average duration of development for each nymph stages, age-specific survival rate and average age-specific reproductive rate were calculated. The average duration of development and the average daily fecundity were calculated using the arithmetic mean. The average rate of development used in this paper was computed as:

$$D = \frac{n}{\sum_{i=1}^{n} d_i} \qquad (2\text{-}1)$$

where D is the average rate of development, n is the sample size, d_is are observed developmental duration (in days).

The age-specific survival rate was calculated as:

$$l_x = \frac{N_x}{N_{x-1}} \qquad (2\text{-}2)$$

where l_x is the age-specific survival rate of day x, N_x and N_{x-1} are the number of survival aphids of two consecutive days.

Based on information from the life tables, the intrinsic rate of population increase r_m, a comprehensive parameter that summarizes the developmental rate, survival rate and fecundity of green peach aphids, was calculated using Birch's approximation (Birch 1948):

$$\sum_x e^{-r_m x} . l_x . m_x = 1 \qquad (2\text{-}3)$$

where r_m is the intrinsic rate of population increase; x is the age in days; l_x is the age specific survival rate; m_x is the age temperature and that between the intrinsic rate of population increase and temperature were fitted to Logan et al.'s two models (Logan et al. 1976): the model of exponential outer expansion (see Eqn. 2-4) and the sigmoid outer expansion (see Eqn. 2-5).

$$D(T) = \psi [e^{\rho T} - e^{\rho T_m - \frac{T_m - T}{\Delta T}}] \qquad (2\text{-}4)$$

where $D(T)$ the temperature-dependent rate in question; T in the temperature (°C); ψ was define by Logan as the rate of the process concerned at some base temperature; ρ is a value for critical enzyme-catalyzed biochemical reactions; T_m the maximum temperature in degree above the bass temperature for the life process; ΔT the width of high temperature boundary layer.

$$D(T) = \alpha \{[1 + ke^{-\rho T}]^{-1} - e^{-\frac{T_m - T}{\Delta T}}\} \qquad (2\text{-}5)$$

where α is a value representing the declining speed of the rate of the process in question at T_m; $\kappa = (\alpha - \psi)/\psi$, $d(T)$, ρ, T_m and ΔT have the same meaning as in the exponential outer expansion. A quasi-Newton's method was used to obtain estimations of the parameters in the above models.

Results

Immature developmental rate. Within the range of temperature studied, the immature stage of the apterous parthnogenetic viviparous form of *M persicae* attained its highest developmental rate at 24°C, it took in average 5.3333±0.1421 days for the aphid to finish the development of its immature stages. Below 24°C, the developmental rate of the immature stage increases with temperature, it took as long as 15.1667±0.1741 days for the aphids to finish the nymph development at 12.5°C; above 24°C, the immature developmental rate decreases as temperature increases, it took 7.6667±0.1421 days for the aphids to finish their nymph development at 27.5°C. At 30°C, all the 20 aphids died before finishing the development of the second nymph stage (Table 2-1).

Table 2-1 Parameter estimates (M+SE) of the life table of *M. persicae* under laboratory conditions. (1992, Montfavet)

Temperature (°C)	12.5	16	18	20	24	26	27.5	30
d (days) (M±SE)	15.1667 ±0.1741	10.0833 ±0.0833	7.6667 ±0.1421	6.5000 ±0.1508	5.3333 ±0.1421	6.0000 ±0.1231	7.6667 ±0.1421	*
D (day^{-1}) (M+SE)	0.0659 ±0.0008	0.0992 ±0.0008	0.1304 ±0.0024	0.1538 ±0.0036	0.1875 ±0.0050	0.1667 ±0.0034	0.1304 ±0.0024	/
Σm_x (generation^{-1}) (M+SE)	88.4396 ±22.8645	88.8823 ±18.4216	88.9759 ±17.6432	91.3233 ±15.3425	69.8571 ±12.6416	61.4487 ±11.0102	2.3357 ±0.7765	/
R_o (generation^{-1}) (M+SE)	80.9858 ±31.8558	79.9892 ±31.6676	81.4196 ±32.9936	82.1451 ±26.8991	57.2154 ±22.1787	33.3318 ±23.4574	0.3417 ±2.0640	/
r_m (day^{-1}) (M+SE)	0.1446 ±0.0787	0.2009 ±0.0894	0.2224 ±0.0947	0.3234 ±0.0999	0.3744 ±0.1695	0.2714 ±0.22123	-0.0958 ±0.5383	/
T_g (days) (M+SE)	30.3988 ±17.7010	21.8152 ±9.4010	19.7847 ±8.2266	15.6329 ±5.1959	10.8082 ±4.7817	12.9196 ±9.7655	11.2123 +10.5115	/
T_d (days)	4.7951 ±2.6089	3.4508 ±1.5353	3.1170 ±1.3271	2.1435 ±0.6621	1.8512 ±0.8382	2.5539 ±2.0819	/	/
T_{cr} (days)	6.9178 ±3.7639	4.9785 ±2.2151	4.4969 ±1.9146	3.0924 ±0.9552	2.6708 ±1.2092	3.6845 ±3.0035	/	/

d (days) (M±SE): duration of development;
D(day^{-1}) (M): average developmental rate ($D=1/d$);
Σm_x (generation^{-1}): Total fecundity / generation;
R_o (generation^{-1}): finite population growth rate, ($R_o = \Sigma x l_x . m_x$);
r_m (day^{-1}): intrinsic population growth rate, see Eqn. 2-3;
T_g (days): mean length of generation time($T_g = (\Sigma x . l_x . m_x)/(\Sigma l_x . m_x)$);
T_d (days): time required to double the population ($T_d = ln2/r_m$);
T_{cr} (days): characteristic return time ($T_{cr} = 1/r_m$).
All these parameters were measured from aphids maintained on peach seedlings cultivated in nutritive solution under laboratory conditions. Photoperiod is maintained at 14:10.

The data on the relationship between the rate of the immature development and temperature were well fitted to Logan et al's "exponential outer expansion" equation (Fig. 2-1). The estimated maximum temperature for the development of green peach aphids is 29.4770°C, and the estimates for the high temperature boundary layer ΔT is 5.3700°C (Table 2-2). The predicted value of temperature at which the maximum value for immature developmental rate is attained was calculated to be 24.0981°C by seeking the maximum value of Eqn. 2-4.

Table 2-2 Parameter estimates for the developmental rate as a function of temperature of *M. persicae*, using: $D(T) = \psi[e^{\rho T} - e^{\rho T_m - \frac{T_m - T}{\Delta T}}]$ (Logan' exponential outer expansion).

(1992, Montfavet)

	ψ	ρ	T_m	ΔT	R^2
Mean	0.6730	0.1856	29.4770	5.3700	0.995
SE	2.5631	0.4335	12.1324	1.2342	

D(T): the developmental rate; T is the temperature (°C);
ψ : the rate of the process concerned at some base temperature;
ρ : a value for critical enzyme-catalyzed biochemical reactions;
T_m: the maximum temperature in degree for the life process;
ΔT: the width of high temperature boundary layer.
A quasi-Newton's method was used to obtain estimations of the parameters in the above models.

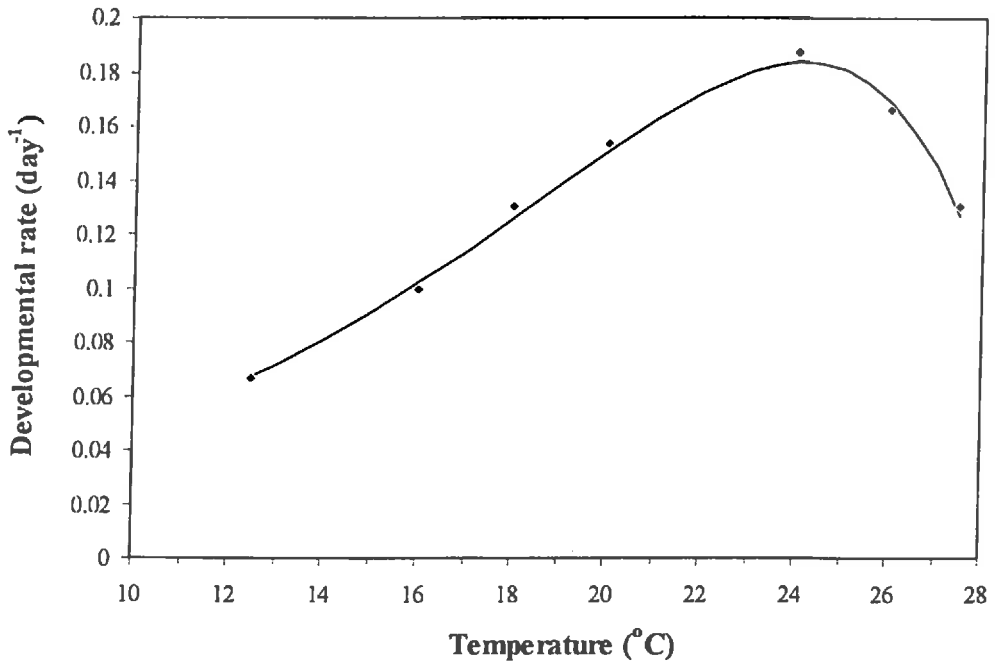

Fig. 2-1 Developmental rate *D* (D=1 day^{-1}) of *M. persicae* in relation to constant temperature (°C). The curve is plotted using predicted values from equation (2-2); the dots are observed values.

Fecundity of the apterous parthnogenetic females. The fecundity of the aphids were described in terms of total fecundity and the age-specific fecundity profile. The total fecundity of the adults attains its maximum at 20°C. Below 20°C, it showed a weak tendency to increase with temperature; above 20°C, the total fecundity declines rapidly as temperature increases, and the decline accelerates as the temperature augments (the slop of the curve becomes steeper toward the right) (Fig. 2-2, Table 2-1). The age-specific fecundity profile (Fig. 2-3) showed that the reproduction of green peach aphids is more concentrated in early adult life under higher temperatures than under lower temperatures. Below the optimal temperature (24°C), as temperature increases, the peaks of age-specific fecundity becomes higher, but the duration of the reproduction becomes shorter. Beyond 24°C, as temperature increases, the peak of age-specific fecundity becomes lower and the duration of reproduction shorter.

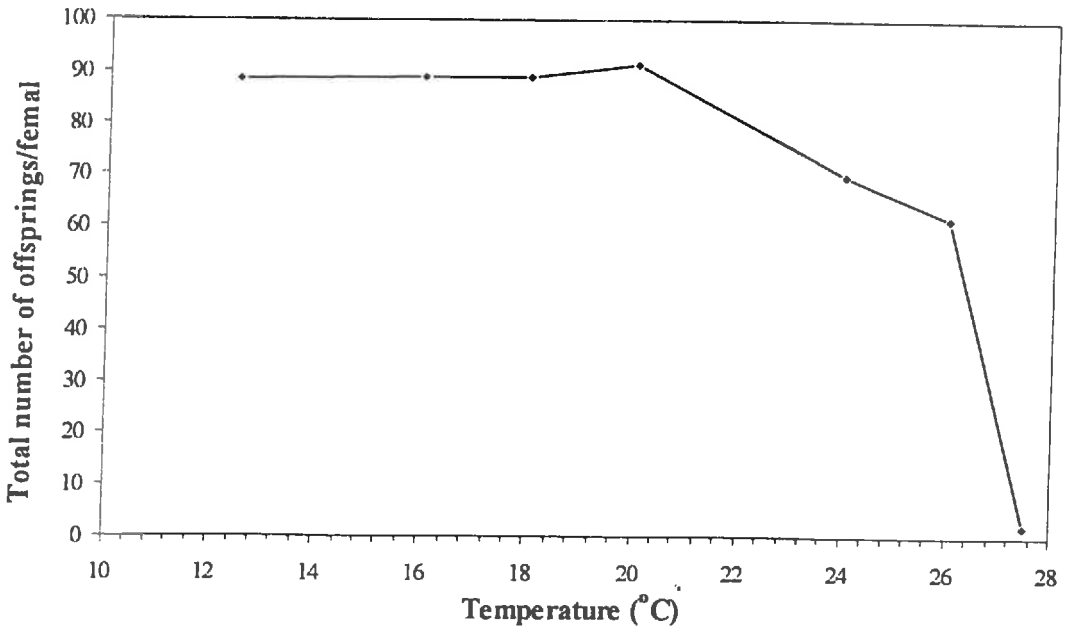

Fig. 2-2 Relationship between the total fecundity of *M. persicae* and temperature (°C) on peach seedlings cultivated with nutritive solution under laboratory conditions. Photo period 14:10.

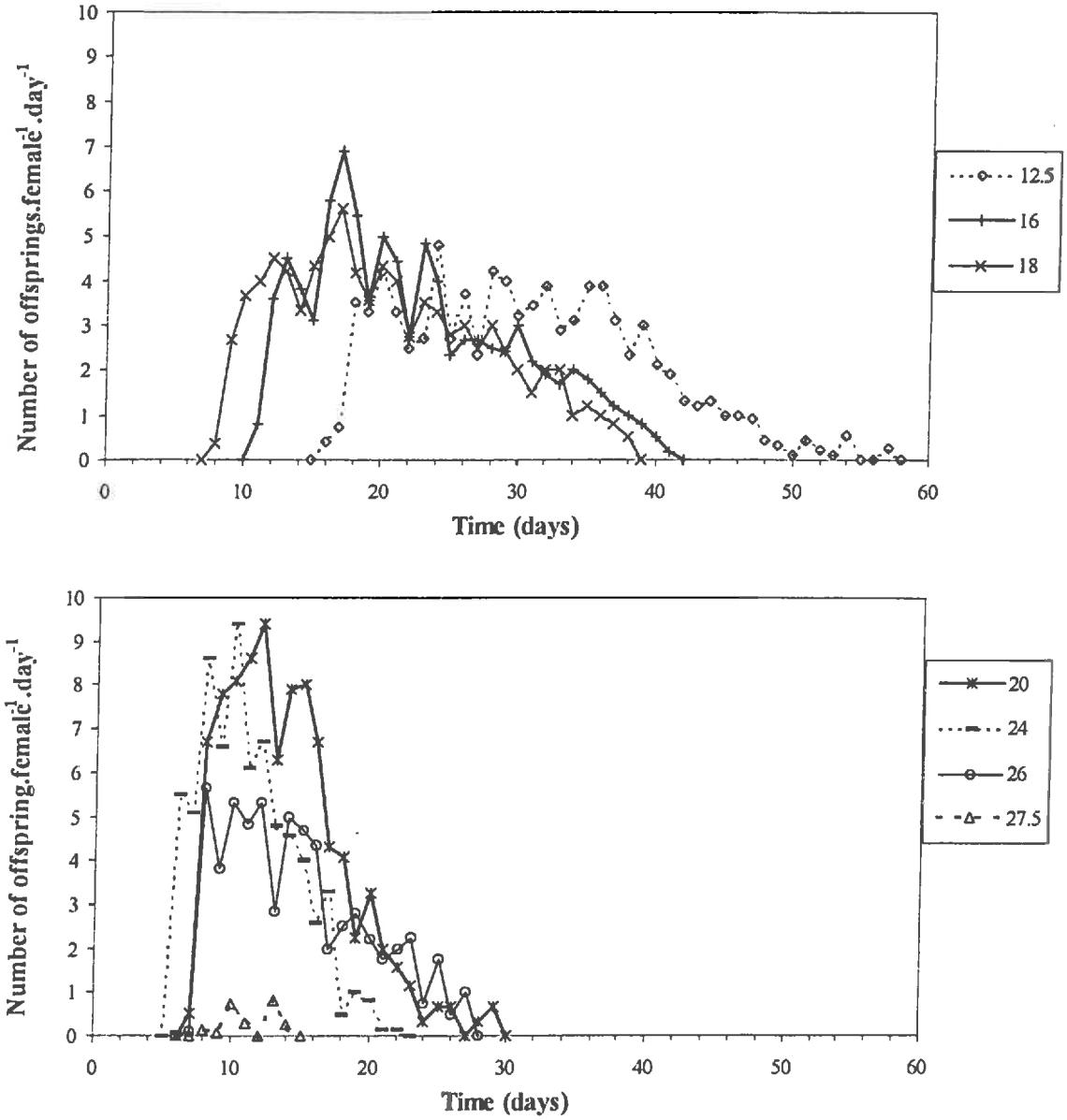

Fig. 2-3 Age-specific fecundity profiles of *M. persicae* in relation to temperature (°C). Observation made under laboratory conditions. The aphids are reared on peach seedlings cultivated in nutritive solutions. Photoperiod is set at 14:10. The numbers in the legend boxes are temperatures in °C

Age-specific survival rate. The life span of green peach aphids was observed to become shorter as temperature augments (Fig. 2-4). It is also shown in Fig. 2-4 that under lower temperatures, most of the death happened during the late adult life and the survival curve appeared more of Deevey's type I, while under higher temperatures, most of the death occurred during the immature stages and the survival curve appeared more close to Deevey's type III.

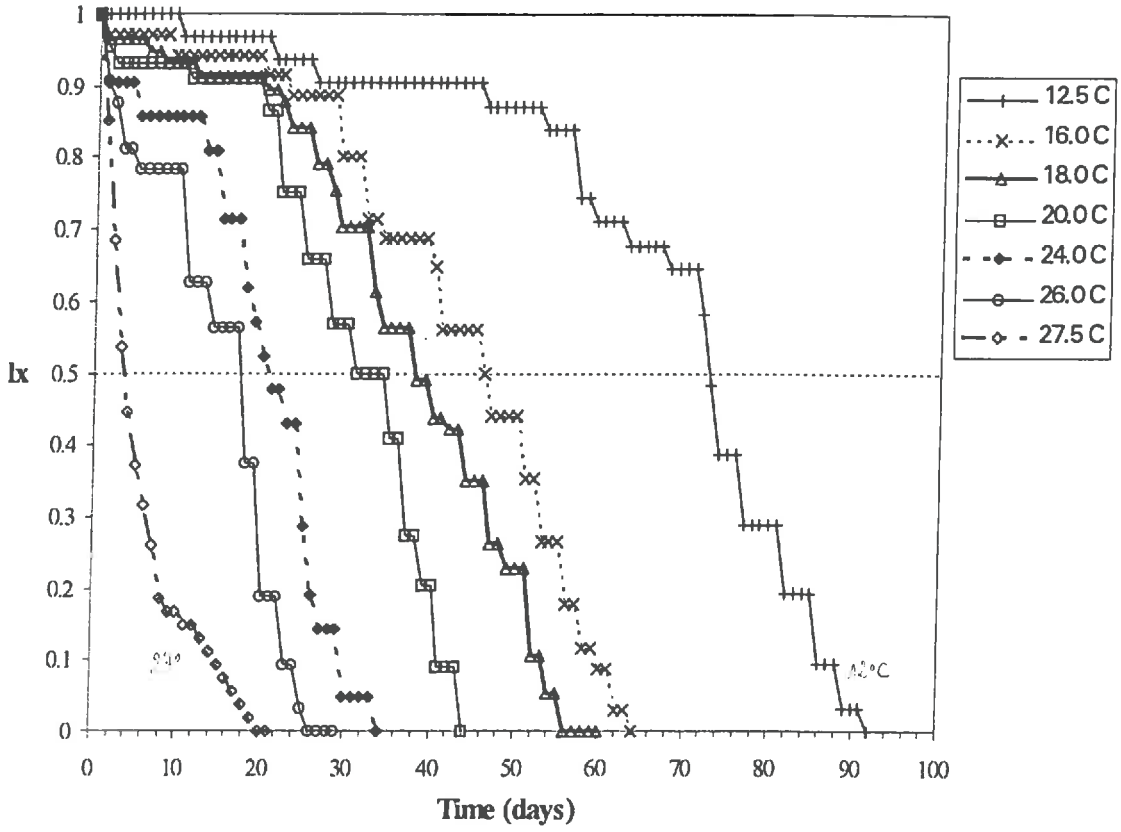

Fig. 2-4 Age-specific survival rate of *M. persicae* in relation to temperature(°C). Observation made under laboratory conditions. $l_x=N_{x-1}/N_x$ is the age specific survival rate of age x. The aphids are reared on peach seedlings cultivated in nutritive solutions. Photoperiod is set at 14:10.

Intrinsic rate of population increase. The relationship between the intrinsic rate of population increase (r_m) of green peach aphids and temperature turned to be similar to that between the developmental rate and temperature. The highest r_m was observed at 24°C (r_m=0.3744). Below 24°C, the value of r_m increases with temperature, but beyond 24°C, the r_m value decreases very rapidly as temperature augments (Fig. 2-5). The maximum temperature threshold for non-negative population increase was estimated, by calculating T (C°) when r_m (as defined in Eqn. 2-5) is set to zero, to be 27.921°C, which is lower than the maximum temperature for immature development. Consequently, the width of high temperature boundary layer for r_m is narrower than that for nymph development (Table 2-2). The predicted value of temperature at which the maximum intrinsic rate of population increase is attained was calculated to be 23.791°C by seeking the maximum value of

Eqn.2-5. The relationship between r_m and temperature was well depicted with Logan et al's "sigmoid outer expansion" model. In comparison with the intrinsic rate of population increase, the net reproductive rate ($R_o=\Sigma x.l_x.m_x$), which represents the population multiplication by generation, attains its largest value (82.1451/generation) at 20°C (Table 2-2). Another useful comprehensive population parameter is the average generation time. Green peach aphids had the shortest generation time (10.8082 days) at 24°C, and became longer as temperature becomes lower. A more immediate index of the speed of population growth is the population doubling time, at 24°C, the green peach aphid could double its population in less than 2 days, compared with 4.7951 days at 12.5°C, 3.4508 days at 16°C, 3.117 days at 18°C, and 2.1435 days at 20°C.

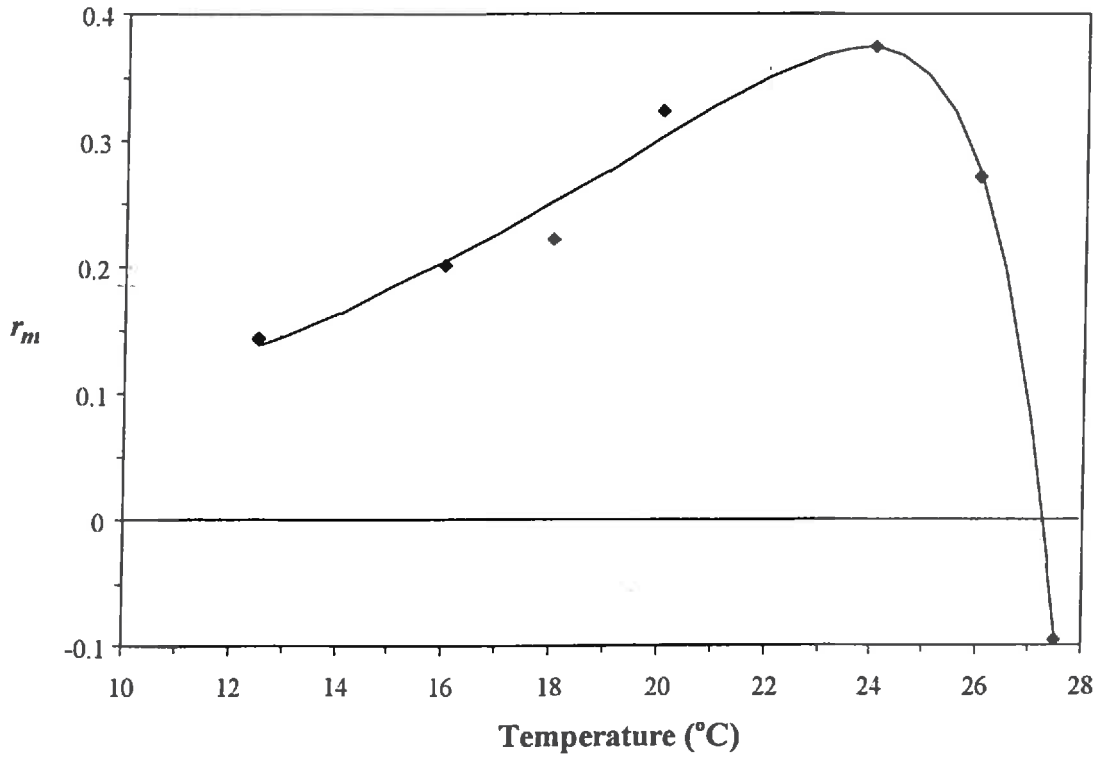

Fig. 2-5. Intrinsic population increase rate r_m of *M. persicae* in relation to constant temperatures (°C). The curve is plotted using predicted values from equation (2-3); dots are values estimated using equation 2-1.

Table 2-3 Parameter estimates for the intrinsic population growth rate as a function of temperature of *M. persicae*, using : $r_m(T) = \alpha\{[1 + ke^{-\rho T}]^{-1} - e^{-\frac{T_m - T}{\Delta T}}\}$ (Logan's sigmoid outer expansion)

(1992, Montfavet)

	α	κ	ρ	T_m	ΔT	R^2
Mean	0.640	30.003	0.170	27.555	1.332	0.998
SE	1.2303	62.2453	0.321	11.6086	0.3881	

$r_m(T)$ is the population growth rate; T is temperature (°C);
α is a value representing the rate of change of $D(T)$ at T_m;
$\kappa = (\alpha - \psi)/\psi$; ψ is the rate of the process concerned at some base temperature;
ρ is a value for critical enzyme-catalyzed biochemical reactions;
T_m the maximum temperature in degree for the life process;
ΔT the width of high temperature boundary layer.
A quasi-Newton's method was used to obtain estimations of the parameters in the above models.

Discussion

The local race of green peach aphids we studied at Montfavet exhibited an adaptation to low temperature on the primary host. Its highest developmental rate occurred at 24°C. it failed to complete development at 30 °C. This pattern is fundamentally consistent with that observed by Barlow (1962) on potato leaves and that by Deloach (1974) on cabbage plants where the aphid had the quickest development at 25°C (both studies were conducted under 5, 10, 15, 20, 25, and 30°C). However, in our experiment the developmental time from the first instar to adult under 10-30°C is significantly longer than that in Barlow's while being shorter than that in Deloach's. Also, while our results is consistent with Barlow's concerning the fact that green peach aphid failed to complete its immature development at 30°C, DeLoach's study (1974) showed that the aphid succeeded in developing into adult at the same temperature on cabbage plants. In this study, the fecundity of apterous viviparous adult females attained its upper bound (about 80 youngs/female, see Van Emden et al. 1969) under temperatures below 20 °C, and declined under temperatures above 20 °C. The peak net reproductive rate (R_o) occurred at 20°C, which is consistent with DeLoach's observation but differs from Barlow's where it

occurred at 15°C. Although the maximum fecundity was observed to occur at 20°C, a higher daily reproductive rate was attained at 24 °C because the reproduction of the female was much more concentrated (Fig 4-3). While the adult reproductive profile from our study is similar to those from Barlow's and DeLoach's, we recorded a much higher total fecundity than did Barlow and DeLoach. The age-specific survival profile of green peach aphid in relation to temperature observed in this study follows a pattern which is similar to that was demonstrated in *Rhopalosiphum padi* (Linnaeus) (Leather, 1980) as well as to those observed in green peach aphid by Barlow and DeLoach on potato and cabbage respectively. In all these studies the aphid manifested a greater longevity and a higher immature survival rate under lower temperatures than under higher temperatures. Nevertheless, the longevity we recorded is somewhat longer than that observed by Barlow but shorter than that by DeLoach; this difference in longevity between the three studies is in accordance with that in developmental time: the aphids in Barlow's system develop faster than that in ours and in DeLoach's, so it has a shorter longevity, and vice versa for the long longevity in Deloach's experiment. Similar to the developmental rate, the intrinsic rate of population increase (r_m) of green peach aphids attained its peak value of 0.3744 at 24°C on peach plants. However, the limitation of temperature on population growth is more severe than that on individual development: the upper limit of temperature for a positive population growth is estimated at 27.555 °C in comparison to that for development, which is estimated at 29.477 °C. This difference was also exhibited by a bigger value of ΔT (width of the high temperature boundary layer) for the population growth rate (r_m) than that for the developmental rate (D) (Table 2, 3). In the studies of Barlow (1962) and DeLoach (1974), the maximum value of r_m of green peach aphid was attained at 25°C, approximately the same level as that in this study (considering their studies were carried out using temperatures 5, 10, 15, 20, 25 and 30°C); both studies showed a negative value of r_m at 30°C; however, the r_m value estimated in this experiment is smaller than that in Barlow's but greater than that in DeLoach's. From above it appears that the general patterns of the demographic characteristics and the intrinsic rate of population increase of green peach aphid in relation to temperature is similar in different studies carried out on different host plants, but the amplitude of specific values varies from

one experimental system to another. The variation in the amplitude of specific values among the studies carried out by Barlow, DeLoach and the author seems to be rooted in the systematic innate variations in the properties of the systems studied instead of in random experimental errors. The difference may mainly result from the species and physiological status of host plants and geographical races of the aphid.

The utility of r_m as a parameter to be used in insect population models has been questioned (Cole 1954) on the basis that it is not a valid measure of population growth unless populations have attained a stable age structure, which is considered unlikely in nature by some author because of constantly fluctuating environmental conditions (Birch 1948, Barlow 1962, Dixon 1989). However, Hughes (1962) found that half of 109 distributions sampled from field aphid population had achieved a stable age structure. In fact, the high reproductive rate of green peach aphid and some density-dependent mechanism in natural populations is quite likely to make the age structure bounded within certain range.

The influences of temperature on biological processes have been an massively studied area. Nevertheless, several basic problems wait for further exploration. A most obvious one is that higher rates of development occur with fluctuating temperatures than with constant temperatures (Cloudsley-Thompson 1953). Messenger (1964b) and Siddiqui et al. (1973) have investigated this phenomenon in aphids and both obtained slightly faster development with fluctuating temperature. Questions remain concerning whether and how the shape of wave and amplitude of fluctuations of temperature may affect the developmental rate. Aphids usually have rapid development and assume parthenogenetic viviparous reproduction at least during part of their life history, the influences of temperature at certain time (or certain time interval) of life may be memorized or have delayed effects on the following life stages or even the following generation; or in other words, aphids that are currently living under the same temperature but had different history of temperature experience may manifest different development, survival and reproductive rates. This may be inherently related to the answer of the previous question.

Chapter 3.

Temperature-dependent functional response of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to *Myzus persicae* (Sulz.) (Homoptera: Aphididae)

Introduction

One of the most important variables determining the effectiveness of a predator is the predation rate, which usually varies with prey density and temperature (Frazer and Gilbert 1976, Gutierrez et al. 1981, Mack and Smilowitz 1982). Information about the predation rate of the predator in relation to prey density and environmental temperature is essential to allow a valid evaluation of the potential effectiveness of *Harmonia axyridis* Pallas as a biological control agent against *Myzus persicae* (Sulz.) and the development of strategies for field releases.

The functional response describes the relationship between the number of prey attacked per predator per unit time and the number of prey present (Solomon 1949, Holling 1959, Hassell 1978). Three types of functional responses have been recognized, of which the type II response is primarily suitable for describing the predation of many invertebrate predators (Holling 1959, Hassell 1978; Hassell and Waage 1984). This type of response is characterized by the number of prey captured increasing rapidly with prey density and leveling off at high density of prey. One of the mathematical descriptions of the type II response is given by Holling's disk equation:

$$N_a = \frac{a.N}{1 + a.Th.N} \qquad (3\text{-}1)$$

where N is the number of prey offered to the predator, N_a is the number of prey consumed per predator per unit time, a is the instantaneous attack rate of the predator, and Th is handling time, time that a predator spent in subduing, ingesting and digesting one prey item and the subsequent resting. Alternate models have been proposed by different authors

based on different assumptions (see discussion by Royama 1971, Williams 1980, Williams and Juliano 1996). The most influential of these models are probably those of Royama (1971) and Rogers (1972) who treated the functional response as the time integral rate of predation, taking into account declining prey density over time, in contrast to the instantaneous rate represented by Holling's disc equation. These models may be microscopically more realistic than Holling's equation. However, as Williams (1980) pointed out, most of the models, including Holling's disc equation, are mathematically isomorphic forms of the Michaelis-Menten-Monod equation, which describes the rate of enzyme-catalyzed reactions in a saturation kinetic form. They make little, if any, qualitative difference in macroscopic dynamic structures of the predator-prey system. Moreover, the implicit form of the mathematical expression of the Royama-Rogers model make it difficult to be incorporated into an explicitly defined mathematical model of predator-prey dynamics and add to the cost of computation. Therefore, Holling's disc equation remains the most commonly used model.

As poikilothermic animals, insects have their metabolic rate and other biological rates varying with surrounding temperature. Temperature has additional differential effects on an insect species and its predators. As was demonstrated in the previous chapter, *M. persicae* adapts well to low temperature in terms of its population growth rate (Chapter 2). Determining the effects of temperature on the predation rate and developmental and survival rates (see Chapter 4) of *H. axyridis* is thus critical in determining within what temperature range the predator is likely to be a effective biological control agent and in developing field release strategies concerning the timing and numbers of the releases. Several approaches have been used to describe the temperature-dependent functional response (Messenger 1968, Everson 1980, Goldman and Carpenter 1974, Frazer and Gilbert 1976, Tamaki and Long 1978, Guitirrez et al. 1981, Flinn 1991). A general temperature-mediated functional response model was developed by Mack et al. (1981) by incorporating into Holling's type II response model (Eqn. 3-1) the enzyme kinetics equations that had been used to describe the temperature dependence of growth or development (Eyring and Urry 1975). This model describes the instantaneous attack rate a and the handling time Th as functions of temperature:

$$a(T) = \frac{u_1 . T . e^{-\frac{u_2}{T}}}{1 + u_3 . e^{-\frac{u_4}{T}}} \qquad (3\text{-}2a)$$

$$Th(T) = \frac{1 + v_1 . e^{-\frac{v_2}{T}}}{v_3 . T . e^{-\frac{v_4}{T}}} \qquad (3\text{-}2b)$$

where u_1, u_2, u_3, u_4 and v_1, v_2, v_3, v_4 are curve fitting parameters.

The present chapter deals with the measurement of the predation rate of the larvae of *H. axyridis* in relation to the density of *M. persicae* and temperature, and we try to model the temperature-dependent functions using equation 3-1 and 3-2 a, b.

Materials and methods

The larvae of *H. axyridis* used in these experiments were obtained from the laboratory mass rearing using eggs of *Ephestia kuehniella* Zeller maintained in INRA-Laboratory of Population Biology in Antibes. The green peach aphid used as the prey came from laboratory colonies maintained on the peach seedlings of the variety 305 which were grown in nutritive solution (see Chapter 1). Cylindrical plastic jars (80x50 mm) were used for setting up the arenas. Three young peach leaves measuring about 12 cm long, with the tip of the stalks wrapped with a piece of filter paper saturated with nutritive solution (see Chapter 1), were placed in each of the jars. Apterous nymphs of *M. persicae* in their 3rd or 4th instars were distributed evenly on these peach leaves. Six aphid densities, depending on the stage of the predator larvae and experimental temperature, were used (Table 3-1), with each of the treatments replicated six times.

To keep the age of predators of a given stage roughly identical, we chose larvae of the instar prior to the instar to be observed, which appeared ready to molt, and placed them in the cylindrical jars. Freshly molted individuals, 4-8 hours after the molting, were then used

in observations. A single individual of *H. axyridis* was placed in each of the arenas. Each set of arenas were placed in one of the incubators of different constant temperatures. The consumption of green peach aphids in each of the arenas was checked and the initial number of aphids was restored for each day until all the larvae of the predator developed to the next stage. The larvae that had been used for the observation of a previous stage were not used again in the observation of any of the following stages. The same procedure was repeated for all the four larval instars of *H. axyridis*.

Experiments were conducted under 12.5, 15, 18, 20, 25, 27.5, 30+0.5°C of constant temperatures respectively to measure the effects of temperature on the functional response of each of the active stages of *H. Axyridis* to *M. persicae*. The humidity inside the incubators was maintained at approximately 70+5% RH and the photoperiod was set to 14:10 (L: D) for all the observations. Light was provided by two 8 watt fluorescent tubes. The air circulation of the incubators was made by an installed ventilator.

The average per-capita daily consumption of green peach aphids by each coccinellid larval stage was calculated from the total consumption of the predator during the specific larval stage divided by the length of that larval stage. If at certain low initial aphid density all the aphids offered were consumed for most the experimental replicates, the data points were left out so as to avoid biased estimates of parameters. Holling's (1959) type II functional response model (Eqn. 3-1) was fitted to the data of the average daily consumption of *M. persicae* by each larval stage of *H. axyridis* under each of the temperatures using Woolf linear transformation (Currie 1982):

$$\frac{N}{N_a} = Th.N + a^{-1} \qquad (3\text{-}3)$$

which was suggested to be a method that provides better parameter estimation than other linear transformations and nonlinear regression (Fan and Petitt 1994).

The estimated parameters a and Th for different temperatures were then fitted to equations 3-2 a, b using the nonlinear regression procedure in SYSTAD (SYSTAD Inc. 1990-1993) to describe the effects of temperature on the predation rate.

Table 3-1 Number of *M. persicae* offered to each larva of H. axyridis of different larval stage at different temperatures.

(Montfavet, 1993)

Stage of	Temperature (°C)						
H. axyridis	12.5	15	18	20	25	27.5	30
	5	5	5	10	10	10	10
	10	10	10	20	20	20	20
L_1	20	20	20	40	40	40	40
	40	40	40	60	60	60	60
	80	80	80	100	100	100	100
	160	160	160	200	200	200	200
	20	20	20	25	25	25	25
	40	40	40	50	50	50	50
L_2	60	60	60	75	75	75	75
	120	120	120	150	150	150	150
	200	200	200	200	200	200	200
	300	300	300	300	300	300	300
	25	25	35	50	50	50	50
	50	50	75	100	100	100	100
L_3	100	100	150	200	200	200	200
	200	200	300	400	400	400	400
	300	300	400	500	500	500	500
	400	400	500	600	600	600	600
	35	35	50	50	50	50	50
	75	75	100	100	100	100	100
L_4	150	150	300	300	300	300	300
	200	200	400	400	400	400	400
	300	300	500	500	500	500	500
	400	400	600	600	600	600	600

Values in the table are numbers of green peach aphids offered to *H. axyridis*. L_1, L_2, L_3, L_4 denote the larval stage 1-4 respectively.

Results

The data on the functional response for all the larval instars of *H. axyridis* under different temperatures were satisfactorily fitted to Holling's type II functional response model (Eqn. 3-1), which is characterized by the predation level increasing at a decreasing rate as prey density augments and approaches indefinitely a maximum predation level as prey density goes to infinity (Fig. 3-1).

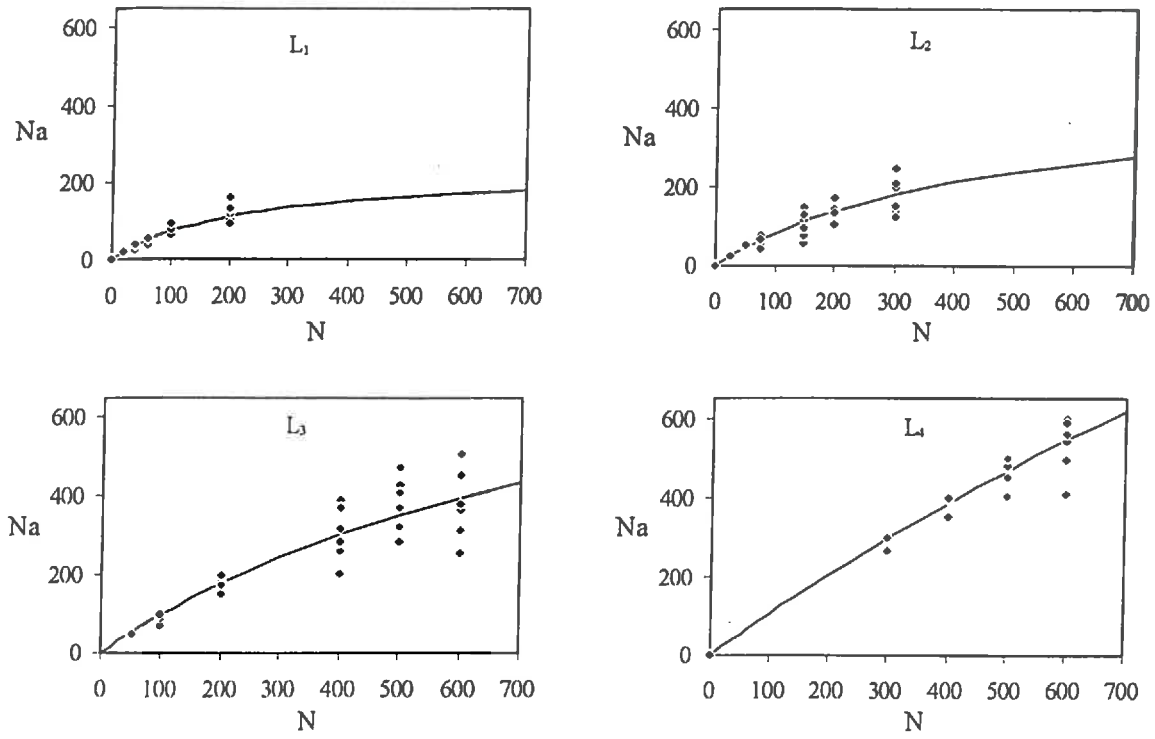

Fig. 3-1 Functional response of larvae of *H. axyridis* to *M. persicae* under 25°C. The solid lines are generated from predicted values, the dots are observed values. The *N* in x-axis is the number of prey offered; The *Na* in y-axis is the number of prey consumed; L_1, L_2, L_3, L_4 are larval instar 1-4 of the predator.

Age-dependence of the functional response of *H. axyridis* to *M. persicae*. The predation rate of larval *H. axyridis* increases with their developmental stages, which is numerically manifested by the difference in the parameter values for different larval stages: the older instar larvae have a larger value of instantaneous attack rate *a* and a smaller value of handling time *Th* than the younger ones (Table 3-2). The instantaneous attack rate *a* determines the rate at which the number of prey attacked (*Na*) increases with the number of prey offered (*N*); and the handling time *Th* determines the voracity - the asymptote of *Na* as *N* increases to infinity. From Table 3-2, we can see that the differences in the values of *a* between different instars are much smaller than the differences in the values of *Th*, which implies that the voracity has a bigger share than the instantaneous attack rate in the differences in the predation rates between different instars of the

predator.

Table 3-2. Parameter estimates for functional responses of Larval *H. aryridis* to *M. persicae* under constant temperatures (°C).

(1992, Montfavet)

Stage	Temperature(°C)	*a* (M±SE)	*Th* (M±SE)	R^2
	12.5	0.2064 ±0.1074	0.0695 ±0.0078	0.8176
	15	0.3468 ±0.1426	0.0318 ±0.0035	0.8784
	18	0.5699 ±0.1552	0.0113 ±0.0016	0.9380
L_1	20	0.8081 ±0.2588	0.0041 ±0.0008	0.9022
	25	0.9257 ±0.2716	0.0039 ±0.0007	0.8697
	27.5	0.9663 ±0.3216	0.0041 ±0.0008	0.8277
	30	0.7598 ±0.2421	0.0100 ±0.0015	0.8014
	12.5	0.3405 ±0.1335	0.0422 ±0.0063	0.8248
	15	0.5224 ±0.1757	0.0165 ±0.0025	0.8180
	18	0.7632 ±0.1792	0.0077 ±0.0014	0.9165
L_2	20	0.9245 ±0.2959	0.0029 ±0.0007	0.8355
	25	0.9898 ±0.3158	0.0022 ±0.0006	0.8495
	27.5	1.0564 ±0.3643	0.0023 ±0.0007	0.8569
	30	0.7897 ±0.2254	0.0080 ±0.0009	0.8143
	12.5	0.4823 ±0.2075	0.0215 ±0.0033	0.9163
	15	0.7658 ±0.2649	0.0099 ±0.0016	0.8061
	18	0.9450 ±0.2919	0.0041 ±0.0008	0.8208
L_3	20	1.0676 ±0.2017	0.0020 ±0.0002	0.8835
	25	1.1036 ±0.2097	0.0010 ±0.0003	0.8341
	27.5	1.1195 ±0.2989	0.0008 ±0.0002	0.8799
	30	0.8131 ±0.2471	0.0047 ±0.0005	0.7925
	12.5	0.6850 ±0.2559	0.0081 ±0.0007	0.8695
	15	0.9768 ±0.2758	0.0036 ±0.0005	0.8460
	18	1.0129 ±0.2642	0.0015 ±0.0004	0.8575
L_4	20	1.0963 ±0.2006	0.0009 ±0.0002	0.8741
	25	1.1296 ±0.0898	0.0004 ±0.0001	0.9048
	27.5	1.1133 ±0.198	0.0007 ±0.0002	0.8124
	30	0.7896 ±0.2634	0.0013 ±0.0007	0.7825

a: the instantaneous attack rate; *Th*: the handling time. These two parameters are estimated by fitting experimental data to Eqn. 3-1, R^2 is the determination coefficient for the linear fit. L_1, L_2, L_3, L_4 denote the larval stage 1-4 respectively.

Temperature-dependence of the functional response of *H. axyridis* to *M. Persicae*. The maximum predation rate of larvae of *H. axyridis* occurred at about 25-27.5°C depending on the developmental stages of the larvae. The estimated instantaneous attack rate *a* had the lowest values at 12.5°C and increased with temperature until attaining its maximum value at the optimum temperature and then declined as temperature increased; the optimum temperature at which the maximum instantaneous attack rate occurred was observed to be 27.5°C for the 1st, 2nd and 3rd instars and 25°C for the 4th instar (Table 3-2. Fig. 3-2). The estimates of handling time *Th* had its peak value at 12.5°C and declined as temperature increased, attaining its lowest value at 25°C for all the 4 instars (Table 3-2, Fig. 3-3).

Table 3-3 Parameter estimates and goodness of fit of the models for the temperature-dependence of *a* and *Th*.

(1992, Montfavet)

Parameters	L_1	L_2	L_3	L_4
$a(T) = \frac{u_1 . T . e^{-\frac{u_2}{T}}}{1 + u_3 . e^{-\frac{u_4}{T}}}$				
u_1	0.1982 +0.1162	0.1022 +0.0567	0.0867 +0.0362	0.0489 +0.0172
u_2	31.778 +9.8700	16.236 +8.228	9.1798 +6.2851	-2.6996 +4.9397
u_3	1370.3 +2150.1	2139.3 +3454	13699 +3191.5	12636 +2921.1
u_4	202.04 +54.578	255.28 +83.30	210.14 +74.989	284.56 +66.739
R^2	0.9818	0.9648	0.9457	0.8691
$Th(T) = \frac{1 + v_1 . e^{-\frac{v_2}{T}}}{v_3 . T . e^{-\frac{v_4}{T}}}$				
v_1	3.3E+09 +3.6E+09	3.3E+09 +4.0E+09	3.3E+09 +6.2E+09	3.3E+09 +1.9E+09
v_2	619.53 +97.192	603.44 +37.7064	610.04 +57.005	620.45 +20.565
v_3	97.689 +47.770	215.47 +69.596	255.36 +109.26	636.06 +177.03
v_4	55.658 +6.3184	59.198 +3.9735	53.001 +5.4351	52.142 +3.5801
R^2	0.9752	0.9968	0.9924	0.9967

a (T): the instantaneous attack rate as a function of temperature; *Th(T)*: the handling time as a function of Temperature; u_1, u_2, u_3, u_4, v_1, v_2, v_3, v_4 are parameters for Eqn. 3-2a and 3-2b, their value are estimated by fitting the *a* and *Th* values listed in Table 1 to Eqn. 3-2a, b using Newton's nonlinear parameter estimation procedure. R^2 is the determination coefficient of the nonlinear regression. L_1, L_2, L_3, L_4 denote the larval stage 1-4 respectively.

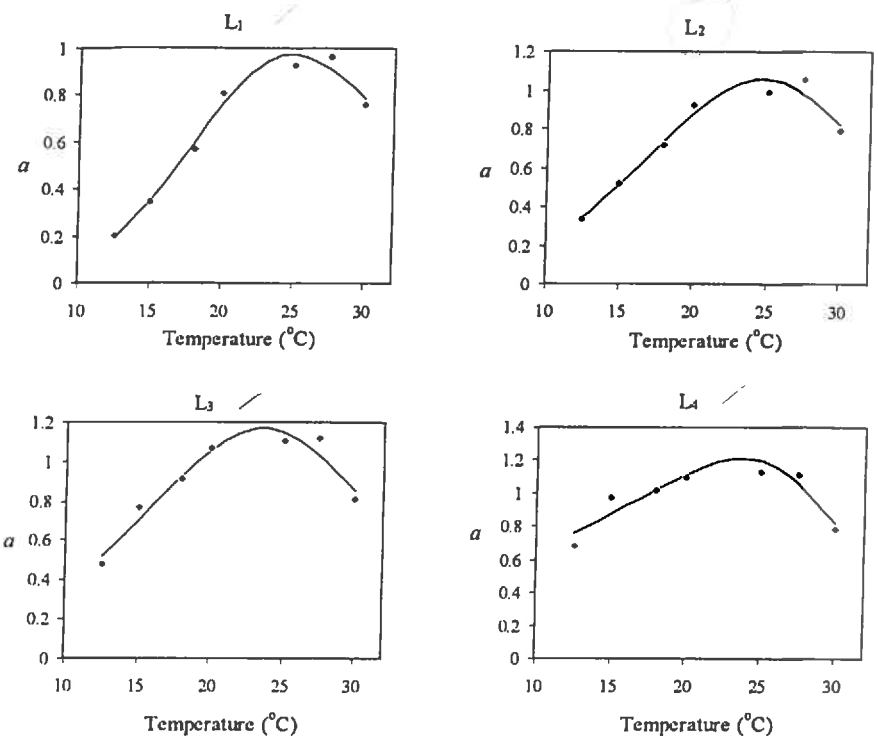

Fig. 3-2 The relationship between instantaneous attack rate a of *H. axyridis* on *M. persicae* and Temperature (°C). L1-4 denotes the larval stadium 1-4.

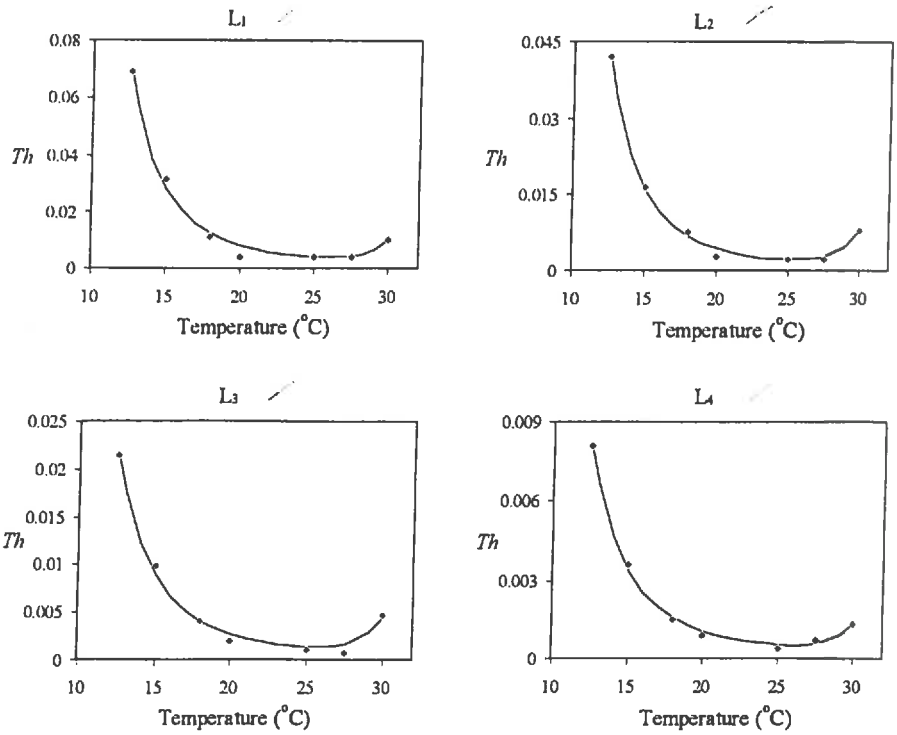

Fig. 3-3 The relationship between instantaneous attack rate a of *H. axyridis* on *M. persicae* and temperature (°C). L_1, L_2, L_3, L_4 denote the larval stages 1-4.

The estimated values of parameters *a* and *Th* under different temperatures for all the larval instars were fitted to equation 3-2a, b (Table 3-3, Fig 3-2, 3-3). The predicted maximum values for the instantaneous attack rate *a* occur at a somewhat lower temperature than that measured directly from the experiment (Fig 3-2).

The parameters *a(T)* and *Th(T)* as temperature forcing functions could be plugged into equation 3-1, from which the temperature-dependent functional response of all larval instars of H. axyridis to M. persicae were plotted in 3-D surfaces to illustrate the dependence of the predation rate on both temperature and prey density (Fig. 3-4)

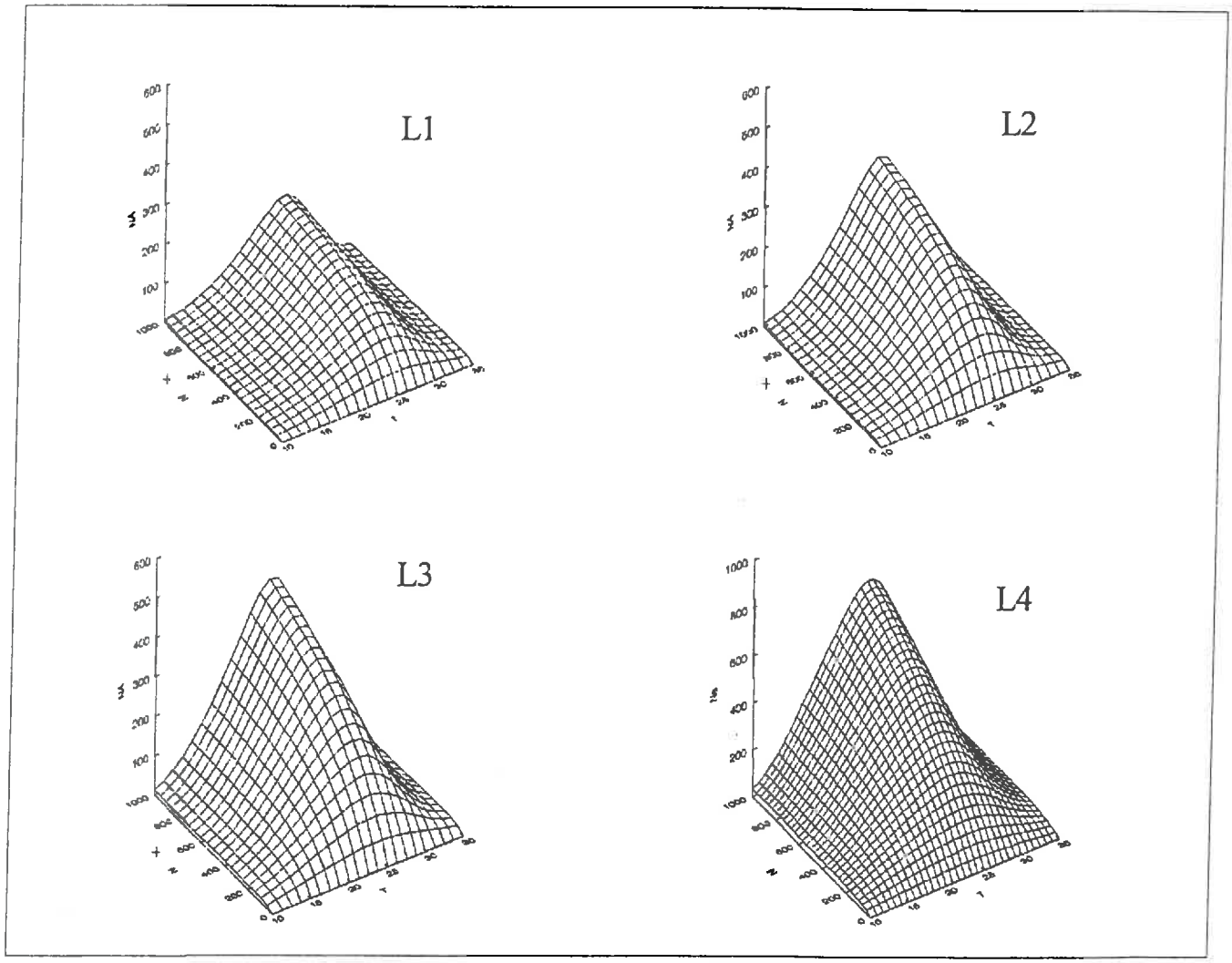

Fig. 3-4. Daily consumption of *M. persicae* by *H. axyridis* in relation to temperature and density of the aphid. Values in plot are calculated from the model.

Discussion

The experiment has shown that the functional responses of all the four instars of *H. axyridis* to *M. persicae* conform Holling's type II response. The 3rd and 4th instar larvae of *H. axyridis* are significantly more effecient in prey searching and more voracious in prey consumption than the 1st and 2nd instars. The difference between the instantaneous attack rate *a* of different larval instars of the coccinellid is significantly smaller than that between the handling time *Th* (Table 3-2). According to Hollong (1959), *Th* signifies the time spent in subduing, ingesting and digesting a prey item and Th^{-1} is in fact the saturation value of prey consumption (*Na*); *a* signifies the searching ability and is the rate at which the saturation consumption is reached as the prey density increases. Therefore, the greater predation rate of the older instar larvae is more a result of being more voracious (having a shorter handling time or a bigger maximum prey consumption) than that of being more effecient in prey searching. Prey consumption of *H. axyridis* is highly dependent on temperature (Fig. 4-4).

The searching rate and the rate at which the prey are ingested and digested increase with temperature, but high temperature has inverse effects on predation rate. Moreover, the increase in developmental rate (see Chapter 4) as a result of increase in temperature naturally results in a higher daily requirement for food. However, we suspect that the total prey consumption might vary only slightly with varying temperature and prey density, because a bigger prey consumption due to the increase of temperature and prey density usually results in a shorter developmental time, thus a shorter period of consumption. It seems that there is such a tendency that the instantaneous attack rate *a* of the younger instar larvae is more sensitive to the variation in temperature than that of the older instars, but the handling time *Th* of the younger instars is less sensitive to the increase in temperature (Table 1).

In this experiment, the green peach aphids are quite evenly distributed in the arenas by the experimental manipulation. It would not be the case for the field populations, which are usually characterized by clustered distribution (Leclant 1976, Tamiki 1973). We suspect that clustered prey distribution may promote the efficiency in the predator's

intensive searching phase but reduce the efficiency in the extensive searching phase. However, the overall searching efficiency is usually higher in the case of prey with clustered distribution (Hassell 1979). Even though, the data from trials using evenly distributed prey still do not lose to be a bottom line for estimating the predator's prey consuming rate.

Chapter 4.

Effects of temperature and density of prey *Myzus persicae* (Sulz.) (Homoptera: Aphididae) on the developmental and survival rates of larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae)

Introduction

The effectiveness of *Harmonia axyridis* Pallas as a biological control agent for inundative release against *Myzus persicae* (Sulz.) depends not only on its predation rate in response to the density of prey, i.e., functional response, but also on the rate of change in its own density in response to the prey density, i.e., the numerical response. Though clearly defined in theoretical frameworks, the numerical response has been more or less neglected in the empirical studies of real-world predator-prey interactions because of the technical difficulties involved in the measurements of the response (Readshaw 1973, Hassell 1978, Frazer 1988). Two elements of numerical responses - aggregative and reproductive numerical responses have been recognized in the interactions of aphids and their natural enemies by Frazer (1988). The aggregative numerical response is the spatial accumulation of predators in response to the prey density, which refers to the movement of predators into a field or patch with higher prey density or out of one with lower prey density (Frazer 1988). The reproductive numerical response is the relationship between the number of offspring reproduced by the predator and the prey density (Frazer 1988). Biological theories and empirical studies (Guterriez 1981, Mills 1981, Hardman and Roger 1991,) tell us that prey density also affects the developmental and survival rates of a predator, which have their shares in the population changes of the predator. This suggests that the developmental and survival numerical response, changes in developmental and survival rates of the predator in response to prey density, are also very important in evaluating the effectiveness of the predator. In the biological control using a predator as an intervention agent for inundative release, we usually do not attempt to introduce the

predator as a long-term regulatory factor of the target pest population as in the classical biological control, but rather want the predator to suppress the prey population instantly during certain critical periods. In the case with *H. axyridis*, we currently have no attempt to have the released predatory force to last for more than a single generation in peach orchards. Hence, in the evaluation of the effectiveness of *H. axyridis* as a biocontrol agent for inundative release against *M. persicae*, the aggregative and reproductive numerical response is of minor importance because the number of the coccinellid larvae is determined by the initial number at release, the survival rate and duration of active stages, instead of being a result of spatial accumulation from other localities or the reproduction of the parent generation. Therefore, the developmental and survival numerical responses of the predator are more important components to study, in the case of using the predator for innundative releases, because they determine how the released predatory force changes in relation to prey density and environmental factors.

As with functional response, numerical response of a predator is affected by temperature, in addition to prey density. While the effect of temperature on numerical response is one of the major factors determining the effectiveness of a predator in suppressing the prey population (Frazer 1976, Barlow and Dixon 1980, Guiterrez et al. 1981), empirical studies in this aspect have been rare. Some remarkable studies as to this point have been done on the temperature-dependent numerical responses of *Typhlodromus pyri* to the European red mite (Hayes and McArdle 1987, Hayes 1988, Hardman and Rogers 1991). As for the interactions between aphids and their coccinellid predators, Mills (1981) studied the effects of temperature on the growth, development and fecundity of *Adalia. bipunctata* when feeding on pea aphids provided at different densities, and found that temperature has some non-linear effects on the adult fecundity and development of the predator. Hardman and Rogers (1991) studied the effects of temperature and prey density on survival and development of immature *Typhlodromus pyri* and found that both the survival and developmental rate of this phytoseiid increase with temperature as well as prey density following nonlinear responses.

We conducted this study because information about the effects of temperature and density of *M. persicae* on the developmental and survival rates of *H. axyridis* is required

in depicting the change in the predation force following a release, which is directly related to the effectiveness of the predator, and in determining the appropriate predator stages, numbers and timing of releases with respect to temperature and prey density for controlling the aphid population. The information is also helpful in providing a better understanding of the consequenses of releases of this ladybug in orchards. Our objective of this study was to develop models describing the temperature-dependent developmental and survival numerical responses of *H. axyridis* to *M. persicae* based on laboratory experiments.

Materials and Methods

The coccinellid larvae used in this study came from the laboratory population reared on the eggs of *Ephestia kuehniella* Zeller maintained in INRA-Laboratory of Population Biology at Antibes. The green peach aphids used as the prey were from laboratory colonies maintained on peach seedlings (see chapter 1) in the laboratory of INRA-Research Station of Zoology at Avignon. Three young peach leaves measuring 12 cm in length or so, with the end of stalks wrapped with a piece of filter paper saturated with nutritive solution to keep the leaves from desiccation, were placed in each of the 80x50 mm cylindrical plastic jars. Apterous aphid nymph of instar 3-4 were placed evenly on these peach leaves. Six aphid densities, namely 10, 20, 40, 80, 160, 200 aphids/jar were offered each to one individual of the predator respectively. The feeding regime had six replicates.

The larvae of the instar prior to the one to be observed, those which appeared close to molt, were kept in round jars. Freshly molted individuals were then separated and moved to the arenas. A single larva was placed in each of the arenas. Each set of arenas (6 treatments x 6 replicates) were placed in one of the incubators in which a constant temperature was maintained. The number of larvae survived and molted to the next stage were recorded for each day. The initial number of aphids was restored after the observation. The larvae that had been used for the observation of a previous stage were

not used again in the observation of any of the following stages. The same procedure was repeated for all the four larval instars of *H. axyridis*.

The experiments described above were conducted under 12.5, 15, 18, 20, 25, 27.5, 30±0.5°C of constant temperatures respectively to measure the impacts of temperature on the numerical responses of each of the larval stages of *A. axyridis*. The humidity inside the incubators was maintained at 70 ± 5% RH and the photoperiod was set to 14:10 (L:D) for all the observations.

The average rate of development used in this paper was calculatted as

$$D = \frac{1}{\bar{d}} = \frac{n}{\sum_{i=1}^{n} d_i} \qquad (4\text{-}1)$$

where D is the average rate of development, n is the sample size, $\bar{d}$ is the average duration of development of individual i of the j^{th} instar, d_i's are observed developmental duration (in days) of individual i.

We used the geometrical average of the survival rate over the number of days required to complete the development of the stadium as the measure of the daily survival rate:

$$S = (\prod_{t=1}^{\bar{d}} S_t)^{\frac{1}{\bar{d}}}$$

because $\bar{d} = \frac{\sum_{i=1}^{n} d_i}{n} = \frac{1}{D}$, and $\prod_{t=1}^{\bar{d}} S_t = \frac{X_j}{X_{j-1}}$, we have

$$S = (\frac{X_j}{X_{j-1}})^D \qquad (4\text{-}2)$$

where S is the average daily survival rate; S_t is the survival rate of the j^{th} instar on day t; X_j is the number of survival larvae at the beginning of the j^{th} instar; $\bar{d}$, d_i and D have the

same meaning as in Eqn. 4-1.

All the parameter estimation involved in the modeling process was conducted using the Quasi-Newton nonlinear regression procedure provided by SYSTAD (SYSTAD Inc. 1990-1993)

Results

Developmental rate of *H. axyridis* as a function of the number of prey offered. As might be expected, the rate of development of *H. axyridis* increased with both temperature and the number of *M. persicae* offered (Table 4-1, Fig. 4-1). Here, we used the analytical strategy that firstly defined the average developmental rate as a function of the number of prey offered, and then incorporate the effect of temperature into the parameters of the density dependent models.

At all the temperatures used for the experiment, the relationship between the rate of development and the number of prey offered followed a saturation curve (Fig. 4-1): a rapid increase with the number of prey offered at beginning and leveling off as the number of prey offered getting larger. This developmental response to the number of prey present is more sensitive at higher temperatures than is at lower ones (Fig. 4-1), i.e. at higher temperatures the development is more food effective. This relationship was modeled using the following formula (see appendix 1 for derivation):

$$D(N) = Dm.[1 - e^{-\beta.N}] \qquad (4\text{-}3)$$

where $D(N)$ is the rate of development as a function of prey density N, Dm the maximum rate of development, β is a parameter with it reciprocal signifying the rate at which the developmental rate approaching the maximum value Dm as more prey are present, i.e. the sensitivity of developmental rate to prey density, a smaller β value implies a greater sensitivity. The parameters Dm and β for each of the larval stadiums were estimated for different temperatures and for different larval stages (Table 4-2).

Table 4-1. Average developmental rate (M+SE) of *H. axyridis* in relation to temperature and the number of *M. ~~axyridis~~ persicae* offered.

(1993, Monfavet)

N	10	20	40	80	160	200
L_1						
12.5 °C	0.0968 ±0.0048	0.1111 ±0.0046	0.1200 ±0.0029	0.1220 ±0.0023	0.1250 ±0.0041	0.1250 ±0.0058
15.0 °C	0.1600 ±0.0060	0.1739 ±0.0056	0.1818 ±0.0075	0.1875 ±0.0070	0.1923 ±0.0054	0.1923 ±0.0054
18.0 °C	0.1875 ±0.0126	0.2222 ±0.0112	0.2381 ±0.0082	0.2500 ±0.0176	0.2500 ±0.0176	0.2500 ±0.0246
20.0 °C	0.2105 ±0.0084	0.3125 ±0.0136	0.3846 ±0.0334	0.4000 ±0.0372	0.4000 ±0.0372	0.4000 ±0.0375
22.0 °C	0.4000 ±0.0373	0.4286 ±0.0351	0.4706 ±0.0323	0.5000 ±0.0000	0.5000 ±0.0930	0.5000 ±0.0930
25.0 °C	0.5000 ±0.0000	0.5405 ±0.0822	0.6000 ±0.1054	0.6000 ±0.1054	0.6667 ±0.1118	0.6667 ±0.1118
27.5 °C	0.5714 ±0.0824	0.6667 ±0.0824	0.8000 ±0.0903	1.0000 ±0.0000	1.0000 ±0.0000	1.0000 ±0.0000
L_2						
12.5 °C	0.1176 ±0.0031	0.1379 ±0.0031	0.1481 ±0.0040	0.1538 ±0.0053	0.1579 ±0.0050	0.1579 ±0.0050
15.0 °C	0.1765 ±0.0070	0.2353 ±0.0087	0.2667 ±0.0140	0.3077 ±0.0146	0.3333 ±0.0366	0.3333 ±0.0335
18.0 °C	0.2667 ±0.0140	0.3125 ±0.0136	0.3333 ±0.0334	0.3333 ±0.0465	0.3636 +0.0278	0.3636 +0.0278
20.0 °C	0.3077 ±0.0146	0.3846 ±0.0351	0.4444 ±0.0294	0.4762 ±0.0192	0.5000 +0.0000	0.5000 +0.0000
22.0 °C	0.3636 ±0.0278	0.5000 ±0.0930	0.6667 ±0.1118	0.8333 ±0.0824	1.0000 ±0.0000	1.0000 ±0.0000
25.0 °C	0.4000 ±0.0373	0.6667 ±0.1118	0.8333 ±0.0824	1.0000 ±0.0000	1.0000 ±0.0000	1.0000 ±0.0000
27.5 °C	0.3636 ±0.0278	0.5000 ±0.0000	0.6667 ±0.1118	0.8333 ±0.0903	1.0000 ±0.0000	1.0000 ±0.0000
L_3						
12.5 °C	0.0667 ±0.0026	0.0833 ±0.0026	0.0976 ±0.0058	0.1053 ±0.0049	0.1071 ±0.0047	0.1081 ±0.0019
15.0 °C	0.0968 ±0.0039	0.1053 ±0.0025	0.1212 ±0.0059	0.1739 ±0.0056	0.1818 ±0.0075	0.1818 ±0.0075
18.0 °C	0.1481 ±0.0066	0.2143 ±0.0105	0.3125 ±0.0136	0.3333 ±0.0334	0.3333 ±0.0334	0.3333 +0.0000
20.0 °C	0.1550 ±0.0107	0.2273 ±0.0214	0.3333 ±0.0334	0.3846 ±0.0339	0.4286 ±0.0351	0.4444 ±0.0360
22.0 °C	0.1667 ±0.0182	0.2500 ±0.0176	0.4000 ±0.0373	0.5000 ±0.0000	0.6000 ±0.1054	0.6667 ±0.1118
25.0 °C	0.2000 ±0.0109	0.2857 ±0.0186	0.4286 ±0.0351	0.6667 ±0.1118	1.0000 ±0.0000	1.0000 ±0.0000
27.5 °C	0.2000 ±0.0000	0.3077 ±0.0146	0.5714 ±0.0824	0.8000 ±0.0904	1.0000 ±0.0000	1.0000 ±0.0000
L_4						
12.5 °C	0.0351 ±0.0021	0.0448 ±0.0019	0.0523 ±0.0021	0.0556 ±0.0017	0.0580 ±0.0017	0.0597 ±0.0013
15.0 °C	0.0521 ±0.0034	0.0702 ±0.0025	0.0800 ±0.0034	0.1111 ±0.0056	0.1143 ±0.0048	0.1176 ±0.0075
18.0 °C	0.0727 ±0.0033	0.1071 ±0.0046	0.1538 ±0.0132	0.1739 ±0.0068	0.1818 ±0.0182	0.1818 ±0.0091
20.0 °C	0.0816 ±0.0028	0.1250 ±0.0050	0.1639 ±0.0105	0.2000 ±0.0134	0.2105 ±0.0091	0.2105 ±0.0123
22.0 °C	0.0952 ±0.0090	0.1379 ±0.0077	0.1739 ±0.0111	0.2222 ±0.0137	0.2727 ±0.0215	0.2727 ±0.0215
25.0 °C	0.1212 ±0.0036	0.1667 ±0.0091	0.2222 ±0.0137	0.2500 ±0.0000	0.2727 ±0.0215	0.2857 ±0.0228
27.5 °C	0.0606 ±0.0023	0.0968 ±0.0040	0.1500 ±0.0061	0.1667 ±0.0091	0.2000 ±0.0134	0.2222 ±0.0137

N denotes the number of green peach aphid offered; values in the table are average developmental rate with standard errors; L_1, L_2, L_3 and L_4 denote the larval instar 1-4 respectively.

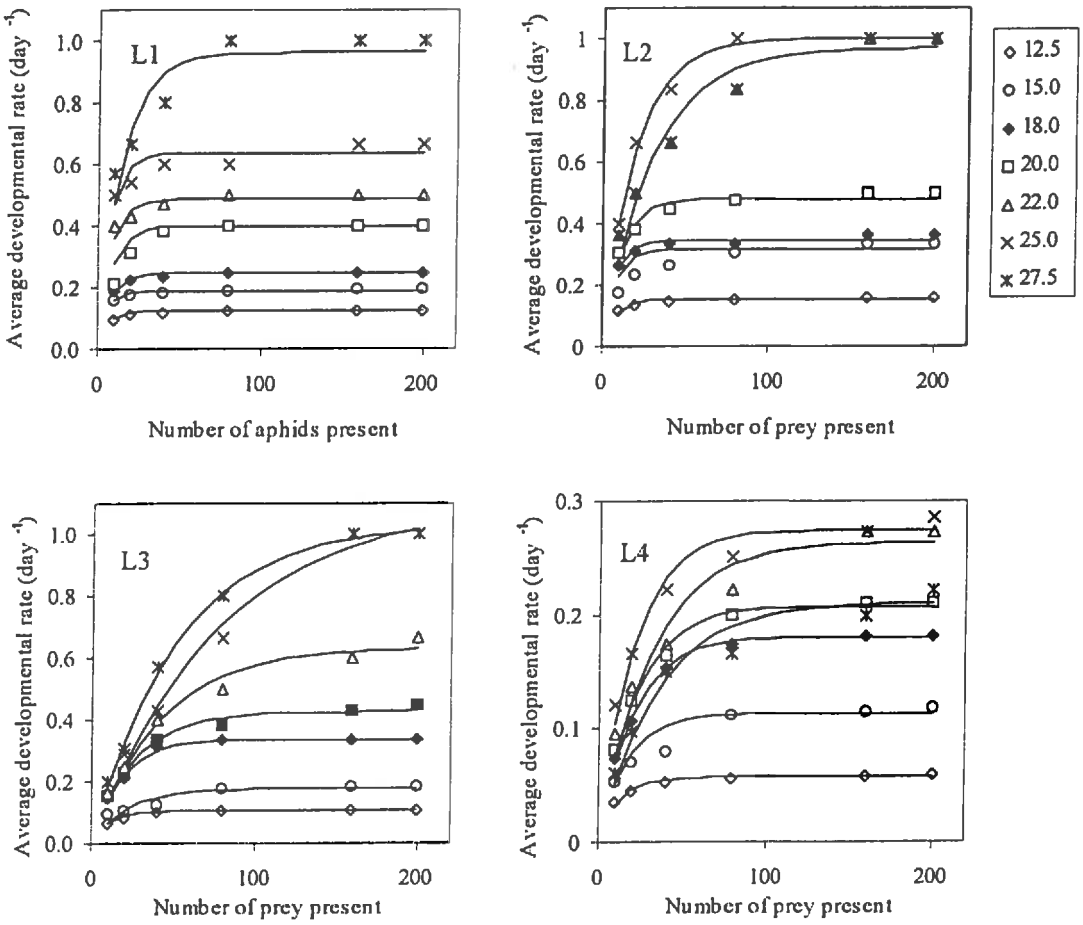

Fig. 4-1 Average developmental rate (day^{-1}) of *H. axyridis* in relation to the number of *M. persicae* present. Values in the legend are temperatures in °C. Lines are predictions from Eqn 4-3, marks are observed values. L_1, L_2, L_3, and L_4 denote the coccinellid larvae of instar 1-4 respectively.

Developmental rate of *H. axyridis* as a function of temperature. When the number of prey offered was fixed, the developmental rate of *H. axyridis* varied with temperatures (Table 4-1) which can be characterized by the variation of parameters in the prey-denpendent developmental rate model as functions of temperatures. From Table 4-2 it can be seen that as temperatures increase the value of maximum developmental rate *Dm* increases, and the value of parameter β decreases. The relationship between the maximum developmental rate *Dm* and temperature *T* is basically of the same form as that of the typical developmental response of poikilothermal animals to temperature (Fig. 4-2). Here it was described using Logan et al's model (1976):

$$Dm(T) = \psi_{HA} \cdot (e^{\rho_{HA} \cdot T} - e^{\rho_{HA} \cdot Tm_{HA} - (Tm_{HA} - T)/\Delta T_{HA}}) \qquad (4\text{-}4)$$

where ψ_{HA} is the rate of physiological process at some base temperature; ρ_{HA} is a value for critical enzyme-catalyzed biochemical reactions; Tm_{HA} is the maximum temperature in degree above the base temperature for the life process; ΔT_{HA} is the width of high temperature boundary layer. Table 4-3 listed the parameters estimated for all the larval stadiums. The maximum temperatures for development (Tm_{HA}) were approximately 29-30 °C; the optimal temperatures for development were about 25-27°C; and the width of high temperature boundary layers (ΔT_{HA}) were around 3-4°C depending on larval stages. The 3rd instar had the highest maximum developmental rate and the 4th instar had the lowest.

The value of parameter β, reciprocal to the sensitivity of developmental rate to the number of prey offered, decreased with temperature T (Fig. 4-3), i.e. the higher the temperature, the more sensitive the developmental rate of *H. axyridis* to the food availability, or, each food item is likely to trigger a greater developmental effects under higher temperatures. This relationship was described using an empirical exponential model.

$$\beta(T) = Bd_1 \cdot e^{-Bd_2 \cdot T} \qquad (4\text{-}5)$$

where Bd_1 and Bd_2 are constants. The estimated values for Bd_1 and Bd_2 is listed in Table 4-3. The average developmental rate can thus be described as a function of both temperature and number of prey offered by substituting for Dm and β in equation (4-1) with $Dm(T)$ and $\beta(T)$, i.e.:

$$D(T, N) = Dm(T) \cdot [1 - e^{-\beta(T) \cdot N}] \qquad (4\text{-}6)$$

The general feature of this model is geometrically sketched as Fig. 4-4.

Table 4-2. Parameter estimates for the average developmental rate (M+SE) of *H. axyridis* as a function of the number of *M. persicae* present:

(1993, Montfavet)

	Dm (M±SE)	β (M±SE)	R^2
L_1			
12.5°C	0.1224 ±0.0017	0.1686 ±0.0135	0.9215
15°C	0.1871 ±0.0030	0.1833 ±0.0243	0.7979
18°C	0.2463 ±0.0033	0.1359 ±0.0111	0.9438
20°C	0.4011 ±0.0011	0.1150 ±0.0009	0.9995
22°C	0.4873 ±0.0120	0.1324 ±0.0272	0.7465
25°C	0.6352 ±0.0220	0.1351 ±0.0328	0.6687
27.5°C	0.9621 ±0.0468	0.0679 ±0.0141	0.8353
L_2			
12.5°C	0.1539 ±0.0025	0.1359 ±0.0138	0.9156
15°C	0.3181 ±0.0124	0.1265 ±0.0120	0.9035
18°C	0.3473 ±0.0083	0.1376 ±0.0204	0.8338
20°C	0.4832 ±0.0122	0.0896 ±0.0111	0.9293
22°C	0.9697 ±0.0466	0.0336 ±0.0058	0.9486
25°C	0.9995 ±0.0144	0.0513 ±0.0028	0.9908
27.5°C	0.9697 ±0.0466	0.0336 ±0.0058	0.9486
L_3			
12.5°C	0.1052 ±0.0023	0.0891 ±0.0094	0.9470
15°C	0.1756 ±0.0137	0.0479 ±0.0154	0.7748
18°C	0.3362 ±0.0052	0.0559 ±0.0033	0.9895
20°C	0.4274 ±0.0112	0.0385 ±0.0036	0.9823
22°C	0.6328 ±0.0274	0.0241 ±0.0033	0.9758
25°C	1.0968 ±0.0663	0.0130 ±0.0019	0.9845
27.5°C	1.0315 ±0.0180	0.0193 ±0.0010	0.9973
L_4			
12.5°C	0.0569 ±0.0014	0.0856 ±0.0101	0.9379
15°C	0.1133 ±0.0061	0.0588 ±0.0095	0.9024
18°C	0.1806 ±0.0020	0.0474 ±0.0019	0.9958
20°C	0.2079 ±0.0038	0.0445 ±0.0030	0.9890
22°C	0.2641 ±0.0144	0.0320 ±0.0062	0.9387
25°C	0.2743 ±0.0089	0.0474 ±0.0064	0.9579
27.5°C	0.2117 ±0.0103	0.0284 ±0.0052	0.9573

Dm: the maximum developmental rate; *b*: the rate by which the average developmental rate approaches *Dm* as the number of prey present increases; the parameters are presented as mean with standard error; R^2: determination coefficient of the nonlinear correlation. Newton's method was used in estimating the parameters. L_1, L_2, L_3, L_4: the larval instar 1-4.

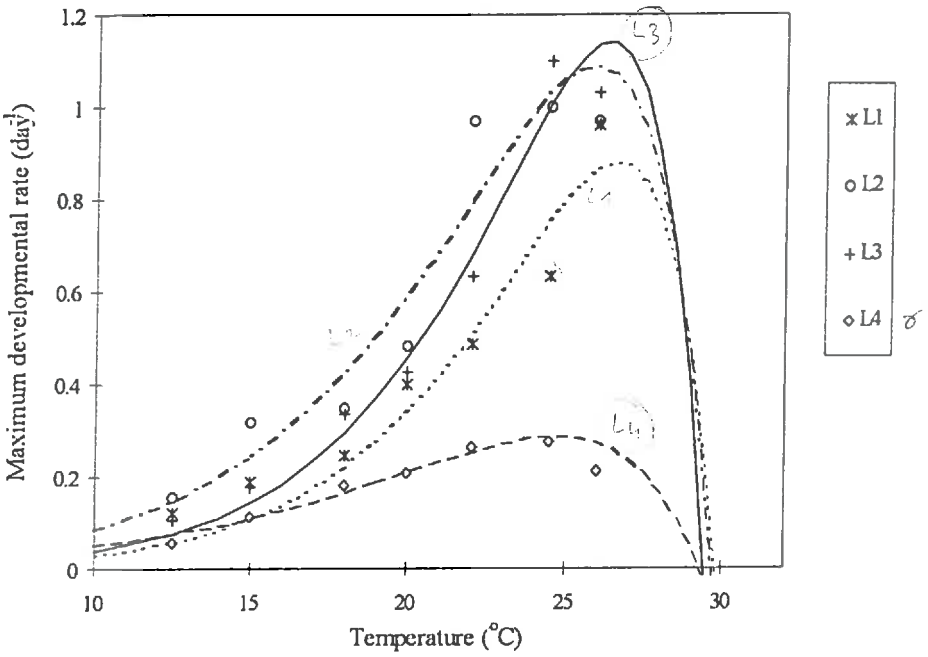

Fig. 4-2 The maximum developmental rate *Dm* of *H. axyridis* in relation to temperature (°C). Solid lines are drawn using predicted values from Eqn. 4-4, marks are observed values. L_1, L_2, L_3 and L_4 denote the larval instar 1-4 respectively.

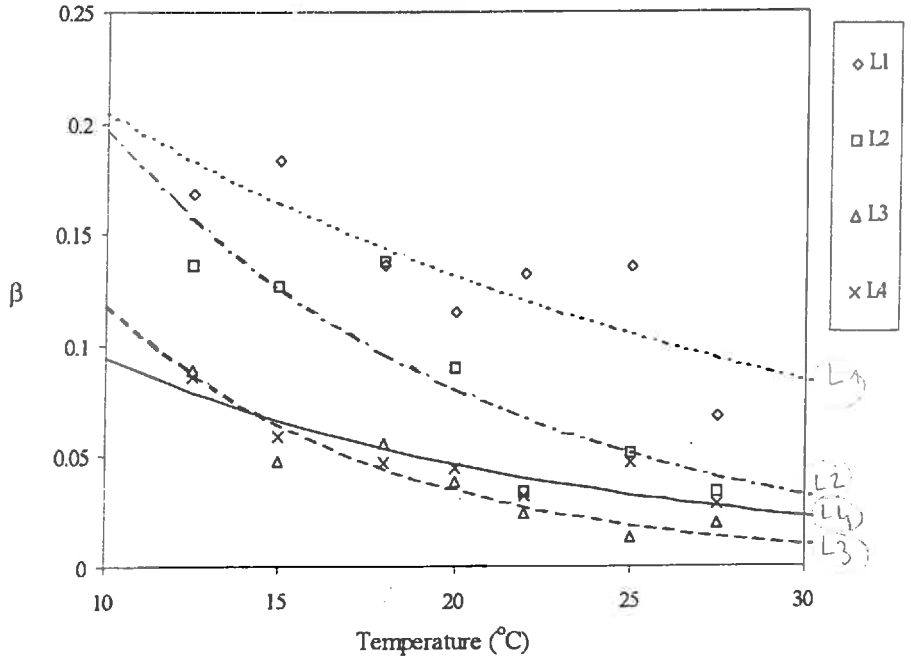

Fig. 4-3 Relationship between the parameter b from Eqn. 4-3 and temperature (oC). Solid lines are drawn using predicted values from Eqn. 4-5, marks are observed values. L_1, L_2, L_3 and L_4 denote the larval instar 1-4 respectively.

Table 4-3. Parameter estimates for equation 4-4 and 4-5, the maximum developmental rate *Dm* and the parameter *b* as functions of temperature.

(1993, Montfavet)

Larval stage	L_1	L_2	L_3	L_4
$Dm(T) = \psi_{HA} \cdot (e^{\rho_{HA} \cdot T} - e^{\rho_{HA} \cdot Tm_{HA} - (Tm_{HA} - T)/\Delta T_{HA}})$				
ψ_{HA}	0.0259 ±.0037	0.0026 ±.0054	0.0048 ±.0015	0.0106 ±.0026
ρ_{HA}	0.2541 ±.0158	0.2884 ±.0326	0.3066 ±.0054	0.1796 ±.0078
Tm_{HA}	29.6976 ±.0103	29.8000 ±.0143	29.4692 ±.0092	29.2809 ±.0096
ΔT_{HA}	3.7050 ±.0215	2.9233 ±.0364	3.0209 ±.0115	3.7741 ±.0164
R^2	0.9257	0.8946	0.9915	0.9684
$\beta(T) = Bd_1 \cdot e^{-Bd_2 \cdot T}$				
Bd_1	0.3191 ±.0758	0.4799 ±.1761	0.3963 ±.1259	0.1907 ±.0525
Bd_2	0.0443 ±.0132	0.0892 ±.0238	0.1212 ±.0220	0.0706 ±.0164
R^2	0.6957	0.7630	0.8705	0.7817

ψ_{HA} : the rate of physiological process at some base temperature; ρ_{HA} : a value for critical enzyme-catalyzed biochemical reactions; Tm_{HA} : the maximum temperature in degree above the bass temperature for the life process; ΔT_{HA} : the width of high temperature boundary layer; R^2: the determination coefficient for the nonlinear correlation. Newton's method was used in estimating parameters. L_1, L_2, L_3 and L_4 denote the larval stadium 1-4 respectively.

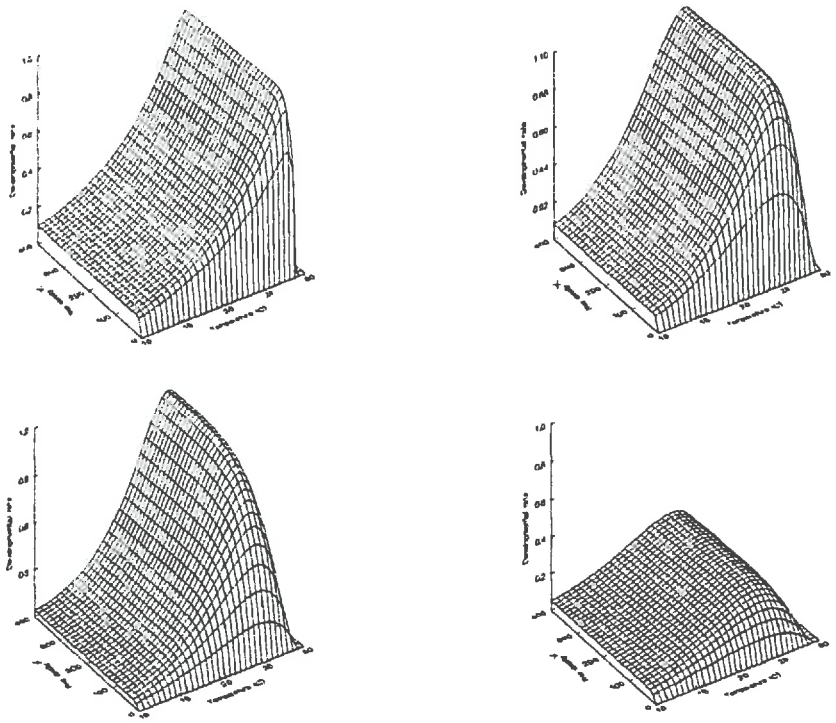

Fig. 4-4 Developmental rate of *H. axyridis* in relation to temperature and the density *of M. persicae*. Graphes were generated from Eqn. 4-6, and parameters in table 3.

Average daily survival rate of *H. axyridis* as a function of the initial number of prey. Here the average daily stage-specific survival rate (equation 4-2), instead of the integral stage-specific survival rate, was used. It is conceptually more legitimate and practically more convenient for this study because in the natural condition the major factors affecting the predator's survival rate, i.e., the prey density and temperature, are changing constantly, and in the simulation model the time-unit for defining the change of temperature, density of prey and predator is one day. Also, the daily age-specific survival rate enables a more direct comparison of the temperature- and prey-dependence of survival between different larval stages, for the effect of duration of development on the survival rate is removed. As with the average developmental rate, the average daily survival rate of *H. axyridis* increased with both temperature and the number of *M. persicae* offered (Table 4-4). We used the same analytical approach as was used for modeling the developmental rate: the average survival rate was defined as a function of the number of prey offered in the first place, and then incorporate the effect of temperature into the parameters of the density-dependent survival model.

The average daily survival rates S of all the larval stages increased with the number of prey available (Fig. 4-5). The survival rates increased as prey densities increased and approached asymptotically the maximum survival rate as the prey density became higher and higher (Fig. 4-5). In general, at the same prey density, older instar larvae had lower daily survival rates than younger ones (Fig. 4-5), which may reflects the trophic requirement increases with age of the larvae. The response of daily survival rate to the number of prey offered was fitted to a sigmoid curve used by Chen (1990) (equation 4-5, see appendix for derivation).

$$S(N) = \frac{1}{1 + Sc_1 . e^{-Sc_2 . N}} \qquad (4\text{-}7)$$

where $S(N)$ is the average daily survival rate of the predator in relation to the number of prey offered N, Sc_1 is a parameter whose reciprocal is related to the average daily survival rate when no prey available, and Sc_2 is a parameter signifying the rate at which $S(N)$

approaches its maximum value (=1 in this case). This model gave a fairly good depict of the prey-dependence of the average daily survival rate of *H. axyridis* (Fig. 4-4, Table 4-5)

Table 4-4. Average daily survival rate (M±SE) of *H. axyridis* in relation to temperature and the number of *M. aryridis* offered.

(1993, Monfavet)

N	10	20	40	80	160	200
L_1						
12.5 °C	0.8745 ±0.0111	0.8748 ±0.0136	0.8959 ±0.0138	0.9189 ±0.0124	0.9280 ±0.0121	0.9381 ±0.0112
15.0 °C	0.8454 ±0.0263	0.8527 ±0.0290	0.9138 ±0.0233	0.9224 ±0.0231	0.9799 ±0.0120	0.9692 ±0.0149
18.0 °C	0.8572 ±0.0319	0.8525 ±0.0419	0.9306 ±0.0312	0.9457 ±0.0295	0.9740 ±0.0203	0.9740 ±0.0203
20.0 °C	0.8484 ±0.0392	0.8618 ±0.0672	0.9192 ±0.0689	0.9500 ±0.0571	0.9500 ±0.0571	1.0000 ±0.0000
22.0 °C	0.8525 ±0.1001	0.8473 ±0.1128	0.8913 ±0.1082	0.9371 ±0.0894	0.9587 ±0.0723	0.9587 ±0.0723
25.0 °C	0.8670 ±0.1312	0.8840 ±0.1370	0.9003 ±0.1475	0.9220 ±0.1303	1.0000 ±0.0000	0.9747 ±0.0865
27.5 °C	0.8660 ±0.1597	0.8560 ±0.2058	0.9071 ±0.2142	0.9387 ±0.2399	0.9664 ±0.1802	0.9664 ±0.1802
L_2						
12.5 °C	0.8679 ±0.0152	0.8652 ±0.0195	0.8884 ±0.0196	0.8989 ±0.0197	0.9099 ±0.0193	0.9225 ±0.0178
15.0 °C	0.8507 ±0.0299	0.8287 ±0.0495	0.9093 ±0.0425	0.9512 ±0.0381	0.9655 ±0.0360	0.9655 ±0.0360
18.0 °C	0.8525 ±0.0550	0.8434 ±0.0719	0.9283 ±0.0524	0.9426 ±0.0467	0.9624 ±0.0429	0.9815 ±0.0299
20.0 °C	0.8473 ±0.0693	0.8534 ±0.0942	0.9255 ±0.0819	0.9487 ±0.0750	0.9487 ±0.0806	1.0000 ±0.0000
22.0 °C	0.8550 ±0.0862	0.8660 ±0.1319	0.8618 ±0.2018	0.8733 ±0.2623	0.9500 ±0.2179	1.0000 ±0.0000
25.0 °C	0.8417 ±0.1040	0.8255 ±0.2265	0.8733 ±0.2623	0.9500 ±0.2179	0.9500 ±0.2179	1.0000 ±0.0000
27.5 °C	0.8550 ±0.0862	0.8367 ±0.1460	0.8973 ±0.1741	0.9159 ±0.2161	0.9500 ±0.2179	1.0000 ±0.0000
L_3						
12.5 °C	0.8706 ±0.0064	0.8648 ±0.0092	0.8892 ±0.0105	0.9081 ±0.0106	0.9065 ±0.0110	0.9284 ±0.0097
15.0 °C	0.8323 ±0.0129	0.8442 ±0.0141	0.8949 ±0.0141	0.9399 ±0.0181	0.9372 ±0.0198	0.9490 ±0.0177
18.0 °C	0.8620 ±0.0220	0.8740 ±0.0364	0.9086 ±0.0540	0.9283 ±0.0524	0.9473 ±0.0447	0.9655 ±0.0360
20.0 °C	0.8498 ±0.0247	0.8340 ±0.0462	0.9086 ±0.0594	0.8953 ±0.0789	0.9558 ±0.0595	0.9775 ±0.0446
22.0 °C	0.8395 ±0.0285	0.8409 ±0.0520	0.8913 ±0.0852	0.9220 ±0.0997	0.9387 ±0.1154	0.9697 ±0.0947
25.0 °C	0.8524 ±0.0358	0.8430 ±0.0630	0.8840 ±0.0976	0.9322 ±0.1416	0.9500 ±0.2179	0.9500 ±0.2179
27.5 °C	0.8326 ±0.0384	0.8320 ±0.0730	0.8484 ±0.1701	0.9192 ±0.2002	0.9000 ±0.3000	0.9500 ±0.2179
L_4						
12.5 °C	0.8786 ±0.0024	0.8745 ±0.0035	0.8866 ±0.0042	0.9145 ±0.0039	0.9326 ±0.0037	0.9326 ±0.0039
15.0 °C	0.8555 ±0.0047	0.8508 ±0.0075	0.8950 ±0.0075	0.9151 ±0.0110	0.9238 ±0.0109	0.9340 ±0.0105
18.0 °C	0.8416 ±0.0082	0.8685 ±0.0132	0.8864 ±0.0210	0.9372 ±0.0185	0.9490 ±0.0177	0.9602 ±0.0156
20.0 °C	0.8565 ±0.0092	0.8409 ±0.0184	0.8926 ±0.0224	0.9175 ±0.0263	0.9412 ±0.0238	0.9541 ±0.0209
22.0 °C	0.8579 ±0.0115	0.8470 ±0.0209	0.8864 ±0.0252	0.9238 ±0.0295	0.9410 ±0.0351	0.9566 ±0.0300
25.0 °C	0.8228 ±0.0187	0.8395 ±0.0285	0.9087 ±0.0324	0.9147 ±0.0373	0.9566 ±0.0300	0.9546 ±0.0329
27.5 °C	0.8340 ±0.0064	0.8177 ±0.0136	0.8348 ±0.0248	0.8754 ±0.0249	0.9311 ±0.0239	0.9564 ±0.0221

N denotes the number of green peach aphid offered; values in the table are average daily survival rate; L_1, L_2, L_3 and L_4 denote the larval stadium 1-4 respectively.

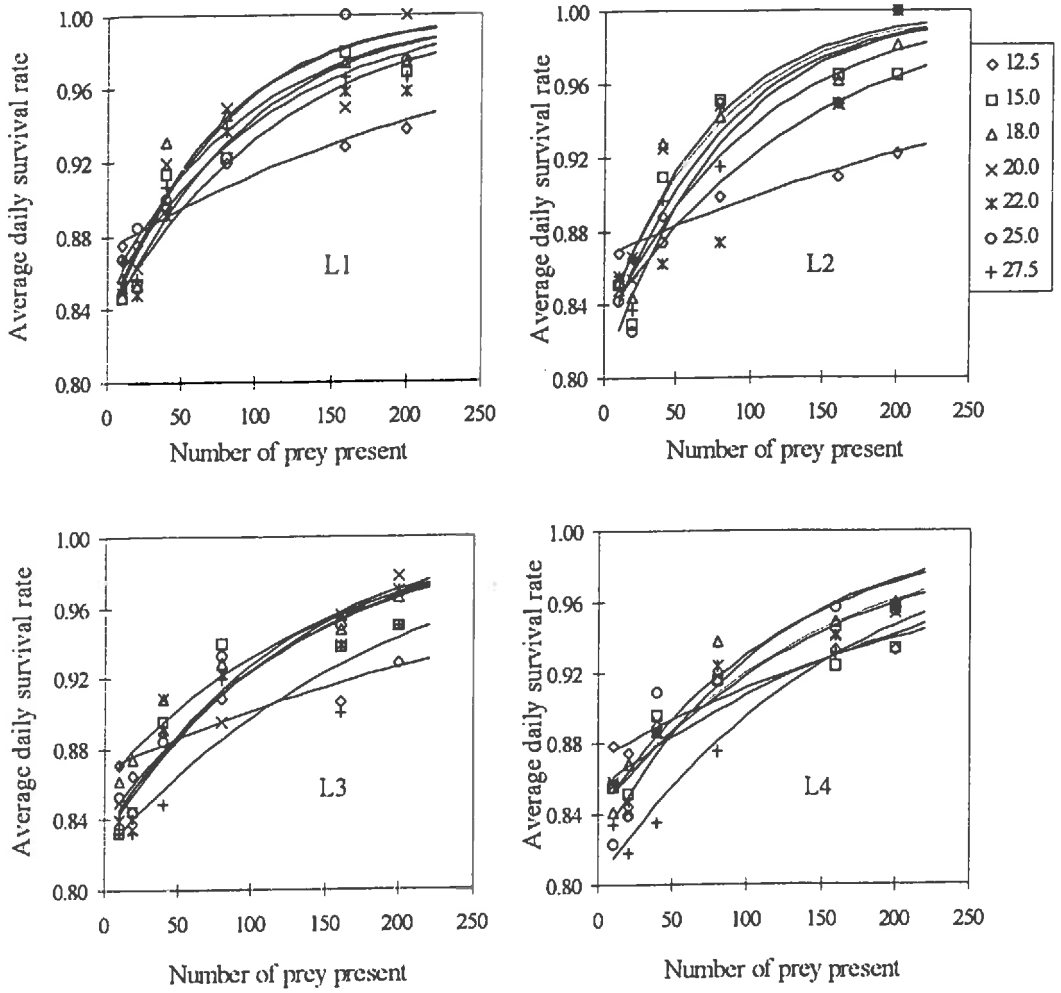

Fig. 4-5 The average daily survival rate of *H. axyridis* in relation to the number of *M. persicae* present. Lines are predicted value computed from Eqn 4-7, marks are observed values. Values in the legend are temperatures in °C. L_1, L_2, L_3 and L_4 denote the larval stadium 1-4 respectively.

Survival rate of *H. axyridis* as a function of temperature. At any fixed density of aphids exposed to the ladybeetle larvae, the daily survival rate of the larvae is dependent on the environmental temperature. The parameters Sc_1 and Sc_2 could, in turn, be defined as functions of temperature (Fig. 4-5, 4-6). The following empirical models were used :

$$Sc_1(T) = Sc_{11}.(1 - Sc_{12}.e^{-Sc_{13}.T}) \qquad (4\text{-}8)$$

$$Sc_2(T) = Sc_{21}.(1 - Sc_{22}.e^{-Sc_{23}.T}) \qquad (4\text{-}9)$$

where Sc_{11}, Sc_{12}, Sc_{13}, Sc_{21}, Sc_{22}, and Sc_{23} are parameters from the curve fitting and do not have explicit biological meaning. The values of these constants were estimated and given in Table 4-6.

Table 4-5. Parameter estimates (M±SE) for the average survival rate of *H. axyridis* as a function of the number of *M. persicae* present: $S(N) = 1 / (1 + Sc_1 . e^{-Sc_2 . N})$.

(1993, Montfave)

T(°C)	12.5	15	18	20	22	25	27.5
L_1							
Sc_1	0.1459 ±.0078	0.2025±.0217	0.1962 ±.0319	0.1951±.0183	0.1744 ±.0195	0.1787±.0170	0.2003 ±.0317
Sc_2	0.0043 ±.0007	0.0124±.0027	0.0151 ±.0050	0.0100±.0020	0.0120 ±.0025	0.0106±.0021	0.0150 ±.0047
R^2	0.9266	0.9379	0.8977	0.9353	0.9285	0.9378	0.9035
L_2							
Sc_1	0.1544 ±.0065	0.2178±.0348	0.2033 ±.0346	0.2062±.0385	0.2025 ±.0294	0.2429±.0342	0.2075 ±.0249
Sc_2	0.0031 ±.0005	0.0142 ±.0051	0.0145 ±.0050	0.0155±.0058	0.0085 ±.0024	0.0143±.0037	0.0112 ±.0025
R^2	0.9239	0.8720	0.8840	0.8779	0.8411	0.9169	0.9147
L_3							
Sc_1	0.1521 ±.0097	0.2004 ±.0285	0.1619 ±.0113	0.2030±.0256	0.2058 ±.0176	0.1932±.0190	0.2155 ±.0256
Sc_2	0.0033 ±.0007	0.0088 ±.0028	0.0079 ±.0012	0.0095±.0024	0.0093 ±.0016	0.0085±.0018	0.0063 ±.0017
R^2	0.8499	0.8388	0.9488	0.8858	0.9412	0.9123	0.8298
L_4							
Sc_1	0.1472 ±.0068	0.1700 ±.0156	0.1885 ±.0167	0.1869±.0159	0.1850 ±.0139	0.2160±.0281	0.2436 ±.0151
Sc_2	0.0042 ±.0006	0.0051 ±.0012	0.0092 ±.0017	0.0075±.0014	0.0076 ±.0013	0.0102±.0028	0.0074 ±.0009
R^2	0.9410	0.8474	0.9348	0.9213	0.9395	0.8866	0.9591

N : the number of prey offered; Sc_1: a parameter whose reciprocal is related to the average daily survival rate when no prey available; Sc_2: a parameter signifying the rate at which $S(N)$ approaches its maximum value (=1 in this case); R^2: the determination coefficient for the nonlinear correlation. Newton's method was used in estimating parameters. L_1, L_2, L_3 and L_4 denote the larval stadium 1-4 respectively.

The survival rate of larvae of *H. axyridis* as a function of both temperature and prey density was then described by incorporating $Sc_1(T)$ and $Sc_2(T)$ into the equation 4-5 :

$$S(T,N) = \frac{1}{1 + Sc_1(T).e^{-Sc_2(T).N}} \qquad (4\text{-}10)$$

The feature of this model within the biologically defined interval was illustrated geometrically as in Fig. 4-7.

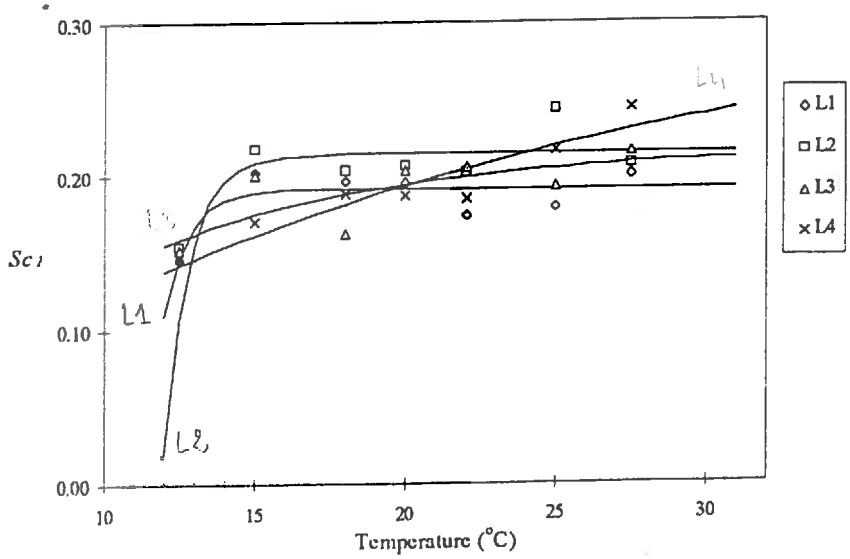

Fig. 4-6 Relationship between the parameter Sc_1 from Eqn. 4-3 and temperature (°C). Solid lines are drawn using predicted values from Eqn. 4-8, marks are observed values.

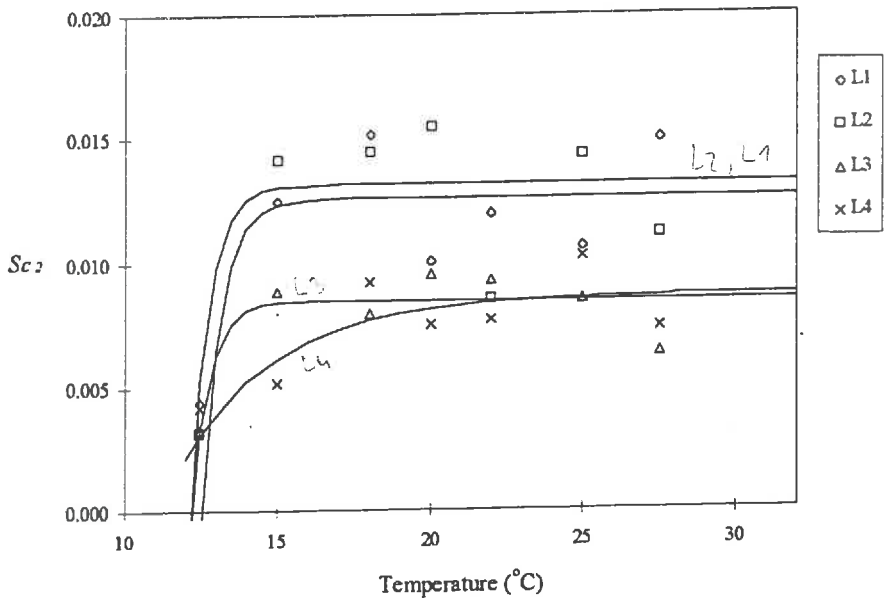

Fig. 4-7 Relationship between the parameter Sc_2 from Eqn. 4-3 and temperature (°C). Solid lines are drawn using predicted values from Eqn. 4-9, marks are observed values.

Table 4-6. Parameter estimates (M±SE) for equation 4-8 and 4-9, the parameter Sc_1 and Sc_2 as functions of temperature.

(1993, Montfavet)

Larval stages	L_1	L_2	L_3	L_4
$Sc_1(T) = Sc_{11}.(1 - Sc_{12}.e^{-Sc_{13}.T})$				
Sc_{11}	0.1915 ±0.0054	0.2141 ±0.0063	0.1968 ±0.0081	0.1996 ±0.0109
Sc_{12}	9.55E+05 ±1.97E+05	1.55E+06 ±2.34E+05	1.55E+08 ±2.64E+07	10.0077 ±8.6534
Sc_{13}	1.2178 ±0.9506	1.1960 ±0.2220	1.4082 ±0.3443	0.2886 ±0.0431
R^2	0.6968	0.6965	0.4952	0.8040
$Sc_2(T) = Sc_{21}.(1 - Sc_{22}.e^{-Sc_{23}.T})$				
Sc_{21}	0.0126 ±0.0021	0.0132 ±0.0026	0.0085 ±0.0024	0.0079 ±0.0212
Sc_{22}	7.50E+08 ±8.12E+08	7.50E+08 ±8.20E+08	7.50E+08 ±7.20E+08	2.35E+06 ±4.63E+06
Sc_{23}	1.6262 ±8.3498	1.6765 ±8.3097	1.6742 ±6.8434	1.0442 ±10.0021
R^2	0.7154	0.7041	0.7717	0.4809

Sc_{11}, Sc_{12}, Sc_{13}, Sc_{21}, Sc_{22}, Sc_{23} are constants from the curve fitting; R^2 is the determination coefficient for the nonlinear correlation; Newton's method was used in estimating parameters. L_1, L_2, L_3 and L_4 denote the larval stadium 1-4 respectively.

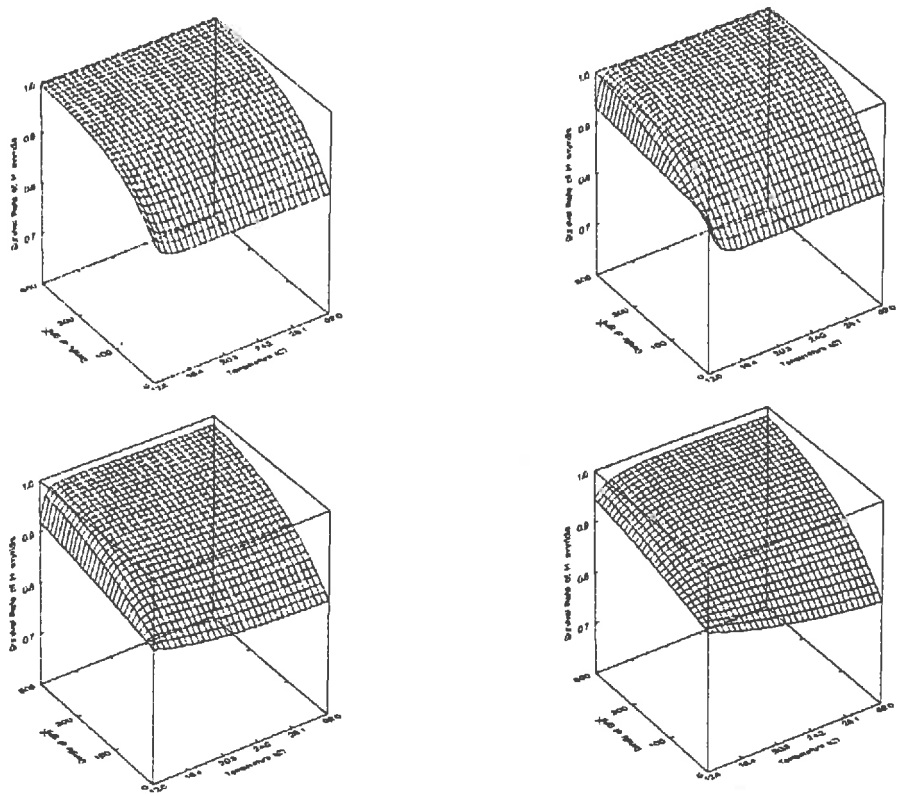

Fig. 4-8 Daily survival rate of H. axyridis in relation to temperature (oC) and the density of M. persicae. Graphes were generated from Eqn. 4-6, and parameters in table 6.

Discussion

In our models developed here to describe the developmental and survival rates of *H. axyridis* as functions of prey density and temperature, one of the independent variables is the number of prey present instead of the number of prey consumed as was used in many similar studies. Many studies indicated that the relationship between the developmental rate and the prey consumption follows a saturation curve (Chen et al. 1985, Hayes and McArdle 1987, Hayes 1988, Hardman and Rogers 1991). The number of prey consumed, in the case of Holling's type II functional response, is itself a function of the number of prey present following a saturation equation. In fact, if we use *Na* in the place of *N* in equation 4-3, and substitute with *Na* with the right hand side of equation 4-12:

$$D(N) = Dm.[1 - e^{-\beta.Na}] \qquad (4\text{-}11)$$

$$Na = \frac{aN}{1 + aThN} \qquad (4\text{-}12)$$

the relationship between *D* and *N* in equation 4-11 still has basically the same numerical and geometrical properties as was described by equation 4-3, only that the parameters have slightly deferent meaning and values. The parameters estimated for the equation 4-11 with *Na* as the independent variable may probably be more accurate than those estimated for equation 4-3 because the developmental rate *D* is more directly related to the number of prey consumed than to the number of prey present and the stochasticity and randomness existing in the relationship between *N* and *Na*. However, equation 4-3 has some advantages: firstly, this loss of accuracy can be partly compensated by reducing experimental error from the manipulation of the system for obtaining the data on *Na*, the error involved in the estimation of parameters in equation 4-12, and the amount of calculation (and thus the round-off error) in the evaluation of the function; secondly, a big amount of trial work load for counting the real *Na* can be saved, in addition, the model with prey density instead of the number of prey attacked can be more readily used for

estimating the developmental and survival rate of the predator in the field conditions.

In this study, we used the average daily survival rate, calculated by taking the geometric average of the stage-specific survival rate of a larval stadium. This measure of survival rate allows us to incorporate the survival rate directly into the simulation model, which is usually run with one day as the time step, and thus the survival rate of any specific day can be calculated from the temperature and prey density of the day. We should be aware that the averaged daily survival rate is only an simplified approximation, because the daily survival rate may depend on the developmental progression within the given instar, rather than a uniform value throughout the whole length of the instar. We adopted the present approach because no data concerning the age-specific survival rate is unavailable and experiments measuring that requires a large quantity of individuals.

Beddington et al. (1976) suggested that the survival rate of a predator in relation to the prey density follow a sigmoid curve, based on a normal distribution of the mean number of prey consumed. His model has not been used very widely to fit experimental data because it is basically suitable for describing survival rate of a generation fits much less well the survival rate data on a daily or stage basis. In addition, the meaning and biological mechanisms of parameters in his model is quite vague. In their study of the predator-prey interactions between *Typhlodromus pyri* and its prey - European red mite, Hardman and Rogers (1991) proposed a saturation curve to describe the survival rate in response to the prey density. Our results supported a sigmoid curve, which has basically the same features as that used by Chen et al. (1985) in his study of the numerical responses of *Chrysopa septenpunctata* to *Myzus persicae*. We derived a model which is different from Beddington's in the underlying mechanism to describe the survival rate of *H. axyridis* in response to the density of *M.persicae*.

Appendix

Derivation of the equation describing the relationship between the developmental rate and number of prey present (equation 4-3).

Consider that the developmental rate (D) of a predator is a function with the number of prey consumed (Na). Since Na is a continuous, differentiable function of N (the number of prey present) in $[0,\infty]$ according to equation 4-12, we can define D as a function of N. let ΔD be the increment of D as N increases by ΔN, we start our derivation from considering the relationship between ΔD and DN, which is a simpler case than the relationship between D and N. Firstly, we assume that: (1) a maximum developmental rate Dm can be attained as the number of prey present increases infinitely; (2) the magnitude of ΔD with respect to ΔN is proportional to Dm-D (the deference between the maximum developmental rate and the actual developmental rate), i.e. an increase in prey density can trigger a larger increase in the developmental rate of the predator when the deference between the maximum developmental rate and the actual developmental rate is bigger. Thus we have:

$$\Delta D = \beta.(Dm - D).\Delta N \qquad \text{(A-1-1)}$$

or $$\frac{\Delta D}{\Delta N} = \beta.(Dm - D) \qquad \text{(A-1-2)}$$

where b is a proportional coefficient.

as $\Delta N \to 0$, A-2 becomes,

$$\frac{dD}{dN} = \beta(Dm - D) \qquad \text{(A-1-3)}$$

$$\frac{dD}{Dm-D}=\beta.dN \qquad \text{(A-1-4)}$$

Integrate both side of A-4,

$$\int\frac{dD}{Dm-D}=\int\beta.dN$$

$$-\ln(Dm-D)=\beta.N+C$$

$$Dm-D=e^{-\beta.N+C}$$

$$D=Dm-C'e^{-\beta.N}$$

When N=0, we have D=0, which lead to C'=Dm. Hence,

$$D = Dm(1-e^{-\beta.N}) \qquad \text{(A-1-5)}$$

Derivation of the equation describing the relationship between the survival rate and number of prey present (equation 4-7).

As with the developmental rate (S), we relate the survival rate directly to the number of prey (N) present. Let ΔS be the increment of S as N increases by ΔN, we derive the S as a function of N from the relationship between ΔS and ΔN. Firstly, we assume that: (1) The daily survival rate approaches its maximum value (Sm=1) as the number of prey present increases infinitely; (2) the magnitude of ΔS with respect to ΔN is proportional to the product of S with 1-S (the deference between the maximum survival rate and the actual survival rate). Thus, we have:

$$\Delta S = Sc_2.S.(1-S).\Delta N \qquad \text{(A-2-1)}$$

or $$\frac{\Delta S}{\Delta N} = Sc_2 . S.(1-S) \qquad \text{(A-2-2)}$$

where Sc_2 is a proportional coefficient

As $\Delta N \to 0$,

$$\frac{dS}{dN} = Sc_2 . S.(1-S) \qquad \text{(A-2-3)}$$

$$\frac{dS}{S.(1-S)} = Sc_2 . dN \qquad \text{(A-2-4)}$$

Integrate both side of A-4,

$$\int \frac{dS}{S.(1-S)} = \int Sc_2 . dN$$

$$-\ln(\frac{S-1}{S}) = Sc_2 . N + C$$

$$\frac{S-1}{S} = Sc_1 . e^{-Sc_2 . N}$$

$$1 - \frac{1}{S} = Sc_1 . e^{-Sc_2 . N}$$

Rearrange the Ababa equation, we get,

$$S = \frac{1}{1 + Sc_1 e^{-Sc_2 N}} \qquad \text{(A-2-5)}$$

Chapter 5:

A simulation model for assessing the potentials of *H. axyridis* (Pallas) as a biological control agent against *Myzus persicae* (Sulz.)

The interactions between *H. axyridis* (Pallas) and *M. persicae* (Sulz.) are dynamic, so it is impossible to evaluate the effectiveness of the predator by evaluating the static characteristics of the predator and the aphid. The predator and green peach aphid interacting with each other comprise a dynamic system which possesses the attribute of behavior, i.e. the evolution of population densities of the predator and the prey as a result of complex inter-specific interactions. In the biological control of green peach aphid we wish to manage certain portion of the behavior by releasing the predator with appropriate timing and numbers so as to minimize the losses to the damage of the aphid at a profitable price. The understanding of the dynamic behavior of the predator-prey interactions is thus the basis for the evaluation of the effectiveness of the predator and the development of optimal release strategies. Models are required toward this end. The form of the model should be determined by the purpose for which it is needed. This chapter is to discuss the general approach and technical details of the simulation model developed for assessing the potentials of *H. axyridis* (Pallas) as a biological control agent against *Myzus persicae* (Sulz.), and to present some results from the sample simulations.

Modeling is an open-ended task, one can never obtain a perfect model. However, one advantage of the modeling approach to problem solving is that sometimes even if the stated objective is not immediately achieved, weakness in our understanding of the system will be exposed, thus suggesting new research projects. In this sense, this study represent an initial step toward an strategy supporting system of the biological control of green peach aphids.

1. The general framework of the simulation model

The appropriate model for this study is one which incorporates an adequate amount of biological realism concerning temperature- and density-dependence of the interaction between *Myzus persicae* and *Harmonia axyridis*, while keeping a considerable degree of tractability. There is little point in having a model that is too complex to manipulate and to understand. Deterministic model was chosen since stochastic model usually require additional information about the variation and probability distribution of each parameter, and add additional complexity in the model structure and computation.

This model includes three major component submodels: 1) the population increase of *M. persicae*; 2) the functional response of *H. axyridis* to *M. persicae*; and 3) the numerical response of *H. axyridis* to *M. persicae*.

Aphid population dynamics can be modeled using two different approaches. One approach assumes that an aphid population has a stable age structure and complete overlapping generations (Hughes and Gilbert 1968) and can thus be modeled as a homogenous entity. The population change is characterized by the rate of population change. The other approach takes into account the population age structure and the population is modeled as an assembly of different age-classes and the population change is characterized by age-specific demographic parameters (Barlow and Dixon 1980). The choice of approach depends on the system, data available and the purpose of the model. In this study, our purpose of modeling the population dynamics of green peach aphid is to use the model as a component model to be coupled with the functional response and numerical response model of *H. axyridis* to study the effects of temperature on the predator-prey interactions. For this purpose, we accepted the holistic approach since it is much easier to handle and its behavior is more tractable. Also, a more complex and detailed age-structured green peach aphid population model will not be of great help to the overall performance of the simulation model, since there has been no information available concerning the predator's attack rate on different age-classes of the aphids and the predator's preference for prey age-classes, which is necessary when an age-structured prey model is used. Because we modeled the green peach aphid population as an homogeneous entity in which each average "individual" makes an equal contribution to the

population, we as well approximate the aphid consumption by the lady beetle larvae as the loss of average "individuals" due to the predation.

A simple Holling's type II functional response was used to model the attack rate of *H. axyridis* on *M. persicae* as a function of temperature. Complex interactions such as predator interference, predator's choice for prey size and the response in the predator's searching efficiency to the aggregation of the aphids are ignored. In practice, we do not want to release and usually can not afford releasing a predator cohort that is so big as to cause significant predator interference.

For the purpose of evaluating the effectiveness of *H. axyridis* as a biocontrol agent for inundative release, no population recruitment of *H. axyridis* was incorporated in the model. The change of the released cohorts of *H. axyridis* was modeled using an age-classed model - the members of one age-class are shifted bodily to the next after a certain amount of thermal time, corresponding to the duration of the age-class, is accumulated. The duration of age-class of *H. axyridis* is dependent on the temperature and abundance of its prey, green peach aphids. A age-specific daily survival rate was applied to the cohort. The age-specific daily survival rate is again a function of temperature and aphid population density.

2. The green peach aphid model

The population course of green peach aphids is simulated with the following approach: the overwintering eggs of green peach aphids hatch in the peach orchards in the early spring when a certain amount of effective thermal time, meaning the accumulation of temperature above the base temperature (4.5°C) is accumulated (Tamacki 1988, Mack and Smilowitz 1982). The parthenogenetic viviparous population will grow through the season, until June when a certain amount of thermal time is accumulated and then all the individuals emigrate out of the peach orchards. The in-orchard migration between colonies during the course of population change was simulated with a random number of uniform distribution. The ladybeetle larvae can be released at any point of time of the season.

We modeled the green peach aphid population using a delayed logistic model under the

assumption that the current value of the intrinsic rate of population increase is determined by the average value of temperature over a period from the current time backward to a previous time $t-\tau$. Here τ is the elapse of time between the current time and the previous time.

$$\frac{dN}{dt} = r_m(\overline{T}_\tau).N.-b.\overline{N}_\tau.N \qquad (5\text{-}1)$$

where N is the population density of the aphid, $r_m(\overline{T}_\tau)$ is the intrinsic rate of population increase driven by $\overline{T}_\tau$, the average temperature over a period from the current time t backward to a delayed time $t-\tau$. In chapter 2, we have characterized the intrinsic rate of population increase of green peach aphid as a function of temperature using Logan's sigmoid outer expansion (Eqn.2-5). That model and parameter will be used here for describing $r_m(\overline{T}_\tau)$:

$$r_m(\overline{T}_\tau) = \alpha\{[1 + ke^{-\rho\overline{T}_\tau}]^{-1} - e^{-\frac{T_* - \overline{T}_\tau}{\Delta T}}\} \qquad (5\text{-}2)$$

The parameters here have the same meaning as those in Eqn. 2-5. The independent variable $\overline{T}_\tau$ is an average of temperature over the time interval $[t-\tau, t]$. The more realistic and more general form of $\overline{T}_\tau$ should be some kind of weighed average with a characteristic weight function. Because of the lack of information concerning this aspect, here we just use the simplest average, the simple arithmetic average, which is defined by

$$\overline{T}_\tau = \int_{t-\tau}^{t} s.T(s)ds \qquad (5\text{-}3)$$

$\overline{N}_\tau$ in Eqn. 5-1 is the average population over a period from the current time t backward to the delayed time τ. Again, it can be a weighed average. Here we use the simple arithmetic average as an approximation:

$$\overline{N}_\tau = \int_{t-\tau}^{t} s.N(s)ds \qquad (5\text{-}4)$$

b in Eqn. 5-1 is the intra-specific competition coefficient and $\frac{r_m(\overline{T}_\tau)}{b}$ represents the carrying capacity which is driven by $\overline{T}_\tau$, the average temperature over a period from the current time t backward to a delayed time t-τ.

In practice, it is impossisible to obtain continuous-time measurement of temperature and population density. Consequently, we sample the state of these continuous-time variables at certain time interval to obtain a discrete-time approximation, such as the average daily temperature, instead of the continuous-time measurement of temperature, and a discrete-time measurement of population, such as daily population count, so that $\overline{T}_\tau$ or $\overline{N}_\tau$ is approximated with the mean of the respective discrete measurements over $[t\text{-}\tau, t]$,

$$\overline{T}_\tau = \frac{1}{\tau} \sum_{s=t-\tau}^{t} T(s) \qquad (5\text{-}5)$$

$$\overline{N}_\tau = \frac{1}{\tau} \sum_{s=t-\tau}^{t} N(s) \qquad (5\text{-}6)$$

In all the equations τ represents the time-lag for the integral time-delay. The average generation time and the duration for immature development can be considered as two of the candidates for τ. Here we accepted the duration for the immature development as τ. Because the duration for immature development is dependent on the temperature, which changes with time, thermal time is used in determining the time-lag for the integral time-delay. Here τ is calculated from the relation

$$1 = \sum_{s=t-\tau}^{t} D(T(s)) \qquad (5\text{-}7)$$

in the computer program, $t-\tau$ is determined by computing the $\sum_{s=t-\tau}^{t} D(T(s))$ backward starting from the current time t until $\sum_{s=t-\tau}^{t} D(T(s)) \geq 1$ is satisfied and then the value of s was taken as $t-\tau$. $D(T(s))$ the immature developmental rate is calculated from Eqn. 2-4 in Chapter 2:

$$D(T) = \psi [e^{\rho T} - e^{\rho T_m - \frac{T_m - T}{\Delta T}}] \qquad (5\text{-}8)$$

where all the parameters and variables have the same meaning as those in Eqn. 2-4. We use the immature developmental time as the length of time over which the integral time delay of temperature- and density-dependence is accounted for by assuming that the current rate of population change is affected by the integral effects of temperature and population density over the immature developmental time. The average generation time or the characteristic return time may also be used as the length of time accounted for integral time delay under different assumptions. The simple average of temperature or population density that is used here is only the simplest case for the integral time delay of temperature- and density-dependence. Weighed averages upon certain patterns of weight distribution over the delayed time period is be expected to be more realistic representations of time delay effect.

3. The ladybeetle model

Functional response. The functional response of the ladybeetle larvae was modeled as a function of the instantaneous temperature and population density of green peach aphid using Holding's type II response (Eqn. 3-1, 3-2a, b).

$$N_{a_i} = \frac{a_i(T).N}{1 + a_i(T).Th_i(T).N} \qquad (5\text{-}9)$$

$$a_i(T) = \frac{u_1 . T . e^{-\frac{u_2}{T}}}{1 + u_3 . e^{-\frac{u_4}{T}}} \qquad (5\text{-}10)$$

$$Th_i(T) = \frac{1 + v_1 . e^{-\frac{v_2}{T}}}{v_3 . T . e^{-\frac{v_4}{T}}} \qquad (5\text{-}11)$$

where the subscript i represents the i^{th} instar larvae of *H. axyridis*, all the other parameters and variables have the same meaning as the in Eqn. 3-1, 3-2a, b.

The total prey consumption of the all the four larval stages of the ladybug is then:

$$N_a = \sum_i N_{a_i}$$

Developmental rate. The developmental progress of ladybug larvae were modeled as a function of the current daily temperature and prey density using Eqn. 4-3, 4-4, 4-5:

$$D_i(T,N) = Dm_i(T).[1 - e^{-\beta_i(T).N}] \qquad (5\text{-}12)$$

$$Dm_i(T) = \psi_{HA} . (e^{\rho_{HA} . T} - e^{\rho_{HA} . (Tm_{HA} - T)/\Delta T_{HA}}) \qquad (5\text{-}13)$$

$$\beta_i(T) = Bd_1 . e^{-Bd_2 . T} \qquad (5\text{-}14)$$

here i signifies the i^{th} instar of larvae. All the other parameters and variables have the same meaning as those in Eqn. 4-3, 4-4, 4-5. The time when larvae enter the next instar was calculated by

$$1 = \sum_{t_o}^{t} D_i(T(s), N(s)) \qquad (5\text{-}15)$$

where $D_i(.)$is the developmental rate of the i^{th} instar larvae as a function of temperature $T(s)$ and prey density $N(s)$ on day s. In the computer program, the time when the i^{th} instar larvae enter the next instar is calculated by computing the $\sum_{t_o}^{t} D_i(T(s), N(s))$ forward starting from t_o, the time when the larvae entered the i^{th} instar from the previous instar, until $\sum_{t_o}^{t} D_i(T(s), N(s)) \geq 1$ is satisfied and then all the individuals that entered the i^{th} instar get to the $i+1^{th}$ instar.

Survival rate. The average daily stage-specific survival rate (Eqn. 4-7, 4-8, 4-9, 4-10) is used for the survival rate of the i^{th} instar ladybug larvae as a function of the current daily temperature and prey density:

$$S_i(T,N) = \frac{1}{1 + Sc_{i1}(T).e^{-Sc_{i2}(T).N}} \qquad (5\text{-}16)$$

$$Sc_{i1}(T) = Sc_{11}.(1 - Sc_{12}.e^{-Sc_{13}.T}) \qquad (5\text{-}17)$$

$$Sc_{i2}(T) = Sc_{21}.(1 - Sc_{22}.e^{-Sc_{23}.T}) \qquad (5\text{-}18)$$

where all the parameters and variables have the same meaning as those in Eqn. 4-7, 4-8, 4-9, 4-10. The change in the density of the i^{th} instar ladybug larvae was then modeled as

$$\frac{dP_i}{dt} = (1 - L_{i-1}).S_{i-1}(T,N).P_{i-1} - [1 - L_i.S_i(T,N)].P_i + U_i(t) \qquad (5\text{-}19)$$

where P_i is the density of the i^{th} instar ladybug larvae, $U_i(t)$ is the number of the i^{th} instar larvae released at time t, L_{i-1} and L_i are logic variables, they assume only two values (0 or

1), when larvae remain in the i^{th} stage, L_i assumes the value 1, when the larvae finished the development of the i^{th} stage and enter the next stage, L_i assumes the value 0.

$$L_i = \begin{cases} 1 & if \quad \sum_{t_0}^{s} D_i(T(s), N(s)) < 1 \\ 0 & if \quad \sum_{t_0}^{s} D_i(T(s), N(s)) \geq 1 \end{cases} \qquad (5\text{-}20)$$

where $D_i(.)$ is the developmental rate of the i^{th} instar larvae as a function of temperature $T(s)$ and prey density $N(s)$ on day s.

The framework for the overall simulation model is then expressed as:

$$\frac{dN}{dt} = r_m(\overline{T}_\tau).N.(1 - \frac{b}{r_m(\overline{T}_\tau)}.\overline{N}_\tau) + \sum_i \frac{a_i N}{1 + a_i Th_i N} \qquad (5\text{-}21a)$$

$$\frac{dP_i}{dt} = (1 - L_{i-1}).S_{i-1}(T,N).P_{i-1} - [1 - L_i.S_i(T,N)].P_i + U_i(t) \qquad (5\text{-}21b)$$

4. The computer simulation program.

The state variables, driving variable, initial conditions, input and output. Temperature is the only driving variable in the model, the temperature data used in the simulation are generated using CLIMGEN, a climate data generating software developed by USDA-ARS, and parameters derived from the Avignon local meteorological record. The only initial condition in this model is the number of overwintering eggs, which can be given by a random number generator or an predetermined estimate. When the aphid population exceeds the level of tolerance, the stage and number of lady beetle larvae are prompted for input. The program outputs the population trajectories of green peach aphids and the ladybeetles.

Time and space scale of the simulation. A Julian day is used as the time scale in this simulation model, considering that it is a most natural and convenient time scale and, also,

all the parameters used in the model were measured in this time scale in the experiments. In cases that thermal time is used to account for the time required to complete certain biological processes, such as the completion of development of given stages, day-degree is used in actual calculations, but it is then converted to Julian days. As a model aiming at addressing fundamental qualitative properties of temperature- and density-dependence of predator-prey interactions, we try to avoid involving spatial complexity such as habitat heterogeneity and predator displacement among aphid colonies, etc., in the simulation. A single aphid colony is used as the spatial scale. We assume that the intra-specific competition coefficient b, the impact of an individual on other individuals in the same colony, is a constant independent of temperature. The carrying capacity, represented by $r_m(T)/b$, is then varying with temperature. In natural conditions, aphids may move into or out of a colony by walking (the apterous forms) or flying (allate forms). This process of within-habitat movement may be density-dependent or/and temperature-dependent, but no sufficient data available as to give a valid pattern that characterizes this process. In this study, we use a random variable of uniform distribution to generate the number of aphids moving into or out of a colony, which is independent of aphid density and temperature. The bias in the results using this method may be viewed as enormous in microscopic scale, but could be considered as being tolerable in macroscopic scale, since the effects of inter-colony movement on population dynamics is much more important under low population density then under high population density of aphids. As the season approaching the end, green peach aphids produce allate forms that emigrate out of the peach orchard to secondary hosts. The proportion of aphids moving out of the orchard is shown to increase as the end of the season is approached (Tamacki 1973, Leclant 1978). Here the number of aphids moving out of the peach orchard is modeled as the product of aphid population density, a uniformly distributed random variable and the proportion of the accumulated day-degree over the total day-degree required to complete the phase of life history of aphids in the peach orchard with an power of x (x is a value to be chosen to obtain expected results):

$$N_{emm}(t) = N(t).RND.(\frac{\sum_{t_*}^{t}(T(t)-T_b)}{DD_{total}})^x \qquad (5\text{-}22)$$

where $N_{emm}(t)$ is the number of aphids moving out of the orchard, $N(t)$ is the current aphid population density, RND is a random variable of uniform distribution, $T(t)$ is the temperature at time t, T_b is the base temperature for the development of aphids, DD_{total} is the total day-degree required to complete the phase of life history of the aphid in the peach orchard, x is a value to be chosen.

The main program. The Main program consists 5 major sections. The first section defines subroutines, functions, arrays and parameter values. The second section reads the temperature data from a data file generated with CLIMGEN and calculates the date when the aphids appears in the orchards. The aphids are supposed to appear in the peach orchards at the point of time when certain effective thermal accumulated above the threshold (4.5°C, Tamacki et al. 1982). Section three initializes the system by assigning initial values to state variables --- populations of green peach aphids and ladybeetle larvae. The initial population of green peach aphids is given by the truncation of number multiplied by a random variable of uniform distribution. A zero is given to the initial population of ladybeetle larvae since the aphid population is supposed to be below the threshold of tolerance. Sections 4-6 include various procedures doing the numerical computations of the simulation, which begins on the date when green peach aphids appear in the orchards and terminates when a thermal time total of 1912 day-degree is accumulated above 4.5°C. Section four calls the subroutine RmLag for calculating the intrinsic rate of population increase of green peach aphids as a function of temperature with integral time delay and the delayed density-dependence due to intra-specific competition (see "section 2. Green peach aphid model" of this chapter). Section five checks whether the aphid population exceeded the threshold of tolerance, if so, a certain number of lady beetle larvae of a chosen larval stage is released. The subroutine ComputY is called to calculate the developmental rate, daily survival rate and prey consumption of the lady beetle larvae as a function of current daily temperature and aphid population. Section six calls the subroutine RungeKutta, a solver of ordinary differential equation, to

compute the population density of aphids and lady beetle larvae of the next day. Section seven writes the data generated by the simulation to a data file.

Subroutine RmLag. This subroutine is called by the main program to calculate the average of daily temperature and the average of aphid population over a delayed time period (as specified by equation 5-3, 5-4), which is the time interval between a time point in the past and the current time during which a thermal time accumulation sufficient for the aphids to complete their immature development (or average generation time) is attained. This time lag is calculated form the current time point backward to a time point in the past at which the accumulation of developmental rate of the aphids, which is a function of temperature, reaches one (see equation 5-7 and the discussion in "Section 2. Green peach aphid model" of this chapter). The average of daily temperature over the delayed time period is then used to calculate the intrinsic rate of population increase $r_m(T)$ using equation 5-2, and the average of aphid population over the same time period is used to account for the delayed density-dependence of the aphid population (see equation 5-1). The daily temperature, aphid population density, relevant parameters and time counter are passed to this subroutine and the intrinsic rate of population change and the average of aphid population over a delayed time period are output as globally shared values.

Subroutine ComputY. This subroutine is called to calculate the prey consumption, developmental rate and survival rate of the lady beetle larvae as functions of temperature and aphid population density. The first part of the subroutine computes the developmental rate of the larvae and the developmental progress in terms of accumulation of developmental rate using equations 5-12 to 5-14. The latter is passed to the subroutine RungeKutta and is used to determine whether the larvae enter the next stage on the next day according to the relation defined in Eqn. 5-15. The second part compute the survival rate which is used in the subroutine RungeKutta as the rate of change of the ladybeetle larvae. The third part of the subroutine compute the instantaneous attack rate and handling time in relation to temperature and is passed to the subroutine RungeKutta for calculating the total consumption of aphids by the ladybeetles.

Subroutine RungeKutta. This subroutine is a simple ordinary differential equation solver using the fourth order Runge-Kutta algorithm. The state system to solved is defined as in

Eqns. 5-21. This subroutine uses the value of rate variable determined by the subroutines RmLag and ComputeY and the total consumption of aphids by the ladybeetles as determined by the function TotalConsum. A step length of 0.1 is used in this algorithm. Values of the state variables, the population densities of aphids and the ladybeetles, are updated each time when the subroutine is called. This subroutine also check whether the development of a certain larval stage has been completed and the individuals should go into the next stage.

Function TotalConsum. This function is called at each time of derivative evaluation in the subroutine RungeKutta for computing the total number of aphids killed by the ladybeetles. The values of the instantaneous attack rate and handling time as well as the population densities of aphids and ladybeetles are passed to the function from the subroutine ComputeY and the main program respectively.

5. Properties of the predator-prey system generated from the simulation model.

Dependence of the effectiveness of larval *Harmonia axyridis* on temperature. The effectiveness of the ladybeetles is accounted in terms of the minimum number of larvae required to bring the aphid population eventually down to zero from a certain aphid population level. The more effective the larval instar, the less individuals are required to eventually eliminate the aphids. This value was estimated using a numerical procedure, in which the number of aphids that move within and out of the orchard is set to zero so that the population collapse of the aphids purely due to predation by the ladybeetle larvae can be observed. The aphid population level at which the ladybeetle larvae are released is assigned 250 aphids/colony (This value was arbitrarily selected, with no practical consideration). In general, for the first three instar larvae of *Harmonia axyrids* more individuals are required to wipe out the aphids on a single colony at lower temperatures than are those at higher temperatures, but the change in the minimum number of larvae required as temperature increases is much stiffer at the two extremes of the effective temperature range than that within the temperature range between 15 and 24°C, corresponding to the overlapping part of suitable temperature ranges for both green peach

aphids and *Harmonia axyrids* (Fig. 5-1 L_1, L_2, L_3). For the 3rd instar, the minimum number of larvae required at 18 °C is somewhat less than those at 21°C and 24 °C (Fig. 5-1 L_3). For the 4th instar, the minimum number of larvae required to bring the aphid population eventually down to zero does not quite follow the pattern of a monotonous decrease along with the increase in temperature (Fig. 5-1 L4). Within the temperature range between 15 and 24 °C the minimum number of the 4th instar larvae required actually increases with temperature, a scheme reverse to that for the 1st and 2nd instars (Fig. 5-1 L_4, 5-2).

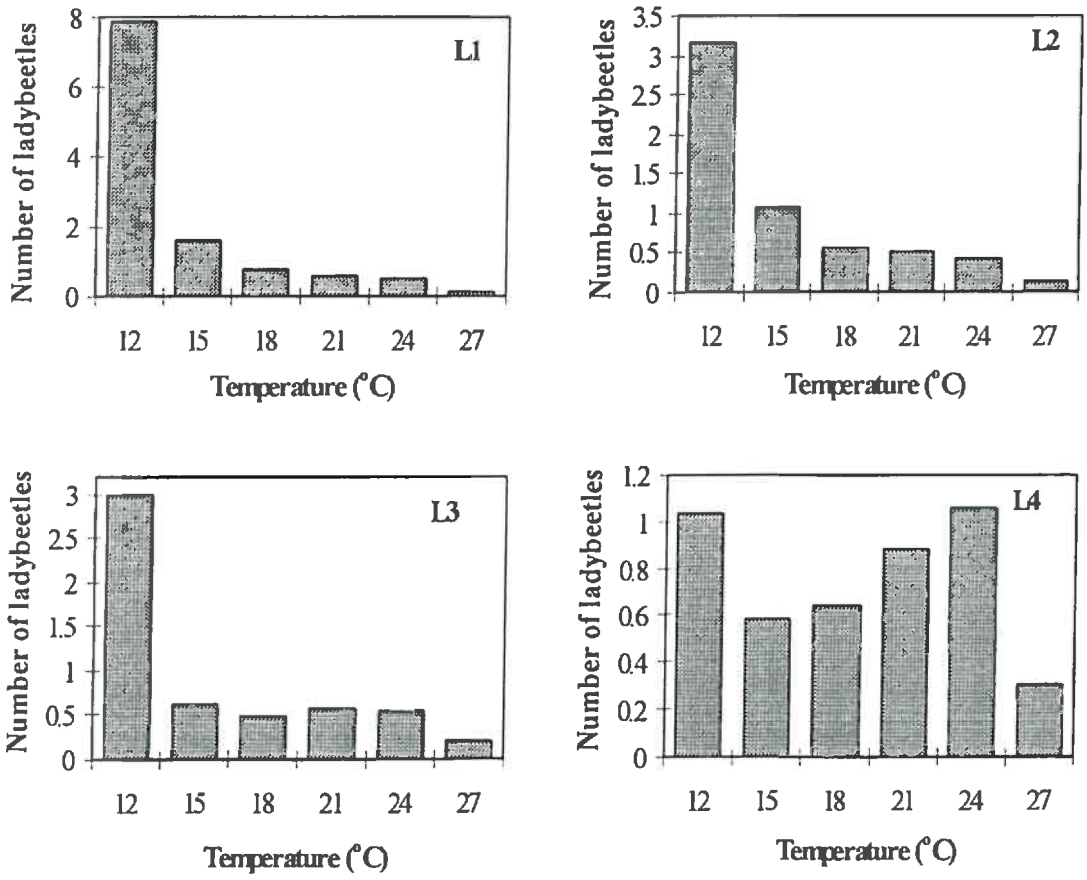

Fig.5-1. Estimated values of the minimum number of larvae of *Harmonia axyridis* required to eventually eliminate the green peach aphids on a single colony in relation to temperature. The predator are released at the aphid population level of 250 aphids/colony. These data are generated with the computer simulation program. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

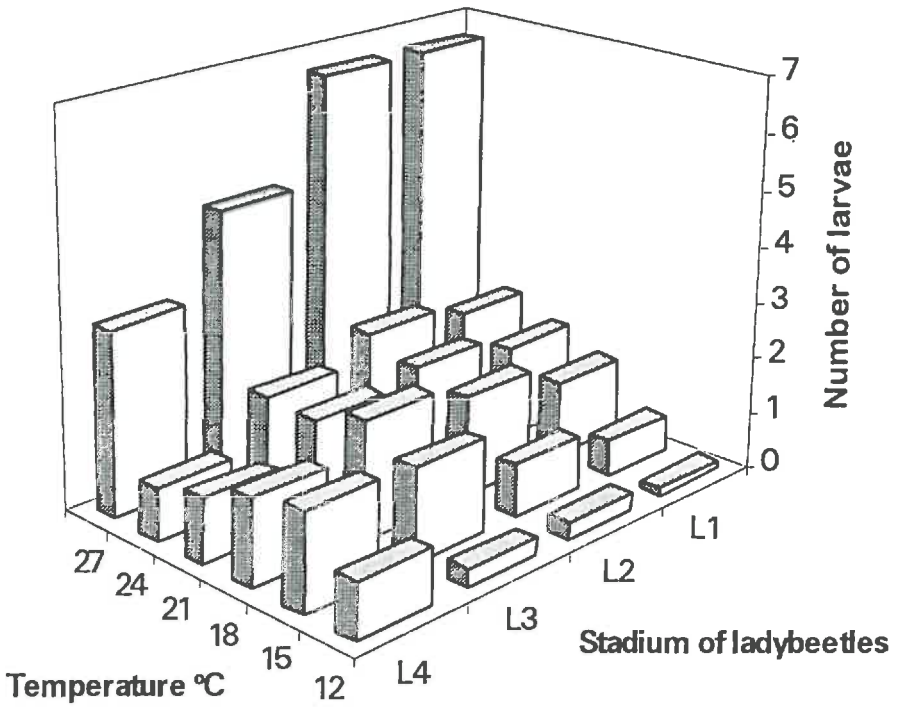

Fig.5-2. The 3-D view of the minimum number of larvae of *Harmonia axyridis* required to eventually eliminate the green peach aphids on a single colony in relation to both temperature and the age of the ladybeetle larvae. The predator are released at the aphid population level of 250 aphids/colony. See the transition of the order along the temperature axis and the lady beetle axis. The data are generated with the computer simulation program. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

The simulation also showed that with the same final consequence of the aphid population eliminated by releasing a minimum number of ladybeetle larvae required to eventually eliminate the aphids, the length of the course of aphid population collapse can be quite different depending on temperatures. The aphid population collapses in a much greater speed under higher temperatures than does under lower temperature (Fig. 5-3, 5-4). Also, younger instar larvae display a greater extent of change in the length of time it takes to eliminate the aphids as temperature increases than do older instars, for example, at 12°C it takes more than 50 days longer for the 1st instar larvae released in the minimum required number to eliminate the aphids than it does at 24 or 27°C, while this change for the 4th instar is only less than 10 days (Fig. 5-3, 5-4).

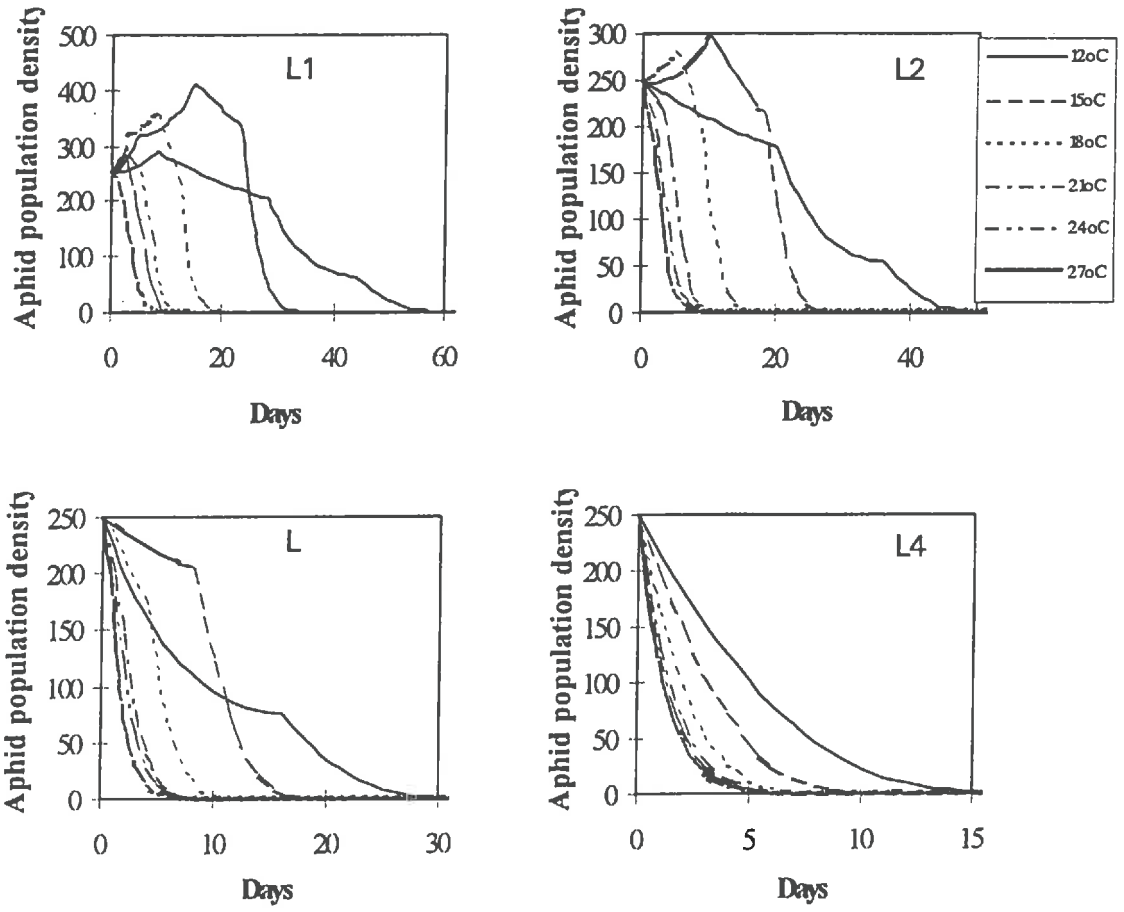

Fig.5-3. Simulated population change of green peach aphid after larvae of *Harmonia axyridis* are released in the minimum number required to eventually eliminate the green peach aphids on a single colony. The predator are released at the aphid population level of 250 aphids/colony. The value of the minimum number of larvae required to eliminate green peach aphids on a single colony is the same as used in Fig 5-1 and Gig. 5-. See that more days are required to completely eliminate the aphids under low temperature than under high temperature, and that the difference in the days required to completely eliminate the aphids is much smaller for the older instar larvae than for the younger instar larvae. The data are generated with the computer simulation program. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

Difference in the effectiveness between different larval stages of *Harmonia axyridis*.

The simulation procedure used here is the same as was described in the above paragraph. The results are just interpreted from another angle. At low temperatures such as 12 and 15 °C, the minimum number of ladybeetle larvae required to wipe out green peach aphids on a single colony decreases as the age of larvae increases, i.e., the value of the minimum

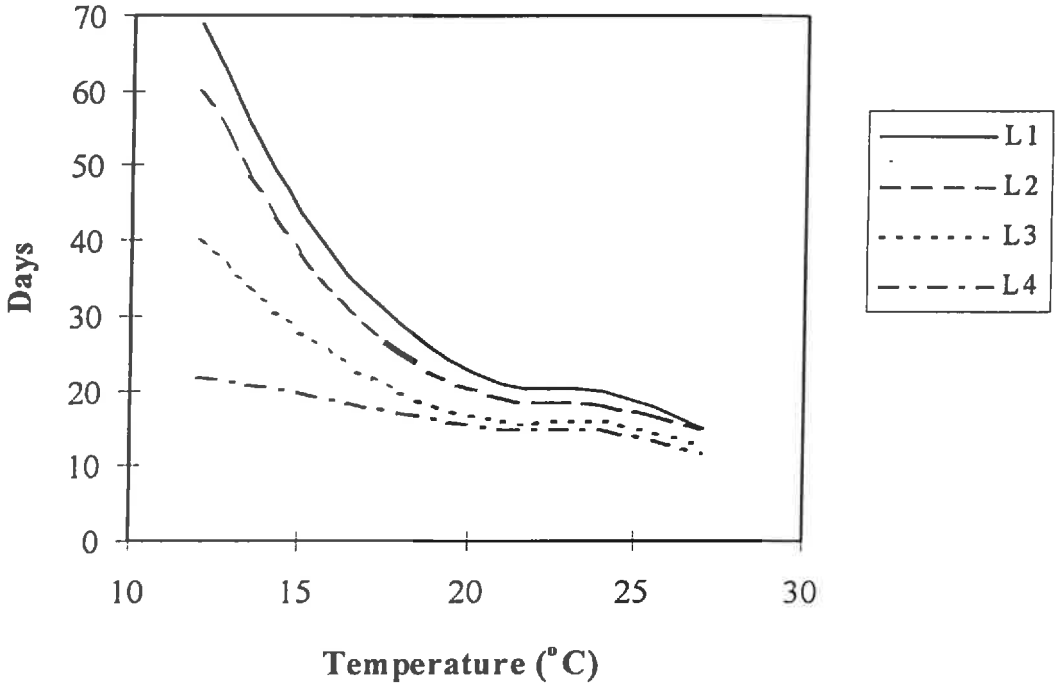

Fig.5-4. Estimates of number of days it take for the aphid population to be brought down to zero by larvae of *Harmonia axyridis* released in the minimum number required to eventually eliminate the green peach aphids on a single colony. See that this value decreases as temperature increases. The data are generated with the computer simulation program. The predator are released at the aphid population level of 250 aphids/colony. The value of the minimum number of larvae required to eliminate green peach aphids on a single colony is the same as used in Fig 5-1 and Fig. 5-. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

number of larvae required to release when the aphid population reaches 250 follows: $L_1>L_2>L_3>L_4$. At the other end of the range of effective temperature such as 27°C, the relative effectiveness switches to the inverse order - the minimum number of larvae required decreases as the age of larvae increases, i.e. $L_4>L_3>L_2>L_1$. Between the two extremes, the order of relative effectiveness of different instars transforms in a sequential manner as temperature increases. As the temperature increases, firstly the order of the minimum number of individuals required to release changes to L1>L4>L2>L3 (Fig. 5-5 18°C), then the order becomes $L_4>L_1>L_3>L_2$ (Fig. 5-5 21°C), and then it changes to $L_4>L_3>L_1>L_2$ (Fig. 5-5 24 °C), and finally, it switches to $L_4>L_3>L_2>L_1$ (Fig. 5-5 27°C). This switch is realized through the fact that as temperature increases, the minimum

number of larvae required to eliminate the aphids decreases to a greater extent for the larvae of younger instars than for that of the older instars (Fig. 5-2, 5-5).

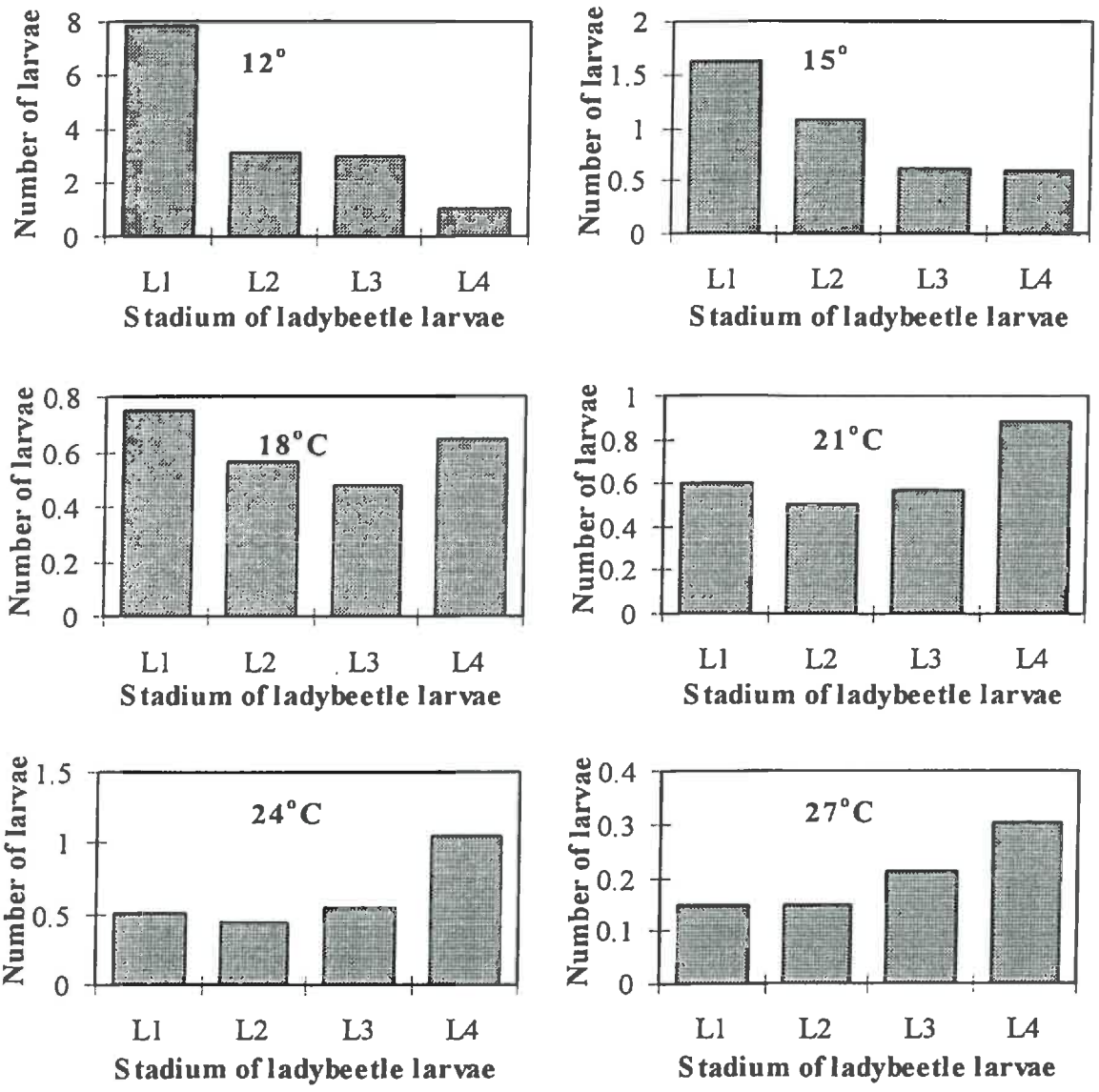

Fig.5-5. Estimated values of the minimum number of larvae of *Harmonia axyridis* required to eventually eliminate the green peach aphids on a single colony in relation to the age of the ladybeetle larvae. The predator are released at the aphid population level of 250 aphids/colony. The order of the minimum number of larvae required to ensure a complete depletion of aphids with respect to the age of the predator switches to the reverse as temperature changes from one end to the other of the effective range. The data are generated with the computer simulation program. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

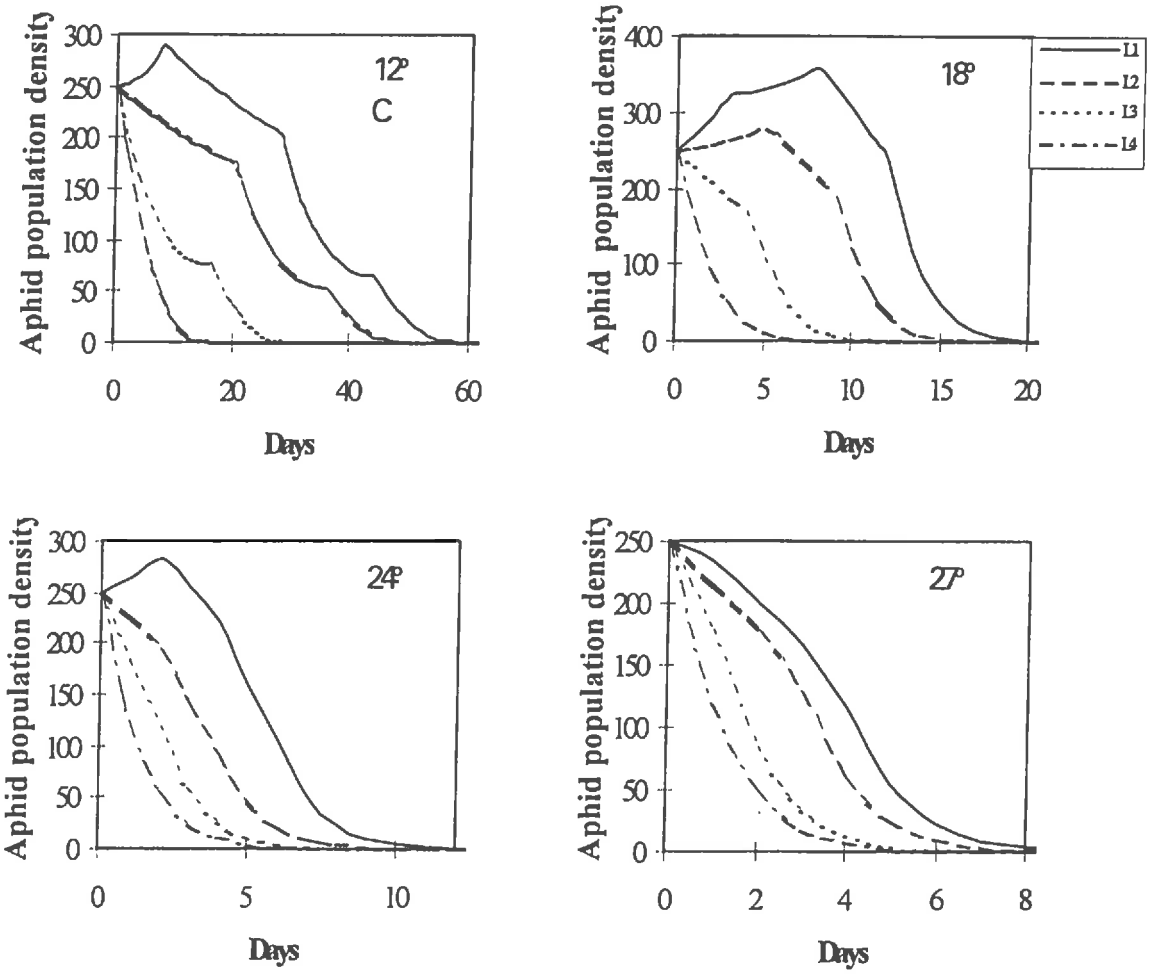

Fig.5-6. Simulated population change of green peach aphid after larvae of *Harmonia axyridis* are released in the minimum number required to eventually eliminate the green peach aphids on a single colony. The predator are released at the aphid population level of 250 aphids/colony. The value of the minimum number of larvae required to eliminate green peach aphids on a single colony is the same as used in Fig 5-1 and Gig. 5-. See that more days are required to completely eliminate the aphids by the younger instar larvae than by the older instar larvae, and that the difference in the days required to completely eliminate the aphids by different instars is much smaller under high temperature than under low temperature. The data are generated with the computer simulation program. L1, L2, L3, L4 represent the larvae or 1st 2nd, 3rd and 4th instars.

When different instars of the ladybeetle larvae are released with each in its minimum number required to ensure a complete depletion of the aphids, the population of green peach aphids collapses in somewhat different speeds. When larvae of a older instar (L_3 or L_4) are released, the aphid population collapses within a comparatively very short time, sometimes almost instantly in the case of 4th instar larvae (Fig. 5-6). In contrary, when

larvae of a younger instar (L_1 or L_2) are released, the aphid population collapse could be a rather long course, and at low temperature the aphid population may even keep growing for a while before finally being eliminated by the predator (Fig. 5-6). The difference in the length of time it takes to eliminate the aphids, when different instars are released with each in its minimum required number, is greater at low temperatures than it does at high temperatures (Fig. 5-4, 5-6).

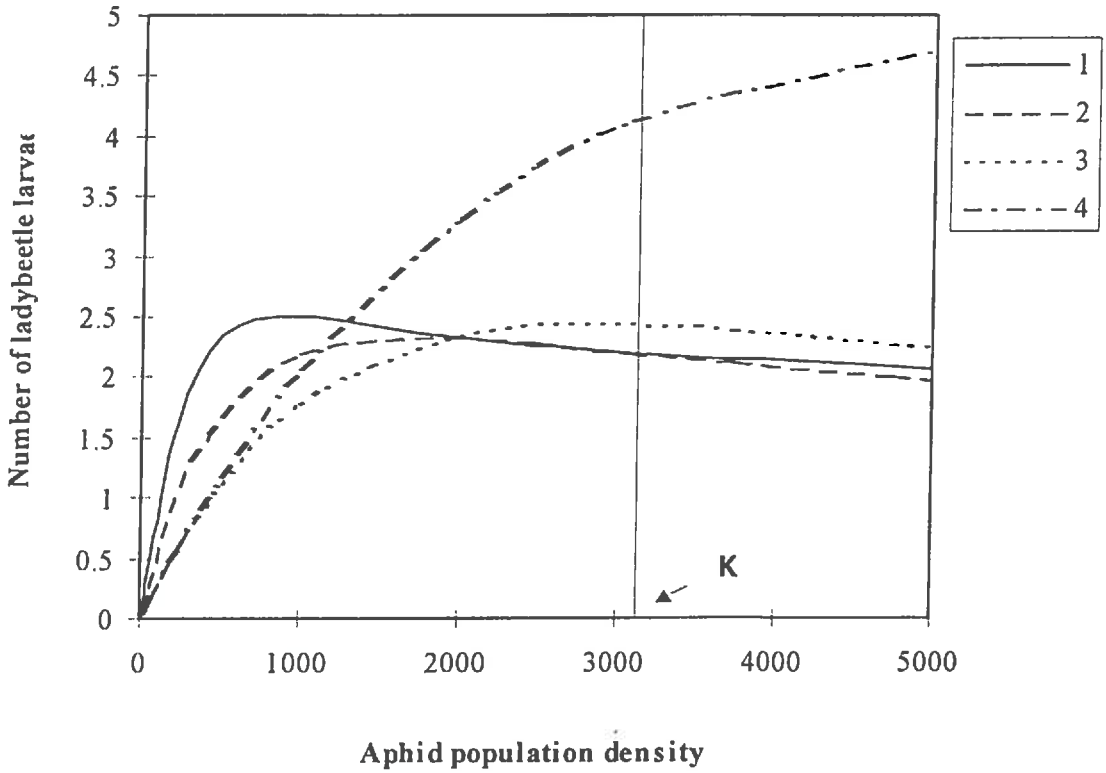

Fig. 5-7. Estimates of the number of larvae of Harmonia axiridis required to eliminate green peach aphids on a colony in relation to the population level of the aphids at which the larvae are released (under 15°C). K (=3074) is the maximum population size when the predator is absent.

The dependence of effectiveness of larvae of *Harmonia axyridis* on the population levels of *Myzus persicae*. Here we calculated the minimum number of ladybeetle larvae required to eventually eliminate the green peach aphids on a single colony in relation to the

aphid population level at which the ladybeetles are released. We illustrate some observed patterns concerning this issue with the results from the simulation using a single constant temperature of 15 °C. For the first three larval instars of *H. axyrids*, at the left part of the x-axis representing the aphid population level, the minimum number of individuals required to ensure a complete elimination of the aphids on a single colony increases sharply as the aphid population level at which the ladybeetle larvae are released increases. Then this value slowly decreases as the aphid population level increases (Fig. 5-7). For the fourth instar, the minimum number of individuals required to ensure a complete elimination of the aphids increases continually as the aphid population level increases (Fig. 5-7).

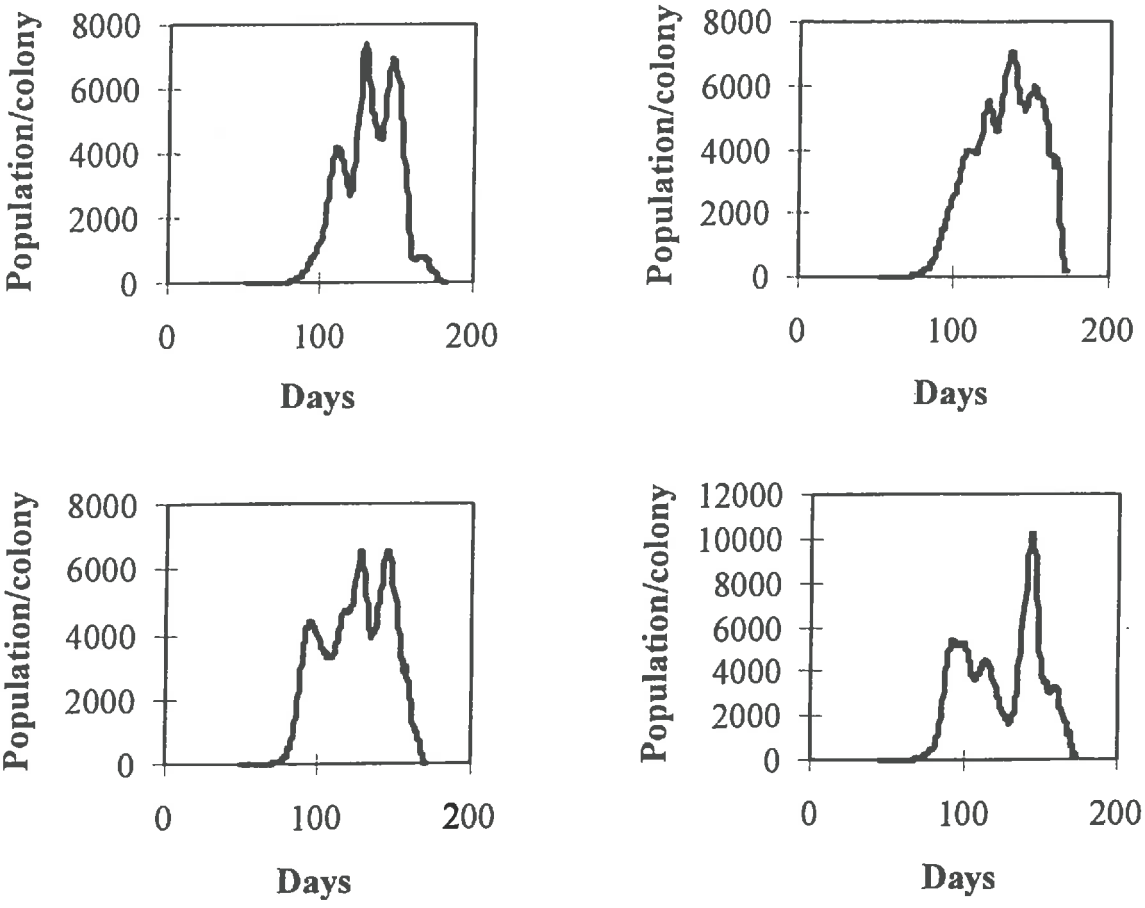

Fig.5-8. Simulated population change of green peach aphid under varible temperature when no Harmonia axyridis are released throughout the season. Temperature data are generated using CLIMGEN, a climate data generator developed by USDA-ARS, with parameters calculated from the local meteo record maintained by INRA-Station de Agroclimatologie at Montfavet.

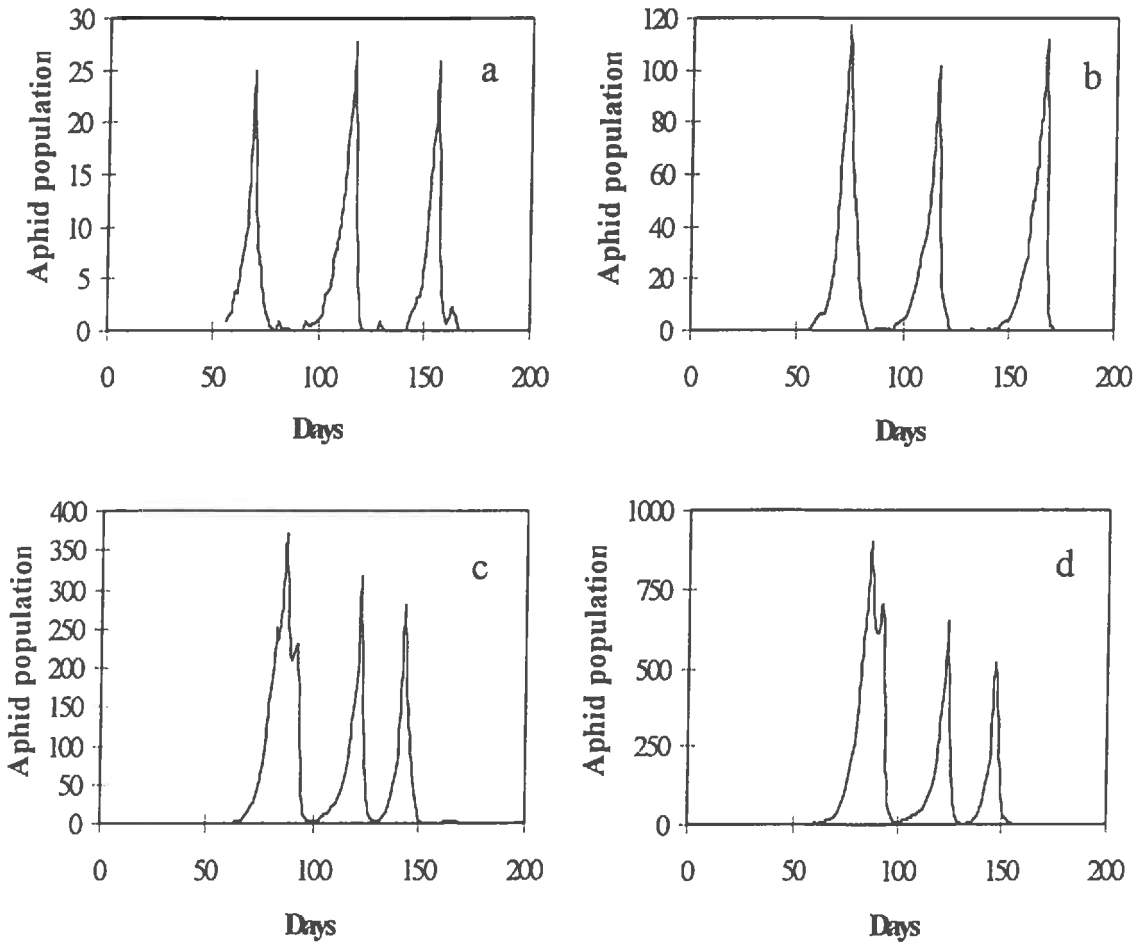

Fig.5-9. Simulated population change of green peach aphid under varible temperature when the 3rd instar larvae of *Harmonia axyridis* are released at different population level of green peach aphids. The aphid population level at which the predator is released --- a: 25 aphids/colony, b: 100 aphids/colony, c: 0.5 larvae/colony, d: 500 aphids/colony. Quantity of 3rd instar larvae of *Harmonia axyridis* released --- a: 0.25-0.25-0.25, b: 1-0.5-0.5, c: 1.5-1-1, d: 2.5-2-2. Temperature data are generated using CLIMGEN, a climate data generator developed by USDA-ARS, with parameters calculated from the local meteo record maintained by INRA-Station de Agroclimatologie at Montfavet.

Dynamical behavior of the simulation model. The computer simulation model generated the following dynamic behaviors: when no ladybeetles are released, the green peach aphid population appears in peach orchards in late February or early March and

disappears from the orchard in mid-June. During the whole course, the population of green peach aphid undergoes fluctuations with 3-4 peaks and is most abundant from April to May (Fig.-8). This pattern conforms somewhat the common sense. However, no field data is available at the moment to perform valid comparison.

Fig. 5-9 shows simulation results concerning the consequence of releasing larvae of *H. axyrids* for biological control against *M. persicae*. The number of larvae required to be released increases with the aphid population level at which the ladybeetle larvae are released. When the predator is released once the aphid population reaches 25 per colony, a very satisfactory result is obtained by releasing the 3rd instar larvae three times each at 0.25 larvae /colony (Fig. 5-9 a). When the predator is released once the aphid population reaches 100 per colony, a similar result is obtained by releasing the 3rd instar larvae three times with each at 1, 0.5, 0.5 larvae /colony respectively (Fig. 5-9 b). If the aphid population level at which the predator is released is set at 250 per colony, the three times releases of 3rd instar larvae with each at 1.5, 1, 1 larvae /colony, the total number of predator to release is much biger than that released at lower prey population levels results in a less satisfactory control over the aphid population (Fig. 5-9 c). If the predator is released at 500 aphids per colony, the three releases of the 3rd instar larvae with each at 2.5, 2, 2 larvae /colony, an almost unrealistic number, gives an almost unacceptable result (Fig. 5-9 d). These simulations also shows that a biger number of predator need to be released at a early time of the season when the temperature is low, than at a late time of the season. Now we can ask the question that whether a better result, in the sense of reducing the releases and the total number of predator released, can be obtained by releasing for the first release a greater number of predator. Fig. 5-10 illustrates the simulation results concerning this question. When the predator are released at the aphid population level of 250 aphids/colony, the number of releases are reduced from three releases to two releases, if a big number of predator are released for the first release. The number of predator released for the first time is 5 larvae for the 1st instar (Fig. 5-10 a), 4 for the 2nd instar (Fig. 5-10 b), 3 for the 3rd and 4th instar (Fig. 5-10 c, d). For the second release, 1 predator is released for all the cases. Increasing the number of predator for the first release is not likely to reduce the total number of predator released, while it do reduce

the number of releases. It is very unlikely to reduce the number of releases any further as to a single release by increasing the number of predator released for the first release within a meaningful extent.

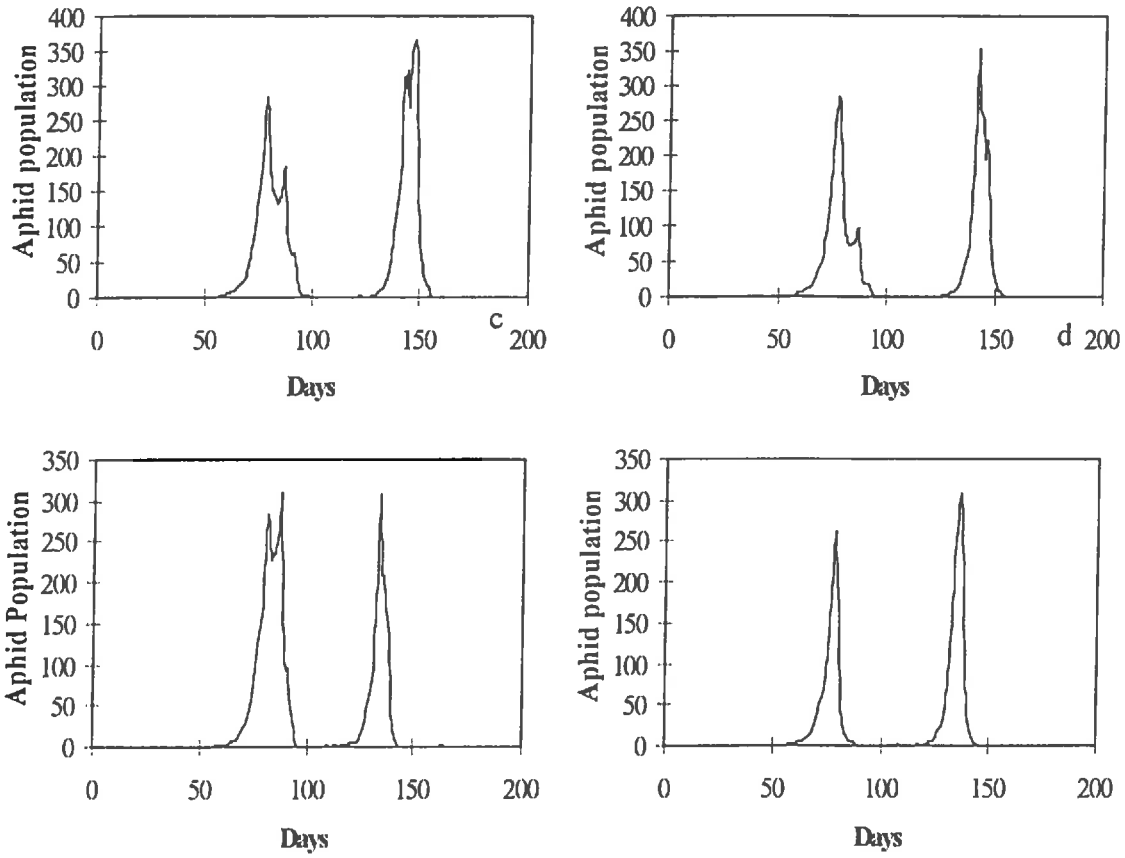

Fig.5-10. Simulated population change of green peach aphid under varying temperature when increasing the number of larvae of *Harmonia axyridis* for the first release at the the aphid population density of 250/colony. The Instar and quantity of larvae of *Harmonia axyridis* released --- a: 1st instar 5-1; b: 2nd instar 4-1, c: 3rd instar 3-1, d: 4th instar 3-1. Temperature data are generated using CLIMGEN, a climate data generator developed by USDA-ARS, with parameters calculated from the local meteo record maintained by INRA-Station de Agroclimatologie at Montfavet.

Discussion

This simulation model is intended to reveal qualitative properties concerning the temperature- and density-dependence in the predator-prey interactions between *H.*

axyridis and *M. persicae*. The results from this model are not attempted to possess much quantitative significance, since a lot of biological and physical details are neglected either for keeping tractability of the behavior of the model or for the lacking of required information. Anyway, this kind of model do generate some qualitative properties which provide insight into the mechanisms underlying various overall behaviors of the predator-prey interactions. And some of the properties may have general implications to a broader context and may serve as testable hypotheses and may eventually add to the accumulation of scientific knowledge.

Two aspects, i.e. the minimum number of predator required to ensure an eventual depletion of aphids and the length of the elapse of time from the day when the predator are released to that when the aphids are completely depleted from the colony, are used to measure the relative effectiveness of larvae of *H. axyridis* in suppressing population of *M. persicae*, since for innundative release, we do not expect the predator to act as a long-term regulator of the prey population, but, in most cases, as depletor of the prey. For all the four larval instars of *H. axyridis*, the minimum number of predator required to ensure an eventual depletion of aphids approaches to zero as temperature approaches the highest extreme for the population growth of the aphids, and it increases to the highest quantity at the other extreme of the range of effective temperature. Within the range of suitable temperature for both species (for example, 15-24°C), the minimum number of the 1st, and 2nd instar larvae of *H. axyridis* required to eventually eliminate the aphids decrease monotonously as temperature increases. Within the same range of temperature, this pattern flattened out for the 3rd instar. For the 4th instar, within the temperature range of 15-24 °C the effectiveness decreases as temperature increases, just the reverse order of that for the 1st and 2nd instars. Within this scenario, the relative order of the effectiveness of different stages of *H. axyridis* switches from $L_1<L_2<L_3<L_4$ under 12°C to $L_4<L_3<L_2<L_1$ under 27°C, with a series of transition at temperatures in between. The elapse of time from the time when the predator is released to the time when the aphids are depleted from the colony also depends on temperature and the age of the predator. For all the four larval stages of the ladybeetle, the length of this elapse of time decreases as temperature increases, and the decrease in the length of this time elapse as temperature increases is

sharper for the younger instar larvae than for the older instar larvae. The length of this time elapse is longer for younger instar larvae than for older instar larvae, and the difference is much greater at lower temperatures than at higher temperatures. Based on above, it is suggested that at lower temperatures, older instar larvae (L_3 and L_4) are more effective because the number of larvae required to release is smaller and they can eliminate the aphids in a much shorter time, and thus are more preferable when the release of predator is required at low temperature. At higher temperature, younger instar larvae (L_1 and L_2) are usually at least not less effective than the older instar larvae since the number of the younger instar larvae that are required to be released is similar (compared with L_3) or smaller (compared with L_4) number and they spend only a little longer time to wipe out the aphids, and thus are more preferable when the release of predator is required at high temperatures. These suggestion may reinforced by practical considerations. At low temperatures, it takes a much longer time for the young instar larvae to wipe out the aphids, which allows a greater chance for the aphids, being frequently disrupted by the predator, to move around and transmit virus diseases. Also, a longer course gives greater probability of predator loss due to dropping on the ground, being died of wind or rain, or being preyed on by general predators, so the risk of failure is greater and in practice a larger number of larvae than that is expected may need to be released. Under high temperature, the older instar larvae can usually quickly end up their development of active stage(s) before wiping out the aphids.

The minimum quantity of ladybeetle larvae required to be released also depends on the population level at which the larvae are released. In most cases, the minimum number of individuals required to ensure a complete elimination of the aphids on a single colony increases sharply as the aphid population level at which the ladybeetle larvae are released increases before it reaches a peak value. Then this value slowly decreases as the aphid population level increases (Fig. 5-7). The left part of the curves Fig. 5-7 describing a sharp increase in the minimum number of larvae that need to be released is most relevant to our practical problem since we expect to suppress the aphid population before it gets very high, and thus, it will be more effective and more economy to release the ladybeetle larvae at a low aphid population level. However, this condition may be limited by two factors: 1)

The temperature dependence of the effectiveness may conflict with this condition --- to release the predator at low aphid density usually implies to conduct the first release at low temperature which usually requires a large number of predator. 2) The behavioral constraints may put limit on the condition. As with many other predators, the ladybeetle may need a minimum rewardable density of prey to initialize and then concentrate its predation on this prey, it is especially true for the ladybeetle larvae like *H. axyridis* from mass production which has grown on food different from the prey.

The left part of the curve in Fig. 5-7 describing a sharp increase in the minimum number of predator required for L_1 - L_3 is fairly easy to understand. However, the right part of the curve in Fig. 5-7 describing a slight decrease in the minimum number of predator required for L_1 - L_3 may be in contradiction with our intuition. The mechanism underlying this is that when aphid population size is beyond $K/2$, the half of the maximum population size, the rate of population change dN/dt of the aphids actually decreases as N increases, .

The simulation also shows that the number of releases of larvae of *H. axyridis* required to ensure the aphid population under check throughout the season may be reduced by increasing the number of individuals released each time, but the total number of larvae that need to be released throughout the season is not reduced by doing this way. In any case, the number of releases of larvae of *H. axyridis* required to ensure the aphid population under check throughout the season is not likely to be reduced to less than two releases.

The feasibility of biological control of green peach aphids using *H. axyridis* depends highly on the level of tolerance to aphid infestation. If the tolerance level is low, once the infestation get intolerablely high, interventions with immediate aphid elimination are usually required. When *H. axyridis* is to be used as a biocontrol agent against the green peach aphids in this case, a large number of 3rd or 4th instar larvae will be required for the release, which may be economically unfeasible. In addition to this, behavioral limits, such as the fact that a considerably high aphid population density may be required for initializing and maintaining a concentrated searching for the aphids by the ladybeetle, or risks of failure due to the randomness and stochasticity of the events that happens after the release may deny the possibility of using *H. axyridis* as a control agent for innundative release if the level of tolerance to aphid infestation is low. In case that the level of

tolerance to green peach aphids is high, the utilization of *H. axyridis* as a biocontrol agent for innundative release seems a feasible alternative to the current control methods.

The most important factor among those which are not incorporated into the model is probably the searching behavior of the ladybeetle larvae. A significant loss of the larvae released was usually the explanation for the failure of almost all of the open-air field release trials that have been conducted. The most satisfactory result of release came probably from the experiment carried out under semi-controlled condition for which full sized peach trees were each caged with fine screen, and the ladybeetle larvae released were confined in the cages (see Chapter 6). The behavioral and demographic fate of the ladybeetle larvae are still greatly unknown at the moment. In this case, we expect our results from the simulation model represent an upper bounds of the effectiveness of *H. axyridis* as a biocontrol agent against *M. persicae*.

Appendix. Q-Basic program of the simulation model

```
'*************************************************************************
'*      Simulation Model for Evaluating the Effectiveness of             *
'*  Harmonia axyridis as a Biocontrol Agent against Green Peach Aphid    *
'*                                                                       *
'*                  Author: Xin Chen                                     *
'*************************************************************************
'
'                   MAIN PROGRAM
'=========================================================================

 DEFINT I-J, L-N
 DEFDBL A-H, K, O-Y

'Declare subprograms

 DECLARE SUB RungeKutta (i, Xave#, r#, SX#, AR#(), Th#(), Totsum, TotThermReq)
 DECLARE FUNCTION TotalConsum# (AR#(), Th#(), Dx#, Yk#())
 DECLARE SUB ComputeY (Stage%, i%, Temp#())
 DECLARE SUB RmLag (i, DayEmer%)

 COLOR 15, 1: CLS
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
'Define dimension of arrays

 DIM X(300), Y(4, 300), Temp(366), Ynew(4)
 DIM DevRatY(4), SurRatY(4), AR(4), Th(4), DmY(4), Bt(4)
 DIM FiY(4), RoY(4), TmY(4), DlY(4), Bt1(4), Bt2(4)
 DIM Sc11(4), Sc12(4), Sc13(4), Sc21(4), Sc22(4), Sc23(4)
 DIM Au1(4), Au2(4), Au3(4), Au4(4), Av1(4), Av2(4), Av3(4), Av4(4)

'=========================================================================
'Parameter values:
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

'Parameters for Green Peach Aphids:
'-------------------------------------------------------------------

'(1) Thermal and population thresholds:
'-------------------------------------

 ThermReqEmer = 365: TotThermReq = 1740: TbX = 4.5
 Threshold = 250: ColonSize = 2!

'(2) Developmental rate of M. persicae as a function of temperature:
'-----------------------------------------------------------

'   DevX(T)=FioX*(EXP(RoX*Temp)-EXP(RoX*TmX-(TmX-Temp)/DlX))        (1)

 FioX = .673: RoX = .1856: TmX = 29.477: DlX = 5.37
```

```
'FioX = .009: RoX = .185: TmX = 27.476: DlX = 1.368
'FioX = .04: RoX = .103: TmX = 27.3: DlX = 1.702
'(3) Population growth rate of M. persicae as a function of temperature:
'--------------------------------------------------------------------

'  dX/dt=r(Temp)*(Tave(t-z))*X-SX*X*Xm(t-z)                    (2)
'  r(Temp)=AlXX*((1+KaXX*EXP(-RoX*Temp))^(-1)-EXP(-(TmX-Temp)/DlX))  (3)

 AlXX = .845: KaXX = 30.121: RoXX = .142: TmXX = 27.921: DlXX = 1.364
 SX = .00006: Em = 10
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

'Parameters for ladybeetles:
'-------------------------------------------------------------------------

'(1) Developmental rate as a function of temperature and prey density.
'--------------------------------------------------------------------

'   DevRatY(X)=DmY(Temp)*(1-EXP(-BtY(Temp)*X)                  (4)
'   DmY(Temp)=FiY*(EXP(RoY*Temp)-EXP(RoY*TmY-(TmY-Temp)/DlY))       (5)
'   BtY(Temp)=Bt1*EXP(-Bt2*Temp)                         (6)

 FiY(1) = .02594:  FiY(2) = .00261:  FiY(3) = .00482:  FiY(4) = .01056
 RoY(1) = .25413:  RoY(2) = .28842:  RoY(3) = .30675:  RoY(4) = .17957
 TmY(1) = 29.69785: TmY(2) = 29.80001: TmY(3) = 29.46918: TmY(4) = 29.28088
 DlY(1) = 3.70503:  DlY(2) = 2.92329:  DlY(3) = 3.02091:  DlY(4) = 3.77412
 Bt1(1) = .31911:  Bt1(2) = .47988:  Bt1(3) = .39625:  Bt1(4) = .19067
 Bt2(1) = .04432:  Bt2(2) = .08924:  Bt2(3) = .12118:  Bt2(4) = .07064

'(2) Daily survival rate as a function of temperature and prey density.
'--------------------------------------------------------------------

'   SurRatY(X)=1/(1+Sc1(Temp)*EXP(-Sc2(Temp))              (7)
'   Sc1(Temp)=Sc11*(1-Sc12*EXP(-Sc13*Temp))                (8)
'   Sc2(Temp)=Sc21*(1-Sc22*EXP(-Sc23*Temp))                (9)

 Sc11(1) = .19146:  Sc11(2) = .21412:  Sc11(3) = .21579:  Sc11(4) = .31085
 Sc12(1) = 955000:  Sc12(2) = 1555555: Sc12(3) = 1.38611: Sc12(4) = 1!
 Sc13(1) = 1.21777: Sc13(2) = 1.19604: Sc13(3) = .13231:  Sc13(4) = .04479
 Sc21(1) = .01258:  Sc21(2) = .01315:  Sc21(3) = .00846:  Sc21(4) = .00964
 Sc22(1) = 7.5E+08: Sc22(2) = 7.5E+08: Sc22(3) = 7.5E+08: Sc22(4) = 32.42401
 Sc23(1) = 1.62623: Sc23(2) = 1.67645: Sc23(3) = 1.67415: Sc23(4) = .31312

'(3) Temperature-dependent functional response:
'----------------------------------------------

'  ConsumY(X)=AR(Temp)*X/(1+AR(Temp)*Th(Temp)*X)             (10)
'  AR(Temp)=(Au1*Temp*EXP(-Au2/Temp))/(1+Au3*EXP(-Au4/Temp))      (11)
'  Th(Temp)=(1+Av1*EXP(-Av2/Temp))/(Av3*Temp*EXP(-Av4/Temp))      (12)

 Au1(1) = .198:   Au1(2) = .102:    Au1(3) = .087:    Au1(4) = .049
 Au2(1) = 31.78:  Au2(2) = 16.236:  Au2(3) = 9.18:    Au2(4) = -2.701
 Au3(1) = 1369.94: Au3(2) = 2138.877: Au3(3) = 1369.701: Au3(4) = 12636.851#
 Au4(1) = 202.034: Au4(2) = 255.308:  Au4(3) = 210.091:  Au4(4) = 284.557
```

```
 Av1(1) = 3.3E+09: Av1(2) = 3.3E+09:  Av1(3) = 3.3E+09:  Av1(4) = 3.3E+09
 Av2(1) = 619.451: Av2(2) = 603.417:  Av2(3) = 610.031:  Av2(4) = 620.522
 Av3(1) = 97.693:  Av3(2) = 215.471:  Av3(3) = 255.433:  Av3(4) = 636.077
 Av4(1) = 55.661:  Av4(2) = 59.203:   Av4(3) = 52.979:   Av4(4) = 52.137
'=============================================================================

'Get weather data and compute phenological date:
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

'Input temperature data.
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

 PRINT "Do simulation with constant temperature or variable temperature?"
 INPUT "Type 'C' for constant temperature or 'V' for variable temperature : ", CV$
 IF UCASE$(CV$) = "C" THEN

' Input a constant temperature:
'---------------------------

      INPUT "Constant temperature = "; TempC
      FOR day% = 1 TO 366
           Temp(day%) = TempC
      NEXT day%
 ELSE

'Input weather data from a data file:
'-----------------------------------

      'INPUT "Input the name of the file where your weather data is put"; Weather$
      weadata = FREEFILE
      Weather$ = "c:\xin.bas\model\avig2000.dat"
      OPEN Weather$ FOR INPUT AS #weadata
      day% = 1
      WHILE NOT EOF(weadata)
           INPUT #weadata, day%, o1, Temp(day%), o2
           day% = day% + 1
      WEND
 END IF
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
'Estimate phenological date:
'-------------------------------------------------------------------

'Time when aphids emerge in the orchard.
'--------------------------------
'
 DayEmer% = 1
 DaydegEmer = 0
 DO UNTIL DaydegEmer >= ThermReqEmer
      IF Temp(DayEmer%) > TbX THEN
           DaydegEmer = DaydegEmer + Temp(DayEmer%) - TbX
      ELSE
           DaydegEmer = DaydegEmer
      END IF
      DayEmer% = DayEmer% + 1
```

```
 LOOP
 PRINT " The aphids emerged in the orchard on the "; DayEmer%; " th day."
'-------------------------------------------------------------------------

'=========================================================================
'Input the initial values of the system.
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
'Initialize the population of green peach aphids:
'-----------------------------------------------

 'PRINT "Numder of aphid eggs emerge in the orchard on the "; DayEmer%; " th day=";
 'INPUT X(DayEmer%)
 INI = RND * 1.5
 X(DayEmer%) = INI
'~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
'Initialize the number of ladybugs.
'---------------------------------

  FOR Stage% = 1 TO 4
      DevY(Stage%) = 0
      Y(Stage%, DayEmer%) = 0
 NEXT Stage%
'=========================================================================
' Print output heading to the screen.
'---------------------------------
 a$ = " ### ###.##  ########  ########  ########  ########  ########"
 PRINT "  TIME   TEMP      GPA      HA L1     HA L2     HA L3     HA L4"
 PRINT "-------------------------------------------------------------------"

'=========================================================================
'Beginning of the main loop:
'--------------------------
 Totsum = 0: Dayend% = DayEmer%: i = DayEmer%
 DO UNTIL Totsum >= TotThermReq
    Totsum = Totsum + Temp(i) - TbX
    IF INKEY$ = CHR$(27) THEN STOP
'Goto subprogram RamLag to compute the parameters r(Tave(t-z)) and Xave.
'-------------------------------------------------------------------
    CALL RmLag(i, DayEmer%)
'Check whether aphid population exceeded the threshold of tolerance
'If "Yes", ask if ladydeetle larvae are to be released.
    IF X(i) >= Threshold THEN
      PRINT "GPA population has exceeded the economic threshold, take actions?"
      INPUT "Yes or no? (Y/N)", act$
'Input the larval stage of and the number of ladybeetle to be released.
      IF UCASE$(act$) = "Y" THEN
        INPUT "Which larval stage of ladybeetle do you want to release (1,2,3,4)?", LS
        INPUT "How many do you want to release (Number per colony)?", Ynew(LS)
        FOR Stage% = 1 TO 4
           IF Stage% = LS THEN Y(Stage%, i) = Y(Stage%, i) + Ynew(LS)
           CALL ComputeY(Stage%, i, Temp())
        NEXT Stage%
        Ynew(LS) = 0: LS = 0
      ELSE
```

```
          FOR Stage% = 1 TO 4
            CALL ComputeY(Stage%, i, Temp())
          NEXT Stage%
        END IF
 'If the aphid population did not exceed the threshold of tolerance
 'No released will be conducted
     ELSE
        FOR Stage% = 1 TO 4
           CALL ComputeY(Stage%, i, Temp())
        NEXT
     END IF

 'Goto subprogram RungeKutta to solve differential equations.
 '-----------------------------------------------------------
     CALL RungeKutta(i, Xave#, r#, SX#, AR#(), Th#(), Totsum, TotThermReq)

 '~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~

 'Write output to the screen:
 '---------------------------

     PRINT USING a$; i + 1; Temp(i + 1); X(i + 1); Y(1, i + 1); Y(2, i + 1); Y(3, i + 1); Y(4, i + 1)
     i = i + 1
  LOOP
  Dayend% = i - 1
 'End of main loop.
 '=============================================================================
 'Write output to a data file.
 '---------------------------
 '
  OPEN "c:\xin.bas\data\SV4-.dat " FOR OUTPUT AS #2
  FOR i = DayEmer% TO Dayend%
       PRINT #2, i, Temp(i), X(i); Y(1, i); Y(2, i); Y(3, i); Y(4, i)
  NEXT i
  CLOSE
 '=============================================================================
 END  'End of main program

 '=============================================================================
 '                  SUBPROGRAKM ComputeY
 '=============================================================================
 '
 SUB ComputeY (Stage%, i, Temp())
  SHARED X(), Y(), FiY(), RoY(), TmY(), DlY(), Bt1(), Bt2()
  SHARED Sc11(), Sc12(), Sc13(), Sc21(), Sc22(), Sc23()
  SHARED Au1(), Au2(), Au3(), Au4(), Av1(), Av2(), Av3(), Av4()
  SHARED DevY(), AR(), Th(), SurRatY(), ColonSize
  J = Stage%

  IF Y(J, i) > 0 THEN

 'Compute intermediate parameter values related to the ladybeetle.
 '----------------------------------------------------------
```

```
'(1) Development Rate as a funcion of temperature and density of prey

      TauY = (TmY(J) - Temp(i)) / DlY(J)
      DmY = FiY(J) * (EXP(RoY(J) * Temp(i)) - EXP(RoY(J) * TmY(J) - TauY))
      BtY = Bt1(J) * EXP(-Bt2(J) * Temp(i))
      DevRatY = DmY * (1 - EXP(-BtY * X(i) / Y(J, i) * ColonSize))
      DevY(J) = DevY(J) + DevRatY
      'PRINT "Dev", DevRatY, DevY(J)

'(2) Survival rate as a function of temperature and density of prey

      Sc1 = Sc11(J) * (1 - Sc12(J) * EXP(-Sc13(J) * Temp(i)))
      Sc2 = Sc21(J) * (1 - Sc22(J) * EXP(-Sc23(J) * Temp(i)))
      IF Sc1 < 0 THEN Sc1 = 0
      IF Sc2 < 0 THEN Sc2 = 0
      SurRatY(J) = 1 / (1 + Sc1 * EXP(-Sc2 * X(i) / Y(J, i) * ColonSize))
      'PRINT "Surv", SurRatY(J)
'(3) Temperature-dependent functional response

      TT = Temp(i)
      IF TT <= 0 THEN TT = .5
      Numeritor1# = Au1(J) * TT * EXP(-Au2(J) / TT)
      Denominator1# = 1 + Au3(J) * EXP(-Au4(J) / TT)
      AR(J) = (Numeritor1# / Denominator1#) / ColonSize
      Numeritor2# = 1 + Av1(J) * EXP(-Av2(J) / TT)
      Denominator2# = Av3(J) * TT * EXP(-Av4(J) / TT)
      Th(J) = Numeritor2# / Denominator2#
      'PRINT "Func", AR(J), Th(J)
 ELSE DevY(J) = 0
 END IF
'=============================================================================
END SUB   'End of subprogram ComputY

DEFSNG M-N
DEFDBL Z
'=============================================================================
'                SUBPROGRAM  RamLag
'=============================================================================
'
SUB RmLag (i, DayEmer%)
SHARED r#, Xave, X(), Temp(), Tb, TempAcum
SHARED FioX, RoX, TmX, DlX, AlXX, KaXX, RoXX, TmXX, DlXX
TempAcum = 0: DevAcumX = 0: XAcum = 0: Lag = i
'-----------------------------------------------------------------------
'Compute developmental rate and the backward time interval for finishing the
'development of the immature stage.

DO WHILE DevAcumX < 1 AND Lag >= DayEmer%
     IF Temp(Lag) > Tb THEN
          TauX = (TmX - Temp(Lag)) / DlX
          DevX = FioX * (EXP(RoX * Temp(Lag)) - EXP(RoX * TmX - TauX))
          TempAcum = TempAcum + Temp(Lag)
     ELSE
          DevX = 0
```

```
            TempAcum = TempAcum
        END IF
        DevAcumX = DevAcumX + DevX
        XAcum = XAcum + X(Lag)
        Lag = Lag - 1
    LOOP
    '-------------------------------------------------------------------
    'Compute the average daily temperature and daily count of average population
    'of aphids over the last interval for finishing the development of immatures

    Tave = TempAcum / (i - Lag)
    Xave = XAcum / (i - Lag)

    'Compute the intrinsic rate of population increase of the green peach aphids

    r = AlXX * ((1 + KaXX * EXP(-RoXX * Tave)) ^ (-1) - EXP(-(TmXX - Tave) / DlXX))
    '===================================================================
    END SUB 'End of subprogram RamLag

    DEFINT M-N
    '===================================================================
    '               SUBPROGRAM RungeKutta
    '===================================================================
    '
    SUB RungeKutta (i, Xave, r, SX, AR(), Th(), Totsum, TotThermReq)
     SHARED SurRatY(), X(), Y(), Stage%, DevY()
     REDIM Y0(4), Yk(4), ky1(4), ky2(4), ky3(4), ky4(4), kave(4)
     h = .1

    'Assign values to intermediate variables

     X0 = X(i): Xk = X0
     FOR Stage% = 1 TO 4
         Y0(Stage%) = Y(Stage%, i)
         Yk(Stage%) = Y(Stage%, i)
     NEXT Stage%

    '-------------------------------------------------------------------
    'Main loop for the solution of differential equations

     FOR T = i TO i + 1 STEP h
    '-------------------------------------------------------------------
         TotNa = TotalConsum(AR(), Th(), Xk, Yk())
         kx1 = h * (r * Xk - SX * Xave * Xk - TotNa)
         Xk = X0 + kx1 / 2
         FOR Stage% = 1 TO 4
             ky1(Stage%) = h * -(1 - SurRatY(Stage%)) * Yk(Stage%)
             Yk(Stage%) = Y0(Stage%) + ky1(Stage%) / 2
             'PRINT "Sur", SurRatY(Stage%), Yk(Stage%)
         NEXT Stage%

    '-------------------------------------------------------------------
         TotNa = TotalConsum(AR(), Th(), Xk, Yk())
         kx2 = h * (r * Xk - SX * Xave * Xk - TotNa)
```

```
        Xk = X0 + kx2 / 2
        FOR Stage% = 1 TO 4
            ky2(Stage%) = h * -(1 - SurRatY(Stage%)) * Yk(Stage%)
            Yk(Stage%) = Y0(Stage%) + ky2(Stage%) / 2
            'PRINT "Sur", SurRatY(Stage%), Yk(Stage%)
        NEXT Stage%

'-------------------------------------------------------------------
        TotNa = TotalConsum(AR(), Th(), Xk, Yk())
        kx3 = h * (r * Xk - SX * Xave * Xk - TotNa)
        Xk = X0 + kx3
        FOR Stage% = 1 TO 4
            ky3(Stage%) = h * -(1 - SurRatY(Stage%)) * Yk(Stage%)
            Yk(Stage%) = Y0(Stage%) + ky3(Stage%)
            'PRINT "Sur", SurRatY(Stage%), Yk(Stage%)
        NEXT Stage%

'-------------------------------------------------------------------
        TotNa = TotalConsum(AR(), Th(), Xk, Yk())
        kx4 = h * (r * Xk - SX * Xave * Xk - TotNa)
        FOR Stage% = 1 TO 4
            ky4(Stage%) = h * -(1 - SurRatY(Stage%)) * Yk(Stage%)
            IF Yk(Stage%) < 0 THEN Yk(Stage%) = 0
            'PRINT "Sur", SurRatY(Stage%), Yk(Stage%)
        NEXT Stage%

'-------------------------------------------------------------------
        X0 = X0 + (kx1 + 2 * kx2 + 2 * kx3 + kx4) / 6
        IF X0 < 0 THEN X0 = 0
        FOR Stage% = 1 TO 4
            kave(Stage%) = (ky1(Stage%) + 2 * ky2(Stage%) + 2 * ky3(Stage%) + ky4(Stage%)) / 6
            Y0(Stage%) = Y0(Stage%) + kave(Stage%)
            IF Y0(Stage%) < 0 THEN Y0(Stage%) = 0
        NEXT Stage%
    NEXT T
'-------------------------------------------------------------------
'Random immigrantion of aphids into the orchard

    RANDOMIZE TIMER

    IMM% = (1 - RND * 2) * .75
    IF IMM < 0 AND X0 - X0 * RND * (Totsum / TotThermReq) ^ 10 < 1 THEN IMM = 0
      X(i + 1) = X0 + IMM - X0 * RND * (Totsum / TotThermReq) ^ 10
    IF X(i + 1) <= 0 THEN X(i + 1) = 0
    FOR Stage% = 1 TO 4
        Y(Stage%, i + 1) = Y0(Stage%)
    NEXT Stage%
    FOR Stage% = 1 TO 4
        IF DevY(Stage%) >= 1 THEN
          IF Stage% + 1 <= 4 THEN
            Y(Stage% + 1, i + 1) = Y(Stage%, i + 1)
            Y(Stage%, i + 1) = 0
            DevY(Stage%) = 0
          ELSE
```

```
            Y(Stage%, i + 1) = 0
          END IF
        END IF
 NEXT Stage%

'=========================================================================
END SUB   'End of subprogram RungeKutta

'=========================================================================
'                FUNCTION TotalConsum
'=========================================================================
'
'
FUNCTION TotalConsum (AR(), Th(), Xk, Yk())
SHARED ColonSize
tmp = 0
 FOR Stage% = 1 TO 4
   IF Yk(Stage%) > 0 AND Xk > 0 THEN
     ConsumY = AR(Stage%) * ColonSize * Xk * Yk(Stage%) / (Yk(Stage%) + AR(Stage%) * ColonSize
* Th(Stage%) * Xk)
   ELSE
     ConsumY = 0
   END IF
   tmp = tmp + ConsumY
NEXT Stage%
TotalConsum = tmp
'PRINT "total", tmp
'=========================================================================
END FUNCTION  'End of Function TotalConsum
```

Chapter 6:
Evaluating the effectiveness of *Harmonia axyridis* Pallas as a biocontrol agent against *Myzus persicae* (Sulz.) with field cage release trial

Introduction

Experimental exclusion techniques have been widely used to assess the effectiveness, especially the short-term performance, of a natural enemy in suppressing a target pest population (Valley and Gradwell 1971, Luck et al. 1988). In the early stage of developing a biological control program, these techniques are particularly useful, for they usually yield a larger amount of useful information because the fate of both the predator and the prey can be traced in details; they may bring to end researches on a species that is unlikely to be a effective natural enemy before much effort and expense are devoted; they may narrow the range of options for large-scale open-air field release trials; and most importantly, some specifically designed experiment can answer specific questions. In our study of evaluating *Harmonia axyridis* as a biocontrol agent against *Myzus persicae*, this kind of experiment was found to be required in several places. Our simulation model predicted that under a suitable temperature and at a relatively low aphid population level, the larvae of *H. axyridis* could be more or less quite effective in eliminating the green peach aphids, even though the overall evaluation of the predator is not quite encouraging. For example, suppose that intervention is carried out whenever the aphid population reaches an average of 25 aphids/shoot, complete depletion of aphids can be obtained by releasing as few as 0.25 ladybeetle larvae of the third instar per shoot, corresponding to 75 individuals/tree for a peach tree with 300 shoots (Chapter 5, Fig. 5-9). However, none of the large-scale open-air field releases carried out by us at several locations demonstrated the predicted consequence, in spite of the fact that sometimes as many as 300 larvae of the 3rd instar were released to each tree. Actually little obvious effects on the aphid population were witnessed in open orchard releases, and little was known concerning what happened to the predator released, since it was extremely difficult to follow the fate of the released cohort

of the predator in the open field conditions. In this case, it is suggested that either the model prediction is totally nonsensical, which implies that some serious mistakes were made during the model construction or numerical computation, or some factors that resulted in an significant loss of the released ladybeetle larvae, other than the normal temperature- and prey density-dependent mortality, existed in open fields. Some suspected causes are: 1) a large number of the ladybeetle larvae were preyed upon by some generalist predators such as birds, ants, etc.; 2) the larvae dropped down the trees passively because they cannot hold on the foliage of the peach tree very well; 3) the larvae fell down the tree in search of more suitable habitats or food because the larvae reared on eggs of *Ephestia kuehniella* Zeller cannot adjust well to the new habitat and food. The objectives of this experiment are two folds: a) to compare qualitatively the observed pattern of population change of *M. persicae* resulting from releasing larvae of *H. axyridis* with the pattern from simulations; b) to acquire some hints about the cause of the loss of released larvae of the predator.

Materials and Methods

Eight peach trees of similar size were selected and pruned to leave approximately the same number of shoots (approximately 250 new shoots/tree). Each of these trees were encaged in a 2.5x2.5x2.5 m fine screen (1 mm) cage. The cages were well closed to prevent insects outside the cages from getting in and the insects inside the cages from getting out. Each tree was infested with green peach aphids from laboratory colonies on the 17th of May. Fifty new shoots from each tree were marked as samples for observation. On the next day, four of the encaged trees were randomly chosen, and onto each of them were released 50 third instar larvae of *H. axyridis*, corresponding to an average of 0.2 larvae per shoots. The larvae of *H. axyridis* came from the mass-rearing with eggs of *Ephestia* maintained by INRA-Laboratory of Population Biology at Antibes. The 50 larvae were put in a petri dish which were placed at the major branching site of the tree.

Monitoring the populations of green peach aphids and the released cohort of *H. axyridis* on the marked shoots was carried out every or every other day. For the ladybeetle larvae, the number of individuals found on the marked shoots was counted. For the aphids, the degree of aphid infestation of each shoot was used as an index of aphid population level. Leclant's classification (Leclant 1967) of tree-level aphid infestation degrees was adapted to colony-level infestation degrees here:

degree 0: no aphids at all, N = 0;

degree 1: slightly infested, number of aphids $0 < N < 5^1$;

degree 2: obviously infested, $5^1 < N < 5^2$;

degree 3: top 2-3 leaves become curled, $5^2 < N < 5^3$;

degree 4: 3-5 leaves curled, aphids crowd the top of the shoot $5^3 < N < 5^4$;

degree 5: aphids crowd all over the top of the shoot and more than 5 leaves, $5^4 < N$.

An index of relative infestation was calculated for each tree using the following formulas:

$$IF = \frac{\sum_0^5 d \cdot f_d}{5 \cdot \sum_0^5 f_d} \qquad (6\text{-}1)$$

where IF is the index of relative infestation, d: $d \in [0,1,2,3,4,5]$ is the degree of infestation; f_d : is the frequency of d.

It is obvious that the maximum value of IF is one, and the minimum zero. The IF value was calculated for each of the trees either with or without ladybeetle larvae. The average IF of the trees with ladybeetle larvae and the trees without were compared.

The data on aphid infestation degree can also be used to estimate the average population density of the aphids on a colony:

$$\bar{N} = \frac{\sum_0^5 f_d \cdot 5^d}{\sum_0^5 f_d} \qquad (6\text{-}2)$$

where $\bar{N}$ is the estimated average of population density of green peach aphids per colony; d: $d \in [0,1,2,3,4,5]$ is the degree of infestation; fd : is the frequency of shoots with a

degree of infestation *d*. Here, for each degree of infestation, we used the upper limits of the range of population density, since we found that in actual observation, the upper limits usually gave much more weight in determining the degree of infestation, for example, 150 aphids/colony is a density falls in the range represented by degree 4 ($5^3<150<5^4$), but this density may often be judged as degree 3 since it is closer to 5^3. Moreover, according to our classification of the degree of infestation, for the degree 5, the corresponding range of population density has only a lower limit ($N>5^4$). We just simply used $d=5$ in the estimation of population, a survey we carried out indicated that this value (5^5) does set an upper limit for the aphid population on a single colony. The estimated aphid populations for both control and treatment were then compared with simulation conducted using temperature data recorded in one of the cages using a self-recording thermometer which was placed in a wooden box. Average daily temperature was calculated from temperatures recorded at 0, 6, 12, 18, and 24 o'clock (see table 1 for data on average daily temperature).

Table 1. Air temperature measured using a self-recording thermometer placed at the height of 76 cm under the tree in the cage.

Date	Temperature (°C)
17-May	19.4
18-May	19.2
19-May	18.8
20-May	18.6
21-May	16.2
22-May	16.5
23-May	17.6
24-May	19.4
25-May	22.8
26-May	23.0
27-May	23.2
28-May	21.3
29-May	21.9
30-May	21.1
31-May	22.6

Results

The Index of aphid infestation of all the four peach trees onto which the 3rd instar larvae of *H. axyridis* were released was observed to have a continuous decline following the release of the predator on May 18 and eventually fell down to zero in about 8-10 days after the release of the predator (Fig. 6-1), while that of the four trees without the ladybeetle larvae kept increasing (except for one tree on which the *IF* had a slight decline) (Fig. 6-2). The comparison of the average value of *IF* for the treatment with that for the control demonstrated more clearly the effect of the released predator on the population change of green peach aphids (Fig. 6-3). On the day prior to the release of predator, both the two group of trees had basically the same average degree of infestation of green peach aphids. And the rate of increase in the average degree of infestation from the first day to the second day had almost the same slop for the two group of trees (Fig. 6-3). Even the frequency distribution of the infestation degree was basically the same for both the treatment and control prior to (May 17) and on the day (May 18) of the release (Fig. 6-4). After the release, for the treatment, the frequency of high degree of infestation declined continuously until all shoots fell into zero degree of infestation, while for the control, the frequency of high degree of infestation kept increasing (Fig. 6-4). The overall average infestation, as was measured by the index of relative infestation, diverged between the treatment and control after the predator was released (Fig. 6-3). The impacts of the predator on the population of the aphids was well manifested by this method.

The fact that the green peach aphids on the trees with ladybeetle larvae were eliminated while those on the trees without the ladybeetle larvae kept increasing suggests that an effective number of active ladybeetle larvae must have well persisted to the moment of the aphid depletion, otherwise there might have been chance for the recovery of the aphid population. The data form observation showed that the larvae of *H. axyridis* had persisted even after the aphids were depleted. Although the relative density of the ladybeetle larvae declined with aphid population (Fig. 6-5), some 4th instar larvae still survived and remained active when green peach aphids had been effectively wiped out from the trees (Fig. 6-6).

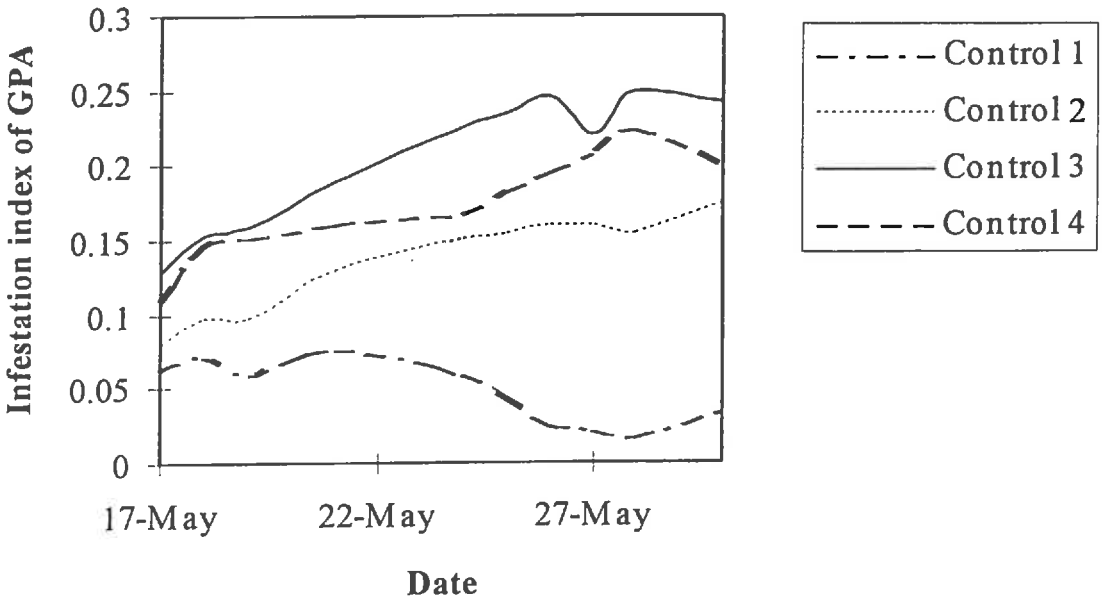

Fig. 6-1 Evolution of index of relative infestation of green peach aphids on encaged peach trees with larvae of *Harmonia axyridis*.

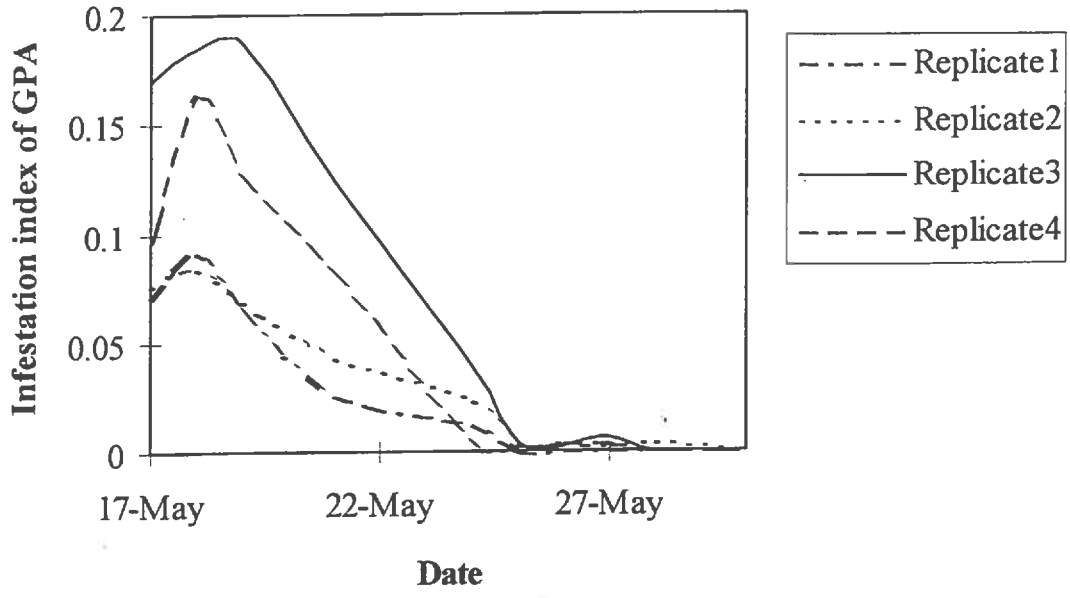

Fig. 6-2 Evolution of index of relative infestation of green peach aphids on encaged peach trees onto each of which 50 3rd instar larvae of *Harmonia axyridis* were released on the 18th of May.

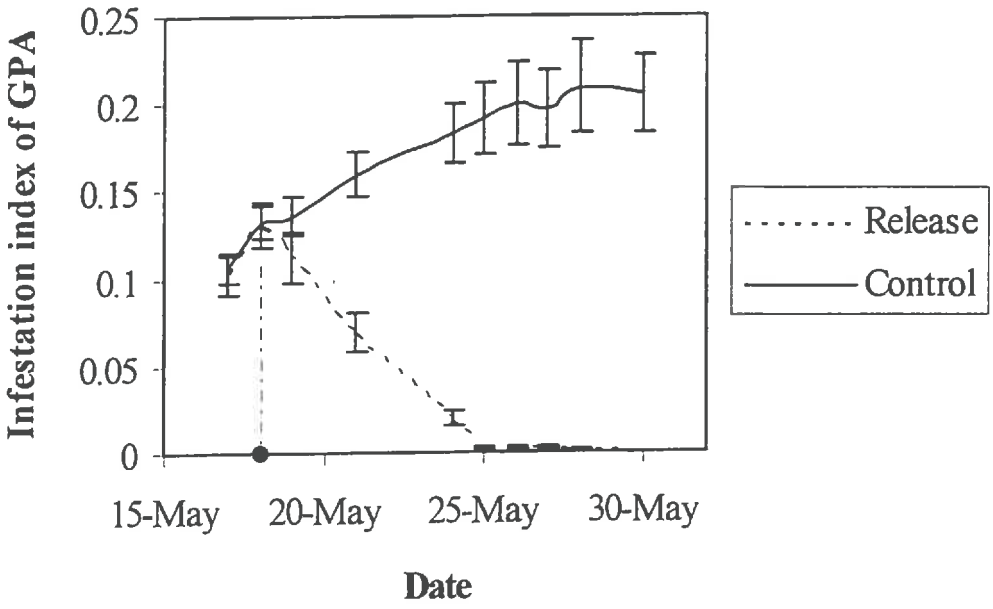

Fig. 6-3 Average of the index of relative infestation (see Eqn. 6-1) of green peach aphids for control (no ladybeetle larvae released) and treatment (50 larvae of *Harmonia axyridis* of the 3rd instar were released on the 18th of May). Error bars are standard errors.

The average per-colony population density of green peach aphids were estimated from the degree of infestation for both control and treatment and plotted against time (Fig. 6-7 a). The observed population changes for both control and treatment were then compared with results from computer simulation using temperature data recorded in one of the cages. The pattern of population change due to the release of the ladybeetle larvae is qualitatively identical for the simulated populations and real populations (Fig. 6-7). The observed population of green peach aphids for the control did not reach as high as the corresponding simulated population (Fig. 6-8 a). The observed declining of aphid population after the release of 3rd instar larvae was much slower than that in the simulation (Fig. 6-8 b), which may partly be owing to the fact that the predator survival rate in the real system is lower than that in the simulation system through most of the course (Fig 6-9). But this is probably not the only cause, since the retardation in the declining of the

aphid population in the real system is more obvious at the beginning (Fig. 6-8 b) when the survival rate of the predator was even higher than that in the simulation (Fig. 6-9).

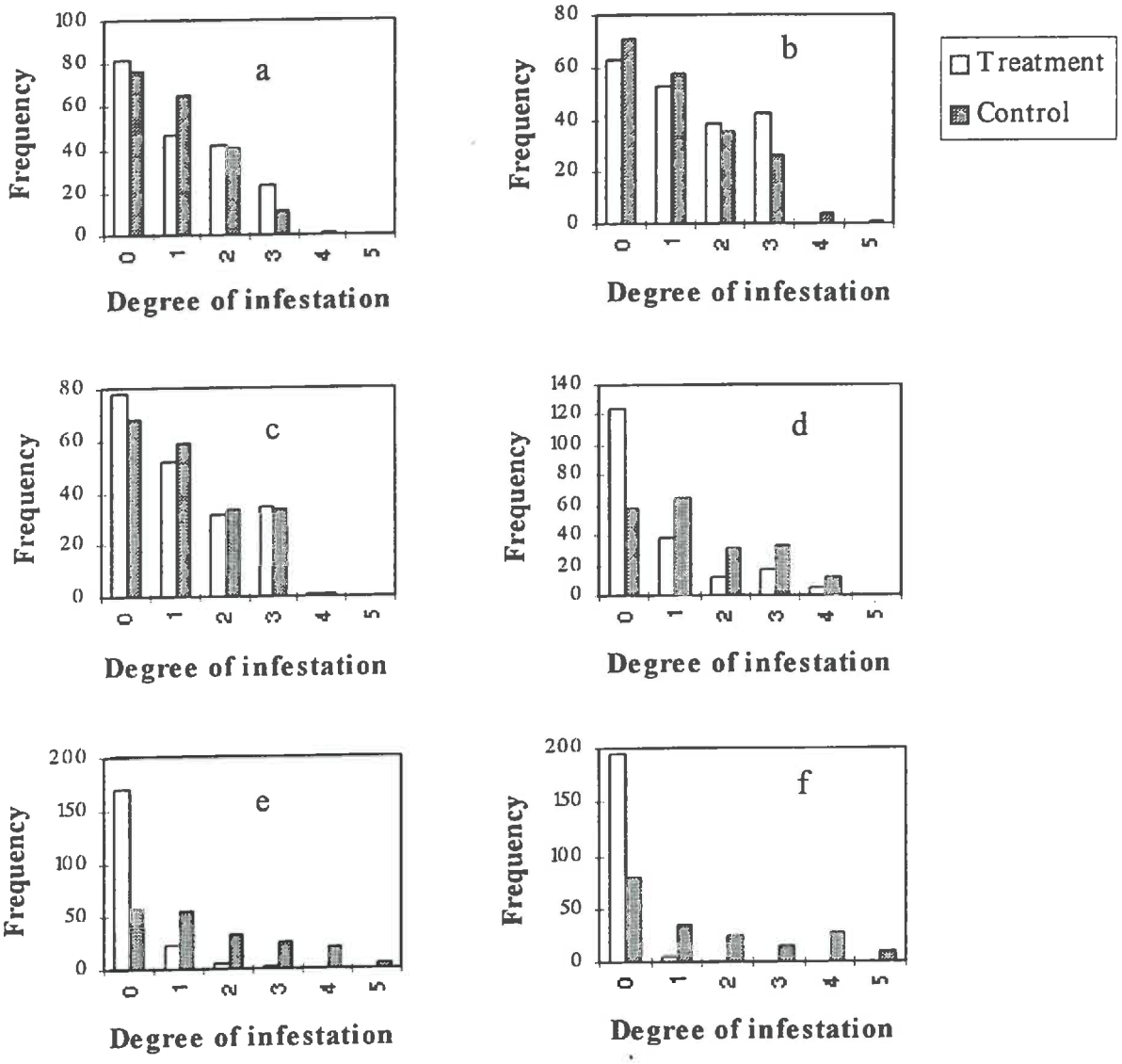

Fig. 6-4 Comparason of frequency of degree of infestation green peach aphids on peach trees with 3rd instar larvae of *Harmonia axyridis* released with that on trees without lady beetle larvae. a: on 17-May; b: on 18-May; c: on 19-May; d: on 21-May; e: on 24-May; f: on 28-May. For the treatment, 50 3rd instar larvae of *Harmonia axyridis* were released on the 18 May.

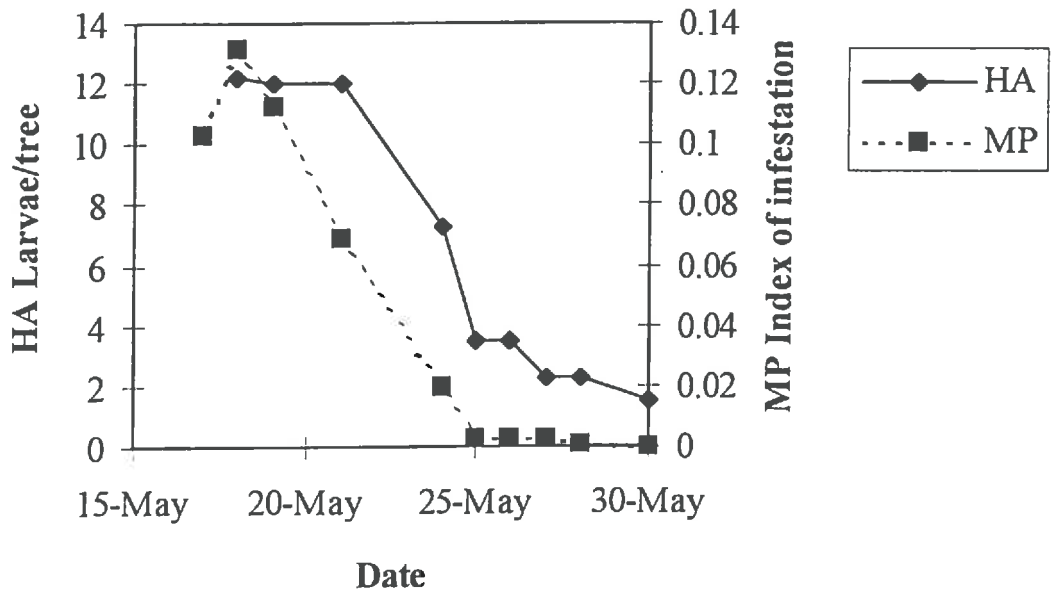

Fig. 6-5 Change in the average number of remaining individuals (the sum of larvae and pupae) of *Harmonia axyridis* (HA) per peach after being released in relation with the declining of population of *Myzus persicae* (MP). Fifty 3rd instar larvae were released onto each tree on the 18 May.

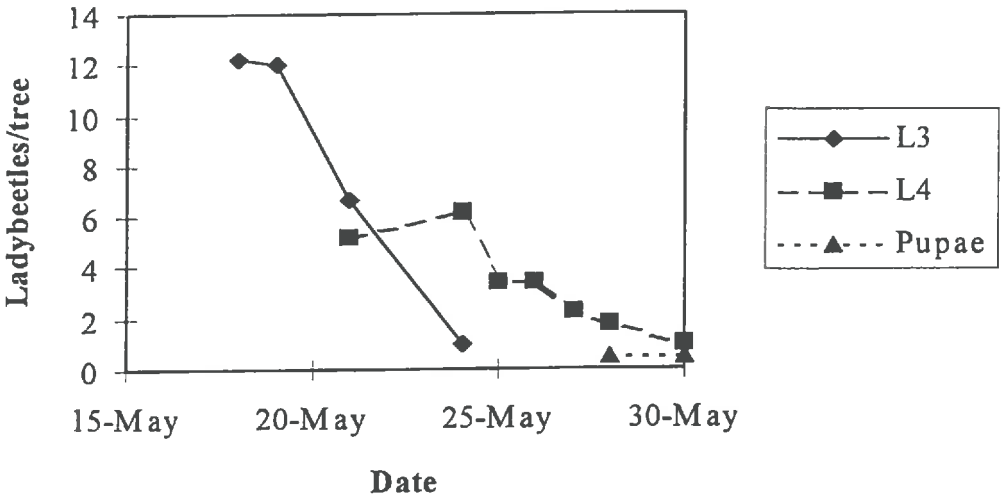

Fig. 6-6 Change in the average number of remaining individuals (including larvae, pupae) of *Harmonia axyridis* (HA) per peach after being released. Showing the succession of the cohort to successive stages. Fifty 3rd instar larvae were released onto each tree on the 18 May.

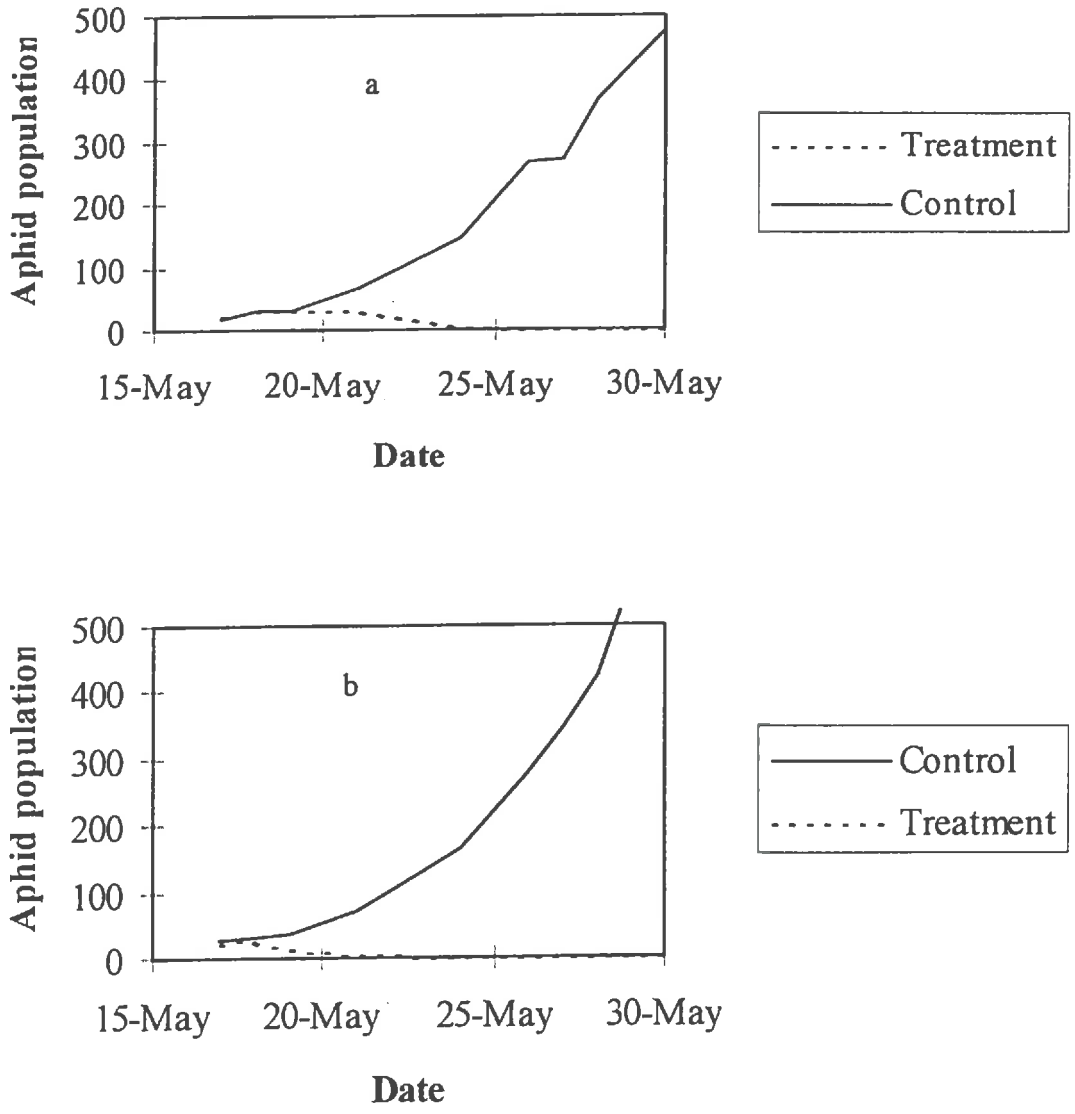

Fig. 6-7 Comparison of the pattern of population change of *Myzus persicae* due to release of larvae of *Harmonia axyridis*. a: observation (50 larvae of 3rd instar released to each tree on the 18 May); b: simulation (0.2 larvae was simulated to be released to each shoot on the same day, coresponding to 50 larvae per tree since there were about 250 new shoots on each tree.).

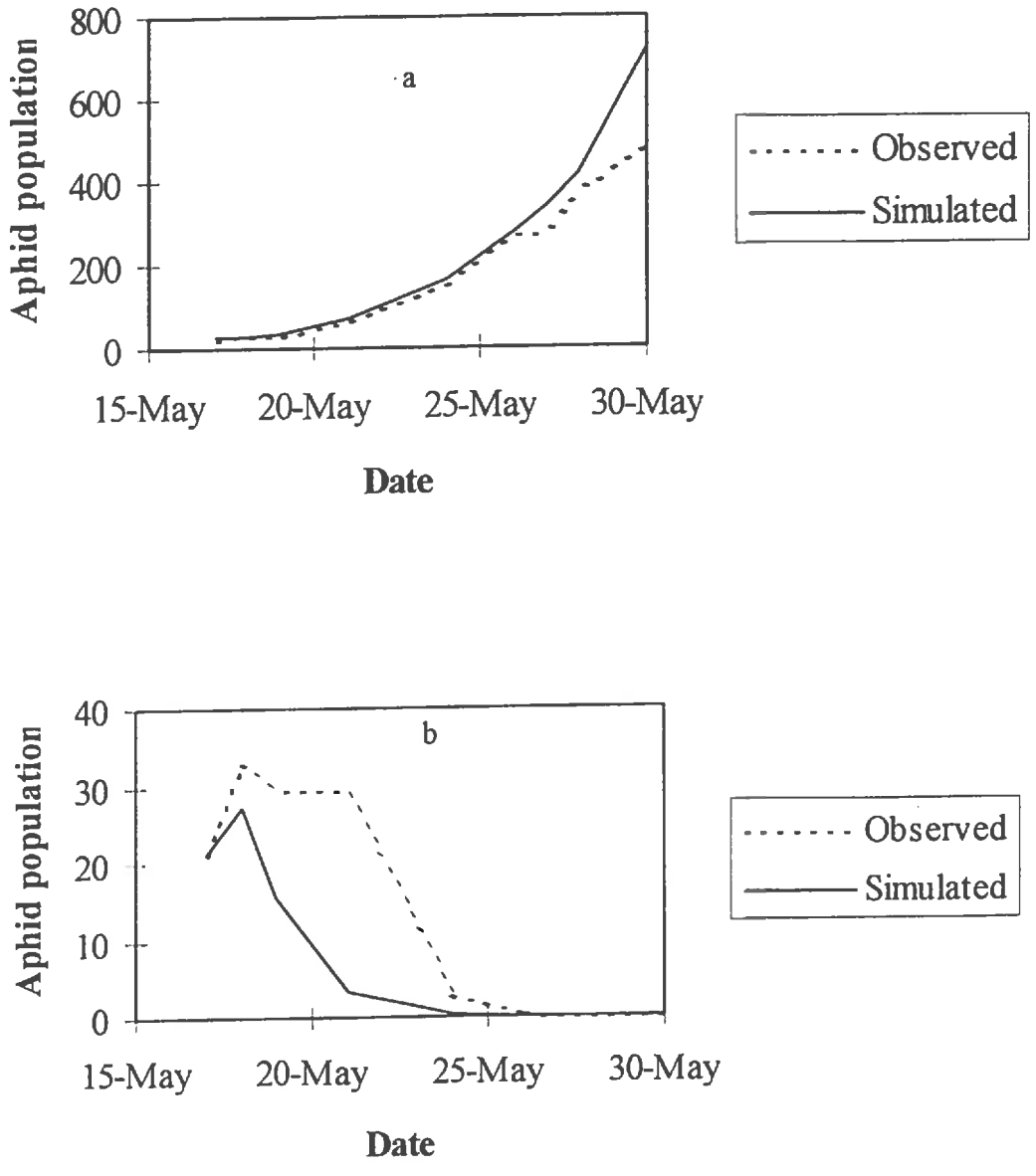

Fig. 6-8. Comparison of population change of *Myzus persicae* in the simulation system with that in the real system. a: Control, no Harmonia axyridis released; b: treatment, 0.2 larvae of 3rd instar/colony were released on the 18 May.

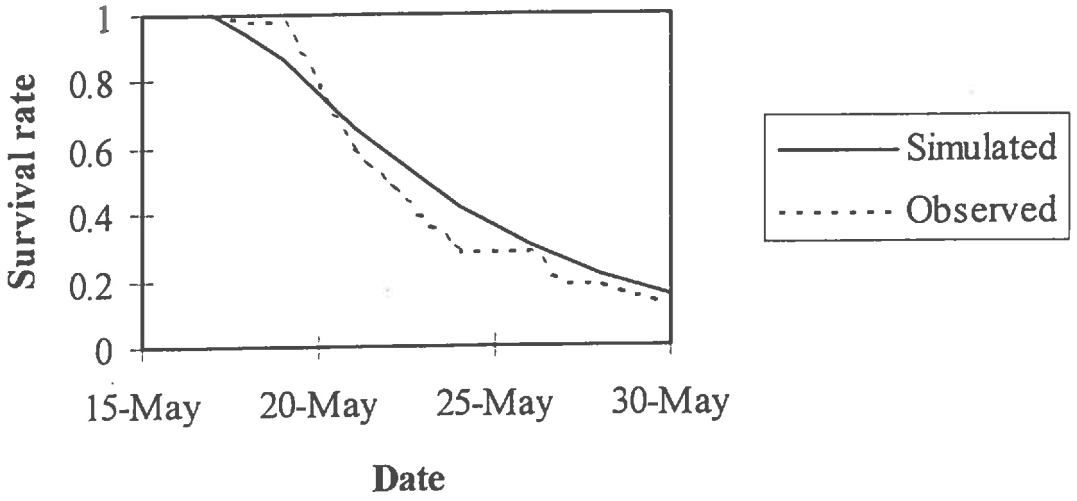

Fig. 6-9. Comparison of change in the number of individuals (the sum of all stages) of *Harmonia axyridis* in the simulation with that in the real system. Release of the predator was carried out on the 18 May.

Conclusion and Discussion

The results from the exclusion experiment showed that a complete depletion of green peach aphids was obtained by releasing 50 third instar larvae and *H. axyridis* at the aphid population level of average 20 aphids/shoot, which is qualitatively coincident with the simulation results. However, the simulation results deviated numerically from the observations to a considerable extent, which shows again that the prediction of the model has only qualitative significance and is meaningful only under certain restricted conditions. The model population of green peach aphids at the absence of *H. axyridis* increased to a much higher level than did the real population. The difference may result from factors limiting the population growth of green peach aphids existing in the real system, such as generalist predators, physiological state of the peach trees, etc. The elimination of aphids is much slower in the real situation than that predicted by the simulation, which may partially be owing to the lower survival rate of the ladybeetle larvae in the real system than

in the simulation, but it is suspected that the major reason may lies in the fact that the ladybeetle larvae must disperse onto the shoots and adapt to the new prey, *M. Persicae*, and may spend a large amount of time traveling around along branches of the tree. That behavioral element was not incorporated into the model. Spatial patchiness and heterogeneity can also result in great deviation of the behavior of the real system from that of the simulation. Even for the best case as was displayed in the results of this chapter, the prediction, even in the qualitative sense, can only be acceptable for short-term time scale, since the deviation may be magnified by orders as time proceeds.

In fact, it will certainly be naive to try to verify a model built mostly upon general biological principles and laboratory experiments by seeking numerical conformities between the model outputs and the trajectories of the field population, since the model system involves much less complexity than the real system. Because of this, here we do not even bother trying to make such numerical comparisons or to claim any credibility for the predictive capacity of this model in predicting field populations. However, a model is useful only if it can reveal at least some properties of the real system or represent, in certain aspects, the characteristics of behaviors of the system. From the results presented above, we can see that the qualitative compatibility of the model output with the behavior of the real system is satisfactory. What was expressed above should not be mistaken as a statement that the validation of a model by comparing the numerical trajectories of the model system with those of the real system is unnecessary or impossible. What is meant here is that delicately designed experiments or observations should be carried out under strictly controlled conditions to test well-defined specific predictions or hypotheses.

Another matter that makes the experiment significant is that the results showed that the ladybeetle larvae reared on eggs of *Ephestia kuehniella* Zeller can indeed get adjusted to their new habitat and food, even though one may argue that this adjustment is the results of being confined within the cage. One critical question is how greater is the probability for a larva dropped on the ground to relocate and get back onto the tree in a cage than that in an open orchard, and whether this probability is sufficiently greater to account fully for the difference between the consequence of releasing the ladybeetle larvae in the cage and that in the open orchard. We may suspect a greater probability for a larvae

dropped on the ground to get back onto the tree, because the larvae were witnessed several times to remount the tree from the sides of the cages which are usually touched by branches of the trees. But the exclusion of general predators of the ladybeetle larvae such as birds by using the cages, may also contribute to the fact that ladybeetle larvae released in the cages wiped green peach aphids while that released in open orchards did not, although a usually much greater number of ladybeetles are released. More experiments need to be carried out concerning this point.

The experiment was carried out in late May, when the aphid population growth rate usually drops down because the peach foliage is becoming less favorable for aphid population growth than that at an earlier time, and a large number of aphids develop into allate forms to move out of the orchard. At this time of the year, naturally occurred enemies of green peach aphids also become more abundant. Under the same condition, the ladybeetle larvae can be very active and voracious. All those contribute to the elimination of the green peach aphids by the ladybeetle. This kind of consequence may have not been obtained if the release was carried out early in the season when the temperature is lower. It will be of great significance to make such an experiment early in the season.

CONCLUDING REMARKS

This study is a part of the research effort on the potential use of *Harmonia axyridis* Pallas for biological control against *Myzus persicae* (Sulz.). Our emphasis is on the evaluation of the effectiveness of *H. axyridis* as a predator of *M. persicae*. Modeling and simulation were used in the attempt to improve the understanding of the basic processes in the predator-prey interactions of this system, and to reveal general qualitative patterns concerning the temperature- and density dependence of the effectiveness of the predator. From the laboratory and field experiments as well as the simulation and analysis of the model system, the following information were extracted:

1. The intrinsic rate of population increase of *M. persicae* augments as temperature increases before a maximum value is attained at 24°C. Then a phase of declining in this value follows. It was also shown that the maximum values for the intrinsic rate of population increase, the developmental rate, the net reproductive rate, and age-specific survival rate, are reached at somewhat different temperatures. The optimal temperature for a maximum survival and net reproduction (20°C) is lower than that for maximum development and population increase (24°C).
2. The number of green peach aphids consumed per individual of *H. axyridis* increases monotonously with prey density following Holling's type II functional response. With a fixed prey density, the prey consumption also increase with temperature until an optimal temperature, beyond which the prey consumption decreases, is reached. The optimal temperature for gaining the maximum prey consumption with a fixed prey density is about 25-27.5°C. Larvae of an older instar are more voracious than those of a younger instar.
3. The developmental rate of larvae of *H. axyridis* augments with the number of prey (green peach aphids) present following a saturation curve - a maximum value is asymptotically approached as the prey density increases. With a fixed prey density, the developmental rate of *H. axyridis* responds to temperature following a typical pattern of developmental response of poikilothermal animals to temperature. The average age-specific daily survival rate of *H. axyridis* increases with prey density following a

sigmoid curve with the asymptote - maximum survival rate being 1. With a fixed prey density, this rate increases with temperature following approximately a saturation curve.

4. Simulation suggested that the effectiveness of young larvae (L1-L3) of *H. axyridis* in eliminating green peach aphids augments as temperature increases, but this pattern does not hold for the 4th instar. From another angle, older instar larvae are always more effective than the younger ones under low temperatures, but this pattern switches to the reverse order at the other end of the effective temperature range, with a series of transition in this patter as temperatures increases within the range of then two extremes.
5. The simulation also suggested that the number of larvae of *H. axyridis* required to eliminate the green peach aphids augments with the aphid population level at which the predator are released, which implies that better results can be obtained by releasing the ladybeetle larvae at a lower prey density.
6. Satisfactory results was obtained in suppressing the population of *M. persicae* using *H. axyridis* by releasing an acceptable number of 3rd instar larvae (50 larvae/tree) at an aphids density of average 20 aphids/shoot. Simulation run with temperature data recorded during the experiment generates results qualitatively consistent with the observation. But the cause underlying the failure of most of the release trials in open-air orchards is not explained by anything from the exclusion experiment as well as the simulation.

The overall evaluation of the potentials of using *H. axyridis* for the biological control of green peach aphids is not conclusive before the economic cost of releasing such coccinellid and the tolerance level to green peach aphid infestation are defined. However, it appears that the inundative release of this coccinellid is unlikely to be used singly for controlling green peach aphids, at least not so for controlling the aphids in commercial gardens, based on the following facts: 1) *H. axyridis* is not very effective under low temperatures, and thus the green peach aphids that appear early in the Spring cannot be controlled very quickly by releasing an feasible number of the predator. 2) the tolerance level for green peach aphids is perceived to be low at present time, so a quick and ensured

depletion of aphids is usually desired. At the present time, this predator may be usede in backyard gardens or as an alternate method to be incorporated into an integrated pest management program, for example, using pesticide spray at the early season, and release the ladybeetle when the aphids resurge later under a higher temperature, so as to minimize the use of spray which may conflict with the integrated control of the other orchard pests, and as a consequence, to reduce the development of pesticide resistance of green peach aphids.

As was emphasized in earlier chapters, the model prediction in Chapter 5 and Chapter 6 has mainly qualitative implication, it should not be surprised if a considerable quantitative deviation from the observation appeared. In fact, it is not our main purpose to build a quantitative predictive model, because it requires more empirical data, which are not available, and by gaining quantitative preciseness and predictability of specific processes, the model's ability in revealing general explanatory, qualitative patterns or properties may be sacrificed. However, this model can serve as a framework for more realistic models. The most required elements to enhance the realism of the model are probably the behavior of *H. axyridis* in responding spatial patchiness and heterogeneity and the mortality of both the predator and aphids due to generalist predators and other non-random events.

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VERSION FRANÇAISE

EFFICACITE DE *HARMONIA AXYRIDIS* (COLEOPTERA: COCCINELLIDAE) COMME AGENT DE LUTTE BIOLOGIQUE CONTRE *MYZUS PERSICAE* (HOMOPTERA: APHIDIDAE).

CHAPITRE 1
DEFINITION DU SYSTEME ET DE L'APPROCHE

LE SYSTEME

LE PUCERON VERT DU PECHER

Le puceron vert du pêcher (*Myzus persicae* Sulzer) est une espèce cosmopolite. Elle est remarquable par sa distribution et la diversité des plante-hôte (Van Emden, et al. 1969). En tant que ravageur des cultures, le puceron vert du pêcher cause non seulement des dommages directs mais peut aussi transmettre plus de 100 maladies virales sur environ trente familles végétales différentes dont beaucoup de cultures importantes.

Dans le Sud de la France, *M. persicae* est un ravageur clé des vergers de pêchers. Ses attaques sur fleurs et bourgeons dès le printemps et son fort potentiel de reproduction favorise des infestations abondantes qui déprécient la qualité des fruits, réduisent la production et affaiblissent les arbres. Une autre conséquence de la présence de cette espèce est la vection de la Sharka, maladie virale des pêchers en Europe, qui a détruit quelques vergers commerciaux et demeure la principale menace pour la production de pêches.

Peu d'approches autres que la lutte chimique permettent une maîtrise satisfaisante des populations de *M. persicae*. L'utilisation exclusive des méthodes chimiques pour prévenir son extension a induit une résistance de cette espèce à plusieurs familles de pesticides, ce qui a souvent conduit à une utilisation plus fréquente et plus intensive des pesticides. La protection intégrée contre les autres ravageurs des vergers s'en est trouvée affectée de même que l'environnement des régions productrices de pêches.

Des méthodes de lutte nouvelles et sans danger pour l'environnement sont à mettre au point, prenant en compte l'utilisation de la résistance variétale des pêchers et la lutte biologique par utilisation des ennemis naturels. Des recherches sont initiées dans ce sens à la Station de Recherche de Zoologie de INRA d'Avignon. C'est dans ce contexte que cette étude a été entreprise.

HARMONIA AXYRIDIS

Harmonia axyridis Pallas est un coccinellidé prédateur originaire de l'Est de l'Asie. C'est une espèce à large distribution et prédatrice de nombreuses espèces de pucerons. Elle a fait l'objet d'études extensives au Japon, en Chine et en Russie pour la lutte biologique par la sauvegarde et la mise en

valeur de ses populations naturelles ou par lâchers. Les recherches ont porté sur la biologie, l'écologie, la physiologie, la biologie des populations, les besoins nutritionnels et l'élevage de masse en laboratoire, ainsi que sur les techniques d'application. Aux U.S.A., cette espèce a été introduite pour le contrôle d'espèces variées, dont principalement les pucerons et les cochenilles. Des populations indigènes ont également été découvertes dans plusieurs localités de l'Amérique du Nord. Un exemple réussi de l'utilisation de cette coccinelle comme espèce exotique pour la lutte biologique classique a été son introduction aux USA pour lutter contre le puceron du pacanier. Le succès de cette introduction fut tel que dans des régions comme le Kentucky ou la Géorgie, cette espèce de puceron n'est plus considérée comme un ennemi majeur.

H. axyridis a été introduit en France au début des années 1980 par le Laboratoire de Biologie des Invertébrés de l'INRA d'Antibes, comme agent potentiel de lutte biologique. Les aspects fondamentaux de la biologie, de l'écologie et du comportement ont été étudiés en détail (Schandler & Ferran 1985, 1988). Les techniques d'élevage de masse à partir d'œufs d'*Ephestia* ont été développées permettant la production commerciale. Des études de laboratoire et de terrain ont été conduites sur les possibilités d'utilisation de cette espèce pour lutter contre divers ravageurs, principalement les pucerons, de nombreuses cultures. Un effort a été fait pour tenter d'utiliser cette coccinelle que ce soit par la lutte biologique classique ou par des lâchers abondants. Cependant, à ce jour, nous n'avons connaissance d'aucun document ou démonstration manifeste prouvant le succès substantiel de l'utilisation de cette coccinelle dans la lutte contre les insectes ravageurs en France. Des études plus détaillées sur l'évaluation de son efficacité en tant qu'agent potentiel de lutte biologique contre différents ravageurs devraient être entreprises avant qu'une conclusion valable ne soit formulée sur l'utilité potentielle de cette espèce comme agent de lutte biologique en France. La présente étude portera plus particulièrement sur l'évaluation de l'efficacité d'*H. axyridis* comme agent de lutte biologique, par lâchers inondatifs, contre le puceron vert du pêcher.

L'APPROCHE

EVALUATION DE L'EFFICACITE DU PREDATEUR

Dans la lutte biologique utilisant des lâchers inondatifs de prédateur, le prédateur n'est habituellement pas destiné à être introduit en tant qu'agent régulateur à long terme de la population de ravageurs, mais plutôt en tant qu'agent de suppression temporaire. Donc la dynamique à long terme du prédateur et de la proie n'est pas d'un grand intérêt pour l'évaluation de l'efficacité du prédateur. La mesure de l'efficacité d'un prédateur utilisé dans la lutte biologique par lâchers inondatifs peut être réalisée selon différentes approches ou associations. Dans le cas de lâchers tentés directement sur le terrain, les résultats obtenus à partir d'échantillonnage seront des indications de cause à effet plutôt que des preuves flagrantes.

Comme alternative, des tables de vie peuvent être établies pour les populations du ravageur et du prédateur lâché en conditions naturelles ou semi contrôlées pour évaluer l'impact du prédateur sur l'évolution démographique du ravageur. Dans ce cas, une surveillance intensive des colonies de pucerons marqués, éventuellement sur plantes ou parties de plantes encagées avec/sans prédateur atteste plus formellement de l'impact du prédateur sur les populations du ravageur. En troisième alternative des populations peuvent être manipulées en laboratoire ou en conditions extérieures strictement contrôlées par des techniques d'exclusion pour déterminer les relations quantitatives pour déterminer les composantes variables majeures du système ; le système est habituellement bien défini et des composantes facilement mesurables et contribuant fortement au comportement du système sont identifiées au sein d'interactions complexes ; les relations mesurées entre les variables constitutives sont synthétisées par un modèle. La première approche est techniquement simple, mais économiquement coûteuse et écologiquement dangereuse si l'essai doit être conduit à très grande échelle en incluant plusieurs options de lâcher ; les résultats de l'évaluation d'efficacité de cette méthode sont directement liés à la situation réelle en pratique, mais permettent peu l'interprétation des conséquences (succès ou échec) du lâcher. La deuxième approche indique clairement l'effet de l'introduction de prédateurs sur la population proie dans un environnement expérimental particulier, mais les résultats dépendent souvent de la situation particulière et ne peuvent être généralisés, de telles expérimentations rencontrant fréquemment des contraintes techniques fortes et étant limitées dans le temps et l'espace. La troisième approche peut permettre l'accumulation d'un grand nombre d'informations concernant les relations quantitatives entre les différentes variables, ce qui est très utile pour répondre à des questions spécifiques telles que "La température est-elle un facteur clé pour l'efficacité du prédateur ?". Les données recueillies par cette méthode peuvent être considérées comme plus générales que celles obtenues d'après les deux précédentes approches, puisque habituellement obtenues sous "conditions idéales" transposables à (presque) toutes les situations. Quelques facteurs spécifiques du système ou de la situation, pouvant ne pas être considérés dans un premier temps, peuvent l'être par la suite selon la nécessité. Cette approche dont le coût est moindre permet souvent une meilleure interprétation des phénomènes observés, ce qui est souvent très utile aux recherches sur le développement des stratégies d'utilisation d'un prédateur comme agent de lutte biologique, et peut conforter la théorie générale de la lutte biologique. Elle présente un défaut qui découle de sa vocation générale, à savoir un moindre réalisme que les deux autres approches, nombre d'éléments considérés comme moins fondamentaux n'étant pas pris en compte dans le modèle. L'utilisation d'une seule approche impose des contraintes et des limitations. Chaque approche est en fait plus appropriée pour répondre à un type de question, pour être utilisée dans telle situation ou à telle étape du projet de recherche. Elles sont plus complémentaires que concurrentes, l'approche modélisation pouvant générer des hypothèses validées ultérieurement par les autres approches. Les lâchers sur le terrain permettront une appréciation finale de l'efficacité du prédateur en conditions naturelles. Les information données par les tables de vie ou le modèle permettent généralement d'éliminer des options de lâcher qui pourraient être retenues bien que sans intérêt, et mieux définir les problèmes posés, ou d'expliciter plus clairement les options à vérifier par les lâchers de terrain.

L'intégration des 3 approches a été adoptée par l'équipe de recherche de la Station de Zoologie de l'INRA d'Avignon. Cette thèse traitera seulement de la partie de l'étude concernant l'approche modélisation. Seront considérées plus particulièrement les capacités de *H. axyridis* comme agent de contrôle biologique contre le puceron vert du pêcher par lâchers inondatifs, en terme de pression potentielle exercée par le prédateur sur le potentiel de croissance de la population d'aphides, chaque population étant réciproquement modifiée par l'autre et par la température.

Le potentiel de croissance des populations de pucerons est représenté par le taux intrinsèque d'accroissement de population, fonction de la température et est soumis à l'effet de la compétition intra-spécifique. Le potentiel de pression prédatrice est exprimé comme indice global du taux d'attaque, de survie et de développement de la coccinelle. Ces éléments sont intégrés dans un modèle pouvant servir à poser ou répondre à des questions quant à l'efficacité de la coccinelle comme prédateur du puceron, ou quant à la gamme de températures permettant l'expression du potentiel de prédation de la coccinelle sur le puceron vert.

APPROCHE DU MODELE DE POPULATION

Un modèle est une construction intellectuelle ou analogue artificiel d'un système physique. Le but de la modélisation d'un système est toujours d'obtenir une représentation de ses éléments constitutifs les plus importants. Le modèle, plus facile à appréhender, sera utilisé en lieu et place du système pour certaines études. C'est dans ce sens qu'une copie parfaite du système est non seulement impossible mais également non nécessaire. De ce fait des simplifications considérables sont toujours requises, un analogue exact du système étant aussi difficile à comprendre et se comportant aussi lentement que le système original.

Différentes approches de la modélisation de la dynamique des populations (qu'il s'agisse d'une espèce seule ou d'un système pluri spécifique) peuvent être distinguées. On distingue tout d'abord les modèles analytiques et les modèles de simulation.

Les modèles analytiques mettent en jeu un nombre limité de variables et de paramètres. Les relations entre les variables y sont mathématiquement explicitées de manière à ce que le modèle soit assez simple pour être utilisable.

Les modèles de simulation peuvent intégrer un grand nombre de variables et de paramètres. Les relations entre variables n'ont pas besoin d'être mathématiquement explicitées, mais peuvent être intégrées implicitement dans l'algorithme du programme informatique.

En fait presqu'aucun modèle ne s'insère parfaitement dans aucune des catégories. La plupart des modèles de simulation utilisent comme cadre des modèles analytiques, et les modèles analytiques nécessitent également l'intégration de techniques de simulation. La distinction entre modèle analytique

et modèle de simulation n'est donc pas toujours très pertinente pour la modélisation d'un système particulier. Il peut être plus utile de caractériser un modèle par sa construction. Un modèle peut être obtenu en ajustant le développement de population à des modèles théoriques simples basés sur des principes biologiques et écologiques fondamentaux. Le modèle peut également être construit directement à partir d'observations ou dérivé d'un ajustement du comportement du système.

Pour la première approche, des séries chronologiques adéquates doivent être compilées et collectées, et le modèle et le système lui-même doivent être assez simples pour être analysables statistiquement. Cette méthode requiert des séries chronologiques stationnaires, ou au moins transformables en séries stationnaires, pour permettre l'étude de changements macroscopiques à long terme des populations sur des pas de temps d'une année. Elle est d'un intérêt limité pour l'étude de changements microscopiques des populations, de populations à fortes variations saisonnières ou soumises à de violentes perturbations, comme chez la plupart des insectes ravageurs.

Pour la seconde approche, le système est structuré pour refléter certains détails biologiques. Il peut être décomposé en sous-unités à plus faible niveau d'organisation et à échelle de temps généralement plus courte. Les paramètres sont dans ce cas biologiquement explicites et peuvent être mesurés directement ou estimés à partir d'autres quantités. Ce type de modèle est comparativement plus simple à construire mais ne permet généralement pas d'expliquer le comportement à long terme d'un système en raison de l'intervention de plusieurs niveaux d'organisation et de différentes échelles de temps et d'espace. Il doit pour cela être utilisé plus spécifiquement sur des échelles limitées, qui constitueront le contexte de notre étude.

Les modèles peuvent également être classés selon leur complexité. Les modèles généralistes à large échelle étaient développés dans les années 70 et au début des années 80. Destinés à une compréhension générale du système, ils incorporaient un très grand nombre de paramètres et de nombreuses interactions. Ils sont apparus plus difficiles à comprendre et à manipuler que les systèmes réels et sont d'un intérêt limité. La tendance actuelle est de revenir à des modèles à objectifs spécifiques caractérisés par un nombre minimum de paramètres.

Notre étude se replace dans une approche de modélisation d'un objectif très spécifique - évaluer l'efficacité de *H. axyridis* comme prédateur de *M. persicae* - ne conservant que les éléments les plus importants.

Trois composants majeurs seront incorporés dans le modèle : le taux d'accroissement des populations de *M. persicae* en fonction de la température, la réponse fonctionnelle de *H. axyridis* à *M. persicae* en fonction de la température, et les taux de survie et de développement de *H. axyridis* en fonction de la température. Ces éléments seront couplés à un modèle de simulation de dynamique.

OBJECTIFS

Il y a deux raisons principales à la modélisation de l'efficacité de *H. axyridis* comme agent de contrôle biologique contre *M. persicae* :

1°/ Un modèle peut servir à identifier les facteurs clés qui déterminent l'efficacité du prédateur, à améliorer notre compréhension des conséquences, à diriger et à affiner l'évaluation des essais de lâchers aux champs.

2°/ Le modèle peut fournir une trame pour le suivi des différentes phases de recherches, pour développer des stratégies de lutte et des outils de prise de décision. Même si le prédateur s'avère insuffisamment performant contre *M. persicae*, le modèle peut être utilisé pour prédire le type d'ennemi naturel qui sera le meilleur agent de lutte potentiel.

L'objectif de l'étude est d'utiliser la modélisation pour évaluer le potentiel de *H. axyridis* comme prédateur de *M. persicae* dans les limites du potentiel de développement de la proie, de la faculté de prospection du prédateur, du maintien du prédateur en fonction de l'abondance de la proie, de la dépendance de ces aspects vis-à-vis de la température, et de fournir des directives pour des évaluations ultérieures en plein champ.

CHAPITRE 2
INFLUENCE DE LA TEMPERATURE SUR LA DEMOGRAPHIE ET LE TAUX DE CROISSANCE INTRINSEQUE DE *MYZUS PERSICAE* (SULZER)

INTRODUCTION

Dans le contexte du développement de stratégies rationnelles pour contrôler *M. persicae* en vergers de pêchers, et en particulier pour évaluer l'efficacité des ennemis naturels, une bonne connaissance de la dynamique de population des pucerons est indispensable. La réalisation de cet objectif requiert l'utilisation de modèles, dont le plus fréquemment utilisé dans la description de la croissance des populations de pucerons est le taux de croissance intrinsèque (r_m). Il inclut des variables constitutives telles que le taux de développement des stades immatures, la fécondité en fonction de l'âge et le taux de survie des stades immatures et adultes (Dixon 1987). Ces variables peuvent être mesurées en établissant les tables de vie des pucerons en conditions spécifiques. Le taux de croissance intrinsèque peut être modifié par la qualité de nutrition, la température, la compétition intraspécifique, la détermination des morphes, etc. (Frazer, 1987). Dans cette étude, nous ne prendrons pas en compte la qualité de nutrition, qui peut dépendre principalement de variations saisonnières chez la plante-hôte. Depuis les premières éclosions en mars en vergers de pêchers, jusqu'en mai, où les pucerons commencent à quitter les pêchers, les pucerons colonisent principalement des pousses en croissance. Cette phase de croissance des populations de *M. persicae* s'effectue donc probablement sur un milieu qui reste favorable. L'effet de la détermination des morphes ne sera pas pris en compte du fait de l'étude exclusive de générations parthénogénétiques de printemps sur pêchers. Les effets de la compétition intraspécifique peuvent être pris en compte en incorporant la valeur de la densité maximum dans le modèle. Pour notre étude, l'effet de la température sur le taux de croissance intrinsèque de la population est d'un intérêt primordial. Les températures ont en effet une tendance saisonnière régulière et de fortes variations aux champs. Elles ont été identifiées comme principal facteur de changement dans l'accroissement des populations de pucerons, ainsi que dans les réponses fonctionnelles et numériques des prédateurs.

Les taux de croissance intrinsèques des populations de *M. persicae* ont été calculés sur des hôtes secondaires de cette espèce tels que la pomme de terre (Barlow, 1962) et le chou (Deloach, 1974), mais n'ont fait l'objet d'aucune étude sur pêchers.

Notre objectif est de mesurer ce taux de croissance intrinsèque chez *M. persicae* et ses variations en fonction de la température, en conditions de laboratoire. Sa connaissance est requise pour établir des

modèles d'évaluation des facteurs de modification extrinsèques de la dynamique de population de *M. persicae*, tels que la prédation ou la résistance variétale de la plante-hôte.

MATERIEL ET METHODES

L'expérimentation est conduite en laboratoire sur des jeunes plants de pêchers (stade 15-20 feuilles, issus de semis de la variété GF 305) servant de plante-hôte aux pucerons. Les colonies de femelles parthénogénétiques vivipares de *M. persicae* proviennent de fondatrices prélevées en mars 1992 dans le verger expérimental de l'INRA de Montfavet. Elles sont maintenues en élevage en chambre climatisée à la température de 21±0,5°C, humidité relative de 60% et photopériode naturelle. L'infestation de chaque plant pour l'expérimentation est réalisée par dépôt d'une femelle adulte pour la production de jeunes larves. Ces adultes et les larves excédentaires sont retirés au bout de quatre heures, une seule jeune larve étant laissée sur chaque plant. Le développement des insectes est suivi dans des cellules incubatrices à 12.5, 16, 20, 24, 26, 27.5 ou 30°C, à raison de 20 répétitions par température. Les mues, la mortalité, et la production de nouvelles larves par les adultes sont enregistrées journellement.

Ces données démographiques pour chaque température sont utilisées pour la réalisation de tables de vie. La durée moyenne de développement de chaque stade larvaire, le taux de survie par âge et le taux de reproduction par âge sont calculés. La durée moyenne de développement et la fécondité journalière moyenne sont estimées en utilisant des moyennes arithmétiques.
Le taux moyen de développement utilisé ici est calculé selon la formule:

$$d = \frac{n}{\sum_{i=1}^{n} D_i} \qquad (2\text{-}1)$$

où d est le taux moyen de développement, n la taille de l'échantillon, D_i's les durées de développement observées (en jours).
Le taux de survie âge spécifique est calculé comme suit :

$$l_x = \frac{N_x}{N_{x-1}} \qquad (2\text{-}2)$$

où l_x est le taux de survie âge spécifique du jour x, N_x et N_{x-1} les nombres de pucerons survivants aux jours x-1 et x.

Le taux intrinsèque d'accroissement de la population r_m, est un paramètre qui synthétise le taux de développement, le taux de survie et la fécondité du puceron vert du pêcher. Il est calculé à partir des tables de vie en utilisant l'approximation de Birch :

$$\sum_x e^{-r_m}.x.l_x.m_x = 1 \qquad (2\text{-}3)$$

où r_m est le taux intrinsèque d'accroissement de la population; x l'âge en jours; l_x le taux de survie âge spécifique; m_x le taux de reproduction âge spécifique.

Le r_m est estimé par maximum de vraisemblance. Les deux modèles de Logan (1976) sont ajustés sur les données reliant le taux de développement et la température d'une part, le taux d'accroissement intrinsèque de la population et la température d'autre part. Le modèle d'expansion exponentielle est exprimé par :

$$D(T) = \psi[\, e^{\rho T} - e^{\rho T_m - \frac{T_m - T}{\Delta T}}\,] \qquad (2\text{-}4)$$

où $D(T)$ est le taux étudié en fonction de la température; T la température (en°C); ψ est défini par Logan comme le taux du processus étudié à une température de base déterminée; ρ correspond à une valeur critique associée aux réactions biochimiques catalysées par les enzymes ; T_m la température maximale (en °C) au dessus de la température de base du processus de vie; ΔT la largeur de la marge limite supérieure de température.

Le dernier modèle est le modèle d'expansion sigmoïde:

$$D(T) = \alpha\{\,[1 + ke^{-\rho T}\,]^{-1} - e^{-\frac{T_m - T}{\Delta T}}\,\} \qquad (2\text{-}5)$$

où α est une constante représentant la vitesse de décroissance du taux du processus étudié à T_m; $\kappa = (\alpha - \psi)/\psi$; $d(T)$, ρ, T_m et ΔT ont la même signification que ci - dessus. Une méthode de quasi-Newton est utilisée dans les deux cas.

RESULTATS

Taux de développement des stades immatures. Dans le cadre des températures étudiées, le taux de développement le plus élevé des larves parthénogénétiques de *M. persicae* est atteint à 24°C avec une durée de développement de 5,33 ± 0,14 jours. En dessous de cette température, le taux de croissance décroît avec la température, le développement larvaire nécessitant 15,17 ± 0,17 jours à la

température de 12,5°C. La durée de développement s'accroît également au-dessus de 24°C (16,67 ± 0,14 jours à 27,5°C). A 30°C les 20 pucerons meurent avant la fin du deuxième stade larvaire (Tableau 2-1). La relation entre températures et taux de développement des stades immatures est bien ajustée à l'équation de Logan (Fig. 2-1). Le seuil supérieur de développement de *M. persicae* est estimé à 29,48°C, la marge supérieure de température ΔT de 5,3700°C (Tableau 2-2) et la température à laquelle le taux de développement maximal est atteint à 24,0981°C.

Fécondité des femelles parthénogénétiques. Elle est décrite en termes de fécondité totale et de profil de fécondité par âge. Elle s'accroît avec la température jusqu'à 20°C, puis décroît rapidement lorsque la température s'élève (Fig. 2-2, Tableau 2-1). A température élevée, la reproduction se concentre pendant les premiers jours de vie des adultes (Fig. 2-3). Jusqu'à la température optimale de 24°C, l'augmentation de la température se traduit par un raccourcissement de la période de reproduction et par une augmentation du pic de fécondité. Au-delà de 24°C, l'augmentation de la température entraîne toujours un raccourcissement de la période de reproduction mais la valeur du pic de fécondité décroît.

Taux de survie par âge. La durée de développement de *M. persicae* diminue lorsque la température augmente (Fig. 2-4). Aux températures basses, la mortalité intervient majoritairement au stade adulte, contrairement aux températures élevées où de fortes mortalités sont enregistrées sur stades larvaires.

Taux de croissance intrinsèque des populations. La relation entre le taux de croissance intrinsèque r_m et la température est analogue à celle qui relie taux de développement et température. La valeur la plus élevée du r_m est observée à 24°C (r_m = 0,3744). En dessous de 24°C, la valeur de r_m augmente avec la température et au-delà, elle décroît très rapidement lorsque la température augmente. Le seuil maximum de température pour un accroissement non-négatif de la population est estimé à 27,92°C, température inférieure au seuil maximum de développement larvaire. En conséquence la largeur de la marge supérieure de température est plus faible pour r_m que pour le développement larvaire (Tableau 2-2).

La température procurant le plus fort taux d'accroissement intrinsèque est estimée à 23,79°C. En comparaison, le taux net de reproduction qui représente la multiplication de la population par génération atteint son maximum (82,15 par génération) à 20°C (Tableau 2-2). Un autre paramètre utile pour la compréhension de la dynamique de population est la durée moyenne d'une génération. Elle est la plus courte (10,81 jours) à 24°C et s'accroît lorsque la température diminue. Le temps de doublement de la population est un indice plus immédiat pour estimer la vitesse de développement de population. Il est inférieur à 2 jours à 24°C, et s'établit respectivement à 4.8, 3.5, 3.1 et 2.1 jours à 12.5, 16, 18, 20°C.

Discussion

La race locale de *M. persicae* étudiée à Montfavet présente une adaptation à basse température sur son hôte primaire. Son taux de développement le plus élevé est atteint à 24°C et son développement ne peut s'achever à 30°, ce qui est conforme aux résultats obtenus par Barlow sur betterave.

La fécondité des femelles vivipares atteint son maximum (80 larves par femelle, Van Emden et al., 1969) à des températures inférieures à 20°C et décline au-delà de cette température. Un fort taux de reproduction journalier est cependant atteint en dessous de 24°, la reproduction des femelles étant alors plus concentrée dans le temps (Fig 4-3).

Le taux de survie par âge de *M. persicae* en fonction de la température est proche de celui de *Rhopalosiphum padi* L. (Leather, 1980). Les basses températures procurent à *M. persicae* une plus grande longévité et un plus fort taux de survie aux stades immatures et chez les adultes jeunes que les températures élevées.

Le taux de croissance intrinsèque est également optimal à 24°C mais l'effet limitant des températures sur la croissance des populations est moins fort qu'il ne l'est sur le développement individuel. Cette différence est également exprimée par une valeur plus forte de DT pour la croissance de la population que pour le taux de développement (Tableau 2-3). Barlow (1962) et De Loach (1974) étudièrent le taux de croissance intrinsèque de *M. persicae* sur betteraves et pommes de terre respectivement. La température optimale qu'ils établissent à 25°C pour le taux de croissance intrinsèque est plus élevée que celle que nous observons (24°C) ou que nous calculons (23,79°C). La différence peut provenir de l'effet de la plante-hôte ou de la variabilité entre races géographiques de *M. persicae*.

CHAPITRE 3

REPONSE FONCTIONNELLE TEMPERATURE DEPENDANTE DE *HARMONIA AXYRIDIS* PALLAS A *MYZUS PERSICAE* SULZER.

INTRODUCTION

L'évaluation de l'efficacité de *H. axyridis* comme agent de contrôle biologique de *M. persicae* et la détermination des stratégies de lâchers requièrent des informations sur l'efficacité du prédateur en relation avec la densité de proie et les températures environnantes. La réponse fonctionnelle décrit la relation entre le nombre de proies attaquées par prédateur par unité de temps de recherche et la densité de proie imposée au prédateur. Trois principaux types de réponses fonctionnelles ont été reconnus parmi lesquels la réponse de type II est la plus utilisée pour modéliser la prédation des invertébrés. L'équation de Holling fournit la description la plus courante de la réponse de type II :

$$N_a = \frac{a.N}{1+a.Th.N} \qquad (3\text{-}1)$$

où N est le nombre de proies imposées au prédateur, Na le nombre de proies consommées par unité de temps de recherche, a le taux d'attaque instantané du prédateur, et Th le temps nécessaire à l'ingestion et à la digestion d'une proie.

Organismes poïkilothermes, les insectes ont un métabolisme dépendant des conditions thermiques. *M. persicae* est apparu bien adapté aux basses températures en terme de taux de croissance de population. Les informations sur la liaison entre température et efficacité prédatrice et taux de développement de *H. axyridis* sont fondamentales pour l'évaluation de cette espèce comme agent de lutte biologique. Un modèle général de réponse fonctionnelle liée à la température incorpore à la réponse de type II de Holling les équations de cinétique enzymatique utilisées pour décrire la relation entre température et croissance ou développement. Ce modèle, que nous utiliserons, décrit le taux d'attaque instantanée a et le temps de prédation Th comme fonctions de la température :

$$a(T) = \frac{u_1.T.e^{-\frac{u_2}{T}}}{1+u_3.e^{-\frac{u_4}{T}}} \qquad (3\text{-}2a)$$

$$Th(T) = \frac{1+v_1.e^{-\frac{v_2}{T}}}{v_3.T.e^{-\frac{v_4}{T}}} \qquad (3\text{-}2b)$$

Ce chapitre décrit la réponse fonctionnelle de *H. axyridis* à *M. persicae* en fonction de la température, et nous essayons de modéliser le taux d'attaque instantané et le temps de prédation en fonction de la température selon l'équation 3-2 a,b.

MATERIELS ET METHODES

Les larves de *H. axyridis* sont produites dans un élevage de masse au Laboratoire de Biologie des Invertébrés d'Antibes, et *M. persicae* provient des élevages conduits sur plants de pêchers au Laboratoire d'Avignon. Les observations sont réalisées dans des enceintes en plastique de 80 mm de diamètre et 50 mm de haut, contenant chacune trois jeunes feuilles de pêchers alimentées par une solution nutritive. Des aptères du 3-4ème stade de *M. persicae* sont introduits tous les soirs dans le dispositif, à six densités différentes. Chacun de ces traitements est répété six fois. Pour homogénéiser l'âge des prédateurs, les larves du stade précédent prêtes à muer sont isolées, et les stades d'observation prélevés 4 à 8 heures après la mue. Une larve de *H. axyridis* est introduite par enceinte. La consommation est contrôlée journellement dans chaque enceinte et le nombre initial de pucerons restauré chaque jour jusqu'à la fin du stade de *H. axyridis*. La même procédure est reproduite pour les quatre stades larvaires et les adultes de *H. axyridis*.

Chaque essai est réalisé aux températures de 12.5, 15, 18, 20, 25, 27.5 et 30 ± 0.5°C, à 70% d'humidité, en photopériode 16:8 (jour:nuit).

L'équation de type II de Holling de la réponse fonctionnelle est appliquée aux données de consommation journalière de chaque stade du prédateur aux différentes températures, en utilisant la transformation de Woolf :

$$\frac{N}{N_a} = Th.N + a^{-1} \qquad (3\text{-}3)$$

Elle assure de meilleurs paramètres d'estimation que les autres transformations linéaires ou la régression non linéaire.

RESULTATS

Les données de la réponse fonctionnelle de tous les stades de *H. axyridis* à toutes les températures s'ajustent bien au modèle de réponse fonctionnelle défini précédemment, caractérisé par un niveau de prédation qui s'accroît avec la densité de proie puis se stabilise lorsque cette densité de proie tend vers l'infini (Fig 3-1).

L'efficacité prédatrice des larves de *H. axyridis* s'accroît avec l'âge, ce qui se traduit par une augmentation du taux d'attaque instantané et par une diminution du temps de prédation (Tableau 3-1).

Le maximum d'efficacité prédatrice des larves est atteint expérimentalement à 25 - 27.5°C. La valeur du taux d'attaque instantané *a* est la plus basse à 12.5 et 30°C pour les larves des quatre stades, la plus haute à 27.5°C pour les trois premiers stades et à 25°C pour le quatrième (Tableau 3-1, Fig. 3-2). Pour les quatre stades, le temps de prédation *Th* est le plus long à 12.5 et 30°C, le plus court à 25°C (Tableau 3-1, Fig. 3).

Les valeurs calculées pour les paramètres *a* et *Th* indiquent pour le taux d'attaque instantané *a* une valeur maximale à une température inférieure à celle estimée directement par les données expérimentales. La représentation 3-D de la réponse fonctionnelle en fonction de la température pour chaque stade larvaire indique que la consommation de proie par *H. axyridis* est hautement corrélée à la densité de proie et à la température (Fig. 3-4).

Discussion

Les larves des troisième et quatrième stades consomment significativement plus que les premiers et deuxièmes stades. Cette différence entre les stades résulte moins du taux d'attaque instantané que du temps de prédation, ce qui peut expliquer une plus grande différence de consommation entre les stades aux fortes densités de proies qu'aux faibles densités (Fig. 3-1).

La consommation de proies est fortement liée à la température (Fig. 4-4), son accroissement influençant directement l'activité de recherche et la vitesse à laquelle les proies sont ingérées et digérées. Par ailleurs, l'accroissement de taux de développement accompagnant un accroissement de température se traduit par une exigence alimentaire accrue. On peut cependant s'attendre à ce que la consommation totale ne varie que faiblement avec la température et la densité de proie, une consommation accrue liée à ces deux facteurs résultant habituellement en un temps de développement plus court et par là même à une période de consommation réduite.

Le taux d'attaque instantané des jeunes stades est plus sensible à l'accroissement de la température que celui des stades âgés, mais le temps de prédation *Th* est moins sensible à un accroissement de température chez les jeunes stades que chez les stades âgés.

Dans le cadre de cette expérimentation, les larves de *M. persicae* sont dispersées chaque jour dans l'enceinte. Ce n'est pas le cas des populations naturelles caractérisées par une distribution agrégative, qui peut favoriser la phase de recherche intensive du prédateur mais réduire l'efficacité de la phase de recherche extensive. L'efficacité de recherche reste généralement supérieure en cas de distribution agrégative de la proie. Cette contrainte expérimentale appliquée à la proie ne doit cependant pas modifier fondamentalement le taux de prédation.

CHAPITRE 4

EFFET DE LA TEMPERATURE ET DE LA DENSITE DE PROIE SUR LES TAUX DE SURVIE ET DE DEVELOPPEMENT DES STADES IMMATURES DE *H. AXYRIDIS*

INTRODUCTION

L'efficacité de *H. axyridis* comme agent de lutte biologique contre *M. persicae* par lâchers inondatifs ne dépend pas uniquement de la réponse fonctionnelle mais également de la réponse numérique, à savoir le changement de densité du prédateur en réponse à la densité de la proie. Bien que clairement définie, la réponse numérique a été peu étudiée en raison des problèmes techniques posés par son évaluation. Dans le cadre des interactions entre les pucerons et leurs ennemis naturels, deux éléments de réponse numérique sont généralement distingués, la réponse numérique agrégative et reproductive. La réponse numérique agrégative correspond à la concentration du prédateur en réponse à la densité de proies. La réponse numérique reproductive est la relation entre le taux de reproduction du prédateur et la densité de proie. On doit ajouter à ces deux principaux éléments les changements de taux de développement et de survie en fonction de la densité de proie qui sont également importants pour évaluer l'efficacité du prédateur. Dans le cas de lâchers inondatifs, le but n'est pas d'établir un équilibre entre la proie et le prédateur mais de supprimer momentanément la proie pendant certaines périodes critiques. Les populations introduites de *H. axyridis* ne se maintenant pas plus d'une génération dans les vergers, les réponses numériques agrégatives et reproductives sont d'un intérêt limité. Le nombre initial de larves du prédateur dans les vergers est déterminé par la date du lâcher et non par l'effet du déplacement ou de la reproduction des générations précédantes.

Comme pour la réponse fonctionnelle, la réponse numérique d'un prédateur est affectée par la température et la densité de proie. Bien que l'effet de la température sur la réponse numérique soit considéré comme un élément majeur pour déterminer la capacité du prédateur à supprimer la population de proie, peu d'études expérimentales concernent cet aspect.

L'objet de notre analyse, qui vise à déterminer les effets de la température et de la densité de *M. persicae* sur les taux de survie et de développement de *H. axyridis*, est de définir le stade et la densité de prédateur appropriés à la maîtrise des populations de pucerons. Cette étude doit également permettre la compréhension des performances de la coccinelle après des lâchers en vergers.

MATERIELS ET METHODES

Le dispositif ainsi que les modalités concernant la proie et le prédateur sont identiques à ceux utilisés pour l'étude de la réponse fonctionnelle. Les nombres de larves survivantes et ayant évolué au stade suivant sont relevés chaque jour, et le nombre de pucerons restauré comme précédemment après chaque observation. Cette procédure est reproduite six fois pour chacun des quatre stades de *H.*

axyridis, aux températures constantes de 12.5, 15, 18, 20, 25, 27.5, 30 ± 0.5°C. Le taux moyen de développement est calculé comme suit :

$$d = \frac{n}{\sum_{i=1}^{n} D_i} \qquad (4\text{-}1)$$

où d est le taux moyen de développement, n la taille de l'échantillon, D_i's les durées de développement observées (en jours).
Le taux de survie journalier a été estimé comme la moyenne géométrique calculée sur le nombre de jours nécessités pour compléter le développement du stade :

$$S = \left(\frac{X_i}{X_{i-1}}\right)^D \qquad (4\text{-}2)$$

où S est le taux moyen de survie journalier, Xi-1 et Xi le nombre de larves survivantes au début et à la fin du ième stade, D le taux de développement moyen.

Toutes les estimations paramétriques rencontrées dans la phase de modélisation sont réalisées par une procédure de régression non linéaire de quasi-Newton.

RESULTATS

Taux de développement de *H. axyridis* en fonction du nombre de proies offertes. Comme on pouvait s'y attendre, le taux de développement de *H. axyridis* augmente à la fois avec la température et avec le nombre de *M. persicae* offert (Tableau 1). Nous avons utilisé une stratégie analytique modélisant tout d'abord le taux moyen de développement comme une fonction du nombre de proies offertes. Les paramètres de ces modèles sont ensuite modélisés comme fonction de la température. A toutes les températures testées, la relation entre taux de développement et nombre de proies offertes journellement suit une courbe de saturation (Fig 1), modélisée selon :

$$D(N) = Dm.[1 - e^{-\beta.N}] \qquad (4\text{-}3)$$

où $D(N)$ est le taux de développement en fonction de la densité de proies N, Dm le taux maximal de développement, β un paramètre dont l'inverse correspond à la vitesse à laquelle le taux de développement approche Dm quand le nombre de proies augmente (sensibilité du taux de développement au nombre de proies offertes). Une valeur de β plus faible correspond à une plus

grande sensibilité. Les paramètres Dm et β ont été estimés pour tous les stades larvaires et pour les différentes températures (Tableau 2).

Taux de développement de *H. axyridis* en fonction de la température. La relation entre le taux maximum de développement et la température (Fig 2) est de même forme que la réponse typique des animaux poikilothermes à la température, décrite ici selon le modèle de Logan :

$$Dm(T) = \psi_{HA} \cdot (e^{\rho_{HA} \cdot T} - e^{\rho_{HA} (Tm_{HA} - T)/\Delta T_{HA}}) \qquad (4\text{-}4)$$

où ψ_{HA} est le taux du processus physiologique à une température de base donnée; ρ_{HA} est une valeur correspondant aux réactions biochimiques critiques catalysées par les enzymes; Tm_{HA} est la température maximale (en °C) au dessus de la température de base du processus de vie; ΔT_{HA} la largeur de la marge supérieure de températures. Les estimations de ces paramètres pour tous les stades larvaires sont données en tableau 4 . La température maximale de développement (Tm_{HA}) est d'environ 29-30 °C, l'épaisseur de la marge supérieure de températures (ΔT_{HA}) d'environ 3-4 °C pour les 4 stades larvaires.

Le paramètre β, (l'inverse de la sensibilité du taux de développement à la densité de proies) décroît avec la température T (Fig. 3). Plus la température est élevée, plus le taux de développement est sensible à la disponibilité en nourriture : chaque portion de nourriture induit un effet sur le développement plus important quand la température augmente. Cette relation est modélisée empiriquement via un modèle exponentiel :

$$\beta(T) = Bd_1 . e^{-Bd_2 T} \qquad (4\text{-}5)$$

où Bd_1 et Bd_2 sont deux constantes. Les estimations de Bd_1 et Bd_2 sont données dans le Tableau 3.
Le taux moyen de développement peut donc être décrit comme une fonction de la température et de la densité de proies en introduisant $Dm(T)$ et $\beta(T)$ dans l'équation (1) :

$$D(T,N) = Dm(T)\,[1 - e^{-\beta(T) N}] \qquad (4\text{-}6)$$

L'allure générale de ce modèle est donnée en Fig. 4.

Taux de survie journalier moyen de *H. axyridis* en fonction du nombre initial de proies. Comme pour le taux de développement moyen, le taux moyen de survie journalier augmente avec la température et avec le nombre de proies offertes (Tableau 4). De même que précédemment nous définissons ce paramètre comme une fonction du nombre de proies offertes et incorporant l'effet de la température dans les paramètres du modèle. Le taux journalier de survie s'accroît avec la disponibilité en proie selon une courbe sigmoïde :

$$S(N) = \frac{1}{1 + Sc_1 . e^{-Sc_2 . N}} \qquad (4\text{-}7)$$

où S(N) est le taux de survie journalier moyen du prédateur fonction du nombre de proies offertes N; Sc1 un paramètre dont l'inverse est relié au taux de survie journalier moyen quand il n'y a pas de proie disponible, Sc2 un paramètre décrivant la vitesse à laquelle S(N) s'approche de sa valeur maximale. Ce modèle décrit bien la dépendance à la proie du taux de survie journalier moyen de *H. axyridis* (Fig. 4, Tableau 5).

Taux de survie de *H. axyridis* en fonction de la température. Pour un nombre de proies disponibles donné, le taux de survie de H. axyridis dépend de la température (Fig. 5, 6) de son environnement. Les paramètres Sc1 et Sc2 peuvent également être modélisés en fonction de la température (Fig 5,6). Les modèles empiriques suivants ont été utilisés :

$$Sc_1(T) = Sc_{11} . (1 - Sc_{12} . e^{-Sc_{13} . T}) \qquad (4\text{-}8)$$

$$Sc_2(T) = Sc_{21} . (1 - Sc_{22} . e^{-Sc_{23} T}) \qquad (4\text{-}9)$$

où Sc_{11}, Sc_{12}, Sc_{13}, Sc_{21}, Sc_{22}, et Sc_{23} sont des paramètres calés lors de l'ajustement de la courbe sans signification biologique explicite (Tableau 6).
Le taux de survie des larves de *H. axyridis* en fonction de la température et de la densité de proies est modélisé en introduisant $Sc_1(T)$ et $Sc_2(T)$ dans l'équation 5 :

$$S(T, N) = \frac{1}{1 + Sc_1(T) . e^{-Sc_2(T) . N}} \qquad (4\text{-}10)$$

Le comportement de ce modèle dans les intervalles définis biologiquement est illustré en Fig. 7

Discussion

Dans les modèles développés ici pour décrire les taux de développement et de survie de *H. axyridis* en fonction de la densité de proie et de la température, une des variables indépendantes est le nombre de proies présentes, plutôt que le nombre de proies consommées utilisé dans plusieurs études similaires. La relation entre taux de développement et consommation de proies suit habituellement une courbe de saturation. Dans le cas de la réponse fonctionnelle de Holling de type II, le nombre de proies consommées est lui-même une fonction du nombre de proies présentes suivant une équation de saturation. En fait si nous utilisons *Na* au lieu de *N* dans l'équation 4-3, en substituant *Na* à la partie droite de l'équation 4-12 :

$$D(N) = Dm.[1 - e^{-\beta.Na}] \qquad (4\text{-}11)$$

$$Na = \frac{aN}{1 + aThN} \qquad (4\text{-}12)$$

la relation entre *D* et *N* dans l'équation 4-11 a les mêmes propriétés numériques et géométriques que celles décrites dans l'équation 4-3, pour des paramètres de signification et de valeur légèrement différents. Les paramètres estimés pour l'équation 4-11 avec Na comme variable indépendante sont probablement plus précis que ceux estimés par l'équation 4-3, le taux de développement D étant plus directement relié au nombre de proies consommées qu'au nombre de proies présentes. L'équation 4-3 a cependant quelques avantages : la perte de précision peut être partiellement compensée en réduisant l'erreur expérimentale liée à la manipulation du système pour obtenir les valeurs de *Na*, l'erreur liée à l'estimation des paramètres de l'équation 4-12, et le nombre de calculs dans l'évaluation de la fonction. De plus, une large part de la charge expérimentale liée à l'évaluation de *Na* peut être économisée et le modèle considérant la densité de proie plutôt que le nombre de proies attaquées peut être utilisé plus rapidement pour l'évaluation des taux de survie et de développement du prédateur en conditions de plein champ.

Dans cette étude, nous utilisons le taux de survie journalier moyen calculé par la moyenne géométrique des taux de survie spécifiques de chaque stade larvaire. Cette mesure nous permet d'incorporer directement le taux de survie dans le modèle de simulation, habituellement résolu sur un pas de temps de 1 jour, le taux de survie étant calculé selon la température et la densité de proie du jour correspondant. Nous devons porter attention au fait que le taux de survie journalier moyen n'est qu'une approximation, car il peut être spécifique de l'âge physiologique plutôt qu'une valeur unique pour le stade. Nous adoptons cette approche simplifiée en raison de l'absence de données sur le taux de survie par âge, et de l'impossibilité de les acquérir sans un dispositif contraignant.

Beddington (1976) suggère que le taux de survie du prédateur en fonction de la densité de proie suit une courbe sigmoïde basée sur une distribution normale du nombre moyen de proies consommées. Ce modèle n'a pas fait l'objet de nombreuses validations par des données expérimentales, la signification des paramètres du modèle étant imprécise. Dans leur étude sur les interactions prédateur/proies entre *Typhlodromus pyri* et sa proie, *Panonychus ulmi*, Hardman et Rogers (1991) proposent une courbe de saturation pour décrire le taux de survie en réponse à la densité de proie. Nos résultats se conforment à une courbe sigmoïde, et nous en déduisons un modèle qui diffère du modèle de Beddington pour l'interprétation des mécanismes décrivant le taux de survie de *H. axyridis* en réponse à la densité de *M. persicae*.

CHAPITRE 5 :

LE MODELE DE SIMULATION

1. CADRE GENERAL DU MODELE DE SIMULATION

Le modèle approprié pour cette étude doit comporter une part adéquate de réalisme biologique dans la description de la dépendance à la température et à la densité de proie de l'interaction entre *M. persicae* et *H. axyridis*, tout en conservant un bon degré de tractabilité. Il y a peu à gagner avec un modèle trop complexe à manipuler et à comprendre. Un modèle déterministe est retenu de préférence à un modèle stochastique, qui requiert habituellement des informations complémentaires sur la variation et la distribution de chaque paramètre, et augmente la complexité de la structure et du calcul du modèle.

Ce modèle incorpore trois sous-modèles principaux :

- Le modèle de dynamique des populations de *M. persicae.*
- Le modèle de réponse fonctionnelle de *H. axyridis* .
- Le modèle de réponse numérique de *H. axyridis* .

La dynamique de population des pucerons est modélisée en utilisant deux approches. Une approche suppose qu'une population de pucerons a une structure d'âge stable et un chevauchement complet des générations, et peut être modélisée comme une entité homogène. L'évolution de la population est caractérisée par son taux d'accroissement. La seconde approche prend en compte la structure d'âge de la population, qui est alors modélisée comme un assemblage de différentes classes d'âge; l'évolution de la population est caractérisée par des paramètres démographiques dépendant de l'âge. Le choix de l'approche dépend du système étudié, des données disponibles et du but du modèle. Dans cette étude, notre but est de coupler la modélisation des populations du puceron à la modélisation des réponses fonctionnelles et numériques de *H. axyridis* afin d'évaluer les effets de la température sur leurs interactions. A cette fin, nous adoptons l'approche holistique, plus facile à manipuler et dont le comportement est plus facile à appréhender. Un modèle de population plus complexe et détaillant la structure d'âge du puceron n'améliorerait pas la performance globale du

modèle de simulation, aucune information n'étant disponible quant au taux d'attaque ou à la préférence du prédateur pour une classe d'âge de la proie.

Un modèle de réponse fonctionnelle du type II de Holling est utilisée pour modéliser le taux d'attaque de *H. axyridis* sur *M. persicae* en fonction de la température. Les interactions complexes comme les interférences entre prédateurs, la préférence du prédateur pour une taille de proie et l'efficacité de recherche du prédateur en fonction de l'agrégation du puceron sont ignorées. En pratique, le nombre de prédateurs qu'il est possible ou souhaitable de lâcher est rarement suffisant pour créer une interférence entre prédateurs. Puisque nous modélisons les populations de pucerons comme une entité homogène dans laquelle chaque individu moyen contribue de manière égale à la population, la perte d'individus moyens due à la prédation peut constituer une approximation de la consommation des pucerons par les larves de *H. axyridis* .

Pour évaluer l'efficacité de *H. axyridis* comme agent de contrôle biologique par lâchers inondatifs, aucun recrutement de population de *H. axyridis* n'est incorporé dans le modèle. L'évolution des cohortes de coccinelles lâchées est modélisée avec un modèle de classe d'âge, le contenu de la classe d'âge étant transféré globalement dans la suivante après un certain nombre de degrés-jours, correspondant à la durée de la classe d'âge. La durée d'une classe d'âge de *H. axyridis* dépend de la température et de l'abondance des pucerons. Un taux de survie journalier âge-spécifique, également fonction de la température et de la densité de proie, est appliqué à la cohorte.

2. LE MODELE PUCERON VERT DU PECHER

L'évolution de la population de puceron vert du pêcher est simulée ainsi : les oeufs de pucerons ayant passé l'hiver éclosent en verger de pêcher au début du printemps quand une certaine valeur de degrés-jours (365 degrés jours dans le modèle) est atteinte, le calcul n'étant fait qu'au dessus du seuil de température de 4,5°C. La population se développe durant la saison selon un mode parthénogénétique vivipare jusqu'en juin, après 1740 degrés jours. Tous les individus émigrent alors hors des vergers de pêcher. La migration entre colonies pendant la période étudiée est simulée par tirage aléatoire uniforme. Les larves de coccinelles peuvent être lâchées à n'importe quel moment dans la saison.

La population de *M. persicae* est modélisée par un modèle logistique à effet retard, en supposant que la valeur actuelle du taux intrinsèque d'accroissement de la population est dépendant de la température moyenne calculée sur un intervalle de temps de largeur τ finissant à la date actuelle.

$$\frac{dN}{dt} = r_m(\overline{T}_\tau).N.-b.\overline{N}_\tau.N \qquad (5\text{-}1)$$

N est la densité de population du puceron, $r_m(\overline{T}_\tau)$ le taux d'accroissement intrinsèque de la population fonction de $\overline{T}_\tau$, la température moyenne calculée entre les jours t-τ et t. Le taux intrinsèque d'accroissement de la population de puceron vert du pêcher a été décrit dans le chapitre 2 comme une fonction de la température, en utilisant le développement de Logan selon une sigmoïde (Eqn. 2-5). Nous reprendrons ce modèle avec ses paramètres pour décrire $r_m(\overline{T}_\tau)$:

$$r_m(\overline{T}_\tau) = \alpha\{[1+ke^{-\rho\overline{T}_\tau}]^{-1} - e^{-\frac{T_m-\overline{T}_\tau}{\Delta T}}\} \qquad (5\text{-}2)$$

Les paramètres ont la même signification qu'en Eqn. 2-5. La variable indépendante $\overline{T}_\tau$ est une température moyenne sur l'intervalle de temps [t–τ, t]. Une forme plus réaliste et plus générale de $\overline{T}_\tau$ pourrait être donnée comme une moyenne pondérée avec une fonction de période caractéristique. Nous utiliserons ici une simple moyenne arithmétique dans la mesure où nous ne disposons pas d'information concernant cet aspect :

$$\overline{T}_\tau = \int_{t-\tau}^{t} \tau.T(s)\,ds \qquad (5\text{-}3)$$

$\overline{N}_\tau$ dans l'équation 5-1 correspond à l'effectif moyen de la population entre t-τ et t. Une fois de plus, on pourrait utiliser une moyenne pondérée. En approximation, nous utilisons ici une simple moyenne arithmétique.:

$$\overline{N}_\tau = \int_{t-\tau}^{t} \tau.N(s)\,ds \qquad (5\text{-}4)$$

Le paramètre b dans l'équation 5-1 est le coefficient de compétition intraspécifique et $\frac{r_m(\overline{T}_\tau)}{b}$ représente la capacité de déplacement. Elle dépend de $\overline{T}_\tau$, la température moyenne entre t et t-τ.

En pratique, le modèle de simulation est basé sur des pas de temps journaliers. En conséquence certaines variables, à priori estimées continûement dans le temps, seront remplacées par leur version discrète. On aura en particulier :

$$\overline{T}_\tau = \frac{1}{\tau}\sum_{s=t-\tau}^{t} T(s) \qquad (5\text{-}5)$$

$$\overline{N}_\tau = \frac{1}{\tau}\sum_{s=t-\tau}^{t} N(s) \qquad (5\text{-}6)$$

Dans toutes les équations, t représente l'intervalle de temps utilisé lors des intégrations. La durée moyenne d'une génération et la durée de développement préimaginal sont généralement considérées comme les deux candidats pour t. Nous retenons ici pour t la durée du développement préimaginal. Dans la mesure où cette durée de développement dépend de la température, qui varie dans le temps, une notion de degrés-jours sera utilisée pour déterminer l'intervalle de temps sur lequel sont calculées les intégrations sur le temps. t est calculé à partir de la relation :

$$1 = \sum_{s=t-\tau}^{t} D(T(s)) \qquad (5\text{-}7)$$

dans le programme, $t-\tau$ est estimé en calculant $\sum_{s=t-\tau}^{t} D(T(s))$ en partant de t jusqu'à ce que $\sum_{t-\tau}^{s=t} D(T(s)) \geq 1$ soit satisfait. $D(T(s))$ le taux de développement des immatures, est calculé à partir de l'équation 2-4 du chapitre 2 :

$$D(T) = \psi[e^{\rho T} - e^{\rho T_m - \frac{T_m - T}{\Delta T}}] \qquad (5\text{-}8)$$

où les paramètres et les variables ont la même signification qu'en équation 2-4. Nous utilisons la durée de développement larvaire comme longueur de temps sur lequel est calculée l'intégrale effectuée par rapport au temps de la dépendance à la température et à la densité. On suppose pour cela que le taux instantané d'évolution de la population est influencé par l'intégrale des effets de la température et de la densité de population sur la durée de développement larvaire. La durée moyenne d'une génération ou le temps de retour caractéristique peuvent être également utilisés comme base de temps sur laquelle calculer les intégrales effectuées par rapport au temps si l'on fait d'autres hypothèses. Les simples moyennes de température ou de densité de population que nous

utilisons ici sont les formes les plus simples d'intégration par rapport au temps de la dépendance de la température ou de la densité. On pourrait s'attendre à ce qu'une moyenne pondérée utilisant une distribution de poids donnée soit une représentation plus réaliste.

3. LE MODELE COCCINELLE

Réponse fonctionnelle. La réponse fonctionnelle du ième stade larvaire est modélisée comme une fonction de la température instantanée et de la densité de population de pucerons verts du pêcher via une réponse de Holling de type II (Equations 3-1, 3-2a,b).

$$N_{ai} = \frac{a_i(T).N}{1 + a_i(T).Th_i(T).N} \qquad (5\text{-}9)$$

$$a_i(T) = \frac{u_1.T.e^{-\frac{u_2}{T}}}{1 + u_3.e^{-\frac{u_4}{T}}} \qquad (5\text{-}10)$$

$$Th_i(T) = \frac{1 + v_1.e^{-\frac{v_2}{T}}}{v_3.T.e^{-\frac{v_4}{T}}} \qquad (5\text{-}11)$$

où l'indice i représente le ième stade larvaire de *Harmonia axyridis*, tous les autres paramètres et variables ayant la même signification que dans les équations 3-1, 3-2a, b.

Le nombre total de proies consommées par une coccinelle est alors :

$$N_a = \sum_i N_{ai}$$

Taux de développement. Le développement temporel d'une larve de coccinelle est modélisé par une fonction de la température instantanée et de la densité de proie en utilisant les équations 4-3, 4-4, 4-5:

$$D_i(T,N) = Dm_i(T).[1 - e^{-\beta_i(T).N}] \qquad (5\text{-}12)$$

$$Dm_i(T) = \psi_{HA}.(e^{\rho_{HA}.T} - e^{\rho_{HA}(Tm_{HA}-T)/\Delta T_{HA}}) \qquad (5\text{-}13)$$

$$\beta_i(T) = Bd_1.e^{-Bd_2 T} \qquad (5\text{-}14)$$

où *i* représente le ième stade de la larve. Tous les autres paramètres et variables ont la même signification que dans les équations 4-3, 4-4, 4-5. Le temps de passage d'une larve dans le stade suivant est calculé en utilisant

$$1 = \sum_{t_0}^{s} D_i(T(s), N(s)) \qquad (5\text{-}15)$$

où $D_i(.)$ est le taux de développement du $i^{ème}$ stade larvaire fonction de la température $T(s)$ et de la densité de proie $N(s)$ au jour s. Dans le programme, le temps de passage du ième stade larvaire au suivant est estimé en calculant $\sum_{t_0}^{s} D_i(T(s), N(s))$ en partant de t_o, le temps d'entrée dans le iéme stade, jusqu'à ce que soit vérifiée l'inégalité $\sum_{t_0}^{s} D_i(T(s), N(s)) \geq 1$. A ce moment, tous les individus du ième stade passent dans le i+1 ième stade.

Taux de survie. Le taux de survie spécifique journalier dépendant de l'âge (Eqn. 4-7, 4-8, 4-9, 4-10) est modélisé comme le taux de survie journalier de la larve de coccinelle au ième stade, fonction de la température instantanée et de la densité de proies :

$$S_i(T, N) = \frac{1}{1 + Sc_{i1}(T).e^{-Sc_{i2}(T).N}} \qquad (5\text{-}16)$$

$$Sc_{i_1}(T) = Sc_{11}.(1 - Sc_{12}.e^{-Sc_{13}.T}) \qquad (5\text{-}17)$$

$$Sc_{i_2}(T) = Sc_{21}.(1 - Sc_{22}.e^{-Sc_{23}.T}) \qquad (5\text{-}18)$$

Tous les paramètres et variables ont la même signification que dans les équations 4-7, 4-8, 4-9, 4-10. L'évolution de la densité de coccinelle du ième stade larvaire est alors modélisé par :

$$\frac{dP_i}{dt} = (1 - L_{i-1}).S_{i-1}(T, N).P_{i-1} - [1 - L_i.S_i(T, N)].P_i + U_i(t) \qquad (5\text{-}19)$$

où P_i est la densité de larves de coccinelles au ième stade larvaire, $U_i(t)$ le nombre de larves du ième stade lâchées au temps t, L_{i-1} et L_i deux variables logiques prenant deux valeurs (0 ou 1). Si une larve reste au ième stade, L_i vaut 1. Quand une larve a fini son développement au stade i et entre dans le stade suivant, L_i vaut 0.

$$L_i = \begin{cases} 1 & if \quad \sum_{t_0}^{s} D_i(T(s), N(s)) < 1 \\ 0 & if \quad \sum_{t_0}^{s} D_i(T(s), N(s)) \geq 1 \end{cases} \qquad (5\text{-}20)$$

où $D_i(.)$ est le taux de développement du ième stade larvaire fonction de la température $T(s)$ et de la densité de proie $N(s)$ le jour s.

Le cadre général du modèle de simulation peut alors s'écrire:

$$\frac{dN}{dt} = r_m(\overline{T}_\tau).N.(1 - \frac{b}{r_m(T_\tau)}.\overline{N}_\tau) + \sum_i \frac{a_i N}{1 + a_i Th_i N} \qquad (5\text{-}21a)$$

$$\frac{dP_i}{dt} = (1 - L_{i-1}).S_{i-1}(T,N).P_{i-1} - [1 - L_i.S_i(T,N)].P_i + U_i(t) \qquad (5\text{-}21b)$$

4. Le programme de simulation

Variables d'état, variable courante, conditions initiales, entrées et sorties. La température est la seule variable courante du système. Les données de température utilisées dans la simulation sont générées par CLIMGEN, un programme de génération de données climatiques développé par USDA-ARS en utilisant les paramètres obtenus à partir des enregistrements météorologiques locaux d'Avignon. La seule condition initiale du modèle est le nombre d'oeufs d'hiver. Il peut être issu d'un générateur de nombres aléatoires ou une simple estimation. Quand la population de pucerons dépasse un niveau donné, le nombre de larves de coccinelles et leur stade doivent être introduits. Le programme retourne les trajectoires des populations de pucerons et de coccinelles.

Pas de temps, d'espace et simulation. Le pas de temps de ce modèle de simulation est le jour circadien, le plus naturel et le plus pratique, et constituant également l'échelle à laquelle ont été mesurés tous les paramètres du modèle. Dans le cas où des degrés jours ont été utilisés pour mesurer le temps nécessaire à l'accomplissement de certains processus biologiques, comme par exemple l'ensemble du développement de certains stades, les degrés jours sont utilisés dans les calculs mais sont ensuite convertis en jours circadiens. Comme modèle s'intéressant aux propriétés qualitatives de base de la dépendance à la température et à la densité des interactions hôte-prédateur, nous chercherons à éviter la complexité spatiale, telle que l'hétérogénéité de l'habitat et le déplacement du

prédateur parmi les colonies de pucerons, etc., dans la simulation. Une seule colonie de pucerons est utilisée comme échelle d'espace. Nous supposons que b, le coefficient de compétition intraspécifique (l'impact d'un individu sur les autres individus de la même colonie) est une constante indépendante de la température. La capacité de déplacement représentée par $r_{m.}(T)/b$, dépend alors de la température .

En conditions naturelles, les pucerons peuvent se déplacer en marchant ou, pour les formes ailées, en volant. Ce processus de déplacement intra - habitat peut être dépendant de la densité ou de la température, mais aucune donnée n'est disponible pour nous permettre de dégager un cadre valide qui puisse caractériser ce processus. Nous avons utilisé dans cette étude un générateur de nombres aléatoires uniformes pour simuler le nombre de pucerons entrant ou sortant de la colonie, et ce de manière indépendante de la densité de pucerons et de la température. Le biais introduit par cette pratique peut paraître énorme à l'échelle microscopique, mais peut être considérée comme acceptable à l'échelle macroscopique, dans la mesure où les effets de déplacement intra-colonie sur la dynamique de population sont très nettement plus importants à faible densité de population qu'à forte densité. Quand la saison se termine, *M. persicae* évolue vers des formes ailées qui émigrent des vergers de pêcher vers des hôtes secondaires. On montre que la proportion de pucerons sortant des vergers augmente quand la saison se termine. Le nombre de pucerons sortant du verger de pêchers est modélisé ici comme le produit de la densité de population de pucerons, de la proportion de degrés jours accumulés sur le nombre total de degrés jours nécessaires à l'accomplissement de la vie des pucerons dans le verger de pêchers à une puissance x (x valeur choisie pour obtenir les résultats attendus) et d'une variable aléatoire uniforme :

$$N_{emm}(t) = N(t).RND.(\frac{\sum_{t_o}^{t}(T(t)-T_b)}{DD_{total}})^x \qquad (5\text{-}22)$$

où $N_{emm}(t)$ est le nombre de pucerons sortant du verger, $N(t)$ la densité de population actuelle, RND une variable aléatoire uniforme, $T(t)$ la température le jour t, T_b le seuil inférieur de température pour le développement du puceron, DD_{total} la quantité de degrés jours nécessaire pour accomplir la phase de vie des pucerons dans le verger de pêcher, x une valeur à fixer.

Programme principal. Le programme principal est formé de 5 grandes parties. Dans la première partie sont définis les sous programmes, les fonctions, les tableaux et les valeurs des paramètres.

Dans la seconde partie, les données de température sont extraites d'un fichier de données créé par CLIMGEN, puis on calcule la date à partir de laquelle les pucerons apparaissent dans les vergers de pêcher, dans ce cas au moment où un total de 192 degrés jours est accumulé au dessus du seuil de 4.5°C. Dans la troisième partie, on initialise le système en affectant aux variables d'état (les populations de pucerons et les larves de coccinelles) leurs valeurs initiales. La population initiale de *M. persicae* est obtenue par troncation d'une valeur aléatoire uniforme. La population initiale de larves de coccinelles est fixée à zéro tant que la population de pucerons est supposée au dessous du seuil de tolérance. Les parties 4 à 6 sont incluses dans la boucle principale du programme, qui démarre le jour où des pucerons apparaissent dans le verger et se termine quand 1912 degrés jours au dessus de 4.5°C ont été accumulés. Dans la quatrième partie, on appelle la subroutine RmLag pour calculer le taux d'accroissement intrinsèque de la population de pucerons qui est fonction de la température via une intégrale retard et une dépendance retard à la densité due à la compétition intraspécifique (voir partie 2, « modèle puceron vert » de ce chapitre). Dans la cinquième partie, on vérifie si la population de pucerons dépasse un seuil de tolérance auquel cas un certain nombre de larves d'un stade donné est lâché. Dans la subroutine ComputY on calcule le taux de développement, le taux de survie journalier et la consommation de proies des larves de coccinelles en fonction de la température instantanée et de la population de pucerons. Dans la sixième partie on appelle la subroutine RungeKutta, qui donne la solution d'une équation différentielle ordinaire, pour calculer les densités de population de pucerons et de larves de coccinelles le jour suivant. Les résultats ainsi générés sont écrits dans un fichier dans une septième partie.

Subroutine RmLag. On appelle cette subroutine dans le programme principal pour calculer la température journalière et la population moyenne de pucerons sur un intervalle de temps (comme précisé dans l'équation 5-3, 5-4) qui est l'intervalle de temps entre une date passée et la date actuelle pendant lequel les degrés jours accumulés permettent le développement préimaginal des pucerons (ou le temps de génération moyen). Cet intervalle est calculé à partir de la date courante en reculant dans le temps jusqu'au moment où l'accumulation de taux de développement de pucerons (fonction de la température) atteint 1 (voir équation 5-7 et la discussion en section 2 de ce chapitre). La température moyenne sur un intervalle de temps est ensuite utilisée pour calculer le taux d'accroissement intrinsèque de la population moyenne de pucerons en utilisant l'équation 5-2. La

population moyenne de pucerons sur la même période est utilisée pour prendre en compte la dépendance retard à la densité de population de pucerons (voir équation 5-1). La température journalière, la densité de population de pucerons, les paramètres utiles et le compteur de temps sont des entrées de cette subroutine. Le taux intrinsèque d'évolution de la population, la population moyenne de pucerons sur un intervalle de temps sont des sorties ainsi que des valeurs globales partagées.

Subroutine ComputY. Dans cette subroutine on calcule la consommation de proies, le taux de développement et le taux de survie des larves de coccinelles en fonction de la température et de la densité de population de pucerons. Dans une première partie de cette subroutine, on calcule le taux de développement des larves et l'évolution du développement en terme d'accumulation de taux de développement, en utilisant les équations 5-12 à 5-14. Cette dernière est introduite dans la subroutine RungeKutta pour déterminer si une larve passe dans le stade suivant le jour d'après, selon la relation définie par l'équation 5-15. Dans la deuxième partie on calcule le taux de survie utilisé dans la subroutine RungeKutta comme taux d'évolution des larves de coccinelles. Dans la troisième partie de cette subroutine on calcule le taux d'attaque instantané et le temps de manipulation en fonction de la température. Ce taux est utilisé dans la subroutine RungeKutta pour calculer la consommation totale de pucerons par la coccinelle.

Subroutine RungeKutta. Cette subroutine est une simple résolution d'équation différentielle utilisant l'algorithme d'ordre 4 de RungeKutta. Le système à résoudre est défini par les équations 5-21. Cette subroutine utilise la valeur de la variable de taux calculée par les subroutines RmLag et ComputY ainsi que la consommation totale de pucerons par les coccinelles calculée par la fonction TotalConsum. On utilise dans cet algorithme un pas de longueur 0,1. Les valeurs des variables d'état, en densités de populations de pucerons et de coccinelles, sont mises à jour à chaque fois que cette subroutine est appelée. Elle vérifie également si le développement d'un stade larvaire donné est terminé et si les individus doivent entrer dans le stade suivant.

Fonction TotalConsum. Cette fonction est appelée pour toutes les évaluations de dérivées dans la subroutine RungeKutta, pour calculer le nombre total de pucerons tués par les coccinelles. Les

valeurs du taux instantané d'attaque et du temps de manipulation, de même que la densité de population de pucerons et de coccinelles sont des entrées issues de la subroutine ComputY et du programme principal.

5. Proprietes du systeme proie-predateur genere par le modele de simulation

Influence de la température sur l'efficacité de *H. axyridis*. L'efficacité des coccinelles est évaluée en terme de nombre minimum de larves requis pour l'extinction de la population de pucerons, à partir d'un niveau de population initial donné. Plus le stade larvaire est efficace, plus le nombre d'individus nécessaires à l'élimination des pucerons est réduit. Cette valeur est estimée par une procédure numérique, dans laquelle le nombre de pucerons qui entre ou sort du verger est établi comme nul. L'observation ne porte ainsi que sur l'extinction des pucerons liée à la prédation par les larves de coccinelles. Le niveau de population de pucerons auquel les larves de coccinelles sont lâchées est fixé à 250. En général, pour les trois premiers stades larvaires de *H. axyridis* , un plus grand nombre d'individus est requis à basse température qu'à température élevée pour éteindre une colonie. La décroissance du nombre minimum de larves requises lorsque la température augmente est plus rapide aux deux extrêmes de la gamme de températures favorables, de 12°C à 27°C, qu'aux températures favorables à la fois à *H. axyridis* et *M. persicae*, de 15 à 24°C (Fig. 5-1 L1, L2, L3). Pour le troisième stade, le nombre de larves minimum requis au-dessous de 18°C est plus faible qu'à 21 et 24°C (Fig. 5-1 L3). Pour le quatrième stade, le nombre minimum de larves requis pour l'extinction de la population de pucerons ne suit pas exactement une décroissance monotone avec l'augmentation des températures (Fig 5-1 L4). Dans la gamme de température 15-24°C, le nombre minimum de larves du quatrième stade requis augmente avec la température, schéma inverse de celui des stades 1 et 2 (Fig 5-1 L4, 5-2).

La simulation montre également que la même extinction finale de la population de pucerons, avec un nombre minimum de larves de coccinelles, est obtenue plus rapidement à hautes qu'à basses températures (Fig. 5-3, 5-4). Ces variations de temps utile pour l'élimination des pucerons en fonction de la température sont plus fortes pour les jeunes stades larvaires que pour les stades âgés. A 12°C, le temps nécessaire à l'extinction des pucerons par des larves de premier stade excède de 50

jours le temps d'extinction à 24 ou 27°C. Cet excédent est inférieur à 10 jours pour les larves de quatrième stade (Fig. 5-3, 5-4).

Différence d'efficacité entre les stades de H. axyridis . La procédure de simulation est la même que précédemment, mais les résultats sont interprétés sous un autre angle. A basses températures (12-15°C), le nombre minimum de larves de coccinelles nécessaire à l'extinction d'une colonie décroît quand l'âge augmente, le nombre minimum de larves requis pour une population de 250 pucerons suivant l'ordre L1>L2>L3>L4. A l'autre extrémité de la gamme de température favorable (27°C), l'efficacité relative suit un ordre inverse, à savoir un nombre minimum de larves requis diminuant quand l'âge des larves augmente (L4>L3>L2>L) Entre les deux extrêmes, l'ordre relatif d'efficacité des différents stades se transforme de manière séquentielle quand la température augmente. Quand la température augmente, l'ordre du minimum d'individus à lâcher passe tout d'abord à L1>L4>L2>L3 (Fig 5-5 24°C), puis devient L4>L1>L3>L2 (Fig 5-5 21°C) et ensuite L4>L3>L1>L2 (Fig. 5-5 24°C). Ce changement est dû au fait que lorsque la température augmente, le nombre minimum de larves requis pour éliminer les pucerons décroît plus vite pour les jeunes stades de coccinelles que pour les stades âgés (Fig. 5-2, 5-5)

Quand différents stades de la coccinelle sont lâchés avec pour chacun le nombre nécessaire à l'extinction des pucerons, cette extinction est obtenue plus ou moins rapidement. Avec des larves âgées (L3 ou L4), l'extinction des populations de pucerons est obtenue comparativement dans un délai très court, presque instantanément dans le cas du 4ème stade (Fig. 5-6). En lâchant des stades L1 ou L2, l'extinction est obtenue après un temps plus long, et à basse température la population de pucerons peut même continuer à croître avant d'être finalement éteinte par le prédateur (Fig 5-6). La différence de délai d'élimination des pucerons par différents stades de coccinelle lâchés à leur effectif minimum est plus grande à basse température qu'à température élevée (Fig 5-4, 6-6).

La dépendance de l'efficacité prédatrice de *H. axyridis* vis-à-vis des populations de pucerons. L'influence de la taille de la population de pucerons sur le nombre de *H. axyridis* efficace pour l'extinction de cette population est évaluée par simulation à la température constante de 15°C. Pour les trois premiers stades de *H. axyridis*, à gauche de l'axe des x représentant le niveau de population de pucerons, le nombre minimum d'individus requis pour une élimination complète des pucerons sur une colonie unique s'accroît rapidement quand la population de pucerons au moment du lâcher

augmente. Cette valeur décroît ensuite lentement quand le niveau de population du puceron augmente (Fig. 5-7). Pour le quatrième stade, le nombre minimum d'individus requis pour l'élimination complète des pucerons augmente de manière continue quand les populations de pucerons augmentent (Fig 5-7).

Comportement dynamique du modèle de simulation. Le modèle de simulation génère les comportements dynamiques suivants : en l'absence de lâcher de coccinelle, les populations du puceron vert du pêcher apparaissent en vergers fin février - début mars et en disparaissent mi - juin. Pendant toute cette période, la population de *M. persicae* connaît des fluctuations avec 3 - 4 pics et une plus forte abondance en avril - mai (Fig. 8). Ces résultats, quelque peu attendus, n'ont pu être comparés avec des données de terrain. La figure 5-9 montre les résultats de la simulation concernant les conséquences du lâcher de coccinelle pour contrôler *M. persicae*. Le nombre de larves requises augmente avec la population de pucerons au moment du lâcher. Si le prédateur est lâché lorsque la population de pucerons s'élève à 25 par colonie, un résultat très satisfaisant est obtenu avec le 3ème stade en effectuant trois lâchers de 0.25 larves de coccinelle par colonie. (Fig. 5-9 a). Si le lâcher intervient quand l'effectif de pucerons s'élève à 100 par colonie, un résultat similaire est obtenu par trois lâchers à respectivement 1, 0.5 et 0.5 larves par colonie (Fig. 5-9 b). Si la population de pucerons atteint 250 par colonie, un résultat moins satisfaisant que précédemment est obtenu en portant l'effectif des trois lâchers de coccinelles à respectivement 1.5, 1 et 1 larve par colonie (Fig. 5-9 c). A 500 pucerons par colonie, trois lâchers de 2.5, 2 et 2 larves du troisième stade, nombres presque irréalistes, donnent des résultats presque inacceptables (Fig. 5-9 d). Ces simulations montrent également qu'un nombre plus élevé de prédateurs doit être lâché en début de saison à basse température que plus tard dans la saison. On peut se demander si un meilleur résultat serait obtenu en augmentant l'effectif de prédateurs du premier lâcher. Cette question est illustrée par la Fig. 5-10. A 250 pucerons par colonie, le nombre de lâchers est ramené de 3 à 2 si un grand nombre de prédateurs est lâché la première fois. L'effectif du premier lâcher est de 5 L1, de 4 L2 ou de 3 L3 / L4 (Fig. 5-10 a,b,c,d). L'effectif du second lâcher est de 1 dans chaque cas. L'augmentation de l'effectif du premier lâcher ne réduit pas le nombre total de prédateurs lâchés mais réduit le nombre de lâchers. La réduction à 1 du nombre de lâchers impliquerait une trop forte augmentation de l'effectif lâché.

DISCUSSION

Le modèle de simulation est prévu pour révéler des propriétés qualitatives concernant la dépendance à la température et à la densité de l'interaction prédateur - proie entre *H. axyridis et M. persicae.* Ce modèle n'est pas doté de grandes significations quantitatives dans la mesure où beaucoup de détails biologiques et physiques sont ignorés, soit pour conserver la tractabilité du modèle, soit par manque d'informations. Quoi qu'il en soit, ce type de modèle génère des propriétés qualitatives qui éclairent sur des composantes diverses de l'interaction prédateur - proie. Quelques unes des propriétés ont des implications générales dans un plus large contexte, peuvent servir à tester des hypothèses et éventuellement à accroître les connaissances scientifiques.

Deux aspects, à savoir le nombre minimum de prédateurs requis pour assurer une éventuelle extinction des pucerons et la durée de la période nécessaire à cette extinction après la date du lâcher, sont considérés pour estimer l'efficacité des larves de *H. axyridis* pour éteindre les populations de *M. persicae.* Dans le cas de lâchers inondatifs, le prédateur n'est pas attendu comme un agent de régulation à long terme, mais plus souvent comme un agent d'élimination de la proie. Pour les quatre stades larvaires du prédateur, le nombre d'individus nécessaire à l'extinction des pucerons tend vers zéro quand la température tend vers l'extrême supérieur pour la croissance de la population de pucerons, et il tend vers les valeurs les plus élevées à l'autre extrémité de la gamme des températures efficaces. Dans la gamme des températures favorables aux deux espèces (15 - 24°C), le nombre minimum efficace de larves 1 et 2 du prédateur décroît de façon monotone quand la température augmente. Pour le quatrième stade, dans cette même gamme de températures, l'efficacité décroît quand la température augmente dans l'ordre inverse par rapport aux premier et deuxième stades. Avec ce scénario, l'ordre relatif d'efficacité des différents stades de *H. axyridis* passent de L1<L2<L3<L4 à 12°C à L4<L3<L2<L1 à 27°C, avec une série de transitions aux températures intermédiaires. Le temps d'élimination des pucerons à partir du lâcher du prédateur dépend également de la température et de l'âge du prédateur. Pour les quatre stades de la coccinelle, la durée de cette période décroît quand la température augmente, et cette décroissance en relation avec la température est plus forte pour les jeunes stades que pour les stades âgés. Il est donc suggéré qu'à basse température, les stades âgés sont plus performants car ils sont efficaces plus rapidement et à effectifs inférieurs. Leur utilisation doit être préférée lorsqu'une intervention est nécessitée à basse

température. Aux températures élevées, les stades jeunes sont en général au moins aussi efficaces que les stades âgés, dans la mesure où ils doivent être lâchés en effectif équivalent (cas des L3) ou inférieur (cas des L4) à celui des stades âgés, et où ils ne nécessitent qu'un temps légèrement supérieur pour l'élimination des pucerons. Leur utilisation est donc préférable à haute température. Cette suggestion peut être renforcée par des considérations pratiques. A basse température, les jeunes stades sont plus longs à éliminer les pucerons, qui ont donc plus de chance d'échapper au prédateur. Ce délai plus long accroît également la probabilité de voir le prédateur tomber au sol ou périr sous l'action des prédateurs généralistes ou des intempéries. A température élevée, les stades âgés peuvent achever leur développement rapidement avant d'avoir pu éliminer les pucerons.

Le nombre minimum de larves de coccinelles requise dépend du niveau de population de pucerons au moment du lâcher. Dans la plupart des cas ce nombre augmente rapidement avant d'atteindre un pic, puis décroît lentement, quand la population de pucerons augmente (Fig. 5-7). Ces courbes suggèrent un lâcher préférable sur de faibles populations de pucerons. Quoi qu'il en soit, cette condition peut être limitée par deux facteurs :

1) l'influence de la température sur cette efficacité (lâcher le prédateur sur de faibles densités de pucerons implique généralement d'intervenir à basse température, donc d'utiliser un grand nombre de prédateurs).

2) comme beaucoup de prédateurs, la coccinelle peut nécessiter une quantité de proies initiale minimale pour se fixer sur les colonies, ce qui est particulièrement vrai pour une espèce comme *H. axyridis* provenant d'un élevage de masse sur proies de substitution. La partie gauche de la courbe en Fig. 5-7, décrivant un fort accroissement du nombre de prédateurs requis aux stades L1 - L3 est facile à comprendre. Mais la partie droite de cette courbe, décrivant une légère diminution de l'effectif minimum de lâchers pour ces mêmes stades est inattendue. Le mécanisme sous-jacent est que lorsque la population de pucerons est supérieure à $K/2$, la moitié de la taille maximale de population, le taux de changement de population dN/dt de pucerons décroît quand N augmente.

La simulation indique également que le nombre de lâchers de prédateurs nécessaire peut être réduit en augmentant l'effectif de chaque lâcher, mais l'effectif total de prédateurs nécessaire s'en trouverait augmenté. Dans tous les cas, le nombre de lâchers pendant une saison ne pourra pas être inférieur à deux.

En pratique, dans les zones infestées par le virus de la Sharka, le seuil de tolérance de *M. persicae* est très bas pour prévenir la transmission du virus. Cela implique des interventions très précoces et efficaces rapidement. Un grand nombre de larves 3 ou 4 de *H. axyridis* serait alors requis, ce qui est économiquement irréaliste. Par ailleurs, des limites comportementales, comme la forte population initiale de pucerons pour fixer le prédateur sur ses colonies, sont en contradiction avec les objectifs de la lutte dans les zones infestées par la Sharka. En dehors de ces zones, l'utilisation de *H. axyridis* est techniquement possible, mais sa faisabilité économique dépend du coût de production et de lâcher et du bénéfice attendu des interventions.

Parmi les facteurs non incorporés dans le modèle, le plus important est sans doute le comportement de recherche des larves de coccinelle. Une perte significative de prédateurs explique l'échec de nombre d'essais de lâchers en plein champ. Le résultat de lâchers le plus satisfaisant vient probablement d'essais conduits en conditions semi-contrôlées, par lâchers de coccinelles sur des arbres encagés. Dans ce cas, nous attendons du modèle une représentation du maximum d'efficacité de *H. axyridis* comme agent de lutte biologique contre *M. persicae*.

CHAPITRE 6 :
EVALUATION DE L'EFFICACITE DE *HARMONIA AXYRIDIS* COMME AGENT DE LUTTE BIOLOGIQUE CONTRE *MYZUS PERSICAE* PAR ESSAI SUR ARBRES ENCAGES AU CHAMP

INTRODUCTION

La technique d'exclusion a été largement expérimentée pour évaluer l'efficacité, particulièrement à court terme, d'un ennemi naturel pour supprimer les populations d'un ravageur. Dans les premiers stades de développement d'un programme de lutte biologique, cette technique est particulièrement utile car elle permet généralement de collecter un grand nombre d'informations sur le ravageur et sur la plante. Elle peut permettre de conclure rapidement à l'inadéquation d'un prédateur au contrôle d'un ravageur donné. Elle peut réduire le nombre d'options pour des essais à grande échelle en plein champ. Dans notre étude de l'évaluation de *H. axyridis* pour le contrôle de *M. persicae*, ce type d'expérimentation a été jugé utile pour plusieurs raisons. Notre modèle de simulation prédisait qu'à température adéquate et à relativement faible niveau de population de pucerons, les larves de la coccinelle pouvaient être plus ou moins efficaces dans l'élimination des populations de la proie. A titre d'exemple, une intervention sur des populations de pucerons atteignant en moyenne 25 individus par rameau nécessiterait pour une extinction complète des populations un lâcher de 0.25 coccinelles du troisième stade larvaire par rameau, soit 75 individus pour un arbre de 300 rameaux. Cependant, aucun des essais que nous avons conduits en plein champ n'a permis la vérification de cette hypothèse, malgré des lâchers parfois supérieurs à 300 larves du troisième stade par arbre. L'effet des prédateurs sur les populations de pucerons n'a pu être précisé, le devenir des insectes lâchés étant par ailleurs très difficile à suivre dans ces conditions de plein champ. Il est supposé dans ce cas que la prédiction du modèle est totalement fausse, ce qui implique quelques erreurs sérieuses dans sa conception, ou que des facteurs autres que la dépendance à la température et à la densité de proie influent significativement sur les insectes lâchés en plein champ. Plusieurs raisons peuvent être évoquées :

- un grand nombre de larves de coccinelles est la proie de prédateurs généralistes tels les oiseaux et les fourmis.

- les larves tombent du feuillage faute de pouvoir s'y fixer convenablement.
- en raison d'un conditionnement préalable sur oeufs d'*Ephestia*, les larves quittent les arbres à la recherche d'habitat ou de proies plus favorables.

Les objectifs de cette expérimentation sont de deux ordres :

- comparer qualitativement aux résultats de la simulation les changements de populations *de M. persicae* induits par le lâcher de larves de *H. axyridis*.
- acquérir quelques indications sur les causes de la disparition des prédateurs lâchés.

MATERIELS ET METHODES

Huit pêchers de taille similaire sont sélectionnés et taillés pour conserver approximativement le même nombre de rameaux (250 par arbre). Chacun de ces arbres est enfermé dans une cage de 2.5 x 2.5 x 2.5 m en grillage moustiquaire de maille 1 mm. Chaque arbre est infesté le 17 mai par des pucerons verts provenant de l'élevage du laboratoire. Cinquante pousses par arbre sont marquées comme échantillon à observer. Le lendemain, quatre arbres encagés sont tirés au sort, et chacun d'entre eux reçoit 50 larves du troisième stade de *H. axyridis*, correspondant à une moyenne de 0.2 larves par pousse. Ces larves proviennent de l'élevage de masse sur oeufs d'*Ephestia,* conduit au laboratoire des invertébrés d'Antibes. Ces 50 larves sont introduites dans une boite de Pétri placée au principal point de ramification de l'arbre. Les populations de pucerons et les larves de coccinelles lâchées sont dénombrées chaque jour sur les pousses marquées. Pour les larves de coccinelles, on compte les individus. Pour les pucerons, le degré d'infestation de chaque pousse est évalué par l'indice de population suivant :

degré 0 : pas de pucerons, $N=0$.

degré 1 : faible infestation, $0<N<5^1$

degré 2 : infestation modérée, $5^1<N<5^2$

degré 3 : 2 - 3 feuilles apicales déformées, $5^2<N<5^3$

degré 4 : 3 - 5 feuilles apicales déformées, $5^3<N<5^4$

degré 5 : infestation de tout l'extrémité du rameau, $5^4<N$

Un indice d'infestation relative est calculé pour chaque arbre selon la formule :

$$IF = \frac{\sum_0^5 d \cdot f_d}{5 \cdot \sum_0^5 f_d} \qquad (6\text{-}1)$$

où *IF* est l'indice d'infestation relative, *d*: $d \in [0,1,2,3,4,5]$ le degré d'infestation; f_d : la fréquence de *d*. Il est clair que la valeur maximum de IF est 1, et le minimum 0. La valeur de IF est calculée pour chaque arbre avec ou sans larve de coccinelle. On compare la moyenne des IF des arbres avec et sans larve de coccinelles.

Les données sur le degré d'infestation des pucerons peuvent aussi être utilisées pour estimer la densité moyenne des pucerons sur une colonie :

$$\overline{N} = \frac{\sum_0^5 f_d \cdot 5^d}{\sum_0^5 f_d} \qquad (6\text{-}2)$$

où $\overline{N}$ est la densité moyenne estimée de la population de pucerons par colonie; *d*: $d \in [0,1,2,3,4,5]$ le degré d'infrstation; f_d : la fréquence de *d*.

Ici, pour chaque degré d'infestation, nous utilisons la limite supérieure de la classe de densité de population qui donne habituellement une meilleure estimation de l'infestation : une colonie de 150 pucerons devrait être classée au degré 4, mais sera le plus souvent estimée comme degré 3, car plus proche de 5^3; qui plus est, le degré 5 n'a qu'une limite inférieure. Les populations de pucerons des deux traitements sont ensuite comparées à la simulation conduite en utilisant les températures enregistrées dans une des cages. La température moyenne d'une journée est calculée par la moyenne des températures à 0, 6, 12, 18, et 24 heures.

RESULTATS

L'infestation des 4 arbres sans coccinelles s'accroît, sauf un arbre dont le IF connaît une légère décroissance (Fig. 6-1). L'indice d'infestation des 4 pêchers sur lesquels les larves de coccinelles sont lâchées décroît de manière continue à partir de la date du lâcher, le 18 mai, et tombe à zéro après 8 - 10 jours (Fig. 6-2). La comparaison des valeurs moyennes de IF pour les arbres traités et témoins démontrent plus clairement l'effet du lâcher du prédateur sur l'évolution des populations de pucerons (Fig. 6-3). Le jour précédant le lâcher, l'évolution du degré d'infestation est la même dans

les deux groupes d'arbres, de même que la distribution de fréquence des degrés d'infestation (Fig. 6-4). Après le lâcher, la fréquence des hauts degrés d'infestation décroît de manière continue jusqu'à ce que toutes les pousses soient ramenées au degré d'infestation zéro, tandis que la fréquence des hauts degrés d'infestation continue à croître sur les arbres témoins (Fig. 6-4).

Le fait que les populations de pucerons des arbres traités soient éliminées tandis que les populations des arbres témoins poursuivent leur accroissement suggère qu'un nombre efficace de larves actives de coccinelles s'est maintenu jusqu'à l'extinction des populations de pucerons. Les observations montrent que c'est effectivement le cas. Bien que la densité relative des larves de coccinelles décroisse avec la population de pucerons (Fig. 6-5), quelques larves de quatrième stade survivent et restent actives après la disparition de la proie (Fig. 6-6).

La densité moyenne de population de pucerons par colonie est estimée et suivie dans le temps par le degré d'infestation des arbres traités et témoins (Fig. 6-7a). La population observée dans les deux cas diffère des résultats de la simulation. Le changement de population dû au lâcher de coccinelles est qualitativement identique dans la simulation et dans les populations réelles (Fig. 6-7), contrairement à la population de pucerons dans les témoins, inférieure aux populations prévues par le modèle de simulation (Fig. 6-8a). Le déclin effectif des pucerons après le lâcher est moins rapide que dans la prédiction du modèle de simulation (Fig.6-8b), peut-être en raison d'une plus faible survie du prédateur en situation réelle que dans la simulation (Fig. 6-9). Ce n'est peut-être pas la cause principale, le retard par rapport à la simulation du déclin de l'infestation étant plus évident juste après le lâcher, à un moment où la survie du prédateur est plus forte dans la réalité que dans le modèle de simulation (Fig. 6-9).

Conclusion et discussion

Les résultats des tests d'exclusion indiquent qu'une complète élimination de *M. persicae* à la population initiale de 20 individus par rameau est obtenue en lâchant 50 L3 de *H. axyridis*, ce qui correspond qualitativement aux résultats de la simulation. La simulation dévie numériquement des observations d'une manière très sensible, indiquant à nouveau que la prédiction du modèle a une signification essentiellement qualitative et sous certaines conditions. La population simulée de pucerons en l'absence du prédateur s'accroît plus fortement que la population réelle. Cette différence peut résulter de facteurs limitant la croissance de la population, tels que des prédateurs

généralistes, l'état physiologique de la plante, etc. Sur arbres traités, l'élimination des pucerons est plus lente dans le système réel que dans la simulation, ce qui peut être dû partiellement à une faible survie des coccinelles, mais plus sûrement au temps passé par les larves à se déplacer le long des branches. Cet élément comportemental n'est pas incorporé dans le modèle. Bien que la simulation de l'évolution qualitative des populations des pucerons paraisse acceptable, nous hésitons à conclure sur la crédibilité du modèle pour différentes raisons. Les températures observées pendant l'expérimentation fluctuaient dans une marge étroite, plus favorables aux pucerons, et dans laquelle le comportement du modèle est attendu pour être plus stable qu'aux températures extrêmes. La population initiale des pucerons dans le système réel et dans la simulation était basse. A cette faible densité, les effets négatifs dus à la compétition intraspécifique, à la prédation, etc. sont habituellement minimisés, le changement de population de *M. persicae* dans le système réel étant alors plus proche du maximum que ce que prévoit le modèle. A haute densité de population de pucerons, la déviation de la simulation par rapport à l'observation peut s'accroître. L'hétérogénéité spatiale peut entraîner également une forte déviation du système réel par rapport à la simulation. Même en situation favorable, la prédiction ne peut être acceptable que pour une courte échelle de temps, la déviation se trouvant accrue sur une échelle de temps plus grande.

La validité de l'expérimentation est accrue par le fait que les larves de coccinelles élevées sur oeufs d'*Ephestia* semblent en mesure de s'adapter à leur nouvel habitat et à leur nouvelle alimentation, même si on peut argumenter du fait que cette adaptation est le résultat d'un confinement dans les cages. Une interrogation est posée sur la plus forte probabilité pour une larve tombée au sol de remonter dans l'arbre en cage ou en verger, et si cette probabilité est suffisante pour induire un résultat différent des lâchers en cage et au verger. L'exclusion des prédateurs généralistes de la coccinelle par l'utilisation de cages peut aussi contribuer à expliquer la meilleure élimination des pucerons en cage qu'en plein champ, malgré des effectifs lâchés plus importants dans cette dernière situation.

L'expérimentation est conduite fin mai, à une période où la population de pucerons s'accroît en général moins fortement en raison d'un feuillage moins favorable, et où une forte population de pucerons évolue vers des formes ailées pour quitter le verger. A cette période de l'année, les ennemis naturels des pucerons deviennent également plus abondants. Dans les mêmes conditions, les larves de coccinelles peuvent être très actives et voraces. Tout cela contribue à l'élimination des pucerons

par la coccinelle. Ce type de conséquence aurait pu ne pas être obtenu par un lâcher plus précoce dans la saison, à température moins élevée. Il serait d'un grand intérêt de reproduire cette expérimentation plus tôt en saison.

1997

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EFFICACITÉ DE *HARMONIA AXYRIDIS* (COLEOPTERA: COCCINELLIDAE) COMME AGENT DE LUTTE BIOLOGIQUE CONTRE *MYZUS PERSICAE* (HOMOPTERA: APHIDIDAE).

Résumé. Le puceron vert du pêcher, *Myzus persicae* Sulzer, est à l'origine de pertes croissantes dans les vergers commerciaux de pêchers du sud de la France. Des recherches sont entreprises à l'INRA sur la possibilité de contrôle biologique des populations de *M. persicae* à l'aide d'une coccinelle prédatrice introduite, *Harmonia axyridis* Pallas. Nous analysons ici l'efficacité de *H. axyridis* comme agent de lutte biologique contre *M. persicae* , par la modélisation de l'interaction proie-prédateur en fonction de la température. Les données de base pour la caractérisation de ces interactions et l'élaboration d'un modèle de simulation sont établies en laboratoire à la station de Zoologie de l'INRA d'Avignon. Le taux intrinsèque d'accroissement des populations de *M. persicae* atteint son maximum à 24°C, alors que les températures procurant la consommation de proies maximale par la coccinelle se situent aux environs de 25-27.5°C. Le taux de développement des larves de *H. axyridis* approche une valeur maximale lorsque la densité de proies augmente, et présente une réponse à la température typique des organismes poikilothermes. Le taux moyen de survie journalier âge -spécifique de *H. axyridis* s'accroît avec la densité de proies selon une courbe sigmoïde, et répond également à la température. La simulation atteste que l'efficacité des jeunes larves (L1-L3) de *H. axyridis* dans l'élimination de *M. persicae* augmente avec la température. Cette réponse ne se retrouve pas chez les larves de 4ème stade. Les larves âgées sont toujours plus efficaces que les jeunes larves à basses températures, et cet ordre s'inverse à l'autre extrémité de la gamme de températures efficaces (10-30°C), avec une série de transitions lorsque la température augmente. La simulation et les résultats d'expérimentations en conditions semi contrôlées n'établissent pas clairement les conditions de la maîtrise des populations de *M. persicae* par lâchers inondatifs de *H. axyridis* en vergers. L'efficacité du prédateur est moindre en conditions de basses températures, où la proie connaît au contraire un très fort taux d'accroissement de population. Des résultats satisfaisants sont obtenus sur arbres encagés où le lâcher d'un nombre approprié de larves de 3ème stade (50 par arbre) permet l'extinction de populations initiales de 20 pucerons par rameau. La simulation réalisée à partir des températures relevées au cours de l'expérimentation génère des résultats qualitativement conformes à l'observation.