

Article

Some dynamic models for development of insecticide resistance in insect population

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Abstract

In present study, we proposed a fundamental model for development of insecticide resistance in insect population, which comprises two differential equations and an algebraic equation

$$\frac{dx}{dt} = r_1(c, t)x - f_1(c, t)x + g_1(c, t)y - \alpha(c, t)xy$$

$$\frac{dy}{dt} = r_2(c, t)y - g_2(c, t)y + f_2(c, t)x - \beta(c, t)xy$$

$$c = u(t)$$

where t : time (insect generation, year, etc.); $x(c, t)$: resistant subpopulation at t ; $y(c, t)$: susceptible subpopulation at t ; c : dosage / concentration of the insecticide. Two special models for election theory and induce variation theory were derived from the fundamental model. We provided the solution of the model and analyzed some of the model behavior. Resistant strength was proposed based on the model, which is positively related to the common used resistance indices, e.g., LC_{50} . Finally, an alternative model, revised from Lotka-Volterra competition model was given. The mechanism of formation and development of insecticide resistance may change with various factors including insect species and environmental conditions. The present models are expected to provide a fundamental for further research.

Keywords insecticide resistance; susceptible subpopulation; resistant subpopulation; differential equation; dynamic model.

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1 Introduction

Insecticide resistance is the consequence of selective adaptation of insect pests to insecticides. It is inheritable (Ni and Pu, 2006). There are two major theories of insecticide resistance, election and induce variation (Tang, 2002). The election theory argues that there have been resistance genes in some individuals of insect

population before insecticide use. Insecticide resistance of these individuals is not able to be expressed in the usual natural selection. But under insecticide pressure, the resistance is expressed, and resistant insects survive, reproduce, and inherit this resistance to the next generation. Because this resistance gene had already existed in some individuals, so the resistance is a pre-adaptation phenomenon. Insecticides only play a selection role in the resistance development. The induce variation theory suggests that some individuals in the insect population do not have resistance genes. Due to insecticide use, some individuals in the population mutate, resulting in a resistance gene. It is a post-adaptation for insecticide resistance and the insecticide played a major role in mutagenesis of genes.

It is well known that there are some remarkable differences in morphological, physiological and biological characteristics between resistant and susceptible insects. The fitness of resistant insect genotype under insecticide selection is generally higher than that of the susceptible genotype, however the fitness of the resistant genotype is usually inferior when the insecticide pressure is reduced. When the insecticide is reduced, the fitness of the resistance genotype is degraded by the decline in the frequency of the resistance gene (Georghiou, 1983; Rough and Mckenzie, 1987). The development of insecticide resistance is dependent upon insect heredity, insecticide and insect fitness, etc (Tang, 2002; Liu et al., 2008).

Biological fitness usually refers to the ability of an organism to survive in an ecological environment and to pass on its characteristics to the next generation, including survival and fecundity (Liu et al., 2008). Biological fitness of both resistant and susceptible subpopulations is dependent upon a lot of factors. The reduction in the fitness may directly lead to a significant reduction in insect competitiveness, which in turn affects the subpopulation growth (Chevillon et al., 1999; Johnston et al., 2003).

Up till now, there is seldom research on dynamic models for insecticide resistance development. In this study, we try to propose some dynamic models for population modeling and simulation of development of insecticide resistance. They are expected to provide a fundamental for further research.

2 Models

Maintaining the certain dosage / concentration of an insecticide in the environment, the insecticide susceptible subpopulation of an insect species may evolve to the insecticide resistant subpopulation. Reproductive transition rates from susceptible subpopulation to resistant subpopulation and from resistant subpopulation to susceptible subpopulation depend on the insecticide pressure. Adaptation and fitness of susceptible subpopulation and resistant subpopulation are different under different insecticide pressure. Therefore, we propose the following dynamic model for development of insecticide resistance in insect population, which compost of two differential equations and an algebraic equation (Zhang, 2018)

$$\frac{dx}{dt} = r_1(c, t) x - f_1(c, t) x + g_1(c, t) y - \alpha(c, t) x y$$

$$\frac{dy}{dt} = r_2(c, t) y - g_2(c, t) y + f_2(c, t) x - \beta(c, t) x y \quad (1.1)$$

$$c = u(t) \quad (1.2)$$

where t : time (insect generation, year, etc.); $x(c, t)$: resistant subpopulation at t ; $y(c, t)$: susceptible subpopulation at t ; c : dosage / concentration of the insecticide. $r_1(c, t)$: c -dependent growth rate (fitness) function of resistant subpopulation, $r_1(c, t) \geq 0$; $\alpha(c, t)$: competition coefficient of susceptible subpopulation to resistant subpopulation, $\alpha(c, t) \geq 0$; $r_2(c, t)$: c -dependent growth rate (fitness) function of susceptible subpopulation, $r_2(c, t) \geq 0$. $\beta(c, t)$: competition coefficient of resistant subpopulation to susceptible

subpopulation, $\beta(c, t) \geq 0$; $f_1(c, t)$: reduction rate of resistant subpopulation due to the reproduction transition from resistant to susceptible insects, $f_1(c, t) \geq 0$; $f_2(c, t)$: growth rate of susceptible subpopulation due to the reproduction transition from resistant to susceptible insects, $f_2(c, t) \geq 0$. $f_2(c, t) = f_1(c, t)$, if there is no subpopulation loss. $g_2(c, t)$: reduction rate of susceptible subpopulation due to transition from susceptible to resistant insects under insecticide pressure, $g_2(c, t) \geq 0$; $g_1(c, t)$: growth rate of resistant subpopulation due to transition from susceptible to resistant insects under insecticide pressure, $g_1(c, t) \geq 0$. $g_1(c, t) = g_2(c, t)$, if there is no subpopulation loss. $f_1(c, t)$ and $f_2(c, t)$ are decrement functions of c . The functions, $g_1(c, t)$ and $g_2(c, t)$ are increment functions of c .

For election theory, $f_1(c, t)=g_1(c, t)=g_2(c, t)=f_2(c, t)=0$, the dynamic model for development of insecticide resistance is

$$\frac{dx}{dt} = r_1(c, t) x - \alpha(c, t) x y$$

$$\frac{dy}{dt} = r_2(c, t) y - \beta(c, t) x y \tag{1.3}$$

$$c = u(t) \tag{1.4}$$

For induce variation theory, $f_1(c, t)=f_2(c, t)=0$, the dynamic model for development of insecticide resistance is

$$\frac{dx}{dt} = r_1(c, t) x + g_1(c, t) y - \alpha(c, t) x y$$

$$\frac{dy}{dt} = r_2(c, t) y - g_2(c, t) y - \beta(c, t) x y \tag{1.5}$$

$$c = u(t) \tag{1.6}$$

Let $\mathbf{x} = (x, y)$, then eq. (1.1-1.2), (1.3-1.4), or eq (1.5-1.6) can be represented by

$$\frac{dx}{dt} = \mathbf{f}(\mathbf{x}, t) \tag{2}$$

3 Model Analysis

3.1 Model solution

Eq. (2) has a solution as the following (Zhang, 2010, 2016, 2018)

$$\mathbf{x}(t) = \mathbf{x}(t_0) + \int_{t_0}^t \mathbf{f}(\mathbf{x}, \tau) d\tau \tag{3}$$

As a simple form of solution, eq. (2) can be discretized as

$$\mathbf{x}(t_{k+1}) = \mathbf{x}(t_k) + h \mathbf{f}(\mathbf{x}(t_k), t_k) \quad k=0, 1, 2, \dots \tag{4}$$

where, $h = t_{k+1} - t_k$, is the time step. The numerical solution of the differential equation can thus be approximately solved in this way.

More precisely, we can use Runge-Kutta method to obtain numerical solution of the differential equation

(2). The Runge-Kutta method is calculated as follows (Zhang, 2010, 2016)

$$\begin{aligned} K_1 &= h f(\mathbf{x}(t_k), t_k) \\ K_2 &= h f(\mathbf{x}(t_k) + K_1/2, t_k + h/2) \\ K_3 &= h f(\mathbf{x}(t_k) + K_2/2, t_k + h/2) \\ K_4 &= h f(\mathbf{x}(t_k) + K_3, t_k + h) \end{aligned}$$

where $h = t_{k+1} - t_k$ is the step length of iteration. The numerical solution is

$$\mathbf{x}_{k+1} = \mathbf{x}_k + (K_1 + 2K_2 + 2K_3 + K_4) / 6 \quad k = 0, 1, 2, \dots \quad (5)$$

Based on eq. (4) or (5) and (1.2), the dynamics for development of insecticide resistance in insect population can be achieved.

3.2 Population outcomes

Four typical outcomes, dependent upon c , are expected in the certain period:

- (1) Resistant subpopulation (x) persists and susceptible subpopulation (y) disappears.
- (2) Resistant subpopulation disappears and susceptible subpopulation persists.
- (3) Both resistant and susceptible subpopulations disappear.
- (4) Resistant and susceptible subpopulations stabilize at their relative equilibrium states.

4 Resistance Strength

Based on eq. (1.1), we can measure the insecticide resistance strength by μ

$$\mu(c, t) = \frac{dx}{dy} = (r_1(c, t) x - f_1(c, t) x + g_1(c, t) y - \alpha(c, t) x y) / (r_2(c, t) y - g_2(c, t) y + f_2(c, t) x - \beta(c, t) x y) \quad (6)$$

or

$$\mu(c, t) = \frac{x}{x+y} \quad (7)$$

Resistance strength increases with $\mu(c, t)$. It is positively related to the common used resistance indices, e.g., LC_{50} , or LD_{50} , etc. That is, the magnitude of LC_{50} is the direct consequence of resistance strength:

$$LC_{50} = F(\mu) \quad (8)$$

Further research is needed to explore the quantitative relationship between resistance strength and LC_{50} (or LD_{50}).

5 Cases of Model Behavior

Use a highly simplified form of eq. (1.1-1.2). Set $\alpha(c, t) = 0.0009$, $\beta(c, t) = 0.0008$, $r_1(c, t) = 0.11$, $r_2(c, t) = 0.13$, $f_1(c, t) = 0.03$, $g_1(c, t) = 0.02$, $f_2(c, t) = 0.03$, and $g_2(c, t) = 0.02$. Initial subpopulations $x = 100$, $y = 100$. It means that the susceptible subpopulation possesses better fitness than the resistant subpopulation, as illustrated

in Fig. 1 (a), which is modeled with eq. (1.1-1.2). Fig. 1(b) shows another case in which the resistant subpopulation possesses better fitness than the susceptible subpopulation.

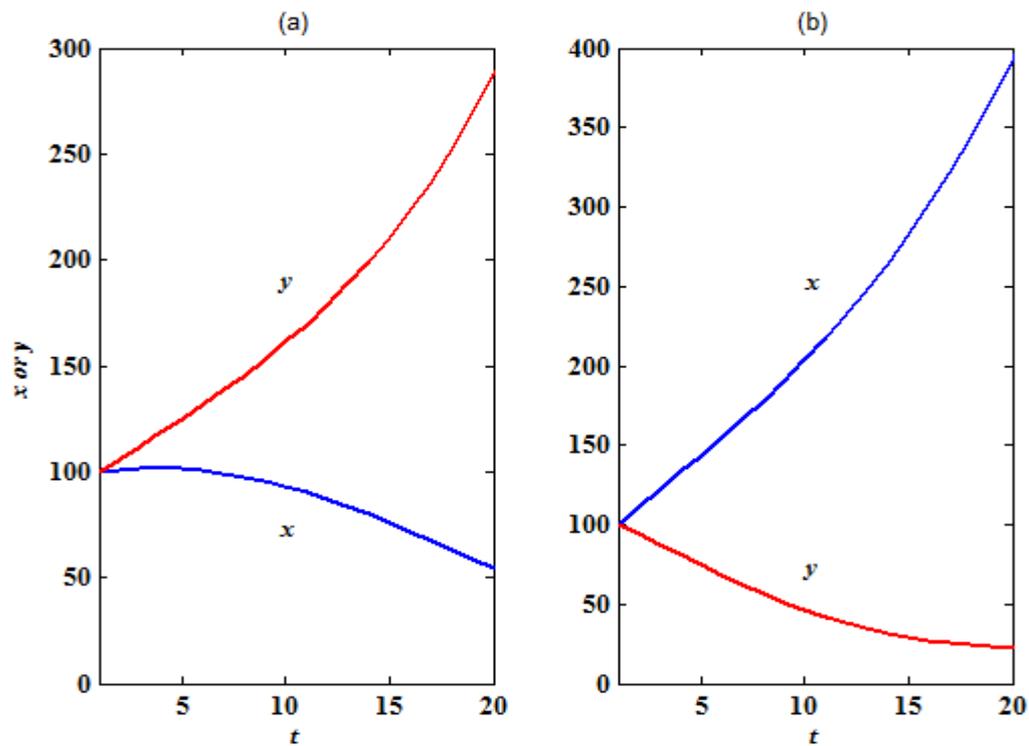


Fig. 1 Dynamics of susceptible and resistant subpopulations, modeled with a highly simplified form of eq. (1.1-1.2). (a) $\alpha(c, t) = 0.0009$, $\beta(c, t) = 0.0008$, $r_1(c, t) = 0.11$, $r_2(c, t) = 0.13$, $f_1(c, t) = 0.03$, $g_1(c, t) = 0.02$, $f_2(c, t) = 0.03$, and $g_2(c, t) = 0.02$. (b) $\alpha(c, t) = 0.0008$, $\beta(c, t) = 0.001$, $r_1(c, t) = 0.11$, $r_2(c, t) = 0.03$, $f_1(c, t) = 0.03$, $g_1(c, t) = 0.12$, $f_2(c, t) = 0.01$, and $g_2(c, t) = 0.02$. Initial subpopulations: $x=100$, $y=100$.

6 An Alternative Model

In addition to eq. (1.1-1.2), I propose another alternative model, which is revised from Lotka-Volterra competition model (Lotka, 1925; Volterra, 1926; Elsadany et al., 2012; Shakil et al., 2015a, 2015b; Ferrarini, 2015)

$$\frac{dx}{dt} = r_1(c, t) x (1 - x / k_1 - \alpha(c, t) y / k_1) - f_1(c, t) x + g_1(c, t) y$$

$$\frac{dy}{dt} = r_2(c, t) y (1 - y / k_2 - \beta(c, t) x / k_2) - g_2(c, t) y + f_2(c, t) x \tag{9.1}$$

$$c = u(t) \tag{9.2}$$

where k_1 : environmental capacity parameter of resistant subpopulation; k_2 : environmental capacity parameter of susceptible subpopulation.

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