



Modelling tritrophic interactions mediated by induced defence volatiles

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ABSTRACT

Many plant species defend themselves against herbivorous insects indirectly by producing and releasing induced volatiles to attract natural enemies of the herbivores. In this paper, we consider the recruitment of natural enemies attracted by plant-induced volatiles and introduce the An–Liu–Johnson–Lovett model into the Lotka–Volterra model in an attempt to add this missing vital link in tritrophic interaction. Increase in attraction strength of plant-induced volatiles to the natural enemy leads to high fluctuation amplitude of plant biomass and herbivore population. When the attack strength of natural enemies reaches a certain level, fluctuation amplitude of plant biomass and herbivore population will decrease and plant biomass will approach to its environmental carrying capacity. The simulation demonstrates that plant volatile compounds induced by insects have led to the introduction of a third tritrophic level, e.g., natural enemies, into the plant–herbivore system, resulting in the coexistence of plants, insects, and natural enemies during the evolution process.

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1. Introduction

Over a long evolution, plants have developed a multitude of defence mechanisms against herbivore attacks (Karban and Baldwin, 1997; Arimura et al., 2002). One such defence mechanism is referred to as induced indirect defence, e.g., the production and emission of volatile compounds that attract natural carnivorous enemies of the herbivores (Turlings et al., 1990; Arimura et al., 2002). Recent studies showed that the plant volatiles induced by herbivores play an important role in regulating the natural defence systems of certain plants against herbivorous insects (Buell, 1998; Mauricio et al., 1997; Stotz et al., 2000). Over 100 plant species, such as cucumber, corn, cotton and lima bean, if attacked by herbivores, have been demonstrated to be able to release volatiles as attractants to recruit the natural enemies of those herbivores (Janssen, 1999; Venzon et al., 1999; Turlings et al., 1990; van Tol et al., 2001). The induction of plant volatiles potentially alters the interaction between plants and their environment in many ways, e.g., by modifying interactions with herbivores, carnivores and/or with competing plants (Dicke and van Loon, 2000). By combining transcript and metabolite analysis, Mercke et al. (2004) identified

the genes involved in spider mite-induced volatile formation in cucumber plants. The induced plant volatiles are also implicated as defence agents and their emissions may contribute to the sustainability of forestry and agriculture (Boege and Marquis, 2005). Such volatile-mediated interaction among plants, herbivores and natural enemies is called a “tritrophic relationship”, and has received increasing attention worldwide in the past two decades due to serious public and environmental concerns about using synthesized pesticides, increasing pesticides resistance, and its potential as an alternative in improving crop protection against pests and diseases (Heil, 2001).

Many studies demonstrate that diurnal periodicity (Loughrin et al., 1994, 1997; Ping, 2001) and systemic release (Dicke et al., 1990; Turlings and Tumlinson, 1992; Potting et al., 1995) are the characteristics of herbivore-induced plant volatiles, which are thought to result in the co-evolution between plants and the natural enemies of herbivores (Dicke and van Loon, 2000). Loughrin et al. (1997) have shown that when Japanese beetles (*Popillia japonica* Newman) feed on the leaves of grapes (*Vitis labrusca* L.), such plants defend themselves by releasing induced volatiles. The release of these volatile compounds increase gradually until the emission reaches a peak and then decreases. A periodicity is shown for the leaves of grape induction. In addition, the release of induced volatiles is not limited to the site of damage but can also occur systemically (Dicke and van Loon, 2000; Turlings et al., 1990).

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In the past few decades, interest has been growing steadily in the design and study of mathematical models of population interactions to acquire fundamental insight and to provide better tools in aiding management of natural resources and agricultural practices (Yang, 2002). The core research of population ecology is the number of interacting species in the dynamics. In the basic prey–predator system, the model usually comprises a logistic prey growth function, a linear function, a linear predator numerical response and predator functional responses, e.g., given by the multispecies version of Holling’s disk equation (Abrams et al., 1998). The Volterra model (1926) describes the dynamic process of the population in the prey–predator system. The behavior of this model tends to be cyclic. The Lotka–Volterra model is modified by predator self-regulation modelled by the logistic equation and is further developed to describe a three species interaction, e.g., prey–predator–superpredator tritrophic relationship (Chen, 1988). There have been many attempts to apply the Lotka–Volterra model to real world oscillatory phenomena (Williamson, 1972). Chattopadhyay et al. (2001) analyzed the population dynamics of plant indirect defence in a plant–herbivore–parasitoid system with the help of the basic prey–predator mathematical models based on experimental data. Their work shows that parasitoids might determine plant fitness. Courchamp et al. (2000) simulated the indirect effects of an introduced prey species on an indigenous prey species, through a population of introduced predators. However, those attempts ignore the recruitment of natural enemies attracted by induced volatiles of plants, which is a vital link among plants, herbivores and their natural enemies. The effect of plant-induced volatiles on tritrophic interactions is missing. Dicke and van Loon (2000) indicated that in natural ecosystems herbivore-induced plant volatiles in the info-chemical web affect the behavior of organisms at various trophic levels. As a result, many interactions in a food web are altered, resulting in temporally and spatially variable multitrophic interactions. Better knowledge of this cause-and-effect relationship is important in understanding the chemical-mediated defence system of plants. Therefore, from a chemical ecology point of view, it is desirable to theoretically explicate the mechanisms of plants attracting natural enemies of herbivores and its dynamics. It could promote more efficient use of pesticides and better management of pests in agriculture practice.

The An–Liu–Johnson–Lovett model (An et al., 2003; Martins, 2006) describes the dynamics of allelochemical synthesis in living plants and their release into the environment. Liu et al. (2006) further developed this model to simulate the dynamic emission of induced volatiles of plants in response to herbivore attacks. In this paper, we consider the recruitment of natural enemies attracted by plant-induced volatiles in the tritrophic interactions among plant, herbivore and their natural enemies and introduce the modified An–Liu–Johnson–Lovett model (Liu et al., 2006) into the Lotka–Volterra model in an attempt to add the missing vital link among plants, herbivores and their natural enemies. This may better reflect the induced defence volatiles-mediated tritrophic relationships among plants, herbivores, and natural enemies, and their long-term dynamic behaviors. Due to the mathematical complexity of modelling these interactions, we have used only computer simulation techniques to present outcomes of the resultant models.

2. Model description

2.1. Modelling plant–herbivore system

The Lotka–Volterra model, also known as the predator–prey model, is frequently used to describe the dynamics of biological systems in which two species interact, such as both compet-

ing for resources or one predator and its prey. Although the Lotka–Volterra model reveals the oscillatory phenomenon in the population dynamics of predator–prey system and in the natural prey–herbivore system, many observations show that the dynamic behavior of populations exhibits a stable equilibrium (May, 1972). Both-side destruction is very much possible – predators are likely to migrate or vanish due to the extinction of their prey. The revised model (Holling, 1959, 1966; Watt, 1959; Caughley and Lawton, 1981) is written as follows:

$$\begin{cases} \frac{dx}{dt} = r_x x \left(1 - \frac{x}{K_x}\right) - yF(x, y) \\ \frac{dy}{dt} = yG(x, y) \end{cases} \quad (1)$$

where all parameters are positive, x and y are the biomass of plants and the population size of herbivores at time t , respectively. The parameter r_x denotes the intrinsic growth rate of the plants. K_x is the environmental carrying capacity of plants. $F(x, y)$ denotes the functional response of plant abundance to herbivore. $G(x, y)$ describes the numerical response of herbivore, which is related to the density of predator. In the absence of herbivores, the model becomes a logistic equation in which plant growth is determined by the intrinsic rate of r_x and its environmental carrying capacity, K_x . We assume the population size of herbivore declines at a rate (r_y) proportional to their numbers in the absence of plants ($x=0$), and we consider herbivores compete to their limited resource. Therefore the dynamics of the population size of herbivores and the amount of plants can be written as follows:

$$\begin{cases} \frac{dx}{dt} = r_x x \left(1 - \frac{x}{K_x} - \sigma_1 \frac{y}{K_y}\right) \\ \frac{dy}{dt} = r_y y \left(-1 + \sigma_2 \frac{x}{K_x} - \frac{y}{K_y}\right) \end{cases} \quad (2)$$

where the parameter K_y denotes the environmental carrying capacity of herbivores, σ_1 and σ_2 are positive constants.

The population equilibrium occurs when neither the density of plants nor the population of the herbivore changes. The possible steady state of Eq. (2) can be evaluated as $E_0(0, 0)$, $E_1(K_x, 0)$ and

$$E^* \left(\frac{K_x(\sigma_1 + 1)}{1 + \sigma_1\sigma_2}, \frac{K_y(\sigma_2 - 1)}{1 + \sigma_1\sigma_2} \right).$$

To determine the local stability character of E^* , we compute the Jacobi matrix of Eq. (2), which is denoted by J :

$$J(x, y) = \begin{pmatrix} r_x - \frac{2r_x}{K_x}x - \frac{\sigma_1 r_x}{K_y}y & -\frac{r_x \sigma_1}{K_y}x \\ \frac{r_y \sigma_2}{K_x}y & -r_y + \frac{\sigma_2 r_y}{K_x}x - \frac{2r_y}{K_y}y \end{pmatrix}$$

Let

$$\begin{aligned} p &= -tr(J) = - \left[\left(r_x - \frac{2r_x}{K_x}x - \frac{\sigma_1 r_x}{K_y}y \right) + \left(-r_y + \frac{\sigma_2 r_y}{K_x}x - \frac{2r_y}{K_y}y \right) \right] \Big|_{E^*} \\ &= \left(\frac{r_x}{K_x}x + \frac{r_y}{K_y}y \right) \Big|_{E^*}, \end{aligned}$$

And

$$\begin{aligned} q &= \det(J(E^*)) = \begin{vmatrix} r_x - \frac{2r_x}{K_x}x - \frac{\sigma_1 r_x}{K_y}y & -\frac{r_x \sigma_1}{K_y}x \\ \frac{r_y \sigma_2}{K_x}y & -r_y + \frac{\sigma_2 r_y}{K_x}x - \frac{2r_y}{K_y}y \end{vmatrix} \Big|_{E^*} \\ &= \left(\left(\frac{r_x r_y}{K_x K_y} + \frac{r_x r_y \sigma_1 \sigma_2}{K_x K_y} \right) xy \right) \Big|_{E^*} \end{aligned}$$

The equilibrium point is stable with the conditions of $p > 0$ and $q > 0$. So E^* is stable with the condition of $\sigma_2 > 1$. This case illustrates a

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