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A simulation model for vegetable－insect pest－insect nucleopolyhedrovirus epidemic system

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Abstract: A generalized model for the epidemiology of baculoviruses in an insect population was implemented in the multi－platform computer language Java. The model consists of a basic insect life table model，supplemented with all relevant infection pathways for the baculovirus and a simple crop growth and damage model. The simulation model is developed to provide a research tool and a teaching model for the epidemiology of pest insect diseases. The model simulates insect population dynamics，active baculovirus dynamics as well as crop injury. The model can be parameterized for various crops，pest insects，and accommodates variable temperatures. It can be used to study the likely behavior of genetically modified baculovirus in agro－ecosystems.

Key words: simulation model；insect；virus disease；vegetable crop

昆虫杆状病毒流行病模拟模型及 Java 模拟软件

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摘要：研究昆虫杆状病毒流行病模拟模型，对确定基因工程改造杆状病毒的主攻方向，明确病毒病田间流行的机制与关键因素，以及制定生物防治策略，均具有重要的理论与实践意义。本研究研制了用于昆虫杆状病毒流行病模拟的数学模型和 Java 模拟软件，该模型包括描述种群动态的一个微分方程组，描述气温变化、作物生长及病毒动态的若干模型等。模拟软件用工具包 JDK 和 JavaScript 开发，由主计算类、图形类、结果显示类、参数输入界面类、警告信息类、主页、用户指南页、版权页、计数页等组成。在参数文件中编入有关作物、病毒、害虫等方面的参数，输入初始的各龄健康、染病虫量、叶面积、病毒密度等，运行后可输出各龄健康、染病及病死的虫量，作物损失，病毒积累等动态，以及图形等等。该模型适用于各种杆状病毒，各种有叶作物，各种食叶性的全变态昆虫。

应用该模拟模型，对温度、病毒施用虫龄、病毒施用时间、病毒施用剂量等进行了灵敏度分析，得到了一些重要结论。

关键词：昆虫杆状病毒；流行病；模拟模型；灵敏度分析；Java 软件

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1 Introduction

Nucleopolyhedroviruses（NPVs）are highly specific insect pathogens that are infectious to major pest insect species，including the armyworms *Spodoptera exigua* and *Spodoptera litura*. Armyworms often have a vast host range including major high value cash crops

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in large portions of the world, such as cotton, field vegetables and ornamentals, and all are difficult to control due to the development of insecticide resistance. Therefore, the development of nucleopolyhedroviruses as biocontrol agents for these insect pests is urgent.

The practical implementation of nucleopolyhedroviruses is hampered by the long incubation time of NPV – induced disease. Insects continue feeding for 5 – 7 days after infection. A large worldwide genetic engineering effort has been going on in the last decade to develop nucleopolyhedroviruses with improved speed of kill (Bianchi *et al.*, 2001, 2002). Many such viruses have been successfully constructed by the deletion of the *egt* gene, which codes for an enzyme that protracts the survival and feeding of infected insects and hence increases virus yield as well as damage to the crop. Improved viruses have been also constructed by the insertion of a toxin gene.

The field evaluation of these improved insect viruses is in its infancy, due to regulatory constraints, and a modeling framework is desirable to assist in this evaluation.

Computer simulation may be used to screen the effectiveness of nucleopolyhedroviruses, to set up field experiments and reduce the number of field experiments when model simulations are in line with field experiments (Bianchi *et al.*, 2001). Furthermore, simulation models can be used to gain insight in the relative importance of viral characteristics for crop protection.

The purpose of this study is to build a simulation model for the epidemiology of genetically improved nucleopolyhedroviruses in field and glasshouse crops, and to assist in the evaluation of the efficacy, persistence and biosafety of these viruses in agroecosystems. Of course, such evaluation can not be made without experimentation, but Modelling helps to focus the questions that should be asked in experimental research. Some questions can be answered with Modelling, e. g. on virus persistence in agro – ecosystems, when main aspects of virus behavior in insects and crops are known.

A detailed simulation model for evaluating the efficacy of wild type and genetically modified nucleopolyhedroviruses against *S. exigua* in glasshouse chrysanthemums was recently developed by Bianchi *et al.* (2001, 2002). An earlier generalized simulation model developed by Zhang *et al.* (1997) was dedicated to evaluate the epidemiology of polyhedroviruses. Building on the works accomplished by Bianchi *et al.* and Zhang *et al.*, we develop here a model that can be more easily adapted to different crops and cropping systems than the detailed and system – specific model of Bianchi *et al.* Thus, the model should fulfill the following criteria: (1) *simple*; (2) *general*; (3) *transparent*; (4) *predictive*; and (5) *easy to use.*

The model is in principle applicable to various pest insects. Some realism and specificity to the modeled system is inevitably lost in the process of generalization, but the wider applicability of the generalized model will hopefully more than compensate for these drawbacks. The new model will be general enough to be readily adaptable to new cropping systems, yet realistic enough to produce credible outcomes. This will enhance practical application.

The model is based on general principles governing the dynamics of insect populations, crop growth characteristics, temperature dynamics, nucleopolyhedrovirus infection cycle, and transmission routes, etc. The model can be used to simulate the dynamics of uninfected and infected insect populations, crop injury, active baculovirus dynamics, etc. The model is applicable to various crops, pest insects, and variable temperature, and the efficacy of genetically modified nucleopolyhedroviruses may be evaluated by using this model.

The major objective of this report is to present users with a detailed documentation in which model concept, model description, parameterization, software description, and program codes are included. In the chapters 2 and chapter 3 the model concept and description are described, respectively. The parameterization of the model is described in chapter 4. Chapter 5 describes the software features. Program codes are included in appendices.

The model is programmed in Java, to enable interactive running on the World Wide Web, to allow easy access to users worldwide and for use in teaching programs and online researches and courses.

In insect – NPV systems, the nucleopolyhedrovirus can infect and kill the host insect. The elementary infectious units of nucleopolyhedroviruses are nucleocapsids which are embedded in a polyhedron (Vlak, 1993). The larvae of insects ingest leaf material together with the active polyhedra on the leaf. The polyhedra dissolve into infectious nucleocapsids and the latter propagate in the body. After an incubation time which is defined as the time between the moments of ingestion of polyhedra and death, and which is affected by temperature (Stairs, 1978), the larvae die of infection and the bodies disintegrate to release the infectious polyhedra. Polyhedra that are ingested by uninfected larva can cause new infections. The susceptibility to virus infection decreases in later instars. Polyhedra are inactivated by the ultra violet light (Bianchi *et al.*, 2000, 2001), which is the major factor responsible for inactivation of polyhedra by direct sunlight in the field (Ignoffo *et al.*, 1997; Zhang *et al.*, 1997).

Three routes are available for the infection of larvae. The first is the direct ingestion of sprayed polyhedra by uninfected larvae. The second, horizontal transmission, is the ingestion of polyhedra, produced by virus victims within the system, by other larvae. The third route, vertical transmission, is the direct transfer of virus from adults to their eggs. Vertical transmission results when later larval instars ingest polyhedra but do not die off and carry viral infection sublethally into the adult stage (Smits and Vlak, 1988b; Bianchi *et al.*, 2001, 2002).

2　Model Concept

Continuous processes are simulated in the present simulation model. The order of calculation in continuous models is indicated in Fig. 1. In the initial part, starting values are assigned to the state variables. Auxiliary variables, rate variables, output variables, and state variables are calculated in this order in the integration loop (van Kraalingen, 1995; Bianchi *et al.*, 2001, 2002).

Spatial details of virus epidemics are highly dependent on the specific crop and cropping system. Insect foraging behavior is specific to insect species. As inclusion of specific spatial foraging behaviors would reduce the generality of the simulation model, all spatial processes in the insect – NPV – crop dynamics were treated as spatially homogeneous.

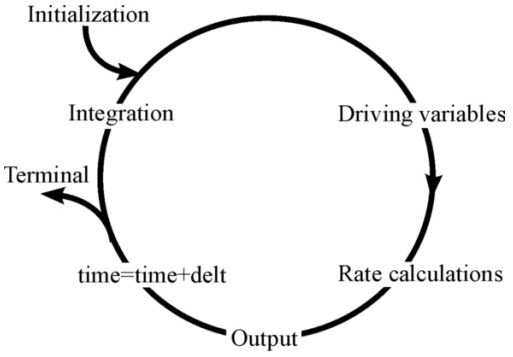

Fig. 1　Integration order of continuous models (after Bianchi *et al.*, 2001)

In an open environment, immigration and emigration of adults must be considered (Zhang *et al.*, 1997).

For the continuous processes described by differential equations, the fourth order Runge – Kutta integration algorithm was used to obtain numerical solutions.

The linear interpolation and linear extrapolation were used in the production of unknown values from known values for two temperatures.

3　Model Description

A relational diagram for the simulation model is provided in Fig. 2. The processes for temperature time course, crop growth, polyhedron inactivation, virus contamination by cadavers, virus contamination due to secretions by infected larvae, infection by horizontal transmission and polyhedron ingestion, infection by vertical transmission, insect population dynamics, and crop injury were included in this model. Immigration and emigration of adults were also incorporated in the model.

The population dynamics of insect are simulated with a group of differential equations which are developed according to the principles of compartment modeling of Zhang *et al.* (1997) and Bianchi *et al.* (2001, 2002).

The main state variables in the model are the densities of the healthy and infected stages of the insect, the densities of viral entities (polyhedron inclusion bodies; PIBs) on the leaves, and the leaf area of the crop.

Densities of m healthy larval stages, L1 – Lm, are denoted as x_1, …, x_m. The number of larval instars is flexible and can be input as a parameter (m). The densities of pupae, adults and eggs are denoted as, respectively, x_{m+1}, x_{m+2}, and x_{m+3}. The model takes only female individuals into account. The sex ratio is thus applied to reduce egg laying from total eggs to female eggs. Male adults are assumed to be sufficient in number to fertilize all female adults.

The densities of the $m+3$ stages of infected individuals are written down as y_1, …, y_{m+3}. Virus – killed individuals are indicated by the symbol z, indexed by stage. A portion of cadavers dying from infection is lost from leaves by falling to the ground, and does not contribute to the horizontal transmission.

3.1 Temperature time course

Temperature over time is simulated with trigonometric functions (Figure 3.2), improved from Zhang (1993):

$$T=(T_0-T_1)/2\times\cos(\pi(1+t-t_{max})/(1-t_{max}+t_{min}))+(T_0+T_1)/2,\quad 0\leqslant t\leqslant t_{min}$$

$$T=(T_2-T_1)/2\times\sin(\pi(t-(t_{max}+t_{min})/2)/(t_{max}-t_{min}))+(T_2+T_1)/2,\quad t_{min}\leqslant t\leqslant t_{max}$$

$$T=(T_2-T_3)/2\times\cos(\pi(t-t_{max})/(1-t_{max}+t_{min}))+(T_2+T_3)/2,\quad t_{max}\leqslant t\leqslant 1 \qquad (1)$$

where t is time (d) in a day, T is temperature (℃) at time t, t_{max} is the time (d) with the highest temperature during a day, t_{min} is the time (d) with the lowest temperature during a day, T_0 is yesterday´s highest temperature, while T_2 and T_1 are today´s highest temperature and lowest temperature, respectively. Finally, T_3 is tomorrow´s lowest temperature.

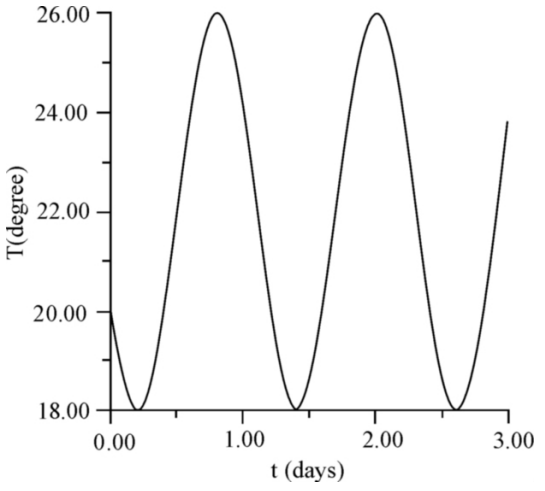

Fig. 2 Trigonometric function to describe temperature time course. In this figure, $T_0=T_2$, $T_1=T_3$.

3.2 Crop growth

In a situation without insect injury, the growth of leaf area is in logistic form (Fig. 3):

$$\frac{dL}{dt}=rL\left(1-\frac{L}{L_{max}}\right) \qquad (2)$$

where t is cumulative effective day degrees, L is leaf area (m^2 leaf per m^2 ground) at physiological time t, L_{max} is the maximum leaf area, r is the relative growth rate of leaf area, $r>0$. The time of inflexion for the equation, a, is measured from

$$a=\frac{1}{r}\ln\left(\frac{L_{max}-L_0}{L_0}\right) \qquad (3)$$

where L_0 is the initial leaf area, $L_0>0$.

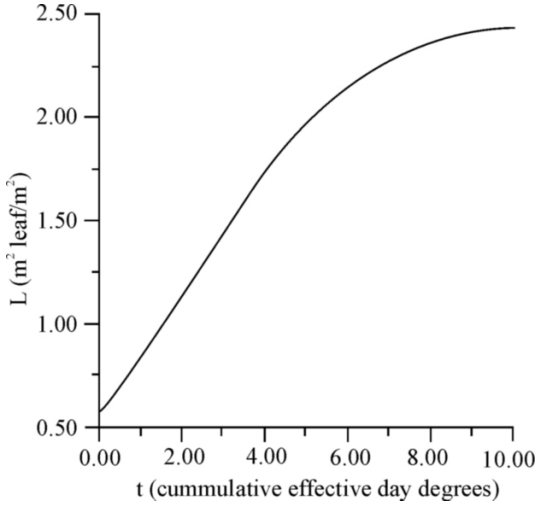

Fig. 3 Logistic function to describe growth of leaf area of crop

3.3 Polyhedron inactivation

It is assumed that the background polyhedra (sprayed polyhedra) are homogeneously distributed on a crop plant. Polyhedra on the crop are inactivated by UV radiation. Polyhedra have exponential inactivation profiles over time (Zhang *et al.*, 1997; Bianchi *et al.*, 2000, 2001), hence inactivation of sprayed polyhedra can be described by assuming a constant relative inactivation rate (Fig. 4):

$$V = V_0 e^{-rt} \qquad (4)$$

where t is time (d), V is the density per m^2 ground of infective polyhedra on leaves (PIBs per m^2 ground) at time t, V_0 is the initial polyhedra on leaves, and r is the relative inactivation rate of polyhedra.

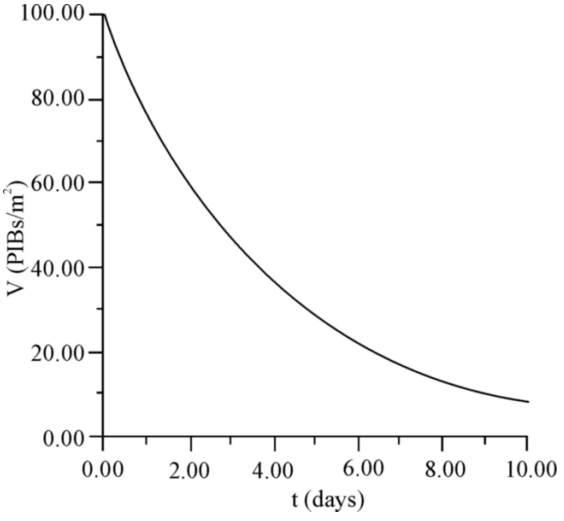

Fig. 4　Exponential function to describe inactivation of polyhedra

3.4 Virus contamination by cadavers

The dynamics of virus – killed larvae can be described as:

$$dz_i/dt = b_i'' \times y_i,\ i = 1,\ 2,\ \cdots,\ m \qquad (5)$$

where z_i is the cumulative number of dead virus – killed larvae, b_i'' is the dying rate of the ith instar infected larvae due to infection (1/d), while y_i is the number of infected larva per m^2 ground, $i = 1, 2, \cdots, m$.

It is assumed that the virus – killed larvae are distributed homogeneously on a plant, and that the larvae that die off due to infection are either (1) instantaneously broken down on the leaf, or (2) never break down, or (3) drop down from leaf. Bodies of infected larvae that die by attrition (background mortality) are not considered infectious. Overlap of leaf area contaminated by different larvae within one time step is negligible and therefore not accounted for. Except for the situation of heavy rain, etc., the virus droping down from leaf is not considered to be effective for the infection because the complex mechanism exist in this aspect.

The dynamics of contaminated leaf area is obtained by summing up over all larval instars the rate of production of new cadavers per m^2, multiplied with factors accounting for loss of cadavers to the ground, and overlap between new and existing contaminated leaf area, and taking into account the leaf area contaminated by a single larva:

$$dP/dt = \sum_{i=1}^{m} dz_i/dt \times (1 - F_i) \times G_i \times (1 - P/L_p) \qquad (6)$$

where dP/dt is the rate at which contaminated leaf area (P) increases, L_p is the present leaf area per m^2 ground, P is the contaminated leaf area at time t, F_i is the fraction loss of bodies of virus – killed larva due to falling from leaves and bodies that didn´t break down on leaves, and G_i is the leaf area (m^2) contaminated per dying larva of instar i, when it is naturally broken down, $i = 1, 2, \cdots, m$.

The rate of increase of the amount of polyhedra released by cadavers on contaminated leaves is

$$dV/dt = \sum_{i=1}^{m} dz_i/dt \times (1 - F_i) \times E_i \qquad (7)$$

where E_i is the polyhedron production of ith instar per virus – killed larva (PIBs per virus – killed larvae), $i = 1, 2, \cdots, m$. V is the cumulative number of polyhedra on contaminated leaves by time t.

Infected larvae that turn into cadavers spill polyhedra on the leaves, and these polyhedra are assumed to be inactivated in the same fashion as sprayed polyhedra (Bianchi *et al.*, 2000, 2001).

The present polyhedra density on contaminated leaves (S; PIBs per m^2 contaminated leaf area) is then

$$S = (dV + V) / (dP + P) \qquad (8)$$

3.5 Infection by horizontal transmission and polyhedron ingestion

It is assumed that larvae forage and ingest polyhe–

dra homogeneously on a plant.

The relative infection rate by background polyhedron (sprayed polyhedra) ingestion is then expressed as

$$d_i' = C_i \times \alpha \times V_s / L_p \times P_i, \quad i = 1, 2, \cdots, m \tag{9}$$

where C_i is the leaf consumption rate (m^2/d) by a single uninfected larvae, α is the fraction polyhedra intercepted by foliage when spraying, V_s is the total sprayed dosage (PIBs per m^2 ground), and P_i – the infection chance per ingested polyhedron for the *i*th instar uninfected larvae, $i = 1, 2, \cdots, m$.

Horizontal transmission is the infection of uninfected larvae by ingestion of polyhedra secreted by infected larva and spilled by cadavers on leaves.

The relative infection rate by horizontal transmission can be calculated as

$$d_i'' = C_i \times S \times P_v \times P_i, \quad i = 1, 2, \cdots, m \tag{10}$$

where P_v is the probability of an uninfected larva meeting a cadaver – contaminated area on a plant. S is indicated in equation (8). It can be reasonably assumed that larvae ingest horizontal transmitted polyhedra on contaminated leaves of a plant with the probability that equals the fraction contaminated leaf area. For this situation,

$$P_v \approx (dP + P) / L_p \tag{11}$$

The total *per capita* infection rate is thus

$$d_i = \min\{d_i' + d_i'', 1\} \quad i = 1, 2, \cdots, m \tag{12}$$

3.6 Infection by vertical transmission

Vertical transmission is the direct transfer of virus from infected female adults to their eggs. The rate of infection by vertical transmission, i. e., new emerged number of contaminated eggs per unit time, is given by

$$h\beta_1' e'_{m+2} y_{m+2} dt \tag{13}$$

where h is the proportion of contaminated eggs deposited per infected female adult, β'_1 is the sex ratio (females/adults) for infected adults, e'_{m+2} is the oviposition rate of infected adults (eggs/d), y_{m+2} is the living number of infected adults per m^2 ground, dt is the time interval.

3.7 Insect population dynamics

Following the structure indicated in the relational diagram (Zhang *et al.*, 1997; Fig. 3.1), the dynamics of the insect pest can be simulated with a group of coupled differential equations (Zhang *et al.*, 1997). There are a total of 2 $(m+3)$ differential equations; $m+3$ equations for healthy insect stages and $m+3$ equations for infected insect stages.

The equations are given below

Healthy L1s:

$$dx_1/dt = e_{m+3} x_{m+3} - (b_1 + e_1) x_1 - d_1 x_1 \tag{14}$$

The first term in the differential equation for healthy L1s denotes egg hatch, the second term attrition plus development into L2, and the third term infection.

Healthy L2s – L*m*s: $dx_i/dt = e_{i-1} x_{i-1} - (b_i + e_i) x_i - d_i x_i$; $i = 2, \cdots, m$ (15)

The meaning of terms in the equations for L2 – L*m* is analogous to those for L1.

Healthy pupae: $dx_{m+1}/dt = e_m x_m - (b_{m+1} + e_{m+1}) x_{m+1}$ (16)

The meaning of terms in the equation for pupae is analogous to those for the larvae. The third term is lacking because pupae do not feed and therefore do not contract infection.

Healthy adults: $dx_{m+2}/dt = e_{m+1} x_{m+1} - (b_{m+2} + W_1) x_{m+2} + R_1$ (17)

The first term in the equation for healthy adults indicate emergence of pupae. The second term includes attrition and emigration. The third term is immigration.

Healthy eggs: $dx_{m+3}/dt = \beta_1 e_{m+2} x_{m+2} - (b_{m+3} + e_{m+3}) x_{m+3} + \beta_1' (1-h) e'_{m+2} y_{m+2}$ (18)

The first term in the equation for eggs is the production of female eggs. The second term includes attrition and development into L1. The third term includes the production of uninfected eggs by infected female adults.

Infected L1s: $dy_1/dt = e'_{m+3} y_{m+3} - (b'_1 + e'_1) y_1 - b_1'' y_1 + d_1 x_1$ (19)

The first term in the differential equation for infected L1s indicates the hatching of infected eggs into infected L1s. The second term includes attrition and development into infected L2. The third term is the death rate of infected L1s due to virus infection. The final term is the recruitment of new infected L1s, due to horizontal or spray – induced infection.

Infected L2*s* – L*ms*: $dy_i/dt = e'_{i-1}y_{i-1} - (b'_i + e'_i)\ y_i - b_i''y_i + d_i x_i;\quad i = 2, \cdots, m$ (20)

The terms in the equation for infected L2 – L*m* are analogous those in the equation for infected L1.

Infected pupae: $dy_{m+1}/dt = e'_m y_m - (b'_{m+1} + e'_{m+1})\ y_{m+1} - b_{m+1}''y_{m+1}$ (21)

The equation for infected pupae is analogous to those for larvae, without the last term, which quantifies horizontal and spray – induced infection in larvae.

Infected adults: $dy_{m+2}/dt = e'_{m+1}y_{m+1} - (b'_{m+2} + W'_1)\ y_{m+2} - b_{m+2}''y_{m+2} + R'_1$ (22)

The equation for infected adults has four terms. The first indicates emergence of the infected pupae. The second term includes attrition and emigration of infected adults. The third term is virus – induced death. The fourth term is immigration.

Infected eggs: $dy_{m+3}/dt = h\beta'_1 e'_{m+2}\ y_{m+2} - (b'_{m+3} + e'_{m+3})\ y_{m+3}$ (23)

The equation for infected eggs has two terms. The first term indicates laying of infected eggs (vertical transmission) by infected females, taking into account the probability of passing the virus on to the egg (h) and the sex ratio (β'_1). The second term covers attrition and development into L1.

The meaning of symbols in the above equations is explained bellow:

• x_i is the number of uninfected 1st – *m*th instar larvae, pupae, adults, and eggs per m^2 ground, $i = 1, 2, \cdots, m+3$;

• y_i is the living number of individuals for all infected (contaminated) larval instars and stages per m^2 ground, $i = 1, 2, \cdots, m+3$;

• e_i is the development (emergence) rate (1/d) of 1st – *m*th instar uninfected larva and pupae, $i = 1, 2, \cdots, m+1$;

• e_{m+2} is the oviposition rate of uninfected females (eggs/female/d);

• e_{m+3} is the development (hatching) rate (1/d) of uncontaminated eggs;

• e'_i is the development rate (1/d) or oviposition rate (eggs/female/d) of infected instars or stages, $i = 1, 2, \cdots, m+3$;

• b_i is the attrition rate (1/d) of uninfected larval instars or stages (fraction attrition mortality × e_i, 1/duration oviposition for uninfected adult), $i = 1, 2, \cdots, m+3$;

• b'_i is the attrition rate (1/d) of infected larval instars or stages (fraction attrition mortality × e'_i, 1/duration oviposition for infected adult), $i = 1, 2, \cdots, m+3$;

• b''_i is the dying rate (1/incubation time) of infected larval instars or stages due to virus infection, $i = 1, 2, \cdots, m+2$;

• h is the fraction of contaminated eggs deposited per infected female adult;

• R_1 is the immigration rate of uninfected adults (adults/d per m^2 ground);

• R'_1 is immigration rate of infected adults (adults/d per m^2 ground);

• W_1, W'_1 is the emigration rate of uninfected and infected adults, respectively (1/d);

• β_1, β'_1 is sex ratio (females/adults) for uninfected and infected adults, respectively.

In all of the above equations, the parameter values for *per capita* attrition rate (b and b') are calculated as the proportion attrition mortality in an instar, as measured in experiments, multiplied by the development rate (e and e'). For the adult stage, one over the duration of oviposition is used as development rate in this calculation.

3.8 Crop injury

The consumption of leaf area per unit time (dw/dt. m^2 leaf) per m^2 ground is calculated as the sum of foliage consumption of uninfected and infected larva

$$\frac{dw}{dt} = \sum_{i=1}^{m} C_i x_i + C'_i y_i \quad (24)$$

The meanings in the equation were indicated in the previous equations.

The cumulative leaf injury (per m^2 ground) over time up till time t is:

$$L_{loss} = \sum_{i=1}^{m} \int_{t0}^{t+dt} (C_i \times x_i(\tau) + C'_i \times y_i(\tau))\ d\tau \quad (25)$$

The meanings in the equation were indicated in the previous equations.

Crop leaf area (per m^2 ground) at time $t + dt$ is calculated as the leaf area without insect injury, L, minus the cumulative leaf area loss, L_{loss}:

$$L_p = L - L_{loss} \quad (26)$$

At the end of each time interval, the loss of effective polyhedra resulting from foliage loss in this time interval is deducted from the total effective polyhedra at that time.

At the start of each integration step, the temperature, infection, population dynamics are calculated, at the end of integration, leaf area and crop injury are calculated.

4 Model Parameterization and Inputs – Outputs

4.1 Inputs

1 Start time of simulation (h, t_0)

2 Simulation time (t_m)

3 Time step of integration (dt, preferably 0.01, or 0.05)

4 Total number of larval instars (m)

5 Initial leaf area (L_0, m^2 leaf area/m^2 ground)

6 Initial density per m^2 ground of polyhedra on leaves (PIBs/m^2 ground)

7 Initial density of all stages, healthy and infected, per m^2 ground: $x_1(0)$, $x_2(0)$ …, $x_{m+3}(0)$, $y_1(0)$, $y_2(0)$, …, $y_{m+3}(0)$

4.2 Outputs

1 The density of all stages per m^2 ground during simulation: $x_1(t)$, $x_2(t)$ …, $x_{m+3}(t)$, $y_1(t)$, $y_2(t)$, …, $y_{m+3}(t)$

2 The density of newly virus – killed larvae during simulation (z_1, z_2, …, z_m)

3 The total density of polyhedra on leaves at every time interval

4 Theoretical leaf area (L, i. e., the leaf area without insect injury), actual leaf area (L_p), and the cumulative foliage consumption due to insect ingestion (L_{loss}, m^2), at every time interval

Information entered in input interface and output into the output interface can be saved in a result file.

4.3 Model Parameters and Parameterization

4.3.1 Parameter File Description

The following sections are included in the parameter file:

Seasonal Section

1 The time (h) of the highest temperature in a day (t_{max}), and the time of the lowest temperature (t_{min})

Crop Section

1 Base temperature of crop development (B_0)

2 Upper temperature limit for crop development (B_u)

3 Maximal leaf area per m^2 ground (L_{max}, m^2 leaf/m^2 ground)

4 Relative growth rate of leaf area (r; 1/d)

Virus Section

1 Relative inactivation rate of polyhedra (r; 1/d)

2 Fraction of polyhedra that is deposited on the crop spraying

3 Proportion of virus – killed larvae that do not contribute to contamination of the crop surface with virus because the cadavers drop from the plant or are not broken down (F_1, F_2, …, F_m)

4 Infection chance per ingested polyhedron for uninfected larva (P_1, P_2, …, P_m) as a function of temperature (Zhang *et al.*, 1997)

5 Polyhedron production per virus – killed larvae (E_1, E_2, …, E_m) as a function of temperature (Fuxa &Tanada, 1987)

Insect Section

1 The development rates (1/d) of 1st – mth instar uninfected larva and pupae (e_1, e_2, …, e_{m+1}) as a function of temperature, the oviposition rate (eggs/d) of uninfected adult (e_{m+2}) as a function of temperature, and the development rate (1/d) of uncontaminated egg (e_{m+3}) as a function of temperature

2 The development rate (1/d) or oviposition rate (eggs/d) of infected (contaminated) larval instars or stages (e'_1, e'_2, …, e'_{m+3}) as a function of temperature

3 The fraction attrition mortality (or 1/duration of oviposition for adults) of uninfected (uncontaminated) stages (for calculating b_1, b_2, …, b_{m+3}) as a function of temperature

4 The fraction attrition mortality (or 1/duration of oviposition for infected adult) of infected stages (for calculating b'_1, b'_2, …, b'_{m+3}) as a function of temperature

5 The dying rate (1/incubation time) of infected classes due to infection (b''_1, b''_2, …, b''_{m+2}) as

a function of temperature

6 The leaf consumption rate (m^2/d) of uninfected larvae (C_1, C_2, …, C_m) as a function of temperature

7 The leaf consumption rate (m^2/d) of infected larvae (C'_1, C'_2, …, C'_m) as a function of temperature

8 Fraction infected eggs deposited per infected female adult (h) as a function of temperature

9 Emigration rate of uninfected and infected adults respectively (W_1, W'_1, 1/d) as function of temperature

10 Sex ratio for uninfected and infected adults respectively (β_1, β'_1) as a function of temperature

Temperature Section

For the first day, yesterday's highest temperature (T_0). For every day (three days in this sample parameter file), today's highest temperature (T_2) and lowest temperature (T_1), tomorrow's lowest temperature (T_3).

Immigration Section

For every day, immigration rate of uninfected and infected adults (R_1, R'_1, adults/d per m^2 ground) respectively.

Spraying Section

Polyhedral spraying day, and dosage sprayed (PIBs/m^2 ground).

4.3.2 Model Parameterization

1 The time of minimum temperature in a day (h, a value in interval [0, 24]), and the time of maximum temperature emerges in a day (h, a value in interval [0, 24]): 5:30 and 15:00, respectively. These times will vary different seasons, latitudes, and altitudes. Users may need to consult astronomical records for their regions.

2 Base temperature of crop development (℃, for leaf growth), upper limit of temperature for crop development (℃, for leaf growth), maximum leaf area per square meter ground (m^2 leaf/m^2), and relative (logistic) growth rate of leaf area (1/(d℃)): 5.0, 40.0, 7.01, and 0.008, respectively. For many of the vegetable crops, base temperature and upper limit of temperature for development can be taken as 5.0℃ and 40.0℃. Maximum LAI (7.01) are taken from Bianchi *et al.* (2001, 2002). Relative growth rate of leaf area (0.008) are derived from Bianchi *et al.* (2001, 2002).

Description	Value	Unit
Maximum LAI	7.01	m^2 leaf/m^2
Relative growth rate of leaf area	0.008	1/(d* ℃)
Base temperature of crop development	5.0	℃
Upper limit of temperature for crop development	40.0	℃

3 Relative inactivation rate of polyhedra (1/d), and proportion of polyhedra not deposited on the plant when spraying: 0.15 and 0.50 respectively. The relative inactivation rate of 0.15 d^{-1} is synthesized from Zhang *et al.* (1997) and Bianchi *et al.* (2001, 2002).

4 Proportion of cadavers that do not contribute to horizontal transmission: 0.1, 0.1, 0.1, 0.1, and 0.1 for $1^{st}-5^{th}$ larval instar respectively for any temperature. This proportion may be affected when the virus is genetically modified by inclusion of genetic material coding for the AiT toxin, as infected larvae are paralyzed and drop from the plant easily.

5 Infection chance per ingested polyhedron. In the following, three sets of parameters for three temperature treatments are listed, which are interpolated and estimated from the data of Bianchi *et al.* (2001, 2002) and Zhang *et al.* (1997).

Temperature	1^{st}	2^{nd}	3^{rd}	4^{th}	5^{th}
20	0.029	0.026	0.025	0.0026	0.000085
25	0.028	0.025	0.024	0.0024	0.000083
30	0.023	0.022	0.021	0.0020	0.000075

6 Polyhedron production per virus-killed larva for every larval instar as a function of temperature (PIBs per larva). The following polyhedron productions for $1^{st}-5^{th}$ infected larva are drawn and estimated from Bianchi *et al.* (2001, 2002) and Pu (1995): 3800000, 115000000, 394000000, 685000000, 0.

7 The development rate of 1st-*m*th instar unin-

fected larva and pupae as a function of temperature (1/d, the reciprocal of the duration of the stage), the oviposition rate of uninfected adult as a function of temperature (eggs/d), and the development rate of uncontaminated egg as a function of temperature (1/d). The oviposition rate of uninfected adults are synthesized from Zhang *et al.* (1997), and the remaining parameter values are drawn from Bianchi *et al.* (2001, 2002).

Temperature	1st	2nd	3rd	4th	5th	Pupae	Adult*	Egg
14	0	0	0	0	0	0	0	0
20	0.278	0.345	0.357	0.303	0.164	0.096	35	0.179
25	0.313	0.526	0.588	0.476	0.244	0.130	65	0.345
30	0.385	0.667	0.833	0.833	0.769	0.400	65	0.500
33	0.500	0.833	0.833	0.769	0.400	0.196	50	0.556

* Synthesized from Zhang *et al.* (1997)

8 The development rate of 1st – *m*th instar infected larva and pupae as a function of temperature (1/d), the oviposition rate of infected adults as a function of temperature (eggs/d), and the development rate of contaminated egg as a function of temperature (1/d). The oviposition rate of infected adults are synthesized from Zhang *et al.* (1997), and the remaining parameter values are drawn from Bianchi *et al.* (2001, 2002).

Temperature	1st	2nd	3rd	4th	5th	Pupae	Adult*	Egg
14	0	0	0	0	0	0	0	
20	–	–	–	–	–	0.096	32	0.179
23	0.186	0.186	0.186	0.159	0.159	–	58	–
25	–	–	–	–	–	0.130	56	0.345
28	0.270	0.270	0.270	0.296	0.296	–	52	–
30	–	–	–	–	–	0.196	52	0.500
33	0.374	0.374	0.374	0.374	0.374	–	43	0.556

* Synthesized from Zhang *et al.* (1997). Unmeasured values are represented by dashes (–).

9 The fraction mortality due to unspecified non – viral causes (attrition) of uninfected (uncontaminated) stages: 0.4, 0.2, 0.12, 0.05, 0, 0, 0, and 0 for 1st – 5th larval instars, pupae, adult, and eggs, respectively for any temperature. The parameter values are drawn and synthesized from Bianchi *et al.* (2001, 2002).

10 The fraction mortality (attrition) of infected (contaminated) larval instars or stages as a function of temperature. The parameter values are assumed and synthesized from Bianchi *et al.* (2001, 2002) and Zhang *et al.* (1997):

Temperature	1st	2nd	3rd	4th	5th	Pupae	Adult	Egg
20	0.5	0.3	0.15	0.06	0.01	0.01	0.01	0.01
25	0.48	0.26	0.14	0.05	0.01	0.01	0.01	0.01

11 The death rate of infected stages (except for egg) due to infection as a function of temperature (1/incubation time (d)). The parameter values are calculated and synthesized from Bianchi *et al.* (2001, 2002) and Zhang *et al.* (1997):

Temperature	1st	2nd	3rd	4th	5th	Pupae	Adult
20	0.3	0.25	0.23	0.2	0.18	0	0
27	0.35	0.26	0.25	0.22	0.2	0	0

12 The leaf consumption rate of uninfected larvae as a function of temperature (ingested square meters leaf area per day). The parameter values are drawn and synthesized from Bianchi *et al.* (2001, 2002):

Temperature	1st	2nd	3rd	4th	5th
20	0.0000012	0.0000032	0.000012	0.000082	0.00020
27	0.0000030	0.0000051	0.000024	0.000100	0.00045

13 The leaf consumption rate per infected larvae as a function of temperature (square meters leaf area per day). The parameter values are assumed based on Bianchi *et al.* (2001, 2002) and Zhang *et al.* (1997):

Temperature	1st	2nd	3rd	4th	5th
20	0.0000006	0.0000020	0.000007	0.000050	0.00010
27	0.0000007	0.0000021	0.000008	0.000051	0.00012

14 Fraction infected eggs deposited per infected female adult as a function of temperature (efficiency of vertical transmission). The value is 0.15 (Bianchi *et al.*, 2001, 2002) in this file for one symbolic temperature treatment.

15 Emigration rate (proportion of adults emigrating out of the field per day) of uninfected and infected adults respectively as a function of temperature(1/d).

The emigration rates uninfected and infected adults are 0 and 0 respectively in this file.

16　Sex ratio for uninfected and infected adults respectively as a function of temperature. The sex ratios for uninfected and infected adults are drawn based on Bianchi *et al*.（2001，2002）：0.5，0.5，respectively.

17　For the first day，yesterday´s highest temperature（T_0℃）. For every day（three days in this sample parameter file），today´s highest temperature（T_2℃）and lowest temperature（T_1℃），tomorrow´s lowest temperature（T_3℃）.

T_0	T_2	T_1	T_3
28			
	23	19	18
	25	21	20
	26	20	17

18　For every day，immigration rate of uninfected and infected adults（number of adults immigrated to plant per square meters ground per day）respectively. The following are the default values for three days：

Uninfected adults	Infected adults
0	0
0	0
0	0

19　Polyhedral spraying day，and dosage sprayed（PIBs per square meters ground，including the polyhedra sprayed on plant and dropped down on ground）. The following are the assumed values for two times of sprayings.

Spraying day	2	3
Dosage sprayed	100000	100000

5　Software Description and User Guidance

5.1　Software Description

The software is embedded in a home page edited in HTML and JavaScript. The software was developed using Java Development Kit 1.1.8© It is an Internet on－line computational tool and comprises 7 classes，plus a HTML file（Fig. 5－7）.

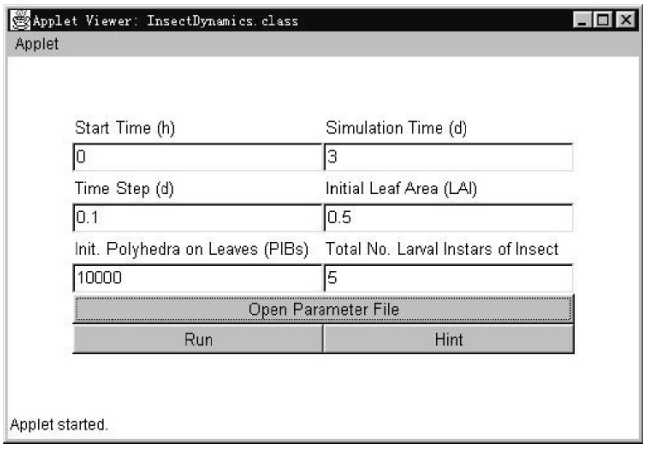

Fig. 5　The window of InsectDynamics class

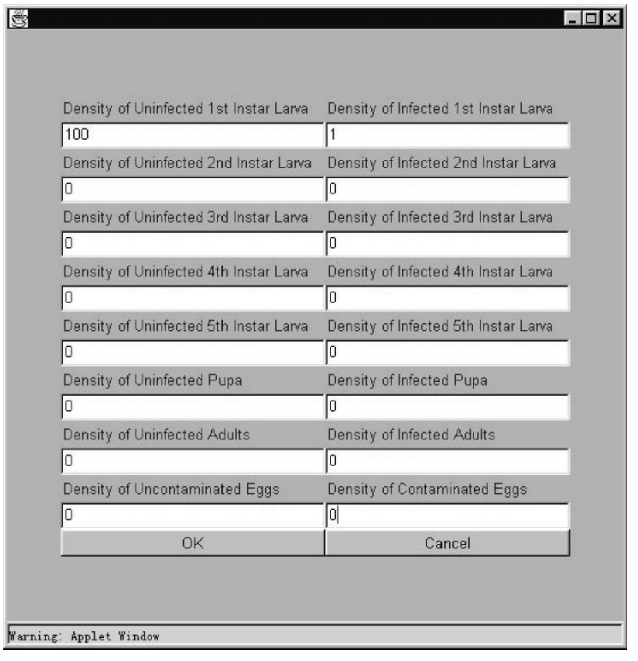

Fig. 6　The window of ParaInput class

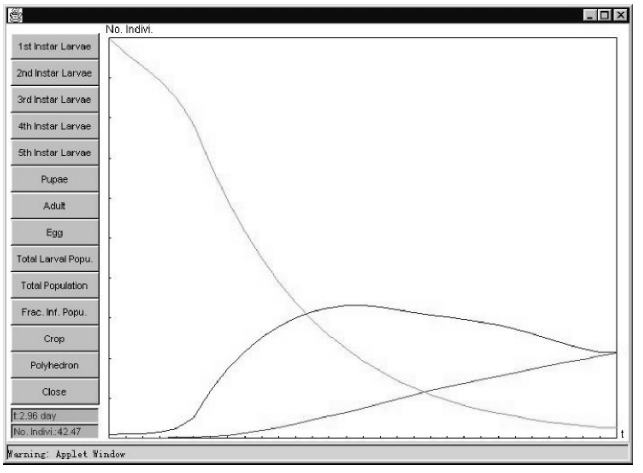

Fig. 7　The window of graphic dynamics

5.2 User Guidance

Before use the simulation software, have your browser be set by pressing "Setting" button on this page and set it as indicated in this new pop - uped window. You may also consult the detailed document of simulation model by pressing "Model Documentation" button on this page.

Temperatures, polyhedra spraying, etc. are all included in the parameter file and, after running the program, it will continuously display results and no interactive windows pop up.

The input window will be poped up after the above choice was made. In the window the data in the input boxes are entered after the window pops up. The data to be entered are:

1 Start time of simulation (h, a value in interval [0, 24], e. g., 3, 7, etc.)

2 Simulation time (d, e. g., 3, 10, etc. In the sample parameter file (for analysis of epidemiologic mechanism) given below, it is 3)

3 Time step of simulation (d, generally it is 0.05 or 0.1. In the sample parameter file (for analysis of epidemiologic mechanism) given below, it is 0.1)

4 Total No. instars of insect larva (how many larval instars are in the insect to be simulated, e. g., for *Spodoptera exigua*, it is 5, and for *Spodoptera litura*, it is 6)

5 Initial leaf area (use the LAI unit, i. e., square meters leaf area per square meters ground, e. g., 0.5, 1, etc.)

6 Initial polyhedra density on leaves (initial PIBs on the leaf per square meters ground, e. g., 1000, 100000, etc.)

When the prompt focus move away from the No. 4 box (total No. instars of insect larva), a new window will be poped up for entering initial density (per square meters ground) of individuals of every larval instars or stages. In this window the data in the input boxes are entered after the window pops up. The initial number of individuals per square meters ground should be entered for every instars or stages.

Before running the program, open parameter file by pressing "Open Parameter File" button on this window. A dialog box will pop up and a parameter file should be selected.

You may restart the simulation by pressing "Run" button on input window. A short hint can be found by pressing "Hint" button on this window.

The result output can be saved by pressing "Save" button on the output window. In the graphics window, by pressing any button the corresponding instar or stage of population dynamics can be displayed. Just move the mouse on graphics interface and read the time (d) and dependent values (number of individuals, leaf area per square meter ground, effective PIBs on the leaf per square meters ground, etc.).

In result outputs, the displayed uninfected and infected population density (per square meters ground) is for 1st - *m*th larval instars, pupae, adult, and egg, respectively.

In graphics window, for insect graphics, the green, blue, and red curve represents infected, uninfected insect, and cumulative cadaver. Pupae, adult and egg graphics have not red curves. For "Crop" graphics, the green, blue, and red curve represents theoretical, actual, and ingested leaf area (per square meters ground). For "Polyhedra" graphics, the blue curve is the dynamics of number of infectious polyhedra on leaf (per square meters ground).

The parameter file is a plain text file with extension ". txt", which can be editted in NotePad (See Start→Programs→Accessoies→NotePad) or, in edit window of MS - DOS.

5.3 Example Parameter File

The values in example parameter file and corrseponding explanations are indicated bellow.

15.00 5.30

Explanation: The time when highest temperature emerges in a day (h, a value in interval [0, 24]), and the time when lowest temperature emerges in a day (h, a value in interval [0, 24])

5.0
40.0
7.01
0.008

Explanation 1: Base temperature for crop development (℃, for leaf growth)

Explanation 2: Upper limit of temperature for crop development (℃, for leaf growth)

Explanation 3: Maximal leaf area per square meters ground (Square meters leaf area)

Explanation 4: Relative growth rate of leaf area (Logistic increase of leaf area per cummulative effective degree day, 1/(d* ℃))

0.15
0.50

Explanation 1: Relative inactivation rate of polyhedra (Negative exponential decay of activation of polyhedra on the leave, 1/d)

Explanation 2: Fraction loss of polyhedra from plant when spraying

1
0.1　0.1　0.1　0.1　0.1

Explanation: Fraction loss of bodies of died larva from plant due to infection and bodies that didn't break down as function of temperature (In this sample parameter file, there are 5 instars of larva for the insect simulated, so five values should be given. The first term "1" means only one set of parameters are available, i. e., these parameters are considered to be obtained in one temperature treatment and the temperature value should not be given in the data set, as done in the following sections)

3
20 0.029 0.026 0.025 0.0026 0.000085
25 0.028 0.025 0.024 0.0024 0.000083
30 0.023 0.022 0.021 0.0020 0.000075

Explanation: Infection chance per ingested polyhedron for uninfected larva as function of temperature (The probability for one polyhedra successfully infected a larvae. In this sample file, 3 sets of parameters under 3 temperature treatments were available, the temperature for each set should be given in the situation with more than one temperature, as done in the following sections)

1
3800000　115000000　394000000
6850000000

Explanation: Polyhedron production per died larvae due to infection as function of temperature (PIBs per died larvae due to infection. In this sample file, the values under one temperature, i. e., normal indoor temperature, was given)

5
14　0　0　0　0　0　0　0　0
20　0.278　0.345　0.357　0.303　0.164　0.096　35　0.179
25　0.313　0.526　0.588　0.476　0.244　0.130　65　0.345
30　0.385　0.667　0.833　0.833　0.769　0.400　65　0.500
33　0.500　0.833　0.833　0.769　0.400　0.196　50　0.556

Explanation: The development rate of 1st – *m*th instar uninfected larva and pupae as function of temperature (1/d, the reciprocal of time duration of an insect in a larval instar or stage), the oviposition rate of uninfected adult as function of temperature (eggs/d), and the development rate of uncontaminated egg as function of temperature (1/d) (In this data set, the values for five temperatures are measured and given)

7
14　0　0　0　0　0　0　0　0
20　–　–　–　–　–　0.096　32　0.179
23　0.186　0.186　0.186　0.159　0.159　–　58　–
25　–　–　–　–　–　0.130　56　0.345
28　0.270　0.270　0.270　0.296　0.296　–　52　–
30　–　–　–　–　–　0.196　52　0.500
33　0.374　0.374　0.374　0.374　0.374　–　43　0.556

Explanation: The development rate of 1st – *m*th instar infected larva and pupae as function of temperature (1/d, the reciprocal of time duration of an insect in a larval instar or stage), the oviposition rate of infected adult as function of temperature (eggs/d), and the development rate of contaminated egg as function of

temperature (1/d)

1
0.4 0.2 0.12 0.05 0 0 0 0

Explanation: The fraction mortality (attrition) of uninfected (uncontaminated) larval instars or stages as function of temperature (the fraction mortality for uninfected insects due to non-infected reasons. In this example file, 1 set of parameters was available)

2
20 0.5 0.3 0.15 0.06 0.01 0.01 0.01 0.01
25 0.48 0.26 0.14 0.05 0.01 0.01 0.01 0.01

Explanation: The fraction mortality (attrition) of infected (contaminated) larval instars or stages as function of temperature (the fraction mortality for infected insects due to non infected reasons)

2
20 0.3 0.25 0.23 0.2 0.18 0 0
27 0.35 0.26 0.25 0.22 0.2 0 0

Explanation: The dying rate of infected larval instars or stages (except for egg) due to infection as function of temperature (1/incubation time (d))

2
20 0.0000012 0.0000032 0.000012 0.000082 0.00020
27 0.0000030 0.0000051 0.000024 0.000100 0.00045

Explanation: The leaf consumption rate per uninfected larvae as function of temperature (ingested square meters leaf area per day)

2
20 0.0000006 0.0000020 0.000007 0.000050 0.00010
27 0.0000007 0.0000021 0.000008 0.000051 0.00012

Explanation: The leaf consumption rate per infected larvae as function of temperature (square meters leaf area per day)

1
0.15

Explanation: Fraction infected eggs deposited per infected female adult as function of temperature (efficiency of vertical transmission. One fraction parameter for one temperature was available in this file)

1
0 0

Explanation: Emigration rate of uninfected and infected adults respectively as function of temperature (1/d, what proportion of adults emigrated to outside field per day, for each temperature, the rate for uninfected and infected adults is given respectively. In this file 1 set of parameters (for one temperature treatment) was available)

1
0.5 0.5

Explanation: Sex ratio for uninfected and infected adults respectively as function of temperature (proportion female adults in total adults, for each temperature, the ratio for uninfected and infected adults is given respectively. 1 set of parameters was available in this file)

3
28
23 19 18
25 21 20
26 20 17

Explanation: For the first day, yesterday´s highest temperature (℃. It is 28℃ in this file). For every day (three days in this sample parameter file),

today´s highest temperature (℃) and lowest temperature (℃) , tomorrow´s lowest temperature (℃)

3
0　0
0　0
0　0

Explanation: For every day, immigration rate of uninfected and infected adults (number of adults immigrated to plant per square meters ground per day) respectively

2
2　　3
100000　　100000

Explanation: Polyhedral spraying day, and dosage sprayed (PIBs per square meters ground, including the polyhedra sprayed on plant and droped down on ground) . Two times of sprayings were conducted in this example file.

6 Simulation and Results

The basic behaviors of the simulation model are similar to that described in the fundamental model of Hammer (1906) , and Anderson and May´s model (1981) . Periodic oscillation will occur in some situations. Frequently the fraction infected population will maintain a relative steady state after a longer time.

6.1 Effect of Incubation Time of Virus

For all larval instars, decreasing the incubation time by 20% , 40% , and 60% , respectively. Initial population is 30 uninfected first instar larva and 1 infected first instar larva . Start time is 0, simulation time is 30 days and the time step for integration is 0. 1 day. Initial leaf area is 1 and no initial spraying of polyhedra. Holding basic temperatures and increasing all the highest temperature and lowest temperature by 5´C, respectively. The 30 day´s simulations showed that for the temperatures under the optimal temperature of development, as the decrease of the incubation time of virus, the insect population size and the crop injury decreases significantly. However, because of the faster dying of infected insects, the proportion infected insect, i. e. , prevalence, drops drown as the decrease of incubation time of virus.

Basic Temperatures

Tot. Uninf. Larva　Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

Basic Incubation Time 9. 2318 36. 4514 49. 33% 0. 40% 2. 612258616810866E9

Incubation Time - 20% 6. 355 22. 3794 46. 61% 0. 28% 2. 0674804674509308E9

Incubation Time - 40% 3. 7296 10. 9613 42. 33% 0. 17% 1. 385662596405567E9

Incubation Time - 60% 1. 6306 3. 4779 34. 81% 0. 08% 6. 715179958554987E8

Temperatures + 5´C

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

Basic Incubation Time 38. 0486 97. 8051 46. 47% 0. 91% 7. 472413446654591E9

Incubation Time - 20% 24. 5079 56. 1605 43. 82% 0. 59% 5. 72493994197629E9

Incubation Time - 40% 13. 3171 25. 5553 39. 75% 0. 33% 3. 678979361301264E9

Incubation Time - 60% 5. 4621 7. 6918 32. 83% 0. 15% 1. 7416609031823866E9

6.2 Effect of Infection Chance of Polyhedron

For all larval instars, increasing the infection chance of polyhedron by 20% , 40% , and 60% , and decreasing it by by 20% , 40% , and 60% respectively. The simulations indicated that as the increase of infection chance of polyhedron, the population size and crop injury decreases but decreasing slowly after a certain value of infection chance was reached.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

Infection Chance - 60% 10. 1675 40. 1622 49. 34% 0. 44% 2. 859368526344558 2E9

Infection Chance - 40% 9. 7912 38. 6682 49. 33% 0. 43% 2. 760820077392384 5E9

Infection Chance - 20% 9. 4221 37. 2063 49. 33% 0. 41% 2. 662943592741286E9

Basic Infection Chance 9. 2318 36. 4514 49. 33%

0.40% 2.612258616810866E9

Infection Chance +20% 9.1005 35.9309 49.33% 0.39% 2.5772636667880435E9

Infection Chance +40% 8.9773 35.442 49.33% 0.39% 2.5442119041864915E9

Infection Chance +60% 8.902 35.1434 49.33% 0.39% 2.523880213575725E9

6.3 Effect of Inactivation Rate of Polyhedra

Initial population is 30 uninfected first instar larva and 1 infected first instar larva. Increasing the inactivation rate by 0.2, 0.4, and 0.6 respectively. The simulations indicated that the population size and crop injury slowly increase as the increase of inactivation rate of polyhedra.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

Basic Inacti. Rate 9.2318 36.4514 49.33% 0.40% 2.612258616810866E9

Inacti. Rate +0.2 9.2467 36.5107 49.33% 0.4% 1.6433660921769638E9

Inacti. Rate +0.4 9.2608 36.5666 49.33% 0.4% 1.214922338471944E9

Inacti. Rate +0.6 9.2767 36.6294 49.33% 0.4% 9.733373399087689E8

6.4 Effect of Vertival Transmission

Initial population is 30 uninfected first instar larva and 1 infected first instar larva. Increasing the fraction infected eggs laid by female adult by 20%, 60%, and decreasing it by 20%, 40%, and 100% (no vertical transmission) respectively. The simulations indicated that the population size and crop injury decreases as the increase of efficiency of vertical transmission.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

No Verti. 12.1389 37.6951 38.10% 0.43% 2.84468146577488E9

Verti. -40% 10.3544 36.9663 44.83% 0.41% 2.704805346156465E9

Verti. -20% 9.7864 36.7118 47.08% 0.41% 2.658461020416935E9

Basic Verti. 9.2318 36.4514 49.33% 0.40% 2.612258616810866E9

Verti. +20% 8.6905 36.1853 51.59% 0.39% 2.5661989734965706E9

Verti. +60% 7.648 35.6359 56.12% 0.38% 2.4745113172597303E9

6.5 Effect of Polyhedron Spraying Dosage

Initial population is taken as 30 uninfected first instar larva. Polyhedra are sprayed on crop in at the start of simulation. Holding basic temperatures and increasing all the highest temperature and lowest temperature by 5°C, respectively. The simulation results showed that polyhedra spraying is important to control the population of insect and to protect crop from insect injury. The necessity and efficiency for control with polyhedra spraying will be different with the change of temperature. Below the optimal temperature for development, as the increase of temperature, the importance of polyhedra spraying becomes more distinctive. The control efficiency will reach 98% for lower temperatures and reach 100% for higher temperatures with 10000000 PIBs spraying. The control efficiency has a relative distinctive increase with the increase of spraying dosage but basically stops increasing after reaching a certain dosage (10000000 PIBs).

Basic Temperatures

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

No Spraying 1956.2411 0.0 0.0% 19.89% 0.0

100000 PIBs 9.4119 37.1708 49.33% 0.41% 2.665085213618224E9

1000000 PIBs 8.4786 33.4697 49.33% 0.37% 2.413115564440661E9

10000000 PIBs 7.1558 27.0604 49.13% 0.30% 1.9492159309426908E9

100000000 PIBs 6.8968 27.1944 49.31% 0.30% 1.9766727688509068E9

Temperatures +5°C

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

No Spraying > 4517.0295 0.0 0.0% 100.0% 0.0

100000 PIBs 39.0907 100.4746 46.47% 0.94% 7.631813781159305E9

1000000 PIBs 34.9335 89.8055 46.47% 0.84% 6.978386706155912E9

10000000 PIBs 29.1981 75.0829 46.48% 0.7% 6.024913473658888E9

100000000 PIBs 29.1974 75.0811 46.48% 0.7% 6.024886307791693E9

6.6 Effect of Polyhedra Spraying Time

Initial population is taken as 30 uninfected first instar larva and polyhedra are sprayed on crop just at the start of simulation and at the end of 1 day, 6 day, 12 day, and 18 day with the dosage of 10000000 PIBs per square meters ground, after start of simulation. The simulations indicated that without initial background polyhedra on crop the earlier polyhedra spraying, the little crop injury and population size. The reasonable timing of polyhedra spraying is important in controlling insect population.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

0st day Spraying 6.9481 27.3979 49.31% 0.30% 1.990917922683845E9

1st day Spraying 10.9858 43.4028 49.34% 0.48% 3.0821611376041036E9

6th day Spraying 43.0809 168.9651 48.89% 1.80% 9.287239462283693E9

12th day Spraying 90.1470 338.2492 47.11% 3.27% 1.3740855574515907E10

18th day Spraying 197.8341 644.6446 43.04% 5.83% 1.5774306467603977E10

6.7 Effect of Spraying Larval Instar

Initial population is taken as 30 uninfected first, second, third, fourth, and fifth instar larva, respectively, and initial polyhedra on leaves are 10000000 PIBs/m^2 ground. The results showed that polyhedra spraying in early larval instars will be largely beneficial to the control of insect population. As the increase of larval instar the efficiency of control with polyhedra spraying will significantly decrease.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

1st Instar Spraying 7.1558 27.0604 49.13% 0.3% 1.9492159309426908E9

2nd Instar Spraying 19.9941 79.306 49.43% 0.9% 5.205278878408237E9

3rd Instar Spraying 46.0400 182.16 49.42% 2.11% 9.427252820150648E9

4th Instar Spraying 94.6442 370.7922 49.28% 4.32% 1.3216927361707972E10

5th Instar Spraying 189.3258 729.2557 49.00% 8.02% 1.6405234411245085E10

6.8 Effect of Temperature

Initial population is 30 uninfected first instar larva and 1 infected first instar larva. Decreasing the highest temperature and lowest temperature by 2℃, 5℃, and increasing them by 2℃, 5℃ respectively. The simulation results indicated that below the optimal temperature for insect development, as the decrease of temperature the population size and crop injury decrease significantly, which shows that the temperature is an deterministic environmental factor to influence the population dynamics and crop injury.

Tot. Uninf. Larva Tot. Inf. Larva Propor. Inf. Popu. Leaf Loss Polyhedra

Temperatures - 5℃ 0.5123 3.7471 49.30% 0.20% 3.949377609811456E8

Temperatures - 2℃ 4.4867 20.9193 48.55% 0.28% 1.1573239996378636E9

Basic Temperatures 9.2318 36.4514 49.33% 0.40% 2.612258616810866E9

Temperatures + 2℃ 16.0970 52.6391 48.47% 0.55% 4.195586694567865E9

Temperatures + 5℃ 38.0486 97.8051 46.47% 0.91% 7.472413446654591E9

7 Conclusion

(1) Polyhedra spraying is an efficient and important way to control insect population on crop. Polyhedra spraying and no spraying will result in distinct difference in the dynamics of insect population and crop injury.

(2) Timing of polyhedra spraying is the most important consideration in the control of insect pest on crop. Generally the earlier the spraying time and the younger the spraying larval instar, the better the con-

trol efficiency.

(3) Incubation time of virus is an important factor to affect the dynamics of insect population and crop injury. It will substantially affect the behavior of the model. The incubation time at certain values will result in the periodic oscillation of insect population, and below certain value will result in the extinction of insect population. Therefore the improvement of action speed of virus is an important way to enhance the sustainable efficiency of virus.

(4) Increasing the spraying dosage, infection chance of polyhedron, and vertical transmission efficiency will enhance the control efficiency with polyhedra spraying. However, for each of the above this efficiency will not be significantly improved after a certain value is reached. The infectivity of virus is negatively related to the population size and crop injury.

(5) Although vertical transmission of virus will surely enhance the epidemiologic level as indicated above, it does not play a substantial role in epidemiology of insect NPV while the horizontal transmission is acting as the predominant epidemiologic factor. The vertical transmission, as shown by Anderson and May (1981), is even not able to maintain an epidemiologic disease without horizontal transmission. This conclusion together with present results, indicated that the horizontal transmission is probably the most important transmission route of NPV in the epidemiology. The major role played by vertical transmission is to maintain the virus population in the insect and triggers an epidemiologic disease while no significant epidemiologic disease develops in the insect population (Fuxa *et al.*, 1987).

(6) The change of inactivation rate of polyhedra will not significantly affect the population size and crop injury. The effort to strength the polyhedra's anti-inactivation in insecticide formulation is thus not distinctively effective.

(7) Temperature is a deterministic factor to govern the dynamics of insect population and crop injury. For this reason, in any spraying practices the temperature situation should be considered as a major factor to affect control efficiency of polyhedra spraying.

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References

Anderson RM, May RM, 1981. The population dynamics of microparasites and their invertebrate hosts. *J. Anim. Ecol.*, 291: 451-524.

Bianchi FJJA, 2001. Process-based modeling of the control of beet armyworm, *Spodoptera exigua*, with baculoviruses in greenhouse chrysanthemum. PhD Thesis, Wageningen University, 143.

Bianchi FJJA, Vlak JM, Rabbinge R, van der Werf W, 2002. Biological control of beet armyworm, *Spodoptera exigua*, with baculoviruses in greenhouses: development of a comprehensive process-based model. *Biological Control*, 23: 35-46.

Bianchi FJJA, Snoeijing I, van der Werf W, Smits PH, Vlak JM, 2000. Biological activity of SeMNPV, AcMNPV and three deletion mutants of AcMNPV against *Spodoptera exigua* larvae (Lepidoptera: Noctuidae). *J. Invertebr. Pathol.*, 75: 28-35.

Bianchi FJJA, Joosten NN, Vlak JM, van der Werf W, 2000. Greenhouse evaluation of dose- and time-mortality relationships of two nucleopolyhedroviruses for the control of beet armyworm, *Spodoptera exigua*, on chrysanthemum. *Biological Control*, 19: 252-258.

Brown GC, 1987. A modeling approach to epizootiological dynamics of insect host-pathogen interactions and an implementation example. In: Shoemaker CA, Brown GC, eds. Insect Pest Management Modelling. John Wiley & Sons, New York.

Fuxa JR, Tanada Y, 1987. Epizootiology of Insect Diseases. John Wiley & Sons, New York, 534.

Hammer WH, 1906. Epidemic disease in England-the evidence of variability and the persistence of type. *The Lancet*, 11: 733.

Ignoffo CM, Garcia C, Saathoff SG, 1997. Sunlight stability and rain-fastness of formulations of *Baculovirus heliothis*. *Environ. Entomol.*, 26: 1470-1474.

Smits PH, Vlak JM, 1988b. Biological activity of *Spodoptera exigua* nuclear polyhedrosis virus against *S. exigua* larvae. *J. Invertebr. Pathol.*, 107-114

Stairs GR, 1978. Effects of a wide range of temperature on the development of *Galleria mellonella* and its specific baculovirus. *Environ. Entomol.*, 7: 297-299

van der Werf W, de Moed GH, Smits PH, 1991. A comprehensive simulation model of the epidemiology of *Spodoptera exigua* nuclear polyhedrosis virus on beet armyworm in glasshouse chrysanthemums. IOBC/WPRS Bulletin, XIV, 108-117.

Vlak JM, 1993. Genetic engineering of baculoviruses for insect control.

In: Whitten MJ, Oakeshot JG, eds. Molecular approaches to pure and applied entomology. Springer Series in Experimental Entomology, 90 – 127.

Zhang WJ, Pang Y, Qi YH, Chen QJ, 1997. Simulation model for epizootic disease of *Spodoptera litura* F. baculovirus. *Acta Scientiarum Naturalium Universitatis Sunyatseni*, 36 (1): 54 – 59. [张文军，庞义，齐艳红，陈其津，1997. 斜纹夜蛾杆状病毒流行病模拟模型研究. 中山大学学报（自然科学报），36 (1): 54 – 59]

Zhang WJ, Pang Y, Qi YH, Gu DX, 1997. Relationship between temperature and development of *Spodoptera litura* F. *Acta Scientiarum Naturalium Universitatis Sunyatseni*, 36 (2): 6 – 9. [张文军，齐艳红，庞义，古德祥，1997. 斜纹夜蛾生长与温度的关系. 中山大学学报（自然科学报），36 (2): 6 – 9]

Zhang WJ, Pang Y, Qi YH, Chen QJ, 1997. Relationship between temperature and development of SlNPV – infected larvae of *Spodoptera litura* F. *Acta Scientiarum Naturalium Universitatis Sunyatseni*, 36 (6): 16 – 19. [张文军，庞义，齐艳红，陈其津，1997. 斜纹夜蛾 NPV 染病幼虫发育与温度的关系. 中山大学学报（自然科学报），36 (6): 16 – 19]

Zhang WJ, Pang Y, Qi YH, Chen QJ, 1997. Quantitative equations to determine field decay and application dosage of insect virus. *Chinese Journal of Biological Control*, 13 (3): 135 – 139. [张文军，庞义，齐艳红，陈其津，1997. 确定昆虫病毒田间衰减和施用剂量的定量方程. 中国生物防治，13 (3): 135 – 139]

Zhang WJ, Gu DX, 2001. A non – linear partial differential equation to describe spatial and temporal changes of insect population. *Ecologic Science*, 20 (4): 1 – 7. [张文军，古德祥，2001. 昆虫种群的一类时间动态模型研究. 生态科学，20 (4): 1 – 7]

Zhang WJ, Qi YH, 2002. Statistic test and network software on statistic significance of biological diversity and evenness. *Modern Computer*, 2002 (8): 6 – 9. [张文军，齐艳红，2002. 生物多样性和均匀度显著性的统计检验及网络计算软件. 现代计算机，2002 (8): 6 – 9]

Zhang WJ, Qi YH, Schoenly KG, 2002. Functional link artificial neural network and agri – biodiversity analysis. *Biodiversity Science*, 10 (3): 345 – 350. [张文军，齐艳红，Schoenly KG，2002. 泛函连接网络计算机软件及其在生物多样性研究中的应用. 生物多样性，10 (3): 345 – 350]

Zhang WJ, 2007. Methodology for Ecology Research. Guangzhou: Sun Yat – sen University Press. [张文军，2007，生态学研究方法. 广州：中山大学出版社]

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in Chinese fir forests. *Chinese Journal of Biological Control*, 15 (1): 8 – 11. [丘玲，1999. 应用管氏肿腿蜂防治粗鞘双条杉天牛. 中国生物防治，15 (1): 8 – 11]

Storeck A, Poppy GM, van Emden HF, Powell W, 2000. The role of plant chemical cues in determining host preference in the generalist aphid parasitoid *Aphidius colemani*. *Ent. Exp. Appl*, 97: 41 – 46.

Vet LEM, Dicke M, 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Ann. Rev. Entomol.*, 37: 141 – 172.

Vet LEM, Groenewold AW, 1990. Semiochemicals and learning in parasitoids. *J. Chem. Ecol.*, 16: 3119 – 3135.

Vet LEM, Lewis WJ, Papaj DR, vanLenteren JC, 1990. A variable – response model for parasitoid foraging behavior. *J. Insect Behav.*, 3: 471 – 490.

Wu H, Wang XY, Li ML, Yang ZQ, Zeng FX, Wang YH, Bai L, Liu SJ, Sun J, 2008. Biology and mass rearing of *Sclerodermus pupariae* Yang *et* Yao (Hymenoptera: Bethylidae), an important ectoparasitoid of the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae) in China. *Acta Entomologica Sinica*, 51 (1): 46 – 54. [武辉，王小艺，李孟楼，杨忠岐，曾繁喜，王红艳，白玲，刘松君，孙进，2008. 白蜡吉丁肿腿蜂的生物学和生态学特性及繁殖技术研究. 昆虫学报，51 (1): 46 – 54]