Biological control of cotton aphid (*Aphis gossypii* Glover) in cotton (inter) cropping systems in China; a simulation study

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Biological control of cotton aphid (*Aphis gossypii* Glover) in cotton (inter) cropping systems in China; a simulation study

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op maandag 2 juni 1997
des namiddags te vier uur in de Aula.

XIA, Jingyuan

Biological control of cotton aphid (*Aphis gossypii* Glover) in cotton (inter) cropping systems in China; a simulation study / XIA Jingyuan. [S.l. : s.n.]
Thesis Landbouwuniversiteit Wageningen. - With ref. - With summary in Dutch and Chinese.

ISBN 90-5485-713-7
Subject headings: *Aphis gossypii* / *Coccinella septempunctata* / biological control / cotton / simulation

Cover: cotton–wheat intercropping and a larva of *Coccinella septempunctata* L., the key predator of *Aphis gossypii* Glover on cotton.

Propositions

1. Current cotton–wheat intercropping systems have an "overcapacity" for biological control of *Aphis gossypii.*
   This thesis

2. Two mechanisms, "disruptive crop" and "natural enemies", explain the reduced *Aphis gossypii* densities in intercropped cotton.
   Vandermeer, J., 1989. The ecology of intercropping. Cambridge University Press, Cambridge, UK, 237 p.
   This thesis

3. *Coccinella septempunctata* plays a key role in suppressing *Aphis gossypii* populations in monocultures of cotton but its numbers increase too late to prevent damage.
   This thesis

4. Predation on mixed *Aphis gossypii* stages by *Coccinella septempunctata* can be modeled as a competitive process.
   This thesis

5. Dispersal of foraging *Coccinella septempunctata* from intercropped wheat into intercropped cotton can be modeled as a diffusion process, and the resulting distribution ratio over cotton and wheat rows is equal to the quotient of the residence times.
   This thesis

6. Cotton–wheat intercropping at the "strip" scale is the optimal cotton growing strategy, in view of the conflicting objectives of pest and disease control, seed and lint quality, labor productivity and land productivity.
   This thesis

7. Without a systems perspective, more efforts are made for the less important processes while less efforts are made for the more important processes.

8. Intercropping of cotton with wheat in China has received more interest from growers than from researchers.

9. Short-term chemical control strategies "rear" the cotton bollworm (*Helicoverpa armigera*).

10. Social and environmental aspects are decisive for acceptance of biological control.

10. Biotechnology is a valuable instrument for improving components of agricultural systems, but an ecotechnological systems approach is indispensable to put the components in the proper place.

12. In nowaday's research, interdisciplinary efforts are needed for picking the "top tree apples".

Propositions associated with the Ph.D. thesis of XIA Jingyuan:

Biological control of cotton aphid (*Aphis gossypii* Glover) in cotton (inter) cropping systems in China; a simulation study

Wageningen, 2 June 1997

中国单作棉田与套作棉田棉蚜（*Aphis gossypii* Glover）生物防治系统模拟研究

夏 敬 源

This thesis is dedicated to my wife WANG Shumin and my son XIA Yining

Abstract

Cotton aphid (*Aphis gossypii* Glover) is the key pest of seedling cotton in China, particularly in the North China cotton region. Biological control with naturally-occurring seven-spot beetle (*Coccinella septempunctata* L.) is crucial for integrated control of aphids and other pests in cotton. The objective of this study is to obtain quantitative insight in the coccinellid–aphid system in cotton (inter) cropping and explore intercropping strategies for cotton aphid biological control applying a systems approach.

Life table parameters of *A. gossypii* as influenced by temperature, and life history parameters of *C. septempunctata* as influenced by temperature and food quantity, were determined in the laboratory. Relationships of life cycle parameters with abiotic and biotic factors were described with mathematical equations and incorporated in a simulation model of the temporal dynamics of the coccinellid–aphid system in cotton. The functional responses of five foraging stages of *C. septempunctata* on three size-groups of *A. gossypii* as influenced by temperature were determined in the laboratory. All functional responses were of type II and were adequately described by Rogers' random predator equation. They were incorporated in the simulation model.

The model was tested and evaluated at three levels of complexity: laboratory, field cage and open field. At each level of complexity, processes were added to the model, based on discrepancies between "original model" behaviors and observations, and additional experimentation. Simulations with the final validated model at the open field level show that *C. septempunctata* plays a key role in controlling *A. gossypii* in cotton monoculture, though its numbers increase too late to guarantee a sufficient biological control. Variations in abundance of the seven-spot beetle are the most important factor causing year to year differences in aphid population dynamics.

A simulation model of the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercropping was developed by complementing the temporal model with calculations accounting for dispersal of the seven-spot beetle within the intercrop. Simulations show that the low abundance of *A. gossypii* in the current cotton–wheat intercropping systems is mainly due to greater and earlier mortality caused by predation and parasitism, where predation by *C. septempunctata* is the most important factor. Other beneficial effect is a 90% decrease in cotton aphid settlement.

Simulations with the spatio-temporal biological control model shows that current cotton–wheat intercropping system has an "overcapacity" for cotton aphid biological control. This "overcapacity" provides opportunities for modifying intercropping systems in the direction of strip cropping, which is advantageous with respect to labor requirement, fiber and seed quality, and suppression of *Helicoverpa armigera* Hübner and *Verticillium dahliae* Kleb. by cultural practices.

Key words: *Aphis gossypii, Coccinella septempunctata*, prey–predator system, biological control, dispersal, population dynamics, simulation model, cotton monoculture, cotton–wheat intercropping

提要

棉蚜（*Aphis gossypii* Glover）是中国，特别是北方棉区棉花苗期的主要害虫。增殖保护利用自然发生的七星瓢虫（*Coccinella septempunctata* L.）是综合治理棉蚜及其它棉花害虫的关键。本研究旨在应用系统分析方法，揭示单作和套作棉田七星瓢虫一棉蚜系统的数量动态规律，开发适合于棉蚜生物防治的棉花套作技术。

室内研究了温度对棉蚜生命表参数及温度与猎物密度对七星瓢虫个体发育史参数的影响。所有这些参数与非生物及生物因子的关系均用数学方程定量描述，后者用于建立棉田七星瓢虫一棉蚜系统时间动态模拟模型。室内还研究了3个棉蚜体积组及温度对七星瓢虫5个捕食虫态的捕食功能反应的影响。所有的功能反应均属II型，并用Rogers 随机捕食模型进行了定量描述。全部捕食功能反应方程用于建立棉田七星瓢虫一棉蚜系统时间动态模拟模型。

所建立的七星瓢虫一棉蚜系统时间动态模型在室内、田间罩笼和大田进行不同系统复杂性层次的检验与评价；根据模拟值与观察值的离散程度和新的参数试验结果，在每一层次引入有关的生态学过程，最终形成单作棉田七星瓢虫一棉蚜系统时间动态模拟模型。大田模拟研究表明，七星瓢虫是单作棉田棉蚜种群的关键调控因子，但因其发生数量上升太晚而不能有效地控制住蚜害。

基于单作棉田七星瓢虫一棉蚜系统时间动态模拟模型，进一步引入七星瓢虫扩散及有关的生态学过程，从而建立了麦套棉田七星瓢虫一棉蚜系统时空动态模拟模型。模拟研究表明，现行麦套棉系统的棉蚜发生数量较低主要是因较高和较早的捕食与寄生死亡率所致，其中以七星瓢虫的捕食最为重要；其次为有翅蚜的迁入率降低90%。

时空动态生物防治模拟研究表明，现行麦套棉系统的棉蚜生物防治能力过剩。这种过剩的生物防治能力将有助于改进现行的麦套棉系统朝着麦棉条带种植的方向发展，从而提高农事操作的机械化程度，改进纤维和种子品质，减轻棉铃虫（*Helicoverpa armigera* Hübner）和棉花黄萎病（*Verticillium dahliae* Kleb.）的猖獗为害。

关键词： 棉蚜　七星瓢虫　捕食者一猎物系统　生物防治　扩散　种群动态
模拟模型　单作棉　麦套棉

Preface

The work reported in this dissertation was funded by the "Sandwich PhD Program" of the Wageningen Agricultural University (WAU), the Netherlands, and the "Integrated Cotton Pest Management Project" of the State Science and Technology Committee (SSTC), China. The idea for this research was formed during my first visit to the Department of Theoretical Production Ecology (TPE), WAU (from July to October 1992). The experimental work was done at the China Cotton Research Institute (CCRI), the Chinese Academy of Agricultural Sciences (CAAS). The experimental data analysis and simulation started during my second visit to TPE-WAU (from September 1993 to March 1994). The work was finalized during my third visit to TPE-WAU. I gratefully acknowledge the support given by WAU, TPE-WAU, SSTC-China and CCRI-CAAS.

I am indebted to Prof. Rudy Rabbinge, my promotor, for his scientific guidance, understanding and moral support. His interest in my research has been a constant source of inspiration. His sharp ideas on the systems analysis and rich experience in simulation modelling were extremely useful for setting the experimental plan and the whole framework of this thesis. His short visit to CCRI was of prime importance for the layout of the series experiments. His critical comments and constructive suggestions on the manuscripts of all chapters of this thesis have been very valuable to me. His broad and deep thinking enabled me to gain more knowledge from the work throughout the programme. I am also grateful to his wife Marja for her hospitality.

My co-promotor Dr. Wopke van der Werf's day to day advice was indispensable for the successful completion of this thesis. His professional skills in systems modelling and strong background in applied mathematics were very helpful for analysing the experimental data and developing the simulation models. His visit to CCRI was extremely important for the successful completion of the experiments. The thesis would never have come out like such shape without his critical review of each page. My sincere thanks is also extended to his wife Saskia for her hospitality.

Dr. Kees G. Eveleens was one of those who encouraged me to work on this topic and initialize this study. His experience in cotton IPM and critical comments on the manuscripts of all chapters of this thesis have been very valuable to me.

Prof. Frits W.T. Penning de Vries was also one of the those who encouraged me to work on this topic and initialize this study. Parts of the thesis received valuable comments and suggestions from him. My sincere appreciation is also extended to his wife Coby for her hospitality.

I am very appreciative to Gon van Laar for her help in setting the final layout of the thesis and checking the manuscripts of the thesis word by word. Her editorial skills and valuable advice have been very useful for the final representation of this thesis.

I thank Prof. Jan Goudriaan and Dr. Peter A. Leffelaar for their help with simulation and programming. Drs Walter Rossing and Joop de Kraker are acknowledged for the scientific discussions of some mathematical equations, and Ing. Rob T. Dierkx for the technical assistance in using the computer software. I am also grateful to Prof. Martin Kropff for his understanding and friendship.

I wish to thank Mrs Lien Uithol, Ria Boleij and Alexandra Nagel for their excellent secretarial assistance.

My deep gratitude and heartfelt thanks are due to Prof. ZHU Dewei, the vice-president of CAAS, for his encouragement, understanding and moral support. My profound appreciation is also due to Mr. QIAN Yongzhong, the assistant director of CCRI, and Mr. SONG Xiaoxuan, the vice-chairman of the Plant Protection Department (PPD) of CCRI, for taking over responsibilities during my stay overseas.

I wish to express my earnest thanks and deep appreciation to MA Yan, WANG Chunyi, CUI Jinjie, XI Jianping, WANG Yueheng and ZHANG Shiliang of PPD-CCRI for their day to day assistance with the tremendous amount of experimental work, which was indispensable for the successful completion of this thesis.

My sincere indebtedness is extended to Mr. Tom Schiphorst, the senior expert of horticulture of the Netherlands A. M. Schiphorst b.v. for his warm heart help and philosophical discussions, which made my stay at Wageningen memorable. My deep sense of gratitude is also extended to Ms. ZHANG Liru for her kindness and help.

Many thanks to my office mates Ms. Jacaranda van Rheenen and Mr. Daniel Rodriguez, and my Chinese friends at Wageningen, for their friendship.

Finally, a special thanks goes to my dear wife WANG Shumin and my lovely son XIA Yining for all their understanding and moral support throughout this thesis research. Their patience with a stressed husband and father and their tolerance of the extended periods of separation significantly contribute to the overall success of this study. Shumin, you have done a marvellous job in keeping everything organized, and your editorial skills regarding the production of the thesis is more than appreciated. Yining, you have done a wonderful job in your study, and your excellent studying record comforted me a lot even though you were neglected during the last four years. Last but not least, I wish to thank my parents, my elder sister and my elder brother who have always supported me in my professional development.

XIA Jingyuan
Wageningen, April 1997

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Chapter 1

General introduction

1.1 Introduction

Cotton plays a significant role in the economic and social development of China. It produces natural fibre, vegetable oil and animal feed. Since the mid 1980s, China has become the largest cotton producer in the world (Liu & Deng, 1984). About 5.5 million ha (1/6 of the world's total) are grown with cotton annually, yielding a total lint production of 4.5 million metric tons (1/4 of the world's total) (Wang, 1996). Cotton is the basis of the nation's textile industry and a major source of foreign exchange. About 1/3 of the nation's export earnings come from cotton textile fabrics (Wang, 1993). At present, around 100 million farmers are associated with cotton production and 80 million people are involved in cotton textile industry (Wang, 1992).

Cotton is widely cultivated in China, from 19 °N to 45 °N, from 124 °E to 75 °E, and from 150 m below sea level to over 2000 m above sea level (CCRI, 1983; Xia, 1991). Three cotton producing regions are generally distinguished: the North China cotton region, the South China cotton region, and the Northwest inland (Xinjiang) cotton region. Of the three regions, the North China cotton region is the most important as it represents over 60% of the nation's cotton production and cotton areas (Liu & Deng, 1984; Xia, 1991).

The North China cotton region is located in a warm temperate zone, with a frost-free period of 180–230 d, an average annual temperature of 11 °C and an annual precipitation of 400–700 mm (CCRI, 1983). It comprises the major cotton producing provinces of Shandong, Henan, Hebei, Shanxi and Shaanxi as well as the North part of Huai River in the provinces of Anhui and Jiangsu (CCRI, 1983; Xia, 1991). The principal cotton cropping systems are cotton monoculture and cotton–wheat intercrop (Wang, 1990; Fang et al., 1992). All cultivated cottons belong to *Gossypium hirsutum* L. (upland cotton), with direct seeding (50%), plastic mulching (30%) and seedling transplanting (20%) (Wang, 1990; Xia, 1991).

Cotton suffers from more arthropod pests than other field crops in the North China cotton region. Over 300 species of arthropod pests have been recorded to be injurious to cotton, with 30 species of major significance. The key pests are cotton aphid (*Aphis gossypii* Glover) and cotton bollworm (*Helicoverpa armigera* Hübner) (CCRI, 1983;

Xia, 1991). Estimated annual losses caused by cotton aphid amount to 10–15% of the attainable yield (CCRI, 1983; Fang et al., 1992; Xia, 1993).

1.2 Cotton cropping systems

1.2.1 Cotton monoculture

Before the 1980s, the principal cotton cropping system in the North China cotton region was cotton monoculture, constituting over 90% of the region's cotton land (CCRI, 1983). At present, single cotton cropping covers less than 40% of cotton acreage in this region due to the expansion of cotton–wheat intercropping (Xia, 1994b). Cultivars with early-medium or medium maturation are used for cotton monoculture, with a growing period of 160–170 d or 180–200 d (CCRI, 1983).

Two developmental stages are generally distinguished for pest management purpose: seedling and square-boll. At the seedling stage, the key pest is cotton aphid, and the secondary pests are cutworm [*Agrotis ypsilon* (Rott.)], cotton thrips (*Thrips tabaci* Lindeman) and red spider mite (*Tetranychus urticae* Koch). At the square-boll stage, cotton bollworm is the most destructive, and the pests of minor importance include plant bugs (*Adelphocoris* sp.), pink bollworm (*Pectinophora gossypiella* Saunders), spiny worm (*Earias* sp.) and small measuring worm (*Anomis flava* Fabricius) (CCRI, 1983; Xia, 1991; Fang et al., 1992).

1.2.2 Cotton–wheat intercrop

Since the early 1980s, there has been a rapid development of cotton–wheat intercropping in the North China cotton region because of the increased human populations who demand more food and fiber from the limited lands (Wang, 1990; Wang et al., 1993). The cotton–wheat intercropped acreage increased from 0.4 million ha in 1978 to 2.3 million ha in 1993, covering more than 60% of the region's cotton land (Xia, 1994b).

Cotton–wheat intercropping (actually cotton–wheat relay cropping) refers to intercropping of an early-medium maturing cultivar of cotton with an early-medium maturing cultivar of winter wheat. The wheat is sown in the mid October upon harvest of cotton, with a designated row width left out for cotton. The cotton is sown in mid April, with the whole seedling stage overlapping with the maturation phase of wheat. Three patterns of cotton–wheat intercropping are commonly practised: three rows of wheat with one row of cotton (3–1 pattern), three rows of wheat with two rows of cotton (3–2 pattern), and four rows of wheat with two rows of cotton (4–2 pattern)

(Wang, 1990). The 3–2 pattern is the most common as it brings about desirable yields of both crops (Mao & Gou, 1992).

There are two advantages of cotton–wheat intercropping: substantially increased productivity per unit land and reduced damage by cotton aphids at the seedling stage (Wang, 1990; Xia, 1994b). For instance, one ha land with a 3–2 pattern of wheat–cotton intercropping typically produces approximately 3000 kg of wheat grain and 850 kg of cotton lint. To obtain such amounts of wheat grain and cotton lint in monocultures, one would need about 1.5 ha of land as, in general, one ha of single cropped wheat produces 5000 kg of wheat grain and one ha of single cropped cotton produces 1000 kg of cotton lint.

Wheat is the major winter crop in the North China cotton region, where most cotton insect pests and their natural enemies overwinter and multiply in early spring. Thus, structures of insect communities and the dynamics of major insect pests in cotton–wheat intercrop are quite different from those in cotton monoculture, particularly at the seedling stage (Xia et al., 1997). It is well known that cotton aphid population numbers at the seedling stage remain below economic damage levels in cotton–wheat intercrop if naturally-occurring natural enemies on wheat, especially the seven-spot ladybird beetle (*Coccinella septempunctata* L.), are preserved (Chen et al., 1991; Wang et al., 1993; Xia, 1994b).

1.3 Cotton–aphid–enemy system

1.3.1 Cotton aphid

Aphis gossypii is extremely polyphagous with over 10 species of primary hosts (e.g. *Hibiscus syriacus* L. and *Zanthoxylum simulans* Hance) and more than 60 species of secondary hosts (e.g. cotton, soybean, citrus, and many vegetable crops and ornamental plants) (CCRI, 1983; Slosser et al., 1989; Fang et al., 1992).

The cotton aphid is holocyclic in the North China cotton region, where it overwinters as eggs on primary hosts (CCRI, 1983; Zhang et al., 1987). Egg hatch occurs in March when temperature rises above 6 °C. The aphid multiplies two to three generations on the overwintering hosts before alate adults are produced due to crowding and deteriorated nutrition. Alate adults immigrate into cotton fields upon emergence of seedlings from late April to mid May, where 15–17 generations are produced before the cotton harvest. In autumn, gynoparae and males appear in response to short daylength and low temperature. These morphs return to the primary hosts, where the gynoparae produce oviparae which oviposit eggs after mating with the males (CCRI, 1983; Fang et al., 1992). There are two aphid peaks in cotton fields. The first peak ("spring aphid") occurs at the seedling stage (from mid May to early June) and the second one ("summer aphid") appears at the square-boll stage (from late June to late July) (CCRI, 1983; Luo & Gao, 1986). Biological control is considered a promising option for the "spring aphid" (CCRI, 1983; Zhang, 1985).

Damage to cotton at the seedling stage by the cotton aphid results from distortion of leaves and stunted growth of young plants, which severely retards the development and closure of the leaf canopy and decreases light interception and production. Replanting is required in severe cases of irreversible stunting and seedling mortality (CCRI, 1983; Fang et al., 1992). At the square-boll stage, premature defoliation and decreased photosynthesis directly reduce yield formation (Luo & Gao, 1986). At the boll opening stage, accumulation of honeydew and the development of sooty molds lower the quality and grading of the lint (Luo et al., 1990). In recent years, honeydew on the lint (sticky cotton) has caused serious problems in the milling process in many cotton producing nations, such as China (Luo et al., 1990), Egypt (Attia & El-Hamaky, 1987), Israel (Broza, 1986), Sudan (Abdelrahman & Munir, 1989) and USA (Slosser et al., 1989; Hardee & O'Brien, 1990).

The cotton aphid has five developmental stages: four nymphal instars and the adult (apterous and late). Its field population dynamics is influenced by (a) temperature, relative humidity, rainfall and wind (both speed and direction) (CCRI, 1983; Fang et al., 1992); (b) crowding (Xie & Sterling, 1987; Li & Xie, 1990b); (c) natural enemies (CCRI, 1983; Zhang et al., 1983; Zhang, 1985; Jiu et al., 1986; Fan et al., 1991); and (d) resistant cultivars, cotton developmental stages and its physiological conditions (Gao, 1987; Liu & Wang, 1990; Wu et al., 1990; Liu & Yang, 1993). Quantitative information on field population dynamics of the cotton aphid is generally lacking.

1.3.2 Natural enemies

More than 850 species of natural enemies have been described to attack insect and mite pests on cotton in China, though only a small proportion of these have a significant impact (Xia, 1991). About 60 beneficial species commonly attack *A. gossypii*, including predators, parasites and fungal pathogens, with the major ones presented in Table 1.1. The importance of natural enemies, particularly predators, in controlling the cotton aphid has been noted for a long time (CCRI, 1983; BU, 1984).

Predators Of the major predators listed in Table 1.1, ladybird beetles, particularly *Coccinella septempunctata*, play the most important role in controlling *A. gossypii* on cotton. (CCRI, 1983; BU, 1984; Fang et al., 1992).

Coccinella septempunctata passes through five generations annually in the North China cotton region (Zhu & Li, 1981). The adults overwinter at the surface soil in winter wheat, oil-seed rape and vegetables, and start egg-laying in March. The first two generations occur mainly on wheat and oil-seed rape from March to May. Some coccinellid adults of the overwintering generation and the first generation may colonize single cotton cropped fields, depending on the availability of the cotton aphid.

Table 1.1. Major natural enemy species of *A. gossypii* on cotton in the North China cotton region.

Group	Order	Family	Species
Predator	Hemiptera	Anthocoridae	*Orius minutus* L.
		Lygaeidae	*Geocoris sp.*
		Nabidae	*Nabis sinoferus* Hsiao
			N. stenoferus Hsiao
	Neuroptera	Chrysopidae	*Chrysopa formosa* Brauer
			C. phyllochroma Wesmael
			C. septempunctata Wesmael
	Coleoptera	Coccinellidae	*Coccinella septempunctata* L.
			Scymnus hoffmanni Weise
			Adonia variegata (Goeze)
			Leis axyridis (Pallas)
			Propylaea japonica (Thungberg)
	Diptera	Syrphidae	*Syrphus corollae* Fabricius
			Melanostoma scalare Fabricius
			Epistrophe balteata De Geer
			Lasiopticus selenitica (Meigen)
	Arachnida	Erigonidae	*Erigonidium graminicolum* (Sundevall)
		Lycosidae	*Lycosa T-insignita* (Boes. et Str.)
		Theridiidae	*Theridion octomaculatus* (Boes. et Str.)
Parasite	Hymenoptera	Aphidiidae	*Aphidius gifuensis* (Ashmead)
			Lysiphlebia japonica (Ashmead)
			Trioxys rietscheli Mackauer
	Acari	Trombidiidae	*Allothrobium neapolitum* Willmann
			A. pulvinum Ewing
Pathogen	Entomophthorales	Entomophthoraceae	*Entomophthora fresenii* Batk *E. virulenta* Hall. et Dunn

Source: CCRI (1983); BU (1984); Jiu et al. (1986); Fang et al. (1992); Zhao (1995).

The most important colonization wave of seven-spot beetle adults in cotton occurs during the second generation, when wheat and oil-seed rape are maturing and aphid populations on these crops decline. The large number of seven-spot beetles and other predators (Table 1.1) immigrating into cotton at this time can destroy any remaining aphids within a few days. After cotton aphid populations have been destroyed, the landscape offers insufficient resources for coccinellids, causing them to migrate long distance, presumably to cooler areas such as the mountains and the seashore (Tsai et al., 1980; Zhu & Li, 1981). The remaining coccinellids complete the third and fourth generation in cotton and vegetables during June and July. They aestivate on corn, sorghum and cotton during August and September. A fifth generation lives on vegetables during late September to late October. Adults of the fifth generation and the ones migrating back from the mountains and the seashore move into wheat, oil-seed rape and vegetables for overwintering (Zhu & Li, 1981; CCRI, 1983; BU, 1984; Fang et al., 1992).

The seven-spot beetle is the key predator of the cotton aphid. It has seven developmental stages: eggs, four larval instars, pupae and adults (females and males). The foraging stages of the seven-spot beetle can attack all life stages of the cotton aphid. Several observations have been made for consumption rates of the different foraging stages of the seven-spot beetle when supplied with excess cotton aphids at fluctuating temperatures in the laboratory (BU, 1984). No detailed studies have been carried out on the functional response of foraging stages of the seven-spot beetle as influenced by predator stage, prey stage and temperature.

Field population dynamics of the seven-spot beetle is largely determined by (a) temperature, relative humidity and rainfall (Zhu & Li, 1981), (b) overwintering numbers and cannibalism (CCRI, 1983; BU, 1984), (c) prey density (Dong & Wang, 1989), and (d) natural enemies including predators, parasites and entomophagous pathogens (Zhu & Li, 1981; BU, 1984; Li, 1986). Few quantitative studies have been made on field population dynamics of the seven-spot beetle, particularly in cotton–wheat intercropping.

Parasites Two groups of parasites commonly attack the cotton aphid: external and internal. Mites from the genus *Allothrombium* (Table 1.1) externally parasitize alate adults on winter hosts (Chen et al., 1994). Parasitized alate adults can fly and colonize cotton, but longevity and fecundity are substantially reduced (Dong et al., 1992). The percentage of alate immigrants carrying *Allothrombium* ranges from 10% to 50%, depending on the weather conditions and the time of year (Dong et al., 1992). These parasitic mites have a major impact on cotton aphid population growth in the early season when other natural enemies of the cotton aphid are rare (Dong et al., 1992; Chen et al., 1994).

Three hymenopterous parasitoids (Table 1.1) commonly parasitize the cotton aphid at the mid-late seedling stage (4–8 leaves). *Lysiphlebia japonica* is the most common (Xie & Sterling, 1987; Wang & Liu, 1989). Percentage of parasitization of the cotton aphid varies from season to season and from place to place, ranging from 5% to 30% (CCRI, 1983; Xie & Sterling, 1987). Cotton aphid populations decline rapidly when parasitization is more than 30% (CCRI, 1983; Fang et al., 1992).

Fungal pathogens Fungal pathogens of the genus *Entomophthora* commonly attack the cotton aphid (Table 1.1), but only occasionally are fungal diseases important in suppressing "spring aphid" populations. Early impact may occur in years with high rainfall in early June (Zhang et al., 1983). Quite frequently fungal epidemics have a significant effect on "summer aphid" populations, particularly in years with high temperature and heavy rainfall in late June and July (CCRI, 1983). Introduction of *Entomophthora* for "spring aphid" control has not been successful (Zhang et al., 1983; Xia, 1992).

1.3.3 Cotton plant

Resistant cultivars Development of resistant cultivars is an effective method for cotton aphid control. Over 1000 accessions of cotton germplasm have been evaluated for resistance to the cotton aphid, with 300 exhibiting medium to high degrees of resistance (Xia, 1996). Resistance to the cotton aphid is associated with (a) morphological characters such as nectarines and hairiness, and (b) increased content of chemical defence such as gossypol or tannin (Guo et al., 1990; Liu & Yang, 1993). Although three aphid-resistant cultivars have been released into production, they are not frequently used as their yield is 10–15% lower than that of the susceptible ones (Guo et al., 1990; Xia, 1996).

Development stage Cotton aphid population development is related to plant growth stage. Survival of the cotton aphid is highest when fed on 4-leaf seedlings, lowest on 8-leaf seedlings, and intermediate on 2-leaf seedlings (Wu et al., 1990). Biochemical analysis indicates that cotton seedlings before the 4-leaf stage are nutritionally more suitable for the aphid than thereafter (Gao, 1987; Wu et al., 1990).

Physiological conditions Population growth of the cotton aphid is influenced by the physiological condition of the cotton plant, which depends on management practices, particularly the application of fertilizer. Liu & Wang (1990) found that the cotton aphid was most abundant in plots with a high rate of nitrogen fertilizer. The content of soluble nitrogen and protein in cotton plants is increased by applying nitrogen, which, in turn, increases survival and fecundity of the cotton aphid (Liu & Wang, 1990; Zuo et al., 1991; Fang et al., 1992).

1.4 History of cotton aphid control

Cotton has been cultivated in China for over 2000 years. Through the centuries, *A. gossypii* was suppressed by naturally-occurring natural enemies such as *C. septempunctata* (Liu & Deng, 1984). In the early 1950s, insecticides were introduced against the cotton aphid in the North China cotton region, when it occurs only at the seedling stage. In the 1960s, chemical control of the cotton aphid became predominant, which resulted in a rapid development of insecticide resistance (Xia, 1993). Subsequently, outbreaks of the cotton aphid occurred not only at the seedling stage but also at the square-boll stage because of resistance to insecticides and suppression of natural enemy populations (CCRI, 1983; Xia, 1993).

The interest in biological control revived in the early 1970s, following the areawide failure to control the cotton aphid with insecticides (Zhang, 1985; Xia, 1993). During that period, some success was achieved with biological control by preserving ladybird beetles through seed or soil treatment with systemic pesticides (e.g. carbufuran and phorate), and by mass releasing the seven-spot beetle collected on wheat (BU, 1984; Liu, 1985). In the early 1980s, biological control of the cotton aphid was discontinued because newly introduced synthetic pyrethroids provided effective control (Fang et al., 1992; Xia, 1993). But resistance developed soon and natural enemies were suppressed, resulting in resurgence of a range of pests apart from the cotton aphid (Zuo et al., 1986; Tan, 1988; Tang, 1988; Wu & Liu, 1992; Xia, 1993). The red spider mite and cotton thrips caused injuries at the seedling stage, while the cotton bollworm became more damaging at the early square-boll stage due to serious disruption of natural enemy communities by chemical control of the cotton aphid in early season (Wu & Liu, 1992). Towards the late 1980s, the cotton aphid had developed resistance to nearly all kinds of conventional insecticides (Tan, 1988; Tang, 1988; Xia, 1993), and serious outbreaks of the cotton bollworm occurred (Xia & Wen, 1993; Xia, 1994a; Xia, 1997). The interest in biological control of the cotton aphid by naturally-occurring natural enemies increased again after the mid 1980s, following the crisis induced by aphid control with pyrethroids. Several strategies for biological control of the cotton aphid were tested, including augmentation, preservation and mass release of natural enemies (Fang et al., 1992; Xia, 1992). Much success was obtained with augmentation of naturally-occurring natural enemies by intercropping cotton with wheat or oil-seed rape (Wang et al., 1993; Xia, 1994b). Nowadays, biological control of the cotton aphid by naturally-occurring natural enemies, particularly by the seven-spot beetle, is considered the pivot of the integrated cotton pest management program both for cotton monoculture and cotton–wheat intercrop in the North China cotton region (Wang et al., 1993; Xia et al., 1996).

A historical analysis of cotton aphid control in the North China cotton region reveals that the sole reliance on insecticides has led to a rapid development of insecticide resistance, serious outbreaks of key pests, resurgence of secondary pests, and risk for man and environment. Induction of cotton aphid outbreaks by insecticides in cotton has become a major problem also in other cotton producing countries, such as Australia (Forrester, 1986), Egypt (Attia & El-Hamaky, 1987), Israel (Broza, 1986), Sudan (Abdelrahman & Munir, 1989) and USA (Kerns & Gaylor, 1993).

Biological control of the cotton aphid is the first priority for integrated pest management in cotton to avoid early season application of insecticides and lay a foundation for effective biological control during the season.

1.5 Objective of the study

Experience has shown that biological control of *A. gossypii* on cotton with *C. septempunctata* is effective and feasible. There are basically three strategies for using the seven-spot beetle as a biological control agent: (1) augmentation of the seven-spot beetle by intercropping cotton with wheat, (2) preservation of the seven-spot beetle by using selective instead of broad spectrum insecticides and seed or soil treatment with systemic pesticides, and (3) mass release of the seven-spot beetle collected on wheat. Intercropping cotton with wheat is the most commonly used approach for cotton aphid control. However, there exist several disadvantages in current cotton–wheat intercropping, such as decreased fiber and seed quality due to the delayed maturation of cotton, increased outbreaks of cotton bollworm and verticillium wilt (*Verticillium dahliae* Kleb.) due to a high survival of overwintering pests, and difficulties with mechanization due to the narrow space between cotton and wheat rows (Wang, 1990; Wang, 1992, 1993; Xia & Wen, 1993; Xia, 1994a; Wang & Xiang, 1997). Nowadays, there is an increased demand for development of more sociologically, economically and ecologically sound cotton–wheat intercropping systems. Biological control of the cotton aphid should play an important role in such cropping systems. A better quantitative understanding of the dynamic behavior of the *C. septempunctata–A. gossypii* system both in cotton monoculture and cotton–wheat intercrop is helpful in applying intercropping strategies for biological control of the cotton aphid.

Systems analysis and simulation are powerful tools to analyse biological control systems and prototype promising biological control strategies (Rabbinge et al., 1989). To date, little research has been done along this line in China. This thesis research aims at: (1) better understanding and characterizing the major processes in the *C. septempunctata–A. gossypii* system quantitatively, both in cotton monoculture and cotton–wheat intercrop; (2) developing a simulation model of the temporal dynamics of the coccinellid–aphid system in cotton monoculture, and a simulation model of the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercrop, by integrating process-level knowledge; and (3) using the models to obtain insight in the dynamic behavior of the predator–prey system and explore intercropping strategies that are not only favorable for biological control of cotton aphid but also advantageous with respect to fiber and seed quality, labor requirement, and suppression of the cotton bollworm and verticillium wilt by cultural control measures.

The insights gained in this study are useful in: (1) allowing more effective use of the seven-spot beetle as a biological control agent of the cotton aphid, (2) obtaining better biological control of the cotton aphid with the whole natural enemy complex rather than the seven-spot beetle alone, and (3) maximizing the natural control potential but minimizing the insecticide application when managing cotton insect pests throughout the season.

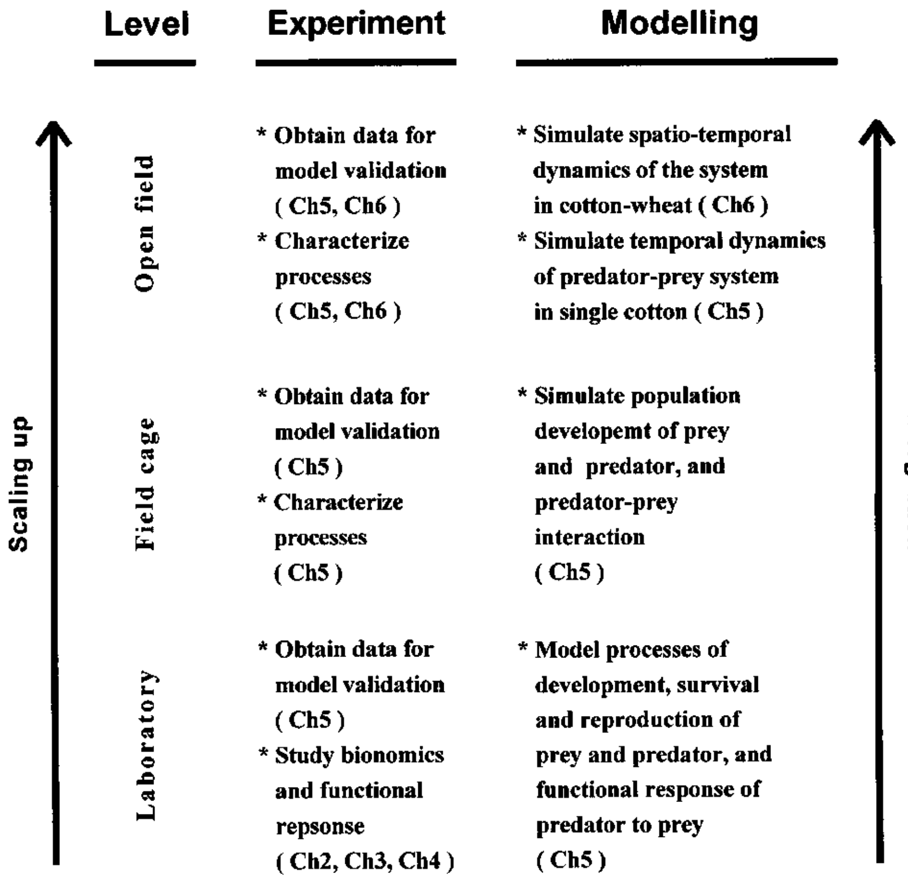
1.6 Approach of the study

A Holistic–Reductionistic–Holistic (HRH) approach (Bouma, 1997; Rabbinge, personal communication) is applied in this thesis research. The main idea for applying this approach is to answer questions at higher levels of system complexity by integrating detailed knowledge at lower levels. Based on the questions formulated in the previous section, detailed knowledge is gathered about the bionomics of *A. gossypii* and *C. septempunctata* in North China, the stage structured predator–prey interaction, and the migration and dispersal of *A. gossypii* and *C. septempunctata* in cotton monoculture and cotton–wheat intercrop. Because of the complex interrelationships involved in the coccinellid–aphid system, three levels of system complexity are distinguished in the systems analysis: laboratory, field cage and open field (Fig. 1.1). The major component processes are worked out at the respective levels, by experimentation and modelling. A comprehensive model is finally developed by integrating all process-level knowledge about the system, and the model is then used to study the dynamics behavior of the system, to develop management strategies and to set research priorities at the field level.

The detailed experimental–simulation methodology is presented in Fig. 1.1. At each level of the system complexity, relevant processes were added to the model, based on additional experimentation, and the adapted model was validated with experimental data collected at the respective level. Only when the integrated model at a lower level explains the observed behavior of the system at that level, it can be subjected to tests at a higher level. Otherwise, more research and modelling work should be done at the lower level until a satisfactory explanation has been reached.

1.7 Outline of the thesis

The thesis describes experiments at laboratory, field cage, and open field level, and uses simulation modelling as an integrative tool and bridge between integration levels. Laboratory experiments addressed the bionomics of *A. gossypii* and *C. septempunctata*, and the functional response (Chapters 2, 3 and 4). In Chapter 2, life table parameters of the cotton aphid as influenced by temperature are determined, and their relationships with temperature are described with mathematical equations. In Chapter 3, life history parameters of the seven-spot beetle as influenced by temperature and by food quantity are determined, and their relationships with these two factors are



Level	Experiment	Modelling
Open field	* Obtain data for model validation (Ch5, Ch6) * Characterize processes (Ch5, Ch6)	* Simulate spatio-temporal dynamics of the system in cotton-wheat (Ch6) * Simulate temporal dynamics of predator-prey system in single cotton (Ch5)
Field cage	* Obtain data for model validation (Ch5) * Characterize processes (Ch5)	* Simulate population developemt of prey and predator, and predator-prey interaction (Ch5)
Laboratory	* Obtain data for model validation (Ch5) * Study bionomics and functional repsonse (Ch2, Ch3, Ch4)	* Model processes of development, survival and reproduction of prey and predator, and functional response of predator to prey (Ch5)

Fig. 1.1. Outline of the combined experimental–simulation methodology for a simulation study on biological control of *A. gossypii* in cotton (inter) cropping systems in China.

described with mathematical equations. Chapter 4 describes the functional responses of foraging stages of *C. septempunctata* to *A. gossypii* as influenced by predator stage, prey size and temperature.

On the basis of data gathered in Chapters 2–4, a preliminary model of the *C. septempunctata–A. gossypii* system is developed and validated with experimental data collected in the laboratory. Field cage studies are used to refine the laboratory-validated model by integrating additional process-level knowledge, and to validate the refined model. The refined and validated model at the field cage level is in its turn subjected to scrutiny, improvement and validation by comparison with field observations in cotton monoculture. A simulation model of the temporal dynamics of the coccinellid–aphid system in cotton monoculture is finally developed and used to study the dynamic behavior of the system (Chapter 5).

The temporal model established in Chapter 5 is further expanded to include the dispersal of the seven-spot beetle between wheat and cotton, and some other processes related to cotton–wheat intercropping. A comprehensive model of the spatio-temporal dynamics of the coccinellid–aphid system is then established and validated with experimental data obtained in cotton–wheat intercropped fields. This model is used to study the dynamic behavior of the coccinellid–aphid system in the cotton–wheat intercrop and to explore possible adaptations of the intercropping strategies for biological control of the cotton aphid (Chapter 6).

The thesis is concluded with a general discussion of the scientific approach, research findings, practical implications and the future research (Chapter 7).

Chapter 2

Influence of temperature on population growth of *Aphis gossypii* on *Gossypium hirsutum*

Abstract Life table parameters of *Aphis gossypii* Glover (Homoptera: Aphididae) on *Gossypium hirsutum* L. were determined at six temperatures (10, 15, 20, 25, 30, and 35 ± 0.5 °C) in the laboratory. Relationships of life table parameters with temperature were described with mathematical equations. Development was fastest at 30 °C, with a pre-larviposition period of 4.6 d. The greatest survival from birth to adult (81%) was obtained at 25 °C. The highest fecundity was attained at 25 °C, with a total fecundity of 28.3 nymphs per female and a mean reproductive rate of 3.1 nymphs per female per day. Threshold temperatures for development in the first through fourth instar and the adult stage were 8.2, 8.0, 7.2, 6.2 and 7.9 °C, respectively; and the thermal constants were 24.2, 23.7, 23.0, 25.5 and 168.8 degree-days (D°), respectively. *A. gossypii* obtained a maximum net reproductive number (24.4 nymphs per female) and the greatest intrinsic rate of increase (0.386 d^{-1}) at 25 °C. The high relative rate of population increase at 25 °C resulted in a daily population increase of 47% and a doubling time of only 1.8 d, illustrating the tremendous growth capacity of *A. gossypii* under favorable conditions. Comparison to similar records from other crops indicates a relatively high heat tolerance of *A. gossypii* populations on cotton. The data obtained are used to construct a simulation model of *A. gossypii* population dynamics in cotton.

2.1 Introduction

Cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae) is the key insect pest at the seedling stage of cotton (*Gossypium hirsutum* L.) in China, particularly the North China cotton region (CCRI, 1983; Fang et al., 1992; Xia, 1991, 1992). The development of integrated pest management (IPM) systems for this aphid requires insight in the effect of environmental conditions, notably temperature, on the rate of its population growth.

Effects of temperature on *A. gossypii* population growth have been studied on cotton in USA (Isely, 1946; Akey & Butler, 1989) and Egypt (Khalifa & El-Din, 1964; Attia & El-Hamaky, 1987), and on other host plants such as cucumber (Wyatt & White, 1977), cucurbit (Liu & Peng, 1987), squash (Aldyhim & Khalil, 1993) and citrus (Komazaki, 1982). However, such information has not been gathered on cotton in China. *A. gossypii* is worldwide distributed and extremely polyphagous. Populations from particular crops or particular geographic locations may differ in their life table parameters due to differences in genotypic adaptation to environmental conditions (Blackman & Eastop, 1985; Attia & El-Hamaky, 1987; Akey & Butler, 1989; Aldyhim & Khalil, 1993). Thus, data on *A. gossypii* population growth should be used with caution if applied to a new crop or location.

The objective of this study is to determine the temperature-dependent life table parameters of *A. gossypii* on cotton. The study is undertaken to provide basic data for a quantitative analysis of biological control of *A. gossypii* with *Coccinella septempunctata* L. in cotton–wheat intercropping in the North China cotton region, using simulation modelling as an analytical and explorative tool.

2.2 Materials and methods

2.2.1 Experiments

The study was carried out at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07 °N latitude and 114.22 °E longitude) in 1993. The experiments were conducted in a Multi–Unit–Chamber (Messrs. Brabender, KSE–S 6–125/RN) at six temperatures (10, 15, 20, 25, 30 and 35 ± 0.5°C). At all temperatures, the humidity was 70–90% r.h. and the photophase was 14 h.

A laboratory colony was started with field-collected aphids from CCRI 12, a cultivar of *Gossypium hirsutun* L. which is commonly cultivated in the North China cotton region. The colony was maintained in field cages (3 m x 3 m x 2 m high). Three generations were completed before tests were initiated. Adults from the colony served as the parent stock for all rearing experiments.

For each temperature, approximately 100 adults collected in field cages were kept in 40 glass petridishes (15 cm diameter and 2.5 cm deep) for 12 h to produce offspring. Around 100 newly born aphids were individually reared on cotton leaflets in glass tubes (2 cm diameter and 10 cm long). The third and fourth true leaves of cotton seedlings were used as rearing substrate in all tests. All cotton leaves were grown in field cages and free of aphid damage. Moulting and mortality were monitored every 24 h at 10, 15 and 20 °C, and every 12 h at 25, 30 and 35 °C. After each observation, the cotton leaf was replaced. During the adult stage, the aphids were individually reared in glass petridishes (10 cm diameter and 2 cm deep), where newly born aphids were counted and then removed. Observations were continued until death of all adults.

2.2.2 Analysis

We estimated the following life history parameters: development time of the first to fourth nymphal instar, and total nymphal period; duration of the pre-reproductive period, reproductive period, reproductive plus post-reproductive period, and the entire adult longevity; duration from birth to first larviposition, and the life span from birth to death; total fecundity (number of nymphs produced per female in her lifetime); and the mean reproductive rate during the reproductive period (number of nymphs produced per female per day). Parameters were compared among temperature treatments using the General Linear Models (GLM) procedure of SAS 6.1 for PC (SAS Institute, 1993–1995). Differences were considered significant at $P < 0.05$ in t-tests (LSD).

From the data collected, the age-specific survival (l_x) and age-specific fecundity (m_x) were calculated. The intrinsic rate of increase (r_m, d^{-1}) was determined using the method of Birch (1948):

$$\Sigma\, l_x\, m_x \exp(-r_m x) = 1 \tag{2.1}$$

where x is the age. the net reproductive number (number of nymphs produced per capita, $R_o = \Sigma\, l_x\, m_x$), generation time ($t = \ln R_o / r_m$, d), finite rate of increase [$\lambda = \exp(r_m)$, d^{-1}] and population doubling time ($\tau = \ln 2 / r_m$, d) were also calculated according to the method of Birch (1948).

Developmental rate (R_d, d^{-1}) of each life stage was calculated as the reciprocal of the stage duration. Logan et al.'s (1976) model was used to describe the response of the developmental rate to temperature:

$$R_d = a_1 \{ \exp[a_2 (T - T_l)] - \exp[a_2 (T_u - T_l) - (T_u - T) / a_3] \} \tag{2.2}$$

where T is the temperature (°C), T_l is the lower threshold temperature (°C), T_u is the upper lethal temperature (°C); and a_1, a_2 and a_3 are coefficients. The upper lethal temperature was assumed to be the same for all life stages: 38 °C as estimated in growth chambers by Xie & Sterling (1987). The lower threshold temperature of each life stage was determined by linear regression, excluding the data for the higher temperature where the relationship becomes nonlinear (see Siddiqui et al., 1973):

$$R_d = b_1 + b_2 T \tag{2.3}$$

where T is the temperature (°C); b_1 and b_2 are coefficients representing the lower threshold temperature and thermal constant, respectively.

Mortality and fecundity in the adult stage are not only temperature- but also age-dependent. Twenty age classes were discerned to describe the age dependency of fecundity and mortality according to the method of Rabbinge (1976, pp. 58–61). The duration of each age class was determined by dividing the maximum period of living by the total number of age classes. The maximum period of living was defined as the mean life span plus 3 SD (standard deviation). The relative mortality rate (R_m, d^{-1}) of each life stage and each adult age class was computed using the method of Rabbinge (1976, p. 57):

$$R_m = (\ln N_t - \ln N_{t+\Delta t}) / \Delta t \tag{2.4}$$

where N_t is the number of insects at time t, $N_{t+\Delta t}$ is the number of insects at time $t+\Delta t$, and Δt is the time interval between observations (i.e. duration of a life stage or an age class). The relationship between relative mortality rate and temperature was described with a parabola:

$$R_m = c_1 + c_2 T + c_3 T^2 \tag{2.5}$$

where c_1, c_2 and c_3 are coefficients.

Weibull's (1951) model was used to describe the relationship of temperature with total fecundity (A), mean reproductive rate during reproductive period (B) and mean reproductive rate of each adult age class (C):

$$Y = d_2 / d_1 d_3 [(T - T_l) / d_1]^{(d_2 - 1)} \exp \{ - [(T - T_l) / d_1]^{d_2} \} \tag{2.6}$$

where Y stands for A, B or C; T and T_l have the same meaning as in Equation 2.2; and d_1, d_2 and d_3 are coefficients. An equation modified from Bieri et al. (1983) was used to describe the relationship between mean reproductive rate of each age class (R_q) and the adult age:

$$R_q = e_1 q / (e_2)^q \tag{2.7}$$

where q is the adult age class; and e_1 and e_2 are coefficients.

Models or equations were selected on basis of a biologically appropriate shape, Root Mean Square Error (RMSE) and coefficient of determination (r^2). All parameters in nonlinear models or equations were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

2.3 Results

2.3.1 Development

Development period of pre-reproductive stages of *A. gossypii* feeding on cotton decreased with temperature up to 25–30 °C and then increased (Table 2.1). The duration from birth to first larviposition was shortest (4.6 d) at 30 °C (5 times of 23.0 d at 10 °C). Duration of the reproductive, and reproductive plus post-reproductive adult stages decreased with temperature. The longest period of the reproductive plus post-reproductive adult (26.0 d) at 10 °C was 7 times of 3.8 d at 35 °C (Table 2.1).

The response of the developmental rate (R_d) in all life stages to temperature was satisfactorily described by Logan et al.'s (1976) model (Fig. 2.1). RMSE ranged from 0.040 to 0.046 d^{-1} for the first through fourth instar, 0.17 d^{-1} for the pre-reproductive adult, and 0.0053 d^{-1} for the reproductive plus post-reproductive adult; and r^2 ranged from 0.94 to 0.99. Developmental rate of pre-reproductive stages increased exponentially from the lower threshold temperature to an optimum (around 30 °C) and then declined until the upper lethal temperature had been reached; while it increased up to 35 °C and then decreased in the reproductive plus post-reproductive adult (Fig. 2.1).

2.3.2 Survival

Survival in all pre-reproductive stages increased with temperature up to 25 °C and then decreased (Table 2.1). The greatest survival from birth to first larviposition was attained at 25 °C (81%), which was approximately 3 times of 26% at 10 °C and two times of 33% at 35 °C (Table 2.1).

A parabola adequately described the relationship between temperature and the relative mortality rate (R_m) of pre-reproductive stages (Fig. 2.2). RMSE ranged from 0.0015 to 0.0073 d^{-1}, and r^2 from 0.95 to 0.99. The relative mortality rate was higher at 10 °C and 35 °C, while it was lower at 20–25 °C (Fig. 2.2). The relationship between temperature and the relative mortality rate of each adult age class was also adequately described by a parabola (Table A–1 in Appendix A). The relative mortality rate increased with adult age at all six temperatures, and it also increased with temperature in each adult age class (Fig. 2.3).

2.3.3 Fecundity

Total fecundity and the mean reproductive rate were highest at 25° C (Table 2.1). For instance, total fecundity (28.3 nymphs per female) at 25 °C was about 5 times of 6.1

Table 2.1. Effect of temperature on life history parameters (means ± SE) of *A. gossypii* on cotton[1].

	Temperature (°C)					
	10	15	20	25	30	35
Nymphs (d)						
first instar	4.6 ± 0.24 (99)[2] a [67.7][3]	3.5 ± 0.23 (54) b [75.9]	2.9 ± 0.19 (51) c [84.3]	1.4 ± 0.08 (68) d [92.6]	1.1 ± 0.04 (66) d [92.4]	1.3 ± 0.06 (87) d [86.2]
second instar	5.3 ± 0.25 (67) a [71.6]	3.5 ± 0.19 (41) b [85.4]	2.0 ± 0.13 (43) c [93.0]	1.3 ± 0.06 (63) de [93.7]	1.0 ± 0.06 (61) e [91.8]	1.6 ± 0.09 (75) cd [77.3]
third instar	5.8 ± 0.29 (48) a [72.9]	2.7 ± 0.14 (35) b [85.7]	2.0 ± 0.14 (40) c [90.0]	1.3 ± 0.05 (59) de [96.6]	1.0 ± 0.06 (56) e [91.1]	1.6 ± 0.12 (58) cd [70.7]
fourth instar	6.8 ± 0.38 (35) a [74.3]	3.0 ± 0.27 (30) b [86.7]	1.9 ± 0.11 (36) c [91.7]	1.3 ± 0.05 (57) de [96.5]	1.1 ± 0.07 (51) e [90.2]	1.7 ± 0.11 (41) cd [70.7]
total nymphal stage	23.0 ± 0.9 (26) a [26.3]	13.0 ± 0.5 (26) b [48.2]	8.5 ± 0.20 (33) c [64.7]	5.0 ± 0.10 (55) d [80.9]	4.6 ± 0.09 (46) d [69.7]	5.4 ± 0.20 (29) d [33.3]
Adults (d)						
pre-reproductive	3.2 ± 0.28 (26) a [76.9]	2.4 ± 0.24 (26) b [88.5]	1.0 ± 0.10 (33) c [97.0]	0.6 ± 0.04 (55) cd [96.4]	0.6 ± 0.06 (46) d [95.7]	0.9 ± 0.10 (29) c [82.8]
reproductive	19.3 ± 2.2 (20) a	20.7 ± 2.2 (23) a	12.6 ± 1.4 (32) b	9.3 ± 0.90 (53) bc	6.2 ± 0.65 (44) cd	2.8 ± 0.26 (24) d
pre-reprod. plus post-reprod.	26.0 ± 2.9 (20) a	23.0 ± 2.6 (23) a	14.2 ± 1.5 (32) b	10.3 ± 1.0 (53) bc	6.8 ± 0.69 (44) cd	3.8 ± 0.40 (24) d
entire adult stage	29.0 ± 3.2 (20) a	25.4 ± 2.4 (23) a	15.6 ± 1.4 (32) b	10.9 ± 1.0 (53) c	7.4 ± 0.70 (44) cd	4.7 ± 0.40 (24) d
Age at first larviposition (d)	25.9 ± 1.1 (20) a	15.1 ± 0.4 (23) b	9.7 ± 0.2 (32) c	5.6 ± 0.08 (53) e	4.9 ± 0.13 (44) e	7.2 ± 0.32 (24) d
Age at death from ageing (d)	53.4 ± 3.6 (20) a	38.4 ± 2.5 (23) b	24.2 ± 1.5 (32) c	15.8 ± 1.0 (53) d	12.0 ± 0.7 (44) d	10.2 ± 0.4 (24) d
Fecundity/female	6.1 ± 1.69 (20) d	21.4 ± 2.5 (23) b	24.6 ± 2.0 (32) ab	28.3 ± 2.5 (53) a	14.6 ± 1.4 (44) c	4.0 ± 0.35 (24) d
Fecundity/female/day	0.4 ± 0.14 (20) d	1.2 ± 0.10 (23) c	2.2 ± 0.12 (32) b	3.1 ± 0.13 (53) a	2.7 ± 0.20 (44) a	1.7 ± 0.21 (24) b

[1] Means in each row followed by the same letter are not significantly different ($P < 0.05$) in t-test (LSD) of GLM.

[2] Values in parentheses are number of aphids tested.

[3] Numbers in square brackets are survival (%) from one stage to the next.

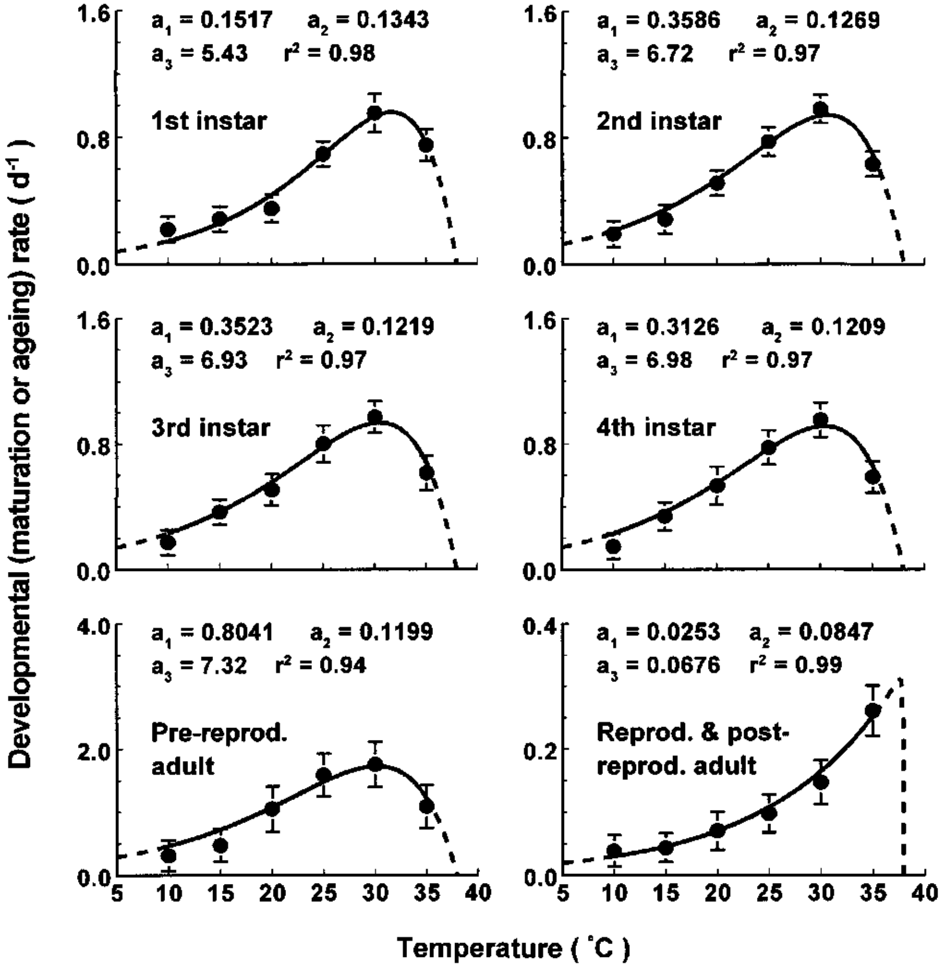


Fig. 2.1. Relationship between temperature (T, °C) and the developmental (maturation or ageing) rate (R_d, d^{-1}) of *A. gossypii* on cotton. Curves are described by Equation 2.2., where the lower threshold temperature (T_l) is presented in Table 2.2, and the upper lethal temperature (T_u) is 38 °C. Bars represent observations with 95% confidence limits.

nymphs per female at 10 °C and 7 times of 4.0 nymphs per female at 35 °C. The mean reproductive rate (3.1 nymphs per female per day) at 25 °C was about 8 times of 0.4 nymphs per female per day at 10 °C and 2 times of 1.7 nymphs per female per day at 35 °C (Table 2.1).

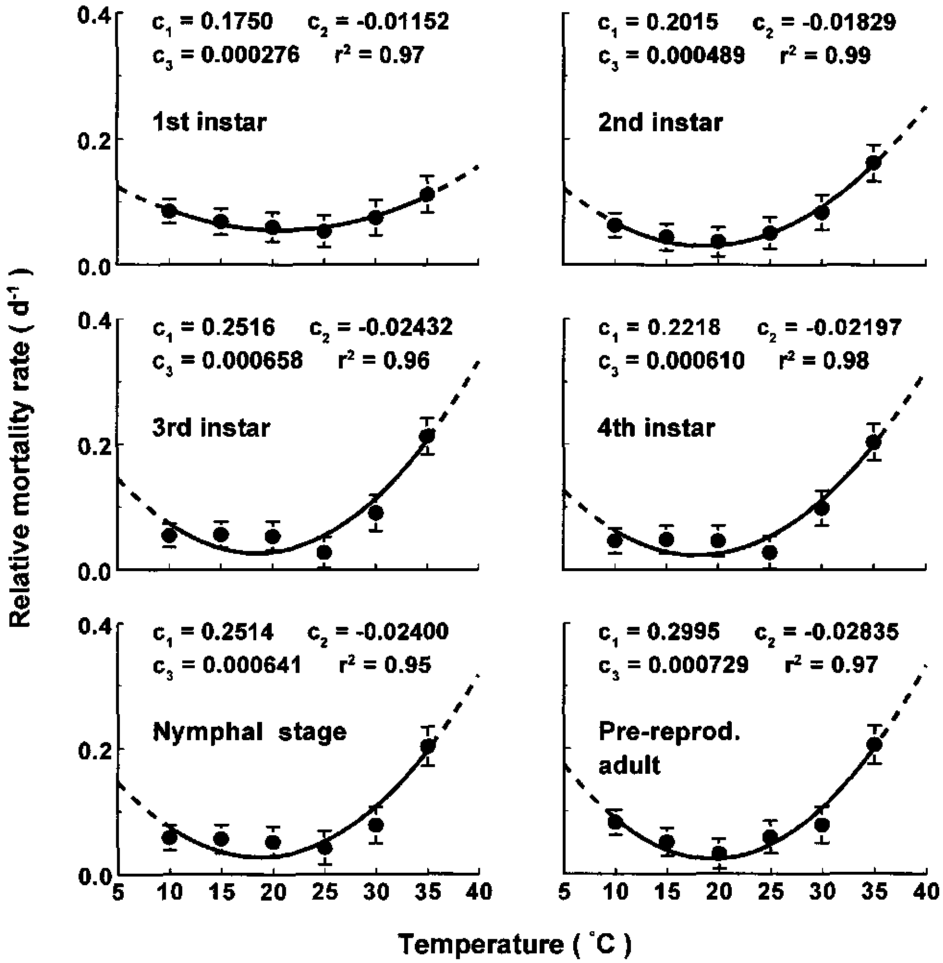


Fig. 2.2. Relationship between temperature (T, °C) and the relative mortality rate (R_m, d^{-1}) of *A. gossypii* on cotton. Curves are described by Equation 2.5. Bars represent observations with 95% confidence limits.

Weibull's (1951) model adequately described the relationships of temperature with total fecundity and the mean reproductive rate (Fig. 2.4). RMSE was 2.9 nymphs per female for the total fecundity (Fig. 2.4A) and 0.4 nymphs per female per day for the mean reproductive rate (Fig. 2.4B), and r^2 exceeded 0.95. Total fecundity and the mean reproductive rate increased exponentially from the lower threshold temperature to an optimum (around 27 °C), and then decreased dramatically with temperature (Fig. 2.4).

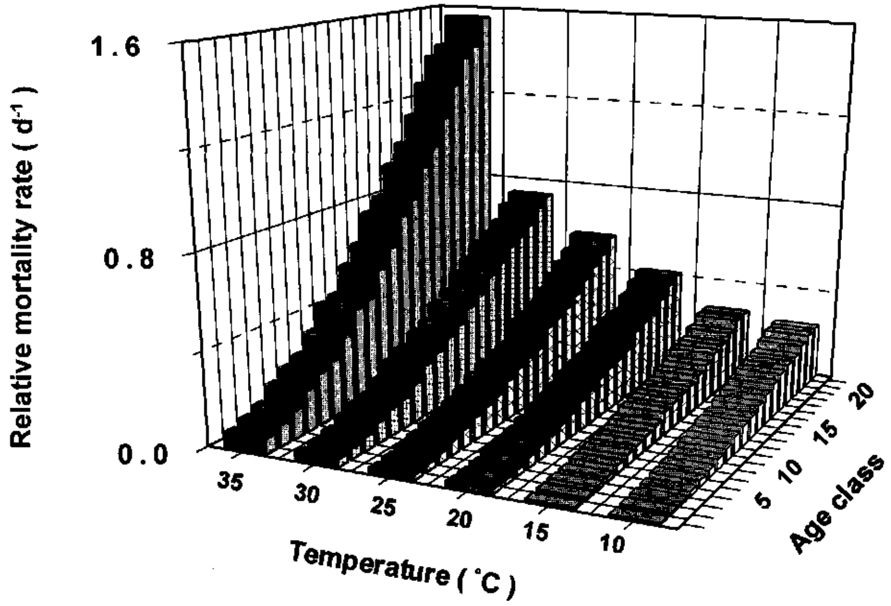


Fig. 2.3. Age class-dependent relative mortality rate (d^{-1}) of *A. gossypii* adults on cotton at six temperatures.

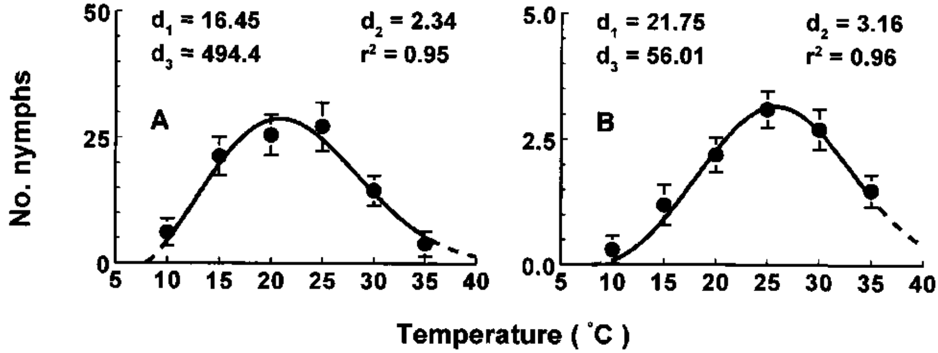


Fig. 2.4. Relationships between temperature (T, °C) and total fecundity (total nymphs per female, A), and the mean reproductive rate during the reproductive period (nymphs per female per day, B) of *A. gossypii* on cotton. Curves are described by Equation 2.6, where the lower threshold temperature (T_l) is 7.9 °C. Bars represent observations with 95% confidence limits.

optimum (around 27 °C) and then decreased dramatically with temperature (Fig. 2.4). The response of the mean reproductive rate of each adult age class to temperature was also satisfactorily described by Weibull's (1951) model (Table A–2 in Appendix A).

The relationship between the mean reproductive rate of each age class (R_q) and adult age at each temperature was adequately described by Equation 2.7 (Fig. 2.5).

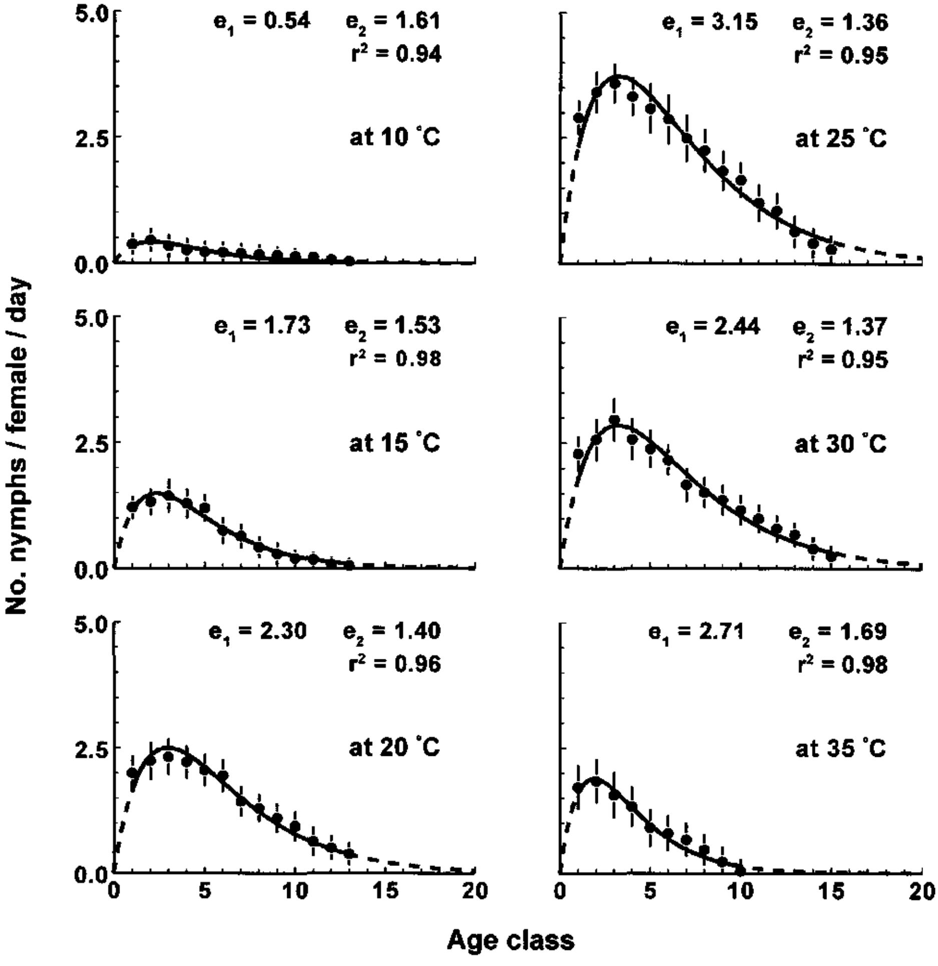


Fig. 2.5. Relationship between adult age class (q) and the mean reproductive rate (nymphs per female per day, R_q) of *A. gossypii* on cotton at six temperatures. Curves are defined by Equation 2.7. Bars represent observations with 95% confidence limits.

RMSE was 0.02, 0.08, 0.21, 0.24, 0.09 and 0.08 nymphs per female per day for 10 °C through 35 °C, respectively; and r^2 ranged from 0.94 to 0.98. The adult age-dependent mean reproductive rate was relatively low at 10 °C and 35 °C, with the reproduction terminated before age class 10; while it was relatively high at 20–30 °C, with the reproduction ending after age class 15 (Fig. 2.5).

2.3.4 Threshold temperature

Threshold temperature decreased in successive nymphal instars from 8.2 °C in the first instar to 6.2 °C in the fourth instar and then increased with adult age up to 7.9 °C in the reproductive plus post-reproductive adult (Table 2.2). The thermal constants needed to complete the development of nymphal instars ranged with narrow bounds, ranging from 23.0 to 25.5 degree-days (D°). The thermal constant of the adult stage was 168.9 D° (about 2 times of 99.4 D° for the entire nymphal period) (Table 2.2).

2.3.5 Rate of population increase

The net reproductive number (R_0) had a maximum value of 24.4 nymphs per female at 25 °C, compared to 18.5 nymphs per female at 20 °C and 10.2 nymphs per female at 30 °C. At the extreme temperatures of 10 °C and 35°C, the net reproductive number was only 2.6 and 2.0 nymphs per female, respectively (Table 2.3). The trend of

Table 2.2. Threshold temperature and thermal constant (means ± SE) of *A. gossypii* on cotton.

Stage / period	Threshold temperature (°C)	Thermal constant (D°)	r^2
First instar	8.2 ± 2.5	24.2 ± 3.6	0.95
Second instar	8.0 ± 1.2	23.7 ± 1.5	0.99
Third instar	7.2 ± 1.1	23.0 ± 1.5	0.99
Fourth instar	6.2 ± 1.1	25.5 ± 1.5	0.99
Total nymphal stage	7.1 ± 2.5	99.4 ± 14.2	0.96
Pre-reproductive adult	6.3 ± 1.7	11.4 ± 2.0	0.91
Pre-reprod. plus post-reprod. adult	7.9 ± 2.6	156.2 ± 30	0.95
Entire adult stage	7.9 ± 2.4	168.8 ± 24	0.96
Age at first larviposition	7.7 ± 2.2	105.3 ± 12	0.97
Age at death from ageing	7.4 ± 1.5	275.4 ± 23	0.98

Table 2.3. Effect of temperature on the rate of increase of *A. gossypii* populations on cotton.

Parameters	Temperature (°C)					
	10	15	20	25	30	35
Net reproductive number (R_0)[1]	2.6	13.8	18.5	24.4	10.2	2.0
Intrinsic rate of increase (r_m, d^{-1})	0.033	0.142	0.255	0.386	0.360	0.092
Finite rate of increase (λ, d^{-1})	1.03	1.15	1.29	1.47	1.43	1.10
Population doubling time (τ, d)	20.8	4.9	2.7	1.8	1.9	7.5
Generation time (t, d)	28.9	18.5	11.4	8.3	6.4	7.6

[1] Number of aphids multiplied in one generation.

intrinsic rate of population increase (r_m) over temperature was quite similar: a maximum of 0.386 d^{-1} at 25 °C compared to 0.255 d^{-1} and 0.360 d^{-1} at 20 °C and 30°C, respectively. At the extreme temperatures of 10 and 35 °C, the intrinsic rate of population increase was 0.033 d^{-1} and 0.092 d^{-1}, respectively (Table 2.3). The high relative rate of population increase at 25 °C resulted in a daily population increase of 47% and a doubling time of only 1.8 d, illustrating the tremendous growth capacity of *A. gossypii* under favorable conditions (Table 2.3).

2.4 Discussion

The intrinsic rate of increase (r_m) is a useful summary parameter to characterize the influence of abiotic factors, in particular temperature, on growth potential of insect populations (Birch, 1948; Messenger, 1964; DeLoach, 1974; Wyatt & White, 1977; Nowierski et al., 1983). It should be considered as a relative measure as the conditions under which it has an absolute value are nearly never met. As demonstrated in Fig. 2.6A, the temperature response of the local population of *A. gossypii* near Anyang, Henan, in the middle of the North China cotton region, differed from results obtained with different local populations. At the lower temperatures, the r_m of aphid populations fed on squash (Aldyhim & Khalil, 1993) and citrus (Komazaki, 1982) was greater than that fed on cotton (Fig. 2.6A). The maximum r_m was attained at 27 °C on cotton, at 25 °C on squash but at 22 °C on citrus (Fig. 2.6A). As shown in Fig 2.6B, the responses of the developmental rate to temperatures varied among the three local populations. They showed a similar trend of development with temperatures increasing from 10 °C to 25 °C (Fig. 2.6B). With the temperature increasing from 25 °C to 30 °C, however, the

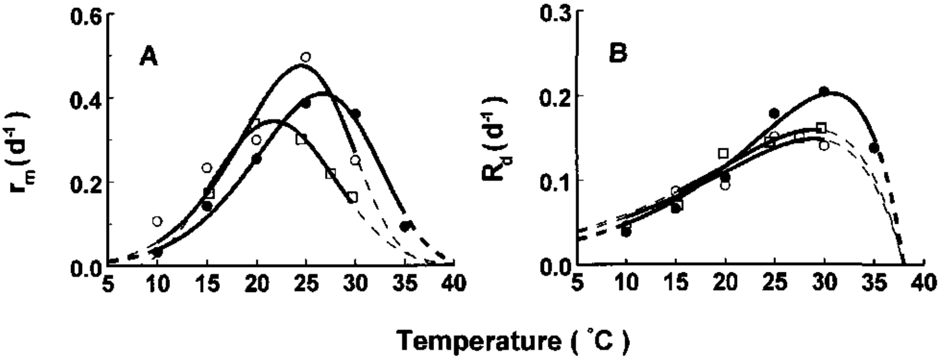


Fig. 2.6. Comparison of the temperature responses of the intrinsic rate of increase (r_m, A) and the rate of development from birth to first larviposition (R_d, B) for *A. gossypii* reared on cotton (●) (this study), squash (○) (Aldyhim & Khalil, 1993) and citrus (□) (Komazaki, 1982).

developmental rate of aphid populations fed on cotton was much higher than those fed on squash (Aldyhim & Khalil, 1993) and citrus (Komazaki, 1982) (Fig. 2.6B). These variations may be attributed to the differences in nutrition in crops (Auclair, 1963) and/or in adaptation to the surrounding environment (Blackman & Eastop, 1985; Akey & Butler, 1989).

A. gossypii populations on cotton were more tolerant to high temperatures than those on the other host plants examined. We observed that the cotton aphid was able to complete its life cycle and to give birth even at 35 °C (Table 2.1), while it hardly survived to the adult stage on squash (Aldyhim & Khalil, 1993) and citrus (Komazaki, 1982) at such high temperatures. This ability to live under high temperatures also exceeds results obtained on cotton in USA (Isely, 1946; Akey & Butler, 1989). High extreme and optimum temperatures for population growth and development (Fig. 2.6) may be an adaptation to the high temperatures in cotton fields in the North China cotton region and contribute to a propensity of the cotton aphid for outbreaks at the square-boll stage ("summer aphid") in the North China cotton region, where the daily temperature in the late summer fluctuates between 28–38 °C (Luo & Gao, 1986; Fang et al., 1992).

A. gossypii obtained its highest rate of increase on cotton at 25–30 °C. This favors population growth on cotton seedlings during late May and early June in the North China cotton region, when ambient temperatures are 20–30°C. Cotton seedlings are vulnerable to aphid injury, and yield losses 10–15% may result or it may be necessary to replant in some areas (CCRI, 1983; Pan et al., 1986; Fang et al., 1992).

Threshold temperatures of *A. gossypii* were 8.2, 8.0, 7.2 and 6.2 °C for the first through fourth instar, respectively (Table 2.2), which was close to the values of 8.0, 8.2, 6.7 and 6.7 °C found by Li & Xie (1990a). Thermal constants of each nymphal instar were almost identical in the four nymphal instars (Table 2.2). This result coincides with results of a study of Hughes (1963), who found similar thermal constants in nymphal instars of cabbage aphid, *Brevicoryne brassicae* (L.).

Results of this study provide a basis for a further analysis of factors regulating population growth of *A. gossypii* on cotton in fields, using simulation modelling of the spatio-temporal population interaction between *A. gossypii* and natural enemies as an analytical and explorative tool.

Chapter 3

Influence of temperature and prey density on population growth of *Coccinella septempunctata* feeding on *Aphis gossypii* on *Gossypium hirsutum*

Abstract Life history parameters of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) feeding on *Aphis gossypii* Glover on *Gossypium hirsutum* L. were determined in two series of experiments. The first experimental set-up addressed the effect of temperature (15, 20, 25, 30 and 35 ± 0.5 °C) on *C. septempunctata* bionomics supplied with unlimited food. The second experiment addressed the effect of food quantity on the beetle's bionomics at 25 °C. Relationships of life cycle parameters with temperature and prey density were described by mathematical equations. *C. septempunctata* developed most rapidly at 35 °C, with a pre-imaginal period of 10.8 d. The highest survival from egg to adult (47%) was obtained at 25 °C. Oviposition was greatest at 25 °C, with a total oviposition of 287.4 eggs per female and a mean oviposition rate during the reproductive period of 22.4 eggs per female per day. Threshold temperature for development of the respective stages ranged from 10.9 to 13.9 °C, with 12.6 °C for the entire life span. The thermal constant was 42.0 degree-days (D°) for eggs, 103.7 D° for larvae, 63.6 D° for pupae and 302.9 D° for adults. Over the range of prey densities tested, a 3.5-fold increase in prey density resulted in a 2-fold reduction in larval development time and a 3-fold increase in larval survival. A 2-fold increase in prey density brought about a 2-fold increase in total oviposition and the mean oviposition rate. The data gathered are used to construct a simulation model of *C. septempunctata* population dynamics in cotton.

3.1 Introduction

Seven-spot ladybird beetle, *Coccinella septempunctata L.* (Coleoptera: Coccinellidae) is a key predator of cotton aphid (*Aphis gossypii* Glover) at the seedling stage of cotton (*Gossypium hirsutum* L.) in the North China cotton region. Biological control of the cotton aphid is a priority for integrated cotton pest management to avoid early season application of insecticides, thus laying a foundation for biological control throughout the season (Xia, 1992; Fang et al., 1992; Xia et al., 1996). Development of biological control systems for the cotton aphid requires insight in population growth of *C. septempunctata* under different climatic conditions (notably the temperature) and different prey densities.

Effects of temperature on *C. septempunctata* bionomics have been studied with several aphid species as food, such as cabbage aphid, *Lipaphis erysimi* Katt. (Sethi & Atwal, 1964; Singh & Malhotra, 1979; Rhamahalinghan, 1987; Zhu, 1987); pea aphid, *Acrythosiphon pisum* (Harris) (Butler, 1982; Frazer & McGregor, 1992); black bean aphid, *Aphis fabae* Scopoli (Hodek, 1958); and Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Michels & Flanders, 1992). Impact of prey density on *C. septempunctata* bionomics has been investigated with pea aphid (Pandey et al., 1984; Evans & Dixon, 1986). Such information on *C. septempunctata* feeding on *A. gossypii* on cotton is generally lacking in China.

C. septempunctata is worldwide distributed and extremely polyphagous. Populations coming from different geographic locations or feeding on different prey species may differ in their life cycle parameters due to genetic adaptation (Hodek, 1973; Hämäläinen & Markkula, 1972; Chen et al., 1980). Thus, data on development, survival and oviposition of *C. septempunctata* should be used with caution if applied to a new location or prey species.

The objective of this study is to determine the effect of temperature and prey density on life history parameters of *C. septempunctata* feeding on *A. gossypii* on cotton. The study is undertaken to provide basic data for a quantitative analysis of *A. gossypii* biological control with *C. septempunctata* in cotton–wheat intercropping in the North China cotton region, using simulation modelling as an analytical and explorative tool.

3.2 Materials and methods

3.2.1 Experiments

This study was carried out at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07 °N latitude and 114.22 °E longitude) in 1993. Two experiments were conducted. The first experiment addressed the effect of temperature on the bionomics of *C. septempunctata*. Five temperatures were set: 15, 20, 25, 30 and 35 ± 0.5 °C. Coccinellids were fed on excess *A. gossypii*. The second experiment addressed the effect of food quantity on the beetle's bionomics, which was done at a constant temperature of 25 °C. Six levels of prey density were supplied for each predator stage (Table 3.1). All experiments were conducted in a Multi–Unit–Chamber (Messrs. Brabender, KSE–S 6–125/RN), where the humidity was 70–90% r.h. and the photophase was 14 h.

Table 3.1. Prey densities of *A. gossypii* on cotton offered for determining the effect of food quantity on the bionomics of *C. septempunctata* at a constant temperature of 25 °C.

Predatory stage	Level of prey density[1]					
	I	II	III	IV	V	VI
First instar	10	15	20	25	30	35
Second instar	15	20	25	30	35	40
Third instar	20	30	40	50	60	80
Fourth instar	40	60	80	100	120	150
Adult	50	80	110	140	170	200

[1] Young *A. gossypii* adults.

A laboratory colony was started with *C. septempunctata* pupae. The pupae were collected in mid May on 85-Zhong-33, a cultivar of winter wheat [*Triticum aestivum* (L.)] which is commonly cultivated in North China. The collected pupae were maintained in glass petridishes (15 cm diameter and 2.5 cm deep) at 25 °C for emergence. Newly emerged adults were paired (female + male), held in plastic containers (10 cm diameter and 8 cm deep) at 25 °C, and fed with excess aphids obtained on field-grown cotton for oviposition. Eggs were used for rearing experiments.

In the first experiment, 300 freshly laid eggs were kept in glass petridishes (15 cm diameter and 2.5 cm deep) for each temperature. They were observed for hatching every 24 h at 15 °C and 20 °C, and every 12 h at 25, 30 and 35°C. At each temperature, 100 newly hatched larvae were individually held in plastic containers (6 cm diameter and 8 cm deep) and supplied with excess aphids of mixed instars. Moulting and mortality were monitored at time intervals of 24 h at the two lower temperatures and 12 h at the three higher temperatures. Each day, aphids were added and the cotton leaves were replaced. Newly emerged adults were transferred to larger glass containers (10 cm diameter and 15 cm high) after copulation had been observed. Eggs in each container were counted and then removed every 12 h at 15 °C and 20 °C, and every 6 h at 25, 30 and 35 °C. Observations ended after death of the females.

In the second experiment, 30–35 newly hatched larvae were individually reared for each prey density and supplied daily with different amounts of young *A. gossypii* adults according to their developmental stage (Table 3.1). The procedure of observations was the same as in the first experiment.

3.2.2 Analysis

In both experiments, we estimated the following life cycle parameters: development time of each larval instar, duration of all larval stages together, pupal stage duration, and the pre-imaginal period (the time from egg to emerged adult); duration of the pre-oviposition period, oviposition period, and oviposition plus post-oviposition period as well as the total adult longevity; entire life span (from birth to death); total oviposition (number of eggs laid per female in her lifetime); and the mean oviposition rate during the reproductive period (number of eggs laid per female per day). All parameters were compared among treatments of temperature, and of prey density, using the General Linear Models (GLM) procedure of SAS 6.1 for PC (SAS Institute, 1993–1995). Differences were considered significant at $P < 0.05$ in t-test (LSD).

Developmental rate (R_d, d^{-1}) of each life stage was computed as the reciprocal of the stage duration in both experiments. Logan et al.'s (1976) model was used to describe the relationship between the developmental rate and temperature:

$$R_d = a_1 \{ \exp [a_2 (T - T_l)] - \exp [a_2 (T_u - T_l) - (T_u - T) / a_3] \} \tag{3.1}$$

where T is the temperature (°C), T_l is the lower threshold temperature (°C), T_u is the upper lethal temperature (°C); and a_1, a_2 and a_3 are coefficients. The upper lethal temperature was assumed to be the same for all life stages: 38 °C as estimated in growth chambers by Sethi & Atwal (1964). The lower threshold temperature of each life stage was determined by linear regression, excluding the data for the higher temperature where the relationship becomes nonlinear (see Kawauchi, 1982):

$$R_d = b_1 + b_2 T \tag{3.2}$$

where T is the temperature (°C); b_1 and b_2 are coefficients representing the lower threshold temperature and thermal constant, respectively. The relationship between the developmental rate and prey density was described with a negative exponential satiation curve:

$$R_d = f_1 + f_2 [1 - \exp (- f_3 D_a / f_2)] \tag{3.3}$$

where D_a denotes the cotton aphid density; and f_1, f_2 and f_3 are coefficients.

Mortality and fecundity in the adult stage are not only temperature- but also age-dependent. Twenty age classes were distinguished to describe the age dependency of fecundity and mortality according to the method of Rabbinge (1976, pp. 58–61). The duration of each age class was determined by dividing the maximum period of living by the total number of age classes. The maximum period of living was defined as the mean life span plus 3 SD (standard deviation). The relative mortality rate (R_m, d^{-1}) of each life stage and each adult age class was computed as:

$$R_m = (\ln N_t - \ln N_{t+\Delta t}) / \Delta t \tag{3.4}$$

where N_t is the number of insects at time t, $N_{t+\Delta t}$ is the number of insects at time t+Δt, and Δt is the time interval between observations (i.e. duration of a life stage or an age class). The relationship between temperature and the relative mortality rate was described with a parabola:

$$R_m = c_1 + c_2 T + c_3 T^2 \tag{3.5}$$

where c_1, c_2 and c_3 are coefficients. A negative exponential decay equation was used to describe the response of the relative mortality rate to prey density:

$$R_m = g_1 \exp (- g_2 D_a) \tag{3.6}$$

where D_a is the prey density; and g_1 and g_2 are coefficients.

Weibull's (1951) model was used to describe the relationship between temperature and total oviposition (A), mean oviposition rate during the reproductive period (B), and the mean oviposition rate of each adult age class (C):

$$Y = d_2 / d_1 d_3 [(T - T_l) / d_1]^{(d_2 - 1)} \exp \{ - [(T - T_l) / d_1]^{d_2} \} \tag{3.7}$$

where Y stands for A, B or C; T and T_l have the same meaning as in Equation 3.1; and d_1, d_2 and d_3 are coefficients. Equation 3.3 was used to describe the response of total oviposition and the mean oviposition rate to prey density. An equation modified from Bieri et al. (1983) was used to describe the relationship between the mean oviposition rate (R_q) and adult age class:

$$R_q = e_1 q / (e_2)^q \tag{3.8}$$

where q is the adult age class; and e_1 and e_2 are coefficients.

Models or equations were selected on basis of a biologically appropriate shape, Root Mean Square Error (RMSE) and coefficient of determination (r^2). All parameters in nonlinear models or equations were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

3.3 Results

3.3.1 Effect of temperature

Development The time to complete development of the pre–adult stage of *C. septempunctata* decreased with temperature from 69 d at 15 °C to 11 d at 35 °C (Table 3.2). Longevity of the adult decreased with temperature from 38 d at 20 °C to 14 d at 35 °C (Table 3.2).

Relationship between temperature and the developmental rate (R_d) of all life stages was adequately described by Logan et al.'s (1976) model (Fig. 3.1). RMSE ranged from 0.018 to 0.034 d^{-1} for eggs through the third larval instar, and from 0.0013 to 0.0094 d^{-1} for the fourth larval instar through the oviposition plus post-oviposition adults. All r^2 exceeded 0.97. Developmental rate of each larval instar and the pupa increased exponentially from the lower threshold temperature to an optimum (around 33 °C, Fig. 3.1) and then declined dramatically until the upper lethal temperature had been reached. However, the developmental rate increased nearly linearly with temperature up to 35 °C and then decreased sharply in eggs, pre-oviposition adults, and the oviposition plus post-oviposition adult (Fig. 3.1).

Survival Survival of all pre-adult stages (except for the second instar) increased with temperature up to 25 °C and then decreased (Table 3.2). The highest survival of the pre-adult period (47%) at 25 °C was about 3 times of 16% at 15 °C and 2 times of 26% at 35°C (Table 3.2). No adult could survive to the oviposition phase at 15 °C.

A parabola satisfactorily described the relationship between temperature and the relative mortality rate (R_m) of each pre-oviposition stage (Fig. 3.2). RMSE ranged from 0.0016 to 0.0042 d^{-1} for eggs through the second larval instar, and from 0.00034 to 0.00095 d^{-1} for the third larval instar through the pre-oviposition adult; and r^2 ranged from 0.97 to 0.99. In most cases, relative mortality rate was fairly low at 20–25 °C but slightly higher at 15 °C and much higher at 35 °C (Fig. 3.2). The relationship between temperature and the relative mortality rate of each adult age class was also adequately described by a parabola (Table A–3 in Appendix A). As shown in Fig. 3.3, the relative mortality rate increased with adult age at all four temperatures, and it also increased with temperature in each adult age class.

Oviposition Total oviposition and mean oviposition rate were highest at 25 °C but lowest at 15 °C and 35 °C (Table 3.2). Total oviposition increased with temperature from 191.6 eggs per female at 20 °C to 287.4 eggs per female at 25 °C and then

Table 3.2. Effect of temperature on life history parameters (means ± SE) of *C. septempunctata* feeding on *A. gossypii* on cotton[1].

	Temperature (°C)				
	15	20	25	30	35
Eggs (d)	9.3 ± 0.13 (89, 71.9)[2]	5.8 ± 0.05 (64, 82.8) b	3.0 ± 0.02 (77, 88.3) c	2.3 ± 0.03 (62, 85.5) d	1.6 ± 0.02 (95, 74.7) e
Larvae (d)					
first instar	9.1 ± 0.20 (64, 51.6) a	4.6 ± 0.13 (53, 73.6) b	2.0 ± 0.06 (68, 85.3) c	1.4 ± 0.04 (53, 83.0) d	1.1 ± 0.06 (71, 76.1) d
second instar	7.5 ± 0.34 (33, 81.8) a	3.2 ± 0.09 (39, 89.7) b	2.1 ± 0.05 (58, 89.7) c	1.2 ± 0.06 (44, 93.2) d	1.1 ± 0.06 (54, 88.9) d
third instar	8.3 ± 0.16 (27, 88.9) a	4.5 ± 0.13 (35, 91.4) b	2.0 ± 0.08 (52, 92.3) c	1.4 ± 0.05 (41, 90.2) d	1.2 ± 0.06 (48, 89.6) d
fourth instar	14.5 ± 0.3 (24, 83.3) a	7.4 ± 0.17 (32, 87.5) b	3.6 ± 0.11 (48, 89.6) c	2.3 ± 0.06 (37, 89.2) d	2.2 ± 0.08 (43, 86.1) d
total larval period	38.7 ± 0.5 (20, 31.3) a	19.3 ± 0.3 (28, 52.8) b	9.7 ± 0.16 (43, 63.2) c	6.2 ± 0.07 (33, 62.3) d	5.6 ± 0.10 (37, 52.1) e
Pupae (d)	16.4 ± 0.3 (20, 70.0) a	10.1 ± 0.2 (28, 85.7) b	5.7 ± 0.11 (43, 83.7) c	3.6 ± 0.08 (33, 78.8) d	3.8 ± 0.07 (37, 67.6) d
Age at emergence(d)	68.8 ± 0.6 (14, 15.7) a	25.1 ± 0.2 (24, 37.5) b	18.3 ± 0.2 (36, 46.7) c	12.3 ± 0.1 (26, 41.9) d	10.8 ± 0.1 (25, 26.3) d
Adults (d)[3]					
pre-oviposition	33.4 ± 1.5 (7) a	16.7 ± 0.9 (13, 76.9) b	11.1 ± 0.7 (19, 89.5) c	7.8 ± 0.51 (15, 73.3) d	6.2 ± 0.42 (15, 53.3) d
oviposition	-	18.9 ± 1.8 (10) a	13.1 ± 1.3 (17) b	9.9 ± 1.1 (11) bc	6.1 ± 0.85 (8) c
ovip. plus post-ovip.	-	21.4 ± 1.9 (10) a	15.6 ± 1.6 (17) b	11.6 ± 1.4 (11) b	7.0 ± 1.05 (8) c
entire adult period	-	37.6 ± 2.1 (10) a	27.1 ± 1.6 (17) b	19.3 ± 1.4 (11) c	13.7 ± 1.0 (8) d
Total life span (d)		72.6 ± 2.0 (10) a	45.3 ± 1.6 (17) b	31.4 ± 1.5 (11) c	23.9 ± 0.9 (8) d
Ovip./female	-	191.6 ± 21 (10) b	287.4 ± 24 (17) a	207.3 ± 17 (11) b	54.1 ± 5.6 (8) c
Ovip./female/day	-	11.1 ± 1.1 (10) b	22.4 ± 1.6 (17) a	20.5 ± 1.2 (11) a	10.9 ± 0.1 (8) b

[1] Means in each row followed by the same letter are not significant ($P < 0.05$, GLM) in t-tests (LSD).

[2] The first value in parentheses is the number of beetles tested, and the second one is the survival (%) to the next stage.

[3] Only females were taken into account.

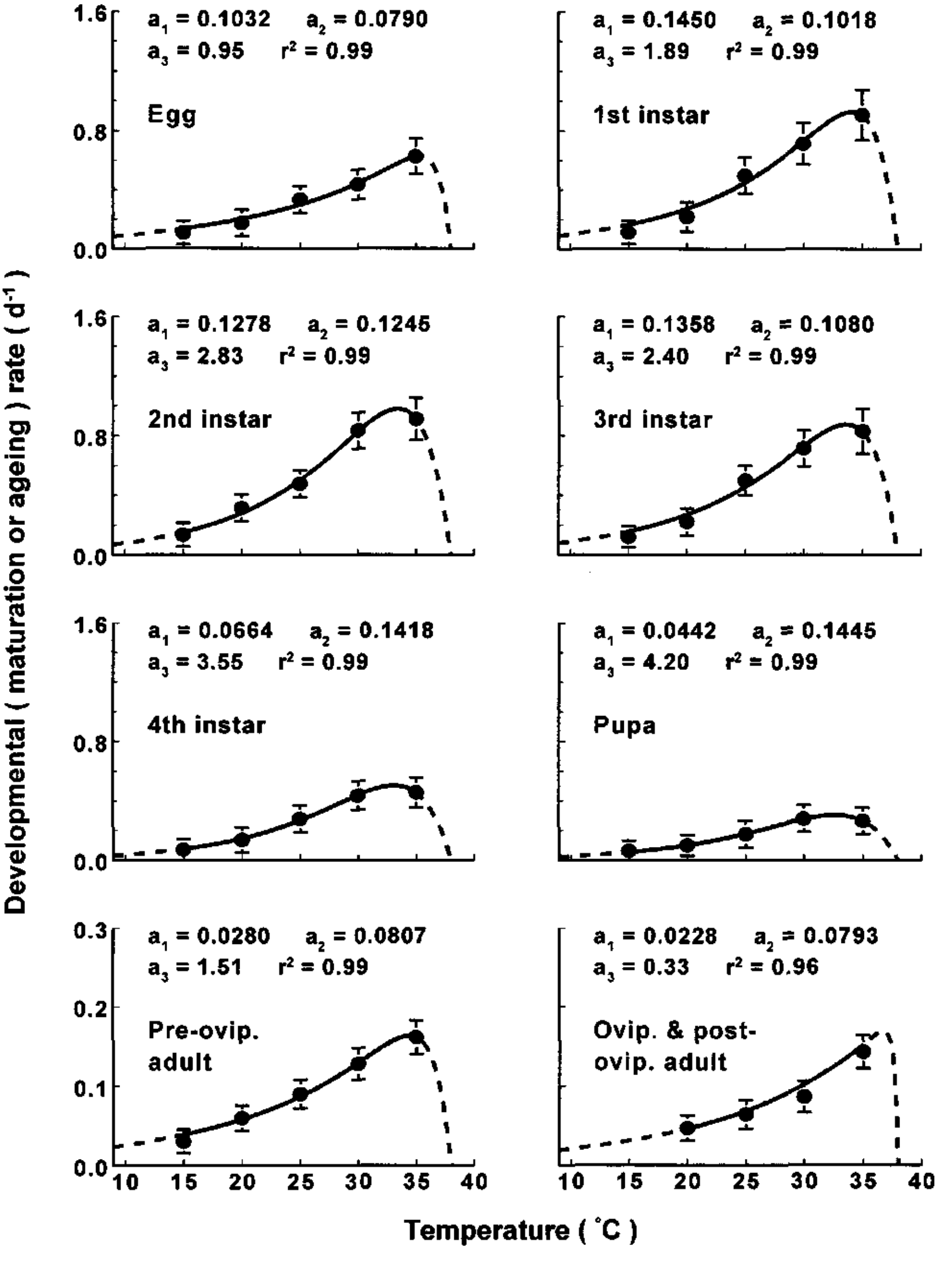


Fig. 3.1. Relationship between temperature (T, °C) and the rate of development (maturation or ageing) (R_d, d^{-1}) of *C. septempunctata* feeding on *A. gossypii* on cotton. The best fit is given by Equation 3.1, where the lower threshold temperature (T_l) is presented in Table 3.3, and the upper lethal temperature (T_u) is 38 °C. Bars represent observations with 95% confidence limits.

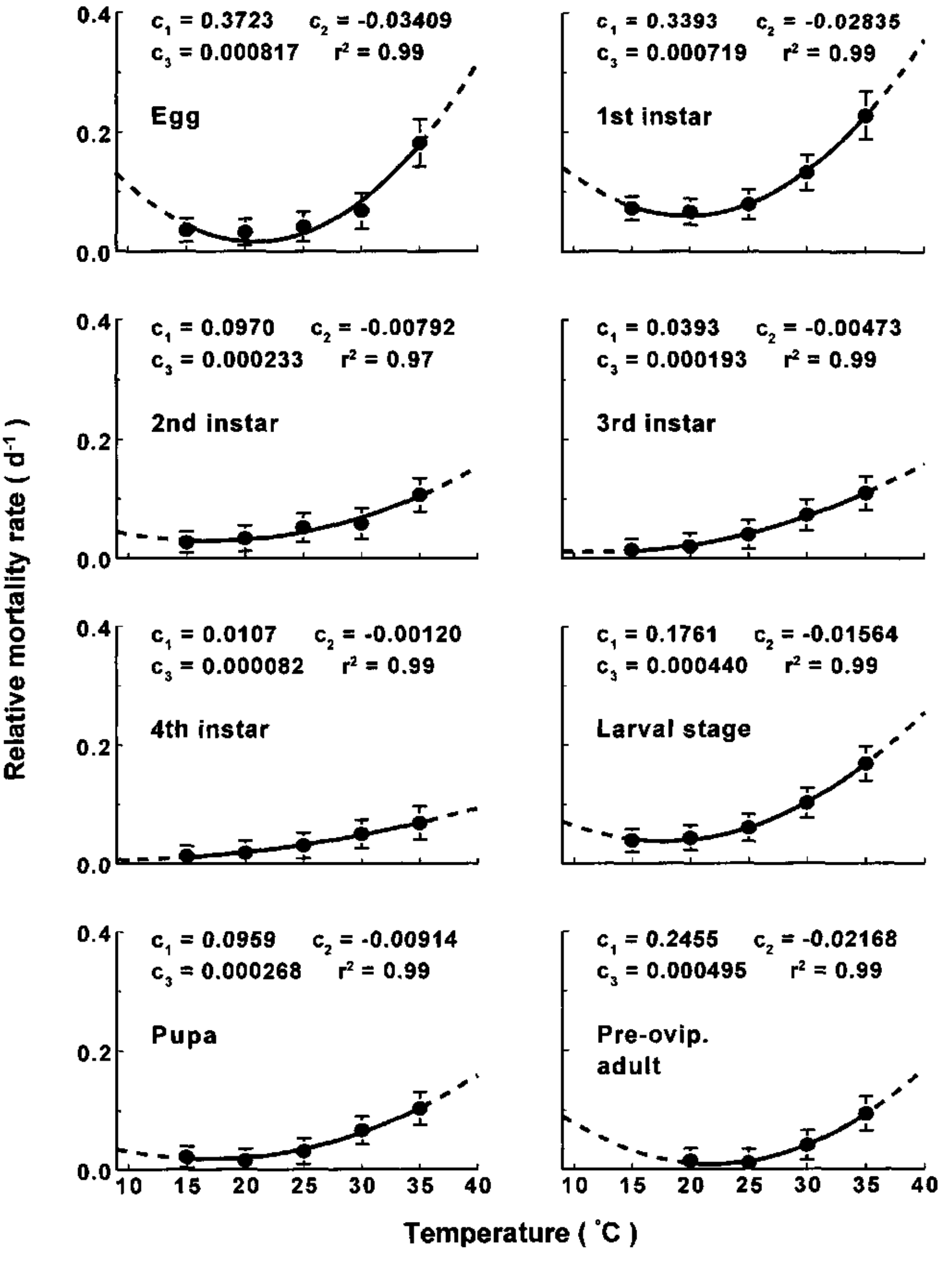


Fig. 3.2. Relationship between temperature (T, °C) and the relative mortality rate (R_m, d^{-1}) of *C. septempunctata* feeding on *A. gossypii* on cotton. The best fit is given by Equation 3.5. Bars represent observations with 95% confidence limits.

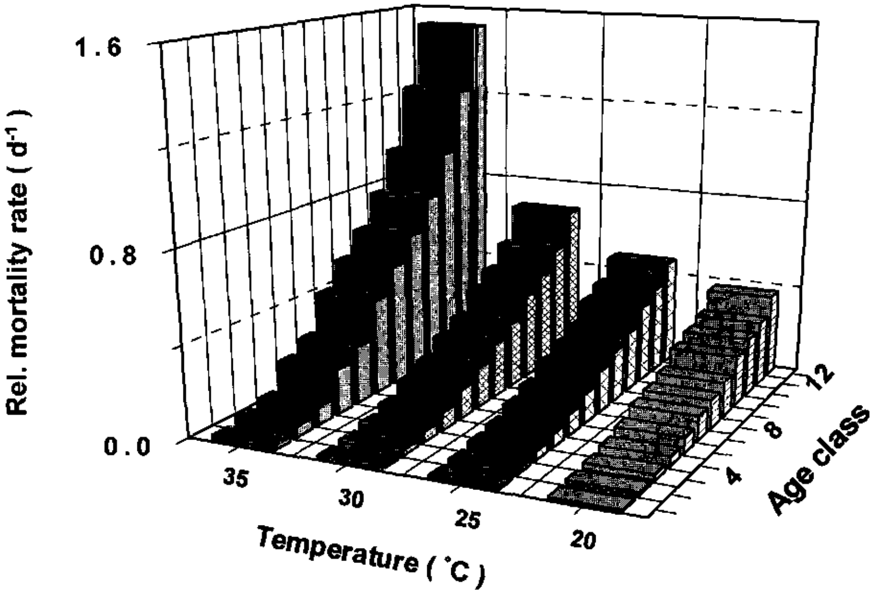


Fig. 3.3. Age class-dependent relative mortality rate (d^{-1}) of *C. septempunctata* adults feeding on *A. gossypii* on cotton at four temperatures.

decrease down to 54.1 eggs per female at 35 °C. The mean oviposition rate (20.5–22.4 eggs per female per day) at 25–30 °C was 2 times as large as at 20 °C and 35 °C (Table 3.2).

Weibull's (1951) model adequately described the relationship of total oviposition and the mean oviposition rate with temperature (Fig. 3.4). RMSE was 46.2 eggs per female for the total oviposition (Fig. 3.4A) and 3.3 eggs per female per day for the mean oviposition rate (Fig. 3.4B); and r^2 was 0.99 for both. Total oviposition and the mean reproductive rate increased exponentially from the lower threshold temperature to an optimum (around 26 °C) and then decreased exponentially with temperature (Fig. 3.4). The relationship between temperature and the mean oviposition rate of each adult age class was also satisfactorily described by Weibull's (1951) model (Table A–4 in Appendix A).

As shown in Fig. 3.5, the relationship between the mean oviposition rate of each age class (R_q) and adult age was well described by Equation 3.8 at all four temperatures. RMSE was 1.1, 3.1, 8.5 and 4.1 eggs per female per day for 20 °C through 35 °C, respectively; and r^2 ranged from 0.96 to 0.99.

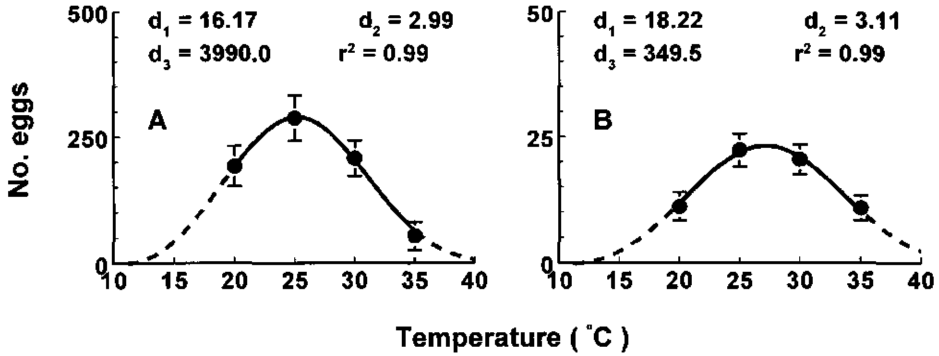


Fig. 3.4. Relationship between temperature (°C) and total oviposition (total eggs per female, A), and the mean oviposition rate (eggs per female per day, B) of *C. septempunctata* feeding on *A. gossypii* on cotton. The best fit is given by Equation 3.7, where the lower temperature (T_l) is 11 °C, and the upper lethal temperature (T_u) is 38 °C. Bars represent observations with 95% confidence limits.

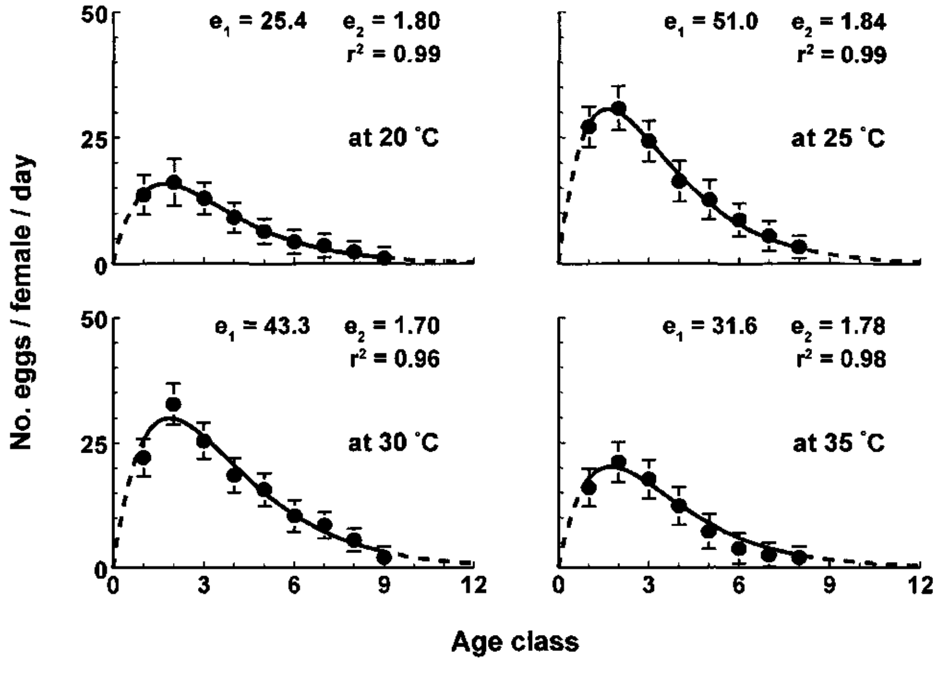


Fig. 3.5. Relationship between adult age class (q) and the mean oviposition rate (eggs per female per day, R_q) of *C. septempunctata* feeding on *A. gossypii* on cotton at four temperatures. The best fit is given by Equation 3.8. Bars represent observations with 95% confidence limits.

Threshold temperature Threshold temperatures ranged from 12.9 to 13.9 °C for the first larval instar through pupae and from 10.9 to 11.5 °C for eggs and the adult, with 12.6 °C for the entire life span (Table 3.3). The thermal constant for the adult stage was 302.9 degree-days (D°), which accounted for over 50% of 546.3 D° for the total life span (Table 3.3).

3.3.2 Effect of prey density

Development Development time of the total larval period of *C. septempunctata* decreased rapidly with prey density from level I to level IV and then decreased slightly (Table 3.4). Over the range of prey densities tested, an average 3.5-fold increase in prey density resulted in a 2-fold decrease in larval developmental time (Tables 3.1 and 3.4). Duration of the pupal stage only slightly decreased with prey density (Table 3.4). Adult life span decreased sharply at prey density up to level III and then decreased slightly (Table 3.4). The response of the developmental rate (R_d) to prey density was well described by Equation 3.3 for the first through fourth instar (Fig. 3.6A). RMSE ranged from 0.0041 to 0.0183 d^{-1}, and all r^2 exceeded 0.97. The developmental rate of all larval stages negatively accelerated with prey density and approached to an asymptote at the higher prey densities (Fig. 3.6A).

Table 3.3. Threshold temperature and thermal constant (means ± SE) of *C. septempunctata* feeding on *A. gossypii* on cotton.

Stage / period	Threshold temperature (°C)	Thermal constant (D°)	r^2
Eggs	11.5 ±.1.4	42.0 ± 4.2	0.98
First instar	13.8 ±.1.2	22.8 ± 2.4	0.98
Second instar	13.6 ± 1.7	20.4 ± 2.5	0.96
Third instar	13.6 ± 1.3	23.1 ± 4.3	0.98
Fourth instar	13.9 ± 1.3	38.0 ± 6.2	0.98
Total larval period	13.7 ± 1.2	103.7 ± 11	0.98
Pupae	12.9 ±.1.6	63.6 ± 8.6	0.97
Pre-oviposition adult	10.9 ± 0.6	151.9 ± 7	0.99
Ovip. plus post-ovip. adult	11.1 ± 1.0	166.1 ± 24	0.99
Total adult period	12.4 ± 1.5	302.9 ± 28	0.98
Entire life span	12.6 ± 0.5	546.3 ± 15	0.99

Table 3.4. Effect of prey density on life history parameters (means ± SE) of *C. septempunctata* fed on *A. gossypii* on cotton at 25 °C[1].

	Level of prey supply					
	I	II	III	IV	V	VI
Larvae (d)						
first instar	4.2 ± 0.28 (35)[2] a [71.4][3]	3.8 ± 0.15 (30) a [76.7]	3.3 ± 0.14 (30) b [80.0]	2.9 ± 0.11 (30) bc [83.3]	2.7± 0.11 (30) c [86.7]	2.6 ± 0.10 (30) c [90.0]
second instar	3.2 ± 0.33 (25) a [68.0]	2.7 ± 0.19 (23) b [73.9]	2.4 ± 0.14 (24) bc [79.2]	2.2 ± 0.08 (25) cd [88.0]	2.0 ± 0.10 (26) cd [88.5]	1.8 ± 0.08 (27) [92.6]
third instar	3.6 ± 0.14 (17) a [76.5]	3.1 ± 0.12 (17) b [82.4]	2.6 ± 0.12 (19) c [84.2]	2.2 ± 0.10 (22) d [86.4]	2.1 ± 0.07 (23) d [91.3]	2.0 ± 0.05 (25) [92.0]
fourth instar	7.0 ± 0.21 (13) a [61.5]	6.0 ± 0.25 (14) b [71.4]	5.4 ± 0.17 (16) c [75.0]	4.6 ± 0.21 (19) d [79.0]	4.4 ± 0.20 (21) d [85.7]	4.2 ± 0.15 (23) [87.0]
total larval period	18.1 ± 0.5 (8) a [22.9]	15.7 ± 0.5 (10) b [33.3]	13.8 ± 0.4 (12) c [40.0]	11.9 ± 0.3 (15) d [50.0]	11.3 ± 0.3 (18) de [60.0]	10.6 ± 0.2 (20) e [66.7]
Pupae (d)	6.5 ± 0.42 (8) a [62.5]	5.9 ± 0.32 (10) ab [80.0]	5.7 ± 0.23 (12) b [83.3]	5.4 ± 0.23 (15) b [93.3]	5.3 ± 0.19 (18) b [88.9]	5.2 ± 0.18 (20) [95.0]
Adults (d)[4]						
pre-oviposition	35.8 ± 1.7 (4) a	24.9 ± 1.6 (7) b	16.4 ± 0.9 (7) c	14.5 ± 0.7 (8) cd	12.9 ± 0.6 (9) d	12.7 ± 0.6 (10)
oviposition	-	28.4 ± 2.4 (5) a	19.7 ± 1.6 (5) b	16.3 ± 1.2 (6) bc	14.9 ± 1.0 (7) c	14.1 ± 1.0 (8) c
ovip. plus post-ovip.	-	34.6 ± 2.6 (5) a	24.2 ± 2.0 (5) b	20.2 ± 1.9 (6) bc	17.7 ± 1.2 (7) c	16.1 ± 1.1 (8) c
total adult period	-	59.5 ± 3.7 (5) a	40.6 ± 2.6 (5) b	34.6 ± 2.2 (6) bc	30.6 ± 1.4 (7) c	28.7 ± 1.5 (8) c
Ovip. /female	-	137.5 ± 16 (5) b	225.0 ± 13 (5) a	243.9 ± 14 (6) a	266.1 ± 19 (7) a	272.5 ± 16 (8) a
Ovip. /female/day	-	5.2 ± 1.22 (5) d	11.9 ± 1.0 (5) c	15.8 ± 1.6 (13) bc	18.6 ± 1.5 (7) ab	20.1 ± 1.4 (8) a

[1] Means in each row followed by the same letter are not significantly different ($P < 0.05$, GLM) in t-tests (LSD).

[2] Values in parentheses are the number of beetles tested. [3] Numbers in square brackets are survival (%) to the next stage.

[4] Only females were taken into account.

Survival Survival of all pre-adult stages increased with prey density and was greatest at the highest prey density (Table 3.4). From instars to the adult stage, a 3.5-fold increase in prey density brought about a 3-fold increase in survival (Tables 3.1 and 3.4). Equation 3.6 satisfactorily described the relationship between prey density and the relative mortality rate (R_m) of each larval stage (Fig. 3.6B). RMSE ranged from 0.00075 to 0.00291 d^{-1} and r^2 from 0.92 to 0.95.

Oviposition Total oviposition and the mean oviposition rate increased monotonously with prey density (Table 3.4). A 2-fold increase in prey density led to a 2-fold increase in total oviposition and the mean oviposition rate (Tables 3.1 and 3.4). Equation 3.3 adequately described the response of total oviposition and the mean oviposition rate to prey density (Fig. 3.7). RMSE was 39.0 eggs per female for the total oviposition (Fig. 3.7A) and 0.7 eggs per female per day for the mean oviposition rate (Fig. 3.7B), and r^2 was 0.99 for both. Total oviposition and the mean oviposition rate negatively accelerated with prey density and reached a plateau at the higher prey densities (Fig. 3.7).

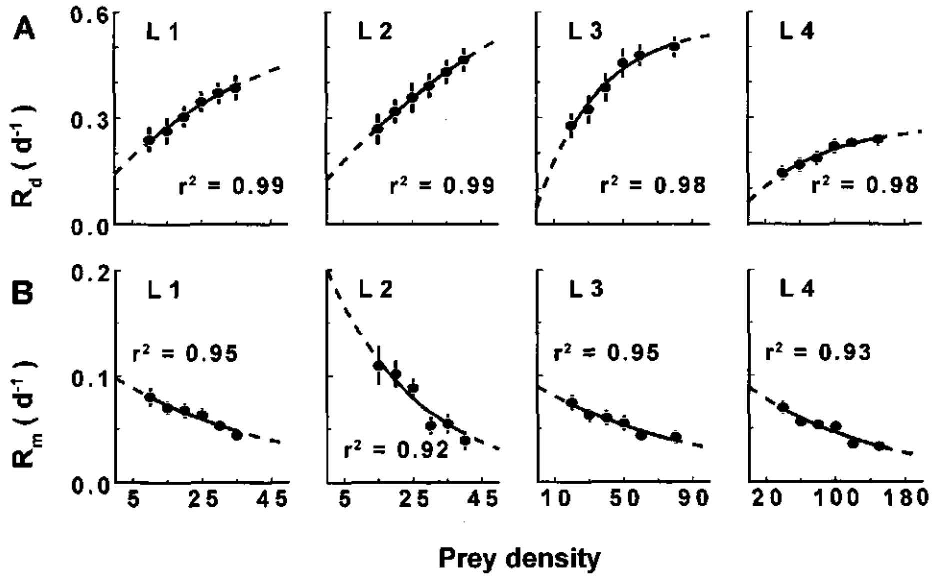


Fig. 3.6. Relationship between prey density (D_a) and the developmental rate (R_d, d^{-1}, A), and the relative mortality rate (R_m, d^{-1}, B) of the first through fourth instar (L1 to L4) of *C. septempunctata* feeding on *A. gossypii* on cotton. The development response is described by Equation 3.3 and the mortality response by Equation 3.6. Bars represent observations with 95% confidence limits.

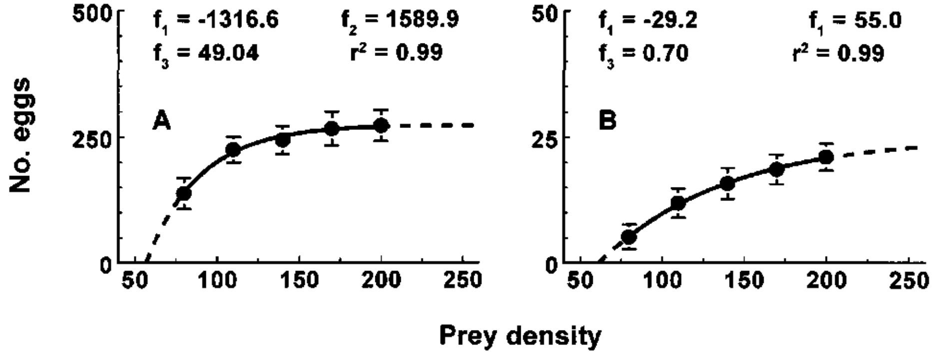


Fig. 3.7. Relationship between prey density (D_a) and total oviposition (total eggs per female, A), and the mean oviposition rate (eggs per female per day, B) of *C. septempunctata* feeding on *A. gossypii* on cotton. The best fit is given by Equation 3.3. Bars represent observations with 95% confidence limits.

3.4 Discussion

It is common that *C. septempunctata* attains its most rapid development at 35 °C (Hodek, 1958, 1973; Sethi & Atwal, 1964; Singh & Malhotra, 1979; Kawauchi, 1982, 1985; Zhu, 1987). High temperature, however, exerts a deleterious effect through increased respiration cost (Mills, 1981), resulting in a reduction of survival and oviposition (Table 3.2). This may be the major cause for the seven-spot beetle to aestivate or enter in diapause in the North China cotton region (Zhu & Li, 1981; Qin, 1978). As shown in Fig. 3.8, developmental rate (R_d) of the pre-adult stage of the seven-spot beetle differs little between acquisitions from different parts of the world: China (this study), Europe (Hodek, 1958), India (Sethi & Atwal, 1964) and Japan (Sakurai et al., 1991), though it shows some differences at high temperatures. These results confirm the comment made by Hodek (1973) that differences among distant populations of *C. septempunctata* are mostly related to its survival near the upper temperature limit.

C. septempunctata obtained greater survival and oviposition at 20–30 °C than at 10 °C and 35 °C. This may explain why *C. septempunctata* populations in the North China cotton region are relatively higher in May and in September when average field temperatures vary between 22 and 30 °C but much lower in July and August when field temperatures fluctuate between 30 and 39 °C. Therefore, *C. septempunctata* is considered an effective biological control agent of *A. gossypii* only at the seedling stage of cotton but not at the square-boll stage (CCRI, 1983; BU, 1984; Fang et al., 1992; Xia et al., 1986).

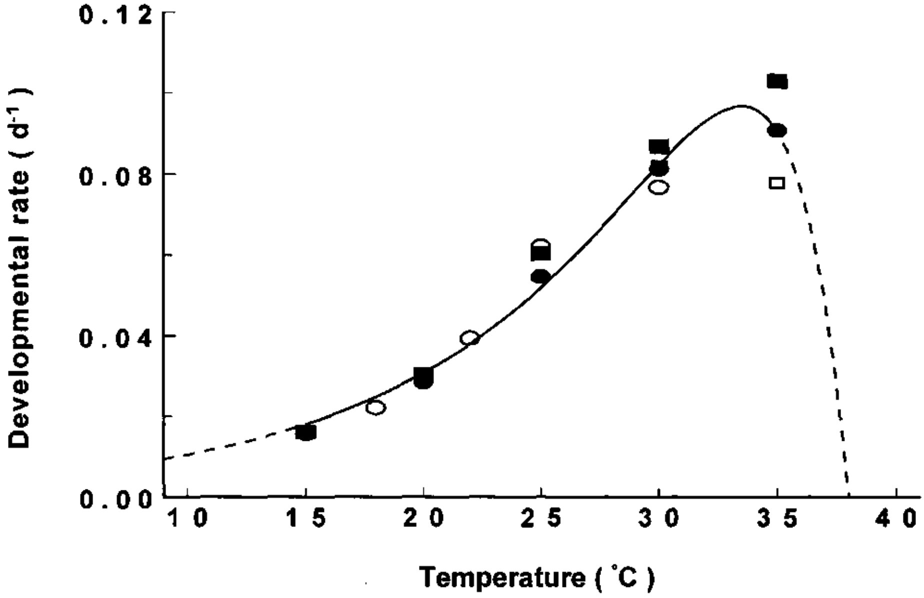


Fig. 3.8. Comparison of developmental rates to the adult stage of *C. septempunctata* in China (●) (this study), Japan (○) (Sakurai et al., 1991), Europe (■) (Hodek, 1958), and India (□) (Sethi & Atwal, 1964).

A linear relationship of the developmental rate, survival and oviposition with prey density is commonly observed in predatory arthropods (Beddington et al., 1976). The present study, however, indicated that the developmental rate, relative mortality rate, total oviposition and the mean oviposition rate of *C. septempunctata* were non-linear dependence of prey density (Figs. 3.6 and 3.7). Such non-linearity was also observed in other coccinellid species, such as *Adalia bipunctata* (Fabricius) feeding on *A. pisum* (Mills, 1981, 1982b), and *Cheilomenes lunata* (Fabricius) feeding on *A. craccivora* (Ofuya & Akingbohungbe, 1988). Development time of all life stages (except for the second larval instar) of *C. septempunctata* fed with aphids at the highest density at 25 °C (Table 3.4) were slightly longer than those fed with excess aphids of mixed instars at the same temperature (Table 3.2). This difference may be attributed to the suitability of food. As observed by Chen et al. (1980) and Sinha et al. (1982), *C. septempunctata* most favoured the third nymphal instar of aphids. In this study, however, only young *A. gossypii* adults were used as food for all life stages of the seven-spot beetle.

Temperature and food quantity are two major factors affecting *C. septempunctata* population dynamics in the North China cotton region. In some years, development and reproduction of the seven-spot beetle in wheat are enhanced by favorable temperatures and abundant prey, especially [*Sitobion avenae* (Fabricius)]. This results in large beetle populations that immigrate for the greater part to (monoculture) cotton and provide for biological control of *A. gossypii* beneath damaging levels. In years in which temperatures in April and May fall substantially below the beetle's optimum, development is prolonged, mortality increased and reproduction reduced, such that – even if prey is abundant – the beetle abundance is significantly lowered and its impact on the cotton aphid reduced. Effective control of the cotton aphid in cotton monoculture is, therefore, most likely if temperature and wheat aphid density favors the bionomics of seven-spot beetles in wheat during April and May.

Results of this study provide a basis for a further analysis of factors regulating population growth of *A. gossypii* on cotton in fields, using simulation modelling of the spatio-temporal population interaction between *A. gossypii* and natural enemies as an analytical and explorative tool.

Chapter 4

Functional response of *Coccinella septempunctata* to *Aphis gossypii* on *Gossypium hirsutum*: effects of predator stage, prey size and temperature

Abstract The functional response of four larval instars and adults of *Coccinella septempunctata* L. on three size-groups of *Aphis gossypii* on *Gossypium hirsutum* L. was determined at five temperatures (15, 20, 25, 30 and 35 ± 0.5 °C) in the laboratory. All functional responses were of type II. They were adequately described by Rogers' random predator equation. The search rate, i.e. the initial slope of the functional response (proportion of prey captured per unit time), increased linearly with temperature. From 15 °C to 35 °C, the search rate increased with a factor of 3–8. The handling rate (the plateau of the functional response) showed a curvilinear relation to temperature and was lowest at 15 °C. There was a considerable variation in the latter response curves in different predator–prey stage combinations. In some predator–prey interactions, handling rate increased consistently with temperature, while in other combinations, the relationship had a maximum at an intermediate temperature. Search rate increased with 50–100% from one larval predator instar to the next but search rates of the adult predator were somewhat lower than those of the fourth larval instar. There was only moderate difference in search rate between prey-size groups for the same predator stage (< 50% between extremes). Handling rate increased with 50–100% from one predator stage to the next. Handling rates of the fourth larval instars and adults were similar. Handling rate towards the early instar, late instar and adult prey varied with a ratio of approximately 3:2:1. The functional responses are incorporated in a simulation model for *C. septempunctata–A. gossypii* population interaction and dynamics in cotton.

4.1 Introduction

Preservation and utilization of the seven-spot ladybird beetle (*Coccinella septempunctata* L.) [Coleoptera: Coccinellidae] is an important component of integrated management of cotton aphid (*Aphis gossypii* Glover) [Homoptera: Aphididae] on seedling cotton (*Gossypium hirsutum* L.) in the North China cotton region (BU, 1984; Xia, 1994b; Xia et al., 1996). A better understanding of *C.*

septempunctata–A. gossypii interactions is helpful in developing effective biological control strategies through manipulation of cropping systems and rational application of selective insecticides.

The interaction between *C. septempunctata* and *A. gossypii* is complicated. Five life stages of the prey (four nymphal instars and the adult) and five foraging stages of the predator (four larval instars and the adult) are involved. Predators of all foraging stages can attack each life stage of the prey, though they are more likely to accept the younger prey, depending mainly on the hunger level of the predator and its size (Frazer & Gilbert, 1976; Ofuya, 1986; Dong & Wang, 1989).

Two important components are involved in the predation process, functional and numerical responses (Holling, 1959, 1966). The functional response, describing the changes in the number of prey consumed by predators per unit time in relation to the changes in prey density, provides a basis of the interaction between predators and their prey. A number of studies have examined in detail the functional response of several coccinellid predators preying on aphids, such as *C. septempunctata* preying on wheat aphid [*Sitobion avenae* (Fabricius)] (Cai & Yan, 1991; Li, 1991) and mustard aphid (*Lipaphis erysimi* Kalt) (Sinha et al., 1982); *C. californicus* Mannerheim, *C. trifasciata* L. and *C. undecimpunctata* L. preying on pea aphid [(*Acyrthosiphon pisum* (Harris)] (Frazer & Gilbert, 1976; Frazer et al., 1981); *Coleomegilla maculata* (De Geer) preying on green peach aphid [*Myzus persicae* (Sulzer)] (Mack & Smilowitz, 1982a); and *Cheilomenes vicina* (Muls.) preying on cowpea aphid (*A. craccivora* Koch) (Ofuya, 1986). Few studies have investigated the effect of prey stage of *A. gossypii* on the functional response of *C. septempunctata* adults (Dong & Wang, 1989). No observation has been made for the functional response of *C. septempunctata* to *A. gossypii* on cotton as influenced by predator stage, prey size and temperature.

The objective of this study is to determine the functional responses of all five foraging stages of *C. septempunctata* to three size-groups of *A. gossypii* at five temperatures. The study is undertaken to provide basic data for a quantitative analysis of biological control of *A. gossypii* with *C. septempunctata* in cotton–wheat intercropping in the North China cotton region, using simulation modelling as an analytical and explorative tool.

4.2 Materials and methods

4.2.1 Experiments

The study was conducted at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07 °N latitude and 114.22 °E longitude) in 1993. The functional response of all foraging stages (four larval instars and the female adult) of *C. septempunctata* was determined with six densities of three size-groups of *A gossypii*. The first size-group included the mixed first and second nymphs (hereafter referred to as early instars), the second size-group included the mixed third and fourth nymphs instars (hereafter referred to as late instars), and the third size-group included adults. Density levels were adjusted to the predator–prey stage combination (Table 4.1). Each combination was tested at five temperatures (15, 20, 25, 30 and 35 ± 0.5 °C). At all temperatures, the humidity was 70–90% r.h. and the photophase was 14 h. All measurements were carried out in a Multi–Unit–Chamber (Messrs. Brabender, KSE–S 6–125/RN). Size-groups were defined because they are easier to be distinguished in

Table 4.1. Prey densities of different size-groups of *A. gossypii* offered for predation by foraging stages of *C. septempunctata* on cotton.

Prey size-group[1]	Predator stage	Level of prey densities					
		I	II	III	IV	V	VI
Early instar	First instar	20	30	40	50	60	80
	Second instar	40	60	80	100	120	150
	Third instar	60	90	120	150	180	220
	Fourth instar	90	130	170	210	250	290
	Female adult	100	150	200	250	300	350
Late instar	First instar	10	20	30	40	50	70
	Second instar	20	30	40	50	60	80
	Third instar	40	60	80	100	120	140
	Fourth instar	50	80	110	140	170	210
	Female adult	60	100	140	180	220	270
Adult	First instar	10	15	20	25	30	35
	Second instar	15	20	25	30	35	40
	Third instar	20	30	40	50	60	80
	Fourth instar	40	60	80	100	120	150
	Female adult	50	80	110	140	170	200

[1] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

the field. Of the adult predators, only females were tested. There is little difference in the predation rate between the two sexes (CCRI, 1983; BU, 1984; Li, 1991; Dong et al., 1992; Fang et al., 1992).

C. septempunctata pupae were collected on wheat in mid May and held in glass petridishes (15 cm diameter and 2.5 cm deep) at 25 °C until emergence. Newly emerged adults were transferred in pairs (female + male) to glass containers (10 cm diameter and 15 cm high) and reared with aphids from field-caged cotton. Their progeny was used for experiments.

Plastic containers (6 cm diameter and 8 cm deep) were used as experimental arenas (each with a surface area of 200 cm^2). A fresh cotton leaflet with a surface area of 30 ± 5 cm^2 (approximately equivalent to one fully expanded true leaf at the seedling stage) served as substrate. All cotton leaves used were grown in field cages and free of aphid injury. A piece of moistened filter paper was laid on the bottom of each arena, and the top was covered with a piece of nylon mesh.

Predators were preconditioned before testing to standardize their level of hunger. The larvae were 6-h old after the last moult and starved for 12 h. Female adults were 24-h old and starved for 24 h. Predation was measured for six densities of each prey size-group (Table 4.1) for 24 h. Ten replicates were made for each combination. Controls identical to the respective predation tests except for the absence of predators were used for correction of background mortality of aphids (Abbott, 1925).

4.2.2 Analysis

Predator feeding rate in the experimental arena can be described as:

$$\mathrm{dN/dt} = -\,a\,\mathrm{N} \,/\, (\,1 + a\,T_\mathrm{h}\,\mathrm{N}\,) \tag{4.1}$$

where N is the number of prey, a is the search rate (arena d^{-1}) and T_h is the handling time (d). The number of prey eaten in a day follows the integrated form of the above equation:

$$\mathrm{N_e} = \mathrm{N_o}\,\{\,1 - \exp\,[\,a\,(\,T_\mathrm{h}\,\mathrm{N_e} - \mathrm{T_t}\,)\,]\,\} \tag{4.2}$$

where N_e is the number of prey eaten, N_o is initial prey density, and a and T_h have the same meaning as in Equation 4.1. We used this equation (developed by Rogers, 1972) to estimate search rate (arena d^{-1}) and handling rate (the reciprocal of handling time, h^{-1}) from the experimental results. Equation 4.1 with estimated parameters will be used later in a simulation model for *C. septempunctata–A. gossypii* interactions in the field cage and open field conditions (Chapters 5 and 6). Rogers' predator equation was used as it takes away the need to replace the consumed prey during the experiments. Parameters of Equation 4.2 were estimated by nonlinear regression (Juliano, 1993), using the NLIN procedure of SAS 6.1 for PC (SAS Institute, 1993–1995).

A linear model was used to describe the relationship between search rate and temperature:

$$a = h_1 + h_2 T \tag{4.3}$$

where a is the search rate (arena d^{-1}), T is temperature (°C), and h_1 and h_2 are coefficients. An optimum type of equation, simplified from Eyring & Urry (1975) (see also Mack & Smilowitz, 1982b), was used to describe the relationship between handling rate and temperature:

$$R_h = j_1\, T \exp(-j_2 / T) / [1 + j_3 \exp(-j_4 / T)] \tag{4.4}$$

where R_h is the handling rate (h^{-1}); T is the temperature (°C); and j_1, j_2, j_3 and j_4 are coefficients. Equations 4.3 and 4.4 were chosen based on a biologically meaningful shape, Root Mean Square Error (RMSE) and coefficient of determination (r^2). Parameters of Equations 4.3 and 4.4 were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

4.3 Results

All observed functional responses of *C. septempunctata* to *A. gossypii* on cotton were of type II (Holling, 1959, 1966; Mills, 1981, 1982b) and were adequately described by Rogers' random predator equation. RMSE ranged from 0.3 to 2.7 aphids per day in the first instar predator, 0.5–5.9 aphids per day in the second instar, 1.1–5.2 aphids per day in the third instar, 2.1–7.1 aphids per day in the fourth instar, and 0.8–11.1 aphids per day in the female adult. r^2 ranged from 0.89 to 0.99. As an example, the 15 functional response curves observed at 25 °C are presented in Fig. 4.1. At the other four temperatures, the 60 responses followed a similar pattern (not shown). The functional response parameters estimated for 15 different predator–prey stage combinations, five temperatures and six prey densities examined for each functional response are summarized in Tables 4.2 and 4.3. Table 4.2 presents the estimated search rate for each predator–prey combination at five temperatures, and Table 4.3 lists the estimated handling rate.

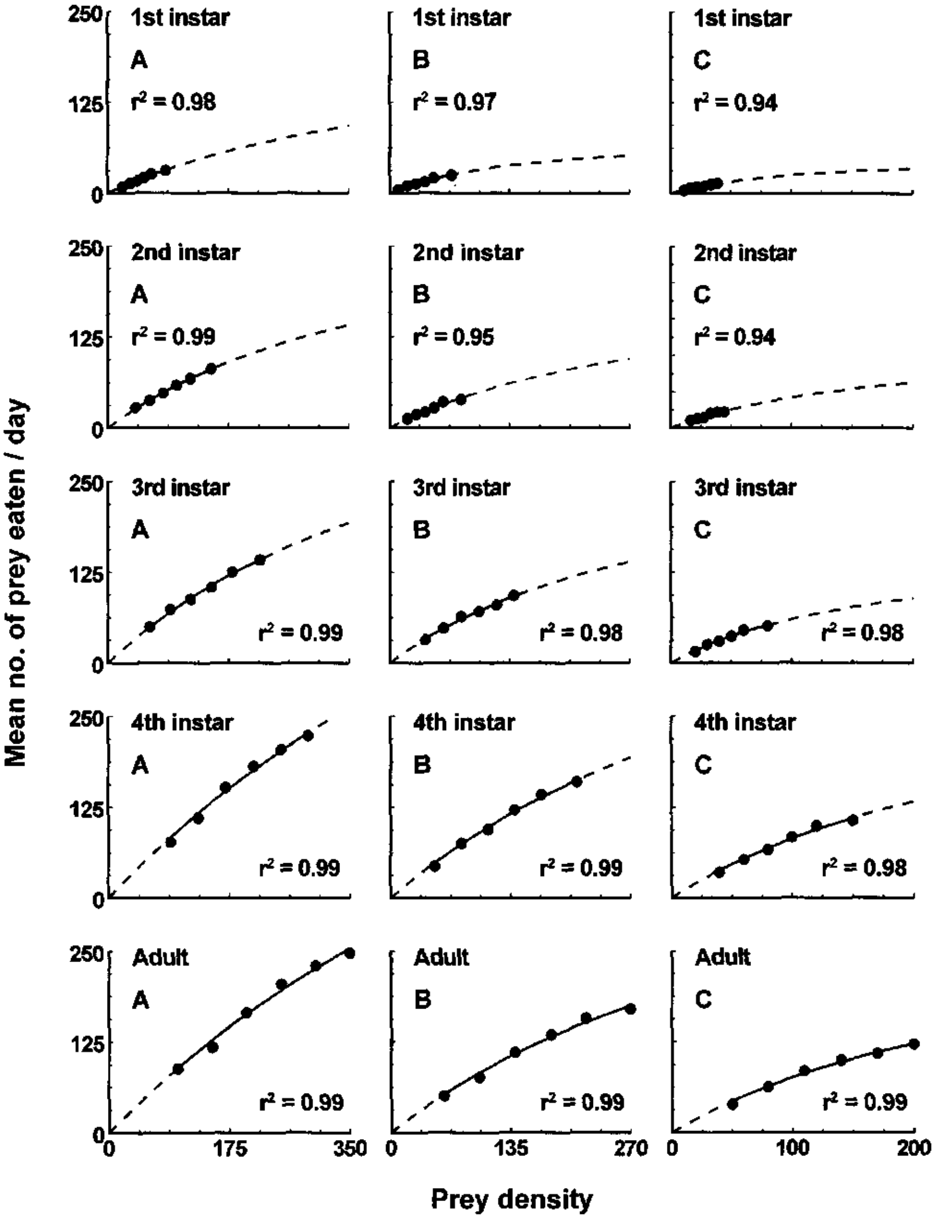


Fig. 4.1. Functional response of five foraging stages of *C. septempunctata* towards early instars (A), late instars (B), and the adults (C) of *A. gossypii* on cotton at 25 °C. Data were fitted with Equation 4.2. Parameters are given in Tables 4.2 and 4.3. Each data point represents a mean of 10 replicates.

4.3.1 Effect of predator stage

At all temperatures tested, search rate (*a*) generally increased by 43–112% from one predator instar to the next, though search rates of the female adult were slightly lower than those of the fourth instar predator (Table 4.2). The search rate defines how steeply the curve approaches the upper asymptote and estimates the proportion of arena area (30 cm^2) searched per unit time (d). This parameter may be converted into units of area

Table 4.2. Search rate (*a*, mean ± SE, d^{-1}) of five foraging stages of *C. septempunctata* preying on three size-groups of *A. gossypii* on cotton at five temperatures[1].

Prey size-group[2]	Predator stage[3]	Temperature (°C)				
		15	20	25	30	35
Early instar	L1	0.36 ± 0.039	0.53 ± 0.030	0.63 ± 0.068	1.00 ± 0.096	1.35 ± 0.241
	L2	0.52 ± 0.055	0.94 ± 0.086	1.20 ± 0.050	1.53 ± 0.356	2.23 ± 0.259
	L3	0.80 ± 0.104	1.42 ± 0.173	1.95 ± 0.191	2.27 ± 0.341	3.00 ± 0.379
	L4	1.70 ± 0.232	2.41 ± 0.434	3.07 ± 0.532	3.26 ± 0.310	4.58 ± 0.851
	FA	0.84 ± 0.196	1.47 ± 0.204	2.56 ± 0.452	2.59 ± 0.342	3.40 ± 0.737
Late instar	L1	0.45 ± 0.037	0.60 ± 0.028	0.71 ± 0.106	1.05 ± 0.058	2.23 ± 0.556
	L2	0.63 ± 0.040	0.95 ± 0.122	1.04 ± 0.220	2.26 ± 0.167	3.04 ± 0.677
	L3	0.90 ± 0.063	1.46 ± 0.215	2.03 ± 0.285	2.81 ± 0.481	3.21 ± 0.907
	L4	1.71 ± 0.321	2.51 ± 0.571	3.40 ± 0.489	5.80 ± 1.043	5.80 ± 1.043
	FA	0.94 ± 0.155	1.69 ± 0.111	2.38 ± 0.326	4.00 ± 1.003	5.28 ± 0.458
Adult	L1	0.39 ± 0.076	0.66 ± 0.056	0.73 ± 0.137	1.08 ± 0.132	1.73 ± 0.277
	L2	0.45 ± 0.046	1.02 ± 0.114	1.28 ± 0.291	3.19 ± 0.565	3.56 ± 0.828
	L3	0.65 ± 0.067	1.59 ± 0.294	2.13 ± 0.371	3.26 ± 0.593	3.66 ± 0.416
	L4	1.28 ± 0.109	2.55 ± 0.344	3.32 ± 0.683	6.44 ± 1.414	7.13 ± 1.528
	FA	0.67 ± 0.130	1.73 ± 0.263	2.29 ± 0.232	3.43 ± 0.412	5.12 ± 0.185

[1] The search rate was estimated from Equation 4.2.

[2] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

[3] L1, L2, L3 L4 and FA denote the first through fourth larval instars and the female adults of *C. septempunctata*, respectively.

searched per unit time by multiplication with the leaf area within arena. For instance, the estimated search rate on the adult prey at 25 °C increased from 22 $cm^2\ d^{-1}$ in the first larval instar to 38 $cm^2\ d^{-1}$ in the second larval instar (73% increase), to 64 $cm^2\ d^{-1}$ in the third larval instar (68% increase), to 100 $cm^2\ d^{-1}$ in the fourth larval instar (56% increase), and to 70 $cm^2\ d^{-1}$ in the female adult (30% decrease) (Table 4.2).

Handling rate increased with 47–112% from one predator stage to the next, though there was less difference in handling rate between the fourth larval instar and adult predator (Table 4.3). The handling rate is the upper asymptote of the functional response curve and represents the potential number of prey that can be killed per unit

Table 4.3. Handling rate (T_h, mean ± SE, h^{-1}) of five foraging stages of *C. septempunctata* preying on three size-groups of *A. gossypii* on cotton at five constant temperatures[1].

Prey size-group[2]	Predator stage	Temperature (°C)				
		15	20	25	30	35
Early instar	First instar	2.2 ± 0.62	5.3 ± 1.40	7.1 ± 2.11	6.2 ± 1.02	7.1 ± 1.96
	Second instar	4.5 ± 1.00	8.7 ± 2.00	9.5 ± 0.91	10.9 ± 2.84	9.1 ± 1.49
	Third instar	9.4 ± 2.31	13.3 ± 3.20	12.6 ± 1.76	13.8 ± 2.82	12.7 ± 1.60
	Fourth instar	16.1 ± 2.52	21.0 ± 6.08	18.5 ± 3.77	17.9 ± 2.31	17.4 ± 2.77
	Female adult	22.2 ± 4.28	24.2 ± 4.66	21.0 ± 5.16	22.4 ± 3.95	19.9 ± 4.00
Late instar	First instar	1.0 ± 0.10	2.2 ± 0.19	2.8 ± 0.91	2.6 ± 0.21	3.1 ± 0.71
	Second instar	2.2 ± 0.22	4.0 ± 1.11	5.5 ± 1.64	4.3 ± 0.37	4.2 ± 0.88
	Third instar	4.7 ± 0.47	7.1 ± 1.58	8.1 ± 1.56	7.6 ± 1.26	8.4 ± 2.43
	Fourth instar	10.5 ± 2.66	13.1 ± 3.88	11.8 ± 1.52	10.3 ± 0.96	10.3 ± 0.96
	Female adult	7.8 ± 1.50	13.1 ± 1.01	12.6 ± 1.60	12.3 ± 1.79	11.4 ± 0.39
Adult	First instar	1.0 ± 0.25	1.3 ± 0.22	1.8 ± 0.46	1.6 ± 0.36	1.9 ± 0.22
	Second instar	1.8 ± 0.42	2.0 ± 0.42	2.9 ± 0.84	2.7 ± 0.54	2.5 ± 0.60
	Third instar	3.3 ± 0.83	4.5 ± 1.41	5.0 ± 1.25	4.2 ± 0.67	4.0 ± 0.35
	Fourth instar	6.3 ± 0.75	7.4 ± 0.99	7.5 ± 1.23	6.4 ± 0.65	6.1 ± 0.60
	Female adult	7.8 ± 1.65	8.5 ± 1.51	8.6 ± 0.74	9.1 ± 0.76	8.8 ± 0.15

[1] The handling rate was estimated from Equation 4.2.

[2] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

time (maximum number of prey killed daily or hourly). For example, the estimated handling rate on the adult prey at 25 °C increased from 1.8 aphid per hour in the first larval instar predator to 2.9 aphids per hour in the second larval instar (60%), to 2.0 aphids per hour in the third larval instar (70% increase), to 7.5 aphids per hour in the fourth larval instar (50% increase), and to 8.6 aphids per hour in the female adult (15% increase) (Table 4.3).

4.3.2 Effect of prey size

Differences in the search rate between prey size-groups for the same predator stage were present but not large (less than 50% between extremes), and the effect of prey sizes on the search rate varied with temperature (Table 4.2). At 15 °C, *C. septempunctata* obtained the greatest search rate on the late instar prey (Table 4.2). At the other four temperatures, the highest search rate was generally attained on the adult prey (Table 4.2).

Handling rate was greatest on early instar prey at all five temperatures (Table 4.3). Compared to adult prey, the handling rate on early instars was a factor 3.1 larger and the handling rate on late instars was a factor 1.6 larger (Table 4.3). This result suggests that one adult unit of *A. gossypii* on cotton is nutritionally equivalent to 1.6 late instars or 3.1 early instars in terms of the maximum predation by *C. septempunctata.*

4.3.3 Effect of temperature

Search rate increased linearly with temperature (Fig. 4.2). RMSE was 0.04–0.19 arena d^{-1} for the first larval instar predator, 0.13–0.61 arena d^{-1} for the second larval instar, 0.15–0.31 arena d^{-1} for the third larval instar, 0.53–1.39 arena d^{-1} for the fourth larval instar, and 0.41–0.59 arena d^{-1} for the female adult; and r^2 ranged from 0.87 to 0.99. All estimated parameters are given in Table A–5 (Appendix A). The search rates of each foraging stage on all prey size-groups at 35 °C were 3–8 times as large as those at 15 °C (Table 4.2 and Fig. 4.2). For instance, the search rate on the adult prey in the first larval instar predator increased from 12 cm^2 d^{-1} at 15 °C to 52 cm^2 d^{-1} at 35 °C, from 14 to 107 cm^2 d^{-1} in the second larval instar, from 20 to 110 cm^2 d^{-1} in the third larval instar, from 38 to 214 cm^2 d^{-1} in the fourth larval instar, and from 20 to 154 cm^2 d^{-1} in the female adult (Table 4.2 and Fig. 4.2).

Changes in handling rate of all foraging stages to each prey size-group with temperature were well described by Equation 4.4 (Fig. 4.3). RMSE was 0.3–4.4 aphids per hour in the first instar larval predator, 0.5–3.7 aphids per hour in the second larval instar, 0.8–3.8 aphids per hour in the third larval instar, 0.9–7.4 aphids per hour in the

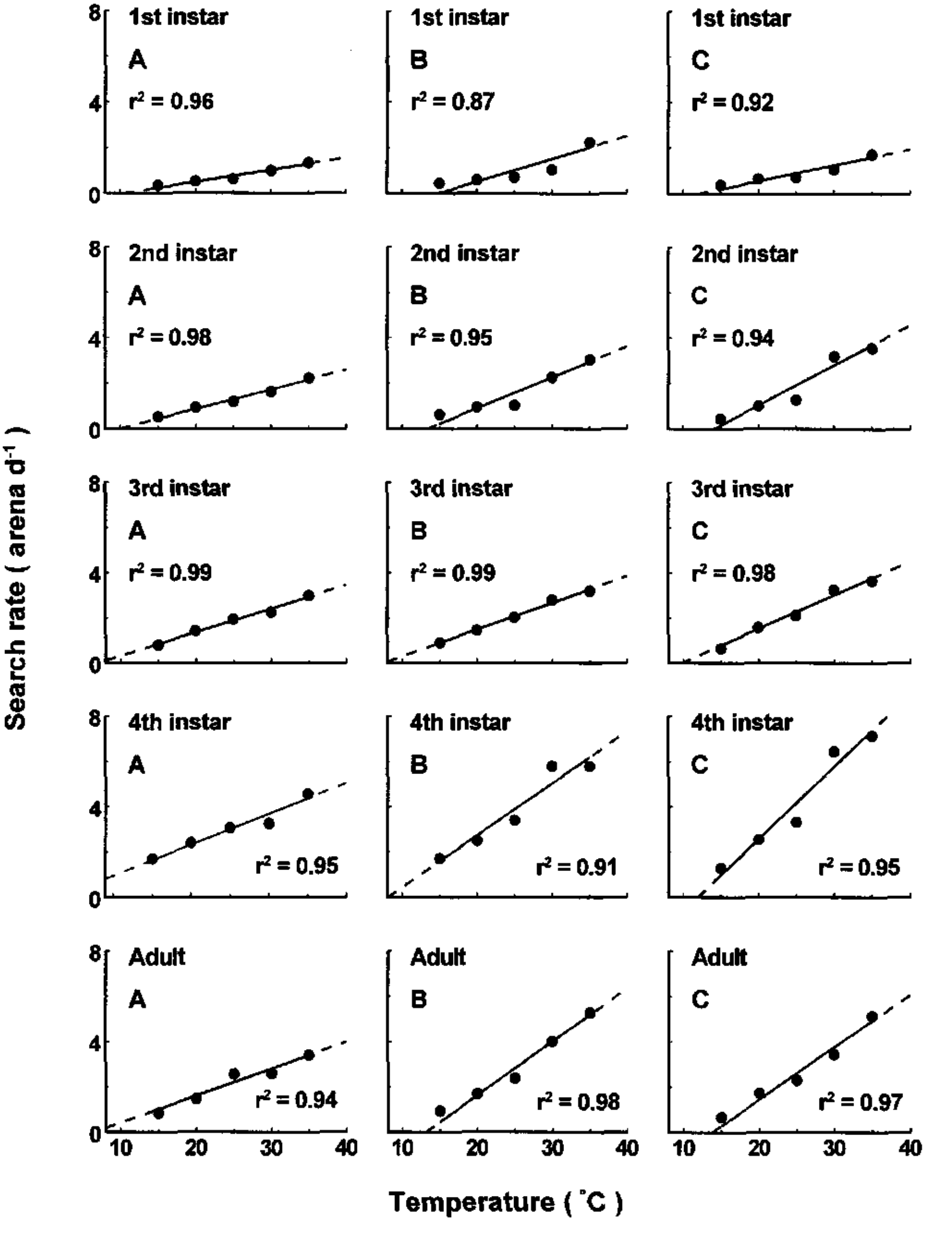


Fig. 4.2. Relationship between temperature (°C) and the search rate (a, arena d^{-1}) of five foraging stages of *C. septempunctata*, feeding on early instars (A), late instars (B) and the adults (C) of *A. gossypii* on cotton. Good fit was obtained using Equation 4.3. The estimated parameters are given in Table A–5 (Appendix A).

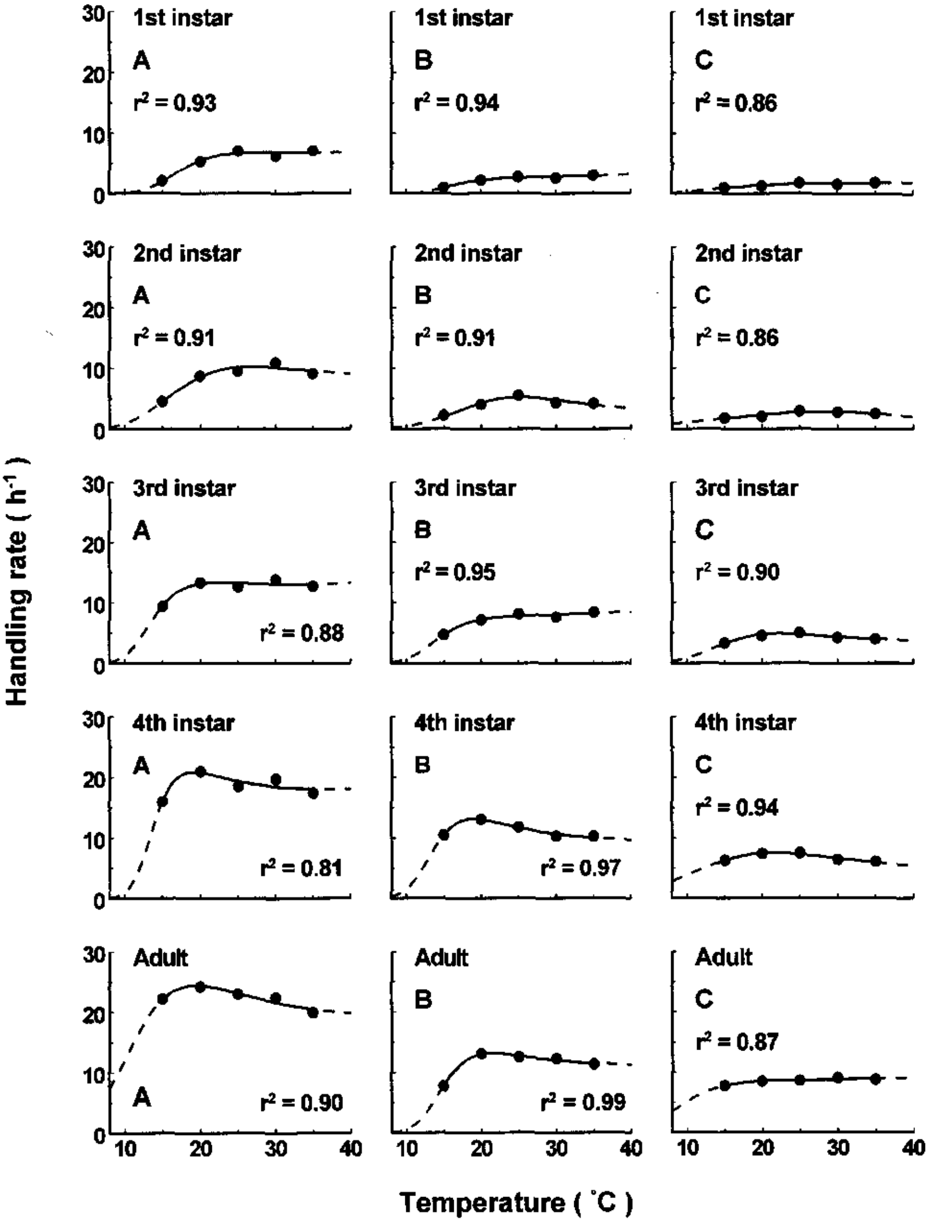


Fig. 4.3. Relationship between temperature (°C) and the handling rate (R_h, h^{-1}) of five foraging stages of *C. septempunctata*, feeding on early instars (A), late instars (B) and the adults (C) of *A. gossypii* on cotton. The best fit was determined using Equation 4.4. The estimated parameters are given in Table A-6 (Appendix A).

fourth larval instar, and 1.1–4.8 aphids per hour in the female adult. r^2 ranged from 0.86 to 0.97. All estimated parameters are shown in Table A–6 (Appendix A). In all predator–prey combinations, handling rate increased substantially from 15 to 20 °C, less so from 20 to 30 °C, and there was a tendency to decline from 30 to 35 °C (Table 4.3 and Fig. 4.3).

4.4 Discussion

An increase in search and handling rate in successive developmental predator stages has been observed in several coccinellids (Hodek, 1973; Frazer et al., 1981; Ofuya, 1986; Fan et al., 1989; Cai & Yan, 1991; Li, 1991; Dong et al., 1992). Our data (Tables 4.2 and 4.3) fit in the general pattern described in the literature. The increase in search and handling rate with developmental stages of a predator are consequences of the increase in its size which affects behavior, e.g. capture efficiency (Hodek, 1973; Thompson, 1978b; Isenhour & Yeargan, 1981).

With increase in *A. gossypii* size, the search rate of foraging stages of *C. septempunctata* increased but the handling rate decreased (Tables 4.2 and 4.3). Similar results were obtained with other coccinellids by Ofuya (1986). Aphids exhibit various defence responses against attacks by coccinellid predators, such as kicking, pulling free the seized appendage, running away and dropping on the ground (Dixon, 1958; Brown, 1974; Frazer & Gilbert, 1976). The effectiveness of these defences increases with aphid developmental stage (Brown, 1974; Frazer & Gilbert, 1976).

Carter et al. (1982) estimated that an adult unit of *S. avenae* on wheat was equivalent to 1.5 fourth instar, 2.0 third instar, 3.5 second instar and 5.0 first instar nymphs, based on the size differences of the various instars. Xie & Sterling (1987) observed that an adult unit of *A. gossypii* on cotton was equivalent to 1.7 fourth instar, 4.6 third instar, 11.1 second instar or 50.0 first instar nymphs, based on the body weight of various instars. Our observations indicated that an adult aphid unit was equivalent to 1.6 late instar nymphs and 3.1 early instar (Table 4.3), based on the relative increase of handling rate of *C. septempunctata* with the size-group of *A. gossypii* averaged over five temperatures.

A linear increase in the search rate with temperature has been found in *C. californicus* (Frazer & Gilbert, 1976), *Ischnura elegans* (van der Linden) (Thompson, 1978a), *Phytoseiulus persimilis* Athias-Henriot (Everson, 1980), and *Orius insidiosus* (Say) (McCaffrey & Horsburgh, 1986). A curvilinear increase in handling rate with temperature was also reported for *C. septempunctata* preying on *S. avenae* (Cai & Yan, 1991), *I. elegans* (Thompson, 1978a), and *P. persimilis* (Everson, 1980). Search rate of foraging stages of *C. septempunctata* preying on *A. gossypii* adults at 15 °C was lower than on the early and late instar prey (Table 4.2 and Fig 4.4). This anomaly may be explained by the different sensitivity of the seven-spot beetle and cotton aphid at low temperatures. The threshold temperature of *A. gossypii* (6–8 °C) (see Table 2.2) is lower than that of *C. septempunctata* (11–14 °C) (see Table 3.3). If we assume that the behavioral sensitivity to low temperature follows this same pattern, low temperature would reduce the activity of the predator more than that of the prey. Consequently, predator capture efficiency would diminish at low temperature. Handling rate of *C. septempunctata* increased rapidly from 15 to 20 °C, reached a maximum between 20 °C and 30 °C, and decreased slightly from 30 to 35 °C (Fig. 4.3). This range of temperature for the maximum feeding is consistent with that for the optimum development and maximum oviposition of *C. septempunctata* (Chapter 3).

Temperature affects most components of the feeding behavior of arthropod predators. High temperature accelerates rates of the ectotherm's chemical processes (Mack et al., 1981; Kharboutli & Mack, 1993), resulting in increased energy demand and hunger (Everson, 1980). Increased temperature may affect the search rate by enhancing the walking speed of the predator and it may also affect the handling rate by decreasing the time spent in pursuit of each prey (Sandness & McMurtry, 1972; Glen, 1975; Nakamura, 1977; Everson, 1980). The tendency of a decline in handling rate gl with temperature rising from 30° to 35 °C (Fig 4.3) was probably the result of predators trying to escape, as we observed during the experiment. Such a response to high temperature may explain why, in the hot months of July and August, *C. septempunctata* are scare in cotton fields in North China, and unable to control "summer aphid" populations (Luo & Gao, 1986; Xia et al., 1996).

The impact of predator stage, prey size and temperature on the functional response of *C. septempunctata* to *A. gossypii* on cotton was clearly demonstrated in this study. The data obtained support the idea to use this predator as a biological control agent of the cotton aphid at the seedling stage of cotton because quite substantial predation is exerted at the temperature range common during the period of May and June in the North China cotton region. Based on these data, it is possible to model the field predation rate on mixed prey stages of *A. gossypii* by mixed predator stages of *C. septempunctata* on whole plants under field conditions. This can be achieved by modelling the predation on mixed prey stages as a competitive process (Rabbinge, 1976; Rabbinge et al., 1989) while taking into account the effect of plant leaf surface on predation by *C. septempunctata* (Chapters 5 and 6).

Chapter 5

Temporal dynamics of the predator–prey system *Coccinella septempunctata–Aphis gossypii* in single cotton cropping: experiments and simulation

Abstract A simulation model of the temporal dynamics of the predator–prey system *Coccinella septempunctata* L.–*Aphis gossypii* Glover in cotton monoculture was developed. Six submodels were distinguished, cotton aphid, seven-spot beetle, predator–prey interaction, parasitism, cotton plant, and abiotic factors. The model was tested and evaluated at three levels of complexity: laboratory, field cage and open field. At each level, processes were added to the model, based on discrepancies between "original model" behaviors and observations, and additional experimentation. Processes included in the model at the laboratory level were temperature-dependent development, survival and reproduction of both insects; and prey density, prey size-group and temperature-dependent predation. Adaptations for the field cage level were density dependence of wing induction and reproduction of *A. gossypii*, extrapolation of the functional response from single stage interaction in experimental arenas in the laboratory to multiple stage interactions on plants, and a higher mortality for *C. septempunctata* than observed in the laboratory. Adaptations for the open field level were immigration of both insects; prey density-dependent departure of seven-spot beetle adults; time-dependent parasitization of alate immigrants by *Allothrombium* mites, and apterous aphids and seven-spot beetle pupae by hymenopterous parasitoids; prey density and prey size-group dependent predation by *Propylaea japonica* (Thungberg); and accumulated degree-days (D°)-driven cotton canopy growth. The simulated and observed data were in reasonable agreement at all levels, though discrepancies increased with the level of scale. Simulations at the open field level show that *C. septempunctata* plays a key role in controlling *A. gossypii* in cotton monoculture, but its numbers increase too late to guarantee a sufficient biological control. With *C. septempunctata* alone, aphid populations are kept below action thresholds at a predator–prey ratio of 1:50. Variations in temperature or alate immigration alone can not explain between-season differences in aphid population dynamics. Immigrating numbers of *C. septempunctata* adults is the key factor. Significance of the findings and further development of the model to explore biological control strategies for *A. gossypii* with *C. septempunctata* are discussed.

5.1 Introduction

Cotton aphid (*Aphis gossypii* Glover) [Homoptera: Aphididae] is the key insect pest of cotton (*Gossypium hirsutum* L.) at the seedling stage in China, particularly in the North China cotton region. The resulting annual losses amount to 10–15% of the attainable yield (CCRI, 1983; Xia, 1991; Fang et al., 1992). Preservation and utilization of naturally-occurring natural enemies, notably the seven-spot ladybird beetle (*Coccinella septempunctata* L.) [Coleoptera: Coccinellidae], is an effective biological control method of the cotton aphid (CCRI, 1983; BU, 1984; Zhang, 1985; Wang et al., 1991). Thus, *A. gossypii* populations can be brought down below economic damage levels by augmenting the seven-spot beetle through cotton–wheat intercropping (Wang, 1990; Wang et al., 1993; Xia, 1994b), by preserving the seven-spot beetle through the selective application of pesticides to minimize their adverse impact (CCRI, 1983; Fang et al., 1992; Xia, 1992; Xia et al., 1996), and by mass releasing the seven-spot beetle collected on wheat (BU, 1984).

These biological control measures have been empirical. Extension consultants and cotton growers face difficult decisions and feel uncertain in applying biological control. The main reason for this is the lack of a quantitative understanding of the dynamic behavior of the *C. septempunctata–A. gossypii* system and insufficient predictability of biological control with the seven-spot beetle.

Modelling complex predator–prey systems can help to gain understanding and develop workable biological control strategies (Rabbinge et al., 1989; van der Werf et al., 1989). Several biological control systems have been developed within the framework of a systems research approach, featuring modelling, e.g. biological control of *Panonychus ulmi* Koch with *Amblyseius potentillae* (Garman) on apple (Rabbinge, 1976); biological control of *Myzus persicae* (Sulzer) with *Coleomegilla maculata* (De Geer) on potato (Mack & Smilowitz, 1982b); biological control of *Acyrthosiphon pisium* (Harris) with *C. canifornicus* Mannerhein, *C. trifasciata* L *and C. undecipunctata* L. on alfalfa (Frazer & Gilbert, 1976); and biological control of *Liriomyza bryonae* (Kaltenbach) with *Dyglyphus isaea* Walker on greenhouse tomato (Boot et al., 1992). No effort has been made to analyse, quantify and explain biological control of *A. gossypii* by *C. septempunctata* in cotton.

The objective of this study is to develop a simulation model of the temporal dynamics of the predator–prey system *C. septempunctata–A. gossypii* in cotton monoculture, and to use the model to gain more insights in the dynamic behavior of the coccinellid–aphid system and the mechanisms of biological control of *A. gossypii* by *C. septempunctata* for exploring promising biological control strategies in cotton in North China.

5.2 Materials and methods

5.2.1 Model development

The model was constructed following the generally accepted principles in systems analysis and simulation (Rabbinge et al., 1989; Xia et al., 1991). It is a dynamic, deterministic and short-term model, designed to simulate temporal dynamics of the predator–prey system *C. septempunctata–A. gossypii* at cotton seedling stage (from sowing to first square, i.e. from mid April to mid June) in cotton monoculture. The model simulates changes in density (number per plant) for both insects on a whole field basis. Spatial heterogeneity was not considered here (but see Chapter 6). For both prey and predator, the fractional boxcar train was used to simulate dispersion in development of each pre-reproductive stage, while the escalator boxcar train was applied to mimic adult ageing because of the age-dependent reproduction (Rabbinge, 1976; Rabbinge et al., 1989). Numbers of boxcar trains used were calculated from the data presented in Tables 2.1 and 3.2, using the method developed by (Goudriaan & van Roermund, 1993). The model was written in a PC version of the Continuous System Modelling Program (IBM, 1975). The rectilinear integration method was applied with a time step of 0.01 d, 1/10 of the smallest time coefficient in the model. Six submodels are distinguished: (1) cotton aphid, (2) seven-spot beetle, (3) predator–prey interaction, (4) parasitism, (5) cotton plant, and (6) abiotic factors.

5.2.1.1 Cotton aphid

Populations of *A. gossypii* are distinguished in five developmental stages: the first through third instar, fourth instar (apteriform and alatiform) and the adult (apterous and alate). Adults are further distinguished in the pre-reproductive and the reproductive plus post-reproductive phases. Apterous and alate adults were not distinguished except where mentioned explicitly.

Immigration and emigration The model initializes aphid population dynamics with measured daily net immigrations of alates (the number of alates settling on cotton per plant per day). The net immigration was determined by field counts (see Section 5.2.2.1 and Fig. 5.3 in Section 5.3.1.1) and input into the model as forcing functions. Immigrations until 20 May were considered as after that time few immigrants were found on winter hosts (e.g. *Hibiscus syriacus* L.) (see Section 5.2.2.1).

Alate immigrants were supposed to be reproductively mature on arrival and to remain in the cotton field until death. Alate adults produced on cotton were assumed to disappear from the cotton field upon their emergence.

Development and survival Development of the cotton aphid is mainly determined by temperature (Chapter 2). The relationship between temperature and the developmental rate (R_d, d^{-1}) of pre-reproductive stages was described with Equation 2.2. T_l is given in Table 2.2; T_u is assumed to be 38 °C for all life stages (Xie & Sterling, 1987); and a_1, a_2 and a_3 are found in Fig. 2.1. The relationship between temperature and the ageing rate computed as the reciprocal of the mean duration plus 3 SD (standard deviation) of the reproductive plus post-reproductive adult (Table 2.1) was linearly interpolated using the CSMP-AFGEN function (IBM, 1975). The ageing rate of alate immigrants was multiplied by 0.9 as they live 10% longer than apterous adults (Xie & Sterling, 1987).

Survival of the cotton aphid at cotton seedling stage is greatly influenced by temperature (Chapter 2), predation (Chapter 4), and parasitism (Dong et al., 1992; Fang et al., 1992). The relationship between temperature and the relative mortality rate (R_m, d^{-1}) was described with Equation 2.5. Values of c_1, c_2 and c_3 are presented in Fig. 2.2 for the pre-reproductive stages, and in Table A–1 (Appendix A) for the adult stage. Effects of predation and parasitism are described in the respective submodels.

Reproduction and morph determination Fecundity of the cotton aphid depends on temperature and adult age (Chapter 2), morph (alate or apterous) (Xie & Sterling, 1987), and crowding (Li & Xie, 1990a). Mean reproductive rate (R_a, the number of nymphs produced per female per day) of each adult age class at different temperatures was calculated with Equation 2.6. T_l is shown in Table 2.2; and d_1, d_2 and d_3 are given in Table A–2 (Appendix A). The mean reproductive rate of alate immigrants was multiplied by 0.8 as their fecundity was about 80% that of the apterous adults (Xie & Sterling, 1987). The mean reproductive rate of apterous adults was multiplied by a factor (F_r), which was inversely related to density and calculated by an equation adapted from Li & Xie (1990a):

$$F_r = \exp\left[-0.0666 \left(R_a / T_d \right) D_a \right] \tag{5.1}$$

where T_d is the temperature above the lower developmental threshold (Table 2.2), and D_a is the total aphid density per plant.

Wing formation is the result of combined effects of crowding (Xie & Sterling, 1987), and physiological conditions and stages of the plant (Zuo et al., 1991). Only the effect of crowding was taken into account. The relationship between aphid density (D_a) and the fraction of the fourth alate instars (F_a) was determined in single caged potted-plants (see Section 5.2.2.1) and described by:

$$F_a = k_1 + k_2 \exp\left(-D_a / k_3 \right) \tag{5.2}$$

where k_1, k_2 and k_3 are coefficients (see Fig. 5.1 in Section 5.3.1.1).

5.2.1.2 Seven-spot beetle

Populations of *C. septempunctata* are distinguished in seven developmental stages: eggs, four larval instars, pupae, and the adults (females and males). Adults are further distinguished in the pre-oviposition and the oviposition plus post-oviposition phases. Females and males were assumed to be the same except for oviposition, with the sex ratio of 1:1.

Immigration and emigration The model simulates seven-spot beetle population dynamics from the start of migration by estimating daily net immigrations of the beetle adults (the number of adults settling in cotton per plant per day). The net immigration was obtained through field counts (see Section 5.2.2.2) and input into the model as forcing functions (see Fig. 5.3 in Section 5.3.1.2). Immigrations until late May (the early season immigration) were considered as after that time a large number of seven-spot beetle adults move into cotton from ripening wheat and oil-seed rape. These late season immigrants do not reproduce in cotton.

Adult immigrants were supposed to be reproductively mature on arrival and not to emigrate unless temperature was above 35 °C and prey density was below 10 per plant (Xie & Sterling, 1987).

Development and survival Development of the seven-spot beetle is mainly driven by temperature and prey density (Chapter 3). The relationship between temperature and the developmental rate (R_d, d^{-1}) of pre-oviposition stages was described by Equation 3.1. Values for T_l are given in Table 3.3; T_u is assumed to be 38 °C for all life stages (Sethi & Atwal, 1964); and a_1, a_2 and a_3 are presented in Fig. 3.1. The relationship between temperature and the ageing rate (the inverse of mean duration plus 3 SD) of the oviposition plus post-oviposition adult (Table 3.2) was linearly interpolated using the CSMP-AFGEN function. Food was assumed to be sufficient during the simulated period.

Survival of the seven-spot beetle at the seedling stage of cotton is greatly influenced by temperature and prey density (Chapter 3), cannibalism (BU, 1984; Fang et al., 1992), and parasitism (Li, 1986). The relationship between temperature and the relative mortality rate (R_m, d^{-1}) was described by Equation 3.5. Values of c_1, c_2 and c_3 are given in Fig. 3.2 for the pre-oviposition stages, and in Table A–3 (Appendix A) for the adult stage. As the relative mortality rate was measured in the laboratory by individual rearing (Chapter 3) it might not hold in the field situations. Thus, the stage-specific survival was verified in a field cage study (see Section 5.2.2.2) and estimated by Kiritani & Nakasuji's (1967) equation:

$$S_i = 1 - F_i / F \tag{5.3}$$

where S_i is the fraction of survival of the ith stage, F_i is the total time cumulated density of the ith stage, and F is the total time cumulated density of all stages from the ith stage inclusive. Equation 5.3 is applied based on the assumption that survival rate per unit time is the same in all life stages for the entire sampling period (Kiritani & Nakasuji, 1967). From the estimated stage-specific survival (see Table 5.2 in Section 5.3.1.2), the stage-specific relative mortality rate was calculated as:

$$R_{mi} = - R_{di} \ln (S_i) \tag{5.4}$$

where R_{mi} is the relative mortality rate of the ith stage, and R_{di} is the developmental rate of the ith stage.

Oviposition Fecundity of the seven-spot beetle is largely dependent on temperature, adult age and prey density (Chapter 3). The relationship between temperature and the mean oviposition rate (Y, the number of eggs laid per female per day) of each adult age class was described by Equation 3.7. T_l is shown in Table 3.3; and d_1, d_2 and d_3 are presented in Table A–4 (Appendix A).

5.2.1.3 Predator–prey interaction

In addition to the seven-spot beetle, also the turtle beetle, *Propylaea japonica* (Thungberg) [Coleoptera: Coccinellidae], plays a role in reducing aphid populations at the cotton seedling stage (Song et al., 1988). Both predators have five foraging stages: four larval instars and the adult (females and males). Individuals of each foraging stage can attack all life stages of the cotton aphid. It was assumed that the seven-spot and turtle beetles do not interfere directly with each other's predation activity.

Predation by the seven-spot beetle The functional response of each foraging stage of the seven-spot beetle to early instars (mixed first and second nymphs), late instars (mixed third and fourth nymphs) and the adults of the cotton aphid was determined at five temperatures, 15, 20, 25, 30 and 35 °C (Chapter 4). Predation on the mixed prey stages was modelled by representing the prey stage selection as a competitive process:

$$P_{.} = a_{.} D_{.} / (1 + a_i T_{hi} D_i + a_j T_{hj} D_j + a_k T_{hk} D_k) \tag{5.5}$$

where the subscripts i, j and k represent early instar, late instar, and the adult prey, respectively; $P_{.}$ is the number of prey in a certain stage consumed per day by one predator of a given stage; a is the search rate (arena d^{-1}); T_h is the handling time (d); and D_i is the density of prey size-group i. Values of a and T_h at different temperatures (Tables 4.1 and 4.2), parameterized in an experimental arena of 30 cm^2 under laboratory conditions, were linearly interpolated using the CSMP-AFGEN function.

The relative mortality rates (R_n) in a given prey size-group due to predation by all predator stages present was calculated as :

$$R_n = (P_{n1} B_1 + P_{n2} B_2 + P_{n3} B_3 + P_{n4} B_4 + P_{n5} B_5) / D_n \tag{5.6}$$

where the subscript n denotes the prey size-group, and the subscripts 1 to 5 represent the first through fourth instar and adult predator, respectively; B is the number of predators in a given stage per plant; D is the density of the prey size-group expressed per plant; P is the predation rate in a given prey size-group by one predator of a given stage, which is calculated from Equation 5.5.

To account for the effect of plant leaf surface on the predation rate under field conditions, we converted the search rate on a proportion of arena basis, measured in experimental arenas with 30 cm^2 leaf area, into units of leaf area (cm^2) per day by multiplying with 30 cm^2. The densities of prey and predator were expressed per cm^2 leaf area by dividing them with total leaf area per plant (two-sided). The leaf area per plant was calculated as a function of accumulated degree-days (D°) (see Section 5.2.2.3). The so-constructed model for mixed predator stages or mixed prey stages on whole plants under field conditions was tested in field cages.

Predation by the turtle beetle The functional responses of foraging stages of the turtle beetle to early instars, late instars and adults of the cotton aphid were worked out under laboratory conditions by Zu et al. (1986) and Song et al. (1988). In both studies, glass test tubes were used as the experimental arena, with a leaf area of about 20 cm^2. For their data to be used in the model, we re-estimated a and T_h (see Table A–9 in Appendix A) with Equation 4.2, applying the NLIN procedure of SAS 6.1 for PC (SAS Institute, 1993–1995).

Calculation of predation rate and total relative predation rate, and conversion of units from arena to whole plants were the same as described for the seven-spot beetle. The number of turtle beetles observed in the field (see Fig. B–1 in Appendix B) was input into the model as a forcing function.

5.2.1.4 Parasitism

Parasitism in the cotton aphid Two kinds of parasites commonly attack the cotton aphid, external and internal. Mites from the genus *Allothrombium* (Table 1.1) externally parasitize alate adults on their overwintering hosts (Chen et al., 1994). Although parasitized alate aphids are able to fly and colonize cotton, their longevity is reduced to less than 5 d and fecundity is reduced by over 50% (Dong et al., 1992). It was assumed that all deaths of parasitized alate immigrants occurred at their arrival and the fraction killed was time-dependent. The relationship between day of year (D_y) and the fraction parasitized (P_m) was estimated from field observations (see Section 5.2.2.1) and described by:

$$P_m = l_1 + 4\, l_2 \exp [(- (D_y - l_3) / l_4] / \\ \{ 1 + \exp [- (D_y - l_3) / l_4] \}^2 \qquad (5.7)$$

where l_1, l_2, l_3 and l_4 are the coefficients (see Fig. 5.2A in Section 5.3.1.1).

Hymenopterous parasitoids internally parasitize the cotton aphid at the 4–8 leaf stage. Three parasitoid species attack the cotton aphid (Table 1.1). All deaths from parasitism by these parasitoids were supposed to occur at the adult moult, and the fraction killed was assumed to be time-dependent. The relationship between day of year and the fraction parasitized was estimated by field counts (see Section 5.2.2.1) and described by Equation 5.7 (see Fig. 5.2B in Section 5.3.1.1). Mortality caused by the parasitoids is usually underestimated by counting the number of mummies in the field, because mummies appear with a delay compared to the moment at which parasitization stops reproduction of the victimized aphids, and because mummies may get lost and be not observed. To compensate for this, the observed fraction parasitized was multiplied arbitrarily by 2 in the model (see also Carter et al., 1982).

Parasitism in the seven-spot beetle Several stage-specific parasitoids commonly attack the seven-spot beetle, e.g. *Homalotylus flaminus* Dalman parasitizing larvae, *Tetrastichus coccinellae* Kurjumov parasitizing pupae, and *Dinocampus coccinellae* (Schrank) parasitizing adults (BU, 1984). *T. coccinellae* plays a role in suppressing *C. septempunctata* populations (Zhu & Li, 1981; Li, 1986). It was supposed that all deaths of parasitized pupae occurred at adult emergence and the fraction of parasitization was time-dependent. The relationship between day of year and the fraction of parasitization was estimated by rearing field-collected pupae (see Section 5.2.2.2) and described with Equation 5.7 (see Fig. 5.2C in Section 5.3.1.2).

5.2.1.5 Cotton plant

Detailed cotton growth and development processes are not strictly relevant in this study. It was assumed that cotton plant is an unlimited food resource, and that changes in its physiological conditions have no effect on survival, reproduction and wing formation of the cotton aphid. Thus, a simple model to predict changes in the cotton leaf area though time was developed as input to predation, by fitting an expolinear equation (Goudriaan & van Laar, 1994, pp. 7–28) to field-collected data (see Section 5.2.2.3):

$$L_a = (m_1 / m_2) \ln \{ 1 + \exp [m_2 (D_d - m_3)] \} \qquad (5.8)$$

where L_a is the leaf area (cm^2); D_d is the accumulated degree-days (D°) above 12.5 °C (CCRI, 1983) starting from sowing; and m_1, m_2, and m_3 are coefficients (see Fig. 5.4 in Section 5.3.1.3).

5.2.1.6 Abiotic factors

Dynamics of the coccinellid–aphid system in cotton can be influenced by temperature, relative humidity, rainfall, light and wind (CCRI, 1983; BU, 1984). Of them, temperature is the most important driving variable as it affects nearly all processes in the system (see Chapters 2–4). A diurnal temperature course was constructed based on daily maximum and minimum temperatures, following the method of Goudriaan & van Laar (1994, pp. 29–49), in which a sinusoidal progression during the daytime and a decreasing exponential curve at night were used. The transition between curves was made at sunrise (minimum temperature) and sunset. The phase and the form of such dynamics pattern depended on the day of year, solar time in hours, daylength, and degree of latitude.

5.2.2 Experiments for process quantification

During model development, experiments were carried out to characterize processes of the coccinellid–aphid system quantitatively. Equations chosen to describe the processes were based on a biologically appropriate shape, Root Mean Square Error (RMSE) and coefficient of determination (r^2). Parameters of selected equations were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

All experiments were conducted at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07 °N latitude and 114.22 °E longitude) in 1992–1995. Cotton cultivar used is CCRI 12, commonly planted in cotton monoculture and cotton–wheat intercrop in the North China cotton region. Experiments were done on potted and field grown plants in small or large cages and in the open field. Clay pots were 15 cm (diameter) x 15 cm (high). Small cages (35 cm x 35 cm x 60 cm high) and field cages (3 m x 3 m x 2 m high) were made of metal frames and white nylon mesh. The single cotton cropped field was 0.4–0.5 ha, where cotton was sown on 18–20 April (80 cm between rows). No insecticides were used for seed treatment but fungicides were included for preventing damage from seedling diseases. Conventional crop management measures were practised except above-ground spray of insecticides at the seedling stage of cotton. Plant populations were 10–15 seedlings per m row before thinning and 3–5 thereafter.

5.2.2.1 Experiments for the cotton aphid

Density-driven wing formation Wing formation in growing aphid populations was studied at two occasions in May and June 1993. Each time, 10 single potted-plants (2–3 leaves) were infested with newly emerged apterous adults (one per plant) and covered individually with a small cage. All plants were observed daily for numbers of the first, second, third and fourth (apteriform and alatiform) instars, and the adult (apterous and alate) until aphid populations had collapsed.

Time-dependent parasitization Parasitization of alate *A. gossypii* immigrants by *Allothrombium* was observed in 1992 and 1993. Each year, from first arrival of alate immigrants until early June, 30 field plots were randomly laid out, each with 20 plants. All plants per plot were inspected every 5 d for the number of healthy and parasitized alate aphids. Parasitization of apterous aphids by hymenopterous parasitoids was observed in 1993–1995. Each year, from first appearance of mummies to mid June, 20–30 field plots (30 before thinning and 20 thereafter) were randomly laid out, each with 10–15 plants (15 before thinning and 10 thereafter). All plants in each plot were monitored every 5 d for numbers of apterous aphids alive and mummies.

Immigration rate The net immigration of alate aphids from winter hosts into single cotton cropped fields was measured in 1992–1995. Each year, 20–30 field plots were randomly laid out, each with 10–15 plants which were marked with plastic labels. From their first appearance until 20 May, alate aphids were counted daily on all marked plants, which was then removed. In addition, each year, from first occurrence to disappearance of alate aphids on winter hosts, 50–100 randomly selected tree branches (each 15 cm long) were thoroughly inspected every 5 d for winged *A. gossypii*.

5.2.2.2 Experiments for the seven-spot beetle

Stage-specific survival Two experiments were done in June 1993. The first one looked at egg survival. Ten clay pots, each with two plants having 3–4 leaves and over

50 aphids per plant, were individually covered with a small cage. One pair of ovipositing seven-spot beetle adults released in each cage and allowed to lay eggs for 24 h. Cages (each with more than 20 eggs) were monitored daily for the egg hatch until all eggs had disappeared. The second experiment was made to determine survival of the other immature stages. Three large cages were erected in the field, each with 50 plants (5–6 leaves) and more than 100 aphids per plant. Newly hatched larvae were released in each cage (one per plant). All caged plants were thoroughly monitored every 2 d for the number of different larval instars, pupae and adults until all adults had emerged.

Time-dependent parasitization Parasitization by hymenopterous parasitoids was observed in 1994 and 1995. Each year, from first pupal appearance in single cotton cropped fields to the end of June, 100–300 pupae were collected every 5–10 d and reared in an insectarium. Emergence of adults and parasitoids was observed daily.

Immigration rate Early season immigration of seven-spot beetle adults into single cotton cropped fields was measured in 1992–1995. Each year, 30–50 field plots were randomly laid out, each with 20–25 plants. Until the end of May, all plants and the underground surface of each plot were inspected daily for the number of beetle adults which were then removed.

5.2.2.3 Experiments for the cotton plant

The experiment for determining the relationship between the leaf area of cotton seedlings and accumulated degree-days (D°) was carried out in 1994 in a single cotton cropped field (3 ha) under the conventional crop management. Fifty plants were randomly sampled every 5 d to measure the total leaf area, using a Portable Leaf Area Meter (LI–3000, LI–Cor).

5.2.3 Experiments for model validation

The model was validated at three levels of the system complexity: laboratory, field cage and open field. At each level (say n), a "naive" model was constructed on the basis of data gathered at lower levels of complexity (< or = n–1) and compared with experimental data collected at level n. Extra information gathered at level n was added to the model to correct for lack of correspondence between the naive model and experiments. The adapted model was further tested as a naive model for level n+1 (Table 5.1). At all levels, validation was made by a subjective comparison of simulated and observed densities of the cotton aphid and the seven-spot beetle through time (Rabbinge et al., 1979; Carter et al., 1982).

Table 5.1. Processes included at different levels of the system complexity for testing and improving models of the temporal dynamics of the *C. septempunctata–A. gossypii* system in cotton.

Level	Processes included (I), added (A) or substituted (S)[1]		
	A. gossypii	*C. septempunctata*	Predator–prey interaction
Laboratory	a) Temperature-dependent development (I) b) Temperature-dependent survival (I) c) Temperature and age-dependent reproduction (I)	a) Temperature-dependent development (I) b) Temperature-dependent survival (I) c) Temperature and age-dependent oviposition (I)	a) Prey density, prey size-group and temperature-dependent predation (I)
Field cage	d) Density-dependent wing formation (A) e) Density-dependent reproduction (A)	d) Stage-specific survival (S)[2]	b) Cotton leaf area-dependent predation (A)
Open field	f) Immigration (A) g) Time-dependent parasitization in alate immigrants and apterous aphids (A)	e) Immigration in early and late seasons (A) f) temperature and prey density-dependent emigration (A) g) Time-dependent parasitization of pupae (A)	c) Accumulated degree-days (D°)-dependent cotton canopy growth (A) d) Prey density and prey size-group dependent predation by *P. japonica* (A)

[1] Details on each process are given in Section 5.2.1.

[2] Process b of the beetle is replaced with d.

5.2.3.1 In the laboratory

The model's structure and its ability to simulate the basic processes of the predator–prey system were evaluated (Table 5.1). All validation experiments were carried out in an insectarium, where fluctuating temperatures were recorded with a thermograph.

Experiments for validating the temperature-dependent development, survival and reproduction of the cotton aphid were conducted in June 1992 and May 1993. The basic experimental set-up was described in Chapter 2. In both years, two tests were made. In the first, 100 newly born aphids were reared individually in glass tubes, where moulting and mortality were monitored every 12 h until all survivors had become adults. In the second test, 50 freshly emerged adults were reared individually in glass petridishes, where newly born aphids were counted and then removed every 12 h until all adults had died.

Experiments for validating the temperature-dependent development, survival and oviposition of the seven-spot beetle were done in June 1992 and August 1993. Basic experimental procedures were described in Chapter 3. In both years, two trials were performed. In the first trial, 100 newly hatched larvae were reared individually in plastic containers, where moulting and mortality were inspected every 12 h until all adults had emerged. In the second trial, 20 pairs of freshly emerged adults were reared in plastic containers, where eggs were counted and removed every 4 h until all females had died.

Experiments for validating the functional response of the seven-spot beetle at fluctuating temperatures in plastic containers were conducted in July 1992. The basic experimental design was described in Chapter 4. Predation of five foraging stages was measured with five densities of three prey size-groups (see Table A–7 in Appendix A) for 24 h. Ten replicates were made for each combination. Controls were used for correction of background mortality of the prey (Abbott, 1925).

5.2.3.2 In the field cages

The model's ability to simulate the population development of the cotton aphid and the seven-spot beetle as well as their interactions in the absence of natural enemies was evaluated in field cages (Table 5.1). Ambient temperatures were measured with a thermograph, which was located in a white wooden box (50 cm x 50 cm x 50 cm) with two vertical sides open. The box was fixed at plant level.

Experiments for validating the population development of the cotton aphid were conducted twice in May and June 1993. In May, three cages, each with 100 plants at the 2–3 leaf stage, were erected in the field. Each plant in the cage was infested with one newly emerged alate adult. The number of nymphs and apterous adults were monitored every 2 d and the alate adults produced in the cage were removed daily until aphid populations had started collapsing. The experiment in June was similar to that in May except that there were only 50 plants (3–4 leaves) in each cage, and each plant was infested with two newly emerged apterous adults.

Experiments for validating the seven-spot beetle population development were carried out in June 1993 and May 1994. In 1993, three cages were erected, each with 40 plants at the 4–5 leaf stage and over 100 aphids per plant. In each cage five pairs of ovipositing adults were released and allowed to lay eggs for 15 days. Eggs, immatures, pupae and adults were counted every 2 d until all adults had emerged. The experiment in 1994 was the same as that in 1993 except that there were 60 plants (3–4 leaves) and over 50 aphids per plant in each cage.

An experiment for validating the functional responses of foraging stages of the seven-spot beetle was done in June 1994. Twenty-five cages, each with 40 plants at the 2–3 leaf stage, were assigned to five groups, A, B, C, D and E. One, two, three, four and five newly emerged apterous adult aphids were released per plant in cage groups A to E, respectively. The number of leaves and apterous aphids per plant was observed daily. When prey populations reached the designated density for predation by a given stage in five cages (see Table A–8 in Appendix A), 40 predators of that stage were released in each cage and allowed to prey for 24 h. The released larvae of each instar were 6–12 h old and starved for 12 h, and the adult was 2–5 d old and starved for 24 h.

An experiment for validating the beetle's ability to control the cotton aphid was made in July 1995. Four groups of three cages were erected, each with 40 plants at the 4–5 leaf stage. Two, four, eight and ten freshly emerged apterous adult aphids were released per plant in cage groups labelled A to D. The number of leaves and apterous aphids per plant was counted in all cages every 2 d. On the 6th day after infestation, newly emerged adult beetles were released in each cage group at predator–prey ratios of 1:50, 1:100, 1:200 and 1:400 (3 cages for each ratio). Observations were ended on the 10th day after predators had been released.

5.2.3.3 In the open field

The model's ability to simulate the temporal dynamics of the predator–prey system in single cotton cropping was evaluated in open fields (Table 5.1). All validation experiments were carried out at CCRI in the years 1992, 1993, 1994 and 1995. In each year, a validation experiment was conducted in an open filed (1 ha) with single cotton cropping, where the basic treatments were the same as described in Section 5.2.2. The daily maximum and minimum temperatures were obtained from a meteorological station at CCRI (see Fig. B–5 in Appendix B).

Dynamics of cotton aphid populations Each year, from first appearance of alate immigrants to mid June, cotton aphid populations were monitored every 5 d. At each observation, 20–30 field plots were randomly laid out, each with 10–15 plants. All plants in each plot were inspected for the number of apterous and alate aphids.

Dynamics of major predator populations Each year, from first arrival of seven-spot beetle adults to mid June, numbers of the major predators were sampled every 5 d. At each sampling date, 30–50 field plots were randomly laid out, each with 20–25 plants. All plants and the underground of each plot were carefully inspected for the number of (a) eggs, first to fourth larval instars, pupae and adults of the seven-spot beetle; (b) larvae and adults of the turtle beetle; and (c) other predators in their foraging stages.

5.2.4 Sensitivity analysis

Sensitivity analyses were carried out by omitting processes from the model (coarse sensitivity analysis) and by altering parameter values with a biologically possible range (fine sensitivity analysis) to assess the overall effect in the system (Rabbinge et al., 1979; Carter et al., 1982). Sensitivity analyses were done at the two higher levels: field cage and open field. At the field cage level, the role of density-dependent wing induction and reproduction of the cotton aphid, and cannibalism-inflicted mortality of the beetle, was evaluated by the coarse sensitivity analysis. The simulation was made for the field cage condition in June 1993.

At the open field level, the role of parasites (external and internal), predation by the seven-spot beetle, predation by the turtle beetle, and total natural enemy-inflicted mortality, was evaluated by the coarse sensitivity analysis. The importance of temperature was assessed by increasing or decreasing daily maximum and minimum values by 2 °C. The effect of immigration of late immigrants and of beetle adults was determined by increasing or decreasing their daily values by 20%. In all cases, the simulation was made for the open field condition in 1992.

5.3 Results

5.3.1 Process quantification

5.3.1.1 Process quantification for the cotton aphid

Density-driven wing formation Proportion of winged fourth instars of *A. gossypii* feeding on cotton increased with aphid density, from 0 below 20 aphids per plant to 0.9 at 300 per plant (Fig. 5.1). The relationship, convex and increasing over the whole range, was adequately described by Equation 5.2 (RMSE = 0.043, r^2 = 0.96) (Fig. 5.1). The maximum carrying capacity of cotton seedlings with 3–6 leaves was about 300 aphids per plant.

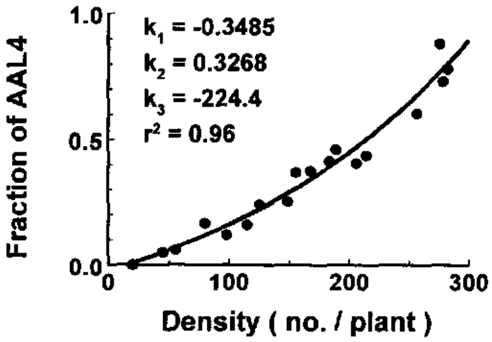


Fig. 5.1. Relationship of total density per plant (D_a) with the fraction of the fourth winged instars (AAL4) induced (F_a) of *A. gossypii* at the seedling stage of cotton. The best fit is given by Equation 5.2.

Time-dependent parasitization Parasitization of alate aphids by *Allothrombium* increased from early May up to a maximum of 13% in mid May and then decreased in both 1992 and 1993 (Fig. 5.2A). The pattern was adequately described by Equation 5.7 (RMSE = 0.006, r^2 = 0.97) (Fig. 5.2A). Parasitization of apterous aphids by hymenopterous parasitoids increased from mid May up to a maximum of 11% in mid June and decreased thereafter in 1993, 1994 and 1995 (Fig. 5.2B). The trend was somewhat different among the three years, but a common curve was chosen to describe the data with Equation 5.7 (RMSE = 0.003, r^2 = 0.95) (Fig. 5.2B).

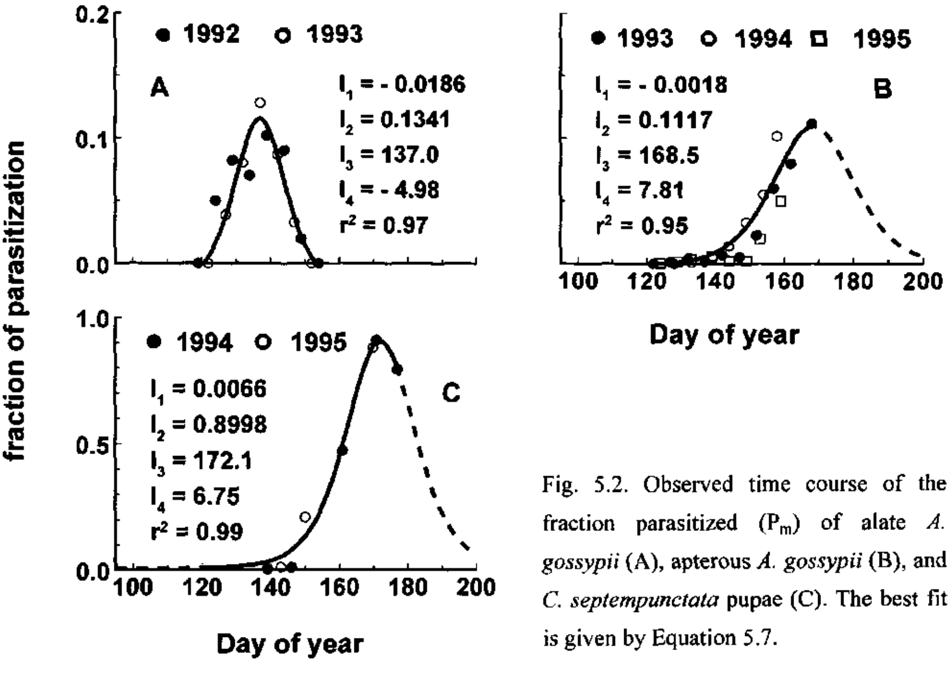


Fig. 5.2. Observed time course of the fraction parasitized (P_m) of alate *A. gossypii* (A), apterous *A. gossypii* (B), and *C. septempunctata* pupae (C). The best fit is given by Equation 5.7.

Immigration rate In all four years, immigration of alate *A. gossypii* immigrants into cotton started early May, peaked mid May and then decreased (Fig. 5.3). The mean daily net immigration over the entire period was greatest in 1995 (0.56 alates per plant per day), lowest in 1994 (0.19 alates per plant per day) and intermediate in 1992 and 1993 (Fig. 5.3).

5.3.1.2 Process quantification for the seven-spot beetle

Stage-specific survival Survival of larval instars and pupae of the seven-spot beetle was above 70 % and that of eggs below 40%, with a total survival of 9% in the pre-adult period (Table 5.2). Cannibalism (both sibling and non-sibling) was the major cause for mortality in the pre-adult stages, particularly among eggs.

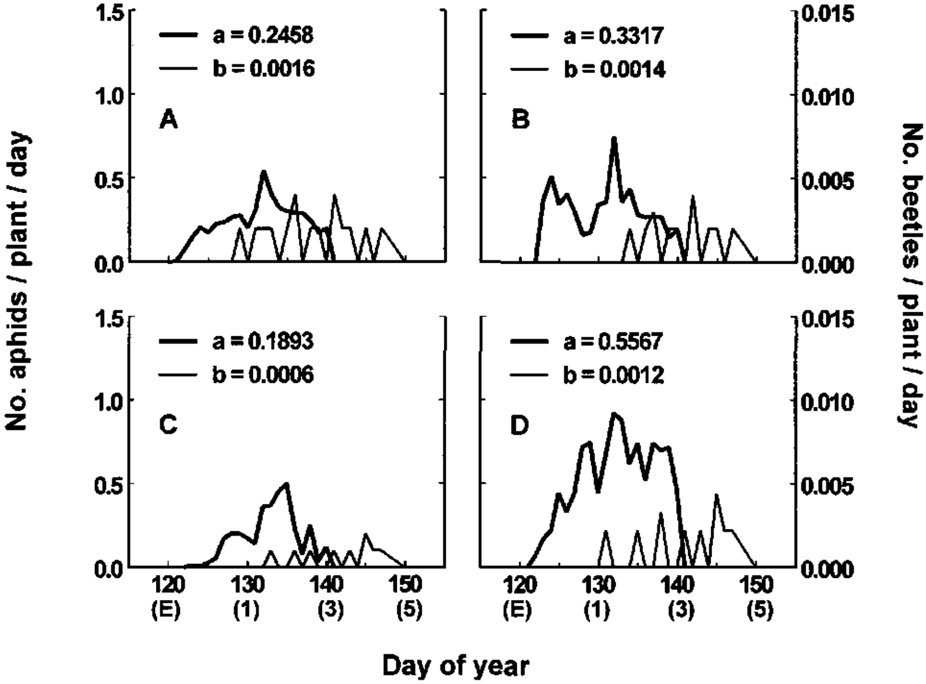


Fig. 5.3. Observed net immigration (number per plant per day) of alate *A. gossypii* immigrants and *C. septempunctata* adults into cotton at the seedling stage in single cotton cropped fields in 1992 (A), 1993 (B), 1994 (C), and 1995 (D). The a and b represent average daily net immigration over the entire period of *A. gossypii* and *C. septempunctata*, respectively.

Table 5.2. Stage-specific survival (%) of *C. septempunctata* in the field cage estimated with the method of Kiritani & Nakasuji (1967).

Eggs[1]	First instar	Second instar	Third instar	Fourth instar	Pupae	Total survival
36.8	76.0	77.7	75.2	74.2	74.6	9.0

[1] Determined in caged single potted-plants.

Time-dependent parasitization Parasitization of *C. septempunctata* pupae by hymenopterous parasitoids increased from late May up to a maximum around 88% in mid June and decreased thereafter in both 1994 and 1995 (Fig. 5.2C). The pattern of parasitization was satisfactorily described by Equation 5.7 (RMSE = 0.019, $r^2 = 0.99$) (Fig. 5.2C).

Immigration rate Immigration of seven-spot beetle adults into cotton started mid May and peaked late May in all four years (Fig. 5.3). The mean daily net immigration rate was highest in 1992 (0.0016 adults per plant per day over a period of 22 d), lowest in 1994 (0.0006 per plant per day over a period of 16), and intermediate in 1993 and 1995 (Fig. 5.3).

5.3.1.3 Process quantification for the cotton plant

The relationship between the leaf area of cotton seedlings in cotton monoculture and accumulated degree-days (D°) was accurately described by Equation 5.8 (RMSE = 34.4 cm^2, $r^2 = 0.99$) (Fig. 5.4).

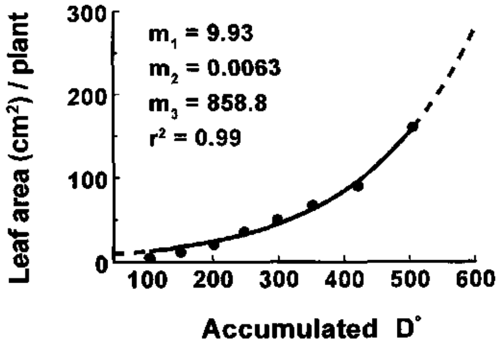


Fig. 5.4. Relationship between cotton leaf area per plant (L_a, cm^2) and the accumulated degree-days above 12.5 °C (D_d, D°) from sowing to the first square in the single cotton cropped field in 1994. The best fit is given by Equation 5.8.

5.3.2 Model validation

In this section, the simulated results were compared with observations at three levels of the system complexity: laboratory, field cage and open field. The model was adapted at each level as summarized in Table 5.1. An interpretation of the results and the insights gained at the different levels are given in the Discussion (see Section 5.4).

5.3.2.1 Validation in the laboratory

A basic model on the development, survival and reproduction of the cotton aphid and the seven-spot beetle as well as their interaction was constructed based on the data gathered in the laboratory (Chapters 2–4). Processes included are shown in (Table 5.1). The simulated results were compared with experimental data obtained in the laboratory.

The model simulated the phenology of instars (Fig. 5.5A), the survivorship of nymphs and adults (Fig. 5.5B), and the accumulated larviposition (Fig. 5.5C) of the cotton aphid in the laboratory experiments in June 1992 and May 1993. Similarly, the model simulated the phenology of immature stages (Fig. 5.6A), the survivorship of immature and adult stages (Fig. 5.6B), and the accumulated oviposition (Fig. 5.6C) of the seven-spot beetle in the laboratory experiments in June 1992 and August 1993. The functional response curves of five foraging stages of the seven-spot beetle to three prey size-groups of the aphid in plastic containers were described by the model (Fig. 5.7).

Above results show that the model can be subjected to more demanding tests at higher levels of the system complexity.

5.3.2.2 Validation in the field cage

A simulation model of the population development of the cotton aphid and the seven-spot beetle as well as their interaction in the field cage was built up by integrating into the laboratory-validated model (a) density-dependent wing formation and reproduction of the cotton aphid, (b) stage-specific survival of the seven-spot beetle, and (c) leaf area-dependent predation of the seven-spot beetle (Table 5.1). The adapted model was validated with population counts from the field cage experiments.

As shown in Fig. 5.8, the model adequately predicted the dynamics of nymphs, apterous adults and total populations of the cotton aphid in field cages in May and June 1993. Compared to the observed data in both cases, the predicted peak was delayed by 2 d, the decreasing phase occurred slightly later, and the peak population size was somewhat larger (Fig. 5.8). In May, the aphid numbers were overestimated throughout

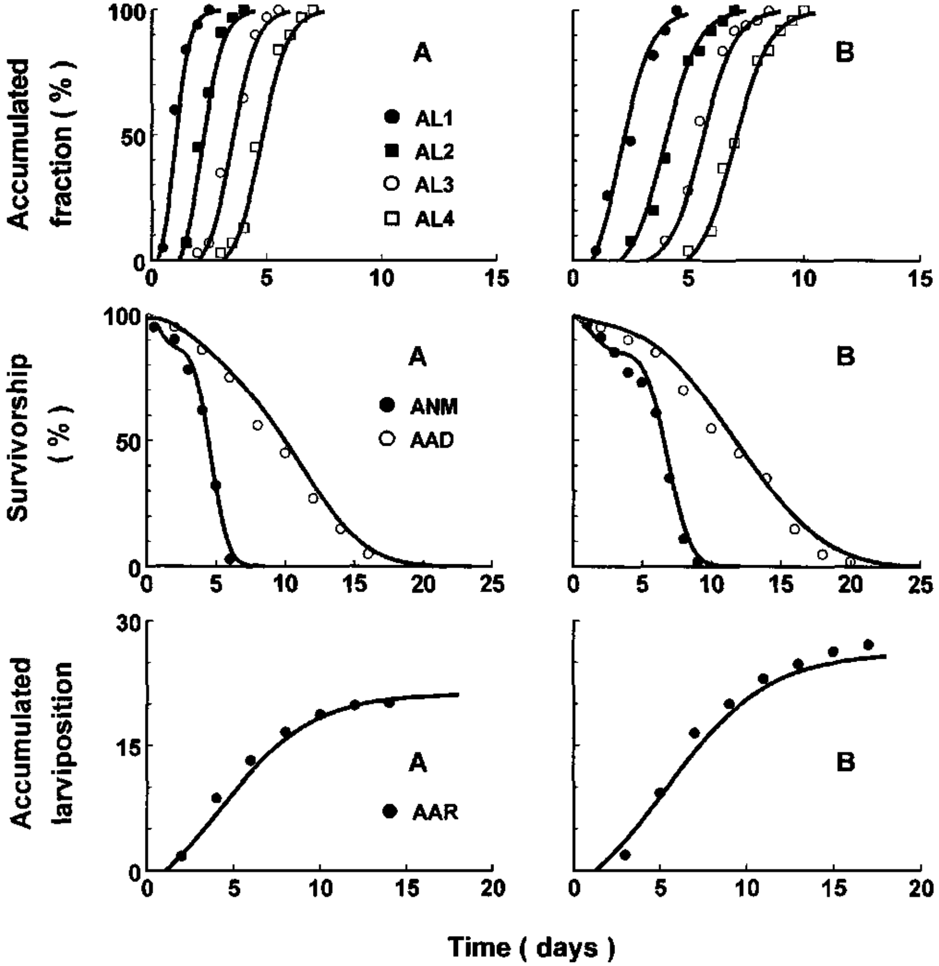


Fig. 5.5. Simulated (——) and observed (symbols) phenology of the first (AL1), second (AL2), third (AL3) and fourth (AL4) instars; survivorship of nymphs (ANM) and adults (AAD); and accumulated larviposition (AAR) of *A. gossypii* at fluctuating temperatures in the laboratory in June 1992 (A), and May 1993 (B).

(Fig. 5.8A). In June, initially they were slightly underestimated but overestimated later on (Fig. 5.8B).

The pattern of population development of eggs, larvae, pupae, and adults of the seven-spot beetle in field cages was simulated both in June 1993 and May 1994 (Fig. 5.9). Compared to observed data in both years, the simulated peak occurred 2 d earlier

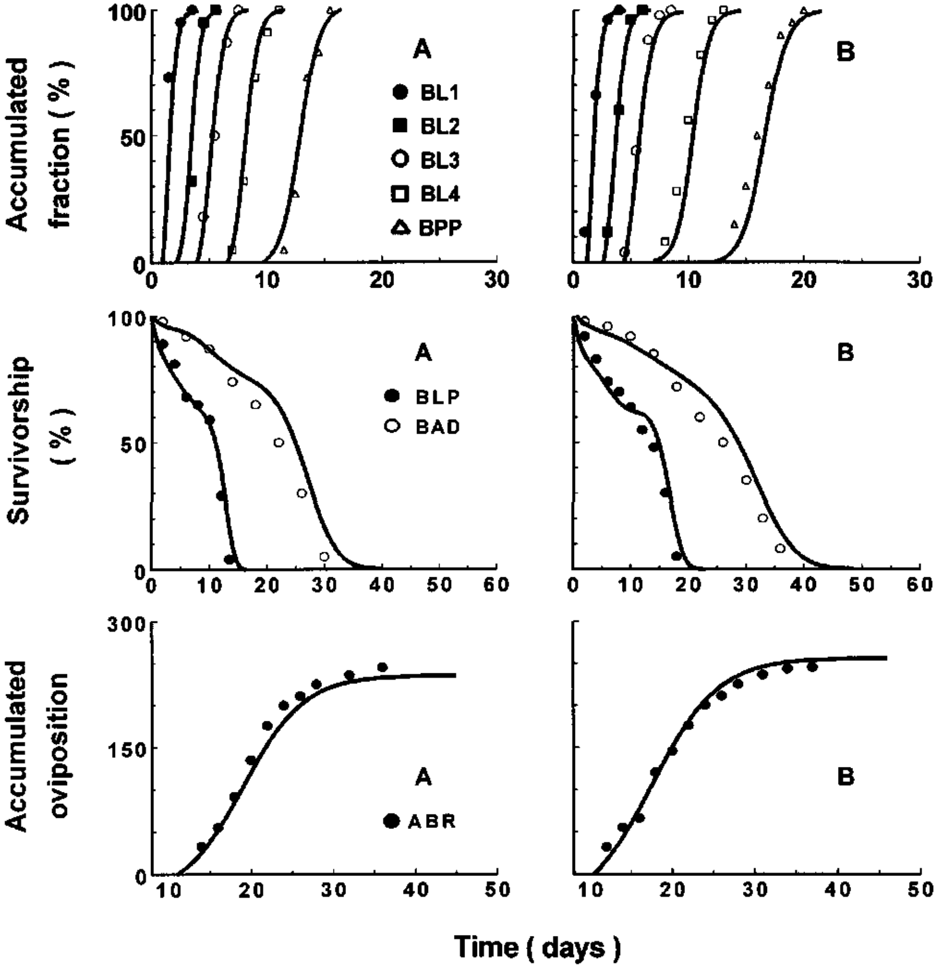


Fig. 5.6. Simulated (——) and observed (symbols) phenology of the first (BL1), second (BL2), third (BL3) and fourth (BL4) larval instars and pupae (BPP); survivorship of immatures (BLP) and adults (BAD); and accumulated oviposition (ABR) of *C. septempunctata* at fluctuating temperatures in the laboratory in June 1992 (A), and August 1993 (B).

in immature stages but 4 d later in the adult stage. In both years, simulated numbers of all stages were greater than observed, particularly in the foraging stages (Fig. 5.9).

The model described the functional response of all five foraging stages of the seven-spot beetle in field cages (Fig. 5.10). In most cases, predation rates were slightly overestimated, especially at the higher prey densities (Fig. 5.10).

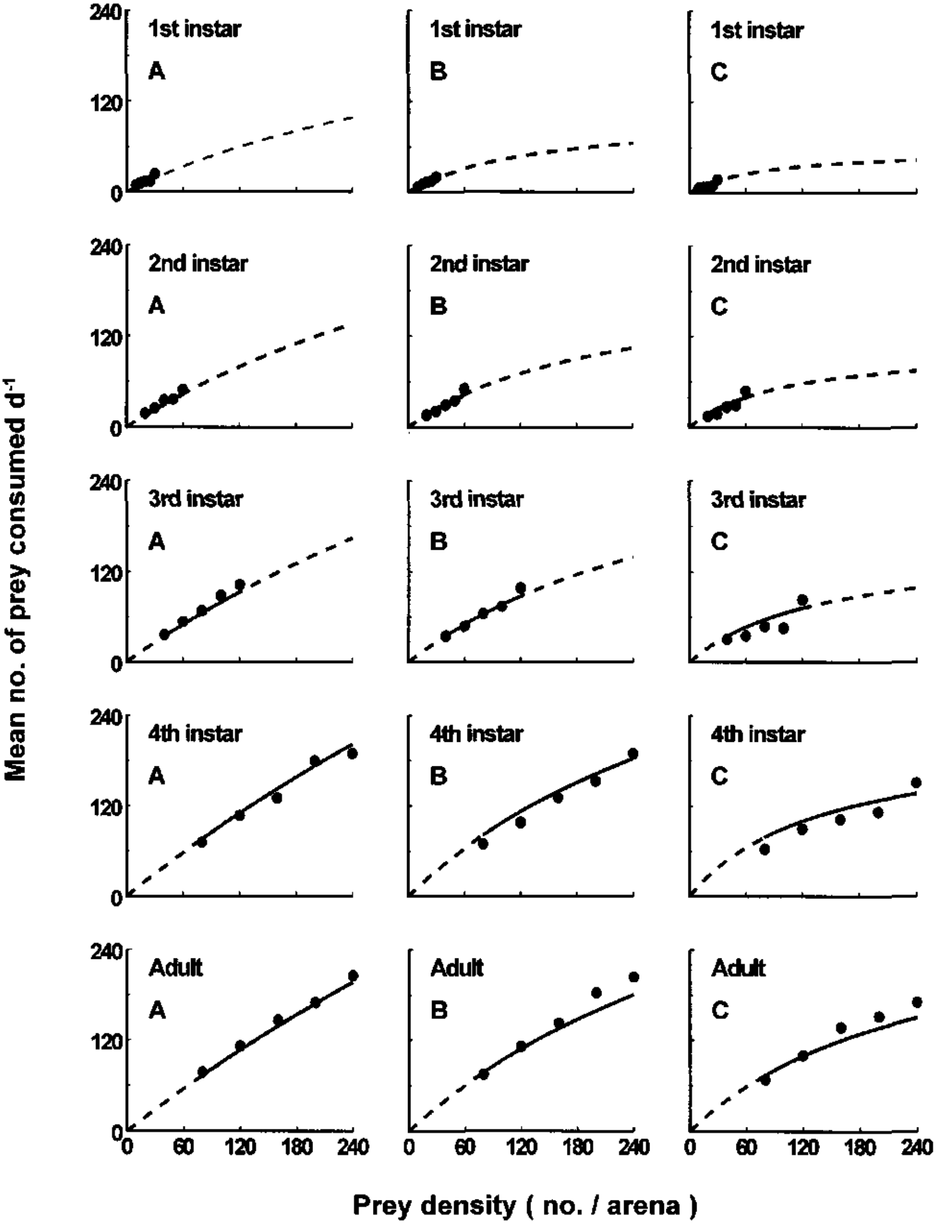


Fig. 5.7. Simulated (——) and observed (●) mean number of early instars (A), late instars (B), and adults (C) of *A. gossypii* consumed daily by five foraging stages of *C. septempunctata* as a function of prey density at fluctuating temperatures in plastic containers in the laboratory in June 1992.

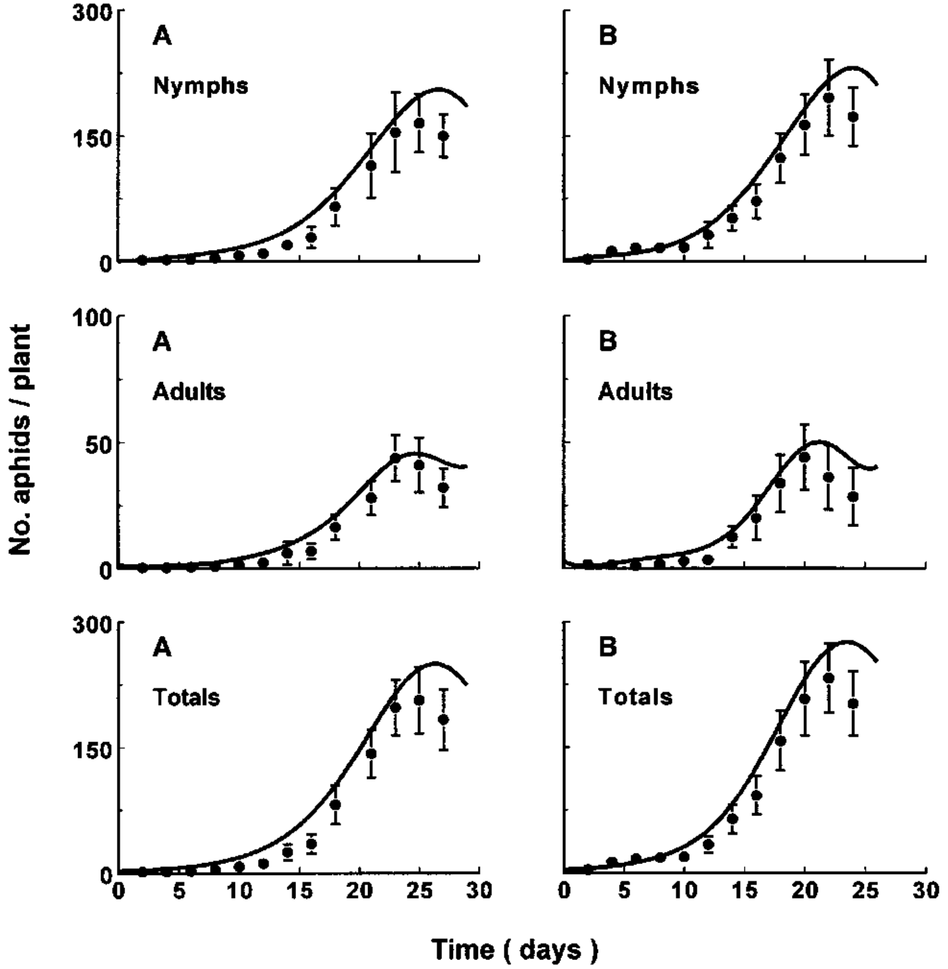


Fig. 5.8. Simulated (——) and observed (●) time courses of the densities of nymphs, apterous adults and total populations of *A. gossypii* in field cages in May (A), and June (B) 1993. Bars represent observations with 95% confidence limits.

Efficacy for the adult predator to control the cotton aphid was simulated at each of four predator–prey ratios, 1:50, 1: 100, 1:200 and 1:400 (Fig. 5.11). There was a tendency for the model to correctly predict cotton aphid densities before the predators were released and underestimated thereafter (Fig. 5.11). The effective period for the prey populations to be brought down below action thresholds (50 aphids per plant at the 5–7 leaf stage) was 10 d at a coccinellid–aphid ratio of 1:50 and 5 d at a ratio of

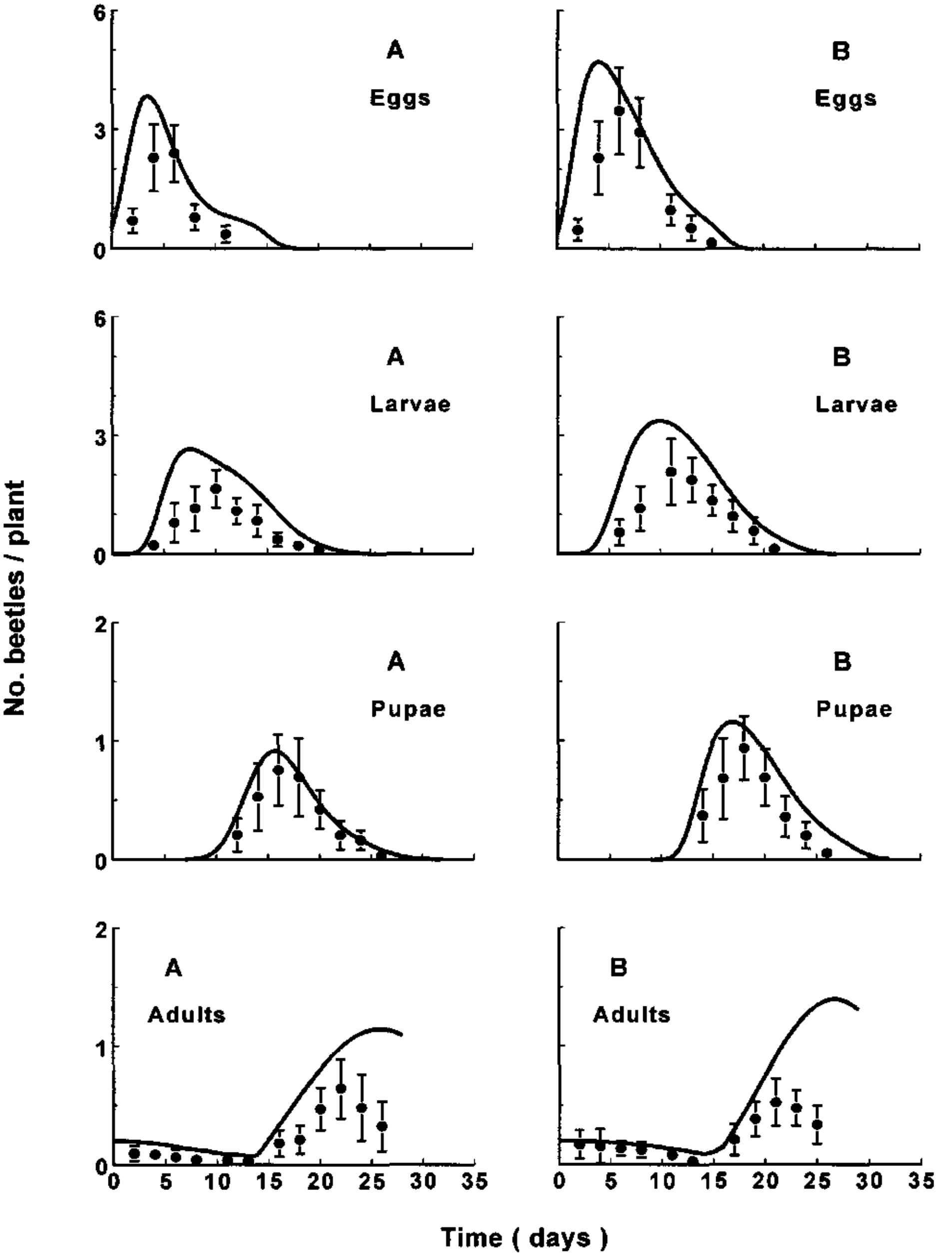


Fig. 5.9. Simulated (——) and observed (●) time courses of the densities of eggs, larvae, pupae and adults of *C. septempunctata* in field cages in June 1993 (A), and May (B) 1994. Bars represent observations with 95% confidence limits.

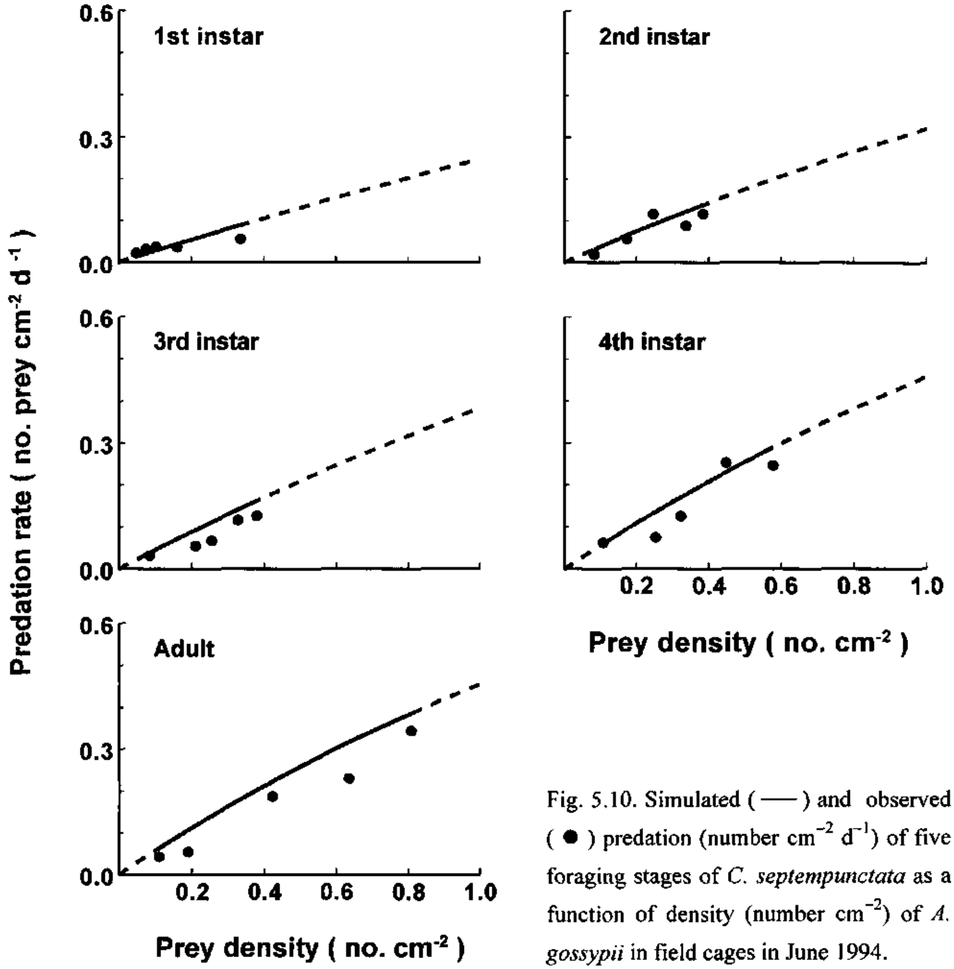


Fig. 5.10. Simulated (——) and observed (●) predation (number cm^{-2} d^{-1}) of five foraging stages of *C. septempunctata* as a function of density (number cm^{-2}) of *A. gossypii* in field cages in June 1994.

1:100 (Figs. 5.11A and B). At the two lower ratios, the predator was simply unable to suppress the prey populations below the defined action threshold (Figs. 5.11C and D).

Above results indicate that the model can be subjected to further tests under the open field situations.

5.3.2.3 Validation in the open field

A comprehensive model of the temporal dynamics of the coccinellid–aphid system was developed by integrating into the cage refined model (a) field-measured immigration of both insects, (b) prey density-dependent emigration of the seven-spot

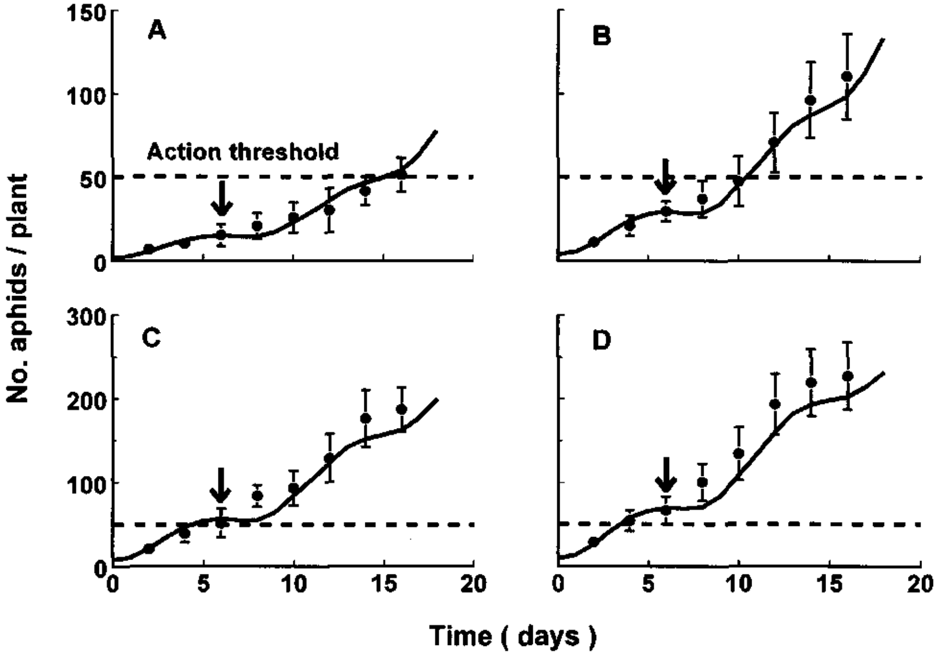


Fig. 5.11. Simulated (——) and observed (●) population dynamics of *A. gossypii* when *C. septempunctata* adults were released in field cages at different time and different predator–prey ratios in July 1995. The ratios used were 1:50 (A), 1:100 (B), 1:200 (C), and 1:400 (D). The arrows indicate the time predators were released at the ratios mentioned, and bars represent observations with 95% confidence limits.

beetle, (c) time-dependent parasitization of both insects, (d) predation by the turtle beetle, and (e) accumulated degree-days (D°)-dependent cotton canopy growth (Table 5.1). The integrated model was validated with experimental data collected in single cotton cropped fields in 1992–1995.

A. gossypii populations increased from early May up to late May and then decreased in 1992–1995 (Fig. 5.12). The patterns of aphid population dynamics were adequately simulated in all four years (Fig. 5.12). The aphid population sizes were somewhat overestimated, particularly later on. The timing of the aphid peak was simulated satisfactorily, the size of the peak was overestimated by 10–30 %, and the predicted population collapse occurred 4–5 d later than observed (Fig. 5.12).

Each year, populations of *C. septempunctata* larvae increased from mid May up to early June and then decreased (Fig. 5.13). The trend of larval population development

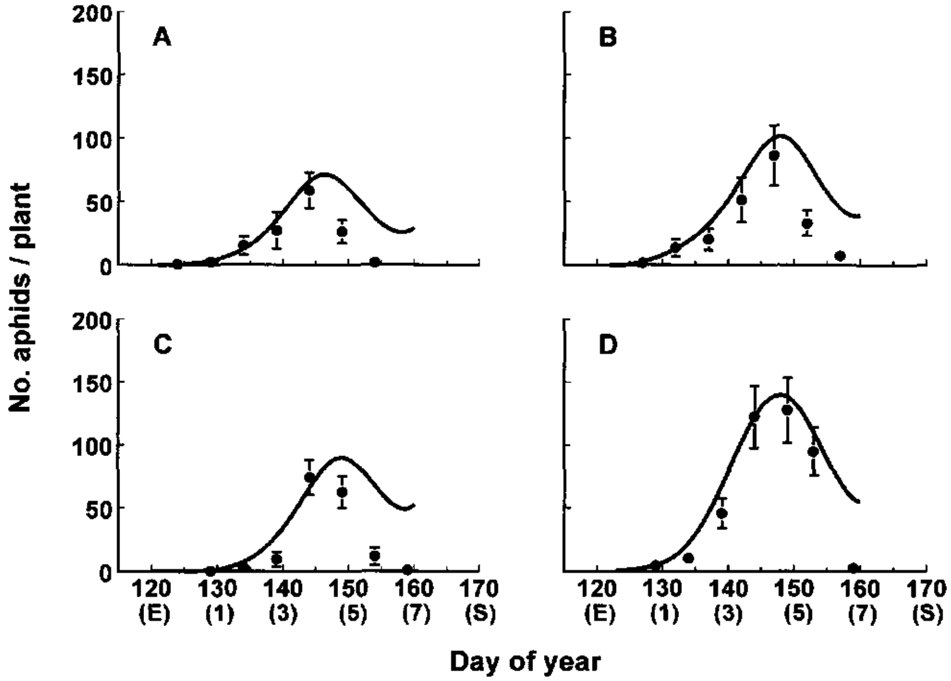


Fig. 5.12. Simulated (——) and observed (●) population dynamics of *A. gossypii* at the seedling stage in single cotton cropped fields in 1992 (A), 1993 (B), 1994 (C), and 1995 (D). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 3, 5, 7 and S are emergence of cotton seedlings; 1, 3, 5 and 7 true-leaf stage; and squaring, respectively.

was described by the model (Fig. 5.13). Compared to observed data in all four years, the simulated peak was delayed by 2–5 d, and the peak density was overestimated by a factor of 1–2 (Fig. 5.13).

In all four years, the initial build-up of adult populations of the seven-spot beetle was simulated (Fig. 5.13). Later on, the beetle adults immigrating from ripening wheat and oil-seed rape were included as a forcing function in addition to the adults produced from pupae in cotton. This late season immigration was the main cause of aphid population collapse in early June (Fig. 5.12).

Above results imply that the model works satisfactorily in single cotton cropping and it can be used as a tool for studying the dynamic behavior of the coccinellid–aphid system in cotton monoculture to gain insights in the system.

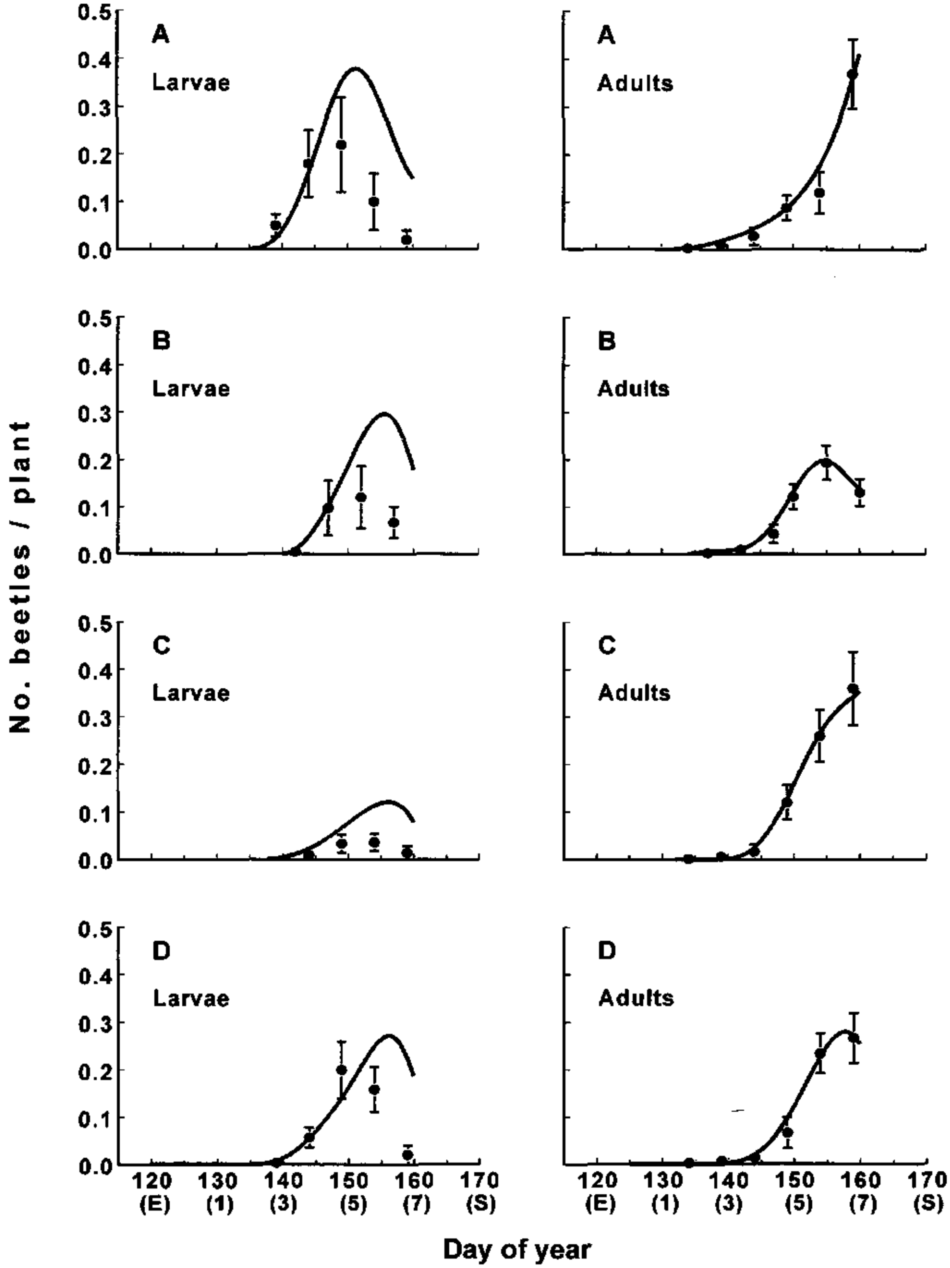


Fig. 5.13. Simulated (——) and observed (●) population trends of *C. septempunctata* larvae and adults in single cotton cropped fields in 1992 (A), 1993 (B), 1994 (C), and 1995 (D). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 3, 5, 7 and S are emergence of cotton seedlings; 1, 3, 5 and 7 true-leaf stage; and squaring, respectively.

5.3.4 Sensitivity analysis

The role of different components and processes in the coccinellid–aphid system was evaluated with the model in this section. The insights gained are given in the Discussion (see Section 5.4).

Obviously, in the absence of density-driven wing formation and reproduction, populations of *A. gossypii* in field cages increased exponentially (Fig. 5.14A). Without cannibalism-inflicted mortality, the larval population size of *C. septempunctata* in field cages increased by a factor 3 (Fig. 5.14B).

Cotton aphid populations increased exponentially up to mid June in the absence of total natural enemy-inflicted mortality (line 1 in Fig. 5.15). Without predation by the seven-spot beetle, the aphid populations increased quickly, with the occurrence of the peak delayed by 8 d and the height of the peak doubled (line 2 in Fig. 5.15). The absence of predation by the turtle beetle did not affect the timing of the aphid peak but the peak number was increased by 5% (line 3 in Fig. 5.15). Without parasitism of alate immigrants by *Allothrombium* and apterous aphids by hymenopterous parasitoids, the aphid populations fluctuated at a slightly higher level throughout, though it exerted no effect on the timing of the aphid peak, with the peak density increased by 6% (line 4 in Fig. 5.15).

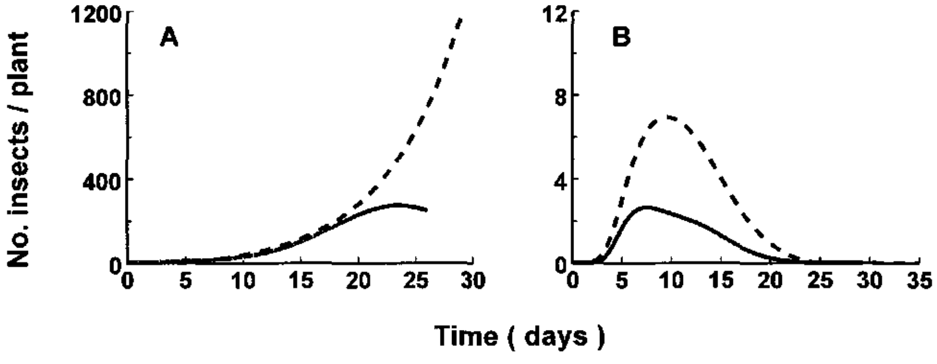


Fig. 5.14. Effects on simulated *A. gossypii* population dynamics in the absence of natural enemies of omitting the density-driven wing formation and reproduction (A), and on simulated *C. septempunctata* larval population development in the absence of natural enemies of omitting the cannibalism-inflicted mortality (B). Simulations are made for the field cage condition in June 1993 (dashed lines). The solid lines represent the simulation with the full model.

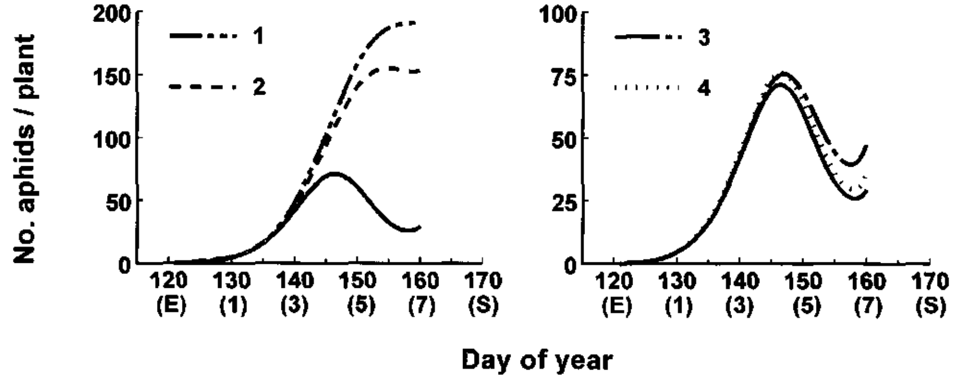


Fig. 5.15. Simulated *A. gossypii* population trends as influenced by omitting the natural enemy-inflicted mortality (line 1), predation by *C. septempunctata* (line 2), predation by *P. japonica* (line 3), and parasitism in alate aphids by *Allothrombium* and apterous aphids by hymenopterous parasitoids (line 4). Simulations are made for 1995 open field conditions. The solid lines represent the simulation with the full model. Crop development is indicated below the abscissa: E, 1, 3, 5, 7 and S are emergence of cotton seedlings; 1, 3, 5 and 7 true-leaf stage; and squaring, respectively.

An increase in the daily maximum and minimum temperatures by 2 °C advanced the timing of the aphid peak by 1 d and increased the peak number by 20% (Fig. 5. 16A). An decrease with 2 °C delayed the timing of the aphid peak by 1 d and decreased the peak number by 30% (Fig. 5.16A). A 20% increase or decrease in the alate *A. gossypii* immigration rate exerted no effect on the date of the aphid peak but brought about a similar increase or decrease in the peak density (Fig. 5.16B). A 20% increase or decrease in the early season immigration rate of seven-spot beetle adults advanced or delayed the occurrence of the aphid peak by 1 d, and decreased the peak number by 7% or increased it by 10% (Fig. 5. 16C).

5.4 Discussion

The present model was tested and validated at three levels of the system complexity, and relevant processes were included at each level, based on discrepancies between “original model” behaviors and observations, and additional experimentation (Table 5.1). Simulated and observed data were in reasonable agreement at all three levels, though the discrepancies increased with the level of scale (Figs. 5.5–5.13). Factors underlying the discrepancies and insights gained are discussed with respect to each level of the system complexity.

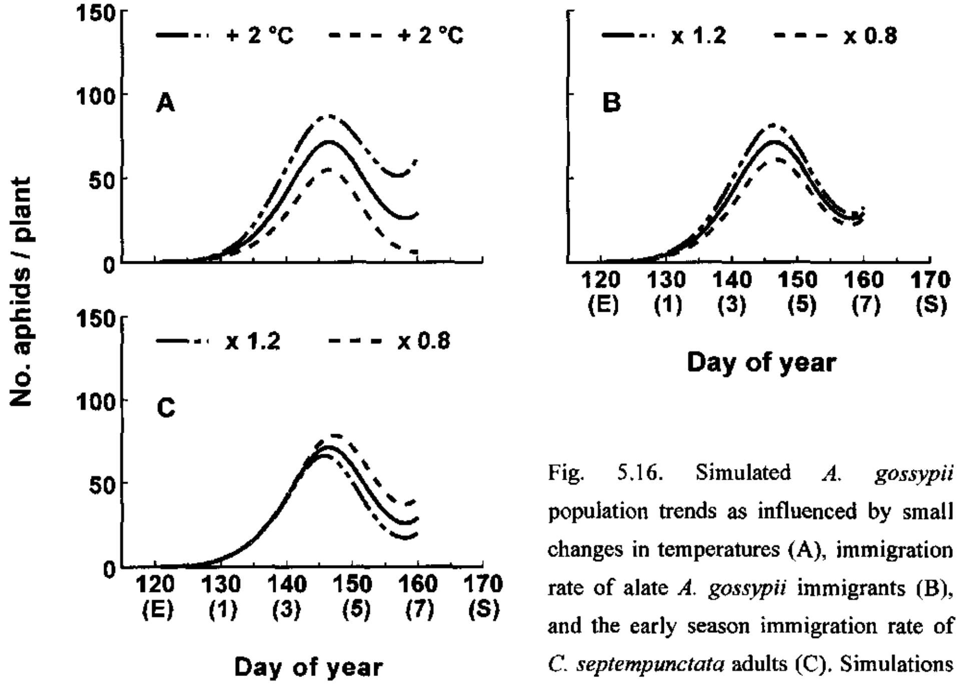


Fig. 5.16. Simulated *A. gossypii* population trends as influenced by small changes in temperatures (A), immigration rate of alate *A. gossypii* immigrants (B), and the early season immigration rate of *C. septempunctata* adults (C). Simulations are made for the open field conditions in 1992. The solid lines represent simulation with the full model.Crop development is indicated below the abscissa: E, 1, 3, 5, 7 and S are emergence of cotton seedlings; 1, 3, 5 and 7 true-leaf stage; and squaring, respectively.

5.4.1 In the laboratory

The model simulated the temperature-dependent development, survival and reproduction of *A. gossypii* (Fig. 5.5) and *C. septempunctata* (Fig. 5.6) as well as the temperature-mediated functional responses of the seven-spot beetle to the cotton aphid (Fig. 5.7). A slight discrepancy between simulations and observations at this level can be ascribed to a higher rate of development, reproduction, and predation at fluctuating than at the constant temperatures (Sethi & Atwal, 1964; Siddiqui et al., 1973).

Evaluation of the model at the laboratory level suggest: (1) the basic structure of the model is reasonably good; (2) the number of boxcars trains chosen is sufficient to calculate the dynamically changing age-structure of both prey and predator populations, and to mimic the dispersion in time during the development and ageing; and (3) the time step calculated for integration is small enough for simulating the temporal dynamics of the coccinellid–aphid system in cotton.

5.4.2 In the field cage

The model simulated the population growth of *A. gossypii* (Fig. 5.8) and *C. septempunctata* (Fig. 5.9) as well as their interaction in the absence of natural enemies (Figs. 5.10–5.11). An overestimation of the aphid population size at the late phase (6–8 leaves) (Fig. 5.8) may be attributed to the fact that the maximum carrying capacity of cotton seedlings determined in single caged potted-plants (around 300 aphids per plant, see Fig. 5.1) is greater than that in the field (about 200 aphids per plant) (Xie & Sterling, 1987; Li & Xie, 1990b). As observed by Wu et al. (1990), survival of the aphid on cotton seedlings increases from 1 to 4 leaf stage, declines thereafter and is lowest at the 8 leaf stage.

A delay of the simulated peak of all pre-adult stages of *C. septempunctata* (Fig. 5.9) was due to a delayed oviposition as it took time for released adults to adapt to the new surroundings before starting egg-laying. A great oversimulation of the population sizes of all foraging stages (Fig. 5.9) may be due to overlooking the hiding beetles and a high cannibalism in field cages. As shown in Fig. 5.9, the discrepancies between simulations and observations are much greater in active than in the static stages, indicating a larger bias in field-sampling for foraging stages of the seven-spot beetle (see also Frazer & Gilbert, 1976). Cannibalism in coexistence of multiple stages in field cages might have been greater than in a single cohort, particularly at such a high artificial density in our field cages (Agarwala & Dixon, 1992; Osawa, 1992).

The slight overestimation of predation rates by the seven-spot beetle in field cages (Fig. 5.10) may be due to a continuous process of predation assumed in the model. In reality, predators do not start preying upon release but search around first and then settle down (Frazer & Gill, 1981). It seems that predation rates of the seven-spot beetle in the field cage increases linearly rather than curvilinearly with prey density (Fig. 5.10). These results agree with those of Frazer & Gilbert (1976).

An underestimation of the aphid populations after release of the seven-spot beetle adults at all predator–prey ratios (Fig. 5.11) is attributed to a continuous predation process assumed in the model and a failure to remove all alate adults in field cages. It is commonly recommended that the action threshold of the cotton aphid at the seedling stage be the predator–prey ratio of 1:100–150 (CCRI, 1983; BU, 1984). This threshold is practical in the presence of other abiotic and biotic mortality factors, but may not hold with the seven-spot beetle alone (Fig. 5.11).

Evaluation of the model at the field cage level indicate: (1) density-driven wing formation and reproduction are the key factor regulating the aphid population dynamics in the absence of natural enemies; (2) cannibalism is the key factor regulating the population fluctuations of the seven-spot beetle in the absence of natural enemies; (3) with the seven-spot beetle alone, aphid populations can be brought down below action thresholds at a coccinellid–aphid ratio of 1:50; and (4) conversion of the search rate and the densities of both prey and predator into proper units is a practical and feasible way to model the field predation rate of the seven-spot beetle.

5.4.3 In the open field

The model simulated the population dynamics of *A. gossypii* and *C. septempunctata* larvae in 1992–1995 (Figs. 5.12–5.13). An overestimation of aphid numbers in all four years (Fig. 5.12) may be easily due to the incomplete accounting for abiotic and biotic mortality factors in the model. Some polyphagous predators (spiders and carabids) and rainfall can play a role in suppressing aphid populations at the early seedling stage (1–3 leaves) (CCRI, 1983; Chen et al., 1994). At the mid seedling stage (3–5 leaves), *Chrysopa* sp., *Syrphus corollae* (Fabricius) and *Erigonidium graminicolum* (Sundevell) are often found to attack cotton aphid (Zhang, 1985). At the late seedling stage (5–8 leaves), a large number of seven-spot and turtle beetles as well as some other predators such as *Adonia variegata* (Goeze), *Leis axyridis* (Pallas), *Scymnus hottmanni* Weise and *Orius minutus* L. move into cotton from ripening wheat and oil-seed rape, which can destroy any remaining aphid populations within a few days (Zhang, 1985; Xia, 1996). *Entomophthora* sp. can also contribute to the collapse of cotton aphid at the late seedling stage, particularly with high rainfall in early June (CCRI, 1983), though this was not the case in 1992–1995. Altogether, the reasonable correspondence between simulation results and field observations indicates that the major mortality factors, notably the seven-spot beetle, were included in the model.

The gradual divergence of predicted densities of seven-spot beetle larvae from the observed (Fig. 5.13) may have been caused by model incompleteness regarding biotic mortality factors and sampling errors. Over 20 species of natural enemies commonly attack the seven-spot beetle (BU, 1984). Except for *T. coccinellae*, ants, mantids, ground carabids and some birds are often found to attack various life stages of the seven-spot beetle (Zhu & Li, 1981). As to sampling, all current methods of counting coccinellids in the field (including direct visual counts as practised in this study) usually underestimate the true densities (Frazer & Gilbert, 1976). This is particularly true when cotton seedlings get larger. In addition, at the late seedling stage, there may be substantial cannibalism, particularly among young larvae when huge numbers of seven-spot beetle adults migrate into cotton from ripening wheat and oil-seed rape, causing aphid shortage. Nevertheless, the general agreement between simulations and observations indicates that the major mortality factors, particularly cannibalism-inflicted mortality, were included in the model.

The role of natural enemies in controlling cotton aphid populations is clearly shown in Fig. 5.15. Seven-spot beetle is the most important, though it comes too late to effect biological control (line 2 in Fig. 5.15). The pattern of aphid population dynamics in 1992–1995 (Fig. 5.12) was mainly affected by the density variation in this influential predator (Fig. 5.13). Thus, although the mean immigration rate of alate *A. gossypii* was 20% higher in 1992 than in 1994 (Fig. 5.3), the peak aphid density was 30% lower in 1992 than in 1994 (Fig. 5.12). This contrary results can be explained by the difference in abundance of the seven-spot beetle between the two years (Figs. 5.13). Compared to 1994, the early season immigration of *C. septempunctata* adults in 1992 was 60% higher, the peak density of larvae was 70% greater, and the adult number at the aphid peak was 40% larger (Figs. 5.3 and 5.13), resulting in a relative low aphid density despite relatively larger immigration (Fig. 5.12). The turtle beetle can help to reduce aphid populations at the mid-late phase (line 3 in Fig. 5.15). Combination of *Allothrombium* and hymenopterous parasitoids plays a role in killing aphid populations throughout the seedling stage (line 4 in Fig. 5.15). Compared to the seven-spot beetle, the turtle beetle, *Allothrombium* and hymenopterous parasitoids play a minor role.

Temperature exerts a large and complex effect on the aphid population growth (Fig. 5.16A). Increased temperature accelerates the development of the prey and the predator, consequently advancing the occurrence of their density peaks, and the effect of decreased temperature is opposite (Fig. 5.16A). Thus, due to comparatively high temperatures in 1992 and 1994 (Fig. B–5 in Appendix B), the simulated and observed aphid peaks occurred 1–3 d earlier in these two years than in the cooler years 1993 and 1995 (Fig. 5.12). Variations in temperature alone (Fig. B–5 in Appendix B), however, can not explain between-season differences in aphid population abundance (Fig. 5.12). Thus, the aphid population size (Fig. 5.12) in the cooler year 1995 was larger than in the warmer year.

The level of alate immigration had an approximately 1:1 effect on the aphid population size over the range of changes made (Fig. 5.16B). Variations in alate immigration alone can not explain between-season differences in aphid population fluctuations (Figs. 5.3C and 5.12C). For instance, compared to 1994, the mean immigration rate of alate immigrants in 1995 increased by 190% (Fig. 5.3), while the aphid peak number increased by only 90% (Figs. 5.12).

A small changes in the early season immigration of the seven-spot beetle adults affects not only the timing of the aphid peak but also the abundance of the aphid throughout the mid-late seedling stage (Fig. 5.16C). Abundance of the seven-spot beetle in the different seasons (Fig. 5.13) was closely related to the immigrating numbers of its adults (Fig. 5.3).This component needs to be determined accurately as it is the key factor in the system.

The importance of *C. septempunctata* in controlling *A. gossypii* was clearly demonstrated in this study. In the North China cotton region, the seven-spot beetle overwinters as adults at the surface soils in winter wheat, oil-seed rape and vegetables (CCRI, 1983; BU, 1984). Its first two generations occur mainly on wheat and oil-seed rape in March–May. Intercropping cotton with wheat has turned out to be a successful approach for biological control of the cotton aphid by enhancing impact of the seven-spot beetle (Wang et al., 1993; Xia, 1994b). Further development of this biological control approach can benefit from detailed simulation studies aimed at optimizing the spatial layout of intercropping patterns of cotton and wheat. The present model can be further developed for such a purpose.

Evaluation of the model at the open field level implies: (1) *C. septempunctata* plays a key role in suppressing *A. gossypii* in cotton monoculture but its number increases too late to guarantee a sufficient biological control; (2) immigrating numbers of *C. septempunctata* adults are the key factor, which should be estimated sufficiently, especially early on; (3) the model can serve as a tool for investigating the processes governing the temporal dynamics of the coccinellid–aphid system under study, for identifying the major mortality factors in the system, and for predicting the field population dynamics of the prey and the predator; and (4) the model can be further developed to simulate the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercropping to evaluate and exploring intercropping strategies for biological control of *A. gossypii* with *C. septempunctata* in cotton (Chapter 6).

Chapter 6

Spatio-temporal dynamics of the predator–prey system *Coccinella septempunctata–Aphis gossypii* in cotton–wheat intercropping: experiments and simulation

Abstract A simulation model of the spatio-temporal dynamics of the predator–prey system *Coccinella septempunctata* L.–*Aphis gossypii* Glover in cotton–wheat intercropping was developed. Six submodels were distinguished: temporal dynamics of cotton aphid populations on cotton, temporal dynamics of seven-spot beetle populations on wheat, seven-spot beetle dispersal, predator–prey interaction, cotton plant, and abiotic factors. Processes, experimentally characterized, included (a) immigration and emigration of both insects; (b) temperature-dependent development, survival and reproduction of the aphid, and temperature-dependent development and ovipostion of the coccinellid; (c) density-dependent wing formation and reproduction of the aphid, and stage-specific survival of the coccinellid; (d) prey density-dependent dispersal of foraging coccinellids from wheat into cotton; (e) prey density, prey size-group, and temperature-dependent predation by *C. septempunctata* and *Propylaea japonica* (Thungberg); (f) time-dependent parasitization in alate and apterous aphids, and in seven-spot beetles pupae; and (g) accumulated degree-days (D°)-dependent cotton canopy growth. Dispersal of foraging stages of *C. septempunctata* from wheat into cotton was modelled as a diffusion process. There was a reasonable correspondence between simulated and observed population dynamics of both insects and dispersal of foraging *C. septempunctata* from wheat into cotton in both 1994 and 1995. Factors underlying differences between model results and experiments were identified and analysed. Simulations reveal that the low abundance of *A. gossypii* in the current cotton–wheat intercropping system is due to a combined effect of increased predation and parasitism, and decreased aphid immigration. Predation by *C. septempunctata* is of overwhelming importance. Year to year differences in immigration of *C. septempunctata* adults into wheat and dispersal of foraging predators into cotton have a profound effect on the system. Current cotton–wheat intercropping has an "overcapacity" for biological control of *A. gossypii*. Simulations suggest that it is possible to develop cotton–wheat strip cropping as a means for overcoming the disadvantages of current cotton–wheat intercropping system and maintaining the biological control of *A. gossypii* on cotton.

6.1 Introduction

Since the early 1980s, there has been a rapid expansion of cotton–wheat intercropped areas in the North China cotton region (Wang, 1990). The intercropped acreage increased from 0.4 million ha in 1978 to 2.3 million ha in 1993, constituting more than 60% of the region's cotton areas (Xia, 1994b). This profound change in cropping systems has brought about significant effects on the structures of arthropod communities and the dynamics of major insect pest populations in cotton (Xia, 1994b; Xia et al., 1997). Cotton aphid (*Aphis gossypii* Glover) [Homoptera: Aphididae] is the key pest at the seedling stage of cotton (*Gossypium hirsutum* L.) in single cotton cropping in the North China cotton region (CCRI, 1983; Fang et al., 1992). The aphid populations, however, remain below economic damage levels throughout the seedling stage of cotton in cotton–wheat intercropping if the seven-spot ladybird beetle (*Coccinella septempunctata* L.) [Coleoptera: Coccinellidae] on intercropped wheat is preserved (Wang et al., 1993; Xia, 1994b). Furthermore, spray of insecticides against cotton bollworm (*Helicoverpa armigera* Hübner), the key pest at the square-boll stage of cotton, is substantially delayed and decreased at the early square stage (mid June) of intercropped cotton as huge numbers of natural enemies directly move into cotton from intercropped wheat (Wang et al., 1993; Xia et al., 1996).

Several mechanisms are responsible for the low abundance of the cotton aphid in cotton–wheat intercropping system: decreased colonization, increased emigration and increased mortality (Wang et al., 1993; Xia, 1994b). Understanding these mechanisms quantitatively is useful not only in optimizing biological control strategies of the cotton aphid by the seven-spot beetle in the current cotton–wheat intercropping system but also in designing new cropping systems for sustainable natural control of the cotton aphid. For reaching such end, it is essential to gain better insight in the spatio-temporal dynamics of the coccinellid–aphid system in the present cotton–wheat intercropping.

A systems approach can be helpful in gaining insight in the spatio-temporal dynamics of complex predator–prey systems and prototyping feasible biological control strategies (Rabbinge et al., 1989; van der Werf et al., 1989). Several biological control systems have been established within the framework of a systems research approach, featuring modelling, e.g. biological control of *Panonychus ulmi* Koch by *Amblyseius potentillae* (Garman) on apple (Rabbinge, 1976), biological control of *Myzus persicae* (Sulzer) by *Coleomegilla maculata* (De Geer) on potato (Mack & Smilowitz, 1982b), and biological control of *Liriomyza bryonae* (Kaltenbach) by *Dyglyphus isaea* Walker on greenhouse tomato (Boot et al., 1992). No study has been carried out to analyse, quantify and explain the biological control of *A. gossypii* by *C. septempunctata* in cotton–wheat intercropping.

The objective of this study was to develop a simulation model of the spatio-temporal dynamics of the predator–prey system *C. septempunctata–A. gossypii* in cotton–wheat intercropping and to use that model to gain more insights in mechanisms of biological control for exploring intercropping strategies for biological control of *A. gossypii* on cotton in the North China cotton region.

6.2 Materials and methods

6.2.1 Model development

Three patterns of cotton–wheat intercropping are commonly practised: 3–2 (three rows of wheat with two rows of cotton), 3–1 (three rows of wheat with one row of cotton, and 4–2 (four rows of wheat with two rows of cotton) (Wang, 1990). The 3–2 pattern is taken into account in the present study as it is the most common and produces desired yields of both crops (Mao & Gou, 1992).

The model was constructed following the general principles in systems analysis and simulation (Rabbinge et al., 1989; van der Werf, 1989; Xia et al., 1991). It is a dynamic, deterministic and short-term model, designed to simulate the spatio-temporal dynamics of the predator–prey system *C. septempunctata–A. gossypii* at the seedling stage of cotton (from sowing to first square, i.e. from mid April to mid June) in cotton–wheat intercropping. Principal simulation techniques applied (i.e. types and numbers of boxcar trains, integration method and time step, and the simulation language) are the same as described in Chapter 5. Six submodels are distinguished: (1) temporal dynamics of cotton aphid populations, (2) temporal dynamics of seven-spot beetle populations, (3) seven-spot beetle dispersal from wheat into cotton, (4) predator–prey interaction, (5) cotton plant, and (6) abiotic factors.

6.2.1.1 Temporal dynamics of cotton aphid populations

The submodel of the temporal dynamics of *A. gossypii* populations on intercropped cotton was adapted from a field-validated model of the temporal dynamics of the coccinellid–aphid system in cotton monoculture developed in Chapter 5. It simulates changes in cotton aphid density (number per plant) on a whole field basis.

Immigration and emigration The model initializes cotton aphid population dynamics from the start of migration by incorporating field estimates of the daily net immigration rate of alates (the number of alates colonizing cotton per plant per day). The net emigration rate was obtained from daily field counts (see Section 6.2.2.1 and Fig. 6.4 in Section 6.3.1.1) and was input into the model as a forcing function. The period from their first appearance to May 20 was considered effective for alate aphids to immigrate into cotton from winter hosts (see Chapter 5).

Alate immigrants were assumed to be reproductively mature on arrival in cotton and to stay until death. Alate adults produced on cotton were assumed to leave the field upon emergence.

Development, survival, reproduction and wing formation Processes of the temperature-dependent development, survival and reproduction as well as the density-driven wing formation and larviposition were included and assumed to be the same as in cotton monoculture (see Chapter 5).

Parasitism Both external and internal parasites (see Chapter 5) are found to attack the cotton aphid in cotton–wheat intercrop (Wang, 1990). Parasitization in alate immigrants by externally parasitic *Allothrombium* was assumed to be identical to that in cotton monoculture (see Fig. 5.2A) as the parasitization is initiated on the winter host of the cotton aphid.

Of the three hymenopterous parasitoid species parasitizing the cotton aphid (Table 1.1), none of them is known to attack wheat aphids, *Sitobion avenae* (Fabricius), *Schizaphis graminium* (Rond), and *Rhopalosiphum padi* (L.) (Wang, 1990). It was supposed that all deaths from parasitism in apterous aphids occurred at the adult moult and that the fraction of aphids killed was time-dependent. The relationship between the fraction of parasitization and day of year was estimated from field observations (see Section 6.2.2.1) and described by Equation 5.7 (see Fig. 6.3A in Section 6.3.1.1).

6.2.1.2 Temporal dynamics of seven-spot beetle populations

Understanding *C. septempunctata* population dynamics on wheat is essential in simulating the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercropping as populations of this predator do not originate from cotton but disperse from wheat into cotton. The submodel of the temporal dynamics of the seven-spot beetle on intercropped wheat was adapted for a field-validated model of the temporal dynamics of the coccinellid–aphid system in cotton monoculture developed in Chapter 5. It simulates changes in predator density (number per m row) on a whole field basis.

Immigration and emigration The model initializes seven-spot beetle population dynamics with measured daily net immigrations of adults (the number of adults arriving in wheat per m row per day). The net immigration rate was determined through daily field observations (see Section 6.2.2.2 and Fig 6.4 in Section 6.3.1.2) and was input into the model as a forcing function. Immigrations until mid May were considered as a new generation of aphids appears from the end of May onward. In general, after mid May the seven-spot beetle adults are hardly found on intercropped wheat before the second generation in late May (see Fig. 6.11 in Section 6.3.2.2).

Adult immigrants were supposed to be reproductively mature on arrival in wheat and not to emigrate. Adults produced in wheat may remain or may emigrate, depending on the availability of cotton and wheat aphids, the development stage of wheat and cotton, and the prevailing weather conditions. In the present model, it was assumed that emigration of seven-spot beetle adults during wheat maturation (after May) was dependent only on *S. avenae* density. The relationship between the relative emigration rate (R_e, d^{-1}) of seven-spot beetle adults in the late season of wheat and wheat aphid density (D_w, the number of wheat aphids per tiller) was estimated by field trials (see Section 6.2.2.2) and described by:

$$R_e = n_1 (D_w)^{n_2} \tag{6.1}$$

where n_1 and n_2 are coefficients (see Fig. 6.5 in Section 6.3.1.2). Data on the wheat aphid density were collected from field counts (see Section 6.2.3.2 and Fig. B–3 in Appendix B) and input into the model as a forcing function.

Development, survival and oviposition Processes of the temperature-dependent development and oviposition as well as the stage-specific survival were included as described in Chapter 5. The assumption was made that the temperature-dependent development and oviposition of the seven-spot beetle feeding on wheat aphids was the same as when feeding on cotton aphids, and that their stage-specific survival on wheat was identical to that on cotton.

Parasitism As in cotton monoculture, *Tetrastichus coccinellae* Kurjumov parasitizing pupae of *C. septempunctata* play a role in suppressing its populations on intercropped wheat (Li, 1986). It was supposed that all deaths of pupae from parasitism occurred upon adult emergence, and that the fraction of parasitization was time-dependent. The relationship between the fraction killed and day of year was determined through rearing field-collected pupae (see Section 6.2.2.2) and described with Equation 5.7 (see Fig. 6.3B in Section 6.3.1.2).

6.2.1.3 Seven-spot beetle dispersal from wheat into cotton

Dispersal of *C. septempunctata* from wheat into cotton is the key process for simulating the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercrop. In the present study, dispersal of foraging stages of the seven-spot beetle from wheat into cotton was modelled as a diffusion process (de Wit & van Keulen, 1975; Kareiva, 1982; Leffelaar, 1993), with hypotheses made as follows:

(1) all foraging stages of the seven-spot beetle move to adjacent crop rows only by walking with negligence of the possibility for beetle adults to depart by flight;

(2) each foraging stage of the predator on wheat, and on cotton has a specific residence time or relative dispersal rate (the reciprocal of the residence time);

(3) residence time on bare soil is negligible as the wheat canopy among rows is highly overlapped and the distance from wheat to cotton is only 20 cm (nearest) to 80 cm (farthest) while the beetle's movement on soil is very fast according to our observations;

(4) dispersal is one-dimensional across rows as both crops are planted in rows and dispersal within rows is not considered; and

(5) residence time is the population level consequence of individual behavior of "area-restricted search" (Kareiva & Odell, 1987), i.e. residence time of the predator on the wheat and the cotton is mainly determined by the density of the wheat and cotton aphids with negligence of the effect of weather conditions.

Diffusion process For an analytic purpose, it is convenient to represent the 3–2 intercropping pattern by a single unit with the outer two rows connected to each other. Dispersal of foraging seven-spot beetles among wheat and cotton rows by walking can be illustrated by a simplified relational diagram (Fig. 6.1). Space is split up into five slices, each representing one row of wheat or cotton. It was assumed that the relative dispersal rate of a given foraging stage was the same on each wheat row or on each cotton row, and that the total relative dispersal rate from a slice was divided into two halves, each denoting the relative dispersal rate from one side of the slice (Fig. 6.1). Relative dispersal rate of each foraging stage on the wheat or on the cotton was dependent on the prey density on them.

A simple diffusion model of the dispersal of foraging stages of the seven-spot beetle among wheat and cotton rows in the 3–2 intercropping pattern was developed based on the relational diagram of Fig. 6.1. The model was written in Continuous System Modelling Program (CSMP) (IBM, 1975; de Wit & Keulen, 1975; Leffelaar, 1993). The rectilinear integration method was applied with a time step of 0.01 d, 1/10 of the smallest time coefficient in the model.

Runs of this simple diffusion model with field data (see Section 6.2.2.2) indicated that the distribution ratio (number per m row on intercopped cotton / number per m row on intercropped wheat) of each selected stage of the seven-spot beetle reached an equilibrium within 1–2 d which was equal to the quotient of its residence time on these two crop rows (see Fig. B–4 in Appendix B). Further simulation runs with the diffusion model brought about similar trends in the other commonly-practised intercropping patterns, 3–1 and 4–2. Thus, it was possible (at least for those above-mentioned intercropping patterns) to assume that at any time, in the temporal model of

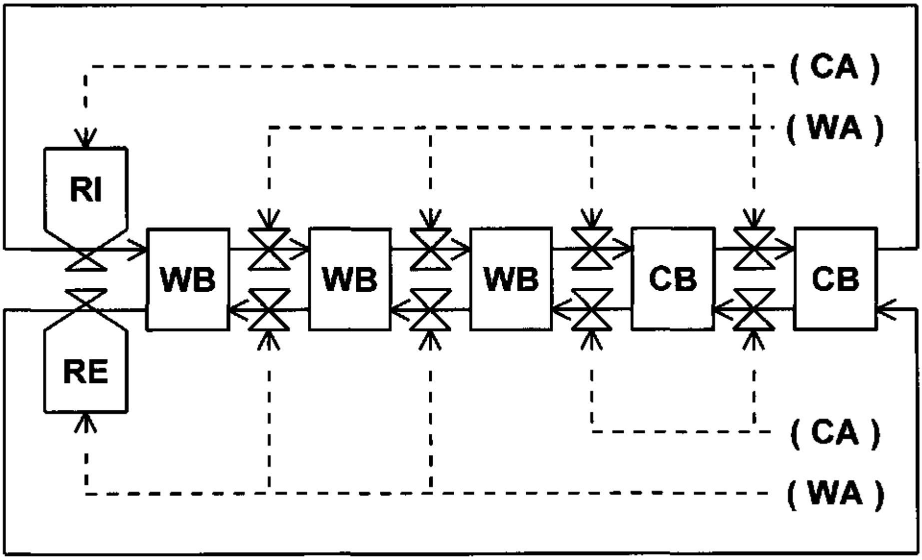


Fig. 6.1. Relational diagram for dispersal of *C. septempunctata* from wheat into cotton in cotton–wheat intercropping with a 3–2 pattern (three rows of wheat with two rows of cotton). Boxes, valves, and parentheses represent state, rate, and driving variables, respectively; and solid and broken lines indicate flow of materials and information, respectively. WB and CB are the seven-spot beetles on the wheat and on the cotton, respectively; RI and RE are the relative rates of walking in and walking out, respectively; and WA and CA are the wheat and the cotton aphids, respectively.

the seven-spot beetle, the dispersal model was in equilibrium, so that the number of predators of each foraging stage dispersing from wheat into cotton row could be calculated based on the ratio of their residence time on the two crop rows. Predation of the cotton aphid was, then, calculated using the density of the seven-spot beetle temporarily dispersing from wheat into cotton (see Section 6.2.1.4).

Prey density-dependent residence time All foraging stages of the seven-spot beetle can disperse from wheat into cotton or the other way around, depending mainly on the availability of wheat and cotton aphids. In this study, the prey density-dependent residence time was determined for the fourth larval instars and the adults of the seven-spot beetle by field observations (see Section 6.2.2.2) and described by:

$$t_r = o_1 [1 - \exp (- o_2 D_p)] \tag{6.2}$$

where t_r is the residence time (d); D_p is the wheat (number per tiller) or cotton aphids (number per plant); and o_1 and o_2 are coefficients (see Fig. 6.6 in Section 6.3.1.2).

According to field observations (see Section 6.2.3.2), the distribution ratio of the first, second and third larval instars of the seven-spot beetle dispersing from wheat into cotton was about 10%, 75% and 75% of that of the fourth larval instar, respectively. Thus, the distribution ratio of the first to third larval instar was found by multiplying the distribution ratio of the fourth instar with 0.1, 0.75 and 0.75, respectively. This implies that the young larvae of the seven-spot beetle spend less time on intercropped cotton than the older ones. The field-observed distribution ratio of foraging stages of the turtle beetle [*Propylaea japonica* (Thungberg)] [Coleoptera: Coccinellidae] dispersing from wheat into cotton and their population numbers on wheat per m row were obtained by field counts (see section 6.2.3.2) and was input into the model as a forcing function (see Fig. B–2 in Appendix B).

6.2.1.4 Predator–prey interaction

Cotton aphid in cotton–wheat intercrop suffers greater predation than in cotton monoculture as most of its predators originate from wheat (Wang, 1990; Wang et al., 1993). Seven-spot beetle is the predominant predator in cotton–wheat intercrop (Xia et al., 1994b). In addition to the seven-spot beetle, the turtle beetle plays a role in reducing the aphid populations at the seedling stage in cotton–wheat intercrop (Wang et al., 1993). Both species have five foraging stages involved in the predation process: four larval instars and the adult (female and male). Individuals of each foraging stage can attack all life stages of both cotton and wheat aphids. While dispersing from wheat into cotton they prey on cotton aphid. Two assumptions are made: (1) temperature, prey density and prey size-group dependent predation rate on the cotton aphid by seven-spot and turtle beetles in cotton–wheat intercrop are the same as in cotton monoculture, and (2) seven-spot and turtle beetles temporarily dispersing from intercropped wheat into intercropped cotton do not directly interfere with each other's predation activity. Predation on mixed prey stages in intercropped cotton was modelled by representing prey stage selection as a competitive process (see Chapter 5).

The relative predation rate in different size-groups of the cotton aphid by foraging stages of seven-spot and turtle beetles were calculated following the same method as described in Chapter 5. The number of cotton aphid, seven-spot beetle and the turtle beetle per plant was converted into the density per unit leaf area (cm^2) by division with total leaf area per plant (double-sided). Dispersal of foraging stages of seven-spot and turtle beetles from wheat into cotton is described in Section 6.2.1.3, and accumulated degree-days (D°)-dependent cotton leaf area is explained in Section 6.2.1.5.

6.2.1.5 Cotton plant

Compared to cotton monoculture, development of cotton seedlings in cotton–wheat intercrop is delayed by 5–7 d, depending on the intercropping patterns or the distance between wheat and cotton strips (Wang, 1990; Wang et al., 1993). A simple model to predict changes in cotton leaf area at the seedling stage in cotton–wheat intercrop was developed as input to predation, using field-collected data (see Section 6.2.2.3) and Equation 5.8 (see Fig. 6.7 in Section 6.3.1.3).

6.2.1.6 Abiotic factors

Compared to those in cotton monoculture, solar radiation, temperature and wind speed in cotton–wheat intercrop are reduced by 5–10%, 0.5–1.5 °C and 10–40%, respectively, while relative humidity and soil moisture are increased by 5–30% and 15–45%, respectively (Wang, 1990; Wang et al., 1991; Wang et al., 1993). Temperature is a major driving variable for the spatio-temporal dynamics of the prey–predator system at cotton seedling stage in cotton–wheat intercrop. Because of the lack of data on the temperatures obtained from cotton–wheat intercropped fields, it was assumed that the fluctuating temperature in cotton–wheat intercrop was the same as in cotton monoculture. The diurnal course of actual temperature was simulated from the daily maximum and minimum temperatures, following the method of Goudriaan & van Laar (1994, pp. 29–49, see Chapter 5).

6.2.2 Experiments for process quantification

During model development, experiments were carried out to characterize processes governing the spatio-temporal dynamics of the coccinellid–aphid system quantitatively. Equations chosen to describe processes were based on a biologically appropriate shape, Root Mean Square Error (RMSE) and coefficient of determination (r^2). Parameters of the selected equations were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows, 1983–1993).

All experiments were conducted at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07 °N latitude and 114.22 °E longitude). The experimental field was 0.5–1.0 ha with a 3–2 intercropping pattern. Wheat cultivar was the early-medium maturing 85-Zhong-33, which was sown in mid October of the previous year upon cotton harvest and harvested at mid June. Wheat row distance was 15 cm (150 tillers per m row). A space (80 cm between wheat strips) was left out for planting cotton next season. Cotton cultivar was the early-medium maturing CCRI 12, which was sown in mid April. The entire seedling period until 6–8 leaf stage overlapped with wheat. Distance between the narrow rows (i.e. within a cotton strip) was 60 cm but 80 cm between the wide rows (i.e. between wheat strips). Plant populations were 10–15 seedlings per meter row before thinning and 4–6 thereafter. Conventional management was carried out except that no seed treatment or above-ground spray was allowed against any insect pests on both crops before wheat harvest.

6.2.2.1 Experiments for the cotton aphid

Time-dependent parasitization Time-dependent parasitization of apterous cotton aphids by hymenopterous parasitoids was observed in 1994 and 1995. Each year, from first appearance of mummies to mid June, 30–50 field plots (50 before thinning and 30 thereafter) were randomly laid out, and each plot consisted of two narrow cotton rows (1 m long each) with 10–30 cotton plants (30 before thinning and 10 thereafter). All plants in each plot were inspected every 5 d for numbers of apterous aphids alive and mummies.

Immigration rate The daily net immigration rate of alate aphids landing on intercropped cotton was measured in 1994 and 1995. Each year, 20–30 field plots were randomly laid out, where each plot consisted of two narrow cotton rows (1 m long each) with 10–30 plants marked with plastic labels. From their first appearance until 20 May, all marked plants in each plot were observed daily for the number of alate adults that had settled. These were then removed.

6.2.2.2 Experiments for the seven-spot beetle

Time-dependent parasitization Time-dependent parasitization of seven-spot beetle pupae by *T. coccinellae* on intercropped wheat was determined in an insectarium in 1994 and 1995. Each year, from first pupal appearance to the wheat harvest, 100–300 pupae were collected on intercropped wheat every 5–10 d and reared in glass petridishes (15 cm diameter and 2.5 cm deep). Emergence of adults and parasitoids was observed daily.

Immigration rate The immigration rate of seven-spot beetle adults landing on intercropped wheat was observed in 1994–1995. Each year, 30–50 (50 before heading and 30 thereafter) field plots were randomly laid out. Each plot consisted of three wheat rows (1 m long each) and was isolated by weeding wheat tillers at both edges by 0.5 m long. Starting from 10 April to 20 May, all tillers and the underground of each plot were inspected daily for numbers of adult beetles which were then removed.

Density-dependent relative emigration rate Experiments for measuring the prey density-dependent relative emigration rate of seven-spot beetle adults from wheat during the wheat maturation (from ripening to the harvest) were conducted twice in late May 1994. Each time, five experimental arenas were made based on wheat aphid density, and each arena (about 0.5 m^2) consisted of three wheat rows (1 m long each). All arenas were individually isolated by a ditch, with plastic sheathing on the sides and filled with water. Upon release of target predators, numbers of wheat aphids per tiller was recorded in all arenas and non-target predators were removed. Twenty field-collected adults (mostly 2–5 d old) marked with white correction fluid ("uni" correction pen, Mitsubishi Pencil Co. Ltd.) were released in each arena. The number of marked adults was monitored at the time intervals of 1 h, 2 h, 4 h , 6 h, 8 h, 1 d, 2 d, and 3 d after release. The relative emigration rate (R_e) at a given prey density was estimated from:

$$N_t = N_o \exp (- R_e \Delta t) \tag{6.3}$$

where N_o is the initial number of marked seven-spot beetle adults released per m row, and N_t is the remaining beetles per m row after the time interval (Δt, d).

Density-dependent residence time Experiments for determining the relationship of residence time of the fourth larval instars and adults of the seven-spot beetle with the density of wheat or cotton aphids in cotton–wheat intercrop were carried out in late May and early June 1995. Ten experimental arenas were created in the field. Each arena (about 1 m^2) was comprised of three wheat rows and two cotton rows with 11 locations recognized (Fig. 6.2). All arenas were individually isolated by a ditch, with plastic sheathing on the sides and filled with water, and they were randomly assigned to two groups, A and B. For group A, 20 target predators were released on the wheat row adjacent to cotton (location 6, see Fig. 6.2), while 10 on the wheat row (location 6) and 10 on the cotton row (location 8, see Fig. 6.2) were released for group B. Upon release of target predators (marked with correction fluid), numbers of wheat aphids per tiller and cotton aphids per plant were recorded in all arenas with the non-target predators removed.

Prey density-dependent residence time of the fourth larval instar was measured twice. In the first measurement, 20 field-collected larvae, mostly fourth instars and also a few third instars, were released in each arena of groups A and B. Observations of locations of the larvae were made after 0.5, 1.5 and 2.5 d. In the second measurement, 20 field-collected fourth instars were released in each arena of group B. The number of dispersed predators at the different locations was checked after 10 min, 40 min, 1 h, 2 h, 1 d, 2 d, and 3 d.

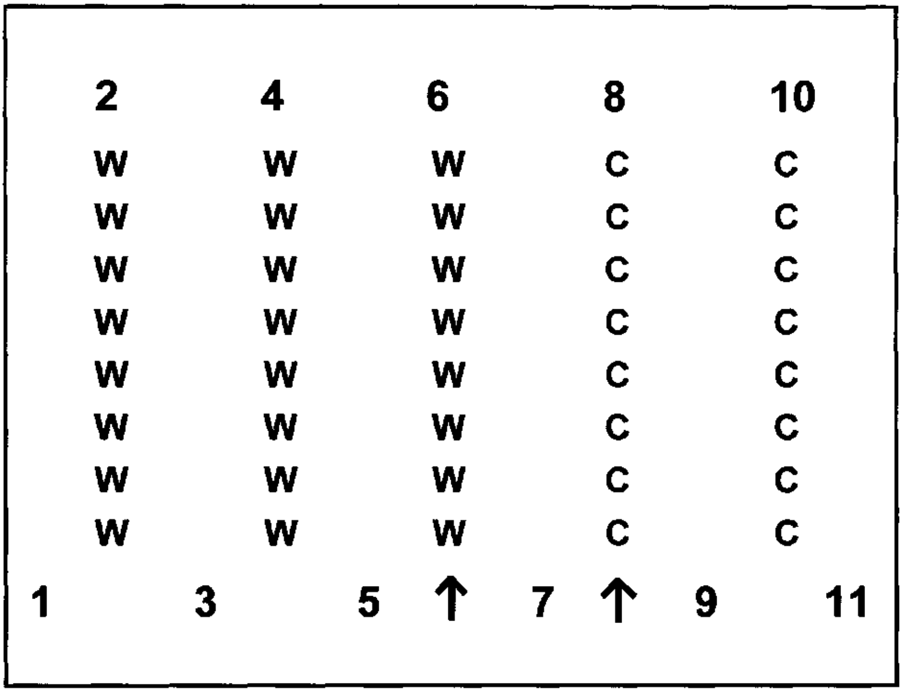


Fig. 6.2. An experimental layout for determining the dispersal rate of *C. septempunctata* among wheat and cotton rows in cotton–wheat intercropping with a 3–2 pattern (three rows of wheat and two rows of cotton). W and C represent wheat and cotton, respectively; and numbers 1–11 are the locations 1 through 11, respectively, with the even number denoting crop rows and the odd one denoting bare soils. Arrows indicate the location for release of target predators.

Prey density-dependent residence time of seven-spot beetle adult was also measured twice. Each time, 20 field-collected adults (mostly 2–5 d old) marked with white correction fluid were released in each arena of groups A and B. The number of marked beetles at different locations was monitored at the time intervals of 10 min, 30 min, 1 h, 2 h, 1 d, 2 d, and 3 d after release. The residence time (t_r) at a given prey density was estimated from:

$$\ln(N_t) = \ln(N_0) - t / t_r \tag{6.4}$$

where N_0 is the initial number of the target predators per m row, and N_t is the remaining target predators per m row after the time interval (t, d).

6.2.2.3 Experiments for the cotton plant

An experiment for determining the relationship of accumulated degree-days (D°) with cotton leaf area was done in 1994 in an intercropped field (3 ha) under conventional management. From the 1 to 8 leaf stage, 50 plants were randomly sampled every 5 d, and their leaf area was measured using a Portable Leaf Area Meter (LI–3000, LI–Cor).

6.2.3 Experiments for model validation

The model was developed by integrating all process-level knowledge in the coccinellid–aphid system (Table 6.1). Its ability to simulate the spatio-temporal

Table 6.1. Processes included in the model of the spatio-temporal dynamics of the predator–prey system *C. septempunctata–A. gossypii* in cotton–wheat intercropping[1].

Temporal dynamics of *A. gossypii*	Temporal dynamics of *C. septempunctata*	Dispersal of predators from wheat into cotton	Predator–prey interaction
a) Temperature-dependent development b) Temperature-dependent survival c) Temperature and age-dependent reproduction d) Density-dependent wing formation e) Density-dependent reproduction f) Immigration into cotton g) Time-dependent parasitization in alate immigrants and apterous aphids	a) Temperature-dependent development b) Temperature and age-dependent oviposition c) Stage-specific survival d) Immigration into wheat e) Prey density-dependent emigration of adults from ripening wheat f) Time-dependent parasitization in pupae	a) Prey density-dependent relative dispersal rate on wheat b) Prey density-dependent relative dispersal rate on cotton c) Time-dependent distribution ratio of *P. japonica* on cotton	a) Prey density, prey size-group and temperature-dependent predation by seven-spot beetle b) Prey density and prey size-group dependent predation by *P. japonica* c) Cotton leaf area-dependent predation d) Accumulated degree-days (D°)-dependent cotton canopy growth

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[1] Details on each process are given in Section 6.2.1.

dynamics of the predator–prey system in cotton–wheat intercropping was validated by a subjective comparison of simulated and observed data through time (Rabbinge et al., 1979; Carter et al., 1982). All validation experiments were conducted at CCRI in 1994 and 1995. Each year, the validation experiment was carried out in an open field (1 ha) with a 3–2 intercropping pattern, where the basic treatments were the same as described in Section 6.2.2. Daily maximum and minimum temperatures were obtained from a meteorological station at CCRI (see Fig. B–5 in Appendix B).

6.2.3.1 Dynamics of cotton aphid and major predators on cotton

Each year, from the first appearance of alate immigrants on intercropped cotton to mid June, populations of the cotton aphid and major predators were monitored every 5 d. At each observation, 30–50 field plots were randomly selected, each consisting of two narrow cotton rows (1 m long each) with 10–30 plants. All plants in each plot were thoroughly inspected for the number of apterous and alate aphids. All plants and the underground of each plot were carefully observed for the number of (a) eggs (if any), first to fourth instars, pupae (if any) and adults of the seven-spot beetle; (b) larvae and adults of the turtle beetle; and (c) other predators in their active stages.

6.2.3.2 Dynamics of wheat aphid and major predators on wheat

Each year, from early April to wheat harvest, numbers of wheat aphids and major predators were inspected every 5 d. At each sampling date, 30–50 field plots were randomly laid out. Each plot was composed of three wheat rows (1 m log each) with 400–450 tillers. Twenty to fifty tillers in each plot were checked for wheat aphids. All tillers and the underground of each plot were thoroughly inspected for the number of (a) eggs, first to fourth instars, pupae and adults of the seven-spot beetle, (b) larval instars and adults of the turtle beetle, and (c) other predators in their active stages.

6.2.4 Sensitivity analysis

Sensitivity analysis was performed by omitting processes from the model (coarse sensitivity analysis), and by changing parameter values within a biologically possible range (fine sensitivity analysis) to evaluate the overall effect in the system (Rabbinge et al., 1979; Carter et al., 1982). The role of total natural enemy-inflicted mortality, predation by the seven-spot beetle, predation by the turtle beetle, and parasitism by parasites (external and internal), was assessed by coarse sensitivity analysis. The importance of temperature was evaluated by increasing or decreasing the daily maximum and minimum values by 2 °C. The effect of immigration rate of alate aphids on intercropped cotton, immigration rate of seven-spot beetle adults on intercropped wheat, and relative dispersal rate of the seven-spot beetle between wheat and cotton, was determined by increasing or decreasing their values by 20%. In all cases, simulations were made for 1995 field conditions.

6.2.5 Scenario studies

The possibility to adapt cotton–wheat intercropping patterns and maintain biological control of *A. gossypii* were explored by carrying out scenario studies with the model. The first study was made to explore how aphid populations are influenced if the daily net immigration rate of alate adults is increased with increasing distance between wheat strips. This was done by increasing the immigration rate by 2, 4, 6, 8, and 10 times, respectively, as it is often observed that immigration rate of alate aphid adults is 8–10 times greater in cotton monoculture than in cotton–wheat intercrop.

The second study was made to explore how aphid populations are influenced if the immigration rate of alate immigrants is increased with increasing width of cotton and wheat strips, but the distribution ratio of foraging predators and the parasitization of apterous aphids are decreased. This was done by testing four increase–decrease combinations: (1) a 2-fold increase in the immigration with a 20% decrease in the dispersal ratio and parasitization, (2) a 4-fold increase with a 40% decrease, (3) a 6-fold increase with a 60% decrease, and (4) a 8-fold increase with a 80% decrease. In all cases, simulations were made for 1995 field conditions.

6.3 Results

6.3.1 Process quantification

6.3.1.1 Process quantification for the cotton aphid

Time-dependent parasitization Parasitization of apterous aphids by hymenopterous parasitoids on intercropped cotton increased from mid May up to late May, with a maximum fraction killed of 0.8 (Fig. 6.3A) and then decreased in both 1994 and 1995. The pattern was adequately described by Equation 5.7 (RMSE = 0.044, $r^2 = 0.97$) (Fig. 6.3A). The peak parasitization occurred 10 d earlier in cotton–wheat intercrop than in cotton monoculture, and the maximum fraction killed was 6 times greater (see Fig. 5.2B). The measured parasitization in cotton–wheat intercrop may be somewhat inflated as some parasitized wheat aphids drop down on cotton and mummify there.

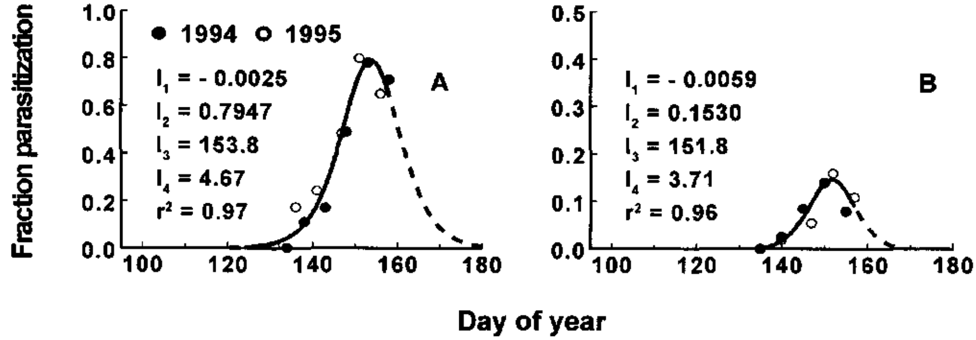

Fig. 6.3. Observed time course of the fraction of parasitization (P_m) in apterous *A. gossypii* by hymenopterous parasitoids on intercropped cotton (A), and *C. septempunctata* pupae by hymenopterous parasitoids on intercropped wheat (B). The best fit is given by Equation 5.7.

Immigration rate In both 1994 and 1995, immigration of alate aphids started early May, peaked mid May and then decreased, with an average immigration rate over the entire period of 0.06 alates per plant per day (Fig. 6.4). Aphid immigration on intercropped cotton was delayed by 5–7 d compared to cotton monoculture (see Fig. 5.3) and the mean immigration was decreased by 80–90%.

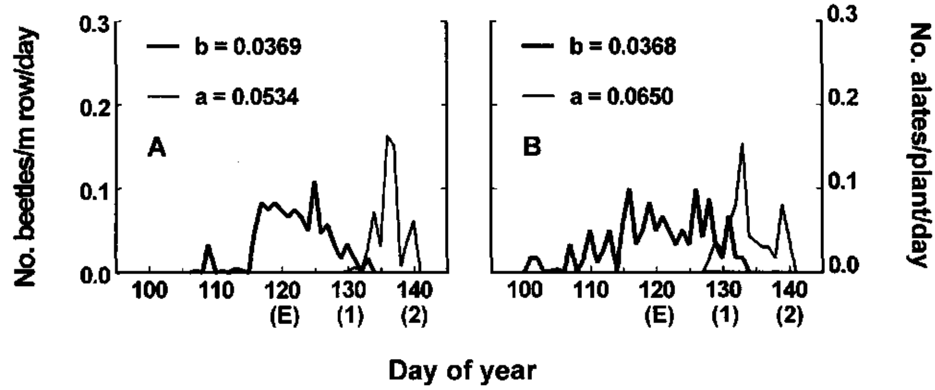

Fig. 6.4. Observed net immigration (number per plant per day) of alate *A. gossypii* into intercropped cotton and *C. septempunctata* adults into intercropped wheat in 1994 (A), and 1995 (B). The a and b represent the mean daily net immigration rate over the entire period of *A. gossypii* and *C. septempunctata*, respectively.

6.3.1.2 Process quantification for the seven-spot beetle

Time-dependent parasitization Parasitization of seven-spot beetle pupae by *T. coccinellae* on intercropped wheat increased from mid May up to late May with a maximum fraction killed of 0.11 (Fig. 6.3B) and then declined in both 1994 and 1995. The trend was satisfactorily described with Equation 5.7 (RMSE = 0.008, $r^2 = 0.96$) (Fig. 6.3B). Apparently, the pupal parasitization on intercropped wheat was much lower than on cotton monoculture (see Fig. 5.2C).

Immigration rate In both years, 1994 and 1995, immigration of seven-spot beetle adults on intercropped wheat started early April, increased from late April up to early May and then decreased, with a mean immigration rate over the entire period of 0.037 adults per m row per day (Fig. 6.4). The immigration occurred 7 d later in 1994 than in 1995, but the mean immigration rate was almost identical in the two years (Fig. 6.4).

Prey density-dependent relative emigration rate Relative emigration rate of seven-spot beetle adults departing from ripening wheat by flight at each wheat aphid density was estimated by Equation 6.3. RMSE ranged from 0.0911 to 0.1758 d^{-1} and r^2 from 0.76 to 0.99. With increase in prey density, the relative emigration rate decreased rapidly, approaching to zero (Fig. 6.5). The pattern was adequately described by Equation 6.1 (RMSE = 0.0399 d^{-1}, $r^2 = 0.94$) (Fig. 6.5).

Prey density-dependent residence time Residence times of the fourth larval instars of the seven-spot beetle related to walking alone and the adults related to walking and flying together at each prey density of wheat aphids and of cotton aphids were adequately estimated by Equation 6.4. For the fourth larval instar and the adult on wheat, RMSE ranged from 0.062 to 0.279 d and r^2 from 0.74 to 0.99. For both of them on cotton, RMSE ranged from 0.018 to 0.230 d and r^2 from 0.87 to 0.99. In all cases, residence time increased quickly with prey density up to 10 aphids per tiller or per plant, and then reached an maximum (Fig. 6.6). The relationship between the residence

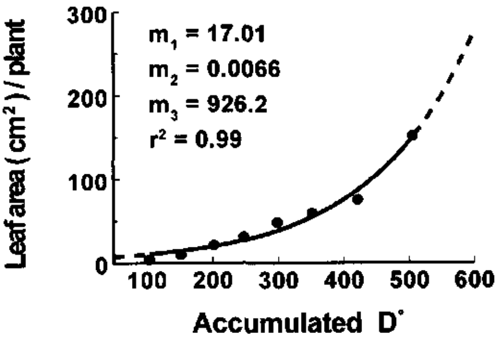

Fig. 6.5. Relationship between prey density of wheat aphids (D_w, number per tiller) and the relative emigration rate (R_e, d^{-1}) of *C. septempunctata* adults from the ripening wheat. The best fit is given by Equation 6.1.

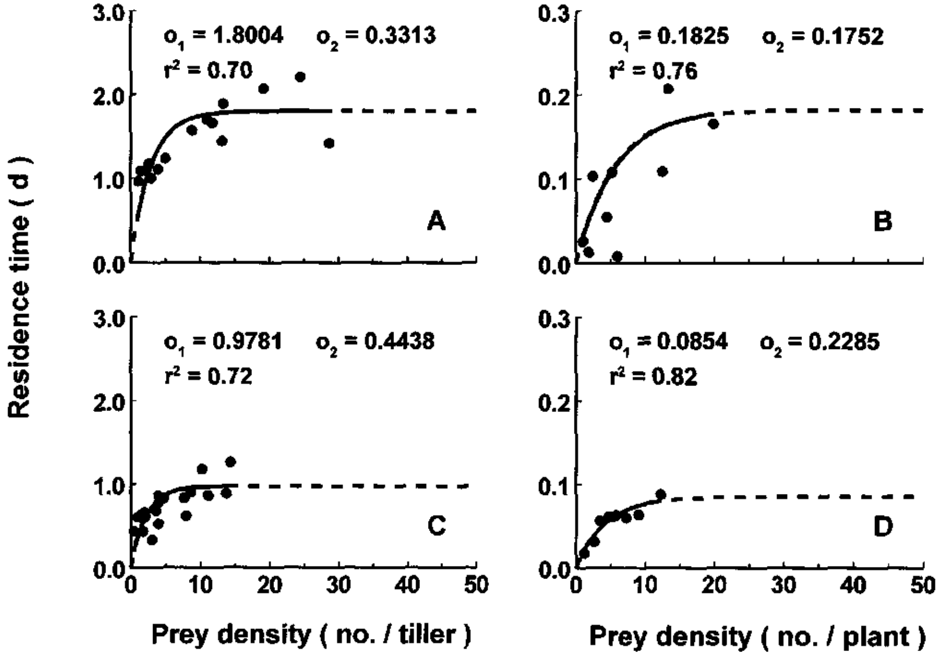

Fig. 6.6. Relationship between prey density (D_p) of wheat aphids (number per tiller) or cotton aphids (number per plant) and the residence time (t_r, d) of the fourth *C. septempunctata* larval instars on intercropped wheat (A) and on intercropped cotton (B), and *C. septempunctata* adults on intercropped wheat (C) and on intercropped cotton (D). The best fit is given by Equation 6.2.

time of both foraging stages and prey density on the two crops was described with Equation 6.2 (Fig. 6.6). The maximum residence time of the fourth larval instars on wheat (1.8 d) was about 10 times as long as on cotton (0.18 d) (Figs. 6.6A and B). The maximum residence time of the adults on wheat (0.99 d) was approximately 12 times as long as that on cotton (0.089 d) (Figs. 6.6C and D). The maximum residence times of the fourth larval instars on wheat and on cotton were about 2 times as long as those of the adults (Figs. 6.6).

6.3.1.3 Process quantification for the cotton plant

The relationship between the leaf area of cotton seedlings and accumulated degree-days (D°) in cotton–wheat intercrop was adequately described by Equation 5.8 (RMSE = 58.6 cm^2, r^2 = 0.99) (Fig. 6.7).

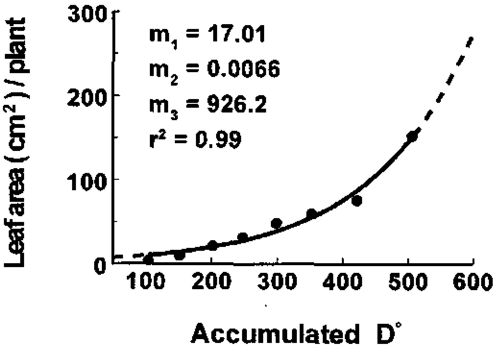

Fig. 6.7. Relationship between leaf area of cotton seedlings per plant (L_a, cm^2) and the accumulated degree-days above 12.5 °C (L_a, D°) from sowing to the first square in cotton–wheat intercrop. The best fit is given by Equation 5.8.

6.3.2 Model validation

The model was developed by integrating all processes presented in Table 6.1. In this section, the simulated results are compared with experimental data collected in cotton–wheat intercropped fields in 1994 and 1995. An interpretation of the results and the insights gained are given in the Discussion (see Section 6.4).

6.3.2.1 Temporal dynamics of cotton aphid populations

In both years, 1994 and 1995, *A. gossypii* populations increased from mid May up to late May with a maximum density of 6 aphids per plant and then collapsed (Fig. 6.8).

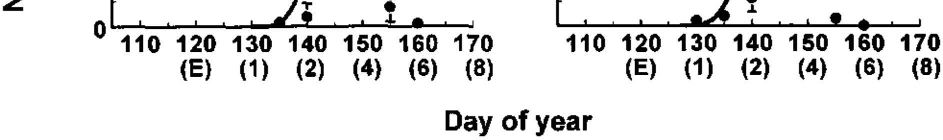

Fig. 6.8. Simulated (——) and observed (●) population trends of *A. gossypii* on intercropped cotton at the seedling stage in 1994 (A), and 1995 (B). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

This dynamic pattern was described by the model, though the population sizes were overestimated, particularly later on (Fig. 6.8). In both cases, the timing of the aphid peak simulated satisfactorily, the peak density was overestimated by 20–30%, and the predicted population collapse appeared 3–5 d later than observed (Fig. 6.8).

6.3.2.2 Temporal dynamics of seven-spot beetle populations

Larval populations of the seven-spot beetle on intercropped wheat increased from early April up to mid May and then declined in both 1994 and 1995. The pattern was simulated by the model, though their numbers were overestimated throughout (Fig. 6.9). In both years, the date of the larval peak was simulated correctly, while the peak density was overestimated by 20% in 1994 (Fig. 6.9A) and 130% in 1995 (Fig. 6.9B).

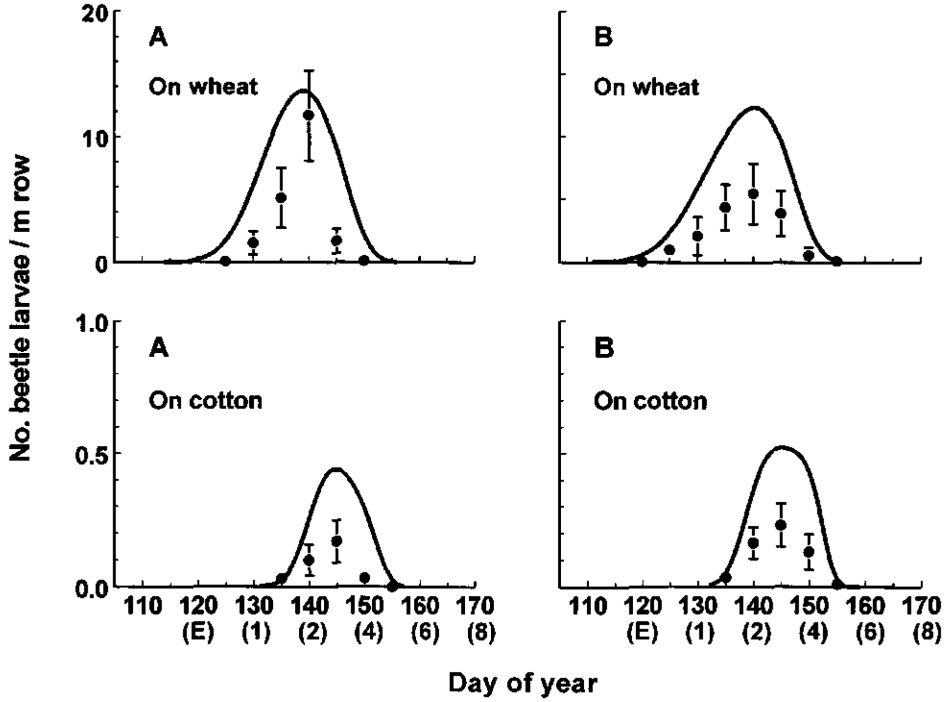

Fig. 6.9. Simulated (——) and observed (●) population trends of *C. septempunctata* larvae on intercropped wheat and on intercropped cotton at the seedling stage of cotton in 1994 (A), and 1995 (B). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

Pupal populations of the seven-spot beetle on intercropped wheat increased from mid May up to late May and then decreased in both 1994 and 1995 (Fig. 6.10). The trend was described by the model (Fig. 6.10). In both years, the predicted peak was delayed by 3–5 d, the peak number was underestimated by 10–20%, and the simulated population collapse occurred 5 d later than observed (Fig. 6.10).

In both years, 1994 and 1995, there were two peaks of seven-spot beetle adults on intercropped wheat: in early May (the peak of adult immigrants) and in late May (the peak of field-produced adults) (Fig. 6.11). The simulated and observed trends were in reasonable agreement (Fig. 6.11). In both cases, the predicted first peak occurred 3–4 d later than observed, with the peak number overestimated by 50–60%, while the predicted second peak was delayed by 2–3 d, with the peak density overestimated by 5–10% (Fig. 6.11).

6.3.2.3 Dispersal of seven-spot beetles into cotton

The predicted distribution ratio of the fourth larval instars of the seven-spot beetle temporarily dispersing from wheat into cotton in both 1994 and 1995 was slightly underestimated at very early seedling stage (1–2 leaves) but overestimated later on (Fig. 6.12). The timing of the larval peak on intercropped cotton was predicted

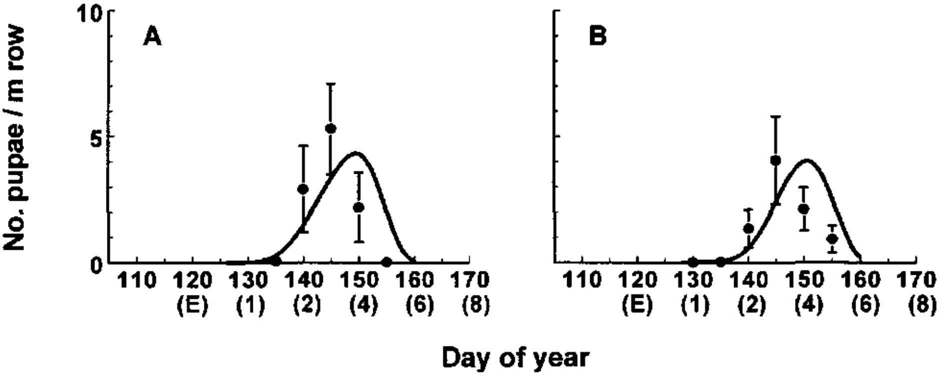

Fig. 6.10. Simulated (——) and observed (●) population trends of *C. septempunctata* pupae on intercropped wheat at the seedling stage of intercropped cotton in 1994 (A), and 1995 (B). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

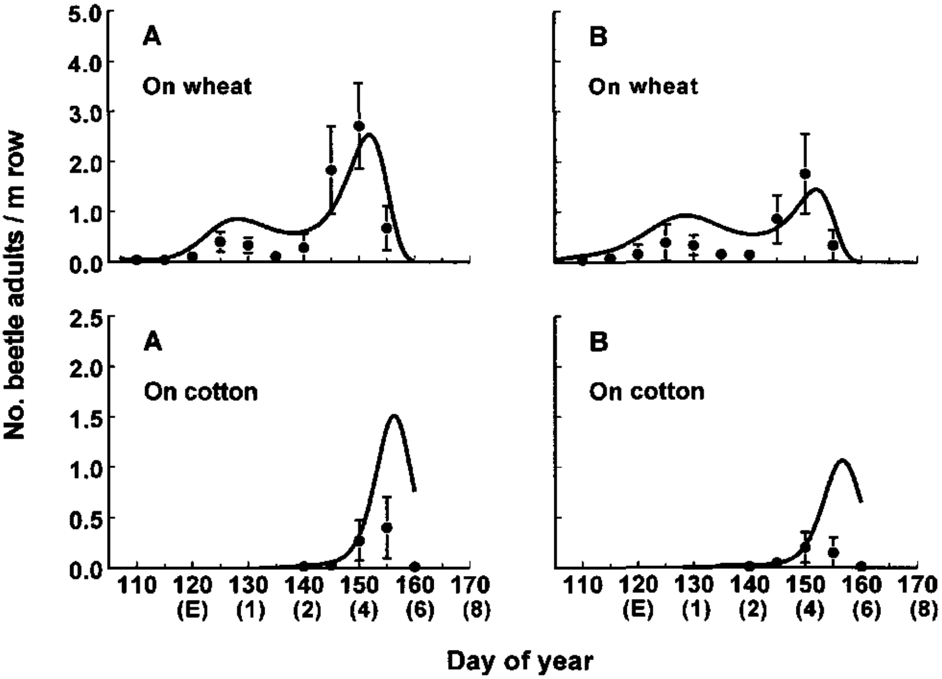

Fig. 6.11. Simulated (——) and observed (●) population trends of *C. septempunctata* adults on intercropped wheat and on intercropped cotton at the seedling stage of cotton in 1994 (A) and 1995 (B). Bars represent observations with 95% confidence limits. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

correctly, but the peak density was 2–3 times greater than observed (Fig. 6.9). In both years, seven-spot beetle larvae peaked 5–7 d later on intercropped cotton than on intercropped wheat (Fig. 6.9).

The time course of the distribution ratio of seven-spot beetle adults temporarily dispersing from wheat into cotton in 1994 and 1995 was well simulated by the model (Fig. 6.12). Similar to the fourth larval instars, the simulated ratio was slightly underestimated at the very early seedling stage and slightly overestimated thereafter in both years (Fig. 6.12). The predicted peak of seven-spot beetle adults on intercropped cotton was delayed by 2–6 d and the peak number was 5–6 times higher than observed (Fig. 6.11). In both years, seven-spot beetle adults occurred 5–7 d later on intercropped cotton than on intercropped wheat (Fig. 6.11).

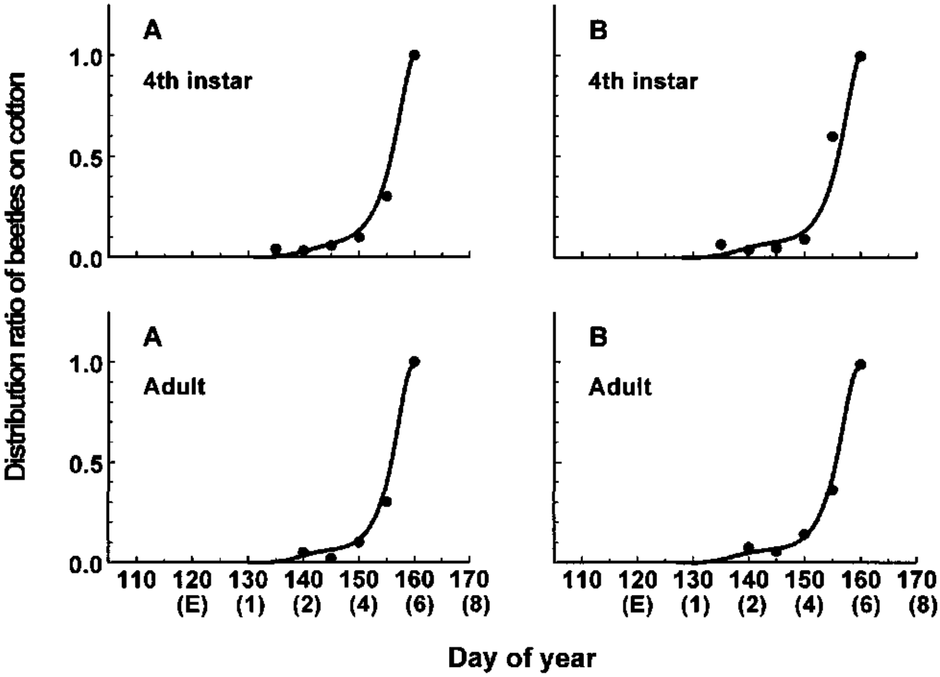

Fig. 6.12. Time course of simulated (——) and observed (●) distribution ratios of *C. septempunctata* larvae and adults temporarily dispersing from intercropped wheat into intercropped cotton at the seedling stage of cotton in 1994 (A), and 1995 (B). Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

6.3.3 Sensitivity analysis

The role of different components and processes in the coccinellid–aphid system in cotton–wheat intercropping are evaluated in this section. Interpretations are given in the Discussion.

Without natural enemy-inflicted mortality, *A. gossypii* populations grew exponentially to damaging levels of more than 100 aphids per plant during the seedling stage (line 1 in Fig. 6.13). In the absence of predation by the seven-spot beetle, the aphid populations increased to a maximum of 25 aphids per plant and then declined slightly. Compared to the full model, the occurrence of the aphid peak was delayed by 7 d and the peak density increased by 260% (line 2 in Fig. 6.13). Absence of predation by the turtle beetle delayed the timing of the aphid peak by 2 d and increased the number by 10% (line 3 in Fig. 6.13). With no parasitism in alate aphid immigrants by

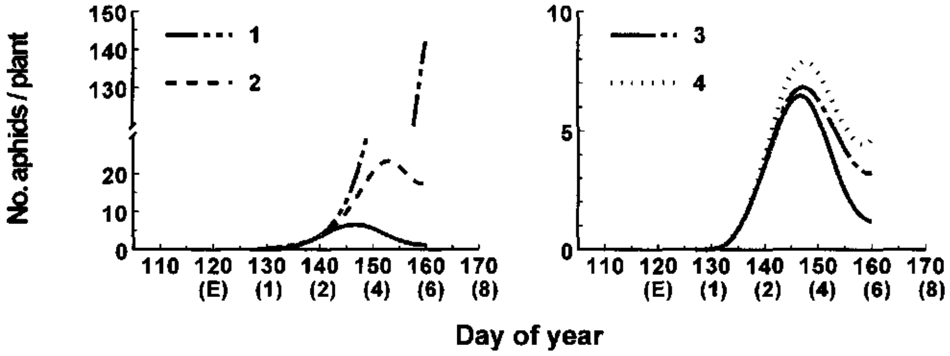

Fig. 6.13. Simulated *A. gossypii* population dynamics on cotton at the seedling stage in the cotton–wheat intercropped field in 1995 as influenced by omitting natural enemy-inflicted mortality (line 1), predation by *C. septempunctata* (line 2), predation by *P. japonica* (line 3), and parasitism of alate *A. gossypii* by *Allothrombium* and apterous aphids by hymenopterous parasitoids (line 4). Solid lines represent the simulation with the full model. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

Allothrombium and apterous aphids by hymenopterous parasitoids, the aphid peak was delayed by 2 d and the peak density increased by 30% (line 4 in Fig. 6.13).

An increase or decrease in daily maximum and minimum temperatures by 2 °C had almost no effect on the timing of the aphid peak but the peak number was increased by 25% or decreased by 20% (Fig. 6.14A). A 20% increase or decrease in the immigration rate of alate aphids on intercropped cotton resulted in no effect on the date of the aphid peak, but the peak number was increased by 15 % or decreased by 14% (Fig. 6.14B). A 20% increase or decrease in the immigration rate of seven-spot beetle adults on intercropped wheat advanced or delayed the aphid peak by 1 d and decreased the peak density by 6% or increased it by 14% (Fig. 6.14C). A 20% increase or decrease in the relative dispersal rate of the seven-spot beetle on both crops had the same result as a 20% changes in the immigration rate of seven-spot beetle adults into intercropped wheat (Fig. 6.14D).

6.3.4 Scenario studies

The results of scenario studies are analysed in this section. An interpretation of the results and practical implications for biological control of *A. gossypii* are presented in the Discussion (see Section 6.4).

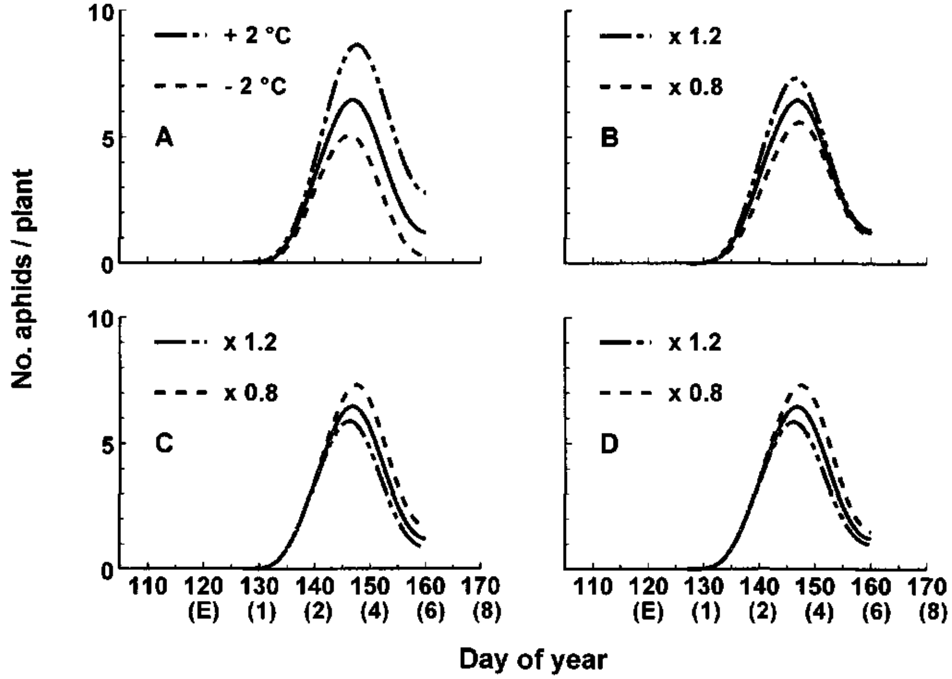

Fig. 6.14. Simulated *A. gossypii* population dynamics on cotton at the seedling stage in the cotton–wheat intercropped field in 1995 as influenced by small changes in temperatures (A), immigration rate of alate *A. gossypii* immigrants into cotton (B), immigration rate of *C. septempunctata* adults into wheat (C), and the relative dispersal rate of foraging *C. septempunctata* from wheat into cotton (D). Solid lines represent the simulation with the full model. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

An increase in the daily net immigration rate of alate *A. gossypii* adults with a factor 2, 4, 6, 8 and 10 exerted no effect on the timing of the aphid population peak, but the peak number was increased with a factor 1.7, 3.1, 4.5, 6.0 and 8.0, respectively (Fig. 6.15). With the immigration increased by a factor of 6, the aphid populations were still below the generally recommended action thresholds of cotton aphid in cotton–wheat intercropping, i.e. 10–20 aphids per plant at the 1–2 leaf stage and 30–40 at the 3–5 leaf stage (Fig. 6.15).

As shown in Fig. 6.16, a 2-fold increase in the daily net immigration rate of alate aphids combined with a 20% decrease in the distribution ratio of foraging predators and the parasitization of apterous aphids, delayed the timing of the aphid peak by 2 d and increased the peak number by a factor 2. A 4-fold increase in the immigration combined with a 40% decrease in the distribution ratio and parasitization, delayed the occurrence of the aphid peak by 4 d and increased the peak number by a factor 5. A 6-fold increase in the immigration combined with a 60% decrease in the distribution ratio and parasitization, delayed the timing of the aphid peak by 5 d and increased the peak number by a factor 9. A 8-fold increase in the immigration combined with a 80% decrease in the distribution ratio and parasitization, delayed the timing of the aphid peak by 5 d and increased the peak number by a factor 15. The aphid population

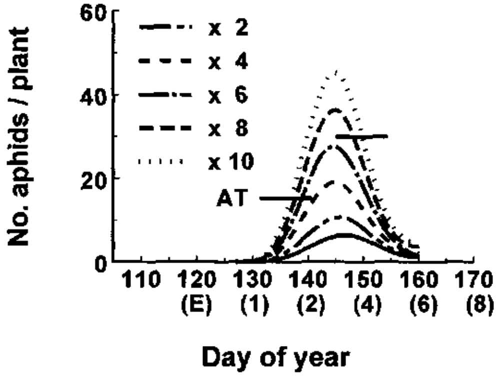

Fig. 6.15. Simulated *A. gossypii* population dynamics on intercropped cotton in 1995 as influenced by increasing the immigration rate of alate aphids. Solid lines represent the simulation with the full model. AT stands for action thresholds. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

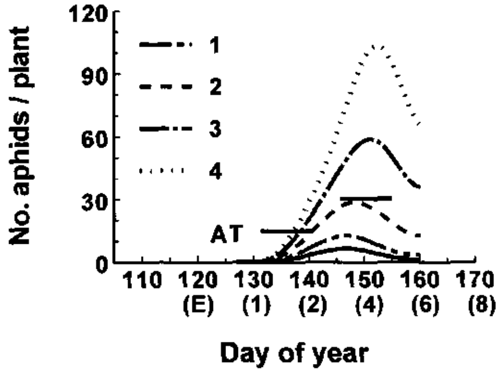

Fig. 6.16. Simulated *A. gossypii* population dynamics on intercropped cotton as influenced by simultaneously increasing the immigration rate of alate aphids, and decreasing the distribution ratio of foraging *C. septempunctata* and *P. japonica* and the parasitization in apterous aphids. Four combinations of increase in immigration with decrease in distribution ratio and parasitization were made: a 2-fold increase with 20% decrease (line 1), a 4-fold increase with 40% decrease (line 2) a 6-fold increase with 60% decrease (line 3), and a 8-fold increase with 80% decrease (line 4). Solid lines represent the simulation with the full model. AT stands for the action threshold. Crop development is indicated below the abscissa: E, 1, 2, 4, 6 and 8 are emergence of cotton seedlings; and 1, 2, 4, 6 and 8 true-leaf stage, respectively.

numbers exceeded the action thresholds if the immigration rate was increased by more than 4 times, while the distribution ratio and parasitization were decreased by more than 40% at the same time (Fig 6.16).

6.4 Discussion

Validation of the model shows a reasonable correspondence between simulated and observed population dynamics of *A. gossypii* (Fig. 6.8) and *C. septempunctata* (Figs. 6.9–6.11) as well as the dispersal of *C. septempunctata* from wheat into cotton (Fig. 6.12). Discrepancies between simulations and observations were more apparent in *C. septempunctata* than in *A. gossypii*. In this section, further discussion is provided on the dynamics of the prey and predator populations, dispersal of predators from wheat into cotton, mechanisms for biological control in cotton–wheat intercropping, and the development of intercropping systems for biological control.

6.4.1 Dynamics of cotton aphid and coccinellid populations

An overestimation of the aphid population sizes throughout may be due to the incomplete accounting for biotic mortality factors. Abundance and diversity of natural enemies, in particular predators, in cotton–wheat intercrop are greater than in cotton monoculture (Xia, 1997). Some polyphagous predators (spiders and carabids) can play a role in suppressing the aphid populations at the early seedling stage (1–3 leaves) (Wang et al., 1993). At the mid-late seedling stage (4–8 leaves), in addition to the seven-spot and turtle beetles, predators preying on wheat aphids are found to attack the cotton aphid, such as *Adonia variegata* (Goeze), *Leis axyridis* (Pallas) and *Scymnus hottmanni* Weise; *Chrysopa sinica* Tieder and *C. phyllochroma* Wesmael; *Syrphus corollae* (Fabricius) and *S. nites* Ettertedt; *Orius minutus* L., and *Nabis sinoferus* Hsiao; and *Erigonidium graminicolum* (Sundevell) (Chen et al., 1991; Wang et al., 1991; Dong et al., 1992; Wang et al., 1993; Chen et al., 1994; Xia et al., 1997). Frequency for these predators to disperse into cotton increases with wheat ripening, reaching a high level only upon wheat harvest, when they contribute to the destruction of remaining aphid populations within a few days (Zhang, 1985; Xia, 1996). Even though, the pattern of *A. gossypii* populations on intercropped cotton was satisfactorily simulated in both 1994 and 1995 (Fig. 6.8). This indicates that the major biotic mortality factors were included in the model, such as *C. septempunctata*, *P. japonica* and hymenopterous parasitoids.

The temporal trend of population development of larvae, pupae, adults of the seven-spot beetle on intercropped wheat was described by the model, but there were discrepancies between simulated and observed densities (Figs. 6.9–6.11). These discrepancies may be due to a lower survival of *C. septempunctata* in the model than in the field, and also to sampling errors. Stage-specific survival of the seven-spot beetle was determined in caged cotton plants (see Chapter 5). Presumably, the mortality by cannibalism in the dense wheat canopy is lower than that in the more open cotton canopy as a larger area index (like wheat) may reduce the encounter rate and hence the chance of cannibalism (Mills, 1982a; Carter et al., 1984; Honek, 1993). Stage specific-survival of *C. septempunctata* in wheat may be measured for further validation of the model. As to sampling, it is difficult to sample foraging seven-spot beetles with a great accuracy, especially in early season as some of them may hide at the surface soil nearby wheat plants (BU, 1984; Zhu & Li, 1981).

Variations in temperature or alate immigration alone can not explain between-season differences in aphid population dynamics on intercropped cotton. Thus, the temperature was about 2 °C higher in 1994 than in 1995 (Fig. B–5 in Appendix B) and the mean immigration rate of alate aphids was 20% higher in 1995 than in 1994 (Fig. 6.4). These two factors are likely to result in higher aphid populations in 1994. Nevertheless, the peak aphid density was somewhat similar in both years (Fig. 6.8).

6.4.2 Dispersal of coccinellids from wheat into cotton

Dispersal of *C. septempunctata* is the key process for simulating the dynamics of the coccinellid–aphid system in the cotton–wheat intercrop, as populations of this predator do not originate from cotton but disperse from wheat into cotton. In this study, dispersal of foraging *C. septempunctata* from wheat into cotton and the other way around was treated as a diffusion process, which was modelled by relating the relative dispersal rate to prey densities. Because the distribution ratio of foraging predators on wheat and cotton rows reached an equilibrium within 1–2 d and was equal to the quotient of its residence time on these two crop rows, the dispersal model was assumed to be in equilibrium at any time. The number of predators temporarily dispersing from wheat into cotton was, therefore, calculated based on the ratio of their residence times on the two crop rows.

As shown in Fig. 6.12, changes in distribution ratios of *C. septempunctata* on intercropped cotton through time were quite satisfactorily simulated. Slight discrepancies may be due to the difference in temperatures between the dense and cool wheat row and the more open and warmer cotton row. In early season, the searching beetles may prefer a warmer environment (i.e. cotton). With the season progressing and air temperature increasing, the searching beetles may prefer staying in the dense wheat row as temperatures there are lower than in the open cotton row (Wang, 1990;

Wang et al., 1993; Honek, 1993). The overall agreement between simulation results and observations indicates that dispersal of *C. septempunctata* (presumably also other coccinellid predators) from wheat into cotton in the 3–2 pattern of cotton–wheat intercropping can be simulated using the ratio of prey density-dependent residence times on the two crops. This principle may be also used in other intercropping patterns.

Complicated behaviors are involved in diffusion processes of foraging predators, e.g. spatially-varying mobility and density-dependent diffusion (Kareiva, 1982). The approach used in this study was rather simple and descriptive. The behavioral components were not considered explicitly but summarized in the prey density-dependent diffusion. This simple (and for some conditions likely incomplete) approach made it feasible to determine the parameters and validate the model in the field.

6.4.3 Mechanisms of biological control in intercrops

Compared to single cropped cotton (see Fig. 5.3), the starting date of immigration of alate *A. gossypii* into intercropped cotton is delayed by 5–7 d and the net immigration rate is decreased by a factor of 8–10 (Fig. 6.4). Thus, cotton–wheat intercropping can substantially reduce the immigration of monophagous cotton aphids (see also Power, 1987, 1988). In the absence of total natural enemy-inflicted mortality, however, the aphid population number (line 1 in Fig. 6.13) exceeds the generally recommended action thresholds throughout the seedling stage of intercropped cotton despite low immigration. The simulation results suggest that the low abundance of the cotton aphid in cotton–wheat intercropping is mainly due to predation and parasitism (lines 2–4 in Fig. 6.13). Predation by the seven-spot beetle is of overwhelming importance (line 2 in Fig. 6.13). Simulations further show that effective biological control can still be achieved even if the immigration of alate aphids in cotton–wheat intercropping is increased by a factor 6 (Fig. 6.15). The role of natural enemies, particularly the seven-spot beetle, in controlling cotton aphid populations in cotton–wheat intercrop has been widely demonstrated (Yan, 1988; Wang et al., 1993). When natural enemies are killed by applying wide spectrum insecticides against wheat aphids on intercropped wheat, one or two sprays are usually required against the cotton aphid on intercropped cotton (Chen et al., 1991; Wang et al., 1993; Xia, 1993). Otherwise, no spray is needed for the cotton aphid control (Xia, 1994b; Xia et al., 1996).

Population dynamics of *A. gossypii* in cotton–wheat intercropping is influenced directly by a reduction of its immigration, and indirectly by an increase in abundance of natural enemies, which, in turn, exerts a great impact on the aphid abundance. This agrees with observations made in other intercropping systems (Wetzler & Risch, 1984; Power, 1987; Trujillo-Arriaga & Altieri, 1990). Diversified agroecosystems, of which intercrops are the prime example, often show reduces herbivore attack (Risch et al., 1983). Three explanations for reduced pest attack in intercrops have been put forward (Vandermeer, 1989): the disruptive-crop mechanism, the trap-crop mechanism and the enemies mechanism. In cotton–wheat intercropping, two mechanisms lead to reduced aphid attack to cotton: decreased immigration and increased enemy inflicted-mortality, where the second one is most important. On one hand, wheat plants disrupt the ability for the monophagous cotton aphid to efficiently colonize cotton plants, directly reducing its attack to intercropped cotton (the disruptive mechanism). On the other hand, wheat plants support a large number of natural enemies because of the presence of wheat aphids and other prey species (the enemies mechanism). These natural enemies disperse from wheat into cotton and consequently reduce cotton aphid populations through predation and parasitism.

6.4.4 Development of cropping systems for biological control

There are several disadvantages to the current cotton–wheat intercropping system, such as decreased fiber and seed quality due to delayed maturation of cotton, and increased outbreaks of the cotton bollworm and verticillium wilt (*Verticillium dahliae* Kleb.) due to a high survival of overwintering pests. Furthermore, mechanization is difficult due to the narrow space between cotton and wheat rows (Wang, 1990; Wang, 1992; Xia & Wen, 1993; Xia, 1994a).

Simulations shows that current cotton–wheat intercropping has an "overcapacity" for biological control of *A. gossypii*. Effective biological control can still be achieved when the immigration rate of alate aphids is increased by a factor 4, and the proportion of the seven-spot beetle foraging on cotton and the parasitization of apterous aphid are decreased by 40% (Fig. 5.16). These results suggest that it is possible to increase the distance between cotton and wheat from a few rows in the current intercropping system to the "strip" scale, and maintain effective biological control. Strip cropping would be favorable for cotton lint and seed quality, labor requirement, and allow more effective suppression of the cotton bollworm and verticillium wilt by cultural control measures. The model developed and insights gained in this study are a basis for further analysis of options of cotton–wheat strip cropping that enable biological control of *A. gossypii* on cotton and are more acceptable in other respects.

Chapter 7

General Discussion

7.1 Scientific approach

This study provides basic biological insights that are necessary for understanding how cotton–wheat intercropping strategies provide for biological control of the cotton aphid (*Aphis gossypii* Glover) [Homoptera: Aphididae] with naturally-occurring natural enemies, particularly the seven-spot ladybird beetle (*Coccinella septempunctata* L.) [Coleoptera: Coccinellidae] in cotton. An integrated modelling approach was followed to investigate the relevance of insect bionomics and behaviorale processes at higher levels of integration and to provide an instrument for explorative studies. Because of complex interrelationships involved in the *C. septempunctata*–A. *gossypii* system under study, three levels of the system complexity and integration were distinguished: laboratory, field cage and open field. At each level, relevant processes affecting the dynamics of the coccinellid–aphid system' were first identified based on the discrepancies between "original model" behaviors and observations, and then characterized quantitatively using additional experimentation. The collected information was integrated into simulation models which were validated at the same level and subjected to tests at a higher level. Comprehensive models were finally developed by integrating all detailed process-level knowledge and validated with population counts from single cotton cropped and cotton–wheat intercropped fields. These models were then used to gain better insights of the dynamics behavior of the coccinellid–aphid system in both cotton cropping systems. The insights gained were used to evaluate the effect of different cotton–wheat intercropping strategies for biological control of *A. gossypii* on cotton. Here, the techniques for modelling the field predation rate of coccinellid predators and their dispersal are further discussed.

7.1.1 Modelling field predation rate of coccinellid predators

Modelling field predation rate of a predator is essential in quantitative understanding of the dynamic behavior of predator–prey systems. It can be modelled descriptively by relating measured predation rate to predator density and other independent variables (e.g. prey density, search area and temperature) (Frazer & Gilbert, 1976), or explanatorily by calculating predation rates on the basis of underlying behavioral processes as walking, searching and digestion (Fransz, 1974; Rabbinge, 1976; Rabbinge et al., 1989; van der Werf et al., 1989; Mols, 1993). In several coccinellid–aphid systems studied, the data on functional response gathered from laboratory experiments are transferred to the field by taking into account the hunger and satiation (Barlow & Dixon, 1980; Mills, 1982b), and the effect of temperature (Frazer & Gilbert, 1976; Gutierrez et al., 1981; Mack & Smilowitz, 1982a, 1982b), or by converting the number of various prey instars into instar units based on the size differences (Carter et al., 1982).

Predation on mixed *A. gossypii* stages by the seven-spot beetle and the turtle beetle [(*Propylaea japonica* (Thungberg)] [Coleoptera: Coccinellidae] in this study was modelled by representing prey stage selection as a competitive process. The data on the functional responses gathered from laboratory experiments were transferred to the field by converting the search rate on a proportion of arena basis into units of leaf area (cm^2) per day. The densities of prey and predator were expressed per m^2 leaf area, with both sides of the leaf considered. The so-constructed model for mixed predator stages or mixed prey stages on whole plants under field conditions was first validated in field cages (Figs. 5.11 and 5.12) and then further used for simulating the open field situations (Chapters 5 and 6). This approach was in essence descriptive. Behavioral components were not considered explicitly but summarized in the search rate. Such population-based approach made it feasible to utilize the information available in literature, to estimate parameters, to use the resulting stage-structured functional response in a population model and to validate the models in the field. Presumably, this approach can be also applicable for coccinellid–aphid systems in other field crops with broad leaves, e.g. soybean, corn, potato, tomato and cucumber.

7.1.2 Modelling dispersal of coccinellid predators in intercrops

Spatial heterogeneity is one of the most important factors influencing population dynamics (Kareiva, 1982). Dispersal of spatially distributed populations is a key process for simulating the dynamics of spatially distributed predator–prey systems, particularly in intercrops (Kareiva & Odell, 1987; Vandermeer, 1989). Modelling dispersal of *C. septempunctata* is essential in understanding the dynamic behavior of the coccinellid–aphid system in cotton–wheat intercropping as populations of this predator do not originate from cotton but disperse from intercropped wheat into intercropped cotton and prey on the cotton aphid there.

Three explanations for the low herbivore abundance in intercrops have been put forward (Vandermeer, 1989): the disruptive-crop mechanism, the trap-crop mechanism and the enemies mechanism. The disruptive-crop mechanism implies that a second crop species disrupts the ability of a pest to efficiently find and exploit its proper host, and applies mainly to specialist herbivores. The trap-crop mechanism implies that a second crop species attracts a pest that would normally be detrimental to the principal crop species. This mechanism mainly applies to generalist herbivores. The enemies mechanism implies that the intercropping situation attracts, for whatever reason, more predators and parasites than the monocultures, thus reducing the pests through predation or parasitism. These mechanisms may operate individually or jointly, depending on the types of intercropping. All three mechanisms ultimately involve movements of pests and/or their natural enemies. These movements may be regarded as a Markov process or as a problem of diffusion (Kareiva, 1982, 1983, 1990; Kareiva & Odell, 1987; Vandermeer, 1989).

In the present study, dispersal of selected foraging stages of *C. septempunctata* from wheat into cotton and the other way around was treated as a diffusion process (de Wit & van Keulen, 1975; Kareiva, 1982; Kareiva & Odell, 1987; Leffelaar, 1993) and was modelled descriptively by relating the relative dispersal rate (the reciprocal of residence time) to the prey density. The simulation results show that the distribution ratio of each selected foraging predator stage on the wheat and cotton rows reaches an equilibrium within 1–2 d and is equal to the quotient of its residence time on these two crop rows. It was assumed that at any time, in the temporal model of the seven-spot beetle, the dispersal model was in equilibrium. Therefore, the number of foraging predators temporarily dispersing from wheat into cotton was calculated based on the ratio of its residence times on the two crop rows (Chapter 6). As shown in Fig. 6.12, the distribution ratio of foraging stages of the seven-spot beetle temporarily dispersing from wheat into cotton was quite satisfactorily simulated throughout the seedling stage of intercropped cotton. These results indicate that dispersal of the *C. septempunctata* (presumably also other coccinellid predators) from wheat into cotton in the 3–2 pattern of cotton–wheat intercropping can be simulated using the ratio of prey density-dependent residence times on the two crops. This principle may be also used in other intercropping patterns.

The mathematical theory of diffusion processes of foraging predators embraces a great diversity of complicated behaviors, e.g. spatially varying mobility and density-dependent diffusion (Kareiva, 1982, 1990; Kareiva & Odell, 1987; Vandermeer, 1989). The approach used in this study was rather simple and descriptive. The behavioral components were not considered explicitly but summarized in the prey density-dependent diffusion. This population-based approach made it easy and feasible to determine the parameters and validate the model in the field. It may be also applicable for predator–prey systems in other intercrops.

7.2 Research findings

Given the knowledge of the separate component processes involved in the *C. septempunctata–A. gossypii* system in both cotton monoculture and cotton–wheat intercrop, simulation models of their combined action have yielded the following general insights in the dynamics of the system (Chapters 5 and 6).

Firstly, temperature is an important driving variable in the coccinellid–aphid system. The rates of development, survival and reproduction of *A. gossypii* (Chapter 2) and *C. septempunctata* (Chapter 3), and the rates of predation by foraging stages of *C. septempunctata* (Chapter 4) all increase with temperature. Nevertheless, variations in temperature can not explain between-season variations in aphid population dynamics.

Secondly, density-dependent wing formation and reproduction are the major regulatory mechanisms for cotton aphid population development in the absence of natural enemies (Fig. 5.14A). Cannibalism (both sibling and non-sibling) is the major regulatory mechanism for the seven-spot population growth in the absence of natural enemies (Fig. 5.14B).

Thirdly, with *C. septempunctata* alone, cotton aphid populations at the seedling stage of cotton can be effectively kept below commonly used action thresholds at a predator–prey ratio of 1:50 (Fig. 5. 12).

Finally, variations in the immigration of alate *A. gossypii* is not the major cause for the between-season differences in *A. gossypii* population fluctuations. Immigrating numbers of *C. septempunctata* adults, however, have a large effect on the aphid population dynamics.

7.2.1 Outbreaks of cotton aphids in cotton monoculture

A. gossypii colonizes single cropped cotton at a high rate upon emergence of seedlings (Fig. 7.1). The aphid obtains its highest rate of increase on cotton between 25 °C and 30 °C (Chapter 2). The field temperature throughout the seedling stage of cotton in the North China cotton region fluctuates between 20 °C and 30°C, which favors aphid population growth. Although *C. septempunctata* plays a key role in controlling the cotton aphid in cotton monoculture, its numbers increase too late to guarantee a sufficient biological control. Predation by *P. japonica* and parasitism by *Allothrombium* and hymenopterous parasitoids play only a minor role (Chapter 5). The high relative rate of population increase and low natural enemy-inflicted mortality of the cotton aphid in single cotton cropping (Fig. 7.1) results in large populations and severe damage, with yield losses of 10–15% or even a need for replanting in some areas (CCRI, 1983; Pan et al., 1986; Fang et al., 1992).

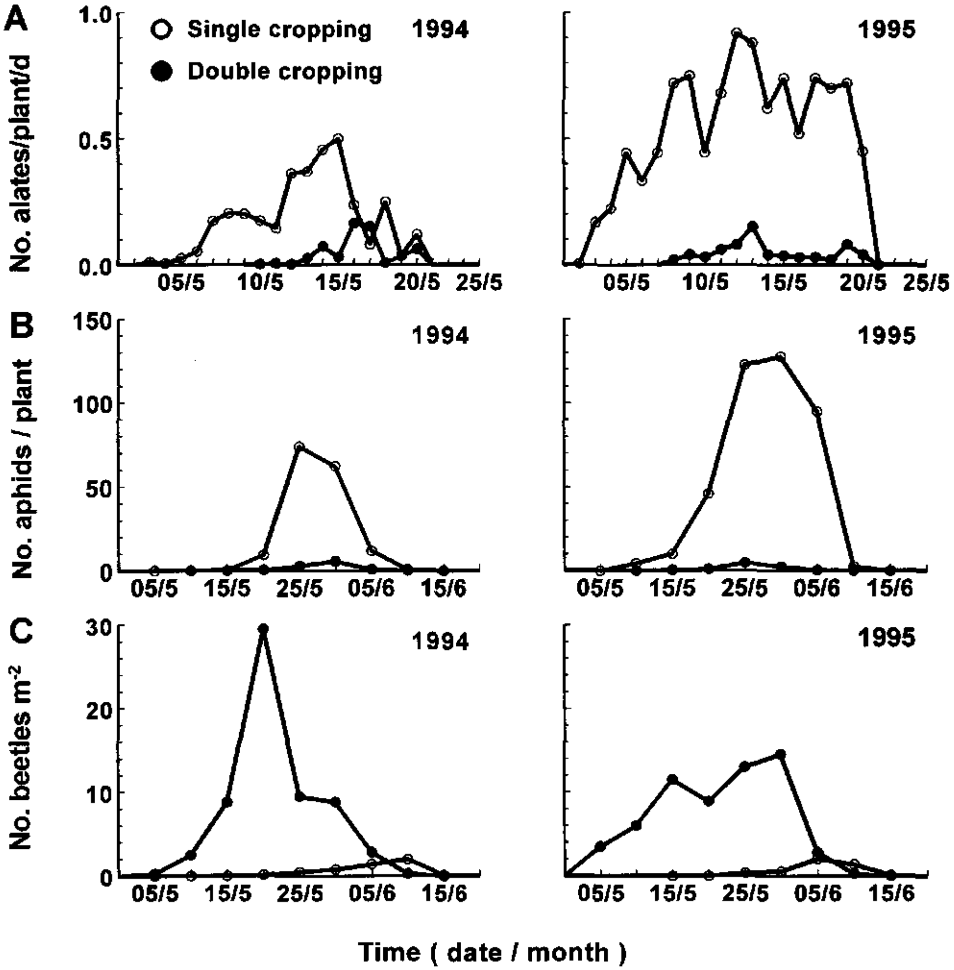

Fig. 7.1. Time course of the observed immigration of alate *A. gossypii* (A), number of apterous *A. gossypii* (B), and number of foraging *C. septempunctata* (C) in cotton monoculture and cotton–wheat intercrop in 1994 and 1995.

7.2.2 Low abundance of cotton aphids in cotton–wheat intercrop

Two mechanisms lead to reduced aphid attack in intercropped cotton: decreased immigration and increased mortality due to natural enemies. The second mechanism is the most important (Chapter 6). Compared to cotton monoculture, the starting date of immigration of alate *A. gossypii* into intercropped cotton is delayed by 5–7 d and the net immigration rate is decreased by a factor of 8–10 (Fig. 7.1). Intercropped wheat imposes a "curtain" barrier that disrupts the ability for the monophagous cotton aphid to efficiently colonize intercropped cotton plants (the disruptive-crop mechanism), which directly reduces its distribution on intercropped cotton.

Seven-spot beetle, the key predator of the cotton aphid, is much more abundant in cotton–wheat intercrop than in cotton monoculture (Fig. 7.1). Wheat plants support a large number of natural enemies, particularly the seven-spot beetle and hymenopterous parasitoids, because of the presence of wheat aphids and some other prey species. These natural enemies disperse from wheat into cotton and consequently reduce aphid populations through predation and parasitism (the enemies mechanism). Simulations show that in the absence of natural enemy-inflicted mortality, cotton aphid populations can still exceed the recommended action thresholds throughout the seedling stage of intercropped cotton (Gao et al., 1989; Wen et al., 1990) despite relative low immigration. Simulations further show that effective biological control can still be achieved if the immigration of alate aphids in the current cotton–wheat intercropping is increased by a factor 6 (Fig. 6.15). Apparently, low abundance of the cotton aphid in the current cotton–wheat intercropping system is mainly due to the earlier and greater predation and parasitism (lines 2–4 in Fig. 6.12), where predation by the seven-spot beetle is the most important (line 2 in Fig. 6.12 and Fig. 7.1). This is supported by the practical experience that one or two sprays are required to control cotton aphids on intercropped cotton at the seedling stage when natural enemies are killed by applying wide spectrum insecticides against wheat aphids on intercropped wheat (Yan, 1988; Wu & Wang, 1990; Wang et al., 1991; Wang et al., 1993; Xia, 1993).

It is concluded that the low abundance of *A. gossypii* in the current cotton–wheat intercropping system is due to a combined effect of increased predation and parasitism, and reduced aphid immigration. Similar findings have been reported in other intercropping systems. For instance, the attack of leaf hopper (*Empoasca* sp.) to beans was substantially reduced by intercropping with nonhost grasses (the disruptive mechanism) (Risch, 1981). *Rhopalosiphum maidis* (Fitch) experienced higher attack by several species of arthropod predators in corn tricultures with faba bean (the enemies mechanism) (Trujillo-Arriaga & Altieri, 1990). Working with the Mexican bean beetle (*Epilachna varivestis* Mulsant) in a tomato–bean intercrop, McGuinness (1987) showed convincingly that both the disruptive crop and the enemies mechanisms were simultaneously operative in reducing the beetle abundance.

7.3 Practical implications

In cotton monoculture, *A. gossypii* is numerous throughout the seedling phase due to the early colonization and high immigration of alate aphids, and the late occurrence and low abundance of natural enemies (Fig. 7.1). Three to five sprays are generally required to prevent cotton aphids from damage. At the other hand, in cotton–wheat intercrops, *A. gossypii* populations are sparse throughout the seedling stage due to the delayed and reduced colonization of alate aphids, and the early and numerous occurrence of natural enemies (Fig. 7.1). No spray is needed against aphids on intercropped cotton, provided that naturally-occurring natural enemies, especially the seven-spot beetle, are preserved on intercropped wheat. However, there exist also several disadvantages in current cotton–wheat intercropping systems, e.g. decreased fiber and seed quality due to delayed maturation of cotton, increased outbreaks of the cotton bollworm (*Helicoverpa armigera* Hübner) and verticillium wilt (*Verticillium dahliae* Kleb.) due to a high survival of the overwintering pests, and a more difficult mechanization due to the narrow space between cotton and wheat rows (Table 7.1) (Wang, 1990; Wang, 1992; Xia & Wen, 1993; Xia, 1994a).

In terms of biological control of *A. gossypii*, the rich resource of natural enemies is not fully utilized in the current cotton–wheat intercropping system, as the aphid populations are far below action thresholds over the entire seedling stage of intercropped cotton (Fig. 6.8). Simulations shows that the aphid populations can be kept below the generally recommended action thresholds even if the immigration rate of alate aphids is increased by a factor up to 6 in current cotton–wheat intercropping. Effective biological aphid control can be achieved even if the immigration rate of alate aphids is increased by a factor of 4, and the distribution ratio of foraging predators and the parasitization of apterous aphids is decreased by 40%. These results suggest that it is possible to increase distance between cotton and wheat from a few rows in the current intercropping system to the "strip" scale, and maintain effective biological

Table 7.1. Comparison of advantages and disadvantages among three cotton cropping systems[1].

	Cotton–wheat intercropping	Cotton–wheat strip cropping	Single cotton cropping
Biological control of *A. gossypii*	++	+	–
Suppression of *H. armigera*	–	+	+
Suppression of *V. dahliae*	–	+	+
Land use efficiency (yield)	++	±	–
Fiber and seed quality	±	+	+
Labor requirements	–	±	+

[1] ++ means high advantage, + advantage, ± in between, and – disadvantage.

control of the cotton aphid. Strip cropping would be also advantageous with respect to fiber and seed quality, labor requirement, and allow more effective suppression of the cotton bollworm and verticillium wilt by cultural practices (Table 7.1).

The model developed and insights gained in this study are a basis for further analysis of options of cotton–wheat strip cropping that enable biological control of *A. gossypii* on cotton and are more acceptable in other respects. In terms of cotton aphid biological control, the pattern of cotton–wheat strip cropping can be worked out as proposed in Fig. 7.2. Both immigration of alate *A. gossypii* and dispersal of *C. septempunctata* are functions of distance from wheat to cotton strips. The optimum distance between the wheat and cotton strips are determined, where the aphid populations throughout the seedling stage of cotton can be fully controlled by naturally-occurring natural enemies, particularly the seven-spot beetle, without application of any chemical insecticides.

7.4 Future research

Systems analysis and simulation used in this study have been a powerful tool to reach the goal of evaluating and exploring cotton–wheat intercropping strategies for biological control of *A. gossypii* on cotton. To validate the proposed strategy of cotton–wheat strip cropping for cotton aphid biological control, field work is required. More research is needed to determining the effect of distance from wheat to cotton on the immigration of alate *A. gossypii* into cotton, dispersal of the major predators from wheat into cotton and back, and parasitization of apterous *A. gossypii* by hymenopterous parasitoids. Dispersal of the major predators by flight should be considered and characterized quantitatively. Ives (1981) observed that local dispersal of coccinellids was significantly influenced by temperature. High temperature

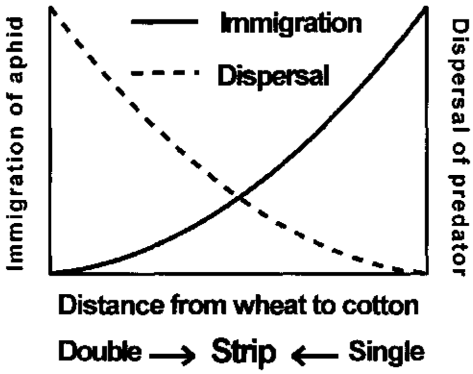

Fig. 7.2. Theoretical relationships between distance from wheat to cotton strips and the immigration of *A. gossypii*, and the dispersal of major predators, for explanation see text.

resulted in a high dispersal rate, which was modified only slightly by the availability of local prey. The effect of temperature on dispersal of the major predators between cotton and wheat should be determined as there exist variations in temperature between the dense wheat row and the loose cotton row (Wang, 1990). The importance of these parameters is indicated in Chapter 6, but they are seldom measured. With these parameters included in the model of Chapter 6, promising strategies of cotton–wheat strip cropping can be identified more precisely and tested on a large scale. Observations should be also made on the effectiveness and profitability of the proposed strategy for further improvement and development of cotton cropping systems in the North China.

The model of Chapter 6 and the proposed strategy have to be subjected to validation and tests in agro-ecological zones in the North China cotton region. Ideally, the model should be further developed by coupling with a cotton growth model (Wu et al., 1988). The relationship between yield losses and aphid density at different developmental stages should also be incorporated (Gao et al., 1989; Wen et al., 1990). The combined model can be used for calculating the reduction in yield due to different aphid numbers, and for formulating the economic threshold of the cotton aphid based on the economic factors (e.g. price of lint, cost of pesticides, etc.). Such a combination model can serve as a useful tool to optimize cotton–wheat strip cropping patterns that enable effective biological control of *A. gossypii* and are more acceptable in other respects. Thus, cotton aphid on seedling cotton in the North China cotton region can be controlled by biological measures, hence laying a foundation for integrated insect pest management through the cotton growing season.

Summary

Cotton aphid (*Aphis gossypii* Glover) is the key insect pest of seedling cotton (*Gossypium hirsutum* L.) in China, particularly in the North China cotton region. The resulting annual losses amount to 10–15% of the attainable yield. Sole reliance on insecticides against the cotton aphid in the past four decades has brought about a rapid development of insecticide resistance, serious outbreaks of key pests, resurgence of secondary pests, and risk for man and environment. Biological control of the cotton aphid by naturally-occurring seven-spot beetle (*Coccinella septempunctata* L.) is the first priority for integrated pest management in cotton to avoid early season application of insecticides and lay a foundation for biological control of aphids and other pests during the season. Augmentation of the seven-spot beetle by intercropping cotton with wheat is the most commonly used approach for cotton aphid biological control. Disadvantages of intercropping are decreased fiber and seed quality, increased outbreaks of cotton bollworm (*Helicoverpa armigera* Hübner) and verticillium wilt (*Verticillium dahliae* Kleb.), and difficulties with mechanization. There is, therefore, a demand for developing more sociologically, economically and ecologically sound cotton–wheat intercropping systems. Systems research provides an appropriate framework to analyse biological control systems and prototype promising biological control strategies. The objective of this study is (1) to better understand and quantify the major processes in *C. septempunctata–A. gossypii* system in cotton monoculture and cotton–wheat intercrop; (2) to develop simulation models of the dynamics of the coccinellid–aphid system in both cotton cropping systems by integrating process-level knowledge; and (3) to use the models to obtain insight in the dynamic behavior of the system and explore intercropping strategies that are not only favorable for biological control but also advantageous with respect to labor requirement, fiber and seed quality, and suppression of the cotton bollworm and verticillium wilt by cultural practices.

A major factor affecting *A. gossypii* population growth is temperature. Life table parameters of the cotton aphid were determined at 10, 15, 20, 25, 30 and 35 ± 0.5 °C in the laboratory (Chapter 2). The relationship of temperature with the developmental rate of each life stage (the reciprocal of the stage duration) was described using Logan curves. The relationship of temperature with the relative mortality rate of each pre-reproductive stage and each adult age class was described using parabolas. The relationship of temperature with the mean reproductive rate of each adult age class was described using the Weibull model. Development of *A. gossypii* was fastest at 30 °C, with a pre-reproductive period of 4.6 d. The greatest survival from birth to adult (81%)

was obtained at 25 °C. Fecundity was maximum at 25 °C, with a total fecundity of 28.3 nymphs per female and a mean reproductive rate of 3.1 nymphs per female per day. Threshold temperatures for development of the first to fourth instar and the adult were 8.2, 8.0, 7.2, 6.2 and 7.9 °C, respectively; and the thermal constants were 24.2, 23.7, 23.0, 25.5 and 168.8 degree-days (D°), respectively. *A. gossypii* obtained its greatest intrinsic rate of increase (0.386 d^{-1}) at 25 °C. High relative rate of population increase at 25 °C resulted in a daily population increase of 47% and a doubling time of 1.8 d, illustrating the tremendous growth capacity of *A. gossypii* under favorable conditions. Comparison to similar records from other crops indicates a relatively high heat tolerance of *A. gossypii* on cotton in North China. The data gathered are used to construct a simulation model of *A. gossypii* population dynamics in cotton.

Temperature and food quantity are two major factors affecting *C. septempunctata* population growth. Life history parameters of the seven-spot beetle feeding on *A. gossypii* were determined in two experiments in the laboratory (Chapter 3). The first experiment addressed the effect of five temperatures (15, 20, 25, 30 and 35 ± 0.5 °C) on the beetle bionomics, while the second one addressed the effect of food quantity on the beetle bionomics at a temperature of 25 °C. The relationship between temperature and the developmental rate of each life stage was described with Logan curves. The relationship of temperature with the relative mortality rate of each pre-oviposition stage and each adult age class was described with parabolas. The relationship between temperature and the mean oviposition rate of each adult age class was described with the Weibull model. *C. septempunctata* developed most rapidly at 35 °C, with a pre-imaginal period of 10.8 d. The highest survival from egg to adult (47%) was obtained at 25 °C. Oviposition was greatest at 25 °C, with a total oviposition of 287.4 eggs per female and a mean oviposition rate of 22.4 eggs per female per day. Threshold temperatures for development of eggs, larvae, pupae and adults ranged from 10.9 to 13.9 °C, with 12.6 °C for the entire life span; and thermal constants were 42.0, 103.7, 63.6 and 302.9 D°, respectively. Over the range of prey densities tested, a 3.5-fold increase in prey density resulted in a 2-fold reduction in larval development time and a 3-fold increase in larval survival. A 2-fold increase in prey density led to a 2-fold increase in total oviposition and the mean oviposition rate. The data gathered are used to construct a simulation model of *C. septempunctata* population dynamics in cotton.

Functional responses of five foraging stages of *C. septempunctata* on three size-groups of *A. gossypii* (mixed first and second nymphs, mixed third and fourth nymphs, and adults) at five temperatures (15, 20, 25, 30 and 35 ± 0.5 °C) were determined in the laboratory (Chapter 4). All functional responses were of type II and were adequately described by Rogers' random predator equation. The search rate increased linearly from 15 to 35 °C with a factor of 3–8. The handling rate showed a curvilinear relation to temperature and was lowest at 15 °C. There was a considerable variation in the latter response curves in different predator–prey stage combinations. In some predator–prey interactions, handling rate increased consistently with temperature, while in other combinations, the relationship had a maximum at an intermediate temperature. Search rate increased with 50–100% from one larval predator instar to the next but decreased from the fourth instar to the adult predator. There was only moderate difference in search rate between prey size-groups for the same predator stage (< 50% between extremes). Handling rate increased with 50–100% from one predator stage to the next, but it was somewhat similar in the fourth instar and adult predators. Handling rate towards early instar, late instar and adult prey varied with a ratio of about 3:2:1. The functional responses are incorporated in the simulation model of *C. septempunctata–A. gossypii* population interaction and dynamics in cotton.

In Chapter 5, a simulation model of the temporal dynamics of the coccinellid–aphid system in cotton monoculture was developed by integrating process-level knowledge. Six submodels were distinguished: cotton aphid, seven-spot beetle, predator–prey interaction, parasitism, cotton plant, and abiotic factors. The model was tested and evaluated at three levels of the system complexity: laboratory, field cage and open field. At each level of complexity, processes were added to the model, based on discrepancies between "original model" behaviors and observations, and additional experimentation. Processes included in the model at the laboratory level were temperature-dependent development, survival and reproduction of both insects; and prey density, prey size-group and temperature-dependent predation. Adaptations for the field cage level were density dependence of wing induction and reproduction of *A. gossypii*, extrapolation of the functional response from single stage interaction in experimental arenas in the laboratory to multiple stage interactions on plants, and a higher mortality for *C. septempunctata* than observed in the laboratory. Adaptations for the open field level were immigration rates of both insects; time-dependent parasitization of alate immigrants by *Allothrombium*, apterous aphids by hymenopterous parasitoids and seven-spot beetle pupae by *Tetrastichus coccinellae* Kurjumov; prey density-dependent departure rate of seven-spot beetle adults; prey density and prey size-group dependent predation by *Propylaea japonica* (Thungberg); and accumulated (D°)-driven cotton canopy growth. The simulated and observed data were in reasonable agreement at all levels, though discrepancies increased with the level of scale. Simulations at the open field level show that *C. septempunctata* plays a key role in controlling *A. gossypii* in cotton monoculture, but its numbers increase too late to guarantee a sufficient biological control. Predation by *P. japonica* and parasitism by *Allothrombium* and hymenopterous parasitoids play only a minor role. Variations in temperature or immigration of alate *A. gossypii* alone can not explain between-season differences in aphid population dynamics. Immigrating numbers of seven-spot beetle adults is the key factor.

Based on the model of Chapter 5, a simulation model of the spatio-temporal dynamics of the coccinellid–aphid system in cotton–wheat intercropping was developed in Chapter 6. Six submodels were distinguished: temporal dynamics of *A. gossypii* populations, temporal dynamics of *C. septempunctata* populations on wheat, seven-spot beetle dispersal from wheat into cotton, predator–prey interaction on cotton, cotton plant, and abiotic factors. In addition to the processes common in cotton monoculture and cotton–wheat intercrop, processes related to the cotton–wheat intercrop were experimentally characterized and included: (a) immigration of alate aphids into intercropped cotton and seven-spot beetle adults into intercropped wheat; (b) prey density-dependent emigration of seven-spot beetle adults from ripening wheat by flight; (c) prey density-dependent dispersal of foraging predators from wheat into cotton by walking; (d) time-dependent parasitization in apterous aphids and seven-spot beetle pupae; and (e) accumulated (D°)-driven cotton canopy growth. Dispersal of foraging seven-spot beetles from wheat into cotton was modelled as a diffusion process. There was satisfactory correspondence between the simulated and observed data. Simulations show that the low abundance of the cotton aphid in the current cotton–wheat intercropping system is due to a combined effect of increased predation and parasitism, and decreased aphid immigration, of which predation by the seven-spot beetle is the most important. Current cotton–wheat intercropping has an "overcapacity" for biological control. Simulations indicate that effective biological control can still be achieved when the immigration rate of alate aphids is increased by a factor 4, and the proportion of the seven-spot beetle foraging on cotton and the parasitization of apterous aphid are decreased by 40%. These results suggest that it is possible to increase distance from wheat to cotton strips in the current intercropping system and maintain effective biological control of the cotton aphid.

Based on models developed and insights gained in this study, a promising strategy of cotton–wheat strip cropping was proposed, which would be not only favorable for *A. gossypii* biological control but also advantageous with respect to labor requirement, fiber and seed quality, and suppression of the cotton bollworm and verticillium wilt by cultural practices. For its validation, field work is required. More research is needed to determine the effect of distance from wheat to cotton strips on immigration of alate aphids into cotton and dispersal of major predators from wheat into cotton. With these parameters included in the model of Chapter 6, the promising strategy of cotton–wheat strip cropping can be identified and tested on a large scale. Observations should be also made for effectiveness and profitability of the proposed strategy for further improvement and development of cotton cropping systems in North China.

Samenvatting

De katoenluis (*Aphis gossypii* Glover) is in Noord China de belangrijkste plaag van katoen (*Gossypium hirsutum* L.) gedurende de zaailingfase. Opbrengstverliezen bedragen ongeveer 10 tot 15%. Eenzijdige en intensieve chemische bestrijding van katoenluis heeft de laatste vier decennia meermalen geresulteerd in een snelle ontwikkeling van resistentie, en leidt ook tot het optreden van secundaire (geïnduceerde) plagen en risico's voor mens en milieu. Biologische bestrijding van katoenluis door van nature voorkomende natuurlijke vijanden, zoals het zevenstiplieveheersbeestje *Coccinella septempunctata* L., is een belangrijke voorwaarde voor het welslagen van geïntegreerde plaagbestrijding in katoen. Daardoor kunnen namelijk vroege toepassingen van pesticiden worden vermeden en wordt de basis gelegd voor biologische bestrijding van bladluizen en andere plagen gedurende de rest van de teelt.

Biologische bestrijding van katoenluis wordt bevorderd door mengteelt van katoen met wintertarwe. In deze mengteelt worden enkele rijen tarwe (vaak drie) afgewisseld met een of twee rijen katoen. De tarwe wordt gezaaid in het najaar en geoogst in juni. De katoen wordt gezaaid in het voorjaar in vrije banen tussen de tarwerijen, en geoogst in oktober. Het katoengewas neemt na de oogst van de tarwe alle ruimte in het perceel in beslag. Natuurlijke vijanden kunnen in de mengteelt een gemakkelijke overstap maken van de tarwe, waarop ze zich voeden met graanluizen, naar de katoen. Daardoor wordt de impact van natuurlijke vijanden op katoenluis bevorderd.

In dit proefschrift is een systeemanalytische aanpak gehanteerd om de werking van dit biologische bestrijdingssysteem verder te onderzoeken en veelbelovende bestrijdingsstrategieën te prototyperen. Het doel van deze studie is (1) kwantitatief inzicht te verkrijgen in de voornaamste processen in het populatiesysteem *C. septempunctata–A. gossypii* in katoenmonocultuur en mengteelt; (2) simulatiemodellen te ontwikkelen voor de dynamica van coccinellide–bladluissystemen in beide teeltsystemen door het integreren van op procesniveau verkregen informatie; en (3) de ontwikkelde modellen te gebruiken om inzicht te verwerven in het dynamisch gedrag van genoemde systemen en opties te verkennen voor mengteeltsystemen die niet alleen voordelen bieden ten aanzien van biologische bestrijding, maar die tevens gunstig uitwerken in andere opzichten zoals arbeidsbehoefte, vezel- en zaadkwaliteit, en de uitvoerbaarheid van cultuurmaatregelen die gericht zijn op de voorkoming en bestrijding van verwelkingsziekte (veroorzaakt door de schimmel *Verticillium dahliae* Kleb.) en de rupsen van de gevreesde "cotton bollworm" (*Helicoverpa armigera* Hübner).

Levenscyclusparameters en potentiële populatiegroei van *A. gossypii*, het plaag insect, worden voornamelijk bepaald door de temperatuur. In klimaatkamers bij 10, 15, 20, 25, 30 en 35 °C werden ontwikkeling, overleving en reproductie gemeten (Hoofdstuk 2). De ontwikkeling verliep het snelst bij 30 °C. Bij deze temperatuur werd het adulte stadium in 4.6 dagen bereikt. De hoogste overleving (81%) werd gevonden bij 25 °C, evenals de hoogste reproductie: 28.3 larven per bladluis over de gehele levensduur en een gemiddelde reproductiesnelheid gedurende de reproductieve periode van 3.1 larven per adult per dag. De laagste temperaturen waarbij nog ontwikkeling plaatsvond in de eerste vier larvestadia bedroegen respectievelijk 8.2, 8.0, 7.2 en 6.2 °C. Ontwikkeling van deze stadia was compleet bij een temperatuursom (met inachtneming van de genoemde drempels) van 24.2, 23.7, 23.0 en 25.5 graaddagen (°Cd). De duur van het adulte stadium bedroeg 168.8 °Cd boven een drempel van 7.9 °C. De hoogste intrinsieke groeisnelheid (0.386 d^{-1}) werd gevonden bij 25 °C. Bij deze temperatuur kan een populatie in theorie dagelijks toenemen met 47%, en is de verdubbelingstijd 1.8 dagen. De relaties tussen temperatuur en levenscyclusparameters werden beschreven met de best passende wiskundige vergelijkingen: Logan-curves voor de ontwikkelingssnelheid, (dal)parabolen voor de relatieve sterftesnelheid, en Weibull-curves voor de reproductiesnelheid. Deze kwantitatieve beschrijvingen werden geïntegreerd tot een temperatuurgestuurd populatiemodel voor katoenluis.

Temperatuur en prooiaanbod zijn de voornaamste factoren die de levenscyclusparameters en potentiële populatiegroei van de predator *C. septempunctata* bepalen. Ontwikkeling, overleving en reproductie werden bepaald in twee series laboratoriumexperimenten (Hoofdstuk 3). In de eerste serie experimenten werd de invloed van de temperatuur gekwantificeerd (15, 20, 25, 30 en 35 °C) bij overvloedig prooiaanbod, terwijl in de tweede serie experimenten de invloed van zes niveaus van prooiaanbod werd gekwantificeerd bij 25 °C. *C. septempunctata* ontwikkelde zich het snelst bij 35 °C: het traject van ei tot adult werd bij die temperatuur in 10.8 dagen afgelegd. De hoogste overleving van ei tot adult (47%) werd gevonden bij 25 °C. Ook reproductie was het hoogst bij 25 °C: 287 eieren per vrouwtje, en een gemiddelde eilegsnelheid gedurende de reproductieve periode van 22.4 eieren per vrouwtje per dag. Temperatuursommen benodigd voor het doorlopen van het ei-, larve (L1-L4)- en pop-stadium bedroegen 42, 104 en 64 °Cd, bij stadiumafhankelijke ontwikkelingsdrempels tussen de 10.9 en 13.9 °C. De totale levensduur bedroeg 303 °Cd bij een drempel van 12.6 °C. Verhoging van het prooiaanbod vanaf het laagste niveau met een factor 2 resulteerde in een verdubbeling van reproductie. Verhoging met een factor 3.5 resulteerde in een halvering van de ontwikkelingsduur en een verdrievoudiging van de larvale overleving. Invloeden van temperatuur en voedselaanbod op levenscyclusparameters werden uitgedrukt in wiskundige formules en verwerkt in een populatiemodel voor *C. septempunctata*.

In Hoofdstuk 4 wordt de kwantificering van de functionele respons beschreven. De functionele respons is de relatie tussen de dichtheid van de prooi (katoenluis) en de predatiesnelheid per individuele predator (zevenstip-lieveheersbeestje). De functionele responsen van vijf foeragerende stadia van *C. septempunctata* (L1-L4 en adult) werden bepaald bij vijf temperaturen (15, 20, 25, 30 en 35 °C) en voor drie grootteklassen van de katoenluis: kleine larven (L1 + L2), grote larven (L3 + L4), en adulten (Hoofdstuk 4). Alle functionele responsen waren van het type II; dat wil zeggen dat er bij lage dichtheid van de prooi een nagenoeg lineaire relatie was tussen prooidichtheid en predatiesnelheid, terwijl deze relatie bij hogere dichtheid geleidelijk steeds verder afvlakte, totdat er een maximum predatiesnelheid werd bereikt bij hoge prooidichtheid. De gemeten responsen konden wiskundig goed worden gekarakteriseerd met Rogers' formule voor predatie door een lukraak foeragerende predator. Deze formule bevat - naast de tijdsduur van het experiment - twee parameters: de zoeksnelheid, welke de initiële helling van de respons voorstelt, en de behandelingssnelheid, welke de maximaal bereikte predatiesnelheid voorstelt. De zoeksnelheid nam van 15 tot 35 °C toe met een factor 3 tot 8, afhankelijk van de combinatie van predatorstadium en bladluisgrootteklasse. De behandelingssnelheid vertoonde een kromlijnig verband met de temperatuur en was het laagst bij 15 °C. Er was aanzienlijke variatie in de vorm van deze respons tussen verschillende combinaties van predatorstadium en bladluisgrootteklasse. Bij sommige combinaties nam de behandelingssnelheid monotoon toe met temperatuur over het hele traject, terwijl bij andere combinaties er een maximum gevonden werd bij intermediaire temperaturen. De zoeksnelheid nam toe met 50 tot 100% van het ene naar het volgende larvale predatorstadium, en was lager in het adulte- dan in het L4-stadium. Er waren niet al te grote verschillen in zoeksnelheid tussen de verschillende prooigrootteklassen (minder dan 50% verschil tussen extremen). De behandelingssnelheid nam van het ene naar het volgende predatorstadium met 50 tot 100% toe, en de behandelingssnelheden waren ongeveer gelijk in het L4-stadium en de adult. De behandelingssnelheden van kleine larven, grote larven en adulten verhielden zich ongeveer als 3:2:1. De functionele responsen zijn geïntegreerd met de populatiemodellen van katoenluis en zevenstip-lieveheersbeestje tot een stadiumgestructureerd predator-prooimodel onder invloed van temperatuur.

Het model werd getoetst en verder ontwikkeld door vergelijking met additionele gegevens op drie niveaus van complexiteit: laboratorium, veldkooi en open veld in katoenmonocultuur en mengteelt. In Hoofdstuk 5 wordt het opschalen van het model van laboratorium naar open veld monocultuur beschreven. Op elk van de drie niveaus wordt het model, zoals dat is gestructureerd en geparameteriseerd op eenvoudiger niveaus van complexiteit, vergeleken met nieuwe experimentele gegevens, en worden op indicatie van discrepanties tussen modelresultaten en waarnemingen model-aanpassingen aangebracht. Deze aanpassingen zijn gebaseerd op additionele waarnemingen, procesanalyses, procesbeschrijvingen en parameterisaties op dit hogere niveau van complexiteit. Op het niveau van de veldkooi werden dichtheidsafhankelijke inductie van gevleugelde bladluizen en dichtheidsafhankelijke reproductie als nieuwe elementen aan het model toegevoegd. Voor het zevenstip-lieveheersbeestje werd een in de veldkooi gemeten, hogere mortaliteit ingevoerd. De functionele respons werd opgeschaald naar plantniveau en interacties tussen gemengde ontwikkelingsstadia van prooi en predator. Op het niveau van het open veld werden een aantal nieuw opgelegde, tijdsafhankelijke omgevingsvariabelen ingevoerd: immigratie van katoenluis, immigratie van *C. septempunctata*, predatie door een andere coccinellide, *Propylea japonica* (Thunberg), en parasitering door mijten van het genus *Allothrombium* en door sluipwespen. Verder werd een aantal nieuwe processen beschreven: dichtheidsafhankelijke emigratie van katoenluis, prooidichtheidsafhankelijke emigratie van *C. septempunctata*, en temperatuurafhankelijke bladoppervlaktegroei van de katoenplant. De bladoppervlakte per plant is nodig in de berekening van de functionele respons op plantniveau. Simulaties met het uiteindelijke model op veldniveau zijn in overeenstemming met veldwaarnemingen. Verschillen tussen simulaties en waarnemingen nemen toe met het niveau van complexiteit. Dit is enerzijds toe te schrijven aan de moeilijkheid om de complexe processen in het veld adequaat in modelstructuur en parameters te "vangen", anderzijds zijn naar alle waarschijnlijkheid onnauwkeurigheden in de bemonstering deels ook debet aan gevonden afwijkingen. De hoofdzaak is dat de modelbouw tot nieuwe inzichten leidt en dat het uiteindelijke model de werkelijkheid voldoende goed weergeeft om als experimenteeromgeving voor scenariostudies te kunnen fungeren. Enkele gevoeligheidsanalyses tonen aan dat variaties van jaar tot jaar in het tijdstip van verschijning en aantallen van het zevenstip-lieveheersbeestje in katoen monocultures de voornaamste verklaring zijn voor de fluctuaties van jaar tot jaar in de dichtheden die *A. gossypii* in de monocultuur bereikt. Het zevenstip-lieveheersbeestje levert dus een belangrijke bijdrage aan biologische katoenluisbestrijding in monocultuur, hoewel deze bijdrage van jaar tot jaar fluctueert en in het algemeen niet toereikend is.

In Hoofdstuk 6 wordt het uiteindelijke model van Hoofdstuk 5 uitgebreid met de dispersie (verspreiding) van lieveheersbeestjes tussen tarwe en katoen in een rijenmengteelt. Het dispersiemodel is gebaseerd op de gemiddelde verblijfstijden van zevenstip-lieveheersbeestjes op tarwe- en katoenrijen. Deze verblijfstijden zijn afhankelijk van de bladluisdichtheden op deze gewassen en liggen voor tarwe ruwweg een factor 10 hoger dan voor katoen. Prooidichtheidsafhankelijke verblijfstijden zijn gemeten in het veld. De mate van dispersie is omgekeerd evenredig met de verblijfstijd. In het populatiemodel voor de interactie tussen katoenluis en zevenstip-lieveheersbeestje in mengteelt wordt ervan uitgegaan dat dit dispersieproces voortdurend in evenwicht verkeert. De verdelingsratio van lieveheersbeestjes in katoen en tarwe is dan gelijk aan de ratio van de verblijfstijden. De bladluisdichtheid op tarwe is een opgelegde tijdsafhankelijke omgevingsvariabele, terwijl de dynamiek van katoenluis wordt gesimuleerd als beschreven in Hoofdstuk 5 voor de monocultuur. Er was overeenkomst tussen modelberekeningen en veldwaarnemingen. Gevoeligheidsanalyses met het model tonen aan dat predatie door *Coccinella* veruit de belangrijkste sterfteoorzaak voor katoenluis is in mengteelt, en dat de mengteelt over een aanzienlijke "overcapaciteit" beschikt in dit opzicht. Andere mechanismen van plaagonderdrukking, zoals sterk gereduceerde immigratie van katoenluis vanaf winterwaarden en parasitering door mijten en sluipwespen, leveren een substantiële bijdrage aan het katoenluisonderdrukkende effect van mengteelt, maar zijn ondergeschikt aan het effect van predatie door *C. septempunctata*.

In de discussie worden de implicaties van de resultaten van de studie in een breder verband bekeken. Er wordt naar voren gebracht dat mengteelt niet alleen voordelen maar ook nadelen heeft. Zo is het in het rijenmengteeltsysteem moeilijk om in het voorjaar grondbewerking toe te passen, waardoor het optreden van rupsenplagen van de "cotton bollworm" *H. armigera* in de hand wordt gewerkt. Verder leidt een rotatie met jaarlijkse teelt van katoen en tarwe op één perceel tot problemen met verwelkingsziekte, veroorzaakt door *V. dahliae*. Mechanisatie is lastig in het mengteeltsysteem met afwisselend drie rijen tarwe en twee rijen katoen, dat thans het meest gangbaar is. De arbeidsbehoefte is er hoog en door concurrentie in het zaailingstadium en de verkorting van het katoenseizoen is de zaad- en vezelopbrengst in dit mengteeltsysteem lager en van minder goede kwaliteit dan in katoenmonocultuur. Gezien deze factoren zou overwogen kunnen worden om over te stappen naar een mengteeltsysteem dat uit bredere "gewasbanen" bestaat dan thans gebruikelijk is. De in simulaties vastgestelde overcapaciteit aan biologische bestrijding in de huidige rijenmengteelt suggereert dat mengteeltsystemen op grotere schaalniveaus vanuit het oogpunt van biologische bestrijding van katoenluis ook goed zouden kunnen voldoen, en wellicht een betere combinatie van doelstellingen kunnen bewerkstelligen. Veldwerk zal moeten uitwijzen of dit werkelijk zo is. Het verder ontwikkelen en gebruik van het in dit proefschrift beschreven model voor de biologische bestrijding van katoenluis in mengteelt en monocultuur kan een waardevolle bijdrage leveren aan de verbetering van biologische bestrijding in katoenteeltsystemen in China en daarbuiten.

小　结

棉蚜（*Aphis gossypii* Glover）是中国，特别是北方棉区棉花苗期的主要害虫；每年因其为害损产10%—15%．由于长期依赖化学农药防治棉蚜，致使害虫抗药性剧增，主要害虫更猖獗，次要害虫大发生，环境污染日趋严重．增殖保护利用自然发生的七星瓢虫（*Coccinella septempunctata* L.）防治棉蚜是棉花害虫综合治理的首选措施，以避免早期用药，保护自然天敌，为棉花全生育期害虫的生物防治奠定基础．麦棉套种是目前最常用的棉蚜生物防治技术。然而，现行麦套棉系统有三点不足：纤维和种子品质降低，棉铃虫（*Helicoverpa armigera* Hübner）和棉花黄萎病（*Verticillium dahliae* Kleb.）发生为害加重，田间机械作业难度较大。因此，发展具有较高经济、生态和社会效益的麦套棉种植方式乃当务之急。系统研究是分析生物防治系统、优化生物防治技术的有效途径．本研究旨在：（1）进一步分析和定量研究单作棉田及麦套棉田七星瓢虫—棉蚜系统的主要生态学过程；（2）通过对不同层次生态学过程知识的综合，建立单作棉田及麦套棉田七星瓢虫—棉蚜系统动态模拟模型；（3）运用所建立的模型，揭示不同耕作制度条件下七星瓢虫—棉蚜系统的数量动态规律，开发不仅适合于棉蚜生物防治，而且有助于提高农事操作的机械化程度、改进纤维和种子品质、减轻棉铃虫和棉花黄萎病发生为害的麦棉套作技术及种植方式．

温度是影响棉蚜种群增长的重要因子。室内研究了10，15，20，25，30及35 ± 0.5°C条件下棉蚜的个体生态学（第二章）．温度与各虫态发育速率（发育历期之倒数）之关系用 Logan 曲线拟合．温度与生殖前期各虫态及成虫各年龄组相对死亡率之关系用二次抛物线拟合。温度与成虫各年龄组平均产仔率之关系用 Weibull 模型拟合。30°C时棉蚜的发育速度最快，其生殖前期历期仅为4.6 d； 25°C时存活率最高(81%)，繁殖力和平均产仔率最大（分别为28.3头幼蚜/成虫和3.1头幼蚜/成虫/天）。1—4龄若蚜及成蚜的发育起点温度分别为8.2， 8.0， 7.2， 6.2和7.9°C，有效积温分别为24.2，23.7，23.0， 25.5和168.8 日度（D°)。25°C时棉蚜的内禀增长率最高（0.886 d^{-1})，种群日增长率47%，种群加倍时间1.8 d。由此表明， 只要环境条件适应，棉蚜种群增长潜能极强。与文献报道的相似研究相比，中国北方棉蚜种群较耐高温。本实验数据用于建立棉田棉蚜种群动态模拟模型。

温度和食物是影响七星瓢虫种群增长的两个重要因子。室内研究了15，20，25，

30和35 ± 0.5℃条件下及25℃时不同猎物密度条件下，七星瓢虫的个体生态学（第三章）。温度与各虫态发育速率之关系用 Logan 曲线拟合，温度与各产卵前期及成虫各年龄组相对死亡率之关系用二次抛物线拟合，温度与成虫各年龄组平均产卵率之关系用 Weibull 模型拟合。35℃时，七星瓢虫的发育速度最快，其成虫前期仅为10.8 d；25℃时的存活率最高（47%），繁殖力和平均产卵率最大（分别为28.7粒卵/雌和22.4粒卵/雌/天）。卵、幼虫、蛹和成虫的发育起点温度为 10.9—13.9℃（全生育期为12.6℃），有效积温分别为42.0，103.7，63.6和302.9 D°。在所测定的猎物密度范围内，猎物密度增加3.5倍，幼虫发育历期缩短2倍，存活率提高3倍；猎物密度增加2倍，生殖力和平均产卵率亦提高2倍。本实验数据用于建立棉田七星瓢虫种群动态模拟模型。

室内研究了15，20，25，30和35 ± 0.5℃条件下，七星瓢虫5个捕食虫态捕食棉蚜三个体积组（1—2龄若蚜、3—4龄若蚜和成蚜）的功能反应（第四章）。全部功能反应均属II型，且用 Rogers 随机捕食模型进行了定量描述。结果表明，七星瓢虫捕食虫棉蚜的搜索率随温度增加呈直线上升，从15℃到35℃，增加3—8倍。捕食率随温度增加呈曲线上升，15℃时最低，但不同捕食者一猎物组合功能反应曲线的后半部变异较大。有些组合的捕食率随温度增加呈上升趋势，有些组合的捕食率则在中间温区为最高。搜索率随捕食者龄期的增长而提高（50%—100%），但自4龄幼虫至成虫期略有下降。同龄期捕食者对不同体积组棉蚜的搜索率差异不大（极值差小于50%）。捕食率随捕食者年龄的增长而提高（50%—100%），但4龄幼虫与成虫的捕食率基本相同。七星瓢虫捕食1—2龄若蚜、3—4龄若蚜及成蚜呈3:2:1的比例变动。全部功能反应方程用于建立棉田七星瓢虫—棉蚜种群互作及其动态模拟模型。

第五章通过对不同层次生态学过程知识的综合，组建了单作棉田七星瓢虫一棉蚜系统时间动态模拟模型。该模型包括6个子模型：棉蚜，七星瓢虫，捕食者一猎物相互关系，寄生，棉花和非生物因子等，并经过室内、田间罩笼、大田等不同系统复杂性层次的检验与评价。根据模拟值与观察值的离散程度和新的参数试验结果，在每一层次引入有关的生态学过程。室内层次主要包括：两种昆虫由温度制约的发育率、存活率和生殖率，以及猎物密度、猎物体积和温度调控的捕食率。田间罩笼层次主要包括：棉蚜密度制约的有翅蚜形成率和生殖率，七星瓢虫特定发育阶段的存活率，以及棉株上七星瓢虫各捕食虫态捕食不同体积组棉蚜的功能反应。大田层次主要包括：两种昆虫的迁人率，依时间变动的有翅蚜、无翅蚜及七星瓢虫蛹寄生率，依猎物密度变动的七星瓢虫迁出率，依棉蚜密度与体积组变动的龟纹瓢虫〔*Propylaea japonica*

(Thungberg)〕捕食率，以及由有效积温调控的株冠生长率。各层次的模拟值与观察值基本吻合，但离散程度随系统复杂性的增加而上升。大田模拟研究表明，七星瓢虫是单作棉田棉蚜种群的关键调控因子，但因其发生数量上升太晚而不能有效地控制住蚜害。龟纹瓢虫、有翅棉蚜寄生螨和膜翅目寄生蜂的控害作用甚微。温度或有翅蚜迁入率的差异不能解释各年份间棉蚜种群动态的差异，但七星瓢虫成虫的迁入数量则为关键因子。

基于第五章建立的模型，第六章进一步组建了麦套棉田七星瓢虫一棉蚜系统时空动态模型。该模型包括6个子模型：棉花上棉蚜种群的时间动态，小麦上七星瓢虫种群的时间动态，七星瓢虫自小麦向棉花扩散，捕食者一猎物相互关系，棉花和非生物因子等。除单作棉和麦套棉共有的生态学过程之外，对麦套棉特有的生态学过程进行了试验研究和定量描述。这些过程包括：棉花上的有翅蚜迁入率和小麦上的七星瓢虫成虫迁入率，小麦成熟期猎物（麦蚜）密度制约的七星瓢虫成虫迁出率，猎物（麦蚜或麦蚜）密度制约的七星瓢虫扩散率，依时间变动的无翅蚜和七星瓢虫蛹寄生率，以及由有效积温调控的株冠生长率。七星瓢虫各捕食虫态自小麦向棉花的运动过程用偏微分随机扩散技术模拟。模拟研究表明，现行麦套棉系统的棉蚜发生数量较低主要是因较高和较早的捕食与寄生死亡率所致，其中七星瓢虫的捕食最为重要。其次为有翅蚜的迁入率降低90%。现行麦套棉系统的棉蚜生物防治能力过剩。模拟研究揭示：即使棉花上有翅蚜迁入率增加4倍、七星瓢虫自小麦向棉花上扩散的比例及无翅蚜的寄生率降低40%，棉蚜种群数量仍低于防治指标。这些结果展示：适当增加现行麦套棉系统中的麦棉距离，仍能使棉蚜得到有效地控制。

基于本研究所建立的模型和揭示的规律认为，在中国北方棉区应提倡麦棉条带种植方式。这样不仅适合于棉蚜的生物防治，而且有助于提高农事操作的机械化程度，改进纤维和种子品质，减轻棉铃虫和棉花黄萎病的猖獗为害。验证麦棉条带种植方式的可行性需要做大量的试验研究工作，重点揭示麦棉条带种植的距离对有翅蚜迁入率和主要捕食性天敌自小麦向棉花扩散的影响。将这些参数引入第六章所建立的模拟模型，即可确定麦棉条带种植的最佳方式，并进行大面积示范试验。与此同时，应进行麦棉条带种植的有效性和经济效益分析，以便进一步改进和发展中国北方棉区的棉花耕作系统。

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Appendix A

Tables

Table A–1. Relationship between temperature (T, °C) and the relative mortality rate (R_m, d^{-1}) of different age classes of *A. gossypii* adults on cotton, based on the parabola: $R_m = c_1 + c_2\ T + c_3\ T^2$, where c_1, c_2 and c_3 are coefficients (see Sections 2.2.2 and 2.3.2). RMSE is the Root Mean Square Error.

Age class	c_1	c_2	c_3	RMSE	r^2
1	0.042	–0.0043	0.00014	0.0010	0.97
2	0.059	–0.0065	0.00021	0.0012	0.98
3	0.083	–0.0088	0.00028	0.0018	0.99
4	0.117	–0.0126	0.00040	0.0036	0.98
5	0.156	–0.0163	0.00052	0.0053	0.98
6	0.165	–0.0167	0.00054	0.0068	0.98
7	0.231	–0.0240	0.00076	0.0091	0.98
8	0.310	–0.0331	0.00104	0.0115	0.99
9	0.273	–0.0274	0.00092	0.0108	0.99
10	0.396	–0.0403	0.00127	0.0183	0.99
11	0.462	–0.0472	0.00148	0.0255	0.98
12	0.590	–0.0616	0.00188	0.0303	0.98
13	0.568	–0.0584	0.00185	0.0354	0.98
14	0.705	–0.0733	0.00227	0.0410	0.97
15	0.756	–0.0769	0.00239	0.0523	0.98
16	0.678	–0.0672	0.00218	0.0421	0.99
17	0.830	–0.0840	0.00266	0.0617	0.98
18	0.934	–0.0930	0.00292	0.0810	0.98
19	0.905	–0.0871	0.00281	0.0793	0.98
20	1.007	–0.0989	0.00318	0.1026	0.97

Table A-2. Relationship between temperature (T, °C) and the mean reproductive rate (Y, number of nymphs produced per female per day) of each age class of *A. gossypii* adults on cotton, based on Weibull's (1951) model: $Y = d_2 / d_1 d_3 [(T - T_1) / d_1]^{(d_2 - 1)} \exp \{ - [(T - T_1) / d_1]^{d_2} \}$, where T_1 is the lower threshold temperature (7.9 °C); and d_1, d_2 and d_3 are coefficients (see Sections 2.2.2 and 2.3.3). RMSE is the Root Mean Square Error.

Age class[1]	d_1	d_2	d_3	RMSE	r^2
1	20.3	2.89	52.7	0.45	0.94
2	20.3	2.96	57.6	0.51	0.94
3	20.1	3.14	59.0	0.43	0.97
4	19.7	3.06	52.3	0.33	0.97
5	19.4	3.24	47.5	0.27	0.98
6	19.4	3.43	42.3	0.13	0.99
7	19.2	3.69	33.3	0.15	0.99
8	19.1	3.92	29.7	0.11	0.99
9	19.1	3.82	25.7	0.04	0.99
10	19.1	4.24	21.2	0.03	0.99
11	19.9	4.90	15.0	0.09	0.98
12	20.1	5.30	12.7	0.07	0.98
13	20.4	5.06	9.3	0.09	0.94
14	20.1	8.97	4.3	0.01	0.99
15	20.0	9.98	3.0	0.01	0.99

[1] No nymphs were produced in age classes 16–20.

Table A–3. Relationship between temperature (T, °C) and the relative mortality rate (R_m, d^{-1}) of different age classes of *C. septempunctata* adults feeding on *A. gossypii* on cotton, based on the parabola: $R_m = c_1 + c_2 T + c_3 T^2$, where c_1, c_2 and c_3 are coefficients (see Sections 3.2.2 and 3.3.1). RMSE is the Root Mean Square Error.

Age class	c_1	c_2	c_3	RMSE	r^2
1	0.034	–0.0028	0.00007	0.0002	0.98
2	0.116	–0.0091	0.00020	0.0007	0.98
3	0.094	–0.0070	0.00019	0.0013	0.98
4	0.680	–0.0553	0.00118	0.0058	0.99
5	0.670	–0.0533	0.00118	0.0067	0.99
6	1.468	–0.1172	0.00249	0.0161	0.99
7	1.504	–0.1213	0.00268	0.0248	0.99
8	1.807	–0.0750	0.00132	0.0339	0.98
9	2.256	–0.1791	0.00392	0.0289	0.99
10	2.788	–0.2217	0.00484	0.0603	0.99
11	3.836	–0.3095	0.00672	0.0796	0.99
12	5.358	–0.4202	0.00887	0.0753	0.99

Table A–4. Relationship between temperature (T, °C) and the mean oviposition rate (Y, number of eggs laid per female per day) of each age classes of *C. septempunctata* adults feeding on *A. gossypii* on cotton, based on Weibull's (1951) model: $Y = d_2 / d_1 d_3 [(T - T_l) / d_1]^{(d_2 - 1)} \exp \{ - [(T - T_l) / d_1]^{d_2} \}$, where T_l is the lower threshold temperature (11.1 °C); and d_1, d_2 and d_3 are coefficients (see Sections 3.2.2 and 3.3.1). RMSE is the Root Mean Square Error.

Age class[1]	d_1	d_2	d_3	RMSE	r^2
1	18.6	2.81	443.9	11.1	0.95
2	19.4	3.19	558.7	6.9	0.99
3	19.7	2.94	453.0	6.5	0.98
4	19.7	3.07	310.2	4.3	0.98
5	18.9	3.68	214.2	2.8	0.99
6	18.4	3.87	136.0	1.6	0.99
7	18.8	4.33	97.7	2.3	0.95
8	19.1	4.39	62.7	1.2	0.94
9	15.3	3.88	20.7	0.1	0.99

[1] No eggs were laid in age classes 10–12.

Table A–5. Relationship between temperature (T, °C) and the search rate (a, arena d^{-1}) of five foraging stages of *C. septempunctata* preying on three size-groups of *A. gossypii* on cotton, based on a linear model: $a = h_1 + h_2 T$, where h_1 and h_2 are coefficients (see Sections 4.2.2 and 4.3.3). RMSE is the Root Mean Square Error.

Predator stage	Prey size-group[1]	h_1	h_2	RMSE	r^2
First instar	Early instar	–0.56	0.053	0.09	0.96
	Late instar	–1.49	0.100	0.04	0.87
	Adult	–0.84	0.070	0.19	0.92
Second instar	Early instar	–0.86	0.086	0.13	0.98
	Late instar	–1.82	0.136	0.38	0.95
	Adult	–2.49	0.177	0.61	0.94
Third instar	Early instar	–0.74	0.105	0.15	0.99
	Late instar	–0.88	0.119	0.15	0.99
	Adult	–1.45	0.149	0.31	0.98
Fourth instar	Early instar	–0.42	0.137	0.53	0.95
	Late instar	–1.85	0.230	1.31	0.91
	Adult	–3.83	0.320	1.39	0.95
Female adult	Early instar	–0.76	0.119	0.41	0.94
	Late instar	–3.09	0.237	0.50	0.98
	Adult	–3.19	0.231	0.59	0.97

[1] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

Table A–6. Relationship between temperature (T, °C) and the handling rate (R_h, h^{-1}) of five foraging stages of *C. septempunctata* preying on three size-groups of *A. gossypii* on cotton, based on the model of Eyring & Urry (1975): $R_h = j_1 \, T \exp(-j_2 / T) / [1 + j_3 \exp(-j_4 / T)]$, where j_1, j_2, j_3 and j_4 are coefficients (see Sections 4.2.2 and 4.3.3). RMSE is the Root Mean Square Error.

Predator stage	Prey size-group[1]	j_1	j_2	j_3	j_4	RMSE	r^2
First instar	Early instar	36.3	82.4	585.1	127.6	4.4	0.93
	Late instar	58.9	97.6	1337.6	120.9	0.5	0.94
	Adult	0.3	20.4	14.3	68.1	0.3	0.86
Second instar	Early instar	3.7	31.7	81.5	108.2	3.7	0.91
	Late instar	1.4	35.2	236.4	146.7	1.4	0.91
	Adult	0.1	1.3	209.2	201.1	0.5	0.86
Third instar	Early instar	131.5	71.4	921.8	105.9	3.8	0.88
	Late instar	18.7	55.0	195.6	88.7	1.5	0.95
	Adult	1.7	30.0	93.3	98.6	0.8	0.90
Fourth instar	Early instar	703.3	87.6	4016.7	125.7	7.4	0.81
	Late instar	51.0	57.4	698.1	106.4	1.5	0.97
	Adult	0.6	3.7	30.1	95.6	0.9	0.94
Female adult	Early instar	4.2	12.1	31.5	72.0	4.8	0.90
	Late instar	92.7	72.9	992.3	118.1	1.3	0.99
	Adult	1.3	8.2	12.6	51.7	1.1	0.87

[1] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

Table A–7. Prey densities (number per arena) of *A. gossypii* on cotton offered for predation by five foraging stages of *C. septempunctata* at fluctuating temperatures in plastic containers with 30 cm^2 leaf in the laboratory experiment (see Section 5.2.3.1).

Predator	Number of prey per arena at different density levels[1]				
stage	I	II	III	IV	V
First instar	10	15	20	25	30
Second instar	20	30	40	50	60
Third instar	40	60	80	100	120
Fourth instar and adult	80	120	160	200	240

[1] The experiment was done for three prey size-groups: early instars (mixed first and second nymphs), late instars (mixed third and fourth nymphs) and adults.

Table A–8. Prey densities (number cm^{-2} leaf) of *A. gossypii* on cotton offered for predation by five foraging stages of *C. septempunctata* at fluctuating temperatures in field cages (see Section 5.2.3.2).

Predator	Number of prey cm^{-2} at different density levels[1]				
stage	I	II	III	IV	V
First instar	0.05	0.10	0.15	0.20	0.25
Second instar	0.10	0.15	0.20	0.25	0.30
Third instar	0.10	0.20	0.30	0.40	0.50
Fourth instar and adult	0.20	0.30	0.40	0.50	0.60

[1] Mixed instars and adults.

Table A–9. Search rate (a, mean ± SE, arena d^{-1}) and handling time (T_h, mean ± SE, d) of five foraging stages of *P. japonica* preying on three size-groups of *A. gossypii* on cotton in glass containers with 20 cm^2 leaf in laboratory (see Section 5.2.1.3)[1].

Predator stage	Prey group[2]	a	T_h	RMSE	r^2
First instar[3]	Early instar	0.91 ± 0.266	0.0134 ± 0.0234	1.27	0.81
	Late instar	1.08 ± 0.421	0.0451 ± 0.0424	0.91	0.68
	Adult	0.54 ± 0.094	0.0999 ± 0.0315	0.30	0.88
Second instar[4]	Early instar	1.77 ± 0.527	0.0187 ± 0.0060	2.32	0.94
	Late instar	0.97 ± 0.219	0.0143 ± 0.0077	1.60	0.96
	Adult	0.84 ± 0.146	0.0056 ± 0.0118	0.69	0.98
Third instar[4]	Early instar	3.03 ± 0.649	0.0237 ± 0.0026	1.56	0.97
	Late instar	2.17 ± 0.484	0.0318 ± 0.0034	1.55	0.95
	Adult	1.91 ± 0.451	0.0291 ± 0.0078	1.05	0.95
Fourth instar[4]	Early instar	2.03 ± 0.220	0.0264 ± 0.0018	0.84	0.99
	Late instar	1.82 ± 0.334	0.0400 ± 0.0059	0.77	0.96
	Adult	1.24 ± 0.215	0.0406 ± 0.0077	0.71	0.95
Adult[3]	Early instar	1.07 ± 0.207	0.0058 ± 0.0032	2.88	0.87
	Late instar	0.80 ± 0.179	0.0059 ± 0.0046	2.98	0.81
	Adult	0.48 ± 0.080	0.0117 ± 0.0051	1.70	0.82

[1] The a and T_h were estimated from Rogers' (1972) random predator equation, where RMSE is the Root Mean Square Error (aphids d^{-1}).

[2] Early instar refers to mixed first and second nymphs, and late instar to mixed third and fourth nymphs.

[3] Data were obtained by Song et al. (1988) at a constant temperature of 25 °C, with 70–90% r.h.

[4] Data were gathered by Zu et al. (1986) at fluctuating temperatures of 21–23 °C, with 82–92% r.h.

Appendix B

Figures

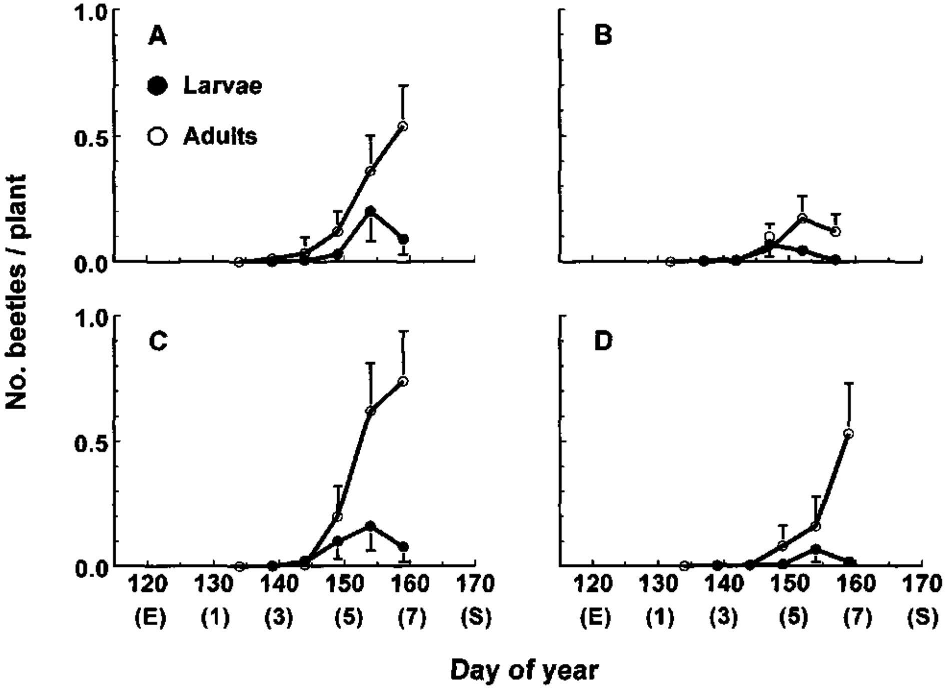

Fig. B–1. Observed larvae and adults (number per plant) of *P. japonica* on cotton at the seedling stage in single cotton cropped fields in 1992 (A), 1993 (B), 1994 (C), and 1995 (D). Bars represent observations with 95% confidence limits (see Section 5.2.1.3).

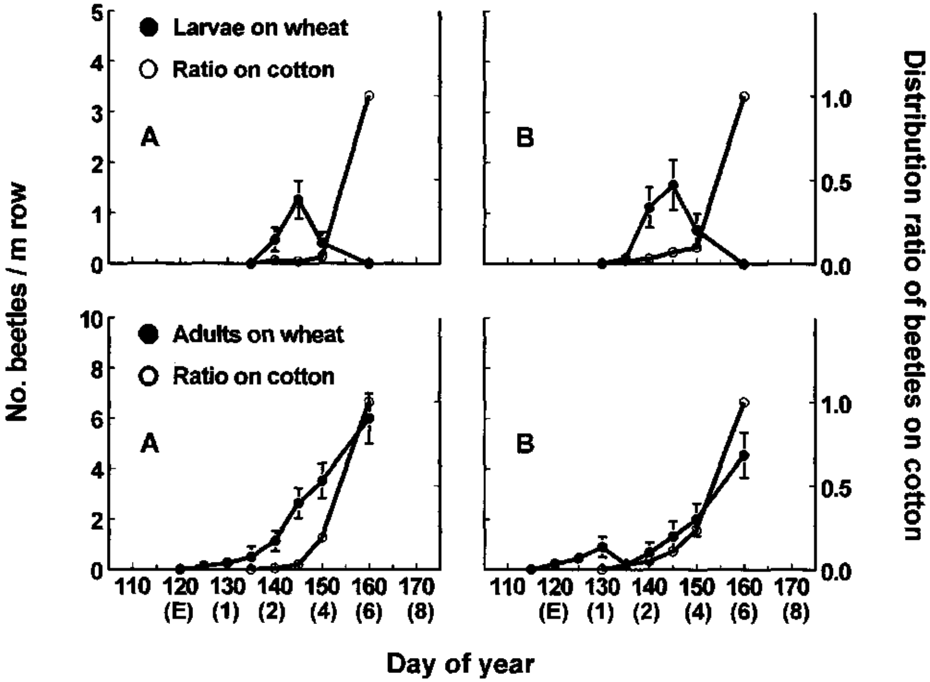

Fig. B–2. Observed larvae and adults of *P. japonica* (number per m row) on intercropped wheat from tillering to harvest, and their distribution ratios on intercropped cotton at the seedling stage in 1994 (A), and 1995 (B). Bars represent observations with 95% confidence limits (see Section 6.2.1.3).

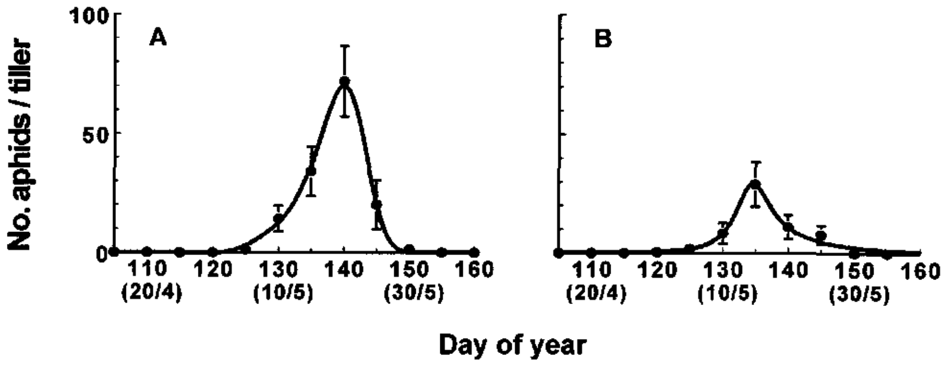

Fig. B–3. Observed wheat aphids on intercropped wheat (number per tiller) from tillering to harvest in 1994 (A), and 1995 (B). Bars represent observations with 95% confidence limits (see Section 6.2.1.2).

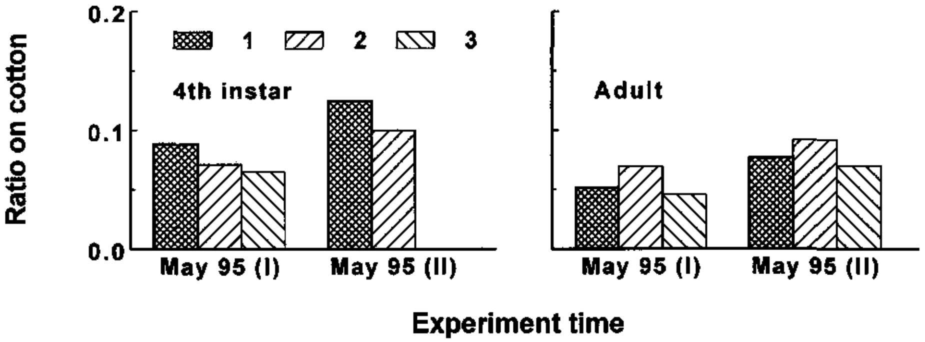

Fig. B–4. Simulated (1) and observed (2 and 3) distribution ratios of the fourth larval instars and adults of *C. septempunctata* temporarily dispersing from wheat into cotton in experimental arenas (1 m^2) in the cotton–wheat intercropped field in 1995. The 2 and 3 represent verification and validation, respectively. Details are given in Section 6.2.1.3.

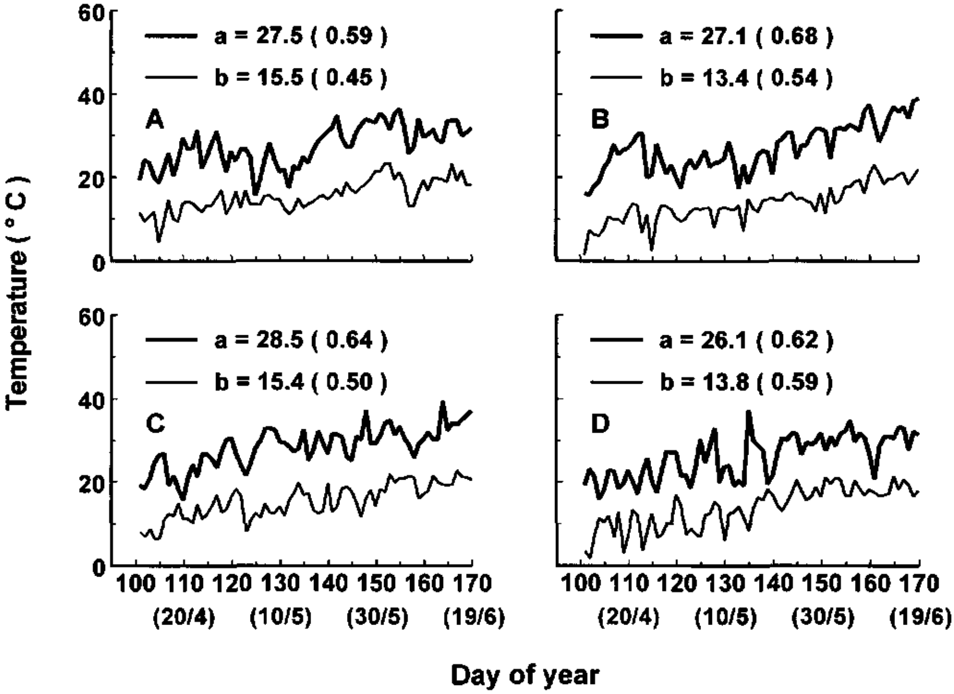

Fig. B–5. Daily maximum (thick line) and minimum (thin line) temperatures (°C) monitored at a meteorological station of the China Cotton Research Institute (CCRI), Anyang, Henan province, China, from April to June in 1992 (A), 1993 (B), 1994 (C), and 1995 (D). The a and b represent the mean daily maximum and minimum temperatures with SE (in parentheses) over the entire period, respectively (see Sections 5.2.3.3 and 6.2.3).

Curriculum vitae

Jingyuan Xia was born on 3 March 1958 in Xishui county, Hubei province, China. From 1978 to 1991, he studied at the Huazhong (Central China) Agricultural University, where he obtained his BSc degree with a specialization in plant protection. From 1982 to 1984, he worked as a research assistant at the China Cotton Research Institute (CCRI) of the Chinese Academy of Agricultural Sciences (CAAS). Here, he was mainly involved in research on biological control of cotton insect pests. From March to July 1984, he followed a training course on "Plant Protection" at the Egyptian International Agricultural Center in Cairo, Egypt. From 1985 to 1988, he studied at the International Rice Research Institute (IRRI) and the University of Philippines at Los Baños (UPLB) in the Philippines, where he got his MSc degree in Entomology with a thesis research entitled "Simulation of the population dynamics of yellow stemborer, *Scirpophaga incertulas* (Walker)". Since 1989, he has been working as assistant professor and associate professor at CCRI, where he has been mainly engaged in research on systems simulation and integrated management of cotton insect pests. He is team leader of the Chinese project on integrated pest management (IPM) in cotton, and vice-chairman of the state action committee for cotton bollworm management. He is advisor of the China National Scientific Committee (CNSC) for insecticide resistance management in cotton, and of the World Bank project on cotton IPM in China. He is head of Plant Protection Department (PPD) of CCRI, and deputy director of CCRI. From July to October 1992, he worked as a visiting research fellow at the Department of Theoretical Production Ecology (TPE) of the Wageningen Agricultural University (WAU) in the Netherlands. Since 1993, he has been involved in a "Sandwich PhD Program" of WAU, which resulted in this thesis.