The Effect of the Area and Configuration of Hibernation Sites on the Control of Aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in Agricultural Landscapes: A Simulation Study

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ABSTRACT The lady beetle *Coccinella septempunctata* L. is an important predator of aphids in arable crops, but depends on noncrop landscape elements, such as hedgerows, for hibernation. We studied the effect of the shape, area, and fragmentation of noncrop landscape elements on the control of aphids by *C. septempunctata* using a spatially explicit simulation model. The model is based on a description of the phenology and population dynamics of aphids and *C. septempunctata*, as well as the predation dynamics and dispersal characteristics of *C. septempunctata*. The study compares biocontrol in 12 landscapes consisting of field crops and hedgerows that differ in the shape, proportion (1, 4, 9, and 16%), and fragmentation of the hedgerow elements (hedgerow area divided into 1, 4, or 16 elements) in the landscape. Linear hedgerow elements provided better control than square elements in 3 of the 12 simulated landscapes and resulted in similar levels of control in the other nine landscapes. The total area of hedgerow habitat was the key factor for the control of aphid populations. Landscapes with 9% and 16% noncrop habitat had large enough local populations of *C. septempunctata* to control aphid infestations, whereas landscapes with only 1% or 4% of hibernation area had no potential for improved aphid control. In landscapes with sufficient noncrop habitat, the best control was achieved when small hedgerow elements were evenly distributed over the landscape.

KEY WORDS biological control, landscape ecology, aphid, lady beetle, modeling

NONCROP LANDSCAPE ELEMENTS, such as field margins, hedgerows, and forests may function as refuge habitats for natural enemies of field crop pests. Such habitats provide alternative food sources, hibernation sites, and shelter from environmental extremes, pesticides, or disturbances (Landis et al. 2000). Presence of refuge areas may have a profound effect on the survival of natural enemies and their ability to invade crops that are infested with pest insects. Increased natural enemy populations have been observed near field margins (Kromp and Steinberger 1992, White et al. 1995, Long et al. 1998, Thies and Tscharntke 1999), uncultivated areas (Thomas et al. 1991, 1992; Colunga-Garcia et al. 1997; Thies and Tscharntke 1999), hedgerows (Landis and Haas 1992, Zhou et al. 1994, Marino and Landis 1996), trees (Corbett and Rosenheim 1996) and forests (Landis and Haas 1992, Marino and Landis 1996). The control of pest insect populations by natural enemies may therefore be affected by the area and spatial configuration of noncrop landscape elements.

It is difficult to assess from empirical studies how much of a specific noncrop landscape element is needed for effective biocontrol of predators and what is the optimal spatial configuration of such elements. For such questions, a modeling approach may be advantageous. Improved understanding of the relation between the area and configuration of landscape elements that act as refuge habitats of natural enemies and the suppression of pest insect populations may contribute to the development of more ecologically based agricultural production systems with reduced pesticide inputs.

Aphids are an important group of pests of many agricultural crops in the temperate zone. Crop injury is caused by feeding on the phloem, by the production of honeydew, and by transmission of viruses. Aphids cause serious economic losses. For example, in the United Kingdom the estimated loss as a result of direct feeding alone is in the order of £100 million per year (Tatchell 1989). Lady beetles are known to be an effective group of aphid predators that are able to control aphid populations in agricultural crops, but depend on uncultivated habitats in the landscape for hibernation such as hedgerows, forest edges, and grass tussocks (Van Emden 1965, Honěk 1989, Roach and Thomas 1991, Maredia et al. 1992, Zhou et al. 1994, Colunga-Garcia et al. 1997). Lady beetles are an at-

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Table 1. Overview of *Coccinella septempunctata* phenology, development, and predation parameters

Stage	Value	Egg	L1	L2	L3	L4	Pupa	Adult	Unit	Reference
Emergence date	150								Julian date	Honěk, 1989
Reproduction date	180								Julian date	Honěk, 1989
Fecundity	200								–	Xia et al. 1999a
Residence coefficient	0.002								d	Ives et al. 1993
Developmental rate		0.172	0.217	0.313	0.222	0.135	0.099		d^{-1}	Xia et al. 1999a
Relative mortality rate		0.017	0.076	0.032	0.022	0.020	0.020	0.027	d^{-1}	Xia et al. 1999a
Search rate[a]			39.1	35.8	42.8	100.2		139.5	cm^2/d	Xia et al. 2003
Handling time			0.0323	0.0208	0.0093	0.0056		0.0049	d	Xia et al. 2003

[a] Search rates determined under ambient conditions in the field.

tractive group for modeling the effects of landscape configuration on predatory impact because their behavior and phenology (Hodek and Honěk 1996), bionomics (Xia et al. 1999a), predation dynamics (Xia et al. 2003), and, to a lesser extent, the dispersal dynamics (Van der Werf et al. 2000) are well studied.

We developed a dynamic spatially explicit simulation model for the control of aphids by the aphid predator *Coccinella septempunctata* L. in a diverse landscape. The model includes the phenology, population dynamics, and dispersal characteristics of aphids and *C. septempunctata.* The model applies to a landscape that consists of landscape elements with specific characteristics to support populations of aphid and *C. septempunctata.* Compared with other population models for insects that incorporate spatial processes (Banks et al. 1988, Corbett and Plant 1993, Brewster et al. 1997), our model contains a more detailed description of aphid and *C. septempunctata* phenology, population, and predation dynamics, which results in biologically realistic simulations of the processes underlying of aphid control. This enables a credible evaluation of the pest suppressiveness of landscapes for the aphid–*C. septempunctata* system.

The aim of this study is to investigate the effect of the area and the spatial configuration of landscape elements that function as hibernation areas for *C. septempunctata* on the control of aphids in agricultural landscapes.

Model Description

The model is developed in the GIS software package PcRaster (Wesseling et al. 1996). It applies to a landscape of 400 × 400 m, which is built up from cells, each measuring $10 \times 10\ m^2$. Calculations on the population dynamics of *C. septempunctata* and aphids are performed for each individual cell. Dispersal results in a relocation of individuals between cells. The time step of the model is 1 h to simulate the rapid dispersal dynamics of Coccinellidae (Frazer 1988, Duelli 1990, Ives et al. 1993, Van der Werf et al. 2000). Because most of the dispersal by *C. septempunctata* occurs predominantly at high temperatures during daytime, e.g., from ≈10 a.m. to 8 p.m. in Utah alfalfa (Van der Werf et al. 2000), 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 behavior, are affected by temperature. Because the study of day-to-day variability of these processes is not the objective of the current model, constant temperatures of 15, 20, or 25°C are used. All simulations are conducted for 20°C unless otherwise indicated.

Landscape. The landscape consists of wheat and hedgerows. The latter landscape elements function as hibernation sites for *C. septempunctata.* Wheat and hedgerows have specific characteristics for maintaining aphid populations during the growing season and the searching behavior of *C. septempunctata.* The carrying capacity for aphids (K, aphids/m^2), which limits the capacity for aphid population growth during the growing season, is 5000 aphids/m^2 for both wheat and hedgerows (Sunderland and Vickerman 1980). Because wheat and hedgerows have pronounced differences in leaf area index (LAI) and vegetation structure, the area searched for aphids by *C. septempunctata* differs. The different searching areas of *C. septempunctata* in wheat and hedgerows are accounted for by a "search area index" (SAI, m^2m^{-2}) of the landscape element. Search area index 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 top leaves, stem, and ear, where the majority of the aphids are situated (Frazer 1988, p. 235). The SAI in wheat is assumed to be 0.6. In contrast, in hedgerows the SAI is assumed to be 4 because of the high leaf area index and heterogeneous vegetation structure.

Aphid Population Dynamics. Aphids emerge in early May (Julian date 130, Williams et al. 1999). The population dynamics of aphids during the growing season is described by the logistic growth equation (equation 1).

$$RA = rgr \cdot A \cdot \left(1 - \frac{A}{K}\right) - P \qquad [1]$$

where *RA* is the growth rate of the aphid population (aphids/d), *A* is the density of aphids (aphids/m^2 ground area), *rgr* is the relative growth rate (d^{-1}), *K* is the carrying capacity (aphids/m^2 ground area), and *P* is the rate at which aphids are removed by *C. septempunctata* (aphids/d). The relative growth rate of the aphid population is 0.25 d^{-1}, which is a representative value for many aphid species on a range of crops at 20°C (Girma et al. 1990, Xia et al. 1999b). No aphid

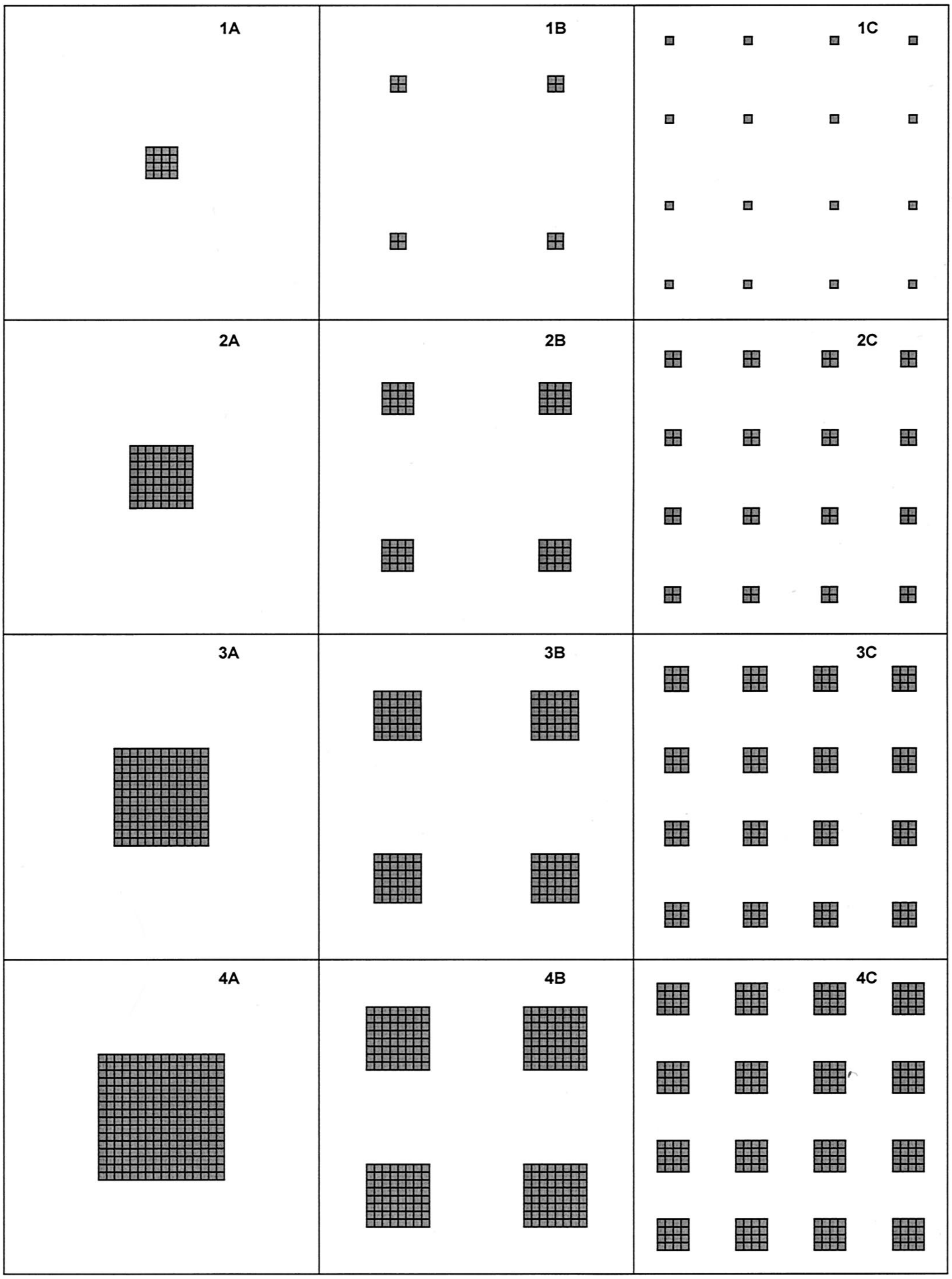

Fig. 1. Twelve landscapes consisting of wheat crops (white area) and hedgerows (gray area) with 1%, 4%, 9%, and 16% of hedgerows (from top to bottom) and increasing level of fragmentation (1, 4, and 16 hedgerow elements, left to right).

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

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		d^{-1}	Xia et al. 1999a
	20	0.172	0.217	0.313	0.222	0.135	0.099		d^{-1}	Xia et al. 1999a
	25	0.333	0.5	0.476	0.5	0.278	0.175		d^{-1}	Xia et al. 1999a
Relative mortality rate	15	0.045	0.076	0.031	0.012	0.011	0.019	0.032	d^{-1}	Xia et al. 1999a
	20	0.017	0.060	0.032	0.022	0.020	0.020	0.027	d^{-1}	Xia et al. 1999a
	25	0.031	0.080	0.045	0.042	0.032	0.035	0.037	d^{-1}	Xia et al. 1999a
Search rate	15		11.7	13.5	19.5	38.4		20.1	cm^2/d	Xia et al. 2003
	20		19.8	30.6	47.7	76.5		51.9	cm^2/d	Xia et al. 2003
	25		41.1	38.4	63.9	99.6		68.7	cm^2/d	Xia et al. 2003
Handling time	15		0.0417	0.0233	0.0127	0.0066		0.0053	d^{-1}	Xia et al. 2003
	20		0.0323	0.0208	0.0093	0.0056		0.0049	d^{-1}	Xia et al. 2003
	25		0.0233	0.0143	0.0083	0.0056		0.0049	d^{-1}	Xia et al. 2003

dispersal is accounted for in the model after the initial colonization of the wheat crops.

***Coccinella 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. 1999a). Development is simulated using the mass proportionality transition. This implies that densities in a stage are shifted to the following stage according to the developmental rate of each stage. The mean development time of each stage equals the reciprocal of the developmental rate (e.g., when the egg stage has a developmental rate of 0.1 d^{-1} the mean developmental time of the egg stage is 10 d). Mortality is accounted for by incorporation of relative mortality rates for each stage. The developmental rates and relative mortality rates for the egg, the four larval stages, the pupal stage, and the adult stage are given in Table 1.

Adult *C. septempunctata* hibernate in hedgerows and not in wheat crops (Honěk 1989). Hibernated *C. septempunctata* emerge somewhat later in spring than aphids (Julian date 150, Honěk 1989) and have a single generation per year in Western Europe. After a dispersal phase the hibernated female adults of *C. septempunctata* are assumed to deposit 200 eggs (Xia et al. 1999a) at the end of June (Julian date 180, Honěk 1989). The sex ratio of *C. septempunctata* is set to 0.5.

A disadvantage of the mass proportionality transition for modeling population development is that the degree of variance produced exceeds the variance that is observed in field situations. However, the assumption of egg deposition at a single day, which produces less variance than observed in field situations, compensates for the excess of variance produced by the mass proportionality transition. The resulting population development is plausible for field situations.

***Coccinella septempunctata* Predation Dynamics.** *Coccinella septempunctata* feed on aphids during the larval and the adult stages. The predation dynamics of *C. septempunctata* are described using a Holling type 2 functional response (equation 2).

$$PR = \frac{sr \cdot (A/SAI)}{1 + sr \cdot ht \cdot (A/SAI)} \qquad [2]$$

where *PR* is the *per capita* predation rate (aphids/*C. septempunctata* /d), *sr* is the search rate (m^2 leaf area/d), *A/SAI* is the aphid density in the searching area of *C. septempunctata* (aphids/m^2 leaf area), and

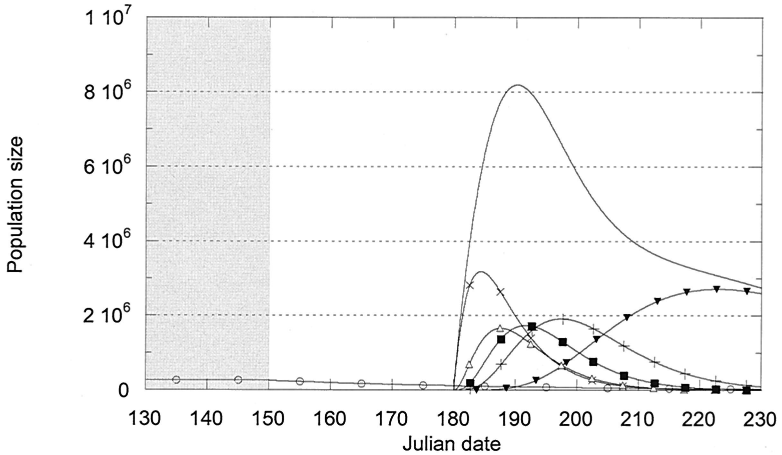

Fig. 2. Population dynamics of carnivorous stages of *Coccinella septempunctata* in landscapes with an area of 16% of hedgerows from Julian date 130–230. The gray area indicates the hibernation period. Legend: hibernated adults (○), first instars (×), second instars (△), third instars (■), fourth instars (+), adults (▼), population totals (no marker).

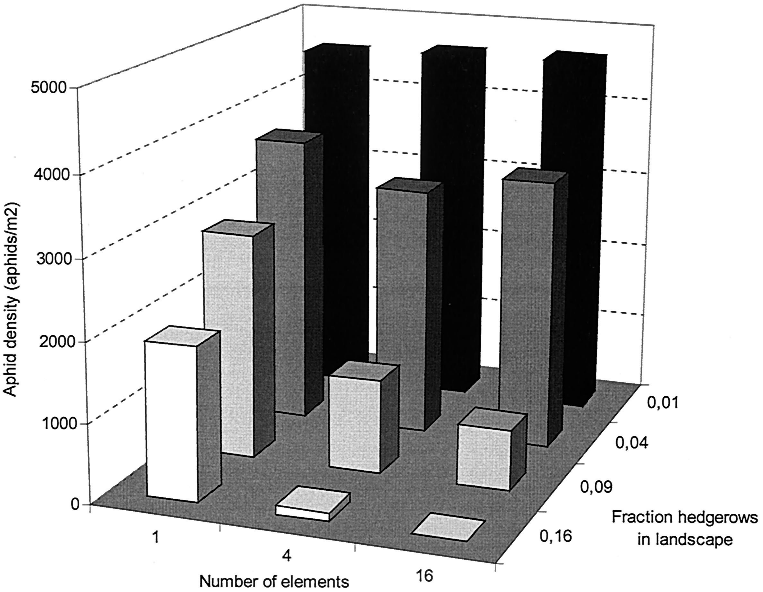

Fig. 3. Density of aphids in wheat at Julian date 230 in twelve landscapes with 1, 4, 9, and 16% of hedgerows divided into 1, 4, or 16 square elements. Landscapes with 1, 4, 9–16% hedgerows contained initial numbers of 16.000, 64.000, 144.000, and 256.000 *Coccinella septempunctata*, respectively, corresponding to 0.1, 0.4, 0.9, and 1.6 lady beetles/m^2 over the whole landscape.

ht is the handling time (d). Each carnivorous stage of *C. septempunctata* has a specific search rate and handling time (Table 1).

Coccinella septempunctata **Departure Dynamics.** Adults of *C. septempunctata* can disperse by flight. The larvae can walk but are assumed to remain in the 10 × 10 m^2 cell where the eggs are deposited. Adult *C. septempunctata* are assumed to be in a nonmigratory movement phase where dispersal is directed only by search for prey and where no long-range dispersal takes place. The dispersal dynamics of *C. septempunctata* adults can be characterized by the departure dynamics, i.e., the number of adults that leave each cell per unit of time, and by the dispersal kernel (Brewster and Allen 1997) of the dispersing adults.

Departure dynamics of *C. septempunctata* have been studied by Ives et al. (1993) who found that densities of *C. septempunctata* remaining in aphid-infested patches of fireweed followed negative exponential curves in time. Therefore, the departure dynamics of *C. septempunctata* adults in each cell is described by a fraction of the adult population leaving per unit of time (relative departure rate), which leads to an exponential decline of the density of *C. septempunctata* adults in time. Relative departure rates of *C. septempunctata* adults are affected by the level of prey availability (Ives et al. 1993, Xia 1997, Van der Werf et al. 2000). Ives et al. (1993) showed that residence times of *C. septempunctata* adults increased linearly from 1 to 25 h with increasing aphid densities. Van der Werf et al. (2000) found residence times of *C. septempunctata* adults increasing from 1.6 to 12.5 h in alfalfa fields with increasing densities of aphids. Consequently, residence times of *C. septempunctata* adults are assumed to be proportional to the aphid density that is present in their searching area (equation 3).

$$RT = rc \cdot \frac{A}{SAI} \qquad [3]$$

where *RT* is the mean residence time (d), *rc* is the residence coefficient (d/(aphids/m^2 search area)), 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 results in residence times that correspond with observations of Ives et al. (1993) and Van der Werf et al. (2000) (Table 1). The relative departure rate of *C. septempunctata* is calculated as the reciprocal of the residence time.

Coccinella septempunctata **Dispersal Dynamics.** *Coccinella septempunctata* adults that disperse are redistributed to all directions in the surrounding landscape. The dispersal kernel is rotationally symmetric and is characterized by a negative exponential decline in space (equation 4).

$$C = e^{-b \cdot x} \qquad [4]$$

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 slope of distance distribution curves of *C. septempunctata* (*b*) is estimated by fitting equation 4 to measured distance distribution data of *C. septempunctata* in alfalfa fields (Van der Werf et al. 2000) using the non-

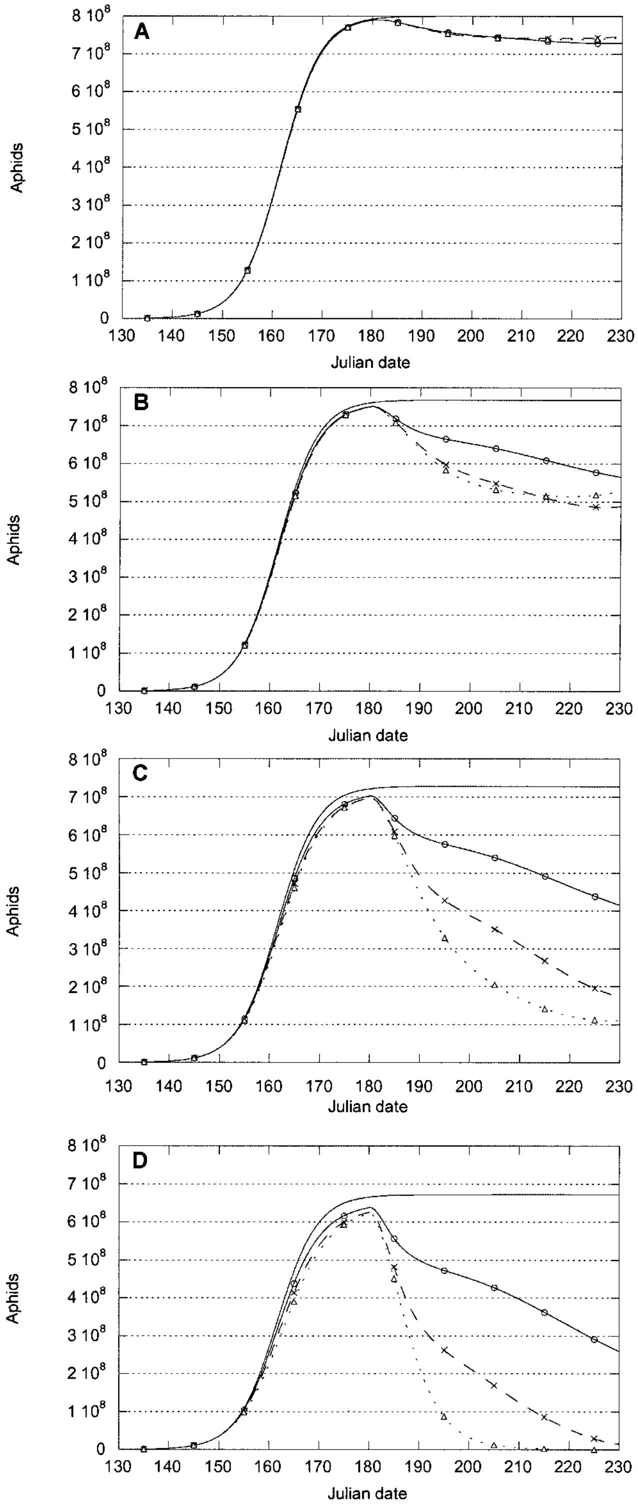

Fig. 4. Development of aphid populations in wheat in landscapes with an area of 1% (A), 4% (B), 9% (C), and 16% (D) of hedgerows divided into 1 (○), 4 (×), or 16 (Δ) square-shaped elements from Julian date 130–230. Aphid development in absence of *Coccinella septempunctata* is indicated by the solid lines without marker.

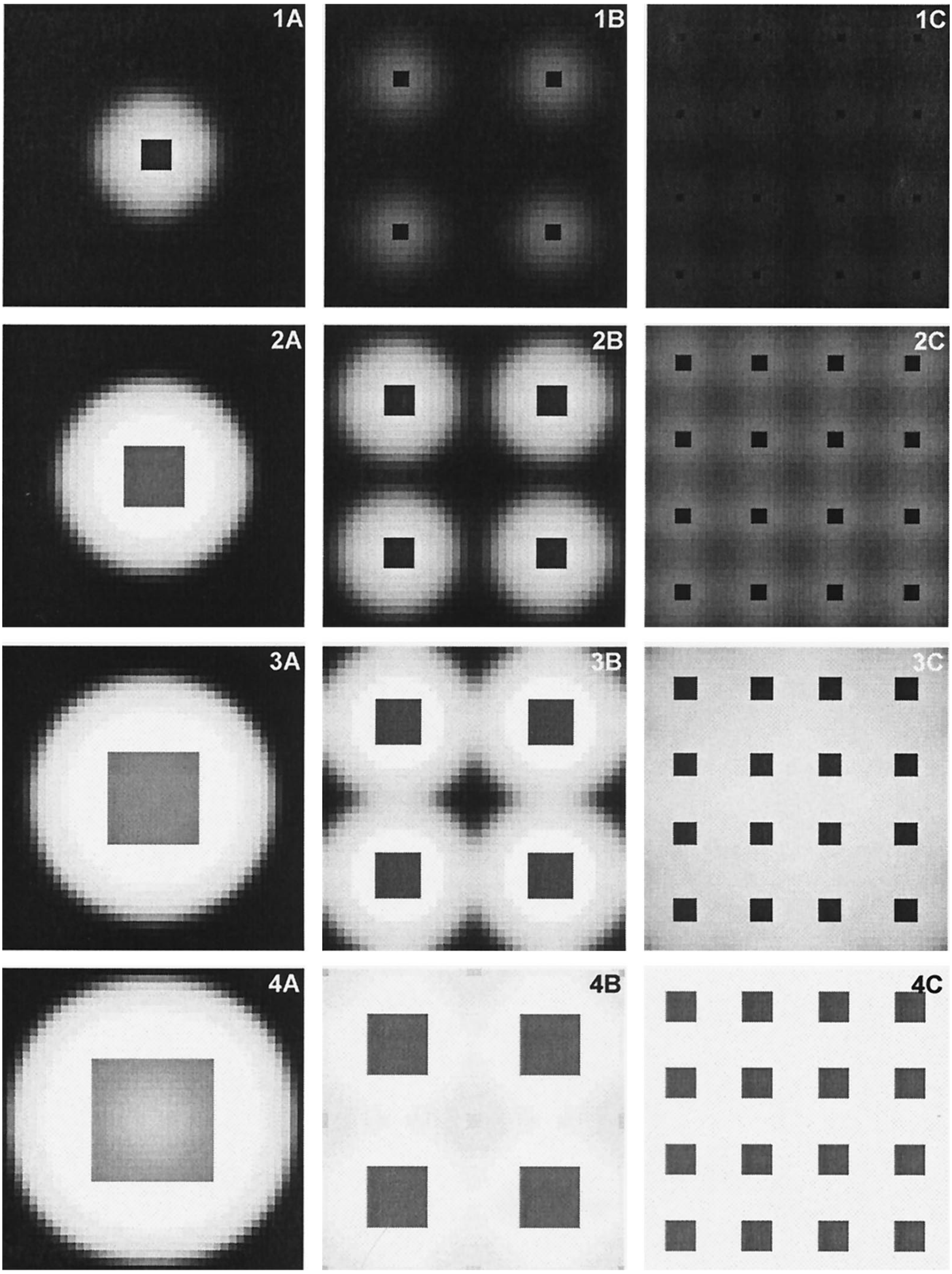

Fig. 5. Spatial distribution of aphid density in 12 landscapes with square hedgerow elements with 1%, 4%, 9%, and 16% of hedgerows (from top to bottom) and increasing level of fragmentation (1, 4, and 16 hedgerow elements, left to right) at Julian date 230. White and black represent densities of 0 and 5,000 aphids/m^2, respectively.

linear regression procedure 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 three repetitions and resulted in an average estimate of the slope of *b* of $0.31 \pm 0.045\ \mathrm{m}^{-1}$ (mean ± SEM). Dispersal is assumed to take place from the center of each 10 × 10-m^2 cell. Because a fraction of *C. septempunctata* adults only move for a short distance, a portion of the dispersing adult population lands in the same cell from which they took off. Individuals that would be distributed outside the map area are redistributed within the map

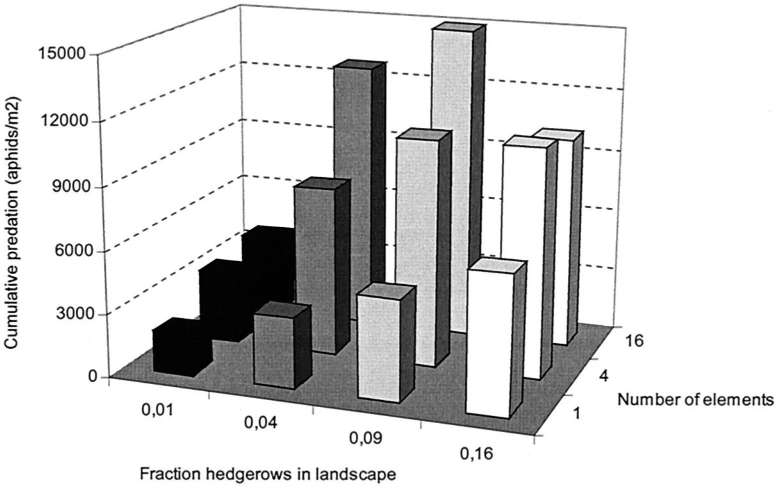

Fig. 6. Total number of aphids removed by *Coccinella septempunctata* in wheat up to Julian date 230 in twelve landscapes with 1, 4, 9, and 16% of hedgerows divided into 1, 4, or 16 square elements.

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.

Scenario Studies

The model was used to study the effect of the area and spatial configuration of hedgerows and wheat crops on the control of aphids by *C. septempunctata.* Because spatial configuration may comprise both the level of fragmentation and the shape of hedgerow elements, these aspects were investigated separately.

A first study focused on the effects of the area and fragmentation of hedgerow elements. The control of aphids by *C. septempunctata* is simulated in 12 landscapes with square hedgerow elements that vary in area and number (Fig. 1). The landscapes are designed in such way that there is a gradient in the area covered by hedgerows increasing from 1, 4, 9, to 16%, and a second gradient in which the number of hedgerow elements increases from 1 in the most clumped configuration, 4 for the intermediate configuration, to 16 for the most fragmented configuration.

In a second study, the effect of the shape of hedgerow elements was investigated. The control of aphids by *C. septempunctata* is simulated in landscapes that contain an area of 9% hedgerows divided into four elements. The elements have a square, block, cross, fractal, open square, or line shape. For the shape that provides the best control, a similar study as for square elements was then conducted to determine the potential for biocontrol in landscapes containing 1, 4, 9, and 16% hedgerows elements divided into 1, 4, and 16 elements (Fig. 1).

A third study focused on sensitivity of model output for uncertain or variable parameters. Because temperatures in May to August may deviate from the default temperature of 20°C, we included simulations in which the developmental rates, relative mortality rates, search rates, and handing times of *C. septempunctata* were to reflect their behavior at 15 and 25°C (Table 2). In addition, the slope of the distance distribution curves of *C. septempunctata* (*b*, equation 4) is poorly documented. Therefore, we studied effects of doubling and halving the parameter *b*. These simulations were conducted for a landscape with 13.5% of hedgerows divided into four square elements with variable sizes.

Initially, aphids are distributed homogeneously over the landscape at a density of two aphids/m^2 in both wheat crops and hedgerows. In contrast, *C. septempunctata* is only present initially in hedgerows at densities of 10 *C. septempunctata* adults/m^2, which is suggested as its maximum hibernation density (Honěk 1989). Landscapes with greater areas of hedgerows give rise to higher numbers of *C. septempunctata* because the hibernation density is kept constant. The number of *C. septempunctata* are 16.000, 64.000, 144.000, and 256.000 for landscapes containing 1, 4, 9, and 16% hedgerows, respectively. Simulations were started when the aphids emerge in spring (Julian date 130) and were terminated when the wheat crop was harvested on Julian date 230. The total period of simulation was, therefore, 100 d.

Results

Area and Fragmentation of Hedgerow Elements.

The dynamics of the total population of *C. septempunctata* in the landscape during the growing season is presented in Fig. 2. Hibernated adults of *C. septempunctata* emerge on Julian date 150 and reproduce at Julian date 180. At the end of the growing season (Julian date 230) almost all offspring developed into adult lady beetles.

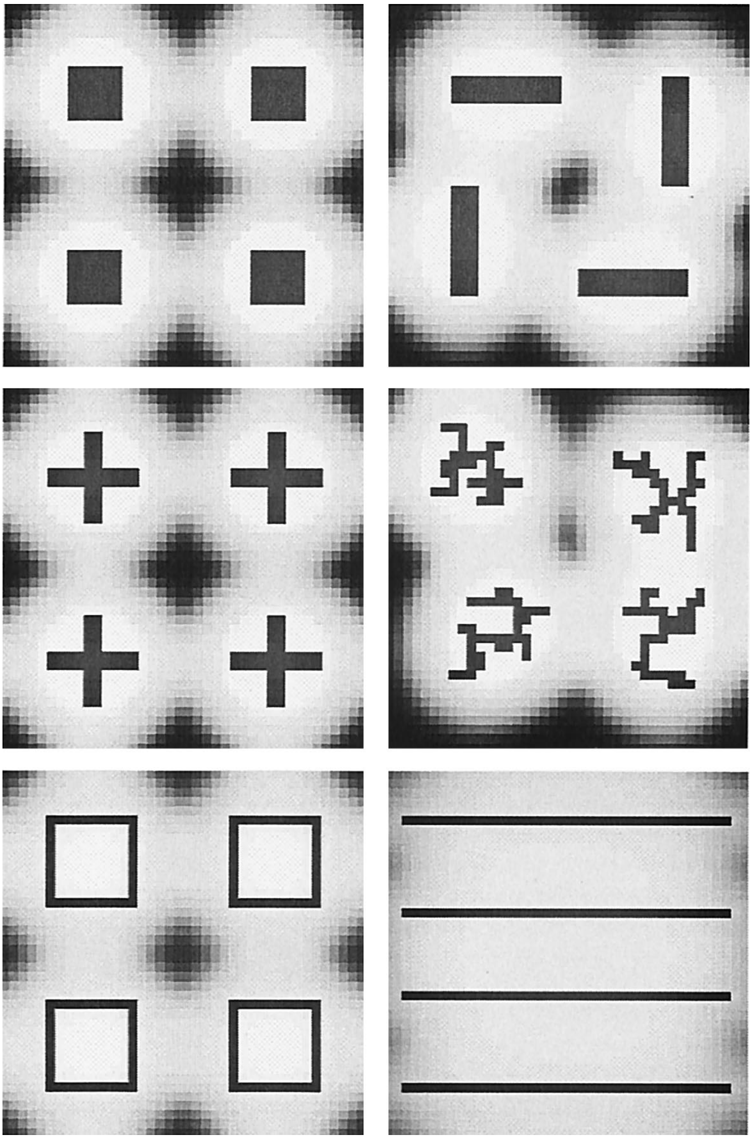

Fig. 7. Spatial distribution of aphid density at Julian date 230 in six landscapes with a square, block, cross, fractal, open square, and line shape. All landscapes contain an area of 9% hedgerows divided into four elements. White and black represent densities of 0 and 5,000 aphids/m^2, respectively.

The initial number of *C. septempunctata* in the landscape has a clear effect on the density of aphids in wheat at the end of the growing season at Julian date 230 (Fig. 3). The 16.000 and 64.000 *C. septempunctata* adults present at the start of the growing season in the landscapes with 1 and 4% of hedgerows (0.1 and 0.4 individuals per m^2, respectively, averaged over the landscape) were not able to provide adequate control. In these landscapes, the mean density of aphids at the end of the growing season was always at least 3,500 aphids/m^2. In contrast, the 144.000 and 256.000 *C. septempunctata* adults in landscapes with 9 and 16% hedgerows (0.9 and 1.6 individuals per m^2, respectively, averaged over the landscape) suppressed aphid densities to 1,000 aphids/m^2 or less at the end of the growing season. However, this level of aphid control was only achieved in landscapes with 4 or 16 hedgerow elements and not in the landscape elements in which the overwintering habitat was aggregated into a single square. When the initial numbers of *C. septempunctata* were too low to provide adequate aphid control, the configuration of the hedgerow elements had no effect on the level of aphid control (Fig. 4A and B). However, when the initial *C. septempunctata* numbers were as high as 144.000 and 256.000 per landscape, the configuration of the hedgerow elements did affect aphid control (Fig. 4C and D). In all simulations, emerging *C. septempunctata* adults were not able to suppress

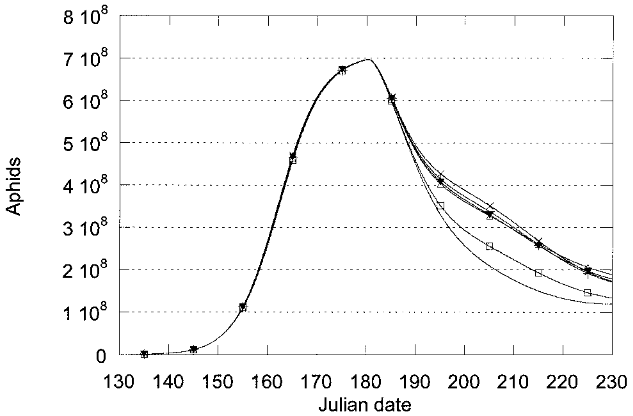

Fig. 8. Development of aphid populations in wheat in landscapes with a square (×), block (▼), cross (+), fractal (△), open square (☐), and line shape (no marker) from Julian date 130–230.

aphid populations early in the season, rather reductions of aphid densities took place only after reproduction of *C. septempunctata* (Fig. 4).

The configuration of hedgerows resulted in different spatial patterns of aphids in the landscape (Fig. 5). Clumped hedgerow configurations lead to strongly suppressed aphid densities near hedgerows while aphids reach densities close to carrying capacity at greater distances from the hedgerows. The area with suppressed aphid densities increased with larger size of the hedgerow, with larger hedgerows providing greater initial numbers of *C. septempunctata.* In landscapes with 4 and 16 hedgerow elements aphid populations show less spatial heterogeneity because of a more even distribution of *C. septempunctata* in the landscape. In landscapes with 16% hedgerows (Fig. 5: 4B and 4C) aphid densities in wheat are reduced to almost zero with little spatial variation.

The number of aphids removed by *C. septempunctata* during the growing season is presented in Fig. 6. In landscapes with 1% of hedgerows the number of removed aphids increased slightly with fragmentation of hedgerow elements but it never exceeded 4,000 aphids/m^2. In contrast, in landscapes with 4 and 9% of hedgerows predation levels increased rapidly up to 12,000 aphids/m^2 with increasing levels of fragmentation. In landscapes containing 16% of hedgerows, predation levels did not exceed 10,000 aphids/m^2 be-

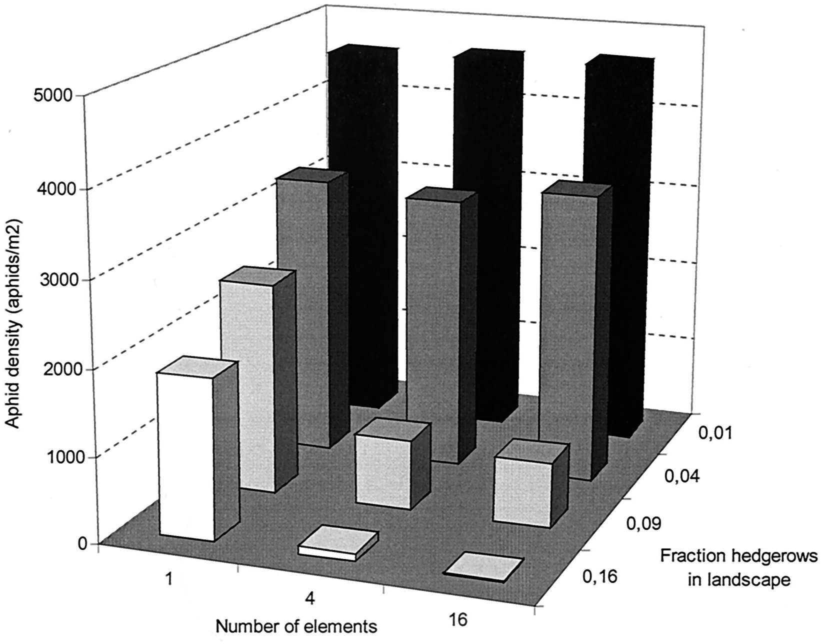

Fig. 9. Density of aphids in wheat at Julian date 230 in twelve landscapes with 1, 4, 9, and 16% of hedgerows divided into 1, 4, or 16 linear elements.

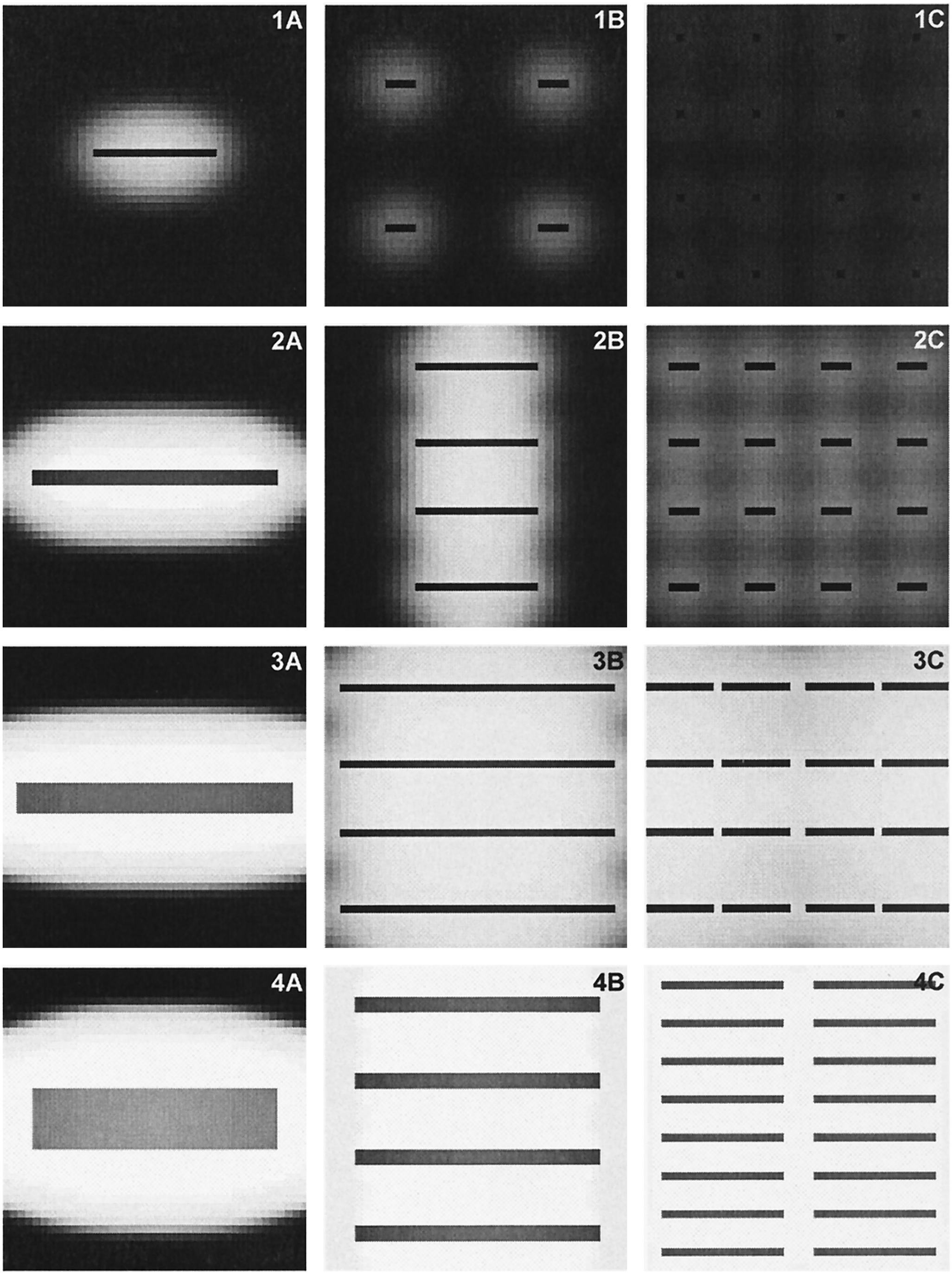

Fig. 10. Spatial distribution of aphid density in 12 landscapes with linear hedgerow elements with 1%, 4%, 9%, and 16% of hedgerows (from top to bottom) and increasing level of fragmentation (1, 4, and 16 hedgerow elements, left to right) at Julian date 230. White and black represent densities of 0 and 5,000 aphids/m^2, respectively.

cause of the limited aphid availability, resulting from early predation impact curtailing aphid population growth and later *C. septempunctata* feeding.

Shape of Hedgerow Elements. Modification of the shape of the hedgerow elements resulted in differences in the level of aphid control (Fig. 7). Landscapes with square, block, cross, and fractal shaped hedgerow elements had similar levels of aphid control, whereas open square and, in particular, line-shaped hedgerow elements provided improved levels of aphid control

Table 3. Sensitivity analysis of the development rates, relative mortality rates, search rates, and handling times of *Coccinella septempunctata* at 15, 20, and 25°C (see Table 2) and the slope of the distance distribution curve of *C. septempunctata* (b) on the aphid density in wheat at the end of the growing season (Julian date 230)

Parameterization	Aphid density (aphids/m^2)	Deviation (%)
15°C, b×2	4830	+108.7
15°C, b	4253	+83.8
15°C, b×½	4245	+83.4
20°C, b×2	4381	+89.3
20°C, b	2314	0
20°C, b×½	1807	−21.9
25°C, b×2	4374	+89.0
25°C, b	2838	+22.6
25°C, b×½	2908	+25.7

Deviations of aphid densities relative to the default parameterization (20°C, b) are indicated.

(Fig. 8). Landscapes with linear hedgerow elements provided the most even distribution of *C. septempunctata* hibernation sites over the landscape resulting in suppressed aphid populations all over the landscape. In contrast, in landscapes with square, block, cross, fractal, and open square shaped hedgerow elements, aphids reached carrying capacity at isolated locations, far from the nearest hedgerow, at the end of the growing season (Fig. 7).

The control of aphids by *C. septempunctata* in landscapes with linear hedgerow elements covering an area of 1, 4, 9, and 16% of the landscape and divided into 1, 4, or 16 elements is given in Figs. 9 and 10. Linear hedgerow elements, as compared with square elements, led to somewhat suppressed aphid densities in landscapes 2A (−9%), 3A (−12%), and 3B (−31%; Figs. 5 and 10). Therefore, the shape of hedgerow elements had a modest effect on the potential level of aphid control.

Sensitivity Analysis. The potential of *C. septempunctata* to control aphids appeared sensitive to changes in temperature (Table 3). At 15°C, lady beetles have a low activity, which is reflected in low search rates (Table 2). In addition, the majority of the lady beetles were still larvae at the end of the growing season because of the low developmental rates. The low activity combined with the long duration of the larval stages in which lady beetles are immobile resulted in poor biocontrol. Temperatures of 20°C provided best biocontrol. Biocontrol at 25°C was lower than that at 20°C. Although lady beetles are more active at 25°C, they have a short life span at this temperature, which is reflected in high relative mortality rates (Table 2). Hence, at 25°C there are fewer *C. septempunctata* alive at the end of the growing season than at 20°C.

Biocontrol by *C. septempunctata* appeared to be sensitive to a reduction in dispersal capacity, but less sensitive to an increase in dispersal capacity. Doubling the slope of the distance distribution curve (b) resulted in almost complete arrest of lady beetles in hedgerows (Fig. 11). This led to aphid densities close to carrying capacity in wheat for all three temperatures (Table 3). Halfing the value of b resulted in a more even suppression of aphids in the landscape (Fig. 11). However, the increased dispersal capacity resulted in a reduction of 22% in aphid density at 20°C, whereas at 15°C and 25°C the increased dispersal capacity resulted in similar aphid densities as the standard dispersal capacity (Table 3).

Discussion

The shape of hedgerow elements had only a minor effect on the control of aphids by *C. septempunctata.* Although linear hedgerow elements were clearly the best shape for hedgerows in landscapes consisting of 9% of hedgerows divided into four elements (Fig. 7), linear hedgerows only resulted enhanced aphid control in 3 of the 12 landscapes (Fig. 5 and 10: 2A, 3A, and 3B). In the other landscapes, no effect of element shape was observed because (1) the number of *C. septempunctata* was too low to cause aphid suppression at all (1A, 1B, and 1C), (2) the number of *C. septempunctata* was sufficient to suppress the total aphid population (4B and 4C), or (3) the level of fragmentation already ensured an effective distribution of *C. septempunctata* over the landscape (3C).

The area of hibernation sites (hedgerows) for *C. septempunctata* appeared to be the key factor for the control of aphid populations in landscapes. The level of fragmentation of the hedgerow elements will only affect aphid control when a sufficient area of hibernation habitat is present to maintain effective densities of *C. septempunctata.* The simulations indicate that the critical area for this fragmentation effect lies between 4 and 9% hibernation habitat (Figs. 3 and 9).

Threshold values have also been reported for the area of habitat needed for the long-term conservation of species in landscapes (e.g., Fahrig 2001, With and Crist 1995). Habitat fragmentation is known to have a detrimental effect on survival of species when the area of habitat is below this critical threshold (Fahrig 1998). On the contrary, in the current study we found that fragmentation of hibernation habitat of *C. septempunctata* may result in enhanced levels of aphid control. The discrepancy between the outcome of these two types of studies lies in the fact that in conservation studies the area outside the habitat area is regarded as completely unsuitable for survival, whereas in the current study *C. septempunctata* relies on hedgerows for hibernation only and that wheat crops are excellent habitat during the growing season.

The highest predation levels do not necessarily result in best control (Fig. 3 and 6). For instance, in the landscape with 4% hedgerows divided in 16 elements over 12,000 aphids/m^2 were removed while the density of aphids at the end of the growing season was still 3,500 aphids/m^2. In contrast, in the landscape with 16% hedgerows divided in 16 elements, complete control was achieved with a mean predation level of only 10,000 aphids/m^2. This difference can be explained by the huge reproduction capacity of aphids (more than 300 aphids/d at population densities of 2500 aphids/m^2, see equation 1) and the limited capacity of *C. septempunctata* to remove aphids. Complete control

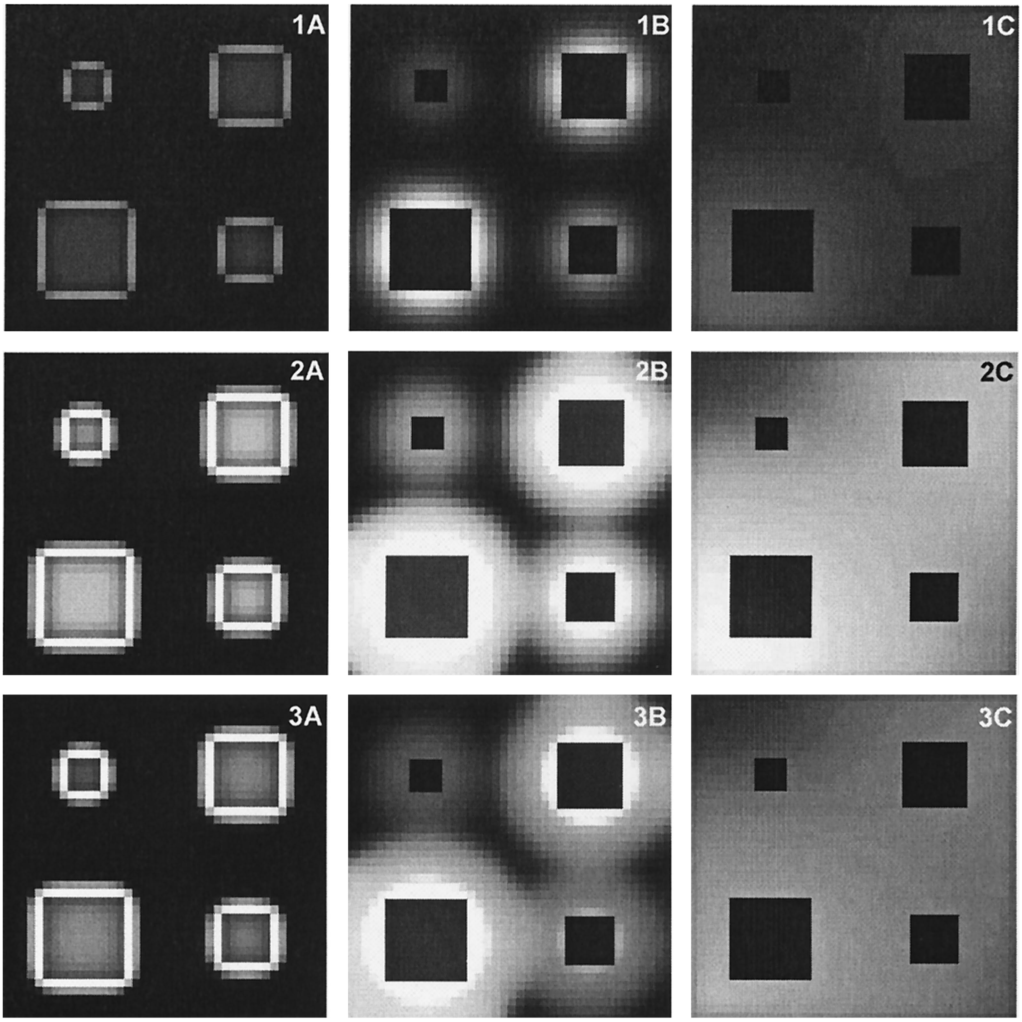

Fig. 11. Spatial distribution of aphid density at Julian date 230 in nine landscapes with four square hedgerow elements with different sizes. Simulations conducted with developmental rates, relative mortality rates, search rates, and handling times of *Coccinella septempunctata* representative for 15, 20, and 25°C are shown from top to bottom. Simulations with double, standard, and half values of the slope of the distance distribution curve (*b*) of *Coccinella septempunctata* are represented from left to right. White and black represent densities of 0 and 5,000 aphids/m^2, respectively.

can only be established when *C. septempunctata* is present at large enough densities to remove more aphids per unit of time than are reproduced. When the capacity of *C. septempunctata* to remove aphids does not exceed the aphid reproduction capacity, large numbers of aphids may be removed without reaching adequate control.

The potential of *C. septempunctata* to control aphid infestations has been studied at 15°C, 20°C, and 25°C. Biocontrol was best at 20°C. At 15°C, the effectiveness of *C. septempunctata* is hampered by low activity and slow development, whereas at 25°C their survival is limited because of high respiration cost (Mills 1981). However, under warm conditions *C. septempunctata* is likely to have more than one generation per year. The occurrence of multigenerations of lady beetles per year can be expected to boost biocontrol. As to the dispersal capacity of *C. septempunctata,* we assumed in this study that the lady beetles exhibit short distance dispersal at a scale of several meters, which is associated with the searching for prey within foraging habitats. However, lady beetles may fly between or within foraging habitats at a scale of at least 50 m (Osawa 2000). *Coccinella septempunctata* is therefore likely to be more mobile in field situations than in our simulations. The sensitivity analysis revealed that the aphid densities at the end of the growing season were relatively insensitive for increased lady beetle dispersal. Halfing the value of the slope of the distance distribution curve (*b*) resulted in a 22% reduction of the aphid density at 20°C and had only a marginal effect at 15°C and 25°C (Table 2). This suggests that the simulations may still be noteworthy despite of the uncertain data on *C. septempunctata* dispersal.

The simulations indicate that landscapes with <4% of good quality hibernation area do not maintain a sufficient local population of *C. septempunctata* to control aphid infestations successfully. Long distance migration of lady beetles from hibernation sites at larger distances may boost the level of control in such landscapes, but then densities of colonizing lady beetles should be in the order of 10,000 per hectare. Enlarging the area of noncrop landscape elements that are associated with *C. septempunctata* hibernation to 9 to 16% of the landscape could potentially lead to enhanced aphid control. An even distribution of noncrop landscape elements near aphid infested crops is advantageous, e.g., as was suggested for grass-sown earth banks by Thomas et al. (1991, 1992). However, because the simulations in our study represent the theoretical maximal impact of *C. septempunctata* on aphids, actual levels of aphid control are likely to be lower. Yet, in real landscapes in addition to *C. septempunctata*, other predators, parasitoids, pathogens, and fungi will contribute to biological control of aphid populations.

The management of refuge habitats of natural enemies is a promising approach to enhance their impact in agroecosystems (Landis et al. 2000, Pickett and Bugg 1998). Besides empirical studies that investigate the impact of natural enemies on arthropod pests in relation to the surrounding landscape, the use of spatially explicit models may contribute to an improved understanding of these systems by providing a theoretical framework in which hypotheses can be formulated and tested. In the current study two hypotheses have been derived: (1) the area of hibernation habitat is a key factor for biocontrol provided by predators and (2) fragmentation of hibernation habitat will only lead to enhanced levels of biocontrol when a sufficient area of hibernation habitat is present. These rules of thumb may be useful for the design and evaluation of the landscapes with enhanced predator impact and may contribute to the development of sustainable agricultural production systems with reduced pesticide inputs.

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