

Resource versus Space Competitions in a Plant Growth Model*

A. El Hamidi

Laboratoire LASIE, Université de La Rochelle, La Rochelle, France

Abstract. In this tutorial note, we present a spatiotemporal model for plant growth, combining two different mechanisms of competition. The first mechanism concerns the biomass growth via resources while the second concerns the space-biomass expansion. The pure time mechanism is described by the standard underlying Kolmogorov model for interacting populations. The spatial mechanism, more adapted to plant growth, expresses the motility of each species and their capability to exclude the others from its territory.

1 Introduction

The spatial and/or temporal behaviors of interacting species in ecological systems represent an important field in mathematical population ecology. In particular, competitive dynamics of interacting species have been the subject of a sizeable literature. Various mathematical models have been proposed to study problems of coexistence or exclusion of competing species. Consider, for example, two substances (species, chemicals, etc.) that are activating or inhibiting each other according to some law of reaction and diffusing in a spatial domain by linear Fick's law. The density of the two substances at time $t > 0$ and place $x \in \Omega$ are denoted by $u_1(x, t)$ and $u_2(x, t)$ respectively, where Ω is a bounded domain in \mathbb{R}^2 .

The well-known competitive Lotka-Volterra-Gause type model is given by

$$\begin{cases} \frac{\partial u_1}{\partial t} - \mu_1 \Delta u_1 = u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2), & t > 0, \quad x \in \Omega \\ \frac{\partial u_2}{\partial t} - \mu_2 \Delta u_2 = u_2(\alpha_2 - \beta_2 u_2 - \gamma_2 u_1), & t > 0, \quad x \in \Omega \end{cases} \quad (1)$$

where μ_i is the diffusion rate of u_i , α_i is the intrinsic growth rate, β_i is the intra-specific competition rate and γ_i is the inter-specific competition rate.

Consider the case where all rates are positive constants and zero-flux boundary conditions

$$\nabla u_i(x, t) \cdot \mathbf{n}(x) = 0 \quad \text{on} \quad \partial\Omega \times]0, +\infty[,$$

* his work has been partially funded by CNRS (National Centre for Scientific Research) within the framework of the "PEPS Rupture" call 2011

where $\mathbf{n}(x)$ is the unit outward pointing normal at the point x to the boundary $\partial\Omega$ of Ω . The initial conditions are

$$u_i(x, 0) \geq 0, \quad \text{for every } x \in \Omega.$$

It is well-known that stable attractors of (1) should be equilibrium solutions. This implies that solutions of (1) become spatially homogeneous asymptotically, that is, stable equilibrium solutions of the pure dynamical system associated to (1)

$$\begin{cases} u_1'(t) = u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2), & t > 0, \\ u_2'(t) = u_2(\alpha_2 - \beta_2 u_2 - \gamma_2 u_1), & t > 0, \end{cases} \quad (2)$$

If the two species u_1 and u_2 are (ecologically) strongly competing, that is

$$\frac{\beta_1}{\gamma_2} < \frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2},$$

the competitive exclusion principle between the u_1 and u_2 occurs [18, 17]. More precisely, any non-negative solution (u_1, u_2) converges to either $(\alpha_1/\beta_1, 0)$ or $(0, \alpha_2/\beta_2)$. However, observations in natural fields show that strongly competing species can coexist. In [27], the authors show that this phenomenon can be assigned to the repulsive effect between competing species. Indeed, they introduced cross-diffusion terms which represent the environmental pressures due to the inter-specific interferences:

$$\begin{cases} \frac{\partial u_1}{\partial t} - \Delta[(\mu_1 + au_2)u_1] = u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2), & t > 0, \quad x \in \Omega \\ \frac{\partial u_2}{\partial t} - \Delta[(\mu_2 + bu_1)u_2] = u_2(\alpha_2 - \beta_2 u_2 - \gamma_2 u_1), & t > 0, \quad x \in \Omega \end{cases} \quad (3)$$

where a, b stand for the cross-diffusion pressures and are nonnegative constants.

In what follows, we will present a model without cross-diffusions where the authors [9] show that species with strong **spatial** competition can lead to their coexistence. Indeed, the strong spatial competitions give rise to degenerate diffusions which guarantee patterns formation and thus coexistence.

On the other hand, it is well known that System (2) has 4 equilibrium points: $(u_1, v_1) = (0, 0)$, $(u_2, v_2) = \left(\frac{\alpha_1}{\beta_1}, 0\right)$, $(u_3, v_3) = \left(0, \frac{\alpha_2}{\beta_2}\right)$, $(u_4, v_4) = \left(\frac{\alpha_2\gamma_1 - \alpha_1\beta_2}{\gamma_1\gamma_2 - \beta_1\beta_2}, \frac{\alpha_1\gamma_2 - \alpha_2\beta_1}{\gamma_1\gamma_2 - \beta_1\beta_2}\right)$. Also, 4 situations of interest hold true, in terms of the inter-specific competitions γ_1 and γ_2 :

- (i) $\frac{\gamma_1}{\beta_2} < \frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$ (moderate competitions \implies coexistence of populations)
- (ii) $\frac{\beta_1}{\gamma_2} < \frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$ (strong competitions \implies extinction of the initially disadvantaged one)
- (iii) $\frac{\alpha_1}{\alpha_2} > \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} > \frac{\gamma_1}{\beta_2}$ (strong vs weak competition \implies extinction of the weak one)

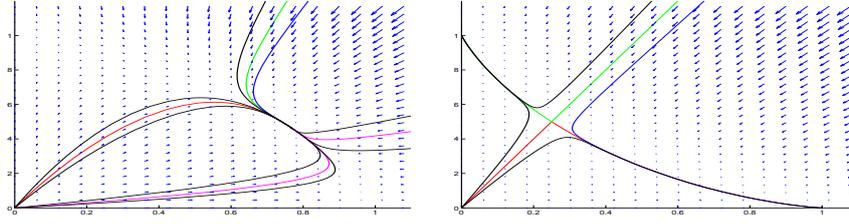


Fig. 1. Left: Situation (i), right: Situation (ii).

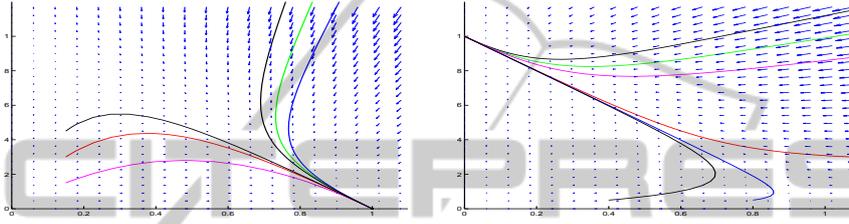


Fig. 2. Left: Situation (iii), right: Situation (iv).

- (iv) $\frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$ (weak vs strong competition \implies extinction of the weak one)

Notice that in all cases, the steady point $(0, 0)$ is linearly unstable. Let us describe the (linear) nature of the other steady states. In case (i), (u_2, v_2) and (u_3, v_3) are saddle points and (u_4, v_4) is asymptotically stable. In case (ii), (u_2, v_2) and (u_3, v_3) are stable and (u_4, v_4) is a saddle point.

On the other hand, we will see that the spatial competitions lead to similar situations, linking the spatial and the time biomass competitions. In the best of our knowledge, this fact is new and deserves more theoretical and numerical studies.

2 Spatial Competitions: Diffusion Degeneracy and Coexistence

In what follows, we present a simple pde's model, without cross diffusions, that allows coexistence and patterns formation, even for strongly competitive populations.

Consider the pde's system

$$\begin{cases} \frac{\partial u_1}{\partial t} - \operatorname{div}(\mu_1(u_2)\nabla u_1) = u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2), & t > 0, \quad x \in \Omega, \\ \frac{\partial u_2}{\partial t} - \operatorname{div}(\mu_2(u_1)\nabla u_2) = u_2(\alpha_2 - \beta_2 u_2 - \gamma_2 u_1), & t > 0, \quad x \in \Omega. \end{cases} \quad (4)$$

For a given parameter $\eta_1 \geq 0$, assume that

$$\mu_1(u_2) > 0 \quad \text{if} \quad 0 \leq u_2 \leq \eta_1 \quad \text{and} \quad \mu_1(u_2) = 0 \quad \text{if} \quad u_2 > \eta_1.$$

This system is degenerated because at least one diffusion term is not positive. In this situation, species u_1 can not diffuse in locations where $u_2 > \eta_1$ and diffuses with the rate $\mu_1(u_2) > 0$ wherever $0 \leq u_2 \leq \eta_1$. The parameter η_1 can be thus interpreted as the ability of species u_2 to resist to the species u_1 intrusion; that is, if η_1 is small then the exclusion ability of the species u_2 is large and vice versa. We expect that this kind of degenerated diffusion can allow patterns formation without the presence of cross-diffusion terms.

We will show that the role of η_1 in space competition is similar to that of γ_1 , in resources competition. More precisely, for simplicity, consider the degenerated system

$$\begin{cases} \frac{\partial u_1}{\partial t} - \operatorname{div}(\mu(u_2)\nabla u_1) = u_1(\alpha_1 - \beta_1 u_1 - \gamma_1 u_2), & t > 0, \quad x \in \Omega \\ \frac{\partial u_2}{\partial t} - \operatorname{div}(\mu(u_1)\nabla u_2) = u_2(\alpha_2 - \beta_2 u_2 - \gamma_2 u_1), & t > 0, \quad x \in \Omega \end{cases} \quad (5)$$

where

$$\mu(s) > 0 \quad \text{if} \quad 0 \leq s \leq \eta \quad \text{and} \quad \mu(s) = 0 \quad \text{if} \quad s > \eta.$$

The carrying capacity of the species u_1 and u_2 respectively $K_1 := \alpha_1/\beta_1$ and $K_2 := \alpha_2/\beta_2$, that is, the biomass u_1 satisfies the inequality $0 \leq u_1(x, t) \leq K_1$ for every $(x, t) \in \Omega \times [0, +\infty[$, provided that the initial condition $u_1(\cdot, 0)$ satisfies the same condition: $0 \leq u_1(x, 0) \leq K_1$, for every $x \in \Omega$. This fact is due to the positivity of the diffusion μ and the Kolmogorov structure of the system (5). Similar properties can be cited about the biomass u_2 .

In this special case, 4 situations of interest linking the spatial competition

- **Infinite Spatial Competition:** $\eta = 0$. In this situation, u_1 and u_2 can not coexist in the same locations. In particular, u_1 and u_2 can not coexist in locations where $u_1(x, 0) > 0$ or $u_2(x, 0) > 0$.
- **Strong Spatial Competition:** $0 < \eta < \min\{K_1, K_2\}$. In this situation, u_1 and u_2 can coexist but only in subdomains where the initial conditions satisfy: $0 \leq u_1(x, 0) \leq \eta$ or $0 \leq u_2(x, 0) \leq \eta$.
- **Weak Spatial Competition:** $\eta > \max\{K_1, K_2\}$. In this situation, the system behaves as a non-degenerated one and the presence of diffusions does not impact the linear stability of equilibrium points of (2). The exclusion principle takes place, if at least one inter-specific competition rate is large (See Figure 3).
- **Moderate Spatial Competition:** $\min\{K_1, K_2\} < \eta < \max\{K_1, K_2\}$. In this situation, the species with the greatest carrying capacity, that is, u_1 if $K_1 > K_2$ or u_2 if $K_1 < K_2$, will be present alone in locations where its density exceeds η and miscibility can occur elsewhere.

In the following, we present two simulations corresponding to the system (5) with homogeneous Neumann boundary conditions on $\partial\Omega$,

$$\mu_1(u_2) \nabla u_1 \cdot \mathbf{n} = \mu_2(u_1) \nabla u_2 \cdot \mathbf{n} = 0 \quad \text{on} \quad [0, +\infty[\times \partial\Omega.$$

The nonlinear diffusion coefficient is the truncation function

$$\mu(s) = C \exp\left(\frac{\eta^2}{s^2 - \eta^2}\right), \quad \text{if} \quad 0 \leq s < \eta \quad \text{and} \quad \mu(s) = 0, \quad \text{if} \quad s \geq \eta > 0.$$

We set $C = \exp(1)$ and hence $0 \leq \mu(s) \leq 1$. The parameters in the temporal dynamical system (2) are such that the second species u_2 has a competitive advantage on the first species, i.e unique stable equilibrium point

$$\left(u_1 = 0, u_2 = \frac{\alpha_2}{\beta_2} > 0 \right)$$

with

$$\alpha_1 = 1, \alpha_2 = 1.3, \beta_1 = 1.2, \beta_2 = 0.8, \gamma_1 = 3., \gamma_2 = 1.1.$$

We focus ourselves on two situations: the *weak spatial competition* and the *weak spatial competition* cases. We test the competitive advantage of space exclusion that corresponds to $\eta \ll 1$ by comparing to the situation with quasi uniform diffusion $\eta \gg 1$.

The initial condition for the benchmark problem is a collection of well separated sharp bell function

$$\exp \left[-\frac{\text{dist}((x, y), M_j)}{\nu} \right],$$

that plays the role of initial "seeds of population density", centered on a set of points M_j - see Figure 3 and 4 at $T = 0$. We use a similar number of "seeds" for both species.

The numerical implementation is straightforward. We use a regular Cartesian grid with a second order finite volume approximation in space and a second order Crank-Nicolson implicit time stepping.

When we run the simulation, we observe at early time the diffusion process that represents plant colonization. After some time, we start to see some interaction with narrow fronts layers where both species compete. This boundary layer that separates the species is more or less diffused depending on how small is the ν value.

In these figures we use the following convention: the space invaded by the first species (respt. the second species) is marked by black label (respt. red label). The simulation exhibit then nice pattern formation for each species.

In the figures area where density is above 0.5 is indicated by circles 'o', while the area with lower concentration in the interval (0.1, 0.5) is indicated by dots '.'. This helps to visualize area where the first species is strongly dominant, i.e red circle zone, areas where the second species diffuses every where black dot point area, and overlapping zone where competition occurs.

As expected, for weak spatial competition, i.e $\eta \gg 1$, the most competitive species ($0, \alpha_2/\beta_2$) wipe out the other one that goes to extinction, that is, weak competition has no effect on the stability of uniform equilibrium points.

However, for strong spatial competition, i.e $\eta \ll 1$, the stability of the uniform equilibrium point ($0, \alpha_2/\beta_2$) can be modified by the strong spatial competition, which leads sometimes to coexistence between strong competitive populations.

Eventually for infinite spatial competition, i.e $\eta = 0$, the less competitive species will always survive, and perhaps get most of the field thanks to its initial fast space invasion. In particular, the linear stability of equilibria is completely modified by this *infinite spatial competition*.

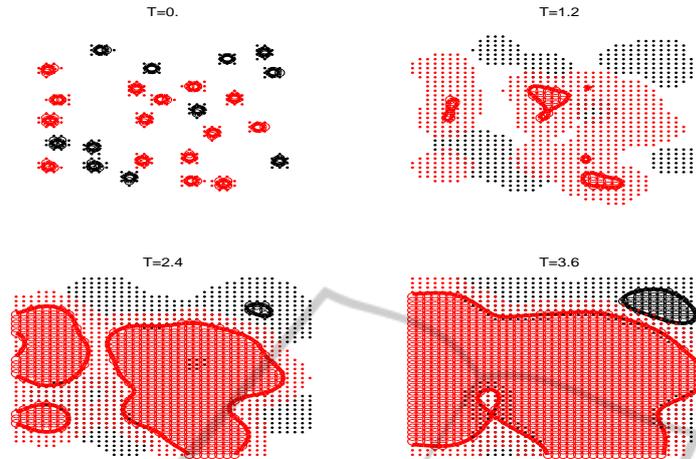


Fig. 3. Two species system with weak spatial competition: $\eta = 100$, $K_1 = 1/1.2$ and $K_2 = 1.3/0.8$.

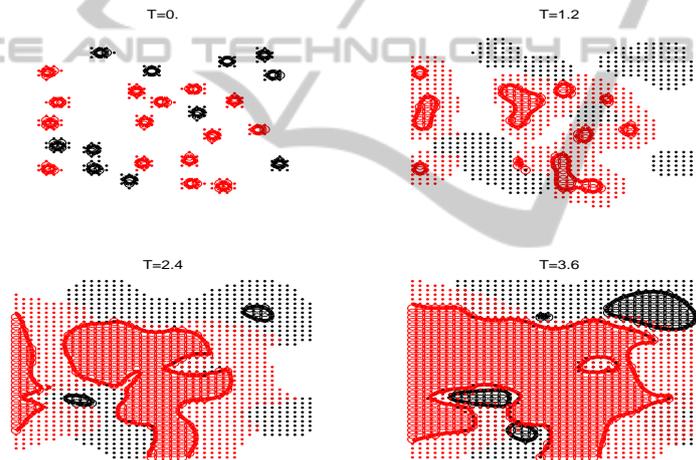


Fig. 4. Two species system with strong spatial competition $\eta = 0.1$, $K_1 = 1/1.2$ and $K_2 = 1.3/0.8$.

References

1. H. Amann, Nonhomogeneous linear and quadilinear elliptic and parabolic boundary value problems. Function Spaces, Differential Operators and Nonlinear Analysis. H.J. Schmeisser, H. Triebel (editors), Teubner, Stuttgart, Leipzig. (1993), 9-126.
2. R. Aris, The mathematical theory of diffusion and reaction in permeable catalysts. Vol. I: The theory of the steady state. Oxford University Press. XVI, (1975).
3. F. Brauer, C. Castillo-Chavez, Mathematical Models in Population Biology and Epidemiology. Springer Verlag, Texts in applied mathematics 40, (2000)
4. S. N. Busenberg, C. C. Travis, Epidemic models with spatial spread due to population migration. J. Math. Biol. 16 (1983), 181 – 198.

5. V. Capasso, A. Di Liddo, L. Maddalena, Asymptotic behaviour of a nonlinear model for the geographical diffusion of innovations, *Dyn. Syst. Appl.* (2) 3 (1994), 207 – 219.
6. E. L. Cussler, *Multicomponent Diffusion*, Chemical Engineering Monographs, Elsevier Scientific Publishing Compagny, Amsterdam, (3) (1976).
7. J. M. Cushing, *An Introduction to Structured Population Dynamics*, CBMS-NSF Regional Conf. Series in Appl. Math. 71, SIAM, Philadelphia, (1998).
8. M. Farkas, Comparison of different ways of modelling cross-diffusion, *Differential Equations Dynam. Systems* (7) 2 (1999), 121 – 138.
9. A. El Hamidi, M. Garbey, N. Ali, A PDE model of clonal plant competition with nonlinear diffusion, *Ecological Modelling* 234 (2012) 83 – 92.
10. P. L. Garcia-Ybarra, P. Calvin, *Cross transport effects in premixed flames*, Progress in Astronautics and Aeronautics, The American Institute of Aeronautics and Astronautics, New York, 76 (1981), 463 – 481.
11. V. Grimm, S.F. Railback, *Individual-based Modeling and Ecology*, Princeton series in theoretical and computational biology, ed. S.A. Levin, Princeton Univ. Press 428, (2005).
12. M. E. Gurtin, R. C. MacCamy, On the diffusion of biological population. *Math. Biosci.* 33 (1977), 35 – 49.
13. J. Journé, Negative ionic cross-diffusion coefficients in electrolytic solutions, *J. Theor. Biol.* 55 (1975), 529 – 532.
14. J. Journé, The Diffusive Lotka-Volterra Oscillating System, *J. Theor. Biol.* 65 (1977), 133 – 139.
15. E. F. Keller, L. A. Segel, Initiation of slime mold aggregation viewed as an instability, *J. Theor. Biol.* 26 (1970), 399 – 415.
16. M. Kirane, S. Kouachi: Asymptotic behaviour for a system describing epidemics with migration and spatial spread of infection, *Dyn. Syst. Appl.* (1) 2 (1993), 121 – 130.
17. K. Kishimoto, H. Weinberger, The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains. *J. Differential Equations* 58 (1985), 15 – 21.
18. J. D. Murray, *Mathematical biology*. Springer-Verlag, 1993.
19. Beáta Oborny, Growth Rules in Clonal Plants and Environmental Predictability – A Simulation Study, *The Journal of Ecology*, Vol 2, N0 2, 341-351, 1994.
20. Beáta Oborny, Tamás Czárán, Ádám Kun, Exploration and Exploitation of Resource Patches by Clonal Growth: a Spatial Mode on the Effect of Transport Between Modules, *Ecological Modelling* 141 (2001) 151 – 169.
21. A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Springer Verlag, (1991), 169 – 184.
22. S. W. Pacal, D. Tilman, Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments, *American naturalist*, Vol. 143-2, (1994), 222–257.
23. G. Rosen, Effect of diffusion on the stability of the equilibrium in multi-species ecological systems, *Bull. Math. Biol.* 39 (1977), 373 – 383.
24. J. Savchik, B. Chang, H. Rabits, Application of moments to the general linear multicomponents reaction-diffusion equations, *J. Phys. Chem.* 87 (1983), 1990 – 1997.
25. H. L. Toor, Solution of the linearized equations of multicomponent mass transfer: I, *A. I. Ch. E. Journal*, 10 (1964), 448 – 455.
26. H. L. Toor, Solution of the linearized equations of multicomponent mass transfer: II. matrix methods, *A. I. Ch. E. Journal*, 10 (1964), 460 – 465.
27. N. Shigesada, K. Kawasaki, E. Teramoto, Spatial segregation of interacting species. *J. Theoret. Biol.* 79 (1979), 83-99.
28. J. Smoller, *Shock waves and reaction-diffusion equations*. Springer-Verlag, New York (1983).