

Four Decades of Progress in Monitoring and Modeling of Processes in the Soil-Plant-
Atmosphere System: Applications and Challenges

Water limitation and negative plant-soil feedback explain
vegetation patterns along rainfall gradient

Addolorata Marasco^a, Annalisa Iuorio^b, Fabrizio Carteni^b, Giuliano Bonanomi^b,
Francesco Giannino^b, Stefano Mazzoleni^{b*}

^a *Dipartimento di Matematica e Applicazioni "R. Caccioppoli", University of Naples Federico II, via Cintia, 80126, Naples, Italy*

^b *Dipartimento di Agraria, University of Naples Federico II, via Università 100, 80055, Portici (Na), Italy*

Abstract

The formation of vegetation patterns has been widely studied and discussed over the years and it has been related to two different mechanisms: depletion of water in the center of vegetation patches and production of toxicity by the decomposition of plant residues in soil. In this work we present a spatially explicit model that combines these two processes showing that negative plant-soil feedbacks can explain the development of different vegetation patterns also when water is not a limiting factor. This also demonstrates that the toxicity effects may change the stability properties of the vegetation patterns.

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1. Introduction

Regular vegetation patterns fascinated plant ecologist since long time [1]. The occurrence of spotted vegetation patches, fairy rings, tiger bush bands, and stripes have been reported in different environmental conditions, especially for semiarid ecosystems (review in [2]). As a consequence, in order to explain such vegetation patterns, water limitation has been proposed as the causal mechanism in both empirical and modeling studies.

* Corresponding author.

E-mail addresses: stefano.mazzoleni@unina.it (S. Mazzoleni).

Several models were formulated as systems of partial differential equations (PDE) representing plant biomass, soil-water and surface water [3]. In such conditions, the emergence of regular vegetation patterns is related to the positive feedback mechanisms between biomass and water, with plant patches increasing the infiltration rate of surface water thus promoting plant growth. In other words, in these models, the balance between water infiltration, evaporation, plant uptake and surface runoff is considered the key process for the emergence of regular patterns.

An alternative explanation for the occurrence of regular vegetation patterns has been related to the so called plant-soil negative feedback (NF). Species-specific NF has been defined as the development of negative conditions for plants induced by the accumulation in the soil of toxic compounds released by decomposing litter of the same plant species [4]. Several mechanisms are involved in such negative plant-soil feedback including soil-borne pathogens, the changing composition of soil microbial communities [5], and the accumulation of autotoxic compounds from decomposing plant litter [6]. It is well established that negative plant-soil feedback affects plant coexistence and allows the maintenance of species diversity at community scale [7]. In this context, a recent theoretical study explored the possibility that negative plant-soil feedback may explain the formation of ring patches in clonal plants [8]. Based on a simple theoretical PDE model, this study demonstrated that plant-soil negative feedback alone may lead to the formation of ring patches in clonal plants, also where water is not a limiting factor.

Previous studies considered water limitation and negative plant-soil feedback as alternative explanations for the development of regular vegetation patterns. Here, for the first time, we explored the hypothesis that both water limitation and negative plant-soil feedback contribute in the formation of regular and irregular vegetation patterns. In detail, we present a spatially explicit model that studies biomass dynamics related to the impact of water and toxicity. First, we developed a stability analysis of the homogeneous steady-state solutions, then, we perform a linear stability analysis to spatially heterogeneous perturbations, supposing a direct effect of toxicity on biomass dynamics. The same analysis was also done by assuming no toxicity effects on biomass dynamics. This allowed us to compare our model with other previous published work based only on the water limiting hypothesis [2].

2. The mathematical model

We develop a new model for vegetation patterns starting from the Klausmeier [9] and Carteni et al. [8] models. We recall that in the Klausmeier model the vegetation pattern formation is only a result of positive feedbacks between biomass and water in semi-arid ecosystems. Differently, in the Carteni et al. [8] it is proved that also in ecosystems without limiting water conditions the negative plant–soil feedback leads to the emergence of vegetation patterns. In our opinion, the mechanisms underlying the vegetation pattern formation are a result of both positive and negative local scale feedbacks.

The Soil-Plant-Atmosphere System is schematically represented in Figure 1. Soil water content is affected by the rain, evaporation and plant uptake (considered as equal to transpiration). Plant biomass grows according to water availability. Litter produces toxic compounds that are degraded in the soil according to environmental conditions (precipitation and temperature), exerting a negative effect on plant growth performance.

2.1. Model description

The proposed model consists of three nonlinear partial differential equations describing the dynamics of three state variables: plant biomass B (kg/m^2), water W (kg/m^2) and toxic compounds T (kg/m^2) (see Fig. 1). The plant biomass, representing the whole system of roots and shoots (as in clonal plants), exponentially grows proportionally (c) to water availability. Plant mortality is due to a constant loss rate d

and an extra loss induced by the NF of T concentration. The NF effect depends on parameter s . Plant vegetative propagation is represented by a dispersal term of coefficient D_B . Furthermore, water W representing both soil and surface water, is supplied uniformly due to precipitation at rate p and lost due to evaporation at rate lW ; plants take up water at rate rB^2W , and, finally water diffusion is modeled as in Von Hardenberg et al. [10] in which the coefficient D_W is reduced by the presence of the plant biomass with a constant factor β . Moreover, toxic compounds are produced by a fraction of the dead biomass γ and are reduced by decay and water precipitation process by means of the parameters k and ε , respectively. For simplicity no diffusion of T is considered.

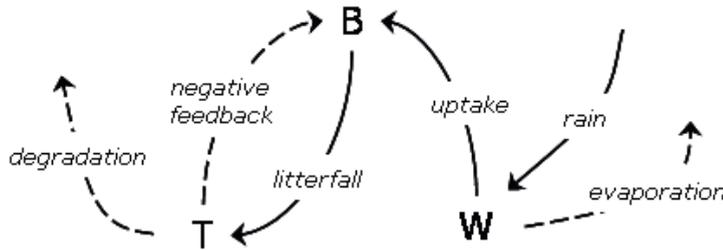


Fig. 1: Soil-Plant-Atmosphere System: Schematic representation of the feedbacks/interactions among plant biomass (B), toxic compounds (T) and soil water (W). The continuous and dashed lines indicate positive and negative effects, respectively.

The model parameters are summarized in Table 1; their values are chosen according to Klausmeier [9] and Carteni et al. [8], or set to order-of-magnitude feasible values. The spatial variable is $x=(x,y)$, while t is the time variable.

Table 1. List of model parameters

Parameter	Description	Unit	Assigned value
c	Growth rate of B due to water uptake	$m^4 \text{ day}^{-1} \text{ kg}^{-2}$	0.1
d	Death rate of B	day^{-1}	0.1
s	Plant sensitivity to T	$m^2 \text{ kg}^{-1} \text{ day}^{-1}$	Between 0 and 0.1
D_B	Plan biomass propagation coefficient	$m^2 \text{ day}^{-1}$	0.05
p	Rainfall	$\text{kg day}^{-1} \text{ m}^{-2}$	Between 0.1 and 0.5
r	Water uptake due to biomass growth	$m^4 \text{ day}^{-1} \text{ kg}^{-2}$	0.3
l	Water loss due to evaporation and	day^{-1}	0.1
D_W	Water diffusion coefficient	$m^2 \text{ day}^{-1}$	0.8
β	Biomass effect on water diffusion	-	Between 0 and 0.1
γ	Proportion of toxic products by litter	-	0.01
k	Decay rate of T	day^{-1}	Between 0.01 and 0.2
ε	Washing effect due to precipitation	$m^2 \text{ kg}^{-1}$	Between 0 and 0.001

According to the above description, the model equations are

$$\begin{aligned}
\frac{\partial B}{\partial t} &= cB^2W - (d + sT)B + D_B\Delta B, \\
\frac{\partial W}{\partial t} &= p - rB^2W - lW + D_W\Delta(W - \beta B), \\
\frac{\partial T}{\partial t} &= \gamma(d + sT)B - (k + \varepsilon p)T.
\end{aligned}
\tag{1}$$

In the model, we assume only positive values for the parameters c, d, p, r and γ , whereas $l, \beta, s, \varepsilon, k, D_B, D_W$ are non negative.

Introducing the dimensionless variables

$$\tilde{B} = \sqrt{\frac{r}{d}}B, \quad \tilde{W} = \frac{c}{\sqrt{dr}}W, \quad \tilde{T} = \frac{1}{\gamma}\sqrt{\frac{r}{d}}T, \quad \tilde{x} = \sqrt{\frac{d}{D_W}}x, \quad \tilde{y} = \sqrt{\frac{d}{D_W}}y, \quad \tilde{t} = dt,$$

we obtain the following non-dimensional form of the model (for convenience, we omit the superscript)

$$\begin{aligned}
\frac{\partial B}{\partial t} &= B^2W - \delta BT - B + \vartheta\Delta B, \\
\frac{\partial W}{\partial t} &= \varphi - B^2W - \lambda W + \Delta W - \zeta\Delta B, \\
\frac{\partial T}{\partial t} &= B - \rho T + \delta BT,
\end{aligned}
\tag{2}$$

where the new non-dimensional parameters are:

$$\delta = \frac{s\gamma}{\sqrt{dr}}, \quad \vartheta = \frac{D_B}{D_W}, \quad \varphi = \frac{cp}{d\sqrt{dr}}, \quad \lambda = \frac{l}{d}, \quad \zeta = \frac{c\beta}{r}, \quad \rho = \frac{(k + \varepsilon p)}{d}.
\tag{3}$$

3. Results

In order to study the mechanisms underlying the vegetation pattern formation as a result of both positive feedback between biomass and water and negative plant–soil feedback due to the presence of the toxic compounds T, we perform a stability analysis of the spatially homogeneous equilibria of Eqs. (2). In addition, we numerically integrate Eqs. (2) fixing the dimensionless parameters $\delta, \vartheta, \lambda, \zeta$ and varying the precipitation p and the decay rate k of T, i.e., the numerical values of φ and ρ , respectively.

In the following, we prove that our model not only exhibits multiple stable states as in the Klausmeier [9] original model, but unlike this model the presence of irregular patterns can be explained by the interplay between positive and negative feedbacks and not only by slight topographic soil variation (represented in [9] by the advection term).

3.1. Stability analysis of the spatially homogeneous equilibria

In this section, we perform a stability analysis of the spatially homogeneous equilibria in two cases:

a) the parameter s (and consequently the non-dimensional parameter δ) is strictly positive, i.e., we assume that the negative plant–soil feedback affects biomass dynamics;

b) the parameters s and δ are zero, i.e., the nonlinear partial differential Eqs. (2) are decoupled respect to the toxic compounds (Klausmeier [9] model in which no topographic soil variations are considered).

Since *b*) is a particular case of *a*), we limit our analysis to the general case *a*) and summarize in Table 2 the results on the stationary solutions for these two different cases.

The first stage in our study consists of finding the stationary solutions of the spatially homogeneous system, i.e., the solutions of the algebraic equations

$$\begin{aligned} B^2W - \delta BT - B &= 0, \\ \varphi - B^2W - \lambda W &= 0, \\ B - \rho T + \delta BT &= 0. \end{aligned}$$

Biologically feasible equilibrium points are the non-negative solutions of the above system, i.e.,

- if $\lambda > 0 \Rightarrow (B_1, W_1, T_1) = \left(0, \frac{\varphi}{\lambda}, 0\right)$;
- if $\lambda = 0 \Rightarrow (B_2, W_2, T_2) = \left(\frac{\rho\varphi}{\rho+\delta\varphi}, \frac{(\rho+\delta\varphi)^2}{\rho^2\varphi}, \frac{\varphi}{\rho}\right)$;
- if $\lambda > 0, \delta > 0, \varphi > 2\sqrt{\lambda}, \rho \geq -\frac{4\delta\lambda\varphi}{4\lambda-\varphi^2} \Rightarrow$

$$\begin{aligned} (B_3, W_3, T_3)^- &= \\ &\left(\frac{\rho\varphi - \sqrt{-4\lambda\rho^2 - 4\delta\lambda\rho\varphi + \rho^2\varphi^2}}{2(\rho+\delta\varphi)}, \frac{2\delta\lambda\rho + 2\delta^2\lambda\varphi + \rho(\rho\varphi + \sqrt{\rho(\rho\varphi^2 - 4\lambda(\rho+\delta\varphi))})}{2\lambda(\delta^2\lambda + \rho^2)}, -\frac{2\delta\lambda - \rho\varphi + \sqrt{\rho(\rho\varphi^2 - 4\lambda(\rho+\delta\varphi))}}{2(\delta^2\lambda + \rho^2)}\right), \\ (B_3, W_3, T_3)^+ &= \\ &\left(\frac{\rho\varphi + \sqrt{-4\lambda\rho^2 - 4\delta\lambda\rho\varphi + \rho^2\varphi^2}}{2(\rho+\delta\varphi)}, \frac{2\delta\lambda\rho + 2\delta^2\lambda\varphi + \rho(\rho\varphi - \sqrt{\rho(\rho\varphi^2 - 4\lambda(\rho+\delta\varphi))})}{2\lambda(\delta^2\lambda + \rho^2)}, \frac{-2\delta\lambda + \rho\varphi + \sqrt{\rho(\rho\varphi^2 - 4\lambda(\rho+\delta\varphi))}}{2(\delta^2\lambda + \rho^2)}\right). \end{aligned}$$

The Jacobian matrix $J(B, W, T)$ associated to system (2) is given by

$$J(B, W, T) = \begin{pmatrix} -1 + 2BW - \delta T & B^2 & -\delta B \\ -2BW & -B^2 - \lambda & 0 \\ 1 + \delta T & 0 & \delta B - \rho \end{pmatrix}.$$

Then, the linear analysis of stability allows us to obtain the following results

- the equilibrium (B_1, W_1, T_1) (corresponding to *bare soil*) is asymptotically stable if and only if $\rho > 0$. In fact, the Jacobian matrix at (B_1, W_1, T_1) admits the eigenvalues $\lambda_1 = -1, \lambda_2 = -\lambda, \lambda_3 = -\rho$;
- at the equilibria (B_2, W_2, T_2) and $(B_3, W_3, T_3)^\pm$ (corresponding to *uniform vegetation*) the stability properties involves all model parameters in a non trivial way. Then, the linear analysis of stability of these equilibria should be examined only on varying the ecologically relevant parameters p and k whereas for the other we assume that:

$$\delta = \frac{1}{100\sqrt{3}}, \quad \vartheta = \frac{1}{16}, \quad \lambda = 1, \quad \zeta = 0, \quad \varphi = \frac{10p}{\sqrt{3}}, \quad \rho = 10k \tag{4}$$

Then, we obtain that (B_2, W_2, T_2) does not exist (since $\lambda \neq 0$), $(B_3, W_3, T_3)^-$ is always unstable, and $(B_3, W_3, T_3)^+$ is always stable to homogeneous perturbations.

Performing a linear analysis of stability in the case *b*) we obtain that the only stable equilibria are $(\overline{B_1}, \overline{W_1}, \overline{T_1})$ and $(\overline{B_3}, \overline{W_3}, \overline{T_3})^+$, whereas $(\overline{B_3}, \overline{W_3}, \overline{T_3})^-$ is always unstable.

Owing to the above results, in Sec. 3.2 we perform a stability analysis to non-uniform infinitesimal perturbations only for the steady states (B_1, W_1, T_1) and $(B_3, W_3, T_3)^+$.

Table 2. Stationary solutions for model equations (2) with different biomass-toxicity dynamics

$\delta \neq 0$		$\delta = 0$	
if $\lambda > 0$	$(0, \frac{\varphi}{\lambda}, 0)$	if $\lambda > 0$	$(0, \frac{\varphi}{\lambda}, 0)$
if $\lambda = 0$	$(\frac{\rho\varphi}{\rho + \delta\varphi}, \frac{(\rho + \delta\varphi)^2}{\rho^2\varphi}, \frac{\varphi}{\rho})$	if $\lambda = 0$	$(\varphi, \frac{1}{\varphi}, \frac{\varphi}{\rho})$
if $\lambda > 0,$ $\varphi > 2\sqrt{\lambda},$ $\rho \geq -\frac{4\delta\lambda\varphi}{4\lambda - \varphi^2}$	$(\frac{\rho\varphi \pm \sqrt{-4\lambda\rho^2 - 4\delta\lambda\rho\varphi + \rho^2\varphi^2}}{2(\rho + \delta\varphi)}, \frac{\delta\lambda\rho + \delta^2\lambda\varphi + \rho^2\varphi - \rho(\rho + \delta\varphi)B_3^\pm}{\lambda(\delta^2\lambda + \rho^2)}, \frac{\varphi - \lambda W_3^\pm}{\rho})$	if $\lambda > 0,$ $\varphi \geq 2\sqrt{\lambda},$ $\rho > 0$	$(\frac{\varphi \pm \sqrt{-4\lambda + \varphi^2}}{2}, \frac{\varphi - B_3^\pm}{\lambda}, \frac{B_3^\pm}{\rho})$

3.2. Linear stability analysis to spatially heterogeneous perturbations

In order to investigate the effect of the biomass and water diffusion on the model system (2) we perform the linear stability analysis of the stationary homogeneous solutions (B_1, W_1, T_1) and $(B_3, W_3, T_3)^+$ to nonuniform infinitesimal perturbations.

We consider the perturbed solutions

$$B(\mathbf{x}, t) = B_* + a_B(t)e^{i\mathbf{x}\cdot\mathbf{h}} + cc, \quad W(\mathbf{x}, t) = W_* + a_W(t)e^{i\mathbf{x}\cdot\mathbf{h}} + cc, \quad T(\mathbf{x}, t) = T_* + a_T(t)e^{i\mathbf{x}\cdot\mathbf{h}} + cc$$

where (B_*, W_*, T_*) is a spatially stable equilibrium solution, $\mathbf{x} = (x, y)$ is the space variables vector, $\mathbf{h} = (h_1, h_2)$ is the wave vector of the perturbation, $\mathbf{a}(t) = (a_B(t), a_W(t), a_T(t))$ is the perturbation amplitudes vector and “cc” stands for complex conjugate.

Substituting the above perturbed solutions in (2) and keeping terms to first-order only, we obtain the following system of linear ODEs for the perturbation amplitudes $\mathbf{a}(t)$:

$$\begin{aligned} \frac{da_B}{dt} &= (-1 + 2B_*W_* - \delta T_* - h^2\vartheta)a_B + B_*^2a_W - \delta B_*a_T, \\ \frac{da_W}{dt} &= (-h^2 - 2B_*W_* + h^2\zeta)a_B - (B_* + \lambda)a_W, \\ \frac{da_T}{dt} &= (1 + \delta T_*)a_B + (\delta B_* - \rho)a_T, \end{aligned} \tag{5}$$

where $h = |\mathbf{h}|$ is the perturbation's wave number.

Assuming exponential growth for the perturbations amplitudes, i.e.,

$$a_B(t) = a_B(0)e^{\lambda t}, \quad a_W(t) = a_W(0)e^{\lambda t}, \quad a_T(t) = a_T(0)e^{\lambda t},$$

we obtain the eigenvalue problem

$$J(h)\mathbf{a} = \lambda\mathbf{a}, \tag{6}$$

where

$$J(h) = \begin{pmatrix} -1 + 2BW - \delta T - k^2\vartheta & B^2 & -\delta B \\ -h^2 - 2h^2\zeta B & -B^2 - \lambda & 0 \\ 1 + \delta T & 0 & \delta B - \rho \end{pmatrix}. \tag{7}$$

The solution of problem (6) give the dispersion relations which provide information about the stability of the stationary homogeneous solution (B_*, W_*, T_*) . In fact, the growth rate of a perturbation characterized by a wave number h is given by the largest real part of the eigenvalues $\lambda = \lambda(h)$.

When we estimate the eigenvalues of the Jacobian matrix $J(h)$ at the steady-states we obtain

- when $\lambda > 0$, at (B_1, W_1, T_1) the Jacobian matrix admits the eigenvalues $\lambda_1 = -1 - k\vartheta$, $\lambda_2 = -\lambda$, $\lambda_3 = -\rho$ which are all negative if $\rho > 0$. Then, the *bare soil* equilibrium (B_1, W_1, T_1) is stable to heterogeneous perturbations if and only if $\rho > 0$ and in this case it can never lead to Turing patterns;
- owing to (4), the equilibrium $(B_3, W_3, T_3)^+$ exists only for $\varphi > 2$, $\rho \geq -\frac{\varphi}{25\sqrt{3}(4-\varphi^2)}$, i.e., $p > \frac{\sqrt{3}}{5}$, $k \geq \frac{p}{-300+2500p^2}$. At $(B_3, W_3, T_3)^+$ the Jacobian matrix (5) admits eigenvalues with negative real part for every value of the wave number h . Then, the uniform vegetation state is asymptotically stable for every discrete value of p different from 0.1, 0.3. Therefore, Turing conditions for vegetation patterns formation are not satisfied. Nevertheless, numerical simulations will show that vegetation patterns occur with our assumptions on parameters (see Fig. 2). These numerical results suggest us to further investigate the spatio-temporal dynamics of the system on varying other parameters than p and k . Finally, we remark that for $p = 0.1, 0.3$ we have only the stable equilibrium (B_1, W_1, T_1) . However, since in our numerical simulations the initial data are outside the basin of attraction of (B_1, W_1, T_1) , the solutions do not converge toward bare soil, but tend to assume different vegetation patterns (see Fig. 2 for $k = 0.01$).

4. Discussion

We numerically integrate Eqs. (2) fixing the non-dimensional parameters $\vartheta, \lambda, \zeta$ as in (4) and varying the precipitation p , the decay rate k of T , and the plant sensitivity to toxic compounds s , i.e., the numerical values of φ, ρ , and δ , respectively.

Figure 2 shows the simulated spatial distributions of plant biomass according to precipitation rate p (rows), decay rate of toxicity k (columns), and plant sensitivity to toxic compounds s . Two values were chosen for plant sensitivity to toxicity: $s = 0.1$ (first three columns) showing simulations of the complete model; $s = 0$ (last column) reporting simulations of the reduced model, which includes only two

equations without NF effect. In this situation the model behaves independently of toxicity T (any k), reproducing the typical stable spatial patterns, reported in the literature for arid and semi-arid environments ([2], [3] and [9]): as the precipitation rate increases, plant biomass spatial distribution goes from bare soil to homogeneous cover, passing through spots, labyrinths and gaps.

On the other hand, in the presence of NF ($s = 0.1$), the same stable patterns described above are formed for sufficiently high values of k (third column). In this case the toxicity is degraded too fast to affect the biomass distribution on the vegetation pattern. Differently, reducing the decomposition rate (second and first column), the longer permanence of toxicity in the soil produces increasing effects on the system. In particular, the total plant biomass decreases with higher toxicity, and the transitions from one spatial pattern to another are shifted towards higher values of precipitation. It is noteworthy that for sufficiently low values of k ($k = 0.01$, first column), all spatial patterns change in time and space, i.e., spots and labyrinth stripes of plants constantly move, escaping from the accumulated toxicity in the previously occupied soil patches.

This spatio-temporal dynamics is consistent with several empirical observations (e.g. [11]), but, so far, it was never obtained with previous formulations of plant-water systems. Differently to the Klausmeier model [9], our numerical simulations show the existence of these patterns when p , k and s assume values in a finite range. In particular, our model can justify the occurrence of vegetation patterns even on flat ground, whereas Klausmeier explained their emergence with the presence of topographic variations. Future analytical and numerical studies are required in order to deeply comprehend the reasons beyond the formation of vegetation patterns even when Turing conditions are not satisfied.

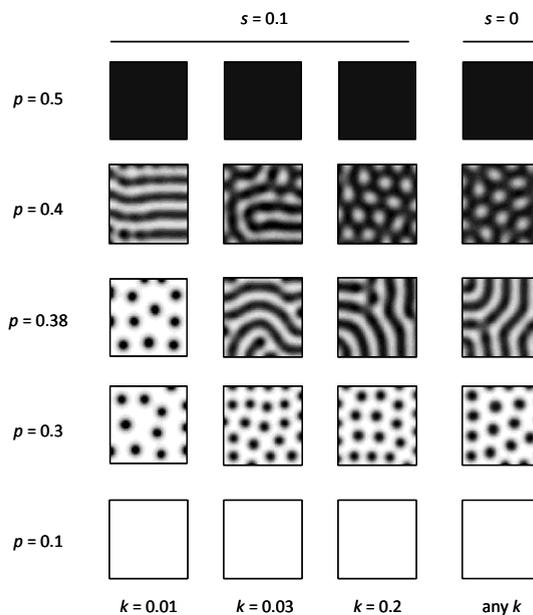


Fig. 2: Model simulations at different values of s (plant sensitivity to Toxicity), k (decay rate of toxicity) and p (rain). Each panel shows a grey-scale map of biomass distribution with darker shade representing higher biomass density. Simulations are performed with numerical integration and stopped after 20000 time steps. Other model parameter values are shown in Table 1 with $\beta = 0$ and $\varepsilon = 0$. Initial data: random plant peaks ($B = 3$) in 5% of a rectangular grid of 50x50 elements, $W = 2$, $T = 0$.

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