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Flow of genetic information through agricultural ecosystems: a generic modelling framework with application to pesticide-resistance weeds and genetically modified crops

O. Richter, R. Seppelt*

Department of Environmental Systems Analysis, Institute of Geoecology, Technical University Braunschweig, Langer Kamp 19c, 38106 Braunschweig, Germany

Abstract

Unintended spatial spread of genetic information is one of the major problems in modern agriculture. The vertical distribution of transgenic properties and the spatial spread of resistant weeds and pests are likely to develop under long-term pesticide use. These are complex systems that require an integrated view of population dynamics, genetics, and physical transport processes. Mathematical models may be utilised to support of risk assessment and to derive appropriate risk management strategies. In this contribution we propose a generic modelling framework that provides an explicit simulation of the spatial patterns of gene flow through agro-ecosystems.

Pollen dispersal is modelled with traditional transport equations from atmospheric physics that are applied to outcrossing studies of genetically modified maize. Transport equations were coupled to models of population dynamics and genetics with partial differential equations that combine dispersal, growth and genetics. The overall model consists of a set of coupled partial differential equations for pollen dispersal, and the spatial and temporal dynamics of each biotype involved. Initial boundary value problems are set up for the dispersal of resistance in dependence on spatial spread patterns, which are solved by finite element methods.
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1. Introduction

In modern agriculture gene flow is important because of (i) the development and spread of resistant biotypes from the extended use of pesticides, and (ii) the large-scale release of transgenics. Gene flow is a complex process embracing population dynamics, genetics, and the flow of genetic information via pollen and seed dispersal. In order to establish mathematical models for risk assessment and management, these processes have to be integrated. Each of these processes have been published with adverse set of mathematical approaches:

- deterministic matrix population models (Richter et al., 2002),
- stochastic models (Paice et al., 1998),
- cellular automaton models for dispersal of resistant weeds (Colbach and Sache, 2001; Ermentrout and Edelstein-Keshet, 1993; Richter et al., 2002),
- air pollution models stemming from atmospheric diffusion theories (Lavigne et al., 1998; Okubo and Levin, 1989), and
- population dispersal in terms of partial differential equations (Murray, 1989).

* Corresponding author. Tel.: +49-531-391-5608; fax: +49-531-391-8170.

E-mail address: R.Seppelt@tu-braunschweig.de (R. Seppelt).

Each approach has its own merits and justification in specific contexts and scales. However, our aim is to find a general mathematical framework for the integration of all processes into an aggregated, transferable and modular model structure.

The processes taken into consideration for integrated modelling of biosafety issues are population dynamics, genetics, and dispersal of genetic information. If gene flow is considered at the field and landscape scale, a convenient general mathematical structure is a system of partial differential equations. For each of the processes involved, relations in the form of ordinary or partial differential equations can be formulated, and then bound into one system of equations. Advantage of a mathematically homogeneous approach includes:

(i) the processes can be formulated in a concise way that
(ii) leads to well defined mathematical problems, and
(iii) for which advanced numerical solution schemes are available.

Furthermore, a concise mathematical formulation is advantageous in that general dynamic patterns can be explained by the structure of the differential equations. This is not feasible for models, which are merely defined in algorithmic form, for instance rule based systems in cellular automaton models (cf. Richter et al., 2001).

The paper is structured as follows: Section 2 describes the proposed integrative modelling framework comprising population dynamics, dispersal, and genetics. Section 3 applies this framework to different experimental data sets. Sub-modules of the framework are used for model analysis and calibration. These results are finally discussed in Section 4.

2. Modelling framework for gene flow in agro-ecosystems

Modelling the spatial spread of genetic information requires coupling of three components: population dynamics, dispersal, and genetics. First a general model for spatially explicit population dynamics based on partial differential equations is developed. This sub-model acts as a source for pollen emission. Second, Lagrangian and the Eulerian approaches for the atmospheric transport processes are incorporated

to model the dispersal of pollen. The third part of the modelling concept is a genetic model that couples pollen imission-events of out-crossing, with the phenomenological pattern of the crop.

2.1. Population dynamics

First we consider $n = 2$ and $n = 3$ populations of different biotypes of a species with the population density denoted by N_i ($i = 1, \ldots, n$). The approach can be extended to an arbitrary number of biotypes.[1] The following basic equation formulates the processes of crop growth and spatial spread, and exchange of genetic information.

$$\frac{\partial N_i}{\partial t} = \underbrace{r_i(\vec{N}, \vec{P})}_{(a)} - \underbrace{\mu_i N_i \left(1 + \sum_{j=1}^{n} \alpha_{i,j} N_j\right)}_{(b)}$$
$$+ \underbrace{\nabla \cdot D_i \nabla N_i}_{(c)}, \quad i = 1, \ldots, n \qquad (1)$$

Population growth and the underlying genetic processes are incorporated by the Term (a). In Section 2.3 we will present a two-loci genetic model for the specification of r_i. P_i denotes the available pollen of biotype N_i.

Term (b) models the species dependent mortality with a parameter μ_i and the interspecific competition between the biotypes i and j defined by parameters $\alpha_{i,j}$. If only a single biotype is considered, the Terms (a) and (b) are equivalent to the logistic growth equation. The last Term (c) of Eq. (1) describes the spatial spread of species by a simple diffusion-type process. The specification of the coefficient D can incorporate different strategies for spatial spread by rhizomes or due to clonal growth. D depends on habitat suitability or abiotic parameters (cf. Seppelt, 2003, chapter 3). Note the model is also applicable to insect populations with immobile (larvae) and mobile (adult) life stages. If exchange of genetic information between the biotypes is neglected, Term (a) becomes a simple growth rate. The equation system of this sub-model can be used to study spatially explicit habitat-dependent population dynamics.

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[1] We will carefully point out if there are any special considerations according to the number of species.

2.2. Pollen dispersal

Several studies from recent literature have examined the outcrossing probability of genetic modified crops (Lavigne et al., 1998; Emberlin et al., 1999; Treu and Emberlin, 2000). However, comparisons between pollen dispersal experiments is difficult because of the strong dependence on the shape and area of the source and receptor plots, and the strong influence of different weather conditions, even for the same crop (Lavigne et al., 1998). Models are needed that relate dispersal distances to such measurable parameters as wind speed and settling velocity. This allows comparisons among different environments, rather than conventional phenomenological models (Okubo and Levin, 1989). Two approaches (Lagrange and Eulerian) are used for modelling the spatial spread of genetic information. Further, differences between phenomenological- and physical-based model approaches are considered.

2.2.1. Lagrange approach

The Lagrange approach describes the concentration statistics in terms of the stochastic properties of the paths of ensembles of particles. Transport of a particle in the three-dimensional space from a location (x, y, z) to a location (x', y', z') is modelled by a density function $f(x - x', y - y', z - z')$, also known as a transfer function. The amount of particles, which are emitted from a location (x', y', z') and reach a location (x, y, z), is given by the product of the density of pollen donators $S_i(x', y', z')$ of biotype i at location (x', y', z') and the transfer function $f(x - x', y - y', z - z')$. The total amount of pollen, which reaches a single plant in (x, y, z), is then derived by the integral over all donators (Lavigne et al., 1998).

$$F_i(x, y, z) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} f(x - x', y - y', z - z')$$
$$\times S_i(x', y', z')\mathrm{d}x'\mathrm{d}y'\mathrm{d}z' \qquad (2)$$

A frequent choice for f is a transfer function of Gaussian-type with covariance matrix Σ in a general for written as:

$$f(\vec{x}) = \frac{1}{(2\pi)^{3/2}\left|\Sigma^{1/2}\right|}$$
$$\times \left(\exp\left[-\frac{1}{2}(\vec{x} - \vec{x}')\Sigma^{-1}(\vec{x} - \vec{x}')\right]\right) \qquad (3)$$

with $\vec{x} = (x, y, z)$, $\vec{x}' = (x', y', z')$ and the general covariance matrix $\Sigma \in R^{3\times3}$. This ansatz is supported by the fact that the general form of the analytical solution of the atmospheric diffusion equation for an instantaneous source in a constant velocity field in x-direction is given by such a Gaussian-type function (cf. Seinfeld and Pandis, 1998).

$$f_1(x, y, z, t) = \frac{S}{8(\pi t)^{3/2}(K_{xx}K_{yy}K_{zz}t)^{1/2}}$$
$$\times \exp\left[-\frac{(x - ut)^2}{4K_{xx}t} - \frac{y^2}{4K_{yy}t} - \frac{z^2}{4K_{zz}t}\right]$$
$$(4)$$

Here u denotes the wind velocity, S is the source strength and K_{ii} is the Eddy diffusion coefficients.

Several experimental investigations (Schütte et al., 2001) showed that spatial spread of pollen is characterised by short and long distance transport. A possible explanation is that pollen in the upper layers of the canopy has a higher diffusion resistance than pollen in the upper layers of the atmosphere (Nichols and Hewitt, 1994). This effect can be modelled by the superposition of transfer functions of Gaussian type. The superposition of two Gaussian-type transfer-functions with covariance matrices Σ_1 and Σ_2 as:

$$f_S(\vec{x}) = S_i\left(\beta\exp\left[-\frac{1}{2}(\vec{x} - \vec{x}')\Sigma_1^{-1}(\vec{x} - \vec{x}')\right]\right.$$
$$\left. + (1 - \beta)\exp\left[-\frac{1}{2}(\vec{x} - \vec{x}')\Sigma_2^{-1}(\vec{x} - \vec{x}')\right]\right)$$
$$(5)$$

yields a typical biphasic profile of spatial spread. Fig. 1 illustrates the superposition of two Gaussian-type functions.

For each biotype i, model parameters include the weighting factor β, and the six elements (in the three-dimensional case or three elements in the two-dimensional case) of the symmetric covariance matrices. These parameters reflect the previous history concerning wind velocity and other meteorological variables and the time overlap of anthesis of the donor population and fertilisation sensitivity of the recipient population.

2.2.2. Eulerian approach

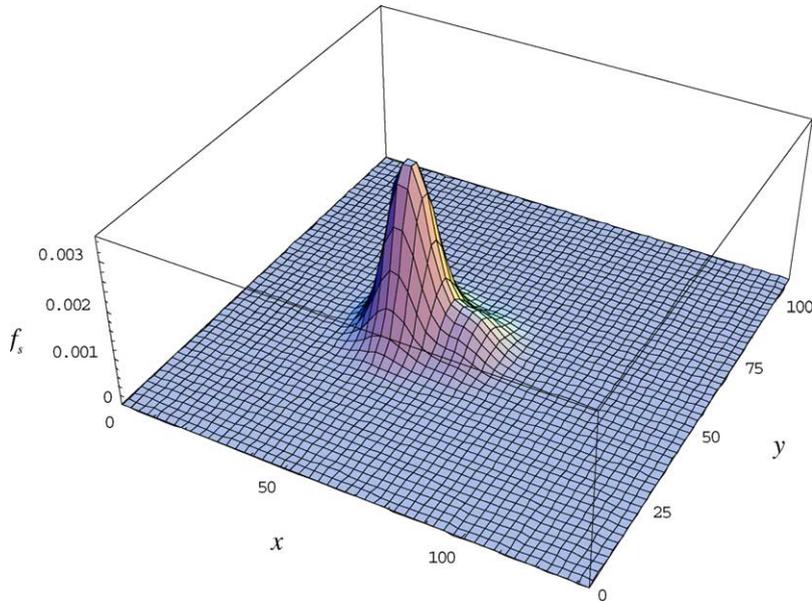The Eulerian approach describes the spatial spread of an ensemble of particles relative to a fixed co-

Fig. 1. Superposition f_S of two Gaussian-type functions f with distinct diffusion coefficients.

ordinate system. The mass balance equation for an infinitesimally small representative volume leads to a partial differential equation. Under simplifying assumptions (molecular diffusion negligible compared to turbulent diffusion, and incompressible atmosphere) spatial spread of pollen P_i of biotype i is described by the following partial differential equation:

$$\frac{\partial P_i}{\partial t} = \nabla \cdot K \nabla P_i - \nabla \cdot \vec{u} P_i + S_i(\vec{x}, t) \tag{6}$$

P_i denotes the particle density, e.g. pollen, K is the diffusion coefficient and S_i is a source term.

The wind velocity profile above canopy is given by an empirical formula:

$$u_x(z) = u_y(z) = u_0 \left(\frac{z}{h_0} \right)^s, \quad u_z = -g \tag{7}$$

The wind velocity field is thus given by $\vec{u} = (u_x, u_y, u_z)$. Gravitational settling of pollen is specified by the parameter g. u_x and u_y specify the velocity of a wind field and thus define the boundary condition for Eq. (6). u_0 denotes an average wind speed and h_0 is the height of the canopy. s is a shape parameter. Based on field measurements the parameters u_0 and h_0 can be measured directly. The shape parameter can

be identified with parameter estimation techniques (Richter and Söndgerath, 1990). Fig. 2 illustrates the boundary condition for the function $u_x = u_y$ with data from Raupach and Thom (1981).

2.2.3. Different mobility of pollen

Eq. (1) may be applied to model spatial spread of crops, weed or insect populations. In this equation dispersal is modelled by a single parameter D. Analysis of gene flow through populations, and the spread of genetic properties necessitates distinguishing populations N_i and their emitted pollen P_i. To now the density of a certain population N_i was available. The emitted pollen from population, N_i, is given by the equation:

$$S_i(x, y, t) = \alpha_i N_i(x, y, t) f(t) \tag{8}$$

As a first approach, it is assumed that pollen emissions are proportional to the plant density, as embodied in the coefficient α_i. The time dependent factor $f(t)$ incorporates phenological stages, e.g. blossom of the crop and the genotype N_i. Note Eq. (8) specifies the source strength of pollen used in Eqs. (2), (4) and (6) and couples the population dynamics sub-model with the one for dispersal.
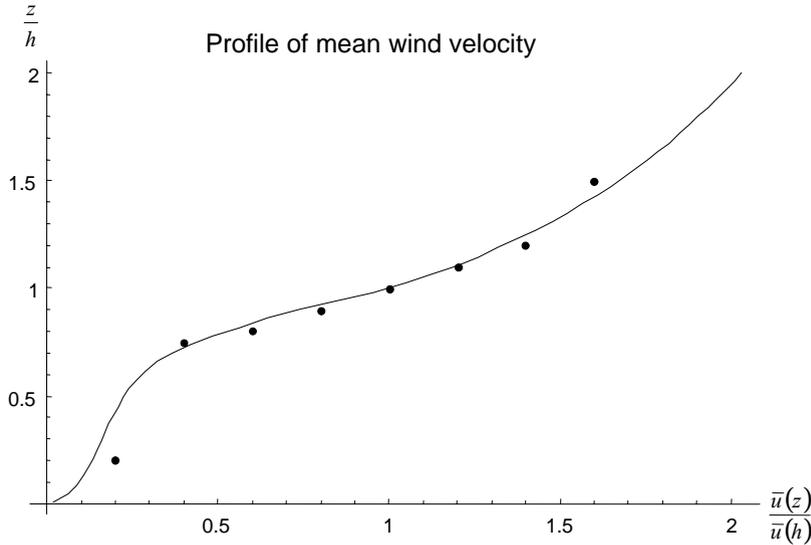
Fig. 2. Profile of mean wind velocity in a maize canopy ($h_0 = 2.45$ m) with a measured wind velocity at the top of $u_0 = 1.13$ m s^{-1}.

2.2.4. Outcrossing probability

Test and analysis of the sub-models was conducted by the estimation of the probability of out-crossing events for one genotype in a field of a differing genotype. This probability was calculated for genotype k by estimating the available pollen of genotype k by the pollen from the donator, as well as for all recipient populations at location $\vec{x}$:

$$p_k(\vec{x}) = \frac{P_k(\vec{x})}{\sum_{i=1}^{n} P_i(\vec{x})} \tag{9}$$

In the following we will focus on two populations, a genetic modified population N_1 (with pollen P_1) and a non-modified population N_2 (with pollen P_2). This reduces Eq. (9) to:

$$p_1(\vec{x}) = \frac{P_1(\vec{x})}{P_i(\vec{x}) + P_2(\vec{x})} \tag{10}$$

2.3. Genetics

Estimating the probability of out-crossing events is a first indicator for gene flow in an agricultural ecosystem. If interest is in the phenological results of gene flow, then simulation of mating process of different genesis is needed. The functions $r_i(\vec{N}, \vec{P})$ (Eq. (1), Term (a)) which couple the sub-model of dispersion

(Eqs. (4) and (6)) with the population dynamics sub-model (Eq. (1)), need to be defined.

We focus on a diploid species with three genotypes ($n = 3$): "AA", "Aa", and "aa". The functions $r_i(\vec{N}, \vec{P})$ are derived from the Hardy–Weinberg theory (Nisbet et al., 1989):

$$r_1(\vec{N}, \vec{P}) = r_1 \frac{1}{P} \left(P_1 + \frac{1}{2} P_2 \right) \left(A_1 N_1 + \frac{1}{2} A_2 N_2 \right)$$
$$r_2(\vec{N}, \vec{P}) = r_2 \frac{1}{P} \left[\left(P_3 + \frac{1}{2} P_2 \right) \left(A_1 N_1 + \frac{1}{2} A_2 N_2 \right) \right.$$
$$\left. + \left(P_1 + \frac{1}{2} P_2 \right) A_3 N_3 \right]$$
$$r_3(\vec{N}, \vec{P}) = r_3 \frac{1}{P} \left(P_3 + \frac{1}{2} P_2 \right) \left(A_3 N_3 + \frac{1}{2} A_2 N_2 \right)$$
$$\tag{11}$$

with $P = P_1 + P_2 + P_3$. Here A_i ($i = 1, \ldots, 3$) denote the number of seed of biotype i, and r_i is the rate of germinating (plants) or hatching (insects).

2.4. Model overview and numerical solution

Fig. 3 summarises the equations and functions of all sub-models introduced previously. An overview of all parameters is given in Table 1. The framework consists of generic models for population dynamics

Sub-model 1: Population dynamics for biotype i including dispersal

$$\frac{\partial N_i}{\partial t} = r_i(\vec{N}, \vec{P}) - \mu_i N_i \left(1 + \sum_{j=1}^{n} \alpha_{i,j} N_j\right) + \nabla \cdot D_i \nabla N_i$$

Source strength of pollen

$$S_i(x, y, t) = \alpha_i N_i(x, y, t) f(t)$$

Sub-model 2: Spatial spread of pollen

a) Lagrange Approach

Density function of pollen emission

$$f_i(\vec{x}) = \frac{1}{(2\pi)^{3/2} |\Sigma^{1/2}|}$$
$$\left(\exp\left[-\frac{1}{2}(\vec{x} - \vec{x}')\Sigma^{-1}(\vec{x} - \vec{x}')\right]\right)$$

Integral of source strength and density functions

$$P_i(x, y, z) = \iiint_{R^3} f(x - x', y - y', z - z')$$
$$S_i(x', y', z') dx' dy' dz'$$

b) Eulerian approach

$$\frac{\partial P_i}{\partial t} = \nabla \cdot K \nabla P_i - \nabla \cdot \vec{u} P_i + S_i(\vec{x}, t)$$

Wind field

$$\vec{u}(z) = \begin{pmatrix} u_{0,x} \\ u_{0,x} \\ 0 \end{pmatrix} \left(\frac{z}{h_0}\right)^s + \begin{pmatrix} 0 \\ 0 \\ -g \end{pmatrix}$$

Sub-model 3: Genetics.

Probability of cross pollinating of genotype k in total population

$$p_k(\vec{x}) = \frac{1}{\sum_{i=1}^{n} P_i(\vec{x})} P_k(\vec{x})$$

Specification of growth term in Sub-model 1

$$r_1(\vec{N}, \vec{P}) = r_1 \frac{1}{P}\left(P_1 + \frac{1}{2}P_2\right)\left(A_1 N_1 + \frac{1}{2}A_2 N_2\right)$$

$$r_2(\vec{N}, \vec{P}) = r_2 \frac{1}{P}\left[\left(P_3 + \frac{1}{2}P_2\right)\left(A_1 N_1 + \frac{1}{2}A_2 N_2\right) + \frac{1}{P}\left(P_1 + \frac{1}{2}P_2\right)A_3 N_3\right]$$

$$r_3(\vec{N}, \vec{P}) = r_3 \frac{1}{P}\left(P_3 + \frac{1}{2}P_2\right)\left(A_3 N_3 + \frac{1}{2}A_2 N_2\right)$$

Fig. 3. Summary of model framework.

Table 1
List of parameters

Sub-model 1	Population dynamics, Eq. (1)
$\alpha_{i,j}$	Interspecific competition
μ_i	Mortality
D_i	Dispersal
Sub-model 2a	Lagrange approach, Eqs. (2)–(5)
Σ, $\Sigma_i \in R^{3 \times 3}$	General covariance matrix
Special case	Two-dimensional superposition of two Gaussian-type functions, Eqs. (4) and (5)
K_{xx}, K_{yy}, K_{zz}	Eddy diffusivity
β	Far-field/near-field relation
S_i	Source strength of biotype i
Sub-model 2b	Eulerian approach, Eqs. (6) and (7)
K	Diffusivity
u_0	Average wind speed at top of canopy
h_0	Height of canopy
s	Shape parameter
g	Gravitational settling of pollen
S_i	Source strength of biotype i
Sub-model 3	Genetics, Eq. (11)
r_i	Germination rate
A_i	Number of seeds of biotype i

(Sub-model 1), two possible approaches for spread of pollen through the atmosphere (Sub-models 2a, 2b) and a sub-model for the mating of a diploid species (Sub-model 3).

The mathematical task of solving these coupled non-linear partial differential equations is performed by advanced finite element methods (FEM) with the MatLAB toolkit Femlab® (Comsol, 2001). The solution of the models requires the following steps:

- Selection of a general class of model equations (here general convection–diffusion equation).
- Definition of geometry either in accordance to a real world situation or certain specific testing purposes.
- Spatially explicit specification of model parameters based on defined geometric objects, initial and boundary conditions.
- Generation of finite element mesh.
- Selection of numerical solver (here a backward differentiation formulae (BDF) for non-linear ordinary differential equations, a full multi-grid with adaptive mesh-control was chosen).

In this study we focus on experiments with simple geometry restructured from real world data. However, topographical data derived from a Geographic Information System can also be used for simulating real world situations, cf. Seppelt (2003).

3. Applications and results

Three case studies are presented to test the modelling toolkit with a focus on the gene flow parts (i.e. Sub-models 2 and 3).

3.1. Out-crossing

Sub-models 2a and 2b (see Fig. 3) were tested within a cross-pollination monitoring study carried out at the Federal Biological Research Centre for Agriculture and Forestry (BBA) in Braunschweig, Germany. In the experiment a 100 m × 100 m plot of genetically modified maize (herbicide resistance) was placed within a field (ca. 5 ha) of ordinary maize of the same variety. Sixteen sampling arrays in equally spaced distances were configured around the source plot.

Sixteen sampling arrays (denoted by "A" to "Q") surrounded the source plot in equally spaced distances (22.5° intervals). Each array was composed of six sampling points in distances of 3, 4.5, 7.5, 13.5, 25.5 and 49.5 m from the edge of the source. A minimum of 2497 maize kernels up to 4996 maize kernels were examined per sampling point to allow valid statements for cross-pollination rates above 0.5%. The maize grains were germinated in a greenhouse, and seedlings were treated with the herbicide Glufosinate. The seedlings that survived the treatment were identified as genetically modified with herbicide resistance. This approach quantifies the amount of genetically modified maize seeds and the percentage of cross-pollination events can be calculated.

Assuming constant population levels for each biotype, the model concept may be applied to the experimental design by setting:

$$N_1(\vec{x}) = \begin{cases} 1, & \text{for } \vec{x} \in \text{GMO}-\text{Plot} \\ 0, & \text{else} \end{cases}$$

for the GM maize population and

$$N_2 = 1 - N_1$$

for the ordinary maize population.

The computed log-scaled cross-pollination rates $(\log(p_1))$ of the Gaussian type model for the geometry of the $100\,\text{m} \times 100\,\text{m}$ transgenic plot show asymmetry reflecting the prevailing wind direction, see Fig. 4. The experimental design and the results of the spatially explicit simulation of the cross-pollination probabilities of the gene dispersal model are shown in Fig. 5. The parameter estimation technique based on a subset of the available measured data. A training data set was used to estimate the model parameters. Application of the calibrated model to the entire field data set ("test data") showed good model performance. For instance, the data from transect "L" was used to train the model for the cardinal point "East" and data from the sampling points of the transects "I" through "N" were used to test the model, see Loos et al. (2003) for detailed information. The model is capable of reproducing the prevailing wind as well as local
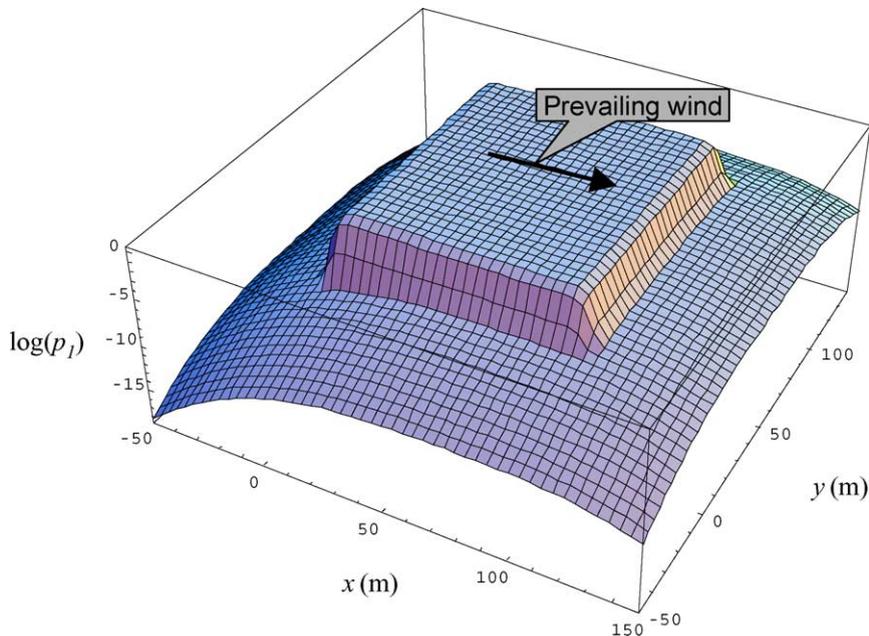

Fig. 4. Simulation of probability of outcrossing as a function of distance from the edge of a field with GM crops. Note, log-scale is used for the outcrossing probability $(\log(p_k))$.
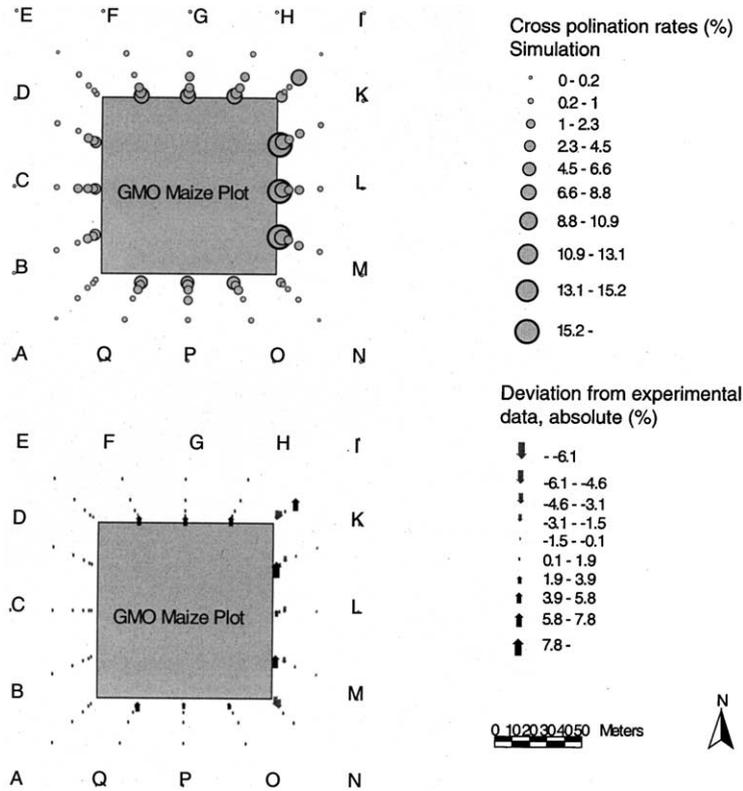
Fig. 5. Comparison of the simulation based on the Gaussian model with the observed field data displayed by the absolute deviations (left, $K_1 = 1.076 \, \text{m}^2 \, \text{s}^{-1}$, $K_2 = 149.439 \, \text{m}^2 \, \text{s}^{-1}$, $u_x = 0.926 \, \text{m} \, \text{s}^{-1}$, $u_y = 0.108 \, \text{m} \, \text{s}^{-1}$, $\beta = 0.632$). The upper figure shows the model results, the lower part displays the absolute deviations from the experimental measurements. A–Q denote the 16 sampling arrays of the experiment (cf. Loos et al., 2003).

characteristics of the field. Fig. 6 shows outcrossing rates along a transect in the prevailing wind direction and the corresponding model fit. The log-scaling clearly illustrates two main dispersal processes for short versus long ranges. For a detailed analysis of this sub-model, see Loos et al. (2003). In this publication an additional approach introduced by Raupach (1987) is compared, which makes use of a special analytic solution of the Euler approach distinguishing between near field and far field transport.

3.2. Spatially explicit spread of pollen

The use of a finite-element-solver allows a simulation with the Eulerian approach of Eq. (6) numerically. This model describes atmospheric transport of particles using a physical approach. Fig. 7 shows the spatial spread of pollen over a closed canopy with
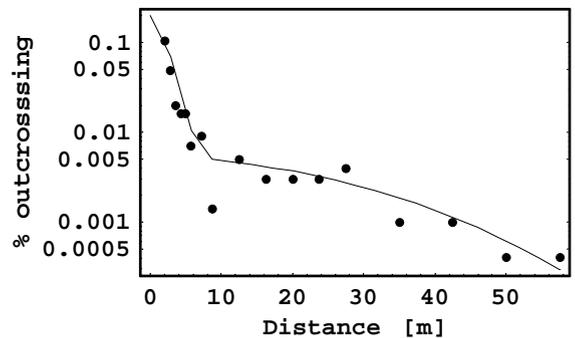

Fig. 6. Spatially explicit results of cross-pollination probabilities from the $100 \, \text{m} \times 100 \, \text{m}$ sized GMO field (cf. Fig. 5) with genetic modified maize along the transect of the prevailing wind. This additional transect with 17 sampling points (between transect L and M) is not plotted in Fig. 5.
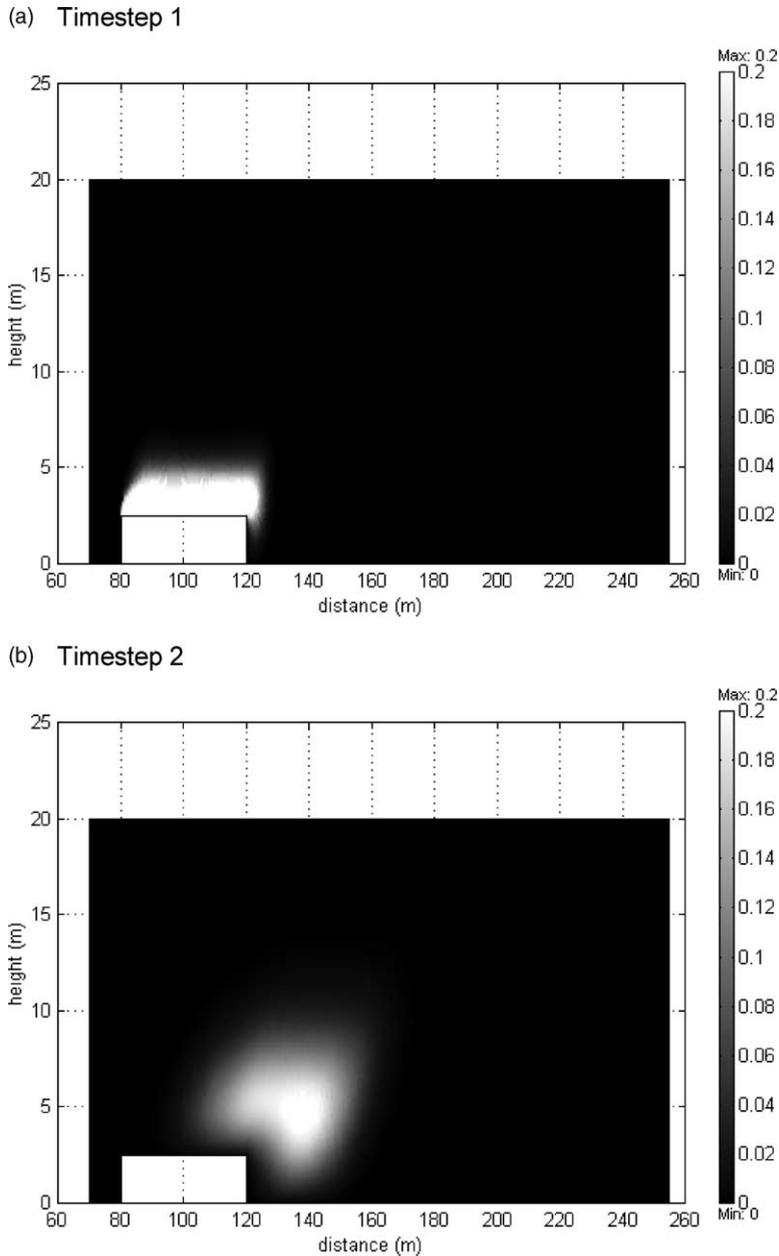
(a) Timestep 1

(b) Timestep 2

Fig. 7. Simulated patterns of dispersal based on the Eulerian approach. Two time steps are selected for detailed study and a transect of 200 m length and 20 m height is chosen. The grey-scale denotes the density of pollen in pollen/m3. Note the gravitational settling of the pollen in the vicinity of the edge of the canopy.

a Neumann boundary condition (prescribed flux, see Eq. (7)) at the surface of the canopy. The wind profile above the canopy causes long-range transport in the upper layers, whereas particles near the bound-

ary layer are transported only a short range because of gravitational settling and low velocities within the boundary layer. The empirical Lagrange approach reproduced these effects. It is an important question

to relate the more empirical approach to physically measurable data. This would allow to run the empirical model without the calibration step based on a field experiment but with measured values on climatic conditions (e.g. wind profile within and outside the canopy). Loos et al. (2003) studied a simplification of this model based on theoretical considerations proposed by Raupach (1987) and compared the results.

3.3. Spread of pesticide resistance

An important application of the above model is modelling the spatial spread of pesticide resistant pest (or weed) populations. We use the modelling framework above to study the spread of pesticide resistance using an artificial simulation experiment.

A diploid population ($n = 3$) is considered, in which the property of resistance is conferred to the next generation by one single dominant gene. In Section 2.3 the model for the underlying genetics is discussed. In this application it is assumed the atmospheric transport of pollen is negligible by setting $P_i = S_i$ for all $i = 1, \ldots, 3$. Thus, this application couples sub-models 1 and 3 (see Fig. 4) with simulation results based on Eqs. (1), (10) and (11).

The parameters with the property of resistance are the mortality rates μ_i. These parameters depend on the pesticide concentration at location $\vec{x}$, and hence on the degree of resistance of the considered biotype. The hypothetical study area consists of three plots "B", "C", and "D", see Fig. 8. A pesticide (or herbicide) is applied to Plots "B" and "C". Plot "D" remains untreated. Starting from an infested spot "A" on Plot "B" a resistant biotype begins to spread in the study area. Fig. 8 shows the geometry of the field together with a finite element mesh required for the solution of the initial boundary value problem. The resultant spatial distributions of resistant (AA and aA) and sensitive (aa) biotypes are shown in Fig. 9 for two time steps. The resistant biotypes invade the treated plots, whereas the sensitive biotype retreats to the untreated plot, which may serve as a refuge.

4. Discussion

In general the modelling approaches of the sub-models (population dynamics, transport, genetics) are highly aggregated, so the entire model is therefore applicable to a broad range of spatial and temporal scales. However, the emphasis here was focused on the field or plot scale of an agro-ecosystem. To scale up to the landscape, simulation with the atmospheric transport model is needed, which considers the topography of the study area. For this sub-model the two approaches (Lagrangian, Eulerian) for transport modelling of pollen through the atmosphere are equivalent under coordinate transformation. However, the
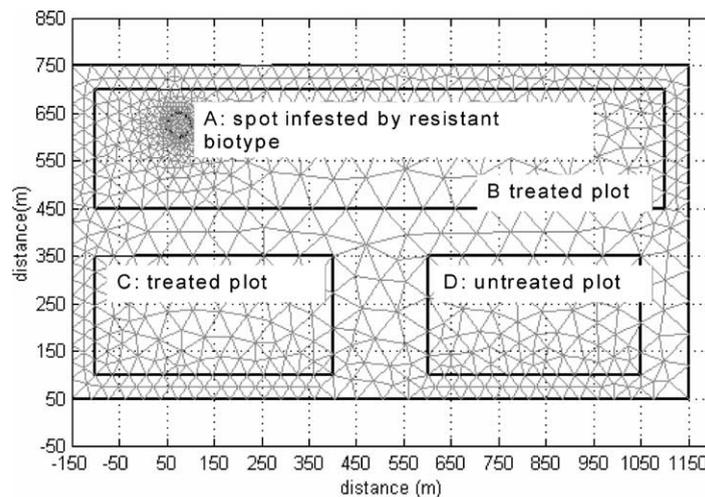

Fig. 8. Finite-element mesh for the numerical simulation of the dispersal of resistance for a test geometry: Plots B and C are treated with a pesticide. On Plot B a resistant biotype is located in spot A.
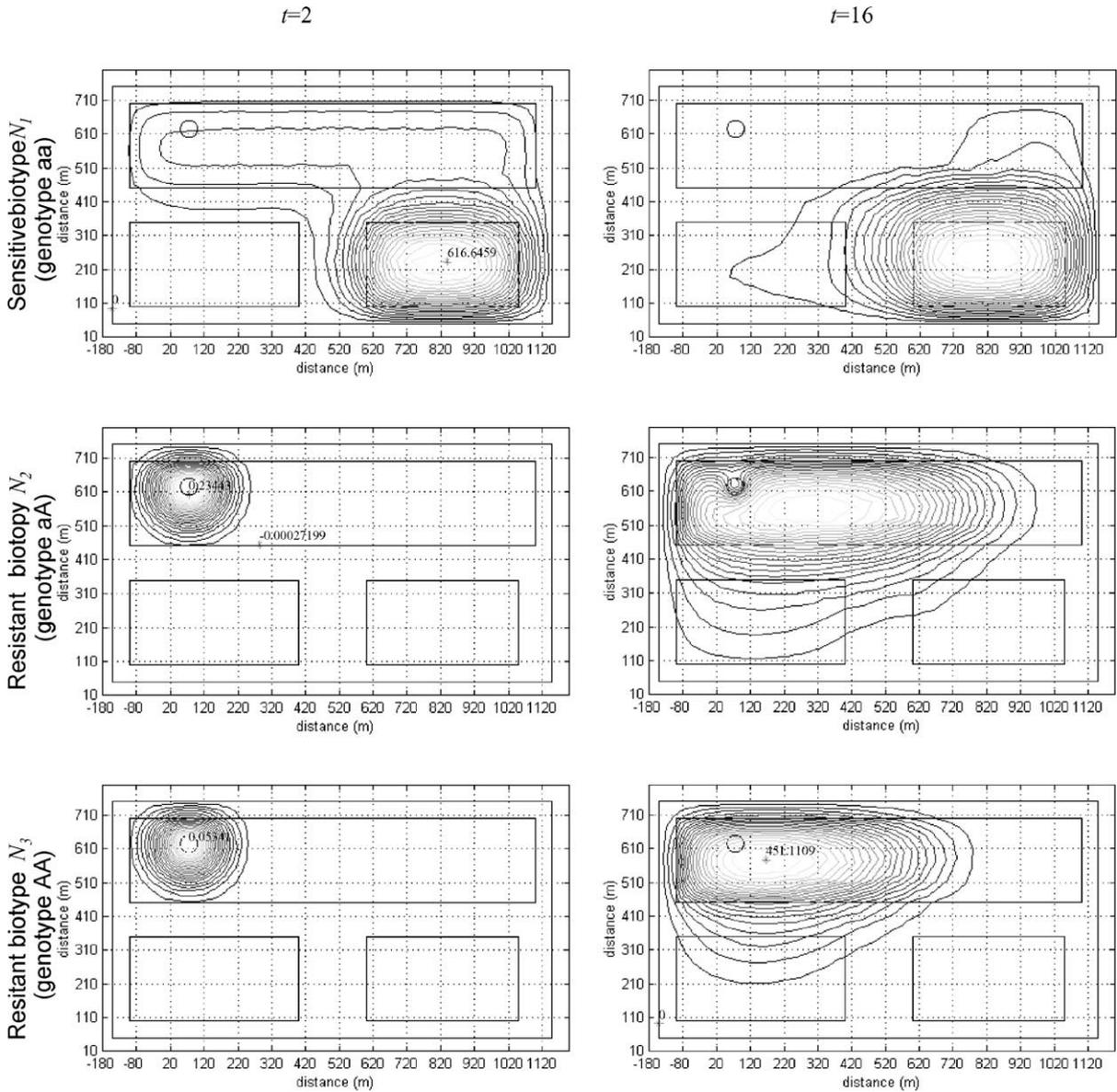
Fig. 9. Spatial spread of three biotypes (sensitive: upper, resistant: lower and middle) for two time steps.

two approaches differ in several general ways. The Lagrangian model is set up by the superposition of analytical solutions of Eq. (6). Parameters can be identified only by the application of parameter estimation procedures. This requires sufficient experimental data, and the transfer of quantitative results to other sites with other environmental forcing is difficult. The advantages of this approach are the small number of free parameters, simplicity in defining different spatial configurations of the donor and recipient field, and less computational effort. The Eulerian model can be specified by physically measurable parameters. This supports model applications at different investigation sites. Scaling up of the Eulerian approach can be supported by the use of topography data in the FEM-solver obtained from Geographic Information Systems.

Amalgamation of all the processes (dispersal, growth and genetics) into the same mathematical structure (i.e. partial differential equations) allows a broad spectrum of applications that encompass developments of anti-resistance strategies, as well as risk assessment of spread of transgenic properties. However, for a detailed mapping of the life cycle of plants, it is more appropriate to use time discrete models that are embedded into cellular automaton models (Seppelt, 2003, chapter 3). A major drawback of cellular automaton models is that the range of dispersal in one time step is limited by the order of the Moore radius. Cellular automata models are therefore not capable of modelling pollen dispersal on a large (landscape) scale. In order to achieve both a realistic description of plant (or insect) development in terms of a time discrete scheme and a realistic simulation of long-range dispersal, both systems have to be integrated into a hybrid model.

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