PHYSICAL REVIEW E **66**, 010901(R) (2002)

Localized vegetation patches: A self-organized response to resource scarcity

O. Lejeune and M. Tlidi
Faculté des Sciences, Code Postal 231, Université Libre de Bruxelles, B-1050 Bruxelles, Belgium

P. Couteron
Ecole Nationale du Génie Rural des Eaux et des Forêts, UMR-CNRS 5120, 648 rue J.F. Breton, 34033 Montpellier Cédex 1, France

(Received 2 January 2002; revised manuscript received 5 March 2002; published 29 July 2002)

We show that spatial self-organization allows vegetation to survive greater resource limitation. Isolated vegetation patches observed in nutrient-poor territories of South America and West Africa are interpreted as localized structures arising from the bistability between the bare state and the patchy vegetation state.

DOI: 10.1103/PhysRevE.66.010901 PACS number(s): 87.23.Cc, 05.65.+b, 87.18.Hf, 89.75.Fb

Spatio-temporal patterning is a central problem in ecology, scaling up from individuals and populations to whole ecosystems [1]. In vegetation, plants showing spatial patterns, i.e., nonuniform, nonrandom phytomass distributions, is the rule rather than the exception [2]. Considering their origin, three classes can be distinguished: morphological patterns, reflecting plant structure and growth; environmental patterns, developed in response to a key factor gradient; and sociological patterns, produced by interactions between plants [3].

Periodic and aperiodic vegetation patches observed worldwide in water-limited and/or nutrient-poor territories belong to this third class. Striped, spotted, or arc-shaped patterns are known to be widespread in arid as semiarid regions of Africa, Australia, North America, and Middle East. The annual rainfall (50–750 mm) is low in regard to potential evapo-transpiration ($\mathrm{PET} \geqslant 1.5\ 10^3 \mathrm{mm}$). Sparsely populated or bare areas alternate with dense vegetation patches. They are made of either herbs and grasses (λ: wavelength ≈ 10 m) or trees and shrubs ($\lambda \approx 100$ m) [4]. Such patterns mark the transition between homogeneous savannas and deserts. Similarly, in Africa and South America, patches of trees on a grassy background, see Fig. 1, are found at the transition between tropical rain forests and grasslands in humid yet nutrient-poor environments [5]. For both resource-limited contexts, there is no evidence of any edaphic or topographic discrepancy preexisting the pattern. Hence, the latter is likely to stem from biotic interactions.

In contrast with models for which some anisotropy is necessary [6], Lefever and Lejeune [7] have proposed a generic interaction-redistribution model of vegetation dynamics, which is able to generate patterns even under strictly homogeneous and isotropic environmental conditions. It is grounded on a spatially explicit formulation of the balance between facilitation and competition [8], which has been recently recognized as a governing factor for most plant communities [9]. It involves a Turing-like symmetry breaking instability [10] that is a classical mechanism to explain morphogenesis in biology [11]. Recently, this theoretical approach of vegetation patterning has been developped in the framework of models of reaction-diffusion type [12].

In this Rapid Communication, we account for the formation of aperiodic vegetation patterns such as those observed in nutrient-poor environments. Indeed, stable localized structures corresponding to isolated vegetation patches are one possible outcome of the model. This kind of structures is well known in chemistry [13], hydrodynamics [14], and in optics [15]. Here, in the context of plant ecology, they are interpreted as a spatial compromise between the patchy vegetation and bare stable states. In addition, the analytical bifurcation diagram of vegetation states as a function of the control parameter measuring environmental adversity is con-

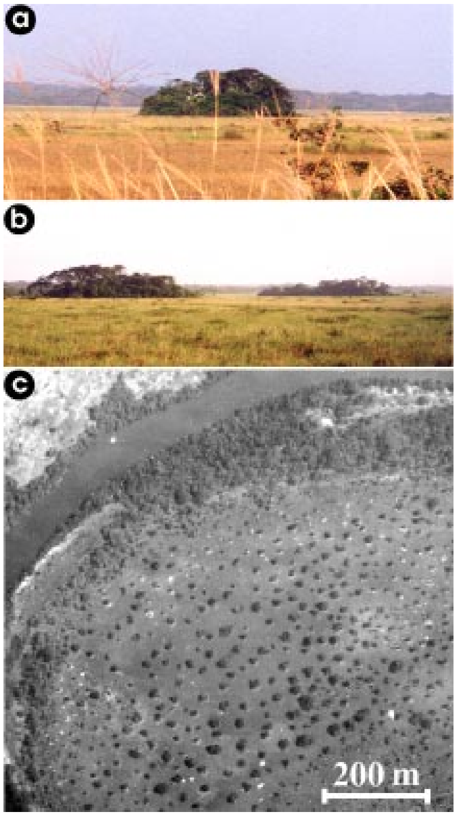

FIG. 1. (Color online) Pattern of isolated dense tree patches that marks the transition from the tropical rain forest to grasslands. (a), (b) Ground pictures from French Guiana (South America). (c) Aerial photograph from Marahoué National Park in Ivory Coast (West Africa): woody vegetation is dark gray, whilst grassland is light gray. Both locations are characterized by nutrient-poor soils (Pleistocene fluvial sands) and by a climate with a ratio of rainfall/PET between 0.9 (Marahoué) and 1.9 (Guiana).

structed. In agreement with numerical integration, the branch of patterns may extend beyond the one of homogeneous distributions. Spatial self-organization appears therefore as a natural response of vegetation to resource limitation.

For the idealized situation of a strictly isotropic and homogeneous environment, the phytomass density $\rho(\mathbf{r},t)$ evolves according to the dimensionless kinetic equation

$$\frac{\partial\rho}{\partial t}=(1-\mu)\rho+(\Lambda-1)\rho^2-\rho^3+\frac{1}{2}(L^2-\rho)\Delta\rho-\frac{1}{8}\rho\Delta^2\rho, \tag{1}$$

where Δ is the two-dimensional Laplacian. The single state variable is defined as total plant biomass per unit area, encompassing all species present, divided by the carrying capacity of the territory. It is assumed that species multiplicity as well as genetic variations, phenotypic differences and age class effects in monospecific subpopulations are not essential to vegetation patterning. The equation is derived in a low density and weak gradient limit from a generalized logistic equation [16] describing nonlocal interactions [17]. This approximation is suitable to resource-poor contexts where average phytomass density is low with respect to the carrying capacity (closed-packing density) of unstressed vegetation, and for which pattern wavelengths are large in comparison with the average size of the dominant plant form.

The phenomenon is characterized by three positive defined parameters: μ is the decrease-to-growth rate ratio; Λ is the facilitation-to-competition susceptibility ratio; L is the facilitation-to-competition range ratio. Plants interact by altering their nearby environment. The susceptibility is the amplitude of the response of the environment to plants. Note that the control parameter μ can be viewed as an indirect measure of resource scarcity. Indeed, a less favorable environment implies usually a lower rate of phytomass production, and possibly a higher rate of phytomass decrease [18]. Vegetation patterning is interpreted as the outcome of an interplay between short-range facilitative and long-range competitive plant interactions. Indeed, in adverse environments aerial parts of established plants have generally a positive effect on the growth of other plants, by providing shadow, nutrient-rich litter, and protection against fire or herbivores [19]. On the other hand, in the presence of water and/or nutrient shortage, superficial roots are known to track scarce resources far away from the limits of epigenous parts, thereby resulting in competitive effects that are long ranged in comparison with facilitative influences [20].

The homogeneous steady states of Eq. (1) are $\rho_0=0$ and $\rho_\pm=[\Lambda-1\pm\sqrt{(\Lambda-1)^2+4(1-\mu)}]/2$. The first solution, ρ_0, represents a territory totally devoid of vegetation. Obviously, it exists for all values of the parameters. The two other solutions, $\rho_\pm$, correspond to uniform plant distributions when they are real and positive. Two cases must be distinguished according to the value of the parameter Λ. If $\Lambda\leqslant 1$, only the homogeneous steady state ρ_+ defines a phytomass density, for $\mu\leqslant 1$. It decreases monotonously with μ (i.e., adversity) and vanishes at $\mu=1$. If $\Lambda>1$, the branch of physical solutions ρ_+ extends up to the turning point $\mu=\mu^*=1+(\Lambda-1)^2/4>1$. In the range $1\leqslant\mu\leqslant\mu^*$, the lower state ρ_0 and the upper state ρ_+ coexist with an intermediate state ρ_-. Overcoming facilitation $(\Lambda>1)$ allows vegetation community to survive where individual plants could not $(\mu>1)$. This situation corresponds to the vegetation systems presented in Fig. 1. Indeed, isolated trees hardly resist fire while patches may survive thanks to mutual protection.

The homogeneous steady state ρ_+ undergoes a Turing-like pattern formation instability when the phytomass density reaches the critical value ρ_c satisfying the equation $2\rho_c^2(1-\Lambda+2\rho_c)=(L^2-\rho_c)^2$. At this threshold, the critical wave number is $k_c=\sqrt{2(1-L^2/\rho_c)}$. Beyond that bifurcation point, the evolution of ρ towards a stationary, spatially periodic distribution is spontaneously triggered by inherent fluctuations. For simplicity and without important loss of generality, the analysis is restricted to stripes, or equivalently to one-dimensional systems, in the strong facilitation case, $\Lambda>1$. Such kind of solutions can be written as a truncated Fourier mode expansion $\rho(\mathbf{r},t)=\psi_0(t)+\frac{1}{2}[\psi_1(t)\,e^{i(\phi_1(t)+\mathbf{k}.\mathbf{r})}+\text{c.c.}]$, where c.c. denotes the complex conjugate. The homogeneous term ψ_0 is the average phytomass density $\langle\rho\rangle$. The inhomogeneous term is characterized by an amplitude ψ_1 and a phase ϕ_1. The modulus of the wave vector is the critical wave number, $|\mathbf{k}|=k_c$. Application of standard nonlinear analysis leads to the following amplitude equations

$$\frac{d\psi_0}{dt}=\psi_0\left(\alpha_0+\beta_0\,\psi_0-\psi_0^2-\frac{3}{2}\psi_1^2\right)+\tilde{\beta}_0\,\psi_1^2, \tag{2}$$

$$\frac{d\psi_1}{dt}=\psi_1\left(\alpha_1+\tilde{\beta}_1\,\psi_0-\frac{3}{4}\psi_1^2-3\,\psi_0^2\right), \tag{3}$$

where $\alpha_0=1-\mu$, $\alpha_1=\alpha_0-L^2k_c^2/2$, $\beta_0=\Lambda-1$, $\tilde{\beta}_0=\beta_0/2+k_c^2/4-k_c^4/16$, and $\tilde{\beta}_1=\beta_0+2\tilde{\beta}_0$. These ordinary differential equations are independent of the phase that evolves according to the equation $\psi_1\,d\phi_1/dt=0$. Equations (2) and (3) admit two classes of stationary solutions. The first one, $\psi_{0s}^H=\rho_s\equiv\{\rho_0,\rho_\pm\}$ and $\psi_{1s}^H=0$, corresponds to the homogeneous steady states of the phytomass density. The second one, $\psi_{0s}^P\neq\rho_s$ and $\psi_{1s}^P\neq 0$, corresponds to spatially periodic vegetation patches. On the other hand, the stationary phase, ϕ_{1s}, is a constant determined by the initial condition.

The results of the nonlinear analysis are summarized in the bifurcation diagram displayed in Fig. 2(a), where we plot the extrema values of the phytomass density, ρ_{min} and ρ_{max}, together with its average value, $\langle\rho\rangle$, for stripe patterns. When increasing the adversity parameter μ from the region $\mu<\mu_c$, the branch of pattern solution emerges supercritically at the instability point $\mu=\mu_c$. The unstable homogeneous steady state ρ_+ exists only for $\mu\leqslant\mu^*$. However, as a consequence of the interaction between the critical $(|\mathbf{k}|=k_c)$ and the homogeneous $(|\mathbf{k}|=0)$ modes, the branch of vegetation patterns exists even beyond the turning point, up to the limit point $\mu=\mu_{lp}$.

In the region $1<\mu<\mu_{lp}$ of the bifurcation diagram Fig. 2(a), the system exhibits a bistable behavior between the uniformly zero and the spatially periodic states. In that domain, another type of solution, the localized structure (LS),

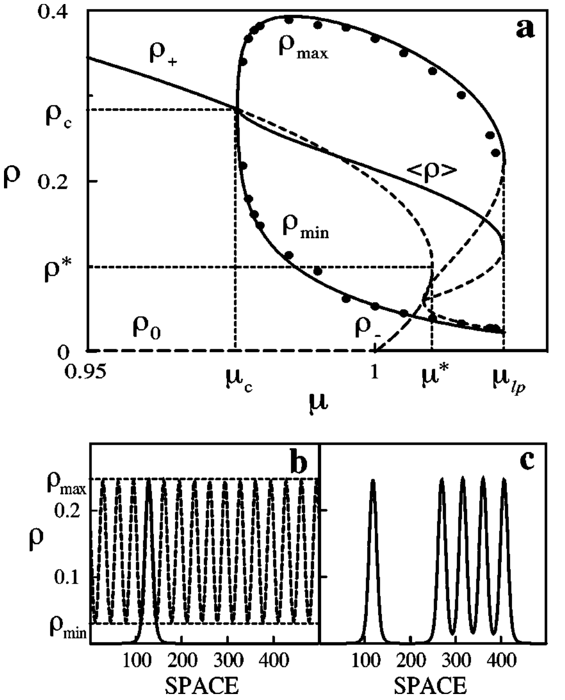

FIG. 2. 1D bifurcation diagram and localized structures. (a) Stationary states of the amplitude equations as functions of the control parameter μ for $\Lambda=1.2$ and $L=0.2$. The full and broken lines correspond to stable and unstable solutions, respectively. The bare state ρ_0 becomes stable beyond $\mu=1$. The branch of homogeneous vegetation states $\rho_\pm$, which extends up to $\mu=\mu^*>1$, loses its stability at $\mu=\mu_c$. The supercritical branch of vegetation patterns emerging from that bifurcation point extends up to $\mu=\mu_{lp}>\mu^*$. The maximum and minimum phytomass densities, ρ_{max} and ρ_{min}, are compared with the values obtained by numerical integration (black disks). The average of the phytomass density is given by the mean of its extrema values, $\langle\rho\rangle=(\rho_{max}+\rho_{min})/2$. (b) A single LS obtained for $\mu=1.02$ is plotted against the corresponding pattern (dashed line) that spatially oscillates between ρ_{min} and ρ_{max}. The maximum phytomass densities almost coincide. (c) For the same parameter values, a LP is formed by several LS's.

connects smoothly these two stable states. A single LS is plotted together with the corresponding Turing-like pattern in Fig. 2(b). Periodic boundary conditions are used for numerical integration. The maximum phytomass density of the LS, reached in the core of the vegetation patch, is nearly equal to the one of the coexisting spatially periodic pattern. On the other hand, the width of the LS is approximately given by half its wavelength. Moving away from the peak, the phytomass density decreases quickly and becomes vanishingly small. The stationary LS can be interpreted as a nonlinear front that undergoes a self-trapping (pinning effect) between the spatially periodic vegetation and the absence of vegetation. Hence, the size of an isolated patch is intrinsically determined by the vegetation dynamics and not by some spatial variation of the environment. It neither grows in spite of available free space, nor decreases in spite of adverse conditions. An example of localized pattern (LP) formed of several LS's is shown in Fig. 2(c); it is obtained for the same parameter values as Fig. 2(b). The number of peaks generated by the dynamics and their spatial distribution depend only on the initial condition.

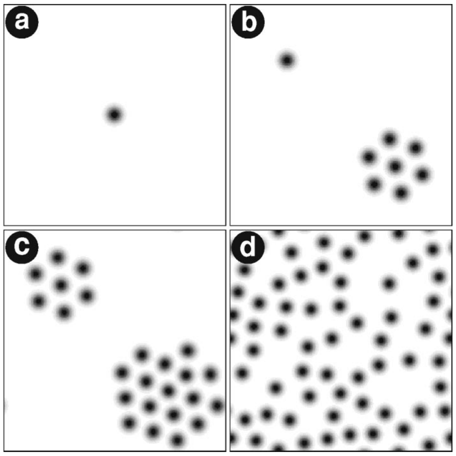

FIG. 3. 2D localized structures and patterns. Parameter values are $\mu=1.02$, $\Lambda=1.2$, and $L=0.2$. (a) A single LS corresponding to an isolated vegetation patch (black) on a bare soil. (b) Several LS's form a LP. (c) They can be self-organized. (d) Their distribution can be random.

In two-dimensional (2D) systems, there is a large variety of LP's. A sample of them is displayed in Fig. 3. They are obtained for the same parameter values; they only differ by the initial condition. A single stationary LS is shown in Fig. 3(a). The peaks forming the LP's in Figs. 3(b,c) are spatially self-organized because of their interaction. On the contrary, in Fig. 3(d), they are randomly distributed. All the peaks appearing in Fig. 3 are identical. Therefore, plant patches of specific size forming aperiodic patterns, see Fig. 1, may be more or less regular distributions of localized structures. The study of the particular case of Fig. 1(c) supports this interpretation. The size of vegetation patches ranges from 10 to 30 m. The space scale of Eq. (1) is the interplant competition range. Its value is approximately given by the radius of the superficial root system of dominant trees. This value is estimated to be of the order of 5 m. The half-height width of 2D localized structures has been determined numerically for $1/10<L<1/2$ and $1<\Lambda<2$ in the vicinity of the turning point $\mu=\mu^*>1$. It varies between three and five dimensionless space units, hence between 15 and 25 m. This interval is consistent with field observations. The time scale of Eq. (1) is the inverse of the vegetation growth rate. It corresponds roughly to the time spent by dominant trees to reach adult size. Its value is estimated to be of the order of 10 years. The generating time of 2D localized structures is typically 10^1–10^2 dimensionless units, hence 10^2–10^3 years. On that time scale, the environment (rainfall, temperature, light, wind, etc.) is likely to be constant on average.

As resource availability diminishes, we show that the vegetation distribution goes through the following stages: homogeneous cover, periodic pattern, or scattered patches of fixed size, no plant. It comes out that the average phytomass density of vegetation patterns, though decreasing with resource shortage, may be higher than the one of the corresponding homogeneous steady state. This result broadens the perspective about vegetation production in the presence of resource limitations, an issue that has been up to now only addressed through source-sink models calling upon passive reallocation of scarce resources through wind or run-off [21]. Obviously, spatial interactions between plants can, alone, account for scarce resource concentration and conservation resulting in productivity enhancement.

It is a pleasure to acknowledge fruitful and stimulating discussions with Professor René Lefever. O.L. and M.T. received support from the FNRS (Belgium). This research was supported in part by Fonds Emile Defay. The support of the Instituts Internationaux de Physique et de Chimie Solvay, and of the Center for Nonlinear Phenomena and Complex Systems (ULB) is also acknowledged.

[1] S.A. Levin, Ecology **73**, 1943 (1992).
[2] P. Greig-Smith, J. Ecol. **67**, 755 (1979).
[3] K.A. Kershaw, Ecology **44**, 377 (1963).
[4] L.P. White, J. Ecol. **59**, 615 (1971); C. Valentin, J.M. d'Herbès, and J. Poesen, Catena **37**, 1 (1999); M.R. Aguiar and O.E. Sala, TREE **14**, 273 (1999).
[5] D.U.U. Okali, J.B. Hall, and G.W. Lawson, J. Ecol. **61**, 439 (1973); V.M. Ponce and C.N. Cunha, J. Biogeogr. **20**, 219 (1993).
[6] A. Mauchamp, S. Rambal, and J. Lepart, Ecol. Modell. **71**, 107 (1994); J.M. Thiéry, J.-M. d'Herbès, and C. Valentin, J. Ecol. **83**, 497 (1995); D.L. Dunkerley, Plant Ecol. **129**, 103 (1997); C.A. Klausmeier, Science **284**, 1826 (1999).
[7] R. Lefever and O. Lejeune, Bull. Math. Biol. **59**, 263 (1997).
[8] O. Lejeune and M. Tlidi, J. Veg. Sci. **10**, 201 (1999); O. Lejeune, P. Couteron, and R. Lefever, Acta Oecol. **20**, 171 (1999); R. Lefever, O. Lejeune, and P. Couteron, in *Mathematical Models for Biological Pattern Formation*, edited by P. K. Maini and H. G. Othmer, IMA Volumes in Mathematics and its Applications Vol. 121 (Springer, New York, 2000), p. 83; P. Couteron and O. Lejeune, J. Ecol. **89**, 616 (2001).
[9] M.D. Bertness and S.M. Yeh, Ecology **75**, 2416 (1994); A.R. Berkowitz, C.D. Canham, and V.R. Kelly, *ibid.* **76**, 1156 (1995); R.M. Callaway and L.R. Walker, *ibid.* **78**, 1958 (1997); M. Holmgren, M.S. Scheffer, and M.A. Huston, *ibid.* **78**, 1966 (1997).
[10] A.M. Turing, Philos. Trans. R. Soc. London, Ser. B **237**, 37 (1952); P. Glansdorff and I. Prigogine, *Thermodynamic Theory of Structure, Stability and Fluctuations* (Interscience, New York, 1971).
[11] H. Meinhardt, *Models of Biological Pattern Formation* (Academic Press, New York, 1982); J. D. Murray, *Mathematical Biology*, Biomathematics Texts Vol. 19 (Springer-Verlag, Berlin, 1989).
[12] J. von Hardenberg, E. Meron, M. Shachak, and Y. Zarmi, Phys. Rev. Lett. **87**, 198101 (2001); R. HilleRisLambers, M. Rietkerk, F. van den Bosch, H.H.T. Prins, and H. de Kroon, Ecology **82**, 50 (2001); T. Okayasu and Y. Aizawa, Prog. Theor. Phys. **106**, 705 (2001).
[13] S. Koga and Y. Kuramoto, Prog. Theor. Phys. **63**, 106 (1980); K.L. Lee, W.D. McCormick, Q. Ouyang, and H. Swinney, Science **261**, (1993); P. Coullet, C. Riera, and C. Tresser, Phys. Rev. Lett. **84**, 3069 (2000).
[14] Y. Pomeau, Physica D **23**, 3 (1986); O. Thual and S. Fauve, J. Phys. (France) **49**, 1829 (1988); O. Jensen, V.O. Pannbacker, E. Mosekilde, G. Dewel, and P. Borckmans, Phys. Rev. E **50**, 736 (1994).
[15] M. Tlidi, P. Mandel, and R. Lefever, Phys. Rev. Lett. **73**, 640 (1994); L.Yu. Glebsky and L.M. Lerman, Chaos **5**, 424 (1995).
[16] J. L. Harper, *Population biology of plants* (Academic, New York, 1977); F. C. Hoppenstead and C. S. Peskin, *Mathematics in Medicine and the Life Sciences*, Texts in Applied Mathematics Vol. 10 (Springer-Verlag, Berlin, 1992).
[17] S.A. Levin and L.A. Segel, SIAM Rev. **27**, 45 (1985); M. Kot, M.A. Lewis, and P. van den Driessche, Ecology **77**, 2027 (1996).
[18] N. Fowler, Annu. Rev. Ecol. Syst. **17**, 89 (1986); R. Kadmon, J. Ecol. **83**, 253 (1995).
[19] O.R. Vetaas, J. Veg. Sci. **3**, 337 (1992).
[20] A.J. Belsky, Ecology **75**, 922 (1994); P. Mordelet, S. Barot, and L. Abbadie, Plant and Soil **182**, 171 (1996); S.N. Martens, D.D. Breshears, C.W. Meyer, and F.J. Barnes, J. Veg. Sci. **8**, 655 (1997); D.A. Coomes and P.J. Grubb, Ecology **79**, 768 (1998).
[21] I. Noy-Meir, Annu. Rev. Ecol. Syst. **4**, 25 (1973); J.A. Ludwig and D.J. Tongway, Land. Ecol. **10**, 51 (1995); J.A. Ludwig, D.J. Tongway, and S.G. Marsden, Catena **37**, 257 (1999).