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Mathematical analysis of a model for plant invasion mediated by allelopathy

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ABSTRACT

Exotic plants threaten the biodiversity of natural habitats and the integrity of agricultural systems throughout the World. Therefore, understanding, predicting and controlling plant invasions became issues of great practical importance. In the present paper, a model for plant invasion based on allelopathic suppression is proposed and studied through analytical methods and numerical integration. Employing linear stability analysis the conditions for plant coexistence as well as one species extinction were determined for the spatially homogeneous system. These conditions demonstrate the advantage conferred to the alien plant by its phytotoxin. It was shown that the system exhibits bistability between two distinct fixed points, either associated to species coexistence or to the extinction of one species. Numerical simulation is also included to support such results. Further, the invasion spreading starting from a single, spatially localized initial focus was investigated by numerical integration of the model's equations. As obtained for the spatially homogeneous system, at strong interspecific competition the outcome is the extinction of one plant species. In contrast, at low interspecific competition, the rule is the coexistence between the invader and native plants. So, under weak competition alien species can invade, but genetic diversity can be sustained.

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1. Introduction

Recently there is much current interest in understand biological invasions, a world-wide phenomena which represents a major threat for ecosystems functioning and biodiversity conservation, water availability, attractiveness of natural areas, and agriculture (Rejmánek, 1989; Shigesada and Kawasaki, 1997; Dean, 1998; Chow, 1999). Preventing the spreading of invasive species and/or predicting their patterns of spreading emerge as imperative tasks in an ecologically sustainable world. In turn, from the mathematical viewpoint, patterns of biological invasion are interesting examples of spontaneous symmetry breaking in complex systems. In a homogeneous environment (Petrovskii and Shigesada, 2001) invasion frequently generates regular (smooth) stationary travelling population waves, but more complicated regimes in which the travelling fronts become transient or oscillatory before the formation of spatial patterns can be observed in heterogeneous environment or under the influence of other species (Shigesada et al., 1986; Sherratt et al., 1995).

The leading theory for plant invasion is the escape of invader species from the pathogens and herbivores that hold them constrained in their original habitat, freeing them to focus their full potential on resource competition (Crawley, 1996). Thus, it is tacitly assumed that plant communities are “individualistic”, composed primarily of individuals exhibiting similar adaptations to explore the resources of a given physical environment. However, instead of being passively shaped by fluctuations in the resources they require, plant communities can emerge from direct chemical, biological and physical root–root and root–microbe interactions occurring within the plant rhizospheres (Bever et al., 2010; Bais et al., 2004). The race of plants and microbes for adapt to the chemicals synthesized by their neighbors may drive species coexistence and community composition. Furthermore, some exotic invasive plants may use competitive mechanisms to disrupt inherent, coevolved interactions among long-associated native species constituting the communities they invade (Callaway and Aschehoug, 2000; Bais et al., 2003). One such mechanism is allelopathy, i.e., the suppression of germination or growth of neighboring plants by the release of toxic secondary chemical compounds. If an invasive species releases a toxic compound and the individuals comprising a given natural community lacks resistance to it, the result may be disruption of the existing plant community. Therefore, community and invasion ecology are

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naturally interconnected because both the persistence of a species in a community or its invasion success abroad its native habitat primarily depends on its ability to increase from low density (Morton and Law, 1997; Shea and Chesson, 2002). Hence, understanding the dynamics of two plant species interacting through allelopathic suppression emerges as a main issue in theoretical ecology.

In the literature, the problem of chemical competition between algae (Fergola et al., 2007) and bacterial (Iwasa et al., 1998) species or strains was rather intensively investigated and modeled mathematically. Nonetheless, the plant–plant interaction dynamics mediated by chemical compounds was much less theoretically considered (Dubey et al., 2010; Souza et al., 2007).

In this paper we propose a mathematical model to investigate the dynamics of two competing plant species in which one of them is an invader and produces a phytotoxin affecting the other. Further, the role of allelopathy in the asymmetry of the competition process is discussed. The paper is organized as follows. In Section 2, the model based on partial differential equations is introduced. In Section 3, a linear stability analysis of its spatially homogeneous, stationary solutions is performed. In Section 4, the resulting dynamical scenarios, supported by the numerical integration of the associated ordinary differential equations, and the correspondent phase portraits are reported. A hallmark of such spatially homogeneous system is the bistability between the extinction of one species and the coexistence of both plants. In Section 5, the non-homogeneous spatio-temporal solutions of the model are investigated numerically. Finally, in Section 6 some conclusions are drawn.

2. The model for allelopathic invasion

In order to describe the population dynamics of two competing plant species in which one of them is an invader and produces a phytotoxin affecting the other, the following reaction-diffusion system was proposed:

$$\begin{aligned} \frac{\partial N}{\partial t} &= \mu N \left(1 - \frac{N + \alpha_1 I}{K_N} \right) - N\Phi(P) + \vec{\nabla} \cdot (D_N(P)\vec{\nabla}N) \\ \frac{\partial I}{\partial t} &= \delta I \left(1 - \frac{I + \alpha_2 N}{K_I} \right) + D_I \nabla^2 I \\ \frac{\partial P}{\partial t} &= \nu I - \gamma PN - \tau P + D_P \nabla^2 P. \end{aligned} \quad (1)$$

Here N stands for the native plant, I for the invasive species, and P for its phytotoxin. Also, μ is the reproduction rate of the native plant and K_N its carrying support. Analogously, δ is the reproduction rate and K_I the carrying support of the invasive plant. A classical interspecific competition for the environmental resources is assumed for the plants. The parameters α_1 and α_2 are the competition coefficients which measure the extent to which each species presses upon the resources used by the other. The factor ν is the rate of phytotoxin exudation from the roots of the invasive plants, while τ is its natural degradation rate. The term $-\gamma PN$ represents phytotoxin consume by the native species with an absorption rate γP which depends on the toxin's level in a linear way. The term $-N\Phi(P)$ represents native plant decrease as they uptake the phytotoxin P . A Holling type I functional response with a threshold for phytotoxin effects and saturation of the allelopathic suppression is assumed:

$$\Phi(P) = \begin{cases} 0, & \text{if } P \leq \theta \\ \beta \frac{P - \theta}{\xi + (P - \theta)}, & \text{otherwise} \end{cases} \quad (2)$$

This functional response was chosen in order to simplify the mathematical analysis. The parameters β and ξ control the

phytotoxin's efficiency in poisons native plants, i.e., the slope β/ξ of the response at the threshold concentration θ . Finally, the diffusion terms model plant spreading in space through stochastic seed dispersal and germination, as well as the spread of the phytotoxin in the soil. For simplicity, the diffusion coefficients D_P and D_I are considered to be constant, uniform and $D_I < D_P$. In turn, since the phytotoxin decreases the chance of native plant seed germination, the diffusion coefficient D_N is assumed to be a decreasing function of the phytotoxin concentration above its threshold. Specifically,

$$D_N(P) = \begin{cases} D_0, & \text{if } P \leq \theta \\ \frac{D_0}{1 + \eta(P - \theta)}, & \text{otherwise} \end{cases} \quad (3)$$

where D_0 is the constant, uniform diffusion coefficient of the native plant in the absence of the invasive species and η a conversion factor having the units of inverse of concentration, respectively. For simplicity, $D_0 = D_I$ is used. All parameters are positive real numbers.

The carrying capacities K_N and K_I , the inverse of the native plants growth rate μ^{-1} and the poisoning threshold θ represent characteristic population densities, timescale and phytotoxin concentration, respectively. Thus, it is convenient to introduce the dimensionless variables $N' = N/K_N$, $P' = P/\theta$, $I' = I/K_I$, $t' = \mu t$, and $\vec{x}' = \vec{x}/\Delta$, in which Δ is a typical length scale (e.g., the rhizosphere radius), in order to transform the model equations (1) into the dimensionless system

$$\begin{aligned} \frac{\partial N'}{\partial t'} &= N'(1 - N' - \bar{\alpha}_1 I') - N'\bar{\Phi}(P') + \vec{\nabla}' \cdot (\bar{D}_N \vec{\nabla}' N') \\ \frac{\partial I'}{\partial t'} &= \bar{\delta} I'(1 - I' - \bar{\alpha}_2 N') + \bar{D}_I \nabla'^2 I' \\ \frac{\partial P'}{\partial t'} &= \bar{\nu} I' - \bar{\gamma} P' N' - \bar{\tau} P' + \bar{D}_P \nabla'^2 P' \end{aligned} \quad (4)$$

where $\bar{\alpha}_1 = \alpha_1 K_I / K_N$, $\bar{\nu} = \nu K_I / \mu$, $\bar{\gamma} = \gamma K_N / \mu$, $\bar{\tau} = \tau / \mu$, $\bar{\delta} = \delta / \mu$, $\bar{\alpha}_2 = \alpha_2 K_N / K_I$, $\bar{D}_P = D_P / \mu \Delta^2$, $\bar{D}_I = D_I / \mu \Delta^2$. The re-scaled response function $\bar{\Phi}$ and diffusion coefficient \bar{D}_N are given by

$$\bar{\Phi}(P') = \begin{cases} 0, & \text{if } P' \leq 1 \\ \bar{\beta} \frac{P' - 1}{\bar{\xi} + (P' - 1)}, & \text{if } P' > 1 \end{cases} \quad (5)$$

and

$$\bar{D}_N(P') = \begin{cases} \bar{D}_0, & \text{if } P' \leq 1 \\ \frac{\bar{D}_0}{1 + \bar{\eta}(P' - 1)}, & \text{if } P' > 1 \end{cases} \quad (6)$$

respectively. In these expressions $\bar{\beta} = \beta \theta / \mu$, $\bar{\xi} = \xi / \mu$, $\bar{D}_0 = D_0 / (\mu \Delta^2)$, and $\bar{\eta} = \eta \theta$. Henceforth, we omit the 's for clarity.

3. Linear stability of the spatially uniform stationary solutions

In this section, we analyze the model equations (4) when spatial fluctuations and correlations are neglected. In this case, the system (4) is reduced to the following ODEs:

$$\begin{aligned} \frac{dN}{dt} &= N(1 - N - \alpha_1 I) - N\Phi(P) \\ \frac{dI}{dt} &= \delta I(1 - I - \alpha_2 N) \\ \frac{dP}{dt} &= \nu I - \gamma NP - \tau P \end{aligned} \quad (7)$$

Clearly, Eq. (7) has a trivial fixed point $\vec{x}_0^* \equiv (N_0^*, I_0^*, P_0^*) = (0, 0, 0)$ whose linear stability is that of a saddle point (eigenvalues $\lambda_1 = 1$, $\lambda_2 = \delta$, and $\lambda_3 = -\tau$). In consequence, both plant species will never be lead to extinction simultaneously. Further, the system (7) has

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