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Modeling spatial spread of genetic information via pollen dispersal: coupling of population dynamics and genetics

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Abstract: The spatial spread of pollen is modeled by transport equations from atmospheric physics. These equations are coupled with a population dynamic and genetic model. The resulting model consists of a set of coupled partial differential equations which is solved by finite element methods. Due to recent advances in software tools it is possible to solve complex systems of partial differential equations within reasonable computing time. Simultaneous simulation of spatial spread and population genetics enable the evaluation of anti-resistance management strategies.

Keywords: resistance modelling, spatial spread of genetic information

1. INTRODUCTION

Unintended spatial spread of genetic information is one major problem in modern agriculture. This concerns vertical distribution of transgenic properties as well as spatial spread of resistant biotypes of weed and pests, which may have developed from a long-term application of pesticides.

These systems are complex and require an integrated view at population dynamic and physical transport processes. Mathematical models, which describe these processes in a concise and consistent way may support the steps of risk assessment and help to derive appropriate management strategies for risk reduction.

2. MODELING SPATIAL SPREAD

Two principle approaches are used for modeling spatial spread of genetic information: The Lagrange and the Eulerian ansatz.

2.1 Lagrange-Approach

The Lagrange ansatz describes the dispersal of particles in terms of the stochastic properties of the paths of ensembles of particles. Transport of a particle from a location (x,y) to a location (x',y') is modeled by a density function $f(x-x',y-y')$. This function may also be called a transfer function. The amount of particles, which are emitted from a location (x',y') and reach a location (x,y) is given by the product of the density of pollen donators $g(x',y')$ at location (x',y') and the transfer function $f(x-x',y-y')$. The total amount of pollen, which reaches a single plant in (x,y) is then derived by the integral over all donators [Lavigne *et al.* 1998]

$$F(x,y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} f(x-x',y-y')g(x',y')dx'dy' \quad (1)$$

Several experimental investigations [Schütte *et al.* 2001] showed that spatial spread of pollen is characterized by a short and long distance transport. A possible explanation of this phenomenon is that pollen remaining in the upper layers of the canopy has a higher diffusion resistance than pollen which has moved into upper layers of the atmosphere. This effect can be modeled for instance by the superposition of two transfer functions of gaussian type:

$$f(x,y) = c \exp \left[-\frac{(x-u_x\tau)^2}{4K_x\tau} - \frac{(y-u_y\tau)^2}{4K_y\tau} \right] \quad (2)$$

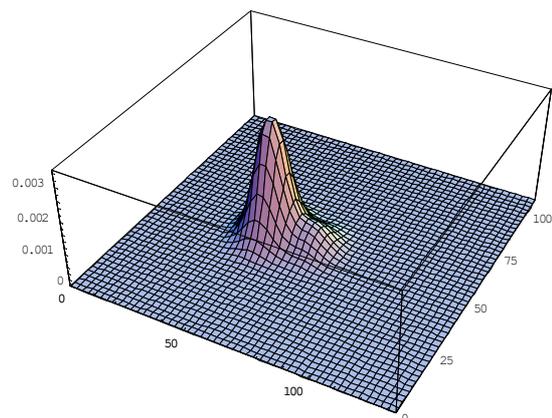


Figure 1: Superposition of two Gaussian-type functions with distinct diffusion coefficients.

The constant c is chosen to scale the integral of the function to unity, so $f(x,y)$ has the meaning of a

probability density function. The parameters u_x and u_y denote the components of the average wind speed during the phase of spatial spread. The superposition of two Gaussian-type transfer-functions with different diffusion coefficients K_1 , K_2

$$f_S(x, y) = c \left(\alpha e^{-\frac{(x-u_{x1}\tau)^2}{4K_{x1}\tau} - \frac{(y-u_{y1}\tau)^2}{4K_{y1}\tau}} + (1-\alpha) e^{-\frac{(x-u_{x2}\tau)^2}{4K_{x2}\tau} - \frac{(y-u_{y2}\tau)^2}{4K_{y2}\tau}} \right) \quad (3)$$

yields a typical biphasic profile of spatial spread. To estimate the probability of genetic transfer via wind pollination, transfer functions are used for the donator as well as for the recipient population. In case of two biotypes F_1 , F_2 the probability of wind pollination at location (x, y) is given by

$$p(x, y) = \frac{F_1(x, y)}{F_1(x, y) + F_2(x, y)} \quad (4)$$

Figure 2 shows an application of the this model to a data set published by Handel [1983] for outcrossing of cucumber (*Cucumis sativus*).

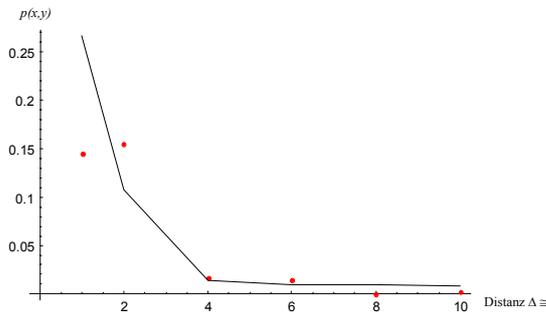


Figure 2. Simulation of probability of outcrossing as a function of distance from the edge of a field (data for cucumber, Handel [1983])

2.2 Eulerian Approach

The Eulerian approach describes the spatial spread of an ensemble of particles relative to a given coordinate system. The mass balance equation for an infinitesimal 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 is described by the following partial differential equation

$$\frac{\partial P}{\partial t} = \nabla \cdot K \nabla P - \nabla \cdot \vec{u} P + S(\vec{x}, t) \quad (5)$$

P denotes the particle density, e.g. pollen, K the diffusion coefficient and S a source term.

The wind velocity profile above the canopy is given by the empirical formula

$$u_x(z) = u_y(z) = a z^s \quad (6)$$

The wind velocity field is thus given by $\vec{u} = (u_x, u_y, -u_z)$. The negative sign of the z-axis component is due to the gravitational settling of the pollen.

Figure 3 shows the evolution in time of spatial spread of pollen emanating from a closed canopy with a Neuman boundary condition (prescribed flux) on the surface of the canopy. The resulting initial boundary value problem was solved by the finite element tool Femlab[®] [Comsol 2001].

The wind profile above the canopy causes a long-range transport in upper layers, whereas particles near the boundary layer have only a short range due to gravitational settling and the low velocities in the boundary layers. The empirical Lagrange approach reproduces this effect.

3. A HIGHLY AGGREGATED MODEL FOR SPATIAL SPREAD OF GENETIC INFORMATION

3.1 Populations dynamics

Modeling spatial spread of genetic information requires the coupling of the three components genetics, growth and dispersal. For the case in hand we consider n populations of different biotypes of a species N_i ($i=1, \dots, n$). The following basic equation covers the processes of spatial spread (term (c)) of pollen or seed, growth (term (a)), inter-specific competition (term (b)), and exchange of genetic information (also term (a)) in a general form

$$\frac{\partial N_i}{\partial t} = \underbrace{r_i(\vec{N}, \vec{P})}_{(a)} - \underbrace{\mu_i N_i \left(1 + \sum_{j=1}^n \alpha_{i,j} N_j \right)}_{(b)} + \underbrace{\nabla \cdot D_i \nabla N_i}_{(c)} \quad (7)$$

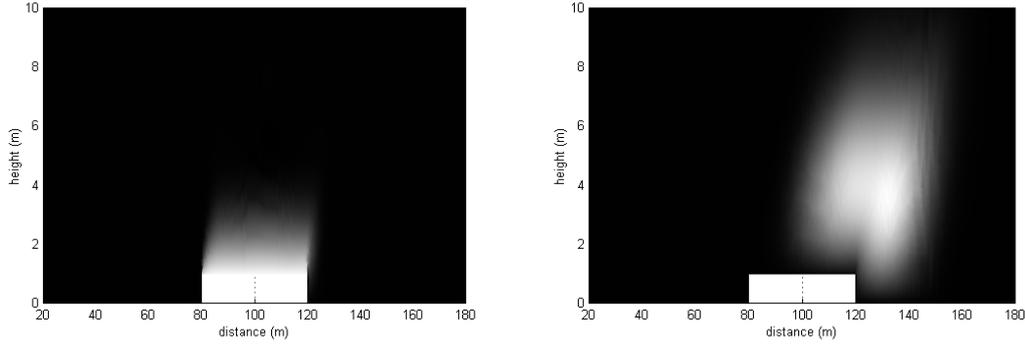


Figure 3: Simulated patterns of dispersal based on the Eulerian approach. The figures show two snapshots of a cross section through a field (80–120 m) from which pollen is emitted. A wind profile is assumed with a wind direction from left to right. Pollen concentration is displayed by gray scale. Note the gravitational settling of the pollen in the vicinity of the edge of the canopy.

The functions $r_i(\bar{N}, \bar{P})$ (term (a)) model the growth rate in dependence of the given biotype i and the mating frequencies between different biotypes (c.f. example below).

For a diploid species with three genotypes (AA, Aa, aa) for instance the functions $r_i(\bar{N}, \bar{P})$ are derived from the Hardy–Weinberg theory [Nisbet et al., 1980].

$$\begin{aligned}
 r_1(\bar{N}, \bar{P}) &= r_1 \frac{1}{P} \left(P_1 + \frac{1}{2} P_2 \right) \left(A_1 N_1 + \frac{1}{2} A_2 N_2 \right) \\
 r_2(\bar{N}, \bar{P}) &= r_2 \frac{1}{P} \left(P_3 + \frac{1}{2} P_2 \right) \left(A_1 N_1 + \frac{1}{2} A_2 N_2 \right) + \\
 &\quad \frac{1}{P} \left(P_1 + \frac{1}{2} P_2 \right) A_3 N_3 \\
 r_3(\bar{N}, \bar{P}) &= r_3 \frac{1}{P} \left(P_3 + \frac{1}{2} P_2 \right) \left(A_3 N_3 + \frac{1}{2} A_2 N_2 \right)
 \end{aligned} \tag{8}$$

with $P = P_1 + P_2 + P_3$. Here A_i ($i=1, \dots, 3$) denotes the number of seed of biotype i , and r_i denotes the resulting rate of germinating (plants) or hatching (insects). Growth is limited by the nonlinear term of mortality (b), which incorporates the interspecific competition between different biotypes. In case of only one single biotype the terms (a) and (b) are equivalent to the familiar logistic growth equation.

The last term (c) of equation (7) describes the dispersal by a simple diffusion process with the coefficient of diffusion D_i .

Equation system (7) has to be closed by a set of equations for the spatial spread of pollen P_i . In a

highly aggregate model version the equation system is closed by assuming that $P_i = N_i$. Note that the above model is also applicable to insect populations with immobile (larvae) and mobile (adult) life stages.

3.2 Different mobility of seed and pollen

In case of different mobility of seed and pollen additional equations of the type of Eqn. (5) for dispersal are required. The source term is specified by

$$S_i(x, y, t) = \alpha_i N_i(x, y, t) f(t) \tag{9}$$

assuming that pollen production is time dependent (factor $f(t)$) and proportional to plant density.

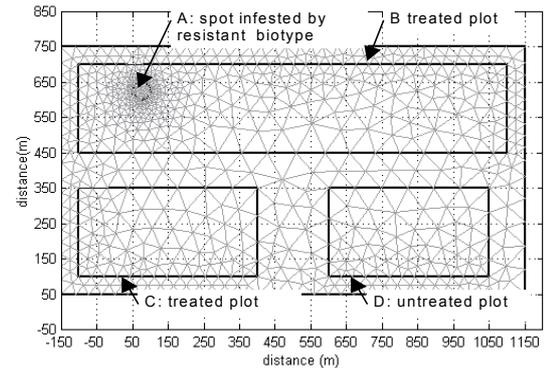


Figure 4: Finite-element mesh for the numerical simulation of the dispersal of resistance based on the partial differential equations system (7), (8). Plots B and C are treated with a pesticide. On plot B a resistant biotype is located in spot A.

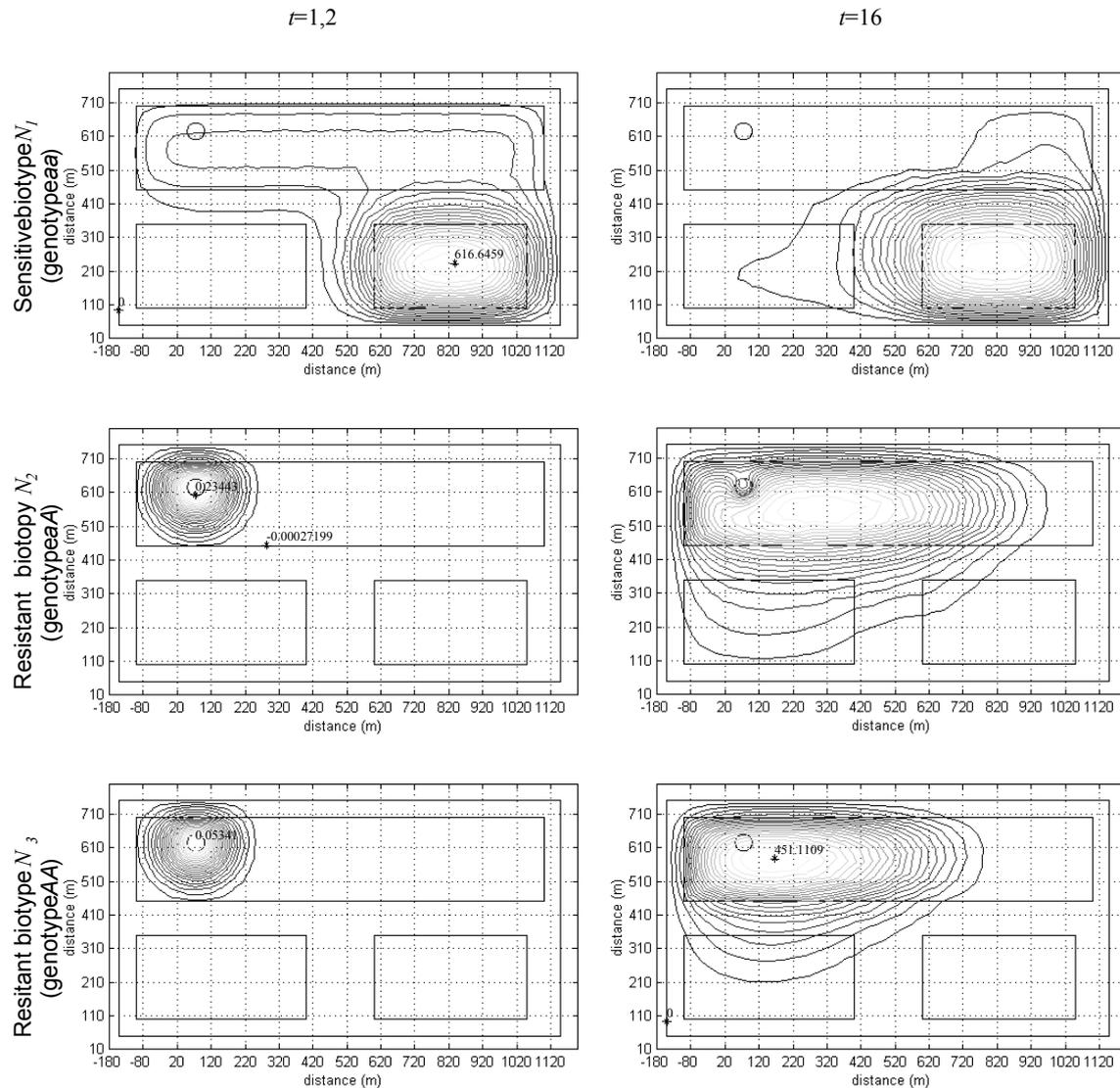


Figure 5: Spatial spread of three biotypes (sensitive: upper, resistant: lower and middle) for two time steps.

4. APPLICATIONS

An important application of the above model is the simulation of the spatial spread of resistant pest (or weed) populations. A diploid population is considered, in which the property of resistance is conferred to the next generation by one single dominant gene. The parameters carrying the property of resistance are the mortality rates μ_i .

These parameters depend on the location (x,y) and on the degree of resistance of the considered biotype. The following simulation results are based on Eqn. (7) and (9) without distinguishing between spatial spread of pollen or seed. The hypothetical study area consists of three plots B, C, and D. 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. 4 shows the geometry of the field together with a finite element mesh required for the solution of the initial boundary value problem. The resulting spatial distributions of resistant (AA and aA) and sensitive (aa) biotypes are shown in Fig. 5 for two time steps. The resistant biotypes invade the treated plots, whereas the sensitive biotype moves back to the untreated plot, which may serve as a refuge.

5. DISCUSSION

The modeling approaches presented here are highly aggregated and therefore applicable to a broad range of spatial and temporal scales. They have the advantage, that all processes involved – dispersal, growth and genetics- are translated into the same mathematical structure, i.e. into partial

differential equations. A broad spectrum of applications exists. These 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 an approach based on time discrete models embedded into cellular automaton models is more appropriate [Richter et al. 2002]. A major drawback of cellular automaton models is that the range of dispersal in one time step is limited by the choice of the order of the Moore radius. Cellular automata models are therefore not capable of modeling 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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