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Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes

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Abstract

The availability of alternative prey is considered to be an important factor for the conservation of predators in agro-ecosystems. However, only a limited number of studies have investigated the effect of prey availability in non-crop habitats on predator impact. We studied the potential of the generalist predator *Coccinella septempunctata* to control pest aphids in wheat fields in landscapes with varying levels of prey in non-crop habitats using a spatially explicit simulation model. Simulations indicate that *C. septempunctata* reproduction and the associated control of pest aphids is affected by both the availability of non-pest aphids in non-crop habitats and the infestation date of pest aphids in wheat fields. When the infestation of wheat by pest aphids takes place early in the season, prey availability of pest aphids alone is sufficient to allow *C. septempunctata* to attain its maximal reproduction. However, when the infestation by pest aphids is somewhat delayed, *C. septempunctata* becomes increasingly dependent on aphids in non-crop habitats. Scarcity of prey may prevent *C. septempunctata* from reproducing or initiate long distance migration. Therefore, prey availability in non-crop habitats may play a significant part in the conservation of ladybeetles and the related biological control in agro-ecosystems.

Keywords: Biological control; Conservation; Aphid; Ladybeetle; Alternative prey; Modelling

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1. Introduction

There is increasing interest for ecologically based agricultural production systems with reduced pesticide inputs. Conservation biological control is an approach that can contribute to the realisation of such production systems by increasing the levels of biocontrol provided by natural enemies. Conservation biological control entails the manipulation of the environment to enhance the effectiveness of natural enemies of arthropod pests. This can be achieved by the provision of alternative food sources (e.g. flowers providing nectar), alternative prey or hosts, improved microclimate and hibernation habitats (Landis et al., 2000). Conservation biological control thus comprises a broad spectrum of habitat management methods that improve the availability of resources required by natural enemies.

Conservation biological control has recently received a great deal of attention (see for review: Barbosa, 1998; Picket and Bugg, 1998; Landis et al., 2000). The fast majority of these studies adopt an empirical approach. This is necessary because of the frequent case-specific nature of the interactions between natural enemies, insect pests and the environment.

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However, the use of a solely empirical approach holds the danger that experiments are primarily based on intuition and lack a theoretical framework (Gurr et al., 1998). Therefore, the integration of both empirical and theoretical approaches is advantageous. Mathematical models offer the possibility to unravel and study the processes underlying habitat management strategies and generate hypotheses that can be tested in empirical studies. Ultimately, models may be used to evaluate and identify promising habitat management strategies.

The augmentation of prey availability in non-crop habitats is one of the habitat management strategies that may preserve predators in agricultural landscapes and increase their effectiveness. Increased levels of prey may be achieved by a careful selection of plant species in non-crop habitats or cover crops that support aphid species that do not interfere with the crop (Bugg et al., 1987; Kozar et al., 1994; Wyss, 1996; Goller et al., 1997). Unfortunately, this habitat management strategy received relatively little attention, possibly because of the complexity of population and dispersal dynamics of predators, and pest and non-pest insect species. In this paper we will explore the potential of ladybeetles to control pest aphid infestations in landscapes with varying levels of prey availability in non-crop habitats, using a simulation model.

Ladybeetles are an important group of aphid predators in agricultural crops (Hodek and Honek, 1996). Hibernation takes place in non-crop habitats, such as hedgerows, forest edges, grass tussocks and debris (Honěk, 1989; Hodek et al., 1993). In early spring, emerged ladybeetles depend on prey in hibernation areas when aphid densities in the fields are still low (Banks, 1955; Altieri and Whitcomb, 1979; Honěk, 1989). Since the level of food supply affects the fecundity (Ferran et al., 1984; Dixon and Guo, 1993; Xia et al., 1999) and migration behaviour of ladybeetles (Hodek et al., 1993) the availability of aphids in non-crop landscape elements is likely to impact the numbers and distribution of ladybeetles and the associated biocontrol.

We developed a spatially explicit simulation model for the population interactions between aphids and the sevenspotted ladybeetle *Coccinella septempunctata* at the landscape level. A spatial explicit approach has been adopted to account for the different dispersal abilities of the larval and adult stages of *C. septempunctata*. The model applies to a landscape that consists of crop and non-crop landscape elements that support populations of pest and non-pest aphid species, respectively. Compared to other population models for insects that incorporate spatial processes (Banks et al., 1988; Corbett and Plant, 1993; Brewster et al., 1997; Grunbaum, 1998; Legaspi et al., 1998; Winder et al., 2001), our model contains in general a more detailed description of phenology, reproduction, dispersal, population and predation dynamics. This results in biologically realistic simulations of the processes underlying aphid control and enables a credible evaluation of the pest suppressiveness of landscapes for the aphid-*C. septempunctata*system.

Aim of the study is to investigate the effect of the availability of prey in non-crop landscape elements during the start of the growing season on the potential of *C. septempunctata* to control pest aphids that infest adjacent fields. The outcome of this study may indicate whether habitat management strategies that aim at an increased availability of prey in hibernation habitats of predators hold potential to enhance predatory impact in agricultural landscapes.

2. Model description

The model is developed in the GIS software package PcRaster (Wesseling et al., 1996). It applies to a landscape of 400 m × 400 m which is built up from cells, each measuring 10 m × 10 m. Calculations on population dynamics of *C. septempunctata* and aphids are performed for each individual cell. Dispersal drives relocation of individuals between cells. The time step of the model is 1 h to simulate the rapid dispersal dynamics of Coccinellidae (Ives et al., 1993; Minoretti and Weisser, 2000; Van der Werf et al., 2000). Since dispersal by *C. septempunctata* occurs predominantly at high temperatures during daytime (Honěk, 1985), flight activity and predation on aphids is only simulated during 10 activity hours per day. Many processes that are incorporated in the model, such as insect development, mortality and searching behaviour, are affected by temperature. As the study of day-to-day variability of these processes is not the objective of the current model, constant temperatures ranging from 15 to 35 °C are used. All simulations are conducted for 20 °C except when otherwise indicated.

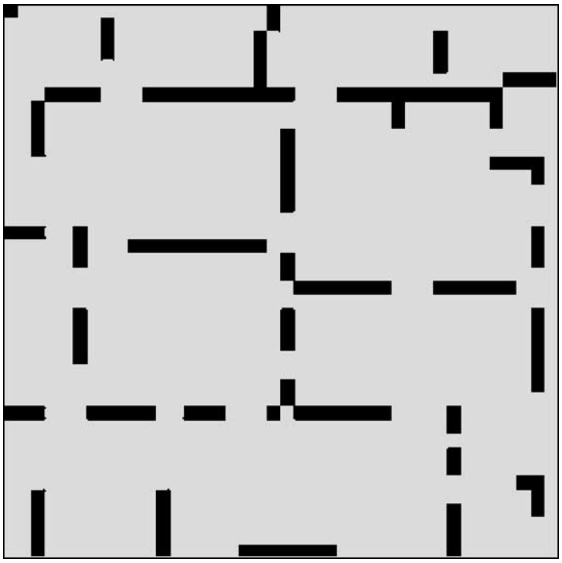

Fig. 1. Landscape map used for simulations. The landscape (400 m × 400 m) is built up from 10 m × 10 m cells consisting of wheat crops (white) and field margins (black).

2.1. Landscape

The landscape consists of wheat crops and field margins (Fig. 1). *C. septempunctata* has different searching areas in wheat and field margins. The different searching areas of *C. septempunctata* in wheat and field margins are accounted for by a "search area index" (SAI; $m^2\,m^{-2}$) of the landscape element. SAI is defined as the leaf area searched for aphids by *C. septempunctata* per unit of ground area. In wheat *C. Septempunctata* is assumed to have a searching profile that is restricted to the upper part of the wheat plants (0.6 m^2 leaf area m^{-2} ground surface) where the majority of aphids can be found. In field margins *C. Septempunctata* has a similar searching profile, but the search area has been set to 1 m^2 leaf area m^{-2} ground surface because of the more heterogeneous vegetation structure. It is assumed that the SAI is constant during the simulation.

2.2. Aphid population dynamics

Two aphid species are simulated: a non-pest aphid species that is only present in field margins and a pest species that only infests wheat crops. *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* represent the latter aphid group in Western Europe. The population dynamics of both aphid species during the growing season is described by the logistic growth equation (Eq. (1)).

$$\mathrm{RA} = \mathrm{rgr}(t) \times A\left(1 - \frac{A}{K}\right) - P \qquad (1)$$

where RA is the growth rate of the aphid population (aphids m^{-2} ground area per day), rgr(t) is the relative growth rate as function of time (per day), A is the density of aphids (aphids m^{-2} ground area), K is the carrying capacity (aphids m^{-2} ground area) and P is the rate at which aphids are removed by *C. septempunctata* (aphids m^{-2} ground area per day). The aphid species of the field margins is assumed to become active in early spring (Julian date 60). The population dynamics of the non-pest aphid species is characterised by a slow population increase with a relative growth rate of 0.1 per day because of the low temperatures early in the season (Michels and Behle, 1989; Girma et al., 1990). The carrying capacity of field margins is set to 2500 aphids m^{-2} ground area. Aphids that infest wheat are assumed to colonise wheat crops somewhere in late spring between Julian dates 120 and 150. After colonisation, the wheat aphid population is assumed to grow with a relative growth rate of 0.25 per day (Michels and Behle, 1989; Girma et al., 1990; Rossing et al., 1994). The carrying capacity of wheat is set to 5000 aphids m^{-2} (Sunderland and Vickerman, 1980). No aphid dispersal is accounted for in the model after the initial colonisation of the wheat crops.

The population dynamics of aphids in wheat are affected by plant quality. Wheat is a suitable host for aphids during the start of the growing season, but later in the growing season it becomes less suitable for aphid development. Initially, as long as the plants are suitable hosts for aphids, the aphid population grows exponentially with a constant relative growth rate of 0.25 per day. From early June onwards (Julian date 161), aphid development is described using a relative growth rate that decreases linearly with time, indicating a deterioration of plant quality for aphid development with time (Fig. 2; Way, 1967; Rossing et al., 1994; Williams et al., 1999). This description is representative for the development of *Sitobion avenae* in winter wheat in Western Europe (Rossing et al., 1994). Field margins are assumed to support non-pest aphid populations during the entire growing season

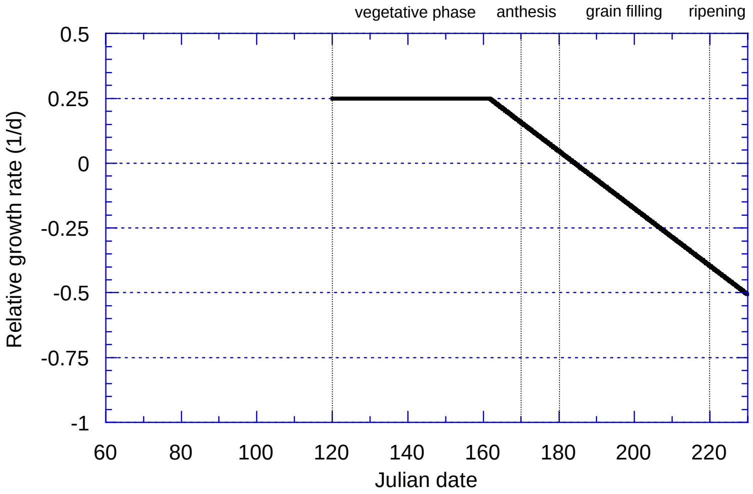

Fig. 2. Development of the relative growth rate of pest aphids in wheat. The developmental stages of wheat are indicated in the heading.

because the assemblage of grasses, herbs and shrubs permits the maintenance of different aphid species that colonise the vegetation during subsequent periods.

2.3. *C. septempunctata* population dynamics

The life cycle of *C. septempunctata* includes an egg stage, four larval stages, a pupal stage and an adult stage. Each stage has specific developmental rates and mortality rates (Xia et al., 1999). Development is simulated by shifting a fraction of the population from one stage to the following stage according to the developmental rate of each stage. The development rate of each stage equals the reciprocal of the developmental time (e.g. when the egg stage has a developmental time of 10 days the developmental rate of the egg stage is 0.10 per day). Mortality is accounted for by incorporation of relative mortality rates for each stage. The values for the developmental rates and relative mortality rates for the egg, the four larval stages, the pupal stage and the adult stage are specified in Table 1.

Adult *C. septempunctata* hibernate in field margins and not in wheat crops (Honěk, 1989). Hibernated *C. septempunctata* are further assumed to emerge in midspring (Julian date 120) after which they remain 30 days in the field margins feeding on non-pest aphids. Thirty days after emergence (Julian date 150) *C. septempunctata* adults become more active and start to disperse. After a dispersal phase the hibernated female adults of *C. septempunctata* are assumed to deposit eggs in early summer (Julian date 175; Honěk, 1989). The sex ratio of *C. septempunctata* is set to 0.5 (Table 1).

The fecundity of *C. septempunctata* females is determined by the aphid consumption between emergence (Julian date 120) and reproduction (Julian date 175). Aphid species in field margins and wheat are assumed to have the same nutritional value. *C. septempunctata* females have a minimum requirement of aphids to enable egg deposition (Honěk, 1978; Xia et al., 1999). This threshold value for reproduction has been set to 500 aphids during the 55 days between emergence and reproduction (Fig. 3). The consumption dependent reproduction is calculated at the population level, i.e. all individual ladybeetles in the landscape are assumed to have a similar reproduction. The mean number of aphids that has been consumed beyond the threshold value is converted to eggs by an egg to aphid conversion factor of 0.4 eggs per aphid. Egg deposition can never exceed the maximum value of 300 eggs per female (Xia et al., 1999).

2.4. *C. septempunctata* predation dynamics

Larval and adult *C. septempunctata* feed on aphids. The predation dynamics of *C. septempunctata* are described using a Holling type 2 functional response (Eq. (2)).

$$\mathrm{PR} = \frac{\mathrm{sr} \times (A/\mathrm{SAI})}{1 + \mathrm{sr} \times \mathrm{ht} \times (A/\mathrm{SAI})} \qquad (2)$$

Table 1
Overview of parameters for *Coccinella septempunctata*

Parameter	Value	Egg	L1	L2	L3	L4	Pupa	Adult	Unit	Reference
Emergence date	120								Julian day	Honěk (1989)
Dispersal date	150								Julian day	Honěk (1989)
Reproduction date	175								Julian day	Honěk (1989)
Developmental rate[a]		0.172	0.217	0.313	0.222	0.135	0.099		Per day	Xia et al. (1999)
Relative mortality rate[a]		0.017	0.060	0.032	0.022	0.020	0.020	0.027	Per day	Xia et al. (1999)
Search rate[b]			39.1	35.8	42.8	100.2		139.5	cm^2 per day	Xia et al. (2003)
Handling time[a]			0.0323	0.0208	0.0093	0.0056		0.0049	Per day	Xia et al. (2003)
Reproduction threshold	500								–	Derived from Xia et al. (1999)
Egg-aphid conversion	0.4								–	Derived from Xia et al. (1999)
Maximal reproduction	300								–	Xia et al. (1999)
Residence coefficient	0.002								Day	Derived from Van der Werf et al. (2000)
Slope of dispersal kernel	0.31								m^{-1}	Derived from Van der Werf et al. (2000)

[a] Parameter values for 20 °C.
[b] Search rates determined under ambient conditions in the field.

where PR is the per capita predation rate (aphids per *C. septempunctata* per day), sr is the search rate (m^2 leaf area per day), A/SAI is the aphid density in the searching area of *C. septempunctata* (aphids m^{-2} leaf area) and ht is the handling time (day). Each carnivorous stage of *C. septempunctata* has a specific search rate and handling time (Table 1). Handing times were determined in the laboratory at 20 °C, whereas search rates were determined under ambient conditions in the field (Xia et al., 2003). These parameter values were used in all simulations except when otherwise indicated.

2.5. *C. septempunctata departure dynamics*

Adults of *C. septempunctata* can disperse by flight. The larvae can walk but are assumed to remain in the 10 m × 10 m cell where the eggs are deposited.

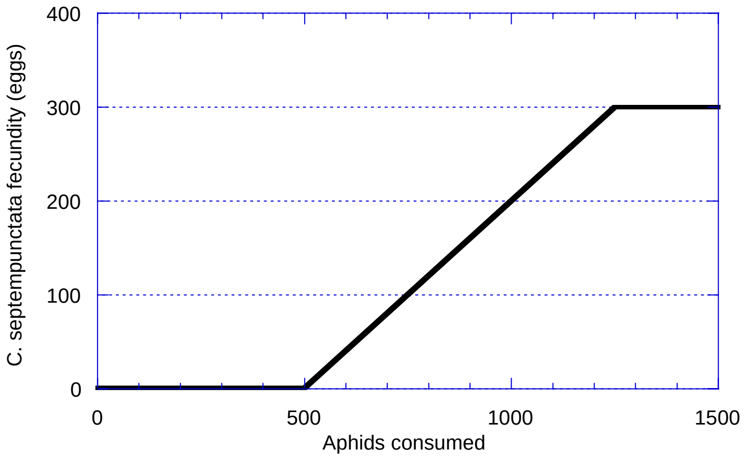

Fig. 3. Relation between the number of aphids consumed between emergence and reproduction and the number of eggs deposited by *Coccinella septempunctata*.

The model only incorporates movements over short distances, which is associated with search for prey. The dispersal dynamics of *C. septempunctata* adults can be characterised by the departure dynamics, i.e. the number of adults that leave each cell per unit of time, in combination with the dispersal kernel of the dispersing adults (Brewster and Allen, 1997).

The departure dynamics of *C. septempunctata* adults are characterised by a linear positive relationship between *C. septempunctata* residence times and aphid densities in their searching area (Ives et al., 1993; Van der Werf et al., 2000; Minoretti and Weisser, 2000). Therefore, residence times of *C. septempunctata* adults are assumed to be proportional to the aphid density that is present in their searching area (Eq. (3)).

$$\mathrm{RT} = \mathrm{rc} \times \frac{A}{\mathrm{SAI}} \tag{3}$$

where RT is the mean residence time (day), rc is the residence coefficient (day (aphids m^{-2} leaf area)$^{-1}$), which is a scaling factor, A is the aphid density (aphids m^{-2} ground area) and SAI is the search area index (m^2 leaf area m^{-2} ground area) of the landscape element. The residence coefficient of *C. septempunctata* is set to 0.002, which corresponds with observations of Ives et al. (1993) and Van der Werf et al. (2000) (Table 1). The relative departure rate of *C. septempunctata* adults is calculated as the reciprocal of the residence time.

2.6. *C. septempunctata dispersal dynamics*

C. septempunctata adults that disperse are redistributed to all directions in the surrounding landscape. The dispersal kernel is rotationally symmetric and is characterised by a negative exponential decline along a transect extending from the origin of dispersal (Eq. (4)).

$$C = \mathrm{e}^{-bx} \tag{4}$$

where C is the density of *C. septempunctata* (*C. septempunctata* m^{-2} ground area) settling at distance x from the source (m), and b is the slope of the decline of *C. septempunctata* density with distance (m^{-1}). The slopes of the dispersal kernels (b) of *C. septempunctata* were estimated by fitting Eq. (4) to measured distance distribution data of *C. septempunctata* in alfalfa fields (Van der Werf et al., 2000) using non-linear regression in Genstat. The negative exponential model gave a good description of measured *C. septempunctata* distance distribution data with r^2 values exceeding 0.95 for 3 repetitions, resulting in an overall estimate of b of $0.31 \pm 0.045\,\mathrm{m}^{-1}$ (mean ± S.E.M.). Dispersal is assumed to take place from the centre of each $10\,\mathrm{m} \times 10\,\mathrm{m}$ cell. Because a fraction of *C. septempunctata* adults only move for a short distance, a part of the dispersing adults lands in the cell from which they took off. Individuals that would be distributed outside the map area are redistributed within the map area by proportionally increasing the numbers that are directly distributed within the map. As a result, there is mass conservation of individuals in relation to dispersal.

3. Scenario studies

The model is used to study the control of aphids by *C. septempunctata* in an agricultural landscape that consists of 10% field margins and 90% wheat crops (Fig. 1). Initial densities of non-pest aphids in field margins are 0, 1, 2, 5 or 10 aphids m^{-2} reflecting non-crop habitats with increasing prey availability. Infestations of wheat aphids result in a homogeneous density of 1 wheat aphid m^{-2} in wheat crops. The date of the colonisation of wheat by wheat aphids varies between Julian dates 120–150. *C. septempunctata* is initially present in field margins only at densities of 10 *C. septempunctata* adults m^{-2}, which is suggested as the upper limit for hibernating adults (Honěk, 1989). Simulations start when the aphids in field margins emerge in early March (Julian date 60) and are terminated when the wheat crop is harvested on Julian date 230. Therefore, the total period of simulation takes up 170 days.

3.1. *Sensitivity analysis*

Sensitivity analyses were conducted to study the influence of model parameters that are uncertain or highly variable under field conditions. A first analysis focussed on the sensitivity of model output for changes in (1) the carrying capacity of non-pest aphids in field margins, (2) the relative growth rate of non-pest aphids in field margins, (3) the carrying capacity of wheat aphids, (4) the relative growth rate of wheat aphids, (5) the egg to aphid conversion factor, (6) the reproduction threshold and (7) the slope of the dispersal kernel of adult *C. septempunctata*. The sensitivity analysis was conducted for a landscape with an initial density of 5 aphids m^{-2} in field margins and which was infested by wheat aphids at Julian date 133. This scenario results in a reproduction of *C. septempunctata* that is approximately half of the maximum reproduction level that is realised in very aphid-rich landscapes. Effects of deviations of 10% of the parameter values on reproduction of *C. septempunctata* and the aphid load in wheat fields during the growing season were studied.

A second analysis focussed on effects of deviations in temperature from the default temperature of 20 °C on the *per capita* egg production of *C. septempunctata* and the aphid load in wheat. The *per capita* egg production of *C. septempunctata* was calculated as the number of eggs deposited at the reproduction day divided by the initial number of hibernating ladybeetles. Developmental rates, relative mortality rates, search rates and handing times of *C. septempunctata* determined at 15, 20, 25, 30 and 35 °C were used to characterise their behaviour at these temperatures (Table 2). Parameter values at intermediate temperatures were derived by linear interpolation between the parameter values at the two nearest temperatures. All parameters, including the search rates, were derived from experiments under controlled conditions in the laboratory (Xia et al., 1999, 2003). The initial density of aphids in field margins was set to 5 aphids m^{-2} and the infestation date of wheat aphids was Julian date 133.

4. Results

A density of 10 hibernating *C. septempunctata* m^{-2} field margin results in an initial population of 160,000 adults, which corresponds with a mean density of 1 adult m^{-2} over the whole 400 m × 400 m landscape. This initial population leads to a peak density of approximately 21 *C. septempunctata* m^{-2} when the maximal reproduction of 300 eggs per female is attained (Fig. 4A). Initial densities of non-pest aphids in field margins of 0, 1, 2, 5 or 10 aphids m^{-2} resulted in increasing levels of prey availability at the emergence date of *C. septempunctata* at Julian date 120 (Fig. 4B). The densities of aphids in field margins were 0, 340, 600, 1100 and 1530 aphids m^{-2}, respectively. The population build up of the pest aphid population in absence of predation in wheat is presented in Fig. 4C. An early infestation of wheat fields by wheat aphids enables a rapid population build up, up to densities close to carrying capacity, because of the prolonged period that wheat is a favourable host for aphids (Fig. 2). When the wheat infestation is delayed, the period that wheat is a favourable host for aphids becomes shorter and, as a consequence, peak aphid densities become dramatically lower (Fig. 4C). When wheat infestations take place at Julian dates 120, 130, 140 and 150, peak densities of wheat aphids are 4950, 4470, 2050 and 280 aphids m^{-2}, respectively. Infestations by wheat aphids at these dates result in levels of prey availability of 1270, 410, 12 and 1 aphid m^{-2} at the time *C. septempunctata* starts to invade the wheat fields at Julian date 150.

Both the density of non-pest aphids in field margins and the date at which wheat aphids infest the fields affect reproduction of *C. septempunctata* (Fig. 5). When the infestation by wheat aphids take place early, e.g. at Julian date 120, prey availability in wheat is sufficient to allow *C. septempunctata* to reach maximal reproduction, even when aphids in field margins are absent. However, when the infestation by wheat aphids is delayed, *C. septempunctata* becomes increasingly dependent on aphids in field margins. For instance, when the wheat infestation takes place at Julian date 130, *C. septempunctata* reproduction in absence of prey in field margins is limited to 125 eggs per female, whereas at the highest level of prey availability in field margins *C. septempunctata* reproduction still reaches 265 eggs per female. Eventually, when the infestation of wheat aphids takes place at an extremely late moment, e.g. at Julian date 145, scarcity of prey prevents *C. septempunctata* from reproducing, even at the highest initial aphid level of 10 aphids m^{-2} field margin. Thus, high levels of prey in non-crop habitats favour *C. septempunctata* reproduction, but availability of wheat aphids is indispensable.

The timing of wheat infestations has a strong impact on the population dynamics of wheat aphids and the level of pest suppression provided by ladybeetles. Early infestations of wheat aphids at Julian date 120 lead to a high aphid load of 2.9×10^6 aphid-days m^{-2} wheat in the absence of *C. septempunctata*, whereas late infestations (Julian date 150) lead to an aphid load

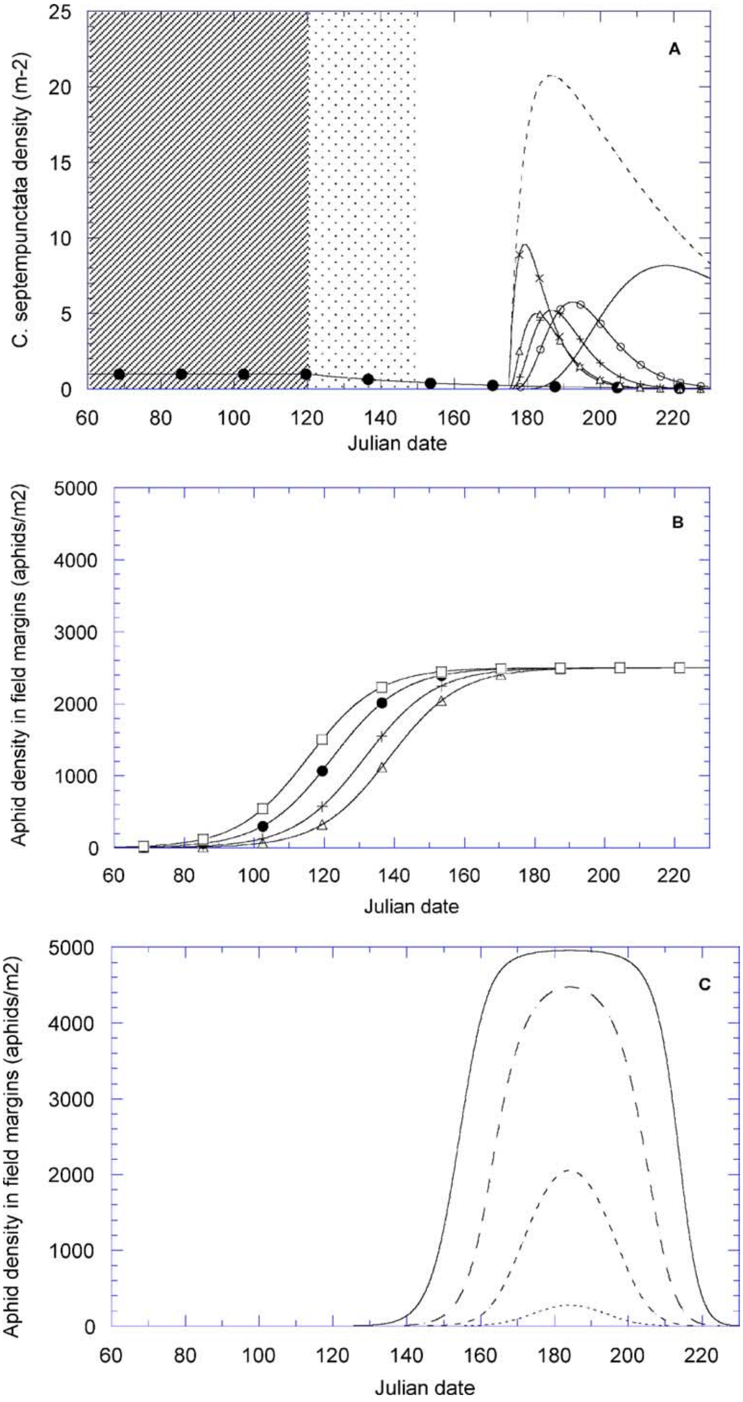

Fig. 4. (A) Population dynamics of carnivorous stages of *Coccinella septempunctata*. The hatched area indicates the hibernation period and the dotted area the pre-dispersal period. Hibernated adults (●), first instars (×), second instars (△), third instars (+), fourth instars (○), adults (—) and population totals (- - -). (B) Population dynamics of non-pest aphids in field margins at initial densities of 1 (△), 2 (+), 5 (●) and 10 (□) aphids m^{-2} ground area in absence of *Coccinella septempunctata*. (C) Population dynamics of pest aphids in wheat at infestation dates 120, 130, 140 and 150 in absence of *Coccinella septempunctata*. Arrows indicate infestation dates.

Table 2
Overview of *Coccinella septempunctata* parameters used for the sensitivity analysis of temperature effects

Stage	*T* (°C)	Egg	L1	L2	L3	L4	Pupa	Adult	Unit	Reference
Developmental rate	15	0.108	0.110	0.133	0.120	0.069	0.061		Per day	Xia et al. (1999)
	20	0.172	0.217	0.313	0.222	0.135	0.099		Per day	Xia et al. (1999)
	25	0.333	0.5	0.476	0.5	0.278	0.175		Per day	Xia et al. (1999)
	30	0.435	0.714	0.833	0.714	0.435	0.278		Per day	Xia et al. (1999)
	35	0.625	0.909	0.909	0.833	0.455	0.263		Per day	Xia et al. (1999)
Relative mortality rate	15	0.045	0.076	0.031	0.012	0.011	0.019	0.032	Per day	Xia et al. (1999)
	20	0.017	0.060	0.032	0.022	0.020	0.020	0.027	Per day	Xia et al. (1999)
	25	0.031	0.080	0.045	0.042	0.032	0.035	0.037	Per day	Xia et al. (1999)
	30	0.085	0.136	0.069	0.071	0.049	0.063	0.052	Per day	Xia et al. (1999)
	35	0.180	0.228	0.105	0.110	0.069	0.104	0.073	Per day	Xia et al. (1999)
Search rate[a]	15		11.7	13.5	19.5	38.4		20.1	cm^2 per day	Xia et al. (2003)
	20		19.8	30.6	47.7	76.5		51.9	cm^2 per day	Xia et al. (2003)
	25		41.1	38.4	63.9	99.6		68.7	cm^2 per day	Xia et al. (2003)
	30		32.4	95.7	97.8	193.2		102.9	cm^2 per day	Xia et al. (2003)
	35		51.9	106.8	109.8	213.9		153.6	cm^2 per day	Xia et al. (2003)
Handling time	15		0.0417	0.0233	0.0127	0.0066		0.0053	Per day	Xia et al. (2003)
	20		0.0323	0.0208	0.0093	0.0056		0.0049	Per day	Xia et al. (2003)
	25		0.0233	0.0143	0.0083	0.0056		0.0049	Per day	Xia et al. (2003)
	30		0.0263	0.0154	0.0099	0.0065		0.0046	Per day	Xia et al. (2003)
	35		0.0217	0.0167	0.0104	0.0068		0.0047	Per day	Xia et al. (2003)

[a] Search rates determined under controlled conditions in the laboratory.

of only 6.9 × 10^4 aphid-days m^{-2} (Fig. 4C). Accordingly, especially for early wheat infestations there is a need for aphid control. When wheat infestations occur in early May (Julian date 125), *C. septempunctata* is able to reduce the aphid load to a level of 52% of the 2.4 × 10^6 aphid-days m^{-2} that would have been on the crop in the absence of predators (Fig. 6A). Initial densities of 0 and 10 non-pest aphids m^{-2} result in similar levels of control because in both cases *C. septempunctata* is able to reach high reproduction

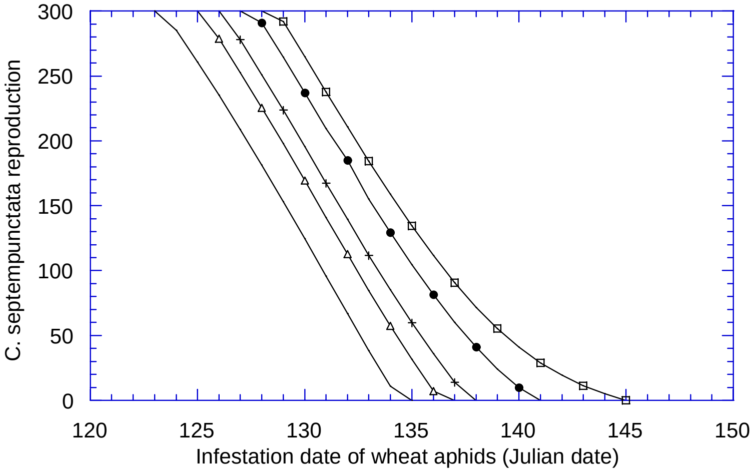

Fig. 5. Reproduction of *Coccinella septempunctata* as function of the infestation date of wheat by pest aphids and five initial densities of non-pest aphids in field margins: 0 (no marker), 1 (△), 2 (+), 5 (●) and 10 (□) aphids m^{-2}.

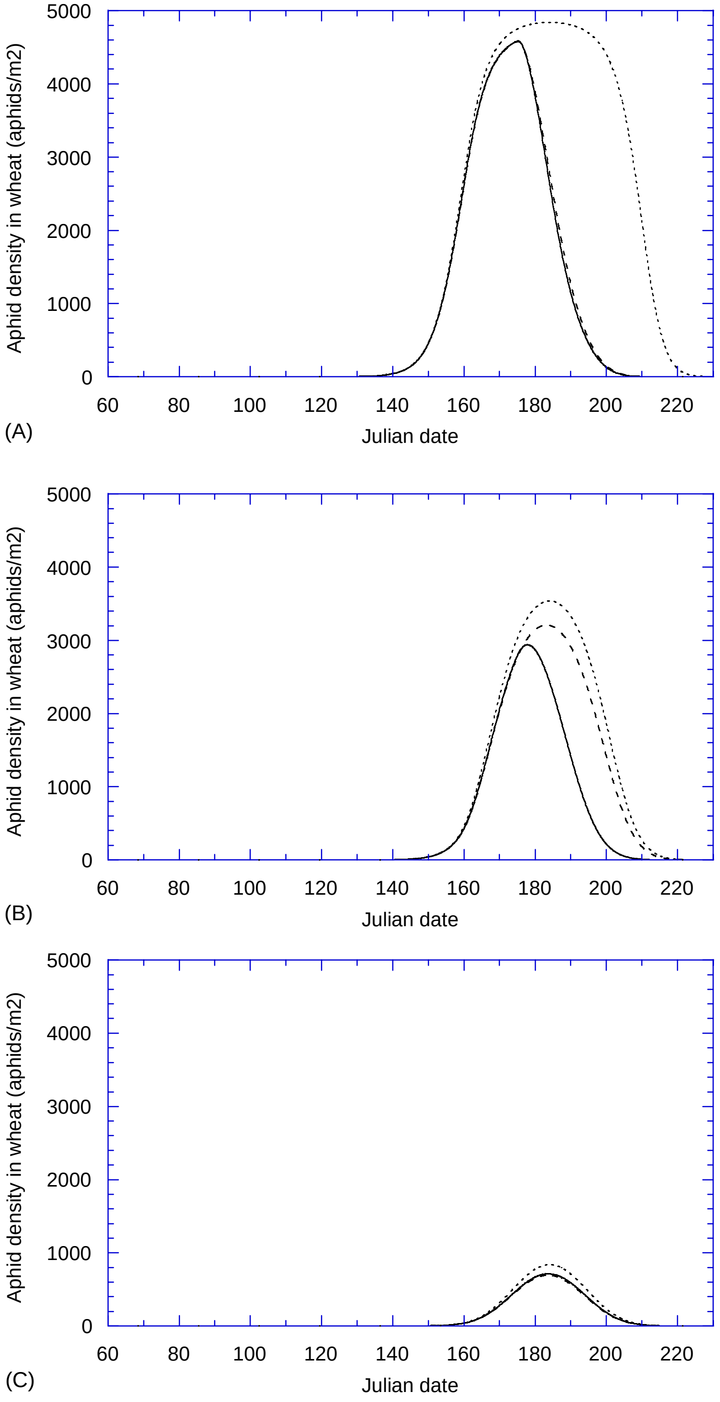

Fig. 6. Density of pest aphids in wheat after infestations at Julian dates 125 (A), 135 (B) and 145 (C). Dotted lines indicate development of pest aphids in wheat in absence of *C. septempunctata*, dashed lines indicate development of pest aphids in the presence of *C. septempunctata* but with no prey in field margins, while solid lines indicate development of pest aphids in presence of *C. septempunctata* and an initial density of 10 non-pest aphids per m^2 field margin.

levels. When wheat infestations occur 10 days later (Julian date 135), the aphid load in the absence of *C. septempunctata* is 1.2×10^6 aphid-days m^{-2} (Fig. 6B), i.e. 50% less than in earlier infestations. *C. septempunctata* is able to reduce this aphid load by a further 40% when an initial density of 10 non-pest aphids m^{-2} is present in field margins. Without alternative prey in the field margins, the aphid load is only reduced by 14%. When no alternative prey is available *C. septempunctata* is not able to reproduce because of food scarcity, whereas in presence of alternative prey, females of *C. septempunctata* lay 135 eggs. Finally, when wheat infestations occur at Julian date 145, the aphid load in absence of *C. septempunctata* is 2.2×10^5 aphid-days m^{-2} (Fig. 6C), i.e. only 8% of the aphid load following early infestation. Presence of *C. septempunctata* reduces the aphid loads by only 17 and 19% for initial densities of 0 and 10 non-pest aphids m^{-2} in field margins, respectively. At this late infestation date, no reproduction of *C. septempunctata* takes place, even at the high level of alternative prey, but even so the aphid load is limited because of the poor quality of wheat for aphid development.

Differences in the infestation date of wheat aphids in landscapes with initial densities of 0 and 10 non-pest aphids m^{-2} in field margins lead to distinct spatial patterns of the aphid load and aphid predation in the landscape (Figs. 7 and 8). When wheat infestations take place early (Julian date 125) the aphid density in wheat is already high when *C. septempunctata* adults start to invade wheat fields from the field margins at the end of May (Fig. 4). Once the wheat aphid populations are suppressed near the non-crop habitats *C. septempunctata* gradually move toward the field centres where wheat aphid densities are higher. Reproduction results in an increased number of predators in cells, which can strongly suppress aphid densities because *C. septempunctata* larvae do not leave the 10 m × 10 m cells. Once *C. septempunctata* larvae develop into adults they are able to leave the cell in search for cells with higher aphid densities. These processes account for the general pattern of suppressed aphid densities and high predation levels near the field margins and peak aphid densities and lower predation levels in the field centres (Figs. 7 and 8: 1A and 1B). When the wheat infestation takes place later (Julian dates 135 and 145) the density of wheat aphids upon arrival of *C. septempunctata* in the fields becomes lower. Since residence times of *C. septempunctata* adults at lower aphid densities become shorter, *C. septempunctata* will become increasingly mobile. This leads to the homogenous patterns of aphid load and predation levels at wheat infestation dates 135 and 145 (Figs. 7 and 8: 2A, 2B, 3A and 3B).

Field margins become increasingly important as foraging habitats of *C. septempunctata* when wheat infestations are delayed. In landscapes without prey in non-crop habitats, aphid predation responds strongly to a delay of wheat infestation from Julian dates 125–135 as a result of reduced reproduction of *C. septempunctata* (Fig. 8: 1A and 2A). In contrast, aphid predation levels in landscapes with initial densities of 10 aphids m^{-2} in non-crop habitats are less sensitive to delayed wheat infestations (Fig. 8: 2B), resulting in a lower aphid load than landscapes without alternative prey (Fig. 7: 2A and 2B). In a situation of a late wheat infestation (Julian date 145) the arrest of *C. septempunctata* in field margins where alternative prey is present results in slightly lower predation levels of aphids in wheat fields than in a situation where no alternative prey is available (Fig. 8: 3A and 3B; Fig. 6C).

4.1. Sensitivity analysis

The first sensitivity analysis is conducted for a landscape with an initial density of 5 aphids m^{-2} field margin and an infestation of wheat aphids at Julian day 133. The default parameterisation resulted in a reproduction of *C. septempunctata* of 156 eggs per female and a wheat aphid load of 8.4×10^5 aphid-days m^{-2} during the growing season. Model output was sensitive to changes in parameter values (Table 3). Reproduction of *C. septempunctata* was most sensitive to changes in the relative growth rate of wheat aphids, followed by the relative growth rate of aphids in field margins, the *C. septempunctata* reproduction threshold and the egg to aphid conversion factor. Reproduction was less sensitive to changes in carrying capacity of aphids in wheat and field margins and the slope of dispersal kernel of *C. septempunctata*. The load of wheat aphids was less sensitive to changes in parameter values than the reproduction of *C. septempunctata*. The greatest sensitivity of aphid load was towards changes in the relative growth rate of wheat aphids, followed by the relative growth rate of aphids in field margins and the carrying capacity of aphids in

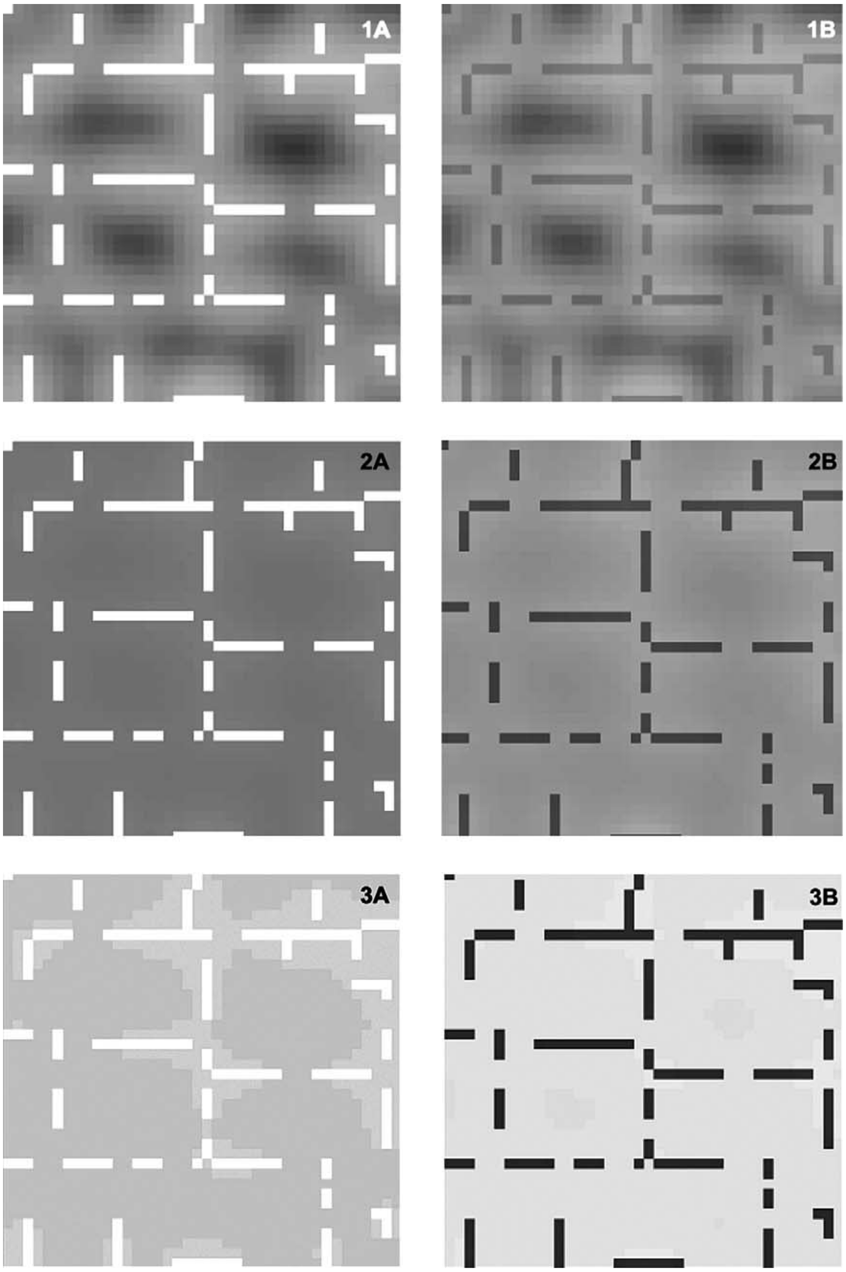

Fig. 7. Spatial distribution of the load of pest and non-pest aphids (aphid-days) during the growing season in landscapes with initial densities of 0 (A) and 10 (B) non-pest aphids m^{-2} in field margins. Infestation dates of pest aphids in wheat are Julian dates 125 (1), 135 (2) and 145 (3).

wheat. Aphid load was not very sensitive for changes in the other parameters.

In the second analysis, we studied the sensitivity of the *per capita* egg production of *C. septempunctata* and aphid load in wheat towards developmental rates, relative mortality rates, search rates and handing times of *C. septempunctata* representative for temperatures ranging from 15 to 35 °C (Table 2). The *per capita*

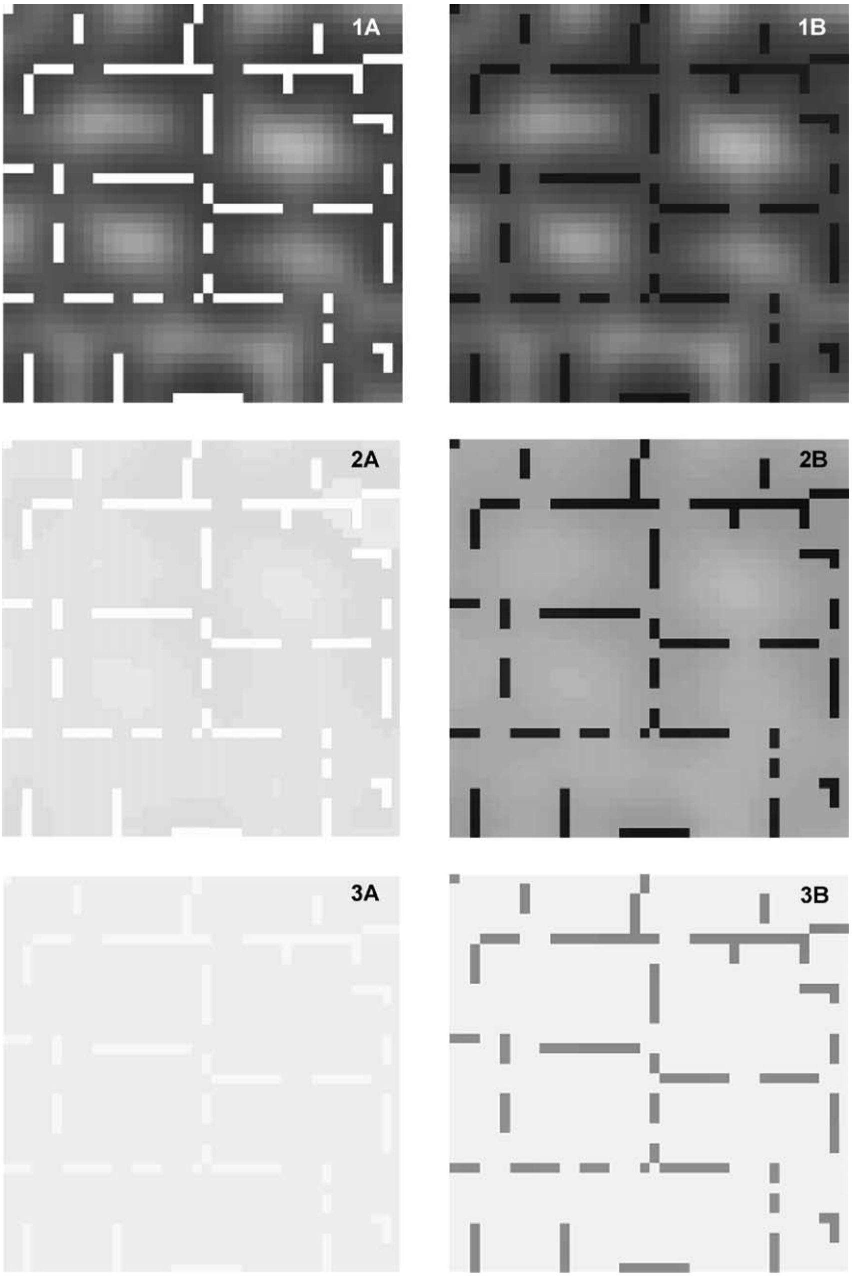

Fig. 8. Spatial distribution of cumulative aphid predation during the growing season in landscapes with initial densities of 0 (A) and 10 (B) non-pest aphids m^{-2} in field margins. Infestation dates of pest aphids in wheat are Julian dates 125 (1), 135 (2) and 145 (3).

egg production of *C. septempunctata* was sensitive for changes in temperature and peaked at 28 °C (Fig. 9). At temperatures between 15 and 20 °C, the low search and handling rates prevented *C. septempunctata* from reaching the aphid consumption threshold needed for reproduction, resulting in a *per capita* egg production equal to zero. At temperatures between 21 and 28 °C, the increasing *per capita* reproduction rate at

Table 3

Sensitivity analysis of a selection of parameters on reproduction of *Coccinella septempunctata* and aphid load in wheat during the growing season (aphid-days m^{-2})

Parameter	Deviation (%)	Deviation in reproduction	Deviation in aphid load
rgr of aphids in field margins	+10	+23.6	−4.5
	−10	−23.7	+5.9
Carrying capacity of field margins	+10	+5.0	−0.9
	−10	−5.3	+1.3
rgr of aphids in wheat	+10	+53.7	+22.4
	−10	−53.4	−32.1
Carrying capacity of wheat	+10	+5.0	+4.4
	−10	−5.6	−5.7
Egg-aphid conversion	+10	+10.0	−2.4
	−10	−10.0	+2.6
Reproduction threshold	+10	−12.8	+3.4
	−10	+12.8	−3.0
Slope of dispersal kernel	+10	+0.2	−0.7
	−10	−0.6	+1.3

higher temperatures, enabled by the increasing search rates and decreasing handling times, exceeded the effect of the decreasing number of hibernated adults that reached the reproduction date, caused by the increasing relative mortality rates. In contrast, at temperatures exceeding 28 °C, the mortality effect surpassed the reproduction effect resulting in a decrease in the *per capita* egg production. The wheat aphid load was not very sensitive to changes in temperature (Fig. 10). At temperatures increasing from 15 to 30 °C, the higher *per capita* egg production and predation activity of *C. septempunctata* resulted in improved pest suppression. At temperatures exceeding 30 °C, the decreasing *per capita* egg production and shorter life span of

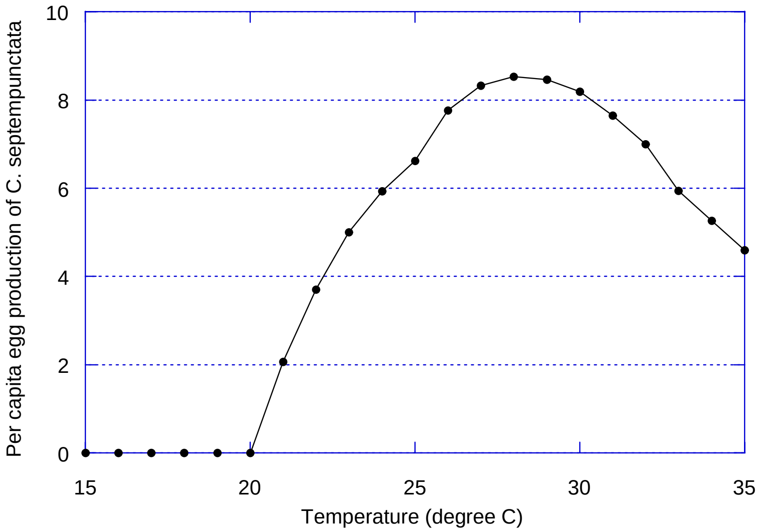

Fig. 9. *Per capita* egg production of *Coccinella septempunctata* simulated with developmental rates, relative mortality rates, search rates and handing times representative for temperatures ranging from 15 to 35 °C (Table 2).

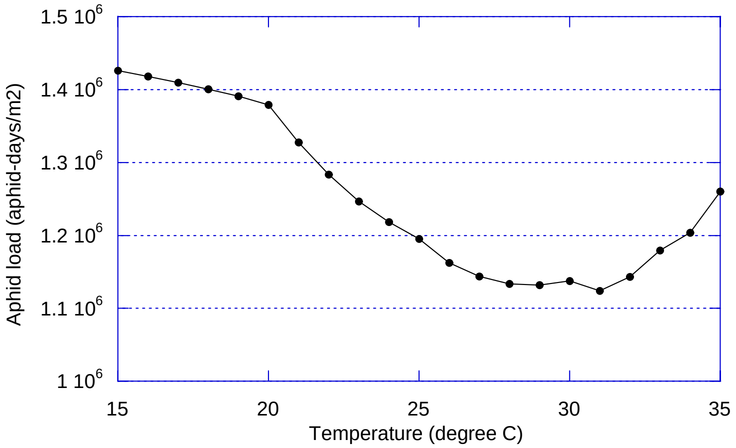

Fig. 10. Aphid load in wheat simulated with developmental rates, relative mortality rates, search rates and handing times of *Coccinella septempunctata* representative for temperatures ranging from 15 to 35 °C (Table 2).

C. septempunctata, reflected in high relative mortality rates, resulted in declining pest suppression.

5. Discussion

The availability of alternative prey is considered to be an important factor for the conservation of predators of pest insects in agro-ecosystems (Landis et al., 2000). However, only a limited number of studies have investigated effects of increased prey availability on biocontrol (Bugg et al., 1987; Kozar et al., 1994; Wyss, 1996; Goller et al., 1997). We simulated the control of a pest aphid species by the generalist predator *C. septempunctata* at varying levels of prey in non-crop habitats in a computer landscape. Because the temporal and spatial dynamics of aphids and ladybeetles in crop and non-crop habitats are extremely complex (Kindlmann and Dixon, 1996), this paper intends to reveal trends of biocontrol in landscapes with varying levels of prey availability rather than to give absolute predictions.

Simulations demonstrated that prey availability in non-crop habitats may play a significant role for the population dynamics of *C. septempunctata* (Fig. 5). Ladybeetle populations in landscapes with low prey availability in non-crop habitats are likely to be more vulnerable to periods of food shortage, e.g. in years when aphid infestation in crops occurs later in the season, than in landscapes with high prey availability. However, Honěk (1978) demonstrated that *C. septempunctata* is able to synchronise its reproductive activity with aphid density levels in the field. This mechanism may cause a delay in *C. septempunctata* reproduction as a response to the late aphid infestations, providing a longer period for *C. septempunctata* to attain a food intake level suitable for egg deposition. Such a trait may prevent a complete block of *C. septempunctata* reproduction induced by late aphid infestations in field situations (Fig. 5). On the other hand, periods of food shortage may trigger long distance dispersal of ladybeetles (Hodek et al., 1993). Possibly, landscapes with low prey availability in non-crop habitats may be subject to increased emigration by ladybeetles during periods of food scarcity. Higher emigration rates and reduced reproduction of ladybeetles in landscapes with low prey availability may result in the depletion of the number of predators and reduced levels of biocontrol.

In simulations, the timing of the infestation of crops by wheat aphids resulted in distinct dynamics of wheat aphids and ladybeetles. Early infestations of crops lead to high densities of wheat aphids and a strong increment in ladybeetle numbers as a result of their high reproduction. Subsequently, the wheat aphid population is suppressed by the large ladybeetle population (Fig. 6A). This scenario is likely to result in high densities of hibernating ladybeetles that may control aphid outbreaks in the following year. In contrast, late infestations of wheat aphids will result in low wheat aphid densities and to a limited ladybeetle reproduction as a result of food scarcity (Fig. 6C). Although the consequences for the control of aphids in the current year are not so important, as the aphid load will stay low anyway, the consequences for aphid control in the following year may be serious because of the low density of hibernating ladybeetles.

The sensitivity analysis indicated that reproduction of *C. septempunctata* and the aphid load in wheat during the growing season were sensitive to changes in the relative growth rates of aphids in wheat as well as non-crop habitats. Both parameters have a strong effect on the number of available prey for *C. septempunctata*. This finding underscores the importance for prey availability on *C. septempunctata* population dynamics and its potential to control aphid outbreaks. Thus, the population dynamics of non-pest aphids in non-crop elements is an interesting field for empirical study.

The strong negative response of *C. septempunctata* reproduction to late infestations by wheat aphids (Fig. 5) suggest that there is an important period at the start of the growing season that may be decisive for the biocontrol provided by predators during the rest of the growing season. This effect is likely to be stronger for specialist predator species that rely on a limited number of prey species than for generalist predators that may feed on a variety of prey species. Since successful biocontrol is more likely to be realised in landscapes where a whole spectrum of generalist and specialist natural enemies are active, prey availability at early stages in the growing season is a factor that needs to be addressed for the realisation of landscapes with enhanced natural enemy impact in crops.

From a theoretical perspective, habitat management focussing at raising levels of alternative prey for predators in non-crop landscape elements seems to hold promise. However, since predators such as ladybeetles act at a landscape scale, such strategies should be implemented at a scale that corresponds with the predator's habitat use. Minimum area requirement for habitat improvement for ladybeetles would be at least in the order of hundreds of meters given their capacity to fly between foraging habitats (Osawa, 2000). Furthermore, this strategy will only be effective when other prerequisites for the preservation of predators are adequate to maintain sufficient large populations of natural enemies to control aphid outbreaks. This puts restrictions on the use of pesticides and minimum area requirements on and the amount of hibernation and refuge habitat. The implementation of effective habitat management strategies is therefore extremely complex, but holds the prospect of sustainable agricultural production systems in an environmentally safe and biologically sound manner.

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