Article

About a dynamic model of interaction of insect population with food plant

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Received 13 July 2011; *Accepted 16 August 2011*; *Published online 1 December 2011*
IAEES

Abstract
In present paper there is the consideration of mathematical model of food plant (resource) – consumer (insect population) – pathogen system dynamics which is constructed as a system of ordinary differential equations. The dynamic regimes of model are analyzed and, in particular, with the help of numerical methods it is shown that trigger regimes (regimes with two stable attractors) can be realized in model under very simple assumptions about ecological and intra-population processes functioning. Within the framework of model it was assumed that the rate of food flow into the system is constant and functioning of intra-population self-regulative mechanisms can be described by Verhulst model. As it was found, trigger regimes are different with respect to their properties: in particular, in model the trigger regimes with one of stable stationary points on the coordinate plane can be realized (it corresponds to the situation when sick individuals in population are absent and their appearance in small volume leads to their asymptotic elimination); also the regimes with several non-zero stationary states and stable periodic fluctuations were found.

Keywords population dynamics; mathematical model; trigger regimes; insect population outbreak.

1 Introduction

In modern literature it is possible to find a lot of various publications that are devoted to the analysis of resource-consumer system dynamics (see, for example, Varley et al., 1973; Smith, 1974; Berryman, 1981, 1982; Nedorezov, 1986; Berryman et al., 1987; and others). Formally, we can also consider the predator-prey system as a resource-consumer system. In both situations we have the interaction of two species, which belong to various trophic levels. On the other hand, in interaction between forest insects and its food plants it is possible to point out several specific features which can't be observed in interaction between populations of animals (see, for example, Isaev et al, 1984, 2001, 2009; Nedorezov and Utyupin, 2011). In particular, interaction between fir beetle (*Monochamus urussovi* Fisch.) with food plant (fir Abies sibirica) leads to the realization of the following effect: increasing of population size leads to the increasing of the volume of food (which is suitable for larva eating) in system (Isaev et al, 1984, 2001). The similar effect is typical for *Xylotrechus altaicus* Gebl. (Rozhkov, 1982) and for *Protocryptis sibiricella* Falk. (Ermolaev, 2011a, 2011b) with interaction of these species with Larix sibirica.

Analysis of two-component (insect population – food plants) system dynamics within the framework of non-parametric system of ordinary differential equations (model of Kolmogorov' type; Kolmogoroff, 1937) showed (Isaev et al, 2009; Nedorezov, 1986, 1997) that at positive feedback in this relation the regimes of various modifications of fixed outbreak can only be realized (population size can be stabilized at one of two various stable levels). And this result corresponds to considering in boreal forests fluctuations of *Monochamus urussovi* Fisch. and *Xylotrechus altaicus* Gebl. populations (Isaev et al, 1984, 2001, 2009; Rozhkov, 1982). If negative feedback is observed in insect – food plant system all types of mass propagations of forest insects can be realized within the framework of non-parametric model (Nedorezov, 1986, 1997).

Epizootics, which are arose in insect populations, for example, at any critical population levels, play very important regulative role in population dynamics (Berryman, 1981, 1982; Varley et al., 1973; Isaev et al, 1984, 2001, 2009; Vorontsov, 1963, 1978; Isaev and Girs, 1975). Some authors assume that epizootics can play the most important role in development of any types of mass propagations of forest insects (Berryman, 1981, 1982; Berryman et al., 1987; Konikov, 1978). For some particular cases this opinion is supported by the analysis of mathematical models (Nedorezov, 1986, 1997; Nedorezov and Utyupin, 2011).

Up to current time moment the problem about combined influence of epizootics and food plants onto forest insect population dynamics is open. One of the main questions of analysis of this situation is following: what kind of types of insect outbreaks can be realized at combined influence of these regulators? And what are the conditions for realization of outbreak regimes?

In current publication we analyze some particular cases of this problem. Analysis of non-parametric models in multi-dimensional situation has a lot of serious problems; at the same time analysis of parametric models (models of Volterra's type; Volterra, 1931; Nedorezov, 2011) doesn't allow obtaining the whole spectra of dynamic regimes, which can be realized in considering system. But some basic regimes, which are typical for considering situation, can be obtained within the framework of parametric model.

2 Description of Model

Let $x(t)$ be the number of healthy individuals in a population, $y(t)$ be the number of sick individuals, and $P(t)$ be the volume of suitable food for consumption in a system at time t.

Let's assume that the following processes have the direct influence on the dynamics of variable $x(t)$: natural birth process and natural death process of individuals (with an intensity α_x; within the framework of model we shall assume that the amount of this intensity α_x depends on the relation of numbers of population groups $x(t)$ and $y(t)$, and volume of food $P(t)$), intra-population competition between individuals (with positive coefficient β_x), and interaction between healthy and sick individuals that leads to the decreasing of number of healthy individuals with the rate $\gamma_x xy$, $\gamma_x = const > 0$ (that corresponds to the "principle of pair interaction" by V. Volterra, 1931). It is very important to note that within the framework of considering model we don't take into account the possibility of appearance of sick individuals in population as a result of very high concentration of individuals. It can realize, for example, on the peak phase of insect outbreak development (Isaev et al., 1984, 2001, 2009).

Dynamics of variable $y(t)$ is determined by the influence of the following processes: natural death of individuals (with an intensity α_y; in model we shall assume that the value of this coefficient depends on the relation of numbers of population groups $x(t)$ and $y(t)$, and volume of suitable food $P(t)$), intra-population competition between individuals (with positive coefficient β_y), and inflow of new sick individuals which appear in a result of interaction between sick and healthy individuals (with the rate $\gamma_x xy$).

Let's also assume that dynamics of variable $P(t)$ is determined by the influence of following processes: inflow into the system of suitable food with the rate P_0 (within the framework of considering model it is assumed that this rate is constant; in general case the amount of this rate depends on the level of influence of insects onto the food plant; Isaev and Girs, 1975), flow of food out of the system that doesn't depend on the interaction between insect population and food plants (with an intensity α_p), and, respectively, outflow of food that correlates with influence of insects onto food plants (with coefficient γ_p).

Taking into account all assumptions about the basic processes in considering system made above, we have the following system of ordinary differential equations:

$$\frac{dx}{dt} = \alpha_x x - \beta_x x(x+y) - \gamma_x xy\,,$$
$$\frac{dy}{dt} = \gamma_x xy - \beta_y y(x+y) - \alpha_y y\,,$$
$$\frac{dP}{dt} = P_0 - \alpha_p P - \gamma_p P(x+\delta y)\,, \tag{1}$$

where parameter δ describes the inequality of influence of sick and healthy individuals onto food plants (note, that sick individuals need in bigger volume of food, and, thus, we have $\delta = const > 1$).

Let c_1 and c_2 be the parameters, which are equal to the rates of food consumption by healthy and sick individuals respectively (for example, grams per day, grams per hour etc.). Thus, the difference $\omega = c_1 x + c_2 y - P$ corresponds to food conditions in the system at every time moment. If $\omega \le 0$ it means that in the system there is enough big volume of food and competition between individuals for food is absent. At realization of this inequality it is naturally to assume that death rates don't depend on the value of ω: at $\omega \le 0$ Malthusian parameters in system (1) are constant, $\alpha_x = \alpha_x^0$ и $\alpha_y = \alpha_y^0$, $\alpha_x^0 > 0$, $\alpha_y^0 > 0$. Consequently, in domain $\omega \le 0$ dynamics of considering system will describe by the following differential equations:

$$\frac{dx}{dt} = \alpha_x^0 x - \beta_x x(x+y) - \gamma_x xy\,,$$
$$\frac{dy}{dt} = \gamma_x xy - \beta_y y(x+y) - \alpha_y^0 y\,,$$
$$\frac{dP}{dt} = P_0 - \alpha_p P - \gamma_p P(x+\delta y)\,, \tag{2}$$

If $\omega > 0$ in the system there is not sufficient volume of food and, respectively, in this situation there exists intra-population competition between individuals for food. For this situation we'll assume that amounts of Malthusian parameters can be described as following linear functions:
$\alpha_x = \alpha_x^0 - \alpha_x^1 \omega$, $\alpha_y = \alpha_y^0 + \alpha_y^1 \omega$,
where $\alpha_x^1 > 0$, $\alpha_y^1 > 0$ are non-negative parameters. Respectively, if $\omega > 0$ dynamics of considering system is described by the following system of differential equations:

$$\frac{dx}{dt} = \alpha_x^0 x - \alpha_x^1 x(c_1 x + c_2 y - P) - \beta_x x(x+y) - \gamma_x xy\,,$$
$$\frac{dy}{dt} = \gamma_x xy - \beta_y y(x+y) - \alpha_y^0 y - \alpha_y^1 y(c_1 x + c_2 y - P)\,,$$
$$\frac{dP}{dt} = P_0 - \alpha_p P - \gamma_p P(x+\delta y)\,. \tag{3}$$

Remark. It is also possible to assume that increase of values of ω leads to the decrease of the intensity of birth rate. And it seems rather natural that decrease of this intensity of population growth can be described by exponential function.

3 Properties of Model (2)-(3)

(1) There exists a stable invariant compact set Δ in non-negative part of phase space; trajectories of system of ordinary differential equations (2)-(3) can't intersect the boundaries of this compact set:

$$\Delta = [0, x_{\max}] \times [0, y_{\max}] \times [0, P_{\max}],$$

where

$$P_{\max} = \frac{P_0}{\alpha_p},\ x_{\max} = \frac{\alpha_x^0}{\beta_x},\ y_{\max} = \frac{\gamma_x x_{\max} - \alpha_y^0}{\beta_y}.$$

It means that for every non-negative initial values of model variables, population size and volume of food in the system are non-negative and bounded for every time moment $t > 0$.

(2) If initial value $y_0 = 0$ (this is the situation when we have no sick individuals in the system at initial time moment) all trajectories of model (2)-(3) belong to coordinate plane $y = 0$. It means that if the number of sick individuals at initial time moment is equal to zero it would be equal to zero for every time moment $t > 0$ (as it was pointed out above this property doesn't realize in common situation – if number of healthy individuals is greater than certain level, sick individuals can appear in the system, for example, in a result of over concentration of individuals).

If initial value $x_0 = 0$ (there are no healthy individuals in the system at initial time moment) trajectories of model (2)-(3) belong to coordinate plane $x = 0$. It means that if $x_0 = 0$ the number of healthy individuals in the system will be equal to zero for every time moments $t > 0$. Taking into account all assumptions made above, in this situation population eliminates at all possible values of other variables of model (2)-(3). In other words, all trajectories converge to stationary state $(0,0,P_0/\alpha_2)$ asymptotically. Also it means that this stationary point $(0,0,P_0/\alpha_2)$ can be a stable knot (in particular, when intensity of birth rate is less than intensity of death rate of individuals) or saddle point (plane $x = 0$ is a surface of incoming separatrixes; in all cases axis P is incoming integral curve).

(3) Stationary states of model in the domain $\omega \le 0$.

We'll assume that coefficients of self-regulation β_x and β_y are positive, β_x, $\beta_y = const > 0$, and population doesn't eliminate for all initials values of variables. In this case in model the following stationary states can appear:

(3.1) Point $(0,\ 0,\ P_0/\alpha_p)$ is unstable stationary state (a saddle point; out-coming separatrix belongs to plane $y = 0$). Note, that for all possible values of model parameters this equilibrium point belongs to the domain $\omega \le 0$. Thus, for all possible sufficient small initial values of healthy individuals $x_0 > 0$ model trajectories go out of this stationary state; if and only if initial number of healthy individuals is equal to zero trajectory asymptotically converges to this stationary point (population eliminates and volume of food stabilizes at constant level P_0/α_p). There are no other stationary states, which belong to coordinate lines.

Let's denote as $R_1 = R_1(x,y,P)$, $R_2 = R_2(x,y,P)$, and $R_3 = R_3(x,y,P)$ the right-hand sides of equations of model (2)-(3) for variables x, y, and P respectively. For equations (2) we have the following relations:

$$\frac{\partial R_1}{\partial x} = \alpha_x^0 - 2\beta_x x - \beta_x y - \gamma_x y, \ \frac{\partial R_1}{\partial y} = -\beta_x x - \gamma_x x, \ \frac{\partial R_1}{\partial P} = 0;$$

$$\frac{\partial R_2}{\partial x} = -\beta_y y + \gamma_x y, \ \frac{\partial R_2}{\partial y} = \gamma_x x - 2\beta_y y - \beta_y x - \alpha_y^0, \ \frac{\partial R_2}{\partial P} = 0;$$

$$\frac{\partial R_3}{\partial x} = -\gamma_P P, \ \frac{\partial R_3}{\partial y} = -\gamma_P \delta P, \ \frac{\partial R_3}{\partial P} = -\alpha_p - \gamma_P (x + \delta y).$$

The Jacobian matrix calculating in point $(0,\, 0,\, P_0/\alpha_p)$ for the system (2) has the following form:

$$J\left(0,\, 0, \frac{P_0}{\alpha_p}\right) = \begin{pmatrix} \alpha_x^0 & 0 & 0 \\ 0 & -\alpha_y^0 & 0 \\ -\dfrac{\gamma_p P_0}{\alpha_p} & -\dfrac{\gamma_p \delta P_0}{\alpha_p} & -\alpha_p \end{pmatrix}.$$

Thus, we have the following result: if $\alpha_x^0 > 0$ stationary state $(0,\, 0,\, P_0/\alpha_p)$ is unstable saddle point.
(3.2) Stationary state

$$\left(\frac{\alpha_x^0}{\beta_x},\, 0,\, \frac{P_0}{\alpha_p + \dfrac{\gamma_p \alpha_x^0}{\beta_x}} \right)$$

corresponds to the situation when there are no sick individuals in the system. Let

$$P^* = \frac{P_0}{\alpha_p + \dfrac{\gamma_p \alpha_x^0}{\beta_x}} = \frac{\beta_x P_0}{\alpha_p \beta_x + \gamma_p \alpha_x^0}.$$

If the following inequality is truthful

$$\frac{c_1 \alpha_x^0}{\beta_x} < P^*,$$

or

$$c_1 \alpha_x^0 (\alpha_p \beta_x + \gamma_p \alpha_x^0) < P_0 \beta_x^2 , \tag{4}$$

this point belongs to the domain $\omega < 0$. If the inverse inequality is realized in (4) for model parameters this point must belong to the domain $\omega > 0$ (but in this situation we have to recalculate point's coordinates using equations (3)). The Jacobian matrix calculating in considering point for the system (2) has the following form:

$$J\left(\frac{\alpha_x^0}{\beta_x}, 0, P^*\right) = \begin{pmatrix} -\alpha_x^0 & -\dfrac{\alpha_x^0(\beta_x + \gamma_x)}{\beta_x} & 0 \\ 0 & -\alpha_y^0 + \dfrac{\alpha_x^0(\gamma_x - \beta_y)}{\beta_x} & 0 \\ -\gamma_p P^* & -\gamma_p \delta P^* & -\alpha_p - \dfrac{\gamma_p \alpha_x^0}{\beta_x} \end{pmatrix}.$$

Thus, we have the following characteristic values:

$$\lambda_1 = -\alpha_x^0 ,\ \lambda_2 = -\alpha_y^0 + \frac{\alpha_x^0(\gamma_x - \beta_y)}{\beta_x} ,\ \lambda_3 = -\alpha_p - \frac{\gamma_p \alpha_x^0}{\beta_x} .$$

Taking into account that $\lambda_1 ,\ \lambda_3 < 0$, considering point is a stable equilibrium of the system if the following inequality is observed for model parameters:

$$-\alpha_y^0 + \frac{\alpha_x^0(\gamma_x - \beta_y)}{\beta_x} < 0 . \tag{5}$$

This point is unstable equilibrium if in (5) we have the inverse inequality. On the coordinate plane $y = 0$ (when there are no sick individuals in the system) this point is global stable knot. There are no other stationary points on coordinate planes.

(3.3) Let

$$A = \frac{\alpha_x^0 \beta_y + \alpha_y^0 \beta_x + \alpha_y^0 \gamma_x}{\beta_y} > 0 ,$$

$$B = \frac{\beta_x \beta_y + (\gamma_x - \beta_y)(\gamma_x + \beta_x)}{\beta_y} .$$

Stationary point $\left(x^{**}, y^{**}, P^{**}\right)$, where

$$x^{**} = \frac{A}{B},\ y^{**} = \frac{(\gamma_x - \beta_y)x^{**} - \alpha_y^0}{\beta_y},\ P^{**} = \frac{P_0}{\alpha_p + \gamma_p(x^{**} + \delta y^{**})},$$

exists if the following inequalities are realized:

$$\beta_x + \gamma_x - \beta_y > 0,\ (\gamma_x - \beta_y)x^{**} - \alpha_y^0 > 0. \tag{6}$$

Taking into account that point's coordinates must be positive the first inequality in (6) can be omitted. It is obvious, that two first equations for variables x and y of the system (2) don't depend on third equation. Thus, analysis of the behaviour of trajectories on the plane (x, y) can give us basic properties of non-trivial stationary state. Trajectories on the plane (x, y) are bounded. Use of Dulac criteria (Andronov et al., 1959) with function $1/(xy)$ allows us to prove that in positive part of the plane (x, y) there are no limit cycles. Thus, unique non-trivial stationary state is global (on the plane) stable equilibrium. Consequently, point $\left(x^{**}, y^{**}, P^{**}\right)$ in the domain $\omega \le 0$ is asymptotically stable. It also means that we cannot have limit cycles which belongs to the domain $\omega \le 0$ only.

(4) Stationary states in the domain $\omega > 0$. It is obvious that number of non-trivial stationary states in this domain is less or equal to two.

(5) Numerical experiments. Provided calculations showed that within the framework of model (2)-(3) the following dynamic regimes could be realized:

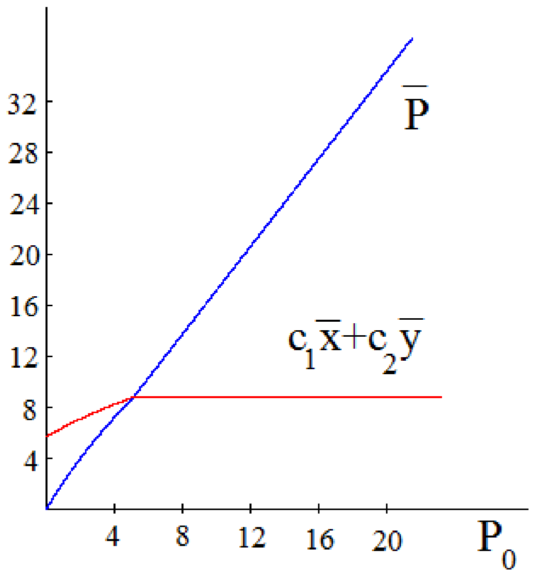

Fig. 1 Changing of stationary level $\overline{P}$ of variable $P(t)$ at increase of food flow into the system P_0 (blue line). Red line is determined by the equation (7).

(5.1) Regime with unique global stable state in phase space (all variables converge to this equilibrium asymptotically at non-zero initial values). This equilibrium can belong as to domain $\omega \le 0$, as to domain

$\omega > 0$. On Fig. 1 the changing of stationary value $\overline{P}$ of $P(t)$ at increase of speed flow of food into the system P_0 is presented (blue line). The red line on this fig. 1 is determined by the following equation:

$$P = c_1\overline{x} + c_2\overline{y}, \qquad (7)$$

where $\overline{x}$ and $\overline{y}$ are the stationary levels of the respective variables of the model. This picture was obtained for the following values of model parameters: $c_1 = 0.004$, $c_2 = 1.1$, $\alpha_p = 0.15$, $\alpha_x^0 = 80$, $\alpha_x^1 = 5$, $\beta_x = 0.01$, $\gamma_x = 10$, $\beta_y = 0.5$, $\alpha_y^0 = 0.1$, $\gamma_p = 0.0009$, $\delta = 60$, $\alpha_y^1 = 7$, $P_0 \in [0,25]$.

As we can see on this picture, at sufficient small values of P_0 global stationary state belongs to the domain $\omega > 0$. After the intersection of these color lines red line becomes equal to constant: in this situation we have a big value of food in the system and stationary levels $\overline{x}$ and $\overline{y}$ of population don't change.

(5.2) Trigger regime (regime with two stable stationary states in phase space) was also observed. For example, this regime was realized for the following values of model parameters (Fig. 2): $c_1 = 0.004$, $c_2 = 6$, $P_0 = 120$, $\alpha_p = 2$, $\alpha_x^0 = 10$, $\alpha_x^1 = 5$, $\beta_x = 0.2$, $\alpha_y^0 = 0.1$, $\gamma_p = 0.0009$, $\delta = 60$, $\alpha_y^1 = 7$, $\gamma_x \in [0,3]$. For every fixed value of γ_x amount of parameter β_y was calculated with following formula:

$$\beta_y = \gamma_x - \frac{\beta_x}{\alpha_x^0}(\alpha_y^0 - 0.0001). \qquad (8)$$

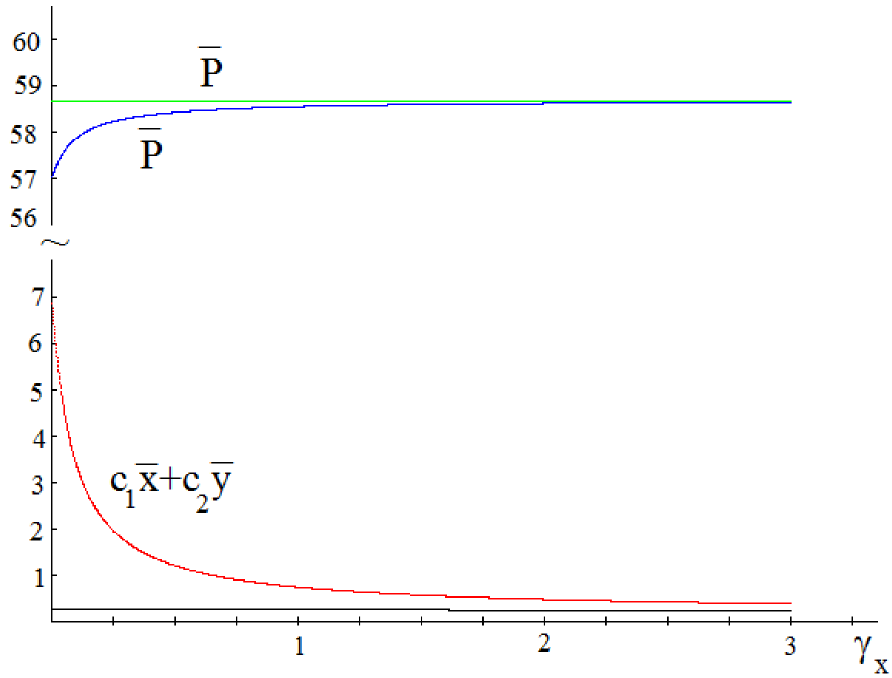

Fig. 2 Changing of stationary levels $\overline{P}$ of variable $P(t)$ at increase of coefficient of interaction between sick and healthy individuals γ_x and β_y determined by the equation (8) (blue and green lines). Red and black lines are determined by the equation (7).

First point which corresponds to green line (black line corresponds to this point and determines by equation (7)) belongs to coordinate plane $y = 0$. The second point which corresponds to blue line (red line corresponds to this point and also determines by equation (7)) belongs to the domain $\omega > 0$. It is obvious, that there exists a saddle point and surface of saddle's incoming separatrixes separate domains of attractiveness of these two stable states. It is important to point out that such kind of dynamic regimes can be observed in nature for some species of forest insects (Isaev et al., 1984, 2001, 2009). In particular, this dynamic regime can be realized in boreal forest zone for *Xylotrechus altaicus* Gebl. (Rozhkov, 1982; Vorontsov, 1978). Analysis which was provided by I.V. Ermolaev and presented in his publications (Ermolaev, 2011a, 2011b), showed that respective dynamic regime is realized for *Protocryptis sibiricella* Falk.

4 Conclusion

Analysis of three-component system which describes in simplest case the process of interaction between insect population and food plant and pathogens, showed that even in the case when the speed of inflow of the food into the system is constant and doesn't depend on level of population size, we may have dynamic regimes with several stationary states in phase space. Before (Isaev et al., 1984, 2001, 2009) this regime was called as fixed outbreak, and such kind of regimes can be observed in nature. Within the limits of two-component insect – food plant system such kind of dynamic regimes can also be observed (Nedorezov, 1986, 1997). But its realization depends on the reaction of food plant on population size increasing: it must have sufficient strong negative or positive feedback.

Within the limits of the inset – pathogen system analogs of fixed outbreak can be realized too (Nedorezov, 1986, 1997). But realization of this regime requires specific relations between components of the system. In considered model we had very simple assumptions about interaction between various components of the system. Nevertheless, simple assumptions can lead to realization of complicated dynamical regimes.

Acknowledgement

This publication was supported by RFFI grant 11-04-01295-a.

References

Andronov AA, Vitt AA, Khaikin SE. 1959. Theory of Fluctuations. Fizmatgiz, Moscow, Russia (in Russian)

Berryman AA. 1981. Population Systems: A General Introduction. Plenum Press, New York, USA

Berryman AA. 1982. Biological control, thresholds and pest outbreaks. Environmental Entomology, 11(3): 544-549

Berryman AA, Stenseth NChr, Isaev AS. 1987. Natural regulation of herbivorous forest insect populations. Oecologia, 71: 174-184

Ermolaev IV. 2011a. Behaviour of *Protocryptis sibiricella* Falk. in Natural Locations. Report 1. Zoological Journal, 90(2): 156-161

Ermolaev IV. 2011b. Behaviour of *Protocryptis sibiricella* Falk. in Natural Locations. Report 2. Zoological Journal, 90(3): 325-330

Isaev AS, Girs GI. 1975. Interaction between Trees and Xylophagous Insects. Nauka, Novosibirsk, Russia (in Russian)

Isaev AS, Khlebopros RG, Nedorezov LV, et al. 1984. Population Dynamics of Forest Insects. Nauka, Novosibirsk, Russia (in Russian)

Isaev AS, Khlebopros RG, Nedorezov LV, et al. 2001. Forest Insect Population Dynamics. Nauka, Moscow, Russia (in Russian)

Isaev AS, Khlebopros RG, Nedorezov LV, et al. 2009. Forest Insect Population Dynamics. KMK, Novosibirsk, Russia

Kolmogoroff AN. 1937. Sulla theoria di Volterra della lutta per l'esistenza. Giornale dell'Inst Italiano degli attuary, 7: 74-80

Konikov AS. 1978. Regulators of Forest Insect Populations. Nauka, Novosibirsk, Russia (in Russian).

Nedorezov LV. 1986. Modeling of Forest Insect Outbreaks. Nauka, Novosibirsk, Russia (in Russian)

Nedorezov LV. 1997. Escape-effect and population outbreaks. Ecological Modelling, 94: 95-110

Nedorezov LV, Utyupin YuV. 2011. Continuous-Discrete Models of Population Dynamics. State Public Scientific-Technical Library of the Siberian Branch of Russian Academy of Sciences, Novosibirsk, Russia (in Russian)

Nedorezov LV. 2011. Analysis of some experimental time series by Gause: application of simple mathematical models. Computational Ecology and Software, 1(1): 25-36

Rozhkov AS. 1982. Tree and Insect. Nauka, Novosibirsk, Russia (in Russian)

Smith JM. 1974. Models in Ecology. Cambridge University Press, Cambridge, UK

Varley GC, Gradwell GR, Hassell MP. 1973. Insect Population Ecology: an Analytical Approach. Blackwell Scientific, Oxford, UK

Volterra V. 1931. Lecons sur la theorie mathematique de la lutte pour la vie. Gauthiers-Villars, Paris, France

Vorontsov AI. 1963. Basic Biology for Forest Protection. Visshaya Shkola, Moscow, Russia (in Russian)

Vorontsov AI. 1978. Forest Pathology. Forest Industry, Moscow, Russia (in Russian)