

**Imperial College
London**

**STUDIES ON TRITROPHIC INTERACTIONS BETWEEN
CRUCIFERS, THE DIAMONDBACK MOTH AND AN
ENDOLARVAL PARASITOID**

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This thesis is dedicated:

To the loving memory of my father, who taught me honesty, and to my beloved mother, who taught me forgiveness, with gratitude for their love and encouragement in all stages of my life.

To my wife, Marzieh, for her love, patience and support, and especially to my lovely son, Parsa, who made my life meaningful.

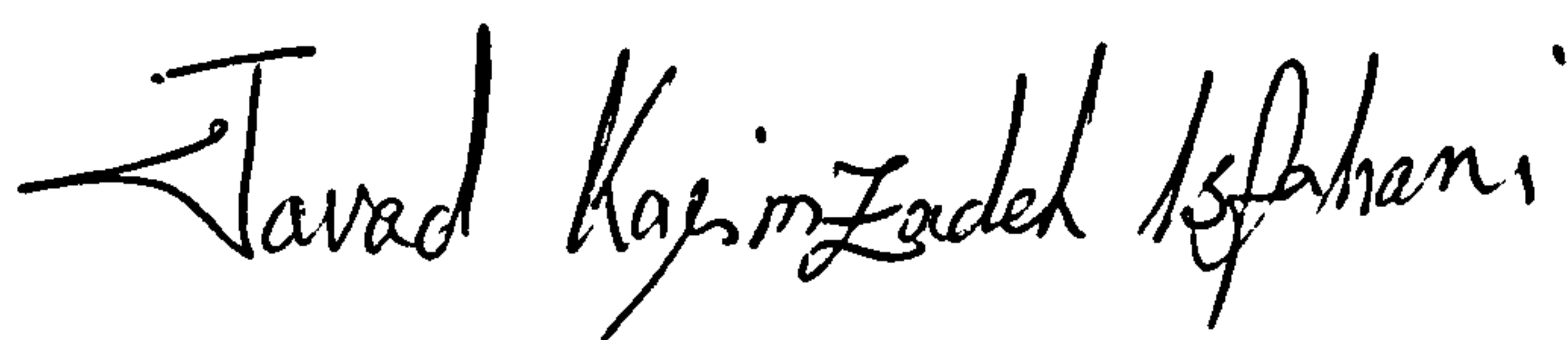
To my dearest sister, who deeply impresses me with her thoughts and feelings, and to my dear brothers for their spiritual supports.

Declaration

The work presented in this thesis is entirely my own and have not been submitted anywhere else with the following exception:

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Abstract

The diamondback moth (DBM), *Plutella xylostella* has become the most destructive pest of crucifers worldwide due to mainly to the overuse of insecticides, and there is an urgent need for more sustainable management strategies. An understanding of population biology is necessary to establish a more ecological approach, integrating sustainable technologies such as host plant resistance and biological control. The hymenopteran parasitoid, *Cotesia plutellae* is a key natural enemy in controlling DBM and is also a useful model system. Studies on the effects of host plant resistance on the population dynamics of DBM and *C. plutellae* showed that this did not affect equilibrial abundance of DBM, but it did affect the dynamics of DBM populations. The mean population size of DBM showed no significant difference between *Brassica rapa* (susceptible host plant) and *B. napus* (partially-resistant host plant) either in presence or absence of the parasitoid. Time series analysis suggested that the dynamics of DBM on *B. rapa* were underpinned by a delayed density-dependent process. However, DBM dynamics on *B. napus* were influenced by a direct density-dependent process. Although, measures of parasitism showed a significantly higher rate by *C. plutellae* on DBM feeding on *B. napus* compared with *B. rapa*, a survival analysis exhibited no significant difference in the persistence time of the host-parasitoid interaction between the two host plants. Olfactometer results revealed that *Cotesia plutellae* did not differentiate between different plant types when both the plant types offered were susceptible or were partially resistant. In contrast, *C. plutellae* could differentiate between the odours from susceptible (young Chinese cabbage) and partially-resistant (old common cabbages) plants whether plants were uninfested or infested with feeding DBM larvae. *Cotesia plutellae* showed a strong tendency to choose young Chinese cabbage in comparison to old common cabbages whether plants were infested or uninfested with feeding DBM larvae. The effects of learning varied depending on the host plant on which the parasitoid had been reared and the host plant on which the parasitoid had experience. In cage experiments, with short exposure times, *C. plutellae* preferred to parasitize DBM larvae on a susceptible host plant compared with DBM larvae on a partially-resistant host plant. However, this preference disappeared when the exposure time to the parasitoid was increased. The number of *C. plutellae* cocoons on susceptible host plants was significantly greater compared with partially-resistant host plants for both short and

long exposure time. Parasitism and immune system studies showed that DBM reared on a partially-resistant host, the common cabbage cv. Wheelers Imperial, had a significantly greater parasitoid egg load and proportion of parasitized hosts compared to a fully susceptible host, Chinese cabbage. The encapsulation proportion of *Cotesia plutellae* larvae was significantly greater on Chinese cabbage than on common cabbages, which in turn had significantly greater encapsulation compared with the fully-resistant host, the cauliflower cv. Early Green Glazed. However, the encapsulation ability of DBM larvae was not strong enough to affect parasitism. In unparasitized DBM, phenoloxidase activity was significantly greater in larvae reared on Chinese cabbage or cv. Wheelers Imperial compared with larvae reared on cv. Red Drumhead or Early Green Glazed. However, there was no significant difference in phenoloxidase activity in parasitized larvae reared on the different host plants. Superparasitism had no effect on the ability of DBM larvae to encapsulate *Cotesia plutellae* larvae. The greater parasitism rate of DBM larvae reared on partially-resistant host plants compared with Chinese cabbage appears to be due to the greater proportion of larvae parasitized by *C. plutellae* rather than the number of eggs laid. Modelling predicted that the biological mechanisms for the persistence of resource-herbivore-parasitoid tritrophic interaction are sufficiently low herbivore mortality or handling time and relatively high parasitoid conversion factor and attack rate or relatively low parasitoid handling time. The strong effects of host-plant resistance whether on herbivore mortality or herbivore handling time will destabilize the tritrophic system. For a sustainable ecosystem, therefore, highly-resistant host plants are not recommended, since they will exclude natural enemies. In this regard, partially-resistant host plant may be more applicable for sustainable strategies looking for compatibility of host-plant resistance and parasitoids. In addition, parasitoids with high attack rate, high conversion factor and low handling time, which can stabilize the system, are useful for sustainable biological control or IPM. Underlying mechanisms for host-plant resistance effects on *C. plutellae* parasitism, the effects of host-plant resistance on searching efficiency of *C. plutellae*, and the effects of bottom-up and top-down forces on population dynamics of crucifers-DBM-parasitoid systems were discussed.

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Chapter 1:

Introduction and Literature Review

1.1 Overview

In recent decades, the dependence on short-term, single-technology strategies for pest control, particularly those based on chemical pesticides, has created an increasing need for sustainable pest management systems (Zeng, 1993; Sar *et al.*, 1998; Trottier, 1998; van Lenteren, 1999; Groot & Dicke, 2002; Agnello *et al.*, 2003; Sharma *et al.*, 2004). Nowadays, there are considerable concerns related to the regular use of chemical insecticides, such as resistance (Elzen & Hardee, 2003; Ceccatti, 2004; Stankovic *et al.*, 2004), pest resurgence (Hardin *et al.*, 1995; Trumper & Holt, 1998; Kerns & Stewart, 2000; Zhu *et al.*, 2004), acute and chronic health (Akgur *et al.*, 2003; Fonseka *et al.*, 2003; Kamel & Hoppin, 2004), environmental pollution (Delpuech & Meyet, 2003; Gupta & Saxena, 2003; Holmes & de Vlaming, 2003; Gama-Flores *et al.*, 2004) and uneconomic crop production (Hallman & Lowenberg-DeBoer, 1999; Reitz *et al.*, 1999; Toenniessen *et al.*, 2003).

A basic understanding of population biology is necessary to establish a more ecological approach to pest management, integrating sustainable technologies such as host plant resistance and biological control (Suarez, 1999; Thomas, 1999; Coll *et al.*, 2000; Blom *et al.*, 2002). Furthermore, in order to have sustainable and profitable pest management strategies, it is essential to understand and work in harmony with nature's checks and balances (Lewis *et al.*, 1997; Rieux *et al.*, 1999; Matteson, 2000; Smeding & de Snoo, 2003). Recent findings have demonstrated that plants, herbivores and natural enemies are tightly entwined in ecological systems (Dicke, 1999; Walker & Jones, 2001; Stinchcombe, 2002), illustrating the importance of multitrophic interactions for effective pest management strategies (Vet & Dicke, 1992; Lewis *et al.*, 1997; Verkerk *et al.*, 1998; Norris & Kogan, 2000; Dicke *et al.*, 2003).

This chapter begins with the aims and objectives of the project. It then provides an introduction to cruciferous crops and the management of their most important pest, the diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae),

including the role of parasitoids in multitrophic context. There is then a more detailed review of tritrophic interactions, where key topics, such as induced plant defence, semiochemicals, foraging and host location behaviours of parasitoids, the insect immune system and population dynamics are discussed.

1.2 Aims and objectives

The overall aim of this study was to elucidate aspects of the behavioural and population ecology of DBM and its parasitoid *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae), especially those features that can be mediated by host plants. The specific objectives were: (1) to test the effects of bottom-up and top-down forces on diamondback moth population dynamics; here a long term experiment was set to test the effects of susceptible versus partially-resistant host plants on DBM and *C. plutellae* populations in a ditrophic (host plant-DBM) and a tritrophic (host plant-DBM- *C. plutellae*) system; (2) to study the olfactory behaviour of *C. plutellae* towards host plants and DBM; here a four-way olfactometer was used to test the preferences of *C. plutellae* for different host plants and complexes of host plants and DBM; (3) to determine if host-plant resistance can suppress the DBM immune system; here measures of encapsulation rate and phenoloxidase specific activity, the cellular and humoral effectors of immune system respectively, were used to determine the host-plant effects on the host immunity ; and (4) to model and analyse different tritrophic systems; here, four mathematical models with different (herbivore) feeding and (parasitoid) functional responses were formularised. Stability and bifurcations of the models were then examined analytically and numerically (by simulations in *Mathematica*) to explore the models' behaviours, seeking for possible periodic or chaotic behaviours.

1.3 Background

1.3.1 The diamondback moth: a specialist herbivore of crucifers

Crucifers are a morphologically diverse group of crop plants belonging to the mustard family (Cruciferae or Brassicaceae), a large family with over 3500 species in about 350 genera (Warwick *et al.*, 2004). Crucifers have great economic value worldwide as leafy, stored and processed vegetables (e.g. radish, cabbage, broccoli, turnip, cauliflower and

Brussels sprouts), condiment source (mustard), source of edible and industrial oil (rapeseed), animal fodder, green manure, ornamental species (e.g. sweet alyssum) and annual wildflowers and weeds that blanket so many landscape in spring and summer (Nieuwhof, 1969; Vaughn *et al.*, 1976; Tsunoda *et al.*, 1980; King, 2000). Cruciferous vegetables are particularly important crops in Asia as they form an essential part of the diet (Sivapragasam *et al.*, 1997). On a worldwide basis, the extent of harvesting area in year 2003 for cabbage, cauliflowers and mustard seed were about 3.18, 0.86 and 0.88 million hectares respectively (FAO, 2004).

Since 1980s, as interest in the use of animal oils and fats in food has declined, primarily through the impact of health concerns, it has been an intensification and diversification of vegetable oils (NNFCC, 2004). Between 1400 species of oil crops, brassica oilseed production has increased to become one of the most important world sources of vegetable oil (Kimber & McGregor, 1995a), with a global harvesting area of about 22.9 million hectares in year 2003 (FAO, 2004). Rapeseed oil is now the third (after soybean and palm oils) in world production of the principal vegetable oils (Kimber & McGregor, 1995b; NNFCC, 2004). Improvement in the quality of rapeseed (also called rape, oilseed rape or in some cultivars, Canola) oil (with low erucic acid) and meal (with high-protein) for animal feed have culminated in recognition of the oil as a nutritionally superior edible oil, and the meal as an important source for animal feeds (Kimber & McGregor, 1995a).

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), has become the most destructive insect pest of cruciferous plants throughout the world, the estimated annual management cost in the 1980s being US \$ 1 billion (Talekar, 1992). DBM feeds on commonly cultivated crops, such as cabbage, cauliflower, broccoli, radish, turnip, Brussels sprouts, Chinese cabbage, kohlrabi, mustard, rapeseed, collard, pak choi, saishin, watercress and kale as well as a large numbers of cruciferous weeds (Talekar & Shelton, 1993). DBM now occurs wherever crucifers are grown and it is believed to be the most universally distributed of all the Lepidoptera. Despite the numerous attempts made to manage this pest, outbreaks and poor control have been reported in many countries (Sivapragasam *et al.*, 1997).

One of the significant features of Brassicaceae is that most members of this family contain groups of sulfur-containing secondary metabolites called glucosinolates

(mustard oil glucosides) (Fahey et al., 2001). Glucosinolates and their metabolites are effective deterrents to generalist insect species, but are essential for specialists in host-plant selection (Kerfoot *et al.*, 1998; Renwick & Lopez, 1999; Lambdon *et al.*, 2003). Glucosinolates are amino acid-derived compounds, which are stored in the vacuoles of plant cells. Intact glucosinolates have limited biological activity, but following tissue damage and exposure to the endogenous plant myrosinase, a β -thioglucosidase, they are hydrolysed to a complex array of products, generally including thiocyanates, isothiocyanates or nitriles (van Loon *et al.*, 1992; Bones & Rossiter, 1996; Halkier & Du, 1997; Rask *et al.*, 2000). These hydrolysis products have diverse biological activity ranging from feeding deterrence for generalist insects to oviposition stimulation for specialists (Rask *et al.*, 2000; Ratzka *et al.*, 2002; Wittstock *et al.*, 2003). Nevertheless, they may also be toxic to crucifer specialists including DBM (Li *et al.*, 2000).

The glucosinolate-myrosinase system, also referred to as “the mustard oil bomb”, has long been suggested to be involved in the defence against herbivores due to the toxic nature of the released hydrolysis products (Bones & Rossiter, 1996). In crucifers, this system is thought to function as a first defence against a variety of invading organisms (Feeny, 1977). The glucosinolates and their isothiocyanate products in crucifers act as antibiotics, fungal growth inhibitors, toxins to nematodes, feeding deterrents to caddis flies, snails and amphipods (Fahey et al., 2001; Newman et al., 1992), deterrents and toxins against a wide range of generalist herbivores (Chew, 1988), and allelopathic compounds (Brown & Morra, 1997; Vaughn & Berhow, 1999). However, many insects have adapted to these defences, and several such species have become major and specialised pests of crucifers. These insects have either developed a way of handling the plants defence system (e.g. rapid excretion, hydrolysis of the glucosides, or sequestering the glucosinolates) or they manage to avoid triggering it (e.g. inhibition of hydrolysis by protective enzymes) (Schoonhoven *et al.*, 1998; Aliabadi & Whitman, 2001; Müller *et al.*, 2001; Müller *et al.*, 2002).

Although the glucosinolate-myrosinase system in crucifers is activated by insect attack (Bernays & Chapman, 1994; Bones & Rossiter, 1996; Pontoppidan *et al.*, 2003), crucifer specialists often use the glucosinolates or isothiocyanates as positive cues for host-plant recognition (Schoonhoven, 1972; Chew, 1988). The isothiocyanates may serve to attract specialist insects to their hosts, whereas the glucosinolates often trigger

oviposition or feeding after an insect lands on the plant (Renwick *et al.*, 1992; van Loon *et al.*, 1992; Chew & Renwick, 1995; Mewis *et al.*, 2002; Marazzi & Stadler, 2004; Marazzi *et al.*, 2004). This close association of crucifer specialists with these compounds has evolved into a type of chemically-dependent host-plant location and acceptance based on perception of volatile isothiocyanates and contact with glucosinolates, respectively (Renwick, 2002). For example, oviposition of *Pieris rapae* depends on glucosinolates at the leaf surface (van Loon *et al.*, 1992; Renwick *et al.*, 1992). *P. rapae* neonate larvae are able to feed in the absence of glucosinolates, but after feeding experience on the diet containing these compounds, they refuse to feed unless glucosinolates are present (Renwick & Lopez, 1999).

Glucosinolates have been prominently considered in the evolution of chemical defences of cruciferous plants against herbivores, pathogens and weeds (Agrawal *et al.*, 2002; Shelton, 2004; Wittstock *et al.*, 2004). With regard to herbivores, glucosinolates are proposed to act primarily as qualitative and quantitative chemical defences against non-adapted generalist herbivores. In contrast, specialist herbivores, such as DBM, are not sensitive to variation in the glucosinolate-myrosinase system, being able to overcome this host-plant chemical defence, even to the point of using them as feeding and oviposition stimulants (Bodnaryk, 1991; Giamoustaris & Mithen, 1995; Hopkins *et al.*, 1998; Lambrix *et al.*, 2001; Kliebenstein *et al.*, 2002).

Glucosinolates and glucosides have been reported as oviposition and feeding stimulants for DBM, respectively (Talekar & Shelton, 1993; Siemens & Mitchell-Olds, 1998). DBM has shown highly dependent on glucosinolates to recognize the host plant for oviposition (Reed *et al.*, 1989). While allyl isothiocyanate is a volatile secondary substance that attracts DBM to the host plant (Gupta & Thorsteinson, 1960). In addition, an optimal amount of allyl isothiocyanate, which is generally an inhibitory substance to most generalist herbivores, serves as an oviposition stimulant to DBM (Olsson & Jonasson, 1994). DBM is able to disarm glucosinolate-myrosinase system of crucifers by using glucosinolate sulfatase, which largely prevents the formation of toxic hydrolysis products arising from this plant defence system. The enzyme acts on all major classes of glucosinolates, enabling DBM to use a broad range of cruciferous host plants (Ratzka *et al.*, 2002).

1.3.2 Diamondback moth management: the role of parasitoids in a multitrophic context

The overuse of insecticides against DBM has led to several problems such as insecticide resistance in many field populations of diamondback moth (Leibee & Savage, 1992; Abro *et al.*, 1993; Kuwahara *et al.*, 1995; Leibee & Capinera, 1995; Iqbal & Wright, 1997; Verkerk & Wright, 1997; Perez *et al.*, 2000; Ninsin *et al.*, 2000; Mohan & Gujar, 2003; Ninsin & Miyata, 2003). There is also concern about insecticide residues on the crop and in the environment, and the deleterious effects of synthetic insecticides on natural enemies leading to pest resurgence (Furlong & Wright, 1993; Ivey & Johnson, 1998; Shelton *et al.*, 2000; Branco & Medeiros, 2001; Xu *et al.*, 2001; Boone *et al.*, 2004; Ding *et al.*, 2004; Haseeb *et al.*, 2004; Xu *et al.*, 2004). Resistance to synthetic pesticides has led to the development of integrated pest management (IPM) system based on biocontrol technologies including parasitoid wasps and *Bt* sprays (Chilcutt & Tabashnik, 1997; Ivey & Johnson, 1998; Chilcutt & Tabashnik, 1999; Schuler *et al.*, 2003). However, DBM has now developed resistance to *Bt* in the field (Iqbal *et al.*, 1996; Tabashnik *et al.*, 1996; Perez & Shelton, 1997; Gonzalez-Cabrera *et al.*, 2001; Sayyed *et al.*, 2003). Thus, alternative and more sustainable methods are needed urgently to control DBM (Talekar & Shelton, 1993; Verkerk & Wright, 1996b; Verkerk & Wright, 1997; Schuler *et al.*, 2003; Reddy *et al.*, 2004).

With reference to host-plant resistance, *Brassica* plants with glossy-wax leaves have shown some resistance to DBM in comparison with those with normal-wax leaves (Eigenbrode *et al.*, 1991; Eigenbrode & Shelton, 1992; Verkerk & Wright, 1996a; Eigenbrode & Pillai, 1998; Ulmer *et al.*, 2002). In other words, the available host plants (normal-wax leaved) just are partially resistant, and the highly resistant host plants (glossy-wax leaved) are not commercially available because of lack of marketability. Host-plant resistance is not therefore a viable method if used alone because of its inadequate control. However if partially resistant host plants can be used in combination with other methods such as biological control pest damage can be minimized (Endersby & Morgan, 1991; Verkerk & Wright, 1996b; Eubanks & Denno, 2000; Stout *et al.*, 2002; Braman *et al.*, 2003; Schmale *et al.*, 2003; Marley *et al.*, 2004). Regarding *Bt* plants, there is concern for their environmental impact, such as the fate of *Bt* insecticidal proteins (Cry toxins) in the environment, their direct and indirect effects on natural

enemies and non-target organisms, and their out-crossing with the risk of horizontal gene transfer to other organisms (Sharma & Ortiz, 2000; Shelton *et al.*, 2002). Biological control alone is probably insufficient to reduce DBM populations to an acceptable level and is better as a component of IPM programmes (Gonzalez-Rodriguez & Macchiavelli, 2003; Guilloux *et al.*, 2003). Consequently, particular attention should be given to the compatibility of partial plant resistance and biological control (Verkerk *et al.*, 1998; Krips *et al.*, 1999; Schmale *et al.*, 2003).

Since parasitoids may play an important role in regulating diamondback moth populations, introduction and conservation of parasitoids will be basic to any sustainable IPM programme (Biever *et al.*, 1992; Talekar & Shelton, 1993; Iga, 1997; Mitchell *et al.*, 1999; Martinez-Castillo *et al.*, 2002; Miura, 2003; Wang *et al.*, 2004). Over 90 parasitoid species are reported to attack DBM and about 60 of them appear to be important (Goodwin, 1979; Talekar & Shelton, 1993; Kfir, 1997). Among the latter six species attack DBM eggs, 38 attack larvae and 13 attack pupae (Lim, 1986; Talekar & Shelton, 1993). The most predominant and effective parasitoids are larval parasitoids, many of which are relatively host specific and belong to two genera, *Diadegma* (Ichneumonidae) and *Cotesia* (= *Apanteles*) (Braconidae) (Talekar & Shelton, 1993). The solitary endolarval parasitoids, *Cotesia plutellae* (Kurdjumov) and *Diadegma semiclausum* (Hellen), are key natural enemies (Waterhouse & Norris, 1987; Mushtaque & Mohyuddin, 1987; Noda *et al.*, 1996; Liu *et al.*, 2000; Wang *et al.*, 2004). They have shown some success in controlling DBM populations in Southeast Asia and provide a model for the basics of a successful IPM program (Ooi, 1992; Talekar & Shelton, 1993; Verkerk & Wright, 1997).

Parasitoids of herbivores have evolved and function within a multitrophic environment (Dicke & van Loon, 2000; Hilker & Meiners, 2002; Gentry, 2003; Montoya *et al.*, 2003). Their physiology and behaviour are thus influenced by elements from other trophic levels particularly their host and its plant food. Parasitoids base their foraging decisions on information from these different trophic levels and chemical information plays an important role (Vet & Dicke, 1992; Dicke *et al.*, 2003). It is evident that in a tritrophic system the different components (plants, herbivores and parasitoids) are tightly interwoven, clarifying the importance of multitrophic perspectives for the effective and sustainable pest management strategies (Lewis *et al.*, 1997). In this regard,

a multitrophic approach to research may assist in the development of more sustainable methods to manage DBM populations (Verkerk & Wright, 1996b; Roy & Pell, 2000).

1.4 Tritrophic (host plant-herbivore-natural enemy) interactions

In a significant paper, Price *et al.* (1980) introduced the theory of plant-herbivore-enemy (three trophic levels) interactions. At that time several areas of theoretical ecology, including theories of plant chemical defence and food webs, and models of insect population dynamics had covered the relationships between plants, herbivores and natural enemies but not in the same context. Price *et al.* (1980) declared that plant-herbivore (ditrophic) interactions without understanding the role of natural enemies (third trophic level) or prey-predator (ditrophic) interactions without understanding the role of plants (first trophic level) could not be realized. They discussed the effects of plant individuals, populations and communities on higher trophic levels, stating a basic position for plants in tritrophic system.

In their reviews of tritrophic interactions, Price (1986) and Thomas & Waage (1996) categorised the factors involved in tritrophic interactions between host plant, insect herbivore and natural enemy into three main areas: (1) semiochemically-mediated interactions, (2) chemically-mediated interactions, and (3) physically-mediated interactions. In the present chapter only semiochemically- and chemically-mediated interactions will be reviewed.

1.4.1 Semiochemically-mediated interactions

The term “semiochemicals” proposed by Law & Regnier (1971) refers to chemicals that mediate interactions between organisms from either the same or different species. Vet & Dicke (1992) put forward a new term, “infochemicals”, which means information-conveying chemicals, as a sub-category of semiochemicals. They remarked that infochemicals convey information between two individuals, evoking a behavioural or physiological response in the receiver. Semiochemicals are classified into pheromones and allelochemicals, which mediate intraspecific and interspecific interactions, respectively (Nordlund, 1981). Allelochemicals have an important role in tritrophic

interactions, inducing different behavioural responses in the receiver organism. If the response is adaptively favourable to only the first organism (releaser) or to the second organism (receiver), or to both organisms, the allelochemical will be named allomone, kairomone and synomone, respectively (Vet & Dicke, 1992). Apart from these major groups of allelochemicals, Nordlund (1981) quoted another sub-group, apneumones, which refer to the allelochemicals that emanate from a non-living material and benefit the receiver organism but are detrimental to the organism being found in or on the non-living material. Whitman (1988) included another group, antimones, which refer to substances that evoke a behavioural or physiological response being detrimental to both emitter and receiver.

1.4.1.1 Insect-plant interactions and induced plant defences

In response to herbivory, plants release volatile compounds (semiochemicals), which act as an airborne signal, revealing the presence of the herbivore to its natural enemies (Chadwick & Goode, 1999; van Tol *et al.*, 2001; Hilker & Meiners, 2002; Lou & Cheng, 2003). For example, Brussels sprouts attacked by *Pieris brassicae* larvae release volatiles that attract the parasitoid *Cotesia glomerata* to the damaged plants (Mattiacci *et al.*, 2001). Females of *Roptrocerus xylophagorum* (Ratzeburg), a larval-pupal parasitoid of bark beetles, *Ips grandicollis* Eichhoff (Coleoptera: Scolytidae), showed attractive to infested bark of loblolly pine but not to uninfested one (Sullivan *et al.*, 2000). There were quantitative differences in volatile composition between infested (by bark beetle, *Ips typographus*) and uninfested logs of Norway spruce, *Picea abies* (Pettersson & Boland, 2003).

The quantity and the quality (composition) of the volatile emissions both are important for attraction of natural enemies (Hoballah *et al.*, 2002). The composition of allelochemicals often differs with different plant species or cultivars. However, for the same plant species, those are under herbivore attack produce a greater quantity and variety of volatiles in comparison with intact ones (Geervliet *et al.*, 1997; Gouinguene *et al.*, 2001). Quantitative differences in volatiles mainly arise from different kind of damage to plant (uninfested, herbivore-infested, or mechanically-damaged) or different stages of plant (Steinberg *et al.*, 1993; Pettersson & Boland, 2003).

The blend of semiochemicals released by the plant can vary subtly with the species of herbivore damaging the plant and differs from the mixture released upon purely mechanical damage (Mattiacci *et al.*, 1994; Geervliet *et al.*, 1997; Tumlinson *et al.*, 1999). This specificity is important because in order for the signals to be effective to recruit the natural enemies of the herbivore, invalid signals must be avoided (Chadwick & Goode, 1999; Pettersson *et al.*, 2000). For instance, females of *Cotesia plutella*, a parasitoid of diamondback moth, preferred the odour of host-infested host plants to non-infested, artificially damaged and nonhost-infested host plants (Bogahawatte & Van Emden, 1996; Shiojiri *et al.*, 2000a,b). The parasitic wasp *Trogus pennator* (Hymenoptera: Ichneumonidae) preferred plants damaged by host larvae, genera *Eurytides* and *Papilio* (Lepidoptera: Papilionidae), to plants damaged by non-host (saturniid) larvae (Sime, 2002).

Plants distinguish between mechanical and feeding damage because of the presence of herbivore oral secretions, which contain a group of compounds called elicitors. It is thought that the presence of particular elicitors in herbivore secretions causes the subtle changes in volatile profile, which allow highly specific natural enemies to locate their prey accurately (Chadwick & Goode, 1999). For example, N-(17-hydroxylinolenoyl)-L-glutamine (or volicitin), which isolated from the regurgitant of *Spodoptera exigua* larvae, is an elicitor of maize volatiles (terpenoids) that are highly attractive to the parasitoid *Microplitis croceipes* (Turlings *et al.*, 2000).

Herbivore-induced volatiles are not just released by the parts of the plant under attack but also by undamaged parts of the plant (Mattiacci *et al.*, 2001; Pickett *et al.*, 2003). The basis of this phenomenon is the exquisitely sensitive molecular recognition of semiochemicals by the natural enemies (Chadwick & Goode, 1999).

1.4.1.2 Role of allelochemicals in host location

Successful parasitism depends on the following factors: (a) host habitat location, (b) host location, (c) host acceptance, (d) host suitability and (e) host regulation. Factors a-c, which form the host selection process, can be sub-divided in seven stages: habitat preference, potential host community location, host location, host examination, ovipositor probing, ovipositor drilling, and oviposition (Vinson, 1984; Lauziere *et al.*,

2000; Zhang & Schlyter, 2004). Allelochemicals appear to play a major role at almost every level of the host selection process. Parasitoids learn to respond to the different allelochemicals to indicate the location of their hosts (Noldus, 1989; Lewis & Martin, 1990; Mattiacci *et al.*, 2000; Zhang & Schlyter, 2003; Zhang *et al.*, 2003).

The searching efficiency of parasitoids is basic to the host-parasitoid population dynamics, the evolution of host and parasitoid behaviour, and in biological control programmes (Bottrell *et al.*, 1998; Vet, 2001; Gingras & Boivin, 2002; Schellhorn *et al.*, 2002). Female parasitoids respond to a hierarchy of physical and/or chemical stimuli leading them to their potential host. When parasitoids forage for hosts, they use a great amount of chemical information (Vet & Groenewold, 1990; Lewis *et al.*, 1991; Tumlinson *et al.*, 1993; Erbilgin & Raffa, 2001; Olson *et al.*, 2003a,b). The efficiency of the strategies used by these insects to locate their potential host depends on type of cues (semiochemicals) provided by the host or its environment (Vinson, 1984; Lewis & Martin, 1990; Vet & Groenewold, 1990; Tumlinson *et al.*, 1993; Schofield *et al.*, 2002; Darwish *et al.*, 2003; Takasu & Lewis, 2003). For instance, ectoparasitoids *Tiphia vernalis* Rohwer and *Tiphia pygidialis* Allen (Hymenoptera: Tiphidae) located their host larvae, the Japanese beetle *Popillia japonica* Newman and masked chafers *Cyclocephala* spp. (Coleoptera: Scarabaeidae), using contact kairomones present in grub body odour trails and frass (Rogers & Potter, 2002). On the contrary, *Pholetesor bicolor*, a larval parasitoid of the apple leafminer, *Phyllonorycter pomonella*, did not rely on host-derived kairomones but used plant-derived semiochemicals for host location behaviour (Dutton *et al.*, 2000). In addition, although the parasitoid *Aphidius* sp. showed responsive to kairomones from tea aphid *Toxoptera aurantii* and to synomones released by aphid-damaged tea shoots, the interaction between synomones and kairomones enhanced the responses to the plant-host complex (Han & Chen, 2002).

Parasitoid host location consists of a series of behaviours, being influenced by information from the surroundings. Female parasitoids have to search different plants or varied plant habitats to find their hosts. In this regards, various allelochemicals are involved, which vary with the distance from the host at which they are active (Lewis & Martin, 1990). The allelochemicals that act at long range may only convey information indicating a habitat likely contains suitable hosts (Molck *et al.*, 2000; Neveu *et al.*, 2002; Sullivan & Berisford, 2004). As the parasitoid gets closer to the host, host or the

host plant produce the allelochemicals, which act at short range and convey information on the availability and location of the host (Vet & Groenewold, 1990; Morehead & Feener, 2000; Schaffner & Muller, 2001). For example, as far as long-range host location was concerned, in comparison to uninfested host plants, *Pieris brassicae* larvae and faeces were more attractive to the larval parasitoid *Cotesia glomerata*. However, artificially-damaged and herbivore-damaged plants were much more attractive than host larvae and faeces. In addition, the plant-host complex, with host larvae actively feeding on the plant, was the most attractive odour source for the parasitoid (Steinberg *et al.*, 1993; Mattiacci *et al.*, 1994). *C. glomerata* were also attracted by infochemicals from the host plant containing nonhost herbivores (Geervliet *et al.*, 1996; Vos *et al.*, 2001). In short-range, *C. glomerata* was able to discriminate between first (which are more suitable hosts) and fifth (which are very risky hosts) larval instars of *P. brassicae* without contacting the caterpillars, through exploiting instar-related cues, which are contacted after arrival at a caterpillar-infested leaf (Mattiacci & Dicke, 1995a), including cues on the margin of the feeding damage and cues in the host frass and silk (Mattiacci & Dicke, 1995b).

1.4.1.3 Specificity (detectability versus reliability) of signals

Parasitoids require signals in order to detect suitable hosts over large distances and indicate reliably the presence of a host (Vet & Dicke, 1992; Hoffmeister & Gienapp, 1999; Wertheim *et al.*, 2003). Kairomones from the host or its frass have been shown to be more reliable than synomones from the plant (Dicke, 1994; Smith *et al.*, 1994; Fujiwara *et al.*, 2000; Darwish *et al.*, 2003; Colazza *et al.*, 2004a; Mbata *et al.*, 2004). Kairomones are closely associated with the presence of a host, whereas synomones from the plant may persist after the host has left the plant (Lou & Cheng, 2001; Benedet *et al.*, 2002; Colazza *et al.*, 2004b). Furthermore, kairomones tend to be more specific for the host species and even for the host developmental stage (Aldrich & Zhang, 2002; Romani *et al.*, 2002; Borges *et al.*, 2003; Conti *et al.*, 2003). For example, *Microplitis rufiventris*, a larval parasitoid of *Spodoptera littoralis*, which can only successfully parasitize second and early third instar *S. littoralis* larvae, was attracted to the herbivore-induced synomones emitted from maize plants. However, the parasitoid was not able to differentiate between the odours (with small difference in phenethyl acetate

and alpha-humulene) of maize plants attacked by different instar larvae (Gouinguene *et al.*, 2003).

Specificity is essential in order to avoid wasting time and energy of parasitoids searching for the wrong host species or developmental stages (Vet & Dicke, 1992; Conti *et al.*, 2004; Morrison & King, 2004). Specific host signals are used more in the microhabitat around the host because of their limited detectability. In contrast, herbivore-induced synomones are more long-range because of their production in large amounts but are less reliable (Dicke, 1994; Wertheim *et al.*, 2003). Synomones are more distinguishable between different plant species than between different herbivores on the same plant (Turlings *et al.*, 1995; Micha *et al.*, 2000). The effects of feeding by several herbivores on the same plant species mainly result in quantitative differences in the synomone bouquet; although it can cause qualitative differences such as the production of different compounds (Turlings *et al.*, 1995; Smid *et al.*, 2002). The ratio of compounds in a herbivore-induced bouquet changes depending on the herbivore. However, the exact combinations of chemicals and their ratio that act to attract specific parasitoids are still unknown (Dicke, 1994).

The quantity of synomones released may simply be a result of the amount of pest damage (Colazza *et al.*, 2004a). Whereas differences in regurgitates of different species are most likely to induce qualitatively different synomones (Thompson, 1996). For example, females of the larval parasitoid *Cotesia glomerata* (L.) use plant-associated cues to locate their host, *Pieris rapae* L. The parasitoids were attracted to host plant species differentially, but they did not discriminate among host larvae based on the dietary history of their hosts (Benrey *et al.*, 1997). In long range, *Cotesia glomerata* was not able to discriminate between plants infested by different host species (*Pieris brassicae*, *P. rapae*, *P. napi* and *Aporia crataegi*), not even between plants infested by host and non-host species (*Plutella xylostella* and *Mamestra brassicae*) (Geervliet *et al.*, 1996; Vos *et al.*, 2001; Perfecto & Vet, 2003). However, *C. glomerata* can discriminate between different larval instars of *P. brassicae* through the short-range semiochemicals (Mattiacci & Dicke, 1995a). The volatile emitted from cabbage plants infested by *P. brassicae* and *P. rapae* showed mainly quantitative difference. However, herbivore-induced volatiles from cabbage varieties and nasturtium differed considerably in a qualitative way (Geervliet *et al.*, 1997).

Consequently, herbivore-induced synomones are important signals in long-range host-searching of parasitoids mainly because of their detectability. They may contain enough information to be specific for certain hosts. However, other cues such as kairomones and visual cues, increase the specificity once the parasitoid has reached the microhabitat of the host (Thompson, 1996).

1.4.1.4 Role of learning in foraging

Learning is an important source of behavioural variability in foraging natural enemies (Vet & Dicke, 1992; Kaiser *et al.*, 2003; Olson *et al.*, 2003a). Responses to chemical and visual cues change with experience (Keasar *et al.*, 2001; Takasu & Lewis, 2003). Learning to respond to cues can be adaptive when the environment is unpredictable between generations but predictable during the parasitoid's lifetime. In general, parasitoids are able to learn in confronting an environment that varies in a regular and predictable way (Vet & Dicke, 1992; Kaiser *et al.*, 2003; Olson *et al.*, 2003b).

Parasitoids that forage for herbivore hosts by using infochemicals may have a problem concerning the reliability and detectability of these stimuli (see Section 1.4.1.3). In other words, host stimuli are highly reliable in indicating host presence, accessibility and suitability but are generally hard to detect at a distance, while stimuli from the host plants are very detectable but are generally less reliable as indicators (Vet *et al.*, 1991; Wiskerk & Vet, 1994; Guerrieri, 1997; Sime, 2002; Wang & Messing, 2003). Parasitoids have evolved different non-exclusive strategies to solve this problem including: (1) using infochemical detour; in this action parasitoids resort to chemical information from other, more detectable, host stages than the one under attack (Vet *et al.*, 1991; Wiskerk *et al.*, 1993; Buitenhuis *et al.*, 2004); (2) using herbivore-induced synomones; parasitoids can use specific plant volatiles that are released upon damage by a specific herbivore species (Powell & Pickett, 2003; Steidle & van Loon, 2003; Colazza *et al.*, 2004b); and (3) associative learning; parasitoids are able to link easy-to-detect stimuli to reliable but hard-to-detect stimuli through associative learning (Kaiser *et al.*, 2003; Meiners *et al.*, 2003; Bleeker *et al.*, 2004).

Associative learning is a major solution to the reliability-detectability problem in foraging parasitoids. The responses of parasitoids to cues are mainly modified through

the process of associative learning (Fukushima *et al.*, 2001; Hu & Mitchell, 2001). Through associative learning parasitoids innately recognize host-derived stimuli (unconditioned stimuli) upon contact, and associate these stimuli with surrounding stimuli (conditioned stimuli) to which it originally shows no or limited responsiveness (Guerrieri *et al.*, 1997; Takasu & Lewis, 2003). Subsequently, by linking highly detectable cues to highly reliable cues through associative learning, parasitoids may temporarily increase the reliability of the detectable indirect cues, and become responsive to the newly learned stimuli and use them in their searches for hosts (Vet *et al.*, 1991; Turlings *et al.*, 1993; Vet *et al.*, 1995; Fukushima *et al.*, 2002). For example, an oviposition experience on an infested banana by female *Leptopilina boulardi*, a larval parasitoid of frugivorous *Drosophila spp.*, resulted in responses of *L. boulardi* females to the learned odour (the fruit odour) alone through associative learning (Couty *et al.*, 1999). Flight responses of female *Cotesia kariyai*, a specialist endolarval parasitoid of the common armyworm *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), to the infested plant were increased after searching experience on a host-infested corn plant. When the females experienced only the host by-products or the infested leaf volatiles, the successive responses did not change. However, females experience on the host by-products together with the infested leaf volatiles resulted in an increased response (Fukushima *et al.*, 2001).

For larval parasitoids, there are implications for the value of learning depending on individuals to be time-limited or egg-limited (Garcia *et al.*, 2001; Zijp & Blommers, 2002; Tylianakis *et al.*, 2004). Under time-limited conditions, the host encounter rate is more important than finding a better host (De Vis *et al.*, 2003). In this situation, any predictable environmental cue, mostly plant-derived, is expected to be learned as long as its use increases the host encounter rate. These cues can be rather general, indicating merely host presence, not suitability (Vet *et al.*, 1995). Whereas, egg-limited parasitoids have stronger selection on fitness gain per host and therefore also on investment in quality, especially when the lifetime number of eggs is small (Godfray, 1994; Heimpel & Rosenheim, 1998). In other words, the preference is to obtain the specific and therefore reliable information about the presence of suitable host (Getz & Mills, 1996). As a result, in this situation, learning may be of less importance, because the parasitoid needs to rely more on innate responses to reliable host-derived cues to avoid making

mistakes. Time and egg limitations are probably a characteristic of a foraging individual rather than of a species (Vet *et al.*, 1995).

Many parasitoids, particularly larval parasitoids, function within a tritrophic context and their foraging strategy can be formed by information from both the first and second trophic level (Olson *et al.*, 2003a; Takasu & Lewis, 2003). The degree of specificity at trophic levels can influence the variability that parasitoids encounter both over generations and within their foraging life (Vet & Dicke, 1992; Meiners *et al.*, 2002). Hence, dietary specialization is expected to be an ecological factor setting specific values for learning, as learning of semiochemicals for foraging occurs frequently in generalist carnivores and rarely in specialists (Vet *et al.*, 1995; Gandolfi *et al.*, 2003; Steidle & van Loon, 2003). To illustrate, the differential effect of experience on the host-finding behaviour of two closely related parasitoids *Cotesia glomerata* and *C. rubecula*, which overlap in niche, can be exemplified. At both host and host-plant levels, *C. glomerata* and *C. rubecula* are considered as generalist and specialist, respectively (Shenefelt, 1972; Laing & Levin, 1982). The pierid hosts of *C. glomerata* feed mainly on cruciferous food plants, but also on the plants from the families Tropaeolaceae, Rosaceae and Berberidaceae. However, preferred host plants of host of *C. rubecula* are restricted to plant species that contain glucosinolates (Terofal, 1965; Feltwell, 1982; Tax, 1989). After multiple experiences with host larvae, female *C. glomerata* showed a clear preference for volatiles from *Pieris brassicae*-infested Brussels sprouts leaves over *P. rapae*-infested Brussels sprouts leaves. On the contrary, female *C. rubecula* did not show any preference for *P. rapae* or *P. brassicae* damaged leaves regardless the type of experience (Geervliet *et al.*, 1998).

1.4.2 Chemically-mediated interactions: effects of food plant status of herbivores on their parasitoids

Effects of host-plant quality on natural enemies may be positive (compatible) or negative (incompatible). Negative interactions between poor quality/partially-resistant host plant and natural enemy may occur when this poor nutritional status affects antagonistically parasitoid life history (Godfray, 1994; Verkerk *et al.*, 1998). It also can happen when feeding on acceptable but nutritionally inferior host plants result in an

increased survival of parasitized host (Singer & Stireman, 2003), because of negative effects of sequestered secondary metabolites in host body tissues on parasitoid larva (Bowers, 1993; Weller *et al.*, 1999). Here, the two most important chemically-mediated, compatible interactions between host plants and parasitoids (i.e. slow-growth-high-mortality and reduced host cellular defence hypotheses) will be considered in next sections.

1.4.2.1 Host developmental period and parasitism risk

Host-plant characteristics may influence the herbivore's developmental rate, and indirectly benefit natural enemies (Godfray, 1994; Haggstrom & Larsson, 1995). Variation in nutritional quality of host plant cause a different growth rate of herbivores feeding on these plants (Chown & Block, 1997; Pereyra & Sanchez, 1998). Because most herbivorous insects have a vulnerable stage to parasitism, and development of herbivores on a plant with weak nutritional status takes a longer time, parasitoids can take advantage of longer exposure to this prolonged stage. This has known as the theory of "slow-growth-high-mortality" (Clancy & Price, 1987; Benrey & Denno, 1997). For example, *Cotesia glomerata*, a larval parasitoid of cabbage butterfly *Pieris rapae*, prefer to oviposit in first two instars of host larvae, because of high rate of encapsulation in third and higher instars (Brodeur & Vet, 1995). On the host plant species on which larval development was delayed, the window of vulnerability (time spent in the first two larval instars) was prolonged, and rates of parasitism was increased (Benrey & Denno, 1997).

1.4.2.2 Host immune function and parasitism success

The control potential of combining partial plant resistance with biological control relies on the assumption that biological control will be greater on resistant compared with susceptible host-plant varieties (Verkerk *et al.*, 1998; van Emden, 1999). Tritrophic interactions between the host plant, insect herbivore and natural enemy, affecting the immunity of insect pests to natural enemies, may explain some effects of host plants on host-parasitoid relationship (Blumberg, 1997). Thus, plant nutrients and resistance may influence defence of herbivores against natural enemies, parasitoids benefiting from

developing in a suboptimal (e.g. nutritionally deficient) host less capable of mounting an immune defence (Godfray, 1994; Price 1986; Thomas & Waage, 1996; Calatayud *et al.*, 2002).

1.4.2.2.1 *Insect immune system*

The immune system is the primary internal defence of insects toward parasitoids (Strand & Pech, 1995; Ponnuvel & Yamakawa, 2002; Brown *et al.*, 2003; Dimopoulos, 2003). The insect immune reaction involves humoral and cellular responses, overall immunity resulting from a complex interplay of the two systems (Gillespie *et al.*, 1997; Bulet *et al.*, 1999; Lavine & Strand, 2002; Brivio *et al.*, 2004). Cellular immune reactions include haemocyte-mediated responses such as phagocytosis, nodulation (nodule formation) and encapsulation (Bulet *et al.*, 1999; Lavine & Strand, 2002). In contrast, humoral immune responses refer to synthesis of antimicrobial peptides (Meister *et al.*, 2000; Lowenberger, 2001), production of reactive nitrogen and oxygen intermediates (Bogdan *et al.*, 2000; Hao *et al.*, 2003) and activation of proteinase cascades such as the blood clotting system (Muta & Iwanaga, 1996) and the prophenoloxidase activation system (Ashida & Brey, 1997; Soderhall & Cerenius, 1998). Here, only cellular responses and phenoloxidase cascade has been taken into consideration.

Phagocytosis refers to the engulfment of biotic (like bacteria, yeast and apoptotic bodies) or small abiotic (like synthetic beads) targets by an individual haemocyte, which is a granular cell or plasmatocyte in Lepidoptera and mainly plasmatocyte in *Drosophila* (Yokoo *et al.*, 1995; Lavine & Strand, 2002). On the contrary, nodulation and encapsulation are complex processes starting by binding of haemocytes to the target, resulting in formation of an overlapping sheath of haemocytes (which are granular cells or plasmatocytes in Lepidoptera and lamellocytes in *Drosophila*) around the target. However, the target in nodulation is aggregations of bacteria, while encapsulation act against larger targets like parasitoid eggs and larvae, nematodes and chromatography beads (Gillespie *et al.*, 1997; Schmidt *et al.*, 2001; Lavine & Strand, 2002). In some insect species, nodules and capsules melanize due to activation of phenoloxidase (Strand & Pech, 1995).

Encapsulation is a common reaction against foreign invaders, and plays a major role in the insect defence against parasitoids (Nappi & Vass, 1993; Strand & Pech, 1995; Stettler *et al.*, 1998; Beerntsen *et al.*, 2000). Encapsulation may require coordination of both cellular and humoral factors, and proceeds as a biphasic process (Cox-Foster & Stehr, 1994; Pech & Strand, 1996). The first step is recognition of the foreign invader by haemocytes (Lackie, 1988; Gillespie *et al.*, 1997). The recognition of intruder occurs either directly through interaction between surface receptors on haemocytes and molecules on the invading organism or indirectly through recognition of humoral receptors, which bind to the surface of the invader and opsonize it (Lavine & Strand, 2002). The second is the formation of a hard, melanized capsule by concentric layers of flattened haemocytes (Kanost *et al.*, 2004; Yu & Kanost, 2004). It is thought that the capsule restricts encapsulated invader metabolism by the production of oxygen radicals or restriction of nutrients resulting in death. Furthermore, lysis of host cells at the capsule-invader interface is thought to release cytotoxic molecules (Gotz and Boman, 1985).

For example, immune reactions against foreign invaders attacking the greater wax moth *Galleria melonella* have been well studied (Blumberg & Ferkovich, 1994; Thurston *et al.*, 1994; Gillespie *et al.*, 2000; Brivio *et al.*, 2004). Regarding cellular events, once foreign invaders such as parasitoid eggs/larvae, fungal spores, nematodes or foreign tissue implants enter the haemocoel of *G. melonella* larvae, granulocytes adhere to the foreign invader and degranulate (Ratcliffe and Gagen, 1977; Cox-Foster & Stehr, 1994; Vey *et al.*, 2002). The prophenoloxidase cascade is then activated (see section 1.4.2.2.2). Finally, plasmatocytes adhere and flatten on melanizing granulocytes-invader mass, where granulocytes have lysed next to the foreign tissue, completing the capsule (Schmit and Ratcliffe, 1977; Slepneva *et al.*, 1999; Whitten *et al.*, 2004). Despite important role in multicellular encapsulation, plasmatocytes also act as phagocytic (Ratcliffe, 1993). *G. melonella* also shows an humoral immune response measurable as antibacterial activity in cell-free haemolymph (Wiesner, 1992; Griesch *et al.*, 2000; Vilcinskas & Wedde, 2002; Kavanagh & Reeves, 2004).

1.4.2.2.2 Enzymes linked to encapsulation

The best-known enzyme associated with the encapsulation response is phenoloxidase (Cox-Foster & Stehr, 1994; Cerenius & Soderhall, 2004; Kanost *et al.*, 2004). It is a copper-containing enzyme that catalyzes two kinds of reactions, oxygenation of monophenols to *o*-diphenols and oxidation of *o*-diphenols to *o*-quinones, which are key steps in the synthesis of the black pigment, melanin (Ashida & Brey, 1997). This enzyme is present in the insect cuticle, midgut and haemolymph and is thought to play a role in pigment formation, sclerotization, wound healing and defence reactions against foreign matters entering the haemocoel (Wilson *et al.*, 2001; Cotter & Wilson, 2002). The phenoloxidase in insect haemolymph is present as a proenzyme, prophenoloxidase, which is spontaneously activated when haemolymph is collected (Ashida & Yamazaki, 1990). Prophenoloxidase has been shown to be activated through the action of the prophenoloxidase cascade or prophenoloxidase activating system (Fabrick *et al.*, 2004; Garcia *et al.*, 2004). Insect phenoloxidases, indeed, seem to be synthesized as inactive zymogens and their activation is finely tuned developmentally and in response to traumatic stress and microbial invasion (Ashida & Yamazaki, 1990; Sugumaran & Kanost, 1993; Ashida & Brey, 1997). This cascade is triggered by microbial cell-wall components, such as bacterial lipopolysaccharide, lipoteichoic acid and peptidoglycan, and fungal β -1,3-glucans, and is considered to be an integral part of insect defence systems (Ashida & Brey, 1997; Yu *et al.*, 2002; Cerenius & Soderhall, 2004; Jiang *et al.*, 2004; Lee *et al.*, 2004).

The prophenoloxidase cascade is proposed to play an important role in the encapsulation of parasitoid eggs (Stoltz & Guzo, 1986; Ashida & Yamazaki, 1990; Armitage *et al.*, 2003; Wilson *et al.*, 2003) and is also a part of the insect recognition system of foreign invader, which is the first step in the insect immune system (Ashida & Brey, 1997; Asgari *et al.*, 2003; Jiang *et al.*, 2003; Yu *et al.*, 2003). It is present in both plasma and haemocyte lysate supernatant but the activation of the cascade *in vivo* seems to take place mainly in plasma (Ashida & Brey, 1997; Park & Kim, 2003; Yu & Kanost, 2003).

Phenoloxidase, dopachrome isomerase and quinone isomerase work together to form melanized and physically rigid (sclerotized) layers around foreign objects invading

insects (Shelby *et al.*, 2000; Sugumaran *et al.*, 2000a,b; Sugumaran, 2002). Dopachrome isomerase and quinone isomerase are present as active forms, and activation of prophenoloxidase is therefore the key step for the initiation of melanization and sclerotization (Ashida & Brey, 1997). Variation in phenoloxidase activity has been linked to the ability to mount a successful defence against a foreign invader (Moreau *et al.*, 2000; Siva-Jothy & Thompson, 2002; Tucker & Stevens, 2003; Cotter *et al.*, 2004).

Another enzyme involved in encapsulation is FAD-glucose dehydrogenase (GLD), which has been proposed to participate in the strengthening and sclerotization during encapsulation and in the killing response (Cox-Foster & Stehr, 1994; Cox-Foster *et al.*, 1995). FAD-GLD is a flavoprotein enzyme that catalyzes the oxidation of glucose to gluconolactone and participates in the immune reaction by giving electrons during regeneration of its cofactor FAD (Lovallo *et al.*, 2002). These electrons can be transferred to quinones as electron acceptors and result in production of superoxide anion radicals, which are highly reactive with proteins (Felitsky, 1997; Fenimore, 1998; Lovallo *et al.*, 2002). GLD activity is strongly induced by either latex implants or implants of heat-killed yeast incorporated into ultra-pure agarose within 15 min (Cox-Foster & Stehr, 1994). Because of the specific induction of FAD-GLD during foreign invasion and encapsulation (Cox-Foster & Stehr, 1994), this enzyme may be used as an indicator of initial activation of the cellular immune response (Lovallo & Cox-Foster, 1999).

1.5 Interactions at population level

Population dynamics is an old discipline that has ever been one of the central areas of study in ecology. Modern population ecology, however, has been built up over the past thirty years (Cappuccino & Price, 1995). In the early twentieth century, population dynamicists were interested whether biotic or climatic factors controlled populations (Howard & Fiske, 1911; Uvarov, 1931; Nicholson, 1933). For last fifty years, density dependent regulation, its strength and frequency in nature, and its necessity for persistent populations have been the main controversy among population ecologists (Andrewartha & Birch, 1954; Milne, 1958; Dempster, 1958; den Boer, 1968; Strong, 1984; Cappuccino & Price, 1995). Time-series analysis is the traditional method of

study of population dynamics, looking for regulation (Cappuccino, 1995; Hunter, 2001; Poysa & Pesonen, 2003). Recent empirical studies show that the frequency of detection of density dependence in populations increases with the length of time series, indicating most field populations are regulated (Woiwod & Hanski, 1992; Harrison & Cappuccino, 1995; Turchin, 1995; Malgras & Debouzie, 1997).

A regulated population in broad sense has bounded fluctuations or a stationary probability distribution, which includes even cycles and chaos (Murdoch & Walde, 1989; Turchin, 1995). The main question, therefore, is no longer about existence of regulation, which can be commonly found by analysis of sufficiently long time-series data, but is about how a population is regulated, and which form of regulation takes place (Cappuccino, 1995). The comparative approach of using time-series data typically looks for ecological and life-history characteristics associated with outbreak dynamics (Southwood, 1981; Auerbach *et al.*, 1995). Novel approaches of population dynamics emphasize on raising a new synthesis by integration of the elements such as plant-herbivore interactions, chemical ecology, behavioural ecology, broad comparative ecology, experimental biology, integrated empirical and theoretical ecology, evolution and international integration (Price & Hunter, 1995).

1.5.1 Intraspecific interactions: competition and density dependence

One of the central questions in population ecology is how important is competition among individuals within species (intraspecific) and between species (interspecific) in determining the fitness of individuals in populations (Stoll & Prati, 2001; Sallam *et al.*, 2002; Eccard & Ylonen, 2003; Relyea & Hoverman, 2003). Intraspecific competition occurs when the resources are in limited supply, and leads to decreased contribution of individuals to the next generation (Begon *et al.*, 1996). For herbivores competing for food, the competition impacts directly on survivorship or fecundity, or both (Ferrenberg & Denno, 2003; Dunham *et al.*, 2004). The most important feature of intraspecific competition is density dependence, signifying that the greater number of competitors results in the greater effects of competition on individuals (Capurro *et al.*, 1997; Choquenot & Ruscoe, 2000; Umbanhowar & Hastings, 2002; Webster, 2004).

The density-dependent effects of intraspecific competition are of central importance in the dynamics of natural populations (Fox & Morin, 2001; Keeley, 2001; Spataro & Bernstein, 2004; Webster, 2004). The extreme forms of competition are scramble and contest. In scramble competition all individuals get an equal share of resources but less than their need, resulting in death of whole population. While, in contest competition some individuals get an adequate share of resources, and survive. But other individuals get no resources at all, and therefore die. In term of fecundity, scramble results in the production of no offspring, while contest leads to production of the maximum number of offspring in some individuals and no offspring for the rest of population (Begon *et al.*, 1996).

Density dependence is a dependence of per capita population growth rate on present and/or past population density (Murdoch & Walde, 1989; Turchin, 1995). If population growth rate is negatively or positively affected by density, then density dependence would be direct or inverse, respectively (Turchin, 1995). It is now generally accepted that population regulation cannot occur in the absence of direct density dependence (return tendency) (Murdoch, 1994; Turchin, 1995; Cooper, 2001). Furthermore, return tendency (the tendency to shift back and forth) must be strong enough to counteract the disruptive effects of density-independent factors. In addition, the lag with which return tendency performs must not be too long, otherwise it may result in diverging oscillations (Turchin, 1995).

It is known that intraspecific competition and density dependence are closely bound (Huffaker, *et al.*, 1999), such that, intraspecific effects whether on survival, fecundity or a combination of the both are always density dependent (Begon *et al.*, 1996). Density-dependent effects lead to a tendency for population size to be regulated (Rodenhouse *et al.*, 2003; Webster, 2004). Regulation refers to the return of a population to an equilibrium density as the result of density-dependent processes, implying population size is subject to negative feedback (Dempster & McClean, 1998). However, as already mentioned if density-dependent effects are weak or happens after a time delay, it may not actually regulate population size to the equilibrium (Begon *et al.*, 1996).

1.5.2 Interspecific interactions: bottom-up vs. top-down forces

The importance of the role of multitrophic interactions and the regulatory effects of bottom-up versus top-down forces on population abundance and distribution has been a controversial theme in ecology (Eickwort, 1977; Price *et al.*, 1987; Power, 1992; Gange & Brown, 1997; Hunter *et al.*, 1997; Dyer & Letourneau, 1999; Schmitz *et al.*, 2000; Walker & Jones, 2001). Tritrophic top-down hypothesis predicts that plants and natural enemies are resource limited while herbivores are consumer limited. In contrast, the bottom-up hypothesis states that the biomass of herbivores and carnivores is dependent on total primary productivity and lost energy through transfer up the trophic chain (Lindeman, 1942; Slobodkin, 1960; Dyer & Letourneau, 1999). Despite the general acceptance of the influences of bottom-up and top-down forces on herbivore populations (Hartvigsen *et al.*, 1995; Hunter *et al.*, 1997; Gratton & Denno, 2003), these ecological processes are often considered to be specific to particular ecosystems (Power, 1992). For instance, top-down effects are considered more influential in aquatic systems (Power *et al.*, 1996; Polis *et al.*, 1998). In contrast, the bottom-up effects of plants may be more effective in trophic interactions in terrestrial systems (Power *et al.*, 1996; Stiling & Rossi, 1997; Polis *et al.*, 1998; Ernest *et al.*, 2000; Ostfeld and Keesing, 2000). For example, in a survey of the literature published between 1970 and 1994, Harrison and Cappuccino (1995) found that resources (bottom-up forces) were much more common as a regulating factor than natural enemies in a variety of different terrestrial systems.

The role of bottom-up effects and, in particular, food limitation in regulating insect populations is of prime importance (Bonsall & Eber, 2001; Umbanhowar & Hastings, 2002) as the population dynamics of both herbivore and herbivore–natural enemy interactions may be influenced by variation in host-plant characteristics (Hunter & Price, 1992; Godfray, 1994). For instance, variation in host-plant quality may affect the body size of herbivorous insects, which, in turn, can determine life-history parameters such as fecundity, longevity, and survival, all directly relevant to population dynamics (Connor & Beck, 1993; Bezemer & Jones, 1998; Bjorkman, 2000; de Bruyn *et al.*, 2002; Teder & Tammaru, 2002). Furthermore, the effects of resource variation, which impacts on the behaviour or the physiology of herbivores, may cascade up to the

population dynamics of higher trophic levels due to significant influences on the fitness and performance (such as survival, development, size, longevity, fecundity, and sex ratio) of natural enemies (Hare & Luck, 1991; Polgar *et al.*, 1995; Moon *et al.*, 2000; Sumerford *et al.*, 2000; Raymond *et al.*, 2002; Teder & Tammaru, 2002; Harvey *et al.*, 2003).

It is now evident that both host-plant quality and quantity govern the pattern of spatial and temporal heterogeneity amongst herbivore populations (Hunter & Price, 1992). Furthermore, variation in host-plant quality and quantity can be influential in determining the core characteristics of populations (such as density and distribution in space and time) at higher trophic levels (Hunter & Price, 1992; Price & Hunter, 1995). However, variation in host-plant characteristics may have differential effects on a herbivore and its associated natural enemies (Teder & Tammaru, 2002). Consequently, understanding the relative contributions of bottom-up effects on consumer and natural enemy trophic levels will provide a more focused comprehension of multispecies insect population dynamics (Ohgushi, 1995).

Top-down effects of predation and grazing significantly affect abundance and diversity of herbivores and primary producers, having regulatory effects on plant-herbivore relationship, mainly in aquatic ecosystems (Sinclair *et al.*, 2000; Krivtsov *et al.*, 2001; Kneitel & Miller, 2002; Enderlein & Wahl, 2004; Thompson *et al.*, 2004). Similar to bottom-up effects, top-down effects also exhibit a trophic cascade when perturbing the stock of a higher trophic level results in observable changes in the stocks of lower trophic levels (Schmitz *et al.*, 2000; Suttle, 2003; Herendeen, 2004). Top-down forces have community-scale effects in aquatic systems such as intertidal, marine, lake and river systems (Paine, 1966; Menge, 1976; Estes *et al.*, 1978; Carpenter *et al.*, 1987; Power, 1990). In terrestrial ecosystems, predation on herbivores has been shown to affect plant damage, biomass, productivity and diversity (Barton, 1986; van Bael *et al.*, 2003; Matsumoto, *et al.*, 2003; Schmitz, 2004). However, there has been debate about the generality and large-scale importance of such interactions (Strong, 1992; Polis & Strong 1996; Polis, 1999; Polis *et al.*, 2000; Shurin *et al.*, 2002).

By distinction between “regulation” as a result of density dependence (Dempster & McClean, 1998) and “influences” as a result of density independent processes (Hassell

et al., 1998), Walker & Jones (2001) argued that in terrestrial plant-insect herbivore-natural enemy systems, the majority of top-down and bottom-up forces have influential but not necessarily regulatory role on population dynamics. The researches on terrestrial tritrophic interactions have been focused on study of the relative role of top-down and bottom-up forces to find fundamental ecological questions, compatibility of host-plant resistance and natural enemies, and life table of long-term observations. Integrating the data from these studies can develop a synthesis to assess the relative “influential” role of the top-down and bottom-up forces on such a tritrophic systems (Walker & Jones, 2001). However, to evaluate the relative “regulatory” role of the top-down and bottom-up forces on population dynamics of insect herbivores, an integration of time-series analysis of long-term observational data, laboratory and field experiments, and population models is necessary (Hassell *et al.*, 1998).

Chapter 2:

The population dynamics of the DBM and *Cotesia plutellae* on different host plants

2.1 Abstract

The effects of host-plant resistance on the population dynamics of the DBM and *C. plutellae* were studied in replicated time-series experiments. Host-plant resistance did not affect the equilibrial abundance of the DBM, but it affected the dynamics of DBM populations. The mean population size of DBM showed no significant difference between *Brassica rapa* (a susceptible host plant) and *Brassica napus* (a partially resistant host plant) either in the presence or absence of the parasitoid. Time-series analysis suggests that the dynamics of DBM on *B. rapa* were underpinned by delayed density-dependent processes. In contrast, the dynamics of the DBM on *B. napus* were influenced by a direct density-dependent process. Although measures of short-term parasitism showed a significantly higher rate of parasitism by *C. plutellae* on DBM feeding on *B. napus* compared with *B. rapa*, this individual performance does not translate into differences in the population dynamics. Analysis showed no significant difference in the persistence time of the population-level interaction between the host and parasitoid on the two different host plants.

It is shown that host-plant type does not affect the equilibrial abundance of an insect herbivore but does impact on the population dynamics of the herbivore. However, in the presence of a natural enemy, the underlying host-plant type has little impact on the persistence time of the whole system. The study concludes by discussing the possible ecological processes and mechanisms leading to these similarities and differences.

2.2 Introduction

Understanding the role of top-down and bottom-up forces on population dynamics of herbivores is central in insect ecology (Wratten, 1992; Cappuccino and Price, 1995; Bizina, 1997). Interactions between such that forces may regulate herbivore populations (Eber, 2001; Denno *et al.*, 2002). However, variation in resource quality and quantity can result in synergistic or antagonistic interactions with natural enemies (Agrawal *et*

al., 2000; van der Meijden & Klinkhamer, 2000; Denno *et al.*, 2003). As far as population regulation in terrestrial multitrophic systems is concerned, the role of bottom-up effects of plants and resulted effects of food limitation have shown more effective than top-down effects of natural enemies (Harrison and Cappuccino, 1995; Stiling & Rossi, 1997; Ostfeld and Keesing, 2000; see section 1.5.2).

In the past decade, the effects of host-plant resistance on fitness and performance of higher trophic levels have received considerable attention (Kareiva & Sahakian, 1990; Reed *et al.*, 1992; Heinz & Zalom, 1996; Brewer *et al.*, 1998; Farid *et al.*, 1998a, b; Fuentes-Contreras & Niemeyer, 1998; Hoover *et al.*, 1998; Nwanze *et al.*, 1998; Agrawal & Klein, 2000; McAuslane *et al.*, 2000; Fuentes-Contreras & Niemeyer, 2002; Giles *et al.*, 2002; Kennedy, 2003). However, little effort has been made to study the effects of host-plant resistance on the populations of herbivores and their natural enemies (Romanow *et al.*, 1991; Zeng *et al.*, 1993; Helms *et al.*, 2004). Furthermore, these population studies have been focused on the effects of host plants on demographic aspects of herbivore population growth, such as the intrinsic rate of increase, rather than host plant-mediated processes driving population dynamics.

Here, however, the objective was to explore the bottom-up effects of plant resistance on the dynamics of populations at higher trophic levels. In particular, the aim of this study was to test the effects of host-plant resistance on the population dynamics of a herbivore and its specialist parasitoid over several generations. Specifically, interest lies in determining the possible regulatory effect of different host-plant types on both the single-species (herbivore) interaction and the predator-prey interaction.

2.3 Materials and methods

To explore the impact of host-plant type on the dynamics of an insect herbivore–parasitoid interaction, a tritrophic laboratory system was developed. In particular, the system was composed of two host plants, *Brassica rapa* (Plant Introduction 469895) and *B. napus* (Plant Introduction 470055), DBM and *C. plutellae*. This system was chosen for a number of reasons. First, it has been shown that above-mentioned *B. rapa* and *B. napus* are susceptible and partially resistant to attack by DBM, respectively (Ramachandran *et al.*, 1998). Second, there is considerable information available on the

biology of DBM and *C. plutellae* (Talekar & Shelton, 1993; Kawaguchi & Tanaka, 1999; Shi *et al.*, 2002). Finally, DBM is a worldwide pest species of crucifers (Talekar, 1992; Sivapragasam *et al.*, 1997) and understanding its population dynamics is central to developing an integrated management strategy for its control (Wright & Verkerk, 1995; Verkerk & Wright, 1996a; Verkerk & Wright, 1997; Verkerk *et al.*, 1998; Schuler *et al.*, 2003).

2.3.1 Plant–insect rearing protocols

Brassica pekinensis (Chinese cabbage) cv. Tip Top (Chiltern Seeds, Ulverston, UK), *B. rapa* (Canola) Plant Introduction 469895 and *B. napus* (Canola) Plant Introduction 470055 (North Central Regional Plant Introduction Station, Ames, Iowa, USA) were sown initially in small peat pellets. Then, 1-2 week-old seedlings were transferred to individual pots (13 cm in diameter) containing a multipurpose compost (Levington®, Fisons, UK) and were grown under the glasshouse conditions of 25 ± 5 °C and 16:8 (L:D) photoperiod. No pesticide was applied in the glasshouse.

A DBM insecticide susceptible strain (originally from the Philippines) and *C. plutellae* were both obtained from Rothamsted Research (Harpenden, Hertshire, UK). Cultures of DBM were maintained on 3-4-week-old Chinese cabbage in ventilated Perspex oviposition cages (35 x 35 x 35 cm). The adults were fed with honey solution (20%). Three to four week-old plants were offered to the adults for 24 h to lay eggs. These plants with eggs were kept until the larvae reached the second instar, and then they were transferred to the similar cages and were fed with fresh plants from the same type and age until pupation.

The cultures of *C. plutellae* were maintained on DBM larvae developing on Chinese cabbage in ventilated Perspex oviposition cages (45 x 45 x 45 cm). Five mated female wasps, fed on honey solution (50%), were offered individual plants infested with about 200 second instar DBM for 24 h. Plants with the parasitized larvae were then transferred to the similar cages and fed with fresh plants (as described above) until cocoon formation. Both cultures were kept in a standard constant environment (25 ± 2 °C, $70\pm10\%$ RH and 16:8 h L:D photoperiod).

2.3.2 Levels of parasitism

To test the hypothesis that parasitism by *C. plutellae* differs between DBM on partially resistant and susceptible host plants, DBM larvae reared on the different host plants were exposed to attack by the parasitoid. In particular, DBM larvae were reared on 6-week-old host plants, *B. rapa* and *B. napus*, until the second instar. Ten 2-day-old second instar larvae were then transferred into a plastic Petri dish (5 cm in diameter) and a single, mated 2-day-old female wasp (reared from DBM feeding on Chinese cabbage, a third host plant, to prevent any innate parasitoid experience of the tested host plants) was released into the dish. For each larval type (reared on partially resistant or susceptible host plants) two exposure treatments were undertaken: one-hour exposure to parasitism and two-hour exposure to parasitism. The exposure of the larvae to the parasitoid was performed in absence of the host plant to minimise any olfactory effects of the host plants on the parasitoid. All DBM larvae were then reared on the leaves of the appropriate host plant until they died, pupated or formed the parasitoid cocoons. Each treatment was replicated 10 times.

2.3.3 Population dynamics

To explore the hypothesis that differences in plant resistance affect the population dynamics of DBM a long-term resource-limited population dynamic experiment was established using the two different host plants (*B. rapa* and *B. napus*) in the presence or absence of *C. plutellae*. The treatments were replicated four times in a randomised block design, and maintained under constant environmental conditions (28 ± 2 °C, $70 \pm 10\%$ RH and 16:8 h L:D photoperiod).

To start the experiment, one 5-week-old plant, six pairs (male and female) of newly emerged DBM adults, and aqueous honey solution (35%) were placed in each cage (55 x 28 x 45 cm). A new plant of the same age was put in the cages every 4 days. Each plant was kept in the cage for 12 days (equal to the developmental period of DBM and *C. plutellae* from adult to adult). This resource renewal regime ensured that there was a low probability of removing part of the population during plant replacement. The adult food supply (honey solution) was replaced every 48 h. For sanitation, the cages of one of the blocks were replaced by clean ones every week. By this way all cages were

cleaned once a month. Furthermore, partially cleaning of other cages was done by cleaning the bottom of the cages with absolute ethanol and surface disinfectant (Virkon®, Antec International Ltd., Suffolk, UK) every week.

After 5 weeks, when a sufficient population of DBM with overlapping generations (all stages present) had established, two 2-day-old mated female *C. plutellae* were introduced to each cage (in parasitoid-present treatments only). The ditrophic interactions between the host plants and DBM, and the tritrophic interactions between the host plants, DBM and *C. plutellae* were monitored by weekly census counts of live adults (moth and wasp), and the data used as a measure of abundance for the population dynamics. The experiment was run until 14 generations of DBM were completed.

2.3.4 Statistical analyses

Differences in the levels of parasitism between the two host-plant types were analysed using logistic analysis of deviance techniques (Crawley, 2002). The population dynamic experiments were analysed using a series of descriptive and detailed statistical techniques (Royama, 1992; Chatfield, 1996). Autocorrelation (ACF) and partial autocorrelation (PACF) functions were examined to identify potential patterns (trends, persistent effects of preceding densities, or random shocks) present in the time-series data (Tabachnick & Fidell, 2001). Moreover, the PACF values also indicate the time lags at which negative feedback may be operating (the order of density dependence). The significance of lagged densities in the ACFs and PACFs were tested with Bartlett's band ($\pm 2/\sqrt{n}$), where n is the length of time series (Royama, 1992; Chatfield, 1996; Crawley, 2002). To explore the role of density dependence on the interactions, the net reproductive rate of the DBM population was calculated as $R_t = \ln(N_{t+1}/N_t)$, where N_t and N_{t+1} are population abundance at time t and $t+1$, respectively. Density dependence processes were then detected by testing the relationship between R_t and the natural log-transformed population abundance at times t , $t-1$, and $t-2$. The most parsimonious linear autoregressive model was obtained by initially fitting the maximal model [$R_t \sim \ln(N_t) + \ln(N_{t-1}) + \ln(N_{t-2})$] and then removing non-significant terms through model simplification (Ylloja et al., 1999; Crawley, 2002). All statistical analyses were completed in S-Plus 6.1 (Insightful Corp., Seattle).

2.4 Results

2.4.1 Levels of parasitism

There was a significantly different rate of parasitism (Fig. 2.1) by *C. plutellae* on DBM reared on the two host plants (1-h exposure: z-value = -6.187, d.f. = 18, $P < 0.001$; 2-h exposure: z-value = -3.505, d.f. = 17, $P < 0.001$). The proportion of hosts on *B. napus* attacked by *C. plutellae* was significantly greater than for DBM reared on *B. rapa* (0.875 versus 0.320 under 1-h exposure and 0.960 versus 0.712 under 2-h exposure). The extension of exposure time resulted in increasing parasitism rate for DBM on the both host plants (*B. rapa*: from 0.320 to 0.712; *B. napus*: from 0.875 to 0.960). However, this prolonged exposure time reduced the difference between host plants for the proportion of hosts parasitized (1-h exposure: 0.556; 2-h exposure: 0.248).

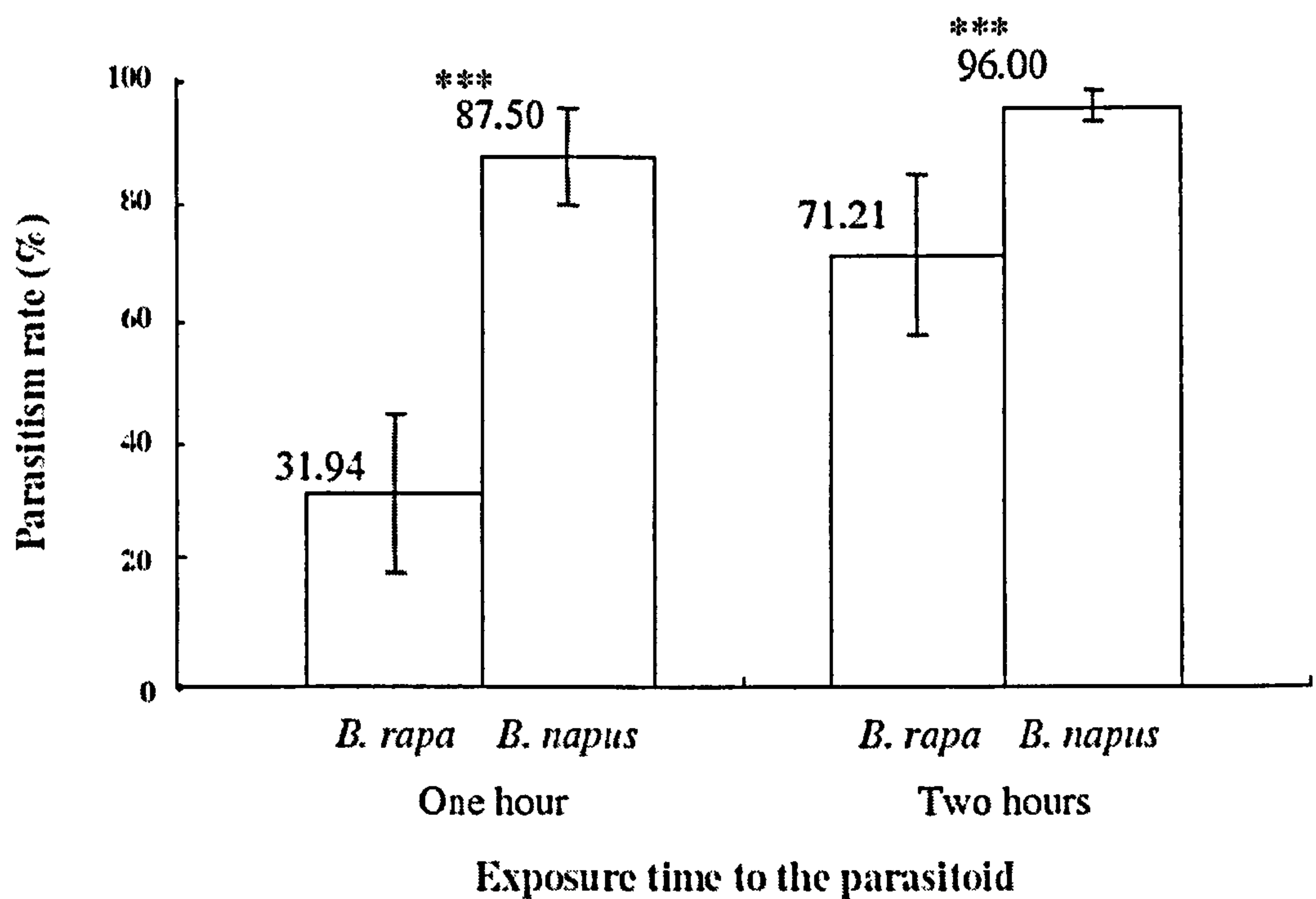


Fig.2.1. Parasitism rate of DBM by *C. plutellae* on *B. rapa* and *B. napus* (logistic analysis of deviance). *** represents a p-value < 0.001 .

2.4.2 Population dynamics: the effects of host-plant resistance on the population dynamics of DBM

2.4.2.1 Descriptive analysis

In absence of the parasitoid, all four replicates of DBM on both host plants persisted throughout the 24 weeks of the experiment (Figs. 2.2-2.9). In general, the pattern of fluctuations exhibited neither a noticeable trend, nor systematic changes with time. This indicates that the populations are statistically stationary and therefore possibly regulated around an equilibrial level. The mean number of DBM adults per week per cage on *B. rapa* varied from 92.4 to 122.8, and between 94.4 and 143.3 for DBM on *B. napus* (Table 2.1). Comparison of the two overall mean abundances for DBM on *B. rapa* and *B. napus* showed no significant difference ($t_6 = 1.44$, $P = 0.2042$).

Table 2.1. Summary statistics of DBM populations on *Brassica rapa* and *B. napus* in absence of the parasitoid over the 24-week period of the experiment.

Replicate	DBM populations on <i>B. rapa</i>			DBM populations on <i>B. napus</i>		
	μ^a	σ^b	CV^c	μ	σ	CV
I	92.4	69.6	0.75	142.3	139.1	0.98
II	122.8	127.2	1.04	143.3	129.3	0.90
III	93.0	122.4	1.32	94.4	76.7	0.81
IV	121.0	140.3	1.16	131.2	105.1	0.80
Overall	107.3	117.0	1.09	127.8	115.0	0.90

^a mean number of live adults per cage per week

^b standard deviation

^c Coefficient of Variation (σ / μ)

The time series also show no evidence for any regular fluctuations or cycles. Examination of the autocorrelation functions (Figs. 2.2-2.9) supported this idea that there were no periodic forcings or components in the population behaviour of DBM on either of the two host-plant types. As the autocorrelation functions rapidly dampen out (Figs. 2.2-2.9) and the effect of long time lags have little influence on changes in current

population size, these correlation statistics also indicate that the dynamics of DBM are potentially driven by density-dependent processes.

To examine the variability in the population dynamics, comparisons within and between time-series treatments were made using coefficients of variation (as the variances were not constant and increased with the mean). Among time series of the same treatment, DBM populations feeding on *B. rapa* showed more variability [coefficient of variation (*CV*) between 0.75 and 1.32] compared to those on *B. napus* (*CV* from 0.80 to 0.98) (Table 2.1). Similarly, this result was consistent when overall variability between plant treatments was compared, indicating greater variability for DBM populations developing on *B. rapa* than on *B. napus* (1.09 versus 0.90).

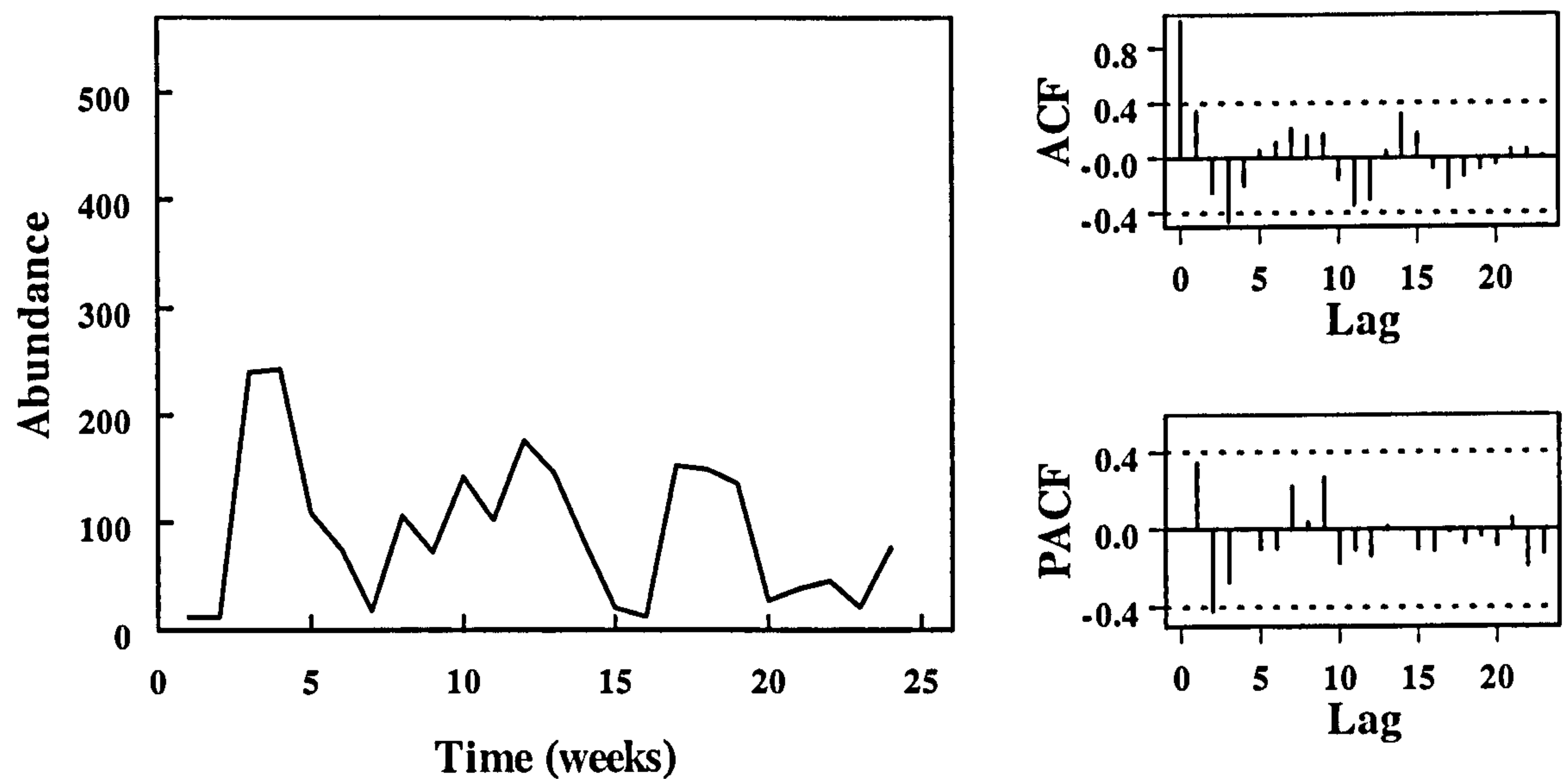


Fig. 2.2. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. rapa* (Replicate I).

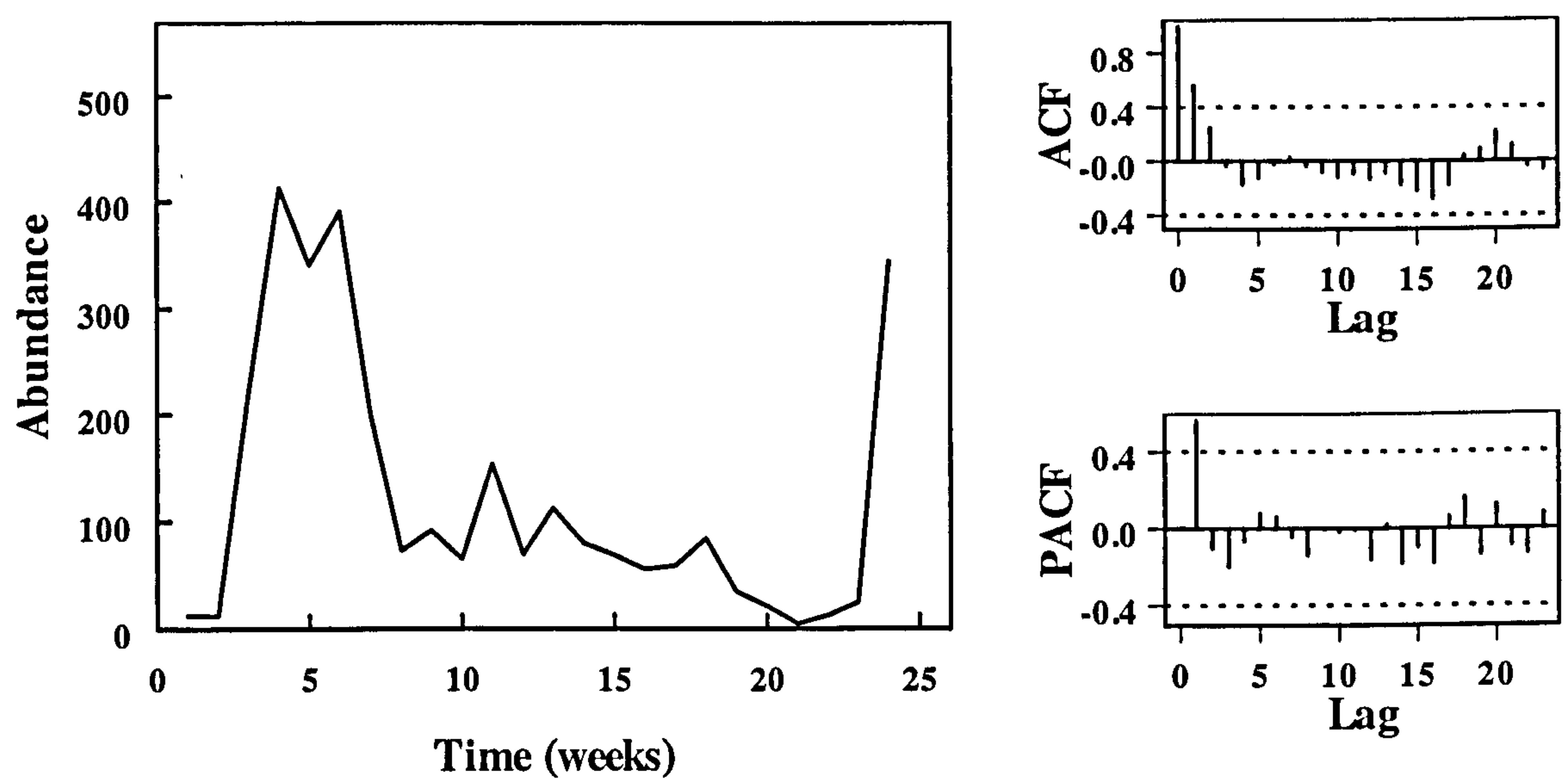


Fig. 2.3. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. rapa* (Replicate II).

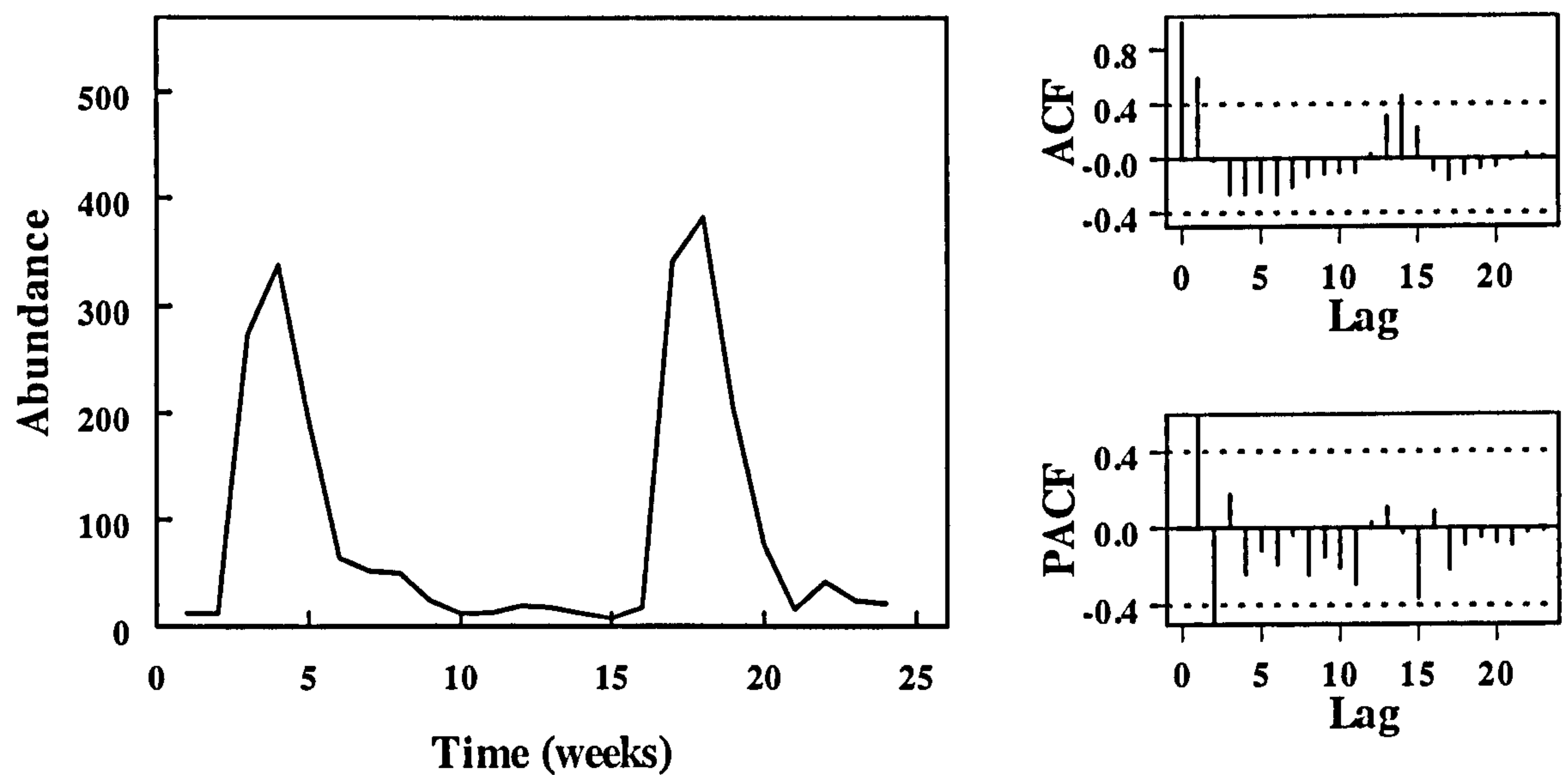


Fig. 2.4. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. rapa* (Replicate III).

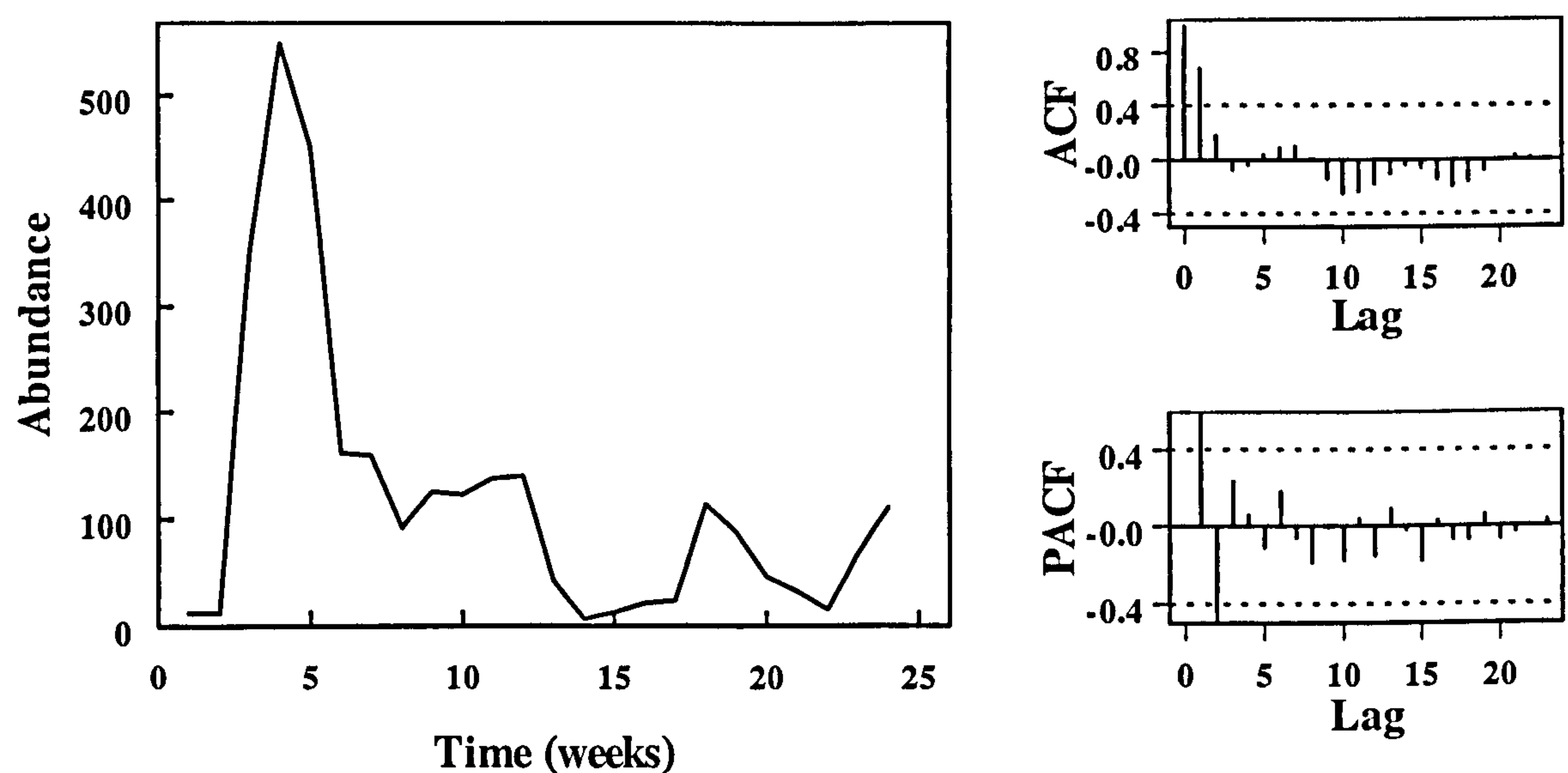


Fig. 2.5. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. rapa* (Replicate IV).

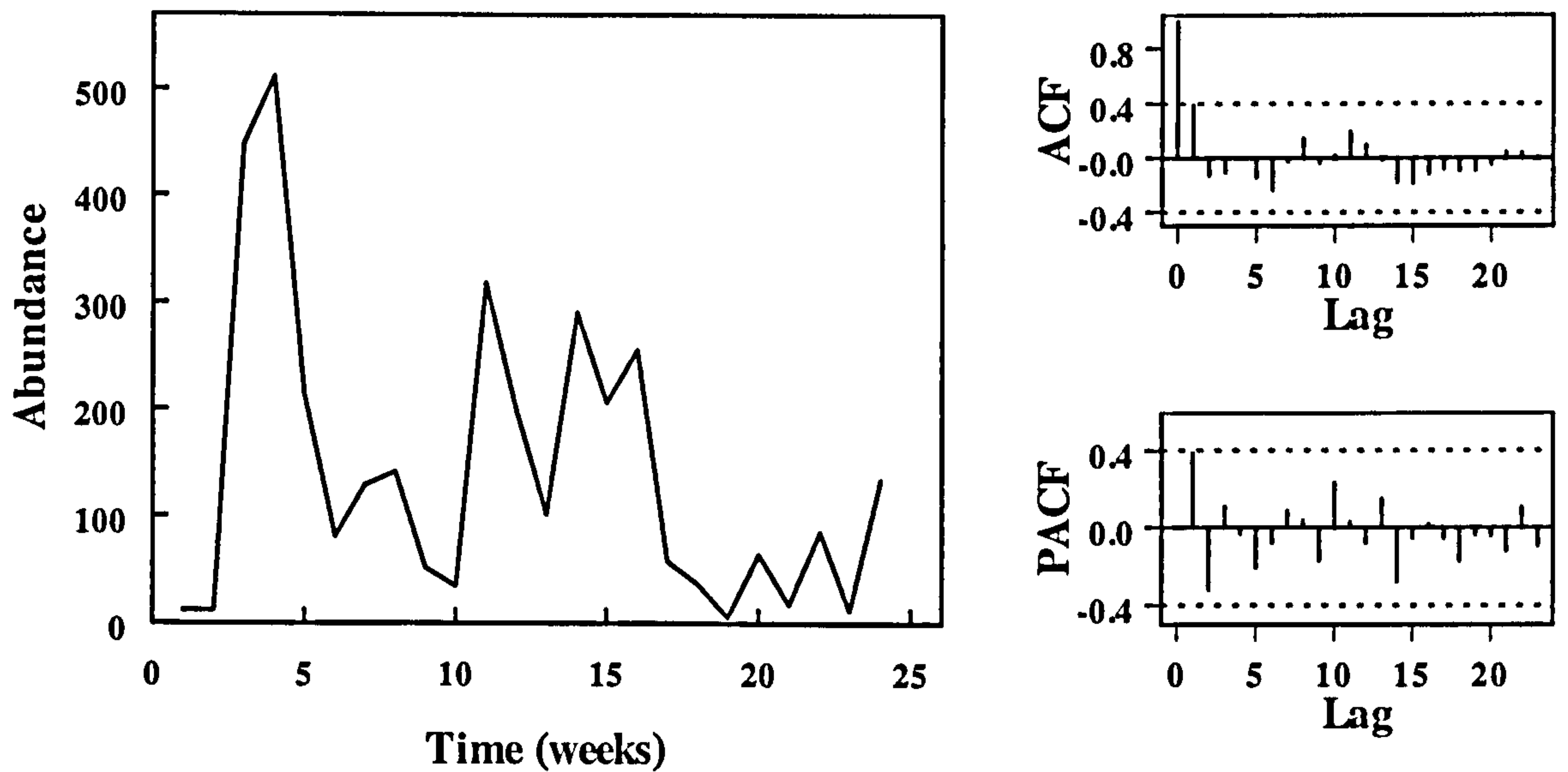


Fig. 2.6. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. napus* (Replicate I).

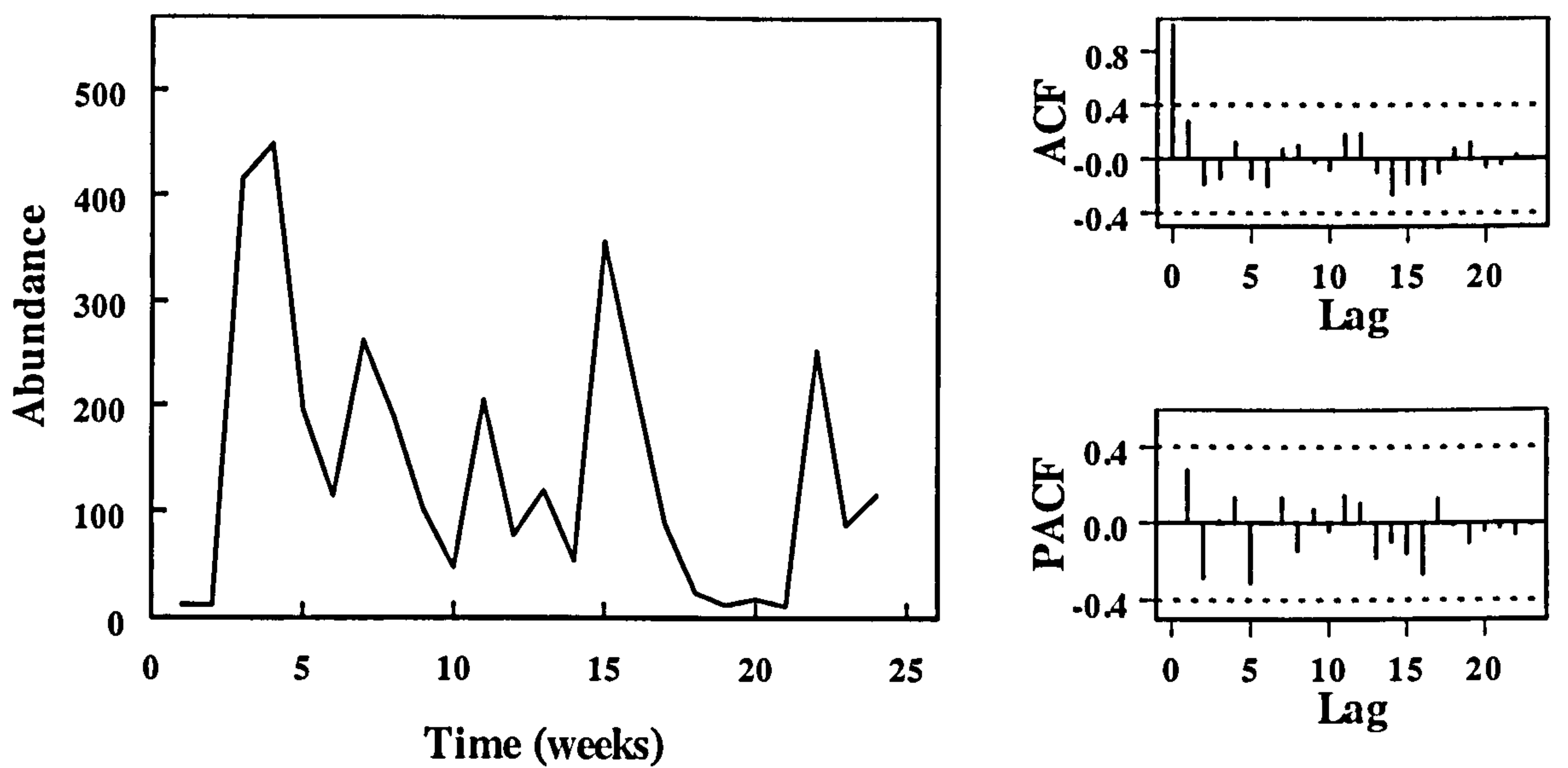


Fig. 2.7. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. napus* (Replicate II).

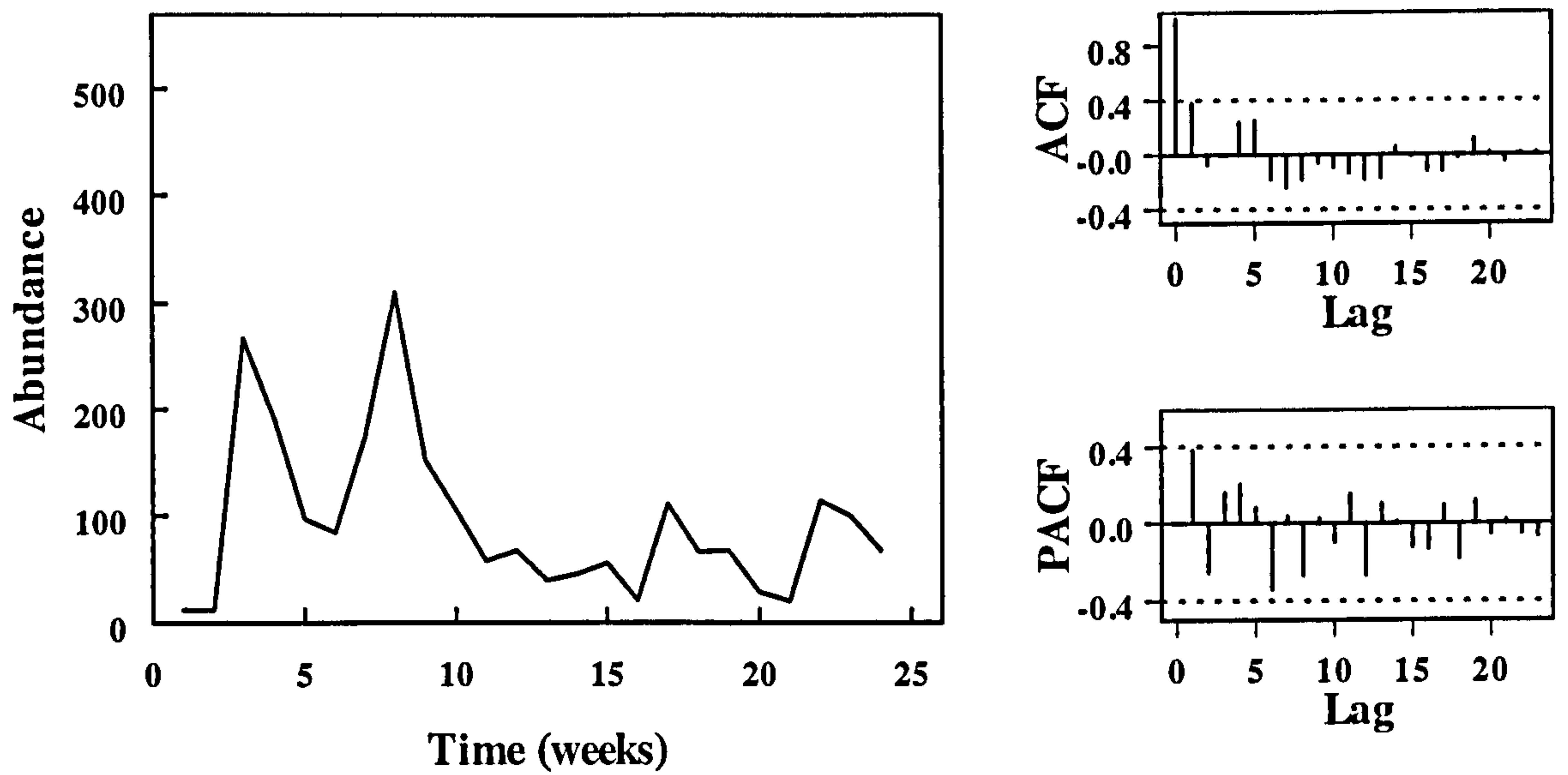


Fig. 2.8. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. napus* (Replicate III).

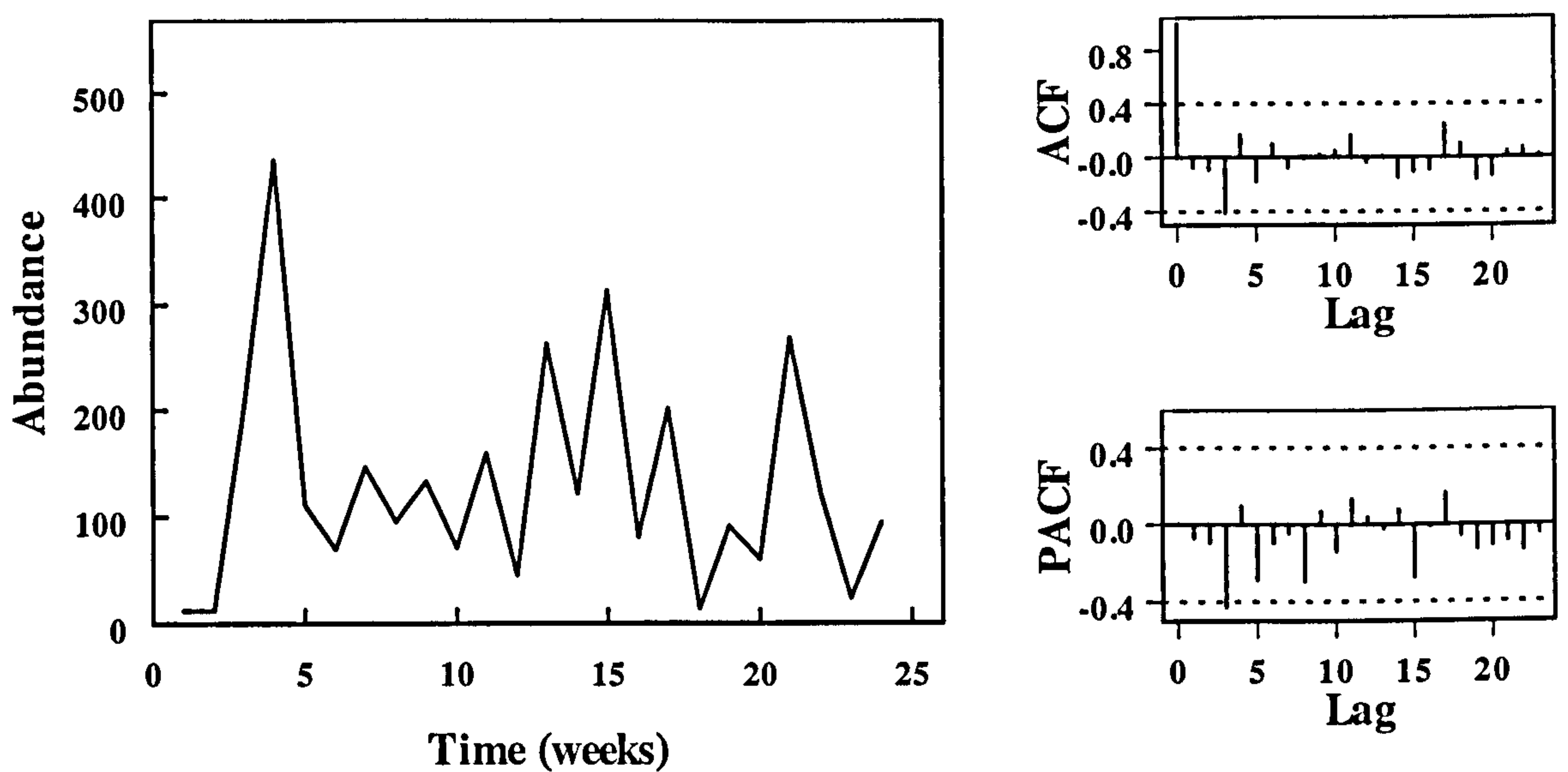


Fig. 2.9. Time series (of total live adults), autocorrelation (ACF) and partial autocorrelation (PACF) plots for DBM populations on *B. napus* (Replicate IV).

2.4.2.2 Density dependence analysis

The PACF correlograms showed differences between DBM populations on the two host plants (Figs. 2.2-2.9). For DBM populations on *B. rapa*, the PACFs exhibited significant correlations at lag one, two, or both, suggesting the dynamics are underpinned by a first- or second-order density dependent model (Figs. 2.2-2.5). Whereas the PACFs for DBM populations on *B. napus* revealed that only one of the four replicates had a significant correlation at lag three (Figs. 2.6-2.9). To explore these descriptive patterns, autoregressive models of the net reproductive rate versus lagged population densities were used. These models showed that the population dynamics of DBM on *B. rapa* were underpinned by delayed density dependence [$\ln(N_t) = 2.43 + 0.66 \ln(N_{t-1}) - 0.25 \ln(N_{t-2})$] (Fig. 2.10a). In contrast, direct density-dependent processes [$\ln(N_t) = 3.23 + 0.27 \ln(N_{t-1})$] determined the dynamics of DBM populations on *B. napus* (Fig. 2.10b).

2.4.3 Population dynamics: the effects of host-plant resistance on the population dynamics of DBM-*C. plutellae*

None of the replicates of the DBM-*C. plutellae* interaction on the two host plants persisted for longer than 16 weeks (Figs. 2.11-2.12). In general, *C. plutellae* drove DBM to extinction within five to nine generations after its introduction. However, in one population on *B. rapa*, DBM population escaped extinction while *C. plutellae* was itself driven to extinction (Fig. 2.11, Replicate II). Comparisons of the persistence time of the DBM-*C. plutellae* interaction (Fig. 2.13) on the two different plants showed no significant difference ($t_6 = 0.3884$, $P = 0.7126$).

In the presence of *C. plutellae*, the mean number of DBM adults per week per cage on *B. rapa* varied between 74.3 and 111.4, and from 70.7 to 133.0 for DBM on *B. napus* (Table 2.2). However, comparison between the overall mean of DBM population size on the different host-plant types showed no significant difference ($t_6 = 0.066$, $P = 0.95$).

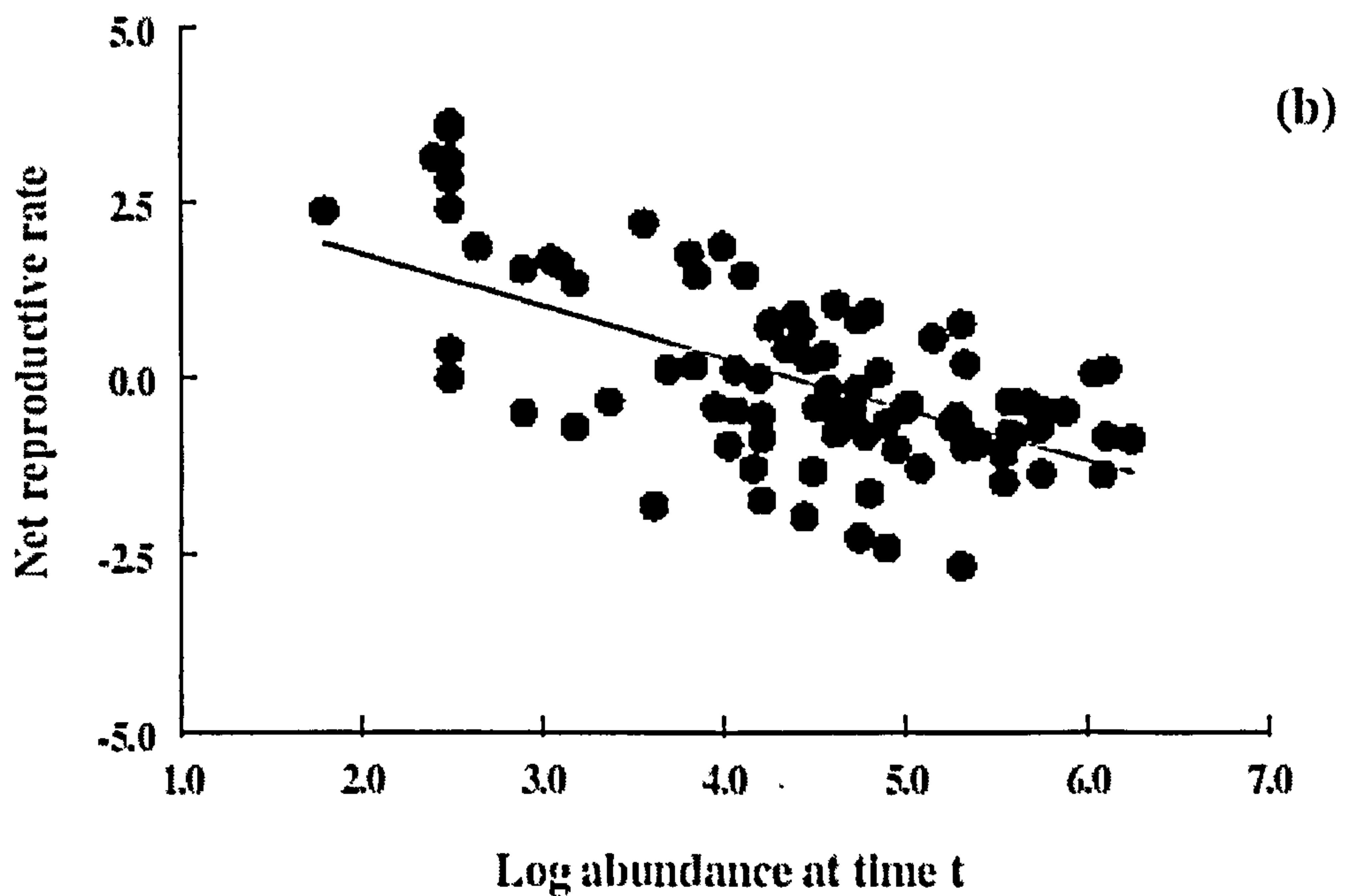
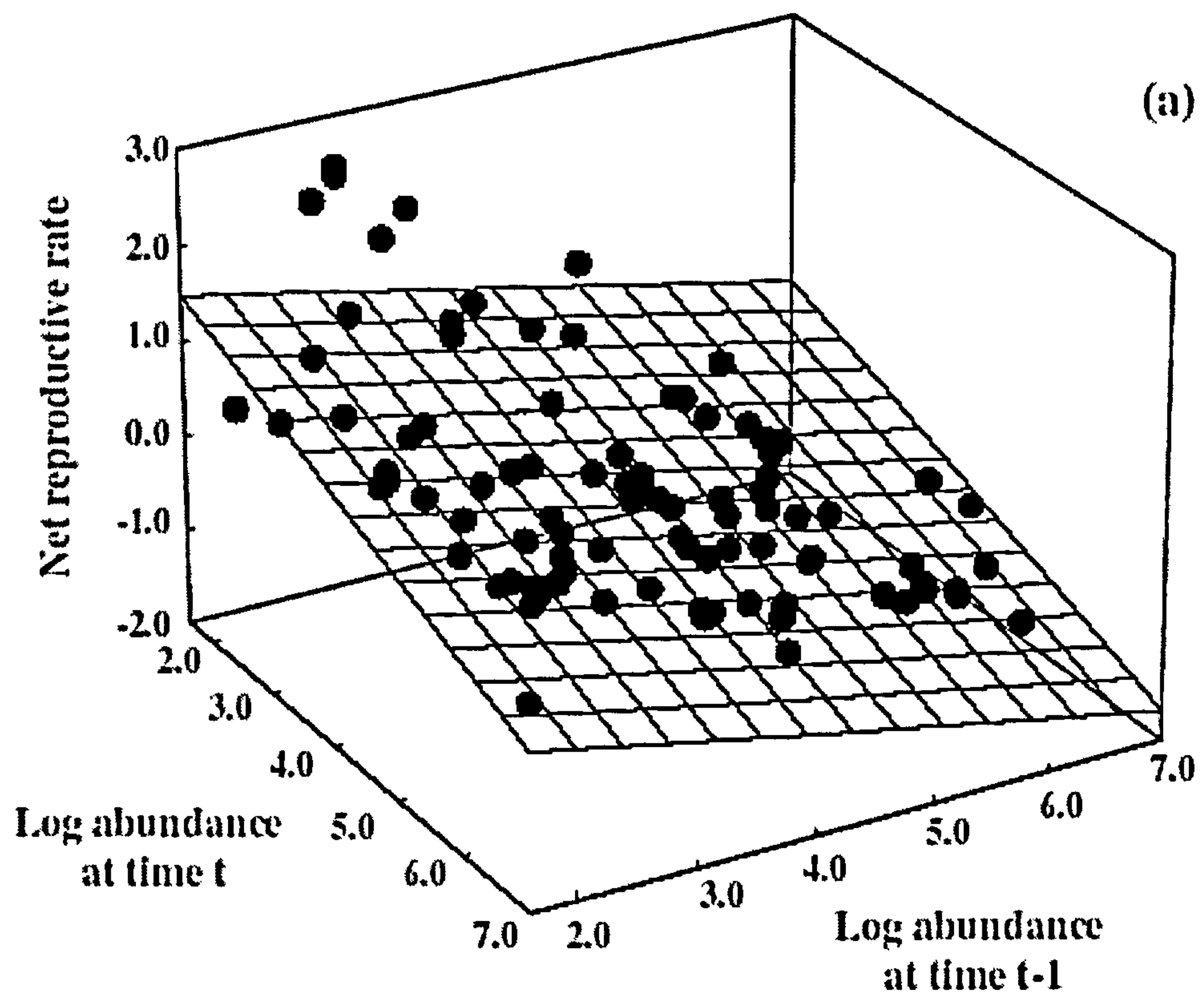


Fig. 2.10. Phase plots of net reproductive rate, $R_t = \ln(N_{t+1}/N_t)$, of DBM populations on *B. rapa* (a) and DBM populations on *B. napus* (b), plotted against natural log transformed population abundance (N_t and N_{t-1}). The best linear autoregressive models were a second-order model [$R_t = -0.2492 (0.1003) \ln(N_{t-1}) - 0.3415 (0.1013) \ln(N_t) + 2.4309 (0.4072)$, $r^2 = 0.29$] for DBM populations on *B. rapa*, and a first-order model [$R_t = -0.73177 (0.09813) \ln(N_t) + 3.22687 (0.44271)$, $r^2 = 0.37$] for DBM populations on *B. napus*. The numbers in parentheses represent the standard errors.

Furthermore, comparison between the overall means of the treatments with and without parasitoids on the same plant (Tables 2.1-2.2) did not show any significant difference (DBM on *B. rapa*: $t_6 = 0.7634$, $P = 0.4742$; DBM on *B. napus*: $t_6 = 1.542$, $P = 0.1768$).

Table 2. Summary statistics of DBM populations on *B. rapa* and *B. napus* in presence of the parasitoid over the period of the experiment.

Replicate	DBM populations on <i>B. rapa</i>			DBM populations on <i>B. napus</i>		
	μ^a	σ^b	CV^c	μ	σ	CV
I	95.4	127.2	1.33	70.7	109.5	1.55
II	111.0	151.8	1.37	113.7	130.0	1.14
III	111.4	136.9	1.23	79.2	93.4	1.18
IV	74.3	101.3	1.36	133.0	163.3	1.23
Overall	100.4	132.2	1.32	96.9	124.6	1.29

^a mean number of live adults/cage/week

^b standard deviation

^c Coefficient of Variation (σ/μ)

When overall variability was compared, in the presence of *C. plutellae*, DBM populations feeding on the two host plants showed no difference (Table 2.2). However, as might be expected, the presence of the parasitoid increased the variability of DBM abundance on both host plants in comparison with the parasitoid-free treatments (Tables 2.1-2.2). In sum, in the presence of the parasitoid, DBM populations on the two host plants revealed no difference in population size, variability, or persistence time.

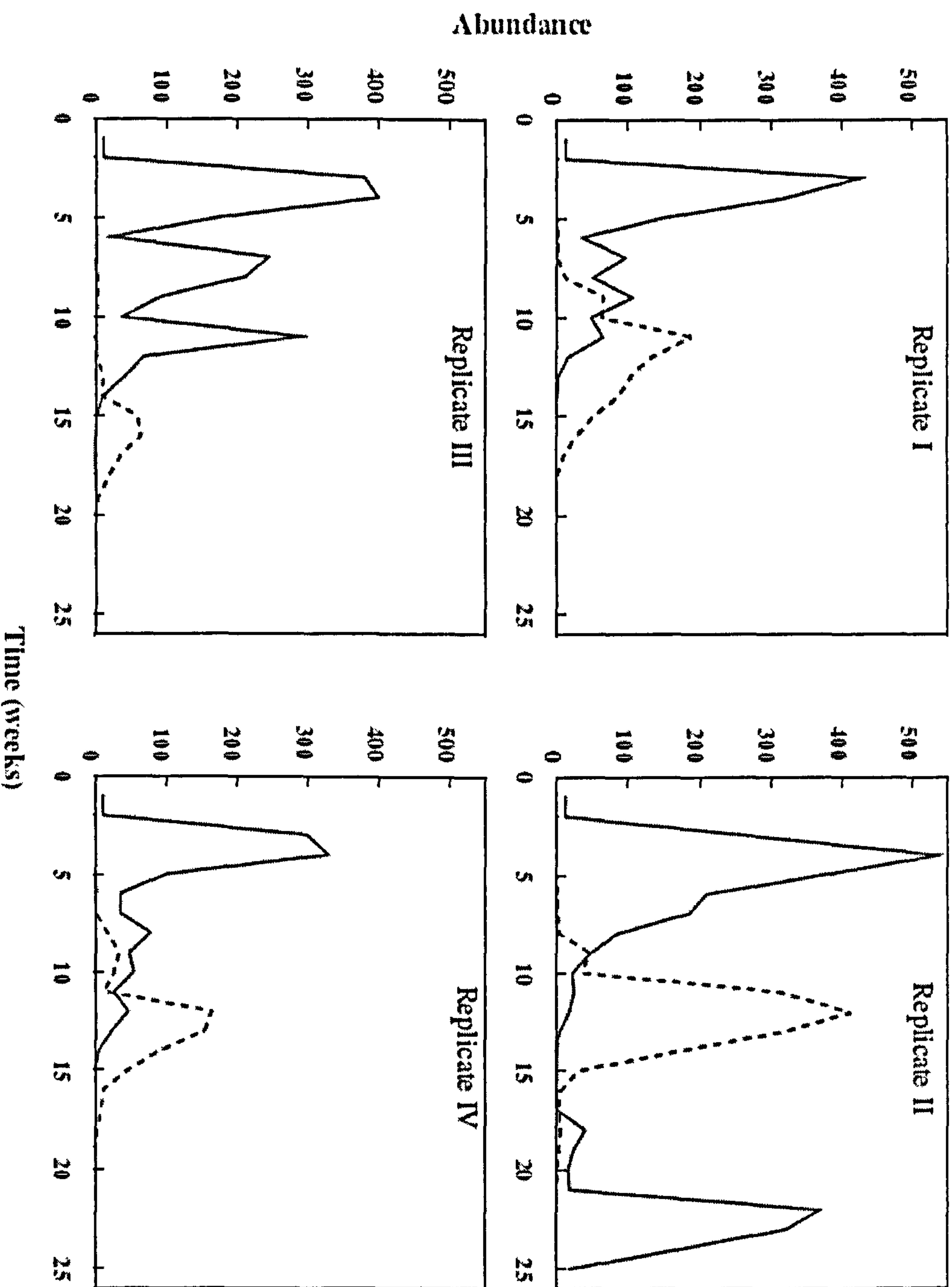


Fig. 2.11. Time series (of total live adults) plots for DBM and *C. plutellae* populations on *B. rapa*. Solid and dashed lines are DBM and *C. plutellae*, respectively.

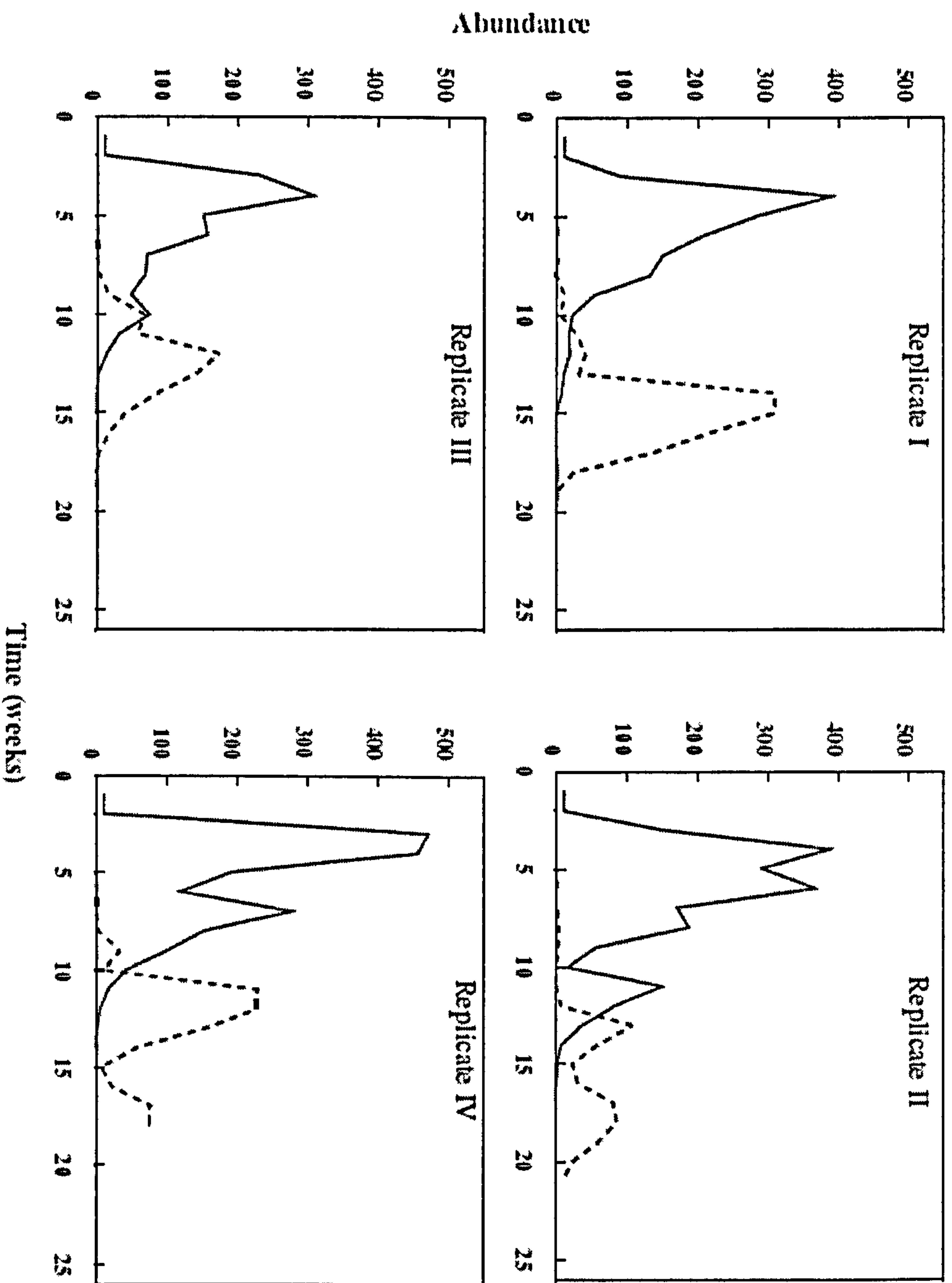


Fig. 2.12. Time series (of total live adults) plots for DBM and *C. pluteellae* populations on *B. napus* . Solid and dashed lines are DBM and *C. pluteellae*, respectively.

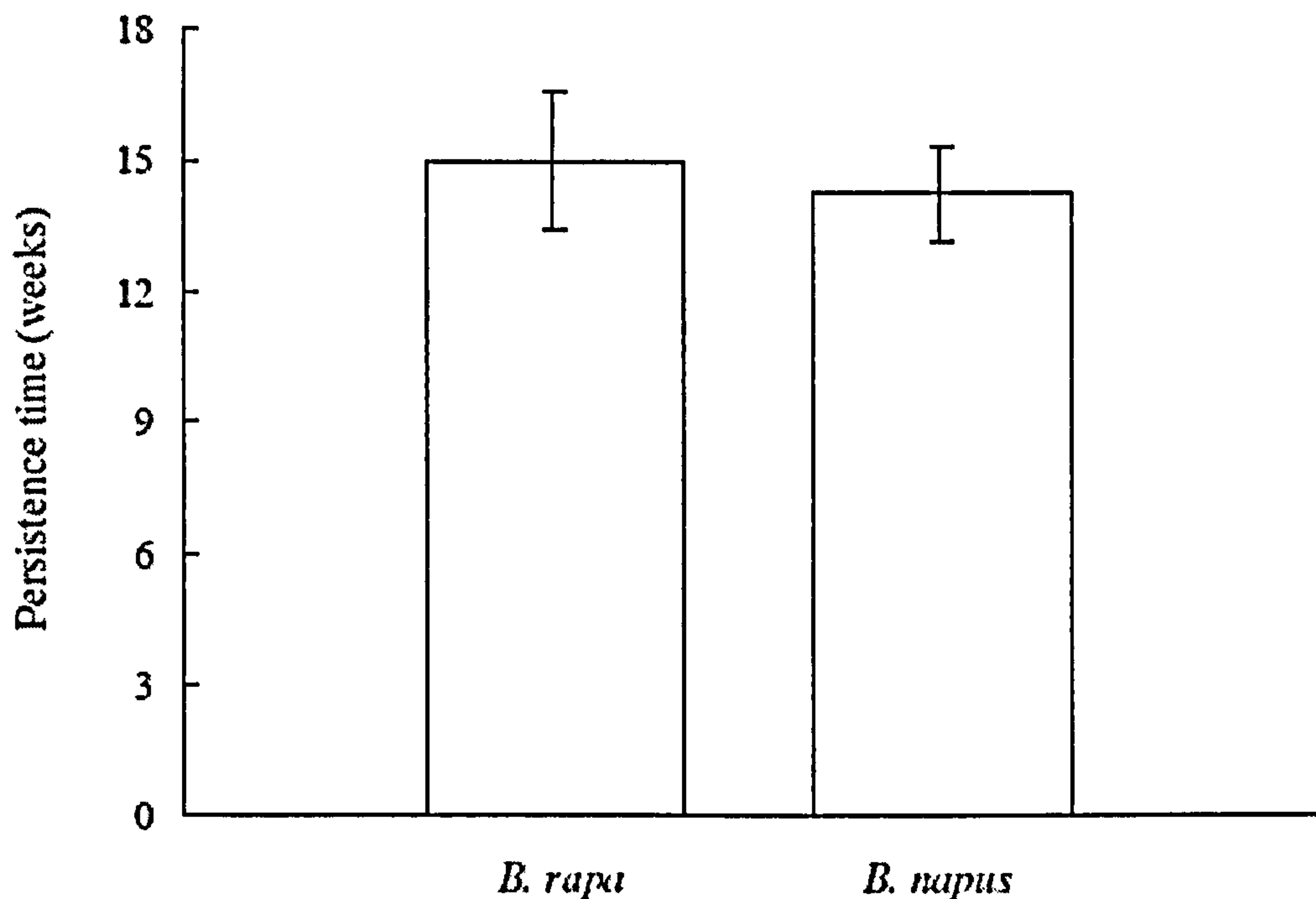


Fig. 2.13. Persistence time (survival) of DBM-*C. plutellae* interactions on *B. rapa* and *B. napus*.

2.5 Discussion

Here, using a series of replicated population dynamic and single cohort experiments it has been shown that differences in individual performance do not necessarily translate into differences in the population dynamics. Despite clear evidence of host plant-mediated effects on the short-term rates of parasitism (functional response) by *C. plutellae* on DBM, underlying plant resistance or type had no effect on longer time scales and on the persistence time of the trophic interaction between the moth and the parasitoid. In a similar way, even though host-plant resistance did not affect the equilibrial abundance of diamond back moth, it clearly had a principal role in governing the different observed population dynamics.

Understanding this relationship between performance and dynamics is paramount in disentangling the effects of top-down and bottom-up effects. For instance, from a series of short-term experiments, Ramachandran *et al.* (1998) have shown that survival of DBM larvae on *B. rapa* was three times greater than that for DBM larvae on *B. napus*

(50% vs. 17%). In comparison, the results of the work presented here show no difference in mean number of DBM on the two host plants at the population level. These contrasting results highlight that marked differences in individual performance do not necessarily translated directly into differences in the population dynamics. It has been well documented that feeding preference decisions (non-preference) by first-instar DBM larvae is the principal mechanism of host-plant resistance (Eigenbrode & Shelton, 1990; Eigenbrode *et al.*, 1990; Eigenbrode *et al.*, 1991a,b; Eigenbrode & Shelton, 1992a,b; Verkerk & Wright, 1996a; Eigenbrode & Pillai, 1998; Ramachandran *et al.*, 1998). Therefore, it is hypothesised that increased survival of DBM larvae on susceptible host plants will result in an increase in population size of competing larvae. In the absence of resource limitation this would lead to higher adult populations. However, the present study was run under resource-limited conditions in which high larval competition for food can result in reduced survival to adults. This happens not because of larval non-preference or host-plant antibiosis (Ramachandran *et al.*, 1998) but because of scramble competition (Begon *et al.*, 1996) and the rapid consumption of resource by the larval population of DBM. This clearly has implications for the population dynamics through the manifestation of density-dependent processes.

Understanding the process governing population dynamics is fundamental in ecology (Ohgushi, 1995). Here, the results from the time series showed that the dynamics of DBM were principally influenced by density-dependent processes. Furthermore, the DBM populations on the two different host plants exhibited different dynamics due to different density-dependent effects. DBM populations on *B. napus* were affected by direct density-dependent processes and instantaneously responded to changes in their density [$N_{t+1} = f(N_t)$]. In contrast, the dynamics of DBM populations on *B. rapa* were determined by a delayed density-dependent process and there was a time lag in the response of DBM populations on *B. rapa* to its own density [$N_{t+1} = f(N_t, N_{t-1})$]. Intraspecific competition between DBM larvae, which is likely to be more intense for DBM populations feeding on *B. rapa* compared with those on *B. napus*, has a strong negative feedback on population growth rate, which can result in delayed density dependence. However, this negative feedback may not only be due to competition for food (limited resources) but also due to physical contact between individuals in high-density interactions (Møller, 1988).

As mentioned, delayed density dependence introduces time lags into the response of population change to population abundance. These effects can give rise to fluctuations in the herbivore populations leading to cycles or chaotic population dynamic behaviour. One of the principal ways that time lags can be generated and lead to oscillatory population dynamics is through maternal effects (Ginzburg & Taneyhill, 1994; Dwyer, 1995). Indeed, population quality can influence population size through maternal effects either directly in the current generation or in a delayed way in subsequent generations (Prout & McChesney, 1985; Rossiter, 1995). It is entirely plausible that host-plant quality can affect DBM through such delayed, maternal effects (Behmer & Grebenok, 1998; Sayyed & Wright, 2001). This effect is likely to be sufficient to influence the population dynamics such that offspring performance (survival and fecundity) is influenced by the bottom-up effects of the host plant and remains an area for future work.

The results presented here show that host-plant resistance can affect the rate of parasitism of DBM by *C. plutellae*. However, in the long-term tritrophic population study, the population size and variability of DBM, and the persistence time of the interaction were not influenced by host-plant type. These results again highlight that the results of individual performance may be totally different from those observed at the population level.

Here, it has been shown that the lack of persistence of the interaction between DBM and *C. plutellae* was principally due to the extinction of DBM (seven cases). The time to extinction was not determined by host-plant type (as host-only interactions persisted) but was due to the dynamical interaction between the insect herbivore and its parasitoid. The observed diverging oscillations between a host and its parasitoid are a consequence of overexploitation of the moth by *C. plutellae*, leading to the rapid extinction of the interaction (Nicholson & Bailey, 1935). Given that the host-only populations are regulated, the limited persistence of the DBM–*C. plutellae* interaction suggests that the lack of available (temporal or spatial) refuges from a randomly foraging natural enemy is the principal mechanism that underpins the observed host–parasitoid dynamics.

In summary, it has been demonstrated that known individual performance on different host-plant types does not necessarily affect equilibrial population abundances but can

affect the mechanisms by which populations are regulated. In tritrophic interactions, differences in host-plant type might be overwhelmed by the response of the natural enemy. Understanding the role of these bottom-up and top-down forces on the dynamics and persistence of DBM remains a central focus for developing integrated control strategies for this pest species.

Chapter 3:

Host plant-mediated foraging behaviour and success of *Cotesia plutellae*

3.1 Abstract

The effect of host plant resistance on plant and plant-host foraging behaviour and on parasitism success of *C. plutellae* were studied in a series of olfactometer tests (using a 4-way olfactometer) and cage experiments. *Cotesia plutellae* did not differentiate between different plant types when both the plant types offered were susceptible or were partially resistant. In contrast, *C. plutellae* could differentiate between the odours from susceptible (young Chinese cabbage) and partially-resistant (old common cabbages) plants whether plants were uninfested or infested with feeding DBM larvae. *Cotesia plutellae* showed a strong tendency to choose uninfested young Chinese cabbage in comparison to uninfested old common cabbages whether *C. plutellae* reared on Chinese cabbage or reared on common cabbage/turnip but experienced on Chinese cabbage. In contrast, experience by the parasitoid larva and adult on common cabbage did not lead *C. plutellae* towards uninfested old common cabbages, either young Chinese cabbage and old common cabbages or two different cultivars of old common cabbages were compared.

Cotesia plutellae also had a strong preference for infested young Chinese cabbage compared with infested old common cabbages, regardless of the host plant on which the parasitoid were reared. However, *C. plutellae* preferred infested old common cabbage to uninfested young Chinese cabbage. The effects of learning thus varied with the host plant on which the parasitoids reared and with the host plant on which adult parasitoid experience happened. In cage experiments, with short exposure times, *C. plutellae* preferred to parasitize DBM larvae on a susceptible host plant compared with DBM larvae on a partially-resistant host plant. However, this preference disappeared when the exposure time to the parasitoid was increased. The number of *C. plutellae* cocoons on susceptible host plants was significantly greater compared with partially-resistant host plants for both short and long exposure time. The present study therefore suggests that partially-resistant host plants negatively affect searching efficiency and parasitism

success of *C. plutellae*. Integration of such plants and *C. plutellae* for control of DBM is therefore incompatible.

3.2 Introduction

Understanding the behavioural ecology and in particular the host location behaviour of *C. plutellae* is essential to construct an IPM programme based on partially-resistant host plants and *C. plutellae* (see Section 1.4.1.2). It has been shown that *C. plutellae* is able to respond to DBM sex pheromone, larval frass volatiles and host-plant volatiles (Reddy *et al.*, 2002). Olfactory studies have demonstrated that host plants can strongly affect foraging behaviour of *C. plutellae* (Liu & Jiang, 2003). In short-range foraging, *C. plutellae* preferred the odour of a partially-resistant host plant on which they had developed compared with the odour of infested and damaged leaves of a susceptible host plant (Bogahawatte & Van Emden, 1996). In tests with young plants, females of *C. plutellae* were more responsive to the volatiles from Chinese cabbage than those from common cabbage, when both plant species were either infested or uninfested (Liu & Jiang, 2003). However, within one plant type the odour from infested leaves was preferred to that from uninfested, undamaged leaves (Bogahawatte & Van Emden, 1996). Antennal-searching behaviour happened only on the host-infested sites (compared with non host-infested or artificially-damaged), suggesting the involvement of both the plant and regurgitant of feeding DBM larvae in the production of the attractive infochemicals (Shiojiri *et al.*, 2000b).

Studies on long-range attraction of adult female *C. plutellae* have indicated that they use predominantly plant-derived stimuli in their in-flight searching behaviour, since while both mechanically-damaged and DBM larvae-damaged plants were attractive, host-damaged leaves remained attractive to the parasitoid after removal of the host larvae (Potting *et al.*, 1999). In its flight response, *C. plutellae* showed preference for host-infested over uninfested, mechanically damaged and non host-infested host plants (Shiojiri *et al.*, 2000a). In addition, *C. plutellae* females could not distinguish between *Bt* plants and wild-type host plants but were more responded to *Bt* plants damaged by *Bt*-resistant DBM than *Bt* plants damaged by susceptible DBM, due to more extensive feeding damage (Schuler *et al.*, 2003). These studies reveal the ability of *C. plutellae* to

show specific responses toward different plant-host complexes. *Cotesia plutellae* is also capable of learning odours as its response to the volatile cues increases significantly after an oviposition experience or contact with host-damaged leaf (Potting *et al.*, 1999; Wang & Keller, 2002; Liu & Jiang, 2003).

The objective of the present study was to test *C. plutellae* olfactory responses to infochemicals emitted by various host plant species and varieties with different resistance levels to DBM. In particular, this study aimed to compare innate preferences of *C. plutellae* for different plant and plant-herbivore complexes in order to determine those that enhance its foraging efficiency. The possible effects of learning in altering parasitoid performances and the effect of host plant resistance on parasitism success were also investigated.

3.3 Materials and Methods

3.3.1 Plants and insects

Brassica pekinensis (Chinese cabbage) cv. Tip Top (TT) (Chiltern Seeds, Ulverston, UK) and cv. F₁ One Kilo SB (SB), *B. oleracea* var. *capitata* (common cabbage) cv. Wheelers Imperial (WI) and cv. Red Drumhead (RD), *B. rapa* (turnip) cv. Snowball (Suttons Seeds, Devon, UK), *B. rapa* Plant Introduction (PI) 469895 and *B. napus* PI 470055 (North Central Regional Plant Introduction Station, Ames, Iowa, USA) were grown organically under glasshouse conditions (Section 2.3.1). An insecticide-susceptible strain of DBM (Roth population) and *C. plutellae* were both obtained from Rothamsted Research (Harpenden, UK). Insects were cultured as described in Section 2.3.1.

3.3.2 Olfactometer description and set-up

A 4-way olfactometer (Fig. 3.1) similar to one described by Douloupaka & van Emden (2003) and modified by P. Vamvatsikos was used. The central arena into which parasitoids were released was a Perspex pot (45 mm dia. x 30 mm high) linked to four odour source chambers by Perspex tubing (5 mm internal dia. x 40 mm long). Each source chamber consisted of a plugged Perspex cylinder (25 mm internal dia. x 95 mm

long). The far end of each source chamber was connected to a plastic pot (25 mm dia. x 30 mm high) filled with activated charcoal to clean the air. The pots were covered with perforated plastic lids that enable air to come through olfactometer. The central chamber was linked to an electric pump CAPEX 8C (Charles Austen Pumps Ltd., Surrey, UK) with airflow control. The pump was set to suck air through the apparatus at approximately 1700 ml/min. Smoke tests showed that this rate is optimum to produce four even streams from the source chambers into the central arena. The smoke was created from the mixture of diethylamine $[(C_2H_5)_2NH]$ and acetic acid $[CH_3COOH]$ in a glass vial (Pham-Delegue *et al.*, 1991) which was then connected to the olfactometer. The olfactometer was placed inside a 60 x 60 x 60 cm wooden frame whose inner sides were covered with white paint to diffuse illumination from a top fluorescent light. To check for any possible bias in the olfactometer, a control test with empty arms was undertaken.

3.3.3 Olfactometer tests

Ten, mated 3-day-old female *C. plutellae* were released into the central arena of the olfactometer and were given a choice between two different plants or plant-host complexes. The choice after 30 minutes (the number of the wasps in each arm) was used as the preference index. The number of the wasps remaining in the central arena was recorded as being non-responsive. Each test was replicated eight times. For half of the replicates opposite arms had the same treatment and for half of the replicates adjacent arms contained the same treatment. After each replicate the whole apparatus was also washed with ethyl alcohol (70% v/v), then kept in an odourless detergent (Lipsol liquid 5% v/v; Bibby Sterilin Ltd., Staffordshire, UK) overnight and finally rinsed in distilled water. The olfactometer was then rotated by 90 ° compared with its previous position before the next replicate test was conducted. All tests were undertaken between 1000 h and 1600 h, the period of day in which wasps showed the greater activity.

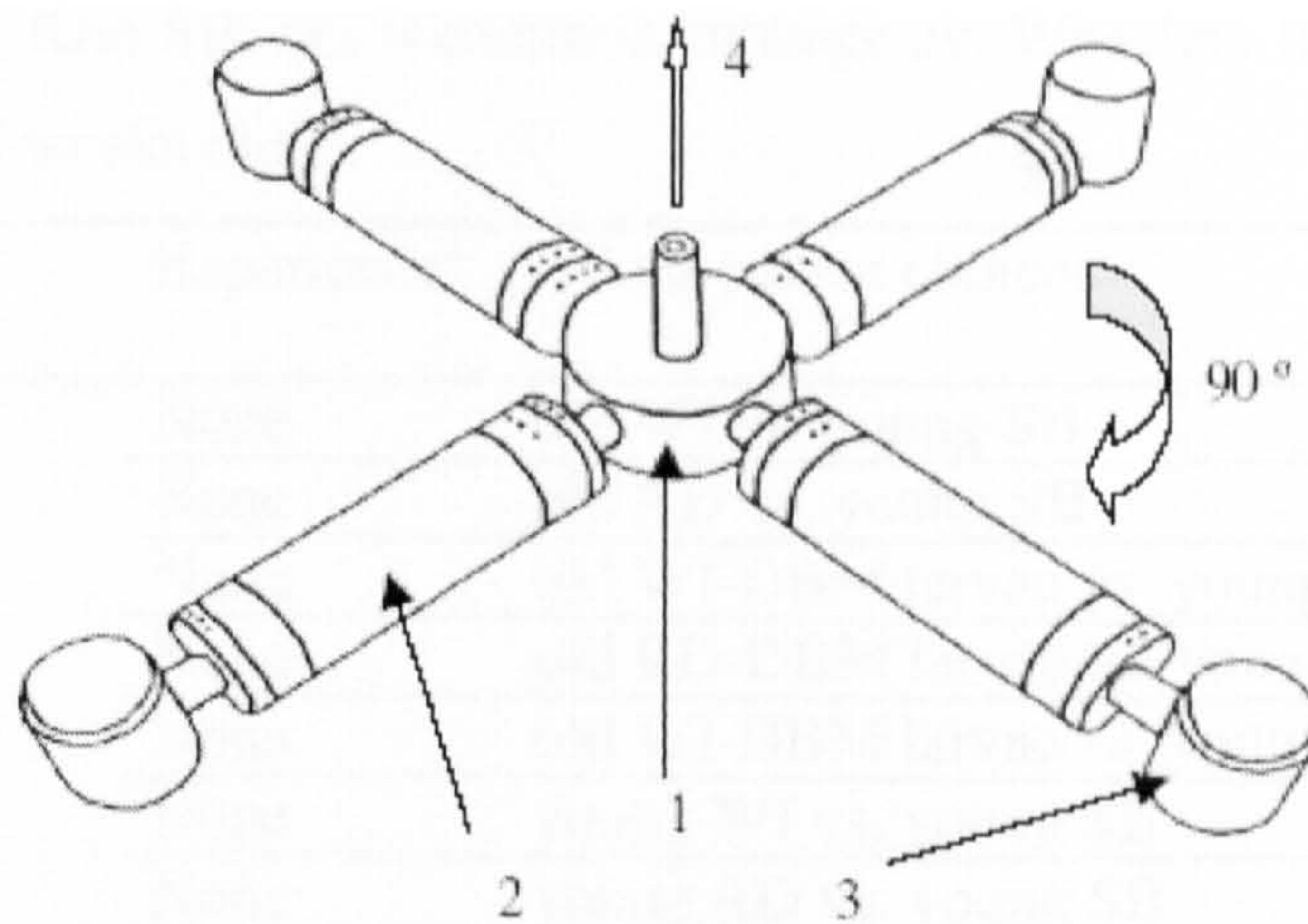


Fig. 3.1. Schematic picture of the 4-way olfactometer used in experiments. The parts 1, 2 and 3 are refer to the central arena, odour source chamber and plastic pot; the number 4 shows the direction of flow suction; the curved arrow shows 90 ° rotation after each replicate.

The following factors were examined: (1) origin of parasitoids: here the effect of the host plant on which the parasitized DBM larvae developed on *C. plutellae* attraction was tested; (2) intact and infested plants: for the tests with intact plants, a piece of rolled leaf from each host plant was placed in an odour source chamber immediately before performing the test; for tests with the plant-host complex, 20 early third instar DBM larvae were added to the piece of leaf in an odour source chamber and both ends of the chamber were covered with cotton 2 h before performing the test; (3) adult parasitoid learning: here the effects of oviposition experience on DBM larvae by the parasitoid on its response to plants or plant-host complexes were tested; for oviposition experience, 10, mated 2-day-old female *C. plutellae* were released into a Perspex ventilated cage (30 x 30 x 30 cm) containing a host plant with 200 early third instar DBM larvae for 24 h; these experienced parasitoids were then used immediately for one replicate of the experiment.

Table 3.1. Olfactometer tests. RD = common cabbage cv. Red Drumhead; SB = Chinese cabbage cv. F₁ One Kilo SB; WI = common cabbage cv. Wheelers Imperial; young = 4 weeks old; old = 15 weeks old.

Source of parasitoids ¹	Experience ²	Odour source choices
(a) young SB	None	old WI vs. young SB
	None	old RD vs. young SB
	None	old WI-DBM larvae vs. young SB-DBM larva
	None	old RD-DBM larvae vs. young SB-DBM larva
	None	old WI-DBM larvae vs. young SB
	None	young WI vs. young SB
	None	young RD vs. young SB
	None	old WI vs. old RD
	young SB	old WI vs. young SB
	old WI	old WI vs. young SB
	young SB	old WI-DBM larvae vs. young SB-DBM larva
	old WI	old WI-DBM larvae vs. young SB-DBM larva
	old WI	old WI vs. old RD
	old RD	old WI vs. old RD
(b) young WI	None	old WI vs. young SB
	young SB	old WI vs. young SB
	old WI	old WI vs. young SB
	None	old WI-DBM larvae vs. young SB-DBM larva
	young SB	old WI-DBM larvae vs. young SB-DBM larva
	old WI	old WI-DBM larvae vs. young SB-DBM larva
(c) young turnip	None	old WI vs. young SB
	young SB	old WI vs. young SB
	old WI	old WI vs. young SB
	None	old WI-DBM larvae vs. young SB-DBM larva
	young SB	old WI-DBM larvae vs. young SB-DBM larva
	old WI	old WI-DBM larvae vs. young SB-DBM larva

¹ Plant on which parasitoids were reared from DBM larvae.

² Plant on which parasitoids experienced multiple ovipositions on DBM larvae before performing the test.

Olfactometer tests were categorised into three groups: (1) tests with *C. plutellae* reared from DBM larvae that had developed on young Chinese cabbage; (2) tests with *C. plutellae* reared from DBM larvae that had developed on young common cabbage; (3) tests with *C. plutellae* reared from DBM larvae that had developed on young turnip (as a third host plant). Each category included tests with inexperienced and experienced *C. plutellae* and responses towards intact plants and plant-host complexes (Table 3.1).

3.3.4 Cage experiments

To explore the role of host plant resistance on parasitism success by *C. plutellae* series of cage experiments were conducted. For each experiment four plants from two different types, a susceptible and a partially-resistant host plant (two of each) were placed together in a well ventilated cage (90 x 75 x 60 cm). Each plant was placed in a separate corner of the cage such that plants from the same type were in opposite corners. Each plant was infested with 50 late second instar DBM larvae. These larvae were from the same type and age of the plants used in the experiments. Plants were placed in trays filled with water and were prevented from touching the sides of the cage to impede movement of DBM larvae between plants. Aluminum foil was used as a horizontal barrier around each pot to prevent larvae from falling in the water. After 24 h, the sufficient time for larvae to establish on the plants, two or four mated female *C. plutellae* were released in each cage. Depending on the experiment, parasitoids were removed after 24 h or after 4 days.

For each cage, replacement plants were provided *ad lib*, from the same type and age as the original plants, until DBM larvae pupated or *C. plutellae* cocoons formed. Each treatment was replicated four times in a randomised block design, and maintained under constant environmental conditions ($25\pm 2^{\circ}\text{C}$, $70\pm 10\%$ RH and 16:8 h L:D photoperiod). In total, five experiments were conducted that can be categorized into two groups: (1) longer exposure experiments: two female *C. plutellae* were released in each cage and the exposure time to the parasitoid was 4 days; (2) shorter exposure experiments: four female *C. plutellae* were released in each cage with an exposure time to the parasitoid of 24 h (Table 3.2).

Table 3.2. Cage experiments. *B. rapa* = PI 469895, *B. napus* = PI 470055, TT = Chinese cabbage cv. Tip Top, and WI = common cabbage cv. Wheelers Imperial.

<i>Experiment</i>	<i>Parasitoid source¹</i>	<i>Number of parasitoids released</i>	<i>Exposure time to parasitoids</i>	<i>Host plants²</i>
1	TT	2	4 days	<i>B. rapa</i> (6) vs. <i>B. napus</i> (8)
2	Turnip	2	4 days	TT (4) vs. WI (15)
3	TT	4	24 h	TT (4) vs. WI (8)
4	TT	4	24 h	TT (5) vs. WI (15)
5	WI	4	24 h	TT (5) vs. WI (15)

¹ Plant on which parasitoids were reared from DBM larvae.

² The number in parentheses refers to the age of plants in weeks.

3.3.5 Statistical analyses

The data from the olfactometer tests (the number of parasitoids responding to different plants or plant-host complexes) were pooled and compared against a null hypothesis of random choice using Chi-square test. Non-responsive wasps were not included in the analyses. The data from cage experiments were analysed for percentage parasitism and wasp cocoon numbers. The difference in percentage parasitism between the host plants were analysed using logistic analysis of deviance. The difference in the number of parasitoid cocoons between the host plants were analysed using student’s t-test (Crawley, 2002). All analyses were completed in S-Plus 6.1 (Insightful Corp., Seattle).

3.4 Results

3.4.1 Olfactometer tests

Random distribution of the results from the control test with empty arms (in absence of odours) indicated no directional bias in attraction within the olfactometer apparatus (Fig. 3.2).

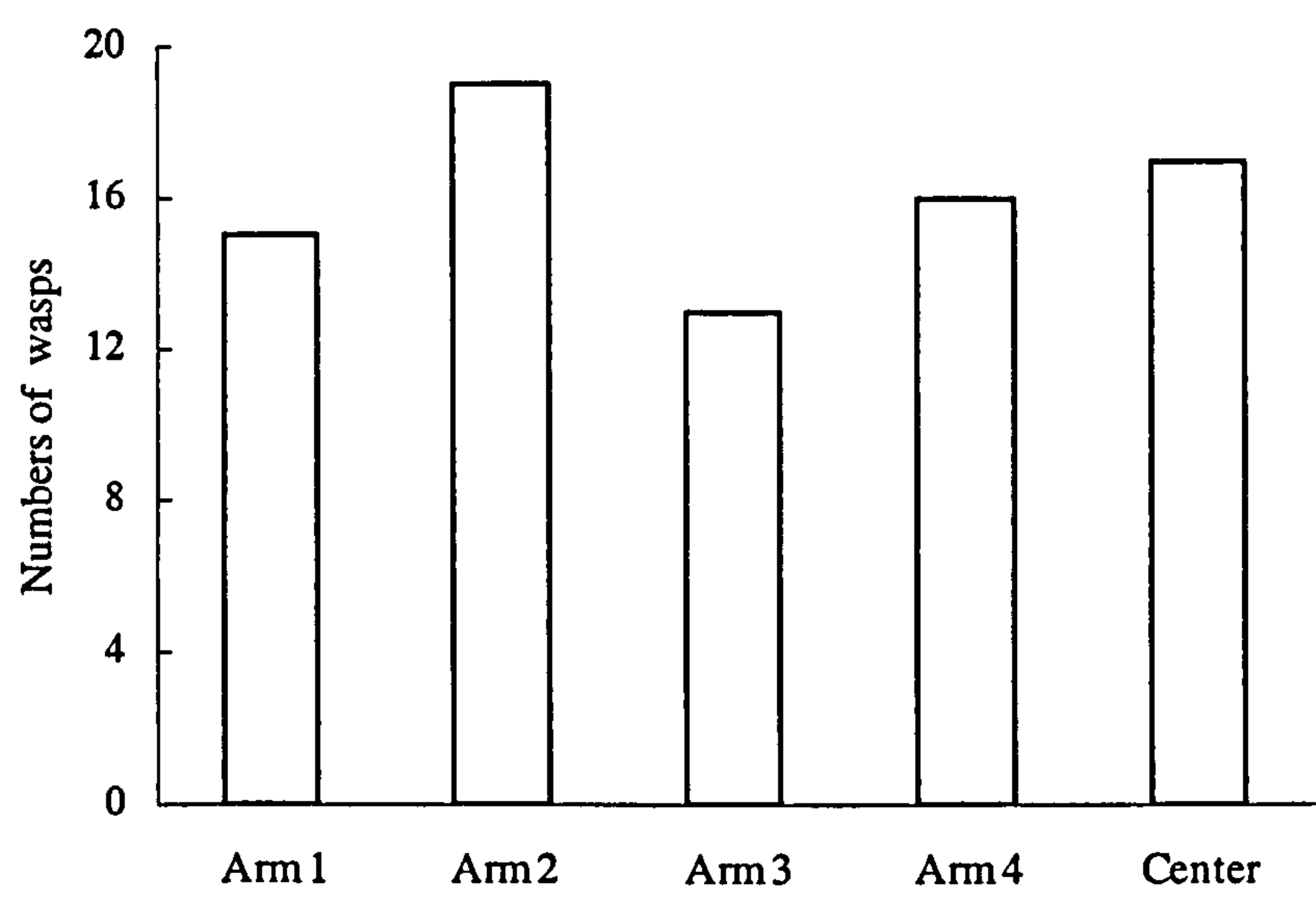


Fig. 3.2. Olfactometer control test with *C. plutellae* using empty arms ($\chi^2 = 1.25$, $P > 0.05$).

3.4.1.1 Tests with the parasitoids reared from Chinese cabbage

Olfactometer tests with naive (inexperienced) *C. plutellae* reared from DBM larvae feeding on Chinese cabbage revealed that *C. plutellae* significantly ($P < 0.001$) preferred the odour from young Chinese cabbage to the odours from old common cabbages (Fig. 3.3A-B). Similarly, the odour from young Chinese cabbage-DBM larvae complex was significantly ($P < 0.001$ and $P < 0.005$) preferred to those from old common cabbage-DBM larvae complexes (Fig. 3.3C-D).

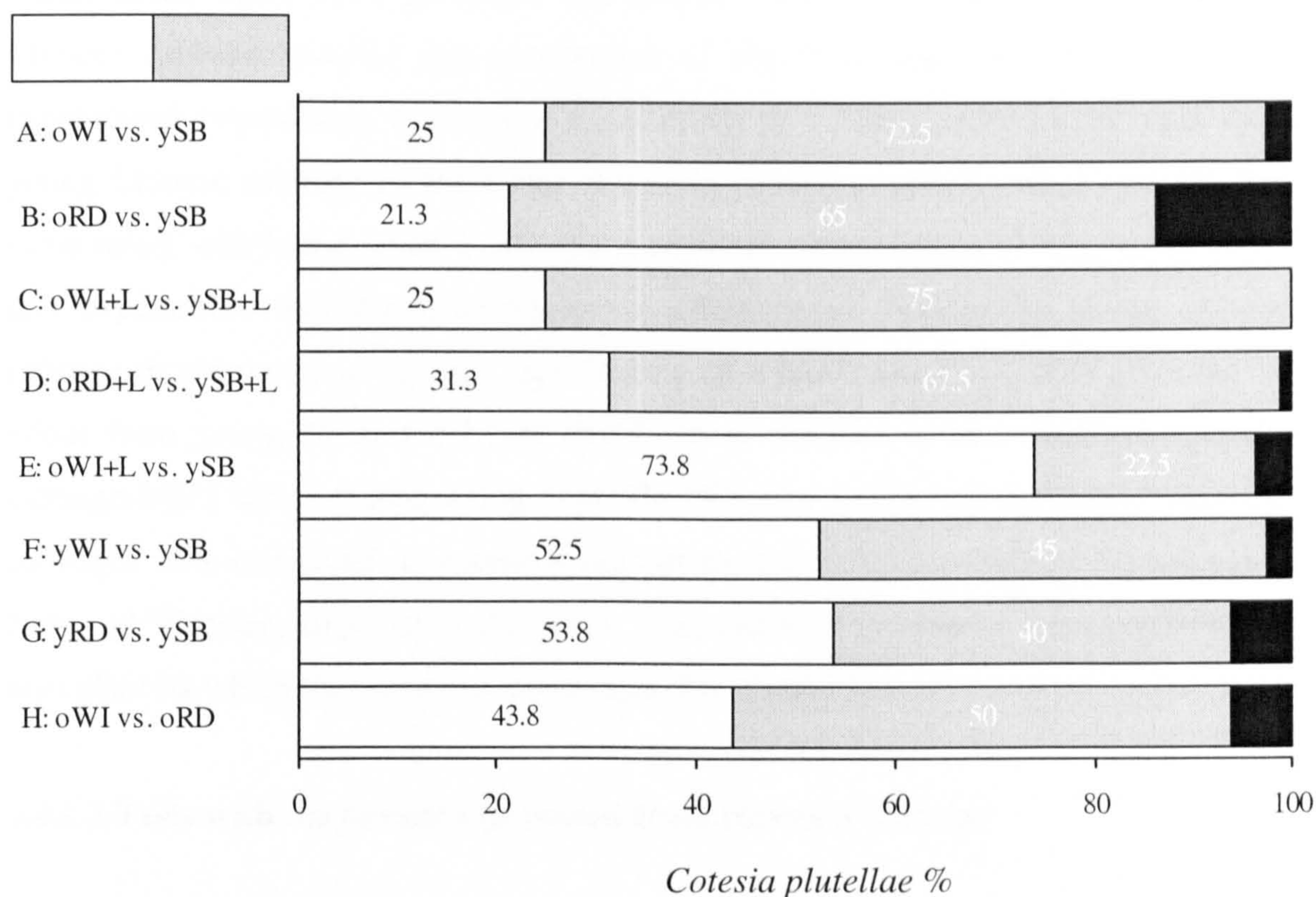


Fig. 3.3. Preferences of naive *C. plutellae* (reared from DBM larvae feeding on Chinese cabbage) towards different plants and plant-host complexes. (A) $\chi^2 = 18.5$; (B) $\chi^2 = 17.8$; (C) $\chi^2 = 20.0$; (D) $\chi^2 = 10.6$; (E) $\chi^2 = 21.8$; (F) $\chi^2 = 0.46$; (G) $\chi^2 = 1.61$; (H) $\chi^2 = 0.33$; white and grey bars indicate the percentage of the wasp preferred for the treatments, and black bars indicate non-responsive wasps; SB = Chinese cabbage cv. F₁ One Kilo SB; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; y = young (4 weeks old); o = old (15 weeks old); L = DBM larvae; asterisks indicate significant differences between choice tests: ***, ** and NS show P-values of < 0.001, < 0.005 and > 0.05, respectively.

However, *C. plutellae* was significantly ($P < 0.001$) more responsive to common cabbage-DBM larvae complex than Chinese cabbage alone (Fig. 3.3E). The different results emerged when young common cabbages were used. *C. plutellae* did not show any significant ($P > 0.05$) preference between the odour from young Chinese cabbage and the odours from young common cabbages (Fig. 3.3F-G). In addition, when two different cultivars of common cabbage were compared *C. plutellae* equally responded to the odours from old Wheelers Imperial and old Red Drumhead (Fig. 3.3H).

Olfactometer tests with experienced *C. plutellae* reared from DBM larvae feeding on Chinese cabbage showed that irrespective of the host plant on which the wasps experienced ovipositions, *C. plutellae* significantly ($P < 0.001$) preferred the odour from young Chinese cabbage to the odour from old common cabbage (Fig. 3.4A-B). The same result was found when plant-host complexes were compared. *Cotesia plutellae* that experienced multiple ovipositions on DBM larvae feeding on young Chinese cabbage or old common cabbage significantly ($P < 0.001$ and $P < 0.005$) preferred the odour from young Chinese cabbage-DBM larvae complex to that from old common cabbage-DBM larvae complex (Fig. 3.4C-D). When two different cultivars of common cabbages were compared, *C. plutellae* did not significantly ($P > 0.05$) prefer the odour from old Wheelers Imperial or the odour from old Red Drumhead, irrespective of the host plant on which the wasp had experience (Fig. 3.4E-F).

3.4.1.2 Tests with the parasitoids reared from common cabbage

Olfactometer tests with naive and experienced *C. plutellae* reared from DBM larvae feeding on common cabbage cv. Wheelers Imperial showed that when naive parasitoids were used, *C. plutellae* did not show any significant ($P > 0.05$) preference for the odour from young Chinese cabbage or the odour from old common cabbage (Fig. 3.5A). This result was repeated when *C. plutellae* experienced parasitization of DBM larvae on old common cabbage before performing the test (Fig. 3.5C). However, after multiple ovipositions experience on DBM larvae feeding on young Chinese cabbage, *C. plutellae* significantly ($P < 0.05$) preferred the odour from young Chinese cabbage to that from old common cabbage (Fig. 3.5B).

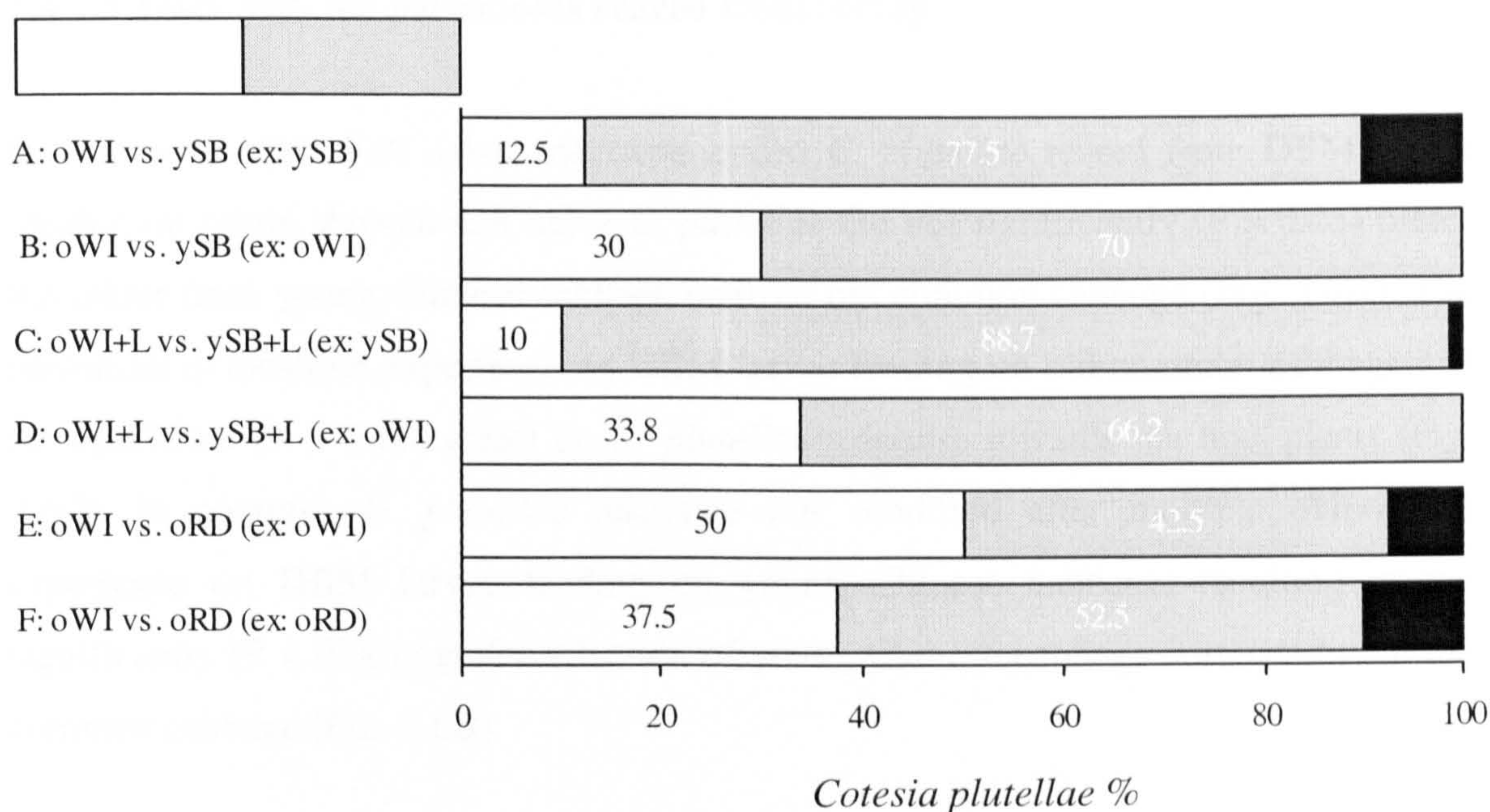


Fig. 3.4. Preferences of experienced *C. plutellae* (reared from DBM larvae feeding on Chinese cabbage) towards different plants and plant-host complexes. (A) $\chi^2 = 37.6$; (B) $\chi^2 = 12.8$; (C) $\chi^2 = 50.2$; (D) $\chi^2 = 8.45$; (E) $\chi^2 = 0.49$; (F) $\chi^2 = 2.0$; white and grey bars indicate the percentage of the wasp preferred for the treatments, and black bars indicate non-responsive wasps; SB = Chinese cabbage cv. F₁ One Kilo SB; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; y = young (4 weeks old); o = old (15 weeks old); L = DBM larvae; ex = the host plant on which the parasitoids experienced multiple ovipositions on DBM larvae before performing the test; asterisks indicate significant differences between choice tests: ***, ** and NS show P-values of < 0.001, < 0.005 and > 0.05, respectively.

When plant-host complexes were compared, naive *C. plutellae* significantly ($P < 0.05$) chose the odour from young Chinese cabbage-DBM larvae complex compared with old common cabbage-DBM larvae complex (Fig. 3.5D). The parasitoid oviposition experience on DBM larvae feeding on young Chinese cabbage did not change the parasitoid preference towards plant-host complexes (Fig. 3.5E). In contrast, the parasitoid oviposition experience on DBM larvae developing on old common cabbage altered the parasitoid preference towards plant-host complexes, resulting in no significant ($P > 0.05$) preference for any of plant-host complexes (Fig. 3.5F).

3.4.1.3 Tests with the parasitoids reared from turnip

Olfactometer tests with naive and experienced *C. plutellae* reared from DBM larvae feeding on turnip showed that naive *C. plutellae* did not significantly ($P > 0.05$) prefer the odour from young Chinese cabbage or from old common cabbage (Fig. 3.6A). The parasitoid oviposition experience on DBM larvae feeding on old common cabbage had no significant ($P > 0.05$) effect on *C. plutellae* response towards the host plants (Fig. 3.6C). In contrast, *C. plutellae* response was modified after multiple oviposition experience on DBM larvae feeding on young Chinese cabbage, resulting in the significantly ($P < 0.001$) greater selection of young Chinese cabbage compared with old common cabbage (Fig. 3.6B).

When plant-host complexes were compared, naive *C. plutellae* significantly ($P < 0.005$) preferred the odour from young Chinese cabbage-DBM larvae complex compared with the odour from old common cabbage-DBM larvae complex (Fig. 3.6D). The parasitoid oviposition experience did not alter the parasitoid preference towards plant-host complexes (Fig. 3.6E-F).

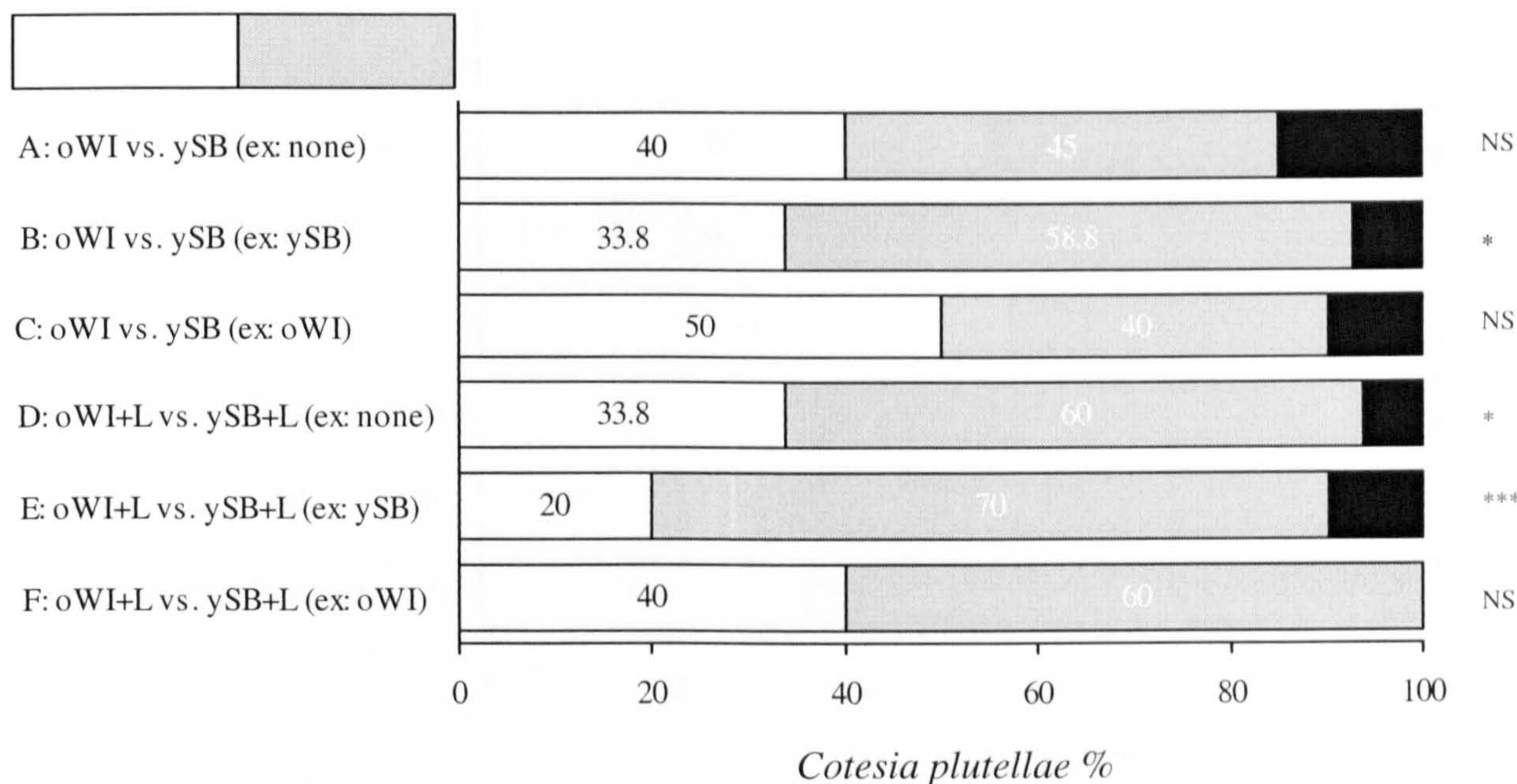


Fig. 3.5. Preferences of naive and experienced *C. plutellae* (reared from DBM larvae feeding on common cabbage cv. Wheelers Imperial) towards different plants and plant-host complexes. (A) $\chi^2 = 0.24$; (B) $\chi^2 = 5.41$; (C) $\chi^2 = 0.89$; (D) $\chi^2 = 5.88$; (E) $\chi^2 = 22.2$; (F) $\chi^2 = 3.20$; white and grey bars indicate the percentage of the wasp preferred for the treatments, and black bars indicate non-responsive wasps; SB = Chinese cabbage cv. F₁ One Kilo SB; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; y = young (4 weeks old); o = old (15 weeks old); L = DBM larvae; ex = the host plant on which the parasitoids experienced multiple ovipositions on DBM larvae before performing the test; asterisks indicate significant differences between choice tests: ***, * and NS show P-values of < 0.001, < 0.05 and > 0.05, respectively.

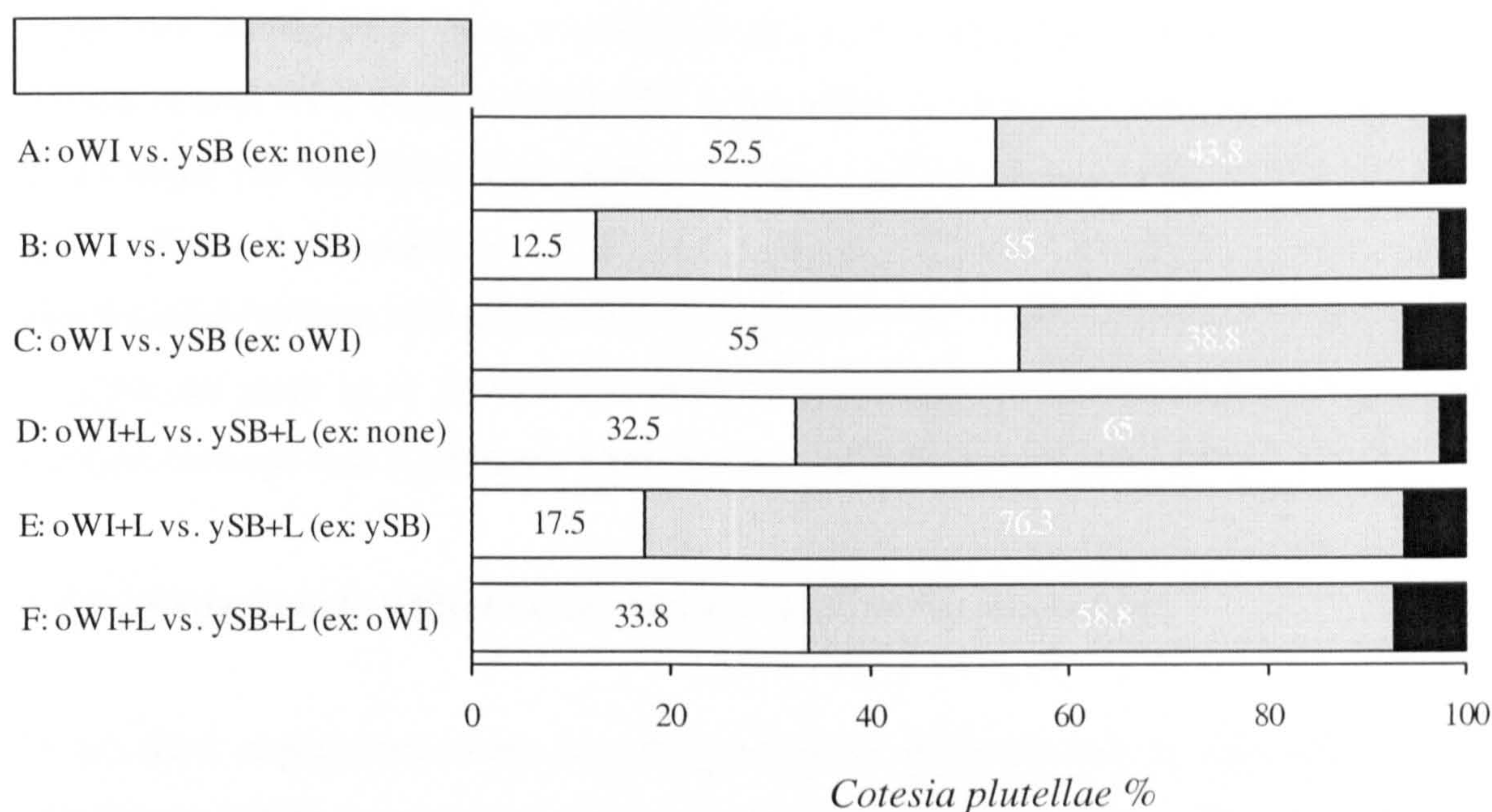


Fig. 3.6. Preferences of naive and experienced *C. plutellae* (reared from DBM larvae feeding on turnip) towards different plants and plant-host complexes. $\chi^2 = 0.64$; (B) $\chi^2 = 43.1$; (C) $\chi^2 = 2.25$; (D) $\chi^2 = 8.67$; (E) $\chi^2 = 29.5$; (F) $\chi^2 = 5.41$; white and grey bars indicate the percentage of the wasp preferred for the treatments, and black bars indicate non-responsive wasps; SB = Chinese cabbage cv. F₁ One Kilo SB; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; y = young (4 weeks old); o = old (15 weeks old); L = DBM larvae; ex = the host plant on which the parasitoids experienced multiple ovipositions on DBM larvae before performing the test; asterisks indicate significant differences between choice tests: ***, **, * and NS show P-values of <0.001, <0.005, <0.05 and >0.05, respectively.

3.4.2 Cage experiments

3.4.2.1 Experiments with longer exposure time to the parasitoids

In the first experiment, percentage parasitism by *C. plutellae* on DBM larvae feeding on the two host plants showed no significant difference (Table 3.3; z-value = 1.120, d.f. = 6, P = 0.263). However, the mean number of *C. plutellae* cocoons per plant was

significantly different between the two host plants ($t_6 = 3.1516$, $P < 0.05$). The number of cocoons formed on *B. rapa* was significantly greater than that on *B. napus*.

Similar results were observed in the 2nd experiment, in which the level of parasitism by *C. plutellae* did not differ significantly between DBM larvae feeding on the two host plants (Table 3.3; z -value = -1.225, d.f. = 6, $P = 0.221$). Nonetheless, there was a significant difference between the two host plants for the mean number of the parasitoid cocoons per plant ($t_6 = 2.5828$, $P < 0.05$). The number of cocoons formed on young Chinese cabbage was significantly greater than on old common cabbage.

3.4.2.2 Experiments with shorter exposure time to the parasitoids

In the third experiment, there was a significantly different rate of parasitism by *C. plutellae* on DBM larvae reared on the two host plants (Table 3.4; z -value = -10.03, d.f. = 6, $P < 0.001$). The proportion of hosts on young Chinese cabbage attacked by *C. plutellae* was significantly greater than for DBM larvae feeding on intermediate common cabbage. The mean number of *C. plutellae* cocoons per plant also differed significantly between the two host plants ($t_6 = 6.4828$, $P < 0.005$). The mean number of cocoons formed per plant on young Chinese cabbage was significantly greater than that on intermediate common cabbage.

Similar results were observed in the 4th and 5th experiments, in which a susceptible host plant (young Chinese cabbage) and a partially-resistant host plant (old common cabbage) were compared (Table 3.4). In the 4th experiment, percentage parasitism of DBM larvae by *C. plutellae* (reared from DBM larvae on Chinese cabbage) on the two host plants was significantly different (z -value = -11.61, d.f. = 6, $P < 0.001$). The proportion of hosts on young Chinese cabbage attacked by *C. plutellae* was significantly greater than for DBM larvae feeding on old common cabbage. Moreover, the mean number of cocoons per plant was significantly greater on young Chinese cabbage compared with old common cabbage ($t_6 = 11.4799$, $P < 0.001$).

Table 3.3. Cage experiments with long exposure¹ to the parasitoid. TT = Chinese cabbage cv. Tip Top, and WI = common cabbage cv. Wheelers Imperial.

<i>Experiment</i>	<i>Parasitoid source^{2,3}</i>	<i>Host plants</i>	<i>Mean (± s.e.) cocoons per plant</i>	<i>P-value</i>	<i>Percentage parasitism</i>	<i>P-value</i>
1	TT (4)	<i>B. rapa</i> (6)	34.9 ± 2.0	< 0.05	96.5	> 0.05
		<i>B. napus</i> (8)	25.6 ± 2.1		94.5	
2	Turnip (4)	TT (4)	31.8 ± 1.8	< 0.05	71.6	> 0.05
		WI (15)	25.3 ± 1.8		75.9	

¹Two female *C. plutellae* released per cage; exposure time to parasitoid = 4 days.

²Plant on which parasitoids were reared from DBM larvae.

³The number in parentheses refers to the age of plants in weeks.

Table 3.4. Cage experiments with short exposure¹ to the parasitoid. TT = Chinese cabbage cv. Tip Top, and WI = common cabbage cv. Wheelers Imperial.

<i>Experiment</i>	<i>Parasitoid source^{2,3}</i>	<i>Host plants</i>	<i>Mean (± s.e.) cocoons per plant</i>	<i>P-value</i>	<i>Percentage parasitism</i>	<i>P-value</i>
3	TT (4)	TT (4)	38.4 ± 1.6	<0.005	83.7	<0.001
		WI (8)	19.0 ± 2.5		45.9	
4	TT (4)	TT (5)	35.4 ± 1.8	<0.001	81.6	<0.001
		WI (15)	9.6 ± 1.3		31.4	
5	WI (4)	TT (5)	29.3 ± 1.9	<0.001	69.0	<0.001
		WI (15)	6.5 ± 0.7		19.1	

¹Four female *C. plutellae* released per cage; exposure time to the parasitoid = 24 h.

²Plant on which parasitoids were reared from DBM larvae.

³The number in parentheses refers to the age of plants in weeks.

In the 5th experiment, which was a repeat of 4th but with the parasitoids reared from DBM larvae feeding on common cabbage, there also was a significant difference between the two host plants for level of parasitism (z-value = -11.576, d.f. = 6, $P < 0.001$). The proportion of DBM larvae feeding on young Chinese cabbage attacked by *C. plutellae* was significantly greater than that on old common cabbage. In addition, the mean number of *C. plutellae* cocoons per plant was significantly different on the two host plants ($t_6 = 10.9551$, $P < 0.001$). The mean numbers of cocoon formed per plant on young Chinese cabbage were significantly greater than that on old common cabbage.

3.5 Discussion

In the present study, a series of olfactometer tests and cage experiments have shown that host plant resistance can significantly influence foraging behaviour and parasitism success of *C. plutellae*. The searching efficiency of parasitoids is basic to the host-parasitoid population dynamics, the evolution of host and parasitoid behaviour, and in biological control programmes (Bottrell *et al.*, 1998; Vet, 2001; Gingras & Boivin, 2002; Schellhorn *et al.*, 2002). Plant volatiles play a major role in searching efficiency of parasitoids towards their host (Chadwick & Goode, 1999; van Tol *et al.*, 2001; Hilker & Meiners, 2002; Lou & Cheng, 2003). Olfactometer tests demonstrated that *C. plutellae* did not differentiate between different plant types when both the plant types offered were susceptible (young Chinese cabbage vs. young common cabbage) or partially resistant (old Wheelers Imperial vs. old Red Drumhead). In contrast, *C. plutellae* exhibited the capability to distinguish between the odours from susceptible (young Chinese cabbage) and partially-resistant plants (old common cabbages) whether plants were uninfested or infested with feeding larvae.

In the present study, *C. plutellae* was found to have a strong tendency to choose uninfested young Chinese cabbage in comparison to uninfested old common cabbages. This plant-mediated response happened either when *C. plutellae* was reared on Chinese cabbage or when *C. plutellae* was reared on common cabbage or turnip but experienced on Chinese cabbage. The former may be due to experience by the parasitoid larva of plant chemicals present in the DBM larval body (Bogahawatte & van Emden, 1996); whereas the latter is experience by the parasitoid adult on plant or plant-host

allelochemicals (Potting *et al.*, 1999; Liu & Jiang, 2003). In contrast, experience by the parasitoid larva and adult on common cabbage did not affect *C. plutellae* choice towards uninfested old common cabbages, either when young Chinese cabbage and old common cabbages or when two different cultivars of old common cabbages were compared.

Secondary plant products, such as glucosinolates and their relatives, can vary markedly among host plants of DBM (van Etten *et al.*, 1976; Verkerk & Wright, 1994b; Harvey *et al.*, 2003). It is known that the glucosinolate contents of crucifers, which play an important role in producing allelochemicals that attract parasitoids (Bradburne & Mithen, 2000), vary by plant age (Karowe *et al.*, 1997). The reduction of glucosinolate contents and the specific activity of myrosinase in old crucifers (Porter *et al.*, 1991; Renwick *et al.*, 1992; Kiddle *et al.*, 1994; Mevy *et al.*, 1997; Wallace & Eigenbrode, 2002; Lambdon *et al.*, 2003) is likely to be the reason for non-preferential response of *C. plutellae* towards old common cabbages. Furthermore, the fact that increased glucosinolate production in young crucifers favours both herbivores and parasitoids (Benrey *et al.*, 1998; Harvey *et al.*, 2003) may explain the preference of *C. plutellae* for a susceptible host plant, young Chinese cabbage.

It was also shown that *C. plutellae* have a strong preference for infested young Chinese cabbage compared with infested old common cabbages, regardless of the host plant on which the parasitoid reared. Parasitoid learning in this regard appeared to have no influence on *C. plutellae* preference. The distinct response of *C. plutellae* for young Chinese cabbage-DBM complex is plausible to be because of highly release of herbivore-induced synomones (Mattiacci *et al.*, 1994; Geervliet *et al.*, 1997; Souissi *et al.*, 1998) by infested young Chinese cabbage. However, the significant attraction of *C. plutellae* towards the old common cabbage-DBM larvae complex compared with uninfested young Chinese cabbage points to the importance of the host as a paramount factor in the host location behaviour by this parasitoid (Bogahawatte & Van Emden, 1996; Potting *et al.*, 1999; Shiojiri *et al.*, 2000a,b).

The effects of learning varied with the host plant on which the parasitoids reared and with the host plant on which adult parasitoid experience happened. When parasitoids were reared on Chinese cabbage, oviposition experience appeared to slightly increase the number of the parasitoids responded to the host plants. However, this effect was not

significant. When parasitoids were reared on common cabbage or turnip, oviposition experience on DBM larvae feeding on young Chinese cabbage led *C. plutellae* to choose young Chinese cabbage to a significantly greater extent. Interestingly, oviposition experience on DBM larvae feeding on old common cabbage did not alter the *C. plutellae* preference towards host plants. When plant-host complexes were compared, learning was not influential; except when the parasitoids (reared on common cabbage) experienced oviposition on old common cabbage, resulting in modification of *C. plutellae* preference; in contrast to naive parasitoids (which showed significant preference for infested young Chinese cabbage), experienced *C. plutellae* did not prefer any of plant-host complexes.

The cage experiments indicated that for short exposure times *C. plutellae* preferred to parasitize DBM larvae kept on susceptible host plant (young Chinese cabbage) compared with DBM larvae on partially-resistant host plants (intermediate or old common cabbage). Such a preference was likely because of the greater attraction *C. plutellae* towards infested Chinese cabbage (as was found by olfactometer results). *Cotesia plutellae* has also been reported to have a narrow-area search around feeding damage sites (Wang & Keller, 2002). This implies that *C. plutellae* would remain in a preferred microhabitat (such as infested Chinese cabbage) rather than searching other microhabitats. However, this preference disappeared when the exposure time to the parasitoid was increased. This has implications for patch use and redistribution of parasitoids based on the frequency of unparasitized host encountered by parasitoids (Godfray, 1994).

The greater number of *C. plutellae* cocoons (as a measure of successful parasitism) on susceptible host plants (*B. rapa* or young Chinese cabbage) compared with partially-resistant host plants (*B. napus*, intermediate or old common cabbages) may be due either to the preference of *C. plutellae* for susceptible host plants (as was indicated by olfactometer tests) or due to a lower rate of survival of parasitized larvae on partially-resistant host plants (Verkerk & Wright, 1994a). Studies of tritrophic interactions have shown that plant quality may influence the success of natural enemies (Raymond *et al.*, 2002; Kopelke, 2003; Campan & Benrey, 2004; Helms *et al.*, 2004). Despite beneficial interactions in compatible integration of partially-resistant plants and parasitoids (Biswas & Singh, 1998; McAuslane *et al.*, 2000; Schmale *et al.*, 2003), plant resistance

may negatively affect on development and success of parasitoids (Campbell & Duffey, 1979; Orr & Boethel, 1986; Mannion *et al.*, 1994).

In the present study, the negative effects of partially-resistant host plants on *C. plutella*, in terms of both reduced preference for and less parasitism success on such plants, indicates that the use of such plants and *C. plutellae* is incompatible for management of DBM.

Chapter 4:

Effects of host-plant resistance on the innate immune response of *Plutella xylostella*

4.1 Abstract

The effects of host-plant resistance on the diamondback moth (DBM), *Plutella xylostella*, innate immune system were studied using measures of cellular (encapsulation) and humoral (phenoloxidase activity) effectors in unparasitized larvae and in larvae parasitized by *Cotesia plutellae*. Host-plant resistance affected the percentage of parasitized larvae, the intensity of superparasitism and the encapsulation proportion of parasitoid larvae. DBM reared on a partially-resistant host, the common cabbage cv. Wheelers Imperial, showed a significantly greater parasitoid egg load and proportion of parasitized hosts compared to a fully susceptible host, Chinese cabbage. The encapsulation proportion of *Cotesia plutellae* larvae was significantly greater on Chinese cabbage, than on Wheelers Imperial. Encapsulation was significantly greater on Wheelers Imperial compared with another partially-resistant common cabbage cv. Red Drumhead, and all three had significantly greater encapsulation compared with the fully-resistant host, the cauliflower cv. Early Green Glazed. However, the encapsulation ability of DBM larvae was not strong enough to effect parasitism. In unparasitized DBM, phenoloxidase activity was significantly greater in larvae reared on Chinese cabbage or cv. Wheelers Imperial compared with larvae reared on cv. Red Drumhead or Early Green Glazed. However, there was no significant difference in phenoloxidase activity in parasitized larvae reared on the different host plants. Superparasitism had no effect on the ability of DBM larvae to encapsulate *Cotesia plutellae* larvae. The greater parasitism rate of DBM larvae reared on partially-resistant host plants compared with Chinese cabbage appears to be due to the greater proportion of larvae parasitized by *C. plutellae* rather than the number of eggs laid.

4.2 Introduction

A herbivore's ability to encapsulate parasitoid eggs and larvae can be influenced by plant nutrition, resistance and allelochemicals (Cheng, 1970; Rhoades, 1983; Benrey & Denno, 1997; Blumberg 1997; Souissi & Le Ru, 1998; Turlings & Benrey, 1998; Calatayud *et al.*, 2002). In general the success of the encapsulation reaction depends on the vigour of the herbivore, which can be decreased by host plant-induced stresses such as poor nutrition, starvation, or high level of allelochemicals (Muldrew, 1953; Salt 1956, 1964; van den Bosch, 1964; Cheng, 1970; Beckage & Riddiford, 1982; Vinson & Barbosa, 1987; Benrey & Denno, 1997; Turlings & Benrey, 1998). A plant with toxins or of low nutritional quality, which causes the host to become weak, may suppress the insect's immune system and thereby benefit the parasitoid (Godfray, 1994; Turlings & Benrey, 1998; Siva-Jothy & Thompson, 2002).

No-choice studies with *C. plutellae* have shown significantly greater rates of parasitism of DBM maintained on a partially-resistant host plant compared with a susceptible one (Verkerk & Wright, 1994b; Karimzadeh *et al.*, 2004). The results suggested that parasitism successes might be affected by plant intrinsic nutritional quality. Considering that parasitization in these experiments took place in the absence of the host plant, it seems that a physiological rather than a behavioural basis for the observed host plant-mediated effects on parasitism rate was involved. It has been suggested that differential host encapsulation resulting from reduced host nutritional status is the main reason for different rates of parasitism of DBM by *C. plutellae* on different host plant groups (Verkerk & Wright, 1994b).

Here, the objective was to test the hypothesis that host plant resistance can challenge the DBM innate immune system. Specifically, cellular (encapsulation) and humoral (phenoloxidase activity) immune functions in unparasitized and parasitized DBM larvae developing on susceptible, partially-resistant and highly-resistant host plants were compared.

4.3 Materials and Methods

4.3.1 Plants and insects

Chinese cabbage, *Brassica pekinensis* cv. Tip Top (Chiltern Seeds, Ulverston, UK), common cabbage, *B. oleracea* var. *capitata* cvs. Wheelers Imperial and Red Drumhead (Suttons Seeds, Devon, UK) and cauliflower, *B. oleracea* var. *botrytis* cv. Early Green Glazed (Plant Introduction 234599; Northeast Regional Plant Introduction Station, Geneva, New York, USA) were grown organically under glasshouse conditions (Section 2.3.1). Four-week-old Chinese cabbage, 15-week-old common cabbages and 12-week-old cauliflower were used as susceptible, partially-resistant and highly-resistant host plants to DBM attack, respectively. An insecticide-susceptible strain of DBM (Roth population) and *C. plutellae* were obtained from Rothamsted Research (Harpenden, UK). Insects were cultured as described in Section 2.3.1.

4.3.2 Development rate of DBM

Individual plants were placed in oviposition cages with DBM adults for 8 h during scotophase. The plants were then removed and kept as above until the larvae reached to the second instar (L2). Batches of 10 L2 DBM were then placed on leaf discs (4.8 cm dia.) within individual Petri dishes (5 cm dia.) containing a moistened filter paper. Leaf discs were cut from randomly selected leaves of different plants for each plant group used in experiments. To prevent starvation of larvae, the leaf discs were replaced every 24 h. Pupa were transferred to Petri dishes and kept until eclosion. Each treatment was replicated 6 times. The experiments were conducted under the standard environmental conditions (Section 2.3.1). The life stage and mortality was recorded daily until all insects either died or emerged as adults. The time from oviposition to pupation (TP) and from oviposition to emergence (TE) was calculated. The percentage survival was calculated at the end of each experiment (Møller, 1988; Verkerk & Wright, 1994a).

4.3.3 Parasitism and encapsulation

In a preliminary test to observe the effects of the host plant on the encapsulation capability of DBM, first instar larvae were reared on different host plants until early third instar. Two different methods were used to examine parasitism: (1) multiple oviposition, where a single, mated three-day-old female of *C. plutellae* was introduced into a plastic Petri dishes (5 cm dia.) containing 10 early L3 DBM; the parasitoid was removed from the Petri dish after 1 h. This treatment was replicated 10 times; (2) single oviposition, where an individual early L3 DBM was exposed to a single, mated three-day-old female of *C. plutellae* and the larva removed immediately after a single oviposition by the parasitoid. Each parasitoid was only offered one larva. This treatment was replicated 50 times. In both methods the DBM larvae were then allowed to feed on the same plant type on which they had fed before parasitism. Insects were maintained under the standard environmental conditions (Section 2.3.1).

After 3 days, the DBM larvae were dissected, and the parasite stage(s) present and a visual estimation of the proportion encapsulation (Cotter & Wilson, 2002) for each parasitoid larvae was recorded using a 10% incremental scale. Identification of *C. plutellae* larval instars was based on Lim (1982). In brief: (1) the first instar larva (caudate-mandibulate form) has a large sclerotized head with distinct mandibles and labrum and a prominent and distinctive caudal horn; (2) the second instar larva (vesiculate form) has no visible sclerotized head and 3-lobed mouth parts (labium and a pair of maxillae). The caudal horn is still present but inconspicuous and largely being masked by the prominent anal vesicle; (3) the third instar larva (hymenopteriform) tapers anteriorly with distinct segmentation and no anal vesicle.

The single oviposition method was used in two further experiments, except that in one experiment the host larvae were dissected after 5 days after parasitism, and in other experiment the larvae were reared until the host had pupated or the parasitoid cocoon had formed.

To compare the effects of the parasitoid egg load (superparasitism) on the encapsulation ability of DBM larvae, five early L4 DBM larvae (reared on Chinese cabbage) were

exposed to the batches of 5 or 20 mated 3-day-old female *C. plutellae* for 1 h. The host larvae then reared on Chinese cabbage and were dissected after 4 days. Each treatment was replicated 10 times.

4.3.4 Phenoloxidase assay

For examination of enzyme activity in unparasitized larvae, batches of 10, 2-day-old L2 DBM were placed in individual Petri dishes (5 cm dia.) and reared on leaf discs from the appropriate host plant (as described in Section 4.3.3) until the late L4 stage but prior to cessation of feeding. For studies on parasitized larvae, the single oviposition method (Section 4.3.3) was used and the DBM larvae were then reared on leaf discs as above until the late L4 stage.

To measure phenoloxidase (PO) activity, haemolymph (2 µl) was collected from late fourth instar DBM larvae and placed into 30 µl of phosphate-buffered saline (PBS), pH 7.4, in a 0.5 ml Eppendorf tube on ice. Haemolymph samples were immediately frozen at -80°C to disrupt haemocyte membranes. Frozen samples were then thawed to 4°C on ice and centrifuged at 12000 g at 4°C for 10 min and the supernatant was removed and used for the assay. An aliquot (2 µl) of the supernatant was immediately used for protein assay and a second aliquot (20 µl) was incubated for 20 min at 20°C to activate PO. Phenoloxidase activity was then assayed spectrophotometrically using 3,4-D-L-dihydroxyphenylalanine (L-DOPA) as a substrate. One ml of 10 mM L-DOPA in PBS was added to 20 µl of the supernatant and the absorbance was measured at 490 nm after 5 and 15 min at 20°C. Negative controls contained 10% w/v 1-phenyl-2-thiourea (PTU), a known inhibitor of phenoloxidases (Reeson *et al.*, 1998; Moreau *et al.*, 2000; Wilson *et al.*, 2001; Siva-Jothy & Thompson, 2002). Protein concentration was measured by the Bradford micro-assay using bovine serum albumin as the standard (Bradford, 1976; Sedmak & Grossberg, 1977). PO specific activity was calculated as units per mg protein. One unit represents 0.001 absorbance at 490 nm per min.

4.3.5 Data analysis

Differences in the levels of parasitism and the survival rates were analysed using logistic analysis of deviance (binomial error). The developmental periods were analysed using nested ANOVA (except pupal periods, which were analysed using Student's t-test). The number of *C. plutellae* larvae per DBM larva were analysed using analysis of deviance (Poisson error). Encapsulation proportions were arc-sine transformed and analysed using one-way ANOVA (for single oviposition data) and nested ANOVA (for multiple oviposition data). PO data were analysed using one-way ANOVA. Pair comparisons were performed using Student's t-test (Crawley, 2002). All statistical analyses were completed in S-Plus 6.1 (Insightful Corp., Seattle).

4.4 Results

4.4.1 Developmental rate of DBM

The egg-pupa (d.f. = 10, F = 244.18, P<0.001) and egg-adult (d.f. = 10, F = 257.47, P<0.001) development times for DBM on old common cabbage were significantly greater than on young Chinese cabbage (Table 4.1). In contrast, the plant groups showed no significant difference for pupal period ($t_{10} = -0.953$, P>0.05) or survival rate (d.f. = 10, F = 1.4833, P > 0.05).

Table 4.1 Mean ($\pm$ s.e) development time and survival rate of DBM on different plant groups at 25 °C.

Parameter	Host plant ²		P-value
	TT	WI	
Egg-pupa period (days)	10.0 $\pm$ 0.2 ¹	18.1 $\pm$ 0.5	< 0.001
Egg-adult period (days)	15.4 $\pm$ 0.2	23.8 $\pm$ 0.5	< 0.001
Pupal duration (days)	5.5 $\pm$ 0.2	5.7 $\pm$ 0.1	> 0.05
Survival (%) ¹	76.7 $\pm$ 7.1	66.7 $\pm$ 4.9	> 0.05

¹ Survival from L2 to adult emergence.

² TT = Chinese cabbage cv. Tip Top; WI = common cabbage cv. Wheelers Imperial.

4.4.2 Preliminary parasitism study

Cotesia plutellae eggs were not found to be encapsulated. The parasitoid larvae were observed to be encapsulated at the first and early second instar.

4.4.3 Multiple oviposition experiment

The proportion of DBM larvae parasitized by *C. plutellae* kept on common cabbage was significantly greater (d.f. = 18, F = 9.2923, P < 0.005) than that on Chinese cabbage (Table 4.2). The number of *C. plutellae* larvae per parasitized DBM larva feeding on common cabbage was significantly greater (d.f. = 172; z-value = 2.418; P < 0.05) than on Chinese cabbage (Table 4.2). DBM larvae reared on Chinese cabbage showed a significantly greater (d.f. = 10, F = 7.5165, P < 0.05) encapsulation proportion compared with DBM larvae reared on common cabbage (Table 4.2).

Table 4.2. Effects of host-plant resistance on *C. plutellae* egg load and DBM encapsulation ability.

Parameter	Host plant ¹		P-value
	TT	WI	
Parasitized DBM larvae %	56.9	88.5	< 0.005
Mean parasitoid larvae/parasitized host	1.02	1.43	< 0.05
Mean encapsulation proportion	0.65	0.35	< 0.05

¹ TT = Chinese cabbage cv. Tip Top; WI = common cabbage cv. Wheelers Imperial.

4.4.4 Single oviposition experiment

At 3 days after parasitism, there was a significant (d.f. = 155, F = 111.45, P < 0.001) difference in the proportion of late 1st instar parasitoid larvae encapsulation proportion between host plants. The encapsulation proportion of parasitoid larvae in DBM larvae feeding on Chinese cabbage was significantly greater than on common cabbage cv. Wheelers Imperial (Table 4.3), which in turn was significantly greater than on common

cabbage cv. Red Drumhead. Encapsulation for all these treatments was significantly greater than on the highly resistant cauliflower, Early Green Glazed.

At 5 days after parasitism, there was a significant (d.f. = 169, F = 6.4508, P < 0.001) difference in the encapsulation proportion of 2nd instar parasitoid larvae between host plants. The encapsulation proportion of parasitoid larvae in DBM larvae feeding on Chinese cabbage was significantly greater than on other host plants (Table 4.3). When parasitized larvae reared until DBM pupation or parasitoid cocoon formation, there was no significant difference between (d.f. = 36, F = 6.338 x 10⁻⁶, P > 0.05) host plants regard to parasitism success.

Table 4.3. Effects of host-plant resistance on DBM encapsulation ability and the parasitism success of *C. plutellae*.

Parameter		Host plant ^{1,2}				P-value
		TT	WI	RD	PI	
Encapsulation proportion	Late 1 st instar parasitoid larvae	0.28 a	0.08 b	0.04 c	0.01 d	< 0.001
	2 nd instar parasitoid larvae	0.01 a	0 b	0 b	0 b	< 0.001
Parasitism success (%)		100 a	100 a	100 a	100 a	> 0.05

¹ TT = Chinese cabbage cv. Tip Top; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; PI = cauliflower cv. Early Green Glazed (Plant Introduction 234599).

² Values sharing a common letter are not significantly different (P > 0.05).

PO specific activity varied significantly (d.f. = 36, F = 5.1968, P < 0.01) between unparasitized DBM larvae feeding on different host plants. DBM larvae reared on Chinese cabbage and common cabbage cv. Wheelers Imperial showed a significantly greater phenoloxidase specific activity than DBM larvae reared on common cabbage cv. Red Drumhead and Early Green Glazed (Fig. 4.1). In contrast, parasitized DBM larvae reared on the different host plants did not show any significant (d.f. = 36, F = 0.4857, P > 0.05) difference for phenoloxidase specific activity.

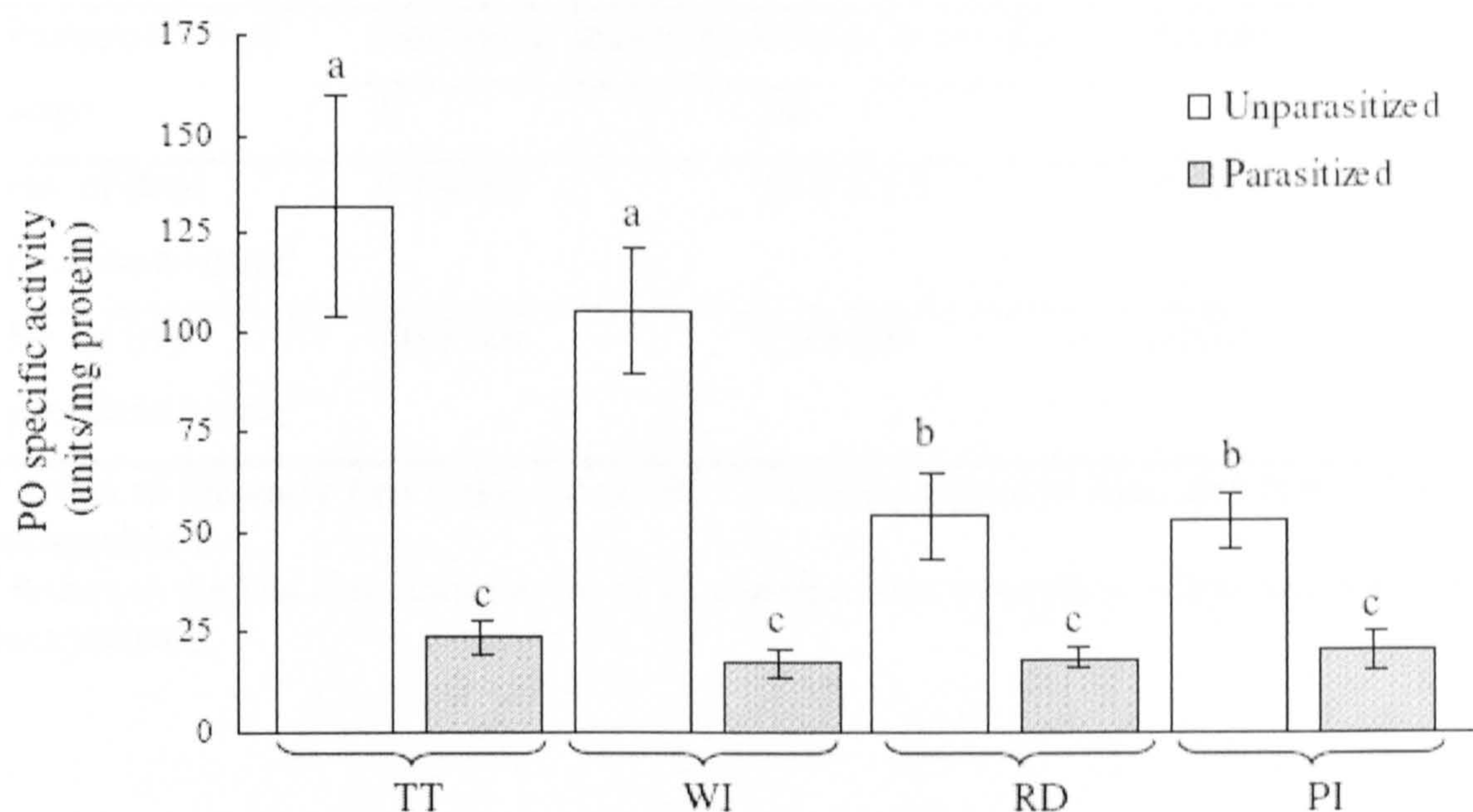


Fig. 4.1. Effects of host-plant resistance on phenoloxidase activity of unparasitized and parasitized DBM larvae. TT = Chinese cabbage cv. Tip Top; WI = common cabbage cv. Wheelers Imperial; RD = common cabbage cv. Red Drumhead; PI = cauliflower cv. Early Green Glazed (Plant Introduction 234599); The common letters show non-significant ($P > 0.05$) means. One unit represents 0.001 absorbance at 490 nm per min.

4.4.5 Superparasitism experiment

At 4 days after parasitism there were two different larval categories of *C. plutellae* inside the parasitized DBM larvae: early first instar larvae, which were dead and fully (100 %) encapsulated (hereafter called non-predominant larvae), and late first instar larvae of *C. plutellae* that were alive, active and not (0 %) encapsulated (hereafter called predominant larvae). There were significantly (d.f. = 92, z-value = -20.99, $P < 0.001$) different numbers of non-predominant *C. plutellae* larvae between treatments (Table 4.4) but no significant (d.f. = 92, z-value = 8.37×10^{-18} , $P > 0.05$) difference between the number of predominant *C. plutellae* larvae.

Table 4.4. The effects of superparasitism by *C. plutellae* on encapsulation ability of DBM.

Parasitoid larval stage	Number of parasitoid females in the test		P-value
	5	20	
No. of dead parasitoid larvae ¹	5.7 ± 0.6	23.5 ± 1.7	< 0.001
No. of live parasitoid larvae ²	1.0 ± 0.0	1.0 ± 0.0	> 0.05

¹ Refers to the early first instar larvae of *C. plutellae* that were dead and fully (100 %) encapsulated.

² Refers to the late first instar larvae of *C. plutellae* that were alive, active and not (0 %) encapsulated.

4.5 Discussion

The greater rate of parasitism of DBM maintained on a partially-resistant host plant compared with a susceptible one has been reported previously (Verkerk & Wright, 1994b; Karimzadeh *et al.*, 2004). In the multiple oviposition test, *C. plutellae* showed a tendency to parasitize DBM larvae feeding on common cabbage compared with Chinese cabbage. However, it was not clear from the test that either the greater proportion of parasitized hosts or the greater number of parasitoid eggs laid per host were responsible for the greater rate of parasitism on the partially-resistant host plant. It has been noted that the probability of at least one egg surviving encapsulation in solitary parasitoids is greater when the host contains several eggs (Puttler, 1974; Berberet *et al.*, 1987; Blumberg, 1997; Sagarra *et al.*, 2000). In other words, host cellular immune response may be exhausted by several parasitoid eggs (the multiple target hypothesis; Godfray, 1994).

When considering the lower parasitoid egg load per host larvae and the greater encapsulation proportion for *C. plutellae* larvae in host larvae reared on Chinese cabbage compared with common cabbage the fact that superparasitism may affect the host immune system must be taken in account. From the multiple oviposition test it was not clear whether the greater encapsulation proportion may result in suppression of *C. plutellae* larva or not. The single oviposition test, on the other hand, revealed that DBM

larvae reared on a susceptible host plant had a greater ability to encapsulate *C. plutellae* larva at 3 days post-parasitism compared to DBM on partially- and highly-resistant host plants. However, the degree of encapsulation was reduced in the next developmental stage of the parasitoid larvae (5 days post-parasitism) and all escaped from encapsulation and produced cocoons in each host plant treatment.

The above results indicate that the encapsulation ability of DBM larvae can be completely suppressed by *C. plutellae*. Hymenopteran endoparasitoids are known to be able to impair the host immune response via expression of polydnavirus genes, preventing parasitoid eggs or larvae to be encapsulated (Glinski & Jarosz, 1996; Shelby *et al.*, 1998; Moreau, 2003). Polydnaviruses are symbiotic proviruses of some ichneumonid and braconid wasps that modify the physiology, growth and development of host lepidopteran larvae (Beckage, 1998; Shelby & Webb, 1999). It has been found that *C. plutellae* has numerous virus-like particles (similar to polydnavirus of other Microgastrinae) in the lateral oviduct lumen (Bae & Kim, 2004). The suppression of DBM encapsulation ability is most probably because of the injection of such virus-like particles into the host larval haemocoel at the time of oviposition by *C. plutellae*. It has been also found that DBM larvae parasitized by *C. plutellae* do not undergo pupal metamorphosis (Bae & Kim, 2004). This can explain the present results where complete success of parasitism was achieved after a single oviposition regardless of the host plant on which the DBM larvae fed.

The greater PO specific activity of unparasitized DBM larvae on susceptible and intermediate host plants (Chinese cabbage and common cabbage cv. Wheelers Imperial) compared with partially- and highly-resistant host plants (common cabbage cv. Red Drumhead and Early Green Glazed) implies that host plant resistance may affect the DBM immune system. However, the loss of such a differences in parasitized hosts, where in each treatment the PO activity was greatly reduced, again stresses the overwhelming ability of *C. plutellae* to suppress the DBM immune system. It is well documented that defensive melanization of haemolymph (phenoloxidase activity) may be dramatically inhibited during parasitism and the effect is inducible by polydnavirus (Beckage, 1998; Shelby *et al.*, 2000; Moreau *et al.*, 2003). These results further support the conclusion that the DBM immune system is not able to suppress parasitism by *C. plutellae*, regardless of the host plant on which the host larvae develop.

The superparasitism experiment indicated that the egg load by *C. plutellae* was not determinative. Only one, predominant *C. plutellae* larva succeeded in developing to the 2nd instar, and DBM larvae were able to fully encapsulate all other *C. plutellae* larvae at the early 1st instar regardless of the number of the parasitoid larvae in the host's haemocoel. It was also clear from single oviposition data that DBM larvae were not able to fully encapsulate, and therefore suppress, the only available *C. plutellae* larvae in its haemocoel. The results support the proposal of Vinson (1990), that the multiple target hypothesis is unlikely to be responsible for increased parasitism success in hosts with several eggs. The complete encapsulation of non-predominant *C. plutellae* larvae seems to be because of their interaction with the predominant parasitoid larva, which is likely to have killed or wounded any non-predominant larvae before complete encapsulation. The interaction between competitive solitary endolarval parasitoids can be in the form of physical conflict, chemical attack or resource competition. Physical conflict, which happens between endoparasitoid larvae of approximately the same age, often results in wounding, and these wounded larvae can be easily targeted by host immune system (Godfray, 1994).

The present work shows that following either a single oviposition or superparasitism one predominant larva escapes encapsulation and completes its development. Host-plant effects were not strong enough to change this situation. The egg load, therefore, is unlikely to be responsible for the greater parasitism rate of DBM larvae on partially-resistant host plants. On the contrary, the greater proportion of larvae parasitized by *C. plutellae* on common cabbage seems to be the main reason for the greater parasitism rate of DBM larvae on such a plant. This may be because of olfactory interactions between the host and the parasitoid (not obvious here because of lack of an alternative choice) or because of the reduced fitness of DBM larvae feeding on sub-optimal host plants, resulting in DBM larvae failing to escape from the parasitoid prior to oviposition.

Chapter 5:

Host plant-herbivore-parasitoid models with different functional responses

5.1 Abstract

To study the long-term population dynamics of host plant-herbivore-parasitoid systems, four three-dimensional continuous time models, extending from the logistic Lotka-Volterra predator-prey model, with different functional responses were studied. To explore the local dynamics, the models were analytically and numerically solved for stability and bifurcations. Transcritical, Hopf, fold-Hopf and period-doubling bifurcations were found. For model I, which had linear functional responses, the only possible attractors were fixed points (no periodic solution), including the equilibrium which represents persistence of all three species and equilibria that reflect the extinction of the parasitoid or the herbivore. In addition to fixed points, model II, embedded with a type II functional response for the herbivore and a linear functional response for the parasitoid, showed the existence of periodic orbits (limit cycles for resource-consumer interactions). Model III, with a linear functional response for the herbivore and a type II functional response for the parasitoid, however, showed fixed points as well as tritrophic (resource-consumer-parasitoid) limit cycles. Finally, model IV, with a type II functional response for both herbivore and parasitoid, not only showed all above-mentioned behaviours but also showed chaotic motions. The chaotic motions were numerically explored, tested for sensitivity to initial conditions, and confirmed by calculation of the largest Lyapunov exponent. The route to chaos was found to be via a period-doubling mechanism. The precise numerical integration of the model indicated the processes of period-doubling and period-halving for chaotic regions of model IV. Different strange attractors were found and the effects of different parameter variation on qualitative changes of the model behaviour are discussed. Bottom-up effects of host-plant resistance and top-down effects of parasitoids on the stability of tritrophic system, with special reference to crucifer-DBM-parasitoid systems, are considered. The effects of plant resistance, in this regards, seems to be more fundamental than the relative roles of parasitoids towards establishing sustainable pest management of DBM.

5.2 Introduction

One of the primary themes of theoretical ecology is using mathematics to model and analyse the dynamics of interacting populations (e.g. AlvarezBuylla *et al.*, 1996; Ives & Jansen, 1998; Holt & Polis, 1997; Holt, 2002; Kuijper *et al.*, 2003; Ramos-Jiliberto, 2005). The most famous of all ecology models is the Lotka-Volterra Predator-Prey model, which has been most repeatedly used to describe the dynamics of food chains (e.g. Persson *et al.*, 2001; Letellier *et al.*, 2002; Cavani & Romero, 2003; Kooi *et al.*, 2004; Rui *et al.*, 2004). The classical Lotka-Volterra model, which is composed of a pair of differential equations, shows regular-period cycles in a resource-consumer interaction; the model emerged from the independent works by Lotka (1925), who derived the model to describe the oscillations of chemical concentrations, and Volterra (1926), who proposed the same model to describe the population dynamics of two interacting fish species (a predator and its prey). In contrast with other classical models (e.g. Thompson, 1924; Nicholson, 1933; Varley, 1947; Hassell, 1978; May and Hassell, 1988), which describe synchronized host-parasitoid system with discrete generations, the Lotka-Volterra model assumes that the generations of the interacting populations overlap completely and that birth and death processes are continuous (Mills & Getz, 1996; Hassell, 2000).

For a long time, the Lotka-Volterra predator-prey model has been studied as a two-dimensional flow to explore the general behaviour of the classical, logistic and stochastic versions of the model (see Wangersky, 1978 for a review; Bomze, 1983; Hua *et al.*, 1996; Fernandez-Nunez, 1998; Ahmad & de Oca, 2002; Zeeman, 2002). More recently with increasing importance of the resource-herbivore-natural enemy interactions in food chain dynamics (Section 1.4) attention has focused on analysing the three-dimensional versions of the Lotka-Volterra model to explore fixed points or periodic orbits (van den Driessche & Zeeman, 1998; Xiao & Li, 2000; Shahruz & Kalkin, 2001; Lu & Luo, 2003; Wang, 2003; Rui *et al.*, 2004; Wang & Wu, 2004). The further studies of three-dimensional Lotka-Volterra models have documented chaotic behaviour for deterministic and forced tritrophic models (Hastings & Powell, 1991; Blasius *et al.*, 1999; Blasius & Stone, 2000; Afraimovich *et al.*, 2001; Vandermeer *et al.*, 2001; Aziz-Alaoui, 2002; Letellior & Aziz-Alaoui, 2002).

The present population dynamics study (Chapter 2) revealed some underlying mechanisms of crucifer-DBM-*C. plutellae* dynamics. However, the implementation of similar long-term studies in the field can be a difficult and time-consuming work. In this regard, theoretical tools such as simulation of resource-herbivore-parasitoid dynamics based on appropriate mathematical models might be helpful for our understanding of what may happen in nature. The aim of this work was to study the dynamics of tritrophic (plant-herbivore-parasitoid) food chains using the analysis of three-dimensional logistic models, arising from the extension of predator-prey Lotka-Volterra model embodied types I and II Holling's functional responses. The specific objectives here were to determine the qualitative behaviour of the models in the sense of stability and bifurcations. The possible effects of bottom-up (e.g. host plants) and top-down (e.g. parasitoids) forces on stabilizing these systems and persistence of plant, herbivore and parasitoid populations with special reference to crucifers-DBM-parasitoid systems were sought.

5.3 The model

The model is a three-dimensional, autonomous, nonlinear system extended from classical predator-prey Lotka-Volterra model (Gillman & Hails, 1997; Hassell, 2000). The model is deterministic (no forcing) and assumes that populations have overlapping generations. In the absence of herbivore, the resource dynamics are given by the Logistic equation. The model has the form of:

$$dR/dT = rR(1 - R/K) - \alpha RH \quad (5.1)$$

$$dH/dT = c_1 \alpha RH - d_H H - \gamma HP \quad (5.2)$$

$$dP/dT = c_2 \gamma HP - d_P P \quad (5.3)$$

Where dR/dT , dH/dT and dP/dT are the rate of change of population size of resource (R or host plant), herbivore (H) and parasitoid (P), respectively; r is intrinsic growth rate of resource; K is carrying capacity of environment; α is the rate at which the plant population is eaten by the herbivore (feeding rate of herbivore); γ is the number of parasitoid attack per unit time per herbivore (attack rate of parasitoid); c_1 and c_2 are the conversion factors; d_H and d_P are the death rate of herbivore and parasitoid, respectively.

Equations (5.1)-(5.3) are true for Holling type I feeding response of a herbivore (αR) and functional response of a parasitoid (γH). Those equations can be written for a Holling type II feeding [$\alpha R/(1+\alpha\beta R)$] and functional [$\gamma H/(1+\gamma\mu H)$] responses (Holling, 1959), where β and μ are handling times, as below:

$$dR/dT = rR(1 - R/K) - \alpha RH/(1+\alpha\beta R) \quad (5.4)$$

$$dH/dT = c_1 \alpha RH/(1+\alpha\beta R) - d_H H - \gamma HP/(1+\gamma\mu H) \quad (5.5)$$

$$dP/dT = c_2 \gamma HP/(1+\gamma\mu H) - d_P P \quad (5.6)$$

By considering the two types of feeding and functional responses, four possible models are imaginable. The first model includes type I feeding response by herbivore (αR) and type I functional response of parasitoid (γH) and it is composed of the equations (5.1)-(5.3). The second model includes type II feeding response by herbivore [$\alpha R/(1+\alpha\beta R)$] and type I functional response of parasitoid (γH). It is composed of equations (5.3) and (5.4) as well as the following equation:

$$dH/dT = c_1 \alpha RH/(1+\alpha\beta R) - d_H H - \gamma HP \quad (5.7)$$

The third model includes a type I feeding response by herbivore (αR) and a type II functional response of parasitoid [$\gamma H/(1+\gamma\mu H)$]. It is composed of equations (5.1) and (5.6) as well as the following equation:

$$dH/dT = c_1 \alpha RH - d_H H - \gamma HP/(1+\gamma\mu H) \quad (5.8)$$

The fourth model includes a type II feeding response by herbivore [$\alpha R/(1+\alpha\beta R)$] and a type II functional response of parasitoid [$\gamma H/(1+\gamma\mu H)$] and it is composed of the equations (5.4)-(5.6).

Some specific words are defined in Table 5.1.

Table 5.1. A glossary for the specific words

<i>Word</i>	<i>Meaning</i>
autonomous	not explicitly contain the independent variable (usually time)
bifurcation	a qualitative change in the dynamical behaviour of a system
Cartesian coordinates	rectangular coordinates (the three axes of three-dimensional Cartesian coordinates are linear and perpendicular)
codimension	the number of bifurcation parameters
dimension	the number of dynamical variables
flow	continuous-time dynamical system
Holling's type I functional response	a linear increase in consumption rate with host density up to a threshold level
Holling's type II functional response	a hyperbolic increase in consumption rate that is a function of available host, parasitoid attack rate and handling time
Hopf bifurcation	the bifurcation of a fixed point to a limit cycle
nonlinear	not proportional to the variables
octant	the region of space in Cartesian system (i.e. any one of the eight regions into which space is divided by the three planes of the Cartesian coordinate system)
origin	the point with all zero coordinates in Cartesian coordinates (in three dimensions, where the x-axis, y-axis and z-axis meet)
transcritical bifurcation	the exchange of stability between two equilibrium points

5.4 Analysis of the model

The local behaviour of the nonlinear systems near a hyperbolic (i.e. all the eigenvalues of the Jacobian matrix have non-zero real parts) equilibrium point is qualitatively determined by the behaviour of their linear system near the origin (Perko, 1991). Hence, the linearization method was used to analyse the models. The local stability of equilibria was determined based on the signs of eigenvalues of the characteristic equations resulted from the related Jacobian matrices. To determine stability, simple characteristic equations were solved analytically. Where it was not possible to symbolically solve complicated characteristic equations, Descartes' rule of signs (Kot, 2001) was applied and the results were confirmed by numerical analysis (simulation). To find the solutions, integration method using the fourth order Runge-Kutta (Sprott, 2003) with a uniform time step was used. To ensure relatively high precision integration, the time step was set at 0.01. The parameters that were considered determinative in stability were chosen for bifurcation analysis. The different bifurcation conditions were mathematically tested to find out which bifurcation was happening when the bifurcation parameters changed. All simulations were performed using Mathematica 5.0 (Wolfram Research, Illinois). The detailed analysis has given in Appendix I.

5.5 Results

5.5.1 Model I

Model I has 8 parameters that can make the analysis difficult and the model, therefore, must be simplified. By defining $x = R/K$, $y = \alpha H/r$ and $z = \gamma P/d_H$ as dimensionless variables, and $t = rT$ as dimensionless time variable, the original equations (5.1-5.3) were modified to the following ones with only 4 parameters:

$$\left\{ \begin{array}{ll} dx/dt = (1-x-y)x & (5.9) \\ dy/dt = a(x-b-bz)y & (5.10) \\ dz/dt = c(dy-1)z & (5.11) \end{array} \right.$$

, where $a = c_1 \alpha K/r$, $b = d_H/c_1 \alpha K$, $c = d_P/r$, and $d = c_2 \gamma r/\alpha d_P$ are all positive parameters.

There are four equilibria for the system (5.9-5.11) in the positive octant as $E_i = [x^*, y^*, z^*]$ which are: (1) $E_1 = [0, 0, 0]$; this is the origin of the phase space and happens when all populations go extinct and there is no system; (2) $E_2 = [1, 0, 0]$; this happens when herbivore and parasitoid population go extinct but the resource population persist at carrying capacity level; (3) $E_3 = [b, 1-b, 0]$; this happens when the resource-herbivore interaction persists but the parasitoid population goes extinct; and (4) $E_4 = [1-(1/d), 1/d, (1-(1/d)-b)/b]$; this happens when the whole system (resource-herbivore-parasitoid interaction) persists.

As the equilibria are hyperbolic, the linearization method can reveal the stability of the model, which has nonlinear terms (the Hartman-Grobman theorem; Nayfeh & Balachandran, 1995; see Appendix I for full stability analysis). As E_1 is always unstable the resource population never goes extinct. The behaviour of the model exhibits that there is always a fixed point (no periodic solution). Based on the Routh-Hurwitz criterion (Kot, 2001) the behaviour of the model can be summarised as: (1) When $b > 1$ [i.e. $d_H > c_1\alpha K$], the herbivore and parasitoid populations go extinct but the resource population persists at an equilibrial level. The equilibrium (E_2) is a node (Figs. 5.1 and 5.2a); (2) When $1-(1/d) < b < 1$ [i.e. $c_1\alpha K(1-\alpha d_P/c_2\gamma r) < d_H < c_1\alpha K$], the parasitoid population goes extinct while the resource-herbivore interaction persists at equilibrial levels. The equilibrium (E_3) is a node or a spiral node (Figs. 5.1 and 5.2b); (3) When $b < 1-(1/d)$ [i.e. $d_H < c_1\alpha K(1-\alpha d_P/c_2\gamma r)$], the whole system (resource-herbivore-parasitoid interaction) persists at equilibrial levels. The equilibrium (E_4) is node or spiral node (Figs. 5.1, 5.2c and 5.3). The bifurcation diagram (Fig. 5.1) shows that the model undergoes transcritical bifurcations at $b = 1$ and $b = 1-(1/d)$. At $b = 1$ [i.e. $d_H = c_1\alpha K$], where the equilibria E_2 and E_3 exchange stability, the Jacobian matrices of the equilibria E_2 and E_3 have a zero eigenvalue (Gwaltney *et al.*, 2004). Similarly, at $b = 1-(1/d)$ [i.e. $d_H = c_1\alpha K(1-\alpha d_P/c_2\gamma r)$], where the equilibria E_3 and E_4 switch stability, the Jacobian matrices of the equilibria E_3 and E_4 have a zero eigenvalue.

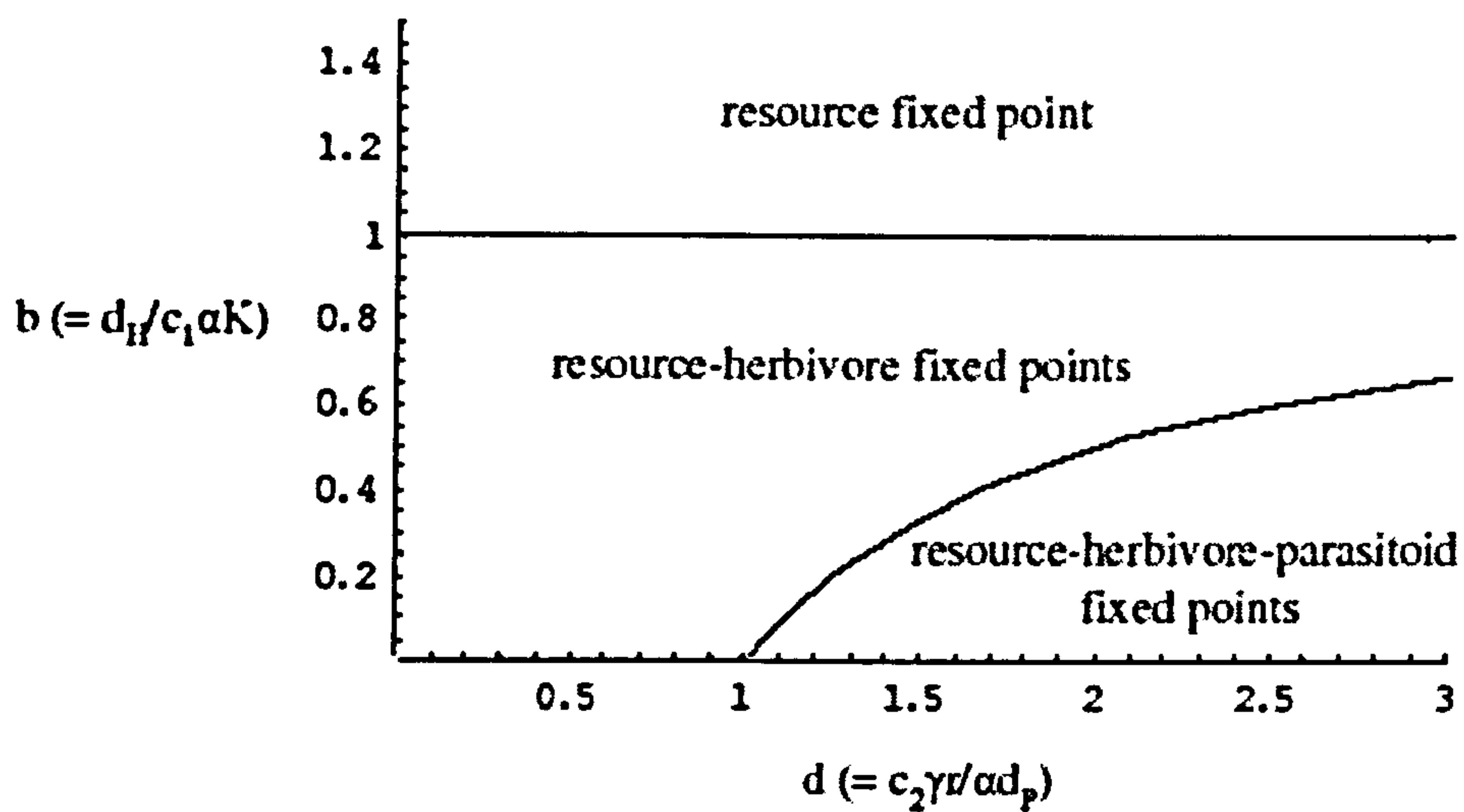


Fig. 5.1. The codimension-two bifurcation diagram of model I. Where b is the scaled death rate of herbivore, and d is the product of scaled conversion factor and attack rate of parasitoid; the parameter values: $a = 1/6$ and $c = 1/30$.

To understand the results in biological sense, the above-mentioned inequalities must be simplified [note that since a and c are constant, the original parameters (c_1 , α , K , r and d_P) constituting these dimensionless parameters were also presumed constant]. By defining two new constant parameter as $\omega_1 = c_1 \alpha K$ and $\omega_2 = \alpha d_P / r$, the model reveals that if herbivore mortality is higher than a threshold [$d_H > \omega_1$] then the herbivore and parasitoid populations will go extinct, and only resource population will persist at carrying capacity levels. In contrast, if herbivore mortality is lower than such a threshold [$d_H < \omega_1$] both ditrophic and tritrophic systems can persist depending on the values of the attack rate and the conversion factor of parasitoid. If the parasitoid attack rate is smaller than a function of parasitoid conversion factor and herbivore mortality [$\gamma < \omega_1 \omega_2 / c_2 (\omega_1 - d_H)$], then coexistence of resource and herbivore populations at equilibrial level will happen. In this situation, parasitoid attack to the system will result in parasitoid exclusion. However, if the parasitoid attack rate is greater than such a function [$\gamma > \omega_1 \omega_2 / c_2 (\omega_1 - d_H)$] this will result in the persistence of the resource-herbivore-parasitoid interaction.

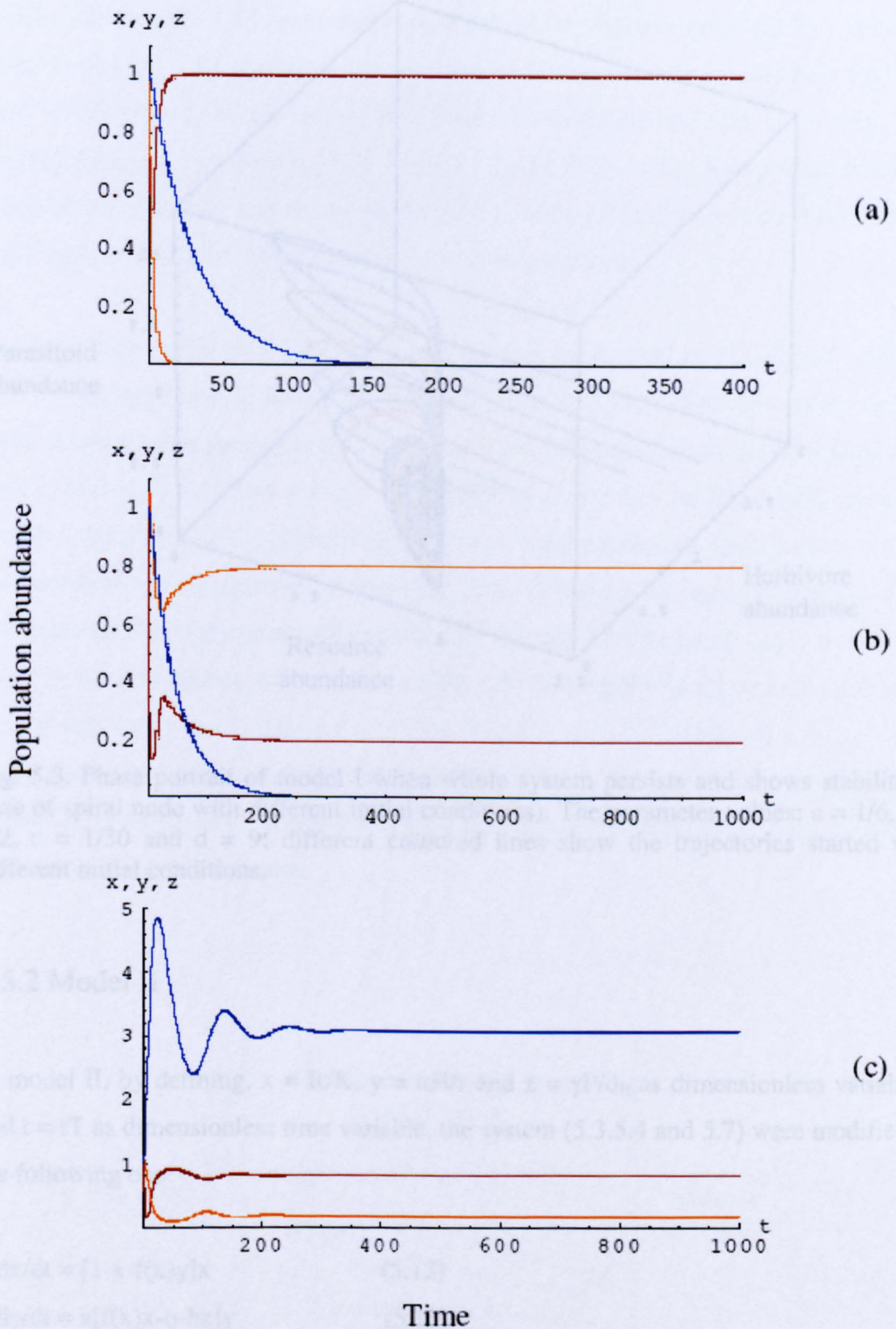


Fig. 5.2. Time plots of model I. (a) Where only the resource persists as a node (the parameter values: $a = 1/6$, $b = 1.2$, $c = 1/30$ and $d = 0.5$); (b) where the resource-herbivore interaction persists as a spiral node (the parameter values: $a = 1/6$, $b = 0.2$, $c = 1/30$ and $d = 0.5$); (3) where the whole system of tritrophic interaction persists as a spiral node (the parameter values: $a = 1/6$, $b = 0.2$, $c = 1/30$ and $d = 5.5$); brown, orange and blue lines indicate modified resource (x), herbivore (y) and parasitoid (z) abundance, respectively.

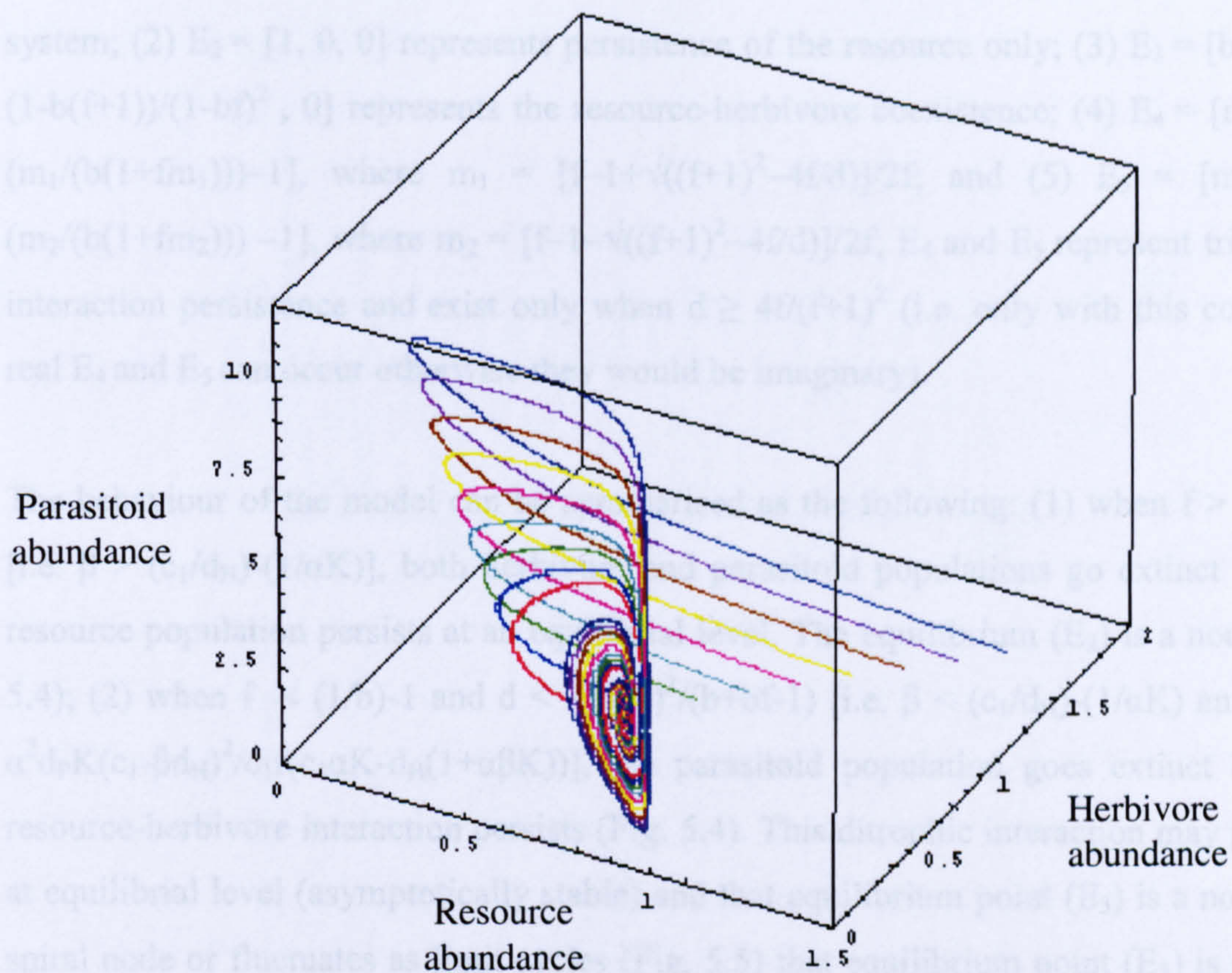


Fig. 5.3. Phase portrait of model I when whole system persists and shows stability (a case of spiral node with different initial conditions). The parameter values: $a = 1/6$, $b = 0.2$, $c = 1/30$ and $d = 9$; different coloured lines show the trajectories started with different initial conditions.

5.5.2 Model II

In model II, by defining, $x = R/K$, $y = \alpha H/r$ and $z = \gamma P/d_H$ as dimensionless variables, and $t = rT$ as dimensionless time variable, the system (5.3,5.4 and 5.7) were modified to the following one:

$$\begin{cases} dx/dt = [1-x-f(x)y]x & (5.12) \\ dy/dt = a[f(x)x-b-bz]y & (5.13) \\ dz/dt = c(dy-1)z & (5.11) \end{cases}$$

, where function $f(x) = 1/(1+fx)$, and parameters a, b, c, d and $f = \alpha\beta K$ all are positive.

There are five equilibria for the system (5.11-5.13) in the positive octant including: (1) $E_1 = [0, 0, 0]$ is the origin of the phase space and represents the extinction of whole

system; (2) $E_2 = [1, 0, 0]$ represents persistence of the resource only; (3) $E_3 = [b/(1-bf), (1-b(f+1))/(1-bf)^2, 0]$ represents the resource-herbivore coexistence; (4) $E_4 = [m_1, 1/d, (m_1/(b(1+fm_1))) - 1]$, where $m_1 = [f-1+\sqrt{((f+1)^2-4f/d)}/2f]$; and (5) $E_5 = [m_2, 1/d, (m_2/(b(1+fm_2))) - 1]$, where $m_2 = [f-1-\sqrt{((f+1)^2-4f/d)}/2f]$; E_4 and E_5 represent tritrophic interaction persistence and exist only when $d \geq 4f/(f+1)^2$ (i.e. only with this condition real E_4 and E_5 can occur otherwise they would be imaginary).

The behaviour of the model can be summarised as the following: (1) when $f > (1/b)-1$ [i.e. $\beta > (c_1/d_H)-(1/\alpha K)$], both herbivore and parasitoid populations go extinct but the resource population persists at an equilibrial level. The equilibrium (E_2) is a node (Fig. 5.4); (2) when $f < (1/b)-1$ and $d < -(bf-1)^2/(b+bf-1)$ [i.e. $\beta < (c_1/d_H)-(1/\alpha K)$ and $c_2\gamma < \alpha^2 d_P K(c_1-\beta d_H)^2/c_1 r(c_1 \alpha K-d_H(1+\alpha \beta K))$], the parasitoid population goes extinct but the resource-herbivore interaction persists (Fig. 5.4). This ditrophic interaction may persists at equilibrial level (asymptotically stable) and that equilibrium point (E_3) is a node or a spiral node or fluctuates as limit cycles (Fig. 5.5) that equilibrium point (E_3) is a spiral saddle with index 2; (3) where $f < (1/b)-1$ but $d > -(bf-1)^2/(b+bf-1)$ [i.e. $\beta < (c_1/d_H)-(1/\alpha K)$ and $c_2\gamma > \alpha^2 d_P K(c_1-\beta d_H)^2/c_1 r(c_1 \alpha K-d_H(1+\alpha \beta K))$], the whole system of tritrophic interaction persists as an asymptotically stable equilibrial point (Fig. 5.4). The fixed point here (E_4) is a spiral node.

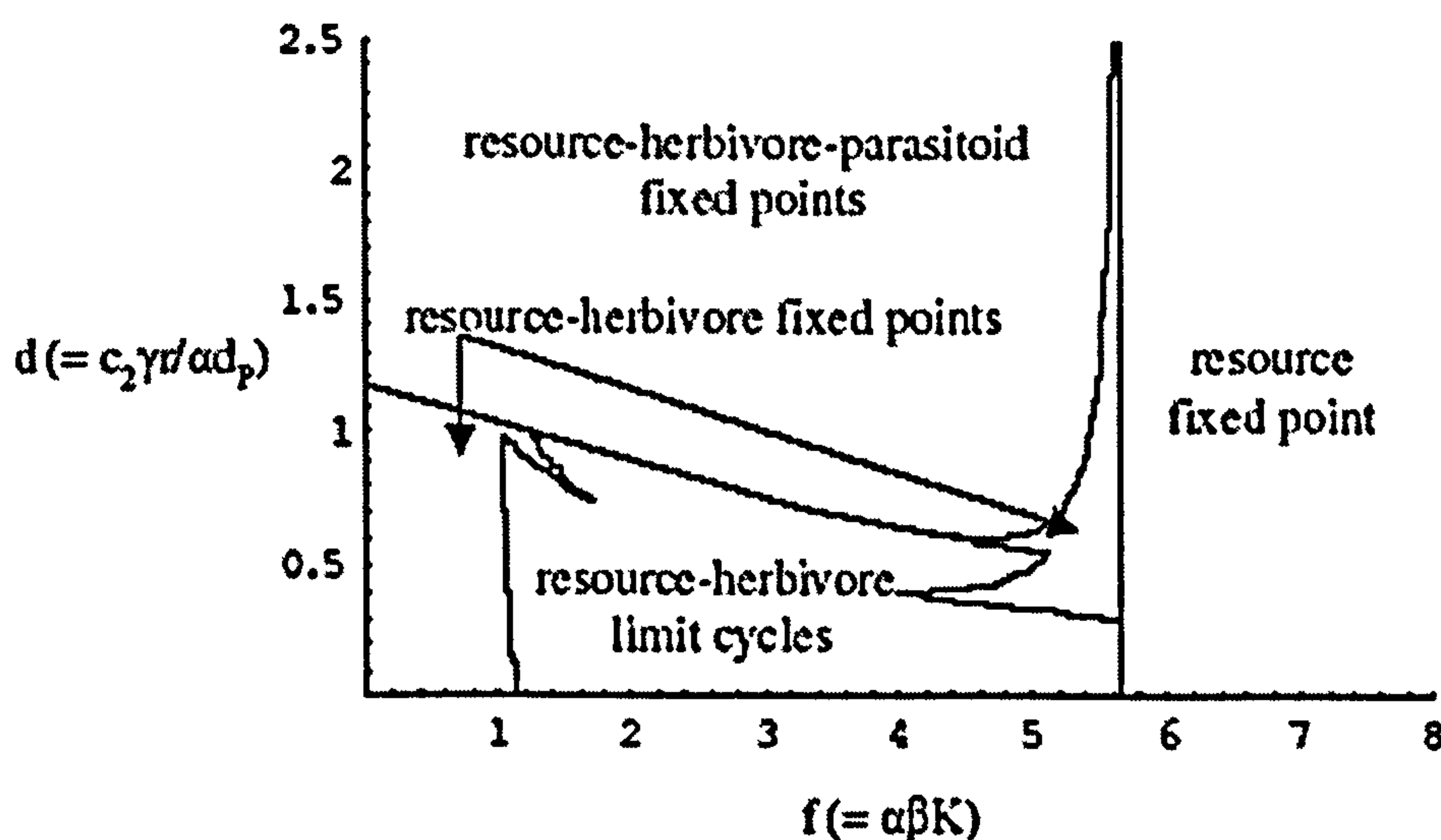


Fig. 5.4. The codimension-two bifurcation diagram of model II. Where d is the product of scaled conversion factor and attack rate of parasitoid, and f is the scaled herbivore handling time; the parameter values: $a = 1/6$, $b = 0.15$ and $c = 1/30$.

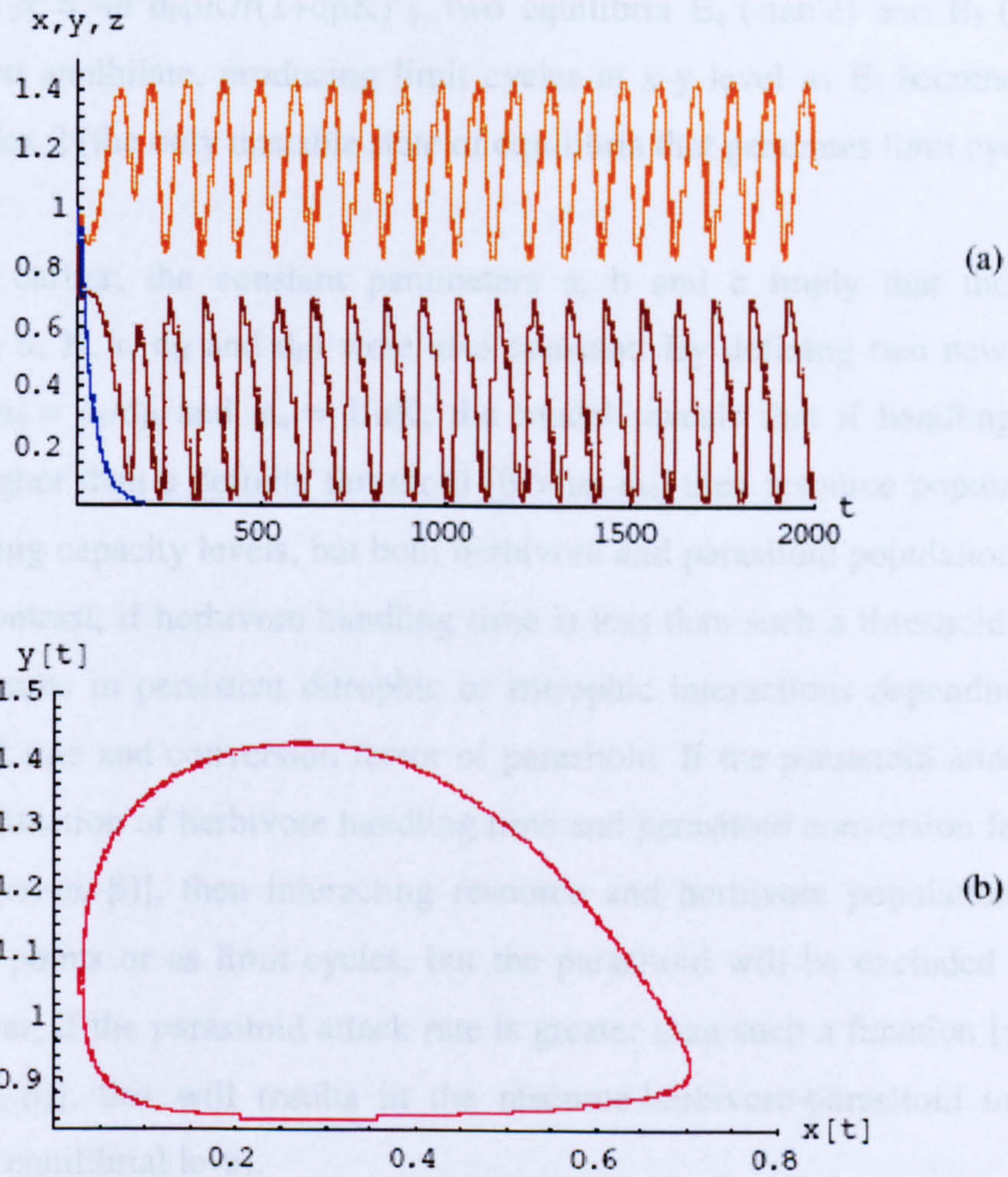


Fig. 5.5. Time plot and phase plot of model II where resource-herbivore interaction fluctuates as limit cycles. (a) Time plot: brown, orange and blue lines indicate modified resource (x), herbivore (y) and parasitoid (z) abundance, respectively; t represent the modified time; (b) phase plot; the parameter values: $a = 1/6$, $b = 0.15$, $c = 1/30$, $d = 0.2$ and $f = 3$.

The bifurcation diagram (Fig. 5.4) shows transcritical bifurcations at $f = (1/b)-1$ and $d = -(bf-1)^2/(b+bf-1)$. When the parameters pass the line $f = (1/b)-1$ [i.e. $\beta = (c_1/d_H)-(1/\alpha K)$] the equilibria E_2 and E_3 exchange stability. While passing through $d = -(bf-1)^2/(b+bf-1)$ [i.e. $c_2\gamma = \alpha^2 d_P K (c_1 - \beta d_H)^2 / c_1 r (c_1 \alpha K - d_H (1 + \alpha \beta K))$] cause a stability switching either between E_3 and E_4 where $f < 1.67$ or $4.00 < f < (1/b)-1$, or between E_3 and E_5 where $1.67 \leq f \leq 3.99$. Another form of bifurcation that happens is fold-Hopf bifurcation, which exists whenever the Jacobian matrix of equilibria has a zero eigenvalue and a pair of conjugate purely imaginary eigenvalues (Gwaltney *et al.*, 2004). This happens where $d = 4f/(f+1)^2$ for $f > 1.01$, and therefore E_4 and E_5 become the same. By intersecting $d =$

$4f/(f+1)^2$ [i.e. $c_2\gamma = 4\alpha^2d_P\beta K/r(1+\alpha\beta K)^2$], two equilibria E_4 (stable) and E_5 (unstable) collide and then annihilate, producing limit cycles at x-y level as E_3 become a spiral saddle with index 2 (the only unstable state of equilibria that generates limit cycle).

As mentioned earlier, the constant parameters a , b and c imply that the original parameters (c_1 , α , K , r , d_H and d_P) were also constant. By defining two new constant parameter as $\omega_3 = c_1/d_H$ and $\omega_4 = 1/\alpha K$, the model reveals that if handling time of herbivore is higher than a definite threshold [$\beta > \omega_3 - \omega_4$] then resource population will persist at carrying capacity levels, but both herbivore and parasitoid populations will be excluded. In contrast, if herbivore handling time is less than such a threshold [$\beta < \omega_3 - \omega_4$] this can results in persistent ditrophic or tritrophic interactions depending on the values of attack rate and conversion factor of parasitoid. If the parasitoid attack rate is smaller than a function of herbivore handling time and parasitoid conversion factor [$\gamma < \omega_2(\beta - \omega_3)^2/c_2\omega_3(\omega_3 - \omega_4 - \beta)$], then interacting resource and herbivore populations persist either as fixed points or as limit cycles, but the parasitoid will be excluded from the system. However, if the parasitoid attack rate is greater than such a function [$\gamma > \omega_2(\beta - \omega_3)^2/c_2\omega_3(\omega_3 - \omega_4 - \beta)$], this will results in the resource-herbivore-parasitoid interaction persisting at an equilibrial level.

5.5.3 Model III

In model III, by defining, $x = R/K$, $y = \alpha H/r$ and $z = \gamma P/d_H$ as dimensionless variables, and $t = rT$ as dimensionless time variable, the system (5.1, 5.6 and 5.8) was modified to the following one:

$$\begin{cases} dx/dt = (1-x-y)x & (5.9) \\ dy/dt = a[x-b-bh(y)z]y & (5.14) \\ dz/dt = c[dh(y)y-1]z & (5.15) \end{cases}$$

, where function $h(y) = 1/(1+hy)$, and parameters a , b , c , d and $h = \gamma\mu r/\alpha$ all are positive.

There are four equilibria for the system (5.9, 5.14 and 5.15) in the positive octant as follow: (1) $E_1 = [0, 0, 0]$ is the origin of the phase space and happens when whole system goes extinct; (2) $E_2 = [1, 0, 0]$ represent extinction of the herbivore and parasitoid populations while the resource population persists; (3) $E_3 = [b, 1-b, 0]$ indicate persistence of resource-parasitoid interaction. Parasitoid attack to such a ditrophic system will results in exclusion of the parasitoid; and (4) $E_4 = [(d-h-1)/(d-h), 1/(d-h), d((1-b)(d-h)-1)/b(d-h)^2]$ represents persistence of resource-herbivore-parasitoid interaction.

The behaviour of the model can be summarised as: (1) when $b > 1$ [i.e. $d_H > c_1\alpha K$], only the resource population will persist at equilibrial level, but higher trophic levels will go extinct. The equilibrium (E_2) is a node; (2) when $b < 1$ and $d < h + 1/(1-b)$ [i.e. $d_H < c_1\alpha K$ and $c_2/d_P - \mu < c_1\alpha^2 K / \gamma r (c_1\alpha K - d_H)$], the parasitoid population will be excluded, while the resource-herbivore interaction persists at equilibrial level (Fig. 5.6). The equilibrium (E_3) is a node or a spiral node; (3) when $b < 1$ and $d > h + 1/(1-b)$ [i.e. $d_H < c_1\alpha K$ and $c_2/d_P - \mu > c_1\alpha^2 K / \gamma r (c_1\alpha K - d_H)$], the tritrophic interaction persists (Fig. 5.6) either at an equilibrial level, which the equilibrium (E_4) is a node or spiral node, or as limit cycles (Fig. 5.7), which the equilibrium (E_4) is a spiral saddle index 2.

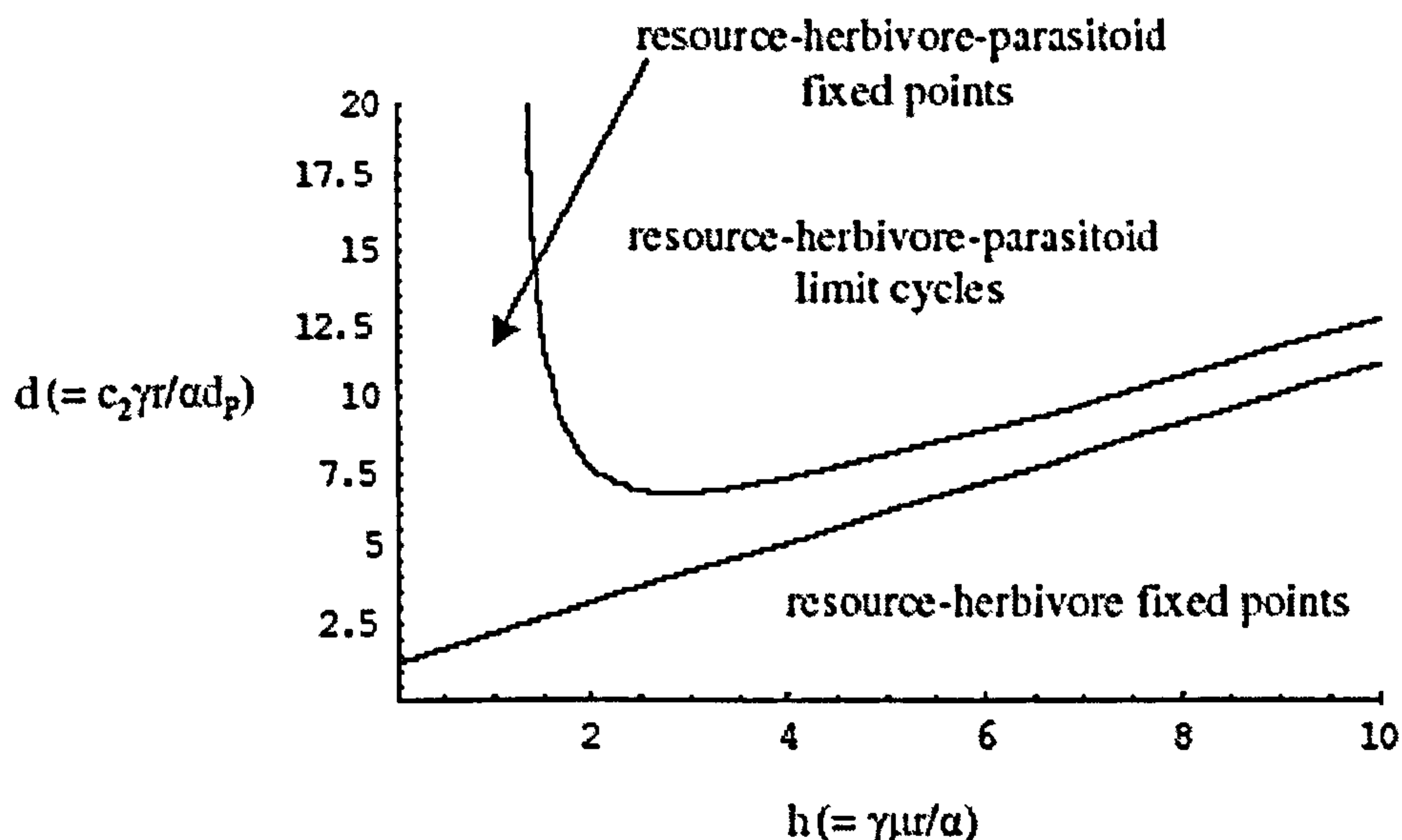


Fig. 5.6. The codimension-two bifurcation diagrams of model III. Where d is the product of scaled conversion factor and attack rate of parasitoid, and h is the product of scaled handling time and attack rate of parasitoid; the parameter values: $a = 1/6$, $b = 0.15$ and $c = 1/30$.

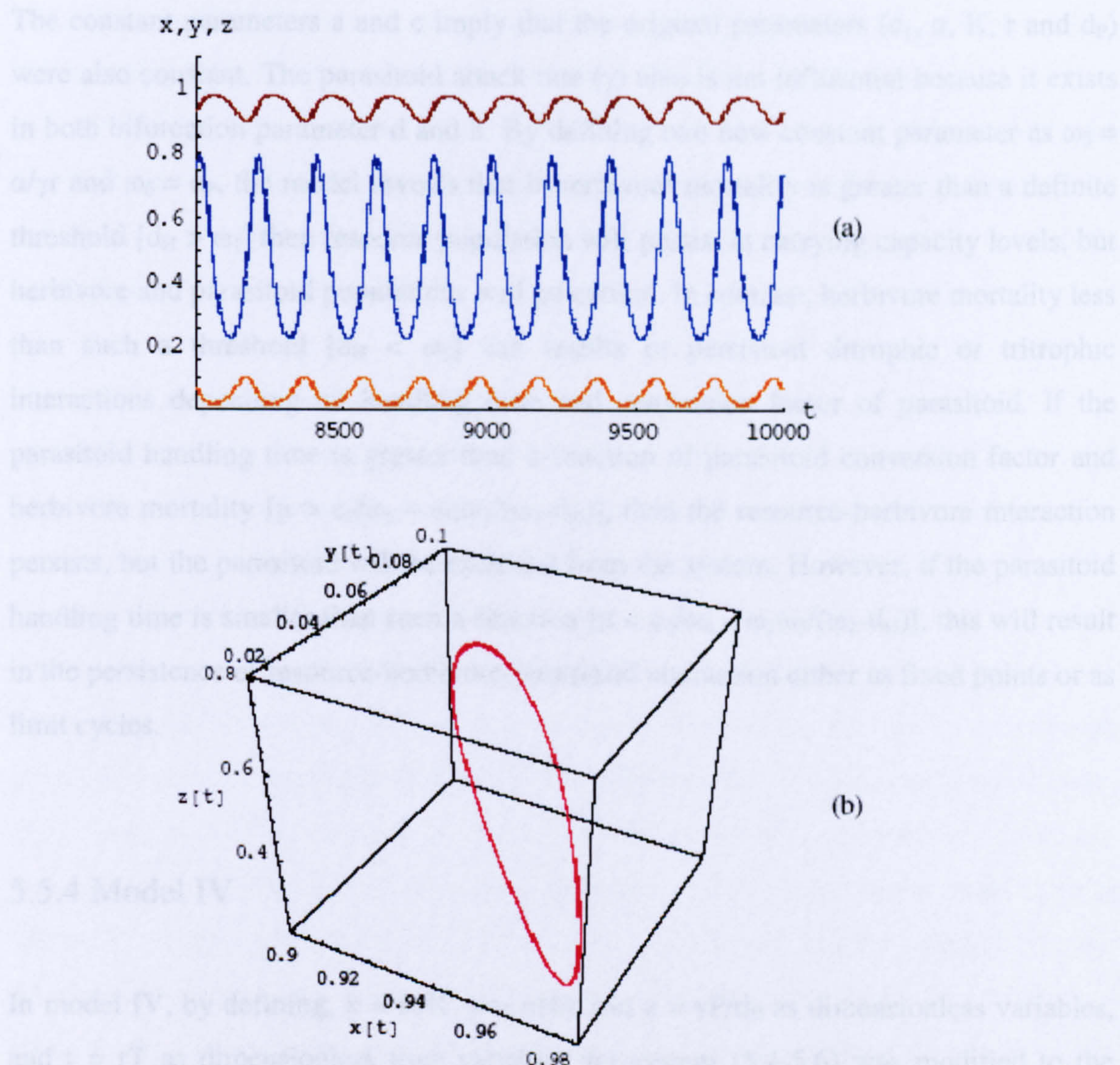


Fig. 5.7. Time plot and phase portrait of model III where x-y-z fluctuate as limit cycles. (a) Time plot: brown, orange and blue lines indicate modified resource (x), herbivore (y) and parasitoid (z) abundance, respectively; t represent the modified time; (b) phase portrait; the parameter values: $a = 1/6$, $b = 0.7$, $c = 1/30$, $d = 25$ and $h = 5.5$.

The bifurcation diagrams (Fig. 5.6) show transcritical and Hopf bifurcations. When the parameters pass line $d = h + 1/(1-b)$ [i.e. $c_2/d_P - \mu = c_1 \alpha^2 K / \gamma r (c_1 \alpha K - d_H)$], a transcritical bifurcation happens, as the equilibria E_3 and E_4 exchange stability. Whereas, a Hopf bifurcation happens (since the Jacobian matrix of the equilibrium E_4 have a pair of conjugate purely imaginary eigenvalues; Gwaltney *et al.*, 2004), as resource-herbivore-parasitoid persistence switches between fixed points and limit cycles. The bifurcation line for this Hopf was too complicated to be shown here.

The constant parameters a and c imply that the original parameters (c_1 , α , K , r and d_p) were also constant. The parasitoid attack rate (γ) also is not influential because it exists in both bifurcation parameter d and h . By defining two new constant parameter as $\omega_5 = \alpha/\gamma r$ and $\omega_6 = d_p$, the model reveals that if herbivore mortality is greater than a definite threshold [$d_H > \omega_1$] then resource population will persist at carrying capacity levels, but herbivore and parasitoid populations will go extinct. In contrast, herbivore mortality less than such a threshold [$d_H < \omega_1$] can results in persistent ditrophic or tritrophic interactions depending on handling time and conversion factor of parasitoid. If the parasitoid handling time is greater than a function of parasitoid conversion factor and herbivore mortality [$\mu > c_2/\omega_6 - \omega_1\omega_5/(\omega_1-d_H)$], then the resource-herbivore interaction persists, but the parasitoid will be excluded from the system. However, if the parasitoid handling time is smaller than such a function [$\mu < c_2/\omega_6 - \omega_1\omega_5/(\omega_1-d_H)$], this will result in the persistence of resource-herbivore-parasitoid interaction either as fixed points or as limit cycles.

5.5.4 Model IV

In model IV, by defining, $x = R/K$, $y = \alpha H/r$ and $z = \gamma P/d_H$ as dimensionless variables, and $t = rT$ as dimensionless time variable, the system (5.4-5.6) was modified to the following one:

$$\begin{cases} dx/dt = [1-x-f(x)y]x & (5.12) \\ dy/dt = a[f(x)x-bh(y)z]y & (5.16) \\ dz/dt = c[dh(y)y-1]z & (5.15) \end{cases}$$

, where functions $f(x) = 1/(1+fx)$ and $h(y) = 1/(1+hy)$, and parameters a , b , c , d , f and h all are positive.

There are five equilibria for the system (5.12,5.15 and 5.16) in the positive octant as follow: (1) $E_1 = [0, 0, 0]$; this is the origin of the phase space, and represents the extinction of whole system; (2) $E_2 = [1, 0, 0]$; this represents persistence of the resource at carrying capacity and extinction of the higher trophic levels; (3) $E_3 = [b/(1-bf), (1-b(f+1))/(1-bf)^2, 0]$, where $f \neq 1/b$; this represents the persistence of resource-herbivore

interaction and exclusion of parasitoid population; (4) $E_4 = [n_1, 1/(d-h), d(n_1 - b(1+fn_1))/(b(d-h)(1+fn_1))]$, where $n_1 = [f-1+\sqrt{((f+1)^2-4f/(d-h))}]/2f$, and $d \neq h$; (5) $E_5 = [n_2, 1/(d-h), d(n_2 - b(1+fn_2))/(b(d-h)(1+fn_2))]$, where $n_2 = [f-1-\sqrt{((f+1)^2-4f/(d-h))}]/2f$, and $d \neq h$; E_4 and E_5 represent the persistence of resource-herbivore-parasitoid interaction and exist only when $d \geq h+4f/(f+1)^2$ or $d < h$ [i.e. otherwise E_4 and E_5 would be imaginary].

The behaviour of the model can be summarised as:

(i) With f and h as the bifurcation parameters (Fig. 5.8a): (1) where $f > (1/b)-1$, the herbivore and parasitoid populations go extinct but the resource population persists at an equilibrial level. The equilibrium (E_2) is a node; (2) where $f < (1/b)-1$: (2.1) where $f < [(2-d+h)-\sqrt{((d-h)(d-h-4b))}]/(2b)$ or $f > [(2-d+h)+\sqrt{((d-h)(d-h-4b))}]/(2b)$, the parasitoid population goes extinct but the resource-herbivore interaction persists including: (2.1.1) where $f < [1-b-\sqrt{(1-6b+b^2)}]/2b$ or $f > [1-b+\sqrt{(1-6b+b^2)}]/2b$, the resource-herbivore interaction persists at equilibrial level. The equilibrium (E_3) is a node or a spiral node; (2.1.2) where $[1-b-\sqrt{(1-6b+b^2)}]/2b < f < [1-b+\sqrt{(1-6b+b^2)}]/2b$, the resource-herbivore interaction persists as a limit cycle. The equilibrium (E_3) is a spiral saddle index 2; (2.2) where $[(2-d+h)-\sqrt{((d-h)(d-h-4b))}]/(2b) < f < [(2-d+h)+\sqrt{((d-h)(d-h-4b))}]/(2b)$, the tritrophic interaction persists at equilibrial level. The equilibrium (E_4) is a node or a spiral node. Transcritical bifurcations happen when the parameters pass the lines $f = (1/b)-1$, where E_2 and E_3 switch stability, and $f = [(2-d+h)-\sqrt{((d-h)(d-h-4b))}]/(2b)$ and $f = [(2-d+h)+\sqrt{((d-h)(d-h-4b))}]/(2b)$, where E_3 and E_4 exchange stability. In addition, Hopf bifurcations happen for E_3 when the parameters pass the lines $f = [1-b-\sqrt{(1-6b+b^2)}]/2b$ and $f = [1-b+\sqrt{(1-6b+b^2)}]/2b$.

(ii) With d and h as the bifurcation parameters (Fig. 5.8b): (1) $d < h-((bf-1)^2/(b+bf-1))$: parasitoid population goes extinct but resource-herbivore interaction persists as a limit cycle. The equilibrium (E_3) is a spiral saddle index 2; (2) $d > h-((bf-1)^2/(b+bf-1))$: (2.1) the tritrophic interaction persists at equilibrial level. The equilibrium (E_4) is a node or a spiral node; (2.2) the tritrophic interaction persists either as limit cycles or chaos. The equilibrium (E_4) is a spiral saddle index 2. Transcritical bifurcations happen when the parameters pass the line $d = h-((bf-1)^2/(b+bf-1))$, where E_3 and E_5 exchange stability. There is also a Hopf bifurcation for E_4 , however, the symbolic formula for such a line is too complicated to be shown here.

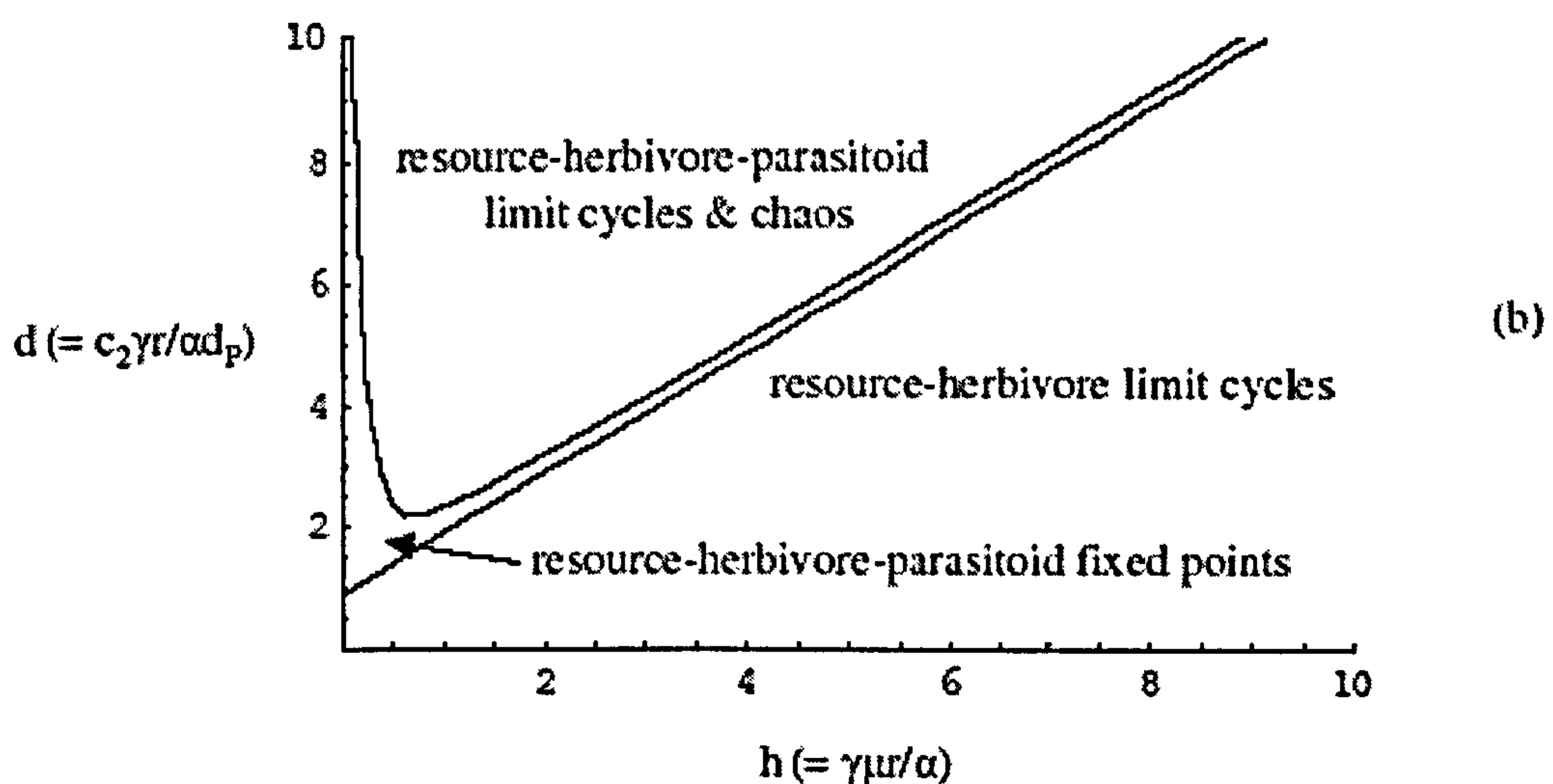
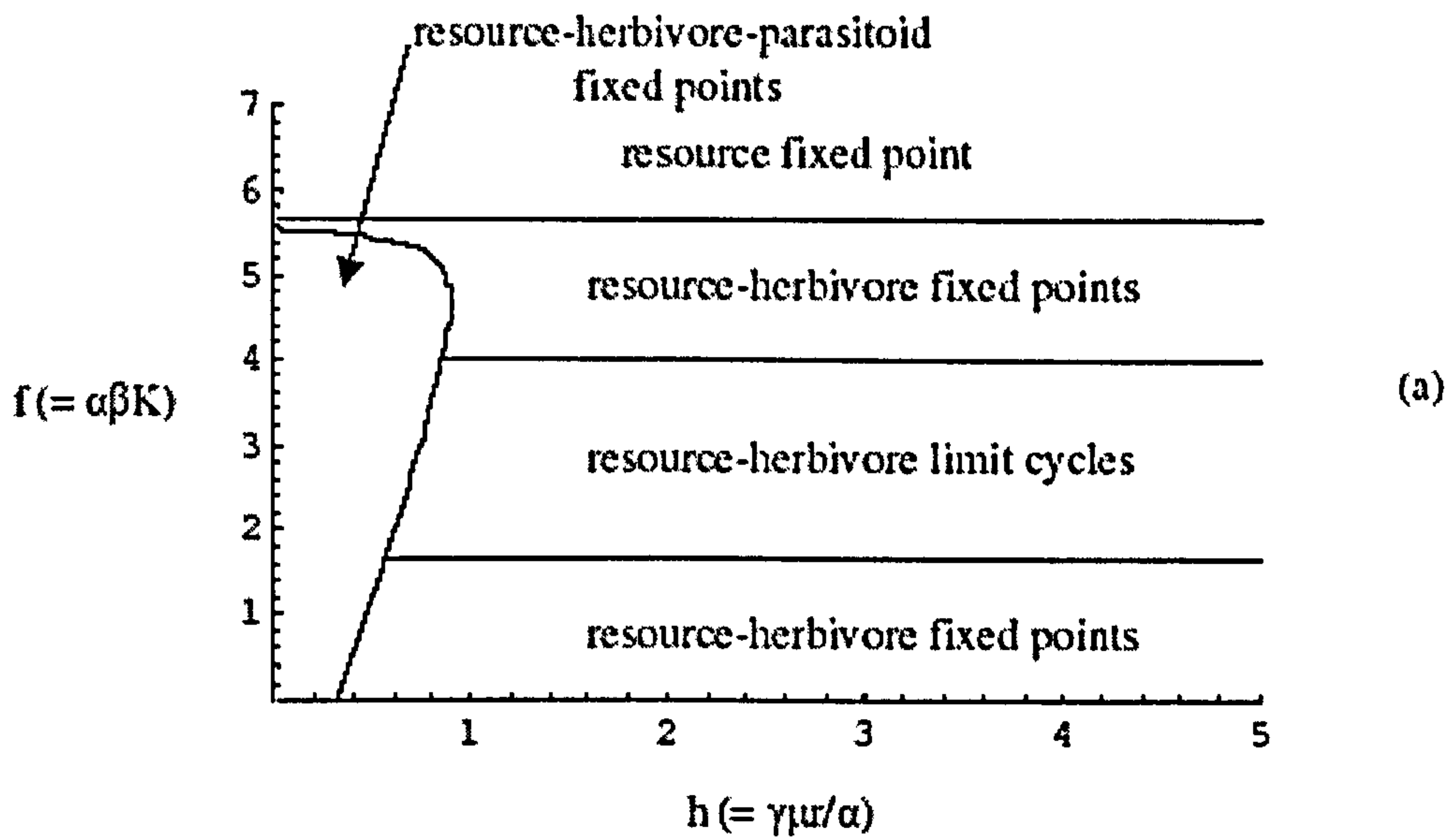


Fig. 5.8. The codimension-two bifurcation diagrams of model IV. (a) With f and h as the bifurcation parameters, where f is the scaled handling time of herbivore, and h is the product of scaled handling time and attack rate of parasitoid (the constant parameters: $a = 1/6$, $b = 0.15$, $c = 1/30$ and $d = 1.5$); (b) with d and h as the bifurcation parameters, where d is the product of scaled conversion factor and attack rate of parasitoid, and h is the product of scaled handling time and attack rate of parasitoid (the constant parameters: $a = 1$, $b = 0.12$, $c = 0.1$ and $f = 2$).

By combining (i) and (ii) the model behaviour can be categorized as: (1) where $f > (1/b) - 1$ [i.e. $\beta > (c_1/d_H) - (1/\alpha K)$], the resource population will persist at equilibrium level, but the higher trophic levels will go extinct; (2) where $f < (1/b) - 1$ and $d < h - (bf - 1)^2 / (b + bf - 1)$ [i.e. $\beta < (c_1/d_H) - (1/\alpha K)$ and $c_2\gamma < \alpha^2 d_P K (c_1 - \beta d_H)^2 / c_1 r (c_1 \alpha K - d_H(1 + \alpha \beta K)) + \gamma \mu d_P$], the resource-herbivore interaction persists either at equilibrium level

or as limit cycle; (3) where $f < (1/b)-1$ and $d > h-(bf-1)^2/(b+bf-1)$ [i.e. $\beta < (c_1/d_H)-(1/\alpha K)$ and $c_2\gamma > \alpha^2 d_P K(c_1-\beta d_H)^2/c_1 r(c_1\alpha K-d_H(1+\alpha\beta K))+\gamma\mu d_P$], the resource-herbivore-parasitoid interactions can persist as equilibrial points, limit cycles or chaos.

Chaos is the aperiodic, long-term behaviour of a bounded, deterministic system that exhibits sensitive dependence on initial conditions (Sprott, 2003). In the bifurcation diagram (Fig. 5.8b) in the top area some regions show limit cycles and some others show chaotic behaviour. One of the routes by which a stable equilibrium becomes chaotic is period-doubling (Sprott, 2003). For instance by setting the parameter $d = 5$, for a range of the parameter h from 1 to 2.04 the model shows the behaviours starting by a limit cycle, continuing by period-doubling conducting to chaotic behaviour (Figs. 5.9-5.10). As it can be seen, a process of period-doubling happens, such that a limit cycle ($h = 0.5$; Figs. 5.9a and 5.10a) becomes a two-point limit cycle ($h = 1$; Figs. 5.9b and 5.10b), and the two-point limit cycle becomes a four-point limit cycle ($h = 2$; Figs. 5.9c and 5.10c), and the latter becomes an eight-point limit cycle ($h = 2.02$; Figs. 5.9d and 5.10d) and so on until it becomes chaotic ($h = 2.04$; Figs. 5.9f and 5.10f) and is no longer periodic. In addition, the model also shows the process of period-halving that starts by chaos and results in limit cycle. For example, by setting the parameter $d = 4$, and an increment of parameter h from 2.4 to 2.7 the model shows the process of period-halving (Fig. 5.11).

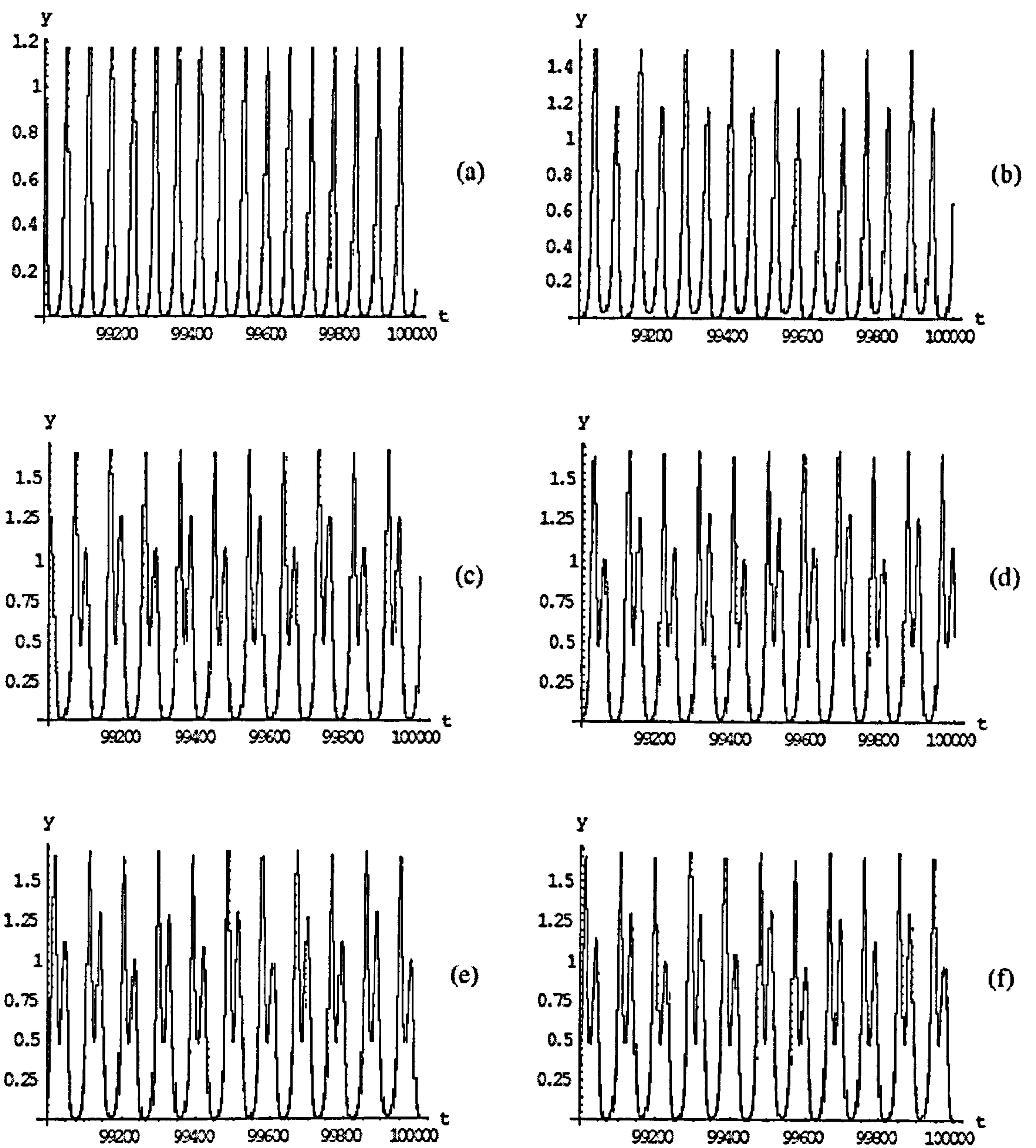


Fig. 5.9. Time plots of model IV for modified herbivore (y) populations from limit cycle to chaos (period doubling). The parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 5$ and $f = 2$; (a) $h = 0.5$; (b) $h = 1$; (c) $h = 2$; (d) $h = 2.02$; (e) $h = 2.03$; (f) $h = 2.04$; t represent the modified time.

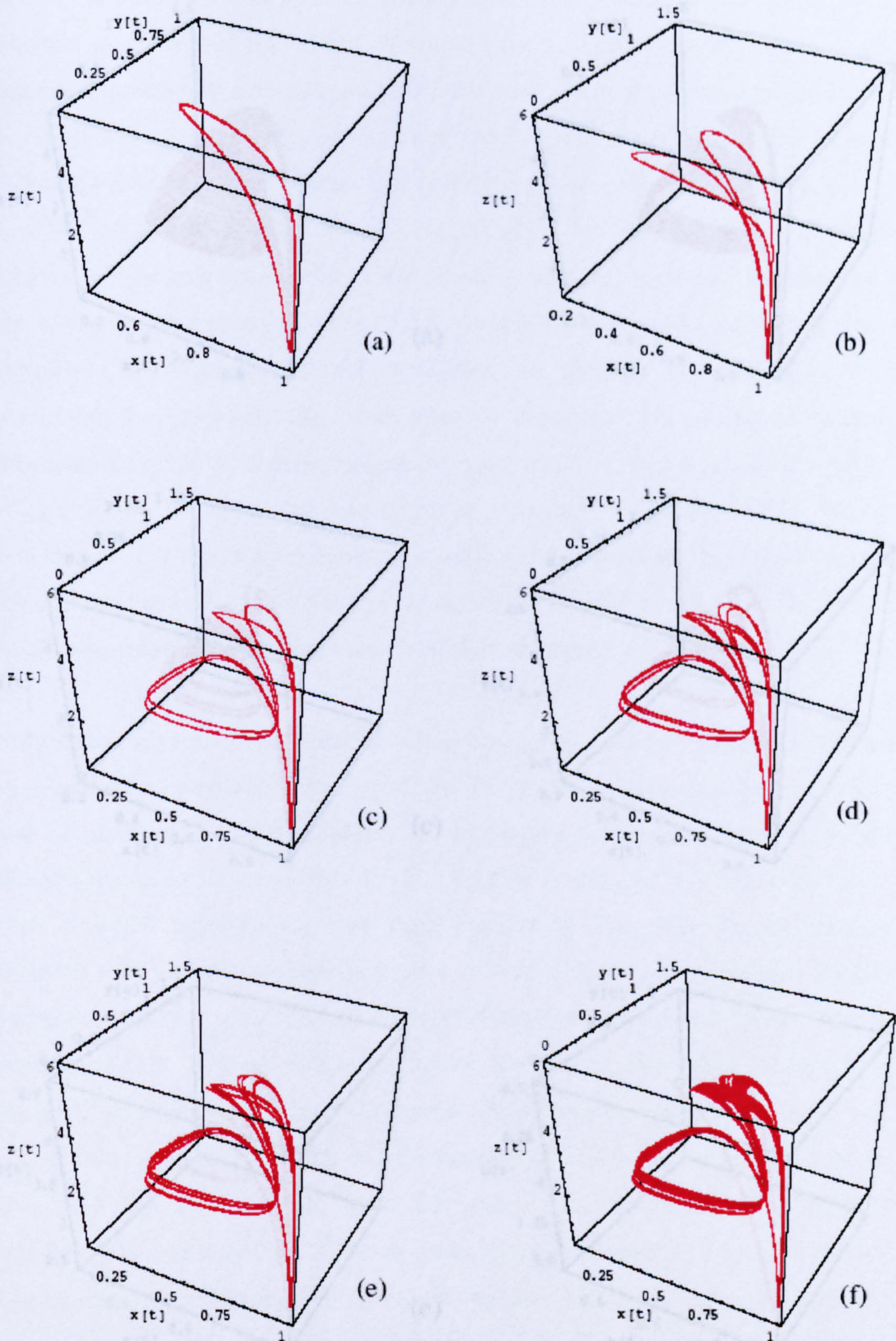


Fig. 5.10. Phase portraits of model IV, showing the transition to chaos through period-doubling. (a) $h = 0.5$; (b) $h = 1$; (c) $h = 2$; (d) $h = 2.02$; (e) $h = 2.03$; (f) $h = 2.04$; x , y and z show the modified resource, herbivore and parasitoid abundance, respectively; the parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 5$ and $f = 2$.

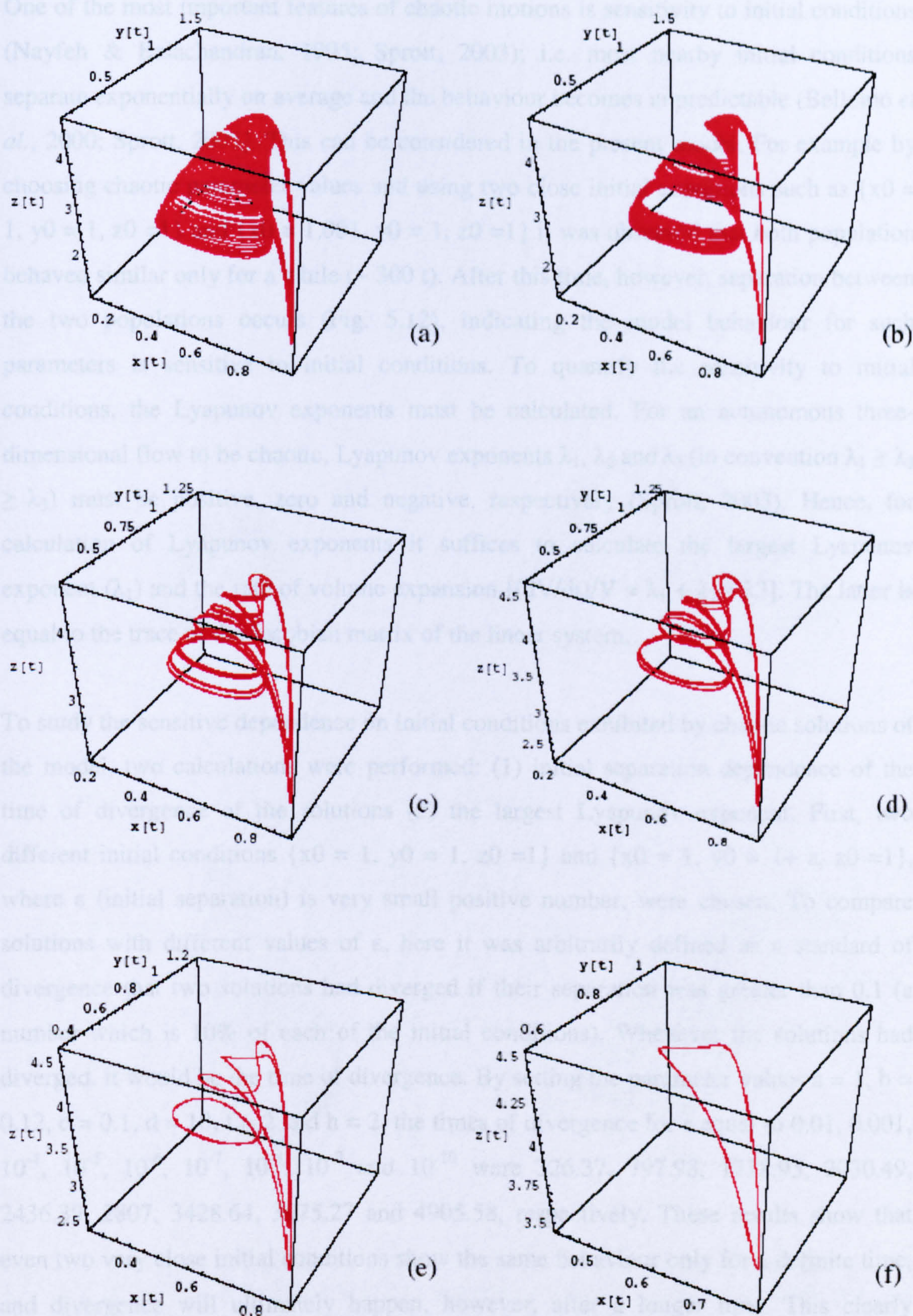


Fig. 5.11. Phase portraits of model IV, showing period-halving from chaos to limit cycle. (a) $h = 2.4$; (b) $h = 2.5$; (c) $h = 2.6$; (d) $h = 2.63$; (e) $h = 2.64$; (f) $h = 2.7$; x , y and z show the modified resource, herbivore and parasitoid abundance, respectively; the parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 4$ and $f = 2$.

One of the most important features of chaotic motions is sensitivity to initial conditions (Nayfeh & Balachandran, 1995; Sprott, 2003); i.e. most nearby initial conditions separate exponentially on average and the behaviour becomes unpredictable (Bellomo *et al.*, 2000; Sprott, 2003). This can be considered in the present model. For example by choosing chaotic parameter values and using two close initial conditions such as $\{x_0 = 1, y_0 = 1, z_0 = 1\}$ and $\{x_0 = 1.001, y_0 = 1, z_0 = 1\}$ it was observed that both population behaved similar only for a while (~ 300 t). After this time, however, separation between the two populations occurs (Fig. 5.12), indicating the model behaviour for such parameters is sensitive to initial conditions. To quantify the sensitivity to initial conditions, the Lyapunov exponents must be calculated. For an autonomous three-dimensional flow to be chaotic, Lyapunov exponents λ_1, λ_2 and λ_3 (in convention $\lambda_1 \geq \lambda_2 \geq \lambda_3$) must be positive, zero and negative, respectively (Sprott, 2003). Hence, for calculation of Lyapunov exponents it suffices to calculate the largest Lyapunov exponent (λ_1) and the rate of volume expansion $[(dV/dt)/V = \lambda_1 + \lambda_2 + \lambda_3]$. The latter is equal to the trace of the Jacobian matrix of the linear system.

To study the sensitive dependence on initial conditions exhibited by chaotic solutions of the model, two calculations were performed: (1) initial separation dependence of the time of divergence of the solutions (2) the largest Lyapunov exponent. First, two different initial conditions $\{x_0 = 1, y_0 = 1, z_0 = 1\}$ and $\{x_0 = 1, y_0 = 1 + \epsilon, z_0 = 1\}$, where ϵ (initial separation) is very small positive number, were chosen. To compare solutions with different values of ϵ , here it was arbitrarily defined as a standard of divergence that two solutions had diverged if their separation was greater than 0.1 (a number which is 10% of each of the initial conditions). Whenever the solutions had diverged, it would be the time of divergence. By setting the parameter values $a = 1, b = 0.12, c = 0.1, d = 10, f = 2$ and $h = 2$, the times of divergence for ϵ equal to 0.01, 0.001, 10^{-4} , 10^{-5} , 10^{-6} , 10^{-7} , 10^{-8} , 10^{-9} and 10^{-10} were 326.37, 797.98, 1718.95, 2030.49, 2436.39, 2807, 3428.64, 3975.27 and 4905.58, respectively. These results show that even two very close initial conditions show the same behaviour only for a definite time, and divergence will ultimately happen, however, after a longer time. This clearly indicate how difficult predictability is.

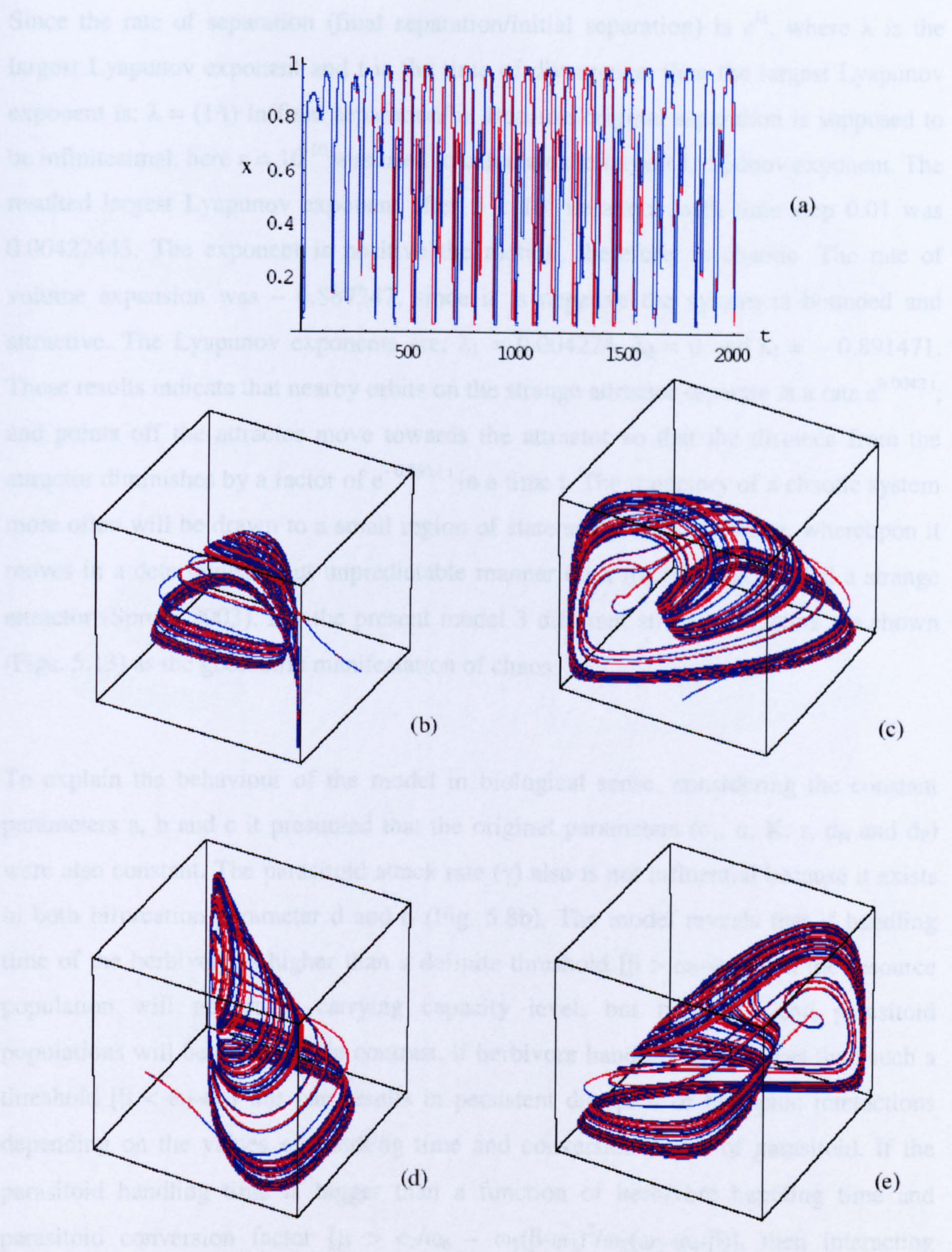


Fig. 5.12. Time plot and phase portraits of model IV for chaotic parameters ($a = 1$, $b = 0.12$, $c = 0.1$, $d = 5$, $f = 2$ and $h = 2.1$) indicating sensitivity to initial conditions. (a) Time plot of resource populations (x and t are modified resource abundance and time, respectively); (b-e) phase portraits from different views; red and blue lines show the population and trajectory started with initial conditions $(1,1,1)$ and $(1.001,1,1)$, respectively.

Since the rate of separation (final separation/initial separation) is $e^{\lambda t}$, where λ is the largest Lyapunov exponent and t is the time of divergence, then the largest Lyapunov exponent is: $\lambda = (1/t) \ln(\text{final separation}/\epsilon)$. Because original separation is supposed to be infinitesimal, here $\epsilon = 10^{-10}$ was used to calculate the largest Lyapunov exponent. The resulted largest Lyapunov exponent after 5×10^5 iterations with time step 0.01 was 0.00422443. The exponent is positive the motion, therefore, is chaotic. The rate of volume expansion was -0.887247 , since it is negative the system is bounded and attractive. The Lyapunov exponents are: $\lambda_1 = 0.004224$, $\lambda_2 = 0$ and $\lambda_3 = -0.891471$. These results indicate that nearby orbits on the strange attractor separate at a rate $e^{0.0042 t}$, and points off the attractor move towards the attractor so that the distance from the attractor diminishes by a factor of $e^{-0.8914 t}$ in a time t . The trajectory of a chaotic system more often will be drawn to a small region of state space as time evolve, whereupon it moves in a deterministic but unpredictable manner on a fractal object called a strange attractor (Sprott, 2003). For the present model 3 different strange attractors are shown (Figs. 5.13) as the geometric manifestation of chaos.

To explain the behaviour of the model in biological sense, considering the constant parameters a , b and c it presumed that the original parameters (c_1 , α , K , r , d_H and d_P) were also constant. The parasitoid attack rate (γ) also is not influential because it exists in both bifurcation parameter d and h (Fig. 5.8b). The model reveals that if handling time of the herbivore is higher than a definite threshold [$\beta > \omega_3 - \omega_4$] then the resource population will persist at carrying capacity level, but herbivore and parasitoid populations will be excluded. In contrast, if herbivore handling time is less than such a threshold [$\beta < \omega_3 - \omega_4$] this can results in persistent ditrophic or tritrophic interactions depending on the values of handling time and conversion factor of parasitoid. If the parasitoid handling time is bigger than a function of herbivore handling time and parasitoid conversion factor [$\mu > c_2/\omega_6 - \omega_5(\beta - \omega_3)^2/\omega_3(\omega_3 - \omega_4 - \beta)$], then interacting resource and herbivore populations persist either as fixed points or as limit cycles, but the parasitoid will be excluded from the system. However, if the parasitoid handling time is smaller than such a function [$\mu < c_2/\omega_6 - \omega_5(\beta - \omega_3)^2/\omega_3(\omega_3 - \omega_4 - \beta)$] the resource-herbivore-parasitoid interaction will persists as fixed points, limit cycles or chaos.

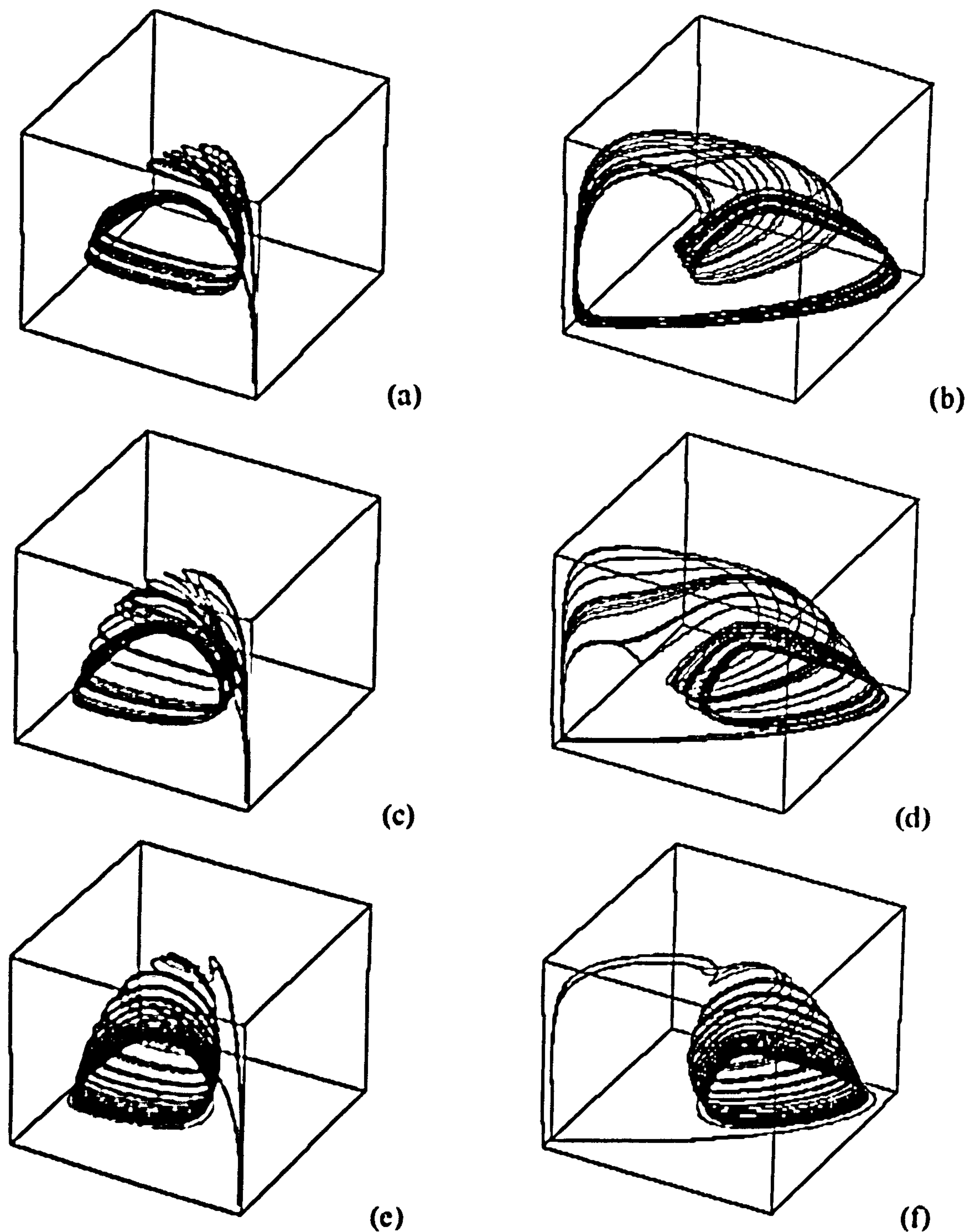


Fig. 5.13. Phase portraits of three different strange attractors of model IV from two different views. (a-b) The parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 5$, $f = 2$ and $h = 2.1$; (b) the parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 10$, $f = 2$ and $h = 5$; (c) the parameter values: $a = 1$, $b = 0.12$, $c = 0.1$, $d = 10$, $f = 2$ and $h = 8$; the model was run enough before drawing graphs to remove the transient trajectories.

5.6 Discussion

Four three-dimensional continuous time dynamical systems, modeling tritrophic food chains, based on a modified Lotka-Volterra predator-prey model were studied. The models were deterministic and differed in the type of functional responses for herbivore and parasitoid. The local behaviours of the models were explored. It was shown that the only attractors identified in model I were fixed points, including the equilibrium which represents persistence of all three species and the equilibria which represent the extinction of parasitoid or herbivore; no periodic orbit was found in this model. Fixed points as well as limit cycles for resource-consumer interactions were found in model II; however, limit cycles for tritrophic interactions were not found in this model. In addition to fixed points, the periodic solutions at the tritrophic level were found in model III. However, limit cycles for resource-consumer interactions were not found in this model. All the behaviours identified in the other models were explored by model IV. Furthermore, chaotic behaviours were found only in model IV. The chaotic motions were numerically explored, tested for sensitivity to initial conditions, and confirmed by calculation of the largest Lyapunov exponent. The route to chaos was found to be period-doubling through which a limit cycle becomes a strange attractor.

To understand how the original parameters can affect the behaviour of the models it is useful to define the stable state for whole system. Here, the whole system stability (WSS) means when all three species persist (i.e. none of population goes extinct). The biological mechanisms for model I (which assumes c_1 , α , K , r and d_p are constant) that result in WSS are sufficiently low herbivore mortality [$d_H < \omega_1$], and relatively high values of parasitoid attack rate and conversion factor [$c_2\gamma > f_1(d_H)$]. Similarly, for model II (which assumes c_1 , α , K , r , d_H and d_p are constant) WSS is satisfied with sufficiently low herbivore handling time [$\beta < \omega_3 - \omega_4$], relatively high values of the parasitoid attack rate and high conversion factor [$c_2\gamma > f_2(\beta)$]. For model III (which assumes c_1 , α , K , r and d_p are constant), WSS is satisfied with sufficiently low herbivore mortality [$d_H < \omega_1$], relatively high parasitoid conversion factor, and relatively low parasitoid handling time [$\mu/c_2 < f_3(d_H)$]. Finally, for model IV (which assumes c_1 , α , K , r , d_H and d_p are constant), sufficiently low herbivore handling time [$\beta < \omega_3 - \omega_4$], relatively high

parasitoid conversion factor, and relatively low parasitoid handling time [$\mu/c_2 < f_4(\beta)$] will satisfy WSS.

The bottom-up effects, such as the effects of host-plant resistance, on the stability of these systems are mainly via feeding rate of herbivore (α), which here assumed to be constant. However, variation in herbivore mortality (d_H) and handling time (β) can be considered to determine the effects of host-plant resistance. Models I and III show that a resistant plant, which causes a high level of herbivore mortality, can destabilize the system. Similarly, models II and IV show that a resistant plant, which increases the handling time of herbivore, may destabilize the system. However, experimental studies are required to evaluate the thresholds for herbivore mortality or handling time that affect the stability of specific tritrophic systems.

As for the crucifer-DBM-parasitoid system, host-plant resistance can affect the system in different ways. First, non-preference of first instar DBM larvae, as the main mechanism of plant resistance to DBM (Sections 1.3.2 and 2.5), can affect the crucifer-DBM-parasitoid system via DBM feeding rate or handling time. Handling time of DBM larvae on highly-resistant crucifers (with glossy-wax leaves) has been shown to be longer than on susceptible host plants (Eigenbrode *et al.*, 1991a; Eigenbrode & Shelton, 1992b; Eigenbrode & Pilliai, 1998). Based on models II and IV, if the increase in handling time of DBM exceeds a threshold level the system will be destabilized, resulting in extinction of both herbivore and parasitoid.

Second, plant resistance to DBM also acts on later larval stages or throughout larval development. This effect, which is found in partially-resistant crucifers (with normal-wax leaves) (Eigenbrode *et al.*, 1991b), can influence DBM mortality because of sub-optimal intake (i.e. feeding on plants with low nutritional status or toxicants). Based on models I and III, if the mortality rate of the herbivore exceeds a threshold, then the system becomes unstable and the herbivore and parasitoid populations will be excluded from the system. As a result, the strong effects of host-plant resistance whether on herbivore mortality or herbivore handling time will destabilize the tritrophic system. For a sustainable ecosystem, therefore, highly-resistant host plants are not recommended, since they will exclude natural enemies. In this regard, partially-resistant host plant may

be more applicable for sustainable strategies looking for compatibility of host-plant resistance and parasitoids.

On the other hand, top-down effects revealed by models II and I indicate that parasitoids with high attack rate and conversion factor, which can stabilize the system, are useful for sustainable biological control or IPM. The models III and IV also reveal that parasitoids with high conversion factor and low handling time also can stabilize the system and are helpful for sustainable strategies in agro-ecosystems. The functional responses of consumers are central to any model describing predation or parasitism (Hassell, 2000). In contrast to Type I functional response, which is more frequent among filter feeders (Holling, 1959; Rigler, 1961; Hassell, 2000; Jeschke *et al.*, 2004), Holling's prey-dependent Type II functional response has been used as the basis of the predator-prey theory (e.g. Chiu & Hsu, 1998; Wang & Ferro, 1998; Angerbjorn *et al.*, 1999; Redpath & Thirgood, 1999; Cantrell *et al.*, 2001; Heikinheimo, 2001; Rinaldi *et al.*, 2004). In models III and IV, which have Holling's Type II functional response for parasitoid, handling time of parasitoid was one of the important factors affecting stability of the systems. Such a known stabilizing effect of parasitoid handling time on dynamical systems (Weisser *et al.*, 1997; Mukherjee & Roy, 1998; Saleem *et al.*, 2003) might be an important factor in selecting the parasitoids of DBM either in sustainable biological control or in IPM programmes against this pest. However, based of model behaviours it is clear that if herbivore mortality or handling time exceeds a threshold level the system will be destabilized, regardless of the magnitude of parasitoid attack rate, handling time or conversion factor. Consequently, it must be borne in mind that the relative role of the factors influencing top-down forces (such as parasitoid handling time) completely depends on the basic role of the factors acting via bottom-up forces (such as host-plant effects on herbivore mortality and handling time). Further empirical and theoretical studies are needed to assess the effects of feeding rate of DBM (as influenced by host-plant resistance) on the stability of crucifer-DBM-parasitoid systems.

Chapter 6:

Summary and General Discussion

6.1 Key findings of the results

Non-choice individual performances:

- A significantly higher percentage parasitism by *C. plutellae* was found on DBM feeding on a partially-resistant host plant (*B. napus*) compared with a susceptible host plant (*B. rapa*).
- DBM reared on a partially-resistant plant (old common cabbage cv. Wheelers Imperial) showed a significantly greater parasitoid egg load and proportion of parasitized hosts compared to a fully susceptible plant (young Chinese cabbage).

Cage experiments:

- With short exposure times, the parasitism level of DBM larvae by *C. plutellae* on a susceptible host plant was significantly greater than on partially-resistant one. This difference disappeared when longer exposure times to the parasitoid were used.
- The number of *C. plutellae* cocoons on susceptible host plants was significantly greater than on partially-resistant host plants.

Olfactory responses:

- *Cotesia plutellae* did not differentiate between different plant types when both the plant types were susceptible or were partially resistant, but it could differentiate between the odours from susceptible (young Chinese cabbage) and partially-resistant (old common cabbages) plants.
- When uninfested plants were tested, *C. plutellae* reared from Chinese cabbage showed a strong tendency to choose young Chinese cabbage in comparison to old common cabbages. In contrast, naive *C. plutellae* reared from common cabbage or turnip did not differentiate between young Chinese cabbage and old common cabbage. *Cotesia plutellae*, which experienced multiple ovipositions of DBM larvae on young Chinese cabbage preferred this plant to old common

cabbages. However, such an experience on old common cabbages was not influential.

- When infested plants were tested, *C. plutellae* showed a strong tendency to choose infested young Chinese cabbage in comparison to infested old common cabbages.

Immune system:

- The encapsulation proportion of *C. plutellae* larvae in DBM larvae feeding on a fully-susceptible plant (young Chinese cabbage) was significantly greater than on common cabbage cv. Wheelers Imperial, which in turn was significantly greater than on common cabbage cv. Red Drumhead. Encapsulation for all these treatments was significantly greater than on the highly resistant cauliflower, Early Green Glazed. However, the encapsulation ability of DBM larvae was not strong enough to affect parasitism success of *C. plutellae*.
- In unparasitized DBM, phenoloxidase activity was significantly greater in larvae reared on Chinese cabbage or Wheelers Imperial compared with larvae reared on Red Drumhead or Early Green Glazed. However, there was no significant difference in phenoloxidase activity in parasitized larvae reared on the different host plants.
- Superparasitism had no effect on the ability of DBM larvae to encapsulate *C. plutellae* larvae.

Population dynamics:

- Ditrophic interactions: host-plant resistance (HPR) did not affect the equilibrial abundance of DBM, but it clearly had a principal role in governing DBM population dynamics. DBM populations on a partially-resistant (*B. napus*) and a susceptible (*B. rapa*) host plant were affected by direct and delayed density-dependent processes, respectively.
- Tritrophic interactions: HPR had no effect on the population size and variability of DBM, and the persistence time of DBM- *C. plutellae* interaction.
- The individual interactions, such as the effects of HPR on DBM development and parasitism by *C. plutellae*, did not translate into differences in the population dynamics.

Modelling:

- Model I predicted that sufficiently low herbivore mortality and relatively high values of parasitoid attack rate and conversion factor will result in stability of the system. Model II predicted that stability is satisfied with sufficiently low herbivore handling time, and relatively high values of parasitoid attack rate and conversion factor. Based on model III predictions, stability is satisfied with sufficiently low herbivore mortality, relatively high parasitoid conversion factor, and relatively low parasitoid handling time. Finally, model IV predicted that sufficiently low herbivore handling time, a relatively high parasitoid conversion factor, and a relatively low parasitoid handling time will result in system stability.
- Based on the above models, if the increase in handling time or mortality rate of DBM exceeds a threshold level the system will be destabilized, resulting in extinction of both herbivore and parasitoid. Highly-resistant host plants, therefore, will exclude natural enemies from the system. Consequently, partially-resistant host plants may be more applicable for sustainable strategies looking for compatibility of host-plant resistance and parasitoids.
- Parasitoids with a high attack rate and conversion factor, and a low handling time, can stabilize the system and thus are predicted to be the most suitable for sustainable biological control or IPM.

6.2 Underlying mechanisms for HPR effects on *C. plutellae* parasitism

The observed higher level of parasitism by *C. plutellae* on DBM feeding on a partially-resistant host plant (*B. napus*) compared with a susceptible host plant (*B. rapa*) in non-choice studies has been previously observed for another partially-resistant (old common cabbage) and susceptible (young Chinese cabbage) host plants by laboratory and greenhouse works (Talekar & Yang, 1991; Verkerk & Wright, 1994b). In contrast, field studies by Verkerk & Wright (1997) did not show such a difference; however, the age of common cabbage used in their studies (4 or 8 weeks old) might be the main reason for lack of such a difference.

HPR had significant effects on cellular immune function of DBM larvae. However, the effect was not influential enough to suppress parasitism. HPR also influenced humoral

immune function of unparasitized DBM larvae. This significant effect was suppressed by *C. plutellae* in parasitized DBM larvae. These results suggest that short term effects of HPR on *C. plutellae* are unlikely to be due to the nutritional status of host plant affecting DBM innate immune function. It is also unlikely to be due to effects of HPR on egg load by *C. plutellae* in DBM larvae since DBM larvae suffer from the lack of ability to fully encapsulate the only *C. plutellae* larvae in their haemocoel; but it might be because of the tendency for *C. plutellae* to parasitize DBM larvae feeding on a partially-resistant host plant. One possible reason for this tendency could be olfactory responses of the parasitoid to the plant-host semiochemicals. However, double-choice olfactory experiments failed to support such a hypothesis. Female *C. plutellae*, in fact preferred the susceptible host plant (young Chinese cabbage) to the partially-resistant host plant (old common cabbage). Short-exposure cage experiments supported the olfactory results; the level of parasitism by *C. plutellae* being significantly greater on DBM larvae on a susceptible plant compared with a partially-resistant one.

Another explanation for the higher parasitization of DBM larvae on a partially-resistant host plant might be the reduced fitness of DBM larvae feeding on sub-optimal host plants, resulting in DBM larvae failing to escape from the parasitoid attack. Since extending the exposure time to *C. plutellae* in non-choice studies reduced the difference in the level of parasitism between treatments, it is also possible that even longer exposure times would eliminate such differences completely. The results of cage experiments also indicated that observed differences in the level of parasitism disappeared with extended exposure times to the parasitoid. Population dynamics studies also showed that HPR has no effect on persistence of the DBM-*C. plutellae* interaction. Differences in HPR, which in ditrophic experiments influenced the population dynamics of DBM, were overwhelmed in tritrophic experiments by the response of *C. plutellae*. In conclusion, it seems that HPR may affect *C. plutellae* parasitism but this effect is not persistent and disappears over long-term host-parasitoid interactions.

6.3 The effects of HPR on searching efficiency of *C. plutellae*

It is well documented that *C. plutellae* responds to volatiles derived from host plants and plant-host complexes (Bogahawatte & Van Emden, 1996; Potting *et al.*, 1999; Shiojiri *et al.*, 2000a,b; Reddy *et al.*, 2002; Wang & Keller, 2002; Liu & Jiang, 2003; Schuler *et al.*, 2003). It has been also found that plant-host derived synomones are the most attractive volatile to *C. plutellae* (Bogahawatte & Van Emden, 1996; Potting *et al.*, 1999; Shiojiri *et al.*, 2000b).

From the IPM viewpoint, the attraction of *C. plutellae* to different plant-host complexes is fundamental to the success of combining HPR and *C. plutellae*. Bogahawatte & van Emden (1996) studied preference of *C. plutellae* for odours from a partially-resistant host plant (cabbage cv. Blue Lake) and a susceptible host plant (cauliflower cv. Early Phenomenal). They found that *C. plutellae* preferred the odour of the plant on which they were reared. In contrast, the present study indicated *C. plutellae* preferred a susceptible host plant (young Chinese cabbage) to a partially-resistant (old common cabbage) plant, irrespective of whether the plants were infested or uninfested. In the latter case this preference occurred either when *C. plutellae* were reared on the susceptible host plant or when *C. plutellae* were reared on the partially-resistant plant but had an experience on the susceptible host plant. Bogahawatte & van Emden (1996) also showed that *C. plutellae* reared on a third host plant (cabbage cv. Brunswick) failed to discriminate between the susceptible and the partially-resistant host plant. Similar results were obtained in the present study when *C. plutellae* had no experience.

Bogahawatte & van Emden (1996) also found that *C. plutellae* reared from a partially-resistant host plant preferred such a plant even to an infested susceptible plant. In contrast, the present study showed that a partially-resistant infested plant (less attractive under equal conditions) was preferred to an uninfested susceptible host plant. The different results obtained in these two studies suggest that *C. plutellae* responses to volatiles from different plant-host complexes are specific to plant species and cultivars. It is possible that the lower responsiveness of *C. plutellae* to old common cabbage in the present study might be due to reduced secondary plant products, such as glucosinolates, and reduced myrosinase activity in older crucifers (Porter *et al.*, 1991; Renwick *et al.*,

1992; Kiddle *et al.*, 1994; Mevy *et al.*, 1997; Wallace & Eigenbrode, 2002; Lambdon *et al.*, 2003). Chemical studies on DBM-damaged crucifers are required to determine the quality and quantity of the semiochemicals that attract *C. plutellae*. Ultimately, field studies are necessary to consider the consequences of combining such a partially-resistant host plants and *C. plutellae* for DBM management during the crop cycle.

6.4 The effects of bottom-up and top-down forces on population dynamics of crucifers-DBM-parasitoid systems

Studies on the population dynamics of host-parasitoid interactions in crucifers-DBM-parasitoid systems have focused on population densities of DBM and its parasitoids (RigginBucci & Gould, 1997; Haseeb *et al.*, 2001; Guilloux *et al.*, 2003; Miura, 2003) rather than the mechanisms by which populations are regulated.

The present study was the first attempt at understanding the process governing population dynamics of DBM-*C. plutellae* interactions. Long-term studies of DBM-*C. plutellae* populations on susceptible and partially-resistant host plants are necessary to understand the role of these bottom-up and top-down forces on the dynamics and persistence of DBM in field. Such long-term studies are very difficult to do. In this regard, theoretically predictions of population behaviours using appropriate population models can be a helpful accompaniment for empirical data (Hassell, 2000).

In the present study, an example of the one of the most important models of tritrophic systems, model IV with Holling's type II functional responses, was explored. The model IV predicts that handling time of the parasitoid is one of the important factors in the stability of tritrophic systems. It was suggested earlier (Section 6.2) that the most likely reason for higher level of parasitism by *C. plutellae* on partially-resistant host plants could be the reduced fitness of DBM larvae, which in turn results in an easier handling of the host larvae by *C. plutellae*. It therefore can be hypothesized that a more resistant host plant, which reduces the fitness of DBM larvae, may decrease *C. plutellae* handling time, resulting in stability of the tritrophic system (Section 5.6). On the other hand, highly-resistant host plants, which increase herbivore mortality or herbivore handling more than an appropriate threshold, will exclude the parasitoid from the

tritrophic system. For a sustainable ecosystem, therefore, partially-resistant host plant may be more applicable. In ditrophic systems (Section 2.5) it was argued how the observed delayed density-dependent process of DBM population on a susceptible host plant might give rise to fluctuations in DBM populations leading to cycles or chaotic behaviour. For tritrophic systems, on the other hand, model IV showed that increasing handling time can result in cycles or chaotic behaviour of all three populations or extinction of parasitoid populations. Studies on handling time of DBM parasitoids are rare (Wang & Keller, 2002) and experimental data are required to compare handling time of DBM parasitoids and the effects of HPR.

6.5 Conclusions and further directions

The present study showed that HPR effects on *C. plutellae* parasitism were not persistent and disappeared over long-term host-parasitoid interactions mainly because in the present study DBM was a fully permissive host of *C. plutellae*. Other DBM and *C. plutellae* biotypes may show differences in host resistance and parasitoid virulence, respectively. If the field populations of DBM show full permissiveness for *C. plutellae*, the host-parasitoid interactions might be destabilized due to lack of an effective refuge from parasitism. This could drive the parasitoid population or both the host and parasitoid populations into extinction. However, the lack of a physiological refuge (successful host resistance to attack) is not sufficient for such consequences to occur in the field populations; this also requires the lack of temporal and spatial refuges from a foraging parasitoid that is unlikely in heterogeneous environments. As a result, establishment and persistence of parasitoids as an effective natural check to DBM populations require the conservation of biodiversity in agroecosystems. In other words, selective pressures (such as using chemical pesticides or genetically-modified plants) in such ecosystems must be limited.

The present study also showed that HPR could affect DBM-*C. plutellae* population dynamics via herbivore fitness costs, handling time or mortality. However, partially-resistant plants may be more applicable than highly resistant ones in a sustainable ecosystem, as the latter can destabilize tritrophic interaction excluding the parasitoid from the system. Using partially-resistant plants may also slow down the adaptation of

DBM biotypes that are able to overcome resistant plants. The failure in attraction of *C. plutellae* by common cabbages stresses the need for future studies on compatibility of HPR and parasitoids to be focused on developing semiochemically-based partially-resistant host plants that are attractive to the parasitoids. Studies on the compatibility of parasitoids with HPR should also compare the relative importance of aspects of behaviour such as conversion factor, attack rate and handling time of different parasitoids. The findings in this and future studies on insect multitrophic interactions can help underpin sustainable pest management strategies as long as governments can provide support to farmers to insure against potential economic losses arising from non-chemical methods of pest control.

References

- Abro, G. H.; T. S. Corbitt; P. T. Christie & D. J. Wright (1993) Sublethal effects of abamectin on *Plutella xylostella* L and *Spodoptera littoralis* Boisduval larvae. *Crop Protection* 12: 39-44.
- Afraimovich, V. S.; S. B. Hsu & H. E. Lin (2001) Chaotic behavior of three competing species of May-Leonard model under small periodic perturbations. *International Journal of Bifurcation and Chaos* 11: 435-447.
- Agnello, A. M.; W. H. Reissig; J. Kovach & J. P. Nyrop (2003) Integrated apple pest management in New York State using predatory mites and selective pesticides. *Agriculture Ecosystems and Environment* 94: 183-195.
- Agrawal, A. A.; R. Karban & R. G. Colfer (2000) How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. *Oikos* 89: 70-80.
- Agrawal, A. A. & C. N. Klein (2000) What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores. *Journal of Animal Ecology* 69: 525-535.
- Agrawal, A. A.; J. K. Conner; M. T. J. Johnson & R. Wallsgrave (2002) Ecological genetics of an induced plant defense against herbivores: Additive genetic variance and costs of phenotypic plasticity. *Evolution* 56: 2206-2213.
- Ahmad, S. & F. M. de Oca (2002) Average growth and extinction in a two dimensional Lotka-Volterra system. *Dynamics of Continuous Discrete and Impulsive Systems-Series A-Mathematical Analysis* 9: 177-186.
- Akgur, S. A.; P. Ozturk; I. Solak; A. R. Moral & B. Ege (2003) Human serum paraoxonase (PON1) activity in acute organophosphorous insecticide poisoning. *Forensic Science International* 133: 136-140.
- Aldrich, J. R. & A. Zhang (2002) Kairomone strains of *Euclytia flava* (Townsend), a parasitoid of stink bugs. *Journal of Chemical Ecology* 28: 1565-1582.
- Aliabadi, A. & D. W. Whitman (2001) Semiochemistry of crucifers and their herbivores. In: T. N. Ananthakrishnan (ed.), *Insects and plant defence dynamics*, pp. 71-94, SP Science Publishers, Enfield.
- AlvarezBuylla, E. R.; R. GarciaBarrios; C. LaraMoreno & M. MartinezRamos (1996) Demographic and genetic models in conservation biology: Applications and perspectives for tropical rain forest tree species. *Annual Review of Ecology and Systematics* 27: 387-421.
- Andrewartha, H. G. & L. C. Birch (1954). *The distribution and abundance of animals*. University of Chicago Press, Chicago, pp.
- Angerbjorn, A.; M. Tannerfeldt & S. Erlinge (1999) Predator-prey relationships: Arctic

foxes and lemmings. *Journal of Animal Ecology* 68: 34-49.

Armitage, S. A. O.; J. J. W. Thompson; J. Rolff & M. T. Siva-Jothy (2003) Examining costs of induced and constitutive immune investment in *Tenebrio molitor*. *Journal of Evolutionary Biology* 16: 1038-1044.

Asgari, S.; G. M. Zhang; R. Zareie & O. Schmidt (2003) A serine proteinase homolog venom protein from an endoparasitoid wasp inhibits melanization of the host hemolymph. *Insect Biochemistry and Molecular Biology* 33: 1017-1024.

Ashida, M. & H. I. Yamazaki (1990) Biochemistry of the phenoloxidase system in insects: with special reference to its activation. In: E. Ohnishi & H. Ishizaki (ed.), *Molting and metamorphosis*, pp. 239-265, Springer-verlag, Berlin.

Ashida, M. & P. T. Brey (1997) Recent advances in research on the insect prophenoloxidase cascade. In: P. T. Brey & D. Hultmark (ed.), *Molecular mechanisms of immune responses in insects*, pp. 135-172, Chapman & Hall, London.

Auerbach, M. J.; E. F. Conner & S. Mopper (1995) Minor miners and major miners: population dynamics of leaf-mining insects. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 83-110, Academic Press, San Diego.

Aziz-Alaoui, M. A. (2002) Study of a Leslie-Gower-type tritrophic population model. *Chaos Solitons and Fractals* 14: 1275-1293.

Bae, S. & Y. Kim (2004) Host physiological changes due to parasitism of a braconid wasp, *Cotesia plutellae*, on diamondback moth, *Plutella xylostella*. *Comparative Biochemistry and Physiology a-Molecular and Integrative Physiology* 138: 39-44.

van Bael, S. A.; J. D. Brawn & S. K. Robinson (2003) Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences of the United States of America* 100: 8304-8307.

Barton, A. M. (1986) Spatial variation in the effect of ants on an extrafloral nectary plant. *Ecology* 67: 495-504.

Beckage, N. E. & L. M. Riddiford (1982) Effects of parasitism by *Apanteles congregatus* on the endocrine physiology of the tobacco hornworm *Manduca sexta*. *General and Comparative Endocrinology* 47: 308-322.

Beckage, N. E. (1998) Modulation of immune responses to parasitoids by polydnviruses. *Parasitology* 116: S57-S64.

Beerntsen, B. T.; A. A. James & B. M. Christensen (2000) Genetics of mosquito vector competence. *Microbiology and Molecular Biology Reviews* 64: 115-137.

Begon, M.; M. Mortimer & D. J. Thompson (1996). *Population ecology: a unified study of animals and plants*. Blackwell science, Oxford, 247 pp.

- Behmer, S. T. & R. J. Grebenok (1998) Impact of dietary sterols on life-history traits of a caterpillar. *Physiological Entomology* 23: 165-175.
- Bellomo, N.; L. Preziosi & A. Romano (2000). *Mechanics and dynamical systems with Mathematica*. Birkhauser Verlag AG, Boston, 417 pp.
- Benedet, F.; T. Leroy; N. Gauthier; C. Thibaudeau; E. Thibout & S. Renault (2002) Gustatory sensilla sensitive to protein kairomones trigger host acceptance by an endoparasitoid. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269: 1879-1886.
- Benrey, B. & R. F. Denno (1997) The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. *Ecology* 78: 987-999.
- Benrey, B.; R. F. Denno & L. Kaiser (1997) The influence of plant species on attraction and host acceptance in *Cotesia glomerata* (Hymenoptera: Braconidae). *Journal of Insect Behavior* 10: 619-630.
- Benrey, B.; A. Callejas; L. Rios; K. Oyama & R. F. Denno (1998) The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biological Control* 11: 130-140.
- Berberet, R. C.; L. J. Willson & M. Odejar (1987) Probabilities for encapsulation of eggs of *Bathyplectes curculionis* (Hymenoptera, Ichneumonidae) by larvae of *Hypera postica* (Coleoptera, Curculionidae) and resulting reduction in effective parasitism. *Annals of the Entomological Society of America* 80: 483-485.
- Bernays, E. A. & R. F. Chapman (1994). *Host-plant selection by phytophagous insects*. Chapman & Hall, New York, pp.
- Bezemer, T. M. & T. H. Jones (1998) Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* 82: 212-222.
- Biever, K. D.; R. L. Chauvin; G. L. Reed & R. C. Wilson (1992) Seasonal occurrence and abundance of lepidopterous pests and associated parasitoids on collards in the northwestern United States. *Journal of Entomological Science* 27: 5-18.
- Biswas, S. & R. Singh (1998) Interaction between host plant resistance and the biocontrol of a cereal aphid: a laboratory study. *Biological Agriculture and Horticulture* 16: 25-36.
- Bizina, E. V. (1997) The relative strength of top-down versus bottom-up factors in the regulation of community structure and functioning: Review of hypotheses. *Zhurnal Obshchei Biologii* 58: 26-45.
- Bjorkman, C. (2000) Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia* 123: 223-231.
- Blasius, B.; A. Huppert & L. Stone (1999) Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature* 399: 354-359.

- Blasius, B. & L. Stone (2000) Ecology: nonlinearity and the moran effect. *Nature* 406: 846-847.
- Bleeker, M. A. K.; H. M. Smid; A. C. Van Aelst; J. J. A. Van Loon & L. E. M. Vet (2004) Antennal sensilla of two parasitoid wasps: a comparative scanning electron microscopy study. *Microscopy Research and Technique* 63: 266-273.
- Blom, P. E.; S. J. Fleischer & Z. Smilowitz (2002) Spatial and temporal dynamics of Colorado potato beetle (Coleoptera : Chrysomelidae) in fields with perimeter and spatially targeted insecticides. *Environmental Entomology* 31: 149-159.
- Blumberg, D. & S. M. Ferkovich (1994) Development and encapsulation of the endoparasitoid, *Microplitis croceipes* (Hym, Braconidae), in 6 candidate host species (Lep). *Entomophaga* 39: 293-302.
- Blumberg, D. (1997) Parasitoid encapsulation as a defense mechanism in the Coccoidea (Homoptera) and its importance in biological control. *Biological Control* 8: 225-236.
- Bodnaryk, R. P. (1991) Developmental profile of Sinalbin (p-hydroxybenzyl glucosinolate) in mustard seedlings, *Sinapis alba* L, and its relationship to insect resistance. *Journal of Chemical Ecology* 17: 1543-1556.
- Bogahawatte, C. N. L. & H. F. vanEmden (1996) The influence of the host plant of diamond-back moth (*Plutella xylostella*) on the plant preferences of its parasitoid *Cotesia plutellae* in Sri Lanka. *Physiological Entomology* 21: 93-96.
- Bogdan, C.; M. Rollinghoff & A. Diefenbach (2000) Reactive oxygen and reactive nitrogen intermediates in innate and specific immunity. *Current Opinion in Immunology* 12: 64-76.
- Bomze, I. M. (1983) Lotka-Volterra equation and replicator dynamics: a two-dimensional classification. *Biological Cybernetics* 48: 201-211.
- Bones, A. M. & J. T. Rossiter (1996) The myrosinase-glucosinolate system, its organisation and biochemistry. *Physiologia Plantarum* 97: 194-208.
- Bonsall, M. B. & S. Eber (2001) The role of age-structure on the persistence and the dynamics of insect herbivore-parasitoid interactions. *Oikos* 93: 59-68.
- Boone, M. D.; R. D. Semlitsch; J. F. Fairchild & B. B. Rothermel (2004) Effects of an insecticide on amphibians in large-scale experimental ponds. *Ecological Applications* 14: 685-691.
- Borges, M.; S. Colazza; P. Ramirez-Lucas; K. R. Chauhan; M. C. B. Moraes & J. R. Aldrich (2003) Kairomonal effect of walking traces from *Euschistus heros* (Heteroptera : Pentatomidae) on two strains of *Telenomus podisi* (Hymenoptera : Scelionidae). *Physiological Entomology* 28: 349-355.
- van den Bosch, R. (1964) Encapsulation of the eggs of *Bathyplectes curculionis* (Hym.:

- Ichneumonidae) in larvae of *Hypera brunneipennis* and *Hypera postica* (Col.: Curculionidae). *Journal of Insect Pathology* 6: 343-367.
- Bottrell, D. G.; P. Barbosa & F. Gould (1998) Manipulating natural enemies by plant variety selection and modification: a realistic strategy? *Annual Review of Entomology* 43: 347-367.
- Bowers, M. D. (1993) Aposematic caterpillars: life-styles of the warningly colored and unpalatable. In: N. E. Stamp & T. M. Casey (ed.), *Caterpillars: ecological and evolutionary constraints on foraging*, pp. 331-371, Chapman & Hall,
- Bradburne, R. P. & R. Mithen (2000) Glucosinolate genetics and the attraction of the aphid parasitoid *Diaeretiella rapae* to *Brassica*. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267: 89-95.
- Bradford, M. M. (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry* 72: 248-254.
- Braman, S. K.; R. R. Duncan; W. W. Hanna & M. C. Engelke (2003) Arthropod predator occurrence and performance of *Geocoris uliginosus* (Say) on pest-resistant and susceptible turfgrasses. *Environmental Entomology* 32: 907-914.
- Branco, M. C. & M. A. Medeiros (2001) Impact of insecticides on diamondback moth parasitoids on cabbage in the federal district of Brazil. *Pesquisa Agropecuaria Brasileira* 36: 7-13.
- Brewer, M. J.; J. M. Struttman & D. W. Mornhinweg (1998) *Aphelinus albipodus* (Hymenoptera : Aphelinidae) and *Diaeretiella rapae* (Hymenoptera : Braconidae) parasitism on *Diuraphis noxia* (Homoptera : Aphididae) infesting barley plants differing in plant resistance to aphids. *Biological Control* 11: 255-261.
- Brivio, M. F.; M. Mastore & M. Moro (2004) The role of *Steinernema feltiae* body-surface lipids in host-parasite immunological interactions. *Molecular and Biochemical Parasitology* 135: 111-121.
- Brodeur, J. & L. E. M. Vet (1995) Relationships between parasitoid host-range and host-defense: a comparative study of egg encapsulation in 2 related parasitoid species. *Physiological Entomology* 20: 7-12.
- Brown, P. D. & M. J. Morra (1997) Control of soil-borne plant pests using glucosinolate-containing plants. *Advances in Agronomy* 61: 167-231.
- Brown, M. J. F.; Y. Moret & P. Schmid-Hempel (2003) Activation of host constitutive immune defence by an intestinal trypanosome parasite of bumble bees. *Parasitology* 126: 253-260.
- Buitenhuis, R.; J. N. McNeil; G. Boivin & J. Brodeur (2004) The role of honeydew in host searching of aphid hyperparasitoids. *Journal of Chemical Ecology* 30: 273-285.

- Bulet, P.; C. Hetru; J. L. Dimarcq & D. Hoffmann (1999) Antimicrobial peptides in insects; structure and function. *Developmental and Comparative Immunology* 23: 329-344.
- Calatayud, P. A.; M. A. Polania; C. D. Seligmann & A. C. Bellotti (2002) Influence of water-stressed cassava on *Phenacoccus herreni* and three associated parasitoids. *Entomologia Experimentalis Et Applicata* 102: 163-175.
- Campan, E. & B. Benrey (2004) Behavior and performance of a specialist and a generalist parasitoid of bruchids on wild and cultivated beans. *Biological Control* 30: 220-228.
- Campbell, B. & S. Duffey (1979) Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control. *Science* 205: 700-702.
- Cantrell, R. S.; C. Cosner & W. F. Fagan (2001) How predator incursions affect critical patch size: the role of the functional response. *American Naturalist* 158: 368-375.
- Cappuccino, N. (1995) Novel approaches to the study of population dynamics. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 3-16, Academic Press, San Diego.
- Cappuccino, N. & P. W. Price (ed.) (1995). *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, 429 pp.
- Capurro, A. F.; M. Gatto & G. Tosi (1997) Delayed and inverse density dependence in a chamois population of the Italian Alps. *Ecography* 20: 37-47.
- Carpenter, S. R.; J. F. Kitchell; J. R. Hodgson; P. A. Cochran; J. J. Elser; M. M. Elser; D. M. Lodge; D. Kretchmer; X. He & C. N. Vonende (1987) Regulation of lake primary productivity by food web structure. *Ecology* 68: 1863-1876.
- Cavani, M. & S. Romero (2003) A simple food chain model with delay. *Positive Systems, Proceedings* 294: 273-280.
- Ceccatti, J. S. (2004) Resisting insects: shifting strategies in chemical control. *Endeavour* 28: 14-19.
- Cerenius, L. & K. Soderhall (2004) The prophenoloxidase-activating system in invertebrates. *Immunological Reviews* 198: 116-126.
- Chadwick, D. & J. Goode (ed.) (1999). *Insect-plant interactions and induced plant defence*. John Wiley & Sons, Chichester, 281 pp.
- Chatfield, C. (1996). *The analysis of time series: an introduction*. Chapman & Hall, 241 pp.
- Cheng, L. (1970) Timing of attack of *Lypha dubia* Fall (Diptera: Tachinidae) on the winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae) as a factor affecting parasite success. *Journal of Animal Ecology* 39: 313-320.

- Chew, F. S. (1988) Biological effects of glucosinolates. In: H. G. Cutler (ed.), *Biologically active natural products: potential use in agriculture*, pp. 155-181, American Chemical Society, Washington DC.
- Chew, F. S. & J. A. A. Renwick (1995) Host plant choice in *Pieris* butterflies. In: R. T. Cardé & W. J. Bell (ed.), *Chemical ecology of insects 2*, pp. 214-238, Chapman & Hall, New York.
- Chilcutt, C. F. & B. E. Tabashnik (1997) Host-mediated competition between the pathogen *Bacillus thuringiensis* and the parasitoid *Cotesia plutellae* of the diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology* 26: 38-45.
- Chilcutt, C. F. & B. E. Tabashnik (1999) Simulation of integration of *Bacillus thuringiensis* and the parasitoid *Cotesia plutellae* (Hymenoptera : Braconidae) for control of susceptible and resistant diamondback moth (Lepidoptera : Plutellidae). *Environmental Entomology* 28: 505-512.
- Chiu, C. H. & S. B. Hsu (1998) Extinction of top-predator in a three-level food-chain model. *Journal of Mathematical Biology* 37: 372-380.
- Choquenot, D. & W. A. Ruscoe (2000) Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology* 69: 1058-1070.
- Chown, S. L. & W. Block (1997) Comparative nutritional ecology of grass-feeding in a sub-Antarctic beetle: the impact of introduced species on *Hydromedion sparsutum* from south Georgia. *Oecologia* 111: 216-224.
- Clancy, K. M. & P. W. Price (1987) Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. *Ecology* 68: 733-737.
- Colazza, S.; A. Fucarino; E. Peri; G. Salerno; E. Conti & F. Bin (2004a) Insect oviposition induces volatile emission in herbaceous plants that attracts egg parasitoids. *Journal of Experimental Biology* 207: 47-53.
- Colazza, S.; J. S. McElfresh & J. G. Millar (2004b) Identification of volatile synomones, induced by *Nezara viridula* feeding and oviposition on bean spp., that attract the egg parasitoid *Trissolcus basal*. *Journal of Chemical Ecology* 30: 945-964.
- Coll, M.; S. Gavish & I. Dori (2000) Population biology of the potato tuber moth, *Phthorimaea operculella* (Lepidoptera : Gelechiidae), in two potato cropping systems in Israel. *Bulletin of Entomological Research* 90: 309-315.
- Connor, E. F. & M. W. Beck (1993) Density-related mortality in *Cameraria hamadryadella* (Lepidoptera, Gracillariidae) at epidemic and endemic densities. *Oikos* 66: 515-525.
- Conti, E.; G. Salerno; F. Bin; H. J. Williams & S. B. Vinson (2003) Chemical cues from *Murgantia histrionica* eliciting host location and recognition in the egg parasitoid *Trissolcus brochymenae*. *Journal of Chemical Ecology* 29: 115-130.

- Conti, E.; G. Salerno; F. Bin & S. B. Vinson (2004) The role of host semiochemicals in parasitoid specificity: a case study with *Trissolcus brochymenae* and *Trissolcus simoni* on pentatomid bugs. *Biological Control* 29: 435-444.
- Cooper, G. (2001) Must there be a balance of nature? *Biology and Philosophy* 16: 481-506.
- Cotter, S. C. & K. Wilson (2002) Heritability of immune function in the caterpillar *Spodoptera littoralis*. *Heredity* 88: 229-234.
- Cotter, S. C.; L. E. B. Kruuk & K. Wilson (2004) Costs of resistance: genetic correlations and potential trade-offs in an insect immune system. *Journal of Evolutionary Biology* 17: 421-429.
- Couty, A.; L. Kaiser; D. Huet & M. H. Pham-Delegue (1999) The attractiveness of different odour sources from the fruit-host complex on *Leptopilina boulardi*, a larval parasitoid of frugivorous *Drosophila* spp. *Physiological Entomology* 24: 76-82.
- Coxfoster, D. L. & J. E. Stehr (1994) Induction and localization of FAD-glucose dehydrogenase (Gld) during encapsulation of abiotic implants in *Manduca sexta* larvae. *Journal of Insect Physiology* 40: 235-249.
- Coxfoster, D. L.; J. E. Stehr; W. Closshey; M. Pieffer & S. Z. Zheng (1995) FAD-glucose dehydrogenase: essential role in encapsulation of fungal invaders in insects. *Journal of Cellular Biochemistry* 206-206.
- Crawley, M. J. (2002). *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley & Sons, Chichester, 761 pp.
- Darwish, E.; M. El-shazly & H. El-Sherif (2003) The choice of probing sites by *Bracon hebetor* Say (Hymenoptera : Braconidae) foraging for *Ephestia kuehniella* Zeller (Lepidoptera : Pyralidae). *Journal of Stored Products Research* 39: 265-276.
- de Bruyn, L.; J. Scheirs & R. Verhagen (2002) Nutrient stress, host plant quality, and herbivore performance of a leaf-mining fly on grass. *Oecologia* 130: 594-599.
- de Vis, R. M. J.; H. Mendez & J. C. van Lenteren (2003) Comparison of foraging behavior, interspecific host discrimination, and competition of *Encarsia formosa* and *Amitus fuscipennis*. *Journal of Insect Behavior* 16: 117-152.
- Delpuech, J. M. & J. Meyet (2003) Reduction in the sex ratio of the progeny of a parasitoid wasp (*Trichogramma brassicae*) surviving the insecticide chlorpyrifos. *Archives of Environmental Contamination and Toxicology* 45: 203-208.
- Dempster, J. P. (1958) The natural control of populations of butterflies and moths. *Biological Reviews of the Cambridge Philosophical Society* 58: 461-481.
- Dempster, J. P. & I. F. G. McClean (1998) Definition of terms. In: J. P. Dempster & I. F. G. McClean (ed.), *Insect populations: in theory and in practice*, pp. 1-4, Kluwer.

- den Boer, P. J. (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18: 165-194.
- Denno, R. F.; C. Gratton; M. A. Peterson; G. A. Langellotto; D. L. Finke & A. F. Huberty (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology* 83: 1443-1458.
- Denno, R. F.; C. Gratton; H. Dobel & D. L. Finke (2003) Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84: 1032-1044.
- Dicke, M. (1994) Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. *Journal of Plant Physiology* 143: 465-472.
- Dicke, M. (1999) Are herbivore-induced plant volatiles reliable indicators of herbivore identity to foraging carnivorous arthropods? *Entomologia Experimentalis Et Applicata* 91: 131-142.
- Dicke, M. & J. J. A. van Loon (2000) Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis Et Applicata* 97: 237-249.
- Dicke, M.; J. G. de Boer; M. Hofte & M. C. Rocha-Granados (2003) Mixed blends of herbivore-induced plant volatiles and foraging success of carnivorous arthropods. *Oikos* 101: 38-48.
- Dimopoulos, G. (2003) Insect immunity and its implication in mosquito-malaria interactions. *Cellular Microbiology* 5: 3-14.
- Ding, Y.; C. A. White; J. V. Bruckner & M. G. Bartlett (2004) Determination of deltamethrin and its metabolites, 3-phenoxybenzoic acid and 3-phenoxybenzyl alcohol, in maternal plasma, amniotic fluid, and placental and fetal tissues by HPLC. *Journal of Liquid Chromatography and Related Technologies* 27: 1875-1892.
- Douloupaka, S. & H. F. van Emden (2003) A maternal influence on the conditioning to plant cues of *Aphidius colemani* Viereck, parasitizing the aphid *Myzus persicae* Sulzer. *Physiological Entomology* 28: 108-113.
- van den Driessche, P. & M. L. Zeeman (1998) Three-dimensional competitive Lotka-Volterra systems with no periodic orbits. *Siam Journal on Applied Mathematics* 58: 227-234.
- Dunham, K. M.; E. F. Robertson & C. C. Grant (2004) Rainfall and the decline of a rare antelope, the tsessebe (*Damaliscus lunatus lunatus*), in Kruger national park, South Africa. *Biological Conservation* 117: 83-94.
- Dutton, A.; L. Mattiacci & S. Dorn (2000) Plant-derived semiochemicals as contact host location stimuli for a parasitoid of leafminers. *Journal of Chemical Ecology* 26: 2259-2273.

- Dwyer, G. (1995) Simple models and complex interactions. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 209-227, Academic Press, San Diego.
- Dyer, L. A. & D. K. Letourneau (1999) Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia* 119: 265-274.
- Eber, S. (2001) Multitrophic interactions: the population dynamics of spatially structured plant-herbivore-parasitoid systems. *Basic and Applied Ecology* 2: 27-33.
- Eccard, J. A. & H. Ylonen (2003) Who bears the costs of interspecific competition in an age-structured population? *Ecology* 84: 3284-3293.
- Eickwort, K. R. (1977) Population dynamics of a relatively rare species of milkweed beetle (*Labidomera*). *Ecology* 58: 527-538.
- Eigenbrode, S. D. & A. M. Shelton (1990) Behavior of neonate diamondback moth larvae (Lepidoptera, Plutellidae) on glossy-leafed resistant *Brassica oleracea* L. *Environmental Entomology* 19: 1566-1571.
- Eigenbrode, S. D.; A. M. Shelton & M. H. Dickson (1990) Two types of resistance to the diamondback moth (Lepidoptera, Plutellidae) in cabbage. *Environmental Entomology* 19: 1086-1090.
- Eigenbrode, S. D.; K. E. Espelie & A. M. Shelton (1991a) Behavior of neonate diamondback moth larvae [*Plutella xylostella* (L)] on leaves and on extracted leaf waxes of resistant and susceptible cabbages. *Journal of Chemical Ecology* 17: 1691-1704.
- Eigenbrode, S. D.; K. A. Stoner; A. M. Shelton & W. C. Kain (1991b) Characteristics of glossy leaf waxes associated with resistance to diamondback moth (Lepidoptera, Plutellidae) in *Brassica oleracea*. *Journal of Economic Entomology* 84: 1609-1618.
- Eigenbrode, S. D. & A. M. Shelton (1992a) Resistance to diamondback moth in *Brassica*: mechanism and potential for resistant cultivars. In: N. S. Talekar (ed.), *Management of diamondback moth and other crucifer pests. Proc. 2nd. Internat. Workshop*, pp. 65-74, AVRDC, Shanhua.
- Eigenbrode, S. D. & A. M. Shelton (1992b) Survival and behavior of *Plutella xylostella* larvae on cabbages with leaf waxes altered by treatment with S-ethyl dipropylthiocarbamate. *Entomologia Experimentalis Et Applicata* 62: 139-145.
- Eigenbrode, S. D. & S. K. Pillai (1998) Neonate *Plutella xylostella* responses to surface wax components of a resistant cabbage (*Brassica oleracea*). *Journal of Chemical Ecology* 24: 1611-1627.
- Elzen, G. W. & D. D. Hardee (2003) United States department of agriculture: agricultural research service research on managing insect resistance to insecticides. *Pest Management Science* 59: 770-776.
- van Emden, H. F. (1999) Are two methods better than one? *International Journal of*

Pest Management 45: 1-2.

Enderlein, P. & M. Wahl (2004) Dominance of blue mussels versus consumer-mediated enhancement of benthic diversity. *Journal of Sea Research* 51: 145-155.

Endersby, N. M. & W. C. Morgan (1991) Alternatives to synthetic chemical insecticides for use in crucifer crops. *Biological Agriculture and Horticulture* 8: 33-52.

Erbilgin, N. & K. F. Raffa (2001) Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. *Oecologia* 127: 444-453.

Ernest, S. K. M.; J. H. Brown & R. R. Parmenter (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88: 470-482.

Estes, J. A.; N. S. Smith & J. F. Palmisano (1978) Sea otter predation and community organization in the western Aleutian islands, Alaska. *Ecology* 59: 822-833.

van Etten, C. H.; M. E. Daxenbichler; P. H. Williams & W. F. Kwolek (1976) Glucosinolates and derived products in cruciferous vegetables: analysis of the edible part from twenty-two varieties of cabbage. *Journal of Agriculture and Food Chemistry* 24: 452-455.

Eubanks, M. D. & R. F. Denno (2000) Host plants mediate omnivore-herbivore interactions and influence prey suppression. *Ecology* 81: 936-947.

Fabrick, J. A.; J. E. Baker & M. R. Kanost (2004) Innate immunity in a pyralid moth: functional evaluation of domains from a beta-1,3-glucan recognition protein. *Journal of Biological Chemistry* 279: 26605-26611.

Fahey, J. W.; A. T. Zalcmann & P. Talalay (2001) The chemical diversity and distribution of glucosinolates and isothiocyanates among plants. *Phytochemistry* 56: 5-51.

FAO (2004). Website of Food and Agriculture Organization of the United Nations. <http://www.fao.org/>.

Farid, A.; J. B. Johnson; B. Shafii & S. S. Quisenberry (1998a) Tritrophic studies of Russian wheat aphid, a parasitoid, and resistant and susceptible wheat over three parasitoid generations. *Biological Control* 12: 1-6.

Farid, A.; S. S. Quisenberry; J. B. Johnson & B. Shafii (1998b) Impact of wheat resistance on Russian wheat aphid and a parasitoid. *Journal of Economic Entomology* 91: 334-339.

Feeny, P. (1977) Defensive ecology of the Cruciferae. *Annals of the Missouri Botanical Garden* 64: 221-234.

Felitsky, D. J. (1997). An investigation of the role of quinones as electron acceptors for FAD-glucose dehydrogenase, The Pennsylvania State University.

- Feltwell, J. (1982) Large white butterfly: the biology, biochemistry and physiology of *P. brassicae* (L.). *The Hague* 273-273.
- Fenimore, J. A. (1998). Production of reactive oxygen species by hemocytes of *Manduca sexta*, tobacco hornworm, during an in vitro encapsulation response, The Pennsylvania State University: 150.
- Fernandez-Nunez, J. (1998) Lagrangian structure of the two-dimensional Lotka-Volterra system. *International Journal of Theoretical Physics* 37: 2457-2462.
- Ferrenberg, S. M. & R. F. Denno (2003) Competition as a factor underlying the abundance of an uncommon phytophagous insect, the salt-marsh planthopper *Delphacodes penedetecta*. *Ecological Entomology* 28: 58-66.
- Fonseka, M. M. D.; K. Medagoda; Y. Tillakaratna; S. B. Gunatilake & H. J. de Silva (2003) Self-limiting cerebellar ataxia following organophosphate poisoning. *Human and Experimental Toxicology* 22: 107-109.
- Fox, J. W. & P. J. Morin (2001) Effects of intra- and interspecific interactions on species responses to environmental change. *Journal of Animal Ecology* 70: 80-90.
- Fuentes-Contreras, E. & H. M. Niemeyer (1998) DIMBOA glucoside, a wheat chemical defense, affects host acceptance and suitability of *Sitobion avenae* to the cereal aphid parasitoid *Aphidius rhopalosiphi*. *Journal of Chemical Ecology* 24: 371-381.
- Fuentes-Contreras, E. & H. M. Niemeyer (2002) Direct and indirect effects of wheat cultivars with different levels of resistance on parasitoids and entomopathogenic fungi of cereal aphids. *Ecoscience* 9: 37-43.
- Fujiwara, C.; J. Takabayashi & S. Yano (2000) Oviposition experience on a host-infested plant affects flight and antennal searching behavior of *Cotesia kariyai* toward the host-plant complex. *Entomologia Experimentalis Et Applicata* 97: 251-256.
- Fukushima, J.; Y. Kainoh; H. Honda & J. Takabayashi (2001) Learning of host-infested plant volatiles in the larval parasitoid *Cotesia kariyai*. *Entomologia Experimentalis Et Applicata* 99: 341-346.
- Fukushima, J.; Y. Kainoh; H. Honda & J. Takabayashi (2002) Learning of herbivore-induced and nonspecific plant volatiles by a parasitoid, *Cotesia kariyai*. *Journal of Chemical Ecology* 28: 579-586.
- Furlong, M. J. & D. J. Wright (1993) Effect of the acylurea insect growth-regulator Teflubenzuron on the endo-larval stages of the hymenopteran parasitoids *Cotesia plutellae* and *Diadegma semiclausum* in a susceptible and an Acylurea-resistant strain of *Plutella xylostella*. *Pesticide Science* 39: 305-312.
- Gama-Flores, J. L.; S. S. S. Sarma & S. Nandini (2004) Acute and chronic toxicity of the pesticide methyl parathion to the rotifer *Brachionus angularis* (Rotifera) at different algal (*Chlorella vulgaris*) food densities. *Aquatic Ecology* 38: 27-36.

- Gandolfi, M.; L. Mattiacci & S. Dorn (2003) Mechanisms of behavioral alterations of parasitoids reared in artificial systems. *Journal of Chemical Ecology* 29: 1871-1887.
- Gange, A. C. & V. K. Brown (ed.) (1997). *Multitrophic interactions in terrestrial systems*. Blackwell Scientific, 448 pp.
- Garcia, P. V.; E. Wajnberg; M. L. M. Oliveira & J. Tavares (2001) Is the parasitization capacity of *Trichogramma cordubensis* influenced by the age of the females? *Entomologia Experimentalis Et Applicata* 98: 219-224.
- Garcia, E. S.; E. M. M. Machado & P. Azambuja (2004) Effects of eicosanoid biosynthesis inhibitors on the prophenoloxidase-activating system and microaggregation reactions in the hemolymph of *Rhodnius prolixus* infected with *Trypanosoma rangeli*. *Journal of Insect Physiology* 50: 157-165.
- Geervliet, J. B. F.; L. E. M. Vet & M. Dicke (1996) Innate responses of the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae) to volatiles from different plant-herbivore complexes. *Journal of Insect Behavior* 9: 525-538.
- Geervliet, J. B. F.; M. A. Posthumus; L. E. M. Vet & M. Dicke (1997) Comparative analysis of headspace volatiles from different caterpillar-infested or uninfested food plants of *Pieris species*. *Journal of Chemical Ecology* 23: 2935-2954.
- Geervliet, J. B. F.; A. I. Vreugdenhil; M. Dicke & L. E. M. Vet (1998) Learning to discriminate between infochemicals from different plant-host complexes by the parasitoids *Cotesia glomerata* and *C. rubecula*. *Entomologia Experimentalis Et Applicata* 86: 241-252.
- Gentry, G. (2003) Multiple parasitoid visitors to the extrafloral nectaries of *Solanum adherens*: is *S. adherens* an insectary plant? *Basic and Applied Ecology* 4: 405-411.
- Getz, W. M. & N. J. Mills (1996) Host-parasitoid coexistence and egg-limited encounter rates. *American Naturalist* 148: 333-347.
- Giamoustaris, A. & R. Mithen (1995) The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus* ssp. *oleifera*) on its interaction with specialist and generalist pests. *Annals of Applied Biology* 126: 347-363.
- Giles, K. L.; R. C. Berberet; A. A. Zarrabi & J. W. Dillwith (2002) Influence of alfalfa cultivar on suitability of *Acyrtosiphon kondoi* (Homoptera : Aphididae) for survival and development of *Hippodamia convergens* and *Coccinella septempunctata* (Coleoptera : Coccinellidae). *Journal of Economic Entomology* 95: 552-557.
- Gillespie, J. P.; M. R. Kanost & T. Trenczek (1997) Biological mediators of insect immunity. *Annual Review of Entomology* 42: 611-643.
- Gillespie, J. P.; A. M. Bailey; B. Cobb & A. Vilcinskas (2000) Fungi as elicitors of insect immune responses. *Archives of Insect Biochemistry and Physiology* 44: 49-68.
- Gillman, M. & R. Hails (1997). *An introduction to ecological modelling: putting*

practice into theory. Blackwell Science, Oxford, 202 pp.

Gingras, D. & G. Boivin (2002) Effect of plant structure, host density and foraging duration on host finding by *Trichogramma evanescens* (Hymenoptera : Trichogrammatidae). *Environmental Entomology* 31: 1153-1157.

Ginzburg, L. R. & D. E. Taneyhill (1994) Population-cycles of forest lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* 63: 79-92.

Glinski, Z. & J. Jarosz (1996) Polydnviruses of hymenopteran endoparasitoids knock out the host insect immune response. *Folia Biologica-Krakow* 44: 87-94.

Godfray, H. C. J. (1994). *Parasitoids: behavioural and evolutionary ecology*. Princeton University Press, Princeton, 473 pp.

Gonzalez-Cabrera, J.; S. Herrero & J. Ferre (2001) High genetic variability for resistance to *Bacillus thuringiensis* toxins in a single population of diamondback moth. *Applied and Environmental Microbiology* 67: 5043-5048.

Gonzalez-Rodriguez, A. L. & R. Macchiavelli (2003) Dynamics of diamondback moth, *Plutella xylostella* (Lepidoptera : Plutellidae), in cabbage under intercropping, biological control and *Bt*-based sprays. *Journal of Agriculture of the University of Puerto Rico* 87: 31-49.

Goodwin, S. (1979) Changes in the numbers in the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera) in Victoria. *Australian Journal of Zoology* 27: 981-989.

Gotz, P. & H. G. Boman (1985) Insect immunity. In: G. A. Kerkut & L. I. Gilbert (ed.), *Comprehensive insect physiology, biochemistry and pharmacology* Vol. 3, pp. 453-485, Pergamon Press, Oxford.

Gouinguene, S.; T. Degen & T. C. J. Turlings (2001) Variability in herbivore-induced odour emissions among maize cultivars and their wild ancestors (teosinte). *Chemoecology* 11: 9-16.

Gouinguene, S.; H. Alborn & T. C. J. Turlings (2003) Induction of volatile emissions in maize by different larval instars of *Spodoptera littoralis*. *Journal of Chemical Ecology* 29: 145-162.

Gratton, C. & R. F. Denno (2003) Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* 134: 487-495.

Griesch, J.; M. Wedde & A. Vilcinskas (2000) Recognition and regulation of metalloproteinase activity in the haemolymph of *Galleria mellonella*: a new pathway mediating induction of humoral immune responses. *Insect Biochemistry and Molecular Biology* 30: 461-472.

Groot, A. T. & M. Dicke (2002) Insect-resistant transgenic plants in a multi-trophic context. *Plant Journal* 31: 387-406.

- Guerrieri, E. (1997) Flight behaviour of *Encarsia formosa* in response to plant and host stimuli. *Entomologia Experimentalis Et Applicata* 82: 129-133.
- Guerrieri, E.; F. Pennacchio & E. Tremblay (1997) Effect of adult experience on in-flight orientation to plant and plant-host complex volatiles in *Aphidius ervi* Haliday (Hymenoptera, Braconidae). *Biological Control* 10: 159-165.
- Guilloux, T.; R. Monnerat; M. Castelo-Branco; A. Kirk & D. Bordat (2003) Population dynamics of *Plutella xylostella* (Lep., Yponomeutidae) and its parasitoids in the region of Brasilia. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie* 127: 288-292.
- Gupta, P. D. & A. J. Thornsteinson (1960) Food plant relationship of the diamondback moth (*Plutella maculipennis* (Curt.)). II. Sensory relationship of oviposition of the adult female. *Entomologia Experimentalis Et Applicata* 3: 305-314.
- Gupta, S. K. & P. N. Saxena (2003) Carbaryl-induced behavioural and reproductive abnormalities in the earthworm *Metaphire posthuma*: a sensitive model. *Atla-Alternatives to Laboratory Animals* 31: 587-593.
- Gwaltney, C. R.; M. P. Styczynski & M. A. Stadtherr (2004) Reliable computation of equilibrium states and bifurcations in food chain models. *Computers and Chemical Engineering* 28: 1981-1996.
- Haggstrom, H. & S. Larsson (1995) Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. *Oecologia* 104: 308-315.
- Halkier, B. A. & L. C. Du (1997) The biosynthesis of glucosinolates. *Trends in Plant Science* 2: 425-431.
- Hallman, A. & J. Lowenberg-DeBoer (1999) Cost, average returns, and risk of switching to narrow row corn. *Journal of Production Agriculture* 12: 685-691.
- Han, B. Y. & Z. M. Chen (2002) Behavioral and electrophysiological responses of natural enemies to synomones from tea shoots and kairomones from tea aphids, *Toxoptera aurantii*. *Journal of Chemical Ecology* 28: 2203-2219.
- Hao, Z. G.; I. Kasumba & S. Aksoy (2003) Proventriculus (cardia) plays a crucial role in immunity in tsetse fly (Diptera : Glossinidae). *Insect Biochemistry and Molecular Biology* 33: 1155-1164.
- Hardin, M. R.; B. Benrey; M. Coll; W. O. Lamp; G. K. Roderick & P. Barbosa (1995) Arthropod pest resurgence: an overview of potential mechanisms. *Crop Protection* 14: 3-18.
- Hare, J. D. & R. F. Luck (1991) Indirect effects of citrus cultivars on life-history parameters of a parasitic wasp. *Ecology* 72: 1576-1585.
- Harrison, S. & N. Cappuccino (1995) Using density-manipulation experiments to study

- population regulation. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 131-147, Academic Press, San Diego.
- Hartvigsen, G.; D. A. Wait & J. S. Coleman (1995) Tri-trophic interactions influenced by resource availability: predator effects on plant performance depend on plant resources. *Oikos* 77: 463-468.
- Harvey, J. A.; N. M. van Dam & R. Gols (2003) Interactions over four trophic levels: foodplant quality affects development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid. *Journal of Animal Ecology* 72: 520-531.
- Haseeb, M.; Y. Kabori; H. Amano & H. Nemoto (2001) Population density of *Plutella xylostella* (Lepidoptera : Plutellidae) and its parasitoid *Cotesia plutellae* (Hymenoptera : Braconidae) on two varieties of cabbage in an urban environment. *Applied Entomology and Zoology* 36: 353-360.
- Haseeb, M.; T. X. Liu & W. A. Jones (2004) Effects of selected insecticides on *Cotesia plutellae*, endoparasitoid of *Plutella xylostella*. *Biocontrol* 49: 33-46.
- Hassell, M. P. (1978). *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, 237 pp.
- Hassell, M. P.; M. J. Crawley; H. C. J. Godfray & J. H. Lawton (1998) Top-down versus bottom-up and the Ruritanian bean bug. *Proceedings of the National Academy of Sciences of the United States of America* 95: 10661-10664.
- Hassell, M. P. (2000). *The spatial and temporal dynamics of host-parasitoid interactions*. Oxford University Press, Oxford, 200 pp.
- Hastings, A. & T. Powell (1991) Chaos in a 3-species food-chain. *Ecology* 72: 896-903.
- Heikinheimo, O. (2001) Effect of predation on the low-density dynamics of vendace: significance of the functional response. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1909-1923.
- Heimpel, G. E. & J. A. Rosenheim (1998) Egg limitation in parasitoids: a review of the evidence and a case study. *Biological Control* 11: 160-168.
- Heinz, K. M. & F. G. Zalom (1996) Performance of the predator *Delphastus pusillus* on *Bemisia* resistant and susceptible tomato lines. *Entomologia Experimentalis Et Applicata* 81: 345-352.
- Helms, S. E.; S. J. Connelly & M. D. Hunter (2004) Effects of variation among plant species on the interaction between a herbivore and its parasitoid. *Ecological Entomology* 29: 44-51.
- Herendeen, R. A. (2004) Bottom-up and top-down effects in food chains depend on functional dependence: an explicit framework. *Ecological Modelling* 171: 21-33.
- Hilker, M. & T. Meiners (2002) Induction of plant responses to oviposition and feeding

- by herbivorous arthropods: a comparison. *Entomologia Experimentalis Et Applicata* 104: 181-192.
- Hoballah, M. E. F.; C. Tamo & T. C. J. Turlings (2002) Differential attractiveness of induced odors emitted by eight maize varieties for the parasitoid *Cotesia marginiventris*: Is quality or quantity important? *Journal of Chemical Ecology* 28: 951-968.
- Hoffmeister, T. S. & P. Gienapp (1999) Exploitation of the host's chemical communication in a parasitoid searching for concealed host larvae. *Ethology* 105: 223-232.
- Holling, C. S. (1959) Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385-398.
- Holmes, R. W. & V. De Vlaming (2003) Monitoring of diazinon concentrations and loadings, and identification of geographic origins consequent to stormwater runoff from orchards in the Sacramento river watershed, USA. *Environmental Monitoring and Assessment* 87: 57-79.
- Holt, R. D. & G. A. Polis (1997) A theoretical framework for intraguild predation. *American Naturalist* 149: 745-764.
- Holt, R. D. (2002) Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research* 17: 261-273.
- Hoover, K.; J. L. Yee; C. M. Schultz; D. M. Rocke; B. D. Hammock & S. S. Duffey (1998) Effects of plant identity and chemical constituents on the efficacy of a baculovirus against *Heliothis virescens*. *Journal of Chemical Ecology* 24: 221-252.
- Hopkins, R. J.; B. Ekbom & L. Henkow (1998) Glucosinolate content and susceptibility for insect attack of three populations of *Sinapis alba*. *Journal of Chemical Ecology* 24: 1203-1216.
- Howard, L. O. & W. F. Fiske (1911) The importation into the United States of the parasites of the gipsy moth and the brown-tail moth. *Bull. USDA Bur. Entomol.* 91:
- Hu, G. Y. & E. R. Mitchell (2001) Responses of *Diadegma insulare* (Hymenoptera : Ichneumonidae) to caterpillar feeding in a flight tunnel. *Journal of Entomological Science* 36: 297-304.
- Hua, D. D.; L. Cairo; M. R. Feix; K. S. Govinder & P. G. L. Leach (1996) Connection between the existence of first integrals and the Painleve property in two-dimensional Lotka-Volterra and quadratic systems. *Proceedings of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences* 452: 859-880.
- Huffaker, C. B.; A. Berryman & P. Turchin (1999) Dynamics and regulation of insect populations. In: C. B. Huffaker & A. P. Gutierrez (ed.), *Ecological Entomology*, pp. 269-312, Wiley,

Hunter, M. D. & P. W. Price (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.

Hunter, M. D.; G. C. Varley & G. R. Gradwell (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences of the United States of America* 94: 9176-9181.

Hunter, M. D. (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic and Applied Ecology* 2: 295-309.

Iga, M. (1997) Effect of release of introduced ichneumonid parasitoid, *Diadegma semiclausum* (Hellen) on Diamondback Moth, *Plutella xylostella* (L) in experimental cabbage field. *Japanese Journal of Applied Entomology and Zoology* 41: 195-199.

Iqbal, M.; R. H. J. Verkerk; M. J. Furlong; P. C. Ong; S. A. Rahman & D. J. Wright (1996) Evidence for resistance to *Bacillus thuringiensis* (Bt) subsp *kurstaki* HD-1, Bt subsp *aizawai* and abamectin in field populations of *Plutella xylostella* from Malaysia. *Pesticide Science* 48: 89-97.

Iqbal, M. & D. J. Wright (1997) Evaluation of resistance, cross-resistance and synergism of abamectin and teflubenzuron in a multi-resistant field population of *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research* 87: 481-486.

Ives, A. R. & V. A. A. Jansen (1998) Complex dynamics in stochastic tritrophic models. *Ecology* 79: 1039-1052.

Ivey, P. W. & S. J. Johnson (1998) Integrating control tactics for managing cabbage looper (Lepidoptera : Noctuidae) and diamondback moth (Lepidoptera : Yponomeutidae) on cabbage. *Tropical Agriculture* 75: 369-374.

Jeschke, J. M.; M. Kopp & R. Tollrian (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews* 79: 337-349.

Jiang, H. B.; Y. Wang; X. Q. Yu; Y. F. Zhu & M. Kanost (2003) Prophenoloxidase-activating proteinase-3 (PAP-3) from *Manduca sexta* hemolymph: a clip-domain serine proteinase regulated by serpin-1J and serine proteinase homologs. *Insect Biochemistry and Molecular Biology* 33: 1049-1060.

Jiang, H. B.; C. C. Ma; Z. Q. Lu & M. R. Kanost (2004) B-1,3-Glucan recognition protein-2 (beta GRP-2) from *Manduca sexta*: an acute-phase protein that binds beta-1,3-glucan and lipoteichoic acid to aggregate fungi and bacteria and stimulate prophenoloxidase activation. *Insect Biochemistry and Molecular Biology* 34: 89-100.

Kaiser, L.; R. Perez-Maluf; J. C. Sandoz & M. H. Pham-Delegue (2003) Dynamics of odour learning in *Leptopilina boulardi*, a hymenopterous parasitoid. *Animal Behaviour* 66: 1077-1084.

- Kamel, F. & J. A. Hoppin (2004) Association of pesticide exposure with neurologic dysfunction and disease. *Environmental Health Perspectives* 112: 950-958.
- Kanost, M. R.; H. B. Jiang & X. Q. Yu (2004) Innate immune responses of a lepidopteran insect, *Manduca sexta*. *Immunological Reviews* 198: 97-105.
- Kareiva, P. & R. Sahakian (1990) Tritrophic effects of a simple architectural mutation in pea-plants. *Nature* 345: 433-434.
- Karimzadeh, J.; M. B. Bonsall & D. J. Wright (2004) Bottom-up and top-down effects in a tritrophic system: the population dynamics of *Plutella xylostella* (L.)-*Cotesia plutellae* (Kurdjumov) on different host plants. *Ecological Entomology* 29: 285-293.
- Karowe, D. N.; D. H. Seimens & T. MitchellOlds (1997) Species-specific response of glucosinolate content to elevated atmospheric CO₂. *Journal of Chemical Ecology* 23: 2569-2582.
- Kavanagh, K. & E. P. Reeves (2004) Exploiting the potential of insects for in vivo pathogenicity testing of microbial pathogens. *Fems Microbiology Reviews* 28: 101-112.
- Kawaguchi, M. & T. Tanaka (1999) Biological characteristics of a larval endoparasitoid, *Cotesia plutellae* (Hymenoptera : Braconidae): host stage preference, subsequent sex ratio of progeny and mate location of males. *Applied Entomology and Zoology* 34: 213-221.
- Keasar, T.; M. Ney-Nifle; M. Mangel & S. Swezey (2001) Early oviposition experience affects patch residence time in a foraging parasitoid. *Entomologia Experimentalis Et Applicata* 98: 123-132.
- Keeley, E. R. (2001) Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* 82: 1247-1259.
- Kennedy, G. G. (2003) Tomato, pests, parasitoids, and predators: tritrophic interactions involving the genus *Lycopersicon*. *Annual Review of Entomology* 48: 51-72.
- Kerfoot, W. C.; R. M. Newman & Z. Hanscom (1998) Snail reaction to watercress leaf tissues: reinterpretation of a mutualistic 'alarm' hypothesis. *Freshwater Biology* 40: 201-213.
- Kerns, D. L. & S. D. Stewart (2000) Sublethal effects of insecticides on the intrinsic rate of increase of cotton aphid. *Entomologia Experimentalis Et Applicata* 94: 41-49.
- Kfir, R. (1997) Parasitoids of *Plutella xylostella* (Lep.: Plutellidae) in South Africa: an annotated list. *Entomophaga* 42: 517-523.
- Kiddle, G. A.; K. J. Doughty & R. M. Wallsgrove (1994) Salicylic acid-induced accumulation of glucosinolates in oilseed rape (*Brassica napus* L) Leaves. *Journal of Experimental Botany* 45: 1343-1346.
- Kimber, D. & D. I. McGregor (ed.) (1995a). *Brassica oilseeds: production and*

utilization. CAB International, Wallingford, 394 pp.

Kimber, D. & D. I. McGregor (1995b) The species and their origin, cultivation and world production. In: D. Kimber & D. I. McGregor (ed.), *Brassica oilseeds: production and utilization*, pp. 1-7, CAB International, Wallingford.

King, G. J. (ed.) (2000). *Proceedings of the third international symposium on Brassicas and twelfth crucifer genetics workshop*. ISHS, Leiden, 144 pp.

Kliebenstein, D.; D. Pedersen; B. Barker & T. Mitchell-Olds (2002) Comparative analysis of quantitative trait loci controlling glucosinolates, myrosinase and insect resistance in *Arabidopsis thaliana*. *Genetics* 161: 325-332.

Kneitel, J. M. & T. E. Miller (2002) Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* 83: 680-688.

Kooi, B. W.; L. D. J. Kuijper & S. A. L. M. Kooijman (2004) Consequences of symbiosis for food web dynamics. *Journal of Mathematical Biology* 49: 227-271.

Kopelke, J. P. (2003) Natural enemies of gall-forming sawflies on willows (*Salix spp*) (Hymenoptera : Tenthredinidae : *Euura*, *Phyllocolpa*, *Pontania*). *Entomologia Generalis* 26: 277-312.

Kot, M. (2001). *Elements of mathematical ecology*. Cambridge University Press, Cambridge, 453 pp.

Krips, O. E.; P. E. L. Willems & M. Dicke (1999) Compatibility of host plant resistance and biological control of the two-spotted spider mite *Tetranychus urticae* in the ornamental crop gerbera. *Biological Control* 16: 155-163.

Krivtsov, V.; C. Goldspink; D. C. Sigee & E. G. Bellinger (2001) Expansion of the model 'Rostherne' for fish and zooplankton: role of top-down effects in modifying the prevailing pattern of ecosystem functioning. *Ecological Modelling* 138: 153-171.

Kuijper, L. D. J.; B. W. Kooi; C. Zonneveld & S. A. L. M. Kooijman (2003) Omnivory and food web dynamics. *Ecological Modelling* 163: 19-32.

Kuwahara, M.; P. Keinmeesuke & N. Sinchaisri (1995) Present status of resistance of the diamondback moth, *Plutella xylostella* L, to insecticides in Thailand. *Applied Entomology and Zoology* 30: 557-566.

Lackie, A. M. (1988) Immune mechanisms in insects. *Parasitology Today* 4: 98-105.

Laing, J. E. & D. B. Levin (1982) A review of the biology and a bibliography of *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae). *Biocontrol News and Information* 3: 7-23.

Lambdon, P. W.; M. Hassall; R. R. Boar & R. Mithen (2003) Asynchrony in the nitrogen and glucosinolate leaf-age profiles of Brassica: is this a defensive strategy against generalist herbivores? *Agriculture Ecosystems and Environment* 97: 205-214.

- Lambrix, V.; M. Reichelt; T. Mitchell-Olds; D. J. Kliebenstein & J. Gershenzon (2001) The *Arabidopsis epithiospecifier* protein promotes the hydrolysis of glucosinolates to nitriles and influences *Trichoplusia ni* herbivory. *Plant Cell* 13: 2793-2807.
- Lauziere, I.; G. Perez-Lachaud & J. Brodeur (2000) Behavior and activity pattern of *Cephalonomia stephanoderis* (Hymenoptera : Bethyridae) attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera : Scolytidae). *Journal of Insect Behavior* 13: 375-395.
- Lavine, M. D. & M. R. Strand (2002) Insect hemocytes and their role in immunity. *Insect Biochemistry and Molecular Biology* 32: 1295-1309.
- Law, J. H. & F. E. Regnier (1971) Pheromones. *Annual Review of Biochemistry* 40: 533-548.
- Lee, M. H.; T. Osaki; J. Y. Lee; M. J. Baek; R. Zhang; J. W. Park; S. Kawabata; K. Soderhall & B. L. Lee (2004) Peptidoglycan recognition proteins involved in 1,3-beta-D-glucan-dependent prophenoloxidase activation system of insect. *Journal of Biological Chemistry* 279: 3218-3227.
- Leibee, G. L. & K. E. Savage (1992) Evaluation of selected insecticides for control of diamondback moth and cabbage looper in cabbage in central Florida with observations on insecticide resistance in the diamondback moth. *Florida Entomologist* 75: 585-591.
- Leibee, G. L. & J. L. Capinera (1995) Pesticide resistance in Florida insects limits management options. *Florida Entomologist* 78: 386-399.
- van Lenteren, J. C. (1999) Fundamental knowledge about insect reproduction: essential to develop sustainable pest management. *Invertebrate Reproduction and Development* 36: 1-15.
- Letellier, C.; L. A. Aguirre; J. Maquet & M. A. Aziz-Alaoui (2002) Should all the species of a food chain be counted to investigate the global dynamics? *Chaos Solitons and Fractals* 13: 1099-1113.
- Letellier, C. & M. A. Aziz-Alaoui (2002) Analysis of the dynamics of a realistic ecological model. *Chaos Solitons and Fractals* 13: 95-107.
- Lewis, W. J. & W. R. J. Martin (1990) Semiochemical for use with parasitoids: status and future. *Journal of Chemical Ecology* 16: 3067-3089.
- Lewis, W. J.; J. H. Tumlinson & S. Krasnoff (1991) Chemically mediated associative learning: an important function in the foraging behaviour of *Microplitis croceipes* (Cresson). *Journal of Chemical Ecology* 17: 1309-1325.
- Lewis, W. J.; J. C. vanLenteren; S. C. Phatak & J. H. Tumlinson (1997) A total system approach to sustainable pest management. *Proceedings of the National Academy of Sciences of the United States of America* 94: 12243-12248.
- Li, Q.; S. D. Eigenbrode; G. R. Stringham & M. R. Thiagarajah (2000) Feeding and

growth of *Plutella xylostella* and *Spodoptera eridania* on *Brassica juncea* with varying glucosinolate concentrations and myrosinase activities. *Journal of Chemical Ecology* 26: 2401-2419.

Lim, G. S. (1982) *The biology and effects of parasites on the diamondback moth, Plutella xylostella* (L.). PhD thesis. The University of London, London, 244 pp.

Lim, G. S. (1986) Biological control of diamondback moth. In: N. S. Talekar & T. D. Griggs (ed.), *Diamondback moth management. Proc. 1st. Internat. Workshop*, pp. 159-171, AVRDC, Shanhua.

Lindeman, R. L. (1942) The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.

Liu, S. S.; X. G. Wang; S. J. Guo; J. H. He & Z. H. Shi (2000) Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera : Plutellidae) in Hangzhou, China. *Bulletin of Entomological Research* 90: 221-231.

Liu, S. S. & L. H. Jiang (2003) Differential parasitism of *Plutella xylostella* (Lepidoptera : Plutellidae) larvae by the parasitoid *Cotesia plutellae* (Hymenoptera : Braconidae) on two host plant species. *Bulletin of Entomological Research* 93: 65-72.

van Loon, J. J. A.; A. Blaakmeer; F. C. Griepink; T. A. van Beek; L. M. Schoonhoven & A. de Groot (1992) Leaf surface compound from *Brassica oleracea* (Cruciferae) induces oviposition by *Pieris brassicae* (Lepidoptera: Pieridae). *Chemoecology* 3: 39-44.

Lotka, A. J. (1925). *Elements of physical biology*. Williams & Wilkins, Baltimore. Reprinted in 1956 as A. J. Lotka. *Elements of mathematical biology*. Dover, New York, 465 pp.

Lou, Y. G. & J. A. Cheng (2001) Host-recognition kairomone from *Sogatella furcifera* for the parasitoid *Anagrus nilaparvatae*. *Entomologia Experimentalis Et Applicata* 101: 59-67.

Lou, Y. G. & J. A. Cheng (2003) Role of rice volatiles in the foraging behaviour of the predator *Cyrtorhinus lividipennis* for the rice brown planthopper *Nilaparvata lugens*. *Biocontrol* 48: 73-86.

Lovallo, N. & D. L. Cox-Foster (1999) Alteration in FAD-glucose dehydrogenase activity and haemocyte behaviour contribute to initial disruption of *Manduca sexta* immune response to *Cotesia congregata* parasitoid. *Journal of Insect Physiology* 45: 1037-1048.

Lovallo, N.; B. A. McPherson & D. L. Cox-Foster (2002) Effects of the polydnavirus of *Cotesia congregata* on the immune system and development of non-habitual hosts of the parasitoid. *Journal of Insect Physiology* 48: 517-526.

Lowenberger, C. (2001) Innate immune response of *Aedes aegypti*. *Insect Biochemistry and Molecular Biology* 31: 219-229.

- Lu, Z. Y. & Y. Luo (2003) Three limit cycles for a three-dimensional Lotka-Volterra competitive system with a heteroclinic cycle. *Computers and Mathematics with Applications* 46: 231-238.
- Malgras, J. & D. Debouzie (1997) Can ARMA models be used reliably in ecology? *Acta Oecologica-International Journal of Ecology* 18: 427-447.
- Mannion, C. M.; J. E. Carpenter; B. R. Wiseman & H. R. Gross (1994) Host corn earworm (Lepidoptera, Noctuidae) reared on meridic diet containing silks from a resistant corn genotype on *Archytas marmoratus* (Diptera, Tachinidae) and *Ichneumon promissorius* (Hymenoptera, Ichneumonidae). *Environmental Entomology* 23: 837-845.
- Marazzi, C. & E. Stadler (2004) Arabidopsis thaliana leaf-surface extracts are detected by the cabbage root fly (*Delia radicum*) and stimulate oviposition. *Physiological Entomology* 29: 192-198.
- Marazzi, C.; B. Patrian & E. Stadler (2004) Secondary metabolites of the leaf surface affected by sulphur fertilisation and perceived by the cabbage root fly. *Chemoecology* 14: 87-94.
- Marley, P. S.; D. A. Aba; J. A. Y. Shebayan; R. Musa & A. Sanni (2004) Integrated management of *Striga hermonthica* in sorghum using a mycoherbicide and host plant resistance in the Nigerian sudano-Sahelian savanna. *Weed Research* 44: 157-162.
- Martinez-Castillo, M.; J. L. Leyva; J. Cibrian-Tovar & R. Bujanos-Muniz (2002) Parasitoid diversity and impact on populations of the diamondback moth *Plutella xylostella* (L.) on Brassica crops in central Mexico. *Biocontrol* 47: 23-31.
- Matsumoto, T.; T. Itioka & T. Nishida (2003) Cascading effects of a specialist parasitoid on plant biomass in a citrus agroecosystem. *Ecological Research* 18: 651-659.
- Matteson, P. C. (2000) Insect pest management in tropical Asian irrigated rice. *Annual Review of Entomology* 45: 549-574.
- Mattiacci, L.; M. Dicke & M. A. Posthumus (1994) Induction of parasitoid attracting synomone in brussels sprouts plants by feeding of *Pieris brassicae* larvae: role of mechanical damage and herbivore elicitor. *Journal of Chemical Ecology* 20: 2229-2247.
- Mattiacci, L. & M. Dicke (1995a) Host-age discrimination during host location by *Cotesia glomerata*, a larval parasitoid of *Pieris brassicae*. *Entomologia Experimentalis Et Applicata* 76: 37-48.
- Mattiacci, L. & M. Dicke (1995b) The parasitoid *Cotesia glomerata* (Hymenoptera, Braconidae) discriminates between first and fifth larval instars of its host *Pieris brassicae*, on the basis of contact cues from frass, silk, and herbivore-damaged leaf tissue. *Journal of Insect Behavior* 8: 485-498.
- Mattiacci, L.; E. Hutter; D. Schoch; N. Scascighini & S. Dorn (2000) Plant-odour mediates parasitoid host handling and oviposition in an endophytic tritrophic system.

Chemoecology 10: 185-192.

Mattiacci, L.; S. Rudelli; B. A. Rocca; S. Genini & S. Dorn (2001) Systemically-induced response of cabbage plants against a specialist herbivore, *Pieris brassicae*. *Chemoecology* 11: 167-173.

May, R. M. & M. P. Hassell (1988) Population dynamics and biological control. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 318: 129-169.

Mbata, G. N.; S. Shu; T. W. Phillips & S. B. Ramaswamy (2004) Semiochemical cues used by *Pteromalus cerealellae* (Hymenoptera : Pteromalidae) to locate its host, *Callosobruchus maculatus* (Coleoptera : Bruchidae). *Annals of the Entomological Society of America* 97: 353-360.

McAuslane, H. J.; A. M. Simmons & D. M. Jackson (2000) Parasitism of *Bemisia argentifolii* on collard with reduced or normal leaf wax. *Florida Entomologist* 83: 428-437.

van der Meijden, E. & P. G. L. Klinkhamer (2000) Conflicting interests of plants and the natural enemies of herbivores. *Oikos* 89: 202-208.

Meiners, T.; F. Wackers & W. J. Lewis (2002) The effect of molecular structure on olfactory discrimination by the parasitoid *Microplitis croceipes*. *Chemical Senses* 27: 811-816.

Meiners, T.; F. Wackers & W. J. Lewis (2003) Associative learning of complex odours in parasitoid host location. *Chemical Senses* 28: 231-236.

Meister, M.; C. Hetru & J. A. Hoffmann (2000) The antimicrobial host defense of *Drosophila*. *Origin and Evolution of the Vertebrate Immune System* 248: 17-36.

Menge, B. A. (1976) Organization of the New England rocky intertidal community: the role of predation, competition, and environmental heterogeneity. *Ecological monographs* 46: 355-393.

Mevy, J. P.; J. Rabier; A. Quinsac; M. Krouti & D. Ribailier (1997) Glucosinolate contents of regenerated plantlets from embryoids of horseradish. *Phytochemistry* 44: 1469-1471.

Mewis, I. Z.; C. Ulrich & W. H. Schnitzler (2002) The role of glucosinolates and their hydrolysis products in oviposition and host-plant finding by cabbage webworm, *Hellula undalis*. *Entomologia Experimentalis Et Applicata* 105: 129-139.

Micha, S. G.; S. Kistenmacher; G. Molck & U. Wyss (2000) Tritrophic interactions between cereals, aphids and parasitoids: discrimination of different plant-host complexes by *Aphidius rhopalosiphi* (Hymenoptera : Aphidiidae). *European Journal of Entomology* 97: 539-543.

Mills, N. J. & W. M. Getz (1996) Modelling the biological control of insect pests: a

review of host-parasitoid models. *Ecological Modelling* 92: 121-143.

Milne, A. (1958) Theories of natural control of insect populations. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 253-271.

Mitchell, E. R.; G. Y. Hu; J. S. Okine & J. E. Carpenter (1999) Parasitism of diamondback moth (Lepidoptera : Plutellidae) larvae by *Cotesia plutellae* (Hymenoptera : Braconidae) and *Diadegma insulare* (Hymenoptera : Ichneumonidae) in cabbage fields after inundative releases of *C. plutellae*. *Journal of Entomological Science* 34: 101-112.

Miura, K. (2003) Suppressive effect of the egg parasitoid *Trichogramma chilonis* Ishii (Hymenoptera : Trichogrammatidae) on the population density of the diamondback moth. *Applied Entomology and Zoology* 38: 79-85.

Mohan, M. & G. T. Gujar (2003) Local variation in susceptibility of the diamondback moth, *Plutella xylostella* (Linnaeus) to insecticides and role of detoxification enzymes. *Crop Protection* 22: 495-504.

Molck, G.; H. Pinn & U. Wyss (2000) Manipulation of plant odour preference by learning in the aphid parasitoid *Aphelinus abdominalis* (Hymenoptera : Aphelinidae). *European Journal of Entomology* 97: 533-538.

Møller, J. (1988) Investigation on a laboratory culture of the diamondback moth, *Plutella maculipennis* (Curt.) (Lep., Tineidae). *Journal of Applied Entomology* 105: 360-373.

Montoya, J. M.; M. A. Rodriguez & B. A. Hawkins (2003) Food web complexity and higher-level ecosystem services. *Ecology Letters* 6: 587-593.

Moon, D. C.; A. M. Rossi & P. Stiling (2000) The effects of abiotically induced changes in host plant quality (and morphology) on a salt marsh planthopper and its parasitoid. *Ecological Entomology* 25:

Moreau, S. J. M.; G. Doury & P. Giordanengo (2000) Intraspecific variation in the effects of parasitism by *Asobara tabida* on phenoloxidase activity of *Drosophila melanogaster* larvae. *Journal of Invertebrate Pathology* 76: 151-153.

Moreau, S. J. M. (2003) Relationships between parasitoid Hymenoptera and the immune system of their hosts: the "active" and "passive" mechanisms redefined. *Annales De La Societe Entomologique De France* 39: 305-314.

Moreau, S. J. M.; P. Eslin; P. Giordanengo & G. Doury (2003) Comparative study of the strategies evolved by two parasitoids of the genus *Asobara* to avoid the immune response of the host, *Drosophila melanogaster*. *Developmental and Comparative Immunology* 27: 273-282.

Morehead, S. A. & D. H. Feener (2000) Visual and chemical cues used in host location and acceptance by a dipteran parasitoid. *Journal of Insect Behavior* 13: 613-625.

- Morrison, L. W. & J. R. King (2004) Host location behavior in a parasitoid of imported fire ants. *Journal of Insect Behavior* 17: 367-383.
- Mukherjee, D. & A. B. Roy (1998) On local(ly) ESS of a pair of prey-predator system with predatory switching. *Mathematical Biosciences* 151: 165-177.
- Muldrew, J. A. (1953) The natural immunity of the larch sawfly (*Pristiphora erichsonii*) to the introduced parasite *Mesoleius tenthredinis*, in Manitoba and Saskatchewan. *Canadian Journal of Zoology* 31: 313-332.
- Muller, C.; N. Agerbirk; C. E. Olsen; J. L. Boeve; U. Schaffner & P. M. Brakefield (2001) Sequestration of host plant glucosinolates in the defensive hemolymph of the sawfly *Athalia rosae*. *Journal of Chemical Ecology* 27: 2505-2516.
- Muller, C.; J. L. Boeve & P. Brakefield (2002) Host plant derived feeding deterrence towards ants in the turnip sawfly *Athalia rosae*. *Entomologia Experimentalis Et Applicata* 104: 153-157.
- Murdoch, W. W. & S. J. Walde (1989) Analysis of insect population dynamics. In: P. J. Grubb & J. B. Whittaker (ed.), *Towards a more exact ecology*, pp. 113-140, Blackwell Science, Oxford.
- Murdoch, W. W. (1994) Population regulation in theory and practice: the Robert H. Macarthur award lecture presented August 1991 in San-Antonio, Texas, USA. *Ecology* 75: 271-287.
- Mushtaque, M. & A. I. Mohyuddin (1987) *Apanteles plutellae* Kurdj. (Braconidae: Hymenoptera), an effective parasite of the diamondback moth, in Pakistan. *Pakistan J. Zool.* 19: 341-348.
- Muta, T. & S. Iwanaga (1996) The role of hemolymph coagulation in innate immunity. *Current Opinion in Immunology* 8: 41-47.
- Nappi, A. J. & E. Vass (1993) Melanogenesis and the generation of cytotoxic molecules during insect cellular immune reactions. *Pigment Cell Research* 6: 117-126.
- Nayfeh, A. H. & B. Balachandran (1995). *Applied nonlinear dynamics: analytical, computational and experimental methods*. Wiley, New York, pp.
- Neveu, N.; J. Grandgirard; J. P. Nenon & A. M. Cortesero (2002) Systemic release of herbivore-induced plant volatiles by turnips infested by concealed root-feeding larvae *Delia radicum* L. *Journal of Chemical Ecology* 28: 1717-1732.
- Newman, R. M.; Z. Hanscom & W. C. Kerfoot (1992) The watercress glucosinolate-myrosinase system: a feeding deterrent to caddisflies, snails and amphipods. *Oecologia* 92: 1-7.
- Nicholson, A. J. (1933) The balance of animal populations. *Journal of Animal Ecology* 2: 132-178.

- Nicholson, A. J. & V. A. Bailey (1935) The balance of animal populations. Part I. *Proceedings of Zoological Society of London* 3: 551-598.
- Nieuwhof, M. (1969). *Cole crops: botany, cultivation and utilization*. Leonard Hill, London, 353 pp.
- Ninsin, K. D.; J. C. Mo & T. Miyata (2000) Decreased susceptibilities of four field populations of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera : Yponomeutidae), to acetamiprid. *Applied Entomology and Zoology* 35: 591-595.
- Ninsin, K. D. & T. Miyata (2003) Monitoring acetamiprid resistance in the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera : Yponomeutidae). *Applied Entomology and Zoology* 38: 517-521.
- NNFCC (2004). The National Non-Food Crops Centre. <http://www.nnfcc.co.uk/>.
- Noda, T.; S. Miyai & S. Yamada (1996) Larval and pupal parasitoids of diamondback moth, *Plutella xylostella* (L) in cabbage fields in Morioka, Japan. *Japanese Journal of Applied Entomology and Zoology* 40: 164-167.
- Noldus, L. P. J. J. (1989) Semiochemicals, foraging behaviour and quality of entomophagous insects for biological control. *Journal of Applied Entomology* 108: 425-451.
- Nordlund, D. A. (1981) Semiochemicals: a review of the terminology. In: D. A. Nordlund; R. L. Jones & W. J. Lewis (ed.), *Semiochemicals: their role in pest control*, pp. 13-28, John Wiley & Sons, New York.
- Norris, R. F. & M. Kogan (2000) Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. *Weed Science* 48: 94-158.
- Nwanze, K. F.; Y. V. R. Reddy; F. E. Nwilene; K. G. Kausalya & D. D. R. Reddy (1998) Tritrophic interactions in sorghum, midge (*Stenodiplosis sorghicola*) and its parasitoid (*Aprostocetus* spp.). *Crop Protection* 17: 165-169.
- Ohgushi, T. (1995) Adaptive behavior produces stability in herbivorous lady beetle populations. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 303-319, Academic Press, San Diego.
- Olson, D. M.; T. A. Hodges & W. J. Lewis (2003a) Foraging efficacy of a larval parasitoid in a cotton patch: influence of chemical cues and learning. *Journal of Insect Behavior* 16: 613-624.
- Olson, D. M.; G. C. Rains; T. Meiners; K. Takasu; M. Tertuliano; J. H. Tumlinson; F. L. Wackers & W. J. Lewis (2003b) Parasitic wasps learn and report diverse chemicals with unique conditionable behaviors. *Chemical Senses* 28: 545-549.
- Olsson, K. & T. Jonasson (1994) Leaf feeding by caterpillars on white cabbage cultivars with different 2-propenyl glucosinolate (sinigrin) content. *Journal of Applied Entomology* 118: 197-202.

- Ooi, P. A. C. (1992) Role of parasitoids in managing diamondback moth in the Cameron Highlands, Malaysia. In: N. S. Talekar (ed.), *Management of diamondback moth and other crucifer pests. Proc. 2nd. Internat. Workshop*, pp. 255-262, AVRDC, Shanhua.
- Orr, D. B. & D. J. Boethel (1986) Influence of plant antibiosis through four trophic levels. *Oecologia* 70: 242-249.
- Ostfeld, R. S. & F. Keesing (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15: 232-237.
- Paine, R. T. (1966) Food web complexity and species diversity. *American Naturalist* 100: 65-75.
- Park, Y. & Y. Kim (2003) *Xenorhabdus nematophilus* inhibits p-bromophenacyl bromide (BPB)-sensitive PLA(2) of *Spodoptera exigua*. *Archives of Insect Biochemistry and Physiology* 54: 134-142.
- Pech, L. L. & M. R. Strand (1996) Granular cells are required for encapsulation of foreign targets by insect haemocytes. *Journal of Cell Science* 109: 2053-2060.
- Pereyra, P. C. & N. E. Sanchez (1998) Effects of different host-plant species on growth, development and feeding of the bud borer, *Epinotia aporema* (Lepidoptera : Tortricidae) in La Plata, Argentina. *Revista Chilena De Historia Natural* 71: 269-275.
- Perez, C. J. & A. M. Shelton (1997) Resistance of *Plutella xylostella* (Lepidoptera: Plutellidae) to *Bacillus thuringiensis* Berliner in central America. *Journal of Economic Entomology* 90: 87-93.
- Perez, C. J.; P. Alvarado; C. Narvaez; F. Miranda; L. Hernandez; H. Vanegas; A. Hruska & A. M. Shelton (2000) Assessment of insecticide resistance in five insect pests attacking field and vegetable crops in Nicaragua. *Journal of Economic Entomology* 93: 1779-1787.
- Perfecto, I. & L. E. M. Vet (2003) Effect of a nonhost plant on the location behavior of two parasitoids: the tritrophic system of *Cotesia* spp. (Hymenoptera : Braconidae), *Pieris rapae* (Lepidoptera : Pieridae), and *Brassica oleraceae*. *Environmental Entomology* 32: 163-174.
- Perko, L. (1991). *Differential equations and dynamical systems*. Springer-Verlag, New York, 396 pp.
- Persson, A.; L. A. Hansson; C. Bronmark; P. Lundberg; L. B. Pettersson; L. Greenberg; P. A. Nilsson; P. Nystrom; P. Romare & L. Tranvik (2001) Effects of enrichment on simple aquatic food webs. *American Naturalist* 157: 654-669.
- Pettersson, E. M.; B. T. Sullivan; P. Anderson; C. W. Berisford & G. Birgersson (2000) Odor perception in the bark beetle parasitoid *Roptrocercus xylophagorum* exposed to host associated volatiles. *Journal of Chemical Ecology* 26: 2507-2525.

- Pettersson, E. M. & W. Boland (2003) Potential parasitoid attractants, volatile composition throughout a bark beetle attack. *Chemoecology* 13: 27-37.
- Pickett, J. A.; H. B. Rasmussen; C. M. Woodcock; W. Matthes & J. A. Napier (2003) Plant stress signalling: understanding and exploiting plant-plant interactions. *Biochemical Society Transactions* 31: 123-127.
- Polgar, L. A.; B. Darvas & W. Volkl (1995) Induction of dormancy in aphid parasitoids: implications for enhancing their field effectiveness. *Agriculture Ecosystems and Environment* 52: 19-23.
- Polis, G. A. & D. R. Strong (1996) Food web complexity and community dynamics. *American Naturalist* 147: 813-846.
- Polis, G. A.; S. D. Hurd; C. T. Jackson & F. Sanchez-Pinero (1998) Multifactor population limitation: variable spatial and temporal control of spiders on gulf of California islands. *Ecology* 79: 490-502.
- Polis, G. A. (1999) Why are parts of the world green?: multiple factors control productivity and the distribution of biomass. *Oikos* 86: 3-15.
- Polis, G. A.; A. L. W. Sears; G. R. Huxel; D. R. Strong & J. Maron (2000) When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15: 473-475.
- Ponnuvel, K. M. & M. Yamakawa (2002) Immune responses against bacterial infection in *Bombyx mori* and regulation of host gene expression. *Current Science* 83: 447-454.
- Pontoppidan, B.; R. Hopkins; L. Rask & J. Meijer (2003) Infestation by cabbage aphid (*Brevicoryne brassicae*) on oilseed rape (*Brassica napus*) causes a long lasting induction of the myrosinase system. *Entomologia Experimentalis Et Applicata* 109: 55-62.
- Porter, A. J. R.; A. M. Morton; G. Kiddle; K. J. Doughty & R. M. Wallsgrove (1991) Variation in the glucosinolate content of oilseed rape (*Brassica napus* L) leaves. I. Effect of leaf age and position. *Annals of Applied Biology* 118: 461-467.
- Potting, R. P. J.; G. M. Poppy & T. H. Schuler (1999) The role of volatiles from cruciferous plants and pre-flight experience in the foraging behaviour of the specialist parasitoid *Cotesia plutellae*. *Entomologia Experimentalis Et Applicata* 93: 87-95.
- Powell, W. & J. A. Pickett (2003) Manipulation of parasitoids for aphid pest management: progress and prospects. *Pest Management Science* 59: 149-155.
- Power, M. E. (1990) Effects of fish in river food webs. *Science* 250: 811-814.
- Power, M. E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73: 733-746.
- Power, M. E.; M. S. Parker & J. T. Wootton (1996) Disturbance and food chain length in rivers. In: G. A. Polis & K. O. Winemiller (ed.), *Food Webs*, pp. 286-297, Chapman

& Hall,, New York.

Poysa, H. & M. Pesonen (2003) Density dependence, regulation and open-closed populations: insights from the wigeon, *Anas penelope*. *Oikos* 102: 358-366.

Price, P. W.; C. E. Bouton; P. Gross; B. A. McPheron; J. N. Thompson & A. E. Weis (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11: 41-65.

Price, P. W. (1986) Ecological aspects of host plant resistance and biological control: interactions among three trophic levels. In: D. J. Boethel & R. D. Eikenbary (ed.), *Interactions of plant resistance and parasitoids and predators of insects*, pp. 11-30, Wiley & Sons, Chichester.

Price, P. W.; H. Roininen & J. Tahvanainen (1987) Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? *Oecologia* 74: 1-6.

Price, P. W. & M. D. Hunter (1995) Novelty and synthesis in the development of population dynamics. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 389-412, Academic Press, San Diego.

Prout, T. & F. McChesney (1985) Competition among immatures affects their adult fertility: population dynamics. *American Naturalist* 126: 521-558.

Puttler, B. (1974) *Hypera postica* and *Bathyplectes curculionis*: encapsulation of parasite eggs by host larvae in Missouri and Arkansas. *Environmental Entomology* 3: 881-882.

Ramachandran, S.; G. D. Buntin; J. N. All & P. L. Raymer (1998) Diamondback moth (Lepidoptera: Plutellidae) resistance of *Brassica napus* and *B. oleracea* lines with differing leaf characteristics. *Journal of Economic Entomology* 91: 987-992.

Ramos-Jiliberto, R. (2005) Resource-consumer models and the biomass conversion principle. *Environmental Modelling and Software* 20: 85-91.

Rask, L.; E. Andreasson; B. Ekbom; S. Eriksson; B. Pontoppidan & J. Meijer (2000) Myrosinase: gene family evolution and herbivore defense in Brassicaceae. *Plant Molecular Biology* 42: 93-113.

Ratcliffe, N. A. & S. J. Gagen (1977) Studies on the in vivo cellular reactions of insects: an ultrastructural analysis of nodule formation in *Galleria mellonella*. *Tissue Cell* 9: 73-85.

Ratcliffe, N. A. (1993) Cellular defence responses of insects: unresolved problems. In: S. N. Thompson & B. A. Federici (ed.), *Parasites and pathogens of insects Vol. 1*, pp. 267-304, Academic Press, London.

Ratzka, A.; H. Vogel; D. J. Kliebenstein; T. Mitchell-Olds & J. Kroymann (2002) Disarming the mustard oil bomb. *Proceedings of the National Academy of Sciences of*

the United States of America 99: 11223-11228.

Raymond, B.; A. Vanbergen; I. Pearce; S. E. Hartley; J. S. Cory & R. S. Hails (2002) Host plant species can influence the fitness of herbivore pathogens: the winter moth and its nucleopolyhedrovirus. *Oecologia* 131: 533-541.

Reddy, G. V. P.; J. K. Holopainen & A. Guerrero (2002) Olfactory responses of *Plutella xylostella* natural enemies to host pheromone, larval frass, and green leaf cabbage volatiles. *Journal of Chemical Ecology* 28: 131-143.

Reddy, G. V. P.; E. Tabone & M. T. Smith (2004) Mediation of host selection and oviposition behavior in the diamondback moth *Plutella xylostella* and its predator *Chrysoperla carnea* by chemical cues from cole crops. *Biological Control* 29: 270-277.

Redpath, S. M. & S. J. Thirgood (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology* 68: 879-892.

Reed, D. W.; K. A. Pivnick & E. W. Underhill (1989) Identification of chemical oviposition stimulants for the diamondback moth, *Plutella xylostella*, present in three species of Brassicaceae. *Entomologia Experimentalis Et Applicata* 53: 277-286.

Reed, D. K.; S. D. Kindler & T. L. Springer (1992) Interactions of Russian wheat aphid, a hymenopterous parasitoid and resistant and susceptible slender wheat grasses. *Entomologia Experimentalis Et Applicata* 64: 239-246.

Reeson, A. F.; K. Wilson; A. Gunn; R. S. Hails & D. Goulson (1998) Baculovirus resistance in the noctuid *Spodoptera exempta* is phenotypically plastic and responds to population density. *Proceedings of the Royal Society of London Series B-Biological Sciences* 265: 1787-1791.

Reitz, S. R.; G. S. Kund; W. G. Carson; P. A. Phillips & J. T. Trumble (1999) Economics of reducing insecticide use on celery through low-input pest management strategies. *Agriculture Ecosystems and Environment* 73: 185-197.

Relyea, R. A. & J. T. Hoverman (2003) The impact of larval predators and competitors on the morphology and fitness of juvenile treefrogs. *Oecologia* 134: 596-604.

Renwick, J. A. A.; C. D. Radke; K. Sachdev-Gupta & E. Stdler (1992) Leaf surface chemicals stimulating oviposition by *Pieris rapae* (Lepidoptera: Pieridae) on cabbage. *Chemoecology* 3: 33-38.

Renwick, J. A. A. & K. Lopez (1999) Experience-based food consumption by larvae of *Pieris rapae*: addiction to glucosinolates? *Entomologia Experimentalis Et Applicata* 91: 51-58.

Renwick, J. A. A. (2002) The chemical world of crucivores: lures, treats and traps. *Entomologia Experimentalis Et Applicata* 104: 35-42.

Rhoades, D. F. (1983) Herbivore population dynamics and plant chemistry. In: R. F.

- Denno & M. S. McClure (ed.), *Variable plants and herbivores in natural and managed system*, pp. 155-204, Academic Press, New York.
- Rieux, R.; S. Simon & H. Defrance (1999) Role of hedgerows and ground cover management on arthropod populations in pear orchards. *Agriculture Ecosystems and Environment* 73: 119-127.
- RigginBucci, T. M. & F. Gould (1997) Impact of intraplot mixtures of toxic and nontoxic plants on population dynamics of diamondback moth (Lepidoptera: Plutellidae) and its natural enemies. *Journal of Economic Entomology* 90: 241-251.
- Rigler, F. H. (1961) The relation between concentration of food and feeding rate of *Daphnia magna* Straus. *Canadian Journal of Zoology* 39: 857-868.
- Rinaldi, S.; A. Gagnani & S. De Monte (2004) Remarks on antipredator behavior and food chain dynamics. *Theoretical Population Biology* 66: 277-286.
- Rodenhouse, N. L.; T. S. Sillett; P. J. Doran & R. T. Holmes (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2105-2110.
- Rogers, M. E. & D. A. Potter (2002) Kairomones from scarabaeid grubs and their frass as cues in below-ground host location by the parasitoids *Tiphia vernalis* and *Tiphia pygidialis*. *Entomologia Experimentalis Et Applicata* 102: 307-314.
- Romani, R.; N. Isidoro; F. Bin & S. B. Vinson (2002) Host recognition in the pupal parasitoid *Trichopria drosophilae*: a morpho-functional approach. *Entomologia Experimentalis Et Applicata* 105: 119-128.
- Romanow, L. R.; O. M. B. De Ponti & C. Mollema (1991) Resistance in tomato to the greenhouse whitefly: analysis of population dynamics. *Entomologia Experimentalis Et Applicata* 60: 247-259.
- Rossiter, M. (1995) Impact of life-history evolution on population dynamics: predicting the presence of maternal effects. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 251-275, Academic Press, San Diego.
- Roy, H. E. & J. K. Pell (2000) Interactions between entomopathogenic fungi and other natural enemies: implications for biological control. *Biocontrol Science and Technology* 10: 737-752.
- Royama, T. (1992). *Analytical population dynamics*. Chapman & Hall, London, 371 pp.
- Rui, X.; M. A. J. Chaplain & F. A. Davidson (2004) Periodic solution for a three-species Lotka-Volterra food-chain model with time delays. *Mathematical and Computer Modelling* 40: 823-837.
- Sagarra, L. A.; D. D. Peterkin; C. Vincent & R. K. Stewart (2000) Immune response of the hibiscus mealybug, *Maconellicoccus hirsutus* Green (Homoptera : Pseudococcidae),

- to oviposition of the parasitoid *Anagyrus kamali* Moursi (Hymenoptera: Encyrtidae). *Journal of Insect Physiology* 46: 647-653.
- Saleem, M.; A. K. Tripathi & A. H. Sadiyal (2003) Coexistence of species in a defensive switching model. *Mathematical Biosciences* 181: 145-164.
- Sallam, M. N.; W. A. Overholt & E. Kairu (2002) Intraspecific and interspecific competition between *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera : Braconidae), gregarious larval endoparasitoids of lepidopteran stemborers. *Biocontrol Science and Technology* 12: 493-506.
- Salt, G. (1956) Experimental studies in insect parasitism. IX. The reaction of a stick insect to an alien parasite. *Proceedings of the Royal Society of London, B: Biological Sciences* 146: 93-108.
- Salt, G. (1964) The ichneumonid parasite *Nemeritis canescens* in relation to the wax moth *Galleria mellonella*. *Trans. Roy. Entomol. Soc. London* 116: 1-14.
- Sar, S. A.; B. M. Wayi & R. D. Ghodake (1998) Review of research in Papua New Guinea for sustainable production of taro (*Colocasia esculenta*). *Tropical Agriculture* 75: 134-138.
- Sayyed, A. H. & D. J. Wright (2001) Cross-resistance and inheritance of resistance to *Bacillus thuringiensis* toxin Cry1Ac in diamondback moth (*Plutella xylostella* L) from lowland Malaysia. *Pest Management Science* 57: 413-421.
- Sayyed, A. H.; T. H. Schuler & D. J. Wright (2003) Inheritance of resistance to *Bt* canola in a field-derived population of *Plutella xylostella*. *Pest Management Science* 59: 1197-1202.
- Schaffner, U. & C. Muller (2001) Exploitation of the fecal shield of the lily leaf beetle, *Lilioceris lili* (Coleoptera : Chrysomelidae), by the specialist parasitoid *Lemophagus pulcher* (Hymenoptera : Ichneumonidae). *Journal of Insect Behavior* 14: 739-757.
- Schellhorn, N. A.; T. R. Kuhman; A. C. Olson & A. R. Ives (2002) Competition between native and introduced parasitoids of aphids: nontarget effects and biological control. *Ecology* 83: 2745-2757.
- Schmale, I.; F. L. Wackers; C. Cardona & S. Dorn (2003) Combining parasitoids and plant resistance for the control of the bruchid *Acanthoscelides obtectus* in stored beans. *Journal of Stored Products Research* 39: 401-411.
- Schmidt, O.; U. Theopold & M. Strand (2001) Innate immunity and its evasion and suppression by hymenopteran endoparasitoids. *Bioessays* 23: 344-351.
- Schmit, A. R. & N. A. Ratcliffe (1977) The encapsulation of foreign tissue implants in *Galleria mellonella* larvae. *Journal of Insect Physiology* 23: 175-184.
- Schmitz, O. J.; P. A. Hamback & A. P. Beckerman (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American*

Naturalist 155: 141-153.

Schmitz, O. J. (2004) Perturbation and abrupt shift in trophic control of biodiversity and productivity. *Ecology Letters* 7: 403-409.

Schofield, P.; M. Chaplain & S. Hubbard (2002) Mathematical modelling of host-parasitoid systems: effects of chemically mediated parasitoid foraging strategies on within- and between-generation spatio-temporal dynamics. *Journal of Theoretical Biology* 214: 31-47.

Schoonhoven, L. M. (1972) Secondary plant substances and insects. *Rec. Adv. Phytochem.* 5: 197-224.

Schoonhoven, L. M.; T. Jermy & J. J. A. van Loon (1998). *Insect-plant biology: from physiology to evolution*. Chapman & Hall, London, 409 pp.

Schuler, T. H.; R. P. J. Potting; I. Denholm; S. J. Clark; A. J. Clark; C. N. Stewart & G. M. Poppy (2003) Tritrophic choice experiments with *Bt* plants, the diamondback moth (*Plutella xylostella*) and the parasitoid *Cotesia plutellae*. *Transgenic Research* 12: 351-361.

Sedmak, J. J. & S. E. Grossberg (1977) A rapid, sensitive, and versatile assay for protein using Coomassie brilliant blue G250. *Analytical Biochemistry* 79: 544-552.

Shahruz, S. M. & D. A. Kalkin (2001) Limit cycle behavior in three- or higher-dimensional non-linear systems: the Lotka-Volterra example. *Journal of Sound and Vibration* 246: 379-386.

Sharma, H. C. & R. Ortiz (2000) Transgenics, pest management, and the environment. *Current Science* 79: 421-437.

Sharma, H. C.; K. K. Sharma & J. H. Crouch (2004) Genetic transformation of crops for insect resistance: potential and limitations. *Critical Reviews in Plant Sciences* 23: 47-72.

Shelby, K. S.; L. Cui & B. A. Webb (1998) Polydnavirus-mediated inhibition of lysozyme gene expression and the antibacterial response. *Insect Molecular Biology* 7: 265-272.

Shelby, K. S. & B. A. Webb (1999) Polydnavirus-mediated suppression of insect immunity. *Journal of Insect Physiology* 45: 507-514.

Shelby, K. S.; O. A. Adeyeye; B. M. Okot-Kotber & B. A. Webb (2000) Parasitism-linked block of host plasma melanization. *Journal of Invertebrate Pathology* 75: 218-225.

Shelton, A. M.; F. V. Sances; J. Hawley; J. D. Tang; M. Boune; D. Jungers; H. L. Collins & J. Farias (2000) Assessment of insecticide resistance after the outbreak of diamondback moth (Lepidoptera : Plutellidae) in California in 1997. *Journal of Economic Entomology* 93: 931-936.

Shelton, A. M.; J. Z. Zhao & R. T. Roush (2002) Economic, ecological, food safety, and social consequences of the deployment of *Bt* transgenic plants. *Annual Review of Entomology* 47: 845-881.

Shelton, A. L. (2004) Variation in chemical defences of plants may improve the effectiveness of defence. *Evolutionary Ecology Research* 6: 709-726.

Shenefelt, R. D. (1972) Braconidae IV, Microgasterinae, *Apanteles*. *Hymenopterorum catalogus* 7: 429-668.

Shi, Z. H.; S. S. Liu & Y. X. Li (2002) *Cotesia plutellae* parasitizing *Plutella xylostella*: host-age dependent parasitism and its effect on host development and food consumption. *Biocontrol* 47: 499-511.

Shiojiri, K.; J. Takabayashi; S. Yano & A. Takafuji (2000a) Flight response of parasitoids toward plant-herbivore complexes: a comparative study of two parasitoid-herbivore systems on cabbage plants. *Applied Entomology and Zoology* 35: 87-92.

Shiojiri, K.; J. Takabayashi; S. Yano & A. Takafuji (2000b) Herbivore-species-specific interactions between crucifer plants and parasitic wasps (Hymenoptera : Braconidae) that are mediated by infochemicals present in areas damaged by herbivores. *Applied Entomology and Zoology* 35: 519-524.

Shurin, J. B.; E. T. Borer; E. W. Seabloom; K. Anderson; C. A. Blanchette; B. Broitman; S. D. Cooper & B. S. Halpern (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5: 785-791.

Siemens, D. H. & T. Mitchell-Olds (1998) Evolution of pest-induced defenses in *Brassica* plants: tests of theory. *Ecology* 79: 632-646.

Sime, K. R. (2002) Experimental studies of the host-finding behavior of *Trogus pennator*, a parasitoid of swallowtail butterflies. *Journal of Chemical Ecology* 28: 1377-1392.

Sinclair, A. R. E.; C. J. Krebs; J. M. Fryxell; R. Turkington; S. Boutin; R. Boonstra; P. Secombe-Hett; P. Lundberg & L. Oksanen (2000) Testing hypotheses of trophic level interactions: a boreal forest ecosystem. *Oikos* 89: 313-328.

Singer, M. S. & J. O. Stireman (2003) Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* 100: 554-562.

Siva-Jothy, M. T. & J. J. W. Thompson (2002) Short-term nutrient deprivation affects immune function. *Physiological Entomology* 27: 206-212.

Sivapragasam, A.; W. H. Loke; A. K. Hussan & G. S. Lim (eds.) (1997) *The management of diamondback moth and other crucifer pests. Proc. 3rd. Internat. workshop*. Kuala Lumpur, Malaysia. 29 October -1 November, 1996, MARDI, Kuala Lumpur, Malaysia, 356pp.

Slepneva, I. A.; V. V. Glupov; S. V. Sergeeva & V. V. Khramtsov (1999) EPR

detection of reactive oxygen species in hemolymph of *Galleria mellonella* and *Dendrolimus superans sibiricus* (Lepidoptera) larvae. *Biochemical and Biophysical Research Communications* 264: 212-215.

Slobodkin, L. B. (1960) Ecological energy relationships at the population level. *American Naturalist* 94: 213-236.

Smeding, F. W. & G. R. de Snoo (2003) A concept of food-web structure in organic arable farming systems. *Landscape and Urban Planning* 65: 219-236.

Smid, H. A.; J. J. A. van Loon; M. A. Posthumus & L. E. M. Vet (2002) GC-EAG-analysis of volatiles from Brussels sprouts plants damaged by two species of *Pieris caterpillars*: olfactory receptive range of a specialist and a generalist parasitoid wasp species. *Chemoecology* 12: 169-176.

Smith, G. S.; J. C. S. Allison & N. W. Pammenter (1994) Bioassay study of response by a parasitoid to frass and feeding substrates of its host, the stalk borer *Eldana saccharina*. *Annals of Applied Biology* 125: 439-446.

Soderhall, K. & L. Cerenius (1998) Role of the prophenoloxidase-activating system in invertebrate immunity. *Current Opinion in Immunology* 10: 23-28.

Souissi, R. & B. Le Ru (1998) Influence of the host plant of the cassava mealybug *Phenacoccus manihoti* (Hemiptera : Pseudococcidae) on biological characteristics of its parasitoid *Apoanagyrus lopezi* (Hymenoptera : Encyrtidae). *Bulletin of Entomological Research* 88: 75-82.

Souissi, R.; J. P. Nenon & B. Le Ru (1998) Olfactory responses of parasitoid *Apoanagyrus lopezi* to odor of plants, mealybugs, and plant-mealybug complexes. *Journal of Chemical Ecology* 24: 37-48.

Southwood, T. R. E. (1981) Bionomic strategies and population parameters. In: R. M. May (ed.), *Theoretical ecology*, pp. 30-52, Blackwell, Oxford.

Spataro, T. & C. Bernstein (2004) Combined effects of intraspecific competition and parasitoid attacks on the dynamics of a host population: a stage-structured model. *Oikos* 105: 148-158.

Sprott, J. C. (2003). *Chaos and time-series analysis*. Oxford University Press, Oxford, 507 pp.

Stankovic, S.; A. Zabel; M. Kostic; B. Manojlovic & S. Rajkovic (2004) Colorado potato beetle [*Leptinotarsa decemlineata* (Say)] resistance to organophosphates and carbamates in Serbia. *Journal of Pest Science* 77: 11-15.

Steidle, J. L. M. & J. J. A. van Loon (2003) Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. *Entomologia Experimentalis Et Applicata* 108: 133-148.

Steinberg, S.; M. Dicke & L. E. M. Vet (1993) Relative importance of infochemicals

from first and second trophic level in long-range host location by the larval parasitoid *Cotesia glomerata*. *Journal of Chemical Ecology* 19: 47-59.

Stettler, P.; T. Trenczek; T. Wyler; R. Pfister-Wilhelm & B. Lanzrein (1998) Overview of parasitism associated effects on host haemocytes in larval parasitoids and comparison with effects of the egg-larval parasitoid *Chelonus inanitus* on its host *Spodoptera littoralis*. *Journal of Insect Physiology* 44: 817-831.

Stiling, P. & A. M. Rossi (1997) Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology* 78: 1602-1606.

Stinchcombe, J. R. (2002) Can tolerance traits impose selection on herbivores? *Evolutionary Ecology* 16: 595-602.

Stoll, P. & D. Prati (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82: 319-327.

Stoltz, D. B. & D. Guzo (1986) Apparent hemocytic transformations associated with parasitoid-induced inhibition of immunity in *Malacosoma disstria* larvae. *Journal of Insect Physiology* 32: 377-383.

Stout, M. J.; G. W. Zehnder & M. E. Baur (2002) Potential for the use of elicitors of plant resistance in arthropod management programs. *Archives of Insect Biochemistry and Physiology* 51: 222-235.

Strand, M. R. & L. L. Pech (1995) Immunological basis for compatibility in parasitoid host relationships. *Annual Review of Entomology* 40: 31-56.

Strong, D. R. (1984) Density-vague ecology and liberal population regulation in insects. In: P. W. Price; C. N. Slobodchikoff & W. S. Gaud (ed.), *A new ecology: novel approaches to interactive systems*, pp. Wiley, New York.

Strong, D. R. (1992) Are trophic cascades all wet?: differentiation and donor-control in speciose ecosystems. *Ecology* 73: 747-754.

Suarez, I. (1999) Mastering chaos in ecology. *Ecological Modelling* 117: 305-314.

Sugumaran, M. & M. R. Kanost (1993) Regulation of insect haemolymph phenoloxidases. In: N. E. Beckage; S. N. Thompson & B. A. Tederici (ed.), *Parasites and pathogens of insects. Vol.I: parasites*, pp. 317-342, Academic Press, New York.

Sugumaran, M.; K. Nellaiappan; C. Amaratunga; S. Cardinale & T. Scott (2000) Insect melanogenesis. III. Metabolon formation in the melanogenic pathway: regulation of phenoloxidase activity by endogenous dopachrome isomerase (decarboxylating) from *Manduca sexta*. *Archives of Biochemistry and Biophysics* 378: 393-403.

Sugumaran, M.; K. Nellaiappan & K. Valivittan (2000) A new mechanism for the control of phenoloxidase activity: inhibition and complex formation with quinone isomerase. *Archives of Biochemistry and Biophysics* 379: 252-260.

- Sugumaran, H. (2002) Comparative biochemistry of eumelanogenesis and the protective roles of phenoloxidase and melanin in insects. *Pigment Cell Research* 15: 2-9.
- Sullivan, B. T.; E. M. Pettersson; K. C. Seltnann & C. W. Berisford (2000) Attraction of the bark beetle parasitoid *Roptrocercus xylophagorum* (Hymenoptera : Pteromalidae) to host-associated olfactory cues. *Environmental Entomology* 29: 1138-1151.
- Sullivan, B. T. & C. W. Berisford (2004) Semiochemicals from fungal associates of bark beetles may mediate host location behavior of parasitoids. *Journal of Chemical Ecology* 30: 703-717.
- Sumerford, D. V.; W. G. Abrahamson & A. E. Weis (2000) The effects of drought on the *Solidago altissima*-*Eurosta solidaginis*-natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. *Oecologia* 122: 240-248.
- Suttle, K. B. (2003) Pollinators as mediators of top-down effects on plants. *Ecology Letters* 6: 688-694.
- Tabachnick, B. G. & L. S. Fidell (2001). *Using multivariate statistics*. Allyn & Bacon, Boston, pp.
- Tabashnik, B. E.; F. R. Groeters; N. Finson; Y. B. Liu; M. W. Johnson; D. G. Heckel; K. Luo & M. J. Adang (1996) Resistance to *Bacillus thuringiensis* in *Plutella xylostella*-the moth heard round the world. *Molecular Genetics and Evolution of Pesticide Resistance* 645: 130-140.
- Takasu, K. & W. J. Lewis (2003) Learning of host searching cues by the larval parasitoid *Microplitis croceipes*. *Entomologia Experimentalis Et Applicata* 108: 77-86.
- Talekar, N. S. & J. C. Yang (1991) Characteristic of parasitism of diamondback moth by two larval parasites. *Entomophaga* 36: 95-104.
- Talekar, N. S. (ed) (1992) *Diamondback moth and other crucifer pests*. Proc. 2nd. Internat. Workshop. Tainan, Taiwan, 10-14 December, 1990, AVRDC, Taipei, Taiwan, 603pp.
- Talekar, N. S. & A. M. Shelton (1993) Biology, ecology and management of the diamondback moth. *Annual Review of Entomology* 38: 275-301.
- Tax, M. H. (1989). *Atlas van de nederlandse dagvlinders's gravenhage: vereniging tot behoud van natuurmonumenten in Nederland*. Vlinderstichting, Wageningen, 248 pp.
- Teder, T. & T. Tammaru (2002) Cascading effects of variation in plant vigour on the relative performance of insect herbivores and their parasitoids. *Ecological Entomology* 27: 94-104.
- Terofal, F. (1965) Zum problem der wirtsspezifität bei pieriden (Lep.): unter besonderer berücksichtigung der einheimischen arten *Pieris brassicae* L., *P. napi* L. und *P. rapae* L. *Mitteilungen m Uncheneer Entomologischen Gesellschaft* 55: 1-76.

- Thomas, M. & J. Waage (1996). *Integration of biological control and host plant resistance breeding: a scientific and literature review*. CTA, Wageningen, 99 pp.
- Thomas, M. B. (1999) Ecological approaches and the development of "truly integrated" pest management. *Proceedings of the National Academy of Sciences of the United States of America* 96: 5944-5951.
- Thompson, W. R. (1924) La theori mathematique de l'action des parasites entomophages et le facteur du hasard. *Annales de la Faculte des Science de Marseille* 2: 69-89.
- Thompson, W. M. (1996). Plants and parasitoids of herbivorous insects: a mutually beneficial relationship.
- Thompson, R. C.; T. A. Norton & S. J. Hawkins (2004) Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. *Ecology* 85: 1372-1382.
- Thurston, G. S.; W. N. Yule & G. B. Dunphy (1994) Explanations for the low susceptibility of *Leptinotarsa decemlineata* to *Steinernema carpocapsae*. *Biological Control* 4: 53-58.
- Toenniessen, G. H.; J. C. O'Toole & J. DeVries (2003) Advances in plant biotechnology and its adoption in developing countries. *Current Opinion in Plant Biology* 6: 191-198.
- van Tol, R. W. H. M.; A. T. C. van der Sommen; M. I. C. Boff; J. van Bezooijen; M. W. Sabelis & P. H. Smits (2001) Plants protect their roots by alerting the enemies of grubs. *Ecology Letters* 4: 292-294.
- Trottier, R. (1998) Sustainable pest management safe utilization of new organisms in biological control: introduction. *Phytoprotection* 79: 1-2.
- Trumper, E. V. & J. Holt (1998) Modelling pest population resurgence due to recolonization of fields following an insecticide application. *Journal of Applied Ecology* 35: 273-285.
- Tsunoda, S.; K. Hinata & C. Gomez-Campo (ed.) (1980). *Brassicas crops and wild allies*. Japan Science Society Press, Tokyo, pp.
- Tucker, T. M. & L. Stevens (2003) Geographical variation and sexual dimorphism of phenoloxidase levels in Japanese beetles (*Popillia japonica*). *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: S245-S247.
- Tumlinson, J. H.; T. C. J. Turlings & W. J. Lewis (1993) Semiochemically mediated foraging behavior in beneficial parasitic insects. *Archives of Insect Biochemistry and Physiology* 22: 385-391.
- Tumlinson, J. H.; P. W. Pare & W. J. Lewis (1999) Plant production of volatile semiochemicals in response to insect-derived elicitors. In: D. Chadwick & J. Goode (ed.), *Insect-plant interactions and induced plant defence*, pp. 95-109, John Wiley &

Sons, Chichester.

Turchin, P. (1995) Population regulation: old arguments and a new synthesis. In: N. Cappuccino & P. W. Price (ed.), *Population dynamics: new approaches and synthesis*, pp. 19-40, Academic Press, San Diego.

Turlings, T. C. J.; F. L. Wackers; L. E. M. Vet; W. J. Lewis & J. H. Tumlinson (1993) Learning of host-finding cues by hymenopterous parasitoids. In: D. R. Papaj & A. C. Lewis (ed.), *Insect learning: ecological and evolutionary perspectives*, pp. 51-78, Chapman & Hall, New York.

Turlings, T. C. J.; J. H. Loughrin; P. J. McCall; U. S. R. Rose; W. J. Lewis & J. H. Tumlinson (1995) How caterpillar-damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences of the United States of America* 92: 4169-4174.

Turlings, T. C. J. & B. Benrey (1998) Effects of plant metabolites on the behavior and development of parasitic wasps. *Ecoscience* 5: 321-333.

Turlings, T. C. J.; H. T. Alborn; J. H. Loughrin & J. H. Tumlinson (2000) Volicitin, an elicitor of maize volatiles in oral secretion of *Spodoptera exigua*: isolation and bioactivity. *Journal of Chemical Ecology* 26: 189-202.

Tylianakis, J. M.; R. K. Didham & S. D. Wratten (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85: 658-666.

Ulmer, B.; C. Gillott; D. Woods & M. Erlandson (2002) Diamondback moth, *Plutella xylostella* (L.), feeding and oviposition preferences on glossy and waxy *Brassica rapa* (L.) lines. *Crop Protection* 21: 327-331.

Umbanhowar, J. & A. Hastings (2002) The impact of resource limitation and the phenology of parasitoid attack on the duration of insect herbivore outbreaks. *Theoretical Population Biology* 62: 259-269.

Uvarov, B. P. (1931) Insects and climate. *Trans. Roy. Entomol. Soc. London* 79: 1-249.

Vandermeer, J.; L. Stone & B. Blasius (2001) Categories of chaos and fractal basin boundaries in forced predator-prey models. *Chaos Solitons and Fractals* 12: 265-276.

Varley, G. C. (1947) The natural control of population balance in the knapweed gall fly (*Urophora jaceana*). *Journal of Animal Ecology* 16: 139-187.

Vaughn, J. G.; A. J. MacLeod & B. M. G. Jones (ed.) (1976). *The biology and chemistry of the Cruciferae*. Academic Press, London.

Vaughn, S. F. & M. A. Berhow (1999) Allelochemicals isolated from tissues of the invasive weed garlic mustard (*Alliaria petiolata*). *Journal of Chemical Ecology* 25: 2495-2504.

Verkerk, R. H. J. & D. J. Wright (1994a) Interactions between the diamondback moth,

- Plutella xylostella* L and glasshouse and outdoor-grown cabbage cultivars. *Annals of Applied Biology* 125: 477-488.
- Verkerk, R. H. J. & D. J. Wright (1994b) The potential for induced extrinsic host plant resistance in IRM strategies targeting the diamondback moth. In: *Proc. Brighton Crop Prot. Conf.: Pests and Diseases*, 1994, pp. 457-462, BCPC, Farnham, UK.
- Verkerk, R. H. J. & D. J. Wright (1996a) Common cabbage resistance mechanisms against the diamondback moth: still an open book? *Annals of Applied Biology* 128: 571-577.
- Verkerk, R. H. J. & D. J. Wright (1996b) Multitrophic interactions and management of the diamondback moth: a review. *Bulletin of Entomological Research* 86: 205-216.
- Verkerk, R. H. J. & D. J. Wright (1997) Field-based studies with the diamondback moth tritrophic system in Cameron Highlands of Malaysia: implications for pest management. *International Journal of Pest Management* 43: 27-33.
- Verkerk, R. H. J.; S. R. Leather & D. J. Wright (1998) The potential for manipulating crop-pest-natural enemy interactions for improved insect pest management. *Bulletin of Entomological Research* 88: 493-501.
- Vet, L. E. M. & A. W. Groenewold (1990) Semiochemicals and learning in parasitoids. *Journal of Chemical Ecology* 16: 3119-3135.
- Vet, L. E. M.; F. L. Wackers & M. Dicke (1991) How to hunt for hiding hosts?: the reliability-detectability problem in foraging parasitoids. *Netherlands Journal of Zoology* 41: 202-213.
- Vet, L. E. M. & M. Dicke (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37: 141-172.
- Vet, L. E. M.; W. J. Lewis & R. T. Cardé (1995) Parasitoid foraging and learning. In: R. T. Cardé & W. J. Bell (ed.), *Chemical ecology of insects* 2, pp. 65-101, Chapman & Hall, New York.
- Vet, L. E. M. (2001) Parasitoid searching efficiency links behaviour to population processes. *Applied Entomology and Zoology* 36: 399-408.
- Vey, A.; V. Matha & C. Dumas (2002) Effects of the peptide mycotoxin destruxin E on insect haemocytes and on dynamics and efficiency of the multicellular immune reaction. *Journal of Invertebrate Pathology* 80: 177-187.
- Vilcinskas, A. & M. Wedde (2002) Insect inhibitors of metalloproteinases. *Iubmb Life* 54: 339-343.
- Vinson, S. B. (1984) How parasitoid locate their hosts: a case of insect espionage. In: T. Lawis (ed.), *Insect communications. 12th Symp. Roy. Entomol. Soc. London*, pp. 325-348, Academic Press, London.

- Vinson, S. B. & P. Barbosa (1987) Interrelationships of nutritional ecology of parasitoids. In: F. Slansky & J. G. Rodriguez (ed.), *Nutritional ecology of insects, mites and spiders and related invertebrates*, pp. 673-695, John Wiley & Sons, New York.
- Vinson, S. B. (1990) How parasitoids deal with the immune system of their host: an overview. *Archives of Insect Biochemistry and Physiology* 13: 3-27.
- Volterra, V. (1926) Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Accad. Naz. dei Lincei. Ser. VI*, 2: 31-113.
- Vos, M.; S. M. Berrocal; F. Karamaouna; L. Hemerik & L. E. M. Vet (2001) Plant-mediated indirect effects and the persistence of parasitoid-herbivore communities. *Ecology Letters* 4: 38-45.
- Walker, M. & T. H. Jones (2001) Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant-insect herbivore-natural enemy systems. *Oikos* 93: 177-187.
- Wallace, S. K. & S. D. Eigenbrode (2002) Changes in the glucosinolate-myrosinase defense system in *Brassica juncea* cotyledons during seedling development. *Journal of Chemical Ecology* 28: 243-256.
- Wang, B. & D. N. Ferro (1998) Functional responses of *Trichogramma ostrinae* (Hymenoptera : Trichogrammatidae) to *Ostrinia nubilalis* (Lepidoptera : Pyralidae) under laboratory and field conditions. *Environmental Entomology* 27: 752-758.
- Wang, X. G. & M. A. Keller (2002) A comparison of the host-searching efficiency of two larval parasitoids of *Plutella xylostella*. *Ecological Entomology* 27: 105-114.
- Wang, X. G. & R. H. Messing (2003) Egg maturation in the parasitoid *Fopius arisanus* (Hymenoptera : Braconidae): do host-associated stimuli promote ovarian development? *Annals of the Entomological Society of America* 96: 571-578.
- Wang, Y. S. (2003) The necessary and sufficient conditions for the existence of periodic orbits in a Lotka-Volterra system. *Journal of Mathematical Analysis and Applications* 284: 236-249.
- Wang, X. G.; J. Duff; M. A. Keller; M. P. Zalucki; S. S. Liu & P. Bailey (2004) Role of *Diadegma semiclausum* (Hymenoptera : Ichneumonidae) in controlling *Plutella xylostella* (Lepidoptera : Plutellidae): Cage exclusion experiments and direct observation. *Biocontrol Science and Technology* 14: 571-586.
- Wang, Y. & H. Wu (2004) Dynamics of competitive Lotka-Volterra systems that can be projected to a line. *Computers and Mathematics with Applications* 47: 1263-1271.
- Wangersky, P. J. (1978) Lotka-Volterra population models. *Annual Review of Ecology and Systematics* 9: 189-218.
- Warwick, S. I.; A. Francis & G. A. Mulligan (2004). Brassicaceae of Canada: Minister of Public Works and Government Services. <http://res.agr.ca/ecorc/cwmt.crucican/>.

- Waterhouse, D. F. & K. R. Norris (1987). *Biological control: pacific prospects*. Inkata Press, Melbourne, pp.
- Webster, M. S. (2004) Density dependence via intercohort competition in a coral-reef fish. *Ecology* 85: 986-994.
- Weisser, W. W.; V. A. A. Jansen & M. P. Hassell (1997) The effects of a pool of dispersers on host-parasitoid systems. *Journal of Theoretical Biology* 189: 413-425.
- Weller, S. J.; N. L. Jacobson & W. E. Conner (1999) The evolution of chemical defenses and mating systems in tiger moths (Lepidoptera: Arctiidae). *Biological Journal of the Linnean Society* 68: 557-578.
- Wertheim, B.; L. E. M. Vet & M. Dicke (2003) Increased risk of parasitism as ecological costs of using aggregation pheromones: laboratory and field study of *Drosophila leptopilina* interaction. *Oikos* 100: 269-282.
- Whitman, D. W. (1988) Allelochemical interactions among plants, herbivores and predators. In: P. Barbosa & D. K. Letourneau (ed.), *Novel aspects of insect-plant interactions*, pp. 11-64, John Wiley & sons, New York.
- Whitten, M. M. A.; I. F. Tew; B. L. Lee & N. A. Ratcliffe (2004) A novel role for an insect apolipoprotein (Apolipophorin III) in beta-1,3-glucan pattern recognition and cellular encapsulation reactions. *Journal of Immunology* 172: 2177-2185.
- Wiesner, A. (1992) Characteristics of inert beads provoking humoral immune-responses in *Galleria mellonella* larvae. *Journal of Insect Physiology* 38: 533-541.
- Wilson, K.; S. C. Cotter; A. F. Reeson & J. K. Pell (2001) Melanism and disease resistance in insects. *Ecology Letters* 4: 637-649.
- Wilson, K.; R. Knell; M. Boots & J. Koch-Osborne (2003) Group living and investment in immune defence: an interspecific analysis. *Journal of Animal Ecology* 72: 133-143.
- Wiskerke, J. S. C.; M. Dicke & L. E. M. Vet (1993) Larval parasitoid uses aggregation pheromone of adult hosts in foraging behavior: a solution to the reliability-detectability problem. *Oecologia* 93: 145-148.
- Wiskerke, J. S. C. & L. E. M. Vet (1994) Foraging for solitarily and gregariously feeding caterpillars: a comparison of two related parasitoid species (Hymenoptera, Braconidae). *Journal of Insect Behavior* 7: 585-603.
- Wittstock, U.; D. J. Kliebenstein; V. Lambrix; M. Reichelt & J. Gershenzon (2003) Glucosinolate hydrolysis and its impact on generalist and specialist insect herbivores. In: J. T. Romeo (ed.), *Integrative phytochemistry: from ethnobotany to molecular ecology*, pp. 101-125, Elsevier, London.
- Wittstock, U.; N. Agerbirk; E. J. Stauber; C. E. Olsen; M. Hippler; T. Mitchell-Olds; J. Gershenzon & H. Vogel (2004) Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proceedings of the National Academy of Sciences of the*

United States of America 101: 4859-4864.

Woiwod, I. P. & I. Hanski (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology* 61: 619-629.

Wratten, S. (1992) Population regulation in insect herbivores: top-down or bottom-up. *New Zealand Journal of Ecology* 16: 145-147.

Wright, D. J. & R. H. J. Verkerk (1995) Integration of chemical and biological: control systems for arthropods: evaluation in a multitrophic context. *Pesticide Science* 44: 207-218.

Xiao, D. M. & W. X. Li (2000) Limit cycles for the competitive three dimensional Lotka-Volterra system. *Journal of Differential Equations* 164: 1-15.

Xu, J. X.; A. M. Shelton & X. N. Cheng (2001) Variation in susceptibility of *Diadegma insulare* (Hymenoptera : Ichneumonidae) to permethrin. *Journal of Economic Entomology* 94: 541-546.

Xu, Y. Y.; T. X. Liu; G. L. Leibee & W. A. Jones (2004) Effects of selected insecticides on *Diadegma insulare* (Hymenoptera : Ichneumonidae), a parasitoid of *Plutella xylostella* (Lepidoptera : Plutellidae). *Biocontrol Science and Technology* 14: 713-723.

Ylioja, T.; H. Roininen; M. P. Ayres; M. Rousi & P. W. Price (1999) Host-driven population dynamics in an herbivorous insect. *Proceedings of the National Academy of Sciences of the United States of America* 96: 10735-10740.

Yokoo, S.; P. Gotz & S. Tojo (1995) Phagocytic activities of hemocytes separated by two simple methods from larvae of two lepidopteran species, *Agrotis segetum* and *Galleria mellonella*. *Applied Entomology and Zoology* 30: 343-350.

Yu, X. Q.; Y. F. Zhu; C. Ma; J. A. Fabrick & M. R. Kanost (2002) Pattern recognition proteins in *Manduca sexta* plasma. *Insect Biochemistry and Molecular Biology* 32: 1287-1293.

Yu, X. Q.; H. B. Jiang; Y. Wang & M. R. Kanost (2003) Nonproteolytic serine proteinase homologs are involved in prophenoloxidase activation in the tobacco hornworm, *Manduca sexta*. *Insect Biochemistry and Molecular Biology* 33: 197-208.

Yu, X. Q. & M. R. Kanost (2003) *Manduca sexta* lipopolysaccharide-specific immulectin-2 protects larvae from bacterial infection. *Developmental and Comparative Immunology* 27: 189-196.

Yu, X. Q. & M. R. Kanost (2004) Immulectin-2, a pattern recognition receptor that stimulates hemocyte encapsulation and melanization in the tobacco hornworm, *Manduca sexta*. *Developmental and Comparative Immunology* 28: 891-900.

Zeeman, E. C. (2002) Classification of quadratic carrying simplices in two-dimensional competitive Lotka-Volterra systems. *Nonlinearity* 15: 1993-2018.

- Zeng, S. (1993) Sustainable agriculture and integrated pest management in China. *Ciba Foundation Symposia* 177: 228-232.
- Zeng, F.; G. Pederson; M. Ellsbury & F. Davis (1993) Demographic-statistics for the pea aphid (Homoptera, Aphididae) on resistant and susceptible red clovers. *Journal of Economic Entomology* 86: 1852-1856.
- Zhang, Q. H.; F. Schlyter; A. Battisti; G. Birgersson & P. Anderson (2003) Electrophysiological responses of *Thaumetopoea pityocampa* females to host volatiles: implications for host selection of active and inactive terpenes. *Journal of Pest Science* 76: 103-107.
- Zhang, Q. H. & F. Schlyter (2003) Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. *Oikos* 101: 299-310.
- Zhang, Q. H. & F. Schlyter (2004) Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology* 6: 1-19.
- Zhu, Z. R.; J. Cheng; M. X. Jiang & X. X. Zhang (2004) Complex influence of rice variety, fertilization timing and insecticide on population dynamics of *Sogatella furcifera* (Horvath), *Nilaparvata lugens* (Stal) (Homoptera : Delphacidae) and their natural enemies in rice in Hangzhou, China. *Journal of Pest Science* 77: 65-74.
- Zijp, J. P. & L. H. M. Blommers (2002) Apple sawfly *Hoplocampa testudinea* (Hym., Tenthredinidae) and its parasitoid *Lathrolestes ensator* in Dutch apple orchards (Hym., Ichneumonidae, Ctenopelmatinae). *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie* 126: 265-274.

Appendix I: Detailed model analysis

A.I.1 The classification of equilibria

For a three-dimensional hyperbolic flow such as the present model, equilibrium can fall in the following categories (Sprott, 2003): (1) if there are three real and negative eigenvalues, the equilibrium is called a node that is an attractive point (stable); (2) if there are one real and a pair of complex conjugate eigenvalues and all are negative, the equilibrium is a spiral node that is an attractive point (stable); (3) if there are three real and positive eigenvalues, the equilibrium is called a repellor (unstable); (4) if there are one real and a pair of complex conjugate eigenvalues and all are positive, the equilibrium is a spiral repellor (unstable); (5) if there are three real eigenvalues such that at least one negative and one positive eigenvalue exist, the equilibrium is called a saddle point (unstable); (6) if there are one real and a pair of complex conjugate eigenvalues such that at least one negative and one positive eigenvalue exist, the equilibrium is a spiral saddle (unstable); saddle points and spiral saddles can be index one or two based on the number of positive eigenvalues. The index is geometrically the number of the outset (the unstable manifold). Saddles both attract and repel and are especially conductive to chaos.

A.I.2 The model analysis using linearization method

A.I.2.1 Model I

By using linearization method, the Jacobian matrix (community matrix) of the system (5.9-5.11) was appeared in form of:

$$J_i = \begin{pmatrix} 1-2x^*-y^* & -x^* & 0 \\ ay^* & a(x^*-b-bz^*) & -aby^* \\ 0 & cdz^* & c(dy^*-1) \end{pmatrix}$$

The matrix J_i for E_1 is: $J_1 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -ab & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_1 are 1, -ab and -c, which show that the equilibrium E_1 is a saddle point index 1 and thus, unstable. From the Jacobian matrix J_1 it is clear that the stable manifold of E_1 is y-x plane and the unstable manifold of E_1 is x axis; i.e. the origin is a hyperbolic saddle point that attracts in y and z directions but repels in x direction.

The matrix J_i for E_2 is: $J_2 = \begin{pmatrix} -1 & -1 & 0 \\ 0 & a(1-b) & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_2 are -1, $a(1-b)$ and -c, which show that the equilibrium E_2 is a node (stable) for $b > 1$ and a saddle point index 1 (unstable) for $b < 1$.

The matrix J_i for E_3 is: $J_3 = \begin{pmatrix} -b & -b & 0 \\ a(1-b) & 0 & -ab(1-b) \\ 0 & 0 & c(d(1-b)-1) \end{pmatrix}$

One of the eigenvalues of the matrix J_3 is $\lambda_1 = c(d(1-b)-1)$ and other two can be found by solving the following matrix:

$$M = \begin{pmatrix} -b & -b \\ a(1-b) & 0 \end{pmatrix}$$

The eigenvalues λ_2 and λ_3 are the roots of the characteristic equation $\lambda^2 - T\lambda + D = 0$, where T and D are the trace and the determinant of the matrix M , then: $\lambda_{2,3} = [-b \pm \sqrt{(b^2 - 4ab(1-b))}]/2$. It is clear that λ_1 is real and can be positive or negative if $d > 1/(1-b)$ or $d < 1/(1-b)$, respectively. λ_2 and λ_3 can be real or complex if $b > 4a/(1+4a)$ or $b < 4a/(1+4a)$, respectively. If λ_2 and λ_3 are complex, they are negative too (since their signs are determined by the real part, which is $-b/2$). But when λ_2 and λ_3 are real, they can be both negative if $b < 1$, and of opposite signs if $b > 1$. Consequently the following states can happen: (1) If $b > 1$ then there are two negative real roots and a positive real root. That is indicative of a saddle point index 1 (unstable); (2) If $4a/(1+4a) < b < 1$ and $1 - (1/d) < b < 1$ then there are three negative real roots, which indicate a node (stable); (3) If $4a/(1+4a) < b < 1 - (1/d)$, this is same as state 1; (4) If $1 - (1/d) < b < 4a/(1+4a)$ then there are a negative real root and two negative complex roots. This indicates a spiral node (stable); (5) If $b < 1 - (1/d)$ and $b < 4a/(1+4a)$ then there are a positive real root and two negative complex roots, which indicate a spiral saddle index 1 (unstable).

The matrix J_i for E_4 is: $J_4 = \begin{pmatrix} (1/d)-1 & (1/d)-1 & 0 \\ a/d & 0 & -ab/d \\ 0 & c(d(1-b)-1)/b & 0 \end{pmatrix}$

The characteristic equation for J_4 is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where $A = 1 - (1/d)$, $B = (a/d)[c(d(1-b)-1) + 1 - (1/d)]$, and $C = ac[(1/d)-1][1 - (1/d) + b]$. By applying Descartes' rule of signs (Kot, 2001), the signs of A , B and C can be determined and the following states can be considered: (1) If $d < 1$, the characteristic equation has 3 real (2 positive and 1 negative) roots, which is indicative of a saddle point index 2 (unstable); (2) If $1 < d < (c-1+\sqrt{(1+c)^2-4bc})/(2c(1-b))$, the characteristic equation has 3 real (1 positive and 2 negative) roots, which indicate a saddle point index 1 (unstable); (3) If $(c-1+\sqrt{(1+c)^2-4bc})/(2c(1-b)) < d < 1/(1-b)$, the characteristic equation has 1 real positive root and 2 complex negative roots, which reveal a spiral saddle index 1 (unstable); (4) If $d > 1/(1-b)$, the characteristic equation has 3 negative (1 real and 2 complex) roots. This implies a spiral node (stable).

The behaviour of the model has been summarized in Table A.I.1.

Table A.I.1. The behaviour of model I for constant value of $a = 1/6$ and $c = 1/30$, and different values of b (varied between 0.01 and 1.5) and d (varied between 0.01 and 3).

Area	Parameter values		E_2	E_3	E_4	Persistent components	
1	$b>1$	$d<1$	N	SPI_1	SPI_2	x	
2		$1<d<n$	N	SPI_1	SPI_1	x	
3		$d>n$	N	SPI_1	SSI_1	x	
4	$b<1$	$d<1$	$b<4a/(1+4a)$	SPI_1	SN	SPI_2	x, y
5		$b>4a/(1+4a)$	SPI_1	N	SPI_2	x, y	
6		$1<d<n$	$b<4a/(1+4a)$	SPI_1	SN	SPI_1	x, y
7		$b>4a/(1+4a)$	SPI_1	N	SPI_1	x,y	
8		$n<d<1/(1-b)$	$b<4a/(1+4a)$	SPI_1	SN	SSI_1	x, y
9		$b>4a/(1+4a)$	SPI_1	N	SSI_1	x, y	
10		$d>1/(1-b)$	$b<4a/(1+4a)$	SPI_1	SSI_1	SN	x, y, z
11		$b>4a/(1+4a)$	SPI_1	SPI_1	N	x, y, z	

$n = (c-1+\sqrt{((c+1)^2-4bc)})/(2c(1-b))$, N = node, SN = spiral node, SP = saddle point, SS = spiral saddle, I_1 = index 1 (one positive eigenvalue), I_2 = index 2 (two positive eigenvalues).

A.I.2.2 Model II

The Jacobian matrix for E_1 is: $J_1 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -ab & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_1 are 1, $-ab$ and $-c$, which show that the equilibrium E_1 is a saddle point index 1 and thus, unstable (same as the origin of model I).

The Jacobian matrix for E_1 is: $J_2 = \begin{pmatrix} -1 & -1/(f+1) & 0 \\ 0 & a(-b+1/(f+1)) & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_2 are -1 , $-c$ and $a(-b+1/(f+1))$ which show that the equilibrium E_2 is a node (stable) for $f > (1/b)-1$ and a saddle point index 1 (unstable) for $f < (1/b)-1$.

The Jacobian matrix for E_3 is: $J_3 = \begin{pmatrix} b(f+1+2/(bf-1)) & -b & 0 \\ -a(b+bf-1) & 0 & a b (-1+b+bf)/(bf-1)^2 \\ 0 & 0 & c(-1-d(b+bf-1)/(bf-1)^2) \end{pmatrix}$

The characteristic equation for J_3 is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where
 $A = c-b-bf+bcd/(bf-1)^2+(cd-2b)/(bf-1)$,
 $B = -[b(a(bf-1)^3(b+bf-1)+c((bf-1)^2+d(b+bf-1))(1+f(b+bf-1)))]/(bf-1)^3$, and
 $C = -[(b+bf-1)((bf-1)^2+d(b+bf-1))]/(bf-1)^2$.

By applying Descartes' rule of signs and then testing by simulation, it was revealed that E_3 could be a node, spiral node, saddle point index 1, spiral saddle index 1, spiral saddle index 2 and spiral repellor for different values of d and f .

The Jacobian matrix for E_4 is: $J_4 = \begin{pmatrix} 1-2m_1-1/d(fm_1+1)^2 & -m_1/(fm_1+1) & 0 \\ a/d(fm_1+1)^2 & 0 & -ab/d \\ 0 & cd(-1+m_1/(b+bfm_1)) & 0 \end{pmatrix}$

The characteristic equation for J_4 is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where
 $A = 2m_1-1+1/d(1+fm_1)^2$,
 $B = [a(m_1-cd(1+fm_1)^2(b-m_1+bfm_1))]/d(1+fm_1)^3$,
 $C = -[ac(b-m_1+bfm_1)(1+d(2m_1-1)(1+fm_1)^2)]/d(1+fm_1)^3$,

By applying Descartes' rule of signs and then testing by simulation, it appeared that E_4 could be a node, spiral node, saddle point index 1, saddle point index 2 and spiral saddle index 1 for different values of d and f .

Table A.I.2. The behaviour of model II for constant value of $a = 1/6$, $b = 3/20$, and $c = 1/30$, and different values of d (varied between 0.01 and 2.5) and f (varied between 0.01 and 12).

Area	Parameters		E ₂	E ₃	E ₄	E ₅	Persistent components
1	f > (1/b)-1	d > 4f/(f+1) ²	N	SPI ₁	SPI ₁	SPI ₁	x
2			N	SPI ₁	SPI ₁	SPI ₂	x
3		d < 4f/(f+1) ²	N	SPI ₁	-	-	x
4	f < (1/b)-1,	d > 4f/(f+1) ²	SPI ₁	N	SPI ₁	SPI ₁	x, y
5			SPI ₁	N	SPI ₁	SPI ₂	x, y
6		d < -(bf-1) ² / (b+bf-1)	SPI ₁	SN	SPI ₂	SPI ₁	x, y
7	SPI ₁		SN	SSI ₁	SPI ₁	x, y	
8		d < 4f/(f+1) ²	SPI ₁	N	-	-	x, y
9			SPI ₁	SN	-	-	x, y
10				SPI ₁	SSI ₂	-	-
11	f < (1/b)-1,		SPI ₁	SPI ₁	SN	SPI ₂	x, y, z
12			SPI ₁	SSI ₁	SN	SPI ₁	x, y, z
13	d > -(bf-1) ² / (b+bf-1)		SPI ₁	SR	SN	SPI ₁	x, y, z
14				SPI ₁	SPI ₁	N	SPI ₂
15			SPI ₁	SR	SN	SSI ₂	x, y (limit cycle); x, y, z

N = node, SN = spiral node, SP = saddle point, SS = spiral saddle, I₁ = index 1 (one positive eigenvalue), I₂ = index 2 (two positive eigenvalues).

The Jacobian matrix for E_5 is: $J_5 = \begin{pmatrix} 1-2m_2-1/d(fm_2+1)^2 & -m_2/(fm_2+1) & 0 \\ a/d(fm_2+1)^2 & 0 & -ab/d \\ 0 & cd(-1+m_2/(b+bfm_2)) & 0 \end{pmatrix}$

The characteristic equation for J_4 is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where

$$A = 2m_2-1+1/d(1+fm_2)^2,$$

$$B = [a(m_1-cd(1+fm_2)^2(b-m_2+bfm_2))]/d(1+fm_2)^3,$$

$$C = -[ac(b-m_2+bfm_2)(1+d(2m_2-1)(1+fm_2)^2)]/d(1+fm_2)^3.$$

By applying Descartes' rule of signs and then testing by simulation, it appeared that E_5 could be a saddle point index 1, saddle point index 2 and spiral saddle index 2 for different values of d and f . This means that E_5 is always unstable.

The behaviour of model has been summarized in Table A.I.2.

A.I.2.3 Model III

The Jacobian matrix for E_1 is: $J_1 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -ab & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_1 are 1, $-ab$ and $-c$, which show that the equilibrium E_1 is a saddle point index 1 and thus, unstable (same as the origin of model I).

The Jacobian matrix for E_2 is: $J_2 = \begin{pmatrix} -1 & -1 & 0 \\ 0 & a(1-b) & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_2 are -1 , $-c$ and $a(1-b)$ which show that the equilibrium E_2 is a node (stable) for $b > 1$ and a saddle point index 1 (unstable) for $b < 1$.

The Jacobian matrix for E_3 is: $J_3 = \begin{pmatrix} -b & -b & 0 \\ a(1-b) & 0 & ab(1-b)/(h(b-1)-1) \\ 0 & 0 & c((d(b-1)/(h(b-1)-1))-1) \end{pmatrix}$

The characteristic equation for J_3 is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where $A = b-c(((d(b-1))/(h(b-1)-1))-1)$, $B = b(a(1-b)+c-((cd(b-1))/(h(b-1)-1)))$, and $C = abc(b-1)((d(b-1)/(h(b-1)-1))-1)$.

The eigenvalues of the matrix J_3 are $\lambda_1 = c((d(b-1)/(h(b-1)-1))-1)$ and $\lambda_{2,3} = (-b \pm \sqrt{b^2 + 4ab(b-1)})/2$ which show that the equilibrium E_3 can be a node, spiral node, saddle point index 1, saddle point index 2 and spiral saddle index 1.

The Jacobian matrix for E_4 is: $J_4 = \begin{pmatrix} (1/(d-h))-1 & (1/(d-h))-1 & 0 \\ a/(d-h) & ah(h(b-1)+d(1-b)-1)/d(d-h) & -ab/d \\ 0 & -c(1+d(b-1)+h(1-b))/b & 0 \end{pmatrix}$

By applying Descartes' rule of signs for the characteristic equation of J_4 and then testing by simulation, it appeared that E_4 might be a node, spiral node, saddle point index 1, spiral saddle index 1 and spiral saddle index 2.

The behaviour of model has been summarized in Table A.I.3.

Table A.I.3. The behaviour of model III for constant value of $a = 1/6$ and $c = 1/30$, and different values of d (varied between 0.01 and 20) and h (varied between 0.01 and 10).

Area	Parameter values		E_2	E_3	E_4	Persistent components
1	$b > 1$		N	SPI_1	N	x
2			N	SPI_1	SN	x
3			N	SPI_1	SPI_1	x
4			N	SPI_2	SPI_1	x
5			N	SPI_2	SSI_1	x
6	$4a/(1+4a) < b < 1$	$d < h + (1/(1-b))$	SPI_1	N	SPI_1	x-y
7		$d > h + (1/(1-b))$	SPI_1	SPI_1	SN	x-y-z
8			SPI_1	SPI_1	N	x-y-z
9			SPI_1	SPI_1	SSI_2	x-y-z limit cycle
10	$b < 4a/(1+4a)$	$d < h + (1/(1-b))$	SPI_1	SN	SPI_1	x-y
11		$d > h + (1/(1-b))$	SPI_1	SSI_1	SN	x-y-z
12			SPI_1	SSI_1	N	x-y-z
13			SPI_1	SSI_1	SSI_2	x-y-z limit cycle

N = node, SN = spiral node, SP = saddle point, SS = spiral saddle, I_1 = index 1 (one positive eigenvalue), I_2 = index 2 (two positive eigenvalues).

A.I.2.4 Model IV

The Jacobian matrix for E_1 is: $J_1 = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -ab & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_1 are 1, -ab and -c, which show that the equilibrium E_1 is a saddle point index 1 and thus, unstable (same as the origin of model I).

The Jacobian matrix for E_2 is: $J_2 = \begin{pmatrix} -1 & -1/(f+1) & 0 \\ 0 & a(-b+1/(f+1)) & 0 \\ 0 & 0 & -c \end{pmatrix}$

The eigenvalues of the matrix J_2 are -1, -c and $a(-b+1/(f+1))$ which show that the equilibrium E_2 is a node (stable) for $f > (1/b)-1$ and a saddle point index 1 (unstable) for $f < (1/b)-1$.

The Jacobian matrix for E_3 is:

$$J_3 = \begin{pmatrix} b(f+1+2/(bf-1)) & -b & 0 \\ -a(b+bf-1) & 0 & a b (b+bf-1)/((bf-1)^2-h(b+bf-1)) \\ 0 & 0 & c(-1-d(b+bf-1)/((bf-1)^2-h(b+bf-1))) \end{pmatrix}$$

By applying Descartes' rule of signs for the characteristic equation and then testing by simulation, it was revealed that E_3 could be a node, spiral node, saddle point index 1, saddle point index 2, spiral saddle index 1, spiral saddle index 2 and spiral repellor for different parameter values.

The Jacobian matrix for E_4 is:

$$J_4 = \begin{pmatrix} 1-2n_1-1/(d-h)(fn_1+1)^2 & -n_1/(fn_1+1) & 0 \\ a/(d-h)(fn_1+1)^2 & -ah(b-n_1+bf n_1)/d(1+fn_1) & -ab/d \\ 0 & -c(d-h)(b-n_1+bf n_1)/b(1+fn_1) & 0 \end{pmatrix}$$

By applying Descartes' rule of signs for the characteristic equation and then testing by simulation, it was revealed that E_4 could be a node, spiral node, saddle point index 1, saddle point index 2 and spiral saddle index 2 for different parameter values.

The Jacobian matrix for E_5 is:

$$J_5 = \begin{pmatrix} 1-2n_2-1/(d-h)(fn_2+1)^2 & -n_2/(fn_2+1) & 0 \\ a/(d-h)(fn_2+1)^2 & -ah(b-n_2+bf n_2)/d(1+fn_2) & -ab/d \\ 0 & -c(d-h)(b-n_2+bf n_2)/b(1+fn_2) & 0 \end{pmatrix}$$

By applying Descartes' rule of signs for the characteristic equation and then testing by simulation, it was revealed that E_5 could be a spiral node, saddle point index 1, saddle point index 2 and spiral saddle index 2 for different parameter values.

