Modelling Dispersal of Genetic Information in Structured Agricultural Landscapes with Partial Differential Equations

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Abstract: We present a model for plant dispersal in agricultural landscapes to evaluate the gene dispersal from genetically modified plants. Dispersal from seed and pollen is modeled with partial differential equations. In scenarios we investigated the effect of roadside application of non-selective herbicides on dispersal of herbicide tolerant oilseed rape (HT OSR). We showed that OSR growing on side of roads and lanes facilitates OSR dispersal and can help to bridge areas with unfavorable conditions for OSR growth. Herbicide application gives advantage to the HT OSR and gene dispersal is more widespread. The model can help to evaluate co-existence management measures such as spatial isolation between GM and non-GM cultivars on the adventitious presence of GM in non-GM harvest.

Keywords: gene dispersal, Oilseed rape, Genetically Modified Plants, co-existence, landscape structure.

1. Introduction

Introduction of Genetically Modified (GM) crops into agriculture has lead to concerns about transgenes escaping from GM fields into the surrounding landscape. Due to cost and time restraints it is not possible to investigate all aspects of gene flow with field experiments especially on the landscape scale. Therefore models are needed to investigate the whole range of factors determining gene flow in agricultural landscapes (Devos et al., 2005). To predict gene flow in real landscapes it is necessary to consider landscape structure, land use and field patterns (Colbach et al., 2001). In order to study the combined effect of seed and pollen dispersal and spillage from machinery alongside roads on the propagation of genetic information we developed a new aggregated model framework using partial differential equations (PDEs) (Lipsius et al., 2007). The model is applied to a theoretical biosafety study of a genetically modified crop, which has been made tolerant to non-selective systemic herbicides such as GM oilseed rape (OSR) tolerance for active ingredients such as glyphosate or glufosinate. A diploid population with two alleles denoted as a and A respectively is considered. Resistance is assumed to be transferred by allele a. At the phenotype level, resistance affects the mortality rates under herbicide applications. The scheme of the hypothesized genetic interactions is shown in Figure 1. OSR grows not only on cultivated fields, but feral populations can frequently be found on the borders of country roads and lanes and along railway tracks. GM OSR generally behaves like conventional OSR. Possible consequences are the propagation of GM OSR along these pathways which might be further enhanced by the application of the herbicide. We present simulation results for an exemplary agricultural landscape.

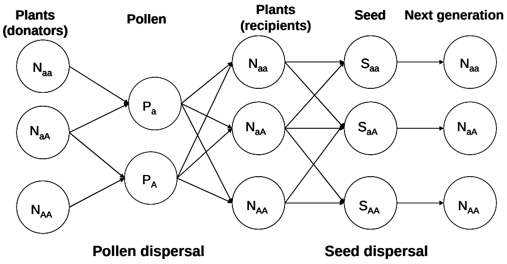

Figure 1. Conceptual model of the genetic interactions

2. Governing equations

Nomenclature

i,j:	index for the two alleles a and A
a	allele conferring resistance
A	allele of the wild type
N_{ij}	plant densities of genotype ij
S_{ij}	seed densities of genotype ij
P_i	density of genotype i pollen
r_{ij}	plant growth factor

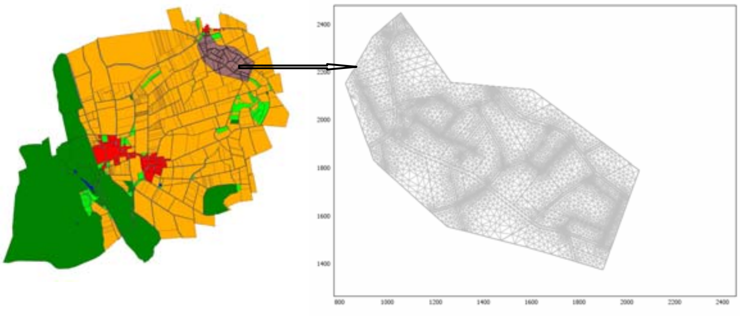

Figure 2. Land use map of a small river catchment in northern Germany. The shaded area is imported into COMSOL. The Finite Element Mesh of the imported area consists of 8140 elements (modified after Richter, 2008)

$K_{ij}(x,y,t)$	plant environmental capacity
α_{ij}	maximum density of seedlings
K_{ms}	half saturation constant
$D_{Pi}(x,y,t)$	pollen dispersion coefficient
$\beta_{Pi}(t)$	pollen production
$\mu_{Pi}(t)$	pollen mortality rate
$D_{Sij}(x,y,t)$	seed dispersion coefficient
$\beta_{Sij}(t)$	seed production
$\mu_{Sij}(t)$	seed mortality rate

The general approach of the model is to combine space operators $L[N_j]$ with reaction terms f_i describing population dynamics and -genetics.

$$\frac{\partial N_i}{\partial t} = L[N_i] + f_i(N_1, N_2 \ldots N_n) \qquad i = 1 \cdots n \tag{1}$$

This equation is applied to pollen (P), seed (S) and plants (N_{ij}) omitting the dispersal term for the latter. The equation for plant growth

$$\frac{\partial N_{ij}}{\partial t} = r_{ij} \cdot N_{ij}\left(1 - \frac{N_{ij}}{K_{ij}(x,y,t)}\right) + \alpha_{ij}\frac{S_{ij}}{S_{ij} + K_{ms}} \tag{2}$$

is comprised of a logistic growth term and a source term due to seed import.

Pollen and seed dispersal are modeled by reaction diffusion equations

$$\frac{\partial P_i}{\partial t} = \nabla \bullet (D_{P_i}(x,y,t)\nabla P_i - \vec{u}P_i) + f_i(N_{ij}, t) - \mu_p(t) \cdot P \tag{3}$$

There are two types of haploid pollen, a and A, which are produced by the three possible genotypes aa, aA and AA. The source terms thus take the form

$$f_i(N_{ij}, t) = \beta_p(t)\left(\frac{N_{ij}}{2} + N_{ii}\right)_i \tag{4}$$

where the second reaction term is the pollen mortality rate. For the three possible genotypes of seeds, aa, aA and AA, the following reaction diffusion equations are set up

$$\frac{\partial S_{ij}}{\partial t} = \nabla \bullet (D_{S_{ij}}(x,y,t)\nabla S_{ij} - \vec{v}S_{ij}) + f_{ij}(N_{ij}, P_i, t) - \mu_{ij}(t) \cdot S_{ij} \tag{5}$$

Assuming random mating (cf. Figure 1) the source terms for AA, aA and aa seeds are given by

$$f_{AA}(N,P,t) = \beta_s(t)\left(\left(\frac{N_{aA}}{2} + N_{AA}\right)\left(\frac{P_A}{P_a + P_A}\right)\right) \tag{6}$$

$$f_{aa}(N,P,t) = \beta_s(t)\left(\left(\frac{N_{aA}}{2} + N_{aa}\right)\left(\frac{P_a}{P_a + P_A}\right)\right) \tag{7}$$

$$f_{aA}(N,P_i,t) = \beta_s(t)\left(\left(\frac{N_{aA}}{2} + N_{aa}\right)\left(\frac{P_A}{P_a + P_A}\right) + \left(\frac{N_{aA}}{2} + N_{AA}\right)\left(\frac{P_a}{P_a + P_A}\right)\right) \tag{8}$$

The second reaction term is the mortality rate of the seeds. A temporal structure is imposed on the model by the explicit time dependence of seed and pollen production, plant mortality, herbicide application and environmental capacity. Spatial structures enter the model via the dispersal coefficients which are a measure of local spatial resistance reflecting the pattern of landscape elements such as roads and the capacity coefficients which reflect the cultivation pattern.

The following remark is in order: the model is a highly aggregated approach to model gene flow in landscapes combining physical, genetic and agricultural elements in a system of PDE's and must therefore be considered as semi-empirical.

3. Methods

Preliminary remark: the simulations carried out are hypothetical and serve to demonstrate the model behavior. The model is applied to a (fictive) co-existence study of GM and conventional oilseed rape (OSR). The GM OSR is endowed with a transgenic tolerance for a non-selective herbicide. Model parameters chosen are in plausible ranges but have not yet been derived from experimental co-existence studies.

Table 1: Spatially independent Parameter values (rate coefficients [month^{-1}])

Parameter	Value for GM variety	Value for non GM variety
r_{ij}	0.095	0.105
α_{ij}	0.7	0.7
β_{Pi}	0.09	0.09
μ_{Pi}	0.1	0.1
β_{Si}	0.09	0.11
μ_{Sij}	0.01	0.01
K_{ms}	10	10

Parameters are specific for each genotype (Table 1). Generally GM varieties have the same physiological and ecological characteristics as their conventional counterparts, but the modification can lead to differences depending on the transgenic trait. In our example, we study herbicide tolerant (HT) oil seed rape. Because the GM plant has to spend energy to produce the enzyme make-up for the herbicide tolerance, we assumed a slightly lower growth rate and lower seed production for the GM OSR varieties.

To integrate landscape structure into the model, parameters were defined individually for each landscape element imported from GIS maps. Field geometries and land use are imported from GIS data with the ArcToolbox ”Export to CAD” (Richter, 2008) (Fig. 2).

Our exemplary landscape (Fig. 3) consists of agricultural fields, a set aside area with trees and roads and lanes. On each agricultural field we assumed a three year crop rotation of OSR, followed by winter wheat and winter barley. Model parameters are functions of time, because the model considers crop rotations to predict plant development and dispersal behavior.

Land use patterns determine the distribution of the spatially dependent parameter values (Tab. 2). Dispersion coefficients are inverse proportional to the resistance of a landscape element against dispersal. For example hedges and trees exert higher resistance against pollen dispersal than agricultural fields. Spillage from machinery facilitates seed dispersal alongside roads and lanes reducing the resistance against seed dispersal and resulting in higher values of $D_{Sii}(x,y,t)$ (Tab. 2). So to each landscape element a specific dispersion coefficient was assigned.

Table 2: Spatially and temporally dependent Parameter values in the model (HA=herbicide application, nHA=no herbicide application; dispersal coefficients [m^2 month^{-1}])

Parameter	OSR fields		Roads		Others
$D_{Pi}(x,y,t)$	150		150		>40
$D_{Sii}(x,y,t)$	25		500		<25
	HA	nHA	HA	nHA	
$K_{aa}(x,y,t)$	150	150	4	4	<5
$K_{aA}(x,y,t)$	150	150	4	4	<5
$K_{AA}(x,y,t)$	1	150	0.5	4	<5

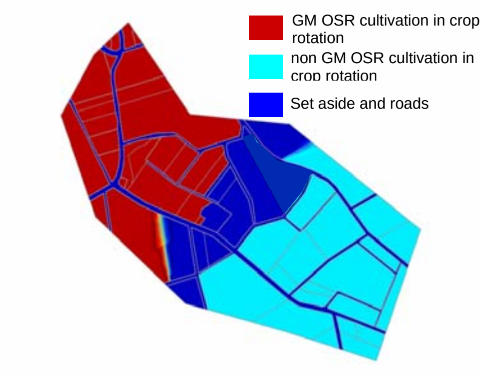

Figure 3. Map of the land use in the model landscape, showing the areas with GM OSR cultivation and non GM OSR cultivation separated by at least 150 m by a set aside area

Values for K_{ij} are spatially and temporally variable, because the environmental fitness of the OSR is influenced by crop rotation. Values for K_{ij} are set to high values when conditions for development are favorable, which is true for fields in years with OSR cultivation (Tab. 2). Differences in the environmental behavior between the conventional OSR and the HT OSR only manifest when herbicides are applied. In those landscape elements where the non-selective herbicide is applied, the environmental capacities K_{ij} of the sensitive OSR of genotype *AA* are set to very low values with respect to values of the herbicide tolerant genotypes OSR, *aA* and *aa* (Tab. 2). Note that in the logistic growth term a decrease of the capacities is equivalent to an additional mortality rate.

The distribution of OSR of GM and conventional (homozygote, N_{AA}) genotypes was modeled for the FEM shown in Fig. 2. GM OSR cultivation was clustered west and conventional OSR cultivation east of the set-aside in the middle of the landscape (Fig. 3). The set aside area separating GM and conventional OSR cultivation has a width of at least 150 m. It is analyzed if this isolation distance suffices to completely separate GM and conventional OSR. The set aside isolation area has very low K_{ij} values for both GM OSR and conventional OSR. Models were run for 16 years with OSR being cultivated every third year in the crop rotations. Fields with OSR in the first, second, and third year, respectively, were allocated randomly. We considered different scenarios, where roads and lanes were or were not treated with the herbicide for which the GM OSR is tolerant. The scenarios compare the effect of no herbicide application along roads and lanes, with non-selective herbicide application only along the main road, presumably a railway track, from east to west and herbicide application along all roads.

4. Results

Figure 4 shows the distribution of GM OSR densities of genotype NaA, at the end of the simulation. High densities can be found in the fields with OSR cultivation in the final year, due to high K_{ij} values. Gene dispersal and admixture between both clusters, i.e. the area with GM OSR cultivation in the west and the area with conventional OSR cultivation in the east, occured for all scenarios. The intensity and velocity of gene dispersal differed between the scenarios. Figure 4a shows the densities for no herbicide application along roads, Figure 4b for herbicide application only along the main road from east to west and Figure 4c for herbicide application along all roads.

The more roads were treated with herbicides, the more widespread were high GM OSR densities. When no herbicides were applied along roads, the fields furthest east stayed GM OSR free throughout the whole simulation period.

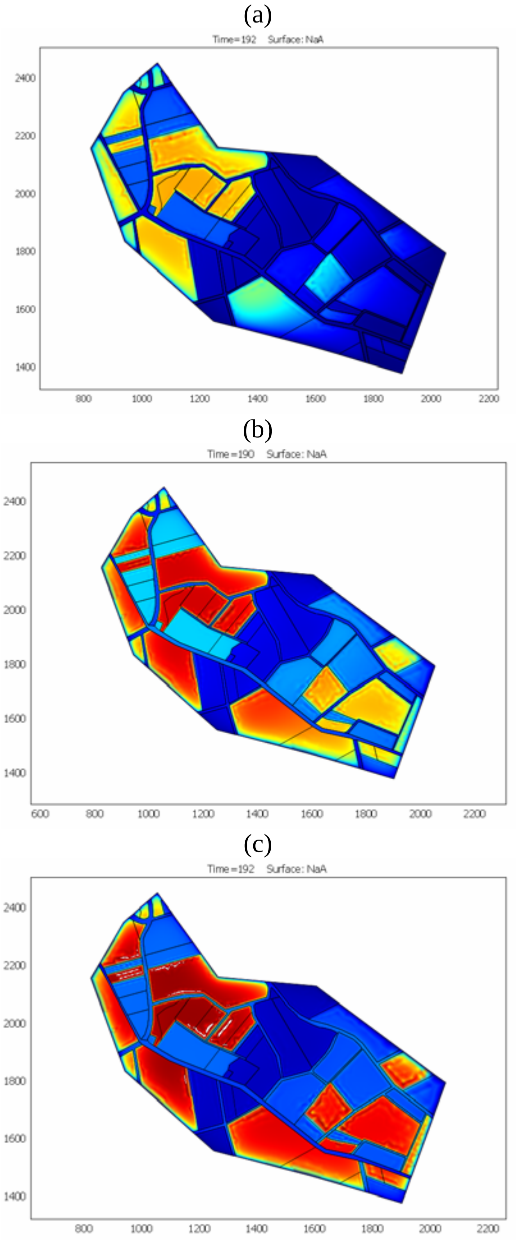

Figure 4. Distribution of herbicide tolerant oilseed rape densities after modelling 16 years of crop rotation for scenarios without herbicide application along roads (a), with herbicide application along the main road (b) and along all roads (c). Values range from 0 to 20, colormap “jet”, lowest value dark blue.

The development of the GM OSR population densities over time at one point in the landscape east of the isolation area is shown in Figure 5. It can be seen that for the scenario with no herbicide application along the roads GM OSR first appeared after 180 months or 15 years. The set aside area separating the GM and non-GM OSR cultivation areas was bridged by GM OSR seeds for the first time after 11 years for the scenario with no herbicide application (not shown here).

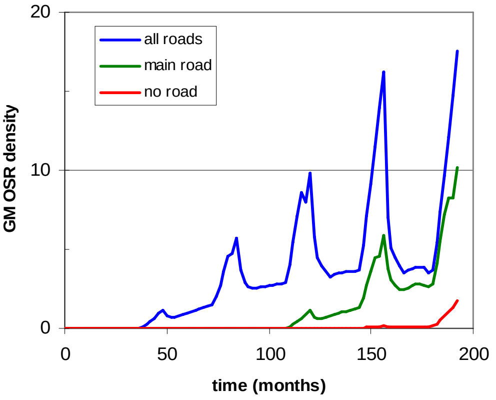

Figure 5. GM OSR densities at position (1880, 1620) in a field in the eastern part of the landscape where conventional GM OSR was cultivated for three scenarios of herbicide applications along roads

For both scenarios with herbicide application the GM OSR densities oscillated with the crop rotation, with the peaks coinciding with OSR cultivation (Fig. 5). The highest GM OSR densities were reached in the scenario with non-selective herbicide being applied along all roads and lanes, where GM OSR was dispersed at high densities throughout the whole model domain within the 16 years of simulation.

The ratio of GM OSR to total OSR densities is shown in Figure 6. When no herbicides were applied along roads (Fig. 6a) the conventional OSR dominated the OSR populations east of the set aside and gene dispersal was limited. The ratio of GM to non-GM OSR was very high along roads where herbicide was applied. When only the main road was treated with herbicide, the GM ratio was raised in comparison to the no herbicide scenario throughout the whole cluster east of the isolation area, where originally only conventional OSR was cultivated (Fig. 6b). The GM ratio was highest with herbicide application along all roads (Fig. 6c).

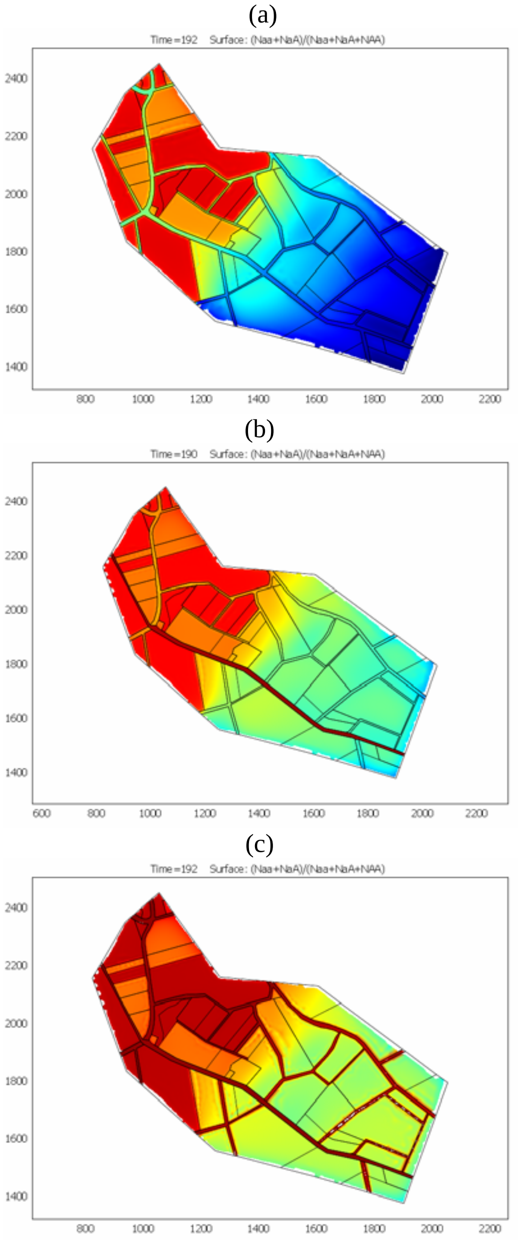

Figure 6. Ratio of transgenic to overall oilseed rape densities after modelling 16 years of crop rotation for scenarios without herbicide application along roads (a), with herbicide application along the main road (b) and along all roads (c). Values range from 0 to 1.

5. Discussion

We compared gene dispersal of GM OSR with and without non-selective herbicide usage along roads. When herbicides were applied GM

OSR dominated the OSR populations, because competition from conventional OSR was prevented. Absolute densities of OSR along roads were very low, because of low environmental capacities compared to OSR fields. However, the seed dispersal along roads was much faster, because spillage from machinery is added to the natural seed dispersal. The GM OSR thus could rapidly disperse along roads and lanes, whereas in low densities. In this pathways the isolation area, i.e. the set aside area in the middle of the landscape, is bridged and the GM OSR is admixed with the conventional OSR. If the GM OSR from the feral population along roadsides is able to fertilize OSR plants in OSR fields, high GM OSR densities in the fields are possible, when conditions for OSR growth are favorable in the years when OSR is cultivated.

Thus, the roads and lanes can act as fuses for the gene dispersal and bridge isolation areas. The OSR densities over time were mainly determined by the environmental capacities. The resulting oscillation leads to GM dispersal similar to traveling waves. The roads facilitate gene flow of OSR and compromise the co-existence of GM and conventional OSR.

6. Conclusions

Our explorative analysis has shown that growth of feral OSR at the borders of country roads and lanes facilitates the OSR gene dispersal in landscapes because of increased seed dispersal. While the plant densities are low along roads and lanes, they can still act as fuses to bridge isolation areas and promote gene dispersal. The competition from conventional OSR limits the GM OSR gene dispersal along the roads, but does not prevent admixture completely. Conventional OSR usually cannot survive where non-selective herbicides are applied and subsequently GM herbicide tolerant OSR dominates the OSR populations. When non-selective herbicides are applied along roads and lanes the GM herbicide tolerant OSR exclusively grows along roadsides, which act as pathways for gene dispersal in the landscape, without competition from conventional OSR. The subsequent fertilization of conventional OSR on cultivated fields from feral GM OSR along roads compromises the co-existence with conventional OSR, because even with large isolation distances the admixture can be high.

The approach to couple PDEs and population dynamics with geoinformation from GIS provides a model framework for gene flow at landscape scale allowing explicit integration of landscape heterogeneity. The model is capable of describing aggregated effects of landscape structure on pollen and seed dispersal and distribution of plants over space and time. We showed how the model can be used to test scenarios with different types of agronomical practices and management. Possible applications of the model are optimization of crop rotation and crop allocation schemes and evaluation of isolation distances. The highly aggregated approach results in very few model parameters, so parameter estimation from field observations is feasible. This is the next step to be taken to endow the model with realistic parameter sets.

8. References

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9. Acknowledgements

Part of this research was funded by the EU project Sustainable Introduction of GMO into European Agriculture (SIGMEA) (Contract: FOOD-CT-2004-591986 (STREP)).