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Mathematical Modelling of Spatially Inhomogeneous Non-Stationary Interaction of Pests with Transgenic and Non-Modified Crops Considering Taxis

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Abstract

Introduction. This paper addresses a unified spatially inhomogeneous, non-stationary model of interaction between genetically modified crop resources (corn) and the corn borer pest, which is also present on a relatively small section of non-modified corn. The model assumes that insect pests influence both types of crops and are capable of independent movement (taxis) towards the gradient of plant resources. It also considers diffusion processes in the dynamics of all components of the unified model, biomass growth, genetic characteristics of both types of plant resources, processes of crop consumption, phenomena of growth and degradation, diffusion, and mutation of pests. The model allows for predictive calculations aimed at reducing crop losses and increasing the resistance of transgenic crops to pests by slowing down the natural mutation rate of pest.

Materials and Methods. The mathematical model is an extension of Kostitsin's model and is formulated as an initial-boundary value problem for a nonlinear system of convection-diffusion equations. These equations describe the spatiotemporal dynamics of biomass density changes in two types of crops — transgenic and non-modified — as well as the specific populations (densities) of three genotypes of pests (the corn borer) resulting from mutations. The authors linearized the convection-diffusion equations by applying a time-lag method on the time grid, with nonlinear terms from each equation taken from the previous time layer. The terms describing taxis are presented in a symmetric form, ensuring the skew-symmetry of the corresponding continuous operator and, in the case of spatial grid approximation, the finite-difference operator.

Results. A stable monotonic finite-difference scheme is developed, approximating the original problem with second-order accuracy on a uniform 2D spatial grid. Numerical solutions of model problems are provided, qualitatively corresponding to observed processes. Solutions are obtained for various ratios of modified and non-modified sections of the field.

Discussion and Conclusion. The obtained results regarding pest behavior, depending on the type of taxis, could significantly extend the time for pests to acquire *Bt* resistance. The concentration dynamics of pests moving in the direction of the food gradient differs markedly from the concentration of pests moving towards a mate for reproduction.

Keywords: mathematical modelling, genetically modified corn, crops, fast and slow taxis

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Оригинальное эмпирическое исследование

Математическое моделирование пространственно-неоднородного нестационарного взаимодействия вредителей с трансгенной и немодифицированной агрокультурами с учетом таксиса

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Аннотация

Введение. Рассматривается объединенная пространственно-неоднородная нестационарная модель взаимодействия генетически модифицированного растительного ресурса (кукурузы) при наличии на поле вредителя — кукурузного мотылька, также локализованного на относительно небольшом участке поля немодифицированной кукурузы. Предполагается, что на обе растительные культуры воздействуют насекомые-вредители, способные к самостоятельному перемещению (таксису) в направлении градиента растительного ресурса. Также рассматриваемая модель учитывает диффузионные процессы в динамике всех компонентов объединенной модели, рост биомассы, генетические особенности обоих видов растительного ресурса и процессов выедания агрокультур, явления роста и деградации, диффузии и мутации вредителей и дает возможность, на основе прогностических расчетов, с одной стороны, уменьшить потери урожая, с другой стороны — повысить стойкость трансгенной агрокультуры к воздействию вредителя за счет снижения скорости его естественной мутации.

Материалы и методы. Математическая модель представляет собой развитие модели Костицына и является начально-краевой задачей для нелинейной системы уравнений конвекции-диффузии, которые описывают пространственно-временную динамику изменения плотности биомассы двух типов агрокультуры — трансгенной и немодифицированной, а также удельные численности (плотности) образовавшихся в результате мутаций трех генотипов вредителей (кукурузного мотылька).

Авторами выполнена линеаризация уравнений диффузии-конвекции по правым частям на временной сетке — нелинейные члены, входящие в каждое из уравнений, берутся с запаздыванием на предыдущем временном слое. Члены, определяющие таксис, представлены в так называемой симметричной форме, гарантирующей кососимметричность соответствующего непрерывного оператора, а при аппроксимации на пространственной сетке — и разностного оператора.

Результаты исследования. Построена устойчивая монотонная разностная схема, аппроксимирующая исходную задачу со вторым порядком на пространственной равномерной 2D сетке. Приведены результаты численного решения модельных задач, качественно согласующиеся с реально наблюдаемыми процессами. Получены решения для различных соотношений модифицированного и немодифицированного участков поля.

Обсуждение и заключения. Полученные результаты учета поведения вредителей в зависимости от типа таксиса могут позволить существенно увеличить время приобретения *Bt*-устойчивости. При этом динамика концентрации вредителей, перемещающихся в направлении градиента поиска пищи, значительно отличается от концентрации вредителей, перемещающихся в направлении партнёра для размножения.

Ключевые слова: математическое моделирование, генетически модифицированная кукуруза, агрокультура, быстрый и медленный таксис

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Introduction. A unified spatially inhomogeneous non-stationary model is considered, describing the interaction of genetically modified crop resources (corn) [1–5] in the presence of pests, specifically the corn borer, which is also localized within a relatively small section of the field growing non-modified corn. It is assumed that insect pests affect both types of crops and are capable of moving independently in the direction of the plant resource gradient, thus accounting for the phenomenon of taxis [6, 7]. Furthermore, the model incorporates diffusion processes in the dynamics of all components of the unified model.

The arrangement of two types of crops of the same species — transgenic and non-modified — on the same plot of land (field), with the non-modified crop occupying a significantly smaller area, allows for the localization of a large proportion of pests in this smaller area [8–13]. By selecting the relative size of this area and considering factors such as soil fertility, biomass growth, diffusion, and genetic characteristics of both types of crop resources, predictive calculations based on the developed model can be used to reduce crop losses. The processes of crop consumption, growth, degradation, taxis, diffusion, and pest mutation are also accounted for additionally, this approach increases the resistance of transgenic crops to pest damage by slowing the natural mutation rate of pests.

Materials and Methods. The mathematical model is formulated as an initial-boundary value problem for nonlinear convection-diffusion equations with nonlinear functions on the right-hand side [14–17]. These equations describe the spatiotemporal dynamics of biomass density changes for two types of crops — transgenic and non-modified — as well as the density of three pest genotypes, which arise due to mutations in the corn borer.

Transgenic corn lines resistant to pests, producing *"Cry 3 Bt"* toxin crystals, are engineered using the bacterium *Bacillus thuringiensis var*. Tenebrionis. It is assumed that the gene responsible for *Bt*-resistance in an individual pest can exist in two states, referred to as alleles: the *Bt*-susceptible allele (*s*-allele) or the *Bt*-resistant allele (*r*-allele) [15–17]. These two alleles form three pest genotypes: *Bt*-susceptible genotypes (*ss* and *rs*, if *Bt*-resistance is recessive) and the *Bt*-resistant genotype (*rr*). The proposed approach is based on a modified demo-genetic model of Kostitsin [1, 15–21], which describes the dynamics of competing pest genotypes using Lotka-Volterra equations [2, 3].

In this work, the convection-diffusion equations were linearized on the time grid, where the nonlinear terms [22, 23] in each equation were taken with a delay from the previous time layer. The terms defining taxis are analogous to advective transport terms and are presented in a symmetric form that ensures the skew-symmetry of the corresponding continuous operator. When approximated on a spatial grid, this also ensures the skew-symmetry of the finite-difference operator. This approach, with relatively mild restrictions on the time step during the approximation on a 2D spatial grid, allows for the construction of a stable monotonic finite-difference scheme.

Formulation of the Initial-Boundary Value Problem. Let $R = R(x, y, t)$ represent the biomass growth of the studied crop, and r_R be the Malthusian growth rate coefficient. The well-known equation for the dynamics of biomass density takes the form:

$$\frac{\partial R}{\partial t} = \delta_R \Delta R + r_R R\left(1-\frac{R}{K_R}\right) - aRN, \tag{1}$$

$$r_R = r_R + g(x,y,t).$$

where $g(x, y, t)$ is a function accounting for the fertility of a specific field section.

It is assumed that two types of plant resources exist — "regular" and transgenic crops:

$$R = R_1 + R_2, \tag{2}$$

where $R_1 = \alpha(x, y)\, R$ is the initial biomass of the regular plant resource, $R_2 = (1 - \alpha\,(x, y))R$ is the initial biomass of the transgenic plant resource, $N = N_{ss} + N_{rs} + N_{rr}$ is the total pest population density, $N_{ij} = N_{ij}(\mathbf{x}, y, t)$ is the density of genotype ij at point $(\mathbf{x}, y) \in \Omega$ at time t ($i, j = r$ или s); N_{ss}, N_{rs}, N_{rr} are the pest population densities correspond to the respective genotypes, K_R is the carrying capacity of the environment, δ_R is the diffusion coefficient for the plant resource, $\alpha(x, y)$ is the competition coefficient between the two types of plant resources (which can be neglected if the distance between patches exceeds 5 meters).

For each pest genotype, where necessary, indices are used in the notation: *ss* and *rs* for *Bt*-susceptible genotypes and *rr* for the *Bt*-resistant genotype.

Recall that the goal of using transgenic crops to suppress the pest population in agricultural fields is to reduce the risk of the pest adapting to the *Bt*-toxin [8–13, 15, 16], produced by the transgenic crop, within the given spatial configuration of the system and under the prescribed "high-dose/refuge" strategy scenarios recommended for managing pest resistance to *Bt* plants. The "high-dose" means that the toxicity level of the *Bt*-crops is sufficiently high to kill nearly all pest larvae. The small percentage of surviving (*Bt*-resistant) individuals should be controlled by designating special areas on or near the transgenic fields where non-modified crops (refuges) are planted. These refuges serve as a source of *Bt*-susceptible individuals, which, by mating with *Bt*-resistant individuals, should decrease the proportion of resistant offspring.

The biomass growth for both types of crops, considering diffusion, is modeled by the following equations:

$$\begin{cases} \dfrac{\partial R_1}{\partial t} = \delta_R \Delta R_1 + r_R R_1\left(1-\dfrac{R}{K_R}\right) - aR_1 N, \\ \dfrac{\partial R_2}{\partial t} = \delta_R \Delta R_2 + r_R R_2\left(1-\dfrac{R}{K_R}\right) - aR_2 N_{rr}. \end{cases} \tag{3}$$

Let's introduce the functions that describe the offspring distribution f_{ij}, where the indices *i, j* represent the genotypes *ss, rs, ss:*

$$f_{ij}:\begin{cases} f_{ss}\left(N_{ss},N_{sr},N_{rr}\right)=W_{ss}\dfrac{1}{N}\left(N_{ss}+\dfrac{N_{rs}}{2}\right)^2, \\ f_{sr}\left(N_{ss},N_{sr},N_{rr}\right)=W_{rs}\dfrac{2}{N}\left(N_{ss}+\dfrac{N_{rs}}{2}\right)\left(\dfrac{N_{rs}}{2}+N_{rr}\right), \\ f_{rr}\left(N_{ss},N_{rs},N_{rr}\right)=W_{rr}\dfrac{1}{N}\left(\dfrac{N_{rs}}{2}+N_{rr}\right)^2. \end{cases} \tag{4}$$

The primary *Bt*-resistance management strategy, the "high-dose/refuge" approach, is modeled as follows. It is assumed that the pest's habitat Ω may consist of an arbitrary number of areas planted either with *Bt*-corn (Ω_{Bt}), or regular corn (Ω_{ref}). Let $\sigma \in (0,1)$ be the selection coefficient for *Bt*-resistance. Then, the fitness of the pest genotypes is expressed as:

$$\begin{gathered} W_{rr}=1-c, \text{ на всем } \Omega; \\ W_{rs}\left(\mathbf{x}\right)=\begin{cases}1-h_c\,c, & \mathbf{x}\in\Omega_{ref}; \\ 1-\sigma+h_\sigma\left(\sigma-c\right), & \mathbf{x}\in\Omega_{Bt}; \end{cases} \\ W_{ss}\left(\mathbf{x}\right)=\begin{cases}1, & \mathbf{x}\in\Omega_{ref}; \\ 1-\sigma, & \mathbf{x}\in\Omega_{Bt}, \end{cases} \end{gathered} \tag{5}$$

where *c* is the cost that the *Bt*-resistant genotype pays for the advantage it has on *Bt*-fields; h_σ is the dominance level of selection for *Bt*-resistance; h_c is the dominance level of the cost *c*, the parameters σ, c, h_σ, $h_c \in [0,1]$ are determined empirically.

Let *a* represent the search activity coefficient of the corn borer, characterizing its sensitivity to the heterogeneity of corn distribution, *b* be the fertility coefficient, μ — the mortality rate of genotypes, α — the competition coefficient between them. $W_{ij} \in [0,1]$ denotes the fitness coefficient of genotype *ij* in the environment, determining its survival depending on its localization in the habitat (on *Bt*-plants or in a refuge). It is worth noting that when the coefficients (i. e., the habitat is homogeneous and serves as a refuge), summing the system of equations leads to a simple logistic growth equation for the entire population.

Results. To solve the task at hand, we modify the Kostytsyn›s demo-genetic model (1) by adding terms accounting for taxis:

$$\begin{cases} \dfrac{\partial N_{ss}}{\partial t}+\nabla(N_{ss}v_{ss})=\delta\Delta N_{ss}+eaRW_{ss}\dfrac{1}{N}(N_{ss}+\dfrac{N_{rs}}{2})^2-\mu N_{ss}, \\ \dfrac{\partial N_{rs}}{\partial t}+\nabla(N_{rs}v_{rs})=\delta\Delta N_{rs}+eaRW_{rs}\dfrac{2}{N}(N_{ss}+\dfrac{N_{rs}}{2})* \\ *(N_{rr}+\dfrac{N_{rs}}{2})-\mu N_{rs}, \\ \dfrac{\partial N_{rr}}{\partial t}+\nabla(N_{rr}v_{rr})=\delta\Delta N_{rr}+eaRW_{rr}\dfrac{1}{N}(N_{rr}+\dfrac{N_{rs}}{2})^2-\mu N_{rr}, \end{cases} \tag{6}$$

where $K_R=\left(b-\mu\right)/\alpha$ is the environmental capacity, δ_R is the diffusion coefficient of the plant resource, W_{ij} are the adaptability coefficients for pests with the *ij*-th genotype, f_{ij} proportions determining the distribution of pest offspring among the three considered genotypes *ij* (*ss*, *sr*, *rr*) (4), $N_{ij}=N_{ij}(\mathbf{x},y,t)$ is the density of the *ij* genotype at point $(\mathbf{x}, y) \in \Omega$ at time *t* ($i, j = r$ or s), N_{ss}, N_{rs}, N_{rr} are the densities of the corresponding pest genotypes, $N = N_{ss} + N_{rs} + N_{rr}$ is the total population density, μ is the mortality coefficient for the genotypes, v_{ss}, v_{sr}, v_{rr}, или $v_{ij}(x, y, t)$ are the velocities of pest movement in the spatial variables *x* and *y* for the corresponding types in the direction of the plant resource gradient.

For two types of taxis (fast and slow), the biological significance and the equations governing them will be presented below. Each type is characterized by its ability to locate areas with high prey concentrations. The moth's search behavior is modeled based on the assumption that the acceleration of the pest's movement is proportional to the gradient of plant density or the change in biomass growth:

$$\frac{\mathrm{d}v_{ij}}{\mathrm{d}t}=k\nabla R+\delta_v\Delta v_{ij}, \tag{7}$$

where $R = R(x, y, t)$ represents the biomass growth of the plant resource population at point (x, y) at time *t*; $v_{ij}(x, y, t)$ denotes the velocities of pest movement, Δ is the Laplace operator, ∇ is the gradient operator.

Here and further, the habitat boundaries of the community are assumed to be uninhabited, meaning that both diffusion and advective flows of individuals across the boundaries are absent:

$$\nabla N_{ij} \bullet n = 0,\ v \bullet n = 0,\ (x, y) \in \partial\Omega\ . \tag{8}$$

Here n is an external normal to the border $\partial\Omega$; Ω is the spatially two-dimensional region representing the pest's habitat; $(x, y) \in \Omega$ (x, y) the closure of this region Ω. Such a formulation of boundary conditions allows for a natural ecological interpretation, specifically the spatial isolation of the trophic community.

Let us now consider the pest dynamics equations, where pest activity is determined by the sum of the densities of two species of insect pests:

$$N = N^{(1)} + N^{(2)} \tag{9}$$

where $N^{(1)}$ и $N^{(2)}$ and are the pest densities in the passive and active state, respectively.

Considering equation (9), the system of equations (6) for the passive behavior of pests can be rewritten as equations (10):

$$\begin{cases} \dfrac{\partial N_{ss}^{(1)}}{\partial t} + \nabla(N_{ss}^{(1)} v_{ss}^{(1)}) = \delta^{(1)} \Delta N_{ss}^{(1)} + eaR_1 W_{ss} \dfrac{1}{N^{(1)}} \left(N_{ss}^{(1)} + \dfrac{N_{rs}^{(1)}}{2} \right)^2 - \mu N_{ss}^{(1)} - \beta N N_{ss}^{(1)}, \\ \dfrac{\partial N_{rs}^{(1)}}{\partial t} + \nabla(N_{rs}^{(1)} v_{rs}^{(1)}) = \delta^{(1)} \Delta N_{rs}^{(1)} + eaR_1 W_{rs} \dfrac{2}{N^{(1)}} \left(N_{ss}^{(1)} + \dfrac{N_{rs}^{(1)}}{2} \right) \cdot \left(N_{rr}^{(1)} + \dfrac{N_{rs}^{(1)}}{2} \right) - \mu N_{rs}^{(1)} - \beta N N_{rs}^{(1)}, \\ \dfrac{\partial N_{rr}^{(1)}}{\partial t} + \nabla(N_{rr}^{(1)} v_{rr}^{(1)}) = \delta^{(1)} \Delta N_{rr}^{(1)} + eaRW_{rr} \dfrac{1}{N^{(1)}} \left(N_{rr}^{(1)} + \dfrac{N_{rs}^{(1)}}{2} \right)^2 - \mu N_{rr}^{(1)} - \beta N N_{rr}^{(1)}, \\ (x, y) \in \Omega(x, y),\ 0 < t \le T, \\ N_{ij}^{(1)}(x_0, y_0, 0) = N_{ij}^*, R_1(x_0, y_0, 0) = R_1^*, \\ \nabla N_{ij}^{(1)} \bullet n = 0,\ \nabla v_{ij}^{(1)} \bullet n = 0, (x, y) \in \partial\Omega. \end{cases} \tag{10}$$

In the active state, considering that the pest, which is susceptible to the pesticide, only consumes the conventional plant resource (and not the transgenic crop), we derive the following system of equations (11):

$$\begin{cases} \dfrac{\partial N_{ss}^{(2)}}{\partial t} + \nabla(N_{ss}^{(2)} v^{(2)}) = \delta^{(2)} \Delta N_{ss}^{(2)} + eaR_1 W_{ss} \dfrac{1}{N^{(2)}} \left(N_{ss}^{(2)} + \dfrac{N_{rs}^{(2)}}{2} \right)^2 - \mu N_{ss}^{(2)} - \beta N N_{ss}^{(2)}, \\ \dfrac{\partial N_{rs}^{(2)}}{\partial t} + \nabla(N_{rs}^{(2)} v^{(2)}) = \delta^{(2)} \Delta N_{rs}^{(2)} + eaR_1 W_{rs} \dfrac{2}{N^{(2)}} \left(N_{ss}^{(2)} + \dfrac{N_{rs}^{(2)}}{2} \right) \cdot \left(N_{rr}^{(2)} + \dfrac{N_{rs}^{(2)}}{2} \right) - \mu N_{rs}^{(2)} - \beta N N_{rs}^{(2)}, \\ \dfrac{\partial N_{rr}^{(2)}}{\partial t} + \nabla(N_{rr}^{(2)} v^{(2)}) = \delta^{(2)} \Delta N_{rr}^{(2)} + eaRW_{rr} \dfrac{1}{N^{(2)}} \left(N_{rr}^{(2)} + \dfrac{N_{rs}^{(2)}}{2} \right)^2 - \mu N_{rr}^{(2)} - \beta N N_{rr}^{(2)}, \\ (x, y) \in \Omega(x, y),\ 0 < t \le T, \\ N_{ij}^{(2)}(x_0, y_0, 0) = N_{ij}^{**}, R_1(x_0, y_0, 0) = R_1^*, \\ \nabla N_{ij}^{(2)} \bullet n = 0,\ \nabla v_{ij}^{(2)} \bullet n = 0, (x, y) \in \partial\Omega. \end{cases} \tag{11}$$

By summing the first three equations, we obtain (11*):

$$\begin{cases} \dfrac{\partial N_{ss}^{(2)}}{\partial t} + \nabla(N_{ss}^{(2)} v^{(2)}) = \delta^{(2)} \Delta N_{ss}^{(2)} + eaR_1 N^{(2)} - \mu N_{ss}^{(2)} - \beta N N^{(2)}, \\ (x, y) \in \Omega(x, y),\ 0 < t \le T, \\ N_{ij}^{(2)}(x_0, y_0, 0) = N_{ij}^{**}, R_1(x_0, y_0, 0) = R_1^*, \\ \nabla N_{ij}^{(2)} \bullet n = 0,\ \nabla v_{ij}^{(2)} \bullet n = 0, (x, y) \in \partial\Omega. \end{cases} \tag{11*}$$

Slow taxis in the passive state for the three types of insect pests is described by the following equations (12):

$$\begin{cases} v_{ss}^{(1)} + \alpha\left(\dfrac{\partial v_{ss}^{(1)}}{\partial t} + \nabla(N_{ss}^{(1)} v_{ss}^{(1)})\right) = \delta_v^{(1)} \Delta v_{ss}^{(1)} + k^{(1)} \nabla R_1, \\ v_{rs}^{(1)} + \alpha\left(\dfrac{\partial v_{rs}^{(1)}}{\partial t} + \nabla(N_{rs}^{(1)} v_{rs}^{(1)})\right) = \delta_v^{(1)} \Delta v_{rs}^{(1)} + k^{(1)} \nabla R_1, \\ v_{rr}^{(1)} + \alpha\left(\dfrac{\partial v_{rr}^{(1)}}{\partial t} + \nabla(N_{rr}^{(1)} v_{rr}^{(1)})\right) = \delta_v^{(1)} \Delta v_{rr}^{(1)} + k^{(1)} \nabla R, \\ (x,y) \in \Omega(x,y),\ 0 < t \le T, \\ N_{ij}^{(1)}(x_0, y_0, 0) = N_{ij}^{*}, R(x_0, y_0, 0) = R^{*}, \\ \nabla N_{ij}^{(1)} \bullet n = 0,\ \nabla v_{ij}^{(1)} \bullet n = 0, (x,y) \in \partial\Omega. \end{cases} \tag{12}$$

Fast taxis in the active state is described by a single equation for pesticide-resistant insect pests (13), since genotype-specific traits are not significant when searching for a mating partner:

$$v^{(2)} = k^{(2)} \nabla N^{(2)} + \delta_v^{(2)} \Delta v^{(2)}. \tag{13}$$

In equations (12)–(13), all velocities $v_{ij}^{(1)}, v_{ij}^{(2)}, ij \in (ss, sr, rr)$ are spatially two-dimensional vectors.

To linearize the system (3)–(11), considering the initial and boundary conditions, we construct a uniform time grid ω_τ over the time interval $0 < t \le T$, where T is the characteristic period of crop maturation (from early spring to late summer), with a time step τ:

$$\omega_\tau = \{ t_k = k\tau, k = 0,1,\ldots,N; N\tau = T \}. \tag{14}$$

On this constructed time grid, we build a sequence of linearized initial-boundary value problems, which are interconnected at each step by the initial and final values. The idea behind such linearization is that all nonlinear terms in the corresponding partial differential equations are taken from the values at the previous time layer relative to the current one. For the first time layer, the appropriate initial conditions are used.

Let the solutions of the sequence of linearized initial-boundary value problems be denoted the same as the solution to the original nonlinear problem (3)–(13).

Initially, for each t_k, starting from the initial moment t_0 the velocities of slow and fast taxis are determined from equations (15) and (16), respectively. The value of k, $k = 1,\ldots,N$ is fixed for all initial-boundary value problems of the linearized system of partial differential equations solved at the given time layer $t_{k-1} < t \le t_k$, $k = 1,\ldots,N$:

$$\begin{cases} \dfrac{\partial v_{ij}^{(1),(k)}}{\partial t} + \dfrac{1}{2}(v_{ij}^{(1),(k)} \nabla N_{ij}^{(1)}(t_{k-1}) + \nabla(N_{ij}^{(1)}(t_{k-1}) v_{ij}^{(1),(k)})) + \\ + \dfrac{1}{\alpha} \Delta v_{ij}^{(1),(k)} = \dfrac{1}{\alpha}(\delta_v^{(1)} \Delta v_{ij}^{(1),(k)} + k^{(1)} \nabla R_1^{(k-1)}(t_{k-1})), \\ v_{ij}^{(1),(0)} = V_{ij}^{*}, v_{ij}^{(1),(k)}(t_{k-1}) = v_{ij}^{(1),(k-1)}(t_{k-1}), k = 1,\ldots,N, \\ t_{k-1} < t \le t_k, (x,y) \in \Omega(x,y), \\ N_{ij}^{(1)}(x_0, y_0, t_0) = N_{ij}^{(1)}(x_0, y_0, 0) = N_{ij}^{*}(x,y), R_1^{0}(x_0, y_0, 0) = R^{*}(x,y), \\ \nabla(N_{ij}^{(1)} \bullet n) = 0,\ \nabla v_{ij}^{(1),(k-1)} \bullet n = 0,\ ij \in (ss, sr, rr), (x,y) \in \partial\Omega. \end{cases} \tag{15}$$

$$\begin{cases} v^{(2),(k)} = k^{(2)} \nabla N^{(2),(k-1)} + \delta_v^{(2)} \Delta v^{(2),(k)} \\ v_{ij}^{(2),(0)} = V^{**},\ N_{ij}^{(2),(0)}(x_0, y_0, t_0) = N_{ij}^{**}(x,y), \\ v_{ij}^{(2),(k)}(t_{k-1}) = v_{ij}^{(2),(k-1)}(t_{k-1}), \\ t_{k-1} < t \le t_k,\ k = 1,\ldots,N,\ (x,y) \in \Omega(x,y). \end{cases} \tag{16}$$

In relations (15) and (16), the initial conditions $V_{ij}^{*}, V^{**}, R^{*}(x,y), N_{ij}^{*}(x,y), N_{ij}^{**}(x,y)$ are represented by known functions. For the sake of brevity, we will not separately specify the initial and boundary conditions for systems (17)–(19).

Here and throughout, for the system (17)–(19), the value of the parameter k is fixed and is the same as in equations (15)–(16). It remains constant across all systems (17)–(19) until the corresponding initial-boundary value problems are solved within the given time interval $t_{k-1} < t \le t_k$.

For system (3), we have the following:

$$\begin{cases} \dfrac{\partial R_1^{(k)}}{\partial t} = \delta_R \Delta R_1^{(k)} + r_R R_1^{(k)} \left(1 - \dfrac{R_1^{(k-1)}(t_{k-1}) + R_2^{(k-1)}(t_{k-1})}{K_R}\right) - a R_1^{(k)} \left(N^{(1),(k-1)}(t_{k-1}) + N^{(2),(k-1)}(t_{k-1})\right), \\ \dfrac{\partial R_2^{(k)}}{\partial t} = \delta_R \Delta R_2^{(k)} + r_R R_2^{(k)} \left(1 - \dfrac{R_1^{(k-1)}(t_{k-1}) + R_2^{(k-1)}(t_{k-1})}{K_R}\right) - a R_2^{(k)} N_{rr}^{(k-1)}(t_{k-1}), \\ R_1^{(k)}(t_{k-1}) = R_1^{(k-1)}(t_{k-1}), R_2^{(k)}(t_{k-1}) = R_2^{(k-1)}(t_{k-1}), \\ t_{k-1} < t \le t_k,\ k = 1,\dots,N,\ (x,y) \in \Omega(x,y). \end{cases} \tag{17}$$

For system (10), we have the following:

$$\begin{cases} \dfrac{\partial N_{ss}^{(1),(k)}}{\partial t} + \dfrac{1}{2}\left(\nabla(N_{ss}^{(1),(k)} v_{ss}^{(1),(k-1)}) + \nabla N_{ss}^{(1),(k)} v_{ss}^{(1),(k-1)}\right) = \delta^{(1)} \Delta N_{ss}^{(1),(k-1)} + \\ + ea R_1^{(k-1)}(t_{k-1}) W_{ss} \dfrac{1}{N^{(1),(k)}} \left(N_{ss}^{(1),(k)} + \dfrac{N_{rs}^{(1),(k-1)}(t_{k-1})}{2} \right)^2 - \mu N_{ss}^{(1),(k)} - \beta N^{(k)} N_{ss}^{(1),(k)}, \\ \dfrac{\partial N_{rs}^{(1),(k)}}{\partial t} + \dfrac{1}{2}\left(\nabla(N_{rs}^{(1),(k)} v_{rs}^{(1),(k-1)}) + \nabla N_{rs}^{(1),(k)} v_{rs}^{(1),(k-1)}\right) = \delta^{(1)} \Delta N_{rs}^{(1),(k-1)} + \\ + ea R_1^{(k-1)}(t_{k-1}) W_{rs} \dfrac{1}{N^{(1),(k)}} \left(N_{ss}^{(1),(k-1)}(t_{k-1}) + \dfrac{N_{rs}^{(1),(k)}}{2} \right) \cdot \\ \cdot \left(N_{rr}^{(1),(k-1)}(t_{k-1}) + \dfrac{N_{rs}^{(1),(k)}}{2} \right) - \mu N_{rs}^{(1),(k)} - \beta N^{(k)} N_{rs}^{(1),(k)}, \\ \dfrac{\partial N_{rr}^{(1),(k)}}{\partial t} + \dfrac{1}{2}\left(\nabla(N_{rr}^{(1),(k)} v_{rr}^{(1),(k-1)}) + \nabla N_{rr}^{(1),(k)} v_{rr}^{(1),(k-1)}\right) = \delta^{(1)} \Delta N_{rr}^{(1)} + \\ + ea\left(R_1^{(k-1)}(t_{k-1}) + R_2^{(k-1)}(t_{k-1})\right) W_{rr} \dfrac{1}{N^{(1),(k)}} \left(N_{rr}^{(1),(k)} + \dfrac{N_{rs}^{(1),(k-1)}(t_{k-1})}{2} \right)^2 - \mu N_{rr}^{(1),(k)} - \beta N^{(\mathrm{k})} N_{rr}^{(1),(k)}, \\ R_1^{(k)}(t_{k-1}) = R_1^{(k-1)}(t_{k-1}), R_2^{(k)}(t_{k-1}) = R_2^{(k-1)}(t_{k-1}), \\ N_{ss}^{(1),(k)}(t_{k-1}) = N_{ss}^{(1),(k-1)}(t_{k-1}), N_{rs}^{(1),(k)}(t_{k-1}) = N_{rs}^{(1),(k-1)}(t_{k-1}), \\ N_{rr}^{(1),(k)}(t_{k-1}) = N_{rr}^{(1),(k-1)}(t_{k-1}), t_{k-1} < t \le t_k, k = 1,\dots,N;\ (x,y) \in \partial\Omega. \end{cases} \tag{18}$$

For the system of equations (11*), we have the linearized formulation (19).

Subsequently, all linearized initial-boundary value problems are approximated on an extended uniform two-dimensional grid using implicit schemes with second-order accuracy with respect to spatial grid steps and first-order accuracy with respect to the time step. Considering the limited speed of pest movement and the symmetric form of the terms describing taxis (skew-symmetry of the corresponding grid operator), it is possible (by selecting a sufficiently small time step) to satisfy the conditions for the applicability of the discrete maximum principle and the positive definiteness of the grid operator for each equation in the system (15)–(19) in the Hilbert space of grid functions. Consequently, we obtain a stable difference scheme. Due to the considerable complexity and volume of work, these studies are expected to be carried out in future research planned on this topic.

$$\begin{cases} \dfrac{\partial v^{(2),(k)}}{\partial t} + \dfrac{1}{2}\left(\nabla(N^{(2),(k)}(t_{k-1}) v^{(2),(k-1)}) + \nabla N^{(2),(k)}(t_{k-1}) v^{(2),(k-1)}\right) = \\ = \delta_v^{(2)} \Delta N^{(2),(k)} - \beta N^{(k)} N^{(2),(k)}, \\ \\ R_1^{(k)}(t_{k-1}) = R_1^{(k-1)}(t_{k-1}), R_2^{(k)}(t_{k-1}) = R_2^{(k-1)}(t_{k-1}), \\ N_{ss}^{(1),(k)}(t_{k-1}) = N_{ss}^{(1),(k-1)}(t_{k-1}), N_{rs}^{(1),(k)}(t_{k-1}) = N_{rs}^{(1),(k-1)}(t_{k-1}), \\ N_{rr}^{(1),(k)}(t_{k-1}) = N_{rr}^{(1),(k-1)}(t_{k-1}), t_{k-1} < t \le t_k, k = 1,\dots,N;\ (x,y) \in \partial\Omega. \end{cases} \tag{19}$$

The resulting system of difference equations, which approximates the sequence of initial-boundary value problems (15)–(19) with a sufficiently small time step (hundreds or thousands of seconds), exhibits strict diagonal dominance. It is advisable to solve it using the Seidel method, which converges at a rate of geometric progression.

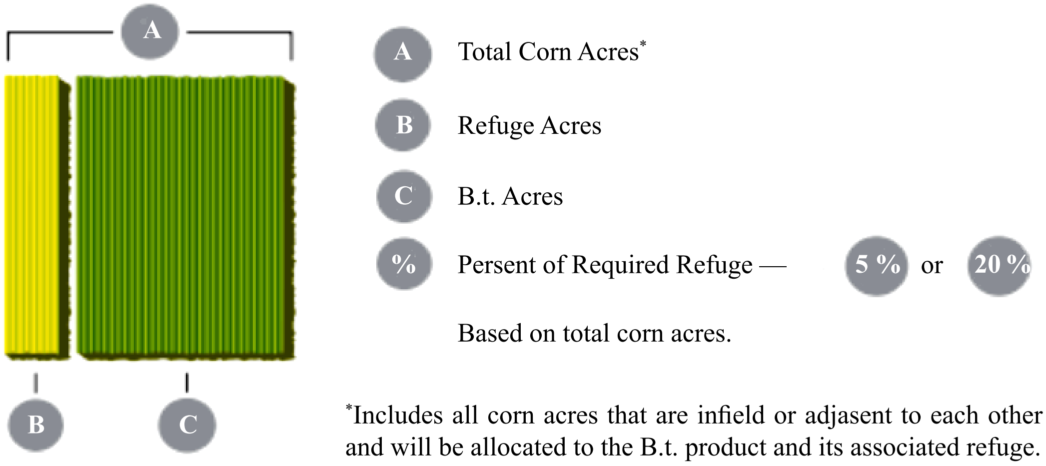
To model possible scenarios of the behavior of a biological system consisting of predators and prey, a software package was developed [21]. A two-dimensional grid of size 100×100 units is considered, with a spatial step of 1 and a time step of 0.01. The weight for the difference scheme is set to 0.5. At the initial moment of simulation, the prey concentration was set to a constant value of 1, while the initial predator concentration is shown in Figures 9 and 10. The following parameters were used to simulate changes in population concentrations: the mortality coefficients for the plant resource $\beta_1 = \beta_2 = 1$, the predator growth coefficient, which is taken as the product of the pest's efficiency coefficient e and the pest's resource search efficiency coefficient a: $ea = 1$, and the taxis coefficients $k^{(1)} = k^{(2)} = 40$. For equations (1)–(7), it is assumed that the mobility of the different moth genotypes is the same $\delta = 1$ the pest mortality coefficient $\mu = 6.84$, the carrying capacity of the environment $K_r = 5*106$ kg/km^2, and the Malthusian growth coefficient $r_R = 25.3$ year^{-1}. In all numerical experiments, it was assumed that at the initial moment, the pest density was uniformly distributed over space at $N^0 = 2{,}948 \times 10^6$ individuals/km^2.

According to the authors' assumptions, at the beginning of the study period, there are pests with dominant (*ss*) and mixed (*rs*) genes that lack resistance to transgenic crops. Pests with recessive traits (*rr*-genotype) emerge as a result of crossbreeding by the end of the first month after the first generation reproduces. For the first few months, recessive traits manifest only in individuals with slow taxis. The movement of pests is directed inward, towards areas planted with conventional crops (referred to as "refuges"). Here, through crossbreeding, the insects lose their resistance to transgenic crops.

As food sources are depleted, the boundaries of these areas "smooth out", naturally evening out the spatial distribution of pests [18, 20, 21]. Pest behavior changes by the second year. Over the first two years, the dynamics of the pests shift significantly depending on their activity — whether they are feeding or reproducing. Rapid consumption of the conventional plant resource inevitably leads pests towards the biomass gradient of the transgenic crops. However, successful reproduction is only possible in areas with conventional crops, which highlights the significant role of both fast and slow taxis in the model. Consequently, the movement of all pests is directed away from the "refuge" areas. As they deplete the conventional crop zones, the pests move toward regions where its biomass increases, eventually entering the transgenic fields, where they reproduce and gradually acquire resistance to transgenic plant varieties.

It should be noted that the main field cannot border other modified crops. Figures 1 and 2 present recommendations for farmers from the company's official website.

As the total area of "refuges" increases (>20 %), the acquisition of Bt-resistance slows down, which aligns with the widely accepted recommendations for the size of "conventional" plots on genetically modified fields — ranging from 5 % to 20 % (Fig. 1).

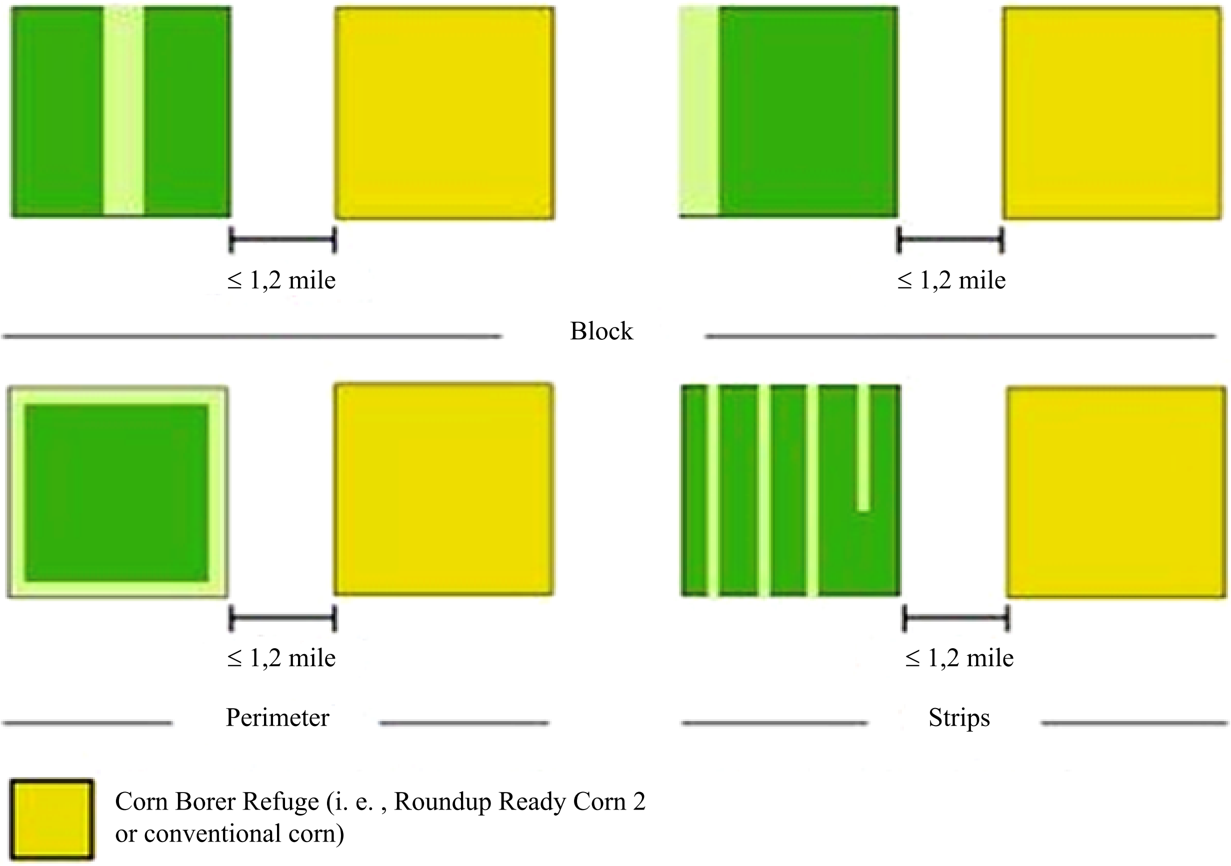


*Includes all corn acres that are infield or adjasent to each other and will be allocated to the B.t. product and its associated refuge.

Fig. 1. Recommended sizes of "refuges"

while the transgenic variety is indicated in green (Fig. 1 and 2). Here, the "striping of refuges" may be uneven across the field, and their placement depends on the agro-climatic conditions (Fig. 2).

Now, let us consider the dynamics of pest distribution under various configurations of "refuges" on fields with modified crops. The study period for pest dynamics is set at $t = 10$ conditional years. It is reasonable to assume that the boundaries of the main field should be "surrounded" by corn that does not possess *Bt*-resistance to facilitate easier access to the "refuge" for pests.



Let us consider the first type of refuge placement, where a single plot of conventional corn is located at the center of the field.

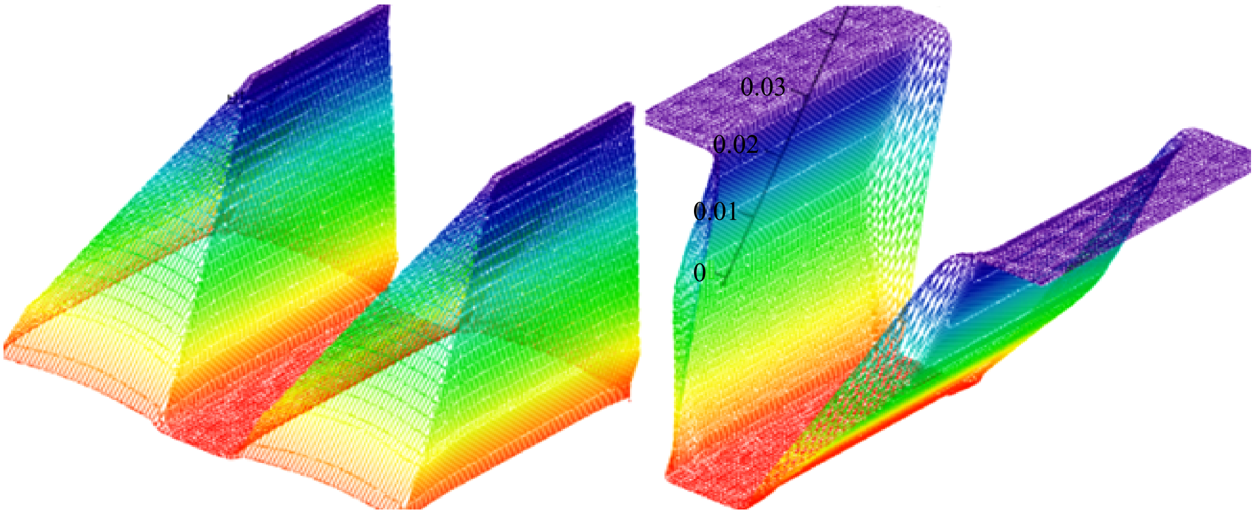


Fig. 3. Depletion of plant resource on transgenic field with a single “refuge” at $t = 10$

By depleting the safe areas of “conventional” crops, the pest is driven in search of food toward the transgenic region. Let us examine the depletion of plant resources by the pest in more detail. Fig. 3 illustrates two areas of depletion, where the boundary consists of conventional and transgenic crops. The plots of “conventional” crops are depleted more rapidly.

In May 2013, RapidEye began monitoring large agricultural plots from space, allowing for the first comparison between numerical research results and the actual conditions of agricultural lands. An overview of satellite images of the U.S. Corn Belt revealed a predominance of the fourth type of distribution, which is easily explained in terms of cultivation convenience and field management. The color differences between the plots (an example of the adjacency of “conventional” and modified varieties of corn is presented in Fig. 4) are attributed to the quality of the plants, their adaptability to the environment, and their immunity to pests.

Fig. 4. Proximity of conventional and modified corn varieties[1]

The influence of the spatial configuration of refuges on the effectiveness of the "high dose — refuge" strategy was investigated for fixed values of refuge percentage and pest mobility in the simplest case, where the pest's range is represented as a rectangle $\Omega = [0, L_x] \times [0, L_y]$. Numerical experiments with the demo-genetic model demonstrated that for a total moth range of 16 km by 16 km, positioning a single strip of refuge in the center of the field approximately halves the time T_{10}, significantly increasing the level of infestation of the *Bt*-field by moths. Dividing a single strip of "refuge" into several strips enhances refuge effectiveness.

A comparison of the results of numerical simulations in cases where the boundaries were also "refuges" or belonged to the main transgenic part of the field indicated the superiority of the first type of distribution.

The depletion of food with a "striped" arrangement of "refuges" is clearly illustrated in Fig. 5. Depletion occurs more rapidly at the boundaries of the area than in the central "refuges", and the presence of boundary "refuges" facilitates quicker depletion of the "conventional" crop.

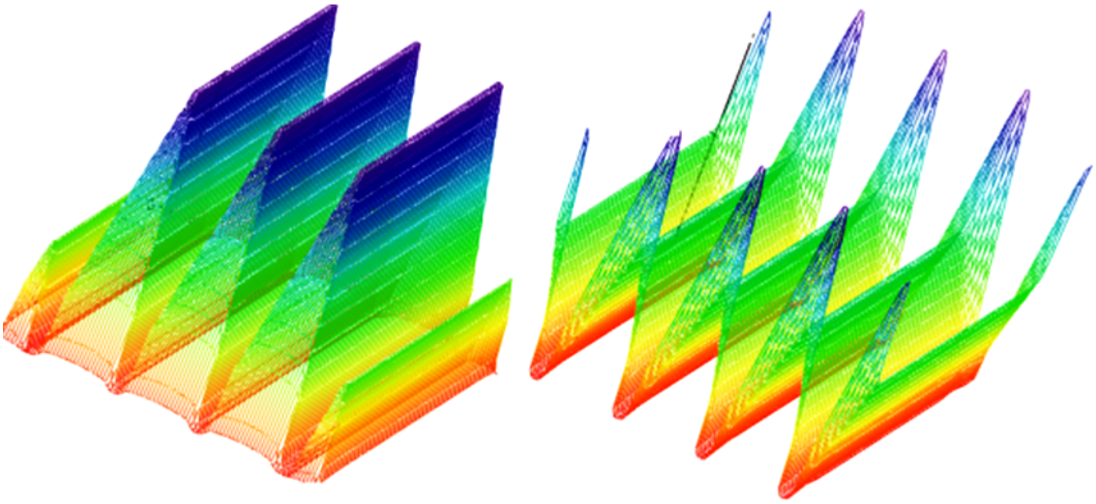


Fig. 5. Depletion of plant resource on transgenic field with four "refuges"

A similar effect is observed for refuges of rectangular or square shapes (Fig. 6 and 7). Let us consider a refuge arrangement where four square plots of "conventional" corn are positioned at the center of the transgenic field. The presence of "refuges" of varying sizes and arrangements is justified only in cases of significant height variation across the field. However, in such cases, a three-dimensional model of pest dynamics would need to be developed. The results obtained confirm our hypothesis that the distribution of "refuges" across the main field area should not touch the boundaries of the region; otherwise, we reduce the likelihood of pests accessing the "refuges".

Forecasting pest dynamics over a period of $t = 100$ reveals that the overall behavioral model of pests during resource depletion remains consistent (Fig. 7). The foliage and fruits of plants are most adversely affected by insect pests, which aligns with natural observations.

It is noteworthy that even with a single "refuge", the depletion pattern can be quite unusual, depending on the selective characteristics of the corn variety and the landscape features (Fig. 8).

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[1] Photo from http://www.monsanto.com

The number of pests increases much more slowly relative to the decrease in their mortality coefficients, indicating the need to investigate the influence of other model parameters on population dynamics.

Let us now examine the dynamics of pests based on various mortality coefficients. For the European corn borer, *Ostrinia nubilalis*, this coefficient is $\mu = 6.845$. Other corn pests exhibit significantly greater survivability. In the area under consideration, let the adaptation coefficients of the genotypes to the environment be $w_{ss} = w_{rs} = 0.45$, $w_{rr} = 0.1$ (with *Bt*-resistance at 10 %), he duration of the study is set at 2 years.

Figure 9 illustrates the dynamics of concentration with a linear increase in pest survivability.

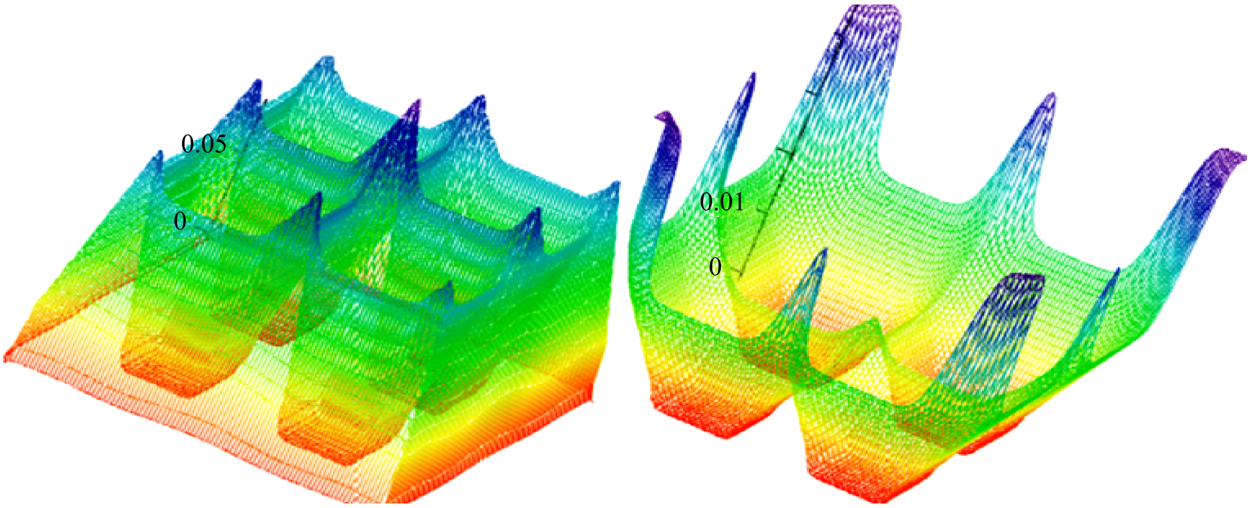

Fig. 6. Depletion of plant resource on transgenic field with four rectangular "refuges"

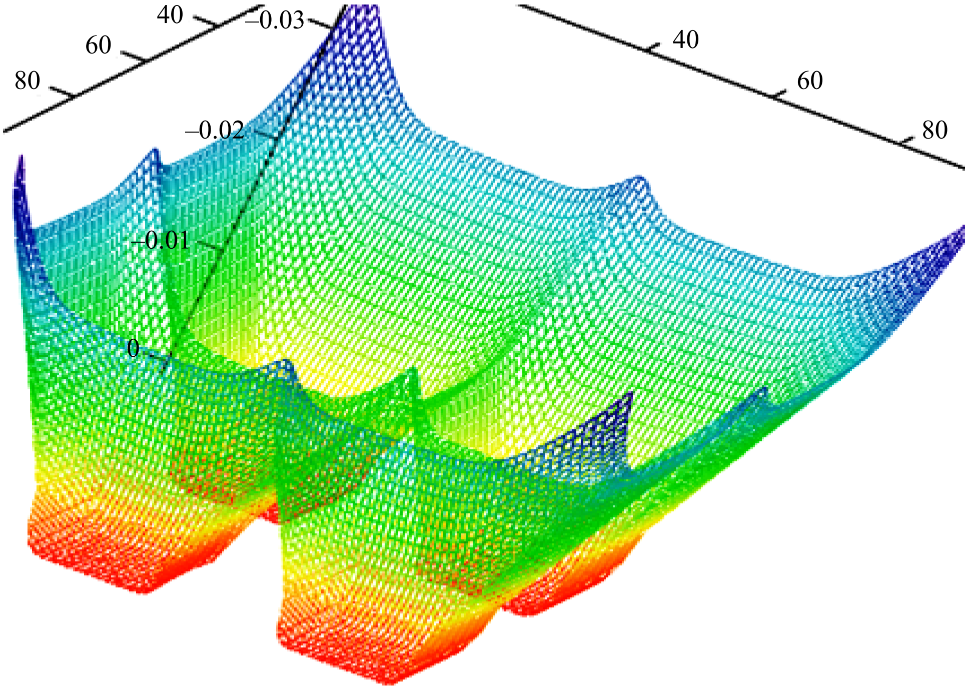

Fig. 7. Depletion of plant resource on transgenic field with four square "refuges"

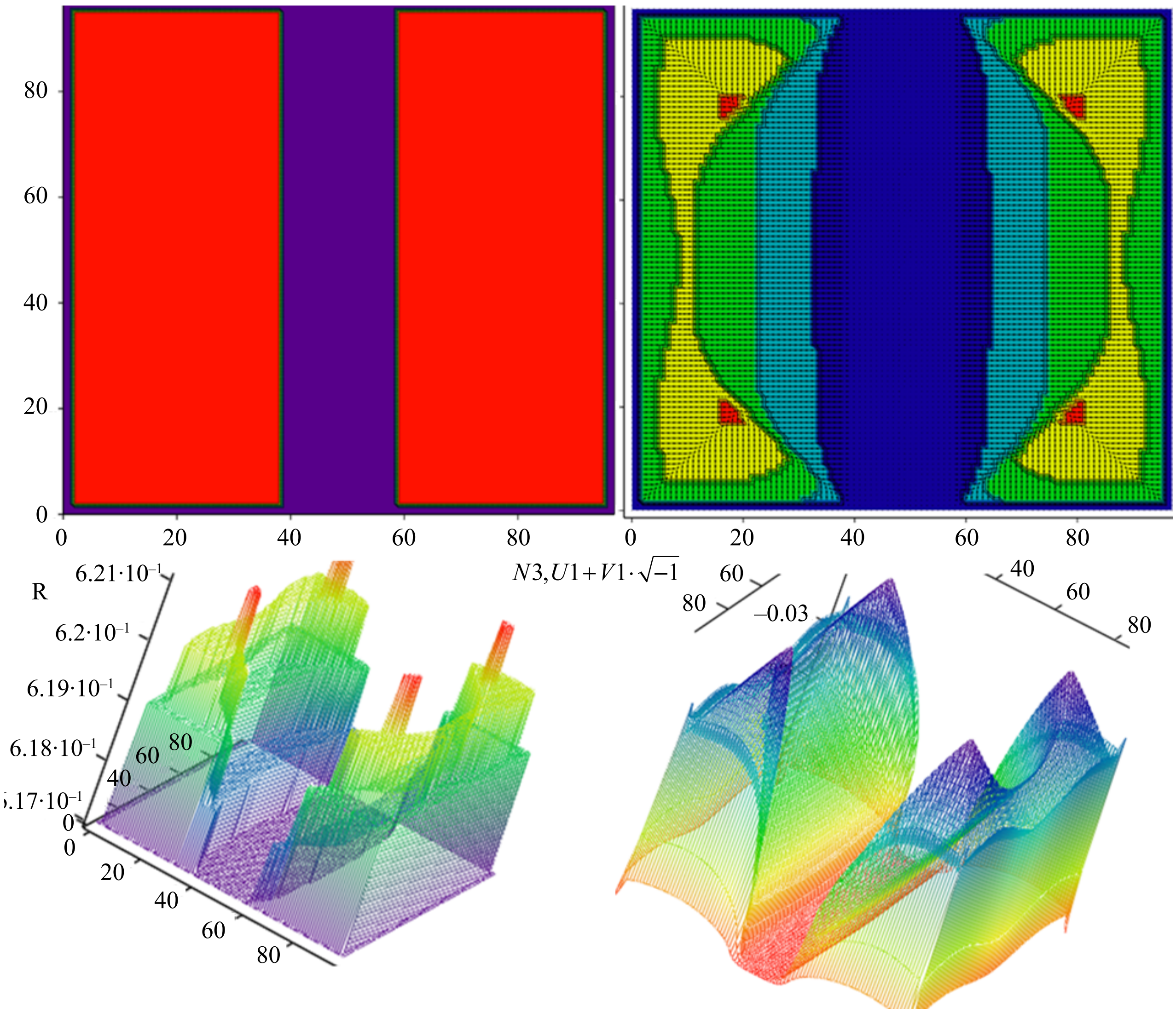

Fig. 8. Forecasting pest dynamics on a field with a single "refuge"

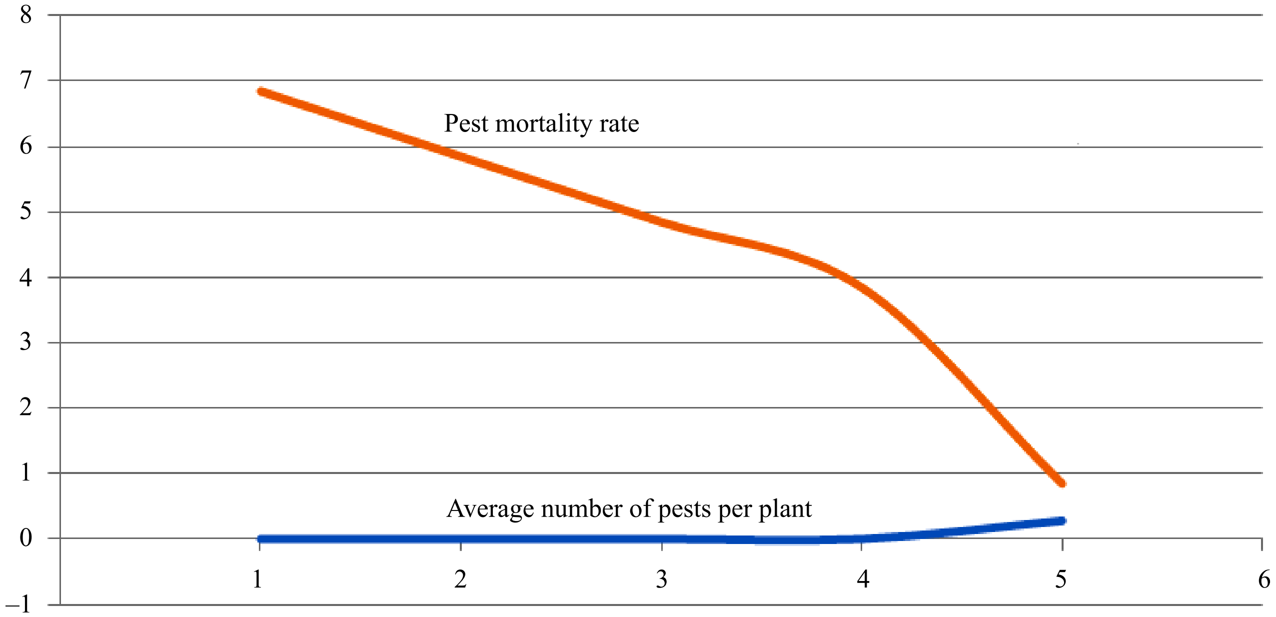

Fig. 9. Pest concentration dynamics at different mortality coefficients

Discussion and Conclusion. Despite the fact that the total area of “refuges” remains unchanged relative to the total field area at 20 %, the depletion of resources occurs faster with a larger number of “refuges” For a given habitat size increasing the number of refuges by reducing their size while maintaining the overall 20 % refuge area can decrease the effectiveness of the “high dose — refuge” strategy. It is reasonable to assume that the easier it is for pests to reach the “refuges”, the quicker they lose their resistance to the toxin. To make it easier for pests to access the “refuges”, it is necessary to reduce the size of the refuges while preserving the 20 % ratio of the total field area. A key feature of the model presented is the differentiation of pests based on the type of taxis they exhibit, which significantly influences the pest population dynamics.

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