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Periodic solutions in a herbivore-plant system with time delay and spatial diffusion

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ABSTRACT

Empirical studies indicate that many populations of herbivorous insects exhibit periodic outbreaks, but the intrinsic causes of this behavior are not well understood. Thus, in this study, we investigated a herbivore-plant system with time delay based on reaction-diffusion equations. Using normal formal theory and the center manifold theorem for partial functional differential equations, we show that this model exhibits the property of Hopf bifurcation. Therefore, interactions between the time delay and spatial diffusion will induce periodic outbreaks in herbivore populations. These results may suggest a new mechanism for herbivore outbreaks.

1. Introduction

The interactions between plants and herbivores have important roles in natural ecosystems, agriculture, and grazing regions. In general, the presence of excessive herbivores has a negative impact on plants in terms of their growth, reproduction, and diversity [1,2]. Hence, plants protect themselves from feeding by herbivores via the adoption of resistance strategies, which mainly comprise chemical defenses, structural defenses, and the induction of natural enemies [3–6]. Moreover, periodic increases in the population size of herbivores are threats to the plants that they consume, which can result in changes in the plant community structure and abundance of plant species. For example, during 2003, outbreaks of spruce budworm and mountain pine beetle damaged four million hactare of forest in British Columbia, Canada [7]. In contrast to abiotic factors such as storms, drought, and fires, herbivore outbreaks can have persistent effects on plants. Therefore, the key to preventing outbreaks of herbivores is understanding the critical factors that determine herbivore outbreaks.

Previous studies have considered various factors that might cause herbivore outbreaks, include inducible resistance, physical stress, interactions between herbivores and enemies, limited resources, and environmental forcing [8–24]. Recently, Sun et al. proposed another mechanism related to periodic herbivore outbreaks, where they suggested that herbivores will exhibit periodic outbreaks when a time delay exceeds a certain threshold [25]. They considered a nonlinear diffusion system

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Table 1
Descriptions and values of parameters.

Para.	Description	Value	Source
α	Maximum induction rate per herbivore population	200	[25]
β	Per-unit reduction of induction rate by self-limitation	1	[25]
δ	Per-unit induction decay rate	0.75	[25]
b	Half-maximum of herbivore damage effectiveness	5	[25]
θ	Herbivore damage effectiveness shape tuning parameter	3	[25]
r	Intrinsic growth rate of herbivore populations	1	[25]
K	Carrying capacity of herbivore populations	10	[25]
m	Mortality rate of herbivore populations by induction	0.01	[25]
τ	Time delay between herbivore damage and deployment of inducible defenses		Computation
d_1	Diffusion coefficient of the plant		Assumption
d_2	Diffusion coefficient of the herbivore		Assumption

combined with induced defense in plants and a time delay. However, they only considered the case where herbivore populations are diffused in space. In fact, the seeds of plants can be carried to other areas by the wind, where new plants will grow in the following year. Hence, in our model, we assume that both the plant and herbivore populations are spatially diffused. In addition, herbivore outbreak can be studied based on reaction-diffusion systems with delay [26–29].

The remainder of this paper is organized as follows. In Section 2, we establish a spatial herbivore-plant system with time delay and we discuss the existence of a Hopf bifurcation with spatial diffusion. In Section 3, we analyze the properties of Hopf bifurcating periodic solutions, including the direction of the Hopf bifurcation, stability, and the period of the bifurcating periodic solutions, where we mainly use the center manifold theorem and normal formal theory. In Section 4, based on numerical simulations, we show that the herbivore will exhibit periodic outbreaks if the delay exceeds a threshold. Finally, we give some conclusions and discuss our findings.

2. Mathematical model and existence of a hopf bifurcation

2.1. Model formulation

It might not be possible to identify the mechanisms responsible for periodic outbreaks of herbivore populations based on empirical evidence because long time series of data are difficult to obtain. Instead, we can employ mathematical models to characterize the interactions between inducible plant defenses and herbivore populations. Sun et al. proposed a mathematical model for describing the interaction between induced plant defenses and herbivore populations [25],

$$\begin{cases} \dfrac{\partial I(x,t)}{\partial t} = [\alpha - \beta I(x,t)]\dfrac{H^{\theta}(x,t-\tau)}{b^{\theta}+H^{\theta}(x,t-\tau)} - \delta I(x,t), \\ \dfrac{\partial H(x,t)}{\partial t} = rH(x,t)\left[1-\dfrac{H(x,t)}{K}\right] - mI(x,t)H(x,t) + \dfrac{\partial^2}{\partial x^2}[D_0 + \chi I(x,t)H(x,t)], \end{cases} \tag{1}$$

where $I(x, t)$ represents the density of plant inducible defenses and $H(x, t)$ denotes the density of the herbivore population.

Sun et al. [25] considered that only herbivore populations have spatial movements, but some plants can also move in space due to environmental factors such as wind. Thus, we consider that the induced plant defenses and herbivores are distributed uniformly in a certain one-dimensional domain. Assuming that the populations cannot move through the boundary of the domain, the system with Neumann boundary conditions is revised into the following form:

$$\begin{cases} \dfrac{\partial I(x,t)}{\partial t} = [\alpha - \beta I(x,t)]\dfrac{H^{\theta}(x,t-\tau)}{b^{\theta}+H^{\theta}(x,t-\tau)} - \delta I(x,t) + d_1\dfrac{\partial^2 I(x,t)}{\partial x^2}, \\ \dfrac{\partial H(x,t)}{\partial t} = rH(x,t)\left[1-\dfrac{H(x,t)}{K}\right] - mI(x,t)H(x,t) + d_2\dfrac{\partial^2 H(x,t)}{\partial x^2}, \quad t>0, \quad x\in(0,\pi), \\ \dfrac{\partial I}{\partial x}\Big|_{x=0,\pi} = 0,\ \dfrac{\partial H}{\partial x}\Big|_{x=0,\pi} = 0, \quad t\ge 0, \\ I(x,t)=\phi_1(x,t)\ge 0, H(x,t)=\phi_2(x,t)\ge 0, \quad (x,t)\in[0,\pi]\times[-\tau,0], \end{cases} \tag{2}$$

where all of the parameters are positive. The descriptions and values of the parameters are given in Table 1. $\frac{\partial^2}{\partial x^2}$ is the Laplacian operator, $\phi = (\phi_1, \phi_2)^T$, and $\psi = (\psi_1, \psi_2)^T$. We assume that $\phi, \psi \in \wp = C([-\tau, 0], X), \tau > 0$ and X is defined as follows:

$$X = \left\{(I,H)^T : I, H \in W^{2,2}(0,\pi);\ \frac{\partial I}{\partial x}\Big|_{x=0,\pi} = \frac{\partial H}{\partial x}\Big|_{x=0,\pi} = 0\right\},$$

with the inner product, $\langle \cdot, \cdot \rangle$.