SZENT ISTVÁN UNIVERSITY

MODELLING THE POPULATION DYNAMICS OF WESTERN CORN ROOTWORM (*DIABROTICA VIRGIFERA VIRGIFERA* LECONTE) ON LANDSCAPE LEVEL

Theses of PhD dissertation

MÁRK SZALAI

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Head of the PhD School: **Dr. László Heszky**
Professor, member of the Hungarian Academy of Sciences
SZIU, Faculty of Agriculture and Environmental Sciences
Institute of Genetics and Biotechnology

Supervisors: **Dr. József Kiss**
Professor
SZIU, Faculty of Agriculture and Environmental Sciences
Plant Protection Institute

Dr. Stefan Toepfer
Adjunct professor
SZIU, Faculty of Agriculture and Environmental Sciences
Plant Protection Institute
CABI Europe - Switzerland

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Dr. László Heszky   Dr. József Kiss   Dr. Stefan Toepfer

Head of the PhD school   Supervisor   Supervisor

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1. Background and objectives

Maize yield can be diminished by feeding damage to roots by larvae of *Diabrotica virgifera virgifera* LeConte (western corn rootworm; Coleoptera: Chrysomelidae)(Chiang, 1973).The pest was accidentally introduced on several occasions from North America into Europe between the early 1980s and early 2000s (Miller et al., 2005; Szalai et al., 2011b). Rotation of maize is an effective and widely used control method against this univoltine pest in Europe (Kiss et al., 2005). However, farmers usually prefer avoiding the rotation of maize, because maize is currently among the most profitable field crops in many European agricultural regions (Fall & Wesseler, 2008). Moreover, rotation of maize fields in each year may be unnecessary to control *D. v. virgifera*, because (i) a certain time period is needed for the pest populations to recover after rotation, and (ii) inter-field dispersal of adults can dilute *D. v. virgifera* populations in infested fields. Therefore, the population dynamics of *D. v. virgifera* require understanding both spatial and temporal factors preferably on landscape level, when investigating population dynamics under different control strategies, such as crop rotation schemes, within the rather complex framework of integrated pest management (Boller et al., 1997). Because such large-scale landscape approaches can hardly be addressed experimentally; models are often developed and used to answer pertinent research questions.

The first simulation model of *D. v. virgifera* population dynamics (and *Diabrotica barberi* [*D. longicornis* in the model] population dynamics) was developed in 1976 (Mooney & Turpin, 1976). The model aimed to forecast pest damage in a maize field and therefore to avoid unnecessary soil insecticide treatments. The situation of a single continuous maize field was modelled, and pest development was evaluated under different weather regimes. The adult dispersal considered as an additional mortality factor in the focal maize field. Similar model structures were developed by Hein & Tollefson (1987) and Elliott & Hein (1991) to investigate *D. v. virgifera* population dynamics of a single continuous maize field in their daily time step, temporally discrete models. Elliott & Hein (1991) evaluated their model at several different levels of input factors to conduct one-at-a-time sensitivity analysis, and factors describing temperature-dependent development rates of immature rootworms and maize plants were found as most influential input factors. Later, population-genetics models were introduced. First, the adaptation of *D. v. virgifera* to crop rotation was modelled by investigating frequency of the hypothesised allele of behavioural tolerance to rotation (Onstad et al., 2001b). Then, in line with the introduction of transgenic *Bacillus thuringiensis* maize, the resistance of *D. v. virgifera* to the bacterial toxin was modelled by simulating the proportion of allele frequencies (Crowder & Onstad, 2005; Crowder et al., 2005; Onstad et al., 2001a; Onstad & Meinke, 2010). These studies were based on temporally discrete models with daily and generational (=annual) time steps, because of the univoltine nature of *D. v. virgifera* and the one-season growing system of maize per year. The studies of Crowder et al. (2005) and Crowder & Onstad (2005) developed the same model structure with generational and daily time steps, respectively and obtained comparable simulation results (Crowder & Onstad, 2005). All these models are not spatially explicit models or can be assumed only as quasi-explicit models (Czárán, 1998). This approach of assuming ergodicity, i.e. the perfect spatial mixing of individuals, is acceptable when models describe a single field or a simple landscape, such as the strict rotation of soybean and maize in the USA corn belt. However, simulating population dynamics in a more diverse landscape requires spatially explicit models (Czárán, 1998; Durrett &

Levin, 1994a), particularly for a mobile pest insect as *D. v. virgifera*. Therefore, spatial models were also developed to explain the population dynamics of *D. v. virgifera* population dynamics. For example, Storer (2003) studied the development of resistance to the *B. thuringiensis* toxin in *D. v. virgifera* populations in a 10x10 lattice of fields, encapsulated into a torus. The adult dispersal was allowed within a defined range of cells in a daily time step model. The model output was the allele frequency of resistance as in the above cited models. Similar aims were addressed in the model of Pan et al. (2011), but containing two submodels, i.e. a daily time step submodel for the adults and an annual time step submodel for the larvae. A single maize field was modelled, which was, however, heterogeneous considering different insect resistance management schemes. The adult dispersal was modelled using a grid covering the considered maize field. The *D. v. virgifera* abundance was also a model output; although, this model investigated resistance management practices focusing on allele frequencies. Only recently, O'Rourke & Jones (2011) considered landscape diversity in the modelling of population dynamics of maize pests, i.e. *D. v. virgifera* and *Ostrinia nubilalis*. An agricultural landscape was coded as 128x128 lattice of different habitat patches. The logistic model of population growth was assumed in the preferred habitats of the pests, i.e. patches covered by maize for *D. v. virgifera* populations. However, maize rotation, which is a crucial factor for *D. v. virgifera* development, was randomly applied at 50% for the entire modelled landscape. Next to the population dynamics and resistance development models, several spatially explicit models were developed to simulate the geographical spread of *D. v. virgifera*. The rotation tolerant population spread was modelled for the corn belt of the USA (Onstad et al., 1999). Then, because of the European introduction of the pest, the speed of the spread and the possible infestation area of *D. v. virgifera* in Europe were studied (Baufeld & Enzian, 2001; Dupin et al., 2011; Edwards et al., 1998; Hemerik et al., 2004). Moreover, the worldwide expansion of the pest due to a possible climate change was also modelled (Aragon et al., 2010; Aragon & Lobo, 2012). In the most of recent European models of *D. v. virgifera* population dynamics, eradication programmes and containment measures were addressed (Baufeld & Enzian, 2001; Carrasco et al., 2012; Carrasco et al., 2010a; Carrasco et al., 2010b; Carrasco et al., 2010c; Krügener et al., 2011), instead of considering established *D. v. virgifera* populations. Carrasco et al. (2012) also considered stakeholders' decision in the simulations of the spread of the pest through in the UK. In this model decision making was influenced by personal experience as well as by decisions of their neighbours. However, the modelled stakeholders for the UK had no or limited knowledge about the pest, because of its recent invasive status compared with other European regions. Therefore, this decision making assumption has limitations for regions with established *D. v. virgifera* populations.

Despite the large amount and diversity of modelling approaches for *D. v. virgifera*, it appears that there is no appropriate model structure available that allows the investigation of pest control strategies, such as crop rotation schemes, in view of agricultural landscape aspects as well as of temporal population dynamics and spatiotemporal dispersal aspects of the pest insect. I therefore aimed to develop a new discrete, spatiotemporal, lattice-based and cellular automaton-like integrated particles system model that ultimately allows complex developments or improvements of pest management recommendations against *D. v. virgifera* such as within the framework of integrated pest management (Boller et al., 1997). In addition to the development of the appropriate model structure, running simulations with realistic values was also aimed. Therefore, two crucial biological parameters, i.e. generational growth rate of the pest and the colonisation of uninfested maize fields by *D. v. virgifera* adults, were investigated in field studies.

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2. Material and Methods

2.1 Determining the generational growth rate of *Diabrotica virgifera virgifera* populations

Modelling population dynamics of the maize pest *D. v.virgifera* requires knowledge on the growth rate (=net reproductive rate) of the species. We investigated the generational (=annual) growth rate of *D. v. virgifera* in isolated maize fields in southern Hungary and eastern Croatia over several years. The population densities of *D. v. virgifera* were assessed by absolute counts of emerging adults in 90 gauze cages per study field. Emergence ranged from 1.3 to 30.7 adults per m^2 in continuous maize field sections, and from 0.3 to 5.1 adults per m^2 in adjacent first-year maize sections. The annual growth rates of *D. v. virgifera* ranged from 0.5 to 13, and averaged in close to 4. These experimentally assessed growth rates could complement growth estimates in population dynamic models, particularly those for forecasting the population growth to economic thresholds or for estimating population build-ups after new introductions of this alien species in Europe. The determined growth rate was used to estimate that the first documented successful introduction of this species into Europe occurred between 1979 and 1984, which is 8-13 years before the detection of this species and its larval damage in maize fields near Belgrade, Serbia, in 1992.

2.2 Colonisation of first-year maize fields by *Diabrotica virgifera virgifera* populations from adjacent infested maize fields

The larvae of *D. v. virgifera* are largely restricted to the roots of maize as food source, and their feeding damage can cause yield losses. The adults are active flyers in search for pollen sources or for new maize fields to colonise. The *D. v. virgifera* colonisation of first-year maize fields from adjacent continuous maize fields was studied in a 20 km^2 intensive agricultural area near Dalmand in South-Western Hungary between 2008 and 2010. Using non-baited yellow sticky traps the infestation levels of adult *D. v. virgifera* were compared between six first-year maize fields and seven to 12 adjacent continuous maize fields during a seven week period in July and August in each year. The infestation in the continuous maize fields accounted for more than 60% of the variation in the adult *D. v. virgifera* captures in the adjacent first-year maize fields indicating that adjacent maize fields are the major source of dispersal into first-year maize and not, or to a lesser extent, the area-wide infestation levels. The findings of this study are considered in the dispersal range of *D. v. virgifera* adults in the population dynamics lattice model.

2.3 Structure of the *D. v. virgifera* simulation model

The *D. v. virgifera* population dynamics lattice model is calculating the densities of the pest insect in the individual maize fields of an agricultural landscape. The considered agricultural landscape was simplified into an n×n lattice of uniform cells encapsulated into a torus to avoid edge effect. The cells of the lattice, i.e. the fields of the modelled landscape, had the following states during the simulations: continuous maize field (C), first year maize field (F) or a non-maize crop field (E). Population dynamics of *D. v. virgifera* were simulated in the lattice as an interacting particle system (Czárán, 1998) using the following basic assumptions:

i. An alien invasive species usually lacks effective and specific natural enemies in the area of invasion, which is also the case of *D. v. virgifera* in Europe. Consequently, the model follows the population dynamics of this species only according to the states of the field cells.
ii. Adult dispersal for oviposition appears among maize fields only. Minor oviposition into non-maize was neglected for the European situation.
iii. Occurrence of a new generation, i.e. successful larval development and adult emergence, is considered in continuous maize only.
iv. All of the modelled fields have the same size, because of uniformity of cells in the lattice. Thus, *D. v. virgifera* population densities can be used in the same way as total abundance values to describe the population dynamics of the pest insect.
v. The model time horizon is 10 years as this is a foreseeable time period in agriculture, i.e. under similar management practices and in a similar economic environment. The agricultural factors remain constants for the simulated 10 years period.

Considering the aforementioned assumptions the simulation steps of the *D. v. virgifera* population dynamics lattice model were as follows:

I. The development of lattices of the simulated agricultural landscape
   a. Randomisation of a starting lattice according to the percentages of maize fields and rotated maize fields as well as other agricultural factors in the considered landscape for the first simulated year
   b. The generation of lattices for the 2nd, 3rd ...10th year using updating rules taking into account the agricultural factors as constants for the 10 simulated years
II. When all lattices were available, the simulation of population dynamics of *D. v. virgifera*
   a. Placement of initial populations into continuous maize fields of the starting lattice
   b. Calculation of the population dynamics of *D. v. virgifera* on the available lattices considering the two discrete time steps in each year (Fig 1.)
      i. Density dependent generational growth in continuous maize fields
      ii. Dispersal of pest adults among maize fields: a density dependent portion of the population dispersed and arrived for oviposition into other maize fields
   c. Comparison of ovipositing *D. v. virgifera* population densities, i.e. after adult dispersal, with the economic threshold level in each maize field of each year
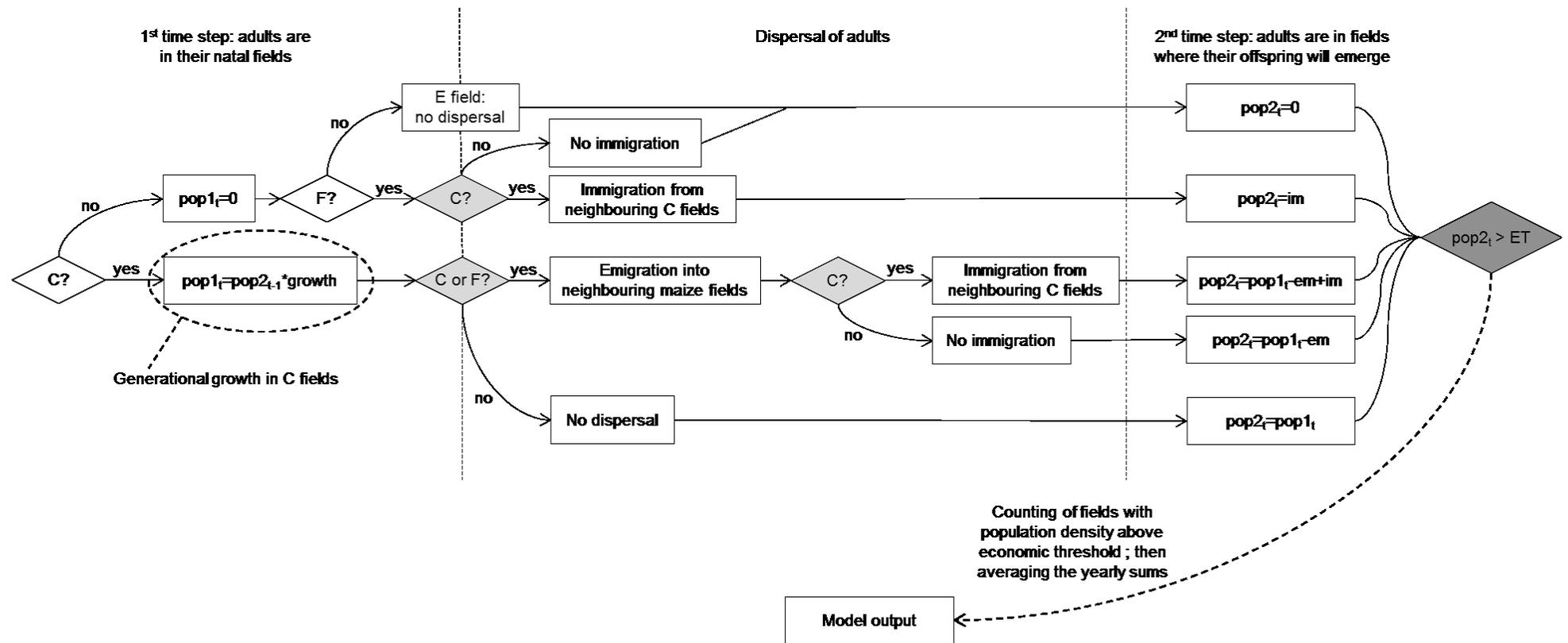
Fig 1. Model structure with the yearly processes of spatiotemporal population dynamics of *Diabrotica virgifera virgifera*. These processes were done for each cell of the simulated landscape in each year (t). *Diabrotica v. virgifera* populations in rectangles: pop1: population density before the dispersal; pop2: population density after the dispersal; growth: generational growth rate. Adult dispersal was separated artificially: emigration (em) is the dispersal of adults out of their natal field to any maize field; immigration (im) is the arrival of dispersing adults in maize fields for oviposition. The rhombuses are the decision steps. The white decisions are for the states of the cell processed (where C is for continuous maize field, F is for first year maize field and E is for non-maize crop field). The light grey decisions are for the states of cells (=fields) in the reachable neighbourhood; and the dark grey one is for the comparison of the population density with the economic threshold level (ET). Model output is the average percentages of maize fields reaching *D. v. virgifera* populations above a threshold in an agricultural landscape and over the period of 9 generations, i.e. from the 2nd to 10th simulated year.

2.3.1 Model output

The average percentages of maize fields reaching *Diabrotica v. virgifera* populations above a threshold in an agricultural landscape and over the period of 9 generations, i.e. from the 2nd to 10th simulated year, was the model output. This output was the result of modelling *D. v. virgifera* population levels in each maize field of a modelled agricultural landscape in each year. Preliminary model evaluations had been conducted to find large enough lattice size for which the output is not affected any more by altering the lattice size. This was at 100x100 lattice size, which was then taken for model evaluations. It would equal for example to a 1500km^2 agricultural landscape in case of 15 ha fields as lattice cells. The model output was studied considering the following 20 varying input factors in their defined ranges (Table 1).

2.3.2 Agricultural input factors

Field size: This refers to the average field size (ha) in the arable land of a considered agricultural landscape, and therefore also the size of the cells in the model lattice.

Percentage of maize in arable land (% maize): This is defined as the percentage of maize fields among all fields of arable land of an agricultural landscape, and therefore also of the lattice of the model. Because of the uniformity of lattice cells, this factor also referred to the percentage of area grown with maize in an agricultural landscape. The used range of 20 to 60% covers almost every maize growing region of Europe (Baufeld & Enzian, 2005).

Percentage of first year maize among all maize fields (% rotated maize): This refers to the percentage of first year maize fields among all maize of the lattice.

Farmers' decisions to rotate first year or continuous maize fields: Farmers may not rotate each of their maize field with equal probability. Such preference resulted in different 'age distribution' of continuous maize fields. For example, for a given percentage of rotated maize, a landscape could be found, where most continuous maize fields are grown with maize for 2 consecutive years, as well as a landscape with maize fields of 5 or 6 consecutive years maize (particularly heavily infested, 'old' maize fields) besides the rotated fields and second year, 'younger', continuous maize fields. As such age distributions of continuous fields can drive different pest population dynamics, the farmers' decisions to rotate first year or continuous maize fields was used as a ratio of two probabilities of rotation and simulated in the lattice updating processes of the model (see below).

Agro-policy legislation: This refers to an agro-policy legislation of mandatory rotation, i.e. a rotation scheme for rotating single fields after 3, 4 or 5 consecutive years of maize growing according to agricultural legislations or integrated pest management recommendations. A strict level of this factor (rotation after 3 years of maize) was applied in accordance with the Hungarian regulations (FVM, 2008) Each rotation scheme was uniformly applied across the entire lattice.

Economic threshold: This is the population density of *D. v. virgifera* adults in numbers of adults per plant that can lead to economic larval damage in the subsequent year. This factor can be set according to the different production systems (grain, seed, silage maize etc.) and economic environment. However, I chose thresholds typical for conventional grain maize production (Table 1.).

Table 1. Input factors of the *Diabrotica v. virgifera* population dynamics lattice model with their range and most likely values to simulate percentages of maize fields reaching *D. v. virgifera* populations above threshold.

Input factors	Min.	Most likely	Max.	Source [a]
Field size (ha)	2	15	100	Bavaria (A. Kunert 2009. pers. comm.), Tolna county (Szalai et al., 2011a)
% maize	20	40	60	(Baufeld & Enzian, 2005)
% rotated maize [b]	5/35	NA	95	(Leteinturier et al., 2007); Agosti, 2008 pers. comm.; Kiss, 2005; Ripka, 2008
Farmers' decisions to rotate first year or continuous maize	0.5	1	2	Own estimation
Agro-policy legislation [c]	NA	'no legislation'	NA	FVM, 2008; European Commission, 2003
Economic threshold (adult/plant)	0.7	1	2	(Edwards et al., 1994; Higgins et al., 1995; Willson, 1992)
Population growth rate in low-populated continuous maize	1.1	4	10	(Szalai et al., 2011b)
Population growth rate in high-populated continuous maize	0.8	1	1.5	Own estimation
Lower limit of population density effects on growth rate (adult/plant)	5	10	15	Own estimation
Upper limit of population density effects on growth rate (adult/plant)	30	40	50	Own estimation
Intensity of environmental year effect on growth rates (% of mean)	10	30	50	(Toepfer & Kuhlmann, 2005)
SD of randomization of population growth rates (% of mean)	10	30	50	Own estimation
Population dispersal range (km)	1	2	3	(Carrasco et al., 2010a; Szalai et al., 2011a)
% emigration from low-populated continuous maize	10	20	40	(Levay et al., 2008)
% emigration from high-populated continuous maize	40	60	80	(Levay et al., 2008)
Lower limit of population density effects on % emigration (adult/plant)	0.3	0.6	1.2	Own estimation
Upper limit of population density effects on % emigration (adult/plant)	5	10	20	Own estimation
SD of randomization of % emigrations (% of mean)	10	30	50	Own estimation
Initial population (% of threshold)	50	80	95	(Bazok et al., 2011; Sivcev et al., 2009)
SD of randomization of initial population (% of mean)	10	30	50	Own estimation

a: References cited here are the sources of the presented values and ranges. The numerous references on similar phenomena but without values are not listed here.

b: In the sensitivity analysis at least 35% rotated maize was used to involve 3 levels of the agro-policy legislation. Moreover, the entire range was investigated in each series of model evaluations; thus, a most likely value of this factor did not exist.

c: Agro-policy legislation is not a numerical input factor. The 'no legislation' level was used for testing all other factors as well as the legislations of the mandatory rotation after 3, 4 or 5 years of consecutive maize growing.

2.3.3 Biological input factors

Population growth rate: This is the annual (=generational) growth rate of *D. v. virgifera* including fecundity, sex ratio and mortality of all life stages. The growth rate of *D. v. virgifera* may depend on the population density; although, experimental studies of density dependence in the growth of pest generations are lacking (Szalai et al., 2011b). For simplicity, I considered a linear negative density dependence of the growth rate within two density independent stages in a 'Z' shape curve that was determined by the following four input factors: population growth rate in maize fields with populations below the lower limit of population density effects on growth rate (referred to as population growth rate in low-populated continuous maize); population growth rate in maize fields with populations above the upper limit of population density effects on growth rate (referred to as population growth rate in high-populated continuous maize); lower limit of population density effects on growth rate; and the upper limit of population density effects on growth rate. For each year, an environmental year effect on the growth rate was randomised to determine if that was an average, optimal or bad year for the reproduction of *D. v. virgifera*. This was uniformly applied across the considered agricultural landscape. The difference between the best and the worst possible years for *D. v. virgifera* reproduction during the 10 simulated years was determined by the intensity of environmental year effect on growth rates. Moreover, a remaining range of variability of growth rates among the continuous maize fields was considered, and the intensity of this variability was defined as the standard deviation of randomization of population growth rates.

Population dispersal: Dispersal of *D v. virgifera* adults can occur in search for food or in order to oviposit, but only the latter was relevant for this study. Therefore, dispersal for oviposition reasons was modelled as interfield movements among maize fields in the lattice, i.e. between continuous maize fields (C), as well as between continuous and first year maize fields (F) (Fig 1.). Inter-maize-field movement for oviposition was assumed for a range of 1-3km according to the flight range of the majority of the dispersing adults (Table 1) and measured as Chebishev distance based neighbourhood in the lattice. Adult dispersal was separated into emigration from the natal continuous maize field and immigration into all other maize fields (see flowchart in Fig. 1). The percentage of emigrants was considered density dependent in a similar way as the growth rate of *D v. virgifera* but in an 'S' shape, i.e. a positive density dependence, and determined by: the percent emigration from maize fields with populations below the lower limit of population density effects on emigration (referred to as % emigration from low-populated continuous maize); the percent emigration from maize fields with populations above the upper limit of population density effects on emigration (referred to as % emigration from high-populated continuous maize); lower limit of population density effects on percent emigration; and by the upper limit of population density effects on percent emigration. Moreover, a remaining range of the variability of emigration from single continuous maize fields was considered and its intensity was also an input factor as the standard deviation of randomization of percent emigrations. Immigration was calculated using the emigration factors described above; consequently, no particular input factor was used for this phenomenon.

Initial population: Normally distributed initial populations of adults were assumed for the continuous maize fields of the starter lattice of the first simulated year. The mean initial population was described as a percentage of the economic threshold. The SD of the distribution was also used in the model as an input factor.

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2.3.4 Update of the cells according to rotation schemes in the agricultural landscape

The states of the fields, i.e. first year maize (F), continuous maize (C) and non-maize (E), and thus model cells in the starting lattice were randomised in accordance with agricultural factors of % maize (a), % continuous maize (b), % rotated maize ($1-b$), farmers' decisions to rotate first year or continuous maize (Q) and agro policy legislations of mandatory rotation after 3, 4 or 5 consecutive year of maize growing. In the presence of agro policy legislations, the 'age' of C fields was also recorded and updated. However, for the population dynamics of *D. v. virgifera*, states of F-C-E were relevant; consequently, only these three states were subsequently considered.

Three probabilities were calculated for each considered agricultural landscape to describe that the fields will be maize (C or F) next year if they were C, F or E in this year, respectively: p_C: probability of the C→C update, p_F: probability of the F→C update, p_E: probability of the E→F update.

Absence of agro-policy legislation

The frequencies of the six possible updates in the entire lattices were as follows:

C→C: $a \cdot b \cdot p_C$ F→C: $a \cdot (1-b) \cdot p_F$ E→F: $(1-a) \cdot p_E$

C→E: $a \cdot b \cdot (1-p_C)$ F→E: $a \cdot (1-b) \cdot (1-p_F)$ E→E: $(1-a) \cdot (1-p_E)$

The proportions of the different states of cells remained constant in the simulated 10 year period. Hence, the equal proportions of C, F and E states were used to calculate the update probabilities

The F state can be reached from E fields only: $(1-a) \cdot p_E = a \cdot (1-b) \implies p_E = a \cdot (1-b)/(1-a)$

C can be reached from states F or C: $a \cdot b \cdot p_C + a \cdot (1-b) \cdot p_F = a \cdot b \implies p_F = (1-p_C)/(1/b-1)$

Introducing farmers' decisions to rotate first year or continuous maize:
$Q = p_F/p_C \implies p_C = 1/(Q \cdot (1/b-1)+1)$

There are two limitations, one for the relationship of a and b (I.); and one for the relationship for Q and b (II.) based on that the update probabilities are in the interval of [0,1]:
I.: $b \geq 2-1/a$; II.: $b \leq Q/(2Q-1)$ if $Q > 0.5$.

In the presence of agro-policy legislation

For simplicity, the probability of rotation of continuous maize fields with any 'age', except the maximum allowed with mandatory rotation, were the same. $p_C = p_{C2} = p_{C3}...$ The value of p_E is the same as in the absence of the agro-policy legislation. Considering the sum of the proportion of the states is always 1; and introducing $A = b/(Q(1-b))$ the following three equations was resulted for the legislation of mandatory rotation after 3, 4 or 5 consecutive years maize growing in a field, respectively: $p_C^2 + p_C - A = 0$; $p_C^3 + p_C^2 + p_C - A = 0$; $p_C^4 + p_C^3 + p_C^2 + p_C - A = 0$

These were solved by Maxima (v 5.27.0, (The Maxima Development Team, 2012) with graphical interface wxMaxima (v12.04.0, (Vodopivec, 2012). The limitations for the relationship of these four agricultural factors based on that the update probabilities are in the interval of [0,1] were not solved analytically. These limitations were checked in the code and model evaluations with agricultural factors which not matched with the limitations were excluded.

2.3.5 Population dynamics of *D. v. virgifera* in the lattice

Normally distributed initial population of adults were placed in continuous maize fields of the starter lattice (C) which were the natal fields of *D .v virgifera* adults in the first year. Then a part of the population dispersed (Fig. 1).

Dispersion was separated into emigration of adults out of their natal field to any maize field; and immigration of dispersing adults arriving in maize fields for oviposition. First, the density dependent proportional emigration was calculated for continuous maize fields with other neighbouring maize field closer than the Chebishev distance in accordance with dispersal of majority of adults (= reachable neighbourhood). In the few cases, when other maize field could not be found in the reachable neighbourhood of a continuous maize field, then this field was considered isolated and no emigration was simulated out that field (Fig 1.) An additional, multiplicative factor was randomised (with normal distribution, mean of 1 and SD according to the input factor) for each field to cover the variability among single continuous maize fields. Then the emigrating adults from each continuous maize field were divided for the number of all maize fields in first, second etc. neighbourhood. This subdivision of emigrating adults considered the following steps: The range of adult dispersal was the nth neighbourhood, meaning that there was emigration into the 1st, the 2nd and up to the nth neighbourhoods. Assuming there were N_i maize fields in the ith neighbourhood, the emigrants were divided into $\sum_{i=1}^{n}(n - i + 1) \cdot N_i$ parts. This quotient of adults was the emigration portion. Immigration to a maize field was the sum of emigration portions from the continuous maize fields within the range of adult dispersal. When continuous maize field could not be found in the reachable neighbourhood of a maize field, then this field was considered isolated and no immigration was simulated into that field (Fig 1.). After the dispersal process *D. v. virgifera* population densities of each maize field were compared with the economic threshold, and the fields with population density above threshold were counted (Fig. 1).

In each subsequent year, the new generation emerged multiplied by the density dependent generational growth rate in the continuous fields (Fig. 1). For each year the growth rates were multiplied by the environmental year effect, which had uniform distribution with a mean of 1 and within the interval determined by the 'intensity of environmental year effect on growth rates'. An additional multiplication factor was also randomised (with normal distribution, mean of 1 and SD according to the input factor) for each continuous maize field to cover the variability of growth rates among single continuous maize fields.

The described yearly processes were evaluated for 10 simulated years, and the counts of fields with population density above the threshold were averaged for the 10 year simulated period (= model output). The model was coded in R (R Development Core Team, 2011).

2.4 Sensitivity analysis of model inputs

Global sensitivity analysis was conducted with low discrepancy Sobol sequence covering the entire input space to identify the key input factors according to their account for variance of the model output (Saltelli et al., 2010; Saltelli et al., 2008). Two sensitivity indices were calculated for each input factor according to its single effect and its contribution to interactions with other input factors

(Saltelli et al., 2010). This method requires independent input factors (Saltelli et al., 2008); therefore, the limitations of agricultural input factors had to be considered. Consequently, at least 35% rotated maize was used to involve each level of agro-policy legislation also in the sensitivity analysis. However, a slight dependency remained among these factors. This was approximately 6% of all model evaluations of sensitivity analysis, and was assumed as a low enough value to allow the appropriate use of the described sensitivity analysis method.

2.5 Fit of the metamodels

Two metamodels (also referred to as surrogate models) were fitted to the simulation results of the entire model to develop a more user-friendly tool for determining percentage of maize fields reaching *D. v. virgifera* population above threshold on landscape level (Saltelli et al., 2008). Linear models were fitted, and the selection of input factors used as explanatory variables in the metamodels was based on the sensitivity analysis showing their significant influence on model output. One metamodel with the legislation of mandatory rotation after 3, 4 or 5 years consecutive maize growing was fitted and one without such legislation.

3. Results

3.1 Model output sensitivity to input factors

Only two among the 20 factors appeared to be of high importance in their influence on the percentage of maize fields reaching *D. v. virgifera* populations above threshold according to their account for the variance of the model output. These were the percentage of rotated maize among all maize fields, as well as *D. v. virgifera* population growth rate of 1.1 to10 in maize fields with populations below the lower limit of population density effects on growth rates (below at least 5 adults / plant, Table 1). Of comparatively low importance were farmers' decisions to rotate first year or continuous maize fields, as well as typically 1 to 3 km range of population dispersal, the considered 2 to 100 ha field sizes and the chosen agro-policy legislations for mandatory rotation after 3, 4 or 5 consecutive years of maize growing. All other 14 factors appeared to be of very low importance or had hardly any importance in their influence on the model output.

3.2 Model output depending on input factors

The percentage of maize fields reaching *D. v. virgifera* populations above threshold varied between 0% and 100% depending on the level of input factors (Fig. 2-4). In general, increases in the percentage of maize rotation led to a logistic shape of decreases in fields reaching *D. v. virgifera* thresholds (Fig. 2 and 4d). When considering the most likely values of all other input factors, then

nearly all maize fields were at risk of reaching *D. v. virgifera* thresholds when less than approximately 40 percent of maize field were only rotated (Fig. 4d). In contrast, only a small percentage of maize fields reached *D. v. virgifera* thresholds when percent rotation of maize was above approximately 70 %. Between 40 to 70% of maize rotation, a steep and highly variable decrease of this model output was observed when percent maize rotation increased. This relationship appeared to be robust, and only the second most influential input factor, i.e. the population growth rate in low-populated continuous maize, affected this pattern (Fig. 2). This is that an increased growth rate in low-populated continuous maize resulted in more maize fields reaching *D. v. virgifera* populations above threshold.
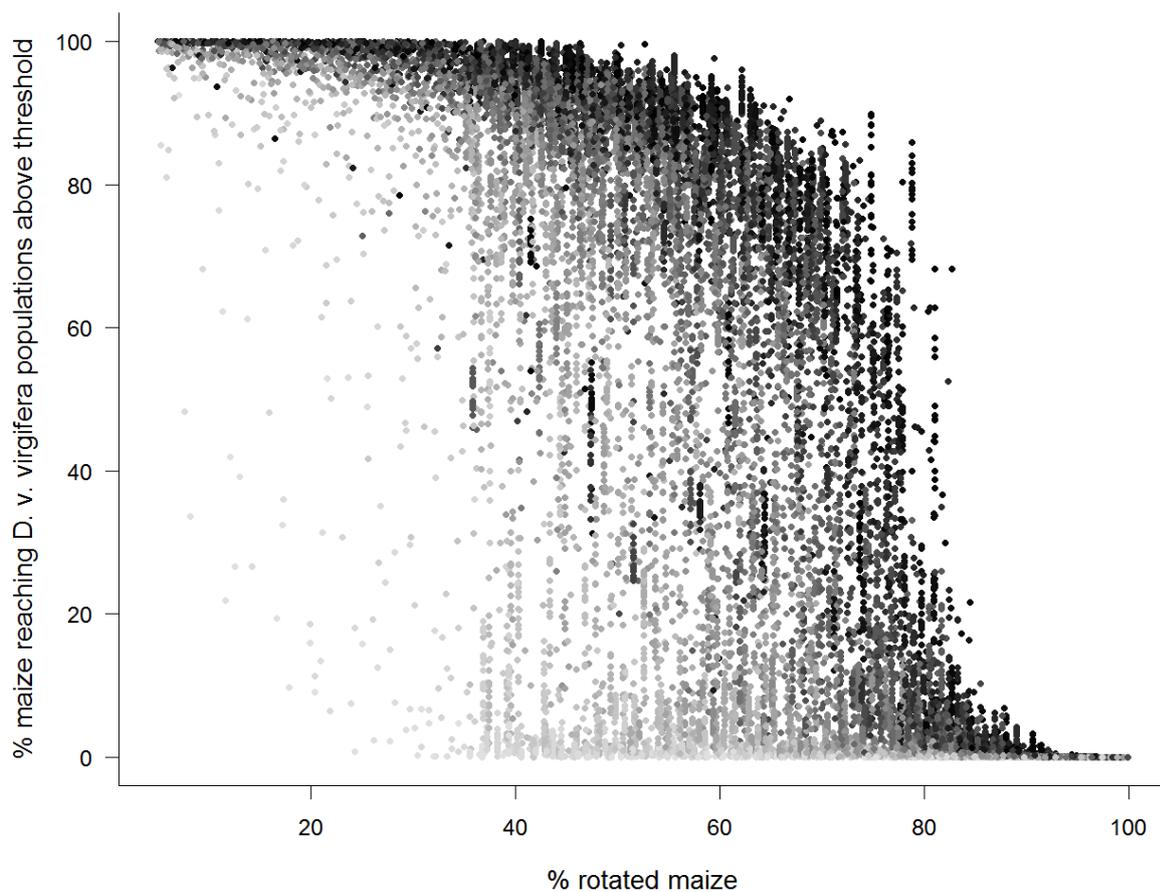

Fig. 2 The percentage of maize fields reaching *Diabrotica v. virgifera* populations above threshold (=model output) depending on the two most influential input factors of the model, i.e. (1) on the percentage of rotated maize among all maize fields (x axis), and (2) on the different *D. v. virgifera* population growth rates in low populated maize fields in the range of 1.1 to 10 presented in different colours of dots (e.g. lightest grey dots from growth rate 1.1 to darkest coloured dots to a growth rate of 10). All other 18 input factors were inserted in their respective ranges (see Table 1).

Farmers' decisions for rotating first year or continuous maize appeared to be of comparatively low importance for the model output (Fig. 3). However, at a given percentage of rotated maize, a more frequent decision of farmers not to rotate first year maize led to more second year maize fields and less 'older' continuous maize fields, because the probability of rotating a first year maize decreased whilst the probability of rotating a continuous maize field increased. This resulted in less maize

fields with extremely high population levels (e.g. above 50 adults / plant), and therefore in slightly less maize fields with *D. v. virgifera* populations above threshold (Fig. 3).
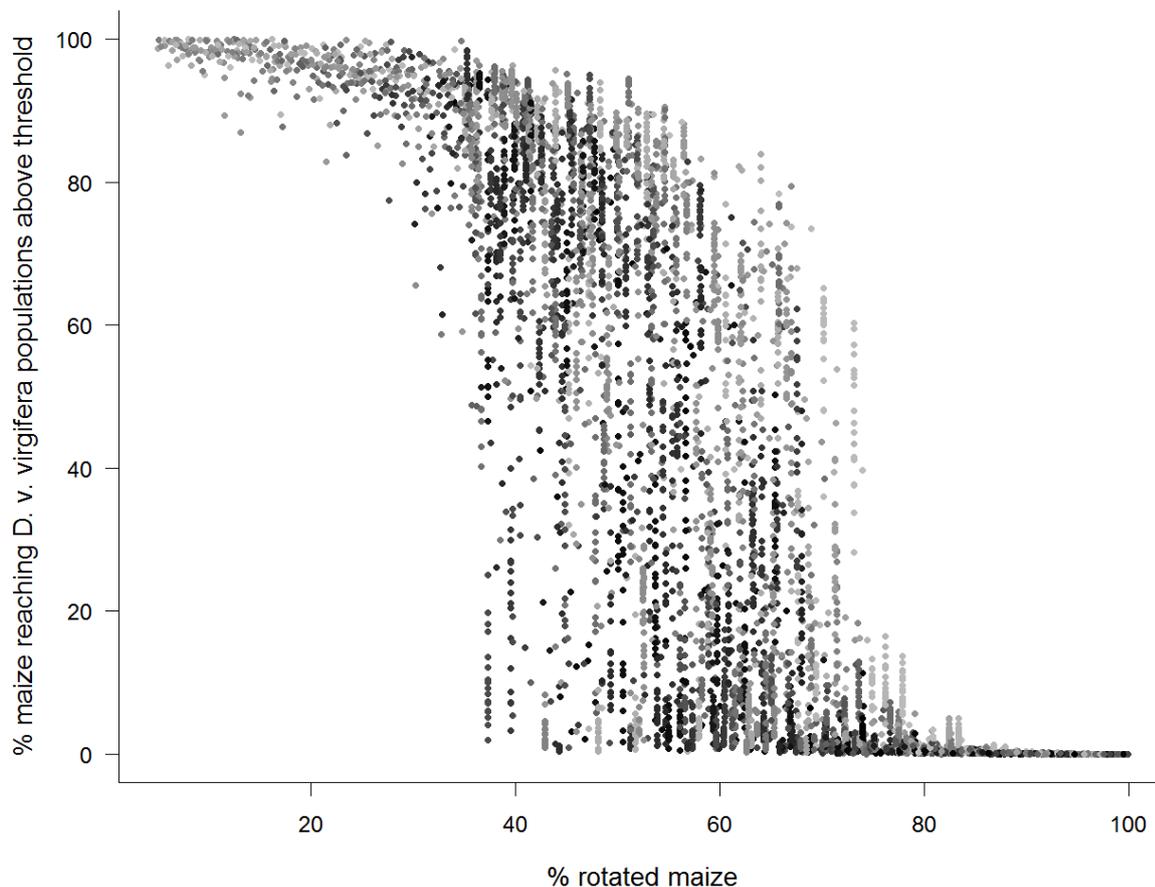

Fig. 3 The percentage of maize fields reaching *Diabrotica v. virgifera* populations above threshold (=model output) depending on the percentage of rotated maize among all maize fields (x axis), and on the different farmers' decisions to rotate first year maize or continuous maize in the range of 0.5 to 2 presented in different colours of the dots (e.g. lightest grey dots from 0.5 to darkest coloured dots of 2). All other 18 input factors are inserted in their respective ranges (Table 1), except the extremities of growth rate were excluded (2.5< and >5.5) to improve graph readability.

The here-chosen agro-policy legislations for mandatory rotations after 3, 4 or 5 consecutive years of maize growing appeared to be of comparatively low importance in their influence on the percentage of maize fields reaching *D. v. virgifera* populations above thresholds (Fig. 4). The greatest effect had the strictest chosen legislation, i.e. a rotation of each maize field within three years. With this legislation about 20% less maize fields would need to be rotated to keep *D. v. virgifera* populations below threshold in the majority if maize fields compared with absence of legislation (Fig 4a, d). Applying the legislation of mandatory rotation of each maize field within four years, only 5% less would need to be rotated (Fig. 4b, d). Mandatory rotation after 5 consecutive years maize growing resulted in comparable percentages of maize fields reaching *D. v. virgifera* populations above threshold as the 'no legislation' situation (Fig. 4c-d).
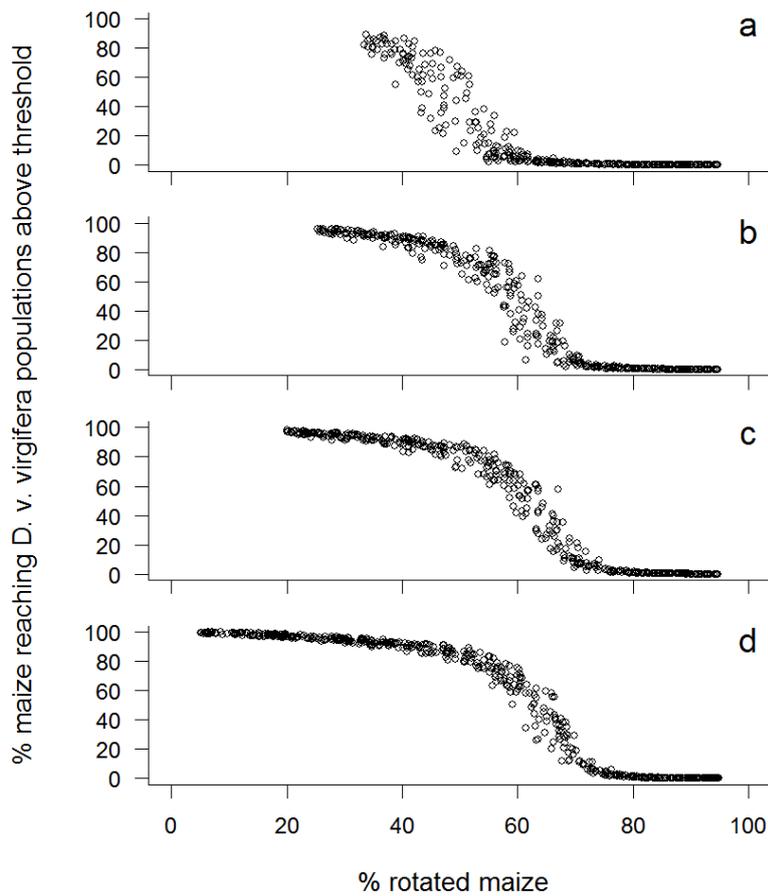
Fig. 4 The percentage of maize fields reaching *Diabrotica v. virgifera* populations above threshold (=model output) depending on the percentage of rotated maize among all maize fields (x axis), and on agro-policy legislations, i.e. (a) maize must be rotated after three years of consecutive maize growing; (b) maize must be rotated after four years; (c) after five years; and (d) no legislation was applied. All other 18 input factors were kept, for simplicity, at their most likely value (see Table 1).

3.3 Metamodels

Two metamodels were created to facilitate an easier use of the model. They only include input factors that appeared to have low to high importance in influencing the percentage of maize fields reaching *D. v. virgifera* populations above threshold in the sensitivity analyses. The population dispersal range and field size were combined into one covariant of the fit according to the number of fields reachable for *D. v. virgifera* adults as follows:

Fr = (*adultrange*^{2})/(*fieldsize*·10000), where *adultrange*: population dispersal range (km); *fieldsize*: average field size (ha) of the considered agricultural landscape

Metamodel 1 without agro-policy legislation of mandatory rotation (R^2 of the fit was 0.90):

logit(y+10^{-5})=-3.03-1.94·logit(*rot*)+0.73· *growth* -0.49·*Q*+0.00365· *Fr* -0.06·logit(*rot*)·*growth*-0.51·logit(*rot*)·*Q*

Metamodel 2 with agro policy legislation of mandatory rotation (R^2 of the fit was 0.88):

$logit(y+10^{-5})$=-6.26 -1.16·$logit(rot)$+ 0.94·$growth$-0.97·Q+0.53· $legisl$ +0.00594· Fr -0.18·$logit(rot)$·$growth$-0.13·$logit(rot)$·$legisl$-0.00544·$logit(rot)$· Fr

> *y*: proportion of maize fields reaching *D. v. virgifera* populations above threshold (=model output in proportions)
> *rot*: proportion of rotated maize among all maize
> *growth*: population growth rate of *D. v. virgifera* in low-populated continuous maize fields
> *Q*: farmers' decisions to rotate first year or continuous maize fields
> *Fr*: number of fields reachable for *D. v. virgifera* adults
> *legisl*: integer of 3, 4 or 5 in accordance with the mandatory rotation legislation

4. Discussion

A new discrete spatially explicit cellular automaton-like, lattice-based model was successfully developed. It allows the investigation of the population dynamics of *D. v. virgifera* on landscape level under the effect of different rotation strategies and agricultural landscape structures with an integrated pest management approach. Also other control options can be implemented into the model. Moreover, user-friendly metamodels were extracted to facilitate further usage and model dissemination.

After the serious damage caused by *D. v. virgifera* in the early 2000s in Hungary, the pest seems to be finally managed without major problems, because the percentage of continuous maize fields largely decreased compared to previous years. For example in Békés, Csongrád, Baranya and Somogy counties of Hungary, continuous maize decreased from 40-50% to 20% or below during the last ten years (Kiss, 2005; Ripka, 2008). This suggested that a 80% of rotation can control *D. v. virgifera* on the large majority of maize fields; although, maize rotation is not the unique control option used in the cited regions. In Serbia, it is suggested that even a 60% rotation would be sufficient (Sivcev et al., 2009). These experiences confirmed the outputs of the here-presented model, showing that total (=100%) rotation of maize is not necessary to keep *D. v. virgifera* populations below the economic threshold on landscape level, as well as only a small percentage of fields would be at risk of reaching populations above threshold when percentages of rotated maize are above approximately 70 %. Consequently, a 100% mandatory rotation of maize fields, such as in Switzerland should not to be advised for farmers for *D. v. virgifera* control; although, this rotation scheme can be sensible for many reasons. On the contrary, percentage of continuous maize growing currently reaches up to 80% in certain regions of Europe, e.g. of Belgium and the Netherlands (Fall & Wesseler, 2007; Leteinturier et al., 2007) and even up to 85% in Brescia province in northern Italy (Agosti, 2008, pers. comm.). Such percentages of continuous maize in regions are likely to be too high to keep populations of *D. v. virgifera* below economic thresholds, a fact that was also proposed by (Krügener et al., 2011).

However, in many European countries the aim is the eradication of *D. v. virgifera* or using containment measures to stop or slow down the spread of the pest (European Commission, 2003,

2006a, b). The latter can be implemented into my model structure; however, the threshold for containment is below the limit of the investigated threshold range (Table 1). Consequently, new model evaluations would need to be conducted at lower initial population and threshold values with the entire model, instead of directly using the metamodels.

Control options, such as seed treatments, soil insecticides, entomopathogenic nematodes or -fungi against the larvae, as well as insecticide sprays against the adults can also be considered by reducing generational growth in accordance with the control efficacy of the measure. Moreover, other maize production systems, such as for seed, silage and sweet maize or under different practises such as organic and conventional, can also be studied with the presented model structure through adjusting economic threshold levels.

The logistic pattern of the model output met the expected boundary conditions of (i) extremely low percentage of rotated maize below 20% resulting in rapid growth of *D. v. virgifera* populations, which, therefore, reached thresholds in almost all maize fields; and (ii) extremely high percentages of rotated maize above 90% resulting in pest extinction, in other words no maize fields reaching population levels above the threshold. This finding is in line with field trials that proved the high efficacy of maize rotation under European conditions (Kiss et al., 2005; Toepfer et al., 2011). In my model, increasing the generational growth rate in maize fields with populations below the lower limit of population density effects on growth rate resulted in more maize fields reaching *D. v. virgifera* populations above thresholds. High growth rate is necessary for a species to become a serious agricultural pest (Knipling, 1979), because this factor ensures the rapid population build ups even after control measures. Field studies on generational growth rates are limited for *D. v. virgifera*; moreover, in the most models of *D. v. virgifera* population dynamics lack detailed analyses on growth rates (Szalai et al., 2011b). The other factors describing the generational growth of *D. v. virgifera* were found to have very low or hardly any influence on the model output. However, the properties of the here-chosen simple density dependence function may have affected the model output. Moreover, the effect of density dependence and year effect on growth rate can be hardly separated in field situations (Szalai et al., 2011b). Consequently, examining the generational growth rate of the pest insect in field studies can be suggested to build more reliable population dynamics model of *D. v. virgifera*.

The found effect of farmers' decisions to rotate first year or continuous maize indicated that many continuous maize fields with maize grown for 2 consecutive years resulted in less maze fields reaching populations above the threshold, than considering a few heavily infested 'old' maize fields among rotating other maize fields. Consequently the 'age distribution' of continuous maize fields seems important in managing *D. v. virgifera* on landscape level. This factor was kept uniform in the model; however, stakeholders may make different decisions and follow different rotation schemes in the case of presence of *D. v. virgifera* (Cullen et al., 2008). In addition, also the legislation of mandatory rotation after 3, 4 or 5 consecutive years maize growing in a field affects the 'age distribution' of the continuous maize fields and the presence of heavily infested fields that could serve as a source for many and rapid new infestations. Therefore the existence of such legislations could reduce the need for rotated maize even down below 60% without more maize fields reaching *D. v. virgifera* populations above thresholds. The stricter legislation was applied the higher was this effect. The 'weakest' tested legislation of mandatory rotation after 5 consecutive years of maize growing in a field resulted in almost the same output of model runs without any legislation.

Consequently, applying mandatory rotation after 5 or more years of consecutive growing with maize cannot be suggested as a strategy for the control *D. v. virgifera*.

The model output is the percentage of maize fields reaching *D. v. virgifera* populations above threshold; therefore, equal results were obtained when 1.1 or 10 fold higher population densities than the threshold existed in a maize field. Density dependence affected the population dynamics mostly above threshold levels. Presumably, this shifted many input factors towards being of very low importance or to hardly any importance. Lower values of initial population sizes may have affected the percentage of maize fields reaching *D. v. virgifera* populations above threshold. A slight difference appeared to be between model evaluations of 50% and 80% of threshold as initial population. However, maize was assumed to be a preferable crop and *D. v. virgifera* a serious pest; thus, average populations in the agricultural landscape were not assumed to be far below thresholds. The rapid growth of *D. v. virgifera* populations in continuous maize fields might mask the effect of different threshold levels on the output. The here-chosen range of threshold (0.7 to 2 adults per plant) was only three fold, while the most likely applied growth rate was 4. Consequently, the threshold values had hardly any importance on the model output.

Astonishingly, most input factors supposedly determining the adult dispersal in the lattice of the modelled agricultural landscape appeared to have almost negligible effect on the percentage of maize fields reaching *D. v. virgifera* populations above threshold. Other neighbourhood definition can be developed in a lattice, for instance von Neumann neighbourhood based on Manhattan distance (Weisstein, 2012), and may then affect the dispersal processes and therefore the model output. However, I have not varied it as neighbourhood constructions are known to have usually only negligible effect on simulation results in cellular automatons or other lattice models (Durrett & Levin, 1994b)

Finally it must be stated that in my simulations, at least few maize fields always had a chance to reach population levels above the threshold even at rotational percentages of the agricultural landscape above 90% and even at the minimum and maximum values of the ranges of most of the considered input factors . Therefore, the here-presented model cannot substitute risk assessments and decision making at the field level. Therein, regular monitoring of *D. v. virgifera* populations and defining thresholds for local situations are the appropriate practices.

4.1 Conclusion

Current legislations of 100% rotation in the presence of *D. v. virgifera* are too strict in terms of pest management. In the future the here-presented model could be used by regional or country-wide decision makers in their agro-policy developments as well as for recommendations for appropriate integrated pest management guidelines.

5. New Scientific results

1. The generational (=annual) growth rate of *D. v. virgifera* populations averaged in close to 4 using adult emergence data of maize fields in south-Hungary and eastern-Croatia.

2. Using the determined growth rate, the first documented successful introduction of this species into Europe occurred between 1979 and 1984, which is 8-13 years before the detection of this species and its larval damage in maize fields near Belgrade, Serbia, in 1992.

3. Adjacent infested maize fields are the major source of *D. v. virgifera* adult dispersal into first-year maize and not, or to a lesser extent, the area-wide infestation levels, because infestation in the continuous maize fields accounted for more than 60% of the variation in the adult captures in the adjacent first-year maize fields.

4. A new discrete spatially explicit cellular automaton-like, lattice-based model was successfully developed. It allows the investigation of the population dynamics of *D. v. virgifera* on landscape level under the effect of different rotation strategies and agricultural landscape structures with an integrated pest management approach. Based on the simulation results the followings can be concluded:

    i. Only two factors were found to be of high importance in their influence on the percentage of maize fields reaching *D. v. virgifera* populations above thresholds: the percentage of rotated maize among all maize fields and the generational growth rate of the pest in low populated fields.

    ii. Total (100%) rotation of maize was not necessary to keep *D. v. virgifera* populations below the threshold level on landscape level.

    iii. Mandatory rotation after 3 or 4 consecutive years of maize growing reduces the need for rotation. The stricter legislation resulted in less need for rotation. However, the percentage of maize fields reaching *D. v. virgifera* populations above thresholds with mandatory rotation after 5 consecutive years of maize was comparable to those without such legislation.

    iv. An increased growth rate in low-populated maize resulted in more maize fields reaching *D. v. virgifera* populations above threshold.

5. Two metamodels were created to facilitate an easier use of the model. They only include input factors that appeared to have low to high importance in influencing the percentage of maize fields reaching *D. v. virgifera* populations above threshold in the sensitivity analyses:

    With legislation of mandatory rotation after 3, 4, or 5 years of consecutive maize growing:
    $$\text{logit}(y+10^{-5})=-6.26-1.16\cdot\text{logit}(rot)+0.94\cdot growth-0.97\cdot Q+0.53\cdot legisl+0.00594\cdot Fr-0.18\cdot\text{logit}(rot)\cdot growth-0.13\cdot\text{logit}(rot)\cdot legisl-0.00544\cdot\text{logit}(rot)\cdot Fr$$

    No legislation situation:
    $$\text{logit}(y+10^{-5})=-3.03-1.94\cdot\text{logit}(rot)+0.73\cdot growth-0.49\cdot Q+0.00365\cdot Fr-0.06\cdot\text{logit}(rot)\cdot growth-0.51\cdot\text{logit}(rot)\cdot Q$$

    y: proportion of maize fields reaching *D. v. virgifera* populations above threshold
    rot: proportion of rotated maize among all maize
    growth: growth rate of *D. v. virgifera* in low-populated continuous maize fields
    Q: farmers' decisions to rotate first year or continuous maize fields
    Fr: number of fields reachable for *D. v. virgifera* adults
    legisl: integer of 3, 4 or 5 in accordance with the mandatory rotation legislation

6. References

Aragon, P., Baselga, A., & Lobo, J.M. (2010) Global estimation of invasion risk zones for the western corn rootworm *Diabrotica virgifera virgifera*: integrating distribution models and physiological thresholds to assess climatic favourability. *Journal of Applied Ecology*, **47**, 1026-1035.

Aragon, P. & Lobo, J.M. (2012) Predicted effect of climate change on the invasibility and distribution of the Western corn root-worm. *Agricultural and Forest Entomology*, **14**, 13-18.

Baufeld, P. & Enzian, S. (2001) Simulation model spreading scenarios of Western Corn Rootworm (*Diabrotica virgifera virgifera*) in case of Germany. In Proceedings of 21st IWGO Conference (ed. by G. Carollo), pp. 63-67, Legnaro, Italia.

Baufeld, P. & Enzian, S. (2005). Maize growing, maize high-risk areas and potential yield losses due to western corn rootworm (*Diabrotica virgifera virgifera*) damage in selected European countries. In Western corn rootworm: ecology and management (ed. by S. Vidal, U. Kuhlmann & C.R. Edwards), pp. 285-302.

Bazok, R., Sivcev, I., Kos, T., Barcic, J.I., Kiss, J., & Jankovic, S. (2011) Pherocon AM Trapping and the "Whole Plant Count" Method - A Comparison of Two Sampling Techniques to Estimate the WCR Adult Densities in Central Europe. *Cereal Research Communications*, **39**, 298-305.

Boller, E.F., Malavolta, C., & Jörg, E. (1997) Guidelines for integrated production of arable crops in Europe: IOBC Technical guideline 3. In IOBC wprs Bulletin, Vol. 20, pp. 2-10.

Carrasco, L.R., Cook, D., Baker, R., MacLeod, A., Knight, J.D., & Mumford, J.D. (2012) Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents. *Ecological Economics*, **76**, 95-103.

Carrasco, L.R., Harwood, T.D., Toepfer, S., MacLeod, A., Levay, N., Kiss, J., Baker, R.H.A., Mumford, J.D., & Knight, J.D. (2010a) Dispersal kernels of the invasive alien western corn rootworm and the effectiveness of buffer zones in eradication programmes in Europe. *Annals of Applied Biology*, **156**, 63-77.

Carrasco, L.R., Mumford, J.D., MacLeod, A., Harwood, T., Grabenweger, G., Leach, A.W., Knight, J.D., & Baker, R.H.A. (2010b) Unveiling human-assisted dispersal mechanisms in invasive alien insects: Integration of spatial stochastic simulation and phenology models. *Ecological Modelling*, **221**, 2068-2075.

Carrasco, L.R., Mumford, J.D., MacLeod, A., Knight, J.D., & Baker, R.H.A. (2010c) Comprehensive bioeconomic modelling of multiple harmful non-indigenous species. *Ecological Economics*, **69**, 1303-1312.

Chiang, H.C. (1973) Bionomics of the northern and western corn rootworms. *Annual Review of Entomology*, **18**, 47-72.

Crowder, D.W. & Onstad, D.W. (2005) Using a generational time-step model to simulate dynamics of adaptation to transgenic corn and crop rotation by western corn rootworm (Coleoptera: Chrysomelidae). *Journal of Economic Entomology*, **98**, 518-533.

Crowder, D.W., Onstad, D.W., Gray, M.E., Pierce, C.M.F., Hager, A.G., Ratcliffe, S.T., & Steffey, K.L. (2005) Analysis of the dynamics of adaptation to transgenic corn and crop rotation by western corn rootworm (Coleoptera: Chrysomelidae) using a daily time-step model. *Journal of Economic Entomology*, **98**, 534-551.

Cullen, E.M., Stute, J.K., Raymond, K.L., & Boyd, H.H. (2008) Farmers' Perspectives on IPM Field Scouting During a Period of Insect Pest Range Expansion: A Case Study of Variant Western Corn Rootworm (Coleoptera: Chrysomelidae) in Wisconsin. *American Entomologist*, **54**, 170-178.

Czárán, T. (1998) Spatiotemporal models of population and community dynamics Chapman & Hall, London.

Dupin, M., Reynaud, P., Jarosik, V., Baker, R., Brunel, S., Eyre, D., Pergl, J., & Makowski, D. (2011) Effects of the Training Dataset Characteristics on the Performance of Nine Species Distribution Models: Application to *Diabrotica virgifera virgifera*. *Plos One*, **6**, e20957.

Durrett, R. & Levin, S. (1994a) The Importance of Being Discrete (and Spatial). *Theoretical Population Biology*, **46**, 363-394.

Durrett, R. & Levin, S.A. (1994b) Stochastic Spatial Models: A User's Guide to Ecological Applications. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **343**, 329-350.

Edwards, C.R., Igrc Barcic, J., Berger, H.K., Festic, H., Kiss, J., Princzinger, G., Schulten, G.G.M., & Vonica, I. (1998) Overview of the FAO western corn rootworm management program for central Europe. *Pflanzenschutzberichte*, **57**, 3-14.

Edwards, C.R., Larry, W.B., & Turpin, F.T. (1994) Field crop insects, managing corn rootworms. Purdue University, Cooperative Extension Service, E-49, 1-6, West Lafayette.

Elliott, N.C. & Hein, G.L. (1991) Population-Dynamics of the Western Corn-Rootworm - Formulation, Validation, and Analysis of a Simulation-Model. *Ecological Modelling*, **59**, 93-122.

European Commission (2003) Commission Decision 2003/766/EC of 24 October 2003 on Emergency Measures to Prevent the Spread within the Community Of *Diabrotica virgifera* Le Conte. *Official Journal of the European Union*, **2003/766/EC**.

European Commission (2006a) Commission Decision 2006/564/EC amending Decision 2003/766/EC of 17 August 2006 on emergency measures to prevent the spread within the Community of *Diabrotica virgifera*. *Official Journal of the European Union*, **2006/564/EC**.

European Commission (2006b) Commission Recommendation 2006/565/EC of 11 August 2006 on containment programmes to limit the further spread of *Diabrotica virgifera* Le Conte in Community areas where its presence is confirmed. *Official Journal of the European Union*, **2006/565/EC**.

Fall, E.H. & Wesseler, J.H.H. (2007). Report on environmental and socio-economic analysis (WP 2 Task 3), Diabr-Act, (Diabr-Act -Harmonise the strategies for fighting *Diabrotica virgifera virgifera*).

Fall, E.H. & Wesseler, J.H.H. (2008). Practical compatibility and economic competitiveness of each biological control option with chemical control and with cultural control of WCR (WP 2 Task 3), Diabr-Act, (Diabr-Act -Harmonise the strategies for fighting *Diabrotica virgifera virgifera*).

Hein, G.L. & Tollefson, J.J. (1987) Model of the biotic potential of western corn rootworm (Coleoptera: Chrysomelidae) adult populations, and its use in studying population dynamics. *Environmental Entomology*, **16**, 446-452.

Hemerik, L., Busstra, C., & Mols, P. (2004) Predicting the temperature-dependent natural population expansion of the western corn rootworm, *Diabrotica virgifera. Entomologia Experimentalis et Applicata*, **111**, 59-69.

Higgins, R., Brooks, L., & Sloderbeck, P.E. (1995) Insect Management for Corn in 1995 Cooperative Extension Service, Kansas State University.

Kiss, J. (2005). WCR risk estimation for developing IPM in maize. GTFS/RER/017/ITA "Integrated Pest Management for Western Corn Rootworm in Central and Eastern Europe" FAO Project Report

Kiss, J., Komaromi, J., Bayar, K., Edwards, C.R., & Hatala-Zseller, I. (2005). Western corn rootworm (*Diabrotica virgifera virgifera* LeConte) and the crop rotation systems in Europe. In Western corn rootworm: ecology and management (ed. by S. Vidal, U. Kuhlmann & C.R. Edwards), pp. 189-220.

Knipling, E.F. (1979) The Basic Principles of Insect Population Suppression and Management United States Department of Agriculture, Wahington DC, USA.

Krügener, S., Baufeld, P., & Unger, J.-G. (2011) Modelling of population dynamics of the Western Corn Rootworm (*Diabrotica virgifera virgifera*) – examination of various containment measures. *Journal für Kulturpflanzen*, **63**, 69-76.

Leteinturier, B., Tychon, B., & Oger, R. (2007) Diagnostic agronomique et agro-environnemental des successions culturales en Wallonie (Belgique). *Biotechnol. Agron. Soc. Environ.*, **11**, 27-38.

Levay, N., Toepfer, S., Kiss, J., & Terpo, I. (2008) Colonization of first year maize fields with *Diabrotica v. virgifera* adults from infested continuous maize fields. In International DiabrAct symposium on:"Western Corn Rootworm management in Europe: Future research and action needs" 25 - 29 May 2008 (ed. by S. Vidal), Göttingen, Germany.

Miller, N., Estoup, A., Toepfer, S., Bourguet, D., Lapchin, L., Derridj, S., Kim, K.S., Reynaud, P., Furlan, L., & Guillemaud, T. (2005) Multiple transatlantic introductions of the western corn rootworm. *Science (Washington)*, **310**, 992.

Mooney, E. & Turpin, F.T. (1976) ROWSIM:a GASP IV based rootworm simulator. In Research Bulletin 938, Purdue Agriculture Experiment Station West Lafayette, IN.

O'Rourke, M.E. & Jones, L.E. (2011) Analysis of landscape-scale insect pest dynamics and pesticide use: an empirical and modeling study. *Ecological Applications*, **21**, 3199-3210.

Onstad, D.W., Guse, C.A., Spencer, J.L., Levine, E., & Gray, M.E. (2001a) Modeling the dynamics of adaptation to transgenic corn by western corn rootworm (Coleoptera: Chrysomelidae). *Journal of Economic Entomology*, **94**, 529-540.

Onstad, D.W., Joselyn, M.G., Isard, S.A., Levine, E., Spencer, J.L., Bledsoe, L.W., Edwards, C.R., Di Fonzo, C.D., & Willson, H. (1999) Modeling the spread of western corn rootworm (Coleoptera : Chrysomelidae) populations adapting to soybean-corn rotation. *Environmental Entomology*, **28**, 188-194.

Onstad, D.W. & Meinke, L.J. (2010) Modeling Evolution of *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) to Transgenic Corn With Two Insecticidal Traits. *Journal of Economic Entomology*, **103**, 849-860.

Onstad, D.W., Spencer, J.L., Guse, C.A., Levine, E., & Isard, S.A. (2001b) Modeling evolution of behavioral resistance by an insect to crop rotation. *Entomologia Experimentalis et Applicata*, **100**, 195-201.

Pan, Z.Q., Onstad, D.W., Nowatzki, T.M., Stanley, B.H., Meinke, L.J., & Flexner, J.L. (2011) Western Corn Rootworm (Coleoptera: Chrysomelidae) Dispersal and Adaptation to Single-Toxin Transgenic Corn Deployed With Block or Blended Refuge. *Environmental Entomology*, **40**, 964-978.

R Development Core Team. (2011) *R: A language and environment for statistical computing.*, Version 2.14.1. R Foundation for Statistical Computing Vienna. URL: www.r-project.org

Ripka, G. (2008) Egy állandósult, de nem megoldhatatlan növényvédelmi gond: az amerikai kukoricabogár. *Gyakorlati agrofórum*, 64-66.

Saltelli, A., Annoni, P., Azzini, I., Campolongo, F., Ratto, M., & Tarantola, S. (2010) Variance based sensitivity analysis of model output. Design and estimator for the total sensitivity index. *Computer Physics Communications*, **181**, 259-270.

Saltelli, A., Ratto, M., Andres, T., Campolongo, F., Cariboni, J., Gatelli, D., Saisana, M., & Taratola, S. (2008) Global Sensitivity Analysis. The Primer John Wiley & Sons Ltd, Chichester, West Sussex PO19 8SQ, UK.

Sivcev, I., Stankovic, S., Kostic, M., Lakic, N., & Popovic, Z. (2009) Population density of *Diabrotica virgifera virgifera* LeConte beetles in Serbian first year and continuous maize fields. *Journal of Applied Entomology*, **133**, 430-437.

Storer, N.P. (2003) A spatially explicit model simulating western corn rootworm (Coleoptera: Chrysomelidae) adaptation to insect-resistant maize. *Journal of Economic Entomology*, **96**, 1530-1547.

Szalai, M., Koeszegi, J., Toepfer, S., & Kiss, J. (2011a) Colonisation of First-year Maize Fields by Western Corn Rootworm (*Diabrotica virgifera virgifera* LeConte) from Adjacent Infested Maize Fields. *Acta Phytopathologica et Entomologica Hungarica*, **46**, 213-223.

Szalai, M., Komaromi, J.P., Bazok, R., Barcic, J.I., Kiss, J., & Toepfer, S. (2011b) Generational growth rate estimates of *Diabrotica virgifera virgifera* populations (Coleoptera: Chrysomelidae). *Journal of Pest Science*, **84**, 133-142.

The Maxima Development Team. (2012) *Maxima, a Computer Algebra System*, Version 5.27.0.

Toepfer, S. & Kuhlmann, U. (2005). Natural mortality factors acting on western corn rootworm populations: a comparison between the United States and Central Europe. In Western corn rootworm: ecology and management (ed. by S. Vidal, U. Kuhlmann & C.R. Edwards), pp. 95-119.

Toepfer, S., Zellner, M., & Kuhlmann, U. (2011) Oviposition of *Diabrotica* in non-maize crops and implications on crop rotation. *IWGO-Newsletter*, **31**, 40.

Vodopivec, A. (2012) *wxMaxima*, Version 12.04.0.

Weisstein, E.W. (2012) von Neumann Neighborhood. In MathWorld -A Wolfram Web Resource.

Willson, H.R. (1992). Scouting and Thresholds in Insect Control, Corn Rootworm. In Insect Control Guide, pp. 36-37. Meister Publishing Company, Willoghby, OH.

7. Related publications

Peer-reviewed journal articles:

M. Szalai, J. Kiss, Sz. Kövér, S. Toepfer (2012): Simulating crop rotation strategies with a spatiotemporal lattice model to improve the management of the maize pest *Diabrotica virgifera virgifera. Ecological Modelling*, submitted.

M. Szalai, J. Papp Komáromi, R. Bažok, J. Igrc Barčić, J. Kiss, S. Toepfer (2011): Generational growth rate estimates of *Diabrotica virgifera virgifera* populations (Coleoptera: Chrysomelidae). *Journal of Pest Science,* 84(1) 133-142, DOI: 10.1007/s10340-010-0336-z. (**IF: 1,509**, 2011)

M. Szalai, J. Kőszegi, S. Toepfer, J. Kiss (2011): Colonisation of First-year Maize Fields by Western Corn Rootworm (*Diabrotica virgifera virgifera* LeConte) from Adjacent Infested Maize Fields. *Acta Phytopathologica et Entomologica Hungarica,* 46(2) 213-223, DOI: 10.1556/APhyt.46.2011.2.5.

Szalai M., Lévay N., Papp Komáromi J., S. Toepfer, Kiss J. (2010): Az amerikai kukoricabogár populációjának térség szintű szabályozása: egy sejtautomata modell és szimuláció. (Management of the western corn rootworm at landscape level: a discrete spatiotemporal simulation model) *In Hungarian, Növényvédelem,* 46(9) 417-424.

Conference abstracts:

M. Szalai, S. Toepfer, Sz. Kövér & J. Kiss (2012): Simulation of rotation strategies to improve management of Western Corn Rootworm in Europe. *6th Annual Workshop of International Pest Risk Mapping Workgroup (Advancing risk assessment models for invasive alien species in the food chain: contending with climate change, economics and uncertainty), Tromso, Norway 23 – 26 July, 2012*

M. Szalai, Sz. Kövér, J. Kiss & S. Toepfer (2011): Simulating maize rotation strategies to develop IPM for *Diabrotica v. virgifera* in Europe. *24th IWGO Conference & 3rd International Conference of Diabrotica Genetics, Freiburg, Germany, 24 – 26 October, 2011*

M. Szalai, S. Toepfer, Sz. Kövér & J. Kiss (2011): Simulating crop rotation at landscape level to improve management of Western Corn Rootworm. *7th European Conference on Ecological Modelling, Riva del Garda, Italy, 30 May – 2 June, 2011*

Szalai M., S. Toepfer, Kövér Sz. & Kiss J. (2011): A vetésváltás térség szintű vizsgálata szimulációs modellel az amerikai kukoricabogár elleni védekezésben. *KÖSzi 2011 4. Kvantitatív Ökológiai Szimpózium, Szeged, 2011. április 7–8*

J. Kiss, **M. Szalai** & S. Toepfer (2011): Developing IPM for WCR in a spatial and temporal context. *„Leben mit dem Maiswurzelbohrer" Worksohop, Klagenfurt, 1-2 March, 2011*

M. Szalai, J. Papp Komáromi, J. Kiss & S. Toepfer (2010): A discrete spatiotemporal population model for management of western corn rootworm (*Diabrotica virgifera virgifera* LeConte; Coleoptera: Chrysomelidae) at landscape level. *9th European Congress of Entomology Conference, Budapest, Hungary, 22–27 August, 2010*

M. Szalai, N. Levay, S. Toepfer & J. Kiss (2009): How to develop discrete spatiotemporal population models for the western corn rootworm at landscape level. *23rd IWGO Conference, Munich, Germany, 5–8 April, 2009*

Szalai M., Lévay N., S. Toepfer & Kiss J.: Szimulációs modell kidolgozása az amerikai kukoricabogár térségi szintű kezelésére. *55. Növényvédelmi Tudományos Napok, Budapest, 2009. február 24–25*

Szalai M., Papp Komáromi J., R. Bažok, S. Toepfer & Kiss J.: Az amerikai kukoricabogár populációbecslése: egy relatív módszer szolgáltathat annyi információt, mint egy abszolút? *55. Növényvédelmi Tudományos Napok, Budapest, 2009. február 24–25*

Szalai M., Lévay N., Papp Komáromi J., Juhász M. & Kiss J.: Az amerikai kukoricabogár szaporodási rátájának, mint a populációdinamikai modellalkotás egyik sarokpontjának meghatározása. *KÖSzi 2008 3. Kvantitatív Ökológiai Szimpózium „Életre keltett adatok", Budapest, 2008. március 18–19*

M. Szalai, N. Levay, J. P. Komaromi, M. Juhasz & J. Kiss (2008): Defining the growth rate of WCR (*Diabrotica virgifera virgifera* LeConte): An important factor for modelling its population dynamics. *"Harmonise the strategies for fighting Diabrotica virgifera virgifera" Diabr-Act Symposium Göttingen, Germany, 25-29 May, 2008*

B. Pai, **M. Szalai** & J. P. Komaromi (2008): Diel flight activity of male western corn rootworm (Diabrotica virgifera virgifera LeConte) adults *"Harmonise the strategies for fighting Diabrotica virgifera virgifera" Diabr-Act Symposium Göttingen, Germany, 25-29 May, 2008*